Chapter 1

The diversity of life

1.1 A vast array of life forms

Every day, each of us encounters an incredible diversity of life forms (Fig. 1.1). Our stomachs contain bacteria, we catch colds caused by viruses and we wear leather shoes made from the skin of a mammal. We eat mushrooms, fish and vegetables sitting at a table made out of a tree, which we cover with a cloth made from the seeds of a cotton plant. We keep dogs, lizards and stick insects as pets, grow flowers in our gardens and use drugs that were first isolated from plants or fungi. Our bread is made from the seeds of grass plants, and we put yeast cells in it to make it rise. We use the juices of fruits so that our soaps and shampoos smell pleasant. The list of

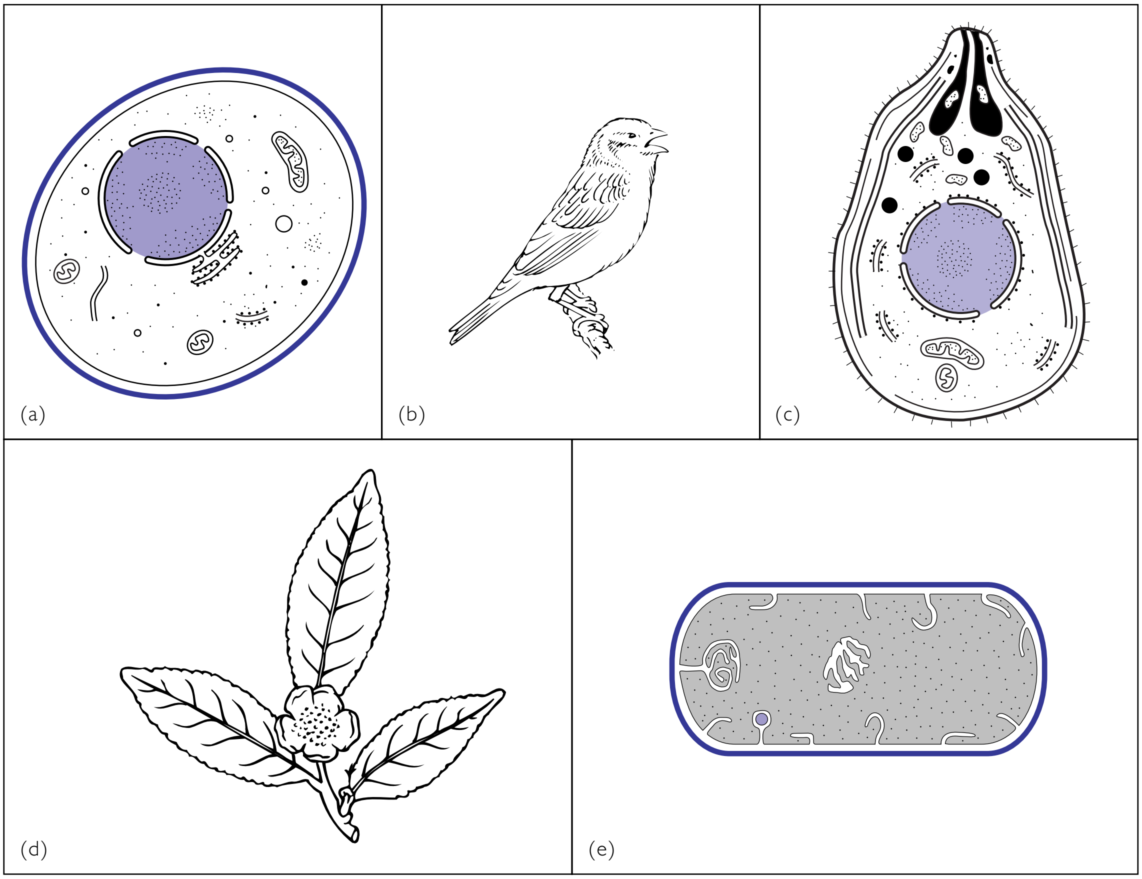

Fig. 1.1 People encounter and use organisms from all the major groups. (a) The fungus *Saccharomyces*, which is used as yeast in brewing and baking. (b) The canary (*Serinus canaria*), which is kept as a pet. (c) The parasite *Plasmodium falciparum*, which causes malaria. (d) The leaves of the tea plant (*Camellia sinensis*), which are infused to make a drink. (e) The bacterium *Lactobacterium*, which is used in the culture of yoghurts.

ways in which we meet organisms, or materials made from them, is seemingly endless.

One reason that people come across organisms in such a variety of ways is that the world has such a vast array of different life forms. Currently, the best estimates of the number of different kinds of organisms in the world vary from about 2 million upwards to 50 or 100 million, and these estimates do not even include bacteria or viruses. Ecology is concerned with every one of these types of organisms, and it is also concerned with the physical environment in which they live, so that an ecologist needs to know not only about biology but also about chemistry, physics and geography. The task of the ecologist is made more difficult by the fact that we do not even know for certain how many different types of living organism have so far been discovered and named, because there is no central list. The only thing that can be said with certainty is that the number of known kinds of organism is well in excess of a million.

It may seem remarkable that humans know so little about the ecology of their planet, especially since it must be one of the oldest subjects of human investigation—men and women must have been trying to understand the life around them ever since they first evolved conscious thought. Moreover, they have always practised applied ecology, in the form of hunting, agriculture and other ways of obtaining food.

An apparent lack of knowledge can be frustrating for the ecologist, who sees scientific colleagues in other fields (such as medicine, physics or chemistry) developing intricate theories and experiments that lead to cures for diseases, exploration into space, or useful inventions such as versatile plastics or labour-saving machines. Nevertheless, the potential ecologist should not despair, because inquisitive ecologists have one major advantage over these other scientists. The fact that ecological scientists have so far discovered so little of what there is to know means that every interested ecologist can add to the sum of human understanding and knowledge and, as often as not, he or she can do so without spending vast sums of money.

More significantly, ecologists know that their science is ultimately just as important as anything else any human has ever done. As the number of people in the world continues to rise, and as increasing numbers of people come to expect the privileged lifestyle enjoyed in places like Western Europe, Japan and North America, the pressures on our planet threaten to become intolerable. This is not simply a matter of the threat of extinction for tigers and giant pandas (which humans happen to find attractive), it is the possibility of serious human and environmental disasters occurring worldwide (Fig. 1.2).

If the world's human population does not properly understand the ecological system in which it lives, it will never really understand how to solve any of its problems. This does not imply that the average ecologist is trying to feed millions of starving mouths, nor does it mean that this book is in any way intended to be political, because it is not. This is a book that will introduce the reader to the fascinating array of different questions that ecologists study, and which make the life of the scientific ecologist exciting, fun, frustrating and fulfilling.

1.2 What is ecology?

If ecology is about every kind of living organism, in every place on the planet and at every time, then it is clearly an extremely large topic. Ecologists could not hope to make any progress in understanding their subject without taking the time to define some sensible limits to what ecology is. Broadly speaking, scientific ecologists tend to have two definitions of their subject, each of which captures something different about what we mean by ecology. The first definition is that ecology is concerned with the interaction between organisms and their environment. The second stresses that ecologists are trying to understand the distribution and abundance of organisms. Each of these definitions has strengths and weaknesses, and it is necessary to understand the two definitions in more detail before progressing any further in trying to understand the subject.

