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- Chapters progress logically from the small scale to the large; from individual species through to species interactions, populations and communities.
- Applications sections at the end of each chapter highlight the practicality of ecological concepts, showing how ecological information and concepts can be useful in agriculture, horticulture and forestry.
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- Summaries at the end of each chapter provide a brief recap, and will help with preparation for tests and exams.
- Questions and discussion topics at the end of each chapter encourage independent and creative thinking.

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Cover illustration: a three-trophic-level interaction illustrated by two sawfly larvae (*Croesus septentrionalis*: Hymenoptera: Tenthredinidae) sitting in a defensive posture on their hazel host plant (*Corylus avelana*: Fagaceae) in Europe.
Photograph by Gyögy Csóka, Forest Research Institute, Matrafüred, Hungary.

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Insect Ecology

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Behavior, Populations and Communities

P. W. Price, R. F. Denno
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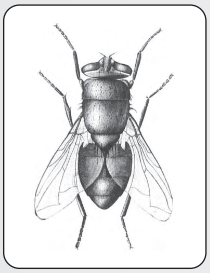

Insect Ecology

Behavior, Populations and Communities

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CONTENTS

PREFACE

The first edition of *Insect Ecology* was published in 1975, and remained the only textbook in the field for over 20 years, passing through a second edition in 1984, and a third edition in 1997. By the time this book had been in print for 30 years, a change in design and coverage seemed propitious. I (PWP) was fortunate to team up with Dr. Robert Denno, and we engaged in a stimulating, enjoyable and fruitful collaboration designing and writing this new book, *Insect Ecology: Behavior, Populations and Communities*. His tragic death in 2008 left his influence and perspective unrepresented as the book progressed, but some former graduate students of his were eager to see the project completed, and they agreed to write chapters. Hence, we have five authors contributing to the book, giving it a fresh complexion.

We have written this textbook for advanced undergraduates, graduate students, faculty and other kinds of researchers. Our emphasis is on providing an introduction to ecology for entomologists, and an introduction to entomological concerns for ecologists. Providing a conceptual basis for investigating insects to satisfy the empirical and problem-solving motivations broadens the scope of understanding and research from a merely descriptive phase to a hypothesis-testing, theory-building enterprise. Research studies that contribute to entomology and ecology simultaneously can add new dimensions to each field, and ecologists who include entomological studies in their comparative work with other taxa broaden the scope of investigation. Therefore, this book should contribute to the increasing synthesis of science.

We have generally taken the approach of introducing a conceptual area of ecology, with its strengths, weaknesses, hypotheses and debates, and gone on to use published studies to illustrate the relevant research. The reader is introduced to the practical way in which concepts and hypotheses are refined and advanced, through the scientific method.

The book is designed to be covered in a one-semester course of about 15 weeks. The 15 chapters move through behavior and social insect ecology, to communities, biodiversity and large-scale interactions. Major conceptual themes are introduced such that a student will be able to appreciate most of the literature in ecology, and fit it into the various sub-disciplines.

Citations and references

As a professional approach to the field develops we recognize that scientists remember information, discuss it and write about it using three kinds of categorical information, as in the indexes in the book: the subject matter, the organisms studied and the scientists involved. The year of publication is also important as a reference tool. Therefore, citations to published papers in the text are a necessary part of scientific coverage, followed by full details in the reference section of the book. We employ extensive reference to the literature in the book for several important reasons. (1) We give credit to ideas and data where credit is due. (2) The sources provide the reader with original works to which reference can be made for more detail, methodology, conceptual development, and further references. The interested and resourceful reader may enjoy a virtually limitless path of enquiry. (3) References also provide information on the types of journals relevant to the field, particularly for those training for a professional career. (4) The use of citations also illustrates how an argument is developed in the scientific literature; the use of the building blocks in the literature on which we depend to construct new science.

Figures and tables

An integral part of the delivery of information in this book is the figures and tables. They should be studied in detail to gain an appreciation of a concept, a set of results or support for an argument. Figures and tables are not necessarily easy to understand, although we have explained them as best we can. They are a fundamental way of communicating quantitative and qualitative information in science, so students are well advised to familiarize themselves with these illustrative materials, and to even commit to memory some of them. Former students may well remember examination questions which require a relevant figure. Tables also can provide large bodies of information in compact form. They can present the weight of evidence for a particular argument developed in the text.

To the figures we have added small images where appropriate representing the type of organism to which the figure refers. This adds interest and may help some students not well versed in entomology to appreciate the kind of insect involved. However, the illustrations only provide a general picture of the insect type, not necessarily an exact match to the species in question.

Names of species and higher taxa

Our emphasis has been on making the treatment of names as understandable as possible. An introductory course in entomology would help the reader to know the kinds of species we discuss, although this is not a necessary course requirement. Without such a course a helpful text would be *Borror and DeLong's Introduction to the Study of Insects*, by C. A. Triplehorn and N. F. Johnson (2005. 7th edition. Belmont, CA: Thompson Brooks/Cole). We follow the taxonomy in this book including the common names of insect families and higher taxa, and also the web site *Common Names of Insects and Related Organisms* by the Entomological Society of America. Other introductory texts in entomology would also be worth consulting.

The naming of species and higher taxa changes periodically, posing a challenge for the writer and reader. Our solution has been usually to employ the Latin binomial used in the original paper, or to use an updated name if the species is well known. We have also usually provided a way of knowing the group to which the species belongs, such as the family name or common name, or order.

For plant names and systematics we have referred to *Plant Systematics: A Phylogenetic Approach* by W. S. Judd *et al.* (2002. 2nd edition. Sunderland, MA: Sinauer Associates), which is a helpful reference when the relatedness of plants is of interest.

Remembering the names of species is a challenge for the student, but an essential part of communicating in science.

Important terms in boldface

Throughout the text we have used boldface font to emphasize important terms which the student should remember.

Glossary

Boldface terms in the text are collected into a glossary near the end of the book for speedy reference, and to help the student with reviewing terms and committing them to memory.

Applications

At the end of each chapter we have a section on how ecological information and concepts can be useful in the cultivation of plants for human needs, and the regulation of pest species. We feel compelled to make connections from basic ecology to practical landscape management because this linkage is important, but also intangible to many. We hope that this section will stimulate the reader to conjure up more examples of relevant examples and to read the primary literature with a view to possible applications.

Summaries

Each chapter is provided with a summary statement written to provide a brief recap of the chapter, which should be helpful with preparation for tests and examinations.

Questions and discussion topics

Chapters are concluded with these items designed to encourage independent and creative thinking, and writing skills. The answers will involve essay-type responses or class discussions, in which specific examples should be encouraged where appropriate, and full justification of the position taken is provided.

Further reading

We have included this section in each chapter, with five references which provide a broad perspective for enhanced learning, giving the reader the opportunity to delve more deeply into aspects covered in the chapter.

Debate

A fascinating aspect of the biological sciences, including insect ecology, is the ongoing debate about interactions and processes. Because of the complexity of nature – so many species and environments – little is resolved to the point of becoming solid scientific theory, which is agreed upon by the majority of scientists in the field. So the best we have in ecology is hypotheses, and frequently several alternatives, which form the basis for discourse, and the impetus for research to resolve differences in evidence and opinion, or to broaden perspective, which will encompass and unify formerly disparate views. There is a large opportunity in ecology for synthesis, broad comparative studies and the development of theory. Much of theoretical ecology is more about generating hypotheses than resolving the questions raised, and much of theoretical ecology remains untested with empirical studies. For the empiricist there is much to do, with entomologists well motivated to contribute basic knowledge which will contribute to the resolution of debates in ecology. We have not attempted to resolve debates in all cases in this book because the text should contain heuristic elements of importance in promoting discussion, and further study of the developing literature.

We hope that this fascination for science is stimulated in the student, and enriched in the professional reader. Insect ecology is a rapidly developing field which offers opportunities and challenges to be enjoyed.

ACKNOWLEDGMENTS

The pleasures and challenges of writing this book have contributed to a rewarding experience which we share with many collaborators. They do not necessarily endorse what is written, but we thank them wholeheartedly for the many reviews of chapters, and contributions of relevant papers: Anurag Agrawal, Joseph Bailey, Randy Bangert, Judith Bronstein, Timothy Craig, Sanford Eigenbrode, Daniel Gruner, Daniel Herms, David Margolies, Nicholas Mills, Yong-Lak Park, Robert Peterson, Jay Rosenheim, John Schneider, Jennifer Schweitzer, Stephen Shuster, Sherilyn Smith, John Spence, Courtney Tobler, Gina Wimp and several anonymous reviewers. Their time, effort and expertise devoted to improving the book are greatly appreciated. Also, Barbara Denno and Courtney Tobler provided invaluable help with figures. Photographs were graciously provided by Thomas and Maria Eisner, David Dussourd, György Csóka and Michael Loeb. These and other photographs and figures are acknowledged in the figure captions, or cited in the reference section of the book. At Cambridge University Press several editors have contributed to this book over the years, most notably Dominic Lewis, Commissioning Editor for Life Sciences, and Sophie Bulbrook, the Textbook Development Editor. We are grateful for their involvement in this project.

Robert Denno was not able to complete this book with us, but he exerted strong impact on its contents, and with the chapters he wrote. We cherish his memory, his friendship, his scholarship and his jovial attitude to life. Bob's passion for insect ecology inspired a new generation of scientists who were fortunate enough to experience the zeal with which he approached his classroom lectures, and the devotion with which he showered his students and post-docs. We (M.D.E., D.L.F. and I.K.) are just a few of the many graduate students who had the privilege of learning the science of insect ecology and the art of life from Bob. We are honored with the opportunity to extend Bob's legacy by taking part in this project, and we hope to reflect his perspective and spirit in our contributions to the work.

P.W.P.
M.D.E.
D.L.F.
I.K.

Part I Introduction

CONTENTS

Chapter 1 **The scope of insect ecology**

We introduce insect ecology by looking at the many remarkable features of the insects: their long evolutionary history, important design characteristics, including wings and flight, and the prodigious numbers of species and numbers of individuals per species. Inevitably, such vast richness entails many kinds of interaction, the basis for the study of insect ecology, because individuals and species provide part of the environment which any insect experiences. Ecology is the science of relationships of organisms to their environment: the physical and the biotic components with which they interact. How they relate depends on their design and their behavior, the latter aspect forming Part II of this book.

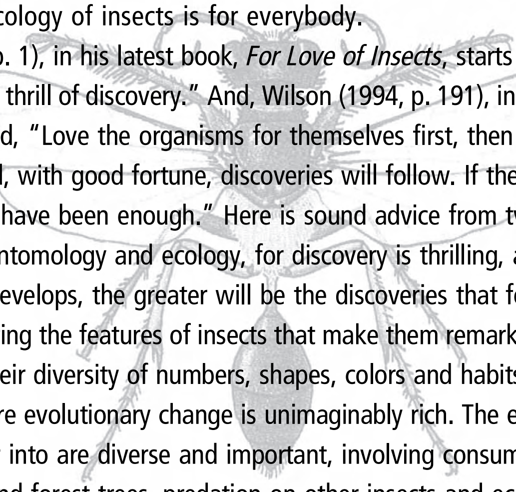
With millions of species of insects comes the question of how so many can evolve and coexist, subjects addressed in this chapter and other parts of the book. Also, we consider the roles that insects play in ecosystems, and the scientific method employed in their study.

These introductory considerations set the stage for expanding many themes in subsequent parts and chapters. Part II is devoted to behavioral ecology, Part III to species interactions and Part IV to population ecology. Moving to larger arrays of interacting species we devote Part V to food webs and communities, and Part VI to patterns and processes over the Earth's surface.

We generally are innately fascinated by insects and other arthropods at a young age, but cultural defects tend to diminish this enjoyment, while enhancing dread and avoidance. With more understanding provided by insect ecology we can recover a sense of wonder, and a knowledge of belonging with insects on this planet.

1

The scope of insect ecology



Everybody is conscious of insects, and even concerned about them. In fact, we each have an ecological relationship with their kind. We share our houses and gardens with them, our walks and picnics, and our adventures. So should we not understand them? Their richness in species and interactions, their beauty and behavioral intricacy, all enrich our lives if we understand who they are, and what they are doing. Therefore, the ecology of insects is for everybody.

Eisner (2003, p. 1), in his latest book, *For Love of Insects*, starts by writing that "This book is about the thrill of discovery." And, Wilson (1994, p. 191), in his autobiographical, *Naturalist*, advised, "Love the organisms for themselves first, then strain for general explanations, and, with good fortune, discoveries will follow. If they don't, the love and the pleasure will have been enough." Here is sound advice from two of the greatest practitioners of entomology and ecology, for discovery is thrilling, and the deeper the fascination one develops, the greater will be the discoveries that follow.

When considering the features of insects that make them remarkable, many attributes come to mind; their diversity of numbers, shapes, colors and habits are incredible. Their potential for future evolutionary change is unimaginably rich. The ecological interactions that insects enter into are diverse and important, involving consumption of plants, including crops and forest trees, predation on other insects and ecosystem processes, such as cycling of nutrients and decomposition. Some insects are highly beneficial for humans, while others are harmful. Thus, insect ecology serves the needs of both the desire to understand nature as a basic contribution to knowledge, and the need to solve the practical problems posed by insect pests concerning human hygiene, animal husbandry, agriculture, forestry, horticulture and the urban environment. We will elaborate on these features of insects, and the need to study and understand them, in the following sections of this chapter, and in the remainder of the book. First we discuss the evolution and design of insects, before looking at the richness of the insect fauna and their relationships. In the later part of the chapter we turn our attention to how insects have become so numerous and diverse through adaptive radiation, and their roles in ecosystem processes.

1.1 Fascination with insects

While developing a fascination with insects we necessarily enter into the whole realm of Nature, because insects interact with almost all other living species in one way or another. By studying insects for their own enjoyment, "with good fortune" we may perform good science. "Nature first, then theory" was the order advised by Wilson (1994, p. 191).

The fascination with insects derives from many of their characteristics. Their charms and annoyances are multifaceted. Insects have inspired art, design and literature, they act as a significant source of food in some parts of the world, they afflict millions with bites and infections while providing essential services in pollination and ecosystem processes. Their interactions with humans, agricultural crops, forests, livestock and other domesticated animals make insects of ubiquitous concern. Seldom will a day pass without seeing or interacting with insects. They are so common locally, and widespread geographically, that virtually all humans experience their presence. But, in spite of their commonness, many people misunderstand insects, regarding them as vermin, and are even frightened by some. However, the study of insect ecology can only contribute to our fascination with them, and our admiration for the roles they play in nature and in environments modified by humans.

1.2 Antiquity of insects

The earliest insect fossils date back to about 400 million years ago (Kukalová-Peck 1991, Labandeira 2002, Grimaldi and Engel 2005), deep in the Devonian Period and Palaeozoic Era. Plants diversified during the Siluro-Devonian "explosion" (420–360 MYA), followed by a rapid radiation of insects during the Carboniferous, with an extraordinary emergence of flying insect taxa by 300 million years ago. We can see from Figure 1.1 that already in the Devonian (400 MYA) there is fossil evidence of insects feeding on plants, including generalized foliage feeding, boring internally, and piercing and sucking types, and by 250 million years ago most types of insect feeding were evident and most types of plant parts were fed upon by insects. In the tree fern swamp forests of the late Carboniferous (308 MYA) the first evidence of gall-inducing insects has been described, and seed predation on seed ferns was evident. As plants diversified, so too did the insects, providing a rich paleoecological background for studies of plant and herbivore interactions.

Insects shared the land with other arthropods such as centipedes, millipedes and spiders through the Devonian and Carboniferous, their distributions being widespread and presumably with high abundance. Their lives were uncomplicated by the presence of vertebrate predators for perhaps 20–25 million years. But in the late Devonian, amphibians made a partial entry into the terrestrial fauna, while still breeding in water. Both on land and in water amphibians were no doubt preying on insects, although impact was probably small, and 20–25 million years is a pretty good run without vertebrate predators for the insects.

The evolution of flight in insects constituted a breakthrough to an extraordinary adaptive radiation in the late Carboniferous – an adaptive radiation never equaled on this Earth. This was about 150 million years before pterosaurs, birds and bats flew. The conquest of the air, so early among terrestrial animals, was no doubt of prime importance in the spread of insects across the globe. Add to this the sheer age of insects, and the time for diversification, and we can begin to understand why insect species are so numerous, and in some ways dominant on Earth.

1.3 Insect body plan

The body plan features of insects have, without a doubt, contributed in key ways to the impressive radiation of the group. Two characters in particular

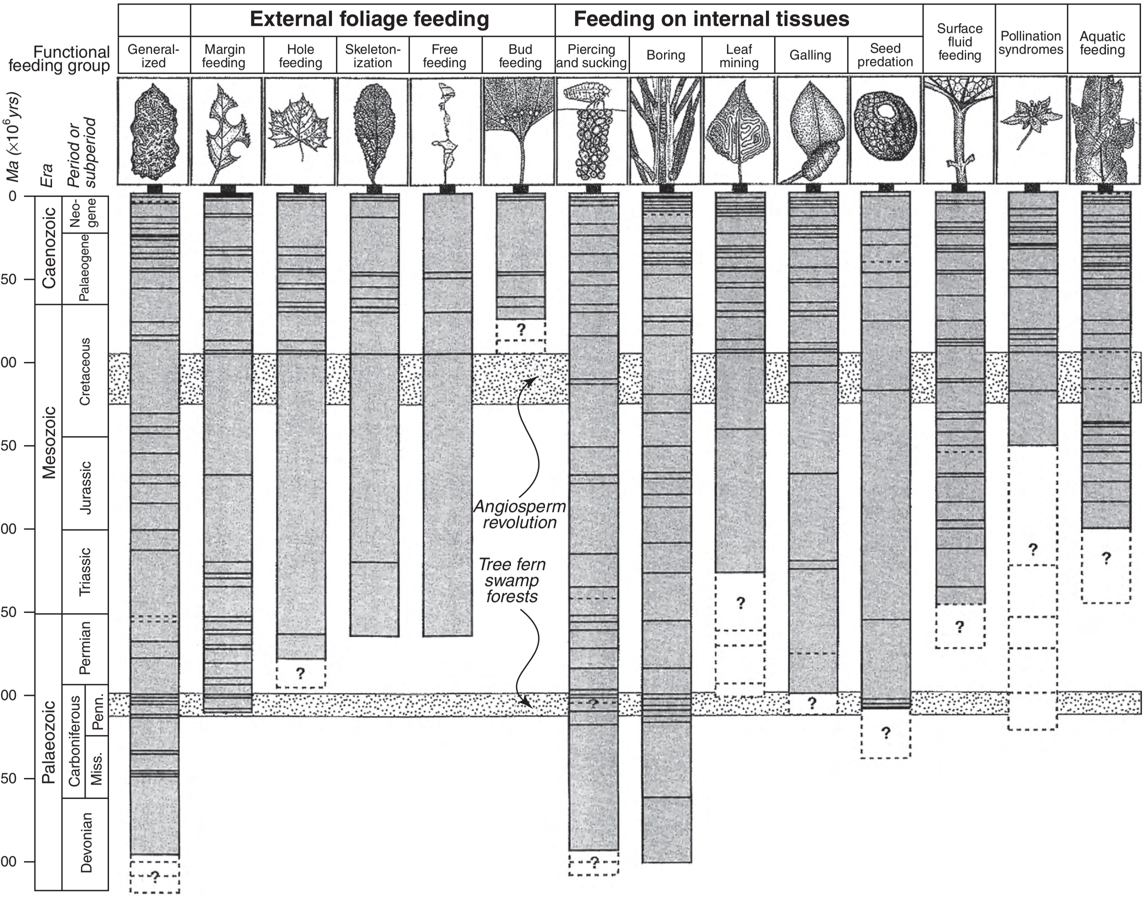


Figure 1.1 The fossil record of insects associated with plants according to the functional feeding groups of insects. Shaded columns represent the geochronological duration of each feeding group, with horizontal lines in columns showing actual records. External feeding and internal feeding categories are grouped. Major features of host plants include tree fern swamp forests and the adaptive radiation of the angiosperms, shown as horizontal shaded bars. Abbreviations: Miss. = Mississipian; Penn. = Pennsylvanian. From Labandeira 2002. Reprinted with permission from Blackwell Science.

permitted a series of novelties which resulted in their richness on Earth: they were primitively terrestrial and they had an exoskeletal integumentary system. Together, these traits facilitated a tracheal system of integumentary invaginations dividing through the body, providing air almost to the cells at work. With a permeability constant for oxygen through air of 660 cm^2/atm.h compared to a permeability through water of 2×10^{-13} cm^2/atm.h, tracheae were extraordinarily efficient, thereby allowing insects to be highly active (Alexander 1971, see also Chapman 1998). However, every adaptation, such as an exoskeleton, has its own constraints: a hard exoskeleton limited size. This was because, to grow, an insect needed to cast its integument, while replacing it with a larger one. But this left the individual briefly vulnerable and subject to bodily collapse since the supporting exoskeleton had been abandoned. Nevertheless, the tough integument, tracheal system and small size provided extraordinary potential for evolutionary innovation, and we look at each of these in turn in this section.

1.3.1 Metamorphosis

The constraint of the exoskeleton and the requirement for molting also provided a new opportunity in insect design: an insect could change its shape from one molt to another. This metamorphosis resulted in larvae evolving with shapes and habits very different from adults. The caterpillar of a moth, butterfly or sawfly spends its life feeding and differs remarkably in design from the adult, while adults may or may not feed, but are involved mainly with reproduction: courting, mating and ovipositing. All insects with winged adults change from immature wingless forms to winged adults. About 9% of insects are **hemimetabolous**, with **incomplete metamorphosis**, for the immature **nymphs** are similar to adults except that they lack wings. But the large majority of insects are **holometabolous**, with **complete metamorphosis**, in which **larvae** are very different from adults, as in the caterpillar and butterfly. About 90% of insect species are holometabolous, including all the very large orders – Coleoptera, Hymenoptera, Lepidoptera, and Diptera (Figure 1.2b), with the origin of holometaboly about 300 MYA (Kukalová-Peck 1991, Grimaldi and Engel 2005). This leaves about 1% of insects that are primitively wingless, including hexapods now classified outside the Class Insecta (Protura, Collembola and Diplura), although they are commonly included in ecological studies on insects. These percentages are based on numbers of described species per insect order provided in Triplehorn and Johnson (2005). They illustrate a remarkable breakthrough in animal design through metamorphosis, especially the holometabolic form. Larval forms and habits are enormously varied, from maggots (vermiform larvae), to grubs (scarabaeiform larvae), to caterpillars (eruciform larvae), to active and often predatory campodeiform larvae, and long and slender elateriform larvae (cf. Triplehorn and Johnson 2005). Maggots may squirm through mud, or animal bodies, mine in plants or live in water, while caterpillars are active as external foliage feeders, wood borers, leaf miners and gall inducers. Certainly, metamorphosis has contributed significantly to the adaptive radiation of the insects.

1.3.2 Exoskeleton and flight

The exoskeleton provided great strength in small structures, a strong skeleton to support heavy-duty muscular contractions and considerable protection against many enemies. Small size meant that gravity exerted a relatively weak force, equivalent to adhesion and cohesion for insects around 1 mm in length (Went 1968), enabling adhesion to leaves, walls and ceilings, but making a drop of water a disabling hazard. Small size, the exoskeleton and the tracheal system also contributed to the evolution of the first flying animals on Earth. With gravity as a relatively weak force, gliding may well have been a possibility, with hardly any particular special

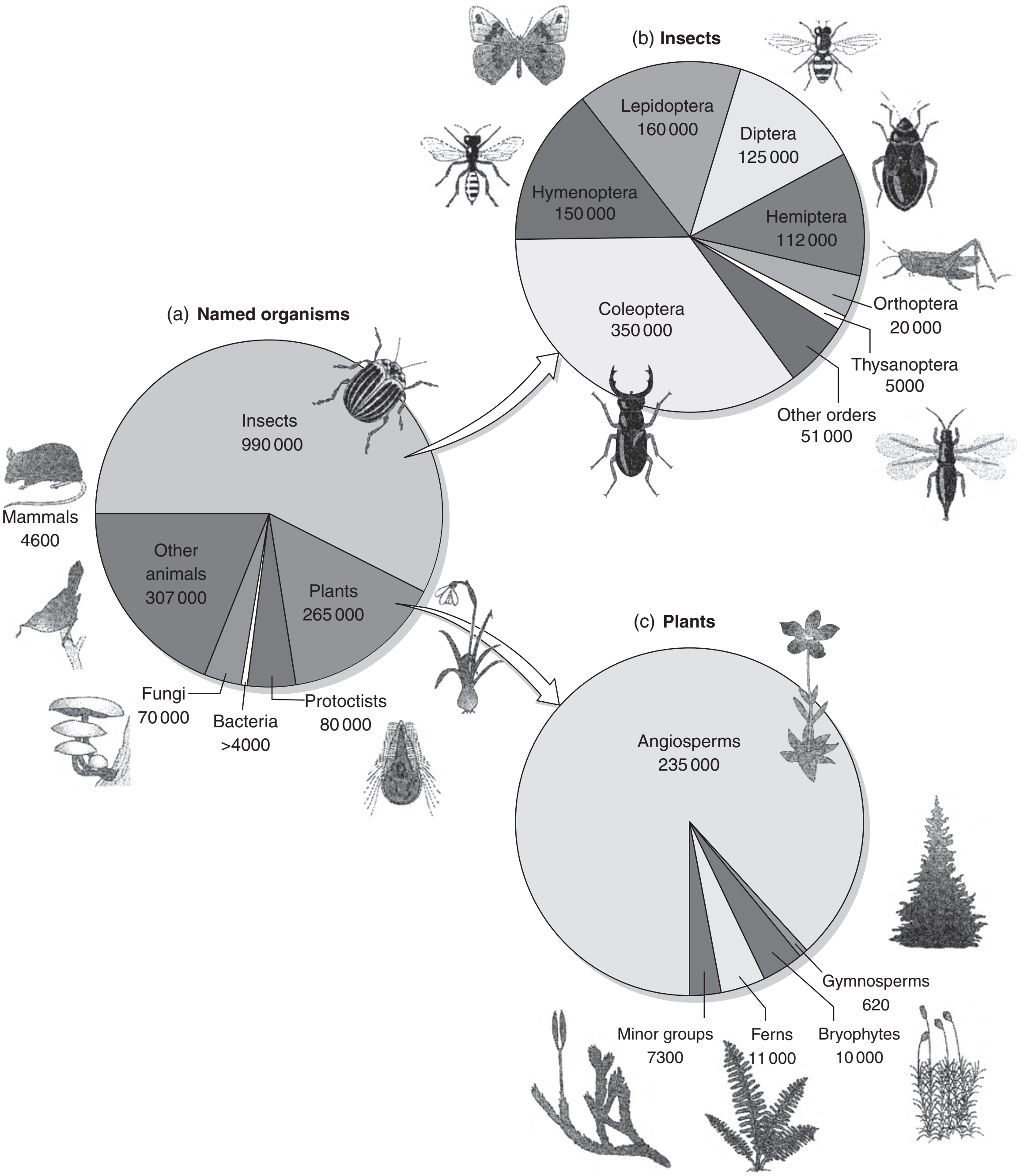


Figure 1.2 The estimated numbers of named species on Earth (a), the insects (b) and the plants (c). Note the large proportion of angiosperm plants (the flowering plants), and the large size of insect orders composed of many herbivores, many of which depend on flowering plants for food. From Price 2002a. Reprinted with permission from Blackwell Science.

adaptation for flight. Any extension of the cuticle would improve the possibility of effective gliding, and articulation would result in controlled flight. Alternatively, articulated flaps acted as gills or gill covers in aquatic insects, that secondarily became modified for flying. No matter which processes were involved in the evolution of flight, and there are many hypotheses (e.g. Kukalová-Peck 1978, 1983, 1987, 1991, Gullen and Cranston 2005, Grimaldi and Engel 2005), flying became a reality for the insects, and a major breakthrough in their adaptive radiation. Approximately 99% of insects can fly in the adult stage, or are derived from a lineage with flight (Price 2002a). The primitively wingless insects and other hexapods have remained a relatively depauperate group.

1.3.3 Small size

Small size, combined with flight, results in insects' ability to exploit small and scattered resources, with narrowly defined **ecological niches**, or places to live. As a consequence they have specialized in the colonization of dung, carrion, tree holes, rotting logs, birds and their nests, other insects, pools, temporary streams and endless other microhabitats (see Gullan and Cranston 2005). Additional resources include pollen and nectar, blood, fungi, plant sap, fruits, seeds and other plant parts, often available in small quantities and briefly in the year. Just these few examples highlight insects as living almost everywhere, each species specialized for a particular way of life utilizing a particular resource. Even on small, remote, subarctic islands on which no indigenous terrestrial mammals and few birds are found, hundreds of invertebrates exist. About 120 invertebrate species have been recorded from Marion Island (46°S) alone, with 17 families in 7 orders of insects present (Mercer *et al.* 2001). (Marion Island lies at 2300 km southeast of Cape Town, South Africa, with intervening islands, and a surface area of about 290 km^2 [Chown 1992].) Insects are also found in thermal pools at 25–40° C in Yellowstone National Park, in brine lakes and deep in caves (e.g. Culver 1982, Fincham 1997).

The "success" of insects is often noted, although usually without defining what success actually means. Clearly the term is subjective, so that quantifiable criteria are best employed to express the impressive adaptive radiation of the group. Most often used is the sheer number of species, but other factors need consideration, such as the diversity of morphology, lifestyles, their biomass per unit area, the rich relationships with each other and among species, and their many roles in natural and managed systems. We will examine some of these criteria in the following paragraphs.

1.4 Richness of the insect fauna

Figure 1.2 shows the estimated number of named species on Earth. As we can see from Figure 1.2b the named insects number about 1 million species (Foottit and Adler 2009). However, most insects have not been named, and their numbers are unknown, but debated none the less. Some estimates converge on approximately 5–10 million species, or about 90% of all terrestrial animal species (e.g. Gaston 1991, 1992, Ødegaard 2000), but others, based on sampling in the tropics, consider 30 million species more likely (Erwin 1982, 1988). Among the described insects, 90% are members of orders including many herbivorous species, with very large orders represented: Coleoptera, Hymenoptera, Lepidoptera, Diptera, Hemiptera, Orthoptera and Thysanoptera (Figure 1.2).

The number of insect species is vastly greater than any vertebrate group, and even all vertebrates combined: fish, amphibians, reptiles, birds and mammals, which add up to about 45 000 species. Bird species number something a little less than 9000 species and mammals about 4600 species; depauperate groups indeed. ("Other animals" in Figure 1.2a includes vertebrates other than mammals, and the many invertebrate groups such as sponges, corals, flatworms, crabs, spiders, snails and worms.) Compare these numbers for whole classes of vertebrates with the species numbers for single families of insects. For the ants, family Formicidae, 8804 species were described by 1990, but quite likely 20 000 species exist on Earth (Hőlldobler and Wilson 1990). In the parasitoid wasp family Ichneumonidae about 15 000 species have been described, with a likely 60 000 species in the world fauna (Townes 1969). Townes notes than an ichneumonid genus is more or less equivalent taxonomically to a bird family.

Insect biomass is equally impressive, with just ants and termites representing an estimated 33% of all animal biomass in the Amazonian *terra firme* rain forest (Hőlldobler and Wilson 1990). "Insects, at an estimated weight of 27 billion tons, outweigh the human population by about six times. In terms of biological mass, or biomass, insects are by far the dominant animal life form on Earth" (Grissell 2001, p. 35).

The numbers of individuals per species are also staggering in some cases. In an outbreak of forest caterpillars, numbers may reach 10^4–10^5 individuals per 100 m^2. Ants may number 20 million individuals per hectare in the tropics, and some driver ant colonies may even contain 20 million workers. Early naturalist explorers were amazed at the mass dispersal of Lepidoptera, like "snowing butterflies." Even in our own gardens and landscaping around our houses, probably more than a hundred species live, represented by thousands of individuals.

Such biodiversity of insects needs protection as much as any other group. All species are impacted by reduced habitat through deforestation, expansion of agriculture and urbanization, and the fragmentation of habitat into smaller and smaller parcels, rendering populations at greater risk of local extinction. Thus, the conservation of insect species and populations is attracting greater attention and stronger resolve (e.g. Gaston *et al.* 1993, Samways 1994, 2005, Bossart and Carlton 2002, and see also the *Journal of Insect Conservation*). Protection of breeding sites for aquatic insects like dragonflies, restoration of habitat for others and monitoring of populations are all part of the conservation strategy and insect ecology. Naturally, much ecological research is needed to understand the status of species and populations, and the risks to which they are exposed, so conservation biology will be discussed repeatedly in this book.

1.5 Richness of relationships

Needless to say, the richness of insect species means that they are involved with an even richer set of interactions, for each individual species interacts with a multitude of others. Table 1.1 shows us that many species exploit plants in one way or another, exhibiting a wide range of resource exploitation, for every part of a plant may be utilized by one insect species or another. For example, a large oak tree may support several hundred species of insect, with almost all parts vulnerable to attack, including all stages from seed, to seedling, to the mature plant (Figure 1.3). Here, we discuss direct and indirect relationships by looking at feeding links and community interactions.

1.5.1 Feeding links and types

Moving up the feeding links, or **food chain**, the herbivores are in turn fed upon by carnivores, both insects and other animals such as reptiles and birds. Feeding on animals such as insects involves three main types: predators, parasitoids and parasites. **Predators** generally kill their prey and consume most or all of the dead body. **Parasitoids** are parasitic in the larval stage but free-living as an adult, with a female parasitoid that searches for hosts in or on which to lay an egg. Thus, parasitoid species can be regarded as mainly parasitic because of usually long

Table 1.1 **The resources provided by plants utilized by insects, and their kinds of exploitation**

Resources provided	Name of exploiter
Living plant or plant parts in general	Herbivore, phytophage
Eating plants and animals	Omnivore
Shoots	None
Leaves	Folivore
Buds	None
Flowers	Florivore
Nectar	Nectarivore
Anthers and/or pollen	Anthophage
Carpel and/or fruit	Frugivore
Seeds	Granivore
Spores	None
Cones	None
Wood/xylem	Xylophage
Cambium	None
Bark/cortex/ periderm	None
Roots/rhizomes	Rhizophage
Tubers, corms, bulbs	None
Sap (phloem and xylem)	None
Exudates/oozes	None
Dead plant material	Saprophage, detritivore, decomposer

Slightly modified from Price 2002a. Reprinted with permission.

association with an insect host, or predatory because a female adult searches like a predator, usually dooming the host to death. This is because of larval feeding in or on the host and, as a consequence, the parasitoid acts like a predator in relation to the population dynamics of the prey. **Parasites** of insects include microorganisms (bacteria, protozoa, fungi), mites, nematodes and the larval stages of parasitoids. A parasite can be defined as an organism that lives in or on another living organism, which obtains part or all of its food from that organism, which is usually adapted by morphology, physiology and behavior to living with its host and which causes some measurable damage to its host (see Price 1980, Bush *et al*. 2001).

These categories of herbivores and carnivores cover only a small selection of relationships among insects, and their food sources (Table 1.2). Some interactions may be beneficial to each species, constituting a **mutualism**, such as in pollination. Mutualists may live intimately with each other, like the protozoa in the paunches of termites, with the protozoa and termites forming a **symbiosis**. Symbioses are not restricted to mutually positive relationships, as they also include parasites and their hosts in close association. **Competition** may be observed among any organisms that exploit the same resource in limited supply. And competition was thought to be most likely among members of the same **guild**: species that exploit the same resource in a similar manner (Figure 1.4, Root 1973). Such competition may be very one-sided – **asymmetric competition** – with one species hardly affected, but the other negatively impacted (a 0— interaction), and competition now appears to be frequent outside guild membership (e.g. Kaplan and Denno 2007, Denno and Kaplan 2007, see Chapter 5 on Competition).

1.5.2 Community interactions

Clearly, these interactions are very rich in any one locality. Such interacting species comprise a

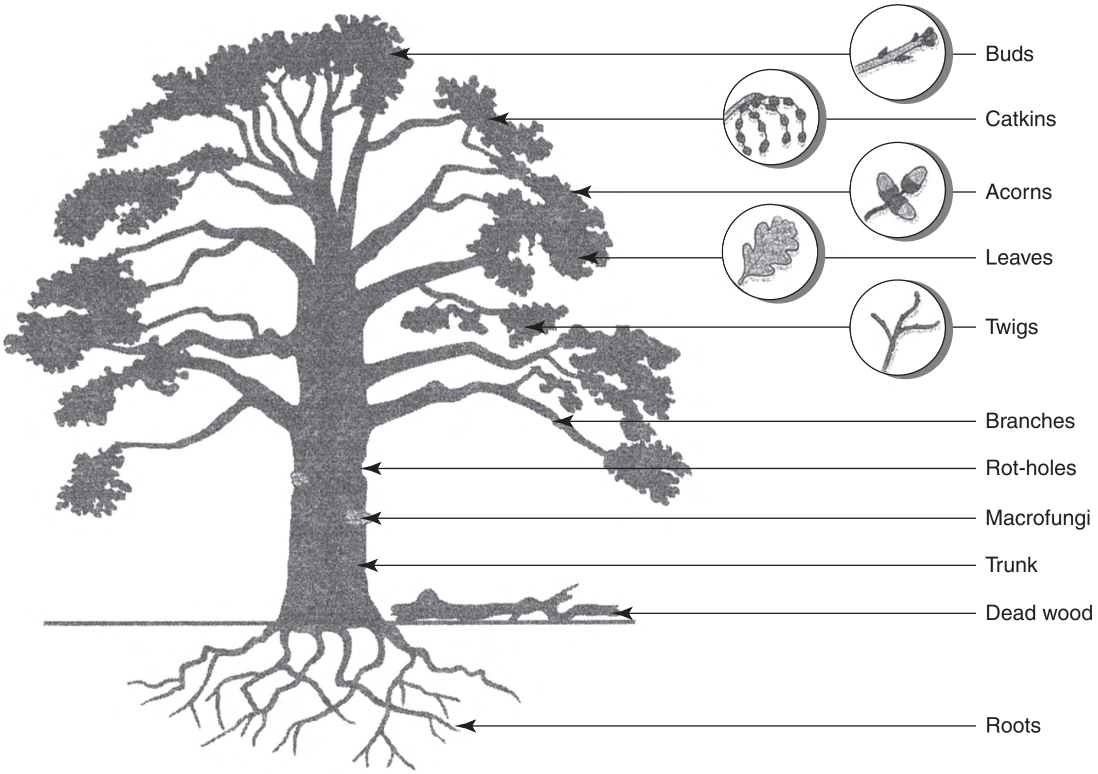


Figure 1.3 A large oak tree, such as the pedunculate oak, *Quercus robur*, in the British Isles, provides many food resources for insects and other animals, and many habitats to live in. Modified from Morris 1974. Reprinted with permission from the Botanical Society of the British Isles.

community of species, defined as a group of organisms that interact in a given area. These interactions may occur among species on the same **trophic level**, meaning the same feeding type such as herbivores on plants or carnivores feeding on herbivores (Figure 1.4). The hierarchy of feeding relationships in a community can then be regarded as a **food chain**, or **food web**, with linkages from plants to herbivores, to primary carnivores, to secondary carnivores and so on up the trophic system (Figure 1.4). Very simple communities may be more chain-like in structure, but usually web-like sets of interactions are observed, especially as predators tend to be more general feeders than herbivores and parasitoids.

However, the diversity of relationships goes well beyond **direct interactions** because feeding, especially on plants, actually changes the properties of the plant. A caterpillar may roll a leaf which later becomes a haven and domicile for smaller herbivores like aphids and thrips. The aphids may excrete honeydew which attracts ants, and these may become predatory on other members of the community. Feeding damage may also change the chemistry of leaves, with beneficial or detrimental impacts on other herbivores. Herbivores on plant stems may result in altered architecture, with impact on others. Indeed, the **indirect interactions** of insects on others may be far richer than the direct effects (Ohgushi 2005, Ohgushi *et al.* 2007, Figure 1.5).

Table 1.2 **The kinds of interaction between species**

Type	Definition
Mutualism (++)[a]	Both species benefit from an association
Symbiosis (++, +−, +0 or −0)	The close association of two or more species living together, no matter which kind of influence one has on the other
Antagonism (+−, −−)	One species has a negative effect on the other species (predation, parasitism), or both species exert a negative effect (competition)
Amensalism (−0)	One species has a negative effect on the other, but there is no measurable reciprocal effect (e.g. highly asymmetric competition)
Competition (−−)	Exploitation of a common and limiting resource by two or more species
Commensalism (+0)	One species benefits from an association without any benefit to, or harm from, the other species
Parasitism (+−)	Individuals of one species live in or on a living host, sapping the host's resources for a relatively prolonged period, and exerting a negative, but not necessarily a fatal, effect on the host
Predation (+−)	Individuals of one species kill and eat individuals of another species − the prey species
Inquilinism (+0, +−)	One species enters the domicile of another habitually, with or without causing damage to the host species
Browsing (+−)	Eating tender plant shoots, twigs or leaves of woody plants
Grazing (+−)	Feeding on growing herbage such as grass, nibbling or cutting at surface growth while passing across a patch of vegetation
Cropping (+−)	Cutting off the upper or outer parts of a plant
Exophytic (+−)	External feeding on a plant
Endophytic (+−)	Internal feeding on a plant
Obligate	A necessary relationship for the existence of a species or individual
Facultative	A relationship that may be used, but is not essential
Specialist	A species with a narrowly defined diet
Generalist	A species that feeds broadly across many host or prey species
Direct interaction	A species has an immediate effect on another by directly influencing the recipient of the interaction
Indirect interaction	A species influences another recipient species by altering the conditions to which the recipient species is exposed

[a] +, − and 0 symbols denote a beneficial relationship, a negative effect or no effect on the other species, respectively. Modified from Price 2002a. Reprinted with permission.

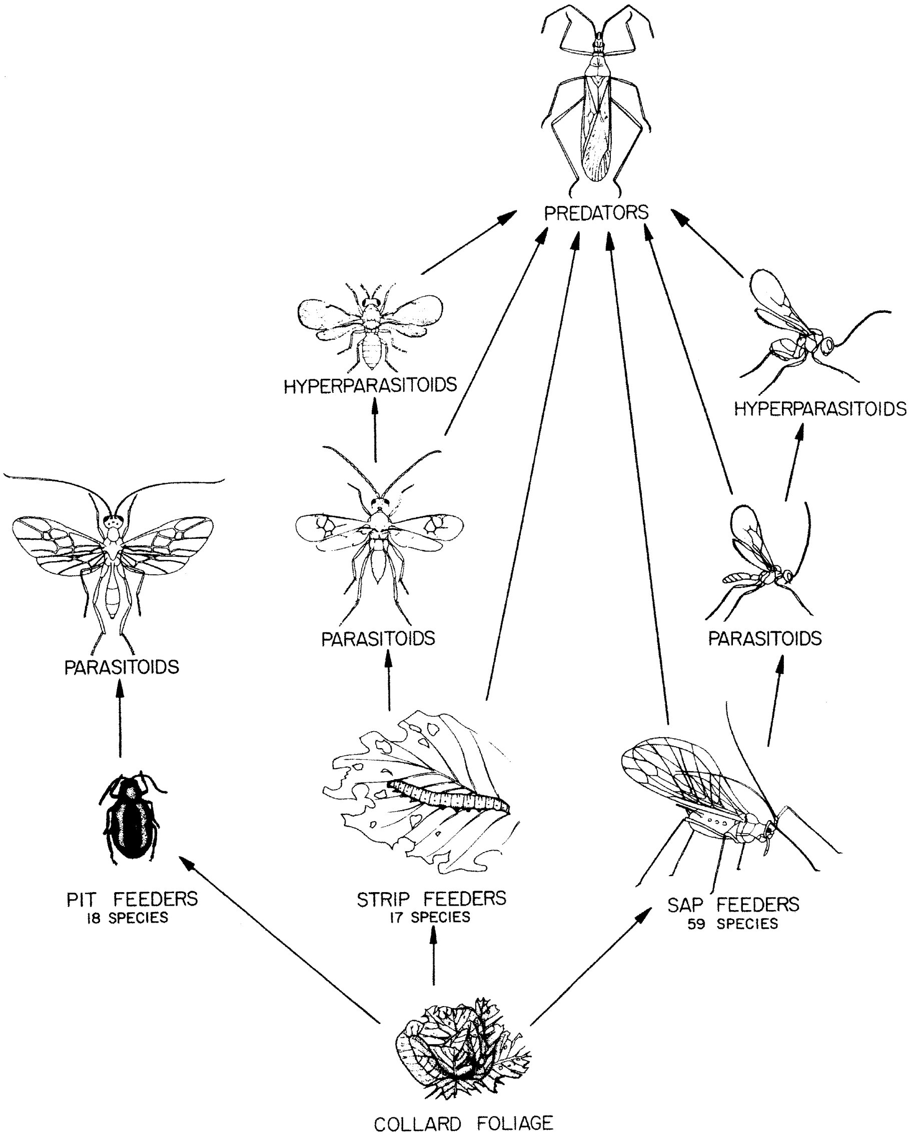
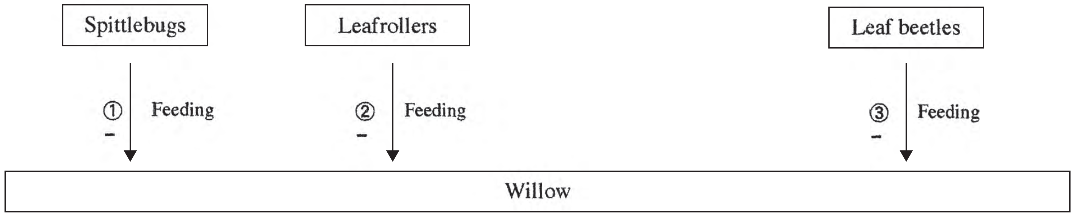


Figure 1.4 A simplified food web based on collard plants, *Brassica oleracea*, showing three major guilds of herbivores, their parasitoids, hyperparasitoids and predators. Note that the predatory nabid bug feeds on the second, third and fourth trophic levels showing a general feeding pattern typical of many predators. Pit feeders include flea beetles, strip feeders are caterpillars and sap feeders are sucking insects such as aphids. Based on Root 1973. Reprinted from Price 1984a, with permission from John Wiley & Sons, Inc.

(a) Food web



(b) Indirect interaction web

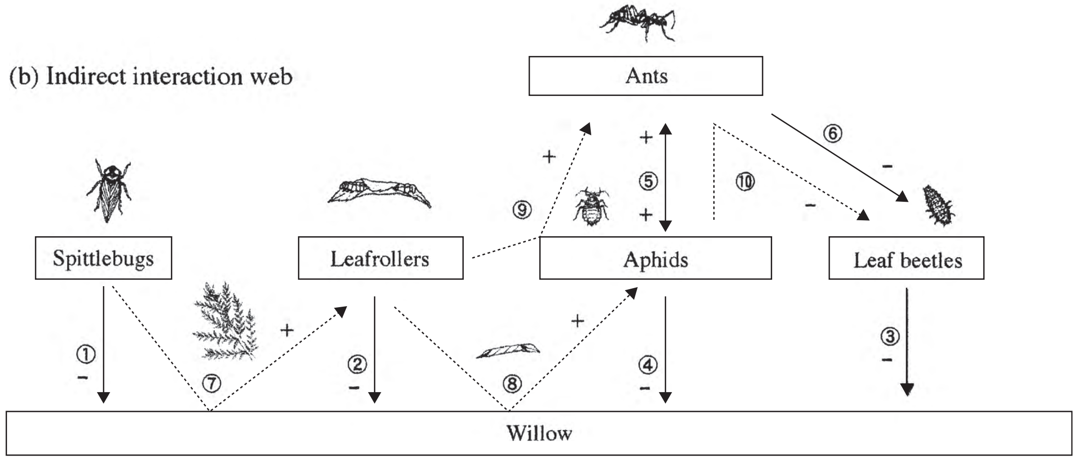


Figure 1.5 The difference between feeding relationships of insects on willow in Japan, with three species feeding directly on the willow (a), and an indirect interaction web (b) showing that insect activity on a plant changes plant traits which influence other herbivores, increasing the number of interactions among species from three in (a) to ten in (b). In the latter case, spittlebugs oviposit into shoots, killing the shoot tip, and promoting new vigorous growth basal to the damage (interaction 7). This growth is attractive to leafrollers, whose rolls act as shelters for aphids (8), and aphid honeydew becomes attractive to three species of ants (9). Ants have a negative impact on leaf beetles (6), while aphids have an indirect effect on leaf beetles (10). In all, this indirect interaction web included six direct interactions (1–6 and solid lines), and four indirect interactions (7–10 and dashed lines), and three direct interactions were newly established, which resulted from earlier indirect relationships (4–6). From Ohgushi 2005. Reprinted, with permission, from the *Annual Review of Ecology, Evolution, and Systematics*, Volume 36, © by Annual Reviews *www.annualreviews.org*

1.6 Adaptive radiation

This richness of the insect fauna and the richness of their interactions obviously raises the question of how insects could become so numerous and diverse. We have discussed above body-plan features which are central to the insect way of life – small size, a tracheal system, metamorphosis and flight in particular – and the antiquity of the group, but clearly there is much more to understanding how so many species are extant today. This subject enters into the realm of evolutionary biology, and especially **adaptive radiation**: the relatively rapid evolutionary divergence of members of a single lineage into a series of adaptive zones with different kinds of ecological niches. An **adaptive zone** is a way of life common to a group of species characterized by a particular mode of exploiting the environment. Hence, the adaptive radiation of beetles (Coleoptera) would include many adaptive zones such as leaf feeding (e.g. Chrysomelidae), wood boring (Cerambycidae and Buprestidae), dung feeding (many Scarabaeoidea), and aquatic and terrestrial predators (Dytiscidae and Carabidae respectively). Adaptive radiation is a large subject which will be discussed and amplified in other parts of the book, but here we focus on three contributing factors to the richness of insects. The first is the richness of plant species on which many insects feed, the second is the richness of herbivores which provide food for predators, and the third is the mechanisms by which insects divide into new species.

1.6.1 Plant diversity for herbivores

The basis for understanding the evolution of the multitude of insects rests on their relatively small size, trophic level linkages and the richness of plants at the base of the food web. Plants are **primary producers**, generating plant biomass through photosynthesis, which then becomes available to other organisms, **consumers** of various sorts: herbivores, decomposers and mutualists, like pollinators, mycorrhizal fungi and nitrogen-fixing bacteria. Plants provide a carpet of green over most of the Earth, but only a small part of this biomass is palatable and nutritious enough for any particular species. Therefore, there are many thousands of ways in which plant biomass can be exploited. Each of the named plant species, numbering over a quarter of a million (Figure 1.1) may support several to many insect herbivore species, each herbivore specialized to a different plant part. As they are small and generally able to fly, insects utilize very small resources such as seeds (e.g. Bruchidae), and widely dispersed resources such as pollen (e.g. Apidae), so each plant species provides many different resources. That is, plants provide a diverse array of **ecological niches** for insects: the resources needed by a species to maintain its population indefinitely. Many herbivorous insects are specific to a single, or a few, plant species, and a particular plant part. For example, fruit flies respond to specific fruit odors of their host plant species (Linn *et al.* 2003). Indeed, many such insects act as parasites on their host plants; living in or on the host plant for much of their lives and feeding on the plant, thereby inflicting some damage (see Table 1.2 for the definition of a parasite). Hence, once a lineage colonizes a new adaptive zone, such as seed feeding or stem boring, it can spread through speciation across many plant species, with each host plant hosting its own insect species in that adaptive zone. With many lineages radiating in this way, for example herbivorous Hemiptera, Diptera, Lepidoptera, Hymenoptera, and Coleoptera, it is evident that any plant species will be colonized multiple times, resulting in a rich community of insects on host plants.

1.6.2 Herbivore diversity for carnivores

This scenario can be applied to higher trophic levels involving the primary and secondary carnivores. Parasitoids, in particular, are likely to be specific to a single host, or a highly circumscribed group of hosts, because their parasitoid larval stage lives in intimate association with host chemistry and defense. For example, in an abandoned damp field in southern England, 15 aphid species were parasitized by 18 primary parasitoid species and 28 secondary parasitoid species (Godfray and Müller 1998, Müller *et al.* 1999, Figure 1.6). The **primary parasitoids** lay eggs inside the living aphid host, which then attaches itself to the host plant, and the exoskeleton hardens into a shell-like aphid “mummy.” A group of 18 **secondary parasitoids** attack the aphid and the primary parasitoid while both are still active, before mummification. These are called **hyperparasitoids** because they attack the primary parasitoids. Another group of 10 species attack the mummified stage of the aphid, the “**mummy parasitoids**,” killing both the

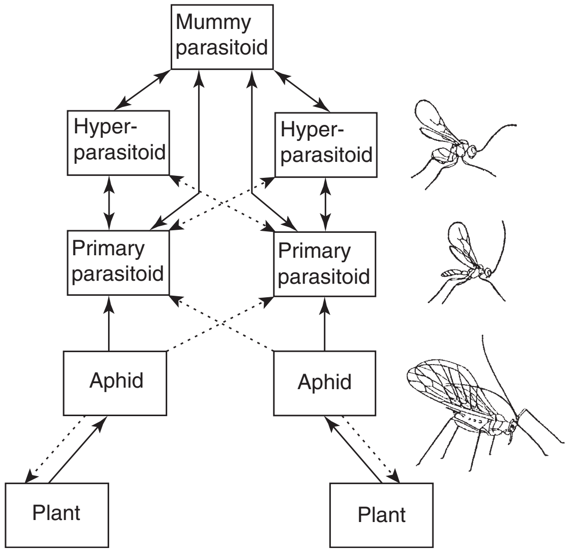


Figure 1.6 Part of a food web based on two plant species, and two aphid species, with primary parasitoids and hyperparasitoids, and mummy parasitoids attacking both primary and hyper parasitoids. Solid lines and arrows illustrate what are thought to be some of the strong influences in the dynamics of the community. Dotted lines and arrows show less important interactions. Modified from Godfray and Müller 1998. Reprinted with permission from Kluwer Academic Publishers.

primary parasitoid and the hyperparasitoid if it is present. Thus, a small number of plant species, less than 20 species, supports 15 aphid species, attacked by 18 primary carnivores and 28 secondary carnivores, some of which act as tertiary carnivores when they attack hyperparasitoids in mummies, for a total of 61 insect species! And this just enumerates the aphids and their parasitoids in one field. Multiply this number by the many other kinds of herbivores and detritivores in the field, and their natural enemies, and we can easily imagine hundreds of species coexisting, each in their own ecological niche, all in one small damp field about 18 000 m^2 in area. Then multiply this number per unit area around the world, and the numbers of insect species at the various trophic levels grows to staggering richness.

1.6.3 Species formation

Of course, an important component of adaptive radiation is the process of **speciation**. Although this is regarded at times as a controversial subject (e.g. Howard and Berlocher 1998) we know speciation happens, and there are relevant points worth mentioning here. The parasitic lifestyle of many insects, both herbivores and parasitoids, means that they tend to be specific to their plant or animal hosts (see Chapter 8 on Parasite and host interactions). They are adapted to find hosts, and to live with hosts, in specialized ways. Once a host is colonized, relatives of the host may be vulnerable to exploitation simply involving a **host shift**: a jump from one host to a related host. This may result in reproductive isolation and speciation, a process that may be repeated many times. Host shifting may occur within the same locality, resulting in **sympatric speciation**, or it could occur on either side of a geographic barrier involving **allopatric speciation**, or speciation in different locations (see Price 1996 for details). For example, it is apparent that during the radiation of the goldenrod plant genus, *Solidago*, two species formed in northern USA and southern Canada: *S. altissima* and *S. gigantea*. The specialist gall fly, *Eurosta solidaginis*, appears to have speciated into two reproductively isolated sibling species, one on each goldenrod host species (Abrahamson *et al.* 2003). In addition, speciation has occurred on the next trophic level involving originally a stem-boring predatory beetle, *Mordellistena convicta*, which has now divided into the stem borer and a new gall-fly predator in the galls (Eubanks *et al.* 2003). Thus, speciation has moved up the trophic system from plants, to herbivores, to predators, representing what must be occurring commonly in countless other species associations. This **sequential radiation** was named by Abrahamson *et al.* (2003, p. 781) to represent the "escalation of biodiversity up the trophic system."

Insect genera are frequently very large, numbering in the hundreds of species per genus, suggesting rapid speciation without great morphological differentiation. The superficially simple scenario of host shifting could account for this taxonomic situation. For example, the cicadellid genus, *Erythroneura*, includes about 500 species, involving many host shifts among woody plant species (Ross 1962). "Species fission by a host transfer mechanism" was Ross's considered view on the spectacular radiation of the genus *Erythroneura* (Ross 1962, p. 188). The details involved are probably unique to each species and genus.

Another suggestive feature of these large genera with many species on different plant species is that **sibling species** are common. Species that are very difficult even for a taxonomist to tell apart, or **cryptic species**, remain hidden from the taxonomist's eye unless particularly careful study is involved or molecular variation is considered. Sibling species would arise, in one scenario, by simple host-plant shifts, with most habits retained on the new host, without demands for adaptation morphologically to the new host. Strong morphological similarity also suggests rapid speciation and rather recent speciation, or we would expect greater morphological divergence simply by **genetic drift**, or random genetic changes. Such sibling species are found in the genus *Erythroneura* itself (Figure 12.5), in sawflies, cynipids, fruit flies and many other groups. Among the fruit flies, one species pair in the genus *Rhagoletis* could be distinguished initially only by electrophoresis, with one of the species appropriately named *Rhagoletis electromorpha* (Berlocher 1984, an electromorph being an enzyme allele detected by electrophoresis).

Adaptive radiation, and its component of speciation, is a rich blend of ecological, behavioral and evolutionary interactions. The ecology involves plant and insect interactions, insect host and parasitoid interactions, predators with prey species and the relationships among all these species in space and time. Therefore, this subject will be revisited many times in this book.

1.7 Ecosystem processes

Insects play important roles in ecosystem processes, as the list below indicates. All these roles that insects fulfill will be discussed in greater detail later in the book.

(1) Insect herbivores convert plant and algal biomass into animal biomass.
(2) Insects then become important food sources for primary carnivores, including many other insects and vertebrates such as reptiles, amphibians, birds and mammals. Insects feeding in fresh-water systems on algae and leaf litter become important food for predaceous aquatic insects, amphibians and fish. Insects are vital components in moving energy up the food chain and food web.
(3) Insects as herbivores and saprophages play a role in decomposition of plant biomass and its recycling of energy and nutrients. Chewed leaves pass out as frass, which typically falls to the ground, along with dead insects and cast integuments after molting. Insects chew up dead leaves, and bore into dead and dying trees, speeding up bacterial and fungal colonization and decay. Recycling of nutrients is accelerated.
(4) Decomposition is also accelerated in animal corpses by colonization by flies, burying beetles and others, while dung is invaded, or carried off, also by many flies and beetles. These kinds of insects contribute importantly to the hygiene of natural landscapes.
(5) We could argue with considerable justification that insects are their own worst enemies. So many species are predators or parasitoids on other insects that one can wonder how their prey species can persist at all (see Clausen 1962). Undoubtedly, carnivorous insects play significant roles in regulating their prey populations, but in turn they become food for higher trophic levels. Insects have been used extensively as agents in the biological control of other insects, in some

cases with great success (e.g. DeBach 1964, Thacker 2002, Anonymous 2003, Hajek 2004).

(6) Herbivorous insects also can have strong impacts on plant populations, either killing plant individuals or weakening them, thereby altering plant community composition and diversity. Forests may be killed by defoliators or bark beetles. Insect predation on seeds and seedlings may play a significant role in plant demography. The biological control of weeds relies in many cases on the activity of insect herbivores, be they defoliators, stem or root borers, gall inducers or seed predators (e.g. Van Drieshe *et al.* 2002, Myers and Bazely 2003, Hajek 2004). Insect herbivores also act as important pests in agriculture and horticulture.

(7) Pollination by insects is another essential function, for many plant species depend entirely on insects to transport pollen from one individual to another. Many crop plants depend almost exclusively on insect pollination, with a total value of these crops estimated at over $24 billion in 1988 in the USA (Metcalf and Metcalf 1993). The economic value of pollination worldwide in 2005 was estimated at 153 billion Euros (~ 198 billion US dollars), with by far the largest benefits for fruits, edible oil crops and vegetables (Gallai *et al.* 2009). Crops range from apples, pears and peaches, to peas, beans and squash, and on to alfalfa, clover, cotton and sunflowers, with over 30 crop species included in the list. Native bees alone have been estimated to contribute over $3 billion per year in pollinating services for US crops (Losey and Vaughan 2006).

(8) Insects even provide an important source of nutrition for humans in many countries (Menzel and D'Aluisio 1998). Caterpillars, dragonflies, cerambycid grubs, scorpions and tarantulas all make culinary delights for those accustomed to their crunchy, proteinacious and fatty treats. Add to the direct consumption of insects (entomophagy) the consumption of honey, and we can guess that the majority of people in any country eat insects or insect products.

(9) Insects are critical in vectoring diseases of plants and animals. Many plant diseases are transmitted, especially by sucking insects (e.g. Carter 1973, Maramorosch and Harris 1979). Serious diseases in animals, wild and domestic, and humans are transmitted by insects, resulting in millions of deaths per year, and many more with debilitating conditions; malaria, dengue, yellow fever, sleeping sickness, plague, Chagas' disease, West Nile virus and Lyme disease are but a few. The cost in human health, morbidity, mortality and suffering is almost incalculable (Busvine 1976, Service 2004, Lehane 2005, Goddard 2003). Insects and other arthropods also cause direct discomfort by biting, sucking and stinging animals and humans. Ticks, mites, mosquitoes, tabanid flies, blackflies, bed bugs, lice, fleas and assassin bugs all afflict members of the Animal Kingdom, as well as the stinging wasps, bees and some parasitoids. Malaria, caused by various *Plasmodium* protist species and vectored by many mosquito species, infects vertebrate species from snakes and lizards to birds, bats, rodents and primates, including humans. Over 300 million acute cases of malaria occur in human populations with over a million deaths annually; 90% in Africa, most in young children, accounting for 40% of public health costs (Bush *et al.* 2001, Roll Back Malaria website 2009).

Thus, there is a lot of ecology to understand. Who eats what, and how much? Why isn't more eaten? What limits the extent of feeding on plants, or on animals? And, how do humans influence such interactions, or benefit from them? How does floral design evolve in relation to pollinators, and what adaptations do the pollinators have that promote pollen transfer and nectar acquisition? The questions are endless, always providing entertainment while we hike, or spend time in the garden and yard. On the practical side, there are a multitude of questions about how best to manage medical, forest and agricultural pests, how to manage landscapes which minimize problems and pesticide use, how to conserve rare and endangered species of insects, and the habitats that they require for survival.

1.8 Ecological questions and answers

As the questions posed above indicate, insect ecology involves the interactions of insects with each other and with other organisms and their physical environments. And, as the title of this book also suggests, we need to develop a conceptual framework in which to work, and the evidence this is based upon. Then this knowledge can be applied to understanding the ecology of natural environments and those influenced by humans, such as in agriculture, horticulture and forestry. Such understanding would contribute to solutions of problems posed in the management of landscapes, and the protection of species, communities and ecosystems.

There are many fundamental questions to be addressed. How do food webs function, and how do species interact among the various trophic levels? How important are interactions within and among trophic levels; how important are the processes of intra- and interspecific competition, mutualism, amensalism, parasitism and predation in community organization? For all these within- and between-trophic-level interactions, many questions relate to the impact of physical factors, or abiotic factors; the role of precipitation, drought, fire, climate and weather. Another interesting area of research is quantifying the genetic variation in populations and elucidating its adaptive significance. The genetic relationships among species, or their phylogenetic relationships, provide a valuable basis for asking about the comparative ecology of a species group. In relation to phylogeny, are there trends in behavior, host relationships, or population structure and dynamics; does the phylogeny expose some evolutionary pathway involving changing ecological relationships; are there phylogenetic constraints on the kinds of ecology we see in a lineage? Can patterns be detected? Here we have entered into the realm of **evolutionary ecology** which often addresses the question “Why?” Why does this flower have this design? Why does that insect eat only one species of plant? Why are there so few natural enemies attacking this particular insect species?

On a larger scale, ecology addresses questions about ecosystem function, landscape patterns and effects, and geographical distributions. How does nitrogen cycle in an ecosystem and what is the role of insects, above ground and below? How does increased carbon dioxide in the atmosphere and climate change influence ecosystem processes? How does natural vegetation affect pests in field crops? What landscape design maximizes persistence of a butterfly species? What is the richness of species on a geographical gradient such as altitude change up a mountain range, or latitude from polar regions to the tropics, and what factors influence the pattern?

The answers to the questions rely on basic components of the **scientific method**. First, an interesting question must be asked. This provides the impetus for the money, time and energy expended in answering the question. Second, the question may be translated into a **hypothesis**, which provides a tentative, testable answer to the question. The hypothesis is framed in a way that allows scientific evidence to be gathered, which is either consistent with the hypothesis, or which falsifies the hypothesis. The hypothesis is either accepted or rejected based on objective, repeatable, verifiable scientific evidence. Third, observations are needed to provide data relevant to the question and the hypothesis. These observations should be extensive enough to discover a pattern in the relationship under study. The broader the pattern that is discovered, the wider will be its application and usefulness. Experiments should be employed whenever possible to help unravel the complex of interacting factors that may be observed in the field. These data result in acceptance or rejection of the hypothesis. In either case, additional research is probably needed to deepen the level of understanding and/or to extend knowledge more broadly. Fourth, once broad patterns in nature are discovered and the mechanisms driving the pattern are defined, then together they form the basis for **theory**: an empirically and factually based mechanistic explanation for a broad pattern in nature. This understanding can then be applied to a wide range of questions and problems relating to both natural and managed systems. “Study major, broad, repeatable patterns,” admonished Tilman (1989, p. 90). “Because the purpose of ecology is to understand the causes of patterns in nature, we should start by studying the largest, most general, and most repeatable patterns” (Tilman 1989, p. 90).

This definition of theory differs from looser uses, such as in theoretical ecology, which often involves the study of hypotheses, and their implications for what is possible in nature. The word “theory” is also used as “just an idea” as if it is merely a hypothesis. But in this book we will use the terms hypothesis and theory as we have defined them. This is because the distinction is important, and the goal of science is the development of theory as defined above.

Applications

Contributions to many disciplines

Insects cause enormous damage to human populations and on their managed lands, and they provide great benefits to humans. The costs of human suffering inflicted by insects are hard to assess, but damage to crops are more tangible. About 10 000 species of insects routinely attack our crop plants, with damage to any one crop ranging from 5–20% of the crop’s value, and estimated total losses adding up to about $15 billion in the USA annually (Metcalf and Metcalf 1993). Insects are our tormenters, our strong competitors for food, and yet they perform important services also (e.g. Losey and Vaughan 2006). Thus, the entomologist and ecologist face many challenges to gain an understanding of human relationships with insects.

For entomologists, ecology may be the most central conceptual field for their science. Plant–insect interactions play significant roles in agriculture, forestry and horticulture. Insect vectoring of plant and animal diseases is very much an ecological topic. Insect physiology includes a strong environmental component. Toxicology encompasses the movement of compounds and breakdown products in food webs, and in the physical environment. Regulation of weedy species and insect pests through biological control involves the ecology of multitrophic-level systems, as does integrated pest management, which strives to maximize crop health, and minimize pest problems in a cost-effective and environmentally responsible way.

From these concerted and long-term efforts involving ecological aspects of entomology many important contributions to the literature have resulted, in terms of major advancement in science, and textbooks in general ecology written by entomologists, or others that studied insects early in their careers (Price 2003b). Much conceptual ecology has been derived from studies designed to solve pressing problems: for example, the control of stored grain pests, forest insects, introduced weeds and insects, conservation and plant protection. Indeed, it is probably these urgent needs to understand insects that have made knowledge of them so important for the development of ecology. The field of ecology then contributes to, and blends with, the problem-solving areas of entomology in a continuum of interaction and advance. Every study is likely to have a useful application, and every problem solved probably contributes to a conceptual advance in ecology. Therefore, any terms, such as basic and applied science, should reflect only emphases rather than differences in disciplines. Insect ecology has benefited through the years from the free interplay between concepts and problem solving.

Ecology also plays an intermediary role between such areas as conservation and agriculture. “In fact, these endeavors are two sides of the same coin, with a shared heritage in decades of population and community ecological theory and experimentation” (Banks 2004, p. 537). Banks goes on to explain this shared heritage in several fields of ecology and how they have been applied to agriculture. The integration of cross-disciplinary knowledge provides a great benefit to understanding natural landscapes and those influenced by humans. Insect ecology can play a major role in integrating many aspects of the environmental sciences. The following chapters expand on the theme that insect ecology has many applications to solving problems involving insects encountered by humans.

Summary

This introductory chapter provides fundamentals on which the rest of the book is based. We have noted some important attributes of insect design which define the way they can relate to their environments: the basis for their ecology. These include a tough exoskeleton, a tracheal system delivering oxygen rapidly to the body, metamorphosis, flight and constraints on size. This blend of characteristics contributes to an understanding of how so many species can evolve and coexist on this planet: several million species, and a high proportion of the animal biomass in any one place.

The diversity of feeding links and types, and the richness of interactions result from the diversity of insects and the richness of habitats into which they blend. This diversity is also key to understanding the extensive adaptive radiation of insect species. Insects generally occupy specialized ecological niches, particularly when living species such as plants and animals act as habitat and food. Thus interactions flow up the food web from plant species with their own specialized requirements, to insect herbivores relating to particular plant species, and carnivorous insects feeding on a relatively narrow spectrum of insect species. Biodiversity increases at each trophic level starting with a species-rich flora, to herbivores, to the predators and parasites which depend on living insects for food.

With such vast resources, the opportunities to expand into new ecological niches is almost infinite. The process of this expansion involves speciation in the same locality via host shifts, or through geographic isolation. The diversity of insect species resulting from speciation and adaptive radiation means that their roles in the environment are rich, intricate and complex.

Insects contribute many activities important to ecosystem function, by converting plant biomass into animal biomass, a source of food for carnivores, including both living, dying and dead plant parts. Decomposition, pollination and transmission of diseases are all included in the beneficial and deleterious impacts of insects based on our own human perspective. To understand all these ecological issues we ask questions and try to gain understanding through the scientific method, resulting in scientific hypotheses and theories. With this knowledge we can address issues relating to our management of land for plant production, our attempts at regulation of vector-borne diseases of plants and animals, and the improvement of human health and hygiene. Insect ecology plays an integral role in the development of human welfare and the conservation of our environments.

Questions and discussion topics

1 In which ways does insect flight influence their ecology?

2 In which ways do you think that the size of insects contributes to the number of species: (a) globally and (b) in local habitats?

3 Discuss from your own perspective the most fascinating aspects of insects and their ecology.

4 Which methods would you advocate for estimating the number of all insect species in a plot of land?

5 Discuss the relative importance of insects as beneficial and deleterious components of ecosystems in relation to their roles in natural habitats.

Further reading

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Part II **Behavioral ecology**

CONTENTS

Behavior links the organism to its environment. At every moment of the day and night behavioral responses to environmental cues, and internal drives, guide an individual through its often perilous existence. Behavior determines success or failure in the efforts to reproduce. Discovering the many cues that insects use to inform them of their environment, and their responses to these stimuli, is an ongoing pursuit of behavioral ecologists. This is because insects can be much more specialized than humans in the cues employed to locate food, and cues that stimulate feeding. Indeed, the ways in which they relate to their surroundings is often notably different from we humans. As a result, behavioral ecology is a broad and fascinating subject which reaches well beyond this section of the book, into Part III on species interactions and other parts of the book.

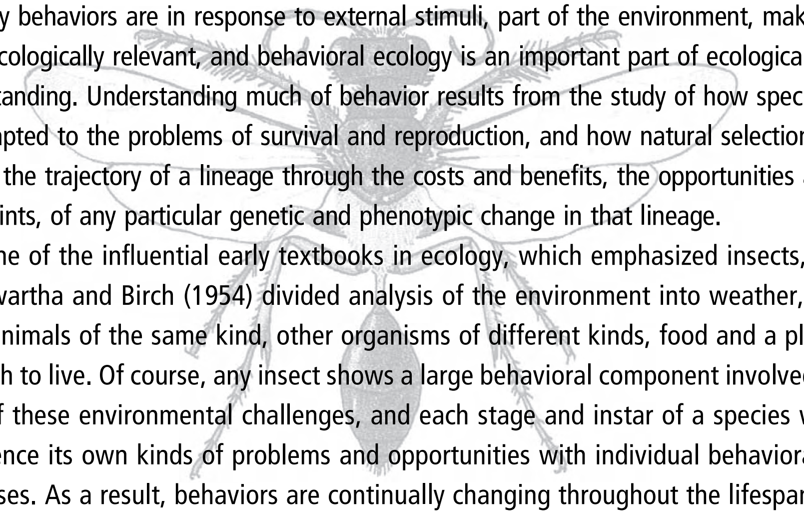
We introduce behavioral ecology by concentrating on the essentials of life, those that deal with existential and environmental challenges: survival, finding food and a place to live, communicating with others of the same and different species, and reproduction. A logical progression in the book, after the introduction, is to concentrate on individuals and how they act. Then we move to interaction among species, populations and communities in later parts, expanding the scale of the ecology we consider.

The second chapter in Part II is devoted to social insects. Their behaviors are complex and integrated into communal living, which has advanced beyond human achievements in many ways. Therefore, they generate impressive impact on their environments, including many species of plants and animals within their range. Few humans can pass their lives without encountering, for good or ill, social insects and most people rely on pollinators such as bees for a large proportion of their food.

Once we have appreciated the existence of insects at the individual and social levels we can progress to other parts of the book, but never forgetting that the understanding of behavior is essential in the comprehension of larger-scale interactions in ecology.

2

Behavior, mating systems and sexual selection



Behavior can be defined as anything that an individual does during its life, involving action in response to a stimulus. Eating behavior is stimulated by hunger; sleeping or resting behavior is in response to fatigue; escape is a response to attack and reproductive behavior is in response to physiological urges and stimulation by members of the opposite sex. Throughout the life of an individual insect it is behaving constantly in one way or another, making behavior a large and important subject.

Many behaviors are in response to external stimuli, part of the environment, making them ecologically relevant, and behavioral ecology is an important part of ecological understanding. Understanding much of behavior results from the study of how species are adapted to the problems of survival and reproduction, and how natural selection shapes the trajectory of a lineage through the costs and benefits, the opportunities and constraints, of any particular genetic and phenotypic change in that lineage.

In one of the influential early textbooks in ecology, which emphasized insects, Andrewartha and Birch (1954) divided analysis of the environment into weather, other animals of the same kind, other organisms of different kinds, food and a place in which to live. Of course, any insect shows a large behavioral component involved in each of these environmental challenges, and each stage and instar of a species will experience its own kinds of problems and opportunities with individual behavioral responses. As a result, behaviors are continually changing throughout the lifespan of an insect, from its embryogenesis to its death, creating a challenge to an adequate sampling of this diversity. Added to the multitude of behaviors within individuals and species is the variety of insect and other arthropod species, each with a unique array of behaviors. Therefore, this chapter will adopt a broad approach to behavior, working through generally experienced challenges as insects pass through their life cycles: survival, foraging, where to live, communication and reproduction, and their behavioral responses to such challenges.

2.1 The reproductive imperative

The essentials of life are organization, metabolism, development, reproduction, interaction with the environment and genetic control (Hickman *et al.* 1988). Maintaining these essentials depends heavily on the behavior of each organism, and each is influenced by their interactions with abiotic and biotic impacts: ecology and behavior are closely associated – hence behavioral ecology. Ultimately, the primary reason for an individual's life is to reproduce its own kind and its own genes, or to aid close relatives in achieving this end. Metabolism, development and growth depend on foraging and feeding, two components of central concern in behavioral ecology. This activity results in success or failure, with finding mates, mating and reproductive achievement often involving complex behavioral sequences, and many diverse strategies for accomplishing successful reproduction. Alternative mating strategies may even be observed within the same species, as is commonly the case (e.g. Shuster and Wade 2003). Therefore, we must regard behavior, and behavioral ecology, as central to the understanding of any insect species or group of insects.

2.2 The life-cycle approach

It is difficult to isolate kinds of behavior into convenient subjects because an individual insect habitually integrates stimuli into a pattern of behavior appropriate for a particular moment in its life. An insect is likely to respond simultaneously to motivations to feed, avoid predation and to communicate. Also, communication, breeding and avoidance of predation are probably closely associated with adult behavior. However, each major aspect of behavior justifies book-length treatments, so discrete units are treated in isolation. Here, in this chapter, we concentrate on ecological aspects of behavior, and following Alcock's (2005) example, we are guided loosely by the life history of the insect from egg to reproduction and death. Therefore, survival and feeding behavior, and habitat and microhabitat selection, are considered before communication and reproductive behavior. To be successful, all stages in the insect life cycle, from nymphs and larvae to adults, must survive, feed, and find and occupy a suitable place to live. Communication may involve the whole life of an insect, including defensive secretions against enemies and signaling to potential mates. But reproductive behavior is usually concentrated in the adult stage of the life cycle, although inevitably among insects, there are exceptions. This, then, is the order in which subjects will be treated in the chapter. Chapter 3 will consider additional aspects of behavior involving social systems and the evolution of sociality.

2.3 The experimental necessity

As in all science, experiments are essential for the objective interpretation of behavior. To understand the stimulus-response, cause and effect, of a behavior, a particular stimulus must be isolated from the range of stimuli that could possibly be used. For example, when a digger wasp locates the burrow it is provisioning with caterpillars as food for its progeny, is it using its eyes to locate the burrow itself or local landmarks, is it using olfaction or perhaps it is orienting in relation to the sun? Early investigators realized that teasing apart the mechanisms of behavior required experiments, they became masters of this approach, and they endowed the field with a rich legacy of experimental methodology, still prominent in the field today.

Amplifying on the example of the digger wasp, the famous ethologist, Niko Tinbergen (1935, Tinbergen and Kruyt 1938) examined the orientation behavior of the digger wasp, *Philanthus triangulum* (Hymenoptera: Sphecidae: Philanthinae). Members of this subfamily provision nests in sandy soil with bees,

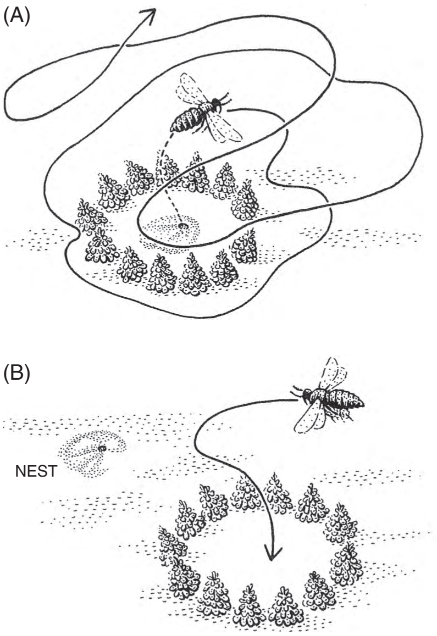


Figure 2.1 An illustration of Tinbergen's experiment on the digger wasp's ability to learn landmarks, which guide the wasp to its nest. (A) The wasp takes an orientation flight over its nest entrance before it goes foraging for prey, and learns to associate it with the ring of pine cones. (B) The pine cones have been displaced from the nest hole. The wasp returns with prey and goes to the center of the pine-cone ring. From Alcock 1975.

and are called "bee-killer wasps" or "bee wolves." After burrowing, a female spirals in flight around the nest area and then flies in search of bees. It returns and easily discovers its nest site. Tinbergen thought that the wasp must exhibit learning behavior, and the cues it oriented to were small local landmarks. Figure 2.1 illustrates the experiment he conducted. He placed a ring of pine cones around the nest while the female was therein. He allowed the female to leave and spiral around, and while she foraged he moved the pine cones a small distance from the nest. The female returned with prey for its larvae and headed straight for the center of the pine-cone ring. This demonstrated unequivocally that the female used the learning of landmarks as the mechanism by which it relocated its nest.

Even more remarkable is the learning ability of the sphecid digger wasp, *Ammophila pubescens*, studied by Baerends (1941), which provisions many of its nests on the same day. Up to 15 nests may be provisioned every day, beginning with an inspection of each nest, which enables assessment of the size of progeny, and the number and size of caterpillar larvae needed for that day. After this initial evaluation the female proceeds with provisioning each nest in turn with the appropriate food supply for that day. When Baerends experimentally manipulated the number or size of prey larvae after the initial inspection, the female did not change her provisioning plan originally developed. In fact, she could learn and remember each morning the amount of food required per nest for that day, and provisioned accordingly for the whole day: a remarkable feat, surpassing what most people could achieve without a note book.

Before these studies, Karl von Frisch had translated the dance language of the honey bee (starting in 1914, and described in von Frisch 1967), using elegant and simple experiments which demonstrated color perception by bees and their learning ability. The discussions that follow in this chapter will rely heavily on experimental methods, without necessarily describing the methodology. Therefore, you are encouraged to examine the original literature to learn of the many clever, creative ways in which behavior is investigated.

2.4 Survival

Environmental threats to survival include weather, food supply, including competition, and natural enemies: predators, parasitoids and pathogens. We now examine these threats in order, together with insect behavioral responses.

2.4.1 Weather

Presumably all organisms have evolved to cope with normal fluctuations in the local climate, and there is a large literature on how particular species are adapted, for example to winter cold, long-term dry spells and excessive heat. This subject of physiological ecology is covered well in many books and journals, for example Wiggleworth's (1984) classic *Principles of Insect Physiology*, Chapman's (1998) *The Insects: Structure and Function*, Chown and Nicolson's (2004) *Insect Physiological Ecology* and the journals *Environmental Entomology* and *Physiological Entomology*. In addition, more specialized treatments cover *Seasonal Adaptations of Insects* (Tauber *et al.* 1986), the ecology of overwintering (Leather *et al.* 1993), insect thermoregulation (Heinrich 1981), and dispersal and migratory behavior allowing insects to escape inclement conditions (e.g. Johnson 1969, Dingle 1996). However, most adaptations to severe and threatening conditions are more physiological than behavioral, so are not treated in this book. Behavioral responses to threatening conditions involve finding protected hiding places or leaving the locality. Overwintering in cold temperate and arctic climates usually involves hiding in concealed, insulated habitats; under bark, in the soil or litter, at the forest edge or under snow. Leaving a locality to escape threats from the weather definitely involves behavior: movement, probably flight, dispersal or migration. Hiding within the same habitat would involve **foraging movement** to find a protective place and **ranging movement** which explores an area for a suitable habitat, according to Dingle's (1996) classification (Table 2.1). These behaviors contrast with **migration behavior**, as explained next.

The understanding of migration involves several areas of biology: behavior, ecology, physiology, genetics and evolution. But the definition of migration is best treated as "a distinct and specialized behavior" (Dingle 1996, p. 25). The behaviors include:

(1) "persistent movement of greater duration than occurs during the station keeping or ranging movements of the same organism;
(2) straightened-out movement that differs from the relatively frequent turning that occurs during ranging and station keeping, especially the latter;
(3) initial suppression or inhibition of responses to stimuli that arrest other movements but with their subsequent enhancement;
(4) activity patterns particular to departure and arrival; and
(5) specific patterns of energy allocation to support movement." (Dingle 1996, p. 25).

Flight tends to be unidirectional and persistent, without orienting to local resources such as food. Flight is often preceded by adaptive changes in behavior and physiology which make flight possible, such as a photopositive response of root-feeding aphids. Likewise, a photonegative response after migration ensures that such aphids return to host-plant roots. Before flight, individuals are likely to store energy as fat and suppress egg production, and after alighting egg production may proceed: the **oogenesis–flight syndrome** (Johnson 1969, Dingle 1996). However, since flight usually precedes reproduction, and flight may even stimulate reproduction, this phenomenon is better labeled as the **flight–oogenesis syndrome**. Thus, migration may be in one direction, or with a return journey, usually in insects by a subsequent generation, and an equivalent term in the literature is **long-distance dispersal**, although dispersal involves the concept of scattering or spreading out of a population.

Considering the escape of insects from life-threatening weather, this qualifies as **seasonal migration** in Dingle's (1996) classification. But the migratory behavior also results in the opportunistic exploitation of abundant resources which develop as cold weather changes into spring and summer in cold temperate latitudes. Migration can be both an escape from winter and a plunge into the exuberance of plant growth in the summer. It may also include a bet-hedging strategy in which progeny from one

Table 2.1 **A glossary of behaviors involving movement of individuals through space**

Movements	Characteristics	Examples
Movements within the home range or directed to resources		
Stasis	Individual is stationary	Resting stages of insects: diapause etc.
Station keeping	Individual stays within home range: an area required to provide the resources for survival and reproduction	Local movement to food, shelter, mates etc.
Kinesis	Changes in rate of movement or turning	An insect responding to an attractive pheromone or kairomone
Foraging	The search for food or other resources, stopping when resource is discovered	A parasitoid searching for hosts, or a butterfly searching for a host plant
Commuting	Regular foraging on a short-term basis which ends when resource is found	Ant foraging, bee or wasp provisioning behavior
Territoriality	Guarding of an area against intruders, and aggressive behavior against trespassers	Mating territories of dragonflies or butterflies where resident males drive off intruding conspecific males
Ranging	Exploration of an area beyond the home range, ending when suitable resources are discovered	Dispersal from one habitat to another such as from feeding to overwintering sites
Movement independent of resources or home range		
Migration	Undistracted movement with stimulus to end provided by movement itself	Annual movement of monarch butterflies, coccinellids, noctuids, aphids, to and from wintering sites
Movement not under control of individual		
Accidental displacement	Passive movement by wind, water or thermals	Small insects such as aphids carried by wind

From H. Dingle (1996). *Migration: The Biology of Life on the Move*. Reprinted by permission of Oxford University Press, Inc.

female spread out and experience new and different environmental conditions (Holland *et al.* 2006).

The migration of the monarch butterfly, *Danaus plexippus*, will be familiar to many (Figure 2.2). Large aggregations of adult butterflies overwinter in fir tree forests in a mountain range in central Mexico. In the spring they migrate to the north and east, colonizing the southern United States (Figure 2.2A). Subsequent generations move northwards into cooler states in the summer. Additional overwintering populations are found in California, which spread east and north in the spring and summer. The monarch butterflies oviposit on milkweeds (*Asclepias*), some species of which (e.g. *A. syriaca*)

(A)

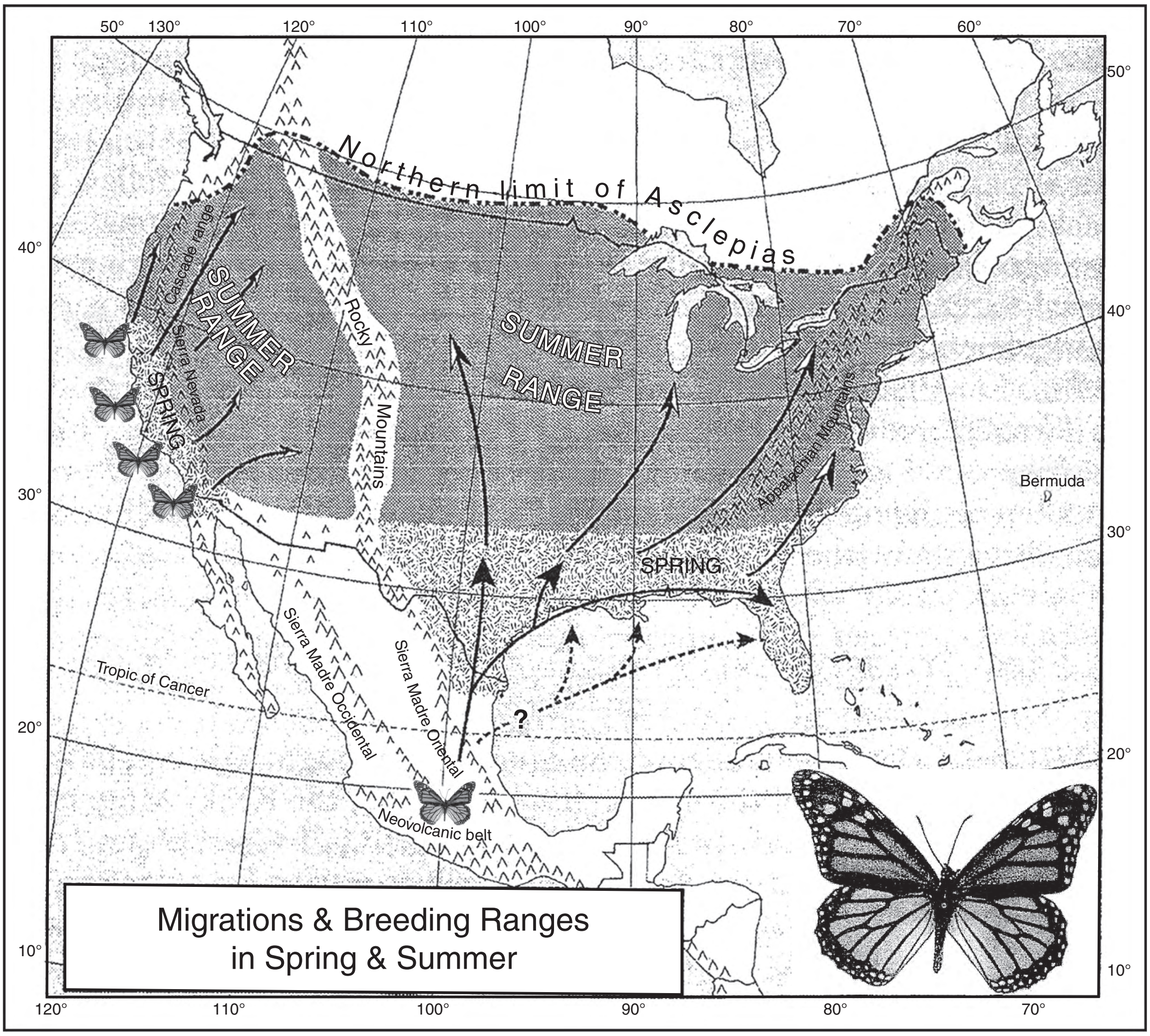


Figure 2.2 (A) The spring and summer migrations of the monarch butterfly in North America. Overwintering occurs in Mexico in fir forests in the mountains of the Transvolcanic Range, and along the California coast. The population from Mexico colonizes eastern North America over two or more generations, and populations in California move into western states. (B) Fall migrations result in returns to overwintering sites. The question marks are discussed in Brower 1995. From Brower 1995.

have become common weeds in disturbed and agricultural land, providing abundant food in summer for the larvae. However, these plants are herbaceous perennials; they die back in the fall, leaving a cold and desolate habitat in which monarchs are unable to overwinter. It is now known that individual monarch adults migrate in the fall from northern latitudes to overwintering sites, with some covering 3000 km, or about 1875 miles, into the fir forests of central Mexico, illustrated in Figure 2.2B. (Brower [1995] provides an excellent summary of monarch migrations, with many

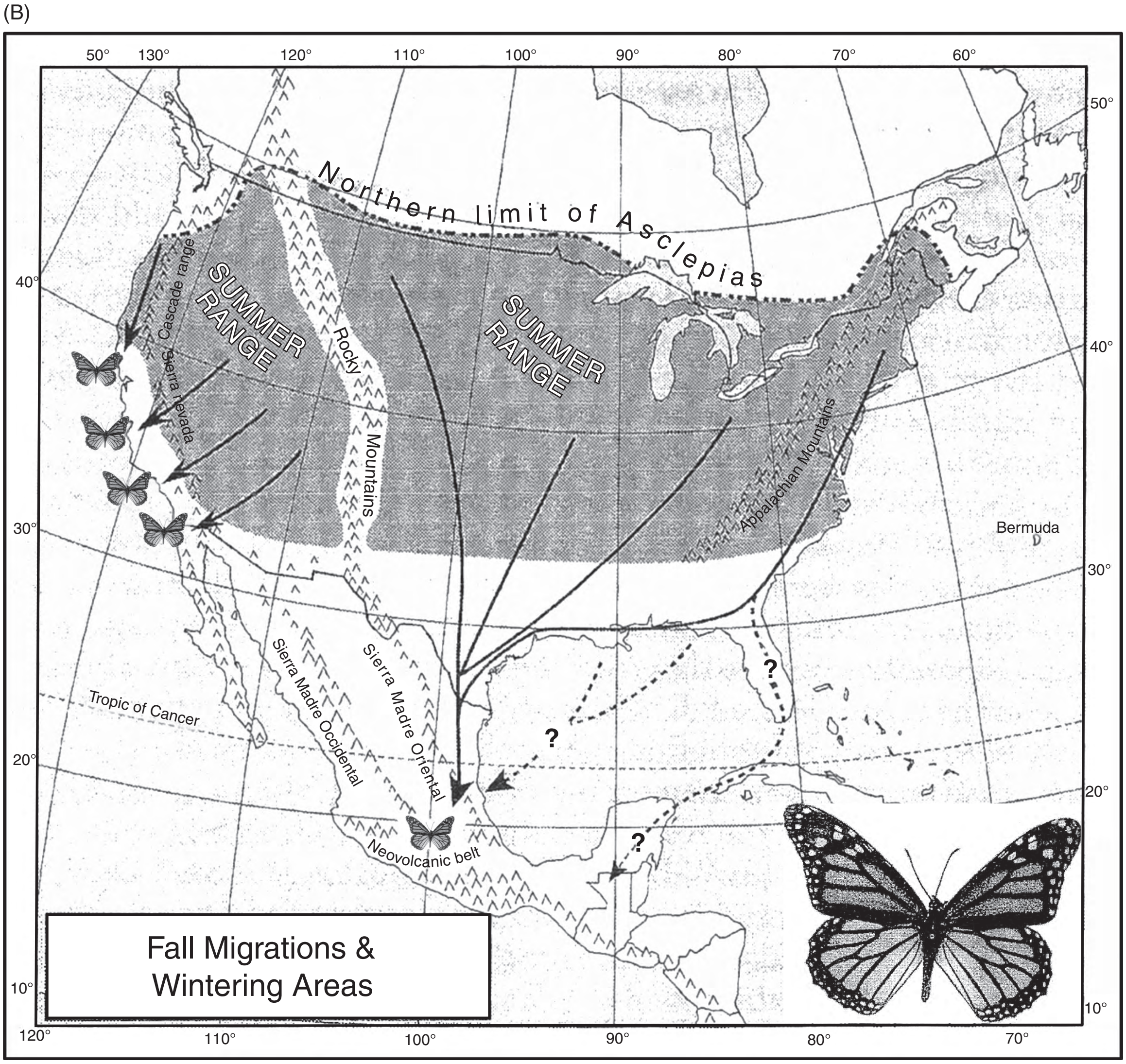


Figure 2.2 (*cont.*)

questions remaining.) Orientation during migration appears to be directed by a time-compensated sun-compass mechanism (Mouritsen and Frost 2002).

Many kinds of insects migrate. Some examples include dragonflies, grasshoppers, aphids, leafhoppers, butterflies, moths, beetles, flies, ants and sawflies (Johnson 1969, Dingle 1996, Gatehouse 1997, Chapman *et al.* 2008). Migration ranks as a major adaptive strategy resulting in the avoidance of severe weather and the colonization of new favorable conditions.

2.4.2 Food supply, competition and natural enemies

Insects at all trophic levels encounter problems while obtaining food. Plant food may be toxic or low in nutrition, and animal food may also be well defended. These kinds of machinations between members of interacting trophic levels are discussed in Chapter 4 on plant–herbivore interactions, Chapter 7 on prey and predator interactions, and Chapter 8 on host and parasite interactions. In addition, lateral effects, such as competition, which reduces access to resources, and the probability of survival, are treated in Chapter 5 on lateral interactions.

2.5 Foraging behavior

Foraging involves searching for food, and feeding results after a food item has been discovered and accepted as a suitable plant part, prey item or host of a parasitoid. The process appears to be simple enough for humans, but for small insects with specialized diets, and a complex environment in which to search, the adaptations that overcome such challenges become complex. This point is illustrated by the path of behavioral decisions made by a parasitoid from finding an appropriate habitat to host acceptance and oviposition, and manipulation of the host. While some specifics are provided here, the scheme of decision-making resulting in the narrowing of the field of search may be generalized to the sequence of behaviors that the majority of insects must pass through in order to find food. This is the case whether an individual is finding food for itself or for its progeny.

One of the most thoroughly studied species regarding foraging behavior is the parasitoid, *Cardiochiles nigriceps* (Hymenoptera: Braconidae), which uses as a host the tobacco budworm, *Heliothis virescens* (Lepidoptera: Noctuidae). The species has been studied over many years in Vinson's research group, with a detailed flow chart of interactions resulting, as shown in Figure 2.3 (Vinson 1975, De Moraes *et al.* 1998, De Moraes and Lewis 1999). The remarkable number of behaviors involved in the progression from finding a suitable habitat in which to search, to finding a host and accepting it, and ovipositing in the host, is well illustrated in the figure. First, females must locate a suitable habitat (1) in which the host is likely to be found, and they are attracted to brightly lit, open areas in which tobacco plants may be growing. Once in the habitat (2), females search for host plants (3) and examine them for damage (4). They land on plants that are damaged by the tobacco budworm larvae in response to a host-seeking stimulant (5). This chemical, a mixture of three methyl triacontanes, originates in the mandibular gland of the host caterpillar, which then becomes deposited on leaf surfaces as the caterpillar feeds. The parasitoid, on detecting this compound (6), starts actively searching the leaf surface, with antennae pressed against the leaf. She follows the path of the compound until she finds a host (7). The mandibular gland secretion that provides an adaptive advantage to the receiving parasitoid, but is produced by the individual the parasitoid is searching for, is called a **kairomone** (see Table 2.3).

Once the host caterpillar is discovered, the host-acceptance stage in the sequence of behaviors is reached (8) (Figure 2.3). A specific host compound on the cuticle appears to provide a stimulus for oviposition, although the host may be rejected if it has been parasitized previously, based on a host-marking chemical left by the original female. A previous parasitoid attack also leaves an internal repellent to subsequent oviposition, which is detected by a second female once the ovipositor is inserted below the cuticle. This results in rejection of that host. However, if the host is accepted, oviposition follows and the host regulation phase of the interaction develops (9). With the egg are injected substances that enhance larval parasitoid survival, modifying physiological processes in the host that benefit parasitoid fitness.

This sequence of stimulus-response behaviors is remarkable in its complexity. However, it is no doubt representative of the kinds of interactions when insects are searching for food, be they parasitoids, predators or herbivores. At the contrasting scales of large complex environments and small insects, many adaptations for finding food have evolved using chemical communications. Often, it is simply the body odor (BO) of the host plant or insect, which acts

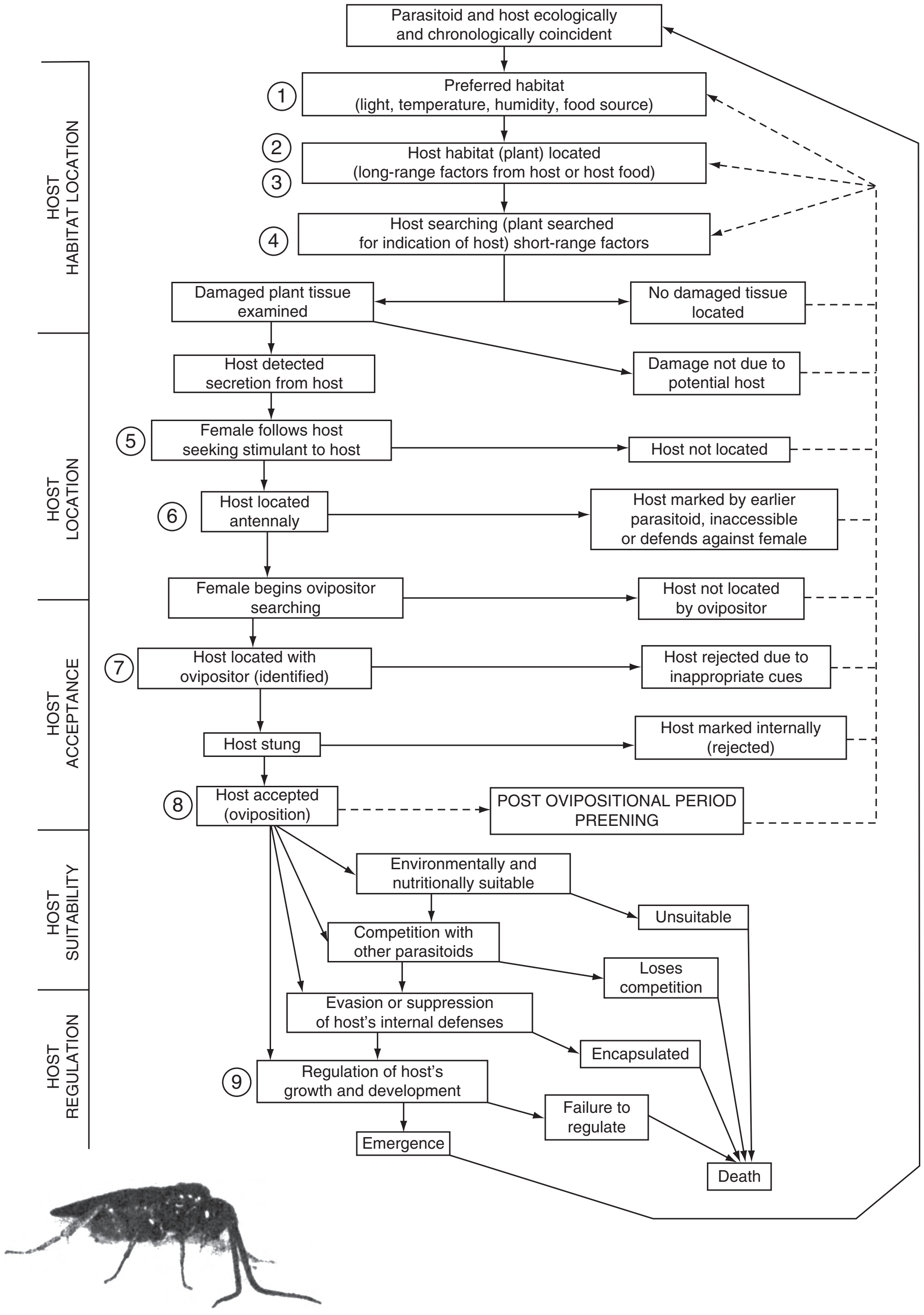


Figure 2.3 The progress of a female parasitoid, from locating the host insect's habitat to host discovery, host acceptance, and successful utilization of the host, resulting in emergence of another adult which repeats the process. From Vinson 1975.

as a stimulus, or odors from particular glands, scales or frass (Price *et al.* 1980, Price 1981). (See also Chapter 13 on Multitrophic interactions.)

In addition to using innate responses to stimuli, insects can learn to find food more efficiently (Papaj and Lewis 1993). Parasitoids learn to associate the discovery of hosts with odors emanating from food, such as from yeasts or apples – **associative learning**. They can even learn to associate hosts with chemicals exotic to their environment, such as perfumes, vanilla and chocolate. Flower-visiting insects learn to improve their access to rewards in individual flowers with experience, and some may learn routes along which nectar or pollen can be found – **trap-lining**.

The local path followed by a searching predator or parasitoid has attracted much attention, partly because it reveals the efficiency of a potential biological control agent, and partly because the rate of discovery affects the population dynamics of the natural enemy and prey or host interaction. The question most simply put is how much time should a searching predator, or parasitoid, spend in a patch before giving up the search. Three scenarios for this **patch time allocation** have been proposed (e.g. van Alphen and Vet 1986):

(1) **number expectation** in which an enemy leaves a patch after finding a certain number of hosts
(2) **time expectation** in which an enemy leaves a patch after a fixed amount of time
(3) **giving-up time** in which the enemy gives up searching and leaves the patch if it has not found a suitable host within a fixed time.

The number-expectation scenario is supported by *Cardiochiles nigriceps*, which leaves a patch after successfully attacking one host. But, in general, the number of cues that affect a search pattern are too numerous for any simple model to apply effectively. The ichneumonid parasitoid, *Venturia canescens*, searches for its host, the Indian meal moth, *Plodia interpunctella* (Lepidoptera: Pyralidae), which feeds on stored grain and meal, and spins a web as it moves through the medium. The wasp is attracted by the silk and turns frequently after contact (Figure 2.4) remaining in the patch until the stimulus is no longer effective. But if a host is found and oviposition occurs, then the parasitoid increases its sensitivity to the patch edge, thereby continuing to search within the patch. Therefore, time spent in a patch depended very much on the number of hosts discovered in that patch, but the time in the patch did not correlate with host density, or with expectations based on the fixed giving-up time model. With so many variables relevant to a searching parasitoid (e.g. Wajnberg 2006), inevitably significant interactions among factors are likely to occur, making the discovery of patch residence rules more problematic (Muratori *et al.* 2008).

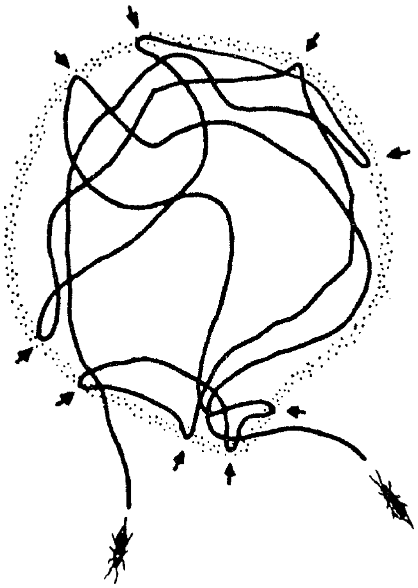


Figure 2.4 The search pattern of a female parasitoid, *Venturia (=Nemeritus) canescens*, on a glass plate, within a patch of host secretions. The edge is marked by stippling in the figure. Arrows show where the female turned abruptly at the edge of the patch. From Waage 1978.

Van Alphen and Vet (1986, see also Wajnberg 2006, Wajnberg *et al.* 2008) list a series of factors which may influence patch time allocation, emphasizing the need to know their influence and relative importance before an adequate patch time model can be formulated:

(1) Patch structure, for example, patch size and roughness
(2) Kairomone concentration – as concentrations increase patch time is likely to increase
(3) Unparasitized hosts in a patch increase patch time as oviposition takes time and often stimulates more intensive search
(4) Parasitized hosts decrease the likelihood of a female staying in a patch because rewards decline
(5) Other parasitoids, either con- or heterospecific, may leave trail odors which are repellent to an arriving female
(6) Previous experience in other patches may reduce patch time, including when mixed host patches have been experienced
(7) Travel time between patches probably increases the patch time as motivation to search increases.

An additional factor that has become increasingly realized recently is the importance of plant-provided food – nectar, pollen, sap, extrafloral nectaries etc. – so that patch dynamics is strongly influenced by alternative foods to prey because predators and parasitoids are frequently omnivores (Eubanks and Styrsky 2005, van Rijn and Sabelis 2005, Wäckers *et al.* 2005).

When considering predators many of the factors remain the same as for parasitoids. However, whereas many parasitoids attack slow-moving or stationary hosts, predators may cause a scattering of prey individuals (Sih 2005). When this occurs, such as when backswimmers (Hemiptera: Notonectidae) attack mosquito larvae which have escape responses, the notonectid's preference for high-density prey is offset by an increased scattering of mosquito larvae, resulting in no correlation between prey and predator densities. In addition, if mosquito larvae benefit from a predation refuge, a negative correlation between prey and predator results. Nevertheless, most modeling has assumed stationary prey, applying optimal-patch-use approaches or the concept of **ideal-free-distribution** studies. The former emphasizes the individual's response to prey and the latter the population response. The ideal-free distribution assumes a set of habitats or patches that differ in quality (e.g. prey density), and the predator is free to search, having an ideal knowledge of patch densities of prey. Predators will then show an **aggregative response** to prey density, causing prey density in the patch to decline, after which predators will find other patches more profitable. Eventually then, the predator population is distributed such that each individual is acquiring food at the same rate: a **stable ideal-free distribution**.

Such distributions have been observed in predator/prey, parasitoid/host and herbivore/plant interactions. For example, one of a small number of unsimplified studies under natural conditions shows an ideal-free distribution for the gall-inducing aphid, *Pemphigus betae*, selecting breeding sites according to leaf size of the host plant, *Populus angustifolia* (Whitham 1980, 1981). The mechanisms involved include females jousting for the best locations and are discussed in Chapter 4 in Subsection 4.3.9: Spatial and temporal variation in plant allelochemistry and nutrition pose tracking problems for insect herbivores, and are illustrated in Figure 4.11.

Obviously, foraging and feeding are large topics which will be covered in other parts of the book as well, particularly where food is toxic or of low nutritional status (Chapter 4), where there is competition for food (Chapter 5), when symbionts open up new resources (Chapter 6), when feeding and host specificity of parasites is considered (Chapter 8) and when community structure and multitrophic level interactions are discussed (Chapters 12 and 13). Indeed, much of ecology concerns the behaviors involved with food, feeding and foraging.

2.6 A place to live

Just as with finding food, every individual of every species (or its mother) has to find a place to live if it is

Table 2.2 **A place to live and care for progeny: some of the microhabitats in which insects and other arthropods live**

(1) Females place eggs in favorable sites for larvae. Preference-performance linkage, e.g. *Pemphigus* aphids, *Euura* sawflies, bruchid weevils and many others (Price 2003a)

(2) Females make habitats for progeny, e.g. galls, leaf folds and rolls, nests of bees, wasps, ants, termites, dung beetles, carrion beetles

(3) Provisioning, usually by females including sterile workers, for larvae in concealed places, e.g. cells in nests, dung balls, carrion fed to silphid larvae in nest (a subset of (2) above)

(4) Plant-provided microhabitats, e.g. domatia for predatory mites, myrmecodomatia, hollow stems, abandoned galls, flaky bark

(5) Animal-provided habitats, e.g. pelts of mammals, feathers of birds for parasites, noses, ears, under skin, blood, organs etc.

(6) Weaving tents, webs and cocoons, e.g. webworms, tent caterpillars, web-weaving spiders, nest-weaving ants, silken cocoons for pupae

(7) Burrowing in substrates:

  (a) Into dead or dying wood: passalid, lucanid, cerambycid and buprestid beetles, carpenter bees, carpenter ants, termites

  (b) Into ground: scarabaeid beetles, crickets, elaterids, ants, solitary wasps

  (c) Into living plants: larvae of many herbivorous insects, e.g. curculionid and bruchid weevils, gall formers, leaf miners, fruit feeders

  (d) Into living animals: parasitoids, some bot flies, chiggers, scabies mites

  (e) Into sand, pebbles, or under rocks, litter or other organic debris, e.g. larvae of some moths, spiders, beetles, aquatic insects such as caddis flies

(8) Abandoned oviposition, i.e. oviposition away from a safe feeding site for larvae, e.g. some arctiid moths and stick insects drop eggs to the ground, many moths oviposit onto substrates largely irrelevant to where larvae will feed: rocks, tree trunks, leaf litter. Therefore larvae lead a dangerous, exposed life until they establish a feeding site on a plant

(9) Feeding in open, e.g. many free-feeding herbivores, tenebrionids, carabids, many other predators

(10) Living in or on water, e.g. water striders, corixids, brine flies, black fly, mosquito larvae

(11) Urban environments, e.g. roaches, spiders, ants, termites

to survive, so the subject of habitat and microhabitat selection and use is of general interest in ecology. How an insect navigates a complex, heterogeneous locality to find a profitable place to live, and the cues that illicit appropriate behaviors relating to habitat use, are enduring questions, with many kinds of adaptations and strategies involved. Some of the diverse major categories concerning where insects live are listed in Table 2.2, and are divided into distinct types of answers to the challenge of occupying a safe place to live. Some examples include:

(1) Females oviposit exactly where the larvae will begin to feed
(2) Females construct or induce habitats for progeny
(3) Females provision cells in which larvae feed
(4) Plants provide microhabitats protective for insects and others

(5) Animals provide microhabitats for parasites
(6) Weaving insects and spiders make nests for themselves
(7) Burrowing by adults and larvae into substrates provides shelter and food
(8) Indiscriminate oviposition behaviors
(9) Feeding in the open
(10) Living in or on water
(11) Living in urbanized environments.

It is hardly surprising that, for small organisms, they can be found almost everywhere. These examples are discussed in more detail below.

2.6.1 Females oviposit exactly where their nymphs or larvae will begin to feed (Table 2.2, (1))

A female that is highly selective in oviposition behavior shows a strong **ovipositional preference** for a certain quality of resource for its progeny, among a range in resource variation. Females have evolved to be specialists, and show a remarkable capacity in a complex environment to make excellent choices. We can judge a female's quality of choice only by evaluating the performance of her progeny. Thus we look for a high **ovipositional preference – larval performance linkage**. Larval performance is often measured as the probability of survival, or growth rate.

Such linkage is relatively straightforward to measure in gall-inducing insects because the gall is initiated by a female in some cases, showing her preference for a particular site, and the progeny's performance is evident within the gall. For example, stem mothers of the aphid, *Pemphigus betae*, are first instar nymphs, only about 0.6 mm in length, and they must crawl from a tree trunk into the foliage of a large tree to initiate a gall in which they and their progeny will feed (Whitham 1978, 1979, 1980). They show strong preference for the largest leaves on a tree (Figure 2.5), and they joust for the best position on the largest leaves. At these sites they are highly successful at initiating galls and producing more progeny than on smaller leaves (see Figure 4.11). A very similar preference–performance linkage is shown by the shoot-galling sawfly, *Euura lasiolepis*, in which long shoots are preferred as oviposition sites by females, and larvae survive best on these shoots (Figure 2.6, Craig *et al.* 1986, 1989). These kinds of examples promoted the development of the **plant vigor hypothesis** which argues that many insect herbivores select and perform best on plants and plant modules which are growing vigorously in a population of plants or modules (Price 1991a, 2003a, see also Chapter 4 on the plant stress and plant vigor hypotheses).

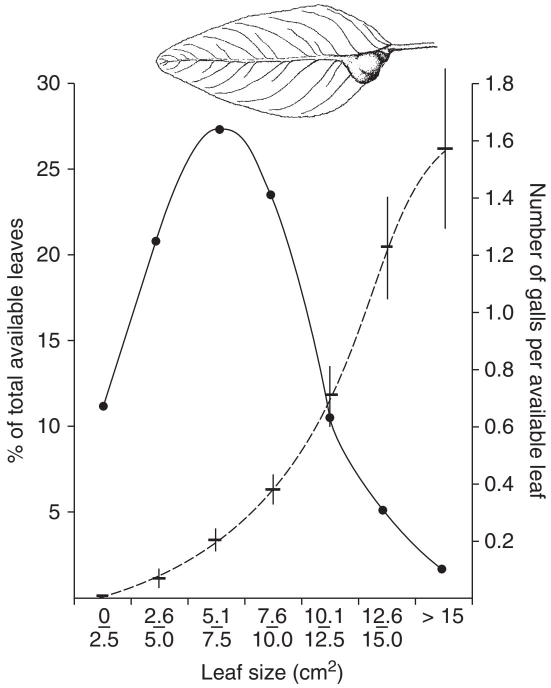


Figure 2.5 The availability of leaves in leaf size classes (solid circles and solid line) in a narrowleaf cottonwood tree, *Populus angustifolia*, and the choice of stem mothers of the aphid, *Pemphigus betae* (solid bars and dashed line). Note the strong preference for the largest leaf area classes, which are the least abundant classes in the leaf population. From Whitham 1981.

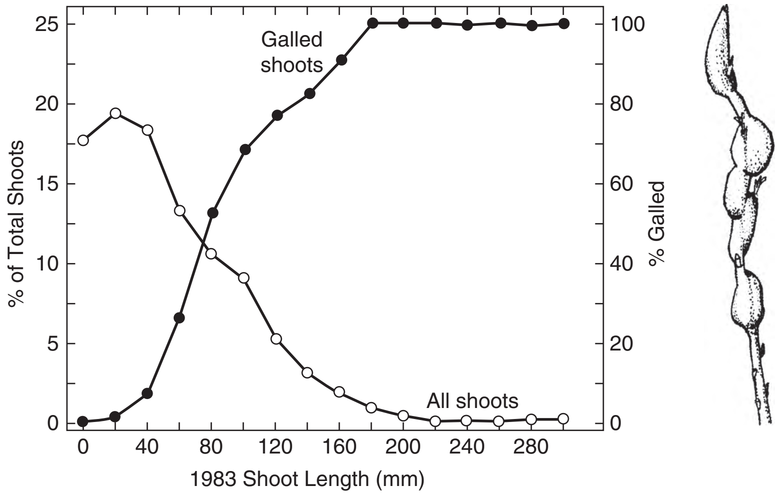


Figure 2.6 The availability of shoots, in shoot length classes, on clones of arroyo willow, *Salix lasiolepis* (open circles), and the attack by females of the gall-inducing sawfly, *Euura lasiolepis*. Note that the strongest preference is for the longest shoot length classes, which are the rarest in the shoot population. From Craig *et al.* 1986.

2.6.2 Females make habitats for progeny (Table 2.2 (2))

In the gall-inducer examples above, the young female aphid stimulates gall formation and she and her progeny live in the gall. The adult female sawfly oviposits into plant tissue, stimulates a gall, lays an egg, and the larva feeds within the gall. Other structures can be induced by ovipositing females such as leaf folds and rolls in which their larvae feed. Major nest builders include bees, wasps and the termites. Some carrion beetles also construct a nest under the carcass they have buried, and feed their larvae rather like birds feeding chicks in a nest. Dung beetles construct dung balls in which they lay an egg, and the larva feeds within the ball (see Figures 2.17, 6.17A, B).

2.6.3 Females provision cells in which larvae feed (Table 2.2 (3))

Provisioning larvae in cells is a general trait in many social insects and solitary wasps, as we discussed in Section 2.3 and illustrate in Figure 2.1. We provide much more detail on provisioning in Chapter 3 on social insects.

2.6.4 Living plants provide microhabitats (Table 2.2 (4))

Insects and other arthropods can search for and find many microhabitats on plants which provide protection and food. This is illustrated in the oak tree example (Figure 1.3) and the typical plant example (Figure 4.1). The text associated with each of these figures provides a little more detail on these kinds of microhabitats.

2.6.5 Living animals provide microhabitats (Table 2.2 (5))

Parasites live in and on animals just as on plants. An example of the many microhabitats that can be used is given in Figure 8.1, showing human skin and all the places occupied by mites. Humans also provide head, body and pubic lice a habitat to occupy, and chewing lice on other animals usually specialize on a particular part of the body of a vertebrate host so that several species may coexist on one host.

2.6.6 Weaving insects and spiders produce protection for themselves (Table 2.2 (6))

Webworms and tent caterpillars construct protective defenses from silk, while many insects tie leaves together: leaf-tying lepidopterans roll leaves or flatten leaves together and feed within the protected area; weaver ants in the genus *Oecophylla* pull leaves together and use larval silk to construct a nest of tied leaves.

2.6.7 Burrowing into substrates (Table 2.2 (7))

The designs and behaviors of burrowing insects is a diverse and fascinating subject. The burrowing way of life is arguably the most common behavioral strategy in the insect world in relation to a place to live. Insects seem to burrow into everything, including substrates not listed in Table 2.2: construction timber, furniture, antlers, horns, turtle carapaces, dead skin, dung, carcasses, sea wrack (seaweed washed onto beaches) and all kinds of other places. One prodigious burrower bores down vessel cells of birch trees from the top shoots to the bottom of the trunk, up to 15 meters, then it emerges and burrows into the ground to pupate. This maggot, the birch cambium fly, *Phytobia betulae* (Diptera: Agromyzidae), is slim enough as a larva to worm its way down the cambium of host trees (Ylioja *et al.* 1999).

2.6.8 Indiscriminate oviposition (Table 2.2 (8))

An interesting example of unselective oviposition is seen in many stick insect species which drop eggs from vegetation to the ground. But ants may collect eggs and carry them to their nest so that nymphs emerge in a safe place, even though away from plant food. Some moth species are known to oviposit on rocks, or tree trunks, even vehicles, and will oviposit in brown paper bags when given the opportunity. Some also drop eggs whilst in flight.

2.6.9 Feeding in the open (Table 2.2 (9))

Another very common place to live is as a free-feeding insect in the open, the strategy of many herbivores, predators and adult parasitoids. Many adult insects fly to find substrates on which to feed or lay eggs: fruits, seeds, flowers, dung, carcasses, living plants or animals, and so on. Living in the open water provides some protection against terrestrial predators, but there are many predatory species in fresh water from which to hide.

2.6.10 Living in or on water (Table 2.2 (10))

This category covers many microhabitats mentioned above for terrestrial habitats: similar behaviors function well in all kinds of environments.

2.6.11 Urban environments (Table 2.2 (11))

Again, this heading acts as an umbrella for the diverse ways in which insects find or create a place to live, mentioned above. This category reminds us that people have constructed houses, bridges, drains, sewage systems, canals, ponds, lawns, golf courses and gardens, many of which provide ideal places in which insects can live.

We can appreciate that there must be a great diversity of behaviors associated with a place to live, all relevant to the ecology of the interaction of the animal and the resource which is utilized. Interesting to contemplate are the details of the stimulus-response sequences needed in each case to search, occupy, construct and live, or lay an egg, in any particular place by any particular insect, as, for example, set out in Figure 2.3 for a parasitoid finding a position for its progeny. Or, for a migrating butterfly, finding food (nectar) for itself and for its progeny (e.g. Figure 2.2), or the bee-killer wasps (Figure 2.1). Such detail is beyond the scope of this chapter even if it were known, so we will progress to the next important set of behaviors in the life of insects.

2.7 Communication

Communication is the act of transmitting information from a signaler to a receiver: a stimulus-response interaction is involved. Some treatments of communication restrict the subject to cases in which signaler and receiver benefit, and both are behaviorally involved in the interplay (e.g. Smith 1977, Greenfield 2002). In books on behavioral ecology communication has received little attention (e.g. Klopfer 1962, Morse 1980), or the emphasis is on signals that benefit the emitter (e.g. Dawkins and Krebs 1978, Krebs and Davies 1978). The bias toward benefits to one or both participants serves behaviorists well by limiting the subject of communication largely to within-species messaging: courtship and other sexually related behaviors, pheromones, aggressive signals, displays and social cohesion and integration. However, for the insect ecologist the subject of communication is much broader than this view because communication can be active or passive. For example, a beetle may actively defend itself by ejecting a noxious spray when attacked, or a caterpillar may leave secretions on a leaf while feeding that provide a cue for a parasitoid searching for the caterpillar, a passive, non-adaptive form of communication.

Here we will concentrate on communication via chemical signals because for insects they play such a critical role in life; for survival, and for finding food and mates. We will examine the many types of communication and then see how they play a role in food webs working up the trophic system from communication from plants to herbivores, then within the herbivore trophic level, and on to communication between herbivores and carnivores.

2.7.1 Chemical communication

Taking chemical communication as an example of the diversity of pathways used in a typical community, plants may communicate passively, by releasing volatiles, which can be considered as body odors (BO), and such chemicals may become attractive to herbivores, or natural enemies of herbivores (Price *et al.* 1980, Vet and Dicke 1992). But an insect may produce strongly repellent chemicals against a would-be predator or parasitoid, and actively reject them at the time of attack, as does the bombardier beetle illustrated later in this chapter. The treatments of communication behavior generally omit consideration of plants as communicators and interactions among individuals from different species, topics of central concern for the insect ecologist. Floral odors are a major component in pollination biology and phytochemicals communicate various kinds of signals, depending on which species the receiver is.

In order to discuss chemical communication relevant to insect ecology we need a specialized lexicon on interactions. Terminology follows Nordlund (1981). **Semiochemicals** are chemicals that mediate interactions between individuals of the same or different species: literally they are signaling chemicals. These may be divided into chemical communication among individuals of the same species – **pheromones** – or among individuals of different species – **allelochemicals** (Table 2.3). Pheromones are used in different ways: as **sex pheromones**, **alarm pheromones** and **epideictic pheromones**. An epideictic pheromone stimulates dispersal from overcrowded conditions, or from conditions that are likely to become overcrowded, thereby causing a more expanded population structure (Prokopy 1981). Allelochemicals are those that mediate interspecific interactions and are divided into four classes: (1) **Allomones** are repellent chemicals which benefit the producer, but are detrimental to the receiver, such as toxic phytochemicals, or stings of bees and wasps.

Table 2.3 **Definitions of terms used for types of signals in chemical ecology**

Hormone A chemical agent, produced by tissue or endocrine gland, which controls various physiological processes within an organism
Semiochemical A chemical involved in the interaction between organisms
Pheromone A substance that is secreted by an organism to the outside and causes a specific reaction in a receiving organism of the same species
Allelochemical A substance that is significant to organisms of a species different from its source, for reasons other than food as such
Allomone A substance produced or acquired by an organism which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral response or a physiological reaction which is adaptively favorable to the emitter, but not to the receiver
Kairomone A substance produced or acquired by an organism which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or physiological reaction which is adaptively favorable to the receiver, but not to the emitter
Synomone A substance produced or acquired by an organism which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral or physiological reaction which is adaptively favorable to both emitter and receiver
Apneumone A substance emitted by a non-living material that evokes a behavioral or physiological reaction which is adaptively favorable to a receiving organism but detrimental to an organism of another species which may be found in or on the non-living material

From Nordlund 1981.

(2) **Kairomones** benefit the receiver rather than the emitter, for which they are detrimental. This class includes body odors of plants or insects which stimulate searching and attack by their enemies. (3) **Synomones** are those chemicals that are beneficial to the emitter and the receiver, such as plant odors that attract predators of herbivores, or floral odors attractive to pollinators. (4) **Apneumones** form another important category of semiochemicals in which a non-living substrate emits attractive odors beneficial to individuals responding to the odors, but detrimental to another species in the medium. Parasitoids attacking host larvae in carrion, dung, meal or grain may use the odor of the substrate while searching for hosts.

All these allelochemical terms relate to interactions involving finding food; this means that different trophic levels are involved. Given the evidence that natural enemies may find herbivores by responding to plant odors, clearly at least three-trophic-level interactions are involved (Price *et al.* 1980).

2.7.2 Multitrophic-level interactions

The term multitrophic-level interactions is now generally used to discuss the many ways in which species interact in a food web or interaction web (e.g. Tscharntke and Hawkins 2002, Ohgushi *et al.* 2007). The subject is much more extensive than just chemical interactions, but it was the study of phytochemicals that gave the subject its initial research energy (e.g. Sondheimer and Simeone 1970). By 1981 the subject of semiochemicals could be treated in a comprehensive way (e.g. Nordlund *et al.*

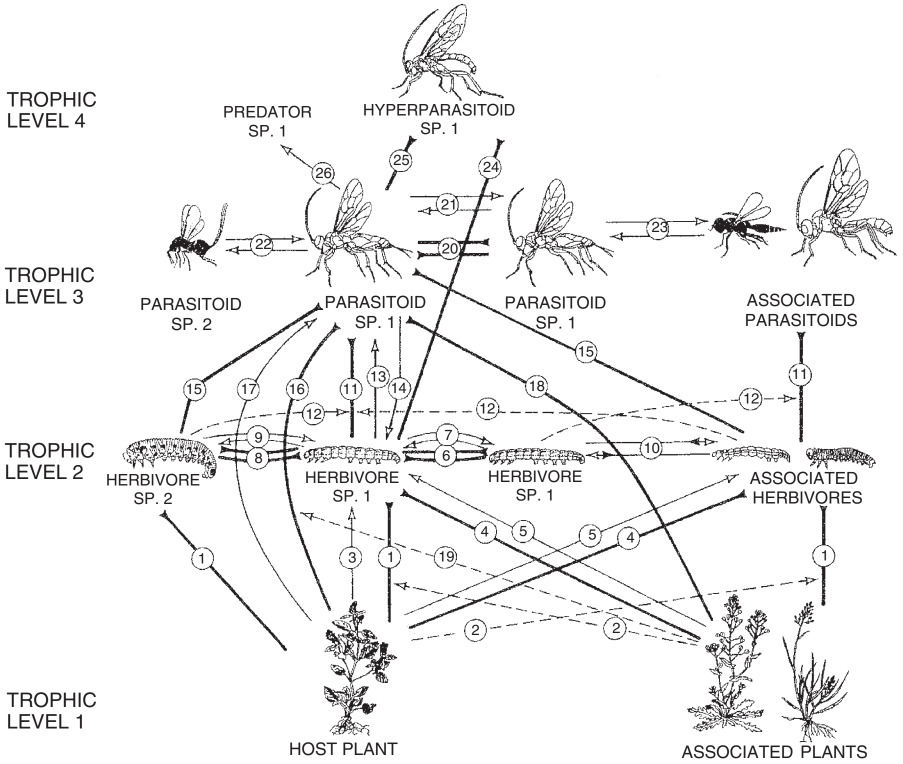


Figure 2.7 Semiochemically mediated interactions among members of four trophic levels, based on a composite of examples in the literature. Arrows are placed against the responding organism. Thick solid lines and solid arrows indicate attraction of a stimulus (e.g. 1, 4, 11, 24). Thin solid lines and open arrows indicate repulsion (e.g. 3, 13, 17, 26). Thin dashed lines show indirect effects such as interference with another response (e.g. 2, 12, 19). From Price 1981.

1981), and multitrophic-level interactions were emphasized by Price (1981), who provided references in the literature for the following examples.

Interactions between trophic levels 1 and 2, the plants and herbivores, are very extensive, including attractants, repellents and antifeedants (Figure 2.7). For example, specialist insects on crucifers (Brassicaceae) are attracted to mustard oils, or glucosinolates, released from potential hosts, also providing the characteristic odors humans associate with cabbage, radish, mustard and other members of the cabbage family. Glucosinolates are attractive to the major species of the herbivore trophic level on crucifers (Louda and Mole 1991, Figure 2.7, interaction 1). The chemical structures of a glucosinolate and a mustard oil are illustrated in Figure 4.9. In the Diptera, the gall midge, *Dasineura brassicae*, and the cabbage rootfly, *Delia brassicae*, are attracted to allylglucosinolate. The specialist beetles on crucifers are also attracted: the red turnip beetle, *Entomoscelis americana*, the curculionid seed weevil, *Ceutorhynchus assimilis*, and flea beetles in the genus *Phyllotreta*. Lepidopterans such as the large white butterfly, *Pieris brassicae*, and its congeners, *P. rapae* and *P. oleracea*, which are more generalist feeders, are stimulated by glucosinolates to lay eggs. However, for other generalist feeders, glucosinolates act as repellents (Figure 2.7, interaction 3), including aphids, grasshoppers, lepidopterans and mites not specialized as crucifer feeders. Mustard oils also cause digestive and other metabolic problems in mammals. Many other kinds of compounds are discussed as active ingredients in plant–herbivore interactions in Rosenthal and Berenbaum (1991): alkaloids, terpenoids, cyanogenic glycosides, cardenolides, coumarins and others.

In Figure 2.7, interaction 2, associated plants may play a role in attraction or repellency to the host plant. When host crucifers were planted in mixtures with non-food plants with aromatic BO, the crucifers were less attacked by flea beetles, *Phyllotreta cruciferae* (Tahvanainen and Root 1972). This interference the authors called **associational resistance**. Associated plants may also act as attractants to adults by providing nectar, pollen or chemical cues to herbivores (interaction 4), or they may be directly repellent to herbivores (interaction 5).

Interactions within trophic level 2 include attracting conspecifics with sex pheromones (interaction 6) or repellency through epideictic pheromones (interaction 7). These kinds of interactions may be interspecific, as when bark beetle attacks attract other species (interaction 8), or in other cases repel attack by other species (interaction 9). Associated herbivores may have similar effects, as in interactions 8 and 9 (interaction 10).

Interactions among trophic levels 2 and 3 include influences from all three trophic levels. Many cases have been found in which a predator or parasitoid is attracted to a herbivore by a kairomone (interaction 11). As was stated earlier in this chapter, *Cardiochiles nigriceps* finds its hosts, *Heliothis (=Helicoverpa) virescens*, in response to three chemicals in the mandibular gland secretion of the host larvae. *Microplitis croceipes* (Hymenoptera: Braconidae) finds larvae of the moths *Heliothis zea* and *Heliothis virescens* by a chemical in larval frass – 13-methylhentriacontane. Scales left by ovipositing moths provide kairomones for the egg parasitoid *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). Similar interactions involve predators, such as larvae of *Chrysoperla carnea* (Neuroptera: Chrysopidae) being attracted to scales from adults of *Heliothis zea* which stimulate egg predation, and bark beetle pheromones are strongly attractive to specialist predatory clerid beetles. Chemicals from a non-target herbivore may also interfere with host searching by natural enemies (interaction 12). Of course, herbivores have their own defenses, many of them chemical (e.g. Evans and Schmidt 1990). Interaction 13 is illustrated by the everted osmeterium of *Papilio* butterflies, which releases foul-smelling odors, like rancid butter, which are butyric acid derivatives, detected even by humans. Sawfly larvae feeding on conifers store resin from the host plant in diverticula of the gut and regurgitate it when attacked. Many plant toxins are sequestered by herbivores, such as cardiac glycosides by milkweed-feeding insects. Aphids release alarm pheromones which attract ants, and the ants repel parasitoids and predators. The ants may well repel enemies of other species on the same plant, providing an example similar to interaction 12. Herbivores may also reduce kairomonal cues by cutting and dropping leaves on which they have fed, or by feeding nocturnally and leaving the feeding site during the day when tachinid parasitoids are active (interaction 14). Enemies may also be attracted to herbivores associated with the target species, or their products, such as honeydew (interaction 15).

Interactions among trophic levels 1 and 3 involve plant hosts which are attractive or repellent to natural enemies, or associated plants which act in a similar way. Chemical signals may involve kairomones from plants directly, kairomones from the herbivore, such as frass which contains plant constituents, synomones such as floral fragrances or apneumones from such things as fermentation products from rotting plant parts. An example of interaction 16 concerns corn plants which contain tricosane, which also appears on the eggs of the corn earworm, *Heliothis zea*, and this chemical becomes a kairomone for the egg parasitoid *Trichogramma evanescens*, as also mentioned under interaction 11. A similar case concerns heptanoic acid present in potatoes which appears in the frass of the potato tuberworm, *Phthorimaea operculella*, which then acts as a kairomone for the parasitoid, *Orgilus lepidus*. Plants may also be repellent to natural enemies of herbivores (interaction 17), as when the odor of pines is repellent to the tachinid parasitoid, *Eucarcelia rutilla*, during its preovipositional period, while oaks are attractive, housing aphids producing honeydew. When the parasitoid is ready to lay eggs, pine becomes attractive, on which it finds its major host, the pine looper, *Bupalus piniarius* (Lepidoptera: Geometridae). Trichome exudates may also bar small parasitoids which become entangled, as with small wasps attacking the tobacco hornworm, *Manduca sexta*, on tobacco, and they are commonly effective on other solanaceous plants. Interaction 18 concerns associated plants acting as attractions to natural enemies on target plants. Commonly, flowering plants in orchards are attractive to parasitoids, such that codling moth, *Cydia pomonella*, and eastern tent caterpillar, *Malacosoma americanum*, were attacked more by the ichneumonid, *Itoplectis conquisitor*, when nectar was available. Conversely, associated plants may interfere with searching by natural enemies and reduce attack rates, as in attacks on the larch sawfly, *Pristiphora erichsonii*, when it occurred in a mixture of other trees and forest shrubs and herbs, with reductions of parasitism from around 86% to 10–13% (interaction 19).

Interactions within the third trophic level follow the same sort as in trophic level 2 (interactions 20–23). For example, trail odors of litter-dwelling parasitoids become repellent to the same and other species, and associated parasitoids may well have similar effects.

At the fourth trophic level hyperparasitoids may be attracted to the presence of the herbivore (interaction 24). For example, the ichneumonid hyperparasitoid, *Euceros frigidus*, lays eggs about 10 cm from a colony of sawfly larvae, and proximal to the tree stem, so that a sawfly colony passes as they feed on needles sequentially down the shoot. *Euceros* eggs hatch, and the planidial larvae crawl onto sawflies, becoming phoretic, and wait, maybe weeks, until a primary parasitoid attacks, after which the *Euceros* planidium becomes parasitic on the primary parasitoid (see Chapter 8 for more information). In interaction 25 a hyperparasitoid may be attracted by odors of the primary parasitoid. For example, the odors of female *Diaeretiella rapae* which attacks aphids on crucifers are attractive to the hyperparasitoid, *Charips brassicae*, which can then find parasitized aphids with wasp larvae it can attack (see Figures 1.4 and 12.1 for a food web based on crucifer plant species). Finally, natural enemies at the third trophic level are commonly defended chemically against attack from the fourth trophic level. Ladybird beetles of many species contain toxins in the haemolymph which are repellent to would-be predators (Blum 1981), and some pupae have a snipping device between abdominal segments, which closes and “bites” when a larva is attacked (Figure 2.8, Schroeder *et al.* 1998, Eisner 2003). Predatory bombardier beetles, aptly named *Brachinus explodens* and *B. crepitans*, explosively eject a hot mixture based on hydroquinones and an oxidizing agent, hydrogen peroxide, which is highly effective against vertebrate and invertebrate predators alike (Eisner 1970, 2003). The African bombardier beetle, *Stenoaptinus insignis*, is brightly colored, aposematic (conspicuously marked) and flightless, all providing a cue to a very toxic spray (Figure 2.9).

The impressive diversity of chemical information transmitted and received illustrates how each species can communicate in a specialized way, perhaps unique in some cases. Although a local air space may be redolent with BO from community members, each signal has a source with a more-or-less specialized receiver. Communication can be precise and effective. However, such signals can be decoded and utilized with surreptitious intent, as with clerid predators of bark beetles using pheromones to find their prey. We observe, as increasingly these kinds of revelations are made, that natural selection has resulted from almost endless kinds of chemically mediated interactions, and that there is probably no end to the ingenuity of nature still to be discovered.

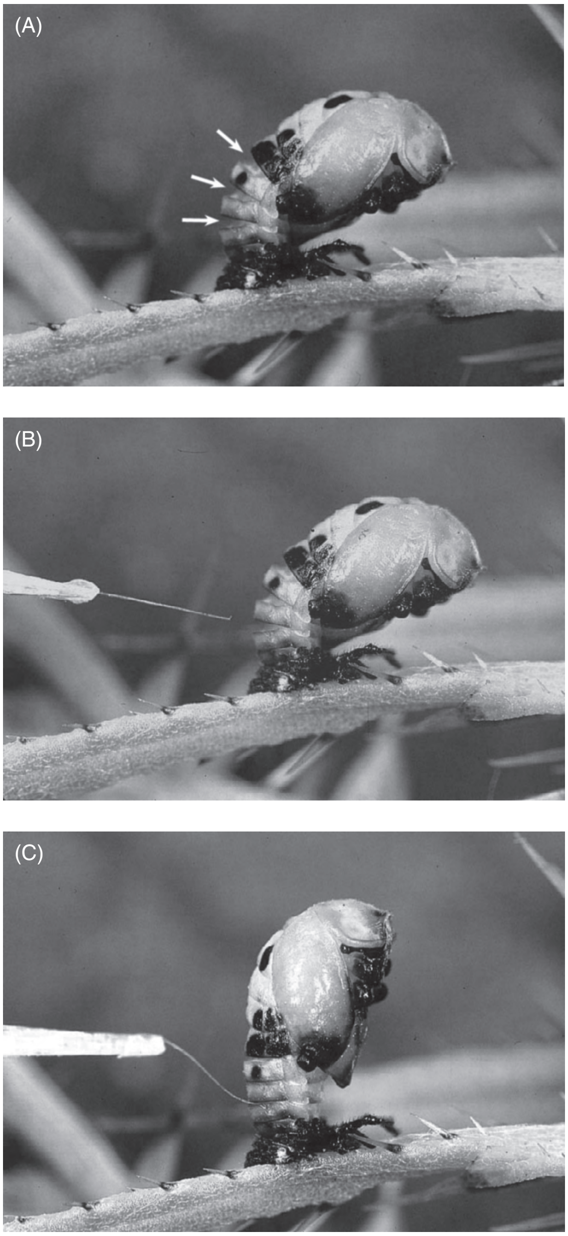


Figure 2.8 Defense of the ladybird beetle pupa, *Cycloneda sanguinea*, formed by pincer-like gaps between abdominal segments (see arrows in frame A). When disturbed from behind by a predator, or in this case a bristle, the pupa flips up, closing the gap and "biting" the aggressor. Photographs by Thomas Eisner, Cornell University. From Schroeder *et al.* 1998, and Eisner 2003. Copyright 1998 National Academy of Sciences, USA. See color plate section.

Of course, an equally diverse scenario of interactions through trophic levels could be developed for physical factors concerned with defense and attack. Some of these are discussed in Chapter 4 on plant defense and herbivore feeding, and in Chapter 7 on prey and predator interrelationships.

2.8 Reproductive behavior

A place to live also involves a place to breed, and the whole reproductive process from finding mates to oviposition in appropriate places, which is treated here as the final aspect of behavior to be discussed in this chapter.

Insect reproductive behavior was reviewed comprehensively from an evolutionary perspective for the first time by Thornhill and Alcock (1983): *The Evolution of Insect Mating Systems*. The book remains a major source of information, fascination, and inspiration. While the field has advanced significantly since that date, the book provides a systematic approach to this large subject, from which we have selected some major aspects to discuss in this chapter. We need to start about 150 years ago with Darwin's (1859) creation of the concept of sexual selection before we move on to the various methods of mate selection, mating strategies and finally parental investment.

2.8.1 Sexual selection

In *The Origin of Species* Darwin (1859, p. 88) introduced the concept of **sexual selection** as a subset of natural selection: "This depends, not on the struggle for existence, but on the struggle between the males for possession of females; the result is not death to the unsuccessful competitor, but few or no offspring. Sexual selection is, therefore, less rigorous than natural selection. Generally the most vigorous males, those which are best fitted for their places in nature, will leave most progeny. But, in many cases, victory will depend not on general vigor, but on having special weapons, confined to the male sex. The hornless stag or a spurless cock would have a poor chance of leaving offspring." Darwin may just as easily have mentioned the stag beetle with the male's large mandibles with which they joust, or the spurs and horns of dung beetles and other scarabs used in displacing opposing males. Indeed, when Darwin (1871) greatly expanded on his theory in *The Descent of Man and Selection in Relation to Sex* he noted many examples in which male beetles exhibited greatly enlarged mandibles or horns (Figures 2.10, 2.11).

Of course, when we consider fitness of individuals, then natural selection and sexual selection become as one, because inability to breed may not kill, but leaving no progeny is genetic death; failure to impart progeny or genes to the next generation. However, the term sexual selection is very useful in emphasizing differences in male and female form and reproductive behavior. The concept was expanded in Darwin (1871) to include two forms, each emphasizing the role of one sex: (1) The competition among males for mating with females, called **intrasexual selection** by Huxley (1938), in which females are likely to be passive. (2) The active choice by females of males which appear to be high quality mates, based on size, color, offensive weapons or vigor; named **epigamic selection** by Huxley.

That males differ greatly in reproductive success, while females are more predictably successful, was elegantly revealed in now famous experiments by

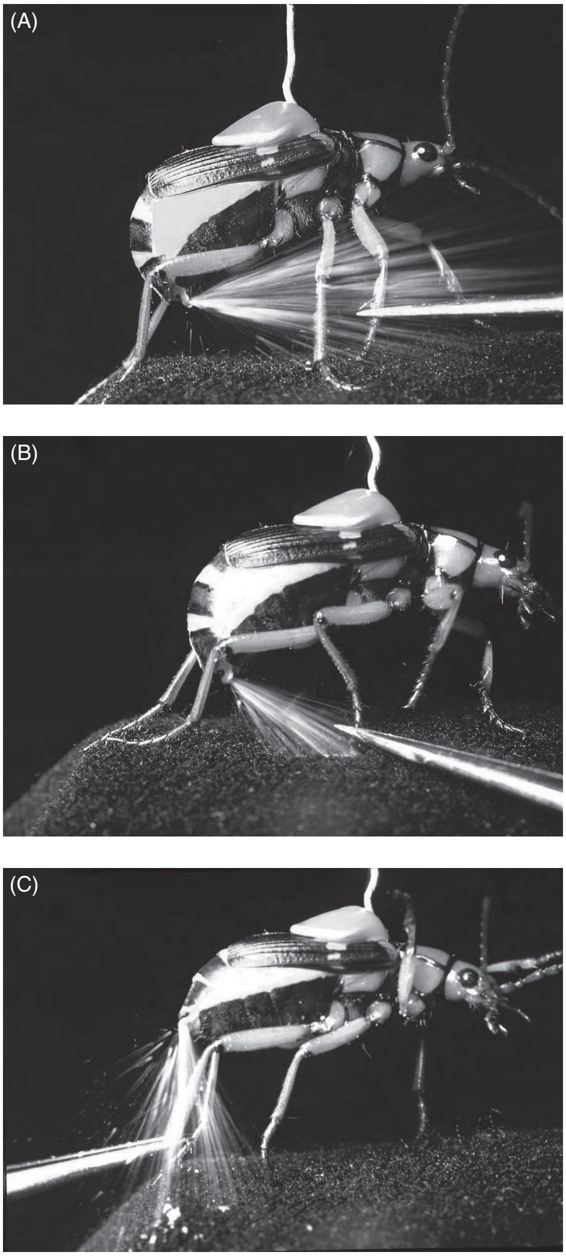
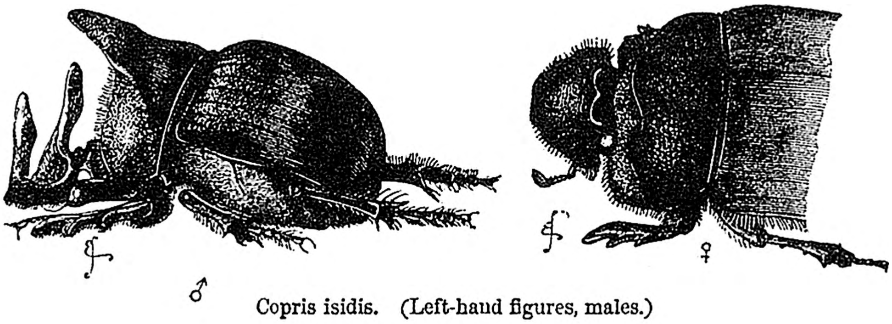
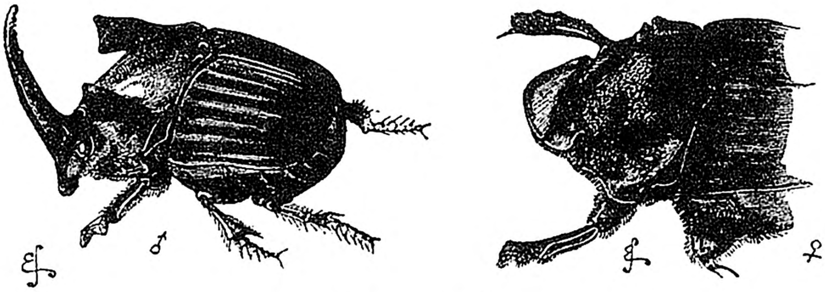


Figure 2.9 The African bombardier beetle blasts off to repel an attack by a pair of forceps which simulated the mandibular grasp of a would-be predator. The blast is directional so that it is projected forward in A, sideways in B, and downwards when the hind leg is pinched, C. Photographs by Thomas Eisner and Daniel Aneshansley,

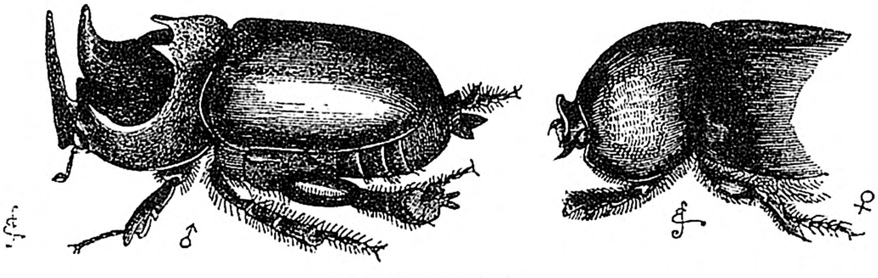
Caption for Figure 2.9 (*cont.*)
Cornell University. From Eisner and Aneshansley 1999, and Eisner 2003. A. Reprinted by permission of the publisher from *FOR LOVE OF INSECTS* by Thomas Eisner, p. 31, Cambridge, Mass.: The Belknap Press of Harvard University Press, Copyright © 2003 by the President and Fellows of Harvard College. B and C. Copyright 1999 National Academy of Sciences, USA. See color plate section.



Copris isidis. (Left-hand figures, males.)



Phanæus faunus.



Dipelicus cantori.

Onthophagus rangifer, enlarged.

Figure 2.10 Illustrations of dung and rhinoceros beetles, in Darwin's (1871) book on *The Descent of Man and Selection in Relation to Sex*. Males are on the left, showing large horns, extensions from the head and thorax, and females are on the right with no such fighting equipment.

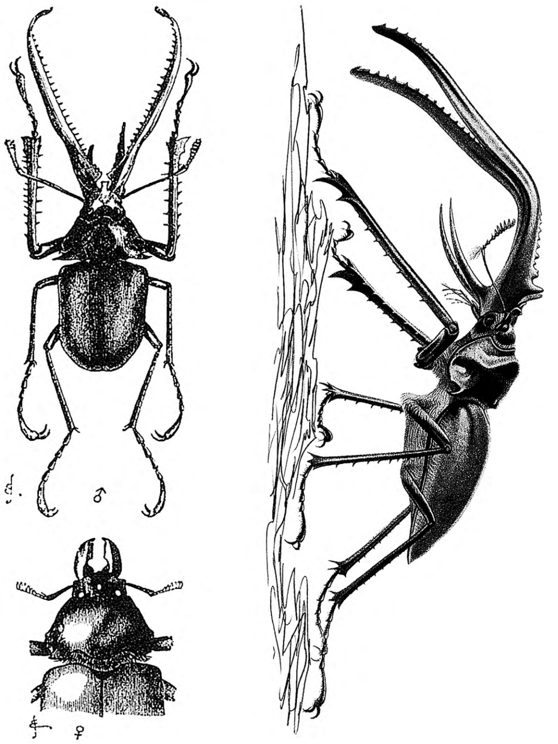


Figure 2.11 The stag beetle, *Chiasognathus granti*, from southern Chile illustrated in Darwin 1871, showing the male with enormous mandibles and the female with normal-sized mandibles. The same species is illustrated in a defensive position on a tree trunk on which a fight will result in one of the males being displaced and falling to the ground. From Linsenmaier 1972.

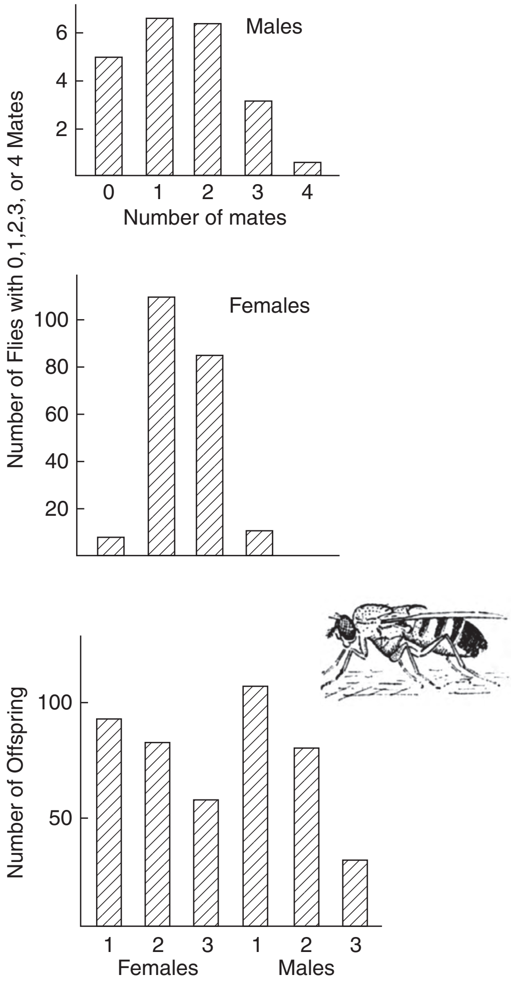


Figure 2.12 Results from Bateman's (1948) experiments, on the variation in male and female mating success, in *Drosophila melanogaster*. Many males have no mates, whereas almost all females mate at least once. Some males had three or four mates whereas most females had only one or two mates. Below, the difference in the number of offspring produced by three females caged with three males is much less variable than among the three males. The spread of reproductive success among females is about 40 progeny, but the range among males reaches 80 progeny. Modified from Thornhill and Alcock 1983.

Bateman (1948). Using adult fruit flies, *Drosophila melanogaster*, in which each had a distinctive dominant marker gene, which would show up in the progeny they produced, Bateman mixed males and females for 3 or 4 days, and measured their success in competition with males for mates and access to females. Males showed much greater variation in reproductive success than females. Many males did not mate even once (21%), while other males mated with as many as four females (Figure 2.12), and some males produced more progeny than others. By contrast, the large majority of females mated once or twice (96%), few more than this, and there was less variation in the number of offspring produced by females than by males. Bateman did not examine the reasons for this differential breeding success among males, but it may well have related to male size, vigor, or the "love songs" with which they courted females (Hoikkala 2006, Drosopoulos and Claridge 2006).

More conspicuously differentiated males and females than in *Drosophila melanogaster* reveal clearly the winners and losers resulting from jousts for access to females. Horned males and hornless females are observed commonly in beetles, as well as enlarged mandibles of males: stag beetles (Lucanidae), rhinoceros beetles (Scarabaeidae: Dynastinae) and dung beetles (Scarabaeidae: Scarabaeinae) are well-known examples. Males assemble at places where females visit and fight for access to females. Such places may be sap flows, shoots or branches, or burrows in plants, or in dung beetles subterranean tunnels in which females are found (Emlen 2000a, Emlen and Nijhout 2000). "Although the resources in question vary considerably from species to species, they share one key characteristic: they all tend to occur in discrete, readily defendable patches. Males with enlarged weapons are able to gain disproportionate access to these contested sites, and consequently, gain disproportionate access to females" (Emlen 2000a, p. 404). In this context, selection will result in larger males with larger horns, until the benefits are outstripped by costs. Such trade-offs have become of great interest in the adaptive radiation of dung beetles in the genus *Onthophagus* (e.g. Emlen 2000a, Moczek and Nijhout 2004, Parzer and Moczek 2008). Although large males win fights, small males may adopt **alternative mating strategies**, as we shall see later in this chapter.

Sexual selection will run as a theme throughout the remainder of this chapter. A summary of the results of sexual selection reveals the diversity of behaviors involved (Table 2.4).

2.8.2 Finding mates

Two central questions relating to sexual selection posed by Darwin (1859) are: first, why males and females of the same species differ from one another, with males showing more exaggerated morphological phenotypes than those observed in females, and second, why males of closely related species show much greater differences in morphology and behavior than females in these species (Shuster and Wade 2003). Clearly, males in most species have to find females, and then compete with other males for access, both activities tending to select for species morphological traits, including enlarged antennae for detecting a female's pheromone, and enlarged appendages or horns for fighting.

However, in many cases males have evolved to find mates as early as possible, thereby avoiding much competition (Thornhill and Alcock 1983). Males are known to search emergence sites when they can mate with emerging virgin females. Examples include bees, wasps, ants, butterflies and beetles. Another strategy is seen in males that find females where the females oviposit, as in scatophagid flies which mate on dung, and many fruit flies in the family Tephritidae, which mate on the fruits into which females oviposit. In other species males have gone to the extreme of detecting virgin females before they emerge as fully mature adults, with forced copulation resulting.

Females may be more active in finding mates in many species where mating occurs at a site away from emergence sites, oviposition sites and food. Females may fly into groups or swarms of males located at landmarks, such as shrubs or trees, or hilltops. Such species include bees, ants, butterflies, midges, mosquitoes and other flies. **Hilltopping** is a common meeting strategy for males and females in which mostly males fly to prominent topographical features and mate with virgin females as they fly through the area.

Table 2.4 **The products of sexual selection in animals in general. Not all products have been observed in insects**

Intrasexual selection
Precopulatory competition for access to potential mates
(1) Skill in mate location
(2) Production of effective mate-attracting signals
(3) Aggressive competence in the defense of mates and territories
(4) Capacity to avoid damaging interactions with rivals
Postcopulatory competition for access to eggs
(1) Mate concealment
(2) Mate guarding
(3) Ability to find and take protected mate from original partner
(4) Ability of sperm to displace competitor ejaculates
Postfertilization destruction of rival zygotes
(1) Ability to induce abortion of fertilized eggs
(2) Infanticide
Epigamic or intersexual selection
Mate discrimination by choosy sex
(1) Rejection of members of wrong species
(2) Selection of genetically superior conspecific partner
(3) Selection of partner with useful resources or services
Attributes that make opposite sex attractive to discriminating sex
(1) Attractive courtship behavior
(2) Morphological characters considered attractive by opposite sex
(3) Material benefit attractive to opposite sex

From Thornhill and Alcock 1983. Reprinted by permission of the publisher from *THE EVOLUTION OF INSECT MATING SYSTEMS* by Randy Thornhill and John Alcock, p. 74, Cambridge, Mass.: Harvard University Press, Copyright © 1983 by the President and Fellows of Harvard College.

This **mate rendezvous hypothesis** (Alcock and Dodson 2008) predicts that:

(1) Most individuals at hilltops are males which gain access to several females and mate with them, but females will be less abundant because they mate once
(2) Females that go to hilltops are likely to be virgins while mated females will be more active at feeding and oviposition sites.

Just on one mountain in Arizona, Alcock and Dodson (2008) recorded six families of Diptera, six families of Lepidoptera, five families of Hymenoptera and one beetle family (Cerambycidae). Some species' males were territorial, driving away others, but different species had males that simply patrolled hilltops without aggressive behavior.

Hilltopping appears to be a rewarding strategy where populations are sparse, so that mates would be hard to find. For example, of the six fly families listed from hilltops by Alcock and Dodson (2008), four were parasitic groups: the bot and warble flies (Cuterebridae and Oestridae), tachinid parasitoids and bombyliids, which are parasitic on other insects such as bees or predaceous on grasshopper eggs. None of the host species would provide dense and predictable resources worth defending territorially, and females of parasitic species disperse widely in search of hosts, so a rewarding strategy appears to be to mate first at a hilltop site, followed by the lonesome search for hosts.

Assemblages of males, independent of food or oviposition sites, are called **leks**. Males aggregate at one spot, set up small adjacent territories and attract females, and the females may select a male for mating and then depart. Males may then mate again with additional females, benefiting from the aggregate attraction of the assembled males (Figure 2.13). This mating system illustrates **lek polygyny**, in which males usually mate more than once, whereas females mate only once. Male tarantula hawk wasps, *Hemipepsis ustulata*, also engage in lek polygyny in the desert of the southwest United States, where they set up territories along ridge tops inhabited by palo verde trees, creosote bushes or jojoba shrubs, which provide conspicuous perches.

Territoriality takes many forms among insect species: a **territory** is defined as any defended area. Where resources are moderately concentrated, relatively patchy, but stable in time and space, a male may increase access to females by becoming territorial. Males may set up a territory where females pass through in order to oviposit, or where females are attracted to oviposition sites or food (see Price 1997 for territory types). The first case of females being intercepted as they fly to oviposition sites is illustrated by the peacock butterfly, *Inachis io*, in which males placed their territories in a field through which females flew in order to oviposit on stinging nettles beyond (Figure 2.14). In the corner of the field surrounded by a hedge on two sides females converged, and the male in territory 1 gained access to four females. Another male with territory 2 by the hedge has three females traverse his territory, but territories 3 and 4, away from the hedge, were less successful. This strategy avoids competition at oviposition and feeding sites, but evidently results in large differences in success among males. A more predictable ploy, but one with a greater competitive risk, is to defend an oviposition site, as does the speckled wood butterfly, *Pararge aegeria* (Davies 1978). Males defended sunspots on the forest floor, which were limiting, so only 60% of males occupied territories. Females were attracted to sunspots because the grass host plants to larvae grow in the brighter areas of the forest floor. Males without territories patrolled the tree canopies searching for mates, but were much less successful than the territory holders.

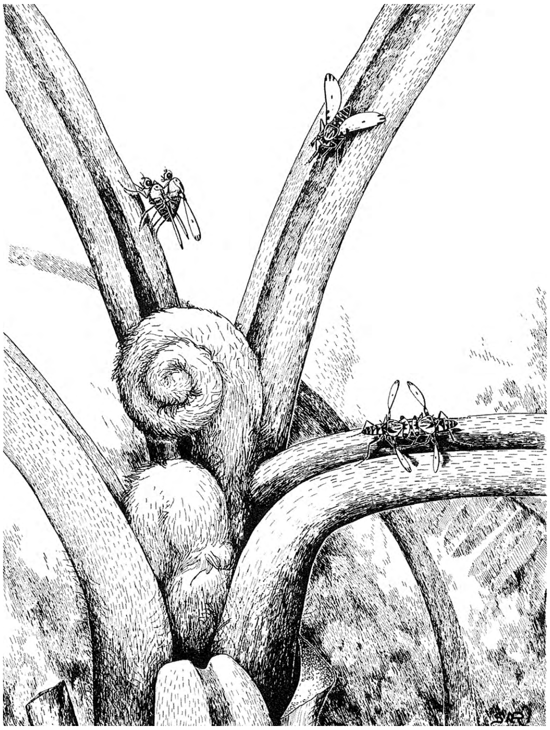


Figure 2.13 A lek of Hawaiian fruit flies, *Drosophila heteroneura*, on a tree fern. The fern provides only an assembly area, with no oviposition sites, food or emerging females. Males joust for a small territory in the lek, at front right. A female visits the lek seeking a mate, top right, and a copulating pair is illustrated on the left. Drawing by L. S. Kimsey. From Thornhill and Alcock 1983.

The complexity of a landscape may be diminished by chemical lures – pheromones – which are sex attractants, usually released by females, which attract males, followed by copulation (Roelofs 1981, Cardé and Baker 1984). Males fly up plumes of odors, gradually orienting to the releasing female, often aided by enlarged antennae relative to those of the female, as in saturniid moths, diprionid sawflies and

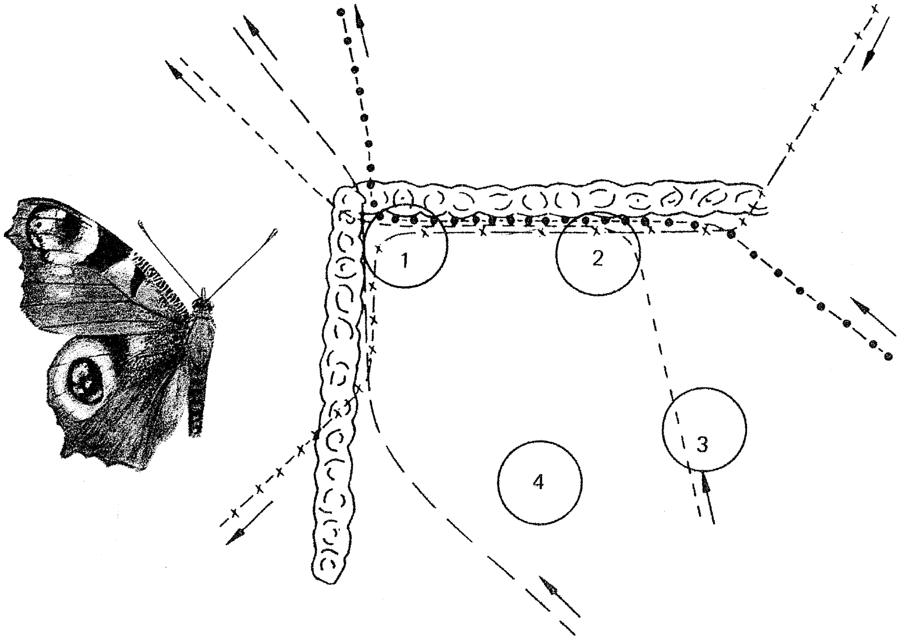


Figure 2.14 The location of male territories of the peacock butterfly, in a field through which females flew to reach oviposition sites. Note differences in success among males in acquiring females based on territory positions. From Baker 1972a. Reprinted with permission from Blackwell Publishing.

scarabaeid beetles. In the giant silkworm moths (Saturniidae), marked males of the cecropia moth, *Hyalophora cecropia*, are known to fly many miles overnight to a female, up to 11 miles in one case, although how far the female's pheromone plume was involved was not investigated (Waldbauer 1996). *Promethea* moths flew 9 miles in 3 days, and even 23 miles in 3 days, to find a virgin female in a trap. With such effective discovery of mates over long distances it is possible for species to persist at very low densities and in highly patchy environments.

2.8.3 Choosing mates

Once a mate has been located there may be almost no courtship behavior before copulation, as in many sawflies, or courtship may be extravagant. Generally males appear to be the "amorous" sex, because they initiate courtship more often than females. Females, on the other hand, appear to be more selective than males because they tend to mate only once. The quality of the father of her progeny is critical. However, because each mating involves one male and one female, the average number of mates for males and females must be equal; that is, there can be no sex difference in average promiscuity between the sexes (Wade and Shuster 2002). Sex differences in mating behavior are often attributed to differences in energetic investment in gametes (sperm are cheap; eggs are expensive). With eggs relatively large and costly in allocation of resources, it becomes important for females to choose males which are likely to father strong and attractive male progeny, and large and fecund female progeny will amplify a female's fitness relative to an unselective female. However, a simpler explanation for these differences is, as Bateman (1948) showed in *Drosophila*, that the correlation between mate numbers and offspring numbers is usually much greater for males than it is for females. Male fitness increases linearly with increasing mate numbers, whereas female fitness increases less rapidly, and may even decrease with multiple mating. Strong selection on males to increase mate numbers and on females to minimize them provides an explanation for why males of many species may attempt to court or copulate with mated females or even with males, while females may kick away a male, fail to adopt a copulatory position or simply fly away (Thornhill and Alcock 1983). This is epigamic selection at work.

Courtship takes many forms. Acoustic signaling is a major method for attracting mates, with stridulation of crickets, katydids, grasshoppers and cicadas commonly experienced by the naturalist, as well as females in these groups. But the fact is that much acoustical and vibrational communication passes unnoticed by the human ear. Like chemical communication, sounds and vibrations made by small insects escaped our attention for many decades. In a wonderful coverage of the literature Drosopoulos and Claridge (2006) included many groups of smaller insects: lacewings and other neuropterids, *Drosophila* flies, stoneflies, planthoppers, leafhoppers, heteropteran bugs, treehoppers, psyllids, whiteflies and bees. Not only is mate location involved with vibrations, but membracids recruit to new feeding sites, gerrids and others locate prey, pergid sawflies use vibrations for group cohesion, ichneumonids, braconids and other parasitoids use them for host location, and some ants recruit to food sources (Virant-Doberlet *et al.* 2006). Also, spiders and scorpions are well known to use vibrations in prey and mate location.

Courtship also includes **nuptial gifts** of food from males to females in many species. The male can display his competence as a hunter and/or provider of food, and the female can make a choice as to whether the gift is adequate. Male gifts may contribute to female fitness by providing a significant meal which enhances her fecundity, and it reduces her risks while hunting for food, and in so doing it promotes male fitness as well (Thornhill and Gwynne 1986). For example, male hanging flies, such as *Hylobittacus apicalis*, a member of the scorpionfly Order Mecoptera, catch insect prey and attract a female. If she accepts the gift she starts feeding and the male is able to copulate (Figure 2.15). In katydids the male delivers a large spermatophore to the female consisting of two parts; one is an ampulla containing sperm, and the other is a food item, free of sperm, called the **spermatophylax** (Figure 2.16). After mating the female eats the spermatophylax while insemination occurs, and then she eats the empty ampulla, acquiring a considerable contribution to egg production from the male, and also acquisition of substances which induce a 4-day-long non-receptive period, ensuring the male's paternity (Thornhill and Gwynne 1986). The **parental investment** of the male in the form of the spermatophore results in an increase in egg size and fecundity of mated females. Some male katydids provide such rich gifts – spermatophores of 25 to 40% of their body weight – that females actually compete aggressively for males,

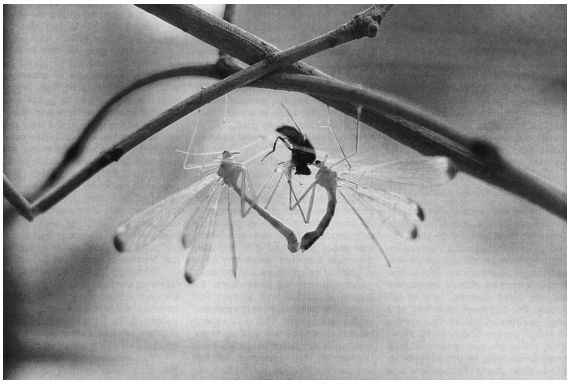


Figure 2.15 A pair of hanging flies, *Hylobittacus apicalis* (Mecoptera: Bittacidae), with the male on the left and the female on the right. The male has captured a blow fly, attracted the female, and has presented her with this nuptial gift which she is consuming. The male can then copulate with the female, as shown, the female's fecundity is increased by the gift and her probability of survival is improved by the reduced need for foraging. Both male and female reproductive success is improved. From Thornhill 1980. See color plate section.

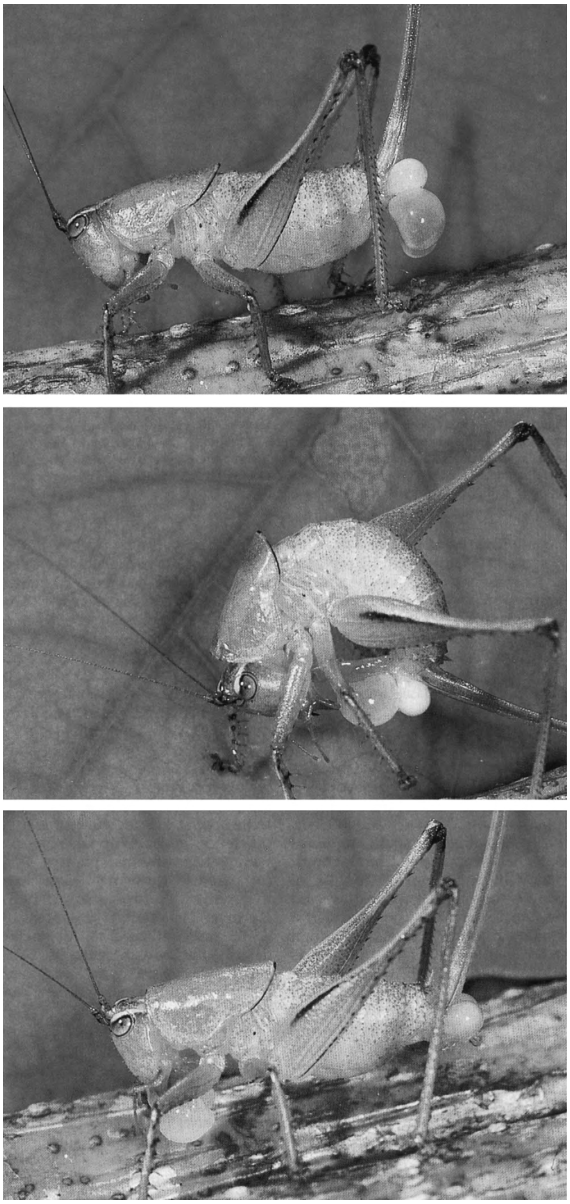


Figure 2.16 Just after mating a female katydid, *Requena verticalis*, has a large spermatophore attached to the base of her ovipositor by the male (top). The female bends down to grasp the nutritious spermatophylax (middle), and consumes it (bottom). The ampulla with the sperm remains in place, releasing sperm, and when this is complete the ampulla is also eaten. The female gains a major donation of food from the male, resulting in increased egg size and fecundity. Adapted from Thornhill and Gwynne 1986. See color plate section.

and males select large fecund females. In the Mormon cricket, *Anabrus simplex*, actually a katydid in the family Tettigoniidae, this reversal of the sex roles is observed (Gwynne 1981, 1984).

Female choice of mates is an important step in bringing mating to fruition, and females make important decisions because, as stated earlier, they may mate only once and their investment in progeny is large relative to that of males. So females make many decisions using a variety of cues to evaluate males. Female cockroaches of *Nauphoeta cinerea* prefer the pheromone of dominant males. Other females may accept the most unusual males of a group – the **rare male advantage** in *Drosophila* for example, in which females are more likely to mate with males with the less common genotypes. Thornhill and Alcock (1983) discuss many methods by which females reject males, prior to, during or after copulation. One intriguing idea, formulated by Eberhard (1985), is the **female choice hypothesis**. This argues that females choose males of their own species on the basis of the male's genitalia: "males with favored genitalic morphologies sire more offspring than others" (Eberhard 1985, p. 70). Then sexual selection on male genitalia by females results in rapid diversifying evolution. Eberhard (1997) expands on this thesis emphasizing cryptic female choice and listing the many mechanisms by which this is achieved. Indeed, it has been long remarked that male genitalia in insects show incredible variety among even closely related species, and often genitalic characters are diagnostic of species differences. A recent example of extreme variation in male genitalia is from *Bembidion* carabid beetles on the Hawaiian Islands, with 23 species showing dramatic variation, including exaggerated male mating organs (heterotrophy) on the male aedeagal flagellar complex (Liebherr 2008, his Figures 3 and 4). The flagellum is involved with placing the male's spermatophore into the female's long spermathecal duct during copulation. "The intimate evolutionary association of an intromittent male structure with the corresponding female receptive structure strongly supports the action of sexual selection during diversification of these beetles" (Liebherr 2008, p. 72). This selection may result during female choice of superior males, or sexual conflict in which females are resistant to mating, which selects for heterotrophy. One can easily imagine that in local populations selection may shift populations in different directions involving genitalic compatibility, resulting in reproductive isolation between populations, speciation and adaptive radiation, in such heterogeneous landscapes as provided by the Hawaiian Islands.

2.8.4 Mating systems and strategies

A **mating system** may be defined as a species-specific pattern of male–female associations. "The term 'mating system' of a population refers to the general strategy employed in obtaining mates. It encompasses such features as: (i) the number of mates acquired, (ii) the manner of mate acquisition, (iii) the presence and characteristics of any pair bonds, and (iv) the patterns of parental care provided by each sex" (Emlen and Oring 1977, p. 222). Thus, much of the preceding parts of this chapter come under the umbrella of mating systems.

Shuster and Wade (2003, p. 36) summarized Emlen and Oring's (1977) ecological classification of animal mating systems as follows.

1. "Males compete with one another for access to females.
2. Like competition for scarce resources, male reproduction is limited by the spatial and temporal availability of sexually receptive females.
3. The intensity of sexual selection depends on the rarity of receptive females in relation to the abundance of competing males.
4. Sexual selection favors male attributes which permit their bearers to find and monopolize their mates.
5. Ecological constraints on male monopolization attempts lead to a species-specific pattern of male-female associations, called a 'mating system.'"

The intensity of competition for mates, or the intensity of sexual selection, is often estimated using the **operational sex ratio**, which is the ratio of adult males to adult females. However, because this ratio can overestimate the success of certain individuals, a better estimator of the intensity of sexual selection is the average number of mates per mating male, a value proportional to both the variance in male mating success and the intensity of sexual selection (Shuster and Wade 2003, Wade and Shuster 2004). This view can result in a classification of mating systems based on male and female mate numbers (Shuster and Wade 2003, Table 2.5). And we have Shuster and Wade to thank for clarifying and simplifying the glossary of terms for mating systems. Differences in mating systems depend on several factors, making males or females more or less accessible. Where both sexes care for young, **monogamy** is likely to prevail, as in *Nicrophorus* beetles (Silphidae) in which both sexes make a nest under a buried carcass and feed their young in the nest. Monogamy appears to be an ancestral trait for bees, wasps and ants, the eusocial insects (Hughes *et al.* 2008). Termites may also form persistent pairs. The term **polygyny** Shuster and Wade apply exclusively where females mate with only one male in their lives, but males may mate with multiple females. This mating system may represent many territorial species, as with territorial hilltoppers such as the tarantula hawk wasps mentioned earlier, and the territorial butterflies and lekking species such as *Drosophila heteroneura* (Figure 2.13). **Polygynandry** is used only as stated in Table 2.5, and Shuster and Wade list only scorpionflies and waterstriders as insect examples. In the scorpionflies, for example, a male may feed and copulate with several females, and he is unable to guard females while hunting for prey, opening opportunities for a female to gain more nuptial gifts, and sperm, from other males.

Table 2.5 **A general classification of mating systems based on male and female mate numbers**

Category	Definition	Variance in mate number	
		Females	Males
Monogamy	Each sex mates once: each sex has a single mate for life	0	0
Polygyny	Females mate once; males are variable in mate numbers	0	++
Polygynandry	Both sexes have variable mate numbers; male mating success is more variable than female mating success	+	++
Polygamy	Both sexes have variable mate numbers; male mating success is approximately equal to female mating success	+	+
Polyandrogyny	Both sexes have variable mate numbers; female mating success is more variable than male mating success	++	+
Polyandry	Males mate once; females are variable in mate numbers	++	0

From Shuster and Wade 2003.

In **polygamy** males and females mate more than once, and males cannot protect females from other males over the longer term. Therefore, conflict among males for females, and intersexual conflict with females rejecting males, may occur as in *Drosophila*, and in damselflies. Sperm competition, discussed later in this chapter, is well known in these insect groups. **Polyandrogyny** is the converse of polygynandry, and refers to mating systems in which females demonstrate the more variable number of mates. We would expect this mating system to prevail under the unusual circumstance in insects of male parental care in which males are constrained in mating because protecting young is paramount, while females are free to mate with several males. An example is the giant water bugs (Belastomatidae, *Abedus*, *Belastoma* and *Lethocerus*) discussed in Chapter 10 on Life histories. **Polyandry** involves males that mate for life with a single female, but females live much longer, or males become devoted to full-time parental care after one mating. These cases are rare in all animals, but one example concerns praying mantids (Order Mantodea) and some spiders in which the female eats the male during or immediately after copulation. Understandably, this classification of mating systems simplifies the diversity seen in nature, and Shuster and Wade provide a more comprehensive survey of major categories and subcategories. One additional strategy is practiced by parthenogenetic individuals or species, some of which do not mate at all.

In any one species of insect one major strategy may appear to be well represented, but **alternative mating strategies** often exist. For example, in many beetles the big males win competitive bouts with smaller males. But small males are unlikely to live until another breeding season, so selection will probably promote an alternative strategy. These alternatives may employ surreptitious behavior and mating, leading to the epithet of sneaky fellow (or something more risqué) for these males. For example, in the dung beetle, *Onthophagus acuminatus*, there is a bimodal distribution of horn lengths, with small males hornless and large males well equipped with horns (Figure 2.17, Emlen 2000a, b, Emlen and

Nijhout 2000). The large males guard burrows under dung, while females burrow below and provision larval cells with dung. Small, sneaking males adopt an alternative strategy involving a side burrow, circumventing the large male, and gaining access to the female. *Onthophagus taurus* exhibits even stronger horn dimorphism than *O. acuminatus* (Stern and Emlen 1999). With both morphs of *Onthophagus* able to mate successfully, presumably selection will maintain this dimorphism indefinitely, if the success of the strategies is more or less matched.

Another case of an alternative mating strategy was described earlier for the speckled wood butterfly, in which some males established territories, while others cruised the tree canopy in search of females.

Thornhill (1981) described alternative mating strategies for the scorpionflies, *Panorpa* species (Mecoptera: Panorpidae), and these are listed in order of likely success in acquiring copulations. Some males defended dead insects which were alluring to receptive females. Others secreted saliva onto leaves, providing a nuptial gift for the occasional female. A third strategy was to force copulation without a gift of any sort. The males made the best strategic choice available to them, and were opportunistic about the strategy they adopted – a **conditional strategy** depending on available resources defined by the competitive milieu in which they found themselves. Grasshopper males also show alternative approaches, and these alternatives may change in individuals over time (Shelly and Greenfield 1985), or in other species some may produce large spermatophores while others attempt to force copulations (Belovsky et al. 1996). Large males of water striders, *Gerris remigis*, are able to swim in fast-flowing water with more food and mate with large females, but smaller males swim in slower water (Rubenstein 1984). Some species of fig wasp have two male morphs (Greef 1995). One type mates within the fig and never leaves, while the other morph can disperse before mating and finds mates on leaves or fruits. The variety of alternative mating strategies among species is extraordinary.

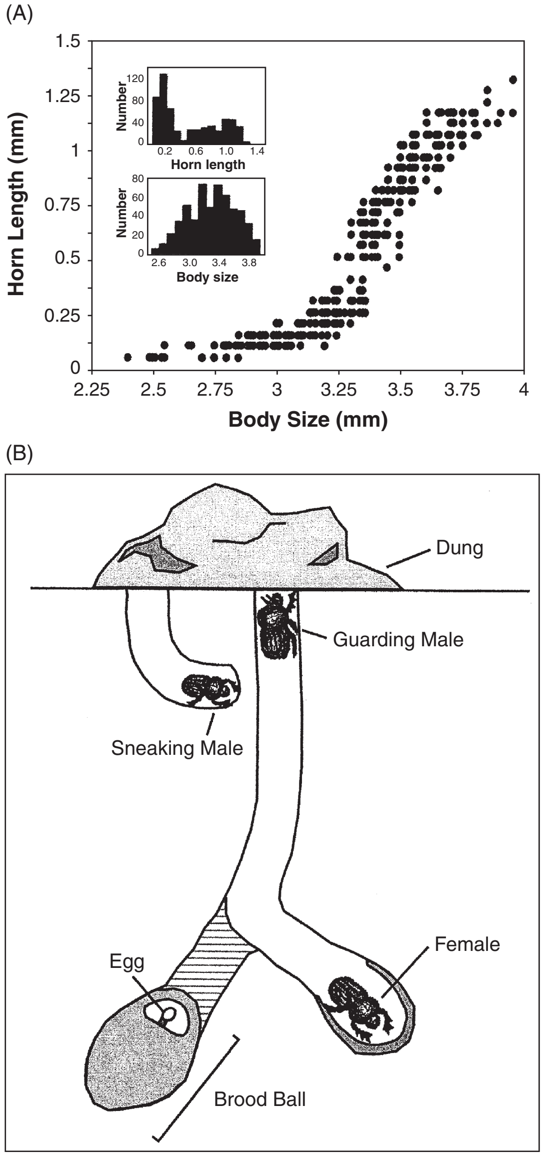


Figure 2.17 (A) The relationship between body size and horn length in male dung beetles, *Onthophagus acuminatus* (Coleoptera: Scarabeidae), in a population on Barro Colorado Island, Panama. The relationship is sigmoidal and the frequency distribution of horn lengths (top inset) is bimodal, with hornless males on the left and horned males on the right. (B) Alternative mating strategies in *Onthophagus acuminatus* with a dominant male possessing large horns guarding the nest entrance below a dung heap, and a smaller hornless male building a side tunnel to sneak access to the female below. From Emlen 1997 (A), 2000a (B). B. Copyright, American Institute of Biological Sciences.

2.8.5 Sperm competition

Once females have mated there is always the chance that a subsequent male will mate with her and displace the sperm in her spermatheca from a previous mating. **Sperm competition** results. This chance is maximized when:

(1) Females mate several times before eggs are fertilized
(2) Inseminated sperm is stored by the female in the spermatheca
(3) Sperm remains viable for a long time
(4) Sperm is used economically, without any waste, and often one sperm is used to fertilize one egg (Parker 1970a).

Under these conditions strong intrasexual selection will result, with inevitable adaptations in males to minimize sperm competition. These strategies include the following and have been reviewed by Parker (1970a) and Thornhill and Alcock (1983):

(1) **Mating plugs** block the genital passages of females after copulation, preventing or reducing possibilities of subsequent copulations. They are formed by secretions of the male accessory glands and are common in Diptera, Hymenoptera and Lepidoptera, but have been observed also in Orthoptera, Coleoptera and Isoptera. The plug may dissolve in a few hours, but probably lasts until a female becomes unreceptive, or it may even induce unreceptivity.
(2) **Prolonged copulation** is common in insects. Insemination may be rapid, but copulations last well beyond this necessary process, to 30 minutes, 60 minutes and even 4 hours, just within the Diptera (Thornhill and Alcock 1983). In the notorious “lovebugs,” *Plecia nearctica* (Diptera: Bibionidae), pairs may remain in copula for up to 3 days! Moths commonly mate for 24 hours. Clearly, males prevent further copulations while joined, and they may induce unreceptivity in females, but forfeiting additional copulations appears to be a high price to pay. Perhaps, when competition for females is high, assuring one successful copulation is a better strategy than going for another female, and risking sperm competition in the original mate?
(3) **Tandem positions** or **passive phases** occur when males remain attached to a mated female but without genital contact. Males defend females against other males, often while the female oviposits. Therefore, postcopulatory passive phases reduce sperm competition. In the dung fly, *Scatophaga stercoraria*, males mate and then guard females on fresh dung, sitting on the back of the female. Without genital contact the female can oviposit into the dung, but the male assures that his sperm fertilizes her eggs. Should he be displaced, a second male will fertilize 80% of the eggs she lays (Parker 1970a, b, c). Tandem positions are adopted in locusts, grasshoppers, most crickets, and in many dragonflies and damselflies.
(4) **Non-contact guarding phases** involve males which guard females they have copulated with, but the pair do not remain in contact. A female may remain in the territory of a male which defends against entry by other males. Both sexes may then be opportunistic in mating, and if populations are dense such opportunities are rich, with extraterritorial males sneaking copulations with females while the guarding male attends to other females which have entered his territory. In the damselfly, *Calopteryx maculata*, males can actively remove sperm in the spermatheca of a female with a specialized organ analogous to a penis, and replace sperm with his own (Waage 1979). Non-contact guarding has been noted in dung beetles in this chapter, and it also occurs in bark beetles and crickets.
(5) **Takeover avoidance** includes any mechanism that improves a male’s probability of inseminating a female and ensuring that his sperm will fertilize her eggs. Tactics may include clasping appendages in the male genitalia which improve the strength

of attachment to a female. Prothoracic legs of males may be modified to grasp females firmly, as in the Dytiscidae, the predaceous diving beetles, with a segment of the tarsus expanded to house suction discs for firm attachment to females. Rejection behaviors by mated males may include kicking at intruding males as in grasshoppers and scatophagid flies. Emigration from dense assemblages of males reduces intramale competition: in the suborder of Diptera, the Nematocera, the long-horned flies, such as mosquitoes, blackflies and midges, pairs form in a swarm, but may drop to the ground to copulate. Male dung flies, *Scatophaga stercoraria*, carry females from dung to surrounding grass with increasing frequency as male densities on dung increase (Figure 2.18). In the cooler conditions away from dung, duration in copula is prolonged, but reduced probability of takeover and reduced disturbance provides a net benefit to fitness (Parker 1971, Borgia 1980, 1982).

Darwin (1871) observed a large range of secondary sexual characters of arthropods from crustaceans to spiders and insects, spending almost 100 pages on this group with most emphasis on insects. He concentrated on visible characters that differed between males and females, which were under the influence of sexual selection. What he did not appreciate was the vast range of behavioral adaptations involved, and the many more cryptic tactics employed in such activities as sperm competition, alternative mating strategies and nuptial gifts. The subject of sexual selection has enjoyed a resurgence since the centennial symposium on the subject (Campbell 1972), before which little progress had been made since Darwin's time. Now, as covered briefly in this chapter, we can see how much studies on the insects have contributed to advances in knowledge on this fascinating subject. Many of the intricacies of sexual selection have been revealed and yet, no doubt, there are rich research opportunities for the future.

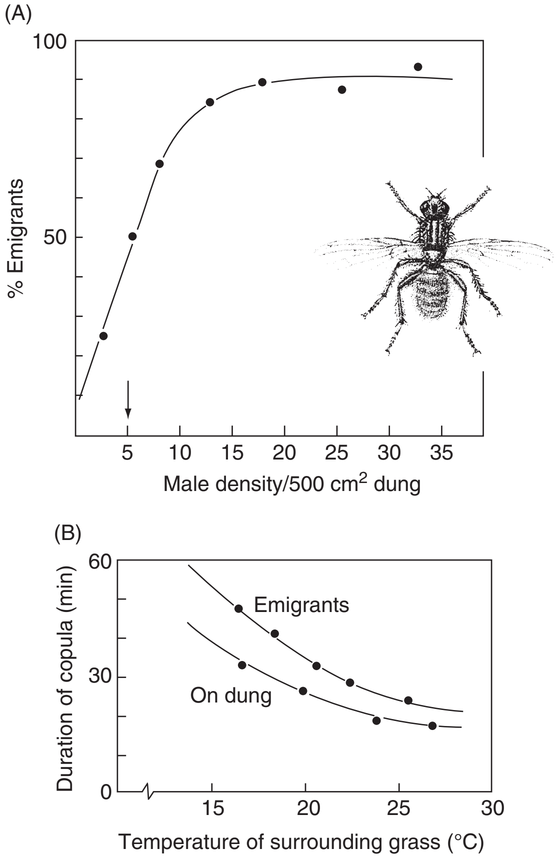


Figure 2.18 Alternative mating strategies in the dung fly, *Scatophaga stercoraria*, which uses fresh, warm dung as mating and oviposition sites. (A) As density of males increases on dung, more males carry females away from the dung to mate in the surrounding grass. The arrow indicates a possible threshold density for emigration. (B) The duration of copulation among emigrants is prolonged relative to those on dung because of the reduced temperature in the grass. From Parker 1971 (A), modified (B). Reprinted with permission from Blackwell Publishing Inc.

2.8.6 Parental investment and care of progeny

Trivers (1972, p. 139) defined parental investment as "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring." Parental investment therefore includes the metabolic cost of primary sex cells as well as provision of food for young and protection of young. In most insects males provide nothing for progeny except sperm. But some males provide nuptial gifts which contribute to the welfare of young, and some males help to feed young and/or guard females against takeovers as we have seen. Among female insects the majority simply lay eggs without further guarding or other investment. However, many females are meticulous in placing eggs in suitable places, spending considerable time finding oviposition sites advantageous to their young. In doing so they become exposed to increased predation risk, with the reduced potential for further reproduction. Many groups, in addition to a complex chorion, provide protective coverings for eggs, such as oothecae in roaches and foamy egg cases or oothecae in mantids, or females cover clutches of eggs with protective secretions, for example in some membracids and reduviids. Some stick insects produce a capitulum on the operculum of the egg which is attractive to ants, like the elaiosome on seeds, stimulating ants to carry the eggs into the safety of their nest.

The function of nuptial gifts from males to females is difficult to evaluate without careful tracking of nutrient use by females. In many cases the nuptial gift functions solely as a **mating investment** rather than a contribution to progeny welfare. However, detailed studies on some species show evidence of considerable male parental investment (Thornhill and Alcock 1983, Thornhill and Gwynne 1986). Spermatophore constituents provided by males to female butterflies are used in egg production, helping to maximize egg number (Boggs and Watt 1981), and advancing early egg maturation when pollen sources are sparse in *Heliconius* and *Danaus* butterflies (Figure 2.19, Boggs and Gilbert 1979). A *Heliconius* butterfly male, with one spermatophore, can provide enough nitrogen to supply 15–30 eggs! Grasshopper males also pass spermatophores to females with nutrients rapidly absorbed into developing eggs, and multiple matings increase fecundity in *Melanoplus sanguinipes*. The 5-hour-long copulation seems to be mostly adaptive for transfer of nutrients, given that sperm can be transferred in 10 minutes.

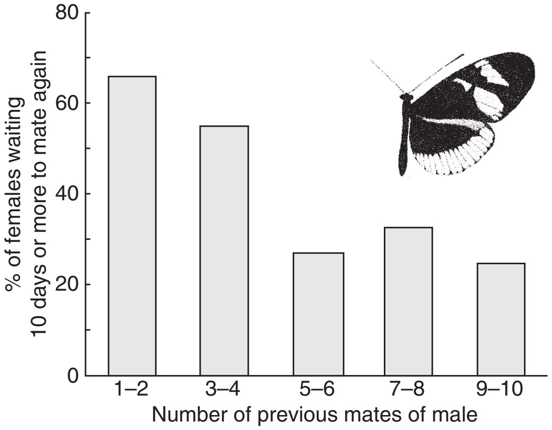


Figure 2.19 When males of the butterfly, *Heliconius cydno*, have mated little before mating with a female, they provide a large spermatophore, with the result that females wait longer to mate again, and lay more eggs fertilized by the male's sperm, compared to waiting times after mating with males which have mated with many females. Data by C. L. Boggs. From Thornhill and Alcock 1983. Reprinted by permission of the publisher from *THE EVOLUTION OF INSECT MATING SYSTEMS* by Randy Thornhill and John Alcock, p. 384, Cambridge, Mass.: Harvard University Press, Copyright © 1983 by the President and Fellows of Harvard College.

Male insects may also show parental care, but rarely. In *Nicrophorus* carrion beetles males will help bury the corpse of a bird or small mammal, excavate a burrow beneath the corpse, masticate corpse material to form a nest in which the larvae develop, and in some species males will aid females in feeding young (Wilson 1971). In some bark beetles males and females collaborate in excavating tunnels and caring for the brood. These kinds of behaviors qualify as **subsocial** – adults care for their own progeny for a period of time (Wilson 1971). In Chapter 10 on Life histories another case of male parental care is discussed – the giant water bugs, where males provide the care exclusively.

Females are more likely to provide parental care because they invest far more than males in their progeny, and therefore they are more limited in the number of progeny they can produce (see Wilson 1971). Female care occurs in the Hemiptera, where females guard egg clutches and young, crickets may dig a burrow in which they feed their young, and many beetle families have species with subsocial behavior.

Perhaps the greatest contribution females typically make toward progeny welfare is the careful placement of eggs. Females are frequently particular and specialized in placing eggs on or in suitable host plants or animals, as illustrated in Figures 2.3, 2.4 and 2.5 and in Chapter 4 on Plant–insect interactions. Some kinds of insects can even decide on whether to place a male or a female egg in a particular position, depending on the resource quality available. In the Hymenoptera, for example, reproduction is **haplodiploid** – males develop from unfertilized eggs; they are haploid. Fertilized eggs become diploid females. This condition has arisen several times in primitively herbivorous insects, including the Hymenoptera, with sawflies at the base of the phylogeny. It constitutes a form of **parthenogenesis** known as **arrhenotoky**: males have no fathers. Four insect orders, with many herbivorous species, include examples of haplodiploidy: Hymenoptera, Hemiptera (Homoptera), Thysanoptera and Coleoptera. Several families of mites are also haplodiploid, including herbivorous spider mites, Tetranychidae (White 1973). The condition has arisen several times in herbivorous groups, but its adaptive value has remained mysterious. However, two studies have shown that sawflies allocate sex ratios in an adaptive manner (Craig and Mopper 1993). Tenthredinid sawfly females lay a greater proportion of female eggs on rapidly growing plants, in which survival is better; females are larger than males and larger females were more fecund than on slower-growing plants. Hence appropriate sex allocation improved female fitness (Craig *et al.* 1992). The second study concerned a diprionid sawfly which laid a higher ratio of female eggs on trees supplemented with water and fertilizer than on trees that were not treated (Mopper and Whitham 1992). On the treated trees females attained a greater mass, and being pro-ovigenic, having all eggs ready to lay on emergence, they were more fecund. Much more work has revealed advantages to sex allocation in haplodiploid parasitoids where female wasps are generally larger than males, and female eggs are more frequently oviposited into larger hosts than male eggs (Figure 2.20, Clausen 1939, Charnov 1982).

What we learn from the study of insect behavior is that detailed observational studies combined with carefully executed experiments are needed to unravel the intricacies of insect life histories (see also Chapter 10). Given their existence on Earth for about 400 million years, since the early Devonian epoch (Grimaldi and Engel 2005), perhaps we should not be amazed at the complexity of interactions between the sexes of insects and their resources such as plants and animals. However, the literature reveals repeatedly fascinating and unexpected details on the life of insects, with many more surprises no doubt awaiting discovery. No wonder then that Vladimir Nabokov (1966, p. 126) wrote “Few things indeed have I known in the way of emotion or appetite, ambition or achievement, that could surpass in richness and strength the excitement of entomological exploration.” Thomas Eisner (2003, p. 1) admitted a lifelong “thrill of discovery . . . In me, love of nature is expressed as an affection for insects. I am an incorrigible entomophile.” Edward Wilson (1994,

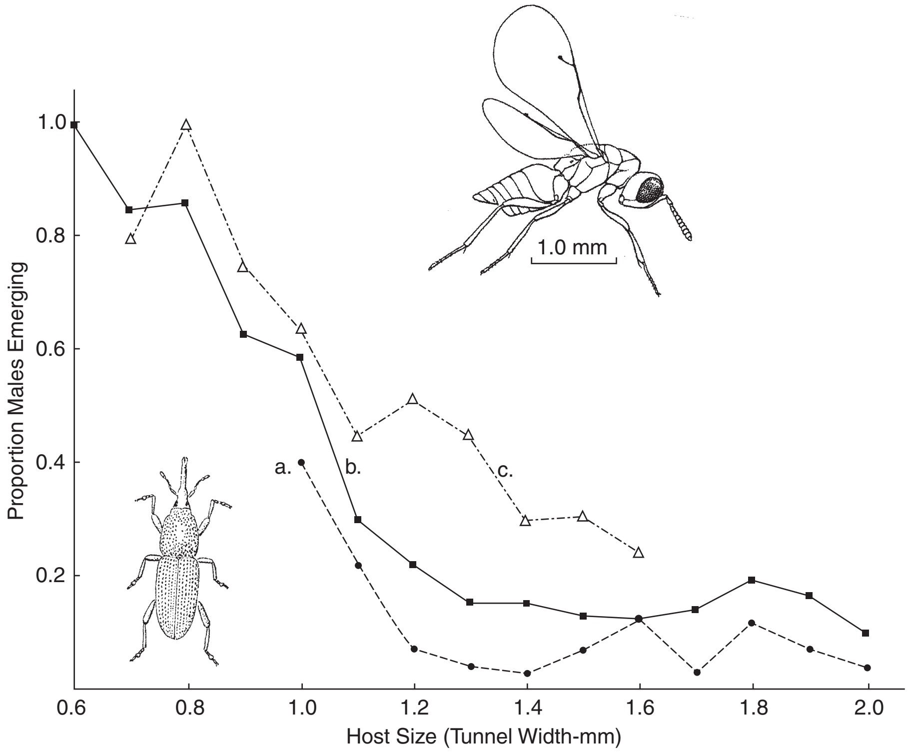


Figure 2.20 As host size increases the proportion of male eggs oviposited into hosts decreases: more females emerge from the larger hosts because of a sex-ratio shift determined by female *Lariophagus distinguendus* (Hymenoptera: Pteromalidae) which attacks larvae of the common granary weevil, *Sitophilus granarius*. The three trends a, b and c result from three experiments with differing conditions. From Charnov 1982.

p. 191) wrote, "Love the organisms for themselves first ..." He concentrated his attention on ants in particular, but these authors illustrate the dedication and focus that made them exceptional. Behavioral studies of insects were of central concern.

Applications

Behavioral approaches to pest regulation

With increasing problems concerning insecticide use – insecticide resistance, environmental contamination, biological concentration, population rebound, non-target species – the discovery of effective alternatives for insect pest population regulation became imperative. Therefore, any methods, or their combination, that impair activity of pest insects, or improve the effect of their natural enemies, using good biological knowledge of field populations, have become a major focus of research and application. Semiochemicals of all kinds hold promise in **behavioral control** of insect pests (e.g. Nordlund *et al.* 1981). "Fortunately, semiochemicals are generally highly pest specific and should cause little or no adverse effect on nontarget organisms. Thus the prospects of managing many of our major pests by taking full advantage of semiochemicals should be welcomed by environmentalists and the public who are increasingly concerned about the maintenance of environmental quality" (Knipling 1981, p. xi). Added to semiochemical use are visual attractants for visually hunting pest species, such as apple maggot flies. Provision of food for natural enemies in or around crop plants is also potentially an important contribution to pest control. The use of plants that provide nectar and pollen, and extrafloral nectaries, can be added as the **indirect defense** of a plant crop to the range of regulatory methods for suppression of insect pests (e.g. Wäckers *et al.* 2005). Many other methods may be integrated into a general strategy of pest regulation involving such approaches as landscape management, hygienic maintenance of farmland and forest, maintenance and enrichment of plant biodiversity, and application of knowledge of multiple-trophic-level interactions (e.g. Tscharntke and Hawkins 2002, Tscharntke *et al.* 2007a). When an insect pest is well understood, physiologically, behaviorally and ecologically, methods may be combined into a comprehensive approach to pest regulation, now known as **integrated pest management** (IPM) (e.g. Pedigo 2002). This involves integrating methodologies for all the major pests on a crop throughout the season, with the key to success being the understanding of their biology.

The integration of cultural, behavioral and biological controls is well illustrated by research on commercial apple orchards by Prokopy and his research group (Prokopy *et al.* 1994). Blending decades of research on apple pests (see Prokopy 1997, Prokopy *et al.* 1994), Prokopy and coworkers devised a six-pronged IPM approach involving management of all classes of pests in apple orchards in Massachusetts, USA:

(1) Monitoring of pest populations using visual traps or direct observation was essential in determining phenology of pests and densities, to decide if early pesticide treatment was necessary, and when to apply it if necessary. Pesticide use was minimized and restricted to early season use, which permitted natural enemies of pests to colonize and multiply through the late spring and summer.
(2) Apple maggot, *Rhagoletis pomonella* (Diptera: Tephritidae), was regulated with the use of a behavioral method: 8 cm red spherical sticky traps baited with a synthetic fruit attractant and a synthetic food attractant placed every 5 meters on perimeter apple trees. The spheres provided supernormal stimuli for the fruit flies, and immobilized the flies on the sticky surface.
(3) Hygiene was used to control codling moth, *Cydia pomonella*, populations by cutting down all apple and pear trees outside the orchard for 100 meters around, a distance rarely traveled by adult moths.
(4) Hygiene was also employed to prevent build-up of codling moth and other pests after apple harvest, by removing dropped fruit.
(5) No direct control methods were used against such pests as leafrollers and scales, because natural enemies became numerous enough after the early insecticide spray.
(6) A blend of herbaceous plants was grown among trees which favored populations of spider mites, *Tetranychus urticae*, and the predacious mite, *Amblyseius fallicis*, providing a reservoir of predaceous mites from which apple trees would be colonized.

The development of this integrated approach was based on a large research program, much of it behavioral in nature, and investigations continue (e.g. Rull and Prokopy 2005). The methods are relatively labor intensive, but the benefits of using more natural approaches to pest regulation are less toxicity in the environment, little impact on non-target species, reduced possibilities of evolved resistance to the methods applied, higher biodiversity and an agricultural ecosystem regulated in a more sustainable way.

Another successful program, reported by Jang *et al.* (2008), targeted one species, the melon fly, *Bactrocera cucurbitae* (Diptera: Tephritidae) in Hawaii. Male trapping, bait spraying, sanitation of crops, the sterile insect technique (see below) and augmentation of a parasitoid were all employed in this effective integrated pest-management plan.

Many other applications of behavioral methods of pest control have been employed (e.g. Jutsum and Gordon 1989, Ridgeway *et al.* 1990, Pedigo 2002). Pheromone traps may be used for monitoring insect populations to determine the need for regulatory methods and their timing. Pheromones and plant derivatives may also be used for mass trapping. Coupled with insecticide in the bait, large numbers of insects can be killed, with successful control of some fruit fly species, cotton boll weevil, *Anthonomus grandis*, bark beetle species and ambrosia beetles (Lanier 1990). Mating disruption can be effective by swamping the environment with pheromone from many point sources so that these compete with females releasing pheromone and males cannot discover mates. Pink bollworm, *Pectinophora gossypiella*, was the first species to be controlled successfully at the commercial level using mating disruption (Cardé 1990), and codling moth has been effectively controlled (Witzgall *et al.* 2008). Other species include oriental fruit moth, *Grapholitha molesta*, and gypsy moth, *Lymantria dispar*. Behavioral modification methods have been used in horticulture, forestry and in field crops, and even in the regulation of such medically important pests as tsetse flies, *Glossina* species (Ridgeway *et al.* 1990).

Other methods of pest regulation also employ a detailed understanding of insect behavior. For example, the regulation of the New World screw-worm fly, *Cochliomyia hominivorax* (Calliphoridae), which was a devastating pest of cattle in the southern USA and Mexico, depended on male and female behavioral characteristics. Females mate only once, meaning that mass releases of sterile males, induced by irradiation, can inundate a population, resulting in most females becoming infertile: the **sterile male technique** (e.g. Pedigo 2002). Males may mate several times so that sterility is propagated effectively. When the method began to fail, it became evident that mass rearing had reduced male competitive ability and general competence, so more effort was devoted to frequent injection of wild-type males into the mass-reared populations. Continual monitoring of male behavior is essential when mass rearing is practiced. Sterile insect mass rearing is now a global enterprise, including many fruit fly species, the screw-worm, moths, such as codling moth and pink bollworm, and tsetse flies (Hendrichs and Robinson 2003).

Many behavioral studies have involved the understanding of foraging by herbivores, predators and parasitoids in a quest to evaluate searching efficiencies (e.g. Waage and Greathead 1986, Hassell 2000). These are frequently in the interest of biological control programs with some work already discussed in this chapter in the section on foraging behavior. Studies were undertaken on glasshouse pests where predictions on activity and effects of interactions could be predicted well in such controlled and enclosed environments (e.g. Dicke 1988, Grostal and Dicke 1999, Krips *et al.* 2001).

Conservation biology necessarily involves behavioral ecology (see Samways 1994, 2005). The behavior of insects informs us of their most profitable habitats, where they go in winter, and the quality of resources most beneficial to a population's survival. Sensitive resources, habitats and landscapes may be identified. Without knowing the migration routes of monarchs, it would be impossible to protect the butterflies where logging threatens winter roosting sites in Mexico. Once these sites were belatedly discovered, a Monarch Butterfly Biosphere Reserve was established, which also received World Heritage status in 2008 (Shea 2008). Insect responses to fragmentation of tropical forest and the ecological importance of forest margins also play a role in conservation efforts (e.g. Tscharntke *et al.* 2007b). Behavior serves as a central theme in the understanding of the ecology of insect communities in tropical forests (e.g. Basset *et al.* 2003) and in the temperate latitudes (see Chapter 12 on Community structure and Chapter 13 on Multitrophic interactions).

There remain considerable opportunities for using the behavioral ecology of insects in the service of humans. Applications rely on increasingly sophisticated technology coupled with the understanding of behavior in life histories of insects. Many natural products, especially in plants, provide repellents and attractants which can be used for pest regulation. Some of these will be discussed in Chapter 4 on Plant and herbivore interactions.

Summary

Behavior covers all activities in the life of an organism from emerging out of an egg to the "last gasp" of the dying. All are related to survival, foraging for food, finding or making a place to live, communication and reproduction. Use of experiments to understand behavior is essential. We have covered survival in response to threats from weather, particularly migration, and the challenges of finding food, competition and avoiding being eaten by carnivores. Foraging behavior is complex, requiring a chain of behaviors in a stimulus-response sequence, as we illustrated with a parasitoid searching for hosts for its eggs. In a local patch time is allocated theoretically according to certain rules such as "giving-up time," but in reality simple motivations are complicated by many significant factors.

Insects need a place to live, which they construct themselves, such as a web or a burrow, or they use places on plants or animals. Behaviors range from females placing eggs exactly where the larva will begin to feed, as in plant tissue, to dropping eggs to the ground from high in vegetation.

Communication among individuals and with the environment by insects is frequently accomplished by chemical signals. All organisms release volatile chemicals which act as body odors available to other species for detection. Thus insects of many kinds detect their host plants by chemical signals, and parasitoids may find hosts by chemicals from insect scales, mandibles or frass, or by finding the host plant first and the insect host second. The lexicon for describing the many kinds of chemical communication, or chemical semaphore involving semiochemicals, includes pheromones, allomones, kairomones, synomones and apneumones, all of which provide coherent information exchange up and down multitrophic level systems.

We treated reproductive behavior under the headings of sexual selection, finding and choosing mates, mating systems, sperm competition, and parental investment. We followed a path from the evolution of differences in form and behavior between males and females of the same species to the tactics involved with finding mates, which may involve hilltopping, leks or territoriality. Courtship enables evaluation of a potential mate, sometimes with tangible nuptial gifts from male to female, while a mating system encompasses a species-specific pattern of male–female association, including mating display, the number of mates, parental care and alternative mating strategies. Sperm competition, when one male displaces sperm in a female from another male, is avoided by many mechanisms such as mating plugs, guarding females, and mating away from meeting places and oviposition substrates. Parental investment is a compromise between increasing the chances of survival of an offspring at the expense of reducing the opportunity to leave more progeny. This often involves parental care of offspring for a period of time, or the careful and time-consuming placement of eggs into high-quality food, or into other well-protected niches.

We completed the chapter with a discussion of the application of behavioral ecology to the regulation of insect pests, and its contributions to integrated pest management. This regulation involves such techniques as the use of semiochemicals for disrupting herbivores searching for host plants, increasing cover and food for natural enemies of pests, use of various trapping methods and the sterile male technique. Behavioral ecology also contributes to conservation of insects, as we need to understand migration routes, breeding and overwintering locations, and the best patterns of habitat over the landscape. Behavior of insects serves as a central theme in the understanding of more complex interactions in communities and ecosystems.

Questions and discussion topics

1. To what extent do you consider behavior of insects to be important in the understanding of their ecology?
2. Which kinds of communication do insects use, and how does this affect their ecology?
3. Discuss the observation that some insects engage in little courtship, while others have evolved complex courtship behaviors. Consider why such differences should evolve.
4. The burrowing habit has evolved many times in insects. Discuss the benefits and costs of burrowing, relating these to specific taxa of insects.
5. Do you think that insect ecology courses should be coupled also with courses in insect behavior and insect evolution?

Further reading

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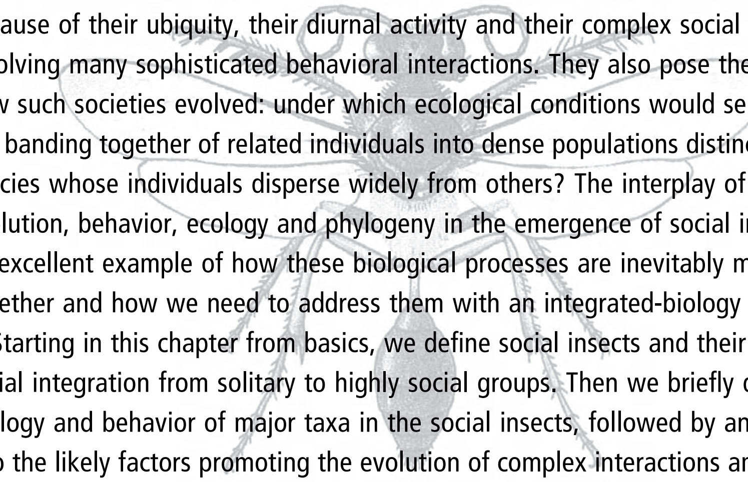
3

Social insects: the evolution and ecological consequences of sociality



Social insects are major components of most ecosystems and are key players in communities. We will see in this chapter that their biomass is impressive, their activities as ecosystem engineers – making nests, trails and moving soil – are massive, and their impacts on other community members are widespread.

Social insects stimulate immense fascination among their human observers because of their ubiquity, their diurnal activity and their complex social structure involving many sophisticated behavioral interactions. They also pose the problem of how such societies evolved: under which ecological conditions would selection favor the banding together of related individuals into dense populations distinct from most species whose individuals disperse widely from others? The interplay of life-history evolution, behavior, ecology and phylogeny in the emergence of social insects offers an excellent example of how these biological processes are inevitably meshed together and how we need to address them with an integrated-biology approach.

Starting in this chapter from basics, we define social insects and their hierarchy of social integration from solitary to highly social groups. Then we briefly describe the ecology and behavior of major taxa in the social insects, followed by an exploration into the likely factors promoting the evolution of complex interactions among closely aggregated individuals. The importance of social insects as participants in community and ecosystem function is then covered in some detail because their impact is multifaceted, complex and strong. Finally, managed lands are colonized by these organized societies, so what we learn about social insects can be applied in agriculture, forestry, horticulture and conservation.

3.1 What are social insects?

An insect **society** is a group of conspecific individuals organized in a cooperative manner. This typically includes helping behaviors, shared resources and cooperational communication. The shared resources can be shelter, defense or food. The majority of insect societies are built on the family unit and how we classify social complexity is largely based on the family relationship (Costa and Fitzgerald 1996). Indeed, the first real attempt to classify social complexity in insects by Wheeler (1928, p. 12) consisted of seven categories distinguished by “constantly increasing intimacy of the mother with her progeny.” The terminology for categorizing insect societies was further developed by Michener (1969) and Wilson (1971). Although this social terminology has been criticized for being overly focused on bees, ants and termites and for not focusing enough on the trade-off between personal reproduction and cooperation inherent in insect societies (Crespi and Yanega 1995, Costa and Fitzgerald 1996, 2005), Wilson’s terminology is still the most widely used. Wilson proposed that insect societies increased in complexity from solitary to highly social via the acquisition of three key traits: cooperative brood care, reproductive castes and overlap of generations (Table 3.1).

3.2 Levels of sociality: the other social insects

Solitary insects, of course, show no cooperation among individuals. **Subsocial** insects, on the other hand, typically form a single-family unit where one or more of the parents care for their own offspring, at least for a short time. **Parental care** is incredibly widespread among insects: it is found in thousands of insect species distributed among at least 15 orders (Tallamy and Wood 1986, Costa 2006). Parental care varies immensely within these species and ranges from passive egg guarding to grooming, feeding, protecting and nesting behaviors. All of the behaviors, however, can be categorized into those that physically protect the young from danger, those that protect resources vital to offspring and those that facilitate offspring feeding (Tallamy and Wood 1986). *Gargaphia solani* lacebugs provide an excellent example of defense from danger. These tiny lacebugs feed on plants in the nightshade genus *Solanum* (Tallamy and Denno 1981). Females produce egg masses that are cemented to the underside of leaves and females remain with their gregarious offspring for all five nymphal instars. When predators approach the nymphs, mothers aggressively charge the predators while fanning their wings. Although the lacebugs are not really capable of harming the far larger and more dangerous

Table 3.1 **The hierarchy of sociality from solitary to eusocial, with intermediate parasocial conditions. 0 = absence, + = presence. Modified from Wilson 1971**

Levels of sociality	Components of sociality		
	Cooperative brood care	Reproductive castes	Overlap of generations
Solitary, subsocial and communal	0	0	0
Quasisocial	+	0	0
Semisocial	+	+	0
Eusocial	+	+	+

Figure 3.1 A *Gargaphia solani* female guards her offspring. Although small and relatively harmless, these lacebugs are very effective at repulsing predators. Photograph and copyright by Michael Loeb. See color plate section.

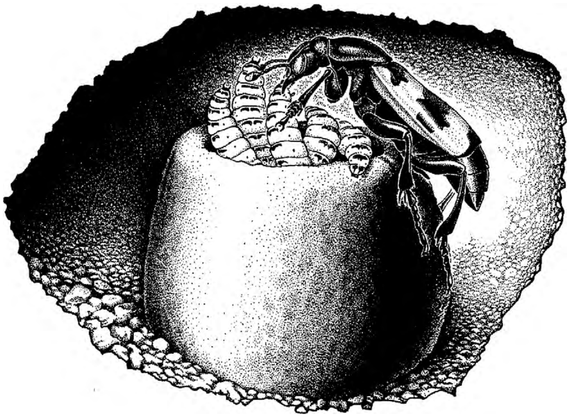


Figure 3.2 Parental care by a carrion beetle, *Nicrophorus vespillo* (Coleoptera: Silphidae), with the adult feeding larvae in a nest-like structure. Original illustration by Sarah Landry, based on a photograph by Erna Pukowski. From Wilson 1971.

predators (lady beetles, lacewings and the like), the displays are very effective: nymphal survival was dramatically higher when mothers were allowed to protect their offspring than when mothers were removed (Tallamy and Denno 1981) (Figure 3.1). Not all parental care is provided by the mother. Male giant water bugs (Hemiptera: Heteroptera: Belastomatidae), for example, protect the eggs that they parent by carrying the eggs on their backs (see detailed discussion in Chapter 10).

Nicrophorus burying beetles provide a rather extreme example of the efforts of some parents to protect resources for their offspring and facilitate offspring feeding (Tallamy and Wood 1986, Costa 2006). Larvae of *Nicrophorus* burying beetles use small vertebrate carcasses as their only food resource (Scott 1998). This resource is essential for reproduction, is unpredictable in space and time and is valuable to many other animals and microorganisms. Consequently, there is strong selection for adult burying beetles to go to great lengths to secure these resources (Scott 1998). Once a female beetle or reproductive pair of beetles discovers a fresh carcass, they move it to a suitable spot for burial and dig beneath it. They also remove the hair or feathers on the carcass and start to shape the carcass into a ball. In addition, they clean the carcass and secrete antimicrobial compounds on it, which significantly delays decomposition. When fully prepared, the carcass may be in a shallow burial chamber that is just a depression under leaf litter or a deep vault that is as much as 60 cm underground. When males cooperate with their mates, carrion is buried significantly faster than when females work alone (Wilson and Fudge 1984). Once all is prepared, the mother *Nicrophorus* lays her eggs in soil near the carcass and she feeds the offspring with regurgitated carrion and continues to defend the carrion and developing larvae from competitors, predators and fungi (Figure 3.2). Frequently her mate will cooperate with these tasks illustrating **biparental care**.

Communal species are those where members of the same generation live together, but without cooperative brood care. This often occurs in species where there is communal oviposition of eggs, but mothers do not actively care for these offspring. This behavior occurs in a wide range of insect orders. For example, females of many species of Psocoptera (book or barklice) will oviposit clutches of eggs in the same location and, upon hatching, groups of several dozen to several hundred nymphs stay together while grazing on lichens and algae (New 1985, Costa 2006; Requena *et al.* 2007). Most teneral adults disperse within a few days of molting (Requena *et al.* 2007) and although some females may be found near aggregations of nymphs, they do not protect their offspring and fly away when threatened (New 1985). Aphids also benefit from living in colonies. Aphids living in colonies are often closely related due to **parthenogenesis** and benefit from group living by two mechanisms: alarm signaling and induction of metabolic sinks in their host plants. When attacked by predators or parasitoids, aphids emit cornicle droplets containing the alarm pheromone E-ß-farnesene (Kislow and Edwards 1972). This alarm signal increases aphid survival by causing clone-mates to stop feeding and walk away or drop from their feeding sites to escape predation (Nault *et al.* 1973). Peel and Ho (1970) found that aphid feeding creates a sink in their host plants whereby photoassimilates are concentrated at the feeding site and this sink effect increases with colony size. Likewise, lepidopteran species in over 20 different families have social larvae and can be classified as communal (Costa and Pierce 1997). In many of these species, gregarious cohorts of larvae cooperate in defense, foraging and nest building, but adult butterflies and moths do not care for the caterpillars (Costa 1997). Many tent caterpillars (family Lasiocampidae), for example, engage in synchronous rearing and flicking of the anterior half of their bodies when threatened by parasitoids or predators, and use trail marking to facilitate group foraging (Fitzgerald 1976, Fitzgerald and Peterson 1988). Very similar behaviors are found in many species of chrysomelid leaf beetles (Jolivet *et al.* 1994) and sawflies (Costa 2006). Gregarious sawfly nymphs, for example, benefit from increased efficacy of chemical defense (Codella and Raffa 1996) and enhanced thermoregulation that results in faster growth rates (Fletcher 2009) as group size increases. Communal living by species of Lepidoptera and Coleoptera often enables them to overcome defenses of their host plants. Caterpillars of the nymphalid butterfly *Chlosyne janais*, for example, gain weight twice as fast when they feed in aggregations on their host plants (*Odontonema callistachyum*) than when they feed alone (Denno and Benrey 1997).

Quasisocial species are socially more complex than communal species because members of the same generation live together and cooperate in brood care. In many allodapine bees in the genus *Exoneura*, for example, multiple sisters will become reproductively active and produce broods in the same nest (Schwarz 1986, Cronin and Schwarz 1999). In several species of *Nicrophorus* burying beetles, multiple, unrelated females will form cooperative breeding associations and jointly prepare large carcasses and share in the feeding of offspring (Trumbo and Wilson 1993). It is thought that the superabundance of food represented by a large carcass promotes cooperation as a mechanism of reducing the probability of nest failure.

In **semisocial** species, there is cooperative brood care of females of the same generation as well as reproductive caste differentiation. This occurs in some wasps and bees. For example, most *Polistes* wasp colonies are semisocial at the beginning of the colony cycle. This occurs when a colony is founded in the spring by a group of females that collectively construct and provision a nest (West 1967). Likewise, *Lasioglossum malachurum* sweat bee colonies will persist in a semisocial state when the colony outlives the founding queen. When the queen perishes, workers of the same generation become reproductively active, produce offspring and share brood care within the colony (Richards 2000).

3.3 Eusociality: the superorganisms

Eusocial species represent the ultimate social condition. The majority of the eusocial insects are ants, wasps, bees and termites. These species engage in cooperative brood care, and have reproductive castes and overlapping generations. The key feature of eusociality is the castes: reproductives are specialized for producing offspring and altruistic workers are specialized for tasks associated with brood care, foraging, nest construction and maintenance, and defense. At maturity, colonies can range in size from a dozen or so individuals up to tens or even hundreds of millions or more (Hölldobler and Wilson 2009). Typical eusocial colonies will contain one or at most a handful of reproductives and a much larger number of workers. In ants, bees and wasps, the reproductives are female queens, while daughters are the workers. In termites, however, a king typically lives with the queen and termite workers are often male and female offspring. Eusocial insects typically use pheromones to evoke particular responses in colony mates such as alarm, attraction, assembly and recruitment, although touch and substrate-borne vibrations may also be involved. Most social insects distinguish nestmates from non-nestmates by evaluating cuticular hydrocarbons. Wilson (1971) has proposed that eusocial insect colonies are "**superorganisms**" due to their integrated communication system, caste-based division of labor and ability to maintain homeostasis via self-regulated, internal feedback loops. The concept of the superorganism is explained by Wilson (1971, pages 469–470) as "Any society, such as the colony of a eusocial insect species, possessing features of organization analogous to the physiological properties of a single organism. The insect colony, for example, is divided into reproductive castes (analogous to gonads) and worker castes (analogous to somatic tissue); it may exchange nutrients by trophallaxis (analogous to the circulatory system), and so forth."

3.3.1 Bees

Apis mellifera, the European or western honey bee, is probably the best studied eusocial insect. Honey bee colonies comprise a single egg-laying queen, up to 80 000 workers, and up to 2000 male **drones** (Winston 1987). The drone's only job is to fertilize new queens. The nest is an array of double-sided wax combs divided into thousands of hexagonal cells. The hexagonal shape holds the most honey for the least wax and the hexagonal array provides strength. During comb construction and repair, wax is produced by glands on the underside of workers' abdomens and it is gathered and shaped with the front legs and mandibles. Worker bees are sterile females and are kept sterile by the queen who produces a pheromone called "queen substance" from mandibular glands (Butler 1954). This pheromone is transferred from bee to bee within the hive and restricts ovarial development within workers.

A queen can lay up to 1500 eggs in a single day and may ultimately lay more than one million eggs over her four-to-five-year life span. When newly emerged, a worker spends her first two days eating pollen and honey. She then spends three weeks working inside the hive as a nurse feeding larvae with **royal jelly** that she secretes from her hypopharyngeal gland. Larvae that are destined to become workers or drones get royal jelly for a few days and then are fed pollen and honey. Larvae that are destined to become queens, on the other hand, are fed royal jelly throughout their development. Nurse bees also produce wax that is used to build new cells and repair the comb. As the worker ages, she switches tasks and becomes a forager. Foragers visit flowers and gather nectar and pollen. Pollen is collected in the **corbiculum** or pollen basket on the outer face of the hind tibia that is specialized for the transport of pollen and nest-building materials. Nectar is stored in an anterior region of the gut called the honey crop and is regurgitated into storage cells or recipient hivemates upon return to the colony (such transfer of food among nest members is called **trophallaxis**).

Honey bee workers share information about the location of nectar- and pollen-producing plants using a remarkable dance language (von Frisch 1967). A figure eight waggle dance of varying speed is performed if the food source is more than 100 meters away. The angle of the waggle run in the middle of the dance relative to the vertical allows the bees to follow a course to the food, relative to the position of the sun (Figure 3.3). If the food is less than 100 meters away, then a round dance is performed.

Workers often aggressively defend the hive. They have a barbed sting such that stinging an intruder is basically suicidal. Another method of defense used against intruders such as hornets is for workers to crowd tightly around the intruder and shiver their thoracic muscles which can generate enough heat to kill the trespasser. When a queen ages, the colony becomes overcrowded or food becomes limited, workers begin to make large queen cells. Just before the first new queen emerges, the old queen and about half the workers leave the colony as a swarm. The first queen to emerge stings unemerged queens and then leaves the hive for a mating flight. The drones compete with each other to mate with the queen and the queen returns to the hive after mating.

3.3.2 Ants

Ants live in colonies ranging from a handful of individuals to hundreds of millions of workers inhabiting underground structures reaching six meters below ground (Hölldobler and Wilson 1990). Worker ants are wingless, while queens and males are winged (queens lose their wings after mating). It is thought that the lack of wings allows workers an advantage when foraging in leaf litter and beneath the soil surface. Chemical communication in ants has reached an extraordinary level. The average ant has more than 40 anatomically distinct exocrine glands involved in pheromone production (Billen and Morgan 1998). Pheromones play important roles in colony regulation, trophallaxis, trail marking, recruitment, recognition of nestmates and defense. Caste is determined by genetic–environment interactions. Ant heads are often modified according to caste and can be very large with massive or otherwise specialized jaws. For example, castes of some species can have jaws modified for crushing seeds, blocking nest entrances or dismembering enemies (Figure 3.4). Head shape and mandible structure inform us well on the ecological roles of ants in their environments. The two largest subfamilies of ants are the Myrmicinae and Formicinae. Myrmicine ants have stings and venom while formicine ants defend themselves by spraying formic acid.

Hölldobler and Wilson (2009) contend that leafcutter ants (primarily *Acromyrmex* and *Atta*) are “Earth’s ultimate superorganisms” because they have one of the most complex communication systems, the most elaborate caste system, air-conditioned nests and colonies that contain up to eight million workers and have a life span of 10 to 15 years. To produce such vast colonies, the queens have become the ultimate reproductive machines. A typical *Atta* queen, for example, can produce 150 to 200 million offspring in her lifetime and store 200 to 320 million sperm cells in her spermatheca (Kerr 1962). The unique aspect of the biology of leafcutter ants is their fungus farming. Leafcutter ants cultivate multiple, distant lineages of fungi, most of them belonging to the family Lepiotaceae (Agaricales: Basidiomycota) (Mueller *et al.* 1998). The fungal cultivars serve as the primary food source for the ants and are provided with cut leaves (Hölldobler and Wilson 1990).

A foundress queen propagates the fungus clonally by carrying inocula in her infrabuccal pocket, a cavity located beneath the opening of the esophagus, during her nuptial flight. After mating, foundress queens establish new colonies by digging chambers in the soil, expelling the fungal pellet that they brought from the natal nest, and initiating the cultivation of their own gardens, which are started by using fecal material provided by the queen. Nestfounding occurs within a chamber that remains closed until the first brood is reared, at which point the new workers begin to feed on the fungus and take over the fungus culture activities, including foraging for new leaves. As fresh clips of leaves are brought into the nest, they are cut into smaller and smaller

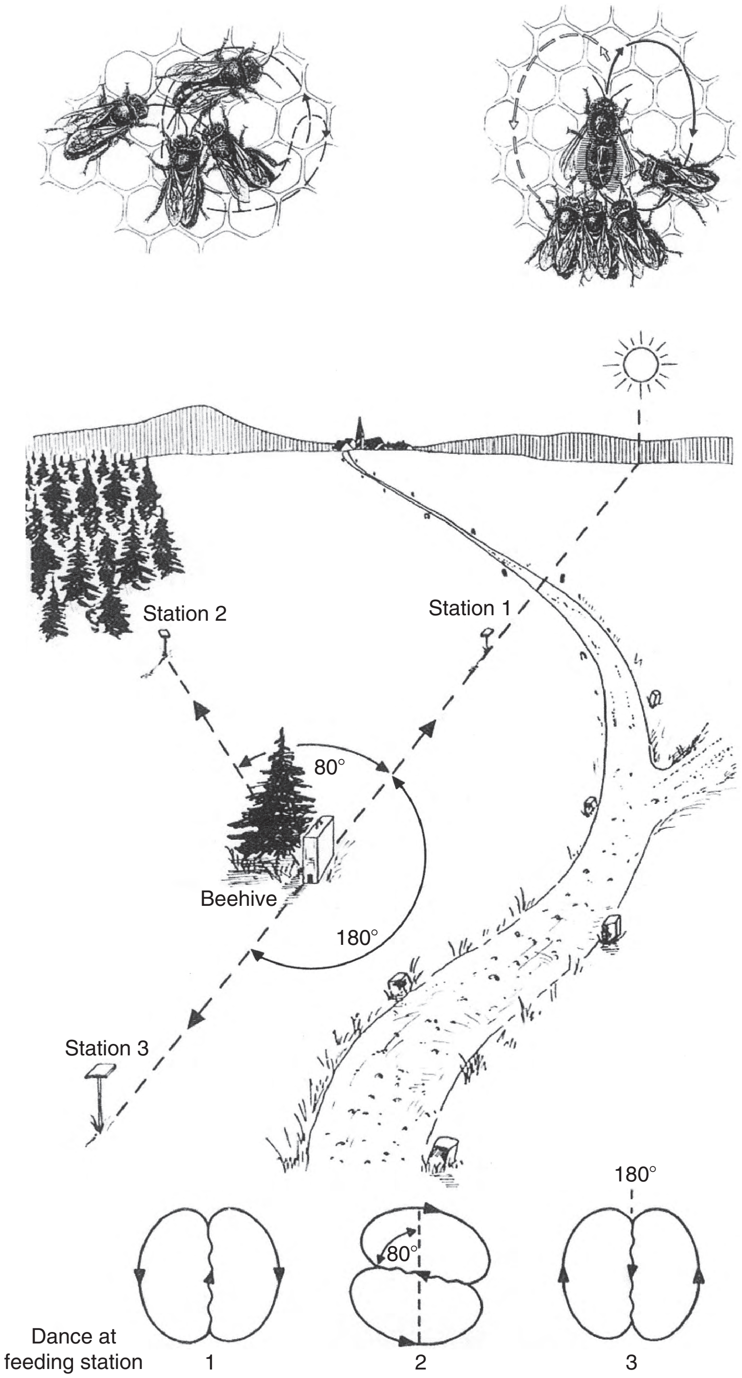


Figure 3.3 Foraging by honey bees (*Apis mellifera*) and the transmission of information to other workers in the nest. If the distance to the food source is less than about 100 meters, the round dance is performed as shown in the top-left figure. If the distance to the food source is greater than 100 meters, then the waggle dance is performed, shown at the top right. The comb surface is vertical so the dances are performed on this vertical surface. The angle of the waggle run in the middle of the dance relative to the vertical tells the bees the course to the food source relative to the sun. For example, flying from the beehive to feeding station 1, directly towards the sun, a bee will return and waggle up the comb vertically and complete the dance by coming down the comb to complete a figure of eight (bottom left) followed by other workers. After visiting feeding station 2 a bee will waggle at 80° off the vertical, and following a visit to feeding station 3, directly away from the sun, a bee will waggle down the comb at 180° from the sun. Based on von Frisch 1967.

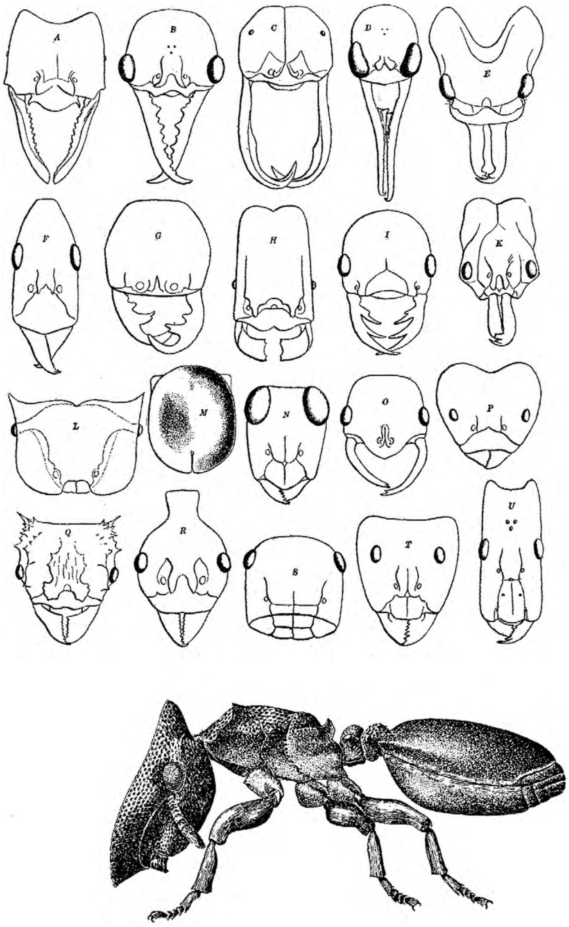


Figure 3.4 A sample of front views of head capsules of ant species showing the great diversity of shapes and a variety of adaptations for different functions. From Wheeler 1910. The ant below is a *Zacryptocerus* species which uses its head to block an entrance to the gallery system, as is the case for example L above in a related species. From Hölldobler and Wilson 1990. The *Colobopsis* head capsule in example S above is also adapted for plugging entrances to nests.

pieces and treated with ant secretions before being inserted into the fungal garden. These secretions are part of the elaborate system of enzymes that are produced directly by the ants and by their microbial symbionts (Currie *et al.* 1999, Fernandez-Marin *et al.* 2009). These enzymes along with "weeding" behaviors (Bass and Cherrett 1994) keep the garden free of bacterial and fungal pathogens and parasites. The workers transplant mycelia to other parts of the garden substrate and stimulate the fungal garden to grow very quickly.

Acromyrmex and *Atta* have highly polymorphic workers and this high level of polymorphism correlates with the complex division of labor that exists within their colonies (Wetterer 1994). In some *Atta* workers, for example, the head width varies eight-fold and the dry weight varies 200-fold. Small workers are required as gardeners of the fungus, large workers are capable of cutting vegetation, and workers of all sizes are capable of brood care (Wilson 1980). Only small workers can take care of the delicate fungal hyphae within the garden, whereas the largest workers with their powerful mandibles designed to cut tough leaves are excellent defenders of the colony. The largest workers are usually recognized as a soldier subcaste or a full caste if really distinct from workers, with a disproportionately large head capsule. It is thought that the queen produces the maximum number of individuals who together can perform all the essential colony tasks. As the colony grows, the range of size dimorphism becomes even more extreme and worker production becomes skewed towards large individuals. **Age polyethism** is also widespread in leafcutter ants: young workers tend to perform tasks inside the nest and older workers tend to labor outside the nest. In a few years, the colony can become a physical monstrosity. The central mound of the underground nest can grow to more than 30 meters wide with smaller, radiating mounds extending out to a radius of 80 meters. The whole underground nest can take up 30 to 600 square meters.

3.3.3 Termites

The most widespread, non-hymenopteran eusocial insects are the termites (Higashi *et al.* 2000). Termites are sometimes called "white ants" because their workers are pale and their social organization is very similar to ants (Thorne 2003). Termites, however, are not closely related to ants at all, but are instead close relatives of cockroaches (Thorne and Carpenter 1992). All termites live in permanent social colonies that range in size from a few dozen individuals to massive, architecturally complex mounds containing millions of termites (Krishna and Weesner 1970). Termite colonies typically contain four castes: primary reproductives (the kings and queens), supplementary reproductives, soldiers and workers. Primary reproductives are originally winged, but shed their wings after a short dispersal or nuptial flight. Colonies typically have a single queen and a few reproductive males. Supplementary reproductives become reproductively active if anything happens to the king or queen. Soldiers are sterile males and females with heavily sclerotized and modified heads. Soldiers are often armed with large jaws or the ability to eject sticky secretions from their heads. For example, soldiers of species in the subfamily Nasutitermitinae have frontal glands in their heads that produce sticky and noxious chemicals. The chemicals are sprayed from a pointed nozzle, or rostrum, at the front of the head. The spray is a viscous entangling agent and irritant, capable of quickly hindering the mobility of ants and other predaceous arthropods. Worker termites of the species *Globitermes sulphureus* take defense to even further extremes. They act as soldiers and have a suicidal self-defense mechanism where they self-destruct by bursting their abdomens and covering their enemies, typically ants, with a sticky secretion (Bordereau *et al.* 1997). Worker termites can be male or female, resemble nymphs, and usually outnumber soldiers 50:1. Much like social hymenopterans, termite workers are responsible for nest construction and maintenance, foraging and brood care. All termites use symbiotic bacteria, protozoa or fungi to digest cellulose. Many of these symbionts are passed throughout the colony by trophallaxis (more detail is provided in Chapter 6).

3.3.4 Thrips, aphids and beetles

Three other, non-hymenopteran insect orders contain species that have recently been described as eusocial. There are at least six species of eusocial thrips (Thysanoptera) that induce galls on Acacia in Australia (Crespi 1992, Crespi *et al.* 1998). Galls are produced in the spring by single, inseminated, winged (macropterous) females. Galling sites on the modified petioles of these plants seem to be in great demand; from gall initiation until gall closure foundresses use their armed forelegs to fight each other over gall ownership. After a foundress is enclosed in the gall, she feeds on gall tissue and oviposits on the inner gall surface. Newly eclosed offspring feed and develop inside the gall. Adult offspring (both males and females) of the foundress are of two discrete types or castes: winged (macropterous) individuals and "normal" forelegs and micropterous (flightless) individuals with much larger forelegs. The micropterous individuals act as soldiers and use their enlarged forelegs to attack kleptoparasitic thrips that try to invade the gall, as well as intruders such as ants. The soldiers are effective defenders and can significantly reduce attacks on the foundress. Female soldiers have significantly smaller oocytes than foundresses and broods are often highly female biased. In the most derived thrips species of this group, the soldiers are almost functionally sterile (Chapman *et al.* 2002) and the macropterous females can function as dispersing reproductives and are analogous to gynes (facultative reproductives) in the eusocial Hymenoptera.

Gall-inducing aphids in two small subfamilies (the Pemphiginae and Hormaphidinae) share a great deal of biology with the eusocial thrips (Aoki 2003, Pike and Foster 2008). These aphids induce galls on their host plants. All members of the gall initially descend from a single foundress, and are therefore clone-mates, but later colonies become chimeric – of mixed genetic origin – with intruders from other colonies. In addition to normal first instar nymphs, there are specially adapted first instar morphs called soldiers

(Foster 1990). These soldiers cluster around the gall's entrance and actively attack predators, piercing them with their stylets and thickened forelegs (Figure 3.5), often losing their lives defending the gall and protecting their relatives (Foster 1990). During the summer there are about 300 aphids per gall in many species, of which approximately 50% are soldiers. The aphids in the gall feed on phloem and defecate honeydew. In some species, the soldiers actively clean the galls, which increases colony growth (Benton and Foster 1992).

A eusocial beetle has recently been discovered (Kent and Simpson 1992). The Ambrosia beetle *Austroplatypus incompertus* lives in galleries in the heartwood of living *Eucalyptus* trees in Australia. Solitary fertilized females initiate gallery systems in the autumn. It takes about seven months for the female to tunnel the 50–80 mm from the bark through the sapwood into the heartwood. Fungal propagules are distributed from mycangia on the pronotum of the female and symbiotic fungi (*Ambrosiella* sp.) establish in the heartwood and sporulate on the tunnel walls. In the following year, the female lays eggs at one end of the gallery. The larvae, like the adults, eat the fungus and take two to three years to develop from egg to adult. After four years there is a marked change in the social order of established colonies. Around that time galleries start to contain unfertilized adult females that extend and maintain the galleries, remove frass and protect against predators. Females residing in the gallery either lose or remove the last four tarsal segments, making it impossible for them to leave the colony. Colonies are extremely long-lived and some are known to persist for up to 37 years.

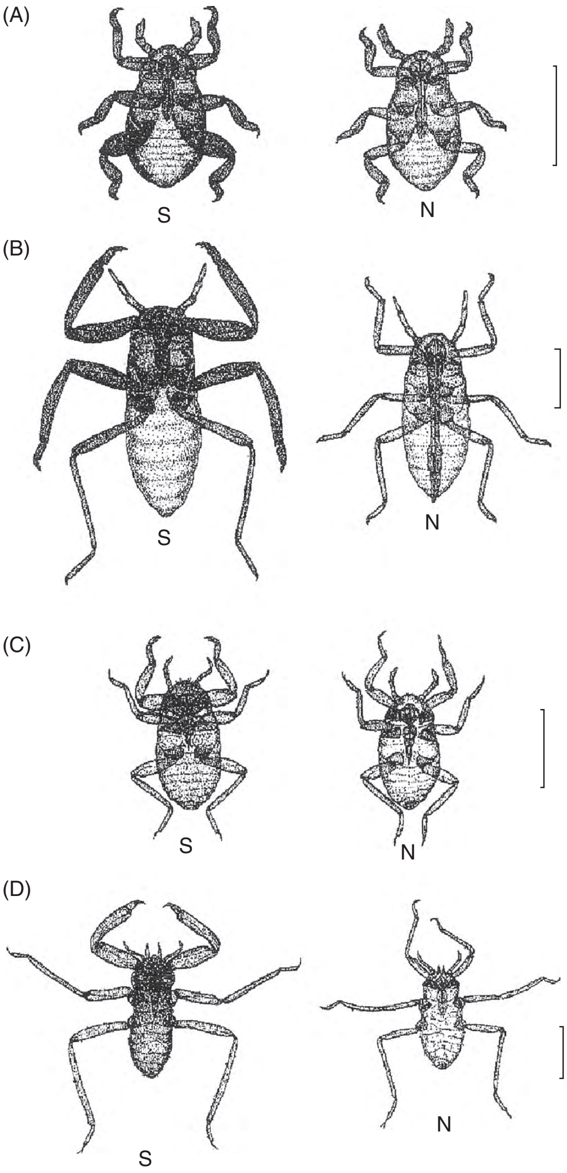


Figure 3.5 Examples of soldier aphids (left) and normal siblings (right) belonging to the species *Pemphigus spirothecae, Colophina monstrifica* and *Pseudoregma bambucicola*. In *Pemphigus spirothecae* (a) a first instar soldier (S) has enlarged legs and a thickened cuticle compared to a normal nymph (N). The soldier of *Colophina monstrifica* (b) is much larger than a normal nymph, and has relatively longer legs, a shorter rostrum, and more sclerotization. In *Pseudoregma bambucicola* the soldiers have

Caption for Figure 3.5 (*cont.*)
enlarged front legs and heavy sclerotization. The soldier in (d) also has longer legs and frontal horns used in impaling intruders. The life cycle of the aphid includes two host plant species. The primary-host soldier (c) is a second instar nymph. The secondary-host soldier (d) is a first instar nymph. The scales are 0.5 mm. From Stern and Foster 1996.

3.4 Evolution of sociality: Darwin's dilemma

Evolutionary biologists have long recognized that altruistic behavior in general, and the presence of sterile workers in particular, is difficult to explain within the concept of individual selection (Sturtevant 1938, Andersson 1984). Darwin was well aware of this problem and noted that sterile workers in eusocial insects posed "one special difficulty, which at first appeared to me insuperable and actually fatal to my whole theory." (Darwin 1859, p. 236). Darwin noted that if the combined offspring of the queen formed a colony that would allow her to produce more offspring than an otherwise comparable, solitary female, sterile castes would evolve as part of the variation of a single hereditary type. That hereditary type, in this case the colony, not the variable forms it produces, would be the unit of selection (Wilson 2005). Thus, Darwin proposed that workers evolve through selection at the level of the colony instead of through selection on individual fitness.

3.4.1 The haplodiploidy hypothesis

Early evolutionary biologists, however, quickly suggested that selection at the colony level could not fully explain why individuals would give up the possibility of passing their genes to offspring (Andersson 1984, Sober and Wilson 1998). Haldane (1932, 1955) began to formulate a solution to this problem when he observed that altruistic behavior could be favored by selection if altruism increased the success of genetically related individuals and he proposed that this is likely to be the case in small populations that typically contain many close relatives. Hamilton expanded this idea into a general theory (Hamilton 1964a). The core concept of this theory was expressed in what has come to be called **Hamilton's rule**: $rb > c$, where b is the benefit to the recipient of the altruistic act, c is the cost to the bearer and r is the degree of relatedness between them. This simple inequality has been incredibly influential, partly because it is so easy to understand. Hamilton's rule demonstrated that natural selection might work to increase **inclusive fitness**, the sum of fitness gained through producing offspring (direct fitness) and through affecting the fitness of individuals that share genes with the altruist (indirect fitness) (Maynard Smith 1964, Herbers 2009). Hamilton immediately applied this idea to the evolution of eusociality within the Hymenoptera (Hamilton 1964b). Hymenoptera are haplodiploid and females develop from fertilized eggs and males from unfertilized eggs. This can create strange patterns of relatedness within families. For example, a male derives all his genes from his mother and thus $r_{\text{son–mother}} = 1$, but the mother gives half her genes to her son and thus $r_{\text{mother–son}} = 0.5$. Most importantly, sisters share three quarters of their genes with each other ($r_{\text{sister-sister}} = 0.75$), but only half with their potential offspring ($r_{\text{mother–offspring}} = 0.5$). Thus for haplodiploid species, helping to raise sisters instead of offspring is a good strategy for getting copies of genes into the next generation (Figure 3.6). This concept provided an excellent framework for studying the context of cooperation and conflict and seemed like an obvious answer to the eusociality conundrum (Herbers 2009). Hamilton's application of **kin selection** to eusociality within the Hymenoptera is often called the **haplodiploidy hypothesis**.

