Chapter 1

AN OVERVIEW OF INSECT ECOLOGY

1.1 INTRODUCTION

In this first chapter we provide a brief overview of the major concepts in insect ecology, and attempt to present a taste of what is to come in the 11 detailed chapters that follow. Unavoidably, a little repetition may therefore occur, in that topics briefly discussed in this chapter will appear again in more detail elsewhere in the book. This overlap is entirely intentional on our part, and we would encourage the random reader to explore this introductory chapter first, and then turn to the details in whichever subject and later chapter takes his or her fancy. Readers who know what they are looking for can, of course, proceed directly to the relevant chapter(s).

We have assumed that most readers will have some knowledge of insect taxonomy, and we have not attempted to provide an in-depth coverage of this topic. Some information is, however, provided to set the scene. Readers who wish to know more are recommended to obtain one of various excellent entomology textbooks such as that by Gullan and Cranston (2005).

1.2 HISTORY OF ECOLOGY AND ENTOMOLOGY

The science of ecology is broad ranging and difficult to define. Most of us think we know what it means, and indeed it can imply different things to different people. It is best considered as a description of interactions between organisms and their environment, and its basic philosophy is to account for the abundance and distribution of these organisms. In fact, ecology encompasses a whole variety of disciplines, both qualitative and quantitative, whole organism, cellular and molecular, from behavior and physiology, to evolution and interactions within and between populations. In 1933, Elton suggested that ecology represented, partly at least, the application of scientific method to natural history. As a science, Elton felt that ecology depended on three methods of approach: field observations, systematic techniques, and experimental work both in the laboratory and in the field. These three basic systems still form the framework of ecology today, and it is the appropriate integration of these systems, which provides our best estimates of the associations of living organisms with themselves and their environment, which we call ecology.

Insects have dominated the interests of zoologists for centuries. Those who could drag themselves away from the charismatic but species-poor vertebrates soon found the ecology of insects to be a complex and rich discipline, which has fascinated researchers for at least 200 years. At first, the early texts were mainly descriptive of the wonders of the insect world. Starting in 1822, Kirby and Spence published their four volumes of *An Introduction to Entomology*. This was a copious account of the lives of insects, written over three decades before Darwin first produced *On the Origin of Species* in 1859. The fact that Kirby and Spence did not have the benefit of explaining their observations on the myriad interactions of insects and their environment as results of evolution did not detract from the clear fascination that the world of insects provided. This fascination has withstood the test of time. Half a century or more after Kirby and Spence, Fabre published insightful and exciting accounts of the lives of insects, starting before the

Table 1.1 Summary of associations in ecology.

Type	Interaction level	Insect example
Competition		
Intraspecific	Individuals within a population of one species	Lepidoptera larvae on trees
Interspecific	Individuals within populations of two different species	Bark beetles in tree bark
Herbivory, or phytophagy	Between autotroph and primary consumer	Aphids on roses
Symbiosis		
Mutualism	Between individuals of two species	Ants and fungi
Sociality	Between individuals of one species	Termites
Predation	Between primary and secondary consumer trophic levels	Mantids and flies
Parasitism	Between primary and secondary consumer trophic levels	Ichneumonid wasps and sawflies

turn of the 20th century (Fabre 1882), wherein he presented in great detail observations made over many years of the ecologies of dung beetles, spider-hunting wasps, cicadas, and praying mantids. These books epitomized the first of Elton's three approaches to ecology, that of field observations. Later work began to enhance the third approach, that of experimental insect ecology, summarized in *Insect Population Ecology* by Varley et al. (1973). This later book was probably the first and certainly most influential, concise account of insect ecology derived from quantitative, scientific research.

1.3 ECOLOGICAL ASSOCIATIONS

The term ''association'' used by Elton covers a great many types of interaction, including those between individuals of the same species, between species in the same trophic level (a trophic level is a position in a food web occupied by organisms having the same functional way of gaining energy), and between different trophic levels. These associations may be mutually beneficial, or, alternatively, involve the advancement or enhancement of fitness of certain individuals at the expense of others. Of course, insects can live in association with other organisms without having any influence on them, or being influenced by them; such associations are ''neutral''.

Ecological associations among insects operate at one of three levels: at the level of individual organisms, at a population level, or over an entire community. Table 1.1 summarizes some of these basic associations. With the exception of primary production, it should be possible to discover insect examples for all other kinds of ecological interactions. The fact that insects are so widespread and diverse in their ecological associations is not surprising when it is considered just how many of them there are, at least on land and in fresh water, how adaptable they are to changing and novel environmental conditions, and how long they have existed in geological time.

1.4 THE INSECTA

1.4.1 Structure

This is not a book about insect morphology or physiology in the main, but both are certainly worthy of some consideration, as the ability of an organism to succeed in its environment is dictated by form and function. Here, we merely provide a few basic details.

The basic structure of a typical adult insect is shown in Figure 1.1 (CSIRO 1979). Comparing the figure with a photograph of a grasshopper (Figure 1.2) will enable any new student of entomology to quickly realize how insects evolved a highly technologically efficient set of specialized body parts and appendages. The three basic sections (called tagmata) of an insect's body are admirably adapted for different purposes. The head specializes in sensory reception and food
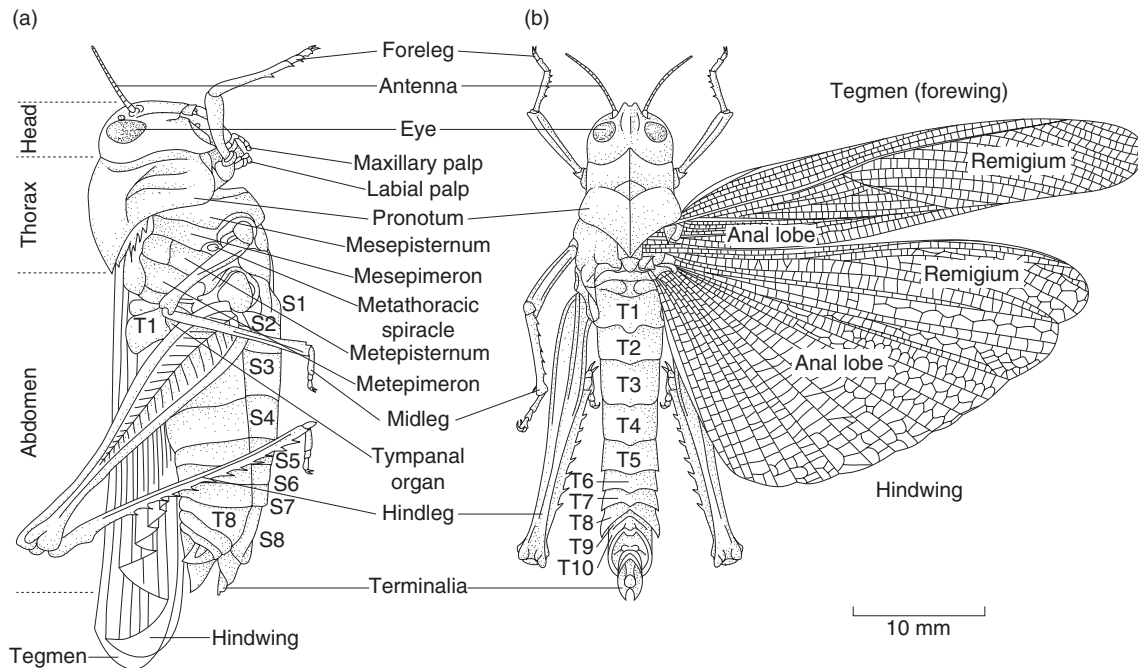
Figure 1.1 The external structure of an adult insect, illustrating general features of a non-specialized species. (From CSIRO 1979.)

gathering, the thorax in locomotion, and the abdomen in digestion and reproduction. All but a minimum number of appendages have been lost when compared with ancestors, leaving a set of highly adapted mouth-parts and a pair of immensely stable tripods, the legs. Throughout the book, we shall refer to these and

Figure 1.2 Side view of grasshopper showing general structure.

other body structures in terms of their evolution and ecology. This basic plan is of course highly variable, and the most specialized insects, for example, blowfly larvae (the fisherman's maggot), bear little or no superficial similarity to this plan.

1.4.2 Taxonomy

We hope that the reader does not get too bogged down with taxonomic nomenclature or classification. We are concerned with what insects do rather than what their names are, and although it is essential that detailed taxonomy is eventually carried out as part of an ecological investigation, in this book we have pro-vided scientific names more as a reference system for comparison with other published work than as some-thing people should automatically learn. However, some introduction to the taxonomic relationships of the insects will help to set the scene.

The class Insecta belongs within the superclass Hexapoda, within the phylum Arthropoda. These in

turn belong to a huge group or clade of invertebrates known as the Ecdysozoa – animals that grow by shedding their cuticles (molting) (Mallatt & Giribet 2006). The Ecdysozoa bring together perhaps unlikely relatives, the nematodes and the arthropods for instance. The arthropod phylum itself is now satisfactorily monophyletic, having survived various attempts over the last few decades to invoke multiple origins for the admittedly hugely diverse group. The place within the arthropods for the insects, and their relationships to other major groups, has also had a rocky ride. For many years, the first edition of this book included, the hexapods containing the insects were placed with the Myriapoda in the Uniramia (otherwise known as the Atelocerata; Mallatt et al. 2004) (Figure 1.3a, b). Now, however, this convenient arrangement has been superseded by techniques involving nuclear and mitochondrial ribosomal RNAs and protein coding genes, with the most likely position for the Insecta shown in Figure 1.3c, d. The crucial point of the new phylogeny is that the Hexapods (most of which are insects) are relatively closely related to the Crustacea (in other words, Hexapods are terrestrial Crustacea), forming an all-encompassing group, the Pancrustacea (or Tetraconata; Richter 2002), whilst

the Myriapods are separate, probably much more closely allied to the Chelicerates (Schultz & Regier 2000). The Pancrustacea makes a lot of sense ecologically, since insects and crustaceans have many similar lifestyles, niches, and so on; one just happens to be in the sea and the other on land (but see Chapter 6). However, controversy still exists; Bitsch and Bitsch (2004) for example found no support for the Pancrustacea concept using comparative morphological characters rather than molecular techniques.

Less controversial is the organization and relatedness of groups within the hexapods. Though the Insecta are by far the most numerous, they share the superclass with three other classes, each of which comprises just one order each, the Diplura, Protura, and Collembola (springtails) (Gullan & Cranston 2005). These latter three were until fairly recently included amongst the apterygote (wingless) insects, but their morphological and physiological features are more likely to mimic those of insects by virtue of convergent evolution than by true relatedness.

The taxonomic classification of the Insecta used in this book follows that described by Gullan and Cranston (2005). There are two orders within the Apterygota (wingless insects): the Zygentoma (silverfish;
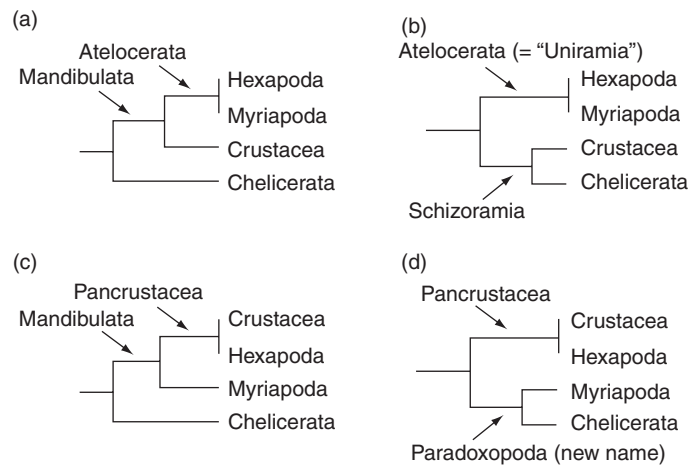
Figure 1.3 Major hypotheses of the relationships of arthropod groups: (a) classic Mandibulata (= Mandibulata + Chelicerata), in which the three groups possessing mandibles formed by the second post-oral appendage (hexapods, myriapods, crustaceans) are distinguished from chelicerates; (b) Atelocerata versus Schizoramia: clades with unbranched versus two-branched appendages; (c) Pancrustacea + Myriapoda within Mandibulata: that is, in the Mandibulata, hexapods group with crustaceans instead of with myriapods; (d) 'Chelicerata + Myriapoda' versus 'Crustacea + Hexapoda.' (From Mallatt et al. 2004.)

Figure 1.4 Silverfish (Thysanura).

Figure 1.4) and the Archaeognatha (bristletails). All other insects belong to the pterygote group (winged insects) and this is in turn divided into the Exopterygota (also known as the Hemimetabola), where wings develop gradually through several nymphal instars, and the Endopterygota (also known as the Holometabola), where there is usually a distinct larval stage separated from the adult by a pupa. Figure 1.5 summarizes the classification of insects, and indicates roughly the number of species so far described from each order. This great species richness within the Insecta is thought to have resulted from low extinction rates throughout their history (see below) (Labandeira & Sepkoski 1993), and it is important to realize that nearly 90% of insect species belong to the endopterygotes, indicating the overwhelming advantages for speciation provided by the specialized larval and pupal stages. As will be seen throughout the book, lay-people and entomologists alike tend to concentrate on adult insects, but the ecology of larval or nymphal stages may well have much more relevance to the success or otherwise of the species or order, as well as having much more direct impact on human life. After all, it is the larvae of peacock butterflies that devour their host plant, nettle, not the adults.

The success of a group of organisms is not just measured in terms of the number of species accrued in the group, but can also be discussed as the range of habitats or food types dealt with, the extremes of environments in which they are able to live, how long the group has been extant, and the relative abundance of individuals. Ecologically, it may be more useful to break down the insect orders into functional groups according to lifestyle or feeding strategies, rather than to merely count the number of species.