1.2.1 Interacting with the environment

One of the commonest descriptions of ecology is that it is the study of the interactions between organisms and their environments. The beauty of this definition is that it starts with the organism. Since all ecology is about organisms, and since evolution acts through the survival and death of particular individuals, ecologists should never forget that their theories and experiments must be explained with reference to **individual** plants, animals, fungi or micro-organisms. The components of

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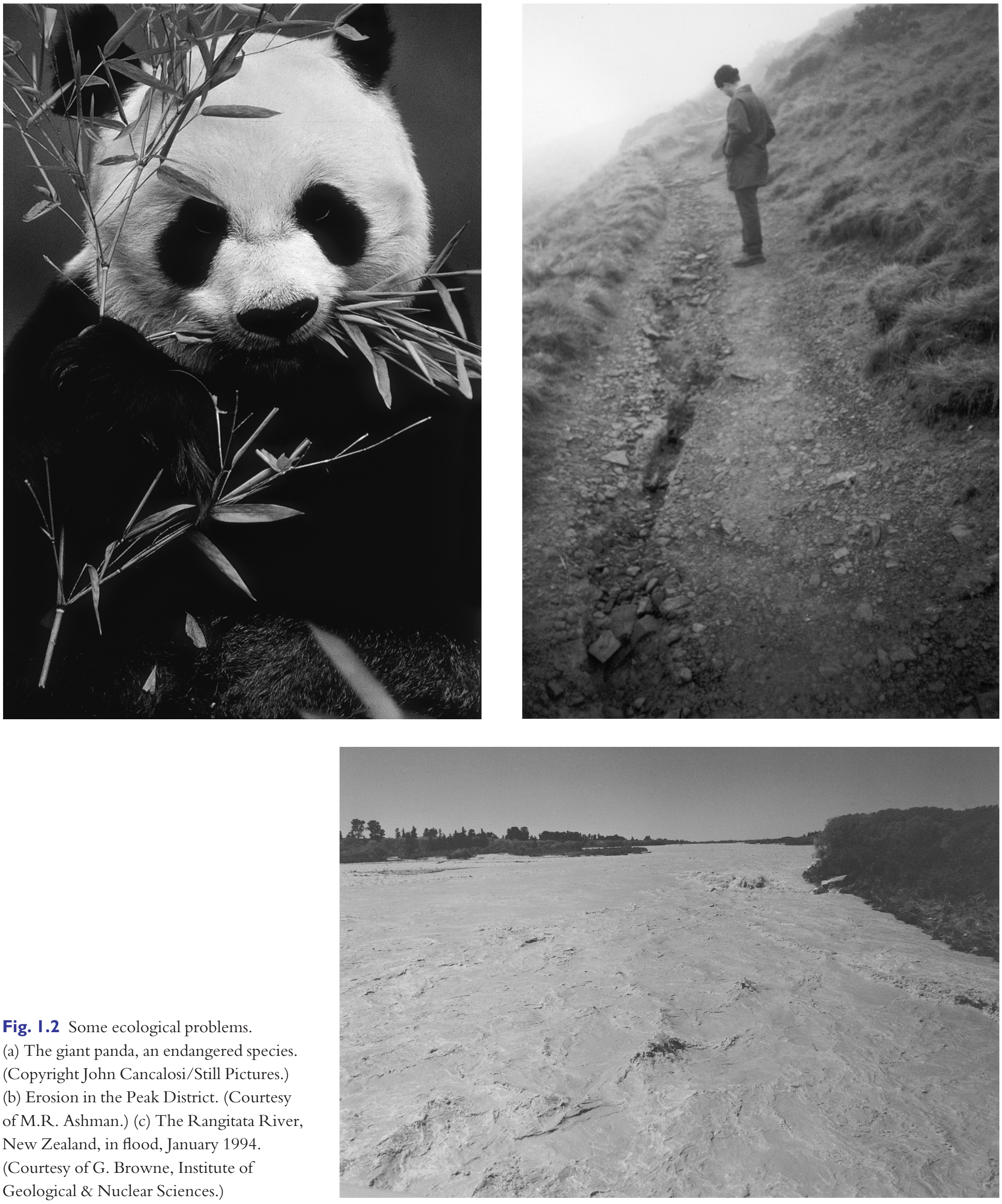

(b)

(c)

Fig. 1.2 Some ecological problems. (a) The giant panda, an endangered species. (Copyright John Cancalosi/Still Pictures.) (b) Erosion in the Peak District. (Courtesy of M.R. Ashman.) (c) The Rangitata River, New Zealand, in flood, January 1994. (Courtesy of G. Browne, Institute of Geological & Nuclear Sciences.)

an organism's environment fall into two categories—the physical and the biological environments. The physical environment includes rocks, soils, rainwater, sunshine, minerals and pollution, while the biological environment includes an organism's food, its parasites, its mate, its offspring and its competitors—all of the other organisms it ever encounters, whether they are of its own species or not.

Ecologists call the living, biological element of the environment the **biotic** environment and the physical element the **abiotic** environment.

1.2.1.1 A problem

The drawback of this first definition of ecology is that it is very broad. In effect, every aspect of every organism involves an interaction with something. Walking, for example, is an interaction with the physical environment, since it involves an animal creating friction with the ground. In other words, if ecologists were to take this definition too literally, they would end up studying every aspect of biology. That would be fascinating, and indeed ecologists should be careful never to ignore any aspect of biology—we can never know when something apparently irrelevant will turn out to shed light on an ecological question. However, ecologists generally find it more useful to restrict their study to interactions that affect the distribution and abundance of organisms.

1.2.2 Distribution and abundance

The second popular definition of ecology is much more limited. By this definition, ecology is the study of the distribution and abundance of organisms. The kind of question that an ecologist might ask about distribution is: Why do we see penguins in the Antarctic but not in the Arctic? Why are bromeliad plants found almost exclusively in South America, while plants in the buttercup family can be found almost throughout the world? Questions of abundance might be something like: Why are there twice as many doves in my garden as there are robins? Why are there fewer pandas in China than there used to be?

The advantage of this second definition of ecology is that it is focused—it allows ecologists to ask specific questions, which is what science is all about. The disadvantage with this definition is that it deals with whole groups of organisms (e.g. all the pandas in China, all the buttercups in the world), not with individual organisms. This is important because of the way the biological world is shaped by natural selection, which is the process by which evolution has created the current ecology of the world, and by which that ecology continues to change as organisms experience selection pressure in each generation. To gain a full understanding of any aspect of ecology, investigators must be certain they understand this process.

1.2.3 Linking the two definitions

In order to tie together the two different definitions of ecology, is it necessary to investigate different **levels of biological diversity**. This allows ecologists to perceive the ways in which individual organisms affect the groups of which they are part, and helps to draw links between the definition of ecology that is based on individuals and the definition that is concerned with whole groups. This concept will be studied in Section 1.3.

The final link joining the two different definitions of ecology will come from an understanding of **evolution by natural selection**, which is the process by which the births, deaths and reproduction of individual organisms combine to govern the composition of a population. This process will be discussed in Section 1.4.

1.3 Levels of diversity

Evolution has created an incredible diversity of form and function in the natural world. There are enormous organisms such as blue whales (*Balaenoptera musculus*) and giant redwood trees (*Sequoia sempervirens*) and also tiny life forms such as viruses. Some organisms, like green plants, make their own food by using the sun's energy to break down gases in the air, while others, such as fungi, digest parts of other organisms. There is life at the bottom of the ocean and at the top of the highest mountains. In fact, the Earth's organisms are so variable that a human lifetime is far too short to appreciate them all fully. A word has been coined that aims to describe this amazing variation—the word is **biodiversity**. But it says much more than a simple statement that there are millions of different kinds of organisms, because biological diversity exists at many different levels.

Perhaps the easiest level to understand is the diversity of **species** on the planet. Most people have some idea of what is meant by the word 'species'. It is normally defined as a set of organisms that are genetically very similiar, and can thus interbreed with one another to produce fertile offspring. This definition works well for most animals and plants. There is a species of badger in Europe and Asia (*Meles meles*) and a related species, also

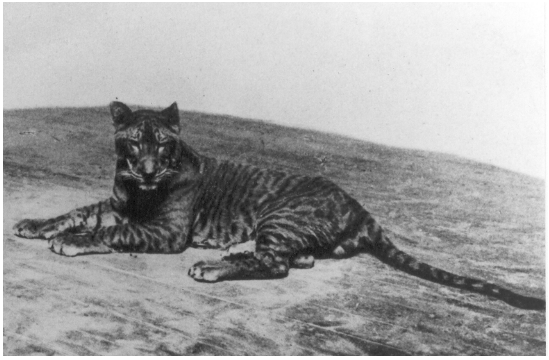

Fig. 1.3 Hybrids like the liger, a cross between a lion and a tiger, are sterile. (Copyright the Zoological Society London.)

known as the badger (*Taxidea taxus*), in North America. Any female Eurasian badger can interbreed with any male Eurasian badger but not with a male American badger. Likewise, any American badger could in theory breed with any other American badger of the opposite sex but not with a Eurasian badger.

