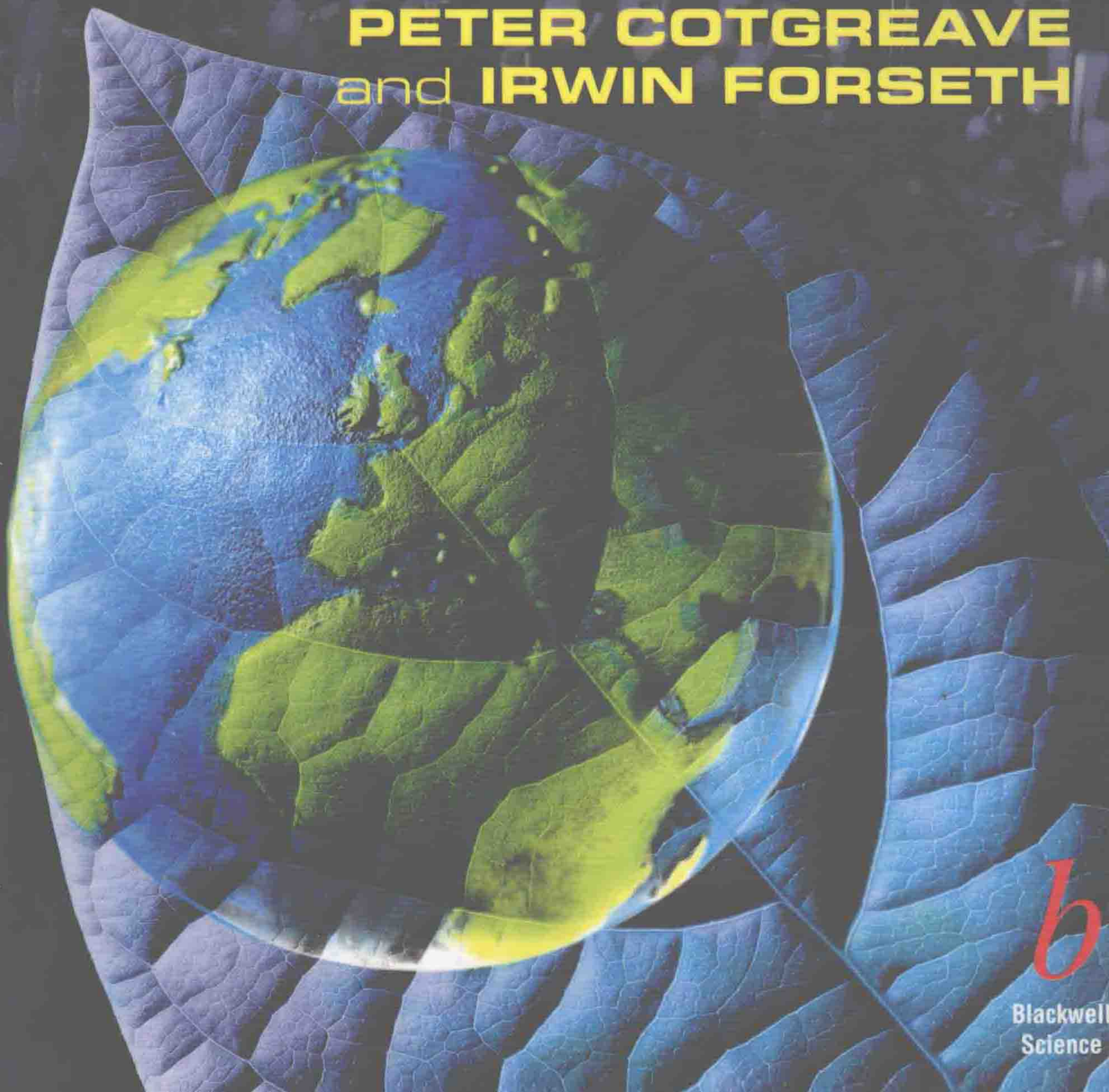
Introductory Ecology

PETER COTGREAVE
and IRWIN FORSETH



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Introductory Ecology

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Preface

The greatest task for humankind over the coming century will be to reconcile the needs of a growing population with the requirement to behave in ways that are environmentally sustainable. As the human species appropriates more and more natural resources for our own purposes, it will be increasingly important for us to understand the processes that drive the natural environment.

