Chapter 2

The Ecology of Evolution

As the great Russian-American biologist Dobzhansky said, "Nothing in biology makes sense, except in the light of evolution". But equally, very little in evolution makes sense except in the light of ecology: ecology provides the stage directions through which the "evolutionary play" is performed. Ecologists and evolutionary biologists need a thorough understanding of each other's disciplines to make sense of key patterns and processes.

Chapter Contents

Key Concepts

In this chapter you will

- appreciate that Darwin and Wallace, who were responsible for the theory of evolution by natural selection, were both, essentially, ecologists
- understand that the populations of a species vary in their characteristics from place to place on both geographic and more local scales, and that some of the variation is heritable
- realize that natural selection can act very quickly on heritable variation—we can study it in action and control it in experiments
- understand that reciprocal transplanting of individuals of a species into each other's habitats can show a finely specialized fit between organisms and their environments
- appreciate that the origin of species requires the reproductive isolation of populations as well as natural selection forcing them to diverge
- realize that natural selection fits organisms to their past—it does not anticipate the future
- realize that the evolutionary history of species constrains what future selection can achieve
- understand that natural selection may produce similar forms from widely different ancestral lines (convergent evolution) or the same range of forms in populations that have become separated (parallel evolution)

2.1   Introduction

The Earth is inhabited by a multiplicity of types of organism. They are distributed neither randomly nor as a homogeneous mixture over the surface of the globe. Any sampled area, even on the scale of a whole continent, contains only a subset of the variety of species present on Earth. One of the greatest of all ecological generalizations is that all species are so specialized that they are always absent from almost everywhere. A great part of the science of ecology tries to explain why there are so many types of organism and why their distributions are so restricted. A proper answer to these ecological questions depends fundamentally on an understanding of the processes of evolution that have led to present-day diversity and distribution.

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Until relatively recently in the history of biology, the emphasis on diversity was to use it (e.g., for medicine, food, and fiber), to exhibit it in zoological and botanic gardens, and to catalogue it in museums (Box 2.1). Without an understanding of how this diversity developed, such catalogues are more like stamp collecting than science. The enduring contribution of Charles Darwin and Alfred Russell Wallace was to provide ecologists with the scientific foundations to comprehend patterns in diversity and distribution over the face of the Earth.

2.2   Evolution by Natural Selection

Darwin and Wallace (Figure 2.1) were both ecologists (although their seminal work was performed before the term was coined) who were exposed to the diversity of nature in the raw. Darwin sailed around the world as naturalist on the 5-year expedition of HMS *Beagle* (1831–6) recording and collecting in the enormous variety of environments that he explored on the way. He gradually developed the view that the natural diversity of nature was the result of a process of evolution in which *natural selection* favored some variants within species through a "struggle for existence". He developed this theme over the next 20 years through detailed study and an enormous correspondence with his friends as he prepared a major work for publication with all the evidence carefully marshaled. But he was in no hurry to publish.

Darwin and Wallace were both ecologists

In 1858, Wallace wrote to Darwin spelling out in all its essentials the same theory of evolution. Wallace was a passionate amateur naturalist. He had read Darwin's journal of the voyage of the *Beagle* and after a visit to the Jardin des Plantes in Paris and the insect room at the British Museum he wrote in 1847, "I should like to take some one family to study thoroughly, principally with a view to the theory of the origin of species." From 1847 to 1852, with his friend H.W. Bates, he explored and collected in the river basins of the Amazon and Rio Negro, and from 1854 to 1862 he made an extensive expedition in the Malay Archipelago. He recalled lying on his bed in 1858 "in the hot fit of intermittent fever, when the idea [of natural selection] suddenly came to me. I thought it all out before the fit was over, and . . . I believe I finished the first draft the next day."

Today, competition for fame and financial support would commonly lead to fierce conflict about priority—who had the idea first. Instead, in an outstanding example of selflessness in science (Darwin wrote to his friend Hooker, "It is miserable in me to care at all about priority"), sketches of Darwin's and Wallace's ideas were presented together

A Brief Catalogue of the Study of Diversity

An awareness of the diversity of living organisms, and of what lives where, is part of the knowledge that the human species accumulates and hands down through the generations. Hunter–gatherer peoples needed (and still need) detailed knowledge of the natural history of their environments to obtain food successfully and at the same time escape the hazards of being poisoned or eaten. The Arawaks of the South American equatorial forest know where to find and how to catch the species of large animals around them and also the names of trees and how they can be used.

The Chinese emperor Shen Nung had compiled what was perhaps the first written "herbal" of useful plants before 2000 BC, and by the first century AD Dioscorides had described 500 species of medicinal plants and illustrated many of them.

Collections of living specimens in zoos and gardens also have a long history—certainly back to Greece in the seventh century BC. The urge to collect from the diversity of nature developed in the West in the 17th century when some individuals made their living by finding interesting specimens for other people's collections. John Tradescant the father (died 1638) and John Tradescant the son (1608–1662) spent most of their lives collecting plants and importing live specimens for the gardens of royalty and the nobility. The father was the first botanist to visit Russia (1618), bringing back many living plants; his son made three visits (1637, 1642, and 1654) to the New World to collect specimens in the American colonies.

Wealthy individuals built up vast collections into personal museums and traveled or sent travelers in search of novelties from new lands as they were discovered and colonized. Naturalists and artists (often the same people) were sent to accompany the major voyages of exploration to report and take home, dead or alive, collections of the diversity of organisms and artefacts that they found. The study of taxonomy and systematics developed and flourished—taxonomy gave names to the various types of organism and systematics provided systems for classifying and pigeon-holing them.
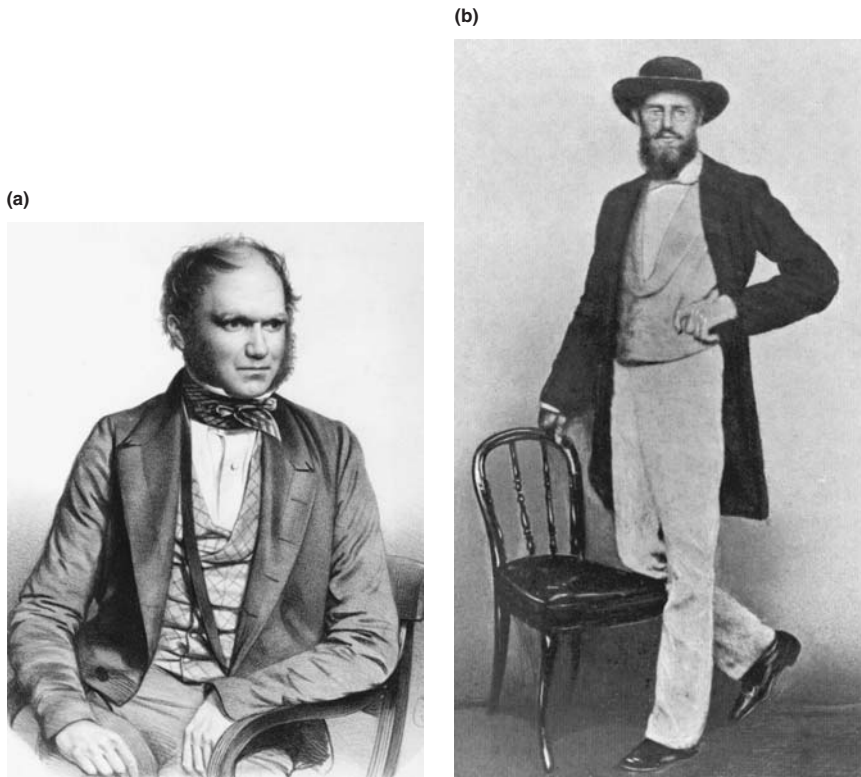
When big national museums were established (the British Museum in 1759 and the Smithsonian in Washington in 1846), they were largely compiled from the gifts of personal collections. Like zoos and gardens, the museums' main role was to make a public display of the diversity of nature, especially the new and curious and rare.

There was no need to explain the diversity—the biblical theory of the 7-day creation of the world sufficed. However, the idea that the diversity of nature had "evolved" over time by progressive divergence from pre-existing stocks was beginning to be discussed in the early 19th century. In 1844 an anonymous publication, *The Vestiges of Creation*, put the cat among the pigeons with a popular account of the idea that animal species had descended from other species.

at a meeting of the Linnean Society in London. Darwin's *On the Origin of Species* was then hastily prepared and published in 1859 as an "abstract" of what was intended eventually to become his "big book". [In fact, most of what Darwin called his big book, with all its detail, footnotes, and references, was not published until 1975 (Stauffer, 1975).] *On the Origin of Species* may be considered the first major textbook of ecology, and aspiring ecologists would do well to read at least the third chapter.

influence of Malthus's essay on Darwin and Wallace

Both Darwin and Wallace had read *An Essay on the Principle of Population*, published by Malthus in 1798. Wallace commented, "The most interesting coincidence in

(b)

(a)

the matter, I think, is that I, as well as Darwin, was led to the theory itself through Malthus." Malthus's essay was concerned with the human population, which, if its intrinsic rate of increase remained unchecked, would, he calculated, be capable of doubling every 25 years and overrunning the planet. Malthus realized that limited resources slowed the growth of populations and placed absolute limits on their size, and that disease, wars, and other disasters also checked population growth. As experienced field naturalists, Darwin and Wallace realized that the Malthusian argument applied with equal force to the whole of the plant and animal kingdoms.

The living world is dominated by reproduction, overcrowding, and death. Darwin and Wallace were almost obsessed by this great truth. They appreciated that all organisms possess a potential to multiply that is impossible to realize. Darwin noted the great fecundity of some species—a single individual of the sea slug *Doris* may produce 600,000 eggs; the parasitic roundworm *Ascaris* may produce 64 million—and as an example of the absurd consequences of unimpeded population growth, he used a population of fish, each laying 2,000 eggs: in eight generations this "would cover like a sheet the whole globe, land and water". But he realized that every species "must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product" (Darwin, 1859, *On the Origin of Species*); and he observed that this was so. In one of the earliest examples of population ecology, Darwin counted all the seedlings that emerged from a plot of

the forces of reproduction, crowding, and death

cultivated ground 3 feet long and 2 feet wide: "Out of 357 no less than 295 were destroyed, chiefly by slugs and insects." Both authors, then, emphasized that most individuals die before they can reproduce and contribute nothing to future generations. Both, though, tended to ignore the important fact that those individuals that do survive in a population may leave different numbers of descendants.

fundamental truths of evolutionary theory

The theory of evolution by natural selection, then, rests on a series of established truths:

1 Individuals that form a population of a species are not identical.
2 Some of the variation between individuals is heritable—that is, it has a genetic basis and is therefore capable of being passed down to descendants.
3 All populations could grow at a rate that would overwhelm the environment; but, in fact, most individuals die before reproduction and most (usually all) reproduce at less than their maximal rate. Hence, each generation, the individuals in a population are only a subset of those that "might" have arrived there from the previous generation.
4 Different ancestors leave different numbers of descendants (descendants, *not* just offspring): they do not all contribute equally to subsequent generations. Hence, those that contribute most have the greatest influence on the heritable characteristics of subsequent generations.