Sometimes, in unusual circumstances, two different species will interbreed, but they cannot normally produce fertile young. Horses (*Equus caballus*), for example, will mate with donkeys (*Equus africanus*) to produce infertile mules. Lions (*Panthera leo*) will breed with tigers (*Panthera tigris*) if they are caged together in zoos or circuses; the offspring, known as tigons or ligers (depending on which species is the mother), are infertile (Fig. 1.3).

In using such a definition, it is essential to recognize that two kinds of organisms may never interbreed, simply because, living in different places, they never have the opportunity. If they did so, however, they might be able to produce fertile young. For example, polar bears (*Ursus maritimus*) live only in the Arctic, and grizzly or brown bears (*Ursus arctos*) live further south in Europe, North America and Asia, so that the two species are separated geographically and rarely have the opportunity to come into contact in the wild. However, when they are brought together in captivity, they can interbreed to produce offspring that are fertile and can themselves go on to produce young of their own. Thus, it appears that by the strict definition of a species, the polar bear and the brown bear may be the same species, but, in fact, they are still classified separately because they live very obviously different lives, and because they never interbreed in the wild.

Human activity may change the degree to which populations have the opportunity to interbreed. For example, the introduction of the ruddy duck (*Oxyura jamaicensis*) into Europe has allowed it to interbreed with the white-headed duck (*O. leucocephala*), a native of Spain and other parts of the Mediterranean. Before human intervention, the ruddy duck was confined to the Americas, and there was no possibility of hybridization occurring. In other areas, as habitats are destroyed and fragmented, organisms may become separated where they would formerly have formed part of the same population.

In reality, as with most definitions in the biological sciences, there are many exceptions to the idealized definition of a species; for example, it is more difficult to define some plant species. In some kinds of plant, for example, each individual can fertilize only itself or a genetically identical individual, so that each genetic type could technically be thought of as a separate species. But for most animals and many plants, the normal definition of a species is a good one, and works well in practice for most ecologists.

The definition works less well for some other kinds of organisms. Bacteria, for example, reproduce in very different ways from animals and plants, with the result that the species concept is less clearly applicable. Nevertheless, such organisms can be roughly classified and, as a framework, the idea of a species tends to be suitable for most things that most ecologists want to think about most of the time.

Each species may be divided into populations. A **population** is a group of individual organisms of the same species living together in the same place and usually at the same time. Different populations of the same species may show variation—the African elephants (*Loxodonta africana*) that live on the plains of East Africa are larger than the forest-dwelling elephants of West Africa, although they belong to the same species and can interbreed. Populations are different because they have a different genetic make-up, so variation at the level of the **gene** is very important to the ecologist.

This brings home an important point about evolution. Although natural selection acts through the life, death and reproduction of **individual organisms**, it is **populations** of organisms that evolve. It is a general feature of all West African forest elephants that they are small—it is a **population** characteristic. However, they are like that because natural selection favoured smaller

individuals in the past, and allowed them to produce more offspring, while larger individuals fared less well. All kinds of biologist, including ecologists, must always remember that natural selection is the major reason why an organism has its particular anatomy, physiology and behaviour. So ecologists must always be careful not to postulate theories about populations, or whole species, that do not take account of individual organisms.

Populations of different species in the same place form **communities**. Thus, all the organisms living together in the Serengeti National Park in Tanzania might form a community. Another community may be all the organisms living in a pond in a garden in Tokyo. An **ecosystem** consists of this biological community and the physical, non-living, or abiotic, environment—the rocks, soils, water and climate.

In a sense, communities and ecosystems are human concepts that we have invented to make our scientific lives easier. In general, we define them at a scale that we happen to find convenient—the scale of a garden pond or a national park, for example. Organisms, of course, live their lives at different scales—to a lion, the Serengeti National Park may seem like a single habitat, but to a grass plant it is a mass of slightly different kinds of soils, some of which are suitable to grow in, while others are not.

In fact, ecologists frequently also define populations at a scale that suits their own purposes. A population may simply be defined as 'all the yeast cells in an uncooked loaf of bread', 'all the squirrels in a single forest', or 'all the redwood trees in California'. Because of this, ecologists tend to use the word population rather loosely, so when they are talking about the distribution and abundance of populations, they might sometimes find it convenient to define an entire species as a population. For example, if people are worried that some kind of organism is in danger of becoming extinct, they may study the distribution and abundance of the whole species.

1.4 Evolution by natural selection

Because there are so many different kinds of organisms and because they do so many different things, it would be easy to be daunted by the complexity of ecology. Indeed, as professional ecologists progress through their careers, they discover that there are many complex aspects of the biological world that they cannot yet even begin to explain. However, ecologists have a single, beautifully simple reference point to which they can always return. Ever since life first evolved, more than 3000 million years ago, the living world has been shaped by the process of natural selection. Charles Darwin (1859) described the process in the verbose language of the nineteenth century but his ideas were very simple in essence.

All organisms need resources—animals need food and shelter, green plants need water and sunlight, and so on. Sometimes, there are not sufficient resources for all the organisms in a locality to obtain enough to survive, so some of the organisms die without ever reproducing. Alternatively, they may not die but may be sufficiently impoverished that they produce a smaller number of offspring than others. **Thus, individuals do not all make the same contribution to the next generation**.

The first important step in Darwin's argument is the observation that the organisms that survive and leave most offspring will be the ones that happen, by chance, to be best suited to the particular environment in which they find themselves. For example, if someone were to take some tawny owls (*Strix aluco*) and put them in the snow-covered habitats of the far north of Europe, they would be unlikely to produce as many offspring as the native snowy owls (*Nyctea scandiaca*), for many reasons. One of these reasons is that snowy owls are better camouflaged in the ice and snow and are thus better able to catch prey. The ill-suited tawny owls, which would be easily seen by the rodents they were chasing, would either die of starvation, or at the very least would fail to provide adequately for their chicks.

The next crucial step in Darwin's argument relies on offspring being similar to their parents—red-flowered pea plants (*Pisum sativum*) often (but not always) produce seeds that grow into red-flowered plants, while plants with white flowers are more likely to produce white-flowered offspring. Darwin had to guess at the mechanism for this inheritance, but it is now known that offspring are like their parents because of the genetic code stored in DNA, and that natural selection acts on the genes that make up this code. Some pea plants contain genes for red flowers and others contain genes for white flowers. These genes are passed into the seeds, so offspring inherit some of their parents' genes and, in consequence, share some of their parents' characteristics (Fig. 1.4).