Although a few researchers warned against an overemphasis on relatedness and pointed to other factors that could play an important role in the evolution of eusociality, such cautions were basically ignored and this idea quickly dominated the field (Andersson 1984). For example, Wilson (1971) stated that "the key to Hymenopteran success is haplodiploidy" and that "nothing but kin selection seems to explain the statistical dominance of eusociality by the Hymenoptera". The evidence seemed overwhelming: 10 out of 11 independent origins of eusociality that were known in the 1960s occurred in the Hymenoptera. Some findings, however, slowly began to raise doubts about the

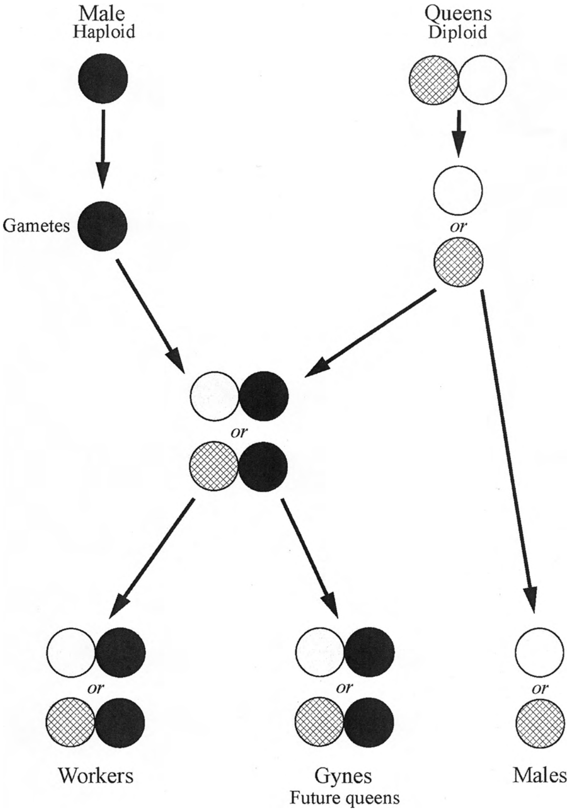


Figure 3.6 The degrees of relatedness within a colony of haplodiploid insects such as ants, bees and wasps, if the king and queen are monogamous. Sisters, on average, share 75% of their genes because each sister gets identical genes from their haploid father. This means that sisters can produce more copies of their genes if they help rear sisters instead of their own offspring. In diploid species, sisters, on average, share 50% of their genes because they have a 50% chance of getting the same genes from their father and mother. Based on Trivers and Hare 1976 and Hamilton 1964b.

overwhelming focus on the importance of haplodiploidy (Andersson 1984). Notably, although all Hymenoptera are haplodiploid, only a very small percentage of hymenopteran species are eusocial. Moreover, most mites and ticks, many thrips, whiteflies, scale insects, some beetles, most rotifers and some nematodes are haplodiploid, yet eusociality is either completely unknown or incredibly rare within these taxa.

3.4.2 More general views

Termite biology provides a particularly strong challenge to the focus on relatedness (Thorne 1997). Termites originated from cockroach-like ancestors and evolved eusociality about 100 million years ago. All termites are diploid and have sterile castes of both sexes. Hence, the asymmetric degree of relatedness inherent between hymenopteran brothers and sisters, and between their sisters and their offspring, is not generated in termites. A number of hypotheses have been proposed to explain the evolution of termite social biology. For example, termites depend on symbiotic intestinal protozoa for digestion of cellulose, and Cleveland *et al.* (1934) suggested this symbiotic relationship predisposes termites to social life. The protozoa are lost at each molt, so developing termites must obtain new protozoa through transfer from other colony members. Hence, the symbiosis with protozoa necessitates social life until adulthood. It has been noted, however, that passing of symbionts does not require advanced sociality; extended parent–offspring contact generated by a simple social system allows for transfer of symbionts in cryptocercid wood roaches, the closest extant relatives of termites (Thorne 1997). Hamilton (1972) proposed that inbreeding could lead to high degrees of relatedness within colonies and facilitate the evolution of eusociality. The problem with this idea is that inbreeding will, over time, also increase the relatedness of parents to offspring and not just among siblings, thus providing little or no selection for the worker caste to forego reproduction.

Thorne (1997) carefully examined the many termite hypotheses and concluded that it is unlikely that eusociality in termites arose as a result of evolutionary forces acting on any one dynamic or on any single life-history component. Instead, she proposes that a suite of ecological and life-history traits of termites and their ancestors predisposed

Table 3.2 **Some ecological and life history characteristics of eusociality. Modified from Thorne 1997**

Nesting habitat
Claustral family associations (e.g., enclosed in a cavity)
Safe, initially small, and persistent habitats, with opportunities for expansion and multigenerational occupation. Nesting in enclosed spaces keeps relatives close and fosters kin selection, and foraging by immatures for each other and the reproductives
Parental care: subsociality
Family groups
Development time: life cycle
Slow development and long generation times with overlap of generations
Long life span, particularly in reproductives
Gradual metamorphosis so helping in the next generation can begin as immatures soon after egg hatch (in termites)
Genetics
Haplodiploidy
Females are more related to sisters than their progeny, so helping the queen to raise sisters increases fitness (in Hymenoptera)
Mating system: single father – monogamy
In haplodiploid groups female progeny share three-quarters of their genes, with likely selection for helping a mother to raise other female progeny (see Figure 3.6)
In diploid species monogamy results in half of an individual's genes being shared with siblings and with progeny, so helping to raise siblings is as genetically profitable as producing progeny
Reproductive cycle: iteroparity
Repeated bouts of reproduction enable offspring to care for new siblings
High risk and/or time investment in dispersal and founding of new nests
Remaining in the parental nest as a helper is likely to be safer than dispersal and establishment of a new nest
Opportunities for replacing reproductives
A mature offspring may take over nest as the reproductive caste, or act as a supplementary reproductive. In either case the individual inherits nest resources
Defense
Group defense of rich resources in the nest essential
Group defense against competitors important
Specialized defense is effective, employing workers and soldiers (use of stings, venoms, biting, etc.)

them for eusocial evolution. These characteristics include familial associations in cloistered food-abundant habitats, slow development, overlap of generations, monogamy, iteroparity, high-risk dispersal for individuals, opportunities for nest inheritance by offspring remaining in their natal nest and advantages of group defense (Table 3.2). In this table Thorne divides factors into ecological, behavioral and life-history categories: nesting habitat, parental care, development, genetics, mating system, reproductive cycle, dispersal and founding nests, inheritance and defense. Each of these factors are explained briefly in the table. However, in real life several factors would combine to promote the evolution of eusociality (Thorne 1997). For instance, primitive termites live under bark where food is plentiful but of low nutritional quality. The nest site is well protected, so a founding queen can remain at this site for a long time while laying eggs, and family groups interact intimately. With hemimetabolous development, the nymphs can act as workers to aid the queen. The life cycle is prolonged because of low food value, and possibly because of the protected nest site, resulting in a likely overlap of generations and cooperation among generations. Monogamy results in a 50% genetic relationship among siblings and a 50% relationship with progeny, so breeding itself or helping siblings are genetically and fitness neutral, but with a significant advantage to staying in the nest and avoiding the dangers of the outside world.

3.4.3 Sequential trait accumulation

This multifaceted array of factors provides a logical start to figuring out how so many traits could be selected for, and in what order they were assembled into the life history and behavior of a social insect species. An intriguing approach was adopted by Hunt (1999, 2007) who argued that tracing essential characteristics of a social group back to their phylogenetic origins will recapture the stepwise aggregation of salient traits. Tracking the evolution of the social wasps (Hymenoptera: Vespidae) the accumulation of traits necessarily started with the most primitive groups in the order (Figure 3.7).

Hunt mapped salient traits on the phylogeny of the Hymenoptera. An abbreviated treatment is provided here.

Trait 1 included at the base of the Symphyta (sawflies, woodwasps, etc.) the possession of mandibles, a lepismatid-type ovipositor (first seen in the primitive silverfish (Thysanura: Lepismatidae)), membranous wings, and the presence of haplodiploidy. Mandibles became important in social wasps in nest building and provisioning the nest. The ovipositor evolved into the sting of wasps critical in the defense of the colony. Membranous wings enabled strong flight for foraging and the carrying of heavy insects as food for larvae. Haplodiploidy resulted in closely related sisters as workers.

At Branch 2, carnivorous larvae evolve from their herbivorous ancestors.

At Branch 3, larvae become legless in the parasitoid wasps and the larval hindgut becomes closed, meaning ultimately that they do not foul the nest. A basal trait of the Apocrita is the petiolate abdomen in which the thread waist of the adult limits nutrition to liquids, although masticated insects can be fed to larvae in the nest.

At Branch 4 the oviduct becomes separate from the ovipositor, such that the ovipositor can evolve into a sting and associated glands become modified to produce venom and pheromones. The sting and venom enable anesthetization of prey and their storage in a nest.

At the origin of the Vespidae, at Branch 5, nest construction and rearing of larvae in the nest evolve, with provisioning by the queen and workers. Additional steps are described by Hunt to conclude the list of the most important traits in the social wasps.

This approach shows how traits originating with the primitive herbivorous insects, parasitoids and predatory solitary wasps all contribute to the evolution of eusociality of the Vespidae. In this lineage behavioral, genetic and ecological traits blend into the evolutionary scenario. They show how many aspects of biology need recognition as contributing to the emergence of a social insect group.

3.4.4 The continuing debate

A growing number of biologists are beginning to rethink the focus on haplodiploidy and relatedness in the evolution of eusociality, and this has ignited a vigorous, ongoing debate (Wilson and Hölldobler 2005a, Foster *et al.* 2006, West and Gardner 2010). The re-evaluation of the importance of haplodiploidy has largely been driven by new discoveries of eusocial animals. Many additional eusocial insects have been discovered, including eusocial aphids, thrips and beetles (see Section 3.3.4). Other

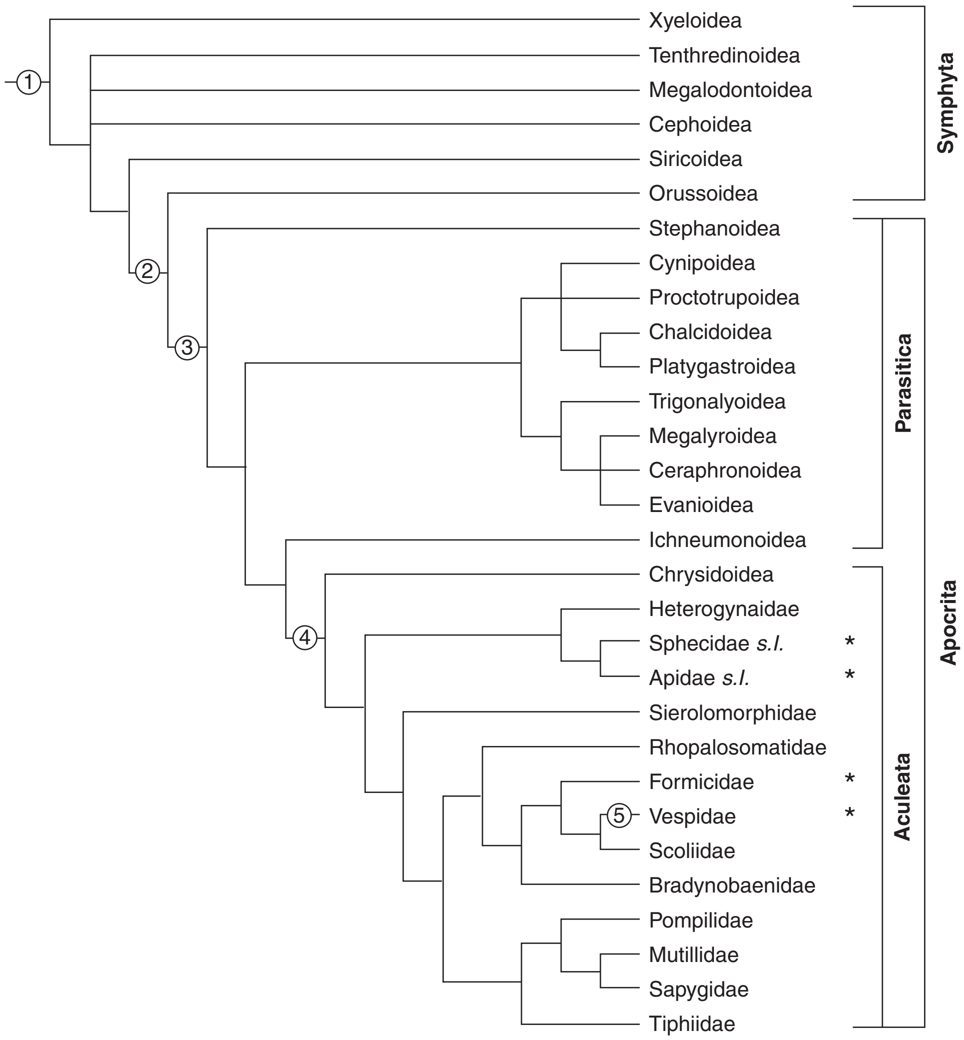


Figure 3.7 A cladogram of the major groups within the order Hymenoptera, with the primitive Symphyta at the top, which includes sawflies (Tenthredinoidea) and woodwasps (Siricoidea), and moving down to include the social wasps (Vespidae) and ants (Formicidae) and other groups containing eusocial species (marked with an asterisk). From Hunt 1999.

invertebrate eusocial species have also been identified, including eusocial sponge-dwelling shrimp (Duffy 1996) and a eusocial tangle-foot spider (Vollrath 1986, Rypstra 1993). Perhaps most surprising, two species of mole-rats were found to be eusocial, the first discovery of eusocial mammals (Jarvis 1981, Jarvis and Bennett 1993). In several cases, these discoveries involve multiple species within the group and multiple independent evolutionary origins of eusociality (e.g., Jarvis and Bennett 1993, Duffy and Macdonald 2010). Because most of these groups are diploid, the association between haplodiploidy and eusociality is no longer statistically viable (Wilson 2005, Herbers 2009).

This does not mean, however, that high levels of relatedness are unimportant in the evolution of eusociality. Indeed, many authors still believe that close relatedness is crucial to the evolution of eusociality. For example, there has always been some dispute in the literature of whether close relatedness is a prerequisite for the evolution of eusociality or a consequence of eusociality. Hughes *et al.* (2008) tested the hypothesis that the evolution of monogamy, in this case breeding with a single male – **monandry**, evolved within eusocial bees, wasps and ants prior to the evolution of eusociality. The idea is that monogamy increases relatedness among offspring, thus increasing the potential for kin selection to act. They found that monogamy was the ancestral state for all eight independent origins of eusociality that they examined. Hughes and colleagues argue that their findings strongly support the hypothesis that high relatedness was important in the evolution of eusociality because monogamy and the evolution of eusociality are strongly linked. Likewise, Duffy and Macdonald (2010) found that eusociality only arose in sponge-dwelling shrimp species with non-dispersing larvae that form tight family groups, suggesting that close relatedness was strongly correlated with eusociality in this group.

There have also been renewed calls for a focus on the role of relevant costs and benefits in the evolution of eusociality, rather than relatedness (Thorne 1997, Herbers 2009). Andersson (1984) was an early critic of the focus on relatedness and suggested that studies evaluating the costs and benefits of brood care and defense of nests or protected cavities and the low success of young adults or solitary pairs that attempt to reproduce on their own would yield important results. Likewise, Queller and Strassmann (1998) have proposed that "fortress defense" (the fortress being a domicile that provides protection and food) and "life insurance" (brood care by non-parents when parents are killed or otherwise unable to rear offspring) are key benefits of eusociality. "Life insurance" will be particularly important for species where the brood have to be continuously provisioned during development (Queller 1994). These analyses, however, are still conducted within the framework of Hamilton's rule ($rb > c$). The idea is that if the benefits are relatively high and the costs are relatively low, then eusociality will be favored even if relatedness is not very high. There are substantial data to support this viewpoint. For example, the probability of foundresses successfully starting a new colony is incredibly low in ants, bees and termites (Hölldobler and Wilson 1990, 2009, Thorne 1997). Studies of facultatively eusocial bees have been particularly insightful. A. R. Smith *et al.* (2007) found that solitary nests of the sweat bee, *Megalopta genalis*, suffer significantly higher levels of failure than eusocial nests and produce significantly fewer broods.

There has also been a renewed focus on **group selection** as an explanation for the evolution of eusociality. Wilson, once a strong advocate for the importance of kin selection, has proposed a multilevel selection model that promotes group selection as the primary "binding force" that favors eusociality (Wilson 2005, Wilson and Hölldobler 2005a, Wilson and Wilson 2007). Group selection, the differential survival and reproduction of entire cooperative groups, was once a widespread explanation of adaptations, but its importance as a force of evolution has been controversial for over 40 years (e.g., Williams 1966). In Wilson's model, close relatedness is a consequence of eusociality, not a causative factor in the evolution of eusociality. Wilson's proposal has been strongly criticized as misinterpreting kin selection theory (Foster *et al.* 2006) and for largely being a semantic argument (Shavit and Millstein 2008). It will be interesting to see if Wilson's latest ideas can be developed into a set of testable hypotheses that will alter widely held views of the evolution of eusociality.

3.5 The ecological consequences of sociality

Social insects are often dominant species in the ecosystems in which they live. Ants, for example, have been one of the most diverse, abundant and ecologically dominant animal groups for over 50 million years (Hölldobler and Wilson 1990, Wilson and Hölldobler 2005b). They comprise 10 to 33% of the biomass of many ecosystems and can reach densities of eight million per hectare in tropical forests (Wilson 1990). It is estimated that their biomass in the Brazilian Amazon is four times greater than all of the terrestrial vertebrates combined (Fittkau and Klinge 1973). Their ecological success is a function of their sociality. Individual ants within the colony can specialize in particular tasks and groups of workers can quickly switch among tasks such as colony maintenance, to group foraging, to colony defense, etc., a major advantage over solitary insects. Ants are classified into a single family, the Formicidae, and comprise 16 subfamilies, 296 genera and over 10 000 species (Bolton 1994). They have a huge geographical range and live in an incredible array of habitats. Ants are among the leading predators of other insects and small invertebrates and are major herbivores and seed predators in many habitats. Omnivorous ants in Polish meadows, for example, can consume up to 3% of the primary production and 40% of the prey biomass available each season (Folgarait 1998). An average-size colony of *Formica polyctena* can consume 6×10^6 insects and 155 liters of honeydew from just a quarter hectare area during one growing season (Horstman 1974). Leafcutter ants can remove 17% of the annual leaf production of a tropical forest (Cherrett 1989), and one *Atta* nest can consume one to two tons of fresh leaf material per year (Folgarait 1998). Ants are also major **ecosystem engineers** (Folgarait 1998, MacMahon *et al.* 2000). For example, they can move tremendous quantities of subterranean soil to the surface. The activities of desert ants may lead to soil turnover rates as high as 420 kg per hectare per year in Australia (Briese 1982) and 842 kg per hectare per year in the USA (Whitford *et al.* 1986). *Camponotus punctulatus* ants move up to 2100 kg of soil per hectare while constructing their mounds in Argentine pastures (Folgarait 1998). Indeed, ants are considered second only to earthworms as biotic sources of soil turbation, but ants have a broader geographical range and are thus more important in many areas of the world (Paton *et al.* 1995, Folgarait 1998). In the tropics, for example, leafcutter ants are the most important agents of soil modification (Alvarado *et al.* 1981) and just one colony of *Atta sexdens* in Brazil deposited over 40 tons of soil in one year (Folgarait 1998). Ant activity can also strongly affect nutrient and energy fluxes within soil. Nests of *Atta colombica* in Panama increase fluxes of 13 chemical elements 38-fold in comparison to surrounding areas of forest, probably due to the greater root activity close to the ant nests (Haines 1978). In Puerto Rico, leafcutter ants have been shown to increase net plant productivity by 1.80 kcal per m^2, probably because ant activity increases the availability of phosphorous in the soil (Lugo *et al.* 1973). Ants can also have dramatic effects on the composition of plant communities via soil and seed dispersal (Horvitz and Schemske 1986, Wilson 1992, MacMahon *et al.* 2000). A ten-year experiment in the Chihuahuan desert of southeastern Arizona found that harvester ant removal resulted in a plant community dominated by small-seeded plant species (Samson *et al.* 1992). This change in the plant community reflected the harvester ants' preference for large seeds.

As noted in Chapter 6 and in Section 3.3.2, many ants form facultative or obligate mutualisms with an incredible range of organisms including fungi, plants and other insects. In many systems, these mutualisms can strongly influence the ecological effects of ants. Many ants, for example, form food-for-protection mutualisms with aphids, scales and other "honeydew"-producing insects (Way 1963, Buckley 1987). In these mutualisms, ants provide protection against arthropod predators and other natural enemies in exchange for carbohydrate-rich excretions from the herbivorous insects. Not surprisingly, these mutualisms often result in dramatic reductions in the number of predators on plants that host honeydew-producing herbivores.

Kaplan and Eubanks (2005), for example, found that cotton-aphid–fire-ant mutualisms dramatically increased the number of foraging fire-ant workers on cotton plants and that fire-ant workers killed over 75% of the predators on aphid-infested plants. It turns out that ant workers that "tend" honeydew-producing insects often kill herbivorous insects as well as predators. Messina (1981), for example, found that *Formica* ants that tend sap-feeding treehoppers on goldenrod plants (*Solidago*) not only protect the treehoppers from predators, but also kill leaf beetles that are major defoliators of the plant. Likewise, fire ants that tend cotton aphids also kill caterpillars and true bugs that feed on cotton plants (Kaplan and Eubanks 2005). These ant–hemipteran mutualisms ultimately result in broad changes in the arthropod community associated with the hemipterans' host plant (Wimp *et al.* 2005). As such, these mutualisms can be considered **keystone interactions** that change the abundance and distribution of many other arthropods, the effects of which cascade down the food web to affect primary production (Eubanks and Styrsky 2006, Chapter 13). In many cases, these changes can actually increase plant fitness. In both examples detailed above (goldenrod and cotton), the defoliators that were killed by hemipteran-tending ants (leaf beetles and caterpillars) were more important herbivores of the plants than the treehoppers and aphids. The mutualisms, therefore, led to increased suppression of these more damaging herbivores and corresponding increases in plant fitness (Messina 1981, Styrsky and Eubanks 2010). A recent review has shown that many ant–hemipteran mutualisms indirectly increase plant fitness in this manner (Styrsky and Eubanks 2007).

Mutualisms involving ants can even shape the ecology of the world's largest terrestrial herbivores. For example, Madden and Young (1992) studied the ecological consequences of the mutualism between the swollen thorn acacia *Acacia drepanolobium* on the plains of Kenya and an ant in the genus *Crematogaster* that nests on these trees. The trees provide the ants with a protected chamber, the swollen thorn, for nesting and nutrient-rich extrafloral nectar for food (see Chapter 6 for a detailed description of the ecology of **myrmecophiles**). In turn, the ants provide protection against herbivory. Madden and Young found that *Crematogaster* ants were highly effective at defending *A. drepanolobium* trees from foraging giraffe calves. They found a very strong, negative relationship between giraffe browsing of acacia trees and the density of swarming ants on the trees.

Although termites have far stricter feeding habits than ants and occupy fewer niches in ecosystems,

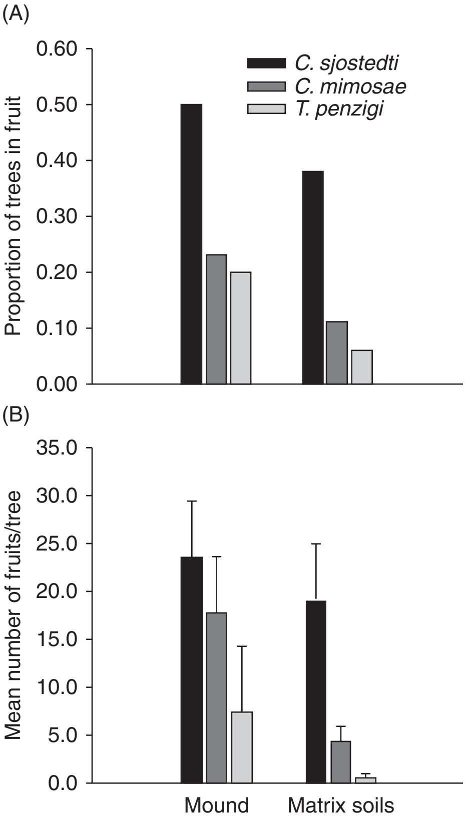


Figure 3.8 *Acacia drepanolobium* trees had a higher probability of fruiting (A) and set more fruit (B) when they were adjacent to termite mounds in Kenya. Different colored bars represent trees inhabited by different ant species (*Crematogaster sjostedti, C. mimosae, and Tetraponera penzigi*, respectively). From Brody *et al.* 2010.

termites have profound ecological effects. They consume up to one-third of the annual production of dead wood, leaves and grass in many habitats and their densities can surpass 8000 per m^2 (Martius 1994, Pearce 1997). Termites can act as ecosystem engineers that influence the physical characteristic of soils and associated habitats and strongly influence biogeochemical cycling (Jones 1990, Decaens *et al.* 2001). A fascinating example of the ecological role of termites occurs in the Kenyan savannas inhabited by *A. drepanolobium* trees. Using observational data, large-scale experimental manipulations and analysis of foliar N, Brody *et al.* (2010) found that *A. drepanolobium* trees growing at the edge of termite mounds were more likely to reproduce than those growing farther away, in off-mound soils (Figure 3.8). Although vertebrate herbivores preferentially used termite mounds, long-term exclusion of mammalian grazers did not significantly reduce *A. drepanolobium* fruit production. Leaf N was significantly greater in trees growing next to mounds than in those growing farther away. Thus, soil enrichment by termites was of primary importance to fruit production near mounds. Pringle *et al.* (2010) found that these termite mounds were not only hotspots of plant growth (primary production), but also local hotspots of animal abundance. Insect abundance and biomass decreased with distance from the nearest termite mound, as did the abundance, biomass and reproductive output of insect-eating predators (Figure 3.9). They also found that the evenly spaced distribution of termite mounds produced dramatically greater abundance, biomass and reproductive output of consumers across all trophic levels than would be obtained in landscapes with randomly distributed mounds. Thus, termites are critically important ecosystem engineers in this system whose distribution plays a fundamental role in **ecosystem function**.

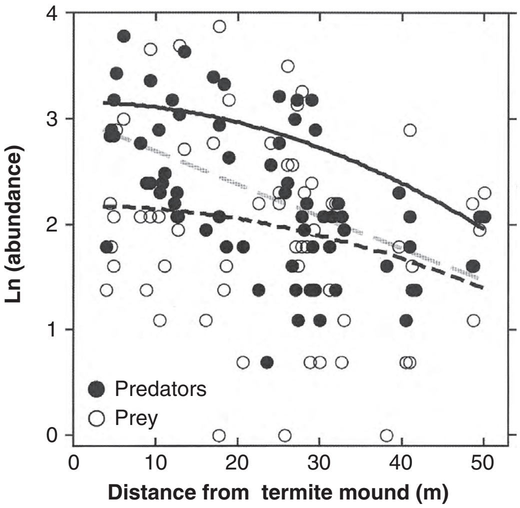


Figure 3.9 The abundance of arthropod predators and prey declined as a function of distance from termite mounds in Kenya. From Pringle *et al.* 2010.

Applications

Social insects as saviors and pests

Honey produced by honey bees was the only sweetener available to humans for centuries, and honey is still a widely used product with an annual value of US$1.25 billion (vanEngelsdorp and Meixner 2010). As detailed in Chapter 6, however, bees and other social insects are incredibly important pollinators of crops and wild plants. By far the most important contribution honey bees make to modern society is the pollination services that they provide. Of the 115 leading global food commodities, 52 depend on honey-bee pollination for either fruit or seed set (Klein *et al.* 2007). Five additional commodities would have 90% yield reductions without honey bees and yield of 16 other commodities would be reduced by 40–90% without honey bees. Smaller reductions would occur in at least 19 additional commodities. In total, 14–23% of all agricultural production is directly reliant on insect pollination and 35% of the human diet is thought to benefit from insect pollination, with honey bees being particularly important (Klein *et al.* 2007, vanEngelsdorp and Meixner 2010). The global value of insect pollination was recently estimated at US$ 212 billion; that represents almost 10% of the total value of agricultural production (vanEngelsdorp and Meixner 2010).

Honey bees and the pollination services they provide have been of great recent interest due to **colony collapse disorder**. Colony collapse disorder is characterized by the rapid loss of adult worker bees from affected colonies as evidenced by weak or dead colonies with excess brood relative to adult bees, noticeable lack of dead workers, and food stores that are not robbed by hive pests or kleptoparasitic bees (vanEngelsdorp *et al.* 2009). In the fall of 2006, US beekeepers reported losses of 30–90% with symptoms consistent with colony collapse disorder. This was followed by two more winters with significant colony losses associated with colony collapse disorder (vanEngelsdorp *et al.* 2007, 2008). Many hypotheses have been proposed and at least partially tested to explain the colony losses, including honey bee parasites (e.g., varroa mites and honey bee tracheal mites), pathogens (e.g., bee viruses and *Nosema* microsporidia), pesticide residues (especially neonicotinoid insecticides) and inbreeding (vanEngelsdorp *et al.* 2009, Ratnieks and Carreck 2010). The latest research on colony collapse disorder suggests that an interaction of factors likely explains colony death, although pathogens, particularly viruses and *Nosema*, appear to be critically important (Cox-Foster *et al.* 2007, Johnson *et al.* 2009, Ratnieks and Carreck 2010).

Many social insects are also economically important predators of crop pests (Way and Khoo 1992). In fact, the manipulation of the weaver ant *Oecophylla smaragdina* to control citrus pests is the oldest known example of biological control and was first documented in 304 AD (Huang and Yang 1987). Weaver ants get their name from their habit of binding leaves and twigs together with silk to form tight nests. The ants spend the night in the nests, but forage outside the nest for their insect prey during the day. These nests have been sold to farmers in Chinese markets for almost 2000 years (Huang and Yang 1987). To take advantage of these ants, a farmer secures a nest on one tree and then connects it to adjacent trees with bamboo strips. These bridges enable the weaver ants to travel among and build nests on neighboring trees. Eventually the whole orchard can be colonized by *O. smaragdina*. These ants were critically important **biological control agents** of citrus and other fruit pests in ancient China and are still extremely valuable in pest management today. For example, weaver ants currently provide economically important biological control in citrus in China and Vietnam, cashew and mango in Australia, and coconut and cocoa in the Solomon Islands and Africa (van Mele 2008). Many other ants are also important predators of crop pests. For example, twig-nesting ants are highly effective at reducing the abundance of leaf miners (De la Mora *et al.* 2008) and coffee berry borers (Larsen and Philpott 2010) in coffee. Recent studies have also documented the importance of ants as important predators of pests in cotton (Styrsky and Eubanks 2010), apple (Mathews *et al.* 2004), collards (Harvey and Eubanks 2004), pecan (Ellington *et al.* 2003) and rice (Way *et al.* 2002), and this is just a small list of the crops where ants play a fundamental role in pest suppression.

Social insects, however, are definitely double-edged swords when it comes to impacts on human society. Invasive ants, even some of the same ant species that are important predators of pests, can be brutally important invasive species. Many ant species, for example, are invasive species that have devastating ecological effects (Holway *et al.* 2002). The red imported fire ant, *Solenopsis invicta*, is a well-known example of an invasive ant in North America (Vinson 1997, Tschinkel 2006). Red imported fire ants were accidentally introduced from Argentina into Alabama approximately 75 years ago, probably in soil ballast discharged from cargo ships arriving from Brazil (Vinson 1997). They have since spread rapidly throughout the Gulf Coast states, east to the coastal areas of South Carolina, North Carolina and Virginia, and west to California, where they continue to expand their range northward (Vinson 1997, Korzukhin *et al.* 2001). Red imported fire ants have also recently been introduced in Taiwan, China and Australia (Morrison *et al.* 2004, Chen *et al.* 2006, Zhang *et al.* 2007). Because they are broadly omnivorous, extremely aggressive and often superabundant as a result of tremendous reproductive potential, red imported fire ants negatively impact invertebrate and vertebrate communities in both natural and managed ecosystems (Vinson 1994, 1997, Wojcik *et al.* 2001, Holway *et al.* 2002). It is thought that escape from coevolved competitors, pathogens and parasites, especially parasitic phorid flies, is responsible for their large populations and rapid range expansion in North America (Porter *et al.* 1992, 1997, Orr *et al.* 1995). It is also believed that the evolution of polygyny, multiple queens per colony, after introduction and its associated reduction in intraspecific territoriality contribute to the high densities and rapid spread of red imported fire ants (Ross and Keller 1995, Ross *et al.* 1996). The evolution of reduced intraspecific competition appears to be an important mechanism contributing to several ant invasions. Argentine ants, *Linepithema humile*, for example, have evolved reduced intraspecific aggression in North America and are far less territorial than Argentine ants in their native range (Holway *et al.* 2002). The corresponding decrease in intraspecific competition leads to faster colony growth, higher Argentine ant densities and faster spread of Argentine ants.

Termites are notorious pests of buildings (Su and Scheffran 2000). Approximately 200 of the 2300 termite species in the world are known to damage buildings and 83 species cause significant economic losses. The global economic impact of termites is unknown, but annual control costs in the United States are over $1.5 billion. Insecticide barriers are typically used to control soil-borne subterranean termites and slow-acting baits for subterranean termites in and near structures. Whole-structure treatments such as fumigation or heat and local treatments such as insecticide injection are the primary control methods for drywood termites. The Formosan subterranean termite, *Coptotermes formosanus*, is a particulary damaging termite pest (Lax and Osbrink 2003). This termite was most likely introduced into the USA when thousands of tons of wooden military cargo such as crates, pallets and dunnage were shipped from the Asian theater to the USA following World War II. New Orleans, Louisiana, was one of the most active ports of entry for these shipments and now hosts one of the densest populations of Formosan termites in the world. This termite lives in large colonies that may contain over a million workers that can cause rapid and significant damage to wooden structures, living plants such as oak trees and even non-cellulosic material such as insulation on buried electrical and telephone cables. The Formosan termite causes over US$300 million annually in damage and control costs in New Orleans, and these voracious termites are spreading within the USA (Woodson *et al.* 2001).

Summary

Social insects are fascinating animals that vary in complexity from small groups comprised of individuals of the same age, to species with intricate parental care, to species of superorganisms that have queens, kings and polymorphic non-reproducing workers. Social behavior is widely distributed among insect taxa, although the evolution of a non-reproducing worker caste has been limited to a few orders (Isoptera, Thysanoptera, Hemiptera, Coleoptera, Hymenoptera). The evolution of non-reproductive workers was a long-standing conundrum in evolutionary biology. Hamilton’s kin selection theory provided a simple and elegant explanation of the evolution of non-reproducing castes. Despite recent challenges, kin selection, especially when the costs and benefits of eusociality are fully considered, is still the best explanation of the evolution of eusociality. Social insects are often dominant species in the ecosystems in which they live due to their high population density and polymorphic workers. They are major predators of arthropods, very important seed predators and dispersers, and ecosystem engineers that play important roles in soil dynamics and pollination. Social insects form facultative or obligate mutualisms with an incredible range of organisms including fungi, plants and other insects, and these mutualisms are often keystone interactions that dictate the abundance and distribution of other species within the community. Social insects also have strong effects on humans. At least 10% of the total value of global agricultural production relies on social insect pollination of crops and social insects like ants are vitally important predators of insect pests. Social insects are also important pests. Invasive ants, wasps and termites, for example, are often urban pests of buildings and landscapes and have had terrible impacts on wildlife such as ground nesting birds, reptiles and amphibians. Termites are often devastating pests of houses and other structures. In total, social insects cause billions of dollars in damage and control costs every year and are typically considered some of the most damaging pests in the world.

Questions and discussion topics

1 Wilson proposed the use of the term "superorganism" to describe eusocial insects. Do you think this is an appropriate term? In what ways is this term an accurate description of eusocial insects? In what ways is this an inaccurate description?

2 The evolution of fungus gardening has been referred to as the evolution of agriculture in insects. In what ways is the evolution of this ant–fungus mutualism analogous to the evolution of agriculture in human society? How does it differ?

3 What is the relative importance of relatedness in the evolution and maintenance of eusociality among different insect taxa?

4 Some biologists have suggested that the order Hymenoptera is the most beneficial group of insects to humans. How does the social biology of this group influence their importance to human society?

5 As noted in the chapter, social insects can also be pests. How does the biology of social insects influence their status as pests? Does sociality alter the ability of humans to suppress the abundance of social insects or mitigate their impact on society?

Further reading

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Part III **Species interactions**

CONTENTS

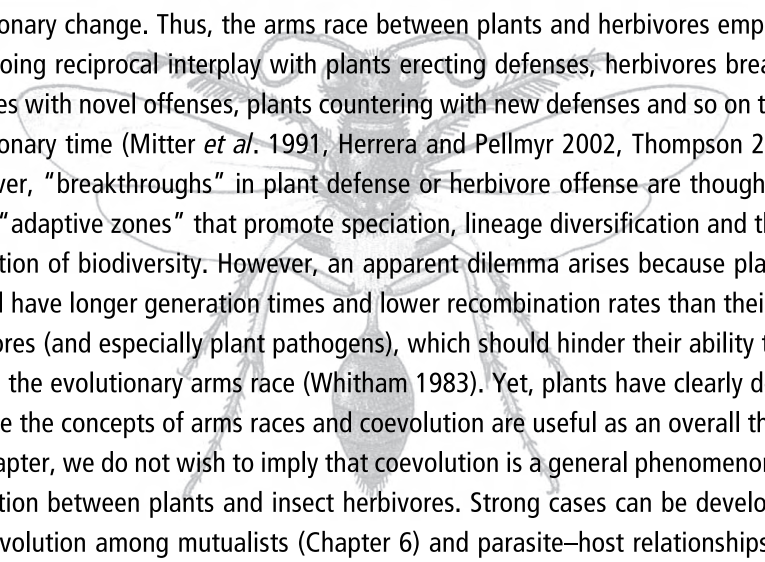
We build from Part II on behavioral ecology, which is devoted to interactions among individuals and within social groups, to interactions between species and trophic levels. Gradually we move up the trophic system, starting with plant and herbivore associations, and then to interactions among herbivores involving competition, strong asymmetric interactions and facilitative interactions. After this, in the next three chapters (6–8), we return to interactions between trophic levels, treating mutualistic relationships, the interplay of prey and predator, and of host with parasite. In aggregate these kinds of relationships constitute the main forms of interactions to be found on any landscape.

Plants are the major primary producers in any ecosystem; they set the stage for interactions passing up the trophic system in a community. Therefore, the insect ecologist needs to understand plants as food and habitat for insects, and their bottom-up role in plant and insect assemblages. This point of view justifies considerable detail on plant and herbivore interactions and a relatively long chapter on this topic. Understandably the subject is of great interest to ecologists with a resultant large literature and many hypotheses, for the subject is fundamental for understanding insects in nature, in agriculture, forestry, horticulture, biological control and conservation. As we saw in Chapter 2, plant characteristics can impact trophic levels above the herbivores because toxins, attractants and repellents may impact predators, parasites and mutualists.

These interactions considered here are the building blocks of communities and ecosystems. Their understanding is necessary as we progress from this part to the subsequent parts of the book which deal with larger scale and more complex arrays of interacting species: Part IV on population ecology, Part V on communities and Part VI on broad patterns in nature. For example, the population dynamics of a species may be profoundly influenced by food supply, competition and natural enemies, and the other interactions discussed here in Part III all have a role to play in community structure. Therefore the contents of this part develop in a logical way the understanding of insect ecology.

4

Plant and herbivore interactions



In their classic paper entitled "Butterflies and plants: a study in coevolution," Ehrlich and Raven (1964) envisioned an "arms race" between plants and herbivores, whereby each player exerted reciprocal selective pressure on the other that resulted in evolutionary change. Thus, the arms race between plants and herbivores emphasizes an ongoing reciprocal interplay with plants erecting defenses, herbivores breaking defenses with novel offenses, plants countering with new defenses and so on through evolutionary time (Mitter *et al*. 1991, Herrera and Pellmyr 2002, Thompson 2005). Moreover, "breakthroughs" in plant defense or herbivore offense are thought to create "adaptive zones" that promote speciation, lineage diversification and thus the generation of biodiversity. However, an apparent dilemma arises because plants in general have longer generation times and lower recombination rates than their insect herbivores (and especially plant pathogens), which should hinder their ability to keep pace in the evolutionary arms race (Whitham 1983). Yet, plants have clearly done so.

While the concepts of arms races and coevolution are useful as an overall theme in this chapter, we do not wish to imply that coevolution is a general phenomenon in the interaction between plants and insect herbivores. Strong cases can be developed for coevolution among mutualists (Chapter 6) and parasite–host relationships (Chapter 8), but there is a shortage of sound evidence that insect herbivores have impacted plant traits in a coevolutionary manner (Futuyma and Agrawal 2009).

In this chapter, we will explore the issue of plant–herbivore interactions in much greater depth and attempt to resolve the apparent disadvantage of plants in their arms race with herbivores. Before doing so, however, we need to learn far more about the players themselves, examine the effects of plants on herbivores at the individual and population levels, and discover more about the complex world of plant–insect interactions. Toward this end, we will elaborate on the incredible taxonomic and ecological diversity of insect herbivores and their variable feeding styles, investigate the barriers (e.g., nutrition and allelochemistry) that plants pose to herbivore attack, explore the counter-ploys herbivores have evolved to overcome plant defenses, visit plant defense theory, determine how herbivores and plants affect each other's distribution and abundance, and examine how such information might be exploited to better manage pest herbivores in agricultural and forest systems. The latter is particularly crucial, given that billions of dollars of potential crop yield are lost directly (herbivory) and indirectly (vectors of plant pathogens) to the feeding activities of insect herbivores (Allard *et al*. 2003, Oerke 2006).

4.1 Taxonomic occurrence of phytophagy

At least half of the estimated 2–10 million described species of extant insects are herbivores (phytophages), feeding on living plant material (Southwood 1973, Speight *et al.* 1999, 2008, Gullan and Cranston 2005, Triplehorn and Johnson 2005). Moreover, fossil evidence for the occurrence of phytophagy (e.g., herbivory, leaf mines, galls and the galleries of wood borers) dates far back in geologic time with numerous records in the Triassic (220 MYA) and Carboniferous (330 MYA) Periods, suggesting that this feeding style is indeed an ancient one (Labandeira and Phillips 1996, Labandeira 2002). Despite the richness of phytophagous species, the habit of herbivory occurs predominantly in only nine of the 29 orders of insects: Orthoptera (grasshoppers and relatives), Phasmatodea (stick insects), Thysanoptera (thrips), Hemiptera (e.g. true bugs, leafhoppers, planthoppers, aphids and scale insects), Psocoptera (bark lice), Coleoptera (beetles), Hymenoptera (sawflies), Lepidoptera (butterflies and moths) and Diptera (flies). Notably, most species of Lepidoptera and Phasmatodea (>95%) and the majority of Orthoptera, Thysanoptera and Hemiptera taxa (>80%) are phytophagous, with a lower incidence of herbivory in the Coleoptera (~35%), Diptera (~30%) and Hymenoptera (~15%). If one includes insect species that consume dead or dying plant material (detritivores, decomposers and shredders) in the category of "herbivores," then the prevalence of phytophagy increases substantially, as this feeding habit occurs in the three orders of non-insect Hexapods (Protura, Diplura and Collembola) as well as in 16 orders of insects. Of the terrestrial detritivores, the most noteworthy by far are the wood-feeding Isoptera (termites), whereas in aquatic systems Trichoptera (caddisflies), Plecoptera (stoneflies) and Diptera (flies) often dominate the feeding assemblage.

4.2 Diet breadth, feeding strategies and herbivore guilds

Most plant species support complex assemblages of herbivores that collectively exploit almost every plant part (Figure 4.1). Synthesizing the incredible diversity of feeding styles and foraging strategies of insect herbivores is a daunting task, but can be simplified by categorizing herbivores according to their **diet breadth** (host-plant range) and **feeding guild** (a group of species exploiting the same resource in a similar manner; *sensu* Root 1973, 2001). Regarding host range, insect herbivores can be **monophagous** (specialists that feed on a single plant

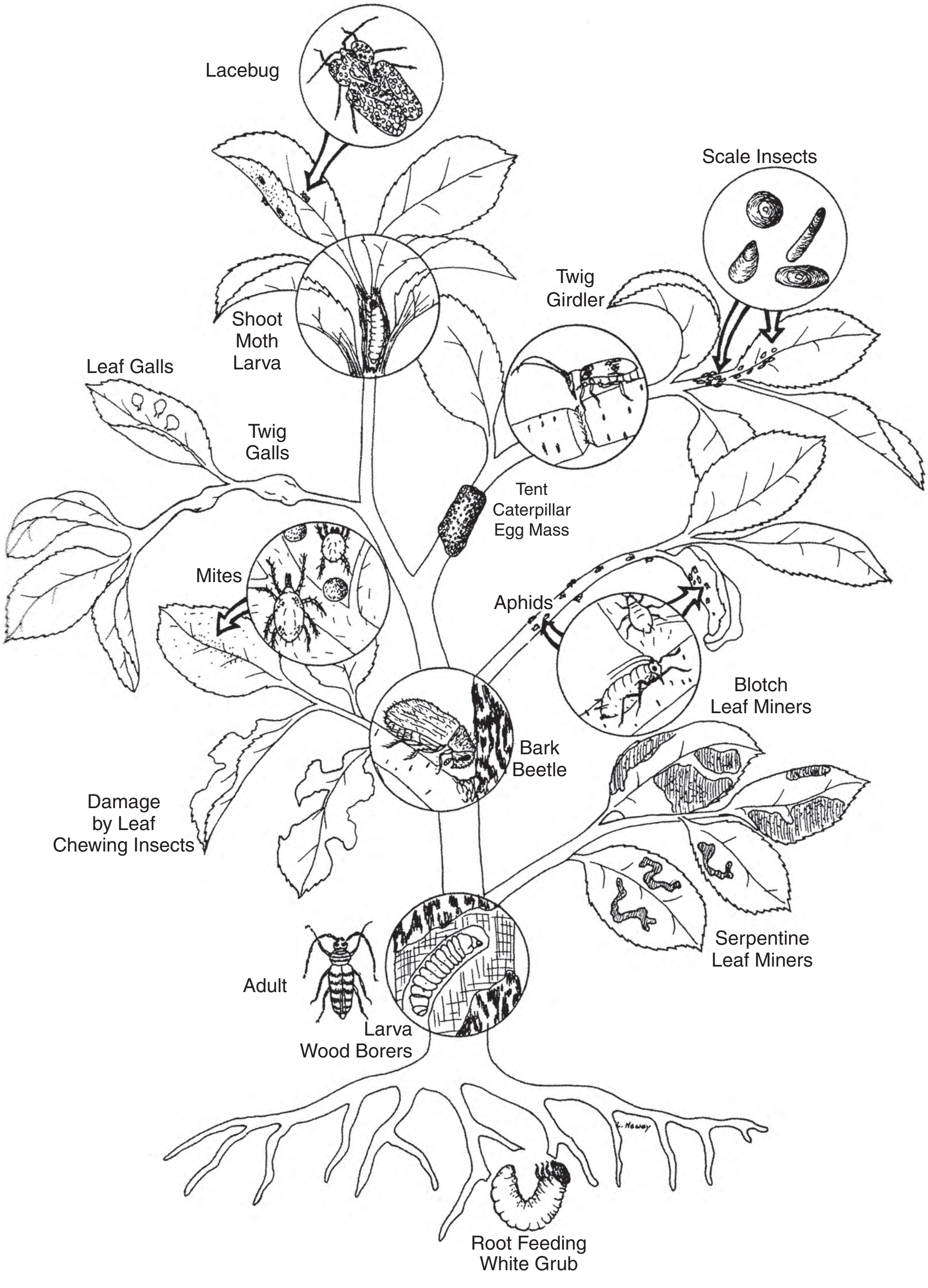


Figure 4.1 Feeding guilds of herbivorous insects and mites that can co-occur on a single host tree including sap-feeders (aphids, scale insects, lacebugs and mites), free-living leaf chewers (tent caterpillars and twig girdlers), leaf miners (blotch and serpentine), borers (shoot moth, bark beetle and wood borer), gall inducers (leaf and twig galls) and root feeders (white grubs). From Johnson and Lyon (1991).

species or plants in the same genus), **oligophagous** (species that feed on plants in several genera, but within the same family) or **polyphagous** (generalists that exploit plants in more than one family) (Strong *et al.* 1984a, Bernays and Chapman 1994). Using swallowtail butterflies as an example, the Oregon swallowtail (*Papilio oregonius*) is monophagous, feeding exclusively on the composite *Artemisia dracunculoides* throughout its range, the short-tailed swallowtail (*Papilio brevicauda*) is oligophagous feeding on several genera of plants in the Apiaceae and the anise swallowtail (*Papilio zelicaon*) is polyphagous exploiting 69 plants in 32 genera in two plant families (Thompson 1998). The fall webworm (*Hyphantria cunea*) and gypsy moth (*Lymantria dispar*) are extremely polyphagous, feeding on over 600 plant species representing dozens of plant families (Miller and Hanson 1989). Complicating matters of diet breadth determination is the fact that herbivores can be locally monophagous, but geographically polyphagous, whereby they specialize on different host-plant taxa elsewhere in their geographic range (Singer and Wee 2005).

Historically, the perception has been that most insect herbivores are monophagous (>70% of species), but this view is based largely on regional assessments of specific taxa such as aphids, planthoppers, butterflies and agromyzid flies, mostly from temperate latitudes (Wilson *et al.* 1994, Dixon 1998, Janz *et al.* 2001). Recent evidence for assemblages of tropical insect herbivores suggests that levels of monophagy may be lower than temperate estimates, at least for some taxa (Basset *et al.* 1996, Mawdsley and Stork 1997, Ødegaard *et al.* 2000). Later in this chapter, factors that enhance or constrain diet breadth, influence host shifts and promote speciation and diversification will be considered.

Insect herbivores can be characterized by their feeding strategy or **guild**, and indeed they exhibit an incredible array of feeding styles on living, dying and dead plant resources (Kirby 1992, Gullan and Cranston 2005, Figure 4.2). Feeding guild is ultimately affected by a variety of factors, including mouthpart type (chewing versus piercing-sucking), the microhabitat where herbivores feed (e.g., leaves, stems, bark, roots, fruits, seeds, dead wood, detritus and fungi), and how plant material is manipulated or processed (e.g., leaf tiers, leaf rollers, gall formers, shredders, collectors and scrapers). For convenience, feeding strategies can be grouped into more general categories such as **chewers** versus **sap-feeders** or **free-living feeders (exophages)** and **concealed feeders (endophages)**. Notably, it is important to distinguish particular herbivore guilds, because they often respond differently to plant nutrition, allelochemistry and natural-enemy attack (e.g., Gross 1991, Inbar *et al.* 1999a, Huberty and Denno 2004).

Of the **free-living chewers**, those that feed in exposed locations on the plant (e.g., on leaves, flowers, pollen, seed heads and fallen seeds), Lepidoptera and Coleoptera are by far the most diverse and abundant followed by Orthoptera (grasshoppers), Hymenoptera (sawflies and ants) and Phasmatodea (stick insects) (Gullan and Cranston 2005). Many chewing insects also feed in concealed locations within living, dying or dead plant tissues. Important guilds of **concealed feeders** include **leaf tiers** (Lepidoptera), **leaf rollers** (Lepidoptera), **leaf miners** that feed internally between the upper and lower epidermis (Lepidoptera, Coleoptera, Diptera, Hymenoptera), **stem borers** (Lepidoptera, Coleoptera, Hymenoptera), **wood borers** (Coleoptera, Lepidoptera, Hymenoptera) that feed within the branches or trunks of woody plants where they consume the bark, cambium, sapwood or heartwood, **fruit borers** (Diptera, Lepidoptera) and **seed/pod borers** that feed internally within seeds or seed pods (Coleoptera, Lepidoptera, Hymenoptera). By their feeding and oviposition activity, mandibulate herbivores (Hymenoptera, Diptera, Lepidoptera and Coleoptera) also induce the formation of galls (structures arising from aberrant plant tissue growth) in which they reside. The diversity of gall sizes and shapes produced by **gall-inducers** is impressive and galls can be induced on most plant tissues. Mandibulate **root feeders** (Lepidoptera, Coleoptera,

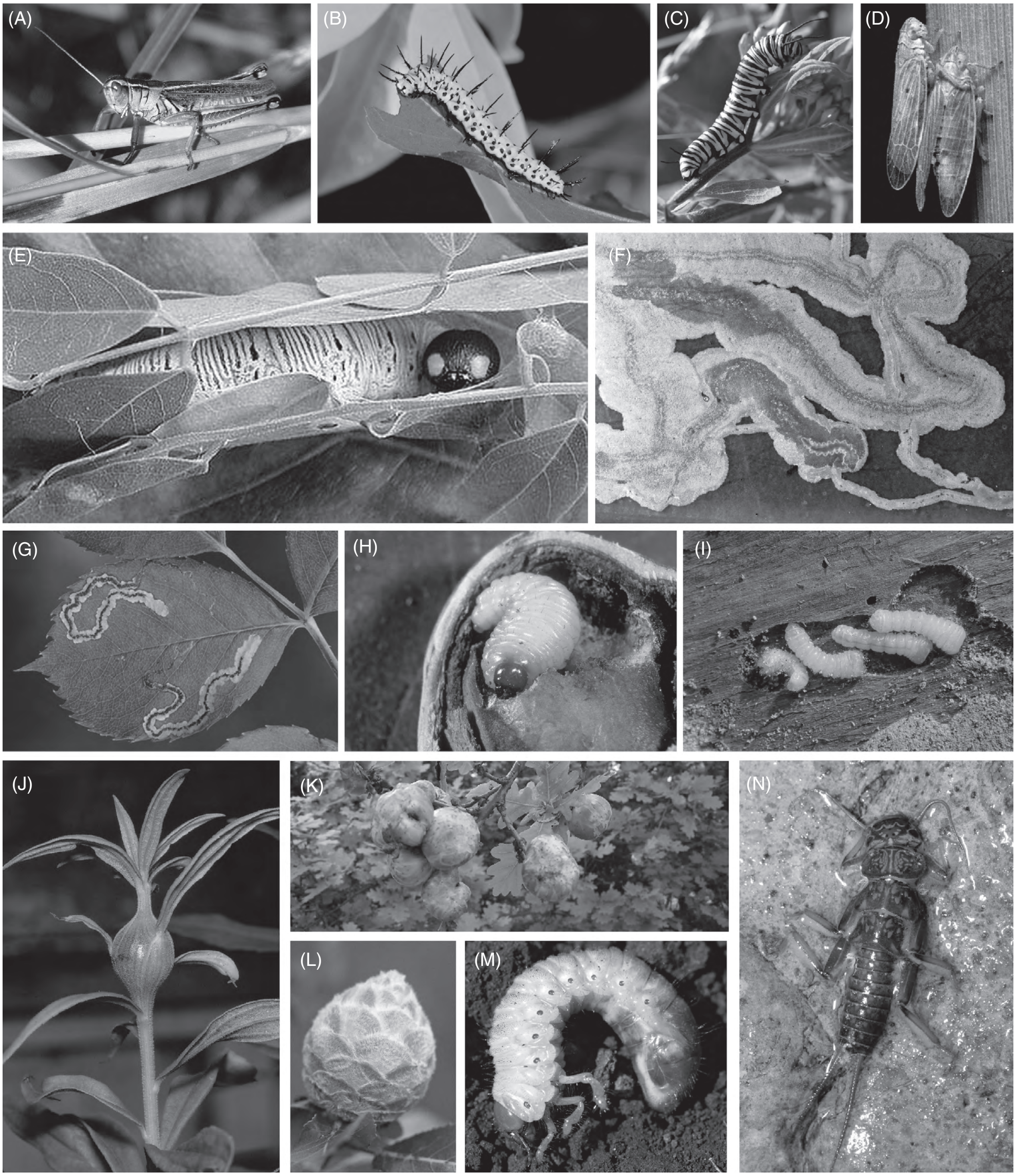


Figure 4.2 Diversity of feeding guilds represented by insect herbivores. Free living mandibulate herbivores include (A) a grasshopper, (B) lepidopteran larva, *Heliconius charitonius*, and (C) caterpillar of the monarch butterfly *Danaus plexippus*. (D) Free-living sap-feeders such as the planthopper *Prokelisia marginata* also feed in exposed positions. Concealed feeders,

Diptera) can be considered concealed feeders simply because they reside in the soil. However, some species feed internally within roots as borers (some Lepidoptera), whereas others feed externally (Coleoptera such as scarab beetles and weevils).

Free-living **sap-feeders** (Hemiptera, Thysanoptera) feed by inserting their stylets into various plant tissues and they are categorized accordingly as **phloem feeders** (e.g., aphids, planthoppers, treehoppers, leafhoppers, scale insects), **xylem feeders** (cicadas, spittlebugs) and **epidermis/mesophyll/parenchyma feeders** (heteropterans and thrips) that insert their mouthparts into non-vascular tissues (Gullan and Cranston 2005). Numerous sap-feeders are also notorious **gall-inducers** (Hemiptera and Thysanoptera), and like their mandibulate counterparts, they (aphids, psyllids and thrips) induce an incredible variety of gall architectures. Several groups of sap-feeders (aphids, mealybugs and scale insects) also feed externally on roots beneath the soil surface.

In aquatic systems, feeding guilds of herbivorous/detritivorous insects are pigeonholed more into functional groups (Merritt and Cummins 1996, Barbour *et al.* 1999, Gullan and Cranston 2005). There are mandibulate herbivores (Lepidoptera, Coleoptera, Diptera) and a few sap-feeders (Hemiptera such as water boatman) that feed externally or internally on living macrophytes or algae. **Shredders** (some Plecoptera, Trichoptera, Coleoptera and Diptera) feed on living or decomposing plant tissues. **Collectors** feed on plant fragments and decomposing bits of organic matter smaller than those usually consumed by shredders. Collectors are often divided into **filter feeders** that strain minute particles from the water column (e.g., blackfly larvae and net-building Trichoptera) and **gatherers** that feed on organic matter on the streambed (several Ephemeroptera, Coleoptera, Trichoptera, Diptera). Notably, shredders break up detritus into smaller fragments, making it available for collectors. **Scrapers** (Ephemeroptera, Coleoptera, Trichoptera, Lepidoptera and Diptera) graze on surface vegetation or on algae that is attached to submerged substrates. Many of the feeding guilds of aquatic insects are omnivorous and consume a variety of microorganisms along with the plant material they ingest.

Terrestrial detritivores, decomposers and dead-wood feeders (e.g., Collembola, Isoptera, Blattodea, Coleoptera) are not often subdivided into feeding guilds, even though they occupy a huge diversity of microhabitats above and below the soil surface (Kirby 1992). Perhaps part of the difficulty in sorting soil and wood-dwelling groups into feeding guilds is that, like their aquatic counterparts, many groups are omnivorous, consuming various combinations of detritus, fungi and dead arthropods. Nonetheless, there are analogs to shredders and gatherers in that larger species (e.g., Isoptera, Coleoptera) process detritus into smaller pieces and fecal material that can then be handled by smaller consumers (e.g., Collembola) (Gullan and Cranston 2005).

From this discourse, it would be wrong to conclude that herbivorous insects are easily pigeonholed into

Caption for Figure 4.2 (*cont.*)
such as (E) the leaf-tying larva of the silver-spotted skipper *Epargyreus clarus*, (F) a leaf-mining larva feeding inside a mangrove leaf, (G) a serpentine leaf miner, (H) the seed-feeding weevil *Curculio nucum* in a hazel nut and (I) wood-boring cerambycid beetle larvae, all feed internally in various plant tissues. Gall inducers, such as (J) the tephritid fly *Eurosta solidaginis*, (K) the cynipid wasp *Biorhiza pallida* and (L) the cecidomyiid fly *Rhabdophaga strobiloides* are also concealed feeders. A great diversity of root-feeders such as (M) the white grub *Melolontha vulgaris* feed beneath the soil surface. Shredders, such as (N) a nymph of a stonefly, feed on living or decomposing plant tissues in aquatic habitats. Photo credits: (A) © Bruce MacQueen/Shutterstock.com, (B) Steve Kaufman/photolibrary, (C) © Ron Rowan Photography/ Shutterstock.com, (D) © Dwight Kuhn, (E) Dale Clark, Dallas County Lepidopterists' Society, (F) Kevin Schafer/photolibrary, (G) Geoff Kidd/photolibrary, (H) Bartomeu Borrell/photolibrary, (I) Keith Douglas/photolibrary, (J) Warren Abrahamson, (K) Brian Hainault, (L) Daniel Mosquin, (M) ©iStockphoto.com/fotosav, (N) Martin Siepmann/photolibrary. See color plate section.

discrete feeding guilds. For instance, within taxonomic groups there are species that feed in different niches, such as aphids on leaves, stems, bark and roots (Dixon 1998) and lepidopteran representatives that can be assigned to virtually all mandibulate feeding guilds like free-living folivores, leaf miners and rollers, wood borers, seed feeders, detritivores and even predators (Covell 1984, Powell *et al.* 1998). Moreover, within a single species, there can be changes in feeding guild throughout development such as occur when miners shift to become free-living folivores and when sap-feeders switch from mesophyll to phloem feeding (Powell *et al.* 1998, Lamp *et al.* 2004). Nonetheless, categorizing herbivores into specific feeding guilds lends organization to the diverse array of feeding strategies that exists for insect herbivores. During the course of evolutionary time, phylogenetic analysis reveals changes in the feeding strategy of numerous herbivorous insect groups (e.g., from concealed to external feeding in the Lepidoptera) (Powell *et al.* 1998) and later in this chapter we will explore underlying causes and the opportunities such shifts offer for radiation and diversification.

4.3 Plant barriers to herbivore attack

Even though half of the world fauna of insects is phytophagous, the restricted occurrence of phytophagy as a predominant feeding habit to only 9 (~30%) of the 29 insect orders (Southwood 1973, Ødegaard 2000, Gullan and Cranston 2005) suggests that plants have evolved formidable barriers to insect attack. These barriers include nutritional constraints, mechanical and **allelochemical defenses**, defensive forces of natural enemies, and features of plant phenology and spatial distribution that render plants inherently difficult to exploit. We will explore each of these obstacles in due course, but suffice it to say for now that once plant barriers are overcome, the evolution of phytophagy vastly accelerates herbivore diversification (Mitter *et al.* 1988, 1991, Winkler and Mitter 2007).

4.3.1 Plant nutrition, ecological stoichiometry and constraints on phytophagous insects

Ecological stoichiometry, the study of the relative balance of key elements in organisms from different trophic levels, provides an integrative approach for analyzing plant–herbivore interactions and specifically the constraints that nutrient-deficient food places on consumers (Elser *et al.* 2000, Fagan *et al.* 2002, Sterner and Elser 2002). All organisms are composed of the same major elements, namely carbon (C), nitrogen (N) and phosphorus (P), but the relative balance of these elements differs dramatically among organisms occupying different trophic levels. Importantly, nutritional imbalances created by organisms feeding at lower trophic levels on nutrient-deficient (N and P) food can severely hamper their ability to meet nutrient demands, grow and reproduce. For example, insect herbivores and detritivores have strikingly higher nitrogen (~ 10% N) and phosphorus (~ 0.5% P) contents than their host plants (~ 2% N, ~ 0.05% P) or detrital resources (~ 2% N, ~ 0.03% P) (Elser *et al.* 2000, Fagan *et al.* 2002, Cross *et al.* 2003, Denno and Fagan 2003). Historically, the stoichiometric mismatch in N content (%) and C:N ratio between plants and insect herbivores has been recognized for decades as imposing fundamental limitations on nitrogen acquisition (McNeill and Southwood 1978, Mattson 1980, White 1993, Awmack and Leather 2002, Matsumura *et al.* 2004, Figure 4.3A–C). Similarly, phosphorous limitation has been shown to have widespread effects in aquatic systems (Sterner and Elser 2002), but only recently has it been shown to adversely affect terrestrial insect herbivores (Schade *et al.* 2003, Perkins *et al.* 2004). In one case where N and P limitations have been compared in the same insect (the planthopper *Prokelisia dolus*), N limitation imposes more severe constraints on growth (Huberty and Denno 2006b), but more studies are needed to confirm any general pattern.

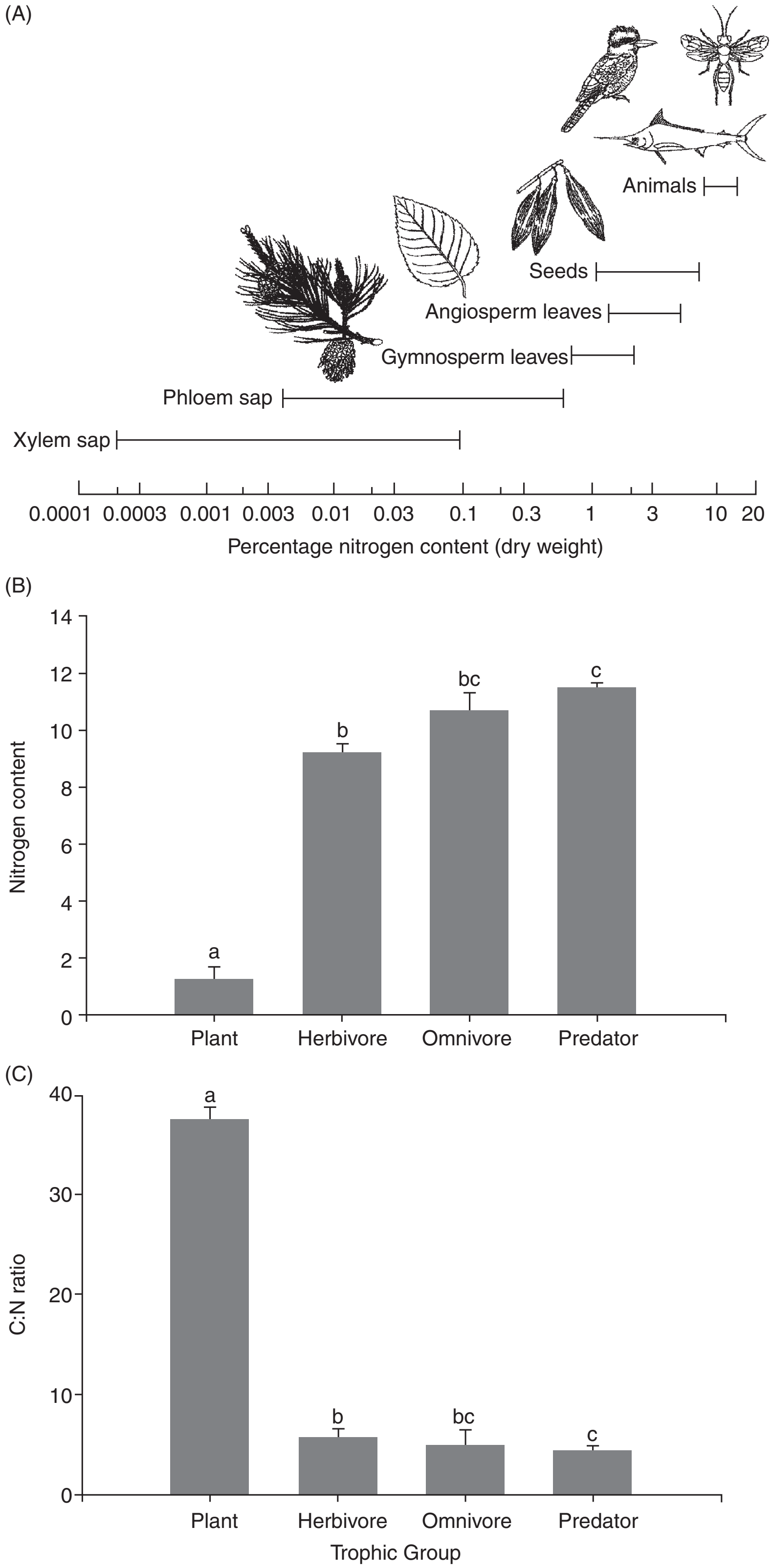


Figure 4.3 (A) Nitrogen content of plant tissues and animals. Original from Mattson (1980); adopted from Speight *et al.* (1999). Nitrogen content (B) and C:N ratio (C) of plants, herbivores, omnivores and predators. Notice the increase in N content and decrease in C:N ratio moving up the food chain from lower to higher trophic levels. From Matsumura *et al.* (2004).

The nutritional mismatch between plants and herbivorous insects persists even though there is considerable variation in the nitrogen content of the different plant groups and plant tissues they exploit (Mattson 1980, Slansky and Scriber 1985, Fagan *et al.* 2002, Figure 4.3A). Of all plant tissues, dead wood and the sap of vascular tissues (xylem and phloem) have the lowest concentrations of nitrogen, whereas reproductive structures, especially seeds, have the highest reported concentrations. The nitrogen content of detritus is also exceptionally low, but can be enhanced when it is enriched with fungi and bacteria (Slansky and Scriber 1985, Cross *et al.* 2003). Overall, phytophagous insects face two obvious problems; not only must they obtain critical nutrients (N and P) from nutrient-poor food, but they must also process and eliminate excess amounts of carbon in doing so (Raven 1983, White 1993, Elser *et al.* 2000). For active consumers that use carbon-based energy for foraging or dispersal, the need to eliminate carbon to achieve elemental balance may be less (Sterner and Elser 2002, Denno and Fagan 2003).

Nitrogen and phosphorus limitation have been featured in studies of phytophagous insect nutrition due to their fundamental roles in protein and RNA synthesis, and maintaining elemental balance (C:N:P) in an organism is essential for metabolism and cell function (Sterner and Elser 2002). Despite elemental mismatches between herbivorous insects and their host plants, herbivores are able to maintain their elemental body composition, at least to some degree, via **homeostatic mechanisms**. Homeostatic regulation in phytophagous insects occurs by the selective uptake, assimilation, storage and excretion of nutrients (Darchambeau *et al.* 2003, Trier and Mattson 2003). A noteworthy case involves sap-feeders (hemipterans such as aphids, leafhoppers and scale insects) that feed in phloem or xylem tissues where they encounter very low concentrations of nitrogen and much higher levels of sugars in the cell sap (Dixon 1998). Homeostasis is achieved by the selective retention of amino nitrogen and elimination of excess sugars as **honeydew**, a process that is achieved by a unique midgut arrangement known as a **filter chamber** whereby most sugar-rich liquid bypasses the absorptive midgut and is excreted. However, homeostasis does not occur without cost, which explains why there are such severe growth penalties when herbivores develop on nutrient-poor foods (Sterner and Elser 2002, Raubenheimer and Simpson 2004).

Given that herbivorous insects are fundamentally nitrogen limited, it is not surprising that elevated host plant quality (%N), either that which occurs naturally or via nitrogen fertilization, can promote increased growth, reproduction and remarkable population outbreaks (McNeill and Southwood 1978, Mattson 1980, Cook and Denno 1994, Herms 2002). However, not all feeding guilds respond similarly to elevated plant nutrition nor do species within the same guild (Scriber 1984, Kytö *et al.* 1996, Awmack and Leather 2002). In general, sap-feeders (e.g., aphids, planthoppers, leafhoppers, scale insects and mirid plant bugs) show consistent population increases on N-enriched host plants, whereas chewing herbivores (e.g., beetles, caterpillars and sawflies) range the gamut of responses including increases, decreases and no change (McNeill and Southwood 1978, Mattson 1980, Strauss 1987, Kytö *et al.* 1996, Awmack and Leather 2002, Denno *et al.* 2003). Unlike mandibulate herbivores, sap-feeders may be more responsive to enhanced plant nitrogen because they feed in vascular tissues, where they benefit from increased soluble nitrogen and yet avoid elevated levels of N-based allelochemicals (e.g. HCN) that are compartmentalized in other leaf tissues (Raven 1983, Huberty and Denno 2004). Likewise, the high reproductive potential characteristic of many sap-feeders may promote their escape from natural enemies on N-enriched host plants, a factor that can compromise potential population increases of slower-growing herbivores. Within the same feeding guild (e.g., leafhoppers and delphacid planthoppers), variable population responses of herbivores to N-enriched host plants have been attributed to species-specific differences in colonization ability, feeding compensation and the level of plant nitrogen at which maximum nitrogen utilization efficiency is achieved (Prestidge 1982, Prestidge and McNeill 1982, Denno *et al.* 2002, Huberty and Denno 2006a).

Although responses of insect herbivores to plant nitrogen can be compromised at the population level by other factors, there is widespread support for the adverse effects of nitrogen limitation on performance at the individual level (Strong *et al.* 1984a, White 1993, Awmack and Leather 2002). There are many examples showing that phytophagous insects in general survive better, grow faster, molt into larger adults and are more fecund if they develop on nitrogen-rich host plants. Their increased performance on N-rich plants is often attributed to increased feeding rates and enhanced nitrogen assimilation and growth efficiencies (Mattson 1980, Slansky and Scriber 1985, Awmack and Leather 2002). Moreover, the extremely slow growth rates (years) of dead-wood borers (cerambycid and buprestid beetles, moths and wood wasps), several aquatic detritivores (stoneflies) and some xylem feeders (17 and 13 year cicadas), all groups that feed on extremely nitrogen-poor food resources, provide further testament to nitrogen limitation (Iverson 1974, Pritchard and Berté 1987, Motomori *et al.* 2001).

Although ecological stoichiometry provides a broad context for highlighting the general nutritional constraints that consumers face, it does not emphasize important details such as the appropriate form of the macronutrient ingested (e.g., nitrogen-containing toxins), amino acid balance in the diet or the need for non-synthesizable nutrients (e.g., sterols required for molting hormone) and limiting trace elements and water-soluble vitamins (e.g., thiamine, riboflavin and ascorbic acid), all of which are necessary for metabolism and development (Prestidge and McNeill 1982, Bernays and Simpson 1990, Singer *et al.* 2002, Singer and Bernays 2003). Moreover, the water content of plants affects cell turgor pressure and the ability of sap-feeders to access plant nitrogen (Huberty and Denno 2004). Similarly, the nitrogen utilization efficiency of chewing herbivores is often diminished under conditions of lowered foliar water content (Slansky and Scriber 1985). Thus, plant condition such as water content and other dietary factors can hinder herbivore performance beyond the general constraints imposed by contrasts in macronutrient stoichiometry with their host plant (Scriber and Slansky 1981).

4.3.2 Coping with nutrient-deficient host plants

Because insect herbivores are inherently nutrient limited, they have evolved a variety of adaptations or feeding strategies that maximize encounters with nutrient-rich resources or buffer them against nutrient deficiencies in their diet (McNeill and Southwood 1978, Cook and Denno 1994, Karban and Agrawal 2002). These adaptations can be organized into six general categories:

(1) Feeding compensation
(2) Selection of nitrogen-rich feeding sites and/or diet mixing
(3) Life-cycle synchronization with nutrient-rich resources
(4) Manipulation of plant physiology by forming nutrient sinks
(5) Obtaining nitrogen from non-plant sources
(6) An evolutionary shift in body nutrient composition.

Feeding compensation: By increasing their feeding rate on nitrogen-deficient plant resources, insect herbivores can partially offset the problem of satisfying their nutrient demands, a phenomenon which occurs in a wide diversity of sap-feeders (Hemiptera: aphids, planthoppers and leafhoppers), chewing herbivores (Orthoptera, Coleoptera, Lepidoptera and Hymenoptera) and detritivores (Plecoptera and Trichoptera) (Iverson 1974, McNeill and Southwood 1978, Bernays and Simpson 1990, Simpson and Simpson 1990, Slansky 1993, Yang and Joern 1994, Kause *et al.* 1999, Swan and Palmer 2006). Feeding compensation, however, is not a completely effective solution to problems of nutrient acquisition because of physiological constraints such as gut capacity and throughput time that limit the degree to which eating more can compensate for eating nutrient-poor food (Simpson and Simpson 1990). For instance, correlated with increased feeding rate on nutrient-deficient food are a shorter gut-retention time and often decreased digestion and nitrogen assimilation. Moreover, increasing consumption rate to compensate for a deficiency in one nutrient may lead to an excess of other carbon-rich compounds or dietary toxins that can negatively affect growth and survival (Slansky and Wheeler 1992, Awmack and Leather 2002). Also, if feeding compensation results in delayed development, then herbivores may also experience higher exposure to natural enemies, the so-called **slow-growth–high-mortality hypothesis** (Price *et al.* 1980, Benrey and Denno 1997, Kaplan *et al.* 2007).

Selection of nitrogen-rich feeding sites and diet mixing: Specialized sap-feeders that are generally less affected by compartmentalized allelochemicals show very strong preferences for nitrogen-rich feeding sites (Mattson 1980, Cook and Denno 1994, Awmack and Leather 2002). Feeding sites where high concentrations of nitrogen occur include actively growing meristems, young leaves, inflorescences, pods, seeds and senescing leaves, and sap-feeders such as aphids often aggregate at these sites, where their performance is dramatically enhanced. Many sap-feeders also shift their feeding position from low- to high-nitrogen sites with the seasonal decline in leaf nitrogen that occurs in many plant species (McNeill and Southwood 1978, Scriber and Slansky 1981). A frequent spatial shift is from leaves to more nitrogen-rich inflorescences or seed heads with the onset of flowering. Chewing folivores (Lepidoptera, Coleoptera, Hymenoptera) show more variable responses than sap-feeders with regard to selecting the most nitrogen-rich feeding sites on a plant, namely young compared to mature leaves (Raupp and Denno 1983). In general, specialist defoliators, which are better adapted than generalists to deal with allelochemicals concentrated in young leaves, show stronger feeding preferences for nitrogen-rich young leaves, but there are exceptions (Raupp and Denno 1983, Awmack and Leather 2002). Although performance is often potentially greater on nitrogen-rich plant tissues, specialized herbivores do not always select such sites for oviposition or feeding because performance is compromised by high concentrations of performance-reducing allelochemicals, increased risk of enemy attack or because herbivores forage selectively elsewhere on the plant for toxins that they sequester for defense (Damman 1987, Awmack and Leather 2002).

Among polyphagous herbivores, such as many grasshoppers and lepidopterans, there is certainly evidence that high-nitrogen diets are selected to meet nutrient demands (Bernays and Simpson 1990, Joern 2000, Awmack and Leather 2002). Similarly, many detritivores like the leaf-shredding caddisfly *Hydatophylax* selectively colonize high-nitrogen litter over less nutritious choices (Cummins and Klug 1979, Motomori *et al.* 2001). However, **diet mixing** (feeding on more than one plant species or food resource) is a common feeding strategy in many herbivorous insects (e.g., numerous grasshoppers and caterpillars) and detritivores as well (e.g., stoneflies and caddisflies) (Joern 2000, Behmer *et al.* 2001, Singer and Bernays 2003, Swan and Palmer 2006). Some herbivores (e.g., many grasshoppers) and detritivores (e.g., stoneflies), and predators for that matter, in fact grow faster and exhibit higher fitness on mixed compared to single-resource diets (MacFarlane and Thorsteinson 1980, Mayntz *et al.* 2005, Swan and Palmer 2006), whereas others do not (several heteropterans and lepidopterans) (Bernays and Minkenberg 1997). Diet-mixing theory, in partial contrast to ecological stoichiometry, emphasizes achieving dietary balance by foraging selectively on limiting macro-nutrients such as protein and carbohydrate (Behmer *et al.* 2001, Raubenheimer and

Simpson 2004, Raubenheimer and Jones 2006). Grasshopper species, for instance, grow best on diets composed of a specific proportion of protein and carbohydrate, their so-called nutritional "intake target." When fed diets deviating in protein-carbohydrate composition from their intake target, performance is reduced. So, it is not surprising that grasshoppers forage selectively on a dietary smorgasbord of protein and carbohydrate choices to achieve their intake target, although targets do differ among species.

Diet mixing theory extends from **optimal-diet theory**, which itself stems from **optimal-foraging theory** (Sih and Christensen 2001). The essential predictions of optimal-diet theory are that foragers should conform as follows:

(1) They should prefer food items that yield more energy per unit handling time.
(2) Individuals should drop low-value items from their diet as higher-value options become available.
(3) They should obey a quantitative threshold rule as to when specific food types should be included or excluded from the diet (Charnov 1976, Sih and Christensen 2001).

The observation that diet mixing can be more beneficial to consumers than simply feeding on the most nitrogen-rich resource challenges the more singular focus of ecological stoichiometry and has led to a multitude of multifaceted hypotheses to explain diet choice and mixing by polyphagous herbivores and omnivores (Bernays and Bright 1993, Joern and Behmer 1997, Joern 2000, Behmer *et al.* 2002, Singer and Bernays 2003, Raubenheimer and Simpson 2004, Raubenheimer and Jones 2006). Besides achieving nutrient balance, alternative hypotheses for diet mixing include feeding on nutrient-deficient resources when superior alternatives are rare, diluting toxins that are ingested from nutritious food resources, diet sampling to assess optimal resources and minimizing exposure to natural enemies. Future development of food-selection theory should seek to combine the constructs of stoichiometry with the complementary views of diet-mixing theory (see Raubenheimer and Simpson 2004). Overall, however, there is overwhelming evidence that nitrogen and phosphorus limitation are pivotal factors directing the feeding strategies of insect herbivores.

Life-cycle synchronization with nutrient-rich resources in time (diapause) and space (dispersal): There is tremendous spatial and phenological variation in plant quality (nutrition and allelochemistry) that occurs within and among plant species (McNeill and Southwood 1978, Hunter *et al.* 1997, Dixon 1998, Awmack and Leather 2002). In general, the nitrogen content of plants such as grasses, forbs and trees follows a distinct seasonal pattern. Leaf nitrogen is highest in spring following bud break, declines rapidly thereafter to a summer low and then rises again during autumn when nutrients from senescing foliage are being translocated to roots. However, among individuals of the same plant species, there is remarkable temporal and spatial variation in the onset of this progression and in the maximum nutrient content that ultimately occurs. Also, within the same habitat, various plant species peak in nitrogen content at different times. Failure to synchronize reproduction and development with "windows of high-nitrogen opportunity" can have drastic consequences for herbivore performance and survival (McNeill and Southwood 1978, Cook and Denno 1994, Hunter *et al.* 1997, Dixon 1998). Two life-history traits, namely **diapause** and **dispersal**, allow herbivores to synchronize reproduction and development with optimal plant nutrition in time and space respectively (Denno 1994a).

Several of the best examples of "nitrogen tracking" occur in the sap-feeding guild (McNeill and Southwood 1978, Dixon 1998). For instance, population size of the Green Spruce aphid (*Elatobium abietinum*) mirrors changes in the amino nitrogen content of its host with peak reproduction occurring in spring when trees are most nutritious (Figure 4.4).

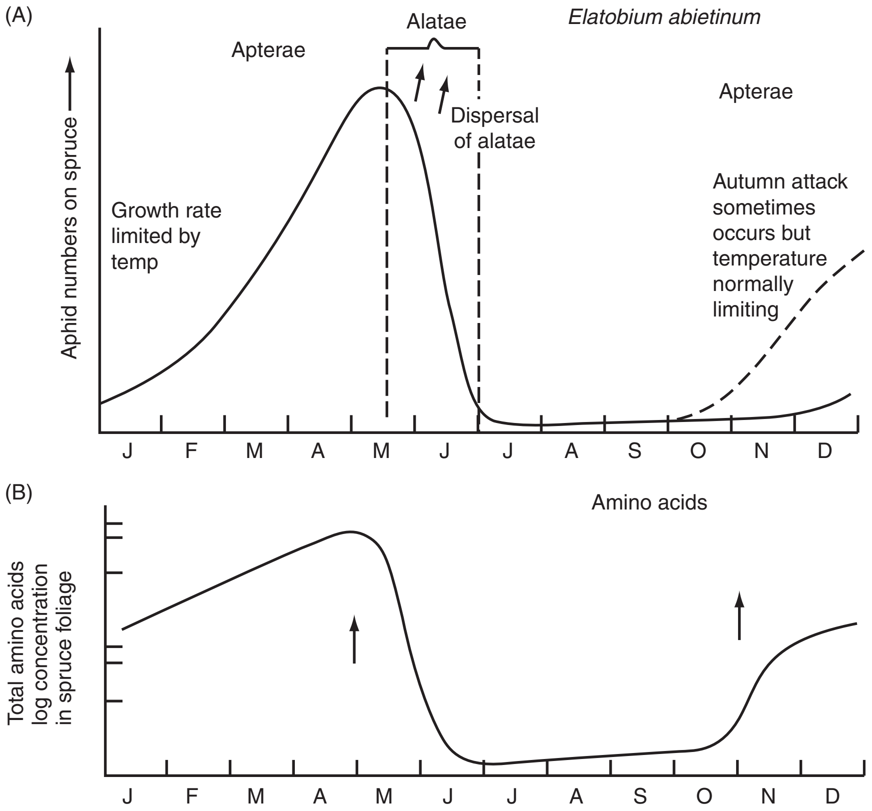


Figure 4.4 (A) Fluctuations in the abundance of the Green Spruce aphid *Elatobium abietinum* in relation to (B) seasonal changes in the amino nitrogen content of its host tree. Fluctuations in aphid population size mirror changes in the amino nitrogen content of spruce with peak reproduction occurring in spring when trees are most nutritious and dispersal (production of winged alatae) is coincident with a precipitous drop in tree amino nitrogen in early summer, when wingless parthenogenetic females (apterae) are present. From McNeill and Southwood (1978).

A second population rise often occurs during autumn and is associated with the mobilization of amino nitrogen and its back translocation to roots. Notably, the production of winged adults (alatae) that can disperse to more nutritious trees elsewhere occurs in summer when there is a precipitous drop in the amino nitrogen content of the resident tree.

Other monophagous herbivores also synchronize their life histories with high plant nitrogen by dispersing to more nutritious plants. For example, the salt marsh planthopper *Prokelisia marginata* meets its high-nitrogen demands by dispersal, which allows for the escape of deteriorating plant patches and the colonization of nutrient-rich plants in other habitats where offspring performance is enhanced (Cook and Denno 1994, Denno and Peterson 2000). By contrast, its sympatric congener *P. dolus* is relatively immobile and copes with declining plant nitrogen by compensatory feeding (Huberty and Denno 2006a). A morphological trade-off in investment between flight muscles (*P. marginata*) and the muscles governing ingestion capacity (*P. dolus*) imposes constraints on how these sap-feeders cope with declining plant nitrogen (Figure 4.5). Thus, dispersal and feeding compensation may be two competing mechanisms for satisfying nitrogen demands that

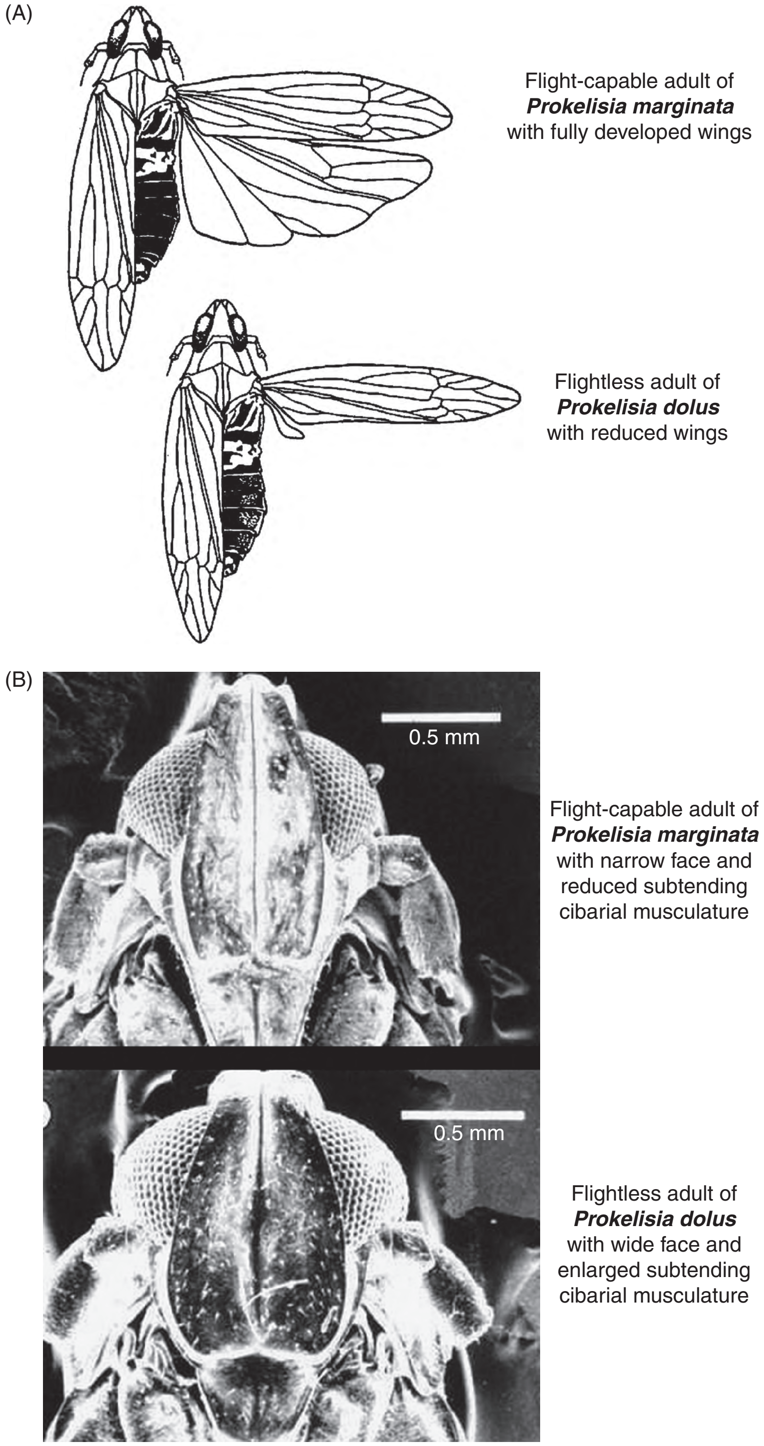


Figure 4.5 (A) Planthoppers are wing-dimorphic as adults with both flight-capable and flightless forms occurring in the same population. Most adults of the planthopper *Prokelisia marginata* are flight capable and meet their nutritional demands

can't both be maximized in the same species. Dispersal allows for avoidance of low-nitrogen conditions, whereas feeding compensation permits tolerance until plant nutrition improves.

Because the nitrogen content of different plant species peaks at different times of the year, polyphagous herbivores can meet nitrogen demands by dispersing to more nutritious plant species as local conditions deteriorate (McNeill and Southwood 1978, Prestidge 1982, Awmack and Leather 2002). For instance the grass bug *Leptopterna dolabrata* and the planthopper *Javesella pellucida* switch host grasses from one generation to the next as they track spatial changes in high-nitrogen availability. Moreover, host alternation in aphids has been linked to nitrogen tracking (Dixon 1998). Host-alternating aphids hatch from overwintering eggs on their primary host, usually a woody tree or shrub. As the amino-nitrogen content of their primary host declines, migratory females are produced that disperse to more nutrient-rich secondary hosts (herbaceous plants) where they undergo several asexual generations until plant quality declines. Subsequently, migratory forms are produced that return to the primary host, where they reproduce and give rise to the egg-laying sexuals. The decrease in quality of the secondary host coincides with the autumn increase in leaf nitrogen content of the primary host.

Other aphid species such as the sycamore aphid *Drepanosiphum platanoides* show similar patterns of precise nitrogen tracking, but do so by entering a reproductive diapause in summer and thus avoiding periods of low nitrogen availability (Dixon 1998). Some herbivorous insects that overwinter as diapausing eggs on their host trees (e.g., treehoppers) detect plant cues in spring and synchronize egg hatch with the onset of sap flow, thereby ensuring development on nitrogen-rich leaves (Wood *et al.* 1990). Other herbivores such as foliar-feeding caterpillars are less able to predict bud break and thus peak leaf nitrogen (Hunter *et al.* 1997). If larvae hatch just following bud break they experience high performance on nitrogen-rich leaves. However, if they hatch too early bud scales preclude access to developing leaves, and if they hatch too late they incur the adverse effects of declining leaf nitrogen and increasing defensive chemicals, both of which result in lower survival.

Manipulation of plant physiology by forming nutrient sinks: Several species of free-living aphids, gall-inducing insects and lepidopterans modify plant nutritional physiology to their own advantage by creating "**nutrient sinks**" (Way and Cammell 1970, Larson and Whitham 1991, Inbar *et al.* 1995, Raman *et al.* 2006). When phloem-tapping herbivores feed, they alter the source–sink dynamics of phloem transport by diverting assimilates from neighboring leaves and drawing them toward feeding sites where their performance is dramatically enhanced. Moreover, by feeding in aggregations, some aphids (*Brevicoryne brassicae*) further facilitate the local accumulation of nutrients and increase the strength of the nutrient sink. Similarly, the developing gall of the lepidopteran *Epiblema strenuana* intercepts the normal flow of nutrients and acts as a nutrient sink.

Caption for Figure 4.5 (*cont.*)
by dispersing to nutrient-rich patches of their host plant where performance is increased. Most adults of *P. dolus* are flightless and do not have this option. From Denno *et al.* (1985). (B) *P. dolus* meets its nitrogen demands by increasing its ingestion rate when plant quality declines. Feeding compensation in *P. dolus* is made possible by a greater investment in cibarial musculature (as evidenced by its wide face where these muscles attach) compared to its congener *P. marginata*, which has reduced compensatory ability. Thus, these planthoppers meet their nutritional demands in different ways and a morphological trade-off in investment between flight muscles (*P. marginata*) and the muscles influencing ingestion capacity (*P. dolus*) imposes constraints on how these sap-feeders cope with declining plant nitrogen. Adapted from Denno *et al.* (1987) and Huberty and Denno (2006a).

Seed-feeding insects can also manipulate seed development to their own advantage (von Aderkas *et al.* 2005). For example, the seed chalcid *Megastigmus spermotrophus* (Hymenoptera: Torymidae) deposits eggs in the ovules of Douglas fir (*Pseudotsuga menziesii*) cones. Oviposition prevents the expected degeneration of unfertilized ovules and at the same time induces the accumulation of energy reserves, which larvae require for development.

Nutrients from non-plant sources: There are two primary ways that insect herbivores obtain supplemental nutrients from sources other than their host plant, namely by **feeding at higher trophic levels** and/or from **symbionts**, microorganisms living in intimate association with their insect host. An extensive literature documents cases of "herbivorous insects" occasionally or frequently feeding at higher trophic levels, where nitrogen is more concentrated in the diet (McNeill and Southwood 1978, Polis 1981, Whitman *et al.* 1994, Douglas 1998, Agrawal *et al.* 1999a, Coll and Guershon 2002, Denno and Fagan 2003, Figure 4.3). These instances include cannibalism, intraguild predation, scavenging on carcasses and feeding on other nitrogen-rich food sources such as dung. A vast array of herbivores exhibit these behaviors, including Orthoptera, Hemiptera, Thysanoptera, Lepidoptera, Coleoptera, Diptera and Hymenoptera. Detritivores such as Trichoptera engage in cannibalism and predation as well (Wissinger *et al.* 1996). By supplementing their diets with nitrogen from other sources, both herbivores and detritivores can increase their growth and fecundity remarkably (Anderson and McFadyen 1976, McNeill and Southwood 1978, Coll and Guershon 2002). Upon hatching, many first-instar caterpillars (e.g., *Ascia monuste*) seek nitrogen-rich meals by regularly consuming their own egg chorion or the eggs of nearby conspecifics (Barros-Bellanda and Zucoloto 2001), whereas other taxa (cockroaches and lepidopterans) often consume their exuviae and partially recover lost nitrogen (Mira 2000). Factors that further motivate herbivores to seek nutrients from other sources include food depletion, reductions in plant quality, high population density and physiological state, such as when females are in the process of maturing eggs (Simpson *et al.* 2006). If plant quality is poor and nitrogen is not available from other sources, females may resorb eggs or embryos, thereby enhancing their own survival (Ohgushi 1996, Awmack and Leather 2002).

Numerous orders of insects have member species that harbor a variety of symbiotic microorganisms such as bacteria, fungi and protozoans (Bourtzis and Miller 2006). Symbiotic mutualists are completely dependent on their hosts, but in turn provide them with nutrients (e.g., amino acids, sterols and vitamins), chemicals that are either rare, absent altogether, or tied up in non-digestible forms in plant diets (Liadouze *et al.* 1995, Baumann *et al.* 1997, Douglas 1998, Bourtzis and Miller 2006). Symbionts are over-represented in groups of insects that feed on nutritionally-poor food or imbalanced diets suggesting that housing symbionts is an adaptation to meet nutrient demands. For example, symbionts occur in phloem and xylem feeders (Hemiptera: aphids, psyllids, whiteflies, scale insects, planthoppers, leafhoppers and cicadas), some folivores (Hymenoptera: leafcutter ants), wood feeders in the Coleoptera (bark, ambrosia beetles and some scarabs and weevils) and Isoptera (termites) and a few omnivores (Blattodea: wood roaches) (Baumann *et al.* 1997, Gullan and Cranston 2005, Bourtzis and Miller 2006). Notably, symbionts are not known to occur in predatory insects that feed on more nitrogen-rich food. Microbial symbionts can occur external to the insect's body (**ecto-symbiotic** fungus grown by leafcutter ants) or within the host (endo-symbiotic gut protozoans in termites), and can be either **extracellular** (bacteria and protozoans in the guts of termites and cockroaches) or **intracellular** (bacteria in the specialized **mycetome** cells of aphids) (see Chapter 6 on Mutualism).

The role of symbionts in host nutrition has been examined by ridding hosts of symbionts with antibiotics, heat-shock treatments or otherwise sterilizing them and then comparing the performance of so-called **aposymbiotic hosts** with symbiotic control groups (Chen *et al.* 1981, Campbell 1989, Douglas 1996, 1998). When symbionts are deactivated, hosts grow slower, molt to smaller adults or exhibit reduced fecundity, a result that has been shown for aphids, planthoppers, bark beetles and termites (Chen *et al.* 1981, Fox *et al.* 1992, Yoshimura *et al.* 1993, Liadouze *et al.* 1995). Moreover, some herbivores such as leafcutter ants (e.g. *Atta*) culture fungal symbionts in their subterranean nests and bark beetles (e.g. *Ips*, *Dendroctonus*) and ambrosia beetles (e.g. *Platypus*) vector them among host trees during colonization (Beaver 1989, Cherrett *et al.* 1989, Fox *et al.* 1992). Depending on the species, these herbivores feed on the ecto-symbiotic fungus either exclusively (*Atta*) or in part (*Ips*), thereby providing essential nutrients for growth and population increase that are available in very limited amounts in leaf tissue or wood. Termites as a group have evolved a variety of mutualisms with different microorganisms that aid in wood digestion, nitrogen acquisition and ultimately balancing their own C:N content when feeding on very carbon-rich food (Breznak 1982, Higashi *et al.* 1992). For the most part, gut microorganisms such as protozoans, bacteria and fungi are required for cellulose digestion (Breznak 1982; Martin 1991). Moreover, several lineages of termites enhance nitrogen intake by harboring bacterial gut symbionts that either fix atmospheric nitrogen or synthesize it (Higashi *et al.* 1992, Moriya *et al.* 1999). Some termites also support methanogenic bacteria in their guts and are thus able to eliminate excess carbon by methane production (Higashi *et al.* 1992, Brauman *et al.* 1992). Overall, the symbioses that termites have evolved with microbes are essential for maintaining their own C:N stoichiometry. Symbionts at large provide herbivores with essential nutrients, particularly nitrogen that is so critical for growth and reproduction. Notably, symbiotic relationships with microorganisms appear to have provided the opportunity for insects to exploit and diversify on nutrient-poor resources that are otherwise very difficult to exploit (see Chapter 6 on Mutualism).

Evolutionary shift in body nutrient composition: Another way that herbivores have partially reduced their chronic demand for nitrogen is to evolve a lower dependence on nitrogen for the construction of body constituents, and thus reduce the stoichiometric mismatch with their plant diet (Fagan *et al.* 2002). At the level of protein subunits, selection may favor amino acids with lower nitrogen contents. Recent research on the elemental composition of bacterial and yeast proteins has shown that shifts in protein composition can evolve in response to elemental shortages (Baudouin-Cornu *et al.* 2001). At the tissue level, selection might, for example, reduce the ratio of protein to chitin in insect cuticle that typically ranges from 1:1 to 4:1 (Chapman 1998). At the whole-body level, selection might alter the relative allocation to muscle, cuticle, fat body and other tissues, all of which differ in nitrogen content (Fagan *et al.* 2002). That herbivorous bugs and beetles have thinner cuticles than their predaceous counterparts is in line with this argument (Rees 1986). Selection at all of these levels of organization may explain why insect herbivores have lower nitrogen content (9.6%) on average than predators (11.0%) (Fagan *et al.* 2002, Matsumura *et al.* 2004). Similarly, selective pressures associated with fundamental limitations in nitrogen may have contributed to reductions in body nitrogen content over evolutionary time. Consistent with this hypothesis is the observation that herbivores in the more derived orders of insects (Lepidoptera and Diptera) contain 15–25% less nitrogen than do those in more basal lineages (Orthoptera and Hemiptera) (Fagan *et al.* 2002). In this context, half of the body mass of rigid grasshoppers is proteinaceous cuticle, which is far more than that for flexible caterpillars (Bernays 1986). Thus, nitrogen conservation may have played a role in the evolution of holometaboly (complete metamorphosis) with the development of a thin cuticle in the larval stage of advanced insect orders (Bernays 1991).

4.3.3 Mechanical and structural barriers to herbivore attack

Besides being nutritionally inadequate, plants possess a variety of mechanical features and structures that pose physical-chemical barriers to herbivore attack. Included in the repertoire of "mechanical and structural defenses" are general tissue **toughness** and **hardness** that deter or prevent feeding (Lucas *et al.* 2000), **trichomes** (plant hairs) that can deny or reduce herbivore access to feeding and oviposition sites (Myers and Bazely 1991, Andres and Connor 2003) and **surface waxes** that can make it difficult for herbivores to colonize and maintain their foothold on plant surfaces (Juniper and Southwood 1986, Eigenbrode and Espelie 1995).

Historically, ecologists have referred to "leaf toughness" as a general mechanical defense against insect herbivores, but usually the structural elements conferring tissue resistance are not explored in detail (e.g., Feeny 1970, Coley 1983, Raupp 1985, but see Peeters 2002). In general, young expanding leaves are less tough than are mature leaves and leaf thickness and the amount of cellulose and lignin, the structural components of plants, have been implicated in tissue toughness (Peeters 2002). Recently, generic "tissue toughness" has been partitioned into two components namely hardness and toughness, both of which can have adverse effects on herbivores (Choong *et al.* 1992, Lucas *et al.* 2000). "Hardness" deters the initial cracking (splitting) of a plant tissue when a herbivore begins to feed, whereas "toughness" results in resistance to crack growth. Thus, a seed coat may be very hard (resist cracking), but be very brittle and therefore not be very tough. The primary source of tissue toughness is the composite cell wall consisting of cellulose microfibrils set in a hemicellulose or lignin matrix, and is roughly proportional to the fraction of plant tissue volume occupied by cell walls. High toughness in plant cells results not from the cell walls themselves, but rather from their plastic ability to collapse. Hardness in plant tissues can be achieved by dense cell walls as in some seed coats or by amorphous silica in leaves, spines or surface structures such as stiff trichomes. Such defenses deter herbivores from contacting plants, but are also responsible for significant abrasion and mandibular wear once feeding has begun (Lucas *et al.* 2000).

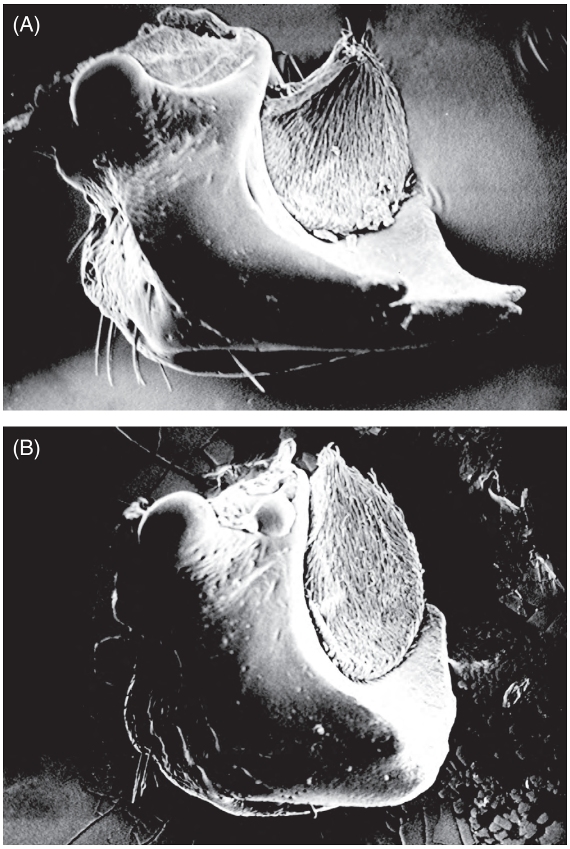


Figure 4.6 Left mandible of an adult willow leaf beetle (*Plagiodera versicolora*) that has fed for one month on (A) tender terminal leaves or (B) tough mature leaves. The incisor of the mandible is completely worn down when beetles feed on tough leaves. From Raupp (1985). Reprinted with permission from Blackwell Publishing.

For mandibulate herbivores such as lepidopterans and beetles, feeding on "tough leaves" results in reduced consumption and delayed growth, which in some cases can be attributed to increased mandibular wear (Raupp 1985, Stevenson *et al.* 1993, Figure 4.6).

Similarly, leaf-shredding caddisflies can show decreased consumption rates on tough litter types (Motomori *et al.* 2001). In several cases, mandibular wear and impaired growth in stem-boring caterpillars have been linked to the high silica content of their grass host (Pathak *et al.* 1971, Hanifa *et al.* 1974), thus implicating tissue hardness as the underlying mechanism. Even more convincing are studies in which the silica content of the host plant was experimentally increased with adverse effects on the growth and digestion efficiency of grasshoppers, lepidopterans and dipterous stem borers (Moore 1984, Massey *et al.* 2006). Notably, sap-feeding herbivores (aphids) in this study were not affected by elevated silica. Sap-feeders may more easily penetrate the cellular spaces between silica-containing cells and as a consequence are not physically excluded from feeding in the vascular tissue. This may explain why herbivore communities on silica-rich grasses are filtered, largely devoid of many chewing herbivores (e.g., free-living lepidopterans and beetles, but not grasshoppers), and are dominated by sap-feeders such as leafhoppers and planthoppers (Cook and Denno 1994). Recent evidence, however, suggests that sap-feeders too incur mandibular (stylet) wear while feeding in plant tissues (Roitberg *et al.* 2005), but mandibular wear has yet to be compared between chewing and sap-feeding herbivores fed the same diet.

Notably, the structural traits of leaves (e.g., blade and cuticle thickness, vein lignification and thickened hypodermis) have also been shown to influence the guild structure of arboreal insect assemblages (Peeters 2002). For example, the density of leaf-chewing herbivores was negatively correlated with a thickened hypodermis and the area of the leaf-vein lignified. In fact, in this extensive study, the functional composition of the herbivore assemblage was better correlated with structural leaf traits than with leaf constituents such as nitrogen and water content. Overall, tissue toughness, hardness and surrogate variables have significant effects on individual performance, population density and community structure.

Trichomes occur in a diversity of forms, sizes and densities and in part serve to protect plants from herbivore attack, although there is substantial variation in their effectiveness (Myers and Bazely 1991, Peter and Shanower 2001, Hare and Elle 2002, Andres and Connor 2003). In addition to their antiherbivore role, trichomes also insulate leaves from solar radiation, deter evaporation, facilitate water and nutrient absorption, or function in salt excretion (Gutschick 1999). Overall, trichomes affect insect herbivores by influencing oviposition, altering herbivore movement, reducing growth and fecundity, and by influencing interactions with natural enemies (Haddad and Hicks 2000, Andres and Connor 2003, Kennedy 2003). Simply, trichomes can be divided into two general types, namely non-glandular and glandular (Levin 1973, Hare 2005). Multiple trichome types can occur on the same individual plant, the same trichome type can vary in density and size among individuals and populations, and some plant species are dimorphic for trichome type with glandular and non-glandular trichomes occurring in different individuals (Hare and Elle 2002, Kennedy 2003). Non-glandular trichomes physically interfere with feeding and colonization, especially for small insects such as first-instar lime aphids (*Eucallipterus tilliae*) that die because they are denied access to the leaf surface where they reach the phloem (Dixon 1998). When the dense bed of stellate trichomes is removed, the young aphids feed and flourish. Similarly, shaving the dendroid trichomes from mullein (*Verbascum*) leaves promotes colonization by the aphid *Aphis verbascae* (Keenlyside 1989). Other small sap-feeding herbivores such as whiteflies and leafhoppers also fail to colonize or successfully grow on cultivars of crop plants rendered resistant by dense beds of leaf trichomes (Butler *et al.* 1991, Goertzen and Small 1993). Larger herbivores too can be very adversely affected by non-glandular trichomes. For instance, larvae of *Heliconius melpomene* that consume a number of passion-vine species (*Passiflora*) are excluded from the widespread *Passiflora adenopoda* (Gilbert 1971). The leaves and tendrils of this vine are covered with hooked trichomes. As larvae attempt to feed, their prolegs catch on the trichomes and tear, haemolymph exudes and the larvae quickly desiccate and die (Figure 4.7A and B). Similarly, the growth and survival of the swallowtail butterfly, *Papilio troilus*, and several noctuid moth caterpillars are negatively affected by leaf pubescence, and in some cases reduced performance and survival occur because trichomes are of lower nutritional quality than other leaf tissues (Lambert *et al.* 1992, Haddad and Hicks 2000, Andres and Connor 2003). It should be emphasized that not all herbivores are negatively impacted by trichomes, and in fact some herbivores prefer plants with dense trichomes for oviposition, and if adapted perform better on such plants.

The exudates from glandular trichomes can deter, mire or poison insect herbivores (Ranger and Hower 2001, Andres and Connor 2003, Kennedy 2003). Small herbivores such as aphids and leafhoppers become entrapped and die in the sticky exudates produced by glandular trichomes on their host plants (Dixon 1998, Kennedy 2003, Figure 4.7C, D and E). However, the exudates of glandular trichomes also contain toxins, which in the case of tomato confer resistance to a variety of herbivores including aphids, whiteflies, lepidopterans and dipteran leaf miners. Although the physical deterrency of non-glandular trichomes is clear, it is often difficult to isolate the effects of mechanical defense, allelochemistry and nutrition when glandular trichomes are involved because the battery of "plant defenses" is so intimately intertwined.

Scaling up to herbivore communities, an extensive study of the insect guilds on manzanita (*Arctostaphylos* species) showed that leaf pubescence has both community-wide and guild-specific effects on folivorous insects because of its selective effects on free-living, but not concealed, feeding guilds (Andres and Connor 2003). Feeding by herbivores can also induce the production of trichomes on the new growth of their host plants, with adverse consequences not only for the inducer, but also for the community of other herbivores feeding on the plant (Baur *et al.* 1991, Agrawal 1998, 1999, 2000a, Traw and Dawson 2002). Induced defenses at large will be dealt with in a forthcoming section of this chapter.

Leaves of some plant species also bear other surface structures that deter herbivore attack. For example, protrusions on the stipules and meristems of *Passiflora* bear an amazing resemblance to the eggs of *Heliconius* butterflies, the primary herbivores on these plants (Benson *et al.* 1975, Williams and Gilbert 1981, Figure 4.8). So-called "egg mimics" significantly reduce the number of potential oviposition sites because adult butterflies avoid placing eggs in their presence. Selection has apparently favored oviposition site scrutiny in these visually oriented butterflies because upon hatching larvae are very cannibalistic and consume other nearby eggs.

In contrast to plants with trichome-laden surfaces, many plants have leaves rendered slippery by the surface waxes that provide protection from desiccation and pathogen invasion (Eigenbrode and Espelie 1995, Eigenbrode *et al.* 2000, Rutledge *et al.* 2003). Such waxes often pose problems of attachment for many herbivores. For example, glossy varieties of cabbage (*Brassica oleracea*) deter foraging and feeding by larvae of the diamondback moth (*Plutella xylostella*), caterpillars of the imported cabbage butterfly (*Pieris rapae*) and cabbage aphids (*Brevicoryne brassicae*), whereas other herbivores such as flea beetles (*Phyllotreta cruciferae*) are able to maintain a foothold. In the cabbage system, complex interactions among the structure of surface waxes and the tarsal morphology of insects combine to influence attachment (Eigenbrode and Jetter 2002). Similar effects have been documented in natural systems, whereby young leaves of some *Eucalyptus* species possess a waxy bloom that precludes attachment and feeding by beetles (Edwards 1982). Overall, the distribution and abundance of leaf

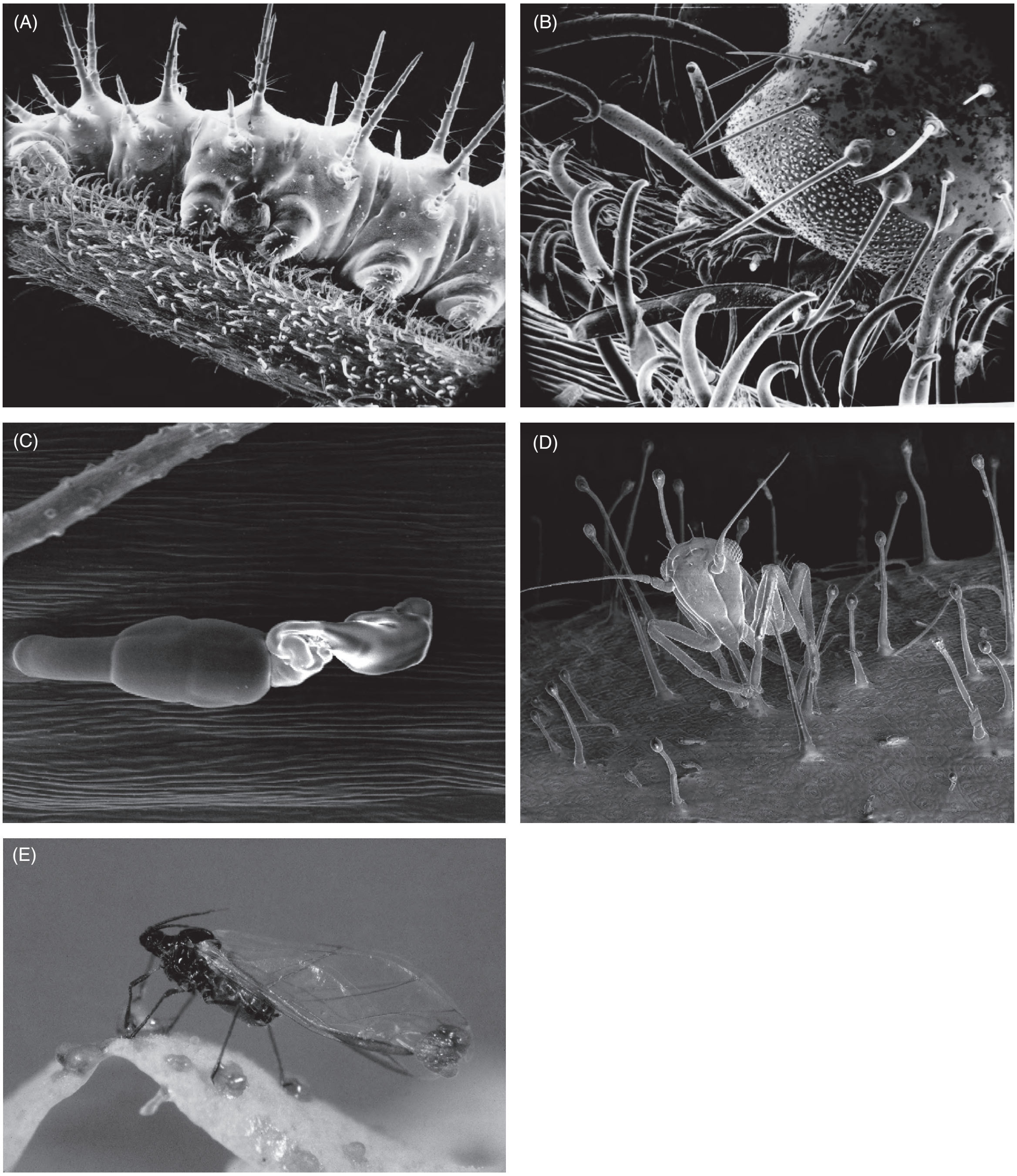


Figure 4.7 (A) Caterpillar of *Heliconius melpomene* caught on the hooked trichomes of *Passiflora adenopoda*. (B) Close-up of trichomes hooked into the caterpillar's proleg. From Gilbert (1971). (C) A glandular trichome of an alfalfa clone resistant to potato leafhopper, *Empoasca fabae* (×1000), which has released exudates after damage. (D) A nymph of the potato leafhopper entrapped in the glandular exudates. From Ranger and Hower (2001). (E) Adult of the aphid *Rhopalosiphum maidis* entrapped in the latex of its lettuce host plant, *Lactuca sativa*. From Dussourd (1995) © Dr. David Dussourd. (A) and (B) From Gilbert, L. E. 1971. Butterfly-plant coevolution: has *Passiflora adenopoda* won the selectional race with heliconiine butterflies? *Science* **172**:585–586. (C) and (D) reprinted with permission from Blackwell Publishing. See color plate section.

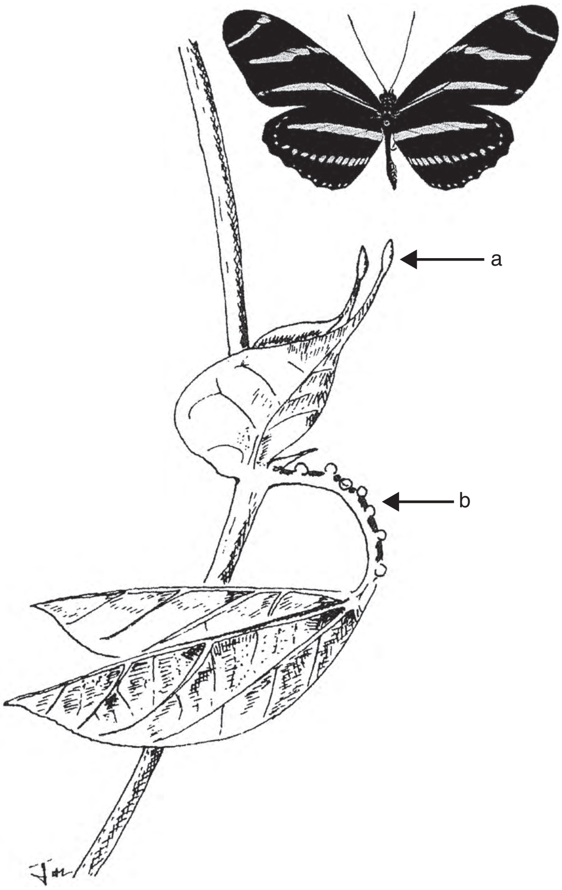


Figure 4.8 Protrusions on the stipules (a) of *Passiflora cyanea* bear a remarkable resemblance to the eggs of *Heliconius* butterflies, the primary herbivores on this group of plants. Adult butterflies avoid placing their eggs in the presence of so-called "egg mimics," significantly limiting the number of potential oviposition sites and ultimately reducing herbivory. Extrafloral nectaries (b) are sugar-secreting glands that provide carbohydrate resources to ants and other predators that further reduce the density of insect herbivores on *P. cyanea*. Original from Gilbert and Raven (1975); adapted from Strong *et al.* (1984a).

feeding beetles on *Eucalyptus* spp. is related to the waxy bloom on the trees and the attachment abilities of the individual beetle species (Edwards and Wanjura 1991).

Although waxy leaf surfaces and dense trichomes often deter some natural enemies, not all predators and parasitoids are adversely affected (Bottrell *et al.* 1998, Eigenbrode and Jetter 2002, Kennedy 2003, Eigenbrode 2004). For example, some natural enemies are better able to negotiate agricultural crop varieties with reduced surface waxes on their leaves, consume more herbivores and thus exacerbate the direct adverse effect of slippery leaves on herbivores. Likewise, fire ants (*Solenopsis invicta*) are not deterred by soybean plants with dense trichomes and in fact suppress lepidopteran caterpillars better on pubescent varieties than on glabrous ones (Styrsky *et al.* 2006). Thus, to assess the general effect of plant surfaces on the abundance of insect herbivores, one must take into account the direct effects of surface structure on herbivore attachment and the indirect effects of altered foraging by natural enemies.

4.3.4 Herbivore counteradaptations to mechanical plant defenses

Insect herbivores have evolved a number of morphologies and behaviors that allow them to cope in part with the mechanical defenses of plants. Concerning leaf hardness, insights can be gained by comparing the morphology of herbivores that feed on silica-rich grasses with that of forb feeders. For instance, the relative head and associated mandibular mass of grass-feeding grasshoppers and lepidopterans is larger than that for related forb feeders (Bernays 1986), and egg size in the Satyridae and Hesperiidae (Lepidoptera) is positively related to the "leaf toughness" of their host grass (Fukuda *et al.* 1984, Nakasuji 1987). Larvae hatching from large eggs have large heads and mandibles which retain their cutting and masticating capability until worn mandibles are renewed at the next molt. Thus, large head and mandible size has apparently allowed some herbivores to exploit grasses, but the price these species have paid for this dietary habit is reduced fecundity. Also, several species of grasshoppers (e.g., the grass-feeding *Chorthippus brunneus*) and lepidopterans (e.g., the Gypsy moth *Lymantria dispar*) can undergo extra molts during their immature development. Supplemental molting allows individuals to replace worn mandibles, and may allow for the exploitation of hard leaf tissues. Moreover, the mandibles of grass-feeding grasshoppers have “chisel-edged incisors” and a well-developed molar region for grinding, whereas forb-feeders do not (Bernays 1991).

Herbivores also have evolved tarsal morphologies for negotiating trichome-bearing leaf surfaces. Some aphids and mirid bugs, for example the specialist oak-feeding aphid, *Myzocallis screiberi*, have tarsal claws modified for grasping trichomes and moving through the densely pubescent leaves (Kennedy 1986, Southwood 1986). Several aphids exploiting host plants with glandular exudates have short tarsi or no tarsi whatsoever, an adaptation which apparently allows them to “tiptoe” through the trichomes (Moran 1986, Bernays 1991). Alternatively, other aphids have solved the problem of accessing the leaf surface by evolving a longer proboscis, which allows them to feed through the dense bed of trichomes (Dixon 1998). Larvae of the Neotropical butterfly, *Mechanitis isthmia*, feed on *Solanum* sp. whose leaves are covered with dense beds of trichomes (Rathcke and Poole 1975, Young and Moffett 1979). Eggs are deposited in masses and upon hatching larvae aggregate on the lower surface of leaves where they collectively spin a “silken scaffolding” over the top of the trichome bed. Subsequently, larvae roam the top of the silken mat where they clip trichomes and safely consume leaf tissue.

Both mandibulate and sap-feeding herbivores have evolved tarsal modifications that allow attachment on waxy leaf surfaces (Bernays 1991). For instance, some chrysomelid beetles, like gecko lizards, are able to hold onto glossy leaf surfaces because of the molecular adhesion provided by thousands of minute setae on their tarsal pads (Stork 1980). Likewise, certain *Empoasca* leafhoppers produce a minute suction cup with their tarsal pads, which provides very effective attachment on smooth leaf surfaces (Lee *et al.* 1986). Notably, the tarsal adaptation works well on preferred glossy leaf surfaces, but is ineffective on pubescent leaves.

4.3.5 Allellochemical barriers to herbivore attack

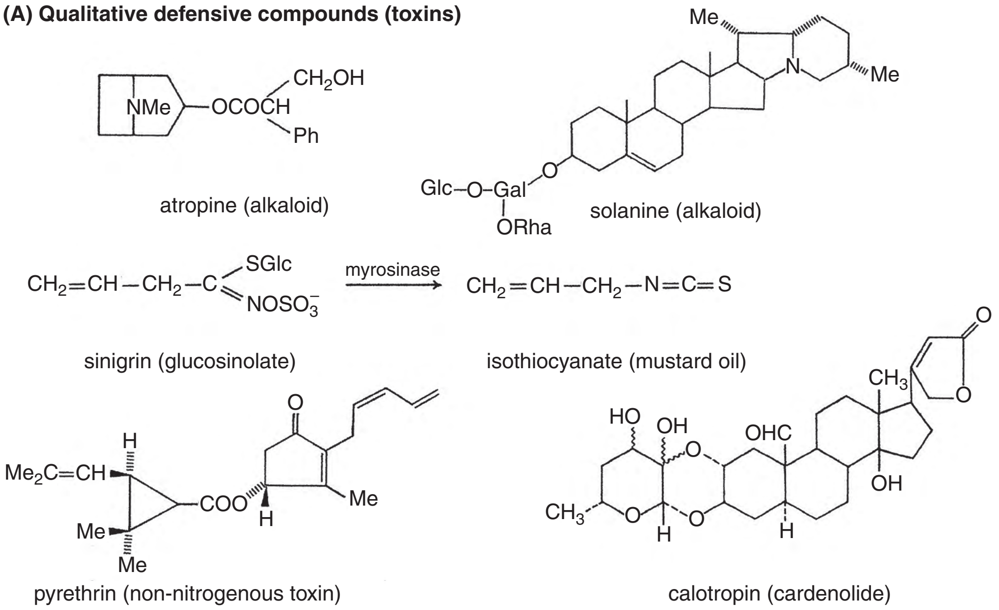
The insecticidal properties of plants have been known for several centuries. For instance, water extracts of tobacco (Solanaceae) were used to kill sap-feeding insects in 1690, rotenone (Fabaceae) was used to kill caterpillars in 1848 and pyrethrum (Asteraceae) has been used as an insecticide since 1880 (Ware 1991). Moreover, the active fractions of these **botanical insecticides** were all isolated prior to 1924 (Matsumura 1985). Despite the long-standing knowledge of the toxic properties of plants by entomologists and natural-product chemists, the role that **secondary metabolites** (also called **secondary chemicals** or **allelochemicals**) play in plant-insect interactions has been realized relatively recently. Brues (1946), Painter (1951), Fraenkel (1959, 1969), Ehrlich and Raven (1964) and Feeny (1968, 1970) were among the first ecologists to promote the importance of allelochemicals as “defenses” against insect herbivores. Since then, the literature documenting the structure, diversity, distribution, concentration, induction, metabolism and antiherbivore properties of allelochemicals has grown enormously (e.g., Rosenthal and Berenbaum 1991, 1992, Tallamy and Raupp 1991, Harborne 1993, Karban and Baldwin 1997, Agrawal *et al.* 1999b, Kessler and Baldwin 2002, Boege and Marquis 2005).

Secondary metabolites are deemed “secondary” because they play little or no known functional role in the **primary plant metabolism** underlying plant growth and reproduction (Whittaker 1970). Literally thousands of secondary metabolites have been isolated from plants and there is unequivocal and widespread evidence that these compounds serve a defensive function in plants against herbivores and pathogens (Rosenthal and Berenbaum 1991, Harborne 1993, Karban and Baldwin 1997, Kessler and Baldwin 2002). For instance, allelochemicals have been shown to affect nearly every aspect of plant–herbivore interactions, including their preference for plants (host-plant selection) and performance (growth, survival, reproduction and dispersal) on particular plants or plant parts. Despite their antiherbivore and pathogen properties, however, there is also a clear indication that secondary metabolites serve other functions, such as protection from ultraviolet radiation (e.g., flavonoids), storage compounds (e.g., nitrogen-containing alkaloids) and plant signaling compounds (e.g., terpenoids) (Rhoades 1979, Chadwick and Whelan 1992, Burchard *et al.* 2000, Theis and Lerdau 2003). Thus, selective pressures associated with herbivory and pathogen attack are not the only forces influencing the evolution of secondary metabolites. Before exploring factors that influence the distribution and abundance of secondary metabolites in plants and the counteradaptations of insect herbivores that allow them to cope with such compounds, we need to consider the diversity of secondary metabolites and their modes of action.

The tremendous diversity of allelochemicals makes it difficult to organize these compounds into a conceptual and useful framework. Most classifications of allelochemicals are oversimplified and are based on modes of action or how allelochemicals are expressed in plants. One approach has been to divide secondary metabolites into two broad functional categories based on their modes of action, namely **qualitative** and **quantitative** defensive compounds, or alternatively **toxins** and **digestibility reducers** respectively (Feeny 1975, 1976, 1992, Rhoades and Cates 1976, Rhoades 1979). Secondary metabolites have also been classified as either **constitutive defenses**, compounds that are continuously present in the plant and do not change following attack, or **induced defenses**, metabolites that are synthesized or released from pre-existing ducts or cells following attack by insect herbivores or plant pathogens (Rhoades 1985, Karban and Baldwin 1997, Seigler 1998, Agrawal *et al.* 1999b, Kessler and Baldwin 2002).

Qualitative defensive compounds such as alkaloids, pyrethrins, glucosinolates, cardenolides, cyanogenic compounds and non-protein amino acids interfere with the metabolism of insect herbivores, thus the synonym toxins. In addition to interfering with metabolism, qualitative defensive compounds are characteristically small molecules, present in low concentrations in plant tissues (<2% dry weight), and possess properties facilitating their rapid synthesis, storage and transport (Rhoades and Cates 1976, Rhoades 1983, Figure 4.9A). Though cheap for plants to synthesize, qualitative defenses are thought to provide limited protection against coevolved specialist herbivores that have developed detoxification or tolerance mechanisms. Notably, naturally occurring plant toxins (e.g., nicotine) often share modes of action that are similar to those of some synthetic insecticides (e.g., the neonicotinoid insecticide imidacloprid) (Bloomquist 2006). For example, the pyridine alkaloid nicotine, naturally present in solanaceous plants such as tobacco, is toxic to insect herbivores because it interferes with neurotransmission (Steppuhn *et al.* 2004, Bloomquist 2006). Specifically, nicotine mimics the neurotransmitter acetylcholine by binding with acetylcholine receptors, which leads to the persistent overstimulation of cholinergic synapses, convulsions, paralysis and rapid death. Similarly, pyrethrins, derived from the flowers of *Chrysanthemum cinerariaefolium* (Asteraceae), are neurotoxins that have potent effects on nerve impulse generation. Cyanogenic compounds (e.g., HCN) that occur commonly in rosaceous plants (e.g., *Prunus* sp.) act on the cytochrome system such that terminal respiration is inhibited, oxygen starvation occurs at the cellular level, and rapid death ensues (Harborne 1993). Other metabolites such as the cardenolides in milkweed plants (Asclepiadaceae, now Apocynaceae) act as sodium-potassium ATPase inhibitors and disrupt the sodium and potassium fluxes in cells (Malcolm 1991, Agrawal 2005).

(A) Qualitative defensive compounds (toxins)



(B) Quantitative defensive compounds (digestibility reducers)

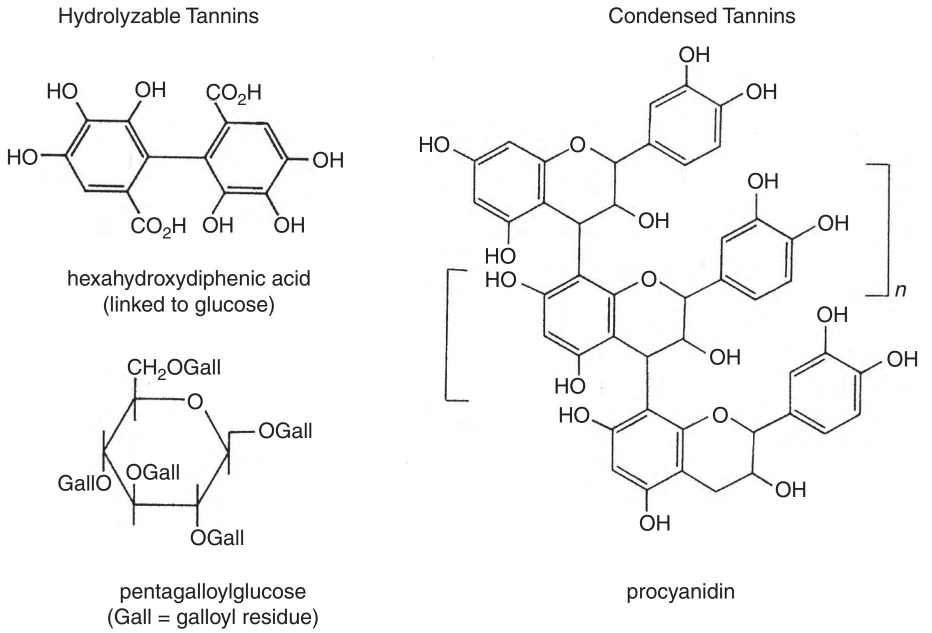


Figure 4.9 Structures of representative (A) qualitative secondary compounds (toxins) and (B) quantitative secondary compounds (digestibility reducers) in plants with known antiherbivore properties. The alkaloids atropine and solanine occur respectively in the solanaceous plants *Atropa belladonna* (deadly nightshade) and *Solanum tuberosum* (potato). After herbivory, the hydrolysis of compartmentalized glucosinolates such as sinigrin by myrosinases to form toxic thiocyanates occurs in crucifers (*Brassica* sp.). Pyrethrin is a non-nitrogenous toxin occurring in *Chrysanthemum cinearifolium* that has been used for years as a naturally occurring botanical insecticide. Calotropin is a common cardenolide present in milkweeds such as *Asclepias curassavica*. Hydrolyzable and condensed tannins in oak trees (*Quercus* sp.) reduce the digestibility of leaves for chewing herbivores. From Harborne (1993). Figures were published in *Introduction to Ecological Biochemistry*, 4th edition by J. B. Harborne. Copyright Elsevier (1993).

Moreover, glucosinolates and their hydrolysis products in mustards and related plants (Brassicaceae) degrade proteins and have adverse effects on respiratory physiology (Tsao *et al.* 2002, Wittstock *et al.* 2003, Halkier and Gershenzon 2006). Another well-studied group of toxins are the furanocoumarins, a photoactivated group of compounds in the parsley (Apiaceae) and citrus (Rutaceae) families that derive their toxicity by cross-linking with DNA strands and inhibiting transcription (Berenbaum *et al.* 1991, Wen *et al.* 2006).

Quantitative defensive compounds include **tannins**, **resins**, **latexes**, **cellulose**, **lignin** and **silica**, all compounds that can act to reduce the digestibility of plant tissues (Feeny 1976, Rhoades and Cates 1976, Rhoades 1983). In fact, most insect herbivores are unable to digest cellulose and lignin at all, the major structural components of plants (Martin 1991). Typically, quantitative defenses are large molecules (e.g., tannins are large polyphenols), occur in relatively high concentrations in plant tissues (5–20% dry weight) and are thought to be more costly to produce than toxins (Figure 4.9B). Though costly, quantitative defenses are thought to provide plants better protection against both specialized and polyphagous herbivores because they act in a dosage-dependent fashion. Although previously discussed as mechanical barriers to herbivore attack, cellulose, lignin and silica are also categorized as quantitative defenses because they reduce herbivore growth in a dosage-dependent manner, occur in high concentrations in plants, render plant tissues tough and difficult to digest, and act by inflicting mandibular wear (Feeny 1975, Rhoades and Cates 1976, Peeters 2002, Massey *et al.* 2006).

Another quantitative defense includes the tannins, a complex suite of high-molecular-weight phenolic compounds that occur abundantly in woody plants, both gymnosperms (e.g., pines) and angiosperms (e.g., oaks, willows, maples, eucalypts and acacias), but do also occur in some grasses (e.g., sorghum) (Haslam 1989, Hemingway and Karchesy 1989, Waterman and Mole 1994). Moreover, tannins are distributed in numerous tissues such as leaves, stems, buds, seeds and even roots. Tannins occur in a diversity of forms and are often divided structurally into **hydrolyzable tannins** (esters of sugars with gallic acid) and **condensed tannins** (polymers of flavonoids) (Harborne 1993, Ayres *et al.* 1997, Figure 4.9B). Tannins are thought to reduce the digestibility of plant tissues by precipitating plant protein from solution under certain conditions (Feeny 1970, Harborne 1993). Thus, when insect herbivores bite into tannin-rich leaves, compartmentalized tannins are brought into contact with plant proteins and digestive enzymes forming tannin–protein complexes that limit the digestion and assimilation of plant proteins (Harborne 1993, Hagerman and Robbins 1993, Zucker 1983, Ayres *et al.* 1997). Overall, however, there is very mixed support for the view that tannins act as a general quantitative defense against insect herbivores, with evidence both for and against (Smith *et al.* 1992, Hunter and Schultz 1995, Ayres *et al.* 1997, Forkner *et al.* 2004). For example, specific condensed tannins differ markedly in their antiherbivore activity and insect herbivores differ in their sensitivity to tannins (Ayres *et al.* 1997). In part, interspecific variation in herbivore response to tannins is likely attributable to differences in gut physiology that can ameliorate tannin effects (Berenbaum 1980, Martin and Martin 1984, Appel and Maines 1995). Complicating matters further is the knowledge that some studies implicate toxicity rather than digestive inhibition as the mode of action of some tannins (Zucker 1983, Steinly and Berenbaum 1985, Ayres *et al.* 1997), thus challenging the broad distinction between quantitative and qualitative defenses.

Many plants also contain **proteinase inhibitors**, enzymes that inhibit the action of digestive protease enzymes (trypsin and chymotrypsin) in the guts of herbivorous insects (e.g. Lepidoptera), thus making plant proteins less available and adversely affecting growth (Ryan 1990). Because proteinase inhibitors are protein-based enzymes, the distinction between primary and secondary metabolites becomes less clear, and suggests that even some "primary metabolites" may play a defensive role (Berenbaum 1995).

Another major group of quantitative defenses are the resins and latexes, sticky plant secretions synthesized in large quantities by many plants, including gymnosperms and angiosperms (Farrell *et al.* 1991, Phillips and Croteau 1999, Becerra *et al.* 2001, Langenheim 2003). Resins are complex mixtures of volatile and non-volatile terpenoids (e.g., monoterpenes, diterpenes, triterpenes and sesquiterpenes) and/or phenolic compounds that, in addition to their defensive function against insect herbivores and pathogens, also play a role in wound repair, water retention and UV protection. Latexes are emulsions (aqueous suspensions of insoluble materials) that contain metabolites such as alkaloids, cardenolides, terpenes and phenolics. Typically, resins are secreted from glands (e.g., creosote bush, *Larrea tridentata*) or trichomes (e.g., hemp, *Cannabis sativa*) on the plant surface or they can be sequestered intercellularly in resin ducts or canals such as the familiar pitchy oleoresins (terpenoids) in coniferous trees (Farrell *et al.* 1991, Langenheim 2003, Keeling and Bohlmann 2006). In contrast, latexes such as the milky secretions in milkweeds (Apocynaceae) and spurges (Euphorbiaceae) are contained in living cells called laticifers. Resins can be deployed either constitutively from surface glands or, like latexes, they can be released (induced) in copious amounts when herbivores sever resin-bearing canals, a subject we will pursue in greater depth shortly. The mode of action of resins and latexes is complex and often involves both physical and toxic components. For example, many resins and latexes inhibit insect herbivores simply by entrapping them or impeding feeding by "gumming up" their mandibles, thus their espoused role as a quantitative defense with dosage-dependent effects (Dussourd 1995, Phillips and Croteau 1999, Langenheim 2003). In this sense, these compounds are not digestibility reducers *per se*, but they do physically deter feeding and may result in digestive costs as well. Additionally, resins and latexes often contain toxins or feeding and oviposition repellents, thus complicating their assignment to general plant defense categories (Dussourd and Hoyle 2000, Langenheim 2003, Keeling and Bohlmann 2006).

Another way to classify secondary metabolites is based on their expression in plants. Once synthesized, **constitutive defenses** are always expressed in plant tissues. There is tremendous diversity in the composition and concentration of naturally occurring constitutive defenses, ranging from mechanical defenses (e.g., cellulose, silica and trichomes in some cases) to digestibility reducers (e.g., resins and tannins) and toxins (e.g., alkaloids and furanocoumarins) (Zangerl and Rutledge 1996, Keeling and Bohlmann 2006). In contrast, **induced defenses** (also called **induced resistance**) are activated by herbivore feeding (e.g., mechanical damage and saliva) or pathogen attack (Karban and Baldwin 1997, Agrawal *et al.* 1999b, Kessler and Baldwin 2002, Traw and Dawson 2002, Traw and Bergelson 2003, Bostock 2005, Stout *et al.* 2006). A vast array of secondary metabolites and trichomes can be induced by herbivore feeding. Allelochemicals known to be induced by herbivores include defensive proteins (proteinase inhibitors), phenolics (phenolic acids, phenolic glycosides, furanocoumarins, condensed and hydrolyzable tannins, and lignin), terpenoids (monoterpenes, diterpenes and cucurbitacins), alkaloids (nicotine, quinolizidine and tropane) and indole glucosinolates (Green and Ryan 1972, Haukioja 1990, Constabel 1999, Kessler and Baldwin 2002). Moreover, some compounds once categorized as constitutive defenses are now known to be inducible (e.g., silica), further challenging the traditional classification of plant defenses (Massey *et al.* 2006).

Induction of phytochemicals by herbivores can take place in two ways, by the release of "preformed chemicals" or by "activated synthesis" both of which can have very negative consequences for herbivores (Karban and Baldwin 1997, Agrawal 1999, Denno and Kaplan 2007). Unlike most activated allelochemicals, the induction of "preformed defenses" does not result exclusively from changes in synthesis or degradation (Karban and Baldwin 1997). Rather, the release of preformed chemicals results from the disruption of tissues where such chemicals are compartmentalized or from the mixing of locally separated substrates and enzymes during tissue damage. Examples of preformed-compartmentalized allelochemicals include the terpenoids stored in the resin ducts of conifers (Raffa 1991, Raffa *et al.* 2005, Keeling and Bohlmann 2006), the cardenolide-containing latex borne in the canal systems of milkweeds (Dussourd and Eisner 1987) and the furanocoumarins housed in oil tubes of wild parsnip plants (Berenbaum and Zangerl 1999, Zangerl 1999). When herbivores puncture such ducts, canals or oil tubes during feeding, the compartmentalized allelochemicals are released, which can entrap and kill herbivores attempting to feed. A classical example involves bark beetles (Coleoptera: Scolytidae) that sever the pressurized resin ducts when boring into conifers (Raffa 1991, Keeling and Bohlmann 2006). When punctured, oleoresins "pitch out" and mire colonizing beetles. A more dramatic case involves plants in the genus *Bursera* (Burseraceae) that hold terpene-containing resins under such high pressure in canals that resins can squirt out or pool up when canals are severed by marauding herbivores (Becerra 1994, 2003). Other canal systems are so sensitive to a herbivore's touch that latexes exude from laticifers and entrap aphids (*Rhopalosiphum maidis*) that simply walk on the surface of wild lettuce plants (*Lactuca sativa*) (Dussourd 1995, Figure 4.7E). Examples of preformed allelochemicals that are induced by the mixing of separated substrates when plant tissue is damaged include the blending of cyanogenic glycosides and catabolic enzymes with the production of hydrogen cyanide in cyanogenic plants (Poulton 1990), the hydrolysis of compartmentalized glucosinolates by myrosinases to form toxic thiocyanates in crucifers (Chew 1988, Bones and Rossiter 1996, Agrawal and Kurashige 2003, Wittstock *et al.* 2003) and the conversion of phenolic glycosides to more active feeding deterrents such as salicin in poplars (Clausen *et al.* 1989).

"Activated allelochemicals" (e.g., proteinase inhibitors, alkaloids and glucosinolates) are synthesized following herbivory and result in an actual increase in the allelochemical pool with adverse effects on some herbivores (Karban and Baldwin 1997, Constabel 1999, Bostock 2005, Mewis *et al.* 2005). Induced increases in allelochemicals can occur over a range of time intervals from a few hours or days (rapid induced response) to the next season (delayed induced response) (Karban and Baldwin 1997, Agrawal *et al.* 1999b). Moreover, different herbivore species can induce very different levels of plant resistance with dramatically different effects on the assemblage of herbivores that feed later that season (Van Zandt and Agrawal 2004a,b, Viswanathan *et al.* 2005). Importantly, however, the distinction between "activated" and "preformed" induced responses is best viewed as a continuum, because some allelochemicals have elements of both. For example, although furanocoumarins, terpenes and glucosinolates occur in preformed states, they can be also induced several-fold by herbivory, suggesting induced synthesis (Lewinsohn *et al.* 1991b, Agrawal *et al.* 1999b, Zangerl 1999). Induced defenses that are activated by herbivore feeding (e.g., mechanical damage and saliva) or pathogen attack are communicated through the plant via signaling pathways that ultimately result in the production of an allelochemical (Felton and Eichenseer 1999, Bostock 2005, Stout *et al.* 2006).

The best-known signaling pathway in plants involves the wound hormone jasmonic acid, which underlies increases in many putative defensive chemicals against insects. Although jasmonic acid is clearly involved in the induction of plant responses to insect herbivores, it is thought that systemin, a small polypeptide hormone, is the compound that actually moves through the plant following herbivory to activate the formation of jasmonates and ultimately the synthesis of allelochemicals (Karban and Baldwin 1997, Staswick and Lehman 1999, Kessler *et al.* 2004, Bostock 2005). Salicylic acid is the corresponding elicitor of metabolites conferring resistance to pathogen attack. Notably, some evidence suggests a negative interaction between jasmonic-acid- and salicylic-acid-mediated response pathways, with a corresponding trade-off in resistance traits such that resistance to pathogens confers susceptibility to herbivores and vice versa (Bostock 2005, Stout *et al.* 2006). Although there is evidence for positive "crosstalk" (coordination) among jasmonic acid, salicylic acid and other phytohormonal signals (e.g. ethylene) as effectors of gene expression for resistance traits, the functional link between herbivore and pathogen resistance is not always clear, but is an exciting and growing area of research (Kessler and Baldwin 2002, 2004, Bostock 2005).

So far, we have discussed phytochemical signaling and induced resistance only in the context of within-plant processes. However, there is evidence that plants "eavesdrop" on herbivore-induced plant volatiles released from neighboring plants when they are attacked by herbivores (Baldwin *et al.* 2006, Kessler *et al.* 2006). The result of this "priming" is the activation of signaling pathways and ensuing defenses before herbivore attack. The hypothesis of "talking trees" was conceived decades ago (Baldwin and Schultz 1983), but is now gaining broader acceptance and may allow researchers to determine whether "fluency" (the ability to detect and respond to volatile signals from attacked neighbors) enhances plant fitness in natural communities (Engelberth *et al.* 2004, Baldwin *et al.* 2006, Kessler *et al.* 2006).

Understanding the biochemical machinery and genetics underlying the expression of resistance traits to herbivores and plant pathogens should allow not only for the elucidation of constraints on the evolution of induced resistance, but also for its genetic manipulation (Kessler and Baldwin 2002, 2004, Taylor *et al.* 2004, Jalali *et al.* 2006). Breakthroughs in our knowledge of signaling pathways in plants have already led to important implications for agriculture. For instance, the use of natural elicitors such as jasmonic acid has implications for the management of pest herbivores (Thaler 1999a,b, 2002a). Specifically, applications of jasmonic acid on tomatoes result in increased levels of proteinase inhibitors and polyphenol oxidases, metabolites implicated in resistance against insect herbivores. Importantly, jasmonic-acid-induced plants can experience lower densities of herbivores and incur much less herbivory than control plants.

Molecular techniques have been used to genetically engineer constitutive defensives into crop plants (Ely 1993, Gould 1998, Cerda and Paoletti 2004, Christou *et al.* 2006, Ferry *et al.* 2006). So-called **transgenic crops** contain resistance-expressing genes that have been artificially inserted into their genomes. The inserted gene sequence (the **transgene**) may derive from other organisms such as unrelated plants or bacteria, and organisms including transgenic crops containing transgenes are called **genetically modified organisms**. For example, corn, rice, cotton and many other crops have been genetically altered to express a bacterial endotoxin (Ely 1993, Christou *et al.* 2006, Ferry *et al.* 2006). Genes expressing the endotoxin are obtained from the soil-dwelling bacterium *Bacillus thuringiensis* (*Bt*), a species that is toxic to many lepidopterans and is marketed worldwide as microbial insecticide (Gill *et al.* 1992, Entwistle *et al.* 1993). Millions of acres of crops engineered with *Bt* endotoxin (e.g. *Bt* corn) have been planted and have proved very effective against serious lepidopteran pests. Potential problems arising from *Bt* crops include the killing of non-target organisms, the development of resistance in targeted pests and the migration of transgenes to other plants via hybridization and introgression (Tabashnik *et al.* 1991, Cerda and Paoletti 2004, Michaud 2005, O'Callaghan *et al.* 2005, Andow and Zwahlen 2006). For instance, under artificial conditions, when genetically modified corn was first deployed, pollen expressing the *Bt* endotoxin drifted to nearby milkweed plants where it killed non-target herbivores such as Monarch butterflies (*Danaus plexippus*) (Losey *et al.* 1999). Further risk assessment showed that the hazard was less than originally observed. Advances in *Bt*-engineered crops have resulted in plants that express the toxin only in certain tissues or crop stages targeted for pest consumption and not in pollen (Cerda and Paoletti 2004, Christou *et al.* 2006). Nonetheless, there is still concern over the use of transgenic crops, which has spurred much research on non-target herbivores and natural enemies as well as resistance management (Cerda and Paoletti 2004, Dively 2005, Andow and Zwahlen 2006, Christou *et al.* 2006).

4.3.6 Herbivore counteradaptations to allelochemical plant defenses

Insect herbivores have evolved a variety of biochemical and behavioral mechanisms that allow them to cope with the qualitative, quantitative and induced defenses of plants (Karban and Agrawal 2002). These mechanisms include **detoxification**, **excretion**, **sequestration**, **behavioral deactivation** or **avoidance**, and **host-plant location**. Detoxification is the most frequent mechanism used by both monophagous and polyphagous insect herbivores to overcome the qualitative defenses (toxins) in their host plants (Brattsten 1992, Schuler 1996, Feyereisen 1999). The major detoxification enzyme systems in insects include **cytochrome P450 monooxygenases** (historically called **mixed-function oxidases**), **glutathione S-transferases** and **esterases**. P450 enzymes are a diverse class of enzymes that play a critical role in the degradation of allelochemicals such as alkaloids, furanocoumarins and pyrethrins, as well as many synthetic insecticides (Berenbaum and Zangerl 1994, Li *et al.* 2003). Moreover, P450s can be induced after exposure to secondary metabolites and their induction is related to diet choice (Hung *et al.* 1997, Feyereisen 1999). For instance, caterpillars of *Manduca sexta* increase their consumption of alkaloid-rich food only after enhancing the midgut activity of P450s, and decrease their choice of alkaloid-containing food when P450 activity is blocked.

Herbivores that specialize in “toxic plants” often employ other more specialized detoxification systems that allow them to metabolize defensive metabolites unique to those plants (Karban and Agrawal 2002). A good example involves the bruchid weevil, *Caryedes brasilensis*, which feeds very successfully on the seeds of the tropical legume, *Dioclea megacarpa*, seeds that are toxic to most herbivores because they contain high concentrations of the non-protein amino acid canavanine (Rosenthal *et al.* 1982). Canavanine derives its toxicity because, as an analog to the protein amino acid arginine, it becomes incorporated into polypeptide chains, thereby disrupting protein function. In *C. brasilensis*, RNA transferase discriminates between arginine and canavanine such that canavanine is not incorporated into polypeptides. Moreover, canavanine is metabolized and the resulting nitrogen-rich compounds become sources for the synthesis of amino acids, thus resulting in great nutritional benefit.

Insect herbivores have also evolved mechanisms to counter the effects of digestibility-reducing metabolites (quantitative defenses). Recall that tannins can reduce the digestibility of plant tissues by precipitating plant proteins. However, the precipitating effects of tannins are most effective under specific midgut conditions such as a low pH. Many lepidopterans offset the adverse effects of tannins by maintaining a high gut pH, surfactants or a specific redox potential, all of which can diminish the protein-binding properties of tannins (Berenbaum 1980, Martin and Martin 1984, Appel and Maines 1995). By inhibiting specific digestive enzymes, proteinase inhibitors also interfere with the digestion of plant proteins. In response, several lepidopterans have apparently countered by developing alternative proteinases that are insensitive to inhibitors in their diet, thereby minimizing growth penalties (Broadway 1996).

Metabolic counteradaptations to both activated and preformed induced defenses are also employed by insect herbivores. Regarding activated defenses, specialist herbivores exhibit feeding behaviors that apparently moderate the induction of certain allelochemicals. For example, feeding by *Manduca sexta* larvae on wild tobacco induces large increases in jasmonic acid pools, but there is little amplification of alkaloid production (Karban and Baldwin 1997). Larvae apparently feed in a "stealthy" fashion, reducing the alkaloid response below that resulting from a comparable amount of artificial defoliation (Baldwin 1988). In this case, it isn't known how larvae interfere with the plant's signal-transduction cascade. However, glucose oxidase, one of the principal components of caterpillar saliva, is responsible for suppressing induced resistance in tobacco by larvae of *Helicoverpa zea* (Felton and Eichenseer 1999, Musser *et al.* 2002). This enzyme prevents the induction of alkaloids by directly inhibiting the wound-signaling elicitor jasmonic acid or by antagonizing its interaction with other signaling pathways.

Specialist herbivores have defeated preformed inducible defenses such as the compartmentalized precursors (glucosinolate and myrosinase) to toxic thiocyanates in crucifers. For instance, larvae of the cabbage white butterfly (*Pieris rapae*) employ a gut protein that prevents the formation of toxic thiocyanates by redirecting glucosinolate hydrolysis to nitriles that are subsequently excreted (Wittstock *et al.* 2004). In contrast, larvae of *Plutella xylostella*, a lepidopteran also specialized to feed on glucosinolate-rich crucifers, desulfate glucosinolates to metabolites that can no longer act as substrates for myrosinases, thus precluding the formation of toxic thiocyanates (Ratzka *et al.* 2002). Likewise, larvae of the Neotropical butterfly, *Heliconius sara*, employ a novel enzyme system that allows them to metabolize compartmentalized cyanogenic glycosides present in their *Passiflora auriculata* host plant to thiols (Engler *et al.* 2000). Moreover, this process precludes the release of hydrogen cyanide (HCN) and allows caterpillars to use the otherwise toxic compound as a nitrogen source.

Other herbivores employ excretion as a mechanism to cope with secondary metabolites. For instance, larvae of the tomato hornworm (*Manduca sexta*) have evolved an excretion system that eliminates non-metabolized nicotine much faster than other herbivores due to a specialized alkaloid transport system in their Malpighian tubules. Malpighian tubules are the excretory organs of insects that remove nitrogenous waste products (also toxic alkaloids) from the haemolymph and deposit them in the hind gut, where they are eliminated.

Many phytophagous insects, especially monophagous species, sequester plant-derived metabolites either as a non-toxic form in the haemolymph or as toxins stored in the cuticle or in specialized glands or organs where their potential toxic effects are isolated (Blum *et al.* 1990, Bowers 1992, 1993, Dyer 1995, Karban and Agrawal 2002). Sequestered toxins include the cardenolides deposited in the integument of monarch butterflies (*Danaus plexippus*) and milkweed bugs (*Oncopeltus fasciatus*), iridoid glycosides present in the integument of checkerspot butterflies (*Euphydryas phaeton*), glucosinolates stored in the haemolymph of sawflies (*Athalia rosae*), pyrrolizidine alkaloids in the haemolymph of leaf beetles (*Oreina cacaliae*) and phenolic glycosides present in the eversible glands of larval chrysomelid beetles (*Phratora vitellinae*) (Brower 1984, Bowers 1992, 1993, Pasteels *et al.* 1983, Hartmann *et al.* 1999, Trigo 2000, Müller *et al.* 2001). Although it is tantalizing to view sequestration as a metabolic process by which herbivores avoid plant toxins, most evidence suggests that the primary selective force underlying sequestration is defense against natural enemies (Pasteels and Gregoire 1983, Denno *et al.* 1990, Karban and Agrawal 2002). For example, many herbivores that sequester toxins are warningly colored (**aposematic**) and unpalatable to predators. Moreover, although many sequestered toxins are acquired during the larval stage, some adult butterflies (Danainae and Ithomiinae) and moths (the arctiid *Utethesia ornatrix*) derive their distaste from toxins (e.g., pyrrolizidine alkaloids) ingested in the nectar of their floral resources and not from larval host plants, further implicating predation in the evolution of sequestration (Bowers 1993). Moreover, sequestration is a costly process and its advantage may be realized only in the presence of natural enemies (Karban and Agrawal 2002). Nonetheless, until shown otherwise, sequestration is a possible mechanism by which plant toxins are rendered innocuous.

Insect herbivores have evolved a suite of behaviors, so-called counterploys, that allow them to avoid or diminish the adverse consequences of secondary metabolites, particularly quantitative defenses like resins and latexes that are contained in ducts or canals (Dussourd 1993, Paine *et al.* 1997, Karban and Agrawal 2002). A classic case involves bark beetles (Coleoptera: Scolytidae) that employ an aggregation pheromone to “mass attack” single pine trees (Seybold *et al.* 2000, Keeling and Bohlmann 2006). The synchronized attack by thousands of individuals boring into a single tree depressurizes the resin canal system, diminishes the “pitching out” of oleoresins that potentially might entrap beetles and facilitates tree colonization. Notably, in some bark beetle species the aggregation pheromone, which is produced by the first arriving colonists, is metabolized from the terpenes in the tree under attack.

Other mandibulate herbivores deactivate canal-borne defenses in many latex- or resin-bearing plants by **clipping veins** or “**trenching**” entire leaves before they feed distal to the cuts on leaves (Dussourd and Eisner 1987, Becerra and Venable 1990, Becerra 1994, 2003, Dussourd and Denno 1991, 1994, Dussourd 1993, Figure 4.10). Vein cutting and trenching block the flow of latex or resin rendering otherwise defended leaf tissues suitable for feeding. Vein-cutting behavior occurs commonly in herbivores associated with milkweed plants (Apocynaceae), such as chrysomelid beetles (*Labidomera clivicollis*), cerambycid beetles (*Tetraopes tetrophthalmus*) and danaid butterflies (*Danaus gilippus* and *D. plexippus*), but has been observed in numerous other families of latex or resin-bearing plants (e.g., Anacardiaceae, Apocynaceae, Bursearaceae, Moraceae). In contrast, trenching behavior occurs on a mutually exclusive group of plants (e.g., Apiaceae, Asteraceae, Caricaceae and Curcurbitaceae). Notably, there is amazing correspondence between behavior and the architecture of the canal systems in latex-bearing plants (Dussourd and Denno 1991). Vein cutting occurs in plants with branching canal architecture, whereas trenching is employed by herbivores on plants with net-like canal systems. Generalist caterpillars which lack these behavioral counterploys perform very poorly on intact plants, but many of them can feed successfully if latex-bearing plants are experimentally depressurized (Dussourd and Denno 1994). The evolution of vascular sap-feeding has allowed these herbivores to largely avoid allelochemicals that are compartmentalized in non-vascular tissues (Raven 1983). For instance, by feeding in the phloem of tobacco, green peach aphids (*Myzus persicae*) avoid ingesting nicotine that occurs in other plant tissues (Guthrie *et al.* 1962).

Last, adapted specialist herbivores have turned the tables on plants by cuing in on “volatile plant toxins” to locate their specific host plants (Visser 1988, Bernays and Chapman 1994, Renwick 2002, Bruce *et al.* 2005). Host selection is a complex continuum between two extremes, namely herbivores choosing their host plant from a distance using olfactory and visual cues, and herbivores selecting their host after contact using gustatory information. The allelochemicals in crucifers (Brassicaceae) are involved in both processes. For instance, glucosinolates often serve as oviposition or feeding stimulants, whereas their volatile hydrolysis products (isothiocyanates) are attractants for several specialists, such as cabbage aphids (*Brevicoryne brassicae*), flea beetles (*Phyllotreta* spp.), diamondback moth (*Plutella xylostella*) and cabbage

Figure 4.10 Deactivating the defenses of latex-bearing plants. Insect herbivores nip the main midrib of their host plant with their mandibles, cut off flow of latex beyond the cut and subsequently feed distally where they avoid the latex. (A) Caterpillars of *Danaus gilippus* on *Asclepias curassavica* (Dussourd and Eisner 1987), (B) the milkweed beetle,

butterflies (*Pieris rapae*) (Renwick 2002, Bruce *et al.* 2005). Similarly, bark beetles (e.g., *Ips* spp. and *Dendroctonus* spp.) use conifer-produced terpenoids to facilitate host selection, colonize particular tree species and identify weakened trees that they can more easily colonize (Paine *et al.* 1997, Seybold *et al.* 2000, Raffa *et al.* 2005, Keeling and Bohlmann 2006). Several bark beetles even use metabolized conifer-derived terpenoids as sex attractants and aggregation pheromones to facilitate the mass colonization of trees. It is important to realize, however, that host-plant recognition often depends on ratios of plant volatiles and not just on the detection of particular compounds.

4.3.7 Leaf abscission as a plant adaptation to deter herbivory

Premature leaf abscission is thought to be an adaptive response to herbivore attack, which has particularly adverse effects on immobile herbivores such as gall-inducers and leaf miners (Faeth *et al.* 1981, Stiling and Simberloff 1989, Connor and Taverner 1997). The gall-inducing aphid *Pemphigus betae*, for example, induces premature leaf drop in cottonwood trees (*Populus*), reducing aphid populations by more than 50% (Williams and Whitham 1986). The induced response is density dependent; leaves with three or more galls are four times as likely to be dropped as leaves with one gall, and twenty times as likely to be abscised as ungalled leaves. Remarkably, 98% of the gall aphids that dropped to the ground died. For leaf-mining herbivores, early abscission can also result in reduced body size, lower fecundity, and increased exposure to predators, although the latter is not always the case (Waddell *et al.* 2001). Not surprisingly, plant growth hormones such as cytokinins, hormones that regulate leaf abscission, do occur in the ovipositional secretions of gall-inducing sawflies (Hori 1992, Schultz 2002). Thus, the biochemical machinery necessary to redirect leaf abscission appears to occur in herbivores that are particularly vulnerable to leaf drop.

4.3.8 Encouraging predators, parasitoids and mutualists as a defense against herbivores

Plants benefit from their association with enemies of insect herbivores, an important element in reducing herbivore damage. However, this large topic will be discussed more appropriately in Chapter 6 on mutualistic associations, and in Chapter 13 on multitrophic level interactions.

4.3.9 Spatial and temporal variation in plant allelochemistry and nutrition pose tracking problems for insect herbivores

We have just explored the tremendous variation in the types of defensive compounds and nutrients that occur in plants. Despite the counteradaptations that insect herbivores have evolved to cope with this chemical diversity, they still face tremendous spatial and temporal variation in plant nutrition, allelochemistry and morphology, making it

Caption for Figure 4.10 (*cont.*)
Tetraopes tetrophthalmus, on *Asclepias syriaca* (Dussourd 1999), (C) the katydid, *Scudderia furcata*, on *Apocynum cannabinum* (Dussourd 2009), and (D) the leaf beetle, *Labidomera clivicollis*, on *Asclepias syriaca* leaf (Dussourd 1999). (E) By trenching leaves of *Lobelia cardinalis*, the lepidopteran, *Enigmogramma basigera*, cuts the flow of latex to leaf tissue within the circumscribed trench where it then feeds (Dussourd 2005). Larvae of *Trichoplusia ni* expend an extensive time and energy trenching leaves of prickly lettuce (*Lactuca serriola*) before feeding distal to the trench; shown are larval trenching efforts after three passes (F) and 15 passes (G) (Dussourd and Denno 1994). (A) From Dussourd, D. E., and T. Eisner. 1987. Vein-cutting behavior: insect counterploy to the latex defense of plants. *Science* **237**:898–901. Reprinted with permission from AAAS. (C) Reprinted with permission from Blackwell Publishing. All photographs are © Dr. David Dussourd. See color plate section.

fundamentally difficult for them to locate optimal resources for oviposition and development (Denno and McClure 1983a, b). Failure to do so can have very negative effects on development and survival with extended effects on population dynamics. Variation in plant defenses and nutrition can be genetic or environmental and can occur within a single plant, among plants in a population, and across plant populations at larger habitat and geographic scales (Denno and McClure 1983a, Fritz and Simms 1992, Hunter *et al.* 1992, Orians *et al.* 2003, Johnson and Agrawal 2005). In the following sections, we elaborate on the sources and spatial scale of such variation and discuss its consequences for herbivores in the context of offsetting the apparent advantage insects have over plants with their short generation times and high recombination rates.

As individual plants develop, there is remarkable spatial and temporal variation in tissue chemistry, morphology and phenology with which herbivores must contend (Hunter *et al.* 1997, Karban and Thaler 1999, Brennan *et al.* 2001, Lawrence *et al.* 2003). In a spatial context, young terminal leaves are often more nutritious (%N) and less tough than mature leaves (Raupp and Denno 1983, Awmack and Leather 2002, Peeters 2002). Based on these two plant characteristics, herbivores should benefit by feeding on young leaves. However, certain allelochemicals that inhibit herbivore growth, such as flavonoid- and terpenoid-based resins, are often more concentrated in the terminal leaves of plants. The elevated resin level denies herbivores access to nitrogen-rich and tender terminals and forces them to feed on sub-optimal basal leaves. Larvae of both diprionid sawflies (*Neodiprion swainei*) on jack pine (*Pinus banksiana*) and the checkerspot butterfly (*Euphydryas chalcedona*) on the chaparral shrub (*Diplacus aurantiacus*) face this feeding compromise (Ikeda *et al.* 1977a, b, Lincoln *et al.* 1982). Likewise, in apple trees, the phenolic compound phloretin is more concentrated in terminal leaves and the within-tree distribution of phenolics is associated with the occurrence of apple-feeding herbivores (Hunter and Hull 1993, Hunter *et al.* 1994). Overall, spatial variation in secondary metabolites is thought to be an important factor influencing the distribution, abundance and population dynamics of insect herbivores (Hunter *et al.* 1996, Forkner *et al.* 2004).

Moreover, there is remarkable ontogenetic and temporal variation in leaf chemistry and morphology that places further constraints on insect herbivores (Denno and McClure 1983b, Krischik and Denno 1983, Forkner *et al.* 2004). A striking case of ontogenetic variation that leads to dramatic structural differences and several chemical discrepancies (e.g., tannin content) between young and mature foliage is called heteroblasty (Brennan *et al.* 2001, Lawrence *et al.* 2003, Gras *et al.* 2005). The genus *Eucalyptus* contains many species that exhibit this phenomenon whereby the foliage changes rapidly from juvenile to adult leaves as trees age. This ontogenetic shift has dramatic consequences for herbivores. For instance, the psyllid *Ctenarytaina eucalypti* develops only on juvenile shoots of *E. globulus*, whereas its congener *C. spatulata* is restricted to adult foliage. Similarly, one of the commonest herbivores on the same heteroblastic eucalypt is the leaf beetle *Chrysophtharta agricola*, which is nine times more abundant in the "adult foliage zone" of trees as it is in the juvenile zone. Thus, as trees undergo heteroblasty there are dramatic shifts in the composition of the herbivore assemblage.

There is also remarkable within-plant variation in plant chemistry and morphology at the seasonal scale. As the season progresses, leaves generally become less nutritious, tougher and more concentrated in digestibility-reducing metabolites such as tannins and resins, although there are certainly exceptions and much variation among specific defensive compounds (Krischik and Denno 1983, Raupp and Denno 1983, Awmack and Leather 2002, Salminen *et al.* 2004). Varley (1967) was the first to observe that the common herbivores such as winter moth (*Operophtera brumata*) on English oak (*Quercus robur*) feed early in the season just following bud break, whereas many rarer lepidopterans feed during the autumn. Feeny (1970) explored this pattern by measuring a variety of plant parameters and concluded that many common herbivores have adjusted their life histories to feed in spring when leaves are most nutritious and tender, and when tannin concentrations are lowest. More recently, seasonal increases in condensed tannin content have been reported for several North American oak species (Forkner *et al.* 2004). Moreover, the densities of several of the abundant herbivores on these oaks are negatively correlated with the tannin concentration. In a similar example, overwintering caterpillars of the checkerspot butterfly, *Euphydryas chalcedona*, emerge from diapause in spring to feed on the nutritious foliage of *Diplacus aurantiacus* when the concentration of leaf resin is at its seasonal low (Mooney *et al.* 1980, 1981). The important take-home message is that many insect herbivores on oaks and other plants face a very narrow seasonal opportunity for development on optimal resources. They are precluded from feeding very early in the season by bud scales that deny access to forming leaves and after bud break they face the rapid onslaught of increasing mechanical and constitutive defenses as the season progresses. Failure to time oviposition and development with optimal leaf resources during the narrow spring window can have very negative consequences for growth and survival (Hunter *et al.* 1997). Immobile herbivores such as leaf miners and gall inducers can face further constraints at the end of the growing season when deciduous trees drop their leaves, thus cutting the growing season short and often inflicting high levels of mortality (Faeth *et al.* 1981, Williams and Whitham 1986, Waddell *et al.* 2001).

An example involving the gall-inducing aphid *Pemphigus betae* on narrowleaf cottonwood (*Populus angustifolia*) highlights the difficulty that herbivores have in tracking suitable resources in a spatial and temporal mosaic of changing leaf morphology and chemistry (Whitham 1978, 1979, 1980, 1983, Zucker 1982). In early spring, when buds just begin to break, female aphids (stem mothers) hatch from overwintering eggs on the trunk, migrate to developing leaves and begin to initiate galls. Females methodically probe developing leaves with their stylets and the proliferating gall tissue soon encloses the aphid. She then produces up to 300 progeny parthenogenetically that develop within the gall. All colonizing females have settled and begun gall initiation within a 5-day period in early spring, and multiple females can initiate galls on the same leaf. The success of gall formation and progeny development, however, is very dependent on leaf size and gall position on the leaf, both of which vary in the concentration of phenolic glycosides. The basal position of the largest leaves on the tree is the optimal site for gall-induction and colonizing females engage in competitive shoving matches to win access to such sites for gall initiation (Figure 4.11A). On the largest available leaves ($>15\,\text{cm}^2$), the probability of females dying during gall formation was 0% whereas 80% of colonizing females die colonizing small leaves ($<5\,\text{cm}^2$). Similarly, female body weight and progeny number were 70% and 220% greater, respectively, on large leaves than on small ones. Remarkably, only 1.6% of all available leaves fall into the most suitable size class, as most leaves are much smaller. Within a leaf, females inducing galls at the leaf base were larger, died less frequently and produced more progeny than females initiating galls in more distal positions (Figure 4.11B). Not coincidentally, the concentration of phenolic glycosides is lowest where aphid performance is best, namely on the largest leaves and at the base of individual leaves.

4.3.10 Sources and consequences of variation in plant resistance: genes and environment

Because secondary metabolites and nutrients often determine the resistance or susceptibility of plants to herbivore attack, there has been great interest in discovering factors that influence the concentration

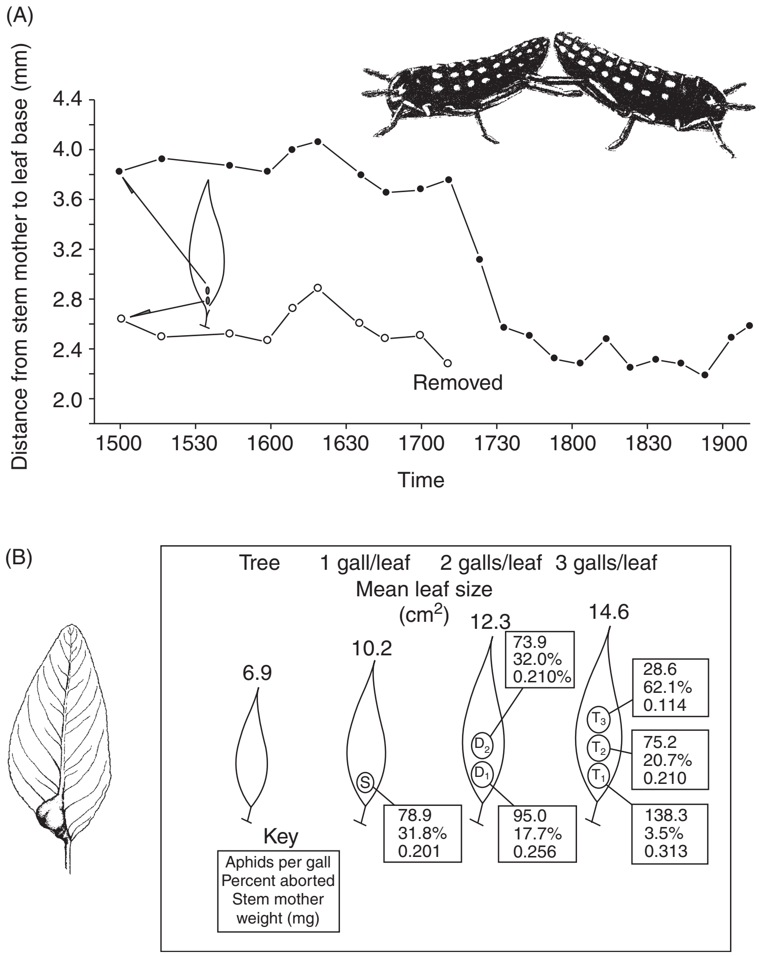


Figure 4.11 (A) Positions of two *Pemphigus betae* females (stem mothers) competing for optimal oviposition sites at base of a cottonwood leaf. When the dominant female is removed at 1710, the displaced female moves down to occupy the better site. (B) Effect of leaf size and gall position on the fitness of *Pemphigus betae* females. Numbers in each box, from top to bottom, refer to the number of aphids per gall, the percent of galls aborted and the weight of the female aphid, respectively. Notice that galls formed at the base of large leaves result in the greatest aphid fitness. From Whitham, T. G. (1980). The theory of habitat selection: examined and extended using *Pemphigus* aphids. *Am. Nat.* 115:449–466. © 1980 by the University of Chicago Press.

of these compounds (Fritz and Simms 1992, Rosenthal and Berenbaum 1992, Orians *et al.* 2003). Like other traits, variation in phytochemistry results from genetic factors, environmental sources, and interactions between the two, namely **gene–environment interactions**. Genetic variation among individual plants for resistance traits is a prerequisite for evolutionary change and has been central to the development of evolutionary theories on plant–insect interactions such as plant defense and coevolution (Stamp 2003, Thompson 2005). Moreover, genetic variation in plant traits has allowed plant breeders or genetic engineers to develop varieties and transgenic crops resistant to pest herbivores (Borojevic 1990, Bos and Caligari 1995, Christou *et al.* 2006, Ferry *et al.* 2006). Also, environmental factors such as nutrient availability, drought stress and elevated atmospheric CO_2 are all known to influence the concentrations of nutrients and allelochemicals in plants. These factors in turn influence "plant resistance, vigor and stress," plant conditions that have played a central role in theories predicting herbivore outbreaks (Price 1991a, Awmack and Leather 2002, Huberty and Denno 2004). For these reasons, it is important to explore the genetic and environmental causes of phytochemical variation in plants and review the hypotheses extending from this variation that have been proposed to predict herbivore performance and population dynamics.

4.3.11 Genetic basis for plant resistance

There are many studies documenting genetic control of the concentration of both primary metabolites such as nitrogen (Caradus 1992, McFerson and Frey 1991, Zangerl and Berenbaum 2004), allelochemicals like alkaloids, phenolics and terpenoids (Berenbaum and Zangerl 1992, Fritz and Simms 1992, Shonle and Bergelson 2000, Orians *et al.* 2003), trichomes (Kennedy and Barbour 1992, van Dam *et al.* 1999) and plant architecture (Rudgers and Whitney 2006). In many of these studies, heritable genetic variation in phytochemistry or other plant traits influenced the density of specific herbivores or the composition of the herbivore community. A good example involves the parsnip webworm *Depressaria pastinacella* (Lepidoptera: Oecophoridae) that feeds selectively on wild parsnip, *Pastinaca sativa*, a plant species that produces toxic furanocoumarins (Zangerl and Berenbaum 1990). Plant genotypes that are avoided by webworms in the field contain high concentrations of furanocoumarins, and when fed to caterpillars in the lab result in reduced performance. In contrast, field-attacked genotypes have lower concentrations of furanocoumarins and foster much higher larval growth rates.

In managed systems, the genetic basis of resistance has been shown by comparing the concentration of defensive metabolites or trichome characteristics between resistant and susceptible crop varieties (Kennedy and Barbour 1992, Sadasivam and Thayumanavan 2003). For example, the concentration of cucurbitacins (triterpenoids) in squash is under genetic control and varieties with high concentrations are resistant to attack by cucumber beetles (*Diabrotica*). Genetic-based variation also occurs in the concentration of alkaloids in tomato and potato, and monoterpenes in pines and mints. Although there is clear evidence for heritable variation in phytochemical-based resistance, environmental factors often influence the expression or strength of resistance, suggesting a gene–environment interaction. An example of a gene–environment interaction involving allelochemicals is evident in wild radish, *Raphanus raphanistrum*, and the induction of glucosinolates by larvae of the cabbage butterfly, *Pieris rapae* (Agrawal *et al.* 2002). Genetic variation for glucosinolate concentration was not detected in undamaged plants, but was found in plants damaged by butterfly larvae. Thus, the expression of glucosinolates in radish depended on environment, namely exposure to herbivory.

The breeding system of a plant and its effect on herbivory provides additional evidence for genetic-based resistance (Carr and Eubanks 2002, Hayes *et al.* 2004, Hull-Sanders and Eubanks 2005). Inbreeding depression resulting from self-pollination often promotes detrimental changes in plants including resistance traits and tolerance to herbivory. For instance, inbred lines of *Mimulus guttatus* (Scrophulariaceae) were both less resistant and tolerant to attack by the spittlebug, *Philaenus spumarius* (Hemiptera: Cercopidae). A study of the herbivores on morning glory, *Ipomoea hederacea* (Convolvulaceae), found that the generalist aphid *Aphis gossypii* grew faster on inbred plants, whereas specialist herbivores such as the tortoise beetle, *Deloyala guttata* (Coleoptera: Chrysomelidae), performed best on vigorous out-bred lines. Variation in herbivore performance in this system was explained by the differential responses of the various herbivore guilds to plant stress and vigor between inbred and out-bred lines.

The study of plant hybrid zones in poplars (*Populus*), willows (*Salix*) and eucalypts (*Eucalyptus*) provides additional evidence for genetic-based resistance, and in several cases links resistance to phytochemistry (Whitham 1989, Fritz *et al.* 1999, 2003, Dungey *et al.* 2000, Orians *et al.* 2000, Bangert *et al.* 2006). It has been argued that hybrids are more susceptible to herbivore attack than the parental species because recombination breaks up coadapted gene complexes that control for resistance traits. Thus, hybrids might act as "**herbivore sinks**" where herbivores accumulate and flourish, a hypothesis that was generated by the observation that the gall-inducing aphid *Pemphigus betae* was far more abundant on hybrids between Freemont cottonwood (*Populus fremontii*) and narrowleaf cottonwood (*Populus angustifolia*) than on either parent (Whitham 1989). Indeed, there is also evidence from eucalypts that some insect herbivores are more abundant on hybrids, and that resistance across parents and hybrids is roughly correlated with phenolic glycoside and terpenoid content, respectively. In the poplar and eucalypt systems, hybrid susceptibility cascades up to affect the composition and abundance of the herbivore assemblage and the associated arthropod community at large (Dungey *et al.* 2000, Wimp *et al.* 2005, Wimp and Whitham 2007). However, there are clear exceptions to the "**hybrid sink hypothesis**," as evidenced by the lower abundance and diversity of some leaf-mining and galling herbivores on oak (*Quercus*) and willow (*Salix*) hybrids (Boecklen and Spellenberg 1990, Fritz *et al.* 2003). Moreover, if coadapted gene complexes controlling for resistance are disrupted during recombination, then F_2 hybrids should exhibit greater susceptibility than F_1 hybrids. Although this is certainly the case for some insect herbivores on hybrid willows, it is not true for others, nor is it the case for all herbivores on hybrid eucalypts (Dungey *et al.* 2000, Fritz *et al.* 2003). Exceptions to the hybrid sink hypothesis may involve the breakup of gene complexes controlling host recognition. For example, if a herbivore uses both parental species, but employs different cues such as leaf volatiles to locate each host, then recombination may disrupt host recognition and result in lower densities on hybrids. Despite the variable responses of herbivores, hybridization studies provide convincing evidence for the genetic basis of resistance.

4.3.12 Environmental influences on plant condition, resistance and herbivore dynamics

Environmental factors such as nutrient runoff and deposition, precipitation, temperature, salinization of soils, air pollution and elevated atmospheric CO_2 can all influence the productivity, vigor and phytochemistry of plants with extended effects on herbivore performance and population dynamics (White 1969, Price 1991a, Polis *et al.* 1997a, b, Whittaker 2001, Awmack and Leather 2002, Huberty and Denno 2004, Throop and Lerdau 2004, Schile and Mopper 2006). With an increasing risk of global warming, changing patterns of drought and precipitation (e.g., El Niño events) and escalating nutrient subsidies from agricultural and urban lands into natural systems (Boyer *et al.* 2002, Howarth *et al.* 2002, Glantz 2006, Shein *et al.* 2006), it is becoming even more important to understand how such factors affect plant–insect interactions. At opposite ends of the plant-physiological spectrum, two hypotheses, namely the **plant stress hypothesis** and the **plant vigor hypothesis**, have figured prominently in explaining how environment-related changes in plant condition influence herbivore attack. These two hypotheses are intimately linked at the level of the individual plant because fluctuating rainfall and temperature can lead to drought stress in one season or year and vigorous plant growth at other times, exposing herbivores to a broad range of phytochemistry and plant growth dynamics.

4.3.13 Plant stress hypothesis

Historically, drought stress has been advocated as a major factor underlying outbreaks of herbivorous insects (White 1969, Mattson and Haack 1987a,b; see also Chapter 11 on Population dynamics). Based on observed outbreaks of the psyllid *Cardiaspina densitexta* on water-stressed *Eucalyptus fasciculosa* trees in Australia, White (1969) formulated the **plant stress hypothesis** (PSH), asserting that outbreaks result from changes in plant physiology, specifically available nitrogen, during times of prolonged water deficit. When plants are water stressed, protein metabolism and amino-acid synthesis are impaired (Hsiao 1973). Under such conditions, proteins can be hydrolyzed, resulting in increased levels of free amino acids (Brodbeck and Strong 1987). Also, to offset the low osmotic pressure resulting from water stress, many plants produce nitrogen-containing osmoprotectants (Aspinall and Paleg 1981). Because nitrogen is so limiting for insect herbivores, White (1969, 1993) suggested that stress-induced increases in available plant nitrogen could result in the improved growth and reproduction of phytophagous insects and thus promote population outbreaks.

However, since the inception of the PSH, an increasing number of experimental studies have failed to support its predictions (Larsson 1989, Mopper and Whitham 1992, Waring and Cobb 1992, Koricheva *et al.* 1998a, Huberty and Denno 2004). Although some phytophagous insects benefit on water-stressed plants, many others do not and are very adversely affected. Such mixed support for the PSH led to modified predictions based on a greater understanding of the physiological responses of plants to water deficit and the effects on specific feeding guilds (Larsson 1989). For example, besides increases in nutritional compounds during water stress, turgor pressure and water content decrease (Hsiao 1973, Inbar *et al.* 2001), allelochemicals often elevate (Gershenzon 1984, Mattson and Haack 1987a,b, Inbar *et al.* 2001), and plant growth is reduced (Price and Clancy 1986, Price 1991a), thus compromising the potential benefits of elevated nitrogen to insect herbivores. Also, certain feeding guilds were thought to respond more positively to water-stressed plants than others because they differentially experience changes in plant nutrition, allelochemistry and growth. Specifically, phloem and cambium feeders, because they feed in vascular tissues with low concentrations of allelochemicals, were suggested to respond more positively to plant stress than free-living chewing insects and gall formers (Larsson 1989). Despite such refinements, however, recent assessments have failed to find consistent support for the PSH and do not explain the discrepancy between early field observations and recent experimental studies (reviewed in Huberty and Denno 2004).

A recent meta-analysis of published experimental studies challenges the historical view that herbivorous insects exhibit elevated performance and outbreak dynamics on water-stressed plants (Huberty and Denno 2004). Overall, strong negative effects of water stress were found on the performance of sap-feeding insects (e.g., aphids and leafhoppers) and gall-inducers (e.g., sawflies and cecidomyiid flies), and inconsistent responses resulted for free-living chewers and leaf miners (e.g., lepidopterans and beetles). Only borers, bark beetles and long-horned beetles showed consistent positive responses on drought-stressed hosts. The positive response of bark beetles likely results from reduced tree resistance during attack, because oleoresin exudation pressure is lower under conditions of drought stress (Mattson and Haack 1987a,b, Lorio *et al.* 1995).

To partly explain the discrepancy between the observed outbreaks of sap-feeders (e.g., phloem-feeding psyllids) on water-stressed plants in nature and the negative effects detected in many experimental studies where plants are continuously stressed, Huberty and Denno (2004) proposed a "**pulsed stress hypothesis**" whereby bouts of stress and the recovery of turgor allow sap-feeders to access and thus benefit from stress-induced increases in plant nitrogen. The finding that phloem-feeding aphids respond positively on intermittently stressed plants, but exhibit poor performance on continuously stressed plants, is consistent with this hypothesis. Together with knowledge of feeding guild, the phenology and intensity of water stress as they mediate nitrogen availability and plant defense likely hold the key to understanding how water stress affects the population dynamics of insect herbivores. Overall, recent assessments suggest that the great majority of insect herbivores are adversely affected on water-stressed hosts. However, White (2009) has stressed that the plant stress hypothesis should be limited to explaining outbreaks of insects feeding on senescing plant parts: senescence feeders which are responding to physiological changes in the host plant.

4.3.14 Plant vigor hypothesis

If plant stress often negatively affects many insect herbivores, then one might expect them to perform well on vigorously growing plants and plant tissues. This expectation has been formalized as the **plant vigor hypothesis**, which was spawned from observations on gall-inducing insects that require rapidly proliferating plant tissue for successful gall formation (Price 1991a; see also Chapter 11). For instance, gall-inducing sawflies (Hymenoptera: Tenthredinidae) and wasps (Hymenoptera: Cynipidae) selectively attack fast-growing shoots over slow-growing ones, and they prefer vigorous-growing plants over slow-growing plants. Also, larval survival within galls can be vastly higher on rapidly growing shoots and plants, a pattern observed for several willow-inhabiting sawflies (*Euura* spp.) and rose-attacking gall wasps (*Diplolepis* spp.), a pattern that is not driven by natural enemies (Craig *et al.* 1986, Price and Clancy 1986, Price *et al.* 1987a,b, Roininen *et al.* 1988). Because tissue growth is dramatically reduced when plants experience water deficit, gall formers often perform very poorly on water-stressed plants. Besides gall-inducers, other insects too show enhanced performance and density on vigorously growing plants or plant tissues (Furniss and Carolin 1977, Price *et al.* 1990, Price 1991a). Foresters have recognized for years that shoot boring herbivores such as tip moths (e.g. *Ryacionia frustrana*) and weevils (e.g. *Hylobius pales* and *Pissodes strobi*) are severe pests on vigorously growing pine seedlings and young trees, and they are far less abundant on mature trees. Also, many insect herbivores selectively attack the new growth or regrowth of trees and shrubs that occurs after rains, artificial defoliation or mammalian browsing (Messina *et al.* 1993, Martinez and Wool 2003, Agrawal and Spiller 2004). Aphids, for example, achieve dense populations on the new shoots of grasses, shrubs and trees that appear following defoliation or pruning (Johnson and Lyon 1991, Brown and Welker 1992). Also, moose-browsed birch trees with extensive regrowth are more heavily attacked than non-browsed trees by insect herbivores in a diversity of feeding guilds, including sap-feeders, gall-inducers and leaf miners (Danell and Huss-Danell 1985).

However, shoot vigor is often confounded by enhanced nutrition and reduced defense. A manipulative field experiment, in which water and nitrogen treatments were applied to willow plants, allowed for an assessment of the relative contributions of shoot length, leaf protein and phenolic content to the density and survival of the gall-inducing sawfly *Euura lasiolepis* (Waring and Price 1988). Across the array of treatment plants, shoot length was a far better predictor of sawfly attack and survivorship than were protein or phenolic content. Similarly, an irrigation experiment in grape vines (*Vitis vinifera*) provides convincing support for the plant vigor hypothesis without any obvious confounding effects of elevated tissue nitrogen (Daane and Williams 2003). Irrigating grape vines with increasing amounts of water resulted in commensurate increases in shoot length, vegetative growth and mid-day leaf-water potential, but not leaf nitrogen content, which in fact declined.

Densities of the variegated leafhopper, *Erythroneura variabilis* (Hemiptera: Cicadellidae), were tightly correlated with vine growth and the amount of water applied, but not leaf nitrogen. It may be though that the elevated leaf water potential on vigorously growing vines allowed leafhoppers to ingest phloem sap more easily as a consequence of elevated cell turgor (Huberty and Denno 2004). For many herbivores, especially free-living ones that do not rely directly on tissue proliferation, isolating the effects of plant and tissue vigor from other correlated variables on herbivore performance remains a challenge.

4.3.15 Other environmental stressors affect plant resistance to insect herbivores

Abiotic stressors including salinity, pollutants such as sulfur and nitrogen dioxide, and elevated levels of atmospheric CO_2 and ozone are growing environmental threats to natural systems (Rogers and McCarty 2000, Hunter 2001a, Whittaker 2001, Hamilton *et al.* 2005). These multiple stressors influence plant–insect interactions largely through their effects on phytochemistry, which in turn influences plant resistance and susceptibility to herbivore attack. In the coming paragraphs we will focus on several of the more important of abiotic stressors and their plant-mediated effects on herbivores.

Soil salinization coupled with rising temperatures can lead to plant stress with consequences for herbivores (Rogers and McCarty 2000, Schile and Mopper 2006). **Salt stress** elicits similar physiological responses in plants as does drought stress (Hasegawa *et al.* 2000, Mansour 2000, Mopper *et al.* 2004). In general, salt stress promotes increases in nitrogen-containing osmoprotectants and reductions in cell turgor, water content, plant growth and productivity. Such changes should have negative consequences for herbivores, especially those that rely on high tissue water content and turgor to feed efficiently and assimilate nitrogen (Slansky and Scriber 1985, Huberty and Denno 2004). Most evidence suggests that the performance of insect herbivores is adversely affected on salt-stressed plants, especially on **glycophytic plants** that are not salt adapted. A manipulative experiment in which the leaf-mining agromyzid fly *Cerodontha iridiphora* was raised on glycophytic iris plants (*Iris hexagona*) grown under saline and freshwater conditions showed that salinity was detrimental to the performance and survival of both the leaf miner and the iris (Schile and Mopper 2006). Likewise, on glycophytic goldenrods (*Solidago*), salt stress also results in the reduced performance of dipteran leaf miners and gall-inducers (Martel 1998, Moon and Stiling 2002b). Not surprisingly, results are more mixed when herbivores are raised on adapted **halophytic plants**. Nonetheless, there is still evidence that stem-boring beetles and lepidopterans, as well as gall inducers, incur reduced performance when their halophytic host plants are salt-stressed (Hemminga and van Soelen 1988, 1992, Moon and Stiling 2002a,b). Interestingly, all of these herbivores are concealed feeders, which often incur fitness penalties when plant growth is reduced. In contrast, salinity had no effect on the performance of lepidopteran leaf miners on sea aster (Hemminga and van Soelen 1992) and it was positively associated with the abundance of dipteran gall formers and the planthopper *Pissonotus quadripustulatus* on their salt-stressed host plants (Gonçalves-Alvim *et al.* 2001, Moon and Stiling 2002a).

The continuous rise in the atmospheric concentration of greenhouse gases (CO_2 and ozone) since the mid-1800s has prompted ecologists and entomologists to study their effects on plant–insect-enemy interactions (Lindroth *et al.* 1995, Hunter 2001c, Whittaker 2001, Percy *et al.* 2002, Mondor *et al.* 2004). In general, when plants are grown under elevated CO_2, photosynthesis, growth and biomass all increase. The accumulation of biomass dilutes the concentration of nitrogen in plant tissues by 15–25% and results in a higher C:N ratio. Also, when plants experience elevated CO_2, carbon-based defenses such as condensed tannins and phenolic glycosides often increase, but there are exceptions. In general, on a poor-quality diet of reduced nitrogen concentration, elevated carbon-based defenses and the diluted effects of nitrogen-based defense, it is logical to think that insect herbivores will show reduced performance and survival. However, there is considerable variation in how insect herbivores respond when fed plants grown under elevated CO_2 (Hunter 2001c, Whittaker 2001). A common response of many herbivores raised on plants exposed to elevated CO_2 is for them to increase their feeding rate, but most herbivores cannot compensate fully and suffer some fitness penalties. As an example, when larvae of the buckeye butterfly, *Junonia coenia*, are fed plants of *Plantago lanceolata* grown under elevated CO_2, they incur higher mortality rates and grow much slower (Fajer *et al.* 1989, 1991). Higher rates of herbivore mortality in some cases have been attributed to nutritional deficiency that results from reduced foliar nitrogen content under elevated CO_2 conditions (Brooks and Whittaker 1999, Stiling *et al.* 2003a). Reductions in gypsy moth performance on aspen trees are associated with CO_2-promoted increases in phenolic glycosides (McDonald *et al.* 1999). Some herbivores, in fact, appear to benefit under elevated CO_2. Larvae of the lycaenid butterfly *Polyommatus icarus* increase their consumption rate and grow faster when reared on *Lotus corniculatus* grown under elevated CO_2, a legume with nitrogen-based defensive metabolites (Goverde *et al.* 1999). Larvae apparently perform better because concentrations of cyanogenic glycosides decrease. Similarly, populations of several aphid species increase when reared on hosts exposed to elevated CO_2 (Awmack *et al.* 1997, Bezemer and Jones 1998, Whittaker 2001). Given the published data at hand, chewing insects in general appear to suffer more from elevated CO_2 effects than do sap-feeders, perhaps because sap-feeders circumvent compartmentalized carbon-based defenses, are preadapted for excreting excess carbohydrate and often have symbiotes that can augment dietary nitrogen.

Elevated CO_2 can also affect interactions between herbivores and their natural enemies. Because feeding compensation with protracted growth is often a consequence of elevated CO_2, herbivores may be at a higher risk of attack from natural enemies (Stiling *et al.* 1999). Lepidopteran leaf miners on several oak species, for instance, experience growth delays and higher attack rates from parasitoids and predators, mortality factors that lead to a reduced density of leaf miners on trees grown under elevated CO_2. Also, coccinellid beetle larvae (*Leis axyridis*) increase their consumption rate of cotton aphids (*Aphis gossypii*) under elevated CO_2, perhaps because the protein content of aphids is lower and beetles compensate with increased predation (Chen *et al.* 2005). The result of increased consumption by beetles is enhanced biological control of aphids. Overall, responses of herbivores to elevated CO_2 are complex and depend on herbivore identity, plant species and genotype, soil nitrogen availability and interactions with natural enemies (Hunter 2001a, Whittaker 2001, Stiling *et al.* 1999, 2003a, Saxon *et al.* 2004). Nonetheless, the consensus is that increasing levels of atmospheric CO_2 will adversely affect many insect herbivores via changes in carbon-based phytochemistry (Percy *et al.* 2002).

Ozone (O_3) effects on phytochemistry and insect herbivores appear to be less than those of elevated CO_2 (Holopainen and Kössi 1998, Costa *et al.* 2001, Whittaker 2001). Elevated O_3 had no effect on the concentration of amino acids, sugars, monoterpenes, resin acids and total phenolics in Scots pine (*Pinus sylvestris*), and there were no negative effects on the reproductive rate of the gray pine aphid, *Schizolachnus pineti* (Kainulainen *et al.* 1994). However, in trembling aspen (*Populus tremuloides*) elevated ozone reduced tree growth, lowered concentrations of phenolic glycosides, but increased cuticular waxes, factors that were associated with improved performance and a greater potential for population outbreaks in the forest tent caterpillar, *Malacosoma disstria* (Percy *et al.* 2002). It is noteworthy that in this aspen system there are significant interactive effects between elevated CO_2 and O_3, such that one gas can offset or exacerbate the effects of the other on phytochemistry and herbivores. For instance, elevated CO_2 reduced the positive effect of O_3 on tent caterpillar performance and on the density of the aphid *Chaitophorus stevensis*. In this system, the long-term suppression of herbivore populations by natural enemies is expected to be less under conditions of elevated CO_2, O_3 or both. Thus, changes in atmospheric gases and their plant- and enemy-mediated effects on herbivores appear to differ between systems (Percy *et al.* 2002, Stiling *et al.* 1999, 2003a).

Atmospheric pollutants such as sulfur dioxide (SO_2) and nitrogen monoxide and dioxide (NO and NO_2) also influence herbivores via altered plant phytochemistry (Whittaker 2001, Jones and Paine 2006). Plants downwind from pollution sources and those growing close to busy roads tend to support higher densities of herbivores. For instance, pine budmoths (*Exoteleia dodecella*) and spruce needle miners (*Epinotia tedella*) achieve much higher densities on conifer trees growing in close proximity to pulp mills, a major source of SO_2 (Oksanen *et al.* 1996). Most experimental studies show that insect herbivores increase in response to elevated SO_2 and NO_2 (Heliövaara and Väisänen 1993). One mechanism by which SO_2 and NO_2 increase the susceptibility of plants to herbivore attack appears to be altered nitrogen metabolism (Deepak and Agrawal 2001, Whittaker 2001, Morikawa *et al.* 2004). Also, both SO_2 and NO_2 can reduce the searching behavior of parasitoids, which leads to lower rates of host parasitism (Gate *et al.* 1995). There are also important interactive effects of air pollutants, such that the combined effects of elevated SO_2 and NO_2 on herbivore performance (e.g., *Elatobium abietinum*) are greater than the singular effect of each dioxide alone. Altogether, alarming changes in pollutants and greenhouse gases with expected, but complex, effects on phytochemistry should foster even more aggressive research in this critical area of environment-mediated plant–insect interactions.

4.4 Plant defense hypotheses

The coevolutionary "arms race" between plants and herbivores emphasizes an ongoing reciprocal interplay whereby each player exerts reciprocal selective pressure on the other resulting in evolutionary change (Ehrlich and Raven 1964). So far, we have taken a very herbivore-centered approach to plant–insect interactions by examining the consequences of plant defenses for phytophagous insects and the counteradaptations which allow herbivores to cope. We will now take the plant's perspective and explore the distribution of phytochemicals within and among plants and the many factors that bear on their expression. Because plants grow, compete with other plants and reproduce, they can't allocate all available energy to defense. Moreover, plants exist in a great diversity of habitats that vary in resource availability (e.g., nitrogen, water and light), and resource limitation is known to affect patterns of allocation to defense in plants. Also, there is tremendous temporal and spatial variation in "herbivore and pathogen pressure" within and among plants and plant populations, thus affecting natural selection for defense. In the context of the diverse selective pressures that bear on plants, several hypotheses have been put forth to explain the existing variation in plant defenses (reviewed in Stamp 2003). In a nutshell, the **optimal defense hypothesis** attempts to explain variation in the allocation of plant defenses in relation to the plant's risk of attack, the value of the attacked tissue to the plant, and production costs of defenses (McKey 1974, 1979, Feeny 1975, 1976, Rhoades and Cates 1976, Rhoades 1979). Mixed results and theoretical advances prompted the development of additional hypotheses including the **carbon–nutrient balance hypothesis** (Bryant *et al.* 1983), the **growth rate hypothesis** (Coley *et al.* 1985), and the **growth-differentiation balance hypothesis** (Herms and Mattson 1992). Although controversial, these hypotheses establish a framework for exploring patterns of plant defense and set the stage for the development of improved theory. Thus, we will examine each of these hypotheses in the forthcoming sections.

4.4.1 Optimal defense hypothesis

The **optimal defense hypothesis** predicts the allocation of plant defenses in relation to the plant's **risk of attack**, the **value** of a tissue to the plant and the **cost** of the defense (McKey 1974, 1979, Feeny 1975, 1976, Rhoades and Cates 1976, Rhoades 1979). The optimal defense hypothesis assumes that plants evolve and allocate defenses in a way that maximizes individual fitness. Thus, plants and plant parts should evolve defenses in direct proportion to their risk from herbivores (historically the **plant apparency hypothesis**), within a plant, tissues should be defended in proportion to their value to plant fitness, allocation to defense varies depending on herbivore presence or absence (allocation to constitutive versus inducible defenses) and defenses are costly because they divert resources from other essential plant needs, such as growth and reproduction (Stamp 2003). Overall, the optimal defense hypothesis predicts that plants should allocate more to defense when the benefits outweigh the costs.

The predictions of the optimal defense hypothesis further presume the following three conditions:

(1) Defenses reduce herbivory
(2) There is genetic variation in secondary metabolites on which selection can act
(3) Herbivory is a major selective force underlying the production of secondary metabolites.

In general, there is support for these presumptions. First, there is an enormous literature documenting that secondary metabolites and other plant defenses indeed reduce levels of herbivory (Rosenthal and Berenbaum 1991, 1992, Karban and Baldwin 1997). Second, there is widespread evidence that the concentration of allelochemicals such as alkaloids, glucosinolates and furanocoumarins is under genetic control (Zangerl and Berenbaum 1990, van Dam and Vrieling 1994, Mauricio 1998, Shonle and Bergelson 2000, Orians *et al.* 2003). Third, there is building evidence from experimental studies that insect herbivores can act as a major selective force underlying the evolution of plant secondary metabolites (Simms and Rausher 1989, Mauricio and Rausher 1997, Shonle and Bergelson 2000). For instance, by manipulating the abundance of insect herbivores on the solanaceous plant *Datura stramonium*, it was shown that insects acted as selective agents on the concentration of two tropane alkaloids, even when levels of herbivory were relatively low (Shonle and Bergelson 2000).

There are also correlative studies showing that on a geographic scale concentrations of secondary chemicals or resistance factors in plants are positively associated with herbivore abundance, a pattern consistent with the view that herbivores are the agents of selection (Hay 1991, Pennings *et al.* 2001, Stamp 2003). An eye-catching example occurs in the Bothnian archipelago where meadow sweet, *Filipendula ulmaria* (Rosaceae), and the specialist leaf beetle *Galerucella tenella* (Coleoptera: Chrysomelidae) colonize islands that are subject to postglacial rebound (Stenberg *et al.* 2006). Postglacial rebound is the rise of land masses that were depressed by the enormous weight of ice sheets during the last glacial age. The result is an array of islands that range in age from very recent to over 1000 years, creating the opportunity to examine plant resistance traits in meadow sweet that have had very discrepant historic exposure to herbivores. Meadow sweet on old islands, those with long-standing exposure to herbivores, had significantly higher concentrations of condensed tannins and individual phenolics than plants growing on young islands. Moreover, beetles performed poorly on well-defended plants from older islands and developed rapidly on less-defended plants in younger populations. These results are entirely consistent with the view that herbivores play a selective role in the evolution of phytochemical defense. Indirect evidence that herbivores are the active agents of selection for secondary metabolites comes from plant lineages that have lost a particular allelochemical when they evolve a substitute defense (Futuyma and Keese 1992). For example, Central American *Acacia* trees that harbor predaceous ants have lost the cyanogenic glycosides that occur in non-ant-defended relatives (Rehr *et al.* 1973). Other studies, however, suggest that herbivorous insects are not the major selective force underlying the abundance and diversity of allelochemicals, as has been suggested for the occurrence of tannins in North American trees (Ayres *et al.* 1997).

The opportunity to test the selective effects of herbivory on allelochemistry arises when plants have been introduced to novel habitats in the absence of their native herbivores (Daehler and Strong 1997, Siemann and Rogers 2001, Castells *et al.* 2005, Lewis *et al.* 2006). By comparing herbivory and phytochemistry on invasive plants in their native and novel range, one can test the expectation that, if costly, plants should evolve reduced defense where herbivore pressure is low. Introduced populations of the Chinese tallow tree (*Sapium sebiferum*) in the southern United States, where herbivory is rare, contain undetectable amounts of tannins, a pattern that contrasts with the high concentrations of tannins in its native China, where herbivory is prevalent (Siemann and Rogers 2001). For invasive plants in general, however, evidence is mixed, with examples in which allelochemistry is not reduced in the invaded area despite a low level of herbivory compared to that in the native range (Willis *et al.* 1999, Lewis *et al.* 2006). Other variables, such as plant pathogens, resource availability and abiotic factors (e.g., UV light) can complicate patterns of plant defense, making it difficult to isolate herbivory as the sole force underlying the occurrence of allelochemicals (Bostock 2005, Carroll and Berenbaum 2006).

A major prediction of the optimal defense hypothesis is that there is a **cost to defense** and the materials and energy allocated to defense cannot be allocated simultaneously to other functions like reproduction and growth (Stamp 2003). Accordingly, when herbivores are absent, less well-defended plants should have higher fitness than better defended individuals. In fact, many studies indicate that there are costs associated with the biosynthesis, maintenance and induction of allelochemicals, costs that are leveled against growth and reproduction (Baldwin 1998, Vrieling and van Wijk 1994, Bergelson and Purrington 1996, Strauss *et al.* 2002). Overall, there is evidence that constitutive defenses, compartmentalized allelochemicals and induced defenses are costly to the plant. For constitutive defenses in the tropical tree *Cecropia peltata*, tannin-rich trees incur less herbivory, but there is a trade-off between defense and growth, as evidenced by an inverse relationship between tannin concentration and leaf production among individual trees (Coley 1986). Regarding compartmentalized allelochemicals, a trade-off between defense and reproduction occurs across genotypes of *Brassica*, whereby an increase in myrosinase (acts on glucosinolates to form toxic isothiocyanates) was correlated with increased resistance to flea beetles (*Phyllotreta cruciferae*), but at the cost of lower seed production (Mitchell-Olds *et al.* 1996). Isolating the cost of a specific resistance factor is now possible with genetic engineering. As an example, transplanting a resistant gene into *Arabidopsis thaliana* reduced seed production by 34%, demonstrating a clear cost to resistance (Bergelson *et al.* 1996).

Because there are explicit fitness penalties associated with the production of constitutive and compartmentalized allelochemicals, “activated allelochemicals” that are not induced until herbivores attack are thought to minimize such costs (Strauss *et al.* 2002, Kessler and Baldwin 2004, Bostock 2005, Walls *et al.* 2005). A field study with *Nicotiana attenuata*, a species in which the alkaloid nicotine is inducible by the wound hormone jasmonic acid, demonstrates this expectation (Baldwin 1998).

Induced plants were attacked less often by herbivores and survived to produce more seed than did their non-induced counterparts. However, if plants were not attacked, jasmonate-induced plants produced less seed than did non-induced plants. In this system, jasmonate-induced responses function as defenses, but are costly, and inducibility allows this species to forgo these costs when defenses are unnecessary.

Evaluating trade-offs between defense, growth and reproduction is complicated by the existence of a "third-party trade-off" with tolerance. In fact, plants cope with herbivore attack in two ways. So far, we have focused on **resistance** (traits that reduce damage), but plants also exhibit **tolerance**, traits that reduce the impact of damage on plant fitness (Stowe *et al.* 2000, Stamp 2003). Tolerance to tissue damage, essentially regrowth ability, involves a variety of factors, including growth rate, storage capacity, flexible photosynthetic rate and nutrient uptake, and developmental plasticity (Rosenthal and Kotanen 1994). Tolerance has likely evolved in response to herbivory, and it is under genetic control (Fineblum and Rausher 1995, Mauricio *et al.* 1997). Plants appear to have one of three strategies: well-developed defense and poor tolerance, well-developed tolerance and poor defense, or an intermediate of both (van der Meijden *et al.* 1988). Thus, there appears to be a negative association between tolerance and resistance, but both can occur together in the same plant (Fineblum and Rausher 1995, Mauricio *et al.* 1997). Overall, there is clear evidence for costs of resistance to plant fitness, but detecting them can be complicated by trade-offs with tolerance, differences in production and maintenance, and induction costs among metabolites, and differences in environmental conditions.

Risk of herbivore attack is another factor thought to influence the distribution and abundance of allelochemicals in plants and plant tissues. Originally proposed as the **plant apparency hypothesis** (Feeny 1975, 1976, Rhoades and Cates 1976), risk of attack is now subsumed as a feature of optimal defense theory (Rhoades 1979). The plant apparency hypothesis posits that plants easily found by herbivores (apparent plants) should invest heavily in costly quantitative defenses such as tannins, which occur in high concentrations and are broadly effective against a diversity of herbivores including both specialists and generalists. Apparent plants include long-lived-trees, shrubs and perennial grasses. In contrast, unapparent plants, due to their rarity, patchiness or short generation times, are expected to escape most herbivory and thus selection should favor low investments in cheap qualitative toxins that are effective against all but specialized herbivores. Unapparent plants include fast-growing annuals, early-successional plants and rare plants. Although there are rough correlations between plant apparency and expected allocations to defense (e.g., tannins predominate in apparent oak trees, which lack glucosinolates, whereas the opposite pattern prevails in ephemeral mustards), there are notable exceptions to this hypothesis (Stamp 2003). For example, in their defensive arsenal, some unapparent plants employ quantitative defenses, whereas even very apparent plants often contain toxins. Further complicating the predictions of the plant apparency hypothesis is the fact that quantitative allelochemicals, such as some tannins and terpenoids, can have both digestibility-reducing and toxic properties (Ayres *et al.* 1997, Langenheim 2003, Keeling and Bohlmann 2006). Most problematic is trying to quantify the "apparency" of a plant to a herbivore, given the tremendous variation among herbivorous insects in their dispersal, sensitivity to plant cues and thus their ability to colonize their host plant (Feeny 1991a, Bernays and Chapman 1994). In short, many herbivores locate their host plant very effectively and synchronize their life history with it, despite its rarity and fleeting existence. Given that most plant species are attacked by a dynamically changing assemblage of many herbivore species with a diversity of host locating abilities, how does one quantify the mean apparency of a plant, the measure on which selection must act? Overall, the plant apparency hypothesis

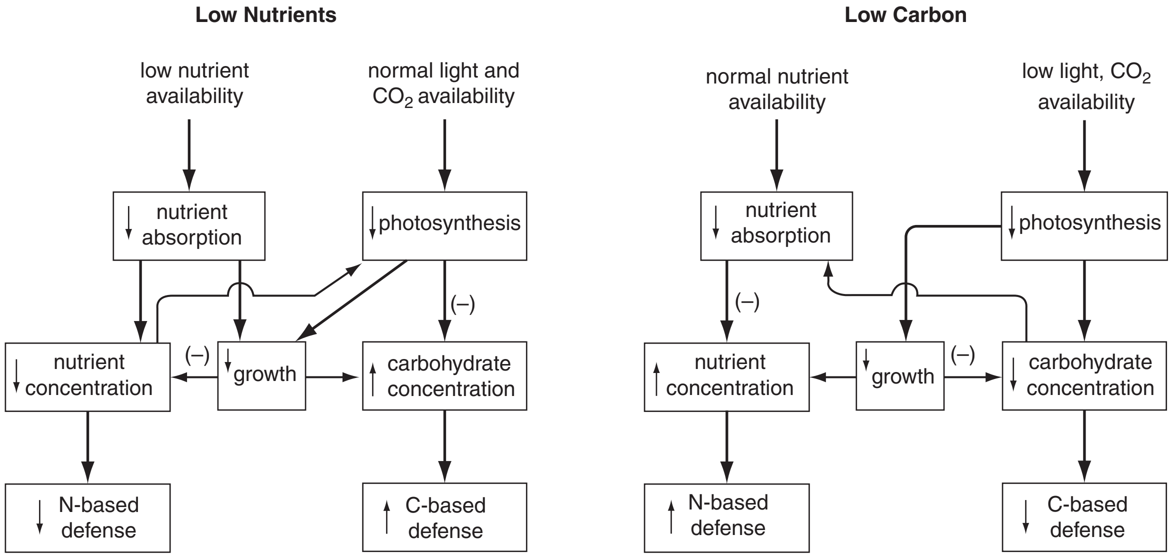


Figure 4.12 Carbon–nutrient balance hypothesis as proposed by Bryant *et al.* (1983). The hypothesis was developed originally to explain the effect of soil nutrients and shade on phytochemical defenses (N-based and C-based) that extend from an altered carbon:nutrient ratio in the plant. Vertical arrows in boxes indicate an increase (↑) or decrease (↓) in a variable. Arrows between boxes (← or →) show a positive effect unless a negative symbol (-) is indicated. The thickness of arrows indicates the relative strength of the effect. From Bryant *et al.* (1983). Reprinted with permission from Blackwell Publishing.

provided a useful framework when it was proposed, and contributed significantly to our knowledge of plant defense, but difficulty with measuring apparency, and the mixed empirical support remain as detractors (Stamp 2003). However, when we consider what humans eat, the preponderance of our vegetable intake is from groups of plants with originally unapparent distributions and toxic defenses, such as in the cabbage, carrot and lettuce families of plants. We do not eat tree leaves, and restrict our diet from trees to nuts and fruits. So from this broad perspective we can see that the plant apparency hypothesis accounts for the human diet effectively.

This hypothesis has proved to be central in the conceptual development of plant defense theory and has general predictive power for the dichotomy in defensive syndromes between short-lived forbs and long-lived trees. However, uncertainty arises because plant apparency is difficult to assess, the predictions of risk and value are often confounded, costs are evaluated without knowledge of the tolerance–resistance relationship in plants and environmental conditions or resource availability and stress were not originally considered. This ambiguity has led to the development of other explanatory hypotheses of plant defense and allelochemical allocation.

4.4.2 Carbon–nutrient balance hypothesis

The **carbon–nutrient balance hypothesis** seeks to explain how the supply of carbon and nutrients in the environment affect the phenotypic expression of defenses in plants and thus resistance to herbivore attack (Bryant *et al.* 1983, Tuomi *et al.* 1988, 1991, Figure 4.12). The carbon–nutrient balance hypothesis was developed originally to explain the effect of soil nutrients and shade on phytochemical defenses that extend from an altered carbon nutrient ratio in the plant. The hypothesis suggests that when plants acquire resources in excess of growth demands, that these resources are shunted into the production of secondary metabolites (Lerdau and Coley 2002). Specifically, plants growing in nutrient-poor soils should allocate more resources to carbon-based defenses (e.g., phenolics), whereas those growing in low-carbon shady environments should allocate more to nitrogen-based defenses (e.g., alkaloids). The carbon–nutrient balance hypothesis further posits that nitrogen fertilization will shift defenses from carbon-based to nitrogen-based. The hypothesis is appealing in its simplicity and because it offers testable predictions (Koricheva *et al.* 1998b, Hamilton *et al.* 2001, Stamp 2003).

However, in the many tests of the carbon–nutrient balance hypothesis, results supporting its predictions are mixed (Koricheva *et al.* 1998b). The domain of the hypothesis is at "higher categorical levels," effectively predicting the total amount of carbon that can be allocated to carbon-based defense. However, predicting the altered concentration of specific compounds requires knowledge of biosynthetic pathways (Koricheva *et al.* 1998b, Lerdau and Coley 2002). For example, this hypothesis successfully predicts changes in the concentration of products of the shikimic acid pathway. As predicted, studies across a large range of plant species growing in many habitats found an increase in condensed tannins with increases in light or decreases in nutrients (Koricheva *et al.* 1998b). Also consistent with this hypothesis is the phytochemical response of silver birch, *Betula pendula*, to fertilization (Mutikainen *et al.* 2000). Fertilization resulted in a decrease in the concentration of condensed tannins, which was associated with decreased tree resistance to the moth *Epirrita autumnata*. Similarly, increases in phenolics and condensed tannins have been found under conditions of elevated CO_2, which increase the C:N ratio in plants (Lindroth 1996, Lerdau and Coley 2002, Percy *et al.* 2002). Results are less predictable for terpenes and alkaloids that are products of non-shikimic acid or multiple metabolic pathways (Koricheva *et al.* 1998b). Moreover, the predictability of the carbon–nutrient balance hypothesis also depends on the phenotypic plasticity of the plant (see Stamp 2003).

Research emerging from tests of the carbon–nutrient balance hypothesis suggests that the defensive responses of plants to variable resources are more complicated than was originally thought (Lerdau and Coley 2002, Stamp 2003). A greater knowledge of the plasticity of plant defense in relation to environmental resources and an understanding of the biosynthetic pathways involved in the synthesis of particular defensive metabolites is necessary to refine predictions stemming from the carbon–nutrient balance hypothesis. Nonetheless, this hypothesis called attention to how resources influence constitutive and induced defenses and contributed to the emergence of the following hypothesis regarding plant defense.

4.4.3 Growth rate hypothesis

The **growth rate hypothesis**, also referred to as the **resource availability hypothesis**, proposes that the pattern of plant defense is largely determined by the inherent growth rate of a plant, which is ultimately determined by available resources (Coley *et al.* 1985). Thus, among plant species, resources limit plant growth and the optimal level of investment in constitutive defense increases with a decrease in plant growth rate (Figure 4.13). The optimal level of defense refers to the expression of defenses at maximal growth rate under conditions of optimal nutrition for each plant species. The growth rate hypothesis predicts that in high resource environments (e.g., agroecosystems and old-field habitats) competition favors fast-growing plant species with little allocation to defense because any herbivore-inflicted damage can be compensated for by rapid growth. Conversely, in low-resource environments (e.g., dry or shaded habitats), resource limitation selects for slow-growing plant species with much greater allocations to defense. Such slow-growing species cannot easily compensate for tissue

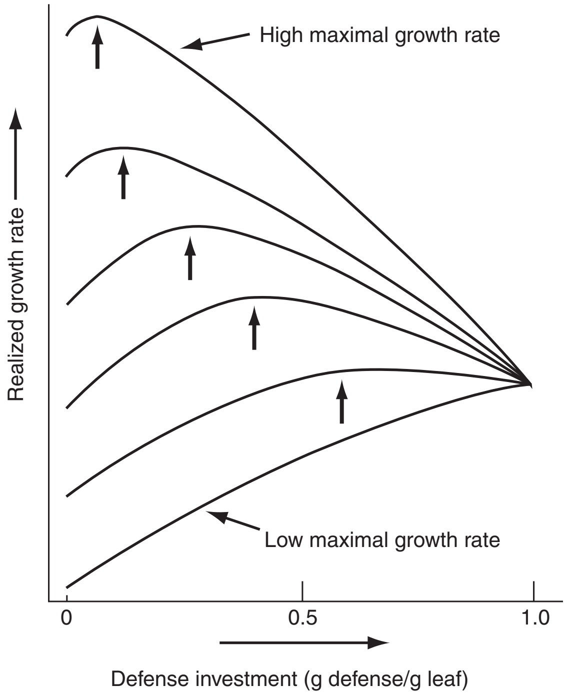


Figure 4.13 Growth rate hypothesis as proposed by Coley *et al.* (1985). The hypothesis posits that the pattern of plant defense is largely determined by the inherent growth rate of a plant, which is ultimately determined by available resources. The graph shows the effect of defense investment on realized plant growth. Each curve represents a plant species with a different maximum inherent growth rate. Levels of defense that maximize realized growth are indicated by an arrow. From Coley, P. D., J. P. Bryant, and F. S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895–899. Reprinted with permission from AAAS.

loss because of their slow growth, so replacement of resources lost to herbivores is more costly for plants in low-resource environments, and thus their higher allocation to defense.

As predicted, there is a negative correlation between the growth rate of Neotropical tree species and their tannin concentration (Coley 1987). More recently, a reciprocal transplant study in Amazonian forests involving tree species growing on nutrient-rich clay soils and nutrient-poor sandy soils found strong support for the growth rate hypothesis (Fine *et al.* 2004). Tree species originating from nutrient-poor soils express higher levels of constitutive defenses (tannins) than those growing on nutrient-rich clay.

Overall, some studies provide support for the growth rate hypothesis (Jing and Coley 1990, Herms and Mattson 1992), whereas others do not (Cates 1996). The major contribution of the growth rate hypothesis is that it makes a compelling case for the evolutionary history of resource availability on the intrinsic growth rate of plants, which in turn is the primary factor responsible for shaping the defensive profile of plants.

4.4.4 Growth–differentiation balance hypothesis

The **growth–differentiation balance hypothesis** predicts how plants balance allocation between differentiation-related processes, such as defense, and growth-related processes across a gradient of environmental conditions (Loomis 1953, Herms and Mattson 1992). Growth is the production of roots, stems and leaves or any process that requires substantial cell division and elongation. Differentiation is everything else, and refers to the enhancement of the structure or function of existing cells (e.g., maturation and specialization). Some differentiation traits bear directly on plant defense. For example, the production of secondary metabolites, trichomes and thick leaf cuticle are examples of differentiation-related processes (Herms and Mattson 1992). Allocation to differentiation includes both the process and the products, so it subsumes enzyme and metabolite costs as well as their transport storage costs. The growth–differentiation balance hypothesis of plant defense is premised on a physiological trade-off between growth and differentiation processes (Herms and Mattson 1992). The trade-off occurs because secondary metabolism and associated structures (e.g., trichomes, latex canals and resin ducts) are physiologically constrained in dividing and growing cells, and because they divert resources from the production of new leaves. Thus, these processes compete directly for photosynthate and plants face the dilemma of growing fast enough to compete with other plants while at the same time maintaining sufficient defenses to survive attack by herbivores and pathogens.

The growth–differentiation balance hypothesis posits that any environmental factor slowing growth more than it slows photosynthesis increases the pool of resources available for allocation to differentiation-related products such as defensive metabolites (Herms and Mattson 1992, Glynn *et al.* 2003). For instance, growth is reduced substantially by shortages of nutrients and water, whereas photosynthesis is less sensitive to such limitations. In such instances, carbohydrates accumulate in excess of growth demands and thus can be converted to secondary metabolites without much cost to plant fitness. Accordingly, the growth–differentiation balance hypothesis explains how the trade-off between growth and defense interacts with the selective forces of herbivory and competition to shape allocational strategies in plants (Herms and Mattson 1992). Thus, a growth–differentiation continuum of allocation exists, whereby at one end of the gradient in resource-rich environments, plant competition selects for growth and at the other end of the continuum in resource-poor habitats, selection favors the differentiation-related strategy of defense. Given that resource limitation affects growth more than does photosynthesis, there should be a curvilinear relationship between allocation to secondary metabolites and resource availability, with peak investment in defensive metabolites occurring at intermediate resource levels (Figure 4.14). Thus, in resource-poor environments, both growth and differentiation are limited, but growth is more limited than defense, resulting in slow growth and some investment in secondary metabolites. At intermediate levels of resource availability, growth is limited to some extent, but photosynthesis is less affected, resulting in high investments in secondary metabolites due to excess photosynthate. Plants growing in resource-rich habitats should not be limited by either photosynthesis or growth, and should allocate a greater proportion of the photosynthate to growth than to defense. There have

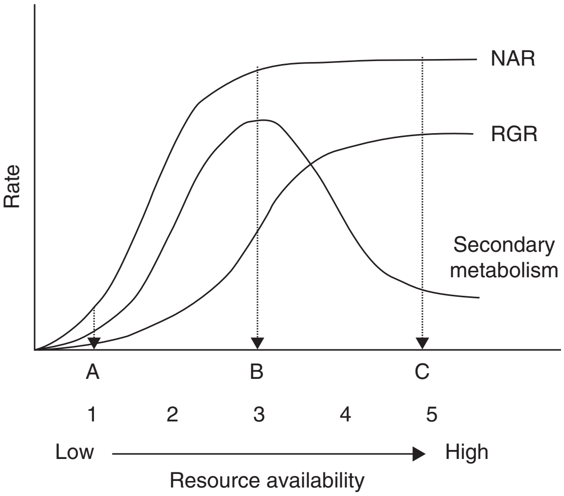


Figure 4.14 The growth–differentiation hypothesis as put forth by Herms and Mattson (1992). The hypothesis proposes that any environmental factor that slows growth more than it slows photosynthesis increases the pool of resources available for allocation to differentiation-related products such as defensive metabolites. Figure shows the relationship of net assimilation rate (NAR), relative growth rate (RGR) and differentiation (secondary metabolism) across a resource availability gradient from low to high, indicated as numbers 1–5, along which resource availability affects growth more than it does photosynthesis. When resource availability is low (A), both growth and photosynthesis are constrained, when resources are moderately available (B), growth is more constrained than photosynthesis and there is more allocation to differentiation (secondary metabolism), and when resource availability is high (C), growth is less constrained and there is more allocation to growth. Original from Herms, D. A. and W. J. Mattson. (1992). The dilemma of plants: to grow or defend. *Q. Rev. Biol.* **67**:283–335. © 1992 by the University of Chicago; adapted from Stamp, N (2003). Out of the quagmire of plant defense hypotheses. *Q. Rev. Bio.* **78**:23–55. © 2003 by the University of Chicago. All rights reserved.

been few studies examining the growth–differentiation balance hypothesis, but two studies provide support for the non-linear relationship between resource availability and allocation to defense. The highest concentrations of terpenes in camphorweed, *Heterotheca subaxilaris* (Asteraceae), occurred at intermediate nitrate levels (Mihaliak and Lincoln 1985) and the highest phenolic content in tomato plants resulted at an intermediate level of nitrogen fertilization (Wilkens *et al.* 1996).

4.4.5 Synthesis and status of plant defense theory

All four of the major hypotheses have made very significant contributions to the theory of plant defense. However, none of the hypotheses is mutually exclusive and there remains an urgent need for integration, synthesis and further theoretical development (Stamp 2003).

The ecologically–based growth–differentiation balance hypothesis has been expanded to model how herbivory and competition have shaped patterns of allocation to growth (primary metabolism) and defense (secondary metabolism) over evolutionary time (Herms and Mattson 1992, Figure 4.15). The conceptual model assumes a trade-off between allocation of photosynthate to growth and defense, with plant competition selecting for enhanced investments in growth and herbivory favoring allocation to defense. Importantly, resource availability mediates the evolutionary outcome. The mix of plant genotypes that survive in the population depends on the pressures exerted by competition and herbivory, with their relative importance being determined by the environment in which the interaction is played out (e.g., resource-rich or resource-poor habitats). Growth-dominated genotypes (genotype A) in resource-rich environments where competition prevails invest heavily in growth and less in defense by evolving phenotypic plasticity (induced resistance) or employing qualitative defenses (Figure 4.15A). In contrast, differentiation-dominated genotypes (genotype B) in resource-poor habitats with frequent herbivory invest heavily in constitutive defenses. A stable polymorphism (genotypes A and B) is maintained by disruptive selection in environments in which the evolutionary importance of herbivory relative to competition is high and low, respectively (Figure 4.15A). Directional selection exerted on genotypes A and B in environments where herbivory and competition are similarly important results in the evolution of intermediate genotypes (genotype C in Figure 4.15B).

By subsuming the other hypotheses and making testable predictions, the expanded growth–differentiation balance hypothesis is the most mature of the plant-defense hypotheses (Stamp 2003). This said, there have been remarkably few studies testing this hypothesis. To further the development of plant defense theory, more experimental tests are clearly needed as is a far more in-depth understanding of the specific biosynthetic pathways involved in the production of defensive metabolites, and the molecular underpinnings of resource-based trade-offs involving plant growth, resistance and tolerance to herbivory. We need to understand much more about how insect herbivores affect plant primary physiological processes, which then cascade to development, growth, yield and fitness effects. An overview of this area is provided by Peterson and Higley (2001).

4.5 The reciprocal effects of plant–insect interactions on distribution and abundance

Plants vary tremendously in physical structure and they grow in spatially diverse arrangements that range from expansive monocultures to mixed communities comprised of hundreds of species. Moreover, insect herbivores can inflict high levels of defoliation and mortality on their host plants. Thus, it is not at all surprising that plants and insect herbivores can influence each other's distribution

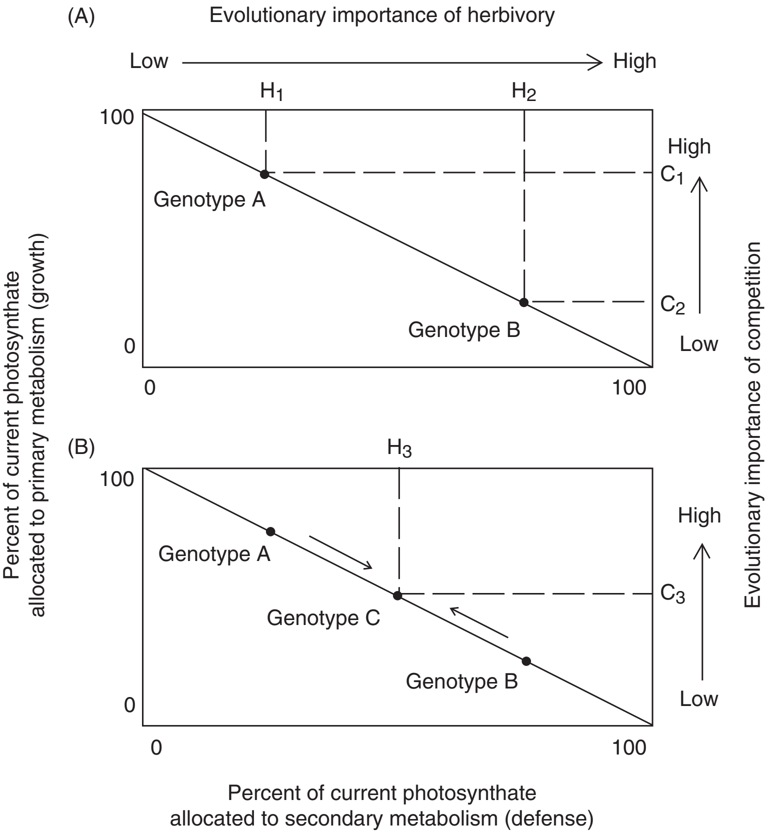


Figure 4.15 Expanded model of the growth–differentiation hypothesis showing how the relative importance of herbivory and competition have shaped patterns of allocation to growth (primary metabolism) and defense (secondary metabolism) over evolutionary time (Herms and Mattson 1992). The mix of plant genotypes that survive in the population depends on the pressures exerted by competition and herbivory, with their relative importance being determined by the environment (resource-rich or resource-poor habitats). (A) Growth-dominated genotypes (genotype A) in resource-rich environments where competition is intense invest heavily in growth and less in defense by evolving phenotypic plasticity (induced resistance) or employing qualitative defenses. In contrast, differentiation-dominated genotypes (genotype B) in resource-poor habitats with frequent herbivory invest heavily in constitutive defenses. A stable polymorphism (genotypes A and B) is maintained by disruptive selection in environments in which the evolutionary importance of herbivory relative to competition is high and low, respectively. (B) Directional selection exerted on genotypes A and B in environments where herbivory and competition are similarly important result in the evolution of intermediate genotypes (genotype C). From Herms, D. A., and W. J. Mattson. 1992. The dilemma of plants: to grow or defend. *Q. Rev. Biol.* **67**:283–335. © by the University of Chicago. All rights reserved.

and abundance. In the paragraphs that follow we examine the direct effects of vegetation structure on the density of phytophagous insects and also consider how insect herbivores influence the spatial arrangement of plants. Admittedly, vegetation and habitat structure can indirectly affect insect herbivores by mediating interactions with their natural enemies. Moreover, the spatial configuration of host-plant resources and habitat patches (e.g., habitat fragmentation and isolation) can have dramatic effects on metapopulation dynamics, food-web dynamics and the diversity of the associated community of arthropods, all topics that we will explore in forthcoming chapters (see Chapters 11–14).

4.5.1 Consequences of vegetation structure for the distribution and abundance of insect herbivores

Several components of **vegetation structure** (**vegetation texture** and **architectural complexity**) are important contributors to variation in the abundance of insect herbivores (Root 1973, Kareiva 1983, Strong *et al.* 1984a, Denno and Roderick 1991, Connor *et al.* 2000, Denno *et al.* 2005a,b). **Vegetation texture** has several elements, namely **patch size** (the area of the plant stand), **plant density** (the distance between individuals of the same species) and **vegetation diversity** (the frequency and identity of non-host-plant individuals). Also, individual host plants can vary in **architectural complexity**, which consists of two components, **plant size** (the spread of plant tissue through space) and **plant part diversity** (the number of different plant parts present such as leaves, petioles, stems, buds and fruits). Together, these elements of vegetation structure define the habitats of phytophagous insects, and variation among these structural components can have large effects on herbivore abundance.

With his experimental studies on the herbivore fauna of collards, Root (1973) was among the first ecologists to formalize the effects of vegetation structure on the abundance of insect herbivores. He discovered that the flea beetle, *Phyllotreta cruciferae*, and larvae of the cabbage butterfly, *Pieris rapae*, attained higher densities on large, pure stands of collards than on plants growing in isolated rows surrounded by diverse meadow vegetation. Two hypotheses which have guided research in this area of plant–insect interactions emerged from this study. First, the **resource concentration hypothesis** posits that herbivores, especially dietary specialists, are more likely to find and remain on host plants growing in dense pure stands and thus achieve higher equilibrium densities there. The high frequency of pest problems in agricultural monocultures is certainly consistent with this hypothesis (Altieri and Nicholls 2004, Gurr *et al.* 2004). Second, plants growing in mixed vegetation possess an **associational resistance** to herbivore attack and thus incur lower densities (Tahvanainen and Root 1972). The mechanisms underlying associational resistance are many and we will explore these in due course. Before exploring associational resistance, however, we will dissect the components of vegetation texture that contribute to the general pattern of increased herbivore abundance on large, pure patches.

Patch size, or the area occupied by the host plant, often has a striking effect on the population density of insect herbivores (Root 1973, Bach 1980, 1981, Rey 1981, Kareiva 1983, Strong *et al.* 1984a, Denno and Roderick 1991, Connor *et al.* 2000). In general, larger patches of host plants often support a higher density of insect herbivores for several reasons, including increased habitat heterogeneity and resource availability, increased colonization rate and reduced probability for extinction. Indeed, by defaunating "islands" of the cordgrass *Spartina alterniflora* in the Gulf of Mexico and monitoring their recolonization by herbivores, it was shown that immigration rates increased and extinction rates declined with island area, which led to higher densities on large islands (Rey 1981; see also Chapters 12 and 14). Importantly, because islands were covered with pure stands of *Spartina* with similar stem densities, patch area effects were not confounded by either mixed vegetation or plant density effects.

Not all herbivores, though, show a positive relationship between density and patch size (Kareiva 1983). Certain combinations of life-history traits (e.g. high dispersal and concealed overwintering stages) favor colonization and persistence on isolated resources, affect the immigration–extinction dynamic and thus influence patterns of herbivore abundance across a range of patch sizes (Denno 1994b, Hines *et al.* 2005). For instance, six resident species of monophagous planthoppers (Delphacidae)

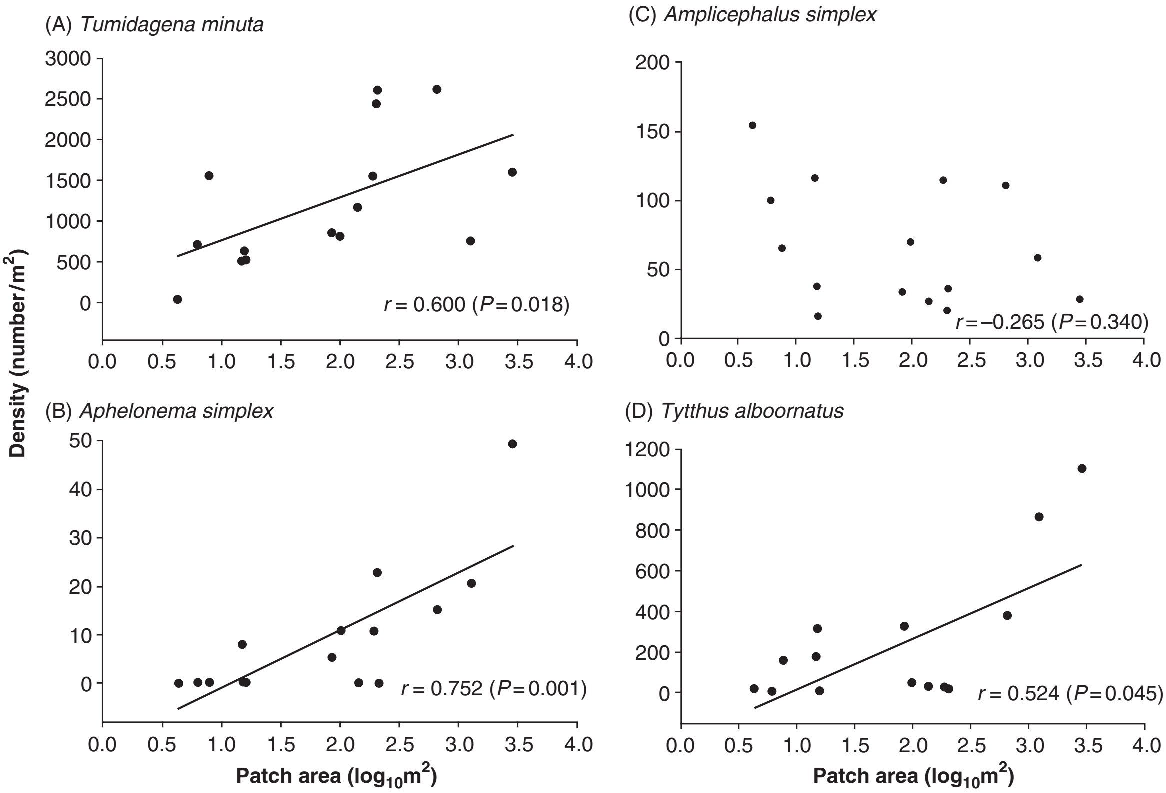


Figure 4.16 Relationship between population density and the area of the host-plant patch for (A and B) the flightless planthoppers *Tumidagena minuta* and *Aphelonema simplex*, (C) the very dispersive leafhopper *Amplicephalus simplex* and (D) the flightless predator of planthopper eggs *Tytthus alboornatus*. Notice that densities of the flightless species are more sensitive to changes in patch area, as evidenced by significant positive relationships. From Hines *et al.* (2005).

and leafhoppers (Cicadellidae) occur abundantly on the cordgrass *Spartina patens*, which grows as an archipelago of pure patches ranging in size from just a few square meters to immense "islands" (> 20 ha). These islets are embedded in a "sea" of another cordgrass species, which is unacceptable as a host for all of the *S. patens* herbivores. Moreover, these herbivores vary in their dispersal capabilities from flightless to fully flight capable. By virtue of where species spend the winter, either as eggs concealed in vegetation or as active nymphs, they also vary in their exposure to the elements and thus incur very different levels of winter mortality, especially on small exposed patches. The combination of these life-history traits explains the relationship between patch size and the abundance of particular sap-feeders. Species with low immigration rates (flightless) and high extinction rates (overwinter as exposed nymphs), such as the planthoppers *Tumidagena minuta* and *Aphelonema simplex*, are least able to maintain populations on small islands, and thus exhibit a positive density–patch-area relationship (Figure 4.16A and B). In contrast, very mobile sap-feeders that overwinter as concealed eggs, such as the leafhopper *Amplicephalus simplex*, persist on and/or effectively colonize small patches and show no significant relationship between density and patch area (Figure 4.16C). In this system, the flightless predator *Tytthus alboornatus* (Hemiptera), which specializes on planthopper eggs, is also rare on small patches and therefore does not likely contribute to the rarity of planthoppers there (Figure 4.16D). Generalist spiders, however, that emigrate from the surrounding matrix habitat may exacerbate problems of herbivore persistence, especially in small patches. Although other factors certainly play a role, the relationship between colonization and extinction rates is central to elucidating patterns of herbivore abundance in relation to patch area in many systems (Rey 1981, Kareiva 1983, Denno 1994b).

By planting agricultural crops at different densities in weed-free plots, one can test the effect of **plant density** on herbivore abundance without the possible confounding effects of mixed vegetation (Dyck *et al.* 1979, Kareiva 1983, Denno 1994b). When this has been done in multiple cropping systems such as oats, soybeans and cucumbers, the densities of the dominant herbivores usually decline with increasing plant density. Another approach to measuring plant-density effects has been to assess herbivore abundance in natural settings where plants occur in sparse and dense arrays (Kareiva 1983, Marques *et al.* 2000). This method has led to highly variable results, with some studies showing a positive relationship between herbivore abundance and plant density, others finding a negative association and yet others showing no relationship. With this approach, plant density is often confounded with plant size, plant nutrition and the diversity of matrix vegetation. In one study where plant size was controlled, the abundance of the parsnip webworm, *Depressaria pastinacella*, declined with increasing plant density, perhaps in response to altered plant quality (Thompson and Price 1977). Possible mechanisms underlying herbivore responses to plant density include variation in their colonization–emigration dynamic, altered microclimate and altered interactions with natural enemies.

Large plants and structurally complex plants often support higher densities of insect herbivores because they provide a greater variety of feeding and oviposition sites, overwintering sites and refuges from natural enemies than do structurally simple plants (Strong *et al.* 1984a, Denno 1994b). Just how **architectural complexity**, both **plant-part diversity** and **plant size**, can affect the abundance of insect herbivores is revealed in a series of manipulative studies undertaken in the intertidal grasslands of North America (Denno 1977, Tallamy and Denno 1979, Denno 1980). The grasses *Distichilis spicata*, *Spartina patens* and *S. alterniflora* dominate the vegetation in these habitats, often grow in pure stands, and possess a persistent and deep thatch layer associated with the base of the living vegetation. Each grass is fed upon by a unique assemblage of planthoppers, leafhoppers and plant bugs that sort out into two subcommunities, those that occur above the thatch layer and those that primarily occur within or below the thatch. When the architectural complexity of each grass species was simplified by removing the thatch layer, the abundances of sap-feeders occupying the different strata changed dramatically. Thatch removal resulted in a large population release for species residing in the upper strata, such as the planthopper *Delphacodes detecta* on *S. patens* that are normally denied access to feeding and oviposition sites within the thatch. In contrast, lower-strata residents such as the planthopper *Tumidagena minuta* greatly declined in abundance with the loss of the thatch layer, a response that was attributed to the loss of specific feeding and oviposition requirements and not to natural enemies. Plant size in these grass systems also affects the abundance of sap-feeders. For example, large plants of *Spartina alterniflora* support more individuals of the planthopper *Prokelisia dolus* than small plants, primarily because large plants offer more oviposition and feeding space. Resource abundance, as measured by leaf biomass per plant, also explains a significant amount of the variation in the abundance of insect folivores in other systems such as desert legumes (Marques *et al.* 2000).

The diversity of the background vegetation in which host plants grow also affects the density of insect herbivores (Root 1973, Atsatt and O'Dowd 1976, Koricheva *et al.* 2000). Host plants growing adjacent to non-host vegetation often gain **associational resistance** to herbivore attack and thereby support lower densities of herbivores (Tahvanainen and Root 1972, Root 1973, Kareiva 1983, Hambäck *et al.* 2000). Manipulative experiments with corn, beans and squash in Costa Rica showed that the density of monophagous species of leaf beetles (Chrysomelidae) was invariably higher when crops were grown in monoculture than in polyculture, where the crops were grown in mixtures (Risch 1980, 1981). However, polyphagous beetles obtained higher densities in polycultures than monocultures, emphasizing, as did Root (1973), that the resource concentration hypothesis is best supported by specialist herbivores. The mechanisms underlying associational resistance are varied and involve hindered herbivore searching behavior, changes in host plant suitability, chemical masking of host location cues or altered interactions with natural enemies, originally stated by Root as the "**enemies hypothesis**." An example of how non-host vegetation interferes with herbivore searching behavior involves the specialist leaf beetle *Galerucella calmariensis* (Chrysomelidae) and its host plant *Lythrum salicaria* (Lythraceae) that grows near thickets of the aromatic shrub *Myrica gale* (Myricaceae) (Hambäck *et al.* 2000). When potted *Lythrum* plants are placed inside and outside thickets of *Myrica gale*, thus controlling for plant quality, *Lythrum* plants nested within *Myrica* thickets incurred lower levels of herbivory and exhibited higher reproductive output than plants outside thickets. Moreover, the pattern of reduced herbivory on experimental *Lythrum* plants was the same as that observed in natural landscapes when *Lythrum* grew nearby *Myrica*. In this study, there was no evidence that the associational resistance was due to increased predation on leaf beetles in *Myrica* thickets, but rather was attributable to the reduced ability of beetles to find their *Lythrum* hosts via visual or olfactory interference.

Other studies demonstrate that host-plant suitability is reduced in the presence of non-host neighbors, thus accounting for associational resistance (Root 1973, Kareiva 1983). A unique case involves the hemiparasitic Indian paintbrush, *Castilleja indivisa* (Scrophulariaceae), when it is grown in the presence of a lupine host (Fabaceae) versus in association with alternative grass hosts (Adler 2000, 2003). *Castilleja* growing in close association with lupines sequesters alkaloids from this host and incurs lower levels of herbivory and sets more seed than plants growing in association with grasses or lupine varieties with low concentrations of alkaloids.

Associational resistance can also result from higher attack rates on herbivores by natural enemies when their host plants grow in complex habitats surrounded by diverse vegetation (Root 1973, Kareiva 1983, Stiling *et al.* 2003b, Shrewsbury and Raupp 2006). Many species of invertebrate predators, for instance, accumulate in complex-structured habitats characterized by diverse vegetation, where their negative effects on herbivore populations are enhanced (Denno *et al.* 2002, Langellotto and Denno 2004, Shrewsbury and Raupp 2006). A good example of enemy-mediated associational resistance is found in the salt marshes of Florida where the gall fly *Asphondylia borrichiae* (Diptera: Cecidomyiidae) attacks two closely related seaside plants, *Borrichia frutescens* and *Iva frutescens* (Asteraceae) (Stiling *et al.* 2003b). In both natural and experimentally manipulated settings, gall densities on *Iva* are significantly lowered by the presence of *Borrichia*. This occurs because bigger parasitoid species that are abundant in large *Borrichia* galls spill over and attack the smaller *Iva* galls. Thus, parasitism rates on *Iva* are higher in the presence of *Borrichia* than where it is absent. The effect is not reciprocal because most parasitoids from *Iva* galls are too small to successfully attack the large *Borrichia* galls, so gall density on *Borrichia* remains unaffected by the presence of *Iva*. The small parasitoids with their short ovipositors simply can't access fly hosts within large *Borrichia* galls.