1.5 FOSSIL HISTORY AND INSECT EVOLUTION

The nature of insect bodies, at least the adults of both Exopterygota and Endopterygota and to some extent the nymphs of the Exopterygota, makes them very suitable for fossilization in a variety of preserving media from sediments to amber. The tough insect cuticle is composed of flexible chitin, and/or more rigid sclerotin. Chitin is certainly an ancient, widespread compound, known in animals from at least the Cambrian period, more than 550 million years ago (Ma) (Miller 1991), but estimating the origins of insects that use it to perfection is difficult and fraught with argument. These days, biologists employ molecular clocks to date events for which there is no physical evidence. With such rather imprecise tools, some remarkable claims of over 1 billion years ago have been made, for example, for when the groups of bilateral animals diversified (Graur & Martin 2004). Using more conservative and exacting molecular clocks, Peterson et al. (2004) have come up with a reasonable origin of the earliest arthropods, somewhere in the early to mid Cambrian, perhaps 540 Ma. Actual fossil hexapods, however, have not been found until more recently. *Rhyniella praecursor* is a fossil springtail (Collembola) found in Scottish sandstones of about 400 million years old (Fayers & Trewin 2005), and for many years this species has held the record for the oldest hexapod. Fragments of another fossil from the same rocks have now been identified as a "proper" insect (Engel & Grimaldi 2004). *Rhyniognatha hirsti* is not only the earliest true insect, but it may well also have had wings. This then places the origin of the Insecta somewhere in the Silurian period (417–443 Ma), arising from a common fairy shrimp-like ancestor (Gaunt & Miles 2002).

The fossil record of insects is therefore relatively complete when compared with that of most other animal groups, and fossil insects turn up extremely frequently in many types of material, from sandstones and shales to coal and amber. Amber is a particularly wonderful substance, a fossil tree resin that traps, entombs, and precisely preserves small particles such as seeds, spiders, and insects. Most amber is Cretaceous or Tertiary in origin, perhaps 30–90 million years old, and is particularly common in the Baltic and Siberia (see, for example, Arillo & Engel 2006), but parts of the Caribbean (Dominica) and Central and South America (Mexico to Peru) also have large
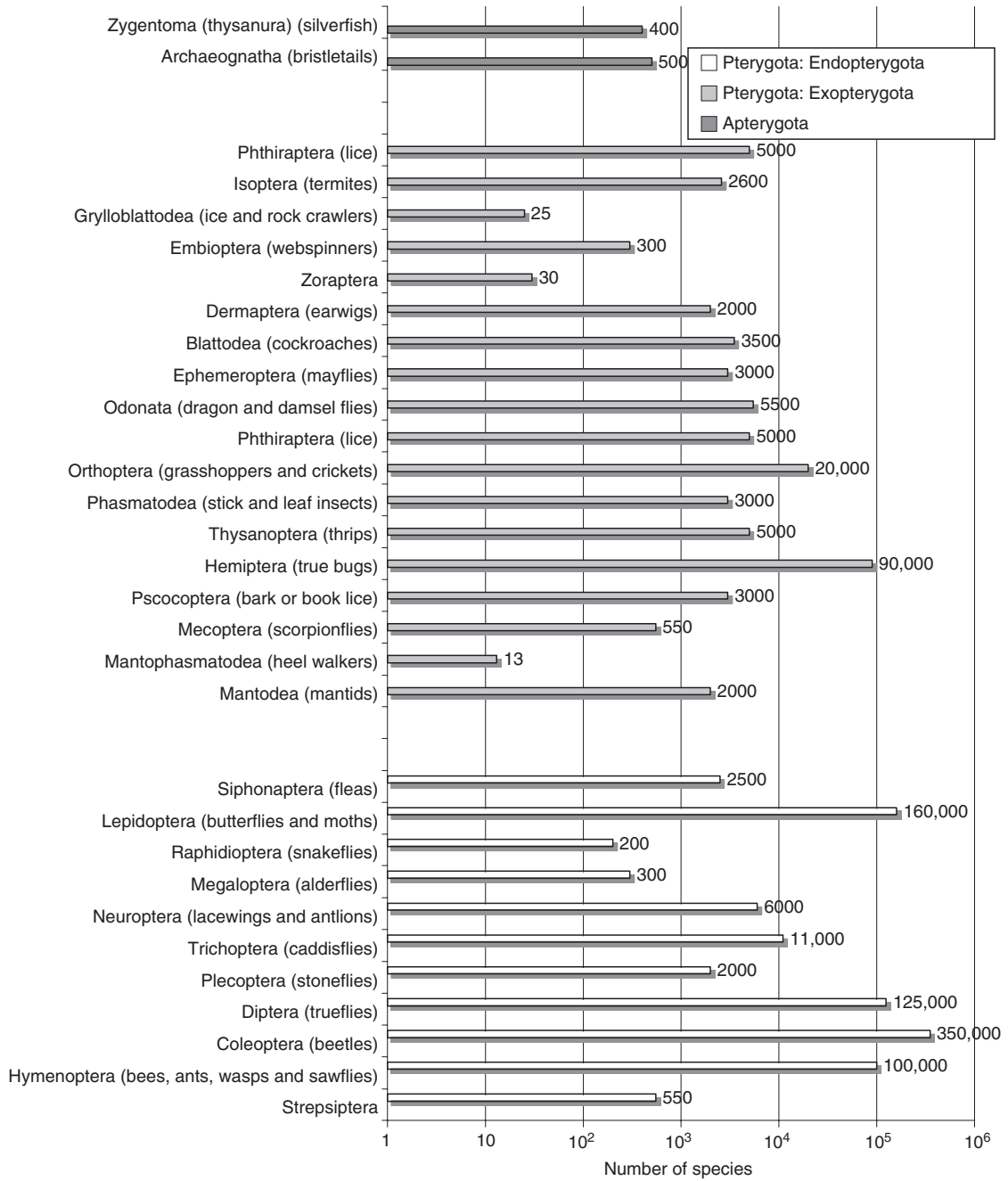
Figure 1.5 Numbers of described species within the orders of insect. (From Gullan & Cranston 2005.)

deposits (see, for example, Wichard et al. 2006). Amber preserves living things so well, in fact, that inferences can be made about whole fossil ecosystems. Antoine et al. (2006) examined amber from the Peruvian Amazon, and discovered diverse collections of fossil arthropods (13 insect families and three arachnid species), as well as large numbers of spores, pollen, and algae. These Middle Miocene deposits are indicative of lush, moist rainforests already in existence in the Amazonian region perhaps 10–18 Mya.

Table 1.2 shows the earliest known fossils from the major insect orders that are still extant today. Though wisdom might suggest that insects such as Odonata (dragonflies and damselflies) are primitive or early when compared with, for example, Hymenoptera (bees, ants, and wasps), there is little evidence from the fossil record of a clear progression or development from one group to the next. Even with modern molecular techniques such as nucleotide sequencing to investigate the relatedness of organisms, it is

Table 1.2 Fossil history of major insect orders alive today. (Data from Boudreaux 1987; Gullan & Cranston 1996.)

Order	Earliest fossils	Million years ago
Archaeognatha	Devonian	390
Thysanura	Carboniferous	300
Odonata	Permian	260
Ephemeroptera	Carboniferous	300
Plecoptera	Permian	280
Phasmatodea	Triassic	240
Dermaptera	Jurassic	160
Isoptera	Cretaceous	140
Mantodea	Eocene	50
Blattodea	Carboniferous	295
Thysanoptera	Permian	260
Hemiptera	Permian	275
Orthoptera	Carboniferous	300
Coleoptera	Permian	275
Strepsiptera	Cretaceous	125
Hymenoptera	Triassic	240
Neuroptera	Permian	270
Siphonaptera	Cretaceous	130
Diptera	Permian	260
Trichoptera	Triassic	240
Lepidoptera	Jurassic	200

difficult to explain the lineages of most modern insect orders. It is not even clear if the largest order, the Coleoptera, for example, is itself a single monophyletic entity (Caterino et al. 2002). In general, it is likely that the divergence of almost all of the orders is very ancient, and may have occurred too rapidly for easy resolution (Liu & Beckenbach 1992).

Most major orders were already distinguishable by 250 Ma, and only a few are known to be much more ancient. The most ancient winged insects probably included primitive cockroaches, the Palaeodictyoptera, whose fossils date back about 370 Ma to late Devonian time (Kambhampati 1995; Martinez-Delclos 1996, Prokop et al. 2006), illustrating the significance of a scavenging lifestyle in terms of early adaptability. Certain ways of life, however, do appear to be more recent than others. Specialist predators such as the praying mantids (Mantodea) are not found as fossils until the Eocene period, around 50 Ma, and sociality might be expected to be an advanced feature of insect ecologies; termites, for example, do not appear in the fossil record until the Cretaceous period, around 130 Ma. In fact, one of the earliest records of termite activity comes from fossil wood found in the Isle of Wight, England, from where Francis and Harland (2006) describe pellet-filled, cylindrical borings in Early Cretaceous deposits (Table 1.3).

Various major orders or "cohorts" have become extinct in the last 250 million years, but relatively few when compared with many other major animal phyla, such as the molluscs and the tetrapods (Figure 1.6). The average time in which an insect species is in existence is conjectured to be an order of magnitude greater than that for, say, a bivalve or tetrapod (May et al. 1995), possibly well in excess of 10 million years. This is not to say that no insect orders have ever gone extinct – indeed they have. The first evidence of the extinction of an insect order comes from the Late Carboniferous (350 Ma), where the Cnemidolestodea vanished (Béthoux 2005). The Permian–Triassic border (around 250 Ma) saw the concurrent extinction of several insect orders (Béthoux et al. 2005), such as the Caloneurodea, an extinct order thought to be related to modern Orthoptera.

At the family level, it would appear that no insect families have become extinct over the past 100 million years or so. In some cases, it is thought that species we find alive today may extend much further back in time even than that. Dietrich and Vega (1995), by examining fossil leaf-hoppers (Hemiptera: Cicadellidae)

Table 1.3 A summary of evolutionary events in the ecology of insects, derived from fossil evidencew (timescales very approximate).

| Event	Period	Approx. time (Ma.)	Reference
Fossil weevils from rocks on the Beardmore Glacier, Antarctica	Pliocene to mid Miocene	15–60	Ashworth & Kuschel (2003)
Trace fossils of insect larvae from dessicating freshwater pools	Upper Oligocene	30	Uchman et al. (2004)
Oldest fossil of Strepsipteran larva	Eocene	45	Ge et al. (2003)
First fossil record of angiosperm leaf mimicry in phasmids	Middle Eocene	47	Wedmann et al. (2007)
Most recent aphid families present	Early Tertiary	50	Helie et al. (1996)
Radiation of higher (Cyclorrhaphan) flies (Dipera)	Tertiary (Paleocene)	55–65	Grimaldi (1997)
Radiation of sweat bees (Halictidae)	Late Cretaceous	80	Danforth et al. (2004)
Fossil bee nests forming oldest evidence of bees	Late Cretaceous	85	Genise et al. (2002)
Midges feeding on the blood of dinosaurs	Cretaceous	88–95	Borkent (1996)
Differentiation of various weevil families	Middle Cretaceous	100	Labandeira & Sepkoski (1993)
Fossils of aquatic hemiptera (Hydrometridae) in amber	Middle Cretaceous	100	Andersen & Grimaldi (2001)
Most recent common ancestor of modern ants groups	Early Cretaceous	115–135	Brady et al. (2006)
Earliest evidence of termite damage to wood	Early Cretaceous	130	Francis & Harland (2006)
Earliest fossil ant	Early Cretaceous	130	Brandao et al. (1989)
Trace fossil of basal Chalcidoidea (Hymenoptera: Parasitica)	Cretaceous/ Jurassic	140	Rasnitsyn et al. (2004)
Bark beetles (Scolytidae) associated with gymnosperms	Late Jurassic	145	Sequeira & Farrell (2001)
Radiation of major lepidopteran lineages on gymnosperms	Late Jurassic	150	Labandeira et al. (1994)
Origin of praying mantids	Late Jurassic	150	Grimaldi (2003)
Establishment of intracellular symbionts in aphids	Jurassic/Permian	160–280	Fukatsu (1994)
Insect grazing damage on fern pinnules and gymnosperm leaves	Late Triassic	240	Ash (1996)
Assymetric wings (e.g. flies and beetles) in fossil record	Permian	250	Wootton (2002)
Evidence of first pollenivory	Early Permian	275	Krassilov & Rasnitsyn (1996)
Resting traces of primitive mayflies or stoneflies from aquatic muds	Early Permian	280	Braddy & Briggs (2002)
Evidence of leaf-mines and galls	Late Carboniferous	300	Scott et al. (1992)
Coprolites (fossil feces) and herbivore-induced plant galls from Holometabola	Late Carboniferous	300	Labandeira & Philips (2002)
Evidence from tree-ferns of insect feeding by piercing and sucking	Carboniferous	302	Labandeira & Phillips (1996)
Evidence of wood boring by insects	Early Carboniferous	330	Scott et al. (1992)

(*Continued*)

Table 1.3 (*Continued*)

Event	Period	Approx. time (Ma.)	Reference
Earliest fossil insect (bristletail) with significant structural detail	Early Devonian	400	Labandeira et al. (1988)
Earliest fossil insect fragment	Early Devonian	396–407	Engel & Grimaldi (2004)
Origin of insects	Silurian	417–440	Engel & Grimaldi (2004)
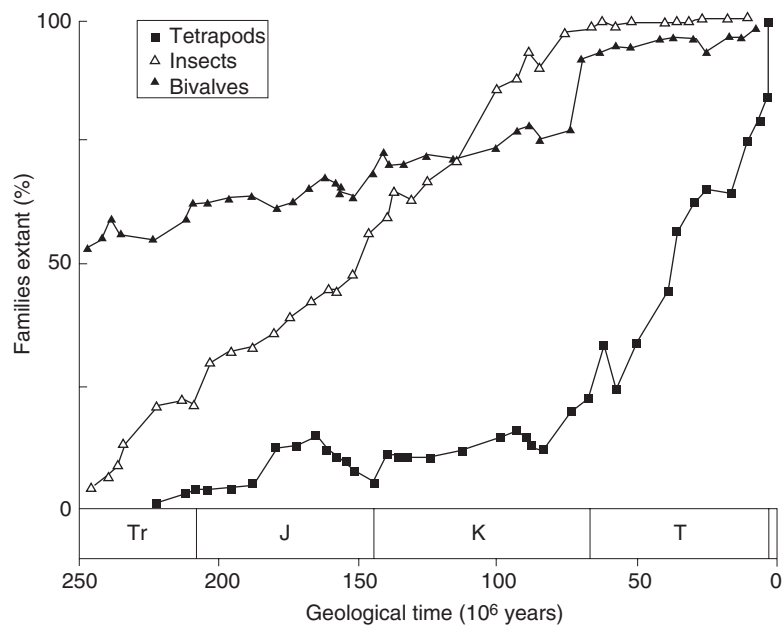
Figure 1.6 The number of families extant at various time periods as a percentage of those alive today. (From May et al. 1995.)

from the Tertiary period, suggested that modern genera of these sap-feeders existed as early as 55 Ma.