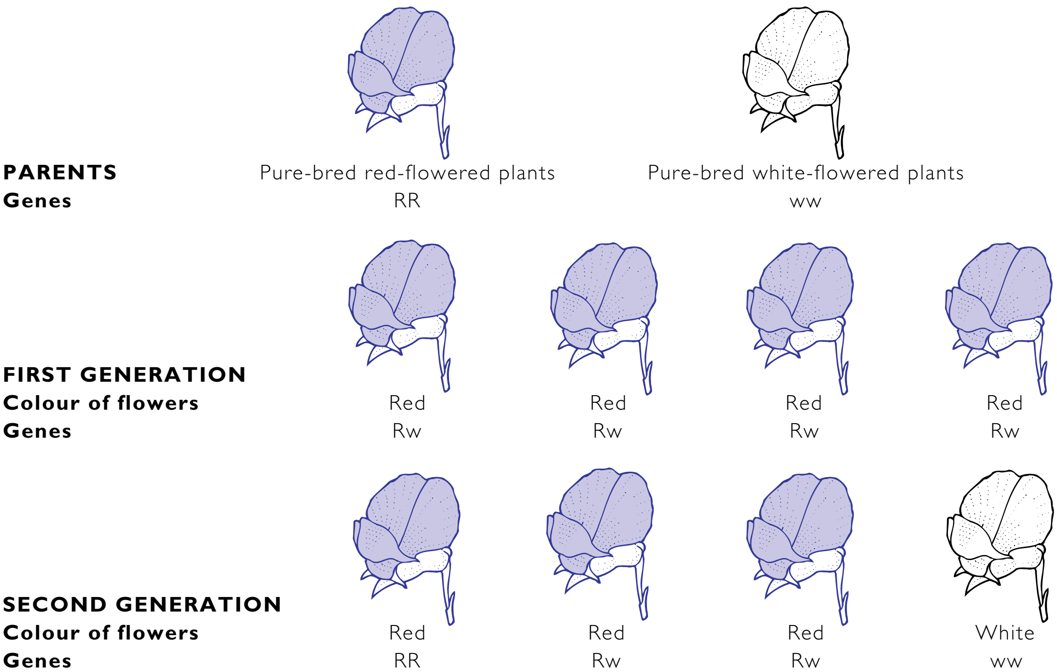

Fig. 1.4 Gregor Mendel (1822–1884) discovered the basis of modern genetics by experimenting with cross-fertilizing pea plants.

Thus, evolution by natural selection can be understood in three points:

1 Some organisms leave more offspring than others.

2 The organisms that leave most offspring are those that are best suited to their environment—they have the highest 'fitness'.

3 The offspring inherit genes from their parents, which means that they also inherit at least some of the characteristics that made their parents well-fitted to the environment, so they too tend to be well-suited.

It is important to note that the word 'fitness' in this context is concerned with 'fitting the environment', not with being 'fit' in the sense of being able to exercise for a long time without getting tired.

Obviously, the environment is not constant—it is always changing in some way. The biological environment could change when a new disease spreads into an area, or if all the local predators became extinct, and the physical environment might change because of, say, global warming. When this happens, evolution will tend to favour those individuals best suited to the new environment, which will probably not be the same ones that would have fared well in the old environment. Thus, natural selection can 'change its mind' about which individuals to favour—there is no single, idealized form that each species is evolving towards. For example, until 65 million years ago, natural selection favoured the set of characters enjoyed by the dinosaurs. But then the environment changed and other animals were favoured at the expense of the dinosaurs. Perhaps a large meteorite struck the Earth and caused a huge cloud of dust and debris that blocked out much of the sun's energy. The colder conditions that would have followed would not have been suitable for the huge lizards, but allowed other, quite different, animals to dominate.

1.4.1 Cadmium tolerance in plants

As an example of how natural selection works, we can look at the many kinds of plants that have evolved tolerance to high levels of cadmium, which is normally extremely toxic both to plants and to animals, including humans. Cadmium is a metal used in a variety of industrial processes and is found at much higher concentrations in the soils of areas that have suffered industrial pollution than in soils of unpolluted areas. Some individuals of some kinds of plants happen to be more tolerant of cadmium poisoning than others, because they have genes that give them a slightly different physiological make-up. In areas of high cadmium pollution, these tolerant plants survive while others simply perish, so that in the next generation, many of the offspring inherit the genes for tolerance and can live in the polluted environment.

However, not all kinds of plants have the same genetic variation and they do not all deal with cadmium in the same way. Some plants, like the soybean (*Glycine max*) and tomato (*Lycopersicum esculentum*), manage to move all the cadmium into a small number of cells so that it does not interfere with the working of the majority of the other cells, while other plants, like rice (*Oryza sativum*) or the water hyacinth (*Eichhornia crassipes*), produce proteins that bind to the cadmium and neutralize its effects (Prasad 1995).

It is important to understand that the particular mechanism that operates in a particular kind of plant depends entirely on which genes the plant has. It so happens that some of the rice plants in polluted areas happened to have genes that produced the binding proteins, but they could equally well have had genes for another kind of mechanism. Equally, it could have been the case that they had no genetic variants capable of dealing with high cadmium levels, in which case that particular kind of plant would not have been able to adapt to the conditions and would have become extinct in areas of cadmium pollution. Natural selection can only operate on the random genetic variation that happens to exist, which is created by mutations in the genetic material of individual organisms.

1.4.2 Evolution is concerned with individuals

An important feature of evolution that must be kept in mind is that it affects the survival and reproduction of individual organisms. Section 1.3 described some of the ways in which those effects are manifest in the composition of populations.

However, it is crucial to avoid the perception that features of organisms can be interpreted in the context of the 'good of the population' or the 'good of the species'. If an organism appears to be generous towards others, it is not concerned with the good of the species. It can almost certainly be shown to be acting in the interests of its own genes.

Many animals, for example, appear to be generous towards others by foregoing their own opportunities to reproduce, and instead helping others to raise their young. This behaviour is not unselfish—it has evolved as the best way, in the circumstances, of increasing the number of copies of the helpers' own genes in the next generation.

Scrub jays (*Aphelocoma coerulescens*), for example, will help their parents to raise more young rather than reproduce themselves. This is because, in some places, their habitat does not provide enough territories for them to have a high chance of raising their own offspring. In these circumstances, while waiting for a suitable territory to become available, the young jays secure more copies of their own genes in the next generation by increasing the survival of their siblings, because two siblings share, on average, one half of their genes. The young jays are not concerned with the good of the species, or the good of the population, and they move away and secure their own territory when they can. In some areas, where the habitat is not fully occupied, the young birds behave in a way that appears much more selfish—they occupy their own territories straight away and do not spend time helping their parents.

1.4.3 Similar solutions to similar problems

Because they have evolved by the same process, different types of organism that live in similar conditions often share many characteristics. For example, there are many places in the world where the temperature falls below the freezing point of water—the Arctic, the Antarctic, and the tops of mountains on all continents. The organisms that live in each of these locations have evolved in isolation from one another but they share many characteristics. In most organisms, the cells are broken if their contents are frozen, so many kinds of organisms, particularly plants and invertebrates, are known to produce chemicals that act to prevent freezing. Many insects (in cold places all over the world) produce glycerol, which lowers the freezing point of the fluid in their cells, exactly as the similar chemical ethylene glycol does when used as antifreeze in the engines of motor vehicles. Plants have evolved an almost identical strategy, using a variety of related chemicals. Some green plants, such as the apple (*Malus*

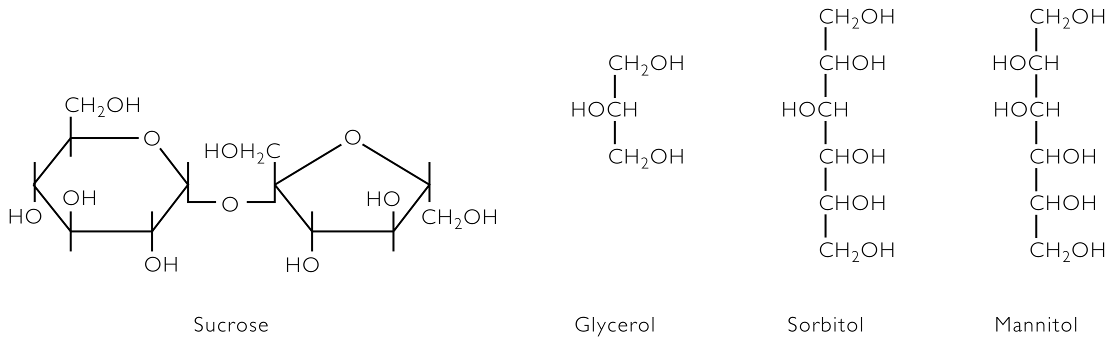

Fig. 1.5 The chemical structure of some molecules used by organisms to prevent their cells from freezing. Many insects produce glycerol and some plants produce chemically similar compounds such as sorbitol and mannitol, but other plants use very different compounds, such as sucrose.

pumila), use the same chemical as most insects or very similar chemicals, such as sorbitol or mannitol. Others, such as ivy (*Hedera helix*) use different sugars, such as sucrose or raffinose (Fig. 1.5).