If we fail, the consequences will be literally unimaginable. To succeed, people in all walks of life will need an ever-deeper understanding of how the human species fits into the wider ecology of the planet; this will involve a detailed comprehension of the effects that our own species continues to have on the physical environment and on other life forms, and an equally detailed comprehension of their effects on us. This understanding will only come through a full appreciation of the fundamental principles of ecology.

Despite the importance of ecology, there is no requirement for a course in ecology in many college syllabuses, even those that involve some degree of specialization in science and biology. The result is that many students leave college or university with only a rudimentary idea of the science of ecology, and of its relevance to the political and societal problems facing countries throughout the world. We have attempted to address this by providing a straightforward text that can be used both by students taking elective courses and by those science students for whom this book may be their only exposure to ecology.

The book aims to give students the kind of basic ecological knowledge and comprehension on which they can build an understanding of how the human species fits into the wider ecology of the planet. We have also attempted to connect basic ecological principles and research with the everyday problems that are becoming increasingly pronounced in today's world. In doing so, we have always emphasized that applied ecology can only be understood in a wider context, in which we interpret ecological experiments, observations and theory to build up a picture of how ecosystems function.

Although only two authors are listed for this book, no text of this type can be developed in a vacuum. Therefore, we acknowledge the contributions that so many others have made to the development of the book, starting with our own teachers, lecturers and mentors, who were so important to our development as naturalists, as scientists and as biologists. Prominent among these are James Ehleringer, Roger Cotgreave and John Lawton.

The other people who have influenced the project are too numerous for us to name, but a small number deserve particular mention. Help, advice and useful ecological examples have come from Andrew Bourke, Brenda Casper, Tim Coulson, Sara Lourie, Mike Peek, Graham Stone and Rosie Woodroffe.

Various people have been kind enough to read sections of the manuscript, and we want to thank Alan Cotgreave, Claire Knapton, Jan Bakker, Martin Kent, John Spicer, Tom Crist, Alan Hastings and anonymous reviewers. Philippa Bayley undertook the unenviable task of giving detailed comments on the entire book.

At Blackwell Science, Ian Sherman was a particularly helpful friend and editor throughout much of the project, and when he moved on, his replacement, Sarah Shannon, demonstrated more than enough energy and enthusiasm to keep us on track. Without their constant advice and encouragement, we would have been even further behind schedule. Simon Rallison, Julie Wilson, Katrina McCallum, Cee Brandson and Jane Andrew all played important roles in seeing the book published.

Writing a book is not as simple as we imagined it would be, and we must thank those who have tolerated and supported us when we have been frustrated and tired. Sometimes we have simply been in need of a break from the plants, animals, and other organisms that so intrigue us, and more often than not, we have been so entranced by them that we have failed to realize it. For coping with us when this happened, we thank Cathy Cooper, Laura Erik and Kirsten Forseth.