It would seem therefore that evolutionary pressures have not dramatically altered the fundamental interactions between insects and their environments for a very long time indeed, despite some major changes to terrestrial ecosystems. How the insects have managed to sustain such taxonomic constancy through large-scale climatic fluctuations is puzzling (Coope 1994), but this puzzle forms the very basis for investigations of insect ecology. Insects do show variations in the patterns of dominance of different species

and families as climates have changed. In Chile, for example, as the ice retreated from the south central lowlands about 18,000 years ago, the beetle fauna was characterized by species of moorland habitat. However, by 12,500 years ago, fossil beetle assemblages from the same region consisted entirely of rainforest species (Hoganson & Ashworth 1992). Thus, insects may not be prone to global extinctions, but are able to move from one region or another as conditions become more or less favorable for their ecologies. They can be thought of as ecologically "malleable" rather than "brittle".

Undoubtedly, the single most important development in the evolution of insects has been the development of wings, and indeed wings are usually the best-preserved structures in fossil insects (Béthoux et al. 2004). From fossil evidence, it is clear that the appearance of the Pterygota (winged insects) coincided with the tremendous diversification of insects that began in the Palaeozoic era (Kingsolver & Koehl 1994). Equally clear are the obvious advantages of flight to an animal, including avoiding predators, finding mates, and locating food, breeding sites, and new habitats. Any organism that has to walk or hop everywhere is bound to be at a disadvantage when compared with one that can fly. Maintaining steady flight in still air is a highly sophisticated process, which in a modern insect is achieved by flapping, twisting, and deforming the wings through a stroke cycle (Wootton 2002). It seems to be the case that insects only ever possessed wings that operated as flight organs on the second and third thoracic segments (the meso- and metathorax; see Figure 1.1) (Wootton 1992), and the fundamental problem concerns the evolutionary steps that led to this final, fully bi-winged state. Various theories exist to explain the origin of wings in insects, and their intermediate functions. One of the most popular suggests that so-called proto-winglets originated from unspecialized appendages on the basal segment of the legs (the pleural hypothesis, according to Kingsolver & Koehl 1994). These winglets were primitively articulated and hence movable, right from the start. Fossil mayfly nymphs (Ephemeroptera) from Lower Permian strata (of around 280 Ma) show both thoracic and even abdominal proto-wings, though this does not imply that that such appendages evolved initially in fresh water. However, other theories that utilize genetic examination of both crustacean and insect species have suggested that wings arose from gill-like appendages called epipodites, which were present on aquatic ancestors of the pterygote insects (Averof & Cohen 1997). Molecular phylogenetic studies have still to confirm this gill-to-wing hypothesis (Ogden & Whiting 2005).

Whatever the origin of proto-wings, there is still confusion as to what purpose or purposes they might have served before they became large enough to assist with aerodynamics. Sexual display and courtship, thermoregulation, camouflage, and aquatic respiration have all been suggested, but perhaps the most traditional idea involves some assistance in gliding after jumping. Whichever early route, once the winglets had increased in size sufficiently to be aerodynamically active, they would have been able to prolong airborne periods, as do for example various modern species of arboreal ant (Yanoviak et al. 2005). Stable gliding would then have become possible, especially with the assistance of long tails (cerci). If we assume that the proto-winglets were articulated from their earliest forms, then fairly easy evolutionary steps to fully powered and controlled flight can be imagined after the gliding habit was perfected. This ability to fly is likely to have been a great advantage in the colonization of new ecospace provided by early tree-like plants such as pteridophytes.

1.6 HABITS OF INSECTS

Not only have many species of insects been on Earth for many millions of years, but their various modern ecological habits also appeared at an early stage. Table 1.3 shows some major events in the development of insect ecology over the last 400 million years. The great radiation of insect species is thought to have begun about 245 Ma, in early Triassic times (Labandeira & Sepkoski 1993), and judging by various insect fossils, it is clear that insects were exploiting terrestrial habitats maybe 100 million years earlier. Note however that aquatic habitats, especially the sea (but see Chapter 6), have not been exploited – a ''mere'' 50,000 or so insect species are known to live in fresh water for at least part of their life cycles (Leveque et al. 2005). On land, conventional wisdom suggests that insect species richness has increased predominantly because of the appearance and subsequent radiation of plants, but examination of the numbers of new species in the fossil record suggests that the radiation of modern insects was not particularly accelerated by the expansion of the angiosperms in Cretaceous times. Instead, the basic ''machinery'' of insect trophic interactions was in place very much earlier. One example from Nishida and Hayashi (1996) describes how fossil beetle larvae have been found in the fruiting bodies of a now-extinct gymnosperm from the Late Cretaceous period in Japan.

In 1973, Southwood described the habits of the major insect orders in terms of their main food supplies, thus defining their general trophic roles (Figure 1.7). If it is assumed that each order has evolved but once, and that all species within the order are to some extent related so that they represent
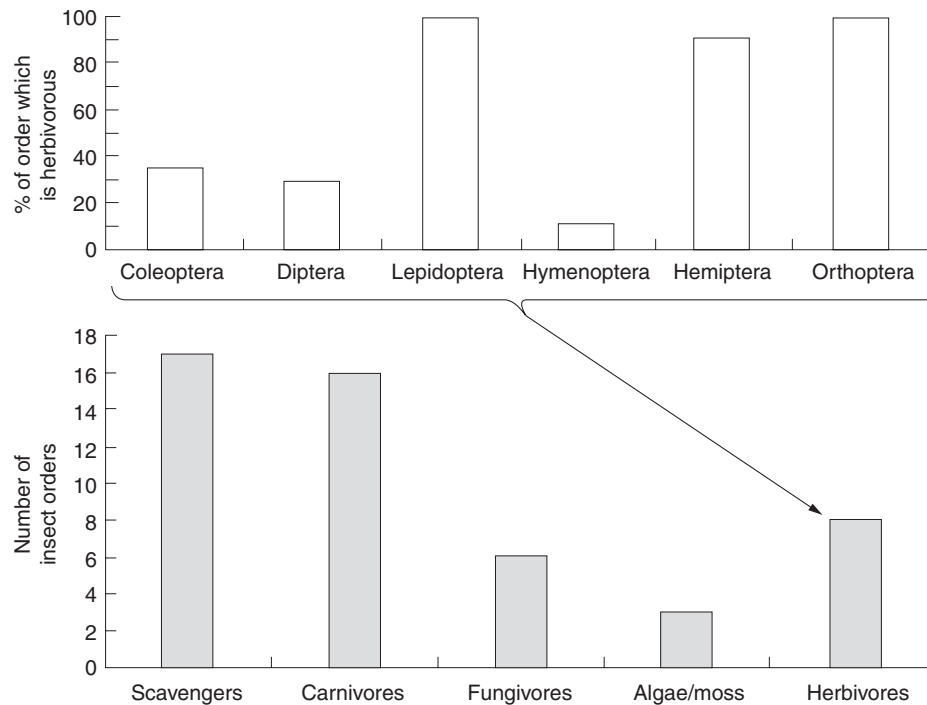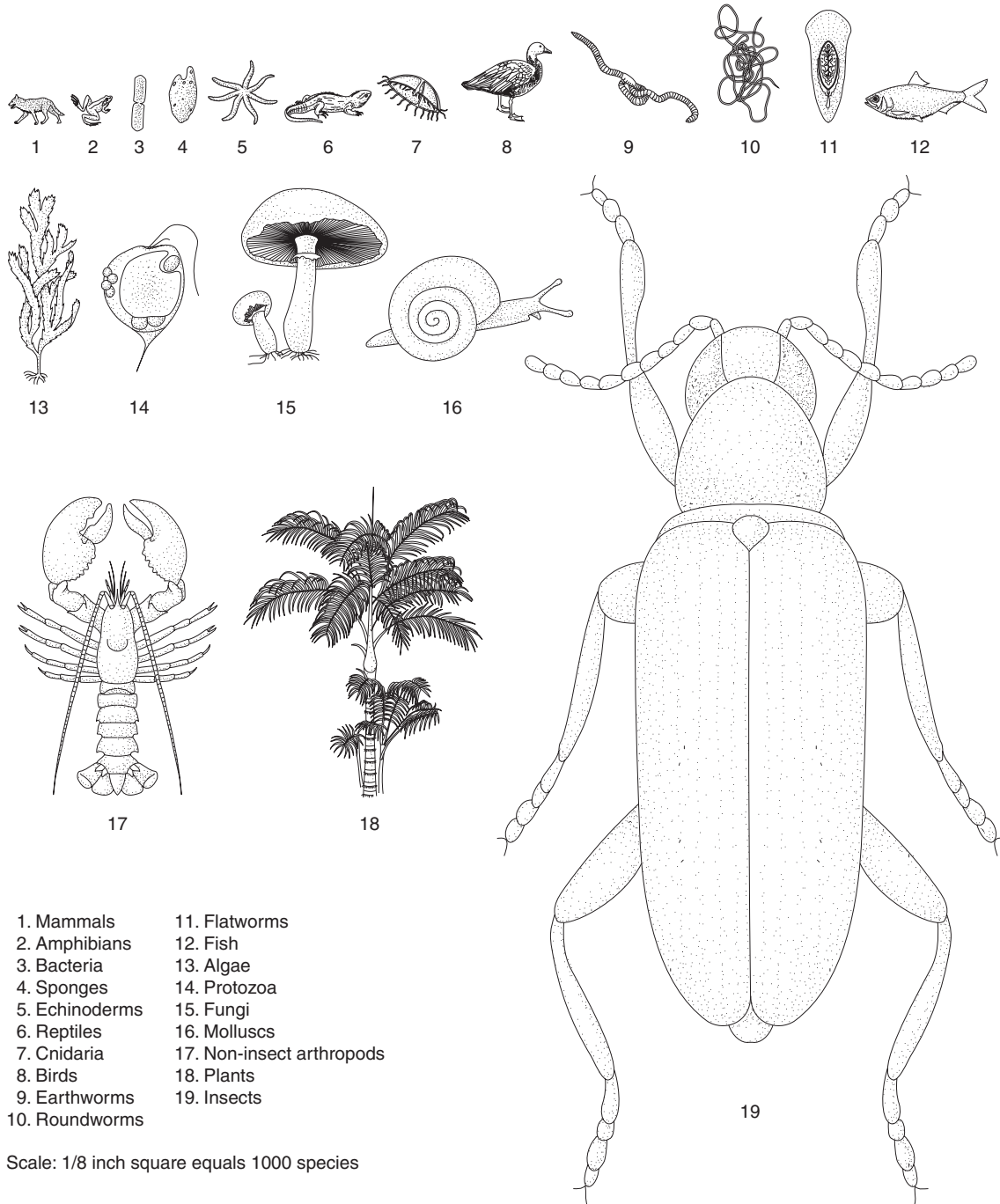
Figure 1.7 Major feeding guilds in the Insecta, showing the importance of herbivory. (From Southwood 1973.)

a common ancestral habit, then it can be seen that the major ''trophic roles'' at order level are scavenging (detritivory) followed by carnivory. Herbivory (or phytophagy), feeding on living plants (or the dead parts of living plants such as heart wood), is represented by only eight major orders, suggestive of what Southwood called an ''evolutionary hurdle''. It is very significant, however, to realize that over 50% of all insect species occur within the orders that contain herbivores, suggesting that once the ''hurdle'' was overcome, rapid and expansive species radiation was able to take place, and indeed it seems that herbivory has repeatedly led to high diversification rates in insects (Janz et al. 2006).

1.7 NUMBERS OF INSECTS: SPECIES RICHNESS

One problem that has at the same time excited and bewildered entomologists since the very earliest days has been the sheer number and variety of insects.

Linnaeus named a large number of insect species in the 18th century in the 10th edition of his *Systema Naturae* (1758), probably thinking that he had found most of them. At that time, only a small percentage of the world had been explored by entomologists (or indeed, anyone else), so it is not surprising that the earliest workers had no concept of the diversity and richness of insect communities, even less the complexities of their interactions. Two hundred years later we are not very much closer to estimating the total number of insect species on the planet with any degree of accuracy, though we do have a better feel for the subject than did Linnaeus. We have now described more than 1.5×10^6 organisms in total, of which more than 50% are insects. Figure 1.8 illustrates the dominance of the Insecta in the list of described species (May 1992). It is revealing to compare the number of species of insects with those of vertebrates (merely a subphylum of the Chordata, when all is said and done): around 47,000 insect species have been described, compared with a trivial 4000 or so for mammals. Furthermore, it is likely that the vast

1. Mammals
2. Amphibians
3. Bacteria
4. Sponges
5. Echinoderms
6. Reptiles
7. Cnidaria
8. Birds
9. Earthworms
10. Roundworms
11. Flatworms
12. Fish
13. Algae
14. Protozoa
15. Fungi
16. Molluscs
17. Non-insect arthropods
18. Plants
19. Insects

Scale: 1/8 inch square equals 1000 species

Figure 1.8 Relative species richness of various animal and plant groups shown as proportional to size of picture. (From May 1992.)

majority of vertebrate species have now been discovered. Insect species meanwhile continue to roll in apace. One problem with this has been the distribution and abundance of taxonomists, rather than that of the species of the other organisms they are dedicated to naming. Gaston and May (1992) have pointed out that there are gross discrepancies between both the number of taxonomists and the groups that they study, and also the regions of the world wherein they collect their animals. For every taxonomist devoted to tetrapods (amphibians, reptiles, birds, and mammals), there are only 0.3 for fish and around 0.02–0.04 for invertebrate species. To make matters worse, if published ecological papers are anything to go by, the study by Gaston and May suggested that 75% or so of authors come from North America, Europe, and Siberia together, whereas the areas of supposed highest species richness, the humid tropics, are seriously understudied.