Chapters 4 and 5 will examine the physical environment of the world in greater depth, and will describe in more detail how evolution has found the same solutions to similar problems in different parts of the world.

1.5 A working definition of ecology

With an understanding of the process of evolution by natural selection, and with a clear idea of what is meant by populations and communities, it is possible to revisit the two different definitions of ecology and unite them into one working definition for the rest of the book.

Recall that the first definition was about organisms interacting with their biological and physical environment, and that the second was about distribution and abundance. The first definition benefits from being centred on the individual organism, but is too unwieldy because it could include any aspect of biology. The second is less cumbersome but has the disadvantage of not concentrating on the individual organisms whose lives we can actually study. Instead it focuses on groups of organisms, such as populations.

These two aspects of ecology are interlinked. Populations evolve because of the action of natural selection on individuals. Thus, in order to preserve the advantages of both trains of thought, it is possible to create a new definition of ecology.

Ecology is the study of how the distributions and abundances of populations (and species) are determined by the interactions of individual organisms with their physical and biological environments.

1.6 Ecological niches

People who live in the tropics may be familiar with day-flying bats, but inhabitants of the temperate zones see bats less frequently, although sometimes on a summer evening, they may notice bats flying around their houses. Because the light is fading, they often have to look twice before they are sure whether they have seen a bat or a bird, or even a large moth. But they do not stop to wonder whether what they have seen was a mouse or a toadstool, because mice and toadstools cannot fly. Likewise, when someone sees something swimming underwater in a pond, they look more closely to see whether it is a frog, a fish or a dragonfly larva but it never crosses their minds that it might be a sparrow or a grass plant. If the water is not a pond but a fast-running stream, they can probably rule out the possibility that what they have seen is a frog. All of this is obvious to the point of being almost trivial.

What is less obvious is the reason whereby people can narrow down what they might have seen. In essence, it is because everyone knows something about ecological niches. Niches are descriptions of what organisms do and where they do it. Usually niches describe the overall attributes of a whole species, although they could refer to populations or even individual animals. Theoretically, the niche occupied by a species defines everything about its needs. Whatever resources are required by organisms—food, shelter, water, space and so on—form part of the niche of a species.

1.6.1 Fundamental and realized niches

The **fundamental niche** of a species defines the places where its members are physiologically capable of living. Most fish cannot live out of water, so dry land is not part of their fundamental niche. In other words, the fundamental niche depends on the physical environment.

In practice, of course, members of a species do not necessarily occur in all the places where they are physiologically capable of doing so. There may be a number of reasons why organisms do not live everywhere that they could theoretically exist. One reason is geography, which is part of the explanation for the lack of wild marsupial mammals, such as kangaroos, in Europe. Bromeliad plants evolved in the Americas and would have had to cross huge oceans to colonize Asia. This interface between geography and ecology is known as biogeography and its effects on biodiversity will be examined in more detail in Chapter 14.

Another reason why organisms of a particular species do not occur in all the places that they might do is that they are excluded by some form of biological interaction. For example, another similar species may already be established and may happen to be a superior competitor. In the prairies of the upper midwest of the United States, the grasses known as little bluestem (*Schizachryium scoparium*) and big bluestem (*Andropogon gerardii*) outcompete grasses such as Kentucky bluegrass (*Poa pratensis*) in obtaining nitrogen from poor, sandy soils. Kentucky bluegrass cannot establish itself in areas where either of the bluestem grasses is already present. However, it can grow in these habitats after a fire creates open space. Alternatively, a piece of habitat may contain a very high density of predators that would very soon eat any member of the species that ventured into the area.

Thus, the **realized niche** of a population is the part of its fundamental niche that it actually occupies, where it is not excluded by predators, competitors, geographic history or anything else.

Both fundamental and realized niches are dynamic, not static—they can change as the biological and physical environment changes. A good example comes from the past ecology of humans and their close relatives. Until about 130 000 years ago, Europe was populated by the Neanderthals, who were either a race of humans or a different but similar species, named after the Neander Valley in Germany, where Neanderthal fossils were first discovered in 1856. Similar fossils are known from a variety of places in Europe, so we know that the fundamental niche of the Neanderthals was wide. But when modern humans evolved and emerged from Africa, they replaced the Neanderthals rather suddenly. The exact degree to which competition played a part is not clear, but there can be little doubt that it was an important factor. As modern humans moved northwards from the Middle East and southern Europe, the realized niche of the Neanderthals receded until they finally became extinct (Fig. 1.6).

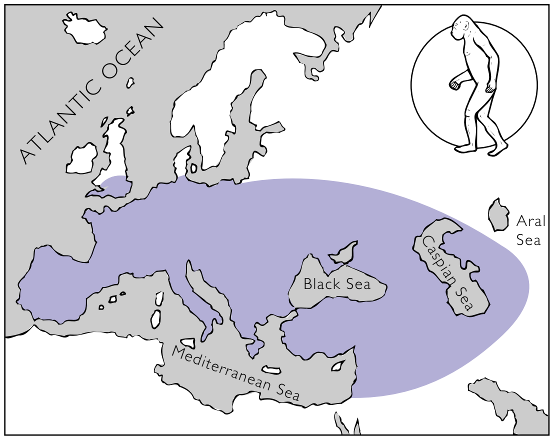

Fig. 1.6 The distribution of the Neanderthal people (*Homo sapiens neanderthalensis*), who were displaced by modern humans (*Homo sapiens sapiens*) about 40 000 years ago. The extent to which the two races interbred is not known, but the realized niche of the Neanderthals certainly contracted as a result of competition from the previously unknown modern humans.

1.6.2 Pitfalls with the niche concept

One way of looking at ecological niches is to say that organisms live in environments to which they are suited. Organisms are adapted to their environment because evolution has selected individuals with characteristics that enable them to survive in the particular conditions that exist. The niche of a species, therefore, reflects the set of conditions to which its members are adapted. However, there are two pitfalls that ecologists must be careful to avoid.

First, it should never be assumed that every aspect of every organism is perfectly adapted for some function. Take, for example, the bactrian camel (*Camelus bactrianus*) and its relative the dromedary (*Camelus

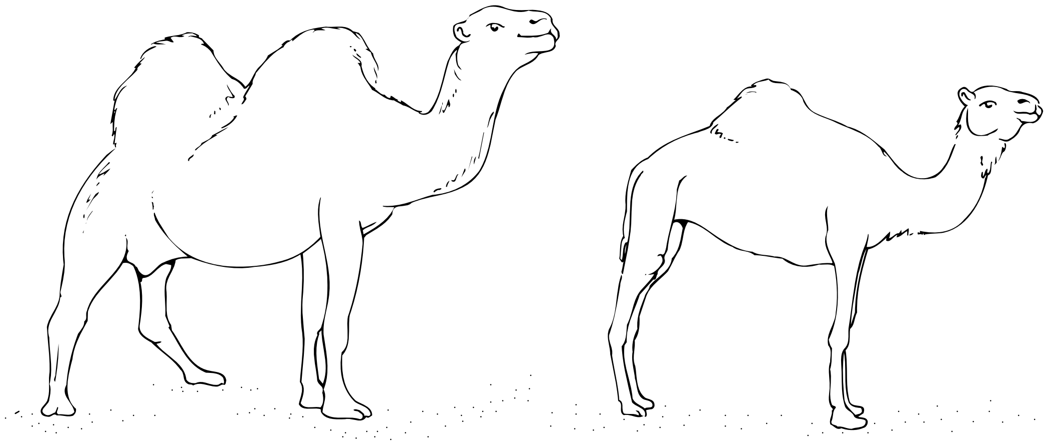

Fig. 1.7 The bactrian camel (*Camelus bactrianus*) has two humps and the dromedary (*Camelus dromedarius*) has only one, but this may just be an accident of history, and the difference may have no adaptive value to individual camels and dromedaries. Ecologists do not need to assume that every piece of variation in the natural world has necessarily been caused by natural selection.

dromedarius). The dromedary, which comes from Arabia, has one hump and the bactrian camel, a native of central Asia, has two (Fig. 1.7). These humps, which are full of fat, are adaptations to life in the desert. They act as a store of energy when food is scarce, and breaking down the fat may also be used as a source of water, although this is doubtful. This is equally true in both species.