Evolution is the change, over time, in the heritable characteristics of a population or species. Given the above four truths, the heritable features that define a population will inevitably change. Evolution is inevitable.

"the survival of the fittest"?

But which individuals make the disproportionately large contributions to subsequent generations and hence determine the direction that evolution takes? The answer is: those that were best able to survive the risks and hazards of the environments in which they were born and grew; and those who, having survived, were left by their environments most capable of successful reproduction. Thus, interactions between organisms and their environments—the stuff of ecology—lie at the heart of the process of evolution by natural selection.

The philosopher Herbert Spencer described the process as "the survival of the fittest", and the phrase has entered everyday language—which is regrettable. First, we now know that survival is only part of the story: differential reproduction is often equally important. But more worryingly, even if we limit ourselves to survival the phrase gets us nowhere. Who are the fittest?—those that survive. Who survives?—those that are fittest. Nonetheless, the term *fitness* is commonly used to describe the success of individuals in the process of natural selection. An individual will survive better, reproduce more, and leave more descendants—it will be fitter—in some environments than in others. In a given environment, some individuals will survive better, reproduce more, and leave more descendants—they will be fitter—than other individuals.

natural selection has no aim for the future

Darwin had been greatly influenced by the achievements of plant and animal breeders—for example, the extraordinary variety of pigeons, dogs, and farm animals that had been deliberately bred by selecting individual parents with exaggerated traits. He and Wallace saw nature doing the same thing—"selecting" those individuals that survived from their excessively multiplying populations—hence the phrase "natural selection". But even this phrase can give the wrong impression. There is a great

difference between human and natural selection. Human selection has an aim for the future—to breed a cereal with a higher yield, a more attractive pet dog, a better hunter, or a cow that will yield more milk. But nature has no aim. Evolution happens because some individuals have survived the death and destruction of the past and reproduced more successfully in the past, not because they were somehow chosen or selected by "Mother Nature" as improvements for the future.

Hence, past environments may be said to have selected particular characteristics of individuals that we see in present-day populations. Those characteristics are "suited" to present-day environments only because environments tend to remain the same, or at least change only very slowly. We shall see later in this chapter that when environments do change more rapidly, often under human influence, organisms can find themselves, for a time, left "high and dry" by the experiences of their ancestors.

Darwin and Wallace placed slightly different emphases on the forces that drive evolution. Wallace emphasized the killing forces of physical conditions such as frost, drought, and predators. Darwin laid more emphasis on competition for limited resources and the lethal effects of crowding that result from overpopulation. We pick up these powerful ecological forces in Chapters 3 (Physical Conditions and the Availability of Resources), 5 (Birth, Death, and Movement), 6 (Interspecific Competition), and 8 (Predation, Grazing, and Disease).

2.3   Evolution within Species

The natural world is not composed of a continuum of types of organism each grading into the next; we recognize boundaries between one sort of organism and another. In one of the great achievements of biological science, Linnaeus in 1789 devised an orderly system for naming the different sorts. Part of his genius was to recognize that there were features of both plants and animals that were not easily modified by the organisms' immediate environment, and that these "conservative" characteristics were especially useful for classifying organisms. In flowering plants, the form of the flowers was particularly stable, whereas the size of leaves and stems was much more readily affected by heat and cold, watering and drought, and the giving and withholding of fertilizers. Nevertheless, within what we recognize as species, there is often considerable variation, and some of this is heritable. It is on such intraspecific variation, after all, that plant and animal breeders work. In nature, some of this intraspecific variation is clearly correlated with variations in the environment and represents local specialization.

to understand the evolution of species we need to understand evolution within species

Darwin called his book *On the Origin of Species by Means of Natural Selection*, but evolution by natural selection does far more than create new species. Natural selection and evolution occur *within* species, and we now know that we can study them in action and within our own lifetime. Moreover, we need to study the way that evolution occurs within species if we are to understand the origin of new species.

2.3.1   Geographical variation within species

Since the environments experienced by a species in different parts of its range are themselves different (to at least some extent), we might expect natural selection to

the characteristics of a species may vary over its geographical range

have favored different variants of the species at different sites. But evolution forces the characteristics of populations to diverge from each other (1) only if there is sufficient heritable variation on which selection can act, and (2) provided that the forces of selection favoring divergence are strong enough to counteract the mixing and hybridization of individuals from different sites. Two populations will not diverge completely if their members (or, in the case of plants, their pollen) are continually migrating between them, mating and mixing their genes.

The sapphire rockcress, *Arabis fecunda*, is a rare perennial herb restricted to calcareous soil outcrops in western Montana—so rare, in fact, that there are just 19 existing populations separated into two groups ("high elevation" and "low elevation") by a distance of around 100 km. Whether there is local adaptation here is of practical importance: four of the low elevation populations are under threat from spreading urban areas and may require reintroduction from elsewhere if they are to be sustained. Reintroduction may fail if local adaptation is too marked. Observing plants in their own habitats and checking for differences between them would not tell us if there was local adaptation in the evolutionary sense. Differences may simply be the result of immediate responses to contrasting environments made by plants that are essentially the same. Hence, high and low elevation plants were grown together in a "common garden" (Figure 2.2), eliminating any influence of contrasting immediate environments (McKay et al., 2001). The low elevation sites were more prone to drought: both the air and the soil were warmer and drier; and the low elevation plants in the common garden were indeed significantly more drought tolerant. For example, they had significantly better "water use efficiency" (their rate of water loss through the leaves was low compared to the rate at which carbon dioxide was taken in) as well as being much taller and "broader" (Figure 2.3).

variation over very short distances

Differentiation over a much smaller spatial scale was demonstrated at a site called Abraham's Bosom on the coast of North Wales. Here there was an intimate mosaic of very different habitats at the margin between maritime cliffs and grazed pasture, and a common species, creeping bent grass (*Agrostis stolonifera*) was present in many of the habitats. Figure 2.4 shows a map of the site and one of the transects from which plants were sampled; it also shows the results when plants from the sampling points along this transect were grown in a common garden. Lengths of shoot taken from this species readily form roots, so that a number of independent rooted plants can be cloned from a single plant taken from the field. Hence, in a careful statistical design, each of four plants taken from each sampling point was represented by five rooted clonal replicates of itself. The plants spread by sending out shoots along the ground surface (stolons), and the growth of the plants was compared by measuring the lengths of these. In the field, cliff plants formed only short stolons, whereas those of the pasture plants were long. In the experimental garden, these differences were maintained, even though the sampling points were typically only around 30 m apart—certainly within the range of pollen dispersal between plants. Indeed, the gradually changing environment along the transect was matched by a gradually changing stolon length, presumably with a genetic basis, since it was apparent in the common garden. Even here, the forces of selection seem to outweigh the mixing forces of hybridization.