Not all plants gain associational resistance in vegetationally diverse settings. In fact, the opposite pattern can occur whereby plants incur greater herbivore attack when they grow in mixed-species plantings (White and Whitham 2000, Rand 2003, Agrawal 2004). **Associational susceptibility** occurs in two salt-tolerant forbs, *Salicornia europaea* and *Atriplex patula* (Chenopodiaceae), that grow in the intertidal marshes of New England and are shared by the common leaf beetle, *Erynephala maritima* (Chrysomelidae) (Rand 2003). Experimental plantings of *Atriplex* with and without *Salicornia* as a neighbor showed that the presence of *Salicornia* enhanced beetle attack on *Atriplex* and lowered its survival and reproductive output. Moreover, surveys of natural marsh habitats found that *Atriplex* growing in close association with *Salicornia* was attacked more by the chenopod specialist than plants not neighbored by *Salicornia*. Also, polyphagous herbivores that reach outbreak proportions often move to nearby less-preferred host plants, a "spillover" effect that results in associational susceptibility (White and Whitham 2000). For example, when larvae of the fall cankerworm, *Alsophila pometaria*, reach high densities on their preferred box elder, *Acer negundo*, host, they disperse to defoliate adjacent cottonwood trees, trees that when growing in open settings incur little herbivory from this moth. Associational susceptibility results from a different mechanism, namely the proximity of oviposition sites, in a milkweed-grass system (Agrawal 2004). The milkweed beetle, *Tetraopes tetrophthalmus* (Coleoptera: Cerambycidae), feeds on the milkweed *Asclepias syriaca* in old-field habitats in southern Canada. In addition to its developmental host, beetles also require grass stems for oviposition, even though they don't consume them. As a consequence, milkweeds growing in association with grasses incur significantly higher levels of herbivory and reproductive losses from adult beetles than do milkweeds growing alone. Moreover, milkweeds suffer root competition from grasses, an effect that is exacerbated by beetle herbivory. In contrast, grasses enjoy competitive release by facilitating herbivory in neighboring milkweeds.

The variable responses of specific insect herbivores to the various components of vegetation texture affect the extent that plants in mixed-species settings experience herbivore attack and thus gain associational resistance or susceptibility (Kareiva 1983, Koricheva *et al.* 2000). Contributing to this variation is the fact that herbivores differ dramatically in their searching abilities and means of host location. Moreover, the mechanisms underlying a herbivore's response to vegetation texture are poorly understood for most insect species. For example, little is known of how vegetation diversity might influence herbivore density via disruption of plant volatile cues both herbivores and enemies use for host location (Visser 1986). Nonetheless, there is little doubt that the structure and diversity of vegetation influences the distribution and abundance of insect herbivores. In the next section, we will explore the reverse interaction, namely how insect herbivores influence the distribution and abundance of plants.

4.5.2 Effect of insect herbivores on plant distribution, abundance and community composition

There is convincing evidence that insect herbivory reduces the productivity, performance and reproduction of a great variety of plant species, including agricultural crops (Marquis 1992, Crawley 1997, Carson and Root 2000, Kranz 2005, Oerke 2006). Moreover, herbivory can directly compromise a plant's competitive ability by reducing leaf and root growth (Louda *et al.* 1990, Carson and Root 2000, Hambäck and Beckerman 2003, Agrawal 2004). We saw in our earlier discussion of plant defense that herbivory also selects for investments in constitutive secondary metabolites, and thus influences a plant's competitive profile in evolutionary time via inherent constraints on growth. So, it should not be surprising that insect herbivores can play a powerful role in determining the abundance and distribution of plants, as well as influencing the composition of the plant community.

An historic example of the biological control of an invasive weed demonstrates what a powerful force insect herbivory can be in affecting plant distribution (Huffaker and Kennett 1959). In the early 1900s, Klamath weed, *Hypericum perforatum* (Hypericaceae), was introduced from Europe into northern California and Oregon and by 1945 it rendered over 4 million acres of rangeland unfit for grazing livestock. In the late 1940s, the leaf beetle *Chrysolina quadrigemina* (Chrysomelidae) was imported from Europe and released on infested rangelands. This beetle soon became established and by 1956 it had largely eliminated Klamath weed in the western United States. Today, small pockets of the weed remain in shady sites where beetle development and survival are reduced, and there is little dynamic evidence that this beetle remains largely responsible for the weed's restricted distribution.

Insect herbivores can also have profound effects on the abundance of their host plant and the plant community at large in natural systems (Carson and Root 2000). Specialist leaf beetles such as *Microrhopala vittata* (Chrysomelidae) often erupt and defoliate the goldenrod, *Solidago altissima* (Asteraceae), in old field habitats in New England. Damage inflicted by this outbreaking beetle drastically reduces the biomass, survivorship and reproduction of *S. altissima*. Moreover, herbivore exclusion promotes the formation of dense stands of goldenrods, under which the abundance and diversity of other plant species are significantly reduced. Overall, *M. vittata* functions as a **keystone species** because beetle herbivory indirectly increases the abundance of invading trees in goldenrod-depleted habitats, thereby increasing the rate of succession by speeding the transition of old fields to tree-dominated communities.

Another example of how insect herbivory influences plant succession comes from studies on Mount St. Helens in Washington State following the eruption of this volcano in 1980 (Fagan and Bishop 2000, Fagan *et al.* 2005). The eruption created a large area of primary successional habitat on the north slope and extirpated all plant and animal species from the area. Shortly thereafter, the nitrogen-fixing lupine *Lupinus lepidus* (Fabaceae) colonized the barren area from remnant populations elsewhere on the volcano and subsequently spread rapidly from its initial invasion focus. By 1990, the lupine population consisted of a large, central core region of extremely high lupine density surrounded by numerous, low-density edge patches. However, by 1992, lupine growth rates in recently founded edge patches dropped to levels far below the extraordinary rates observed during the early stages of colonization, contributing to surprisingly slow rates of spread in recent years. Manipulative experiments suggest that insect herbivores were responsible for the slow rate of lupine spread. For instance, the removal of the dominant herbivore *Filatima* (Lepidoptera: Gelechiidae) increased the growth of existing plants and the production of new plants in the edge region, thereby accelerating the lupine's rate of increase at the front of the lupine reinvasion. In this system, herbivore-generated decreases in lupine reinvasion will likely result in reductions in rates of soil formation, nitrogen input and entrapment of seeds and detritus that are likely to alter the trajectory of primary succession.

Seed- and seedling-feeding insects are also thought to influence the distribution and diversity of plants by affecting where seedling recruits are most likely to survive. Decades ago, Janzen (1970) and Connell (1971) proposed that herbivores and pathogens were key factors in maintaining the high tree-species diversity characteristic of tropical forests. They both hypothesized a disproportionately high mortality of seeds and seedlings near mature trees because host-specific seed predators, herbivores and pathogens are more likely to concentrate their attack where the initial seed input is highest. Thus, due to density-dependent or distance-dependent responses of herbivores, the survival of conspecific seedlings was expected to increase with distance

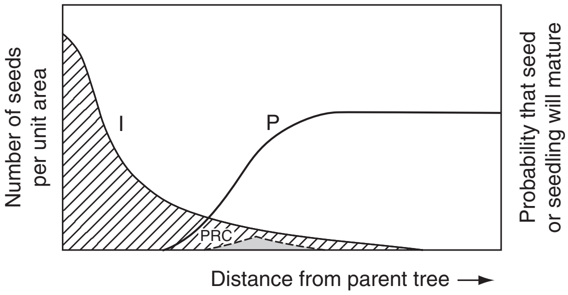


Figure 4.17 Model predicting the probability of seed or seedling survival as functions of seed crop size (I), the probability of escaping from a seed or seedling predator (P) and distance from the parent tree. The product of the "I" and "P" curves gives the population recruitment curve (PRC), where progeny are most likely to survive at some distance from the parent tree. Modified from Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**:501–529. © by the University of Chicago Press.

from the parent tree, a prediction now referred to as the **Janzen–Connell hypothesis** or the **escape hypothesis** (Howe and Smallwood 1982, Clark and Clark 1984, Givnish 1999). Moreover, with high seedling mortality near the parent tree, the probability that other plant species would establish in these sites increases, thus enhancing tree species diversity.

Janzen (1970) envisioned seed input and the probability that a seed or seedling will mature (escape a herbivore or pathogen) as functions of distance from the parent tree (Figure 4.17). Moving away from the parent adult, seed density should decrease because of dispersal limitations and the probability that a seed or seedling will be missed by a herbivore (seed predator) should increase. The interaction between seed density and seed mortality predicts maximum recruitment at intermediate distances from the nearest conspecific adult. Candidate mortality agents in the Neotropics that are both abundant and known to inflict density-dependent mortality on the seeds and seedlings include seed weevils (Coleoptera: Bruchidae), plant pathogens and vertebrates (Janzen 1975, Augspurger 1984, Howe 1986). A study of the Neotropical tree *Dipteryx panamensis* (Fabaceae) supports the expectations of the escape hypothesis in that seedling survival was positively correlated with distance from the parent tree and negatively associated with seedling density (Clark and Clark 1984). Likewise, pod infestation of the neotropical tree *Cassia biflora* (Fabaceae) by the bruchid beetle *Acanthoscelides obrienorum* (Coleoptera: Bruchidae) was strongly density dependent (Silander 1978). Many other studies, but not all, find support for the escape hypothesis (Clark and Clark 1984, Wills *et al.* 1997, Nathan *et al.* 2000, Norghauer *et al.* 2006). However, there has been mixed support for the specific expectation that seedling recruitment is highest at an intermediate distance from the parent tree (Condit *et al.* 1992). Although heavily critiqued over the last few decades, the Janzen–Connell hypothesis has gained recent support with new evidence for the density-dependent mortality of seeds or seedlings and its effect in maintaining plant species diversity (Wills *et al.* 1997, Givnish 1999, Nathan *et al.* 2000). However, seed predation does not increase toward the tropics and many temperate tree species also experience density-dependent seedling mortality (Hille Ris Lambers *et al.* 2002, Moles and Westoby 2003). Thus, unless the strength of density-dependent mortality varies with latitude, this factor alone is not likely to explain the high diversity of tropical forests.

Besides escape from density- or distance-dependent seed and seedling mortality (**escape hypothesis**), seed dispersal can be advantageous by promoting the colonization of suitable, but unpredictable, germination sites such as forest gaps or disturbed roadsides (**colonization hypothesis**), or by directed dispersal to particular sites with a relatively high probability of survival (**directed dispersal hypothesis**) (Howe and Smallwood 1982, Wenny 2001). Support for the colonization hypothesis comes from weedy plants that broadly disperse many small seeds to colonize disturbed habitats where competition is initially low. Birds, mammals and ants that cache or move seeds and nuts in specific sites provide support for the directed dispersal hypothesis. Needless to say, these hypotheses are not mutually exclusive because all three usually predict more successful recruitment away from the parent plant. Teasing apart the factors contributing to spatial patterns of seedling recruitment and survival is an area ripe for future research endeavors. Nonetheless, given that seed and seedling survival increase with distance from the reproducing parent, it is not surprising that plants have evolved a diverse array of seed and fruit adaptations that ensure dispersal by wind, water, explosive seed pods and animals, including insects (Howe and Smallwood 1982, Howe 1986, Wenny 2001).

Many cases of seed dispersal involve mutualisms between plants and animals, in which animals disperse seeds or fruits in exchange for a reward (Howe and Smallwood 1982, van der Pijl 1982, Howe 1986, Rodgerson 1998, Boyd 2001). Mutualistic seed dispersal often involves vertebrate animals such as mammals and birds, and less commonly insects. Of the insects, ants are by far the most important group of seed dispersers (Stiles 1992). Most cases of ant-mediated seed dispersal involve the collection of seeds or fruits that have elaiosomes attached to them, lipid-rich structures that offer a nutritional reward (Rodgerson 1998, Boyd 2001). Ants collect elaiosome-bearing seeds and carry them to their nests where they consume the elaiosome and then leave the seed underground or discard it from the nest. Ant-dispersed seeds are less likely to suffer vertebrate predation because they have been moved to low-risk sites and because some ant-dispersed seeds are tough and less vulnerable to attack from other insect herbivores.

On the whole, insect herbivores clearly affect the distribution and abundance of plants. We have seen that the density-dependent attack of seeds by insect herbivores directly influences where seedling recruitment occurs, and insects also contribute to the multitude of seed mortality factors favoring seed adaptations that encourage dispersal away from the parent plant. Ants are often agents of dispersal in some cases and actually move seeds to sites where germination and survival are higher. We have also seen that insect folivores can have striking effects on plant survival, succession, distribution and the structure of the plant community once seedlings have established. In an even more general sense, there is little question that insect herbivores and plants influence each other's abundance, distribution, evolution and diversification.

4.6 The evolutionary ecology of plant–insect interactions

There is irrefutable evidence that plants and herbivorous insects have influenced each other's evolution (Mitter *et al.* 1988, 1991, Futuyma and Keese 1992, Herrera and Pellmyr 2002, Thompson 2005, Winkler and Mitter 2007). The selective effects of herbivores on the evolution of plant defenses and the counteradaptations of herbivores to the vast array of phytochemical and morphological defenses stand in testament to reciprocal evolutionary effects. Moreover, plant defense theory is premised on the assumptions that plant defenses reduce herbivory and that herbivory is an important selective force underlying the evolution of secondary metabolites. What is far less clear is the extent to which plants and insect herbivores have directed each other's diversification and what conditions influence the degree of coadaptation and coevolution. Implicit in models of coadaptation and coevolution is that herbivorous insects not only promote plant genetic diversity, but they ultimately shift and adapt to novel plant genotypes with consequences for their own diversification (Farrell and Mitter 1990, Mitter *et al.* 1991, Herrera and Pellmyr 2002, Thompson 2005). Thus, factors influencing host-plant specialization, shifts to novel plant genotypes or species and diet breadth evolution (monophagy versus polyphagy) are central to theories on lineage diversification, coadaptation and coevolution. Plant–insect associations provide an ideal model for examining the process of diversification because phytophagy promotes higher rates of diversification than other feeding styles such as predation and saprophagy (Mitter *et al.* 1988, Wiegmann *et al.* 1993, Schluter 2000, Winkler and Mitter 2007). This assertion has been rigorously supported using replicated phylogenetic contrasts between sister lineages, which by definition are of equal age, an assessment that found phytophagous lineages to be far more species rich than their non-phytophagous counterparts. We will explore these issues in greater depth in the sections that follow.

4.6.1 Host shifting and diet breadth evolution

Earlier in this chapter, we learned that most phytophagous insects (>70% of species) are specialized in their use of host plants (monophagous). Historically, dietary specialization and host shifting have been thought to promote herbivore diversification (Futuyma and Keese 1992). Two factors contribute to this expectation. First, a given plant diversity represents a far greater variety of resources for specialist herbivores than generalists, thus providing greater opportunity for reproductive isolation and speciation. Second, specialization might promote herbivore diversity if the property of specialization enhanced the likelihood for speciation. For example, an accidental colonization of a novel host plant might foster specialization and speciation if mating occurs exclusively on the host plant (Jaenike 1990, Caillaud and Via 2000, Berlocher and Feder 2002). Alternatively, it has been argued that polyphagy facilitates radical host shifts because less specialized species are more likely to make "oviposition mistakes" on novel hosts, thus enhancing opportunities for diversification (Janz *et al.* 2006). Because diet breadth is so labile with reversals between monophagy and polyphagy in the same lineage of herbivores, diet breadth is not likely subject to much phylogenetic constraint (Nosil and Mooers 2005, Yotoko *et al.* 2005, Winkler and Mitter 2007). Thus, standard phylogenetic techniques may be less able to shed light on diet breadth evolution such as whether specialization evolves from a polyphagous lifestyle following colonization of a novel host. Counter to the expectation that specialization fosters diversification is the finding that, in a significant majority of 20 phylogenetically controlled comparisons, lineages of concealed feeders (e.g., borers) were less diverse than their external-feeding sister clades, despite the fact that internal feeders tend toward greater host specificity (Winkler and Mitter 2007). Regardless of the underlying mechanisms and the ancestral state of diet breadth, a recent phylogenetic assessment suggests that shifting to novel hosts per se plays a major role in promoting the speciation of phytophagous insects (Winkler and Mitter 2007). Given their importance in the diversification of phytophagous insects and in theories of coadaptation, let's now examine the various factors that are thought to shape the diet breadth and host shifting in phytophagous insects.

The relationship between the oviposition **preference** of females for particular host plants and the **performance** of their offspring on those hosts has played a central role in the evolution of diet breadth in herbivorous insects (Futuyma and Moreno 1988, Thompson 1988, Jaenike 1990). However, other factors, such as host plant abundance, risk of enemy attack and mating on the host plant have been suggested as important contributors to diet breadth as well. In the paragraphs that follow we will explore the many factors that have been proposed to influence diet breadth in insect herbivores (Jaenike 1990), examine the evidence for each and then highlight which factors appear to be most influential in promoting specialized or broad diets (see also Chapter 8 on Host and parasite interactions).

4.6.2 Selective factors favoring narrow herbivore diets

Because of allelochemical and other dissimilarities among plants, most insect herbivores are not likely able to use the vast array of locally available host-plant species (Jaenike 1990). For example, monarch butterflies (*Danaus plexippus*) that rely on unique chemical cues to locate their milkweed hosts, and whose larvae are adapted to cope with the toxic cardenolides therein, are not likely able to either find or develop on introduced *Eucalyptus* trees with vastly different allelochemical signatures. Thus, at a gross plant taxonomic scale, one expects to find a positive relationship between oviposition preference and offspring performance. It was observations like these that led ecologists to view a **positive preference–performance correlation**, namely females preferring to oviposit on plants where their offspring grow and survive best, as a potentially powerful factor favoring dietary specialization (Thompson 1988, Jaenike 1990). However, with more restricted sets of host plants, such as congeners or plants in closely related genera, there has been mixed support for a positive preference–performance relationship (Jaenike 1990, Abrahamson and Weis 1997, Mayhew 1997, Agrawal 2000b). Indeed, some herbivores rank host-plant species for oviposition in the same order as their suitability for offspring performance. Examples include the heliconiid butterfly *Agraulis vanillae* on *Passiflora* species, the cecidomyiid fly *Rhabdophaga terminalis* on willows, and the agromyzid leaf miner *Liriomyza sativae* on agricultural crops (Copp and Davenport 1978, Åhman 1984, Via 1986).

However, many other insect herbivores do not show this positive association (Thompson 1988, Abrahamson and Weis 1997). Low correspondence between preference and performance can arise when females fail to oviposit on plant species that are perfectly suitable for larval development, as occurs in the swallowtail butterfly, *Papilio machaon* (Wiklund 1975). In such cases, selection may have favored larvae that accept a wider array of host plants, while at the same time adults oviposit only on the most suitable hosts in a local patch. Alternatively, females may fail to oviposit on novel introduced plants that are suitable for larval development, simply because they fail to recognize them in the absence of appropriate oviposition cues. Poor correspondence between preference and performance can also arise when females oviposit on host plants where larvae fail to survive or develop very slowly. Such a case occurs in Rocky Mountain populations of the mustard white butterfly, *Pieris napi*, which oviposits on seven crucifer species including two introduced species (*Thalaspi arvense* and *Chorispora tenella*) with glucosinolate profiles similar to those in native hosts, but that are lethal to larvae because of additional toxic constituents (Chew 1977, Rodman and Chew 1980). Likewise, females may oviposit on "poor-quality" host plants because their offspring obtain protection from natural enemies. For example, the sawfly *Neodiprion sertifer* prefers to oviposit on pine trees with high resin acid content (Björkman *et al.* 1997). When natural enemies are excluded, larvae perform poorly on resin-rich trees, whereas in open cages larvae suffer far less mortality from enemies than they do on resin-poor trees because the regurgitated resin is used as an effective defense against parasitoids. Thus, when risk of enemy attack is diminished on plants where performance is reduced, there may appear to be poor correspondence between oviposition preference and performance when performance is assessed in the absence of natural enemies.

It is important to note that there is far better correspondence between preference and performance when herbivores choose among plants of the same species (Jaenike 1990, Price 2003a). Many aphids, planthoppers and sawflies, for example, selectively oviposit on plants where offspring performance is high (Whitham 1983, Cook and Denno 1994, Denno *et al.* 2002, Price 2003a). In several of these cases, increases in soil nitrogen created high-quality patches of plants that were both preferred for oviposition and on which offspring performance was enhanced. Thus, it is important to realize that environmental factors can influence the preference–performance relationships of insect herbivores.

Another potentially powerful factor promoting host-plant specialization is a physiological trade-off in herbivore performance on different host plant species that is evidenced by a **negative cross-host correlation in performance** (Jaenike 1990, Futuyma and Keese 1992, Thompson 1994). Intuitively, if the biochemical machinery necessary to detoxify allelochemicals found in one host plant precludes this ability on another, then such a negative correlation should favor monophagy. One of the few earlier studies that examined performance relationships featured the fall canker worm, *Alsophila pometaria* (Lepidoptera: Geometridae), and its larval performance on several co-occurring tree species (Futuyma and Philippi 1987, Jaenike 1990). Larval clones that grew faster on red maple grew slower on several oak species, providing support for a host-related trade-off in larval performance. More recently, the host races of the planthopper *Nilaparvata lugens* on the native grass *Leersia hexandra* and on rice (*Oryza sativa*) are reinforced by a negative trade-off in performance on the two host plants (Sezer and Butlin 1998). However, other studies seeking support for a negative correlation in cross-host performance have found either no relationship or a positive correlation, such that high performance on one host promotes the same on another (Bernays and Graham 1988, Jaenike 1990, Fry 1996, Thompson 1996).

Earlier studies on preference–performance relationships or cross-host performance correlations were largely phenotypic and were hampered by a nearly complete lack of information on how these processes were genetically related (Via 1986, Thompson 1988). Moreover, it is undeniable that an understanding of the genetic underpinnings of preference and performance traits is central to elucidating factors influencing diet breadth evolution. Several recent studies on aphids find convincing support for genetically based correlations in preference and performance that strongly favor host-plant specialization (Hawthorne and Via 2001, Via and Hawthorne 2002). For instance, highly specialized host races of the pea aphid, *Acyrthosiphon pisum*, occur on alfalfa (*Medicago sativa*) and red clover (*Trifolium pratense*). Using a **quantitative trait locus** (QTL) analysis, evidence was found for both a negative correlation in aphid performance (fecundity) on the two host plant species and for a positive association between host-plant acceptance and performance. A positive genetic correlation between preference and performance could arise by pleiotropy (the same allele affecting both preference and performance) or linkage disequilibrium (alleles affecting preference and performance occurring in close physical proximity on chromosomes, thus increasing their chances of being inherited together) (Falconer and MacKay 1996). In the above aphid example, genetic correlations could be generated by QTL that have either pleiotropic effects or linkage disequilibrium. Not all genetic assessments, however, have found convincing evidence for either a positive association between preference and performance or for a negative correlation in performance across host plants (Joshi and Thompson 1995, 1997, Fry 1996, 2003, Thompson 1996, Abrahamson and Weis 1997, Ballabeni *et al.* 2003).

Natural enemies can also shape the diets of insect herbivores and promote specialization. For many insect herbivores, susceptibility to predators and parasitoids varies as a function of the host-plant species they consume (Bernays and Graham 1988, Jaenike 1990, Berdegue *et al.* 1996). If, for example, herbivores sequester specific plant toxins and use them for defense against generalist predators, the **enemy-free space** (EFS) provided could promote dietary specialization by restricting herbivores to plants where toxins can be obtained. Jeffries and Lawton (1984) define enemy-free space as “ways of living that reduce or eliminate a species’ vulnerability to one or more species of natural enemies.” In fact, seldom is an area of a species’ niche totally free of natural enemies, and studies generally reveal the existence of **enemy-reduced space** (Berdegue *et al.* 1996), a more accurate moniker for this widely used concept. An example consistent with the hypothesis that EFS promotes dietary specialization involves the leaf beetles *Phratora vitellinae* and *Galerucella lineola* that feed on willows in Scandinavia (Denno *et al.* 1990). When disturbed by a predator, larvae of *P. vitellinae* exude droplets of a defensive secretion from dorsal glands. The secretion contains salicyl aldehyde, the precursors for which are plant-derived salicylates like salicin (phenolics). When fed willow species rich in salicylates, larvae defend themselves effectively against predators such as coccinellid beetles. In contrast, when fed salicylate-poor willows, larvae are readily consumed. Herbivores such as *P. vitellinae* obtain enemy-free space on willows where they can acquire the allelochemical precursors for defense. The result appears to be dietary specialization on salicylate-rich willow species, even though they can survive and develop well on salicylate-poor species in the absence of predators. Related herbivores like *G. lineola* that do not employ a plant-derived defense are not so constrained and use a broader range of willow species in the field.

Other evidence that predation can shape the diet breadth of herbivores comes from an experiment involving a taxonomically diverse array of 70 species of Neotropical caterpillars offered to the predaceous ant *Paraponera clavata* (Dyer 1995). Overall, specialist caterpillar species that either sequestered plant chemicals or synthesized them *de novo* were far more protected from ant predation than palatable generalists. Moreover, when specialists that normally sequester plant toxins were reared on toxin-free diets, they became more susceptible to attack than larvae reared on leaves with access to toxins. Thus, both plant chemistry and predators may act in concert to select for dietary specialization in this assemblage of herbivores. As a caveat, however, chemically defended caterpillars that are protected from predation in this assemblage are susceptible to attack from parasitoids (Gentry and Dyer 2002). In fact, specialist lepidopterans at large incur higher attack rates than do more polyphagous species (Dyer and Gentry 1999). Thus, the advantage specialists enjoy from relaxed predation may be offset by increased parasitoid attack. It should be noted also that there are highly polyphagous species, such as the lubber grasshopper, *Romalea microptera*, that sequester toxins from a wide variety of plants and lower their risk of predation by so doing (Blum *et al.* 1990). Thus, EFS achieved by toxin sequestration may not always be associated with dietary specialization.

Crypsis (camouflage by resemblance to the background environment) can also promote narrow diets as a consequence of enemy-free space (Otte and Joern 1977, Jaenike 1990, Crespi and Sandoval 2000). In the case of desert grasshoppers (Orthoptera: Acrididae), species that resemble the specific background of their host plant gain protection from visually orienting predators (Otte and Joern 1977). As a consequence, adaptation to one host background diminishes protection on another and the specificity of crypsis is inversely related to diet breadth. For example, *Bootettix* grasshoppers that live exclusively on and precisely resemble the foliage of their *Larrea* host plant (Zygophilaceae) are very host specific. In contrast, crypsis in stem-inhabiting grasshoppers (e.g. *Ligurotettix coquilletti*) provides effective camouflage across a variety of habitats and these grasshoppers are far more polyphagous. Similarly, *Timema* walking sticks (Phasmatodea: Timemidae) gain protection from vertebrate predators (lizards and birds) by resembling their host plant (Crespi and Sandoval 2000). In this assemblage of walking sticks, selection for crypsis has resulted in dietary specialization. In fact, certain species (*Timema cristinae*) have evolved different plant-associated color morphs, a polymorphism that is maintained by differential risk of predation of the morphs on the respective host plants. Also, host shifts to distantly related plants have occurred because certain walking-stick species possess color patterns that preadapt them for crypsis, and therefore enemy-free space, on novel plants.

Interspecific competition is another factor that may favor dietary specialization (Jaenike 1990). By specializing on different plant species herbivores could reduce competitive interactions that otherwise might result in reduced fitness (Denno *et al.* 1995). This assertion assumes that competition is a consistent and important source of mortality for herbivores, a view that has attracted considerable debate, but is regaining momentum (see Chapter 5). Nevertheless, the great majority of studies testing for interspecific competition between herbivore species involve interactions on the same host-plant species, thus precluding an assessment of how competition might restrict a herbivore to using a subset of available plant species (Denno *et al.* 1995, Denno and Kaplan 2007, Kaplan and Denno 2007). One study, however, sheds light on the issue. For instance, the survival of the plant bug *Megaloceroea recticornis* was reduced by another plant bug *Notostira elongata* when only a single host-plant species was present, but the competitive effect was removed in the presence of an alternate plant species that acted as a refuge for the inferior competitor (Gibson and Visser 1982). This dietary shift is consistent with the view that interspecific competition can be minimized when co-occurring herbivores "specialize on" or occupy different host-plant species.

Host-plant abundance and apparency can also influence the diet breadth of insect herbivores (Courtney and Forsberg 1988, Singer *et al.* 1989, Jaenike 1990, Kuussaari *et al.* 2000). Specializing on host plants that confer high offspring fitness is favored only if the realized fecundity of the female isn't compromised by other factors such as plant rarity. As the abundance of an acceptable host-plant species increases in the habitat, herbivores evolve oviposition preferences for the common host which often translates into increased use. A good example involves the Glanville fritillary butterfly, *Melitaea cinxia* (Lepidoptera: Nymphalidae), that selectively oviposits on *Veronica spicata* as this host-plant becomes more abundant in the habitat relative to an alternative host *Plantago lanceolata* (Kuussaari *et al.* 2000). Alternatively, when the most suitable host-plant species is rare in the habitat, females move down the preference hierarchy and oviposit on less favored hosts (Thompson 1988, Singer *et al.* 1989). This said, "oviposition preference" is a complex process and is influenced by a variety of herbivore-specific factors, including genetic variation in preference rankings among females, a female's motivational state and egg load, learning and age (Jaenike 1990, Radtkey and Singer 1995, Singer and Lee 2000). For instance, females are more likely to oviposit on less preferred hosts if they are old and carrying a large load of undeposited eggs. Regarding learning, apple maggot flies are more likely to oviposit on fruit types on which they have had previous experience (Papaj and Prokopy 1988). Despite the variation imposed by these factors, the spatial use of host plants appears to be driven largely and directly by plant abundance and indirectly by an evolved preference for the regionally abundant acceptable host plant (Kuussaari *et al.* 2000).

Plant ephemerality also influences diet breadth. Among mycophagous drosophilid flies, *Drosophila duncani* and *Mycodrosophila claytoni* specialize on a few species of very persistent bracket fungi, whereas *D. falleni* and *D. putrida* use dozens of species of ephemeral gilled mushrooms (Lacy 1984). Overall, both the abundance and persistence of host plants have played an important role in shaping the diet breadth of phytophagous insects.

If the fitness of an individual choosing a particular host-plant species increases in the presence of other colonizing conspecifics, then host specialization can arise (Jaenike 1990). An example would be species that choose host plants on which they are more likely to encounter mates. So-called cases of **plant-associated assortative mating** (mating with individuals like themselves who in this case prefer the same plant) are thought to strongly favor adaptation to specific host plants. Fruit flies in the *Rhagoletis pomonella* complex (Diptera: Tephritidae) feed as larvae within the fruits of their hosts and provide a classic example whereby assortative mating has promoted specialization on a variety of trees and shrubs including hawthorn (*Crataegus*), apple (*Malus*) and dogwood (*Cornus*) (Bush 1969, Feder *et al.* 1994, Prokopy and Papaj 2000, Berlocher and Feder 2002, Forbes and Feder 2006). Flies in this complex of "host races" mate solely on fruits of their host plant and this behavior likely facilitated a shift of *R. pomonella* from hawthorn to apple in the mid-1800s as apple became more abundant. Host-associated mating minimizes gene flow among the host races, promotes genetically based differences in oviposition preference, and synchronizes the fly's life cycle with the phenology of fruit production, all adaptations that have led to host-plant specialization, mating barriers and perhaps speciation.

A similar situation occurs with the gall-inducing fly *Eurosta solidaginis* (Diptera: Tephritidae) that forms host races on two species of goldenrods, *Solidago altissima* and *S. gigantea* (Asteraceae) (Abrahamson *et al.* 2001, Craig *et al.* 2001, Eubanks *et al.* 2003). Genetic differences between host races in this fruit fly have resulted from host-associated assortative mating as well as strong oviposition preferences. In this system the predaceous tumbling flower beetle, *Mordellistena convicta* (Coleoptera: Morellidae), that attacks the fly has also formed host races on the two *Solidago* species. Notably, host-associated mating also occurs in the beetle and has contributed to local adaptation. This study suggests the interesting possibility that host-race formation by a herbivorous insect can promote subsequent diversification at higher trophic levels, a phenomenon referred to as **sequential radiation** by Abrahamson *et al.* (2003).

Plant-associated mating also encourages specialized diets in other herbivores. For instance, the pea aphid, *Acyrthosiphon pisum*, mates on its alfalfa and clover hosts where specialization on each plant species is facilitated because genes controlling host acceptance, assortative mating and performance are genetically linked (Caillaud and Via 2000, Hawthorne and Via 2001, Via and Hawthorne 2002). Not only does this genetic architecture promote host-plant specialization, but it can also foster reproductive isolation and speciation. Similarly, assortative mating has played an important role in the specialized diets and host-race formation of the *Enchenopa binotata* complex of treehoppers (Hemiptera: Membracidae) (Wood and Guttman 1982, 1983, Wood *et al.* 1999). These sap-feeders exploit a number of tree and shrub species in eastern North America where there is strong evidence for host-race formation. Membracids, like their leafhopper and planthopper relatives, have a unique mate-location system that ties them very closely to their host plant and thus promotes assortative mating. Both sexes locate and communicate with each other during courtship using substrate-borne vibrational signals they produce. Such signals can be detected only by individuals contacting the same plant through which the signals are conducted. Thus, both mating and oviposition into host-plant tissues are closely linked to the same individual plant. Such close linkage has promoted preferences for and adaptation to the specific phenologies of the different host-plant species. Assortative mating in *Rhagoletis* flies, pea aphids and *Enchenopa* treehoppers has been championed as a prerequisite to host-race formation and speciation at a small geographic scale, namely **sympatric speciation** (Wood *et al.* 1999, Hawthorne and Via 2001, Berlocher and Feder 2002). Although the process of sympatric speciation has generated considerable debate, it can hardly be contested that host-associated mating can be an important factor promoting genetic divergence and dietary specialization in insect herbivores given that so many of them mate on their host plants.

Aggregation behavior in herbivores may also promote dietary specialization (Jaenike 1990). For instance, many species of insect herbivores including aphids, lepidopterans, beetles and sawflies feed in coordinated groups (Bowers 1993, Fitzgerald 1993, Dixon 1998, Fordyce 2005, 2006). Also, many herbivores that feed in aggregations are aposematic (warningly colored), sequester toxins from their host plant and are distasteful to predators. Advantages of feeding in aggregations include increased foraging efficiency, feeding facilitation, defense against predators, thermoregulation and overwhelming plant defenses. To a certain point, all of these factors are enhanced with increasing group size and thus are density dependent. Many, but not all, aggregative herbivores on toxic plants are dietary specialists. For example, several tree-feeding Lepidoptera such as *Malacosoma*, *Hyphantria*, *Halisidota* and *Symmerista* are gregarious feeders, but are highly polyphagous (Baker 1972b, Price 2003a pages 155–158). An example of how larval aggregation may promote specialization involves the crimson patch butterfly, *Chlosyne janais* (Lepidoptera: Nymphalidae), that feeds only on the shrub *Odontonema callistachyum* (Acanthaceae) in the subtropics of Mexico (Denno and Benrey 1997). When experimentally manipulated, there is a striking effect of group size on larval growth whereby larvae more than double their weight gain by feeding in large rather than small aggregations on intact plants in the field. However, this group-feeding advantage is lost altogether when larvae are raised on excised leaves in the lab, suggesting that large aggregations may overwhelm an induced allelochemical response. Given the intimacy of the interaction required for herbivores to manipulate plant defenses (Karban and Baldwin 1997), it is unlikely that the benefits of aggregation would be as effective across a broad range of plant species. Thus, aggregation and associated traits such as warning coloration and increased defense against predators may contribute to dietary specialization.

4.6.3 Selective factors favoring broad herbivore diets

When herbivores feed on **small or ephemeral plants** and must move among several individual plants to complete development (e.g., some grasshoppers) grazing behavior can be favored (Thompson 1988, Jaenike 1990). If selection promotes grazing behavior, then it may also favor the ability of larvae to develop on numerous plant species with diverse chemistries. For instance, the salt marsh caterpillar, *Estigmene acrea* (Lepidoptera: Arctiidae), is broadly polyphagous, frequently defoliates individual host plants and wanders widely among many different host species before completing development (Singer *et al.* 2004a,b). In this case, grazing may be favored by the small size of its host plants, but overt diet mixing likely contributes to polyphagy as well. For example, in Arizona, larvae *E. acrea* feed on two asterid host plants, *Senecio longilobus*, which contains pyrrolizidine alkaloids that the caterpillars sequester, and *Viguiera dentata*, which does not contain these alkaloids. Although larvae grow faster on *Viguiera* than on *Senecio*, they are better defended and suffer less parasitism when fed *Senecio*. When the risk from parasitoids is moderate, as it is in nature, a mixed diet provides a survival advantage over pure diets of either *Viguiera* or *Senecio*. Thus, by diet mixing, larvae balance the benefits of enhanced growth and enemy-free space. Regardless of underlying mechanisms, herbivores that feed on rare, small and ephemeral plants are more polyphagous than are those exploiting abundant and larger plants. Herbivores fitting this bill are taxonomically diverse and include *Heliconius* butterflies, grasshoppers and *Drosophila* that breed in mushrooms and cacti.

Risk spreading can also promote broad diets when host-plant suitability is unpredictable and females deposit their eggs across a variety of host plants to ensure that some offspring survive (Jaenike 1990). The oviposition behavior of the cabbage butterfly, *Pieris rapae*, is consistent with risk-spreading behavior (Root and Kareiva 1984). Females exhibit wide-ranging movements that result in oviposition over a large area on many different individual plants and plant species. Females are apparently unable to accurately assess the potential vagaries of plant suitability arising from changes in phytochemistry, defoliation, competitors and predators. Thus, when mortality is unpredictable across the oviposition landscape, females may hedge their bets and scatter their eggs widely (Stearns 1992), a behavior that can promote a broader diet.

Enemy-free space, or more realistically **enemy-reduced space**, arising from ant mutualisms has promoted polyphagy, particularly in lycaenid butterflies (Lepidoptera: Lycaenidae) (Thompson 1988, Jaenike 1990, Baylis and Pierce 1993, Pierce *et al.* 2002). Larvae of many lycaenid species are tended by ants that protect them from natural enemies. Larvae possess exocrine glands and upon solicitation from tending ants produce secretions containing carbohydrates and amino acids that are then consumed by ants. Producing resources is costly to the lycaenids because ant-tended larvae grow slower and pupate at a smaller size than non-tended larvae when natural enemies are excluded (Pierce *et al.* 1987, 2002). In the presence of natural enemies in the field, however, larval survival can be very low if ant mutualists are absent. Thus, there has been strong selection for female butterflies to oviposit where ants are abundant, and for females to use ant cues rather than host-plant cues as oviposition stimulants. In fact, females of some species, such as the Australian *Ogyris amaryllis*, oviposit on the nutritionally inferior mistletoe *Amyema maidenii* with ants rather than on the nutritionally superior *A. preissii* (Atsatt 1981a, b). An important consequence of the mutualism is that ant-tended lycaenids feed on a much greater variety of host-plant species than do non-tended species (Pierce and Elgar 1985, Baylis and Pierce 1993, Pierce *et al.* 2002). For these butterflies, the benefits of ant protection offset the disadvantages of feeding on less nutritious, allelochemically discrepant and rare plants, a net advantage that has contributed to broader diets.

Polyphagy can arise either by a herbivore feeding locally on multiple host-plant species or it can result from populations that specialize on different host-plant taxa throughout its geographic range (Jaenike 1990, Parry and Goyer 2004). **Genetic correlations between preference and performance**, such as those that occur in the clover and alfalfa host races of pea aphids, can lead to local specialization, but at the same time promote "polyphagy" at a larger geographic scale (Hawthorne and Via 2001, Via and Hawthorne 2002). A well-studied system that highlights this possibility involves the checkerspot butterfly, *Euphydryas editha*, which uses plants in five different genera in two families as larval hosts throughout its range in the mountains of California: *Pedicularis*, *Collinsia*, *Castilleja* and *Penstemon* in the Scrophulariaceae and *Plantago* in the Plantaginaceae (Singer *et al.* 1988, 1993, Singer and Parmesan 1993, Singer and Wee 2005). Despite similarities in the composition of plant communities from site to site, checkerspots specialize on plants in one genus at any one site. Moreover, there is evidence that genetic variation for oviposition preference and positive linkages between oviposition preference and larval performance contribute to the regional pattern of host-plant use. However, episodes of logging have disrupted historic patterns of host use and promoted rapid changes in oviposition preference. For example, the traditional host *Pedicularis* is a hemiparasite of trees and becomes far less abundant after clear cutting. Following disturbance, *Collinsia* thrived in the clearings and was incorporated into the diet of the butterflies. However, female butterflies retained their inherent oviposition preference for the historic host *Pedicularis*, therefore disrupting the traditional preference–performance linkage because butterflies no longer preferred the host plant where larvae performed best. Needless to say, anthropogenic disturbance upset the evolutionary equilibrium of the system and set the stage for rapid changes in host-plant preferences. Nonetheless, the positive preference–performance relationships seen in this system, pea aphids, *Rhagoletis* fruit flies and treehoppers demonstrate how this linkage can promote polyphagy at regional spatial scales.

If herbivores undergo eruptive population dynamics and frequently defoliate their host plants, the ability to feed on alternative host plants would be advantageous (Thompson 1988, Jaenike 1990). Thus, frequent **intraspecific competition** could favor polyphagy in herbivores. Forest macrolepidoptera support this notion in that outbreaking species have a greater diet breadth than non-outbreaking taxa (Hunter 1995b). Phylogenetic contrasts reveal that outbreaking species incorporate on average seven more plant genera into their feeding repertoire than do non-eruptive species. Classic examples are forest defoliators like the fall webworm, *Hyphantria cunea*, and the gypsy moth, *Lymantria dispar*, which are among the most polyphagous of all herbivores (Warren and Tadic 1970, Miller and Hanson 1989).

Natural enemies and pathogens often concentrate their attack on plants where prey and hosts are abundant (Hassell 1978, Jaenike 1990, Hajek 2004) and herbivores that distribute themselves across multiple host plants may incur less enemy-inflicted mortality. Thus, concentrated enemy attack might select for broad herbivore diets. Indeed, an early survey of parasitoid attack rates on a large diversity of herbivore taxa found evidence that density-dependent attack was lower on polyphagous herbivores (16%) than on monophagous species (27%) (Stiling 1987). This finding has been confirmed in recent assessments in which parasitism rates were significantly less on polyphagous species than on dietary specialists, a study based on lepidopteran hosts occurring in natural habitats (Dyer and Gentry 1999, Gentry and Dyer 2002). Surveys in agricultural systems found the same result, namely that biological control successes involving parasitoids were higher for specialist pest herbivores than generalists (Stiling 1990, Dyer and Gentry 1999). Altogether, several studies are consistent with the view that density-dependent attack by natural enemies has contributed to the evolution of broad herbivore diets.

4.6.4 Overview of selective forces influencing diet breadth

Although there are several convincing examples, there is no general consensus that positive genetic correlations between oviposition preference and offspring performance or negative cross-host correlations in performance select for narrow diets in herbivorous insects (Thompson 1988, Jaenike 1990, Fry 1996, 2003, Hawthorne and Via 2001, Via and Hawthorne 2002). Indeed, plant-associated mating can reinforce the evolution of host-plant specialization (Hawthorne and Via 2001, Berlocher and Feder 2002). Other factors, however, can either promote or compromise the extent to which herbivores evolve narrow diets (Yamaga and Ohgushi 1999). If “preferred host plants” are rare or ephemeral, offer little enemy-free space or are subject to frequent bouts of defoliation, broader diets may be favored. Moreover, the specific life-history traits of herbivores also bear on diet breadth evolution. If herbivores are both short lived with limited time to search and oviposit and are highly fecund as well, selection resulting from large egg loads may foster oviposition on a broader range of host plants. Feeding guild also appears to influence host shifting, specialization and ultimately diversification (Wiegmann *et al.* 1993, Winkler and Mitter 2007, see Chapter 8). For instance, concealed feeders such as leaf miners and gall inducers are often very specialized compared to free-living herbivores, an intimacy that can deter host shifting and associated rates of increased diversification. As a specific example, Nyman *et al.* (2006) found that internally feeding nematine sawfly clades have colonized significantly fewer plant families than their externally feeding sister groups.

4.6.5 Deme formation and adaptation to individual plants

So far, we have focused primarily on diet breadth at the taxonomic scale of plant species or higher. Specifically, we have considered factors that restrict herbivores or not to single plant species, genera or families. Dietary specialization, however, can occur at the scale of individual plants. The **demic adaptation hypothesis** predicts that populations of small, specialized insect herbivores become genetically isolated over time, subdividing into demes (subpopulations) that are differentially adapted to the traits (e.g., phytochemistry) of individual large perennial plants (Edmunds and Alstad 1978, Alstad 1998). This hypothesis further asserts that as demes become specialized on natal hosts, performance on novel hosts declines, an expectation remindful of the negative genetic correlation in cross-host performance that can promote dietary specialization. The hypothesis was first tested by transferring the scale insect *Nuculaspis californica* (Hemiptera: Diaspididae) back to its natal pine tree and to novel individuals that it had not experienced. This procedure was followed by an assessment of scale performance on natal and novel trees. Because scale insects are notoriously immobile it was originally thought that sessile insects with reduced gene flow would be more likely to form demes than more dispersive herbivores.

Since its inception, the demic adaptation hypothesis has been tested using a variety of insect herbivores, including scale insects, thrips, leafmining lepidopterans, beetles and gall-forming flies (Karban 1989a, Hanks and Denno 1994, Strauss 1997, Cobb and Whitham 1998, Stiling and Rossi 1998, Mopper *et al.* 2000). Overall, recent assessments of experimental studies find general support for the demic adaptation hypothesis, namely that local adaptation to natal hosts results in reduced performance on novel ones (Van Zandt and Mopper 1998, Mopper 2005). However, sessile herbivores were no more likely to exhibit deme formation than more mobile insects. There was a greater tendency for endophagous herbivores (leaf miners and gall inducers) and parthenogenetic species (some aphids, scale insects and thrips) to form demes than free-living and sexually reproducing species. Altogether, several experimental studies show that some herbivores evolve extreme dietary specialization by adapting to the specific properties of individual plants.

4.6.6 Factors facilitating host plant shifts

Coevolutionary scenarios necessarily assume that herbivores are able to shift ultimately to novel plant genotypes or species and thus enter new adaptive zones where they then undergo speciation and diversification (Farrell and Mitter 1990, Mitter *et al.* 1991, Herrera and Pellmyr 2002, Thompson 2005). Thus, understanding factors that facilitate host shifts is critical, not only for diet breadth evolution, as we have just seen, but also for the forthcoming treatment of coevolution. Chemical similarity in plants is most certainly involved in facilitating shifts to novel plants (Futuyma 1983, Jaenike 1990, Becerra 1997, Becerra and Venable 1999, Wahlberg 2001). For instance, related species of butterflies often use plants that are chemically similar. A well-known example involves monarch butterflies and their relatives (Danainae: Nymphalidae) that specialize on milkweed plants in the family Apocynaceae that contain cardenolides (Brower 1984). Moreover, host shifts are more likely to occur between plants with similar allelochemistries, even though the plants are taxonomically distant. For example, many species of swallowtail butterflies, such as the black swallowtail, *Papilio polyxenes* (Papilionidae), are found only on plants in the carrot family (Apiaceae) and citrus family (Rutaceae), both of which contain furanocoumarins (Berenbaum 1983, Feeny 1991b). Likewise, introduced plants are most likely colonized by insect herbivores that feed on chemically similar plants (Strong *et al.* 1984a). The garden nasturtium *Tropaeolum majus* (Tropaeolaceae), for instance, was introduced from Peru to Western Europe more than 300 years ago when the cabbage whites *Pieris brassicae* and *P. rapae* (Lepidoptera: Pieridae) rapidly incorporated it into their repertoires along with their normal mustard hosts (Brassicaceae). The phytochemical commonality is that both mustards and nasturtium contain glucosinolates which adult butterflies use as chemical cues to locate their hosts and to which larvae are adapted (Fahey *et al.* 2001, Renwick 2002, Wittstock *et al.* 2004).

Some herbivores, however, are clear exceptions to the view that chemical similarity facilitates host shifting (Becerra 1997, Becerra and Venable 1999). Although most species of the leaf beetle genus *Blepharida* (Coleoptera: Chrysomelidae) have shifted to *Bursera* species (Burseraceae) with similar terpene chemistries, *Blepharida alternata* has not. In contrast to its congeners, this beetle has colonized a suite of chemically discrepant and phylogenetically unrelated *Bursera* species. Observations like these, coupled with the fact that many herbivores can adapt quickly to both plant toxins and resistant varieties of plants, have prompted ecologists to suggest that the selective forces underlying host shifting and dietary specialization are less likely to lie with toxic barriers than other ecological factors (Futuyma 1983, Jaenike 1990). As we have seen, many of the factors that favor the evolution of broad diets are potentially involved in promoting host shifts. Thus, as a general paradigm, similarity in plant chemistry often sets the stage for a host shift, but other ecological factors appear necessary for it to actually occur.

An examination of cases in which a host shift is in progress or has recently occurred sheds light on the factors facilitating the incorporation of a novel host into a herbivore's diet. Just such a situation involves swallowtail butterflies in the *Papilio machaon* group (Papilionidae) that normally use plants in the carrot family (Apiaceae) as their larval hosts (Murphy 2004, Murphy and Feeny 2006). In Alaska and northwestern Canada, *P. machaon* feeds locally on its ancestral apiaceous host (*Cnidium cnidifolium*), but it has recently added to its diet plants in the distantly related Asteraceae (*Artemisia arctica* and *Petasites frigidus*). All three hosts are chemically similar in that they contain derivatives of hydroxycinnamic acid, which act as oviposition stimulants for the butterfly. Shared chemistry paves the way for this host shift, but enemy-free space from predaceous ants is involved in the actual shift. The growth and survival of caterpillars on all three host plants were measured in the field with plants either exposed or protected from predators. In the presence of predators, larval survival was greater on the novel hosts (Asteraceae) than on the ancestral host (Apiaceae), but in the absence of predators survival and growth were greater on the ancestral host. This study is one of few that fulfill the criteria necessary to rigorously demonstrate the role of enemy-free space in host shifting (Berdegue *et al.* 1996). These are that:

(1) Herbivore fitness is adversely affected in the presence of enemies
(2) Herbivore fitness is greater on the novel host than the normal host when natural enemies are present thus demonstrating enemy-free space
(3) In the absence of natural enemies herbivore fitness is greater on the normal than the novel host, thus documenting a feeding cost on the novel host.

When the benefits of enemy-free space on the novel compared to the normal host outweigh developmental costs, enemy-free space can facilitate host shifting.

The extent to which enemy-free space facilitates host shifting, however, can be conditional on temporal changes in the composition of the natural enemy complex. An example is provided by a study of the leafmining fly *Liriomyza helianthi* (Diptera: Agromyzidae) on its natural sunflower host *Helianthus annuus* (Asteraceae) and several related novel hosts (Gratton and Welter 1999). Larvae were experimentally transplanted into both normal and novel hosts and the level of attack by parasitoids was measured. In years when endoparasitoids dominated the enemy complex, leaf miner mortality was 22% lower on the novel than the normal host plant. However, in years when generalist parasitoids dominated the assemblage, there was no difference in parasitism on novel and normal host plants, documenting that enemy-free space as a force favoring a host shift varies with changes in the composition of the parasitoid complex.

However, historic host shifts can ultimately result in increased enemy attack and thus appear to have occurred despite enemy-enriched space on novel hosts. For the leaf miner *Tildenia inconspicuella* (Lepidoptera: Gelechiidae), stellate trichomes on its horsenettle host plant (*Solanum carolinense*) impair the miner's ability to exit the leaf mine after entering it as a newly hatched small larva, which has apparently selected for an entirely endophagous feeding habit (Gross and Price 1988). In contrast, the related leaf miner *Tildenia georgei* is able to freely enter and re-enter leaves of its groundcherry hosts (*Physalis heterophylla*) because this plant has simple trichomes, and larval movement and mine re-initiation are not hindered. Surprisingly, the horsenettle leaf miner incurs a fourfold higher incidence of parasitoid attack compared to that of the groundcherry leaf miner giving the impression that any host shift to horsenettle occurred directly into enemy-enriched space. However, the increased attack rate on horsenettle occurs as a consequence of several endoparasitoids that likely joined the parasitoid assemblage well after the miner's initial colonization of and adaptation to horsenettle. Thus, current differences in enemy-free space between novel and ancestral host plants may not reflect historic differences in enemy attack rates that promoted the initial host shift.

Ecological factors other than natural enemies also facilitate host shifts. Several native herbivores have recently included agricultural crops in their diet, host-plant shifts that are associated with changing land-use patterns. For example, the sulphur butterfly, *Colias philodice*, historically used only native legumes as its sole larval host plants, but it has now switched to alfalfa in certain areas of the Rocky Mountain region (Tabashnik 1983). In the decades following the host shift, butterflies have not evolved a difference in oviposition preference between hosts, but they do exhibit local adaptation in performance because larvae from alfalfa-feeding populations develop faster on alfalfa than they do on native legumes. Similarly, larvae from populations feeding on native legumes perform better on these hosts than they do on alfalfa, suggesting a negative performance correlation on the two hosts. Nonetheless, the host shift was associated with changes in the abundance of alfalfa in the region.

Global warming has fostered changes or expansions in the geographic distribution of numerous insect herbivores, some of which are accompanied by shifts in host plant use (Parmesan *et al.* 1999, Pimm 2001, Thomas *et al.* 2001). Since the 1970s, the brown argus butterfly, *Aricia agestis* (Lepidoptera: Lycaenidae), has expanded its distribution northward in England (Thomas *et al.* 2001). Along with this range expansion, there has also been a shift in the butterfly's choice of host plants from sun-loving *Helianthemum chamaecistus* (Cistaceae) to various *Geranium* species (Geraneaceae) that grow in habitats previously too cool to support larval development. Females in stationary populations to the south prefer to lay eggs on their developmental hosts, whereas in expanding populations females prefer to oviposit on geraniums. Thus, changes in oviposition preference are also associated with this range expansion. This example emphasizes that subtle change in an environmental factor can provide opportunities for dietary shifts that are otherwise precluded by the developmental constraints of the herbivore.

Hybridization between two related host plants can also facilitate host shifting (Floate and Whitham 1993, Pilson 1999). The so-called "**hybrid bridge**" hypothesis was spawned from a study of the exploitation patterns of seven aphid species on two parental cottonwood species (narrowleaf cottonwood, *Populus angustifolia*, and Fremont cottonwood, *P. fremontii*) and their naturally occurring F_1 and backcross hybrids (Floate and Whitham 1993). The various aphid species are host specific on either *P. angustifolia* or *P. fremontii.* Aphids normally associated with the narrowleaf parent freely exploit the F_1 hybrids, whereas aphids specializing on the Freemont parent do not. This pattern suggests that the hybrid bridge is asymmetric (when unidirectional introgression occurs) and that F_1s share more herbivore species with the parent species to which introgression occurs (*P. angustifolia*) than the parent with which hybridization does not (*P. fremontii*). Genes controlling the expression of traits affecting host-plant recognition and/or herbivore performance in F_1 hybrids derive solely from *P. angustifolia*, thus encouraging the potential one-way shift of herbivores from *P. angustifolia* to *P. fremontii*. When hybrid bridges occur, herbivores experience novel plant genomes and associated plant morphologies and physiologies in gradual steps, which perhaps ease host shifts that would otherwise be more difficult. However, to evaluate the generality of this hypothesis, more studies are needed on how plant hybridization influences herbivore preference and performance, both of which must be positively affected to facilitate a host shift (Pilson 1999).

4.6.7 Coevolution

Coevolution is reciprocally inflicted evolutionary change between interacting species driven by natural selection (Futuyma and Keese 1992, Thompson 2005). However, there is a continuum of coevolutionary interactions that vary in their intensity from tightly coevolved mutualisms between microbial symbionts and their hosts to generally weaker interactions between free-living organisms such as plants and herbivores, flowers and pollinators, and parasites and hosts (see Chapter 6). The term coevolution was first used to describe gene-for-gene interactions between plants and plant pathogens (Mode 1958, 1961). However, coevolution was popularized when Ehrlich and Raven (1964) published their essay on interactions between butterflies and their host plants. They imagined a scenario whereby plants and herbivores exert reciprocal selective pressure on one another, resulting in evolutionary change in both participants. As plants erected new defenses, herbivores ultimately countered with offensive breakthroughs and the "arms race" was on. Key in their coevolutionary scenario is that novel defensive breakthroughs in plants and offensive innovations by herbivores create temporary "adaptive zones" where plants free of herbivore attack and herbivores with novel offenses are favored, which then promotes speciation and diversification. Subsequently, the Ehrlich and Raven model has been hailed as "**escape-and-radiate coevolution**" (Thompson 1989, 2005, Futuyma and Keese 1992). Thus, Ehrlich and Raven interpreted coevolution in a far broader sense than did Mode (1958), who emphasized a gene-for-gene correspondence between the defensive traits of plants and the resistance-breaking adaptations of pathogens.

Much of what we have discussed so far has taken a broad view, emphasizing the interplay between plants and herbivores, how they have shaped each other's evolution, and the various defensive strategies of plants and countertactics of herbivores. However, regarding all the contingencies that single plant and herbivore species face, how many specific pairwise species interactions are indeed strong enough to exert reciprocal selective effects, effects strong enough to promote speciation and diversification? If, for example, a herbivore is rare and polyphagous, how strong can interactions be between a consumer and one of its many host-plant species? Moreover, if a plant must contend with a barrage of pathogens, physical stresses and allocations to growth and reproduction, as well as defense, what is the relative strength of selection from a single herbivore species? One can imagine instances in which plants and herbivores have little reciprocal impact. Alternatively, coevolution is most likely to occur when a herbivore is abundant and monophagous and its host plant harbors few other herbivores or pathogens (Futuyma 1983). Therefore, a continuum of possibilities exist that range from tight coevolved associations to loosely linked interactions (Thompson 2005). Also, authors often use the term coevolution without establishing that evolutionary change has resulted from reciprocal selection. With this in mind, it is a valuable exercise to read original papers and examine the legitimacy of the coevolutionary claim. Often, suggestions are made that coevolution has occurred without any hard evidence, and it is particularly difficult to establish that plant traits have evolved in response to selection by insects. Thus, before examining the evidence supporting coevolution and exploring its consequences for speciation and diversification, we need to better understand the variety of interactions that are subsumed under the guise of coevolution.

There are many studies demonstrating the one-way adaptation of herbivores to plants or vice versa (Fritz and Simms 1992, Shonle and Bergelson 2000, Berlocher and Feder 2002). The evolution of resistance-breaking genotypes of crop pests that allow them to feed on formerly resistant varieties is an example, as are the many cases of host-race formation. However, without evidence for reciprocal effects, the adaptation of a herbivore to a changing plant resource is not coevolution and simply represents **resource tracking**. As an example, the soapberry bug, *Jadera haematoloma* (Hemiptera: Rhopalidae), feeds on the seeds of plants in the Sapindaceae and has rapidly evolved shorter piercing-sucking mouthparts in response to the introduction of goldenrain tree, *Koelreutaria elegans*, in parts of the southern United States (Carroll and Boyd 1992, Carroll *et al.* 1998). The native host plant of soapberry bugs is balloon vine, *Cardiospermum corindum*, which has relatively large fruits. On this native host, the distance from the outside of the fruit to the centrally positioned seeds is large and bugs have long beaks that can pierce the fruit and access the seeds. In contrast, goldenrain tree has small flat fruits and in areas where this invasive tree has established, bugs have evolved shorter mouthparts, while other dimensions of body size have remained unchanged. Beak length in the two races of bugs is under genetic control, thus providing the raw material for selection and local adaptation. In this system, however, there is no evidence yet that soapberry bugs have influenced plant traits.

Most models that portray reciprocal impacts between plants and herbivores, as well as hosts and parasites, describe **pairwise coevolution** or coadaptation between two interacting species (Thompson 1989, 2005, Futuyma and Keese 1992). The analogy of the “coevolutionary arms race” often applies to this model, as do examples of gene-for-gene interactions. Perhaps one of the best species-level examples of pairwise coevolution involves an array of leaf-beetle species in the genus *Blepharida* (Chrysomelidae) that feed on a diversity of trees in the Bursearaceae (Becerra 2003). By calibrating the timescale of the molecular phylogenies of *Bursera* and *Blepharida* beetles, it was shown that examples of defense and counterdefense have synchronous times of origin. Older lineages of tree species employ a system of pressurized canal-born resins in their leaves that when damaged produce a “squirt of resin” that mires non-adapted herbivores. Older lineages of beetles exploiting these trees have countered by cutting the leaf veins, which deactivates the defense. More recent lineages of trees don’t squirt, but have evolved a different defensive strategy consisting of complex mixtures of terpenes. Younger lineages of beetle species don’t cut veins, but are able to metabolize the complex mixtures of defensive chemicals. Because *Blepharida* beetles are monophagous and among the most abundant herbivores in the system, this scenario is consistent with the view that tree and beetle traits have coevolved in pairwise fashion in response to concurrent reciprocal selective pressures.

Most species, however, do not exist in nature as isolated pairs, but as multispecies assemblages. Thus, **diffuse coevolution** refers to the situation whereby a suite of species exert selection on another species or suite of species, resulting in reciprocal changes that cannot be attributed to a single pairwise interaction (Futuyma and Keese 1992, Inouye and Stinchcombe 2001, Stinchcombe and Rausher 2001, Thompson 2005). For instance, a multitude of herbivores and pathogens may select for high tannin concentrations in trees that in turn foster a variety of different counteradaptations in the community of herbivores. Diffuse coevolution proceeds if the effect of multiple herbivores is non-additive such that plants respond to the net selection imposed by the consumer assemblage at large. A variety of ecological mechanisms can generate non-additive effects that enhance or diminish the effect of any one herbivore on the plant (Juenger and Bergelson 1998). For example, a widespread non-additive effect results from induced resistance when prior attack by one herbivore or pathogen diminishes attack by another (Karban and Baldwin 1997, Viswanathan *et al.* 2005, Stout *et al.* 2006). Clearly, the intensity and frequency of a specific plant–herbivore interaction, and thus the opportunity for coevolution, can be affected by the presence of other players in the system.

Reciprocal selection on a specific pairwise interaction often varies among populations because the presence of other species changes the strength of the interacting pair. Thus, pairwise interactions may be subject to reciprocal selection only in certain local communities. These "coevolutionary hotspots" are embedded in a matrix of coevolutionary coldspots resulting in a **geographic mosaic of coevolution**, according to Thompson (2005). A purported example involves the woodland star, *Lithophragma parviflorum* (Saxifragaceae), and its specialist herbivore-pollinator *Greya politella* in the Rocky Mountain region of the United States (Lepidoptera: Prodoxidae) (Pellmyr and Thompson 1996, Thompson and Cunningham 2002, Thompson 2005). With their specialized long ovipositors, moths deposit their eggs in the flower's ovary through the deep corolla tube and in so doing passively pollinate the flowers. Larvae feed on a small fraction of the developing seeds within each inflorescence. Thus, moths impose a cost to plants for the pollination benefits they provide. In some populations flowers are also visited by copollinators like bombyliid flies (Diptera: Bombyliidae), which in some cases are as effective as moths at pollination. Copollinators don't oviposit on plants and therefore impose no cost on the plant. Where copollinators are abundant, pollination benefits provided by *G. politella* are outweighed by the cost of seed consumption. However, where copollinators are rare there is a net benefit to moth pollination. Thus, there is a "geographic mosaic of coevolution" between moths and woodland stars mediated by the presence of copollinators. The interaction changes across the landscape from one of mutualism (coevolutionary hotspots), where copollinators are absent, to one of antagonism where copollinators abound (coevolutionary coldspots). More accurately, this example might be called a geographic mosaic of selection potentials because woodland stars have apparently selected for long ovipositors in moths but the reciprocal effects of moths on *Lithophragma* evolution have not yet been shown.

Escape-and-radiate coevolution is a special case of coevolution, whereby an evolutionary innovation by either partner creates an "adaptive zone" that promotes speciation and subsequent diversification of the lineage (Ehrlich and Raven 1964, Futuyma and Keese 1992, Thompson 2005). An example would be the evolution of a novel defensive trait that liberates a plant lineage from its herbivores, resulting in a radiation of species in that plant lineage. Support for this hypothesis would come from "starbursts of speciation" associated with the evolution of novel defenses or counteradaptations in clades of herbivores and plants (Thompson 2005). So, what evidence do we have that rapid diversification in either plants or their associated herbivore lineages follows an adaptive innovation? The independent evolution of latex and resin canals has occurred in 16 lineages of plants, including milkweeds, figs and composites (Farrell *et al.* 1991). Moreover, evidence abounds for the effectiveness of canal-bearing plants in deterring many insect herbivores. A comparison of sister lineages of canal-bearing and canal-free plants shows a significant pattern, namely that canal-bearing lineages are far more diverse in species, a pattern which is consistent with escape-and-radiate coevolution.

If selection resulting from a pairwise interaction promotes sufficient genetic change in both partners, **cospeciation** can result (Futuyma and Keese 1992, Thompson 2005). Cospeciation has been invoked in "tightly coevolved" mutualisms such as those involving insect herbivores and their symbionts, plants and their protectionist ants, and obligate plant-pollinator systems (Clark *et al.* 2000, Itino *et al.* 2001, Kawakita *et al.* 2004, Hosokawa *et al.* 2006). However, cospeciation could be causal, in which case genetic divergence and speciation in both parties is promoted by reciprocal selective pressures (coevolution), or it may be coincidental, in which case one partner undergoes genetic divergence as a consequence of selective forces external to the interaction and speciation in the other partner simply follows.

Historically, cospeciation between pairs of plants and herbivores has been extended to entire lineages to suggest that phylogenetic relationships within a diversifying group of insect herbivores might mirror those among their radiating host plants (Futuyma and Keese 1992, Mitter *et al.* 1991). Thus, in cases of strong reciprocal selection and diversification, plant and herbivore phylogenies might match with ancestral insect species exploiting ancestral plants and derived insects using derived plant species. **Parallel cladogenesis** then represents instances where corresponding lineages of interacting species groups simultaneously diversify. Parallel cladogenesis was once viewed as the ultimate support for coevolution. Early in the development of coevolutionary theory, Ehrlich and Raven's model of escape-and-radiate coevolution was often overextended to mean cospeciation or parallel cladogenesis. Since its early inception, and with the development of molecular tools for phylogenetic assessments, there have been many studies seeking evidence in support of parallel cladogenesis (see Winkler and Mitter 2007). Like cospeciation, however, parallel cladogenesis could be either causal or coincidental. Several criteria are necessary to support a parallel cladogenesis hypothesis. First, there must be significant cladogram (phylogenetic tree) concordance between the corresponding lineages of players, and second, evidence is required that lineages diverged contemporaneously (Mitter *et al.* 1991). So, let's examine the evidence for such criteria, explore which groups of organisms show parallel cladogenesis or not, examine factors that preclude codivergence, and comment on the mechanistic link between coevolutionary forces as drivers for parallel diversification.

The best evidence for cospeciation and parallel cladogenesis comes from mutualisms involving hosts and their symbiotic microorganisms (Moran *et al.* 1993, 2005, Clark *et al.* 2000, Hosokawa *et al.* 2006). In many cases there is almost perfect cladogram concordance and molecular clock data that support contemporaneous divergence. For instance, molecular phylogenies of *Uroleucon* aphid species and their endosymbiotic bacteria *Buchnera* show very significant phylogenetic congruence (Clark *et al.* 2000; Figure 4.18). The reason underlying the robust pattern of cospeciation in *Buchnera*–aphid associations is that the endosymbionts are **vertically transmitted** from mother to progeny before birth and there is no evidence for "host switching" via the **horizontal transmission** of bacteria. Also, the bacteria are obligate mutualists and can't live outside their hosts. Moreover, *Buchnera* benefit their host aphids by supplying them with nutrients, which are required for host reproduction. In fact, *Buchnera* are genetically specialized to overproduce essential amino acids for their nutrient-limited host aphids (Baumann *et al.* 1997). Such mutualisms provide perhaps the best evidence that cospeciation and parallel cladogenesis have resulted from reciprocal selection, and thus offer evidence for coevolution.

For herbivorous insects and their host plants, phylogenetic concordance is rare and when it does occur, parallel diversification of plant and herbivore taxa is often not contemporaneous but sequential (Percy *et al.* 2004, Winkler and Mitter 2007). There are, however, a few cases involving *Phyllobrotica* leaf beetles (Chrysomelidae) on mints (see Chapter 6) and *Tetraopes* long-horned beetles (Cerambycidae) on milkweeds that show both cladogram match and contemporaneous diversification (Farrell and Mitter

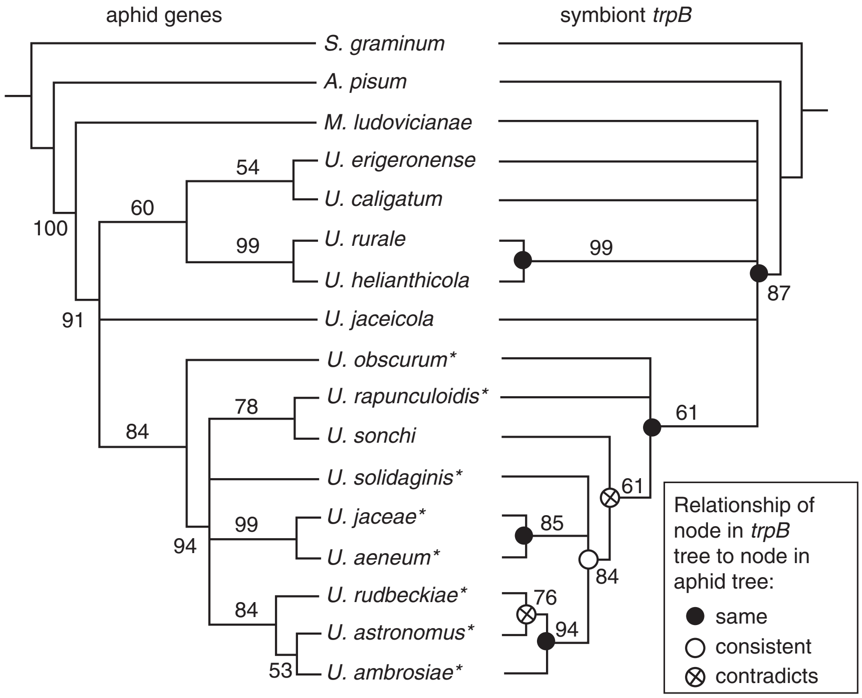


Figure 4.18 Evidence for cospeciation and parallel cladogenesis in *Uroleucon* aphid species and their endosymbiotic bacteria *Buchnera*. Phylogenetic trees for aphids and corresponding *Buchnera* show significant phylogenetic congruence. The *Buchnera* tree is based on partial sequences of *trpB*; the aphid tree is based on mitochondrial and nuclear sequences. Nodes resolved in the *Buchnera* tree are marked as the same, consistent or inconsistent, according to whether they match nodes in the aphid tree. Numbers on branches are bootstrap values, a measure of the statistical support for each branch by the data. Asterisk indicates taxa in which the *trpB* sequence contains an extra codon. From Clark *et al.* (2000).

1990, 1998, Farrell 2001, Figure 4.19). For the *Tetraopes*–milkweed association, there is a phylogenetic progression of increasing toxicity of cardenolides in milkweeds from ancestral to derived taxa that is paralleled by beetle diversification, a pattern consistent with a defensive innovation-counteradaptation scenario. In legume-feeding psyllids (Hemiptera: Psyllidae), however, there is remarkable cladogram concordance, but dating of lineages using molecular clocks showed that the plants diversified 8 million years ago whereas the psyllid radiation was back dated to only 3 million years (Percy *et al.* 2004). Thus, psyllids colonized already-existing plant taxa in phylogenetic sequence, giving the superficial impression of a coevolutionary scenario. Overall, there are numerous examples of plant–insect associations that exhibit phylogenetic concordance, but fail to meet the criterion of synchronous radiation and coevolution (Winkler and Mitter 2007).

Phylogenetic concordance is often precluded because herbivores switch to chemically similar, but distantly related host plants (Miller 1987, Becerra 1997, Becerra and Venable 1999, Kergoat *et al.* 2005, Winkler and Mitter 2007). As a consequence, patterns of herbivore diversification correspond better to plant chemistry than plant relatedness. Swallowtail butterflies in the genus *Papilio*, for example, feed ancestrally on plants in the citrus family (Rutaceae), but have switched, multiple times in some cases,

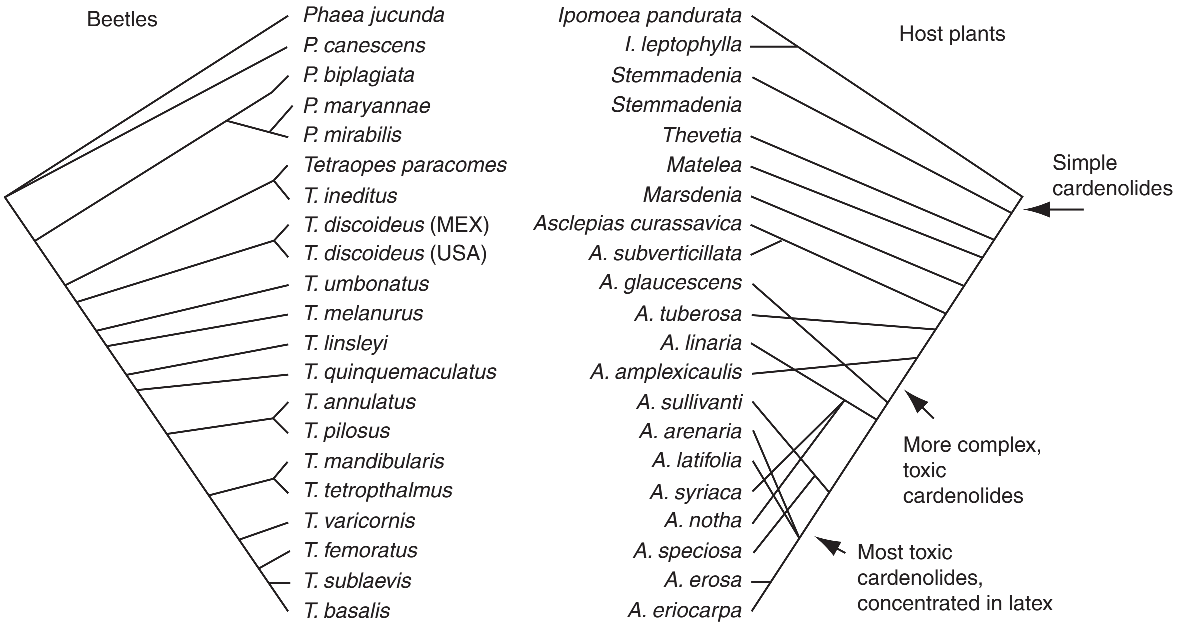


Figure 4.19 Evidence for parallel cladogenesis and contemporaneous diversification in the longhorned beetles *Tetraopes* and *Phaea* species and their host plants. Beetle phylogeny is based on morphology and allozymes, and plant phylogeny was extracted from the literature. There are 13 cospeciation events, and cladogram correspondence is significant ($P < 0.01$). For the longhorned beetle–host plant association, there is a phylogenetic progression of increasing toxicity of cardenolides in host plants from ancestral to derived taxa that is paralleled by beetle diversification. From Farrell and Mitter 1998. Reprinted with permission from Blackwell Publishing.

to more primitive plants in the laurel family (Lauraceae) and more derived plants in the carrot (Apiaceae) and aster (Asteraceae) families (Miller 1987, Zakharov *et al.* 2004). These host shifts in *Papilio* and other lepidopterans are promoted by phytochemical similarities (coumarins and related compounds) among these plant families (Berenbaum 1983, Berenbaum and Passoa 1999).

Although plants and herbivorous insects have certainly influenced each other's evolution, actually demonstrating that reciprocal selection has promoted cospeciation and codiversification has proved more difficult. Evidence for coevolution, cospeciation and parallel cladogenesis comes from tightly linked mutualisms like aphids and their vertically transmitted bacterial symbionts (Clark *et al.* 2000), and from some parasite and host interactions (Chapter 8). In such associations, the intimacy of the relationship intensifies the opportunity for reciprocal adaptation and cospeciation. Indeed, there are credible examples of pairwise coevolution between herbivores and their host plants, and as expected these associations involve herbivores that are monophagous and plants that are fed on by few other consumers (Becerra 2003). For most insect herbivores, however, coevolution is often more diffuse and evidence is found at larger taxonomic scales (Thompson 2005), such as that envisioned by Ehrlich and Raven (1964) with their escape-and-radiate hypothesis. Consistent with the escape-and-radiate model is the fact that elevated diversification in plants is associated with the acquisition of novel defenses like latex and resin canals (Farrell *et al.*

1991). For insects, diversification is associated with the evolution of phytophagy, and among phytophages with the shift from non-angiosperm to angiosperm hosts (Winkler and Mitter 2007). Thus, at this very general scale, there is evidence that plants and insects have had reciprocal influence on each other's evolution. Best then, is to view coevolution as a continuum with tightly coevolved mutualisms at one end of the spectrum and diffuse and spatially dynamic interactions at the other, such as occurs with many plant–herbivore associations (Thompson 2005).

Applications

Plant–insect interaction theory in pest management

Between the 1940s and 1960s, changes from traditional agricultural practices in many developing nations led to significant increases in the agricultural production of crops such as wheat, rice and corn, the so-called "green revolution" (Conway 1999). These changes included planting single crops in expansive monocultures, simplifying habitat structure, deploying high-yielding crop varieties and applying copious amounts of fertilizers, all of which predisposed crops for insect and pathogen attack and led to a heavy reliance on pesticides (Benbrook *et al.* 1996, Norris *et al.* 2003). For the same reasons, parallel pest problems have occurred throughout North America, Europe, northern Asia and Australia. As we have seen, planting crops in monocultures and simplifying habitat structure by removing weeds or tilling fields often promotes resource concentration effects and eliminates any advantage of associational resistance. Also, the heavy use of fertilizers promotes rapid growth and high plant quality, which often encourages pest outbreaks and leads to high levels of nitrogen runoff with adverse consequences for neighboring systems (Tilman 1999, Awmack and Leather 2002, Boyer *et al.* 2002). Moreover, due to trade-offs between growth and defense in plants, high-yielding crop varieties were often left defenseless and became very subject to pest attack (Fritz and Simms 1992). For example, there is an inverse relationship between yield and the alkaloid content among the different varieties of tobacco (Vandenberg and Matzinger 1970). To keep insect pests at bay, pesticides were applied heavily and frequently, which often led to the rapid development of pesticide resistance and the need for more effective pesticides. Thus, toxicologists were placed in the precarious position of developing new pesticides at a rate faster than pests evolved resistance, and the so-called “pesticide treadmill” was on a roll (Benbrook *et al.* 1996). The combination of pest resistance to pesticides, the kill of natural enemies, frequent pest outbreaks, rising production and management costs, increasing risks of pesticide contamination to human health and the environment, and public outcry has led to the development of more ecologically based pest management practices and ultimately to pesticide reductions and more sustainable agriculture (Hoffman and Carroll 1995, Norris *et al.* 2003, Gurr *et al.* 2004).

Currently, **integrated pest management** (IPM) employs an array of complementary control measures to suppress pest herbivores in agricultural, forest and urban systems (Norris *et al.* 2003, Gurr *et al.* 2004). Recently, more emphasis is being placed in agriculture on **ecological engineering**, namely the design of cropping systems for pollution avoidance and resource conservation. In this context, an understanding of plant–herbivore interactions has led to more ecologically sound pest management practices in several ways, including **deploying resistant varieties**, managing vegetation structure by **enhancing associational resistance** and managing habitat structure to **encourage natural enemies**, all of which can reduce dependence on pesticides. Strategies for encouraging natural enemies will be discussed in far greater detail in Chapter 7 on Predator–prey interactions. Specifically, a greater understanding of the molecular pathways involved in the synthesis and expression of constitutive and induced defenses has led to the genetic engineering of varieties and transgenic crops resistant to insect and pathogen attack (Gould 1998, Cerda and Paoletti 2004, Christou *et al.* 2006, Ferry *et al.* 2006). Moreover, techniques are being refined that allow for the expression of resistance traits in the specific tissue or crop stage fed on by the target pest, thus minimizing the migration of transgenes to other plants. Admittedly, concern remains over the use of transgenic crops, but this management technique is in its infancy and much of its potential as a safe control option is yet to be developed (Dively 2005, Andow and Zwahlen 2006, Christou *et al.* 2006). Likewise, advancements in our understanding of the signaling pathways in plants have highlighted the possibility for using natural elicitors such as jasmonic acid as management tools to induce resistance and suppress pests in agricultural crops (Thaler 1999a,b, 2002a, Kessler and Baldwin 2002). Moreover, developments on the genetic basis of resistance-breaking mechanisms in herbivores are providing insights into how, and how fast, pests adapt to resistant varieties and to improved resistance-management strategies (Hare 1994, Gould 1998, Norris *et al.* 2003).

Ecological principles stemming from plant–herbivore interactions have also played a significant role in managing the structure of agroecosystems and in designing urban landscapes in ways that enhance associational resistance and minimize pest problems (Gould 1991, Altieri and Nicholls 2004, Norris *et al.* 2003, Gurr *et al.* 2004). Planting and harvest techniques that can improve associational resistance include growing several crops in polyculture, deploying multiple genetic varieties of the same crop (multilining), strip-harvesting such that some of the crop remains and employing no-till practices, whereby some elements of habitat structure persist. Furthermore, habitat and vegetation structure can be managed to encourage natural enemies and increase pest suppression (Thies and Tscharntke 1999, Landis *et al.* 2000, Gurr *et al.* 2004, Langellotto and Denno 2004). In general, maintaining structural diversity or plant species diversity in managed landscapes often minimizes pest problems because natural enemies accumulate and persist in such habitats (Landis *et al.* 2000, Gurr *et al.* 2004, Shrewsbury and Raupp 2006). This occurs because diverse landscapes often provide refuges for natural enemies during times when fields are fallow or offer resources in the form of nectar, pollen or alternative prey. For example, adding organic matter to irrigated rice fields in Indonesia boosts populations of detritivorous insects (alternative prey), which in turn encourages the retention of generalist predators such as predaceous bugs and spiders that ultimately suppress populations of pests like the brown planthopper, *Nilaparvata lugens* (Settle *et al.* 1996). Likewise, the azalea lacebug, *Stephanitis pyrioides* (Hemiptera: Tingidae), is far less abundant on azaleas (Ericaceae) in complex ornamental plantings consisting of azaleas and many other plant species than it is in simple landscapes comprised of only or mostly azaleas, a pattern that can be attributed to the abundance of spiders in diverse habitats (Shrewsbury and Raupp 2006). As a parting thought for this chapter, it is encouraging to know that strong consideration is being given to increased vegetation complexity as a management tool for reducing pest problems in certain agricultural crops, urban landscapes and home gardens (Grissell 2001, Gurr *et al.* 2004, Shrewsbury and Raupp 2006). We will return to this theme again and again in this book since managing, disturbing and otherwise fragmenting plant-dominated landscapes has been, and will continue to be, a major endeavor in human history (see Chapters 7 and 12).

Summary

Insect herbivores occur in many taxonomic groups, and illustrate many kinds of feeding, from specialists to generalists, from chewers to sucking insects and from external feeders to borers. But plants exhibit many barriers to insect attack offering, for example, a poor balance of nutrients for animals in general, although insects employ various strategies for circumventing nutritional deficiencies, such as feeding compensation, selection of high nitrogen plant parts and mixing sources of food. Plants also develop mechanical barriers to insect consumers with tough tissues, trichomes and waxes, but again insects have adapted to some of these defenses. Chemical barriers in plants are widespread and generally effective against herbivores, and can be divided into qualitative and quantitative defensive compounds, and constitutive and induced defenses. Induced defenses include phytochemicals which can affect neighboring plants, causing allelochemical concentrations to rise in neighbors. Again, herbivores have evolved to cope with plant toxins through deactivation, excretion, sequestration and trenching, among others. Plants may also provide the enemies of herbivores with shelter and food, gaining protection by association with the third trophic level, and genetic heterogeneity in plant populations contributes to variation in food sources for herbivores. Both plant stress and plant vigor influence herbivore nutrition, each with benefits to some feeding guilds and deleterious effects on others.

Plant defense theory uses optimal defense as a guiding theme, with plants evolving to protect the most costly and vulnerable parts effectively. Conspicuous plants on the landscape are likely to defend against all herbivores with digestibility reducers, but ephemeral and patchy plants have evolved with cheap toxins effective against generalists. Optimizing allocation of nutrients and defenses is also applied to the carbon–nutrient balance of plants and how carbon-based and nitrogen-based defensive chemicals are synthesized according to the nutrients available, just as in allocation to growth rate or defense depending on the nutrient and photosynthetic resources available to plants. The same theme runs in the growth–differentiation balance hypothesis on how a plant strategy evolves to allocate resources to growth, which limits differentiation and defense, and then to differentiation which limits growth. However, plant defense theory is in need of further refinement in order to cover the great variety of plant strategies and constituents. At the level of plant communities the habitats available to herbivores are highly heterogeneous, involving patchy communities, variable densities, plant species diversity and architectural complexity. Plant resources can be concentrated or dispersed, and associated plants may improve or degrade a local habitat for herbivores. Natural enemies of herbivores are also greatly influenced by plant species composition and density. Conversely, insect herbivores can influence plant distribution and abundance, especially by seed and seedling predation.

The evolution of diet breadth, specialization and generalist feeders involves many factors. Of course, females may evolve to optimize the wellbeing and survival of their progeny, often by showing a preference for certain plants and plant parts favorable to progeny growth, and/or defense. Other factors involving narrowing of host-plant use include camouflage against the host background, interspecific competition, and host-plant density, apparency and associated plants. Extreme specialization may result in deme formation adapted to individual plants. Broadening of feeding niches may result in small and/or ephemeral plants, a risk-spreading strategy or increasing enemy-reduced space. Host shifting is an important process in the adaptive radiation of insect herbivore lineages, often facilitated by similarities in phytochemistry and habitat use among host plants. Hybridization between plant species may provide a "bridge" for a herbivore species to access a new host plant. The concept of coevolution invokes the view of an arms race between plant species evolving new defenses, which herbivores later evolve to cope with. The mechanisms are debated although the concept of a geographic mosaic of coevolution at the population level in which there are coevolutionary hotspots interspersed in a matrix of passive coexistence between host and herbivore appears to capture a realistic perspective on the interaction.

Concepts of the interaction of plants and herbivores apply well to landscapes managed by humans, with integrated pest management employing many ecological concepts, and indeed contributing importantly to their development.

Questions and discussion topics

1 The body odor of plants in the field and in our food often can be associated with particular plant families. Can you list at least 10 odors, the kinds of chemicals involved and the plant families from which they are derived?

2 How would you describe a way in which hypotheses on plant defense can be synthesized into a general theory? Would a graphical model contribute understanding to the synthesis?

3 The position of herbivores between natural enemies and plants has been described as "between the devil and the deep blue sea," respectively. Discuss the validity of this comparison, and whether you consider plants to be in a similar bind between herbivores and resources.

4 At what scale(s) do you think coevolution should be studied, and what criteria would you use to evaluate an adequate demonstration of coevolution between plants and herbivores?

5 In a plan to regulate a pest population, which would you recommend as the better strategy: a top-down approach using biological control, or a bottom-up approach using host-plant properties? Would you be able to suggest plans which would combine the two approaches?

Further reading

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Rosenthal, G.A. and M.R. Berenbaum, editors. 1991, 1992. *Herbivores: Their Interactions with Secondary Plant Metabolites*. Volumes 1 and 2. 2nd edition. San Diego: Academic Press.

Thompson, J.N. 2005. *The Geographic Mosaic of Coevolution*. Chicago: University of Chicago Press.

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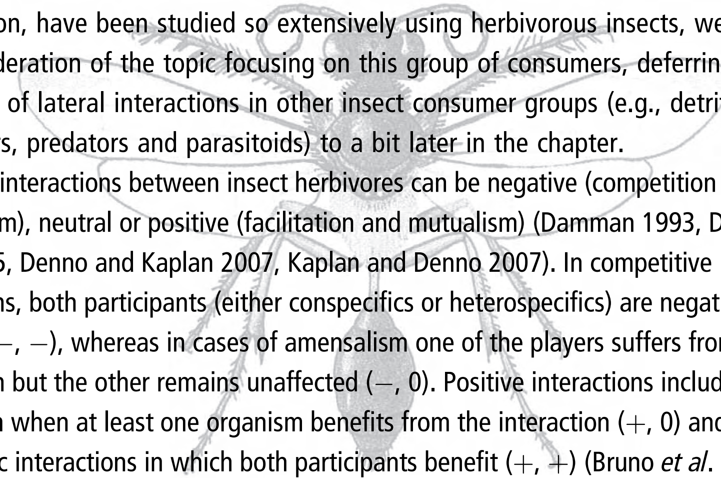
5

Lateral interactions: competition, amensalism and facilitation

In the preceding chapter, we focused on interactions between phytophagous insects and their host plants and saw how species occupying different trophic levels can influence each other's abundance, distribution and evolution. Other important intertrophic level relationships include predator–prey and host–parasitoid interactions, and these will be dealt with in forthcoming chapters (see Chapters 7 and 8). Here we consider **lateral interactions**, those that occur among individuals feeding at the same trophic level, and how such interactions (e.g., **competition**, **amensalism**, **facilitation** and **mutualism**) can affect species' abundance, distribution and community structure. Because lateral interactions, and in particular competition, have been studied so extensively using herbivorous insects, we begin our consideration of the topic focusing on this group of consumers, deferring our treatment of lateral interactions in other insect consumer groups (e.g., detritivores, scavengers, predators and parasitoids) to a bit later in the chapter.

Lateral interactions between insect herbivores can be negative (competition and amensalism), neutral or positive (facilitation and mutualism) (Damman 1993, Denno *et al*. 1995, Denno and Kaplan 2007, Kaplan and Denno 2007). In competitive interactions, both participants (either conspecifics or heterospecifics) are negatively affected (−, −), whereas in cases of amensalism one of the players suffers from the interaction but the other remains unaffected (−, 0). Positive interactions include facilitation when at least one organism benefits from the interaction (+, 0) and mutualistic interactions in which both participants benefit (+, +) (Bruno *et al*. 2003, Bourtzis and Miller 2006). Moreover, mutualisms can involve tightly coevolved obligate interactions, such as aphids and their bacterial symbionts, or they can entail much looser facultative relationships, such as generalist pollinators and their nectar source plants. Because of the complexity and often intertrophic nature of mutualisms (e.g., protectionist ants and plants that offer rewards), we devote a whole chapter to this fascinating topic (Chapter 6). There we discuss only positive interactions between organisms feeding at the same trophic level, although the strength of such interactions (and negative ones as well) are often mediated by basal resources (plants) and natural enemies (Denno *et al*. 1995, Denno and Kaplan 2007, Kaplan and Denno 2007).



In the context of traditional community ecology, negative interactions have received far more attention than positive ones (e.g., Lawton and Strong 1981, Schoener 1982, Strong *et al*. 1984a,b, Denno *et al*. 1995), and until quite recently have dominated ecological theory (e.g., Stachowicz 2001, Bruno *et al*. 2003, Lill and Marquis 2003, Nakamura *et al*. 2003). In our forthcoming consideration of lateral effects, we provide evidence for negative and positive interactions among insect consumers and discuss their consequences for individual fitness and population size. Also, we present the traditional view on the importance of lateral forces (e.g., competition and facilitation) and address the mediating role of host plants and natural enemies. Last, we discuss how the historic perspective on lateral interactions is changing in light of recent information and insights, particularly the relative frequency and importance of competition.

5.1 Competition and resource limitation

Most insects have a tremendous potential for population increase and thus the overexploitation of resources. We see evidence for this potential when lepidopterans such as tussock moths (*Orgyia vetusta*) reach outbreak density, which is followed by widespread defoliation, plant death and ultimately the local demise of the moth population (Harrison 1994). Unless a population is limited by other factors (e.g., climate or natural enemies), competition for limited resources (food, shelter and oviposition sites) ultimately deters population growth via strong negative **density-dependent** impacts on birth rate (fecundity) and survival. Thus, **competition** can be defined as an interaction among individuals, generated by a shared requirement for a limited resource that leads to a reduction in the growth, reproduction or survival of the individuals involved (Begon *et al.* 2006). Several important elements of the process of competition are worth emphasis. First, organisms must overlap in their use of a limiting resource. Two phloem-feeding aphid species feeding exclusively from the nitrogen-rich terminal leaves on the same host plant constitutes resource overlap. If those terminals are in short supply, then the aphids "compete" for a limiting resource, often with dire fitness consequences. A second consequence of competition is that it is envisioned as a negative–negative interaction with both participants adversely affected. However, there is tremendous variation in the symmetry of competitive interactions between individuals or species ranging the gamut from classic cases in which both parties are similarly affected to instances of tremendous asymmetry where only one party suffers, namely amensalism (Denno *et al.* 1995, Kaplan and Denno 2007).

5.1.1 Types of competitive interactions

Interactions over a shared resource can involve individuals of the same species, so-called **intraspecific competition**, or the struggle may entail interactions among individuals of different species, namely **interspecific competition**. Because conspecifics are more likely to share the exact same resources than members of different species, the traditional view is that intraspecific competition should be stronger than interspecific competition (see Strong *et al.* 1984b, Denno *et al.* 1995). We shall explore the evidence for this long-standing tenet of competition theory a bit later in the chapter.

Moreover, there are several different forms of competition (Price 1997, Speight *et al.* 1999, 2008, Begon *et al.* 2006). **Scramble competition**, also referred to as **exploitative competition**, occurs when individuals have the same or similar access to a limited resource and a "free-for-all" results (Nicholson 1954). In such cases, the "scramble" among individuals for resources often results in resource depletion, with severe consequences for most or all of the competing individuals. A classic experimental example involves the sheep blowfly,

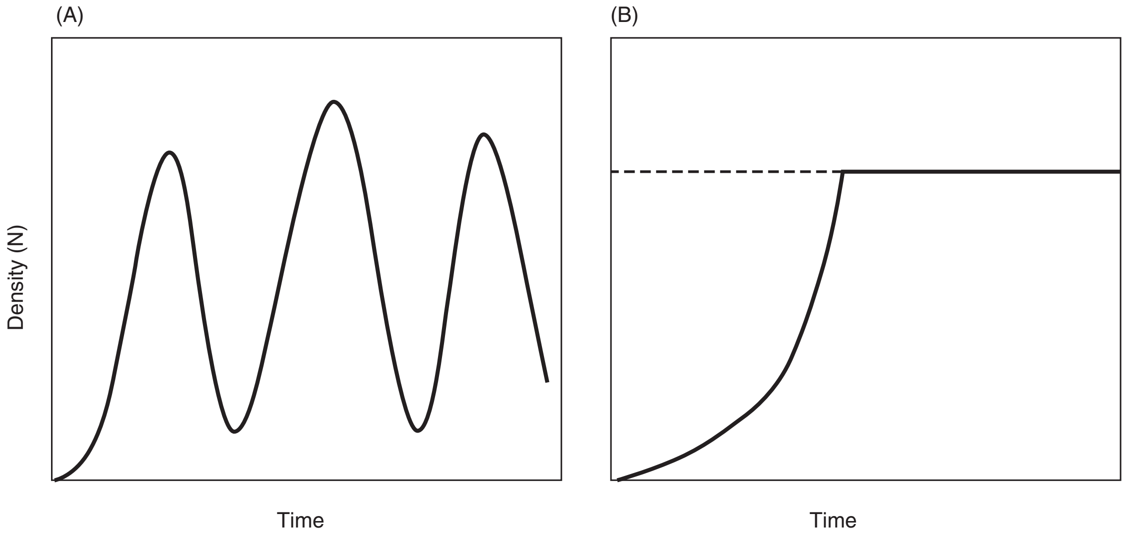


Figure 5.1 Population dynamics resulting from (A) scramble competition and (B) interference competition. With scramble competition, there is overexploitation of resources, high density-dependent mortality, population crashes and unstable population dynamics. Interference competition leads to more stable population dynamics because some individuals retain access to resources as the population grows toward carrying capacity (dashed line) (adapted from Price 1997).

Lucilia cuprina, a carrion-feeder in Australia (Nicholson 1954). When a few larvae (30 maggots) were fed 1 g of carrion, larval competition was weak, larval mortality was low and many adult flies emerged. In contrast, when the larval density was experimentally increased to 80, larval competition intensified on the 1 g of carrion, fewer adults were produced and these flies were small with a low reproductive potential. Above a larval density of 200, food was depleted, larvae experienced mass starvation and no adults emerged. Thus, with scramble competition, there is often widespread overexploitation of resources, high density-dependent mortality and reproductive failure, drastic population crashes and an unstable population dynamic (Figure 5.1A).

In contrast to scramble competition, **contest competition** or **interference competition** occurs when some individuals gain access to more than their share of resources and in so doing deprive other individuals of access, either conspecifics or heterospecifics, to requisite resources (Nicholson 1954). Interactions exhibiting interference competition include those involving direct killing, aggressive displacement behavior and the production of chemicals (deterrents and pheromones) that hinder colonization, feeding or oviposition (Denno *et al.* 1995, Kaplan and Denno 2007). For example, in a guild of stem-borers comprised of lepidopterans, beetles and flies, there is a dominance hierarchy based on either size or aggression, whereby the dominant species (*Chilo demotellus*) kills, but does not consume, the subordinate species when they meet within the same grass stem (Stiling and Strong 1984). Also, larger females of the gall aphid, *Pemphigus betae*, push smaller ones away from optimal oviposition sites on leaves of narrowleaf cottonwood (*Populus angustifolia*) (Whitham 1979, Figure 4.11A). Similarly, male dragonflies engage in aggressive tangles with other males when defending territories along pond edges (Tsubaki *et al.* 1994). By so doing, winning males deny losers access to resources such as prey and mates. Also, many herbivores, predators and parasitoids produce chemical cues (**marking**

pheromones) that indirectly deter potential competitors, either conspecifics or in some cases heterospecifics, from ovipositing or feeding in the same host, host-plant tissue or nearby area (Denno *et al.* 1995, Merlin *et al.* 1996, Hemptinne *et al.* 2001, Nufio and Papaj 2001). Such **pseudointerference** mechanisms have the same effect as direct interference phenomena in that they deny or dissuade a competitor access to shared resources without aggressive interactions. In general, interference competition is thought to lead to more stable population dynamics than exploitative competition because as resources become depleted, some individuals in the population will retain access to sufficient resources for growth, reproduction and survival (Figure 5.1B). Despite our dichotomous treatment of scramble and interference competition so far, populations of many insects likely exhibit a mix of both types of competition. For example, ovipositing females of the bean weevil, *Callosobruchus maculatus*, deposit a marking pheromone on beans which inhibits egg deposition by its congener *Callosobruchus rhodesianus*, but the reverse does not occur (asymmetric interference competition); however, in mixed-species populations where larvae scramble for access to beans, *C. maculatus* often excludes *C. rhodesianus* (asymmetric exploitative competition) (Giga and Smith 1985).

Consumers also compete for "**enemy-free space**" (Jeffries and Lawton 1984), a phenomenon also termed "**apparent competition**" (Holt 1977, 1984, Chaneton and Bonsall 2000, van Veen *et al.* 2006, Kaplan and Denno 2007). Consider a single predator species that attacks two prey species. Both prey species are adversely affected by the predator and the predator benefits by consuming both prey species. Furthermore, an increase in the predator's abundance as a consequence of consuming prey species 1 enhances its negative effect on prey species 2. Thus, prey species 1 indirectly affects prey species 2 and vice versa, in the same way that two prey species might compete exploitatively for a shared food resource (Figure 5.2). A good example of apparent competition between two leafhopper species involves the shared parasitoid (*Anagrus epos*), which resulted in the partial replacement of a native leafhopper (*Erythroneura elegantula*) by an invading species (*E. variabilis*) following its introduction into the vineyards of California (Settle and Wilson 1990). The "competitive displacement" resulted from the selective attack of the native species' eggs, which were inserted closer to the leaf surface and consequently experienced greater parasitism. Thus, the native leafhopper was dramatically reduced by the invader because the invader competed more successfully for enemy-free space, namely deep oviposition sites.

It should be evident by now that the strength of lateral interactions such as competition and facilitation can be mediated by other factors, both biotic and abiotic. As exemplified by herbivorous insects, competition, both intraspecific and interspecific, can be **plant-mediated**, **natural-enemy mediated** or **physical-factor mediated** (Damman 1993, Denno *et al.* 1995, Denno and Kaplan 2007, Kaplan and Denno 2007), all of which constitute **indirect effects**. "Indirect effects occur when the influence of one species, the donor, is transmitted through a second species, the transmitter, to a third species" (Morin 1999). Concerning plant-mediated competition, we learned in Chapter 4 that previous feeding by one herbivore often induces changes in the defensive chemistry, nutrition or morphology (e.g., trichomes) of its host plant that have negative consequences for other herbivore species feeding elsewhere on the same plant or later in the season (Inbar *et al.* 1995, Karban and Baldwin 1997, Constabel 1999, Kaplan and Denno 2007). In such cases of **induced resistance**, herbivores "compete" entirely through feeding-induced changes in the quality or availability of their shared plant resource. Moreover, natural enemies can both mediate the intensity of interspecific competition between insect herbivores and alter the outcome of competition

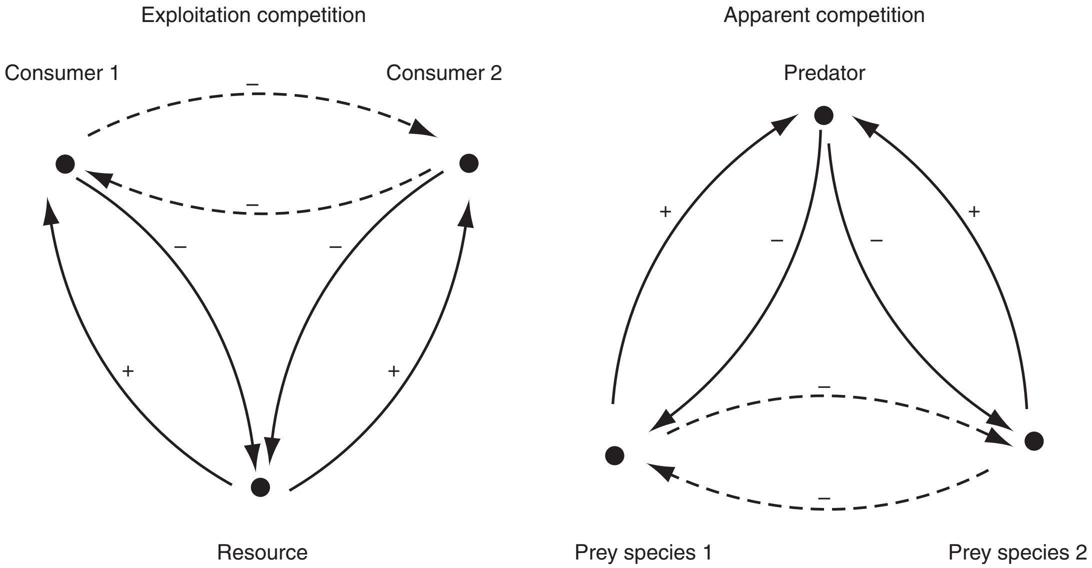


Figure 5.2 Apparent competition (when two prey species are attacked by the same predator) is identical to exploitation competition (when two consumers vie for a shared resource) in that both interactions carry the same signs (+ and −). Solid lines indicate direct interactions, whereas dashed lines show indirect effects. Adapted from Holt, R. D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.* **124**:377–406. © 1984 University of Chicago.

between two species, as evidenced by the parasitoid mediation of leafhopper competition on grapes. Even subtle changes in physical conditions can also shift the competitive outcome of species interactions. For instance, at 30 °C the bean weevil, *Callosobruchus chinensis*, excludes *C. maculatus* in mixed-species cultures, but a 2 °C increase completely reverses the outcome and its rival becomes the superior competitor (Fujii 1967). The take-home message from these scenarios is that competition, and other lateral interactions for that matter, cannot be viewed in isolation of other factors that mediate the frequency and strength of competitive interactions. Suffice it to say for now, recent analyses of published studies on the nature of plant-mediated competitive interactions among insect herbivores are challenging the traditional paradigms of competition theory (Denno and Kaplan 2007, Kaplan and Denno 2007). We will learn more about this evolving issue shortly, and explore in greater depth plant-, enemy- and physical-factor mediated competition and facilitation.

5.1.2 Competition, predation, facilitation and niche theory

How an organism uses resources in time and space, its so-called **niche**, has been intimately linked to competitive interactions throughout much of the historic development of population and community ecology (Damman 1993, Denno *et al.* 1995, Kaplan and Denno 2007). Several stages of niche theory development are often recognized. These include the original formulation of a species' niche as a spatial unit (Grinnell 1904, 1917), the recognition of the niche as a functional unit (Elton 1927), the development of the **competitive exclusion principle** (Gause 1934), the emergence of the multidimensional niche (Hutchinson 1957) and more recently the consideration of multiple factors (competition, predation and facilitation) in the shaping of an organism's niche (Jeffries and Lawton 1984, Bruno *et al.* 2003). Although Darwin was certainly aware of the idea of a species' niche, the concept is credited to Grinnell, who envisioned a species' niche as its distribution in space. Elton broadened the concept and viewed an organism's niche as its functional role in the community, more specifically its "place in the biotic environment and relations to food and enemies." Thus, the niche became an interaction-based concept, and this view persists today.

Gause (1934) was the first ecologist credited with identifying the linkage between niche theory and interspecific competition. He remarked that "as a result of competition, two similar species scarcely ever occupy similar niches, but displace each other in such a manner that each takes possession of certain kinds of food and modes of life in which it has an advantage over its competitor." Emerging from his work was the competitive exclusion principle which posits that two species with identical niche requirements cannot coexist. Gause based this principle on Elton's functional definition of the niche. Hutchinson (1957) later redefined the niche as an "**n-dimensional hypervolume**," an abstract multi-dimensional space identifying the environmental limits within which a species is able to survive and reproduce. Each niche dimension corresponded to a specific requisite such as the range of temperatures required for development, the seed sizes that can be consumed, the thickness of plant tissue within which eggs can be deposited, etc. Hutchinson further defined a species' **fundamental niche** as its pattern of resource use in the absence of competitors and its **realized niche** when competing species or other organisms were present (Figure 5.3A). Thus, as a consequence of interspecific competition, a species' realized niche is predicted to be smaller than its fundamental niche due to **competitive displacement** along part of one or more niche dimensions. The scale insect *Fiorinia externa*, for example, displaces the rival scale *Nuculaspis tsugae* from the nitrogen-rich terminal needles of hemlock trees and relegates it to feeding on mature needles, where it incurs reduced fecundity and heavy mortality (McClure 1980). When *F. externa* is experimentally removed, *N. tsugae* freely expands its distribution along the hemlock shoot by colonizing the terminal needles

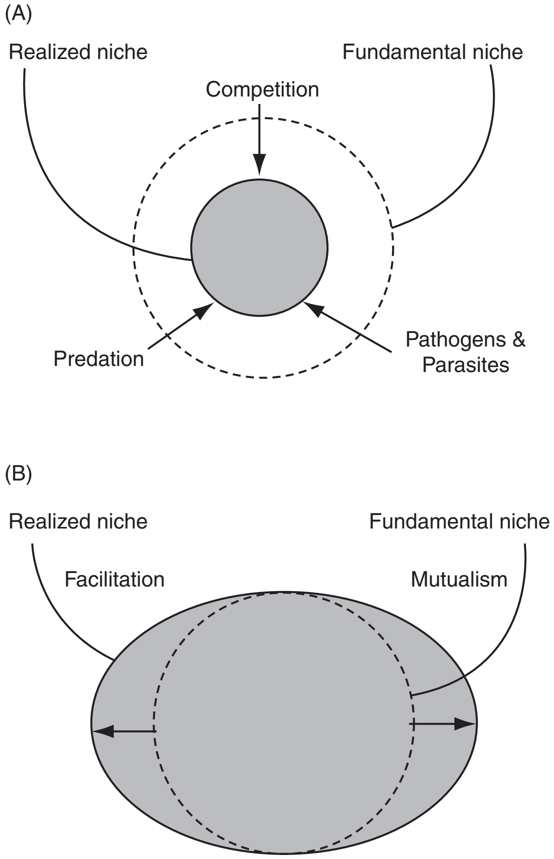


Figure 5.3 (A) The fundamental niche of a species describes its pattern of resource use in the absence of competition, predation and pathogens. The presence of antagonists (e.g., competitors) constrains the use of resources by a species, resulting in a smaller realized niche. (B) Positive interactions with other organisms (facilitation and mutualism) allow a species access to additional resources and broaden its realized niche beyond its fundamental niche. Reprinted from *Trends Ecol. Evol.* 18(3), by J. F. Bruno, J. J. Stachowicz and M. D. Bertness. Inclusion of facilitation into ecological theory. Pages 119–125. Copyright 2003, with permission from Elsevier.

where it thrives. Such "subtraction experiments," in which one competitor is removed, demonstrate **niche release** and document that the realized niche of a species when a competitor is present is smaller than its fundamental niche when that competitor is absent.

Although not emphasized by Hutchinson (1957), predators, parasitoids and pathogens can also influence a species' use of resources and thus its niche (Chaneton and Bonsall 2000, Denno *et al.* 1995, Kaplan and Denno 2007) (Figure 5.3A). We just saw that the "realized niche" (oviposition space in grape leaves) of a native leafhopper species was dramatically restricted by an introduced leafhopper as a consequence of the invasive species' competitive superiority for enemy-free space from a shared parasitoid (Settle and Wilson 1990). Similarly, colonies of the nettle aphid, *Microlophium carnosum*, suffer more rapid declines in density over the growing season on plants adjacent to grassland patches with high densities of the grass aphid, *Rhopalosiphum padi*, than on nettle plants growing close to patches where grass aphids are scarce. Differences in performance and distribution of nettle-aphid colonies resulted from a predaceous ladybird that aggregated on high-density *R. padi* patches and a "spill-over" effect onto neighboring nettle patches (Müller and Godfray 1997). The realized niche of nettle aphids was restricted in the presence of grass aphids due to a shared predator. These and other studies on predator–prey systems suggest that apparent competition can arise when alternative prey species display overlapping temporal dynamics and a predator shifts its attack to include a co-occurring prey species in its diet (Chaneton and Bonsall 2000, Kaplan and Eubanks 2005).

Positive interactions among insect species such as facilitation and mutualism can in fact broaden the realized niche of a species beyond that predicted by its fundamental niche (Bruno *et al.* 2003, Figure 5.3B). In cases of facilitation, resources are made available to one species only by the actions of another species. For example, high levels of defoliation by one herbivore can elicit a positive density response in subsequent herbivores by weakening plant defense systems (e.g., resin flow in conifers), or stimulating a re-flush of young leaves (Kaplan and Denno 2007). All factors considered, a practical definition of an organism's realized niche is its pattern of resource use resulting from interactions with the physical environment (abiotic factors) and other organisms, including conspecifics, other competing species, mutualists and natural enemies (biotic factors). In later sections of this chapter we provide evidence for the relative frequency and strength of negative (competition and amensalism) and positive interactions (facilitation and mutualism) as they influence the distribution and abundance of insect herbivores and consumers at higher trophic levels.

5.1.3 Modeling interspecific competition

Mathematical models have been developed describing the adverse effects of two species on each other's population growth. The first of these endeavors, the **Lotka–Volterra model** of interspecific competition, named for its originators (Lotka 1925, Volterra 1926a,b), extends from the **logistic growth equation** for a single species (Verhulst 1838):

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\left[\frac{(K-N)}{K}\right] \tag{5.1}$$

where N is population size, r is the per capita exponential growth of a population and K is the "carrying capacity" of the environment or the average number of individuals of a species the environment can support. Thus, the equation describes the rate of population change based on the size of the population, its growth rate and how far the current population size is from the carrying capacity of the environment. The term $(K-N)/K$ modifies population growth (r) depending on population size (N) relative to the carrying capacity (K) such that r is positive below K and negative above it. The model possesses a simple equilibrium solution: when a population is small relative to the carrying capacity ($N << K$), the population grows exponentially; however, when the population reaches the carrying capacity ($N = K$) it levels off and remains there due to resource limitation (Figure 5.4A). Equilibrium is reached at the carrying capacity where the population ceases to grow ($\mathrm{d}N/\mathrm{d}t = 0$) and importantly when $(K–N)/K = 0$, which occurs when $N = K$. Simply stated, the logistic growth equation describes intraspecific competition whereby competition among individuals of the same species for limited resources sets the limit on population growth.

The logistic growth model (Equation 5.1) can be extended to consider the effects of interspecific competition on population growth, specifically the consequences of one species' density on the growth of a second species and vice versa. Two equations (the Lotka-Volterra model) are needed to model the reciprocal density effects of two species on each other's population growth. As developed by Lotka (1925) and Volterra (1926a), the two equations, one for each competing species, are:

$$\frac{\mathrm{d}N_1}{\mathrm{d}t} = r_1 N_1 \left[\frac{K_1 - N_1 - \alpha N_2}{K_1}\right] \tag{5.2}$$

$$\frac{\mathrm{d}N_2}{\mathrm{d}t} = r_2 N_2 \left[\frac{K_2 - N_2 - \beta N_1}{K_2}\right] \tag{5.3}$$

where each species has its own characteristic r, N and K (as indicated by the subscripts 1 and 2).

Also, the terms αN_2 and βN_1 have been added to the growth equation (5.1); the competition coefficients α and β convert individuals of one competing species into equivalent units of the other competitor. Thus, α (Equation 5.2) denotes the effect of an individual of species 2 on species 1, and β (Equation 5.3) indicates the effect of an individual of species 1 on species 2. If, for example, $\alpha = 0.8$, each individual of species 2 uses 0.8 of the resources used by an individual of species 1. More specifically, if the population size of species 2 increases by 100 individuals, the population size of species 1 will decline by 80 individuals. In this example, individuals of species 1 suffer more from competition with conspecifics (intraspecific competition) than from interspecific competition with individuals of species 2.

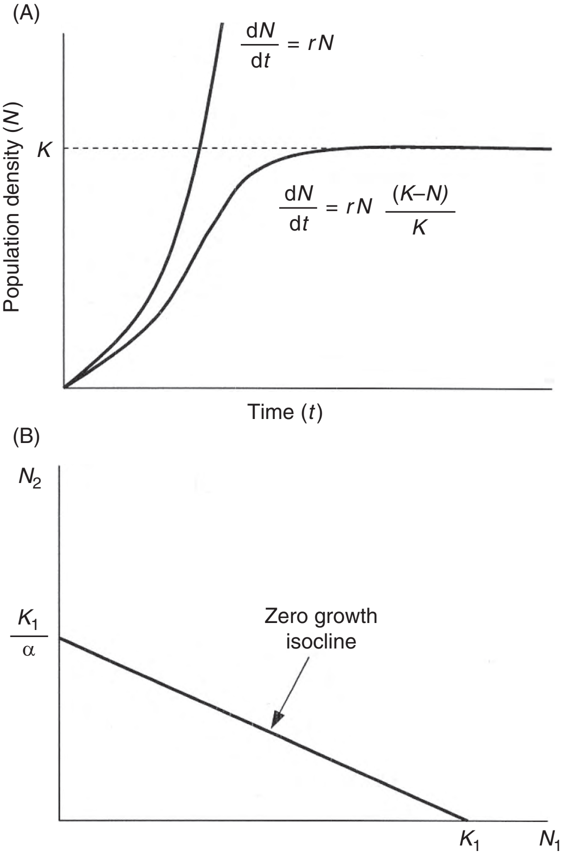


Figure 5.4 (A) Exponential growth (left curve) describes population growth in the absence of resource limitation. In logistic growth (right curve), resource limitation causes the population to level off at the carrying capacity. (B) The "zero-growth isocline" describes the range of equilibrium densities where $\mathrm{d}N/\mathrm{d}t = 0$ for one competing species in the presence of another. Each point along the line represents an equilibrium density for species 1 at differing densities of species 2. The equilibrium density of species 1 declines with increasing densities of species 2 (adapted from Speight *et al.* 1999).

By contrast, if $\beta = 1.3$, an increase in species 1 by 100 individuals would cause the population size of species 2 to drop by 130. In this instance for species 2, interspecific competition with individuals of species 1 is more intense than intraspecific competition. The competitive superiority of species 2 over species 1 ($\beta > \alpha$) might arise because it is either larger or more aggressive.

Equilibrium densities for the two competing species (N_1 and N_2) can be determined by setting $\mathrm{d}N/\mathrm{d}t$ to zero in Equations 5.2 and 5.3. Recall that for a single-species population, $\mathrm{d}N/\mathrm{d}t = 0$ when the population is at carrying capacity ($N = K$). In the two-species model, the equations reduce to:

$$N_1 = K_1 - \alpha N_2 \tag{5.4}$$

and

$$N_2 = K_2 - \beta N_1 \tag{5.5}$$

As a result, the equilibrium density for species 1 (N_1) is no longer expressed as a single density, but varies depending on the density of species 2 (N_2) and its competition coefficient (α). Likewise, this is the case for species 2. These two equations (5.4 and 5.5) describe straight lines with the competition coefficients characterizing the slopes. So-called "zero-growth isoclines" describe the range of equilibrium densities where $\mathrm{d}N/\mathrm{d}t = 0$ for each competing species. The line for species 1 (Figure 5.4B) crosses the x-axis where $N_2 = 0$. Setting N_2 to zero in Equation 5.4 allows us to obtain the value $N_1 = K_1$. Likewise, the line must cross the y-axis when $N_1 = 0$ and by substituting $N_1 = 0$ into Equation 5.4 we can also determine when $N_2 = K_1/\alpha$. In this example, the equilibrium density of species 1 declines with increasing densities of species 2. The zero-growth isocline for species 2 can be calculated in the same way using Equation 5.5 such that the isocline must cross the y-axis at K_2 and the x-axis at K_2/β.

Knowing the equilibrium conditions ($\mathrm{d}N/\mathrm{d}t = 0$) for each competitor (Figure 5.4B) now allows us to predict whether or not their combined equilibrium densities permit coexistence. This can be established by plotting the isoclines for both species on the same graph (Figure 5.5). First let's consider the case where species 1 always excludes species 2 (Figure 5.5A). This occurs because the isocline for species 2 falls entirely within the isocline for species 1. As a consequence, at any density combination between the two isoclines the population trajectory leading to K_1 results in a population increase for species 1 and a decrease for species 2. The reverse case in which species 2 prevails is shown in Figure 5.5B. Here the isocline for species 1 is nested entirely within that for species 2 and the population trajectory of species 2 toward K_2 will promote the demise of species 1. The case of an unstable equilibrium is shown in Figure 5.5C. In this example, the winning competitor depends on the starting densities of the two species and on their relative growth rates. If initial conditions favor a population trajectory where the isocline for species 2 exceeds that for species 1 (upper left triangle), then species 2 will drive species 1 to extinction. The reverse occurs if initial conditions lead the population trajectory into the zone (lower right triangle) where species 1 outcompetes species 2. An unstable equilibrium point exists where the two isoclines intersect, but any environmental factor that causes a change in the density of either species will destabilize the interaction and promote the extinction of one of the competing species.

A stable equilibrium exists between both species (coexistence) only if the isoclines of both cross such that the carrying capacities of each species fall within the isocline of the other species (Figure 5.5D). For coexistence to occur, K_1 must be less than K_2/β on the x-axis and K_2 must be less than K_1/α on the y-axis. In this case, intraspecific competition exceeds interspecific competition and each competitor will limit its own population growth before it drives its competitor to extinction. Stated in other terms, and as predicted by the Lotka–Volterra model, stable coexistence is possible only when the product of the competition coefficients

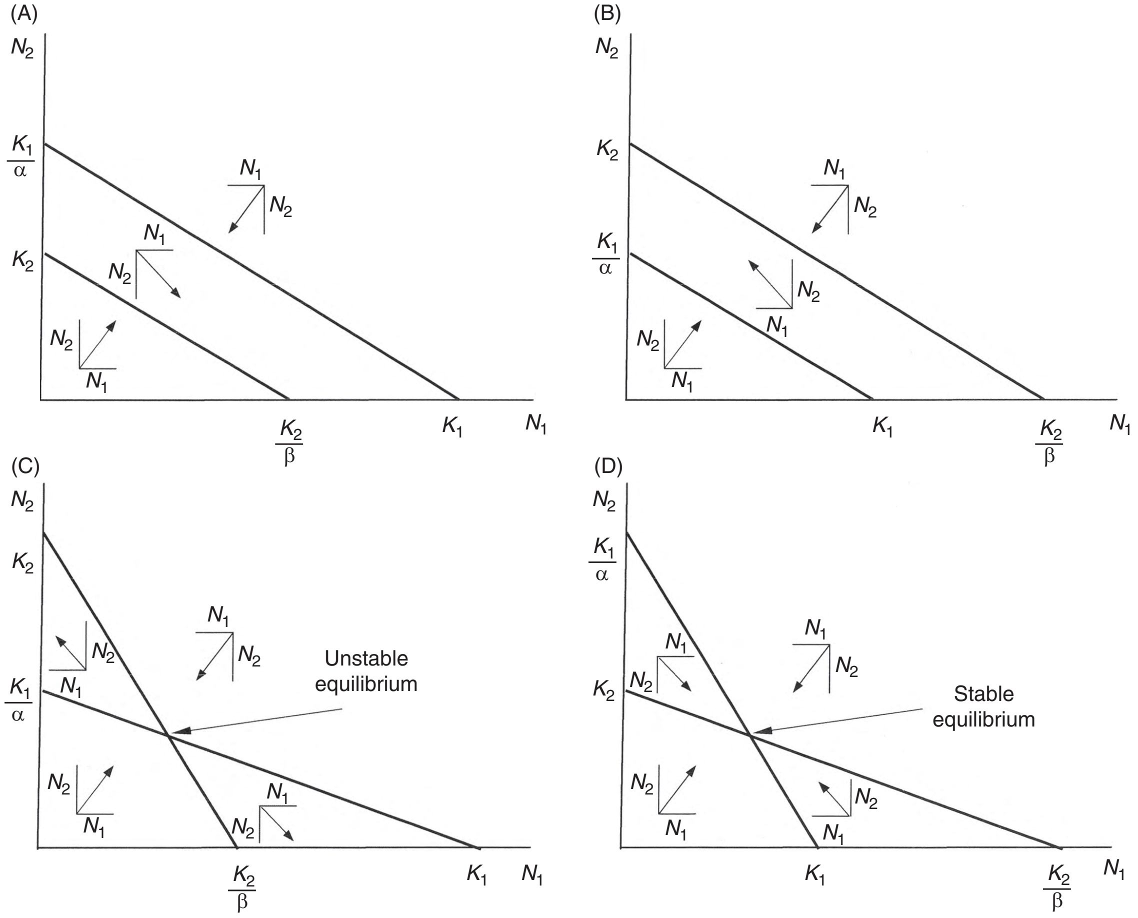


Figure 5.5 Zero-growth isoclines for two competing species and predictions for species coexistence. The four panels describe the case in which (A) species 1 excludes species 2, (B) species 2 excludes species 1, (C) an unstable equilibrium exists and the surviving competitor depends on initial conditions, and (D) a stable equilibrium exists and both species coexist (adapted from Speight *et al.* 1999).

($\alpha\beta$) is less than 1, that is when intraspecific competition is greater than any interspecific effect for either species.

5.1.4 Coexistence and the niche: a theoretical perspective

Given that the Lotka–Volterra model predicts stable coexistence when intraspecific competitive effects are stronger than interspecific ones ($\alpha\beta < 1$), any factor reducing interspecific competition should favor coexistence. Intuitively, any differential use of resources by two competing species (**niche divergence** or **resource partitioning**) should reduce interspecific competition and concentrate intraspecific effects. Also, implicit in the competitive exclusion principle is that niche divergence between species promotes coexistence. What remains unanswered so far in our discussion is how much niche divergence is necessary to ensure coexistence, how much niche differentiation actually occurs in nature, and whether or not "niche divergence along specific resource dimensions indeed reduces interspecific competition?" With regard to the last question, might two phloem-feeding aphid species compete severely for a common phloem resource even though they exhibit niche divergence by feeding at different locations on the plant? We will explore such issues in due course. Nonetheless, the first two questions are longstanding and involved ones that were first addressed by MacArthur and Levins (1967) and later developed by May (1973c).

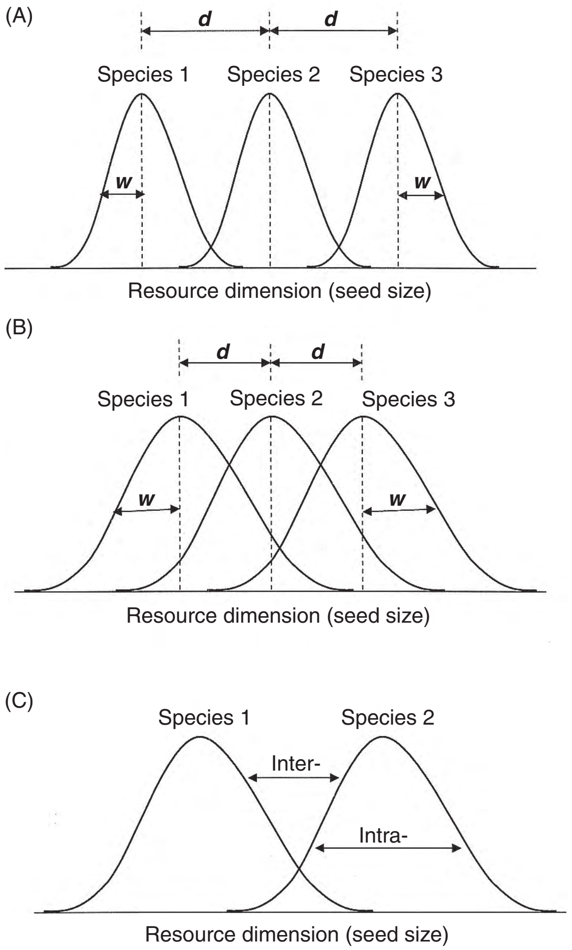


Figure 5.6 Resource utilization curves for three coexisting species along one resource dimension (seed size in this case) where d is the distance between neighboring curves and w is the standard deviation of each curve. (A) describes a case of narrow niches, little niche overlap ($d/w >> 1$) and relaxed interspecific competition. (B) illustrates an example of broad niches, high niche overlap ($d/w < 1$) and intense interspecific competition. (C) Selection from interspecific competition acts to narrow a species' niche, whereas intraspecific competition broadens its niche.

Our rendering of their argument is as follows: Consider three species competing for a single resource that varies continuously along a one-dimensional gradient. Picture for example seeds that vary in size from small to large and an assemblage of three weevil species that bore into the seeds. Each weevil species occupies its own realized niche along the seed-resource dimension. Consider a normal distribution of seed sizes used by each species, namely its resource utilization curve, where each weevil efficiently consumes seeds at the center of its "niche" and fails to exploit seeds beyond the tail ends of the distribution (Figure 5.6). The more the resource utilization curves overlap, the more intense is interspecific competition. Accordingly, the competition coefficient (α) for each species can be expressed as:

$$\alpha = e^{-d^2/4w^2} \tag{5.6}$$

where w is the standard deviation of each curve (an index of relative niche width) and d is the distance between peaks. Consequently, α is small when the three species diverge in their use of seeds toward non-overlap ($d/w >> 1$) (Figure 5.6A) and α approaches one as the utilization curves converge toward complete niche overlap ($d/w < 1$) (Figure 5.6B). Overall, theory predicts that selection resulting from interspecific competition (also apparent competition) acts to narrow a species' niche, whereas intraspecific competition broadens its niche (Figure 5.6C). Moreover, selection resulting from these two opposing competitive pressures should result in an assemblage of species that fully exploits the range of resources, leaving no so-called "**vacant niches**" available. Accordingly, the consequences of these evolutionary "pushing and shoving matches" bear heavily on the number of species able to coexist or "pack" into the community, in what is termed **species**

packing. In this context, the question still remains, however, as to how much niche overlap is permitted before one species excludes another?

May (1973c) explored the issue by assuming that the two peripheral species in a three-species assemblage have the same carrying capacity (K_1 or the suitability of resources available for species 1 and 3), and examined the opportunity for coexistence of another species (species 2) nestled between them with a carrying capacity of K_2 (see Figure 5.6B). Stable coexistence of the assemblage is indicated for different values of K_1/K_2 in relation to d/w (niche overlap) (Figure 5.7). When d/w is low (α is high and interspecific competition is intense), the conditions for coexistence (K_1/K_2) are very constrained. As d/w increases and approaches unity (α declines and interspecific competition is relaxed), stable coexistence becomes possible, but only when available resources are similarly suitable for all species ($K_1/K_2 \sim 1$). Any environmental change that promotes variation in the K_1/K_2 ratio will allow for coexistence only within the stable region of the model (Figure 5.7). Thus, for low values of d/w (high niche overlap) coexistence is very unlikely when K_1/K_2 deviates much from unity. For our weevil example, this might occur when some environmental factor results in relatively lower seed quality for species 2 (K_2) thus increasing K_1/K_2. High values of d/w (reduced interspecific competition) promote stable coexistence, but they are likely selected against in the real world due to intense intraspecific competition. Thus, environmental uncertainty when d/w is low and intraspecific competition when d/w is high suggest that stable coexistence is most likely when d/w is approximately equal to one.

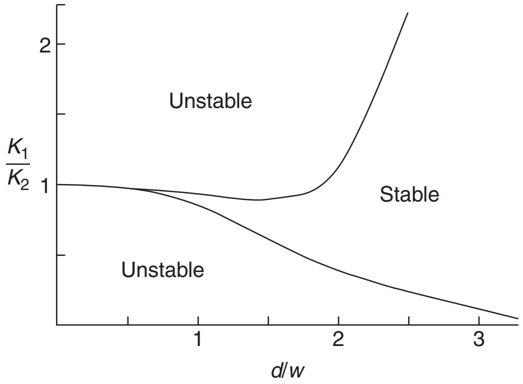


Figure 5.7 Opportunity for the coexistence of a third species (species 2 with a carrying capacity of K_2) with two other species (species 1 and 3 both with a carrying capacity of K_1) in a three-species assemblage. The model predicts that when d/w is low (intense interspecific competition) the conditions for coexistence (K_1/K_2) are very constrained. As d/w increases and approaches one (relaxed interspecific competition), stable coexistence becomes possible but only when available resources are similarly suitable for all species ($K_1/K_2 \sim 1$) (adapted from May 1973c).

Although this model provides a logical estimate of how much niche overlap is allowed for species to coexist, it has several inherent drawbacks. First, the model examines species interactions along a single resource dimension. In fact, most species divide their use of resources among more than one niche dimension. As a consequence, high niche overlap along one dimension may provide little indication of the strength of interspecific competition (α). For instance, our weevils may overlap considerably in the size of seeds they exploit, but if each species specializes on seeds from a different plant species, overlap in seed size use per se is of little consequence for predicting coexistence. Thus, estimates of d/w along multiple resource dimensions must be taken into account to better estimate stable coexistence (see Abrams 1976). Moreover, identifying competition as the sole factor underlying patterns of resource use in the field is an experimental and statistical challenge. Nonetheless, the model identifies a specific limit to how similar species can be and still coexist and suggests that this limit represents a balance between intraspecific competition and resource-based equilibria that are too precarious to prevail in the real world (Begon *et al.* 2006). In other words, we see that coexistence depends on factors other than niche overlap (d/w) such as resource suitability and environmental variance. Again we see that competitive interactions cannot be studied in isolation of other mediating factors.

5.2 Paradigms of competition theory: evidence for and against

Underlying simple competition models (e.g., Lotka 1925, Volterra 1926a,b, Gause 1934, MacArthur and Levins 1967, May 1973c) are several assumptions that bear directly on species coexistence and that have emerged as paradigms of traditional competition theory and thinking. These assumptions regarding competition and coexistence serve as hypotheses to be tested by venturing into the real world of species interactions and seeing how much support is indeed found (Speight *et al.* 1999). The fundamental model assumptions and tenets of competition theory are as follows:

(1) Competition coefficients (α and β) are constants (Equations 5.2 and 5.3).
(2) Competition for limiting resources is density dependent, intensifying as population size (N) approaches K (Figure 5.4).
(3) The only density-dependent forces acting on populations N_1 and N_2 are intraspecific and interspecific competition (Equations 5.2 and 5.3) and no other density-dependent factors such as predation or pathogen attack are limiting.
(4) Coexistence is promoted only if intraspecific competition is greater than interspecific competition (Figure 5.5D).
(5) Patterns of niche divergence along resource gradients result from reciprocal and thus symmetric competitive interactions among interacting species (Figure 5.6B).
(6) Two species with the same niche cannot coexist and resource partitioning diminishes interspecific competition and promotes coexistence (Figures 5.6B and 5.7).
(7) Closely related species or members of the same feeding guild compete intensely.
(8) Species interact and coexistence occurs only under equilibrium conditions (Equations 5.2 and 5.3; Figure 5.5D).

Even from what we have learned so far about competitive interactions, one might deduce that several of these model assumptions are violated in the natural world, at least to some extent. So, we will scrutinize each assumption looking for supporting evidence and discovering the conditions under which each is realized.

5.2.1 Are competition coefficients constants?

A substantial amount of evidence suggests that competition coefficients are not constants and vary depending on environmental factors such as temperature and food quality. By raising two insect herbivores under different temperatures in laboratory cultures, researchers have documented reversals in competitive superiority suggesting that competition coefficients in those studies were in fact temperature dependent. Such temperature-mediated shifts in competitive dominance have been shown in bean weevils (*Callosobruchus chinensis* and *C. maculatus*), stored product beetles (*Rhizopertha dominica* and *Callandra oryzae*) and fruit flies (*Drosophila pseudoobscura* and *D. serrata*) (Birch 1953, Fujii 1967, Ayala 1970). A noteworthy example from the field involves two lepidopterans feeding on English oak, namely the winter moth, *Operophtera brumata*, and the oak tortrix, *Tortrix viridana* (Hunter 1990). The winter moth is the superior competitor when spring temperatures are high, whereas the oak tortrix prevails under low spring temperatures. Collectively, these studies suggest that competition coefficients are context dependent and are not constants. Secondly, they document that fluctuating environmental conditions shift the competitive advantage back and forth between rival herbivores, deter competitive displacement and allow for coexistence. The consequences of fluctuating environments and non-equilibrium conditions for species coexistence have been explored mathematically by many workers; see Chesson (2000) for a nice synthesis.

5.2.2 Is competition density dependent?

A second assumption of competition models is that competition is density dependent, intensifying as population size increases toward carrying capacity. There is certainly a wealth of data showing that this is indeed the case for several insect herbivores with regard to both intraspecific and interspecific competition (McClure 1980, Ohgushi 1992, Denno *et al.* 1995, 2000, Hunter *et al.* 1997, Dixon 1998). For delphacid planthoppers (Hemiptera: Delphacidae), increasing population density (intensifying intraspecific competition) results in dramatic reductions in growth, fecundity and survival (Figure 5.8A). Moreover, for this group of wing-dimorphic insects (see Figure 4.5 for a refresher on wing dimorphism) and many others, such as aphids, dispersal is also density dependent (Denno and Peterson 1995). With increasing density, more and more flight-capable adults are produced in the population which escape the fitness penalties of high-density life and migrate to less crowded host plants elsewhere (Figure 5.8B). Density-dependent fecundity, survival and emigration collectively contribute to density-dependent growth at the population level. For instance, a plot of early-season density (log N_t) of the planthopper *Prokelisia marginata* against its late-season density two generations later (log N_{t+2}) yields an inverse relationship, suggesting that population growth is deterred by intraspecific competition when initial populations are high (Figure 5.8C).

Planthoppers and many other herbivorous insects also suffer from interspecific competition which can be density dependent as well (McClure 1980, Denno and Roderick 1992, Dixon 1998). Two salt-marsh inhabiting *Prokelisia* planthoppers, for instance, compete intensely for their shared phloem resource (Denno *et al.* 2000). When the density of *P. dolus* is experimentally increased, the body size (index of fecundity) of its competing congener *P. marginata* is very negatively affected (Figure 5.8D). Moreover, an increase in the population density of *P. dolus* results in a density-dependent increase in the production of migratory forms in *P. marginata* (Denno and Roderick 1992), an interspecific dispersal response that also occurs in aphids (Lamb and McKay 1987).

For herbivorous insects at large, however, recent reviews suggest that interspecific effects may not be generally density dependent in the way foretold by simple competition models (Denno and Kaplan 2007, Kaplan and Denno 2007). Exceptions occur for species that compete via feeding-induced changes in plant defensive chemistry (see Chapter 4). Although plants generally become more resistant to attack as herbivore damage increases, even very low amounts of damage can induce substantial levels of resistance (Stout and Duffey 1996, Karban and Baldwin 1997). Consequently, herbivores may interact, often with dire consequences, even if their densities are not particularly high. Other studies have also documented strong interspecific effects at defoliation levels where the quantity of available leaf tissue is clearly not limiting for herbivores (e.g., Agrawal 1999, 2000a, Wise and Weinberg 2002, Van Zandt and Agrawal 2004a,b, Viswanathan *et al.* 2005). Such plant defensive responses to low levels of herbivory may explain why the occurrence of interspecific competition via induced resistance is not well correlated with levels of defoliation (Kaplan and Denno 2007). That insect herbivores can induce resistance, and therefore compete at low to moderate densities, challenges the traditional model prediction of density-dependent competition, at least for some species.

5.2.3 Is competition the only density-dependent factor limiting populations?

Needless to say, this assumption extends from a simple mathematical expression designed to predict a two-species interaction and does not reflect the complexity of biotic factors that influence population size in the real world. There is certainly evidence that predators, parasitoids and pathogens attack their prey or hosts in a density-dependent fashion (Veldtman and McGeoch 2004, Bonsall and

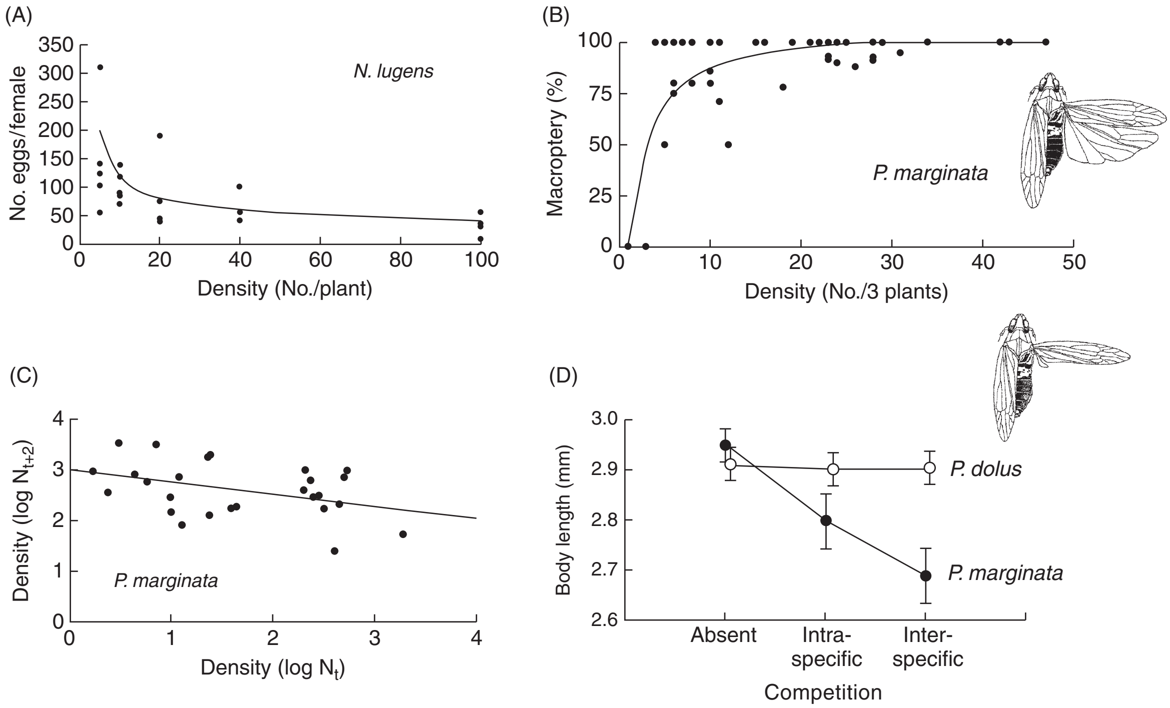


Figure 5.8 Density-dependent competition in delphacid planthoppers. Increasing population density results in (A) declining fecundity (eggs/female) in the rice pest *Nilaparvata lugens* and (B) increased macroptery (% of winged and flight-capable adults) in the salt marsh planthopper, *Prokelisia marginata*. (C) At the population level, there is an inverse relationship between the early-season density (log N_t) of *P. marginata* and its late season density (log N_{t+2}), indicating that intraspecific competition is intensified and population growth is deterred when initial populations are high. (D) Interspecific and intraspecific competition in two co-occurring planthoppers *Prokelisia dolus* and *P. marginata*. The body size (surrogate for fecundity) of *P. dolus* is unaffected by experimental increases in its own density or in the presence of its competitor *P. marginata*. In contrast, *P. marginata* suffers extreme body-size reductions under increased density conditions, both intraspecific density and particularly when feeding on plants exposed to a high density of *P. dolus* (from Denno *et al.* 1994, 2000).

Benmayor 2005, Chapters 7 and 8). It is noteworthy that one of the major observations used by Hairston *et al.* (1960) to argue against the importance of competition between insect herbivores was that "defoliation" was rare, food was not often limiting and that natural enemies (predators and pathogens) maintain herbivores below competitive levels. This pivotal paper triggered controversy as to the importance of competition versus predation in regulating herbivore populations, a controversy which remains today and which we will discuss more fully a bit later in this chapter and in others (Chapters 7 and 13).

Support of the view that natural enemies suppress herbivore populations below densities where competition occurs comes from studies of insect herbivores in their native and introduced ranges where natural enemies are common and rare, respectively. For example, interspecific interactions between scale insects and adelgids on hemlock and pine were studied in their native Japan and in eastern North America where they have been introduced (McClure 1986a,b, 1991). In Japan, natural enemies exhibit density-dependent attack and usually maintain scale and adelgid densities below competitive levels. In contrast, in North America, where specialized natural enemies are far less effective, these herbivores fiercely compete to the point of competitive exclusion in regions of overlap.

Besides influencing the intensity of interspecific competition, natural enemies may also alter the outcome of competition between two species. We have already seen and will explore further how natural enemies mediate competitive interactions between insect herbivores. Whether enemies promote coexistence or accelerate the outcome of competition (e.g., exclusion) depends on which herbivore suffers most from attack. Increased enemy attack of the inferior competitor may hasten its reduction or exclusion, as was the case when a shared parasitoid selectively attacked the scale insect *Nuculaspis tsugae* and accelerated its exclusion from hemlock stands by the competitively superior scale *Fiorinia externa* (McClure 1981, 1988). In contrast, heightened attack of the superior competitor may promote coexistence (Denno *et al.* 1995). For instance, the aphid *Panaphis juglandis* experienced dramatic density increases in commercial walnut orchards following the suppression of the competitive dominant *Chromaphis juglandicola* by a parasitoid (Messenger 1975). These examples underscore that density-dependent factors other than competition act on herbivore populations, but they also emphasize the mediating role of natural enemies in competitive interactions. Thus, it is not an "either or" situation regarding the importance of competition versus predation in herbivore suppression, but it is a "when and under what conditions" do these two factors interact with plants and the physical environment factors to influence herbivore populations!

5.2.4 Is intraspecific competition greater than interspecific competition?

Another central tenet of competition theory is that stable coexistence between two species is promoted only if intraspecific competition is greater than interspecific competition. For free-living folivorous insects, some of the best experimental evidence for the relative strength of intraspecific and interspecific competition comes from a study of eight species of *Erythroneura* leafhoppers that co-occur on sycamore trees in mid-western North America (McClure and Price 1975, see Figure 12.5). The densities of the eight species were experimentally varied in single-species and mixed-species populations that were caged on trees in the field. After a month of interaction, the effects of competition on each species were assessed by measuring leafhopper survival and reproduction. In this study, strong intraspecific competition diminished, but did not preclude, significant interspecific effects. Additional evidence for leafmining lepidopterans also indicates that intraspecific competition can be a more important mortality source than interspecific competition (Bultman and Faeth 1985, Faeth 1992). However, general reviews examining the relative strength of intraspecific and interspecific competition for insect herbivores do not find overwhelming support for the notion that intraspecific competition is generally more intense (Denno *et al.* 1995, Kaplan and Denno 2007). For 70 species interactions, intraspecific exceeded interspecific competition in 40% of the cases, interspecific equaled intraspecific competition in 10% of the cases and interspecific exceeded intraspecific competition in 50% of the cases (Denno *et al.* 1995). A recent meta-analysis of 57 interactions between insect herbivores found a similar result; there was no statistical difference in the magnitude of intraspecific and interspecific competition on growth and fitness (e.g., body size, fecundity, survival and emigration rate) (Kaplan and Denno 2007). However, for every growth and fitness variable assessed there was a tendency for the intraspecific effect to exceed the interspecific effect. Indeed there are specific herbivore interactions in which intraspecific effects exceed interspecific ones, but there are a sufficient number of exceptions to question the assumption that coexistence is broadly dependent on the dominance of intraspecific over interspecific competition.

5.2.5 Are interspecific competitive interactions symmetric?

Inherent in competition theory is that different species vie for resources along resource gradients, that each species is the superior competitor at the peak of its resource utilization curve, and that reciprocal competitive interactions among species promote niche divergence among species ($d/w \sim 1$) along the gradient (Figure 5.6B). This pattern of niche divergence is predicted on the basis of symmetric interspecific interactions that result in the dominance of species at different positions along the gradient. *Erythroneura* and *Eupteryx* leafhoppers feeding on sycamore trees and nettle plants, respectively, provide good examples of symmetric competitive interactions in which oviposition, reproduction and survival are similarly reduced when different species co-occur (McClure and Price 1975, Stiling 1980). Competitive interactions between the bark beetles *Ips paraconfusus* and *I. pini* are also symmetric (Light and Birch 1982, Light *et al.* 1983). For these beetles, the first species to attack a ponderosa pine tree produces an inhibitory pheromone which deters colonization by the other species. This interaction is reciprocal, is an example of interference competition and results in the spatial segregation of beetle species on their pine tree host.

Despite several clear examples of symmetric interactions, reviews of the competition literature on phytophagous insects find widespread evidence that most interspecific interactions (84%) are highly asymmetric (amensalistic) (Denno *et al.* 1995, Kaplan and Denno 2007), a result consistent with the findings of earlier critiques (Lawton and Hassell 1981, 1984, Strong *et al.* 1984a). Plant-mediated competition may hold part of the answer as to why interspecific effects are so asymmetric. However, the mechanisms underlying plant-mediated competitive dominance, and thus asymmetrical interactions, are diverse and include the tolerance of induced allelochemistry and depleted plant nitrogen and the induction of strong metabolic sinks that deprive competitors of essential nutrients (Denno and Kaplan 2007). For instance, early-season feeding by the leaf beetle *Phratora vitellinae* induces increases in phenolic glycosides that the insect is able to tolerate, but which negatively affect generalist herbivores such as the winter moth *Operophtera brumata* (Ruuhola 2001). Likewise, feeding by the whitefly, *Bemisia argentifolii*, induces defensive proteins (e.g., chinases and peroxidases) that have little effect on the whitefly, but adversely affect the development and survival of the leaf-mining dipteran *Liriomyza trifolii* and the foliar-feeding lepidopteran *Trichoplusia ni* (Inbar *et al.* 1999a,b, Mayer *et al.* 2002). Competitive interactions between *Prokelisia* planthoppers are also highly asymmetric (Olmstead *et al.* 1997, Denno *et al.* 2000, Huberty and Denno 2006b, Figure 5.8D). The competitive superiority of *P. dolus* over *P. marginata* results from its greater allocation to cibarial muscle mass and increased ability to compensate for declining plant nitrogen via increased ingestion of phloem sap. In mixed-species crowds, not only does *P. dolus* contribute more to declines in plant nitrogen, but it also tolerates such declines better and experiences less severe performance and fitness costs than *P. marginata*. The asymmetry of interspecific interactions between gall aphids (*Geoica sp.* and *Forda formicaria*) on *Pistachia* trees occurs because *Geoica* occupies the base of leaves where they manipulate phloem transport, form nutrient sinks and direct nutrients away from the distal area of leaves where *Forda* suffers high mortality (Inbar *et al.* 1995).

Natural enemies can also mediate interactions between insect herbivores, tip the competitive balance and generate asymmetric interactions (Denno *et al.* 1995, Kaplan and Denno 2007). When natural enemies selectively attack one competitor, asymmetries often arise.

In the absence of their shared egg parasitoid, two *Erythroneura* leafhopper species possess very similar competitive abilities and exhibit a classic symmetric interaction (Settle and Wilson 1990). However, when the parasitoid is present, *E. variabilis* dominates because *E. elegantula* is selectively parasitized and the interaction now becomes very asymmetric.

Plants and natural enemies can also act in concert to mediate competitive interactions and either promote asymmetries or exacerbate existing ones. Comediation can occur when one herbivore induces the production or release of plant chemicals that increase the risk of enemy attack on a second herbivore. For instance, prior feeding by the mirid bug, *Tupiocoris notatus*, causes native tobacco plants to release volatile organic compounds that attract the generalist predator *Geocoris pallens*, which then selectively attacks caterpillars of the less mobile and co-occurring herbivore *Manduca quinquemaculata* (Kessler and Baldwin 2004). In another study, previous feeding by potato leafhoppers (*Empoasca fabae*) induces chemical and morphological changes in potato plants that result in a significant developmental delay for later-feeding larvae of Colorado potato beetles (*Leptinotarsa decimlineata*) (Lynch *et al.* 2006). The slow-developing beetle larvae on induced plants then incur much higher mortality from the predaceous stinkbug *Podisus maculiventris* than larvae feeding on undamaged plants (Kaplan *et al.* 2007).

5.2.6 Does high niche overlap result in competitive exclusion and does niche divergence promote coexistence?

There are certainly examples of competitive exclusion between insect herbivores sharing the same niche (Denno *et al.* 1995). A clear case involves two scale insects (*Fiorinia externa* and *Nuculaspis tsugae*) that both feed in the mesophyll cells of young hemlock needles (McClure 1980, 1991). Both sap-feeders were introduced into New York City about 90 years ago and since have expanded their distribution in several northeastern states where they can be severe pests. However, during the course of its range expansion and because of its competitive superiority, *F. externa* rapidly excluded *N. tsugae* within four years from numerous forest stands previously dominated by this species. A similar competitive displacement occurred following the invasion of *Matsucoccus resinosae*, a scale insect that displaced the adelgid *Pineus boerneri* from red pine forests in New England, both of which shared the same niche on 3-year-old wood (McClure 1990).

Because high niche overlap can result in competitive displacement between species, we can now ask if niche divergence in general diminishes interspecific competition and fosters coexistence. The competition literature is replete with examples of how species diverge in their use of resources by feeding at different locations on the same resource, at different times of the year, or in different habitats (see review by Denno *et al.* 1995). The paramount question, however, is if such niche differences arose as a consequence of interspecific competition and if competition is therefore diminished? Manipulative experiments can shed light on these issues. Bark-beetle species typically attack their coniferous host at different heights along the tree trunk where they encounter a gradient in bark thickness. Adult beetles must be able to penetrate the bark and deposit eggs in the underlying cambium where their larvae feed, girdle the tree and often kill it. Differences in body size among rival beetle species are often associated with bark thickness with larger species attacking the base of trees and smaller ones colonizing tree tops (e.g., Figure 12.4). By attacking living trees at different heights, during different stages of tree senescence (live, dying and dead), and/or different seasons, bark beetles are thought to reduce interspecific competition (Paine *et al.* 1981, Ayres *et al.* 2001). An example of niche divergence involves the bark beetles *Dendroctonus ponderosae*, which attacks living pines, and *Ips pini* that usually follows by exploiting dying trees (Rankin and Borden

1991). By introducing the aggregation pheromone of *I. pini* onto living trees, the two beetle species can be forced to co-occur. Experimentally forced synchrony of these beetles results in drastic reductions in the survival of *D. ponderosae*, which is attributable to direct competition with *I. pini*, as well as increased mortality from the predators and parasitoids normally associated with *I. pini* (Bergvinson and Borden 1991, Rankin and Borden 1991). Moreover, reciprocal avoidance of aggregation pheromones in bark beetles deters colonization and contributes to their spatial segregation both within and among trees. Also, in the absence of a rival species, bark beetles occupy broader niches than they do in mixed species populations (Paine *et al.* 1981, Rankin and Borden 1991). “Addition experiments” demonstrating drastic fitness reductions and “subtraction experiments” followed by niche release suggest that niche divergence contributes to reduced interspecific competition and promotes coexistence in the bark-beetle guild.

Another interaction between bean weevils also suggests that resource partitioning diminishes competition (Toquenaga 1990, Toquenaga and Fujii 1990). On large beans, *Callosobruchus analis* feeds in the center of the bean and *C. phaseoli* feeds near the outside surface. When these beetles are reared together on small beans, the opportunity to partition the bean is precluded and *C. analis* excludes *C. phaseoli*, suggesting that microhabitat segregation in large-sized beans allows for their coexistence. Manipulative experiments also suggest that temporal partitioning can also reduce interspecific competition. Leaf-mining lepidopterans normally feed later in the season than do many free-living folivores (West 1985). By experimentally forcing a premature “spring generation” of the miner *Phyllonorycter* sp. to coincide with folivorous chewers, the miner’s survival was much lower than that which occurs naturally during its summer generation (West 1985). Recall also that the experimental removal of the scale insect *Fiorinia externa* from terminal hemlock needles resulted in the colonization of this optimal feeding site by *Nuculaspis tsugae* in a clear case of niche release.

It is not only the realized niche of a species that is altered in the presence of a competitor, but its morphology may change as well in what is called **character displacement** (Brown and Wilson 1956). Historically there has been a strong theoretical link between character displacement and interspecific competition, but in fact few examples establish a rigorous connection. The argument is rather straightforward and goes as follows: In areas of sympatry (overlap) between two species, selection resulting from competition will favor differences in morphology that diminish competition for food, oviposition sites, nesting sites, etc. Purported differences include mandible and beak size, ovipositor length and overall body size. In contrast, where two species’ ranges are allopatric (don’t overlap), interspecific competition is lacking, and the character of note should not be under selection to diverge.
A possible example involves two North American ant species, *Lasius flavus* and *L. nearcticus*, that share similar food habits (Wilson 1955). The two ants occur sympatrically in the eastern United States, but only *L. flavus* occurs in the west. Where the two species are sympatric, they diverge in seven head characters that may reflect differences in the food they gather. In contrast, where *L. nearcticus* is absent, *L. flavus* converges in all head characters. A biplot of head width against head length in areas where *L. flavus* occurs sympatrically and allopatrically with *L. nearcticus* demonstrates character displacement by *L. flavus* in the zone of overlap (Figure 5.9). Simply demonstrating that species diverge in their morphology where they co-occur does not mean that interspecific competition is necessarily the underlying cause. For the link between character displacement and interspecific competition to be established, the following must be shown.

(1) The pattern of character displacement is non-random.
(2) Differences in morphology are related to resource use.

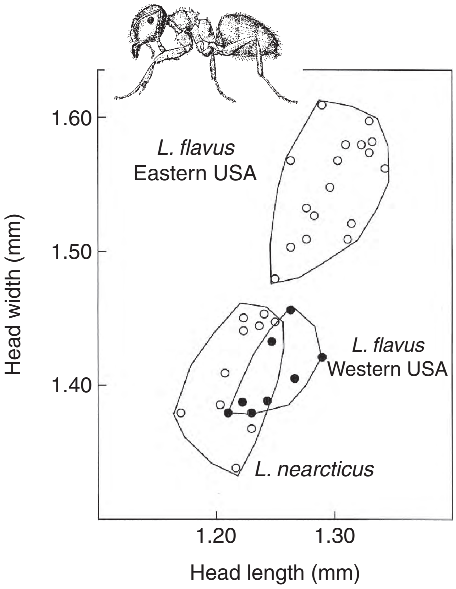


Figure 5.9 Character displacement in the ant *Lasius flavus*. In the zone of sympatry (the eastern USA) where *L. flavus* co-occurs with its congener *L. nearcticus*, the two ants exhibit very different head morphologies (width/length ratio). Where the two species occur allopatrically (*L. flavus* in the west and *L. nearcticus* in the east), both ants have very similar head morphologies. The difference in head morphology and other mandibular characters in the zone of overlap is thought to result from selection that minimizes competition for food. From Wilson 1955. Museum of Comparative Zoology, Harvard University.

(3) Both species consume less prey in areas of sympatry than allopatry.
(4) Resources are similarly available in zones of sympatry and allopatry.
(5) Differences evolved in the zone of sympatry and did not exist prior to co-occurrence when species were allopatric.
(6) Differences are genetically based (Schluter and McPhail 1992, Losos 2000).

Addressing these hypotheses in a single study is certainly a daunting task, but an increasing number of researchers are attempting to do so (Adams and Rohlf 2000).

Further complicating matters is that the morphological differences between two species that we see today may be a reflection of selective pressures resulting from competition during evolutionary history. Thus, character displacement may be the “ghost of competition past” (Connell 1980) and cannot be tested by simply removing the suspected rival species and looking for niche release, because characters may have become fixed in evolutionary time. Nonetheless, the prediction is that the intensity of competition experienced by two species should decline as character displacement proceeds, yielding descendants whose present-day interactions are a “ghost” of their former strength (Pritchard and Schluter 2001). Using stickleback fish species with divergent body size and mouth gape characteristics and with different histories of post-Pleistocene co-occurrence, it was shown that species with a longer history of co-occurrence suffered fewer growth penalties than species with a recent history of co-occurrence, suggesting a decline in the strength of resource competition through time. No such studies are available for insects, but assessing character divergence in native ant species with different histories of interaction with invasive ants may provide an ideal opportunity. Overall, however, evidence is accumulating from several vertebrate systems that character displacement and associated niche divergence have evolved in response to interspecific competition and indeed can reduce its intensity.

Back to insects, niche divergence and the strength of interspecific competition! Although there are several examples involving insect herbivores in which niche divergence reduces interspecific competition, general reviews find mixed results for this traditional notion (Damman 1993, Denno *et al.* 1995, Kaplan and Denno 2007). Exceptions to the view that resource partitioning alleviates competition often arise when plants and natural enemies indirectly mediate interactions among insect herbivores. Induced resistance responses in plants can be rapid (within a single herbivore generation) or quite delayed (across multiple generations), providing the opportunity not only for contemporaneous herbivores to interact, but also those that occur in different seasons (Haukioja and Niemelä 1979, Karban and Baldwin 1997). Even inter-year carryover effects of induced resistance from outbreak defoliators allow plants to mediate interactions between herbivores across different growing seasons (Kaitaniemi *et al.* 1998, 1999). Also, induced responses can be local, occurring in the damaged tissue, or they can be systemic where the response often carries beyond the damaged tissue to other non-damaged tissue, and in several cases even to different non-damaged tissue types (Inbar *et al.* 1995, Karban and Baldwin 1997). Consequently, herbivores that are spatially or temporally separated on the same plant can interact via feeding-induced responses of induced resistance factors or altered nutrition (Denno *et al.* 1995, Denno and Kaplan 2007).

As an example of a competitive interaction arising from induced allelochemistry, the root-feeding wireworm *Agriotes lineates* induces increases in aboveground terpenoids in cotton plants that negatively affect the growth of the leaf-chewing lepidopteran *Spodoptera exigua* (Bezemer *et al.* 2003). Also, on wild radish plants (*Raphanus raphanistrum*), glucosinolates are induced by larvae of *Pieris rapae* that negatively affect the growth, colonization and density of lepidopterans, aphids and leafmining flies feeding later in the season (Agrawal 1998, 1999, 2000a). Feeding-induced reductions in plant nitrogen or altered source-sink dynamics can also negatively affect spatially and temporally separated herbivores. Prior feeding by gypsy moth larvae (*Lymantria dispar*) results in decreased plant nitrogen that negatively affects the growth and survival of later-feeding tiger swallowtail larvae (*Papilio canadensis*) on quaking aspen, *Populus tremuloides* (Redman and Scriber 2000). Moreover, sap-feeding herbivores such as planthoppers, aphids and gall aphids compete intensely for their common phloem resource even though they occupy different plant parts or occur at different times of the year on the same host plant (Moran and Whitham 1990, Inbar *et al.* 1995, Denno *et al.* 2000). Early-season feeding by the planthopper *Prokelisia dolus* depletes the nitrogen content of its *Spartina* host so much that subsequent generations of its nitrogen-sensitive rival *P. marginata* are essentially precluded. Regardless of the specific mechanism, the important generality that emerges from this collection of studies is that induced resistance conferred by altered allelochemistry or plant nutrition can result in substantial competitive effects between insect herbivores that are temporally and spatially separated on the same plant.

Natural enemies can also mediate herbivore interactions across time and space, although their spatiotemporal effects are likely to differ from plant-mediated interactions (Kaplan and Denno 2007). Because many natural enemies aggregate in areas where prey are abundant, their persistence in one habitat, and thus their ability to affect later-occurring herbivores, will likely be less than the effect of a delayed induced defense. Accordingly, the impact of early-season herbivores on late-season herbivores via shared natural enemies may be weak because predators and parasitoids will probably emigrate in search of alternative food after their focal prey disappear. Unlike induced defenses, however, natural enemies can mediate competition between herbivores on different plants, and therefore their spatial reach is far greater than an induced plant defense. The invasion of soybean aphids (*Aphis glycines*) in the midwestern USA has increased the abundance of predaceous coccinellid beetles that colonize alfalfa fields where they severely reduce pea aphid (*Acyrthosiphon pisum*) densities (Harvey 2007). As a consequence, soybean aphids strongly “compete” with pea aphids, even though these two herbivores feed on different host plants in widely separated agricultural fields.

So, is there a consensus regarding niche divergence, relaxed interspecific competition and species coexistence? In fact there is not, at least for insect herbivores. Extensive reviews provide very mixed support for a strong link between niche divergence and relaxed competition (Denno *et al.* 1995, Kaplan and Denno 2007). There is certainly variation among species interactions and perhaps the most prudent conclusion given the current data set is that temporal and spatial differences in resource use can dampen, but not necessarily preclude, interspecific competition. Many clear exceptions for phytophagous herbivores involve plant-mediated and enemy-mediated competitive interactions in which severe competition is not precluded by spatial and temporal niche segregation.

5.2.7 Do closely related species or members of the same feeding guild compete intensely?

It is thought that competition is more likely to occur between closely related taxa because their feeding niches are often so similar (Miller 1967). Even Darwin (1859, p. 110) predicted that "the most closely-allied forms – varieties of the same species, and species of the same genus or related genera – which, from having nearly the same structure, constitution and habits, generally come into the severest competition with each other." Since, the relationship between phylogenetic proximity and the strength of interspecific competition has become a fundamental tenet deeply embedded in competition theory (Kaplan and Denno 2007). Likewise, members of the same feeding guild, because they feed on a similar resource, might compete more intensively than members of different feeding guilds.

Reviews of the literature on phytophagous insects, however, provide mixed support for these hypotheses, in that the degree to which closely related taxa compete depends on their feeding guild (Denno *et al.* 1995, Kaplan and Denno 2007). Phylogenetic similarity was a far better predictor of the strength of interspecific competition for sap-feeding herbivores than mandibulate herbivores. Intense competitive interactions, for instance, occur between congeneric sap-feeders, including aphids (*Uroleucon*), adelgids (*Pineus*), psyllids (*Arytaina*), planthoppers (*Prokelisia*) and leafhoppers (*Erythroneura*), and interactions are less intense when such taxa competed with species in other genera, families or orders. Even so, there are exceptions to this general pattern for sap-feeders. The sap-feeding spittle bug, *Philaenus spumarius*, suffers badly from interactions with larvae of the distantly related plume moth, *Platyptilia williamsii*, which deny spittlebug nymphs access to optimal feeding sites in the buds of their host plant *Erigeron glaucus* (Karban 1986, 1989b). For mandibulate herbivores, intense competition can occur between both closely related species and distantly related taxa representing different families or orders (Van Zandt and Agrawal 2004b, Kaplan and Denno 2007). Early-season feeding on milkweed plants by the stem-feeding weevil *Rhyssomatus lineaticollis* reduces the growth of other beetle species (*Labidomera clivicollis*), as well as more distantly related lepidopterans like the monarch (*Danaus plexippus*), an effect that is likely mediated by a reduction in plant quality.

The consequences of induced resistance via enhanced allelochemistry may be felt by a broader taxonomic range of chewing herbivores than sap-feeders. Because sap-tappers feed in vascular tissues, they may avoid feeding-induced increases of allelochemicals that occur in non-vascular tissues that leaf-chewing herbivores cannot avoid (Denno and Kaplan 2007). Overall, intense interspecific interactions can occur between distantly related herbivores and even organisms in different kingdoms can experience severe competitive effects (Hochberg and Lawton 1990, Stout *et al.* 2006).

Do members of the same feeding guild compete more intensely than herbivores belonging to different feeding guilds? Early reviews of the subject found that sap-feeders (e.g., aphids and leafhoppers) competed more frequently and intensively with each other than with mandibulate herbivores (e.g., grasshoppers and caterpillars) (Strong *et al.* 1984a, Denno *et al.* 1995). However, a recent assessment that included many more plant-mediated studies established that there was no difference in the strength of interactions occurring within versus between members of these feeding guilds (Kaplan and Denno 2007). Due to the limited number of published studies that provided quantitative data necessary for meta-analysis, a comparison of the strength of competition within versus between subguilds was not possible. Older reviews, however, suggest that interspecific competition occurs more often in interactions between species occupying internal feeding niches (e.g., stem borers, wood borers and seed feeders) than in interactions between externally feeding folivores such as grasshoppers, lepidopterans and beetles (Denno *et al.* 1995). Perhaps competition is more intense between species in concealed feeding niches because they, unlike free-living herbivores, are less able to escape the confines of their competitive arena. Whether these patterns will stand the test of time remains to be seen.

5.2.8 Do species interact and does coexistence occur only under equilibrium conditions?

Competition models assume that species exist under equilibrium conditions, that their populations grow to carrying capacity and that the outcome of interspecific competition depends on an even playing surface and the competitive abilities (α and β) of the two species (Equations 5.2 and 5.3). Moreover, species **coexistence under equilibrium conditions** is possible when species partition their use of resources (Figure 5.6B) and when one species limits its own population more than that of its competitor, that is, when intraspecific competition exceeds interspecific competition (Figure 5.5D). In their predictions about competitive exclusion and coexistence, basic competition models don't take into account variable environments, habitat disturbance and the life-history strategies of the competitors. Such factors can interact to promote **coexistence under non-equilibrium conditions.** Poor competitors, for example, can coexist in a system if they are better colonizers of temporary habitats. An example is provided by *Prokelisia* planthoppers (Denno *et al.* 2000). By all measures, *P. dolus* is competitively superior to *P. marginata*, inflicting heavy penalties on its growth and survival when the two occur together. However, *P. marginata* is by far the better disperser and coexists in the spatially diverse tidal marshes of North America because it is able to colonize low-marsh stands of its *Spartina* host grass that are destroyed annually during winter by shifting ice and tidal disturbance, but that become temporarily available in summer with the regrowth of the perennial grass. In this heterogeneous marsh landscape, *P. dolus* finds winter refuge and prevails throughout the year in stable meadows of *Spartina* on the high marsh, and the "fugitive" *P. marginata* persists in the system due to its superior colonizing ability.

In seasonal habitats and on ephemeral resources, consumers must colonize newly available space such as the spring flush of leaves, a fallen carcass or vertebrate dung. In these instances, early arrival is critical to success and often provides the competitive edge in ensuing interactions with other species (Denno *et al.* 1995, Denno and Kaplan 2007). Early arrival tends to confer competitive superiority when coupled with rapid population growth and the preemption of resources resulting from physical exclusion or chemical deterrence. The competitive dominance of the scale insect *Fiorinia externa* over *Nuculaspis tsugae* is completely dependent on the early emergence of scale crawlers, their spring colonization of new hemlock needles and the development of a "standing-room only population," which precludes exploitation of the optimal feeding site by later-emerging immatures of the rival scale (McClure 1980). However, when the advantage of early arrival is experimentally removed for *Fiorinia externa*, its competitive superiority is lost altogether. Similarly, the psyllid *Arytaina genistae* is the competitive dominant on buds of Scotch broom (*Sarothamnus scoparius*) based on one-on-one cage experiments with its congener *A. spartii* (Waloff 1968). However, the early hatch of *A. spartii* eggs in spring allows nymphs to colonize and preempt buds before the superior competitor arrives. These examples demonstrate that inferior competitors can persist and superior competitors can be excluded as a consequence of their life-history strategies, as they facilitate the colonization and monopolization of temporary resources in fluctuating and patchy environments.

Hutchinson (1961) suggested that non-equilibrium coexistence can be attained by organisms with several generations per year whereby changing environmental conditions shift the competitive advantage from one species to the next. We have already seen that competition coefficients change with temperature in bean weevils (*Callosobruchus chinensis* and *C. maculatus*) and lepidopterans on English oak (*Operophtera brumata* and *Tortrix viridana*). In a fluctuating environment the competitive advantage shifts back and forth, neither species excludes the other and both species coexist. Altogether, these examples demonstrate that coexistence is possible under non-equilibrium conditions when **changing environmental conditions** and **habitat disturbance** prevent one species from achieving a density ($N = K$) where competitive exclusion might occur.

5.3 Changing perspectives on competition between insect herbivores

5.3.1 Competition's rocky role as an important factor in species interactions and community structure

The importance of interspecific competition as a factor influencing species interactions and structuring communities of insect herbivores has experienced a very controversial history (Strong *et al.* 1984a,b, Damman 1993, Denno *et al.* 1995, Kaplan and Denno 2007). During the 1960s and 1970s, competition was regarded as a central organizing force in community ecology (Denno and Kaplan 2007). During these decades, field investigations into interspecific competition were dominated by observational studies of resource partitioning as evidence for reduced competition and coexistence. Experimental field studies were noticeably scarce! In the 1980s, the role of competition in the ecology of herbivorous insects was challenged severely, and within a few years it fell from a position of prominence to the status of a weak and infrequent force (Lawton and Strong 1981, Lawton 1982, Lawton and Hassell 1984, Strong *et al.* 1984a,b). Two lines of criticism led to its demise. The first had its origin in a theoretical paper by Hairston *et al.* (1960) who argued that because defoliation was rare, food was not limiting for herbivores, and that natural enemies were responsible for maintaining herbivore densities below competitive levels. A second line of attack came from the analysis of phytophagous insect distributions and co-occurrences. Instances of positive interspecific association and the presence of vacant niches led many ecologists to question the importance of competition, but this view was based largely on observational studies. By the mid 1980s the scientific community had responded to a plea for a more experimental approach, and many more manipulative investigations of competition between insect herbivores began to appear (e.g., McClure 1980, Stiling and Strong 1984, Karban 1986). With such studies came the revitalized perception that insect herbivores frequently compete and subsequent reviews reflect this reversal in thinking (Damman 1993, Denno *et al.* 1995).

In the mid 1990s, an extensive review of experimental studies involving 193 pairwise interactions between insect herbivores found compelling evidence for interspecific competition (Denno *et al.* 1995). Competitive effects on growth and survival were found for 93% of the studies involving sap-feeding herbivores (e.g., aphids, scale insects, planthoppers and leafhoppers) and in 78% of the cases investigating chewing herbivores (e.g., grasshoppers, caterpillars, beetles and sawflies). Most revealing was the discovery that over half of the cases of interspecific competition between mandibulate herbivores were instances of plant-mediated competition. Thus, a major conclusion of this review and others at the time (Damman 1993) was that competitive effects were often plant-mediated via induced resistance and that failure to investigate this indirect mechanism may have vastly underestimated the occurrence and importance of competition in herbivore communities.

In the 1990s and thereafter, more and more studies began to appear documenting that plant-mediated interactions were widespread and that insect herbivores frequently competed via induced resistance (e.g., Masters and Brown 1992, Inbar *et al.* 1995, Agrawal 1998, Redman and Scriber 2000, Nykänen and Koricheva 2004, Van Zandt and Agrawal 2004a,b). Books on induced resistance also appeared during this time, further highlighting that plants mediate interactions among insect herbivores (Tallamy and Raupp 1991, Karban and Baldwin 1997, Agrawal *et al.* 1999b). Competition had thus re-entered the milieu of potentially important factors influencing herbivore interactions and the structuring of herbivore communities.

5.3.2 Emerging view of competition in insect herbivores challenges traditional paradigms

Reviews and a recent meta-analysis of experimental studies of interactions between species of insect herbivores reveal widespread evidence for the occurrence of interspecific competition, thus putting to rest the notion that competition is a weak and infrequent force influencing this group of consumers. Undeniable evidence for interspecific competition was detected in 67% ($n = 99$), 76% ($n = 193$) and 62% ($n = 333$) of the experimental studies analyzed (Damman 1993, Denno *et al.* 1995, Kaplan and Denno 2007). Although these assessments found overwhelming evidence for interspecific competition, they did not find that the traditional paradigms of competition theory accurately predicted the nature of competitive interactions between many insect herbivores.

Meta-analysis revealed that virtually every fundamental paradigm of competition theory tested was violated to some degree (Kaplan and Denno 2007). Interspecific competition was not correlated with levels of defoliation suggesting that it does not always occur in a density-dependent fashion. Moreover, competition occurred frequently between distantly related species and between species in very different feeding guilds. Also, competition was highly asymmetric and was not generally dampened by spatial and temporal resource partitioning. The prevalence of indirect herbivore interactions mediated by plants (induced resistance) and natural enemies, as well as altered species interactions under non-equilibrium conditions, underlie much of the discrepancy between theory and pattern. For example, the majority of competitive interactions were mediated indirectly by plants and natural enemies (62%) and not directly by traditional exploitative and interference mechanisms (38%). As we have seen, plant- and enemy-mediated interactions between insect herbivores promote competitive asymmetries, allow distantly related species in different guilds to compete, and permit intense competition even if herbivores partition resources in space or time. Moreover, changing environments and non-equilibrium conditions permit species to coexist despite their very similar niches. Thus, traditional, niche-based competition theory is a bit too restrictive to adequately account for interspecific interactions involving many species of insect herbivores.

So where does this leave us with regard to resolving the conflict between theory and observation, and how representative are the responses of insect herbivores compared to other consumer groups? In part, the conflict is real. For instance, there is a longstanding record in the ecological literature that interspecific interactions among insect herbivores are asymmetric (Lawton and Hassell 1981, Strong *et al.* 1984a, Denno *et al.* 1995, Kaplan and Denno 2007). Although asymmetric competition in herbivores may be exacerbated by induced resistance, such asymmetries also occur in other consumer groups (detritivores, carrion feeders, predators and parasitoids) in which species interactions are not as clearly mediated by feeding-induced changes in resource quality (see Lawton and Hassell 1981). Failure of theory to predict patterns of resource partitioning in insect herbivores is in part a consequence of the spatial or temporal scale at which species interactions are evaluated. If herbivores induce a whole-plant systemic response or a long-lasting resistance response, one should not expect resource partitioning at small spatial (within-plant) and temporal scales to preclude interspecific competition, even if herbivores are phylogenetically distant or represent different feeding guilds. Thus, such competing herbivores should be evaluated at larger and more meaningful spatial scales (among plants) and over longer temporal periods when resource partitioning may diminish competition. Alternatively, plant-mediated competition may not be the only form of competition taking place in a specific species interaction. For instance, by occurring on different plant parts, aphid species can reduce competition for feeding space (interference) when densities are low even though they ultimately fail to avoid the negative consequences of induced reductions in plant quality as populations grow (Denno *et al.* 1995). Nonetheless, and because there are so many cases that deviate from theoretical expectations, discovering when and where competition and niche theory predict patterns of resource use will be an ongoing challenge for insect herbivores. Let us now move on and examine evidence for competition in other groups of consumers.

5.4 Competition in omnivores, detritivores, predators and parasitoids

Although not as extensively studied as in insect herbivores, there is considerable evidence suggesting that interspecific competition for limited resources occurs in other groups of insects, such as omnivores, detritivores, carrion feeders, predators, parasitoids and parasites. In the paragraphs that follow we shall explore competitive interactions in these trophic groups, and compare the consequences of these antagonistic interactions with those for insect herbivores.

5.4.1 Omnivores

Competition, both intraspecific and interspecific, occurs in omnivorous ants, where it can have dramatic effects on survival, colony size and spacing, and the structure of the ant community (Holway 1998, 1999, Morrison 2000, LeBrun *et al.* 2007). In fact, interspecific competition has been championed as the major factor underlying the displacement of native ant species by introduced invaders such as the Argentine ant (*Linepithema humile*) and the red imported fire ant (*Solenopsis invicta*), both of which were introduced from South to North America in the early 1900s. Subsequent to their introduction, these omnivorous intruders have spread rapidly, with devastating consequences for not only the native ant community, but for the invaded soil-dwelling assemblage of arthropods and food-web structure at large (Holway 1998, Kaplan and Eubanks 2005). The mechanisms of colony take-over in ants are complex and involve both interference and exploitative competition (Hölldobler and Wilson 1990). So-called competitive hierarchies involve asymmetries that arise from both worker attributes such as size, aggression and repellent pheromones (interference phenomena) and colony characteristics like recruitment ability (exploitation) and colony growth and size (Holway 1999). Among many ant species, there is an apparent trade-off between interference and exploitative competition such that species can be categorized as either “opportunists” that arrive early at food sources and exploit them quickly versus “extirpators” that are slow to arrive, but aggressively displace opportunists when they do show up (Wilson 1971). Such diverse foraging strategies are thought to promote coexistence in the ant community. The trade-off is very reminiscent of the pattern for insect herbivores in which "poor competitors" are able to persist under non-equilibrium conditions such as in spatially diverse and changing landscapes due to their superior dispersal ability. At least for the Argentine ant, and unlike most other native ants, the reason for its invasiveness is thought to be its proficiency at both interference and exploitative competition (Holway 1999). This species secures the majority of available resources along the invasion front, both because workers are more aggressive and because of its unique colony structure consisting of multiple queens, which promotes colony growth and the monopolization of resources.

5.4.2 Detritivores

Detritivores, including filter-feeding mosquitoes and stream and pond-dwelling caddisflies, also exhibit intense interspecific competition for shared resources. Interspecific competition during the larval stage of container-breeding mosquitoes is often severe, but competitive superiority can depend on habitat stability (Sunahara and Mogi 1997). In bamboo groves in southwestern Japan the slow-developing mosquito *Tripteroides bambusa* coexists with the fast-growing species *Aedes albopictus*, which often becomes dominant. Both species use water-filled bamboo stumps as breeding sites and larvae of both species co-occur and filter-feed on decaying leaf litter and associated microorganisms. In short-term experiments designed to mimic interactions in an ephemeral habitat that dries up quickly, *A. albopictus* wins in competitive interactions due to its faster larval development. However, in long-lived habitats and over several mosquito generations, the competitive outcome reverses and *T. bambusa* prevails. The greater survival of *T. bambusa* during the later stages of succession likely involves its superior ability in direct interactions with *A. albopictus* (interference competition) and its greater ability to tolerate increased concentrations of chemicals that alter the aquatic habitat as succession progresses. Like herbivorous insects, we see that changing environmental conditions can influence competitive outcome. In other container-breeding mosquitoes, shared larval habitats and shifts in the distribution and abundance of resident *Aedes albopictus* or *A. aegypti* after the establishment of the other species suggest that competitive displacement occurs (Braks *et al.* 2004).

Competition among detritivores in other aquatic habitats is also a common phenomenon. Hydropsychid caddisflies inhabit fast-flowing streams where they build retreats and capture nets between rock crevices. The larvae glean bits of detritus and small animal fragments from the nets that are filtered from the rushing water. The larvae compete both intraspecifically and interspecifically for optimal net-construction sites on the stream bottom (Funakoshi 2005). Fights (interference competition) among larvae are frequent when one individual attempts to take over the retreat of another. Interspecific contests often have a very asymmetric outcome with the larger species (e.g., *Stenopsyche marmorata*) often usurping the net of a smaller rival (e.g., *Stenopsyche sauteri*). However, residents appear to have an advantage over intruders independent of body size.

Intense interspecific competition also occurs in case-building caddisflies such as the limnephilds *Asynarchus nigriculus* and *Limnephilus externus* (Wissinger *et al.* 1996). In this case, larvae of both species feed mainly on vascular plant detritus, but *A. nigriculus* dominates in temporary basins, whereas *L. externus* is more abundant in permanent waters. Exploitative competition for detritus, however, does not explain their differential use of habitats. Rather, the intraguild predation (extreme interference competition) of *L. externus* by larger individuals of *A. nigriculus* explains the prevalence of *A. nigriculus* in temporary waters. The asymmetry of the interaction is driven by the developmental head start of *A. nigriculus*, which results in larger individuals that dominate in aggressive interactions with smaller heterospecifics. The prevalence of *L. externus* in permanent waters is an enemy-mediated indirect effect resulting from selective salamander predation on *A. nigriculus*. In this system, intraguild predation and cannibalism are not density-dependent, suggesting that carnivory in these detritivores may have evolved as a strategy for supplementing a nutrient-poor diet with nitrogen-rich prey. These results also bear on the trophic position of these so-called "detritivores" because they clearly feed on food resources from different trophic levels, thus making them omnivores, at least facultative ones.

Likewise, predation and cannibalism also occur in "herbivores" and may be a way of amending a nitrogen-poor diet. One of the classic and earliest experimental tests of intraspecific and interspecific competition involved two co-occurring species of flour beetles, *Tribolium confusum* and *T. castaneum* (Park 1962, Park *et al.* 1965). Both species were reared in containers of flour that provided necessary oviposition sites and larval food resources. In addition to consuming flour, beetle larvae and adults also attacked and cannibalized each other's eggs, larvae and pupae. Importantly, beetles consumed more individuals of their own species than they did individuals of the other species, demonstrating that intraspecific antagonism exceeded negative interspecific interactions, an outcome thought to lead to stable coexistence (see Figure 5.5D).

5.4.3 Carrion feeders

Competition, both intraspecific and interspecific, is often fierce on nutrient-rich and concentrated resources such as carrion and dung (Hanski and Cambefort 1991, Smith and Wall 1997). Blow flies (Calliphoridae) and flesh flies (Sarcophagidae), for instance, dominate the community of consumers on vertebrate carcasses, where larval competition can be intense (Ullyett 1950, So and Dudgeon 1990, Smith and Wall 1997). Female blow flies can cover a carcass with thousands of eggs, whereas flesh flies deposit a few living larvae. In short order, a carcass can become a seething mass of maggots representing several species. Manipulative laboratory experiments in which two species are raised in pure and mixed species combinations show that the effects of interspecific competition on body size and survival can be stronger than intraspecific effects for some species (e.g., *Lucilia sericata*), whereas the reverse is true for others (e.g., *Calliphora vicinia*) (Smith and Wall 1997). The difference in the relative strength of interspecific versus intraspecific competition promotes an asymmetric competitive outcome, but not to the extent that *C. vicinia* excludes *L. sericata*. Competitive outcome for this pair of calliphorid species in the field, however, depends on the habitat with *L. sericata* emerging in high numbers from mouse carcasses placed in pasture habitats and *C. vicinia* dominating on carcasses in woodland sites. The reversal in dominance is associated with the number of ovipositing adults of each species occurring in the respective habitat types.

In general, studies of mixed-species assemblages of carrion flies show that competitive superiority is affected by the size and age of the carcass, disturbance, habitat type and the life-history strategies of the flies. For example, adult females of *Sarcophaga bullata* arrive within hours to larviposit on fresh rabbit carcasses (Denno and Cothran 1975, 1976). Female sarcophagids are ovoviviparous, meaning that their eggs hatch within the uterus and the female deposits live larvae on the food resource. Early detection of carcass volatiles, early arrival at the carcass, and larviposition allow this sarcophagid to complete its larval development and pupate before the onslaught of calliphorids arrive and inundate the carcass with eggs. When the advantage of early arrival is removed by placing an "aged carcass" in the field, both *S. bullata* and a barrage of calliphorid flies arrive simultaneously at the carcass, but the competitive edge now shifts to the calliphorids and only they successfully complete development.

5.4.4 Predators

Both intraspecific and interspecific competition occur frequently in insect predators occupying terrestrial and aquatic habitats. The form of competition can be direct and involve mechanisms such as interference, cannibalism or intraguild predation, or it can be indirect and mediated through reductions in prey density (Polis *et al.* 1989, Lucas *et al.* 1998, Evans 2004, Van Rijn *et al.* 2005). Intraguild predation, in which one predator species kills and consumes another contending predator, can be viewed as an extreme expression of interference competition. Moreover, both direct and prey-mediated interactions can occur between the same predator–predator interaction. The decline of numerous native ladybird beetle species in North America coincides with the introduction of the seven-spotted ladybird beetle, *Coccinella septempunctata* (hereafter C-7), from Eurasia in the 1970s and 80s and the Asian ladybird, *Harmonia axyridis*, in the mid 1990s (Alyokhin and Sewell 2004, Evans 2004, Van Rijn *et al.* 2005). Moreover, the later establishment of *H. axyridis* in orchards resulted in a local decline of other exotics such as C-7. Resource competition for aphid prey may be a partial explanation for the decline in native species following the establishment of exotics (Evans 2004). For instance, because native ladybirds aggregate in areas of high aphid density, reductions of aphid populations in the alfalfa fields of Utah by C-7 significantly affects the degree to which the habitat retains native ladybirds. Although native and exotic ladybirds clearly compete via resource competition and experience local displacements as a consequence, there is no evidence yet that exotics are better resource competitors than natives.

Intraguild predation between the exotic and native ladybeetles is the most likely reason underlying the spread of exotic species and the subsequent decline of native species or earlier established exotics (Yasuda and Ohnuma 1999, Snyder *et al.* 2004, Yasuda *et al.* 2004, Van Rijn *et al.* 2005). Lab experiments show that intraguild predation of natives by exotics is generally greater than the reverse and that in interactions between the exotics *H. axyridis* is favored. A complicating factor is that these predators not only feed on the larvae of other predator species, but they also cannibalize their own young, an intraspecific effect that may offset the effect of intraguild predation on another rival species. The latter may explain in part why no exotic ladybird has excluded a native species altogether. In interspecific interactions among ladybird beetles and among ladybird beetles and more distantly related taxa such as green lacewings (*Chrysoperla rufilabris*), we see compelling evidence for asymmetric intraguild predation (Lucas *et al.* 1998, Michaud and Grant 2003). In general, success in intraguild interactions was conferred by large body size, better weaponry, such as large mandibles or spines, aggressiveness and high mobility. However, the presence of extraguild prey (aphids) can alter the strength and symmetry of intraguild predation.

Insect predators in aquatic habitats also compete indirectly via intraguild predation and directly for food resources. An excellent example involves naiads of the giant damselfly, *Megaloprepus coerulatus*, that share water-filled tree holes with two other damselfly species (*Mecistogaster linearis* and *M. ornata*) in the seasonal moist forests of Panama (Fincke 1994). As naiads, these damselflies are the top predators in tree holes, where they feed on a variety of other invertebrates, including each other. As an aside, adults of these pseudostigmatid damselflies feed exclusively on web-building spiders that they locate visually. Both *Mecistogaster* species are superior colonizers as adults: their naiads occupy about half of the tree holes within a month of the first seasonal rains. Due to their advanced arrival and oviposition, *Mecistogaster* naiads attain a large size and often eliminate smaller naiads of *Megaloprepus* via intraguild predation, especially from small tree holes. In larger tree holes, *Megaloprepus* gain the competitive edge where they eventually grow large enough to kill individuals of *Mecistogaster* before emergence. In this system, density-dependent cannibalism among conspecific naiads also occurs, but in experiments where cannibalism and intraguild predation were prevented, competition for food reduced naiad growth.

5.4.5 Parasitoids and parasites

Parasitoids, usually small wasps or flies, deposit their eggs on (**ectoparasitoids**) or in (**endoparasitoids**) their hosts (often insects and other arthropods). Females of some parasitoids may lay more than one egg in or on a host, resulting in **superparasitism**, a situation in which more individuals occur in a host than can obtain adequate resources to complete their development. **Multiple parasitism** occurs when a single host is infested by more than one parasitoid species at the same time. The very terms themselves are suggestive of antagonistic interactions and in fact both intraspecific and interspecific competition have been widely documented in parasitoids (Hogarth and Diamond 1984, Luck and Podoler 1985, Amarasekare 2000, Bográn *et al.* 2002).

A compelling example of intraspecific competition involves the gregarious ectoparasitoid *Goniozus nephantidis* (Hymenoptera: Bethylidae), which lays up to 20 eggs on the surface of its caterpillar host *Opisina arenosella* (Lepidoptera: Oecophoridae) (Hardy *et al.* 1992). Female wasps adjust clutch size by depositing more eggs on larger larvae suggesting that host size is limiting. Moreover, when the number of larvae per host is experimentally increased, the size of emerging female parasitoids decreases, as does their fecundity. In some parasitoid–host systems, female parasitoids place marking pheromones on their host during oviposition, which deter conspecific and heterospecific females from ovipositing on the same individual host and thereby minimize the adverse effects of competition (Nufio and Papaj 2001).

Interspecific competition also occurs in parasitoids, often with negative repercussions for one or both of the participating species (Heinz and Nelson 1996, Reitz 1996, Bográn *et al.* 2002). An elegant study demonstrating the complexity of interspecific interactions among an assemblage of parasitoids was conducted in central California (Force 1974). In this region, coyote brush (*Baccharis pilularis*) is attacked by the small gall-forming midge *Rhopalomyia californica* (Diptera: Cecidomyiidae). Gall midges are attacked by several hymenopteran parasitoids, including *Platygaster californica*, an endoparasitoid which oviposits in eggs and develops in midge larvae, the larval ectoparasitoids *Torymus koebelei* and *T. baccharicidis*, and the larval endoparasitoid *Tetrastichus* sp. Under undisturbed field conditions, the two *Torymus* species and *Platygaster* are by far the most abundant parasitoids and *Tetrastichus* is rare accounting for less than 1% parasitism. The parasitoids form a competitive hierarchy with the *Torymus* species near the top followed by *Platygaster* and *Tetrastichus*. In this assemblage, competitive superiority is inversely related to a species' intrinsic rate of increase (*r*), with *Tetrastichus* having the greatest reproductive potential. Competitive superiority results from a variety of mechanisms. *T. koebelei* readily multiply parasitizes hosts and kills the other parasitoids in the process. *T. baccharicidis* also multiply parasitizes hosts with one exception; it never parasitizes hosts already attacked by *T. koebelei*. *Platygaster*, although it initially parasitizes eggs, ultimately incurs high larval mortality from interactions with the larval ectoparasitoids via intraguild predation. *Tetrastichus* rarely attacks hosts previously parasitized by the other ectoparasitoids and it is frequently killed if the other parasitoids oviposit in hosts where *Tetrastichus* is already present. The competitive asymmetries are due in part to the advantage ectoparasitoids enjoy over endoparasitoids; in consuming the host, larvae of ectoparasitoids also devour developing endoparasitoid larvae.

One can ask why *Platygaster* and *Tetrastichus* persist in the community when they are such poor competitors. Fluctuations in the densities of the *Torymus* species hold the answer for *Platygaster*.

Indeed, when the *Torymus* species are abundant, *Platygaster* nearly disappears from the system. However, when *Torymus* is rare, *Platygaster* undergoes niche release and its populations soar. Thus, fluctuations in the abundance of *Torymus* hold the key to coexistence for *Platygaster*. Habitat disturbance provides the answer for *Tetrastichus*. In habitats where *Baccharis* plants are cut to the ground, parasitism by *Tetrastichus* increases from 1% to 46% in galls developing on regrowth. With its high rate of increase and perhaps better dispersal capability, *Tetrastichus* is able to better exploit the new habitat than the *Torymus* species. With time, and as the plant community recovers, the *Torymus* species recolonize, *Tetrastichus* is outcompeted and its parasitism rate declines to the normal low 1%. Thus, the community appears to exist under non-equilibrium conditions, whereby fugitive species coexist due to disturbance and a fluctuating environment.

One of the classic examples of shared niches and competitive displacement comes from the parasitoid world and involves the California red scale (*Aonidiella aurantii*), a common pest of citrus trees in California, and a group of three parasitoids in the genus *Aphytis* all of which attack the immature stages of this scale insect (DeBach and Sundby 1963, Luck and Podoler 1985). Around 1900, the parasitoid *A. chrysomphali* was accidentally introduced from the Mediterranean region and rapidly spread throughout southern California, where it provided effective control of the scale, especially in milder coastal areas. In an effort to improve the biological control of the scale, another congeneric parasitoid, *Aphytis lingnanensis*, was obtained from China in 1948, mass reared and then released in the citrus-growing area. By 1958, *A. lingnanensis* had almost completely displaced *A. chrysomphali* throughout most of its distribution. In the late 1950s yet another parasitoid species, *A. melinus*, was obtained from India and Pakistan, a region with wide annual climatic fluctuations similar to those in California. This parasitoid was reared and released in hopes of achieving better general control of the scale in both mild coastal areas and in the hot interior region of California where *A. lingnanensis* was less effective. By 1961, *A. melinus* broadly displaced *A. lingnanensis* and accounted for most of the parasitism in the interior citrus region. The mechanisms underlying the serial displacement of one *Aphytis* species by the next are complex and likely involve both exploitative competition and interference competition involving pheromones (Huffaker and Laing 1972). In part, *A. melinus* displaced *A. lingnanensis* because it attacked slightly smaller size classes of immature scales, pre-empted resources before they became available to the rival parasitoid and thus gained the competitive edge.

Experimental investigations of interspecific competition in insect parasites are few, but such studies do occur for fleas (Krasnov *et al.* 2000). Fleas (Siphonaptera) are obligate ectoparasites feeding mainly on mammals, especially small burrowing species, and birds. Larvae are not parasitic and feed on organic matter found in the nest of the host, and larval and pupal development occurs entirely off the host. Two flea species, *Xenopsylla conformis* and *X. ramesis*, inhabit the rodent host, the gerbil-like rodent *Meriones crassus*, in the Negev Highlands of Israel. Larval competition between these two flea species was studied in mixed- and single-species cultures in a laboratory setting. Results provide strong evidence for asymmetric interspecific competition, especially when larval food was limiting; *X. conformis* survived poorly in the presence of *X. ramesis*, but the survival of *X. ramesis* was unaffected by heterospecific larvae. The strong competitive interaction likely contributes to the spatial replacement of one species of flea by the other along a habitat moisture gradient in the field.

5.5 Comparative overview of competitive interactions

The above studies provide widespread evidence for strong competitive interactions in detritivores, predators and parasitoids, and these interactions show many characteristics in common with those observed for insect herbivores. Using parasitoids for comparison, we see that parasitoids compete via both exploitative (superparasitoidism) and interference mechanisms (intraguild predation and host marking pheromones) (Hardy *et al.* 1992, Amarasekare 2000, Nufio and Papaj 2001). Species sharing the same niche compete severely and competitive exclusion can occur (DeBach and Sundby 1963, Luck and Podoler 1985, Heinz and Nelson 1996, Bográn *et al.* 2002). Moreover, interspecific competitive interactions among larval parasitoids are often very asymmetric with co-occurring ectoparasitoids often excluding endoparasitoids (Force 1974, Amarasekare 2000).

Mechanisms for coexistence among parasitoids are similar to those for herbivores as well. Under equilibrium conditions, resource partitioning (e.g., attacking different stages of the host) can promote the coexistence of two competing parasitoids (Yu *et al.* 1990). Also, if two interacting parasitoids exhibit aggregated distributions, they will likely encounter more conspecifics than heterospecifics (May and Hassell 1981, Hassell *et al.* 1991). This should result in stronger intraspecific competition than interspecific competition and promote parasitoid coexistence. Non-equilibrium conditions promote coexistence in parasitoids as well. Changing seasonal temperatures, for instance, ensure the coexistence of two parasitoids of olive scale (*Parletoria oleae*) that have different temperature optima (Huffaker and Kennett 1966). Also, habitat disturbance and fluctuations in host productivity can foster the persistence of inferior competitors and fugitive species (Force 1974, Amarasekare 2000).

As in the case of insect herbivores, organisms from trophic levels below and above can also mediate competitive interactions between parasitoid species. Interactions between the parasitoids attacking pea aphids are likely mediated via host physiology (Danyk and Mackauer 1996). For instance, a protective envelope is formed around the eggs of *Praon pequodorum* (Hymenoptera: Aphidiidae) when eggs are deposited in aphids that are already parasitized by other parasitoids (*Aphidius ervi* and *Aphidius smithi*), but not in the presence of conspecific eggs. The envelope has a defensive function; it protects the developing embryo against physical attack by an earlier-hatching larva of another competitor, and allows *P. pequodorum* to coexist in the parasitoid complex. The envelope is produced by the eggs, but the stimulus for its production in the presence of heterospecific eggs is likely communicated via changes in host physiology.

Enemies at higher trophic levels, such as **hyperparasitoids**, can also mediate the strength of competitive interactions between primary parasitoids (May and Hassell 1981, Amarasekare 2000). Coexistence of two primary parasitoids can occur in the face of asymmetric interspecific competition if a hyperparasitoid selectively attacks the superior competitor. Also, a case of apparent competition involves caterpillars of the Glanville fritillary, a specialist primary parasitoid *Cotesia melitaearum*, and the hyperparasitoid *Gelis agilis* (van Nouhuys and Hanski 2000). When the second primary parasitoid (*Cotesia glomerata*) was experimentally added to the system, populations of *Cotesia melitaearum* declined as a consequence of increased attack by a shared hyperparasitoid. The decline occurred even though *C. glomerata* doesn't directly attack caterpillars of the fritillary.

Although there is certainly evidence that closely related parasitoids sharing the same niche can compete intensely, such as the case of competitive displacement involving the *Aphytis* species on California red scale, there is plentiful evidence documenting strong competition between parasitoids in different genera and families (Force 1974, Yu *et al.* 1990, Bográn *et al.* 2002). Moreover, and like insect herbivores (Stout *et al.* 2006), parasitoids can compete with other phyla, including bacteria and viruses, that exploit the same host (Chilcutt and Tabashnik 1997, Nakai and Kunimi 1997). The parasitoid *Cotesia plutellae* and the bacterial pathogen *Bacillus thuringiensis* both attack the same lepidopteran host *Plutella xylostella*, but the outcome of the competitive interaction depends on the degree of host susceptibility to the pathogen (Chilcutt and Tabashnik 1997). In susceptible hosts, the pathogen has a significant negative effect on parasitoid performance, but there is no such reciprocal effect of the parasitoid on the pathogen. In moderately susceptible hosts the interaction between the parasitoid and pathogen is competitive and symmetrical, whereas highly resistant hosts preclude infection by the pathogen and provide a refuge for the parasitoid.

Altogether, the topic of competitive interactions in trophic groups of insects other than herbivores is ripe for review. Based on the examples provided herein, however, we anticipate that the findings of such reviews will similarly challenge the traditional paradigms of competition theory. As for insect herbivores, the more we discover about how organisms from trophic levels above and below mediate interactions between players at the same trophic level (indirect effects), the more we will be able to learn about when and under what conditions predictions from traditional competition theory are realized.

5.6 Facilitation

Now it is time to leave the world of negative interactions and explore the prevalence and importance of positive interactions where again our initial focus will return to insect herbivores. Here we explore the considerable diversity of effects in which insects may improve conditions for other insects feeding on the same plant.

5.6.1 Positive interactions involving insect herbivores

Reviews not only reveal that plants mediate negative interactions between insect herbivores, but they also show that plants promote positive interactions (induced susceptibility) via altered allelochemistry (leaf volatiles), plant nutrition (feeding facilitation), architecture (leaf flush) or protective housing (leaf shelters) (Damman 1993, Denno *et al.* 1995, Nykänen and Koricheva 2004, Kaplan and Denno 2007). In a recent assessment of interspecific herbivore interactions, most interactions were negative (competition), but 11% (38 of 333) were cases of facilitation, nearly all of which were plant mediated (indirect) and very asymmetric (Kaplan and Denno 2007). As already mentioned, positive interactions can in fact broaden a species' realized niche beyond that predicted by its fundamental niche (Bruno *et al.* 2003, Figure 5.3B).

When previous feeding by one herbivore induces allelochemicals that are used by another to locate its host plant, induced susceptibility can occur (Denno and Kaplan 2007). For instance, larvae of *Pieris rapae* feed on wild radish and induce glucosinolates that are used by the specialist flea beetle *Phyllotreta* sp. to locate its host, a response that results in increased beetle colonization and oviposition (Agrawal and Sherriffs 2001). Induced susceptibility can also occur when one herbivore deactivates the preformed defenses of a plant, thus providing another herbivore the opportunity to feed. Heavy feeding by jack pine budworms *Choristoneura pinus* severs resin canals, thereby reducing resin flow and the concentration of monoterpenes (Wallin and Raffa 2001). Deactivation of the resin defense system by budworms encourages colonization by bark beetles (*Ips grandicollis*) and pine sawyers (*Monochamus carolinensis*), resulting in positive density associations among the three herbivores with the added benefit of feeding on a non-defended tree. A similar situation occurs on plants with latex canals. The vein-cutting and trenching behavior exhibited by a wide variety of insect herbivores depressurizes the latex canal system of plants (Dussourd and Eisner 1987, Dussourd and Denno 1994). By feeding distal to the cuts, not only does the inducing herbivore benefit, but so do other species that feed on the undefended leaf tissue (Dussourd and Denno 1991, 1994). For example, armyworm larvae (*Spodoptera ornithogalli*) grow much more rapidly on the leaves of the latex-bearing plant *Lactuca* following trenching by looper larvae *Trichoplusia ni* (Dussourd and Denno 1994) (See Chapter 4 for more on trenching behavior).

Another example demonstrating induced susceptibility between unrelated herbivores involves the root-feeding nematode *Meloidogyne incognita* and foliar-feeding lepidopterans (*Manduca sexta* and *Trichoplusia ni*) on tobacco (Kaplan *et al.* 2008a,b, 2009b). In plants that are not infected with nematodes, above-ground herbivory induces the synthesis and transport of alkaloids from roots to leaves, where the growth of the inducing lepidopterans is negatively affected (induced resistance). However, when roots are infested with nematodes, the synthesis and transport of alkaloids to leaves is precluded, plants become susceptible to attack and leaf-feeding caterpillars benefit tremendously (induced susceptibility). Not surprisingly, above-ground defoliation is highly associated with the presence of root-infesting nematodes among plants in the field. These examples demonstrate that the presence of one herbivore provides opportunities for niche expansion and resource acquisition in another that otherwise are not available.

When herbivores feed, particularly phloem feeders, they often induce nutrient sinks by diverting nutrients from surrounding leaves to their feeding site (Larson and Whitham 1991, Inbar *et al.* 1995). If other herbivores colonize and exploit surrounding sites, they are deprived of nutrients and their performance is often negatively affected (Inbar *et al.* 1995). On the other hand, if other herbivores aggregate locally with the inducers at the site of the nutrient sink, they can benefit tremendously from the enhanced levels of assimilates. For instance, numerous aphid species either selectively colonize the specific feeding sites occupied by other aphid species or shift their feeding site to co-occur with another aphid species (Denno *et al.* 1995). The result is a pattern of positive interspecific association either within a plant or across plants in the field (Waltz and Whitham 1997). Moreover, by occurring in close proximity to an induced nutrient sink, sap-feeders experience enhanced growth, body size and survival (Montandon *et al.* 1993).

Herbivores can also induce changes in plant morphology, such as increased branching and the re-flush of leaves, or alter architecture by building leaf shelters and leaf rolls that favor other herbivore species. Often, induced changes in plant morphology occur well after the initial bout of herbivory or shelter construction, providing the opportunity for temporally displaced herbivores to interact (Ohgushi 2005, Ohgushi *et al.* 2007). Regarding induced changes in plant morphology, damage to the apical meristems of goldenrod *Solidago altissima* by early-season gall formers causes more branching, which results in increased colonization and higher densities of aphids and spittlebugs (Pilson 1992). Similarly, early-season herbivory by caterpillars on oaks and gall-makers on willow stimulate a secondary leaf flush on which aphids, leaf beetles and leaf-rollers thrive (Hunter 1992a,b, Nakamura *et al.* 2003).

By constructing leaf shelters (rolls, folds and ties) or forming leaf galls, herbivores create new habitats for other herbivores that often generate positive associations (Lill and Marquis 2003, Ohgushi 2005). Positive interactions occur because the shelters built by these so-called "**ecosystem engineers**" provide other colonizing herbivores with enemy-free space, improved microclimate or improved food quality (Denno and Kaplan 2007). Importantly, primary shelter makers spend significant time and energy constructing their leaf structures, expenditures that later shelter users do not incur (Fukui 2001). The experimental addition of artificial leaf shelters designed to mimic the structures of early-season leaf-tying and leaf-rolling lepidopterans results in population increases in other shelter-building caterpillars and non-shelter-building herbivores such as aphids, lepidopterans, sawflies and beetles (Lill and Marquis 2003, Nakamura and Ohgushi 2003). In one instance, recruitment of previously occupied artificial ties by secondary leaf tiers is twice that compared to never-occupied ties, implicating feeding-induced volatiles (Lill and Marquis 2003). Not surprisingly, the removal of natural leaf shelters results in remarkable reductions in the densities of other insect herbivores (Lill and Marquis 2003). It is important to realize that the initiating shelter builder can induce positive interactions with other shelter colonists such as aphids, but negative associations with folivores like leaf beetles may result, as these are attacked by ants which tend the aphids (Nakamura and Ohgushi 2003).

From this last example, one might guess that natural enemies can mediate interspecific interactions between herbivores and in fact alter the sign of their interaction (Kaplan and Denno 2007). If one herbivore is attacked by the ants tending another herbivore, then the ant mutualism generates a negative interaction between the two herbivores in a case of apparent competition (see Chapter 6 on Mutualism). On the other hand, "apparent facilitation" can result if the tending ants protect both herbivores from other natural enemies, such as happens when ants tending nymphs of the treehopper *Vanduzea arquata* (Membracidae) on locust trees also protect beetle larvae (*Odontota dorsalis*) from the predaceous bug *Nabicula subcoleoptrata* (Fritz 1983). Survivorship of the beetle was significantly higher in the presence of ants than when ants were excluded from branches. Enemy-mediated facilitation can occur at a larger spatial scale as well. If predators aggregate in high-density patches of one herbivore species or otherwise prefer to feed on that herbivore, this can draw predators away from other herbivores to their benefit (Bergeson and Messina 1998, Koss and Snyder 2005). When aphids are present on potato plants, Colorado potato beetle larvae incur less predation from heteropteran predators than when aphids are absent. The perceptive reader will notice that these indirect herbivore–herbivore interactions are very asymmetric and in fact are plus–minus interactions with the focal prey losing and the alternative prey benefiting. Importantly, the sign of the interaction is very much determined by features of the habitat and the spatial scale at which predators aggregate in relationship to prey, because it is only at this scale where the plus–minus interaction might occur (Östman and Ives 2003).

Taken altogether, we see that positive interactions between insect herbivores share many features in common with competitive interactions (Denno *et al.* 1995, Kaplan and Denno 2007). First, they occur frequently in many habitats and involve herbivores from diverse taxa and not simply close relatives. Moreover, both positive and negative interactions are often mediated indirectly by plants or natural enemies, and they are usually quite asymmetric with one of the interacting players receiving most of the benefit. It is an encouraging sign that positive interactions are finally finding their way into the theoretical literature on niche relationships and community ecology (Bruno *et al.* 2003) and that the fraction of empirical studies investigating facilitation between insect herbivores is increasing as well (see Kaplan and Denno 2007).

5.6.2 Positive interactions in detritivores and predators

A major role of shredders in stream ecosystems is the conversion of large organic plant material such as leaf litter into smaller particles. These finer particles generated by shredders make up a significant component of the food resource base for the stream invertebrate functional group termed collectors

(Cummins *et al.* 1989, Merritt and Cummins 1996). Thus, by breaking detritus into smaller fragments, shredders condition food and make it available for collectors. The stonefly, *Pteronarcys californica*, for instance, shreds alder leaves, making this food resource available to collectors such as larvae of the caddisfly, *Hydropsyche californica*, and the blackfly, *Simulium arcticum* (Short and Maslin 1977). Using radiolabelled phosphorus, the collectors accrued far more of the label when the shredder was present than when it was absent, suggesting that the stonefly facilitated nutrient uptake. The conditioning of detritus and leaf fall by shredders and microbes is thought to have positive effects, not only on collectors, but on the diversity and functioning of aquatic ecosystems at large.

Aquatic systems also provide an excellent example of facilitation between predator species (Soluk and Collins 1988a,b, Soluk and Richardson 1997). Predaceous stoneflies (*Agnetina capitata*) drive mayfly naiads (*Baetis tricaudatus* and *Ephemerella subvaria*) from the undersurface of stones and into exposed situations where they are more susceptible to fish predation and where fish benefit. In stream channels with large predaceous stoneflies, trout gain body mass, whereas in channels without stoneflies fish lose weight. Positive predator–predator interactions occur in terrestrial environments as well (Losey and Denno 1998). When the ladybird *Coccinella septempunctata* forages in the canopy of alfalfa, it triggers an alarm response in pea aphids causing them to drop to the ground into the awaiting jaws of ground-foraging predators like the carabid beetle, *Harpalus pennsylvanicus*. Predation rate on the aphid population increases and the carabids benefit with an enhanced food supply. Moreover, the strength of the synergistic interaction is density dependent, increasing with prey density. Such synergistic interactions occur when the foraging activity of one predator species alters the behavior or feeding niche of the prey, making it more susceptible to attack by another predator species. As for insect herbivores, most instances of positive interactions involving detritivores and predators are overwhelmingly asymmetric with one predator reaping most of the benefits.

5.7 Call for broader theory

Until recently, ecology texts have emphasized interference and exploitative interactions as two direct mechanisms driving competition. However, indirect interactions mediated by host plants and natural enemies provide the vast majority of evidence (>65%) underlying interspecific interactions between insect herbivores (Kaplan and Denno 2007). Moreover, almost all studies of interactions between insect herbivores, plant-mediated or otherwise, involve pairwise assessments (reviewed in Denno *et al.* 1995, Nykänen and Koricheva 2004, Kaplan and Denno 2007). There are only a few studies that have considered multiple species interactions among the major co-occurring herbivores in any one system and most of these are very focused on plant-mediated effects and far fewer on enemy-mediated interactions (Hunter 1992a,b, Agrawal 2000a, Van Zandt and Agrawal 2004b, Ohgushi 2005, Ohgushi *et al.* 2007). Despite the daunting experimental challenge, we must move beyond simple pairwise assessments to a broader approach that includes not only interactions with multiple herbivores, but also considers indirect effects and both negative and positive interactions. Because much of the discrepancy between the predictions of niche theory and patterns of resource use by organisms involves indirect interactions mediated by plants and enemies, it becomes all the more important to determine when and where the expectations of competition and niche theory are realized.

Applications

Humans and insects as competitors

Knowing that taxonomically discrepant organisms can compete intensely for shared resources, it should come as no surprise that insects and humans also compete. This occurs when insects use resources that humans require (food and timber) and when humans destroy insect requisites (habitats, food and breeding sites). Thus, in today's world there is a continuum of "competitive interactions" ranging from insect control in agricultural cropping systems, where we hope to gain the competitive edge via pest management, to insect conservation in disturbed natural habitats, where we aim to deter the exclusion of endangered species.

A classic example of reciprocal competitive interactions between insects and humans involves the Rocky Mountain locust, *Melanoplus spretus* (Orthoptera: Acrididae) (Lockwood 2004). This locust developed massive swarms in the western states of Nebraska, Kansas and Utah during the 1870s. One swarm in 1874 was estimated to contain 12.5 trillion locusts weighing 27.5 million tons and covering 198 000 square miles, an area greater than California. Needless to say, there was widespread crop devastation and famine in the local farming communities. Locusts had outcompeted humans for shared crop resources! Not more than 30 years later, however, the locust was extinct, evidently because critical habitat for oviposition in the soil had been plowed under by farmers. "Just a small contingent of settlers equipped with horse-drawn plows and simple implements effectively eliminated the locust across the continent transforming the fertile river valleys of the Rockies" (Lockwood 2004, p. 257). Without realizing the impact of our farming activities we had caused the extinction of a species. The lesson to be learned here is that even very prolific insects can be driven to extinction when their habitats are destroyed or fragmented as a consequence of human activities (see Samways 2005). We will explore the consequences of habitat destruction, fragmentation and loss more in forthcoming chapters on community ecology and biodiversity (Chapters 12 and 14 respectively).

On a more positive note, understanding how agricultural and forest pests affect each other's density via either induced resistance or susceptibility may become important for developing contemporary pest-management programs, ones that focus on reducing pesticide use. For instance, we may be able to use elicitors like jasmonic acid that are involved in induced resistance between insect herbivores as management tools to control pests in agricultural crops (Thaler 1999a,b, 2002a, Kessler and Baldwin 2002). Also, we may be able to set more realistic **economic thresholds** (the pest density at which a control decision is made) by knowing more about plant-mediated herbivore interactions. For example, knowing that potato leafhoppers (*Empoasca fabae*) induce changes in potato plants that make them more resistant to Colorado potato beetles (*Leptinotarsa decimlineata*) should raise the economic threshold for leafhoppers. In other words, more leafhoppers should be tolerated because of their adverse competitive effect on beetles which also damage plants and reduce tuber yield (Lynch *et al.* 2006, Kaplan *et al.* 2007, 2008c).

At higher trophic levels, how multiple species of predators and parasitoids interact bears heavily on their effectiveness in biological control programs (Rosenheim *et al.* 1995, Losey and Denno 1998, Bográn *et al.* 2002, Finke and Denno 2004). Competitive interactions among natural enemies can decrease their overall impact on target pests resulting in crop loss. On the other hand, if predators facilitate each other's attack of prey, pest suppression can be enhanced. Moreover, negative interactions (intraguild predation) and positive ones (facilitation) among natural enemies can have dramatic consequences for food-web dynamics and community structure. Nowhere is this more evident than in invaded natural habitats where predator incursions (e.g., introduced ants and ladybird beetles) result in the competitive annihilation of native natural enemies with drastic consequences for community structure (Holway 1999, Reitz and Trumble 2002, Van Rijn *et al.* 2005). We will discuss these issues to a far greater extent in forthcoming chapters on predator–prey, host–parasite and food-web interactions (Chapters 7, 8 and 13). We will also consider how plant resources, lateral effects such as competition and natural enemies interact to affect the structure and dynamics of arthropod-based communities (Chapter 12). For now, suffice it to say that there is widespread evidence for competition and facilitation in insects at all trophic levels.

Summary

Lateral interactions in communities covered in this chapter include competition, amensalism and facilitation. Competition may be intra- or interspecific, and involve scramble or contest competition, with the possibility that species with similar niches may compete until one species is displaced or excluded from much of its niche space. Competition has been modeled with the Lotka–Volterra equations with a stable equilibrium in two-species interactions possible when interspecific interactions are weaker than intraspecific competition, often achieved by niche divergence or resource partitioning, with species packing resulting in narrowed niches. But assumptions in basic competition theory are commonly not found to apply in the natural world, for example coefficient "constants" are variable, and much competition is asymmetric or amensalistic. Also, much competition is indirect, being mediated through effects on plant defenses in the form of induced resistance, or through differential impact of natural enemies on two competing species. In general, there is great variation in competitive interactions among insect herbivores, with studies needed to reach understanding on where and when competition is most likely to be observed. Competition also occurs commonly in omnivores, detritivores, carrion feeders, predators, parasitoids and parasites. Among predators intraguild predation is common, representing an extreme case of interference competition, and as with herbivores, mediation of competition by upper and lower trophic levels has been documented frequently.

Facilitation among members of the same trophic level is not as common apparently as competition, and among herbivores it is often mediated through effects on the food plant by one species, which improves conditions for another species: an indirect interaction. Induced effects include phytochemicals and plant architecture, and are asymmetric interactions in many cases. In fact, indirect interactions in competition and facilitation have been found to be more common than direct interactions, with host plants and natural enemies implicated as the mediating agents. Discovering generalities relevant to these interactions remains a challenge.

Insects compete with humans for food, forage and fiber, with humans causing extinction of certain species while protecting others through conservation practices. Inducing plant resistance and the application of biological control provide methods for mitigating insect pest attack on resources produced to benefit humans.

Questions and discussion topics

1 In a natural community how would you evaluate the frequency of important interactions discussed in this chapter, as well as the frequency of no interaction between species? If you erected an hypothesis on the rank order of interaction frequencies, how would you state this hypothesis?

2 Discuss the role of simple models, such as the Lotka–Volterra model, in the conceptual development of a field, including both advantages and disadvantages.

3 This chapter records the changing opinions on the role of competition in communities through time, indicating the roles of debate and evidence in the progress of science. Would you consider that this debate is resolved or are there opportunities for refining conclusions?

4 When you consider cooperation and facilitation among social insects and breeding pairs discussed in earlier chapters, does this modify your perception of the relative importance of competition and facilitation in natural communities?

5 How would you rank competition among humans and insects for agricultural and forestry products in a list of other threats in agriculture and forestry, such as drought and other effects of global change?

Further reading

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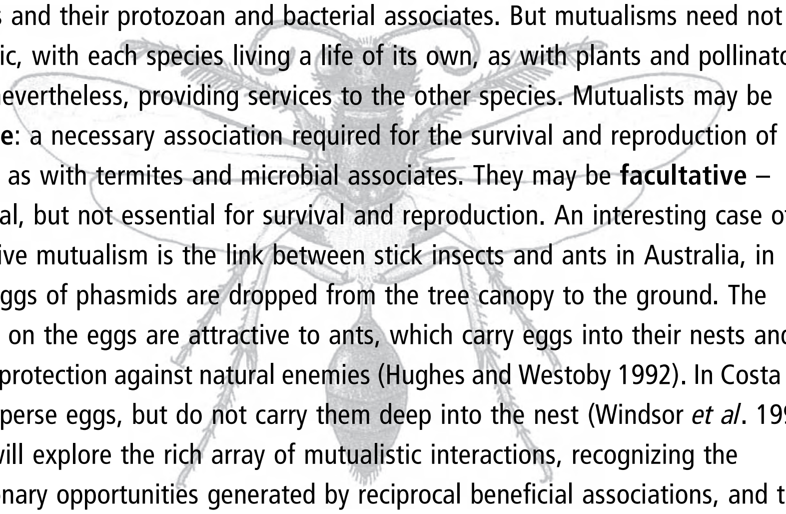
Kaplan, I. and R. F. Denno. 2007. Interspecific interactions in phytophagous insects revisited: a quantitative assessment of competition theory. *Ecol. Lett.* **10**:977–994.

Reitz, S. R. and J. T. Trumble. 2002. Competitive displacement among insects and arachnids. *Annu. Rev. Entomol.* **47**:435–465.

Strong, D. R., D. Simberloff, L. G. Abele and A. B. Thistle, editors. 1984. *Ecological Communities: Conceptual Issues and the Evidence*. Princeton, NJ: Princeton University Press.

6

Mutualisms



Mutualism is the association of two species, which is beneficial to both: a plus–plus relationship (see also Bronstein *et al*. 2006). Such species may live in close association through much of their lives, in which case the relationship qualifies as **symbiotic mutualism.** Some would argue that symbiosis involves the physiological integration between partners, but this criterion is not employed in most of the ecological literature. Examples include the many cases of microbial symbionts of insects, as in termites and their protozoan and bacterial associates. But mutualisms need not be symbiotic, with each species living a life of its own, as with plants and pollinators while, nevertheless, providing services to the other species. Mutualists may be **obligate**: a necessary association required for the survival and reproduction of a species, as with termites and microbial associates. They may be **facultative** – beneficial, but not essential for survival and reproduction. An interesting case of a facultative mutualism is the link between stick insects and ants in Australia, in which eggs of phasmids are dropped from the tree canopy to the ground. The capitula on the eggs are attractive to ants, which carry eggs into their nests and to greater protection against natural enemies (Hughes and Westoby 1992). In Costa Rica ants disperse eggs, but do not carry them deep into the nest (Windsor *et al*. 1996).

We will explore the rich array of mutualistic interactions, recognizing the evolutionary opportunities generated by reciprocal beneficial associations, and the many forms of mutualism involving insects. Then we will enter into the subject of the inevitable costs and benefits of these associations, and cheating the system. Mutualistic relationships have resulted in major adaptive radiations, which we explore with several examples, and then move on to approaches to modeling and how beneficial relationships may become complex and central to community organization, as well as in the practice of agriculture.

6.1 Mutualism as a creative evolutionary force

There can be little doubt that mutualism is among the most creative forms of interaction in nature. As an evolutionary force, the coupling of two species into a beneficial bond becomes a saltational event, frequently allowing, and enabling, a leap into a new adaptive zone, and the exploitation of novel ecological niches. Consider the evolution of the eukaryotic cell, formed by the community of mutualistic prokaryotic species, and the abundance of life derived from these unions (e.g., Lee and Frederick 1987, Margulis 1993, Margulis and Fester 1991, Sapp 1994, Werner 1992, Cavalier-Smith 1987, 2006). Union of prokaryotic cells resulted in “momentous quantum evolutionary episodes of cellular innovation” (Cavalier-Smith 2006, p. 969). Purple bacteria, using respiration as an energy source, colonized a prokaryotic cell to form mitochondria in the eukaryotic cell. In a similar manner, cyanobacteria capable of photosynthesis colonized protist cells which enabled photosynthesis in the eukaryotic cell and the evolution of plants (Figure 6.1).

The creative opportunities provided by mutualism have only expanded since the evolution of the eukaryotic cells. Four new kingdoms of organisms have emerged: protozoa and other Protoctista, plants, animals and fungi (e.g., Margulis 1993), and members of these kingdoms have combined in mutualistic associations with far-reaching consequences, enabling the emergence of large plants – herbs, shrubs and trees – and large animals (Figure 6.1, Price 1991c, 2002a). Large plants could evolve in association with mycorrhizae, pollinators and seed dispersal agents, and large animals depend on large plants for food, with many sequestering microbial digestive agents in rumens or caecae. Even humans enjoy mutualisms with many bacteria in their intestines (Bäckhed *et al.* 2005), and as probably with insects, the **microbiome** may contain 50–100 times more genes than the human genome (Dillon and Dillon 2004). Species themselves should be considered more as ecosystems, than as single individuals or species.

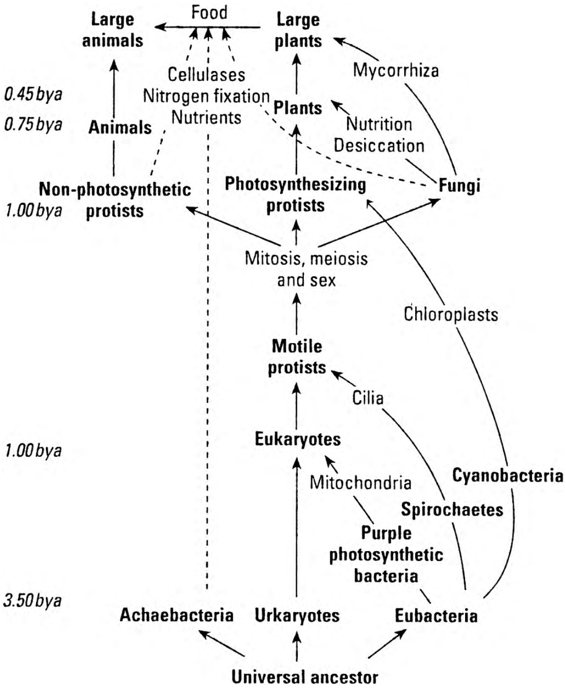


Figure 6.1 An overview of symbiotic interactions through the last 3.5 billion years, which have resulted in major breakthroughs in the development of organismal complexity and ultimately in the emergence of large plants and animals. Bold type indicates major taxonomic groups of organisms. Solid lines and arrows indicate links among evolutionary steps. Dashed lines show utilization of ancient organisms as mutualists enabling exploitation of plants by large animals such as insects and mammals. Light lettering shows the contributions made by various taxa in the evolution of biotic complexity. For example, the Archaebacteria provided methanogenic bacteria, which are critical for digestion in the gut of ruminant animals, and protozoa and bacteria are essential in the breakdown of cellulose in the termite diet. Based on Price 1991c, from Price 2002a.

6.2 The variety of mutualistic interactions

Insects have benefited from mutualistic associations as much as any other group, and perhaps more. For example, insects have radiated into incredibly diverse adaptive zones, frequently utilizing nutritionally inadequate resources such as blood (sucking lice), or plant sap (aphids), or highly refractive substrates, such as cellulose in wood (termites), and keratin in wool, antlers, horns and tortoise carapaces (e.g., Deyrup *et al.* 2005). Clothes moths and trogid beetles are assumed to require mutualistic species, but this is not yet described in the literature, although tineids are known to utilize keratin in which fungi occur (Robinson 2004). It is interesting to note that feeding on fungi is widespread in the Tineoidea and perhaps it is a ground-plan character of the group (Robinson 1981), indicating a long-term association with fungi that can digest material in rotting logs and keratin of various sorts (Robinson 2004).

In fact, we see in Table 6.1 that the range of mutualistic types involving insects is bewilderingly diverse. One estimate of the frequency of mutualism suggested that 45% of insect species in the British Isles are likely to participate (Price 1984b, 1997). However, including insect species that are impacted by mutualism involves many additional species, either directly (as in Table 6.1), or indirectly through the evolution of the angiosperms, or the influence of mycorrhizas on host plants of herbivores, or the radiation of the herbivorous mammals. Thus, major adaptive radiations, such as the flowering plants (angiosperms) or the herbivorous mammals (artiodactyles, perissodactyles, lagomorphs, rodents, etc.) created new resources on which insects themselves could radiate.

There are many ways to categorize and classify mutualistic associations, but we have chosen to emphasize ecological relationships, dividing them into three major kinds. There are **exploitative mutualisms**, or **nutritional mutualisms**, in which, by acquisition of a mutualist, an insect gains the ability to exploit a new resource, from which a novel adaptive radiation may develop. Here the nutritional value of the food source is incomplete, with obligate microbial symbionts providing additional micronutrients (Table 6.1). Or an additional resource is provided, sufficiently valuable to reinforce mutualistic associations, such as sap-sucking insects excreting honeydew, which is utilized as an energy source by tending ants (Table 6.1). Then there are **protective mutualisms** in which plants may provide a protected domicile, such as stems or thorns for ants to nest in, ants that protect sucking insects from natural enemies, or microbes that provide antibiotics for their larger partner, as in polydnaviruses (PDVs) in ichneumonid and braconid wasps (see Chapter 8). In this kind of classification one mutualism may confer two kinds of benefit, as is often the case. For example, aphids provide a new resource for ants in the form of honeydew, and this constitutes an exploitative mutualism for ants, while at the same time ants protect aphids from attacks by predators and parasitoids – a protective mutualism for aphids.

A third kind of mutualism involves the dispersal of propagules such as seeds and fruits (together termed **diaspores**, meaning units of dispersal), the transmission of pollen from one plant to another thereby providing pollination services, or the dispersal of mutalistic mites from one resource to another by larger insect associates (Table 6.1). Such mutualisms can be called **dispersal/transmission mutualisms**, or **transportation mutualisms**. The value of pollination of crops by native (wild) bees in the United States alone is estimated at over $3 billion annually (Losey and Vaughan 2006), providing a glimpse of their probable ecosystem value in natural vegetation (see also Kremen and Ostfeld 2005).

Another category could be added to Table 6.1, namely indirect mutualisms, or complex interactions involving mutualists, but this addition would have to cover an enormous range of phenomena. For example, mycorrhizal fungi have direct effects on the plant associate, but they may alter plant quality, which impacts herbivores and even higher trophic levels (e.g., Gange *et al.* 2003). We will discuss this subject in greater depth later in this chapter, and in Chapter 13 on multitrophic interactions. However, it is worth keeping in mind the inevitable consequences

Table 6.1 **Examples of mutualistic associations involving insects: an ecological perspective**

Services provided by partner	Services provided by insect	Insect taxon	Partner taxon	References
A. Exploitative mutualisms – new resources exploited by insects				
1. Nutritional value of food improved				
(a) Improved nutrition of blood	Transport, inoculation, domicile	sucking lice, bed bugs, tsetse flies, triatomines, hippoboscids, nycteribiids	microbial species	Chapman 1998, Durvasula *et al.* 2003, Aksoy 2003
(b) Digestion and nutrition of keratin, wool, feathers, skin	Transport, inoculation, domicile	chewing lice, clothes moths, trogid beetles	microbial species ?	An assumed association, Robinson 2004
(c) Improved nutrition of plant sap	Transport, inoculation, domicile	thrips, cicadellids, psyllids, coccids etc.	microbial species	Douglas 2003, Vega and Dowd 2005
(d) Improved nutrition of seeds	Transport, domicile	rice weevil	microbes	Nardon and Grenier 1991
(e) Improved nutrition of fruits	Transport, inoculation	tephritid flies	bacteria	Lauzon 2003
2. New resources made available				
(a) Digestion of wood and cellulose	Transport, inoculation, domicile	longhorns, ambrosia beetles, wood wasps, roaches, termites etc.	fungi, yeasts, bacteria	Martin 1987, Six 2003, Suh and Blackwell 2005, Harrington 2005
(b) Digestion of plant parts	Domicile, culture, transport	leaf-cutter ants, termites	fungi	Currie 2001, Aanen and Boomsma 2005, Schultz *et al.* 2005
(c) Nectar and pollen	Transport of pollen, pollination	moths, butterflies, bees, ants	plants	Bentley and Elias 1983, Rico-Gray and Oliveira 2007
(d) Extra-floral nectar	Protection of supplier	ants, parasitoids	plants	Bentley and Elias 1983, Oliveira and Oliveira-Filho 1991

Table 6.1 (*cont.*)

Services provided by partner	Services provided by insect	Insect taxon	Partner taxon	References
(e) Sugar secretions and excretions	Protection of supplier	ants, parasitoids	hemipterans	Beattie 1985, Styrsky and Eubanks 2007
(f) Resins, oils, waxes, fragrances	Pollination	bees	plants, orchids, euphorbs	Steiner and Whitehead 1990, Armbruster 1996
B. Protective mutualisms – Insects protect plants and other insects				
(a) Domicile, food	protection against herbivores	ants	acacias, cecropia melastomes	Janzen 1966, 1967a,b, Davidson *et al.* 1991, Beattie and Hughes 2002
(b) Domatia	Protection against herbivores	predatory mites	plants	Walter and O'Dowd 1992a,b, Walter 1996
(c) Honeydew	Protection against enemies	ants	hemipterans	Beattie 1985, Beattie and Hughes 2002
(d) Sugary secretions	Protection against enemies	ants	lycaenid larvae	Pierce 1989, Pierce *et al.* 2002
(e) Extrafloral nectaries etc.	Protection against herbivores	ants	plants	Wäckers *et al.* 2005, Rico-Gray and Oliveira 2007
(f) Suppress host immune response	Domicile, transport, infection, inoculation	parasitoids: braconids, ichneumonids	virus particles	Schmidt *et al.* 2001
(g) Removal of competitors	Transport among resources	burying beetles	predaceous mites	Wilson 1983
C. Dispersal/transmission mutualisms – insects disperse propagules, pollen, spores				
(a) Elaiosomes as food	Transport, dispersal, protection against predators	ants	many plants	Sernander 1906, Beattie 1985, Heithaus *et al.* 1980, Beattie and Hughes 2002, Rico-Gray and Oliveira 2007

Table 6.1 (*cont.*)

Services provided by partner	Services provided by insect	Insect taxon	Partner taxon	References
(b) Pollen and/or nectar as food	Pollination	bees, butterflies, moths flies, beetles, ants	plants	Faegri and van der Pijl 1971, Proctor and Yeo 1973, Lloyd and Barrett 1996
(c) Spores as food	Transport of spores	flies	mosses, fungi	Bequaert 1921, Erlanson 1930, Alexopoulos 1952, Parker and Bultman 1991, Marino 1991
(d) Seeds as food	Pollination	fig wasps, yucca moths, senita moth etc.	figs, yuccas, senita cactus	Fleming and Holland 1998, Pellmyr 1989, Pellmyr *et al.* 1996a,b, Bronstein 1992
(e) Contaminant removal from nest	Transport	bees	mites	Eikwort 1994
(f) Fruits as food	Transport	ants	plants	Beattie 1985

of mutualistic interactions for other species co-occuring in the same habitat. For example, ants protect aphids against predators and parasitoids, while receiving honeydew as a reward, but the ants may also protect the plant from other herbivores such as leaf beetles and caterpillars (e.g., Laine and Niemelä 1980, Ohgushi 2005, Ohgushi *et al.* 2007). Thus, there is a network of indirect links involving mutualists, food resources and non-feeding interactions, such as providing domiciles or protection, resulting in community structures that are complex and inadequately studied (Ohgushi 2005, Ohgushi *et al.* 2007).

6.3 Mutualism and the evolution of biodiversity

Mutualism is implicated in practically every major step in evolutionary history. Even among the bacteria, and before eukaryotic cells evolved, there were undoubtedly beneficial associations developed in stromatolites, bacterial crusts and other kinds of communities on soil, rock faces and aquatic surfaces. (Stromatolites are many-layered microbial mats forming stable, sedimentary, boulder-like structures in marine environments.) In these interactions one species provided services to another, such as plasmids, which provide mutualistic services to bacteria today (e.g., in the crown gall bacterium), and cooperation was no doubt frequent as it is today in biofilms (e.g., Webb *et al.* 2003, Brockhurst *et al.* 2006, Hansen *et al.* 2007). Once photosynthesizing protists evolved they are thought to have combined with fungi to produce green plants (Figure 6.1): the fungal associate foraged for nutrients and water in the soil, while the alga provided photosynthate and protection against desiccation above ground. Moreover, the first fossil plants were associated with endophytic fungi, which are likely to have been precursors of mycorrhizas today. Thus plants evolved more as ecosystems rather than individual species because of the symbiosis involving the eukaryotic cell, photosynthesizing cyanobacteria, fungi in the thallus of the plant and mycorrhizas adding to the nutrition of plants as they became larger (Figure 6.1).

6.3.1 Herbivore radiations

Once plants had evolved and grown in stature, they formed the resources for herbivore radiations (Price 2002a). The initial problem was that animals and plants have very different structures and chemistries (e.g., C:N ratios), making plants nutritionally poor resources for animals (see Chapter 4). The solution in many cases was for herbivores and detritivores to acquire mutualistic symbiotic bacteria, protists or fungi, preadapted over long periods of evolutionary time to digest plant parts and to synthesize nutrients deficient in plants or detritus. And this is the way in which the adaptive radiations of insect herbivores became so successful. Many insects feeding on nutritionally deficient plant sap are associated with mutualistic symbionts – up to seven species in some cases (Buchner 1965) – including leaf hoppers, aphids, tree hoppers and jumping plant lice (Moran and Telang 1998, Table 6.1). Many wood-associated herbivores depend on fungi and other symbionts for their ability to digest cellulose: longhorn beetles, ambrosia beetles, lucanid and passalid beetles, siricid wasps, termites and wood roaches (Table 6.1). Additional evolutionary innovations have been to use fungi as pathogens which reduce the vigor of trees, or to kill them, thus opening up breeding sites for bark beetles (Beaver 1989, Webber and Gibbs 1989), or to carry fungi from plant to plant in cecidomyiid gall-inducing insects, with the fungal associate providing food for the developing fly larva (Bissett and Borkent 1988).

In these ways plant-based communities have developed, which involve adaptive radiations of species assemblages, more like ecosystems rather than individual species (Price 2002a, Figure 6.2). Even large animals can exploit nutritionally inadequate green plants with the aid of fermenting bacteria and protozoa, such as ruminants as depicted in Figure 6.2, and those with caecal fermentation such as horses, rabbits and hares.

6.3.2 Carnivores with mutualists

But, in the building of food webs, mutualistic associations do not stop with the herbivores. Carnivores also depend on mutualistic microbes in many ways (Table 6.1). These include:

(1) Blood feeders such as sucking lice, bed bugs and tsetse flies, in which microbes provide supplemental nutrients for insects feeding on a relatively homogeneous resource – also hippoboscids, nycteribiids and triatomines like *Rhodnius*. Not included are fleas, mosquitoes and horseflies, whose larvae feed aquatically or on detritus on nutritionally more diverse resources.
(2) Insects that feed on homogeneous or nutrient-poor substrates such as dead skin and keratin (as in horn and wool), which can be exploited probably only with the aid of mutualists (e.g., chewing lice, clothes moths).
(3) Parasitic carnivores on insects which depend on microbial mutualisms to aid in overcoming the defenses of their hosts, as in parasitic wasps and virus particles, or in protecting the host from invading bacteria or fungi, as in nematodes with symbiotic bacteria on scarabaeid larvae (Figure 6.2).

In addition to microbial symbionts, insects themselves may become mutualistic with carnivorous insects.

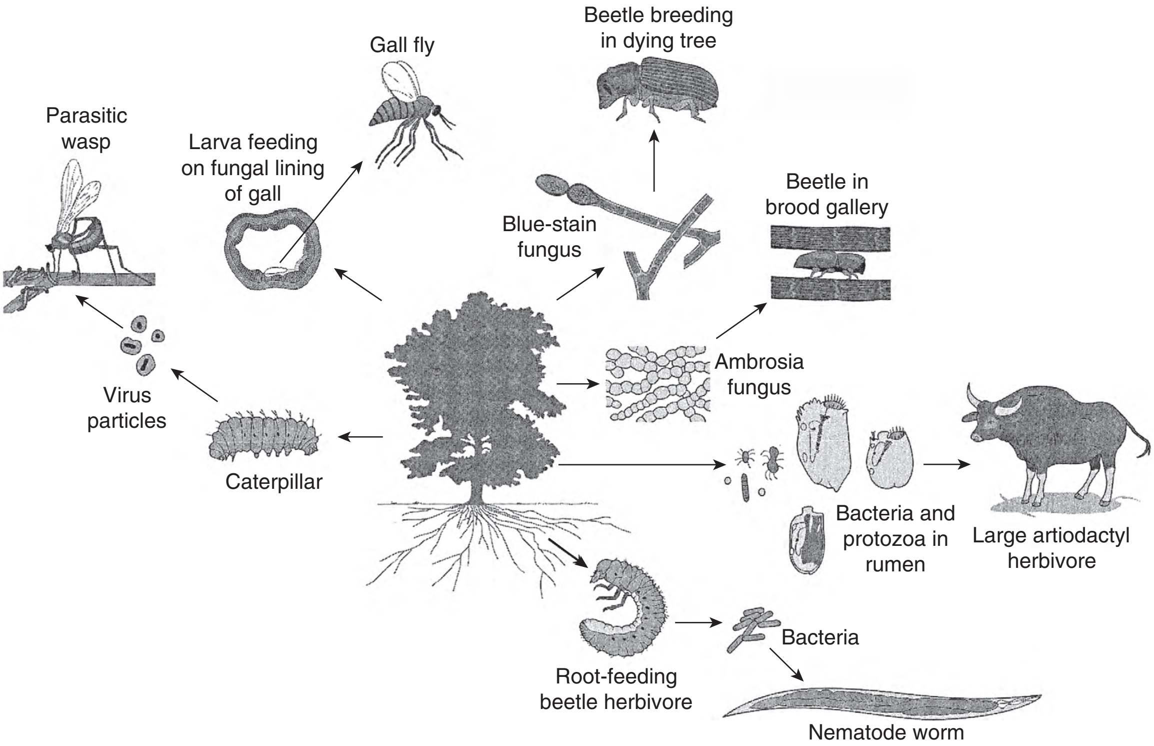


Figure 6.2 Examples of mutualistic and antagonistic interactions which may be found in a community, showing how antagonists of plants and herbivores rely on mutualistic viruses, bacteria, protozoa and fungi as intermediaries. For example, ambrosia fungus makes possible wood (cellulose) digestion and provides otherwise unavailable nutrients for ambrosia beetles (upper right). Bark beetles carry blue-stain fungus, inoculating the tree with pathogenic killers, thereby rendering the tree a suitable breeding site while it dies. Gallmidges also inoculate the host plant with fungi, which become the food source for larvae within the gall. The large artiodactyls, such as antelope, deer, goats and sheep, all depend upon the rumen, a large fermentation chamber containing bacteria and protozoa with cellulases responsible for the digestion of refractive plant material. At the third trophic level, herbivore resistance to parasitoid eggs and larvae is suppressed by inoculated virus particles, and root-feeding scarabaeid larvae have bacteria introduced by a parasitic nematode worm, making the host toxic to competitors. Every food web and ecosystem is likely to be equally populated with such a complexity of mutualistic associations. From Price 2002a.

For example, herbivore products, such as honeydew from aphids and tree hoppers, and sugary secretions from lycaenid caterpillars, also provide nutritional supplements to the generally carnivorous ants (Tables 6.1, 6.2, Styrsky and Eubanks 2007).

It becomes apparent, albeit rather slowly because so many associations are subtle and cryptic, but nevertheless convincing, that mutualisms play vital roles in communities and ecosystem functions, and in the evolution of biodiversity (Quek *et al.* 2004, Eastwood *et al.* 2006). Many ecological and evolutionary opportunities and pathways have been opened up by association of one species with another, with each providing novel resources to the other. This is particularly evident when apprehending the larger picture, although delivered piecemeal in Table 6.1. This complexity results because food webs expand as opportunities provided by mutualisms enable more associations, richer communities and more complex ecosystem functions.

Table 6.2 **Examples of mutualistic interactions involving insects in which benefits and/or costs have been explored**

	Category of mutualism and species	Examples of benefits and/or costs	References
A.	Ants and plants		
	(a) General	Reduced leaf damage and vine overgrowth/ extrafloral nectar, food bodies	Bronstein 1998
	(b) *Solenopsis* ants/ fishhook barrel cactus	Increased fruit set/extrafloral nectar	Morris *et al.* 2005
	(c) Ants in general/ *Chamaecrista*	Reduced herbivory (slight)/extrafloral nectar	Rutter and Rausher 2004
	(d) *Forelius* ants/wild cotton	Reduced herbivory, and higher seed production in some populations/extrafloral nectar	Rudgers and Strauss 2004
B.	Pollinators and seed predators		
	(a) *Perizoma* moth/*Silene dioica*	Pollination/seed predation	Westerbergh 2004
	(b) *Liporrhopalum* fig wasps/*Ficus*	Pollination/seed predation	Moore *et al.* 2003
	(c) Fig wasp spp./*Ficus* spp.	Pollination/seed predation	Jousselin *et al.* 2003
	(d) Yucca moths/*Yucca* sp.	Pollination/seeds for larvae, low costs in time, adaptations, and pollen load	Pellmyr 1997
C.	Ants and lycaenid larvae		
	(a) *Iridomyrmex* ants/*Jalmenus* lycaenid	Reduced natural enemies/reduced pupal and adult weights	Pierce *et al.* 1987, Pierce 1989
	(b) Ant spp./*Hemiargus* lycaenid	Reduced parasitoid attack	Weeks 2003
	(c) Ant spp./*Glaucopsyche* lycaenid	Protection against enemies/increased nutritious secretions and tentacle displays (Figure 7.5)	Axén 2000
D.	Ants and hemipterans		
	(a) *Formica* ants/*Tuberculatus* aphids	Increased longevity of colony/smaller body size and fewer embryos	Yao *et al.* 2000
	(b) Ants/hemipterans, general view	Protection against enemies, higher or lower weights and fecundity, longer development	Stadler *et al.* 2001

Table 6.2 (*cont.*)

	Category of mutualism and species	Examples of benefits and/or costs	References
	(c) *Lasius* ants/*Aphis* aphids	Costs: longer development, later progeny production, fewer embryos etc.	Stadler and Dixon 1998
	(d) Tropical ants/ hemipterans	Ants benefit from plant and insect exudates	Davidson *et al.* 2003
	(e) Tropical ants/ hemipterans	Variable benefits and costs because of variable densities of herbivores (coccids and pseudococcids)	Lapola *et al.* 2005
E.	**Insects and fungi**		
	(a) *Ips pini* bark beetle/ *Ophiostoma* fungus	Increased brood production/reduced colonization of trees	Kopper *et al.* 2004
	(b) *Phorbia* fly/*Epichloe* fungus	Transport of spermatia/consumption of hyphae and ascospores	Parker and Bultman 1991

6.3.3 A trophic-level perspective

Taking a trophic-level approach, plants have mutualists such as ecto- or endomycorrhizas, and other endophytic fungi (e.g., Clay 1988, Arnold and Lewis 2005), any of which may influence the quality of food for insect herbivores, so effects cascade up to higher trophic levels where herbivores may be positively or negatively affected (e.g., Gehring and Whitham 2002, Gange *et al.* 2003). Also, plant food is so poor relative to insects' nutritional requirements, that mutualists generally provide essential enzymes or nutrients, or they concentrate or recycle nitrogen (Chapman 1998, his Table 4.3). Plants also provide floral nectar, pollen and extrafloral nectar (Table 6.1). The herbivores, in turn, provide food for higher trophic levels, such as honeydew for ants, wasps and parasitoids, and sugary secretions from lycaenid butterfly larvae attractive to ants. Secretions by lycaenid larvae are frequently referred to as "honeydew." However, honeydew is "liquid discharged from the anus of certain Hemiptera" (Triplehorn and Johnson 2005, p. 786). Then the virtually ubiquitous ants affect other species in the system, attacking and removing many herbivores, while promoting the welfare of honeydew-excreting aphids, coccids and others. These kinds of interactions are present in many terrestrial ecosystems, but in the tropics additional linkages have evolved, with food bodies provided for ants by the plant genera *Acacia*, *Cecropia*, *Macaranga*, the melastome family and others, and ants and termites practicing agriculture with fungus gardens (Table 6.1). Ants' nests in turn alter nutritional substrates for plants, and ants carry seeds into and onto their nests, where germination and establishment is improved. "Ants create fertilized pockets of substrate that the plants locate by making their seeds and fruits attractive to ants" (Beattie 1985, p. 77). Termites, with their own symbionts, process vast quantities of plant materials, changing soil quality and nutrient status. And so, these ecosystem processes keep revolving in communities, with mutualistic associations a key to integrating the many species and interactions involved.