An inquisitive person may ask why the dromedary has just one hump, while the bactrian camel has two. There is no harm in asking such questions, so long as we are content if there turns out to be no adaptive explanation. It is possible that a one-humped version of the bactrian camel would outcompete the existing two-humped form, but no such animal has ever evolved, so it is impossible to say. The number of humps is just as likely to be an accident of history. Millions of years ago, when the dromedary evolved, the individuals that happened to have the best suite of characteristics for life in the African desert also happened, by chance, to have genes for one hump rather than two. It is possible that there was no selective advantage in having one hump and it is conceivable that they could equally well have had genes for two humps or even three or four, but that is not the way things happened.

The second piece of thinking that ecologists must be careful to avoid is to imagine that the niche of a species represents its 'role' in the system, in the way that a taxi driver, a farmer or a schoolteacher has a role in a human community. This train of thought suggests that the system would be incomplete, or could not function, without the species, just as a human community could not function properly without teachers or farmers. In fact, what happens when a species is removed from a system is that the remaining organisms find themselves in an altered biological environment. This means that some populations are subjected to new pressures by natural selection.

If these pressures are considerable, then other species might become extinct and the area might become less rich in terms of its biological diversity. However, the system would still exist, and new populations might even invade, or existing populations may evolve to create new species. It is unhelpful to think of ecological systems as fixed entities; they are always changing, as the component populations undergo evolution.

Of course, this logic is not an excuse for humankind to bring about extinctions without concern. There is little doubt that human activity has the capacity to cause extinctions so rapidly that the remaining species could be subjected to such fierce selection pressures in such short spaces of time that they could not evolve quickly enough to avoid extinction themselves.

1.7 Four concepts that form a basic framework for the ecologist

Sections 1.3–1.6 have described a powerful set of ideas with which to study the ecology of our planet. The

definition of ecology in Section 1.5 takes account of different strands of thinking and allows ecologists to take a wide overall view without ignoring the importance of individual organisms. Equally important, the study of ecology cannot afford to forget the concept of other **levels of diversity**, such as genes, populations, species and communities, and these were described in Section 1.3. Ecologists must also have an understanding of the process of **evolution by natural selection** (Section 1.4) as a sound theoretical base from which it is dangerous to stray. They also rely on the concept of the **ecological niche**, which places organisms in the context of their physical and biological environments (Section 1.6); in other words, it describes (in ecological terms) each of the different life forms that natural selection has produced.

1.7.1 A final concept: making comparisons

The final idea that is needed before an ecologist can really begin the study of the ecology of planet Earth is one that is common to almost all fields of study—ecologists must develop a habit of making comparisons. It is difficult to learn anything of value, and difficult to be fascinated by anything, without making comparisons. This may sound like an odd statement until one realizes that we compare things all the time without even noticing that we are doing it.

For example, we may study a large oak tree and observe that it produced a total of five acorns this year. This fact would tell us nothing until we compare our tree with oaks in other places, or with the same oak tree in previous years, or even simply make a comparison with a general knowledge of what large trees normally do—drawn from experience of trees in a variety of places and at different times. Knowing about any of these situations would tell us that oak trees usually produce thousands of acorns each year. Armed with this knowledge we can say that our oak tree produced an unusually small crop of acorns this year. If we were being more precise, we would say that the crop is small **compared with our expectation based on previous knowledge**.

1.7.2 Patterns

When making comparisons, ecologists discover patterns in the behaviour, anatomy, distribution and physiology of the organisms around them. Deer and antelope have eyes on the sides of their heads but most monkeys have eyes that face forward. Many plants that live in Australia have woody stems but fewer species from the high Arctic do so. Toadstools are common in the countryside of Wyoming but absent from the Great Barrier Reef. Tuberculosis, sore throats and other diseases caused by bacteria can be cured using antibiotics (like penicillin and tetracycline) but viral illnesses, such as AIDS (acquired immune deficiency syndrome) and influenza, cannot.

If one person sat for a thousand years writing down such patterns about animals, plants, fungi and microorganisms, he or she would not exhaust the possibilities. Ecologists can restrict the list—they are likely to be more interested in why toadstools are rare at the bottom of the sea than they are in why penicillin does not cure common colds. But even if they did their best always to remember a limited definition of ecology and concentrated only on how interactions with the environment affect the distribution and abundance of biodiversity, they would barely have begun their list at the end of a millennium of cataloguing patterns in nature.

Maybe at some far distant point in the future, a group of people will feel the need to spend a lifetime listing ecological patterns and the questions that must be answered if those patterns are ever to be explained. They will perhaps do this when they think that all the big questions have been answered, when all the obvious, universal patterns have been explained. But for the time being, there are plenty of unexplained patterns that are obvious to even the most casual observer.

1.8 Examples of ecological patterns

For the remainder of this chapter, it will be helpful to examine a few of the kinds of patterns in which ecologists are interested. The patterns that will be investigated will represent a small selection, in an attempt to try to illustrate as much variation as possible in the types of questions that ecologists ask. They do not represent the whole spectrum of questions that could be asked, or even of those that researchers are currently studying, but aim to give a flavour of the variety of different spatial and temporal scales with which ecologists are concerned. Some of the examples are of patterns at the scale of the whole globe, while others involve patterns over a few square metres. Some of the patterns describe ecological changes over the course of a single year, others deal with several generations of a population, and yet more are concerned with the effects of changes over millions of years.

1.9 Spatial patterns in ecology

The definition of ecology in Section 1.5 stresses the importance of the distribution and abundance of organisms. These words are simply another way of talking about **where** organisms are situated. The distribution of a population is a description of where in the world its individuals live, while abundance is about where those organisms are placed relative to one another—are they generally placed near to other members of their own species or at a greater distance from one another?

To understand ecological processes, it is necessary to understand spatial patterns in the distribution of organisms.

1.9.1 Large-scale geographical patterns

There are birds almost everywhere there is life on Earth. Emperor penguins (*Aptenodytes forsteri*) tolerate harsh blizzards as they nest on the ice of Antarctica, while white-eyed vireos (*Vireo griseus*) live in the equable woodlands of North America, and malleefowl (*Leipoa ocellata*) incubate their eggs in piles of rotting vegetation in Australia. Birds have been seen flying above the peak of Mount Everest and some species can dive underwater to depths of 50 m. However, despite their universal presence, birds are not distributed evenly over the available habitats. It is possible to make useful insights into ecology by comparing at a broad geographical scale the variety of different birds that live in different places.

About a quarter of all living species of birds are restricted to South America, and it is well-known that an area of tropical rainforest will contain more different types of birds (and other organisms) than an equal area of temperate forest (Fig. 1.8). Likewise, although coral reefs are not especially valuable habitats for birdlife, they harbour a greater diversity of other organisms than do coastal areas at higher latitudes.

Another kind of geographical pattern might relate not to the variety of different species of organisms in each place, but to the characteristics of those organisms. For example, most mammals in Australia have pouches in which to carry their young, while no Japanese mammal has any such pouch. There is plenty of tropical rainforest in West Africa but none in the east of the continent.

The explanations for such large-scale patterns are likely to be complex, and it may often prove most practical to study some smaller aspect of the larger system. But it is always useful to remember that if seemingly simple spatial patterns cannot be explained, then an understanding of ecology will lack any basic generalizations. Under these circumstances, ecologists would end up with a patchwork of interesting results from the four corners of the world, but these results would not make an intellectually satisfying whole.