On the other hand, it would be quite wrong to imagine that local selection always overrides hybridization—that all species exhibit geographically distinct variants with a genetic basis. For example, in a study of *Chamaecrista fasciculata*, an annual legume
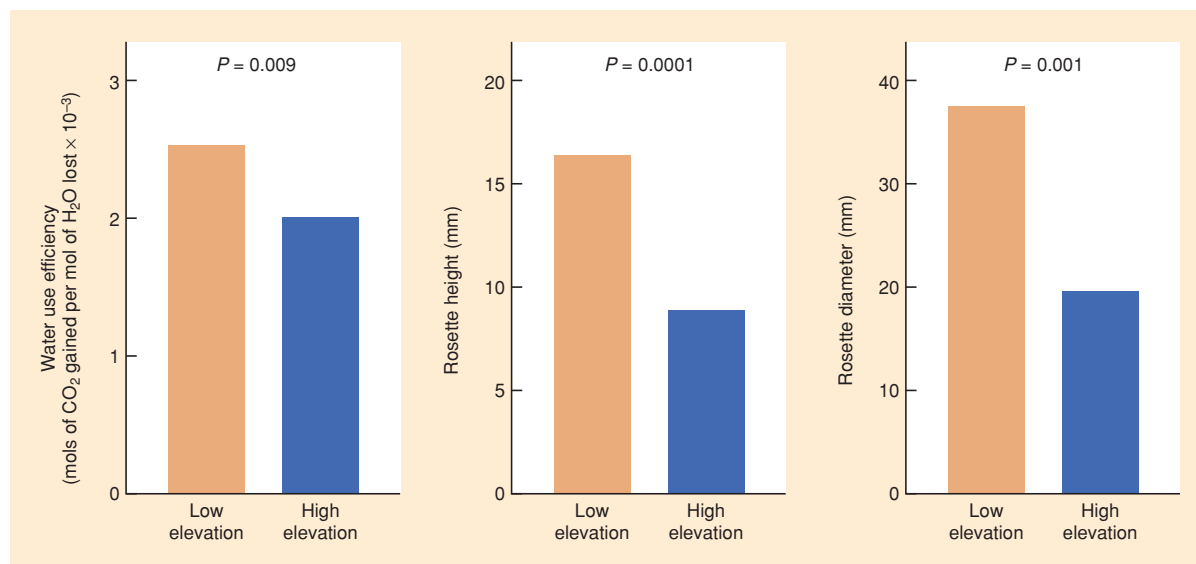
(a) Common garden experiments
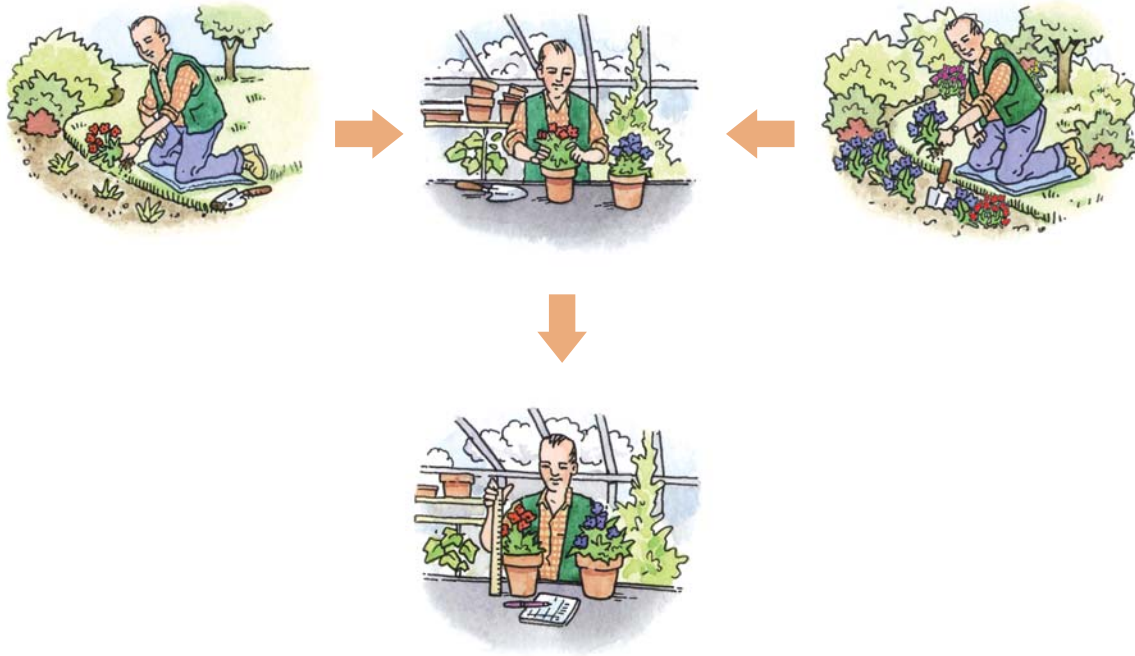
(b) Reciprocal transplant experiments
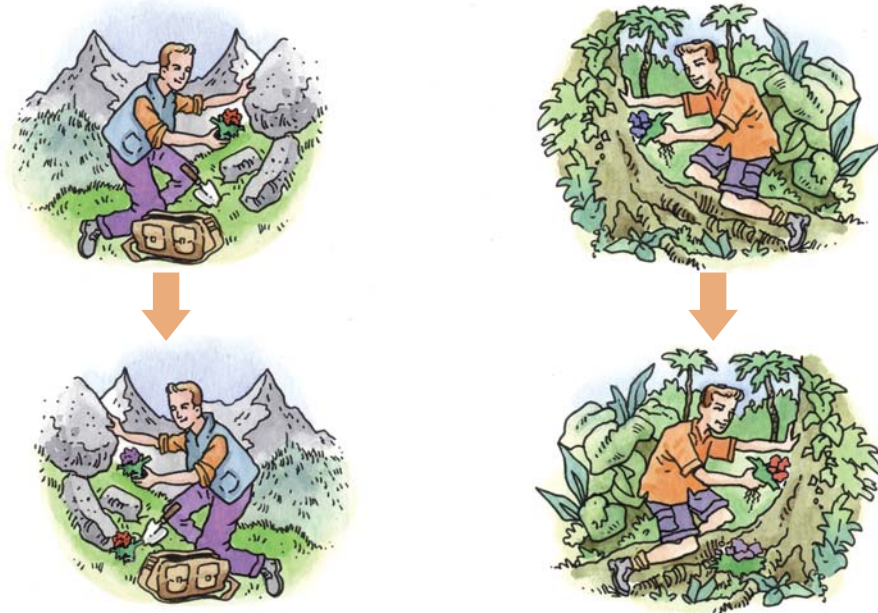
Figure 2.2
Common garden experiments (a) and reciprocal transplant experiments (b).
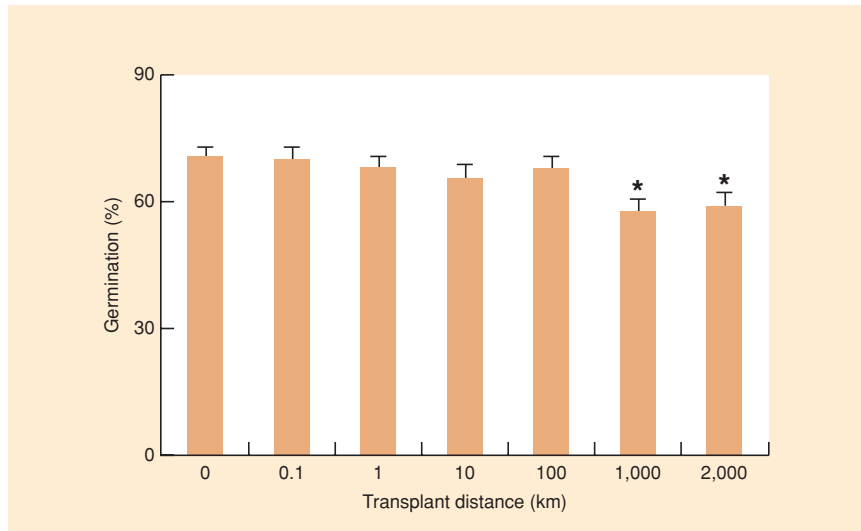
Figure 2.3
When plants of the rare sapphire rockcress from low elevation (drought prone) and high elevation sites were grown together in a common garden, there was local adaptation; those from the low elevation site had significantly better water use efficiency as well as having both taller and broader rosettes. (From McKay et al., 2001.)

Figure 2.4
(a) Map of Abraham's Bosom, the site chosen for a study of evolution over very short distances. The green area is grazed pasture; the pale brown area is cliffs falling to the sea. The numbers indicate sites from which the grass *Agrostis stolonifera* was sampled. Note that the whole area is only 200 m long. (b) A vertical transect across the study area showing a gradual change from pasture to cliff conditions. (c) The mean length of stolons produced in the experimental garden from samples taken from the transect. (From Aston & Bradshaw, 1966.)
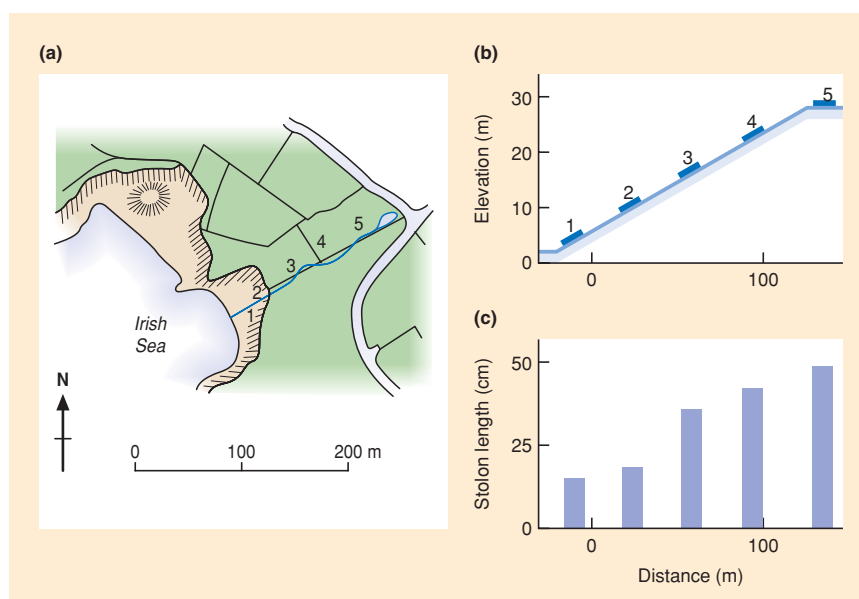
from disturbed habitats in eastern North America, plants were grown in a common garden that were derived from the "home" site or were transplanted from distances of 0.1, 1, 10, 100, 1,000, and 2,000 km (Galloway & Fenster, 2000). The study was replicated three times—in Kansas, Maryland, and northern Illinois. Five characteristics

were measured: germination, survival, vegetative biomass, fruit production, and the number of fruit produced per seed planted; but for all characters in all replicates there was little or no evidence for local adaptation except at the very furthest spatial scales (Figure 2.5). There is "local adaptation"—but it's clearly not *that* local.

We can also test whether organisms have evolved to become specialized to life in their local environment in *reciprocal transplant* experiments (see Figure 2.2), comparing their performance when they are grown "at home" (i.e., in their original habitat) with their performance "away" (i.e., in the habitat of others).

It can be difficult to detect the local specialization of animals by transplanting them into each other's habitat: if they do not like it, most species will run away. But invertebrates like corals and sea anemones are sedentary, and some can be lifted from one place and established in another. The sea anemone *Actinia tenebrosa* is found in pools on headlands around the coast of New South Wales, Australia. Ayre (1985) chose three colonies on headlands within 4 km of each other on which the anemone was abundant. Within each colony, he selected three transplant sites (each 3–5 m long) and at each he set aside three 1 m wide strips—two to receive anemones from the away sites and one to receive "transplanted" individuals from the home site itself. Ayre cleared the experimental sites of all the anemones present and transplanted anemones into them. The anemone multiplies clonally by producing broods of asexual juveniles. The number of juveniles brooded per adult was used as a measure of the performance of the anemones in the various pools (home and away).

The proportion of adults that were found brooding 11 months later is shown in Table 2.1. Anemones originally sampled from Green Island were rather successful in brooding young after being transplanted both home and away and did not show any specialization to their home environment. However, in all the other transplant experiments a greater proportion of anemones brooded young at home than at away sites: strong evidence of evolved local specialization. In later experiments Ayre (1995) lifted anemones from a variety of sites as before, but he then kept them for a period to

reciprocal transplants test the match between organisms and their environment—sea anemones transplanted into each other's habitats

Table 2.1
A reciprocal transplant experiment of the sea anemone *Actinia tenebrosa*. (From Ayre, 1985.)

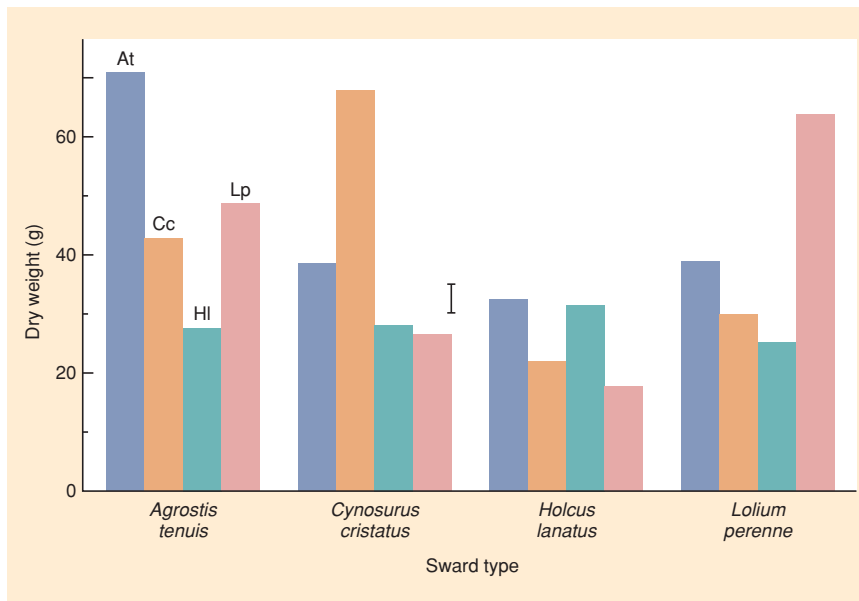| Site of origin		Transplanted to sites at:		
		Green Island	Salmon Point	Strickland Bay
Green Island	a	**0.42**	0.68	0.78
	b	**0.80**	0.63	0.75
	c	**0.67**	0.62	0.61
Salmon Point	a	0.11	**0.42**	0.13
	b	0.18	**0.43**	0.28
	c	0.00	**0.50**	0.40
Strickland Bay	a	0.11	0.06	**0.33**
	b	0.00	0.06	**0.27**
	c	0.04	0.20	**0.27**

a, b, and c are the three replicate sites in each colony. In each case the proportion of adults that were found brooding young is shown. Transplants back to the home sites are shown in bold print.

acclimate at a common site before transplanting them in a reciprocal experiment. This more severe test convincingly confirmed the results in Table 2.1.

a reciprocal transplant experiment involving a plant

Another reciprocal transplant experiment was carried out with white clover (*Trifolium repens*), which forms clones in grazed pastures. Individual clones differ in features such as the pattern of white markings on the leaves, ability to release hydrogen cyanide when damaged or bitten, and susceptibility to various diseases. To determine whether the characteristics of individual clones matched local features of their environment, Turkington and Harper (1979) removed plants from marked positions in the field and multiplied them into clones in the common environment of a greenhouse. They then transplanted samples from each clone into the place in the sward of vegetation from which it had originally been taken, and also to places from where all the others had been taken. The plants were allowed to grow for a year before they were removed, dried, and weighed. The mean weight of clover plants transplanted back into their home sites was 0.89 g, but at away sites it was only 0.52 g, a statistically highly significant difference.