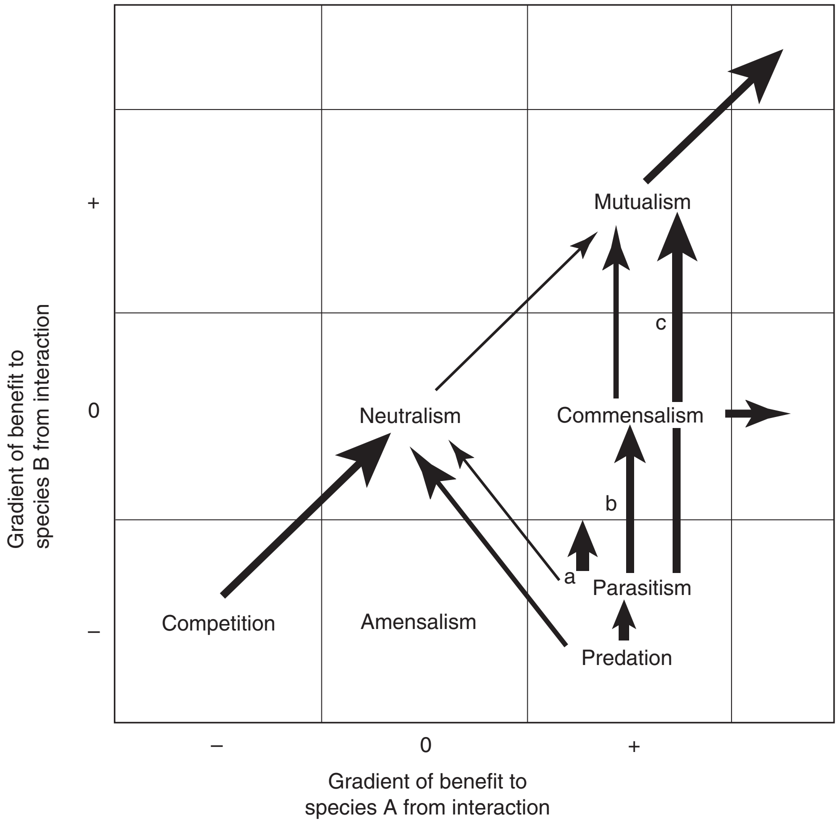


Figure 6.3 The possible relationships between two species, ranging from negative to positive, along hypothetical evolutionary pathways resulting in reduced negative effects. Width of arrows suggests the likelihood of transition from one type of interaction to another. Note that parasitism may evolve into: (a) reduced negative impact, (b) a commensal relationship or (c) a beneficial interaction. The arrow from mutualism beyond the ++ relationship simply suggests the evolution of stronger positive associations. From Price 1984b.

6.4 The origin of mutualisms

The evolution of mutualisms is not easy to study because the transition from two free-feeding species (that is individuals feeding alone without the aid of mutualists) into a mutualistic association is likely to be rapid when the selective advantages to both are great. However, we can speculate that antagonistic relationships such as competition (– –), or parasitism (+ –), are likely to be ameliorated by natural selection (Figure 6.3). In particular, parasites, already in a symbiotic relationship with their hosts, may benefit from the evolution of less pathogenic impact, with movement towards commensalisms, and ultimately mutualism (Price 1984b). Competitors are probably less likely to become mutualists because they utilize the same resource, so aiding each other is problematic. Mutualisms usually develop between organisms utilizing different resources; they are often on different trophic levels, and are taxonomically divergent, as illustrated in Figures 6.1 and 6.2.

Although we do not have an insect example of the observed transition from a parasitic symbiont to a mutualist, in a brief sequence of events, there is such an example between a protozoan and a bacterium.

Only 10 years elapsed before an *Amoeba* culture became fully reliant on a formerly parasitic bacterium, with cloning becoming impossible in the absence of the bacterium (e.g., Jeon 1972, Jeon and Ahn 1978). In another case a parasitic plasmid became a mutualist with a bacterium, *Escherichia*, in a short period of 50 generations (Bouma and Lenski 1988). The time periods involved in the transition from parasitism to mutualism in these cases are as a blink of an eye in relation to the evolutionary history of life in general, and such evolutionary opportunism and saltational adaptation is no doubt continuing unobserved in multitudes of cases today. Many examples have been noted in the literature where the shift from parasitism to mutualism has been suggested, such as mycorrhizas (Harley 1969), other endophytic fungi (Clay 1988), and herbivorous parasites (Westerbergh 2004).

6.5 The give and take in mutualism

Very little is free in nature – there is no free lunch. If an individual gains in fitness, there is usually an associated cost. In the case of mutualism this is particularly clear because of the mutual and reciprocal give and take involved.

6.5.1 Plants, pollinators and seed predators

An example of this gain and loss concerns the senita cactus, *Lophocereus schottii*, which is pollinated by the senita moth, *Upiga virescens* (Pyralidae), in the Sonoran Desert (Fleming and Holland 1998, Fleming 2002). The female moths collect pollen from the cactus on specialized abdominal scales and deliberately deposit pollen on the receptive stigma of the flower. Then the female lays a single egg on a petal. Larvae bore into the ovary and eat young seeds for 6 days, then they leave the ovary, bore into cactus stems and emerge as adults. The cactus is an obligate outcrosser, with reduced nectar production and a limited ability to attract other pollinators. The cactus receives very effective pollination (75% of fruits set in 1995, and 90% in 1996), but at a cost of larval destruction of about 30% of the seeds produced from pollination by senita moths. Although all seeds are consumed by a larva in an ovary, moths evidently pollinate several other flowers without laying eggs. However, many pollinated flowers are aborted resulting from limitation of resources such as water. Consequently, mortality of larvae may be an important regulating factor in the interaction (Holland *et al.* 2002).

For the energetic cost of pollinating flowers, the moth receives a reward of a nutritious food resource for its larvae. There is a net gain in fitness for each species because, in the absence of moths, pollination would be much less effective by default pollinators such as halictid bees, and net seed production would be lower. Thus, without providing the service of pollination, the pyralid would experience a much lower carrying capacity of ovules as larval food. Both cactus and pyralid populations would probably decline in the absence of the mutualism. This mutualism has been modeled by Holland *et al.* (2002), using the net functional responses of pollinator and flower number, incorporating costs and benefits to the interacting species. The results suggest that fruit abortion may enable equilibrium in the mutualism.

Features of the senita and senita moth system are similar to the yucca and yucca moth relationship studied by Pellmyr *et al.* (1996a,b), as pointed out by Fleming and Holland (1998):

(1) Resource-limited fruit set is apparent in both systems, with the limiting resource likely to be water.
(2) Flowers are obligately outcrossing and little nectar is produced.
(3) Flowers are short-lived and open nocturnally.
(4) Female moths collect pollen with specialized structures and deliberately transfer it to stigmatic surfaces of the flower.
(5) Alternative pollinators are unreliable or absent.
(6) Larvae destroy about 20–30% of seeds in a crop and yield a benefit:cost ratio from 2–5.

More recently, Fleming (2002) estimated that the benefit:cost ratio was about 3:1 in the senita mutualism, a ratio similar to that seen in other pollination mutualisms of yuccas and their moths and figs and their fig wasps.

We have mentioned three cases of more-or-less obligate pollinators whose larvae consume developing seeds: the senita cactus, yuccas and figs. We will expand on the yuccas and figs later in this section. A fourth case concerns the globe flower, *Trollius europaeus* (Ranunculaceae), and four fly species in the genus *Chiastocheta* (Diptera: Anthomyidae) (Pellmyr 1989). The flies are thought to be the exclusive pollinators of these globe-like flowers closed to other potentially pollinating species such as bees. The flies mate, feed on pollen and oviposit within the flower, and larvae eat a few seeds each. As in the other pollinator and seed-feeding mutualisms, seeds are the currency in which the benefits and the costs of larval feeding are measured. Hence, it is relatively simple to estimate benefits and costs, which explains why these systems, although uncommon in nature, have been featured in the study of mutualism. As the number of flies increases per flower, pollination increases so the seed initiation frequency increases (Figure 6.4). Also, the number of eggs laid per flower may increase, meaning that more seeds are consumed by fly larvae. However, neither trend is linear and relative seed set remains remarkably stable, around 36% over the range of egg densities per flower observed in nature (from about 2–7 eggs per flower, see also Jaeger *et al.* 2000). At the peak of relative seed set, with four eggs per flower, pollination services yielded a benefit of about 62% of ovules originally available in the ovary, and larval seed predation inflicted a cost of about 14% seed loss, leaving a net benefit of about 48% of seeds. This ratio of benefit to loss is therefore about 3.4:1, comparable to estimates mentioned above for other systems. Further studies have found that the interaction of host plant and pollinators/seed predators was always beneficial for the plant in 20 natural populations in France (Jaeger *et al.* 2001).

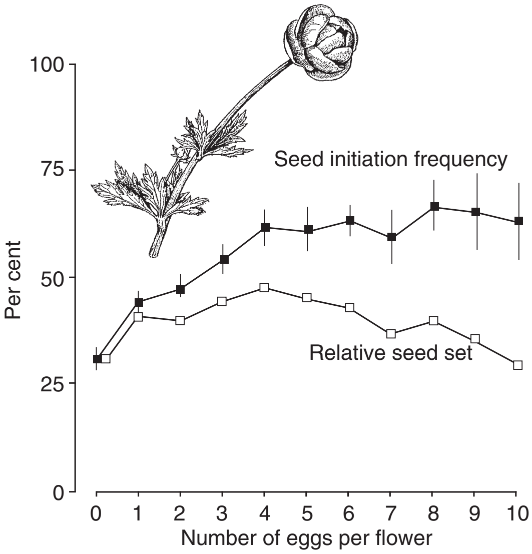


Figure 6.4 Estimates of the benefits and costs of pollination and seed predation in the globe flower, *Trollius europaeus*. The benefit of pollination is measured as seed initiation frequency, which depends on the number of eggs laid per flower by pollinating flies. The cost of pollination is estimated by the number of fly larvae and the average number of ovules eaten per larva, which reduces the number of viable seeds to the relative seed set level. From Pellmyr 1989.

Of course, both species in a mutualism experience costs, so selective conflicts emerge, with each species maximizing gains and minimizing losses. Such conflict was emphasized by Bronstein (1992, see also Anstett *et al.* 1996), in the fig and fig–wasp interactions, where she examined in detail how the evolutionary balance between participants could persist for so long. The pollinating wasp would appear to have an evolutionary advantage, passing through about 100 generations per single fig-tree generation. So, why doesn't the fig wasp evolve with a longer ovipositor, enabling it to reach and utilize more ovules as larval food? What countermeasures have evolved in the fig? Janzen (1983, p. 232) even called mutualisms "reciprocal parasitisms" because the negative effects of partners were more or less balanced. Let's examine the fig and fig-wasp relationship in more detail as it represents a classic case of mutualism.

Fig trees and fig wasps (From Price 1984b, 1997)

More than 900 species of figs (*Ficus*, Moraceae) have been recorded, which are pollinated by very specific wasps in the family Agaonidae (Chalcidoidea), the fig wasps. Many characters in both the figs and wasps show closely coevolved properties, and the two taxa have obviously radiated together as a result of the initial development of a mutualistic relationship (Bronstein and McKey 1989, Kjellberg *et al.* 2005).

The fig is a false fruit formed by the enlarged receptacle of the inflorescence. The flask-shaped fruit encloses a large number of flowers (Figure 6.5), and each inflorescence passes through the following stages (Galil and Eisikowitch 1968, Ramirez 1970, Wiebes 1979): *phase A – prefemale*, in which the inflorescence is closed to entry by fig wasps (Figure 6.6); *phase B – female*, in which the ostiolar scales loosen, female flowers ripen and agaonid wasp females penetrate the inflorescence and oviposit into the ovaries; *phase C – interfloral*, where wasp larvae develop in developing galls formed from the fig ovaries, and unattacked fig embryos develop; *phase D – male*, where male flowers mature, wasps reach maturity and emerge from galls, the males inseminate females and bore holes in the receptacle, the females collect pollen from the male flowers and emerge through the holes bored by males and fly to fig inflorescences in phase B, and *phase E – postfloral*, in which seeds ripen and the receptacle ripens, becoming attractive to fruit-eating animals, which disperse the seeds.

The life cycle of the fig wasps is also complicated, and only a general pattern is depicted here, as there is considerable variation between species. Before females leave the inflorescence in phase D, they load up with pollen, packing it into special receptacles on or near the coxae of the front legs and the abdomen. Then they exit from the inflorescence through holes bored by males, fly to figs in phase B on another tree, and enter the ostiole. On entry they lose their wings and part of their antennae. Males are wingless, and do not leave the fig fruit in which they developed. In the lumen of the fig, females pierce with the long ovipositor the stigmas of the flowers and the length of the styles, ovipositing in the ovary (Figure 6.7). After ovipositing in an ovary they pollinate the flower by scraping pollen out of the receptacle with their legs onto the stigmatic surface. They also pollinate flowers in which no wasp eggs are laid. Eggs hatch and larvae develop in the gall formed from ovary tissue. Males emerge before females, cut holes in the sides of ovaries, and inseminate the female inside the gall. Females then collect pollen and leave the fig, completing the life cycle.

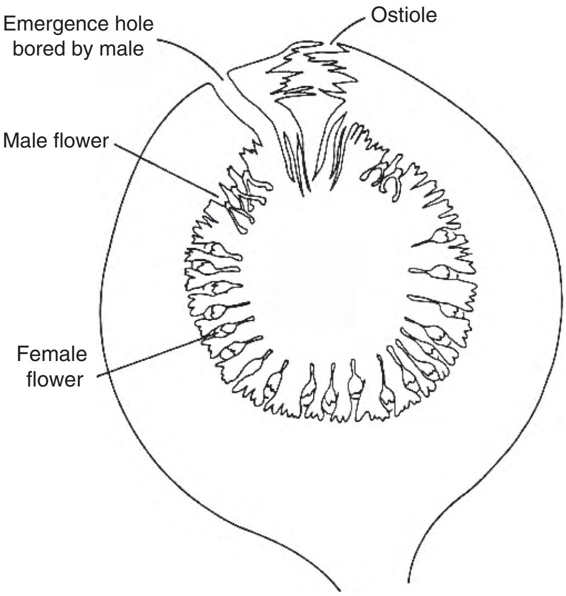


Figure 6.5 Diagramatic cross section of a fig inflorescence showing the distribution of male and female flowers, drawn as if both were mature synchronously. After Galil and Eisikowitch (1968).

Some coevolved traits in the figs include:

(1) The unique false-fruit design, allowing only agaonids and a small number of closely related parasitic wasps to enter the inflorescence.

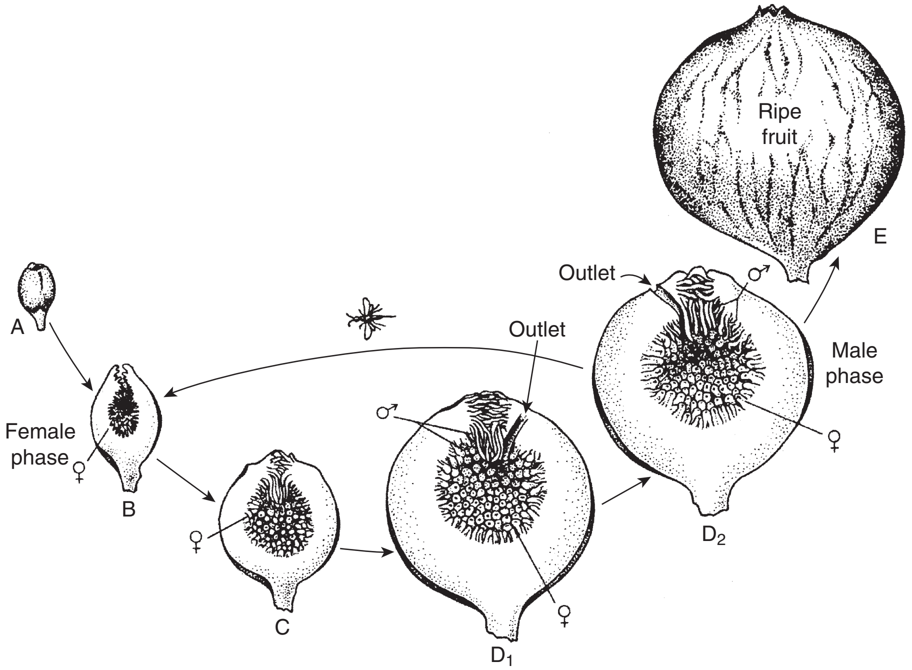


Figure 6.6 Phases in fig development. From Galil and Eisikowitch (1968).

(2) The extreme **protogyny**, with female flowers receptive several weeks before male flowers produce pollen, is clearly adapted specifically to the generation time of the fig wasp.
(3) The inflorescence contains both stalked and unstalked flowers with short and long styles, respectively, making seeds more or less available to ovipositing fig wasps, some sacrificed for the mutualistic wasps and some reserved for seed production.

Some coevolved features of the wasps include:

(1) The specialized morphology of both male and female fig wasps (Figure 6.8), involving: (a) the female body adapted to squeezing through the ostiole of the fig; (b) pollen receptacles on the female; (c) a wingless male with a long abdomen for mating with a female in the gall.
(2) The specialized behaviors of loading and releasing pollen.
(3) The specialized secretions in the female that promote gall formation.
(4) The very specialized relationship, usually between one fig species and one wasp species, reminiscent of the highly specialized parasites discussed in Chapter 8.

Of course, with so many fig and fig-wasp species, few have been studied in detail so that further explorations will yield new and fascinating information. But we now understand that the costs and benefits of this relationship are extensive and multifaceted.

6.5.2 Ants and plants

Since the first benefit and cost analysis of pollinator and seed predator by Pellmyr (1989) these and many other systems have been examined (Table 6.2). Ants benefit plants, and the plants provide food for ants in the form of **extrafloral nectar** and

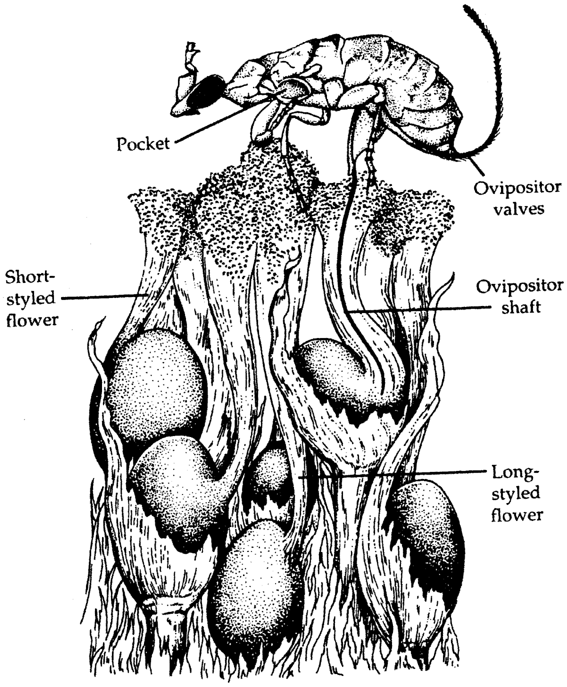


Figure 6.7 Female fig wasp, *Ceratosolen arabicus*, ovipositing in a short-styled flower of *Ficus sycomorus*, and extracting pollen from a pouch to fertilize the flower. From Galil and Eisikowitch (1969).

protein-rich food bodies. Many ant plants, or **myrmecophytes**, also provide shelter in the form of swollen plant parts, as in bull's horn acacias (Janzen 1966, 1967a, b), or hollow stems as in *Cecropia* species (Davidson *et al.* 1991), into which the ants can bore and establish their nests. We will consider these examples in a little more detail as they have become classic examples of mutualism, as in the case of figs and fig wasps.

Bull's horn Acacia and Cecropia species and ants (Partly from Price 1984b, 1997)

More than 90% of species of the genus *Acacia* (Fabaceae: Mimosoideae) in Central America are protected from herbivores by cyanogenic chemicals in the leaves (Rehr *et al.* 1973). The remainder seem to have gained a more potent defense in the form of ants which live in close association with these plants. Belt (1874) discovered that some species, the bull's-horn acacias (e.g., *A. cornigera*), act as hosts to colonies of ants in the genus *Pseudomyrmex* (Figure 6.9), and the ants act as allelopathic agents for the plant (Brown 1960, Janzen 1966, 1967a,b). The ants gain protection from the plant by living in the swollen stipular thorns and food is provided by the plant – sugar is secreted by petiolar nectaries and protein is produced in small **Beltian bodies** growing at the tips of new leaflets (Figure 6.10). The aggressive ants patrol the plant, ward off herbivores and suppress potentially competitive plants by chewing the growing tips (Janzen 1967b). Such suppression of plants around an occupied acacia plant also makes it much less vulnerable to fire, which frequently sweeps through this dry-tropics vegetation (Janzen 1967a).

Similar relationships exist between ants and *Cecropia* (Cecropiaceae) plants (Figure 6.11) (Janzen 1969, Davidson and Fisher 1991, Davidson *et al.* 1991, Hölldobler and Wilson 1990) in which the precision of coevolution can be seen in the production of animal sugar (glycogen) in the **Müllerian bodies** of the host plant, the only known case in the higher plants (Rickson 1971, 1976) (see also Buckley 1982). About 100 species of *Cecropia* in the New World tropics house ants in their hollow stems. The plants provide **prostomata** which are small areas in the internodes through which queen ants can easily cut to gain entrance to the hollow stem, which becomes a brood chamber. After entry the prostoma grows back to close the opening, protecting the queen as she lays her eggs and rears her first brood of workers. Workers open the prostoma again and forage for Müllerian bodies rich in glycogen produced in **trichilia** platforms at the base of petioles (Figure 6.12). Other food types provided by various *Cecropia* species are spongy parenchyma cells on the stem inner walls, pearl bodies rich in lipids on leaf surfaces, and honeydew produced by coccids tended by the ants in the hollow stems (Davidson *et al.* 1991).

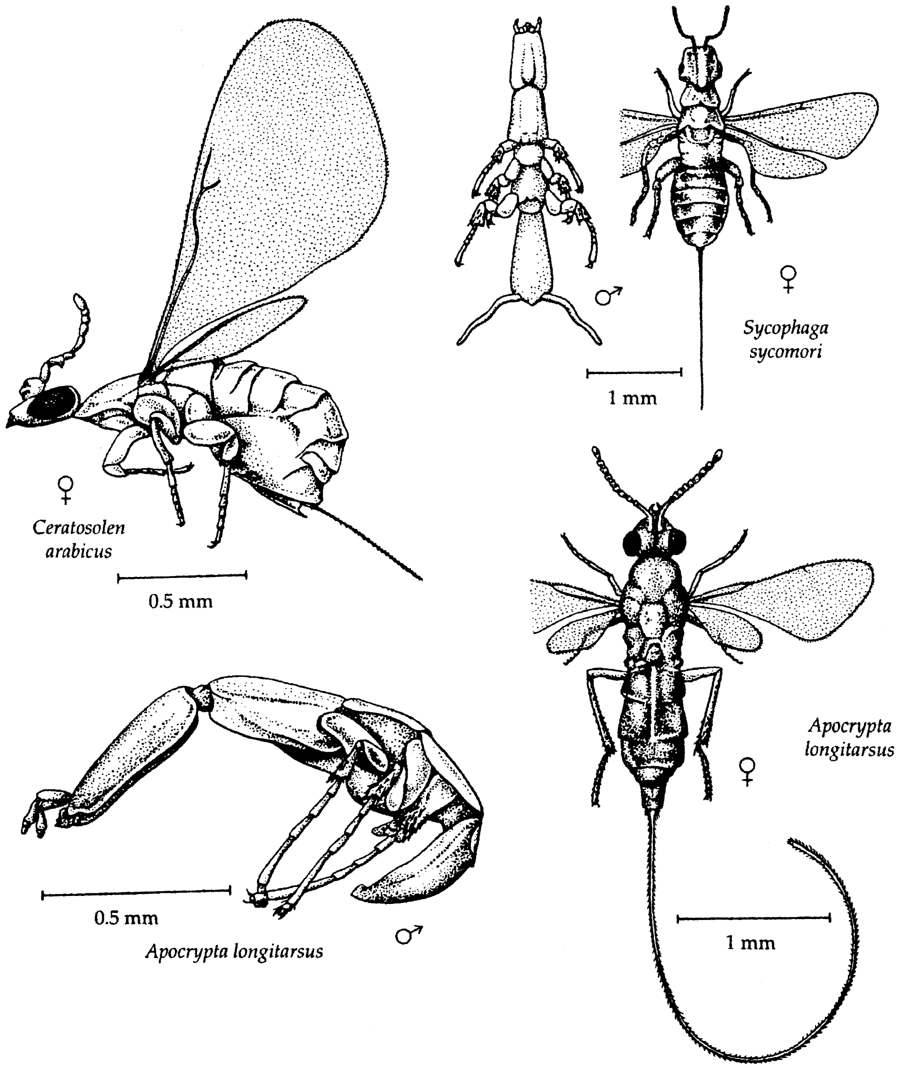


Figure 6.8 Inhabitants of *Ficus sycomorus* inflorescences. The female *Ceratosolen arabicus* (Agaonidae) is the pollinator and mutualist. *Sycophaga sycomori* (Agaonidae) is a parasite of the fig and a competitor with *C. arabicus* because it does not pollinate the fig, but utilizes both long- and short-styled flowers as oviposition sites. *Apocrypta longitarsus* (Torymidae) is an inquiline utilizing galls formed by *Ceratosolen* and *Sycophaga*. From Galil and Eisikowitch (1968).

Other well-studied ant and plant interactions include the plant genera *Leonardoxa* (Caesalpiniaceae) and *Macaranga* (Euphorbiaceae) (Heil and McKey 2003 and references therein), which would be rewarding for the reader to explore. The full array of ant and plant associations is covered by Beattie (1985), Huxley and Cutler (1991), Hölldobler and Wilson (1990), and Rico-Gray and Oliveira (2007).

Ant dwellings, or **domatia** (also **myrmecodomatia**), may also house mutualistic hemipterans such as coccids and pseudococcids, from which the ants derive carbohydrate resources in the form of honeydew. A case is provided in Table 6.2 under ants and hemipterans (Lapola *et al.* 2005). When ants feed on the honeydew produced by a hemipteran, for example, the process is called **trophobiosis** and the provider is a **trophobiont**. Such cohabitation with ants is also called **myrmecophily**, which is practiced by **myrmecophiles**, although this term was originally reserved for the ant's "guests" in the nest (Wheeler 1910). Hence, all hemipterans excreting honeydew and lycaenids secreting sugary liquids were regarded as trophobionts, but only those living in an ant's nest were considered to be myrmecophiles. However, this definition still includes many aphids, coccids and pseudococcids that reside in ants' nests (e.g., Lapola *et al.* 2005), and lycaenid larvae that

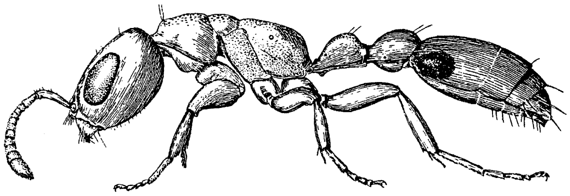


Figure 6.9 The ant, *Pseudomyrmex*, with a long, thin, body form suitable for living in hollow twigs, stems and thorns. From Hölldobler and Wilson 1990.

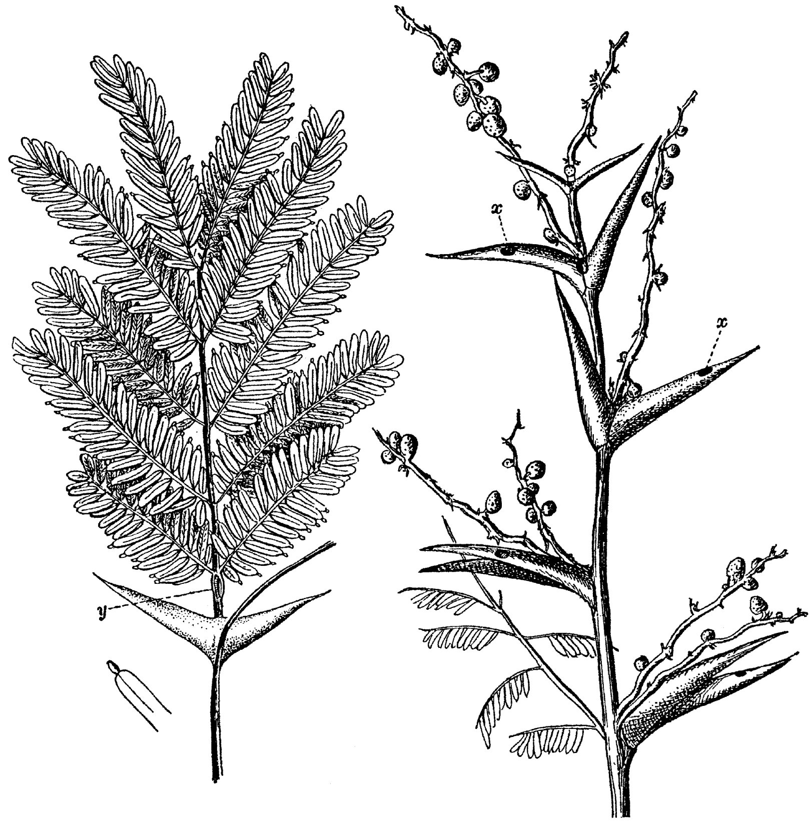


Figure 6.10 Right. The end of a branch of a bull's horn acacia, *Acacia sphaerocephala*, with paired, inflated and hollow thorns inhabited by ants in the genus *Pseudomyrmex*. Entry holes cut by ants are marked with an *x*. Left. A young shoot of the same acacia species, with Beltian bodies at the tips of leaflets (enlarged in inset at lower left), and an extrafloral nectary on the upper surface of the petiole, marked by a *y*. The young thorns have not been occupied by ants. From Wheeler (1910).

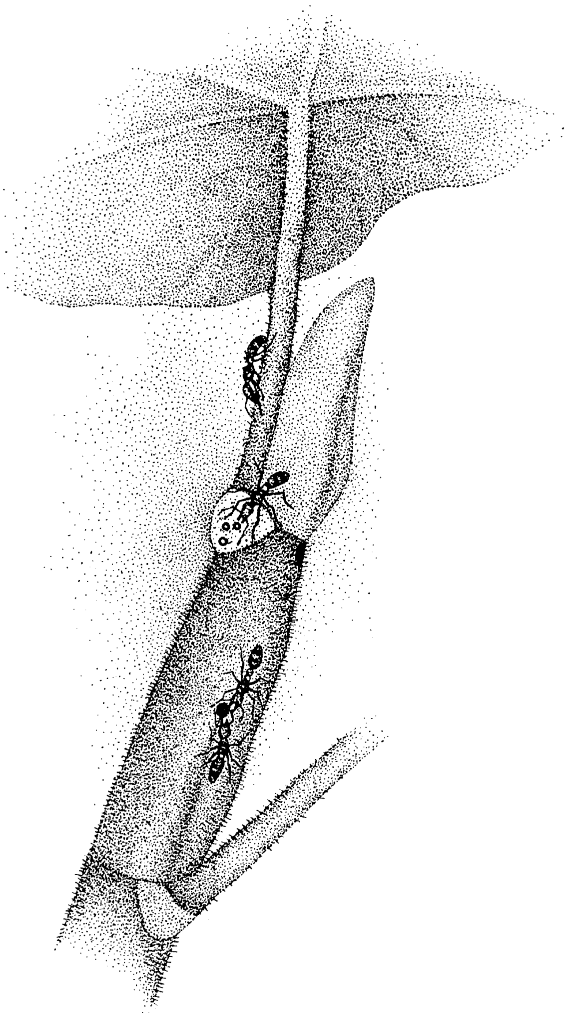


Figure 6.11 Myrmecophytic *Cecropia tessmannii*, showing a swollen stem with an open prostoma (an entry site for ants), and petiolar bases with white trichilia (sites of Müllerian body production). Ants are workers of *Pachychondyla luteola*. The new name for the plant is provisionally *Cecropia pungara*, with the specific name relating to the stinging ant named by the local people. Figure by Ali Partridge based on photograph by Diane Davidson. From Davidson *et al.* 1991.

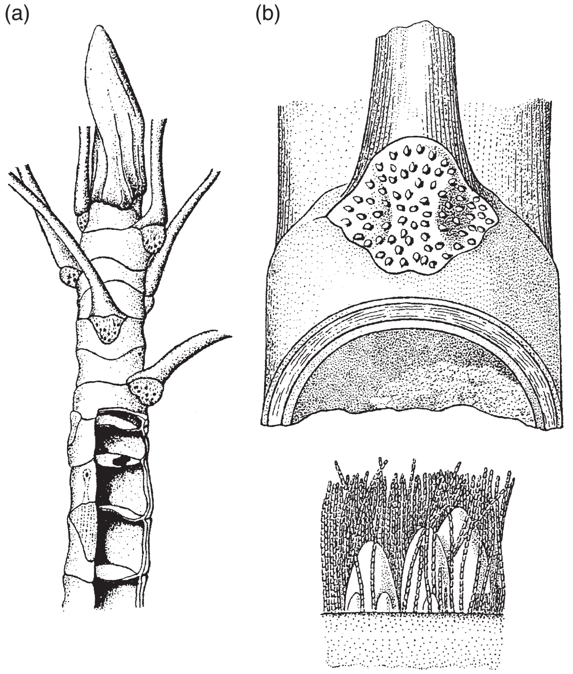


Figure 6.12 Details from the myrmecophyte, *Cecropia adenopus*, which grows in the American tropics, and supports ant colonies in the hollow internodes (a). Note the pads at the base of the petioles which produce Müllerian bodies fed upon by the ants (b). An enlarged surface of a petiolar base shows developing egg-shaped Müllerian bodies. From Hölldobler and Wilson (1990). Reprinted by permission of the publisher from *THE ANTS* by Bert Hölldobler and Edward O. Wilson, Cambridge, Mass.: The Belknap Press of Harvard University Press, p. 222, Copyright © 1990 by Bert Hölldobler and Edward O. Wilson.

enter nests of ants (e.g., Thomas 1980, 1989, 1991). At present the term myrmecophile is defined as "an organism that must spend at least part of its life cycle with ant colonies" (Hölldobler and Wilson 1990, p. 640), which would presumably exclude facultative trophobionts. One case study concerning ants and lycaenid larvae shows how variable relationships are: with this **context dependency** (Bronstein *et al.* 2006) or **conditional mutualism** (Cushman and Whitham 1989, Cushman and Addicott 1991, Bronstein 1994) responses of larvae depended on ant density and ant species (Figure 6.13).

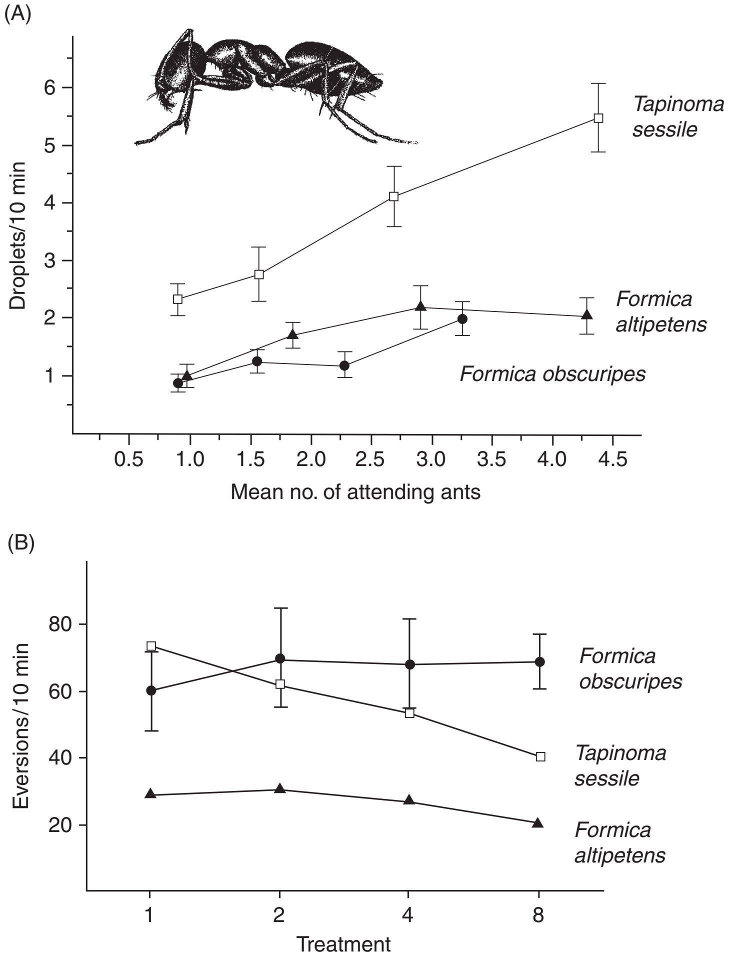


Figure 6.13 Variation in the response of lycaenid larvae, *Glaucopsyche lygdanus*, to different species of tending ants: *Formica altipetens*, *Formica obscuripes* and *Tapinoma sessile*. (A) Droplets of sugary secretions produced by ant-tended lycaenid larvae increased as the number of ants touching and tending larvae increased, particularly when *T. sessile* was tending. (B) Also, tentacle eversions decreased as the number of ants tending increased in *T. sessile* (the treatment axis). Eversible tentacles in lycaenid larvae are thought to release volatiles, which alert ants and increase attendance. Modified from Axén 2000.

In all cases in Table 6.2, and in the literature in general on ant and plant mutualisms, there is an emphasis on benefits and costs to the plant: reduced herbivory, increased fruit and seed set, with the cost of providing extrafloral nectar. Seldom are the ants the focus of a benefit/cost analysis, but see Pierce (1989) discussed below.

Moving on from ant relationships, we list in Table 6.2B cases where pollinators and seed predators have been evaluated in terms of benefits and costs in the relationship. This kind of relationship has been named **brood-site pollination mutualism** (Sakai 2002) and **nursery pollination** (Dufaÿ and Anstett 2003). Again, emphasis has been on the plant's gains and losses in the interaction. However, the example of Pellmyr (1997) actually measured costs to the yucca moth. These were very low: time allocated to pollination, 4.1%; specialized morphology, 0.42% of female body mass; pollen load transport, <4% of female body mass. Pellmyr concluded that with such modest costs, one would expect the pollination/seed predation syndrome to be more common than is observed so far in nature. Perhaps many more cases await discovery, or the "copollinator abundance hypothesis" (Pellmyr 1997, p. 1658) may limit evolutionary opportunities. For example, if copollinators are effective on a plant, then specializing on that plant will be unrewarding because pollinators would not limit seed set. And, indeed, the range of nursery pollination systems noted in the literature has expanded in the last decade (e.g., Sakai 2002, Dufaÿ and Anstett 2003).

6.5.3 Ants and herbivores

Ants and lycaenid larvae, and ants and hemipterans show similar relationships, with ants providing protection against predators and parasitoids, and gaining sugary secretions or honeydew (Table 6.2C). Much of the literature assesses benefits and costs to the herbivorous insect rather than the ant partner. Frequently, the costs of being tended by ants and supplying nutrients appear to be high, as evidenced by reduced pupal and adult weights (decreased by 25%) in lycaenids, and smaller body size, fewer embryos, longer development times and delayed progeny production, all of which have been recorded in aphids and other hemipterans (Table 6.2). Moreover, some species of aphids, coccids, membracids and lycaenids have become obligate associates of ants and are unable to survive in the absence of ants (see Stadler *et al.* 2001 for a good review of costs and benefits of mutualistic interactions with ants). Pierce (1989) assessed benefits to ants tending lycaenid larvae by measuring dry weights of ants ascending trees to tend larvae, and weights as they descended. The increased weights of descending ants documented a significant energetic gain as a consequence of the resources garnered by tending lycaenid larvae. The metabolic cost of foraging was at least compensated for in the tree canopy because of the net gain in weight of ants, but the extent to which such foraging benefited the ant colony at large, and the queen, was not determined.

6.5.4 Insects and fungi

The last category of mutualism treated in Table 6.2 is the associations of insects with fungi. Costs and benefits have not been analyzed frequently in this literature, although it is extensive (see Batra and Batra 1967, Batra 1979, Martin 1987, Pirozynski and Hawksworth 1988, Wilding *et al.* 1989). Specialized pouches for transmission of fungal spores or mycelium (**mycangia** or **mycetangia**) from one host plant to another have evolved repeatedly, being present in wood wasps, bark and ambrosia beetles, cecidomyiid gall-inducing midges, leaf-cutting ants and others. These fungus-bearing pouches are invaginations of the epidermis with external openings (as opposed to internal **mycetomes:** bodies of cells containing symbiotic organisms within host organisms) (Buchner 1965). In an example involving the bark beetle, *Ips pini*, and the blue-stain fungus, *Ophiostoma*, Kopper *et al.* (2004) introduced beetles into the cambium of pine trees which had been inoculated with fungi at various times (0, 3, 7 and 10 days before beetle entry) to determine the effects on bark-beetle colonization and development. As the blue-stain fungus developed longer, colonization rates declined, but the number of progeny increased relative to fungus-free controls. Since attack of dying trees and inoculation of blue-stain fungus by beetles is normally simultaneous, because the fungus is carried by the beetle in mycangia, the mutualistic association benefits the beetle both because more progeny are produced by the colonizing cohort, and because competition from colonizing conspecifics is deterred. Of course, the fungus benefits from highly specific transport from host to host and effective inoculation into the cambium of the host.

Another insect–fungus mutualism involves the *Phorbia* fly and the fungus *Epichloe*. *Epichloe* is an endophytic ascomycete on the grass, *Elymus virginicus* (Table 6.2). This fungus forms stroma on the grass stem surface in the spring, producing spore-like spermatia. The flies are attracted to the stroma and carry spermatia to another stroma of the opposite mating type, thus acting as the equivalent of a pollinator. The flies oviposit on the stroma and larvae feed on fungal tissues, including ascospores, which develop after the "+" and "−"fungal mating types fuse. This example is therefore equivalent to the mutualistic examples of pollinators and seed predators.

There are many interesting questions which remain to be addressed regarding mutualistic associations. What is the variation in the intensity of the mutualistic relationship over the landscape, for example, when different ant species tend lycaenid larvae (e.g., Axén 2000), or when extrafloral nectar traits vary (Rudgers and Strauss 2004). And why don't extrafloral nectaries result in protection of the plant against herbivore attack in some cases (e.g., Rashbrook *et al.* 1992). Also, at least three species are usually involved in a mutualism because the association is often involved with protection against natural enemies, so variation in any one of the players has important and interesting consequences for the strength of the interactions (see review by Bronstein and Barbosa 2002). In ant and plant interactions, hemipterans may become involved, and the species may change with time or across habitats, posing the question of how this alters the ant's protection of the host plant (e.g., Gaume *et al.* 1998). More perplexing and esoteric questions arise in the fig and fig–wasp interactions because some fig-wasp species cannot reproduce in figs with only female "flowers," begging the question as to why they enter such figs only to pollinate (e.g., Moore *et al.* 2003)? It is in the nature of mutualism that interactions are complex and highly variable (Bronstein 1998), with geographic mosaics of coevolution common (Thompson 2005, see Chapter 4). The study of benefits and costs of these interactions force detailed analyses and raise many questions, ensuring a rich future for their continued study.

6.6 Cheating

Where there are rewards, cheaters will materialize, both in human society and in mutualistic systems in the wild. If a pollinator's activity results in an ovary full of seeds, why not use the seeds for larvae without the "bother" of pollination?

6.6.1 Seed predators

Cheaters in the yucca moth and yucca mutualism have evolved at least twice (Figure 6.14, Pellmyr *et al.* 1996a). The cheaters have evolved to be finely tuned to *Yucca* species phenology. Following pollination in *Yucca filamentosa*, fruits with more than seven or eight moth eggs are abscised within 5 days, a response to the inevitable overexploitation of seeds by so many resulting larvae. Fruits that are not abscised will normally have 26% of seeds consumed by larvae from the pollinating moth. However, the early-phenology cheaters oviposit into the fruit after all abscission has been initiated, and consequently do not influence the probability of fruit loss. Thus, cheaters feed on and destroy more seeds than the pollinators, consuming from a mean of 75% of seeds up to 100% in some fruits. Late-phenology cheater species oviposit 2–3 weeks after pollination into the fully grown fruit, using a long ovipositor. When both types of cheater species are present almost all seeds are destroyed. The phylogenetic hypothesis on *Tegeticula* moths suggests multiple host shifts among *Yucca* species, opening up opportunities for one species of pollinator to move to a new host and remain a mutualistic pollinator, while another with a slightly delayed oviposition time could evolve into a cheater. It would appear that the pollinator strategy is more rewarding, in terms of larval survival, than the cheater strategy,

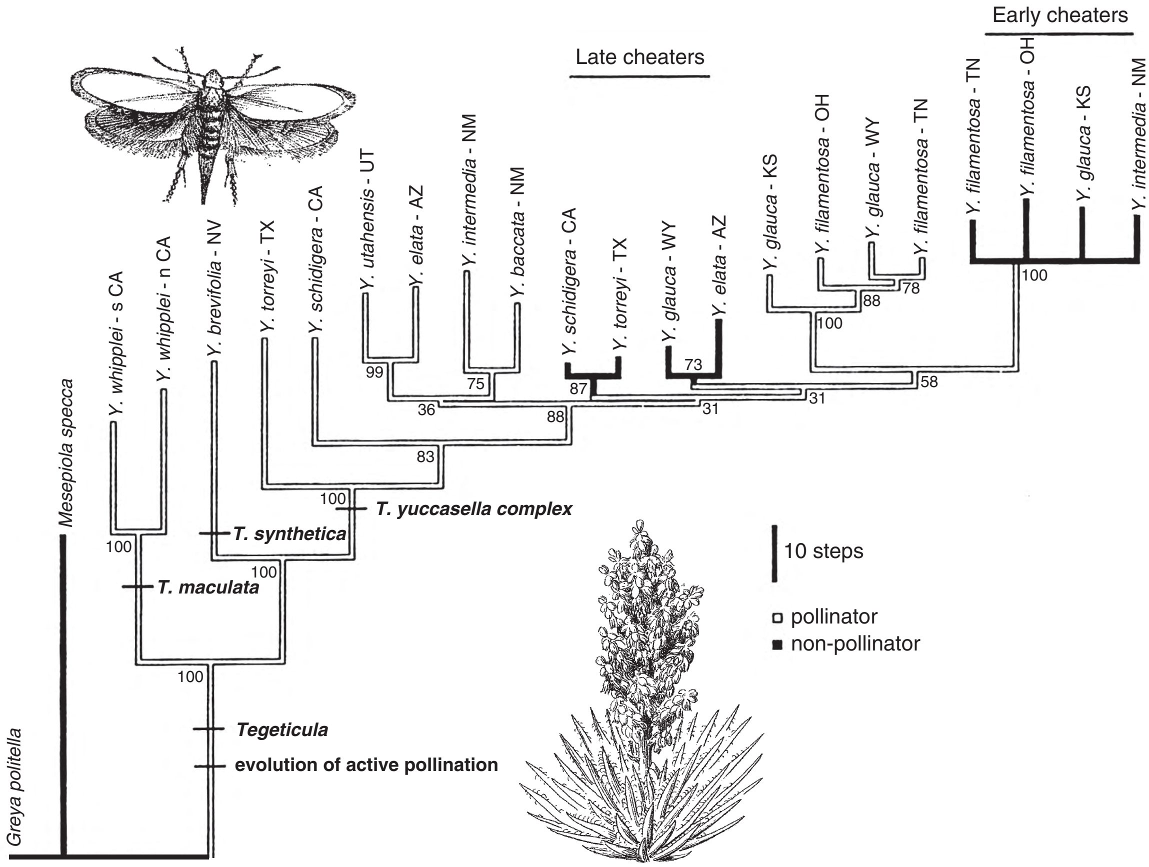


Figure 6.14 Phylogenetic relationships among species of pollinating yucca moths and cheaters in the genus *Tegeticula*. Each moth species is designated by its *Yucca* host species and the geographic source population. The origins of late cheaters and early cheaters, and the species involved, are shown with solid black lines. From Pellmyr *et al.* 1996. Reprinted with permission from Pellmyr, O., J. Leebens-Mack and C. J. Huth. 1996a. Non-mutualistic yucca moths and their evolutionary consequences. *Nature* **380**:155–156 © 1996 Macmillan Publishers Ltd.

or the long-term coexistence of the association would be impossible. Since the genus *Tegeticula* evolved, cheaters have coexisted with pollinators for about 35% of the lineage's existence, a very long persistence time for this potentially destabilizing set of interactions.

6.6.2 Flower visitors

Another form of cheating occurs when nectar is taken from flowers without pollination – **nectar robbing** (e.g., Inouye 1983, Scott *et al.* 1993). This is known to occur in birds, bees and ants, where for example, large carpenter bees in the genus *Xylocopa* pierce the base of the corolla of tubular *Solanum* and ocotillo (*Fouqueiria splendens*) flowers, and suck up nectar without contacting stamens or stigma at the opening of the flower. *Xylocopa* bees are short-tongued and rob many plant species, and together with short-tongued bumblebees (*Bombus* spp.) and stingless bees (*Trigona* spp.) hundreds of plant species are robbed. These bees form a class of

primary robbers, which cut into flowers, but this provides access to nectar for **secondary robbers** whose mouthparts can enter slits at the base of corollas already present. Honeybees, moths and butterflies may all act as secondary cheaters. The costs of nectar robbing to the seed set in flowers appears to be minor, because normal pollination by long-tongued bees, butterflies and moths is not curtailed (Morris 1995). In some cases seed set may be increased by cheaters because reduced nectar supplies results in pollinators visiting more flowers! However, although nectar robbers may range from cheaters to mutualists (Maloof and Inouye 2000), generally they have a detrimental effect on plant reproductive success (Irwin *et al.* 2001), although this effect is highly variable in time and space (Irwin and Maloof 2002).

Cheating is not restricted to the insect and bird pollinators because some plants cheat in the interaction as well. For instance, **deceit pollination** is observed in orchids, begonias and other plant species (Fritz and Nilsson 1996, Schemske *et al.* 1996). In orchids, such as in the genera *Ophrys* (Kullenberg 1961) and *Orchis* (Fritz and Nilsson 1996), flowers provide no apparent reward to pollinating bees, but resemble females of the pollinating species both visually and pheromonally. Males attempt to mate with the flower, and carry away pollinia after flower visitation. This is called **pseudocopulation**. Similar deceitful relationships have evolved in plants with flower parts mimicking the hosts of parasitoids, attracting female parasitoids which sting into the flower and pollinate it – **pseudoparasitism** (Faegri and van der Pijl 1971). Flowers may also mimic other insects, causing bees to attack in territorial defense, which results in pollination via a deceptive process called **pseudoantagonism**, or **pseudoaggression**. Another form of deceit pollination occurs when flowers are unisexual, and female flowers offer no reward to pollinators while males provide pollen, as in the genus *Begonia* (Schemske *et al.* 1996). Although male flowers are larger, displayed more conspicuously, and offer a reward, female flowers attract brief bee visits which result in pollination, by mimicking male flowers. Spectral qualities are similar (UV light absorption is strong by anthers and stigmas), and sepals are similarly reflective in the UV range in male and female flowers. Both male and female flowers are formed, mainly by two conspicuous sepals, and the sex ratio was female biased (about 66% females). Although male flowers were much more attractive to bees than females, experiments with supplemental pollinations produced no more fruits per plant than controls, which received natural pollination, and in both treatment and control about 45% of female flowers produced mature fruits. However, with supplemental pollination, seed set was higher by about 10%. Nevertheless, with little cost to female flowers (except that of looking like males, which is usually avoided in nature), this deceit pollination through intersexual mimicry is effective, evolutionarily stable and of long standing.

Many other forms of cheating occur in mutualistic systems, because the opportunities for cheating are almost limitless. Lycaenid butterfly larvae drink extrafloral nectar provided by the host plants to attract ants involved in protecting both the plant and the caterpillar from natural enemies (DeVries and Baker 1989). Non-pollinating wasps utilize fig fruits pollinated by others (Bronstein 1991), and parasites of mutualisms are commonplace (Yu 2001). **Inquilinism** is the relationship in which a species spends much of its life cycle in the nest of its host species. In fungus-growing nests of ants and termites, and other myrmecophily without rewards for ants, inquilinism is represented by hundreds of species (Hölldobler and Wilson 1990). Nonetheless, the advantages of mutualisms clearly outweigh the drawbacks incurred from conflicts of interest and cheating. However, some clades ancestrally mutualistic show defectors in which species become parasitic or independent (Sachs and Simms 2006), as with the case of cheating yucca-moth species.

6.7 Adaptive radiation in mutualistic systems

Many authors have argued for the importance of dead organic matter as a cradle of evolution for insects (see Hamilton 1978). These kinds of habitats would bring the colonizers into intimate contact with the multitude of microorganisms already adapted for living in and on wood, with the necessary enzymes for digesting organic matter, and toxins for dealing with antagonistic interactions. Acquisition by insects of such organisms, as mutualists, would proceed more rapidly than in the *de novo* evolution of the necessary traits, and result in more efficient exploitation of resources. We provide some examples, starting with radiation in woody substrates, moving to roaches and termite symbionts, and then we consider the role of symbiosis in the radiation of the ants.

6.7.1 Breeding structure in dead trees

Hamilton narrowed the focus to dead trees in his article, *Evolution and diversity under bark*. He emphasized the evolution of breeding structures that resulted in rapid evolution and adaptive radiation:

(1) The origin of wing polymorphisms is frequent, as observed in Zoraptera, Psocoptera, Thysanoptera, Hemiptera, Coleoptera, Diptera and Hymenoptera. Food sources under bark for these groups were fungi, yeasts and small arthropods.
(2) The origin of male haploidy occurred at least five times in this habitat – Hymenoptera, Thysanoptera, *Micromalthus* beetles and some scolytid beetles, as well as some mites.
(3) Eusociality has evolved at least twice, in the termites and ants, and possibly in the social aculeate wasps.
(4) Sexual dimorphism is also common in wood-dwelling insects. Think of the stag beetles, the Lucanidae, with large males with huge mandibles like antlers for fighting, and the smaller females without enlarged mandibles (Figure 2.11). Several orders have species with winged males and flightless females – Dictyoptera, Embioptera, Psocoptera, Hemiptera and Coleoptera.

The breeding structure resulting from these four common attributes of insects in wood results in small interbreeding units in which natural selection and drift may be rapid. Many such isolated demes would indeed create a cradle for evolutionary innovation and many major groups appear to have originated in wood: Dictyoptera, Isoptera, Zoraptera, Dermaptera, Thysanoptera, Hymenoptera (Symphyta like siricid woodwasps) and Coleoptera. In these small interbreeding groups, exchange of beneficial microbial associates would be effective and probably common. Bacteria, protozoa, yeasts and fungi would also be common, yielding plentiful opportunities for symbiotic associations. Wood is difficult to digest, and cellulases, which are not produced by most insect groups, are most commonly found in microbial species and fungi (Table 6.1). Also, wood low in nitrogen provides inadequate nutrition for insects which are contrastingly high in nitrogen and protein. However, this depauperate substrate can be utilized by microbial and fungal partners from whom the insects benefit.

Although Hamilton (1978) emphasized breeding structure he did mention symbiosis as one factor that may facilitate evolutionary change, but the case can be made that symbiosis was perhaps at least as important, if not more so, than breeding structure. This results because, although breeding structure has changed during radiations, symbiosis has been maintained throughout radiations in many cases, suggesting its more central role in the process. We will examine three examples of adaptive radiation of major inset taxa in support of this contention: the Dictyoptera, the Scarabaeoidea and the ants.

6.7.2 Microbes in cockroaches and termites

The Dictyoptera include the termites (Isoptera), mantids (Mantodea) and the cockroaches (Blattodea)

(Triplehorn and Johnson 2005, Gullan and Cranston 2005). The mantids are predatory, so symbiotic microbes are not utilized, but in the termites and cockroaches mutualistic microbes have been basic and central to the adaptive radiation of these two orders (Nalepa *et al.* 2001, p. 194). "We suggest that the evolution of a sophisticated hindgut fauna is a process of internalizing this self-assembled microbial community, accompanied by changes in host-microbe interdependence, the source of microbial inoculum for neonates, and host social behavior," and "The association of these flagellates with the dictyopteran lineage is an ancient one, and may have originated as part of the external rumen in the Carboniferous coal swamps" (i.e., over 300 million years ago). The **external rumen** mentioned here refers to faeces in which microbes act as potential mutualists with the precursors of termites and roaches, providing breakdown of cellulose, detoxification of allelochemicals, a softening of the substrate and a direct source of nitrogen-rich food. Thus, digestion is partially external to the insects, but equivalent to the microbial activity in the rumen of ungulates.

It is argued that the ancestors of the Dictyoptera fed mostly on rotting plant material in which fungi, protozoa and bacteria would be active in decomposition, so associations of microbes and insects were inevitable. After ingestion of an active culture of plant material and microbes, decomposition may well accelerate, and anaerobic fermentation became possible. Some microbes would be retained in the gut and eventually become accommodated in an enlarged paunch, the fermentation chamber in termites. Fecal pellets would provide a rich source of predigested plant material plus microbial protein and potential symbionts, so **coprophagy** (the consumption of faeces) would be highly advantageous (Figure 6.15). Then, association among individuals in small family groups, as envisioned by Hamilton (1978), would promote the coprophagous habit, and eventually highly social units and eusociality. Direct transfer of fecal material among family members, from the anus of one to the mouth of another, or **proctodeal trophollaxis** in cocktail-party parlance, would ensure inoculation of neonates with mutualistic microbes, including groups such as flagellated protists which function in a liquid medium. Such vertical transmission of mutualists from parents to progeny would accelerate coevolutionary adaptation in the host and its gut fauna, and among faunal components themselves. Thus, symbiosis and mutualism appear to be fundamental to the evolution and adaptive radiation of the cockroaches and termites.

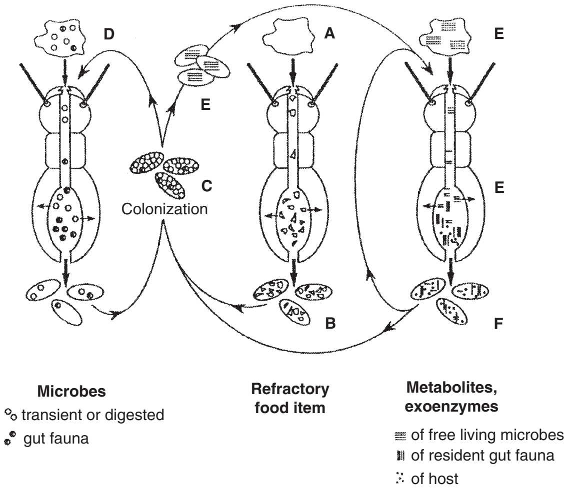


Figure 6.15 Interactions among a detritivorous insect and microbes in its environment. In A the insect feeds on a refractory food, digesting any contents such as starches, sugars and lipids, but masticated organic matter such as cellulose is excreted largely unchanged (B), and fecal pellets provide a substrate for microbial feeding and multiplication. Ingested microbes on substrate (D), or from fecal pellets of conspecific insects (C), may be digested or passed out in feces or be retained selectively as mutualists. Microbes provide metabolites and enzymes of potential benefit to the host insect (E), and fecal pellets (F) provide inoculum via coprophagy to related individuals. From Nalepa *et al.* 2001.

6.7.3 The Scarabaeoidea

Not surprisingly, another adaptive radiation originated from the detritivore habit, that of the superfamily Scarabaeoidea, which includes stag beetles, bess beetles, rain beetles, dung beetles, skin beetles, scarab beetles, white grubs and several families without common names (Table 6.3). But some members are greatly admired and even revered, like the sacred scarab of ancient Egypt, Hercules beetles, the goliath beetle with larvae weighing almost 100 g (Acorn 2007) and some large stag beetles with mandibles of prodigious proportions. The group has been radiating for about 200 million years, from Triassic times, and the existence of Pangaea.

The ancestral scarabs appear to have fed on humus as larvae, and fungus as adults (Figure 6.16, Scholtz and Chown 1995). Present day larvae have an enlarged hind gut which acts as a fermentation chamber (Figure 6.17). This gut morphology must have evolved early in the lineage because the trophic link to humus, dung and rotting wood, necessitating microbial digestion (i.e., fermentation), has remained as a theme throughout the radiation (Figure 6.16, Table 6.3). The fermentation of refractive substrates opened up huge opportunities to exploit a wide range of previously unavailable foods, as listed in Figure 6.16 and Table 6.3. Larvae fed within the medium, often boring into the ground, a **hypogeal** or below-ground-level habitat, and adults would burrow into a substrate to oviposit. Hence, the colonization of wood, dead animals and the nests of ants and termites would result from an instinct to burrow.

In the scarab radiation one clade expanded after the Triassic–Jurassic extinctions at about 208 million years ago – the Mesozoic Clade shown in Table 6.3, and the left-hand clade in Figure 6.16. Another adaptive radiation occurred after the Cretaceous–Tertiary extinctions at 65 million years ago – the Cenozoic Clade shown in Table 6.3, and the right-hand clade in Figure 6.16. This more recent clade radiated into almost all the adaptive zones utilized by the older clade. However, the Cenozoic clade has become much more diverse in terms of species number (Table 6.3), having radiated into the dung habitat more extensively (e.g., Aphodiinae, Scarabaeinae) with the advent of the radiation of mammalian herbivores 55 million years ago. Another scarab radiation was coincident with the extensive radiation of the angiosperms about 50 million years ago, enabling entry into a new adaptive zone provided by the roots, stems and leaves of flowering plants. The extremely species rich Melolonthinae, with an estimated 10 000 species worldwide, includes the May beetles (also known as June bugs), chafers and their larvae, the white grubs, many of which have become serious pests of pastures, lawns and agricultural crops.

The microbial faunas in larval fermentation chambers of scarab beetles have been less studied than those in the roaches and termites, so we do not know if there is a specialized gut fauna, or how it is acquired. Possibly, colonization results simply from the microbes in the substrate, because these communities are likely to be speciose, with potential symbionts occurring in high numbers in rich substrates such as dung and carrion.

The persistence of the mutualistic relationship between scarabaeoid beetles and a fermenting microbial fauna forms a common thread through two radiations with similar results, the Mesozoic and Cenozoic clades. The breeding systems in the species have changed radically from subsocial groups like the Passalidae (Mesozoic Clade), to a solitary lifestyle in many dung beetles, to parental cooperation in some Scarabaeini (e.g., dung rollers) contained in the Cenozoic Clade. The subsocial breeding system may well have contributed to the origin of the group and its diversification, but the mutualistic ecology of the group with microbes has been instrumental in this spectacular adaptive radiation. It remains almost a paradox that on one of the least nutritious substrates, wood, the largest insects grow; the record being a 205 g grub of the rhinoceros beetle, *Megasoma actaeon* (Acorn 2007). Undoubtedly the credit goes to mutualistic microorganisms and the “external rumen,” and as Acorn (2007, p. 63) says

Table 6.3 **Diversification in the Scarabaeoidea; the number of genera and species per family or subfamily, and the feeding ecology of each taxonomic group. The table illustrates the breadth and numerical extent of the radiation, with mutualistic bacteria digesting organic matter as a central enabling interaction. The Mesozoic Clade radiated after the Triassic-Jurassic extinctions, and the Cenozoic Clade radiated after the Cretaceous-Tertiary extinctions. Common names, where available, are from Triplehorn and Johnson (2005)**

	Feeding Ecology			
Taxon	Larvae	Adults	Genera	Species
Mesozoic Clade				
Glaresidae	?	?	1	50
Passalidae (Bess beetles)	Wood/humus	Wood	40	500
Diphyllostomatidae	?	Humus	1	3
Lucanidae (Stag beetles)	Wood	Flowers or do not feed	100	750
Glaphyridae	Roots/humus	Humus/flowers	10	30
Trogidae (Skin beetles)	Keratin	Keratin	3	300
Pleocomidae (Rain beetles)	Roots/mycorrhiza	Do not feed	1	33
Bolboceratidae	Fungi	Fungi	40	350
Geotrupinae (Earth-boring dung beetles)	Fungi/humus/dung	Fungi/dung	25	150
Taurocerastinae	Humus/dung	Dung	2	2
Lethrinae	?	?	1	80
Hybosoridae	Humus/dung	Carrion and carrion insects	28	275
Ceratocanthidae	Fungi/humus (inquilines)	Fungi (inquilines)	25	150
Ochodaeidae	?	?	8	80
Cenozoic Clade				
Aegialiinae	Humus/fungi	Humus	4	50
Aphodiinae (Dung beetles)	Humus/roots/dung	Humus/fungi/dung/carrion	100	2500
Aulonocneminae	Wood	Wood	4	50
Scarabaeinae (Dung beetles)	Humus/fungi/dung/carrion	Humus/fungi/dung/carrion	200	4500
Orphninae	Roots	Spores	10	100

Table 6.3 (*cont.*)

	Feeding Ecology			
Taxon	Larvae	Adults	Genera	Species
Melolonthinae (June beetles, chafers, white grubs)	Humus/roots/dung	Leaves/flowers or do not feed	500	10 000
Dynastinae (e.g., Rhinoceros, Hercules beetles)	Humus/roots	Roots	225	1400
Rutelinae (Shining leaf chafers)	Humus/roots/wood	Leaves	200	4100
Osmoderminae	Wood	Plant saps and oozes	2	10
Cetoniinae (e.g., Flower beetles)	Humus	Plant saps and oozes/ flowers/humus	400	3000
Cremastocheilinae	Humus/ants	Predaceous on ants	50	400
Valginae	Humus/termites	Predaceous on termites	30	200

Source: Scholtz and Chown 1995

"…isn't it interesting that all the real contenders for the largest insect title feed on rotting wood?"

6.7.4 Ants and mutualism

The fourth adaptive radiation involves the ants, which is no less impressive than those in the Dictyoptera and Scarabaeoidea. In fact, the ants constitute one of the most dominant elements in terrestrial faunas (Hölldobler and Wilson 1990, Davidson *et al.* 2003). "Ants are a ubiquitous and dominant feature of the terrestrial landscapes, playing key roles in symbiotic interactions, soil aeration, and nutrient cycling," (Moreau *et al.* 2006, p. 101). Present estimates place the emergence of ants in the late Jurassic about 150 million years ago, but major radiation occurred in the Late Cretaceous to Early Eocene, from about 100 million years ago. This radiation was coincident with the origin of angiosperm-dominated forests (Moreau *et al.* 2006). Accompanying the angiosperm radiation was the expansion of herbivorous insects into tree canopies, such as hemipterans and coleopterans, providing both food and mutualists for the ants. Indeed, Davidson *et al.* (2003, p. 969) found strong evidence that arboreal ants "feed principally as 'herbivores' of plant and insect exudates." Extrafloral nectaries on plants, and food bodies from myrmecophytes, plus hemipteran trophobionts, as well as microsymbionts of ants, probably all play important roles in ant nutrition and the radiation of the group. The microsymbionts of ants are housed in **mycetocytes** (specialized cells with symbionts therein) along the midgut lumen; they are maternally transmitted Proteobacteria, and probably contribute to the ant colony's nitrogen budget (Sauer *et al.* 2000).

The assemblage of symbiotic relationships of ants may well have contributed to their abundance in lowland tropical rainforest canopies where they constitute 94% of all arthopods when fogging samples are taken, and 86% of the biomass (Davidson *et al.* 2003). Mutualistic relationships of microbes with ants include myrmecophytes, trophobionts and

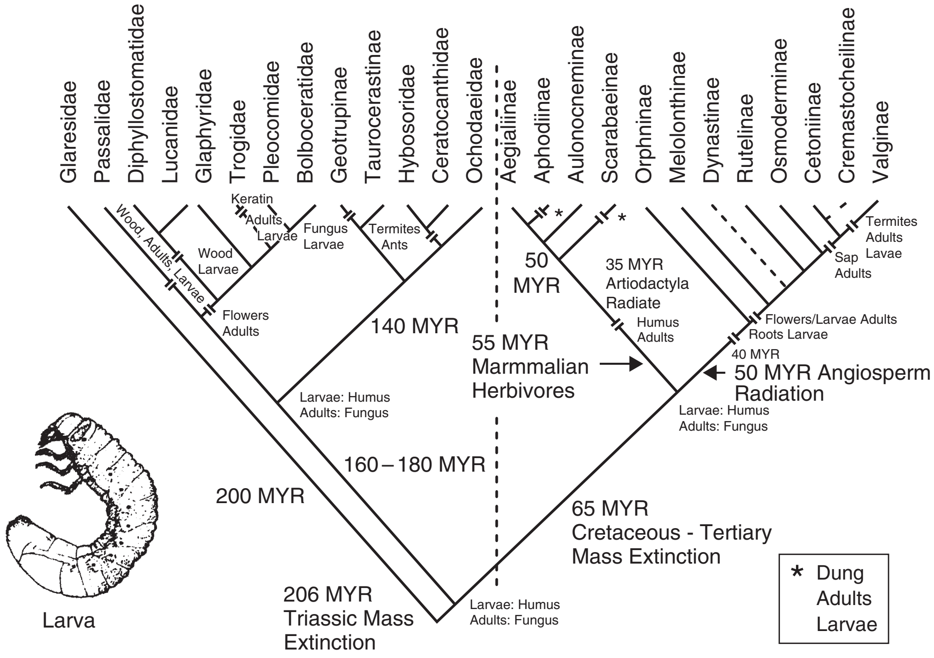


Figure 6.16 Phylogeny of the Scarabaeoidea showing a Mesozoic Clade on the left and a Cenozoic Clade on the right, separated by a vertical dashed line. The early species were hypogean with humus-feeding larvae and fungus-feeding adults. Major changes in larval and adult diet are shown by double lines on the phylogeny. Major new adaptive zones developed with the radiation of the herbivorous mammals, 55–35 million years ago, and the rapid expansion of the angiosperms about 50 million years ago. From Scholtz and Chown 1995.

gut microsymbionts. In addition to these multispecies complexes, the leaf-cutting ants are involved with their fungus-garden mutualists, and parasite-inhibiting bacteria. These bacteria produce antibiotics which inhibit fungi parasitic on the fungi ants cultivate for food (Currie *et al.* 2006). The bacteria are accommodated in cuticular crypts with exocrine glands providing nutrients, a mutualistic relationship that must have enabled the radiation of leaf-cutting ants a long time in the past. This occurred about 4 million years ago, according to Hölldobler and Wilson (1990). The persistence of antibiosis after millions of years of coevolution of ants, fungal cultivars, parasitic fungi and the bacteria is impressive. Yet, how does the ant-bacterium mutualism avoid the evolution of resistance in the parasitic fungi?

The radiation of ants constitutes one of the most impressive adaptive radiations on Earth (Hölldobler and Wilson 1990). It cannot be denied that mutualistic associates have been important in this radiation, but whether they have been critical and fundamental can be debated. It is interesting to note that, as with the Dictyoptera and Scarabaeoidea, the ants were originally, and largely remain, soil dwelling, where they forage in the soil and rotting vegetation on the ground (Hölldobler and Wilson 1990). In a brief consideration of the reasons for the success of ants Hölldobler and Wilson do not include mutualistic relationships, but the arguments developed since their publication may well provide a compelling scenario for their importance (e.g., Davidson *et al.* 2003, Currie *et al.* 2006, Moreau *et al.* 2006).

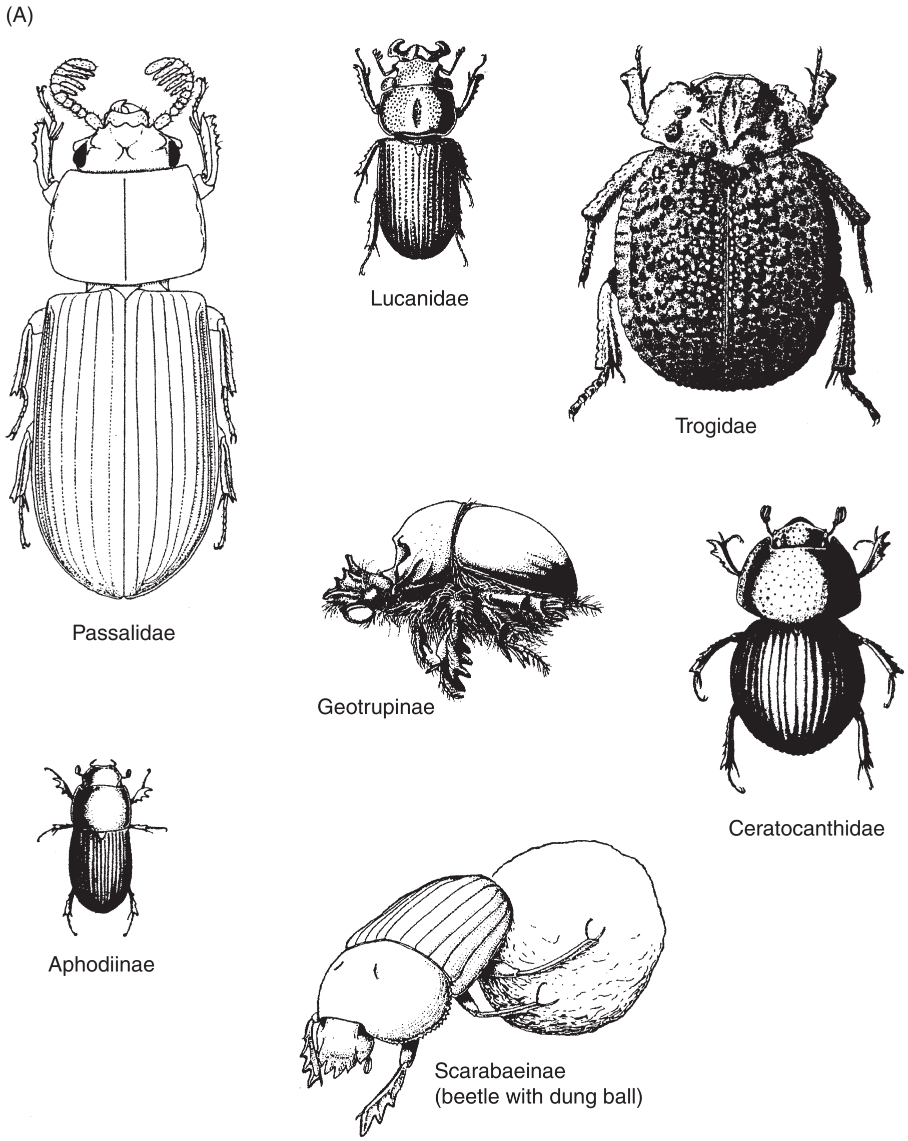


Figure 6.17 Examples of species (not to scale) representing families and subfamilies in the superfamily Scarabaeoidea. In (A) a scarabaeid adult rolls a dung ball away from the source and will bury it at a distance. Note the enlarged terminal segments of larvae (white grubs) in (B) which house an expanded hind gut acting as a fermentation chamber. In (B) top right, various nesting types are illustrated: paracoprids, endocoprids and telecroprids. All examples are from Scholtz and Holm 1985.

Many other adaptive radiations have resulted from mutualistic relationships. Consider the diverse taxa of pollinating bees, moths and butterflies, and other taxa such as beetles and flies (Tables 6.1 and 6.2). The accompanying mutualists, be they angiosperm plants or microbial associates, have also radiated, with microbes and insects often showing cospeciation and probably coevolution (e.g., Norris

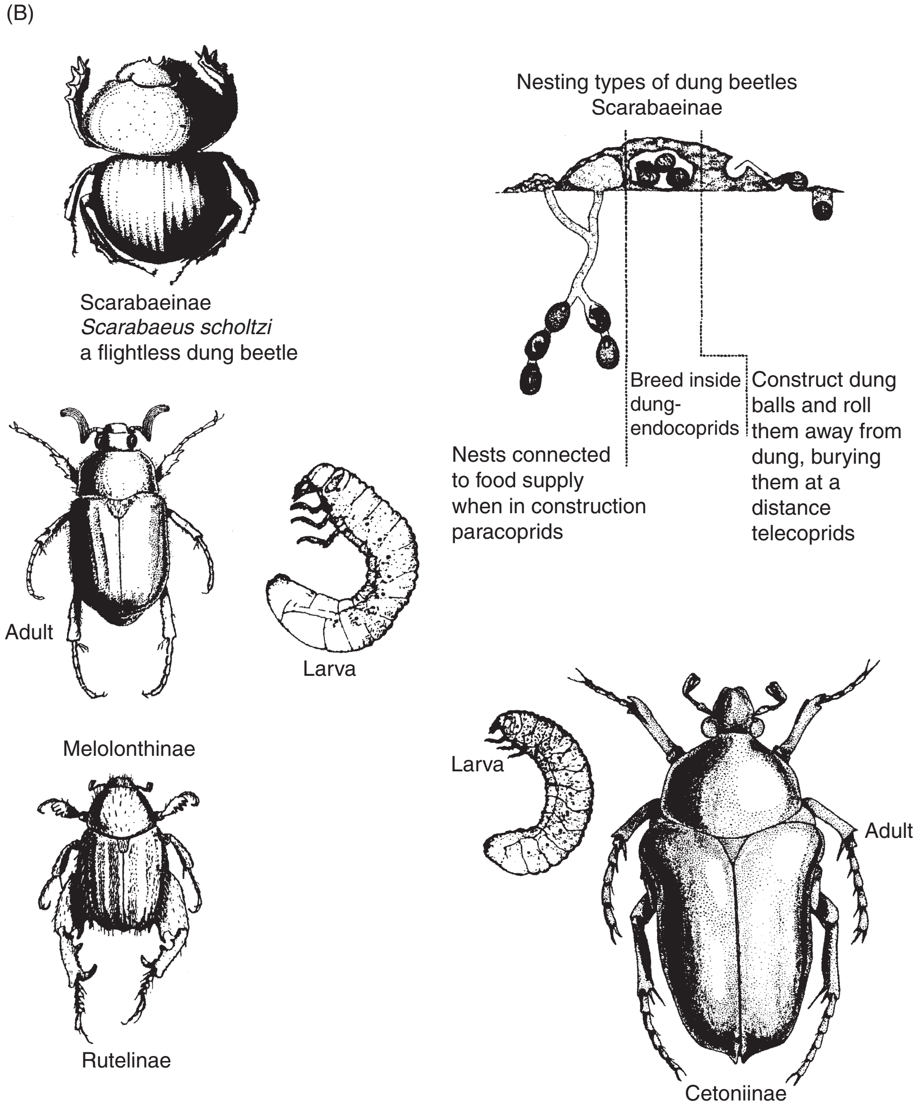


Figure 6.17 (*cont.*)

1979, Currie *et al.* 2006, Sauer *et al.* 2000, Aksoy 2003, Clark *et al.* 2000, Figure 8.9). Overall, mutualism has played a very creative role in the generation of biodiversity, and the expansion of ecology into many fascinating areas. Many of the criteria listed by Boucher (1985a, p. 23) needed to demonstrate that "mutualism is the major organizing principle in nature" have been met, establishing at least that mutualism has emerged as one of the few most important creative interactions in nature.

6.8 Modeling mutualism

Models of mutualism have a relatively long history in ecology, and have emphasized several different aspects of relationships: population stability, benefit and cost, and mutualism/competition models are a few examples. As models usually do, they attempt to clarify a conceptual framework, identify parameters and aid in developing methods for quantifying these parameters.

Gause and Witt (1935) applied the Lotka–Volterra **phase-plane model** to mutualism, and many papers have used this approach since (Boucher 1985a, Wolin 1985). This kind of model plots the population density of one mutualistic species on the horizontal axis and the other on the vertical axis, for instance with pollinating bees and plants. As populations change in size it is usually predicted that one species will benefit at one pair of densities, say low densities, and the other at higher densities. The species will then develop a stable equilibrium density where densities intersect, and four phases can be recognized: phase A, where both densities increase; phase B, in which both densities will decrease; phase C, in which species 1 will increase and species 2 will decrease; and phase D, where species 1 decreases and species 2 increases (Figure 6.18). The two interacting species are assumed to act independently, such as a pollinator species and a plant species, which of course is not relevant to many symbiotic mutualisms, such as those with transovarial transmission, coprophagy and most microbial symbionts. Also, as we have seen repeatedly, seldom are only two species involved in a mutualistic embrace – a third species is often the victim and multiple species are involved.

Nevertheless, much modeling effort has been applied to pairs of species that live independently. May (1973a,b,c, 1976, 1978b, 1981) developed models of mutualism using pollinators and plants as examples of interacting species, adding in the phase-plane models the likelihood of extinction when the density of either population becomes low (Figure 6.19). Resources such as food, in terms of food for the pollinator or transported pollen for the plant, may become too scarce to support the population, and populations would move towards extinction in the shaded area of Figure 6.19. The pollinator population, Y, can be assumed to grow according to the logistic equation (see Chapter 9), with a carrying capacity proportional to the plant population size, X. Therefore, equilibrium numbers of the pollinator, Y, must lie along the plane defined by the line dY/dt. The plant population is assumed to have concave equilibrium values because intraspecific competition limits maximum density, setting a carrying capacity, and plants can propagate by seed only when pollinators are adequate. A threshold density of pollinators is involved, below which plant populations will decline. Above this density the plant population will increase toward the carrying capacity,

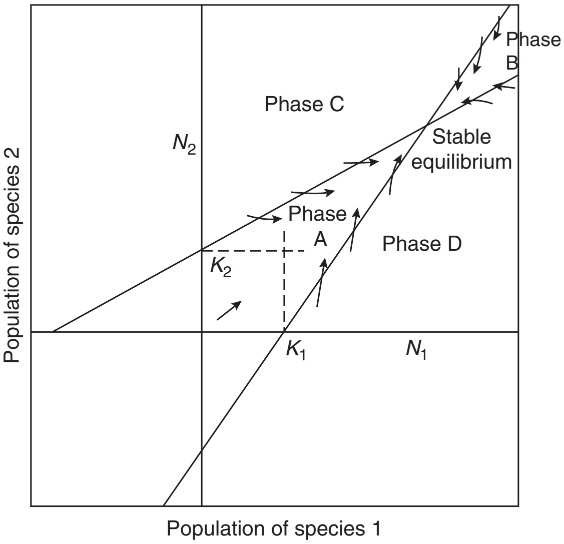


Figure 6.18 A phase-plane model of mutualism for species 1 and 2, with populations N_1 and N_2. K_1 and K_2 represent the maximum population size at which each species can exist without the other – the carrying capacity for species 1 and 2 respectively. The model is based on Lotka–Volterra equations, but with mutual positive effects, as opposed to negative effects in the original model. Arrows show the direction of population trends toward the stable equilibrium. In Phase A both species increase; in Phase B both species decrease, etc. From Hutchinson, G. E. 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven Copyright © 1978 Yale University.

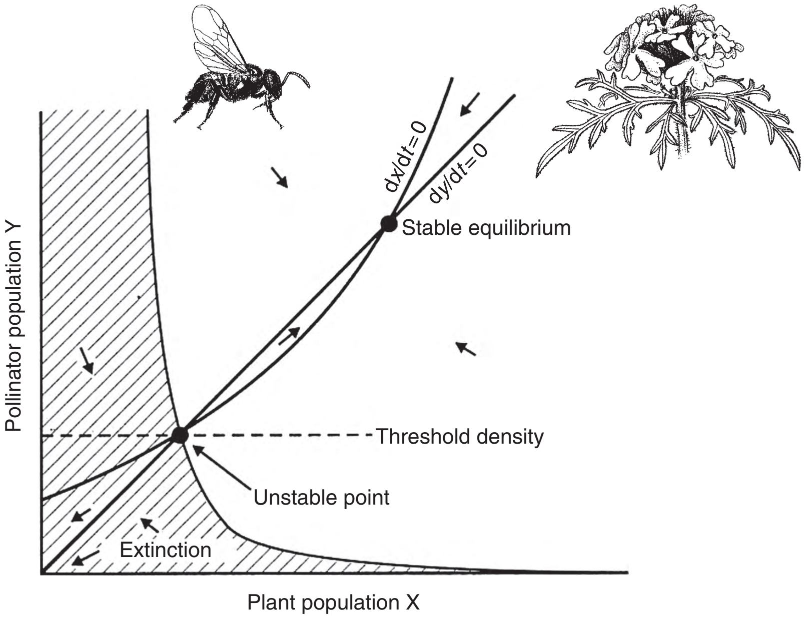


Figure 6.19 May's (1976) model of two mutualistic species *X* and *Y*, with plant and pollinator populations in mind. The threshold density of pollinators is the minimum required to maintain a viable plant population at the unstable point. Arrows show the directions in which populations will move. Modified from May 1976.

hypothetically reaching a stable equilibrium with pollinators, at which point plant populations below equilibrium will increase, and populations above equilibrium will decrease, as shown in Figure 6.19, and in the simpler phase-plane model in Figure 6.18.

Another kind of model emphasizes benefit/cost ratios. One example is Fonseca's (1993) model concerning mymecophytes and their ant mutualists. He assumed that ant colony size on a plant with domatia or extrafloral nectaries, or both, could increase in a linear way, but the benefit to the plant would increase rapidly at low ant colony size and would decline as ants no longer increased their host plant protection, so the benefit of ants would reach an asymptote (Figure 6.20). At extreme ant densities the relationship moves from mutualism to parasitism, when the costs of domatia exceed the benefits of ants. This conceptual model could be tested using energy required to meet the costs, and that saved by the benefits, with the expectation that an optimum ant-colony size would be evident where benefits far exceed costs, shown as the "maximum net benefit" at ant density, *N*, in Figure 6.20 (see also Fonseca and Benson 2003). Fonseca suggests that mymecophytes could limit ant-colony size by setting a low carrying capacity for nesting sites – domatia – on the plant, thereby controlling in evolutionary time the net benefit of ant mutualists. Keeler (1985) reviewed the many kinds of cost/benefit models of mutualism involving a variety of species, finding generalization difficult because of the diverse array of interactions. A promising approach has used net functional responses of pairs of mutualists based on the gross benefits of the mutualism (*GB*), the costs (*C*) and the net effects (*NE*) ($NE = GB - C$) (Holland *et al.* 2002). These variables are estimated as per capita rate of reproduction and/or survival of a mutualist population, Mutualist 2, in response to the population size of Mutualist 1. The modeling was

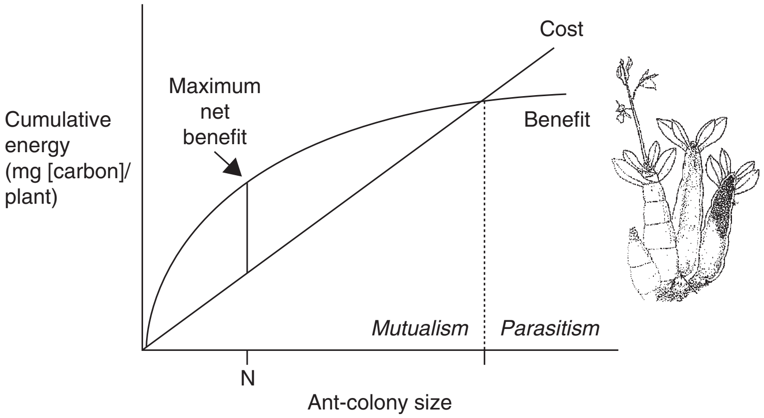


Figure 6.20 Fonseca's (1993) model of the costs and benefits for a myrmecophytic plant when associated with different colony sizes of the protective ants. At *N*, colony size provides the greatest net benefit to the plant host. When costs exceed benefits the ant colony becomes detrimental (parasitic) to plant fitness rather than beneficial (mutualistic). From Fonseca 1993. Reprinted with permission from Blackwell Publishing.

applied to the obligate mutualism of the senita cactus and senita moth already described in this chapter.

There is probably more interest in mutualism today than ever before, reflected in a great diversity of modeling approaches. Mutualism is so diverse in the kinds of interactions involved that it is difficult to generalize models that are helpful in understanding nature. To remain simple, however, models often emphasize two-species interactions. As an example, predator/prey kinds of approaches are used to examine functional responses of fig wasps and fig trees, and yucca moths and their hosts (e.g., DeAngelis and Holland 2006). Models of ants competing in a mutualism with a cactus (Morris *et al.* 2005) and the population dynamics and coevolution of mutualisms (e.g., plants and mycorrhizas) (McGill 2005) take very different approaches. Bronstein *et al.* (2007) explore a resource allocation model for the interesting case of a pollinating moth whose larvae are virtually obligate herbivores on the same host-plant species. The moth is both mutualist and antagonist in different stages of its life cycle. The variety in this literature is impressive, and the quantification of parameters and the testing of models remains a major challenge in the field.

6.9 Complexity of interactions

The diversity, frequency and intimacy of mutualisms should have been clear in the treatment of this subject, but we have yet to emphasize the inevitable community dynamics when several to many species interact. Gilbert (1980) captured this kind of complex scenario very well (Figure 6.21). Two-species systems they are not. Most mutualisms are included in multispecies systems, across diverse landscapes, with complex interactions incorporating many kinds of interplay. Gilbert (1980, p. 23) used the term **keystone mutualists** which he defined as "those organisms, typically plants, which provide critical support to large complexes of mobile links." **Mobile links** are "animals that are significant factors in the persistence of several plant species which, in turn, support otherwise separate food webs" (p.19), such as pollinators, fruit and seed dispersers, and ants that defend plants, with bats, birds, moths, bees and ants as focal players.

The plants are likely to have distinct phytochemicals to which certain insects are attracted, and, together with mutualistic pollinators and ants, much of Neotropical biodiversity is organized,

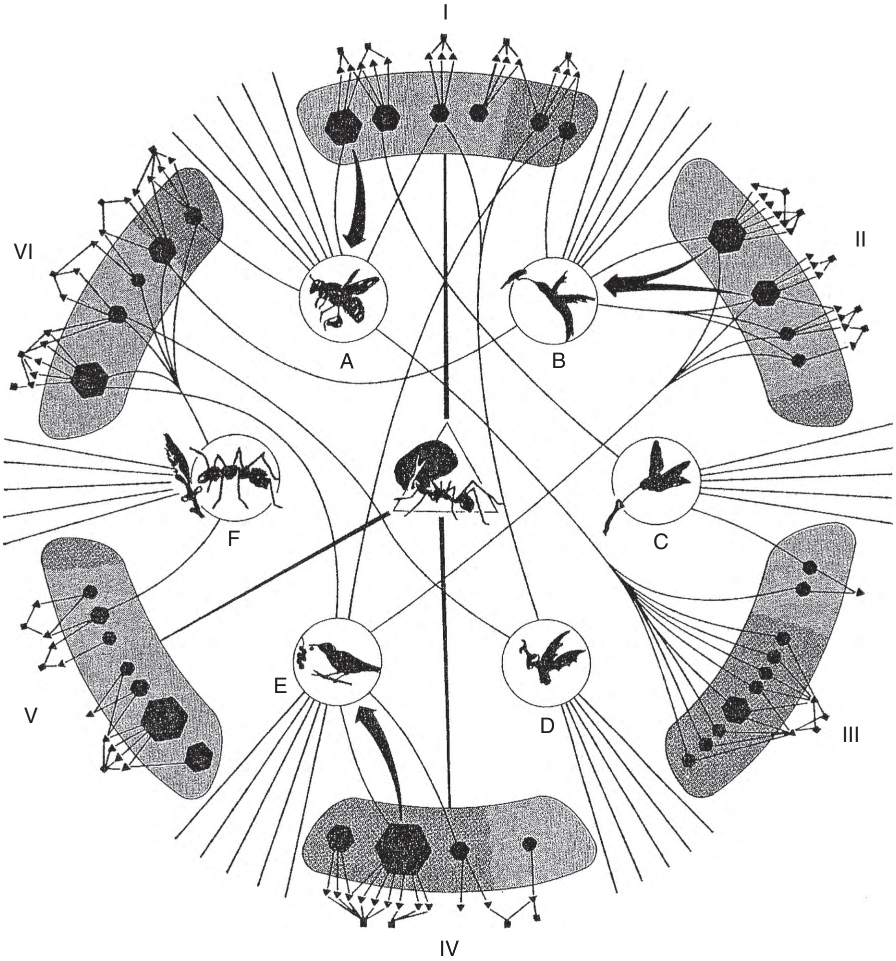


Figure 6.21 Gilbert's (1980) concept of how most Neotropical diversity is organized based on the particular characteristics of plant groups (I–VI), and mutualistic associates such as ants, bees, hummingbirds and bats. See text for details. From Gilbert 1980.

according to Gilbert. Many mutualistic associations could be added, such as mycorrhizas, microbial symbionts in many animals and honeydew-providing hemipterans.

Gilbert's view of complex tropical mutualisms is organized around six plant groups (Figure 6.21): I, the *Solanum* family, Solanaceae; II, the genus *Heliconia*: III, orchids; IV, canopy-emergent trees such as figs; V, grasses; VI, passion-flower vines. The hexagons represent plant species, with hexagon size indicating taxon abundance. Many of these plants act as keystone mutualists, providing important resources for mobile links (see heavy arrows). Specialized herbivores on particular host plants are represented by small solid triangles, and their specialized parasites by small solid boxes, all indicated on the outside of the plant groups in the figure. The large triangle in the middle of the figure represents generalized herbivores such as grasshoppers and leaf-cutter ants. The six large circles show mobile links important in pollination, seed dispersal, and plant protection (A–F), and thin lines show the resources they service including many passing out of the figure to other kinds of plant groups. Heavy arrows indicate plants critical to the support of mobile links, which are themselves mutualists. Added complexity comes at the landscape level on which plant species occur at different stages of succession, on different soil types, and at various places on the topography. The connection among plant groups maintained by mobile links should be noted. Only when habitat heterogeneity prevails, so that the many plant groups coexist as an interwoven community, can the services of these mutualists be supported. This figure would be much more complex were all species included. Nonetheless, "Mutualism plays a crucial role in the maintenance of diversity in the system" (Gilbert 1980, p. 32).

Figures similar to Gilbert's portrayal (Figure 6.21) could be developed for almost any community on Earth, emphasizing the essential roles of mutualists in ecosystems, and the supporting roles they perform in maintaining biodiversity (see examples in Strauss and Irwin 2004).

Modeling approaches have explored several roles of mutualisms in communities, which expand upon Gilbert's empirical example (e.g., Lewinsohn *et al.* 2006, Fortuna and Bascompte 2006). The maintenance of biodiversity was addressed by Bascompte *et al.* (2006) who argued that mutualistic networks should be regarded as coevolved structures with two important traits: (1) **coevolutionary complementarity**, in which pairwise interactions depend on matching characters such as flower depth and pollinator proboscis length; (2) **coevolutionary convergence**, in which species can enter into existing networks because characters such as flower depths or proboscis lengths are convergent. Their modeling suggests that asymmetric relationships between mutualists, one strong and one weak, are important in the maintenance of biodiversity.

Were communities cataloged for the number of interactions involving predation, parasitism and mutualism, we should expect mutualistic interactions to rank along with the other two major forms of interplay. To maintain systems in balance, antagonistic interactions should be matched by reciprocal beneficial ones. Hopefully, a growing literature on mutualistic interactions will eventually reflect this kind of balance.

6.10 An historical note

One wonders why mutualism has been under-rated or even ignored in ecology, even into the recent past. History provides a clue. Elton (1927) in his influential book, *Animal Ecology*, ignored the subject. Andrewartha and Birch (1954) mentioned mutualism once, and Lack (1954, 1966) not at all. Odum (1959) noted how mutualism was widespread and important, but treated the subject only briefly. A small consideration of mutualism was spliced into a chapter on predator and prey relationships by Ricklefs (1973). In May's (1976) rendition of a mutualism model (Figure 6.19) he noted that in unstable environments one or both species would be likely to slip into the shaded zone and move to extinction. Therefore, he concluded that mutualisms will probably persist in stable environments, such as the humid tropics. Of course, this view is not reflected in nature because mutualisms are ubiquitous. One important contributing factor is that many associations are obligatory, involving transovarial transmission, coprophagy and tight social units with easy transmission. Also, many mutualisms can be found in cool temperate climates such as the British Isles where 45% of insect species were estimated to enter into some kind of mutualistic association (Price 1997), and mutualisms such as pollination are common throughout latitudinal gradients.

One of the reasons why mutualism was under-rated in ecology resulted from an early emphasis on mammals and birds (e.g., Elton 1927, Lack 1954, 1966). Although mutualism is common enough in these groups, such as gut symbionts, bird and bat pollinators, bird and mammal seed and fruit dispersers, and the many associations represented in Figure 6.21, these interactions were largely ignored. Andrewartha and Birch (1954) concentrated attention on insects, yet still almost ignored mutualism. This general disregard was widespread in those times, contributing to generations of ecologists not versed in the fascination, ubiquity and importance of mutualism. Fortunately, "Mutualism ... is an idea which has been reborn in the last decade. Never entirely absent from ecological thought, it none the less fell out of favor as modern ecology grew, and only since the early 1970s have we begun to find it important again ... Ecologists once again find it interesting" (Boucher 1985a, p. 1). Now, most general ecology texts devote a chapter to mutualism, but they illustrate the weak development of concept and theory, compared to other interactions such as plant–herbivore interactions, competition and predation.

Applications

Beneficial interactions in agriculture

The growth and propagation of plants are fundamental to agriculture, forestry and horticulture. For these activities to be successful and sustainable, many kinds of organisms are essential, involving nutrition in soil, nitrogen fixation, mycorrhizal symbionts, decomposers, soil conditioners, pollinators and others perhaps, such as endophytic fungi (Price 1984b, Figure 6.22). Many mutualistic relationships are involved. Therefore, the art and science of growing plants should attempt to favor such beneficial activities and to minimize detrimental effects. The use of insecticides may well be lethal to soil organisms and pollinators, and fertilizers may diminish the positive effects of mycorrhizas. Therefore the accomplished farmer, or forester, recognizes the subtle interplay of all components in the ecosystem which is being managed. As demand for organic crops increases, preserving natural pathways of interaction in the soil, above ground and between the two will enhance the quality of the crop, the profitability for the grower, and the welfare of the ecosystem.

Management is well developed for the promotion of crop pollination, where honey bees contribute an estimated \$12–16 billion of crop value per year in the United States, and native bees about \$3 billion (Losey and Vaughan 2006). Not only is direct pollination of crops an important ecosystem service performed by insects, but many animals are supported by the resources supplied by insect-pollinated plants. Hence, animal food, dairy

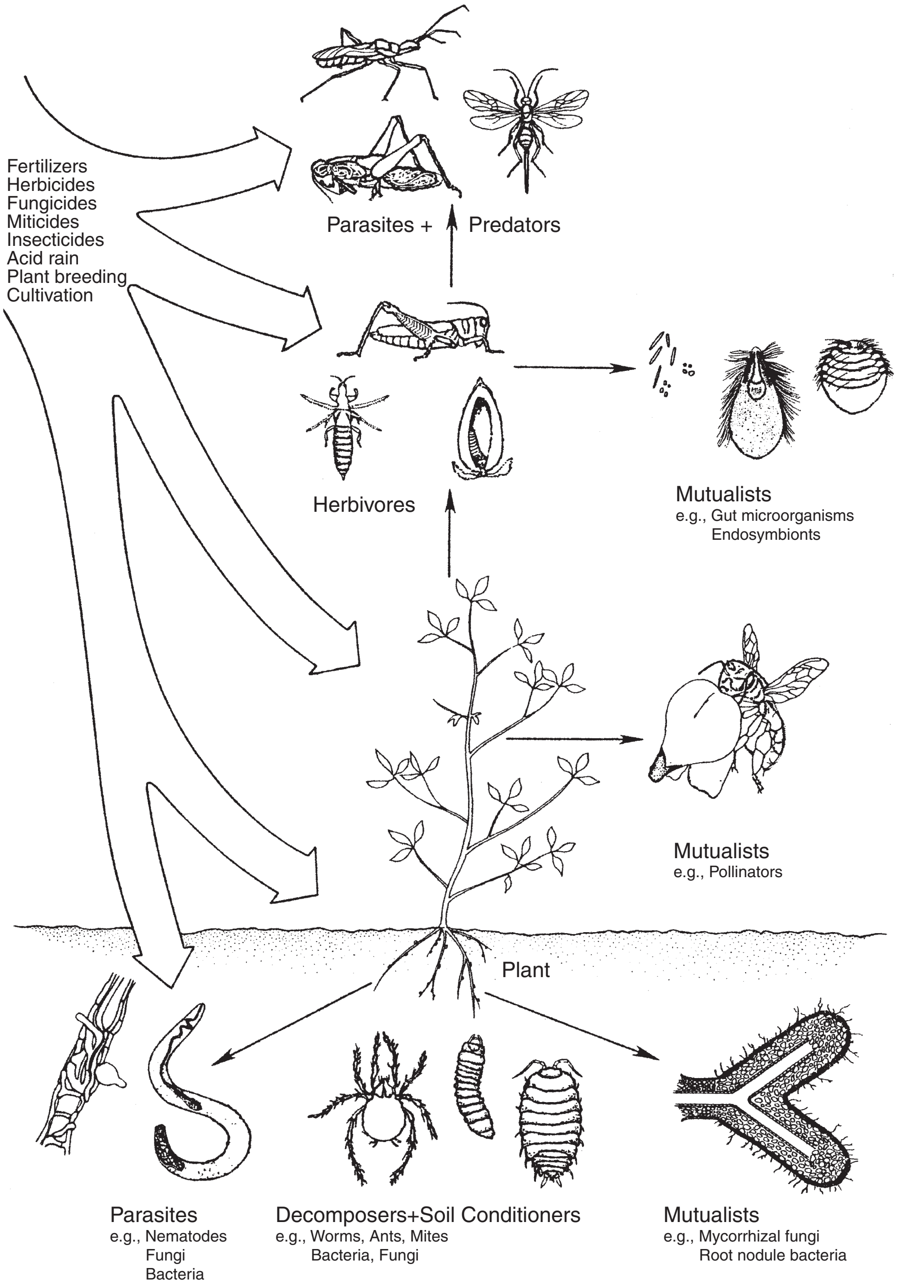


Figure 6.22 The many factors, animate and inanimate, that influence the growth and productivity of a crop plant such as soybean, depicted in the center of the figure. Many of the organisms illustrated are mutualists. From Price 1984b.

products, nuts, vegetables, seeds and oils all contribute to an estimated 15% to 30% of the human diet in the United States which depends upon insect-pollinated crops.

However, the problem of **pollinator decline**, involving dramatic decreases of wild and domesticated bees occurring around the world, is threatening the sustained pollination of crops, and crop yields, the conservation of pollinator populations, and the plants which they service (Buchmann and Nabhan 1996). Papers have been commissioned (e.g., Allen-Wardell *et al.* 1998), and syntheses on pollinator decline have been sponsored, for example by the National Center for Ecological Analysis and Synthesis (e.g., Cane and Tepedino 2001, Keven and Phillips 2001 and associated papers), and the US National Academy of Sciences (Berenbaum *et al.* 2007). On a global scale, loss of pollinators is expected to reduce agricultural production by 3–8% (Aizen *et al.* 2009).

Many ecological questions need attention concerning landscape management, intercropping, floral properties of wild species and horticultural varieties conducive to pollinators, population and community structure of pollinating species, the epidemiology of the parasites afflicting pollinators and the impact of declines on cultivated crop yields and wild plant populations (see Allen-Wardell *et al.* 1998). The predictions of Carson (1962) and Tepedino (1979) that pollinators were threatened have been validated (Buchmann and Nabhan 1996), with declines resulting from "disruption of the delicate '**biofabric**' of interactions that bind ecosystems together" (Wilson 1996, pp. xiv–xv), or on the same theme in Carson's (1962, p. 73) words, the elimination of "the last sanctuaries of these pollinating insects and breaking the threads that bind life to life." These views mirror precisely the complex interplay of species described by Gilbert (1980), and discussed under the section on complexity of interactions in this chapter.

Other mutualistic systems also provide important ecosystem services. Losey and Vaughan (2006) estimate the value at some $0.4 billion per annum of dung burial by dung beetles, their role in the decomposition of dung, the recycling of nitrogen, the reduced fouling of forage and the amelioration of pest fly problems. Pest control by natural enemies, many with symbiotic associations (see below), is estimated at $4.49 billion worth of protection, and insects as food for birds and fish contribute to the economics of recreational activities to the extent of about $50 billion per year in the USA.

We know enough about the kinds of insects providing ecosystem services and the plants that they interact with to realize that a multitude of mutualistic interactions are involved. Many interactions will involve loose mutualisms such as predators and parasitoids feeding on plant products like nectar and pollen, which in turn provide protection of the plant against herbivores. But for many interactions intimate and obligate mutualistic associations have been detected, such as the polydnavirus (PDV) associates of parasitoids, which allow them to defeat the immune systems of their herbivorous hosts (see Chapter 8). Boucher (1985b) in his chapter on “Mutualism in agriculture” discussed the several ways in which humans can make practical use of mutualisms by simply promoting the associations found in nature as described in this chapter. This also involves the husbandry of mutalisms, as well as the focal crop.

Mutualism is also essential in the conservation of biodiversity. Samways (1994) emphasized the importance of maintaining pollinating systems intact in natural vegetation, and fostering ant–insect interactions by preserving ant habitat which is critical to the survival of its mutualistic associates. Although all butterfly host-plant species have remained in one English county, 42% of its butterfly species have been lost, partly due to reduction of suitable sites because of agriculture and urbanization, but also from more subtle changes in the landscape, such as reduced grazing resulting in lowered habitat quality for mutualistic ants. Gilbert’s (1980) concept of keystone mutualists, and the interplay of many plant species connected by their mutualists (Figure 6.21), is essential in promoting conservation efforts that maintain or amplify habitat heterogeneity. This view can also be applied to landscapes dominated by agriculture where natural vegetation is reserved in the landscape for its aesthetic appeal, and for the conservation of species that provide ecosystem services (Bianchi *et al.* 2006, Giliomee 2006). Fields set aside from agriculture can provide successional natural vegetation with plant species composition changing from year to year, thereby contributing to a mosaic of different habitats and insect species such as butterflies (Steffan-Dewenter and Tscharntke 1997a, Kleijn *et al.* 2006). Habitat fragmentation reduces insect diversity both in natural and agricultural landscapes (Kruess and Tscharntke 1994, Steffan-Dewenter and Tscharntke 1997b). Insect services decline as fragmentation increases (Tscharntke and Brandl 2004).

We may also learn critical lessons on how to manage microbial organisms, as insects do with their mutualists. For example, when ants grow their fungus gardens, the parasitic fungi on their gardens have been suppressed for millions of years by the antibiotic produced by bacteria mutualistic with the ants (Currie *et al.* 2006). The authors ask how antibiotic virulence can be maintained in the face of presumably strong selection for resistance to develop in the parasitic fungi. The answer is not yet known, although the solution may be applicable to antibiotic resistance in human medicine.

Another potential application of knowledge on mutualism is to target the microbial mutualists of insects that vector disease-producing organisms among animals, including humans. For example, insect vectors that suck blood, such as sucking lice and triatomine bugs, have symbiotic bacteria that contribute nutrients to their otherwise restricted diet. Genetically altered bacteria could be produced that target the pathogens and disrupt transmission cycles in the insect vector. This approach is under investigation in the reduviid bug, *Rhodnius prolixus*, which transmits *Trypanosoma cruzi*, the causal agent of Chagas' disease. The method is known as **paratransgenesis**, or the **Trojan Horse method**, akin to introducing warriors into the heart of a community (Durvasula *et al.* 2003). The altered bacteria are transmitted transovarially from generation to generation making a lineage permanently pathogenic to the human pathogen (so long as resistance in the human pathogen does not evolve).

In the protection of crops, symbiotic fungi pathogenic to pest insects are likely to become very important. For example, *Beauveria bassiana* has been used as an entomopathogen for many years, but it also becomes an endophytic symbiont with corn (= maize), and many other plant species (Arnold and Lewis 2005). It is transmitted horizontally by dry conidia germinating on a leaf surface when moist, or by sucking insects. Its antibiotic activity is widespread among insect orders. Many other endophytic fungi show entomopathogenic activity which may be harnessed in the service of insect pest management on crops.

Another kind of interaction may prove to be important in control of virus transmission among plants by aphids and other vectors. In this context, plant extracts, such as those from the neem tree, *Azadirachta indica* (Meliaceae), interfere with the metabolism of the *Buchnera* symbiont in aphids, which reduces efficacy of the potato leafroll luteovirus. For instance, at certain low concentrations aphid growth was not impaired, but virus transmission was reduced by 40–70% (van den Heuvel *et al.* 1998). This example shows that microbial symbionts may be targeted with phytochemicals, or synthetic antibiotics, to effect control of the insect herbivores themselves, or the plant pathogens that they may transmit.

Whether in natural or managed environments, mutualisms play a major and even central role, in population, community and ecosystem processes, in the evolutionary biology of species, and in the adaptive radiation of lineages.

The role of mutualism is easily overlooked: a subliminal, but ubiquitous, presence. Researchers and managers should be alert constantly for the likely role of mutualistic associations and the way that they may influence ecology and evolution. Conversely, how humans may influence mutualisms in nature and in managed systems is a subject of enduring interest and importance.

Summary

We have entered into the complex and intriguing world of beneficial relationships among species by recognizing that mutualism has contributed centrally to the development of the eukaryotic cell and life in general. The roles of mutualisms in insect ecology are extensive, involving, by association with a mutualistic species, the exploitation of new nutritional resources, the acquisition of protection or the transportation of propagules. We have investigated how beneficial relationships have resulted in the evolution of biodiversity for insect herbivores, carnivores and the structure of trophic-level relationships. We speculated on the origins of mutualisms, perhaps deriving from parasitic relationships, and recognize that benefits must incur costs in these interactions between species. For example, pollinators may exact a cost on the pollinated plant by ovipositing in the ovary where larvae feed on seeds, protective ants must be sustained by food supplied by the plant and insects produce honeydew for their ant defenders. But cheating mutualistic systems is common, as in pollination, involving species that take nutrients without providing a service.

Four examples serve as reminders of how mutualisms have resulted in adaptive radiation of the taxa involved by opening up novel opportunities for exploiting resources. Breeding in trees, and utilizing woody tissue and organic litter have all been enabled with the acquisition of microbial mutualists. The modeling of mutualisms often employs a modified phase-plane model, with partners living independently, or benefit/cost ratio models; however, such models cannot capture the complex nature of mutualistic interactions, where many linkages among species are generated by species forming a network of associations in the community. The beneficial nature of mutualisms in agriculture are discussed in the applications section, as well as their relevance to conservation biology. Several opportunities exist for interrupting the obligate mutualistic function in pest insects, thereby disrupting their ability to live and breed.

Questions and discussion topics

1 If you were challenged to undertake a study of the relative numbers of interactions in a community involving competition, mutualism, predation and parasitism: (a) which kind of community would you select; (b) which methods would you employ and (c) what sorts of results would you anticipate?

2 Discuss the steps by which specific mutualistic relationships may have evolved.

3 With your experience as an entomologist, can you identify an insect taxon in which its adaptive radiation can be traced back to a key association between species? Consider an example in addition to those treated in Section 6.7.

4 Discuss groups of insects in which mutualism is not likely to be found, and in the light of all the groups involved in mutualism, explain the likely absence of mutualism in those groups.

5 In your opinion, how would the practice of agriculture benefit from greater recognition of mutualism as an important component of agricultural landscapes?

Further reading

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Losey, J. E. and M. Vaughan. 2006. The economic value of ecological services provided by insects. *Bioscience* **56**:311–323.

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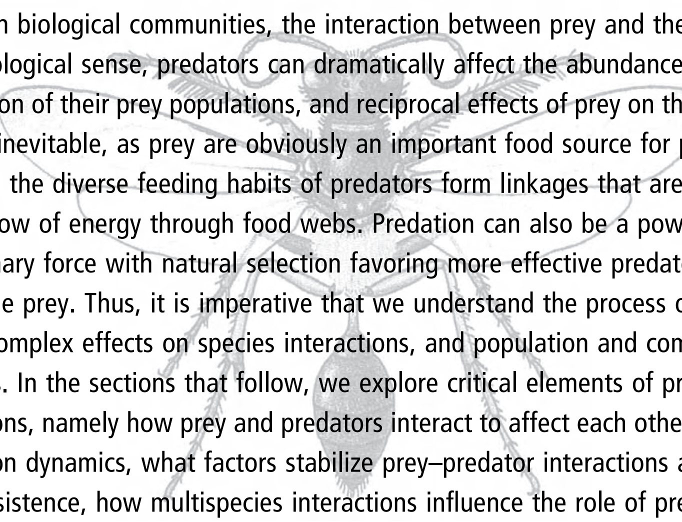
Wäckers, F. L., P. C. J. van Rijn and J. Bruin, editors. 2005. *Plant-provided Food for Carnivorous Insects: A Protective Mutualism and its Applications*. Cambridge: Cambridge University Press.

7

Prey and predator interactions



In Chapter 4 we learned how plants and herbivores can influence each other's abundance, distribution and evolution. Here we consider another important inter trophic level relationship that can have widespread ecological and evolutionary effects on biological communities, the interaction between prey and their predators. In an ecological sense, predators can dramatically affect the abundance and distribution of their prey populations, and reciprocal effects of prey on their predators are also inevitable, as prey are obviously an important food source for predators. Likewise, the diverse feeding habits of predators form linkages that are responsible for the flow of energy through food webs. Predation can also be a powerful evolutionary force with natural selection favoring more effective predators and less vulnerable prey. Thus, it is imperative that we understand the process of predation and its complex effects on species interactions, and population and community dynamics. In the sections that follow, we explore critical elements of prey–predator interactions, namely how prey and predators interact to affect each other's long-term population dynamics, what factors stabilize prey–predator interactions and promote their persistence, how multispecies interactions influence the role of predation in complex food webs, the contribution of behavior to a predator's total impact on prey populations, and how predators and prey have reciprocally influenced each other's evolution.

7.1 What is a predator?

In a very general sense, **predation** can be viewed as the consumption of one living organism (the prey) by another organism (the predator). Usually the whole prey item is killed and eaten. If the prey organism in question is a plant, then this general definition of predation includes herbivory. However, whole plants are usually only killed and eaten by a single predator when the plant is in the seed or seedling stage. Hence the terms seed predator and seedling predator are in common usage. In the context of this chapter, however, we restrict our definition of predation to acts of carnivory in which animals consume other animals. We define predators as animals that kill and consume all or parts of their prey, and require many prey items to reach maturity. This definition distinguishes predators from **parasitoids**, such as some small wasps and flies, which require and eat only one prey item during their life span. Parasitoids are free living as adults, and lay their eggs in or on a host. Larvae hatch from the eggs and live parasitically in or on the host, eventually killing it. For conceptual simplicity we discuss predators and parasitoids as representing distinct biological groups; however, the line distinguishing predators from parasitoids is often blurred, with biological reality perhaps better represented as a continuum rather than discrete categories.

Although a single parasitoid will directly consume a single prey item, an adult female parasitoid that oviposits on many hosts will ultimately be responsible for the death of many individuals. In this way, predators and parasitoids can have comparable ecological impacts, and prey–predator and host–parasitoid interactions share many important similarities. As a result, parasitoids have contributed much to the development of the theory surrounding predation (Raffel *et al.* 2008). Therefore, while the focus of this chapter is on predators and their prey, the relationship between parasitoids and their hosts will also be considered where relevant. A more detailed treatment of the ecological and evolutionary biology of parasitoids, and the parasitic lifestyle more generally, is provided in Chapter 8.

7.2 The generalized feeding habit of predators

While it is convenient to think of predators as occupying a discrete trophic level that is functionally distinct from that of their prey, in reality predators are often generalized in their feeding habits and may consume not only prey, but also other predators and/or plant resources (see Chapter 13). In this circumstance, generalist predators are more accurately described as **omnivores**, consumers that feed from multiple trophic levels. For instance, big-eyed bugs are often labeled as generalist predators, but are actually omnivorous consumers whose diverse range of prey species includes aphid and lepidopteran eggs and larvae, as well as the pods, seeds and leaves of many plant species. To further complicate matters, big-eyed bugs also fall victim to predation by omnivorous fire ants that compete with big-eyed bugs for herbivorous insect prey. This special case of omnivory, when predators consume other predators with which they compete for a common prey resource, is called **intraguild predation**. **Cannibalism** is distinguished from intraguild predation as occurring when predators consume members of their own species. Wolf spiders (*Lycosa* and *Pardosa*), for example, are notoriously cannibalistic, consuming smaller individuals in the population and even their own offspring. As we will see in Chapter 13, generalist predators that engage in omnivorous feeding strategies, including plant feeding and intraguild predation, enhance the complexity of food webs and complicate our understanding of the role of predators in community dynamics.

Although many predators are generalists and feed on a diversity of prey species, there are some very specialized feeders. Ground beetles in the genus *Scaphinotus* feed selectively on mollusks and have a long head and mandibles adapted for reaching deep into snail shells. In contrast to predators, parasitoids commonly exhibit a high degree of specialization, often feeding on only a single life stage of a particular group of insects. This level of specialization is likely the result of the intimate association between parasitoids and their hosts (see Chapter 8). Whether predators are generalists or specialists can have consequences for food web dynamics, as we will see later.

7.3 Predator effects on prey abundance

Excluding predators from or adding predators to natural prey populations provides evidence that predators indeed can reduce populations of their prey, very significantly so in some cases. For example, herbivorous planthoppers (*Prokelisia marginata*) and their wolf spider predators (*Pardosa littoralis*) co-occur on the inter-tidal marshes of North America. When spiders are removed from habitat patches, planthopper populations erupt to very high levels. If spiders are removed, but are then added back into habitat patches at natural densities, planthopper populations remain suppressed (Döbel and Denno 1994).

The biological control of crop pests following the release of natural enemies provides further evidence that predators suppress prey populations. With the accidental introduction of cottony cushion scale (*Icerya purchasi*) from Australia, the California citrus industry became seriously threatened by this severe insect pest. In the late 1800s, a predaceous ladybird beetle (*Rodolia cardinalis*) was collected in Australia and subsequently released into California citrus groves. Shortly after the release of this efficient predator, it completely controlled the scale insect and saved the citrus industry from financial ruin (Caltagirone and Doutt 1989). The introduction of some insect growth regulators in the late 1990s that were highly toxic to *Rodolia* caused a re-emergence of cottony cushion scale, showing again that this predator remains the primary regulator of scale populations (Grafton-Cardwell *et al.* 2006). Since this classic case, the encouragement or release of arthropod predators has frequently resulted in reduced pest populations (Symondson *et al.* 2002). There are cases, however, in which predator removal does not result in increased prey density. Often, such cases involve compensatory mortality, whereby the mortality inflicted by predation is replaced by mortality from another limiting factor like food shortage, or compensatory population growth of prey as a result of reduced intraspecific competition.

It is clear that predators can inflict high mortality on prey populations and that in the absence of predation, prey population eruption is possible (see Chapter 11). But what is the exact nature of this predation, and how do prey and predators interact to affect each other's long-term population dynamics? As we will see later in this chapter, predators can have both consumptive and non-consumptive (i.e., behaviorally mediated) effects on populations of prey. We focus first on the consumptive impacts of predators and how these effects are influenced by a predator's response to changes in prey density, as well as interactions among conspecific and heterospecific predators.

7.4 Predator responses to changes in prey density

The first step in understanding the prey and predator relationship is to understand the response of predators to changes in prey density. This can either be the response of an individual predator in its ability to catch and handle prey (functional response) or an increase in predator population size (numerical response) as prey densities grow (Solomon 1949).

7.4.1 Functional response

The **functional response** of a predator describes how an individual's rate of prey consumption changes in response to prey density. In a practical sense, functional responses can be used to estimate rates of prey depletion, identify predator preferences for particular prey types, characterize linkages across trophic levels and may ultimately contribute to the prediction of community dynamics.

Using a component analysis approach, Holling was able to identify several predator-related factors that contribute to the functional response (Holling 1959a, b, 1961). In his now classic experiment, a blindfolded human "predator" foraged for 4 cm diameter sandpaper disks or "prey" that were tacked to a 9-ft^2 table. The number of disks captured in one minute by tapping the table until finding a disk and removing the disk from the table was recorded across a range of disk densities. These data were used to develop a general model of the predator functional response known as the Holling disk equation. The general disk equation is

$$N_A = \frac{aT_T N_o}{1 + aT_H N_o} \tag{7.1}$$

where N_A is the number of discs removed, N_o is the density of discs offered, T_T is the total time available for searching, T_H is the handling time and a is the searching efficiency or attack rate of the predator. This equation describes what is known as a Type II functional response curve in which the consumption rate of the predator increases at a decelerating rate until it levels off to an upper plateau (Figure 7.1). This saturating response is the result of a trade-off in the time available for a predator to search for prey (T_T) and the handling time (T_H), the time required to subdue, consume and digest each prey item. At low prey densities, predators spend most of their time searching for prey items. At high prey densities most of a predator's time is spent handling captured prey and relatively little time is spent searching for additional prey. Eventually, predators become satiated and the response saturates since predators that are not hungry will not continue to consume additional prey items (Holling 1966). Thus, Holling's work highlights four essential components of the Type II functional response: rate of successful search, time predator and prey are exposed to each other, handling time and hunger.

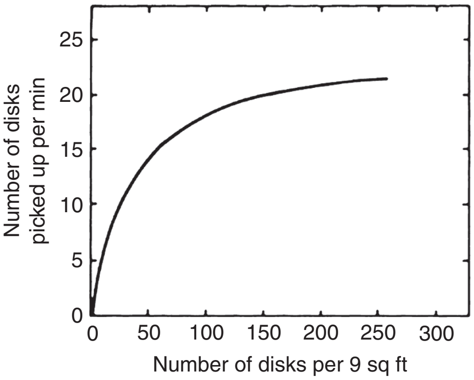


Figure 7.1 Graphical representation of Holling's disk equation showing the rate of discovery by a human "predator" in relation to the density of sandpaper disc prey. From Holling (1959b).

The basic Type II functional response curve originally described by Holling accurately represented the few published responses of natural enemies to prey density that existed at the time, all of which involved parasitoids or invertebrate predators, including eulophid and braconid wasps, corixid bugs and dytiscid beetles (Holling 1961). Further study revealed that alternative relationships between predator consumption rate and prey density were possible under different ecological scenarios. For example, vertebrate predators such as small mammals and birds produced a sigmoidal or S-shaped functional response. Only small variations on the disk equation were necessary to accurately reproduce these alternative functional response curves. Holling (1959a) described three major types of functional response (Figure 7.2):

Type I functional response – For predators exhibiting a Type I functional response, the consumption rate of a single individual is limited only by prey density. Thus, over a wide range of densities, per capita consumption and prey density are linearly related, up to a

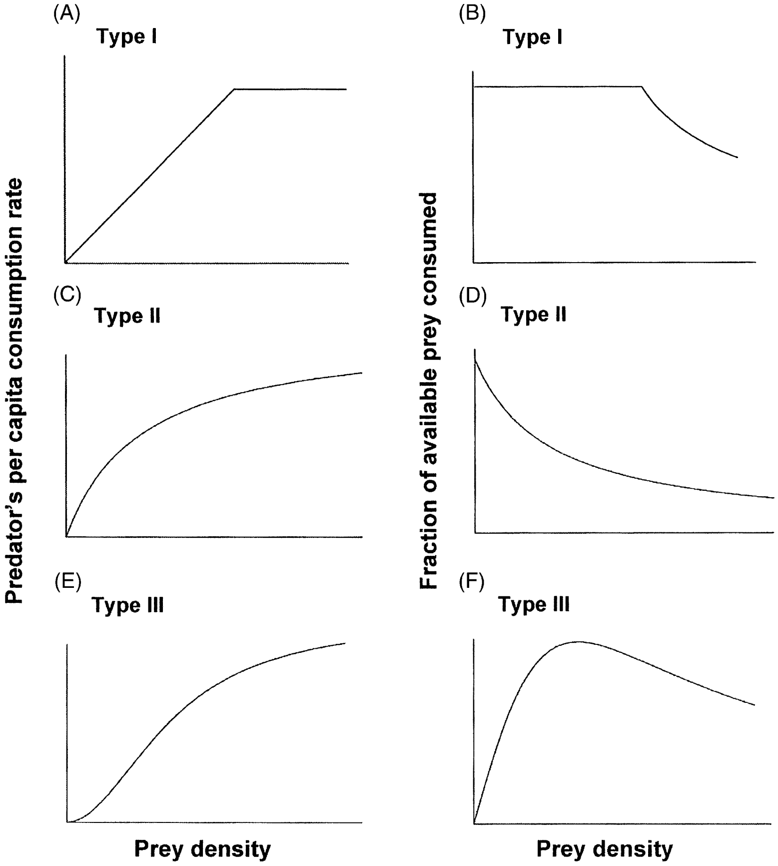


Figure 7.2 Three major types of functional responses. Per capita consumption rates are shown for predators exhibiting Type I, Type II and Type III functional responses (A, C and E, respectively), as is the proportion of prey taken of the total number offered for each type of functional response (B, D and F).

threshold density (Figure 7.2A). In this case, the proportion of prey captured of the total number offered remains constant and independent of prey density (Figure 7.2B). The Type I functional response is a specialized case that may be exclusive to "filter feeders," including web-building spiders, which are able to snare many food items simultaneously (Jeschke *et al.* 2004).

Type II functional response – Most invertebrate predators (e.g., hunting spiders, praying mantids, ladybird beetles) and most parasitoids exhibit the Type II functional response described by the general disk equation above (Luck 1984, Fernández-Arhex and Corley 2003; Figure 7.2C). Notably, for predators with a Type II response, the fraction of prey captured of the available total decreases with increasing prey density (Figure 7.2D). As prey density increases, such predators are less able to reduce prey population growth, thus providing prey with an ever-growing opportunity to escape from predation.

Type III functional response – Many vertebrate (e.g., birds and mammals) and some invertebrate predators and parasitoids show a sigmoidal or Type III functional response (Figure 7.2E). For such predators, consumption rate responds slowly to increases in prey density when prey are scarce. At somewhat higher prey densities, consumption rate rises rapidly, and at very high prey densities consumption rate saturates and is limited by handling time and satiation as in a Type II response. The rapid rise in consumption rate at intermediate prey densities can be the result of multiple mechanisms. Predators may learn to discover and capture prey with increased efficiency (Holling 1959a, Tinbergen 1960), or they may simply increase their searching rate as they encounter more prey (Murdoch and Oaten 1975, Hassell *et al.* 1977). Prey switching can also lead to a Type III functional response (Oaten and Murdoch 1975). Generalist predators often switch to alternative prey when the density of their preferred prey species falls below a certain threshold abundance. Therefore, prey switching can transform a Type II response into a Type III because the consumption rate of focal prey is relaxed at low prey densities. With a Type III response, the fraction of prey consumed of the total offered is initially low, increases with prey density up to a point, and then eventually decreases (Figure 7.2F). The density-dependent predation that occurs at lower prey densities contributes to prey–population regulation and may promote stability in the prey–predator interaction, which we will see later.

7.4.1.1 Functional response to a defended prey

Holling (1965) also recognized that not all prey are uniformly susceptible to predation and that some prey species evolve defensive mechanisms against predators. When prey exhibit defensive behaviors, Holling predicted that the functional response would be humped with the number of prey taken, initially increasing with prey density, but eventually dropping off as the predator learns to avoid the defended prey or as the prey defense becomes more effective at higher prey densities (Figure 7.3). The first experimental demonstration of a humped functional response came from the work of Tostowaryk (1972) who assessed the effect of prey defense on the functional response of a predatory pentatomid, *Podisus modestus*, to varying densities of the colonial sawflies *Neodiprion swainei* and *N. pratti banksianae*. These sawflies display a collective defense behavior, whereby sawfly larvae rear back and produce a resinous regurgitate when threatened by a predator, and this defense becomes more effective as colony size increases. Tostowaryk found that the predator's attack rate on sawfly larvae initially increased with an increase in sawfly density. However, prey eventually reached a density at which their collective defensive response became effective, and the attack rate of the predator declined. When the defensive response of the sawfly larvae was removed by treating the larvae in hot water, the humped functional response was no longer evident and a classic Type II response resulted (Figure 7.4).

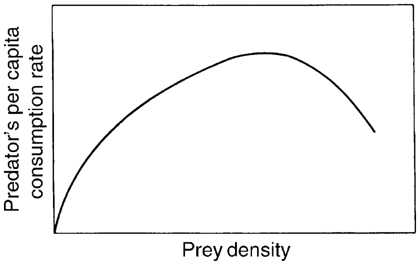


Figure 7.3 Hump-shaped functional response of a predator to a defended or distasteful prey. From Holling (1965).

7.4.1.2 Predator-dependent functional response

So far we have considered only the traditional prey-dependent functional response that describes the number of prey eaten by a predator as a function of prey density (e.g., Figure 7.5A). However, the density of predators co-occurring in a particular habitat may also play a significant role in determining the consumption rates of individual predators due to factors such as adaptive antipredator behavior by prey (e.g., refuge use or lowered activity levels of prey in response to the presence of predators) (Abrams 1993) and mutual interference among predators (Schenk *et al.* 2005). A functional response

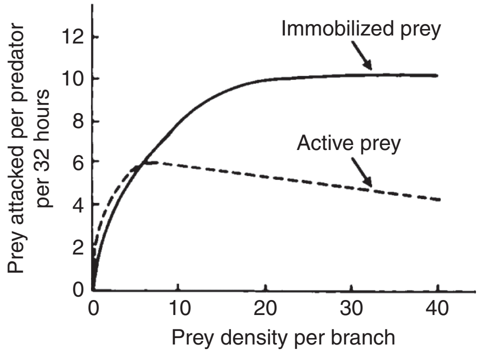


Figure 7.4 Functional response of third instar nymphs of the pentatomid bug, *Podisus modestus*, to normally active second instar larvae of the sawfly *Neodiprion pratti banksianae* that showed a defensive behavior in response to predator attack, and larvae of the same age and species that were immobilized by treatment in hot water and thus incapable of defense. Note that initially the active larvae are more heavily preyed upon as they are more visible to the predator, but as the prey density increases the colonial defensive behavior lowers the predation rate to less than 50% of that on the defenseless larvae. After Tostowaryk (1972).

that is influenced by changes in predator abundance is classified as predator-dependent (Holling 1961; e.g, Figure 7.5B). Ratio-dependent functional responses in which the response depends on the ratio of prey population size to predator population size are a specific case of predator-dependency (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000). In nature, it is unlikely that functional responses will be purely prey- or purely predator-dependent, with interference among predators becoming inevitable at sufficiently high predator densities (a breakdown of prey dependency) and interference among predators improbable at sufficiently low predator densities (a breakdown of predator dependency) (Abrams and Ginzburg 2000).

Field studies measuring functional responses where the densities of both predators and prey are manipulated are rare, but necessary, if we are to understand the impact of predators on prey populations in a broader food-web context.

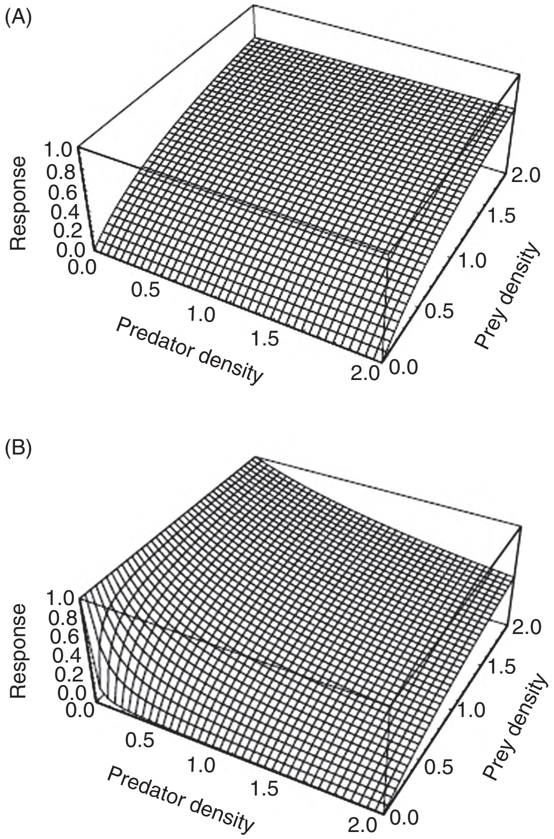


Figure 7.5 Functional responses as a function of both prey and predator densities. The traditional prey-dependent response (A) is unaffected by predator density. The ratio-dependent response (B) increases as predator density decreases. The ratio-dependent functional response is a special case of predator dependency in which the response depends on the ratio of prey population size to predator population size. Reprinted from *Trends in Ecology and Evolution*, Vol. 15, Abrams, P. A. and L. R. Ginzburg. The nature of predation: prey dependent, ratio dependent or neither? pp. 337–341, Copyright (2000), with permission from Elsevier.

A noteworthy case involves the predatory paper wasp, *Polistes dominulus*. Paper wasps are abundant generalist predators in South and Central Europe where they frequently attack larvae of the shield beetle, *Cassida rubiginosa*. Larvae of this beetle carry a fecal shield over their abdomen that provides mechanical protection against predation

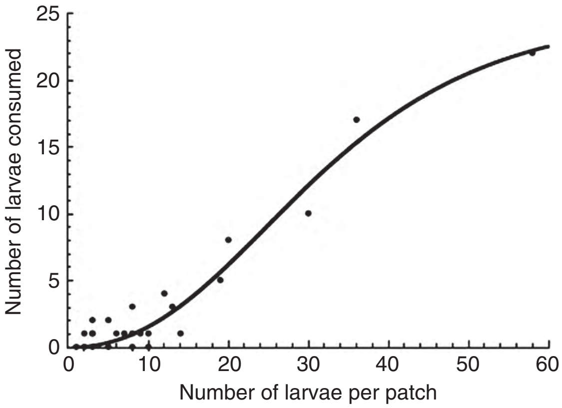


Figure 7.6 Type III functional response of the predatory paper wasp, *Polistes dominulus*, to manipulated densities of tortoise beetle larvae, *Cassida rubiginosa*, in the field. The beetles use fecal shields against natural enemies. From Schenk and Bacher (2002), by permission of Blackwell Publishing Limited.

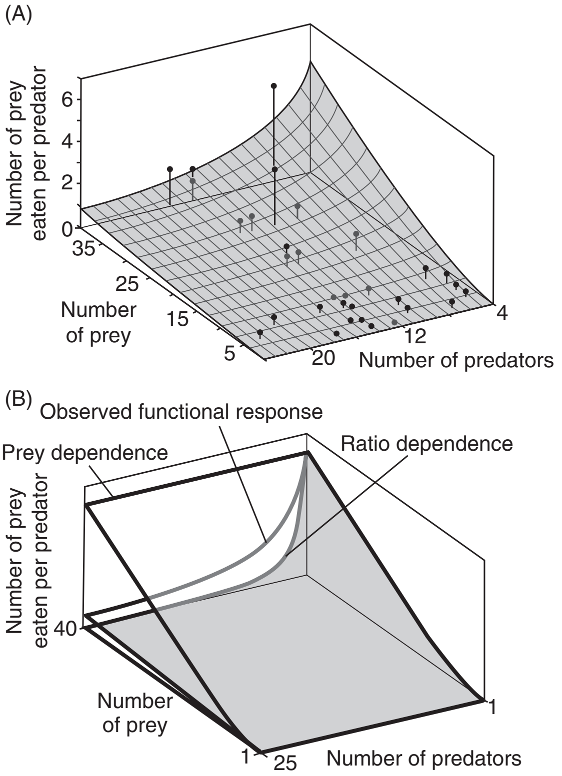


Figure 7.7 (A) The per capita consumption of tortoise beetle larvae, *Cassida rubiginosa*, by paper wasps, *Polistes dominulus*, as a function of both prey and predator densities. (B) The observed functional response of the wasp is dependent on both prey and predator densities, falling somewhere between strict prey- and strict ratio-dependence. From Schenk *et al.* (2005); by permission of Blackwell Publishing Limited.

(Eisner *et al.* 1967, Olmstead and Denno 1993). Initial studies to quantify the functional response of the paper wasp to shield beetle larvae were conducted in natural plots where only prey density was manipulated (Schenk and Bacher 2002). Video surveillance of predation events allowed an estimation of the functional response of the naturally occurring wasp population to the manipulated shield beetle larvae. In this open-field environment that potentially included alternative prey items for the generalist wasps, the functional response was characterized as a Type III (Figure 7.6). If no further study had been done, it might have been concluded that the functional response of the paper wasp is clearly prey dependent with the likely mechanism being that the generalist wasp is switching to alternative prey at low shield beetle densities. However, a follow-up study designed to test for predator dependency of the functional response by manipulating both prey and predator abundance in an open-field setting found that the functional response of this system actually lies somewhere between strict prey dependence and strict ratio dependence (Figure 7.7). Predator dependence in this case is the result of a decrease in the predation rate of paper wasps on shield beetle larvae with an increase in the number of wasps in the environment due to interference among predators (Schenk *et al.* 2005). To further complicate matters, it was found that the presence of a preferred alternative prey enhances the predator-dependent functional response, not by modifying the intensity of interference among predators, but by decreasing the effective number of predators foraging on the target prey (Tschanz *et al.* 2007). As an interesting caveat, there was no evidence of prey switching by the wasps despite the original finding of a Type III functional response. This system corroborates the prediction that precise prey or predator dependence is likely to be rare in nature (Abrams and Ginzburg 2000) and highlights the fact that functional responses are likely to be influenced by species other than the target prey. Experiments such as these that investigate mechanisms of predation in natural food webs are necessary to advance our understanding of the outcomes of prey–predator interactions.

7.4.2 Numerical response

So far, we have considered only the consumption rate of an individual predator under conditions of increasing prey and/or predator density. To gain a complete picture of how predators might control prey populations, we also need to know how many predators are present in the population and how predator population size responds to increasing prey densities, the **numerical response**.

Most predators exhibit a positive numerical response, becoming more abundant as the density of their preferred prey increases. Two independent mechanisms underlie this pattern, predator aggregation and enhanced reproduction. First, predators often aggregate in areas where prey abound. This is a behavioral response of predators to prey that results in a short-term change in the spatial distribution of predators. The local density of the wolf spider *Pardosa littoralis*, for instance, can be dramatically enhanced over a three-day period when prey are experimentally added to its habitat (Döbel and Denno 1994). Likewise, a significant increase in the number of ladybird beetles (e.g., *Hippodamia convergens*) in response to artificially enhanced aphid densities can be detected within as little as one day following aphid manipulation (Evans and Toler 2007). However, it is important to keep in mind that the spatial and temporal scale at which predators detect and respond to changes in the abundance of their prey can vary. For example, some predators may distinguish among individual plants, whereas others distinguish among patches of plants (Schellhorn and Andow 2005). Thus the appropriate spatial scale at which to assess predator aggregation and the numerical response may vary among predators. Second, if prey density remains high for an extended period of time, predator populations may build as a consequence of increased reproduction. For example, the number of eggs produced by ladybird beetle females has been shown to increase with an increase in aphid abundance (Dixon and Guo 1993). Unlike the aggregation of predators that happens relatively quickly in response to changes in prey abundance, the reproductive numerical response is only exhibited after a lag that can be equal to the generation time of the predator. Thus, predator aggregation and enhanced reproduction can both account for the numerical response of a predator to increased prey density, although at different time scales.

7.5 Prey–predator dynamics

Given that predators both affect and respond to changes in prey abundance, it is not surprising that reciprocal interactions between prey and predators can determine the long-term population dynamics of each (Gilg *et al.* 2003). Historic support for the view that a coupled prey–predator interaction can drive population cycles came from an analysis of ∼100 years of fur-trapping records by the Hudson Bay Company in boreal Canada. An analysis of the number of lynx and snowshoe hare pelts showed spectacular periodicity with peaks and valleys of abundance occurring at roughly 10-year intervals. When hares were numerous, lynx increased in numbers, reducing the hare population, which in turn caused a decline in the lynx population. With predation relaxed, the hare population recovered and the cycle began anew. It should be noted, however, that there is controversy over the singular role of predation in driving these population cycles (e.g., Stenseth *et al.* 1997).

An example of a coupled prey–predator population cycle in insects comes from a long-term manipulative study assessing the impact of a natural-enemy complex on the dynamics of southern pine beetle (*Dendroctonus frontalis*) populations in pine forests of the southern United States (Turchin *et al.* 1999). Enemies were excluded from some trees and not others for five years, encompassing one complete pine beetle population cycle with a population peak in abundance bounded by two valleys. When pine beetle populations were increasing from low abundance, predator-imposed mortality was negligible (Figure 7.8A). The strength of predation grew during years of peak pine beetle population size and reached a maximum during the initial period of pine beetle population decline. The relaxation of predation intensity as the pine beetle population declined allowed the beetle population to rebound and avoid extinction. At least one specialist predator in the natural enemy complex, the clerid beetle, *Thanasimus dubius*, exhibited population oscillations that were coupled with those of the pine beetle, indicating that it may play a particularly influential role (Figure 7.8B). However, it is important to remember that, while predation may make a significant contribution to the periodic oscillations in pine beetle populations, this does not preclude the possibility that other cyclical mechanisms may also play a significant role.

7.5.1 Lotka–Volterra model of prey–predator interactions

The first models of the cyclic dynamics of prey–predator interactions were constructed by Alfred Lotka (1925) and Vito Volterra (1926a,b) who independently derived the "predator–prey equations" (Lotka–Volterra equations) to describe the coupled dynamics of a single specialized predator and one prey species. Both men based their models on observations of reciprocal prey–predator cycles in nature. Volterra's ideas were motivated by watching the rise of fish populations in response to decreased fishing pressure during World War I, whereas Lotka was inspired by observing parasitoid–moth cycles.

Lotka and Volterra modeled prey–predator interactions in continuous time using differential equations to describe populations with overlapping generations and continuous reproduction. For the prey population, the rate of population change through time ($\mathrm{d}H/\mathrm{d}t$) is represented by the equation:

$$\frac{\mathrm{d}H}{\mathrm{d}t} = rH - \alpha HP \tag{7.2}$$

where H is prey density, r is the rate of increase of the prey population (birth rate), α is a constant that measures the prey's vulnerability to the predator and P is predator density. Thus, exponential growth of the prey population (rH) is countered by deaths due to predation (αHP). Change in the predator population through time ($\mathrm{d}P/\mathrm{d}t$) is shown by:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = cHP - dP \tag{7.3}$$

where c is a constant, namely the rate that prey are killed and converted to predator offspring, and d is the rate of decrease in the predator population (death rate). The decline in the predator population ($-dP$) due to death is offset by the rate that predators kill prey and convert them into offspring (cHP). The two equations provide a periodic solution in that predator and prey populations oscillate in reciprocal fashion through time (Figure 7.9A). When the dynamics of predator and prey populations resulting from the Lotka–Volterra equations are plotted in two-phase space (i.e., predator density versus prey density), a neutral limit cycle results, whereby both predator and prey populations cycle perpetually in time (Figure 7.9B).

Seeing that simple models could generate prey–predator oscillations prompted numerous researchers

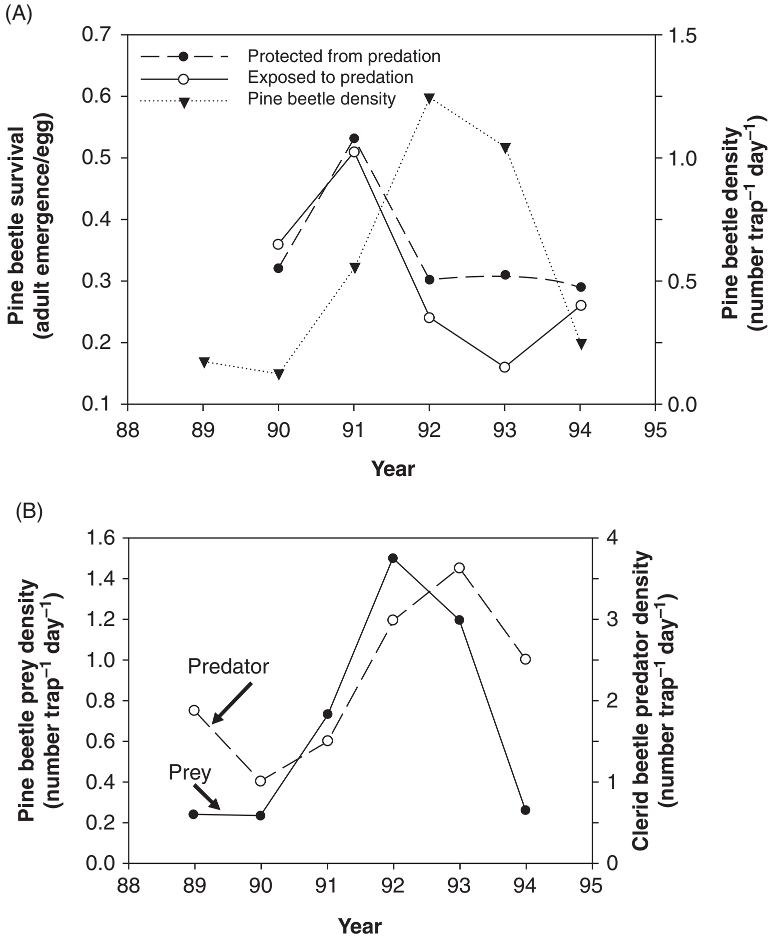


Figure 7.8 Cyclic population dynamics of the southern pine beetle, *Dendroctonus frontalis*, and its natural enemies. (A) The dotted line with solid triangles indicates pine beetle density during the course of a southern pine beetle outbreak. The intensity of predation on the pine beetle population during the outbreak can be estimated as the difference between survival of pine beetles when beetle populations were exposed to predation (solid line, open circle) and survival of pine beetles when protected from predation by caging (broken line, solid circles). (B) Densities of the southern pine beetle (solid circle, solid line) and one of its important predators, the clerid beetle, *Thanasimus dubius* (open circle, dashed line), as measured by a network of pheromone-baited traps. The clerid beetle exhibits population oscillations that are coupled with those of the pine beetle. From Turchin, P., A. D. Taylor and J. D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285:1068–1071. Reprinted with permission from AAAS.

to attempt to duplicate such persistent cycles under simple laboratory conditions. However, these attempts often failed. Gause (1934) was the first to test the Lotka–Volterra model experimentally. His experiments involved the predaceous ciliate protozoan *Didinium nasutum* and its prey, another ciliate, *Paramecium caudatum*. Five *Paramecia* were placed in laboratory cultures and after two days three predators were added. Initially, prey populations exploded in the absence of predators, but with the addition of predators *Paramecium* populations were quickly driven to extinction (Figure 7.10A). In the absence of prey, predators subsequently perished. Only by imposing artificial immigration upon the system, the addition of a single individual predator and prey every third day of the experiment, was Gause able to obtain a persistent prey–predator cycle (Figure 7.10B).

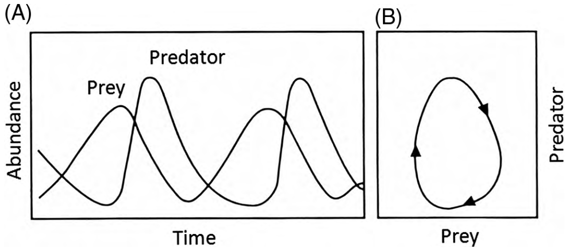


Figure 7.9 Population oscillations of prey and predator abundance predicted by the Lotka–Volterra equations. (A) Abundance plotted against time. (B) Phase diagram indicating perpetual coexistence of predator and prey. From H.G. Andrewartha and L.C. Birch, *The Distribution and Abundance of Animals*. Published by the University of Chicago Press. Copyright © by the University of Chicago Press. All rights reserved.

These unexpected results, and those from many other laboratory attempts, raised the question of why prey–predator cycles couldn't be easily reproduced in the laboratory, why such simple systems were inherently unstable, and why the prey–predator interaction didn't persist. Simply stated, more is needed to understand why prey are not driven to extinction at high predator densities and why predators persist when focal prey are rare. Ecologists have since identified multiple factors missing from the Lotka–Volterra model that introduce realism into prey–predator interactions and lend accuracy in predicting real-world dynamics.

7.5.2 Nicholson–Bailey model of prey–predator interactions

Nicholson and Bailey (1935) criticized the Lotka–Volterra equations on several points, including the unrealistic model expectation that predators and prey respond instantaneously to changes in each other's densities. For many natural enemies, their reproductive response to increases in prey density is lagged, and in some cases may be as long as a

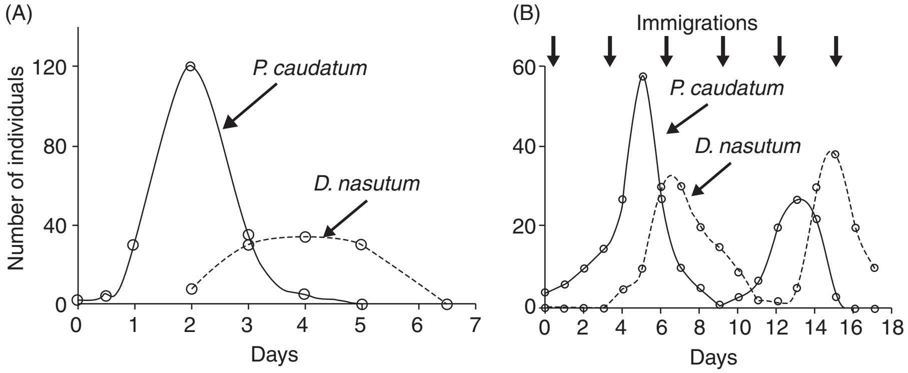


Figure 7.10 Interaction between predator (*Didinium nasutum*) and prey (*Paramecium caudatum*) in laboratory microcosms (A) without immigration and (B) with immigration (the addition of a single individual of the predator and prey once every three days as indicated by arrows). Low-level immigration of predators and prey into the system promoted the cycling and persistence of predator and prey populations. After Gause, G.F. 1934. Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* **79**:16–17. Reprinted with permission from AAAS.

generation of the predator. Thus, Nicholson and Bailey proposed a new model with parasitoids in mind. Rather than using calculus to describe continuous population change, as was done by Lotka and Volterra, a discrete-time model using difference equations was used to represent insect populations with synchronous reproduction and no overlap of generations. Several simplifying assumptions were made:

(1) Predator/parasitoid search is random.
(2) Prey/hosts are distributed uniformly in a uniform environment.
(3) The ease with which prey can be found does not vary with the density of the prey population.
(4) The appetite of predators (i.e., the capacity for parasitoid oviposition) is insatiable, independent of prey population density.
(5) The predator/parasitoid has an "area of discovery" that is a constant. The area of discovery represents the efficiency of the parasitoid in finding its prey and is measured as the proportion of prey found in the total habitat searched by the parasitoid during its lifetime.

Given these assumptions, host abundance in the next generation (H_{t+1}) can be modeled as a function of current host abundance (H_t) using the equation

$$H_{t+1} = rH_t e^{-ap_t} \tag{7.4}$$

where H is host density, r is the rate of increase of the host population (birth rate), a is the area of discovery, P is parasitoid density and t is the generation. The prey population has the capacity to grow exponentially (rH_t); however, only the proportion of prey population that avoids parasitism (e^{-ap_t}) will survive to the next generation. Prey survivorship declines as an exponential function of parasitoid population size due to the assumption of a random probability of encounter between parasitoids and their hosts. Alternatively, the proportion of the prey population succumbing to parasitism would be $1–e^{-ap_t}$, and thus the number of parasitoids alive in the next generation (P_{t+1}) is described as

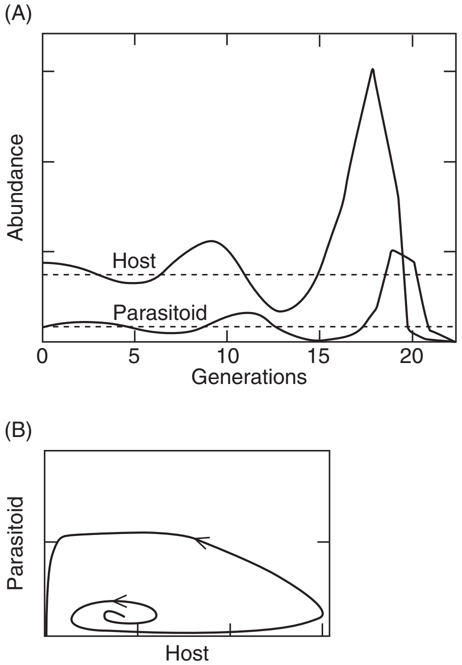


Figure 7.11 Population oscillations of host and parasitoid abundance predicted by the Nicholson–Bailey equation. (A) Abundance plotted against time. (B) Phase diagram indicating increasing oscillations. Steady states are represented by dashed lines. After Nicholson (1933); by permission of Blackwell Publishing Limited.

$$P_{t+1} = cH_t(1-e^{-aP_t}) \tag{7.5}$$

where c is the rate at which hosts are converted into parasitoid offspring. Together, these equations predict that a steady state exists in a constant environment where hosts and parasitoids can remain indefinitely at equilibrium densities. However, this steady state is unstable, with even the slightest environmental disturbance causing coupled oscillations in populations that increase in amplitude until the eventual local extinction of hosts and parasitoids (Figure 7.11).

Given the unstable dynamics predicted by this model, how can it be used to explain the behavior of real populations in nature? Just as Gause obtained stability by imposing immigration, Nicholson and Bailey argued that the stability of populations in the face of localized extinction requires recolonization from other patches. However, Nicholson and Bailey could hardly justify the need for spatial dynamics to induce stability in light of their original assumption that animals are distributed evenly over a uniform area.

7.5.3 Factors stabilizing prey–predator interactions

Despite lacking in realism, the Nicholson–Bailey model has provided a valuable starting point for subsequent investigations that attempt to identify aspects of the prey–predator interaction that can provide stability to the model. In the sections that follow, we will discuss some of the ecological factors that, when added to the model, improve its ability to predict real-world dynamics.

7.5.3.1 Mutual interference and the Hassell–Varley model

In an attempt to more accurately reflect the assumed stability of prey–predator or host–parasitoid interactions in nature, Hassell and Varley (1969) modified the Nicholson–Bailey model to incorporate the effects of **mutual interference** among parasitoids. The major criticism leveled at the Nicholson–Bailey model by Hassell and Varley was that the area of discovery (a) of a parasitoid is not a constant, but rather a function of parasitoid density. In real-world systems, parasitoids often disperse upon encountering other parasitoid individuals or cues that another parasitoid has been present, causing search efficiency to decline with an increase in parasitoid density. Hassell and Varley were able to show that for several species and over several orders of magnitude, the area of discovery was linearly related to parasitoid density in the following manner:

$$\log a = \log Q - (m \log p)$$

where a is the area of discovery, p is the parasitoid density, Q is the "quest constant" and m is the "mutual interference constant." Both Q and m are calculated empirically from the regression line with Q, the attack rate when only a single parasitoid is present, equal to the intercept and m equal to the slope of the line. Given this relationship, the area of discovery (a), rather than being constant, is actually predicted to decline with an increase in parasitoid density (p). Thus, we can solve for a by taking the antilog of the expression, swap this new density-dependent term ($a = Qp^{-m}$) for the a in the Nicholson–Bailey model, and the new "parasite quest equations" become, by substitution:

$$\begin{aligned} H_{t+1} &= rH_t \mathrm{e}^{-Qp_t^{(1-m)}} \text{ and} \\ P_{t+1} &= cH_t\left(1 - e^{-Qp_t^{(1-m)}}\right) \end{aligned} \tag{7.6}$$

where H is host density, r is the rate of increase of the host population (birth rate), c is the rate at which consumed prey are converted into parasitoid offspring and t is the generation. Unlike the Nicholson–Bailey model, the Hassell–Varley model provides for stable dynamics between parasitoids and hosts by incorporating density dependence into the behavior of the parasitoid population (Figure 7.12). The greater the value of the mutual interference constant (m), the greater will be the tendency for the host–parasitoid model to stabilize. Underestimation of m results in unstable dynamics similar to those produced by the Nicholson–Bailey model.

7.5.3.2 Predator aggregation

In addition to mutual interference, there are a multitude of other reasons why simple models inadequately predict prey–predator dynamics and do not capture the complexity of prey–predator interactions in nature. Foremost is that prey–predator interactions do not take place in closed systems in the absence of spatial processes such as emigration and immigration. Prey are highly unlikely to be uniformly distributed throughout a homogeneous environment, as assumed by Nicholson and Bailey, and it is likely that predators will respond to the

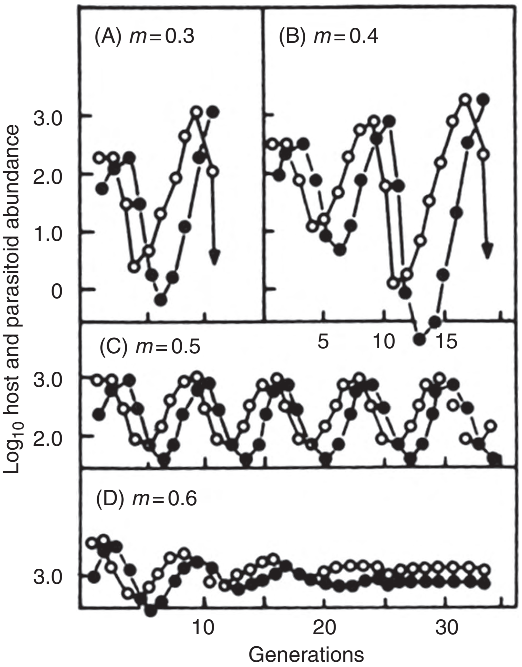


Figure 7.12 Population oscillations of host (open circles) and parasitoid (solid circles) predicted by the Hassell–Varley model with the mutual interference constant, m, increasing from 0.3 in (A) to 0.6 in (D). The greater the value of the mutual interference constant, the greater the stability of the host–parasitoid interaction. From Hassell and Varley (1969).

unequal distribution of prey across habitat patches. For example, at low prey densities, predators often disperse to areas of higher prey density, thus relaxing predation on the local prey population rather than driving it to extinction. Using a modified Nicholson–Bailey model, spatially aggregated attack by enemies in areas of high prey density was shown to promote the long-term persistence of the prey–predator interaction (May 1978a,b). This clumping of predator attacks can mimic the stabilizing effects of mutual interference, as described by Hassell and Varley, and has thus been described as "pseudo-interference" (Free *et al.* 1977, Beddington *et al.* 1978).

However, controversy exists surrounding the role of predator aggregation in stabilizing prey–predator dynamics, and it has been argued that the stability induced by spatial aggregation is merely an artifact of the model rules that govern the colonization of patches by predators (Murdoch and Stewart-Oaten 1989, Rohani *et al.* 1994). For example, subsequent studies document that stability can also arise in response to predator aggregation that is independent of prey density (Pacala and Hassell 1991, Rohani *et al.* 1994, Chesson 2000). These studies predict that the key to stability is variation among prey populations in their vulnerability to attack by enemies, with only a small fraction of prey accounting for most of the risk. Skew in the relative risk of predation among prey can result from individual prey being exposed to different densities of predators, as occurs when predators aggregate their attacks. However, it can also result from the fact that some prey are more difficult to find or attack due to their microhabitat use or phenotypic differences. In this case, stability is enhanced, not because of the spatial behavior of the predator, but because a subset of prey experience refuge from predation and avoid localized extinction.

7.5.3.3 Habitat complexity and refuge from predation

In addition to spatial processes, complex habitat structure and the refuge it provides for prey from predation also lends persistence to prey–predator interactions. A classic example involves interactions between the citrus-feeding spider mite *Eotetranychus sexmaculatus* and its predatory mite *Typhlodromus occidentalis* (Huffaker 1958). The population dynamics of the mites were compared between two experimental habitats: a simple habitat consisting of a monoculture of oranges arranged on trays and a complex-structured habitat where oranges were interspersed among rubber balls and little posts from which prey could disperse on a silken thread (the predator was limited to cursorial movement). In the simple habitat, predatory mites easily dispersed throughout the habitat, prey were driven to a

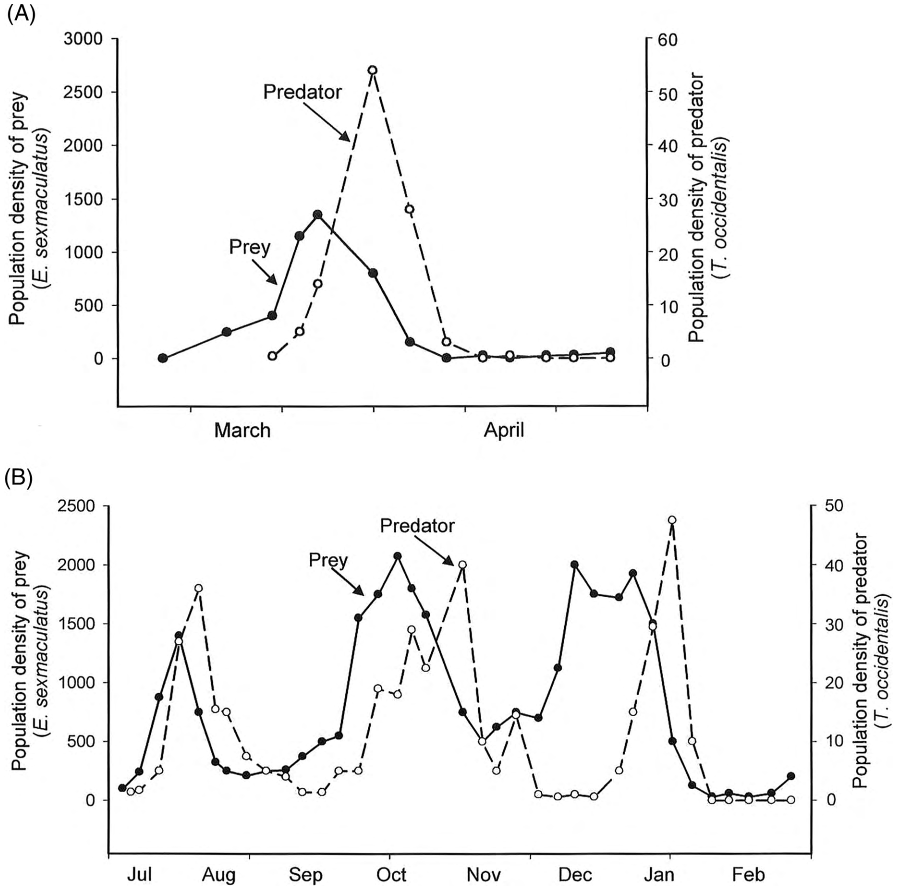


Figure 7.13 Results of Huffaker's test of the influence of refuge from predation on the persistence of prey–predator interactions. In a simple-structured habitat without refuges (A), predatory mites drive herbivorous mites to low densities, leading to the starvation and ultimate extinction of predatory mites. In a complex-structured habitat (B), herbivorous mites find refuge from predation and the prey–predator oscillation persists until food (orange fruit) quality for the prey deteriorates. After Huffaker (1958).

threateningly low density, and the predator went extinct (Figure 7.13A). In the complex habitat, prey dispersed and found refuges from predation, and three complete predator–prey oscillations resulted before the food quality of oranges deteriorated and the system collapsed (Figure 7.13B). Huffaker's study highlights the importance of environmental complexity in promoting the coexistence of prey and predators, but it also emphasizes that other factors such as the spatial arrangement of prey and predators, their relative dispersal capabilities and food quality all bear on the persistence of the interaction.

Like Huffaker, Ellner *et al.* (2001) found that populations of the predatory mite *Phytoseiulus persimilis* and its herbivorous prey, the spider mite *Tetranychus urticae*, persisted longer in complex habitats with clumped host plants as opposed to simple habitats where host plants were uniformly distributed. Using a modeling approach they were able to determine that the mechanism contributing to persistence was not the explicit spatial structure of the habitat (the system could be accurately modeled without consideration of the spatial location of the plants) but the fact that habitat structure reduced the success of predators at locating prey outbreaks. This refuge from predation created by habitat structure resulted in asynchrony in local population dynamics among plants, due to stochastic colonization events, and thus prevented the overall extinction of prey populations across the habitat.

Kareiva (1987) tested the contribution of habitat complexity to dynamic stability in a natural system. He manipulated the complexity of goldenrod (*Solidago canadensis*) habitats by mowing strips in a goldenrod field to create continuous or patchy goldenrod plots. Contrary to the results of Huffaker and Ellner, increasing the complexity of the goldenrod habitat by fragmenting the landscape resulted in more frequent localized outbreaks of aphids (*Uroleucon nigrotuberculatum*) and less stable dynamics. The unstable dynamic was a consequence of the complex-structured habitat interfering with the non-random foraging behavior of the predatory ladybird beetle, *Coccinella septempunctata*. In simple-structured habitats, ladybird beetles rapidly aggregate to and exterminate aphid clusters, which threaten to initiate population outbreaks. However, habitat patchiness promotes aphid outbreaks because it hinders this aggregation behavior of the predator. While this study failed to find support for the importance of habitat patchiness and refuge from predation in stabilizing prey–predator interactions, it confirms ideas about the importance of predator aggregation behavior as discussed above.

Together, these studies highlight the importance of interfacing behavioral qualities of predators and prey with habitat structure to determine the ultimate impact on stability. In all cases, habitat complexity interferes with the ability of predators to effectively track their prey and thus provides refuge from predation, but the dynamical consequences of the refuges vary depending on the intensity of control exerted by the predator. Complex-structured habitats promote stability when they provide refuge for prey from highly mobile and efficient predators, like mites, which are capable of extirpating prey in simple environments. However, the refuge provided to prey by habitat complexity may be just enough to tip the balance towards prey outbreaks and instability when less efficient predators, like ladybird beetles, are present.

7.5.3.4 Type III functional response

Prey species also escape predation, and thus evade extinction and the instability that results, due to constraints on the ability of predators to catch and handle prey (Holling 1959a, 1965). For this reason, it is predicted that predators exhibiting a Type III functional response to changes in prey density are more likely to stabilize prey–predator interactions than those with a Type II functional response (Oaten and Murdoch 1975). Theoretically, stability is imposed with a Type III response because the fraction of prey consumed by a predator is low at low prey densities, preventing predators from driving prey to extinction (Figure 7.2F). Yet, with an increase in prey density, the fraction of prey consumed increases (is density dependent), thus reducing the opportunity for prey to escape predator control. Only at very high densities are predators satiated such that the fraction of prey consumed decreases and the prey population escapes.

To understand why this stable dynamic is predicted to emerge with Type III, but not Type II, responses, we must first consider the growth potential of a prey population, and the amount of mortality necessary to offset that growth and maintain a constant prey population size over time. For a population exhibiting logistic population growth, where the rate of growth is density dependent and gradually decreases to zero at the carrying capacity for the population (see Chapter 9), the percent mortality necessary to exactly offset population growth and result in no net change in population size from one generation to the next (*NEC*) will vary with prey density (Figure 7.14). When prey populations are

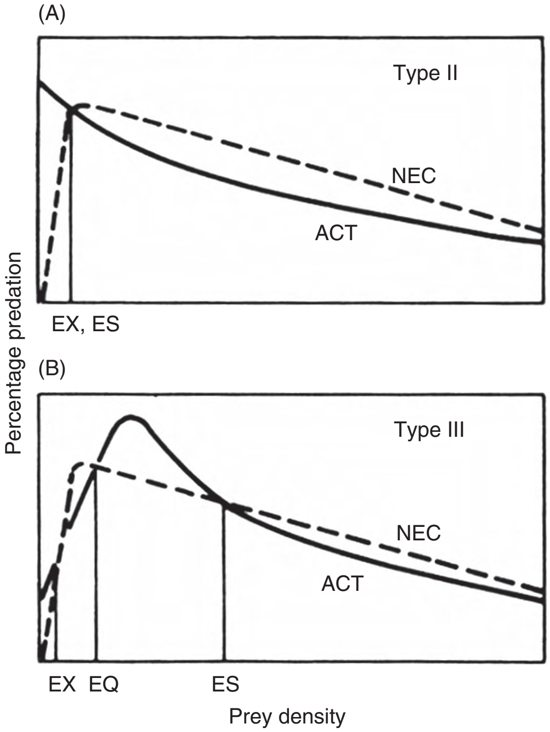


Figure 7.14 Population regulation effects of Holling's Type II (A) and Type III (B) functional responses. *NEC*, percentage predation necessary to stabilize populations; *ACT*, actual percentage predation; *EX*, threshold density for population extinction; *EQ*, equilibrium density; *ES*, threshold density for population escape. After Holling (1965).

very small and individuals have difficulty finding mates, very little mortality is needed to offset the limited amount of reproduction. At moderate prey densities, mates are relatively easy to locate and resources are abundant, resulting in exponential population growth. Thus, at moderate prey densities a higher intensity of predation is necessary to prevent prey outbreak. As prey densities become relatively large and approach the carrying capacity of the environment, resources become limiting and the percentage predation necessary to counterbalance reproduction declines.

Next, we compare the actual percent mortality (*ACT*) exerted across a range of prey densities for predators exhibiting Type II or Type III responses to the amount of mortality that is necessary to offset population growth (*NEC*) (Figure 7.14). Where these lines intersect, the percentage mortality exactly balances population growth and an equilibrium point exists. The equilibrium is considered stable if feedback mechanisms exist that return the population to its equilibrium density following perturbation. Where perturbation away from the equilibrium density results in population extinction or outbreak, the equilibrium is considered to be unstable.

When a predator exhibits a Type II functional response, the actual fraction of the prey population (*ACT*) captured declines with increasing prey abundance (Figure 7.15A), and a single unstable equilibrium emerges at *EX* and *ES* when the *NEC* and *ACT* curves are superimposed (Figure 7.14A). At prey densities below this unstable equilibrium point (*EX*), the level of predation inflicted will always be greater than the growth capacity of the population, driving the prey population to extinction. At prey densities above the unstable equilibrium (*ES*), mortality is never strong enough to prevent prey-population escape. Thus, a Type II functional response by a predator results in an unstable dynamic with even the slightest disturbance away from the equilibrium density causing the eventual extinction or escape of the prey population.

When a predator exhibits a Type III functional response, the outcome can be quite different. In this case, the actual fraction of prey consumed by a predator (*ACT*) is low at low prey densities, increases at intermediate prey densities, and declines again at high prey densities (Figure 7.15B). The result is that the *ACT* curve intersects the *NEC* at three points, creating one stable and two unstable equilibria (Figure 7.14B). As with the Type II response, when prey densities fall below *EX*, the high rate of predation drives the prey to extinction, whereas densities above *ES* result in uncontrolled outbreaks. The key to stability lies in the dynamics that happen when prey populations fall between *EX* and *ES*. At

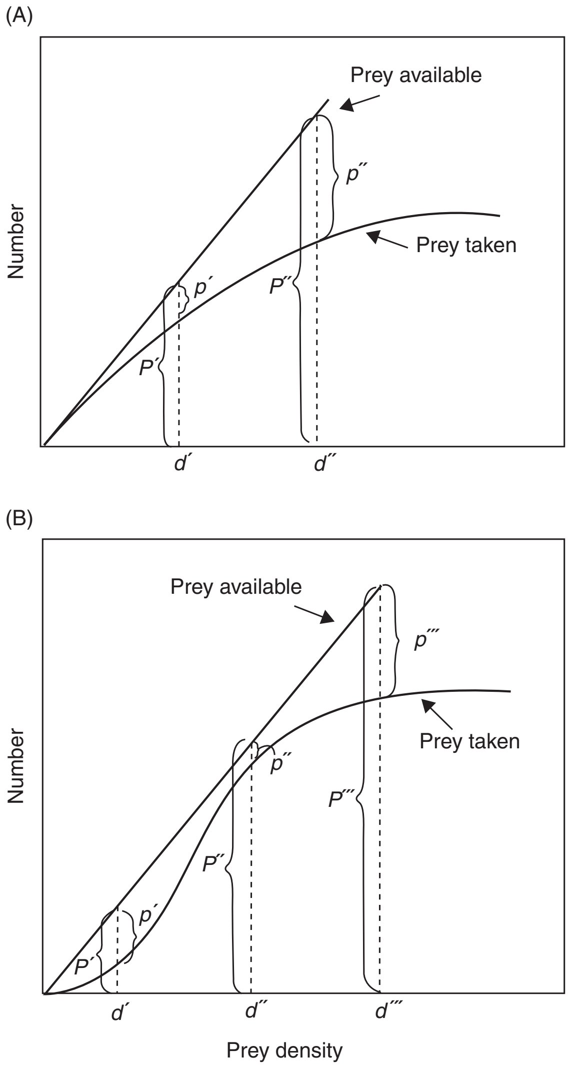


Figure 7.15 Percentage predation as a function of prey density. The Type II functional response (A) results in a constant decline in percent mortality with increasing prey density. At low prey densities (d') the proportion of prey taken $1-(p'/P')$ is large, but as prey density increases (d'') the proportion taken $1-(p''/P'')$ decreases. With the Type III functional response (B), percent predation is low at low densities (d'), high at moderate densities (d'') and low at high densities (d'''). From Price (1975b).

prey densities above *EX*, the actual level of predation is less than what is necessary to limit population growth and the population will increase until it reaches *EQ*. At densities below *ES*, the level of predation inflicted on the prey population is greater than the reproductive potential of the population and the population will decline until it reaches *EQ*. Therefore, *EQ* represents a stable equilibrium density to which the population returns following moderate disturbance. As a result, the Type III functional response is theoretically more likely to stabilize the dynamics of a prey population than is a Type II functional response.

7.6 Predation in complex food webs

So far, our focus has been on interactions between a single prey and predator species, and the reciprocal nature of their population dynamics. However, prey and predators don't occur in isolation from other organisms, but are instead nested within complex food webs of interacting species. The presence of multiple predator and prey species in a system can alter the interaction between a specific prey–predator pair, and complicate predictions of population dynamics.

7.6.1 Interactions among predator species

When multiple predator species are present simultaneously, often their combined effects on prey cannot be predicted simply by knowing the effectiveness of each individual predator species when present alone. If this is the case, the multipredator assemblage is said to have **emergent impacts** on prey (Sih *et al.* 1998), that is, unexpected results based on knowledge of the impacts of individual species. In the absence of emergent impacts, predator effects are **additive** and prey depletion by the total predator assemblage can be accurately determined by merely summing the number of prey consumed by each predator species when present alone. When the combined effects of multiple predator species are subadditive, or less than what is predicted by summing the impacts of individual predator species, the interaction is classified as **antagonistic** and the result is a reduction in the risk of predation for the prey. When predators interact to create superadditive effects on prey, the interaction is **synergistic** and prey experience enhances predation risk when a collection of predators is present, as opposed to when only a single predator is present. Identifying the mechanisms that lead to additive, antagonistic, or synergistic interactions among predators and characterizing the relevant traits of predators that promote one type of interaction over another improves our ability to predict the outcome of prey–predator interactions within complex food webs.

7.6.1.1 Additive interactions

Predators have additive impacts on prey when the effect of one predator species on the prey population is completely independent of the presence of the other predator species. In this case, intraspecific interactions among individual predators dominate and interspecific interactions are relatively unimportant. The most common mechanism contributing to this non-emergent effect of natural enemies on prey is **resource partitioning** (Ives *et al.* 2005, Casula *et al.* 2006). Resource partitioning occurs when enemy species attack different subsets of prey because of interspecific differences in predator traits that affect how, where and when they attack. For example, predators may partition resources because they prefer to attack prey with different phenotypes (Wilby *et al.* 2005), they forage at different times of the day (Tso *et al.* 2007), they exploit different microhabitats (Straub and Snyder 2008) or they are active at different times of the year (Roy *et al.* 2005). When species completely partition the prey population such that there is no overlap in their prey-use patterns, there is limited opportunity for interspecific competition for prey among predators, and additive impacts result. For example, in an old field habitat, the grasshopper *Melanoplus femurrubrum* falls victim to three dominant hunting spider species, the nursery web spider *Pisaurina mira*, the jumping spider *Phidippus rimator*, and the wolf spider *Rabidosa rabida* (Sokol-Hessner and Schmitz 2002). Each spider species prefers to forage within a different microhabitat; the nursery web spider resides in the upper canopy, the jumping spider is most often found in the middle canopy and the wolf spider inhabits the lower canopy (Figure 7.16). Thus, the grasshopper's risk of attack by the various spider species is partitioned vertically across the habitat with the grasshopper only being susceptible to predation by a single spider species within any particular habitat. Therefore, in this system spiders act independently and the net effects of multiple spider species on grasshopper mortality can be

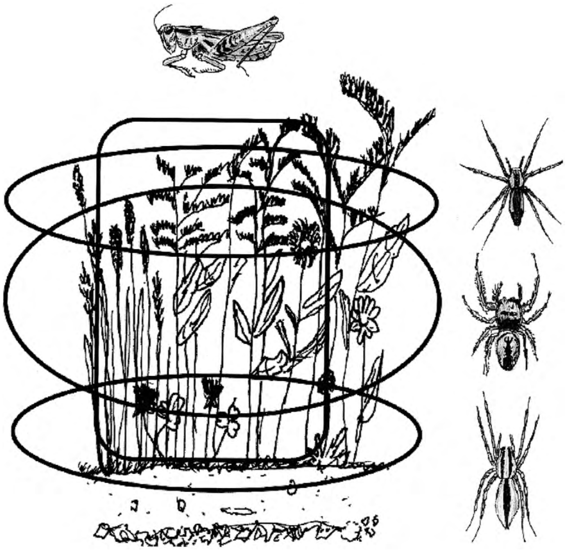


Figure 7.16 Partitioning of a grasshopper prey resource by three hunting spider species in an old-field habitat. The grasshopper prey occupies the entire habitat (vertical rectangle), but each spider species prefers to forage within a different microhabitat (horizontal ellipses). The nursery web spider *Pisaurina mira* resides in the upper canopy, the jumping spider *Phidippus rimator* is most often found in the middle canopy and the wolf spider *Rabidosa rabida* inhabits the lower canopy. From Schmitz (2007).

predicted based on knowledge of the single-species spider effects.

7.6.1.2 Antagonistic interactions

Antagonistic interactions among predators occur when one predator species disrupts the ability of another to capture and consume prey. Often this antagonism results from predators killing one another (i.e., intraguild predation), altering their behavior to avoid falling victim to intraguild predation or being displaced from prime foraging locations due to interference competition. While all of these mechanisms are common and likely contribute to the emergence of antagonistic interactions, intraguild predation has received the most theoretical and experimental attention by far.

Intraguild predation occurs when a top predator (the intraguild predator) consumes an intermediate predator (the intraguild prey) with which it competes for a common prey resource (the shared prey) (Polis *et al.* 1989). Theoretical models of intraguild predation predict that the presence of an intraguild predator will enhance the equilibrium density of the shared prey, due to consumption of the competitively superior intraguild prey by the intraguild predator (Holt and Polis 1997). Therefore, when intraguild predators are present, multispecies predator communities could have the surprising result of increasing the population size of the shared prey. However, experimental evidence is mixed concerning the ultimate impact of intraguild predation on the prey populations. Consistent with these theoretical predictions, some studies have in fact documented relaxed predation on shared prey when intraguild predators are present (e.g., Snyder and Ives 2001, Snyder and Wise 2001, Finke and Denno 2004, Prasad and Snyder 2004). A good example involves heteropteran bugs (*Zelus* and *Nabis*) and lacewing larvae (*Chrysoperla*), all of which prey on the cotton aphid *Aphis gossypii* (Rosenheim *et al.* 1993). In the absence of heteropteran predators, lacewing predation drives the cotton aphid population to a low level. When heteropterans are added to the system, they focus their attack on the more vulnerable lacewings, aphids experience a partial refuge from predation and aphid populations rebound. Conversely, a variety of other studies have shown an overall increase in predation pressure, and a decrease in prey abundance, in the presence of an intraguild predator (e.g., Colfer and Rosenheim 2001, Denno *et al.* 2004, Harvey and Eubanks 2005). For instance, the invasive red imported fire ant (*Solenopsis invicta*) is a major intraguild predator of important beneficial arthropods in cotton and soybean fields in the southern United States; nevertheless, densities of fire ant workers are negatively associated with the abundance of all major herbivore taxa in cotton (Eubanks 2001, Eubanks *et al.* 2002). This unexpected result is likely due to the voraciousness of the fire ant, which indiscriminantly attacks herbivores, intermediate predators and other intraguild predators within the food web. While the voraciousness of the intraguild predator is one factor that may influence the ultimate effect of intraguild predation on prey populations, various other predator- and habitat-related characteristics have also been proposed to explain the variable impacts of intraguild predation across systems. We will address just a few of these features here.

The type of foraging strategy employed by predators, whether predators actively pursue their prey or sit and wait to ambush prey, may shape a predator's probability of encountering prey and thus determine the impact of intraguild interactions on prey populations. Early work predicted that sedentary prey are more likely to be captured by widely foraging predators, whereas sit-and-wait predators are more likely to encounter and consume mobile prey (Huey and Pianka 1981). If we incorporate intraguild predation into this earlier theoretical framework we can predict the outcome of intraguild interactions simply by knowing the foraging strategies and mobility of predators and prey involved (Rosenheim and Corbett 2003). Consider the case of a sedentary herbivore that is effectively suppressed by a widely foraging intermediate predator that in turn falls victim to its own intraguild predator. An intraguild predator with a sit-and-wait strategy is predicted to disrupt the suppression of the sedentary prey by the intermediate predator, since the mobile intermediate predator would be highly vulnerable to attack by the sit-and-wait predator. In contrast, a widely foraging intraguild predator has the opportunity to encounter both the mobile intermediate predator and the sedentary herbivore. Thus, as long as the direct suppressive effect of the intraguild predator on the herbivore offsets its negative effects on the intermediate predator, overall herbivore suppression can still be strong despite the occurrence of intraguild predation (Rosenheim and Corbett 2003).

Rosenheim *et al.* (2004a,b) found empirical support for these theoretical predictions using the predator community associated with sedentary spider mites *Tetranychus cinnabarinus* on papaya. This community includes two widely foraging specialist predators, a ladybird beetle *Stethorus siphonulus* and a phytoseiid mite *Phytoseiulus macropilis*, as well as a sit-and-wait generalist, a tangle-web spider *Nesticodes rufipes*. The ladybird beetle effectively suppressed spider mite populations when alone. However, in the presence of both the beetle and the tangle-web spider, mite populations were enhanced. This result was most likely due to the susceptibility of the widely foraging beetle to intraguild predation by the sit-and-wait spider (Rosenheim *et al.* 2004a). The phytoseiid mite was also capable of suppressing spider mite populations when alone, but unlike the ladybird beetle, when the phytoseiid mite was present in combination with the tangle-web spider, spider mite suppression was not disrupted. The variation in response was likely due to body size differences between the phytoseiid mite and the ladybird beetle. The relatively small body size of the phytoseiid mite means that its foraging requirements to meet its energy demands are moderate, as compared to that of the ladybird beetle. Thus, phytoseiid mites move less often and have limited encounters with tangle-web spider webs (Rosenheim *et al.* 2004b). These results highlight how multiple factors, in this case the combination of both predator foraging mode and body size, can simultaneously determine the outcome of these complex trophic interactions.

The behavioral responses of prey to the presence of predators may also mediate the impact of intraguild predation on prey suppression. It is important to remember that intraguild prey (i.e., intermediate predators), as well as shared prey, are not passive resources waiting to be consumed, but that they have the capacity to respond behaviorally to the threat of predation. The ability of an intermediate predator to avoid foraging in patches where a potential intraguild predator exists would diminish the opportunity for antagonistic intraguild interactions and perhaps enhance the overall exploitation of prey. This avoidance may be the result of predator emigration in the presence of intraguild predators. Moran *et al.* (1996) documented the exodus of hunting spiders from plots to which mantids, avid intraguild predators, were added. Or potential intraguild prey may evade the threat of predation by avoiding patches with intraguild predators altogether. Parasitoids have been shown to detect the volatiles associated with coccinellid beetle trails and avoid patches where these trails exist (Nakashima and Senoo 2002, Nakashima *et al.* 2006). Mites are also capable of assessing patch profitability using volatiles associated with potential intraguild predators (Gnanvossou *et al.* 2003a,b). Phytoseiid mites avoid plants on which minute pirate bugs are already present and consuming thrips, the shared herbivore prey (Magalhaes *et al.* 2004).

Habitat complexity also has the potential to mediate the intensity of multipredator interactions by providing refuge for predators from intraguild predation. For example, leaf surface structure reduces the intraguild predation of beneficial mites (Roda *et al.* 2000, Norton *et al.* 2001) and interference among generalist spiders is diminished in complex-structured habitats (Marshall and Rypstra 1999, Rickers *et al.* 2006). Ultimately, this refuge for predators from intraguild predation can result in greater herbivore suppression and an increase in plant biomass (Finke and Denno 2006). Such is the case for *Prokelisia* planthoppers feeding on *Spartina* cordgrass, which are themselves consumed by the intermediate predator *Tytthus* and the intraguild predator *Pardosa*. In this intertidal system, there is considerable variation in leaf litter due to elevational differences in tidal flushing and decomposition. In litter-rich habitats, *Pardosa* hunting spiders abound and readily aggregate in areas of elevated planthopper density. In these structurally complex habitats, *Tytthus* finds refuge from *Pardosa* predation, the predator complex effectively suppresses planthoppers and cordgrass flourishes. By contrast, in litter-poor habitats, spiders are less abundant, *Tytthus* experiences intraguild predation, and overall predation on planthoppers is relaxed, leading to planthopper outbreak and reduced plant biomass. Thus, both vegetation structure and the predator assemblage interact in complex ways to influence the probability for a **trophic cascade**, the extent to which predator effects cascade to affect herbivore suppression and plant biomass (see Chapter 13 for further discussion of trophic cascades). This example further underscores why understanding prey-predator interactions requires a multitrophic approach.

7.6.1.3 Synergistic interactions

Synergistic interactions among predators result from predator–predator facilitation, whereby one enemy species enables a second species to capture and consume more prey than would be possible if foraging alone. Predator facilitation often involves conflicting behavioral responses of prey to multiple predators, resulting in the prey escaping one predator only to find itself in the clutches of a second enemy (Sih *et al.* 1998). For example, in stream systems, mayflies (*Ephemerella subvaria*) react to the presence of predatory stoneflies (*Agnetina capitata*) by leaving their refuge habitat under rocks, making them more susceptible to attack by fish (*Cottus bairdi*) (Soluk and Collins 1988a,b). Likewise, in alfalfa, the presence of the foliar foraging ladybird beetle *Coccinella septempunctata* elicits an escape behavior in pea aphids (*Acyrthosiphon pisum*) causing them to drop to the ground where they are eaten by the ground-foraging carabid beetle, *Harpalus pennsylvanicus* (Losey and Denno 1998). However, conflicting behavioral responses of prey to predators do not always result in facilitation among enemies. Krupa and Sih (1998) showed that the water strider, *Aquarius remigis*, faces a conflict over which habitat refuge to use when responding to the simultaneous threat of predation by sunfish (*Lepomis*) and fishing spiders (*Dolomedes*). Water striders retreat to the stream banks to avoid sunfish predation, but must move away from the banks to avoid spider predation. Therefore, no effective spatial refuge exists for the water striders in the presence of both predators. However, this conflict in refuge use for the water strider does not result in facilitation between sunfish and spiders as one might predict. In addition to the predator-specific escape responses, the water striders also exhibit a more generalized response to the presence of predators in the form of a reduction in overall activity. This generalized response renders the water striders less conspicuous to predators, despite the loss of their spatial refuge, and precludes a synergistic interaction between the predators.

7.6.2 Predator diversity

A practical extension of studies of predator–predator interactions is to ask what the consequences of changing predator diversity will be for prey suppression and ecosystem functioning at large. In most systems, predator diversity is in a state of flux as it is shaped by the processes of extinction, introduction, and invasion. Extinction acts to depress predator diversity in many ecological communities. Predators, by virtue of their precarious position at the apex of the food chain are often at greater risk of extinction when systems are disturbed (Petchey *et al.* 1999, Purvis *et al.* 2000, Duffy 2003). At the same time, predators are often intentionally introduced into systems as biological control agents for the purposes of controlling insect pests, and several predator species have been particularly successful invaders (Snyder and Evans 2006). Introduced or invasive predators sometimes coexist with native species, but may also displace ecologically similar natives (Snyder and Evans 2006). Thus, predator introduction and invasion can either increase or decrease regional predator diversity.

Recent studies conducted with the explicit goal of examining the relationship between natural enemy diversity and prey suppression differ from previous studies that examine multiple predator impacts on shared prey populations, such as those discussed above, in two important ways. First, while studies of interactions among predator species often include just two enemy species, studies of predator diversity examine communities with higher levels of **species richness**. Second, studies of predator diversity are carefully designed to distinguish the effects of species richness from the effects of other potentially confounding factors, such as total enemy abundance. In this way, the influence of diversity (i.e., species richness) on prey suppression is isolated. Studies utilizing this experimental design provide evidence that the relationship between natural enemy diversity and prey suppression is context dependent, and increasing predator diversity can increase, decrease or not affect pest suppression. In systems where intraguild predators dominate the predator assemblage, promoting predator diversity may inhibit prey suppression (Finke and Denno 2005, Ives *et al.* 2005). Where predators complement each other by partitioning their use of the prey resource or by facilitating the action of other predators, increasing predator diversity can enhance prey suppression (Wilby *et al.* 2005, Snyder *et al.* 2006, Griffiths *et al.* 2008, Ramirez and Snyder 2009). Where different predator species fill similar ecological roles in the community, their effects are redundant and prey suppression is unaffected by an increase in diversity (Sokol-Hessner and Schmitz 2002, Straub and Snyder 2006). Undoubtedly, the key to elucidating the relationship between predator diversity and prey suppression will rest on a clear understanding of the nature of predator–predator interactions and how these interactions are shaped by environmental heterogeneity.

7.6.3 Prey diversity

We have already considered the trophic complexities that can arise when multiple predator species are present and feed on a single prey, but predators are often generalists that forage and develop in habitats where several prey species coexist. How might the presence of multiple prey species alter the outcome of a focal prey–predator interaction? In Chapter 5 we saw how one species can limit the abundance of another species by directly competing for essential resources. However, prey can also compete indirectly and influence the abundance of other prey by mediating the impact of a shared predator.

When prey interact indirectly via **apparent competition** (see Chapter 5), the presence of one prey species can have a negative effect on the abundance of another prey species by enhancing the population size of a shared enemy (Holt 1977). A good example of apparent competition involves two leafhopper species, a native leafhopper (*Erythroneura elegantula*) and an invading species (*E. variabilis*), feeding on domestic grapes in California. Following the introduction of the invading species, densities of the native leafhopper rapidly declined due to an increase in rates of parasitism by a shared egg parasitoid (*Anagrus epos*) (Settle and Wilson 1990). Prey populations were contemporaneous in the case of the leafhoppers, but apparent competition can also occur among prey populations that are displaced in either space or time. The invasion of soybean aphids (*Aphis glycines*) in soybean fields of the Midwestern United States has increased the abundance of predatory ladybird beetles that colonize alfalfa fields where they severely reduce pea aphid (*Acyrthosiphon pisum*) densities (Harvey 2007). As a consequence, soybean aphids influence the susceptibility of pea aphids to predation, even though these two herbivores feed on different host plants in separate agricultural

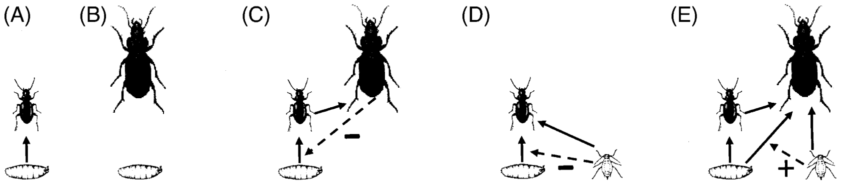


Figure 7.17 Complex species interactions involving anthomyiid fly eggs, small predaceous ground and rove beetles, a larger predatory ground beetle *Pterostichus melanarius* and aphid alternative prey. (A) Smaller beetles readily feed on fly eggs while (B) the larger beetle rarely does. Independently, (C) the larger beetle and (D) the aphid alternative prey benefit fly eggs by reducing attack on eggs by small beetles. However, an emergent indirect effect appears when all species are present together (E) resulting in an unexpected reduction in fly egg abundance. Solid arrows indicate direct interactions and represent energy flow from resource to consumer. Dashed lines indicate behavioral effects and point from the species inducing the changed behavior to the species interaction that is altered; labels on the dashed arrows indicate whether the change in behavior strengthens (+) or weakens (−) the interaction. After Prasad and Snyder (2006a).

fields. Likewise, prey with vastly different phenologies can also interact via apparent competition since predation on early season prey can boost predator populations and intensify their impacts on later-developing prey populations. In tropical rice fields of Southeast Asia, high populations of generalist predators are supported early in the season by feeding on abundant populations of detritus- and plankton-feeding insects. The availability of this early-season alternative prey provides the predators with a head start and increases suppression of pest herbivores that emerge much later in the growing season (Settle *et al.* 1996).

Indirect interactions among prey species that are mediated by a shared natural enemy do not always result in a greater risk of predation. They can also result in a reduction in the predation risk of a focal prey species if the presence of an alternative prey species causes a predator to switch its feeding preferences. Consistent with this prediction, Prasad and Snyder (2006b) found that a guild of small predaceous ground (Carabidae) and rove (Staphylinidae) beetles reduced their consumption of the eggs of root-feeding anthomyiid flies in the presence of aphid alternative prey because the small beetles switch to consuming aphids when given a choice (Figure 7.17D). However, the story is further complicated by the addition of a large top predator, the ground beetle *Pterostichus melanarius*. *Pterostichus* does not itself readily feed on fly eggs, but it does disrupt fly egg predation in the absence of aphids because the smaller beetles reduce their foraging activity due to the threat of intraguild predation by the large beetle (Figure 7.17C). Surprisingly, control of fly eggs is restored when aphids are added as alternative prey because aphids trigger greater foraging efforts, and thus an increase in incidental predation of fly eggs, by the large beetle (Prasad and Snyder 2006a; Figure 7.17E). Thus, in the absence of the top predator, fly eggs benefit from a reduction in predation in the presence of the alternative aphid prey. But when the top predator is present, the indirect interaction between fly eggs and aphids is more consistent with apparent competition (Figure 7.17). This study highlights how our understanding of prey–predator interactions can be enriched when we consider these associations within the context of the complex food webs that are typical of real-world communities.

7.7 Non-consumptive predator impacts on prey

Our focus to this point has been on the changes in prey abundance that result when predators capture, kill and consume their prey, the so-called consumptive effects of predators. The perspective that predators and prey interact solely through consumption has dominated the study of population and community dynamics, and is reflected in the models of prey–predator dynamics that we discussed earlier. In these models, it is assumed that predator populations reduce prey abundance by killing and consuming individual prey, and that any reduction in prey populations must contribute directly to predator population growth. However, prey are not passive victims and they often employ a variety of induced behavioral and morphological defenses under risk of predation (Lima and Dill 1990). These defensive responses can be effective at helping prey avoid being consumed, but they often come at a cost to other aspects of prey biology. Therefore, in addition to influencing prey population density by killing and consuming prey (consumptive effects), predators may also impact prey populations by inducing costly defensive changes in prey traits (non-consumptive effects).

Evidence is building from many systems that predators adversely affect prey populations via both consumptive and non-consumptive effects. For example, when grasshoppers are exposed to non-lethal (i.e., de-fanged) spiders, they undergo a feeding shift from grasses to poor-quality forbs where they avoid spiders, but incur increased mortality due to starvation (Schmitz *et al.* 1997). Notably, the mortality arising from this antipredator behavior rivals that seen when grasshoppers are killed directly by spiders with their fangs intact. Similarly, pea aphids inhabiting alfalfa are frequently disturbed by a diverse guild of natural enemies, causing pea aphids to repeatedly drop from their host plant to the ground (Nelson 2007). We discussed previously how this behavioral escape response can enhance aphid suppression by increasing the susceptibility of aphids to predatory beetles foraging on the ground. However, the dropping behavior alone, in the absence of actual predation, is also sufficient to cause a reduction in pea-aphid population size, since the aphids pay a high cost when they continually drop from their host plant in the form of lost feeding opportunities (Nelson *et al.* 2004). Although these lost feeding opportunities have no direct impact on aphid survival, reduced phloem intake translates into reduced reproductive output by pea aphids and thus a decline in aphid abundance (Nelson 2007). Since predator-avoidance behaviors by herbivores often come at the cost of foraging time, the ultimate impact of predators on prey may depend on the ability of prey to compensate for lost access to resources by adjusting their activity budgets (Preisser and Bolnick 2008, Preisser *et al.* 2009). In the case of pea aphids, there is little opportunity for compensation since aphids feed on nutrient-poor phloem, and thus the amount of time spent feeding is already a primary constraint on aphid growth and reproduction.

In addition to compensation, prey can also limit the costs associated with predator avoidance behaviors by tailoring their behavioral response according to the degree of risk associated with a particular predator. For example, cues from fairly sedentary “sit-and-wait” or “sit-and-pursue” predators are strongly indicative of imminent predation risk, and thus evoke a stronger response by prey than cues from actively hunting predators that may no longer be in the immediate area (Preisser *et al.* 2007). Likewise, the intensity of costly predator avoidance behaviors exhibited by different mayfly species is consistent with their relative rates of predation by stoneflies (Peckarsky 1996). Mayfly species that are more vulnerable to predation show strong induction of costly drift dispersal behavior in the presence of stoneflies, whereas morphologically defended mayfly species demonstrate no escape behaviors.

As more and more studies document behaviorally mediated effects of predators on prey, it is becoming increasingly clear that a complete understanding of prey–predator population dynamics will require consideration of the non-consumptive as well as consumptive effects of predators. Toward this end, Priesser and Bolnick (2008) have constructed a simple prey–predator model based on the models of

Lotka and Volterra that can distinguish the effects of direct consumption by predators from the costs of prey defenses to avoid consumption in reducing prey population growth rates. Furthermore, the non-consumptive effects of predators not only alter the outcome of prey–predator interactions, but also have the ability to cascade through the food web with far-reaching impacts on other trophic levels. For example, feeding cessation to avoid predators can lead to reduced plant damage and an increase in biomass even when herbivore abundance does not change (Preisser *et al.* 2005). As we will see in Chapter 13, the strength of such behaviorally mediated indirect effects on plants can rival the top-down impacts of predators on plants that are induced by the direct killing of herbivores by predators (Schmitz *et al.* 2004).

7.8 Evolutionary response of prey to predation

There is little doubt that predators have exerted selection on prey that has resulted in evolutionary change. For example, prey species have evolved a wide range of defenses in response to selection from predation (Evans and Schmidt 1990). Such defenses can be categorized as primary, secondary or tertiary, depending on when in the predation sequence (detection, capture or handling) they operate.

Primary prey defenses function to prevent the initiation of a capture attempt by a predator, typically by evading detection altogether. With effective primary defenses, the prey save the energetic costs of interacting with predators and avoid the direct risks of injury and death due to predation. However, some traits that help prey evade detection, such as reducing activity when predators are foraging in the vicinity, conflict with other biological demands of the organisms, such as feeding, reproducing and dispersing, resulting in fitness trade-offs like those discussed above (i.e., non-consumptive effects of predators on prey).

There are a wide variety of morphological and behavioral mechanisms that enable prey to evade detection by predators. Prey may eliminate evidence of their presence by concealing their feeding damage (e.g., eating an entire leaf, producing symmetrical damage, or clipping the petioles of partially consumed leaves), or by removing frass that accumulates at their feeding sites. Prey may also be rendered less obvious to a predator if they possess a color pattern or shape that matches their environment. Examples of such **crypsis** include the green coloration of grasshoppers that enables them to blend in with the background vegetation (**eucrypsis**), or the resemblance of prey to an inedible feature of the environment (**mimesis**) (terms advocated by Pasteur 1982 and Lederhouse, 1990). For example, caterpillars in the family Geometridae often resemble twigs, and many early instars of *Papilio* caterpillars mimic bird droppings. Such defenses work best when prey are sparse, otherwise predators may develop search images or other means of more efficiently locating the camouflaged prey (Tinbergen 1960).

While the best defensive strategy for palatable prey species may be to evade attack by avoiding detection, unpalatable prey species may utilize the opposite strategy and evade attack through **aposematism**, or advertizing their unsuitability to predators using conspicuous coloration, sounds or smells. For instance, many tiger moths (Arctiidae) advertise their chemical defense to predators using bold coloration and/or ultrasonic clicks. Interestingly, the warning signals utilized by different tiger-moth species, whether visual or acoustic, vary with respect to the activity patterns of their major predators, birds and bats (Ratcliffe and Nydam 2008). The tiger moth species that are out during spring, when birds are active and bats less so, do not produce ultrasonic clicks. However, those moth species emerging later in the season when bats become more active do produce ultrasonic clicks. Furthermore, tiger-moth species that are most active during the day are visually conspicuous, whereas those that are predominantly nocturnal are visually cryptic. Thus, it appears that this multifaceted warning display is the result of selection from multiple predators.

For aposematism to be effective, the predator must learn to associate the warning signal with an unpleasant experience, and thus it is inevitable that some prey individuals must be attacked initially during the predator's learning period. As a result, two different aposematic species would mutually benefit from converging on a common warning display, since predators would only have to learn to avoid a single display, requiring fewer total prey individuals to be captured than if predators learned two different displays. This evolutionary convergence in appearance, sound or smell of unpalatable species is referred to as **Müllerian mimicry**. A classic example of Müllerian mimicry involves tropical *Heliconius*, or passion-vine, butterflies that are unpalatable comimics that show an amazing amount of convergence in wing pattern across species.

If an aposematic prey avoids predation by advertizing its distastefulness, a palatable prey species could certainly benefit from mimicking the warning display of the aposematic species. This type of deceit is referred to as **Batesian mimicry** and is defined as the evolutionary advergence in appearance, sound or smell of an edible "mimic" toward resemblance of a less palatable "model." True aposematic species benefit from dense populations because the avoidance reaction of the predator is reinforced with repeated unpleasant encounters. Batesian mimics, on the other hand, should be relatively rare within the community so that the predator does not learn to associate their appearance with palatability rather than unpalatability. In addition, mimics must also occur in sympatry with their distasteful models for a Batesian mimicry system to evolve. Consider the African swallowtail butterfly, *Papilio dardanus*, that exhibits a remarkable degree of female polymorphism. *P. dardanus* is a palatable species and subject to heavy predation by birds in particular. The occurrence of different species of distasteful models throughout the geographic range of *P. dardanus*, as well as geographic variation in a broadly distributed model, has been accompanied by the evolution of correspondingly different mimetic morphs of *P. dardanus* females. Each mimetic pattern is only found where the appropriate model is also present, highlighting the importance of sympatry between models and mimics.

A common misconception in ecology is the inclusion of the viceroy butterfly, *Limenitis archippus*, and the monarch butterfly, *Danaus plexippus*, as an example of Batesian mimicry. Viceroys are historically considered palatable mimics of the chemically–defended monarchs, which sequester toxic glycosides from their larval host plants in the milkweed genus *Asclepias*. However, more recent data refutes this interpretation by revealing that viceroys can be equally as unpalatable as the monarch butterfly, and that their palatability varies based on the mix of food plants consumed (Ritland and Brower 1991). Likewise, it now appears that there is great variation in the glycoside content in monarch butterfly populations, from zero to concentrations sufficient to cause emesis (Brower *et al.* 1972). Thus the predators of these butterflies experience a **palatability spectrum**, which complicates the designation of one species as a "model" and another as a "mimic," and suggests that this widely cited example of Batesian mimicry may actually be a dynamic case shifting along a continuum of Batesian to Müllerian mimicry.

When primary defenses fail and prey are detected by a predator, **secondary prey defenses** operate to deter capture. Examples of secondary defenses include escape mechanisms (aphids dropping from leaves in the presence of a foraging ladybird beetle), startle behaviors (moths displaying wings with eye spots to frighten away birds), armored body surfaces (chrysomelid beetles adorning themselves with fecal shields) and evasive behaviors (moths detecting the echolocation of bats and initiating strategic flight-avoidance tactics). **Tertiary prey defenses** interrupt predation after capture and during the handling phase. When a predator succeeds in overcoming prey strategies designed to prevent detection and attack, and prey escape is not a reasonable possibility, the prey must resort to its last defense – counterattack. Such defenses include mechanisms that deter, repel or even kill the predator directly (biosynthesized or sequestered toxins, venoms or morphological structures such as spines). The warning signals of aposematic prey typically advertize the presence of tertiary defenses, blurring the lines between primary and tertiary defenses. In fact, the distinction between primary, secondary and tertiary defenses is often ambiguous. For example, the strategic flight tactics used by some moths function as both primary and secondary defense mechanisms (Fullard 1990). Moths from a variety of families possess simple tympanic organs that enable them to detect the echolocation signals of insectivorous bats. Moths use their tympanic organs to mediate a set of defensive behaviors that can be categorized as primary or secondary defenses depending on the perceived distance of the approaching bat. The faint acoustic signals of distant bats elicit a coordinated avoidance flight intended to remove the moth from the detection area of the bat. This avoidance flight is performed before the bat has detected the echo from its prey and is therefore considered a primary response. Secondary responses are initiated in response to the more intense acoustic stimulation of closer bats. These secondary responses include evasion maneuvers such as flight cessation and are considered a last-ditch effort at escape once the moth has been detected by the bat. Some moths even make ultrasonic clicks of their own that may startle bats, alert bats to the moths' toxic chemistry or interfere with or "jam" the sonar of the bat (Corcoran *et al.* 2009).

Clearly, predation has promoted a wide array of prey defenses and the question arises as to whether there have been counteradaptations in predators. Have predators and prey engaged in an "evolutionary arms race" such that reciprocal selection has promoted a continuing escalation of predator offense and prey defense? Some evidence is consistent with this hypothesis. For instance, the drilling abilities of predaceous gastropods and the shell thickness of their bivalve prey have increased through geologic time (Vermeij 1994). Similarly, marine snails have become more heavily armored, while the correlated response in predaceous crabs has been the evolution of larger claws for crushing the better-defended snails. In both of these instances, predators may have evolved greater weaponry in reciprocal response to improved prey defense (coevolution hypothesis) or predator armaments may have evolved in response to other predators or competitors (escalation scenario).

Overall, however, evidence suggests that reciprocal selection on predators may be weaker than that on prey, thus precluding a classic evolutionary arms race (Brodie and Brodie 1999). In part, the asymmetry arises because many predators are generalist feeders and selection imposed by any one of its prey options is likely small. In general, coevolution between exploiter and exploited is unlikely when the intimacy of the interaction is low. Moreover, selection on predators from effective primary and secondary prey defenses is probably weak. For instance, if a predator fails to detect cryptic prey or catch a stealthy individual it simply searches for another without penalty. The exception occurs when predators interact with dangerous prey that possess tertiary defenses like toxins that can kill the attacker. In such cases, predators experience strong selection from prey and are expected to either evolve innate avoidance behaviors or evolve traits that allow them to exploit dangerous prey. Such is the case with internal parasitoids that are susceptible to their hosts' cellular immune responses, and thus have been under intense selection pressure to overcome these defenses (see Chapter 8). For example, there is a growing body of evidence that coevolution may have occurred between *Drosophila* flies and their parasitoids in the genera *Asobara* and *Leptopilina* (Kraaijeveld and Godfray 1999). Physiological, molecular and artificial selection studies show that *Drosophila* resistance (immune defenses against the early stages of the parasitoids) has influenced parasitoid virulence (ability of eggs and larvae to survive within the host body) and vice versa. However, studies of geographical variation in the intensity of this reciprocal interaction suggest that coevolution in this case is relatively diffuse, reflecting the larger host–parasitoid community structure, rather than a coupled interaction between pairs of species.

Applications

Biological control

The expansion of modern, chemically–intensive agriculture poses one of the single greatest threats to species diversity (Tilman *et al.* 2001). Concern over the impact that this loss of diversity will have on the functioning of agricultural and natural communities, as well as the loss of broad-spectrum insecticides due to changing federal regulations, growing pesticide resistance among pests and concerns about health risks associated with pesticide exposure, has led to growing interest in more sustainable management practices (Bengtsson *et al.* 2005, Hole *et al.* 2005). **Biological control**, or the intentional use or manipulation of natural enemies to control pest organisms, is one alternative to the use of pesticides for controlling insect pests (DeBach and Rosen 1991, Van Driesche and Bellows 1996). There are three distinct approaches to biological pest control. In **classical biological control**, natural enemies of an introduced pest are selected from the country or area of origin of the pest. The foreign natural enemies are introduced, released and expected to establish viable populations capable of regulating pest populations. In this case, both the pest and its enemy are exotic species. **Augmentative biological control** aims to increase the population of an introduced or native natural enemy to levels necessary for successful control of a target pest. Augmentation of natural enemies is usually accomplished by mass-rearing and releasing one or more natural enemies. The final strategy, **conservation biological control**, involves the manipulation of the environment to make conditions more hospitable for natural enemies, either by removing or mitigating adverse factors or providing requisites for natural enemies that are lacking in the habitat (Barbosa 1998). Typically, classical and augmentative biological control focus on interactions involving a single predator or parasitoid species and single pest species, whereas conservation biological control involves the maintenance or enhancement of a diverse guild of natural enemies.

Biological control is considered to be an environmentally sound alternative for the management of insect pests, but it is not without potential ecological side effects (Louda *et al.* 2003a,b). For example, in the context of classical biological control, some exotic biological control agents introduced to control alien pest species have unanticipated effects on non-target native species. In some cases, the impacts of the introduced enemies on native populations appear minimal, occurring at levels that suggest no long-term effects on host densities (Louda *et al.* 2003a,b). However, the impact of exotic enemies on non-target species can sometimes be intense, accelerating the decline of rare native species and enhancing their risk of extinction (Louda *et al.* 2003a,b). No prey–predator or host–parasitoid interaction occurs in isolation from the broader community and thus the ecological risks associated with the deliberate manipulation of natural enemies will ultimately hinge on the myriad of direct and indirect species interactions that emerge, the potential for host switching, dispersal into non-agricultural habitats and the possibility of evolutionary adaptation to new hosts.

The goal of biological control is to induce a trophic cascade, whereby pests are collectively suppressed by the enemy complex and crop yield is enhanced. Therefore, factors that strengthen the impacts of predators on prey and minimize antagonistic interactions among predators would be beneficial in this context. Throughout this chapter we have highlighted many factors, such as a strong numerical response to increasing prey density, partitioning prey use among enemies and refuge for predators from intraguild predation in complex habitats, which influence the intensity of prey suppression and are relevant to the practice of biological control. Traditionally, host specificity is also considered a critical trait for a successful biological control agent, but the ability to feed on alternative prey, and thus persist in a system in the absence of target prey, supports the case for generalist predators (Riechert 1999). One aspect of ecological theory that has the potential to significantly alter the way we think about biological control, but which has yet to be fully incorporated in an applied context, is the non-consumptive effects of predators on prey. If the presence of a natural enemy induces defensive behaviors that result in lost feeding time for the prey, crop yield may be enhanced even when pest abundance does not change

(Preisser *et al.* 2005). Therefore, evaluations of biological control agents based merely on their ability to suppress prey populations by directly consuming prey may underestimate the ultimate impact of some natural enemies on crop yield (Schmitz *et al.* 2004).

Recently, increasing attention has been focused on the manipulation of habitat and vegetation structure to encourage natural enemies and promote pest suppression through conservation biological control (Thies and Tscharntke 1999, Landis *et al.* 2000, Gurr *et al.* 2004, Langellotto and Denno 2004). At the within-plant level, the presence of hair tufts at vein axils (domatia) can increase the abundance of predatory mites (Agrawal and Karban 1997) and cuticular waxes on certain varieties of plants can interfere with predator foraging behavior (Rutledge *et al.* 2003). Thus, through careful crop variety selection the opportunity exists to exploit intraspecific variation in plant traits to enhance the impact of natural enemies. The response of natural enemies to variation in plant traits will be explored in more detail in Chapter 13. At the habitat level, maintaining vegetation diversity in managed landscapes (i.e., by planting polycultures, foregoing tillage, incorporating native plant borders, etc.) often minimizes pest problems because natural enemies accumulate and persist in such habitats (Landis *et al.* 2000, Gurr *et al.* 2004, Shrewsbury and Raupp 2006). This occurs because diverse habitats often provide refuges for natural enemies during times when fields are fallow or offer resources in the form of nectar, pollen or alternative prey. At the landscape level, some parasitoids can be more abundant and parasitism rates of hosts higher within a complex mosaic of agricultural fields embedded within hedgerows and woodlots, as compared to simple agricultural fields lacking diverse landscape features (Marino and Landis 1996). Furthermore, structurally complex landscapes with high connectivity among habitat fragments have been shown to enhance the probability of pest regulation (Tscharntke *et al.* 2007a). Therefore, many opportunities exist to use various forms of habitat manipulation to improve biological control. However, we must also remain mindful of the potential that vegetation diversity, while benefiting predators and parasitoids, may also be favorable to unwelcome pest species.

It is clear that many aspects of prey–predator ecological theory inform the practice of biological control, but is the flip side of the argument also true? Can knowledge gained from the practice of biological control enlighten ecological theory? Biological control has certainly played a key role in shaping ecological theory in the past, with successful natural enemy introductions being viewed as evidence that predators and parasitoids do play a significant role in insect herbivore population dynamics (see Section 7.3). However, Hawkins *et al.* (1999) outline two characteristics of the systems in which biological control is typically employed that have the potential to fundamentally skew the manner in which natural enemies operate. First, biological control is most often utilized in habitats that have been substantially simplified in diversity and structure when compared to the majority of natural habitats. Second, the food webs of systems where biological control is employed are typically dominated by exotic species that share few evolutionary and ecological links with the native flora and fauna. The simplified nature of these food webs may intensify the effects of natural enemies and overestimate the role of predation when applied to more complex, natural communities. A review of the literature reveals that, when herbivore suppression occurs, it is more frequently due to a single parasitoid species when considering exotic insect species on exotic plants in cultivated habitats, whereas for native insect herbivores on native plants in natural habitats it is most often due to a suite of generalist predators (Hawkins *et al.* 1999). Furthermore, the overall success rate of biological control is greater in exotic, simplified, managed habitats than natural habitats, particularly when parasitoids are involved. Thus, biological control may indeed overestimate the extent to which natural enemies, particularly parasitoids, exert control on insect populations and may not be the perfect paradigm for understanding prey–predator interactions in natural systems. This contrast across natural and agricultural systems provides an ideal impetus for exploring the complex role of predation in community dynamics from both applied and theoretical perspectives.

Summary

Predation is a central process in community ecology with widespread ecological, evolutionary and economic effects in both natural and managed habitats. The manipulation of predators, whether done intentionally for experimental or biological control purposes or unintentionally as the result of environmental perturbation, provides evidence that predators can inflict high mortality on prey populations and that prey-population eruption is possible in the absence of predation. Predators can respond to increases in prey density by enhancing the rate at which individual predators catch and handle prey (functional response) or increasing their population size as prey densities grow (numerical response). But just as predators are capable of limiting their prey populations, so too can prey influence populations of their predators as it is also clear that without prey predators would not survive. Thus prey and predators have reciprocal influences on each other's long-term population dynamics. Insights into these coupled prey–predator dynamics are provided by the simple mathematical models of Lotka and Volterra and Nicholson and Bailey. Using a continuous time model, Lotka and Volterra were able to successfully generate persistent prey–predator oscillations; however, these results were not reproducible, even in controlled laboratory systems. Nicholson and Bailey proposed a new discrete-time model that incorporated more biological complexity, but failed to produce stable dynamics and resulted instead in localized extinction. Subsequent modeling efforts have highlighted several factors that may promote the long-term persistence of prey and predator populations, including mutual interference among predators, predator aggregation, habitat complexity and refuge from predation, and a Type III functional response. Predicting the outcome of prey–predator interactions is complicated even further when a prey–predator interaction is considered within the context of an entire food web. When multiple predator species are present they may have emergent, or unexpected, antagonistic or synergistic effects on prey populations. A diverse prey assemblage may also impact the effectiveness of predators, either through apparent competition or prey switching by predators. While the majority of research to date has focused on the impacts that predators have on prey populations by consuming prey, a growing body of work documents the critical role of non-consumptive (i.e., behavior- or trait-mediated) predator effects on prey. Prey must balance their need for obtaining food with the risk of becoming food themselves, and there may be physiological costs to prey associated with defensive behaviors such as increased vigilance or escape responses. Prey are hardly passive victims waiting to be consumed by predators. They have evolved a variety of primary, secondary and tertiary defenses that function to avoid becoming food for predators. Thus, predation can be a powerful evolutionary force with natural selection favoring more effective predators and less vulnerable prey. Understanding the process of predation and its complex effects on species interactions and food-web dynamics has enhanced our ability to use invertebrate predators as effective biological control agents of agricultural pests, increasing crop yields without the adverse consequences of pesticides.

Questions and discussion topics

1 In this chapter, many models of prey–predator interactions were presented. What is the usefulness of discussing prey–predator interactions within a modeling framework? What are some ways in which models can be integrated with empirical studies of prey–predator interactions?

2 While many insect predators exhibit a Type II functional response to increasing prey density, this is not the case for all predators in all circumstances. What are some biological mechanisms that might lead to a Type III functional response?

3 How might the incorporation of non-consumptive effects of predators on prey (and vice versa) alter our current understanding of the role of prey–predator interactions in food webs and community dynamics?

4 Discuss the evidence for and against the existence of a coevolutionary arms race between prey and predators.

5 What types of pre-release tests should be done to thoroughly evaluate the ecological risk (i.e., potential for non-target effects) associated with the release of an exotic biological control agent?

Further reading

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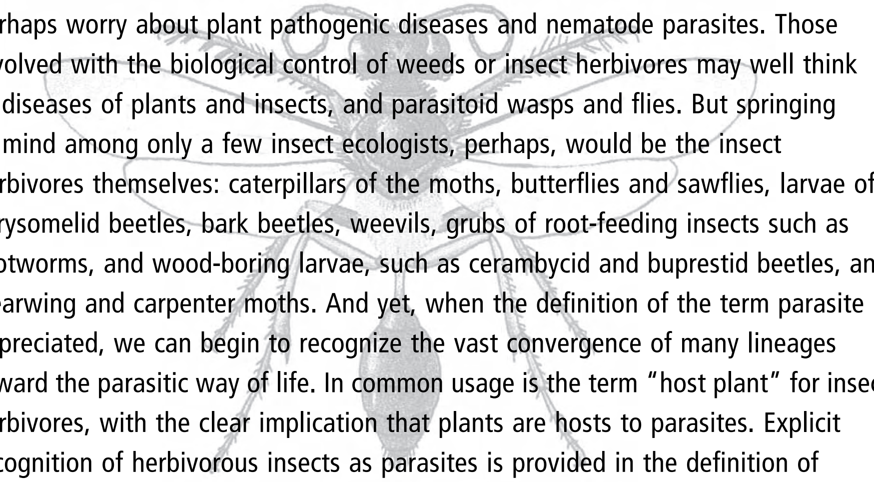
8

Parasite and host interactions



When considering the word “parasite” various kinds of organisms may spring to mind, depending upon the audience. Veterinarians may think of scabies, mange mites, warble flies, helminthes such as liver flukes, bird lice and disease organisms that cause rabies, plague, West Nile Virus and bird flu. Medical entomologists may be more concerned about malaria, sleeping sickness and vectors of disease like mosquitoes and blackflies. Agriculturalists would perhaps worry about plant pathogenic diseases and nematode parasites. Those involved with the biological control of weeds or insect herbivores may well think of diseases of plants and insects, and parasitoid wasps and flies. But springing to mind among only a few insect ecologists, perhaps, would be the insect herbivores themselves: caterpillars of the moths, butterflies and sawflies, larvae of chrysomelid beetles, bark beetles, weevils, grubs of root-feeding insects such as rootworms, and wood-boring larvae, such as cerambycid and buprestid beetles, and clearwing and carpenter moths. And yet, when the definition of the term parasite is appreciated, we can begin to recognize the vast convergence of many lineages toward the parasitic way of life. In common usage is the term “host plant” for insect herbivores, with the clear implication that plants are hosts to parasites. Explicit recognition of herbivorous insects as parasites is provided in the definition of a gall: “Galls are abnormal growths formed from tissues of a plant or other host, due to the parasitic activity of another organism” (Redfern and Shirley 2002, p. 207). This broad view of what is a parasite is somewhat controversial because of the ingrained emphasis on parasites of animals, particularly in the field of parasitology. However, plant pathology treats parasitic diseases extensively and we can observe life-history convergence in parasites on animals and plants (Section 8.6), so we should recognize the common features of all kinds of parasites.

In this chapter we emphasize the diversity of insect parasites, as well as the convergence of many groups toward similar life cycles, their main characteristics and how they relate to host species. We compare parasites with other ways of life such as predation, emphasizing that intimacy and duration of relationships between parasite and host have major importance in understanding evolutionary pathways in parasite lineages: life-history convergence, adaptive radiation and phylogenetic tracking of host lineages. Kinds of damage inflicted on hosts are discussed. Host responses in the form of defenses, how parasites can modify host behavior, and the population dynamics of host and parasite all contribute to a general appreciation of the parasite's ecological and evolutionary roles.

8.1 The parasite and parasitism

A parasite can be defined as an organism living in or on another living organism, obtaining its nutrition from that host organism and causing some degree of measurable damage to the host. We could add that parasites show some degree of adaptive modification to the host, but then every species shows adaptations to its food supply. Altogether, many of the species that are of concern to veterinarians, medical entomologists, agricultural and forest entomologists, and practitioners of biological control, are parasites. And those that study plant and herbivore interactions, parasite and host interactions, and multitrophic level interactions, in many cases are studying parasite–host relationships. Most caterpillars, but not all, spend their lives on a single host plant, eating plant tissues and causing real damage: they qualify as parasites. It is the **durable interactions** that characterize the parasite and its host (Combes 1995, 2001). "This is true no matter what the systematic position of the partners, no matter the way the interaction is borne out, and no matter even that the benefits and costs of the association may be unequally shared" (Combes 2001, p. 4). And so parasitism applies to the majority of insect herbivores.

This view of the widely ranging groups of species that qualify as parasites is neither a trivial nor a semantic exercise. Recognition of broad patterns in nature is basic to the fields of ecology and evolutionary biology, so that the wider the comparative biology can be cast, the more general the hypotheses and theories can become to explain the parasitic phenomenon: the convergence of life styles, the tricks of the parasitic trade, the rates of speciation and adaptive radiation, and even perhaps the best methods of regulating their numbers.

Reflecting upon the definition of a parasite, we should consider which organisms really qualify, and which do not. **Parasitoids** are organisms that have free-living adults that find insect hosts, on or in which they deposit eggs or living larvae. The larvae develop in a parasitic manner in the living host, whether the host continues to feed, or lie in a moribund state, paralyzed by the adult parasitoid. In either case, the host is killed eventually by the parasitic stage. Therefore, the adult parasitoid results in the death of many host insects, and its actions are equivalent to those of a predator. This was recognized by Reuter (1913) who called them "parasite-like predators," the Parasitoidea, from which the word parasitoid is derived. Others have coined terms such as "predatoid" and "carnivoroid" (see Flanders 1973), illustrating a dichotomy of emphases, although the facts are clear: parasitoid adults have impact on insect populations equivalent to predators (e.g., see Chapter 7), although their larvae are parasitic. And, as we shall see, the evolutionary biology of parasitoids is very much influenced by the constraints and opportunities afforded by the parasitic lifestyle.

Those insects that may not qualify as parasites, strictly speaking, but which are considered in texts on medical entomology are the biting flies: mosquitoes, blackflies, biting midges or no-seeums and most adult fleas. Of course, they are important in medical entomology as vectors of serious diseases, but they enjoy only brief encounters with the mammalian, reptilian and avian individuals, and even other insects, from which they obtain a blood meal. Adults are free-living, as are the larvae. Were they true parasites, they would not be effective vectors of diseases at all, because a parasite would live on a single host and not move among hosts as vectors must do to be effective. Even though a flea may stay on one host for a while it can easily hop from one host to another, and is more likely to do so than a small caterpillar feeding on a large tree. However, here we begin to recognize the gradient between parasites and free-living organisms, for as in most of biology, humans' classifications fall short of capturing the reality of nature (see also Lafferty and Kuris 2002).

We should also recognize that, as a way of life, parasites are involved with much of ecology, both basic and applied. They are ubiquitous and exert impacts on almost all living organisms. "Parasites dominate food web links" (Lafferty *et al.* 2006, p. 11 211), and "Parasitism is the most common consumer strategy among organisms" (Lafferty *et al.* 2008, p. 533). They are major contributors to malaise and mortality with often strong impact on host survival, and the distribution, abundance and population dynamics of many species. Parasites play a major role in ecology and evolution. Hence, we should understand them well, recognize common features observed in this lifestyle, and explore the evolutionary potential of these kinds of organisms that are easily overlooked in nature, and often ignored by ecologists.

8.2 Kinds of parasites

While the definition of a parasite is straightforward enough, the range of interactions that are considered in the literature as parasitic is enormous. Some kinds of interactions and their definitions contribute to an appreciation of the scope of parasitism and the considerable variation in the intimacy between host and parasite (Table 8.1). Even the lexicon relating to the parasitoid life cycle has become extensive because of the diversity of interactions involved (Table 8.1).

The recognition that many insect herbivores act as parasites dates back over 30 years (Price 1975c), with Bush (1975) considering speciation in "phytophagous parasitic insects," and Janzen (1975) noting that bruchid weevils act as parasitoids, with the adults finding seed pods and seeds on which they oviposit, while larvae feed slowly in the seeds as parasites, eventually killing them. Just as in our chapter on parasites, Janzen noted that when considering bruchid diversity "it will be most profitable to think of them as parasitoids" (p. 157), noting their impressive host-plant specificity, with 83% of species in his sample known from only one host plant species. (Plant pathogens similarly show narrow host ranges (Van den Ackerveken and Bonas 1997).) It was clear then, as it is now, that intimate and durable relationships between host and parasite necessitates specificity in feeding, fosters isolation between populations and form the engine of adaptive radiation in plant and animal parasites alike.

The importance of finding broad similarity across taxa in the durability and intimacy of interactions, which characterize the parasitic relationship with hosts, lies in the discovery of broad patterns in nature. The broader the pattern, the more general the concepts can become, and the wider-ranging the theory. When we can recognize massive convergence in life-history traits, host relationships and adaptive radiations, across several trophic levels, we have achieved a major conceptual breakthrough.

General characteristics of parasites are considered next, including concepts treated earlier by Price (1977, 1980).

8.3 The number of parasitic insect species

Various estimates have been made of the numbers of parasitic species in any fauna, and their proportional representation in that fauna, ranging

Table 8.1 **Kinds of parasitic insect and other kinds involved with parasitic life cycles. This also includes at the end of the list conditions which may occur in parasite ecology**

Parasite: Insects that live on, or in, and feed on a single living plant or animal for long periods of time, or for most of their lives, sapping energy from the host and causing damage.

Parasitoid: Insects that mature by feeding on a single host parasitically, eventually killing the host, while adults are free-living, finding living hosts and laying eggs in, on or near them.

Primary parasitoid: A parasitoid that attacks a host that is not a parasitoid itself.

Secondary parasitoid: A parasitoid that attacks a host already parasitized by a primary parasitoid, and actually parasitizing the primary parasitoid. It may be obligate or facultative.

Hyperparasitoid: The same as a secondary parasitoid.

Koinobiont: A parasitoid that lives with the living host, when the host continues to feed and to defend itself.

Idiobiont: A parasitoid in which the adult permanently paralyzes the host before the parasitoid egg hatches, and the parasitoid feeds on the moribund host.

Endoparasitoid: A parasitoid that lives within the host integument. Usually koinobionts.

Ectoparasitoid: A parasitoid that lives on the surface of the host. Usually an idiobiont.

Cleptoparasite (=Kleptoparasite): A species that steals food from other species, in insects this usually involves social parasitism such as in cuckoo bees. A better term is **cleptobiosis**, because a living host individual is not parasitized. However, among parasitoids, true cleptoparasitism is common enough.

Social parasite: A species that exploits the social structure of another species rather than an individual host, usually involving inquilines in nests of social insects.

Inquiline: A species that lives within the nest of another species, such as an ant or termite nest, or within the gall tissue of a gall-inducing insect, which may or may not cause harm to the host.

Pathogen: A species that causes disease in other species, usually applied to viruses, bacteria, protozoa or fungi, whether they parasitize plants or animals.

Vector: A species that transmits pathogens from one host to another. A vector may also be a host to the parasite, providing a breeding site, such as a mosquito acting as a host to malarial parasites.

Multiparasitism: The condition in which a host is attacked by more than one species of parasitoid.

Superparasitism: When more eggs are laid on or in a host than can be supported by the resources of that host. Eggs may be from the same or different species.

from about 15 to 50% (e.g., Arndt 1940, Rothschild and Clay 1952, Askew 1971, Bush *et al.* 2001). We can make our own estimate using 1 320 000 (and growing) estimated described animal species in the world (Hawksworth and Kalin-Arroyo 1995), 105 170 metazoan parasites on animals (Poulin 2007), plus 82 131 parasitoid species (Godfray 1994), a total of 187 301 parasite species on animals and 14% of all animal species. Adding in parasites on plants, plus bacterial, protozoan and fungal parasites, would increase the percentage, not to mention the undescribed species concentrated in the bacteria, protozoa, viruses, nematodes, fungi and insects, all with many parasitic species. But if we concentrate on the insect fauna, which after all dominates in numbers of species in any locality, some surprises may be evident. The British insect fauna is well studied and documented, with well-developed species lists (Kloet and Hincks 1945, 1964–1978), which can be employed in estimating the relative abundance of various feeding types (Table 8.2). Most notable in this compilation is the large proportion of the fauna represented by insects with a parasitic lifestyle, a total of 70.7% of the fauna. Also, in every case in which both predators and parasites are represented in an order of insects, parasites have become much richer in species than the predators. The most remarkable example of species richness is the parasitic Hymenoptera, the parasitoids, with 5342 species, representing 89% of the parasites on animals and 26% of the entire British insect fauna. (Even in the updated edition of the British Hymenoptera (Fitton *et al.* 1978, p. v), it was stated that “the total will be considerably increased when the Parasitica are better known”).

When we dissect the richness of parasitic Hymenoptera into families, we also observe that many families rank among the richest in the British fauna (Table 8.3). While the 10 largest families of predatory insects average 45 species per family, herbivorous parasites have a mean of 329 species per family and carnivorous parasites reach a mean of 489 species per family. Among the carnivorous parasites most families are composed of parasitoids, and most are hymenopterans. The Tachinidae with 228 species is a large family of dipteran parasitoids. The Philopteridae (Phthiraptera), with 176 species represented, is the family of bird lice, the only non-parasitoid family listed. Eight of the 10 largest families of carnivorous parasites are hymenopteran parasitoids.

Notable also in Table 8.3 is the large size of many herbivorous parasitic families. The Cecidomyiidae are the gall midges, with an intimate host-plant and parasitic interaction among the species. The weevils (Coleoptera: Curculionidae) are mostly internal parasites of plants as larvae, burrowing in stems, in cambium, under bark and in roots, shoots and fruits. Other families include lepidopterans, hemipterans, sawflies and beetles, so that all the major orders of insects are represented.

In rigorous phylogenetic tests of the extent of adaptive radiation of non-phytophagous versus phytophagous insects using 13 sister-group comparisons, the phytophagous groups were larger in 11 cases or 85% of cases (Mitter *et al.* 1988, see also Mitter *et al.* 1991, Farrell and Mitter 1993 and Chapter 4). However, at the higher trophic level, Wiegmann *et al.* (1993) found that in 9 of 15 comparisons the carnivorous parasitic taxon was smaller than the non-parasitic group (see also Winkler and Mitter 2007). That more local and intensive studies on the British fauna should provide a view different from a world view based on much less detailed studies should not be surprising. Also, detailed research on a tropical fauna using molecular techniques to identify cryptic species is revealing much greater parasitoid species richness and much higher specificity than previously recognized (Smith *et al.* 2006, 2007, 2008, Janzen *et al.* 2009).

The high numbers of species in families that are largely represented by parasitic lifestyles raises the question of why such extensive speciation should be apparent, relative to the smaller families of predatory insects. The answers are discussed in the next two sections.

8.4 Small body size

Obviously, parasites are smaller than their hosts, and usually much smaller. Living in or on the host means that the host not only provides food to the parasite, but also a habitat in which to live. Considering a large plant, like an oak tree, or a large mammal, such as a human, we can begin to appreciate the richness

Table 8.2 **The orders of British insects and other hexapods, the feeding habits of members of each order, and the percentage represented in each feeding type. Based on 20 244 species listed in Kloet and Hincks (1945) of which 16 929 can be readily classified**

Order	Predators	Non-parasitic Herbivores and Carnivores	Parasites on Plants	Parasites on Animals	Saprophages
Thysanura					23
Protura					17
Collembola					261
Orthoptera		39			
Psocoptera		70			
Phthiraptera				308	
Odonata	42				
Thysanoptera			183		
Hemiptera: Heteroptera	123		283		
Hemiptera “Homoptera”			976		
Megaloptera	3				
Neuroptera	54				
Mecoptera	3				
Lepidoptera			2233		
Coleoptera	215	65	909	18	1637
Hymenoptera	170	241	435	5342	36
Diptera	54	231	922	311	1672
Siphonaptera				47	
Total	665	646	5941	6031	3546
Percentage of insect fauna	3.9	3.8	35.1	35.6	21.5

Source: Price 1980

of habitats available on a single host. The mammalian integument is one example of the myriad places in which parasites can live: surface temperatures and humidity vary greatly over the body, pelage can be dense or sparse, sites may be easily groomed or protected, cavities differ, glands differ in shape and secretions, and hairs, and their follicles, vary in size and shape. The landscape of the

Table 8.3 **The 10 largest families in the British insect fauna in the categories of predators, herbivorous parasites and carnivorous parasites. Based on the check list of species in Kloet and Hincks (1945). From Price (1980)**

Predators		Herbivorous Parasites		Carnivorous Parasites	
Dytiscidae	110	Cecidomyiidae	629	Ichneumonidae	1938
Sphecidae	104	Curculionidae	509	Braconidae	891
Coccinellidae	45	Aphididae	365	Pteromalidae	649
Corixidae	32	Tenthredinidae	358	Eulophidae	485
Cucujidae	32	Noctuidae	298	Tachinidae	228
Hemerobiidae	29	Chrysomelidae	248	Philopteridae	176
Vespidae	27	Cicadellidae	242	Platygasteridae	147
Asilidae	26	Cynipidae	238	Encyrtidae	144
Anthocoridae	25	Olethreutidae	216	Diapriidae	125
Saldidae	20	Miridae	186	Ceraphronidae	108
MEAN	45		329		489

mammalian body, such as the human, becomes as varied and topographically complex for a parasitic mite as the State of Arizona may be for a human being (Figure 8.1).

When considering parasites and their small size, as Thompson (1942, p. 77) wrote, "we have come to the edge of a world of which we have no experience, and where all preconceptions must be recast." "We are prisoners of the perceptions of our size, and rarely recognize how different the world must appear to small animals" (Gould 1974, p. 21). We seldom think of our own bodies as ecosystems on which a myriad of species live, and it would take a dermatologist or a microbiologist to fully appreciate the complexity of the body surface, and the ways in which species become fine tuned and adapted to only small and specific locations on the skin (e.g., Marples 1965).

The implications of small size are almost endless. Body design, physiology, life cycle, population size and dynamics, niche occupations, community structure, evolutionary potential and adaptive radiation are all inextricably involved with size of the organism (e.g., Thompson 1942, Bonner 1965, Peters 1983, Calder 1984, Andrews 1991). Ecologically, it is easy to imagine that parasites can live in tiny niches, many species can coexist on a host, but in discrete places, and the amount of food consumed during a life time is miniscule. Also, small distances may result in sufficiently large divergence in the environmental quality that habitable patches may be narrowly defined, with disjunct distributions to be expected, and reproductive isolation occurring over short distances. Short generation times, and high populations, coupled with life on hosts affording discrete microhabitats, may well provide the ingredients for rapid speciation and adaptive radiation. Entering into the lives of parasites provides many challenges, but after all, as ecologists we should try to understand these species that in numbers may well exceed all other kinds of organisms. This perspective and the effects of body size will be discussed many times in this chapter and elsewhere in this book.

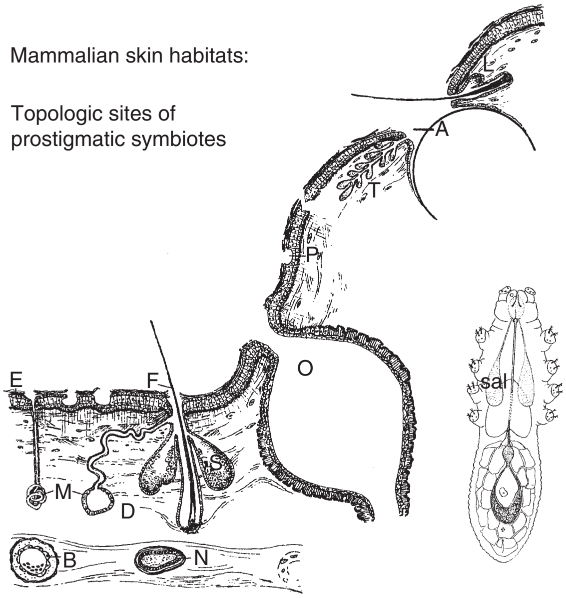


Figure 8.1 Habitats, or ecological niches, available for colonization by prostigmatid mites on the mammalian skin. Letters indicate discrete niches colonized by certain kinds of mites. A = ocular or oral cavity; B = blood vessels; D = dermis; E = epidermis; F = hair in follicle; L = eye lid; M = mixed apocrine and eccrine glands; N = lymph node; O = oral cavity; P = epidermal pits; S = sebaceous holocrine gland; T = tarsal gland. From Nutting (1985).

8.5 Adaptive radiation of parasites

Many reasons exist for the extensive adaptive radiation of parasitic groups, but high specificity to host species appears to be the most salient feature. Parasites are usually highly specific, often adapted to one species of host. This is the general case among parasitic groups on plants, such as leaf-mining flies (Agromyzidae), plant bugs (Miridae), and leaf-mining, leaf-rolling and tying, and gall-inducing lepidopterans in the family Gelechiidae (Table 8.4). It is also a feature common to animal parasites, with parasitoids showing that 53% of ichneumonids and 60% of braconids are recorded from a single host. Molecular studies are showing even higher levels of specificity, with over 90% of parasitoid species attacking only one or two host species (Smith *et al.* 2008). Bird lice are highly specific also, with 87% of species recorded as specific to a single host species. These levels of specificity contrast strongly with predators of seeds and insects, and plant grazers, which typically forage on 10–30 species of food items (Table 8.4). Seldom have arthropod predators been evaluated adequately for diet breadth. One well-studied scorpion, *Paruroctonus mesaensis*, is recorded to consume more than 125 prey species including a small snake (McCormick and Polis 1990, Polis and Yamashita 1991). “So far, there has been a direct relationship between the duration of the study and the number of species determined to be in the diet” (McCormick and Polis 1990, p. 302). Thus, the listings for vespid wasps, spiders and scorpions grossly under-represent the variety of prey. This is because prey are often recorded by higher taxa, such as orders and above.

We begin to see the reasons for high specificity among parasites when the higher and lower ends of the ranges in specialization are examined. Those families with higher than 50% of species with only one host have a very intimate relationship with that host, with individuals living in or on that host for the majority of their life cycles, or all of it in the case of the wingless philopterid bird lice. In contrast, phytophagous mirid bugs are good walkers, even as nymphs, and can move around from plant to plant, encountering several potential host species in a lifetime. The same is true for louse and bat flies (Hippoboscidae), which are parasitic on birds, bats and other mammals. Many species are winged as adults, and pupariate in the soil, so that a disconnection exists between host and parasite, and the freely foraging adult may find opportunistically various hosts before it settles and sheds its wings.

Examining the specificity in families of parasitic insects on mammals and birds supports the hypothesis that intimacy of life cycle between parasite and host selects for higher specificity. Philopterid lice are wingless, with a life spent entirely on the host, with 87% of species recorded from a single host (Table 8.5). Without wings, opportunities for parasite transfer to other hosts arise mainly among conspecific individuals: parent to young in

Table 8.4 **The numbers of host species recorded for parasitic insects on plants, insects, mammals and birds, compared with the number of taxa fed upon by predators of seeds, and insects, and by small mammals and ungulate grazers. The percentage of species in each class of "Number of hosts" or "Number of species . . . in diet" is provided in the table. Based on Price (1980)**

	Parasites on Plants			Parasites on Insects		Parasites on Mammals and Birds	
Number of Hosts	Agromyzidae	Miridae	Gelechiidae	Ichneumonidae	Braconidae	Philopteridae	Hippoboscidae
1	57	22	53+	53	60	87	17
2	20	14	26+	18	14	9	9
3	7	13	6+	11	10	2	15
4	6	21	3+	4	7	1	13
5	4	8	–	5	2	1	7
6	3	6	–	3	1	–	4
7	<1	7	–	1	2	–	4
8	<1	1	–	1	<1	–	4
9	<1	4	–	1	1	–	2
10–19	2	3	–	3	2	–	4
20–29	<1	1	–	<1	–	–	7
30–39	–	–	–	<1	–	–	2
40–49	–	–	–	–	–	–	–
50–59	–	–	–	–	<1	–	2
60–69	–	–	–	–	–	–	–
70–79	–	–	–	–	–	–	–
80–89	–	–	–	<1	–	–	7
Number of species	267	72	112	514	214	122	46

Table 8.4 (*cont.*)

	Predators on					
	Seeds		Insects		Grazers	
Number of Species or Larger Taxa in Diet	Birds	Small Mammals	Bats	Wasps, and Arachnids	Small Mammals	Ungulates
1	–	–	–	–	–	–
2	–	–	–	–	–	10
3	–	9	–	–	5	–
4	–	9	–	–	–	–
5	–	–	–	–	–	–
6	3	–	–	–	5	–
7	9	–	–	–	–	–
8	3	–	–	10+	14	–
9	4	17	–	30+	–	10
10–19	43	35	25	20+	40	20
20–29	20	26	25	–	31	10
30–39	10	–	50	10	–	10
40–49	4	4	–	–	–	10
50–59	1	–	–	–	–	10
60–69	3	–	–	–	–	–
70–79	–	–	–	–	5	–
80–90+	–	–	–	10	–	20
Number of species	70	23	4	10	22	10

+ indicates that numbers of taxa includes species, orders and above.

Sources are in Price 1980, and for predatory wasps and arachnids: Spradbery 1973, McCormick and Polis 1990, and Polis and Yamashita 1991.

Table 8.5 **The numbers of host species recorded for parasitic insects on mammals and birds. For each insect family the percentage of species in each class of number of hosts utilized is provided. From Price (1980)**

Number of Hosts	Philopteridae	Streblidae	Oestridae	Hystrichopsyllidae	Hippoboscidae
1	87	56	49	37	17
2	9	22	19	20	9
3	2	13	7	9	15
4	1	5	6	5	13
5	1	2	6	5	7
6		1	4	6	4
7		1	4	2	4
8			0	3	4
9			4	3	2
10–19			2	9	4
20–29				<1	7
30–39				<1	2
40–49					0
50–59					2
60–69					0
70–79					0
80–89					7
Number of parasites	122	135	53	172	46

particular, and among nestlings. The opportunities for host species shifts are very limited, resulting in close tracking of host lineages and parasite lineages. The ectoparasitic flies on bats (Streblidae) have blood-sucking, winged adults which deposit fully developed larvae on the surface of bat roosts where the larvae pupariate. So adults emerge close to the original host species and are likely to settle on such hosts, maintaining an intimate relationship with that species and even that particular colony. However, other bat species in the roost may be exploited, reducing specificity in this group relative to the bird lice. The bot and warble flies (Oestridae) show less specificity than streblids, presumably because the adults are strong fliers and move freely to find mammalian hosts. However, the parasitic life of the larvae still requires special adaptations for living inside the host, and almost 50% of species are recorded from a single host species. Some of this specialization is determined by the remoteness of the hosts, such as reindeer in the northern tundra, and some strange noses, such as the elephant's, hippopotamus's and giraffe's (Zumpt 1965). Here, the term remoteness applies to geographical isolation, or the uniqueness of nose design or position. The Hystrichopsyllidae is a family of fleas that utilize mostly small mammals as hosts. Adults take blood from hosts, but can jump from host to host, and are long-lived. Larvae are free-living, usually feeding in nest debris. This lifestyle results in relatively loose relationships with hosts, and relaxed specificity, with some species reported from over 20 mammal species. The least host-specific group in this progression is the Hippoboscidae, or louse flies, with the main hosts being birds. The louse flies are related to the streblids, but intimacy with the host is lost when the mature larva drops to the ground to pupariate in the soil. Hence, an emerging adult must fly around in search of hosts and may encounter many species, from which it may gain a blood meal, and so specificity is reduced.

The examples in Table 8.5 show a triangular pattern of host specificity, with high specificity on the left, and no parasitic species attacking more than five host species, and low specificity on the right, with records showing species from over 80 host species. Where there is high host specificity we should anticipate that reproductive isolation becomes stronger when host shifting occurs, and speciation may become more extensive. The number of hosts available in the lineage of hosts is also probably an important contributor to the potential for adaptive radiation of parasites. Host species probably act as ecological islands, just as islands in oceanic archipelagoes act to promote geographic and reproductive isolation in the celebrated cases of adaptive radiation. When we compare numbers of recorded hosts, and parasite specificity, and the number of parasite species per family, a suggestion of such a trend is evident. For example, the philopterid lice on birds exploit about 8600 species of hosts, they are highly specific parasites and exhibit extensive adaptive radiation with about 1500 species worldwide. In contrast, with fewer hosts and/or lower specificity, adaptive radiation in the parasites declines into the hundreds of species (Price 1980).