1.9.2 Small-scale geographical patterns

Imagine that a group of ecologists is looking at the barnacles living on boulders on a rocky shore anywhere in the world. The ecologists have learned to identify the different species and are only interested in one of the species; they draw a map that plots the position of each individual of their chosen species. The distribution could be described as one of three broad types. The barnacles could be spread out regularly, with each one separated from its neighbours by a standard distance, or alternatively they might be scattered randomly across the surface of the rock, with no apparent pattern. The third possibility is that the barnacles might show a clumped distribution, with large aggregations of barnacles living close together, with spaces in between where no barnacles live.

Broadly, all populations can be described in such a manner. Rainforest trees often have either clumped or over-regular distributions. Many rainforest tree species in Costa Rica, Australia, Malaysia and West Africa have been found to be dependent on canopy openings to grow to be larger than saplings. For example, *Trema micrantha* on Barro Colorado Island in Panama requires high light levels for its growth, and is found only in forest gaps larger than 376 m^2. Thus, it has a clumped distribution, as large gaps fill up with trees of this species. In Borneo and Malaysia, trees of the dipterocarp family tend to have clumped distributions because their large seeds fall only short distances from the parent tree.

By contrast, many other rainforest tree species have distributions that are overdispersed; individuals are located further away from one another than might be

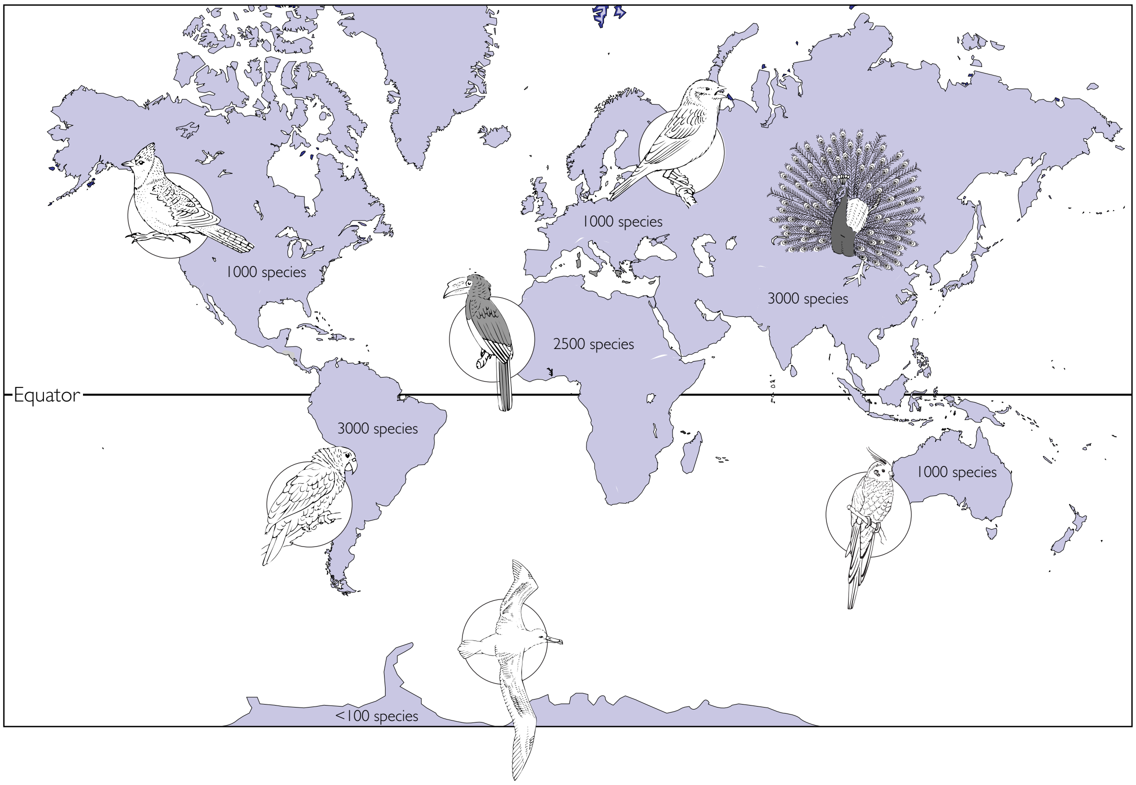

Fig. 1.8 The approximate number of bird species on each of the world's continents.

predicted if seeds were distributed and germinated randomly. In the case of *Platypodium elegans* in Central America, fungal diseases kill so many seeds near to the parents that no saplings are found within 20 m of the parent tree.

1.10 Temporal patterns in ecology

In defining ecology in Section 1.5, it was necessary to understand the difference between the interactions involving an individual organism and the processes that determine the distribution and abundance of a population. One of the most obvious differences is to do with the timescales over which these processes occur.

Individual organisms can only be affected by events that take place within their own lifetimes, whereas populations can be affected by processes and events that operate over many generations. The process of evolution by natural selection, for example, has been occurring for about 3.5 billion years.

One of the most important skills for an ecologist is integrating the effects of short-term and long-term processes.

1.10.1 A timescale of millions of years

Evolution has produced tens of thousands of species of fungi, but it does not appear to have been entirely fair to the different kinds of fungus. Why, for example, are there 16 000 species of Basidiomycotina fungi (such as mushrooms and toadstools) but fewer than 1000 species of Zygomycotina, a different group of fungi that tend to be parasitic and cause infections in other organisms (Fig. 1.9)?

This kind of question can be asked again and again. Why do rodents account for one-half of all mammal species? Why are there millions of animal species but only a few hundred thousand plants? More striking still, why is it that more than one-third of all the known species of animals are beetles? The processes

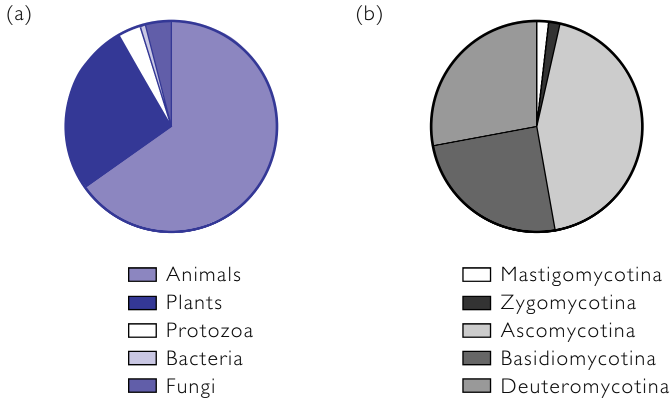

Fig. 1.9 Piecharts showing the relative number of known species in (a) each of the five kingdoms of organisms, and (b) each of the five orders of fungi.

that created these patterns operated over many millions of years.

There are many possible answers to these sorts of questions and, on the whole, they will not be considered in this book. Explaining such patterns is the work of evolutionary biologists, but ecologists cannot ignore the patterns or pretend that they are unimportant.

1.10.2 Timescales that relate to the lifespan of the organisms being studied

Imagine that someone wishes to carry out an ecological study of a population of protozoa in a garden pond. They wish to know how the population changes over time—when the number of protozoa increases and when it decreases. They believe that there may be some patterns that describe what happens to the protozoan population. They consider that temperature might be important—when the weather is hot, the population rises. It is also possible that pollution plays a part in determining the number of protozoa—when pesticides or fertilizers are accidentally spilled into the water, the population declines.

To know whether these hypotheses are true, it would be essential to study the protozoa continuously for some time. To have a real feel for whether the temperature is important, it would be as well to study the population for several years. That way, the investigation would be likely to include some warm summers and some cool ones, as well as harsh and mild winters. Similarly, to understand the importance of fertilizer accidents, it is not going to be enough to show that one April, some chemicals were spilled and the number of protozoa in the pond went down. However convinced the investigator may be that the population crash was caused by carelessness with garden chemicals, validation of the theory will only come if the population is studied during the April of other years, to test that a sudden and dramatic crash is not part of some natural, regular cycle. And the investigator would need to spill some chemicals at other times of the year, over several years.