The clover plants studied were not random samples but had been chosen from patches dominated by four different species of grass. Hence, in a second experiment, clonal samples of the different clovers were planted into dense experimental plots of the four grasses. Again the clovers were removed after 12 months, dried, and weighed; the results are shown in Figure 2.6. The mean yield of clovers grown with their original neighbor grass was 59.4 g; the mean yield with "alien" grasses was 31.9 g, again a highly significant difference. Thus, both clover experiments provide strong direct evidence that clover clones in the pasture had evolved to become specialized, such that they tended to perform best (make most growth) in their local environment and with their local neighbors.

natural selection by predation— a controlled field experiment in fish evolution

In most of the examples so far, geographic variants of species have been identified, but the selective forces favoring them have not. This is not true of the next example. The guppy (*Poecilia reticulata*), a small freshwater fish from northeastern South America, has been the material for a classic series of evolutionary experiments. In Trinidad, many rivers flow down the northern range of mountains and are subdivided by waterfalls that isolate fish populations above the falls from those below. Guppies are present in almost all these water bodies, and in the lower waters they meet various species of predatory fish that are absent higher up the rivers. The populations of guppies in Trinidad differ from each other in almost every feature that biologists have examined. Forty-seven of these traits tend to vary in step with each other (they *covary*) and with the intensity of the risk from predators. This correlation suggests that the guppy populations have been subject to natural selection from the predators. But the fact that two phenomena are correlated does not prove that one causes the other. Only controlled experiments can establish cause and effect.

Where guppies have been free or relatively free from predators, the males are brightly decorated with different numbers and sizes of colored spots (Figure 2.7). Females are dull and dowdy and (at least, to us) inconspicuous. Whenever we study natural selection in action, it becomes clear that compromises are involved. For every selective force that favors change, there is a counteracting force that resists the change. Color in male guppies is a good example. Female guppies prefer to mate with the most gaudily decorated males—but these are more readily captured by predators because they are easier to see.

This sets the stage for some revealing experiments on the ecology of evolution. Guppy populations were established in ponds in a greenhouse and exposed to different intensities of predation. The number of colored spots per guppy fell sharply and rapidly when the population suffered heavy predation (Figure 2.8a). In a field

Figure 2.7
Male and female guppies (*Poecilia reticulata*) showing two flamboyant males, courting a typical dull-colored female. (Courtesy of Anne Magurran.)

Figure 2.8
(a) An experiment showing changes in populations of guppy *Poecilia reticulata,* exposed to predators in experimental ponds. The graph shows changes in the number of colored spots per fish in ponds with different populations of predatory fish. The initial population was deliberately collected from a variety of sites so as to display high variability and was introduced to the ponds at time 0. At time S weak predators (*Rivulus hartii*) were introduced to ponds R; a high intensity of predation by the dangerous predator *Crenicichila alta* was introduced into ponds C; while ponds K continued to contain no predators (the vertical lines show ± two standard errors). (b) Results of a field experiment showing changes in the size, number, and color diversity of guppy spots. A population of guppies originating in a locality with dangerous predators (c) was transferred to a stream having only a weak predator (*Rivulus hartii*) and, until the introduction, no guppies (x). Another stream nearby with guppies and *R. hartii* served as a control (r). The results shown are from guppies collected at the three sites 2 years after the introductions. Note how x and r have converged and changed dramatically from c. (After Endler, 1980.)
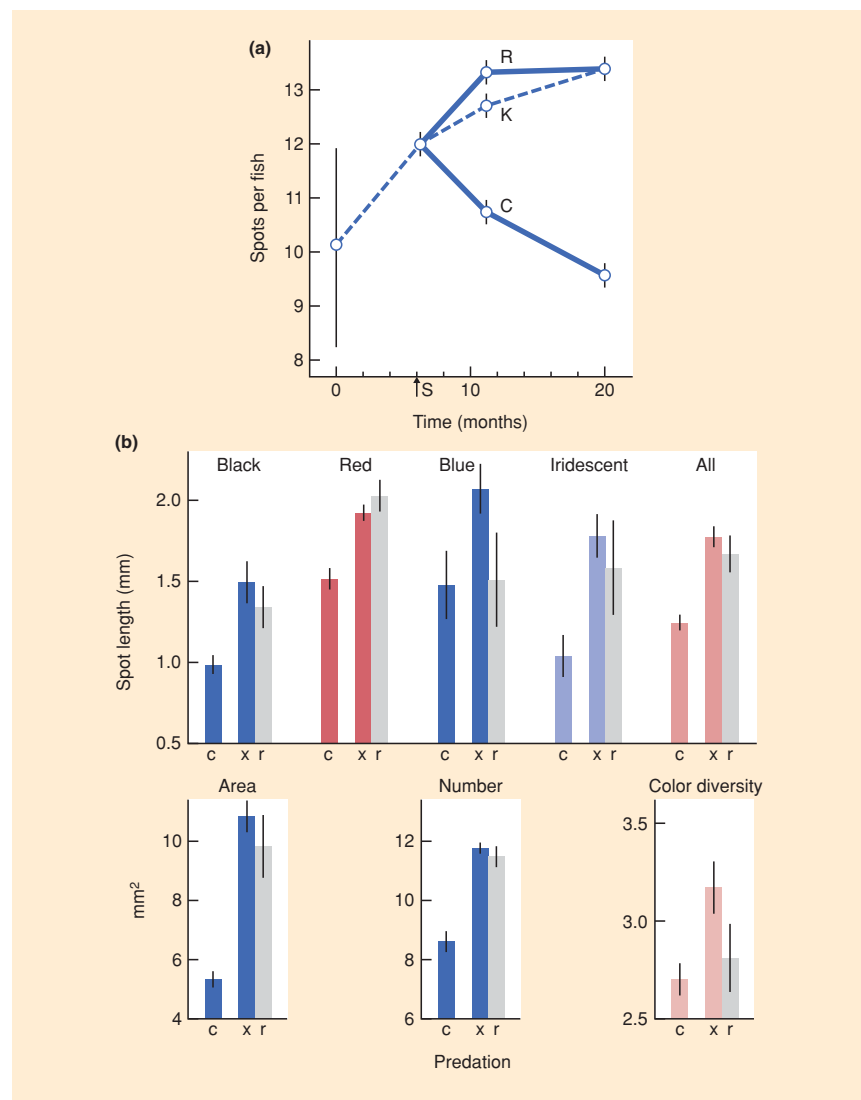
experiment, 200 guppies were moved from a site far down the Aripo River where predators were common and introduced to a site high up the river where there were neither guppies *nor* predators. The transplanted guppies thrived in their new site, and within just 2 years the males had more and bigger spots of more varied color (Figure 2.8b). The females' choice of the more flamboyant males had had dramatic effects on the gaudiness of their descendants, but this was only because predators did not reverse the direction of selection.

The speed of evolutionary change in this experiment in nature was as fast as that in artificial selection experiments in the laboratory. There was plenty of overpopulation (as many as 14 generations of fish occurred in the 23 months during which the experiment took place) and there was considerable genetic variation in the populations upon which natural selection could act. The guppies transplanted into the nearly predator-free environment evolved in other respects too. The females were larger and older at maturity, they produced fewer but bigger offspring, and they began to lose the habit of moving together in schools—behavior that defends them against predators (Endler, 1980; Magurran, 1998).

2.3.2   Variation within a species with man-made selection pressures

It is not surprising that some of the most dramatic examples of natural selection in action have been driven by the ecological forces of environmental pollution—these can provide rapid change under the influence of powerful selection pressures. Pollution of the atmosphere in and after the Industrial Revolution has left evolutionary fingerprints in the most unlikely places. *Industrial melanism* is the phenomenon in which black or blackish forms of species of moths and other organisms have come to dominate populations in industrial areas. In the dark individuals, a dominant gene is responsible for producing an excess of the black pigment melanin. Industrial melanism is known in most industrialized countries, including some parts of the United States (e.g., Pittsburgh), and more than a hundred species of moth have evolved forms of industrial melanism.

natural selection by pollution—the evolution of a melanic moth
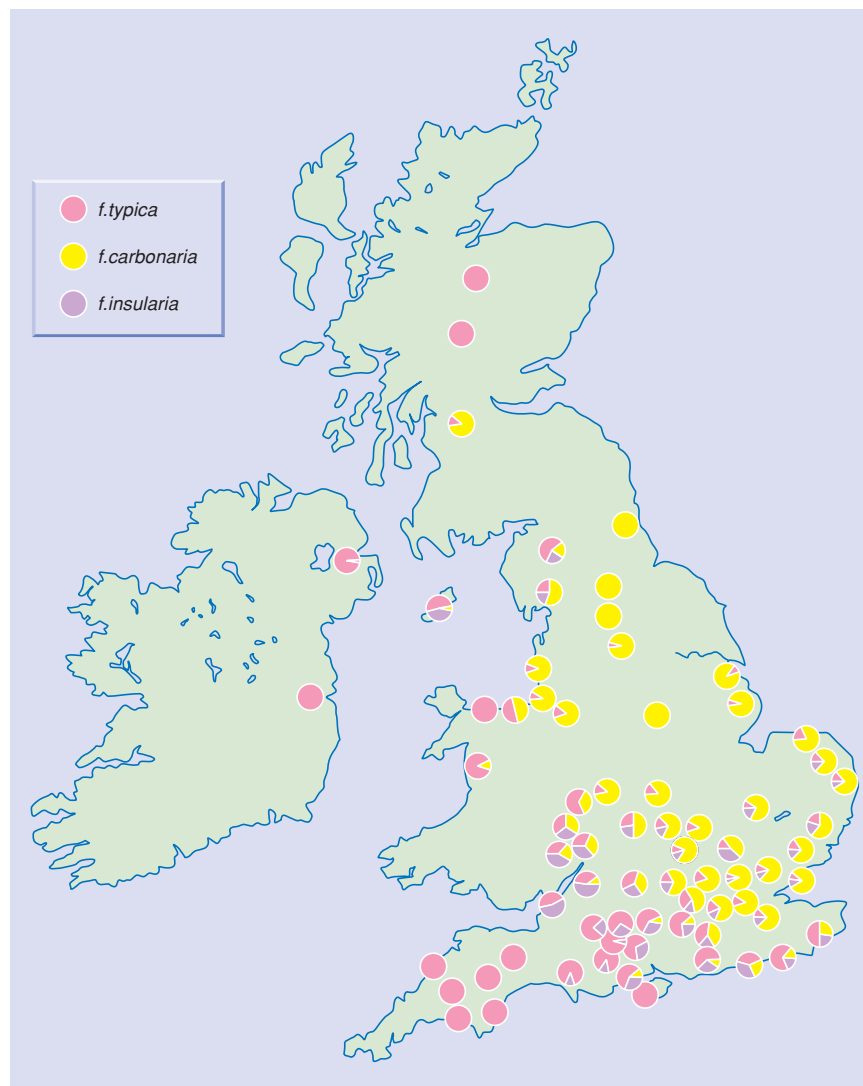
The earliest recorded species to evolve in this way was the peppered moth (*Biston betularia*); the first black specimen was caught in Manchester (England) in 1848. By 1895, about 98 percent of the Manchester peppered moth population was melanic. Following many more years of pollution, a large-scale survey of pale and melanic forms of the peppered moth in Britain recorded more than 20,000 specimens between 1952 and 1970 (Figure 2.9). The winds in Britain are predominantly westerlies, spreading industrial pollutants (especially smoke and sulfur dioxide) toward the east. Melanic forms were concentrated toward the east and were completely absent from unpolluted western parts of England and Wales, northern Scotland, and Ireland.