Similar scenarios can be developed for insect herbivore groups (e.g., Price 2002a), as suggested by the richness of species listed in Table 8.3. For example, the gall midges (Cecidomyiidae) are highly specific to one or a few host-plant species, as is the case in most gall-inducing insects. The extent of adaptive radiation is very high because of this specificity, and the richness of host-plant species in the lineage or lineages exploited. This has been observed within the family Cecidomyiidae (Roskam 1985, Figure 8.2), in other families of galling insects (Price 2005), and in other kinds of arthropod parasites (Price 1980). Altogether, data support **Eichler's rule** (Eichler 1948), developed for animal parasites, which states that the diversity of the parasitic fauna will increase as the diversity of the host taxon increases.

8.6 Life-history convergence

A problem common to many parasites, with their small size and widely scattered hosts, is the transmission from one host to another, or the infection or colonization of new hosts. Overcoming this problem has frequently involved a complex life cycle with the massive generation of individuals of a particular stage adapted for transmission and infection of new hosts. In many cases, complex life cycles have evolved with several distinct stages, some of which involve asexual reproduction and one stage with sexual reproduction. This convergence is observed in flatworms like liver flukes (Platyhelminthes: Digenea), gall aphids, gall adelgids and rust fungi (Figure 8.3), representing three taxa of widely different origins, which utilize vertebrates or plants as hosts. Frequently, more than one host animal or plant species is used in the life cycle, as in the cases shown in Figure 8.3, but also where insect vectors become the transmission agent for microbial organisms causing diseases such as malaria, yellow fever, Chagas disease, sleeping sickness and bubonic plague (Bush *et al.* 2001). Many plant diseases are also vectored among host plants by insect herbivores, particularly sucking insects such as aphids,

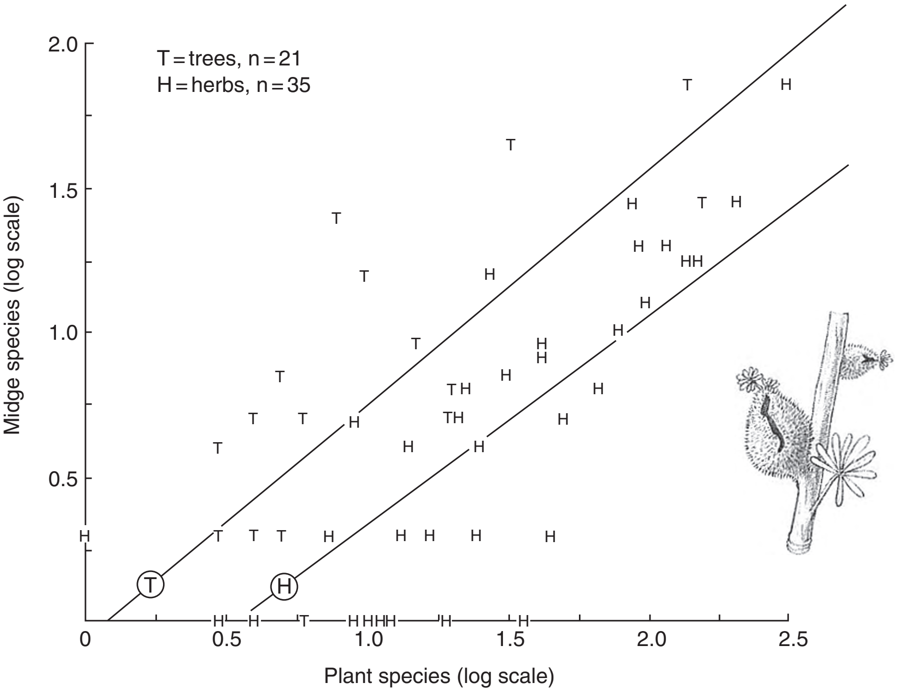


Figure 8.2 The number of gall-midge species correlates positively with the number of species in a plant family, for both midges on trees and on shrubs. From Roskam (1985).

leafhoppers, planthoppers and whiteflies, but also bark beetles. Plant diseases include mosaics, wilts and blights caused by viruses, mycoplasmas, spiroplasmas and bacteria, and many multiply in the vector, causing disease in the vector, but enriching saliva with parasite stages ready for injection into the next host (Maramorosch and Harris 1979, Borror *et al.* 1992, Nault 1994, Maloy and Murray 2001). The high production of propagules for transmission to a new host among disease organisms no doubt causes serious problems for vectors and recipient vertebrate hosts as well. Among humans, for example, high mortality results from the massive reproduction of such propagules, which result to ensure that tiny doses of blood taken up by insect vectors contain at least a few infective stages necessary to continue the parasite's life cycle (Ewald 1983, 1994).

Of course, many insectan parasites are well equipped to move from host to host, because adults are winged and commonly fly efficiently. But they, too, show reproductive capacities consonant with the problems faced in finding hosts, and surviving in hosts. For example, some parasitoids oviposit onto foliage, and infection of a host occurs when an egg is eaten or an active larva hatching from an egg attaches to a passing host. In these cases parasitoid fecundity is very high, compensating for the low chances of host infection (Figure 8.4). At the other extreme are parasitoids which oviposit directly into the host stage in which the life cycle is completed. Fecundity is low in these parasitoids because the probability of survival is high. Again we see convergence in reproductive strategies – this time in parasitoid taxa, such as the hymenopteran ichneumonids and the dipteran tachinids.

As with all adaptive strategies, there are associated inevitable limitations or constraints. When such strategies are broad scale and general, as in the parasitic

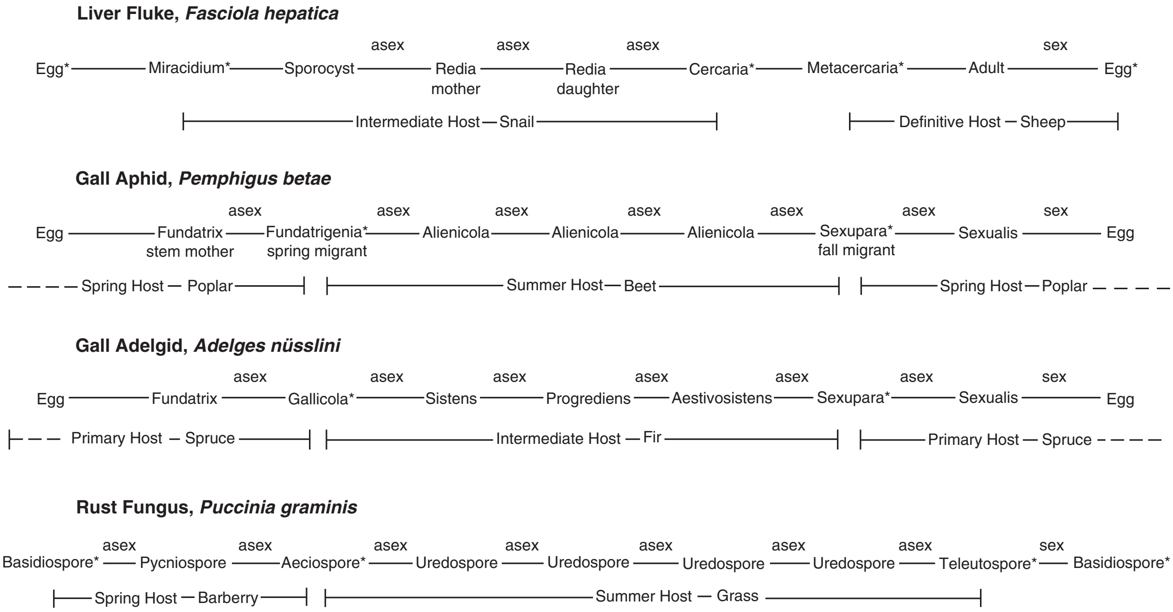


Figure 8.3 The convergence of life cycles among four types of parasite: a trematode liver fluke, a gall aphid, a gall adelgid and a rust fungus. Note the similarity of multiple stages of asexual reproduction (asex) and the single episode of sexual reproduction (sex) resulting in an egg or basidiospore. Asterisks denote stages in which transmission occurs between hosts, which are noted below the life cycle for each species. From Price (1992a).

lifestyle, we observe repeatedly the convergence of traits under similar kinds of natural selection. Parasitoids are constrained by the survivorship curve of the host, as if in a straight-jacket that limits life-history options and selects for convergence (see Figure 8.4). Given the richness of parasite taxa, the opportunities for comparative biologists are immense for the discovery of general patterns in nature.

8.7 Convergence among parasitoids

We concentrate here on parasitoids because of their immense interest to ecologists, their role in pest-population regulation, and because we need to understand with clarity how different parasitoids are from predators when we consider the parasitic way of life.

Evolutionary convergence into the parasitoid way of life provides one of the best and most diverse examples available today; convergence being the paths of disparate taxa evolving towards a common body plan and/or life-history type. We see similar lifestyles evolving even from across orders of insects. Also, within each lineage the adaptive radiation onto new hosts, and into new ecological niches, is extreme in some cases, as, for example, the Ichneumonidae with an estimated 15 000 described species and perhaps 60 000 total species in the world fauna. Godfray (1994) lists the families of insects which contain parasitoids, including 37 families in the Hymenoptera, nine families in the Diptera, five in the Coleoptera, two in Lepidoptera and one in the Neuroptera. Families with 1500 or more named parasitoid species in the world include the Chalcididae (1500), Torymidae (1500), Pteromalidae (3100), Encyrtidae (3000+), Eulophidae (3000+), Diapriidae (2028), Scelionidae (2768), Ichneumonidae (15 000), Braconidae (10 000), Tiphiidae (1500), Bombyliidae (3000), Tachinidae

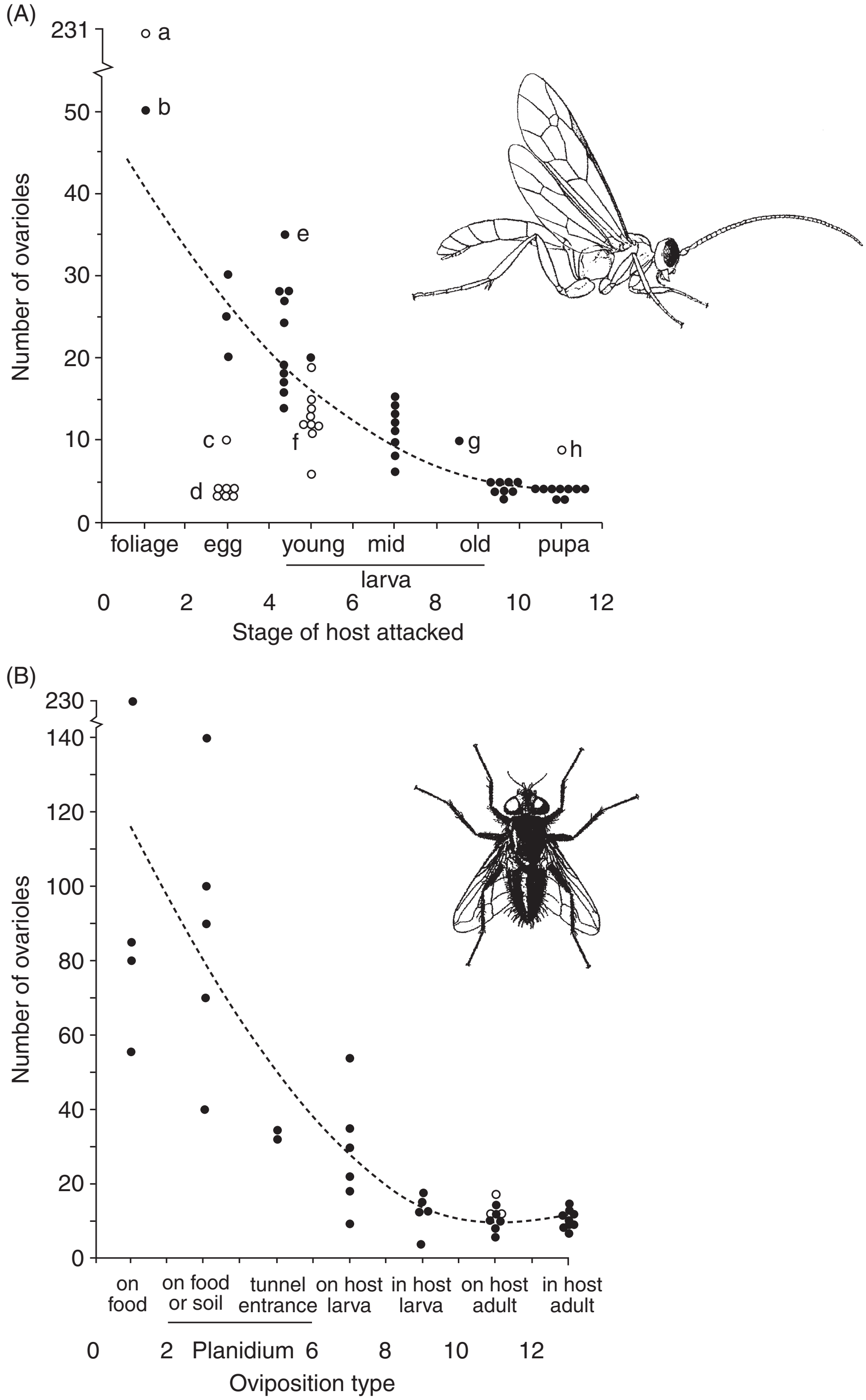


Figure 8.4 Relationships in the Ichneumonidae (A) and Tachinidae (B) between the host stage attacked and the number of ovarioles per ovary, which correlates well with total fecundity per female in these families. Note that in the Ichneumonidae some species oviposit on foliage (a and b), and in the Tachinidae oviposition in certain species may occur on food, soil or at a tunnel entrance. In these cases an active planidial first instar larva hatches and attaches to the host. From Price (1975a) in which details are explained, especially deviations from the trend in A such as the data marked d. These are egg parasitoids of spiders which kill the eggs and emerge from the egg sac, making them equivalent to pupal parasitoids.

(8200) and Meloidae (2000). A total estimated parasitoid fauna in the major insect orders add up to well over 50 000 species in the Hymenoptera, about 15 000 species in the Diptera, and over 3000 species in the Coleoptera. There is hardly an insect family that does not provide hosts for parasitoids, and many other invertebrates are also parasitized.

Parasitoids outnumber all Chordates: fishes, amphibians, reptiles, birds and mammals. With such vast numbers of species we should not be surprised at the impressive diversity in modes of reproduction and life history. Many specializations are not observed in solitary predators: polyembryony, precocious larvae and caste formation, haplodiploidy and sex ratio allocation, parthenogenesis, heteronomy, inbreeding or sib mating, hypermetamorphosis and extended phenotypes. These adaptive traits will be described briefly and more details can be found in other sources (e.g., Charnov 1982, Godfray 1994, Quicke 1997, Strand and Grbic 1997, Combes 2001). The examples illustrate, apparently, how favorable the parasitic habit is to the evolution of novelty, as also seen in morphological innovations. Such creativity argues against the views of earlier biologists who suggested that “parasites as a whole are worthy examples of the inexorable march of evolution into blind alleys” (Noble and Noble 1976, p. 525), “most specialization leads to blind alleys” (Mayr 1963, p. 596) and “specialization is a deepening rut in evolution” (Huffaker 1964, p. 645).

Polyembryony: the formation of multiple embryos from one egg. This condition is known in four families of parasitoid wasps: Encyrtidae, Platygasteridae, Dryinidae and Braconidae (Strand and Grbic 1997). Brood sizes can reach up to 3000 wasp progeny per host, with clear impact on population growth.

Precocious larvae and caste formation: polyembryonic encyrtids produce polymorphic larvae, with one type sterile and precocious. They develop rapidly and act as a soldier caste, which manipulates sex ratio of the reproductive caste and protects the brood from other parasitoids attacking the host caterpillar.

Haplodiploidy and sex-ratio allocation: sex determination in which males result from unfertilized eggs and females are produced from fertilized eggs. Since the ovipositing female can manipulate sex ratio, various adaptive traits appear: males can be produced on poor-quality hosts, perhaps small hosts, and females can be placed on higher-quality hosts. Sex ratios can be strongly skewed in favor of females, thereby increasing population growth.

Parthenogenesis: haplodiploidy is a form of parthenogenesis (arrhenotoky), but in addition, **thelytokous parthenogenesis**, in which only females are produced from unfertilized eggs, is moderately common in parasitoid wasps, reported in 20 families and 205 species.

Heteronomy: parasitoid species in which the two sexes develop in different host types obligatorily. This trait is observed in aphelinid parasitoids in which females develop as an endoparasitoid of homopterans such as mealy bugs, whitefly and scale insects, while males develop as hyperparasitoids, utilizing females of their own species or other species.

Inbreeding or sib mating: where sex ratios are strongly female biased among gregarious parasitoids a few males from one host will mate with their sisters originating from the same host.

Hypermetamorphosis: the life history in which larval instars develop through more than one form, as in blister beetles (Meloidae), with an active long-legged first instar larva, the **triungulin**, which can search for host grasshopper eggs or bees’ nests. They have less active parasitic stages and legless later instars. Also, first instar larvae of many endoparasitic species are equipped for fighting and killing conspecific and heterospecific endoparasitoids: large, rigid head capsules with strong mandibles result in vicious weapons of attack. They usually molt into second instars with smaller mandibles less equipped for physical aggression. **Planidial** first instar larvae of parasitoids, as described below, are equivalent to

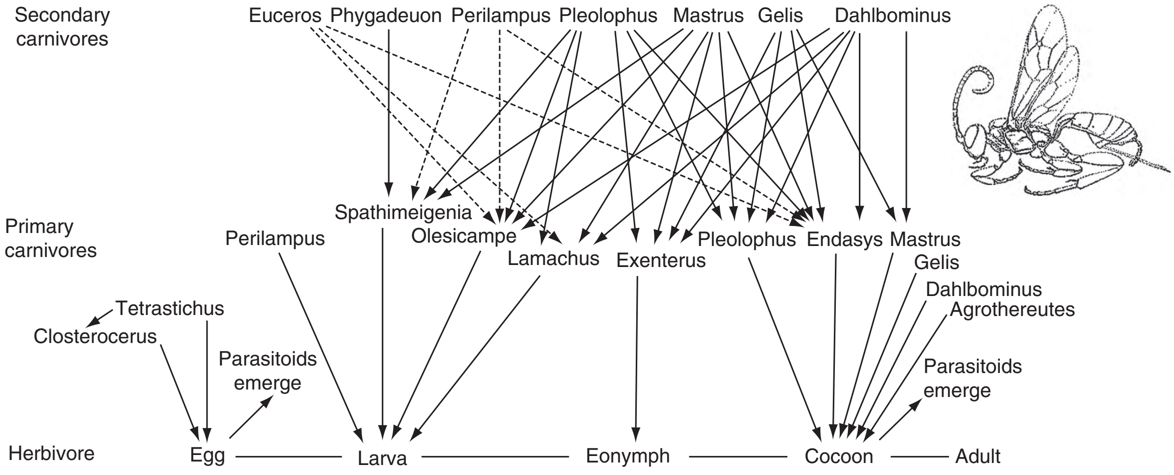


Figure 8.5 The life cycle of the Swaine jack pine sawfly (herbivore), and the parasitoids attacking each stage (primary carnivores) and the parasitoids in the secondary carnivore trophic level. From Price and Tripp (1972).

triungulins (Pinto 2003). Planidial larvae are found, for example, in the Eucharitidae which utilize ant pupae as hosts, Perilampidae (see below), *Euceros* (see below) and acrocerid flies.

Extended phenotypes: parasites can affect their own environments such that the phenotype of the parasite extends beyond the organism itself, such as a gall-inducing insect, a parasite, stimulating gall formation on the host plant (Dawkins 1982). Combes (2001) has emphasized that the "durable interactions" of host and parasite mean that genomes of both interact for much of the life of the parasite. The host becomes the extended phenotype of the parasite, and the parasite becomes the extended phenotype of the host.

The holometabolous insect host offers a series of substantially different resources which can be attacked by parasitoids, each requiring different specializations which ensure success. As an example, a sawfly such as the Swaine jack pine sawfly, *Neodiprion swainei*, passes through four stages: egg, larva, pupa and adult (Figure 8.5). In addition, larvae pass through several instars as they grow, ending with a non-feeding eonymph, which enters the forest litter and spins a cocoon in which it overwinters, pupating in the spring and emerging as an adult. Parasitoids attack eggs, larvae and eonymphs, and larvae, pupae and new adults in cocoons, but not emerged adult sawflies.

Many kinds of life history are illustrated by the *Neodiprion* parasitoids (Price and Tripp 1972). Two species of egg parasitoid attack and emerge from the egg. Larval, eonymphal and cocoon parasitoids are primary parasitoids and emerge from cocoons in the spring. *Perilampus* (Hymenoptera: Perilampidae) oviposits on foliage, active first instar larvae and **planidia**, hatch and wait for a passing sawfly larva, onto which they climb, bore into the host and become endoparasitoids. *Spathimeigenia* (Diptera: Tachinidae) is a larviparous species, which injects first-instar maggots into feeding sawfly hosts, where they become endoparasitoids. *Olesicampe* (Hymenoptera: Ichneumonidae) attacks early instar larvae, and *Lamachus*, in the same family, attacks later instar larvae. All larval parasitoids are koinobionts because they do not interrupt feeding and development of host larvae, but finally kill the host in the spring before it can pupate. *Exenterus*, another ichneumonid, is a specialized eonymphal parasitoid, laying eggs in the cuticle of the host before the sawfly leaves the tree and spins a cocoon. The parasitoid larva hatches onto the surface of the host after a cocoon has been spun and feeds as an ectoparasitoid and a koinobiont. The cocoon parasitoids are mostly ichneumonids: *Pleolophus*, *Endasys*, *Mastrus*, *Gelis* and *Agrothereutes*. All pierce the cocoon with long ovipositors, inject the sawfly host with venom, thereby paralyzing it, and oviposit on the host surface. Larvae feed ectoparasitically as idiobionts.

Among the secondary parasitoids or hyperparasitoids, *Pleolophus*, *Mastrus*, *Gelis*, *Agrothereutes*, *Dahlbominus* (Hymenoptera: Eulophidae) and *Perilampus* are facultative, acting also as primary parasitoids. They attack and parasitize each other in cocoons, and the hosts occupied by larval parasitoids. Two other species are obligate hyperparasitoids, only maturing on primary parasitoids. *Euceros* oviposits onto pine foliage and planidial first instar larvae hatch and climb onto a passing sawfly larva. The parasitic larva waits on the sawfly integument until a primary parasitoid larva becomes available, then it attacks its true host, feeding as an ectoparasitoid koinobiont as a primary parasitoid on a parasitoid host, and a secondary parasitoid on the cocooned sawfly host. The other hyperparasitoid is *Phygadeuon* (Hymenoptera: Ichneumonidae), which is a primary idiobiont parasitoid on fly puparia, but in this case attacks *Spathimeigenia*, the dipteran primary parasitoid on sawfly larvae. Many differences in life-history strategies correlate with these different kinds of host exploitation by parasitoids on the Swaine jack pine sawfly (e.g., Price 1971, 1972, 1974).

Other kinds of parasitoid exploitation patterns are observed, for example in those attacking lepidopterans and weevils, discussed by Mills (1994), for which he recognized 12 parasitoid guilds. These included parasitoids attacking adult weevils, some that attack eggs, but emerge from larvae, early larval, mid larval and larval-pupal parasitoid guilds, and others. The diversity of life cycles is amazing, as is the taxonomic and morphological diversity of families containing parasitoid species.

8.8 Phylogenetic tracking of host lineages

8.8.1 Parasites on animals

When parasites live closely associated with hosts we may well anticipate the parallel evolution of both host and parasite, such that when the host speciates, the parasite will also. This **cospeciation** of host and parasite, if persistent over the long term, would result in phylogenies that run parallel to each other: **parallel cladogenesis**, or various related terms such as **phylogenetic congruence**, **phylogenetic tracking**, **cophylogeny** or **concordance** (e.g., Page 2003). Such terms should not be construed as coevolution because reciprocal selection is not necessarily involved. The concept of parallel cladogenesis has been tested many times with varying results discussed below, but whatever the outcome, they enlighten us on the ecological settings in which species exist and the opportunities for adaptive radiation relevant to different lifestyles. Even among parasitic groups we find very different scenarios (see also Chapter 4).

Among parasitic taxa, various hypotheses are viable for a lineage through time, from no speciation, or extinction, to cospeciation, host shifting, speciation without a host shift and host speciation without speciation in the parasite lineage (Figure 8.6). Under which kinds of conditions will these different modes of lineage development prevail?

In the case of cospeciation we would expect its occurrence where parasites are tightly linked in their life history to the host, with strong phylogenetic constraints preventing deviation from members of a lineage. Examination of Tables 8.4 and 8.5 suggests that lineages showing high specificity of the parasite species with a single host species would be candidates for cospeciation. So the bird lice, Philopteridae, members of the chewing louse group, would provide the most likely examples. Other families of lice should show similar host

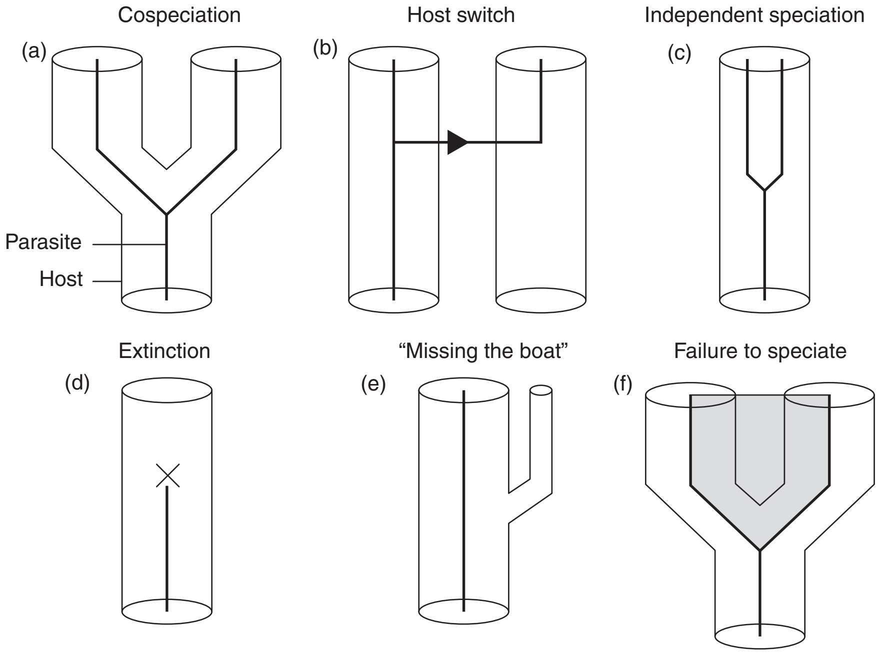


Figure 8.6 Various possibilities in the phylogenetic relationships of host and parasite species through time, with time passing from bottom to top in each example: (a) host and parasite species diverge and speciate in synchrony; (b) a parasite species shifts from one host to another, expanding its range of hosts; (c) speciation in the parasite lineage occurs on a single host lineage; (d) the parasite species goes extinct; (e) the host speciates without the parasite colonizing the new species; (f) the host speciates, but the parasite does not, although it remains on both hosts. From R. D. M. Page. 2003. Introduction. Pages 1–21 in R. D. M. Page, editor. *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. Chicago: University of Chicago Press. © 2003 by the University of Chicago.

relationships. Not only are the lice wingless, but they spend their entire life on the skin, hair or plumage of the host, and are likely to pass from one host generation to another, known as **vertical transmission**. The life of the birds, in many cases, accentuates the isolation of parasite lineages by nesting and roosting in isolation, minimizing opportunities for lice to crawl from one host to another. An additional factor is the high **prevalence** on hosts, meaning the high frequency of infection, and relatively large numbers of individual parasites per host. This reduces the probability of cases (d) and (e) in Figure 8.6, because populations of hosts are unlikely to lose their parasites. Evolved life history of lice with their hosts, and the cloistered ecological conditions in which they live, predispose such lineages to track host phylogenies closely.

As expected, it is in the lice, and their hosts, that we observe the clearest cases of insects illustrating parallel cladogenesis. They support **Fahrenholz's rule** that parasite phylogenies mirror host phylogenies – but not completely. For example, phylogenetic hypotheses on swifts (Apodidae), and their lice parasites in the genus *Dennyus* (Mallophaga: Menopodidiae), show numerous cases of cospeciation (Figure 8.7). Of host nodes, 60% (12 out of 20) were associated with cospeciation events with their lice parasites, and 13 such events were identified in the parasite lineage. Even so, parallel cladogenesis is not as extensive as we may expect over long periods of time. Similar ecological

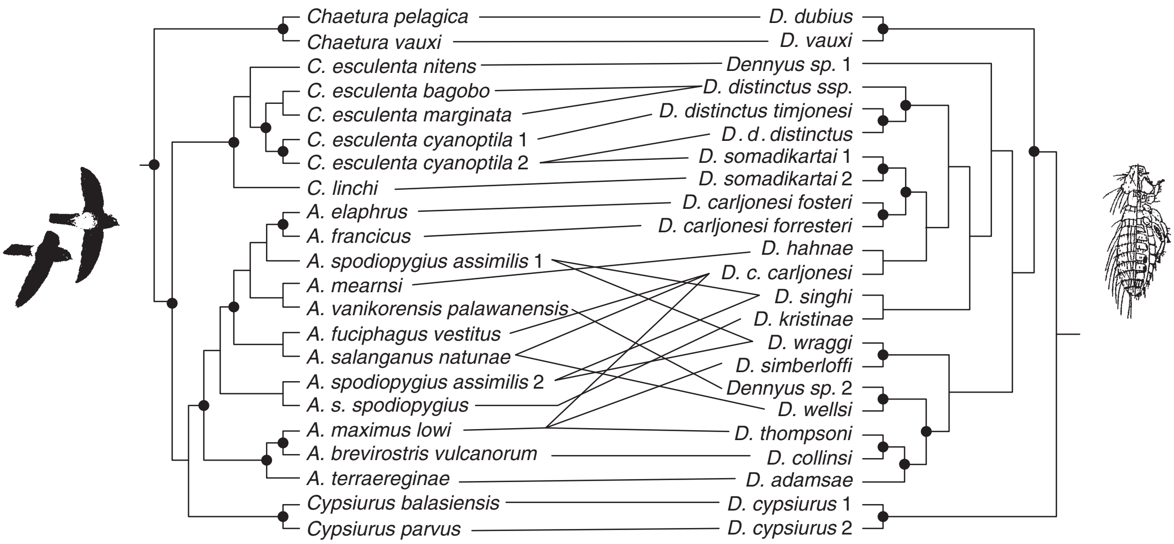


Figure 8.7 Comparison of phylogenetic hypotheses on swifts and lice in the genus *Dennyus*, with bulleted nodes marking cospeciation events. Lines from birds to lice show host–parasite associations. C = *Collocalia*, A = *Aerodramus*, D = *Dennyus*. From D. H. Clayton, S. Al-Tamini and K. P. Johnson. 2003. The ecological basis for coevolutionary theory. Pages 310–341 in R. D. M. Page, editor. *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. Chicago: University of Chicago Press. © 2003 by the University of Chicago.

factors to the swift-louse system also prevail in the pocket gophers as hosts to chewing lice parasites (Hafner *et al.* 2003). Gophers are fossorial, they spend most of their time tunneling in the ground, and typically show a solitary lifestyle in isolated populations (Hafner *et al.* 2003). They construct their own cave-like environment, so that they and their associated parasites become poorly adapted to life on the surface, "meaning that subterranean mammals and many of the organisms that coexist with them are locked into a long-term ecological association" (Hafner *et al.* 2003, p. 199). Biological interaction in the small caverns is high, increasing the opportunity for phylogenetic tracking, and perhaps coevolution. The resulting isolation of individuals, and species, both locally and inevitably at greater geographic distances also, forms the template on which speciation events will be relatively rapid. Phylogenies of hosts and parasites are likely to run in parallel, as in Figure 8.8, for pocket gophers and chewing lice. "All evidence involving tree topology and genetic divergence points to a history of widespread cospeciation between pocket gophers and chewing lice" (Demastes *et al.* 2003, p. 227).

8.8.2 Parasites on plants

Should phytophagous insects with a parasitic lifestyle illustrate similar patterns of phylogenetic congruence as the lice on some animal groups? Some hosts of lice are highly mobile, such as swifts, while plants are sedentary, suggesting initially, perhaps, that herbivorous insects might experience more ecological isolation than carnivorous parasites. However, once adults are winged, and many species have immature stages that can jump or crawl, coupled with plant communities rich in species, this combination of characteristics probably reduces the likelihood of extensive cospeciation. In fact few examples exist in the plant–herbivore literature. Commonly, phylogenies of host plants and insect herbivores indicate opportunistic host shifting

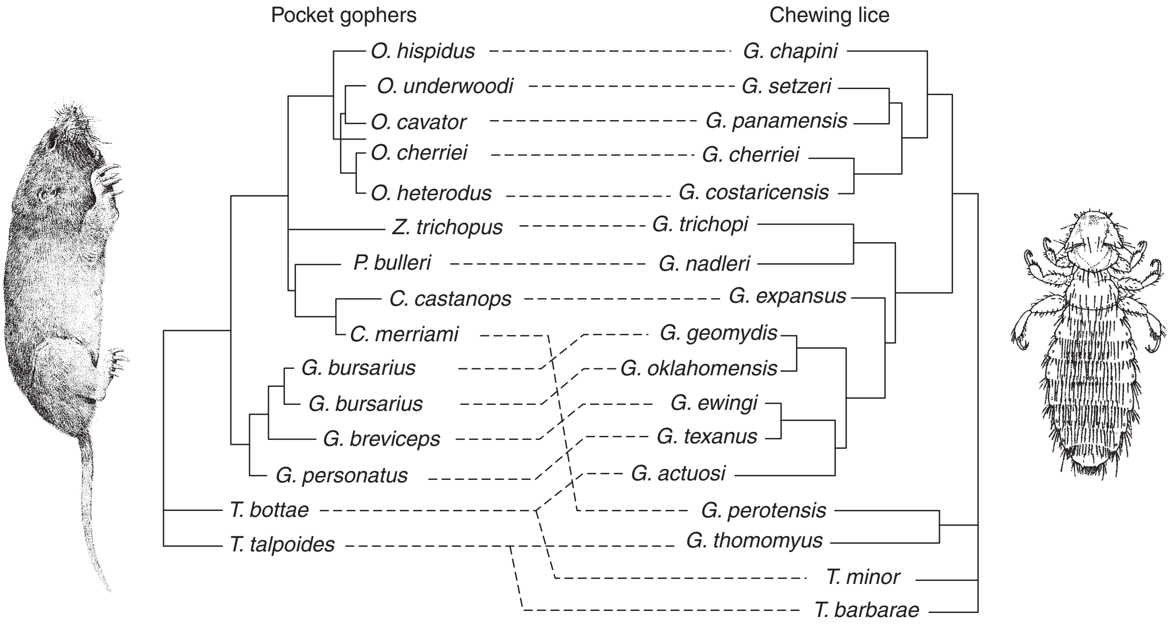


Figure 8.8 Comparison of phlogenetic hypotheses for pocket gopher hosts and their chewing lice parasites. Branch lengths are proportional to the estimated amount of genetic change, indicating that the lice have evolved faster than their hosts in many cases. For pocket gophers genera are: O = *Orthogeomys*; Z = *Zygogeomys*; P = *Pappogeomys*; C = *Cratogeomys*; G = *Geomys*; T = *Thomomys*. Chewing lice genera are: G = *Geomydoecus* and T = *Thomomydoecus*. Note that the two subspecies of *Geomys bursarius* each has its own specific louse species. From M. S. Hafner, J. W. Demastes, T. A. Spradling and D. L. Read. 2003. Cophylogeny between pocket gophers and chewing lice. Pages 195–220 in R. D. M. Page, editor. *Tangled Trees: Phylogeny, Cospeciation, and Coevolution*. Chicago: University of Chicago Press. © 2003 by the University of Chicago.

among hosts in the same environments. Examples include *Rhagoletis* fruit flies and their host plants (Smith and Bush 1997, Chapter 4), tenthredinid sawflies on willows (Nyman 2000), and cynipid gall wasps on oaks, which seem to have radiated after their oak hosts had diversified (Graham Stone, personal communication, in Price 2005, see also Bernays and Chapman 1994, Strong *et al.* 1984a).

However, host-plant chemistry appeared to be a stronger determinant of host-shifting patterns in *Blepharida* beetles (Coleoptera: Chrysomelidae: Alticinae) than geographic proximity of hosts in the genus *Bursera* (Burseraceae) (Becerra and Venable 1999), or host-plant phylogenetic relationships (Becerra 1997, 2003). This can be appreciated when the specialized chemical defenses of *Bursera*, in the form of "squirt gun" responses when canals with resins under pressure are punctured, and the specialized counterplay evolved in the associated beetles are considered (Becerra and Venable 1990, Becerra 1994, Becerra *et al.* 2001, see also Chapter 4).

An unusual case of phylogenetic tracking of host plants by insect herbivores involves *Phyllobrotica* beetles (Coleoptera: Chrysomelidae) utilizing members of the mint family (Lamiaceae) (Farrell and Mitter 1990, Mitter *et al.* 1991). The insects as larvae are endoparasitic in the roots of host plants, indicating an intimate association. In addition, the host plants are aromatic and chemically defended with the iridoids catalpol and aucubin, which may well be sequestered by larvae and passed on to adults which are aposematically colored yellow-orange and

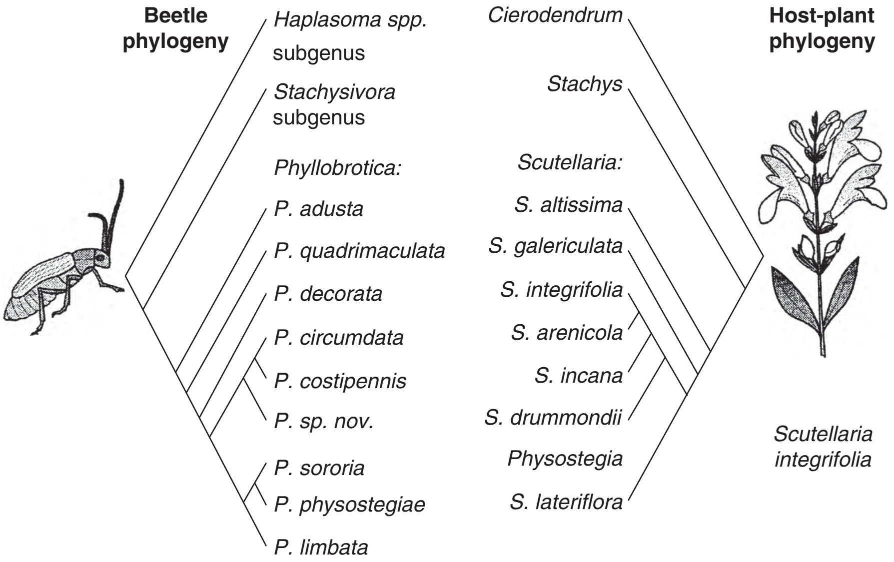


Figure 8.9 Comparison of phylogenetic hypotheses for the beetle genus *Phyllobrotica* and its sister genus *Haplasoma*, and the host plants in *Scutellaria* and related genera. From Price (2002a), based on Farrell and Mitter (1990).

black, and have a bitter taste. Given these conditions selecting for high specificity among beetle species, the phylogenies of beetles and host plants are closely similar (Figure 8.9). But this kind of relationship would be expected to be replicated many times, particularly with endophytic insects, so the remarkable fact is that it has been recorded so rarely.

8.8.3 Microbial symbionts of insects

Rather than asking how parasitic insects track host lineages, we can ask how symbionts of insects track their hosts. Microbial symbionts of insects are typically transmitted vertically, from female parent to offspring, such that cospeciation and phylogenetic tracking are likely. This is indeed the case. Aphids and their symbiotic bacteria in the genus *Buchnera* have diversified in parallel since the origin of aphids 150–250 million years ago (Chapter 4, Figure 4.18, Baumann *et al.* 1997, Clark *et al.* 2000). Similar relationships hold for psyllids and their symbionts (Thao *et al.* 2000) and sharpshooters (Hemiptera: Cicadellidae) (Moran *et al.* 2003), and all other groups studied so far, including ants, weevils, flies, cockroaches and termites (Moran and Bauman 1994, Moran and Telang 1998). The symbiotic bacteria are mutualistic symbionts, however, not parasites, and are housed in specialized cells, the bacteriocytes, and a particular organ, the bacteriome.

Similar studies on parasitic bacteria, such as *Wolbachia*, perhaps surprisingly, show no such congruence with host phylogenies, indicating **horizontal transmission** among hosts outside the maternal lineage (Werren 1997), meaning infection by bacteria across host species. While **vertical transmission** in *Wolbachia* is the norm, involving infection from generation to generation of hosts by sexual means, ensuring infection down a lineage, horizontal transmission affords an escape to other host lineages and a broadening of the exploitation pattern of the parasites. Horizontal transmission in certain strains of *Wolbachia* includes not only that among hosts of the same species, but among different taxa – **intertaxon transmission** (Werren 1997). One strain may be found in several insect orders such as Lepidoptera, Hymenoptera, Diptera and Coleoptera, with divergence times estimated at 0–1.6 million years ago, while their hosts diverged 200 million years ago. The comparatively recent expansion of the host range clearly indicates that horizontal transmission is important and quite commonplace, which precludes phylogenetic concordance of *Wolbachia* with any one host lineage.

8.9 Geographic mosaics of variation and patch dynamics

Another characteristic of parasites is that they are likely to show extensive variation in space and time – a geographic and temporal mosaic of variation in their interactions with hosts. Thompson (2005) has emphasized this in his book *The Geographic Mosaic of Coevolution*, using many examples involving symbiotic species interactions as some of his most intriguing and convincing cases.

8.9.1 Drosophila and its parasitoids

One example concerns the interactions of *Drosophila melanogaster* and relatives with their larval parasitoids in Europe (Kraaijeveld and van Alphen 1994, 1995, Kraaijeveld and Godfray 1999). The parasitoids are internal and thus susceptible to resistance from their hosts' cellular immunological responses, which result in cellular **encapsulation** of parasitoid eggs and death. The parasitoids involved were *Asobara tabida* (Hymenoptera: Braconidae), *Leptopilina heterotoma* and *L. boulardi* (Hymenoptera: Eucoilidae). These are the major parasitoids attacking *Drosophila* in Europe. They differ in their defenses against encapsulation: *Asobara* eggs adhere to host tissue and become invested in a fibrous coat; *Leptopilina* injects with the eggs viral-like particles which appear to prevent encapsulation. Therefore, we may well expect both variation in parasitoid virulence and avirulence, and host resistance and susceptibility.

Asobara virulence in *Drosophila* showed a clear pattern of variation geographically across Europe, from very low in the north to northwest, to high in the south and southeast (Figure 8.10). Interestingly, *Drosophila* resistance by encapsulation to *Asobara* did not correlate with *Asobara* virulence, but showed strong resistance in a central belt across France and Italy, weakening to the north, southwest and southeast (Figure 8.10). Yet another independent "pattern" was evident in *Drosophila* resistance to *Leptopilina boulardi* (Figure 8.11), which illustrated a patchwork of 0% to above 20% encapsulation from Britain to Turkey, Cyprus and Israel, a true mosaic of interaction strengths between hosts and parasitoids.

The interlocking of interactions among *Drosophila* populations involving other species, in addition to *melanogaster*, and the internal parasitoids, plus puparial parasitoids, will be extremely complex. This example illustrates the mosaic of interactions to be expected in the majority of instances where feeding substrates, host and parasitoid species, and geography and climate interact. Variation may be extreme, even from one locality to an adjacent location, and situations are likely to change temporally and rapidly.

8.9.2 Scrub typhus

The precise details of such very local variation in parasite–host interactions is seldom recorded, but we can infer scenarios by the infection patterns in humans working in the field. In arenas of war in Southeast Asia and adjacent islands, soldiers working in one group may experience infection by scrub typhus among a few in the group, whereas other groups working only meters away incur no infection (Price 1980). Foci of infection were often extremely local and these may change over short periods of time. The scenario to be described is characteristic of the epidemiology of many parasite populations. We can start with the complexity of biotic interactions, with several species involved, such that their intersecting lives and distributions, each with their

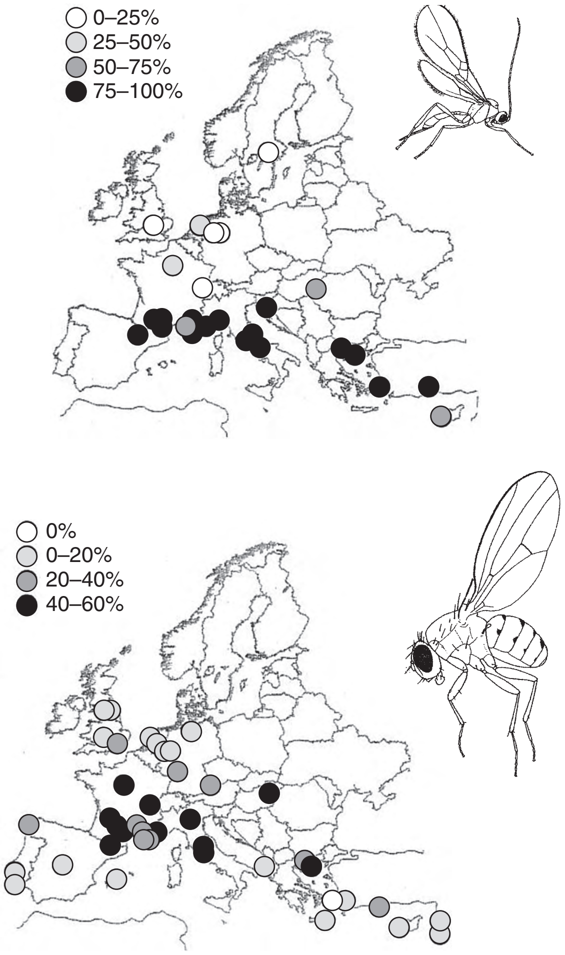


Figure 8.10 (Top) Geographic variation in virulence of the parasitoid *Asobara tabida* in populations of *Drosophila melanogaster* in Europe. Different levels of virulence, indicated by the percentage of parasitoid eggs not encapsulated in a standard strain of the host, are shown by circles increasing from clear to black as encapsulation is reduced. (Bottom) The pattern in Europe of the resistance by encapsulation by *Drosophila melanogaster* populations to parasitoid eggs of *Asobara tabida*. Different levels of resistance are indicated by circles, as estimated using a standard strain of the parasitoid. From Kraaijeveld, A. R., and H. C. J. Godfray (1999). Geographic patterns in the evolution of resistance and virulence in *Drosophila* and its parasitoids. *Am. Nat. Suppl.* 153:S61–S74. © 1999 by the University of Chicago.

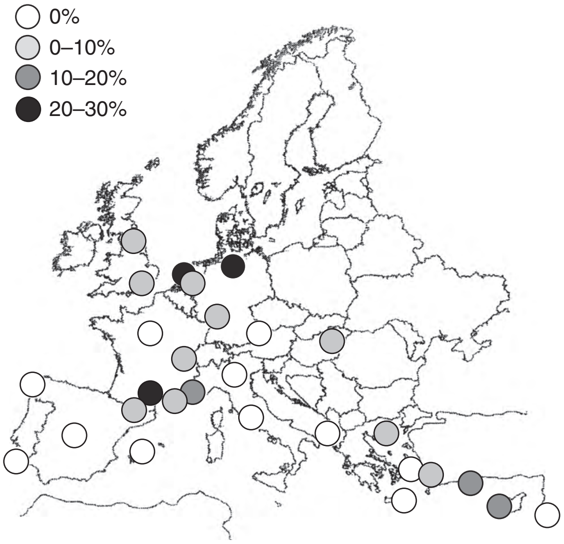


Figure 8.11 Geographic variation of encapsulation of the parasitoid, *Leptopilina boulardi*, in populations of *Drosophila melanogaster* across Europe, with levels of encapsulation increasing from 0 to 30% in a standard strain of the parasitoid. From Kraaijeveld, A. R. and H. C. J. Godfray (1999). Geographic patterns in the evolution of resistance and virulence in *Drosophila* and its parasitoids. *Am. Nat. Suppl.* 153:S61–S74. © 1999 by the University of Chicago.

own mosaic structure over the landscape and in time, just happen to allow transmission in small nodes where all conditions become favorable (Figure 8.12). Transmission would seem to be most unlikely were it not for military operations combing large areas with masses of troops involved.

Scrub typhus, or chigger-borne rickettsiosis, occurs at the confluence of at least six factors involving biotic and abiotic conditions (Traub and Wisseman 1974, Price 1980).

(1) The presence of the pathogen *Rickettsia tsutsugamushi*, which is transovarially transmitted among mites.
(2) The vectors of the pathogens are trombiculid mites in the genus *Leptotrombidium*, which are chiggers.
(3) The chiggers attack small mammals, particularly rats in the genus *Rattus*.

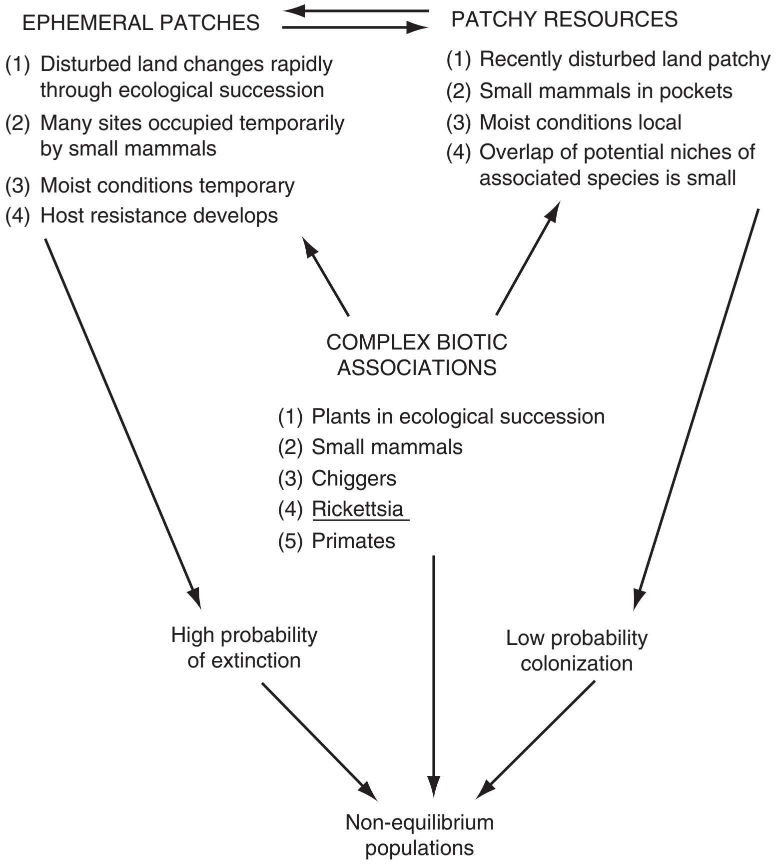


Figure 8.12 The patch dynamics of chigger-borne rickettsiosis, or scrub typhus. Note the many biotic and abiotic factors which interact, thereby affecting parasite transmission. From Price (1980).

(4) The vegetation is characteristically scrubby, recently disturbed and in a passing phase of ecological succession that is overgrown rapidly in tropical climates.
(5) Humans walking through patches with all four preceding elements present, at least in the recent past, are attacked by chiggers which pass on the infection.
(6) Moist conditions increase the probability of infection of humans.

Overlap of all these factors is likely to be very patchy in nature and ephemeral and highly unpredictable for any personnel, resulting in non-equilibrium populations waxing and waning across a landscape (Figure 8.12). "The characteristic localization of chigger-borne typhus is of a dual nature, comprising endemic districts of a large size (ranging from a few square km to extensive geographic areas, such as islands or valleys) and, within such locales, a markedly patchy distribution or highly circumscribed foci or even microfoci, of typhus islands which may be a few meters in diameter" (Traub and Wisseman 1974, p. 244).

Plant demography and dynamics will impact rat dynamics as food supply of seeds varies, and rat dynamics are notoriously eruptive in tropical and subtropical regions: the rat plagues or ratadas. Rats are crucial to the maintenance of chigger populations and *Rickettsia*.

8.9.3 A brine fly and its parasite

The complex pattern of interactions between parasite and host becomes extraordinarily dynamic, and probably generally applicable to parasite–host interactions. For example, under very different circumstances, the same kinds of conditions prevail for the parasitic mite, *Partnuniella thermalis*, on its host the brine fly, *Paracoenia turbida* (Diptera: Ephydridae) in a high productivity alkaline thermal spring in Yellowstone National Park. "The pattern in space of resources for both parasitic and free-living stages of the mite will be a mosaic of high and low density patches with few patches of intermediate density" (Collins 1975, p. 250). Host flies are unpredictably distributed and extremely clumped, with effective defenses, making colonization of clumps hazardous with accompanying high and inevitable mortality (Collins *et al.* 1976). The similarity of this example with that in Figure 8.12 is evident, including complex biotic associations, ephemeral patches, patchy resources and their consequences.

The geographic mosaic of variation and patch dynamics of parasite and host interactions has a miniature dimension commensurate with the sizes of parasites, vectors and suitable breeding places. This contrasts with the huge impact of many parasites through history, and over large geographic areas, and on the population dynamics of natural populations of host species. This brings us to the next characteristic of parasites to be treated in this chapter – the damage that parasites do to their hosts.

8.10 Damage to the host

Many parasites inflict serious damage on hosts, but others have questionable impact, revealing the inevitable continuum between interaction types observed throughout biology.

8.10.1 Early attitudes on parasites

Understandably, parasites damage their hosts – a requirement in the definition of a parasite – but it is not necessarily easy to evaluate this damage. Early in the development of ecology Charles Elton (1927, p. 75), in his influential book *Animal Ecology*, recommended "that it is best to treat parasites as being essentially the same as carnivores … the resemblances between the two classes of animals are more important than the differences." This argument was based on his view, "If parasites are to occupy a special place in the scheme we must, to be consistent, accuse cows of petty larceny against grasses, and cactuses of cruelty to the sun" (p. 75). David Lack (1954, p. 169) in his classic *The Natural Regulation of Animal Numbers* also minimized the role of parasites concluding that, "While further evidence is needed, it seems unlikely that disease is an important factor regulating the numbers of most wild birds." And Lack (1966) continued to downplay the role of parasites in bird populations. These two prominent ecologists, Elton and Lack, may well have had a long-term chilling effect on the study of parasites and diseases in natural populations, for the literature was dominated for many decades by studies on predation, with parasitism remaining in a backwater of ecology.

8.10.2 A change in attitude

Fortunately, and necessarily, these attitudes have changed. Given the massive impact of diseases on human populations throughout history, the attitudes of earlier ecologists were unreasonable, and were founded on a lack of study, and of knowledge, rather than on an understanding of the natural world. Another complicating factor is that parasite life cycles, modes of transmission, vectors of diseases, pathogenicity, resistance, virulence, immunity and susceptibility, all contribute to a more involved set of variables to measure and incorporate into a simple framework of ecology. So the details can be glossed over, as Elton did, or ignored because of lack of knowledge. However, we now have books devoted to such subjects as *Bird–Parasite Interactions* (Loye and Zuk 1991), which documents many adverse effects of parasites on bird behavior, distribution and fitness; *Parasites and the Behavior of Animals* (Moore 2001), *Evolutionary Biology of Parasites* (Price 1980), books devoted to cospeciation of hosts and parasites (e.g., Brooks and McLennan 1993, 2002, Page 2003), and more ecological treatments of parasitology, such as *Parasitism: the Diversity and Ecology of Animal Parasites* (Bush *et al.* 2001), and *Parasitism: The Ecology and Evolution of Intimate Interactions* (Combes 2001, see also Poulin 2007). In addition, research on parasites increasingly appears in the ecological literature (e.g., Sol *et al.* 2003, Elliott *et al.* 2003, Fitze *et al.* 2004, Krasnov *et al.* 2004, Bize *et al.* 2004, Pulkkinen and Ebert 2004, Johnson and Herbers 2006), much of it documenting the negative impact of parasites on their hosts.

Of course, parasitoids have never been shortchanged in the literature because their direct impact on host mortality is obvious. Early biological control attempts on insect herbivore pests, such as the California red scale, *Aonidiella aurantii*, were impressively successful using parasitoids (DeBach and Sundby 1963, DeBach 1964, Murdoch 1994), and early studies on population dynamics implicated parasitoids as important factors (see Chapters 7 and 11). When hosts occur in concealed microhabitats, like under bark, in mines, or in cocoons or puparia, external parasitoids commonly paralyze hosts with a sting into a nerve ganglion, after which an egg is laid and the larva feeds on the moribund host, which never recovers. Parasitoids of this kind have been called **idiobionts** (Askew and Shaw 1986, Table 8.1), meaning "life" (Greek, *bios*), "alone" or as an "individual" (Greek, *idios*), implying life alone without a fully active host. On active and externally feeding hosts parasitoids often lay eggs into the host without immediately impairing its activity. These kinds of parasitoids were called **koinobionts** (Askew and Shaw 1986, Wharton 1993), the term meaning that the parasitoid shares a life (Greek, *bios*) in common (Greek, *koinos*) with the host. The host continues to feed, but eventually the parasitoid larva grows and feeds actively, inevitably killing the host, unless the host encapsulates the egg or larva. Host resistance is suppressed in many cases when female parasitoids inject virus-like inclusions with the parasitoid eggs (Stoltz *et al.* 1976, Stoltz and Vinson 1979, Edson *et al.* 1981, Boucias and Pendland 1998). These inclusions are generally referred to as virus-like particles (VLPs) and belong to a distinct group of polydnaviruses (PDVs) (see Gullan and Cranston 2005). In both cases, of host paralysis or internal parasitoid larvae, the host is usually doomed to die. There is a one-to-one relationship with the larva killing one host, and the impact is easy to document, with hundreds of life tables recording mortality inflicted by parasitoids (see Chapter 9).

Also relatively straightforward to evaluate is the damage to plants by herbivores, many of which act as parasites on the plants. This has been treated extensively in Chapter 4. Even a small amount of chewing on a leaf is recorded for the life of that leaf, which can be readily documented, allowing estimates of damage to be compared in temperate and tropical latitudes (e.g., Coley and Aide 1991, Dyer and Coley 2002), with leaf damage reaching as high as 48% of leaf surface among gap-specialist plants in tropical wet forest (Coley and Barone 1996, Dyer and Coley 2002).

Parasites' negative impact on vertebrates has been much more difficult to evaluate, resulting in the kinds of early underestimates expressed by Elton and Lack already mentioned. Birds' alimentary canals may be packed with thousands of helminth parasites, but hosts show no measurable effects. And the trouble with insect ectoparasites on birds and mammals is that small numbers have little effect (except for vectors of pathogens), and only when populations build up do pathological effects appear, and measurements can be made. However, once host

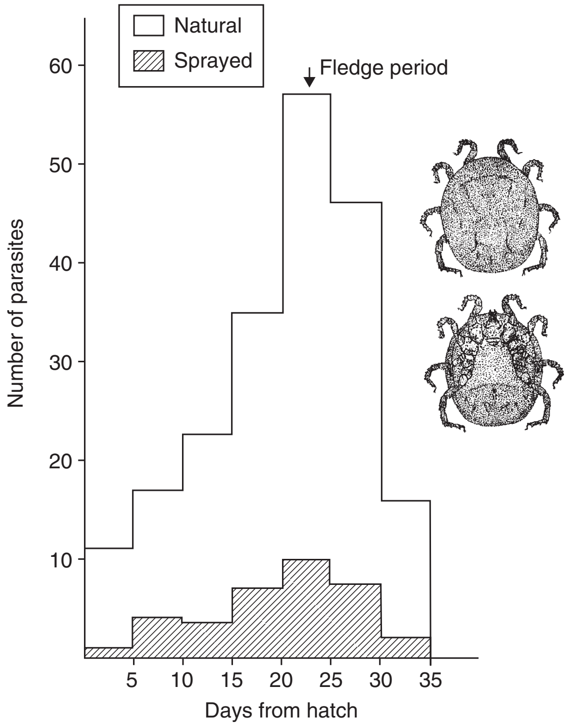


Figure 8.13 The mean number of ectoparasites per trap, or "harborage," in each 5-day period from the start of swallow occupancy of a site through the brooding season until after nestlings fledged. A harborage was a 6×6 cm block of plaster providing dark refuges for ectoparasites, 10 cm below a study colony, into which parasites crawled after feeding. Removal of the block provided a standardized count of the parasite population. Parasites were released after each count. From B. R. Chapman and J. E. George (1991). The effects of ectoparasites on cliff swallow growth and survival. Pages 69–92 in J. E. Loye and M. Zuk, editors. *Bird-Parasite Interactions*. Oxford: Oxford University Press. Reprinted by permission of Oxford University Press, Inc.

Table 8.6 **Mortality of cliff swallow nestlings before fledging according to their position in the hatching sequence, in natural levels of ectoparasites and in sprayed nests. From B. R. Chapman and J. E. George (1991). The effects of ectoparasites on cliff swallow growth and survival. Pages 69–92 in J. E. Loye and M. Zuk, editors. *Bird-Parasite Interactions*. By permission of Oxford University Press**

Hatching Sequence	Mortality % Natural	Mortality % Sprayed	χ^2
1	5.2	4.1	0.23 (NS)
2	8.8	5.4	1.29 (NS)
3	21.1	8.2	7.84 $p<0.01$
4	45.6	11.3	25.76 $p<0.005$

nesting starts, parasites can multiply rapidly and time in the nest becomes a crucial determinant of how the young succeed. In cliff swallows studied by Chapman and George (1991) ectoparasite populations built rapidly, in north-western Texas (Figure 8.13), involving three main species: the cimicid swallow bug, *Oeciacus vicarious*, the small tick, *Argas cooleyi*, and another tick, *Ornithodorus conanensis* (Acari: Argassidae). Many adverse effects were observed on the growth of chicks and fledging success when comparisons were made between nests untreated and nests sprayed with an acaricide. Nestlings grew more rapidly in treated nests, they reached a higher fledgling weight, and with greater percentage success (89 vs. 54% success) from hatching to fledging. In addition, those chicks that hatched early, and experienced lower levels of parasitism, suffered much less mortality than later chicks (Table 8.6). The heaviest mortality was inflicted upon the fourth chick to hatch in a nest with 45.6% mortality in unsprayed nests and only 11.3% in sprayed nests. Further effects were seen in feather lengths of fledglings, blood quality and total mortality which reached 76% in natural nests and only 9% in sprayed nests. Strong impact by arthropod ectoparasites indeed.

Strong effects of parasites have also been documented for *Philornis*, the muscid botflies that feed subcutaneously, mainly on nestlings, but also on adults in the subtropical and tropical latitudes (Delannoy and Cruz 1991). Among sharp-shinned hawks in Puerto Rico they caused 43% more mortality among nestlings than among unparasitized birds. Weaker effects have been found for other dipteran nest parasites, such as *Protocalliphora sialia* (Diptera: Calliphoridae) on tree-swallow nestlings, which live as larvae in the nest material and suck blood from young birds (Rogers *et al.* 1991). Here, high densities of parasites do not preclude 100% fledging or good weight gain, although "Larvae of *P. sialia* indisputably live at their hosts' expense, since nestlings that experience blood loss through parasitism must reallocate energy from maintenance and growth into tissue regeneration and repair, as well as in other physiological responses to parasitism" (Rogers *et al.* 1991, p. 134). The more recent studies on parasites of birds show many and varied effects, but in most cases contrasting with the views of Elton and Lack, and making the differences between predation and parasitism obvious and compelling. An important stepping stone into the current state of investigation was made by authors in Loye and Zuk (1991) from which we have taken our examples.

The life of parasites is made much more problematic by their hosts' responses, which are as diverse and intricate as the parasites themselves. Next we focus on host defenses in response to parasite attack.

8.11 Host defenses against parasites

When parasites impose strong selection on host populations there will develop clear evidence that hosts have evolved with countermeasures. These include immune responses and other physiological mechanisms, association with protective mutualists, various morphological and behavioral modifications, and perhaps secretive lifestyles. All such traits are observed in insects in response to parasitoids.

8.11.1 Defenses against parasitoids

Gross (1993) reviewed the subject of insect behavioral and morphological defenses against parasitoids, dividing traits into three main categories:

(1) Properties of hosts that minimize the chance of being found, such as use of refugia from attack, leaving food plants or feeding damage or moving away from frass or excretions.
(2) Behavioral and morphological defenses that reduce a parasitoid's ability to attack, including use of armor, evasion, defensive secretions and aggressive movements.
(3) Internal physiological mechanisms that kill parasitoid eggs or larvae such as encapsulation, sequestration of plant allelochemicals or synthesis of toxins by the insects themselves.

Gross (1993) concentrated on the middle category, the others having been treated in the recent past, and he emphasized the literature on herbivorous insects, providing examples of each case considered. Even limiting responses to parasitoids in this way, he recognized five categories of defense:

(1) Morphological traits such as a toughened egg chorion, or protective coatings or coverings over eggs, such as in oothecae, scales and silk. In nymphs and larvae a tough integument may be protective, as well as hairs and setae, cases, bags, cocoons, webbing and shelters made of rolled leaves, or shields. Pupae may be protected by retaining a larval cuticle (e.g., a puparium) or setae, or hanging on a silken thread or by a cocoon.
(2) Evasive behaviors include vigorous wriggling, dropping on a silken thread and thrashing.
(3) Aggressive behaviors include biting and secretion or ejection of defensive chemicals, or kicking (by aphids).
(4) Protection by attending ants is effective in many types of insects, such as aphids, scales, membracids and other honeydew producers, gall-inducing insects which include extrafloral nectaries on the gall surface, and lycaenid caterpillars.

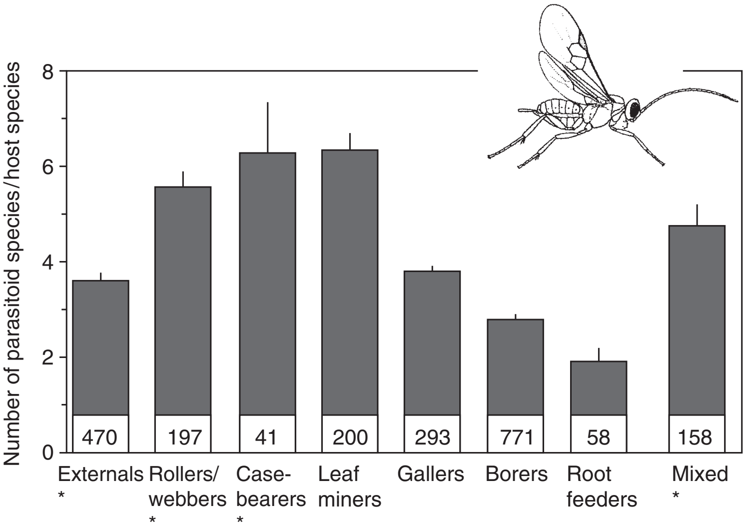


Figure 8.14 The relationship between the host-insect feeding niche in Coleoptera, Diptera, Lepidoptera and Hymenoptera, and the mean number of parasitoid species per host species. At the base of each bar, the number of host species used for the compilation is recorded. Asterisks mark complete or partial externally feeding insects in these herbivore niches. Ranking of the external feeders to root feeders is based on decreasing mobility and increasing concealment in food plants or soil. From Hawkins (1994).

(5) Parental care of eggs or immatures has been observed among species in the Hemiptera, such as the Pentatomidae and Membracidae, and in Coleoptera and Hymenoptera.

This diverse array of defenses has been selected for repeatedly in a multitude of insect species, indicating the strong and ubiquitous adversity imposed by parasitoids. In aggregate, all forms of defense by insects against parasitoids affect both the number of parasitoids adapted to any host species and the level of mortality inflicted.

8.11.2 Relative protection depends on the host's feeding niche

The most general patterns of protection from parasitoids relate to the ecological niche of the host. Hawkins (1994) categorized the host feeding niche as externally feeding, leaf rollers and webbers, case-bearers, leaf-miners, gall-inducers, borers and root feeders, and ordered them in relation to decreasing mobility, and increasing protection by the food plant. A dome-shaped pattern emerged in the mean number of parasitoid species per host species (Figure 8.14). External feeders could escape or defend themselves during an attack, and relatively few parasitoid species had adequate countermeasures. As host larvae became more concealed and constrained, accessibility to parasitoids increased on average until plant parts became major obstacles to attack, such as galls, stems and roots.

A commensurate property of the species richness of parasitoids per host is the mortality they inflict on hosts (Figure 8.15), or putting it another way, the probability of survival of individuals depending on their level of defense. Thus, the host feeding niche, included in Gross's first category of minimizing the chance of being found, and his second of behavioral and morphological defenses, becomes a very significant determinant of a larva's defensive options, and its chances of survival. Added to these defenses are many in the realm of physiological

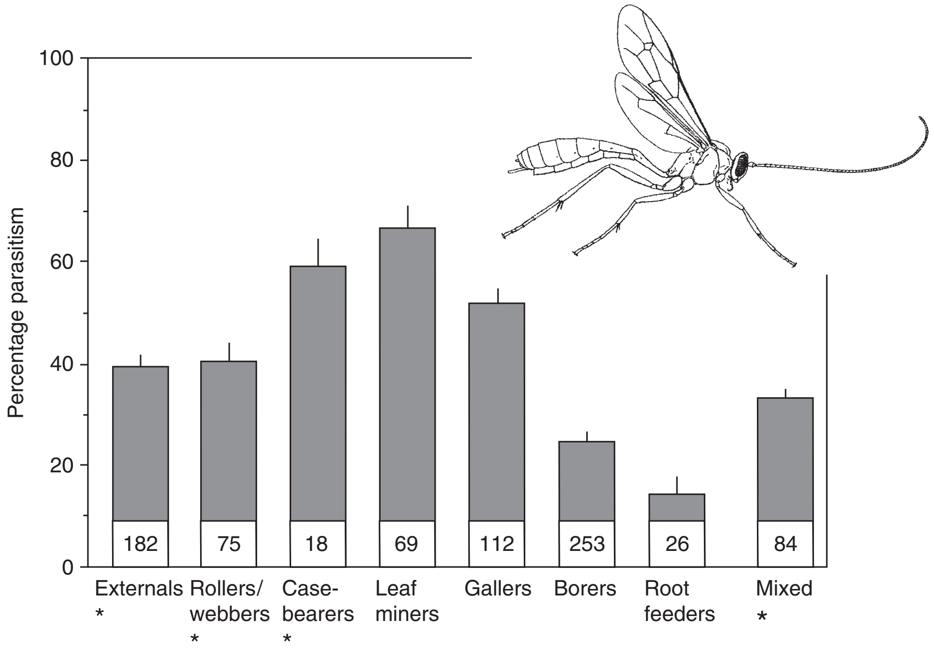


Figure 8.15 The relationship between host-insect feeding niche and the mean of the highest parasitism rate recorded per host species. Conventions are as in Figure 8.14. From Hawkins (1994).

mechanisms. For example, facultative bacterial symbionts in aphids cause high mortality in parasitoid larvae (Oliver *et al.* 2003), and fungal plant endosymbionts synthesize alkaloids, which are sequestered by aphids, and such aphids reduce the developmental rate, survival and fecundity of coccinellid predators (Sassi *et al.* 2006).

Plant defenses against their parasites have been already treated in Chapter 4 on plant and herbivore interactions. Trichome density, toughness, toxins, inducible defenses and abscission all contribute to a battery of defenses. Also, rapid cell death when attacked – **hypersensitivity** – is an important plant defense against gall-inducing insects (e.g., Fernandes 1990, Fernandes and Negreiros 2001, Höglund *et al.* 2005), and as a means of self-protection plants provide various forms of food for the carnivores feeding on herbivores (Wäckers *et al.* 2005). A rich array of multitrophic-level interactions pass up and down food webs.

8.11.3 Vertebrate defenses

As with other organisms attacked by parasites, vertebrates have a battery of defenses of varying efficacy (Moore 2001). Using birds as examples, their most potent defenses against internal parasites are the cellular and humoral immune responses, which are amazingly diverse and complex, and the "games" parasites and hosts play with interacting antigens and antibodies are the subject of much research today. Such defenses do play an important role in arthropod-borne diseases, but they are of less consequence for the arthropod ectoparasites, such as lice, mites, fleas and ticks. Against the ectoparasites and vectors of diseases, like mosquitoes, there are still many and varied defenses. Examples are taken from Loye and Zuk (1991). Grooming is effective against ectoparasites, decimating parasite numbers in areas of the body that can be reached, and direct pecking at mosquitoes is most effective. At high mosquito densities only 3% of individuals may successfully feed on cattle egrets, and 5% on house sparrows, and birds may also fly away from feeding, roosting or nesting sites to escape attack. Some roosting birds protect vulnerable parts from mosquitoes by covering the head under the wing and pulling one leg into the abdominal feathers. Head and foot shaking are also employed, and movement out of dense mosquito zones may be employed when possible, as on altitudinal gradients in Hawaii where native birds move downslope during the day when mosquitoes are inactive. The main malarial vector, *Culex quinquefasciatus*, is principally a nocturnal feeder, and the pathogen, *Plasmodium relictum*, appears to have selected for birds that move between high elevation forest and lowland areas colonized by introduced mosquitoes (van Riper *et al.* 1986, Atkinson and van Riper 1991). Moore (2001) summarizes a large literature on avoiding arthropod vectors and ectoparasites by vertebrates. Behavioral responses include moving away, shifting habitats, adjusting posture, joining a group, swatting, biting and slapping, and the use of camouflage.

Both vertebrates and invertebrates can develop fever in response to being parasitized. Of course, in poikilotherms fever is induced by moving to warmer temperatures, and it is widespread phylogenetically from annelid worms to arthropods, fishes, amphibians and reptiles (Moore 2001). But behavioral chills may also retard parasite development and increase melanization as in roaches infected with the acanthocephalan, *Moniliformis moniliformis*. Metabolic fever in homeotherms has similar effects to behavioral fever, and in both cases the metabolic cost of fever suggests that it is highly adaptive – there is an estimated 13% increase in metabolic rate per 1 °C in homeotherms (Hart 1988), with this relatively high cost indicating a strong selective benefit. The wide range of responses to parasitism indicates the ubiquity of infection and the resulting strong natural selection for defense.

8.12 Host behavioral modification by parasites

While hosts evolve with behaviors that reduce infection and/or transmission of parasites, parasites have evolved to increase the probability of infection (Moore 2001). A clear example is from Moore's own research on the interaction of songbirds such as starlings, with pillbugs, *Armadillium vulgare* (Isopoda), as a prey item, and the acanthocephalan parasite, *Plagiorhynchus cylindraceus*, that lives in the intestines of songbirds. As in the case of many acanthocephalans, an infected pillbug has an altered behavior such that it moves from shady and moist litter into open spaces, where it is more likely to be spotted and devoured by a starling (Figure 8.16). The life cycle of the acanthocephalan is completed, with the pillbug acting as an intermediate host, enabling parasite transmission from one bird host to another (Moore 1983, 1984).

Indeed, arthropods serve commonly as intermediate hosts to helminthes and other kinds of parasites in both aquatic and terrestrial systems: amphipods, isopods, beetles, cockroaches, ants and more, many of which endure behavior modified by parasites that promotes transmission and completion of the parasite life cycle. Also, parasites with direct life cycles, moving from insect to insect, may cause changes in behavior. Celebrated examples concern horsehair worms (Nematomorpha) and mermithids (Nematoda), which breed in water, but parasitize terrestrial insects such as ants and grasshoppers. Parasitized hosts have an inexorable attraction to water – "frantic hydrophilia" in some cases (Moore 2001, p. 76) – in which they drown and the parasite emerges.

Many parasitoids are known to alter host behavior, causing caterpillars to adopt more conspicuous feeding sites, moving higher on foliage, shifting from nocturnal to diurnal feeding and negative phototaxis, the last example resulting in concealment of aphids from possible predators and hyperparasitoids (e.g., Brodeur and McNeil 1989, 1990, 1992, Moore 2001).

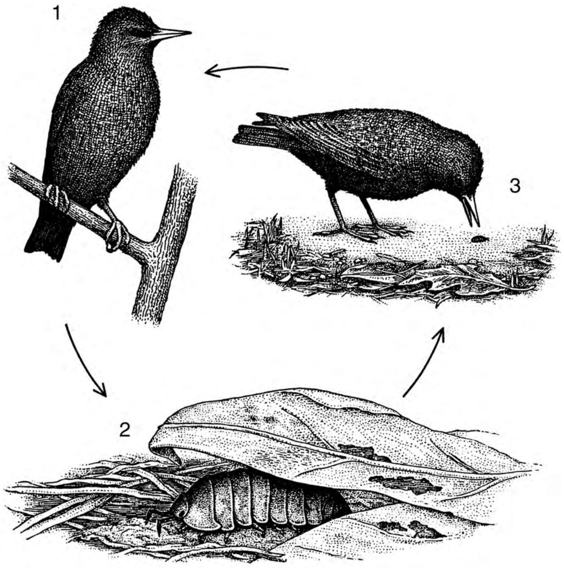


Figure 8.16 The interaction of the acanthocephalan *Plagiorhynchus cylindraceus* when it infects pillbugs, normally secretive in litter, which then move into exposed sites where they are easily spotted and eaten by starlings, the definitive host. In a starling (1) a mature female parasite lays eggs that are released in feces. The pill bug consumes faeces and becomes infected (2). (3) Then the vulnerable pill bug is eaten by a starling, completing the cycle. From Moore (1984).

8.13 Modeling host and parasite interactions

Based on the foregoing discussion on parasites we can now appreciate that there are complexities in life histories beyond those in predator–prey interactions. Models need to cope with these complexities when they attempt to mimic the dynamics of natural populations with greatly simplified conditions, particularly to examine the potential for host population regulation by parasites. Life cycles of parasites commonly include more than one host: a definitive host and a vectoring insect that acts as an intermediate host, or flukes and their relatives, and acanthocephalans, with definitive and intermediate hosts (see Figures 8.3, 8.16). Therefore, the population dynamics of three or more species are involved, and the transmission dynamics of the parasite become critical in epidemiological studies of humans and other species. Added to this life cycle complexity is the variation in immunity of host individuals, either through previous infection or genetic resistance. Also, vector competence in transmission may vary, among mosquito species as one example. In addition, parasites do not kill hosts quickly, or not at all, so the debilitating effects of infection need to be incorporated into models: reduced fecundity, delayed reproduction and the role of hosts in promoting transmission of the parasite. We have also noted that infectious diseases, the hosts they employ and the probability of transmission may be very patchily distributed (e.g., Figure 8.12, and the section on geographic mosaics of variation and patch dynamics). Therefore, spatial models of parasite–host interactions may be more useful and realistic than temporal models: metapopulation models may be relevant to the spatial distribution of parasites (see Chapter 11). However, we should remember from Chapter 7 on prey and predator interactions that parasitoids can be modeled as if the adult females are predators, because one attack usually results in the eventual death of one host individual.

8.13.1 Infectious disease in insect populations

As an example of the way in which models of parasite and host interactions are developed we will use the relatively simple case of infectious disease in the population cycles of insects (Anderson and May 1980, 1981, Anderson 1981). We will employ the basic model while recognizing that there has been an explosion of models since then, particularly relating to human diseases (e.g., Grenfell and Keeling 2007). The simplifying feature of viral, bacterial, protozoan and fungal infections of insects is that transmission is direct from host to host, without any intermediate host, and no long-term immunity is thought to exist,

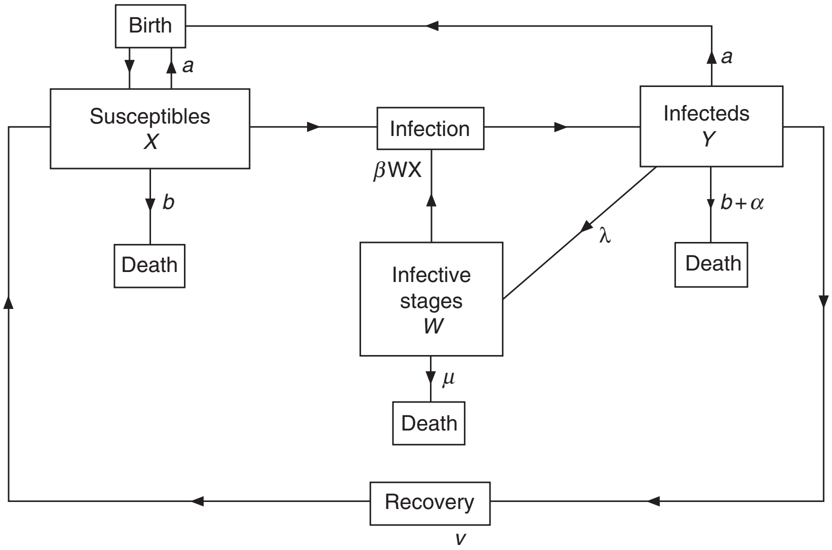


Figure 8.17 The flow of interactions in Anderson and May's (1981) model (Model G in their paper) which includes free-living infective stages of the parasite, and is applicable to insect disease epidemiology such as in the larch budmoth example. Notation is as in the text. Slightly modified from Anderson and May (1981).

so inclusion of an immune class of hosts is not required. A complicating factor is that free-living infective dormant states of microbial pathogens may persist in the environment for many years, so persistence must be incorporated, because this will produce delayed effects on host-population dynamics, and the possibility of cyclic behavior. For example, the fungal pathogen *Entomophaga maimaiga*, which attacks gypsy moths, has long-lived resting spores that persist in the environment at least for several years (Hajek 1999, 2004).

Using Anderson's (1981) notation, the total population of the host insect is N, the densities of susceptible hosts is X, of infected hosts is Y, and infective propagules in the environment is W. Therefore, the transmission of parasites will be proportional to the rate of contact between X and W, given as βWX. When $W(t)$ is the density of infective stages at time t, the model for the dynamics of an infection is as follows.

For the density of susceptible hosts:

$$\mathrm{d}X/\mathrm{d}t = aN - bX - \beta XW + vY \tag{8.1}$$

For the density of infected hosts:

$$\mathrm{d}Y/\mathrm{d}t = \beta XW - (\alpha + b + v)Y \tag{8.2}$$

For the density of infective stages in the habitat:

$$\mathrm{d}W/\mathrm{d}t = \lambda Y - (\mu + \beta N)W \tag{8.3}$$

Where a is the per capita birth rate of the host, b is the natural mortality rate without disease as a factor and v is the rate of recovery of a host from infection. Mortality caused by the disease is denoted as α. The rate at which infective stages are produced by the infected hosts is λ, and these infective stages are reduced by death at a rate of μ, or by entering and infecting hosts at a rate of βN. The flow of interactions is shown in Figure 8.17.

This model predicts cyclic dynamics when the pathogen produces high mortality (high α) and releases high numbers of propagules into the habitat (λ large, and μ small). These cycles may be short or long, depending upon the rate of increase of the host. When the intrinsic growth rate of the host, r, is small, cycles are predicted to be long, while higher r results in shorter cycles (Figure 8.18).

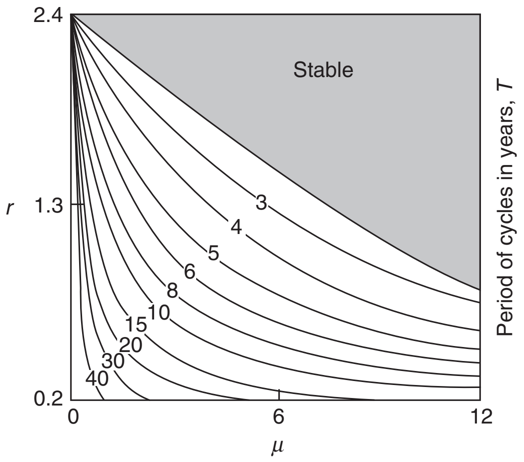


Figure 8.18 Results derived from Equations (8.1), (8.2) and (8.3), when parameter values for μ and r are varied and others are fixed at $\alpha = 9.0$, and $b = 3.3$. μ is the death rate of infective stages, and r is the intrinsic growth rate of the host. When r and μ are high, host populations reach a stable equilibrium, but as r and/or μ decrease cycles are generated, with increasing period of cycles T, in years. From Anderson, R. M. and R. M. May. 1980. Infectious diseases and population cycles of forest insects. *Science* **210**:658–661. Reprinted with permission from AAAS.

Anderson and May (1980, 1981) applied this model to the larch budmoth, *Zeiraphera diniana*, population dynamics in the Swiss Alps, with empirical data provided by Auer (1968). These data provided population densities of the bud moth, and the percentage of larvae infected with a granulosis virus, or the prevalence of the disease (Figure 8.19). Then the model was developed by inserting estimated values for the parameters a, b, α, v, λ and μ in Equations (8.1), (8.2), and (8.3) (see Anderson and May 1980 for parameter values). The results show a pattern of population change and infection rates similar to those in the natural environment. There were two cycles in about 20 years, two epidemics of disease in this period, with the disease outbreaks following closely after the peak of budmoth density.

Anderson and May (1981) discuss other host–parasite models, with complicating factors such as parasitic castration, in which the host is not killed, but reproduction is suppressed, and vertical transmission of infections from females to progeny. Also, parasite pathogenicity may depend on the host's nutritional status (see Smith *et al.* 2005), and after infection a latent period may occur while the host is non-infective. In all, Anderson and May develop seven models covering various possibilities and complicating factors.

Anderson and May (1980, 1981) stimulated many additional modeling efforts which addressed some of the complicating factors avoided in the original models. For example, Dwyer (1994) extended the original model by including density-dependent reproduction of the herbivorous host and its spatial spread, which would also spread the virus, resulting in synchronous population crashes. Then age-structured populations were considered in which susceptibility to the pathogen was limited to the adult insect, or to the larval stage (Briggs and Godfray 1995). Another study tested bottom-up and top-down effects on larch foliage quality and moth interactions with parasitoids (Turchin *et al.* 2003). Evidence indicated that the budmoth–parasitoid interaction accounted for 90% of the variance in budmoth population growth rates. These and other papers illustrate the stimulating effect on an originally simple model and the diverse conclusions that may be reached by invoking various kinds of interactions. They also illustrate the value of long-term data – 28 years for the larch budmoth – covering several cycles of eruption and crash (see Table 11.1 for a list of long-term studies on population dynamics). The challenge remains to include all important variables which contribute to population cycles, while keeping the models tractable.

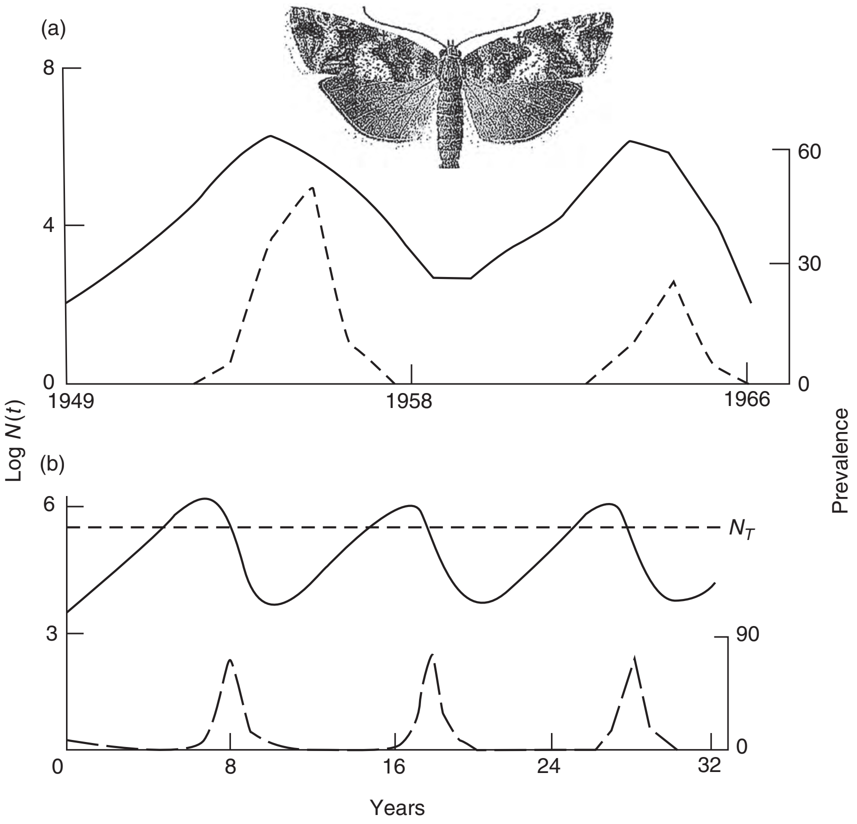


Figure 8.19 (a) The density of the larch budmoth population (solid line) from 1949 to 1966 in the Swiss Alps, and the percentage infected by a granulosis virus (prevalence) (dashed line). (b) Results from the model defined by Equations (8.1), (8.2) and (8.3) which predict host abundance, *N(t)* (solid line), and the prevalence of the parasitic infection (dashed line), over a period of 32 years. From Anderson, R. M. and R. M. May. 1980. Infectious diseases and population cycles of forest insects. *Science* **210**:658–661. Reprinted with permission from AAAS.

The role of disease in insect population dynamics is still debated, and uncertain in many cases. As Myers wrote in 1988 (p. 231), “I may simply be emphasizing the importance of disease because it is the least known factor in studies of insect cycles.” But, modeling approaches have enabled the exploration of possibilities in the host–parasite interaction, and will continue to do so for insect diseases and emerging diseases of humans.

Applications

Harmful and beneficial parasites

Parasites have caused misery and death for countless millions of people through the ages, and many millions are afflicted today (e.g., Zinsser 1935, Garrett 1994, Wills 1996). Domestic animals and crop plants are also vulnerable, and heavily impacted in certain cases. In fact, no living organism is immune to parasite attack, and all populations may well bear the imprint of disease, were we able to document the loss of energy and life wherever parasites struck. Therefore, ecologists should try to understand host–parasite interactions as best they can.

When considering applications of our knowledge of parasites we must enter into a vast field of research and practice, covering most human endeavors involving living organisms, for parasites impact all those species that humans are concerned with: humans themselves, their domesticated animals and plants, the wild animals and plants in need of conservation, and those species in parks and botanical and zoological gardens, and threatened ecosystems, marine, fresh-water and terrestrial (e.g., Thomas *et al.* 2005, Collinge and Ray 2006). And the disciplines and subdisciplines involving concern for parasites, therefore, constitute a lengthy list: crop protection, biological control of weeds, biological control of insect pests, plant resistance and genetic engineering, public health and hygiene, veterinary science, gardening, epidemiology, vector control, forest health, horticultural science, conservation biology, integrated pest management, sustainable agriculture and ecosystem management. Insects play a role in all of these applied domains: they are parasites themselves on humans, other animals and plants, they vector diseases among plants and among animals, they act as enemies of pests in biological control, they become invasive in new countries, they generally compete with human desires for food, fiber, wood products and an aesthetically pleasing environment. Casting the net broadly around the concept of parasitism, as is advocated in this chapter, and in Price (1980), enables a vision of the magnitude of the ecological problems we face.

One example of how an ecological perspective provides advantages for the understanding of parasite problems and epidemiology concerns the extension of malaria into highland areas of western Kenya. Malaria had been eliminated in temperate elevations and latitudes in the 1950s and 1960s, but highland malaria had been increasing again since the 1980s, with particularly severe outbreaks in the 1990s, and into 2002. Local factors appeared to be involved, so Carlson *et al.* (2004, 2009) undertook to understand the factors involved. The inhabitants of the area were involved with making bricks, with clay dug from shallow pits in which water accumulated. A survey of all water bodies in the area showed that these were the primary breeding grounds for *Anopheles* mosquitoes, the vectors of malaria, but larvae were most abundant in the most recently developed pits. In older pits, and in natural aquatic habitats, emergent vegetation had developed, predator diversity was well developed and mosquito larvae were absent or scarce. Probably predators produced a direct effect by eating mosquito larvae, but also an indirect influence of complex vegetation contributed to the predator effects by reducing the probability of intraguild predation (e.g., Finke and Denno 2002). The trophic dynamics of simple and complex aquatic habitats was central to understanding the epidemiology of malaria in highland Kenya. This kind of scenario may also be relevant in temperate latitudes (e.g., Chase and Knight 2003).

In applying our knowledge on parasites one of the most important considerations is their evolutionary potential. The numbers of parasitic species are vast because they evolve rapidly, ecological niches are highly specialized, and therefore almost innumerable, and consequently adaptive radiation has exceeded that in other modes of resource exploitation. Moreover, the evolutionary potential of parasitic species has not diminished in the recent past. We have observed repeatedly the evolution of resistance in insects to insecticides and originally resistant crops, and microorganisms to antibiotics. “Resistance to pesticides in more than 500 species of insects … has taught us not to underestimate the evolutionary potential of pests” (Tabashnik 1994, p. 72). We also understand how natural selection can actually increase the virulence of pathogens. For example, vector-borne diseases of humans, such as malaria, yellow fever, sleeping sickness and epidemic typhus, produce relatively high mortality compared with most directly transmitted diseases because infective stages in human blood must be in high concentration for transmission to be effective, when very small blood meals are taken by mosquitoes, flies and lice (Ewald 1983). In producing such high concentrations of infective stages, high toxin production occurs in the host's blood, causing fever. Also, increased hygiene in hospitals can select for higher virulence of directly transmitted diseases, as transmission is possible when high densities of propagules are released rapidly, as in cholera, for example (Ewald 1994).

The first challenge to applying knowledge to solve parasite-related issues is to develop a sophisticated understanding of the epidemiology of each problem insect or other arthropod we wish to control. This is straightforward ecology, although with complex life cycles, and reservoir hosts, intermediate stages or alternative but important hosts, the basic ecology of the system may be difficult to discover.

The second challenge is to find effective methods of regulating pests, which may involve integrated pest management, biological control and other well-established methods on which large literatures are easily accessed.

The third and most daunting challenge is to prevent the evolution of resistance to whatever mechanism is used. Insecticide resistance and cross resistance among insecticides are well studied and recorded. Microbial resistance to antibiotics is also becoming so grave a problem as to leave few if any sound alternatives to the treatments currently available for some infections. What, then, are the answers to evolved resistance? The discovery of new pesticides and antibiotics is one solution, with novel modes of action so that cross resistance is avoided. Such discovery is slowing down, and resistance develops rapidly. Non-chemical methods, involving behavioral manipulation, genetic resistance, biological control and cultural methods, may play a role. The basic question is how can we slow down, or even prevent, the evolutionary process when it involves parasitic species with high evolutionary potential? This textbook is not intended to be a compendium of pest-control methods, and many compendia are available, but a few ecological ideas are worth discussing here.

One idea is that evolution will work most rapidly in the presence of one strong mortality factor. Selection will be uncompromised by other selective forces, so adaptation that diminishes the factor is likely to be rapid. This is the case in many attempts to regulate pest numbers. But, expose a problem parasite to multiple challenges simultaneously, and evolution of resistance will take much longer – the cocktail hypothesis used in treating HIV infections. An experiment illustrates the idea. House flies, *Musca domestica*, were used as a surrogate parasite on a surrogate host: artificial diet on which survival was near 100%. Then, single toxic chemicals were added to the diet, and one treatment had all toxicants added together. Evolution of

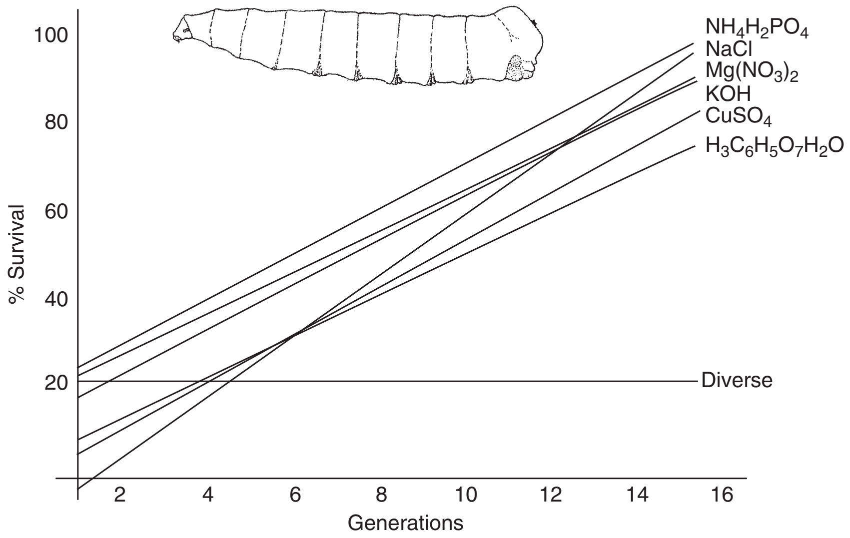


Figure 8.20 The response of house flies to toxic substances in food provided singly and in a diverse mixture. Evolution of "resistance" was rapid in cultures with single toxins, but absent in the diverse treatment. The lines are linear regressions for the responses of the flies over 16 generations. From Pimentel, D. and A. C. Bellotti (1976). Parasite-host population systems and genetic stability. *Am. Nat.* 110:877–888. © 1976 by the University of Chicago.

resistance to the single chemicals was uniformly rapid, reaching over 70% survival in just 16 generations, but there was no evolutionary response to the diverse array of toxins, in which survival remained at around 20% in each generation for 32 generations (Figure 8.20, Pimentel and Bellotti 1976).

Another idea likely to be effective against plant pests is to treat some of the crop with insecticide, leaving other areas untreated. A portion of the pest population remains susceptible to the treatment and dilutes, by mixing, tendencies for resistance to develop in the treated population. In a patchwork of treated and untreated areas, which changes each year, susceptibility may be maintained over the long term. This is indeed the case for the use of Bt transgenic crops of corn, cotton and others (Tabashnik *et al.* 2003). Bt toxins are derived from the bacterium, *Bacillus thuringiensis*, with genes responsible being introduced to the genome of the crop plant in which the toxins are expressed. The case of the cotton crop in Arizona has been studied in detail since before Bt cotton was introduced in 1996 (Carrière *et al.* 2003). The major pest is the pink bollworm, *Pectinophora gossypiella* (Gelechiidae), a lepidopteran specialist on cotton. In general, as the proportion of Bt cotton increased over a large area, so populations moved from increasing to declining, with the best results achieved at Bt cotton approaching 90% of the total cotton crop (Figure 8.21). Over many areas tested, population growth

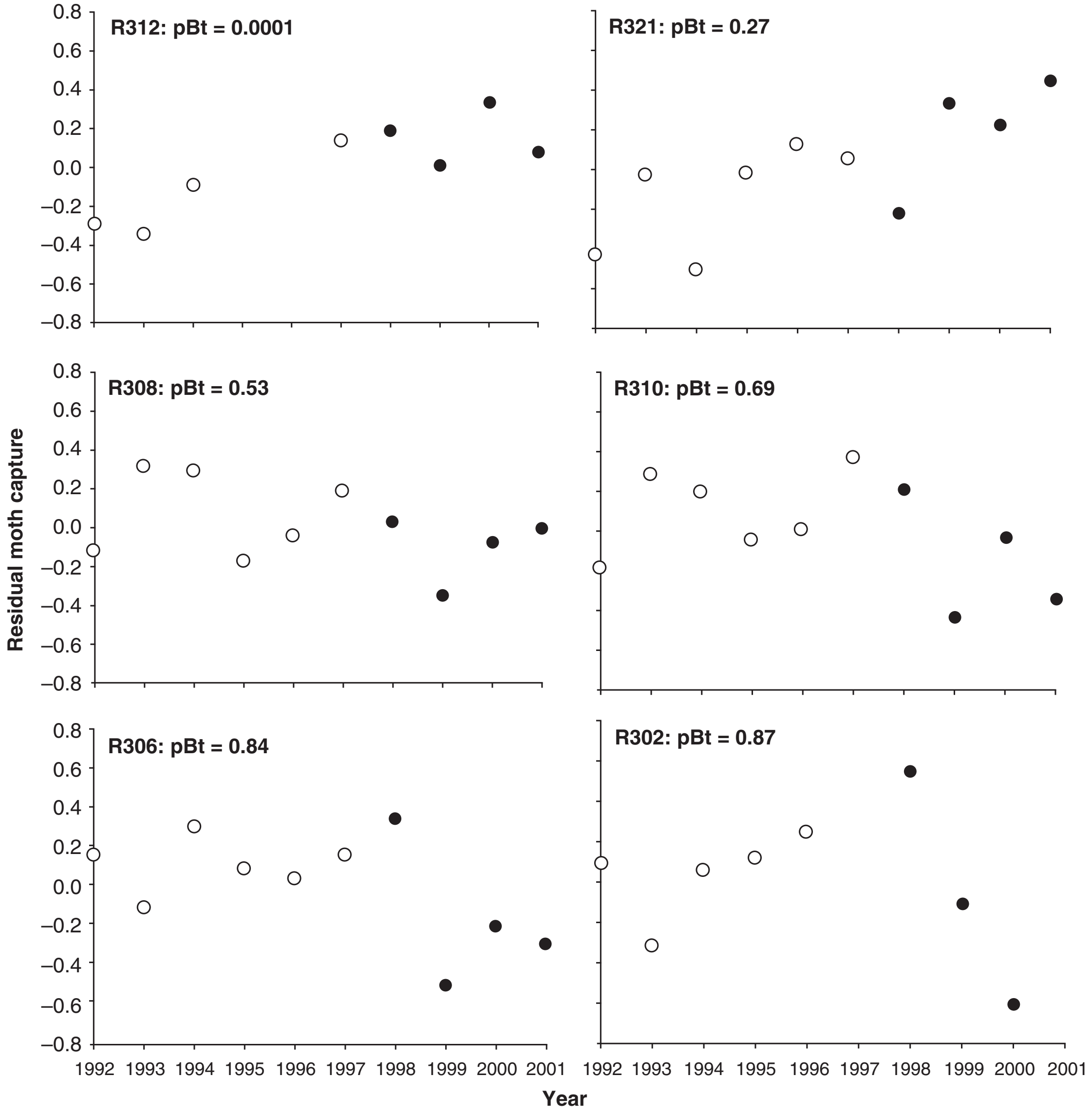


Figure 8.21 Studies on the pink bollworm on cotton in Arizona, 1992 to 2001, in various regions differing in the proportion of Bt cotton per region from 0.0001 in Region 312 (top left) to 0.87 in Region 302 (bottom right). Residual moth capture indicates regional population estimates of adult moths with effects of region and weather removed using multiple regression analysis. Open circles represent populations before reductions in moth populations were observed in any area. Filled circles show populations after reductions in populations began to be recorded. From Carrière *et al.* (2003). Copyright 2003. National Academy of Sciences, USA.

declined dramatically only when high percentages of Bt cotton were grown (Figure 8.22). Use of this refuge strategy of deploying transgenic crops depends on the spatial configuration of the refuges, which is examined in Carrière *et al.* (2004). In addition, models employing **the refuge–high dose**

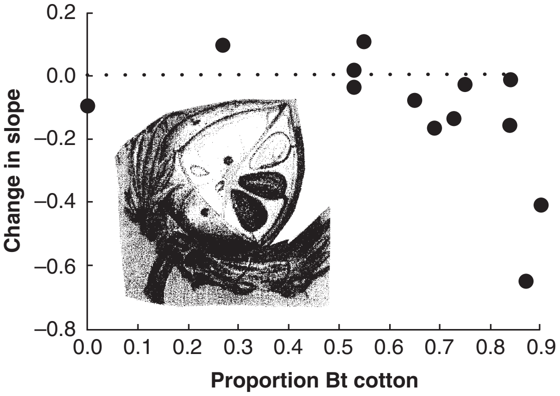


Figure 8.22 The change in slope of population trends before and after Bt cotton showed effects on pink bollworm populations in Arizona, in relation to the proportion of Bt cotton in particular regions. Zero, and the dotted line, indicate no change in moth density. A negative change in slope shows a regional decrease in population growth, with strong declines appearing only at very high proportions of Bt cotton in a region. From Carrière *et al.* (2003). Copyright 2003. National Academy of Sciences, USA.

strategy for Bt crops predict that frequency of resistance can decline in populations, as has been observed in the field populations (Carrière and Tabashnik 2001). The "refuge" refers to the untreated crop, providing a safe place to reproduce for bollworms, and "high dose" means high titers of Bt toxins in transgenic cotton. High-dose plants result in recessive resistance genes in the insect, and all heterozygotes are therefore killed in Bt cotton. Resistance is prevented if, in addition, most resistant adults mate with susceptible adults, requiring high emigration from refuges. Fitness costs accompanying resistance also contribute to the success of this control strategy (Tabashnik *et al.* 2004, 2005). In a 10-year study in Arizona, pink bollworm was suppressed over a large area where Bt cotton was at high frequencies. "Such long-term suppression has not been observed with insecticide sprays, showing that transgenic crops open new avenues for pest control" (Carrière *et al.* 2003, p. 1519). No resistance was observed through 2005 (Yves Carrière, personal communication).

We can think of this interplay of parasites and humans as humans engaging in cultural evolution with the evolutionary potential of their pests and diseases. Thompson (2005) considers these relationships in his chapter on "Applied coevolutionary biology". "The more we learn about the coevolutionary process, the more apparent it is that ongoing coevolution among species permeates every aspect of our societies, including medicine, epidemiology, agriculture, forestry, aquaculture, and conservation efforts" (p. 339). As pests and diseases evolve to be more damaging to our welfare, and new pests and diseases emerge, so we engage in increasing defenses; by selective breeding, genetically modifying organisms and searching for new antibiotics. As entire landscapes are changed, some species are pushed closer to extinction and conservation measures are required, and invasive species take a hold and require management or control. Urbanization and rapid transport increase movement of pests and pathogens of all kinds, and alter epidemiology in favor of the parasites, as is the case in agriculture also. All our efforts to regulate nature in our favor result in increasing numbers of unintended consequences, a fourth challenge in dealing with the parasites we live with.

Summary

The parasite lives surreptitiously and is seldom seen, and yet this insidious way of life impacts all other organisms. We have adopted a broad view of parasites in this chapter to include parasites of animals and plants, including many insect herbivores. We have considered which insects act as parasites, the kinds of parasite and the impressive richness of the parasitic fauna, which raised a question on the characteristics that result in such high species diversity. Small size was seen to be a fundamental feature of parasites, but their adaptive radiation clearly depends on selection for high specificity to hosts and parts of hosts. With constraints imposed on the parasitic way of life such as the challenge in transmission from host to host, and the host as a habitat, we should expect to observe evolutionary convergence. Our examples ranged from the liver fluke and gall-forming insects to rust fungi, and the massive convergence of taxa into the parasitoid way of life.

With such a close relationship between parasite and host, phylogenetic tracking becomes highly probable in those situations in which lineages exist in discrete niches where interchange of parasites is limited. Also, variation in associations is likely to be considerable over the landscape, providing good examples of geographic mosaics in interactions and patch dynamics.

Measurable damage to the host is a necessary part of the parasitic lifestyle, which is clearly evident for herbivores and parasitoids, but more difficult to evaluate for insect parasites of vertebrates. However, strong evidence is presented that some bird species are heavily impacted. Naturally, with so many parasitic species, host defenses have become diverse and often effective, so we considered insect defenses

against parasitoids, including the protection offered by the host's feeding niche, and vertebrate defenses. This is countered in some parasites by modifying host behavior to increase the probability of infection. Damage to the host at the individual and population levels is important in modeling host and parasite interactions, but this exercise is more complex than for predators because infections that do not kill leave hosts with immune resistance, a variable of central importance in epidemiology. But parasites may be harmful or beneficial in managed environments depending upon the trophic level at which they work. Parasites on crops, livestock and humans are clearly deleterious from a human perspective, but parasites on weeds and insect pests are advantageous. These are all dynamic interactions because of the rapid evolutionary potential of the parasites, so that regulation of parasitic pests must meet this challenge.

Questions and discussion topics

1 Discuss the proposition developed in this chapter that it is useful to consider insect herbivores as parasites.

2 So many different life cycles of parasites exist that, at the very least, several models are needed to capture this diversity. Considering the model presented in this chapter, how do you think it should be modified in order to simulate other kinds of life cycles, such as in protozoa vectored by insects, or parasite species with two or more hosts in their life cycle?

3 Discuss the argument that the parasitic way of life results in evolutionary dead ends because, once parasitic, the lineage is unlikely to be able to escape from this kind of life.

4 If you were to undertake a study on the frequency of interactions involving competitors, predators, parasites and mutualists in a natural community of interacting species, what would you anticipate to be the most common type, and what would be the rank order of commonness in these interactions?

5 Whenever we manipulate landscapes and communities there are likely to be unintended consequences. For any particular example of pest regulation, in agriculture, forestry, animal husbandry or parasites of humans, consider the kinds of unexpected results which may be observed, and ways in which detrimental outcomes may be circumvented.

Further reading

Combes, C. 2001. *Parasitism: The Ecology and Evolution of Intimate Interactions*. Chicago: University of Chicago Press.

Godfray, H. C. J. 1994. *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton, NJ: Princeton University Press.

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Part IV **Population ecology**

CONTENTS

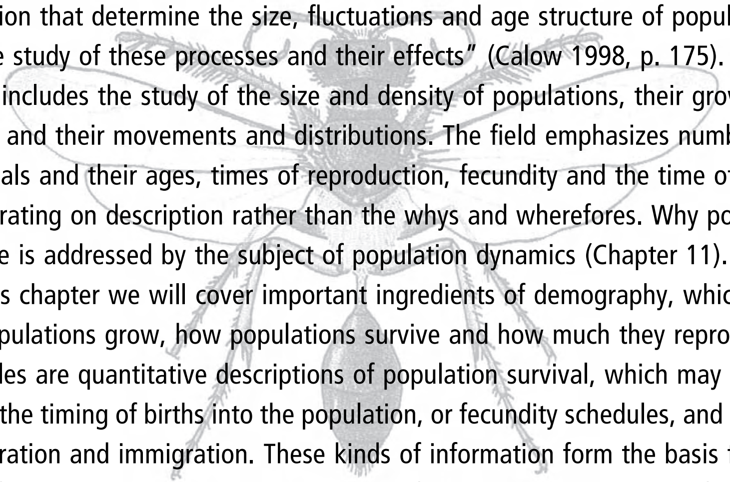
Populations illustrate characteristics such as growth and decline, birth and death, immigration and emigration, life histories adapted to the environment, and dynamical behavior. These are the topics in this part of the book. They are of great interest to the insect ecologist because they provide ways of understanding species in nature and in managed systems. We need these approaches in order to predict population trends and to plan pest-management strategies. Emphasis on population phenomena also provides an intermediary level of understanding between species interactions (Part III), community organization (Part V) and broader patterns over the landscape (Part VI). Naturally, species interactions have population consequences, such as natural enemies impacting prey populations, so comparable to what we did with species interactions, moving up the trophic levels, we now approach Part IV by moving up a complexity gradient from individuals (Part II), to interactions (Part III) and now to their consequences at the population level.

The study of demographics, life histories and population dynamics are at the core of insect ecology. How populations grow and decline, and how they can be documented in life tables, has been a major preoccupation for many decades. The description of insect life histories has also played a central role in entomology for even longer, while population dynamics has occupied attention in forestry and agriculture since humans developed a scientific interest in crop protection and management.

As we will see in later parts of the book, population eruptions produce impacts at the ecosystem level, for example by killing large tracts of forest, and invasive species threaten residents. Climate change alters the distribution and abundance of many species, and fragmentation of habitats has consequences for population sizes, distributions and biodiversity. Therefore, population phenomena remain of central concern through the remaining parts of this book.

9

Demography, population growth and life tables



Demography has been defined as "The processes of birth, death, immigration and emigration that determine the size, fluctuations and age structure of populations. Also the study of these processes and their effects" (Calow 1998, p. 175). Thus, the science includes the study of the size and density of populations, their growth and decline, and their movements and distributions. The field emphasizes numbers of individuals and their ages, times of reproduction, fecundity and the time of death, concentrating on description rather than the whys and wherefores. Why populations fluctuate is addressed by the subject of population dynamics (Chapter 11).

In this chapter we will cover important ingredients of demography, which include how populations grow, how populations survive and how much they reproduce. Life tables are quantitative descriptions of population survival, which may also include the timing of births into the population, or fecundity schedules, and estimates of emigration and immigration. These kinds of information form the basis for the study of population dynamics, so that some of the elementary aspects of population dynamics are treated in this chapter.

9.1 Principles of population growth

There are some essential elements, or principles, which can guide a discussion on population growth. These have been summarized by Berryman (1999, 2003): exponential or geometric growth, cooperation, intraspecific competition, interacting species and limiting factors. Some of these concepts have been covered in Chapter 5, but we need to treat them in logical order here among other principles needed to understand population dynamics.

9.1.1 Exponential growth, or geometric growth

This kind of growth occurs when a population increases by a constant factor in each generation or time period. The population grows steadily, say when each female in a generation is replaced by two female progeny in each subsequent generation, over the course of several generations. This is Malthus's principle, and is usually expressed as the equation

$$\frac{dN}{dt} = rN \tag{9.1}$$

in which N is the number in the population and r is the rate of change per individual, or the per capita instantaneous rate of change (Figure 9.1A, seen also in Figure 5.4A). It may be preferable to use R in place of r (Royama 1977, Berryman 2003), to distinguish it from the correlation coefficient r, and particularly when we use logarithmic equations. Given a constant R-value, or R-function, populations will show linear growth or decline when R is expressed as the per capita logarithmic rate of change in a population (Figure 9.2), or

$$\frac{d(\ln N)}{dt} = R = \text{constant} \tag{9.2}$$

This first principle can be stated as "All populations grow at a constant logarithmic rate unless affected by other forces in their environment" (Berryman 2003, p. 696). The principle forms a basic, or null model, because it defines how a population is expected to grow in the presence of unlimited resources, lack of interaction with other species, and favorable physical conditions. Therefore, finding how R deviates from this constant, and why, becomes the basis for population dynamics studies.

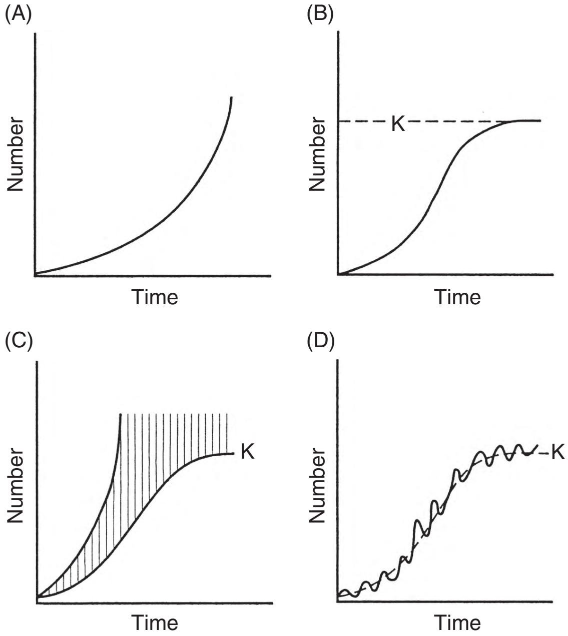


Figure 9.1 Examples of (A) exponential growth, (B) sigmoidal growth or logistic growth up to the carrying capacity, *K*. In (C) the shaded area represents environmental resistance from a resource that cannot support more than *K* individuals. (D) The irregular increase of an insect population towards *K*, with increases in population during the breeding season, and declines as mortality factors reduce numbers in a generation. Numbers are on an arithmetic scale. From Price 1997.

9.1.2 Cooperation

The second principle encompasses the reality that in most populations finding mates is essential, meaning population densities must be high enough so that the probability of discovering a member of the opposite sex is high. Mating aggregations may be a basic component of

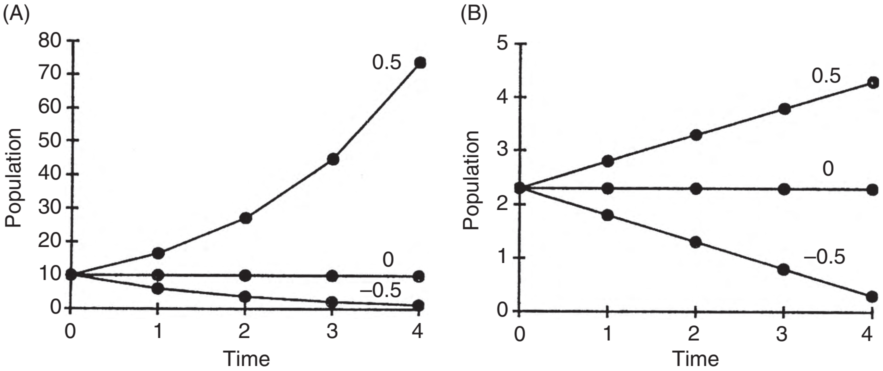


Figure 9.2 Population trajectories through time (four generations) with R values of 0.5, 0 and −0.5, with populations plotted on an arithmetic scale in A and on a logarithmic scale in B. Note that population growth with $R = 0.5$ is linear in B, and an equilibrium number exists when $R = 0$. From Berryman 1999.

reproduction, but feeding aggregations, and grouping that diminishes natural enemy impact, also constitute cooperative units. Such intraspecific cooperation was noted by Allee (1932), and is now known as the **Allee effect**, when cooperation fails at very low population densities. In other words the R-function is likely to be negative at very low densities because mates are hard to find, increasing gradually as N increases, but clearly cooperation has its limits as populations become large and competition ensues (Figure 9.3). The Allee effect is known to be widespread in nature (Kramer *et al.* 2009), with a special feature devoted to this subject (Yamanaka and Liebhold 2009).

9.1.3 Intraspecific competition

This competition increases with population density N, reducing the rate of population change, causing the R-function to decline. Conceptually, it is easiest to consider a maximum amount of food available to a population, which is renewable at that amount, forming a kind of ceiling to which the population can rise, but at which point $R = 0$. This ceiling has been defined as the **carrying capacity**, K, and growth is **logistic** with increasing intraspecific competition reducing R gradually until it becomes zero (Figure 9.1B). As we saw in Figure 5.4A, this concept was defined by Verhulst (1838) and Pearl and Reed (1920) with the equation:

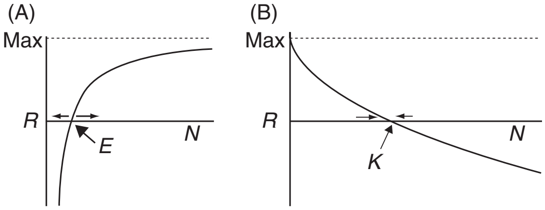


Figure 9.3 Examples of the Allee effect, or cooperation, and positive feedback in (A), and in (B) negative feedback through intraspecific competition until $R = 0$ at the carrying capacity, K. Note that an unstable equilibrium exists at E in (A), because populations tend to move away from E as R is negative below E and positive above E. At K, in (B) the equilibrium is stable because the population will increase up to K, but decrease when above K. The arrows along the N axis indicate the direction of population trends around E and K. Max = the maximum per-capita rate of change in a given environment. From Berryman 2003. Reprinted with permission from Blackwell Publishing.

$$\frac{\mathrm{d}N}{\mathrm{d}t} = rN\frac{(K - N)}{K} \tag{9.3}$$

When $N = K$, growth becomes zero (Figure 9.3). This **logistic growth**, or **sigmoidal growth**, equation is often called the Verhulst–Pearl equation, recognizing the independent contributions of these authors.

Exponential growth represents what Chapman (1928) called the **biotic potential** of a population, and logistic growth shows the effects of intraspecific competition that limits this growth and forms one component of **environmental resistance**, or the combined effects of factors that reduce growth below the biotic potential (Figure 9.1C). In addition to competition, natural enemies (predators, parasitoids, pathogens) and weather are likely to reduce population growth rate, and render it negative periodically such that a population may fluctuate well below a carrying capacity set by food supply, breeding sites, or space in territorial species. Even if the carrying capacity is reached, in insect populations which breed seasonally, increases will be sudden and declines gradual through mortality, yielding a zig-zag approach to K (Figure 9.1D).

9.1.4 Interacting species

The fourth principle recognizes that inevitably other species will impact the focal species' population dynamics. Some species may be beneficial, such as food plants for herbivores, prey for predators, flowering plants for pollinators and the many kinds of mutualists discussed in Chapter 6. Other species will be detrimental to population growth of a species, such as natural enemies and interspecific competitors. Here, food-web structure is of importance, for this structure defines how trophic levels interact and the lateral effects on the same trophic level through interspecific competition, facilitation of one species by another and indirect effects, say through one species causing changes in a host plant that may influence another species (e.g., Hunter 1992b, Hunter and Price 1992, Ohgushi 2005, Ohgushi *et al.* 2007, Kaplan and Denno 2007). Denno and Kaplan (2007) note that one species feeding on a plant may modify plant quality for another species through changes in plant allelochemistry, morphology, nutrition, and risk of attack by enemies (see also Chapter 4).

9.1.5 Limiting factors

This topic encompasses Liebig's (1840) principle, or "law of the minimum," which argues that the resource most limiting to the population will define its population size: shortage of food, low nutrient content of food, low winter temperatures, shortage of water. And excessive conditions may be equally limiting: temperatures too high, too much rainfall, high salt content in food or soil. Therefore, we can consider the tolerance of the organism for environmental factors, stated in Shelford's (1913) "law of tolerance," recognizing both deficiencies and excesses beyond which a species cannot tolerate, therefore defining the presence, absence and abundance of species.

These five principles are likely to operate in every population, although their influence may vary over space and through time. They set the stage for thinking about the ways in which population density may change and the processes that regulate or limit populations.

9.2 Feedback loops, density dependence and population regulation

In the foregoing principles we have seen several examples of feedback loops. Feedback may be positive, tending to increase population growth, or R. An example was seen in Principle 2 on cooperation, in which increasing density of individuals improved their chances of finding mates, avoiding enemies, or feeding on tough foliage as in some gregarious insect species. As density increases from very low levels when mates are rare, or cooperation is weak, where R is negative, positive feedback accelerates growth past $R = 0$ (**positive density dependence**), where the population is at equilibrium, and into the region of $R > 0$ (Figure 9.3A). This creates an unstable equilibrium, *E*, because populations will increase when above *E* and decline when below *E*. That is, there will be no **population regulation** at this point, with population regulation defined as “the return of a population to an equilibrium density, following departure from that density, as a result of density-dependent processes” (Dempster and McLean 1998, p. xx). **Density dependence** is where “one or more demographic parameters (birth, death, immigration or emigration) is a function of population density, i.e. a change in population density allows prediction of a change in a demographic parameter” (Calow 1998) (Figure 9.4). Density-dependent processes can also involve negative feedback loops in which increasing density of individuals slows the growth of the population gradually, perhaps to zero, because of intraspecific competition, natural enemies or limiting factors (**negative density dependence**) (Figure 9.3B). Negative feedback is stabilizing, with **population stability** defined as “a relative constancy in population size, i.e. the population shows no trend, and population fluctuations are in a narrower range than expected from random variation” (Dempster and McLean 1998, p. xx). Stability is produced because, as an example, populations can grow towards the carrying capacity, *K*, but they will decrease when above *K* because of shortage of the limiting resource. Negative feedback, and its stabilizing influence, is also likely to be seen in the action of natural enemies on an insect population in which they become more effective as the insect population grows, killing a greater proportion of the population, reducing *R* until it may become zero, and a stable equilibrium is reached.

The terms feedback loops and density-dependent factors are used interchangeably, although the concept of density dependence has been plagued with confusion and controversy (Berryman *et al.* 2002). However, these terms need to be explained here because they are in common usage. **Negative density dependence** is the negative effect of population density, *N*, on the realized per-capita rate of change, *R* (Figure 9.4). In the literature the terms density

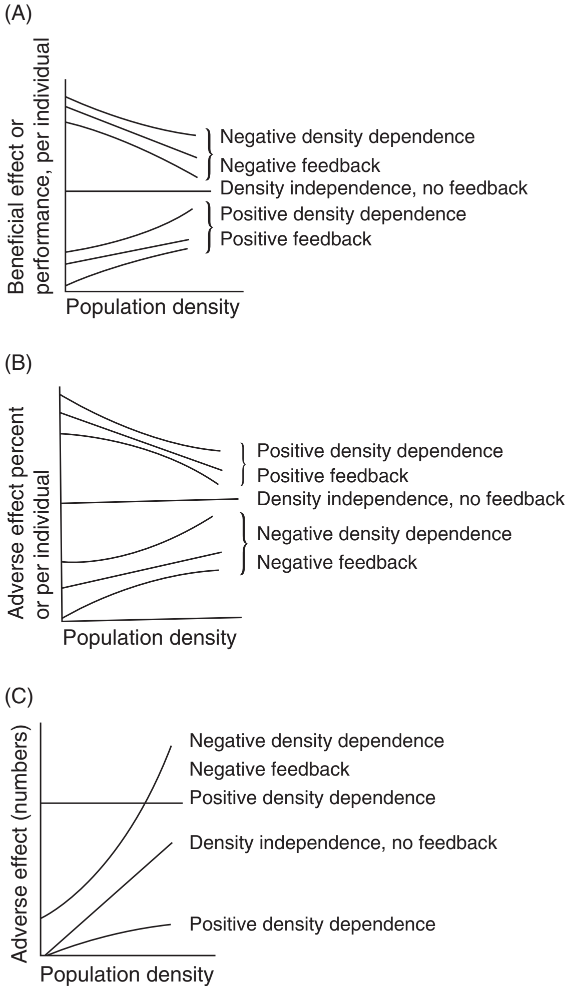


Figure 9.4 Examples of density dependence, or feedback. (A) In relation to the beneficial effect as a percentage or per individual as population density increases. (B) In relation to the adverse effect as a percentage or per individual as population density increases. (C) In relation to adverse effects as *numbers* in the population as population density increases. Note that for negative density dependence, or negative feedback, the proportion of individuals affected in a beneficial way declines in A, and the proportion of individuals affected adversely increases as the population density increases in B. Any positive slope in B illustrates negative density dependence. In C the horizontal trend illustrates positive density dependence because the number of adversely affected individuals remains constant while density increases, resulting in a lower proportion of individuals impacted by the negative effect.

dependence (e.g., Solomon 1949, Dempster and McLean 1998), direct density dependence, and negative density dependence (Calow 1998) have been used interchangeably. (We use negative density dependence for its clarity, its synonomy with negative feedback and its obviously opposite function to positive density dependence.) As population density increases, the strength of the adverse effect of the factor increases, so the percentage of the population affected increases, or the likelihood of an individual being affected increases. This is also negative feedback, which causes R to decline towards $R = 0$, or even $R < 0$ (Figure 9.3B). An **inverse density-dependent factor** is one in which the population density has a positive effect on the population (a reduced adverse effect), and is more clearly stated as positive density dependence, constituting a positive feedback (Figure 9.4). **Density-independent factors** are not influenced by population density, although they may affect R positively or negatively. Royama (1992) has emphasized that confusion can be avoided if the ecological factor under consideration is influenced by the population density of the animal. If it is, then the factor is density dependent; if it is not, it is density independent. For example, insect herbivore population density is likely to have an increasing impact on tree leaves, so food supply is likely to be density dependent, but insects will not affect weather, so weather is a density-independent factor. This view avoids some of the contentious debate between the Nicholson–Bailey (1935) school of thought, which advocated the importance of density-dependent factors, and the Andrewartha and Birch (1954) school, which had little use for the concept of density dependence because they felt that no component of the environment has an influence that is independent of population density.

One important aspect of feedback is that it may be delayed, with the mortality factor acting on generation $t + 1$ rather than on generation t. Such time delay has been called **delayed density dependence**, or a **time lag** in the feedback loop. A time lag may be caused potentially by several kinds of factors. Defoliating herbivores in generation t may influence foliage quality for individuals in generation $t + 1$, reducing food quality and survival of larvae through increased induced defenses in the foliage. Natural enemies may respond to increasing density of prey or hosts through higher reproduction, resulting in a higher density of enemies in the next generation and a stronger negative feedback in that generation. Delayed negative feedback means that population responses to feedback will be slower than with immediate feedback; therefore it is likely to produce oscillations in the population and cyclic behavior. This will be seen to be common in Chapter 11 on Population dynamics, just as population oscillations were predicted from the predator–prey equations discussed in Chapter 7 on Prey and predator interactions.

Another aspect of feedback and density dependence is that they may work over time as densities change, and they may work in space as densities vary over the landscape (Walde and Murdoch 1988, Hassell 2000, Veldtman and McGeoch 2004). Both positive and negative feedback may operate in both time and space. Of course, plot techniques often used in life-table construction are not designed usually to capture spatial heterogeneity, and the possibility of feedback in space. Hence, large plots with much heterogeneity and patchiness, or many small plots covering a similar range of habitat diversity, are needed to capture spatial effects on population dynamics.

A somewhat controversial point that remains is whether populations must be regulated in some way, or whether **population limitation** has a major influence (see Dempster 1998). Population limitation is defined as “the density-dependent reduction in population growth brought about by intraspecific competition as density approaches the carrying capacity of the habitat” (Dempster and McLean 1998, p. xx). This implies that populations can exist at any point below the carrying capacity, but not above it. There is one main limiting factor, such as tree holes

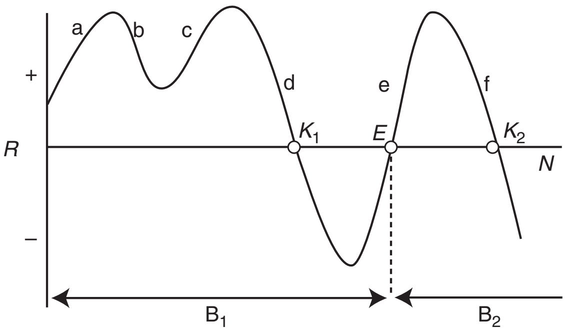


Figure 9.5 A hypothetical example of changes in *R* through time, with zones of positive and negative *R*, stable equilibria at K_1 and K_2, and an unstable equilibrium at *E*. B_1 and B_2 indicate basins of attraction in which populations tend to move toward equilibria K_1 and K_2 respectively. From Berryman *et al.* 2002. Reprinted with permission from Blackwell Publishing.

for hole-breeding mosquitoes and syrphid flies, conifer cones for cone-boring beetles, insect hosts for a parasitoid population or space for territorial animals, as discussed under Section 9.1.5 above on limiting factors. Dempster (1983, 1998) has been a strong advocate of resource limitation of populations. Here resources set a ceiling on population density, whereas with population regulation density-dependent factors result in fluctuations around an equilibrium density. In fact, the difference between the two concepts may be very difficult to distinguish in field populations, and it is unclear which situation is more common in nature.

Assembling the elements of the foregoing discussion on processes involved with population growth and regulation, using a hypothetical case, we can envision the various processes at work (Figure 9.5). In this figure population density, *N*, is on the horizontal axis and the *R*-function is on the vertical axis. Recall that when $R = 0$ the population is neither growing nor declining, as in Figure 9.2B, so that at any time the density meets $R = 0$, an equilibrium exists. If the trajectory of *R* is negative (at K_1 and K_2) then a stable equilibrium will exist, negative feedback or negative density dependence will be in operation, and population regulation will be in effect. The population will tend to behave as in Figure 9.3B. If the trajectory of *R* is positive, then an unstable equilibrium will prevail (at *E*) with the population tending to move away from this point, as in Figure 9.3A. Here, positive feedback, or positive density dependence, prevails, and population regulation is not operating because the factors at work are not bringing *N* back to the equilibrium point at $R = 0$.

Figure 9.5 illustrates three negative feedback segments (b, d and f). Stable equilibrium may be established by different forces, perhaps natural enemies cause negative feedback in segment d and an equilibrium at K_1, and food supply may set an upper equilibrium point at K_2, above which *R* is always below zero and the population *N* will decline. Populations will tend to increase when below an equilibrium point and decrease above one, so that populations exist in **basins of attraction** (B_1 and B_2). Therefore, the population is regulated at some times and not at others, depending on its proximity to an equilibrium point.

9.3 Life tables

The question now arises of how field data can be collected on insect populations which will enable population processes to be studied and how the conceptual framework already discussed can be applied. Many kinds of methods have been proposed to census populations and to gather the necessary details on birth, death, emigration and immigration (e.g., Southwood 1966, Hayek and Buzas 1997, Krebs 1999, Southwood and Henderson 2000), but the method most commonly employed in insect studies is life-table analysis. The first life tables developed for insect populations in the field were prepared on the spruce budworm, *Choristoneura fumiferana*, by Morris and Miller (1954). This insect was a serious defoliator of fir and spruce trees in New Brunswick, Canada, and under intensive study at the time (see Morris 1963a).

Naturally, a life table encompasses the full life of the insect, from birth to death. In the majority of insects studied by this method, the life cycle is more or less synchronous among individuals in a population, simplifying the gathering of data and computation. This emphasis on species with seasonal and synchronous reproduction is partly because most studies have been conducted in temperate latitudes where life cycles are commonly annual, or univoltine, and partly because herbivorous pest insect species have been the focus of attention. Such herbivores have life cycles synchronized with their food supply, which flushes in spring and ages through the season until leaf fall, with rapid changes in availability and suitability of food, imposing usually a single window in the annual cycle in which food is suitable for young larvae to become established.

9.3.1 Spruce budworm life table

The life table attempts to capture the demography of a population: birth, death, immigration and emigration. This is what the spruce budworm life table does (Table 9.1). One advantage in the study of the budworm is that the whole life cycle is spent on the tree branches, on which eggs are laid, larvae feed in buds and pupate in the foliage, and even females lay their first eggs where they emerge. Therefore, sampling branches at intervals, and laboriously searching for and counting each stage of development, provides the basis of the life table: eggs, first instar larvae, the hibernacula in which second instar larvae overwinter, second instar larvae feeding in buds in the spring, larger instars III to VI and pupae (Table 9.1 lists these stages and the number in the cohort at each stage). Pupae can be sexed, so the number of adults can be estimated, the sex ratio and the number of females, and from the females the number of eggs expected in the next generation can be calculated. If the actual number of eggs exceeds the expected number, as is the case in Table 9.1, this provides an estimate of immigration to the population. Should the number of eggs recorded be below the expected number, then this would provide an estimate of emigration by females.

We see that the cohort of eggs starting the life table numbered 174, and this number was gradually depleted by various causes of death until only 0.82 of an adult moth remained. These numbers therefore describe a **survivorship curve** for this population which indicates high mortality in the larval stages, typical of many insect species (Figure 9.6).

In addition to recording numbers of individuals per 10 square feet of branch surface, the standard sampling unit, Morris and Miller were interested in estimating the causes of death, for these would provide a mechanistic understanding of why populations differed from year to year. The particular methods they used are described in a series of papers (Morris 1955, 1957, 1960, 1963a, Miller 1957). Causes of death are listed in Table 9.1, as well as the number dying from each factor. Finally, the percentage of the cohort dying because of each factor, and the total percentage dying per developmental stage, is calculated in the right-hand column of the table. This provides an estimate of the relative importance of each factor.

Therefore, the life table is constructed with a series of columns defined as follows (see also Carey 2001):

Age interval x: this is the age of the cohort defined by the stage in development and the instar of the larvae. Thus, although a sample may contain more than one instar, members of the same instar are grouped in the life table.

Number alive at beginning of x, l_x: the number surviving at the beginning of this age interval. In the case of the spruce budworm this was the mean number per sampling unit of 10 square feet of branch surface.

Number dying during x, d_x: the number of individuals dying during the age interval.

Factor responsible for d_x, d_xF: An estimate of the cause of mortality.

Table 9.1 **Life table for the 1952–1953 generation in a relatively low population of spruce budworm in the Green River watershed, New Brunswick. Modified from Morris and Miller 1954**

Age interval, x	Number alive at beginning of x, l_x	Factor responsible for d_x, d_xF	Number dying during x, d_x	d_x as percentage of l_x, $100q_x$
Eggs	174	Parasites	3	2
		Predators	15	9
		Other	1	1
		Total	19	11[a]
Instar I	155	Dispersion, etc.	74.40	48
Hibernacula	80.60	Winter	13.70	17
Instar II	66.90	Dispersion, etc.	42.20	63
Instars III – VI	24.70	Parasites	8.92	36
		Disease	0.54	2
		Birds	3.39	14
		Other – inter.[b]	10.57	43
		Total	23.42	95
Pupae	1.28	Parasites	0.10	8
		Predators	0.13	10
		Other	0.23	18
		Total	0.46	36
Moths (SR = 50:50)	0.82	Sex	0	0
Females X 2	0.82	Size	0	0
		Other	0	0
		Total	0	0
"Normal" females X 2	0.82	–	–	–
Generation	–	–	173.18	99.53
Expected eggs 62		Moth migration etc.	–513	–827
Actual eggs 575				
Index of population trend:		Expected	–36%	
		Actual	+330%	

[a] Use of whole numbers results in inaccurate summation for total $100q_x$.

[b] Other factors minus mutual interference among all factors.

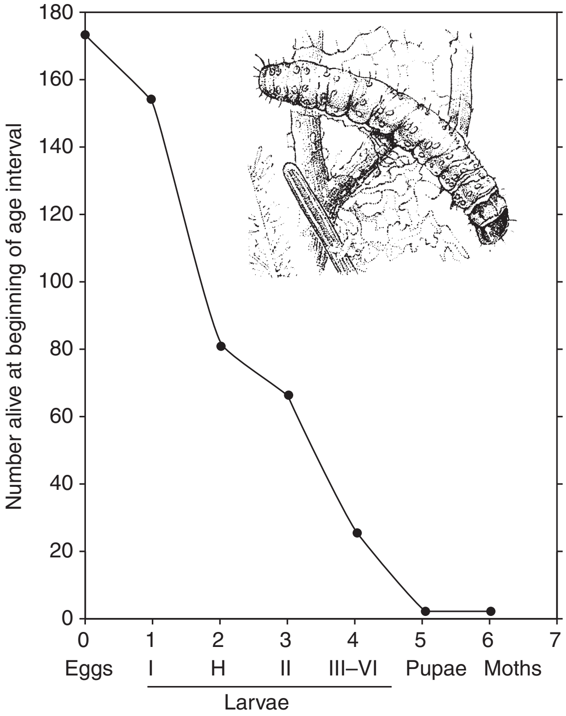


Figure 9.6 Survivorship curve for the spruce budworm derived from the l_x column in Table 9.1. The age intervals are plotted as if evenly spaced in time, although in the field instars I and II exist over a period of almost 10 months from August into May (see Morris 1963a, his Figure 2.1).

d_x as a percentage of l_x, $100q_x$: the mortality rate per 100 individuals which were alive at the beginning of the age interval.

There are some notable features in the spruce budworm life table (Table 9.1). Loss of larvae in instars I and II includes what is called "dispersion" – 48% of the cohort in instar I and 63% of the cohort surviving into instar II. This loss of 116.6 individuals from the original 155 individuals entering instar I, by far the biggest factor depleting the cohort, is caused by larvae each dispersing on a silken thread. They may drift to the ground and die, waft away in wind currents or float out of the sampling area into adjacent trees. The other most important factors are winter mortality in hibernacula (13.70 individuals and 17% of the cohort) and parasitoids attacking instars III – VI (8.92 individuals and 36% of the cohort).

Emigration or immigration was estimated based on the number of females surviving in the cohort, their size and therefore their expected fecundity. Since females have all their eggs mature when they emerge, pupal weight correlates well with fecundity of adults (Miller 1957). Female size in the generation studied in Table 9.1 was normal – that is, not influenced by starvation, so expected fecundity was not depleted (0 was entered in the column d_x). Also, the sex ratio was 50:50 so that Females × 2 provided a good estimate of the adult population. The expected fecundity was 62 eggs, but the actual number was 575, resulting in an expected trend in population of an increase of 330% (575/174), instead of an expected decline of 36% (62/174). Hence, immigration proved to be a very important factor in the dynamics of this population.

It is striking that the emphasis of the life table appears to be the amount of death, and what causes death, suggesting to some that these would be better called "death tables" (e.g., Price 2003a, see also Hunter 2001b who uses the term). However, the number of eggs in a cohort may be influenced strongly by insect female decisions to withhold eggs if conditions are inadequate (e.g., Ohgushi and Sawada 1985, Ohgushi 1992, Preszler and Price 1988). Female herbivorous lady beetles, *Henosepilachna niponica*, stopped laying eggs when leaf damage on the host plant reached 30%, although females laid many more eggs if transferred to undamaged plants (Ohgushi and Sawada 1985). In the stem-galling sawfly, *Euura lasiolepis*, females on poor quality willows retained 85% of their eggs, while on high quality willows only 28% of eggs were retained. In each case much of the dynamics was dictated by female behavior and fecundity, which greatly influenced the cohort size starting a generation. In Hunter's (2001b, Hunter *et al.* 2000) critique of life-table construction, he emphasizes the need for measures of rates of birth and movement, which are likely to diminish the apparent effects in life tables of top-down influences by natural enemies. Carey (2001) notes that adult insect life span needs more attention. Therefore, influences on realized fecundity and birth should be included in life tables if they are to be reliable. This will accomplish the full intent and meaning of the term "life table."

Another concern involving the reality of life tables is the inevitable existence of **compensating mortality** factors. If one mortality factor early in a life cycle is absent, say dispersal by first instar larvae in Table 9.1, then surely other mortality factors, such as natural enemies, will compensate to some extent by causing more mortality. Compensating mortality was recognized in the human actuarial literature, with a method for treating it in the form of the **multiple decrement life table**, which Carey (1989) adapted for use on insect populations. The key is to identify the kinds of mortality that are irreplaceable, and those which can be compensated for. **Irreplaceable mortality** "is the mortality rate from a specific factor that cannot be replaced by another factor" (Peterson *et al.* 2009, p. 2).

Peterson *et al.* (2009) used multiple decrement life tables and irreplaceable mortality analysis on 73 published insect life tables to determine where conventional life tables may over- or underestimate the magnitude of mortality factors. These authors found that mean irreplaceable mortality caused by abiotic impacts such as environmental instability and plant quality factors were higher, at 35% mortality, than that caused by pathogens (~9%), predators (~8%) and parasitoids (~6%). In biological control attempts, introduced natural enemies were estimated to cause only about 5% of irreplaceable mortality, providing a possible explanation for the failure of many biocontrol attempts. A re-evaluation of life-table analyses using the Carey (1989) and Peterson *et al.* (2009) methods would be valuable in both population biology and applied ecology.

One life table captures the demography of one population in one generation. When life-table construction is repeated over several to many generations they provide the basis for understanding population dynamics. They should provide the raw data on changes in density from generation to generation, and the reasons why density changes. This assumes that the salient variables are measured and incorporated in the life table, which may not always be the case. Notably, food quantity and quality was not recorded in many studies or its importance was underestimated (Cornell and Hawkins 1995) and natality was much less emphasized than mortality (Price *et al.* 1990). However, we have a large body of studies with which to examine demographic trends in insect populations.

9.4 Comparison of life tables

Many life tables on insects have been developed, affording an opportunity for comparisons among them, with a view to identifying generalizations and synthesis. Cornell and Hawkins (1995) reviewed patterns to be found in 530 life tables on 124 holometabolous, herbivorous insects. Direct comparisons among large numbers of herbivore species was made possible by uniform timing of life-history stages, egg, larva, pupa, adult, plus three periods within the larval stage, early, mid and late. Every holometabolous insect's developmental sequence could be fitted onto this categorization, survivorship curves could be compared directly, and mortality sources were evaluated to produce generalized pictures for various types of herbivory.

Perhaps an obvious result from Cornell and Hawkins' study was that survivorship curves differed greatly within species (Figure 9.7), meaning that mortality varied greatly from generation to generation, and population to population. This would be expected in populations that are variable through time and space. Another unsurprising result was that survivorship curves differed greatly no matter what category of feeding was examined:

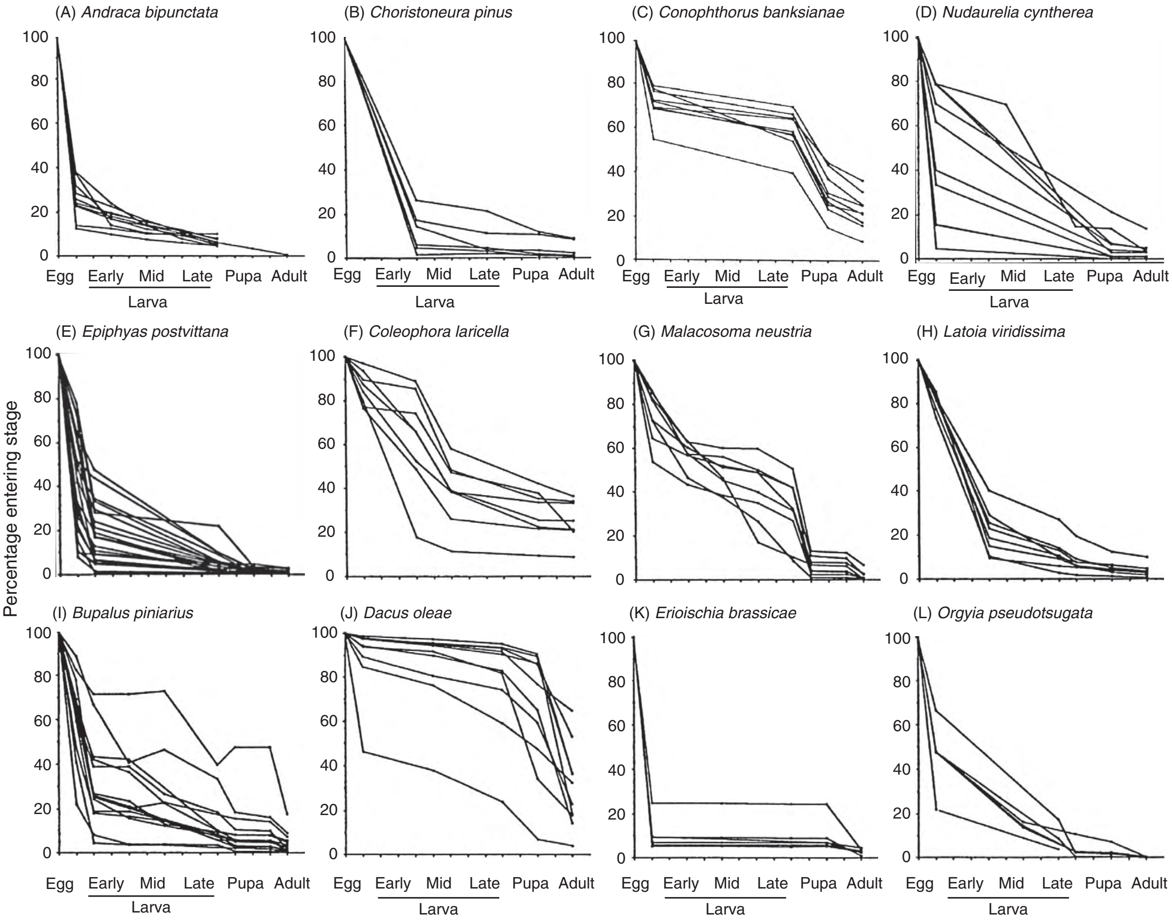


Figure 9.7 Survivorship curves for individual populations of 12 species of insect showing considerable variation within each species in different generations or locations. Each survivorship curve within each species represents a different generation or location. Species characteristics are provided in Table 9.2. From Cornell, H. V. and B. A. Hawkins 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *Am. Nat.* **145**:563–593. © by the University of Chicago.

exophytes, endophytes, leaf rollers, leaf miners, root feeders, native or introduced species, etc. (Figure 9.8). More unexpected was the apparent similarities of external feeders, internal feeders and root feeders, although some endophytes did show relatively high early survival, as might be expected when the egg and larva are protected within plant tissue (see, for example, C in Figure 9.7, of *Conophthorus banksianae*, which bores in the shoots and cones of pines, and example G in Figure 9.8 of native borers, such as bark-boring weevils, cone borers, seed weevils and stem borers). Overall, external feeders were exposed to 5–10% greater mortality than internal feeders. A relevant factor here is that external feeders were on average twice as large as endophytics and twice as fecund, suggesting that greater mortality should be expected when many eggs are laid, and individuals are likely to be easier to find.

The distribution of mortality factors over the life cycle of herbivorous insects was consistent with what

Table 9.2 **Characteristics of species illustrated in Figure 9.7**[a]

	Species name	Common name	Feeding niche	Host plant example
A	*Andraca bipunctata*		external folivore	tea, *Camellia sinensis*
B	*Choristoneura pinus*	jack pine budworm	mixed exo-endophytic	jack pine, *Pinus banksianae*
C	*Conophthorus banksianae*	jack pine tip beetle	mixed exo-endophytic	jack pine, *Pinus banksianae*
D	*Nudaurelia cyntherea*	pine tree emperor moth	external folivore	pines
E	*Epiphyas postvittana*	light brown apple moth	leaf roller/ webber/tier	pear, *Pyrus communis*
F	*Coleophora laricella*	larch casebearer	leaf miner	larch, *Larix decidua*
G	*Malacosoma neustria*	tent caterpillar	leaf roller/ webber/tier	hardwoods
H	*Latoia viridissima*	nettle caterpillar	external folivore	oil palm, *Elaeis guineensis* coconut palm, *Cocos nucifera*
I	*Bupalus piniarius*	pine looper	external folivore	Scots pine, *Pinus sylvestris*
J	*Dacus oleae*	olive fruit fly	borer	olive, *Olea europaea*
K	*Erioischia brassicae*	cabbage maggot	root feeder	cabbage, *Brassica oleracea*
L	*Orgyia pseudotsugata*	Douglas-fir tussock moth	external folivore	Douglas fir, *Pseudotsuga menziesii*

[a] References to studies are in Cornell and Hawkins 1995.

we should expect: external feeders suffer greater mortality from natural enemies than internal feeders (51% vs. 44%), and exophytics are less impacted by plant resistance factors than endophytics (2% vs. 15%) (Figure 9.9). Plant factors work earlier in the life cycle while mortality caused by natural enemies becomes stronger later in larval development.

A surprising result was that mortality from competition and natural enemies did not differ between insect herbivores in the temperate and tropical regions, nor did they differ with stage of ecological succession in which host plants occurred. Given the conventional wisdom that biotic factors, such as competition and natural enemies, are stronger effects in the tropics, and abiotic factors such as weather are stronger in temperate latitudes, the results from Cornell and Hawkins' study provide important real evidence contrary to prevailing views. This should provide a strong stimulus for more detailed comparative studies on latitudinal gradients,

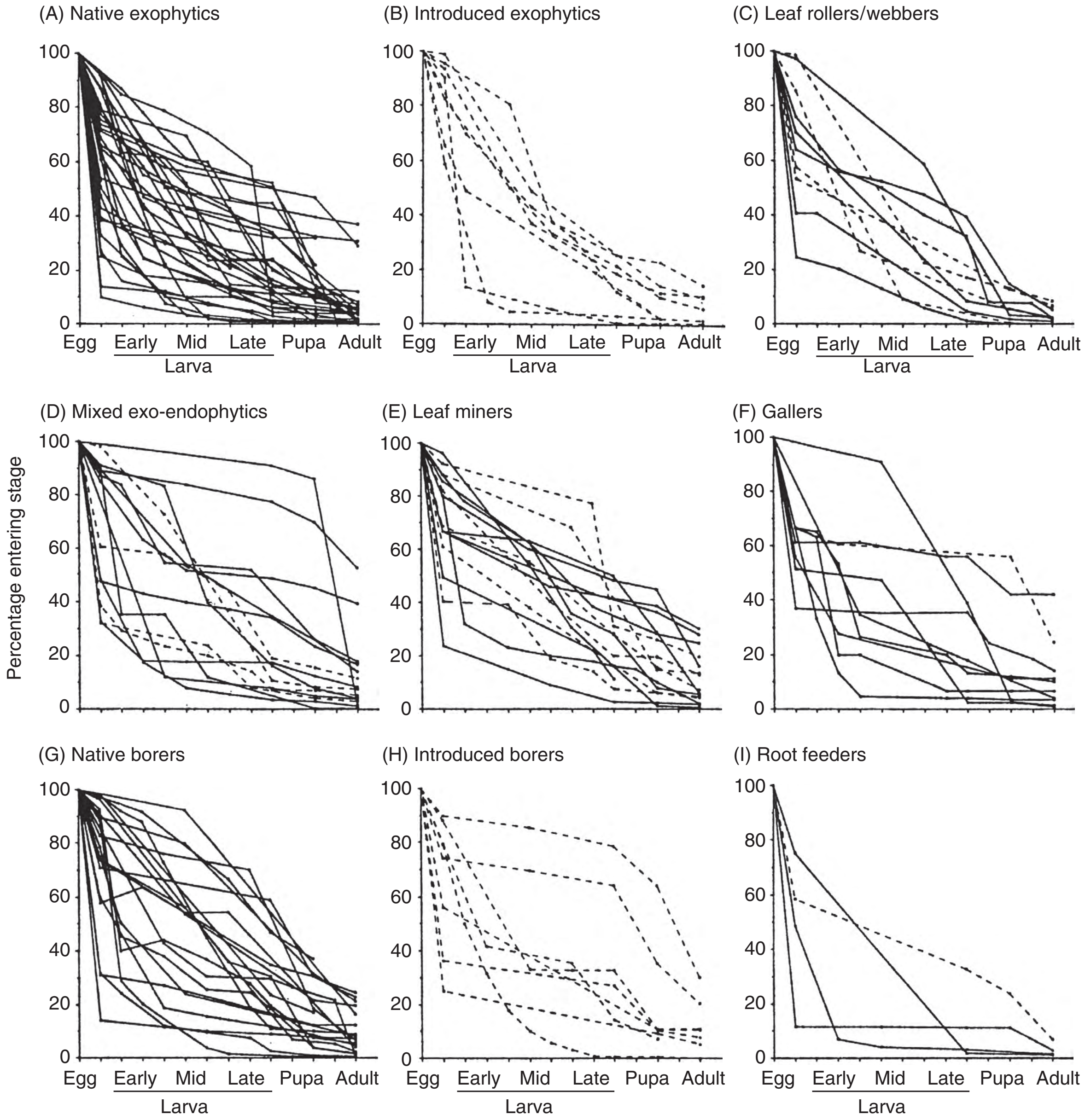


Figure 9.8 Survivorship curves for herbivore species in nine categories based on feeding type, and whether native or introduced. Note the wide variation among species within a feeding category. Solid lines show native species and dashed lines show introduced species. Each curve represents a different species. From Cornell, H. V. and B. A. Hawkins 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *Am. Nat.* **145**:563–593. © by the University of Chicago.

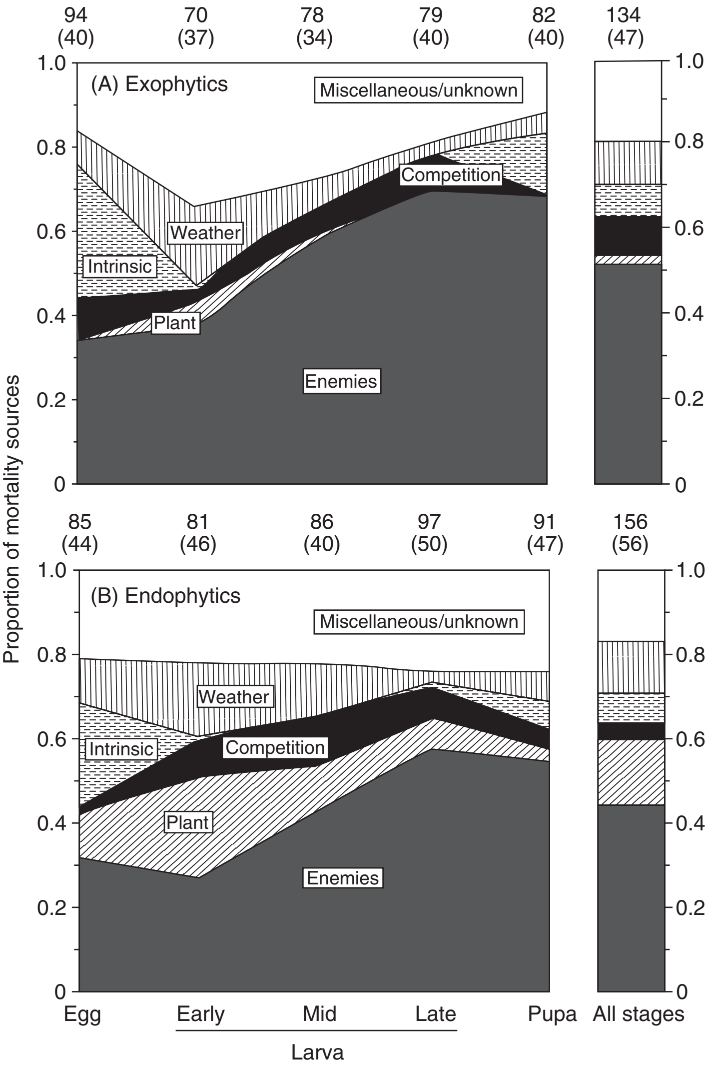


Figure 9.9 The relative importance of six mortality factors for (A), externally feeding larvae, and (B), internal feeders, at each age interval through the life cycle. The figures represent means for over 30 life tables in each case. The columns on the right show the relative importance of each mortality factor over the entire immature period. Numbers above each figure represent the number of cases used to calculate the proportions for each developmental stage (top number), and the number of life tables in which mortality data were available (in parentheses). From Cornell, H. V. and B. A. Hawkins 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *Am. Nat.* **145**:563–593. © by the University of Chicago.

especially on species within the same phylogenetic clade and feeding type, and with additional emphasis on tropical species; in Cornell and Hawkins' study there were almost nine times more temperate species than tropical species. In a subsequent paper (Hawkins *et al.* 1997), which distinguished predators, pathogens and parasitoids, predators and pathogens caused more mortality in the tropics and parasitoids more in temperate regions. Various authors from Humboldt, to Darwin and Wallace, expostulated over the exuberance of life in the tropics, with the rational deduction that biotic interactions must be strong. On Darwin's first entry into tropical forest, for example, he wrote, "If I was to specify any one thing I should give the pre-eminence to the host of parasitical plants" (Darwin 1892, p. 141). Dobzhansky (1950), MacArthur and Wilson (1967), Odum (1969) and Pianka (1970, 1974) were all influential in promoting the idea of strong biotic interactions in the tropics, with more *K*-selected species with presumably lower fecundities, but higher survival of progeny and more convex survivorship curves. These ideas must be re-evaluated, for insect herbivores at least. (*K*-selection will be described in the next chapter on life histories: it refers to natural selection on species usually living near the carrying capacity of the environment, with strong competition and attack by enemies, which select for high parental investment in progeny and therefore low fecundity.)

9.5 Survivorship curves

The life cycle is usually conceived of as starting with the egg. Insect eggs are generally very small, resulting in diminutive first instar nymphs or larvae facing serious challenges in a hostile world. Survivorship curves should capture this early stage in the life history, and evaluate the role of ovipositing females in providing suitable places for immatures to start their lives.

9.5.1 Establishment of larvae

The shape of survivorship curves depends upon the ease with which a newly hatched larva can establish a feeding site on or in the host plant. In all the survivorship curves of individual species shown in Figure 9.7, there is at least one curve per species showing a steep drop in survival between the egg stage and first sample of larvae, as in *Dacus oleae*. This pattern is more frequently evident in most of the other species (e.g., in A, B, D, E and K). The general point to note is that the first instar larva is a critical interval in the life history, and its survival or death may well influence general population trends. The contrast between survival of the cabbage maggot, *Erioischia brassicae*, and the olive fruit fly, *Dacus oleae*, is illuminating. The cabbage maggot female lays eggs at the collar of the young cabbage plant at soil level, and the tiny larvae must burrow down to roots before they can feed, with great loss of individuals through desiccation, difficulty burrowing, perhaps predation, and difficulty establishing a feeding site by tunneling through the plant cuticle. The resulting survivorship curve is strongly concave. In contrast, the olive fruit fly lays eggs directly through the skin of the olive fruit, placing the eggs into the flesh on which the larvae will feed. The larva is protected from desiccation, hard to find by natural enemies and surrounded by food. Thus, the survivorship is strongly convex in most cases.

9.5.2 The role of adult females

These contrasting life cycles raise the question of how well life tables capture the role of females, realized fecundity and maternal care during oviposition. Females of many species emerge with all their eggs mature and ready to lay; they are **pro-ovigenic**. Many moth species, like the spruce budworm, pine looper and emperor moths, as well as diprionid sawflies, are pro-ovigenic, so they lay their eggs soon after emerging as adults and mating, and presumably are rather undiscriminating on where they lay eggs: eggs are laid where females emerge, or away from larval food. Also, predictions on fecundity based on pupal or adult weight or size are likely to be quite accurate (Leather 1995). Hence, counting eggs at the beginning of the life table, as in the spruce budworm, probably captures the role of the female adequately. She lays eggs in clusters, the first clutch right where she emerges, and evidently makes no decisions on where to oviposit relative to where the larvae will establish feeding sites. Larvae are likely to disperse on a silken thread (see Table 9.1) and start to feed in the spring, months after oviposition in the previous August.

Other species have females that are **synovigenic**, maturing eggs after emergence, and usually laying eggs gradually through their adult life, making decisions on food quality and quantity for their progeny, and perhaps withholding eggs when resources are inadequate. Such cases were mentioned earlier in this chapter, concerning the lady beetle, *Henosepilachna niponica*, and the stem-galling sawfly, *Euura lasiolepis*. Food for adult females may also be important, affecting fecundity and longevity (Leather 1995). For example, Mediterranean fruit flies, *Ceratitis capitata*, require protein in order to mature eggs, but can live a long time if only sugary substances are available (Figure 9.10, Carey *et al.* 1998). Carey (2001, p. 92) notes that “the entomology literature contains little [adult] insect life span information,” and he provides a valuable discussion of the available records. He notes that there is a 5000-fold range in adult insect life spans (see Chapter 10 Section 10.8), compared to only a 60-fold difference in life spans of mammals. Clearly the range in insects indicates the potential for huge variation in fecundity and birth rates, which need more attention in demographic studies.

Flanders (1950) emphasized the different roles of pro-ovigenesis and synovigenesis in parasitoids, but it appears that complete pro-ovigenesis may be less common in parasitoids than in insect herbivores (see Jervis *et al.* 2001). But whether we study parasitoids or herbivores, or both together, evaluating the role of maternal responses to resources will be critical in understanding the population dynamics of the species.

Capturing the role of adult females in life tables, and therefore population dynamics, is challenging, but important. The maternal condition and response to food quality can be *the* major factor in population dynamics (Preszler and Price 1988). Capturing this aspect of the life cycle, and the fate of eggs once they are formed in the female, would be achieved if a life table were started with the cohort of eggs inside females, and followed the female’s decisions on laying or withholding eggs, and the nature of the substrates on or in which she oviposits. Such detail probably requires experimental approaches, but for synovigenic species the effort would be rewarding. An example of the maternal response to host plant quality, when 100 eggs are available inside two females per treatment, showed a difference of 72.5

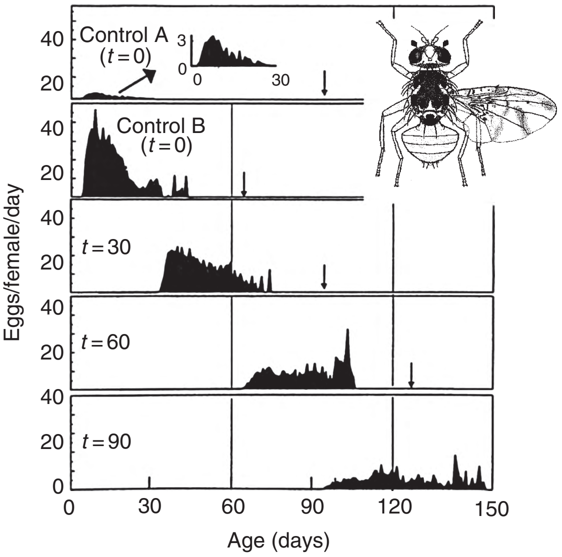


Figure 9.10 The eggs laid per female per day through the life of adult medflies maintained under different conditions during adult life. Control A provided a sugar-only diet, with very low egg production resulting (note enlarged inset). Control B provided a full sugar plus protein diet from emergence of adults to their death ($t = 0$). In the three treatments adults were provided sugar only until day 30, 60 or 90 ($t = 30$, $t = 60$, $t = 90$) and then switched to a full sugar plus protein diet. Egg production was delayed until the diet contained protein and the longer the protein was denied the longer the females lived. Vertical arrows show the time when the last female died. For $t = 90$ the last female died at 173 days. From Carey, J. R., P. Liedo, H.-G Müller, J.-L. Wang and J. W. Vaupel. 1998. Dual modes of aging in Mediterranean fruit fly females. *Science* **281**:996–998. Reprinted with permission from AAAS.

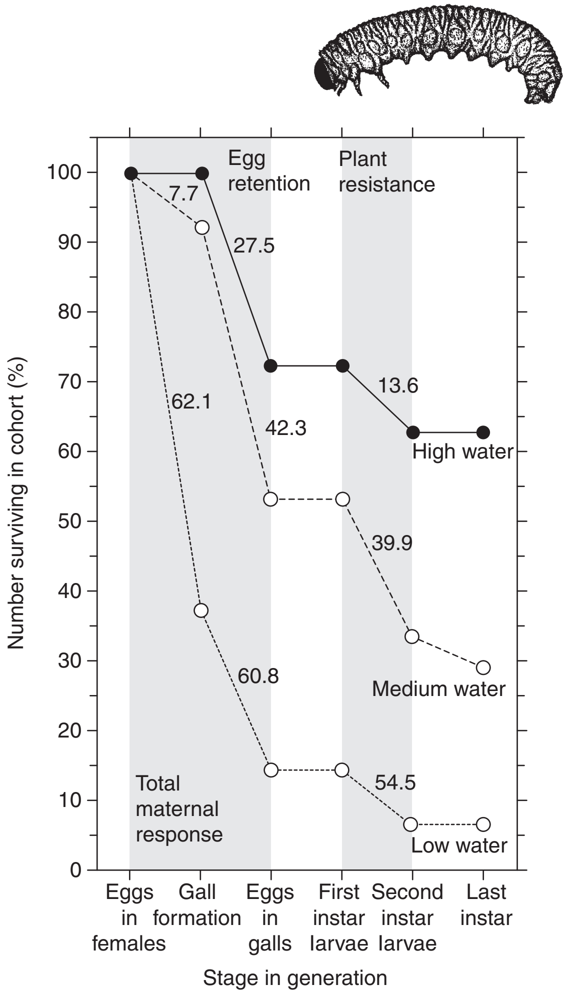


Figure 9.11 Survivorship curves for the stem-galling sawfly, *Euura lasiolepis*, in three treatments of host plants with high, moderate and low water supply. Note the large differences in maternal responses to willow quality (shaded on left) with females not forming galls and withholding eggs much more on willows growing less vigorously. Also note the correlation of low egg retention and low larval mortality, and high egg retention and high larval mortality. No natural enemies were present so larval mortality was caused by plant resistance. From Price *et al.* 1998a.

eggs laid in high-quality plants and 15.0 eggs in low-quality plants (Figure 9.11). In the high water treatment, 100 eggs available in the two females resulted in 100 galls, with 27.5 of eggs retained in the females. In the low water treatment, 100 eggs available resulted in 38 galls, and within these galls 60.8% did not contain eggs. Females laid more of their eggs on willows growing well with ample water and their larvae survived well, with only 13.6% mortality between the first and second instar. On poorly growing plants in a low water treatment, females withheld eggs, and among those that were laid 54.5% died in the first instar.

This gall-inducing species was used by Cornell and Hawkins (1995) as an example, which appears in Figure 9.8F as the species with the highest survival to the adult stage. The survivorship curve was provided in Price and Craig (1984), before the role of maternal responses was understood. In this case the maternal response was likely to result in an extra 40% loss from the potential cohort, which would result in a survivorship curve similar to the gallers with lower survival in the figure. Wherever females oviposit into plant tissue then maternal responses need to be incorporated into life tables and survivorship curves.

Another factor that is probably undersampled in many species is the role of diseases, especially those that act rapidly and then the evidence is lost. For example, even though weekly samples were taken in the Green River study of spruce budworm, much unaccounted loss of the cohort occurred (Royama 1984, 1992). In addition, estimating the role of parasitoids requires careful study for accurate estimation of their real impact (Van Driesche 1983, Van Driesche *et al.* 1991).

Survivorship data and life tables are published frequently, and on a wide variety of insects and other organisms, including aspects of human biology. These approaches have become among the most commonly used in the study of insect ecology, with probably hundreds of studies published each year. They are commonly employed in comparative studies such as comparing herbivore performance on different hosts (e.g., Liu *et al.* 2004), or predator performance on different prey species (e.g., Torres *et al.* 2004), or responses of species to a range of environmental conditions (e.g., Matadha *et al.* 2004, Bayhan *et al.* 2005). Species may also be compared such as among predator species (e.g., Lanzoni *et al.* 2004), and the role of competition (e.g. Agnew et al. 2002). Survivorship curves and life tables offer such a basic methodology with such versatile and widespread application that they have become almost indispensable tools in the study of insect ecology.

Applications

Approaching a problem and planning

Most life tables are developed on economic pests such as aphids (e.g., Bayhan *et al.* 2005, Li *et al.* 2007) and chewing herbivores (e.g., Barrigossi *et al.* 2001, Liu *et al.* 2004, Wermelinger and Seifert 1999, Wang *et al.* 2008) or their natural enemies (e.g., Legaspi 2004, Matadha *et al.* 2004, Torres *et al.* 2004). But other species of insect include butterflies (e.g., Karlsson and Wiklund 2005), insect ectoparasites of birds (e.g., Fitze *et al.* 2004, Bize *et al.* 2004), burying beetles (e.g., Nisimura *et al.* 2002) and ants (Sanders and Gordon 2004). In studying insect populations for almost any reason, be it to estimate population growth rates, the impact of natural enemies or the role of host plants, life tables offer a general method on which quantitative analyses can be based.

For any management project, in agriculture, forestry, medical entomology or conservation, in which insects are of interest, their population growth characteristics and population dynamics are important to understand. So the elements discussed in this chapter provide the groundwork for approaching management questions. In studying the life history of an insect, the life table and survivorship approach provide a structured sampling framework for description, and a method with broad comparative application, as illustrated in the studies by Cornell and Hawkins already discussed in this chapter. The life-table approach helps to focus on many critical issues in the life history of an insect, such as fecundity, oviposition behavior, sex ratio, larval establishment in feeding sites, food plant choice and performance of immatures on various foods, the timing of mortality caused by predators, parasitoids and diseases, the role of weather and many other environmental factors. All can be encapsulated in the life table.

Most long-term studies of insect population dynamics have employed life-table analysis of one kind or another, with many examples provided in Chapter 11 on population dynamics. It is the life table that promises the possibility for understanding the mechanisms underlying changes in populations, and the role of management techniques, including control methods of various kinds, in influencing insect populations. Mere censuses of populations, recording numbers per generation or other time period, can provide only the trends in population from which various deductions can be made and forecasting developed. But only the details of natality and mortality factors can reveal the reasons for population change and the mechanisms of population regulation or limitation, if such exist.

One would think that, with so many life tables published, the opportunities for comparative studies would be great, with promising possibilities for synthesis and generalization. Perhaps a narrower perspective than that adopted by Cornell and Hawkins (1995) would provide new insights, possibly comparing aphid life tables on different kinds of hosts or in different habitats, or microlepidopteran herbivores with different feeding niches. Finding generalizations is important in management because they help with anticipating problems and answers, and they enable us to predict what to expect of a new species of interest when similar species have been studied already. Invasive species, as an example, are of grave concern (e.g., Van Driesche and Van Driesche 2000), and having life tables of such species from their native environment, or of related species, should aid in developing the course of studies to be undertaken, and the possible weaknesses in the life cycle that might be exploited in a management plan.

It is actually hard to imagine a practical problem in field entomology in which life table studies would not be of value. However, we must recognize that they are descriptive and empirical, and while being of enormous value, additional experimental approaches will always be necessary to fully understand the factors critical to the population biology of a species.

Summary

This chapter started with five principles of population growth involving persistent growth being reduced by competition within species and among species, plus natural enemies and other limiting factors, such as poor weather conditions. As a population increases, various feedbacks may change the rate of growth. This may involve positive density dependence or positive feedback when, for example, low populations increase to a point where cooperation is effective, or negative density dependence or negative feedback when, for example, food becomes limiting as competition increases. Negative feedback stabilizes a population at an equilibrium. Influences on populations not related to insect density, such as weather variables, are regarded as density-independent factors, but other variables exercise an effect on the next generation of insects, involving a time lag, or delayed density dependence, such as long-term induced defenses in plants or natural enemies.

Life tables provide a clear method for documenting numbers of insects in a cohort from the egg stage until death, the life tables on the spruce budworm serving as an example of how a life table is constructed, the development of a survivorship curve, and how estimates of the relative importance of mortality factors are determined. They provide a strong basis for comparison among species, among habitats, or on latitudinal gradients, although more attention is required on the influence of female behavior on cohort size, and compensating mortality factors, the latter treated in multiple decrement life tables. Comparison of life tables on herbivores in the tropical and temperate regions showed a surprising result of little difference in the effects of competition and natural enemies on mortality. Survivorship curves illustrated the importance of early larvae establishing a safe feeding site, and high mortality associated with eggs placed at a distance from the larval feeding site. Life tables have been developed extensively for insects of economic importance, and they aid in the development of management plans and their implementation.

Questions and discussion topics

1. Using an insect in a natural setting with which you are familiar, how would you plan a sampling protocol in order to describe a survivorship curve and life table for the species?
2. Select a published life table and discuss ways in which the methods, analysis and conclusions could be improved.
3. In your opinion, would experimental methods, coupled with field observations, improve the realism of life table construction? Which experiments would you conduct and what results would you expect that would change your conclusions on the most important factors in the life cycle of the species?
4. The use of multiple decrement life tables, which identify irreplaceable mortality, show that conventional life tables may overestimate some factors and underestimate others. How, in your opinion, should such modifications in understanding contribute to general concepts on population dynamics and population regulation?
5. Discuss the value of good life tables when planning an integrated pest-management strategy for an insect pest species you are familiar with.

Further reading

Berryman, A. A. 2003. On principles, laws and theory in population ecology. *Oikos* **103**: 695–701.

Cornell, H. V. and B. A. Hawkins. 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. *Am. Nat.* **145**:563–593.

Kramer, A. M., B. Dennis, A. M. Liebhold and J. M. Drake. 2009. The evidence for Allee effects. *Popul. Ecol.* **57**:341–354.

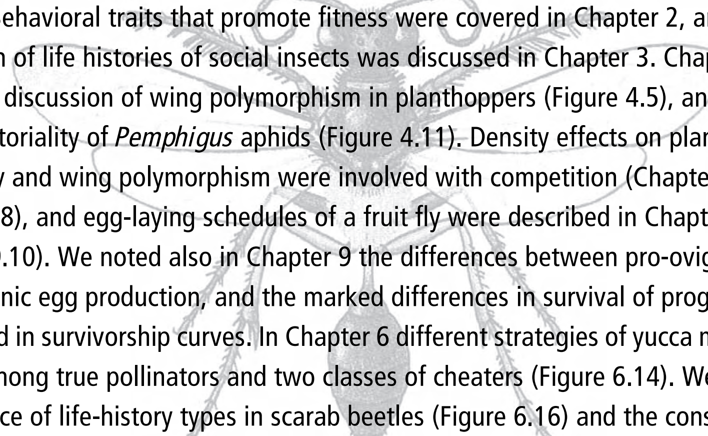
Peterson, R. K. D., R. S. Davis, L. G. Higley and O. A. Fernandes. 2009. Mortality risk in insects. *Environ. Entomol.* **38**:2–10.

Southwood, T. R. E. and P. A. Henderson. 2000. *Ecological Methods*, third edition. Oxford: Blackwell.

10

Life histories

The study of life histories involves the full span of life, from egg or sperm through reproduction and death. The ways in which individuals maximize progeny production and survival are about as diverse as the populations and species themselves. Research interest in life history is therefore strongly comparative, looking at the variation in life-history characteristics within populations, within species and among related species. As with ecology in general, we search for patterns in nature and develop hypotheses and theories, which account for the trends that we observe, and prompt new observations in a cycle of efforts to refine knowledge.



Understanding of life histories is fundamental to insect ecology, and we have covered many examples of life-history studies already in this book, and more will follow. Behavioral traits that promote fitness were covered in Chapter 2, and the evolution of life histories of social insects was discussed in Chapter 3. Chapter 4 included discussion of wing polymorphism in planthoppers (Figure 4.5), and jousting and territoriality of *Pemphigus* aphids (Figure 4.11). Density effects on planthopper fecundity and wing polymorphism were involved with competition (Chapter 5, Figure 5.8), and egg-laying schedules of a fruit fly were described in Chapter 9 (Figure 9.10). We noted also in Chapter 9 the differences between pro-ovigenic and synovigenic egg production, and the marked differences in survival of progeny portrayed in survivorship curves. In Chapter 6 different strategies of yucca moths were noted among true pollinators and two classes of cheaters (Figure 6.14). We also saw divergence of life-history types in scarab beetles (Figure 6.16) and the constraints on ovariole number and fecundity of parasitoid wasps and flies (Figure 8.4). Indeed, the study of life-history traits runs throughout ecology, and this is how it should be, because understanding the evolution of whole life histories is at the heart of understanding insects, and the evolutionary pathways along which they have traveled. This point is taken up again in the last section of this chapter on applications.

In this chapter we focus on the evolutionary strategies and adaptations which have resulted in the variation in life histories among and between species and populations. We will make some comparisons of life-history traits within insect taxa to illustrate the ways in which we can detect patterns and generate explanations. Then we will discuss the costs and benefits of adaptive shifts in life histories, and move on to variation in fecundity among species, the timing of reproduction and a view on stabilizing selection which results from the checks and balances in the evolutionary process.

10.1 Scope of studies

Study of the full span of life of an insect enables us to appreciate the checks and balances, and compromises selectively inflicted upon the evolutionary pathway a population or species is traveling. From the beginning, a species is comprised of, by its basic design, a set of phylogenetic constraints, but it also benefits from an integrated set of adaptations reflecting its evolutionary past. Every evolutionary advance carries a cost and trade-off because the energy, nutrients and time available are limiting. Typical life-history traits that are studied in insects are egg size and number per female, the balance between reproductive effort and adult survival, parental investment in progeny and age of first reproduction, survivorship of progeny and factors that influence stage-specific vulnerability. A central question is how a particular life-history configuration maximizes lifetime fitness in relation to other possibilities: i.e., which strategies promote or maximize the number of high-quality individuals left at the end of a generation?

Environmental variables inevitably influence the evolution of life histories. Ephemeral resources such as small water bodies, or fresh dung or carcasses, may force the evolution of dispersal behavior. This usually involves development and maintenance of wings, flight muscles, a strongly built thorax and the allocation of energy to flight. Costs of flight may detract from resources otherwise available for reproduction, a trade-off commonly observed in insects in which flight muscles atrophy after dispersal, with resources being shunted to reproductive effort. Another strategy widely adopted among insects is for populations to be polymorphic, with some winged individuals and some wingless, as we shall see in an example that follows. Considering all these machinations in the evolutionary trajectories of species makes the field of life-history study a large and rich enterprise, particularly for the insect ecologist with such a huge and diverse range of species–habitat combinations to study. However, such richness of species promises a strength in numbers such that patterns may be easier to detect than in more depauperate taxa with much less variation in life histories.

10.2 Evolutionary strategies and tactics

“Strategies” and “tactics” are words typically employed for the intentional planning of a military campaign, a political movement, or a business enterprise. In evolutionary biology the same terms are used, but without implying that there is a grand plan in the evolutionary process. Rather, the terms are a short hand which covers the more cumbersome, but correct approach, of saying that a particular trait changed passively under the influence of natural selection. Such natural selection may have worked over the long term, gradually resulting in a syndrome of adaptations which meets environmental challenges and promotes population persistence of a species. The full syndrome of adaptations could be seen as the adaptive strategy, or evolutionary strategy, comprising for example, in *Prokelisia* plant hoppers, wing polymorphism, the response to density, cibarial pump design, and changes in fecundity in response to crowding. These combined tactics encompass the individual adaptations and their physiological mechanisms by which the strategy is achieved.

10.3 Comparative life-history studies

Life-history variation and evolutionary conservation can be observed at every level of organization in insects. Related species differ in their evolutionary strategies, while showing some strong effects of phylogenetic constraints. There is variation in life-history traits among populations of a species over whole landscapes, and within populations lineages may also differ in many life-history characteristics. In the following sections we will consider examples of each level of variation to illustrate the way that life-history studies have been approached by insect ecologists.

10.3.1 Comparisons among species: parasitoids

Some features of the parasitoid life cycle have been discussed in previous chapters, so we are familiar with their basic life-history traits. In Chapter 8 (Figure 8.4) convergence in ovariole number per female was illustrated, showing in both ichneumonid wasps and tachinid flies that ovariole number and fecundity declined as species attacked the depleted number of hosts available as the host life cycle progressed from eggs to pupae and adults. High fecundity was selected for when hosts were young and numerous, and could be discovered rapidly. Low fecundity evolved when hosts were sparse, often hidden in an overwintering position, and consequently hard to find. Parasitoids were placed in a proverbial "environmental straitjacket" by the inevitable pattern of survivorship curves of their hosts, forcing convergence to a narrow range of opportunities for variation in fecundity among their species. These features underlie the contrasting reproductive strategies which were described: those of **koinobionts** and **idiobionts** in Chapter 8 and **pro-ovigenic** and **synovigenic** species in Chapter 9.

The pro-ovigenic to synovigenic continuum in parasitoids has been examined in some detail by Jervis *et al.* (2001), using 638 species in 28 hymenopteran families. An **ovigeny index** was developed ranging from 1 to 0, to estimate the proportion of all eggs a female can lay in her lifetime which are mature at the time of adult emergence. A value of 1 is given to females in which the lifetime complement of eggs is mature and ready to oviposit at the time of adult emergence. Zero indicates complete synovigeny, in which no mature eggs are present at the time of adult emergence. Given the range in parasitoid life cycles and evolutionary strategies, it is not surprising that the ovigeny index shows the full range from 1 to 0 in the 638 species studied, suggesting various hypotheses about why such a range should exist.

One hypothesis predicted that early reproductive effort should be correlated with reduced life span. This prediction was based on life-history theory involving costs and benefits or trade-offs: if a high cost of early reproduction results in a shorter life, pro-ovigenic parasitoids should have shorter adult lives than synovigenic species. This hypothesis was supported with 38% of the variation in life span accounted for by the ovigeny index. When species within a genus were compared, more (46%) of the variation was explained, and comparisons among families within a superfamily accounted for 51% of the variation. Life spans differed significantly with a mean of 9 days for pro-ovigenic species and 29 days for synovigenic species.

Among the several other hypotheses proposed by Jervis *et al.* (2001), one concerns contrasts between koinobionts and idiobionts. We can expect koinobionts to exhibit a higher ovigeny index than idiobionts. This is because koinobionts live with the host, they are mostly internal parasitoids, and tend to attack earlier developmental stages of hosts, which are more numerous and easier to find than the more concealed and less numerous hosts utilized by idiobionts (see Figure 8.3). This prediction was upheld, with one test showing an ovigeny index of 0.477 for koinobionts and 0.008 for idiobionts, a highly significant difference. Using the ovigeny index gradient, Jervis *et al.* (2008) have extended the understanding of parasitoid life history diversity, and have applied it to other insect groups such as the Lepidoptera (Jervis *et al.* 2005, 2007), discussed under trade-offs later in this chapter.

These two hypotheses, of the eight proposed, serve to illustrate some valuable points:

(1) Empirical studies, often of individual species, may be descriptive and non-conceptual, but they contribute to a growing database which becomes increasingly valuable with time. Eventually, especially with insects, large bodies of data become available for rigorous testing as with the 638 species used in the Jervis *et al.* (2001) study.
(2) Such data begin to reveal patterns among species contributing to conceptual advances, as with the recognition of koinobionts to idiobionts (Askew and Shaw 1986) and the pro-ovigenic and synovigenic (Flanders 1950) continuum.
(3) These conceptual frameworks provide the basis for testing theory and for erecting hypotheses that contribute to theory. Thus, the gradual accumulation of empirical studies builds eventually to a central goal in ecology; to detect patterns in nature and to develop and test scientific theories.
(4) Another advantage to this sequence in scientific research is that it generates new hypotheses, as we shall see in the next example.

Based on the study by Jervis *et al.* (2001), Boivin *et al.* (2005) reasoned that there must exist similar patterns of variation in male parasitoids. They developed the **spermatogeny index**, with 1 indicating complete prospermatogenic males which emerge as adults with all sperm ready to be used, and 0 for synspermatogenetic males which mature sperm later in their adult lives. As for female parasitoids, a complete range from 1 to 0 was discovered, although adequate data were available for only 16 species. Several hypotheses were erected based on the logic of trade-offs in life-history evolution; just three are used as examples here:

(1) A higher spermatogeny index should correlate with a shorter life span: that is high energy costs early in life will take their toll on longevity.
(2) Species that are more synspermatogenic have a higher probability of feeding on rich protein sources: the cost of foraging and feeding provides the benefit of higher nutrients available for sperm production.
(3) The spermatogeny index should correlate with the ovigeny index: pro-ovigenic females should mate with males producing many sperm early in life.

None of these hypotheses could be tested because of a paucity of data, but the paper provides heuristic encouragement for increased study of male reproductive strategies, and the eventual testing of hypotheses. This illustrates again the reciprocal nature of gathering empirical, descriptive data, and the generation and testing of hypotheses.

10.3.2 Comparisons among species: giant water bugs

A significant puzzle in understanding the life history of giant water bugs (Hemiptera: Heteroptera: Belastomatidae) is that males rather than females protect their brood, a most unusual behavior throughout the animal kingdom (Figure 10.1). Smith (1997 and earlier publications) provided a fascinating look at this **uniparental postzygotic parental care** by males in need of a clear adaptive explanation. Major parental investment by males is rare because, usually, a male can leave more progeny by copulating with many females, and females generally provide a larger investment in progeny because of the large egg size relative to sperm size, so females should evolve to protect their investment rather than males, if progeny need protection at all. But terrestrial insects have an intricate chorion which protects embryos against desiccation and drowning, resulting in few terrestrial insect species exhibiting parental care by either sex, except in the social insects.

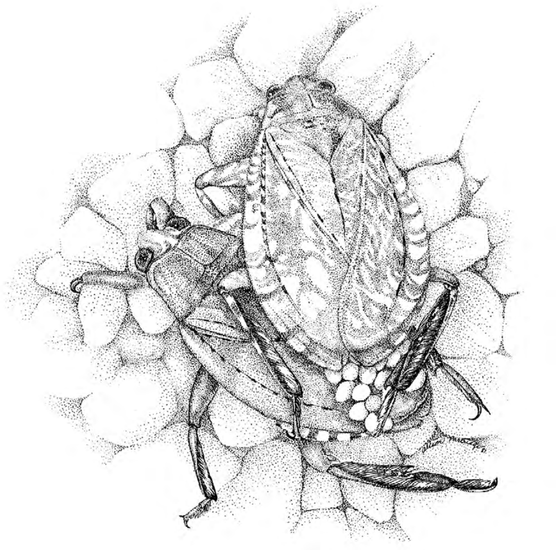


Figure 10.1 An example of uniparental postzygotic parental care in the giant water bug, *Abedus herberti*. The eggs are laid on the back of the male (below) by the female (above) who has just mated with the male, ensuring paternity for the male of the eggs he cares for. Based on an original photograph by Robert L. Smith. Drawing by Alison Partridge. From Price 1997.

How, then, did the male parental care in giant water bugs evolve? Paternal investment is expensive for the following reasons.

(1) The male is unable to mate again until the eggs have hatched.
(2) Brooding is energetically expensive in many species in which males receive eggs on their backs from females, and aerate them by rocking eggs in the water or exposing eggs above the water.
(3) Predatory efficiency of males is reduced by the mass of eggs.
(4) Males become more vulnerable to predators.

These costs must be offset by considerable advantages ensured by mating behavior. First, the male can evaluate the quality of a potential mate and ensure paternity of the eggs he broods. Courtship is complex, composed of sparring, embracing, clasping and pumping up and down, so strength and agility of the mate is gauged. Before oviposition starts in *Abedus herberti*, studied by Smith, the male copulates with the female, and again after every egg or two is laid on his back. In one case a male copulated 100 times in 36 hours during the oviposition of 144 eggs by one female! Insistence on frequent copulation assures that the male is the parent of the eggs he broods. He is not a **cuckold**, or partner to a female which has mated with another male. Second, eggs are relatively large, so that gas exchange would be too slow in water – eggs die without aeration facilitated by males. Third, egg survival is high given parental brooding, usually above 95%. Thus, evolution of large eggs in an aquatic insect required active aeration by an adult; that adult needed to be male because females could not lay eggs on their own backs, making male parental care likely to develop.

But why should eggs be so large? Smith reasons that constraints on egg size are the phylogenetically determined number of instars in the life cycle and **Dyar's Law**. Five instars is the basal or **plesiomorphic character** of the Nepoidea to which belastomatids belong (Figure 10.2). This sets a rigorous constraint on how large eggs must be to enable the development of ultimately large adults because of Dyar's Law (1890). Dyar found that caterpillar head capsules increased by a constant of 1.6 times at each molt, so with a given number of instars constant, evolution of larger egg size is required if adults are to become larger. Evidence from a more diverse array of both hemi- and holometabolous insects showed growth ratios ranging from 1.27 to 1.52 (Cole 1980), but the constraint on egg size directly linked to adult size remains real. Hence, the evolution of large eggs needing specialized brooding and parental care is partially explained.

However, the inevitable question becomes, what selected for larger adults, well beyond the typical size of insects with typical egg sizes that could acquire adequate gas exchange through the chorion? Again, Smith (1997) provides an explanatory scenario.

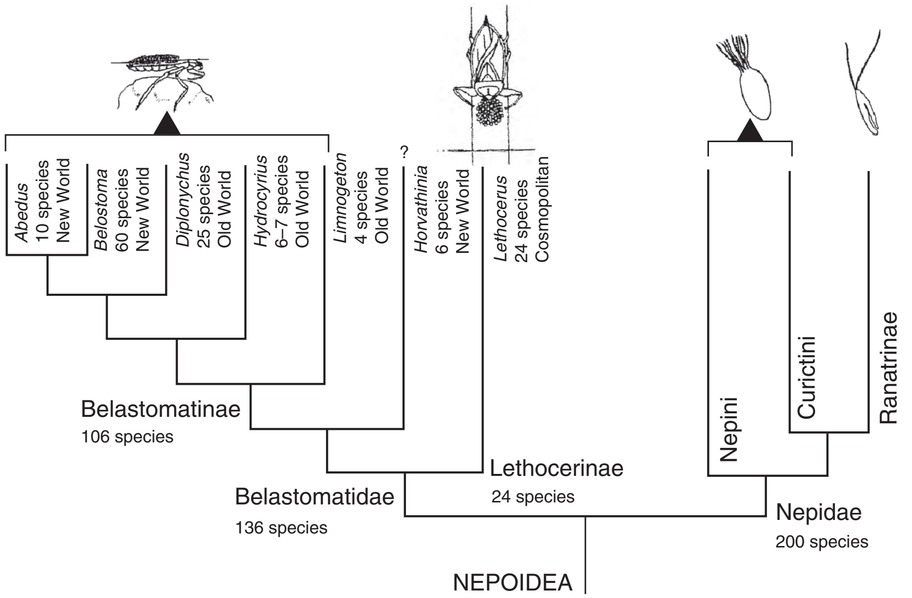


Figure 10.2 A cladogram for the superfamily Nepoidea (Hemiptera), which contains two families, the giant water bugs, Belastomatidae and the waterscorpions, Nepidae. The large eggs characterizing this group show divergent solutions to oxygen exchange: the eggs of Nepidae have respiratory horns, while the belastomatids care for eggs on emergent vegetation (Lethocerinae), or on the backs of males (Belastomatidae). From Smith 1997.

A small water bug of 5–7 mm long survived well when it was able to feed on relatively large prey: tadpoles and small fish for example. It possessed a venomous saliva and raptorial front legs, and a move to vertebrate prey opened a new feeding niche and a new adaptive zone. Selection may well have been rapid in favor of larger individuals in this lineage resulting from the advantage of large food items, necessitating correlated selection on egg size. Eventually this selective pathway resulted in relative gigantism, with some water bugs ranking among the largest insects in any local fauna. Large eggs – large adult size – large meals: even frogs, birds, fish and snakes are killed by some of the impressive predators in the belastomatid lineage. (However, the large eggs and large female body size does not correlate positively in other groups, such as butterflies [Bauerfeind and Fischer 2008]).

The current phylogenetic hypothesis reconstructing the superfamily Nepoidea aids in the understanding of egg incubation and male brooding (Figure 10.2). The Nepidae, or waterscorpions, are not as large as the largest belastomatids, therefore their eggs are not as large, so respiratory horns add sufficient surface area for gas exchange in water, without male brooding. On the belastomatid side of the cladogram, the earliest subfamily is the Lethocerinae, with very large adults at around 6 cm long, and male brooding on emergent vegetation. The large eggs are guarded by males, which enter the water to wet themselves and then "drip-dry" onto the eggs, shade them from the sun and inject water with the proboscis among the eggs. The loss of mating opportunities for male back-brooders is not experienced by *Lethocerus* males because multiple females may be attracted to a guarding male, mate and contribute to the clutch size under his tender

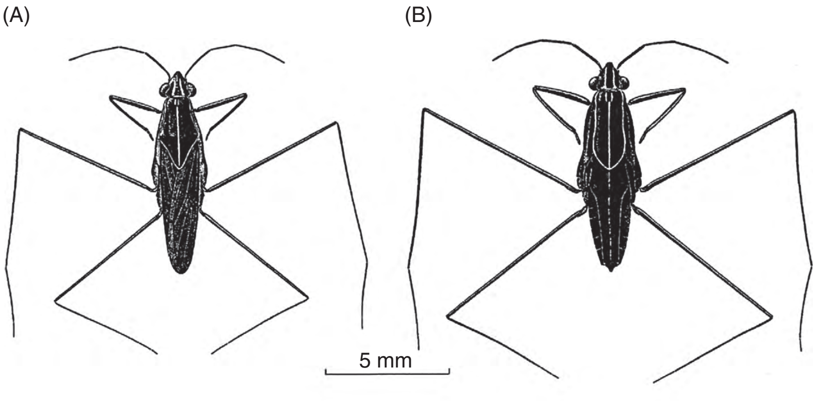


Figure 10.3 The Australian species of water strider, *Limnogonus luctuosus* (Hemiptera: Gerridae), with the smaller macropterous morph (A) and the larger apterous morph (B). Drawing by S. Monteith. From Naumann 1991. Reproduced by permission of CSIRO Australia © CSIRO.

care. So *Lethocerus* provides a stepping stone to the back-brooding type seen in the genera *Abedus* (Figure 10.1), *Belastoma* and others. Back brooding opened opportunities for exploiting habitats without emergent vegetation, and with running water, thereby extending the range of the adaptive radiation.

Smith has been studying giant water bugs for about 40 years; much of his work is captured in his 1997 paper, but new knowledge is developing (e.g., Lytle and Smith 2004). The scope of this long-term study illustrates the advantages of broad comparative research on a group, including life-history variation, phylogenetic relationships and the assimilation of a large range of subjects into the understanding of a remarkable and rare phenomenon: uniparental postzygotic parental care by male insects. The many questions raised by this unusual characteristic have been answered.

We can observe in the Nepoidea cladogram that several either-or options developed in the evolutionary divergence of the group. Stay smaller, as in the Nepidae, but rely on respiratory horns for increased gas exchange in water. Or grow larger, as in the Belastomatidae, requiring larger eggs with higher oxygen demand, and brooding. In the Lethocerinae adaptations moved in the direction of brooding on emergent vegetation, and in the Belastomatinae back brooding evolved. The consistency of types within subfamilies suggests that alternatives were unlikely to be adaptive, and variation within families was limited: polymorphisms incorporating alternative life histories in a mixed strategy have not been observed. Instead, evolution seems to have been constrained by phylogenetic divergences early in the radiation of the group. However, life histories in many other insects show variation within species and within populations, as the examples that follow illustrate.

10.3.3 Comparisons among and within species: water striders

Water striders (Hemiptera: Heteroptera: Gerridae) skim over water surfaces, preying on any hapless insect trapped in the water, and on each other. The Australian species *Limnogonus luctuosus* illustrates a common occurrence in the family in having both winged, **macropterous**, and wingless, **apterous**, females (Figure 10.3). This dimorphism provides different advantages and disadvantages for each morph – every adaptation has its own constraints. The dimorphism provides a good example of trade-offs in life-history evolution. The winged form (Figure 10.3A) is smaller-bodied, having allocated resources to wings, the flight musculature and a strong thoracic housing adapted for flight. Consequently it can fly and colonize new water bodies, escaping local competition and drying ponds; this we can assume is at the expense of increased time to first reproduction and perhaps reduced reproductive effort. The apterous form (Figure 10.3B) is clearly larger than the winged morph and, without the expense of wings and associated adaptations, we predict that it develops faster to reproductive age, it is larger and may devote more resources to reproduction, but the cost is inability to escape from drying water bodies and competition, and a strict limitation on migration, which must be cursorial. Morph differences in total fecundity will be re-examined in the next example.

Similar trade-offs have been observed in gerrids around the world. In Alberta, Canada, four species coexist in ponds and all express the fully winged, macropterous morph (Spence 2000). However, once the bugs fly from terrestrial overwintering sites to ponds where they breed, flight muscles undergo histolysis, with the large energy source contributing to costly egg production. The species differ in both timing and rate of histolysis, with *Gerris pingreensis* rapidly reducing flight muscles, and *G. buenoi* doing so more slowly, while histolysis occurs much later in other species (Figure 10.4). Females with this early-histolysis strategy produced more eggs early in the reproductive season (see May 15), relative to those showing no early histolysis (by 34% in *G. pingreensis* and 26% in *G. buenoi*). These significant advantages are obviously a trade-off with migratory ability, and the ability to escape drying ponds. This example illustrates species differences and changes within species through the season.

Some equivocation was expressed earlier regarding the Australian gerrid species *Limnogonus luctuosus*, when we stated that the winged morph suffers a cost, *perhaps* of reduced reproductive effort, and the apterous morph *may* devote more resources to reproduction. These are the directions predicted by conventional wisdom on trade-offs, but are they supported by data, and are the costs and benefits either in the short term or the long term (i.e., lifetime)? Lifetime fecundity has been only rarely measured for gerrids, but it is an essential statistic for resolving the debate on costs and benefits of wing polymorphism. However, Spence (1989) collected the relevant data on the same species discussed above, *G. pingreensis* and *G. buenoi* (Table 10.1). The notable result was that lifetime fecundity did not differ significantly between morphs in either of the species, nor did survival. Differences did occur in early egg

Table 10.1 **Comparison of wing morph egg production in *Gerris pingreensis* and *G. buenoi* in central Canada. Data from Spence 1989**

Trait	Apterous morph	Macropterous morph
	Gerris pingreensis	
Egg production		
Total lifetime fecundity	202 eggs	192 eggs
First 10 days	57 eggs[a]	24 eggs[a]
First 20 days	134 eggs[a]	84 eggs[a]
Survival	34 days	35 days
Preoviposition period	3.6 days[a]	5.5 days[a]
	Gerris buenoi	
Egg production		
Total lifetime fecundity	148 eggs	122 eggs
First 10 days	44 eggs[a]	18 eggs[a]
First 20 days	106 eggs[a]	71 eggs[a]
Survival	27 days	25 days
Preoviposition period	5.1 days[a]	8.4 days[a]

[a] Comparisons between morphs were significant at the $P < 0.05$ level or less

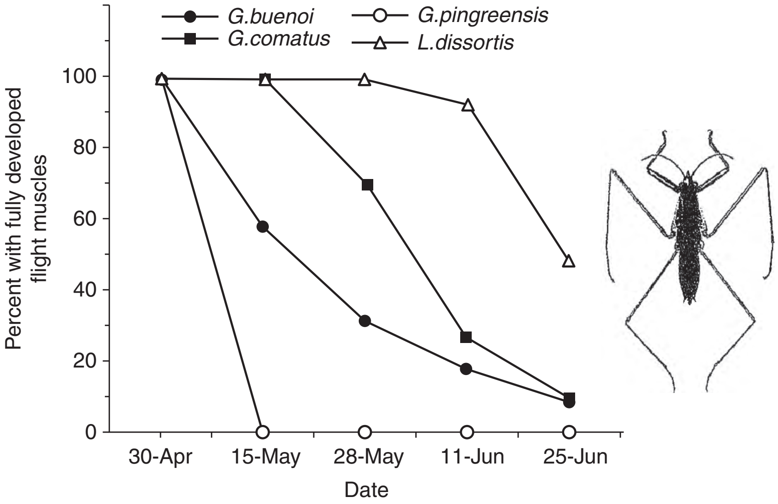


Figure 10.4 Dates of sampling flight muscle condition in four sympatric water-strider species in the genera *Gerris* and *Limnoporus* in Alberta, Canada. Loss of fully developed flight muscles through histolysis, making energy available for oogenesis, was very rapid in *G. pingreensis*, and slower in the other species. From Spence 2000.

production and in the length of the preoviposition period, with the apterous morph producing many more eggs in the first 10 days of adult life than the macropterous morph, and also starting oviposition earlier in the season. Thus, a trade-off between morphs was established, although not the one that is generally expected. The trade-off was also a short-term rather than a long-term, or lifetime, deficit in fecundity for the macropterous morph, but obviously the apterous morph suffered the potential lifetime disadvantage of lacking wings. Given no reduction in survival, the deficit of reduced dispersal ability would be traded off against the benefits accruing from greater early reproductive effort, but these are difficult to measure. We will examine the effects of time of reproduction in a later section of this chapter, showing how time of reproduction has a strong effect on the rate of growth of a lineage.

Many gerrid populations express only, or mainly, a single wing morph: **monomorphism**. Thus, the mix of wing morphs is clearly selected for under differing habitat conditions, although other factors such as diapause, and overwinter survival, need to be integrated into a full understanding of wing polymorphism patterns over a landscape (see Spence 1989). We cannot understand the variety of life-history strategies of any species without knowledge of the habitats they occupy. This is well illustrated by Vepsäläinen's (1978) study of European *Gerris* species, which occupy various aquatic habitats: some freeze in winter, some dry rapidly, and others are permanent; some landscapes provide low isolation among water bodies and some high isolation. Vepsäläinen compared species and populations in Finland at 60° N and Hungary at 47°, finding variation in life-history traits between species, between populations and within populations. Some populations illustrated genetic dimorphisms and others seasonal dimorphism – **polyphenism**: within populations a temporary, environmentally induced change in morph type (Table 10.2). (But individuals do not change their morph.)

Some species (Type I) are monomorphic for long wings (LW), having only the macropterous morph, and individuals are capable of flight and dispersal throughout their adult lives (Table 10.2). Type II species showed seasonal polyphenism with flying, long-winged individuals in the overwintering generation and short-winged (SW), flightless females in the summer generation in Finland, and dimorphism in Hungary. Still others were genetically dimorphic (Type III), and two species were monomorphic for short wings (Type IV).

Table 10.2 **Wing-length patterns of *Gerris* species studied in southern Finland (about 60° N latitude) and Hungary (about 47° N latitude)**

Wing-length pattern	Winter = diapause generation (univoltine populations)	Summer = non-diapause generation of multivoltine populations		Additional notes
		Finland	Hungary	
I. *LW* monomorphism				
G. rufoscutellatus	*LW*	*LW*	*LW*	*SW* known
II. Seasonal dimorphism (seasonal polyphenism)				
G. thoracicus	*LW*	*SW*	*LW*	Type I in Hungary
G. odontogaster	*LW*	*SW*	Dimorphic	
G. argentatus	*LW*	*SW*	Dimorphic	
G. paludum	*LW*	*SW*	Dimorphic	
III. Permanent dimorphism (genetic polymorphism)				
G. lacustris	Dimorphic	*SW*	Dimorphic	Partially Type II
G. lateralis	Dimorphic	?	–	
G. asper	Dimorphic	–	?	
IV. *SW* monomorphism				
G. najas	*SW*	–	?	Dimorphic in Poland
G. sphagnetorum	*SW*	?	–	*LW* unknown

LW = long-winged; *SW* = short-winged; ? = not known; – = does not exist. From Vepsäläinen 1978.

Under what environmental conditions does natural selection result in these different life-history strategies? The template over the landscape onto which these species fit is defined by the permanency of the water body and their isolation (Figure 10.5). In large, permanent lakes, remote from others, populations will be monomorphic and short-winged (Type IV), because the high risk of long-distance travel has selected against flight. Where ponds have a low permanency and low isolation, long-winged morphs are essential for survival of a lineage (Type I). Between these two extremes, the conditions under which most species live, dimorphism is the most adaptive strategy (Types II and III). The intraspecific

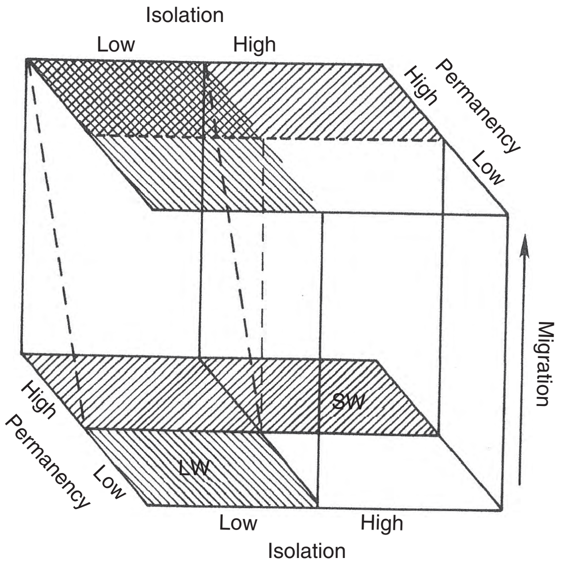


Figure 10.5 The relative predictability and isolation of habitats for *Gerris* species, which select for the wing-length patterns shown in Table 10.2. For example, high permanency and high isolation select for short-winged (*SW*) monomorphic populations, while low permanency and low isolation select for long-winged (*LW*) monomorphic populations. The effect of migration (on the vertical axis) results in mixing of populations, as in the crosshatched area in the upper left-hand corner. From Vepsäläinen 1978.

differences observed in the Type II species between Finland and Hungary are thought to relate to the latitudinal gradient of precipitation and temperature, with Hungary drier and hotter, and therefore water bodies are less predictable and more ephemeral. This would select for a summer generation that retains at least some long-winged morphs. In Finland there is time for a short-winged generation to mature and breed before migration is necessary.

10.3.4 Comparisons within populations: the pitcher-plant mosquito

Alternative reproductive strategies are commonplace among insects, with allocation of time and energy, costs and benefits, and trade-offs entering into each adaptive move in a lineage. The pitcher-plant mosquito, *Wyeomyia smithii* (Diptera: Culicidae), widespread in North America, has proved to be an excellent subject for the study of variation in life-history traits (e.g., Armbruster *et al.* 2001, Bergland *et al.* 2005, Ragland and Kingsolver 2008). The mosquito breeds in water held within pitcher plants, *Saracenia purpurea*, which are distributed from the Gulf of Mexico north to Labrador and across to Saskatchewan. These small amounts of water are susceptible to freezing at unpredictable times in northern latitudes. Therefore, an interesting question becomes, "How do life histories evolve to result in survival sufficient to maintain populations under conditions in which the environment can change rapidly, necessitating the development of diapause before freezing conditions prevail?"

One answer is to evolve with a **mixed reproductive strategy** or a **bet-hedging strategy** (Stearns 1976), which is what Istock (1981) found for *Wyeomyia smithii* in a bog near Rochester, New York State, in the USA. There existed considerable genetic variation in development time and diapause within the population, the characters being correlated to produce fast-developing and diapause-resisting phenotypes, ranging to slowly developing and diapause-prone phenotypes (Figure 10.6). The population included genotypes expressing continuous variation, with phenotypes that ranged from **univoltine** to **multivoltine**. The "fast" extreme produced several generations per season, the "diapause" extreme one generation per season, and a mixed strategy was maintained by matings among the two extreme genotypes. The mixed strategy resulted in some diapausing individuals being produced in the second generation, and some that did not diapause, but instead reproduced for another generation.

The potential net reproductive rate per season, R_s, differs dramatically among the genotypes (Figure 10.6, potential R_s), but which strategy proves

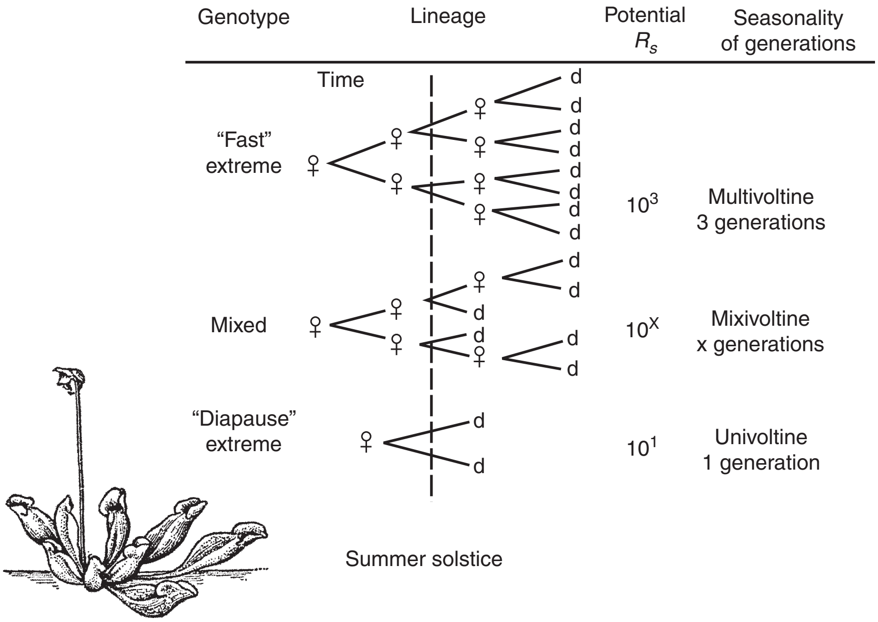


Figure 10.6 Lineages of the pitcher-plant mosquito, *Wyeomyia smithii*, from Kennedy Bog in New York State, illustrating three types of lineage: the "fast" extreme, an intermediate mixed genotype and the "diapause" extreme. The letter "d" shows the production of diapausing females in a lineage. From Istock 1981.

to be the most effective in a given season depends on the weather. If the season is long and food is abundant then the "fast" extreme will leave most progeny at the end of the season. If the season is short and food is scarce the "diapause" extreme will leave most progeny. A moderately long season, which is likely to occur in many years, will favor the mixed-strategy lineages. The simplest explanation for the maintenance of this genetic polymorphism is that the extreme genotypes are homozygotic and the mixed genotype is heterozygotic, and the polymorphism is maintained by a heterogeneous physical environment with unpredictable breeding-season length, in which all strategies succeed some of the time. A theoretical study reached a similar conclusion in which prolonged diapause of more than one winter promoted invasion only when environmental stochasticity was high (Mahdjoub and Menu 2008).

The apparent common feature of the comparisons of life histories discussed so far is that key resources have been identified and characterized, and these form a template on which life histories evolve (e.g., Southwood 1977, 1988, Spence 1989). The term **habitat template** is used in ecology as in industry, as a pattern or guide, but in the evolutionary sense the template provides a pattern of resources in the environment, and a guide to the necessary adaptive trajectories in a lineage which promote fitness. We saw this in the example of parasitoid wasps and flies where the host survivorship curve provided a pattern of resources much too diverse to be exploited by a single species, so each parasitoid adapts to a small segment within the habitat template. With the giant water bugs, the opportunity to exploit larger prey selected for larger eggs, which needed efficient aeration, so the habitat template can be viewed as prey size, or oxygen levels in air and water. The other examples, of water striders and the pitcher-plant mosquito, also involve aquatic insects, clearly because water is a critical resource, and the habitat template is formed by discrete bodies of water which are ephemeral or permanent, small or large, and grouped or distant, all providing a variety of opportunities for various strategies of exploitation to evolve. The cases discussed illustrate the identification of highly variable resources and the life-history responses of a group of species or populations.

10.4 Adaptations, constraints, trade-offs, resource allocation, costs and benefits and alternative strategies

We have seen in the previous section on comparative life-history studies that adaptations are compromised by constraints. With limited resources, a species will evolve to allocate these resources in an optimal manner, without ever achieving "perfection." Allocation to flight is likely to detract from resources for reproduction, or reduced wings and flight muscles reduce the cost of flight and migration with the benefit of increased energy for reproduction. Therefore, the terms adaptations, constraints, and costs and benefits are all employed to convey the idea of inevitable limits on the adaptive strategy, for it will be balanced or compromised by other competing needs in the evolution of the lineage.

Dispersal polymorphism is probably the most extensively studied example of trade-offs in the insect literature (Zera and Denno 1997). Polymorphism is observed in wing size from fully winged, macropterous forms, to brachypterous or apterous morphs, accompanied by allocation to strong flight muscles associated with macroptery, and small or vestigial flight muscles in the brachypterous or apterous morphs. Such polymorphism is widespread in the insects, including Orthoptera, Psocoptera, Thysanoptera, Homoptera, Heteroptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera (Zera and Denno 1997).

Costs and benefits are inevitably associated with these dispersal polymorphisms. A common correlation with the benefit of effective flight ability is the cost of reduced fecundity and increased age at first reproduction. In the water striders discussed above there was a short-term reduction in fecundity (but not lifetime fecundity), and a delayed start to oviposition in the season compared to the apterous morph (Spence 1989). The alternative strategy of greatly reduced allocation to flight commonly results in the benefits of increased fecundity and an advanced start to reproduction, but the cost is a lifetime without migratory ability and all the consequences that this may entail. Flight and migration themselves are risky strategies with fitness costs because individuals become more conspicuous to predators, and destinations are probably unpredictable, or hard to find, and of variable quality (Roff and Fairbairn 2007). The negative effects of strong allocation to flight compete with limited internal resources for reproduction, both of which are energetically expensive. This competition has frequently resulted in temporal separation of the two activities in macropterous morphs, recognized as the flight-oogenesis syndrome (see Section 2.4 on Survival, Zera and Denno 1997).

While the cost-benefit trade-off in dispersal polymorphisms for females has been generally clear enough, males of some species also show wing polymorphism, so an explanation is needed. Studies on the planthopper *Prokelisia dolus* (Hemiptera: Delphacidae) showed that brachypterous males gained several advantages compared to macropterous males, in stable habitats in which migration was not important, and female brachypterous morphs were common:

(1) Brachypterous males were able to obtain 77% of matings with brachypterous females.
(2) Brachypterous males were effective in displacing macropters during courtship.
(3) There was a small tendency of brachypters to arrive before macropters at the site of calling females.
(4) Brachypterous males sired more progeny per female than macropters, indicating that sperm load was larger in the short-winged males.

Macropterous males had a mating advantage with macropterous females, and they retained migratory ability if conditions deteriorated. Survival of both male morphs was about the same (Langellotto *et al.* 2000).

In this planthopper, *Prokelisia dolus*, vegetation structure also played a role in the costs and benefits of alternative wing morphs in males (Langellotto and Denno 2001). Winged males were more successful at locating females and mating with them in sparse vegetation, and at low densities, while flightless males were more effective in dense vegetation and at high female densities. Of course, both morphs could hop, but it appears to be a better method of locomotion than flying in dense vegetation.

Another form of investment trade-off was identified by the Denno research group, involving the ability to disperse and to ingest plant sap (Huberty and Denno 2006a, b). Rather than dispersing as plant quality declined, *Prokelisia dolus* engaged in compensatory feeding, made possible by a relatively large cibarial pump illustrated in Figure 4.5B (see also accompanying text). Increased feeding mitigated the impact of declining plant nutrients, enabling members of this species to remain in a patch, while its congener with a smaller cibarial pump, *Prokelisia marginata*, was driven to seek richer pastures.

Eggs are expensive to produce for a female, providing the expectation that checks and balances will be evident in the evolution of life histories. This was explored for parasitoids early in this chapter using the ovigeny index: recall that it ranged from 1 to 0, with 1 indicating completely pro-ovigenic females, and 0 representing complete synovigeny. Jervis *et al.* (2005, see also Jervis *et al.* 2007) then applied the concept to Lepidoptera and other orders, showing that trade-offs involved with egg-maturation strategies were commonplace in between-species comparisons. A dichotomy in allocation was recognized as between soma, or the capital investment in the body of the insect (“body building”), and non-soma, which is invested in reserves ultimately allocated to eggs and somatic maintenance. In fact, eight correlations were noted as follows, and all make intuitive sense:

(1) As the ovigeny index (OI) increases the allocation to soma decreases, supported in the Trichoptera and Hymenoptera.
(2) As OI increases the reliance on adult feeding declines, observed in the Hymenoptera and Lepidoptera.
(3) As OI increases the degree of polyandry decreases, as do nuptial gifts such as spermatophores, seen in the Lepidoptera.
(4) As OI increases resource reallocation declines, such as egg resorption and histolysis of thoracic muscles, noted in the Hymenoptera and Lepidoptera.
(5) As OI increases life span decreases in the Trichoptera, Hymenoptera and Lepidoptera; a cost of early reproductive effort – or is it that once eggs are all laid early in life, prolonged life is superfluous, with no adaptive value?
(6) When OI is one, female winglessness increases in frequency coupled with a lower probability of adult feeding in the Lepidoptera.
(7) As OI increases female mobility in winged Lepidoptera decreases.
(8) As OI increases larval diet breadth increases in the Lepidoptera, meaning that oviposition strategies are generalized when OI is high, and more specialized when OI is low. Clustering eggs also correlated with high OI.

This list of alternative strategies may seem remarkable, but they are more-or-less inevitable. Cody (1966) called the partitioning of resources that promoted fitness the **principle of allocation**. Energy, nutrients and time are allocated as efficiently as possible, depending on the species involved and the environmental conditions that prevail. But the concept of allocational trade-offs is much older, with a lengthy history recorded by Rensch (1959), under the concept of **material compensation**. Matsuda (1979) provided examples such as the inverse relationship between wing size and hind-leg size in several insect orders, and trade-offs are discussed extensively in textbooks such as Roff (1992), Stearns (1992), and Stearns and Hoekstra (2000).

10.5 Hypotheses on fecundity variation

With the variations in life histories discussed above, and the many others in the literature, we should wonder if any generalizations can be reached about such a basic life-history trait as fecundity. Let's consider a few hypotheses.

Any hypothesis on such a broad topic as fecundity variation, applicable to all insects, or all organisms, is fraught with difficulties. Simple generalizations cannot cover the wide variations seen in nature, because so many factors interact to define the final result – such as fecundity in a species and its variation. So perhaps it is wiser to consider "**explanatory frameworks**," which outline the ways to approach a certain question in ecology or evolutionary biology (Vepsäläinen and Spence 2000, p. 211). This approach is perhaps more suitable for addressing variation in fecundity rather than expecting general hypotheses to pertain. The latter approach has resulted in much debate, dissatisfaction and even a tendency to reject hypotheses based on one or two studies. Therefore, raising awareness about the ways we might consider fecundity variation appears to be a more positive approach to addressing the relevant questions. However, we retain the term hypothesis for each argument because this is how they are named in the literature.

10.5.1 The balanced-mortality hypothesis

We have seen in Chapter 8 on parasitism that parasitoids in the families Ichneumonidae and Tachinidae show clear trends in fecundity variation (Figure 8.4). In these families ovariole number correlates well with total fecundity, and more is known about ovariole number than total fecundity, so the former character works well as a surrogate for fecundity (Price 1975a). In Figure 8.4 we see that high fecundity occurs when parasitoids attack early stages of the host. Internal parasitoids that emerge from a late instar larva are inevitably exposed to the typical mortality factors that shape the survivorship of the host insect, which generally result in high death rates. High fecundity appears to balance or trade off against the high mortality within the host. This has been called the **balanced-mortality hypothesis** (Figure 10.7). This idea that egg production is adapted to balance the hostility of the environment in which a species lives has a long history (e.g., Rensch 1938, Cole 1954). For example, Cole stated that the high fecundity frequently observed among parasites is an adaptation enabling survival when a high probability of death prevails. At the other end of the host survivorship curve, the host may be in a cocoon, or protected in wood, facing low mortality before it emerges as an adult. The parasitoid attacking such stages is equally protected, with a low mortality rate. The host is hard to find, but safe, so parasitoids leave relatively few progeny, but with a good prospect of survival (Figure 10.7).

It could be argued that mortality balances fecundity. Large numbers of small eggs produce individuals that are more likely to die during the life cycle than those deriving from a small number of large eggs. We cannot distinguish the two hypotheses without knowing the primitive state and the trajectory of the adaptive radiation. In the parasitoid example, at least, those with low fecundity attacking late larval instars or pupae are considered to be primitive. Then as species radiated up the host-survivorship curve, fecundity would have to increase to balance the inevitable mortality to be incurred.

10.5.2 The bet-hedging hypothesis

The case of the pitcher-plant mosquito just discussed provides a good example of a bet-hedging strategy. The potential net reproductive rate in a season, R_s, is reduced in some genotypes as a safety precaution against the early onset of inclement weather. On the

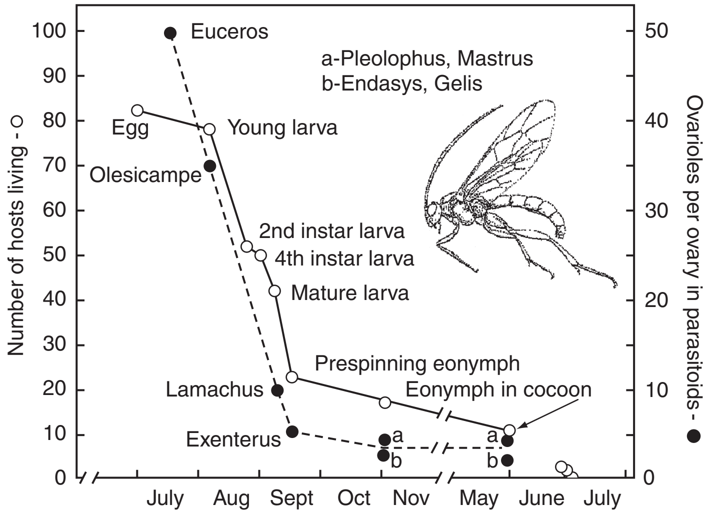


Figure 10.7 A typical survivorship curve of the host, the Swaine jack pine sawfly, *Neodiprion swainei* (open circles and solid line, from McLeod 1972), and the number of ovarioles per ovary in parasitoids attacking this host (solid circles and dashed line), plotted in synchrony with the time at which each species most commonly attacks the host. From Price 1974. The number of ovarioles per ovary correlates closely with total fecundity (see Figure 8.4). For example, the *Euceros* species with 50 ovarioles is estimated to lay about 1000 eggs on foliage, while *Pleolophus* species with four ovarioles per ovary lay about 30–40 eggs into host cocoons (Price 1975a).

other hand, the one-generation-per-season strategy misses breeding opportunities in a long, favorable season. Hence, a mixed strategy is optimal (Stearns 1976). In general then, spreading reproductive effort over a long period spreads the risks of mortality and reduces adult allocation to reproductive effort at any one time, probably increasing adult survival.

10.5.3 *r*- and *K*-selection

MacArthur and Wilson (1967) reasoned that reproductive strategies would differ according to the stability and predictability of the environment. In harsh, unstable environments well north and south of the equator or on mountains, ***r*-selection** will maximize reproductive rate. Populations are likely to be kept well below the carrying capacity by adverse conditions, so that having high *r* is adaptive, but despite having explosive growth potential populations will rarely if ever reach the carrying capacity, *K*, of the habitat. Therefore, high fecundity with no parental care will prevail, and population growth will typically be expressed as in the lower half of the logistic growth curve, before the onset of competition (Figure 9.1), and well below *K*. The contrasting extreme is represented by ***K*-selection**, or selection that adapts a species to living close to the carrying capacity of the environment. Under conditions of high competition and perhaps predation, selection will favor individuals that protect their young, and otherwise invest highly in individual progeny. Allocation of parental care inevitably is accompanied by the trade-off of reduced fecundity, and delayed further bouts of reproduction, as in the male giant water bugs discussed in this chapter. The *K*-selected strategy should be expected in the tropics with stable environmental conditions in which reproduction can continue over several generations, such that the carrying capacity of the habitat is reached. Further population growth is unlikely, but maintaining a lineage through time has its own challenges because of competition and predation. Biotic forces generally predominate in *K*-selecting environments, and abiotic influences prevail in *r*-selecting environments.

The *r*- to *K*-selection continuum has been invoked many times in the literature, often with examples that do not fit the contrast. However, the fact that the hypothesis is used frequently indicates its heuristic value in providing a conceptual framework with which to approach questions about life-history strategies. The hypothesis is also simplified sometimes to contrast just high and low fecundity species, when actually much information is needed before applying the scenarios to any particular example. At least the following five characteristics must be considered:

(1) The relative stability of environmental conditions.
(2) The reproductive rate of the species, *r*.
(3) The carrying capacity, *K*, of the environment relative to mean population density.
(4) The probability of intra- and interspecific competition.
(5) The importance of natural enemies.

As Vepsäläinen and Spence (2000, p. 211) have said, "The most useful generalizations are explanatory frameworks, which are road maps to solutions, rather than solutions themselves." Each particular case studied is likely to yield a unique set of selective factors impacting life histories, but the scenarios discussed in this provide a range of factors needing attention.

10.6 Timing of reproduction

Time is an aspect of the habitat template apparent in the examples of life-history strategies we have discussed. When to reproduce, and how soon to reproduce, are as critical in insect life histories as is the question of how much resource to devote to reproduction. We next consider some general aspects of reproductive timing.

10.6.1 Semelparity vs. iteroparity

In the last chapter on demography, we defined *r* as the rate of change per individual, or the per capita instantaneous rate of change in the population. For population modeling purposes *r* is a useful variable because the population in the next generation can be readily calculated based on any given average clutch or litter size, or population size.

Life-history variation is extensive among, and often within, species, suggesting that *r* is highly variable in nature. We may then consider the effects of natural selection on *r* and how it may be influenced by clutch size and time of reproduction. A classic paper by Cole (1954), "The population consequences of life history phenomena," enters into this field of inquiry.

One of Cole's questions was how breeding once in a lifetime, called **semelparity**, or single breeding, compared to breeding more than once in a lifetime: **iteroparity** or repeated breeding. Many insects lay all their eggs at one time in a single clutch, such as cecropia moths, gypsy moths and bagworms, all of which have short adult lives, and one generation per year. They are excellent examples of semelparity. Other examples include annual plants, century plants (*Agave* species) and bamboos, which reproduce at the end of their lives. Hence, we see that semelparity is associated with many species of short-lived adults and relatively short life cycles, and long-lived plants which mature only to die soon afterwards. Although a number of selective factors probably influence the diversity in the life history of semelparous insects and plants, we will concentrate on why insects are so often semelparous.

Cole modeled the relationship between the clutch (or litter, or brood) size of a semelparous species needed to match *r* of an iteroparous species (Figure 10.8). The iteroparous species is assumed to breed indefinitely. For example, females of an iteroparous species might start to reproduce at day 30 and lay 100 eggs ($b = 100$) in each brood. Then Cole could calculate how many eggs a semelparous species would have to lay to achieve the same

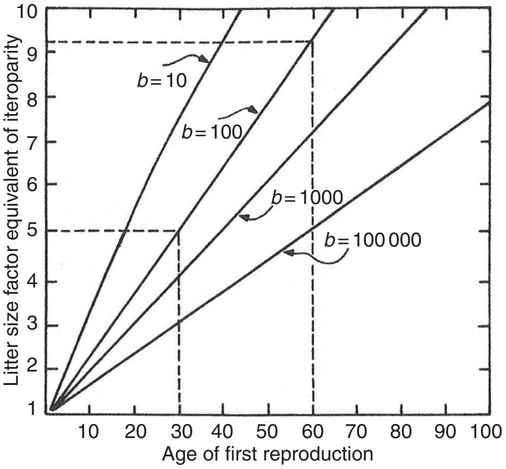


Figure 10.8 The factor by which litter or clutch size must be increased to achieve in a single reproduction the same intrinsic rate of increase, *r*, that would result from indefinite iteroparity. $b =$ brood size of an iteroparous species. The ordinate axis gives the factor by which this must be multiplied. From Cole, L. C. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* **29**:103–137. © 1954 by the University of Chicago. All rights reserved.

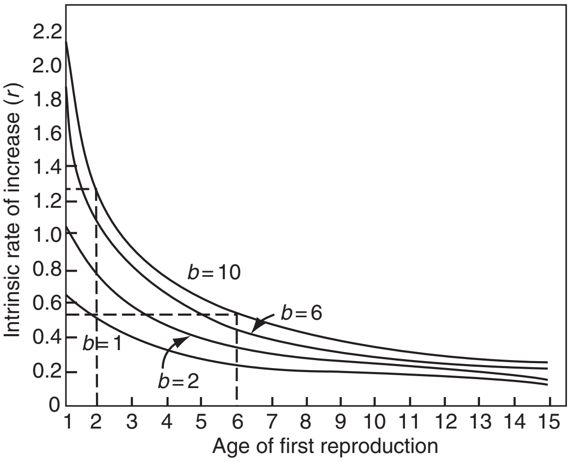


Figure 10.9 The effect of changing the time of first reproduction on the intrinsic rate of increase, *r*, of a population. $b =$ brood size of an indefinitely iteroparous species where a brood is produced at every time interval after first reproduction. From Cole, L. C. 1954. The population consequences of life history phenomena. *Q. Rev. Biol.* **29**:103–137. © 1954 by the University of Chicago. All rights reserved.

population growth rate: $100 \times 5 = 500$ eggs (see dashed lines in Figure 10.8). Several semelparous insect species lay clutches of eggs at around this number: gypsy moth, 750 eggs; satin moth, 650 eggs; fall webworm, 600 eggs; mountain mahogany looper, 350 eggs; pine tussock moth, 300 eggs (e.g., Price 2003a). Another example uses the age at first reproduction as 60 days for an iteroparous species and laying 100 eggs per clutch. For an equivalent population growth a semelparous species would then have to lay 925 eggs in one clutch (Figure 10.8).

With many insect and plant species having annual life cycles, semelparous breeding and high fecundities, Cole reasoned that semelparity would normally have a strong selective advantage over iteroparity. The effect of iteroparity on population growth must be negligble in these kinds of species. For example, if an iteroparous insect species produces 30 eggs in each annual bout of reproduction, a semelparous species would have to produce only 31 eggs in a single clutch to achieve the same rate of population growth. In effect, that one extra egg matures and takes over the reproductive role of the iteroparous female producing a second clutch in a second breeding cycle. With only 30 eggs per clutch, the increase in *r* of an iteroparous species will be less than 1%, making the cost of one extra egg per clutch minute compared to the cost of an extended life and repeated bouts of laying 30 eggs in each breeding season.

Another factor examined by Cole (1954) was the effect of age at first reproduction on population growth, a consideration relevant to the nutritional ecology of insect herbivores which influences age at maturity, and the time to reproduce in water striders, and many other species with only relatively short breeding seasons available. For example, when the brood size is 10 ($b = 10$) the intrinsic rate of increase at time 2 is more than double than when age at first reproduction is at time 6 (Figure 10.9; at 2, $r = 1.29$; at 6, $r = 0.52$). Of course, time of reproduction is

Table 10.3 **Hypothetical life table for an insect population in which maximum longevity is 5 months. R_o = net replacement rate. From Price 1975b**

Age at beginning of interval, x	Age specific survivorship, l_x	Expected daughters, m_x	Reproductive expectation, l_xm_x
0	1.0	0	0
1	0.8	0	0
2	0.5	3	1.5
3	0.3	2	0.6
4	0.1	0	0
5	0	0	0
	Gross reproductive rate	= 5	$R_o = 2.1$

affected by many factors, such as seasonality in temperate latitudes, but all else being equal, life histories are likely to evolve toward the earliest possible time of reproduction in iteroparous species.

10.6.2 Selection on time of reproduction

Another consideration in the evolution of life histories is the effects on population growth of small changes in factors such as age at first reproduction and time of peak reproduction, which may occur as one species colonizes different habitats with different selective regimes. For example, a colonizing species may arrive at a vacant resource, perhaps an island empty of competitors, with different selective pressures compared to those in the parental population.

This kind of species was modeled by Lewontin (1965) who used the shape of the l_xm_x, **reproductive expectation** relationship of a cohort, where l_x is the age specific survivorship (see Table 9.1) and m_x is the expected number of female progeny that will be produced at age x by a female that is still alive at age x (e.g., Table 10.3). Summing the values in the reproductive expectation column, l_xm_x, provides an estimate of R_o, the **net replacement rate**, defined as the number of females that replace an average female in the course of a generation. The shape of the l_xm_x relationship is likely to be roughly triangular, as illustrated by the numbers in Table 10.3, and defined by the age at first reproduction (A), the age at peak reproduction (T), and the age at the end of reproduction (W) (see also Figure 10.13). This defines the **reproductive function** (V_x) of a population, being the shape of the l_xm_x relationship (Figure 10.10).
By varying the position of the reproductive function

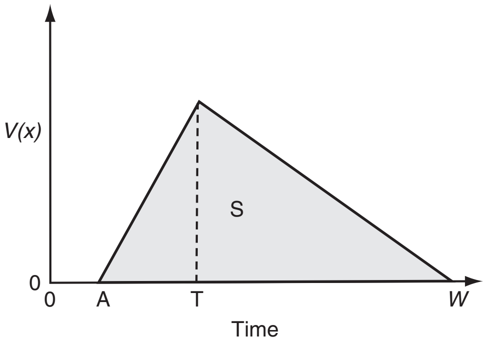


Figure 10.10 A generalized triangular reproductive function, $V_{(x)}$, which represents the l_xm_x curve of a cohort. A = age at first reproduction; T = age at peak reproduction; W = age at last reproduction; S = total number of offspring produced – the total shaded area in the triangle. From Lewontin 1965.

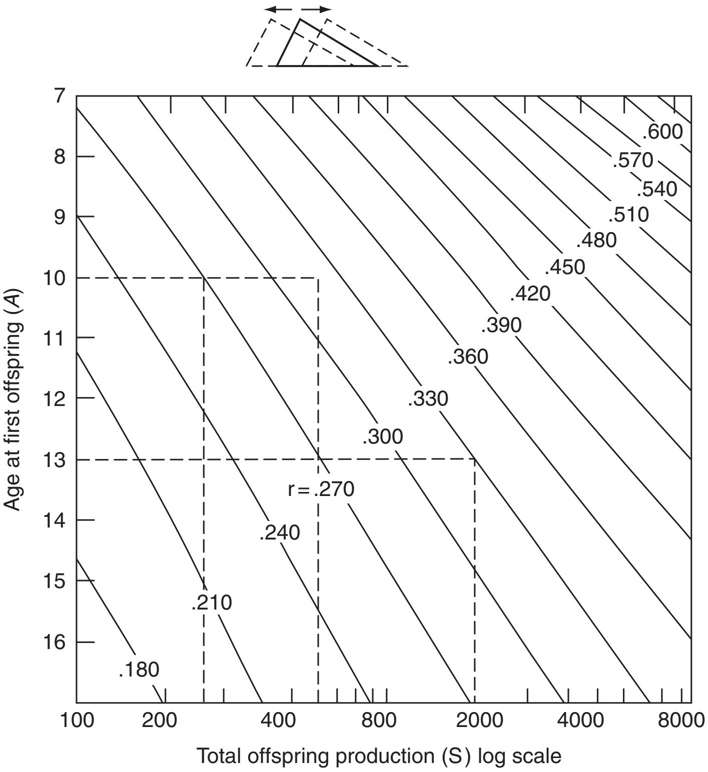


Figure 10.11 The effect of changing the age at first reproduction, *A*, on the intrinsic rate of increase, *r*. Solid lines give equal *r* values for changing *A* and *S*. The change in the reproductive function is given above the graph. From Lewontin 1965.

in time and by changing its shape, Lewontin could compute their effects on *r*. In this way he could compare the relative advantage of increased fecundity of a certain number of eggs as opposed to greater longevity. Or he could ask how much fecundity would have to increase to raise *r* from 0.27 to 0.30. These kinds of comparisons illustrate the directions in which natural selection may move the traits of a population as selective regimes change during colonizing episodes.

One obvious question is about the effect of changing only the time of first reproduction: keeping the shape of the reproductive function constant, but advancing the time of first reproduction (Figure 10.11). Perhaps natural selection may work to advance the time of first reproduction by 3 days, say from day 13 to day 10. What would be the effect on population growth? Keeping fecundity constant at 600 eggs, for example, the rate of increase improves from 0.27 to almost 0.33 (see dashed lines in Figure 10.11). Also, if selection worked on fecundity, a rate of increase of 0.27 could be achieved with only 260 eggs instead of 600 eggs, if the age of first reproduction were reduced from 13 to 10 days (see Figure 10.11). This would constitute a major economy in egg allocation resulting from advancement of the start of reproduction. If reproduction started at day 13, and *r* was increased from 0.27 to 0.33, the number of female progeny needed would have to be 2000 (see Figure 10.11). Contemplating evolutionary shifts in this way illustrates that relatively small changes in fecundity or timing can have considerable impact on the probable population growth in a colonizing population.

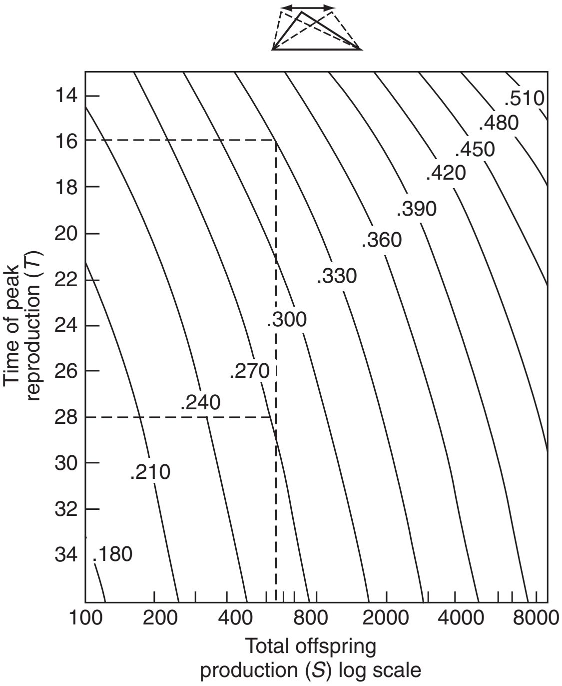


Figure 10.12 The effect of changing the time of peak reproduction, *T*, on the intrinsic rate of increase, *r*. Solid lines provide equal *r* values for changing *T*; *S* does not change. The change in shape of the reproductive function is given above the graph: *T* changes, but *A* and *W* remain unchanged. From Lewontin 1965.

Another example compares changes when *A* and *W* remain the same but *T* changes (Figure 10.12). Advancing the peak of reproduction from day 28 to day 16, *r* increases from 0.27 to 0.33, indicating a probable selective advantage to moving the peak of reproduction forward. This will be independent of the advantage of higher survival to earlier time units of *x*. For example, moving up one unit of time in Table 10.3, from first reproduction at interval 2 to interval 1, would increase R_o from 2.1 to 3.4 $((0.8 \times 3) + (0.5 \times 2) = 3.4)$.

These classic papers by Cole and Lewontin exemplify the kinds of ways we can think about life-history evolution, and the paths that cohorts undoubtedly follow in nature. Unfortunately, there is very little information on how specific insect populations evolve through time as conditions change or as they move from one locality to another in nature.

Life-history studies remain a very active field in ecology and evolutionary biology. No longer is the field easily assimilated as it was in the 1970s and early 1980s, for there are now hundreds of papers published each year across a broad range of journals, covering a very diverse range of subjects. Also, as is usual in the evolution of ecological topics, the kinds of traits studied in a life-history context are becoming more detailed and narrowly conceived. Just a few examples are provided here to illustrate some of the research avenues.

Brook trout were shown to be significant agents of natural selection on life-history traits of mayflies, *Baetis bicaudatus*, in high-elevation streams in Colorado (Peckarsky *et al.* 2002). In the presence of trout, or just chemicals from trout, mayfly larvae developed faster than in the absence of predators, but matured at a smaller body size with lower fecundity. Therefore the benefit of reduced exposure to predation was at the cost of reduced number of eggs.

A trade-off has also been observed among sawfly species in which traits relating to defense are negatively correlated: those species with tough integuments have low levels of haemolymph toxins, and species with a haemolymph defense have a delicate integument which is easily damaged so that they bleed easily, releasing the toxic haemolymph onto the surface of the cuticle (Boevé and Schaffner 2003, Müller *et al.* 2003).

Life-history traits also varied within a species when reared on native host plants and exotics. The hemlock looper, *Lambdina fiscellaria* (Lepidoptera: Geometridae), on Anticosti Island, Canada, which was exposed in nature only to balsam fir as a food plant, matured in fewer instars, showed a more rapid daily fresh-weight increase and a higher fecundity when fed on its natural host plant than when other mainland species acted as hosts (Hébert *et al.* 2006).

But the same species naturally occurring on the mainland produced much higher numbers of eggs per female than the island species on sugar maple, eastern hemlock and balsam fir, which are typical host plants on the mainland.

A fourth example investigated clonal variation in competitive ability of the pea aphid, *Acyrthosiphon pisum*, against the co-occuring vetch aphid, *Megoura viciae* (Hazell *et al.* 2006). One pea-aphid clone showed rapid population growth and outcompeted the vetch aphid, while the other pea-aphid clone grew more slowly and was outcompeted by the vetch aphid. This despite the fact that the clones did not differ in lifetime fecundity. These clonal differences in life-history traits relating to population growth and competitive ability were heritable, illustrating that natural selection (or genetic drift) resulted in variable traits even when clones were collected in the same area.

10.7 Stabilizing selection on life-history traits

In spite of the emphasis on variation in life histories and evolutionary change in this chapter, we should not overlook the evident fact that much remains stable in insect life histories. Species remain remarkably constant in size at any one locality, resulting in the use of body size or appendage size as more-or-less stable characters for identifying species. Stabilizing selection no doubt is at work to limit variation in life-history traits.

This fact appears to be at odds with the many arguments in the literature that, within an insect species, larger body sizes result in higher fecundity and fitness, with the implication that directional selection will favor increases in size. There are at least two points worth considering in debates on the size and fecundity relationship. The first is that the correlation works for some species and not for others (e.g., Leather 1988, 1995, Klingenberg and Spence 1997, Bauerfeind and Fischer 2008). For example, pro-ovigenic species have all eggs ready to oviposit at the time of adult emergence, so pupal or adult weight is likely to be a good correlate of fecundity. But synovigenic species mature eggs as adult life progresses, making fecundity more dependent on adult nutrition, survivorship and clemency of the abiotic environment, resulting in poor correlation between insect size and fecundity. The second point to consider is the compromising features of increased size. Larger size probably correlates with a longer development time in many species, so when breeding time is short larger individuals are at a disadvantage. Delayed onset of first reproduction could be critical, especially in colonizing species in which early arrival at a newly available resource is advantageous. *Drosophila* fruit flies probably benefit from short developmental times during competition for ephemeral rotting fruit, and carrion flies depend on early colonization of a carcass for an edge on rich resources. Small size may provide a critical advantage when timing is of the essence. For a given amount of food, allocation to a smaller body size may result in greater allocation to reproductive effort. Female *Drosophila melanogaster* mating with smaller males have a higher fecundity than when mated with larger males (Pitnick 1991). Smaller males copulated longer and transferred more sperm than larger males. These kinds of trade-offs are almost inevitable and to be expected, thereby stabilizing life-history characteristics within rather narrow bounds. Klingenberg and Spence (1997, p. 66) have even suggested for water striders that size of adults “appears to be selectively neutral, rather than an adaptive trait,” although recognizing that dispersal ability and development time may correlate with size.

As an example of stabilizing selection, let us use the adult size of *Drosophila melanogaster*, a colonizing species in which early occupation on a new resource such as rotting fruit provides a major advantage in competition with later arrivals. Here, the intrinsic rate of natural increase, *r*, can be

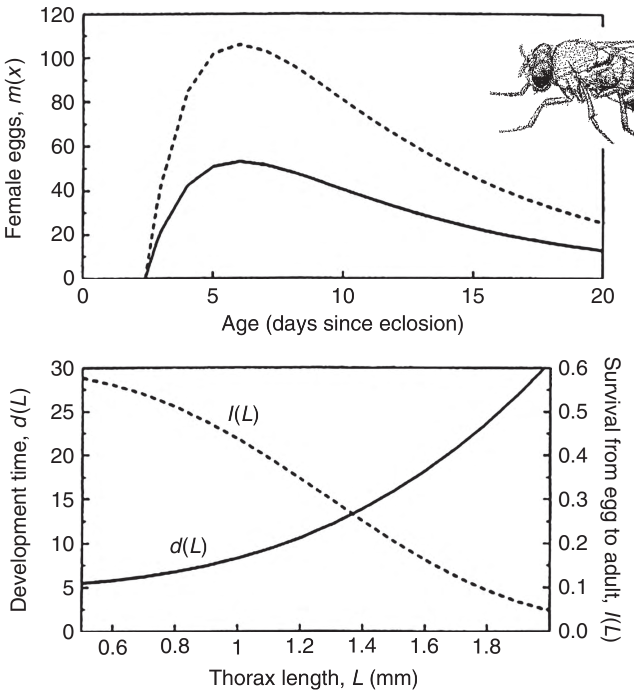


Figure 10.13 The relationship between female age and number of eggs laid, and body size and development time, for *Drosophila melanogaster* used by Roff (1981, 1992) to estimate change in population growth, *r*, with change in body size. The reproductive function (above) is roughly triangular for small females (solid line) and large females (dashed line). In relation to thorax length (below) development time increases with body size, while survival from egg to adult declines. From Roff 1992.

estimated in relation to fecundity, development time from egg to adult and survival over this interval, in relation to adult size (Roff 1981, 1992). Integrating several life-history traits requires a modeling approach and much detailed information on the variables examined, so *D. melanogaster* is a good choice. Its size varies little in the field, with thorax length ranging from 0.90 to 1.15 mm, apparently under the influence of stabilizing selection.