Peter Cotgreave
Irwin Forseth
July 2001

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Contents

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

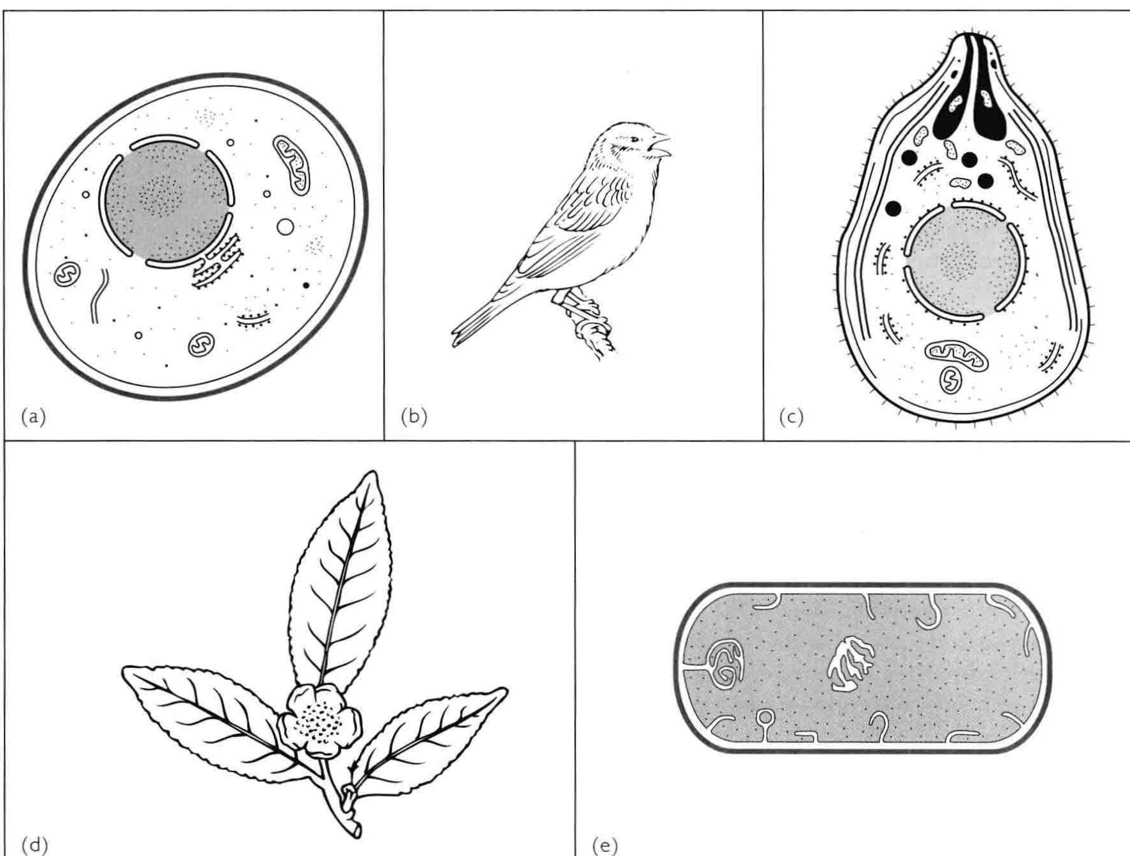


Fig. 1.1 People encounter and use organisms from all the major groups. (a) The fungus *Saccharomyces*, which is used as yeast in brewing and baking. (b) The canary (*Serinus canaria*), which is kept as a pet. (c) The parasite *Plasmodium falciparum*, which causes malaria. (d) The leaves of the tea plant (*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).

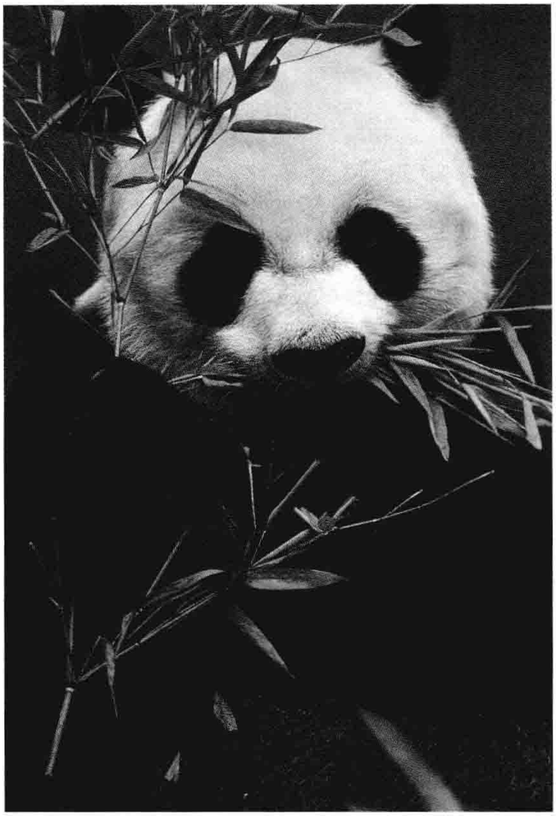
If the world's human population does not properly understand the ecological system in which it lives, it will never really understand how to solve any of its problems. This does not imply that the average ecologist is trying to feed millions of starving mouths, nor does it mean that this book is in any 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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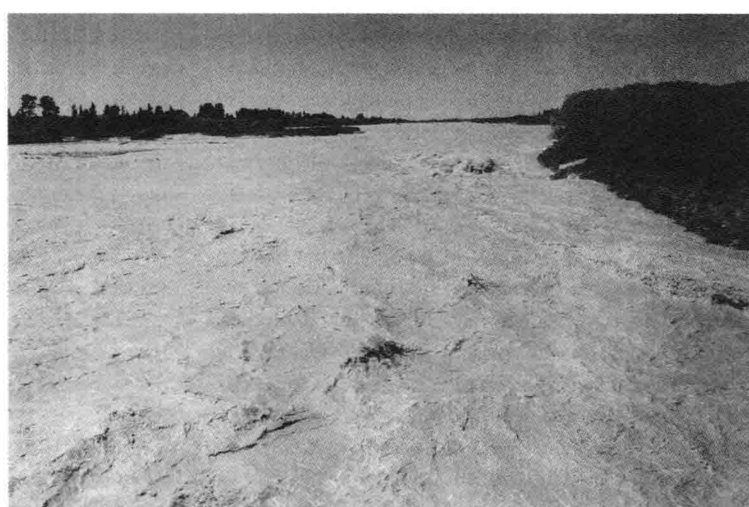