In short, studying populations of organisms takes time, and the amount of time needed for any particular study depends to some extent on the organisms in question. Organisms with short generation times like bacteria could be studied in months, weeks or even days, but those with longer generations will require years or even decades of study.

Even with the simple example of protozoa in a garden pond, the time needed to describe adequately the many factors affecting population change is impractical. Therefore, ecologists tend to manipulate populations, or use simpler versions of the real world, to try to find answers to their hypotheses. For example, they might create a model system of a garden pond by setting up several glass tanks using samples of pond water. Then, they could alter the temperature, or concentration of fertilizers in different tanks, and observe the changes made to the populations of protozoa.

It is not always easy to define the best timescale over which any population should be studied, and in practice, the length of time over which something is studied may depend on the funding available, or the degree to which new ideas or constraints take the investigators away from the study. But there are many ecological patterns to be seen over timescales that people can appreciate. Nine studies of plant ecology reported in a

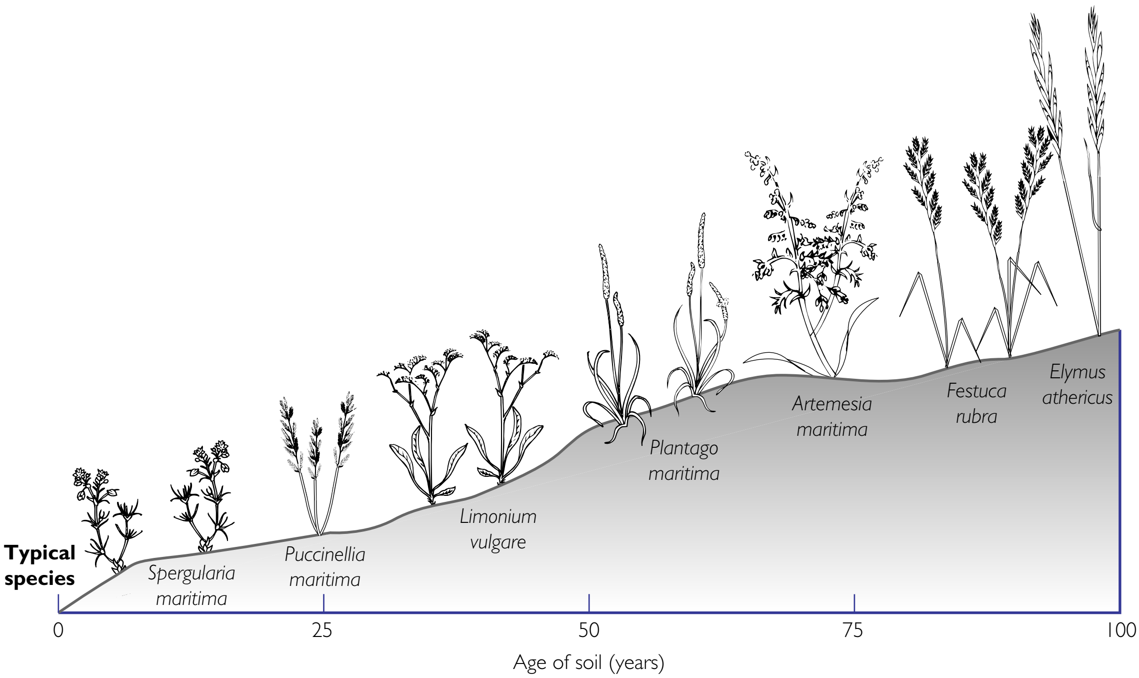

Fig. 1.10 Ecological succession at Schiermonnikoog in the Dutch Frisian islands. When the soils are first deposited, the plant community is characterized by small short-lived plants such as the sea spurrey (*Spergularia maritima*), but as the soil builds up over a century, the community is typified by larger, longer lived species such as red fescue grass (*Festuca rubra*).

single issue of the *Journal of Ecology* vary in timescale from a 'snapshot' study, attempting to make inferences from the structure of an ecological community in Brazil at a single point in time (Fragoso 1997), to an analysis of layers of pollen in a peat bed that give information about the European climate over 3000 years (Tallis 1997). There is one other study of very long-term processes, covering several centuries (Kelly & Larson 1997), but the remaining investigations all cover periods of a few years at most.

One example of a common pattern that occurs on the scale of human lifetime is ecological succession. Suppose that a new habitat opens up, because a fire kills off all the existing vegetation, or because humans abandon a plot of land that they have previously used as farmland. As time progresses, the structure of the ecological community that lives on the land will change, and will often do so according to a predictable pattern.

On the island of Schiermonnikoog in the Dutch Frisian islands, new land is created as the sea deposits silt on the sandy subsoil (Olff *et al.* 1997). Over a period of 100 years, the plant community on the resulting saltmarshes changes in a way that is common to each new saltmarsh. After about 10 years the sea spurrey (*Spergularia maritima*) is one of the dominant plants, but 25 years into the ecological succession, it has almost disappeared, to be replaced by the sea plantain (*Plantago maritima*) and sea lavender (*Limonium vulgare*). After the succession has proceeded for half a century or more, the sea spurrey and sea plantain are completely absent from the saltmarshes and the sea lavender is rare. The dominant plants now form a grassland, with couch grass (*Elymus athericus*) and red fescue (*Festuca rubra*) among the commonest species (Fig. 1.10).

If ecologists want to document the patterns of ecological succession that might occur over a span of 25–1000 years, it is obviously not possible by direct observation. However, many studies of succession have benefited from records and observations taken by different people over historical timescales. The retreat of glaciers in Glacier Bay, Alaska has been documented over the past 200 years and has allowed ecologists to reconstruct the pattern of ecological succession in this area. Often, spatial patterns are used to reconstruct the temporal pattern of succession. Thus, the development of vegetation with increasing distance from the shore of Lake Michigan was used to reconstruct the ecological succession of sand dunes formed by the side of the lake. Likewise, forest succession on the coastal plain of southeastern North America was described by studying a series of abandoned agricultural fields that had been out of cultivation for different periods, ranging from 1 to 200 years.

To understand the processes that act at the scale of a few years in the imaginary population of protozoa described above, or over a human lifetime in the ecological succession on the island of Schiermonnikoog, ecologists need to know both about the ways in which organisms interact with the physical environment and the ways in which they interact with the biological environment. For example, to understand succession on the Dutch islands, it is necessary to know how sea lavender thrives in different kinds of soils and with different concentrations of salt, and also to know how it fares in competition with sea plantain and couch grass, and how all the plant species are affected by grazing by geese or rodents.

When ecologists begin to understand these interactions, they begin to understand the patterns that emerge when they study a single site but make comparisons between different points in time. Once someone has really begun to understand ecology, these explanations for temporal patterns will dovetail neatly with the explanations that they discover for spatial patterns.

1.11 Chapter summary

Ecology is all about the vast diversity of life forms that share our planet. Scientific ecologists classify this biodiversity into different levels and then study it by attempting to understand the ways in which organisms interact with their biological and physical environments. Their explanations never forget the importance of evolution by natural selection.

But before someone can begin to explain the diversity of life, he or she must be able to find those patterns that are common and repeatable. Ecologists uncover these patterns by making comparisons in space and in time. The spatial and temporal variation that they discover is the basis of all ecological study, and it will be investigated in more depth throughout the rest of this book.

Recommended reading

Ghilarov, A. (1996) What does 'biodiversity' mean—scientific problem or convenient myth? *Trends in Ecology and Evolution* **11**: 304–306.

Orr, M.R. & Smith, T.B. (1998) Ecology and speciation. *Trends in Ecology and Evolution* **13**: 502–506.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.

Westoby, M. (1997) What does 'ecology' mean? *Trends in Ecology and Evolution* **11**: 166.

Wilson, E.O. (1992) *The Diversity of Life*. W.W. Norton & Co. Inc., New York.