The moths are preyed upon by insectivorous birds that hunt by sight. In a field experiment, large numbers of melanic and pale ("typical") moths were reared and released in equal numbers in a rural and largely unpolluted area of southern England. Of the 190 moths that were captured by birds, 164 were melanic and 26 were typicals. An equivalent study was made in an industrial area near the city of Birmingham. Twice as many melanics as typicals were recaught. This showed that a significant selection pressure was exerted through bird predation, and that moths of the typical form were

clearly at a disadvantage in the polluted industrial environment (where their light color stood out against a sooty background), whereas the melanic forms were at a disadvantage in the pollution-free countryside (Kettlewell, 1955).

In the 1960s, however, industrialized environments in Western Europe and the United States started to change as oil and electricity began to replace coal and legislation was passed to impose smoke-free zones and to reduce industrial emissions of sulfur dioxide (Chapter 13). The frequency of melanic forms then fell back to near preindustrial levels with remarkable speed (Figure 2.10).

The forces of selection at work, first in favor and then against melanic forms, have clearly been related to industrial pollution, but the idea that melanic forms were favored simply because they were camouflaged against smoke-stained backgrounds
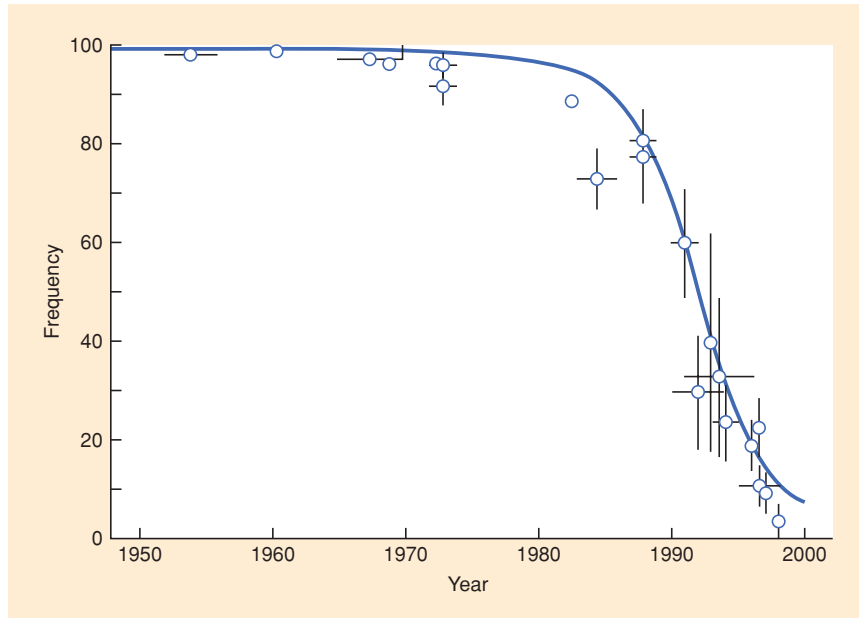
may be only part of the story. The moths rest on tree trunks during the day, and non-melanic moths are well hidden against a background of mosses and lichens. Industrial pollution has not just blackened the moths' background; atmospheric pollution, especially SO_2, has also destroyed most of the moss and lichen on the tree trunks. Indeed the distribution of melanic forms in Figure 2.9 closely fits the areas in which tree trunks were likely to have lost lichen cover as a result of SO_2 and so ceased to provide such effective camouflage for the nonmelanic moths. Thus SO_2 pollution may have been as important as smoke in selecting melanic moths.

Some plants are tolerant of another form of pollution: the presence of toxic heavy metals such as lead, zinc, and copper, which contaminate the soil after mining. Populations of plants on contaminated areas may be tolerant, while at the edge of these areas a transition from tolerant to intolerant forms can occur over very short distances (Figure 2.11). In some cases it has been possible to measure the speed of evolution. Zinc-tolerant forms of two species of grass *Agrostis capillaris* were found to have evolved under zinc-galvanized electricity pylons within 20–30 years of their erection (Al-Hiyaly et al., 1988).

natural selection by pollution— evolution of heavy-metal tolerance in plants

2.3.3   Adaptive peaks and specialized abysses

Natural selection changes the character of a population by sifting out and eliminating much of its variation and leaving behind a residue for future generations with a narrower range and more restricted potential. This is commonly pictured as a force that drives populations toward a peak of *adaptation*—of a perfect match between organism and environment. This is an optimist's view (Figure 2.12a). An alternative picture of

Figure 2.11

The grass *Anthoxanthum odoratum* colonizes land heavily contaminated with zinc (Zn) on an old mine. This is possible because the grass has evolved zinc-tolerant forms. Samples of the grass were taken along a transect from a mine (Trelogan) into surrounding grassland (zinc concentrations in the soil are shown as parts per million), and were tested for zinc tolerance by measuring the length of roots that they produced when grown in a culture solution containing excess zinc. The index of zinc tolerance falls off steeply over a distance of 2–5 m at the mine boundary. (After Putwain, in Jain & Bradshaw, 1966.)
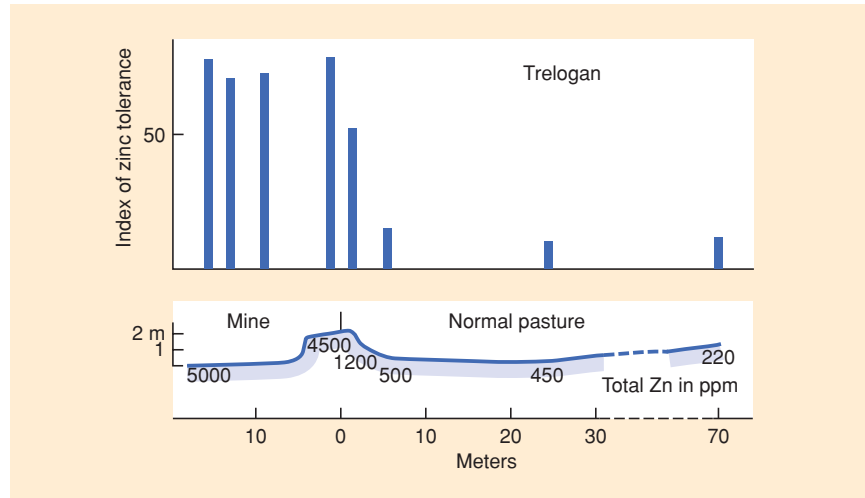
Figure 2.12

Two models of natural selection in action: (a) an optimistic and (b) a pessimistic interpretation of natural selection. In both (a) and (b) a horizontal plane is drawn to represent two dimensions of a range of environmental conditions. On both diagrams ellipses are drawn to show the range of this variation that is tolerated by four populations of organisms. (a) In the optimistic view, the vertical scale is a measure of the range of fitness of the organisms in the populations and natural selection is shown as arrows driving the population to ever higher "adaptive" peaks. Population 1 is highly variable and tolerates a wide range of conditions. Natural selection is relatively weak. Population 2 is a very uniform population, and natural selection is fierce and driving the population to a very high degree of specialization and local fitness. (b) In the pessimistic view, natural selection is shown as arrows driving the populations into ruts, troughs, and pits. The vertical downward axis is a measure of the intensity of specialization. The highly variable population with weak selection is rather safe if the environment changes but population 2 is at extreme risk of extinction. The two depictions should not be seen as one right and one wrong impression of natural selection in action, but rather as two views of the same truths.
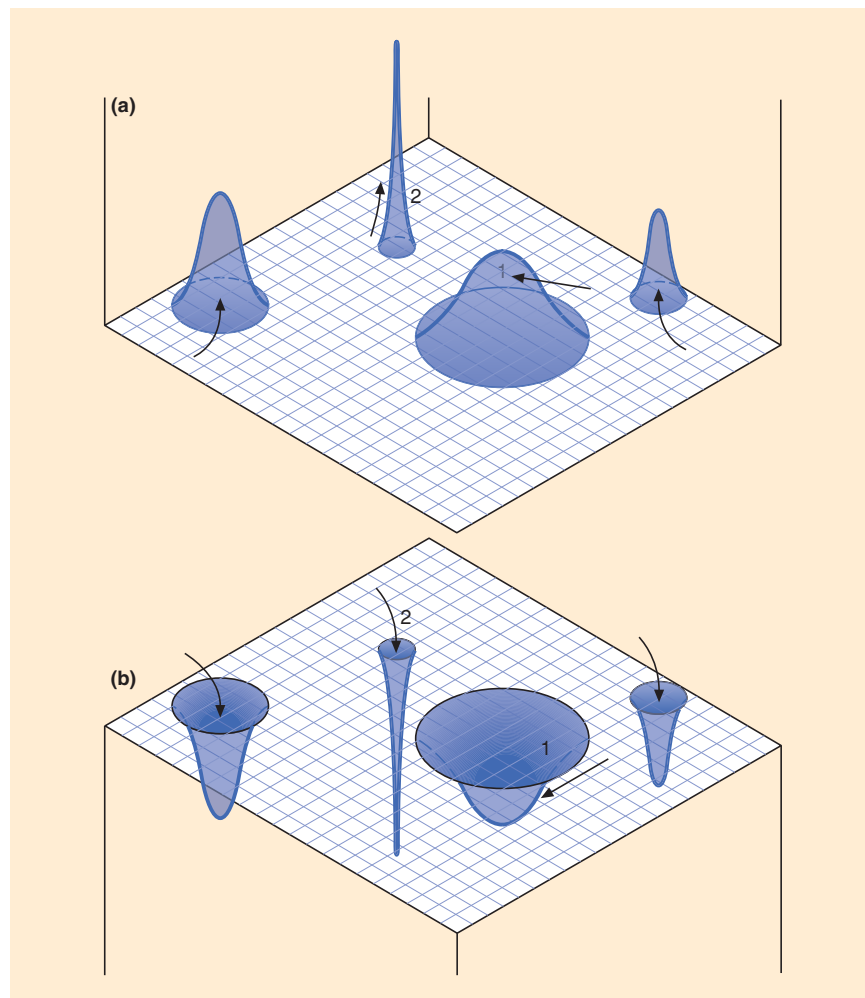
natural selection is that it forces populations into an ever-narrowing rut of overspecialization—an ever-deepening trap (Figure 2.12b). This pessimist's view emphasizes how the effects of natural selection are to limit and constrain, and that the specialization of species means that they risk extinction when the environment changes.