As Gaston and Hudson (1994) have discussed, the total number of insect species in the world is an important but elusive figure. Exactly why it is important is also rather elusive, and different scientists would argue differently as to why we need to know just how many species there are in the world. First, by invoking Gause's axiom, which states that no two species may coexist in the same habitat if their niche requirements completely overlap, then by assessing the number of species in a given place, we can comment on the complexity of niche separation and thus the implied heterogeneity of the particular habitat. (Niche ecology is considered in Chapter 4.) Second, we know that an increase in environmental heterogeneity as associated, for example, with high densities of herbaceous vegetation reduces interspecific competition and this allows species coexistence (Corrêa et al. 2006). Thus a great deal of concern is being expressed worldwide about the decline of natural habitats through anthropogenic activities such as the logging of tropical rainforests and the urbanization of temperate regions (see Chapters 8 and 9). One consequence of habitat decline is species extinction, and with insects, as indeed with all other organisms, it is impossible to assess extinction rates effectively until we know how many species exist in the first place. Certainly, we cannot give a percentage extinction figure unless we know how many species were there originally. Third, in applied ecology, it is important to predict stabilities of forest or agroecosystems, in terms of pest outbreak potential (see Chapter 12). If we are to

rely more heavily in the future on population regulation by insect natural enemies, we need to inventory beneficial species in order to select targets for manipulation. One of the aims of evolutionary biologists is to explain the relationships between organisms, both extinct and extant, and the Insecta provide by far the most diverse group for this type of study. As all species have arisen through natural selection, a knowledge of the number of species must be an important baseline for discussing their origins. Finally, the intrinsic wonder of insect life wherever we turn in the non-marine world must beg the question: ''Just how many are there?''

Different researchers have used different methods to estimate the number of species in the world. Table 1.4 summarizes some of these conclusions. There is a surprising variation in opinion, spanning a whole order of magnitude from 2 or 3 million to a staggering 30 million or even more, though as we shall see, these higher figures seem relatively implausible (Gaston et al. 1996; Gering et al. 2007). The methods for arriving at these estimates vary considerably (May 1992), and only a brief résumé is presented here. In the case of well-known animal groups such as birds and mammals, the tropical species so far described (probably most of them) are twice as numerous as temperate ones. If it is assumed that this ratio also holds true for insects (though this has not been tested), and that we have described the majority of temperate insect species, then we reach an estimate of around 1.5–2 million species in total. As for all such estimates, some of the basic assumptions may be suspect. This theory assumes that insects, with an average size orders of magnitude smaller than those of birds and mammals, would show a proportional increase in species number as their tropical habitats diversify curvilinearly when compared with their temperate ones. Work in Borneo by Stork (1991) showed that the mean number of insect species in a rainforest canopy was 617 per tree, with one tree sample containing over 1000 species. This compares with the species numbers recorded from native British tree species, with an average of around 200 per tree (Southwood 1961) (see below), showing that tropical species might outnumber their temperate counterparts by a good deal more than 2:1.

Taxonomic biases are also to be found within the Insecta. Some orders of insects are better known than others, and have been collected heavily from only certain regions of the world. Butterflies, for example,

Table 1.4 Estimates of the numbers of insect species in the world.

Estimated no. of species (x million)	Method or source of estimation	Reference
2–3	Hemiptera in Sulaweis	Hodkinson & Casson (1991)
3	Insects on plants	Gaston (1991)
3–5	Tropical vs temperate species	May (1992)
4.8	Tropical beetle communities	Ødegaard (2000a)
4.9–5.8	Specialist herbivores in rainforests	Novotny et al. (2002)
6	Butterflies in UK	Hammond (1992)
6.6	Host-plant specialization	Basset et al. (1996)
7–10	Insect host specificity	Stork (1988)
10	Biogeographic diversity patterns	Gaston & Hudson (1994)
12.2	Scale dependence and beetles	Gering et al. (2007)
30	Beetle–tree associations	Erwin (1982)

have fascinated amateur entomologists far longer than almost any other group of insects, and so we should by now know most of the temperate species within this order, and also have a fairly good notion of the tropical ones too. There are 67 species of butterfly in the UK, and between 18,000 and 20,000 world-wide. In total, we have 22,000 or so British insect species, encompassing all the orders, so by using the ratio of 67 : 22,000 and applying it to the 20,000 global butterfly species, we reach a grand total of around 6 million insect species worldwide. This esti-mate again, of course, relies on linear relationships of habitat diversity between temperate and tropical communities, though it seems reasonable to suggest that the latitudinal gradient of insect species richness increasing between these regions is a direct function of plant diversity also increasing in the same direction (Novotny et al. 2006).

Perhaps the most extravagant estimate of the richness of insect species comes from Erwin (1982), who predicted a figure of 30 million species for tropi-cal forests on their own. Amongst other crude as-sumptions, this estimate relies heavily on the concept that tropical insect herbivores are plant-species spe-cialists, so that a ''one beetle, one tree'' system has to operate. However, it is now suspected that host-generalist rainforest insects are more common than might have been thought (Basset 1992; Williams & Adam 1994; Novotny et al. 2002), so that rainforest trees may sustain herbivore faunas ranging from highly specialized to highly polyphagous. Note also

that it may be dangerous to make assumptions that cover all insects equally well. Very small insects, for example, have the ability to produce enormous numbers (see later in this chapter), and also to exploit microniches in their environment unavailable to much bigger species (Finlay et al. 2006). Hence, rules for speciation, diversification, and host special-ization may not apply to the very small or the very large species.

Though the total number of species so far un-described is certainly huge, some groups in some parts of the world are thought to be fairly complete. As mentioned earlier, British butterflies are certainly all described, as would befit a small group of easily recognizable species, as are the majority of other European insects. The degree of completion of species inventories of groups can sometimes be estimated using species accumulation curves and fitting asymp-totic models to the data. Western Palaearctic dung beetle species, for example, are thought to be virtually complete (Cabrero-Sanudo & Lobo 2003), with only about 16% of the family Aphodiidae yet to be described (Figure 1.9).

1.8 VARIATIONS IN SPECIES NUMBER

Merely attempting to estimate the total number of insect species in the world, though a worthwhile exer-cise, conceals a myriad of ecological interactions that
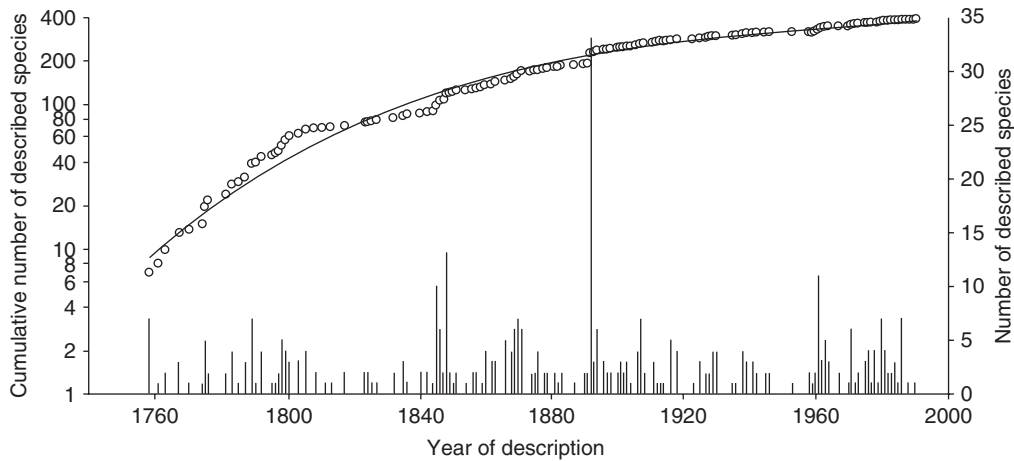
Figure 1.9 Number of described species (bars) and temporal variation in the logarithm of the cumulative number of described dung beetle species (O) from 1758 to 1990 in the western Palaearctic region, taking into account the exhaustive taxonomic information about the Palaearctic species of the three Scarabaeoidea families: Aphodiidae (395 species). The cumulative curves were fitted (continuous line) using the beta-p function & using the quasi-Newton method. (From Cabrero-Sanudo & Lobo 2003.)

influence the number of species found in any particular habitat. Many of these processes will be considered in detail in later chapters, but they are summarized here as an introduction.

1.8.1   Habitat heterogeneity

As stated above, if we invoke Gause's axiom, or the Competitive Exclusion Principle, it is clear that homogeneous habitats with relatively few ''available niches'' should support fewer species than heterogeneous ones. The latter are likely to allow for more coexistence of species by enabling them to partition resources within the habitat and hence avoid interspecific competition (see Chapter 4). From this, we may conclude that habitats that are more diverse in terms of greater plant species richness, for example, should exhibit greater insect species richness as a consequence. Undoubtedly, once Southwood's evolutionary hurdle of herbivory (see above) has been overcome, plants provide an enormous variety of new habitats and niches for insects (Fernandes 1994). Hutchinson's (1959) ''environmental mosaic'' concept describes the system well, and mosaics of mixed natural habitats such as small-sized crops, fields, and natural habitats in the
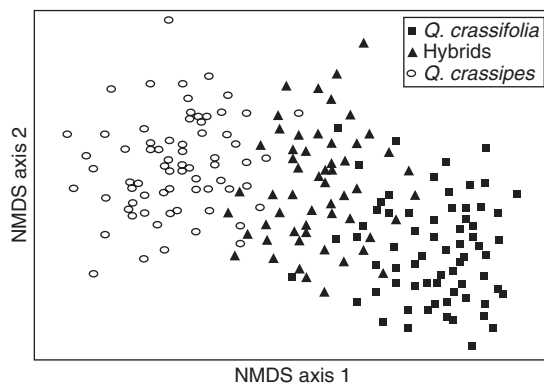
same landscape maximize the richness and diversity of insect species (Duelli et al. 1990; Yu et al. 2003). Such habitat mosaics are also thought to decrease the probability of the extinction of rare species (see Chapters 8 and 9).

Early seral stages of succession, for example, tend to possess higher plant species richness than those close to climaxes, so that it might be expected that early succession is also typified by higher insect species richness as well. A study on bees in set-aside fields in Western Europe illustrates this phenomenon well (Gathmann et al. 1994). Various types of crops and fallow fields in an agricultural landscape were assessed for bee species richness, and it was found that habitats with greater floral diversity offered better and richer food resources for flower visitors. Set-aside fields that were mown, and hence reduced to early successional stages, showed a greatly increased plant species richness, coupled with double the species richness of bees when compared with unmown, late-successional-stage fields.

So far, we have considered floral diversity at a phenotypic level, but it may be that even within a host species, plants with increasing genetic diversity may increase insect species richness (Wimp et al. 2005). A complex derivation of plant species richness involves hybrid zones, areas of habitats where two or

more plant species hybridize to produce a third, F1, phenotype. These areas seem to provide a great diversity of resources for herbivorous insects (Drew & Roderick 2005). In Tasmania, Australia, for example, where two species of eucalyptus hybridize, this area was found to be a center for insect (and fungal) species richness (Whitham et al. 1994). In this study, out of 40 insect and fungal taxa, 53% more species were supported by hybrid trees than in pure (parent plant) zones. In a different study, Floate et al. (1997) found that not only were populations of leaf-galling aphids in the genus *Pemphigus* (Hemiptera: Aphididae) 28 times as abundant in hybrid zones of the host tree cottonwood (*Populus* spp.), but that, in the authors' opinion at least, preserving such small hybrid zones could have a disproportionately beneficial role in maintaining insect biodiversity. Figure 1.10 illustrates the use of multivariate statistics in detecting three distinct clusters of gall-forming and leaf-mining insects associated with two species of *Quercus* in Mexico, and a hybrid of the two (Tovar-Sánchez & Oyama 2006). Clearly, the hybrid supports an intermediate community, adding to both the genetic and

species diversity of the forest ecosystem. Despite all this, the role of hybrid zones in determining insect numbers remains controversial (see Chapter 3).

It is not only herbivore communities that might be expected to show an increased species richness as their plant-derived habitat also becomes more species-rich. Consumer trophic levels such as specialist predators or parasites can also be influenced in this way. Parasitoid guilds constitute an important part of the biodiversity of terrestrial ecosystems (Mills 1994), and because many of them are host specialists, high species richness of their insect hosts results in a similarly higher parasitoid richness. This system parallels that of plant–herbivore interactions well. Insect herbivores feed on many different parts of the plant (see below), so that one plant species can often support many insect species. Similarly, it is possible to recognize a series of guilds, each composed of various species, depending on the life stage of the host insect (Figure 1.11). Habitat heterogeneity may also play an important part in promoting species coexistence, hence adding to regional species richness. Palmer (2003) found that termite mounds increased the complexity of habitats for African acacia-associated ant species, and allowed them to avoid competitive exclusion.

1.8.2 Plant architecture

The term ''architecture'' when applied to plants was coined by Lawton and Schroder (1977). It describes
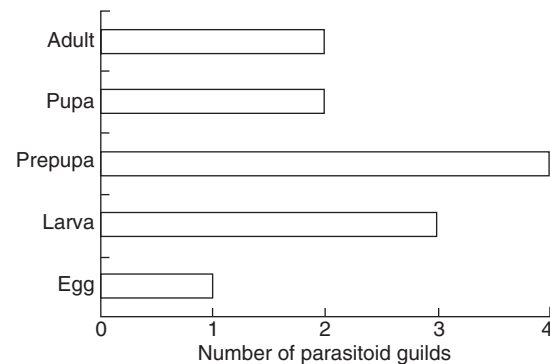

Figure 1.10 Differences in endophagous (gall-forming and leaf-mining insects) community composition among oak host *Quercus crassifolia*, hybrids, and *Q. crassipes*. Each point is a two-dimensional (axis 1 and axis 2) representation of endophagous species composition on an individual tree based on global, non-metric multidimensional scaling (NMDS). Distances between points reflect a dissimilarity matrix created using the Bray–Curtis dissimilarity coefficient. Points that are close together indicate endophagous communities that are more similar in composition. (From Tovar-Sánchez & Oyama et al. 2006.)