Variation in the relevant relationships takes different forms in this study of *D. melanogaster*:

(1) Fecundity increases with body size, and “The actual time course of egg production is triangular in shape” (Roff 1981, p. 407) (Figure 10.13), as used in Lewontin’s models (Figures 10.10–10.12).
(2) The larger the body size is in *D. melanogaster*, the longer is an individual’s development time.
(3) An increased development time is likely to correlate with increased larval mortality. Under a competitive regime, the scramble competition in rotting fruit may leave slow developers starving. These factors will collectively modify *r* in a population growth equation, having mean parameter values obtained largely from the literature. It is apparent that increasing fecundity with size, rising development times with thorax length and declining survival with thorax length will produce stabilizing selection and an optimal thorax size at some intermediate dimension. The net result is a set of predicted rates of increase, *r*, corresponding to a range of thorax lengths provided in Figure 10.14. The changes in *r* reveal the likelihood of positive selection on larger size for small individuals and counter selection on large flies, resulting in stabilizing selection at a thorax length of around 1 mm. In fact the observed range in size of

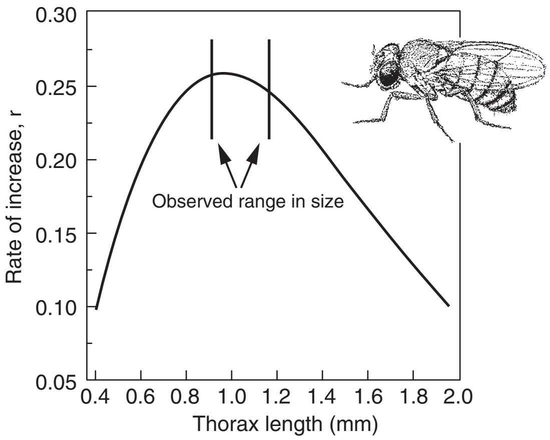


Figure 10.14 Roff's (1981, 1992) estimate of the rate of increase, *r*, a measure of fitness, in relation to thorax length in *Drosophila melanogaster*. Note that the observed range in size of flies coincides well with the predicted optimal female size for maximum fitness. From Roff 1992.

> *D. melanogaster* is very much in accord with that predicted in Figure 10.14, showing that larger body size correlated with higher fecundity will be selected against once the optimum size is passed, despite its association with higher fecundity.

This example using *Drosophila* should provide a salutary influence on the ways in which we examine life-history variation. Simple correlations between two variables, such as size and fecundity, will be modified by complicating factors such as changes in mortality or development time. And it is likely that stabilizing selection will usually prevail, such that individuals with intermediate sizes, fecundities or development times are likely to be fittest. The empirical evidence on species sizes supports this observation, as the following examples suggest. In the gall midge, *Rhopalomyia californica*, egg production appears to be balanced by a limitation on the time available to lay the eggs (Rosenheim *et al.* 2008). And time limitation may be imposed by the temperature dependence of egg maturation and oviposition, as in the butterfly, *Pararge aegeria* (Gotthard *et al.* 2007, Berger *et al.* 2008). If time is limiting, the realized fecundity of a female may well increase in the presence of preferred hosts on which larger clutches of eggs are laid (see Bergstrőm *et al.* 2006). Predation has been shown to increase as butterfly larval size increases, probably imposing stabilizing selection on body size (Berger *et al.* 2006).

Of course, if a population is exposed to a new selective regime, then directional selection may prevail for a time until a new selective equilibrium is reached, and selection exerts a stabilizing influence again. The key to evaluating the fitness consequences of particular life-history traits such as body size or fecundity is to blend such variables into the matrix of other significant factors to evaluate net effects on population growth, *r*, as illustrated in Roff's example, or other integrating methods which evaluate overall fitness.

Another approach to the question of stabilizing selection is to examine how traits vary during the adaptive radiation of a taxonomic group. We know, for example, that acridid grasshoppers become eruptive in many parts of the world. Commonly called locusts, they are some of the most destructive insect herbivores on the planet, no matter which continent they have colonized (Table 10.4). They retain the same basic morphology and habits, ovipositing into the ground and leaving nymphs to forage for whatever food they can find (Price 1997, 2003a, Lockwood 2004). Such conservation of traits, including morphological, life-history and ecological, in a group which has colonized much of the world should impress upon us how stable and predictable lineages and the species in them can be. Once such a successful group as the acridid grasshoppers has evolved, with a certain ground plan and life history, these sets of general adaptations appear to be effective over a broad range of environmental conditions. (See also Section 11.4, An evolutionary hypothesis.)

A similar case can be made for conservation of life-history traits and related ecology in forest moths. In spite of the arguments in the *r*- to *K*-selection hypothesis, life histories of related tree-feeding

Table 10.4 **Grasshoppers (Orthoptera: Acrididae) from around the world which show eruptive population dynamics. From Price 1997**

Species	Common name	Location
Anacridium melanorhodon	Tree locust	Africa
Austriocetes cruciata	Plague grasshopper	Australia
Chortoicetes terminifera	Australian plague locust	Australia
Dociostaurus maroccanus	Moroccan locust	Western Turkey
Gastrimargus musicus	Yellow-winged locust	Australia
Locusta migratoria	African migratory locust	Africa, Asia, Australia
Locustana pardelina	Brown locust	Southern Africa
Melanoplus sanguinipes	Migratory grasshopper	North America
Melanoplus spretus	Rocky Mountain grasshopper	North America
Nomadacris guttulosa	Spur-throated locust	Australia
Nomacridis septemfasciata	Red locust	Tropical Africa
Nomacridis succincta	Bombay locust	India
Schistocerca gregaria	Desert locust	North Africa, Asia

moths appear to be very similar in temperate and tropical forests (Price 2008). For example, in northern pine forests the pandora moth, *Coloradia pandora* (Lepidoptera: Saturniidae), is an eruptive species – to such an extent that native peoples use them as a protein source. Likewise, another saturniid, the mopane worm, *Imbrasia belina*, is eruptive across a mostly tropical belt in southern Africa (15–25°), and again is eaten by native peoples. Both species oviposit egg clusters on host plants independently of foliage quality for small first instar caterpillars, leaving larvae to forage on whatever they can find, and defoliating large tracts of host plants. In fact, when we compare lists of forest Lepidoptera with eruptive population dynamics from north temperate forests in North America (40–50° N), and from equatorial forests in Ghana (5–11° N), the families represented are remarkably similar (Table 10.5). Although the climates are very different, and the host-plant families exploited are completely different, and the localities are thousands of miles apart, 7 out of 12 families are the same in temperate and tropical habitats, showing a high probability that life-history traits and correlated ecology are retained as lineages spread over the globe.

When we consider life histories in such broad terms it becomes clear that phylogenetic constraints and stabilizing selection are important in maintaining suites of traits as lineages diversify in species and geographic locations. The conservation of characters that enable the identification of orders, families, genera and species reveals that many characters are largely stable – an observation that we take for granted, but one that nonetheless illustrates the continuity of life-history traits through time and over geographical regions.

10.8 Life span of adult insects

While discussing briefly the richness of the insect faunas and relationships in Chapter 1, we could well have emphasized the tremendous diversity of life cycles, one component of which is adult life span. The range in adult longevity is

Table 10.5 **A comparison of families of moths and butterflies which occur in forests in temperate North America and tropical West Africa which show eruptive population dynamics. From Price 2008. The number of species per family are shown. © 2008 Regents of the University of California. Published by the University of California Press**

Family	Temperate North America	Tropical Ghana
Nymphalidae	1	1
Pieridae	1	0
Saturniidae	3	2
Lasiocampidae	5	3
Lymantriidae	7	4
Notodontidae	4	3
Arctiidae	3	6
Geometridae	16	3
Dioptidae	1	0
Noctuidae	0	9
Hesperiidae	0	1
Sphingidae	0	1
Limacodidae	0	1
Papilionidae	0	1

Table 10.6 **A classification of factors which may select for increased adult life span in insects and arachnids, with some examples. From Carey 2001. Reprinted, with permission, from the *Ann. Rev. Entomol*. 46, 79–110 © 2001 by Annual Reviews www.annualreviews.org**

Factors	Examples
Environmental	
Food scarce or widely dispersed	*Heliconius* spp., cave dwellers, euglossine orchid bees
Uncertain or adversity	*Polistes* wasp queens, soft ticks, treehole mosquitoes, *Tribolium*, monarch butterflies (migratory phase), *Locusta*, tarantulas, bed bugs
Kinship and cooperation	
Parental care/ monogamy	Tsetse flies, dung beetles, ambrosia beetles, *Bembix* spp. (progressively provisioning wasp)
Nest helpers/kin selection	*Polistes* spp., aposematic saturniid moths, bumble bees, primitive ants
Primary reproductives (eusocial)	Queen termites, ants, bees, wasps

extraordinary; from a few days in mayflies to several decades in social-insect queens (Figure 10.15). This amounts to a 5000-fold difference in adult longevity, the first notable fact on adult life span mentioned by Carey (2001).

The second of Carey's observations was the apparent phylogenetic constraint on adult longevity. No mayflies are long-lived, and most Lepidoptera live relatively brief lives, with exceptions in the genus *Heliconius*, which can live for 5–6 months digesting nutrient-rich pollen.

The third interesting fact is that longevity increases as parental commitments increase, including eusociality. Brood-caring, monogamous dung beetles may live for more than 3 years. Queen ants, termites and bees can be long-lived, with some soil-dwelling species setting longevity records for insects of over 30 years!

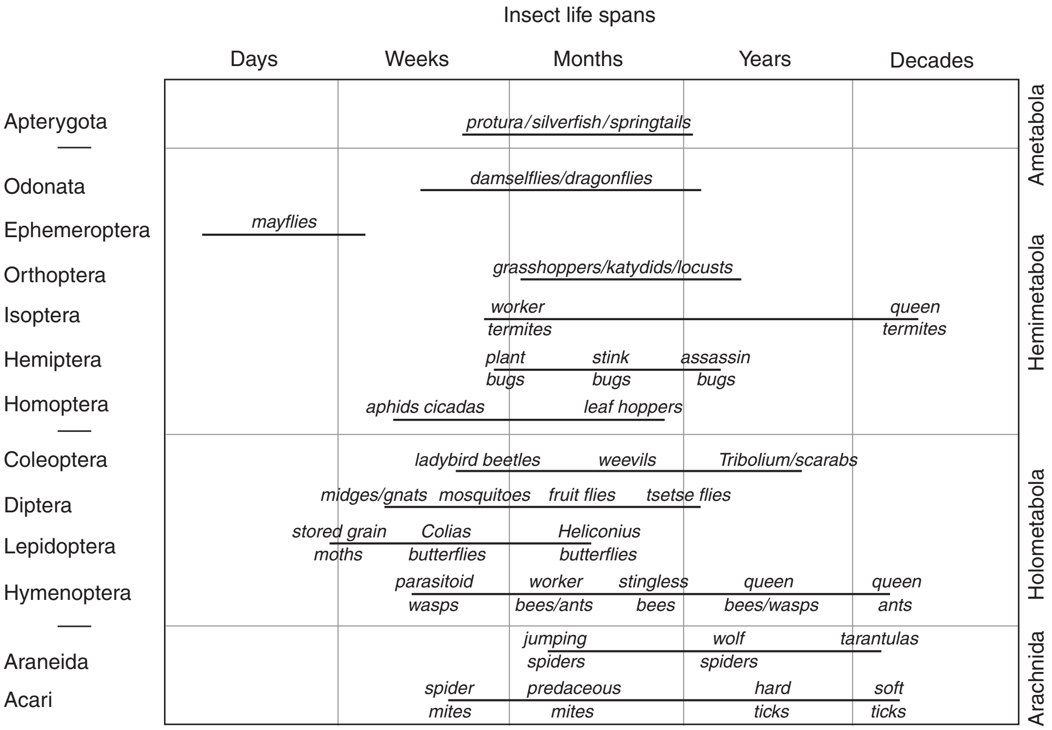


Figure 10.15 Examples of life spans of adult insects and arachnids, ranging from a few days in the mayflies to several decades in some queens of social insects and some arachnids. These arthropods illustrate a 5000-fold difference in adult longevity, much greater than the 60-fold difference in mammals, from small rodents (~2 years) to humans (~120 years). From Carey 2001. Reprinted, with permission, from the *Ann. Rev. Entomol.* **46**, 79–110 © 2001 by Annual Reviews www.annualreviews.org

Fourth, unpredictable environmental variation results in selection for increased longevity in some species, in which individuals may remain reproductively dormant over winter or through a long dry season. Some ticks live for 10–20 years and large tarantulas live somewhat longer.

Fifth, scarce food resources which are hard to find are likely to select for increased longevity, as in *Heliconius* butterflies, euglossine bees, bed bugs and reduviid bugs.

A classification of factors that select for insect adult longevity emphasizes two main drivers: environmental adversity and parental investment and kinship (Table 10.6).

Perhaps we take the diversity of life cycles for granted in the insects, but these examples illustrate well the magnitude of that diversity. We can see the extent to which natural selection can stretch the range of a trait such as adult longevity, and how ecological and behavioral factors play their role in diversification.

Applications

Understanding pest species

Life-history studies are almost boundless in their diversity and contribute substantially to the growth of ecological science and its value in applying knowledge to solving problems in agriculture, forestry and conservation.

"The life cycle of a particular species can be viewed as the story of how a maturation point is attained with maximum combined speed and freedom from risk. Only by studying it as one strategy out of a great many possible strategies can we expect to understand more deeply the way a given species has adapted . . . to the particular environment in which it lives." (Hölldobler and Wilson 1990, p. 143). Life histories or life cycles are studied extensively because they form the basis for understanding a species or a group of related species. They are essential in understanding evolutionary trends and the development of effective management plans for pests or beneficial species. For example, studies may investigate the effects of intercropping on pest species (e.g., Åsman and Ekbom 2006), the potential of trap crops (e.g., Badenes-Perez *et al.* 2006), and the qualities of invasive species relative to natives (e.g., Boivin *et al.* 2008, Mahdjoub and Menu 2008). Collecting descriptions of life histories and using them comparatively fosters an evolutionary perspective on trends, and the multiple ways in which species fit onto the habitat template available to them. Two examples relate to the evolution of aphid life cycles (Moran 1992) and life history evolution in carabid beetles (Sota and Ishikawa 2004). Frequently, research papers and reviews on insect species, early in their treatment, provide a description of the life history of the species as an essential ingredient for understanding subsequent aspects of the treatment. For example, a discussion of the biology of the soybean aphid, *Aphis glycines*, provides the life history, and a figure of the life cycle of the species (Ragsdale *et al.* 2004). Many other papers describe life histories with a view to using such knowledge in more analytical studies on the ecology and management of a species. For example, Yan and Li (2007) studied the life history of two mayfly species as a basis for understanding their role in nutrient cycling and energy flow in the ecosystem, and Njoka *et al.* (2006) described the life history of two weevil species in the Lake

Victoria basin in Kenya as a basis for biological control of water hyacinth, an important weedy species that clogs water bodies throughout the tropics. Additional studies are motivated by an interest in particular species, and these add to the accumulating knowledge for the relevant taxonomic group, for example, on the rolled leaf hispine beetle, *Cephaloleia fenestrate*, in Costa Rica (Johnson 2004) and the nymphalid butterfly, *Phyciodes phaon*, in Florida (Genc *et al.* 2003).

The study of life histories, or life cycles, is so basic to the understanding of an insect species that their applications are almost universal. Who would try to employ population regulation methods on a specific insect without knowing its life cycle, which is likely to reveal the best time of season, and the most vulnerable aspect of the insect's life, for the method to be applied? Textbooks used in insect regulation courses are full of life-history information (e.g., Metcalf and Metcalf 1993). Which forensic entomologist would collect insects from a corpse and interpret their collection without knowing the detailed life history of the species discovered (e.g., Goff 2000, Gennard 2007)? How would conservation management of a species be undertaken in the absence of life-cycle information (e.g., Samways 1994, 2005, Stewart *et al.* 2007)? The implementation of effective monitoring systems for conservation and biodiversity studies is one of the key emphases in the new journal *Insect Conservation and Diversity* (Leather *et al.* 2008). Such monitoring must depend on knowledge of life histories, and conservation studies in general should employ species-level studies as the basis for developing biomonitoring efforts, and the use of indicator species (Spence *et al.* 2008).

Obviously, the more detailed life-history information becomes, including demographic data, the more refined can be the applications in many relevant management plans. Also, as life histories accumulate on related species, the patterns revealed form the basis for predictions about as yet unstudied species, the development of hypotheses and theory on the evolutionary pathways followed by a clade, and the major aspects of natural selection driving this evolution (e.g., review by Spence and Andersen [1994] on the interaction between systematics and ecology, and the review by Nylin and Gotthard [1998] on plasticity in life-history traits). In addition, the possible responses of species may be anticipated, for example to approaches in management, or changes in the habitat template, such as habitat fragmentation (Karlsson and Van Dyck 2005), or climate change (e.g., Musolin 2007). There are, indeed, endless applications of life-history information to solving problems in nature and in managed systems.

"The life cycle, in fact, is the unit of evolution, the unit of innovation and elimination, and it is for this reason more than any other that the life cycle has a central position in the structure of biology" (Bonner 1965, p. 13). "Why study life histories? Life histories lie at the heart of biology: no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles" (Stearns 1992, p. 9).

Summary

Life histories of insects provide the basis for understanding species and, with comparative studies, how the evolutionary process shapes variation among species. We illustrate approaches to life-history studies using parasitoids, giant water bugs, water striders and pitcher-plant mosquitoes. The evolution of all life histories is constrained by limited resources such that adaptations incur a cost, meaning that trade-offs in resource allocation are an inevitable component of life histories. For example, functional wings will probably result in reduced fecundity when compared to individuals with reduced, non-functional wings. Timing of egg production also exacts an expense if all eggs are produced by the time of adult emergence – pro-ovigeny – with many life-history correlates, such as reduced or eliminated adult feeding. Fecundity varies so much within and between taxa that hypotheses have been developed to account for this: the balanced mortality hypothesis, the bet-hedging hypothesis, and *r*- and *K*-selection. Also, the timing of reproduction is considered in relation to semelparity versus iteroparity, and how selection can change the rate of growth of the population by alteration of the reproductive function. Stabilizing selection also plays an important role in insect life histories by maintaining traits which are near optimal, such as mean insect size in a population and the life span of insects. Life histories are critical in preparing management plans for pest and beneficial species, in the use of insects in forensic diagnosis, and in insect conservation.

Questions and discussion topics

1 Many arguments have been made that larger individuals in an insect population have a fitness advantage over smaller individuals, for example larger females can lay more eggs. Discuss the counterarguments that stabilizing selection prevails on size in most populations and for most of the time.

2 What advantages do water-dwelling insects provide for the study of life-history strategies? Suggest terrestrial habitats and species which would have similar advantages.

3 Discuss, using examples, the proposition that every adaptation has its own constraints.

4 Which selective factors are involved in the generation of very large differences in the longevity of adult insects? Are males and females of the same species likely to have different life spans? Can you think of any advantage in insects to living after reproduction has ended?

5 Discuss stages in the life cycle of insects in which behavioral methods of population control or regulation are most likely to be effective.

Further reading

Berger, D., R. Walters and K. Gotthard. 2006. What keeps insects small? – Size dependent predation on two species of butterfly larvae. *Evol. Ecol.* **20**:575–589.

Carey, J. R. 2001. Insect biodemography. *Annu. Rev. Entomol.* **46**:79–110.

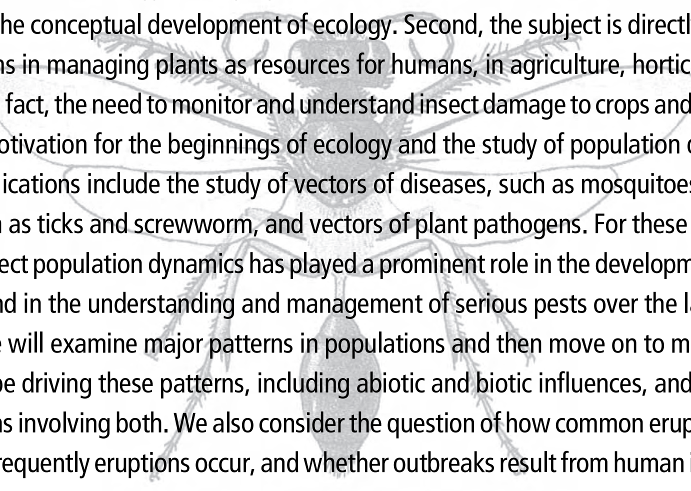
Jervis, M. A., J. Ellers and J. A. Harvey. 2008. Resource acquisition, allocation, and utilization in parasitoid reproductive strategies. *Annu. Rev. Entomol.* **53**:361–385.

Roff, D. A. 1992. *The Evolution of Life Histories: Theory and Analysis.* New York: Chapman and Hall.

Zera, A. J. and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. *Annu. Rev. Entomol.* **42**:207–230.

11

Population dynamics



All natural populations fluctuate: they are dynamic. Chapter 9 introduced the concepts of population growth and regulation. How and why populations change are the subjects of this chapter. Population dynamics has been of major concern in insect ecology for at least two reasons. First, ecology has been defined as the study of the distribution and abundance of species (Andrewartha and Birch 1954, Krebs 1972). Since the study of population dynamics must include both changes in numbers over time and over the landscape, the subject acts as a central theme in ecology: a unifying concept that permeates the science. It is therefore critical to the conceptual development of ecology. Second, the subject is directly applicable to problems in managing plants as resources for humans, in agriculture, horticulture and forestry. In fact, the need to monitor and understand insect damage to crops and forests was a major motivation for the beginnings of ecology and the study of population dynamics. Other applications include the study of vectors of diseases, such as mosquitoes, pests of cattle such as ticks and screwworm, and vectors of plant pathogens. For these reasons the field of insect population dynamics has played a prominent role in the development of basic ecology and in the understanding and management of serious pests over the landscape.

First we will examine major patterns in populations and then move on to mechanisms that may be driving these patterns, including abiotic and biotic influences, and complex interactions involving both. We also consider the question of how common eruptive species are, how frequently eruptions occur, and whether outbreaks result from human interference with natural dynamics. We note that long-term studies are essential in deciphering the reasons for population change, but many potential influences need to be investigated. Bottom-up effects from plants, top-down effects from natural enemies and lateral effects all need attention. Spatial distribution of populations is also important in a fragmented landscape, covered by the field of metapopulation dynamics. Population dynamics is a field of wide application for understanding pest species, epidemiology, biological control and conservation, all requiring information for planning and management.

11.1 Population patterns

Populations change in time and over the landscape. Many studies have undertaken investigations with plot techniques, monitoring populations through time, as with most life-table studies, exemplified by the spruce budworm life tables discussed in Chapter 9. But questions arise on whether eruptions start from a nodal location or epicenter, or whether there is a gradual upwelling of numbers over a landscape. These are critical considerations for management because pinpointing epicenters may enable local control to prevent an eruption. But if broad-scale increases in a pest population are the norm, then a totally different regulative strategy is required. Hence we need to consider temporal and spatial aspects of population change.

11.1.1 Long-term studies

Long-term observations of insect populations are critical for revealing patterns in population fluctuations. When we look at the evidence from long-term studies on insect populations, we can begin to appreciate the kinds of questions that have been investigated in order to understand when, why and how populations wax and wane.

When regulated forestry commenced in Germany in about 1800, monitoring of four insect pests of pine trees was undertaken to determine economic damage and the need for control measures. A population index was calculated based on the amount of damage estimated in each forest district for the pine looper, *Bupalus piniarius*, pine beauty moth, *Panolis flammea*, the nun moth, *Lymantria monacha*, and the common pine sawfly, *Diprion pini*, and data for four districts were provided by Klimetzek (1990). One forest district was in southwestern Germany and the other three were spread out across southeastern Germany, so patterns over a large geographic area could be compared. Data were available from 1801 to 1988, making this the longest-running study with which to examine how insect populations change through time and space.

Several patterns emerged from this long-term data set. Clearly evident in the population history of pine herbivores were outbreak years of high damage interspersed with years when no attack was evident (Figure 11.1). Large magnitude fluctuations in populations were commonplace. A second feature was the synchrony among sites for any one insect species, which was especially evident in the three sites in southeast Germany, about 150 km apart, although major outbreaks were synchronized in the west and east, almost 300 km apart.

A third point to be noted was that for two species, the nun moth and pine beauty, eruptions tended to occur with peaks of pine beauty lagging the nun moth by one year and one generation (on the right of Figure 11.1). However, there was no such synchrony in the other species. Fourth, highest populations occurred usually in areas 2 and 3. A final point is that outbreaks became more frequent after 1930, particularly for the pine looper in southeast Germany.

These patterns provide a heuristic basis for identifying the mechanisms that drive population dynamics in the system:

(1) Widespread synchrony in eruptions suggests that the causes are in common, and that they affect large areas simultaneously. Such a pattern suggests that weather is the likely candidate, with precipitation, temperature or their combination probably involved. Perhaps drought that stresses trees, warm winters which increase survival of insects or warm summers which accelerate larval development are contributing factors.
(2) Areas 2 and 3 with the highest populations were similar in several characteristics. They were located in areas of large continuous forest with a high proportion of pine trees (about 55% pine), and soils were poor and porous. These areas were relatively low in elevation, low in precipitation and hot. Thus, the spatial distribution of the food plant was probably a

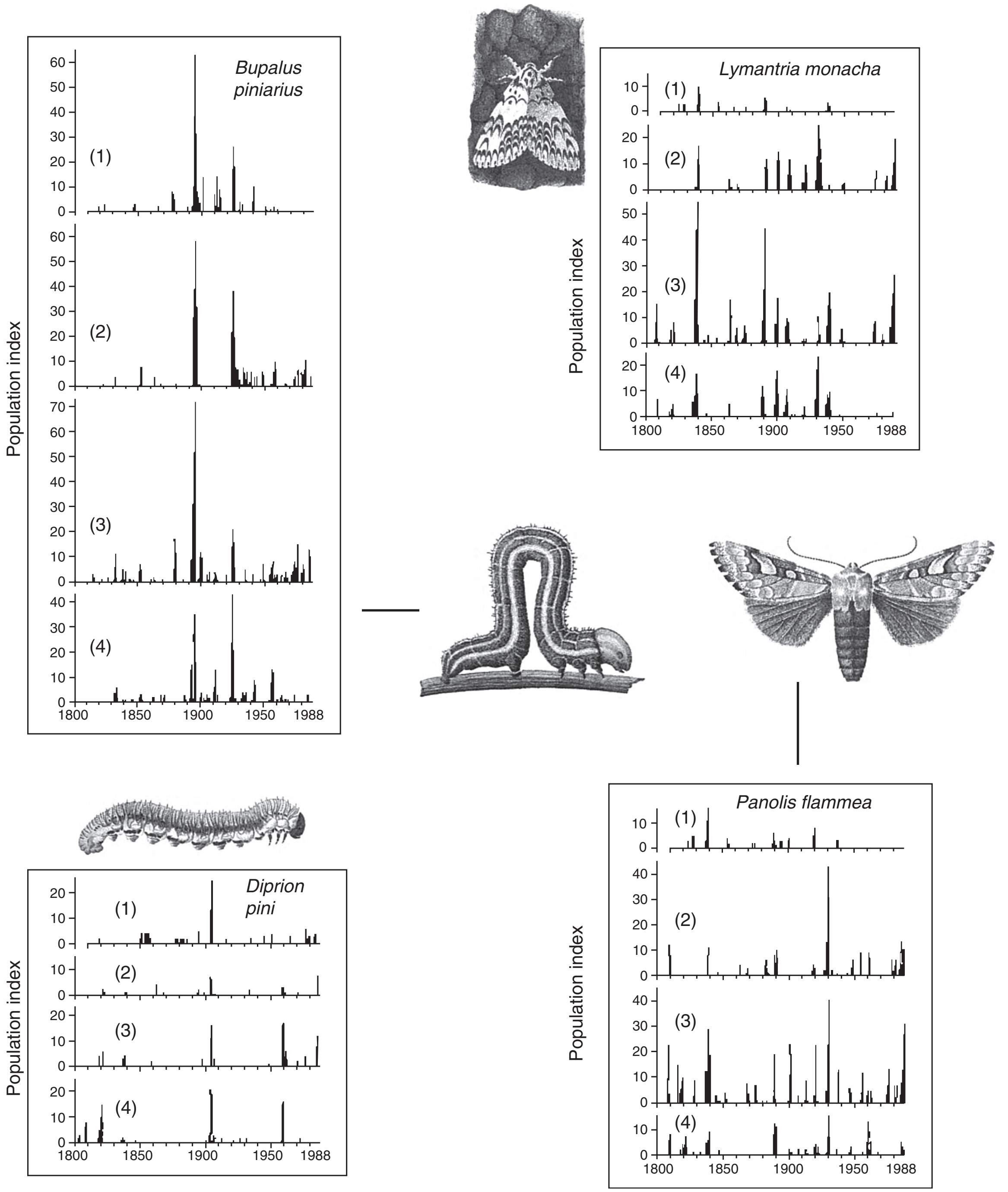


Figure 11.1 Population outbreaks of four pine defoliators, 1801–1988, in four state-owned forests in Germany (Areas 1–4). *Bupalus piniarius* is the pine looper moth, *Lymantria monacha* is the nun moth, *Diprion pini* is the common pine sawfly and *Panolis flammea* is the pine beauty moth. From Klimetzek (1990).

factor in stimulating outbreaks, as was tree nutrient and water status, and possibly the local climate in which the insects developed.

(3) Lower populations in Area 1 may well be associated with a higher proportion of hardwoods in the forest and a tradition of less litter removal, resulting in higher nutrient status of the soils.

The diversity of factors possibly involved in the population dynamics of these four insect species is typical of variables affecting any other insect. Teasing apart the mechanisms becomes a challenge, with experiments and analytical techniques being required to achieve real understanding, and to provide the basis for predicting when and where outbreaks are likely to occur. With many insect pest species and many plant species of economic importance, the field of insect population dynamics has grown to be an important component of insect ecology.

However, the discovery of mechanisms, and establishing that certain factors are important while others are not, became problematic. How much information is necessary in order to understand these tremendous fluctuations in density? While a great effort has been invested in understanding the fluctuations in these species, a complete understanding of all the mechanisms involved has been elusive.

An important step between the damage assessments made in southern Germany, and mechanistic studies, was taken by Schwerdtfeger (1935, 1941), who examined direct estimates of insect densities in pine plantations in Letzlingen in northern Germany. Data were available from 1880 to 1940, showing large population changes over two to five orders of magnitude (Figure 11.2). At the highest population densities trees were defoliated, larvae starved and populations declined. Shortage of food set an upper limit, or carrying capacity, to population density in some years, but in others populations declined without serious defoliation. Neither Schwerdtfeger (1935, 1941), nor Varley (1949), could determine the factors involved because, on the one hand, too many possibilities existed, and on the other, not enough detailed information had been collected. However, this study stimulated Varley to start his own observations on the population dynamics of the winter moth, *Operophtera brumata*. He selected five oak trees, a major food plant, in Wytham Wood, in 1949, and records were kept on population density and mortality caused by natural enemies: predators, parasitoids, and a microsporidian disease (Varley *et al.* 1973). These studies, and similar investigations, launched a long tradition of studies, which attempted to gather sufficient field data that would ultimately explain the reasons for population fluctuations. In 1949 also, a population study of the grey larch tortrix, *Zeiraphera griseana*, was started in the Engadine Valley, in the Alps of Switzerland (Baltensweiler 1968). A little earlier detailed studies were started on the spruce budworm, *Choristoneura fumiferana*, in the Green River and nearby watersheds, New Brunswick, Canada, with a major report covering the years 1945–1959 (Morris 1963a), although decades of less intensive investigations preceded them. These and other studies have contributed to a large literature on long-term studies, some of which are listed in Table 11.1 (more are listed in Price 2003a).

The major factors involved with population regulation or limitation, listed in Table 11.1, range widely from weather, to strong bottom-up effects through the host plant, to strong top-down influences from natural enemies. Most studies employed correlational methods to see which independent variables correlated best with the insect population density changes through time. Weather was apparently important in many studies, from stick insects to moths (Studies 1, 4, 5, 8, 11, 16, 17, 18, 19, 20, 21), but weather also influenced host-plant quality or abundance, resulting in strong bottom-up effects (Studies 5, 6, 8, 15, 19, 21, 22). Natural enemies were frequently implicated in regulating populations, influences that were seen in all types of

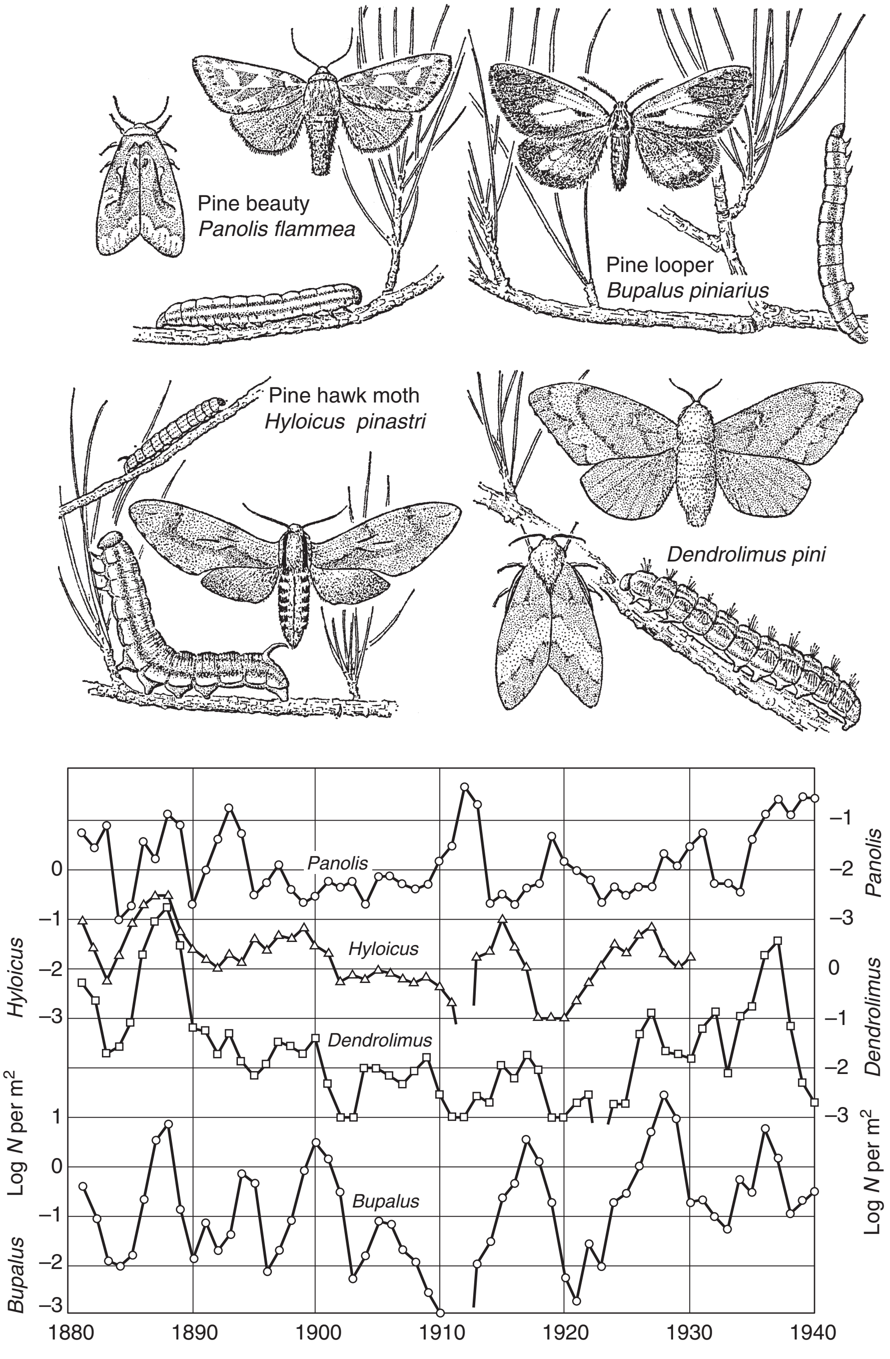


Figure 11.2 The four species of moth that were major defoliators of pine in Letzlingen, Germany, 1880–1940, studied by Schwerdtfeger (1935, 1941), and populations of moth pupae or hibernating larvae per m^2 of pine forest litter. From Varley *et al.* (1973). Illustrations by Rosemary Wise.

Table 11.1 **Examples of long-term studies (15+ years) on insect population dynamics and the major factors apparently involved in regulating or limiting populations (based on Price 2003a)**

Insect species	Taxonomic affinity	Host plant(s)	Locality	Study length	Major factors	Reference
(1) *Didymuria violescens*	Phasmatodea: Phasmatidae	*Eucalyptus* spp.	Australia	17 yr	Weather, bird predation	Readshaw 1965
(2) *Drepanosiphum platanoides*	Homoptera: Aphididae	*Acer pseudoplatanus*	UK	19 yr	Intraspecific competition	Dixon 1990
(3) *Baizongia pistaciae*	Homoptera: Pemphigidae	*Pistacia palaestina*	Israel	20 yr	Unknown	Wool 2002
(4) *Neophilaenus lineatus*	Homoptera: Cercopidae	*Juncus*, *Festuca* spp.	UK	37 yr	Temperature	Whittaker and Tribe 1998
(5) *Lygaeus equestris*	Hemiptera: Lygaeidae	*Vincetoxicum hirundinaria*	Sweden	18 yr	Weather, food quantity	Solbreck 1995
(6) *Phytobia betulae*	Diptera: Agromyzidae	*Betula pubescens*, *B. pendula*	Finland	47 and 65 yr	Tree age and variation	Ylioja *et al.* 1999
(7) *Taxomyia taxi*	Diptera: Cecidomyiidae	*Taxus baccata*	UK	28 yr	Parasitoids	Redfern and Cameron, 1998
				35 yr	Parasitoid and parental density	Redfern and Hunter 2005
(8) *Euura lasiolepis*	Hymenoptera: Tenthredinidae	*Salix lasiolepis*	USA	22 yr	Precipitation, resource quality	Price and Hunter 2005
(9) *Aneugmenus* spp.	Hymenoptera: Tenthredinidae	*Pteridium aquilinum*	UK	19 yr	Disease? Plant quality?	Lawton 2000

Table 11.1 (*cont.*)

Insect species	Taxonomic affinity	Host plant(s)	Locality	Study length	Major factors	Reference
(10) *Diprion hercyniae*	Hymenoptera: Diprionidae	*Picea glauca*, *P. mariana*	Canada	23 yr	Parasitoids, disease	Neilsen and Morris 1964
(11) *Choristoneura fumiferana*	Lepidoptera, Tortricidae	*Abies balsamea*	Canada	15 yr	Temperature, parasitoids, predators	Morris 1963b
				36 yr	Climate, enemies, food web dynamics	Royama 1984, 1992
(12) *Tortrix viridana*	Lepidoptera: Tortricidae	*Quercus robur*	UK	16 yr	Resource limitation, variation	Hunter *et al.* 1997
(13) *Zeiraphera diniana*	Lepidoptera Tortricidae	*Larix decidua*	Switzerland	28 yr	Induced plant resistance	Baltensweiler and Fischlin 1988
(14) *Epinotia tedella*	Lepidoptera: Tortricidae	*Picea*	Denmark	19 yr	Parasitoids	Münster-Swendsen 1985
(15) *Operophtera brumata*	Lepidoptera: Geometridae	*Quercus robur*	UK	16 yr	Mortality of young larvae	Varley *et al.* 1973
				16 yr	Pupal predation	Hunter *et al.* 1997
(16) *Epirrita autumnata*	Lepidoptera: Geometridae	*Betula pubescens*	Finland	115 yr	Sunspot activity weather in north, predation in south	Tenow 1972, Ruohomäki *et al.* 2000

Table 11.1 (*cont.*)

Insect species	Taxonomic affinity	Host plant(s)	Locality	Study length	Major factors	Reference
(17) *Malacosoma californicum*	Lepidoptera: Lasiocampidae	*Alnus rubra*, etc.	Canada	24 yr	Weather, viral disease	Myers 2000
(18) *Malacosoma disstria*	Lepidoptera: Lasiocampidae	*Populus tremuloides*	USA	55 yr	Weather, parasitoids	Hodson 1941
(19) *Lymantria dispar*	Lepidoptera: Lymantriidae	Deciduous trees	USA	73 yr	Weather, oak mast, mammals, predation	Liebold *et al.* 2000
(20) *Orgyia pseudotsugata*	Lepidoptera: Lymantriidae	*Pseudotsuga menziesii*	USA	70 yr	Natural enemies, warm dry zones	Mason and Wickman 1988
(21) *Tyria jacobaeae*	Lepidoptera: Arctiidae	*Senecio jacobaea*	Netherlands	23 yr	Rainfall, food available	van der Meijden *et al.* 1988
(22) *Anthocaris cardamines*	Lepidoptera: Pieridae	*Cardamine pratensis*	UK	18 yr	Food quantity	Dempster 1997

insects (e.g., studies 1, 7, 9?, 10, 11, 14, 15, 16, 17, 18, 19, 20). Intraspecific competition was frequently important in aphids (Study 2, and Dixon 1990). Notable, also, is that these factors overlapped in many cases to limit population size, with combinations of weather, host-plant effects and/or natural enemies being significant. For example, we will see later in this chapter that induced plant resistance results in larvae better able to encapsulate parasitoid eggs (Haukioja 2005). These factors are not likely to be simply additive, and they may well interact in complex ways, so that experimental methods are required to unravel the pathways of interaction.

Just in this short list of studies in Table 11.1, no patterns emerge to predict which kinds of species are likely to be regulated by a particular factor. Taking forest Lepidoptera, for example, major factors include weather, parasitoids, predators, diseases, food shortage and other factors. Practically any factor may play a role in dampening population growth. Such lack of patterns makes general predictions on population dynamics difficult or impossible, even though some individual species show regular patterns of density change.

Regularity of patterns in population variation within species includes cyclical changes in density, and synchrony over a landscape (e.g., Liebhold and Kamata 2000). Such patterns engender hypotheses on why such phenomena should be observed, discussed later in this chapter. Some species show both cyclic behavior and spatial synchrony in parts of their range, such as the grey larch tortrix and the Western tent caterpillar (Figure 11.3). Are such patterns driven by:

(1) Variation in insect quality
(2) Variation in host plant quality
(3) Climatic factors
(4) Disease susceptibility? (Myers 1988, Cory and Myers 2009)

Or are predators and parasitoids implicated in population cycles (e.g., Berryman 1996)?

One of the problems with understanding insect population dynamics is that experiments have not been employed adequately. “There is an unfortunate lack of experimental investigation of population cycles of forest Lepidoptera” (Myers 1988, p. 224). Krebs (1994, 1995), Lambin *et al.* (2002) and many others have emphasized the need for experiments in order to study mechanisms of population change, an issue we will return to when processes and mechanisms are discussed further, later in this chapter.

11.1.2 How numerous are eruptive and latent species?

Notable among the species mentioned in this chapter so far, is that almost all are serious pests; outbreak species with eruptive population dynamics. **Eruptive species** are those showing rapid and large changes in density, in which populations periodically reach high densities damaging to host plants. Therefore, we should enquire about the commonness or rarity of eruptive species. Are they representative of the majority of insects or are they an unusual kind?

Every informed student of insect population dynamics recognizes that eruptive species are unusual and rare compared to the large numbers of species in any particular community. “An impressive variety of caterpillars are found on the foliage of trees, yet surprisingly few species ever reach outbreak numbers” (Mason 1987, p. 31). “Of the vast number of insect species that feed on western North American trees, . . . only 16 are defoliators” (Faeth 1987, p. 136). Hunter (1995b) estimated that at most 1–3% of macrolepidopteran species in forests are eruptive species, and Price (2003a) reckoned that only 3% of tenthredinid sawflies were outbreak species. Nothnagle and Schultz (1987) listed 41 species of macrolepidopterans recorded as reaching outbreak proportions for two or more years in the period from 1962–1981. It is hard to know what proportion of species these represent in forest environments. However, with some 5032 species of Macrolepidoptera in North America (Arnett 1993) in

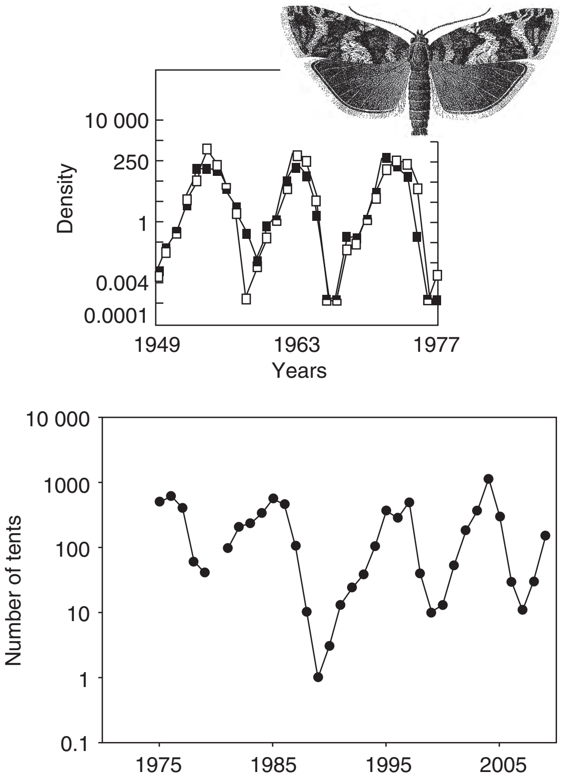


Figure 11.3 Top: Cyclic population dynamics of the grey larch tortrix and synchrony between two populations in the Engadine Valley, Switzerland. Data from Fischlin (1982), figure from Myers (1988). Bottom: A cycling population of the Western tent caterpillar, *Malacosoma californicum*, in British Columbia (personal information from Judith H. Myers 2009). Top: Reprinted from *Adv. Ecol. Res.* **18**, by J. H. Myers. Can a general hypothesis explain population cycles of forest Lepidoptera? Pages 179–242. Copyright 1988, with permission from Elsevier.

all environments, the eruptive forest species compose a tiny 0.8% of the fauna. No matter what kind of comparison one undertakes, eruptive species make up a very small minority of the insect community. Conversely, **latent species**, those showing low fluctuations in density without usually causing conspicuous damage to host plants, probably comprise at least 90–95% of any fauna, but their population dynamics are hardly ever studied and this needs to change.

11.1.3 How frequently do outbreaks occur?

Most outbreaking species spend most of the time at low densities in any one location, causing very little damage. Indeed, individuals may be very hard to find between outbreaks. Long gaps between outbreaks, of over 10 years in many cases, are evident in Figure 11.1. And in Figure 11.2, as was noted earlier, in certain years peaks in populations collapsed before defoliation was evident. In 17 years of studying the grey larch tortrix, damage was evident in only 7 years, when larvae reached densities of well over 100 per 7.5 kg of branches, the standard sampling unit (Figure 11.4).

Myers (1988) reviewed the frequency and cyclicity of outbreaks of forest Lepidoptera in North America and Europe. Average periodicities of outbreaks were 8–11 years, but some such as the western spruce budworm, *Choristoneura occidentalis*, and the eastern spruce budworm, *Choristoneura fumiferana*, showed much longer cycles of 28 and 35 years respectively.

For eruptive species of sawflies, the frequency of outbreaks varies enormously from region to region, but in the majority of species heavy to severe damage to forests occurred once to 10 times in a period of 37 or 38 years (Haack and Mattson 1993). Outbreaks were generally more frequent in Ontario, Canada, than in Minnesota, Wisconsin and Michigan in the United States, and the pine sawflies (Diprionidae) showed eruptive dynamics more frequently than the common sawflies (Tenthredinidae).

The evidence indicates that in more-or-less natural systems of forest vegetation, there are virtually no insect species that exist at persistently damaging densities. There are relatively few species that are eruptive and they are at outbreak densities for a minority of the time. Outbreaks are less frequent than the non-outbreak phases of population change in any one species and locality.

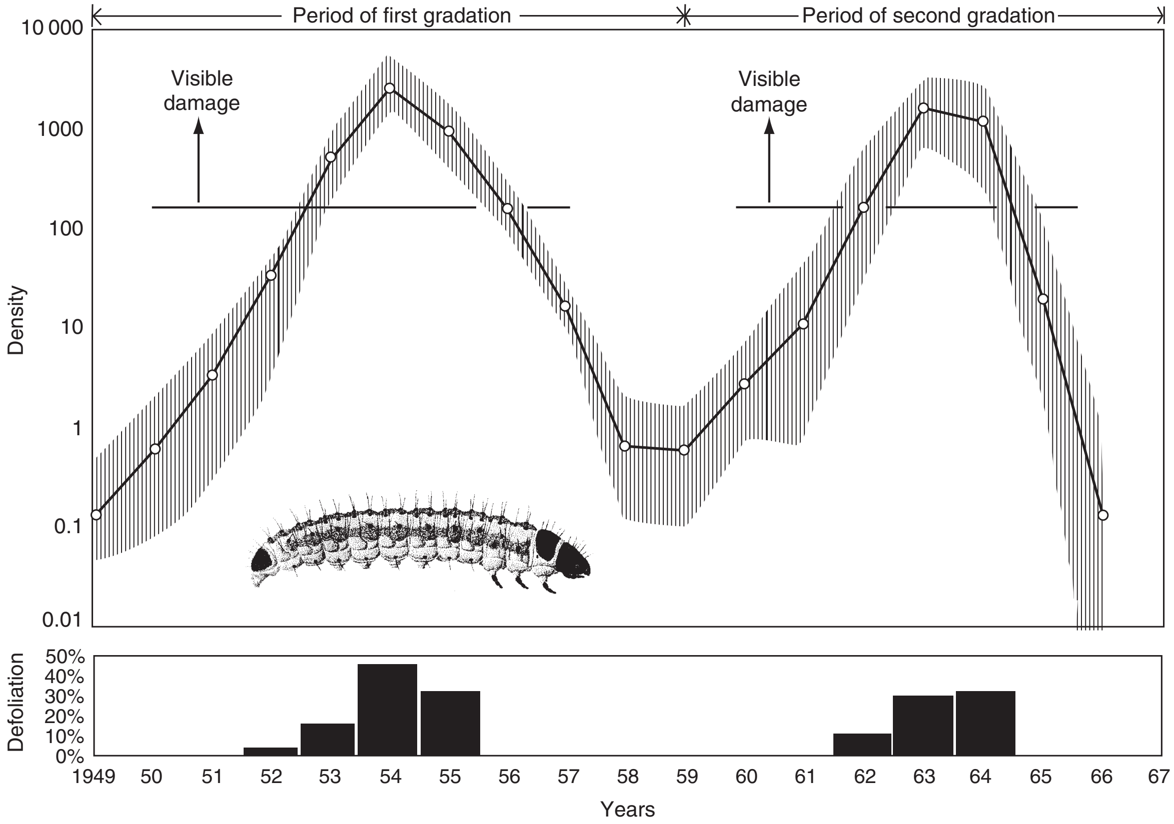


Figure 11.4 Two cycles of the grey larch tortrix, 1949–1966, in the Engadine Valley, Switzerland, showing densities above which damage was visible. Open circles and solid line show the mean density of larvae per sampling unit of 7.5 kg of branches, and the shading shows the range of means in 11 sectors of the Engadine Valley. Defoliation is the percentage of needles lost to defoliation. From Baltensweiler (1968).

11.1.4 Are outbreaks natural?

That outbreaks are natural phenomena, rather than promoted by human management, is illustrated by western spruce budworm in the Sangre de Cristo Mountains, New Mexico (Swetnam and Lynch 1993, Swetnam and Betancourt 1998). Tree-ring analysis revealed nine regional outbreaks of budworm between 1690 and 1989, with a periodicity ranging from about 22 to 33 years, with the duration of effects lasting about 11 years per outbreak. Many outbreaks were recorded before human impact on these forests became significant in the late 1800s. Of course, this does not mean that management practices do not exacerbate eruptive dynamics. Planting pure stands of Scots pine in Germany may well have promoted eruptions, illustrated in Figure 11.1 and 11.2, and use of insecticide spray from 1925 onward on these forests may have increased the frequency of eruptions. But outbreaks of forest insects continue to occur in remote areas such as in Alaska, Canada and Russia, the Rocky Mountains and high-elevation beech forests in Japan.

In eastern Canada tree-ring analysis has also recorded episodic outbreaks of high spruce budworm impact back into the 1700s (Blais 1958, 1962, 1965).

And in Maine, head capsule fossils, probably of budworm larvae, show that outbreaks were occurring more than 10 000 years before the present (Anderson *et al.* 1986). There can be little doubt that eruptive insect populations have occurred in natural vegetation ever since major groups of herbivores evolved, such as grasshoppers, moths, sawflies and bark beetles.

11.2 The mechanistic understanding of why population density change occurs

Nobody expects that populations should be stable over long periods of time, but why should they show such dramatic changes, why should so many be cyclic, and why are changes synchronous in some species over large geographic areas? These are the questions that have been addressed over at least the last 100 years, but the answers are not easy to achieve. Even with long-term studies over 15 years, there may be no certainty about the mechanisms involved (see Table 11.1, Lawton 2000, Wool 2002). And where there are some clear indications of mechanisms, different approaches may yield different processes. For example, vertical interactions, in particular top-down impact of natural enemies, have been emphasized in many studies, but horizontal interactions, within the trophic level of herbivorous insects, may be more important as the subtlety of the plant–herbivore interplay becomes better understood (Faeth 1987). In the well-studied spruce budworms, certain measures of parasitism, predation and temperature, plus the density in the previous generation, entered into the model as the factors which correlated best with population change (Morris 1963b, 1969). The general scenario developed by Morris (1963c) and associates was that populations of spruce budworm were maintained at a low equilibrium by weather conditions and the functional and numerical responses to host-density variation by predators and parasites. Survival rate increased in dense, maturing fir forest, and when several consecutive years of favorable weather prevailed, such populations escaped the low equilibrium because natural enemies became ineffective. The budworm population rose to the carrying capacity of the forest, depleting the food supply, resulting in reduced fecundity and starvation in some years, and causing mass migration to other forest stands. Population eruptions spread from favorable epicenters through mass dispersal. Either trees were not killed and a high equilibrium population was maintained for several years, or trees died and populations crashed locally. The return of unfavorable weather may cause a decline in populations at any time.

After recognizing the assumptions in Morris's model and general scenario, Royama (1992, p. 335) stated that, "My forgoing analyses of the same field data do not support the five major assumptions in the early theory," and Royama listed them as follows:

(1) Budworm larval survival was not as responsive to changes in weather as in Morris's scenario, and forest maturity did not appear to play a role in population outbreaks and larval survival.
(2) Budworm decline in populations tended to be synchronous over the landscape, independent of foliage condition. Food shortage was not a general cause of population decline.
(3) Moth invasions occurred in epidemic and endemic populations; they complemented increasing populations, but did not affect decreasing or endemic populations.
(4) Epicenters of population eruption did not appear to be important in budworm dynamics.
(5) The data did not support the concept of two equilibria in budworm populations, the endemic and epidemic levels.

Royama (1984, 1992) preferred a scenario in which food-web structure was crucial: food supply, other defoliators, primary natural enemies and secondary natural enemies. The relative densities of other defoliators were important, as Faeth (1987) argued, for they provided alternative hosts and prey for generalist enemies. The necessary components needed to explain population change became much more complex. Also, another set of data suggests that cool, wet periods promote budworm outbreaks, rather than dry, warm weather, but this was in the drier southwestern United States, based on dendrochronological studies (Swetnam and Betancourt 1998).

Such discrepancies in the conclusions of Morris and Royama, based on the same available data, deserve careful scrutiny, beyond the scope of this book. However, the alternative views do illustrate the need for clarity and objectivity in presenting data and conclusions, not always evident in the literature.

For these reasons we enter this debate on mechanisms of population change with an open mind, and a critical eye for correlational studies, experimental studies of mechanisms, hypothetical scenarios and empirically based factual explanations. We will start with examples of abiotic factors, such as the influences of soil and weather, and move on to biotic influences, including the bottom-up effects of food supply, lateral effects among herbivores, and top-down impacts of natural enemies. However, in these complex systems involving multiple trophic levels, we should expect no simple answers. Rather, interactions among factors are to be expected in the regulation of populations, and these interactions are likely to become more complex as we understand more about any one species. We will explore these more complicated scenarios at the end of the chapter.

11.2.1 Abiotic factors: direct effects

Rainfall and temperature dictate much of the distribution of plants and animals (Merriam 1894, 1898, Holdridge 1967, Holdridge *et al.* 1971), so these factors could be invoked in understanding the population dynamics of almost all species. That they often are not probably means that the study was limited in its geographical coverage, and limited to a physical environment to which the study organism is well adapted. Clearly, dynamics are likely to be different at the center and at the edge of the geographic range of a species.

Close to the northern edge of its geographic range, the dynamics of the fall webworm, *Hyphantria cunea*, were dominated by the heat available each summer (Morris 1969, reviewed in Price 1997). Outbreaks followed periods of above normal mean August and September temperatures (Figure 11.5). Mechanistic studies showed that the effects of temperature were positive on larval survival, female fecundity and population density in the following generation, food quality, maternal effects on quality of the next generation and parasitoid attack. In addition, a population evolved rapidly in response to warmer summers, for example, and became more vulnerable to cooler summers as a result. Most of the population dynamics of this insect could be explained mechanistically by the amount of heat available each year. Many experiments were needed to understand these links, and they were accompanied by broad-scale surveys of populations each year in New Brunswick, Canada.

Another study in the northern part of an insect's range showed that cool temperatures in September, when females were developing eggs, limited populations (Whittaker and Tribe 1998, and references therein). A model for the lined spittlebug, *Neophilaenus lineatus*, at a high-altitude site in northern England, using the mean minimum monthly temperature for September in the year preceding the sample as the independent variable, accounted for 75% of the variation in population density. Experimentally raising temperatures by 1 °C in the field, using enclosures and unenclosed controls, resulted in a strong positive response in spittlebug density, a result consistent with the mechanistic explanation of density variations for this insect.

Temperature in the spring also impacts early-feeding caterpillars, such as the western tent caterpillar, *Malacosoma californicum pluviale* (Myers 2000), either directly or indirectly through influences

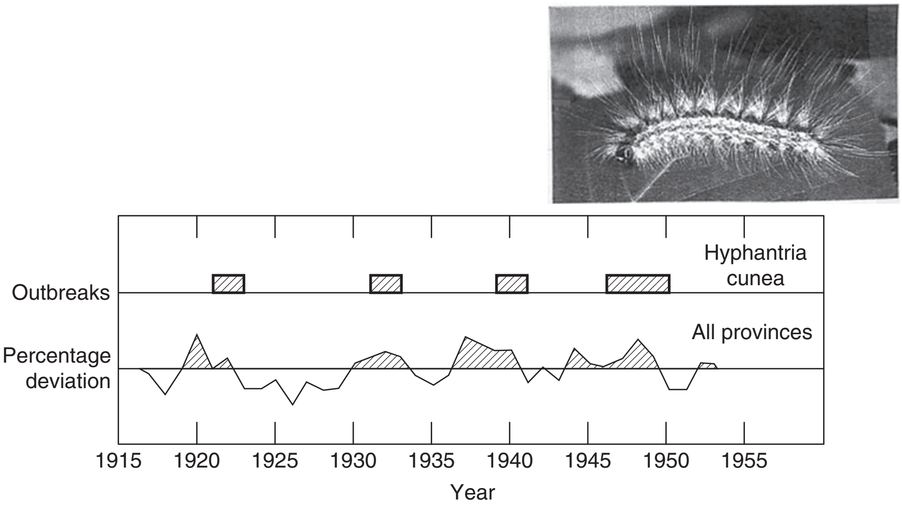


Figure 11.5 The relationship between positive deviations from mean August and September temperatures in eastern and central Canada and fall webworm population outbreaks. From Morris (1964).

of host-plant phenology. The latter effect will be discussed under host-plant effects.

Rainfall and drought are commonly implicated in the population dynamics of insects and, of course, temperature interacts with precipitation to define evapotranspiration and the water available to plants (Holdridge *et al.* 1971). Just what the chain of effects among these factors is, often remains unresolved. For example, "virtually every plant process is affected by drought" (Mattson and Haack 1987a, p. 367). Therefore, effects may be multiple, either directly on the insect population, or mediated through the host plant. Temperature and drought may affect insect herbivores in at least six ways (Mattson and Haack 1987b): increased temperatures may improve development and survival; drought-stressed plants may be more attractive or acceptable; plants may become physiologically more favorable; higher temperatures may increase insect rates of detoxication and improve immune responses; beneficial symbionts may be favored and natural enemies reduced; genetic changes through natural selection or induction of enzyme systems may favor insect survival. Added to this complexity is the frequent failure of experiments to reveal mechanistic linkages between water stress and the insect response. In nature, water stress on host plants is more commonly positive for insects, but in experiments herbivores are typically affected negatively (Waring and Cobb 1992). This discrepancy may well be accounted for by the **pulsed stress hypothesis** proposed by Huberty and Denno (2004), discussed in Chapter 4 in the section on the plant-stress hypothesis.

It is hardly surprising that if host plants grow well, with no water stress, they produce longer shoots, more and larger leaves, and grow more rapidly, all likely to be favorable to many insect species. This argument has been developed as the plant-vigor hypothesis (Price 1991a), which has been supported for many insect species (Price 2003a) (see chapter 4 Section 4.3). The hypothesis was erected in response to the plant-stress hypothesis, proposed by White (1969, 1974, 1976), which promoted the relationship between stressed plants and insect outbreaks. These two hypotheses are more complementary than contradictory, for they apply to different systems and kinds of plants and herbivores, and they

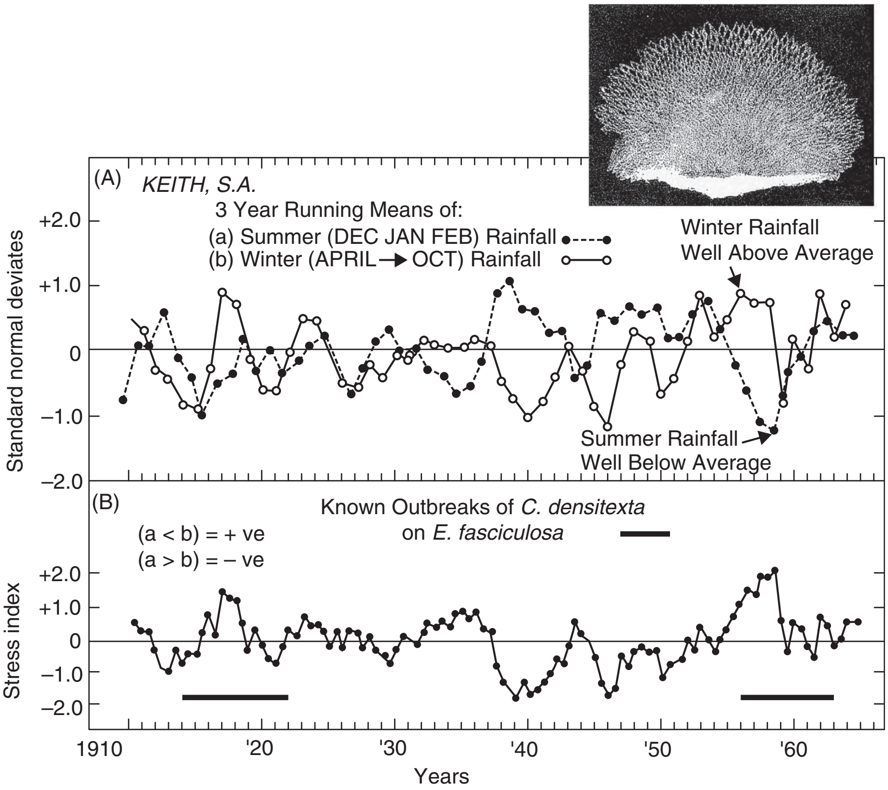


Figure 11.6 The relationship between White's (1969) stress index and outbreaks of *Cardiaspina densitexta* on *Eucalyptus fasciculosa* at Keith, South Australia. High stress created by high winter rainfall followed by low summer rainfall coincided with an outbreak of the psyllid from 1956–1963. However, the earlier outbreak from 1914–1922 started before the stress index became positive. From White (1969).

highlight the likelihood of a continuum of effects of plant-quality variation on insect-population density. Therefore, we will examine a few specific studies as examples of the relevance of plant stress and plant vigor.

White's (1969) initial study concerned outbreaks of the psyllid *Cardiaspina densitexta* on its host plant *Eucalyptus fasciculosa*, in southern Australia. He emphasized the contrast between high winter precipitation and low summer precipitation that produced physiological stress in the eucalyptus trees (Figure 11.6). Outbreaks of *Cardiaspina* occurred when the stress index peaked in the late 1910s and the 1950s. Clearly, the correlation is not perfect, and this should encourage more detailed studies. White (1974, 1984, 1993, 2008) went on to emphasize the role of plant stress in influencing the population dynamics of several insect species, mainly through stress increasing the levels of nitrogen which favored establishment of young larvae.

Bark beetles frequently become epidemic during droughts, as in large areas of the southwestern United States during years of drier than normal weather (e.g., the most recent during 1996 to 2004) (Christensen *et al.* 1995, Ogle *et al.* 2000, Breshears *et al.* 2005). On pinyon pines, a dominant vegetation type over huge areas of the southwest United States, up to 90%+ of trees were killed (Gitlin *et al.* 2006), and where trees did not die, stressed trees were more favorable to the shoot-boring moth, *Dioryctria albovitella* (Mopper and Whitham 1986, Cobb *et al.* 1997). The primary defense in pines and other conifers is resin flow when damage occurs. This resinosis, or pitching out, derives from resin canals and from induced defenses after attack (see Berryman 1988). In both systems resinosis is compromised during drought.

High precipitation increases plant growth, and this is favorable to many insect herbivores. The species that stimulated the development of the plant-vigor hypothesis was the stem-galling sawfly, *Euura lasiolepis*, with a willow host plant. Females prefer to oviposit on the longest shoots available, on which the larvae survive well. There is a strong ovipositional preference and larval performance linkage (Craig *et al.* 1989). High winter precipitation, which influences willow growth in the late spring, results in more and longer shoots, and this results in increased oviposition and higher larval survival in the sawfly. Indeed, most of the gall-inducing sawflies we have studied, as well as many other gall-inducing species, attack the longest shoots they can find (Price 2003a). Robust growth also is beneficial to shoot borers, root feeders, external stem feeders, leaf miners, and some aphids, scale insects and spider mites. Frequently insects are seen close to the meristems of host plants and the herbivores may often attack younger, more vigorous plants.

In addition to temperature and precipitation, edaphic factors such as soil quality are frequently pieces of the puzzle explaining why eruptions of insects occur in one area and not another. Poor, dry soils, such as alluvial sands, or gravelly or cinder soils, are generally thought to promote plant stress, increased larval survival, and outbreaks in certain kinds of insects. We have mentioned several studies in this chapter which included poor dry soils (Klimetzek 1990, White 1974, Christensen *et al.* 1995, Mopper and Whitham 1986, Cobb *et al.* 1997). In addition, a major sawfly pest of jack pine in eastern Canada, *Neodiprion swainei*, usually erupts in poor quality jack pine stands on sandy plains (McLeod 1970), and the highest mortality of pinyon pine, caused directly by drought, was on the west aspect of cinder cones with the hottest conditions (Ogle *et al.* 2000). (Cinder cones are produced by small volcanic eruptions, producing well-drained, dry habitats for plants to colonize.) However, one of the hypotheses advanced by Kamata (2000) on outbreaks of the beech caterpillar, *Syntypistis punctatella*, on Honshu and Hokkaido islands in Japan, invokes soils rich in nitrogen resulting in higher nitrogen in leaves and better survival of larvae. As is typical when we consider any one kind of factor, it may be beneficial for some insect herbivores and deleterious for others. Generalizations are hard to find because studies tend to be idiosyncratic, making synthesis virtually impossible.

The causes of periodicity and synchrony of population change over large areas has been debated for a long time, certainly since Elton (1924) discussed the topic. Abiotic factors that exert influence on species simultaneously across the landscape are likely to contribute to population synchrony. The solar cycle and sunspot activity are factors that have kept recurring in the literature as a possible mechanism producing wide-scale effects on populations. A good example of the correlation between sunspot activity and population outbreaks concerns the autumnal moth, *Epirrita autumnata*, on mountain birch, *Betula pubescens*, in northern Finland (Ruohomäki *et al.* 2000). Sunspot minima covary with low temperatures which kill overwintering eggs. During subsequent warming trends all populations in the region tend to recover and outbreak synchronously (Figure 11.7), a pattern that has been repeated for 12 outbreaks since 1880. The mechanistic link between sunspot activity and outbreaks is unknown, but we will examine this later in the chapter. Killing temperatures are not the key ingredient in population synchrony in

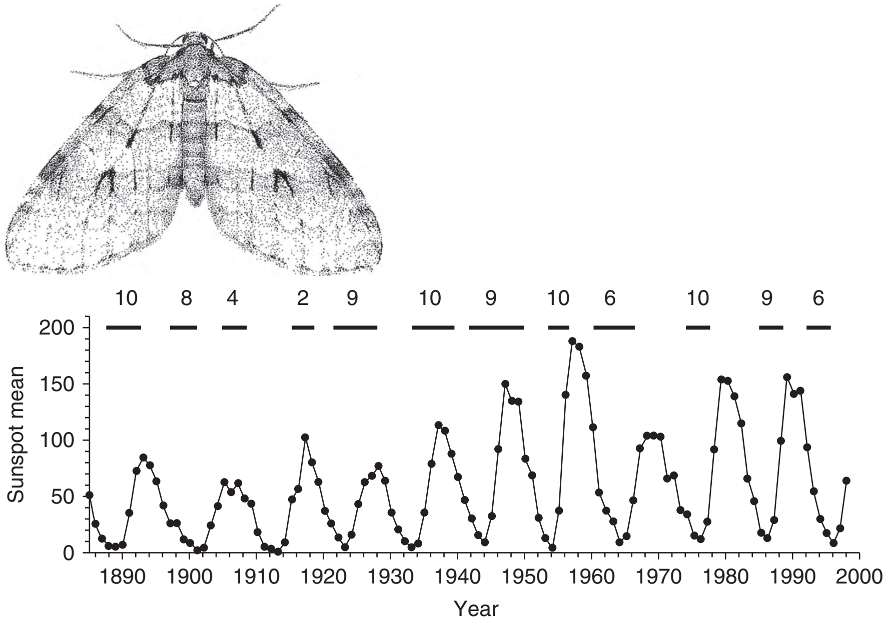


Figure 11.7 Sunspot cycles in northern Europe and outbreaks of autumnal moth shown as bars above the cycles. The number above each bar shows the number of years from the previous sunspot minimum to the first year of the outbreak. From Ruohomäki *et al.* (2000).

other species because similar cycles occur in species that do not suffer egg mortality in cold winters (Myers 1998), and Nilssen *et al.* (2007) have argued against the feasibility of sunspot cycles to explain cyclic outbreaks.

Other weather factors may well act to synchronize population dynamics, such that populations are in unison over large areas. For example, the spruce budworm in eastern North America shows remarkable synchrony of outbreaks from western Ontario into Maine, eastern Quebec Province and Newfoundland (Figure 11.8, Williams and Liebhold 2000). The specific weather factors were not identified, but temperature and precipitation were both widely correlated spatially across this region, and may well have caused synchrony of cycles, because otherwise populations would have cycled independently in each area. This synchronizing effect is now called the **Moran effect** because Moran (1953) originally noted the possibility. "Under this hypothesis, some exogenous factor (most likely a weather condition that affects reproduction or survival) acts synchronously over a large geographic area" (Liebhold *et al.* 2000, p. 263). In the gypsy moth, also, there is considerable synchrony in the beginning of outbreaks over large geographic areas, and in this case the Moran effect may work through the supply of alternative food for a predator (Liebhold *et al.* 2000). Weather is likely to influence acorn crops, and when acorn supply fails small mammal populations decrease, and predation on gypsy-moth pupae decreases, such that there is a synchronous upsurge in the gypsy moth over a large area. Weather may also have more direct effects on the gypsy moth such as minimum temperature in mid-December and mid to late July (Williams and Liebhold 1995a). The correlational studies between temperature and population density did not identify any specific mechanisms involved. Myers (1998) also considered the possible role of the Moran effect, through lows in sunspot activity associated with cold springs, which affected many forest lepidopterans in north temperate latitudes.

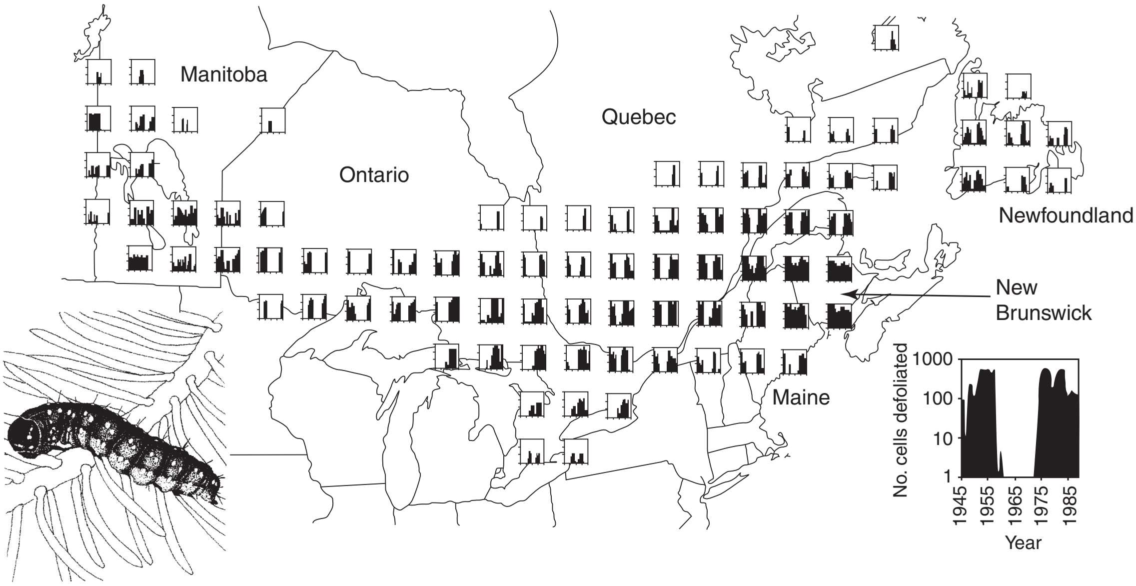


Figure 11.8 The record of detectable defoliation by the eastern spruce budworm from 1945 to 1988 in eastern North America. Each box contains a record of the number of cells, about 5×5 km, defoliated per year, with an example in the lower right box. The maximum number of cells that could be defoliated per year was 1024, and each box represents an area of 160×160 km. From Williams and Liebhold (2000).

11.2.2 Biotic factors

We treat biotic factors in three categories: host-plant effects, lateral effects and natural enemies. In a trophic-level context we can regard these as bottom-up effects from plants, top-down influences from natural enemies and interactions among members of the same trophic level.

11.2.2.1 Host-plant effects

With the emergence of chemical ecology in the 1970s (e.g., Sondheimer and Simeone 1970), a dramatic shift in emphasis took place in insect herbivore population dynamics. Whereas early emphasis was placed on mortality factors in life-table approaches, as we saw in Chapter 9, ultimately the quality of food began to be of major concern. The multitude of ways in which host plants may impact herbivore individuals from the bottom up was addressed in Chapter 4. Here we will emphasize effects of food on population dynamics.

It is intuitively obvious that food should be a major component in the dynamics of organisms, and the examination of the role of plant food has become increasingly sophisticated as the mechanisms of interaction come to be better understood, and inevitably more complex. There are several kinds of influences that plant food can have on insect populations, which we can categorize as:

(1) Direct effects through food quality variation
(2) Direct effects of the quantity of food available
(3) Indirect effects of food.

We will treat these in turn, providing a few examples in the process.

Feeny (1970) showed that larvae of the winter moth, *Operophtera brumata*, which fed in the early spring on very young foliage, benefited from a phenology adapted to maximize larval access to available nitrogen, a limiting nutrient. Soon it became clear that nitrogen in foliage was a key to the growth rate, size and survival of larvae, and fecundity in females (e.g., Mattson 1980, White 1984, Scriber and Slansky 1981, Mattson and Scriber 1987, Slansky and Rodriguez 1987, White 1993).

The direct effects of nitrogen are clear enough in aphids in which population peaks in reproductive rate in a year correspond with peaks in soluble nitrogen availability in leaves (Dixon 1970). Sycamore (*Acer pseudoplatanus*) leaves flush in spring with high nitrogen content and then senesce in the fall, with another peak as nitrogen is withdrawn from the leaf. The densities of the sycamore aphid, *Drepanosiphum platanoides*, follow these trends. White (1993) distinguished between flush and senescence feeders, with each type benefiting from high soluble nitrogen content of leaves in spring and fall, but clearly some species are able to benefit from both flushing and senescing leaves. Many other kinds of insects are strongly influenced by the nitrogen content of food (Slansky and Rodriguez 1987, White 1993), and clearly nutritional quality of leaves is likely to be influenced by soil fertility, drought, flooding, fire and other factors (Tabashnik and Slansky 1987).

The nutritional quality of host plants also changes as plant phenology varies in relation to insect phenology. Many insects feed on the youngest foliage, such as the winter moth, or even in opening buds, as in the spruce budworms, thereby minimizing leaf toughness and maximizing available nitrogen. Should plant phenology become advanced relative to larval activity, leaf quality will decline, and if host phenology is delayed, larvae may starve. Hunter (1992a) was the first to establish a strong link between budburst date and larval density and defoliation. He studied pedunculate oak, *Quercus robur*, and the winter moth interaction, finding a strong positive correlation between trees with early budburst and high larval density. A similar relationship was recorded for the green oak tortrix, *Tortrix viridana*, on the same trees. Budburst phenology was the only variable that accounted for differences in larval density and defoliation for these two defoliating species.

High nitrogen content is usually associated with rapid growth and plant vigor, to which many insects respond positively, both in terms of female ovipositional preference and larval performance: developmental rate, total mass, survival and fecundity. But plant growth may well be stimulated by water availability without a change in soil nutrient status, resulting in lower nitrogen content in plant parts. And yet some insects are still likely to prefer vigorous plant parts. For example, the arroyo willow shoot-galling sawfly, *Euura lasiolepis*, always selects the longest shoots available, on which larvae survive the best, independent of shoot nutrient status (Craig *et al.* 1989, Waring and Price 1988). Many other gall-inducing insects appear to respond in a similar way (Price 2003a), probably because high meristematic activity is needed for an insect to divert the plant's developmental program into its own needs for a gall. "Gall morphogenesis requires that the insects stimulate undifferentiated plant tissues" (Weis *et al.* 1988, p. 469). Other insects respond positively to plant module size, be it leaf, shoot, flower, fruit or seed, including leaf miners, leaf rollers, shoot borers and tephritid flies attacking flowers and fruits.

Plant age is also critical to many herbivores. This is partly because vigor changes with age as physiological aging progresses inexorably through time. The amazing agromyzid fly, *Phytobia betulae*, the larvae of which burrow down vessels in the cambium of birch trees, almost from top to bottom of a tree in their lifetimes, is strongly influenced by tree age (Ylioja *et al.* 1999). Populations rose and fell asynchronously in different areas, but in response to tree age, populations peaked at about 20–30 years of tree age and declined thereafter. Studies of within-year variation showed that populations were higher on rapidly growing trees, and data on among-year variation showed that greater annual diameter growth correlated with higher populations. Another factor in host-plant aging is ontogenetic aging, in which changes in physiology occur at a certain time in the life history of a tree which remain stable thereafter (Kearsley and Whitham 1989, 1997). For example, the narrowleaf cottonwood, *Populus angustifolia*, is susceptible as a young tree to the leaf-feeding beetle, *Chrysomela confluens*, but "**developmental resistance**" sets in as trees mature at a diameter at breast height in the range of 2–5 cm (Kearsley and Whitham 1989, p. 432). However, after maturation trees become susceptible to another herbivore, the leaf-galling aphid, *Pemphigus betae*, which tends to increase in density as trees become large, up to 30 cm in diameter.

The direct effects of food quantity are observed repeatedly during outbreaks of insects when defoliation becomes conspicuous and trees may even begin to die. We have seen many examples in this chapter already. When insect populations grow to over 100 egg masses per m^2 and almost 10 000 larvae per tree, as they have done in the spruce budworm (Royama 1992), the population becomes insatiable, food supply is depleted and larvae starve to death. Even higher densities are known in eruptive grasshopper species, such as the desert locust, *Schistocerca gregaria*, in north Africa, which may reach 103 740 eggs per m^2 (Uvarov 1977: 780 egg pods per m^2, with a mean of 133 eggs per pod). In Brazil, the eruptive spittlebug, *Deois flavopicta*, a pest of pastures, reaches nymphal populations of over 300 per m^2, debilitating pasture grasses (Fontes *et al.* 1995). Adults derived from such populations may cause most leaves in a pasture to die by injecting saliva which induces phytotoxemia.

More subtle effects are seen when exploitation of the food supply by a herbivore also influences the availability of other critical resources for the population. In the larch sawfly, *Pristiphora erichsonii*, in Quebec Province, Canada, larvae will eat any foliage, but females oviposit exclusively into long shoots growing at the tip of a branch. After several years of defoliation long-shoot growth was apparently not possible for attacked trees, eliminating oviposition sites and precipitating a population crash (Cloutier and Filion 1991, Tailleux and Cloutier 1993). Another case of a subtle effect of food supply concerns the jack pine budworm, *Choristoneura pinus*, in which early spring feeding by second-instar larvae occurs preferentially in male cones. Pollen cones provide superior food for larval survival through the spring (over 50%) compared to vegetative buds (less than 20%). However, high populations of budworm defoliate trees, resulting in decreased male cone production in subsequent years. Then, mainly vegetative buds remain as early feeding sites for larvae, survival declines and populations decline (Nealis and Lomic 1994, McCullough 2000).

Indirect effects of host-plant food on insect herbivore populations may take a multitude of forms, with unexpected results. For example, phytochemicals may reduce the efficacy of pathogens of insects, allowing populations to erupt. The gypsy moth, *Lymantria dispar*, appears to outbreak mostly where oaks are most concentrated. These plants have high tannin and other phenolic content in leaves, which are inhibitory to the gypsy-moth polyhedrosis virus, such that survival of larvae on oaks is higher than on other trees in the forests of eastern North America (Foster *et al.* 1992). In experiments with various tree leaf foods, those with the highest hydrolyzable tannins produced the highest survival of virus-infected gypsy moth larvae (Keating *et al.* 1990). Feeding on red and black oaks with high levels of hydrolyzable tannins resulted in about 50% survival of larvae while aspens with very low hydrolyzable tannins led to less than 10% survival. Another indirect effect of plant food is perhaps influenced by the herbivores themselves, through an ecosystem-level modification of plant quality. Hunter (2001a) listed seven mechanisms through which insect herbivores change nutrient cycling and nutrient availability in soils resulting in increased soil quality for plants. All are potentially positive effects. These effects then feed back to the host plant, which gains in foliage nutrients, and possibly loses foliar defenses, both beneficial to herbivore populations. Quality and quantity of foliage may well increase, which affect both herbivore and predator densities (Forkner and Hunter 2000).

Another complex interplay of factors has been proposed by Haukioja (2005) concerning mountain birch and the autumnal moth in Finland. Both herbivory and ultraviolet light (UV-B) induce plant defenses deleterious directly to the herbivore. However, the defensive compounds confer greater immunocompetence to larvae which are able to encapsulate internal parasitoids; parasitism declines dramatically to 1–2% and populations increase, although larvae are smaller. A similar effect of induced defenses increases resistance of gypsy moths to nuclear polyhedrosis virus (Hunter and Schultz 1993).

The effects of plants on insect populations are many and varied. We have illustrated just a few types of effects. The wide range of influences up the trophic system is to be expected because plants provide both food and habitat for insects. And just as human nutrition is proving to have multiple effects on health, we can expect the same for insect herbivores.

11.2.2.2 Lateral effects

Continuing with biotic effects on insect population dynamics, and moving up the trophic system from plant–herbivore interactions, we need to consider herbivore–herbivore interactions. These may be negative, through competition, or positive because one herbivore may modify plant traits in a way that is favorable to another species. These subjects have been treated in Chapter 5 on competition and facilitation, but a few additional considerations are provided here. We have also discussed induced plant defenses in Chapter 4 on plant and herbivore interactions. It is becoming increasingly clear that lateral effects, from one herbivore species to another, are much more common than was generally acknowledged a decade ago. This is largely because of the greater recognition that insects of one species are very likely to influence plant resources for other species; indirect effects via induced plant traits (Ohgushi 2005, Ohgushi *et al.* 2007). For example, a cercopid ovipositing into stems may kill the stem and induce more vigorous growth the next year which is very attractive to leafrollers (Craig and Ohgushi 2002, Ohgushi 2005). The leaf rolls become attractive to aphids, which become tended by ants, which then negatively influence chrysomelid beetle populations (see Figure 1.5). The **interaction web** (Price 2002b) is far more extensive and complex when all kinds of interactions are included rather than when feeding relationships alone are used, as in food webs. Since plant traits induced by herbivores can include defensive phytochemicals, architectural changes, nutritional quality and structures initiated by insects such as leaf rolls and galls, the indirect effects through plant trait alteration become ubiquitous. While induced plant defenses are thought to play a role in the population dynamics of the autumnal moth (Haukioja 2005), and the grey larch tortrix (Baltensweiler and Fischlin 1988), the same induced plant effects are likely to impact other species, in addition to the direct competition for food. Just how much lateral effects, including indirect effects, play a role in population dynamics remains to be seen, because in population dynamics studies the focal insect is emphasized while others are largely ignored.

11.2.2.3 Natural enemies

From the top of the food web down to the insect population under study, natural enemies are likely to play a regulatory role in dynamics. As discussed in Chapters 7 and 8 natural enemies include predators, parasitoids and pathogens. Examination of Table 11.1 on long-term population studies reveals that 12 out of 22 examples have natural enemies implicated as important in the dynamics of their prey or host species. Of course, determining cause and effect is almost impossible without experiments, so the most parsimonious explanation for correlations between insect herbivore population changes and natural enemy changes is a strong bottom-up influence of food supply on the next generation. This is especially valid when population peaks of herbivores are followed by peaks of natural enemies with a time lag of one generation, because food is likely to impact the reproduction and fecundity of one generation and the survival of the next.

Take, for example, an early analysis by Morris (1959) on the relationship between the blackheaded budworm, *Acleris variana*, on spruce and fir, and its parasitoids, and the European spruce sawfly, *Diprion hercyniae*, a defoliator of spruce, and its parasitoids. In both species, Morris found strong correlations between host density and survival after the population had been reduced by parasitoid-caused mortality. He could plot the number of survivors after parasitism in generation *n*, against the number of individuals present in the subsequent generation ($n+1$), and obtain impressively good correlations (Figure 11.9). For the blackheaded budworm, the regression accounted for 86% of the variance, and for the European spruce sawfly, 46% in the fall generation and 69% in the summer generation. Models including more variables hardly improved these estimates (Morris 1969). Morris (1959, p. 580) named this kind of impact by parasitoids a **key factor**, meaning simply that changes in population density from generation to generation are closely related to the degree of mortality caused by this factor, which therefore has predictive power. Morris emphasized in the same paper that "no attempt has been made to establish cause and effect, because single-factor data are scarcely suitable for this purpose" (p. 587). But others have been less rigorous about using correlative data, preferring an interpretation of direct causation between a key factor and population change (e.g., Varley *et al.* 1973). This is, of course, only a preference, without any logical basis. "The only known way to separate causation from spurious correlation is to resort to experiments" (Lambin *et al.* 2002, p. 167).

However, most data in support of natural enemies as regulators of insect herbivore populations is of a correlational nature, so we will take it at its face value. Berryman (1996) argued that cycles in populations of forest lepidopterans are driven by parasitoids in many cases, listing nine species, noting that parasitoids act as second-order feedback, or in a delayed density-dependent way, which produces cycles. Indeed, biological processes are likely to result in cycles because a change in one population is likely to result in a change in an associated organism in the next time period (see Berryman 2002). This lagged effect will drive populations up or down, depending upon the strength of the interaction. So the alternatives are bottom-up or top-down effects, with both potentially playing a role and entering into a **dynamical complex**, as is most likely in the larch budmoth in Switzerland (Turchin *et al.* 2002, p. 140), and quite possible in the autumnal moth in Fennoscandia (Tanhuanppää *et al.* 2002). We would certainly endorse the concept that the majority of, if not all, herbivore populations are in such dynamical complexes, and encourage that this view is espoused as an initial hypothesis when a population dynamics study is undertaken. As Lawton and McNeill (1979, p. 223) expressed it, the insect herbivore is caught "between the devil and the deep blue sea," the "devil" being the natural enemies and "the deep blue sea" the plant food of low nutritional quality.

Where time-series data are coupled with modeling and experiments, the results are most encouraging. A 42-year history of the southern pine beetle, *Dendroctonus frontalis*, in Texas, which attacks pines, including loblolly and shortleaf pines, showed a strong impact of predators on the population dynamics of the beetle (Reeve and Turchin 2002). The main predator was the clerid beetle, *Thanasimus dubius*, whose numbers correlated with *Dendroctonus* numbers in Louisiana (Figure 11.10), and a long-term exclusion experiment lasting 5 years indicated that the predator became effective as a mortality factor as the prey population peaked in the field in 1992 (see Figure 11.10). Of three models tested, the predator–prey model provided the best fit to the cyclical pattern of *Dendroctonus* populations.

A strong case for the role of parasitoids has also been made for the spruce needleminer, *Epinotia tedella* (Lepidoptera: Tortricidae) in Denmark, by Münster-Swendsen (1985, 2002, Münster-Swendsen

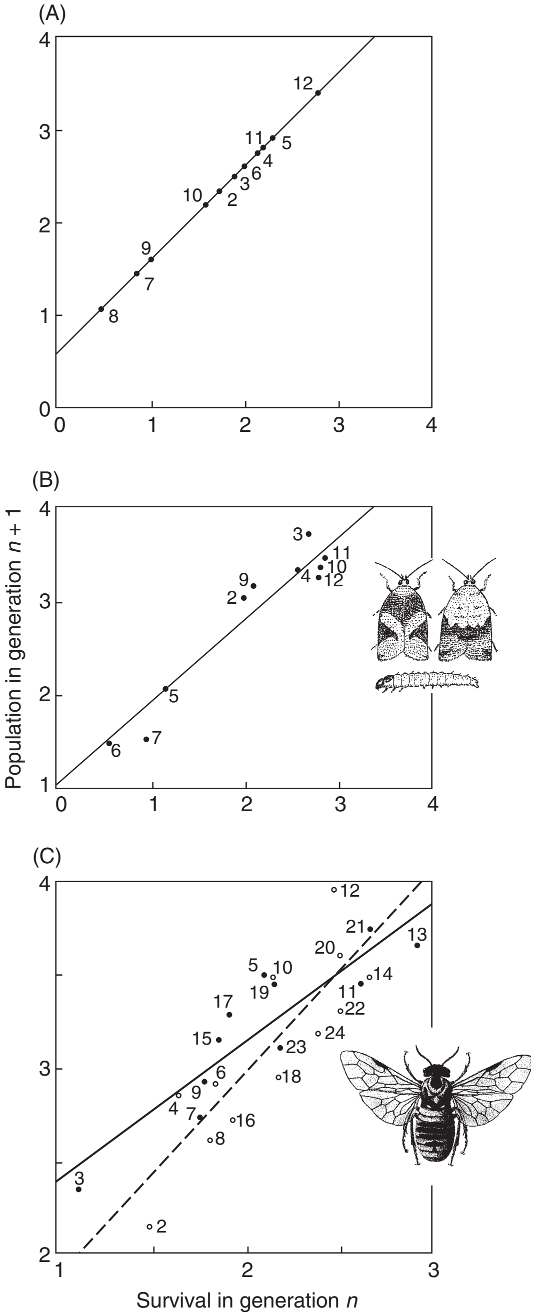


Figure 11.9 The relationship between number of individuals surviving in generation n, and the number of individuals present in the following generation ($n+1$), with values expressed as common logarithms. (A) Results for the

and Berryman 2005). Data were collected for 20 years, 1970–1989, and a time-series analysis on the host–parasitoid interaction indicated that 74% of the variation in needleminer densities could be accounted for. "Parasitism" actually resulted from parasitoid attack and oviposition, which ultimately killed larvae, plus **pseudoparasitism** in which an attack is initiated, but not completed. Gland secretions and sometimes polydnavirus are injected into the host which suppress gonadal development, rendering the resulting adults sterile, but without an internal parasitoid present. This phenomenon accounted for the observation that populations of the needleminer declined when parasitism reached 50%, because an additional 40% of the population suffered from pseudoparasitism. Populations crashed well before defoliation became serious.

The many cases of successful biological control of insect herbivores also suggest that top-down forces can be strong and regulating. However, caution is needed in interpreting results because in natural-enemy introductions, the three trophic levels are frequently exotic species, and food webs are simplified (Hawkins *et al.* 1999). However, this does not alter the fact that natural enemies have been of immense utility in the regulation of insect-pest populations, and there is much to be learned from the literature on biological control.

11.3 Complex interactions

We have seen several examples in which a combination of factors is likely to interact resulting in regulation of an insect population. There are 13 cases out of 22 in Table 11.1 where more than one factor appears to be important: weather and

Caption for Figure 11.9 (*cont.*)
Nicholson and Bailey (1935) model. (B) Blackheaded budworm. (C) European spruce sawfly. Numbers beside the points refer to the $n+1$ generations, and in (C) even numbers are for the fall generations and odd numbers are for the summer generations. From Morris (1959).

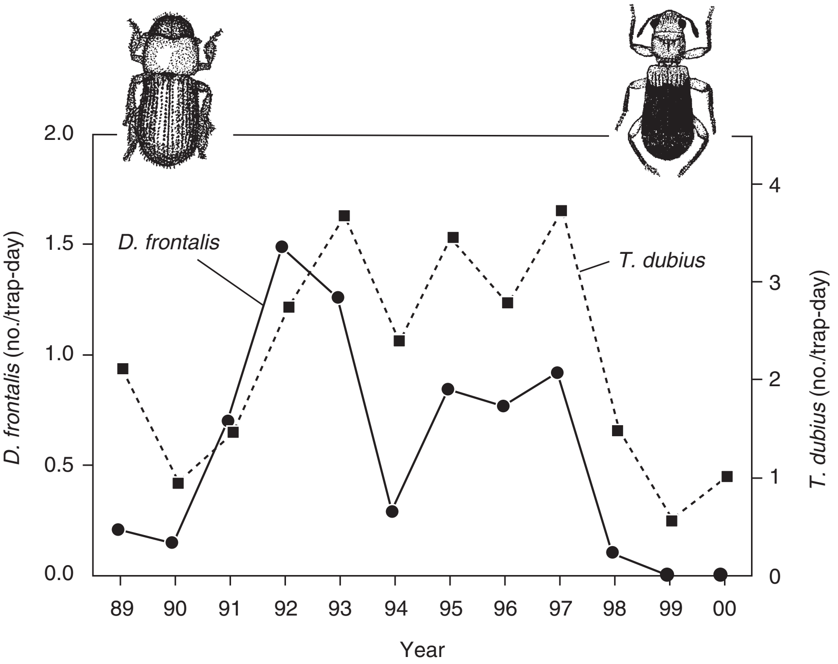


Figure 11.10 Mean trap catches of southern pine beetle, *Dendroctonus frontalis*, and its clerid predator, *Thanasimus dubius*, in Kisatchie National Forest, Louisiana, 1989–2000. From Reeve, J. D., and P. Turchin (2002). Evidence for predator-prey cycles in bark beetles. Pages 92–108 in A. Berryman, editor. *Population Cycles: The Case for Trophic Interactions*, Oxford: Oxford University Press. Reprinted by permission of Oxford University Press, Inc.

predation, temperature and natural enemies, weather and disease, natural enemies and warm, dry zones etc. One example concerns the effects of winter precipitation on willow growth in the spring, which has multiple effects on the arroyo willow stem-galling sawfly, *Euura lasiolepis* (Figure 11.11, Price *et al.* 1998a, Price 2003a). In addition, increased shoot quality results in larger galls, which provide a larger refuge for larvae from parasitoids and percentage parasitism declines. A second example concerns the beech caterpillar, *Syntypistis punctatella*, in Japan (Figure 11.12, Kamata 2000). Defoliation caused a delayed induced defensive response (DIR) in beech trees, including reduced nitrogen and increased tannin in leaves, resulting in reduced survival and body weight of larvae. Low body weight resulted in lowered fecundity, and the percentage of unfertilized eggs increased. Together these factors reduced the quality of beech caterpillar populations. Top-down influences also played their roles, with avian predators being most effective during low-density periods, and the predatory carabid beetle, *Calosoma maximowiczi*, parasitoids and diseases becoming important at peak densities. A final example concerns a rather complex interplay of bottom-up and top-down influences in the mountain birch and autumnal moth interaction in northern Finland (Figure 11.13, Haukioja 2005). When damaged, either by insect feeding or by ultraviolet light, plants respond with a **defense cascade**, in addition to constitutive defenses of phenolics and low nutrient content, which may also play a role in plant defense. The complex defense cascades are induced defensive responses involving various pathways: the octadecanoid, salicylic acid and ethylene signaling

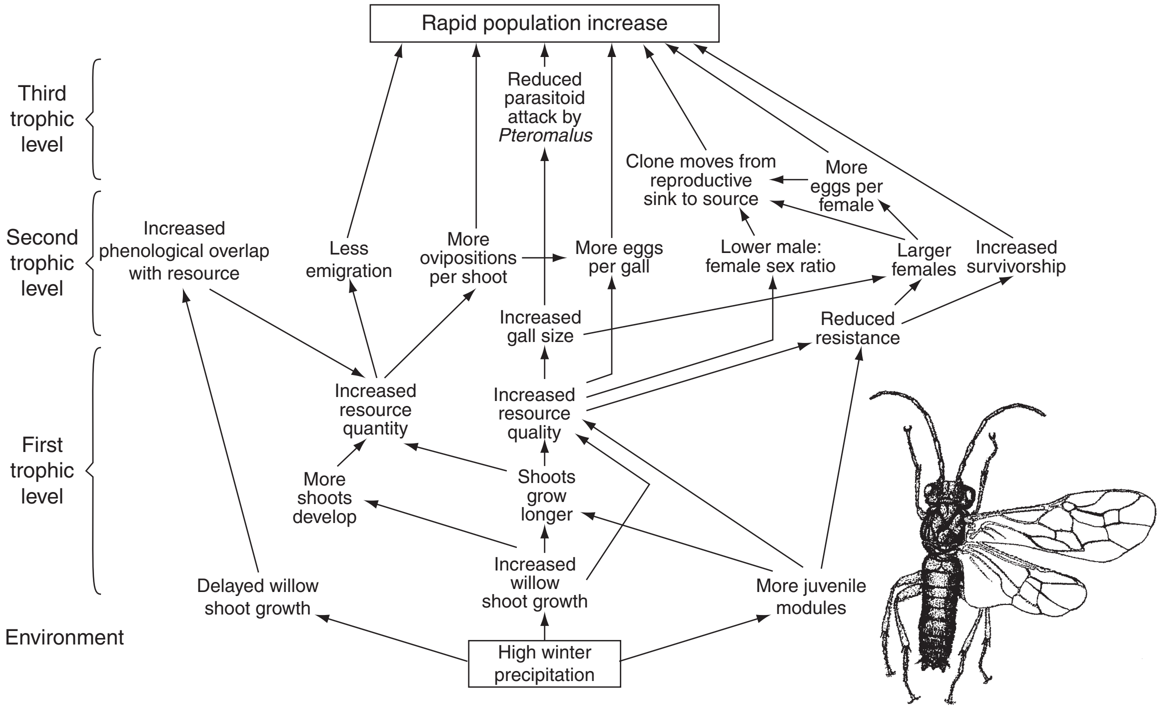


Figure 11.11 The bottom-up effects of relatively high winter precipitation on arroyo willow, *Salix lasiolepis*, the gall-inducing sawfly, *Euura lasiolepis*, and the parasitoid, *Pteromalus* sp., resulting in a rapid population increase. From Price *et al.* (1998a).

pathways discussed in Chapter 4. The constitutive phenolics in leaves had a strongly negative effect on larval growth rate, but survivorship was most influenced by fatty-acid content and the induced octadecanoid pathway. Damage caused by insect feeding also induced production of many volatile compounds including jasmonic acid and salicylic acid, which can induce defensive reactions in neighboring trees, and act as cues to searching predators and parasitoids.

The induced plant defenses caused by feeding larvae were hypothesized to have another effect: that of conferring higher immunity to internal parasitoids through encapsulation, although larvae grow less well, and these effects lagged behind initial feeding damage (Figure 11.13). Thus, populations increase, even though larvae are generally smaller, because encapsulation of parasitoids is so effective. Another plant defense-inducing agent is ultraviolet light (UV-B), which is highest at sunspot minima and, as we saw in Figure 11.7, peak moth densities are seen 3–4 years after sunspot minima (Ruohomäki *et al.* 2000). UV-B triggers the same octadecanoid pathway as chewing insects, such that population increases are likely to be synchronized over large geographical areas. The exact strength of these interactions is yet to be determined, but this intriguing scenario argues for both positive feedback loops (through immunocompetence of larvae) and negative feedback loops (through plant induced defenses and parasitoids), as well as an interplay between abiotic and biotic factors, and bottom-up and top-down effects. So far, one direct test of the hypothesis that variation in the immune response influences population cycles did not support the prediction (Klemola *et al.* 2007).

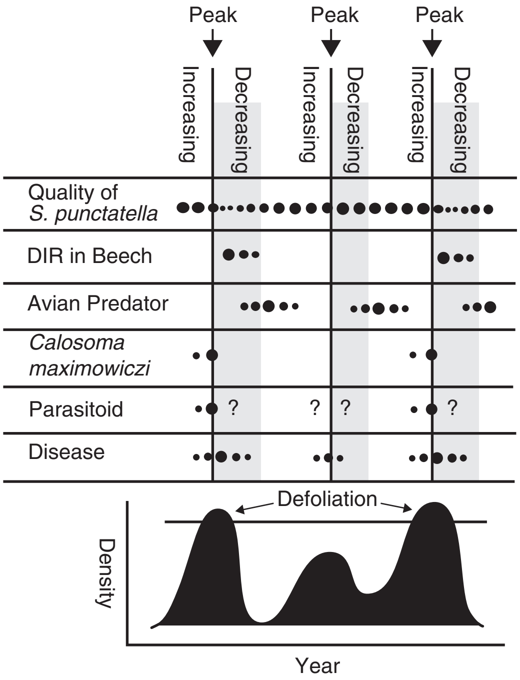


Figure 11.12 The factors involved with the population dynamics of the beech caterpillar, *Syntypistis punctatella*, in Japan, and their relationship to the density fluctuations of the herbivore. DIR = delayed induced defensive response in the beech leaves. Disease appeared to be the factor most likely to be responsible for the cycles. From Kamata (2000).

These three examples illustrate what is likely to be common in insect-herbivore population dynamics: many factors play a role in dynamics, the host plant is highly variable in space and time, and natural enemies must be included in the multiple-trophic-level interplay of constantly varying traits in plants, herbivores and natural enemies.

The examples above are part of a growing concern for integrating bottom-up and top-down, and lateral influences on population dynamics. In a review of experimental approaches to teasing out multiple-trophic-level effects on population regulation, Harrison and Cappuccino (1995) found for herbivorous insects in 20 studies that 9 were regulated from the bottom up, 6 were regulated from the top down and 5 were regulated mostly by lateral effects such as competition or dispersal, and a mean of 60% of studies showed direct negative density dependence. This review highlights the likely limitations on interpreting long-term population dynamics studies which evaluated little more than food quantity in the category of bottom-up effects. In another overview including 604 insect species density dependence proved to be a general feature of population dynamics in a high majority of cases (Brook and Bradshaw 2006).

The motivation to evaluate simultaneously bottom-up and top-down factors in population dynamics is gaining advocates, stimulated in part by the overview by Hunter and Price (1992) with the title “Playing chutes and ladders,” which captures the essence of the idea that effects of factors run up and down food webs. The same view is expressed in the title by Forkner and Hunter (2000): “What goes up must come down?” Progress in this field depends on well-designed experiments which can tease apart multiple potential impacts simultaneously. For example, Denno *et al.* (2002) found that plant nutrition and physical structure mediated natural-enemy impact by spider predators on *Prokelisia* planthoppers. In a native grassland arthropod community, the relative importance of up and down effects showed seasonal variation, with plant quality being important throughout the season, but with cursorial spider effects being limited to early in the season, and then only impacting grazing herbivores (Boyer *et al.* 2003). Albarracin and Stiling (2006) found that up and down effects on a sap sucker and a gall inducer on the salt marsh plant *Borrichia frutescens* were so strong that environmental stress imposed by a salinity gradient did not alter the general properties of the trophic interactions. Another case concerns plant development from young to older individuals of a tropical tree which impacted bird predation on insect herbivores, resulting in changes in herbivore density, species richness and diversity (Boege and Marquis 2006). When these kinds of experiments are coupled with

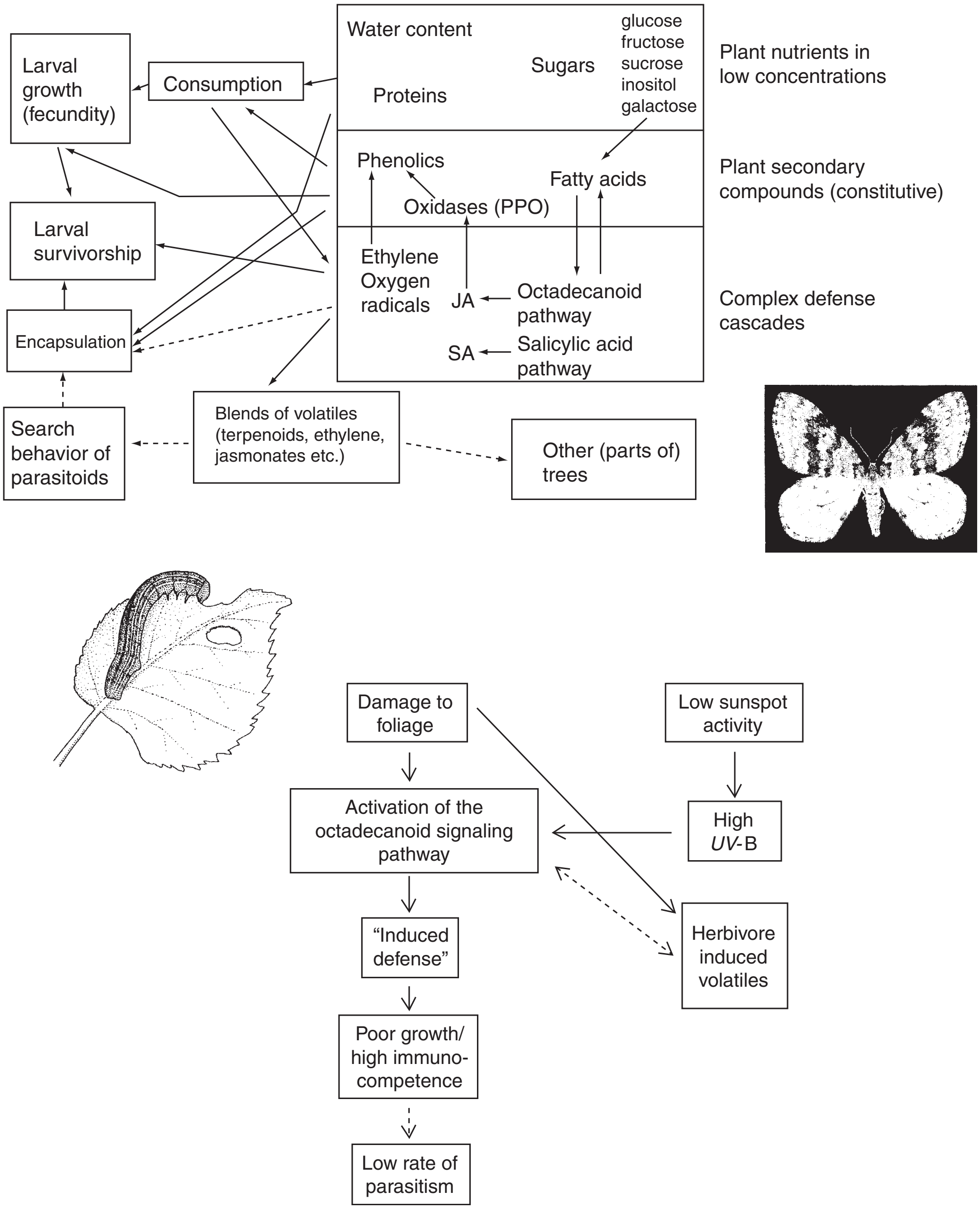


Figure 11.13 A mechanistically based model of birch defense against defoliators in relation to the autumnal moth, *Epirrita autumnata*, in northern Finland (above), and the resulting population fluctuations (below). Dashed lines show relationships known from other systems, but not tested for birch in the study area. JA = jasmonic acid. SA = salicylic acid. Figure is by Erkki Haukioja, and is similar to that published in Haukioja (2005).

longer-term field censuses on population density, the field of insect population dynamics is likely to change significantly.

Long-term studies are as critical as detailed field observations on variations in the trophic system, and experiments to test specific hypotheses. Without the longer-term perspective, time-series analysis and other approaches to modeling of insect populations will be inadequate or impossible, and the predictive value of effective models will be lost, to the detriment of the management of populations and general understanding. Just how much detail is needed in the experiments and long-term data will vary with the species of focal concern. Should spatial and temporal variation be included? Should populations and communities of trophic-level members all receive attention? For how long should experiments be conducted? Prolonged experiments may provide some surprising results and insights as illustrated by Brown *et al.* (2001).

These kinds of studies discussed above, while vital for an understanding of one species' dynamics, are necessarily idiosyncratic. Each species is likely to be changing under a unique set of variables (Table 11.1), and even within the same species, dynamics are often different in various geographic regions or altitudes. Therefore, reaching any kind of general prediction or overview is difficult or impossible. How do we view the wide diversity of patterns in dynamics with a more synthetic approach?

11.4 An evolutionary hypothesis

When searching for broad patterns in ecology it is frequently rewarding to adopt an evolutionary approach using phylogenetic relationships as the basis for comparative studies. While rigorous phylogenetic analysis of traits in groups with outbreak species shows closely related species with very different traits and dynamics (Hunter 1991, 1995a,b), we can still characterize genera and families that have a relatively high number of outbreak species or species with latent population dynamics. For example, acridid grasshoppers have a much higher proportion of eruptive species than the bush katydids (Orthoptera: Tettigoniidae: Phaneropterinae) and diprionid sawflies have a larger proportion of outbreaking species than the tenthredinid sawflies (Price 2003a, Price *et al.* 2005). The fundamental differences between these contrasting groups are the details of their morphology, life history and behavior.

Related species share common morphological, life history and behavioral traits. For example, acridid grasshoppers mostly oviposit into the soil with tough, short elements of the ovipositor; they are not selecting places where tiny first instar nymphs will commence feeding. In contrast, bush katydids have ovipositors adapted for piercing plant tissues, and placing eggs where nymphs will start to feed. Many other traits are correlated with these differences (Price 1997, 2003a). In the phylogenetic-constraints hypothesis such fundamental differences in ovipositor structure are regarded as **phylogenetic constraints**: they limit the path of adaptive radiation to a rather narrowly circumscribed set of evolutionary opportunities. Around this constraint cluster a set of adaptations that mitigate the constraint, the **adaptive syndrome**, which is likely to include behaviors that improve oviposition or larval success. These evolved traits in the phylogenetic constraint and adaptive syndrome then dictate much of the ecology of the group sharing these traits. The ecology can be called the **emergent properties** of the group, including distribution, abundance and population dynamics. For example, the robust, digging ovipositor of acridid grasshoppers (Orthoptera: Acrididae) allows the deposition of egg pods with many eggs in the soil, and it produces selection which results in nymphs that emerge with the ability to fend for themselves, and with a generalized ability to eat whatever they find first. In turn these characteristics produce populations that can become dense and produce outbreaks when there is ample food for first instar nymphs (e.g., Showler 1995, Price 2003a). In contrast, bush katydids (Orthoptera: Tettigoniidae: Phaneropterinae) lay eggs singly or in small groups, in many cases in carefully selected leaves, of which there is likely to be a limited number in any locality. Oviposition is slow and highly selective, and emerging nymphs are specialized to feed on one or a few host plants. Populations will therefore remain low and show latent population dynamics, which explains why there are extraordinarily few pest species in such a large subfamily (Price 2003a).

In a similar way, tenthredinid sawflies are generally non-pest species, with latent population dynamics. These sawflies have the phylogenetic constraint of a flexible ovipositor which is inserted into plant tissue, and thus exhibit highly selective oviposition preferences for soft, rapidly growing plant tissue, which sets a limiting carrying capacity in the environment. There is a strong ovipositional preference and larval performance linkage limiting oviposition usually to a single host-plant species and the most vigorous shoots available in that species (Craig *et al.* 1989). (Why diprionid sawflies, related to the tenthredinids, are so frequently eruptive requires a special explanation provided in Price [2003a].)

Contrasting with these tenthredinid sawflies are the outbreaking forest Lepidoptera found in the same kinds of environments as the sawflies. They have a pad-like **oviporus**, which cannot pierce plant tissue. Eggs are laid on surfaces, such as bark, rocks, twigs and leaves, often months before larvae will commence feeding, and well away from the initial feeding location. For example, gypsy moths typically oviposit low on the trunks of trees, but they will also lay eggs in brown paper bags if placed there, and on vehicle wheels. There is no ovipositional preference for suitable feeding spots for their larvae, and no preference and performance linkage (Price 1994). Larvae necessarily forage for themselves, and over time evolve to become generalists in their capacity to feed on foliage in the forest. Thus, foliage represents a potentially huge resource with a very high carrying capacity, which under favorable ecological conditions will result in eruptive population dynamics and defoliation of large tracts of forest (Price 2003a).

The phylogenetic-constraints hypothesis does not explain when outbreaks will occur or why some species show eruptive dynamics, while related species do not. But it does develop a mechanistic explanation of why certain groups have relatively high probabilities of eruptive dynamics and others remain latent. More comparative studies within and between related groups would be valuable.

11.5 Metapopulation dynamics

Beyond the study of individual populations, groups of populations in a region may interact as sources and sinks, providing and receiving colonists as individual populations wax and wane, and sometimes go extinct. The field of metapopulation dynamics addresses these issues of regional patterns (e.g., Gilpin and Hanski 1991, Hanski and Gilpin 1997). “Populations are defined as ensembles of interacting individuals each with a finite lifetime; metapopulations are ensembles of interacting populations with a finite lifetime, in other words expected time to extinction. The metapopulation concept is thus closely linked with processes of population turnover, extinction and establishment of new populations, and the study of metapopulation dynamics is essentially the study of the conditions under which these two processes are in balance and the consequences of that balance to associated processes” (Hanski and Gilpin 1997, p. 4).

Hanski (1997) noted four conditions that are consistent with a metapopulation structure:

(1) Suitable habitat for a species is patchy over a landscape, and many patches are large enough to sustain an individual breeding population for a generation or more.
(2) All local populations have a risk of extinction.
(3) Recolonization of suitable habitat patches is possible because patches are sufficiently close.

Nearest-neighbor distances between patches are small relative to the dispersal ability of the species of concern.

(4) Local populations are not synchronous in their population dynamics, such that densities in one population may be high, providing potential colonists, while another may be going extinct.

These conditions are met in the dry meadows used by the Glanville fritillary butterfly, *Melitaea cinxia*, on the Åland Islands of southwestern Finland, which is now considered to be a classic case of metapopulation structure. Discrete patches of dry meadow averaged 0.13 ha in area, with a maximum size of 6.80 ha and a total of 1502 patches sampled. Of the 377 local populations present in 1994, the largest contained about 500 butterflies, but even such large populations are known to have gone extinct. The mean nearest-neighbor distance among dry-meadow patches was 240 m, so movement among patches was easy for butterflies that flew a mean of 590 m and a maximum of 3050 m while migrating between patches. Populations were to a large extent asynchronous in their population dynamics. Adding to the interest and complexity of this metapopulation structure is the parasitoids and hyperparasitoids, food plants of the butterfly and a powdery mildew on one host-plant species (van Nouhuys and Hanski 2002a,b, van Nouhuys and Laine 2008). Differential dispersal abilities of all these species create an ever-changing checkerboard of interactions, with coexistence of species dependent on details of the competitive and dispersal abilities of each (e.g., van Nouhuys and Punju 2010).

The kinds of organisms likely to exist with similar metapopulation structure can be easily imagined. Other species of butterfly are obvious candidates (Thomas and Hanski 1997), and about 60% of Finnish butterflies were estimated to qualify as existing in metapopulations similar to that of the Glanville fritillary (Hanski and Kuussaari 1995). Insects in similarly patchy habitats are numerous: dragonflies in ponds and lakes, forest insects occupying dead tree trunks, and fire-adapted insects. Herbivores on patchy weed species, such as the cinnabar moth, *Tyria jacobaeae*, and its parasitoid, *Cotesia popularis*, both dependent upon the host plant, *Senecio jacobaea*, in the Netherlands (van der Meijden and van der Veen-van Wijk 1997) are also candidates for metapopulation dynamics. Any species of plant showing patch dynamics and their herbivores may well illustrate metapopulation structure (e.g., Pickett and White 1985). As habitats become more fragmented because of habitat destruction, plants and their herbivores and pollinators will move toward metapopulation structure. For example, the ancient oak scrub vegetation of Florida has become highly fragmented due to human disturbance (e.g., Menges 1999, Quintana-Ascencio and Menges 1996, Quintana-Ascencio *et al.* 1998). Archipelagoes may be formed by typical aggregations of islands in water, such as the islands of Åland, or they may be habitat islands on a mainland, but in either case such habitat structure is likely to impose a metapopulation structure on the residents (e.g., spiders on Bahamanian islands, Schoener and Spiller 1987, Spiller and Schoener 1990b). Many kinds of parasites have very patchy distributions (Price 1980) in which metapopulation models are applicable, such as in chigger-borne rickettsiosis.

The spatial population dynamics of species with metapopulation structure will depend on the spatial arrangement of habitat patches (Figure 11.14, Harrison and Taylor 1997). The Glanville fritillary represents a "classic model" (Figure 11.14A), the mainland-island model illustrates the case of a large population supplying recruits to small outlying populations that build and go extinct (B). There may be sufficient movement among patches to retain cohesion of a single patchy population (C), or so little recolonization that populations gradually decline to extinction, resulting in a non-equilibrium or declining metapopulation (D). Inevitably, complex combinations of these models are possible (E). Modeling of metapopulations depends on the patchwork nature of the habitat, the probabilities of colonization and extinction, the mobility of individuals, and, not least, the question being addressed. Good introductions to the modeling of

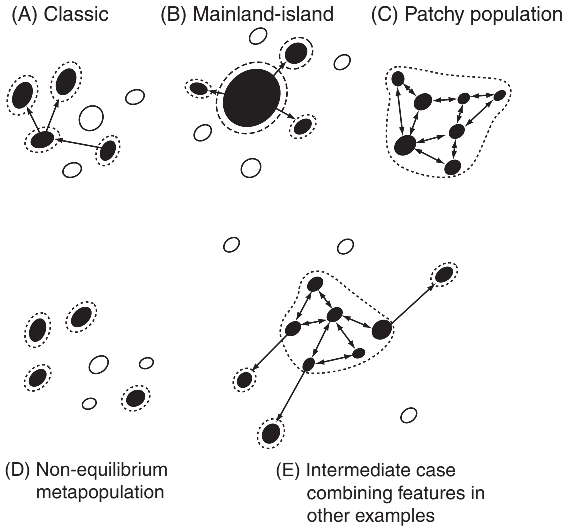


Figure 11.14 Examples of population clusters that represent metapopulations or similar spatial arrangements. Based on Harrison and Taylor 1997.

metapopulation dynamics are provided in Gilpin and Hanski (1991) and Hanski and Gilpin (1997).

It is not only the spatial arrangement of habitat patches, but also the composition of the landscape mosaic which may influence dispersal rates and thus the likelihood of patch extinction and colonization. Cronin (2003) quantified the movement of the prairie planthopper, *Prokelisia crocea*, among discrete patches of its prairie cordgrass host plant, *Spartina pectinata*, in mark-release-recapture experiments. Predictions derived from these dispersal experiments accurately predicted natural planthopper distributions obtained from a survey of 146 cordgrass patches over five generations. The spatial structure of this population resembled that of a mainland-island metapopulation with the dynamics in a few mainland patches being more important than regional processes for the persistence of the population as a whole. Planthopper densities and patch occupancy rates were positively correlated with patch size, but the amount of movement among cordgrass patches was also affected by the surrounding matrix, the habitat encountered by planthoppers when dispersing between patches of host plants. In fact, the composition of the landscape, specifically the presence of mud flats versus non-host grasses in matrix habitats, was relatively more important than patch-related factors such as quality, size or isolation in affecting local population abundance and dispersal rates among patches (Haynes *et al.* 2007). This system highlights the importance of considering the entire landscape context when attempting to predict how population distributions may change over time. These metapopulation and metacommunity studies are also relevant to parasitoid efficacy (e.g., Cronin 2007a,b), and to conservation in patchy environments (e.g., Baum *et al.* 2004).

Applications

Planning and management

Understanding the population dynamics of damaging insect pests is central to any management approach, be it in forestry or agriculture, or the epidemiology of diseases and their insect vectors. Prediction of trends in pest densities is important, and most effectively practiced when a mechanistic understanding of population dynamics is achieved. Then, the driving variables can be monitored and pest population responses can be predicted. Driving variables may be any of those discussed in this chapter: winter precipitation effects on the next generation, sun-spot cycle minima, winter or summer temperatures, and all of these may be influenced by global warming likely to cause more frequent outbreaks, at least in northern latitudes (Kozlov and Selikhovkin 2005). Even if mechanisms are not understood, time-series analysis may allow accurate predictions to be made based on the former dynamics of the population, especially if it is cyclic (e.g., Berryman 1999). Forecasting has become a major management approach for many insect species, both for temporal and spatial change in abundance and distribution (e.g., Tobin *et al.* 2004). Monitoring mosquito populations, and interactions among species and their predators, is vital for effective management of vector populations (e.g., Lounibos *et al.* 1997, 2001). The population dynamics of other pests, such as fire ants, need to be understood at the population level (e.g., Adams and Tschinkel 1995, 2001, Tschinkel *et al.* 1995). Studies on predators, like spiders, and their impact on prey populations encompass many aspects of population dynamics (e.g., Greenstone and Sunderland 1999). Silvicultural practices in forestry may well change the responses of insects, such as to thinning, which in some cases favor population growth of herbivores (e.g., McMillin *et al.* 1996, McMillin and Wagner 1998, Moreau *et al.* 2006). Landscape planning in agriculture is also vital, based on the movement of insects and their dynamics in crop systems, especially when transgenic crop plants are used. The ratio of transgenic genotypes, such as Bt cotton with the gene for the insecticidal toxin from *Bacillus thuringiensis*, to the susceptible genotype, and their spatial arrangement, must be carefully planned for optimal effect (Carrière and Tabashnik 2001, Carrière *et al.* 2001, 2002, 2003).

Many aspects of population dynamics are required to investigate the success or failure of biological control agents. For the control of weeds, knowledge of the demography of the target plant species is needed, as well as the temporal and spatial dynamics of the herbivorous biocontrol agents. Natural enemies of the herbivores may also play a role in diminishing efficacy of the biocontrol strategy (e.g., Goeden and Louda 1976). Likewise, in the biological control of pest insects, the dynamics are likely to involve multiple trophic levels, indirect effects and a complex interplay of interactions (e.g., Price *et al.* 1980, Gange and Brown 1997, Tscharntke and Hawkins 2002).

In conservation biology also, information on the population density and dynamics is a necessary component of planning and management (see Samways 1994, Gaston *et al.* 1993, McGeoch and Samways 2002). The design of nature reserves depends very much on the population structure required in a target species which allows the persistence and hopefully the increase of populations. As habitats become more fragmented through human activity, metapopulation models become increasingly relevant to conservation management. Increasingly isolated habitats become more akin to archipelagoes of habitats in which local colonization, extinction and migration rates must be understood for adequate design of nature reserves. Approaches using the theory of island biogeography (see Chapter 14) and metapopulation dynamics models which emphasize the importance of the spatial linkage among local populations, or within a patchy population (see Figure 11.14C), are necessary if a viable population structure is to be maintained.

With a good mechanistic understanding of population dynamics comes the ability to predict the distribution, abundance and dynamics of species. These are areas of central concern to ecology, and central to the application of ecology to management, in whatever form it takes.

Summary

Population numbers change in time and space. Long-term studies have shown that large-magnitude fluctuations in density are common and may be synchronous over large areas. They also show that many factors impact population changes and combinations of factors are commonly implicated in eruptive dynamics: weather, plant quality, natural enemies and competition may all play a role in insect population dynamics. Twenty-two insect species, each studied for 15+ years, were reviewed to illustrate the range of factors found to be of major influence in the population dynamics. Species with eruptive and damaging population dynamics form a small proportion of species over the landscape, and outbreaks may be relatively brief under natural conditions, and naturally occurring before humans managed ecosystems. Drivers of population dynamics include abiotic factors such as rainfall, temperature and soil quality, and biotic influences including host-plant effects, lateral effects through competition, and natural enemies. However, complex interactions may be common, such as winter precipitation affecting plant growth and vigor, which is beneficial to herbivores as a food source, but also because the herbivores are better protected against natural enemies. Herbivory may also affect plant nutritional and defensive qualities, which can impact fecundity, viability of larvae and resistance to natural enemies. Therefore, a multitrophic-level approach is essential for understanding population dynamics, with bottom-up, lateral and top-down effects evaluated simultaneously, and coupled with experiments which test for mechanistic linkage between independent factors and population responses. However, the many variables involved with population change, and the many approaches adopted for their study, make generalizations difficult to detect and conceptual advances challenging.

An evolutionary hypothesis on population dynamics provides a conceptual approach based on phylogenetic constraints in lineages such as the presence or absence of an ovipositor. Around this constraint an adaptive syndrome evolves and together these evolved characters enable predictions of the emergent properties of populations: the ecological attributes of distribution, abundance and population dynamics. The hypothesis suggests why some taxa are more eruptive than others, but does not explain why related species show different dynamics, presumably explained by ecological differences in their environments.

Beyond the dynamics of populations we treat dynamics among populations, addressing the subject of metapopulation dynamics. Populations are patchy over a landscape and are small enough to go extinct periodically, but emigration and colonization are important factors keeping metapopulations dynamic and persistent. Interest in this subject and its relevance is likely to increase as habitat fragmentation advances.

Planning and management of landscapes depend upon a good understanding of insect population dynamics of pest species, beneficial insects and of the conservation of species.

Questions and discussion topics

1 For any insect species you select, how would you plan a long-term study on its population dynamics using field observations and experiments? Suggest one or more hypotheses which would guide your planning.

2 The existence of interaction webs with strong lateral influences is well established, making the study of several species in the web advisable. Discuss the probability that the dynamics of eruptive and damaging species are impacted by other members of interaction webs, and how studies might be designed to study this phenomenon.

3 How would you develop evidence arguing that the plant-stress and the plant-vigor hypotheses are ends of a continuum of effects of plant quality on insect population dynamics rather than contradictory hypotheses?

4 Consider landscape-scale dimensions and the kinds of combinations of habitat and insect species on this landscape which would probably represent a metapopulation. What would be the value of a metapopulation approach to studying these species rather than focusing on one population?

5 What argument would you employ in generating an impact assessment, for example on road construction, which involves a threatened or endangered species of butterfly or dragonfly in the habitat: (a) that a short-term study of a few weeks will be adequate for accurate predictions to be made; (b) that a long-term study is required for adequate impact assessment; (c) that experiments must be conducted to evaluate impact?

Further reading

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Part V **Food webs and communities**

CONTENTS

We have built the conceptual basis for this part of the book through our earlier treatment of behavior, then interactions among species at the same and different trophic levels. We have also discussed population ecology in Part IV, so that we are aware of the kinds of interaction and variation that species may contribute to the communities they live in. Now, in Part V, we explore concepts and evidence on how species fit together into communities, how communities are organized and the interactions promoting order and predictability.

We are now dealing with groups of species in the same area so we can compare the number of species in communities on similar resources and explore the reasons why communities should differ or are similar in their species richness. Few communities have been investigated at all trophic levels and with all components included, from plants to decomposers, to herbivores and higher trophic levels, including invertebrates and vertebrates. But when this is accomplished, a novel vision of communities is achieved, which we discuss at the end of Chapter 12.

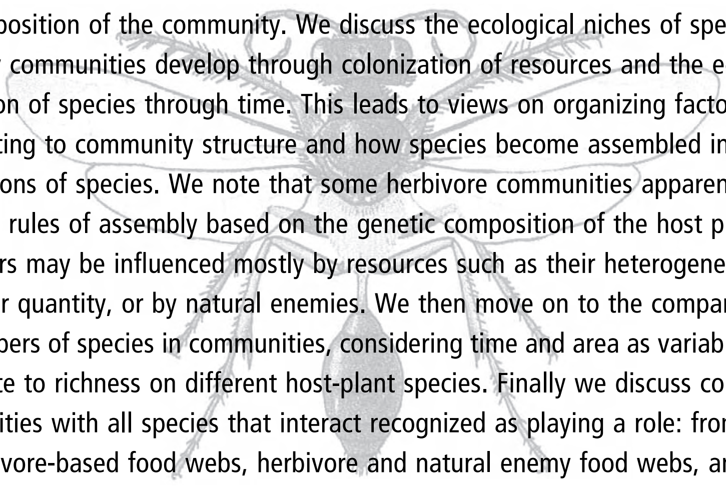
As we saw in Parts II and III of this book, community members may exert a strong impact on members of trophic levels one removed from the immediate interactions. An example is plants attracting or repelling natural enemies of herbivores. Thus, multitrophic levels interact simultaneously requiring a chapter on these kinds of machinations and their consequences. In Chapter 13 we explore this field in which both direct and indirect interactions play their roles in organizing the community. The effects of plants up the trophic system and of predators downwards may impact all trophic levels, producing trophic cascades of interaction and community-wide effects. We will see that many indirect interactions involve non-trophic effects of one species on another, which may not even encounter each other. Such influences include change in plant architecture or phytochemicals caused by one species which influence another herbivore species feeding subsequently. These influences increase greatly the diversity of interactions in a community, largely missed by an emphasis on food webs. Therefore, we revisit a theme which we introduced first in Chapter 1.

After we have dealt with interactions and patterns within communities we can increase our range of interest to broader patterns over the landscape and over the globe, the subject of Part VI on broad patterns in nature. As we will see, gaining a clear understanding of insect biodiversity requires a detailed knowledge generated by understanding all foregoing elements of this book. Also, the discovery of broad patterns still depends upon knowledge of individual species and their interactions with others.

12

Community structure

In this chapter we consider what a community really is and how we conceptualize the composition of the community. We discuss the ecological niches of species and how communities develop through colonization of resources and the ecological succession of species through time. This leads to views on organizing factors contributing to community structure and how species become assembled into associations of species. We note that some herbivore communities apparently illustrate rules of assembly based on the genetic composition of the host plant, but others may be influenced mostly by resources such as their heterogeneity, their quality or quantity, or by natural enemies. We then move on to the comparison of the numbers of species in communities, considering time and area as variables which contribute to richness on different host-plant species. Finally we discuss complex communities with all species that interact recognized as playing a role: from plants to detritivore-based food webs, herbivore and natural enemy food webs, and up to the top predators in the system.



12.1 The community

Various concepts of the **community** coexist in the literature: “the organisms that interact in a given area” (Price 1997, p. 21); “an assemblage of populations that coexist in an area” (Root 2001, p. 295); “the total living biotic component of an ecosystem, including plants, animals and microbes. The term . . . implies interaction between the individuals and species . . .” (Moore 1998, p. 145). Morin (1999) discusses the concept at length, with it being so entrenched in the ecological lexicon that almost any view is viable and acceptable. In this book we prefer to emphasize interactions among species as a necessary criterion of the community, just as interaction is the cornerstone of human communities, a comparison first noted by Elton (1927).

Of course, it is very hard to find groups of species that do not interact: plants with herbivores, parasites with hosts, predators with prey. Whether all species must interact to be included in a community is debatable, but it is unlikely that all species in an ecosystem actually affect each other. Therefore, where interaction is not established and unimportant to the argument, the term **assemblage** is advisable, which may refer to the assemblage of insect herbivores on a tree, or insect detritivores in a pond.

When interactions are emphasized in community ecology there has tended to be a difference in emphasis among terrestrial and aquatic ecologists. Terrestrial communities have frequently been conceived as groups of species on the same trophic level, with **lateral effects** emphasized: competition, coexistence, niche differences, indirect effects and the number of coexisting species, as examples. In aquatic systems there has been more of an emphasis on trophic relationships up and down food webs: predation, trophic cascades and “the trophic-dynamic aspect of ecology” of Lindeman (1942). These differences are by no means absolute, but they reflect the kinds of interests fostered in the rather separate disciplines studying terrestrial and aquatic systems.

The terms community, assemblage and association are used almost interchangeably in the literature, mostly differing in the context of their usage. We, in this book, will use community as a group of interacting species, and an assemblage as a group of species on a particular resource, such as a plant individual, or species, without any assumption of interaction. The term association has been employed for decades in relation to plant assemblages with described characteristics, such as those in a peat bog, an alpine meadow or a riparian habitat (see Gleason 1926, Clements 1936). However, all three terms may be used in the same paper in more-or-less interchangeable ways, for example by Prado and Lewinsohn (2004).

Particularly concerning terrestrial communities involving plants as hosts and insect herbivores, it is convenient to consider the herbivores on a particular plant species as a **component community**, and herbivores on all plants in a habitat as the **compound community** (Root 1973). Component communities on a single plant species are frequently studied as a way of simplifying the interactions to the point where details may be understood. Root (1973) studied the insect community on collard plants (*Brassica oleracea* var. *acephala*), and Van Zandt and Agrawal (2004a,b) inspected insects on milkweed (*Asclepias syriaca*). Community concepts may also apply to whole taxa of plants and insects, such as the insects in flower heads of a tribe in the Asteraceae (Prado and Lewinsohn 2004), going beyond the local habitat. The term community is employed in many ways, as is so common with ecological terms, so authors will no doubt continue to define the term as they wish to use it.

The unit of interest within a community is usually the species, but species differ enormously in their influence within the community. Therefore, some jargon has developed, meaning a technical language rather than any derogatory connotation. Foundation species, core species, dominant species, keystone species, structural species and ecosystem engineers are all terms denoting a particularly important role in a

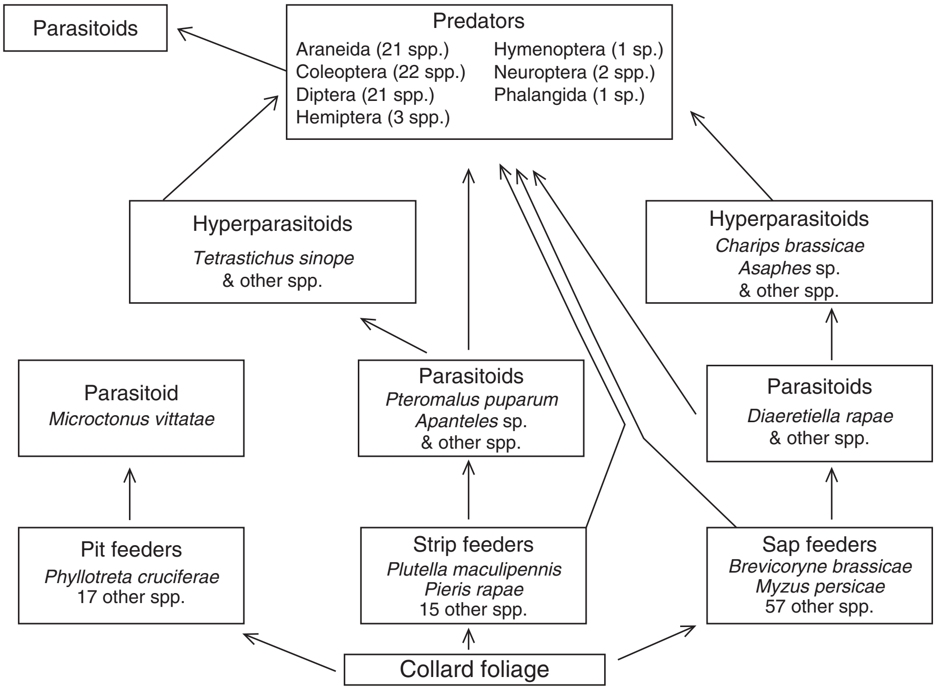


Figure 12.1 The food web of arthropods based on collard plants, with the three major guilds of herbivores indicated as pit feeders, strip feeders and sap feeders. From Root 1973. See also Figure 1.4 in this book.

community or an ecosystem, and all are defined in Ellison *et al.* (2005).

Species may be grouped into a **guild**, which is defined in Chapter 4 as "a group of species that exploit the same class of environmental resources in a similar way" (Root 1967, p. 335, 2001). Such groups define the basic roles that species play in the community; for example, the guilds of species on collard plants identified by Root (1973): the pit feeders, strip feeders and sap feeders (Figure 12.1). Pit feeders chew pits in leaves, for example the three flea beetles in the genus *Phyllotreta* (Coleoptera: Chrysomelidae). The strip feeders are the caterpillars, grasshoppers and snails, the insects with mandibular mouthparts, and the snails with a radula which acts as a scraper and collector. The sap feeders are aphids, cicadellids, mirids and relatives, all with sucking mouthparts, and feeding on plant sap and other fluids. The guild concept therefore focuses attention on groups of species that are most likely to compete, interfere, preempt resources and otherwise interact. Guilds are frequently studied in relation to niche occupation and niche differences among species.

Progressing to larger components of communities, trophic levels and food webs are recognized. A **trophic level** is a stage in the sequence of feeding interactions up a food web from primary producers to top carnivores. These stages in a terrestrial system include plants as primary producers, herbivores as primary consumers, predators and parasitoids as carnivores, and higher trophic levels of parasites and carnivores. The linkage among species defines **food chains** and **food webs**. Elton (1927, p. 56) coined the term food chain as "chains of animals linked together by food, and all dependent in the long run upon plants." Food webs attempt to describe the set of linkages in a community, usually emphasizing feeding interactions, thereby combining the food

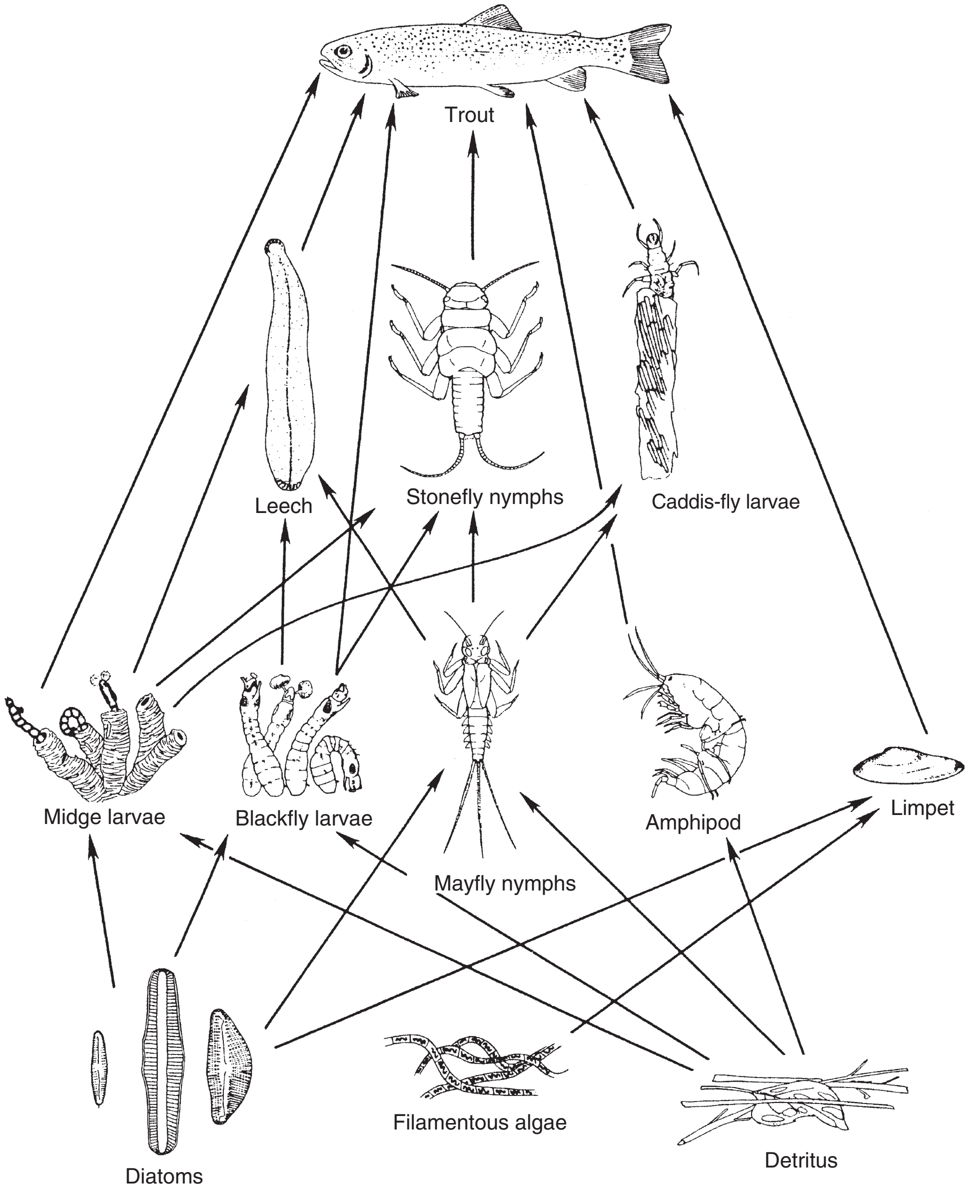


Figure 12.2 A food web of aquatic organisms showing insects and other invertebrates as grazers, detritivores and predators, and the web-like interactions among them. From Price 1984a.

chains and the linkages between them (Figure 12.2). In fact "food webs are … caricatures of nature" (Pimm 1982, p. 1), because in nature they change constantly in space, and with the seasons, interactions differ in frequency and intensity, and they are all simplified to only the major interactions. However, food webs capture the essence of community interactions, they simplify an otherwise bewilderingly complex world and they have stimulated much conceptual development and hypothesis generation in ecology (see Morin 1999). The next chapter on multitrophic-level interactions will discuss food webs more fully.

12.2 The ecological niches of species

Part of the conceptual structure of the community is provided by the roles that species play in that community, or the places in that environment which they occupy. These species characteristics are captured in various definitions of the **ecological niche** (Whittaker and Levin 1975), which was discussed briefly in Chapter 5, and expanded here. Elton (1927, p. 64) wrote that the ecological niche of a species "means its place in the biotic environment, *its relations to food and enemies*" (italics are in the original): the part it plays in the ecological theater. In his paper "The niche-relationships of the California thrasher," Grinnell (1917) emphasized "the requirements and behaviors expressed by a species wherever it normally occurs" (Root 2001, p. 295). This definition encompasses elements of the environment essential to the species, and the role of the species in that environment. But, to actually measure the niche of a species, we need a more formal view, provided by Hutchinson's (1957) definition: an *n*-dimensional hypervolume in the environment, the perimeter of which circumscribes the space in which a species can reproduce indefinitely. This simply means that we can measure the distribution of a species on multiple gradients to form a three-dimensional space, and beyond into multidimensional space, in which the species can persist. For example, gradients may be formed by temperature, stem width and moisture content of wood for bark beetles, as well as other requirements.

Hutchinson's view of the niche enables the measurement of ecological niches by plotting the distribution of a species on one or more gradients, or set of resources. The set of resources may be divided into resource units, such as types of leaf litter or depth of bark, or vegetation types, and ordered on a gradient of such units. Then the proportion of a species, A, occupying each unit can be estimated and plotted on the gradient or resource set (Figure 12.3), and the **niche breadth**, B, can be calculated as:

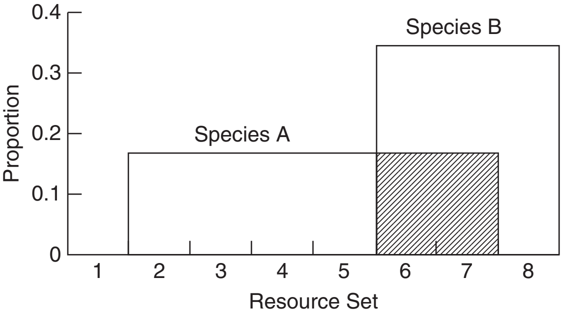


Figure 12.3 Hypothetical distribution of two species, A and B, on a resource set, or gradient, showing the proportional distribution of each species in each resource unit. Species A shows a broad niche with individuals spread evenly across the set of resources. Species B has a narrower niche and a greater proportion of individuals in each unit occupied. The shaded area shows the proportional similarity, but species A overlaps species B more than B overlaps A. From Price 1997.

$$B = 1/\Sigma_{i=1}^{s} p_i^2 (S) \tag{12.1}$$

Where p_i is the proportion of a species found in the ith unit of a resource set, S is the total number of units on each resource set, where $B_{max} = 1.0$, and $B_{min} = 1/S$ (Levins 1968). B can be scaled to vary between 1 and 0, enabling direct comparison among species distributions on resource sets with different numbers of units (e.g., Colwell and Futuyma 1971).

Another species, B, may have a narrower distribution on the same gradient as species A, but it may overlap species A on the gradient (Figure 12.3, with overlap shown as the shaded area). This **niche overlap** can be calculated as:

$$\alpha_{\text{ij}} = \Sigma_{n=1}^{n} p_{ih} p_{jh} (B_i) \tag{12.2}$$

where α_{ij} is the niche overlap of species i over species j, p_{ih} and p_{jh} are the proportion of each species in the

hth unit of a resource set, and B_i is the niche breadth of species i (Levins 1968).

The distribution of species A and B in Figure 12.3 are also similar over two resource units, and **proportional similarity** is estimated by the formula:

$$PS = \Sigma_{i=1}^{n} p_{mi} \text{ or } PS = 1 - {}^{1}\!/_{2}\Sigma_{j=1}^{n}\left|p_{ij} - p_{hj}\right| \qquad (12.3)$$

where p_{mi} is the proportion of the less abundant of a pair in the ith unit of a resource set with n units, and p_{ij} and p_{hj} are the proportions of species i and h respectively, in the resource unit j. $PS_{max} = 1$, and $PS_{min} = 0$ (Whittaker 1952, who used **percentage similarity**).

12.2.1 Actual and realized niches

Niche breadth, overlap and similarity provide some basic measures for niche analysis. Many others have been employed (see Krebs 1999, Southwood and Henderson 2000). These formulae could also be used for analyzing a single species' distribution, when coexisting with other species. This can be called the **actual** or **realized niche**. Also, the niche that could be occupied in the absence of other species may be referred to as the **potential** or **fundamental niche**. Thus, community effects on a species may be quantified.

One of the principles of niche ecology is that no two species can occupy the same ecological niche (Grinnell 1914), which is similar to the so called **Gause's principle** (or **axiom**, or **hypothesis**) (1934) that no two species can live together indefinitely on a single limiting resource. Coexisting species with similar ecology are typically found in different microhabitats, such as bark beetle species occupying different parts of a dying tree (Figure 12.4). The structure of the habitat defines the kinds and sizes of beetles, and to a large extent the time of attack and persistence on a particular resource.

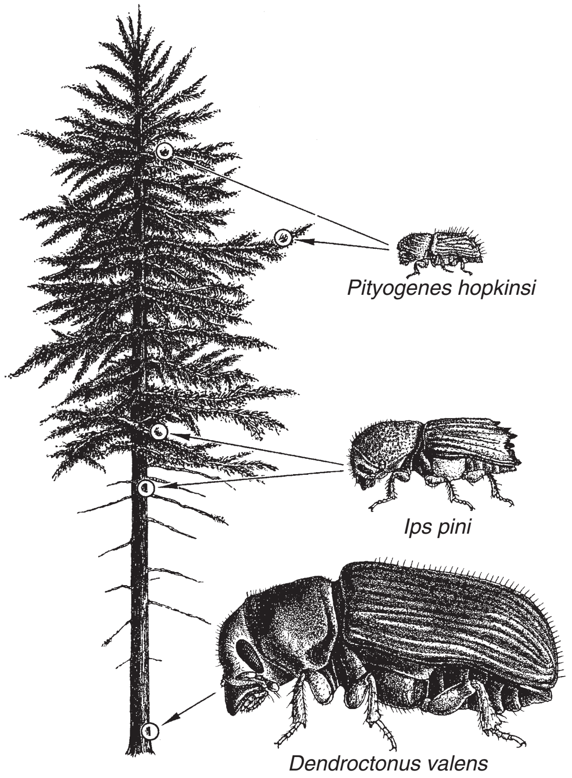


Figure 12.4 Three bark beetle species occupy different regions of dying white pines, *Pinus strobes*, in the northeastern United States and Canada, with the size of beetles correlated with bark thickness. The relative sizes of the beetles are illustrated. The red terpentine beetle, *Dendroctonus valens*, attacks the base of trees. The pine engraver, *Ips pini*, invades the upper trunk and large branches, and is usually much more abundant than the larger beetle. *Pityogenes hopkinsi* enters the bark on smaller branches, which provide a very large area for attack, with this species regarded as one of the most abundant bark beetles in the northeast. Drawing by Alice Prickett. From Price 1975b.

12.2.2 Occupation of the same niche

However, at least two claims have been made in the literature that species do indeed occupy the same niche. Neither has stood up to more detailed scrutiny, but the histories of these cases are instructive. They concern leafhoppers in the genus *Erythroneura*, and bark lice in the genus *Mesopsocus*.

Ross (1957, 1958), an acknowledged expert on cicadellids, found that six species of *Erythroneura* occupied the same niche on sycamores, or plane trees

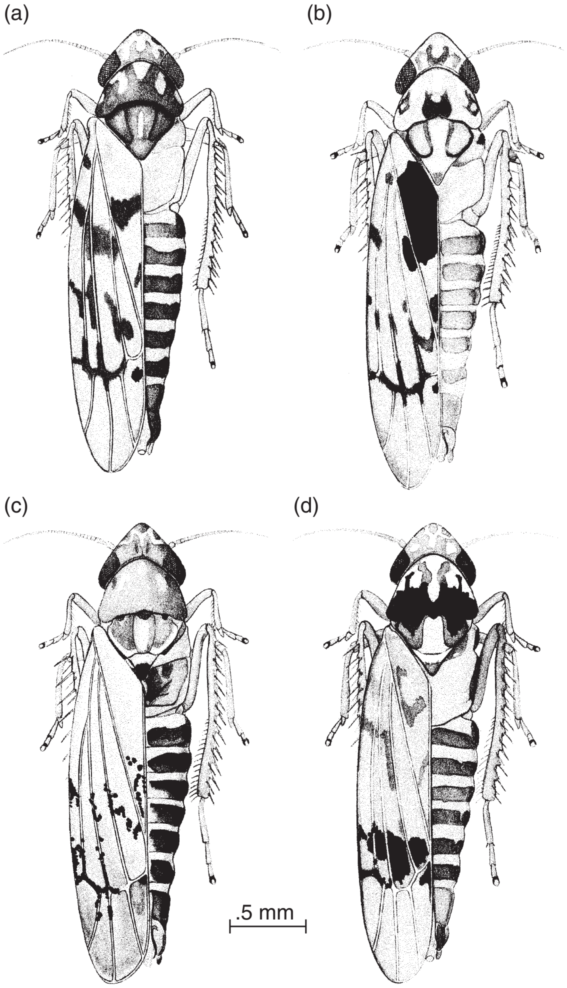


Figure 12.5 Sycamore cicadellids in the genus *Erythroneura*, with males that show distinct pattern differences among the species: (a) sibling species, *E. arta*, *E. ingrata*, *E. lawsoni*, *E. torella* and *E. usitata*, which can be distinguished only on the basis of male genitalia; (b) *E. bella*; (c) *E. hymettana*; (d) *E. morgani*. Drawings by Alice Pricket. From McClure 1975.

(*Platanus occidentalis*), in Illinois (Figure 12.5). All appeared to be intermingled, sucking cell juices from the leaves. The study has been cited many times in support of authors' arguments (see Price 1997). However, McClure's studies indicated that the species were distributed differently over a geographical gradient from Illinois into Kentucky and Tennessee, a range of 43° to 35°N (McClure 1974, 1975, McClure and Price 1975, 1976). These distributions show that the peak of abundance of each species differs somewhat from the others, possibly providing sufficient niche differences to enable coexistence of the species (Figure 12.6). Other factors may have played a role in coexistence, such as the flush of new unoccupied leaves each spring, opening up a large resource, and the vagility of adult leafhoppers enabling them to escape crowded conditions.

The other celebrated case of coexistence of species in apparently the same niche involved bark lice in the moist larch plantations in northern England (Broadhead 1958). Two *Mesopsocus* species were similar in body form, size, food preferences and phenology; they frequented the same twigs, often attaining equally high densities. Further detailed studies by Broadhead and Wapshere (1966) identified an important niche difference involving oviposition sites that were apparently limiting resources. *Mesopsocus immunis* laid most of its eggs in the axils of dwarf side shoots, where *M. unipunctatus* laid few eggs, while the latter species concentrated oviposition in girdle scars and leaf scars (Figure 12.7).

Since these studies, authors evidently have been reluctant to claim that species occupy identical niches (see Morin 1999, and Chase and Leibold 2003, who do not discuss the concept). This results partly from the view of the Hutchinsonian niche with its emphasis on the distribution of species on gradients, such that two or more gradients inevitably show differences in species distributions and resource utilization. In the case of *Erythroneura* it was a geographical gradient, and with *Mesopsocus* position along a shoot provided the key gradient. In addition, natural enemies are likely to impact the fundamental niche of each species differently, resulting in different realized niches. For example, two mite predators of the herbivorous cassava green mite, *Mononychellus tanajoa*, occupy different parts of the cassava plant in Africa, whereas the

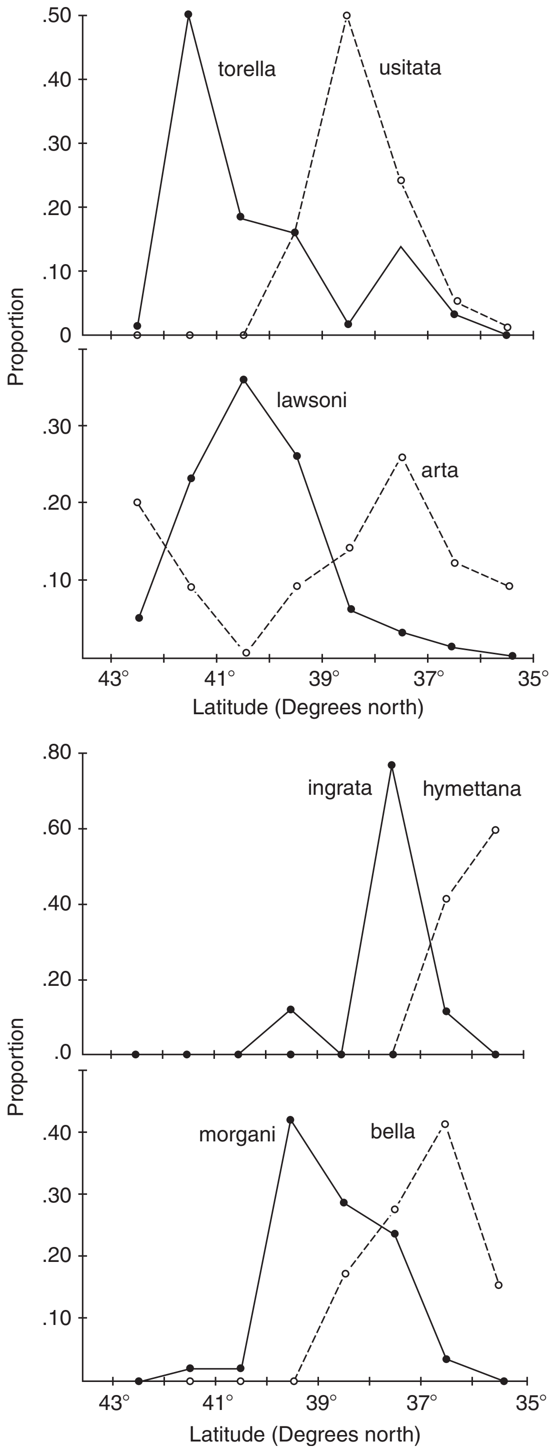
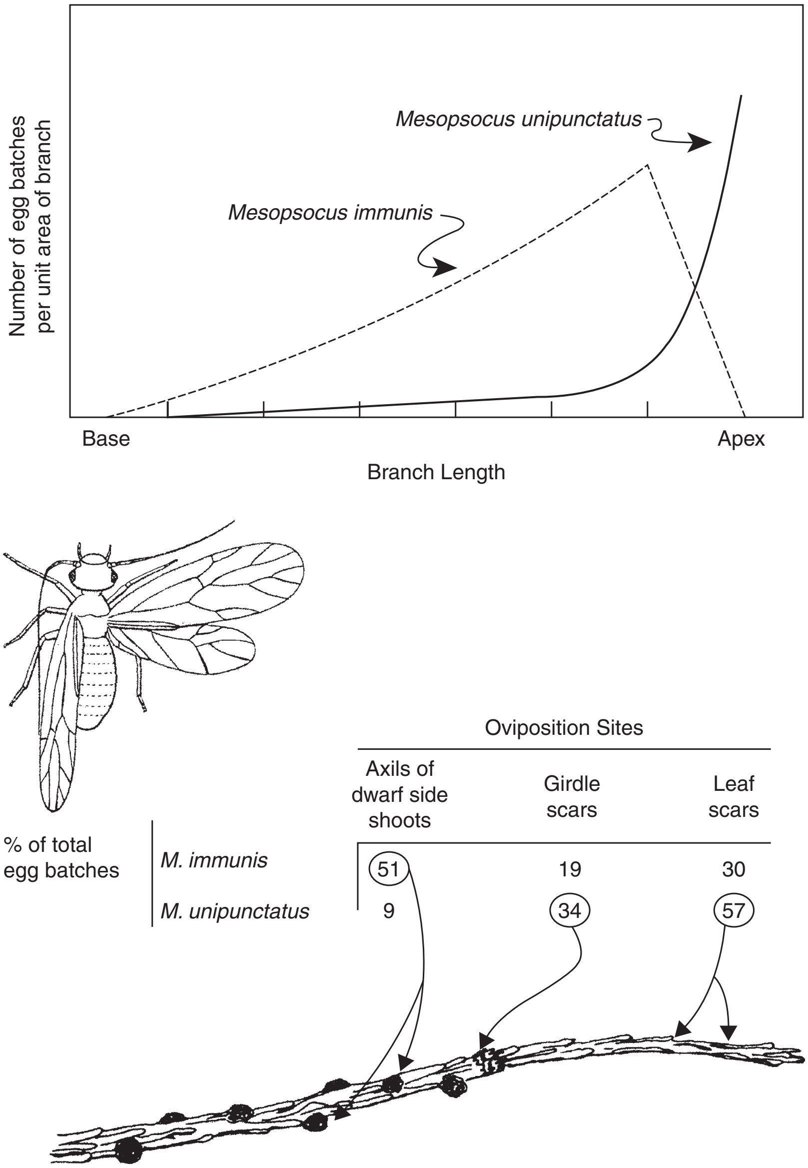


Figure 12.6 The distribution of the eight *Erythroneura* species on a latitudinal gradient from northern Illinois (42.5°N) to the Smoky Mountains, Tennessee (35.5°N). The proportion of individuals in each species is shown in each of the eight sampling areas. From McClure and Price 1976.

herbivorous mite has a fundamental niche of the whole plant. Thus, if one predator occupying young plant parts were present and the other absent, the green mite's occupation would be reduced to a realized niche in the lower foliage (Gnanvossou *et al.* 2003b). Also, the realized niche of the Monterey Pine aphid, *Essigella californica*, may be more affected by biotic factors such as competition and parasitism than climatic conditions (Wharton and Kriticos 2004). Good evidence is provided by Dőbel and Denno (1994) that spiders can reduce population growth of delphacids to zero, essentially limiting the planthopper niche to low predation densities. Indeed, the concept of **ecological refuges** from natural enemies is repeatedly invoked in discussions of planthoppers (Denno and Perfect 1994). As habitat complexity increases, so the denizens of thick organic detritus experience improved chances of survival (Denno *et al.* 2005a), including more refuges from predation (Langellotto and Denno 2004, Finke and Denno 2006). More was discussed on the role of natural enemies in herbivore niche restriction in Chapter 7, Prey and predator interactions.

12.2.3 Vacant niches

Another feature of the Hutchinsonian niche is its ability to recognize and quantify **vacant** or **empty niches.** The concept of the vacant niche has been alive and well for close to a century, soon after the first use of the term niche in an ecological context in 1910 (Johnson 1910, see also Gaffney 1973, Hutchinson 1978). Particularly where clearly structured habitats provide resources for species, such as the structure of a plant with its various modules, this provides a template into which species



		Oviposition Sites		
		Axils of dwarf side shoots	Girdle scars	Leaf scars
% of total egg batches	*M. immunis*	51	19	30
	M. unipunctatus	9	34	57

Figure 12.7 The number of egg batches for each *Mesopsocus* bark louse species per unit area of branch surface along the length of larch branches (above). This distribution prompted more detailed studies to find the oviposition preferences for each species (below). The partial refuges from competition for oviposition sites are circled, and arrows show the sites utilized by females. Larch leaves are not shown. Data are from Broadhead and Wapshere 1966.

can fit. This plant-provided template is replicated more or less in many places by the same or different species which provide similar structure and resources.

An early study revealing many vacant niches studied the records of leaf-mining flies (Diptera: Agromyzidae) on umbelliferous plants (Apiaceae) in Britain. Noting that each plant species provided the

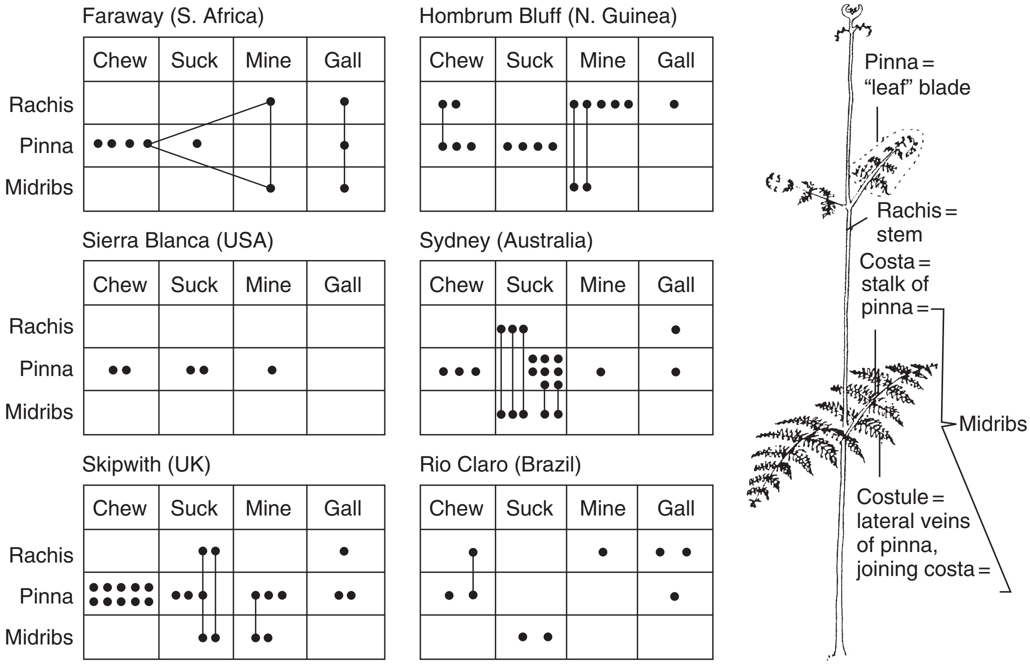
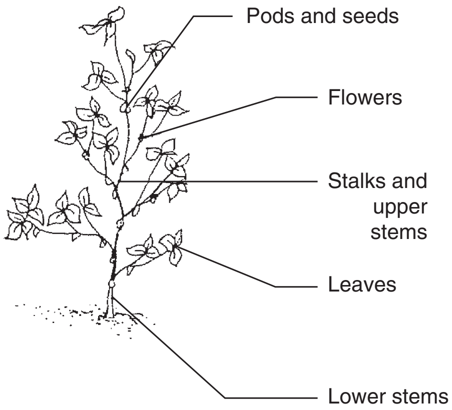


Figure 12.8 Guild matrix for assemblages of insect herbivores (plus a mite species in South Africa) on bracken fern in six geographical regions. The number of species in each guild is indicated by solid circles. Lines join a species that exploits more than one plant part. From Lawton *et al.* 1993. On the right a bracken fern frond illustrates the names applied to plant parts. From Strong *et al.* 1984a.

same resources, particularly leaves, so that each plant species could be expected to support the same number of leaf-mining species, wide differences in the number of coexisting species were actually evident (Lawton and Price 1979). For example, some umbellifer species with a wide geographic range supported up to five agromyzid species, whereas others had none, and herbaceous plants outside the umbellifers supported up to eight miner species, indicating many unoccupied niches on some plant species.

Even more convincing cases of vacant niches derive from studies of the same plant species in different parts of the world: bracken fern (*Pteridium aquilinum*), which occurs naturally over a wide geographic range, and soybean (*Glycine max*) from the Orient, grown commercially as a crop plant in many parts of the world. In each case a matrix can be constructed with the plant resources as one axis and the guilds of insects on these resources on the other axis. Bracken fern was sampled in many localities around the world, summarized by Lawton *et al.* (1993) (Figure 12.8). Immediately apparent are the large differences among locations; clearly, as bracken fern has dispersed distinct herbivore faunas have evolved based on independent sources of colonists in each region.

The highest number of species was found on Skipwith Common in England (21 species), with lower numbers in New Guinea (14 species), and subtropical Brazil (8 species), with only 5 species on the isolated peak of Sierra Blanca in New Mexico. Whole guilds of herbivores on certain resources, well represented in one locality, are absent in others, such as leaf miners on the rachis at Hombrom Bluff, which are absent at Skipwith, Sydney and Sierra Blanca. In fact, in each feeding guild many boxes are free of species, while being occupied in other regions,



	North America		Central and South America		Orient	
Pods and seeds	6+	2	4+	3	5+	1
Flowers	3+	1	2+	1	1+	2
Stalks and upper stems	0	2	3	1	1	1
Leaves	16+	1	10+	2	11+	3
Lower stems	3	2	2+	3	3	3
Niches occupied and vacant	28	8	21	10	21	10
Total niches present	36		31		31	
Percentage of niches vacant	22		32		32	

Figure 12.9 Resources on a soybean plant are illustrated on the left, and the numbers of insect species exploiting each resource are recorded in the top left segment of each box, for North America, Central and South America and the Orient. A + indicates a minimum estimate. In the lower right of each box is the estimated number of vacant niches on that resource, and below the matrix the total estimated number of occupied and vacant niches, the ecological niches present, and the percentage of estimated vacant niches are provided. From Strong *et al.* 1984a.

showing that the niche can be occupied. Even the richest community, at Skipwith Common, had many niches vacant, and most had over 50% of niches empty because an empty box shows that a whole guild is absent, and several species can coexist in any one guild according to the empirical evidence from other localities.

In the case of insects on soybean, Turnipseed and Kogan (1976) summarized the number of insects utilizing each resource on soybean plants in North America, Central and South America, and the Orient (Figure 12.9). Strong *et al.* (1984a) erected a matrix of geographical regions and soybean resources. A third dimension could be feeding guild, as in the bracken fern study. In each box for a region and a resource, such as leaves, the number in the top left half gives the number of species recorded (16+ in North America). In the bottom right of the box, the number of vacant niches is estimated. This derives from a comparison of guild representation in other regions, and shows the number of guilds, such as leaf chewers, leaf suckers or pit feeders, that are present in other regions, but not in the region represented in the box (1 in North America). So the number of vacant niches is actually underestimated, as several species could be present in a guild that is absent in a certain region and on a certain resource. Even so, niche vacancy is high according to these estimates; from 22–32% of niches remain vacant. Vacancy rates could obviously be much higher in local communities, say in a single field, than in these regional views, probably yielding values of well over

50% of niches being vacant at the local level, where species are likely to interact.

Such high niche vacancy rates undermine concepts of the tight species packing in communities, niche compression, saturation of communities, the ubiquitous force of competition and the broken stick model of MacArthur (1957, 1960), in which all resources are fully exploited. Indeed, it was the development of the vacant niche concept, and its use in herbivore and parasite communities, that contributed to the debate on the importance or weakness of competition in community organization (see Strong *et al.* 1984b, and discussion in Chapter 5).

If "absentee" rates among species are so high in communities of insects, can we argue that presence or absence is unimportant in communities and species are expendable? In general, it is extraordinarily difficult to discover the full impact of a species, or a species' extinction, for each species is likely to play subtle roles in the community, which would take years of dedicated study to reveal (see Louda and Rand 2003). "Thus, a judgment of 'ecologically significant' might be logically impossible for evolutionary reasons; as long as we are dealing with true species, which have an independent evolutionary history, we are dealing with entities that have unpredictable and limitless potential for further contributions" (Root 2003, p. 289–290). Species that appear insignificant and expendable now may become major players in ecosystem function in the future. And any one species may yield insights that have important consequences for science and its applications. Hence, there seems to be no scientifically based reason to relegate species to the status of being redundant or expendable (see Kareiva and Levin 2003). While the niches of many species have been described, there remain many details to be discovered and many questions remain about their full role in the community. What is the role of indirect effects in niche restriction (e.g., Figures 1.5, 12.22, 12.30–33)? Knowing from interactions described in Chapters 2 and 4 that induced defenses in plants affect other herbivores, could such effects result in apparently vacant niches, but which actually are not available? What are the relative effects of bottom-up (from plants) and top-down (from enemies) impacts on niche occupation in communities? What is the role of refuges from enemies in community organization?

12.3 Community development

Communities develop both in **ecological time** and in **evolutionary time**. In any one growing season in the temperate latitudes, seeds will germinate and plants will grow, and deciduous trees will flush their leaves. Resources for plant-dwelling arthropods will expand rapidly and colonization will proceed rapidly. In this ecological time, a community will develop through the season, adding species and increasing interactions. In addition, such interactions, with host-plant species, competitors, or with predators and parasites, are likely to result in evolutionary changes which adapt species to their abiotic and biotic environments. Species' ecological niches may narrow or widen depending upon these interactions; more species may evolve which can invade a community. Hence, a community may become more organized in evolutionary time. Therefore, it is useful conceptually to keep in mind these different time scales when considering community development.

12.3.1 Phases in community development

Wilson (1969) envisaged the increase of species in a community as comprising four different processes (Figure 12.10). Rapid colonization of a vacant site initially would be **a non-interactive phase** because so much space and resources would be available, and natural enemies would be slow to colonize until prey were abundant. Of course, colonists would interact with their food sources, such as colonizing plants, but this scenario emphasizes one trophic level, as was the usual emphasis in terrestrial

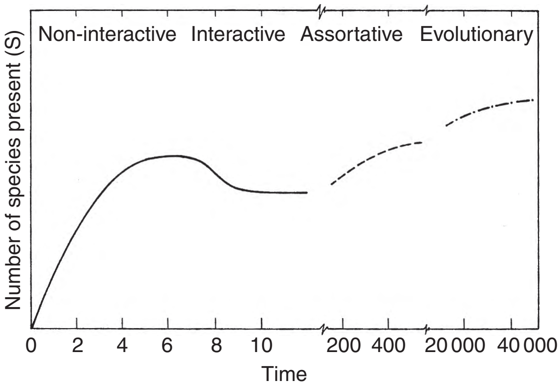


Figure 12.10 Wilson's (1969) conceptual view of the major phases in community development through time. The time scale represents the relative periods of time that it may take to reach an equilibrium community in each phase.

ecology. As populations increased, an **interactive phase** began, reducing the number of coexisting species through competition and enemy attack, achieving a sustainable equilibrium number of species in the community. As time passed, a sorting of species would produce coexisting species better able to live together – the **assortative phase**. And finally an **evolutionary phase** would involve natural selection on species which reduced negative interactions, perhaps by niche compression, by more effective defenses against enemies, and the evolution of mutualistic associations.

The reality of the evolutionary phase is illustrated by the **taxon cycle**, another concept advanced by Wilson (1961). This has been noted particularly on tropical islands with extensive lowland areas and significant relief. A colonizing ant or beetle is likely to be a generalist species from the lowlands of another island with a variety of habitats. Such a species is adapted to expand its range in an archipelago. Following colonization of a new island, the evolution of new species may occur as migration up the mountain slopes proceeds. Dispersal into upland sites is likely to select for more specialized species in mesic forest, and ultimately specialized endemics will colonize the higher rain forests.

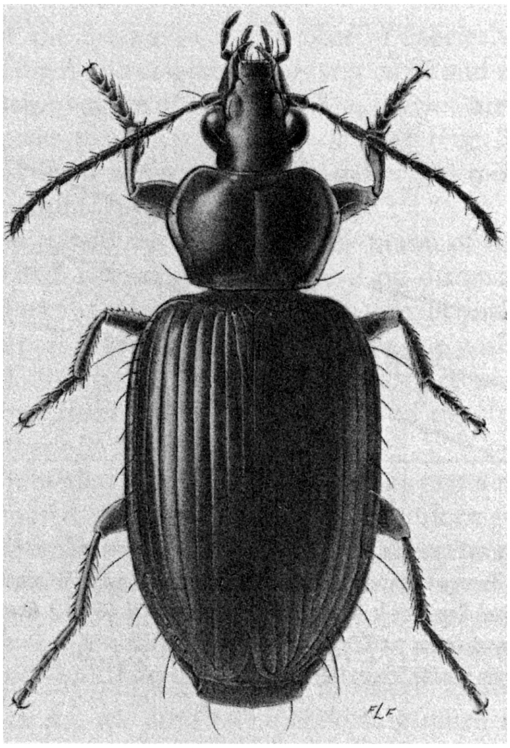


Figure 12.11 A carabid beetle, *Platynus marginissimus*, described by Liebherr (1992), distributed in tropical Mexico, Guatamala and El Salvadore. Drawing by Frances L. Fawcett.

A mountainous tropical island like Hispaniola, with peaks over 10 000 feet, is occupied by 14 related species of *Platynus* (Coleoptera: Carabidae) in five areas of endemism all species are wingless with narrow upland to mountain distributions (Figure 12.11, Liebherr 1992). This study is similar to earlier studies on the taxon cycle. Wilson (1959, 1961) had studied the ponerine ant fauna of Melanesia, including New Guinea, and the mainland fauna of southeastern Asia, showing considerable diversification of species in mountain rain forest on islands (Figure 12.12). The number of species increased in evolutionary time as species became more locally distributed and specialized to mountain habitats with rain forest vegetation. Communities became enriched.

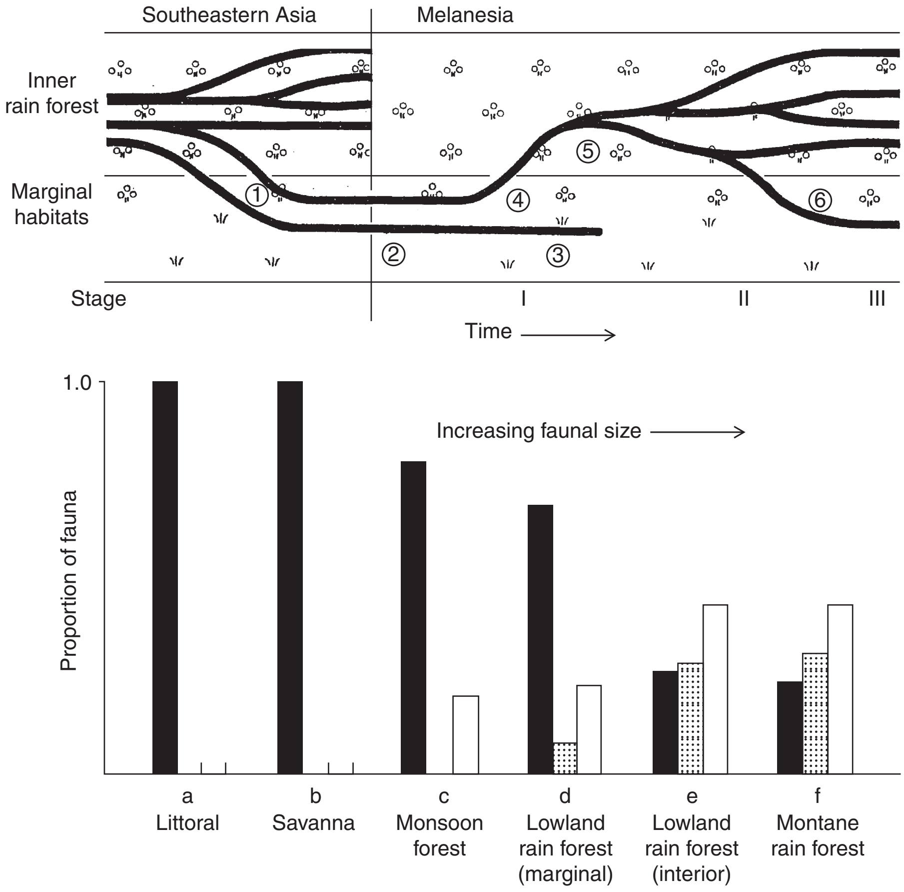


Figure 12.12 Wilson's (1959) conceptual view of how ponerine ants colonized Melanesian islands from mainland southeastern Asia, and radiated on the islands. (Above) Key habitat for ponerines is the inner rain forest, but evidently some species adapted to marginal habitats (1), which preadapted them for colonizing similar habitats in New Guinea (2). Such invading species either went extinct (3) or invaded their original inner rain forest vegetation type on Melanesian islands (4). Speciation results in montaine topography (5) and later marginal habitats may be colonized again (6) providing potential colonists to new islands. On the mainland some extinction occurs making the Melanesian fauna central to the ponerine ant distribution. Stages I, II and III denote the sequence of adaptive radiation from Stage I covering phases (3) and (4) in the figure. Stage II covers the phase of major adaptive radiation (5), and Stage III shows a phase when the Melanesian fauna becomes the center of the ant genus distribution (6). (Below) The proportion of the ponerine ant fauna in New Guinea belonging to Stage I species (black columns), Stage II species (stippled) and Stage III species (white). Note that the most diverse and derived fauna occurs in inland mountain rain forest (right, f), and littoral and savanna habitats are composed of Stage I species (left a and b). From Wilson 1959.

12.3.2 Colonization studies

The early progression of colonization of a habitat was investigated experimentally using mangrove islands in the Florida Keys – in ecological time. Several mangrove islands of different sizes off the west coast of Florida, in Florida Bay, were censused completely for arthropod species, then fumigated with methyl bromide, and censused again to check for surviving

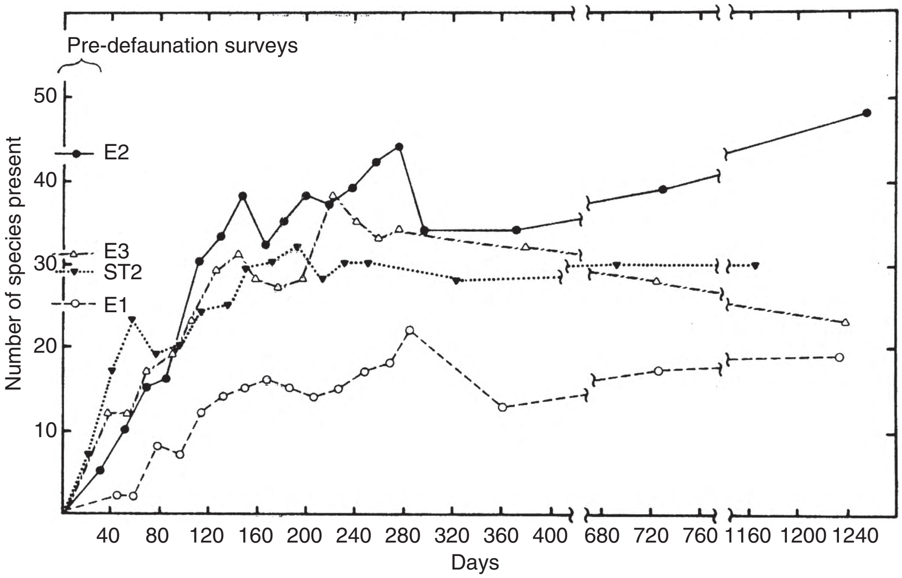


Figure 12.13 Colonization trajectories for more than 3 years for four small mangrove islands in the lower Florida Keys after defaunation. The numbers of species present before defaunation are indicated for each island on the ordinate. The near island, E2, had the most species, while the farthest island, E1, supported the fewest. From Simberloff 1978.

species (Wilson and Simberloff 1969). Then monitoring proceeded regularly to count the species present which had colonized from the mainland (Simberloff and Wilson 1969, 1970, Simberloff 1978). Colonization by arthropods was rapid initially; the number increased beyond that which prevailed before defaunation, and then declined to near before-treatment numbers (Figure 12.13). The rates of colonization differed among islands, depending upon their proximity to the mainland and the source of colonists. The rate was higher on the nearest island (E2), and lowest on the farthest island (E1).

Wilson's (1969) concept of an equilibrium number of species in a community appears to be supported by the defaunation and colonization study. All islands, except E1, increased in species beyond the original number and then declined, as if a real equilibrium in species number were evident (Figure 12.13). E1 was the exception: it was the most distant island and was slow to be colonized. This early simplicity in the fauna allowed two species to reach outbreak numbers, which may have suppressed colonization by other species (Simberloff 1978).

Defaunation studies were also performed on smooth cord-grass, *Spartina alterniflora*, salt marsh islands by Rey (1981, Rey and Strong 1983). Results were similar to the mangrove defaunation experiments with a rapid increase in insect species accumulating on islands, a decrease during winter, but after 20 weeks predefaunation species richness was achieved. Larger islands maintained more species than smaller islands, with higher immigration and lower extinction of species. With time, species persistence increased as the community stabilized (Rey and Strong 1983).

The defaunation experiments suggest that there is some limit in species number, which imposes some sorting of species, each species able to exploit its own discrete set of resources. Some species, no doubt, colonized, but did not survive because resources essential to their persistence were inadequate, or competition or natural enemies were too severe. This self-organizing aspect of the community therefore becomes a very interesting aspect of ecology and poses the question of which factors are involved in setting equilibrium numbers. Clearly, a balance of colonization and extinction is involved, but why do communities differ so much in the number of species that coexist? We will examine some possibilities in the next section of this chapter on community organization and structure.

Community equilibrium and vacant niches may appear to provide contradictory evidence on community structure. However, the first is an ecological phenomenon and the latter is evolutionary. In an equilibrium community vacant niches may still exist, but over evolutionary time more species may increase richness, as suggested in Figure 12.10.

12.3.3 Ecological succession

The Florida Keys study and the *Spartina* study in the subtropics provide realistic scenarios for north temperate insect herbivore communities because, when leaves flush and crops grow in the spring, they provide empty resources available for colonization. The difference is that with herbaceous plants, including crops, the resources expand through much of the season, and conditions change as foliage density increases and canopies close. But the colonization curves for a soybean crop in Illinois are certainly reminiscent of those on the Florida Keys (Price 1976). Other resources are created as vacant habitats, such as dung, carrion, dead trees, ephemeral ponds, fallow agricultural land or old fields, and in many cases we can conceive of enrichment of species as **ecological succession**. Ecological succession has been associated with many patterns (e.g., Odum 1969); not least is the increase in coexisting species, but in succession resulting in temperate forest, a peak is reached in mid succession, followed by a decline as tree species become dominant (e.g., Whittaker and Woodwell 1968, 1969, Whittaker 1970a). The peak occurs when young woody species become mixed with the earlier herbaceous plant stage. The latter become diminished as the trees out-shade the herbaceous species and species richness declines. A 28-year study of an Alaskan stream showed a peak richness of macroinvertebrates at 20–24 years and then a small decline (Milner *et al.* 2008). We know of no equivalent studies on arthropods in plant succession, but it would be interesting to examine the extent to which arthropods follow this trend. Certainly arthropod assemblages change with plant ecological succession: tiger beetles on sand dunes (Shelford 1907), and other arthropods (Shelford 1963, see Figure 14.21); coastal communities (Chevin 1966); spiders (van der Aart 1974, see Figure 14.21); pseudoscorpions (Weygoldt 1969); ants after disturbance resulting from mining (Majer and Nichols 1998, Luque *et al.* 2007). A complicating factor in primary succession is that insect herbivores modify the process of plant colonization on bare substrates, such as the pumice plains left by the eruption of Mount St. Helens. Here pioneering lupine colonization, and therefore subsequent succession, is retarded by caterpillar herbivores (Fagan and Bishop 2000, Fagan *et al.* 2004, Bishop *et al.* 2005). On such terrain "… ecological succession is very complex, proceeding at varying paces along diverse paths, and with periodic setbacks through secondary disturbances" (Dale *et al.* 2005, p. 962).

What is driving patterns in ecological succession and community development has been a long-standing question. Clements (1916, 1936) saw climax vegetation as a "complex organism," with species of plants assembled or associated in the climax like the organs of a complex species: the **Clementsian associational concept**. The opposite viewpoint was adopted by Gleason (1926) who argued that "Every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements" (p. 26): the **Gleasonian individualistic concept**. These early concepts in ecology are akin to the community concept of species influencing each other's distribution and abundance, and the concept of assemblages where no such interaction is assumed. However, the complex organism analogy of Clements fell into disrepute as the term **ecosystem**, proposed by Tansley (1935), gained favor.

The individualistic concept of the community is supported by the Florida Keys study. The equilibrium number of species present was very dynamic. Turnover rates of species were high. "Actual turnover rates at equilibrium were between a half and one species per day" (Simberloff 1978, p. 143). So the **equilibrium number** of species is set by the balance of colonization and extinction in the community. This discovery is in accord with the evidence that many vacant niches exist in communities of insects. This contrasts with the concept of **community saturation**: "the point reached by a local community when no more species can invade from the regional species pool and establish to increase the species richness. In this situation, all resources are fully exploited and biotic interactions (particularly competition) are intense" (Hall 1998, p. 660). Saturation of communities is usually detected in species occupying a single trophic level in which competition, often through territorial interactions, is intense, such as among ant species. "Interspecific competition, involving some degree of colonial warfare, plays a major role in the determination of the saturation curve (Wilson 1961, p. 191). "Undisturbed ant faunas of islands in the Moluccas-Melanesian arc are for the most part 'saturated', that is, approach the size that is correlated closely with the land mass of the island but only weakly with its geographic location" (Wilson 1961, p. 190). However, the terms equilibrium and saturation may not be as distinct as they first seem, and they are used in different ways in ecology, as illustrated in the glossary entry for saturation in MacArthur and Wilson (1967, p. 190): "The equilibrial condition, i.e. the state at which immigration is balanced by extinction."

12.3.4 Experiments on ant communities

The factors influencing community development, and the size of communities, are best studied experimentally in order to achieve an empirical and mechanistic understanding of the processes involved. This is rarely undertaken, but an excellent case was developed by Cole (1983a,b), again using the Florida Keys, but concentrating on highly interactive ant communities. First he surveyed 81 small islands and recorded the ant species present, showing the presence of five major species. This community size was manageable for the detailed experimental work necessary for untangling the causes of presence and absence of ant species on islands of different size. He then conducted experiments on behavioral interactions among species and the suitability of islands for persistent occupation by species. Islands were formed by red mangrove, *Rhizophora mangle*, and all ant species nested in the hollow twigs of this plant. Island volumes sampled ranged from 0.03 m^3 to 877 m^3, a range of over four orders of magnitude.

Cole (1983a) discovered some clear patterns on the islands (Figure 12.14). The smallest islands supported no ant species (0.03–0.3 m^3 in volume). Slightly larger islands supported only zero or one ant species (0.31–5 m^3), and larger islands, starting at 5.09 m^3, began to support two species, and then up to a maximum of five species on two islands. Also, species required a minimum island size before they could colonize, each species showing a unique minimum (Figure 12.14).

Experimental studies revealed two major mechanisms in the assembly of ant species. For two species small islands were unsuitable: food supply was sufficient, but wind and water exposure were too severe. These species were christened primary species because they colonized the smallest inhabited islands: they were *Crematogaster ashmeadi* and *Xenomyrmex floridanus* (Hymenoptera: Formicidae: Myrmicinae). Two other species, *Pseudomyrmex elongatus* (Pseudomymicinae) and *Zacryptocerus varians* (Myrmicinae), were named secondary species

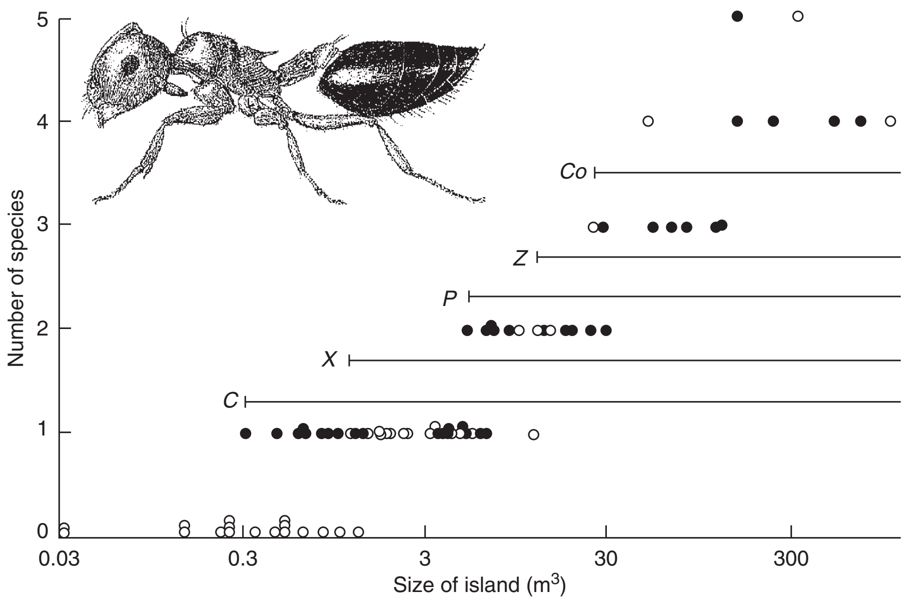


Figure 12.14 The number of ant species present in relation to island size on 81 small mangrove islands studied by Cole (1983a). Solid circles show the presence of *Crematogaster ashmeadi*, open circles show empty islands in the bottom left, and where islands are occupied, the presence of *Xenomyrmex floridanus*. Bars indicate the range of island area occupied by the five species, with species identity shown by a first letter of the genus name, except for Co, which is a *Camponotus* (*Colobopsis*) species. Reprinted with permission from Blackwell Publishing.

because they could persist on islands of any size, but were competitively excluded from islands when *Crematogaster* or *Xenomyrmex* were present.

Pair-wise encounters between species in arenas demonstrated that *Crematogaster* and *Xenomyrmex* were aggressive toward the other three species, and the latter avoided the aggressors. The two primary species, when placed together, showed aggression and avoidance, but when introduced simultaneously to empty islands *Crematogaster* always prevailed, and *Xenomyrmex* never persisted. Once an island was occupied by *Crematogaster* or *Xenomyrmex*, the other species could not invade, so islands were occupied on a first-come basis.

Thus, the assembly of the ant community followed some strict rules of coexistence in relation to island size, summarized by Cole (1983a, Figure 12.15). When a primary species colonizes an island above its minimum size requirement (MSR), in the absence of the other primary species, invasion is successful. When colonization is on an island below its MSR extinction is inevitable. For secondary species, successful colonization depends on the size of the island (above MSR) and the presence or absence of primary species.

Colonizing abilities of the ants were also important in determining the frequency of colonizing events, and the importance of competitive interactions. Cole's (1983b) studies indicated an order of colonizing from *Xenomyrmex* as the best, then *Crematogaster*, *Pseudomyrmex*, *Zacryptocerus* and finally *Camponotus* (*Colobopsis*) as the poorest colonizer. This order reflected some of the sequence of minimum island size that could sustain ant species. *Xenomyrmex* queens, after arriving on an island, produce high numbers of workers which could establish the colony effectively. *Crematogaster* and *Xenomyrmex* have relatively large queens and small workers, so that a founding female can produce relatively many workers during her initial

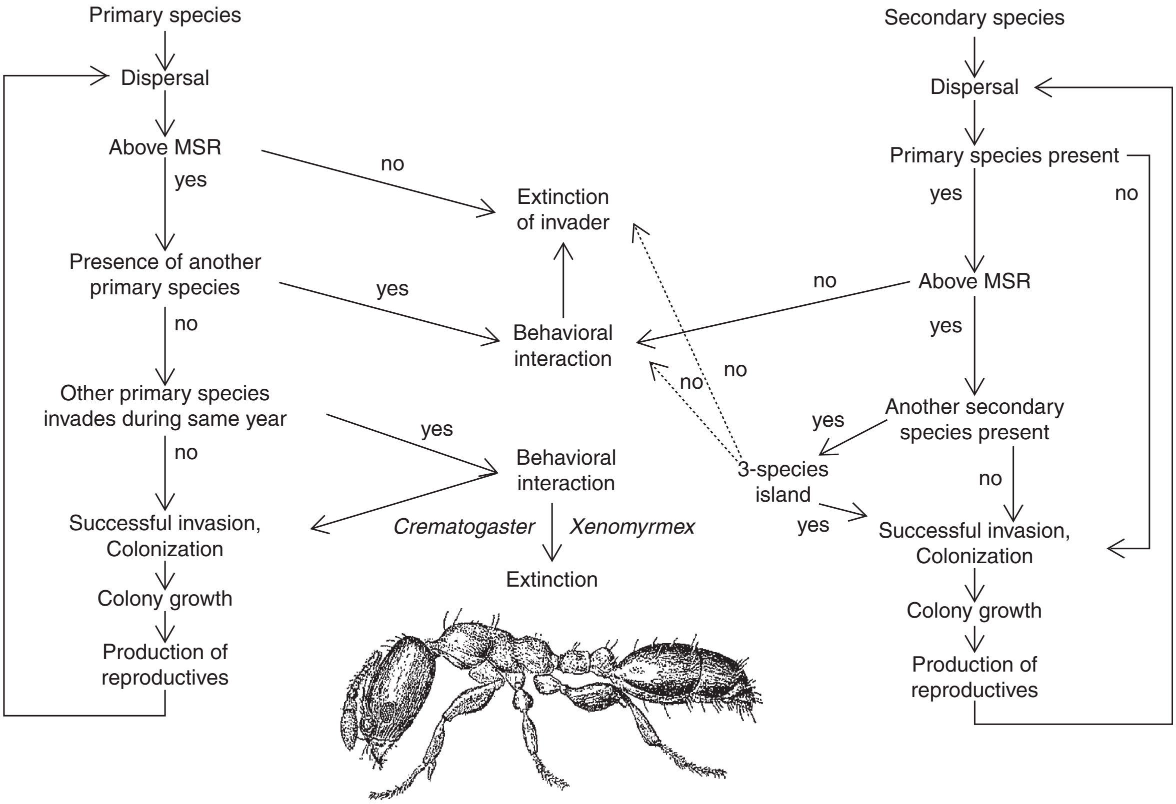


Figure 12.15 The assembly sequences of mangrove ant communities studied by Cole (1983a), starting with primary species (left) and secondary species (right). The paths to successful colonization and colony growth differ for the primary and secondary species. Reprinted with permission from Blackwell Publishing.

confinement, or claustral stage, after arrival. *Pseudomyrmex* selects twigs for nesting at the margins of mangrove trees, reducing interactions with other species. *Zacryptocerus* and *Camponotus*, with a distinct major worker caste, were considered to have reduced colonizing ability because of the more complicated caste structure. This conjecture is based on the lack of a defensive caste early in colony life when the colony is most vulnerable, and other factors discussed by Cole (1983b).

Overall, each ant species showed a unique set of characters, which is to be expected, but considerable dedication was needed to unravel the mechanisms of assembly and coexistence, even with a small community of five ant species with highly tractable experimental methods. Other approaches are simpler and faster, but yield more debatable results. Evident in Cole's studies, also, is that each community, and each member species, will experience a unique set of criteria defining its presence or absence, and frequency in a particular location. This makes generalizations and the development of theory challenging (see Lawton 1999), but empirical and observational studies have contributed significant insights.

12.3.5 Assemblage of communities

Another study showing the way in which communities are assembled concerns the leaf-mining moths on oaks in California (Opler 1974). Here, instead of islands in a marine setting as in the Florida

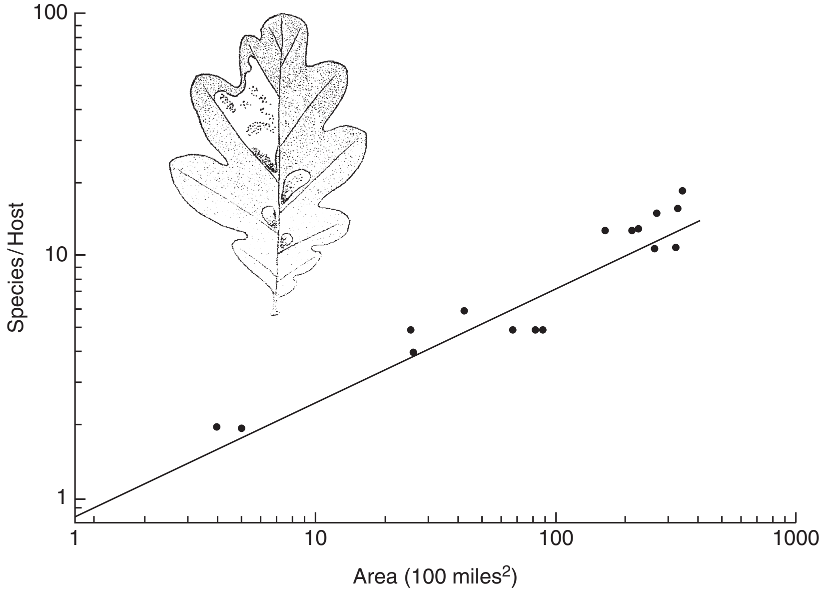


Figure 12.16 The relationships between the area occupied by an oak species and the number of leaf-miner species that have colonized that oak. On these logarithmic scales oak species area accounted for 90% of the variation in leaf-miner species per host. Adapted from Opler 1974.

Keys, oak species were viewed as islands in a terrestrial setting. Such islands were available for colonization in evolutionary time, and again, the effects of island size, or the geographical area over which a species is spread, were considered as an organizing principle. Oaks in California have a similar age in the fossil record, about 18 million years, so the time for colonization by insects has been probably equivalent. Leaf miners tend to be very specific to their host plants, with a high number of species monophagous (see Table 8.4, Agromyzidae). On each oak species they form a guild of species, all living on the leaves of oaks and exploiting them in a similar way by mining with mandibular mouthparts within the leaf mesophyll. Eighteen species of oaks provided food and habitat for 116 species of mining lepidopterans. Some oaks were grouped because of hybridization.

Opler (1974) discovered a strong relationship between the geographic area occupied by an oak species, island size and the number of moth species per host (Figure 12.16). Island size accounted for 90% of the variation in number of miner species per oak host, using a log/log plot, as in the figure. The most widespread oak supported 19 miner species, and the most narrowly distributed had 2 miner species. Even more interesting was how the miner species were assembled on the oak species. “There is an orderly hierarchy by which successful colonization (evolution of new host-specific miners) takes place” (Opler 1974, p. 72). Certain genera were clearly effective colonizers, with species discovering most host species, for example *Cameraria* and *Lithocolletis*, with several species per host on the most widespread oak species (Figure 12.17). Then there was a gradual narrowing of host species colonization until two genera were found only on the biggest island, *Quercus agrifolia*: *Careospina* and *Neurobathra*. As a consequence, each oak species supported a rather predictable assembly of leaf-mining genera, and a predictable species richness. The times of existence for the oak species appeared to

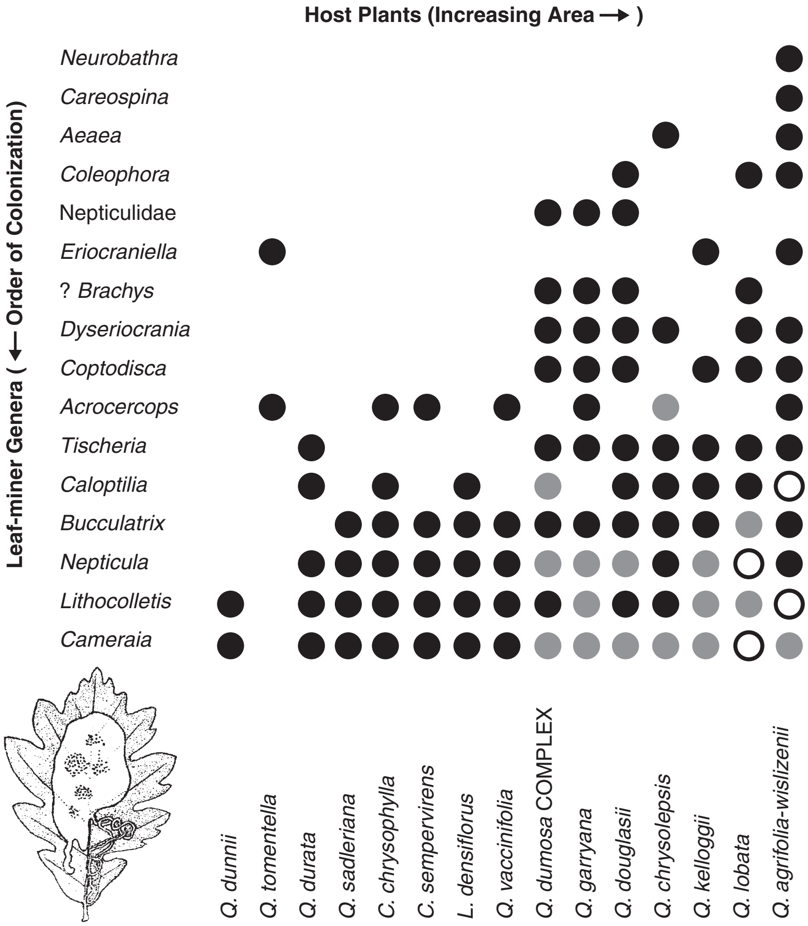


Figure 12.17 The hierarchical colonization of oak species by leaf miners in evolutionary time. Hosts with the narrowest distribution, e.g., *Quercus dunnii*, are on the left, and those with the greatest distribution, like *Quercus lobata* and the *Quercus agrifolia–wislizenii* hybrid group, are on the right. The best colonizers, like *Cameraria* leaf miners, are at the bottom of the figure and slowest colonizers are at the top, such as *Careospina* and *Neurobathra*. Adapted from Opler 1974.

be similar based on the fossil record, as noted earlier, so time could not be invoked as an organizing influence on species richness of leaf miners.

The island-area effects on species richness of colonists in the community have at least four components. First, the larger the island the higher is the probability that it will be discovered and colonized. Second, the larger the area, the more diverse will be the habitat and abiotic conditions, offering a greater variety of conditions in which species can adapt and diversify. Resources and habitats are more heterogeneous. Third, the larger the island, the higher the population sizes are likely to become, reducing the chances of extinction. Fourth, larger islands probably experience lower emigration losses (Cronin 2007a). These components contributing to high species richness on large islands are inextricably coupled, with heterogeneity acting as a key ingredient. We will explore this more in the next section.

12.3.6 Assembly rules

In spite of the promising early studies on assembly of communities by Opler (1974) and Cole (1983a,b), the idea of **assembly rules** has become controversial. The term was originally coined by Diamond (1975), but has become more broadly defined as ecological "restriction on the observed patterns of species presence or abundance that are based on the presence or abundance of one or more other species or groups of species" (Wilson and Gitay 1995, p. 369). Simply said, assembly rules describe the patterns resulting from the interaction among species. Obviously, the mechanisms involved are important to understand, as in Cole's study on ants, and Opler's study on leaf miners on oaks, but some have argued that the patterns themselves provide evidence of the processes resulting in patterns (e.g., Wilson 1999). "Study major, broad repeatable patterns" in nature was Tilman's (1989) admonition, but scientific theory must also explain these patterns, as Tilman went on to say (see Chapter 1, Ecological questions and answers). Therefore, pattern detection comes first, but mechanistic studies light the path to theory and a full understanding of community assemblage. The discovery of broad patterns in assembly rules would provide a major impetus in community ecology, although this remains an elusive goal. However, the development of theory requires both patterns and an understanding of the mechanisms involved.

If assembly is defined for any one community of invertebrates it tends to be specific rather than general. Assembly processes and rules may differ significantly depending upon environment (Drake *et al.* 1999, Gotelli and Ellison 2002), or the sequence of colonization of a habitat (Drake *et al.* 1993), or sequence and population dynamics of colonizing species (Drake 1991).

In addition to finding non-random and repeated patterns in community structure – Stage 1 – and identifying mechanisms driving these patterns – Stage 2 – Bangert and Whitham (2007) advocate a Stage 3: exploration of the genetic basis of variation in resources for communities, such as variation of host-plant genotypes, and correlated leaf quality or phytochemical composition. When a genetic basis for community structure is found, this relationship would provide a **genetic assembly rule**. For example, Bangert *et al.* (2006) examined the effects of cottonwood host-plant genotypes that hybridize, and the effects of a range of plant cross types on the insect and mite herbivores which colonize the trees. The herbivore community was composed of "leaf-modifying arthropods," so changes in leaf structure caused by leaf gallers, tiers, rollers, folders and miners were easily recognized and sampled. The host plants were narrowleaf cottonwood, *Populus angustifolia*, and Fremont cottonwood, *Populus fremontii*, F_1 hybrids, and backcrosses between F_1s and narrowleaf cottonwood. Sampling revealed that each *Populus* cross type supported a distinct arthropod community, even when cross types were separated by about 800 km (Figure 12.18). Among natural stands of cottonwoods, plant genetic diversity accounted for almost 60% of the arthropod diversity variation (Wimp *et al.* 2004). "The **genetic similarity rule** (our bold lettering) indicates that, on average, arthropod communities become more similar as the plants they utilize become genetically more similar" (Whitham *et al.* 2006, p. 518).

The genetic basis of resources, such as host plants, for insect communities is becoming a strong field in ecology, uniting it more intimately with evolutionary biology. The approach makes the study of evolution and communities more tangible and experimentally tractable (Whitham *et al.* 2006). The subject of community genetics will be discussed later in this chapter.

12.4 Community organization and structure

What regulates the number of species and their abundance in communities is a central issue in ecology. Understandably it has generated

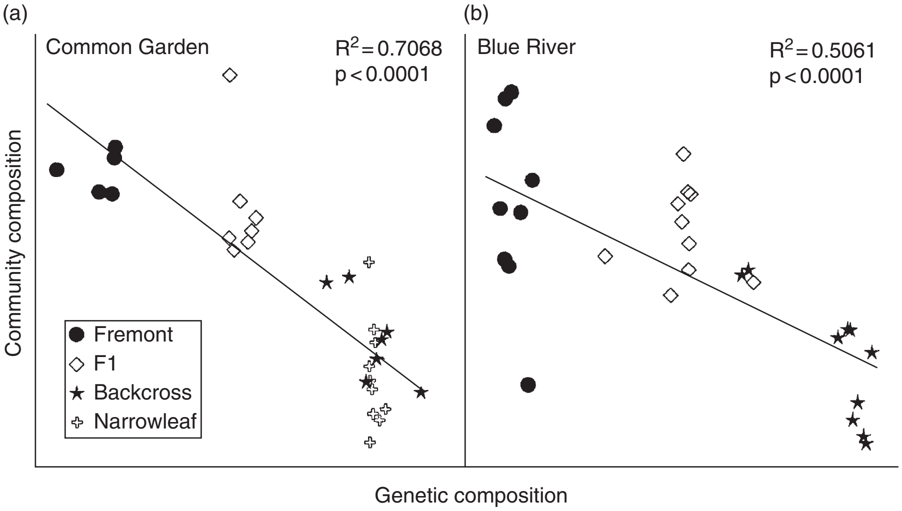


Figure 12.18 The relationship between genetic similarity of cottonwoods and the community similarity of leaf-modifying arthropods in a common garden (a) and a wild population in the Blue River about 800 km away (b). Fremont cottonwood and narrowleaf cottonwood are the parental species which hybridize to form F_1 hybrids and these backcross to narrowleaf forming a hybrid swarm. Some clusters of points for each cross type have outliers that may well indicate different genotypes not partitioned by the genetic characters used in the analysis. Backcrosses and narrowleaf plants blend into each other genetically in (a). From Bangert and Whitham 2007.

considerable research and debate, yielding alternative hypotheses on the major factors involved.

12.4.1 The resource-heterogeneity hypothesis

The more heterogeneous an environment is, the more resources are likely to be provided, and the more ecological niches will be available for colonization. This concept can be called the **resource-heterogeneity hypothesis**. It offers many avenues for exploration, only some of which can be introduced here. There are many forms of heterogeneity. A single plant offers a heterogeneous set of resources, and these change with plant age. A population of plants offers heterogeneity as genetic variation, nutritional variation, variable defenses and differences in microhabitat, including edaphic conditions. Plant species provide greater heterogeneity, and plant communities show ever more complex variation in food and habitat for herbivores. Inevitably, all this heterogeneity affects the number of species that can coexist. The same hierarchy of increasing habitat richness can be envisaged for all kinds of communities, from terrestrial arthropod assemblages, to freshwater ecosystems and marine intertidal communities. Indeed, habitat structure has an enormous range of effects on species and communities (e.g., Bell *et al.* 1991). Most hypotheses on community organization and structure embrace the concept of environmental heterogeneity as a key ingredient. Variation in the environment creates a kind of template into which species can fit to occupy their own unique ecological niches. Southwood's (1977, p. 337) presidential address to the British Ecological Society argued that the habitat provided "the templet for ecological strategies," and this was composed of heterogeneity in time and heterogeneity in space. The majority of species and/or ecological strategies could be categorized on the time/space grid.

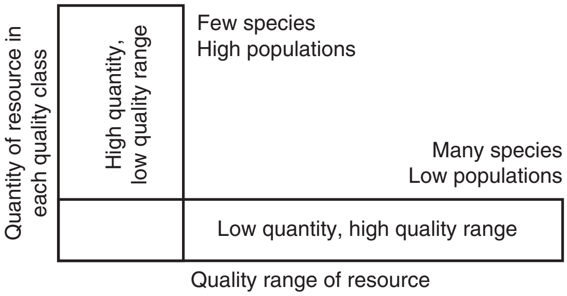


Figure 12.19 Relationships between quantity of resource and quality range of resources in a community, and their impact on the number of species present and population sizes. Quality range may incorporate seed-size variation for granivores, nectar depths in flowers for pollinators or range in bark thickness for bark beetles, as examples. The two extremes illustrated provide equal amounts of resource available. From Price 1984b.

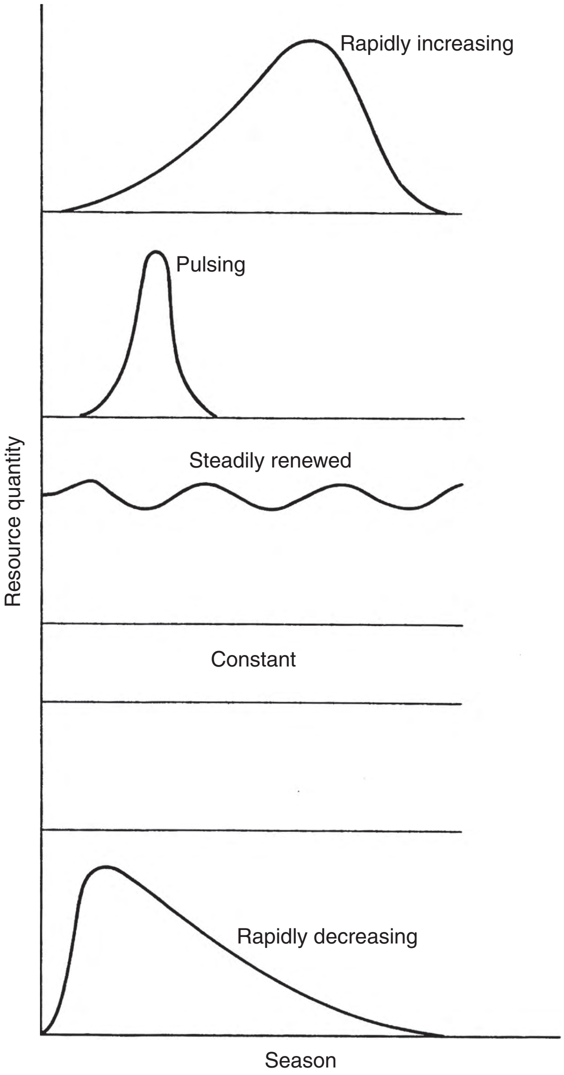


Figure 12.20 Types of resource development that will probably influence exploiting populations in different ways, thereby affecting such ecological factors as competition, population dynamics and community development and persistence. From Price 1984c.

12.4.2 Quality and quantity of resources

In general, a high variation in quality of resources will enable more species to coexist in a community and species abundance will be influenced by the quantity of resource available for each species. Thus, for the same quantity of resources, a low quality range and a high quantity will only allow a high number of a few species. The converse, a wide range of resources with a low quantity of each, will result in many coexisting species with low populations (Figure 12.19). Of course, resources are usually not in constant supply, so the nature of the resources will play a significant role in the organization of communities and the life-history strategies of the species exploiting each kind of resource. For insects we can envisage various types of resource quantity variation through time (Figure 12.20). Rapidly increasing resources are typical of leaf and stem development of trees, shrubs and herbs in temperate latitudes, which become available to herbivores. Then, in the fall, there is a rapid decline in resources as leaves fall, and herbs and grasses die back. The carrying capacity of the resources becomes high rapidly, and resource quality changes rapidly as leaves age (see Chapter 4). This rapid opening up of new resources allows colonization without competition, and herbivores experience a long time period over which they can feed. A contrasting display of resources can be called pulsing, which exist briefly, such as dung, animal corpses, mushrooms, desert pools and many kinds of plant parts attacked by specialists, such as flower buds or very young leaves. These resources must be colonized rapidly to be utilized at all, and competition may be fierce, with utilization of the resource rapid. Dung and carrion are good examples of resources that are often colonized rapidly and dissipated in a brief time period. Steadily renewed resources may include those for animal parasites, or leaves in tropical rain forest. Constant resources are those influenced by neither seasonal change nor exploitation that reduces the resources. Tree holes are an example in which insects do not create the rot holes, nor do they destroy them. The water in the tree hole may vary in time, although the number of them may build with time. Rapidly declining resources, after a flush in production, may be observed for seeds utilized by granivores in desert communities. A pulse of seeds is produced after the brief rainy season, and the resource is reduced by germination or by utilization by seed eaters, probably generating intense competition. Cocooned larvae or pupae, and other resting stages of insects, are like seeds, generated over a short time and gradually reduced by predation, attack by parasitoids and emergence, with competition eventually becoming severe.

This simple view of temporal variation in resources illustrates some kinds of heterogeneity which have strong organizing influences on the kinds of species that have become adapted to exploiting them. An interesting exercise is to recognize the different qualities of insects adapted to each kind of resource: the excellent colonizing ability of flies utilizing dung or carrion; the territorial behavior of male syrphid flies at tree holes waiting for females to mate with, followed by oviposition and development of rat-tailed maggots; the peaceful coexistence of chrysomelids in rolled leaves of *Heliconia* plants in which large leaves are available only briefly, so colonization time is short, and the resource is plentiful, but ephemeral. Such examples are discussed in more detail in Price (1984c, 1997).

Temporal variation in resources is frequently coupled with spatial variation, partly because resource display is not necessarily synchronized over a landscape, individual plants will vary in their phenology and development time. But even a single plant offers a rapidly changing set of resources from a seedling, to maturity and the senescing relic (Figure 12.21). The community becomes more diverse as the plant grows, producing new resources in sequence: stems, leaves, flowers, pollen and seeds, with insects and fungi adapted to each resource (see also earlier discussion of colonization of a soybean field).

12.4.3 The resource-concentration hypothesis and associational resistance

The resource-heterogeneity hypothesis covers many underlying hypotheses. The **resource-concentration hypothesis** proposed by Root (1973) argued that where resources are concentrated, such as in a pure patch of collards, specialist herbivores are more likely to find suitable habitat and food and will probably stay longer and breed more successfully. Populations will increase rapidly in such species, which will dominate the community: herbivore biomass will become concentrated in a few successful species, as in Figure 12.19. The hypothesis is actually the converse argument to the heterogeneity hypothesis, approaching diversity from the simplicity point of view. Even working with the same plant species, but planted in an old-field background vegetation, heterogeneity was increased sufficiently to preclude dominance by a few species. Tahvanainen and Root (1972) found that non-host plants around the collards interfered with finding and feeding on host plants: there was an **associational resistance** to herbivore populations, which reduced the likelihood of herbivore population explosions when compared with monocultures. This **associational-resistance hypothesis** was developed as a mechanism influencing dominance and diversity in communities.

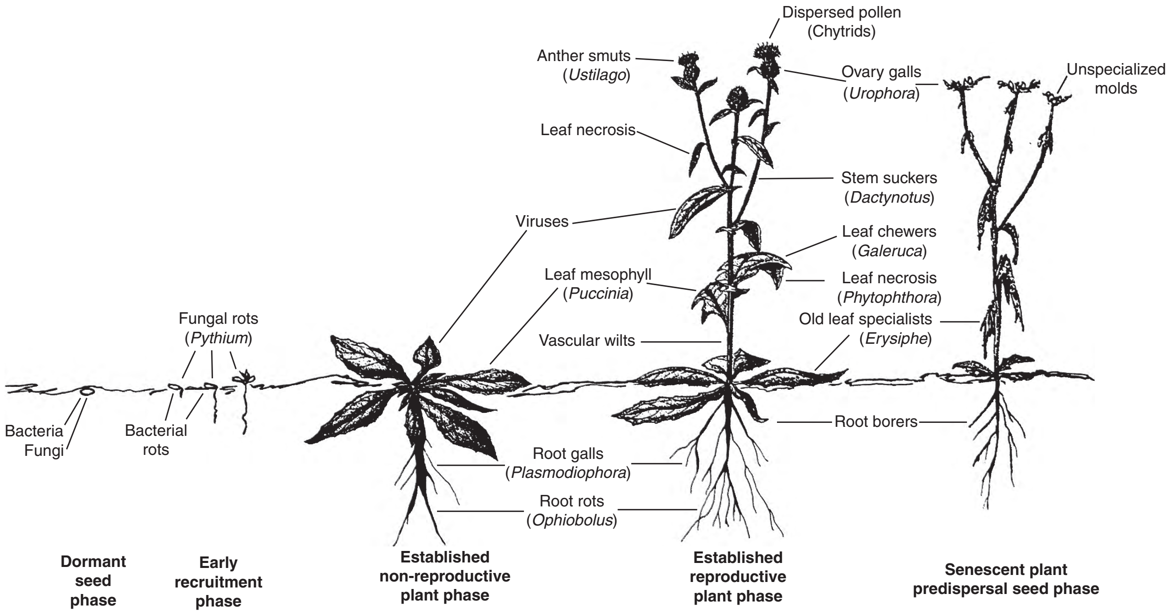


Figure 12.21 The life cycle of a host plant showing four phases of growth and the progression of ecological niches that become available for exploitation by parasitic species, with examples from insect herbivores and plant pathogens. The examples of parasites are not all found on one plant species, but illustrate the diversity of ecological niches available in a plant community or over a landscape. From Price 1992a.

12.4.4 The enemy-impact hypothesis

The above hypothesis contrasted with the **enemy-impact hypothesis** developed earlier from the same kinds of collard experiments by Pimentel (1961). The diversity of plant species associated with collards in the old-field community resulted in a diversity of insect species and a high diversity of predators and parasitoids. The natural enemies found plentiful food in rich plant communities, including insect prey and hosts, nectar, pollen and honeydew. Therefore, populations of natural enemies of insects on the collards were high, and stable, because of alternative prey and hosts, resulting in effective population regulation of the would-be outbreak species on collards. The enemy-impact hypothesis has had long-standing support from other systems, even if it was not the best explanation for the particular case of the collard experiments. The support derives mostly from population dynamics studies (see Chapter 11), biological control of insects (e.g., DeBach 1964, Hajek 2004), and broad evidence of increased mortality correlated with more enemies (e.g., Hawkins and Gross 1992, Hawkins 1994). These kinds of studies have concentrated on individual species, but extrapolating to the community level is straightforward in terms of implications for top-down effects. For example, intraguild predation is reduced in complex habitats, increasing the strength of a trophic cascade on plants in salt marshes (Finke and Denno 2006).

12.4.5 Connectance and quantitative food webs

Direct studies of communities and their natural enemies reveal the complexity of interactions in nature, which studies on individual species do not expose. Take, as an example, the community of

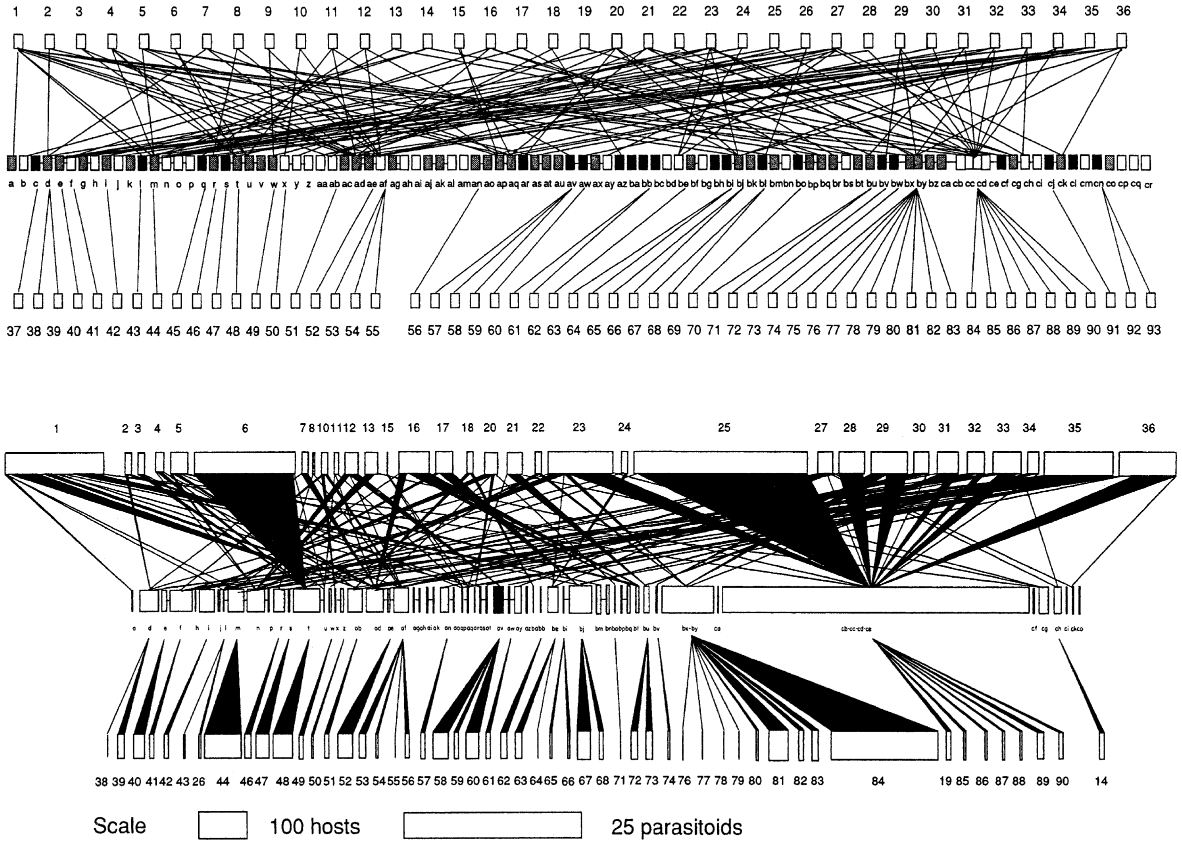


Figure 12.22 A connectance (qualitative) food web (above), and a quantitative food web (below) showing trophic links among leaf-mining insects and their parasitoids in Santa Rosa National Park, Costa Rica. Rectangles represent insect species with leaf miners in the central horizontal row, with a letter for each species, and parasitoids in the upper and lower rows with a number for each species. Parasitoid species with only one host miner are in the lower row, and those with two or more hosts are in the upper row. Miner species on the same host plant are linked by a horizontal line and are coded by various shading to various insect orders provided in the original publication. In the quantitative food web below, the widths of rectangles for leaf miners and parasitoids are proportional to their abundance, and are scaled as shown in the figure. From Memmott *et al.* 1994. Reprinted with permission from Blackwell Publishing.

leaf-mining insects and their parasitoids in Santa Rosa National Park in Guanacaste, western Costa Rica, in an area of regrowth tropical dry forest (Memmott and Godfray 1994, Memmott *et al.* 1994). The study included 88 plant species, 92 leaf-miner species and 93 parasitoid species. The resulting food web showing just the linkage between species, the **connectance food web**, was rich in interactions resembling “uncooked spaghetti” (Memmott and Godfray 1994, p. 311) (Figure 12.22). Thirty-six species of parasitoids attacked more than one host (shown on the top rank of species in the figure: species 1–36), while the remaining species attacked only one host species (the bottom rank: species 37–93). The species along the middle of the figure, labeled a–cr, are the leaf-miner species, with shading that indicates the taxonomic affiliation of each. The “uncooked spaghetti” illustrates the kind of buffering effects that natural enemies may provide in dampening population eruptions of herbivores in complex communities, as Pimentel (1961) argued. When one natural enemy species declines in numbers, other species are likely to compensate.

The connectance food web only provides one part of the picture of interactions in this dry tropical forest. When the relative size of the populations of leaf miners and parasitoids are entered into what is now a **quantitative food web**, a more complete picture of community structure is revealed. Memmott *et al.* (1994) provided the first large quantitative parasitoid web, and the first for the tropics, so we can ask what insights are provided by such a study.

First, developing a clear description of food-web interactions, using both connectance and quantitative food webs, provides the basis for parasitoid community ecology, as well as much information on the complete food web involving plant hosts and leaf miners. In this case it shows a community composed largely of specialists: 88% of miner species were recorded from a single plant species, while 63% of parasitoid species attacked only one host species. So much of the diversity of the community was linked to single chains of interactions. But the "spaghetti" image captures the tremendous compensatory potential of the more generalized species and the lack of **compartmentalization** (= **compartmentation**) of the food web. Many miner species are linked in their ecology from the top down rather than from the bottom up. This result supports much earlier conclusions by Pimm and Lawton (1980, p. 879) that "Polyphagy in higher trophic levels . . . generates non-compartmented food webs in assemblages of polyphagous insects."

Second, an overall estimate of mortality caused by parasitoids was obtained, an important statistic for comparative purposes on both other tropical and temperate herbivore assemblages: of the total mortality of leaf miners, a mean of 32% was caused by parasitoids.

Third, the kinds of parasitoids were shown to play different roles in the community, with endoparasitoid koinobionts much more specific than ectoparasitoid idiobionts. Among the internal parasitoids 37% were recorded from a single host, and none attacked more than four host species. Only 7% of ectoparasitoids attacked a single host and up to 12 miner species were recorded for some. We can see that the endoparasitoids were more important in providing linear, chain-like connectance while the ectoparasitoids were the "spaghetti"-building species. These differences have obvious consequences for the population dynamics of the leaf miners.

Fourth, where more than one miner species attacked a single host plant species, parasitism was higher on each species, meaning that small differences in host-plant range can have large top-down consequences.

Fifth, the quantitative web shows that while a parasitoid may attack several hosts, a major component of abundance derives from one host, so that host may exert an inordinate effect on another leaf-miner species, indirectly through the parasitoid trophic level. Memmott *et al.* (1994) use as examples the parasitoids coded numbers 6, 25 and 36.

12.4.6 Comparison of tropical and temperate food webs

A valuable comparison can be made between this tropical food web and one in England. At Silwood Park, in southern England, four tree species, their leaf miners in the genus *Phyllonorycter*, and parasitoids were studied (Rott and Godfray 2000). The parasitoids were less specific in this north temperate latitude, resulting in rich connectance and no compartmentation in the leaf miner and parasitoid web, and a high potential for indirect interactions among leaf miners through shared parasitoid species. In these respects food webs were similar. However, the parasitoid richness was much higher per host in the north temperate site: 2.25 parasitoid species per host compared to about one per host in the tropics. At Silwood Park, 4 plant species supported 12 *Phyllonorycter* species and 27 parasitoid species, while in Guanacaste 88 plant species were attacked by 92 species of miner and 94 species of parasitoid. The large difference in parasitoid richness per host supports the general patterns found by Hawkins (1994) for leaf miners and other feeding types, with about twice as many parasitoid species on leaf miners in cooler latitudes as in the tropical latitudes.

12.4.7 Compartmented food webs

This picture of non-compartmented food webs in herbivore parasitoid communities contrasts with the lower part of food webs involving plants and herbivores, in certain cases. As in the leaf miners, fruit flies (Diptera: Tephritidae), which infest the flower heads of plants, are quite specific, many attacking a single plant species and most confined to a single tribe, or lower plant taxon in the case of tephritids on the Asteraceae plant family. In the Espinhaço Mountain Range, in the State of Minas Gerais, Brazil, 81 plant species in the composite tribe Vernonieae were attacked by 35 tephritid species (Prado and Lewinsohn 2004). Plant species in the same subtribe or genus were associated with substantially different sets of fruit flies, such that six compartments were recognized with little overlap among compartments. This kind of pattern is likely to be commonplace in specialist herbivore communities on large plant families like the Asteraceae, and even more developed in communities containing several plant families. Compartmentation also becomes more evident as the scale of the study increases, with the Espinhaço Range study much more extensive than the studies in Guanacaste and Silwood Park. However, the compartmentation will break down at the third trophic level of natural enemies in which predators and some parasitoids attack a broad range of herbivores.

On the theme of habitat heterogeneity begets species richness, the plant–herbivore–parasitoid studies are supportive: the more plant species in a habitat, the more herbivores and parasitoids there will be. There is also much evidence that increasing vegetation structure and habitat complexity promotes the presence and efficacy of invertebrate predators in both terrestrial and aquatic environments (Denno *et al.* 2005a). But any one species of plant can exhibit heterogeneity itself, with genetic variation as an important contributor. This recognition has resulted in the relatively new field of **community genetics** (e.g., Agrawal 2003 and associated papers, Whitham *et al.* 2006).

12.5 Community genetics

In his chapter "Toward community genetics," Antonovics (1992, p. 448) emphasized the need for a holistic approach in this "study of the genetics of species interactions and their ecological and evolutionary consequences." He noted that development of the field would have to rely on improvements in genetic analysis, the documentation of genetic variation, experiments that isolate causes and effects, and long-term studies of interactions. He asked questions about the relationship between species diversity and genetic diversity. Over a decade later, a special feature on community genetics in the journal *Ecology*, edited by Agrawal (2003), highlighted the role of genetic variation in producing patterns in nature, and the predictive science of community genetics that would blend the fields of population genetics, ecology and evolution more effectively.

12.5.1 Genetic diversity and species diversity

In a review of the relationship between species diversity and genetic diversity (Vellend and Geber 2005), direct support for a positive relationship was recognized, if the evidence was somewhat preliminary. However, in insect communities on cottonwoods, *Populus* species, in the wild, Wimp *et al.* (2004) found a significant correlation between cottonwood gene diversity in a stand and arthropod species diversity; arthropods that were directly linked to the cottonwoods through the food web based on

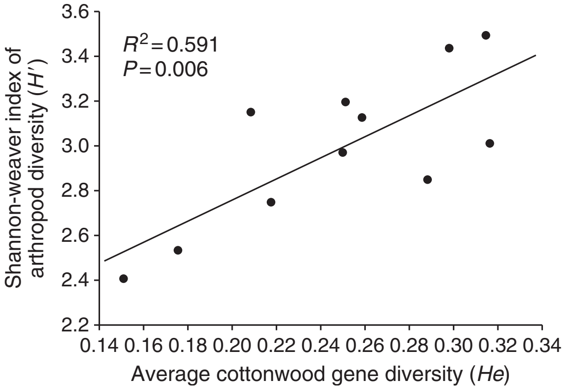


Figure 12.23 The relationship between cottonwood, *Populus*, genetic diversity and arthropod genetic diversity, accounting for almost 60% of variance in diversity of arthropods. The 11 points represent stands of cottonwoods of varying genetic diversity. From Wimp *et al.* 2004.

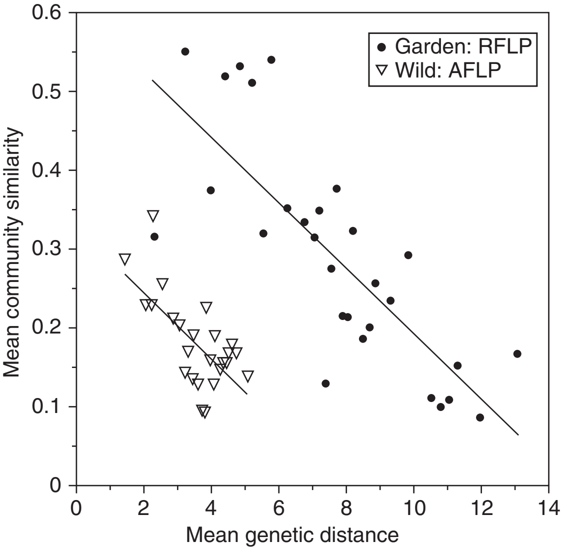


Figure 12.24 The relationship between mean genetic distance among cottonwood trees and the mean community similarity among arthropods on these trees, for both a common garden and a wild population. Small genetic distances are equivalent to high similarity. Genetic variation was estimated using restriction (RFLP) and amplified (AFLP) fragment length polymorphisms in the garden and wild populations, respectively. From Bangert *et al.* 2006.

these host plants (Figure 12.23). Bangert *et al.* (2006) showed that as the mean genetic distance among cottonwood trees increased, as they became less related, so the similarity in the leaf-modifying-arthropod community on these trees declined. This was true both in a common garden and in a natural population (Figure 12.24). Also, in an experimental test where the number of goldenrod genotypes, *Solidago altissima*, was increased, the result was increased arthropod species richness of herbivores, and predators, and increased above-ground net primary productivity (Crutsinger *et al.* 2006). Clearly, there is growing evidence of direct and positive influences of host-plant genetic diversity, and genotypic diversity, on arthropod species richness and community structure.

12.5.2 Cottonwood genetics influences higher trophic systems

Taking the interaction between plant genetics and herbivore responses further, links have been found in cottonwood between genetic markers and leaf phenology, condensed tannin concentration, phenolic glycoside concentration, resistance to an insect, *Pemphigus betae*, and resistance to rust fungi, *Melampsora* species (Whitham *et al.* 2008 and references therein). As a result, the repercussions of genetic variation in plants are extensive, both at the community and ecosystem levels (e.g., Whitham *et al.* 2006, 2008). The first paper to show a link between biological diversity (= phenotypic diversity) and ecosystem processes – carbon and nitrogen cycling – was by Madritch and Hunter (2002), and the first to show that plant genes affected ecosystem function was authored by Schweitzer *et al.* (2004). These authors found that condensed tannins in leaves explained 55–65% of the variation in soil nitrogen mineralization.

Cottonwoods in riparian habitats have been recognized as **foundation species**: “species that structure a community by creating locally stable

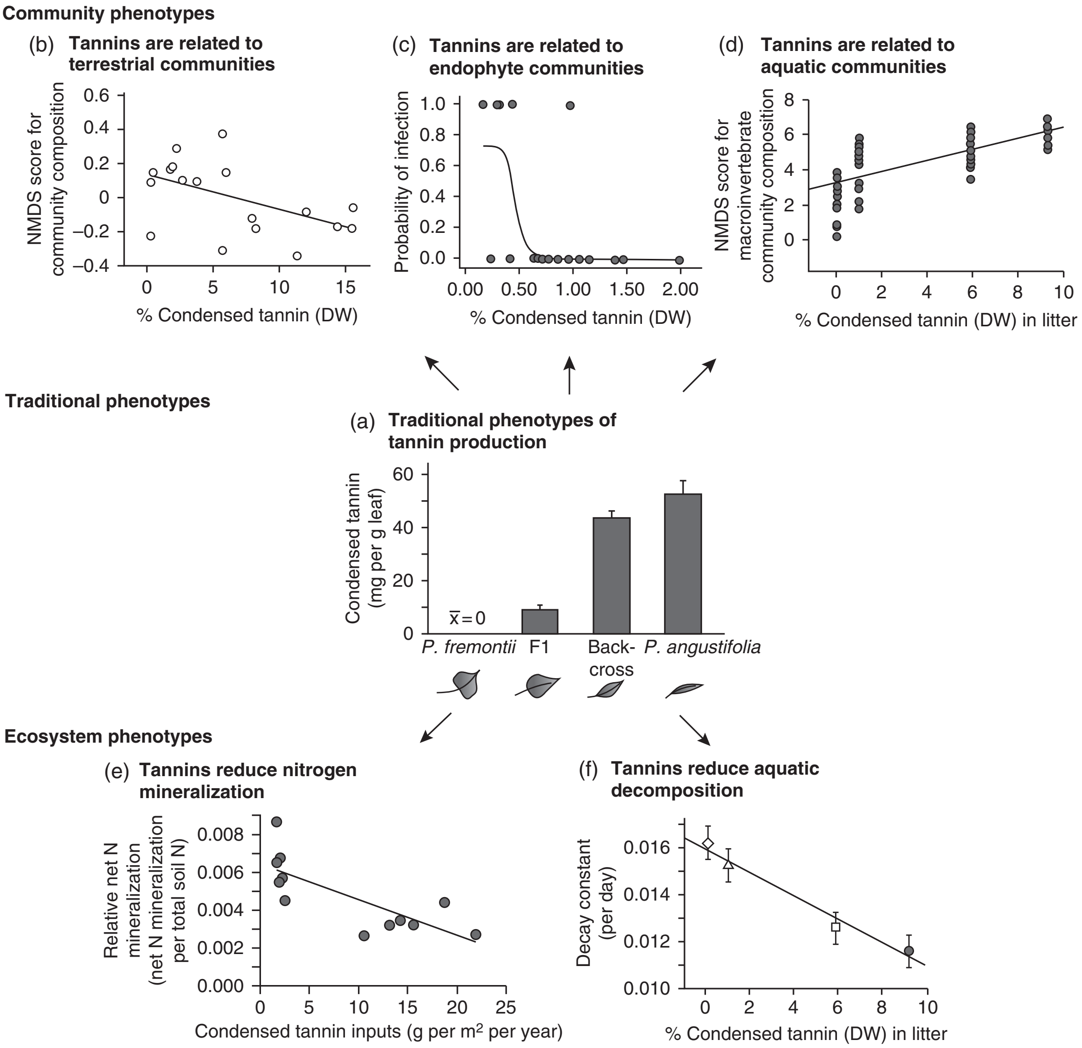


Figure 12.25 Relationships among cottonwood condensed tannin contents (a) and responses of dependent communities: (b) terrestrial (NMDS is non-metric multidimensional scaling – similar scores indicate similar community structure), (c) endophytic fungi and (d) aquatic macroinvertebrates. Ecosystem functions are also related to cottonwood genotypes: (e) tannins reduce nitrogen mineralization and (f) aquatic decomposition. From Whitham *et al.* 2006. Reprinted by permission from Macmillan Publishers Ltd: *Nature Reviews: Genetics*. Whitham, T. G., J. K. Bailey, J. A. Schweitzer *et al.* 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* **7**:510–523 © 2006.

conditions for other species, and by modulating and stabilizing fundamental ecosystem processes" (Whitham *et al.* 2006, p. 511). Therefore, genetic variation in just one trait, such as condensed tannin concentration in trees, can have profound influences on the associated communities of arthropods and ecosystem processes such as litter decomposition and nitrogen mineralization, both in terrestrial and adjacent aquatic environments (Figure 12.25). Also, when leaf litter decomposes it releases carbon,

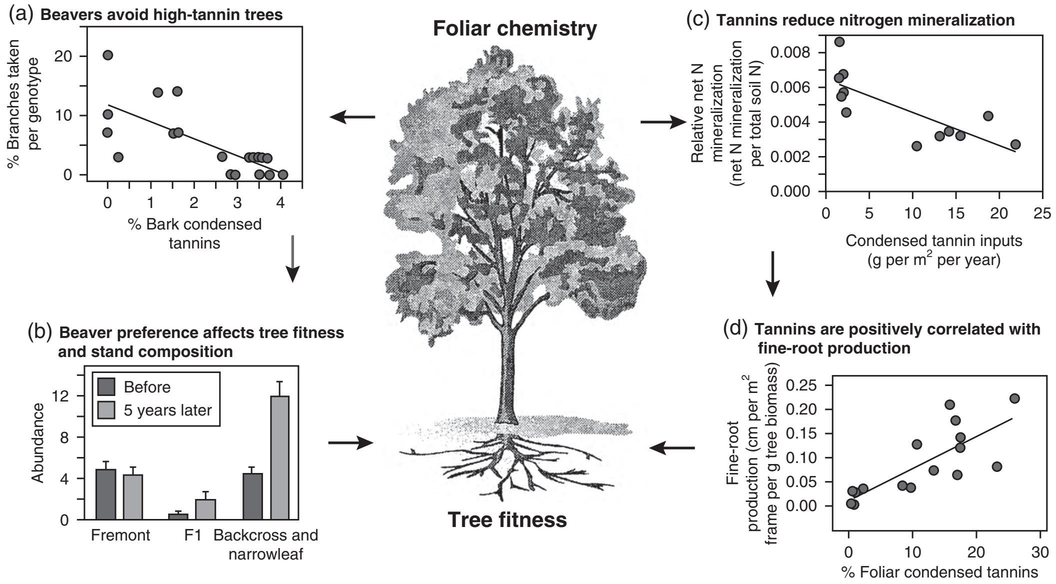


Figure 12.26 Feedback relationships suggesting that natural selection may reinforce cottonwood characters such as tannin content via interactions in the tree's environment. (a) Beavers avoid trees with high condensed tannin concentrations, such that (b) they select for trees with high tannin content (left-hand column of a pair is 5 years earlier in the study, and right-hand column is 5 years later) with genotypes with the highest tannin content – backcrosses and pure narrowleaf cottonwood (see Figure 12.25a) – becoming much more abundant in the riparian woodland within 5 years. Another feedback loop involves (c) tannins that reduce nitrogen mineralization, but (d) stimulate fine-root production. From Whitham *et al.* 2006. Reprinted by permission from Macmillan Publishers Ltd.: *Nature Reviews: Genetics*. Whitham, T. G., J. K. Bailey, J. A. Schweitzer et al. 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* **7**:510–523.

nitrogen and sulfur determined by the genetic identity of the parent plant (Madritch *et al.* 2006), and frass from canopy herbivores was influenced by intraspecific variation in green-leaf chemistry, including C:N ratios and condensed tannins (Madritch *et al.* 2007). In addition, feedback loops from foliar chemistry involving tannin concentrations in leaves may well affect natural selection on the trees through increased fine root production, and decreased beaver preference as tannin concentrations increase (Figure 12.26). Major defoliating herbivores may well be influenced in similar ways and enter into additional feedback loops. Indirect effects may also ramify from tannins to leaves and then to other herbivores (e.g., Bailey and Whitham 2006).

Several studies now show that plant genetic factors account for about 40–70+% of variation in ecosystem functions in the cottonwood system. Water cycles from soil to plant to the atmosphere, with plant genetics accounting for 35–40% of the variation (Fischer *et al.* 2004). Below-ground carbon storage and root production is strongly influenced by plant genetics, accounting for 77% of the variation (Fischer *et al.* 2006). Plant productivity has 45% of its variation influenced by genetics (Lojewski *et al.* 2009), and leaf-litter decomposition and nutrient cycling are similarly influenced, from 34–65% (e.g., Schweitzer *et al.* 2004, LeRoy *et al.* 2006). Biodiversity of microorganisms, herbivores and birds are all influenced by plant genetics ranging from 43–78% of variation accounted for by plant genetics (Wimp *et al.* 2004, Bangert *et al.* 2005, Shuster *et al.* 2006, Bailey *et al.* 2006, LeRoy *et al.* 2006, Schweitzer *et al.* 2008), and plant genotype also influenced microbial community composition (Schweitzer *et al.* 2008). So pervasive are the genetic effects of host plants on communities that we can conceive of a community heritability of arthropods on host plants, with an estimate of 56–63% of total variation in community phenotype explained by the known genotype of cottonwood trees (Shuster *et al.* 2006).

When we can identify feedback loops, such as in Figure 12.26, and establish that natural selection is working, and evolutionary change is being affected, then the case can be made for a coevolutionary system. This would result almost certainly in a geographic mosaic of coevolution because the selection intensities and directions of selection are most likely to differ over a landscape. Therefore, community genetics is important both in natural and cultivated landscapes, including forest ecosystems.

12.6 The time hypothesis or the area hypothesis?

We have focused much attention in this chapter on the way in which individual communities develop and the processes involved, but when community richness is compared across many examples, the “independent variables” may be correlated. This is particularly the case when evolutionary time and geographic area are considered as part of the mechanistic explanation of differences in community richness, resulting in debate about their relative importance.

Time provides a dimension on which communities assemble and develop on ecological scales and evolutionary scales. Both scales are illustrated in Wilson’s concept of community development (Figure 12.10), and colonization of islands in ecological time was documented in the defaunation studies by Simberloff and Rey (Figure 12.13). Space influences communities through size of habitats available for colonization, such as the mangrove islands colonized by ants, studied by Cole (1983a,b) (Figures 12.14, 12.15), and the oak tree hosts colonized by leaf miners (Figures 12.16, 12.17, Opler 1974). Space also is likely to be correlated with variety of habitat structure, and its arrangement over the landscape, both important influences on community development and structure (see Bell *et al.* 1991, Roslin and Kotze 2005). As space for populations to occupy increases, as on oceanic, vegetational or aquatic islands, population size is likely to increase, with persistence and stability probably increasing in concert. Therefore, time and space play important roles in community organization.