It is easy to see that a population of plants faced with repeated drought is likely to evolve a tolerance of water shortage, and an animal repeatedly faced with cold winters is likely to evolve habits of hibernation or a thick protective coat. But droughts do not become any less severe as a result, nor winters milder. Physical conditions are not heritable: they leave no descendants, and they are not subject to natural selection.

But the situation is quite different when two species interact: predator on prey, parasite on host, competitive neighbor on neighbor. Natural selection may select from a population of parasites those forms that are more efficient at infecting their host. But this immediately sets in play forces of natural selection that favor more resistant hosts. As they evolve they put further pressure on the ability of the parasite to infect. Host and parasite are then caught in never-ending reciprocating selection. A result is that both host and parasite become increasingly specialized—caught in an ever-deepening rut. Eventually only a specialized form of the parasite can infect and can do so only on a highly specialized form of the host. We will find examples of this extreme form of natural selection—coevolution—when we consider organisms as habitats in Chapter 7.

natural selection does not act on physical conditions . . .

. . . but parasites, predators, and competitors can all be both forces of natural selection and objects of selection

2.4   The Ecology of Speciation

We have seen that natural selection can force populations of plants and animals to change their character—to evolve. But none of the examples we have considered has involved the evolution of a new species. Indeed Darwin's *On the Origin of Species* is about natural selection and evolution but is not really about the origin of species! Those who studied the evolution of melanism in the peppered moth named the black and normal forms *forma carbonaria* and *forma typica*: they classified them as forms within a species, not as different species. Likewise the different growth forms of the grasses on the cliffs and pastures of Abraham's Bosom and the dull and flamboyant races of guppies are just local genetic classes. None qualifies for the status of distinct species. But when we ask just what criteria justify naming two populations as different species we meet real problems.

2.4.1   What do we mean by a "species"?

Cynics have said, with some truth, that a species is what a competent taxonomist regards as a species! Darwin himself regarded species (like genera) as "merely artificial combinations made for convenience". On the other hand, back in the 1930s, two American biologists, Ernst Mayr and Theodosius Dobzhansky, proposed an empirical test that could be used to decide whether two populations were part of the same or of two different species. They recognized organisms as being members of a single species if they could, at least potentially, breed together in nature to produce fertile offspring. They called a species tested and defined in this way a *biospecies*. In the examples that we have used earlier in this chapter we know that melanic and normal peppered moths

Figure 2.13
The role of isolation in the evolution of species. A uniform species with a large range (1) differentiates (2) into local forms, varieties, or subspecies, which (3) become genetically isolated from each other, for example, separated by geographical barriers or dispersed onto different islands. After evolution in isolation they may meet again (4) when they are unable to hybridize and have become true biospecies.
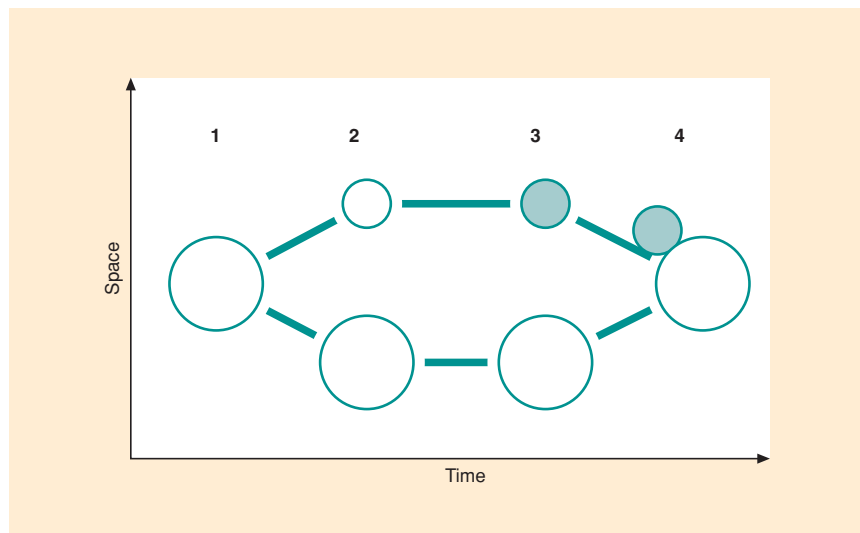
can mate and that the offspring are fully fertile; this is also true of colored and dull guppies and of plants from the different types of *Agrostis*. They are all variations within species—not separate species.

In practice, however, biologists do not apply the Mayr–Dobzhansky test before they recognize every species: there is simply not enough time and resources; but it is there to resolve arguments if they arise. What is more important is that the test recognizes a crucial element in the evolutionary process. If the members of two populations are able to hybridize and their genes are combined and reassorted in their progeny, then natural selection can never make them truly distinct. Although natural selection may tend to force a population to evolve into two or more distinct forms, sexual reproduction and hybridization mix them up again.

biospecies do not exchange genes

Two parts of a population can evolve into distinct species only if some sort of barrier prevents gene flow between them; they might, for example, be isolated on different islands. While isolated from each other they may then evolve and become so different that, if they meet again, they can no longer hybridize and their populations can no longer exchange genes. They are now different biospecies. Figure 2.13 illustrates this process.

Differences that are particularly effective in keeping newly evolved species distinct are different rituals of courtship, different signals of attraction between the sexes, and in flowering plants, different species of insect pollinator. It may sometimes happen that hybrids form between two evolving species but their parental chromosomes have become so different that they fail to pair at meiosis: the hybrids are then sterile (for example, the horse–donkey hybrid is the sterile mule).

evolution in sea gulls

The evolution of species and the balance between natural selection and hybridization are illustrated by the extraordinary case of two species of sea gull. The lesser black-backed gull (*Larus fuscus*) originated in Siberia and colonized progressively to the west, forming a chain or *cline* of different forms, spreading from Siberia to Britain and Iceland (Figure 2.14). The neighboring forms along the cline are distinctive, but
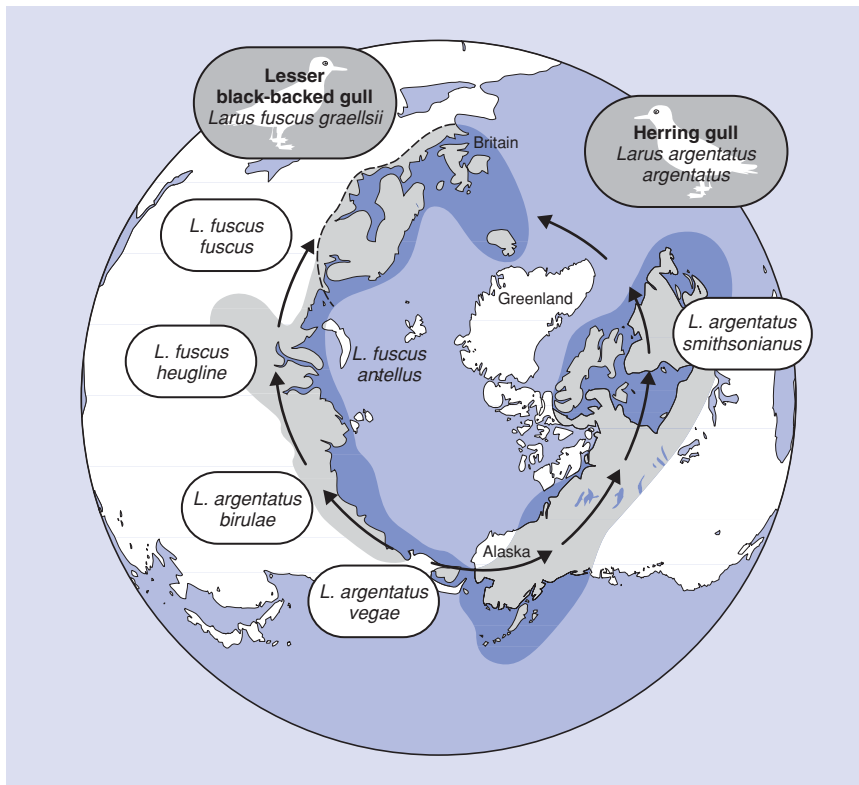
they hybridize readily in nature. Neighboring populations are therefore regarded as part of the same species and taxonomists give them only "subspecific" status (e.g., *Larus fuscus graellsii*, *Larus fuscus fuscus*). Populations of the gull have, however, also spread east from Siberia, again forming a cline of freely hybridizing forms. Together, the populations spreading east and west encircle the northern hemisphere. They meet and overlap in northern Europe. There, the eastward and westward clines have diverged so far that it is easy to tell them apart, and they are recognized as two different *species*, the lesser black-backed gull (*Larus fuscus*) and the herring gull (*Larus argentatus*). Moreover, the two species do not hybridize: they have become true biospecies.

In this remarkable example we can see how two distinct species have evolved from one primal stock, and that the stages of their divergence remain frozen in the cline that connects them. But it is where a population becomes split into completely isolated populations, dispersed onto different islands for example, that they most readily diverge into distinct species.

2.4.2 Islands and speciation

The most celebrated example of evolution and speciation on islands is the case of Darwin's finches in the Galapagos archipelago. Darwin had been chided for

Darwin's finches

underestimating the importance of isolation in the evolution of species but responded (in a letter, 1876), "It would have been a strange fact if I had overlooked the importance of isolation, seeing that it was such cases as that of the Galapagos archipelago which chiefly led me to study the evolution of species."

The Galapagos are volcanic islands isolated in the Pacific Ocean about 1000 km west of Equador and 750 km from the island of Cocos, which is itself 500 km from Central America. At more than 500 m above sea level the vegetation is open grassland. Below this is a humid zone of forest that grades into a coastal strip of desert vegetation with some endemic species of prickly pear cactus (*Opuntia*). Fourteen species of finch are found on the islands, and there is every reason to suppose that these evolved from a single ancestral species that invaded the islands from the mainland of Central America.