Figure 1.11 Number of guilds of parasitoid insect attacking different life stages of insects. (From Mills 1994.)

both the size, or spread, of plant tissues in space, and the variety of plant structures (Strong et al. 1984), from leaves to shoots to wood to roots; Lewinsohn et al. (2005) consider it to be a cornerstone of insect–plant relationships. Figure 1.12 shows the great diversity of niches thought to be available for just one, albeit the largest, order of insects, the Coleoptera (Evans 1977). All imaginable parts of the tree are utilized by one species of herbivore. Clearly, different plant types vary widely in their structures,
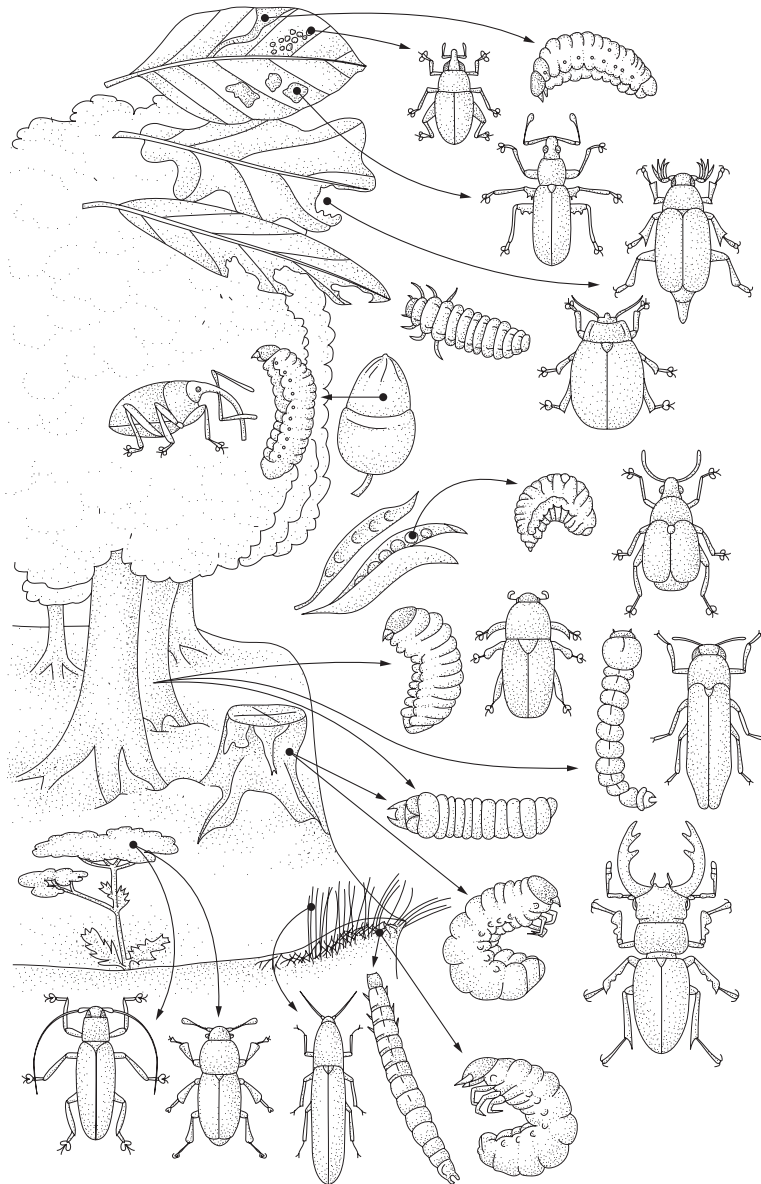
Figure 1.12 An illustration of the diversity of beetles found living on a single tree. (From Evans 1977.)
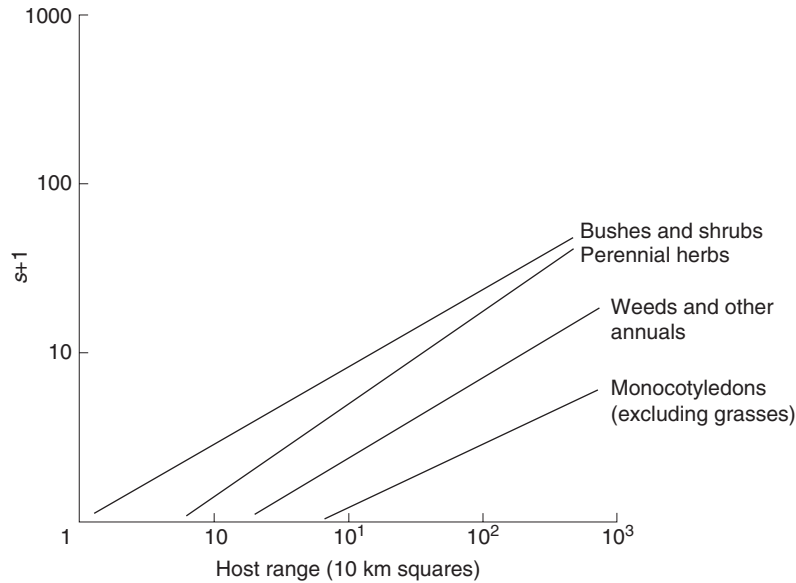
Figure 1.13 Number of insect species on plants with different architectures and varying commonness. (From Strong et al. 1984.)

and thus architectures. Ferns are very much less complex than trees, and hence in terms of habitat heterogeneity, a bush, shrub, or tree would be expected to support more insect species than would a fern, everything else being equal (Figure 1.13). If the ratios of species richness of herbivorous insects between more complex plant types or species and less complex ones are considered (Table 1.5) (Strong et al. 1984), it can be seen that, in all cases, the architecturally more complex plant has considerably more species associated with it. Summing over the ratios in the table, we can ''guesstimate'' that a tree should have something like 50 times as many species associated with it than a monocotyledon, although this is probably somewhat of an overestimate. A most striking case compares Lepidoptera on trees and shrubs with those on herbs and grasses (Niemalä et al. 1982), where there are over 10 times as many species on the former plant types than on the latter.

Table 1.5 Ratio of numbers of herbivore insect species on plants of different structures. (From Strong et al. 1984.)

More complex plant	Ratio	Less complex plant
Trees	27:1	Shrubs
Shrubs	21:1	Herbs
Bushes	1.3:1 to 25:1	Perennial herbs
Perennial herbs	1.5:1 to 27:1	Weeds
Weeds	1.3:1 to 29:1	Monocotyledons

1.8.3 Plant chemistry

Chemicals in plants that may have an influence on the ecology of insects fall into two basic categories: food and defense. Insect herbivores are particularly limited by the suboptimal levels of organic nitrogen provided by plants as food (White 1993). Though many insects are highly resistance to plant toxins (Torrie et al. 2004), plant defenses reduce the efficiencies of feeding processes even further. However,

although plant chemistry influences the abundance of insects, it is difficult to detect a major influence on insect species richness. Jones and Lawton (1991) looked at the effects of plant chemistry in British umbellifers, and though there was thought to be some influence on species richness via changes in natural enemy responses to hosts or prey on biochemically diverse plants, they concluded that there was no evidence that plant species with complex or unusual biochemistries supported less species-rich assemblages of insects. Essentially then, though a ''niche'' on a toxic or low nutrient plant may be harder to utilize, the number of niches (i.e. habitat heterogeneity) remains the same. This result is difficult to reconcile with the fact that most insect herbivores (about 80%) are specialists, unable to feed on plants with different chemistries. Indeed, it seems that feeding specializations in herbivorous insects depend on recognition of stimulants specific to the host plant (del Campo et al. 2003).

1.8.4   Habitat abundance (time and space)

For insects to adapt to a new habitat or resource of any sort, there must be sufficient opportunity for natural selection to do its job, and for selection pressure to ''push'' a species into a new and stable form. This type of opportunity consists of the regional abundance of the resource and/or how long in evolutionary time the resource has been available. The best illustrations of this principle again come from insects feeding on plants.

In the UK, both abundance through time, measured as the number of Quaternary (last million years) remains, and commonness, measured as the number of kilometer squares of the UK wherein the species of tree was recorded, have a significant positive influence on the numbers of insects on the trees, as noted by Southwood (1961) and Claridge and Wilson (1978). Both studies showed that the *Quercus* genus (oaks), which is both the most common and has been in the landscape for the longest time, shows the highest number of insects associated with it. Newly introduced tree species such as the sycamore and horse chestnut have relatively few (see Chapter 8). In summary, there appears to be tremendous variation in numbers of insect species on British trees, all of which may be assumed to possess roughly the same architecture.

1.8.5   Habitat size and isolation

A fundamental concept in ecology is the equilibrium theory of island biogeography, first proposed by MacArthur and Wilson (1967). Simply put, the theory makes predictions about how island area and distance from a source of colonists affect immigration and extinction rates (Schoener 1988; see also Chapter 8). The term ''island'' can indicate an island in the true, geographic sense, but it can also mean any patch of relatively homogeneous habitat that is surrounded by a different one. The latter broad category could include woodlands in farmland, ponds in fields, or even one plant species surrounded by different ones. A nice example is provided by Krauss et al. (2003) who studied butterfly species in different-sized calcareous grasslands in Germany. As Figure 1.14 shows, there is a highly significant relationship (note the log scale on the *x*-axis) between the size of the grassland ''patch'' and the number of species of butterfly living in it. This association is robust enough not to differ between years of sampling.

Theoretically, there should be a balance between the migration of species into an island or habitat patch and extinction rate, such that for a given size of island there is an equilibrium number of species present (Durrett & Levin 1996). The species–area relationship is firmly established in ecology (Hanski
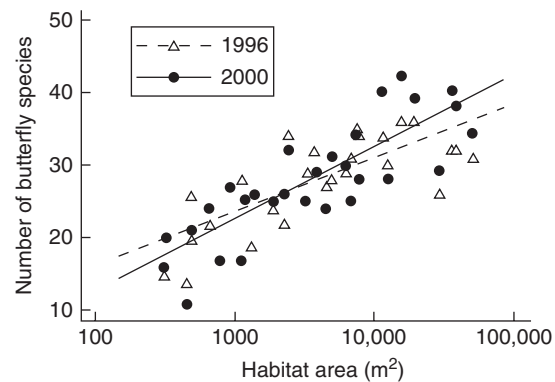
Figure 1.14 Relationship between the number of butterfly species and grassland area ($n = 31$ fragments) in 1996 and 2000. 1996, $y = 1.69 + 7.23 \ \log_{10} x$, $F = 40.37$, $r^2 = 0.582$, $P_R < 0.0001$; 2000, $y = -6.28 + 9.58 \log_{10} x$, $F = 62.48, r^2 = 0.683$, $P_R < 0.0001$. Comparison of regressions: slopes, $F = 2.00$, $P_S = 0.163$. (From Krauss et al. 2003.)

& Gyllenberg 1997), and it describes the rate at which the number of animal and/or plant species increases with the area of island available. The model is represented by the simple equation:

$$s = a^z$$

where s is the number of species, a is the island area, and z is a constant.

There are a host of assumptions to the theory, including those that insist that habitat type, age, and degree of isolation of the ''islands'' being compared are the same. There is some uncertainty about the existence of a maximum value for variability or heterogeneity of physical environments (Bell et al. 1993). It is possible that as islands become larger, their heterogeneity increases apace. However, field data fitted to the species–area model suggest that the curve will asymptote; in other words, the exponent value, z, is less than one. In fact, there are surprisingly few examples where z has been estimated with confidence for insects. Values range from 0.30 and 0.34 for ants and beetles, respectively, on oceanic islands (Begon et al. 1986) to 0.36 for ground beetles (Coleoptera: Carabidae) in Swedish wooded islands (Nilsson & Bengtsson 1988); z-values for specialist butterfly species in Germany were estimated to be 0.399 (Krauss et al. 2003), whereas generalist species only managed 0.096.

As mentioned above, the species–area model has some shortcomings (Williams 1995). There are no limits to the function that describes it, and the model is unable to handle zero values, so that if, by some quirk of fate, a particular island has no species representing the particular animal or plant group under investigation, then that island cannot be included in the model fitting. Despite these drawbacks, the island biogeography theory does fit observed data on occasion, but particularly few insect examples exist. One experimental illustration was carried out by Grez (1992), who set up patches of cabbages containing different numbers of plants, ranging from four to 225. Later sampling of the insect herbivores on and around the cabbages showed that species richness of insects was highest in the large host-plant patches, which also showed an enhanced presence of rare or infrequent species within the general area, when compared with the smaller patches. In a field study, Compton et al. (1989) were able to detect a significant but rather weak tendency for larger patches of bracken

(*Pteridium aquilinum*) to support more species of insect herbivores than smaller ones, in both Britain and South Africa. On the other side of the Atlantic Ocean, the Florida Keys have gained their fauna of longhorn beetles (Coleoptera: Cerambycidae) from both the islands of the West Indies, including the Bahamas and Cuba, and the mainland, represented by the peninsula of south Florida. Both species–area and species–distance relationships for cerambycids were found to conform to the island biogeographic theory (Browne & Peck 1996), even though the islands making up the Keys have been fragmented by rising sea levels for only the last 10,000 years or so. Such relationships may, though, be overshadowed by other biogeography factors, such as historical dispersal patterns. Beck et al. (2006) studied the number of hawkmoth (Lepidoptera: Sphingidae) species in the Malesian region of Southeast Asia (a region covering the Solomon Islands and New Guinea to the east and Peninsular Malaysia and Sumatra to the west). Though species–distance relationships were detectable for some species of hawkmoth, the main determinant of species richness on these islands was the amount and diversity of vegetation, especially rainforest.

The fragmentation of habitat islands may be a natural event over geological time, as evidenced by the Florida Keys above, but many aspects of human activity, such as logging and road building, over a very much shorter timescale, result in fragmentation as well. A particular case in point would be the impacts of landscape-scale modifications to natural habitats from agricultural practices such as the removal or reduction in woodland, the parceling up of land into fields, and the management of field boundaries and hedgerows as windbreaks or stock barriers (Pichancourt et al. 2006). Such practices can produce a further decrease in ''island'' size and an increase in isolation. Animal and plant populations remaining in these fragments constitute metapopulations, that is, local populations undergoing constant migration, extinction, and colonization on a regional rather than global scale (Husband & Barrett 1996). A British example of a metapopulation study is that by Hill et al. (1996) on the silver spotted skipper butterfly, *Hesperia comma* (Lepidoptera: Hesperiidae). The larvae of this butterfly are grass-feeders, preferring short swards where the conditions are warm. Patches of this type of habitat occur on chalk downland in the south of England, and studies of the metapopulation

dynamics of the species showed that habitat patches were more likely to be colonized if they were relatively large and close to other large, occupied patches. Furthermore, adult butterflies were more likely to move between large patches close together, whereas local populations in small isolated patches were more likely to go extinct. A consideration of habitat ''quality'' is also required; two patches of grassland for instance may be of a similar size and equally isolated, but one may be of a higher quality than the other in terms of vegetation height and the abundance of flowers (Öckinger & Smith 2006).