In fact, time and space effects are simultaneously involved in many cases. It takes time for specialist species to colonize a host plant, or any other particular habitat, and evolve to exploit the relevant resource. And, inevitably, a spatial component of the habitat has its effects. Hence, the relative effects of time and space have resulted in some debate. For example, Southwood (1961) examined the number of insect species associated with British trees. He found that as the length of time the tree species had occupied the British Isles increased, based on the fossil record, so the number of insect species increased (Figure 12.27). Also, introduced tree species had depauperate insect communities. However, the fossil record also correlated with the abundance of tree species, so tree availability for colonization had several influences on colonization, length of time, tree geographic range and abundance. Later analyses showed that abundance of host species was a better predictor than tree geographic range (Kelly and Southwood 1999), and interestingly, all groups of insects, including herbivorous Lepidoptera, Hymenoptera and Hemiptera, showed positive correlations with tree abundance, indicating a lack of competitive exclusion and independent colonization.

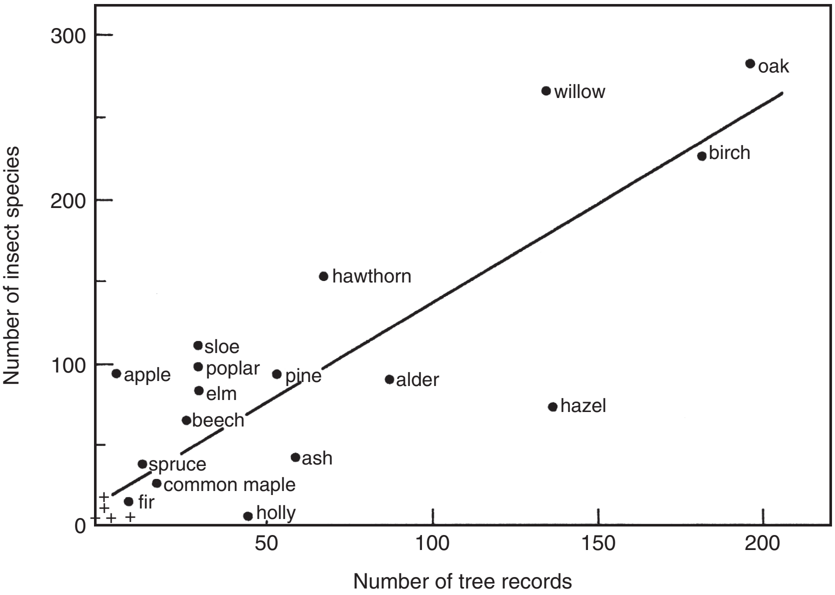


Figure 12.27 The relationship between the abundance of tree fossils coupled with the length of time available in the Quaternary record, which influence the probability of colonization by insects and the number of insect species recorded on British trees. + indicates the number of insect species on introduced tree species. From Southwood 1961. Reprinted with permission from Blackwell Publishing.

Another case studied by Southwood (1960) shows time and host abundance irrevocably correlated, because so much of the flora and fauna in the Hawaiian Islands is endemic. Therefore, colonization of trees by specialized insects must have occurred over evolutionary time. Also, we can presume that abundance of host trees is generally correlated with time. So, specialized insect herbivores would colonize trees in evolutionary time, while generalists would colonize in ecological time. In both cases the same responses to host-tree abundance were observed (Figure 12.28).

Recalling Opler's (1974) study on oaks (Figure 12.16), the time available for colonization did not register as an important factor, while tree geographic range had strong predictive power. This proved to be true also for the insects on British trees when reanalyzed by Strong (1974a,b) (Figure 12.29), and introduced tree species such as apple, lime, larch and sycamore, although present for a much shorter time on the islands, had relatively rich faunas best accounted for by the area they occupied.

Thus, we have a **time hypothesis** and an **area hypothesis** for the number of species in communities, with a correlation between the two in some cases. Time is a simple dimension, but space is complex. As we have noted already, space, such as island size, can influence population size, habitat heterogeneity, distance among resources and colonization rates, to name a few aspects, and spatial ecology is a vigorous field of research (e.g., Roslin and Kotze 2005). Since resources are displayed in space, several community hypotheses are relevant: the resource-heterogeneity hypothesis, the resource-concentration hypothesis, the associational-resistance hypothesis and even the enemy-impact hypothesis.

Population-density responses to space are generally positive, particularly in insect species, relative to birds and mammals (Connor *et al.* 2000). Out of 29 insect species tested, 11 showed very strong

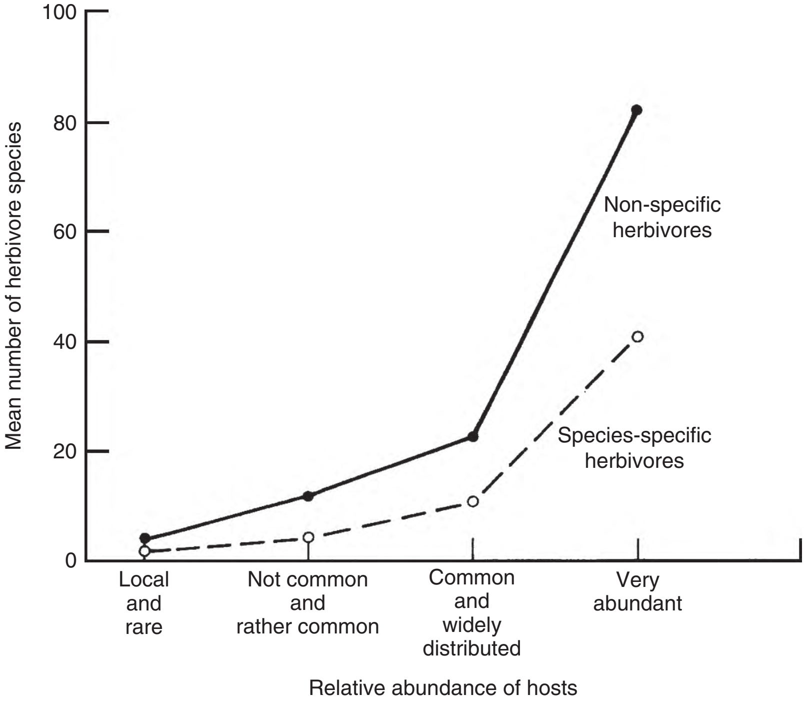


Figure 12.28 The relationship between the commonness of Hawaiian tree species and the mean number of herbivore species recorded on each tree species, both for generalist and specialist species. Based on data provided in Southwood 1960.

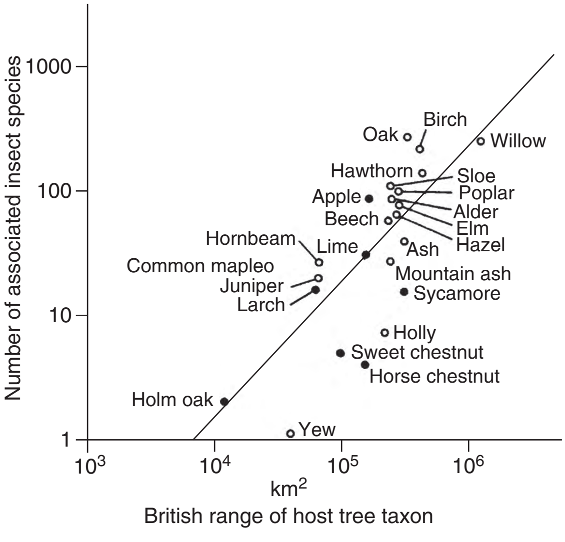


Figure 12.29 Strong's (1974a) analysis of the relationship between geographic area occupied by a tree species in Britain and the number of insect species associated with each tree species. Open circles are for native trees and closed circles are for introduced species.

correlations with area (correlation coefficients 0.8 and above), and 23 species showed positive correlations, while the remaining six were negative. The results were consistent with the resource-concentration hypothesis, although various other mechanisms may be involved. This density response to space is likely to influence the probability of persistence, extinction and dispersal. The topic of area and arrangement of suitable habitat will be examined further in Chapter 14, Biological diversity.

12.7 Compound communities

In the chapter so far we have concentrated on component parts of communities because it is usual to simplify in order to detect and understand the patterns we can find. Also we have largely deferred consideration of complete food webs and interactions

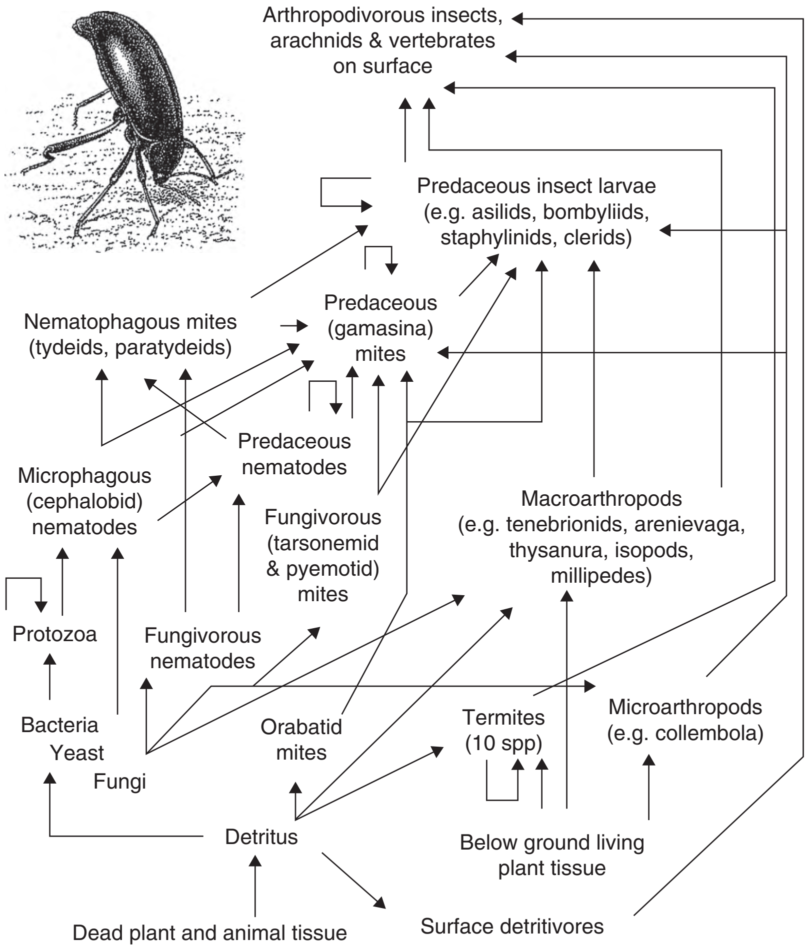


Figure 12.30 The subweb based on dead plant and animal tissue developed by Polis (1991a), from the sandy soils of the Coachella Valley, California. "Food webs in desert communities: complexity via diversity and omnivory" from *The Ecology of Desert Communities*, edited by Gary A. Polis © 1991 The Arizona Board of Regents. Reprinted by permission of the University of Arizona Press.

among trophic levels until Chapter 13. We have considered relationships among organisms on the same trophic level: ecological niches, coexistence of species, herbivores on bracken fern and soybean, and the development of component communities on mangrove islands and cord-grass. Studies on small ant communities on mangrove islands, leaf miners on oaks and community assembly have all focused on insects on one trophic level. Qualitative and quantitative food webs, so far as we have discussed them, have involved insect herbivores on several to many host plants, but studies have been restricted to a particular kind of herbivore such as leaf miners or aphids. Adding more taxonomic groups of herbivores and predators would increase greatly the complexity of food webs. Even these limited webs had to be simplified in order to capture the main interactions, filtering out detail that would make diagrams such as Figure 12.22 almost solidly black.

One begins to wonder if truly complete communities are tractable for ecological research,

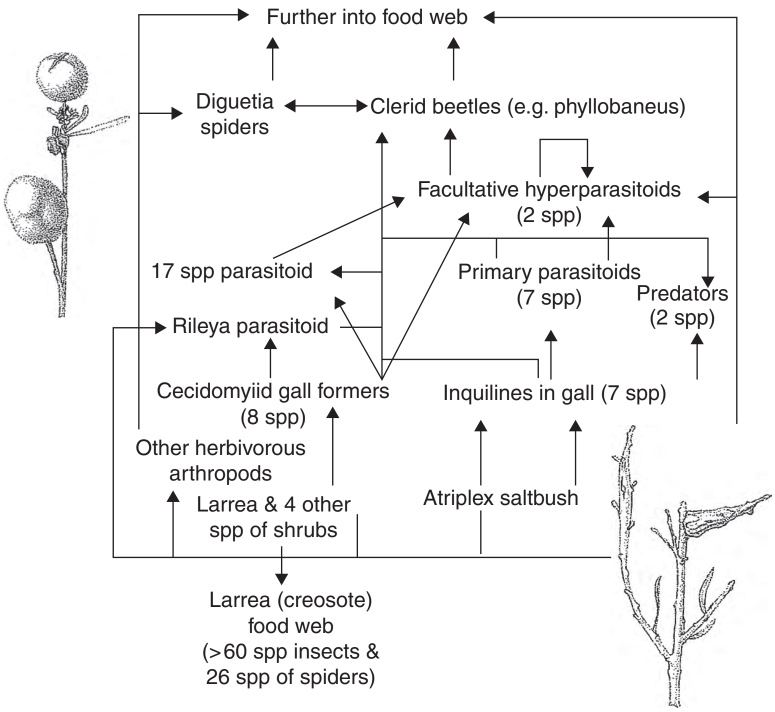


Figure 12.31 An example of a subweb on a living plant species, such as saltbush, with interactions involving cecidomyiid gall-inducers illustrated. There are 8 cecidomyiid gall formers which interact with 67 other species (Hawkins and Goeden 1984), and many of the carnivores also enter the subwebs based on creosote bush, *Larrea divaricata* (Schultz *et al.* 1977). From Polis 1991a. “Food webs in desert communities: complexity via diversity and omnivory” from *The Ecology of Desert Communities*, edited by Gary A. Polis © 1991 The Arizona Board of Regents. Reprinted by permission of the University of Arizona Press.

and what such communities would look like and how informative they would be. The converse view is that simplifying food webs usually results in over simplification and abstractions that may be misleading. Some generalizations about food webs in the literature are listed by Polis (1991a,b), such as food chain lengths are typically three or four trophic levels, omnivory is rare, looping in food chains is rare and species interact with only two to five other species. But this is not what Polis found. Extensive studies of food-web interactions in the desert of the Coachella Valley in Riverside County, California, indicate that generalizations may be overstated. This is partly because of problems with many studies:

(1) Real communities are much more speciose than those usually depicted in food-web studies.
(2) Lumping of species is common.
(3) Dietary information is incomplete, particularly for general predators like scorpions.
(4) Temporal and spatial variation in food-web structure is universal, but seldom captured in a study, with pulsing of food sources being a contributing factor.
(5) Age structure influences who eats whom, age classes of insects and vertebrates change diets: “life-history omnivory” and “ontogenetic diet shifts.”
(6) Looping is common where species feed on their own kind – cannibalism – or when species A eats species B, B eats C and C eats A, or B eats A (mutual predation).

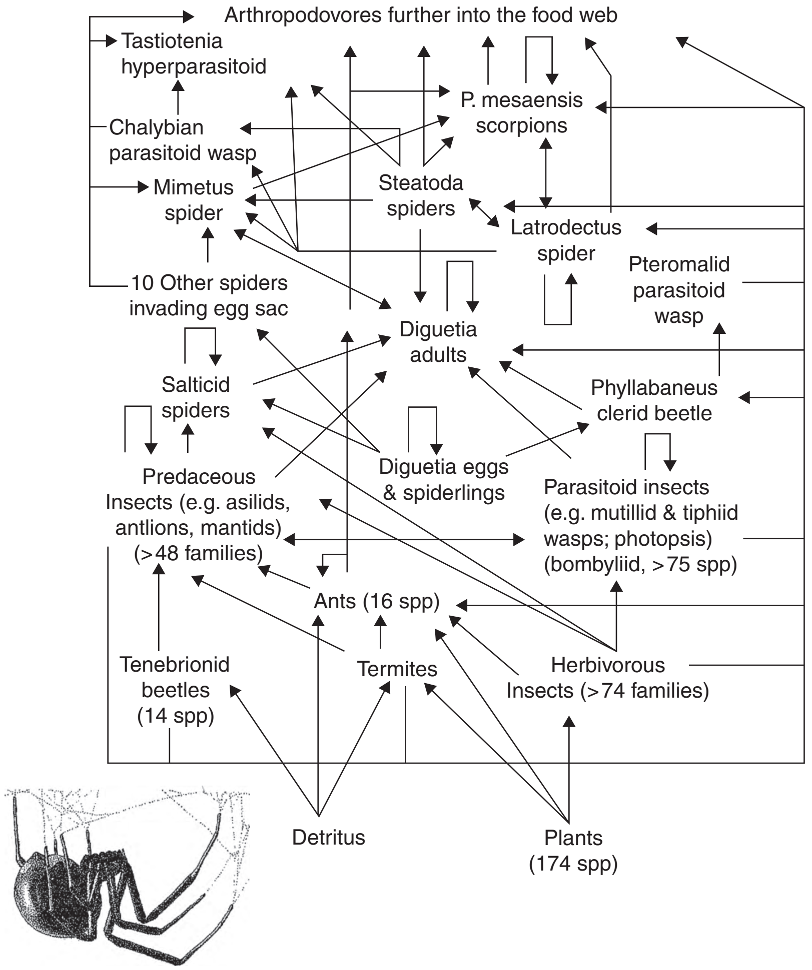
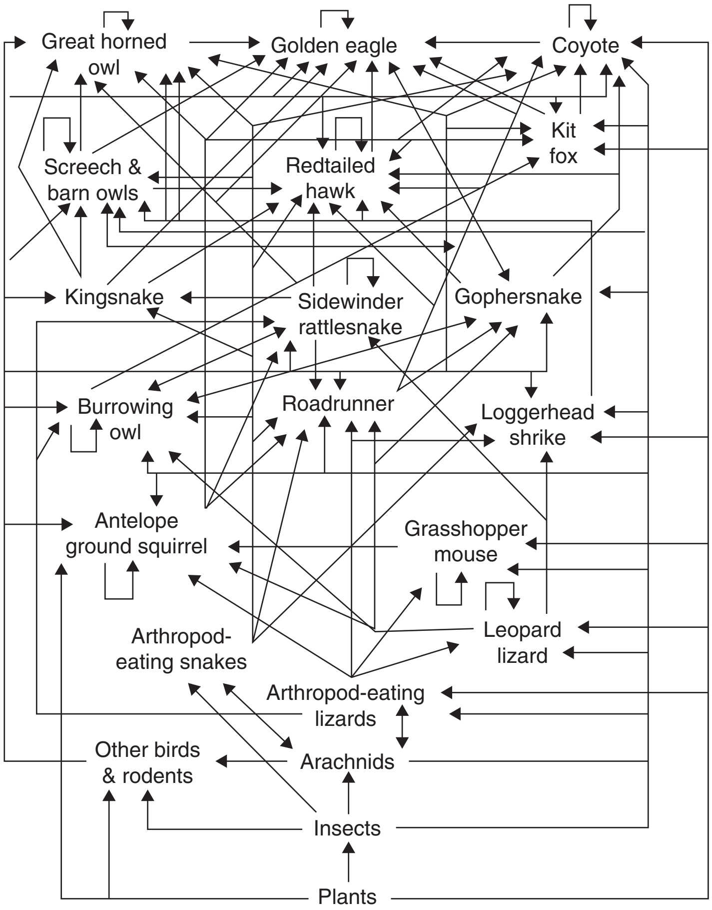


Figure 12.32 The subweb from the Coachella Valley emphasizing predaceous arthropods, showing much cannibalism, intraguild predation, looping involving several species and long chain lengths in the food web. From Polis 1991a. "Food webs in desert communities: complexity via diversity and omnivory" from *The Ecology of Desert Communities* edited by Gary A. Polis © 1991 The Arizona Board of Regents. Reprinted by permission of the University of Arizona Press.

Polis (1991a) depicts the Coachella Valley desert food web in a series of subwebs. Starting from the ground up, he provides a subweb based on dead plant and animal tissue (Figure 12.30). Distinct trophic levels are hard to find, and there is much looping in predaceous groups, such as nematodes, mites and insects. Another set of subwebs concerns living plants and their herbivores and parasitoids, with the saltbush *Atriplex canascens* as an example, which concentrates on the gall-inducing species, their parasitoids, and predators or parasitoids and hyperparasitoids (Figure 12.31). Then, a subweb emphasizing predaceous arthropods illustrates looping of various kinds among predaceous spiders and scorpions (e.g., *Latrodectus* → *Mimetus* → *Paruroctonus mesaensis* → *Latrodectus*) (Figure 12.32).



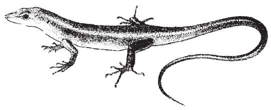


Figure 12.33 The vertebrate subweb in the Coachella Valley showing long food chain length, lack of a trophic level structure because of omnivory (feeding on more than one trophic level) and shifting diet with animal age. From Polis 1991a. "Food webs in desert communities: complexity via diversity and omnivory" from *The Ecology of Desert Communities* edited by Gary A. Polis © 1991 The Arizona Board of Regents. Reprinted by permission of the University of Arizona Press.

All these subwebs feed into the subweb composed of vertebrates, showing multiple examples of omnivory (note arrows going from plants to lizards, mouse, fox, etc.), looping and an intricate web of predation with food-chain lengths reaching up to seven or eight links (Figure 12.33). Several other subwebs are provided by Polis (1991a).

The sandy terrain of the Coachella Valley supports about 175 species of plants, 100 vertebrates, and thousands of arthropods and microbe species. They form a compound community which shows complexity of subwebs, long food chains, the importance of age structure and omnivory. Omnivory in this context refers to feeding on more than one trophic level, not only feeding on both plants and animals. Also, looping is common – predators feed on each other, so focus on a top predator is rare, and species composition and abundances change with time. Few generalizations identified in hypothetical developments in the field of food webs are supported.

Desert communities are commonly regarded as simple or even depauperate, and yet one of the richest webs has been developed for the sandy Coachella Valley. This suggests that other habitats have a greater diversity of species and interactions, and that the literature has failed to capture the reality in nature. However, rather than despairing of ever understanding such complexity, other approaches reveal insights and generalities which will be discussed in the next chapter.

Applications

Insects in environmental assessment

The health of communities and their long-term maintenance and well being are of major concern in the closely related areas of conservation, restoration, climate change, biodiversity and the management of sustainable environments in general. To measure environmental health, communities of various species are commonly employed as indicators of environmental degradation or recovery, so that monitoring approaches and methods have become diverse and multifaceted. Environmental assessment and environmental impact statements are expected to rely on sound-monitoring techniques. Many environmental impacts need to be assessed: urbanization, habitat fragmentation, agriculture, logging in forest ecosystems, various impacts on stream and lake quality, pollution, climate change and global warming. The maintenance of biodiversity during environmental modification is a central theme.

Environmental monitoring

Insect communities provide excellent subjects for monitoring environmental change. Insects are ubiquitous in virtually all environments of interest, or they should become common if recovery from heavy impact is achieved. Individual species numbers are relatively high, and species can be collected, with discretion, making sampling objective, with a record of the specimens available for study. Insects also occupy the many habitats available: the ground surface and below, fresh-water habitats, plants of all sizes, wild and urban environments. Therefore, diverse sampling methods may be employed: cryptozoa boards, pitfall traps, nets of many kinds, direct observation of herbivores on plants, capturing of flying insects, such as flies, dragonflies and butterflies. The display of sampling devices and the analysis of data become major concerns (see Hayek and Buzas 1997, Krebs 1999, Southwood and Henderson 2000). Long-term studies of species and communities are particularly valuable for detecting trends in populations and biodiversity correlated with abiotic and biotic variables such as land use, logging practices, aquatic pollution, habitat fragmentation and climate change. For example, butterfly species and communities have been followed for a decade or more in the United Kingdom, the Netherlands, Spain, Brazil and the USA (e.g., Pollard *et al.* 1995, British Isles, 19 years; Pollard and Moss 1995, British Isles, 67 years; van Strien *et al.* 1997, British Isles, 17 years; Pollard and Greatorex-Davies 1998, British Isles 21 years; Brown and Freitas 2000, Brazil, 26 years; Roy *et al.* 2001, British Isles, 22 years; Thomas *et al.* 2002, Wales, 30 years; Walton *et al.* 2005, USA, 13 years; Wilson *et al.* 2005, Spain, 30 years, Thorne *et al.* 2006, California, 27 years).

Indicator groups and species

Evaluating change or stability in insect communities may be expensive in time and money, and expertise could be hard to find. Simplification is often achieved by focus on a particular insect taxon like butterflies, dragonflies, ants or aquatic groups, or even one representative species of a group. These may be called **indicator groups** and **indicator species**, respectively (e.g., Gaston *et al.* 1993, Samways 1994). Here the concepts of the ecological niche and guild become useful. Guilds of species may be employed as indicator groups, and several guilds could be used to monitor environmental conditions. Or, an indicator species, considered to be representative of its guild, may be the center of focus, thereby reducing the costs of monitoring. Species can be studied for their own intrinsic interest, such as checkerspot butterflies (e.g., McLaughlin *et al.* 2002a,b), or as representatives of a guild or larger taxonomic group, such as ants (e.g., Widodo *et al.* 2004, Bestelmeyer 2005, Forys and Allen 2005).

Agricultural practice

Some examples of estimating environmental impact of human activities such as agriculture and logging will illustrate how insect communities are viewed and used in managed landscapes. Agricultural practices simplify habitats, thereby reducing food supplies and nesting sites for some kinds of insects. Even coffee plantations, formerly planted under a dense-shade canopy of native trees, have been greatly simplified by reducing shade trees, pruning them and applying chemicals. Nesting sites for twig-dwelling ants are diminished, competition may eliminate some species, reducing ant diversity, and their biological control effects on coffee-pest insects is compromised in these agroecosystems (Philpott and Foster 2005). Adding artificial nesting sites to coffee plantations in the form of hollow coffee twigs or bamboo stems increased ant species richness from 14 to 26 ant species, and ant abundance also increased in treatment areas. Effects on insect pests were not measured, but with more ant species present, in greater abundance, and with species composition changing among sites and treatments, considerable differences in biocontrol could be anticipated.

Forestry practice

As in agriculture, logging also simplifies habitats, disturbs soil and low vegetation, and increases runoff into aquatic systems. Impact is extensive and diverse unless extraction techniques are carefully planned to minimize habitat degradation. Insects have been used to evaluate harvesting methods and impact. Sampling of lepidopteran caterpillars on oaks in the Ozark uplands of Missouri, USA, before and after timber harvest, showed subtle effects on species richness and density (Forkner *et al.* 2006). On white oaks postharvest species numbers were reduced by 32%, but on black oaks species richness increased, and in general density of species and community structure remained the same. Continued monitoring in relation to tree-harvest frequency will yield relevant data for management plans with the intent of maintaining insect herbivore diversity and density. Of course, insects serve many functions in forests, as food for birds, mammals, and invertebrates, and in various ecosystem functions (see Chapter 13), so their conservation is desirable.

Logging, including both timber extraction and road building may also affect aquatic insect communities (Kreutzweiser *et al.* 2005a,b). Low intensity logging (29% of basal area of trees removed) had no detectable effect on community structure and abundance, but at 42% of basal area removed, the abundance of five taxa increased, probably resulting from a 2.5× increase in fine particulate organic matter deposited in the stream. In a related study in the same Turkey Lakes Watershed in Ontario, Canada, a road crossing a stream was prepared for logging operations, which released fine sediment downstream. This may have impacted the benthic community through increasing sediment by over six times. Therefore road plans to minimize detrimental effects on aquatic insects were recommended. However, road effects were minimal, with no significant impact on total insect abundance or biomass, although community composition changed with spring shredders declining, and chironomids increasing.

Restoration ecology

Restoration ecology depends heavily on concepts and hypotheses derived from community ecology (Young *et al.* 2001, 2005). Particularly useful are approaches and concepts related to ecological succession and ecological assembly. **Ecological restoration** is defined as "The return of an ecosystem to an approximation of its structural and functional condition before damage occurred" (Cairns 1998, p. 217). This requires extensive knowledge of community dynamics such as how the community develops and mechanisms that may influence assembly of members, and not least, the original conditions which should be restored as far as possible. And while restoration may well involve recreation of environments of a former time – **retrospective restoration** – the plan should encompass a design ensuring a sustainable ecosystem well into the future – **prospective restoration**. Given the anticipated climate change over the next 100 years, for example, some plant genotypes from warmer areas than in the restoration area may well be better adapted for the future conditions than the locally adapted genotypes. For insects, we may well expect them to evolve rapidly enough to remain adapted to changing conditions, but their food plants, especially long-lived species, may need some supplemental genotypes.

There are many other applications of community ecology that relate to multitrophic level systems that will be covered in the next chapter. For example, in the biological control of weeds and insects, attempts are made to establish communities of natural enemies on these pest species. And in the treatment of biodiversity in Chapter 14, other opportunities will be available to discuss the roles of community ecology in maintaining sustainable environments.

Summary

The community involves interacting individuals and species at one location, and we distinguished between component and compound communities. Concepts contributing to community views include the guild, trophic levels, food chains and food webs. Each species within the community occupies its own unique niche which we can measure objectively, but habitats may support more species than at present because vacant niches are evident. Communities develop in ecological time and evolutionary time, with four phases in development recognized, and the final evolutionary phase illustrated by the taxon cycle. Colonization of defaunated islands illustrates that equilibrium numbers of species are eventually realized, with patterns mimicking those observed in ecological succession. Experimental studies on communities show that assembly of species follows certain rules, but these vary according to the kinds of insects studied. The kinds of species of herbivores coexisting in a community may be influenced by the genetic makeup of the host plant.

The organization and structure of a community are influenced by various factors which form the basis of hypotheses, ranging from ideas on the importance of resource heterogeneity, to resource concentration, and the top-down impact of natural enemies. Structure may be described by food webs showing connectance among species, with added information provided in quantitative food webs, and communities may or may not be compartmented into subunits based on discrete resources utilized by rather specialized insects. Plant genetic diversity has been shown to be positively correlated with insect species diversity, and plant molecular traits impact many aspects of community and ecosystem functions.

Comparing community species numbers across equivalent habitats, such as tree species as hosts for insect herbivores, time and area both contribute positively to species richness. Time allows species to colonize and evolve, and large areas offer more diverse habitats and a greater probability of species colonizing. Moving up to compound communities raises questions about generalizations on community structure. The high richness of species and interactions in such communities, their prolonged study, and the recognition that generalized predators modify diet commonly as they grow, all contribute to a much more complex set of relationships

than generally examined, resulting in different conclusions. Nevertheless, studies on insect communities have provided important insights into ways in which we can monitor environments to evaluate various human impacts, for example by using indicator species and groups. Estimating impact can be practiced in agriculture and forestry, and progress in restoration ecology can be evaluated.

Questions and discussion topics

1 The niche concept has been debated at length over the years. In your opinion: (a) what is the most satisfactory view of the ecological niche, (b) is the vacant niche a useful concept and (c) can you define a practical use for the concepts of actual and potential niches of a species?

2 In a community of your choice discuss how you would proceed in describing the structure of the community and the variables that influence this structure.

3 Discuss the argument that communities of insects will be influenced more by bottom-up effects than by top-down effects.

4 In order to understand insect community structure, how would you design a series of experiments to investigate the relative roles of habitat heterogeneity, host-plant genetic heterogeneity and host-plant associational effects?

5 In a newly planted agricultural field, a new plantation of small trees or in a restoration site, how would you plan a study to test for phases in community development, and how would you incorporate research on an unaltered reference or control site?

Further reading

Basset, Y., V. Novotny, S. E. Miller and R. L. Kitching, editors. 2003. *Arthropods of Tropical Forests: Spatio-temporal Dynamics and Resource Use in the Canopy*. Cambridge: Cambridge University Press.

Memmott, J., H. C. J. Godfray and I. D. Gauld. 1994. The structure of a tropical host-parasitoid community. *J. Anim. Ecol.* **63**:521–540.

Morin, P. J. 1999. *Community Ecology*. Oxford: Blackwell.

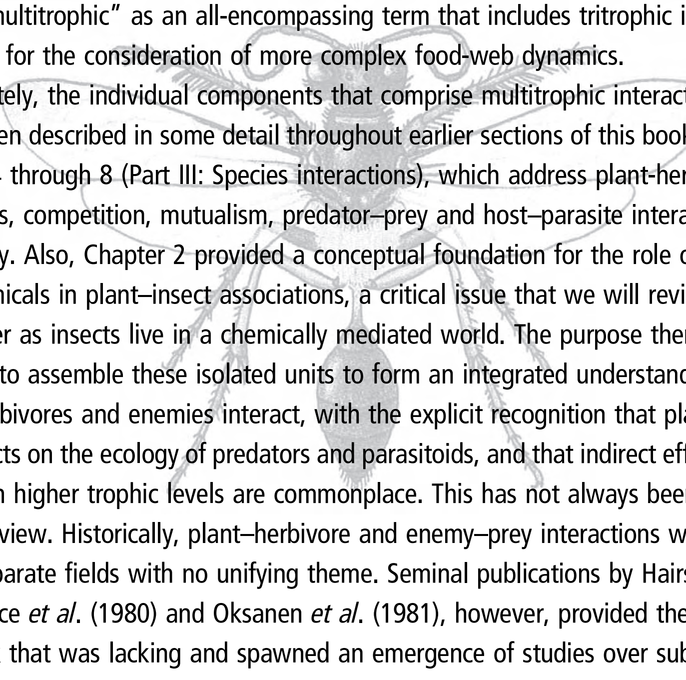
Whitham, T. G., J. K. Bailey, J. A. Schweitzer *et al.* 2006. A framework for community and ecosystem genetics: from genes to ecosystems. *Nat. Rev. Genet.* **7**:510–523.

Young, T. P., D. A. Petersen and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecol. Lett.* **8**:662–673.

13

Multitrophic interactions

Multitrophic interactions are those that link several (i.e., more than two) trophic levels, including plants (first trophic level), herbivores (second trophic level), and predators, parasitoids or pathogens (third trophic level and beyond; hereafter referred to as "enemies"). These types of multispecies consumer-resource dynamics are also referred to as **tritrophic interactions** when they specifically involve three trophic levels. Because food webs typically possess more than three trophic levels, with higher-order predators preying on intermediate predators and hyperparasitoids attacking primary parasitoids, we use "multitrophic" as an all-encompassing term that includes tritrophic interactions, but allows for the consideration of more complex food-web dynamics.



Fortunately, the individual components that comprise multitrophic interactions have already been described in some detail throughout earlier sections of this book, especially Chapters 4 through 8 (Part III: Species interactions), which address plant-herbivore interactions, competition, mutualism, predator–prey and host–parasite interactions, respectively. Also, Chapter 2 provided a conceptual foundation for the role of semiochemicals in plant–insect associations, a critical issue that we will revisit often in this chapter as insects live in a chemically mediated world. The purpose then of this chapter is to assemble these isolated units to form an integrated understanding of how plants, herbivores and enemies interact, with the explicit recognition that plants exert direct effects on the ecology of predators and parasitoids, and that indirect effects linking plants with higher trophic levels are commonplace. This has not always been the prevailing view. Historically, plant–herbivore and enemy–prey interactions were treated as two separate fields with no unifying theme. Seminal publications by Hairston *et al*. (1960), Price *et al*. (1980) and Oksanen *et al*. (1981), however, provided the theoretical framework that was lacking and spawned an emergence of studies over subsequent decades. As a result, the field of multitrophic interactions is among the most productive, innovative and exciting realms of insect ecology.

This chapter is roughly partitioned in two distinct, but related, topics. We begin exploring multitrophic interactions from a highly mechanistic perspective, delving into the specific plant traits that directly and indirectly impact higher trophic levels, and the sophisticated strategies that plants have evolved to minimize enemy impact – although as we will soon learn, they are not always successful in this endeavor! In the latter half of the chapter we discuss broader ecological patterns by which plant and carnivore effects cascade up or down the trophic web to indirectly affect each other's abundance, distribution and diversity. One important theme that we do not address in this chapter is the influence of predators and parasitoids on host shifts and diet-breadth evolution in phytophagous insects via **enemy-free space**. This topic is covered extensively in Chapter 4 under Section 4.6 entitled "The evolutionary ecology of plant–insect interactions."

13.1 The trophic level concept

Before launching into a full-scale discussion of multitrophic interactions, it is worthwhile for us to first spend a moment scrutinizing the concept of trophic levels, as this will place much of the ensuing chapter in its proper perspective (also see Chapter 12). Trophic levels represent the hierarchical positioning of organisms in a food chain. Plants (producers) are the basal resource at trophic level one, herbivores (primary consumers) feed on plants and form the second trophic level, while carnivores (secondary consumers) eat herbivores and comprise the third trophic level. In theory, this linear chain describing who eats whom can extend indefinitely to the fourth trophic level (tertiary consumers) and beyond, depending on how many consumers exist in a given community. Lindeman (1942) originally devised this system to group organisms with similar functional roles in a food web, an approach that is commonly employed in ecology (e.g., feeding guilds). Such abstractions and simple linear food chains, however, suppress the inherent complexity of real communities, which tend to form reticulate webs that are difficult to partition conceptually or tease apart mechanistically (Figures 12.32 and 12.33). This complexity is largely driven by the prevalence of **omnivores**, consumers that feed from multiple trophic levels. Omnivory is a ubiquitous feeding strategy represented in at least 40 families and 12 orders of insects (Coll and Guershon 2002). Certain species of lacewings, for instance, consume pollen as adults, whereas the larval stage is predaceous, feeding on soft-bodied prey items such as aphids (so-called "**life-history omnivores**"; Coll and Guershon 2002). In other words, these insects begin their life as predators, but undergo an ontogenetic shift from predator to herbivore with pupation to adulthood. Similarly, late-instar caterpillars incidentally ingest insect eggs that are embedded in leaf tissue as they forage. Should these insects be assigned to the second or third trophic level? Obviously, caterpillars are almost universally regarded as herbivores, yet these examples demonstrate some of the intrinsic difficulties and challenges associated with the trophic level concept.

Despite their continued and widespread use, several authors have questioned the value of trophic levels because they overly simplify food webs, resulting in a trophic model that bears little resemblance to reality (Polis 1991b). Polis and Strong (1996, p. 815) went so far as to state the following: "We reiterate that the notion that species clearly aggregate into discrete, homogeneous trophic levels is fiction. Especially in species-rich systems, groups of species with diets of similar species do not occur. Omnivory, ontogenetic, and environmentally induced diet shifts and geographical and temporal diet heterogeneity all obscure discrete trophic levels." This extreme position has ignited a contentious debate that has since been countered (Hairston and Hairston 1997). In a recently published quantitative analysis of 58 real food webs, Thompson *et al.* (2007) demonstrated that plants and herbivores are in fact discernable as discrete groups, but these trophic patterns quickly dissipate at the third trophic level and higher because of extensive omnivory. Thus, trophic levels may indeed exist in short food chains, but the concept becomes less applicable as food-chain length increases.

The realism of trophic webs can also be improved by overlaying them with ecologically relevant details, an approach that we have taken throughout this book. For example, in Figure 1.4 herbivores are partitioned into feeding guilds, and in Figure 2.7 plant species are differentiated from one another rather than lumping them into a single trophic group. In spite of the controversy surrounding this topic, we consider trophic levels to provide a valuable framework for envisioning plant–insect assemblages. Nevertheless, it is critical to at least consider the caveats and pitfalls associated with simplifying complex food webs. This will become especially important in our later discussion of trophic cascades, which are founded on the existence of distinct trophic levels and the propagation of strong top-down effects through linear chains.

13.2 Plant traits that affect enemy–prey interactions

Plants possess a variety of ecologically important traits that affect the outcome of enemy–prey interactions, in some cases enhancing enemy attack and in others interfering with it. We know this to be true, at least in part, because of studies that have taken a comparative approach, measuring the impact of predators and parasitoids on herbivore survival, abundance, distribution and damage across several plant species. If plant traits have no bearing on enemy–prey interactions then we would expect predation and parasitism rates to remain approximately constant from one plant species to the next. Of course, between-plant variation in the number of prey consumed by predators or parasitoids can also be attributed to the inherent resistance traits of herbivores themselves, meaning that specialist herbivores on oak trees may experience fewer attacks than specialist herbivores on cottonwood trees because of differing evolutionary trajectories. To isolate the contribution of plants per se, a study would ideally compare attack rates on the same species of herbivore occurring across two or more plant species.

Although there are dozens of good examples of this phenomenon in the published literature and a thorough review of such studies is beyond the scope of this chapter, a particularly robust example comes from Barbosa *et al.* (2001) who presented five years of field data on parasitism levels in a community of 82 macrolepidopteran species on two riparian trees, box elder (*Acer negundo*) and black willow (*Salix nigra*). Overall parasitism levels were twice as high on box elder compared with willow (30.4% vs. 16.5%), a pattern that was remarkably consistent across sampling years and lepidopteran families. Furthermore, box elder caterpillars still experienced substantially higher parasitism rates after removing specialists from the dataset and only comparing caterpillars that co-occur on both trees (i.e., holding the composition of the two herbivore assemblages constant and isolating the effect of tree species). A similar outcome was documented by Lill *et al.* (2002), who used decades of sampling data from the Canadian Forest Insect Survey to assess patterns of differential parasitism across plant species. This dataset provided parasitism rates for 15 species of Lepidoptera from six different families occurring on forest trees and included data obtained from ~21 000 total caterpillar rearings and >4600 parasitism events, making it one of the most convincing assessments yet of the role of plants in parasitoid–host interactions. Comparable to the results obtained by Barbosa and colleagues (2001), a strong host-plant signal was detected on parasitism rates. Lepidoptera feeding on angiosperms experienced higher parasitism than those on gymnosperms (21% vs. 16%) and even more pronounced differences occurred between plant families and genera. Caterpillar parasitism on willow trees (*Salix* sp.), for example, was six times higher than on pine trees (*Pinus* sp.) – 48% vs. 8%. Unlike Barbosa's study, however, patterns of enemy attack occurring across tree species varied strongly depending on herbivore identity, such that a host plant providing enemy-free space to one caterpillar species resulted in elevated risk of attack for a second caterpillar species.

It is important at this point to emphasize that plants can impact multitrophic interactions not just at the species level; the magnitude of enemy effects also vary across different plant genotypes. In some cases this variation can be attributed to gross phenotypic differences in species that are polymorphic for the expression of particular resistance traits (e.g., cyanogenic vs. acyanogenic morphs in *Trifolium repens*, glandular vs. non-glandular trichome types in *Datura wrightii*). Yet multitrophic effects of plant genetic variation can be far more subtle, as demonstrated by the milkweed *Asclepias syriaca*. The abundance of predaceous ants varied 13-fold in a field study of 32 different milkweed genotypes, an effect with both positive and negative consequences for the survival of aphids and monarch caterpillars (Mooney and Agrawal 2008). We will revisit this issue several more times in the chapter as intraspecific plant variation forms the basis for the evolutionary ecology of tritrophic interactions in natural systems, and is central to maximizing host-plant resistance and biological control for pest suppression on agricultural crops.

While the above-cited studies provide clear and unambiguous cases demonstrating how plant heterogeneity alters the outcome of enemy–prey interactions, in most cases the specific mechanisms driving these patterns are unknown. The goal then of this section is to identify and group plant traits according to their mode of action and describe how they function in a multitrophic context. Though not an exhaustive list, we emphasize the key plant traits that are most commonly implicated in predator–prey and host–parasitoid studies. Keep in mind that while we present these traits individually, they are by no means mutually exclusive. Most plants possess several traits that act in concert to shape overall patterns of enemy attack.

Much of the terminology and background information in this section will be abbreviated, as it has already been described in earlier chapters. For an introduction to the ecology of plant defenses and their impact on herbivores, see Chapter 4 under Section 4.3 entitled "Plant barriers to herbivore attack."

13.2.1 Secondary metabolites

Secondary plant metabolites (also called secondary chemicals, secondary compounds or allelochemicals) are compounds that play no role in basic plant metabolism (e.g., growth, development, reproduction), but instead mediate interactions involving plants and their biotic environment (Fraenkel 1959, Whittaker and Feeny 1971). For our purposes we will focus on secondary metabolites that are thought to attract, repel, poison or otherwise harm insects. Three broad classes of compounds will be considered in turn: (a) toxins, (b) digestibility reducers and (c) volatiles. One important feature shared by all three of these groups is that they are known to be expressed constitutively (i.e., the baseline concentration that occurs in undamaged plants), but can also be induced to higher levels after herbivores initiate feeding on plants (Karban and Baldwin 1997). This difference is critical because some compounds have limited impact in their constitutive state, becoming far more meaningful when induced. Constitutive emission of volatiles, for instance, can only attract foraging predators and parasitoids to plants, which may or may not be occupied by herbivores. These allelochemicals become especially functional in their induced state as they guide enemies to the specific location of their prey.

13.2.1.1 Toxins

Toxins (also referred to as qualitative defenses, sensu Feeny 1975, 1976) are chemicals that have toxic properties when ingested and thus poison consumers. Examples include alkaloids, glucosinolates, cardenolides and furanocoumarins. Although toxins kill insects when exposed at sufficiently high doses, virtually all plants possess a community of adapted herbivores that have evolved mechanisms for tolerating these compounds in their diet. As a result, insects can persist, and even thrive, in spite of their host-plant's toxicity. Several strategies, ranging from detoxification to excretion, are available in an insect's counterdefensive arsenal (also termed **herbivore offense** by Karban and Agrawal 2002). However, **sequestration**, the ability to store toxins in specialized tissues or glands, is a particularly notable strategy as it allows herbivores to bioaccumulate secondary compounds at high concentrations (Duffey 1980, Dobler 2001, Nishida 2002).

Because you are what you eat, herbivores that feed on toxic plants are often toxic themselves to enemies via secondary exposure (Nishida 2002, Ode 2006). Therein lies the dilemma for plants; not only do toxins require a metabolic expense to synthesize in terms of **allocation costs**, but if herbivores are able to turn the table and use plant-derived compounds for their own protection then toxins become even more expensive via **ecological costs**. Perhaps the most well-known and classic example of this process entails monarch caterpillars, *Danaus plexippus*, sequestering cardiac glycosides from their milkweed host plants, which then protect adult butterflies from bird predation (Brower *et al.* 1967).

Several factors influence the likelihood for toxins to cascade up the food chain and release herbivores from top-down control by enemies. First, insects that actively sequester toxins, such as monarchs, may be more likely to receive protection than insects that passively acquire toxins. This seems logical, given that sequestering insects accumulate toxins in their body, whereas non-sequestering insects continuously dispose of toxins. Despite this line of reasoning, non-sequestering insects may still receive some level of protection from their diet (Thaler 2002b). A good example can be found in the hornworm, *Manduca sexta*, which feeds on tobacco plants that are laced with the neurotoxic compound nicotine. Hornworms are known to either detoxify or excrete nicotine, but they do not accumulate this chemical in their body tissue via sequestration (Wink and Theile 2002). However, when *M. sexta* larvae that had been parasitized by the wasp *Cotesia congregata* were experimentally reared on an artificial diet that varied in nicotine content from 0 to 0.8%, wasp mortality increased dramatically on high nicotine diets (Barbosa *et al.* 1991). This multitrophic effect of a plant-derived insect toxin can be visualized in the positive relationship between nicotine and wasp mortality in Figure 13.1. What is particularly striking from this example is that variation in nicotine had little to no impact on the performance of hornworm caterpillars, and thus the indirect cascade on enemies was far stronger than the direct effect of the phytotoxin on herbivores. Interestingly, nicotine was more recently found to adversely affect the performance of hyperparasitoids attacking the primary parasitoid *C. congregata* from the fourth trophic level (Harvey *et al.* 2007).

Another factor that may determine the impact of toxins on higher trophic levels is whether the enemy involved is a predator or parasitoid. As demonstrated by the aforementioned example, parasitoids are overly represented in the literature on this topic (Ode 2006). This may in part be a result of convenience; fitness parameters tend to be more easily measured in parasitoids that develop on a single host than predators that consume multiple prey items. There are also potential biological explanations for this divergence. Because parasitoids live entirely within the body of their host and are literally bathed in hemolymph, the sheer level of exposure to phytotoxins is far greater than for predators (Turlings and Benrey 1998). Alternatively, one could argue that because of their intense exposure and specialized lifestyle, parasitoids are adapted to tolerate toxins and are less sensitive to variation in prey chemistry. Last, toxins often reduce the size of developing herbivores, an effect that can severely constrain the

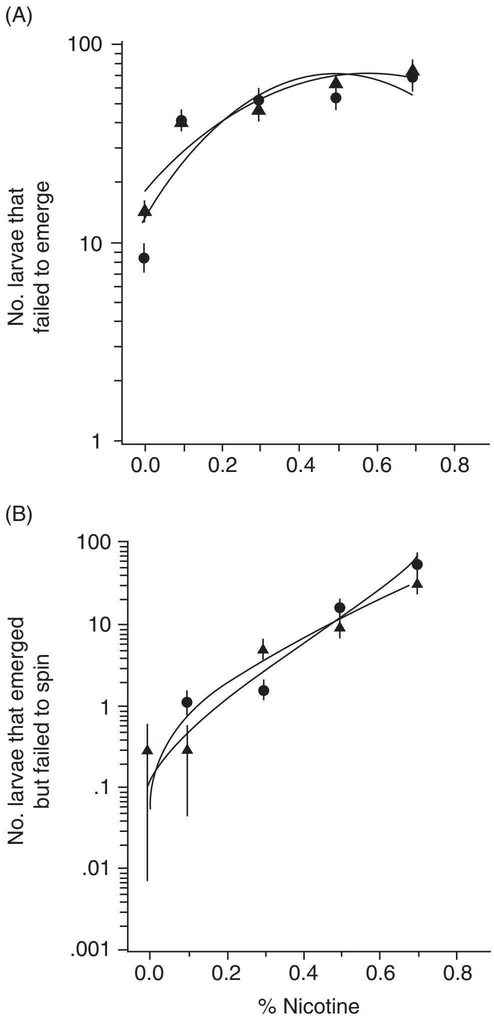


Figure 13.1 The impact of variation in nicotine content in the diet of parasitized hornworm caterpillars (*Manduca sexta*) on the mortality of (A) late larval and (B) prepupal parasitoids (*Cotesia congregata*). Triangles and circles represent two different trials of the same experiment. Note the logarithmic scale on the *y*-axis. From Barbosa *et al.* (1991).

performance of parasitoids, but is unlikely to affect predators that typically engage in compensatory feeding when prey size is limiting. Host range can also mediate this effect – phytotoxins impact the growth and development of polyphagous herbivores more so than monophagous or oligophagous herbivores, and therefore parasitoids associated with generalists are more likely to be affected by toxin-mediated developmental changes (e.g., decreases in host size) than parasitoids of specialists (Harvey *et al.* 2005).

Up until this point we have assumed that herbivores incidentally acquire toxins as they feed on their host plant. Insects are also known to ‘self-medicate’ (also called **pharmacophagy**) by actively seeking out toxic plants, despite the ensuing growth penalties that occur as a result of this foraging strategy. The woolly bear caterpillar, *Grammia geneura*, is a polyphagous herbivore that grazes several species of forbs, yet caterpillar performance is maximized when reared on a single-species diet of the plant *Malva parviflora* (Singer 2001). This begs the question: Why do woolly bear caterpillars eat a mixed-species diet in nature if it compromises their growth? To experimentally test this question, Singer and colleagues collected late-instar caterpillars from the field and reared them on either a monospecific diet consisting of *Malva* or a mixed-species diet of *Malva* and several additional forbs known to be included in *G. geneura*’s host range (Singer *et al.* 2004a). Although caterpillar growth efficiency was highest on the *Malva* only diet, mortality from a community of parasitoids was lower in individuals from the mixed-species treatment. This suggests a fundamental trade-off in food selection between maximizing growth and protection from enemies. Several plant species in the mixed-diet treatment are known to contain high concentrations of pyrrolizidine alkaloids. Furthermore, nearly 50% of woolly bear individuals can be parasitized late in the season by an assemblage of mostly tachinid flies. Thus, the selective pressures necessary for maintaining toxic plants in the diet of woolly bear caterpillars exist in this system.

Two final thoughts regarding the role of toxins in enemy–prey interactions are worth considering here. First, we have primarily emphasized the indirect exposure route of phytotoxins on enemies (i.e., those acquired via herbivores as the intermediary). Direct effects, though far less studied, may also be important, particularly for omnivorous predators that consume plant material in addition to prey, or for plants that express toxins in the glandular exudates of trichomes (see *Morphology* below). Second, we have only considered the possibility that enemies are adversely affected by toxins. While this appears to be mostly true, there are exceptions. The leaf beetle *Chrysomela lapponica* feeds on several species of willow trees that vary in salicyl glucoside (SG) content; the attack rates and performance of phorid and tachinid flies on beetles in this system were in fact higher on SG-rich willows than SG-poor ones (Zvereva and Rank 2003). Smilanich *et al.* (2009) observed that caterpillars of the buckeye butterfly, *Junonia coenia* (Nymphalidae), a specialist on plant families with iridoid glycosides, showed stronger encapsulation and melanization responses to artificial parasitoid eggs when fed lower concentrations of secondary metabolites. They hypothesize that, although specialization to toxic host plants and sequestration of this chemistry provides effective defense from generalist predators, the high energetic costs involved may predispose these herbivores to greater parasitism risk through weakened cellular immune responses.

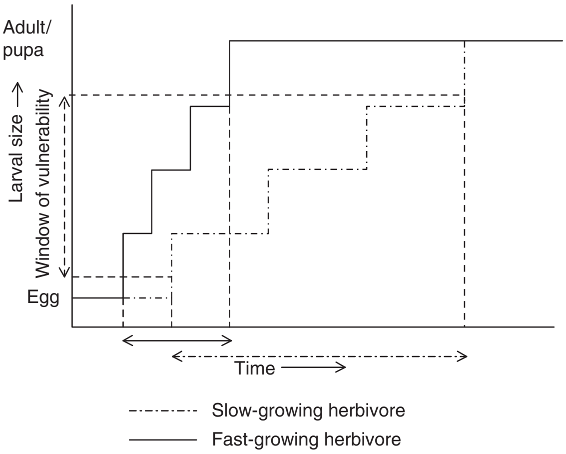


Figure 13.2 The developmental trajectories of two insects, one growing rapidly (solid line) and the other growing slowly (dashed-dotted line). In this hypothetical scenario, the window of vulnerability in which larvae are susceptible to attack from enemies occurs during the first three larval instars (see dashed arrow on the y-axis). Accordingly, the amount of time that slow-growing herbivores are vulnerable to predation or parasitism (dashed-dotted arrow on the x-axis) is more than twice that of fast-growing herbivores (solid arrow on the x-axis). Williams, I. S. 1999. Slow-growth, high-mortality – a general hypothesis, or is it? *Ecol. Entomol.* **24**:490–495. Copyright (1999) Wiley-Blackwell.

13.2.1.2 Digestibility reducers

Digestibility reducers (also referred to as quantitative defenses, sensu Feeny 1975, 1976) are secondary chemicals that reduce the nutritional quality of plant tissue for consumers by preventing access to nitrogen and other growth-limiting resources. Examples include protease inhibitors, tannins, lignin and silica.

Unlike toxins, digestibility-reducing compounds do not directly poison herbivores; hence the term **sublethal plant defenses**. Instead, they reduce herbivore growth rates, thereby increasing development time. Insects often compensate for the low nutritive quality of their host plant by simply consuming more leaf tissue (Slansky and Feeny 1977). As a result, sublethal plant defenses have been described as paradoxical because they tend to increase rather than decrease herbivory (Price *et al.* 1980, Clancy and Price 1987; but see Wise *et al.* 2006). In other words, how can a plant trait be considered defensive if its expression causes *greater* damage to the plant? The proposed resolution to this paradox is that delayed development increases the amount of time that insects are retained in early larval instars and thus vulnerable to enemy attack (Feeny 1976). This concept has since been formalized as the **slow-growth–high-mortality hypothesis**. A key assumption of this hypothesis is that younger growth stages are more susceptible to attack and slow growth increases this window of vulnerability. As demonstrated in Figure 13.2, the slow-growing herbivore (dashed-dotted line along the x-axis)

Table 13.1 **The percentage of observations from published studies (absolute number of observations is listed in parentheses) either supporting or rejecting the slow-growth–high-mortality (SGHM) hypothesis as affected by herbivore feeding guild and natural enemy type. From Williams (1999)**

Herbivore feeding habit	Natural enemy type	Support for SGHM	Rejection of SGHM	No trend
External	Predator	58.3% (7)	33.3% (4)	8.3% (1)
External	Parasitoid	17.6% (3)	58.8% (10)	23.6% (4)
Gall	Predator	0.0% (0)	100.0% (1)	0.0% (0)
Gall	Parasitoid	55.6% (10)	33.3% (6)	11.1% (2)
Gall	Inquilines	100.0% (2)	0.0% (0)	0.0% (0)
Mine	Predator	33.3% (2)	33.3% (2)	33.3% (2)
Mine	Parasitoid	42.9% (3)	14.2% (1)	42.9% (3)
Other internal	Predator	0.0% (0)	100.0% (2)	0.0% (0)
Other internal	Parasitoid	50.0% (1)	50.0% (1)	0.0% (0)
Total		**41.8% (28)**	**40.3% (27)**	**17.9% (12)**

remains in its vulnerable stage more than twice as long as the fast-growing herbivore (solid line along the *x*-axis). The imported cabbageworm, *Pieris rapae*, for example, is mostly vulnerable to parasitism during its first two larval instars. By the third instar, caterpillars begin encapsulating wasp eggs and antipredator behaviors (e.g., thrashing) become far more effective. Consequently, the first and second instars have been used as *P. rapae*'s window of vulnerability (Benrey and Denno 1997).

Experimental support for slow-growth–high-mortality is equivocal at best, with some studies providing evidence in favor (e.g., Häggström and Larsson 1995, Benrey and Denno 1997, Kaplan *et al.* 2007) and a similar number of studies reporting data that are inconsistent with this hypothesis (e.g., Clancy and Price 1987, Lill and Marquis 2001, Medina *et al.* 2005). Recently, Williams (1999) summarized the results from 67 different enemy–prey combinations reported from 41 published studies where the slow-growth–high-mortality hypothesis could be evaluated (Table 13.1). Most of these cases involved parasitic wasps attacking lepidopteran herbivores, while fewer studies reported on predator effects and those involving dipteran, hymenopteran or hemipteran herbivores. Parasitoids and predators were equally implicated, although the data suggest a potential interaction between enemy type and herbivore feeding habit. Studies involving predators of externally–feeding herbivores more often supported the hypothesis, whereas those involving parasitoids of external feeders typically rejected it (Table 13.1). This divergence among enemy types, however, was not apparent with concealed feeders such as gallers and miners. Overall, 28 interactions provided support for slow-growth–high-mortality, 27 rejected the hypothesis and 12 found no trend. Thus, it is difficult at this point to make any definitive statements regarding its validity – the hypothesis appears to explain patterns of enemy attack under a restricted range of ecological contexts that we do not yet fully understand.

One potential problem with applying slow-growth–high-mortality across a broad range of circumstances is that other factors can over-ride the effect of delayed development and render it inconsequential. Benrey and Denno (1997) tested this hypothesis using imported cabbageworm larvae, *P. rapae*, on four different host plants. When caterpillar growth rate was experimentally reduced on each of the four plant species individually (i.e., within-species assessment) parasitism levels greatly increased, but there was no relationship between development time and parasitism when assessed across the four plant species. The implication of this finding is that slow-growth–high-mortality may in fact operate when all else is equal, but such is rarely the case. A multitude of factors in addition to development time vary when herbivores develop on different host plants. A plant that is considered poor quality and leads to slow growth may simultaneously possess other traits (e.g., glandular trichomes, the 'wrong' bouquet of volatiles) that interfere with enemy attraction, retention and foraging. In these cases, delayed development is unlikely to translate into enhanced enemy attack, emphasizing the need for a more holistic perspective, whereby delayed development is viewed in the context of multiple plant traits.

13.2.1.3 Volatiles

Volatiles are one of the most important classes of plant traits to be integrated with digestibility-reducing chemicals (otherwise known as **volatile organic compounds** or **VOCs**). Volatiles are low-molecular-weight chemicals that are readily emitted from plants into the air, providing a distinctive odor to foraging insects. Humans have long recognized the occurrence of volatiles as they provide the unique aromas that we associate with the flowers and leaves of many plants (e.g., basil, eucalyptus, pine trees). Only far more recently have we begun to decipher the ecological relevance of these infochemicals in mediating multitrophic interactions (Vet and Dicke 1992). This is true in part because humans only perceive a small fraction of the >1000 different volatile compounds that have been identified from plants (Pichersky *et al.* 2006).

Because volatile profiles are species-specific and can be detected several meters or more from their source plant, they provide reliable cues that insects exploit in circumnavigating the complex physicochemical environment posed by plants. The orientation of enemies toward plant volatiles, in particular, has received a great deal of research attention from the scientific community in recent decades (Paré and Tumlinson 1999, Turlings and Wäckers 2004). Predators and parasitoids are both known to use plant volatiles in their foraging decisions, although enemies integrate a diverse array of cues while searching for prey, including those derived from the herbivore itself, such as frass (see Figure 2.3). Unlike other enemy-attracting plant traits that are restricted to a subset of species (e.g., extrafloral nectaries), volatiles are ubiquitous. This is likely to be the case because such compounds are multifunctional in nature (i.e., repelling herbivores – De Moraes *et al.* 2001; attracting pollinators – Kessler *et al.* 2008; within-plant signaling – Frost *et al.* 2007), and did not necessarily evolve for the sole purpose of enemy attraction.

Several important distinctions are made in how we classify and discuss volatiles, the first and most critical being constitutive vs. damage-induced (sometimes referred to as HIPVs or **herbivore-induced plant volatiles**). While undamaged plants emit some volatiles, the quantity and number of compounds released increase dramatically upon attack by herbivorous insects. As a result, enemies are typically attracted to undamaged plants, but this level of attraction increases when plants are injured. In a direct comparison of the volatiles emanating from plants and prey, the parasitic wasp *Cotesia glomerata* was most attracted to caterpillar-damaged plants, followed by host larvae and their frass with no plant present, and the least attractive cue was an undamaged plant, thus demonstrating the primacy of induced volatiles in parasitoid foraging decisions (Steinberg *et al.* 1993). The relatively recent discovery of damage-induced volatiles represents a major breakthrough in the field of multitrophic interactions, as it suggests that plants may "call for help" from the third trophic level (Nadel and van Alphen 1987, Dicke and Sabelis 1988, Turlings *et al.* 1990).

Much of our knowledge of enemy responses to induced plants is based on lab-oriented research that compares undamaged vs. injured plants using measurements of volatile compounds and bioassays quantifying enemy preference for plant odors using y-tube olfactometers, or other related techniques. A smaller number of studies have tested the effect of induced volatiles on enemy attack under more realistic field environments using natural populations of predators or parasitoids (De Moraes *et al.* 1998, Thaler 1999a, Kessler and Baldwin 2001, Kost and Heil 2008). Most notably, Kessler and Baldwin (2001) mimicked the herbivore-induced volatile response that is characteristic of wild tobacco, *Nicotiana attenuata*, and found that survival of tobacco hornworm, *Manduca sexta*, eggs decreased from 83% on control plants to 4% on plants with induced volatiles. This substantial decline in egg survival was directly attributed to attraction of and increased predation by the hemipteran predator *Geocoris pallens*.

Another important difference in the classification of induced volatiles is between local and systemic responses. Local induction occurs when compounds are released from the site of tissue damage (i.e., the leaf upon which caterpillars are feeding), whereas systemic induction represents volatiles that are emitted from undamaged tissues of herbivore-injured plants. This distinction has obvious ecological relevance as systemically induced volatiles attract enemies to plants that are occupied by potential prey, but cannot reveal the specific location of that prey within the plant. Given the minute size of parasitoid wasps relative to trees and other large plants, the ability to exploit local cues is highly advantageous in successfully locating hosts. Local and systemic responses, however, are not mutually exclusive processes. Corn seedlings, for instance, emit terpenoids from damaged and undamaged leaves following attack by the beet armyworm, *Spodoptera exigua* (Turlings and Tumlinson 1992). These local and systemic responses are both attractive to the parasitic wasp *Cotesia marginiventris*, although the local response is considerably stronger than the systemic one.

A final important distinction is between those volatile responses that are elicited by mere tissue damage versus those that entail the presence of **elicitors** from the saliva or regurgitant of herbivores. The contribution of elicitors has typically been assessed by comparing plant responses to either: (a) actual insect herbivory vs. artificial herbivory that mimics patterns of insect damage using a scissor or hole-punch, or (b) mechanical damage alone vs. mechanical damage with caterpillar oral secretions or regurgitant applied to the wounded plant tissue. Early work on caterpillar–corn interactions demonstrated that beet armyworm saliva amplifies the damage-induced volatile response that attracts parasitoids (Turlings *et al.* 1990), and subsequent studies have confirmed the generality of this phenomenon across several different tritrophic systems (Mattiacci *et al.* 1994, Kahl *et al.* 2000, Röse and Tumlinson 2005). As a result, a number of labs have begun investigating the chemical composition of caterpillar saliva and regurgitant with the goal of identifying compounds that amplify or suppress plant responses. Considerable progress has been made on this front, with several elicitors now identified, including β-glucosidase in *Pieris brassicae* (Mattiacci *et al.* 1995), volicitin in *Spodoptera exigua* (Alborn *et al.* 1997), and fatty-acid–amino-acid conjugates in *Manduca sexta* (Halitschke *et al.* 2001). Plant responses to elicitors and their underlying phytohormonal pathways, however, appear somewhat idiosyncratic making patterns difficult to flesh out, and at this point a universal elicitor does not exist; even the same elicitor induces very different responses when tested across several plant species (Schmelz *et al.* 2009).

Because different herbivore species produce different elicitors and patterns of leaf damage (i.e., old vs. young leaves, avoiding vs. chewing through major leaf veins), both of which dictate the quantity, number, proportion and type of compounds emitted from plants, we might expect that each plant–herbivore combination generates a unique blend of volatiles. This point is crucial because induced volatiles are most effective in guiding enemies if they reveal the identity of the damaging herbivore (Dicke 1999, Takabayashi *et al.* 2006). Hundreds of species of herbivorous insects may co-occur in a given habitat and each one of these species is attacked by its own suite of enemies. If every herbivore induced a similar plant-volatile profile then the information would be virtually useless for all but the most polyphagous of enemies. Given that predators and parasitoids have restricted host ranges, and many can only attack certain developmental stages of their prey (i.e., larva vs. adult, early vs. late instars), the greater the information content provided by induced volatiles, the more easily foraging enemies can exploit these cues. It is no coincidence that volatiles are referred to as infochemicals! Perhaps the most convincing evidence yet for the specificity of induction mediating tritrophic interactions comes from a study of the parasitoid wasp *Cardiochiles nigriceps* responding to volatiles from tobacco and cotton plants infested with host and non-host caterpillars (De Moraes *et al.* 1998). On both plants, wasps were attracted to infestations with larvae of *Heliothis virescens* (HV), a known host for *C. nigriceps*, compared to herbivore-free control plants (C), but wasps were not nearly as attracted to plants infested with *Helicoverpa zea* (HZ), which is not a host for *C. nigriceps* (Figure 13.3a). The same pattern was documented when caterpillars and damaged leaves were removed, demonstrating that parasitoids were responding to systemic plant signals and not to the herbivore itself (Figure 13.3b).

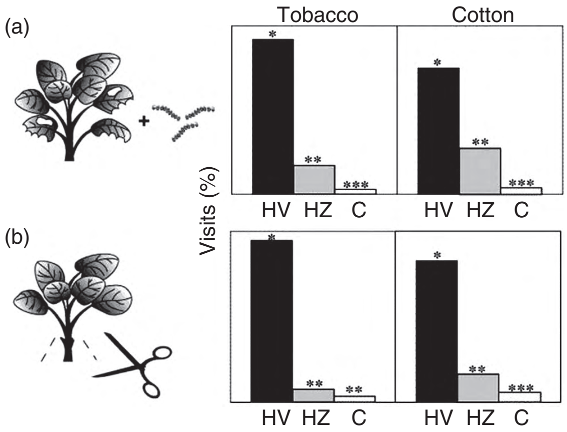


Figure 13.3 Response (% visitation) of the parasitic wasp *Cardiochiles nigriceps* to tobacco and cotton plants infested with larvae of *Heliothis virescens* (HV), a host, or *Helicoverpa zea* (HZ), a non-host. C = undamaged control plants. In experiment 1 (a), caterpillars were present on plants during the trial, whereas in experiment 2 (b) the caterpillars and damaged leaves were removed and therefore wasps could only respond to cues emanating from the plant. Asterisks denote level of statistical significance. Reprinted by permission from Macmillan Publishers Ltd: *Nature* (De Moraes *et al.* 1998), copyright (1998).

The above example clearly illustrates that enemies can recognize and distinguish the induced volatile responses elicited from host and non-host larvae. The fact that the two herbivores are closely related species, consumed the same amount of leaf tissue, and treatment effects were consistent across multiple plant species greatly strengthens the inferences that can be drawn from this example. Although enemy preference for plant volatiles induced by hosts over non-hosts has since been documented in other systems (Guerrieri *et al.* 1999, Shimoda and Dicke 2000, Rasmann and Turlings 2008), there are undoubtedly limits on the information content provided by volatile phytocompounds and it would be mistaken to assume that enemies are omniscient in their exploitation of plant-derived cues (Vet and Dicke 1992). A comparable number of studies have found weak evidence for specificity of induction and/or response in tritrophic systems (McCall *et al.* 1993, Turlings *et al.* 1993, Rodriguez-Saona *et al.* 2005), and similarly variable results were found when testing the ability of enemies to use induced volatiles for differentiating damage by different larval instars of their host (Mattiacci and Dicke 1995, Takabayashi *et al.* 1995, Gouinguené *et al.* 2003).

While this section, and the published literature in general, emphasizes plant volatiles that are elicited by chewing herbivores, mostly lepidopteran larvae, and emitted from leaf tissue, we are only beginning to appreciate the true diversity of volatiles in a tritrophic context. For example, aphids and other insects with piercing-sucking mouthparts that do not defoliate leaf tissue nevertheless induce volatile plant responses that are attractive to aphid enemies (Guerrieri *et al.* 1999, Ninkovic *et al.* 2001, Lou *et al.* 2005). Plant-feeding altogether is not even a requirement. Oviposition by female insects is now known to elicit plant volatiles that attract egg predators and parasitoids (Hilker and Meiners 2006). Last, the general phenomenon is not restricted to leaves or predaceous and parasitic insects, as demonstrated by two recent studies involving quite divergent taxa: entomopathogenic nematodes (Rasmann *et al.* 2005) and insectivorous birds (Mäntylä *et al.* 2008). Larvae of the western corn rootworm (WCR), *Diabrotica virgifera*, are important pests of corn and their nematode parasites are strongly attracted to insect-damaged compared with undamaged or mechanically-damaged roots (Figure 13.4A). Interestingly, the volatile

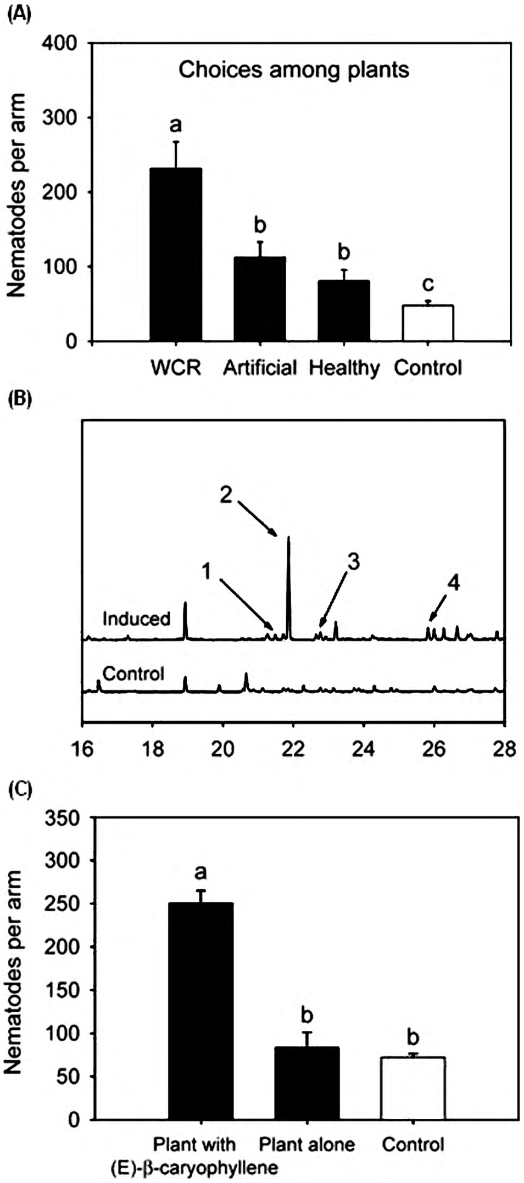


Figure 13.4 (A) Recruitment of the entomopathogenic nematode *Heterorhabditis megidis* when offered the choice of sand ('Control', no plants or insects), undamaged plants ('Healthy'), mechanically-damaged roots ('Artificial') and plants whose roots were infested with larvae of the western corn rootworm ('WCR'), *Diabrotica virgifera virgifera*. (B) Chromatographic traces that depict the volatiles emitted from an undamaged root system ('Control') compared with those emanating from roots with corn root worm herbivory

Caption for Figure 13.4 (*cont.*)
('Induced'). Each peak represents a different volatile compound and, most notably, peak 2 was identified as (*E*)-β-caryophyllene. (C) Nematode preference for sand ('Control', no plants or insects), undamaged plants ('Plant alone') and plants whose rhizosphere was spiked with (*E*)-β-caryophyllene. Reprinted by permission from Macmillan Publishers Ltd: Nature (Rasmann *et al.* 2005), copyright (2005).

compound (*E*)-β-caryophyllene, peak number 2 in Figure 13.4B, is strongly emitted from insect-damaged roots, and this chemical is also known to be highly attractive to nematodes when applied to the soil in the absence of herbivorous insects (Figure 13.4C), suggesting a mechanistic link between below-ground insect herbivory, root volatiles and nematode attraction (Rasmann *et al.* 2005). Perhaps more surprising, a recent study showed birds recruited preferentially and preyed on artificial larvae at greater rates on trees with bagged herbivorous larvae and elevated volatiles compared to sham bagged control trees with lower levels of volatile emissions (Mäntylä *et al.* 2008).

13.2.2 Nutritional resources

Unlike the secondary metabolites discussed in the above section, plants also provide nutritional rewards that encourage the retention of predators and parasitoids, and potentially enhance their impact on prey populations, thereby reducing plant damage. The vast majority of enemies, many of which we consider strict carnivores, are in fact omnivores that require, or at least benefit from, plant-derived resources to fuel flight, growth and/or reproduction (Coll and Guershon 2002, Eubanks 2005, Wäckers *et al.* 2005). Parasitoids, for instance, are carnivorous in their larval stage, but adult wasps are primarily sugar-feeders. Even predators with a reputation for consuming exclusively prey-based diets, such as spiders, are now known to frequent plant nectaries while foraging (Ruhren and Handel 1999, Taylor and Pfannenstiel 2008). Ants are among the most dominant groups of predators in terrestrial ecosystems, yet ants are also extreme omnivores whose success hinges on the availability of plant sugars (Blüthgen *et al.* 2000, 2003, Davidson *et al.* 2003). In fact, the dominance of ants as consumers in arthropod food webs is, in large part, driven by sheer abundance, a biological attribute that is causally linked with diets that are heavily subsidized by plants.

Bear in mind that only a subset of enemies are adapted to use different plant tissues and exudates, resulting in taxonomic differences in resource use. Phylogenetic constraints associated with factors such as mouthpart morphology prevent any given predator or parasitoid from exploiting the full range of resources at their disposal. Hemipteran predators, for example, use their piercing-sucking stylet to tap into leaves, stems and fruits, whereas spiders possess chelicerae and are unable to access plant tissue. This is not entirely surprising when you consider that insects in the order Hemiptera also include aphids and other sap-feeding herbivores. Realize that these are broad generalizations and much remains to be learned about the feeding ecology of enemies in nature. Even biological control agents that have been well studied for decades often have poorly described feeding habits because of the methodological challenges with assessing food selection for polyphagous consumers under realistic field settings. Recent reports show that spiders and larval Lepidoptera, widely considered to be 100% predaceous and herbivorous/detritivorous, respectively, have divergent species that buck the trends (Rubinoff and Haines 2005, Meehan *et al.* 2009).

Plant nutritional resources naturally segregate into two distinct groups: (a) those traits that are adaptations for growth and reproduction (e.g., leaves, flowers and fruits) and (b) structures that are thought to have evolved for the sole purpose of maintaining large enemy populations as bodyguards (e.g., extrafloral nectaries, food bodies). Although resources among these two groups may be virtually identical in their chemical composition and suitability as food, for example, comparing floral vs. extrafloral nectar, the distinction is vital in an evolutionary context. In the first case, enemies are thieves that steal resources intended for pollinators or gametes for reproduction, even though plants may very well benefit as a result. In the second case, plant traits are an emergent outcome of the co-evolutionary dynamics between the first and third trophic levels.

13.2.2.1 Vegetative and reproductive parts

We begin with plant vegetative and reproductive parts, focusing on enemy use of leaves, floral resources, namely nectar and pollen, and developing fruit. As mentioned earlier, omnivorous predators in the order Hemiptera, including the families Anthocoridae, Lygaeidae, Miridae, Nabidae and Pentatomidae, are common foliar-feeders, although thrips also switch between foliage and prey. Leaves fundamentally differ from reproductive structures in several respects that are likely to affect their interaction with omnivores. The principal differences are that flowers and fruits tend to have higher nutritional value than leaves, but leaves are accessible throughout the growing season, while flowers and fruits are ephemeral. From the insect's perspective this means that leaves are a stable albeit poor-quality resource. Due in part to their low nutritional content, predators cannot sustain development for extended periods on a purely leaf-based diet. Leaves are a supplemental resource that can promote survival and longevity when herbivores are scarce, but are by no means a substitute for prey. Given that herbivore population outbreaks and crashes are sporadic and unpredictable, the stability of leaves as a constantly available resource is crucial for buffering omnivores against fluctuations in prey availability, in spite of their nutritional inferiority (Lalonde *et al.* 1999).

A recent review of 26 published studies summarized the response of selected life-history traits (e.g., development rate, survival, size, longevity and fecundity) in omnivorous predators to prey-only diets vs. prey diets supplemented with plant food (Eubanks and Styrsky 2005). In all cases, predator performance was more often enhanced when provided with supplemental plant material such as leaves, resulting in an average increase of 6.4% in development rate, the weakest response, and 60.1% in fecundity, the strongest response. Some have speculated that leaves benefit predaceous hemipterans by providing moisture to avoid desiccation stress and thus do not constitute a true nutritional supplement. The fact that plant availability improved performance-related parameters such as development, size and fecundity in the above review suggests otherwise. Several of the reviewed studies found that predators perform better on a diet of plant leaves and water compared with water alone (Naranjo and Stimac 1985, Ruberson *et al.* 1986). At a more extreme level of dependency, certain predators failed to develop altogether in prey-only environments and required access to plant foliage to reach adulthood. This implies that leaves are providing some key resources above and beyond moisture, although, to our knowledge, no one has quantified precisely what those resources are. Another line of evidence suggesting that leaf material may be used for more than just water comes from a study showing that omnivorous thrips, *Frankliniella occidentalis*, consume approximately half the amount of leaf material and twice the number of prey items on highly resistant host plants (Agrawal *et al.* 1999a). The fact that thrips shifted their position along the herbivore–carnivore gradient, becoming more predaceous and less herbivorous, in response to increasing plant resistance demonstrates that leaf quality indeed matters for omnivorous insects.

Floral resources in the form of nectar and pollen fundamentally differ from leaves in terms of accessibility and biochemistry. Nectar mostly consists of simple sugars, a combination of the disaccharide sucrose and the monosaccharides glucose and fructose, with amino acids, secondary compounds, vitamins and minerals also occurring at low concentrations (Wäckers 2005). The composition of pollen, on the other hand, is the opposite – rich in proteins and amino acids, but lacking in carbohydrates. Unlike leaves or nectar, several predators (e.g., minute pirate bugs, *Orius insidiosus*, the ladybird beetle, *Coleomegilla maculata*) can develop entirely from egg to adult on pollen alone. Similar to vegetative tissue, experimental studies that compare enemy performance with and without floral supplements generally find that nectar/pollen availability benefits predators and parasitoids. Because of their utility in biological control, many such studies assess the impact of nectar-feeding on the performance of parasitoid wasps with the two responses most commonly measured being adult longevity and fecundity. This should not be entirely surprising because wasps that live for a long time and produce many eggs are thought to suppress pest populations more effectively than short-lived wasps with few eggs. As one of many potential examples, adult survival of the egg parasitoid *Trichogramma exiguum* was increased 8.5-fold and fecundity 6.3-fold when provisioned with buckwheat flowers compared with water alone (Witting-Bissinger *et al.* 2008).

Recall from our earlier discussion of insect life histories in Chapters 9 and 10, parasitoids are described as either **pro-ovigenic** when adult females emerge with their lifetime complement of eggs mature and ready to oviposit, and **synovigenic** if eggs are initially immature and develop over the course of adulthood. Floral nectar will not affect the fecundity of pro-ovigenic wasps and can only benefit synovigenic species. Pure pro-ovigeny, however, is exceedingly rare among parasitoids. In a survey of 638 species of hymenopteran wasps from 28 families, 98.1% of the species were synovigenic (Jervis *et al.* 2001). The implication of this finding is that the vast majority of parasitoids in nature stand to benefit from nectar-feeding, at least when quantified in terms of egg production. Indeed, floral visitation is an extremely common practice for parasitic hymenopterans (Jervis *et al.* 1993), although all flowers are not equally accessible to wasps. Variation in floral traits such as morphology, odor and phenology filters the pool of potential colonists to a far smaller subset of species (Wäckers 2004, Fiedler and Landis 2007). Tooker and Hanks (2000) compiled one of the largest known datasets on record of enemies visiting flowering plants, which contained observations of >15 000 individuals from 151 species of parasitic hymenopterans collected over a 33 year period. While certain plant groups (e.g., Apiaceae) possessed attributes such as exposed nectaries and accessible anthers that resulted in higher parasitoid diversity, overall patterns revealed that "most species of wasps were only collected from a small number of plant species, suggesting that many wasp species are oligophagous" (Tooker and Hanks 2000, p. 583).

The above discussion largely addresses the impact of vegetative and reproductive plant tissues on enemy performance and feeding behavior, but we have not yet dealt with the more important question of whether such nutritional rewards increase enemy abundance in the field and ultimately enhance (or detract from) prey suppression. Unfortunately far fewer studies have adequately addressed these issues. Classical community ecology predicts that omnivory will strengthen top-down suppression of herbivores (Crawley 1975, Pimm and Lawton 1977, 1978, Walde 1994, Eubanks and Denno 1999). The logic underlying this theoretical prediction is that plant-feeding decouples enemies from their prey, allowing them to survive periods of prey scarcity and discouraging emigration at low herbivore densities. Unlike strict predators, whose population dynamics typically mirror those of their herbivorous prey leading to boom-bust cycles, omnivorous predators should exhibit more stable population dynamics, remain abundant when herbivores are rare in the environment and drive prey to local extinction.

The alternative point of view in this debate argues that plants distract enemies from killing herbivores, thus reducing their per-capita impact on prey populations. In other words, time and appetite spent feeding on plants is time and appetite lost attacking prey. What then is the net outcome? Does omnivory promote or interfere with prey suppression? This is an ideal case where we can apply our knowledge of the numerical and functional responses from Chapter 7 on predator–prey interactions. Consider a hypothetical example where enemies are 30% more abundant when presented with high-quality plant material such as pollen (increased numerical response), but each individual enemy consumes 60%

fewer herbivores (decreased functional response). In this scenario the decline in functional response outweighs the increase in numerical response and therefore plant-feeding will likely detract from prey suppression. This is a straightforward and simple example; remember that functional and numerical responses are typically non-linear and making such calculations requires knowledge of the shape of those responses.

Let's examine one of the few studies to empirically disentangle the impact of plant quality on the outcome of omnivore–prey interactions. The big-eyed bug *Geocoris punctipes*, an omnivorous hemipteran, feeds on small soft-bodied prey items, including aphids and early-instar caterpillars, but also uses its piercing-sucking stylet to access leaves, stems and fruits. Developing fruit, in particular, is considered a highly nutritious food item with nitrogen content often 3–5 times higher than leaves. Eubanks and Denno (1999, 2000) manipulated the presence of lima bean pods to understand the consequences of variation in plant quality for predation. Big-eyed bugs mounted a strong numerical response to high-quality plants – individuals were far more abundant in open-field plots containing plants with pods compared with those having pods experimentally removed. In fact, the number of pods per plant was the best overall predictor of variation in big-eyed bug density. This increase in abundance, however, was counteracted by a decline in per-capita predation pressure; fewer aphids and lepidopteran eggs were consumed per individual predator on pod-bearing than pod-free plants, presumably because big-eyed bugs were satiated by tapping into nitrogen-rich fruits. This dichotomy presents a similar dilemma to the above-described hypothetical example, but in this case the elevated numerical response overwhelms a weaker functional response. Big-eyed bug nymphs were $> 2 \times$ as abundant (Figure 13.5A) and adults $>5\times$ as abundant (Figure 13.5B) in field plots with plants possessing pods. Aphids (Figure 13.5C) and caterpillars (Figure 13.5D) displayed the reverse pattern; these herbivores were dramatically less abundant in the presence of pods.

One caveat to the preceding discussion is that it relates primarily to omnivores that readily switch back and forth between plants and prey throughout their life cycle. It is not quite as applicable to life-history omnivores that shift their trophic position with ontogeny. Parasitoid wasps, for example, may be attracted to and remain longer in patches of flowering plants, as big-eyed bugs are similarly more numerous on and around pod-bearing plants, but access to floral nectar will likely enhance, rather than interfere with, attack rates on herbivores because nectar is a complimentary resource that fuels flight for adult wasps to locate suitable hosts for their carnivorous offspring. Overall patterns of nectar-feeding on parasitism rates will be discussed below in the Applications section as the majority of studies on this topic seek to enhance biocontrol of herbivorous pests by cultivating floral borders adjacent to crop fields.

Thus far in this section we have only considered the rather straightforward case whereby enemies benefit from plant nutritional resources and herbivore populations indirectly suffer as a consequence. More variable and complex outcomes might be expected if other trophic levels partake. Plant-provided food is equally accessible to all consumers, and plants have no means of selectively allowing exploitation by the third trophic level and filtering out the remainder of the community. One might expect that plants will experience greater damage if herbivores at the second trophic level or hyperparasitoids and other insects acting from the fourth trophic level take advantage of these supplemental resources (Wäckers *et al.* 2007).
A recent study by Winkler *et al.* (2009) analyzed the sugar content in the bodies of field-caught insects in *Brassica oleracea* fields and found that close proximity of flowering plants elevated the energetic state of both herbivores (*Plutella xylostella*) and their parasitoid (*Diadegma semiclausum*). However, the end result may nevertheless be beneficial from the

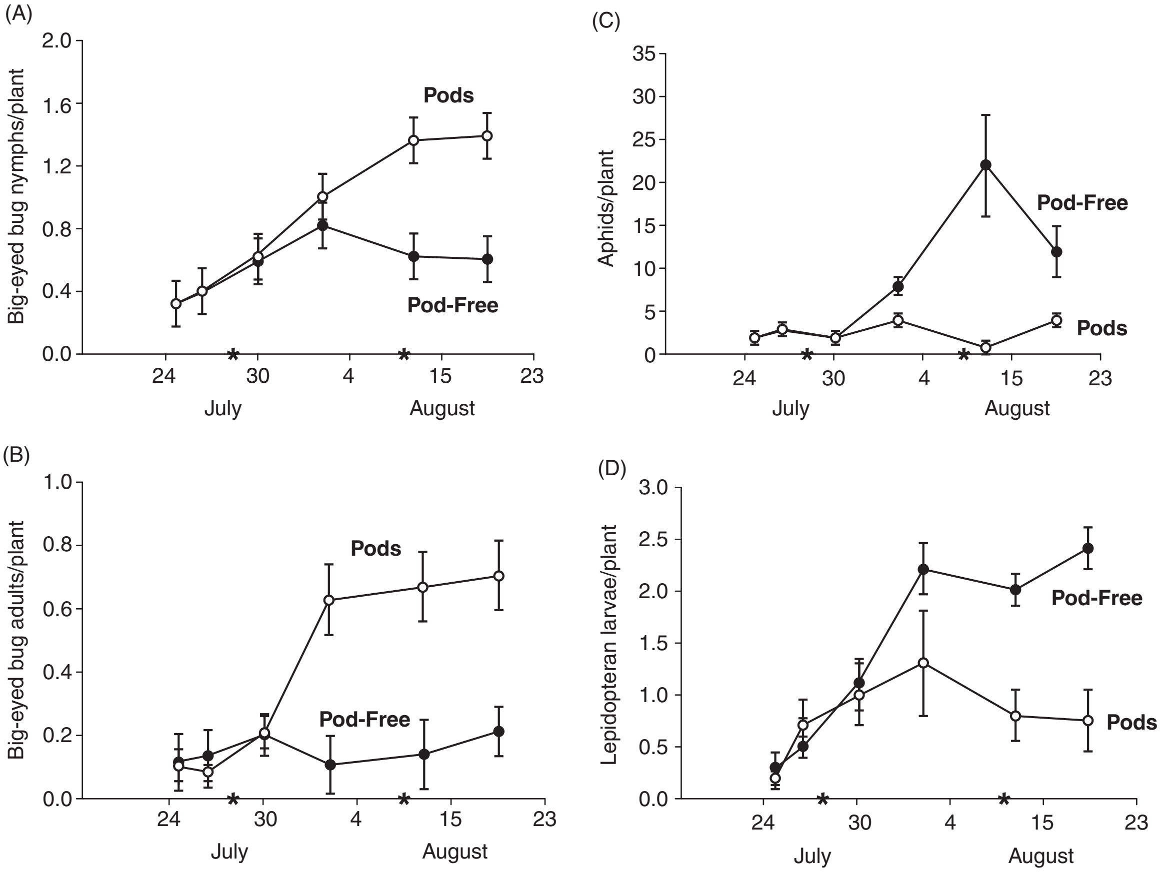


Figure 13.5 The impact of nitrogen-rich bean pods on the abundance of omnivorous predators including big-eyed bug (A) adults, (B) nymphs, and their prey (C) aphids, and (D) caterpillars. From Eubanks and Denno (2000).

plant's perspective. Van Rijn and colleagues (2002) used a combination of manipulative experiments and modeling approaches to demonstrate that pollen presence lowered the equilibrium density of herbivorous thrips, despite the fact that thrips readily consumed pollen alongside their predators. Fewer accounts have reported on fourth trophic level effects, although at least one study suggests that access to flowers induces aphid outbreaks by promoting parasitism of aphidophagous predators (Jonsson *et al.* 2009).

A final consideration to keep in mind is that vegetative and reproductive plant traits are not relegated to affecting the insect assemblages on the plant from which they are produced. Enemies tend to be highly mobile and nutritional rewards provided by one plant can subsidize predators and parasitoids attacking herbivores on a neighboring plant. This runs counter to other plant traits that we discuss in this section, most of which are only applicable to the plant on which they are expressed. Thus, nutritional resource subsidies are spatially dynamic, linking multiple unrelated plant species in natural systems (i.e., associational resistance; Atsatt and O'Dowd 1976), and forming the basis of the "enemies hypothesis" which provides a mechanistic explanation for fewer herbivore outbreaks in diverse habitats (Root 1973).

13.2.2.2 Coevolved traits

Plant traits that may have coevolved with enemies include those that apparently exist for the sole purpose of attracting and maintaining predators and parasitoids as bodyguards. Several features differentiate these traits from the above group. First, like secondary metabolites, they serve no role in primary metabolic processes associated with plant growth and reproduction. Second, enemy and plant mutually benefit from the interaction in a reciprocal fashion, with plants providing enemies with food, and enemies providing plants with protection. Last, traits are expressed in a manner consistent with a defensive function – maximizing protection from herbivory, while minimizing costs to the plant. We consider each of these features for the two best-studied coevolved traits, extrafloral nectaries and food bodies.

Extrafloral nectaries are similar to floral nectaries, except rather than enclosed within the corolla they are strategically positioned on leaves (usually the petiole or mid-rib), stems, bracts and fruits. Structurally, extrafloral nectaries are small openings in the plant surface, typically one to several millimeters in diameter, but sometimes larger, that exude nectar consisting primarily of simple sugars such as sucrose, glucose and fructose (see Figures 4.8 and 6.10). While not all plants possess extrafloral nectaries – they are totally absent in gymnosperms – the trait is widely distributed across flowering plants, occurring on >1000 species in >90 families that include grasses, forbs, vines, shrubs and trees (Koptur 1992, Wäckers 2005). Nectary-bearing plants, however, tend to be more prevalent in tropical compared with temperate zones, where they comprise nearly 30% of the species in certain regions (Heil and McKey 2003, Rudgers and Gardener 2004).

A large number of insects visit extrafloral nectaries; ants are the most commonly reported and frequently monopolize this resource, but other generalist predators, parasitoid wasps and even herbivores are among the visitors. Of 136 lacewing larvae observed foraging in the field, 21% of them fed on nectaries during the observation period (Limburg and Rosenheim 2001). Similar values have been reported for non-web-building wandering spiders (e.g., crab spiders in the family Thomisidae, jumping spiders in the family Salticidae); up to 41% of field-collected individuals tested positive for fructose, indicating recent extrafloral nectar consumption (Taylor and Pfannenstiel 2008). Because of such frequent enemy visits in nature, the nutritional value of nectar to sugar-limited insects and their apparent lack of function, the hypothesis that extrafloral nectaries exist to attract bodyguards that protect plants from herbivorous insects has grown in popularity and is now widely accepted among ecologists (Bentley 1977, Koptur 1992, Heil 2008).

Evidence abounds that enemies benefit from access to sugar sources such as extrafloral nectar (Lingren and Lukefahr 1977, Limburg and Rosenheim 2001, Wäckers 2005, Röse *et al.* 2006, Irvin *et al.* 2007, Lach *et al.* 2009, Taylor and Bradley 2009). The reciprocal benefits that enemies provide to plants are far more variable and complex to disentangle. To establish this causal link, a study would ideally document that nectary-bearing plants experience enhanced enemy attack on herbivores (Pemberton and Lee 1996, Oliveira 1997, Agarwal and Rastogi 2008), reduced plant damage (Stephenson 1982, Oliveira *et al.* 1999, Rudgers 2004, Whitney 2004, Kost and Heil 2005, Sugiura *et al.* 2006, Doak *et al.* 2007) and increased plant fitness (Stephenson 1982, Oliveira *et al.* 1999, Ruhren and Handel 1999, Rudgers 2004, Whitney 2004, Kost and Heil 2008).

While the above-cited studies do in fact demonstrate these benefits, others have either found no impact of extrafloral nectaries on herbivory (O'Dowd and Catchpole 1983, Tempel 1983, Heads and Lawton 1984, Zachariades and Midgley 1999, Mody and Linsenmair 2004) or demonstrated context-dependency of the effects (Barton 1986, Horvitz and Schemske 1990, Rashbrook *et al.* 1992, Di Giusto *et al.* 2001, Whitney 2004, Oliver *et al.* 2007, Chamberlain and Holland 2008). The strength of mutualisms is often conditional on the ecological context in which they occur (Cushman and Addicott 1991, Bronstein and Barbosa 2002), as is true for species interactions in general (Thompson 2005). Numerous factors dictate whether extrafloral nectaries lead to a net beneficial impact on plants and the strength of this effect, including, for instance, the species identity and aggression level of ants patrolling the plant (Lach 2003, Ness 2003a, Ness *et al.* 2006). Another reason for conditional outcomes is that the benefit must be sufficiently strong to offset costs of enemy attraction. In the case of ants, nectary-mediated recruitment can reduce plant reproductive output by deterring pollinators (Ness 2006), or induce ants to attack other, potentially more effective, predators and parasitoids, indirectly benefiting herbivores (Koptur and Lawton 1988). Ant attraction can also promote tending and thus outbreaks of honeydew-producing hemipterans (Offenberg 2000), or provide enemy-free space for stealthy herbivores that evade ant detection (Eubanks *et al.* 1997).

Perhaps the best evidence for a defensive role of extrafloral nectaries derives from observed spatiotemporal patterns of nectar exudation and gland occurrence, which in many cases correspond with optimal defense theory predictions. For example, extrafloral nectar can be induced by feeding damage, with reported increases in the number of nectaries or exudate volume and quality (e.g., sugar and amino-acid concentrations) following attack by herbivorous insects (Koptur 1989, Agrawal and Rutter 1998, Wäckers *et al.* 2001, Ness 2003b, Wooley *et al.* 2007). Inducible extrafloral nectary responses can be mediated by jasmonic acid, a phytohormone that simultaneously regulates secondary chemical expression and other putative plant defenses (Heil *et al.* 2001a). Induced nectar production also tends to be localized, occurring from the nectaries on herbivore-damaged compared with undamaged leaves (Stephenson 1982, Wäckers *et al.* 2001), suggesting that plants are guiding enemies to the exact location of their prey. Several studies show that the timing of peak nectar secretion coincides with herbivore developmental stages that are most vulnerable to predation and parasitism (Tilman 1978, Stephenson 1982). Last, nectaries are often preferentially allocated to tissues such as flowers, fruits and young leaves that are of greatest value to the plant and/or at highest risk of being damaged by herbivores (Heil *et al.* 2000, Wäckers and Bonifay 2004, Radhika *et al.* 2008, Holland *et al.* 2009).

In spite of the overwhelming evidence and widespread acceptance of a defensive function, other explanations have been put forth to explain the evolution of extrafloral nectaries. Koptur (2005) reviewed these alternative hypotheses, which include:

(1) *Plant physiological waste product* – nectaries excrete excess carbohydrates, which may occur if nitrogen or other nutrients are highly limiting.
(2) *Distracting ants from flowers* – if ants harvest floral nectar then pollination services may suffer, therefore nectaries discourage ants from flower plundering by offering an alternative sugar source (Kerner 1878, Wagner and Kay 2002).
(3) *Distracting ants from hemipterans* – similar to the second hypothesis, nectaries lure ants from honeydew-producing hemipterans and thus prevent them from inducing outbreaks of aphids and other such herbivores (Becerra and Venable 1989, 1991).

While all of these competing hypotheses have received some level of support, the body of evidence supporting a protective function is considered to be the most convincing (for additional discussion see Bentley 1977, Sabelis *et al.* 2005).

Food bodies are small epidermal structures rich in proteins and lipids that are harvested by foraging ants (Beattie 1985). These structures are also referred to as Beccarian bodies, Beltian bodies, Müllerian bodies or pearl bodies, all of which describe a particular type of food body that is either unique to certain plant taxa or shares some defining characteristic (see Figures 6.10–6.12). Beltian bodies are found on leaf tips of New World *Acacia* sp. and Müllerian bodies at the petiole base of *Cecropia* trees. Pearl bodies are small (max. 3 mm), contain mostly lipids, and have a “pearl-like luster”; Beccarian bodies are a type of pearl body occurring on plants in the genus *Macaranga* (Beattie 1985).

While food bodies and extrafloral nectaries are comparable in their general purpose as nutritional adaptations to attract enemies for antiherbivore protection, they differ substantially in several important aspects of their ecology. For one, food bodies are both geographically and taxonomically more restricted than extrafloral nectaries. Food-body-bearing plants occur principally in the tropics and have been reported from fewer than 30% as many plant families as extrafloral nectaries (Heil and McKey 2003). Also, a large and diverse assemblage of consumers visit nectaries, but food bodies are harvested by ants (although cheaters have evolved to exploit food bodies in some ant–plant mutualisms; e.g., Letourneau 1990, Dyer *et al.* 1999, Meehan *et al.* 2009). This greater level of specialization with interactions involving food bodies is likely driven by the fact that these structures are frequently used as rewards on **myrmecophytic** plants that house ants in **obligate mutualisms**, whereas extrafloral nectaries are often visited by opportunistic ants resulting in more loose associations called **facultative mutualisms** involving **myrmecophiles** or “ant-loving” plants.

In the case of obligate mutualism involving food bodies, the lives of ants and plants are so tightly intertwined that in many cases neither partner can survive in the absence of the other. This symbiotic interaction fundamentally differs from facultative mutualisms in which both partners may benefit from the association, but are not reliant on one another for survival. The reliance of ants on myrmecophytic plants is not surprising when you consider that ants are both fed and housed entirely by the plant (this latter aspect will be addressed in greater detail below in Section 13.2.3.2, Domatia). Even potential prey items are attacked and driven from the plant instead of being collected and eaten. This is especially the case for mammalian herbivores, but interestingly it also holds true for herbivorous insects that could be used as a supplementary resource. In a study of the myrmecophytic *Piper* plant that houses *Pheidole bicornis* ants, more than half of the insect eggs encountered by ants were taken to the edge of the plant and dropped to the ground rather than consumed as food (Letourneau 1983). This implies that food body provisioning by *Piper* can satiate the appetite of *P. bicornis*. Other studies have demonstrated sophisticated biochemical adaptations that link mutualistic ants to the food provided by their host plant, adaptations that are lacking in non-mutualist ant species (Heil *et al.* 2005). Further evidence for specialization in ant–plant mutualisms comes from empirical work showing that food-body production is inducible (Risch and Rickson 1981) and the harvesting ants preferentially defend higher-value plant parts, as predicted by optimal defense theory (Letourneau 1983, Heil *et al.* 2004a).

Myrmecophytes are similarly dependent on ant partners for their survival. In a classic study of swollen-thorn acacias and their ant inhabitants in Central America, Janzen (1966) experimentally demonstrated that ant removal quickly results in the decimation of plants by herbivorous insects, an outcome since confirmed in other ant-plants (Letourneau 1998, Heil *et al.* 2001b; but see Moraes and Vasconcelos 2009). Ants generally provide broad spectrum and effective antiherbivore protection, especially in tropical regions (Chamberlain and Holland 2009, Rosumek *et al.* 2009). The sheer reliance of plants on ant bodyguards as an **indirect defense**, however, runs counter to the perception that plant tissue is replete with toxic secondary chemicals and structural carbon (e.g., cellulose, lignin), making them relatively unpalatable to consumers (Polis 1999). Herbivory may reduce plant fitness, but it rarely outright kills the plant in nature. Why then are myrmecophytes so susceptible to herbivory in the absence of ants? Janzen (1966) suggested that ant-plants reduce investment in **direct defenses** as a cost-saving mechanism. Why should plants expend energy in resistance traits such as toxins that become redundant on plants that are continuously patrolled by aggressive ants? Despite early evidence (Janzen 1966, Rehr *et al.* 1973), this purported trade-off between chemical and biotic defenses has received variable support (Dyer *et al.* 2001, Heil *et al.* 2002).

As evident from the preceding discussion, ant–plant mutualisms provide an ideal example of trait integration such that it becomes difficult to assess the importance of any one plant trait, in this case food bodies, without referencing other inter-related traits that together function as a single defensive syndrome (sensu Agrawal and Fishbein 2006). Certain ant-plants only offer food bodies (e.g., *Piper* sp., *Cecropia* sp.), others only provide extrafloral nectaries (e.g., African *Acacia* sp.), while still others produce both food bodies and extrafloral nectaries (e.g., Central American *Acacia* sp.) (Heil and McKey 2003). Swollen-thorn acacias, also called bull's-horn acacia, are colonized by ants in the genus *Pseudomyrmex*. The plant provides hollowed thorns that ant colonies live in along with a well-balanced diet consisting of carbohydrate-rich extrafloral nectar and food bodies containing all essential amino acids and fatty acids (Heil *et al.* 2004b). These three traits (domatia, extrafloral nectaries, food bodies) coalesce to form a highly effective biotic defense syndrome revolving around ants as bodyguards. Dissecting the system into its component pieces would poorly depict the sophisticated defenses plants can deploy in their quest to manipulate enemies.

13.2.3 Morphology

The final broad group of plant traits considered in this section includes morphological features such as (a) trichomes, (b) domatia, and (c) architecture. The mechanisms by which variation in plant morphology affects multitrophic interactions are in many ways a departure from those that we have previously considered. Whereas secondary metabolites and nutritional resources require the herbivore, the enemy or both to ingest compounds that are either detrimental or beneficial (with volatiles the lone exception), morphological traits influence the ability of insects to move, forage, grip and otherwise live on the plant surface. They impact survival of predators and parasitoids, but also their efficiency in locating and capturing prey.

13.2.3.1 Trichomes

One of the fundamental challenges, or "evolutionary hurdles," that phytophagous insects must surmount is to remain attached to their host plant (Southwood 1973, 1986). In fact, the problem of attachment is universal for all insects foraging on plants, whether a herbivore searching for leaves or enemy hunting their prey. While the plant surface presents a complex foraging environment that encompasses several morphological features that are relevant to our ensuing discussion (e.g., epicuticular waxes; Eigenbrode 2004), the emphasis of this section, reflecting that of the primary literature, is the role of **trichomes**. As we know from Chapter 4, trichomes are small, epidermal hairs that emerge from leaves, stems and other plant surfaces (Figure 4.7). Their structure varies considerably from simple hair-like protrusions that serve as physical barriers impeding insect movement, to glandular trichomes that express secondary compounds in viscous secretions exuding from the trichome tips. In the latter case, small insects can easily become entrapped and immobilized, and die embedded in the glandular substance or, more simply, be deterred by contact with the toxic chemicals. Plant species and genotypes differ greatly in their level of trichome "pubescence," including density, length and the ratio of glandular to non-glandular hairs.

Although trichomes are routinely cited as a plant defense mechanism (Levin 1973), their effects on insects are highly variable, even beneficial for herbivores in certain instances (Southwood 1986, van Dam and Hare 1998, Gruner *et al.* 2005, Kaplan *et al.* 2009a). Several whitefly species, for example, are repelled by the glandular trichomes of *Datura wrightii*, while the co-occurring and phylogenetically related mirid *Tupiocoris notatus* prefers and performs better on glandular trichome-bearing plants (van Dam and Hare 1998). Species identity may indeed drive such idiosyncratic responses, challenging our ability to predict outcomes in a multitrophic context. Reports of predators and parasitoids altering their behavior (e.g., increased grooming, decreased movement, fewer oviposition attempts and attacks on prey) on relatively hairy or sticky plants are commonplace (Gruenhagen and Perring 1999, De Clercq *et al.* 2000, Lovinger *et al.* 2000, Kennedy 2003, Verheggen *et al.* 2009; but see Styrsky *et al.* 2006, Romero *et al.* 2008). Whether trichomes ultimately disrupt top-down suppression and thus induce herbivore outbreaks, however, depends on the degree to which trichomes impede enemies compared with their phytophagous prey. If herbivores are entirely unaffected or perform better while enemy foraging is disrupted, then trichome expression will benefit herbivores and likely result in higher densities. Yet most cases are not this straightforward. Often trichomes negatively affect both insects and the balance of these two opposing forces determines the net impact on herbivore populations.

A good example of this balance comes from the lepidopteran herbivore *Manduca sexta*, which is widely regarded as a specialist that feeds exclusively on solanaceous plants, although large quantities of *M. sexta* eggs and larvae were recently found on the non-solanaceous plant *Proboscidea parviflora* (Mechaber and Hildebrand 2000). This apparent host range expansion is puzzling because *P. parviflora* is distantly related and chemically distinct from plants in the family Solanaceae. More importantly, *P. parviflora* leaves are coated with a dense mat of sticky trichomes that cause most *M. sexta* eggs to abort or the larvae to die upon hatching (Mira and Bernays 2002). This is in stark contrast with solanaceous host plants from which plant-mediated mortality, including the combined effects of trichomes and other resistance traits, is minimal. Why then should *M. sexta* oviposit on the novel host? The answer most likely lies at the interface of leaf surface morphology and enemy-inflicted mortality. Hornworm eggs and young larvae are heavily attacked by 51 species of natural enemies on solanaceous plants, but predation and parasitism is virtually non-existent on trichome-laden *P. parviflora*. As a result, fewer than 0.5% of all eggs oviposited on solanaceous plants survived to the final larval instar compared with 3% of those on *P. parviflora*. Despite the fact that trichomes severely reduce the survival and performance of *M. sexta*, the benefits of enemy-free space afforded by glandular hairs on the novel host plant far outweigh the direct costs of trichome exposure for herbivore development.

While the above study offers compelling, albeit circumstantial, evidence linking trichomes with relaxed enemy pressure, the two plant types differ in dozens of ecologically relevant traits, making it difficult to implicate pubescence per se. Gassmann and Hare (2005) used two phenotypes of jimsonweed, *Datura wrightii*, one of which is covered with short non-glandular trichomes (the “velvety” phenotype) and the other of which produces glandular trichomes (the “sticky” phenotype), to disentangle the direct negative effect of trichomes on herbivores vs. indirect positive effect via enemy release. In this case, using conspecific plants allowed for greater control over the potentially confounding effects of variation in morphological and biochemical plant traits aside from trichomes. By comparing the mortality of herbivorous chrysomelid beetles (*Lema daturaphila*) on the two plant phenotypes in the presence and absence of several key predators, this study clearly demonstrates the need for a multitrophic perspective in assessing the ecological consequences of trichomes. As shown in Figure 13.6, when occurring in the enemy-free “control” environment, herbivore mortality was 3× greater on “sticky” plants with glandular trichomes compared with “velvety” plants. The opposite pattern, however, was found when

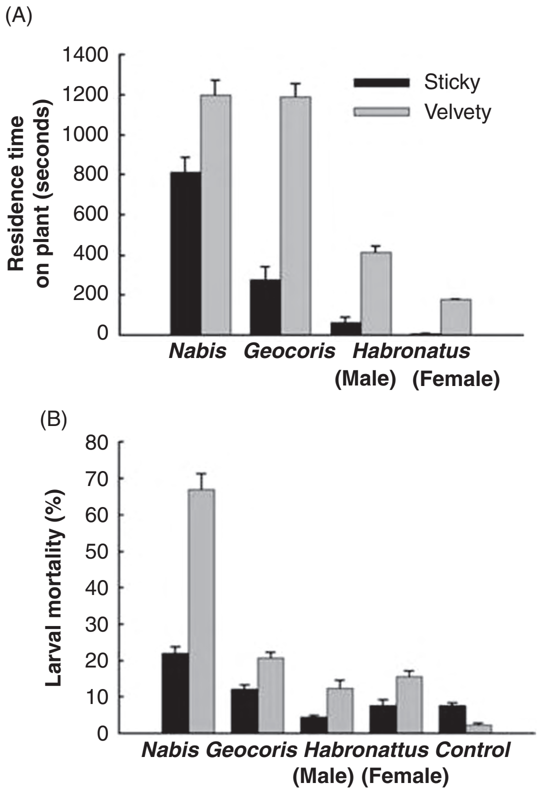


Figure 13.6 *Datura wrightii* produces two distinct phenotypes: velvety (non-glandular trichomes) and sticky (glandular trichomes) plants. (A) Predators avoid foraging on sticky plants, and (B) the mortality of a chrysomelid herbivore *Lema daturaphila* is thus higher on velvety plants that are more heavily patrolled by enemies. With kind permission from Springer Science+Business Media: *Oecologia*, Indirect cost of a defensive trait: variation in trichome type affects the natural enemies of herbivorous insects on *Datura wrightii*, **144**, 2005, p. 62–71, A. J. Gassmann and J. D. Hare, Figures 1 and 3.

comparing herbivore mortality on the two plant types in the presence of the predators *Nabis*, *Geocoris* or *Habronatus*, all of which avoid foraging on "sticky" plants. Trichomes only provided effective resistance to herbivory in a simple bitrophic environment and actually *promoted* herbivore outbreaks when embedded in their naturally occurring food web. Whether this paradigm can be broadly applied to other plant–insect systems will in large part depend on the relative importance of natural enemies (top-down) vs. host plants (bottom-up) in the population ecology of herbivores.

13.2.3.2 Domatia

Upon successfully gripping the plant surface, all insects face the equally daunting task of survival in a harsh environment that includes exposure to desiccation, among other abiotic stresses. Plants can selectively encourage the survival of enemies by providing **domatia**, morphological structures that insects use as refuge or housing (see also Chapter 6 on mutualism). This allows enemies to live directly on or in the plant, a critical advantage in facilitating prey suppression. Speed is of paramount importance in defending plants from herbivores: if enemies arrive several days or more after herbivores initiate feeding, it may be too late. Such a time lag provides herbivores the opportunity to severely injure plants or grow to a larger size class less vulnerable to predation and parasitism. In the case of aphids and other parthenogenetic insects, even a minor gap in predator colonization time is enough for colonies to attain population sizes that escape natural enemy control. Domatia-bearing plants can circumvent this problem because resident predators can discover and attack herbivorous prey nearly instantaneously upon colonization.

The two best examples of domatia-mediated plant defense come from ant–plant and mite–plant mutualisms. In the case of ant–plant mutualisms, we discussed this relationship in the above section on food bodies so we will only briefly mention them here. A large number of opportunistic ant species establish nests in cracks, crevices and cavities naturally formed in branches, stems, leaves, galls, roots and bark (Hölldobler and Wilson 1990). These relationships may occasionally be mutualistic, but are often better described as commensal or parasitic. Fewer, more specialized plant species develop hollowed-out sections, referred to as **myrmecodomatia**, whose only purported function is to house ant colonies, including eggs and developing larvae. Although the most well-cited example is the hollowed out thorn of *Acacia* sp. described by Janzen (1966), other plants also produce domatia whose location and structure vary tremendously. These include swollen internodes, hollow stems or branches, inflated leaf bases or subtending pouches, to name a few. They are often colonized by only one species and the benefits of domatia for plant fitness can be substantial because their ant inhabitants fiercely defend the plant as their home (Gaume *et al.* 2005). As eloquently described by Hölldobler and Wilson (1990, p. 535): "Further evidence of coevolution is provided by the legendary ferocity of many of the guest ants. The vast majority of *Pseudomyrmex* species not occupying domatia are timid and flee even when their nest is broken apart. In sharp contrast, *P. triplarinus*, an obligate resident of *Triplaris americana*, falls upon any intruder touching the nest tree without hesitation or mercy. To be stung by several of these ants within a few seconds is a shocking experience – you pull back at once. Or conversely, if you want to locate *Triplaris* quickly in an Amazonian forest, shake one sapling after another until one produces a swarm of the stinging ants."

Mite–plant mutualisms, while conceptually and functionally similar, are quite different in structure compared with ant–plant mutualisms. In these cases, mites inhabit **leaf domatia**, which are small, localized tufts of non-glandular trichomes in the axils of leaf veins, where small predaceous insects accumulate (see Figure 1 in Romero and Benson 2005 for pictures illustrating the structural diversity of mite-inhabiting domatia). Plants in more than 250 families bear these structures, encouraging high densities of small predators (e.g., thrips and mites) and enhancing their overall effect in reducing herbivore populations (O'Dowd and Wilson 1991, Walter 1996, Romero and Benson 2005). Thus, domatia have been viewed by many ecologists as a mutualistic association between plants and small predators. Domatia can also result in reduced plant fungal infection by housing mycophagous mites (English-Loeb *et al.* 2005), but most current research emphasizes consequences for predator–prey dynamics (Walter and O'Dowd 1992a, 1992b, Grostal and O'Dowd 1994, Agrawal 1997, Agrawal *et al.* 2000, Romero and Benson 2004). The actual benefits incurred by domatia inhabitants include improved microclimate, an important consideration for small, soft-bodied arthropods that are vulnerable to desiccation. Perhaps more importantly, small intermediate predators can escape intraguild predation by larger top predators that are denied entry (Norton *et al.* 2001). In a manipulative study on cotton plants (summarized in Figure 13.7), addition of "artificial domatia" (tufts of cotton fibers) to leaf undersurfaces resulted in upwards of fivefold increases in the densities of small invertebrate predators such as western flower thrips (*Frankliniella occidentalis*), big-eyed bugs (*Geocoris* spp.) and minute pirate bugs (*Orius tristicolor*), and their eggs were found almost exclusively in domatia. In this study, herbivorous mite populations were reduced twofold and cotton yield (boll production) increased by 30% (Agrawal and Karban 1997).

13.2.3.3 Architecture

The final aspect of plants that we will discuss in a multitrophic context is architecture, which is a broad designation that includes a wide range of variables such as leaf shape, petiole length, branching patterns, foliage density and phenological stage (i.e., vegetative vs. reproductive, flowering plants). These traits interact to generate plants that are architecturally simple, complex or intermediate, and this level of complexity varies enormously from one plant species to the next. While architecture certainly affects the strength of predation and parasitism for herbivorous insects (Kareiva and Sahakian 1990, Marquis and Whelan 1996, Casas and Djemai 2002), it remains unclear whether enemies act as selective pressures on architectural complexity or whether such interactions are purely incidental (i.e., abiotic factors select for optimal plant growth patterns and dictate architecture, which inadvertently affects insects).

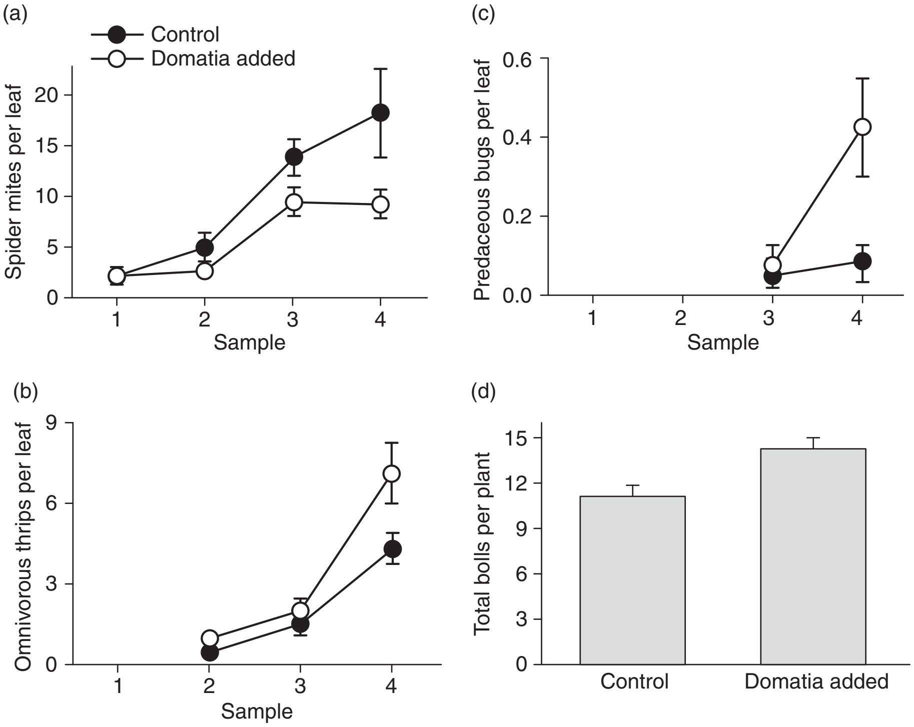


Figure 13.7 Experimental addition of leaf domatia to cotton plants results in (a) decreased herbivore abundance, (b) and (c) increased predator abundance and (d) increased plant fitness. Reprinted by permission from Macmillan Publishers Ltd: *Nature* (Agrawal and Karban 1997), copyright (1997).

Recall from Chapter 7 in our discussion of predator–prey interactions (Section 7.5.3.3: Habitat complexity and refuge from predation), more complex habitats may promote stability by providing a refuge for prey from highly mobile and efficient predators, thus preventing predators from driving herbivores to local extinction. This prediction is based on Huffaker's classic study of mite searching efficiency in structurally complex environments, and we can extend this to predict that architecturally more complex host plants will provide greater refuge for herbivores. Coccinellid and lacewing larvae, for example, are more effective aphid predators on grasses with broad, flat leaves compared with those bearing linear leaves that are tightly rolled inward, the latter of which provide aphids with enemy-free space (Clark and Messina 1998a, 1998b). In other cases, predators and parasitoids are less effective because architecturally more complex plants simply take longer to search and thus locate prey on (Andow and Prokrym 1990, Grevstad and Klepetka 1992). Recent studies have extended this logic to understand predator–predator interactions with the finding that intraguild predation and cannibalism are also diminished in complex foraging environments, leading to greater herbivore suppression (Norton *et al.* 2001, Finke and Denno 2002, Langellotto and Denno 2004). Thus, the net impact of architecturally complex host plants will depend on who receives the refuge (herbivore or intermediate predator), the relative importance of predator–predator interactions, and the foraging behavior of the enemies and prey involved.

13.3 Trophic cascades

We now turn our attention away from plant traits and toward broader ecological patterns, namely **trophic cascades**, defined as indirect effects linking non-adjacent trophic levels. They can propagate either up or down the trophic web and are evaluated using any number of response variables including abundance, biomass and diversity. That being said, the term trophic cascade is most commonly used to describe the indirect positive impact of enemies on lower trophic levels, including plant biomass, via suppression of herbivores. This more strict definition necessitates that two conditions hold true. First, in the absence of enemies, herbivores must suppress plants. This is not a given – terrestrial plants are replete with toxic chemicals and recalcitrant, structural carbon making them relatively inedible to consumers. If herbivores have no impact on plant growth or reproduction in enemy-free environments then trophic cascades simply cannot occur, regardless of what happens at higher trophic levels. Second, enemies must function collectively as a cohesive third trophic level, reducing the abundance of their herbivorous prey, and releasing plants from the potentially devastating effects of herbivory. Again, this is not a given – as discussed earlier in the chapter (Section 13.1: The trophic level concept), the topology of real food webs is such that widespread omnivory, intraguild predation and other trophic complexities obscure the existence of discrete trophic groups (Polis 1991b, Polis and Strong 1996). Thus, strong cascading effects are expected when plants are relatively palatable and enemies attack herbivores instead of one another. Cascades will likely be weak to non-existent when plants are heavily defended and enemies engage in extensive intraguild predation. While these are some of the fundamental conditions for trophic cascades as strictly defined, as we will learn later in this section, cascading effects of enemies on plants occur under a far wider range of circumstances that violate these underlying assumptions.

The conceptual basis for such conditions was originally outlined by Hairston, Smith and Slobodkin in their now classic paper “Community structure, population control, and competition” (Hairston *et al.* 1960). This opinion piece, often referred to as HSS or the **green-world hypothesis**, is organized around a seemingly logical series of observations as follows. First, outbreaks of herbivores are rare in nature and thus plants mostly remain abundant, green and minimally damaged by consumers. Because of this pattern, food availability must not be a factor limiting herbivore abundance. Second, the rare instances of herbivore outbreaks and ensuing depletion of their food plants occur when enemies are absent or inadvertently removed from the environment (i.e., invasive species such a gypsy moth). Third, weather does not regulate numbers of herbivores. The logic then follows that if food availability and weather do not limit herbivores, and population outbreaks tend to occur in predator-free habitats, then enemies must regulate herbivores to low densities, thereby preventing them from outstripping their food resources. This top-down view posits that enemies control the greenness of the world by suppressing herbivores that would otherwise suppress plants.

As might be expected, given the bold and overarching predictions outlined in the green-world paradigm, this predator-driven perspective of population control has since weathered intense criticism (Murdoch 1966, Ehrlich and Birch 1967, Polis 1999). Several arguments refuting the green-world hypothesis were mentioned above (i.e., assumes that leaf tissue is universally edible, underestimating the importance of plant defenses and the stoichiometric mismatch between plants and consumers; species diversity and trophic complexity attenuate top-down effects, preventing cascades from reaching plants, e.g., Polis and Strong 1996). Others have noted that abiotic factors such as temperature, precipitation and nutrients rather than predators truly dictate global patterns of greenness. The green-world model also assumes that only three factors (food availability, enemies and weather) limit herbivore abundance, ignoring density-dependent mechanisms such as territoriality, cannibalism or competition for oviposition sites. Last, green leaf tissue is used as the sole currency for food. Although this is the case for caterpillars and defoliating insects in general (and many vertebrate grazers), it does not account for herbivores in other guilds that feed on phloem, xylem, galls, roots, pollen, nectar, seeds and fruits.

Perhaps because the green-world hypothesis is devoid of supporting data, relying entirely on anecdotal observations, this publication spurred a tremendous growth in experimental studies testing the impact of enemies on herbivores and plants, making it one of the most influential papers in community ecology to date. The legacy of Hairston *et al.* (1960) and trophic cascades will be reviewed below, beginning with an assessment of underlying assumptions, continuing with emerging patterns and syntheses, and ending with a review of factors that enhance or diminish the strength of cascades.

13.3.1 Underlying assumptions

Classic trophic cascade models implicitly assume several underlying conditions in the structure and function of communities. We begin by reviewing evidence for several of the more fundamental assumptions.

13.3.1.1 Cascades are transmitted by changes in whole trophic level biomass

Trophic cascades as classically defined are assessed by quantifying overall changes in plant biomass with the addition or exclusion of trophic levels. Plants are plentiful in the absence of herbivores, their biomass declines with the addition of a herbivorous second trophic level, and a functional third trophic level releases plants from herbivore control. Thus, plant biomass is relatively high in communities with one or three trophic levels, but is depressed in systems with two or four trophic levels (Oksanen *et al.* 1981). This alternating pattern of plant biomass accumulation with increased food chain length is a hallmark of top-down trophic cascades. Many have noted that top-down cascades are weaker in terrestrial compared with aquatic communities (Strong 1992, Polis 1999, Shurin *et al.* 2006), a system-wide divergence that is in large part driven by the inedibility of terrestrial plants. In other words, herbivores simply cannot remove, assimilate and recycle sufficient plant biomass, even in the absence of enemies, to catapult a strong cascade in terrestrial food webs (Power 1992, Gruner *et al.* 2008).

Despite its historic and continued use, we urge caution in relying on a single metric such as plant biomass when assessing the multitrophic consequences of enemies. Schmitz (2003, 2006, 2008) experimentally manipulated the number of trophic levels in a five-year study of old-field plant communities, resulting in plots with either: (a) one trophic level – plants (Figure 13.8A), (b) two trophic levels – plants and grasshoppers (Figure 13.8B) or (c) three trophic levels – plants, grasshoppers and spiders (Figure 13.8C). The addition of grasshoppers alone reduced overall plant biomass, but the further addition of spiders did not allow plants to rebound (compare plant biomass in Figures 13.8A–C). Under this scenario, it would be tempting to conclude that spider predation does not cascade downward to impact plant communities. This, however, is not the case. In the absence of spiders, grasshoppers preferentially consume grasses (e.g., *Poa pratensis*), avoiding less palatable and competitively dominant forbs such as *Solidago rugosa*. Spider presence causes grasshoppers to alter their foraging behavior by taking refuge in forbs, thus consuming less grass and more *S. rugosa* than in spider-free habitats. As a result, spiders induce grasshoppers to suppress the competitively dominant *S. rugosa*, increasing plant species diversity and enhancing ecosystem properties such as nitrogen mineralization rate. Note the progressive decline in *S. rugosa* and concomitant increase in plant diversity with the addition of trophic levels in Figure 13.8. This is an excellent

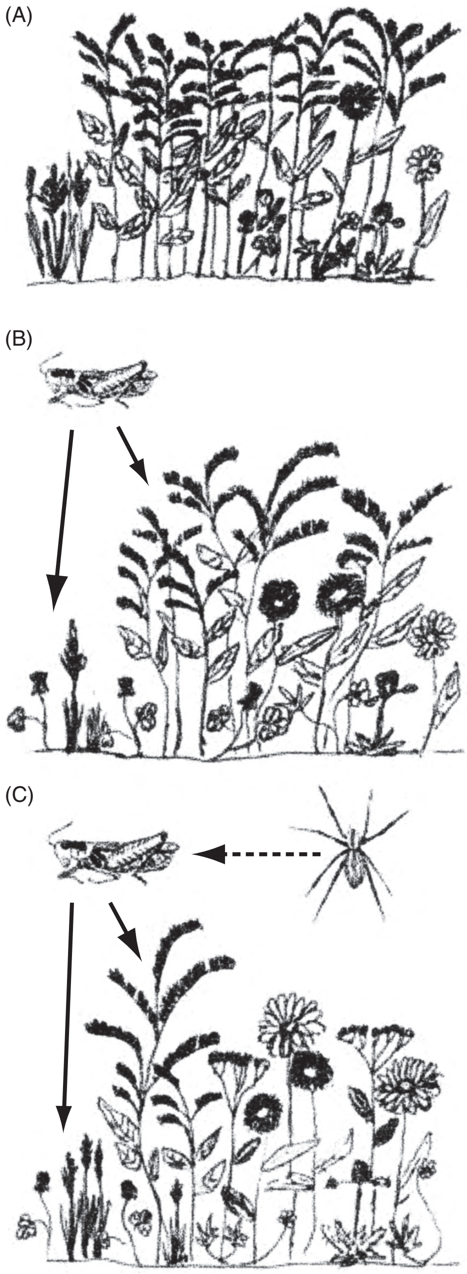


Figure 13.8 The structure and diversity of old-field plant communities in one-, two- and three-trophic-level systems (A–C, respectively). From Schmitz (2003), *Ecology Letters*, John Wiley & Sons, Inc.

example of predators dramatically affecting plant community composition and function, but without a corresponding change in trophic-level biomass (also see Dyer and Letourneau 2003).

13.3.1.2 Cascades are mediated by consumption

As stated by Strong (1992, p. 747): “Trophic cascades mean runaway consumption, downward dominance through the food chain.” Though the emphasis on consumption is not always clearly articulated as it is here, the notion that consumption drives cascades is pervasive. Recall from Chapter 7 that in addition to killing, predators induce changes in prey behavior, physiology and life history, collectively referred to as non-consumptive effects (Section 7.7: Non-consumptive predator impacts on prey). The above example of spiders in old-field plant communities is a cascade entirely mediated by adaptive changes in grasshopper behavior under predation risk. This begs the question: Do trophic cascades necessitate consumption at all? What is the relative importance of consumptive vs. non-consumptive pathways in multitrophic interactions?

These questions are difficult to resolve because non-consumptive predator effects have been recognized only recently and remain underappreciated. These effects are ever-increasingly documented, however, in a wide range of insect taxa including aphids (Nelson *et al.* 2004, Nelson 2007), beetles (Snyder and Wise 2000, Williams *et al.* 2001, Hlivko and Rypstra 2003), caterpillars (Stamp and Bowers 1992, 1993, Griffin and Thaler 2006, Johnson *et al.* 2007, Thaler and Griffin 2008), grasshoppers (Beckerman *et al.* 1997, Schmitz *et al.* 1997), mayflies (Peckarsky 1980, 1996, Peckarsky *et al.* 1993, 2001, 2002), thrips (Janssen *et al.* 1998) and whiteflies (Nomikou *et al.* 2003). Because these prey behavioral responses typically entail herbivores moving and feeding less or shifting habitats to evade detection, in many cases the response cascades down to reduce plant damage (see Table 1 in Schmitz *et al.* 2004). Notably, a recent meta-analytical review concluded that consumptive top-down effects attenuate through the food web, whereas non-consumptive effects amplify (Preisser *et al.* 2005). The implications here are that prey responses to predation and parasitism risk in fact contribute *more* to trophic cascades than killing does. This counterintuitive finding clearly needs to be substantiated in more systems, but it is now evident that consumption is not essential for cascades to occur.

13.3.1.3 Cascades propagate via linear three trophic level food chains

This is perhaps the most hotly debated aspect of green-world theory and one that is by no means fully resolved (Polis and Strong 1996, Hairston and Hairston 1997). Contradicting the green-world perspective of linear food-chain interactions, a large number of enemies attack one another in addition to, or instead of, herbivores. This practice is referred to as **intraguild predation** or **higher-order predation** and it is ubiquitous within insect communities (Polis *et al.* 1989, Rosenheim 1998) (see Section 7.6: Predation in complex food webs for an overview of antagonistic predator interactions).

Is intraguild predation simply background trophic noise that has no bearing on plants, or does it radically alter enemy function? We can certainly cite instances where intraguild predators benefit plants by suppressing herbivores and thereby function as the three-trophic-level system envisioned by Hairston and colleagues (Spiller and Schoener 1990a, 1994, Moran *et al.* 1996, Moran and Hurd 1998). Other studies have found intraguild predation to be highly disruptive to herbivore population suppression (Rosenheim *et al.* 1993, Snyder and Wise 2001, Finke and Denno 2003, Rosenheim *et al.* 2004a, Finke and Denno 2005). In these cases the predator complex either had little to no impact on herbivores or functioned as a four-trophic-level system, elevating plant damage. Similar contradictions have haunted the biocontrol arena, where the relative values of specialist versus generalist predators have been argued (Rosenheim *et al.* 1995, Symondson *et al.* 2002). One clear conclusion is that enemies do not universally benefit plants and this variation is often associated with antagonistic predator–predator interactions.

Unlike intraguild predation models where the top predator feeds on both intermediate predators and herbivores, in certain systems top predators specialize on other enemies. Obligate hyperparasitoids, for instance, attack primary parasitoids and constitute a distinct fourth trophic level. Perhaps the best example of cascading effects of fourth-trophic-level consumers on plants comes from the tropical ant plant *Piper cenocladum* (Letourneau and Dyer 1998, Dyer and Letourneau 1999, Letourneau *et al.* 2004). In this system, *Piper* plants are fed on by an assemblage of defoliating insects, which in turn are attacked by the predaceous ant *Pheidole bicornis*. The larvae of a specialist clerid beetle feed on ant broods inside the hollowed out petioles and inflict substantial mortality. The experimental addition of beetles to plants reduced ant occupancy (Figure 13.9A), causing herbivores to outbreak (Figure 13.9B) and plant performance to suffer (Figure 13.9C). This example is particularly noteworthy because it occurred in a tropical rain forest, the type of hyperdiverse system harboring complex food webs in which antagonistic interactions should weaken linear food chain dynamics (e.g., Gruner 2004). Is this study the exception rather than the rule? In the following section we hope to answer this question (among others) by reviewing evidence for trophic cascades from studies that have manipulated enemy presence and subsequently measured plant responses.

13.3.2 Patterns and syntheses

In the 50 years since Hairston *et al.* (1960) was published, a sufficient number of experimental tests have accumulated in the scientific literature for a rigorous evaluation of patterns. This allows us to make generalizations and pose more specific hypotheses about the overall strength of cascades

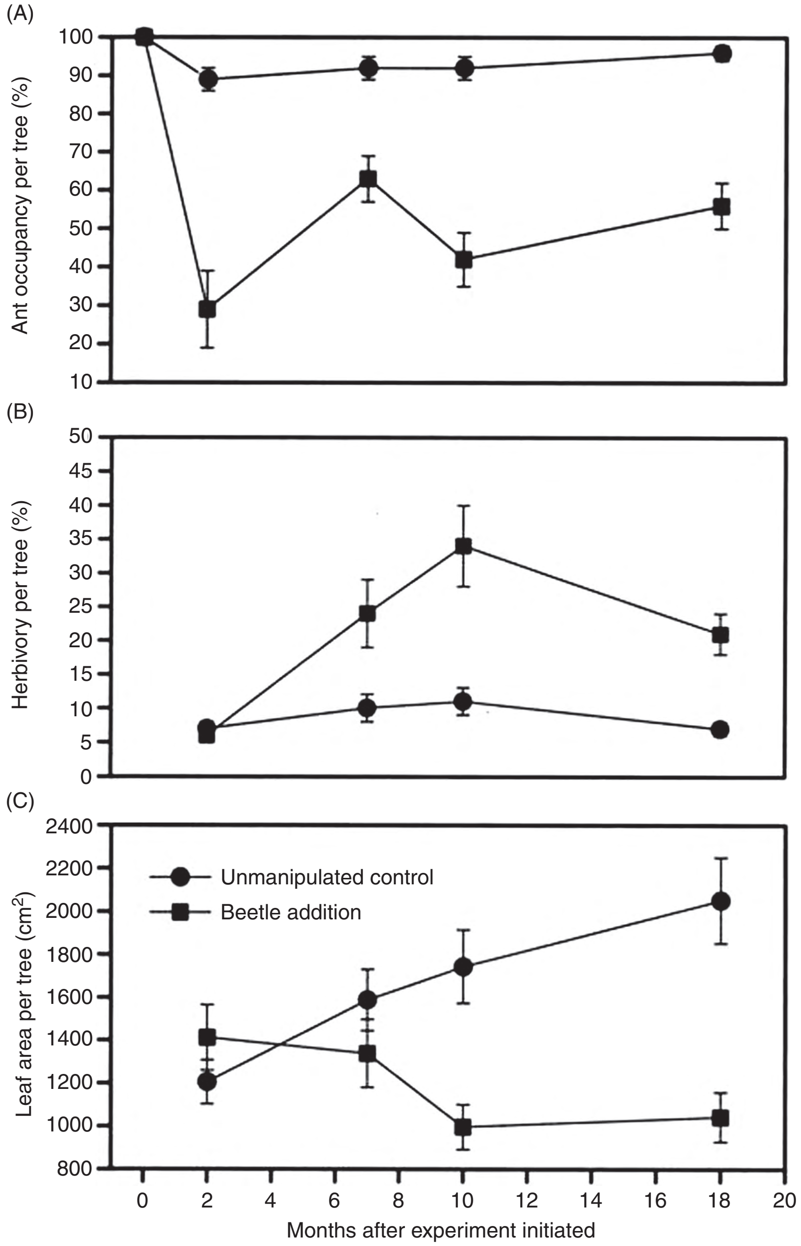


Figure 13.9 Cascading effects of top (fourth trophic level) predator additions on (A) predaceous ant (third trophic level) occupancy of *Piper* plants, (B) insect damage to leaves, and (C) leaf area in a tropical plant-insect food chain. Dyer, L. A., and D. K. Letourneau. 1999. Trophic cascades in a complex terrestrial community. *P. Natl. Acad. Sci. USA* **96**:5072–5076. Copyright (1999) National Academy of Sciences, USA.

and potential differences across habitats and taxa. Fortunately, two independent meta-analytical syntheses were published on terrestrial trophic cascades in plant–arthropod food webs that we will use as roadmaps (Schmitz *et al.* 2000, Halaj and Wise 2001). These reviews largely emerged as a direct response to the strongly held notion that cascades are weak to non-existent on land and thereby a phenomenon restricted to aquatic environments (Strong 1992, Polis 1999, Shurin *et al.* 2006).

The two aforementioned reviews compiled field studies that entailed carnivore removals or additions and measured plant damage, biomass or reproductive output. Because of slight differences in criteria for the inclusion of studies (i.e., Halaj and Wise included tests in agricultural crops, whereas Schmitz and colleagues did not) the two datasets differ substantially, with only 21% overlap, but both are robust assessments. Schmitz's dataset contains 60 experiments reported from 41 studies; Halaj and Wise's dataset has 299 experiments from 40 studies. Both reviews exclusively used studies involving phytophagous insects; however, the enemies investigated ranged from predaceous insects, such as coccinellids, to spiders, lizards and birds. Surprisingly, only one study used parasitoids (Gómez and Zamora 1994), and thus the literature available for review is overwhelmingly biased towards generalist predators. This is an important caveat to bear in mind when interpreting the results which we summarize below. Another point to consider is that negative results are difficult to publish, leading to what has been termed "the file drawer effect."

Both reviews found that predator removal significantly increased herbivore abundance, elevated plant damage and reduced plant biomass and reproduction. In Schmitz's analysis, for instance, 45 of the 60 studies evaluated found evidence that removing predators indirectly affected at least one of the three plant response variables. As a result, the two reviews agree that top-down cascades are widespread and prevalent in terrestrial insect-dominated food webs. In both reviews the magnitude of predator impact on herbivore abundance (effect size $= +0.77$) and plant damage (effect size $= +0.88$) were equivalent, suggesting that enemy effects did not attenuate. Both reviews, however, also documented that the strength of predator impact on plant biomass (effect size $= -0.32$) was comparatively weaker than damage. This may be evidence of cascade attenuation, or more simply that the experimental time scale was not sufficiently long to allow for a biomass response. However, the duration of studies ranged from 1 month to 3.5 years, but did not show temporal trends in the magnitude of herbivore or plant responses. Similarly, predator taxa did not have a consistent or otherwise apparent influence on the outcome of experiments (Table 13.2).

The strength of cascades varied enormously across ecosystems with far stronger effects in agricultural crops than either grasslands or woodlands (Table 13.2). Interestingly, predator impact on herbivore abundance was roughly similar comparing natural vs. managed systems, particularly when comparing crops with woodlands where the two effect sizes are virtually identical: 0.92 vs. 0.93, respectively. Yet predator removals resulted in a strong cascade on crop yield, whereas the cascade was non-existent for natural plant systems. This implies that predation pressure on herbivores is comparable across ecosystems, but some component of natural plant communities buffers the indirect interaction, resulting in effects that are more variable and less predictable. Agricultural crops possess many of the same attributes highlighted earlier in this section that promote trophic cascades (i.e., more edible plant tissue, simplified food web and habitat structure), perhaps explaining this ecosystem-level divergence.

While the two reviews agree that trophic cascades are a ubiquitous process in terrestrial insect communities, they differ dramatically in assessing their overall magnitude, especially when compared with aquatic systems. Both compared their findings with those values reported in Brett and Goldman (1996), a meta-analysis of freshwater trophic

Table 13.2 **The magnitude of natural enemy impact on herbivore density, plant damage and plant biomass according to ecosystem and predator type. Data were obtained from published field studies that experimentally added or removed predators. Effect sizes are directly proportional to the strength of the predator effect and thus larger values indicate that predators have a strong impact. Positive effect sizes signify that the response variable increases following predator exclusion, whereas negative effects indicate a decrease in the response variable after predator removal. The effect size metric (d_+) is calculated by comparing the mean values of the response variable in predator-present vs. predator-free environments, while accounting for the amount of variation within each treatment (i.e., magnitude of standard deviation) and the sample size per treatment. From Halaj and Wise (2001)**

Response variable	*Herbivore Abundance*		*Plant Damage*		*Plant Biomass*	
	No. of comparisons	Effect size (d_+)	No. of comparisons	Effect size (d_+)	No. of comparisons	Effect size (d_+)
Ecosystem						
Crops	61	0.92	35	1.60	46	–0.48
Grasslands	44	0.51	4	0.15[a]	40	–0.20
Woodlands	28	0.93	32	0.35	9	–0.01[a]
Predator Type						
GAPC	57	0.85	31	1.34	43	–0.53
Mantids	7	0.81	. . .	. . .	5	–0.62
Spiders	25	0.61	15	0.61	30	–0.17[a]
Birds	35	0.68	7	1.12	9	–0.23[a]
Lizards	8	0.85	13	0.54[a]	. . .	. . .
Arthropods	90	0.79	51	0.92	86	–0.33
Vertebrates	43	0.71	20	0.81	9	–0.23[a]

[a] = effect size not significantly different from zero (95% confidence interval overlaps zero)

GAPC = ground arthropod predator complex

cascades. Schmitz and colleagues (2000) reported that the average strength of top carnivore effects on terrestrial plants was equal to or stronger than those found in aquatic systems, resulting in the following conclusions: “Trophic cascades are common in many types of environments, and they occur despite variation in carnivore type, food web diversity, and experimental protocol. Moreover, the patterns and strengths of top-down effects of carnivores are equivalent to those found in other types of systems (e.g., aquatic environments)” (p. 150). In contrast, Halaj and Wise (2001) noted that, although carnivore effects on insect herbivore abundance were comparable in magnitude with zooplankton (analogous primary consumers in aquatic food webs), the indirect effects, comparing terrestrial plants with phytoplankton, were substantially weaker on land. As might be expected, these authors then concluded as follows: “Do indirect effects of predation in terrestrial communities flow torrentially down the trophic waterfall, or do they trickle? Our analysis provides a preliminary answer for food webs dominated by generalist arthropod predators. The terrestrial cascade starts strongly but becomes diverted to a trickle when it reaches the pool of primary production, with the exception of those crop systems in which the cascade continues on to cause not a ripple but a splash” (p. 276).

As mentioned, the emphasis in both reviews is on terrestrial grazing (living) food chains, reflecting that of the primary literature. Yet many insects (e.g., mayflies, dragonflies, stoneflies, caddisflies) are also important components of aquatic food webs. The same can be said of detrital systems where ants, collembolans, carabid and staphylinid beetles, among spiders, mites and other arthropods are often the dominant consumers. Do top predators indirectly control rates of decomposition? Preliminary studies have documented variable and complex effects of spiders on forest-floor leaf-litter removal, in some cases enhancing decomposition rates (Lawrence and Wise 2004, Lensing and Wise 2006, Miyashita and Niwa 2006). What is abundantly clear is that trophic dynamics in detrital webs rarely (if ever) correspond to green-world predictions (Scheu and Setälä 2002). However, in cases where below-ground food chains are interconnected with living plant tissue as happens with root-feeding insects and entomopathogenic nematodes, top-down cascades may in fact be prevalent and strong (Strong *et al.* 1996, 1999, Preisser 2003, Denno *et al.* 2008).

A final comparison worth briefly considering here is multitrophic interactions in temperate vs. tropical zones. The vast majority of experimental work on top predators has been in temperate climates. Moreover, the structure of tropical plant–insect assemblages is thought to contrast with the relatively simple structure of agricultural crops, displaying attributes expected to buffer cascades (i.e., poor-quality host plants, extremely high species diversity and habitat complexity). Dyer and Coley (2002) compared published accounts of trophic cascades in temperate vs. tropical ecosystems and, unexpectedly, found stronger cascading effects of carnivores on plants in the tropics. Inference in this comparison was hampered by low sample size and the issue clearly requires more comparative studies. If this pattern did indeed hold it would undoubtedly force a re-evaluation of the factors mediating trophic cascades.

13.3.3 Factors that enhance or diminish the strength of cascades

Even the simplest of ecological communities are extraordinarily complex systems in which variation in multiple biotic and/or abiotic factors can mediate the outcome of species interactions. Such factors inherently vary across systems and even within-system heterogeneity can be substantial. A central goal in community ecology is to understand the causes and consequences of this heterogeneity, and in so doing elucidate the critical factors underlying community-level patterns (Hunter and Price 1992). As illustrated in the trophic diagram in Figure 13.10, heterogeneity in both extrinsic and intrinsic variables at any given trophic level can dictate the strength of cascades either up or down the web. While encompassing heterogeneity may be a daunting task given the sheer number of potential explanatory variables at play, in posing the question “Why do trophic cascades occur?” Polis (1999) provides a framework for grouping factors. Below we review three general circumstances hypothesized to promote top-down cascades on plants with examples from insect food webs.

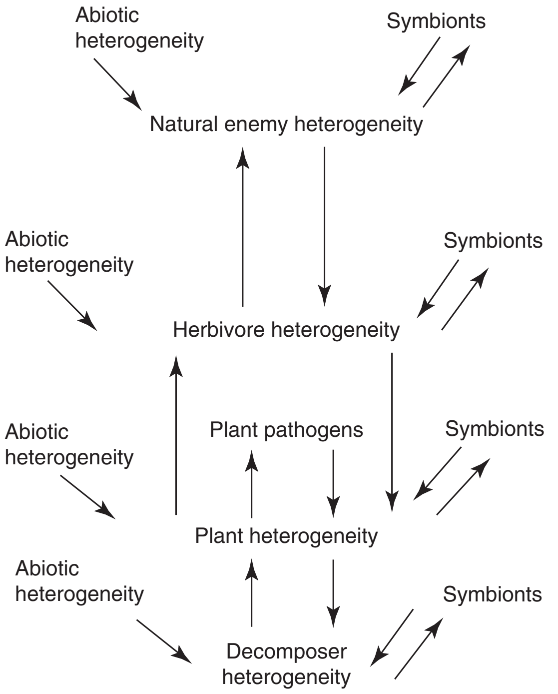


Figure 13.10 Potential influences of variation in intrinsic and extrinsic factors on trophic cascades in three trophic level systems. From Hunter and Price (1992).

13.3.3.1 Appropriate extrinsic environmental conditions

Abiotic factors are notoriously heterogeneous over relatively small spatial and temporal scales. Understanding the consequences of this variation for cascades requires us to first identify precisely what those "appropriate" conditions are. A given habitat's environment encompasses a wide range of variables, including, for example, light, temperature, water, nutrients, carbon dioxide, salinity, and disturbance frequency and severity. Complicating the picture further, most of these variables act either directly or indirectly on multiple trophic levels.

Theory predicts that bottom-up plant traits set the stage on which natural enemies act (Hunter and Price 1992, Power 1992), and therefore much of the research on environmental variation in top-down impact focuses on plant growth patterns. More specifically, the **ecosystem exploitation hypothesis** predicts that green-world dynamics will occur in highly productive plant communities that support a functional third trophic level (Oksanen *et al.* 1981). Thus, trophic cascades should be stronger in high vs. low productivity environments. In support of this theoretical model, herbivore predation and parasitism are routinely reported as being higher on experimentally fertilized plants (Hartvigsen *et al.* 1995, Stiling and Rossi 1997, Fraser and Grime 1998, Uriarte and Schmitz 1998, Forkner and Hunter 2000, Moran and Scheidler 2002, Gratton and Denno 2003, Gruner 2004; but see Denno *et al.* 2002). For instance, the seven-spot ladybird beetle *Coccinella septempunctata* suppresses the aphid *Sitobion avenae* on the grass *Poa annua*, increasing the number of flower heads to control (herbivore-free) levels, but this predator-induced cascade on plant reproduction only occurs on grasses growing in high compared with low soil fertility (Fraser and Grime 1998). Despite the apparent consensus on enemy attack increasing with plant fertility, not all of the above-cited studies documented that higher attack rates on more productive plants necessarily led to improved growth or performance. As a result, environment-mediated alterations in plant quality can provide the platform for strong top-down effects, upon which other factors (i.e., trophic complexity) must align to generate noticeable changes in plant traits.

Unlike soil nutrients that directly impact plants with indirect effects on enemies and their prey, other abiotic factors act directly on insects with important consequences for outbreaks of phytophagous insects. Enemies are considered relatively more susceptible to environmental stress or disturbance compared with herbivores, leading to the prediction that top-down effects will be strong in low-stress habitats (Menge and Sutherland 1987). Moderate to high stress will differentially affect higher trophic levels, decoupling predator from prey and resulting in weak cascades. Intertidal salt marshes are high-stress ecosystems due to frequent tidal inundation, high salinity, and exposure to wind and temperature fluctuations.

In these coastal habitats, the wolf spider, *Pardosa littoralis*, is largely deterred from low elevation marsh grasses where abiotic stress levels are high, taking refuge in high elevation marsh; unlike their planthopper prey which are unaffected by this elevation-mediated stress gradient. Because of such trophic-level differences in stress tolerance, spiders induce strong cascades on grass biomass in high elevation zones, whereas top-down suppression is weak and planthoppers outbreak in the low marsh (Denno *et al.* 2005b, Lewis and Denno 2009).

In certain cases, predicting the impact of environmental stress on trophic interactions requires a thorough understanding of the basic biology of the organisms in question. Entomopathogenic nematodes are ubiquitous parasites of insects below ground and nematodes are highly sensitive to variation in soil moisture (Preisser *et al.* 2006). On the California coast, bush lupine (*Lupinus arboreus*) is severely damaged by root herbivores (the ghost moth, *Hepialus californicus*), but plants remain protected when entomopathogenic nematodes suppress these insect larvae. In simulating soil moisture under ambient weather conditions compared with those characteristic of El Niño/Southern Oscillation (ENSO) events (i.e., increased precipitation), Preisser and Strong (2004) found a dramatic interaction between abiotic stress and the magnitude of trophic cascades. As illustrated in Figure 13.11A, nearly 100% of lupine rhizospheres were occupied by the nematode *Heterorhabditis marelatus* in El Niño-simulated conditions compared with <5% of plants under ambient soil moisture. Consequently, nematodes only suppressed insect herbivores (Figure 13.11B), thereby benefiting plant growth (Figure 13.11C) and reproduction (Figure 13.11D), in the elevated precipitation treatment. This is a striking example of trophic cascades that only occur in the "appropriate" environmental context.

This is a realm of research that has clear applications in predicting the consequences of global change for both plant and insect communities. Severe outbreaks of bark beetles and other forest

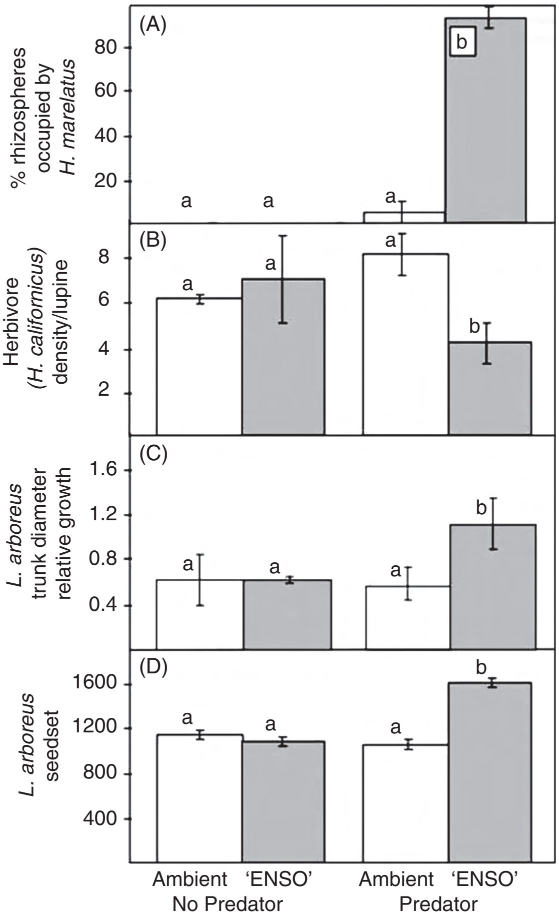


Figure 13.11 Impact of climate ("ambient" = normal precipitation pattern, "ENSO" = elevated precipitation from El Niño/Southern Oscillation) on trophic cascades induced by entomopathogenic nematodes (referred to as the "predator" in this figure) on bush lupine via root-feeding insect herbivores. Elevated precipitation (A) increases survival of nematodes, leading to (B) fewer herbivores, and (C–D) increased plant performance in the presence of enemies. From Preisser and Strong (2004), *American Naturalist*. Published by the University of Chicago Press. Copyright © by the University of Chicago Press. All rights reserved.

pests over large tracts of western North America are one major manifestation of climate warming that is projected to worsen based on current climate models (Logan *et al.* 2003). In one of the only studies that has attempted to uncover patterns and mechanisms underlying climate-change-induced insect outbreaks, Stireman and colleagues (2005) compiled a large dataset of caterpillar attack by hymenopteran parasites over a broad geographic range and found that high climatic variability was correlated with lower enemy attack. Parasitism rates decline from 12% in relatively stable environments to 4% in variable environments (see Figure 15.10) – precisely the pattern predicted by Menge and Sutherland's (1987) environmental stress model. A similar outcome has been reported on tropical islands where major hurricanes resulted in 66% and 59% declines in the abundance of spiders and parasitoid wasps, respectively, but elevated insect herbivory $>3\times$ compared with prehurricane levels (Spiller and Schoener 2007). A growing number of studies in the scientific literature report greater sensitivity of higher trophic levels to climatic disturbances (Voigt *et al.* 2003, Hance *et al.* 2007) and anthropogenic stresses (Duffy 2003).

13.3.3.2 Intrinsic characteristics of key consumers and resources

Plants, herbivores and their enemies each possess a suite of intrinsic biological attributes that may promote trophic cascades. These attributes, however, are quite diverse and rather idiosyncratic. Moreover, we have already discussed several of these characteristics earlier in the section (i.e., vulnerable plants, efficient consumers that mount strong numerical and functional responses, enemy complexes that operate collectively as a third trophic level with minimal intraguild interference). Therefore, we will not devote much additional attention to this topic.

One such intrinsic characteristic that we will briefly revisit here, in part because of its paramount importance, is the foraging behavior of predators and parasitoids. As we know, enemies can act as either third- or fourth-trophic-level consumers, and resolving this "indeterminacy of predator function" (Rosenheim *et al.* 2004a) requires a detailed knowledge of foraging behavior. Rosenheim and Corbett (2003) employed a series of simple rules based on the match (or mismatch) between predator and prey foraging modes as follows: (1) actively foraging predators may be effective regulators of sedentary herbivore populations, (2) sit-and-wait (or ambush) predators are unlikely to suppress populations of sedentary herbivores, but may act as omnivorous top predators, suppressing populations of widely foraging intermediate predators and thereby increasing herbivore densities. The logic underlying these predictions is based on the likelihood of encounter. For instance, actively foraging predators such as coccinellid and lacewing larvae more frequently encounter and thus are more effective consumers of sedentary aphids than ambush predators such as spiders. Using encounter probabilities based on fixed behavioral traits such as foraging modes is a novel perspective that has already received some level of empirical support (Rosenheim and Corbett 2003, Rosenheim *et al.* 2004a). Thus foraging mode, along with the "habitat domain" of predators and their prey (Schmitz 2007), are likely to interact to determine the strength of top-down interactions. For instance, in an elegant series of experiments Schmitz (2008) demonstrated that actively hunting spiders enhanced above-ground net primary production (NPP) and nitrogen mineralization rate through a classic trophic cascade. By contrast, sit-and-wait ambush spiders had opposite effects on NPP and nitrogen mineralization, but also increased plant community diversity and evenness by forcing herbivores behaviorally to concentrate their feeding on competitively dominant plant species.

A second foraging characteristic known to affect the magnitude of cascades is host range. Enemy complexes dominated by strict predators or specialist parasitoids tend to protect plants more effectively than polyphagous species (Finke and Denno 2005, Finke and Snyder 2008). This is not to say that generalist predators are entirely ineffective at suppressing their prey (Symondson *et al.* 2002), but a narrow host range in higher-trophic-level consumers may correlate with stronger localized top-down control in species-level cascades (Polis *et al.* 2000).

13.3.3.3 Multichannel omnivory and subsidized consumers

“Multichannel subsidies produce more consumers than can be supported by current and local resource productivity. These consumers then depress their resources. I suggest that such processes likely underlie most (all?) strong consumer-resource interactions in natural systems” (Polis 1999, p. 10). Subsidy in this case is used as an all-encompassing term to describe the input of resources (e.g., insect prey, leaf litter) that originate outside of the delineated food web. In essence, this area of important research relaxes the assumption that food-chain dynamics occur in closed systems; instead, in open systems there is an exchange of resources and propagules. We will review three general classifications of subsidies: spatial, temporal and detrital.

Spatial subsidies involve the movement of allochthonous resources produced in one ecosystem to an adjacent ecosystem, where they elevate consumer abundance and thereby strengthen trophic cascades in the recipient habitat (Polis *et al.* 1997a, Leroux and Loreau 2008). In arthropod-dominated food webs this realm of research has emphasized unidirectional pulses of aquatic insects emerging from streams and lakes to neighboring riparian zones where they subsidize the diets of terrestrial predators (Nakano and Murakami 2001, Murakami and Nakano 2002, Sabo and Power 2002, Marczak and Richardson 2007, Gratton *et al.* 2008, Gratton and Vander Zanden 2009, Wesner 2010). The larvae of chironomid midges, for example, develop in lakes, but the adults emerge in massive numbers and disperse to terrestrial vegetation to mate, as seen in the swarm of midges in Figure 13.12. Gratton and colleagues (2008) estimate that over a one week period in early August, 189 kg of midges per hectare are deposited in lakeside vegetation each day! Similarly, Murakami and Nakano (2002) documented that insects such as trichopterans and dipterans produced from streams attract insectivorous birds to riparian forests, leading to greater suppression of leaf-rolling caterpillars on Japanese lilac in streamside compared with upland habitats. Cross-habitat linkages can also occur in the opposite direction. Periodical cicadas emerge from the soil at astonishingly high densities every 13 or 17 years and subsidize aquatic ecosystems when their carcasses are inadvertently deposited into streams (Nowlin *et al.* 2007, Menninger *et al.* 2008).

Figure 13.12 A massive swarm of adult midges emerging from Lake Myvatn in Northern Iceland and moving to lakeside vegetation. Photograph by Jamin Dreyer. From Gratton and Vander Zanden (2009). See color plate section.

Subsidies can also manifest themselves through resource pulses that temporarily elevate consumers following an initial time lag (Ostfeld and Keesing 2000, Yang *et al.* 2008). An excellent example of this phenomenon comes from eastern US forests, where mature oak trees produce large acorn crops, referred to as masting, every 2 to 5 years. Because acorns are a preferred food source for rodents, masting events in the autumn increase survival and breeding success of white-footed mice in the subsequent winter and spring, resulting in high mouse densities the following summer. Mice are also important predators of gypsy-moth pupae and studies have now documented that oak masting in year 1 substantially increases consumption of gypsy-moth pupae by rodents in year 2, potentially contributing to the cyclic population dynamics exhibited by this invasive forest pest (Ostfeld *et al.* 1996, Jones *et al.* 1998, Goodwin *et al.* 2005). These periodic pulses of oak acorn resources also affect the prevalence of Lyme disease transmitted by ticks in the northeastern United States (Ostfeld *et al.* 2006).

At a more localized scale, detrital food webs support prey such as Collembola that boost the abundance of polyphagous predators that readily switch back and forth between consuming decomposers and herbivores. This has led to the prediction that influx of detritus to systems will contribute to stronger cascades in grazing food webs by allowing higher densities of generalist predators than could otherwise be supported by grazing herbivores alone (Polis and Strong 1996, Scheu 2001, Halaj and Wise 2002, Miyashita *et al.* 2003). In tropical rice agroecosystems, early-season detrital subsidies pave the way for natural spider control of planthoppers. Before crop pests become abundant, spiders subsist on detritus- and plankton-feeding insects as alternative prey, decoupling these predators from a strict diet of herbivorous insects and providing the “head start” needed to effectively suppress pests later in the season (Settle *et al.* 1996). Other local subsidies similar in function to detritus include hemipterans whose sugary honeydew subsidizes omnivorous hymenopterans. In New Zealand beech forests, the honeydew generated by endemic scale insects fuels population growth of invasive *Vespula* wasps, with ~10 000 wasps per hectare (Beggs 2001). As a direct result of this abundant and readily available carbohydrate source: “the predation rate of wasps on some invertebrate prey species is so high that the probability of an individual surviving through the wasp season is virtually nil” (p. 17). Analogous results have been found with honeydew-producing aphids and invasive ants in terrestrial arthropod food webs (Kaplan and Eubanks 2005, Styrsky and Eubanks 2007).

Applications

Choosing plants to encourage trophic cascades

Because plant attributes necessarily impact predator and parasitoid survival, as well as their capacity to locate, capture and consume prey, the application of multitrophic interactions in agriculture entails selecting plants that maximize biocontrol of pests (Bottrell *et al.* 1998, Cortesero *et al.* 2000). This practice amounts to targeting specific traits of interest (Section 13.2 of this chapter), and measuring the strength of enemy-mediated cascades on crop yield when that trait is expressed (Section 13.3 of this chapter). Thus, manipulating plant–herbivore–enemy dynamics for biologically based management of crop pests is largely a conceptual synthesis of what we have discussed up until this point.

One of the central tenets of integrated pest management (IPM) is that tactics should not counteract or otherwise interfere with one another and, more ideally, the control measures should synergize, resulting in pest suppression that is greater than the sum of the two approaches. Host-plant resistance and biological control are two of the best non-chemical weapons at a farmer's disposal and the success of either of these tactics depends on the degree to which predators and parasitoids are compatible with resistant crop cultivars (Bergman and Tingey 1979, Campbell and Duffey 1979, Boethel and Eikenbary 1986). Although this concern originated with traditional plant breeding programs, the recent and widespread deployment of transgenic crops expressing the *Bt* endotoxin (e.g., corn, cotton) has led to similar concerns for non-target effects on higher trophic levels (Obrycki *et al.* 2001, Groot and Dicke 2002, Poppy and Sutherland 2004).

From a theoretical standpoint, it can be difficult to predict the outcome of interactions between crop resistance and biocontrol. As we learned earlier in the chapter, herbivores tend to move more and develop slower on resistant host plants, both of which are thought to increase susceptibility to attack. On the other hand, herbivores sequester secondary chemicals on toxic plants and resistance traits can impede enemy foraging in the case of surface features such as trichomes. Because of the offsetting nature of these mechanisms, the outcome in any given system will depend on the key resistance traits implicated. In tomato, for example, breeding efforts to disrupt herbivores have focused on the introgression of genes coding for glandular trichomes from wild *Solanum* sp. to cultivated varieties, resulting in plants that disrupt predation and parasitism (Kennedy 2003). In a review of 61 published studies, Hare (2002) concluded that resistant crop cultivars interfered with parasitism in 37% of cases, enhanced parasitism in 10% of cases and additive effects occurred in the remaining 53% of cases. Resistant crops were less likely to deter predation (18% of cases), and more likely to synergize pest consumption by predaceous arthropods (23% of cases); additive effects occurred at a similar frequency with predators (59%) as with parasitoids. Compared with the above studies that used crop varieties bred for resistance, transgenic crops are less likely to disrupt biocontrol efforts owing to their greater level of specificity in expressed traits (Hare 2002, Romeis *et al.* 2006).

Even if crop cultivars are in fact compatible with biocontrol, predation and parasitism may still have minimal impact on pest abundance under field conditions. Often this lack of an effect can be directly attributed to the absence of key factors (e.g., food, shelter) in the landscape. Agroecosystems are characterized by low-diversity habitats in which crops tend to be cultivated in barren monocultures and lack the alternative resources to maintain stable enemy populations. Based on his observations of enemy proliferation in environments with flowering plants, Wolcott (1942) was one of the early voices to emphasize the need to consider resources aside from prey alone, a sentiment that has since been echoed under the umbrella of **conservation biological control** (Barbosa 1998, Pickett and Bugg 1998, Lewis *et al.* 1998, Wäckers *et al.* 2005). Thus, subsidizing enemy diets with nutritional rewards is the other main driver in the application of multitrophic interactions for pest management. Such rewards are typically delivered by enhancing vegetational diversity in the landscape. This can be accomplished through selective planting of border or companion crops, cover crops, intercropping or simply tolerating weed presence in the field or along field margins (Root 1973, Andow 1991, Landis *et al.* 2000). Alternatively, habitat management might be directed towards buffering the abiotic environment for natural enemies; as entomopathogenic nematodes are highly sensitive to high temperatures and low moisture in soils (Figure 13.11), intensive, conventional agricultural practices are often incompatible with conservation of these potent natural enemies of root herbivores (Stuart *et al.* 2006).

While augmenting habitat diversity can benefit enemies in several respects (e.g., more favorable microclimate, access to alternative prey), the most widely cited mechanism involves floral feeding by parasitoid wasps. The major premises of what has been termed the "parasitoid nectar provision hypothesis" are that: (a) parasitoids in the field are generally sugar limited; (b) crop fields are devoid of natural sugar sources and (c) accessibility to floral nectar increases parasitoid longevity, fecundity and/or energetic state, leading to greater pest suppression (Heimpel and Jervis 2005). An abundance of evidence from lab studies demonstrates that access to floral nectar dramatically enhances parasitoid performance, but the mechanistic link between nectar and pest suppression in the field has remained far more elusive. Recent methodological advancements (e.g., chromatographic techniques) for detecting sugars in field-caught wasps have allowed researchers to determine whether wasps increase nectar consumption in experiments where floral strips are added. For applied purposes, however, the ultimate measure of success is whether floral borders lead to lower pest densities. Heimpel and Jervis (2005) reviewed field studies testing this hypothesis and in 7 of 20 cases floral additions increased parasitism of the focal pest, but in only one case did this result in a corresponding decline in pest abundance. In spite of its logical appeal, current evidence surrounding the parasitoid nectar-provision hypothesis remains equivocal, limiting its impact as a reliable habitat manipulation tool for pest managers.

Another means for subsidizing biocontrol agents with nutritional rewards involves cultivating crop varieties that produce the reward themselves. The ancestral form of several key food and fiber crops (e.g., beans, cotton, peach) bear extrafloral nectaries. This offers a distinct advantage in that the resource subsidy occurs on the plant needing protection, unlike floral strips that require enemies to move from flower to crop. Indeed, this has been one of the main criticisms, and perhaps the Achilles' heel, of floral supplements – they are often highly effective within several meters of the floral border, but their efficacy wanes exponentially with distance resulting in a distinct edge effect (Tylianakis *et al.* 2004). Evidence for the biocontrol benefits of extrafloral nectary-bearing crops is substantial in systems where they have been studied. In peach, for instance, most cultivated varieties possess extrafloral nectaries, although recent trends in fruit breeding programs have led to the loss of this trait from some modern cultivars. This prompted Mathews and colleagues (2007) to investigate the consequences of variable nectary expression on a

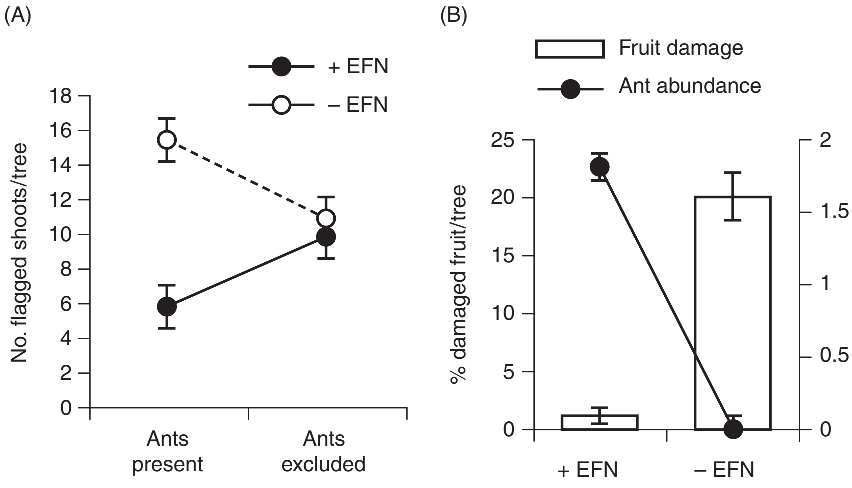


Figure 13.13 Consequences of variable extrafloral nectary (EFN) expression on the attack of peach trees by a key insect pest (A) in the presence and absence of predaceous ants, and (B) the impact of ant recruitment to peach EFNs for crop damage. Flagged shoots are simply those displaying visual evidence of insect pest damage. From Mathews *et al.* (2007).

key peach pest, the oriental fruit moth *Grapholita molesta*. The data in Figure 13.13A demonstrate that extrafloral nectary presence reduced larval infestations of this fruit pest by >50%, and these benefits disappear entirely when predaceous ants are experimentally excluded from trees. In fact, ants exclusively forage on nectary-bearing peach cultivars, resulting in a 95% reduction in pest damage (Figure 13.13B). Parasitism rates were also higher on extrafloral nectary trees and likely contributed to this pattern. Analogous results have been found with cotton varieties (Lingren and Lukefahr 1977, Adjei-Maafo and Wilson 1983, Treacy *et al.* 1987).

The final component of applied multitrophic interactions that we only briefly mention here includes plant-derived attractants to reduce emigration and encourage immigration of enemies. This strategy implicitly assumes that enemies evolved to exploit herbivore-induced plant volatiles, and therefore if we mimic or overexpress these volatile responses in crops then we stand to improve biocontrol of pests (Turlings and Ton 2006). In other words, how can we make the odor of crops “smell” more attractive to predators and parasitoids? Although this realm of research remains in its infancy, preliminary work has been rather encouraging. The goal of enemy attraction and retention can be accomplished using several techniques including synthetically produced and deployed VOCs (Yu *et al.* 2008), spraying crops with phytohormonal defense elicitors such as jasmonic acid (Stout *et al.* 2002), or genetically engineering crops with constitutively enhanced terpene emission (Degenhardt *et al.* 2003, Kappers *et al.* 2005). Most notably, a recent study genetically transformed corn to continuously emit the entomopathogenic nematode-attracting volatile (*E*)-β-caryophyllene from its roots (see Figure 13.4). These plants were far less vulnerable to a key pest (corn rootworm, *Diabrotica virgifera*) in the field because of intense nematode-inflicted mortality compared with untransformed corn lines (Degenhardt *et al.* 2009).

Summary

Plants are intrinsically linked with insect herbivores and their enemies in complex webs that entail direct and indirect interaction pathways. As we have outlined in the chapter above, these interactions often propagate from the base of the food web, with various plant traits (i.e., volatiles, trichomes, domatia, toxins) altering the outcome of predator–prey and parasitoid–host interactions, in some cases enhancing the impact of these enemies, but in others detracting from it. Price and colleagues (1980) highlighted the significance of actively studying plant heterogeneity in tritrophic interactions, and 30 years hence a rich literature on plant–herbivore-enemy dynamics has emerged. We have learned (and continue to learn) about the herbivore-induced mechanisms that shape traits and the phytohormones that underlie such plant responses. These inducible mechanisms continue to unfold as entomologists and ecologists increasingly collaborate across traditional disciplinary boundaries with plant and molecular biologists. This is especially exciting in light of the burgeoning transgenic era that now allows us to amplify the expression of specific plant structures or compounds and observe the outcome when exposed to insects. Apparent from existing studies is that plants represent a ubiquitous and omnipotent force that pervades all plant–insect communities. Our challenge for the future is to elucidate the contribution of key traits across systems and incorporate the inherent diversity of plant phenotypes.

As the review of Price and colleagues (1980) encouraged a generation of insect ecologists to incorporate a bottom-up template in higher-trophic-level interactions, so too did Hairston, Smith and Slobodkin (1960) in provoking the scientific community to consider their top-down perspective on population control. This is the 50th anniversary of the green-world hypothesis and our current understanding of trophic cascades has progressed, to say the least. Although ecologists in a broad sense are still grappling with the triggers and controls that determine the magnitude of cascades in terrestrial arthropod communities (Schmitz *et al*. 2000, Halaj and Wise 2001, Mooney *et al*. 2010), we now can move beyond case studies to make clear hypotheses and more definitive, quantitative predictions from an ever-accumulating body of evidence from field manipulations of top and intermediate predators. As shown by the virtual absence of studies involving parasitoids and pathogens, however, the current literature base is heavily biased across taxa and much remains to be learned from these under-represented groups. The late Gary Polis, among others, dramatically enhanced our knowledge of the factors affecting cascade strength, such as resource subsidies and food web complexity. Moreover, our perspective on these issues has broadened to include non-consumptive predator effects and cascades on plant community diversity and ecosystem function. While such top-down cascades have obvious implications for our basic understanding of food webs, their understanding is also paramount to effectively integrating biocontrol in agriculture and predicting the consequences of global change for plant and insect assemblages.

Questions and discussion topics

1 Given the large number of plant traits that affect the outcome of enemy–prey interactions, can you think of combinations of two or more traits that would be most likely to synergize with one another, resulting in "indirect defense syndromes"?

2 Herbivorous insects are notorious for surmounting plant defenses. If you were engineering a plant to minimize herbivory, would you invest more resources in direct resistance traits (e.g., toxins) or indirect defenses that enhance enemy impact (e.g., extrafloral nectaries)? How would your decision affect the rate at which herbivores counter these strategies over evolutionary time? Discuss the costs and benefits of investing in a direct vs. indirect plant defense system.

3 Many of the plant traits that we discussed in this chapter are expressed constitutively, but are induced to far higher levels when herbivores begin feeding. Aside from allocation costs, why would a plant only emit herbivore-specific volatiles upon attack? Do you think that predators and parasitoids would continue to be attracted to induced volatiles if they were expressed all the time, even when herbivores were not present on the plant, or would they eventually learn to ignore these signals? How long do you think this process would take? Would it differ among classes of enemies (i.e., predators vs. parasitoids, generalists vs. specialists)?

4 Based on what you know of current trends in biodiversity loss resulting from global climate change, invasive species and habitat degradation, among other threats, what are the implications for trophic interactions in plant–insect food webs? Are trophic cascades in the year 2100 and beyond likely to be weaker, stronger, or no different from the present day?

5 If you had the option of introducing a single, specialist biocontrol agent of an invasive crop pest vs. conserving a suite of generalist predators, with the ultimate goal of minimizing crop damage, which approach would you take and why?

Further reading

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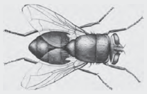


Part VI **Broad patterns in nature**

CONTENTS

This book concludes with discussions on the broadest biological patterns we can observe on this Earth, and the reasons for their existence. We also examine smaller scales of variation that would be seen on the landscape and ecosystem levels. In doing so we pick up various topics discussed in previous chapters, such as the roles of time and space as influences on species richness, and expand this view to the global level, showing that the same factors remain important as we scale up our perspective to interactions on Earth. We also look at the paleobiological record again, as we did in Chapter 1 to note the long evolutionary history of insects, but in this section we examine the record for clues on what might be expected as global changes occur, and if predictions are possible.

It is interesting to note that ecologists have debated some issues in this section over the long term, almost since the dawn of our field, with many hypotheses developed to account for the gradient of increasing diversity into the tropics, as an example. These hypotheses depend on many subjects treated in earlier sections, such as the roles of competition and predation. But it is heartening to realize that from all this debate a synthesis is emerging, which we cover in Chapter 14. When we realize that species–area curves were first described in the mid-1800s we gain an insight on how slowly ecology has progressed in some areas. The bigger the pattern, perhaps, the harder it is to determine the mechanisms responsible?

However, pattern detection has accelerated in some areas of ecology as change over the globe accelerates, a subject we introduce in Chapter 15. Insects have emerged as excellent indicators of global change, leaving a fingerprint with their shifting phenology and geography, indicating a warming trend in many parts of the world. Warming also promotes drought, increased plant stress and susceptibility to insect attack and fire. Ecosystem processes become an important focus of attention. Spatial relationships also continue as a theme in this book, as fragmentation of landscapes increases, as invasions proceed across and among continents, and as conservation designs employ landscape-scale planning.

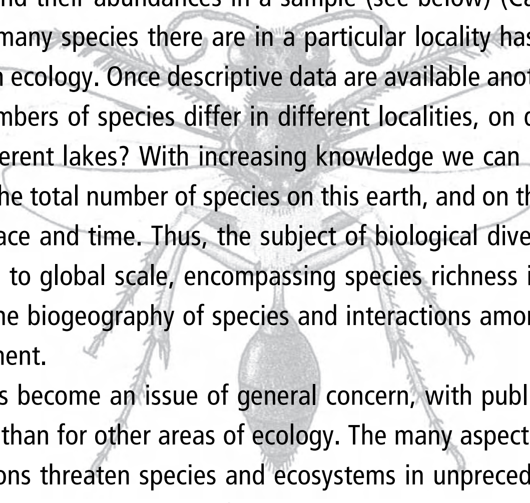
As the challenges of global change increase, ecology will broaden its horizons to understand the implications of change, and to develop management strategies to accommodate change. The opportunities for creative research expand as our perspective broadens to the global scale, so this section of the book completes the trend of increasing focus from individuals, to their interactions and then to populations, communities, ecosystems, and the world.

14

Biological diversity

Biological diversity, or biodiversity, is the number and variety of species and other taxa in any locality, ecosystem, region or the biosphere. The commonest measure of biodiversity is the number of species present in the area of interest. Species number, species richness and species diversity are used almost interchangeably in the ecological literature, although diversity may be employed when considering both the species number and their abundances in a sample (see below) (Calow 1998, 1999).

Learning how many species there are in a particular locality has formed a major basis of enquiry in ecology. Once descriptive data are available another basic question becomes why numbers of species differ in different localities, on different plant species, or in different lakes? With increasing knowledge we can begin to ask questions about the total number of species on this earth, and on the patterns of their distribution in space and time. Thus, the subject of biological diversity reaches the local, to regional, to global scale, encompassing species richness in component communities to the biogeography of species and interactions among species and the physical environment.



Biodiversity has become an issue of general concern, with public awareness greater, perhaps, than for other areas of ecology. The many aspects of human impact on global conditions threaten species and ecosystems in unprecedented ways, with the consequent predictions on rates of species extinction estimated to reach proportions unrivaled in the geological record (Wilson 1988a,b). Therefore, efforts to thwart loss of species are gaining momentum. Conservation of habitats and ecosystems to preserve plants and animal species are increasing.

The problem with protecting insects and other invertebrates is that we hardly know how many species there are locally, or globally, except for a small number of taxa of popular interest: butterflies and dragonflies in particular. We discussed estimated total numbers of insect species in Chapter 1 (Figure 1.2), with perhaps only 10–20% of species named, and with new species being discovered frequently. Also, in Chapter 12 on community structure, the numbers of species in component communities were compared: on bracken fern, on soybean, numbers colonizing defaunated islands, leaf miners on oak trees and in Santa Rosa National Park, and their parasitoids, herbivores on cottonwoods, and trees in Britain and Hawaii. From these studies we know a considerable amount about influences on component community size. So it is appropriate now, in this chapter, to examine larger dimensions of species richness, at the within-habitat, among-habitats and regional-habitats scales. We emphasize the detection of pattern, looking for gradual changes in species diversity over environmental gradients, such as island size and distance from a source of colonists, and latitudinal, altitudinal, time and disturbance gradients. Ultimately we discuss how detection of patterns over the landscape aids in the development of nature reserves and the conservation of biodiversity.

14.1 Scales of biodiversity

In ecological studies it is convenient to recognize a gradient or transect of increasing inclusiveness in the study of species richness, for example while walking from a point across country to the edge of the region of interest. Insect communities can be sampled at the starting point, in the soil or on a plant species or on the whole plant community. This samples the **local community diversity**, which recognizes niche difference among species in their ways of dividing up resources within one habitat (named alpha diversity by Whittaker 1970). Progressing along the transect we encounter additional habitats with additional species, each adapted to specific attributes of the environment. The scale of sampling has increased to **among habitat diversity**, which increases as we pass through more and more habitats (named beta diversity by Whittaker 1970). Finally, we reach the edge of our region of interest, which may be a remnant of tall grass prairie, a county boundary, shores of an island, an international boundary or the limit of a biogeographical realm, such as the Neotropical Realm. The full number of species along the transect can be called **regional diversity** (or gamma diversity). Of course, transects in all directions would be needed to record species for the whole area of the region of interest. Rosenzweig (1995) avoided use of the terms alpha, beta and gamma diversity because alternative names provide more intuitive appreciation of the scales being considered. The next concern becomes how to estimate these diversities.

14.2 Sampling species density

Sampling generally includes both the number of species per sample and the number of individuals per species per sample. Hence the term **species density** captures two important components of a community or locality, the number of species per unit area and the population density of each species. A sample unit may be a quadrant, or an individual plant, with the inevitable question of how many to sample.

The ideal answer is to sample exhaustively until no new species are found. Practically, this is possible in temperate herbivore communities or many aquatic

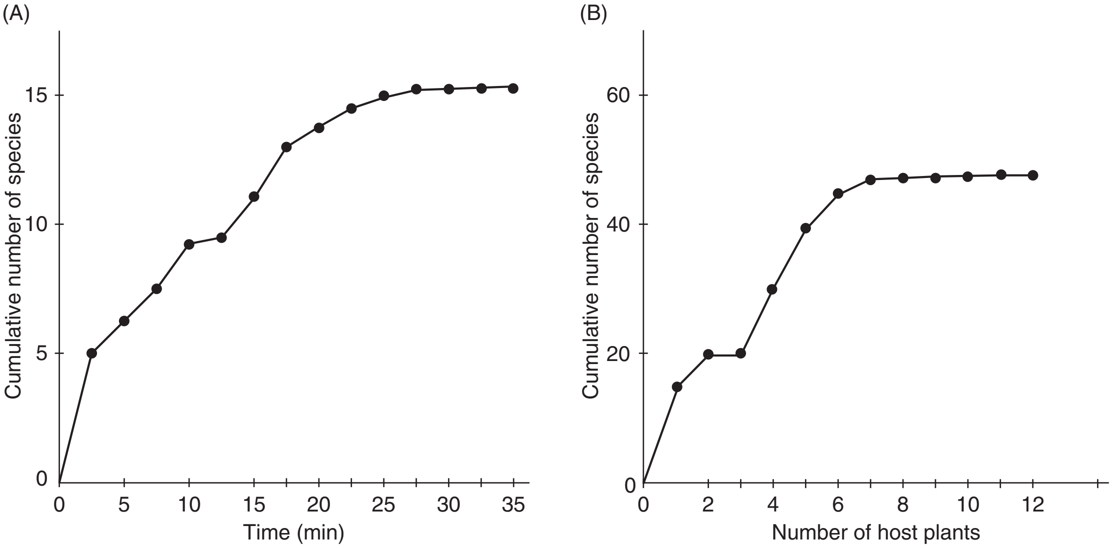


Figure 14.1 Results from sampling herbivores on host plants to determine when sampling is adequate to achieve an asymptotic cumulative number of species. (A) On an individual plant in a timed sample. (B) in a component community to find the number of plants needed to reach an asymptotic number of species.

systems, but in the tropics the species richness may appear to be almost infinite, considering the resources of time and energy available for sampling. While the aspirations to sample the complete community are the same, the methods may diverge, as we discuss below.

14.2.1 Temperate communities

Taking a typical temperate community of herbivores on a particular plant species, we would first like to know how much to sample an individual plant. A timed direct visual census often works well because it is non-destructive, interactions can be observed and early stages in the life cycles, such as eggs and first instar larvae, can be observed. Many other methods are provided in sampling manuals (e.g. Hayek and Buzas 1997, Krebs 1999, Southwood and Henderson 2000, Hill *et al.* 2005). Then timing the discovery of each new species yields a cumulative increase in total species recorded until an asymptote is reached: no new species remain to be discovered on that plant (Figure 14.1). Several such samples provide an estimate of the mean sampling time required per plant. Numbers of individuals per species can be recorded simultaneously. Once the required time to sample an individual plant is determined, which will take perhaps a few minutes to half an hour depending on plant size, the number of plants needed to sample the whole community should be estimated. Again, plants are added to the sample until an asymptote of species richness is achieved (Figure 14.1). Usually 15–30 plants are adequate. This kind of **species accumulation curve** can be used in many ways, such as in comparisons of richness on different plant species, on latitudinal or altitudinal gradients, at different times of the year or at various stages in ecological succession.

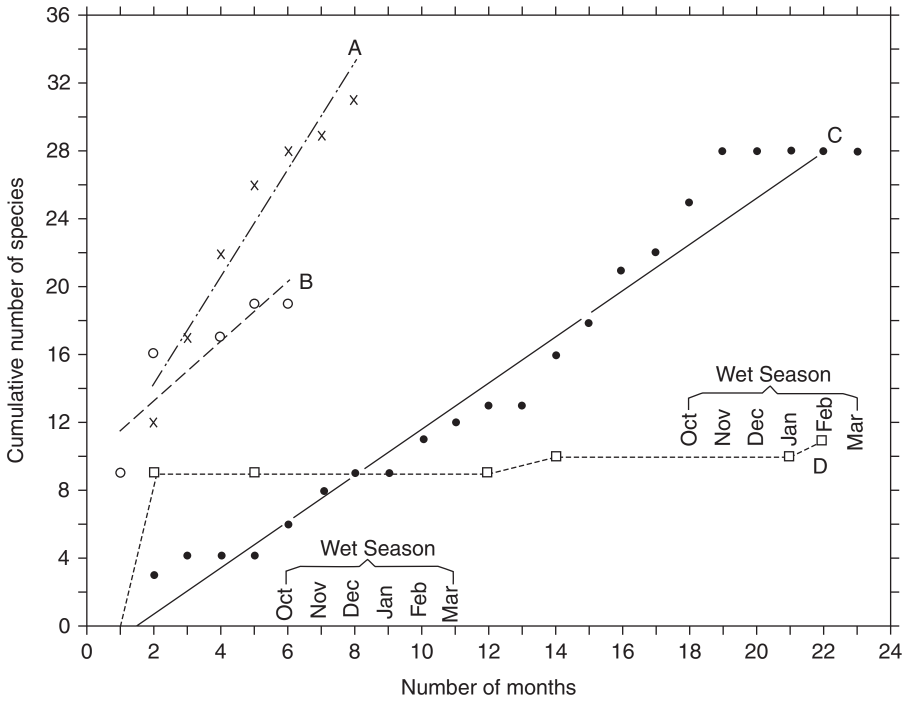


Figure 14.2 Samples of lepidopteran herbivores on host plants in tropical and temperate latitudes. A: Sampling of morphospecies on *Erythroxylum* host plants in cerrado vegetation near Brasilia, Brazil (16° S) for the period June–December (data points x) B: Similar samples, May–October (data points o). C: Specimens reared and identified to genus or species in the same area as in A and B, with sampling lasting for almost 2 years. Note in samples A, B and C, no asymptotic number of species was reached, except perhaps in the last months of sampling in C. D: For comparison, temperate sampling (35° N) of lepidopterans on legume species shows rapid development of an asymptotic number of species. From Price *et al.* 1995.

14.2.2 Tropical communities

Similar methods may work well in the tropics if the scale of study is small, for example on a single plant species such as a herb or a shrub. But even at this scale sampling may yield a non-asymptotic accumulation of species (Figure 14.2). We would also like to know the richness of species in various taxa on a larger scale, such as the number of species in a nature reserve, a national park or a vegetation type. As samples accumulate over time a species accumulation curve develops, but it is likely to be incomplete, particularly in the tropics. For comparative reasons, for conservation purposes and for an appreciation of the full biodiversity of a taxon in an area, an estimated asymptotic number of species is desirable. This requires extrapolation from the known data to achieve predictions of the actual species number present. Such estimation of biodiversity has become a major focus in species-rich communities such as in the La Selva Biological Station studies in Costa Rica, and in Bolivia (Coddington *et al.* 1991, Colwell and Coddington 1994, Mao and Colwell 2005, Mao *et al.* 2005). The methods employed are diverse (e.g., Gotelli and Colwell 2001, Longino *et al.* 2002), and beyond the scope of this book, but the results will enable the evaluation of species loss through time resulting from change of various factors affecting biodiversity.

14.3 Importance of pattern detection

The study of biological diversity probably provides the best opportunity for discovering broad patterns in nature. So it is worth emphasizing again that finding broad, repeatable patterns in ecology is the basis for the development of theory (see Chapter 1). Such patterns do not occur by chance, or they would not be repeated in nature. Therefore, there must be certain processes that result in the patterns, making the mechanistic explanation of patterns tangible, accessible and the foundation of ecological theory.

There should be no surprise, then, that patterns relating to species abundance have contributed importantly to the development of ecology. Early discoveries of patterns related to species diversity on latitudinal gradients, and ecological succession (Table 14.1). Then came studies relating body size to abundance and geographic range, and latitudinal gradients in plant defenses and herbivore damage (Table 14.1). Altitudinal patterns in diversity have also been detected. As Lawton (1999, p. 177) pointed out, when “large sets of species over large spatial scales, or over long time periods” are studied, patterns can be detected with relative ease, and the possible hypotheses to explain such patterns are limited to a few, which are often easy to test. We have entered into the realm of **macroecology**, defined by Brown (1995, p. 10) as “a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution, and diversity.” Relatively large spatial and temporal scales are involved.

Indeed, whenever ecological gradients are studied, the power of the results depends very much on the length of the gradient. We like to include extremes in our comparisons because it makes the trends stronger, the patterns easier to detect, and therefore the mechanistic explanation more likely to be discovered. Also, the longer the gradient and the more comprehensive the study, the more general the emerging theory will be. The creation of broad, general theory should be the preoccupation of ecologists. “To discover general patterns, laws and rules of nature, ecology may need to pay less attention to the ‘middle ground’ of community ecology, relying less on reductionism and experimental manipulation, but increasing research efforts into macroecology.” (Lawton 1999, p. 177).

14.4 Gradients of island size and remoteness

One would be correct if intuition suggested that larger islands would support more species than smaller islands. This appears to be obvious and elementary, but which processes are involved? We saw in Chapter 12 on community structure that defaunated islands were colonized again, tending to reach the before-treatment number of species present (Figure 12.13). But an interesting feature emerging from the census data illustrated a rapid turnover of species, perhaps as high as one species per day (Simberloff 1978). Therefore, the equilibrium number of species on an island must be maintained by a balance of colonization and extinction.

14.4.1 Theory of island biogeography

The empirical result had been anticipated by MacArthur and Wilson (1963, 1967) in their **theory of island biogeography**, which examined the relationships among species number per island, the size of the island, and the distance of the island from the mainland source of colonists. They argued that the rate of colonization of species from the mainland location would not be constant, but would decline as fewer immigrants belonged to new species. Rapidly dispersing species would result in a high immigration rate initially, with slower dispersers reducing the rate gradually, producing a concave **immigration curve** (Figure 14.3). The immigration rate reaches zero at point *P* when all species from the mainland have colonized.

Table 14.1 **Examples of studies on broad patterns in nature**

Kinds of relationships	Kinds of species	References
Latitudinal gradients and species diversity	Beetles	Clarke 1954
	Ants	Fischer 1960
	Dragonflies	Williams 1964
Time gradients – ecological succession	General	Odum 1969
	Plants	Whittaker 1970
	Plants, insect herbivores and carnivores	Price 1991b. See Table 14.6
Body size, abundance and geographic range	Moths, aphids, etc.	Gaston 1988, Gaston and Lawton 1988, Lawton 1991
Latitudinal gradients in chemical defenses	Plants	Coley and Aide 1991, Dyer and Coley 2002 and refs. therein
Latitudinal gradients in herbivore damage to plants	Herbivores	Coley and Aide 1991, Dyer and Coley 2002
Altitudinal gradients	Vegetation	Merriam 1894, 1898, Holdridge 1947, 1967
	Gall-inducing insects	Fernandes and Price 1988, 1991, 1992
	Ferns	Cardelús *et al.* 2006
Area gradients	Insects on plants	See Table 14.2
Phylogenetic patterns in time	Insects	Grimaldi and Engel 2005

Another process will work simultaneously with immigration – species extinction. This will be zero to begin with, when no species have colonized, and will increase as colonist species number increases (Figure 14.3). The prediction was that the **extinction rate** would increase exponentially as the number of species present increased because the chance of extinction would increase, competition between species would become stronger and natural enemies might colonize and cause mortality. Both competition and natural enemies may reduce population sizes per species, increasing the probability of extinction.

At the intersection of the rate curves for immigration and extinction, the processes would be balanced, with equal rates setting an **equilibrium number of species**, $\hat{s}$, on an island.

This equilibrium number of species varied among islands according to their size, when animals easier to census than insects were observed, such as birds (Figure 14.4). Larger islands supported more bird species than smaller islands, forming a linear array of species number per island on a log–log plot. All these islands, from New Guinea, to the Philippines, to the Sunda Islands, to Christmas Island, were grouped

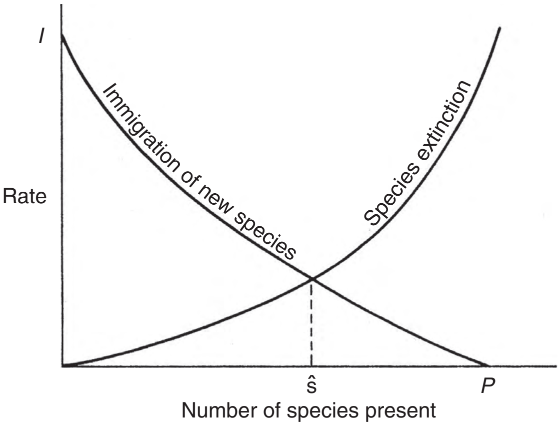


Figure 14.3 The relationship between immigration and extinction rates of species on an island. The balance between the two processes results in an equilibrium number of species, $\hat{s}$, on the island. *I* is the initial immigration rate of species, and *P* is the total number of species in the source of colonists – the mainland. From MacArthur and Wilson 1967.

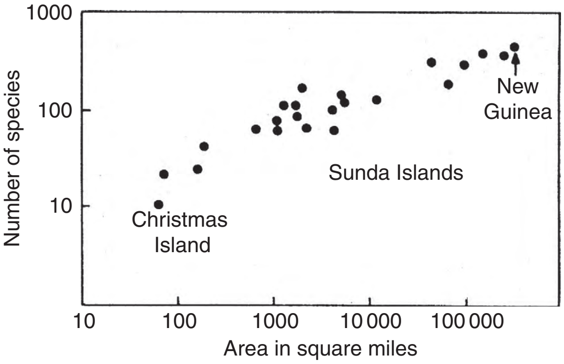


Figure 14.4 The relationship between island area (log scale) and the number of bird species (log scale) in the Sunda Island group, the Philippine Islands and New Guinea. The islands are relatively closely grouped and close to the Asian continent, so they illustrate a strong island-area effect on the equilibrium number of species present. From MacArthur and Wilson 1967.

close together and close to the Asian continent, so distance from the mainland from which colonists could migrate had little influence on the equilibrium number of species present.

However, moving further into the vast Pacific Ocean, remote islands in the Moluccas, Melanesia and Oceania, in the central and south Pacific, supported fewer birds than predicted by their size alone (Figure 14.5). Evidently, distance from the source of colonists, or mainland, imposed a lower equilibrial number of species. Thus, both island size and distance from the mainland needed to be incorporated into the theory of island biogeography.

MacArthur and Wilson reasoned that rates of immigration would be higher on relatively near islands than on relatively far islands. Also, species extinction would be higher on small islands compared to large islands (Figure 14.6). When these processes were balanced, equilibrium numbers of species would be relatively high on near, large islands, $\hat{s}''$, and relatively low on far, small islands, $\hat{s}'$. Nearer islands would receive more colonists per unit of time than further islands, resulting in an

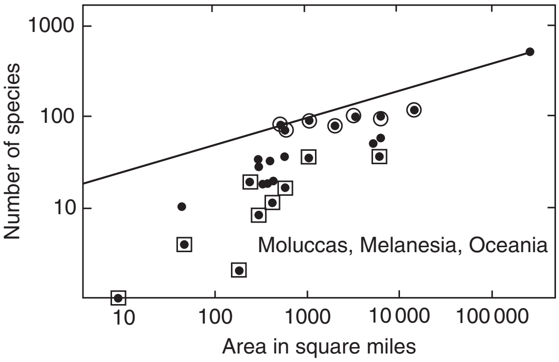


Figure 14.5 The relationship between island area (log scale) and the number of bird species (log scale) in the Moluccas, Melanesia, Micronesia and Polynesia. The regression line is derived from the Sunda Island group in Figure 14.4, with New Guinea at the end of the line. Circled islands are less than 500 miles from New Guinea, with an equilibrium number of species close to that predicted by the regression line. Squared islands are over 2000 miles from New Guinea, in which the equilibrium number of species drops significantly below the expected species richness based on the area alone. Hence, distance of islands from a mainland source of colonists has a strong effect on the equilibrium number of species. From MacArthur and Wilson 1967.

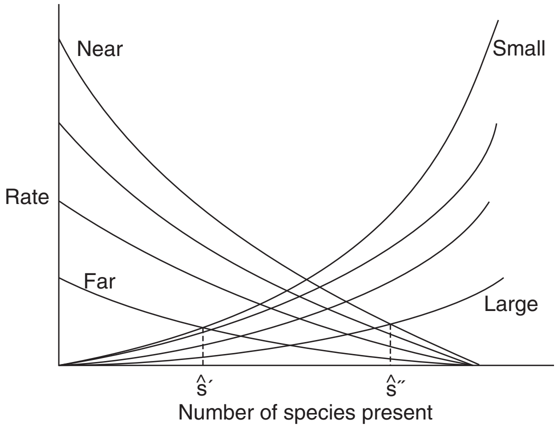


Figure 14.6 The effects of island size and remoteness from the source of colonists on the equilibrium number of species on an island. Near, large islands support more species, $\hat{s}''$, than small, far islands, $\hat{s}'$. From MacArthur and Wilson 1967.

equilibrium number closer to *P*, the number of species in the source area. Larger islands would provide a higher carrying capacity for each species, resulting in the potential for higher populations and lower extinction. Larger islands would also be likely to provide a greater diversity of habitats, which would allow an enriched flora and fauna, and potentially more places in which species can live relatively free of competition.

This theory and the empirical evidence, which examines patterns in biological diversity on gradients of island size and remoteness, has prompted a major research impetus in ecology, and is an important tool for examining patterns in nature. The theory can be applied to ecological islands on continents, such as high-altitude floras and faunas on "archipelagoes" of isolated mountain tops (e.g., Brown 1971), and plant species as islands to be colonized by herbivorous insects, as discussed in Chapter 12 (e.g., Figures 12.16, 12.27, 12.28, 12.29). The theory is also relevant to fields in agricultural settings and the management of landscapes, the prediction and planning necessary for conservation, and the design of nature reserves (see discussion in the Applications section of this chapter).

14.4.2 Species–area relationships

The study of gradients of island size has resulted in a large literature covering what is generally referred to as **species–area relationships**. The studies of insect species richness in relation to island size defined by host plant islands of various kinds, and host animals for their parasites, show a wide range of fidelities to the predicted species–area relationship (Table 14.2). Some oceanic islands and mountain tops are also included in the table. The range of $r^2 \times 100$ values, which estimate the percentage variance accounted for by the regression of species number on area of island, almost covers the gamut of possibilities. However, Boecklen and Gotelli's (1984) summary of values for insects went into the range of negative slopes, in which there were fewer species on larger islands than on smaller islands. The list in Table 14.2 includes many kinds of relationships from herbivores on plant islands to mites on mammals, parasitoids on insect herbivores, fungi on trees and herbivores on agricultural crops. There may have been many more studies showing low or no relationship between species number and island size, which have not been published because weak or negative data are not popular with reviewers and editors. However, this attitude in publishing results certainly biases the literature, and our confidence in patterns and theory (see also Connor and McCoy 1979). But the results in Table 14.2 should make it clear that the species–area relationship cannot be taken for granted. In any case, where predictions or planning are based on species–area relationships, their validity must be founded on empirical evidence concerning the group under consideration.

An example of a species–area pattern that could be used successfully in planning or prediction is that of the butterfly faunas of the West Indies (Davies and Smith 1997). The full range of island sizes is sampled, and a log–log plot results in a linear relationship that accounts for 64% of the variance (Figure 14.7). Not only this, but the relationship has been stable for almost 50 years; the original relationship being based

Table 14.2 **Studies on species–area relationships showing a large range in percentage of the variance accounted for ($r^2 \times 100$). Various models were used for regressions (e.g., log–log plot)**

Arthropod taxon	Host island	$r^2 \times 100$	References
Tenebrionidae	Mountain tops	98	Covarrubias and Elgueta 1991
Curculionidae	Mountain tops	96	Covarrubias and Elgueta 1991
Leaf miners	Oaks	90	Opler 1974
Mites	*Peromyscus* spp.	86	Dritschilo *et al.* 1975
Insects	Woody shrubs	85	Lawton and Schröder 1977
Arthropods	*Astragalus sericoleucus*[a]	71–85	Tepedino and Stanton 1976
Cerambycidae	Bahama Islands	73	Browne *et al.* 1993
Cynipids	Oaks in California	72	Cornell and Washburn 1979
Insects	Perennial herbs	71	Lawton and Schröder 1977
Butterflies	West Indian Islands	64	Davies and Smith 1997
Insects	Trees	61	Strong 1974a,b
Insects	Sugarcane[a]	61	Strong *et al.* 1977
Ants	Bahama Islands	61	Morrison 1998
Insects	Annual plants	59	Lawton and Schröder 1977
Macrolepidoptera	Trees and shrubs	57	Neuvonen and Niemelä 1981
Insects	Monocotyledons	51	Lawton and Schröder 1977
Scarabaeinae	Local faunas	51	Lobo and Martin-Piera 1999
Geotrupinae	Local faunas	51	Lobo and Martin-Piera 1999
Insects	Cacao[a]	47	Strong 1974c
Mites	*Microtus* spp.	46	Dritschilo *et al.* 1975
Hemiptera, arboreal	Urban roundabouts	44	Helden and Leather 2004
Aphodiinae	Local faunas	43	Lobo and Martin-Piera 1999
Cynipids	Oaks (Atlantic)	41	Cornell and Washburn 1979
Mites	Cricetid rodents	37	Dritschilo *et al.* 1975
Parasitoids	Umbelliferae	35	Lawton and Price 1979
Agromyzids	Umbelliferae	32	Lawton and Price 1979
Fungi	Trees	28	Strong and Levin 1975

Table 14.2 (*cont.*)

Arthropod taxon	Host island	$r^2 \times 100$	References
Microlepidoptera	Umbelliferae	24	Lawton and Price 1979
Hoverflies	Forest fragments	20	Ouin *et al.* 2006
Delphacidae	Hawaiian Islands	18	Denno 1994b
	+ island age	71	Denno 1994b
Arthropods	*Phlox bryoides*[a]	10–16	Tepedino and Stanton 1976
Gall-forming insects	Pantanal forest patches	11	Julião *et al.* 2004
Leafhoppers	Trees	0.04	Claridge and Wilson 1976, 1978

[a] Studies on area differences within a host species. All others compare area differences among host species

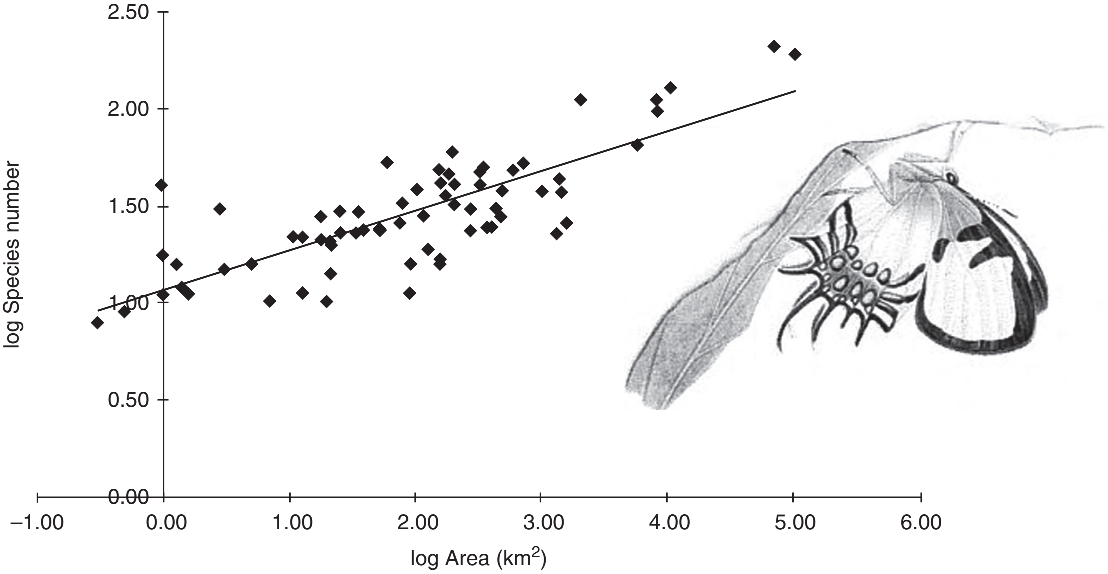


Figure 14.7 The log–log plot of butterfly species number against the area of islands in the West Indies, showing a relatively strong species–area relationship. From Davies and Smith 1997.

on 11 data points (= "islands"), and the current pattern based on 68 islands. The fact that 11 points provided a good prediction for a large set of islands, and that this prediction has been valid for almost 50 years (1948–1997), reinforces the view that species–area relationships can be extremely valuable in basic and applied ecology.

Other studies in Table 14.2 indicate that patch or island size is simply a surrogate for more important biological variables such as the number of plant species available to colonists, or other resources. For example, urban roundabouts in England, around which traffic is routed, are often large enough to support a rich vegetation of trees, shrubs and herbs, with the vegetation on what are islands in the middle of circulating traffic. Given their large range in sizes, from 400 m^2 to 63 680 m^2, which includes nearby parks, the gradient in island sizes is long enough to provide the expectation of significant patterns. Helden and Leather (2004) were not disappointed. The species–area relationship on a log–log plot accounted for 44% of the variance of arboreal hemipteran species richness vs. island area. However, in a multiple regression including island area and number of tree species, area was not significant, and tree species was. In fact the linear regression of number of arboreal hemipteran species vs. number of tree species accounted for 90% of the variance. Number of tree species was a much better predictor of hemipteran richness than area itself. The importance of plant diversity in relation to species richness has also been emphasized in relation to latitudinal gradients in species diversity of insects (see Novotny *et al.* 2006, to be discussed later in this chapter), and in the Chamela-Cuixmala Biosphere reserve in Jalisco, Mexico (Cuevas-Reyes *et al.* 2004). Also, as area sampled increased, genetic marker richness increased, and accounted for 92% of the arthropod species richness on poplar trees in the southwest USA (Bangert *et al.* 2008). The **genetic scaling** was very similar to the species–area relationship, suggesting a strong mechanistic basis for arthropod richness on trees. Genetic scaling is defined as “the expression of genes, that affect plant traits, which in turn affect ecological traits (e.g., community structure) at multiple levels of measurement” (Bangert *et al.* 2008, p. 122).

14.4.3 Mechanisms influencing the species–area relationship

These results bring us to the more general question of the mechanisms driving the species–area relationship. Clearly, plant species richness is an important factor for insect herbivores, which generally increases with island size, but not all species depend so directly on plants, such as dragonflies and soil arthropods. More generally, larger islands will support more habitat types, which are able to support more kinds of species. Rosenzweig (1995) assembled much evidence in support of the **habitat-heterogeneity** or **habitat-diversity hypothesis**, and Stevens (1986) showed for wood-boring insects that this hypothesis was supported: wide-ranging host-plant species covered more habitat types in which more wood-boring communities existed. Also, woodland-patch heterogeneity increased with the area of the patch, and supported more hover fly species (Ouin *et al.* 2006). The habitat heterogeneity hypothesis is well supported in the literature, but alternative explanations need to be considered.

Three hypotheses on the species–area relationship were considered by Connor and McCoy (1979) and Rosenzweig (1995): the habitat heterogeneity hypothesis already discussed, the **area-per-se hypothesis**, and the **sampling hypothesis**. The area-per-se hypothesis invokes a pure effect of island size, as in the theory of island biogeography, which emphasizes the balance of immigration and extinction in relation to island area and distance from the mainland, as in Figure 14.6. The sampling hypothesis acts as a null hypothesis, asserting that larger areas passively receive larger samples than smaller ones, thereby accumulating more species. A contributing factor may well be sampling effort, because larger islands take more time to search for species, increasing the chances of a larger estimated cumulative species number.

The area-per-se hypothesis has been supported experimentally by reducing the area of mangrove islands, with a uniform habitat, with pre- and post-treatment censuses of insect species richness (Simberloff 1976a,b, 1978). Reducing island size would result in non-equilibrium communities – oversaturation – so the prediction was that a new and lower equilibrium would be established when the islands were resampled 7 months later. This

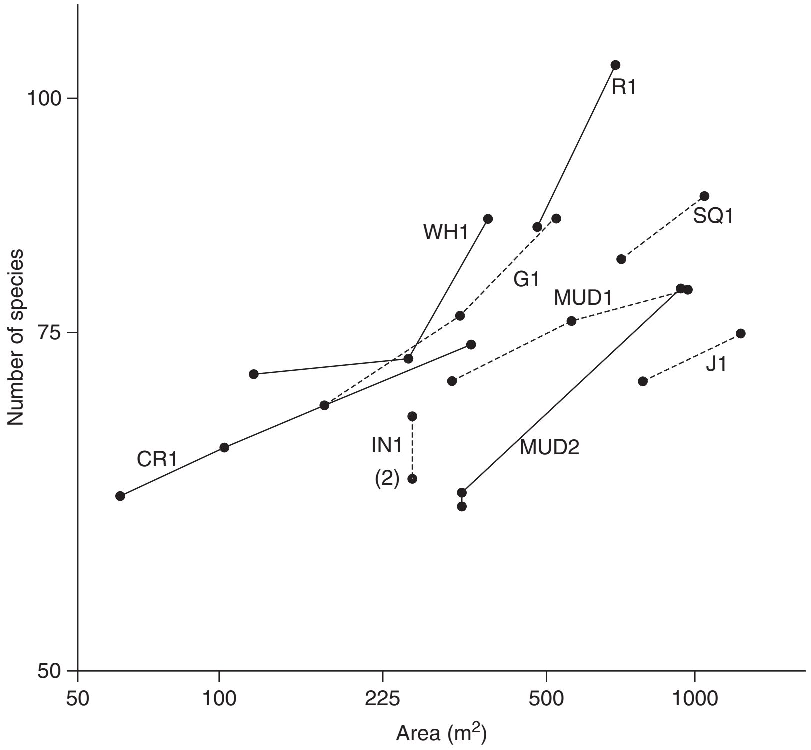


Figure 14.8 Simberloff's (1978) experiment testing the island-size effect on the equilibrium number of arboreal arthropod species on red mangrove islands in Florida Bay, just east of Key West. Islands were reduced in area, except for the control, IN1, with census of arthropods before and after the treatment. Some islands were reduced in area a second time, with three census periods, with island MUD2 acting as a control for the second treatment. From Simberloff 1978.

prediction was affirmed (Figure 14.8). In addition, after the 7-month census, four islands were reduced in area again and censused 1 year later, together with an untreated control island (IN1), and another island (MUD2), which received the original area-reduction treatment, but not the second. Thus, MUD2 acted as a control for the islands with depleted areas at 7 months. The four islands with two area reductions (WH1, G1, CR1 and MUD1) therefore had three census dates, as did MUD2 (Figure 14.8). The control island, IN1, remained the same area and numbers of insect species changed little. Some islands showed strong reductions in species richness and additional reductions with a second decrement in area. The MUD2 control showed a strong reduction in number of insect species after its area was reduced, but richness changed by only one species at the 1-year census when area had not been depleted further.

This experiment supported the area-per-se hypothesis and the theory of island biogeography, but results were not consistent with the habitat heterogeneity hypothesis or the sampling hypothesis. Mangrove islands are remarkably consistent in habitat type, with only one plant species present, and only this species constituting the island at high tide: no soil, mud or other heterogeneity. Therefore habitat diversity was not reduced by reducing island size. The sampling hypothesis could be rejected because the same area on each island was sampled before and after size reduction. The areas to be cut were not sampled. Even though sampling area remained the same, the equilibrium number of species was reduced as island size declined.

Without careful controls, or experiments, to eliminate alternatives, as in the mangrove island example, the three hypotheses on species–area relationships may all remain as viable hypotheses which contribute to the patterns discovered (Connor and McCoy 1979).

Rosenzweig (1995, p. 263) noted that "The theory of island biogeography sparked a revolution in ecology." Whereas scientists assumed that islands were colonized accidentally and passively, the theory invoked a highly dynamic and predictable process. Communities, they argued, were in a dynamic equilibrium, which promoted many investigations on the mechanisms involved. Shortly after the theory was published, Janzen (1968) pointed out that host plants acted as islands for herbivores in evolutionary and contemporary time, and the flurry of research resulting can be seen in the many papers published in the 1970s listed in Table 14.2.

After all that has been written about ecological niches, partitioning of niches, competition, community organization and interactions involved in island biogeography, it may seem counterintuitive to argue that all species are equivalent, ecologically speaking, and that they drift over the landscape in a random way. The landscape has a metapopulation structure, with ecologically equivalent species colonizing, dispersing and going extinct in each local community. Communities experience **ecological drift**, with population sizes changing at random, eventually going extinct, equivalent to the process of genetic drift, but with species involved, not genes. A dynamic process of speciation, dispersal and extinction prevails over the metacommunity landscape. This is the gist of the **neutral theory of biodiversity and biogeography** proposed by Hubbell (2001, 2005, 2006), after studying tropical forest dynamics for over two decades on Barro Colorado Island, Panama.

The remarkable achievement of this hypothesis is that it predicts well many of the patterns observed empirically in communities, including the species–area relationship. This provides both a benefit and a problem: the benefit is that a null model erects the simplest possible hypothesis against which to compare empirical data, and the problem is how to determine the processes involved when the predictions of niche models and neutral models are so similar. Which model accounts best for the patterns observed in nature?

The neutral theory of biodiversity and biogeography has generated much interest and debate (e.g., the special feature on neutral community ecology in the journal *Ecology*: Holyoak *et al.* 2006, May *et al.* 2007). One test of the neutral theory involves estimating ecological drift rates using speciation and extinction rates of known taxa, and comparing these with predictions from the theory. Turnover rates in communities were much faster in reality than in the theory in one test (Ricklefs 2006), and turnovers of species on defaunated islands studied by Simberloff (1976a, 1978) were extremely rapid, both studies indicating ecological factors working faster than speciation and drift. Of course, the dynamics of a community depends on life spans, mobility and age structure. Hubbell measured all trees with a stem diameter of over 1 cm in an area of 50 hectares, meaning that plants were established, and the much higher turnovers in smaller size/age classes were not recorded. In Ricklefs' (2006) study, birds are obviously more mobile and communities more dynamic than long-lived tropical trees, and the insect communities in the Florida Keys are even more changeable because of species with short generation times and high mobility. In spite of such reservations, an integration of neutral and niche models may be possible with the potential for improving our understanding of nature (e.g., Holyoak and Loreau 2006, Liebhold and McPeek 2006).

14.5 Latitudinal gradients

All the early explorer-naturalists were impressed with tropical richness and diversity (Lewinsohn *et al.* 1991a). Comparisons of species number along latitudinal gradients, digesting the spectacle of

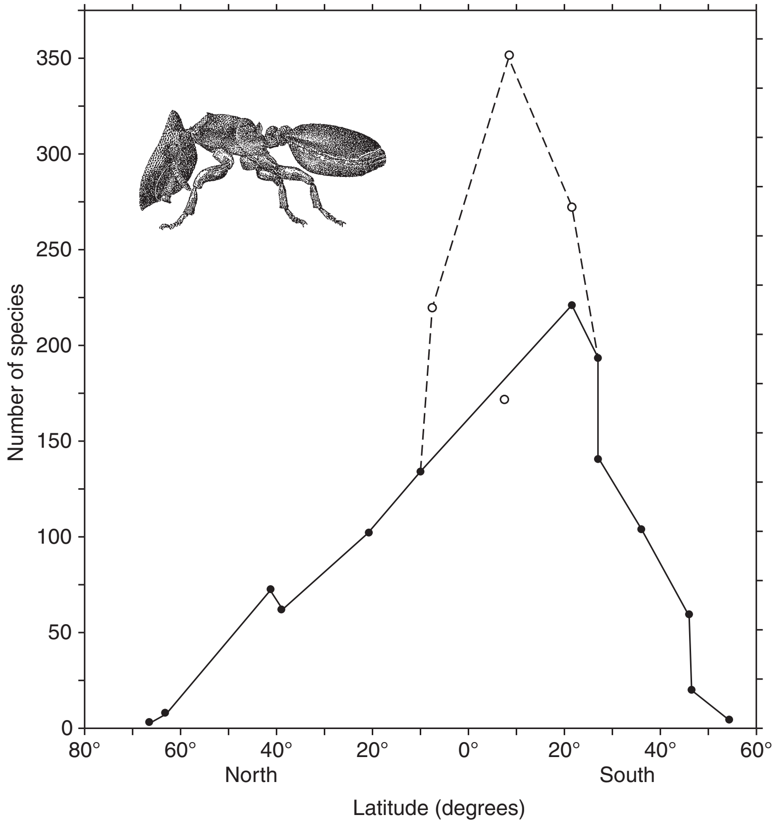


Figure 14.9 The number of ant species on a latitudinal gradient north and south of the equator, based on Kusnezov's (1957) review of the literature (solid circles and lines), supplemented with data in Hölldobler and Wilson (1990) (open circles and dashed lines). This is a crude comparison because areas sampled were not equal, but the trends are strong.

nature down to simple numbers, misses much of the intriguing detail and magnificent ecosystem scale, but numbers reveal trends very well. Early comparisons reported for beetles were 169 in Labrador, 2000 in Massachusetts and 4000 in Florida (Clarke 1954). Alaska had 7 species of ant, Iowa 73 and Trinidad 134 (Fischer 1960). Ants reach to 350 species near the equator in the western Amazon Basin, Peru, declining to near zero by 60° N and S (Kusnezov 1957, Figure 14.9). Termites may number as high as 60 species near the equator, but decline to none in the British Isles (cf., Collins 1989, Kloet and Hinks 1964, Figure 14.10). Plants reach over 250 species in 0.1 hectare plots near the equator, declining to 20 or less above 50° N (Gentry 1988). In North America tiger beetles reach a maximum richness of 20 species in the south, declining to one species in the north, but they number over 50 species on Sri Lanka just north of the equator (Pearson and Cassola 1992, Pearson and Juliano 1993). In the large New World countries of Canada, the USA and Brazil, total tiger beetle richness is 29, 111 and 184, respectively. In the well-studied swallowtail butterflies, diversity drops dramatically from the equator to the north and south (Figure 14.11, Scriber 1995), accompanied by relatively high

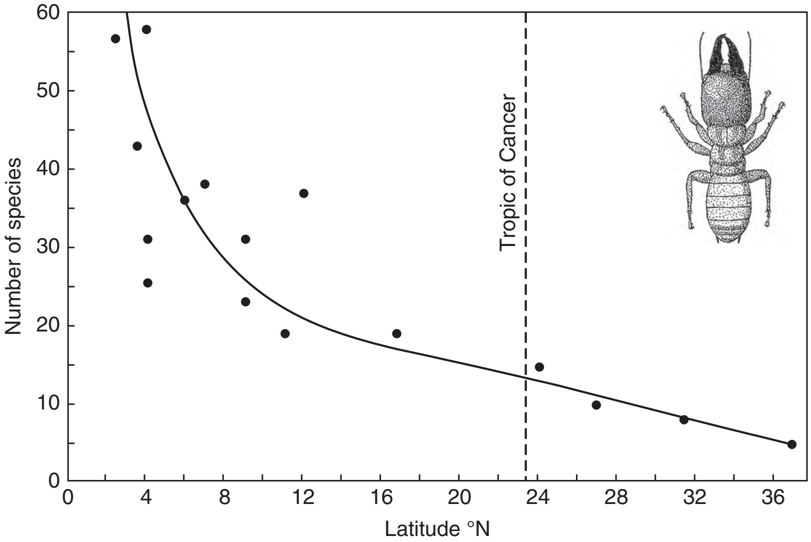


Figure 14.10 The number of termite species from near the equator to the northern latitudes, with the greatest number of species found in equatorial rain forests with a complex canopy structure. The highest richnesses (near 60 species) are recorded in dipterocarp forest in west Malaysia and in Sarawak. Numbers of species are for localities, not adjusted for the area sampled. Based on Collins 1989.

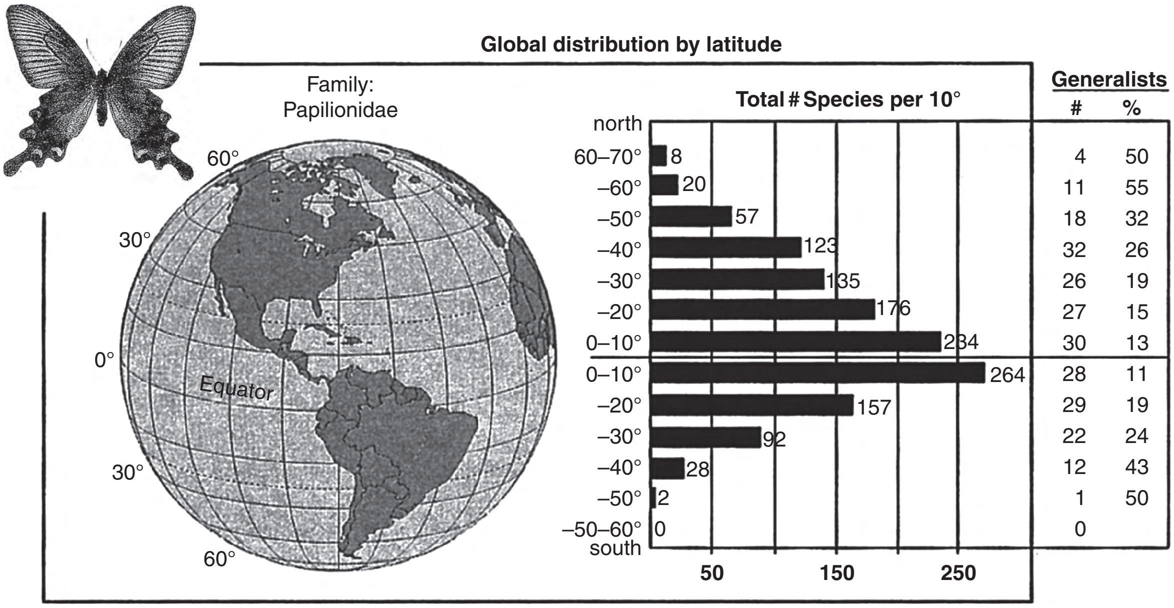


Figure 14.11 The total number of swallowtail butterfly species per 10° of latitude north and south of the equator, with the numbers and percentage of generalist species listed on the right. The world fauna of swallowtails is 563 species. From Scriber 1995.

specificity on host plants in the tropics, and an increasing percentage of generalists into the colder latitudes (generalists were defined as species with larvae feeding on more than one plant family). Rosenzweig (1995), Begon *et al.* (1996) and Brown and Lomolino (1998) provide many examples for taxa other than insects: plants, bats, other mammals, snakes, frogs, lizards, fishes and foraminifera. Almost any comparison of numbers of species on latitudinal gradients appears to support the trend of increasing richness toward and into the tropics. Exceptions will be discussed later in this chapter.

14.5.1 Mechanistic hypotheses on latitudinal gradients

The mechanisms influencing species richness patterns on latitudinal gradients have been debated for decades. Many hypotheses have been proposed, but few are easy to test, with the result that ideas have proliferated, and resolution of the question was long delayed. A good review of the hypotheses was provided by Pianka (1966), with each having some validity, so these will be covered first very briefly (hypotheses 1–6), after which more recent developments will be considered. More of the pros and cons for each hypothesis are provided by Price (1997).

(1) *The time hypothesis*: Older vegetation types such as tropical rain forest have had more time to diversify in species than younger ones, like temperate forests. More species have accumulated over time in the tropics, generating a latitudinal gradient in species richness.

(2) *The spatial-heterogeneity hypothesis*: There is much environmental heterogeneity in the tropics, from dry to wet tropics, and from lowland forests up mountainsides, reaching altitudes equivalent to high latitudes in climate (see Holdridge 1947, 1967, discussed under altitudinal gradients in this chapter). Therefore, many vegetation types are sustained in the tropics, providing many and varied habitats into which animals can colonize. In temperate regions vegetation types, such as broadleaved forest and conifer forest, tend to cover immense swaths of the landscape right across continents, offering much less heterogeneity than in the tropics and hence fewer cumulative species on the gradient.

(3) *The competition hypothesis*: A long-standing argument, fostered by Dobzhansky (1950) among others, has held that competition is more intense in the tropics, niches are narrow and species are more tightly packed than in temperate regions. The clement conditions in the tropics result in the dominance of biotic interactions in the evolutionary process, with competition an important process. In the temperate regions, abiotic forces such as drought and cold are prevalent and mortality indiscriminate, with selection for high reproductive capacity. Species become more generalized and less tightly packed, resulting in lower species richness in temperate versus tropical latitudes.

(4) *The predation hypothesis*: The argument goes that predators and parasites are more abundant in the tropics, reducing competition and increasing the chances for coexistence of more prey species, which in turn fosters the evolution of more predators and parasites. In the temperate regions, natural enemies are less effective, with more competition and less niche space for a rich flora and fauna.

(5) *The climatic-stability hypothesis*: Another argument suggests that regions with stable climates allow finer specialization because resources are more stable and predictable. Therefore, more species can coexist by being tightly packed than in temperate regions where resources are more variable and species are more generalized in their capacity to withstand variable weather conditions.

(6) *The productivity hypothesis*: The position here is that greater productivity in the tropics results in higher species richness. A broader base to the energy pyramid allows for more trophic levels and more species in aggregate.

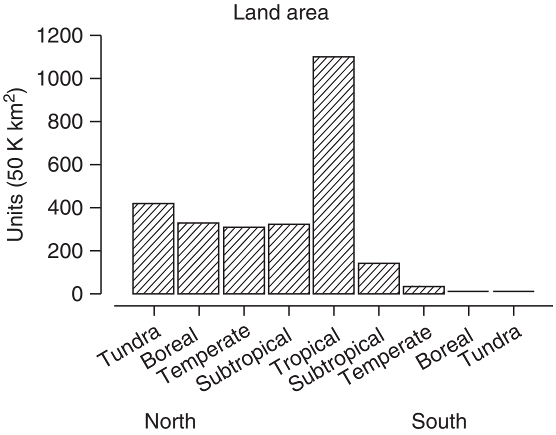


Figure 14.12 Comparison of land areas for major biomes along a north to south latitudinal gradient, showing the large area of the tropical biome. From Rosenzweig 1995.

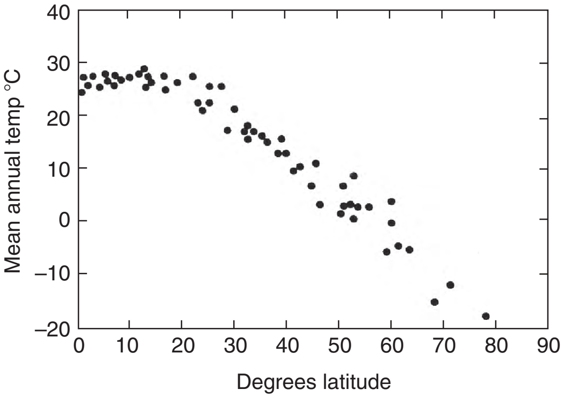


Figure 14.13 Mean annual temperatures of low elevation, mesic continental locations on a latitudinal gradient from the equator. From Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.* **107**:481–501. © 1973 by the University of Chicago.

(7) *The resource-limitation hypothesis*: Resources are very limited in the tropics because high temperatures and high rainfall cause rapid recycling or leaching of nutrients, making soils poor for plant growth. Plant species cannot develop dominance under such conditions so many species coexist, in contrast to temperate regions. Higher plant species richness in the tropics results in higher faunal richness also, compared to temperate latitudes (Tilman and Pacala 1993).

(8) *The animal-pollinator hypothesis*: In the humid tropics wind pollination is ineffective, and most plants are pollinated by animals: the insects, especially bees, the birds and the bats. Wind causes widespread pollen distribution, reducing chances of reproductive isolation among plant species and speciation. However, animal pollination can result in local pollination patterns, and isolation among plant populations, with the consequent possibility of rapid species formation (e.g., Grant 1949, Dressler 1968, Dodson *et al.* 1969). The discrepancy in speciation rates in plants and associated faunas in the temperate and tropical latitudes will result in the latitudinal gradients in species richness so commonly observed.

Obviously, some of these hypotheses conflict, some are not mutually exclusive and some are very similar. All depend on evolutionary processes which are difficult to quantify and to test for validity. Therefore, there is unlikely to be a meeting of minds on which is the most valid hypothesis. However, one hypothesis remains that has a compellingly simple and factual basis, and recent developments discussed later show great promise.

(9) *The large-area hypothesis, or Terborgh's (1973) hypothesis*: Terborgh (1973) noted the symmetry of climates from the North to the South Poles, but only at the equator do the equivalent north and south elements abut; contiguous tropical latitudes from north and south combine to make one huge area. In fact, tropical land covers about three times more area than the next largest biome, the tundra (Figure 14.12, Rosenzweig 1992). Added to this, the latitudinal temperature gradient is non-linear because cloudiness in the tropics decreases temperatures, making a wide band of some 50° latitude total (25° N to 25° S) with similar temperatures (Figure 14.13).

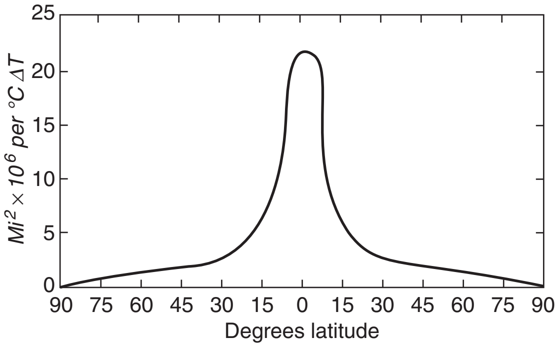


Figure 14.14 A latitudinal gradient of the area of the Earth's land surface in millions of square miles, between 1° C isotherms of mean annual temperature. Note the much greater area of surface around the equator. From Terborgh, J. 1973. On the notion of favorableness in plant ecology. *Am. Nat.* **107**:481–501. © by the University of Chicago.

As a result, the millions of square miles of the Earth's surface between 1° C isotherms is huge relative the areas outside the wide central equatorial belt (Figure 14.14).

The large area allows species to spread widely, increasing chances for speciation, so large areas support more species. Several of the other hypotheses may contribute to the mechanistic explanation of high species richness in the tropics. The fact remains that very large areas in tropical latitudes exist, and a strong area effect has been established repeatedly, as discussed in the previous section of this chapter.

14.5.2 Large area in tropical latitudes

Rosenzweig (1995) summarizes the mechanisms resulting from the great area in the tropical latitudes, with the probability that tropical species have larger geographic ranges than in higher latitudes.

(1) *Larger total population size – low extinction rates*: The larger the geographical range of a species the larger the population is likely to be. This reduces the probability of extinction of the species, and extinction rates in general will be low in the tropics.

(2) *More niche refuges – low extinction rates*: Larger geographical ranges provide more refuges from climatic deterioration and epidemic diseases and their catastrophic effects, resulting in higher population persistence and lower extinction rates.

(3) *More geographical barriers – higher speciation rates*: The larger the geographical range of a species, the more likely a geographical barrier will be encountered, resulting in allopatric speciation in isolated populations. Speciation rates will be highest where species ranges are large.

(4) *Higher evolutionary rates – higher speciation rates*: Species with larger ranges and higher populations support higher genetic heterogeneity, and live in more varied environments, which foster higher evolutionary rates, and ultimately higher speciation rates.

These four scenarios include two mechanisms which reduce extinction rates and two that increase speciation rates, promoting much higher equilibrium numbers of species in the tropics than in the temperate regions.

14.5.3 Plant species richness

The key to understanding tropical species richness must lie in the mechanisms resulting in high plant-species richness. This will translate into high richness of specialists associated with these plants, and a high number of generalists which depend on a variety of foods and other resources spread in space and time. Novotny *et al.* (2006) considered the various factors resulting in the richness of insect herbivores in the tropics. Did greater numbers of species in the tropics compared to the temperate regions result from: (i) host-plant species diversity, (ii) numbers of herbivore species per host or niche partitioning and/or (iii) host specificity of the insect species? Sampling of folivorous insects in Moravia and Slovakia in Central Europe, and in Papua New Guinea, using the same protocols, provided direct comparisons between temperate and tropical conditions, respectively. They found that tree species supported similar richness of herbivores on equal areas of foliage in both latitudes, so niche partitioning could be eliminated as a factor in herbivore richness in the tropics. Likewise, host specificity of herbivores did not differ between the sites. This leaves host-plant species diversity as the key to understanding insect herbivore species diversity. The tropical site contained seven times more tree species than the Moravian site: 152 vs. 21 tree species. Therefore, the effect of increasing tree species per unit area in the tropics has an additive effect on the richness of insect herbivores: more tree species – more insects.

14.5.4 The water-energy balance hypothesis

Of course, plants grow better and show greater species richness in warm and wet climates, so aren't these two variables likely to provide a more mechanistic explanation of plant productivity and richness, which then contributes to species richness at higher trophic levels? Climatic variables can therefore be used as predictors of species richness for plants, vertebrates and invertebrates (Hawkins *et al.* 2003). For plants, in 20 out of 21 studies, variables involving water were the best predictors of plant richness. The best variables differed among studies, but rainfall, annual potential evapotranspiration (PET) and annual actual evapotranspiration (AET) were frequently the most predictive. Levels of evapotranspiration depend on precipitation, but also on the heat to promote evaporation and transpiration, so these variables capture both water and energy supply. Hence, the **water–energy-balance hypothesis**.

For vertebrates the water–energy variables accounted for most variation in species richness in 24 cases, and direct energy measures were better predictors in 17 cases. In many studies temperature was the best predictor, but PET, AET, rainfall and net primary production (NPP) also emerged as the best predictors in others.

The data for invertebrates were all on insects, mostly on butterflies, but also including moths, tiger beetles, dung beetles, termites, ants and others. The best predictors of species richness were similar to those for vertebrates: PET, AET, NPP and rainfall in warm climates, and sunshine and temperature in cooler latitudes (Hawkins *et al.* 2003).

Of the 85 cases included in the study, in 82 examples the richness of flora or fauna were best predicted by measures of energy, water or the water–energy balance. The water–energy hypothesis accounted for an average of over 60% of the variation in species richness over a wide taxonomic sample. In another study, on western Palearctic butterflies, the water–energy-balance hypothesis explained 79% of the variance in species richness derived from range maps (Hawkins and Porter 2003). For dragonfly species richness in Europe and North Africa, the water–energy hypothesis was supported again, with PET and AET being the most predictive variables (Keil *et al.* 2008a).

In general, the water–energy-balance hypothesis on species richness has accounted for well over 50% of the variance in a wide range of taxa, apparently explaining more variation than any other climatic variable can. Alternative hypotheses, such as the metabolic theory (e.g., Brown *et al.* 2004), which predicts species richness correlations principally with temperature, have not been broadly supported, even among insect taxa (Hawkins *et al.* 2007). But, however predictive the water–energy-balance hypothesis is, it throws no light on the evolutionary mechanisms involved in the speciation and adaptive radiation along these climatic gradients, or the variation in the rates of these processes. Perhaps a quantitative test of Rosenzweig's (1995) predictions on the effect of large area in tropical latitudes will contribute to an understanding of species richness.

14.5.5 Anomalous trends

Again, we should not jump to the conclusion that there is an inevitable trend of increasing species richness into the tropics for all plant and animal groups, or that the water–energy-balance hypothesis universally predicts species richness. As with species–area relationships, some healthy circumspection is advisable on how broadly the trends can be applied. Many insect groups, as well as plant genera, show anomalous trends, with more species in temperate regions, or no latitudinal trend. Anomalous groups include herbivores, pollinators, parasitoids, aquatic insects and plants (Table 14.3). Such anomalies are sometimes dismissed as minor and of little consequence. Contrary to this opinion, the estimated numbers of species involved dwarfs the richness of vertebrate groups such as birds, mammals, snakes and lizards, which conform to the general trend. Some of the exceptions have now become generally viewed as interesting and valuable. "The existence of exceptions to the general latitudinal pattern of diversity potentially provides a useful and important tool for testing postulated mechanisms for the overall pattern" (Gaston 1996, p. 467). Also, the exceptions help us to focus on the particular ecology of a group, its evolutionary background and phylogenetic constraints, in order to understand the apparently anomalous distribution. Some examples follow.

For aphids and psyllids, many more exist in the temperate areas than in the tropics – about 80% of aphids and 60% of psyllids (Eastop 1972, 1978). Aphids find hosts by landing and testing hosts and non-hosts, an increasingly inefficient method as plant species richness increases dramatically in the tropics. Being small and delicate, aphids cannot survive long without a host plant to feed on, so increasing difficulty in finding hosts in the tropics reduces the probability of colonizing hosts, which "appear" to aphids as highly fragmented and widely separated islands in a sea of unsuitable green (Dixon *et al.* 1987).

Sawflies are more diverse in the north temperate than in the tropics, probably for a different reason. The common sawflies (Tenthredinidae) have a strong phylogenetic association with willows (*Salix* in the family Salicaceae). Willows are more numerous in the north temperate, and depauperate in tropical latitudes, so sawfly diversity is simply reflecting willow richness (Table 14.3). A similar relationship probably exists between pine sawflies (Diprionidae) and conifers, especially the host-plant genus *Pinus*, which declines in species richness towards the tropics (Table 14.3).

Gall-inducing insects show a strong peak in local species richness in the warm temperate regions, around 35° N or S, where sclerophyllous vegetation dominates; examples are chapparal in North America, cerrado in Brazil and marquis in the Mediterranean (Figure 14.15). A hypothesis to account mechanistically for the high richness in scleromorph vegetation in climatic zones with a long, dry season emphasizes the flow of effects from nutrient-poor soils to the evolution of long-lived tough leaves, coupled with fire as a major environmental factor (Figure 14.16).

A similar peak of richness at 35° N was documented for grasshoppers in the family Acrididae by Davidowitz and Rosenzweig (1998), but for a different reason. The most likely explanation provided is that grass species are a major food source, and many grasshopper species frequent warm, dry, grassy habitats, mostly ranging between 30–55° N in North America. Within this range there is a latitudinal gradient, with increasing grasshopper richness as latitude declines.

Among the pollinators, bees show no greater richness in the tropics than in temperate regions. Bee community richness in lowland tropical areas and temperate areas is similar, but richness is greater in warm, xeric vegetation in Mediterranean latitudes (Table 14.4, Roubik 1992). As variability in resources increases in space and time in the tropics, ecological niches become more flexible and bee species more generalized, with an increased percentage of social

Table 14.3 **Examples of anomalous latitudinal distribution patterns in insect groups and two plant genera**

Taxon	Number of species[a]	Trend	References
Herbivores			
Agromyzid leaf-mining flies	1800	More in temperate	Spencer 1972
Aphids or plant lice	4064	More in temperate	Dixon *et al.* 1987
Psyllids or jumping plant lice	1728	More in temperate	Eastop 1972, 1978
Tenthredinid sawflies	5000	More in temperate	Benson 1950, Smith 1979
Sawflies in general	2842*	Highest in north	Kouki *et al.* 1994, Kouki 1999
Gall-inducing insects	> 8000	More in warm temperate	Price *et al.* 1998b
Grasshoppers, Acrididae	305*	Peak at 35° N	Davidowitz and Rosenzweig 1998
Detritivores, fungivores and necrophages			
Byrrhidae, pill beetles	290	More in temperate	Gaston 1991
Latridiidae, scavenger beetles	1059	More in temperate	Gaston 1991
Cryptophagidae, fungus beetles	800	More in temperate	Gaston 1991
Silphidae, carrion beetles	300	More in temperate	Gaston 1991
Syrphidae	641*	More in temperate or no trend	Keil *et al.* 2008b
Pollinators			
Bees	20 000	No greater richness in tropics	Michener 1979, Roubik 1989, 1992
Bee flies (parasites and predators as larvae)	4500	More in temperate	Hull 1973
Parasitoids			
Ichneumonid wasps	60 000	More in temperate	Townes 1969, Janzen 1981
Braconid wasps	40 000	More in temperate	Quicke and Kruft 1995
Aquatic insects			
Chironomid midges in Australia	87*	No trend	McKie *et al.* 2005

Table 14.3 (*cont.*)

Taxon	Number of species[a]	Trend	References
Insect communities in Australia	1578*	Peak in subtropical and temperate	Arthington 1990
Haliplidae, water beetles	200	More in temperate	Gaston 1991
Plants			
Pines	111	Peak at 30–40° N	Stevens and Enquist 1998
Willows	350	Peak in north	Skvortsov 1999

[a] Number of species in the world, except where an asterisk indicates the number of species in the study. Most groups are shown with the number of described species, but ichneumonids and braconids are listed as the estimated total in the world.

species. In warm, xeric vegetation bees appear to be much more specialized on particular plant species.

14.5.6 Anomalous parasitoid species richness

Ichneumonid and braconid parasitoid species also show an anomalous latitudinal richness pattern (Table 14.3). Several hypotheses have been advanced, mainly concerning ichneumonid species, and have been summarized by Hawkins (1994) and Price (1997).

(1) *The cool-environment hypothesis*: Ichneumonids are adapted to cool, moist conditions, and have radiated extensively in such areas; in cool temperate climates in northern latitudes, or at high elevations in the tropics (Heinrich 1977).
(2) *The microhabitat-specificity hypothesis*: Ichneumonids tend to be microhabitat specific rather than host specific. In the tropics the diversity of ichneumonid species does not increase because microhabitat diversity does not increase (Owen and Owen 1974).
(3) *The host-larval-predation hypothesis*: Parasitized hosts frequently become sluggish, with prolonged development times, making them vulnerable to predation. Predation is higher in the tropics, particularly involving ants, so parasite mortality while in a host is likely to be very high, reducing the probability of survival in the tropics (Rathcke and Price 1976).
(4) *The nasty-host hypothesis*: Tropical woody plants are more toxic than temperate species, and the toxins may pass up the food web to negatively impact parasitoids. Therefore, tropical hosts are more difficult to utilize than temperate hosts, and many will not be exploited (Gauld *et al.* 1992, Gauld and Gaston 1994).
(5) *The resource-fragmentation hypothesis*: As diversity of plant species per unit area increases into the tropics and the diversity of herbivores follows, the density of any one species declines dramatically, making it increasingly more difficult to discover hosts. Faced with rare hosts, selection will favor more generalized species, reducing diversity. Also, rare hosts may become so difficult to find that they cannot be utilized by many species (Janzen 1981).
(6) *The adult-parasitoid-predation hypothesis*: Adult parasitoids are also vulnerable to predators, particularly in the tropics, where predation is high and resources are fragmented, so searching

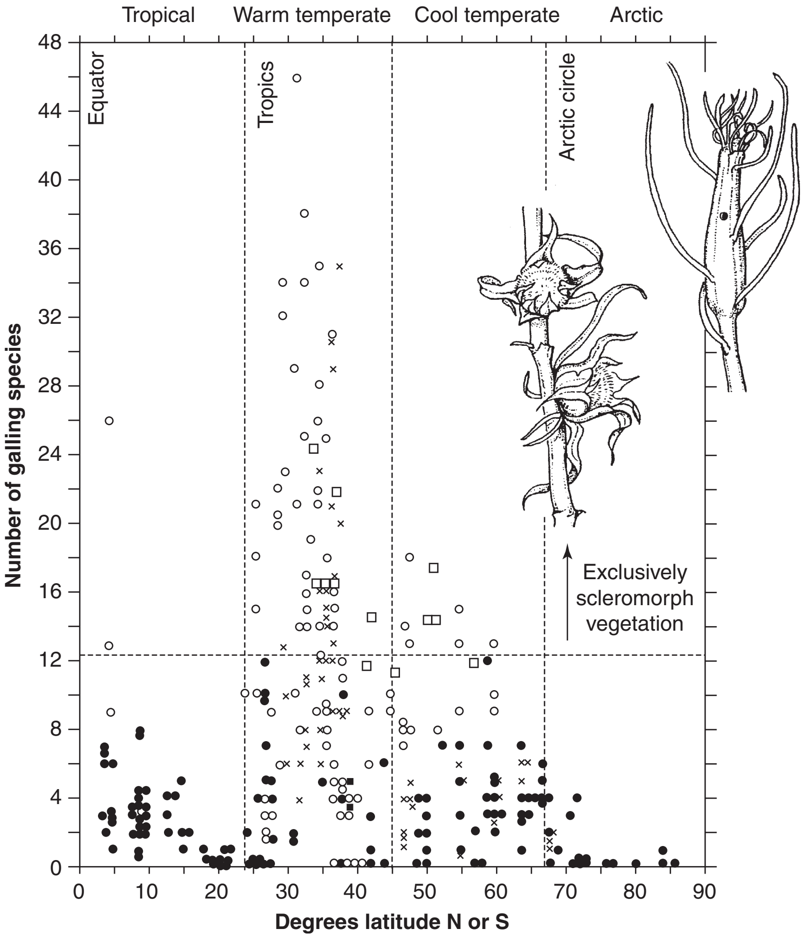


Figure 14.15 The distribution of local gall-forming insect species richness on a latitudinal gradient north or south of the equator, with all samples corrected for altitude, and plotted as if at sea level. Note the strong peak of richness in warm temperate latitudes in scleromorph vegetation (open circles). Samples in mesic sites in non-scleromorph vegetation are in solid circles. Samples in relatively mesic sites in scleromorph vegetation are marked x. Samples from fynbos vegetation in South Africa were collected as an independent test of the pattern (12 open squares), and from riparian woodland (two solid squares). The three open circles from the tropics were from campina vegetation along the Rio Negro River, Amazonia, a scleromorph vegetation on poor white sands. From Price *et al.* 1998b. Reprinted with permission from Blackwell Publishing. The inserted galls were formed by cecidomyiid gall midges on rabbit brush, *Chrysothamnus nauseosus*. From Fernandes *et al.* 2000.

times are prolonged. This additional mortality may reduce parasitoid fitness so that populations are lowered to below a sustainable density (Gauld 1987).