In their remote island isolation, the Galapagos finches have radiated into a variety of species in groups with contrasting ecologies (Figure 2.15). Members of one group, including *Geospiza fuliginosa* and *G. fortis*, have strong bills and hop and scratch for seeds on the ground. *Geospiza scandens* has a narrower and slightly longer bill and feeds on the flowers and pulp of the prickly pears as well as on seeds. Finches of a third group have parrot-like bills and feed on leaves, buds, flowers, and fruits, and a fourth group with a parrot-like bill (*Camarhynchus psittacula*) has become insectivorous, feeding on beetles and other insects in the canopy of trees. A so-called woodpecker finch, *Camarhynchus* (*Cactospiza*) *pallida*, extracts insects from crevices by holding a spine or a twig in its bill. Yet a further group includes a species (*Certhidea olivacea*) that, rather like a warbler, flits around actively and collects small insects in the forest canopy and in the air. Populations of ancestor species became reproductively isolated, most likely after chance colonization of different islands within the archipelago, and evolved separately for a time. Subsequent movements between islands may have brought non-hybridizing biospecies together, and subsequently these have evolved to fill different niches. We will see in Chapter 6 that when individuals from different species compete, natural selection may act to favor those individuals that compete least with members of the other species. An expected consequence is that among a group of closely related species, such as Darwin's finches, differences in feeding and other aspects of their ecology are likely to become enhanced with time.

The entire process of evolutionary divergence of these species appears to have happened in less than 3 million years. Very rarely, hybridization occurs among species that have similar ecologies. However, these occasions are so rare that the species are true or emerging biospecies. We need to remember that the origin of a species is normally a process rather than an event. For the formation of a new species, like the boiling of an egg, there is some freedom to argue about when it is completed!

The evolutionary relationships among the various Galapagos finches have been traced by molecular techniques (analyzing variation in "microsatellite" DNA) (Petren et al., 1999) (Figure 2.15). These accurate modern tests confirm the long-held view that the family tree of the Galapagos finches radiated from a single trunk (i.e., was *monophyletic*) and also provides strong evidence that the warbler finch (*Certhidea olivacea*) was the first to split off from the founding group and is likely to be the most similar to the original colonist ancestors.

The flora and fauna of many other archipelagos show similar examples of great richness of species with many local *endemics* (i.e., species known only from one island or area). The Hawaiian Islands are home to an extraordinary diversity of picture-winged
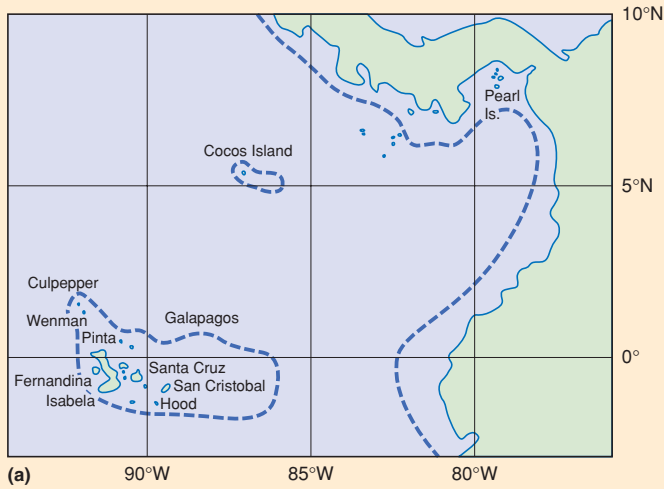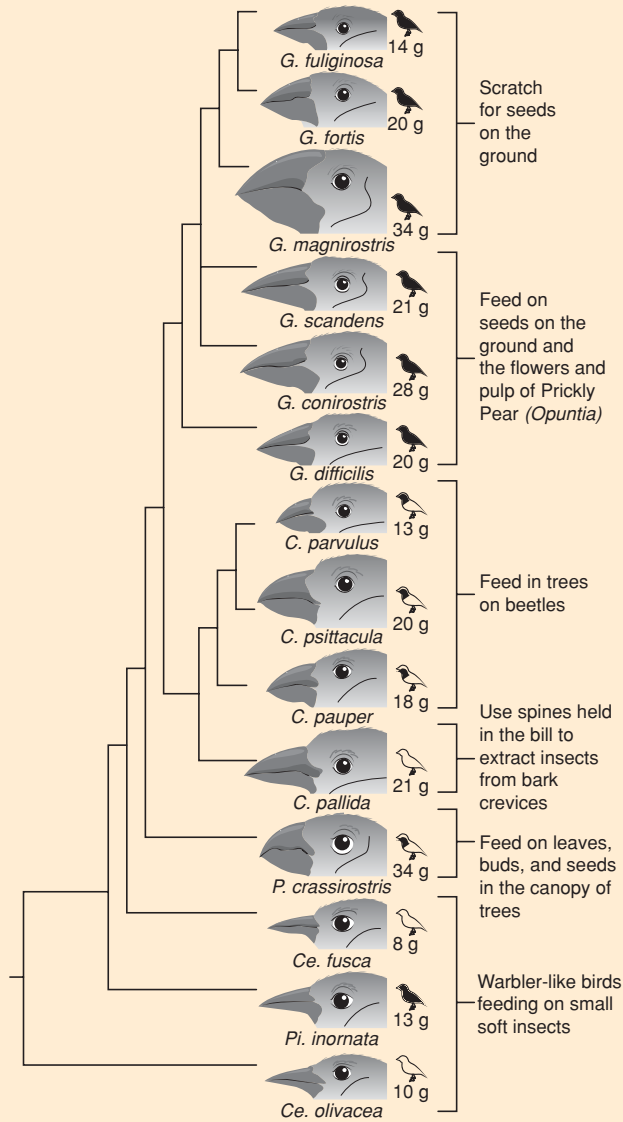
Figure 2.15
(a) Map of the Galapagos Islands showing their position relative to Central America; on the equator 5° equals approximately 560 km. (b) A reconstruction of the evolutionary history of the Galapagos finches based on variation in the length of microsatellite DNA. The feeding habits of the various species are also shown. Drawings of the birds are proportional to actual body size. The maximum amount of black coloring in the male plumage and the average body mass are shown for each species. The *genetic distance* (a measure of the genetic difference) between species is shown by the length of the horizontal lines. Notice the great and early separation of the warbler finch (*Certhidea olivacea*) from the others, suggesting that it may closely resemble the founders that colonized the islands. *C.*, *Camarhynchus*; *Ce.*, *Certhidea*; *G.*, *Geospiza*; *P.*, *Platyspiza*; *Pi.*, *Pinaroloxias*. (After Petren et al., 1999.)

fruit flies (species of *Drosophila*) and closely related species of honey creeper that have diverged in feeding habit and bill shape remarkably like the Galapagos finches. Lizards of the genus *Anolis* have evolved a kaleidoscopic diversity of species on the islands of the Caribbean; and isolated groups of islands, such as the Canaries off the coast of North Africa, are treasure troves of endemic plants. These unusual and often rich communities may pose particular problems for the applied ecologist (Box 2.2).

Invaders onto marine islands may become isolated from other parts of their population and are then free to diverge under natural selection and become different species. But there are other kinds of "islands" in which colonists can also become genetically

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Box 2.2   *Topical ECOncerns*

Deep Sea Vent Communities at Risk

Deep sea vents are islands of warmth in oceans (literally and metaphorically) that are otherwise cold and inhospitable. As a consequence, they support unique communities, rich in endemic species. One of the latest controversies to pit environmentalists against industrialists concerns these deep sea vents (see figure), which are also now known to be sites rich in minerals. This newspaper article by William J. Broad appeared in the *San Jose Mercury News*, January 20, 1998:

> With miners staking claim to valuable metals lying in undersea lodes in the South Pacific, questions surface about how to prevent

A deep sea vent community (© Whoi, J. Edmond, Visuals Unlimited).

disasters in these fragile, little understood ecosystems.

The volcanic hot springs of the deep sea are dark oases that teem with blind shrimp, giant tube worms and other bizarre creatures, sometimes in profusions great enough to rival the chaos of rain forests. And they are old.

Scientists who study them say these odd environments, first discovered two decades ago, may have been the birthplace of all life on Earth, making them central to a new wave of research on evolution.

Now, in a moment that diverse ranks of experts have feared and desired for years, miners are invading the hot springs, possibly setting the stage for the last great battle between industrial development and environmental preservation.

The undersea vents are rich not just in life but in valuable minerals such as copper, silver and gold. Indeed, their smoky chimneys and rocky foundations are virtual foundries for precious metals. . . . The fields of undersea gold have long fired the imaginations of many scientists and economists, but no mining took place, in part because the rocky deposits were hard to lift from depths of a mile or more.

Now, however, miners have staked the first claim to such metal deposits after finding the richest ores ever. The estimated value of copper,

Box 2.2 (cont'd)

silver and gold at a South Pacific site is up to billions of dollars. Environmentalists, though, want to protect the exotic ecosystem by banning or severely limiting mining.

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Consider the following options and debate their relative merits:

1 *Allow the mining industry free access to all deep sea vents, since the wealth created will benefit many people.*

2 *Ban mining and other disruption of all deep sea vent communities, recognizing their unique biological and evolutionary characteristics.*

3 *Carry out biodiversity assessments of known vent communities and prioritize according to their conservation importance, permitting mining in cases that will minimize overall destruction of this category of community.*