1.8.6   Longitude and altitude

On a local scale, insect species richness may still vary even when habitat heterogeneity and abundance, or patch size, are constant. These variations would seem to be influenced by environmental factors such as latitude, longitude, and altitude, presumably via climatic interactions. There are two general predictions of how species richness and altitude are related. Either richness decreases fairly linearly with increasing altitude, or richness peaks at mid-elevations (Sanders 2002). Several examples describe how insects in a particular locale are most species-rich at a certain height above sea level. Libert (1994) found that many species of butterfly observed in Cameroon, West Africa, exhibited a preference for the tops of hills, whereas in Sulawesi, Indonesia, hemipteran communities showed highest species richness at elevations between 600 and 1000 m (Casson & Hodkinson 1991). The explanations of these observations are no doubt complex, and detailed microclimatic and vegetational data would be required to investigate causality. The roles of decreasing diversity with latitude or altitude of host-plant species, decreasing structural complexity, and increasingly unfavorable climatic conditions may all have an influence (Brehm et al. 2003). Indeed, weather conditions can influence insect species richness. In tropical Australia, leaf beetle (Coleoptera: Chrysomelidae) communities were found to be most species-rich during the hottest and wettest times of the year (December to March; Hawkeswood 1988). It can often be difficult in ecology to assign cause and effect with confidence, but various effects of weather and climate on insect ecology are considered in detail in Chapter 2. Suffice it to say for now that, in this example, leaf beetle richness was not correlated with plant richness, though it might be expected that these climatic influences would operate at least in part via the host plants of these totally herbivorous species.

On a larger geographic scale, it is usual to expect that insect species richness will decrease towards the poles. In North America, of 3550 species studied, 71% occurred south of a line along state boundaries from the Arizona–California to Georgia–South Carolina borders (Danks 1994), whereas in Scandinavia, out of a wide range of insect families examined, the number of species was generally highest in the southern provinces, declining to the north and north-west (Vaisanen & Heliovaara 1994). As always in insect ecology, exceptions to neat rules crop up. Also in Finland, Kouki et al. (1994) showed that the species richness of sawflies (Hymenoptera: Symphyta) showed an opposite latitudinal trend, so that species richness is highest in the north, not the south. Kouki et al. explained this by the fact that the principal host-plant group, willows (*Salix*), are also most species-rich further north.

1.8.7   Human interference

Various of the foregoing factors that influence insect species richness can be altered, usually detrimentally, by human activities such as agriculture, forestry, urbanization, and so on. In general, the diversity of insect communities in habitats such as grassland is often negatively correlated with management intensity (Nickel & Hildebrandt 2003). Certainly, the intensive growing of monoculture crops all over the world must result in a reduction in biodiversity of plants and the animals that associate with them (see Chapter 12). Rainforests all over the world are being depleted rapidly, and this also has an undoubted effect on species richness within them. In Sabah (northeast Borneo as was), primary lowland rainforest has largely been reduced to small or medium-sized forest ''islands'', often isolated from each other and surrounded by artificial agricultural ecosystems (Bruhl et al. 2003). Communities of leaf litter ants in these fragments of forest showed a significant reduction in species number and diversity when compared with communities in contiguous forest, with a maximum of only 47.5% of the original richness. Connectivity between habitat islands is crucial for organisms to move between them, and even a forest plantation is better

than no forest at all, as found with dung beetle communities in Chile (Bustamante-Sanchez et al. 2004). In this example, pine plantations maintained the structural and functional biodiversity of native fauna, at least partially, and were able to connect native forest remnants across the landscape. Habitat specialists in particular suffer from this type of habitat isolation (Steffan 2003), whilst generalist species do better in a diverse landscape ''matrix'''.

Reductions in habitat heterogeneity result from practices such as selective logging, but the knock-on effects on insect species richness are not always so predictable. Some species of butterfly actually do better in logged forest, the gap specialists in particular (Hamer et al. 2003), and it has in fact proved difficult to detect significant changes in species richness of everything from moths to beetles when primary rainforest is selectively logged (Speight et al. 2003).

1.9 THE NUMBER OF INSECTS: ABUNDANCE

Species richness is only one measure of the success of insects; their abundance is another equally important one. No-one could deny that a plague of locusts, although very species-poor, is the epitome of success, at least as judged by the number of individuals and their rapacious ability to devour plant material of many kinds. Unfortunately, it is rather more difficult to obtain reliable estimates of the number of individuals (abundance) of a species than it is merely to score the species present in or absent from a habitat (species richness). Common but immobile or concealed species such as aphids or soil- and wood-borers may be underestimated or even completely overlooked by most ecological sampling systems, and it is only when we look very closely at tiny and, in most people's perceptions, inconsequential, insects in novel habitats that we find just how common some groups are. An example of booklice (Psocoptera; Figure 1.15) from Norway spruce canopies in lowland England shows how immensely abundant they are in a seemingly sterile habitat (Ozanne et al. 1997). Using insecticidal mist blowing of tree canopies, an astonishing 6500 per square meter were collected. As a side issue, this example illustrates the importance and magnitude of detritivore pathways in some ecosystems (Foggo et al. 2001). Booklice feed mainly on fungi, lichens, and fragments of leaf and bark material in dark tree

Figure 1.15 Booklice (Pscoptera).

canopies, and are likely to form the staple diet of a myriad of predatory insects and other arboreal arthropods.

The densities of insects that commonly act as disease vectors, such as mosquitoes, tsetse flies, and aphids, are especially significant when it is considered that these can be low-density pests, where only a very few (as few as one) individuals are required to pass on diseases such as malaria, sleeping sickness, or potato leaf curl (see Chapter 9). Although it is one thing to wonder at the sheer numbers of insects in a locust swarm, it is quite another to appreciate the potential for harm inherent in one small individual.

1.9.1 Variations in insect numbers

Of much more fundamental interest to ecologists is the manner in which insect population densities vary within a population through time. Some of the most basic ecological processes have been explored in response to such variations, and the explanation of the patterns and processes in population density changes has taxed ecologists the world over, and still does. Large variations in the population densities of insects occur under two different headings: population cycles and population eruptions (Speight & Wainhouse 1989; Speight & Wylie 2001). Cycles are periodic, with some degree of predictability about the time between peak numbers; high densities are rapidly followed by large declines. Eruptive populations, on the other hand, often remain at low densities for long periods before outbreaks occur suddenly and often unexpectedly. Once such outbreaks have developed, they may be sustained for some time.

1.9.2 Cycles

Most cycles of insect populations have been observed in species that inhabit perennial, non-disturbed habitats such as forests. Figure 1.16 shows a typical population cycle of a forest insect, the larch budmoth, *Zeiraphera diniana* (Lepidoptera: Tortricidae) (Baltensweiler 1984). This species shows remarkably regular cycles of abundance in the Engadine Valley in Switzerland, where outbreaks have a periodicity of 8 or 9 years (Dormont et al. 2006). Mean population density may vary 20,000-fold within five generations, though 100,000-fold increases have been observed locally. These huge numbers of defoliating caterpillars can have an enormous impact on the growth of the host trees, and larch budmoth outbreaks can be ''reconstructed'' over many hundreds of years by examining tree ring widths. In years when large numbers of larvae were eating larch needles, the density of latewood laid down by the trees is much reduced. Figure 1.17 shows that budmoth outbreaks have come and gone in fairly recognizable cycles, averaging every 9.3 years to be exact, for 1200 years. It is only in the last 20 or so years that these predictable outbreaks seem to have been absent (Esper et al.

2007), a possible consequence of climate change (see Chapter 2).

Many other forest insects show similarly predictable cycles; the Douglas fir tussock moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae), has exhibited regular outbreaks at 7–10-year intervals in British Columbia since the first recorded observations in 1916 (Vezina & Peterman 1985). What is more, these cycles may be synchronized over relatively large areas. Larvae of the autumnal moth, *Epirrita autumnata* (Lepidoptera : Geometridae) feed on mountain birch, *Betula pubescens*, over much of Fennoscandinavia, cycling to outbreak densities every 10 years or so. In Figure 1.18 it can be seen that moth outbreaks from 24 different localities, some over 1000 km apart, show remarkably similar patters over the years (Klemola et al. 2006). This spatial synchrony weakens as site distances increase, and it is likely to be linked to climatic variations within and between regions.

In practice, population cycles are very difficult to explain (Turchin et al. 2003). Unless climatic patterns are themselves cyclic (Hunter & Price 1998), most insect population cycles can usually be attributed to biotic interactions, such as competition and predation,
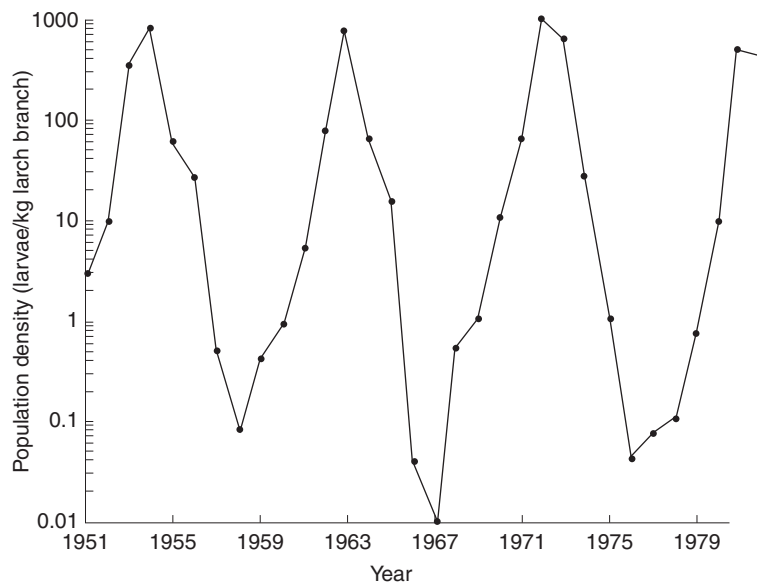
Figure 1.16 Population cycles for *Zeiraphera diniana* on larch in Switzerland. (From Baltensweiler 1984.)
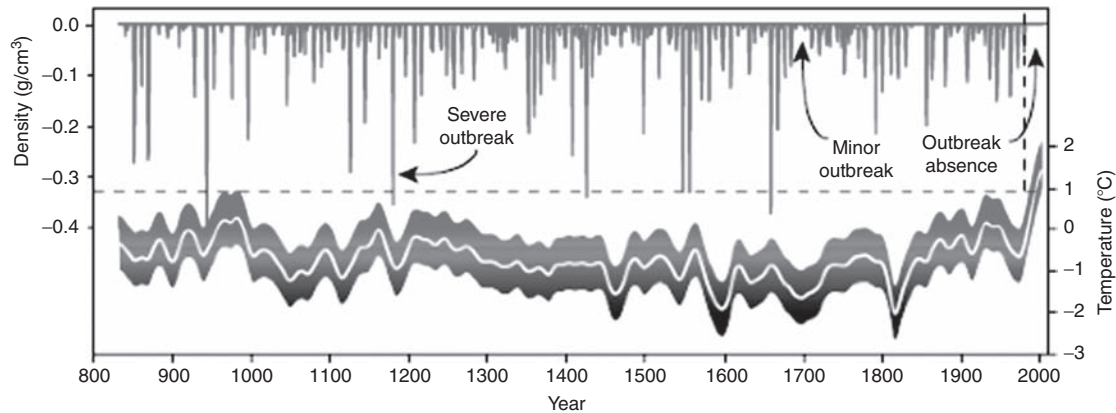
Figure 1.17 Long-term larch budmoth (LBM) and temperature reconstructions for the European Alps. (Top) Maximum latewood density (MXD)-based LBM outbreak reconstruction since AD 832. Time-series is the age-corrected difference series between gap-filled and original MXD data. Values less than $-0.005\,\mathrm{g/cm}^3$ are shown. (Below) The temperature model (white curve) is shown together with the standard error (gray band) derived from the fit with instrumental data. Dashed lines indicate the last LBM mass outbreak in 1981 (vertical) and the upperstandard error Emit recorded in the late ninth century (horizontal). (From Esper et al. 2007.)

that have a delayed action on population growth rates. Delayed density dependence will be considered in detail in Chapter 5, and is introduced below. Population cycles are rarely as neat as in the case of *Zeiraphera*, and long-term examinations of abundance data for insect species, though revealing some degree of cycling, suggest that the levels of peaks and troughs are less regular or predictable.

1.9.3   Regulation

In ecological terms, we recognize that population cycles in insects are at least partially under the
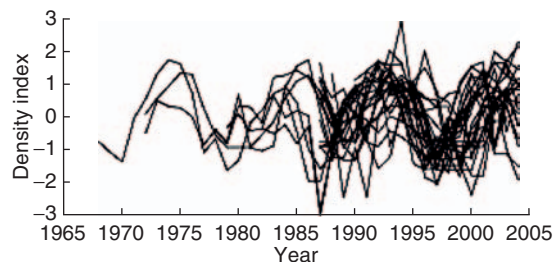
Figure 1.18 Autumnal moth population time series for each of 24 locations in Fennoscandia. (From Klemola et al. 2006.)

influence of a process known as regulation. Regulation describes the way in which a population's abundance varies through time as a decrease in population growth rate as population density increases (Agrawal et al. 2004). Declines in population growth rates with density can be manifested by: (i) increases in the rate (proportion) of mortality that the population suffers; (ii) decreases in birth rate; (iii) increases in emigration rates; or (iv) decreases in immigration rates. When birth, death, or movement rates vary proportionally with density (i.e. they are density dependent), they have the potential to maintain an insect population around some equilibrium density. If the density dependence occurs on a time delay, the population can overshoot this equilibrium, and exhibit cyclic behavior. In general, the higher the insect's fecundity, or the longer the time lag, the more dramatic the oscillation will be.

Various biotic factors are known to be potentially regulatory (i.e. may act in a density-dependent fashion), and each is considered in detail in later chapters. However, it is useful to separate such factors into those that act within a trophic level, such as competition, and those that act between trophic levels, either from below (so-called "bottom-up"), via food supply, or from above (so-called "top-down"), via the action of natural enemies such as predators, pathogens, or parasitoids (see Chapter 5).