(c)

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

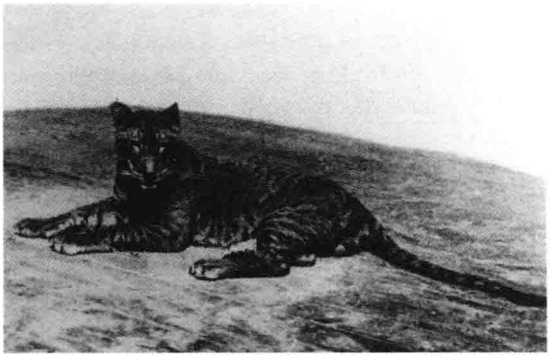

Fig. 1.3 Hybrids like the liger, a cross between a lion and a tiger, are sterile. (Copyright the Zoological Society London.)

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

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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).

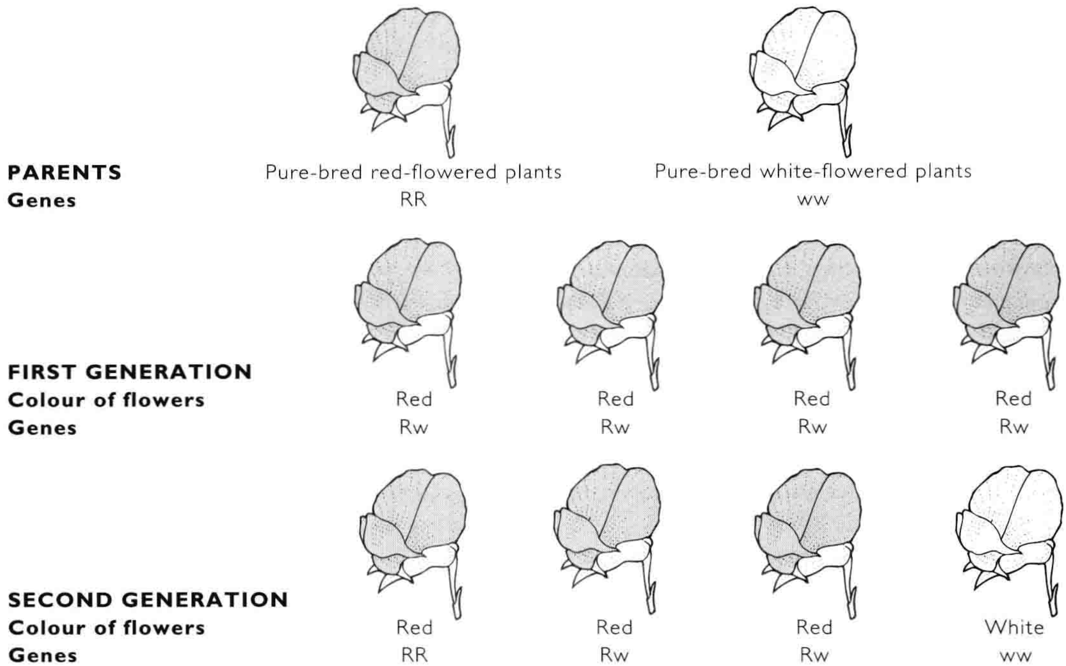


Fig. 1.4 Gregor Mendel (1822–1884) discovered the basis of modern genetics by experimenting with cross-fertilizing pea plants.