(7) *The interphyletic-competition hypothesis*: Insect parasitoids compete more in the tropics with other parasitic groups such as nematodes, fungi and bacteria – all with short life cycles able to outcompete the longer-lived parasitoids. Parasitoid diversity is therefore reduced by competitive exclusion (Eggleton and Gaston 1990).

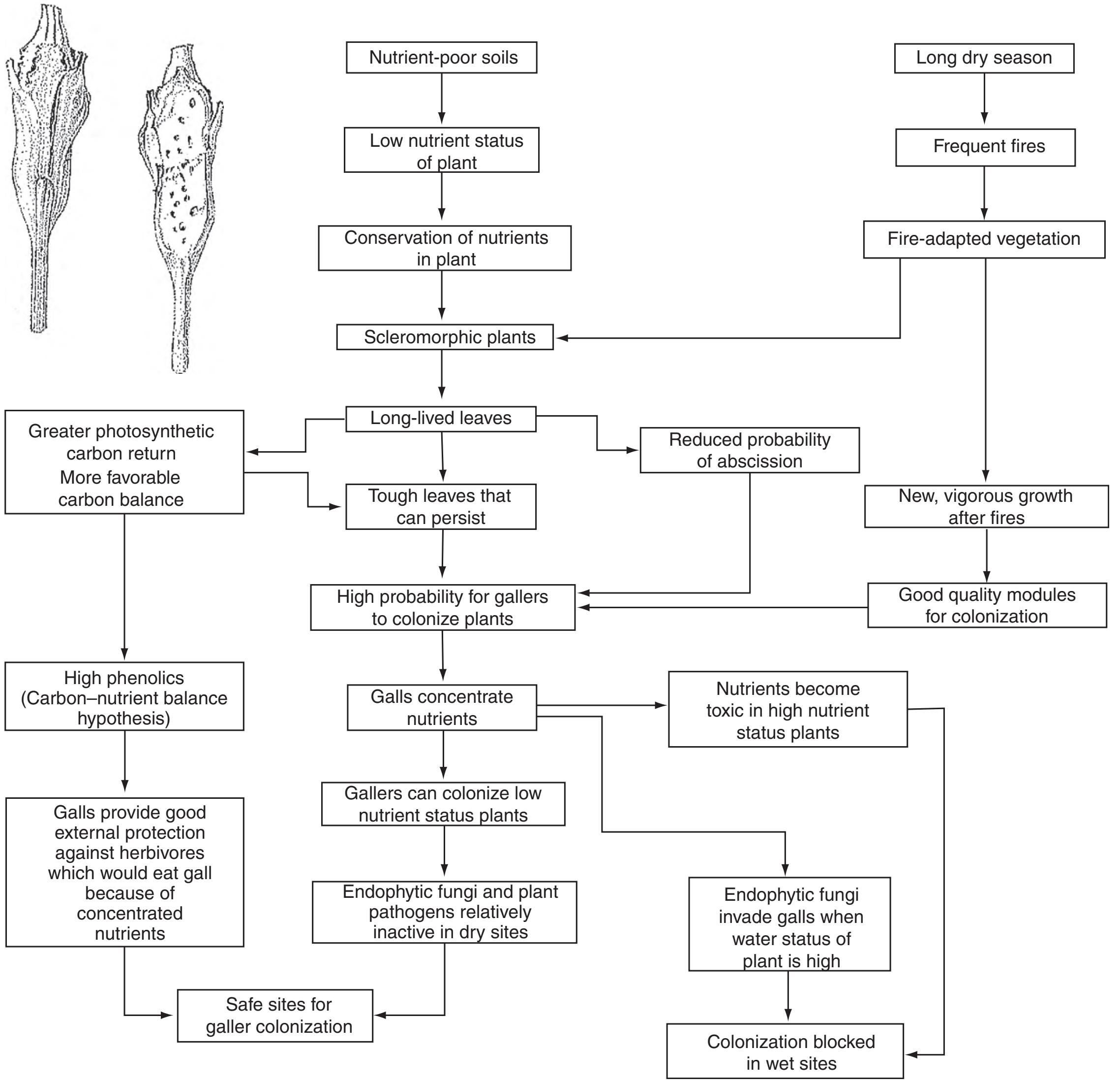


Figure 14.16 A hypothesis proposing the mechanisms that result in high local richness of gall-inducing insect species, based on the evolution of scleromorph vegetation in climate zones with a long dry season. The original hypothesis was developed by Fernandes and Price (1991), and was modified in Price (2003a) to include the favorable effects of fire on plant vigor and resources for gall-inducing insects. From Price 2003a.

These hypotheses are not mutually exclusive. Indeed, they may be complementary, with several playing a role simultaneously. The hypotheses have been simplified in these statements, and the refinements in the original papers provide interesting, testable subhypotheses. Of course, adequate sampling and standardized samples are continuing problems, with some doubting the validity of the anomalous trend (e.g., Hespenheide 1979, Morrison *et al.* 1979). Nevertheless, the trend has been found by many researchers independently, much research has been stimulated,

Table 14.4 **Bee community richness in lowland tropical and temperate locations. From Roubik 1992**

Locality	Number of species	Number of genera	Percent social	References
Lowland tropical				
Central Sumatra	110	20	50	Inoue *et al.* 1990
Belém, Brazil	250	50	50	Ducke (Michener 1979)
French Guiana	245	50	50	Roubik 1990
W. Costa Rica	200	65	25	Heithaus 1979
Central Brazil	230	80	35	Camargo and Mazucato 1986
Xeric scrub				
Central Mexico	230	90	20	Ayala 1990
S. California	500	>100	~15	Timberlake (Michener 1979)
S. W. France	500	>100	~15	Perez (Michener 1979)
Temperate				
Central Japan	170	25	~15	Kakutani *et al.* 1990
Illinois	300	55	10	Pearson 1933
N. Dakota	245	45	5	Stevens (Michener 1979)

and the debate, covered well by Hawkins (1994), will continue.

Recent evidence of higher than expected richness of parasitoid wasps in the tropics changes the complexion of this debate. In the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica, six braconid genera were reared from wild caterpillars (Smith *et al.* 2008). They were identified and sorted by experts into 171 provisional species, but DNA barcoding revealed an additional 142 provisional species, making a total of 313 species discovered in 2597 specimens examined. Perhaps 95% of the species are undescribed, but all are highly host specific; over 90% attack only one or two host species. As an example of the revealing possibilities of DNA barcoding, one species, *Apanteles leucostigmus*, was thought to attack 32 host species based on visual morphotypes, but barcoding revealed 36 provisional, highly specific species. DNA barcoding employs "a standardized short sequence of DNA as a species-level key character" (Janzen *et al.* 2009, p. 2). These results show that originally only 55% of the species revealed by barcoding had been recognized previously as morphospecies, grossly underestimating richness and specificity of parasitoids in contiguous areas of dry forest, cloud forest and wet forest in the tropics.

A similar scenario has been revealed for parasitoid tachinid flies on lepidopteran caterpillars in the ACG (Smith *et al.* 2006, 2007). Before these studies 20 morphospecies of *Belvosia* were recognized, with three generalist species and 17 very host-specific species. The DNA barcoding study recognized the 17 specialized species, but also showed that the putative generalists were groups of equally specialized cryptic species, making a total count of 32 species (Smith *et al.* 2006). A related study examined 16 tachinid parasitoid species thought to be among the most generalized in the ACG, but actually identified 73 taxonomically distinct barcoded morphospecies. Nine species remained as generalists and the remainder were more specialized or highly specialized.

These results place in question the richness of tropical parasitoids and the latitudinal patterns which have resulted in so much debate. Apparently, there are many more cryptic species than previously recognized, resulting in a large underestimate of the actual biodiversity. In each of the three studies just discussed, the percentage of species recognized by barcoding, actually identified before barcoding, was only 55%, 53% and 22%, respectively. Thus, barcoding should be employed widely in inventories of biodiversity and other kinds of ecological studies (Janzen *et al.* 2009), and it would be valuable to develop more comparative studies in tropical and temperate faunas to search for patterns in cryptic species and host specialization.

Hawkins (1994) documented worldwide richness of parasitoid faunas per host species, with richer faunas on exophytic herbivores in the temperate regions, and no trend in endophytic herbivores. These trends in exophytic herbivores are strongest in the Ichneumonoidea (ichneumonids and braconids); dipteran parasitoids show a similar pattern, but chalcidoids are apparently as rich in the tropics as in temperate regions. Why chalcids escape the various effects as listed in the hypotheses above is uncertain, but their smaller size enables use of smaller hosts with denser populations, they become less visible and a lower reward for predators, and they can become more commonly gregarious, making the discovery of a single host sufficient for leaving many progeny (Hawkins 1994). It is likely that barcoding will modify these patterns also.

14.5.7 Anomalous trends in aquatic insects

Among aquatic insect studies in streams, there is a mix of results showing a lack of latitudinal trends in species richness, and the presence of a trend. McKie *et al.* (2005) found none in a survey of chironomids in NE Australia, and Arthington (1990) recorded higher richness in subtropical and temperate streams than in tropical lotic systems. His sampling included Ephemeroptera, Plecoptera, Hemiptera, Diptera, Trichoptera and Coleoptera, all of which conformed to the pattern of lower species richness in tropical streams. Lake *et al.* (1994), as one example, found higher richness of lotic macroinvertebrates in the tropics than in more southern latitudes. However, there appears to be a general appreciation that lotic systems provide a general exception to the pattern of increasing species richness into the tropics. McKie *et al.* (2005) summarize the reasoning for this pattern:

(1) Plant detritus in streams is leached of defensive chemicals so plant diversity plays little role in selecting for a diverse insect fauna.
(2) Aquatic leaf shredders, as a consequence, are more generalized feeders than terrestrial herbivores.
(3) The habitat in streams is more uniform than terrestrial environments, with little variation in the basic substrates of rocks, gravel, sand, wood and leaves.
(4) Temperature, oxygen and nutrient tolerances appear to be broad in at least some taxa, such as midges (Chironomidae), and macroinvertebrates in general.

This diverse array of exceptions to the general trend of increasing species richness into the tropics, summarized in Table 14.3, coupled with the apparently valid explanations for divergence from the prevailing patterns, makes the study of latitudinal gradients much more intriguing than if trends were uniform. Each explanation for an exception is unique, with no generalizations appropriate, except that each taxon has its own environmental requirements and phylogenetic constraints, so it would be remarkable if all taxa followed the same latitudinal trends worldwide. We should also note the very large number of species represented by the anomalous patterns in species richness. The examples are not quirky or trivial, but add up to a significant proportion of the Earth's fauna. Many other taxa could be added to the insect examples, such as marine amphipods and freshwater copepods. More detailed analytical research on specific taxa would benefit our understanding of latitudinal trends in species diversity, including detailed studies on the mechanisms in taxa that follow the general pattern (see Chown and Gaston 2000).

14.6 Altitudinal gradients

Altitudinal gradients are steep in two senses. They frequently involve the steep terrain in mountain ranges with rapidly changing edaphic conditions, and temperature differences are large, declining rapidly up the slope. The cooling effect with altitude results from **adiabatic cooling**: when air is forced up over a mountain it expands with decreasing barometric pressure, loses heat and cools. The rate of cooling is estimated at 10 °C per kilometer increase in elevation, or 1 °C per 100 m in dry air. This change occurs with no condensation of water vapor and no cloud formation, both of which would add to the cooling effect (Brown and Lomolino 1998). Higher elevations also lose heat more rapidly than lower elevations through higher radiation into the atmosphere because of lower air density. These cooling effects translate into rapid climate change up a mountain, equivalent to going north or south in latitude from the equator. Thus, the altitudinal effect on temperature can be converted to a latitudinal-effect equivalent by using an increase of 4° latitude for every 305 m increase in altitude, as Merriam pointed out in his publications in 1894 and 1898.

14.6.1 Life zones

Merriam worked this relationship out when he camped in the San Francisco Peaks in Arizona, and recognized the clear zonation of vegetation types up the mountain and down into the Sonoran Desert, still apparent today (Figure 14.17). Merriam called these bands of vegetation **life zones**, with Sonoran Desert vegetation at the lowest elevations and arctic-alpine components at the peak. South-facing slopes, which received more direct heat from the sun in a north-temperate latitude, allowed plant species to persist higher up the slope, with their distributions declining on northern slopes. The life-zone approach works well in the mountainous west of North America, but less well in the east where Pitelka's (1941) approach emphasizing the structural characters of the vegetation is more applicable. Pitelka recognized **biomes** as terrestrial communities of plants and animals in which a major vegetation type was uniform (Odum 1971). The grassland biome, the temperate deciduous forest biome, northern coniferous forest biome and the tundra would dominate much of eastern North America, but Pitelka (1941) recognized **ecotones** and subregions. An ecotone is a zone of transition, usually between vegetation types, such as the coniferous–deciduous forest ecotone, or the deciduous-forest–grassland ecotone.

Obviously, major shifts in vegetation type and plant species composition exert strong influences on insects in these biomes. However, the high mobility of insects reduces their confinement to particular biomes, and they have not been used in the characterization or classification of biomes. Insects respond to smaller scales of variation in general, such as the distribution of particular plant families, individual species of which may be found in many biomes, such as in the Brassicaceae, Fabaceae and Solanaceae.

The life-zone and biome concepts have been combined by Holdridge (1947, 1967, Holdridge *et al.* 1971, Figure 14.18) using three climatic parameters:

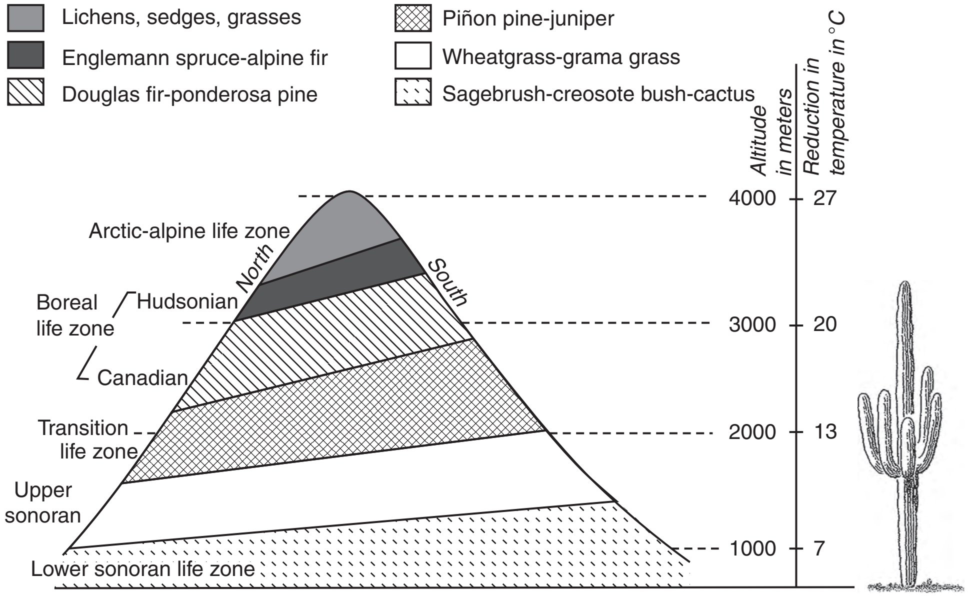


Figure 14.17 Life zones recognized by Merriam on the San Francisco Peaks in northern Arizona. The slope of the vegetation zones from south to north faces results from more insolation on the south face. Figure 1.3, p. 7 from *Ecology of Populations* by Arthur S. Boughey (1968). Reprinted by permission of Pearson Education, Inc.

temperature, precipitation and evaporation. Temperature above 0° C, or **biotemperature**, declines from the equator to the polar regions, so temperature can be plotted as horizontal zones, with parallel lines representing isotherms. Temperature belts are represented on both latitudinal (left) and altitudinal (right) gradients. Precipitation is the average total annual rainfall in millimeters, and is plotted at about a 60° angle from the horizontal axis. The evapotranspiration ratio is the balance between temperature and rainfall. The values represent the number of times actual rainfall could be evaporated in one year at sea-level atmospheric pressure. All scales are logarithmic. Holdridge noted that it is only in the tropics that all life zones are represented – the diversity of zones declines with latitude, resulting in great belts of one vegetation type across northern latitudes: tundra and coniferous forest. The wide range of life zones in the tropics produced by the strong effects of altitude and precipitation relates back to the high species richness in the tropics. Altitudinal and moisture gradients result in much greater environmental heterogeneity in the tropics than in northerly or southerly latitudes, thereby contributing a rich mosaic of habitats which foster rich floras and faunas.

14.6.2 Insect responses to altitude

Insects certainly respond to altitudinal gradients. Hilltops and mountaintops provide focal points on a landscape at which visually oriented insects can meet and mate, as discussed in Chapter 2 under reproductive behavior (Alcock and Dodson 2008). This **hilltopping** behavior is widespread taxonomically and geographically. Taking all insect species that hilltop into consideration, assemblages may become extraordinarily diverse, particularly where peaks are isolated. Taxa represented in the literature include butterflies, true flies in the families of bot flies, big-headed flies, woodlouse flies, flesh flies, tachinid flies, hover flies and mydas flies, tiger

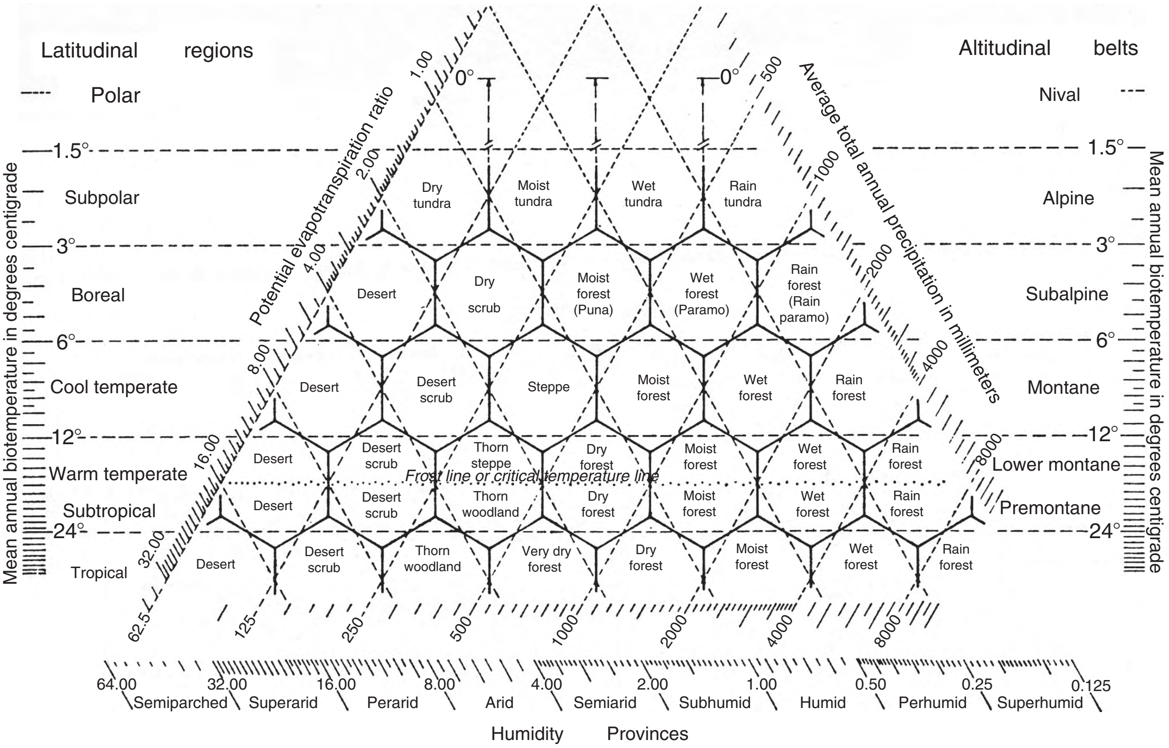


Figure 14.18 The Holdridge system for classifying life zones using temperature, rainfall and potential evapotranspiration to delimit each zone. From Holdridge *et al.* 1971.

beetles and hymenopterans such as carpenter bees, pompilid wasps and vespids. One study in the Swiss Alps yielded 30 species in seven families of flies which were hilltopping (Merz 2000): Stratiomyidae, Empididae, Syrphidae, Muscidae, Sarcophagidae, Tachinidae and Oestridae.

However, more general patterns in biodiversity have been discovered when full altitudinal gradients have been examined. Even then, the trends vary enormously among species and larger taxonomic groups, as reviewed by Hodkinson (2005). Considering altitudinal trends in abundance of individual species, 13 species decreased with altitude, 7 increased and 7 showed little or no trend. Most parasitoids and predators decreased with altitude, while a range of responses has been observed when communities, assemblages or taxonomic groups have been studied (Table 14.5). The examples in the table were selected to illustrate the range of responses to altitude recorded in the literature, but they show that trends depend strongly upon the particular ecology of the group being studied, and the length and location of the altitudinal gradient. Cool-adapted species may well increase with increasing altitude, particularly when mountains emerge from hot, dry conditions. But as elevation increases, the area of vegetation decreases per unit of elevation, and the number of plant species usually decreases, so decreasing numbers of insect herbivore species should be expected on this basis alone, as seen in several cases in Table 14.5. An example of an altitudinal trend in species richness is provided by gall-inducing insects from sea level to the summit of the San Francisco Peaks in Arizona, at 3843 m

Table 14.5 **Selected examples to illustrate the range of recorded responses of insects to altitudinal gradients on a local scale. From Hodkinson 2005**

Insect group	Habitat types	Country	Altitudinal range of transect (m)	Species richness trend up the gradient	References
All insects	*Acacia/ Metrosideros* tree community	Hawaii	2400	Peaking mid-altitude	Gagne 1979
All insects	Tropical forest	Panama	2100	Decreasing	Wolda 1987
All insects	Open fields	USA	1600	Peaking mid-altitude	McCoy 1990
Geometrid moths	Montane rain forest	Ecuador	1800	None or increasing	Brehm and Fiedler 2004
Galling insects	Mixed vegetation	Brazil	700	Decreasing or none	Lara *et al.* 2002
Scarabaeoid beetles	Various habitats	Spain	1080	Increasing	Romero-Alcaraz and Avila 2000
Scarabaeid beetles	Various habitats	Indonesia	2300	Generally decreasing	Hanski 1983
Moths	Montane rain forest	Papua New Guinea	600	Decreasing	Hebert 1980
Galling insects: several groups	Various habitats	Indonesia	400	All decreasing	Fernandes and Lara 1993
General insects	Bryophytes	Australia and New Zealand	1750	No overall trend	Andrew *et al.* 2003
Orthoptera	Open habitats	France	1600	No overall trend	Claridge and Singrao 1978
Hemiptera	Tropical rain forest	Indonesia	1600	No clear pattern	Casson and Hodkinson 1991

(Figure 14.19). The low elevations are dominated by Sonoran Desert vegetation and chaparral, with many scleromorphic plants which support many gall-inducing insects (cf., Figure 14.15). And even in the pinyon/juniper zone elements of the chaparral persist, so that numbers of galling species are relatively high, well above the regression line in these vegetation types. This hump-like distribution in the chaparral and pinyon/juniper zones is similar to records in Table 14.5 where species richness peaks at mid-altitude.

14.6.3 Mid-gradient peaks in richness

This **mid-elevation richness peak** has roused considerable interest (e.g., Cardelús *et al.* 2006). Such peaks in species richness have broader implications when applied to other gradients such as latitudinal trends, and the phenomenon has been called the **mid-domain effect** (e.g., Colwell and Lees 2000, Romdal *et al.* 2005). First, if the elevational or other gradient covers the range of distribution of the taxon under study, we would expect that large-ranged species would overlap most in the mid-gradient, producing a peak in richness. Also, species would tend to peak at the center of the range, having higher populations and larger ranges, reinforcing the peak. Second, a purely random process of placing species ranges on a gradient will result in more overlapping species in the central part of the gradient. Take, for example, a group of Madagascar butterflies with 66 species recorded by Lees *et al.* (1999). Their richness can be plotted over the 12.5° geographic extent of their distributions over the full length of the island, south of the equator in the Indian Ocean (Figure 14.20, Romdal *et al.* 2005). The dome-shaped distribution shows that most species occur in mid range, as predicted by our first consideration. However, two models which place the empirically determined ranges on the gradient at random, or theoretically determined ranges on the gradient at random, mimic the actual distribution in species richness very well, accounting for almost 90% of the variation in the empirical data. The mid-domain effect has been shown on elevational gradients for ants (Sanders 2002), small mammals (McCain 2004) and palms (Bachman *et al.* 2004).

14.7 Time gradients

Time is an important variable to consider. Biological interactions are so dynamic that we can envision communities changing all the time. Capturing this change is a challenge, but studies have nevertheless been a preoccupation for ecologists and evolutionists over many decades.

14.7.1 Ecological succession

The concept of **ecological succession** was developed by Cowles (1899), who studied the rapidly changing conditions on the sand dunes of Lake Michigan, and how plant communities adapted to the changing landscape through time. Ecological succession means the change in vegetation and associated fauna in a directional pattern, usually from bare ground, or at least from disturbed ground, to a mature vegetation type. Some aspects of this topic were discussed in Chapter 12 on community structure.

Sand dunes form when prevailing winds pile up sand along a sea or lake shore, such that the youngest dunes are near the water and the oldest are further inland. The edaphic, floral and faunal changes through the passage of time are therefore displayed in space. Successional change is rapid as one walks from the water's edge inland. Wind-blown, moving dunes become fixed. Organic matter accumulates, salt concentration and wind force decline. The vegetation and fauna follow predictable changes over the dunes and through time (Figure 14.21). On the east coast of Florida the prevailing winds are from the east, and on the west coast of the Netherlands winds are from the west, so dunes retreat in opposite directions, as shown in the figure. In both cases the number of plants increases with

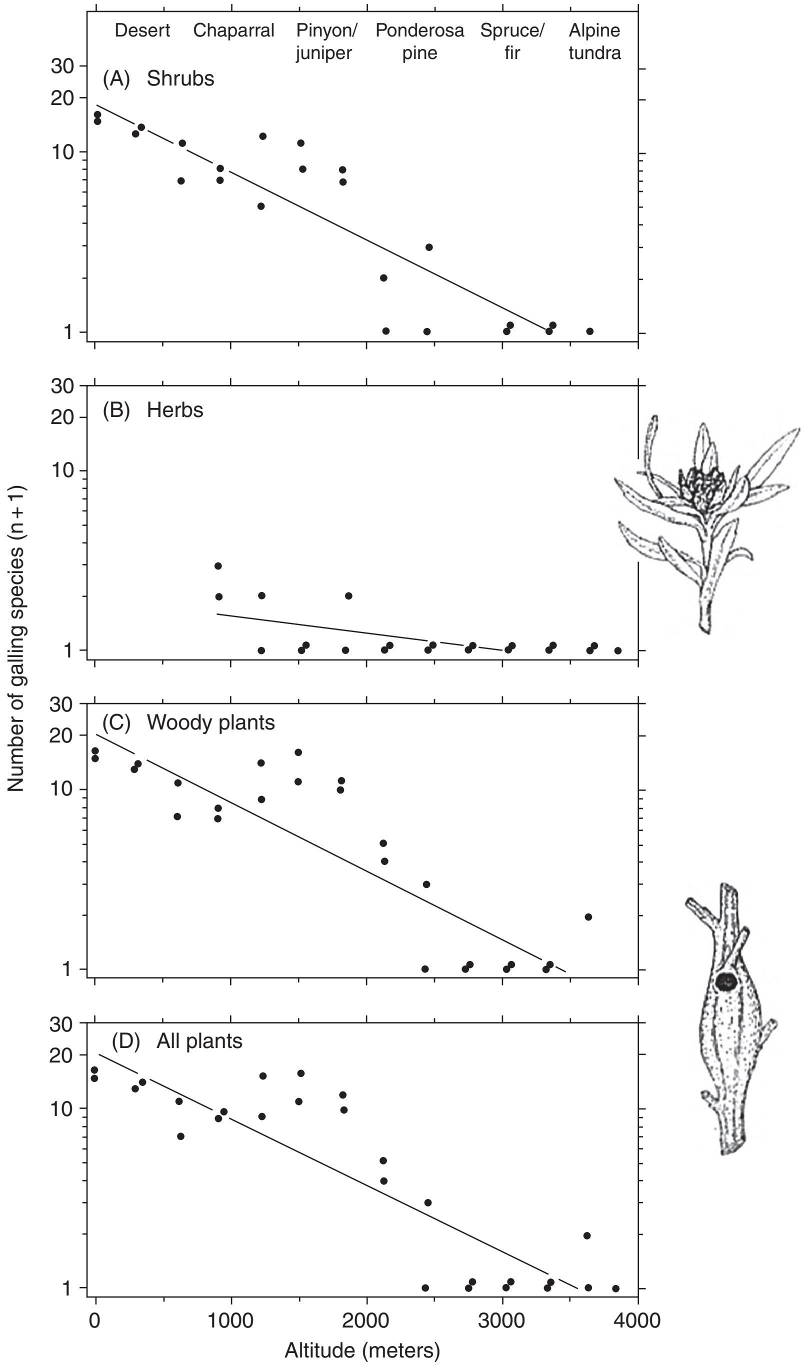


Figure 14.19 Patterns of gall-inducing insect species on an altitudinal gradient from sea level at Bahia Kino, Mexico, on the Gulf of California, north through Arizona to its highest peak, Mt. Humphries, at 3843 m above sea level. The strong trend of increasing gall species richness down the gradient is dominated by galls on shrubs in vegetations with scleromorph plant species in the desert, chaparral and pinyon/juniper zones. From Fernandes and Price 1991.

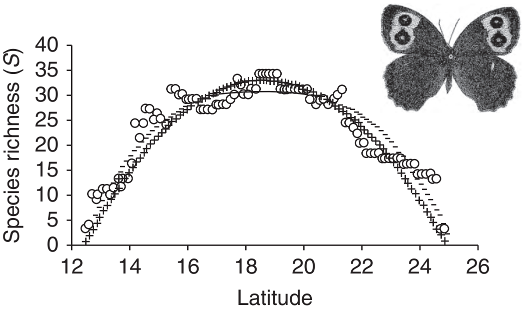


Figure 14.20 The mid-domain effect in butterflies on the island of Madagascar. The butterflies represent an adaptive radiation in the subfamily Satyrinae (Mycalesina), and show a peak in species richness at mid range on a north-south gradient, which runs the length of the island. The empirical data are shown as open circles, and the two model predictions using random placement of distribution are shown with x, and solid dots. From Romdal *et al.* 2005.

time, no doubt accompanied by an increasing number of arthropod species. Table 14.6 shows general trends in north temperate areas for plants, herbivores and carnivores.

Trends in biodiversity with ecological succession show few plant species that colonize open ground, say after fire, but the first colonists ameliorate conditions so that more species can invade. Plant diversity peaks with the early forest stage when some grasses, forbs and shrubs persist, so this illustrates a mid-domain effect resulting from a non-random process (Figure 14.22). After the early forest stage, competition for light and nutrients results in some reduction in plant species diversity. Southwood *et al.* (1979) recorded a much stronger peak in plant species richness in early succession with a strong decline into the woodland stage in England, but the insects showed high, though slightly declining, richness after the peak had passed, and species abundance was greatest in the late successional woodland sites. Coupled with plant species changes, the apparency of plant species increased (as in Feeny 1975, 1976, see Chapter 4), and the palatability of the species decreased (Reader and Southwood 1981).

In tropical latitudes similar patterns have been observed. Nocturnal tiger moths (Arctiidae) in the Ecuadorian Andes showed highest abundance and species richness in advanced successional sites where secondary scrub or young forest was developing. Early successional sites and mature forest under-story were less rich in species, although the mature forest supported most rare species (Hilt and Fiedler 2005). In the Chamela-Cuixmala Biosphere Reserve in western Mexico, gall-inducing insect species richness increased with plant species richness, with later successional woody plants exerting the strongest positive effects on the number of galling species (Cuevas-Reyes *et al.* 2004). In Amazonian rain forest, recovery of vegetation after bauxite mining has left a successional gradient of time-after-mining lasting 21 years (Fernandes *et al.* 2011). The trends in gall species richness peak at about 14–15 years, and then decline slightly. However, for spiders, which appear to frequent more open habitats, local people on Orchid Island, off the coast of Taiwan, open up woodland for cultivation among trees, where spider diversity is higher than in natural forest (Tsai *et al.* 2006). As with altitudinal gradients, when we examine distributions of specific taxa, responses to successional gradients vary.

14.7.2 Adaptive radiations through time

Another kind of time gradient involves the change in richness within phylogenetic lineages, the adaptive radiation of particular groups, and the distribution and spread of species over the globe. These topics become a blend of ecology, evolution and behavior, but as we have seen repeatedly in this book, the ecological opportunities provided by climatic variation and resource variation through time and space create a complex mosaic of interacting forces that shape cladistic trajectories. The radiation of plants and mammals provided expanding resources for scarabaeoid beetles (Figure 6.16, and accompanying text). The radiation of plants has provided an extraordinarily diverse set of resources

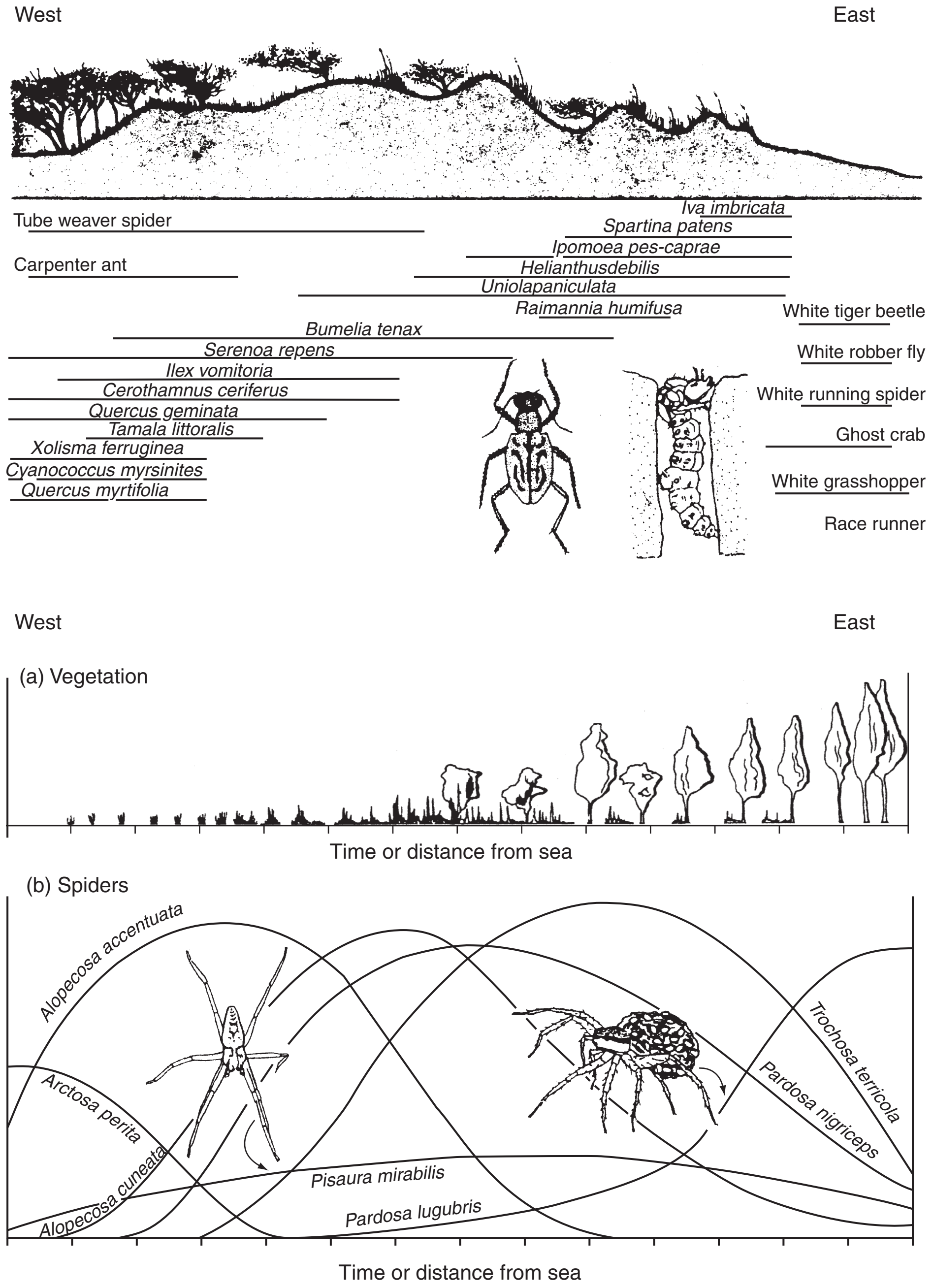


Figure 14.21 Ecological succession on sand dunes. Top: On the east coast of Florida, showing the distribution of plants and arthropods in space and time. The sea is to the east and succession progresses from right to left, with the oldest elements on the left. Prevailing winds are onshore from the east (after Shelford 1963). A tiger beetle adult and larva are illustrated, which are found on open sand in early succession. The race runner, a *Cnemidophorus* lizard (lower right) frequents most of the successional range. Bottom: On the west coast of the Netherlands with (a) change in vegetation from bare sand in the west to woodland in the east, and (b) the change in spider species abundance during succession. Prevailing winds are onshore from the west. After van der Aart 1974.

Table 14.6 **Examples of patterns in ecological succession on three trophic levels, from plants, herbivores and carnivores, in moist north temperate vegetation dominated by forest.**[a] **From Price 1991b**

Characteristic	Early succession	Late succession	References
Plants			
(1) Dominant species	Annual herbs	Large trees	Bazzaz 1968, 1975, 1996
(2) Individual longevity	Short, 1–5 years	Long, 50–500 years	Odum 1959
(3) Size	Small	Large	Odum 1959
(4) Physiological rates	Generally high	Relatively low	Bazzaz 1979
(5) Apparency	Low	High	Feeny 1976
(6) Chemical defense	Toxins	Digestibility reducers	Feeny 1976, Rhoades and Cates 1976
(7) Spatial distribution	Patchy	Extensive tracts	Loucks 1970, Pickett and Thompson 1978, Shugart and West 1981
(8) Biomass per unit area	Low	High	Odum 1969, Whittaker 1970
(9) Biomass of leaves per plant species	Low	High	Ovington 1962, Whittaker and Woodwell 1968, 1969
(10) Number of species per unit area	Low, but increasing rapidly	High	Bazzaz 1975, Whittaker 1970
(11) Structural diversity	Low	High	Southwood *et al.* 1979, Lawton 1983
Herbivores			
(1) Insect species richness	Low	High	Lawton 1983, Southwood *et al.* 1979, Leather 1986
(2) Host plant species specificity	High	Low	Futuyma 1976
(3) Palatability of plant food	High	Low	Reader and Southwood 1981
(4) Flight capacity	High	Can be low or absent	Barbosa *et al.* 1989, Roff 1990
(5) Evolution of egg load per plant	Can be high	Can be absent	Thompson 1983, Price *et al.* 1990

Table 14.6 (*cont.*)

Characteristic	Early succession	Late succession	References
(6) Linkage of ovipositional preference and larval performance	?	Can be low or absent	Price *et al.* 1990
(7) Potential population size	Low	High	Price 1992b
(8) Potential population persistence	Low	High	Price 1992b
(9) Local abundance	Low?	High?	Gaston 1988, Gaston and Lawton 1988
(10) Regional distribution	Low?	High?	Gaston 1988, Gaston and Lawton 1988
(11) Population variation	Low?	High?	Gaston 1988, Gaston and Lawton 1988
(12) Population dynamics	Usually latent?	Many species eruptive	Price *et al.* 1990
(13) Adult size	Small	Large	Niemalä *et al.* 1981
(14) Feeding pattern	Toxin specialists?	Toxin avoiders?	Cates 1980, 1981
Carnivores			
(1) Vertebrate species richness	Low	High	Odum 1950, Johnston and Odum 1956
(2) Vertebrate predator population size	Low	High	Johnston and Odum 1956, Odum 1959
(3) Species richness of parasitoids	Low	High	Hawkins 1988, Hawkins *et al.* 1990
(4) Mortality caused by parasitoids	Low?	High?	Price and Pschorn-Walcher 1988, Gross and Price 1988, Hawkins and Gross 1992
(5) Probability of host limitation by parasitoids	Low	Relatively high	Hawkins and Gross 1992
(6) Host specificity of parasitoids	High	Low	Hawkins *et al.* 1990, Sheehan 1991

[a] Only endpoints are listed; the original literature should be consulted for details and trends in mid succession. Speculative generalizations are followed by a question mark. Most generalities about herbivores apply to the Lepidoptera.

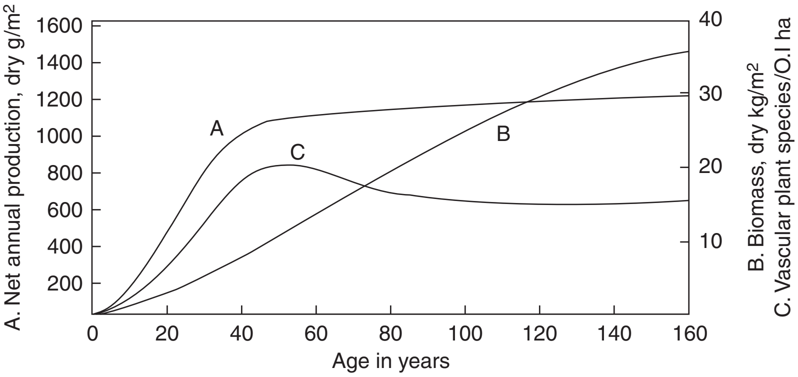


Figure 14.22 Trends in forest succession after fire on Long Island, New York. (A) Net annual production. (B) Biomass. (C) Plant species richness. Note that the peak species richness is reached at about 50 years and then declines. From *Communities and Ecosystems* by R. H. Whittaker (1970). © Robert H. Whittaker. 1970. Reprinted by permission of Pearson Education, Inc.

for insect herbivores to colonize. And up the trophic levels, these insects have become the basis of radiations among parasitoids and predators. As clades expand, so do associated species of mutualists (Chapter 6), parasites (Chapter 8) and up the whole trophic web (Chapter 13). While the cladistic development and radiation of insect taxa is now well described, for example in *Evolution of the Insects* by Grimaldi and Engel (2005), the actual mechanisms and reasons remain speculative on why some groups have radiated extensively and others remain species depauperate. When asked by some theologians about the character of the Creator revealed by the study of nature, J. B. S. Haldane gave the famous answer "An inordinate fondness for beetles," but it required molecular genetic techniques, decades later, to reveal the basis for much of this radiation (Farrell 1998). In the Phytophaga, the oldest and largest herbivorous beetle group, basal lineages remain associated with conifers and cycads, but younger lineages have repeatedly radiated on angiosperms. These "**ecological breakthroughs**" (Farrell 1998, p. 558), occurring within major taxa, have resulted in some of the largest families among the insects: weevils, Curculionidae; long-horn beetles, Cerambycidae and leaf beetles, Chrysomelidae. On a narrow taxonomic relationship, the radiation of milkweed beetles correlates well with the divergence of the host plants (Farrell 2001), and it appears that diversification of milkweeds and beetles was synchronous (Farrell and Mitter 1998). However, there remains much work to be done on the timing of adaptive radiations, the corresponding change and expansion of resources, and the ecological breakthroughs into new adaptive zones.

14.8 Disturbance gradients

Disturbance appears in many guises: wind, flood, fire, erosion, wave action, biotic effects such as herbivory, burrowing and damming, as well as human impacts. Effects of disturbance are widespread, frequent and commonplace, and they have attracted the attention of ecologists for many decades. Tansley and Adamson (1925) excluded rabbits on grassland in southern England and saw a spectacular increase in floral diversity in the exclosures, observed again when myxomatosis killed a large proportion of the rabbit population in the 1950s (Harper 1969). Loucks (1970, p. 17) noted "The natural tendency of forest systems toward periodic perturbation ... recycles the system and maintains a periodic wave of peak diversity ... any modifications of the system that preclude periodic, random perturbation and recycling would be detrimental to the system in the long run." Fire would cause a major disturbance, setting ecological succession back, followed by increasing species diversity, repeated in a wave-like process over decades and centuries. Suppression of fire would allow the forest to reach a climax vegetation with decreased diversity and productivity. Mattson and Addy (1975) noted that major insect herbivores such as the forest tent caterpillar, *Malacosoma disstria*, on aspen, and the spruce budworm, *Choristoneura fumiferana*, on balsam fir, also act as major disturbance factors which influence plant succession, species diversity and primary productivity. Eventually, disturbance became of sufficient interest to warrant a book-length overview: *The Ecology of Natural Disturbance and Patch Dynamics* (Pickett and White 1985).

Connell (1978) reviewed alternative hypotheses on how local diversity of species is maintained over time, dividing processes into those in which species composition is rarely in an equilibrium state, and those in which stability and equilibrium prevail. His long-term studies in tropical rain forests and corals on tropical reefs showed that non-equilibrium conditions prevailed. "The species composition of communities is seldom in a state of equilibrium. High diversity is maintained only when the species composition is continually changing. Diversity is higher when disturbances are intermediate on the scales of frequency and intensity" (p. 1303). He named this the **intermediate-disturbance hypothesis**.

This hypothesis has stimulated a large amount of research effort. The kinds of disturbance relevant to insect species richness are very diverse, including herbivore impact, predation effects, management intensity, urbanization, windstorms, river flow, gradients in salinity, and amplitude of pH and temperature variation. Equally diverse are the results reported, as a few examples will illustrate. Intermediate levels of moose browsing resulted in higher regional species richness of ground beetles (Carabidae) than in non-browsed and heavily browsed areas in Norway (Melis *et al.* 2007). At intermediate densities dragonfly predation on a macroinvertebrate community resulted in the highest species richness (Thorp and Cothran 1984). In the Kruger National Park, South Africa, dragonfly assemblages were richest in rivers with moderate flow fluctuations (Stewart and Samways 1998). Caddisfly richness in the Meurthe River in France was highest at intermediate sites on a salinity gradient (Piscart *et al.* 2005), while weak support for the hypothesis was found for Ephemeroptera, Plecoptera and Trichoptera in a meta-analysis when pH and temperature amplitude fluctuations were considered (Statzner and Resh 1993). After a windstorm blew down trees in an oak-hornbeam forest in France, some support for the hypothesis was found in the response of wood-feeding beetles (Bouget 2005). However, on an urban–suburban–rural gradient with decreasing intensities of human disturbance in Hungary, the hypothesis was not supported by the response of carabid beetles (Magura *et al.* 2004), but a complex of heterogeneity variables accounted for much of the variation, including abiotic factors, cover, decaying wood and prey.

Disturbance of any kind probably impacts many variables, so disturbance itself is not necessarily the factor with the most explanatory power. Hence, for any particular taxon, more specific and relevant gradients may best be employed in order to understand mechanistically the processes involved. Worth noting is that in tropical forest and coral reefs studied by Connell, space is critical to the establishment of new individuals for anchorage and light, and the space created by storms (or experiments) can be accurately and objectively quantified. Therefore Connell's studies set an example of how the intermediate disturbance hypothesis can be applied in ways directly relevant to the organisms under investigation.

Applications

Conserving species richness

An important application using the theory of island biogeography has been in studies of conservation and the maintenance of biodiversity (e.g., Wilson 1988a,b, 1992). Wilson (1992) made a compelling case for the importance of conserving biodiversity and the many highly threatened floras and faunas around the world. Yet there remains inexorable attrition in areas of high diversity and sensitivity, involving habitat destruction, degradation and fragmentation.

As areas of natural vegetation decline, as in the case of tropical rain forest and many other vegetation types, we can employ the theory of island biogeography to predict the associated decline in biodiversity. Using species–area relationships, as in Figures 14.4 and 14.7, we can reverse the area scale and plot the predicted decline of species numbers as island size declines through degradation of habitat (Figure 14.23). This assumes that there is an empirically determined species–area relationship for the particular group of organisms of concern. In the case of Figure 14.23, reptiles and amphibians of the West Indies are the subjects, and they show a general trend in how diversity is lost in a taxon as area declines. We will see later that the rate of loss of insects in the tropics may well be similar to the rate illustrated in the figure. As a general statement, or rule of thumb, there is a 50% loss of species with a 90% reduction in island size (Wilson 1992).

Using this generalization, various authors have estimated rates of extinction as tropical forest area is depleted. Following Wilson's (1992) argument, the predictions are as follows. There may be 10 million species living in tropical rain forest. By 1979 the rain forest was reduced to about 56% of its prehistoric area, and cutting was proceeding at about 1% per year. By 1980 the cutting rate had almost doubled to about 2% per year. This means that about 0.5% of the species are going extinct every year – or about 50 000 species. A conservative estimate would be 27 000 species per year, 74 species each day, and 3 species each hour! At present rates of destruction, 90% of the

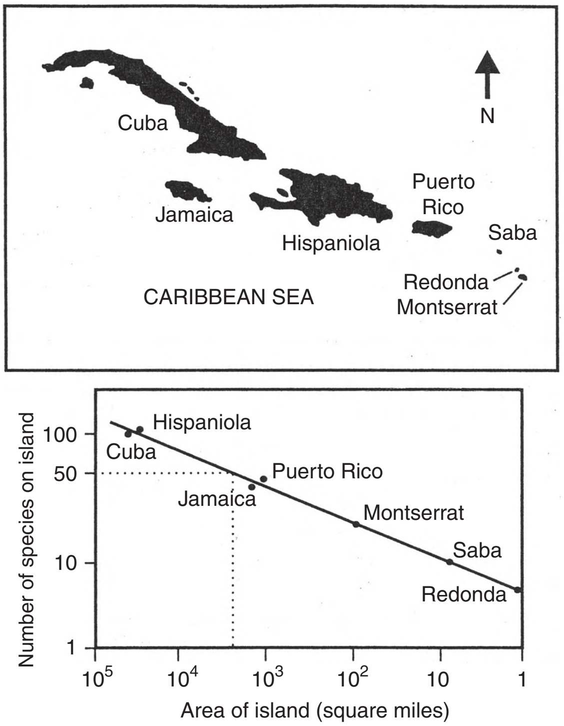


Figure 14.23 The archipelago of the West Indies and the number of reptiles and amphibians recorded on each island, relative to island area (log scales). Note that Cuba and Hispaniola have about 100 species recorded and have an area of about 40 000 square miles. When the number of species drops to 50 per island, the area has declined by about 90%, to 4000 square miles, as indicated by dashed lines. This illustrates the rule of thumb that a reduction of 90% of area results in a loss of 50% of the species. From Wilson 1992. Reprinted by permission of the publisher from *The Diversity of Life* by Edward O. Wilson, p. 222, Cambridge, MA: The Belknap Press of Harvard University Press, Copyright © 1992 by Edward Wilson.

tropical rain forest could be destroyed by about 2040, when it is possible that 50% of tropical species will have gone extinct.

The equation for the species–area relationship, as in Figures 14.4 and 14.23, is:

$$S = CA^z$$

where S is the number of species present, C is a constant, A is the area of an island, be it a habitat island or an oceanic island, and z varies with the group of organisms being considered. Species with a relatively high z value, at about 0.35, are poor dispersers, such as land snails and orchids, resulting in higher levels of endemicity. Therefore, as area is lost, the slope of the species loss is relatively steep. A relatively low value of z is observed for species with high dispersal, such as birds, where a z value may be 0.15. Where are insects likely to place within this range, especially those in tropical rain forest?

Erwin (1988) made some preliminary estimates of the endemicity of canopy-dwelling beetles in South America in the Amazon Basin. In the Tambopata Reserved Zone in Peru, in one upland forest type and in two plots only 50 m apart, the overlap of shared canopy beetle species was only 8.7% of species. The sample included 7 families of beetles and 126 species. This small similarity of beetle assemblages so close together suggests that beetles have specific habitat requirements and are distributed in very local patches of the canopy. Other samples from Manaus, Brazil, add support to the evidence that endemicity is high in these canopy assemblages. In four forest types 70 km or more apart, a total sample of 61 beetle families and 1080 species showed that only 1% of species were found in all four forest types.

Thus, for tropical canopy-dwelling beetles at least, and probably for many insect herbivores, we should anticipate relatively high z values of around 0.30, the value used for the rule of thumb mentioned above. For the West Indian butterfly fauna shown in Figure 14.7, the z value was 0.26 in the original survey in 1948, but declined to 0.20 with the more recent survey (Davies and Smith 1997). Especially with insects, very thorough sampling may result in reduced z values, well below 0.30. Values for z calculated by Fonseca (2009) for some studies listed in Table 14.2 include 0.47 for leaf miners on American oaks (Opler 1974); 0.34 for leafhoppers on British trees (Claridge and Wilson 1976); cynipid gall wasps in the US Atlantic region, 0.25, and California, 0.63 (Cornell and Washburn 1979) and agromyzid flies, 0.14, and Macrolepidoptera, 0.16, on Umbelliferae in Britain (Lawton and Price 1979).

Several studies have shown the high richness of insect herbivores in various vegetation types, but with a high number of rare species (e.g., Price *et al.* 1995, Figure 14.2). Erwin (1988) collected 3099 individual beetles at Tambopata and 1093 species. This averages at less than three individuals per species. Sampling weevils in tropical Panama, Wolda *et al.* (1998) noted the high degree of endemism and the high proportion of rare species. Wolda (1983, 1996) also noted impressive endemism in tropical cockroaches and pselaphid beetles.

Another kind of prediction derived from the theory of island biogeography is the size of a habitat island required to sustain a certain number of species in a nature reserve. The desire would be to develop a reserve larger than the habitat fragments that support just a few current species each, such that all the species could be sustained indefinitely in one conservation area. Therefore, the species–area relationship derived from the habitat fragments needs to be extrapolated to a point where the area is large enough to predict that all species can be supported. Take, for example, the study by Shreve and Mason (1980) on 22 woodland areas in eastern England, which supported a total of 26 butterfly species. Any single wood supported 1 to 22, but none contained all 26 species. How much woodland would be needed to support them all, and what confidence could we have in the estimate?

The area required to support all species is called the **point estimate** (Boecklen and Gotelli 1984), and is derived by extrapolation to the number of species to be preserved. Then we would like to know the confidence we can have in any one area supporting a certain number of species, for which **prediction intervals** are calculated. These are similar to confidence intervals which provide the average number of species a given area will support. However, for conservation purposes we need to preserve all species and know a particular species number for a given area. Thus prediction intervals are wider than confidence intervals, but more realistic if we want to conserve 26 species of butterfly in one area.

When such estimates are made, we begin to see some of the problems involved (Figure 14.24). The point estimate is more than one order of magnitude beyond the empirical data, and we have no idea if the linear species–area model is valid at this scale. In addition, the 95% prediction intervals for area maintaining 26 butterfly species, either side of the point estimate, span over two orders of magnitude (Boecklen and Gotelli 1984). If a planner wanted to be sure of conserving 26 butterfly species with 95% confidence, the safest area to design for would be two orders of magnitude larger than the point estimate, or in the order of 100 000 hectares.

This kind of approach is central to the debate on whether one large area is better to conserve a set of species, or many smaller areas are more effective. This debate has been reduced to “single large or several small” reserves, and the acronym SLOSS has been applied. Concerns revolve around keeping populations large to maintain genetic diversity, and to avoid chance events which cause extinction, maximizing habitat heterogeneity to provide

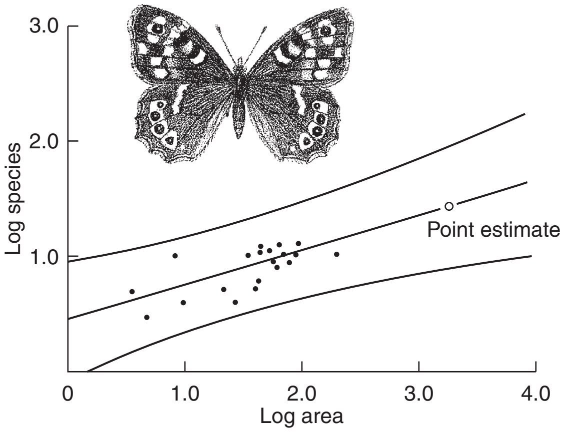


Figure 14.24 The species–area regression on the number of butterfly species in woodlands of eastern England, studied by Shreve and Mason (1980). The regression line is extrapolated to the point estimate (open circle), and the 95% prediction intervals are also estimated. Reprinted from *Biological Conservation* 29(1) by W. J. Boecklen and N. J. Gotelli. Island biogeographic theory and conservation practice: species-area or specious-area relationships? Pages 63–80. Copyright 1984, with permission from Elsevier.

adequate resources for all species of concern, and the maintenance of more than one population to counter the risks of epidemic diseases. Clearly, each planner has a unique landscape to manage, and decisions will depend upon the land and the species to be conserved. Perhaps a bet-hedging strategy would emphasize the need for very small patches to maximize protection of species, with the contrast being a single large reserve vs. plentiful patchy reserves, or SLOPP (Samways 1994). Many considerations are relevant to the planning process (Samways 2005), usually in the face of serious constraints based on the land available for preservation.

One ameliorating factor when land is limited involves corridors of habitat, which allow the movement of species between patches, making the effective conserved area for species larger and more diverse (Samways 1994, 2005). Corridors may take various forms, such as paths, forest roads, hedgerows, roadsides, drainage ditches or any other linear band of habitat along which species can travel relatively easily. Carabid beetles will move along the verges of roads between heathland habitats (Vermeulen 1994), and remnants of indigenous grassland in a forested landscape provide linkages between suitable habitats for adult butterflies in South Africa (Pryke and Samways 2001, 2003). In a large-scale replicated experiment Damschen *et al.* (2006) found that fragments of habitat connected by corridors conserved more plant species than isolated patches, and the benefits of corridors increased over time. Such improved plant species richness would, no doubt, increase the biodiversity of insect herbivores, carnivores and pollinators.

In agricultural and forestry management, the maintenance of biological diversity is seldom of prime concern. Nevertheless, increasing numbers of ecologists are using biodiversity monitoring for metering the preservation of landscape quality in such manipulated landscapes. Some are concerned with diversity in general, some with maximizing natural enemies of pest species, while others emphasize the conservation of butterflies, bees and other pollinators (e.g., Kruess and Tscharntke 1994, Hendrickx *et al.* 2007, Kohler *et al.* 2007). In addition, much concern is devoted to biodiversity of insects as food for wild birds, particularly in Europe (e.g., van Emden and Rothschild 2004). Not surprisingly, high-intensity agriculture generally reduces diversity of arthropods, and natural or seminatural habitats are favorable. As in temperate studies, tropical forest modification and fragmentation were found to affect adversely insect species richness, diversity declining with increased modification and reduced size of forest fragments (Nichols *et al.* 2007). A plea has been made to increase efforts in long-term environmental monitoring, which could include physical factors such as ice melt times and water quality, or biological activity like blooming phenology (Lovett *et al.* 2007), and many publications on insects and other arthropods advocate more testing and application to monitor environmental quality. Insects may be employed as **bioindicators** of environmental change or general quality (McGoech 1998, McGeoch *et al.* 2002), or the efficacy of restoration ecology (e.g., Andersen and Sparling 1997, Andersen *et al.* 2002, 2003). On questions regarding environmental quality and landscape management, insects offer unlimited potential to inform our decisions and to evaluate our impact on the landscape.

Summary

Biodiversity is the number of species in a locality of any size up to and including global biodiversity: it can be measured and studied at any scale. Measuring or estimating biodiversity is a challenge, but a theme in such studies is the detection of pattern. Patterns can be observed when richness of species in relation to island size is measured, and the remoteness of islands from sources of colonists influences the equilibrium number of species present on an island. Equilibrium is maintained by a balance of immigration and extinction of species. Islands may be formed in oceans, lakes, fragments of vegetation or host-plant species for herbivores in a matrix of non-host species, with a general relationship of increasing insect species number with increasing island area. The potential mechanisms resulting in the species–area relationship are multiple, including the possibility of neutral drift playing a role. Another frequently observed trend in biodiversity is that species richness increases from arctic and north temperate latitudes into the tropics. This pattern has generated many hypotheses about the mechanisms involved, with one obvious fact that tropical lands cover a vast area, with several causes for richness evident: the species–area relationship, large population sizes, reduced extinction rates and high speciation rates. With more plant species in the tropics we should expect more insect species, and plants will respond to plentiful water availability present in the wet tropics. However, caution is needed with latitudinal trends because interesting anomalous patterns are observed in a variety of taxa, with the species richness of parasitoids generating several hypotheses on the relatively low richness in the tropics. Aquatic insects also do not adhere well to general trends with latitude. Also observed are altitudinal gradients with biodiversity declining with increasing altitude, although adherence to this trend depends upon the taxon considered. Species composition also changes with altitude such that life zones can be identified. Time gradients in biodiversity are observed in ecological succession and as taxa undergo adaptive radiation, and disturbance gradients often show peak biodiversity at intermediate levels of disturbance.

Clearly, understanding patterns of biodiversity over several different independent variables is important in planning for the conservation of species richness. The species–area relationship allows predictions on the area required to conserve a certain number of species in a particular taxon, and on the loss of species as fragmentation of habitats increases.

Questions and discussion topics

1. If you were challenged to design a plan for the conservation of an insect taxon, which group of insects would you select as being promising candidates, and what would your strategy be?
2. Within an urban setting, many island-type habitats exist. Identify as many of these as you can, suggest the kinds of species adapted to each, and describe how you would undertake a study on patterns of biodiversity.
3. Discuss experimental methods which would advance the understanding of mechanisms influencing biodiversity.
4. As mountains rise the area of an elevational band declines, generating an inevitable correlation between elevational climate change and the species-area curve. Can you suggest methods by which the correlated effects can be partitioned?
5. In a landscape plan for conservation, how would you employ insect species as bioindicators, and which groups of insects would you prefer to use?

Further reading

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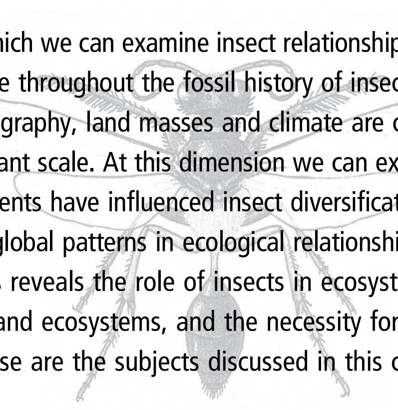
15

Planet Earth: patterns and processes

The largest scales on which we can examine insect relationships with their environments are time and space: time throughout the fossil history of insects, and the space over the globe in which topography, land masses and climate are constantly in flux. Planet Earth provides the relevant scale. At this dimension we can examine the paleobiological record and how past events have influenced insect diversification, the current impacts of climate change and global patterns in ecological relationships. Breaking the planet down into smaller units reveals the role of insects in ecosystems, their importance as invaders of continents and ecosystems, and the necessity for conservation of habitats and their denizens. These are the subjects discussed in this chapter.



15.1 The paleobiological record

The history of life provides clues, or predictions, about what the future may bring. Using families of insects as a measure of richness in the fossil record provides a stable estimate: family richness is high enough to capture diversity changes, and family size is large enough to provide a reliable signal (Labandeira and Sepkoski 1993). In the Carboniferous period numbers of families increased rapidly, it declined during the Permo-Triassic extinctions about 245 million years ago, and then increased at a steady rate for the next 220 million years (Figure 15.1). The jump in richness in the mid-Tertiary resulted from rich fossiliferous deposits from that time, including Baltic amber, and the Florissant shales of Colorado. At the end of the Paleozoic era and the Permo-Triassic boundary, whole orders of insects went extinct, including the Palaeodictyoptera and related clades (Figure 15.2). These were endowed with piercing and sucking mouthparts for feeding on plants, and presumably were impacted by major losses in plant diversity during the extinctions. After the end of the Paleozoic, four major groups of insects, extant today, expanded exponentially through the Mesozoic and Cenozoic eras: the Hemiptera, Coleoptera, Diptera and Hymenoptera. The Lepidoptera were late arrivals in the fossil record, undergoing expansive radiation in the upper Cenozoic (Figure 15.2).

Several aspects of these fossil patterns are noteworthy. The rise in family diversity during the Mesozoic resulted not from a higher rate of origination of families, but from a greatly reduced extinction rate, indicating a durability of taxa at the family level (Labandeira and Sepkoski 1993). This is heartening in the face of dire predictions of extinctions in the current and future times. However, extinctions have occurred, as at the Cretaceous/Tertiary (K/T) boundary in which specialized herbivores were impacted heavily and generalists rebounded to levels in the Cretaceous (Labandeira *et al.* 2002). Another interesting pattern is the expansion of major plant-feeding insect taxa well before the adaptive radiation of the flowering plants, the angiosperms. Angiosperms began to radiate in the Lower Cretaceous, around 140 million years ago, but insect radiations were apparent in the early Mesozoic, in Triassic times, 240 million years ago. So insect-herbivore groups were multiplying for 100 million years before the angiosperms. While many authors have suggested that insect radiations depended on the richness of flowering plants, the converse is a more likely scenario; that insects contributed to the radiation of the angiosperms (Labandeira and Sepkoski 1993). This provides a cautionary view for current declines in pollinator abundance and diversity. A third feature of the fossil record is the response of insects to global warming during previous geological eras. Mean annual temperatures rose about 7–9 °C during the late Paleocene (56 MYA) to the early Eocene (53 MYA),

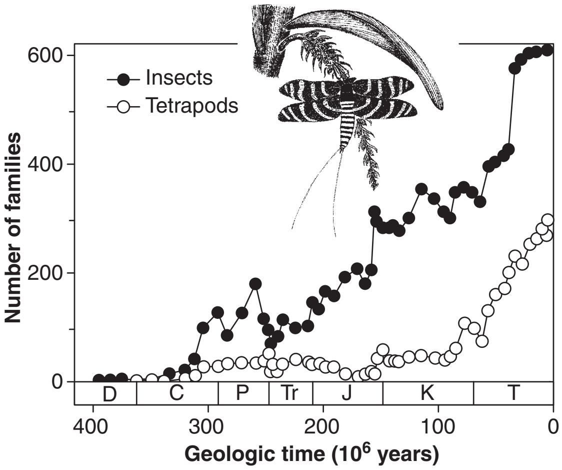


Figure 15.1 The number of families of insects in the fossil record through geologic time: D = Devonian, C = Carboniferous, P = Permian, Tr = Triassic, J = Jurassic, K = Cretaceous and T = Tertiary. The tetrapod fossil record is also shown to illustrate the relatively rich insect fossil record. From Labandeira, C. C., and J. J. Sepkoski 1993. Insect diversity in the fossil record. *Science* **261**:310–315. Reprinted with permission from AAAS.

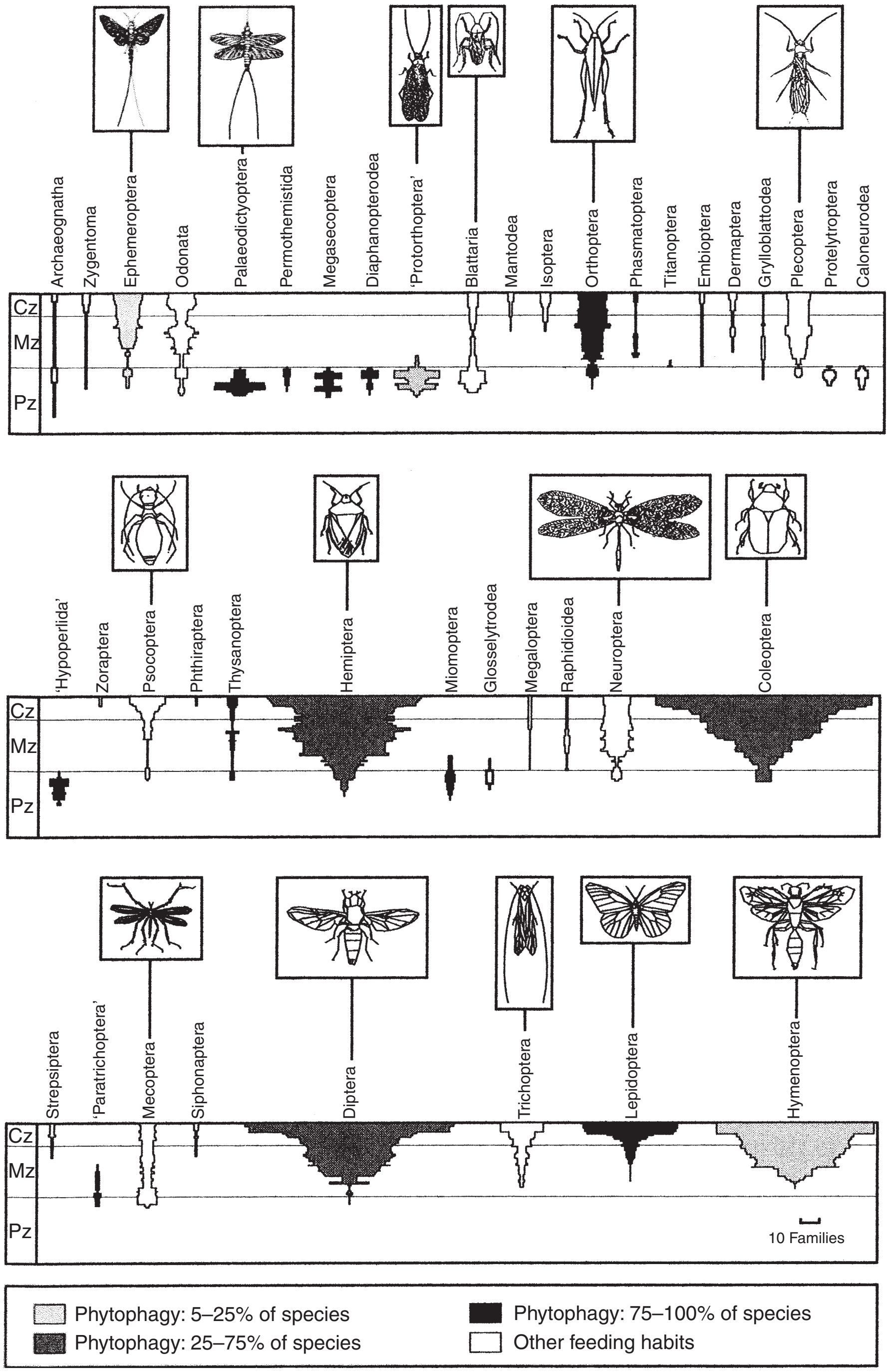


Figure 15.2 The family-level changes in diversity of major insect clades through geological time. Note the massive radiations in the Hemiptera, Coleoptera, Diptera and Hymenoptera, plus the relatively late blooming of the Lepidoptera. Shading within clades illustrates the percentage of species that were phytophagous. The time scale covers the major eras in geologic time: Pz = Paleozoic, Mz = Mesozoic, Cz = Cenozoic. In comparison with Figure 15.1 the Paleozoic covers up to the Permo-Triassic boundary. The Mesozoic era covers from the Triassic to the K/T boundary, and the Cenozoic era spans the Tertiary to the Quaternary. From Labandeira 2002, modified from Labandeira and Sepkoski 1993.

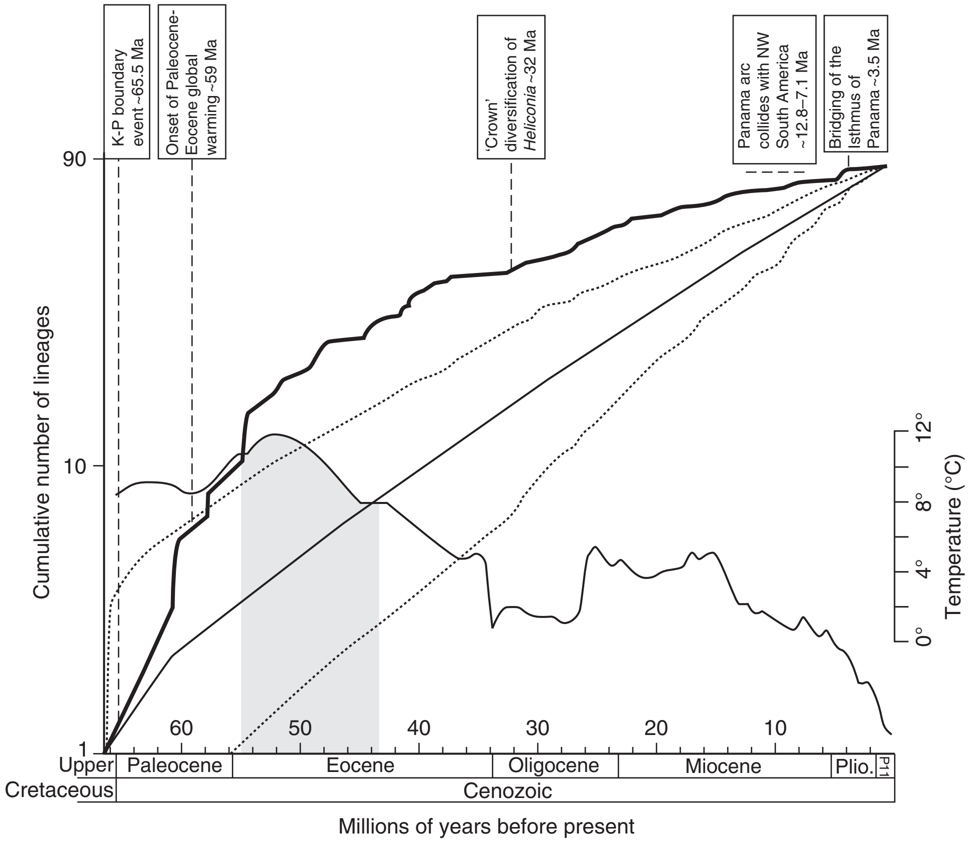


Figure 15.3 A lineage accumulation curve (solid black) showing the evolutionary radiation of the genus *Cephaloleia*, a genus of rolled-leaf hispine chrysomelid beetles, based on a molecular phylogeny. Temperature changes are also shown with a peak at around 50 million years ago, and the scale on the right. A constant diversification rate model is shown as an almost straight line with 95% confidence intervals, and the model is rejected when the empirical black trajectory of richness passes outside the confidence intervals just after the onset of the Paleocene-Eocene global warming at about 59 million years ago. Major geological events are noted in boxes at the top of the figure. "Crown" diversification of *Heliconia* at about 32 million years ago marks the time of origin of the first *Heliconia* ancestor and the radiation of all descendents to the present time. From McKenna and Farrell 2006. Copyright 2006 National Academy of Sciences USA.

causing a shift from temperate to subtropical vegetation (see Figure 15.3). Plant species turnover was above 80% and all dominant plant species were replaced, with a net increase in plant species diversity (Wilf and Labandeira 1999). Resulting from the warming trend was an increase in the variety of damage types on fossil plants, and the intensity of damage. Damage by insects increased on average by about 7%, up to 36% of specimens damaged, with higher levels on the birch family, Betulaceae, with an increase of about 13% (see also Wilf *et al.* 2001). Equivalent increases in herbivory in forests and in agriculture in response to current global warming would be costly, and perhaps devastating in marginal agricultural land.

15.1.1 Warming and adaptive radiation

A closer inspection of the effects of global warming in the past on insect diversity can be derived from phylogenetic studies of particular groups, now using the number of species as the measure of diversity. McKenna and Farrell (2006) asked if speciation rates were constant or spasmodic in the large genus of rolled-leaf hispine chrysomelid beetles, *Cephaloleia*, and if tropical forests acted as cradles of new originations, or museums of old taxa. These are Neotropical leaf beetles which originated over 66 million years ago (Wilf *et al.* 2000) based on diagnostic damage on fossil leaves. As mentioned above, the K/T boundary extinctions impacted specialist herbivores particularly hard, leaving resources open to new adaptive radiations. The global warming of the late Paleocene-Eocene appears to have "triggered" the rapid diversification of *Cephaloleia*, and its host plants, far beyond that predicted by a constant-speciation model (Figure 15.3, McKenna and Farrell 2006, p. 10 948). Additional statistically significant spurts of speciation were noted during the Oligocene adaptive radiation of host plants in the genus *Heliconia*, and a more recent Miocene-Pliocene acceleration of speciation during the collision of the Panama land mass with South America, ultimately connecting North and South America. McKenna and Farrell concluded that accelerated rates of radiation have occurred in leaf beetles, coincident with relatively ancient global warming, as well as relatively recent tectonic landmass movements, and thus the wet tropics have acted both as museums which preserve old lineages and cradles for new adaptive radiations.

15.1.2 Cooling and migration

If warming climatic conditions result in accelerated speciation and origination of higher taxa, does cooling cause the reverse effects: stasis and extinction? The fossil record reveals that insects show remarkable geological persistence (Labandeira and Sepkoski 1993). The extant beetle genus *Tetraphalerus* is close morphologically to a Jurassic fossil from 153 million years ago! And the modern crane fly genus *Helius* has been identified in 93-million-year-old deposits, well into the Cretaceous. Also, an 89-million-year-old fossil fits well into the currently present leaf-mining genus, *Stigmella*. Modern genera and even species are represented in many fossils from 10–40 million years ago from Miocene back to Eocene times. Almost all beetle species from Pliocene and Pleistocene deposits in the northern hemisphere belong to modern species, many showing persistence in the fossil record for well over a million years (Labandeira and Sepkoski 1993).

Coope (1973, 1978) has asserted that stability in morphology is the norm rather than the exception, and that species persist by tracking climatic conditions as the zones shift. For example, an *Aphodius* beetle in Britain during the last glaciation now lives in Tibet, and a *Tachinus* beetle species that occurred with *Aphodius* in Britain is now a resident of Siberia and North America. It appears that rather than extinction during cooling climates, including glaciations, many species migrated together in response to climate changes without showing much if any morphological change.

These kinds of conclusions are based mainly on beetles because the hard exoskeleton fossilizes relatively well. Some beetles found in Britain during the glacial or interglacial times in the late Quaternary, less than 500 000 years ago, are cold-adapted species now found in arctic and alpine localities in Europe, but not in England (Figure 15.4, Elias 1994). Other beetle species were thermophilous in Britain, but are now resident in Spain, Sicily or other parts of southern Europe and North Africa (Figure 15.5). In North America, a southern refugium south of the glaciation enabled cold-adapted beetle species to persist, but they migrated north as the ice receded. Current distributions of some cold-adapted species now occur in Alaska and northern Canada, but with one species, *Amara alpine*, persisting as isolated populations in the Rocky Mountains in the United States (Figure 15.6). Persistence and morphological stability characterize many species,

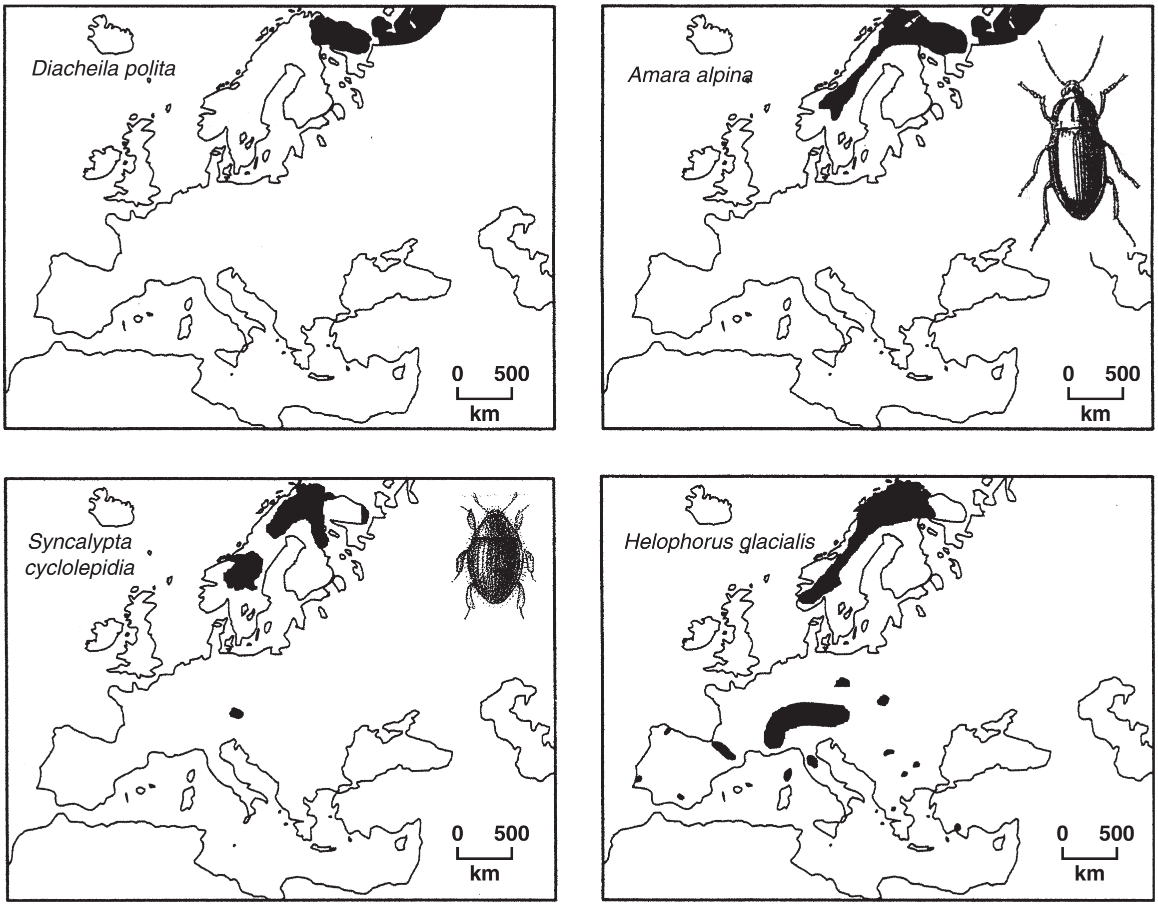


Figure 15.4 Current distributions of four cold-adapted beetle species which were found in British glacial deposits formed during the Quaternary, but which have migrated into colder localities in more northern latitudes or higher altitudes. From Elias 1994.

at least in the beetles, through the cooling impact of glaciations.

15.1.3 No-analog communities

It is easy to imagine that such shifting of species over large distances results in novel communities, new combinations of species, original interactions and perhaps ecological surprises. The result will be **no-analog communities** – "communities that are compositionally unlike any found today" (Williams and Jackson 2007, p. 475). Williams and Jackson found common ground among the paleoecologists and the global-change ecologists who study systems deviating significantly from what can be observed in modern times. These authors adapted a conceptual model from Jackson and Overpeck (2000) to illustrate how local climates may move in climatic space, which shifts the species able to coexist because their fundamental and realized niche space is not coincident (Figure 15.7). Climate space is defined by two variables, 1 and 2, and the **fundamental niches** of species 1, 2 and 3 are constant, and located in this space. The **realized**

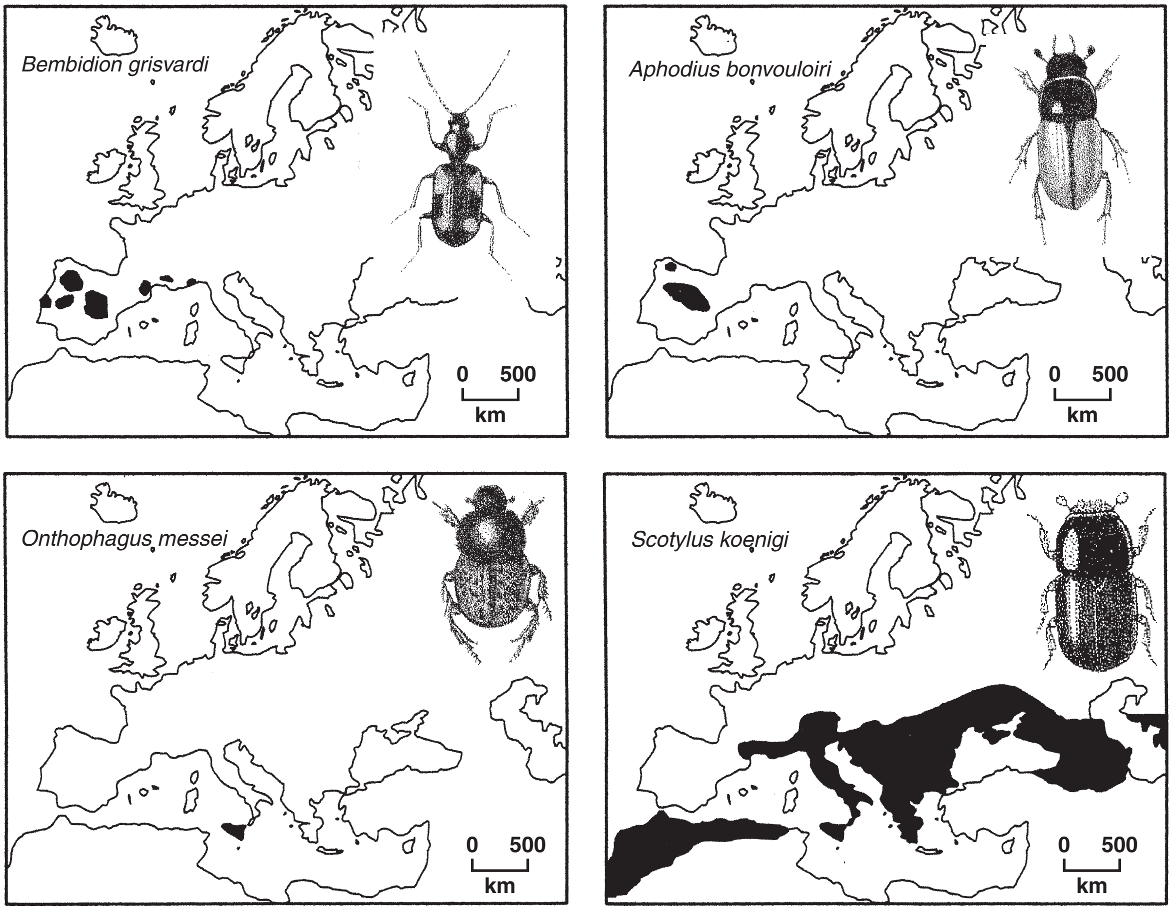


Figure 15.5 Distributions of four thermophilic beetle species present in Britain during the Quaternary, which are currently found in warmer more southern localities. From Elias 1994.

niches of the species move with the climatic conditions within the confines of the fundamental niche space. Species can coexist in a local assemblage only when their distributions overlap within the current climatic conditions. Climate is hypothesized to move from the present, illustrated by an open ellipse, to some time, *t*, in the past or in the future, so the coincidence of realized niches of species changes as the climate changes. Only where the fundamental niches of species overlap, within the current climatic conditions defining their realized niches, will species be found in the same community. In the present, species 1 and 3 may be found together, but species 2 and 3 would not coexist. However, at time *t*, the climate would be conducive to both species 2 and 3, and they would become components of a no-analog community relative to what could be observed by an ecologist in the present day.

All this may sound rather hypothetical, but Williams and Jackson, studying fossil deposits of plants, note that real no-analog communities existed for most of the time from 21 000 to 6000 years before present. Plant communities were particularly divergent from present communities in Alaska and the interior of eastern North America,

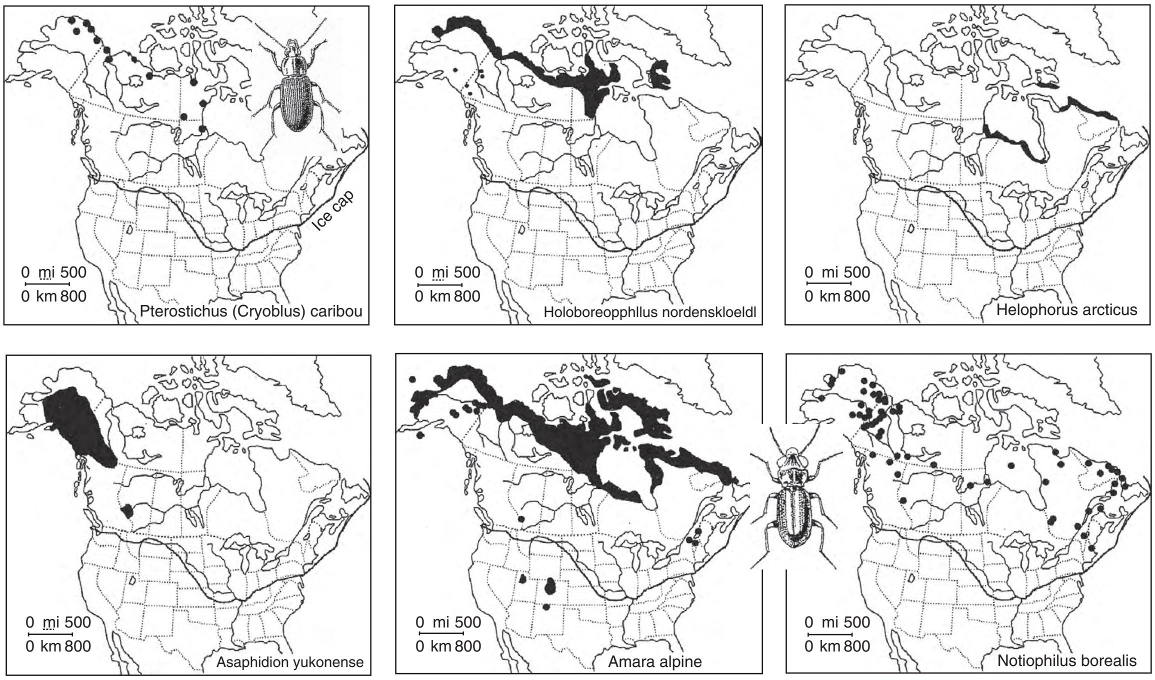


Figure 15.6 Modern North American distributions of six cold-adapted beetle species. The beetles probably survived glaciation in the southern refugium south of the Laurentide ice cap, the limits of which are noted in the top left figure, and shown in the remainder of the figures. From Elias 1994.

between 17 000 and 12 000 years ago during a warming trend. Needless to say, as plant communities change, so do the realized niches of insects at all trophic levels. Host plants move over the landscape, and insects move with them. Both groups interact with different plant species, litter composition varies and the whole geographic mosaic of interactions of the plants, insects and other species changes through time. As we saw in Chapter 12 on Community structure, phenotypes and genotypes of plant species impact herbivore community composition, litter quality, litter decomposition and other ecosystem processes. So conditions in all parts of the changing vegetation will affect the insect denizens of these plant communities. **"Species reshuffling"** (Williams and Jackson 2007, p. 475) has been a feature of the paleobiological past, as it will be in the global climate change of the future.

15.2 Climate change

We can study climate change in many different ways, but here we will concentrate on how insects can inform us about the phenomenon, and how they are impacted by it.

15.2.1 The biological fingerprint

As an introduction to global environmental change, Vitousek (1992) noted the following kinds of changes:

(1) Alteration of the composition of the atmosphere, particularly carbon dioxide (CO_2).
(2) Climate change because of global warming caused by greenhouse gases such as CO_2 and methane.
(3) Declines in stratospheric ozone concentrations with an increase in ultraviolet radiation.

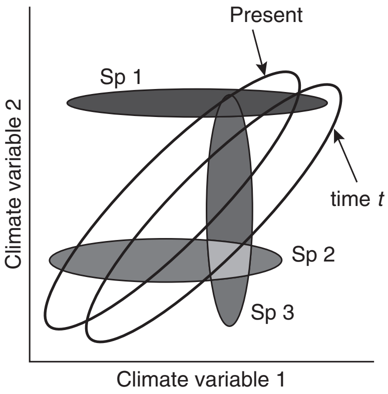


Figure 15.7 The concept of no-analog communities. The fundamental niches of three species are plotted in climate space defined by variables 1 and 2. The realized niches of the species depend on the current climate during the present, or at time, *t*, in the geological past or in the globally warming future. Where species distributions overlap in the fundamental niches within the climatic envelope, they will coexist, as do species 1 and 3 in the hypothetical present, but not at time *t*, when new combinations of species will be observed, not recorded during the present. From Williams and Jackson 2007, based on Jackson and Overpeck 2000.

(4) Land use change which, although local, together alters global budgets of greenhouse gases and threatens major ecosystem types.
(5) Accelerated decline in biodiversity mainly because of land-use change.
(6) Biological invasions, mostly because of increased mobility of humans, and the movement of plants, animals and their products by humans.
(7) Changes in atmospheric chemistry resulting in phenomena such as acid rain and increased nitrogen deposition.

Vitousek (1992, p. 7) noted that most of these environmental changes were well documented but that "human-caused global climate change has not been detected unequivocally as yet." He cited the report by Wigley and Barnett (1990), which appeared in the authoritative Intergovernmental Panel on Climate Change (IPCC) (Houghton *et al.* 1990). Since then anthropogenic climate change has become generally accepted, and the biological evidence for global warming is overwhelming (e.g., Parmesan 2006).

Long-term monitoring of butterfly populations has yielded solid evidence of phenological changes in the dates of first appearance of species, and the duration of the flight period in multibrooded species (e.g., Roy and Sparks 2000). Over the period of 1976 to 1998, the date of first appearance of the red admiral butterfly, *Vanessa atalanta*, advanced by 36.3 days, and the flight period duration increased by 39.8 days (Figure 15.8). For the green-veined white butterfly, *Pieris napi*, the date of first appearance advanced about 2 weeks and the duration of the flight period by over 3 weeks. In cool-temperate climates such as the British Isles global warming has had some beneficial effects, prolonging foraging and breeding seasons. In central California, among 23 species of butterfly, 70% advanced the date of first flights by an average of 24 days over 31 years (Forister and Shapiro 2003), with warmer, drier winters promoting early flight, and accounting for 85% of the variance in flight date.

Another trend in butterfly ecology has been the northward shift in distribution during the 1900s. A sample of 35 European butterfly species revealed that 63% had range shifts northward by 35–240 km in non-migratory species, while only 3% of species shifted to the south (Parmesan *et al.* 1999). Similar changes have been recorded in North America also (Walther *et al.* 2002). Of 35 insect species, 13 showed phenological changes as predicted by climate change, no species changed in a way opposite to that predicted and 22 species remained stable in their distribution (Parmesan and Yohe 2003). Among 52 insect species during 98 years, 34 species shifted north as predicted, 1 species shifted south and 17 remained stable. Taking evidence for plants, birds, insects, reptiles and amphibians, fish and other marine species, Parmesan and Yohe (2003) showed that, in phenological changes among 484 species, 87% were consistent with predicted change and 13% changed in the opposite direction. Distributional changes

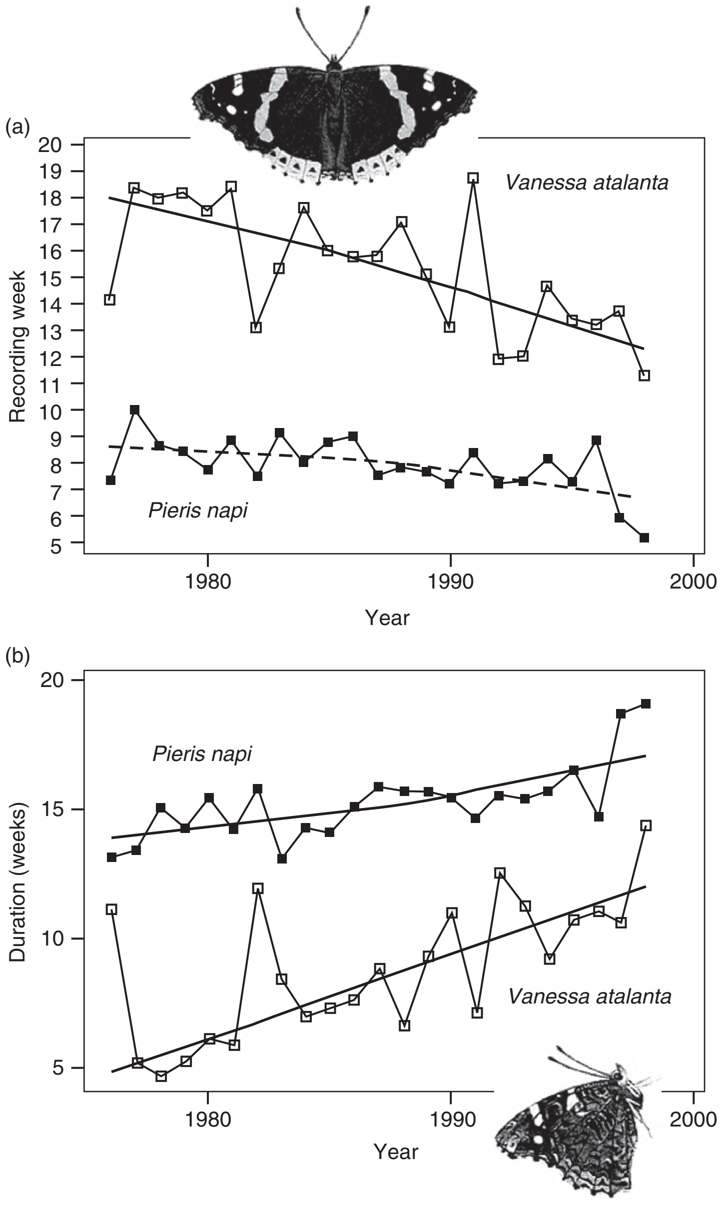


Figure 15.8 Trends from 1976–1998 in (a) the date of first appearance in Britain of *Vanessa atalanta* and *Pieris napi*, and (b) the duration of the flight period. Week 1 is set at the first week in April. From Roy and Sparks 2000. Reprinted with permission from Blackwell Publishing.

were again mostly as predicted for poleward/upper-range boundaries and equatorial/lower-range boundaries, with 81% and 75% of species responding as predicted, respectively.

In addition to phenological and distributional changes in single species, there is likely shifting of these variables in one species relative to another: plant hosts and insect herbivores, and insect prey and their predators. As Visser and Both (2005) point out, we need a yardstick with which to estimate the impact of phenological changes in a species. Will the change be adaptive or maladaptive? They recognize

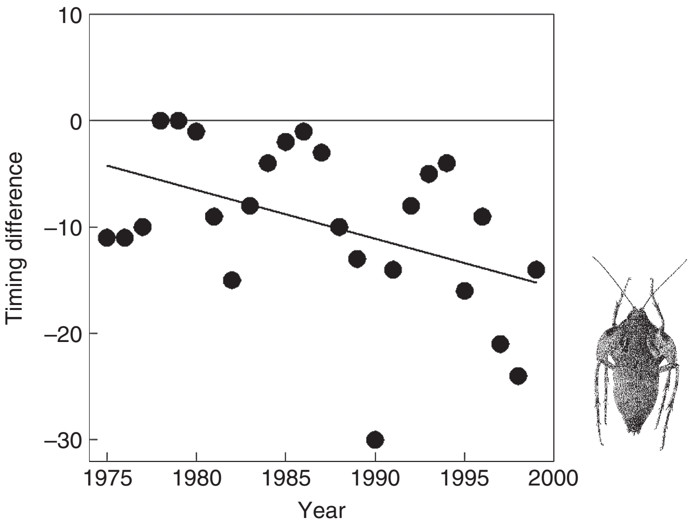


Figure 15.9 The increasing discrepancy between date of egg hatching in the winter moth with the date of bud burst in oaks from 1975–1999. The timing difference, in days, equals the date of egg hatching minus the date of budburst, so that 0 shows complete synchrony. From Visser and Holleman 2001.

that food availability is a suitable yardstick, and for insect herbivores plant phenology does not necessarily shift at the same rate as the herbivores', causing misfits. This subject is in need of more study, but in three cases of insect herbivores, two became less well synchronized and one remained more-or-less synchronized. In the larger literature 8 out of 11 studies documented reduced synchrony between food abundance (prey) and predators. For example, the shift in egg-laying date in great tits became less synchronized with the biomass peak of caterpillar prey in the Netherlands, but not in southern England.

One clear case of an increasing mismatch between plant phenology and insect herbivores concerns the bud-burst phenology of oak trees in the Netherlands and egg hatching by the winter moth, *Operophtera brumata* (Visser and Holleman 2001). There has been a trend of increasing asynchrony between bud burst and egg hatch from 1975 to 1999 (Figure 15.9), with eggs hatching too early so that larvae were without food and perished. Another study involves a remarkable record of 113 years of surveys on 9 butterfly species and 20 moth species which migrate from France, across the English Channel, to England each spring (Sparks *et al.* 2005). As temperatures have risen in the area, migration dates have advanced, but food phenology in Britain has not necessarily advanced to the same extent. For example, the red admiral butterfly uses as a major food plant the stinging nettle, *Urtica dioica*, in which flowering phenology has not advanced, creating a mismatch for the migrating butterfly (Visser and Both 2005). A mitigating factor, perhaps, is that with a warming southern England, the red admiral may become a resident in England which would probably increase synchrony with the nettle food source.

Not all warming trends have been anthropogenic because long-term climate cycles also play their role, such as the North Atlantic oscillation (NAO) which is an important driver of climatic fluctuations in the North Atlantic and surrounding land masses, just as the El Niño in the Pacific Ocean influences the western United States. NAO has tended to be positive and a warming influence since the 1970s.

Added to the well-studied cases of butterflies, with long-term monitoring data, enabling the description of trends, many pest species have been responding to warming trends also, moving north in the northern hemisphere, and upward in elevation. The pine processionary moth, *Thaumetopoea pityocampa*, has expanded its northern range in France by 87 km in the past 32 years, and increased the upper elevational limit of its distribution in Italy by up to 230 m (Battisti *et al.* 2005). Warmer temperatures have resulted in the altered life cycle of the mountain pine beetle, *Dendroctonus ponderosae*, in the Rocky Mountains, from a 2-year to a 1-year cycle, with the consequence of increasing populations and threats to the forests. Mosquitoes are expanding ranges under the influence of climate change, carrying with them in the tropics *Plasmodium* pathogens, which cause malaria and other diseases (Flannery 2005). The potential exists for malaria to spread into high population densities in the tropics from areas which largely precluded human existence because of the severe effects of the disease. Models of malaria transmission under the influence of climate change generally predict increasing ranges of suitable climatic conditions in Africa (e.g., Martens *et al.* 1995, Ebi *et al.* 2005). Tick-borne encephalitis carried by *Ixodes ricinus* has increased in Sweden as numbers of ticks have risen at the northern limit of their distribution (Lindgren and Gustafson 2001). Distribution and abundance of human populations are likely to be negatively impacted.

Here, then, is a small fraction of the evidence that climate change has had a strong influence on species, species interactions, community composition and no doubt ecosystem function: the biological fingerprint of climate change. Parmesan's (2006) overview provides a more complete picture.

15.2.2 Temperature and drought

Rising temperatures result in higher evaporation from the soil and evapotranspiration in plants, and an increased probability of drought, all else being equal. Stressed plants have direct effects on insect communities, commonly negative effects on folivores, and positive effects on bark beetles and other cambium feeders in trees. These effects are now well documented in generally drier climates, such as the western United States.

The mortality rate per year of trees in unmanaged old forests in the western United States has increased dramatically over the period sampled from 1955 to 2007 (van Mantgem *et al.* 2009, p. 521). "Regional warming and consequent increases in water deficits are likely contributors to the increases in tree mortality rates." Rates per year have increased from less than 0.5% before 1960 to over 1.5% after the year 2000, with pines and firs reaching up to 2.0% mortality per year. This increased rate covers a huge area over the Pacific Northwest, California and the interior US, from northern Idaho, to Colorado and Arizona. Mortality rates have increased at all elevations, from less than 1000 m to over 2000 m above sea level, on all size classes of trees, on all major tree species, and on all age classes. All this has occurred without any increase in recruitment rates of young trees, indicating a net loss of trees. Some plots have been attacked by bark beetles, causing increased rates of tree mortality. Other studies have shown that plant species colonize upslope as climate warms, and they die off at lower elevations, producing general elevational shifts in vegetation (Kelly and Goulden 2008, Breshears *et al.* 2008).

In the southwestern United States, in Arizona, New Mexico, Utah and Colorado, there was regional peak death of over 90% of the dominant tree, piñon pine (*Pinus edulis*), in 2002–2003, caused by warmer temperatures and drought, accompanied by bark-beetle outbreaks involving *Ips confuses* (Breshears *et al.* 2005). Within the same area, after the same drought, estimated mortality of dominant tree species and shrubs reached means of 3.3% for one-seeded juniper (*Juniperus monosperma*), 14.6% in manzanita (*Arctostaphylos pungens*), a dominant shrub in the chaparral vegetation of Arizona, 15.4%

in quaking aspen (*Populus tremuloides*), 15.9% in ponderosa pine (*Pinus ponderosa*), 20.7% in Fremont cottonwood (*Populus fremontii*) and 41.4% in piñon pine (Gitlin *et al.* 2006). All the species showed a more localized very high mortality from 24 to 100% in the drier sites with higher water stress. These tree species represent "**barometers of change**" (Gitlin *et al.* 2006, p. 1477), which indicate rapidly effects of climate change, and act as predictors of future climate shifts due to global warming. The high mortality of piñon pine, its large distribution as a codominant in the third largest vegetation type in the United States, and a record of change going back 40 000 years, makes this species an excellent candidate as an **indicator species** for climate change.

For this reason, piñon pine has been the focus of studies on drought effects on insect communities (Trotter *et al.* 2008). Three main effects of chronic drought were as follows:

(1) Community composition was altered significantly, with more predators and parasitoids in low-stress sites.
(2) Trees in more mesic sites had arthropod communities 90% richer than those growing under high stress.
(3) Among the 33 most common herbivore species, 73% showed higher numbers at the low-stress part of the gradient.

On stressed pines both species richness of arthropods and their abundances were reduced. Under low-stress conditions herbivores were 12.7 times, predators 1.5 times and parasitoids 2.7 times more abundant than in the highly stressed trees. In the soil below these trees heterotrophic bacteria were 10 times more abundant among low-stress sites compared to high-stress sites (Kuske *et al.* 2003), but ectomycorrhizal colonization was twice as high in high-stress sites (Gehring *et al.* 1998).

These studies show the dramatic changes caused by drought on all biotic components of the system. Ecosystem functions must change in equal measure. The studies also illustrate the use of moisture and stress gradients as analogs for climate change, with resident species acting as indicator species and indicator communities, and facilitating predictions about future moves in biotic communities and assemblages.

A major feature of drought in coniferous forests is the impact of bark beetles on forest structure, composition and ecosystem function. With beetles causing up to 60% mortality in general and 80–90% mortality in the larger size classes of trees, and impacting several million hectares in North American forests, bark-beetle eruptions act as agents of major disturbances on the landscape (Raffa *et al.* 2008). In the scenario developed by Raffa and associates, among the external controls and releasers for the plant–herbivore interaction, climate plays a major role. Temperature affects the bark beetles directly with increasing survival as temperatures rise, including warmer summers and milder winters. Increased temperature is associated with drought, stressing trees and reducing tree resistance to beetle attack. Reduced snow cover can delay thawing of tree roots and the development of resistance in the trunk to beetles. Environmental change by humans contributes to beetle eruptions also, including suppression of fire and increased homogeneity of tree species, resulting in age structures and landscape coverage conducive to widespread attack by beetles (Raffa *et al.* 2008).

Tropical vegetation, at least in the Amazon Basin, appears to be sustaining or increasing biomass, with recruitment of trees exceeding mortality rates (Phillips *et al.* 2004). Unfortunately, we do not know how insect communities are performing, particularly if herbivore outbreaks are increasing as the climate changes, as in temperate regions.

In the temperate zones most predictions are that global warming will increase the frequency of insect outbreaks, they will be more widespread and durations will increase. Coniferous forests will be particularly vulnerable (Williams and Liebhold 1995b, Ayres and Lombardero 2000, Volney and Fleming 2000, Logan *et al.* 2003, Hóder and Zamora 2004). Effects are likely to act in three major ways:

(1) Direct effects on insect herbivore life cycles with increased development rates and survival.
(2) Physiological changes in trees which reduce tree defenses.
(3) Indirect effects through changes in efficiency of natural enemies and mutualists (Ayres and Lombardero 2000).

An exception perhaps is the larch budmoth, *Zeiraphera diniana*, which has shown a reduced frequency of severe outbreaks in the 1900s, and an absence since the early 1980s in most parts of the European Alps (Esper *et al.* 2007).

Global warming is expected by Stireman *et al.* (2005) to increase the frequency of insect outbreaks through direct positive effects on insect life cycles and because of the negative effects on natural enemies, as also noted by Ayres and Lombardero (2000). Stireman *et al.* found that climatic unpredictability, measured as variation in precipitation, had a negative effect on parasitoid attack on insect herbivores (Figure 15.10). The suggestion is that unpredictable weather, plus its impact on host populations, making them more variable, decreased the ability of parasitoids to track host populations. This would lead to the prediction that host populations are less well regulated by natural enemies, and outbreaks are more frequent in more unpredictable climates. This finding was observed across the latitudinal gradient from Brazil, Ecuador and Panama, to Costa Rica, the United States and Canada. With global warming increasing extreme weather in some areas, the impact on mismatches between herbivore dynamics and natural-enemy responses may become conspicuous, but mechanistic studies are needed to understand the interactions.

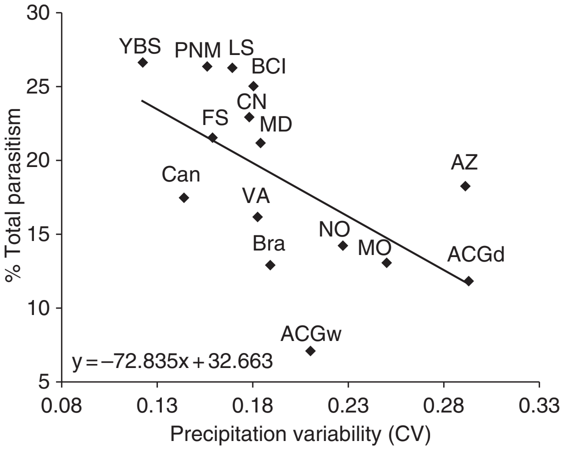


Figure 15.10 The relationship between percentage total parasitism and precipitation variability (coefficient of variation) in 15 large rearing programs covering a latitudinal range from 15°56′S to 45°45′N, from Ecuador to Canada. The regression line accounts for 37% of the variance ($P = 0.016$). Localities are shown beside data points. For example, Can = Canada; CN, MD, VA, NO, MO and AZ are states in the USA; LS, ACGw and ACGd are in wet and dry forest in Costa Rica; PNM, BCI and FS are in tropical forest in Panama; Bra is in Brazil and YBS is in Ecuador. From Stireman *et al.* 2005. Copyright 2005. National Academy of Sciences USA.

15.2.3 Fire and insects

As warming trends develop, drought increases in many areas, insect and pathogen eruptions increase and forests become more prone to wildfire. The fossil record of fire, based on charcoal in sediments, covers up to 12 000 years in some locations. Clear signals of climate change and fire frequency are evident, but they are complicated by changes in dominant tree species, such as about 8000 years ago when lodgepole pine was replaced by less fire-prone white pine and Douglas fir forest during an increase in cooler and wetter conditions (Gavin *et al.* 2007). However, there is no doubt that wildfire activity in western US forests has increased in recent decades: greater frequency of large wildfires, fires that burn longer and extended seasons of wildfires (Westerling *et al.* 2006). During the period 1986–2003, wildfire frequency increased almost four times compared to 1970–1986 and the total area burned increased by over six times. These increases were associated with increased spring and summer temperatures and early snowmelt. Temperature alone accounted for 66% of the variance in fire frequency, with more fires in the warmer years.

Fires have many important impacts on insect life, but pathogens of trees also become involved (Parker *et al.* 2006). For example, in lodgepole pine (*Pinus contorta*) forests, fire returns at 25- to 90-year intervals. It kills trees, but also damages roots and trunks of surviving trees, allowing fungal infection. Fungal attack weakens trees, which become susceptible to attack by mountain pine beetles, *Dendroctonus ponderosae*. Such trees may become foci for eruptive dynamics, killing many more trees and making the forest more fire prone. Bark beetles in surviving, but damaged, trees may spread decay fungi, inoculating other trees, thereby continuing the cycle of interacting fires, bark beetles and pathogenic fungi (Parker *et al.* 2006). Another case of a pathogen, bark beetle and fire interacting concerns dwarf mistletoe, which weakens ponderosa pines, making them more susceptible to bark-beetle attack, followed by tree mortality, fuel build-up and eventually intense forest fires.

Fire and tree stress or death also favor other wood- and cambium-feeding insects, such as woodwasps (Hymenoptera: Siricidae), longhorn beetles (Coleoptera: Cerambycidae), metallic wood-boring beetles (Buprestidae) and ambrosia beetles (Curculionidae: Scolytinae). Also, there is a group of fire-adapted species which attack trees immediately after a fire; some are attracted to smoke and some by heat (Evans 1971, Saint-Germain *et al.* 2008) and are dependent exclusively on fire to provide a suitable substrate for breeding. Scorched trees provide habitat for the buprestids *Melanophila accuminata* and *Buprestis nuttalli* in white spruce stands in Alaska (McCullough *et al.* 1998) and pyrophilous species increase in burned trees (Dajoz 1998), including carabids, buprestids, cerambycids, cucujids and latridiids. Suppression of fire has had severe impact on pyrophilous species in North America and Europe (Saint-Germain *et al.* 2008). Wickman (1964a,b) described attraction and attack by buprestids and cerambycids in fire-killed and scorched pines.

Probably the most important beneficial effect of fire on insects is that fire acts as a major disturbance, which increases the mosaic nature of the landscape, thereby increasing insect biodiversity (e.g., McCullough *et al.* 1998). In each patch of fire, plant succession is altered, tree ages are shifted, nutrient cycling is accelerated, erosion is probably increased, soil communities are impacted, and over the landscape species composition is altered and in aggregate the number of species is increased. Many species respond positively to regrowth after fire, because regrowth is nutrient rich and palatable. In fire-adapted vegetation types such as the cerrado in Brazil, there is a flush of new leaves and flowers after fire which are utilized by insects, in stark contrast to adjacent unburned areas (e.g., Prada *et al.* 1995, Vieira *et al.* 1996, Seyffarth *et al.* 1996).

Fires also affect insects indirectly when frequency increases, by altering levels of carbon dioxide in the atmosphere and opening up forests results in warming of the soil, increased metabolic activity and increased CO_2 emissions from the litter and the soil.

15.2.4 Carbon dioxide effects on insects

Burning fossil fuels releases carbon dioxide (CO_2) into the atmosphere, and this greenhouse gas causes global warming. But CO_2 has direct effects on plants and through plants on insect herbivores, and also directly on insects. Some insects use CO_2 as a cue to locate metabolically vigorous plants during their oviposition behavior, such as the pyralid moth *Cactoblastis cactorum*, and perhaps the sphingid moth *Manduca sexta* (Guerenstein and Hildebrand 2008). CO_2 attracts gravid tephritid flies, *Bactrocera tyroni*, at short range. Remarkably, some plants like Scots pine can reduce CO_2 assimilation in response to insect oviposition, thereby influencing further oviposition. Pollinators may also be attracted by increased CO_2 levels in flowers. The attraction to CO_2 emitted by mammals, including humans, by hematophagous insects is well known. Many taxa respond positively to CO_2 concentrations: mosquitoes, tsetse flies, "kissing bugs" or assassin bugs (Reduviidae), biting midges, sand flies, black flies, ticks and the muscid stable fly, *Stomoxys calcitrans* (Guerenstein and Hildebrand 2008). Social insects employ behaviors and nest design, which regulate CO_2 concentration during the intense metabolic activity of the colony. Climate control is known in honey bees, bumble bees, ants and termites. Direct effects of increased levels of CO_2 during climate change have not been studied extensively, but responses are likely to be individualistic and frequently complex because of interactions with temperature and other variables (Guerenstein and Hildebrand 2008).

Indirect effects of increased CO_2 via plants on insects have been studied in some detail. For example, the Aspen Free Air CO_2 Enrichment (FACE) experiment in northern Wisconsin, which was started in 1998 in an aspen–birch forest, studied CO_2 and atmospheric ozone (O_3) effects on plants and herbivores (e.g., Hillstrom and Lindroth 2008). These authors found that elevated CO_2 slightly reduced numbers of phloem-feeding herbivores and increased numbers of chewing herbivores and parasitoids, and insect community composition was affected significantly. Elevated CO_2 affects plant quality and herbivore performance (Hunter 2001c, Zvereva and Kozlov 2006a). In Hunter's overview of CO_2 impacts, he notes that elevated CO_2 increases photosynthesis and resultant plant biomass. Under constant nutrient availability this inevitably reduces nitrogen concentrations in plant tissues, increasing C:N ratios and allocation of carbon to plant-defense compounds which are carbon rich – phenolics, condensed tannins and lignin. Such compounds generally act as digestibility reducers for herbivores (see Chapter 4, Plant–insect interactions).

Many insect species have the capacity to compensate for low nutrient status plant parts when C:N ratios increase, by feeding more and digesting food more efficiently. Therefore, with increased atmospheric CO_2, damage to plants by insects increases, as found with grasshoppers, other leaf-chewing insects and leaf miners. However, the increased biomass of host plants can more than compensate for increased herbivore damage. Also, lower nutrient status leaves may reduce herbivore survival, so numbers decline, and parasitoid attack has increased in some studies (e.g., Stiling *et al.* 1999, 2002). The net result was that leaf damage in ambient CO_2 was about 31% of leaves damaged on myrtle oak, a major component of scrub-oak vegetation in Florida, but under elevated CO_2 only 19% of leaves were damaged (Stiling *et al.* 2002). More recently, Stiling *et al.* (2009) have shown that on a per-leaf basis herbivore densities have declined under elevated CO_2, but increased leaf production can result in higher herbivore densities per meter squared of oak vegetation, dependent on the oak species involved.

As CO_2 effects pass up the trophic system, the effects appear to be less predictable and species dependent (Hunter 2001c), and interactions with other variables such as light conditions, nutrients or temperature are more complex. However, Bezemer and Jones (1998) identified some general patterns related to elevated CO_2 based on 61 plant–herbivore interactions:

(1) Foliar nitrogen concentrations decreased by about 15%, carbohydrates increased by about 47% and phenolic-based secondary metabolites increased by 31%.
(2) Nitrogen and carbohydrates had the main effects on herbivore feeding.
(3) Both herbaceous and woody plants affected insects in a similar way.
(4) Leaf-chewing insects usually increased foliage consumption by about 30%, and pupal weights were not impacted.
(5) Leaf miners suffered declined pupal weights because feeding compensation was incomplete.

(6) Phloem-feeding insects increased population size and decreased development times under elevated CO_2 (see also Hunter 2001c).

As the number of studies on CO_2 enrichment has increased, and on other kinds of influences, an interaction web of influences has emerged. Based on 688 published studies on the main drivers of global environmental change, including CO_2 enrichment, nitrogen deposition, climate change, biotic invasions and land use, Tylianakis *et al.* (2008) concluded that general results emerge:

(1) Alteration of competitive interactions.
(2) Multitrophic effects on the decomposer food web.
(3) Increases in pathogen infection.
(4) Reduced plant mutualisms.
(5) Increased herbivory.

However, considerable variability has been found in the size of effects and their direction.

Concentrating on the impacts of enriched CO_2, Tylianakis *et al.* (2008) developed a generalized web of interactions, which illustrates the trends in changes in interactions in each case documented in the published literature (Figure 15.11). Twelve interactions are illustrated in the figure; they are listed below using the numbers in the figure, but the original paper should be consulted for details. All interactions are variable to highly variable:

(i) Plant–pollinator interactions show a general benefit to pollinators.
(ii) Plant–fungal interactions often show an increase in colonization by mycorrhizal species.
(iii) Seed dispersal has not been studied under increased CO_2 concentrations.
(iv) Plant–plant competition is affected by shifts in advantage.
(v) Plant–hemiparasite interactions may benefit the parasite.
(vi) Plant–herbivore associations are more negative than positive on the insect species.
(vii) Plant–pathogen relationships more often increase infections.

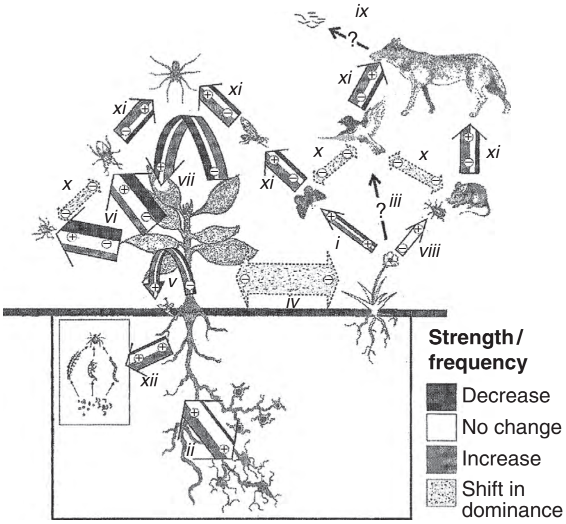


Figure 15.11 Trends in changes among interactions in terrestrial nutrient and energy flow in response to increasing atmospheric CO_2, assembled by Tylianakis *et al.* (2008). Arrows with solid outlines show nutrient and energy flow, for example from plant to insect. Double-headed arrows with dotted outlines show resource competition. Within arrows, + and – indicate benefit or cost to each species (e.g., $-/+$ for the plant–insect interaction, and $+/+$ for the mycorrhizal-fungi–plant mutualism). The proportion of shading within each arrow reflects the proportion of interactions among all studies used showing increases (gray), no effect (white) or decreases (black).

(viii) Seed predation needs more study.
(ix) Parasite–host interactions have not been studied. This does not include parasitoids – see below.
(x) Animal–animal competition shows a shift in advantage, but is not well studied.
(xi) Predator–prey and parasitoid–host interactions generally result in increased rates of attack.
(xii) In decomposer food webs variable results have been observed depending upon the trophic level involved.

There are, of course, complexities to be added when variables, in addition to CO_2, are considered. Interactions among variables with higher-order effects are inevitable. Elevated CO_2 affects climate and the plant–herbivore interaction (Figure 15.12),

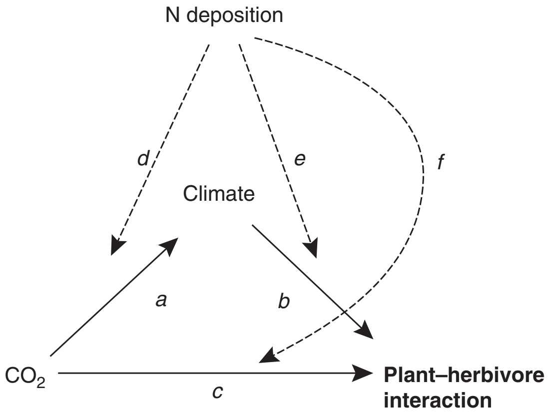


Figure 15.12 An illustration of potential higher-order interactions among increased CO_2 in the environment and another driver of global environmental change, such as nitrogen deposition. In this case, leaf-feeding herbivores and plants are treated as the target interactions. Solid arrows *a*, *b* and *c* are direct effects, while dashed arrows *d*, *e* and *f* are indirect effects which moderate the direct effects, as explained in the text. From Tylianakis *et al.* 2008.

and elevated temperatures impact the plant–herbivore interactions (direct effects *a*, *b* and *c*). Indirect effects from nitrogen deposition (*d*, *e* and *f*) may impact increased plant growth and compensate for increased herbivory (*f*). Increased plant growth could increase CO_2 assimilation during increased biomass production, reducing effects of CO_2 on climate change (*d*), and N deposition and climatic temperature increases could be additive, with positive influences on herbivory (*e*). "We need long-term, multifactorial experiments under field conditions to have any hope of predicting the interactive effects of CO_2 and other ecological variables on the insect pests of crops and trees" (Hunter 2001c, p. 156).

15.3 Ecosystem dynamics

Evidently, changing environmental conditions can impact insect life, but insects can also influence the conditions in the ecosystems they inhabit. They can reset plant succession by killing trees, and accelerate recycling of nutrients by feeding on leaves, by boring into wood which promotes decay, and with other arthropods by regulating decomposition in soils. Early recognition of these processes was reflected in the symposium "The role of arthropods in forest ecosystems" (Mattson 1977). Here, Amman (1977) gave an example of a major insect effect on forest vegetation, which has been mentioned earlier in this book. The mountain pine beetle, *Dendroctonus ponderosae*, kills most of the large and dominant lodgepole pines, *Pinus contorta*, over large areas on a cycle of about 20 to 40 years. Opening up the forest allows more shade-tolerant Douglas fir, subalpine fir and Englemann spruce to take over as dominants, depending on elevation. Or, lodgepole pine may reseed in vacated areas producing a mixed-age forest, and replacing trees which have reached maturity. The result is a healthier forest than in the absence of beetles, with higher productivity than when trees are reaching old age, senescence and death.

Peterman (1978) added more to this scenario by noting that *Dendroctonus* beetles are "managers" of lodgepole pine when they thin and "harvest" trees in pine stands. They create fuel for fires which are essential in the reproduction of these pines: seeds are only released from serotinous cones after extreme heat from fire. This thinning also reduces the likelihood of high-density stands in the next generation, in which growth stagnates, because the seed bank does not increase long enough to produce high seedling density. Peterman even suggested that the age at which trees became susceptible to *Dendroctonus* may well have evolved in response to selection favoring increased fire probability, and tree reproduction when the parental seed crop is adequate for regeneration, but before very dense seedlings would result in intense competition among progeny. Such "management" would provide more breeding sites for beetles eventually because overcrowded stands become stagnant, with trees too small and bark too thin to support beetle populations.

15.3.1 Insects as regulators

In a similar vein, Mattson and Addy (1975) argued that insects are more than just consumers; they are regulators of ecosystem processes. As host-plant conditions change, insects respond, providing feedback to host plants and other components in the ecosystem, such as litter content and decomposition. These authors employed as an example severe defoliation by insects in temperate forest trees, including the forest tent caterpillar, *Malacosoma disstria*, on aspen, *Populus tremuloides*, and the eastern spruce budworm, *Choristoneura fumiferana*, on its favored host, balsam fir, *Abies balsamifera*. Such defoliations have effects as follows:

(1) They change the physiological status of the host tree.
(2) They accelerate litter fall, which includes leaves, twigs, branches and insect frass, exuviae and carcasses.
(3) There is increased leaching of nutrients from the trees into the soil and litter system.
(4) Many trees die in the classes of weakened, old or suppressed trees, thereby changing distributions of light, heat, nutrients and biotic factors for the survivors, enhancing their growth and that of associated plants.
(5) Stimulated activity of soil arthropods and microorganisms results, numbers increase, and nutrient cycling in the ecosystem is accelerated. The insects play an important role in maintaining relatively high primary production and nutrient cycling.

This is the perspective that Mattson and Addy (1975) employed in mapping the relationship between forest tent caterpillar and aspen, as their relationships changed over time (Figure 15.13). At times relationships were mutualistic (+/+), and at others they were negatively impacting each other (−/−). The authors used the periodic coordinate system, in which the coordinates 0°, 90°, 180° and 270° represent interaction types +/0, 0/+, −/0 and 0/−, respectively, and the angles midway between these coordinates represent +/+, −/+, −/− and +/− interactions, respectively. The intensity, or net outcome, of the relationship is specified by the proportional change from a standard reference value, R0. When there is no impact on either species, a net neutral relationship between species (0/0), the relationship is recorded on the reference zero circle (R0), as when trees are 26 and 27 years old and vigorous. Net positive relationships become more distant from the circle outward (not shown in Figure 15.13 but evident in Figure 15.14). Net negative interactions move in from R0, with greater departures from R0 showing stronger negative effects. A comparison of total biomass production (a combination of both aspen production and forest

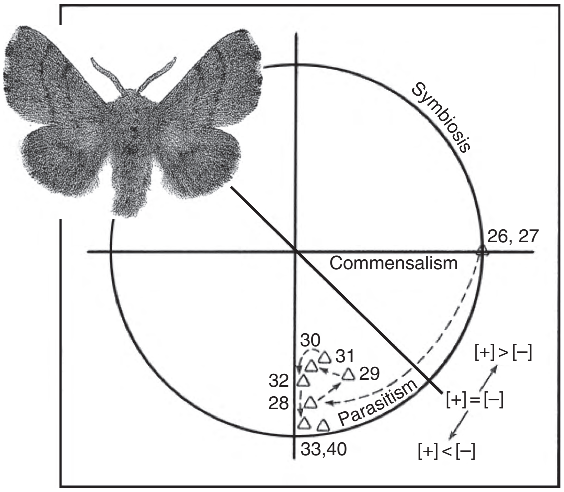


Figure 15.13 Relationships between forest tent caterpillar and aspen trees, plotted on the periodic coordinate system. The circle is reference zero (R0) when total production of insects plus vegetation is equal, whether insects are present or absent. Open triangles represent the position of the insect and plant relationship, and the numbers show the years of tree age in the aspen stand. Dashed lines and arrows indicate the direction of movement of the relationship in the coordinate system. From Mattson, W. J. and N. D. Addy 1975. Phytophagous insects as regulators of forest primary production. *Science* **190**:515–522. Reprinted with permission from AAAS.

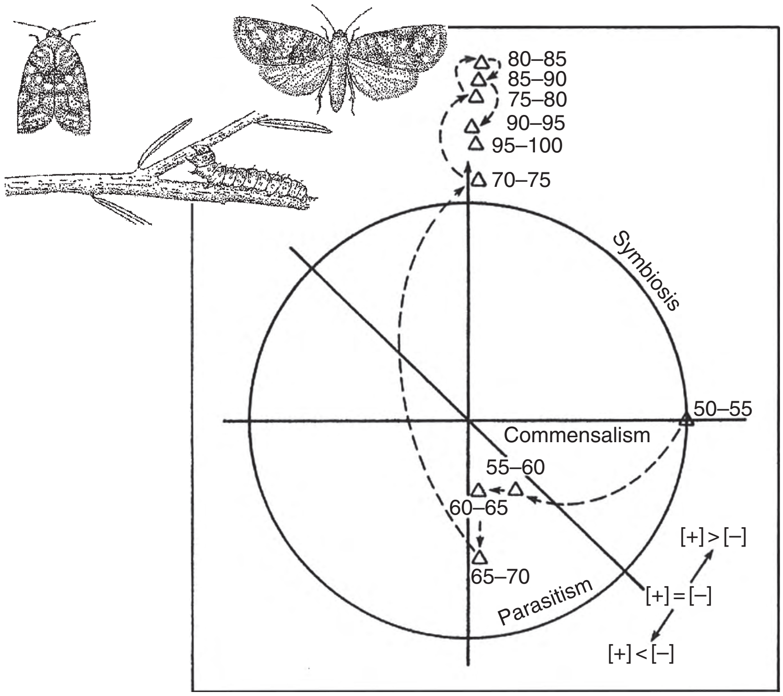


Figure 15.14 Relationships between spruce budworm and balsam fir plotted on the periodic coordinate system as in Figure 15.13. From Mattson, W. J. and N. D. Addy 1975. Phytophagous insects as regulators of forest primary production. *Science* **190**:515–522. Reprinted with permission from AAAS.

tent caterpillar production) with and without insects was employed to evaluate the kind and intensity of interaction involved. The notable result from this plot is that the relationship changes from commensalisms in 26- and 27-year-old stands, to parasitism at ages 28 and above. As trees age from 30 to 40 years, they thin out, with weakened trees dying, and the budworm impact declines towards a net neutral, commensalistic relationship.

An equivalent analysis on the spruce budworm and balsam fir association showed greater shifts among interaction types, from commensalism (0/+) at ages 50–55, to parasitism (+/−) at ages 55–70 and then to the opposite form of commensalism (+/0) at age 70 years and beyond (Figure 15.14). Eventually, these older trees are killed, replaced by young, vigorous trees as dominants and the relationship returns to the 90° position.

Mattson and Addy (1975) concluded that each forest ecosystem supports insects whose impact varies with seasonal and developmental changes in host-plant stand structure. Some insect species respond strongly to these changes, thereby acting as regulators of the forest ecosystem. Insects also act as major disturbances which perturb ecosystems, influencing plant succession, species diversity and primary productivity (see Loucks 1970, Raffa *et al.* 2008).

15.3.2 Insect effects on nutrient cycling

If insects are "regulators" and "managers" in forests, they must be influencing nutrient cycling in major ways. But less conspicuous activity is proceeding constantly throughout the lives of plants. For example, an experiment using potted red oak, *Quercus rubra*, saplings employed additions of insect frass labeled with the isotope ^{15}N as the treatment, and no added frass as the control (Frost and Hunter 2007). The frass was derived from a different set of labeled trees which were fed upon by gypsy-moth larvae, and it was added to soil of treatment plants, this being the only source of labeled N in the experiment. ^{15}N was rapidly taken up by the oak plants, which became available to herbivores feeding later in the season. About 10% of labeled N reached the leaves within the same year, while about 42% of frass N was recovered in the soil. This shows that nitrogen is recycled rapidly, at least in small trees, which benefits later season herbivores. Increased nitrogen in the soil also benefits the nutritional status of trees, and associated species. Insect herbivores on other plants in the community may also benefit from nitrogen deposition, as shown in a different experiment using the milkweed, *Asclepias tuberosa*, and a herbivore, *Aphis nerii*. Added nitrogen resulted in increased leaf nitrogen in the plants and plant biomass, and increased aphid population growth rate (Zehnder and Hunter 2008).

During a moderate outbreak of leaf herbivores there was a threefold increase in frass, soil nitrate availability increased five times and nitrate leaching into streams doubled (Reynolds *et al.* 2000). Herbivores can have strong effects on nitrogen cycles because they consume leaves high in nitrogen, which is dropped as frass, whereas most litter is composed of senescing leaves from which much nitrogen has been removed by the plant before abscission (Hollinger 1986). Therefore, frass deposition has a strong influence on below-ground processes in the ecosystem (e.g., Hartley and Jones 2004, Stadler *et al.* 2004). However, this does not appear to be beneficial to the mycorrhizal fungi, which are generally negatively impacted by above-ground herbivores. This seems to result from reduced carbon availability in roots due to defoliation, while carbon demands of the fungi may reach 10–15% of total primary production in the host plants (Gehring and Whitham 2002).

With the growing realization that plant genetic effects are strong up the trophic system and in the decomposer trophic system (Figures 12.25, 12.26, Whitham *et al.* 2006, Bailey *et al.* 2009, Barbour *et al.* 2009), it will be interesting to learn how other ecosystem processes are influenced, such as cycling of nitrogen and insect frass quality (Madritch *et al.* 2006, 2007).

15.4 Invasions

Organisms are constantly on the move, and insects are no exception. We saw this based on the fossil record early in this chapter. As land masses collided, so migrations followed, as in “The Great American Interchange” when the formerly isolated land masses of North and South America were joined, connecting across Central America (Simpson 1980). Warming trends result in plants and animals moving north in the northern hemisphere, and higher in altitude (e.g., Callaghan *et al.* 2004). As humans transport goods around the globe, insects travel with them (e.g., Haack 2001, 2006).

15.4.1 Invaders of North America from Europe

One interesting pattern in insect faunal changes is the disparity in the movement of species: North America has received many more insect invaders from Europe than the reverse. Counting the number of phytophagous tree-feeding species that invaded from Europe to North America, about 300 species were documented (Niemelä and Mattson 1996, Mattson *et al.* 2007), whereas only 57 species have reached Europe from North America, about a fivefold difference (Table 15.1). As a null hypothesis we should expect a roughly equal flow of species across the Atlantic Ocean, recognizing the centuries-old commercial exchange among the countries on either side.

Table 15.1 **Successful establishment of invasive phytophagous insect species in North America arrived from Europe, and in Europe invaded from North America. Data from Mattson *et al*. 2007**

To North America			To Europe		
Insect order	Number of species	Percentage of species	Insect order	Number of species	Percentage of species
Coleoptera	65	20.9	Coleoptera	9	15.8
Diptera	12	3.9	Diptera	8	14.0
Hemiptera	34	11.0	Hemiptera	4	7.0
Homoptera	83	26.8	Homoptera	22	38.6
Hymenoptera	34	11.0	Hymenoptera	8	14.0
Lepidoptera	77	24.8	Lepidoptera	5	8.8
Orthoptera	1	0.3	Thysanoptera	1	1.8
Psocoptera	1	0.3			
Thysanoptera	3	1.0			
Total number of species	310		Total number of species	57	

Niemelä and Mattson (1996) erected several alternative hypotheses which might account for unbalanced movement of forest-dwelling insects. Based on general characteristics of plant and insect interactions (Chapter 4) they generated a list of factors that would contribute to a species becoming a successful colonizer:

(1) The size of the geographic ranges of all potential host plant species, likely to be species in the same genus or family.
(2) The mean density of hosts in the area.
(3) The similarity of hosts in the newly invaded zone compared to original host plants in relation to phytochemistry, morphology and ecology.
(4) The synchrony of host-plant phenology and insect phenology.

Major aspects of the authors' argument are as follows, forming the **European-crucible hypothesis**.

(1) **Higher rates of host-plant extinction during the Pliocene and Pleistocene in Europe left a rich flora of potential host plants in North America.** The richness of tree species and genera is higher in North America than in Europe (Table 15.2), with about twice as many potential hosts for colonists in North America. The hypothesis accounting for this difference is that compression of floristic zones during glaciation events to the south in Europe resulted from long mountain ranges in an east–west direction. The southern migration was limited and floral elements were fragmented, causing extinctions. The Cantabrian Mountains, and the Pyrenees, blocked migration into Spain, and the Alps, Carpathians and Caucasus ranges blocked southerly movement into southern Europe and the Middle East. The situation in North America differed significantly from Europe because mountain ranges run

Table 15.2 **The number of tree genera and species of gymnosperms and angiosperms in North America and Europe, and the species per genus in each. Based on Niemelä and Mattson 1996**

	In North America		In Europe	
Taxon	Genera	Species	Genera	Species
Gymnosperms	16	97	8	30
Species per genus	6.06		3.75	
Angiosperms	143	503	78	256
Species per genus	3.52		3.28	

mainly north and south, parallel with migrating plants and animals during glaciations. Southerly migration was not impeded by the Appalachian chain in the east, or the Rocky Mountain Range in the west, resulting in little extinction.

(2) **Plant extinctions during the Pleistocene may have selected for insects in Europe to acquire a broader ability to exploit host genera than those in North America.** In Europe, with extinctions of host-plant species and genera, and compaction of host-plant ranges, host shifting or expansion of hosts by herbivores may have been common. Broader host-utilization patterns would be acquired, making members of the fauna better colonizers than their American counterparts.

(3) **North American forests provide a larger and less fragmented landscape than in Europe, promoting easier colonization by European insects.** Europe has been deforested and fragmented more than in North America because agrarian economies developed and expanded earlier in Europe.

(4) **Pleistocene and modern conditions in European forests selected for superior competitors and colonizers.** European glaciations, compaction of plant and animal ranges, expansion northwards after glaciations and fragmentation of forests have contributed major disturbances for plants and insects. This seems to have selected for high colonizing ability and perhaps a competitive edge against resident species in North America. Also, in Europe, polyploidy and parthenogenesis are unusually common, promoting colonizing ability. Polyploids appear to be broadly adapted to a range of landscapes and parthenogenesis enables one female to establish a new population.

(5) **Synchrony of phenologies of plants and insect herbivores has a higher probability when movement is from higher to lower latitudes.** Temperate deciduous forest in Europe lies between about 43–60°N, but in North America it is further south, from about 30–48°N. Therefore, seasonal photoperiodic changes relevant to insect diapause and plant phenology are much greater in Europe than in North America. For example, day lengths at 60°N range from 6–19 hours, but at 30°N only between 10–14 hours. An insect moving to Europe would probably not survive because day lengths in summer would be too long to trigger diapause in time before the rapid onset of winter. However, an insect moving from Europe in summer would encounter shorter day lengths, which would stimulate diapause in good time before winter cold.

The European-crucible hypothesis of Niemelä and Mattson (1996) and Mattson *et al.* (2007) creates a scenario explaining increased colonizing ability from

Europe to North America among insect herbivores on trees. The five components of the hypothesis outlined here cover paleoecological and biogeographical aspects of insect ecology, providing a heuristic basis for future research. Testing hypotheses and sorting among them will be challenging. That European conditions acted as a melting pot, or crucible, digesting down life-history components of insect herbivores, which resulted in effective colonizing ability, remains as an intriguing possibility. The factual imbalance in movements is established, but the mechanisms demand more investigation.

15.4.2 Establishment and spread of invaders

Most species arriving on foreign shores do not establish viable populations. Failure results from several factors reducing the probability of success, but mainly because low numbers in a new population enhance the probability of extinction through stochastic events, finding suitable habitat and food sources is a challenge and the **Allee effect** plays its role (see Chapter 9, and Figure 9.3). Difficulty in finding mates in very small populations, inbreeding depression, vulnerability to predation and insufficient cooperation may all contribute to the Allee effect (Liebhold and Tobin 2008).

Once a new population has established a breeding population in an exotic location, the spread of the most successful invaders can be quite spectacular. Considering the small size of insects in general, range extensions have been remarkable (Table 15.3). Some invaders spread by diffusion, resulting in continuous range expansion: **short-range dispersal**. **Long-range dispersal** may be caused by different processes, perhaps by vehicles transporting insects accidentally. The spread of the gypsy moth in North America was composed of short-distance dispersal of airborne first instar larvae on silken threads, but long-distance dispersal depended on transportation by humans. This compound process, called **stratified dispersal**, can result in leap-frogging dispersal, with populations becoming established well ahead of the general population diffusion, after which populations may coalesce as they spread (Liebhold and Tobin 2008).

15.4.3 The impact of invading insects

"The range of impacts of invasive, non-native species is large, encompassing nearly every ecological relationship imaginable" (Lockwood *et al.* 2007, p. 203). Lockwood and associates classified impacts according to levels of complexity from genes to global impact:

(1) Genetic impacts occur when gene pools of native species are altered, usually by hybridization or introgression (e.g., Rhymer and Simberloff 1996). For example, native plants do hybridize with invading species, which must alter host-plant and insect-herbivore interactions, but examples have yet to emerge.

(2) Individual impacts result in changes in morphology, behavior or demography of natives resulting from introduced predators, parasitoids, pathogens or competitors. For example, introduced plants may offer oviposition cues to native insects, but provide poor nutrition or increased toxicity. One case concerns the monarch butterfly and the introduced dog-strangler vine, *Vincetoxicum rossicum*, from Europe, and in the same family as the native milkweed hosts. Young larvae do not survive on the *Vincetoxicum*, and although monarchs disfavor the vine for oviposition, there is a waste of eggs when milkweed hosts are scarce (Mattila and Otis 2003).

(3) Population impacts may affect population structure, abundance or dynamics of native species. Ant species invaders commonly exert major impacts on native species through competition and predation, with far-reaching consequences in some cases. "Invasional meltdown" was the term used by O'Dowd *et al.* (2003, p. 812) to describe the effects of the yellow

Table 15.3 **Examples of the radial rate of spread of invasive insects in various countries. From Liebhold and Tobin 2008. Reprinted, with permission, from the *Ann. Rev. Entomol*. 53, © 2008 by Annual Reviews www.annualreviews.org**

Order	Species	Common name or general type	Area of invasion	Time period	Radial rate of spread (km per year)
Hemiptera	*Adelges tsugae*	Hemlock woolly adelgid	N. America	1990–2004	8–13
	Cryptococcus fagisuga	Beech scale	N. America	1911–2003	14–15
Coleoptera	*Dendroctonus micans*	European spruce beetle	Europe	1973–1989	15
	Popillia japonica	Japanese beetle	N. America	1920–1940	5–6
	Oulema melanopus	Cereal leaf beetle	N. America	1962–1969	26–90
	Lissorhoptrus oryzophilus	Rice water weevil	Japan	1979–1986	28–470
Lepidoptera	*Lymantria dispar*	Gypsy moth	N. America	1900–2005	3–29
	Cameraria ohridella	Leaf-mining moth	Europe	2001–2003	17–39
	Pieris rapae	Imported cabbageworm	N. America	1868–1883	15–170
	Phyllonorycter leucographella	Leaf-mining moth	Europe	1989–1993	10.3
Thysanoptera	*Frankliniella occidentalis*	Western flower thrips	Europe	1983–2001	209–249
Hymenoptera	*Linepithema humile*	Argentine ant	N. America	1930–2000	15–67
	Solenopsis invicta	Red imported fire ant	N. America	1930–1975	21
	Apis mellifera scutellata	Africanized honey bee	S. and Central America	1957–1989	300–500
	Sphecophaga vesparum vesparum	Wasp parasitoid	New Zealand	1988–1993	1–1.5
Diptera	*Pseudacteon tricuspis*	Fire ant decapitating fly	N. America	1999–2001	20
	Plecia nearctica	Lovebug	N. America	1940–1975	32

crazy ant, *Anoplolepis gracilipes*, in rainforest on Christmas Island in the Indian Ocean, about 350 km south of Java. The ants caused extinction of the major herbivore, the red land crab, which kept the forest floor clear of dense vegetation. An increased richness of seedlings resulted. The ants in the trees fostered high densities of scale insects, large honeydew production and the development of sooty molds, resulting in dieback in the canopy and even death of some trees. These ants therefore impacted the populations of many species, and even drastically altered ecosystem functions.

(4) Community impacts clearly result from any of the effects of populations because relative abundance will change, and perhaps some species will be pushed to local extinction. Many examples have been documented involving insect biological control agents becoming invasive on the native flora and fauna (Louda *et al.* 2003a,b, Louda and Stiling 2004). An interesting case shows the far-reaching consequences of a well-intended biocontrol effort. Two tephritid flies in the genus *Urophora* were introduced to control exotic knapweeds in the genus *Centaurea*. Flies became abundant, but did not necessarily control the weeds, and the maggots in the flower heads supplemented the diet of deer mice, such that mouse populations increased to the point where other small mammal populations declined, and the native plant community was changed (Pearson *et al.* 2000). The red imported fire ant, *Solenopsis invicta*, has enormous impact on communities throughout its new range in North America, on all trophic levels. In cotton fields native predators are active and important in regulating pest species, but when fire ants invade, intraguild predation results in a decline in almost all native predatory species (Eubanks *et al.* 2002). In one case 12 of 13 native predatory species declined in the presence of fire ants, showing negative correlations with increasing ant density. Native predators included lady beetles, lacewings, spiders, big-eyed bugs, minute pirate bugs, ground and rove beetles, and assassin bugs. In greenhouse experiments lady beetles in the genera *Coccinella* and *Hippodamia* had survival reduced by 50% in the presence of ants compared to controls, and green lacewing larvae, *Chrysoperla carnea*, were reduced by 38%. Red imported fire ants also have strong negative impacts on native ant communities (e.g., Porter and Savignano 1990), with cascading effects on other arthropods.

(5) Ecosystem impacts occur whenever processes are changed involving such things as cycling of nutrients, decomposition or ecological succession. Invading diseases such as chestnut blight on American chestnuts, and invasive vectors of disease, including mosquitoes, all cause ecosystem change (e.g., Crowl *et al.* 2008). Plant invaders are probably the most studied in relation to ecosystem function (e.g., Ehrenfeld 2003), but insect communities are impacted, which contributes to changes in the cycling of nutrients. For example, in the Dongtan wetland in the Yangtze River estuary in China, *Spartina alterniflora* has invaded the native *Phragmites australis* salt marsh. Stable isotope studies provide evidence that the native insect fauna shows changes in food-web structure, with the prospect that the saltmarsh ecosystem will change in characteristics mainly because *Spartina* has different impacts than *Phragmites* (Wu *et al.* 2009). Also, in cases where insects cause large-scale decline and death of trees, as we saw in the ecosystem section of this chapter, ecosystem processes are drastically affected. For example, the invasive hemlock wooly adelgid, *Adelges tsugae*, eventually causes tree mortality, with increased litter fall during the process, and changes in the carbon and nutrient fluxes in the southern Appalachian forests (Nuckolls *et al.* 2009).

(6) Landscape, regional and global impacts include human influences on species which may lose or gain from expansion of human populations.

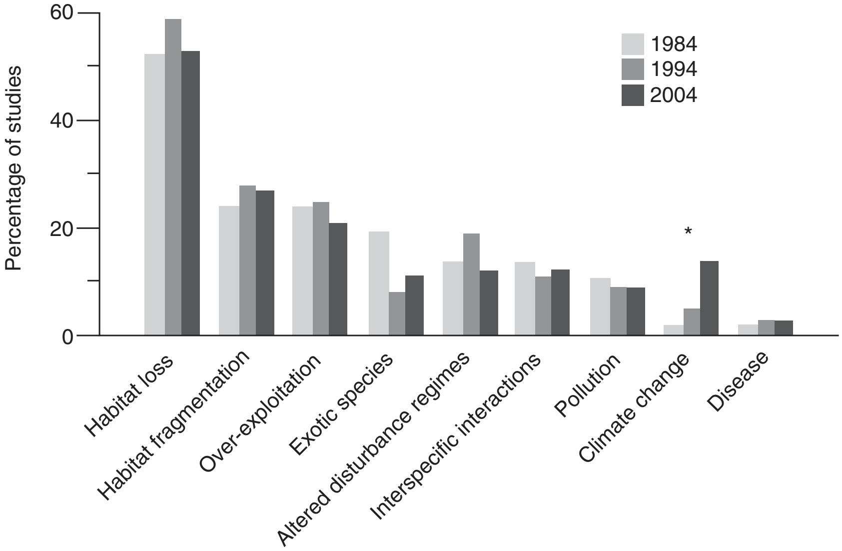


Figure 15.15 The percentage of conservation studies in selected journals which have studied aspects of each of nine threats to biodiversity over 20 years, sampled in 1984, 1994 and 2004. The asterisk shows a significant increase in percentage of studies devoted to climate change. From Lawler *et al.* 2006.

> "Winners" are far outnumbered by "losers" (McKinney and Lockwood 1999, Lockwood *et al.* 2007). As invasions proceed, biodiversity over landscapes and regions changes, but homogenization of biotas is a likely consequence of spreading species. Species interactions change and selective regimes are modified, constantly altering the geographic mosaic of evolutionary change (Olden *et al.* 2004, Thompson 2005).

Invading species clearly have large impacts on indigenous species, floras and faunas, so much so that many conservation efforts have become involved, the subject of the next section.

15.5 Conservation ecology

The 2008 Red List of the International Union for Conservation of Nature and Natural Resources provides a global sum total of only 1259 insect species (or other units such as subspecies or populations) in all their categories of threatened species. A large majority (74%) of these are Lepidoptera and Odonata, mostly species that are diurnal, relatively large and which generate considerable interest among the general public. Our preferential biases are clearly illustrated in this list. Nevertheless, threatened and endangered insects conform well to quantified estimates of threats for all kinds of plants and animals. Habitat degradation and loss affect the majority of threatened species. Invasive species cause major impact, while pollution and overexploitation often exert strong influences (Wilcove *et al.* 1998), and the frequency of publications on threats to species reflects scientific interest in these environmental aspects of threatened and endangered species (Figure 15.15, Lawler *et al.* 2006).

However, much of conservation ecology is concerned with environmental impacts on biodiversity, as well as on individual species (see Samways 2005). This widens the scope of investigations because almost every hectare in most landscapes is impacted by human activity and human effects, climate change and pollution. Also, whatever threatens one species is likely to have an effect on others, and therefore on higher levels of ecological organization. Some examples of threats to biological diversity are discussed next.

15.5.1 Habitat degradation and loss

Habitat loss and degradation is, of course, a catch-all category because habitat quality can be diminished by invading species, pollution, land use changes and urban sprawl. Therefore, over 90% of threatened insect groups are regarded as impacted by habitat degradation and loss, as well as other factors (so percentages of species impacted by each factor add up to well over 100%). The major categories of habitat quality decline and destruction relevant to insects are due to agriculture (56% of species), infrastructure development, including roads (23%), outdoor recreation, including off-road vehicles (41%), pollutants (26%) and land conversion for commercial development (67%) (Wilcove *et al.* 1998). In the last category will be included destruction of vegetation along coastlines, rivers, lakes and salt marshes, for the development of industrial and leisure businesses: just the habitats in which many rather specialized, and often endemic plants and insects live.

A large-scale experiment in the Amazon rainforest to explore the effects of forest disturbance was started in 1979: The Biological Dynamics of Forest Fragments Project (BDFFP) (Laurance 2007). This is the largest experimental study of habitat fragmentation in the world, and the longest in duration. Fragments of 1 hectare to 100 hectares were isolated from continuous forest by distances of 80–650 m, and controls were established in nearby continuous forest. As expected, as area declined so did species richness, and biodiversity was lower in fragments than in the controls. Some beetle, ant, bee, termite and butterfly species were very sensitive to the area of fragments, and some species even went extinct in the largest fragments, including dung and carrion beetles, and butterflies. Edge effects are also strong, with greater light penetration favoring those species attracted to brighter places, including some species of termites, leafhoppers, scale insects, aphids and tending ants, and some butterflies. But other species responded negatively to edges, and were diminished by fragmentation: some flies, bees, wasps, beetles, ants and butterflies. Insectivorous understory birds also avoided edges, as did obligatory ant-following bird species. Distance effects also played a role in reducing movement among patches, with even clearance of 15–100 m in width proving too exposed for such insects as carrion beetles and euglossine bees to venture across. Clearings also impeded movement of insect predators such as bats. Laurance (2007) provides an excellent summary of results from the BDFFP.

Evidently, habitat fragmentation has dramatic effects on populations, species, communities and ecosystem function. Ecological changes in fragmented communities include unusually high rates of change, species invasions and change in trophic structure and in ecosystem processes. These kinds of changes are not restricted to tropical rain forest, but are generally observed (e.g., van Nouhuys and Hanski 2002a, b, Tscharntke and Brandl 2004).

15.5.2 Pollution

Insect communities are impacted by all of the environmental changes we have discussed thus far, and pollution is no exception. Most impacts are predictably negative, and any conservation measures would be focused on reducing or excluding the pollutant. For example, increasing residential land use in coastal Rhode Island results in stream communities being negatively impacted: biodiversity of aquatic insects is decreased, indicating the need for watershed-scale conservation efforts (Lussier *et al.* 2008). But pollutants also may have indirect effects on communities, as was found in Rocky Mountain streams affected by historic mining operations. The metal pollutants increased the negative impact of ultraviolet-B light on macroinvertebrates (Zuellig *et al.* 2008).

In terrestrial environments pollution has multiple effects also (e.g., Heliövaara and Väisänen 1993, Kozlov *et al.* 2009, Zvereva and Kozlov 2009). An interesting set of cases involves insect herbivore outbreaks in polluted areas. For example, a nickel-copper smelter on the Kola Peninsula in NW Russia is a major polluter, releasing sulphur dioxide and heavy metals. In the polluted area leaf-mining moths in the genus *Eriocrania* reach outbreak proportions, and as with other similar situations, the question arises about the mechanisms involved. Zvereva and Kozlov (2006b) found that parasitoid communities were heavily impacted by pollution, resulting in newfound enemy-free space for the leaf miners. Conservation efforts would naturally concentrate on reducing emissions from the smelter in order to re-establish the vigor of the birch host plants and a more natural community of insects.

The key to conservation is really the protection of areas from disturbance of any kind, which are large enough to support biotic communities and ecosystems, or the maintenance of connectedness among smaller areas, with habitat corridors (e.g., Samways 1994, 2005). Designing landscapes for conservation is an essential large-scale goal. Thus, we are reminded of the SLOSS and SLOPP debates and related discussions in Chapter 14 on Biological diversity in the Applications section.

With increasing data being gathered around the globe, more papers are able to synthesize large bodies of data, with the detection of general patterns. We have discussed already gradients in diversity: area, latitude, altitude, time and disturbance (Chapter 14). Meta-analyses are becoming more frequent, which search for general trends among many studies as, for example, the study by Parmesan and Yohe (2003) on the fingerprint of climate change discussed earlier in this chapter. Also, Koricheva *et al.* (1998a,b) were cited in Chapter 4, who examined by meta-analysis the responses of insects to plant stress. Gruner *et al.* (2008) examined results in 83 papers and 191 independent experiments, with a meta-analysis searching for patterns in the effects of bottom-up and top-down effects on plant biomass, and Shurin *et al.* (2006) compared similar up and down effects in aquatic vs. terrestrial food webs. Also, 274 experiments were used by Hillebrand *et al.* (2007) in a meta-analysis comparing up and down control of primary producers in marine, freshwater and terrestrial ecosystems (see also Elser *et al.* 2007). These kinds of papers are resulting in new kinds of generality and understanding.

Applications

Threats and costs

Inevitably, changing environments impact agricultural practices and productivity for better or for worse. Therefore, efforts are in progress to evaluate and predict the impacts, and to estimate their costs. Anticipating change is an important strategy in eventually meeting the challenges posed by change.

Threats to agriculture

Whatever impacts are imposed on natural systems they are also likely to affect managed landscapes as in agriculture, forestry and urban environments. For crop pests winter temperatures are becoming less limiting, and degree-day accumulations in the summer are increasing, both favorable to pest species. Corn, or maize, is one of the most important crops in many parts of the world (see Pollan 2006), which has generated interest in predicting how this crop will perform under the influence of global warming. One set of predictions concerning effects on pests is sobering. Four major pests of corn are predicted to expand their range and perhaps threaten other crops as well: corn earworm (*Helicoverpa zea*), European corn borer (*Ostrinia nubilalis*), northern corn rootworm (*Diabrotica barberi*) and western corn rootworm (*Diabrotica virgifera*) (Diffenbaugh *et al.* 2008). Climate models also predict that summer temperatures will increase, threatening crops around the world and reducing agricultural productivity, agricultural revenues, and reliability of the food supply (Battisti and Naylor 2009). By the end of this century it is predicted that summers will be warmer than the warmest recorded to date over large parts of the Earth, necessitating a vigorous research program to select for crops and varieties which can tolerate higher stress, to improve efficiency of irrigation systems, and clearly to ensure strong resistance to pest insects.

Added to the problems of global warming are the declining numbers of crop pollinators and concerns over their conservation (Gallai *et al.* 2009), with vegetables and fruits as the crops of major importance. Among bumble bees declines have been due to habitat loss, declines in floral abundance and reduced floral diversity, mostly due to increases in agriculture (Goulson *et al.*

2008). Habitat degradation and fragmentation are also important. Invasive parasite species have entered new bumble bee populations through global trade routes. The plight of the bees mirrors much of the troubles observed in many other species and biotas, mostly because bees are ubiquitous, they forage widely, and require a diversity of resources. They therefore act as good indicator species for ecosystem health.

A landscape perspective

To maintain ecosystem services such as pollination and biological control in agricultural systems a landscape perspective is essential, with incentives for farmers to maintain or increase complexity in agricultural landscapes necessary for high biodiversity (Tscharntke *et al.* 2005). Complex habitats are likely to support higher richness of enemies on herbivorous insects, and more specialized species, as was the case with the enemies of nettle aphids, *Microlophium carnosum*, near Göttingen in Germany (Rand and Tscharntke 2007). As habitats and landscapes become simplified species are lost, but higher trophic levels appear to be more vulnerable, with the possibility of trophic collapse and loss of ecosystem services (Roland and Taylor 1997, Ryall and Fahrig 2005, Dobson *et al.* 2006). Landscape design is a key to maintaining biotic complexity in the matrix among agricultural fields, compensating for fragmentation and pollution resulting from cropland (e.g., Hunter 2008).

Landscape design that promotes conservation, trophic complexity and ecosystem services may also be implemented in urban settings (Hunter and Hunter 2008). Promoting urban beauty and green space can be coupled with conservation of insects, resulting from collaborations among landscape architects and insect ecologists. Many elements of urban development can host plant communities conducive to insect life: home gardens, residential areas, recreational spaces, land around schools, greenroofs, roadside corridors, water drainage corridors and urban wetlands. Roadside vegetation can provide effective conservation corridors between suitable habitat for many insect species. Well-designed gardens may provide a cornucopia of resources for insects, both desirable and not so welcome (e.g., Grissell 2001). Integrated community-wide endeavors that take every opportunity to maximize a mixture of natural elements such as grasses, shrubs, trees, ponds and wetlands will promote conservation effects and human enjoyment.

Costs of change

The costs of global change in areas other than agriculture are also large. Take, for example, human disease and vectors such as mosquitoes (e.g., Molyneux 2003). Common themes include the following:

(1) Generalist vectors spread resulting in epidemic disease spread such as malaria, filariasis, leishmaniasis, schistosomiasis and onchocerciasis.
(2) Farming and urban settings provide domestic animals and breeding sites for vectors.
(3) Reduced biodiversity fosters spread of generalist vectors and reservoir hosts.
(4) The more serious malaria pathogen, *Plasmodium falciparum*, increases relative to *Plasmodium vivax*.
(5) Water management such as dams, ponds, ditches and basins change vector-borne disease patterns.
(6) Both deforestation and reafforestation can increase vector-borne infections by fragmentation, edge effects and increases in human and reservoir host populations. These changes can act rapidly and will no doubt accelerate with population growth and accompanying anthropogenic change. The need for epidemiological studies of vectors and diseases outstrips the number of qualified and dedicated investigators.

Costs of invasive species have received considerable attention. Pimentel *et al.* (2000, see also Pimentel 2002) estimated that some 50 000 non-indigenous species have colonized the United States alone, causing environmental damage and losses totaling almost 137 billion dollars per year. This sum includes plants, vertebrates, mollusks and microbes, as well as insects and other arthropods. Among the 4500 arthropod species, over 2500 have colonized Hawaii, and over 2000 have entered the mainland. US crop pests cause the most damage among the arthropods, followed by forest pests, those in lawns, gardens and golf courses, the imported fire ant, Formosan termite and gypsy moth.

Reducing these costs and impacts is the challenge for the ecologist involved with applied problems: a daunting but, at the same time, an exciting challenge, taking all the skill, knowledge and creativity that we can muster.

Summary

The fossil record of insects shows periods of diversification interspersed with extinction events, but, in general, strong increases in the number of families has been realized. Warming trends seem to have accelerated adaptive radiation, while cooling has been accompanied by migration in some taxa. Movement of species is likely to produce no-analog communities. Current warming trends on the planet have produced a strong biological fingerprint, with insect species in temperate regions emerging earlier in the spring, shifting northwards in the northern hemisphere and upwards in elevation, including pest species and disease vectors. Increases in temperature and drought cause stress in trees, thereby increasing mortality and susceptibility to insect attack, as well as increasing fire risk. Carbon dioxide has direct effects on insects, and indirect impact through plant physiology, and rising CO_2 levels in the atmosphere have diverse influences on insect herbivores, varying with species and feeding guilds.

Insects have dynamic influences on ecosystem processes by killing trees and resetting ecological succession, and by accelerating recycling of nutrients when feeding on leaves and quickening decay of organic materials. Insects can act as regulators of ecosystems. They have also been very effective invaders of continents, although with a preponderance of forest insects moving from Europe to North America, with a smaller movement in the opposite direction, and several contributing factors involved. Impacts of invaders on indigenous communities can include effects from genetics, to populations and ecosystem functions. But insects are under threat from many other sources such that the conservation ecology of insects has become a very active field in terms of protecting species, habitats and biodiversity. A major factor threatening insects is habitat degradation in all its guises, with fragmentation a major contributor. Pollution is another.

Global change is likely to affect agricultural landscapes significantly because insect pest species are predicted to their expand ranges and various impacts are reducing pollinating insect numbers and diversity. Maintenance of a rich diversity of habitats over a landscape will contribute to ecosystem services such as pollination and biological control, including in urban environments. The costs of global change are high, posing a challenge to ecologists and others to ameliorate the negative impact on agriculture, with epidemiology of diseases and invasive species as examples.

Questions and discussion topics

1 What reasons would you develop for or against the position that, as more detailed studies are conducted on the paleobiological record, we will obtain a clearer predictive view of how global change will affect insect populations and species?

2 In an area with which you are familiar, which quantitative studies would you recommend and undertake to document any kind of local change in plant and insect species, and communities relating to phenology, area changes, population variation and biodiversity?

3 Discuss the opinion that invasion of species is an ongoing process, that attempts to prevent introductions have been largely ineffective, and equilibrium conditions would be established more rapidly if invasions were unrestricted. Employ specific examples where possible.

4 Do you think that insects have to reach eruptive or outbreak densities in order to act as regulators in ecosystems, or are they likely to be effective at endemic densities?

5 In your opinion is there an inevitable conflict between agricultural productivity and biodiversity conservation? If conflicts arise how can they be mitigated?

Further reading

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GLOSSARY

Definitions apply to usage in this book, and do not necessarily cover all meanings of a word or phrase.

accidental displacement passive movement by wind, water or thermals.

actual niche the ecological niche actually occupied by a species in the presence of competitors and other species such as natural enemies (= realized niche).

adaptive radiation the relatively rapid evolutionary divergence of members of a single lineage into a series of adaptive zones, with different kinds of ecological niches.

adaptive syndrome a set of adaptations clustered in response to a phylogenetic constraint which mitigates the confining effects of the constraint.

adaptive zone a way of life common to a group of species characterized by a particular mode of exploiting the environment.

additive interaction prey depletion by a predator assemblage can be accurately determined by summing the number of prey consumed by each predator species when present alone.

adiabatic cooling the cooling effect with altitude resulting from air being forced upward over a mountain, the air expands with decreasing barometric pressure, loses heat and cools.

age polyethism a division of labor based on age.

aggregation behavior behavior resulting in relatively high densities of a species.

aggregative response natural enemies collect where densities of hosts or prey are high.

alarm pheromone a pheromone released by an attacked individual which warns others of the same species of the threat (such pheromones may also act as synomones).

Allee effect the case in which cooperation fails at very low population densities and populations decline, perhaps to local extinction.

allelochemical a substance that is significant to organisms of a species different from its source, for reasons other than food as such.

allelochemical defense a chemical in, or released by, one species that is toxic or repellent to individuals of another species.

allocation cost the energetic cost of allocating valued plant resources (e.g., nitrogen) away from growth-related processes and toward antiherbivore resistance traits (e.g., secondary chemistry); assumes an inherent trade-off between plant growth and defense.

allomone a substance produced or acquired by an organism which, when it contacts an individual of another species in the natural context, evokes in the receiver a behavioral response or a physiological reaction which is adaptively favorable to the emitter, but not to the receiver (e.g., a defensive chemical).

allopatric speciation the origin of new species when populations are separated into different localities.

alternative mating strategy a mating behavior adopted by a subclass of individuals in a population, usually less competitive males, which circumvents the need for aggression among males.

amensalism an interaction in which one species is negatively affected by the interaction, but the other is unaffected.

among habitat diversity the diversity of species achieved when sampling across habitats – beta diversity.

antagonistic interaction prey depletion by a predator assemblage is less than predicted by summing the number of prey consumed by each predator species when present alone.

apneumone a substance emitted by a non-living material that evokes a behavioral or physiological reaction which is adaptively favorable to a receiving organism, but detrimental to an organism of another species, which may be found in or on the non-living material (e.g., aroma of dung is attractive to parasitoids but detrimental to fly larval hosts in the dung).

aposematic warningly colored.

aposematism advertizing unsuitability to predators using conspicuous coloration, sounds or smells.

aposymbiotic host a host with symbionts experimentally removed.

apparent competition an ecological situation where two species appear to show the effects of interspecific competition, although the result depends on the actions of a third species, such as a predator or parasitoid.

apterous an individual without wings, usually applied to wingless adults.

area hypothesis the hypothesis that larger areas support more species.

area-per-se hypothesis the argument that the pure effect of island size accounts for the relationship between area and species number.

arrhenotoky a form of parthenogenesis in which males develop from unfertilized eggs – they have no father – and females develop from fertilized eggs (= haplodiploid sex determination).

assemblage a fauna or flora in a given area which may or may not interact to qualify as a community.

assembly rule restrictions on the observed patterns of species presence or abundance which are based on the presence or abundance of one or more other species or groups of species.

associational resistance plants in the same community as the herbivore's host plant which interfere with the herbivore's finding of and oviposition on the host plant.

associational resistance hypothesis the argument that non-host plants in a community reduce the likelihood of herbivore population eruptions on host plants because the non-hosts interfere with finding and feeding on host plants.

associational susceptibility plants that are likely to be attacked by herbivores when in association with other species which may act as attractants, or alternative food plants.

associative learning learning to find food or hosts by associating their presence with another cue.

assortative phase the part of community development when sorting of species increases species packing by selecting for species better able to coexist.

asymmetric competition unbalanced exploitation in which organism 1 has a much stronger negative effect on organism 2 than 2 has on 1.

augmentative biological control increasing the population of an introduced or native natural enemy of a target pest through mass-rearing and release of the enemy.

balanced-mortality hypothesis the argument that fecundity evolves as a counter to the probable mortality inflicted upon progeny.

barometer of change a species or group of species that indicate changing conditions, which may increase predictive value on future climate change.

basin of attraction a zone of positive and negative population growth rate in which a population tends toward a stable equilibrium, as if attracted to an equilibrium point.

Batesian mimicry evolutionary advergence in appearance, sound or smell of an edible "mimic" prey organism toward resemblance of a less palatable "model" prey organism.

behavioral control a method of insect pest control employing behavioral manipulation using semiochemicals.

Beltian body a protein package produced by an *Acacia* plant at the tips of new leaves utilized by mutualistic ants as a food source.

bet-hedging strategy a reproductive mode in which more than one outcome is possible, which increases the chances of some progeny surviving (= mixed reproductive strategy).

bioindicator a species used in monitoring environmental condition that is sensitive to environmental change, and presumed to be representative of other species.

biological control the intentional use or manipulation of natural enemies to control pest organisms. There are three different types of biological control including classical, augmentative and conservation.

biome a terrestrial community of plants and animals with a uniform major vegetation type.

biotemperature temperature above 0° C.

biotic potential the possible growth of a population under ideal conditions.

biparental care parental investment that increases offspring survivorship through the cooperation of both male and female parents.

botanical insecticide plant chemicals used as insecticides (e.g., pyrethrum, rotenone).

brood-site pollination mutualism the mutualistic interaction of adult insect pollinators of angiosperms in which larvae of the pollinator are seed predators of the pollinated plant (= nursery pollination).

cannibalism the consumption of one individual by another individual of the same species.

carbon-nutrient-balance hypothesis the hypothesis that plants will allocate to defensive compounds according to the nutrients available in excess of those needed for growth: in nitrogen-rich environments nitrogen-based defenses will be synthesized, and in carbon-rich environments carbon-based defenses will predominate.

carrying capacity a maximum number of individuals that can be sustained by a particular set of environmental conditions, forming a virtual ceiling on population growth.

character displacement the result of interspecific competition between species 1 and 2 in which morphological traits of at least one species diverge, which reduces overlap of the ecological niches of the species 1 and 2 and subsequent competition.

chewer an insect that feeds with mandibles, cutting and ingesting pieces of food.

classical biological control the importation and release of natural enemies of an introduced pest from the country or area of origin of the pest.

Clementsian associational concept the idea that plants are associated in climax vegetation in a predetermined way, like a "complex organism," equivalent to the organs in a complex species.

cleptobiosis (= kleptobiosis) the condition in which one species becomes a social parasite of another species, living in the nest of another species for example.

cleptoparasite (= kleptoparasite) a species that steals food from another species.

coevolution reciprocally selected evolutionary change among interacting species.

coevolutionary complimentarity a mutualistic network in which pairwise interactions depend on matched characters among pairs, such as flower depth and pollinator proboscis length.

coevolutionary convergence in a mutualistic network, species can enter into an existing network because characters such as flower depths or proboscis lengths are convergent.

collector an insect that feeds on small plant fragments and decomposing organic matter.

colonization hypothesis the hypothesis that seed dispersal promotes the colonization of favorable new resources or patches.

colony collapse disorder a phenomenon affecting honey bees that is characterized by a rapid loss of adult worker bees with an absence of dead bees in or near the colony and the presence of abundant brood honey and pollen despite vastly reduced numbers of adult workers.

communal species members of the same generation live together, but do not participate in cooperative brood care.

community a group of species that interact in a given area.

community genetics the study of the effects of genetic diversity in host plants on community organization among herbivores and their natural enemies, other members of the community including birds and mammals, and ecosystem function.

community saturation the point reached by a local community when no more species can invade.

commuting regular foraging on a short-term basis.

compartmentalization (= compartmentation) the division of communities into compartments, or blocks, of more strongly interacting species, for example based on plants in different species with specialist herbivores, although compartmentalization is likely to be less evident at the higher trophic levels with more generalist feeders, as with pollinators or predators.

competition the exploitation of the same resource, which is in limited supply, by two or more organisms of the same or different species.

competitive displacement the prevention of species 1 from occupying its fundamental niche by the activity of a competing species 2, so species 1 is restricted to its smaller realized niche.

competitive exclusion principle the concept that no two species can occupy the same ecological niche, resulting in the exclusion of one.

component community the community of species associated with a particular plant species.

compound community the community consisting of all species in a habitat.

concealed feeder an insect feeding on internal tissues of a plant or animal (= endophage).

concordance the condition in which the phylogenies of two lineages appear to be diversifying together (= cophylogeny).

condensed tannin polymers of flavonoids in plants which act as feeding deterrents and/or digestibility reducers when ingested by insects.

conditional mutualism the interaction between species which varies depending upon the prevailing conditions, from strong mutualism to none in some cases.

conditional strategy a mating strategy that depends upon available resources defined by the competitive milieu in which an individual exists.

connectance food web a food web simply showing the feeding linkages without any estimate of their strengths: a qualitative food web.

conservation biological control the manipulation of the environment to make conditions more hospitable for natural enemies, either by removing or mitigating adverse factors or providing requisites for natural enemies that are lacking in the habitat.

constitutive defense a compound in a plant that is always present in the plant and that does not change following attack.

consumer an organism that eats plants or animals or their products.

contest competition when individuals can protect resources, excluding others, such as in territoriality (= interference competition).

context dependency the interaction between species which varies depending upon the prevailing conditions (e.g., conditional mutualism).

cooperation when two individuals benefit each other as between males and females mating.

cophylogeny the condition in which the phylogenies of two lineages appear to be diversifying together (= concordance).

coprophagy the consumption of feces.

corbiculum a pollen basket on the outer face of the hind tibia that is specialized for the transport of pollen and nest-building materials.

cospeciation concurrent speciation between pairs of species such as host and parasite without necessarily involving coevolution.

crypsis a color pattern or shape that allows an organism to blend in with the environment, either to the substrate color or pattern, or to an object such as a leaf, thorn, twig or bird feces.

cryptic species species that are so similar that their identity is largely hidden from detection (= sibling species).

cuckold the partner of a female in which the female has mated with another male.

cytochrome P450 monooxygenases a major class of enzymes involved with the breakdown of toxic compounds such as alkaloids (= mixed function oxidases).

deceit pollination a plant species that lures an insect to perform the act of pollination without providing a reward.

defense cascade a range of metabolic responses in a plant induced by damage from insects or ultraviolet light etc., which reduces survival of insect herbivores.

delayed density dependence a factor responding to population density with a delayed effect on the density of a population, acting on generation $t + 1$, rather than on generation t.

demic-adaptation hypothesis the hypothesis that populations (demes) of small, specialized insect herbivores become adapted to, and specialized on, individual large perennial host plants.

density dependent (1) a response of species 1 to species 2 which varies according to the density of species 2; (2) where one or more demographic parameters such as birth and/or death is a function of population density.

density-independent factor an environmental influence not affected by the density of a species, such as weather, or a factor causing mortality in a population which is not related to the density of that population.

developmental resistance the case in which a plant changes the level of resistance to herbivores as it develops from juvenile to the mature reproductive stage.

diapause a quiescent phase in an insect life cycle during inclement, usually winter, conditions.

diaspore a plant propagule adapted for dispersal, including fruits and seeds.

diet breadth the range of resources utilized as food by a population or species.

diet mixing feeding on more than one plant species or food source.

diffuse coevolution evolution resulting from a suite of species that selects for traits in another species or group of species, which is reciprocated.

digestibility reducer a secondary compound in a plant with an increasingly deleterious effect on herbivores as concentrations increase and acting to reduce food quality (= quantitative defense).

direct defense plant defensive traits that act directly on the herbivore, such as toxins, as opposed to **indirect defenses** which attract natural enemies as a defense.

directed-dispersal hypothesis the hypothesis that in some species of plants, fruits and seeds have evolved such that they are likely to reach specific favorable sites for germination, often resulting from animal dispersal.

direct interaction the kind of interaction in which an individual has an immediate effect on another individual, such as when a herbivore eats a plant.

dispersal movement away from one area to another usually motivated by the search for food, breeding sites or protective places, often used with the implication that individuals spread out over a landscape.

dispersal/transmission mutualism a mutualism involving the dispersal of pollen, fruits, seeds or symbionts such as beneficial mites (= transportation mutualism).

domatium a plant part adapted for sheltering beneficial arthropods.

drones stingless male bees in a colony of social bees whose only function is to mate with the queen.

durable interaction an interaction over the long term typical of the host and parasite relationship and contrasting with the brief interaction of a predator and its prey.

Dyar's law the general fact that caterpillar head capsules increase by a constant of 1.6 times at each molt (growth ratios of 1.27 to 1.52 better cover a range of taxa).

ecological breakthrough a sudden burst of adaptive radiation in a lineage resulting from the initial colonization of a new set of resources, as when the beetle group, Phytophaga, radiated on the angiosperms, from basal lineages on conifers and cycads.

ecological cost the costs of expressing a plant trait which manifest themselves upon interactions with the biotic community, as opposed to **allocation costs**; for instance, in addition to negatively affecting herbivorous insects, producing secondary plant metabolites may deter pollinators and predators or parasitoids, thus reducing plant fitness.

ecological engineering the design of cropping systems that minimize pest problems and maximize conservation and nutrient cycling.

ecological niche the role of a species in the environment, or the place in the environment which provides all the needed resources for a species which enable it to survive and reproduce.

ecological refuge a place of escape from adversity, often from competition or natural enemies.

ecological restoration the return of an ecosystem to an approximation of its structural and functional condition before damage occurred.

ecological stoichiometry the study of the relative balance of key elements in organisms from different trophic levels (e.g., C:N ratio in plants vs. insect herbivores).

ecological succession the progression of species on the landscape through time in a predictable way, in which plants and animals form different communities as colonists change conditions for subsequent arrivals.

ecological time the time over which ecological phenomena take place.

economic threshold the pest density at which the damage caused justifies the expense incurred in management practices, or the point at which pest density causes an economic loss of yield.

ecosystem engineer a species that modifies the environment, which benefits itself or other species, such as beavers making dams, or insects making leaf rolls.

ecosystem-exploitation hypothesis the number of trophic levels in a community is proportional to plant productivity, with only two trophic levels in low productivity systems and three or four trophic levels in moderate to high productivity systems; the number of trophic levels supported then dictates the direction and strength of top-down cascades on plant biomass (i.e., high plant biomass in one- or three-trophic-level food chains and low plant biomass in two- or four-trophic-level food chains).

ecosystem function an intrinsic ecosystem attribute related to the set of conditions and processes whereby an ecosystem maintains its integrity (e.g., primary productivity, nutrient cycling, food chain, etc.)

ectoparasitoid a parasitoid that lays its eggs and larvae feed externally on the host.

ecto-symbiotic a symbiont–insect relationship that is external to the insect's body.

Eichler's rule the rule indicating that the diversity of the parasitic fauna will increase as the diversity of the host taxon increases.

elicitor specific compounds expressed in the saliva, regurgitant or oral secretions of herbivorous insects such as caterpillars that elicit a characteristic secondary chemical response in plants.

emergent impacts unexpected impacts of multiple predator species on prey based on the summed knowledge of interactions between individual species.

emergent property the ecology of a species defined by the evolutionary background of the lineage, including the phylogenetic constraint and the adaptive syndrome, particularly the ecology of population distribution, abundance and dynamics.

encapsulation the cellular immunological response of a host insect to a foreign body such as a parasitoid egg, which usually kills any living body by enveloping it with blood cells, and which may become melanized and conspicuous.

endoparasitoid a parasitoid that lays eggs inside the body of the host in which the larva feeds.

endophage an insect feeding on internal tissues of a plant or animal (= concealed feeder).

enemies hypothesis the hypothesis that diverse assemblages of plants offer more resources for natural enemies of herbivores than concentrated single-species plant patches, so that specialist herbivore densities can build in dense plant patches, but not in diverse areas.

enemy-free space a location in the niche of a species in which natural enemies are absent, or inflict reduced mortality, relative to other parts of niche space.

enemy-impact hypothesis the idea that a diverse array of plants in a community provides natural enemies with plentiful food and suitable habitat, resulting in high populations and suppression of eruptive species.

enemy-reduced space a location in the niche of a species with reduced natural enemy attack relative to other parts of niche space.

environmental resistance the additive impact of factors such as weather, poor nutrition or natural enemies, that reduce population growth below its biotic potential.

ephemeral plant a plant species with parts available to herbivores and/or pollinators relatively briefly, such as spring ephemerals.

epideictic pheromone a pheromone that stimulates dispersal from overcrowded conditions, or from conditions that are likely to become overcrowded.

epidermis feeder an insect that feeds on epidermal cells of plants, usually by sucking cell fluids.

epigamic selection natural selection operating between the sexes of a species which favors traits that improve attraction and access to mates (= intersexual selection).

equilibrium the concept in population and community ecology in which a stable state prevails in a population, or between species in a community; this may be a dynamic equilibrium maintained by balanced birth and death rates in a population or a return to a former state after perturbation in a community.

equilibrium number the number of species in a community when that community reaches a stable, asymptotic diversity set by the balanced colonization and extinction rates of species.

eruptive species a species with populations that show rapid and large changes in density, which reach damaging populations periodically.

escape-and-radiate coevolution the hypothesis that a genetic mutation in a plant population results in escape of it and its progeny from herbivores, which results in adaptive radiation in that lineage, until a mutation in the herbivore population enables exploitation of the novel lineage, with the result that the specialized insect group radiates; consequently there are step-wise adaptive radiation episodes between plants and insect herbivores.

escape hypothesis the hypothesis that survival of plant progeny increases with distance from the parent plant because density-dependent seed and seedling predation acts more strongly near the parent plant, resulting in progeny well spaced from parents (= Janzen–Connell hypothesis).

eucrypsis a type of crypsis in which an organism blends in with the background.

European-crucible hypothesis the argument that European conditions through time selected for insect herbivores on trees that were good colonizers into North America resulting in an imbalance in the exchange of species with the preponderance of species moving from Europe to North America.

eusocial species species which engage in cooperative brood care, have reproductive castes, and overlapping generations.

evolutionary ecology ecology that is concerned with adaptation, natural selection and the environmental factors influencing evolutionary change.

evolutionary phase the part of community development involving evolutionary shifts in species' niches, reducing negative interactions and increasing the number of coexisting species.

evolutionary time the time over which evolutionary phenomena proceed.

exophage an insect feeding on the external surface of plants or in another open space (= free-living feeder).

explanatory framework an outline of the ways to approach a certain question in ecology or evolutionary biology (as opposed to the alternative of erecting a general hypothesis).

exploitative competition when individuals have about the same access to a limited resource in a free-for-all interaction (= scramble competition).

exploitative mutualism a mutualism enabling the utilization of a new resource (= nutritional mutualism).

exponential growth when a population increases by a constant factor in each generation or time period (= geometric growth).

extended phenotype any influence of one genotype on its environment, such as on the host of a parasite or the gall of an insect.

external rumen a name given to insect feces in which microbes act as potential mutualists, breaking down cellulose etc., and making such feces more nutritious when subsequently ingested by coprophagous species.

extinction rate the rate at which species go locally extinct in relation to the number of species present in the community.

extracellular outside the cell, as in the lumen of the gut.

extrafloral nectary a sugar-producing structure on a plant not within the flower.

facilitation an interaction in which the activity of one individual is beneficial to another.

facultative a non-essential relationship.

facultative mutualism a mutualistic interaction that benefits both parties, but is not essential for either's survival; this term typifies many relationships involving ants and extrafloral nectary-bearing plants.

Fahrenholz's rule the rule that parasite phylogenies mirror host phylogenies.

feedback loop a loop of interactions that increases population growth or retards it, as with cooperation or the action of natural enemies.

feeding compensation increased feeding rate on nitrogen-deficient plant resources which improves the balance of nutrients, especially nitrogen, in the diet.

feeding guild a group of species that exploit the same resource in a similar manner (= guild).

female-choice hypothesis the argument that females choose males of their own species on the basis of the male's genitalia.

filter chamber a design in the alimentary canal of a sucking insect whereby sugar-rich liquid bypasses the absorptive midgut and is rapidly excreted.

filter feeder an insect that strains particles of food from water.

flight-oogenesis syndrome the sequential division of resources in a female insect's body, usually involving those needed for flight first and then the production of eggs second.

food chain the feeding links in a sequence from producers to primary consumers and secondary consumers.

food web the linkages from plants to herbivores, to primary carnivores and so on up the trophic system, involving food chains and cross linkages to others.

foraging movement searching for food or other resources within one locality.

free-living chewer an insect feeding in an exposed position while chewing food with its mandibles.

free-living feeder an insect feeding on the external surface of plants or in another open space (= exophage).

fruit borer an endophytic insect feeding within the fruit of a plant.

functional response the change in an individual predator's rate of prey consumption in response to varying prey density.

fundamental niche the ecological niche which could be occupied in the absence of competitors and/or natural enemies (= potential niche).

gall inducer an organism that causes an abnormal growth on a plant in which a larva or nymph lives and feeds.

gatherer an insect that feeds on organic matter on the streambed.

Gause's principle (axiom or hypothesis) no two species can live together indefinitely on a single limiting resource, or in the same niche.

gene–environment interaction the modification of gene expression by environmental conditions.

genetically modified organism an individual, or crop-plant species, genetically engineered to contain a gene sequence from another species or population.

genetic assembly rule the presence and/or abundance of species in a community is defined by the genetic basis of the host plant supporting that community.

genetic drift random genetic changes in a lineage causing gene frequencies to change.

genetic similarity rule on average, arthropod communities on plant hosts become more similar as the plants they utilize become genetically more similar.

geographic mosaic of coevolution the concept that coevolutionary hotspots of interacting species are embedded in a matrix in which coevolution is not in effect, so that a landscape supports a mosaic of varying levels of reciprocal selection or its absence.

geometric growth when a population increases by a constant factor in each generation or time period (= exponential growth).

giving-up time the hypothesis that an enemy gives up searching and leaves a patch if it has not found a suitable host within a fixed time.

Gleasonian individualistic concept the view that each species responds in a unique way to environmental variation: each species is individualistic in its ecology.

glutathione S-transferases a major class of detoxification enzymes in insects.

glycophytic plant a plant that is not adapted to high salt conditions.

green-world hypothesis a three-trophic-level top-down view of population control proposed by Hairston, Smith and Slobodkin (1960), which states that predators largely regulate patterns of plant biomass (or the greenness of the world) by suppressing herbivores that would otherwise suppress plants.

group selection selection for traits that would benefit a population at the expense of the individual possessing the trait.

growth-differentiation-balance hypothesis the hypothesis that there is a physiological trade-off between growth and differentiation, and the plant engages in one or the other, with the one least impeded by environmental conditions being the most active at any given time.

growth-rate hypothesis the hypothesis that plants that can grow rapidly in nutrient-rich conditions will be less defended, but will compensate for damage, while plants in low nutrient conditions will be well defended and evolve with constitutive defenses.

guild a group of species that exploit the same resource in a similar manner (= feeding guild).

habitat-heterogeneity hypothesis (= habitat diversity hypothesis) the argument that as habitat variability in an area increases so will the species number of occupants in a particular taxon.

habitat template (= habitat templet) a pattern of resources in the environment which affect natural selection, "guiding" adaptive trajectories in a lineage.

halophytic plant a plant adapted to saline conditions.

Hamilton's rule mathematical concept that a gene can increase its evolutionary success by promoting reproduction and survival of related individuals only when $rb > c$, where b is the benefit to the recipient of the altruistic act, c is the cost to the bearer and r is the degree of relatedness between them.

haplodiploid the sex-determination system in which a male develops from an unfertilized egg, which is therefore haploid, and a female develops from a diploid fertilized egg (= arrhenotoky).

haplodiploidy hypothesis idea that the high relatedness among full sisters ($r_{\text{sister-sister}} = 0.75$) in haplodiploids predisposes them to eusociality.

herbivore-induced plant volatile plant volatile compounds that are emitted upon feeding damage by herbivorous insects; as opposed to constitutive volatiles that are released from uninjured plants.

herbivore offense a range of offensive strategies utilized by herbivorous insects (e.g., sequestration, detoxification) to counteract the defensive strategies employed by plants.

herbivore sink a plant population that is attractive to, or favorable for, a herbivore species such that herbivores reach high densities, perhaps in a hybrid zone, relative to low densities in other parts of its range.

heteronomy the condition in which parasitoid species develop males in one host and females in another.

higher-order predation organisms that function as top or intraguild predators, consuming other enemies rather than herbivores.

hilltopping a meeting strategy for males and females of a species, usually with sparce dispersion, employing visually prominent landmarks where individuals aggregate.

homeostatic mechanism various means by which an individual maintains its elemental body composition.

honeydew excretions of excess sugars by sucking insects.

horizontal transmission the transfer, usually of pathogens, from one host to another in the same generation, or across species.

hormone a chemical agent, produced by a tissue or endocrine gland, which controls various physiological processes within an organism (c.f., semiochemical, pheromone).

hybrid-bridge hypothesis the hypothesis that hybrid plant populations can act as a bridge which facilitates host-plant shifts by herbivores from one parental plant to another.

hybrid-sink hypothesis the hypothesis that hybrid plants are better hosts than either parental species, resulting in high herbivore densities in the hybrid zone.

hydrolyzable tannin a defensive compound in a plant formed from esters of sugars with gallic acid, which is biodegradable and can be recycled rapidly.

hypermetamorphosis the life history in which larval instars develop through more than one form, for example from an active first instar with legs, to a legless sedentary form.

hyperparasitoid a parasitoid species that attacks a primary parasitoid, either in an obligatory or facultative manner.

hypersensitivity rapid cell death in a plant which isolates an attacking pathogen or insect in localized necrotic tissue.

hypogeal a below-ground–level habitat.

hypothesis a tentative explanation of a question, which needs further testing.

ideal-free-distribution the assumption that a predator is free to search a set of habitats or patches which differ in quality (e.g., prey density), while having an ideal knowledge of patch densities of prey.

idiobiont a parasitoid in which the adult permanently paralyzes the host before the parasitoid egg hatches, and the parasitoid feeds on the moribund host.

immigration curve the rate at which species immigrate, starting with an empty habitat, in relation to the number of species present in the community.

inclusive fitness the sum of fitness gained through producing offspring (direct fitness) and through affecting the fitness of individuals that share genes with the altruist (indirect fitness).

indicator group a group of species that is effective in showing the condition of the environment, enabling evaluation of change in an economical way, usually in insects involving a taxon that is easily monitored, such as butterflies or dragonflies.

indicator species one or a few species that effectively capture(s), or represents, the state of an ecosystem and its general sustainability, enabling evaluation of change in an economical way.

indirect defense a method using attractive plants to natural enemies, providing pollen and/or nectar for example, so that the enemies are more effective in regulating pest species on a crop in the vicinity.

indirect interaction the kind of interaction in which an individual modifies conditions which influence another individual, often through modifying host-plant quality, which has an effect on another species.

induced defense chemicals that are synthesized, or released from pre-existing ducts or cells, during attack by a herbivore (= induced resistance).

induced resistance chemicals that are synthesized, or released from pre-existing ducts or cells, during attack by a herbivore (= induced defense).

inquilinism the relationship in which a species, the inquiline, spends much of its life in the nest of another insect, the host species.

integrated pest management (IPM) the amalgamation of control methodologies for all the major pests on a crop throughout the active season, and preferably over a landscape.

interaction web a web of interactions in a community not restricted to the food web, but including effects such as induced changes in plant chemistry or architecture by species 1 which modifies the ecology of species 2.

interactive phase the part of community development in which interactions develop, causing some sorting of species.

interference competition when individuals can protect resources in limiting supply, excluding others, such as in territoriality (= contest competition).

intersexual selection natural selection operating between the sexes of a species which favors traits that improve attraction and access of mates (= epigamic selection).

interspecific competition competition between different species.

intertaxon transmission horizontal transmission of a parasite among different species.

intracellular within a cell.

intraguild predation the consumption of one predator by another predator with which it competes for a common prey resource.

intrasexual selection selection on traits that improve competitive ability among males for mating with females.

intraspecific competition competition among members of the same species.

inverse density dependence a term denoting positive density dependence, the latter being the preferred usage.

irreplaceable mortality the mortality from a specific factor that cannot be replaced, or compensated for, by another factor, in the context of life-table studies.

iteroparity repeated breeding within a life cycle.

Janzen–Connell hypothesis the hypothesis that survival of plant progeny increases with distance from the parent plant because density-dependent seed and seedling predation acts more strongly near the parent plant, resulting in progeny well spaced from parents (= escape hypothesis).

***K*-selection** selection that adapts a population or species to living close to the carrying capacity (*K*) of the environment.

kairomone a substance produced or acquired by an organism that, when it contacts an individual of another species in a natural context, evokes in the receiver a behavioral response or physiological reaction that is adaptively favorable to the receiver, but not to the emitter (e.g., a plant attractant to a herbivore).

keystone interactions interactions among organisms in a community which alter the effect of keystone species and the interaction strengths linking multiple species.

keystone mutualist an organism, usually a plant, that provides critical resources to large complexes of mutualistic animals, or mobile links.

kinesis change in rate of movement or turning.

kin selection a theory of natural selection which states that a usually altruistic behavior or attribute that lowers the fitness of a particular individual is selected for if it increases the probability of survival and reproduction of relatives who possess some or all of the same genes as the altruistic individual.

koinobiont a parasitoid that lives with the living host, when the host continues to feed and to defend itself.

larval performance the relative ability of larvae to survive and/or grow rapidly, usually in relation to a mother's ovipositional preference.

latent species a species with populations that pass through relatively low fluctuations in density without usually causing conspicuous damage.

lateral interaction an interaction between species feeding at the same trophic level.

leaf domatia places to hide and live on a leaf for arthropods beneficial to the plant, such as small predatory insects and mites.

leaf miner an endophytic insect feeding within the leaf of a plant.

leaf roller an insect that forms rolls from leaves, and lives and feeds mostly within the roll.

leaf tier an insect that threads plant parts together with silk and feeds within the assembled parts.

lek an assemblage of males independent of food or oviposition sites, which attracts females ready to mate.

lek polygyny a lek in which males may mate repeatedly, but females entering the lek mate only once and leave.

life-history omnivore insects that switch between plant and prey foods with ontogeny; for example, a species that consumes plant tissue as a herbivorous larva, but acts as a predator, eating other insects, after pupating to adulthood.

life zone a band of vegetation on an elevational gradient, particularly evident in the southwest US, characterized by a particular dominant plant species.

limiting factor a resource that constrains population growth because it is in short supply.

local community diversity the richness and abundance of species within a community – alpha diversity.

logistic growth equation a simple model of density-dependent population growth in which growth rate decreases gradually to zero at the carrying capacity for the population.

long-distance dispersal another term for migration: undistracted movement with a stimulus to end the behavior provided by movement itself.

long-range dispersal the extensive and rapid spread of an invasive species, often by transport of infested material, well beyond the front of a diffusing population.

Lotka–Volterra model a basic model of interspecific competition founded on the logistic equation, which used competition coefficients α and β which convert individuals of one competing species into equivalent units of the other competitor.

macroecology (1) a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution and diversity; (2) an ecological and mechanistic approach which attempts to explain the macroevolutionary basis for patterns of distribution, abundance and population dynamics in phylogenetically related species.

macropterous an individual with fully developed, functional wings.

marking pheromone a chemical cue left by an insect on a substrate, usually acting as a deterrent to subsequent members of the same or different species.

mate rendezvous hypothesis the reasoning that males gain access to females at hilltop sites when virgin females pass through briefly and acquire mates.

mating investment a nuptial gift from a male to a female solely to influence the probability of mating, without any contribution of nutrients for egg development or progeny welfare.

mating plug a blockage of the female genital passage placed by a male after copulation which prevents subsequent copulations for a certain time.

mating system a species-specific pattern of male–female associations; the general strategy employed in obtaining mates.

mesophyll feeder an insect that feeds on mesophyll cells of leaves, usually by sucking cell fluids.

metapopulation a group of populations exchanging individuals of a species and experiencing largely independent events of colonization, immigration, emigration and extinction, so that populations act as sources or sinks for other populations.

microbiome the many symbiotic species of microbe that live in the bodies of larger animals such as insects or humans.

mid-domain effect the condition in which species number in a taxon is highest in the middle of a gradient, be it an elevational or latitudinal gradient.

mid-elevation richness peak the condition in which species number in a taxon is highest at an intermediate elevation.

migration behavior undistracted movement with the stimulus to end provided by the movement itself (= long-distance dispersal).

mimesis (1) imitation, mimicry; (2) a type of crypsis in which the organism resembles an inedible feature of the environment (usage as advocated by Pasteur 1982 and Lederhouse 1990).

mixed-function oxidases a major class of enzymes involved with the breakdown of toxic compounds such as alkaloids (= cytochrome P450 monooxygenases).

mixed reproductive strategy a reproductive mode in which more than one outcome is possible, which increases the chances of some progeny surviving (= bet-hedging strategy).

mobile link an animal species playing a significant role as a mutualist connecting several to many plant species, as a pollinator or diaspore disperser, for example.

monandry the state of breeding with a single male at a time.

monogamy each sex mates only once.

monophagous a specialist feeder utilizing a single species as food, or closely related species.

Moran effect the synchronization of population cycles over several to many apparently independent populations by an exogenous factor such as weather.

Müllerian body a glycogen-rich food body produced on the base of the petioles of *Cecropia* trees, which are collected and eaten by resident ants housed in the hollow stem.

Müllerian mimicry evolutionary convergence in appearance, sound or smell of unpalatable prey species.

multiple-decrement life table a life table based on estimates of irreplaceable mortality with the recognition that much mortality is unlikely to be compensated for by other mortality factors.

multiple parasitoidism a condition in which a host individual is occupied by more than one species of parasitoid.

multitrophic interaction any direct or indirect interaction linking more than two trophic levels.

multivoltine having more than one generation per year.

mummy parasitoid a parasitoid that attacks the mummified stage of an aphid, killing and consuming whatever is contained; a primary parasitoid or a hyperparasitoid.

mutual interference interference among predators or parasitoids leading to a reduction in per capita consumption rate that increases with predator or parasitoid density.

mutualism an interaction between species which is beneficial to both.

mycangium a specialized pouch in an insect adapted for transmission of fungal spores or mycelium from one breeding site to another (= mycetangium).

mycetangium a specialized pouch in an insect adapted for transmission of fungal spores or mycelium from one breeding site to another (= mycangium).

mycetome a specialized group of cells which contain symbiotic bacteria.

myrmecodomatium a plant part adapted to the accommodation of ants.

myrmecophile a species that cohabits with ants.

myrmecophily the condition in which a species cohabits with ants.

myrmecophyte a plant adapted to providing shelter for mutualist ants, plus food in some cases.

n-dimensional hypervolume a multidimensional space that defines the environmental conditions under which a species can survive and reproduce indefinitely – the ecological niche of a species.

negative cross-host correlation in performance the condition favoring monophagy in which detoxifying mechanisms adapted for one host-plant species precludes this ability on another host-plant species.

negative density dependence when a factor retards the rate of population growth as the population density increases, as is likely when natural enemies become more effective in dense populations of prey or hosts.

net replacement rate the total of reproductive expectation in a generation, R_0, which is the number of female progeny that replace an average female in the course of a generation.

niche same as ecological niche.

niche breadth the distribution of a species along one important gradient within the fundamental or realized niche of that species.

niche divergence the result of natural selection through competition or other factors which reduces the overlap of ecological niches of two species, resulting in reduced interspecific competition (= resource partitioning).

niche overlap an estimate of the proportional overlap of one species over another on one important gradient within the multidimensional niches of the species.

niche release the expansion of the resource utilization pattern of species 1 when a competing species or a natural enemy reduces its impact in an area of the fundamental niche, allowing species 1 to expand into a larger part of its fundamental niche.

no-analog community a community that is compositionally unlike any found today.

non-contact guarding phase a post-copulatory strategy in which a male guards a female against other males, without contact between the sexes.

non-equilibrium condition the concept in population and community ecology in which a state of flux prevails whether through unbalanced birth, death and immigration rates in a population, or rates of colonization and extinction of species in a community.

non-interactive phase the part of community development at the beginning of colonization of a vacant habitat in which individuals are too sparse to interact.

number expectation the hypothesis that an enemy will leave a patch of prey or hosts after finding a certain number of hosts.

numerical response a change in predator population size, either due to aggregation or reproduction, in response to increasing prey densities.

nuptial gift a lure used in a courtship strategy involving the offering of a token, usually food, to a female by a male, which induces the female to approach and mate.

nursery pollination the mutualistic interaction of adult insect pollinators of angiosperms in which larvae of the pollinator are seed predators on the pollinated plant (= brood-site pollination mutualism).

nutrient sink a place on a plant to which nutrients are drawn by rapid consumption by insects or their effects on the plant, causing rapid cell division (e.g., during gall formation).

nutritional mutualism a mutualism enabling the utilization of a new food resource (= exploitative mutualism).

obligate a required relationship in order to survive.

obligate mutualism a mutually beneficial interaction whereby the interacting partners are reliant on each other for survival; ant-plants are a good example, whereby plants house and feed ant colonies and in return ants protect the plants from herbivores and competitors.

oligophagous a species feeding on a range of other species over several genera, but usually within the same family.

omnivore insects that feed from more than one trophic level; typically used to describe organisms that consume both plant and prey foods.

oogenesis-flight syndrome the sequential division of resources in a female insect's body usually involving those needed for flight first, and then the production of eggs second.

operational sex ratio the ratio of adult males and adult females.

optimal-defense hypothesis the hypothesis that defenses in a plant are adjusted according to the risk of damage, the cost of a module and its value to the plant.

optimal-diet theory the hypothesis that foragers should select food items efficiently to maximize energy and nutrient intake.

optimal-foraging theory the hypothesis that any foraging activity should maximize efficient use of time and effort.

ovigeny index a value from 1 to 0 where 1 is given to females that are fully pro-ovigenic, and 0 to females that are completely synovigenic, so the index estimates the proportion of all eggs a female can lay in her lifetime which are mature at the time of adult emergence.

oviporus the pad-like structure in the Lepidoptera through which eggs are laid.

ovipositional preference selection by a female of a certain quality of resource for oviposition, among a range of resource variation.

ovipositional-preference–larval-performance linkage the relationship between a female's ability to oviposit in high-quality resources and the larval response in terms of high growth rate, pupal weight or survival.

pairwise coevolution evolution in two interacting species with reciprocal selective effects, usually between specialists such as parasites and their hosts, including specialist herbivores.

palatability spectrum continuous variation in the suitability of prey to a predator.

parallel cladogenesis lineages of interacting species diversify concurrently, with or without coevolutionary interactions.

parasite an organism that lives in or on another living organism, which obtains part or all of its food from that organism, which is usually adapted by morphology, physiology and behavior to living with the host, and which causes some measurable damage to its host.

parasitoid an individual that is parasitic in the larval stage, with a free-living adult, which searches for hosts and lays an egg in or on a host, completing the life cycle.

paratransgenesis the disruption of transmission cycles in insect vectors of diseases by producing genetically altered bacteria that target pathogenic species (= Trojan-horse method).

parenchyma feeder an insect that feeds on parenchymatous tissue of plants, usually by sucking cell fluids.

parental care any postzygotic parental investment that increases offspring survivorship.

parental investment any allocation of time or energy by a parent of an individual offspring which increases the offspring's chance of surviving, at the cost of the parent's ability to invest in other offspring.

parthenogenesis unisexual reproduction from an egg by a female without male gametes.

passive phase a post-copulatory strategy in which a male remains attached to a mated female without genital contact, protecting against other males (= tandem position).

patch time allocation the time spent in a patch searching for prey or hosts by a predator or parasitoid, respectively.

pathogen a species that causes disease in other species, usually applied to microbial parasites.

percentage similarity an estimate of how much species overlap on one dimension of multidimensional niche space, based on the percentage of one species that coexists with the other on that dimension.

pharmacophagy seeking out secondary plant compounds and using them to enhance insect fitness (aside from host recognition), for instance by sequestering chemicals to protect from predators, parasitoids or pathogen attack.

phase-plane model the model by Lotka and Volterra to compare the relationship between populations of two species.

pheromone a substance that is secreted by an organism to the outside and causes a specific reaction in a receiving organism of the same species.

phloem feeder an insect that feeds on phloem tissues, usually by sucking sap.

phylogenetic congruence the condition in which phylogenies of interacting species run parallel to each other.

phylogenetic constraint a plesiomorphic trait in a lineage that limits the path of adaptive radiation of that lineage to a rather narrowly circumscribed set of evolutionary opportunities.

phylogenetic tracking the condition in which phylogenies of interacting species run parallel to each other with one lineage tracking the other, as in some host and parasite lineages.

planidium the active first-instar larva of some parasitoid species which can crawl onto a host, after which it and the remaining instars are less active.

plant-apparency hypothesis the hypothesis that plants that are easily found (apparent) should be defended with more costly defenses than plants that are hard to find (non-apparent).

plant-associated assortative mating mating with individuals of the same species which prefer the same plant species.

plant-stress hypothesis the hypothesis that stressed plants provide favorable resources for some kinds of herbivores, resulting in increased herbivore densities.

plant-vigor hypothesis the argument that many insect herbivores select and perform best on plants or plant modules which are growing vigorously relative to mean growth rates in the population.

plesiomorphic character a character of an organism which has an anciently homologous basis of similarity with other members of the same phylogeny.

point estimate the area estimated that will support all species of interest in one conservation reserve, based on extrapolation from smaller areas which support a subset of species.

pollinator decline the problem of reduced survival of wild and domesticated bees which threatens the effective pollination of wild and crop plants.

polyandrogyny both sexes have variable mate numbers, but female mating success is more variable than male mating success.

polyembryony the formation of multiple embryos from one egg.

polygamy both sexes have variable mate numbers with approximately equal mating success of males and females.

polygynandry both sexes have variable mate numbers, but male mating success is more variable.

polygyny males mate more than once, but females mate once.

polyphagous a generalist feeder that exploits other species in more than one family.

polyphenism seasonal dimorphism in which a temporal, environmentally induced change in morph type occurs.

population limitation the density-dependent reduction in population growth brought about by intraspecific competition as density approaches the carrying capacity of the habitat.

population regulation the return of a population to an equilibrium density following departure from that density as a result of density-dependent processes.

population stability a relative constancy in population density.

positive density dependence where a factor improves the rate of growth of a population as the population density increases, as with cooperation.

positive preference–performance correlation the positive relationship between a female's preference for an oviposition site and the progeny's ability to grow and survive well at that site.

postzygotic parental care care of young after fertilization of the egg when the zygote is formed.

potential niche the ecological niche which could be occupied in the absence of competitors and/or natural enemies (= fundamental niche).

precocious larva a rapidly developing larva that can act as a soldier caste in a polyembryonic parasitoid.

predation the consumption of one living organism (the prey) by another organism (the predator).

predator an individual that kills and eats individuals of other species, or members of its own species.

prediction intervals used in conservation planning to provide a confidence envelope around a species–area relationship that will sustain all species of interest (equivalent to a confidence interval, but wider in order to conserve all relevant species).

prevalence the frequency of infection of hosts by a parasite.

primary parasitoid a parasitoid that attacks a host directly and utilizes that host as its food source.

primary plant metabolism metabolic processes devoted to growth and reproduction of a plant.

primary prey defense a prey defense that functions to prevent the initiation of a capture attempt by a predator.

primary producer mostly plants that generate plant biomass through photosynthesis.

primary robber a species that cuts through the corolla base of a flower to take nectar without providing a pollination service to the plant.

proctodeal trophollaxis direct transfer of fecal material among insect family members, from the anus of one to the mouth of another.

prolonged copulation sexual contact beyond the need for sperm transfer, which results in preventing access to the female by other males.

pro-ovigenic a female that emerges with all her eggs mature and ready to lay.

proportional similarity the estimate of how similarly distributed two species are along one gradient in the multidimensional niche space, based on the proportion of one species that overlaps the other.

prospective restoration ecological restoration designed to ensure a sustainable ecosystem over the long term.

prostomata small areas in the internodes of a plant through which queen ants can easily gain entrance to a hollow stem used as a nest site.

protective mutualism a mutualism in which one partner provides protection for the other, such as ants protecting aphids.

proteinase inhibitor an enzyme that inhibits the action of digestive protease enzymes.

protogyny female flowers become receptive before male flowers produce pollen.

pseudoaggression an antagonistic act by an insect towards a flower, resulting in pollination, because the flower mimics the insect shape and coloration, causing a mistaken territorial attack by the insect (= pseudoantagonism).

pseudoantagonism an antagonistic act by an insect towards a flower, resulting in pollination, because the flower mimics the insect shape and coloration, causing a mistaken territorial attack by the insect (= pseudoaggression).

pseudocopulation the act of a male insect attempting copulation with a flower which deceives the male into the copulatory act by appearing and smelling like a female in the same species as the male.

pseudointerference indirect manipulation of individuals by means of a cue, usually chemical, which deters access to a resource, left by another individual of the same or a different species.

pseudoparasitism (1) the act of a parasitoid attempting to attack a flower which mimics the insect host of the parasitoid; (2) the case in which a host insect is attacked by a parasitoid, but no egg is laid, although the host is likely to die from the attack, or be rendered sterile.

pulsed-stress hypothesis the hypothesis that bouts of stress and recovery are beneficial to sap-feeding insects because of repeated increases in plant nitrogen availability.

qualitative defense a secondary compound in a plant with a toxic effect on some herbivores, even at low concentrations (= toxin).

quantitative defense a secondary plant compound with an increasingly deleterious effect on herbivores as concentrations increase (= digestibility reducer).

quantitative food web a food web in which the strengths of interactions are evaluated and illustrated in the food web.

quantitative trait locus (QTL) a genetic locus that is identified with statistical correlation between mapped genetic markers and complex traits, such as growth rate or tannin production in a plant.

quasisocial species members of the same generation that live together and participate in cooperative brood care.

ranging movement exploration of an area beyond the home range.

rare male advantage males with a less common attribute, such as genotype, are more attractive to females of the same species and therefore gain more mates.

realized niche the ecological niche actually occupied by a species in the presence of competitors and other species, such as natural enemies (= actual niche).

refuge–high-dose strategy a pest control plan employing a refuge of untreated crop plants together with large areas of transgenic plants with high titers of Bt toxin.

regional diversity the diversity over a large area or region – gamma diversity.

reproductive expectation the $l_x m_x$ relationship of a cohort showing the average number of female progeny produced in each age interval in a life table.

reproductive function the shape of the reproductive expectation ($l_x m_x$) through a generation, V_x, usually simulated by an inverted V-shaped relationship through time.

resource-concentration hypothesis the hypothesis that specialist herbivores increase populations within concentrated patches of resources because host plants are easier to find, they provide more resources and less associational resistance is present.

resource-heterogeneity hypothesis the argument that more heterogeneous environments provide more resources, and more ecological niches available for colonization.

resource partitioning the division of resources between two competing species, reducing the realized niches of both species and reducing interspecific competition (= niche divergence).

resource tracking the condition in which an insect lineage follows the adaptive radiation of a plant or other host lineage, without any evidence that the insects have exerted selection on host traits.

retrospective restoration ecological restoration of an area which attempts to recreate environments of a former time.

risk spreading behavior that results in spreading out progeny into a diverse array of resources, which increases the probability that some progeny survive.

root feeder an insect that feeds on roots of plants either endo- or exophytically.

royal jelly a secretion of the hypopharyngeal gland of bees that is fed to all young larvae for the first few days and to larvae that will develop into queens throughout development.

***r*-selection** selection on a population or species that maximizes reproductive rate (*r*).

sampling hypothesis the argument that larger areas receive more sampling effort, which increases the discovery of species.

sap feeder an insect that feeds on sap using sucking (haustellate) mouthparts.

scientific method the objective investigative method used to generate factual knowledge based on erecting testable hypotheses and gathering data, including experiments, that are consistent with the hypothesis, or cause its refutation.

scramble competition when individuals have about the same access to a limited resource in a free-for-all interaction (= exploitative competition).

scraper an insect that grazes on the surface of vegetation or on algae attached to submerged substrates.

secondary metabolite a plant product not thought to be used in primary metabolism of the plant, which frequently acts as an allelochemical.

secondary parasitoid a parasitoid that exploits a primary parasitoid.

secondary prey defense a prey defense that operates to deter capture following the initiation of a capture attempt by a predator.

secondary robber a species that uses the cut made by a primary robber in the corolla base of a flower to steal nectar without providing a pollination service.

seed/pod borer an endophytic insect feeding on seeds, including those within the pod of a plant.

semelparity the case in which all breeding activity is confined to once in a lifetime.

semiochemical a chemical involved in the interaction between organisms.

semisocial species cooperative brood care of females of the same generation with reproductive caste differentiation.

sequential radiation the escalation of biodiversity up the trophic system, resulting from speciation of plants, for example, which results in speciation of herbivores and their predators.

sequestration the isolation of toxic compounds within the insect body in a form, or in a place, where the toxin is more or less inactive in the insect, but the toxin may act in defense against natural enemies.

sex pheromone a pheromone that is attractive to the opposite sex of a species which aids meeting and mating.

sex ratio allocation the adaptive allotment of eggs to either male or female sexes in haplodiploid insects.

sexual selection a form of natural selection favoring the acquisition of mates for sexual reproduction, involving both the ability to compete with members of the same sex for a mate, and attraction between the sexes.

short-range dispersal the gradual diffusion-like spread of an invasive species over the landscape.

shredder an insect that feeds on live or dead plant tissue, breaking it up into smaller pieces.

sibling species species that are very similar morphologically (= cryptic species).

sib mating males mate with their sisters.

sigmoidal growth logistic growth in which intraspecific competition reduces population growth rate gradually to zero at the carrying capacity for the population.

slow-growth–high-mortality hypothesis the argument that slow growth on low nutrient resources increases exposure to natural enemies and high mortality.

social parasite a species that exploits the social structure of another species rather than an individual host, as in inquilines in the nests of social insects.

society a group of conspecific individuals organized in a cooperative manner.

speciation the process by which new species evolve.

species accumulation curve the cumulative number of species recorded as sampling effort increases.

species–area relationship the correlation between area and the number of species present, usually concerning oceanic or habitat island area.

species packing the way in which species in a community are ordered along one or more environmental gradients, often including the suggestion that species have overlapping distributions and are more or less tightly "packed" on the available resources.

species reshuffling the repositioning of species relative to others in new community relationships, under the influence of changing climatic conditions.

species richness the number of species present in a community.

spermatogeny index an estimate of the proportion of all sperm produced in a male's lifetime that is mature at the time of adult emergence, similar to the ovigeny index for females.

spermatophylax the part of the spermatophore, free of sperm, which forms a nuptial gift from a male to a female, distinct from the ampulla containing sperm.

sperm competition competition among males to inseminate a female with sperm she actually employs for fertilizing her eggs.

stable ideal-free distribution the distribution of natural enemies resulting from the aggregative response when each individual is acquiring food at the same rate.

stasis a stationary state.

station keeping an individual stays within the home range, an area providing resources for survival and reproduction.

stem borer an endophytic insect that feeds by tunneling through plant stems.

sterile male technique the method of regulating an insect population by releasing sterilized males into a population which render females infertile after mating.

stratified dispersal the compound process of short- and long-range dispersal of an invasive species.

sublethal plant defenses applied to digestibility-reducing plant compounds that delay herbivore development, but are not toxic to the insect.

subsocial a social system in which adults care for their own progeny for a period of time.

superorganism a group of individual organisms which possess features of organization analogous to physiological properties of a single organism.

superparasitoidism the condition in a host individual in which more than one parasitoid larva is present, leaving insufficient resources for all to survive.

survivorship curve a graph of the numbers in a population on a time or age axis.

symbiont an individual or species that participates in symbiosis.

symbiosis the intimate living together of two species, which includes parasitism, some mutualisms and commensalism.

symbiotic mutualism a mutually beneficial relationship between two or more species which live in intimate contact.

sympatric speciation the evolution of a new species within the same locality as the ancestral species.

synergistic interaction prey depletion by a predator assemblage is more than predicted by summing the number of prey consumed by each predator species when present alone.

synomone a substance produced or acquired by an organism which, when it contacts an individual of another species in a natural context, evokes in the receiver a behavior or physiological reaction which is adaptively favorable to both emitter and receiver (e.g., alarm pheromones of aphids which attract ant defenders).

synovigenic the case in which a female matures eggs after emergence, as her adult life progresses.

takeover avoidance any mechanism that improves the male's probability of inseminating a female, preventing access by subsequent males and ensuring that his sperm will fertilize her eggs.

tandem position a postcopulatory strategy in which a male remains attached to a mated female without genital contact, protecting against other males (= passive phase).

taxon cycle an evolutionary concept of events following colonization of a habitat, such as an island, by a generalist species with subsequent speciation and specialization as species move into habitats demanding more specific adaptations, often as species colonize higher altitudes.

territoriality guarding of an area against intruders, and aggressive behavior toward trespassers.

territory any defended area.

tertiary prey defense prey defense that interrupts predation after capture by a predator and during the handling phase.

thelytokous parthenogenesis the condition in which unfertilized eggs result in female individuals.

theory an empirically and factually based mechanistic explanation of a broad pattern in nature.

time expectation the hypothesis that an enemy will leave a patch of prey or hosts after a fixed amount of time.

time hypothesis the argument that the richness of a community correlates positively with the time available for its development, which can involve both ecological and evolutionary time.

time lag a delay in the effect of a factor from one generation to the next, as in delayed density dependence.

toxin a secondary compound in a plant with a toxic effect on some herbivores, even at low concentrations (= qualitative defense).

transgene a gene sequence inserted into a plant usually for the purpose of increased defense.

transgenic crop a crop plant genetically engineered to contain constitutive defenses.

transportation mutualism a mutualism involving the dispersal of pollen, fruits, seeds or symbionts such as beneficial mites (= dispersal/transmission mutualism).

trap-lining the repeated use of learned routes of foraging, usually involving widely dispersed resources such as orchids and other flowers (e.g., by *Heliconius* butterflies or euglossine bees).

trenching clipping veins, or other parts of plants, preventing flow of defensive compounds such as resin or latex, so the herbivore feeds on plant parts with reduced defenses and distal to the trenching.

trichilium a platform at the base of petioles on *Cecropia* plants which produce Müllerian bodies rich in glycogen, and are fed upon by insects.

trichome a hair on a plant surface derived from an epidermal cell.

tritrophic interaction interactions involving plants, herbivores and natural enemies.

triungulin an active first-instar larva of species otherwise with inactive larvae, such as in some parasitoids.

Trojan-horse method the disruption of transmission cycles in insect vectors of diseases by producing genetically altered bacteria that target pathogenic species (= paratransgenesis).

trophallaxis the exchange of regurgitated food or other fluids among colony members.

trophic cascade an indirect effect of predators on plant biomass mediated through changes in herbivore abundance or behavior.

trophobiont an animal in species 1 that provides food for an animal in species 2.

trophobiosis the provision of food by one animal to another, such as honeydew from aphids fed upon by ants.

uniparental care the situation in which only one parent cares for young.

univoltine having one generation per year.

vacant niche a resource hypervolume that could potentially support a species, although such a species is absent in the community (= empty niche).

vector a species that transmits pathogens from one host to another.

vegetation structure the way in which plants and plant parts are displayed over a landscape, which are available to herbivores, such as patch size, plant density or plant diversity.

vertical transmission the transfer of a pathogen or mutualist from parent to progeny.

volatile low-molecular-weight secondary chemicals that plants emit into the air constitutively and following herbivore damage which insects (both herbivores and their enemies) use to locate hosts (= **volatile organic compound or** VOC**).**

wood borer an endophytic insect that lives and feeds by tunneling through xylem tissue.

xylem feeder an insect that feeds on xylem tissue, often implying feeding on xylem sap.

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AUTHOR INDEX

TAXONOMIC INDEX

SUBJECT INDEX

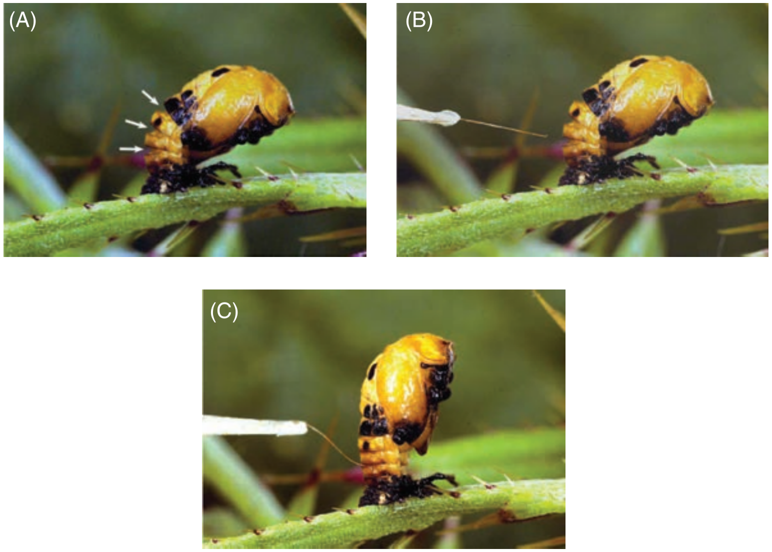

Figure 2.8 Defense of the ladybird beetle pupa, *Cycloneda sanguinea*, formed by pincer-like gaps between abdominal segments (see arrows in frame A). When disturbed from behind by a predator, or in this case a bristle, the pupa flips up, closing the gap and "biting" the aggressor. Photographs by Thomas Eisner, Cornell University. From Schroeder *et al.* 1998, and Eisner 2003. Copyright 1998 National Academy of Sciences, USA.

Figure 3.1 A *Gargaphia solani* female guards her offspring. Although small and relatively harmless, these lacebugs are very effective at repulsing predators. Photograph and copyright by Michael Loeb.

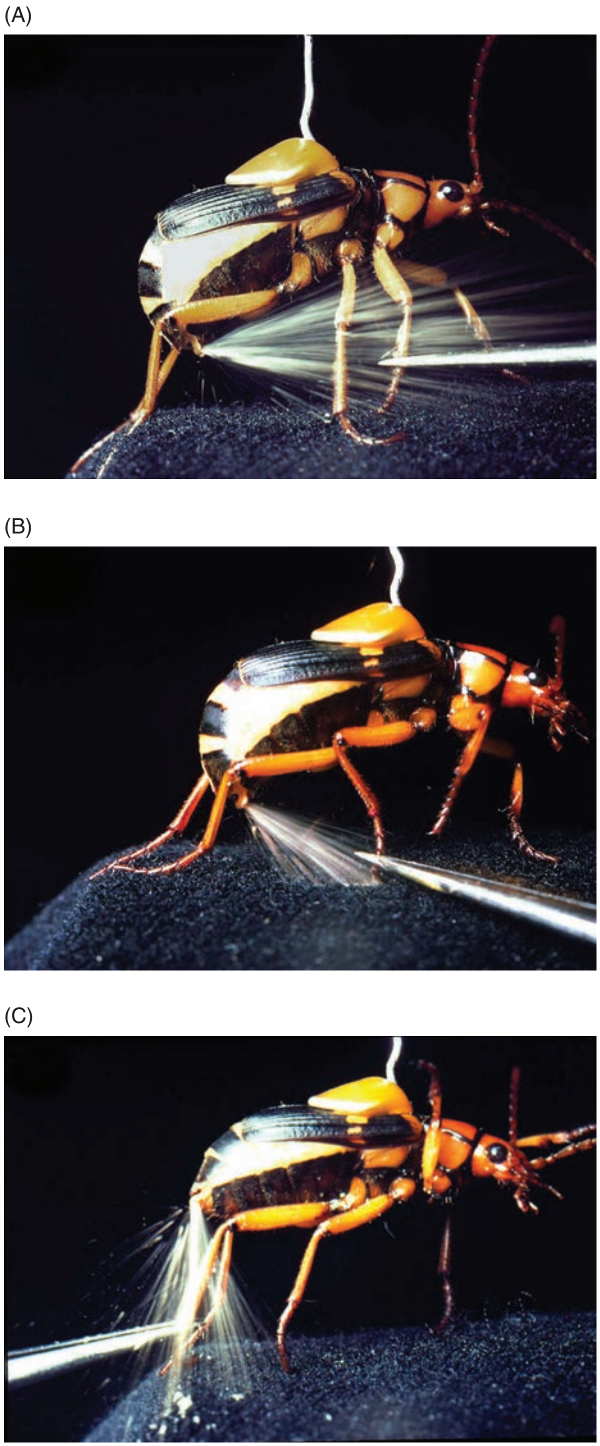

Figure 2.9 The African bombardier beetle blasts off to repel an attack by a pair of forceps which simulated the mandibular grasp of a would-be predator. The blast is directional so that it is projected forward in A, sideways in B, and downwards when the hind leg is pinched, C. Photographs by Thomas Eisner and Daniel Aneshansley, Cornell University. From Eisner and Aneshansley 1999, and Eisner 2003. A. Reprinted by permission of the publisher from *FOR LOVE OF INSECTS* by Thomas Eisner, p. 31, Cambridge, Mass.: The Belknap Press of Harvard University Press, Copyright © 2003 by the President and Fellows of Harvard College. B and C. Copyright 1999 National Academy of Sciences, USA.

Figure 2.15 A pair of hanging flies, *Hylobittacus apicalis* (Mecoptera: Bittacidae), with the male on the left and the female on the right. The male has captured a blow fly, attracted the female, and has presented her with this nuptial gift which she is consuming. The male can then copulate with the female, as shown, the female's fecundity is increased by the gift and her probability of survival is improved by the reduced need for foraging. Both male and female reproductive success is improved. From Thornhill 1980.

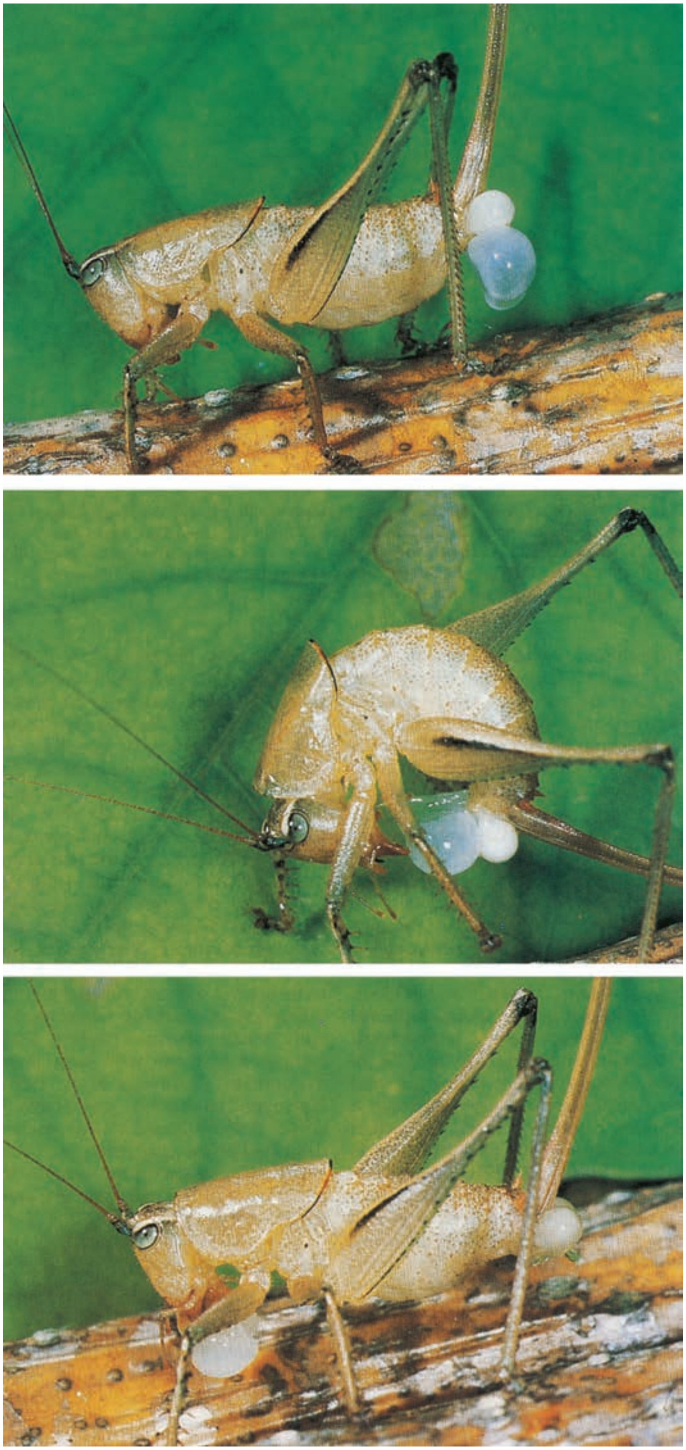

Figure 2.16 Just after mating a female katydid, *Requena verticalis*, has a large spermatophore attached to the base of her ovipositor by the male (top). The female bends down to grasp the nutritious spermatophylax (middle), and consumes it (bottom). The ampulla with the sperm remains in place, releasing sperm, and when this is complete the ampulla is also eaten. The female gains a major donation of food from the male, resulting in increased egg size and fecundity. Adapted from Thornhill and Gwynne 1986.

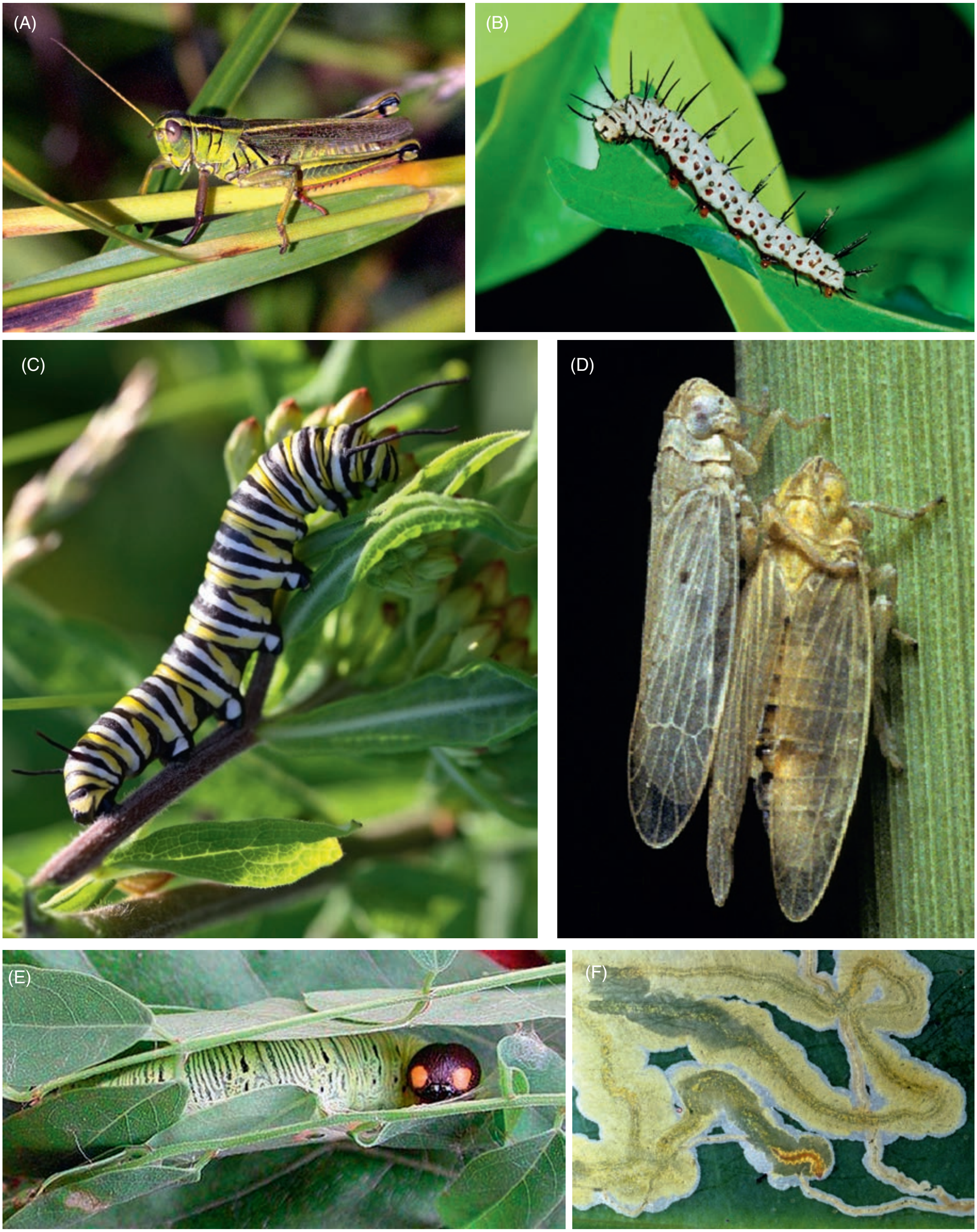

Figure 4.2 Diversity of feeding guilds represented by insect herbivores. Free living mandibulate herbivores include (A) a grasshopper, (B) lepidopteran larva, *Heliconius charitonius*, and (C) caterpillar of the monarch butterfly *Danaus plexippus*. (D) Free-living sap-feeders such as the planthopper *Prokelisia marginata* also feed in exposed positions. Concealed feeders, such as (E) the leaf-tying larva of the silver-spotted skipper *Epargyreus clarus*, (F) a leaf-mining larva feeding inside a mangrove leaf. Photo credits: (A) © Bruce MacQueen/Shutterstock.com, (B) Steve Kaufman/photolibrary, (C) © Ron Rowan Photography/Shutterstock.com, (D) © Dwight Kuhn, (E) Dale Clark, Dallas County Lepidopterists' Society, (F) Kevin Schafer/photolibrary.

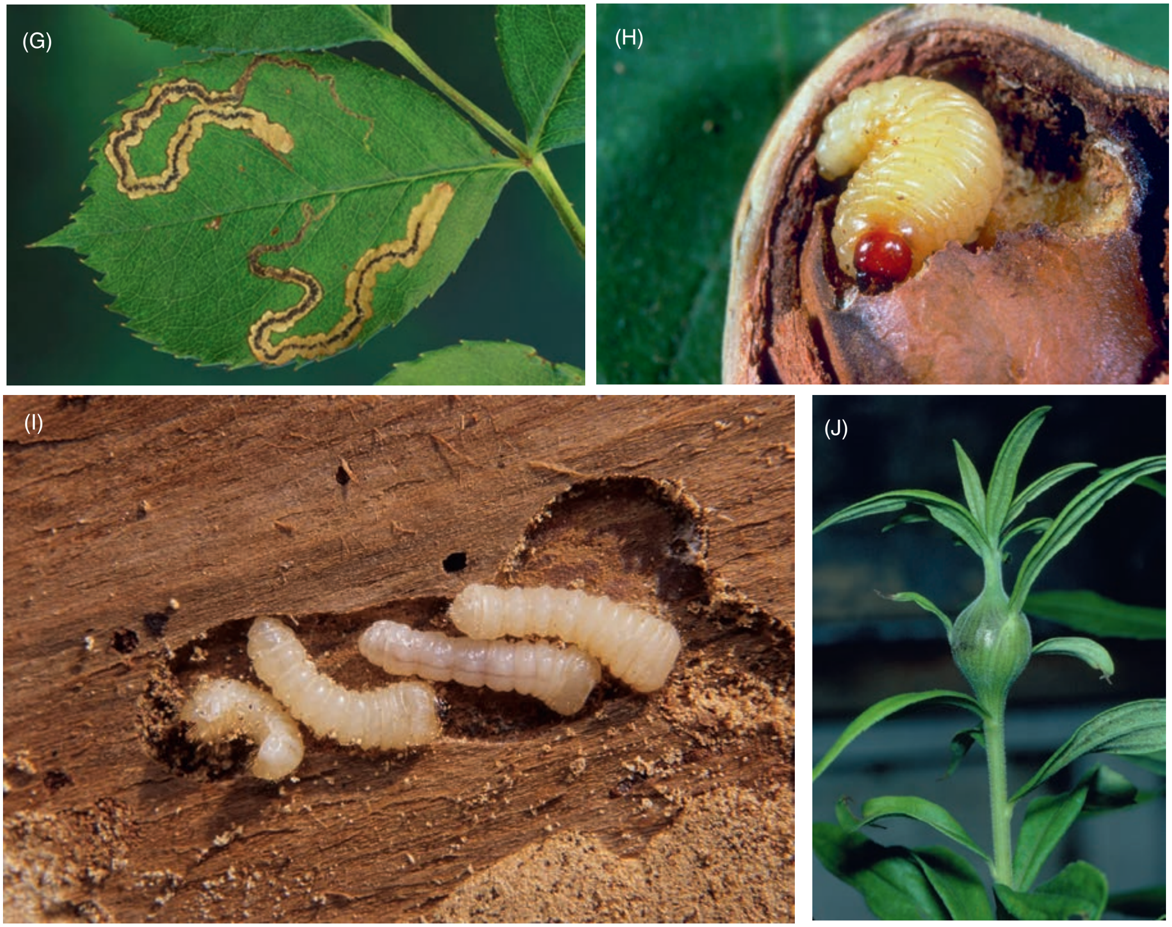

Figure 4.2 (*cont.*) (G) a serpentine leaf miner, (H) the seed-feeding weevil *Curculio nucum* in a hazel nut and (I) wood-boring cerambycid beetle larvae, all feed internally in various plant tissues. Gall inducers, such as (J) the tephritid fly *Eurosta solidaginis*. Photo credits: (G) Geoff Kidd/photolibrary, (H) Bartomeu Borrell/photolibrary, (I) Keith Douglas/photolibrary, (J) Warren Abrahamson.

Figure 4.2 (*cont.*) (K) the cynipid wasp *Biorhiza pallida* and (L) the cecidomyiid fly *Rhabdophaga strobiloides* are also concealed feeders. A great diversity of root-feeders such as (M) the white grub *Melolontha vulgaris* feed beneath the soil surface. Shredders, such as (N) a nymph of a stonefly, feed on living or decomposing plant tissues in aquatic habitats. Photo credits: (K) Brian Hainault, (L) Daniel Mosquin, (M) ©iStockphoto.com/fotosav, (N) Martin Siepmann/photolibrary.

Figure 4.7 (E) Adult of the aphid *Rhopalosiphum maidis* entrapped in the latex of its lettuce host plant, *Lactuca sativa*. From Dussourd (1995) © Dr. David Dussourd.

Figure 4.10 Deactivating the defenses of latex-bearing plants. Insect herbivores nip the main midrib of their host plant with their mandibles, cut off flow of latex beyond the cut and subsequently feed distally where they avoid the latex. (A) Caterpillars of *Danaus gilippus* on *Asclepias curassavica* (Dussourd and Eisner 1987), (B) the milkweed beetle, *Tetraopes tetrophthalmus*, on *Asclepias syriaca* (Dussourd 1999), (C) the katydid, *Scudderia furcata*, on *Apocynum cannabinum* (Dussourd 2009).

Figure 4.10 (*cont.*) (D) the leaf beetle, *Labidomera clivicollis*, on *Asclepias syriaca* leaf (Dussourd 1999). (E) By trenching leaves of *Lobelia cardinalis*, the lepidopteran *Enigmogramma basigera*, cuts the flow of latex to leaf tissue within the circumscribed trench where it then feeds (Dussourd 2005).

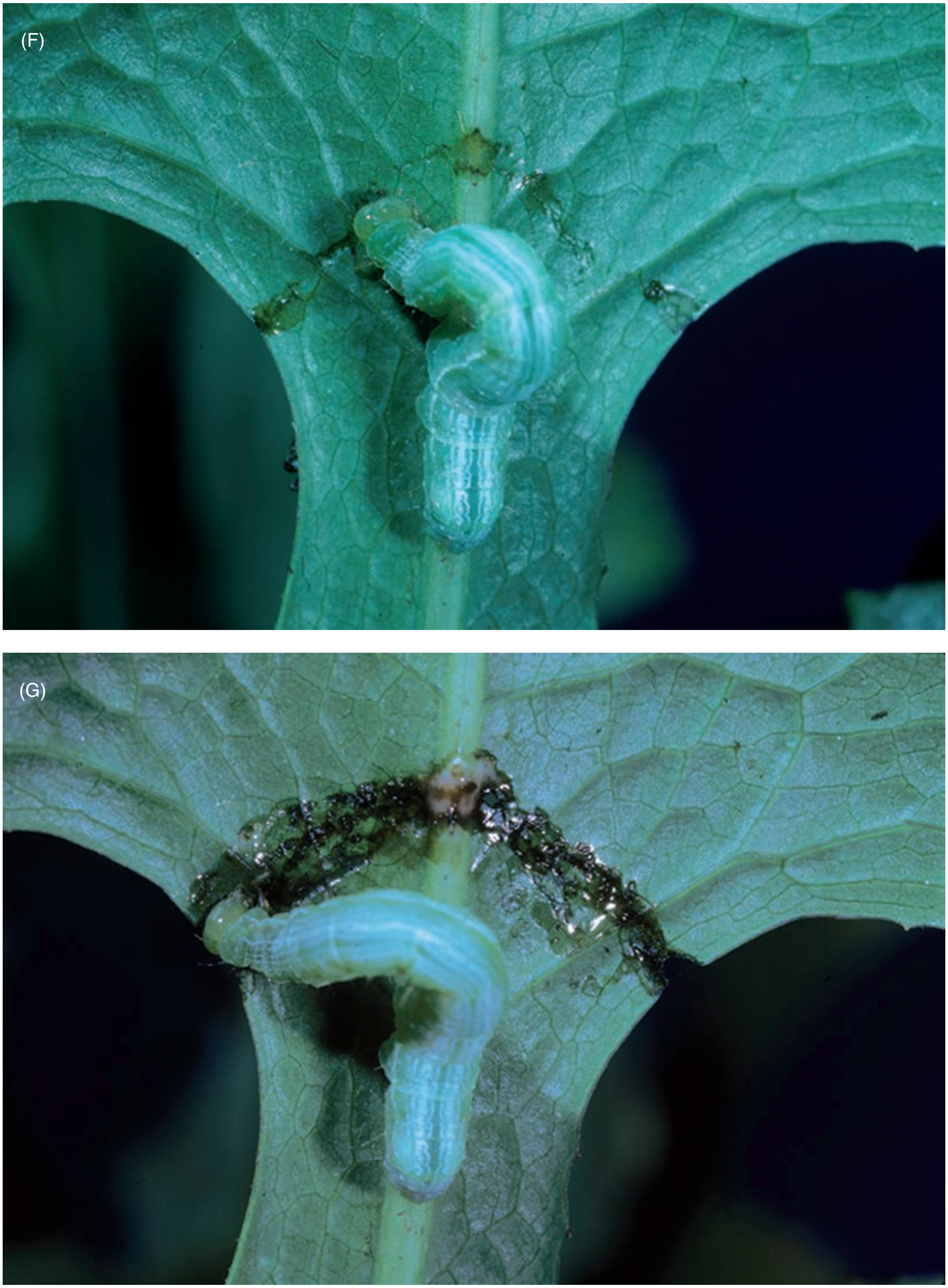

Figure 4.10 (*cont.*) Larvae of *Trichoplusia ni* expend an extensive time and energy trenching leaves of prickly lettuce (*Lactuca serriola*) before feeding distal to the trench; shown are larval trenching efforts after three passes (F) and 15 passes (G) (Dussourd and Denno 1994). (A) From Dussourd, D. E. and T. Eisner. 1987.
Vein-cutting behavior: insect counterploy to the latex defense of plants. *Science* **237**:898–901. Reprinted with permission from AAAS. (C) Reprinted with permission from Blackwell Publishing. All photographs are © Dr. David Dussourd.

Figure 13.12 A massive swarm of adult midges emerging from Lake Myvatn in Northern Iceland and moving to lakeside vegetation. Photograph by Jamin Dreyer. From Gratton and Vander Zanden (2009).