In reality, these factors interact, so that, for example, competition often acts via the amount of food available for individual insects in what is known as resource-driven outbreaks (Steinbauer et al. 2004). Food limitation via intraspecific competition may result in decreased fecundity, or in increased migration (Azerefegne et al. 2001). Experimental studies frequently demonstrate this sort of competition. Cycles in populations of Indian meal moth, *Plodia interpunctella* (Lepidoptera: Pyralidae), for example, in laboratory containers appeared to be caused by density-dependent competition for food amongst the larvae (Sait et al. 1994), but field conditions are, of course, likely to be more complex. Though the cinnabar moth, *Tyria jacobaea* (Lepidoptera: Arctiidae), suffers periodic crashes in abundance because of competition for larval food (Van der Meijden et al. 1991), recovery after a crash is still delayed even with food available, presumably because of the activities of natural enemies and reduced food quality. Clearly, competition for food might be something to avoid if possible. Various behavioral mechanisms have evolved that minimize competition, from eating siblings in tropical damselflies (Fincke 1994), to avoiding oviposition on host plants already bearing eggs in butterflies (Schoonhoven et al. 1990), or by selecting different types or size of food when competition becomes intense, as in stoneflies (Malmqvist et al. 1991).

The role of natural enemies in the population regulation of insects is discussed in full in Chapter 5. Classic work by Varley and Gradwell (1971) has shown that as herbivore populations vary with time, so do the abundances of various predators and parasitoids that feed on them (Figure 1.19). *Philonthus decorus* (Coleoptera: Staphylinidae) is a predatory rove beetle that eats the pupae of winter moth, *Operophtera brumata* (Lepidoptera: Geometridae), in the soil, whereas *Cratichneumon culex* (Hymenoptera:
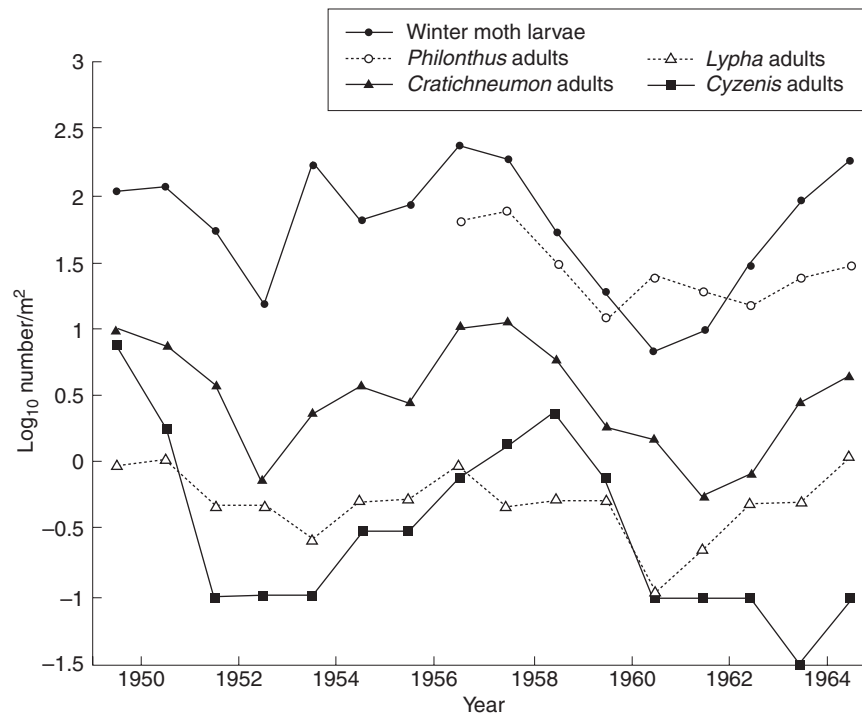

Figure 1.19 Densities of winter moth larva and its natural enemies in Wytham Wood, Oxfordshire. (From Varley & Gradwell 1971.)

Ichneumonidae) is a parasitic wasp, and *Lypha dubia* and *Cyzenis albicans* are both parasitic flies (Diptera: Tachinidae), all of which attack the larval stages whilst feeding in the canopy. Two points are worthy of note. First, the peaks of all the enemies seem to be 1 year (or in the case of *Cyzenis*, 2 years) later than that of the winter moth, illustrating the phenomenon of delayed density dependence described above. Second, it may be tempting to attribute the changes in winter moth abundance to regulation from its enemies. As the moth larvae population increases from year to year, so do the levels of predation and parasitism, thus knocking the herbivore numbers back again. In this instance, however, only pupal predation by *Philonthus* was shown to be density dependent and hence regulatory (Varley & Gradwell 1971). The other enemies, in fact, were merely tracking the variations in the host, with no regulatory impact. These host variations relate to nutrient and defense quality and quantity, and will be discussed in Chapter 3. Variations in predator–prey relationships

may also be detected on a much smaller timescale. Figure 1.20 shows how numbers of the aphid *Metopeurum fuscoviride* (Hemiptera: Aphididae), which feeds on tansy (*Tanacetum vulgare*), vary during one season in association with various natural enemies such as ladybirds, predatory bugs, and hoverflies (Stadler 2004). The increase in predator numbers at the end of July is associated with a sharp decline in aphid numbers, and it is of course tempting to attribute causality – i.e. the enemies are regulating the aphids. However, aphid numbers may decline for various other reasons, such as a decrease in host-plant quality, increased intraspecifc competition, or migration; such interactions therefore need further work to identify the factor or factors responsible for the observations.

Many pathogens are now known to act as regulators of insect populations, with fungi, bacteria, and especially viruses having a great impact on occasion (McVean et al. 2002). Forest insects known to be at least partially regulated by naturally
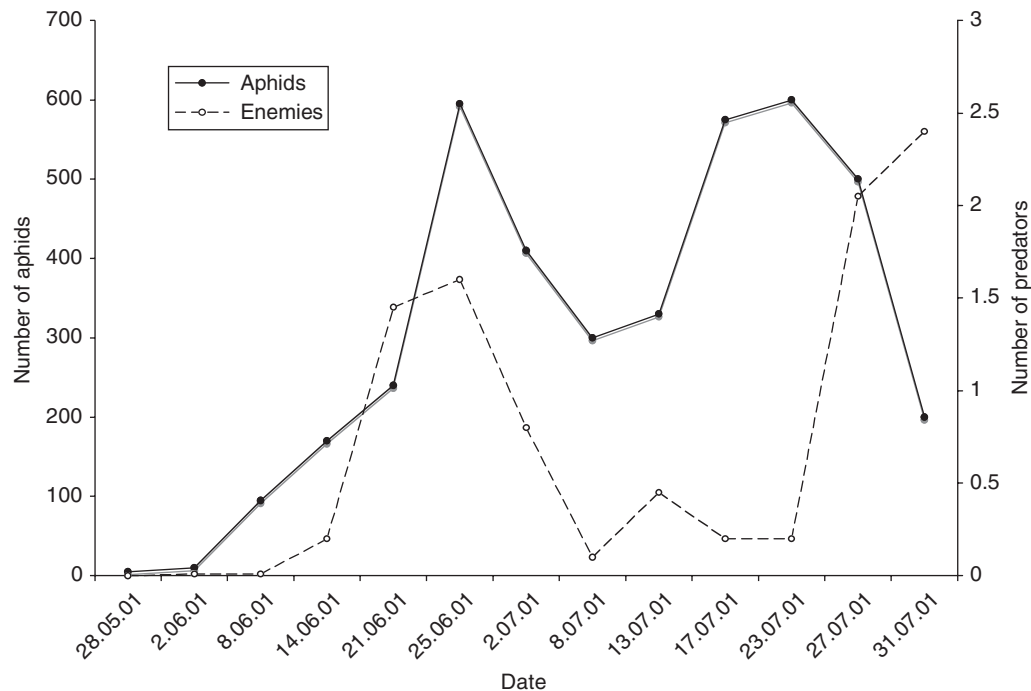

Figure 1.20 Seasonal trends in abundances of the aphid *Metopeurum fuscoviride* and its predators on tansy. (From Stadier 2004.)

occurring viruses include the nun moth *Lymantria monacha* (Lepidoptera: Lymantriidae) (Bakhvalov & Bakhvalova 1990), rhinoceros palm beetle *Oryctes rhinoceros* (Coleoptera: Scarabaeidae) (Hochberg & Waage 1991), and browntail moth *Euproctis chrysorrhoea* (Lepidoptera: Lymantriidae) (Speight et al. 1992). Chapter 12 provides more details.

The host plant may also influence the density of herbivorous insects via a factor or factors that cause feedbacks with time lags of suitable duration (Haukioja 1991). One example involves the autumnal moth, *Epirrita autumnata* (Lepidoptera: Geometridae) in northern Fennoscandia, mentioned earlier. Large-scale defoliation of the host tree, mountain birch, induces changes in the food quality of foliage produced subsequently, such that the reproductive potential of the moth is significantly reduced (see also Chapter 3). So for several years following outbreaks, insect populations are suppressed. However, *Epirrita* larvae also feed on apical buds of birch, which causes a change in plant hormone balance resulting in luxuriant growth of new leaves. This new foliage is particularly suitable for herbivores. Thus the insect population begins to build up again (Haukioja 1991). These complex reactions to herbivore density result in statistically significant cycles of the autumnal moth of 9–10 years' duration. Attempts to attribute *Epirrita* outbreaks to good birch mast years, when tree fruits are especially plentiful, have so far proved more difficult (Klemola et al. 2003).

Controversy has raged for years concerning the relative importance of natural enemies versus resource (e.g. food) limitation in the population ecology of insects and other animals. For now, it is clear that there are no easy answers. The science and practice of biological pest control relies on the ability of predators, parasitoids, and pathogens to regulate pest populations, whereas the ecology of pest outbreaks, and its links to crop husbandry of all types, emphasizes resource limitation as the driving force in insect epidemiology. Figure 1.21 summarizes the potential relationships between various possible mortality factors, and suggests that their relative importances vary as the population of the insect on which they act varies (Berryman 1987). In general terms, the figure suggests that regulation from natural enemies such as predators and, especially, parasitoids might be expected to be effective up to a medium host or prey density, but at high, epidemic levels, regulation via pathogens such as viruses, if present, is more
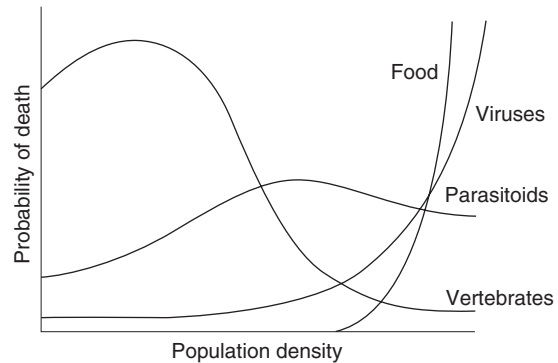
Figure 1.21 Relative importance of various mortality factors on insect populations at different densities. (From Berryman 1987.)

important. Food limitation is often the most important regulatory factor in high-density insect populations. These controversies are of fundamental relevance to insect pest management (see Chapter 10).

1.9.4 Eruptions

Eruptive outbreaks can develop when environmental changes, such as consecutive seasons of favorable weather acting directly on the insect or indirectly via its food supply, permit the rapid growth, dispersal, and/or reproduction of the insect population in question. In essence, regulation at low density is lost because of environmental conditions, and unpredictable outbreaks result. In many cases, this breakdown of natural regulation results from human intervention upsetting the coevolved semistability between insect and habitat, enabling the insect populations to exhibit much higher amplitudes of population oscillations, or indeed to remain at outbreak levels rather than declining again (Moreau et al. 2006).

Locusts are a classic example of this phenomenon. Globally, many species of locust are known to erupt into plagues from time to time, the most common being the desert locust, *Schistocerca gregaria*, migratory locust, *Locusta migratoria*, tree locust, *Anacridium melanorhodon*, Moroccan locust, *Dociostaurus maroccanus*, and Australian plague locust, *Chortoicetes terminifera* (all Orthoptera: Acrididae) (Wright et al. 1988; Showler 1995; Stride et al. 2003; Hunter 2004). Various species of *Schistocerca* are also serious pests

in South America (Hunter & Cosenzo 1990). Many affected countries are some of the poorest in the world and are completely unable to afford control or prevention campaigns (Lecoq 2001). To make matters even worse, one of the major causes of desert locust outbreaks developing these days is armed conflict. Wars and revolutions prevent timely access to locust breeding sites so that the suppression of outbreaks before they occur is prevented (Showler 2003).

Locust plagues (Figure 1.22) have been ravaging crops for many centuries. Swarms of locusts invading southern Europe from Africa were described in Roman times by Pliny the Elder, and countries from Hungary to Spain were particularly badly attacked in the 14th, 16th, and 17th centuries (Camuffo & Enzi 1991). In 1693, for example, a swarm of *L. migratoria* built up on the northwestern shore of the Black Sea and between the rivers Danube and Theiss. Some of the swarm invaded the Tyrol, but most entered Austria via Budapest. Some ended up in Czechoslovakia and Poland, whereas others headed west into Germany. A few individuals actually reached the British Isles (Weidner 1986). Locust eruptions are, of course, still occurring. In the 1980s, for example, devastating plagues occurred in Algeria (Kellou et al. 1990), Argentina (Hunter & Cosenzo 1990), Australia (Bryceson 1989), Peru (Beingolea 1985), Chad (Ackonor & Vajime 1995), China (Kang & Chen 1989; Ma et al. 2005), the Arabian Peninsula (Showler & Potter 1991), and Sudan (Skaf et al. 1990). In the 1990s, successive generations of locusts gave rise to localized eruptions for 18 months as far west as Mauritania in West Africa and as far east as

Figure 1.22 Swarm of immature locusts in Mauritania, West Africa. (Courtesy M. de Montaigne, FAO.)

India (Showler 1995). The damage caused by these eruptions is enormous, as is the cost of control (Showler 2002). During one desert locust plague in Africa, 1.5×10^7L of insecticide were used, at a cost of around US$200 million (Symmons 1992). Not only that, but locust plagues can adversely affect other animal populations. In central Saudi Arabia, many species of birds adapted to feeding on grasses and seeds were recorded inhabiting grassland and savanna areas (Newton & Newton 1997). A plague of desert locusts in spring and summer 1993 combined with poor spring rains to reduce the bird populations to the lowest numbers and species diversity recorded during the 28-month study.