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.

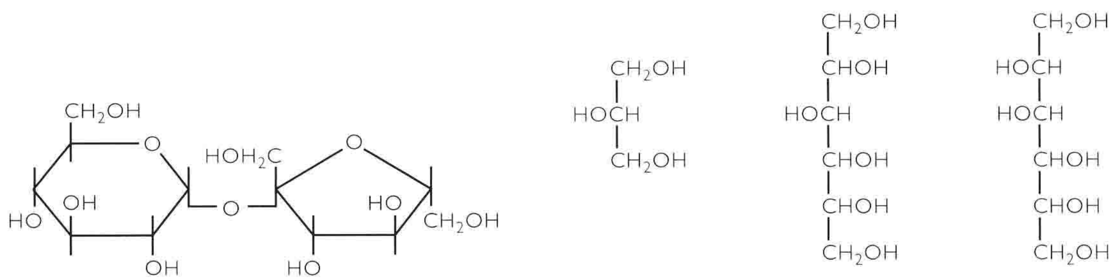
However, it is crucial to avoid the perception that features of organisms can be interpreted in the context of the 'good of the population' or the 'good of the species'. If an organism appears to be generous towards others, it is not concerned with the good of the species. It can almost certainly be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



Sucrose Glycerol Sorbitol Mannitol

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).

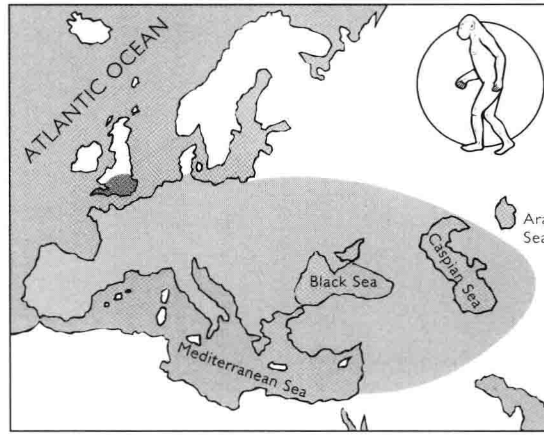


Fig. 1.6 The distribution of the Neanderthal people (*Homo sapiens neanderthalensis*), who were displaced by modern humans (*Homo sapiens sapiens*) about 40 000 years ago. The extent to which the two races interbred is not known, but the realized niche of the Neanderthals certainly contracted as a result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

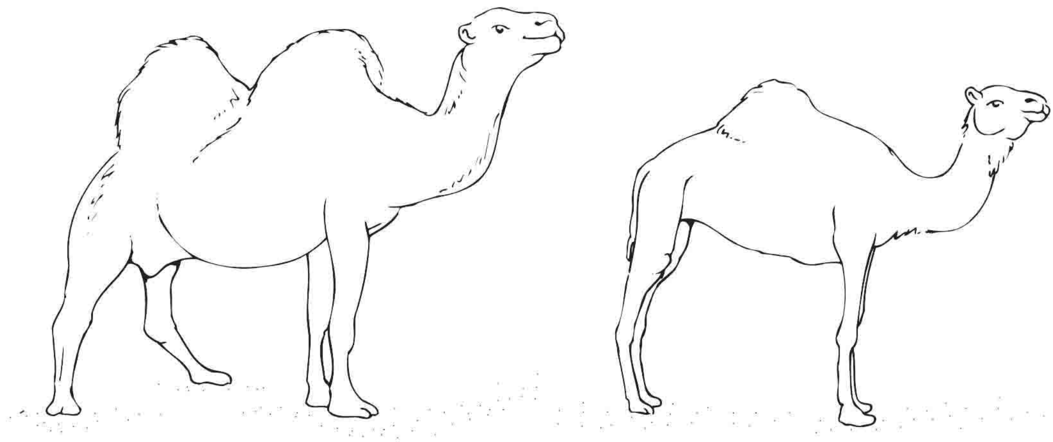


Fig. 1.7 The bactrian camel (*Camelus bactrianus*) has two humps and the dromedary (*Camelus dromedarius*) has only one, but this may just be an accident of history, and the difference may have no adaptive value to individual camels and dromedaries. Ecologists do not need to assume that every piece of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

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