The origins of locust swarms and their subsequent migrations are basically controlled by climatic factors (Camuffo & Enzi 1991; see also Chapter 2). Locust eggs may stay dormant in soil for months, waiting for random events to bring rain to their area. Depending on the type of soil, eggs survive best during rain (Showler 1995), and rain also promotes the growth of vegetation on which the hatching nymphs, or hoppers, can feed (Hunter 1989; Phelps & Gregg 1991; Ji et al. 2006). The El Niño phenomenon is a southward-flowing ocean current off the coasts of Peru and Ecuador. Apparently cyclical changes in the pattern of its flow are the cause of environmental and climatic disturbances that cause widespread damage every few years. In Peru in 1983, El Niño caused up to 3000 mm of rain in an otherwise arid region, resulting in enormous locust swarms (Beingolea 1985). In fact, the detection by satellite imagery of new areas of green vegetation caused by rain is one of the most important tools in international locust plague-monitoring programs (Bryceson 1990; Despland et al. 2004). Once the nymphs have depleted local resources, the migratory phase of a locust plague ensues, whose scale and direction is mainly dependent on winds (Symmons 1986; Camuffo & Enzi 1991). Under the right weather conditions, plagues can last for months or even years. Eventual declines occur because of extremely dry conditions (Wright et al. 1988) or drops in temperature (Camuffo & Enzi 1991). It can be seen, therefore, that population eruptions as typified by locust plagues are rarely if ever under tight regulation by density-dependent factors. Rather, density-independent factors such as climate are the most influential (see also Chapter 2).

Further information, updates, and international status of locust eruptions is provided by the Food and

Agriculture Organization (FAO) of the United Nations via its website.

1.10 INSECTS AND HUMANS

So far, we have briefly considered the success of insects as a function of their enormous species richness and their huge numbers of individuals. Finally, we need to introduce the all-important associations that humans have with insects, to see how the most successful group of animals interact, for better or worse, with ourselves. In this way, we move into the realm of applied ecology.

1.10.1 Pests

The term ''pest'' is entirely anthropocentric and subjective. It tries to attach a label to an organism that, via its ecological activities, causes some sort of detriment to humans, their crops, or livestock. Ecologically, an insect pest is merely a competitor with humans for another limited resource, such as a crop. A crop, after all, is merely a rather special type of host-plant community from the viewpoint of a herbivorous insect. It is only because humans planted the crop for their own uses that this herbivore then assumes pest status (see Plates 1.1 and 1.2, facing p. 000).

Insect pests first appeared in written records thousands of years ago, with lice, mosquitos, and other flies for example achieving mentions in Assyrian texts and the Christian Old Testament (Levinson & Levinson 1990). Plagues of locusts appear in the Book of Exodus, and the early Egyptians of the Third Dynasty (over 3500 years ago) had to fight to keep their mummified ancestors free of insect infestations. In modern times, crop losses on a global scale are rather difficult to assess, but clearly insects can have an enormous detrimental impact on humans and their activities. Crop losses averaged from many published studies reach almost 45% of total yield annually, a colossal loss in food and other products, with potential yield losses to pests (weeds and pathogens as well as insects) ranging from around 50% for wheat to a colossal 80% in cotton (Oerke 2006).

Let us take cotton as an example. This is one of the world's most important cash crops, with the capacity to earn international money for many countries, both developed and developing (Figure 1.23). It is grown on a colossal scale; the world total cotton lint production for the 2005 period exceeded 23×10^6 tonnes (FAO 2007). Despite long and bitter experiences of the development of high levels of resistance in insect pests to insecticides over the years, cotton growers still have to rely predominantly on this method of pest management (see Chapter 12). In the USA in the 1990s, for example, despite an average of six treatments with insecticide per growing season, nearly 7% of the entire crop was lost to insect damage at one stage of growth or another (Luttrell 1994). Australia seems even worse. Here, an average of 10 applications of insecticide may be carried out per year; the average insecticide application per year in the 2002–3 and 2003–4 seasons, for example, for conventional cotton was 135 kg insecticide per hectare (Knox et al. 2006). The true benefits of new technologies such as transgenic crops, genetically engineered to express toxins lethal to feeding insects, can be appreciated. For cotton, crucial benefits of genetically modified varieties are a 70% reduction in insecticide applications in *Bt* cotton fields in India, resulting in a saving of up to US$30 per hectare in insecticide costs, and an 80–87% increase in harvested cotton yield (Christou et al. 2006).

The previous examples involved developed countries. Even more significant perhaps is the fact that developing countries may not have the infrastructure, knowledge, or technology to manage their pests effectively or safely. In Rwanda, as just one example, a country noted for its extreme socioeconomic and political difficulties, insect pests of various types attack common beans, a vital crop for subsistence farmers.

AQ2

AQ3

Figure 1.23 Cotton crop. (Courtesy of C. Hauxwell.)

Trutmann and Graf (1993) reported losses of between 158 and 233 kg/ha, which is equivalent to a national loss to Rwanda of dry beans worth somewhere in the region of an amazing US$32.7 million (£22 million) per year.

In fact, in the early 21st century, we are no closer to removing these threats. Instead, we are constantly attempting to develop new and often highly sophisticated techniques to combat insect pests – based these days on a sound knowledge of the target insect's ecology, how it interacts with its environment, and the influence of other organisms, natural enemies in particular. This is the subject of Chapter 12.

Insect pests also interact directly with humans via stings, rashes, and more serious medical conditions. The tiny hairs on the larvae, pupae, and egg masses of the browntail moth, *Euproctis chrysorrhoea* (Lepidoptera: Lymantriidae), cause very serious reactions in people in the UK, from serious rashes (urticaria; see Plate 1.3, facing p. 000) (Doutre 2006) to temporary blindness and even death via anaphylactic shock (Sterling & Speight 1989). This insect was also an extremely serious problem in the USA, though in recent years it has rather mysteriously reduced it's originally huge range to a mere handful of sites where it still occurs (Elkinton et al. 2006). The pine processionary caterpillar, *Thaumetopoea pityocampa* (Lepidoptera: Lymantriidae), causes similar dermatitic and conjunctivitic reactions in continental Europe (Lamy 1990). There was even a recent record of dogs in the eastern Mediterranean exhibiting severe tongue necrosis after eating processionary caterpillars (Bruchim et al. 2005), obviously a lapse in the evolved defense system of the moth. Contact with *Lonomia achelous* (Lepidoptera: Saturniidae) larvae is known to bring about hemorrhagic diathesis, clinical bleeding with reduced blood clotting, which, on rare occasions, can prove fatal (Arocha-Pinango et al. 1992). Bee and wasp stings are, of course, a regular occurrence, but with the spread of Africanized bees to warmer parts of the USA, for example, worries are increasing about the potential medical effects of multiple stings (Schumacher & Egen 1995).

1.10.2 Vectors

A particular type of insect pest is one that is able to carry diseases from one mammalian host to another, or from one plant to another. These hosts may both be human, or one may be another mammal such as another primate or a rodent. They may be wild plants that provide reservoirs of diseases for infection of crops, or they may both be crops. Both local and global epidemics are vectored in this way by insects; the rising importance of malaria, sleeping sickness, plague, encephalitis, and so on illustrate the vital need to explore the intimate ecology of insect–disease associations, in attempts to reduce the colossal and direct impact on human lives. The World Health Organization (WHO) estimates that malaria causes more than 300 million acute illnesses globally every year, of which at least 1 million die of the disease. Over 80% or so of cases occur in sub-Saharan Africa (Torre et al. 1997). Such problems may appear to those living in developed nations as irrelevant or remote. However, human suffering on such a large scale must impinge on all our lives. A steadily increasing number of Europeans, for instance, are treated in hospital after returning from trips to tropical countries where the disease is rife (see Chapter 11).

Though the Diptera (including mosquitoes, blackfly, and tsetse flies) dominate in terms of the number of human and livestock diseases with which they are associated, other orders such as the Hemiptera (true bugs) and the Siphonaptera (fleas) also have an enormous impact. Bubonic plague, the ''Black Death'', which is carried by fleas, is thought to have killed around a third of the entire population of Britain in a pandemic that first appeared in England in 1348 (Kettle 1995).

Insects also vector numerous pathogenic organisms that cause extremely serious diseases in annual and perennial plant species. The list of major problems includes Dutch elm disease, barley yellows virus, and potato leaf curl, and insects range from Hemiptera (such as aphids and hoppers) to Coleoptera (beetles). The details of the ecology of insect–pathogen–host associations are considered in Chapter 11.

1.10.3 Beneficials

Insects that in some way damage ourselves or our livelihoods tend to be uppermost in people's thoughts, and though we are also familiar with bees and their activities, a very large number of insect species that are important to us are largely ignored. Undoubtedly, insects have a variety of pivotal roles to play in human livelihoods and poverty alleviation. Chapter 12

describes the vital importance of predatory and para-sitic insects in the ever-growing field of biological pest control, and the revenue from diverse systems such as pollination of crops and the silk industry is staggering. In Italy, for instance, the value of crop pollination by insects is estimated at around 2000 billion lire (US $1.2 billion); the profit from honey, wax, and other beekeeping products is about 30 billion lire ($1.8 million) (Longo 1994). In the USA in recent years, two parasitic mites have caused drastic declines in feral honeybee populations, and crop losses associated with a consequent reduction in pollination run into billions of dollars. Silk has been produced from silk-worms (Lepidoptera: Saturnidae) commercially for many hundreds of years, and is now estimated to be worth US$1200 million globally.

On a much broader scale, the roles played by a myriad of insects in food webs are of supreme import-ance to the functioning of a very large number of terrestrial and non-marine aquatic ecosystems. The lives of many bird species, such as blue and great tits in an English oak wood, for example, are utterly dependent on a plentiful supply of lepidopteran larvae when the chicks are in the nest, and partridges in farmland have a similar reliance on insect food for their young.

1.10.4   Esthetics

Insects have been prized for decoration and ritual for thousands of years. Scarab beetles (Coleoptera: Scarabaeidae) were hugely significant in Egypt during the time of the Pharoahs, when their likenesses were used as seals, trinkets, and charms. This widespread decorative use was associated with a much more ser-ious belief that the scarab beetle came into being spontaneously from balls of dung. The Egyptians asso-ciated this with their religious ideology of self-creation and resurrection, and the scarab was worshipped under the name ''Khepri''. Insects, in this case cicadas, were again associated with reincarnation by both the ancient Chinese and the Romans (Kysela 2002) and they were used as jewelry in Europe for many centuries after the Romans.

Most humans, if they have any interest at all in wildlife, will tend to think about higher vertebrates such as birds and especially mammals when it comes to considering the esthetics of the animals around them. The majority of conservation systems in the world are still heavily biased towards this minor sub-phylum, but the perceived value of insects for amenity and as natural and important components of habitats is increasing. Conservation projects are now directed on occasion at targets such as butterflies or dragon-flies, which have really no economic value; they are encouraged for their own sake. The ecology of insect conservation and augmentation is considered further in Chapter 8. Insects can also take part in the educa-tional process, being considered particularly appro-priate to interest and excite pre-college students (Matthews et al. 1997). The handling, rearing, and simple admiration of moths and butterflies, beetles, stick insects and mantids, cockroaches, and locusts can play a very significant role within an educational framework, even beginning at primary school level (see Plates 1.4 and 1.5, facing p. 000).

1.10.5   Food

To a surprisingly large number of people in the world, insects provide a vital source of protein and other nutrients. Insects are undoubtedly very useful nutritional sources (see Plate 1.6, between pp. 000 and 000). Costa-Neto (2003) reports that over 1500 species of edible insects have been recorded from nearly 3000 ethnic groups from more than 120 countries. More than 50 species of edible insects from 11 orders are documented from just one country, Sabah (east Malaysia; Chung et al. 2002). According to Costa-Neto, the most important groups of insects eaten are beetles, bees and wasps, grasshoppers, and moths. Table 1.6 provides some details of the nutri-tional value of a variety of insects used by rural people in the state of Oaxaca in Mexico (Ramos-Elorduy et al. 1997). In some regions, insects are eaten every day as part of the staple diet. They may be roasted, fried, or stewed, usually as larvae. Ants, bees, and wasps are apparently the most popular, as the table suggests, though butterfly caterpillars (*Phasus triangularis*) are also full of fat and high in calories.

Chinese people in Yunnan eat the larvae and pupae of wasps, which are rich in protein and amino acids (Feng et al. 2001). Deep-fried grasshoppers can be bought on street corners in Bangkok, Thailand, and the Tukanoan Indians of the northwest Amazon eat over 20 species of insect, the most important being beetle larvae, ants, termites, and caterpillars (Dufour 1987). Insects provide up to 12% of the crude protein

Table 1.6 Nutritional value of insects used as food in rural Mexican communities. (From Ramos-Elorduy et al. 1997.)

Dietary component	Content or range (%)	Insect with highest dietary content
Dry protein	15–81	Wasp larvae
Fat content	4.2–77.2	Butterfly larvae
Carbohydrate	77.70	Ants
Essential amino acids	46–96*	–
Protein digestibility	76–98	–

* Percentage of total requirements.

derived from animal foods in men's diets, and 26% in those of women. In Irian Jaya (Indonesia), the Ekagi people regularly eat large species of cicada (Hemiptera: Cicadidae) (Duffels & van Mastrigt 1991). The mopane worm, the larva of the mopane emperor moth *Imbrasia belina* (Lepidoptera: Saturniidae), in southern Africa has become a cash "crop", with an annual production of nearly 2000 tonnes. Caterpillars contain high levels of crude protein, more than 50% according to some reports, as well as high concentrations of calcium and phosphorus (Madibela et al. 2007).

Ironically, it is possible that conservation projects attempting to boost populations of large grazing mammals in game reserves in the region may deprive locals of this food source in that, in Botswana at least, local absences of mopane worm may be caused by extensive herbivory on their host plant (Styles & Skinner 1996). Undoubtedly, the "mini-livestock" could be harvested more intensively but sustainably (van Huis 2005) with considerable nutritional and economic consequences for regions such as sub-Saharan Africa.

1.11 CONCLUSION

As we noted at the beginning, all of the concepts introduced in this chapter will appear again later in the book, where they are considered in detail. Although each chapter is necessarily separate, it is important to try to consider insect ecology as a series of interlocking systems. For instance, to fully understand how an insect population can be of great economic significance in a crop, we need to look at its relationships with its host plant, its enemies, its competitors, and with the climatic conditions in its environment, although these aspects are presented in separate chapters.

AUTHOR QUERY

AQ1: Fig. 1.22 kindly supply the new figure.
AQ2: ref. missing.
AQ3: ref. missing.