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isolated from the rest of a population. Mountains isolate valleys from each other and valleys isolate mountains. A few individuals that chance to be dispersed to a habitable site in a mountain range can form the nucleus of an expanding new species. Its character will have been colored by the particular genes that were represented among the colonists—unlikely to be a perfect sample of the parent population. What natural selection can do with this *founder population* is limited by what is in its limited sample of genes (plus occasional rare mutations). Indeed much of the deviation among populations isolated on islands appears to be due to a *founder effect*—the chance composition of the pool of founder genes puts limits and constraints on what variation there is for natural selection to act upon.
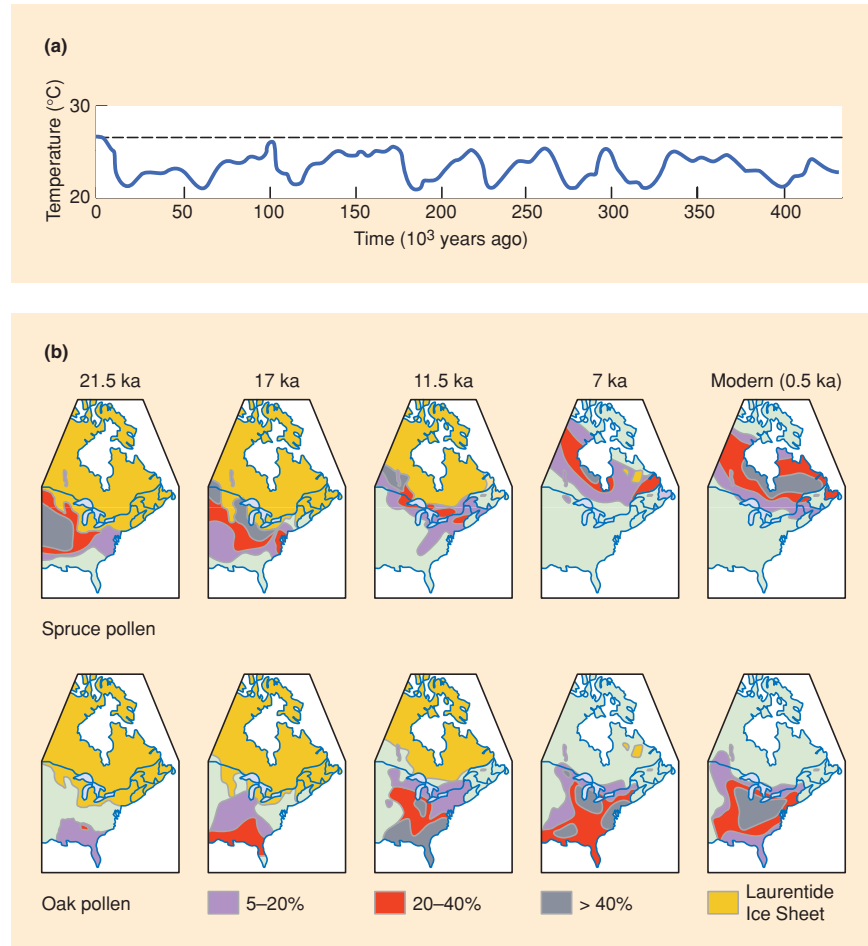
The evolutionary biologist's understanding of island patterns depends on a thorough appreciation of ecological processes such as dispersal (Chapter 5) and interspecific competition (Chapter 6). Likewise, the ecologist's understanding of ecological specialization, species distributions, species diversity, and niche partitioning, among many other ecological phenomena, would be rudimentary indeed without the underpinning provided by the evolutionary processes discussed in this chapter.

2.5 The Effects of Climatic Change on the Evolution and Distribution of Species

Changes in climate, particularly during the ice ages of the Pleistocene (the past 2–3 million years), bear a lot of the responsibility for the present patterns of distribution of plants and animals. As climates have changed, species populations have advanced and retreated, have been fragmented into isolated patches, and may have then rejoined. Much of what we see in the present distribution of species represents phases in a recovery from past climatic change. Modern techniques for analyzing and dating biological remains (particularly buried pollen) are beginning to allow us to detect just how much of the present distribution of organisms is a precise,

(a) An estimate of the temperature variations with time during glacial cycles over the past 400,000 years. The estimates were obtained by comparing oxygen isotope ratios in fossils taken from ocean cores in the Caribbean. The dashed line corresponds to the ratio 10,000 years ago, at the start of the present warming period. Periods as warm as the present have been rare events, and the climate during most of the past 400,000 years has been glacial. (After Emiliani, 1966; Davis, 1976.) (b) Ranges in eastern North America, as indicated by pollen percentages in sediments, of spruce species (above) and oak species (below) from 21,500 years ago to the present. (After Davis & Shaw, 2001.)
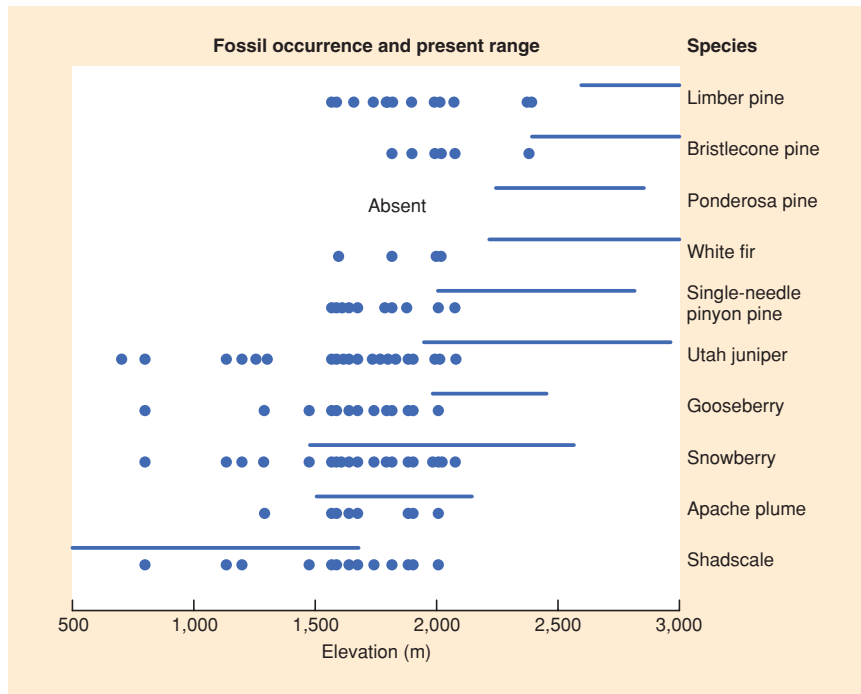

(a)

(b)

21.5 ka   17 ka   11.5 ka   7 ka   Modern (0.5 ka)

Spruce pollen

Oak pollen   5–20%   20–40%   > 40%   Laurentide Ice Sheet

local-evolved match to present environments, and how much is a fingerprint left by the hand of history.

cycles of glaciation have occurred repeatedly

For most of the past 2–3 million years the Earth has been very cold. Evidence from the distribution of oxygen isotopes in cores taken from the deep ocean floor shows that there may have been as many as 16 glacial cycles in the Pleistocene, each lasting for up to 125,000 years (Figure 2.16a). Each cold (glacial) phase may have lasted for as long as 50,000–100,000 years, with brief intervals of only 10,000–20,000 years when the temperatures rose to, or above, those of today. In this case, present floras and faunas are unusual, having developed at the warm end of one of a series of unusual catastrophic warm periods.

the distribution of trees has changed gradually since the last glaciation

During the 20,000 years since the peak of the last glaciation, global temperatures have risen by about 8°C. The analysis of buried pollen—particularly of woody species, which produce most of the pollen—can show how vegetation has changed during this period (Figure 2.16b). As the ice retreated, different forest species advanced in different ways and at different speeds. For some, like the spruce of eastern North America,

there was displacement to new latitudes; for others, like the oaks, the picture was more one of expansion.

We do not have such good records for the postglacial spread of the animals associated with the changing forests, but it is at least certain that many species could not have spread faster than the trees on which they feed. Some of the animals may still be catching up with their plants, and tree species are still returning to areas they occupied before the last ice age! It is quite wrong to imagine that our present vegetation is in some sort of equilibrium with (adapted to) the present climate.

Even in regions that were never glaciated, pollen deposits record complex changes in distributions: range shifts to new regions, large changes in population size, both up and down, and in the mountains of the Sheep Range, Nevada, shifts in elevation range varying in amount and even direction (Figure 2.17). The species composition of vegetation has continually been changing and is almost certainly still doing so.

The records of climatic change in the tropics are far less complete than those for temperate regions. Many believe, though, that during cooler, drier glacial periods, the tropical forests retreated to smaller patches, surrounded by a sea of savanna. Support for this comes from the present-day distribution of species in the tropical forests of South America (Figure 2.18). There, particular "hot-spots" of species diversity are apparent, and these are thought to be likely sites of forest refuges during the glacial periods, and sites too, therefore, of increased rates of speciation (Ridley, 1993). On this interpretation, the present distributions of species may again be seen as largely accidents of history (where the refuges were) rather than precise matches between species and their differing environments.

Figure 2.18 (a) The present-day distribution of tropical forest in South America. (b) The possible distribution of tropical forest refuges at the time when the last glaciation was at its peak, as judged by present-day hot-spots of species diversity within the forest. (After Ridley, 1993.)
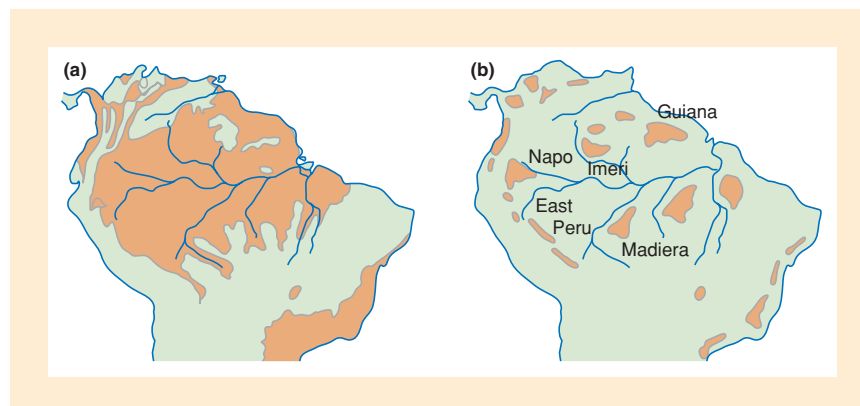
predicted global warming by the "greenhouse effect" is nearly a hundred times faster than postglacial warming

Evidence of changes in vegetation that followed the last retreat of the ice hint at the likely consequences of the global warming (maybe 3°C in the next 100 years) that is predicted to result from continuing increases in "greenhouse" gases in the atmosphere (Chapter 13). But the scales are quite different. Postglacial warming of about 8°C occurred over around 20,000 years, and changes in the vegetation failed to keep pace even with this. But current projections for the 21st century require range shifts for trees at rates of 300–500 km per century compared to typical rates in the past of 20–40 km per century (and exceptional rates of 100–150 km). It is striking that the only precisely dated extinction of a tree species in the Quaternary, that of *Picea critchfeldii*, occurred around 15,000 years ago at a time of especially rapid postglacial warming (Jackson & Weng, 1999). Clearly, future even more rapid change could result in extinctions of many additional species (Davis & Shaw, 2001).

2.6 The Effects of Continental Drift on the Ecology of Evolution

land masses have moved . . .

The patterns of species formation that occur on islands appear on an even larger scale in the evolution of genera and families across continents. Many curious distributions of organisms between continents seem inexplicable as the result of dispersal over vast distances. Biologists, especially Wegener (1915), met outraged scorn from geologists and geographers when they argued that it must have been the continents that had moved rather than the organisms that had dispersed. Eventually, however, measurements of the directions of the Earth's magnetic fields required the same, apparently wildly improbable, explanation and the critics capitulated. The discovery that the tectonic plates of the Earth's crust move and carry the migrating continents with them reconciles geologist and biologist (Figure 2.19). While major evolutionary developments were occurring in the plant and animal kingdoms, their populations were being split and separated, and land areas were moving across climatic zones. This was happening while changes in temperature were occurring on a vastly greater scale than the glacial cycles of the Pleistocene episode.

. . . and divided populations that have then evolved independently

The established drift of the continents answers many questions in the ecology of evolution. The curious world distribution of large flightless birds is one example
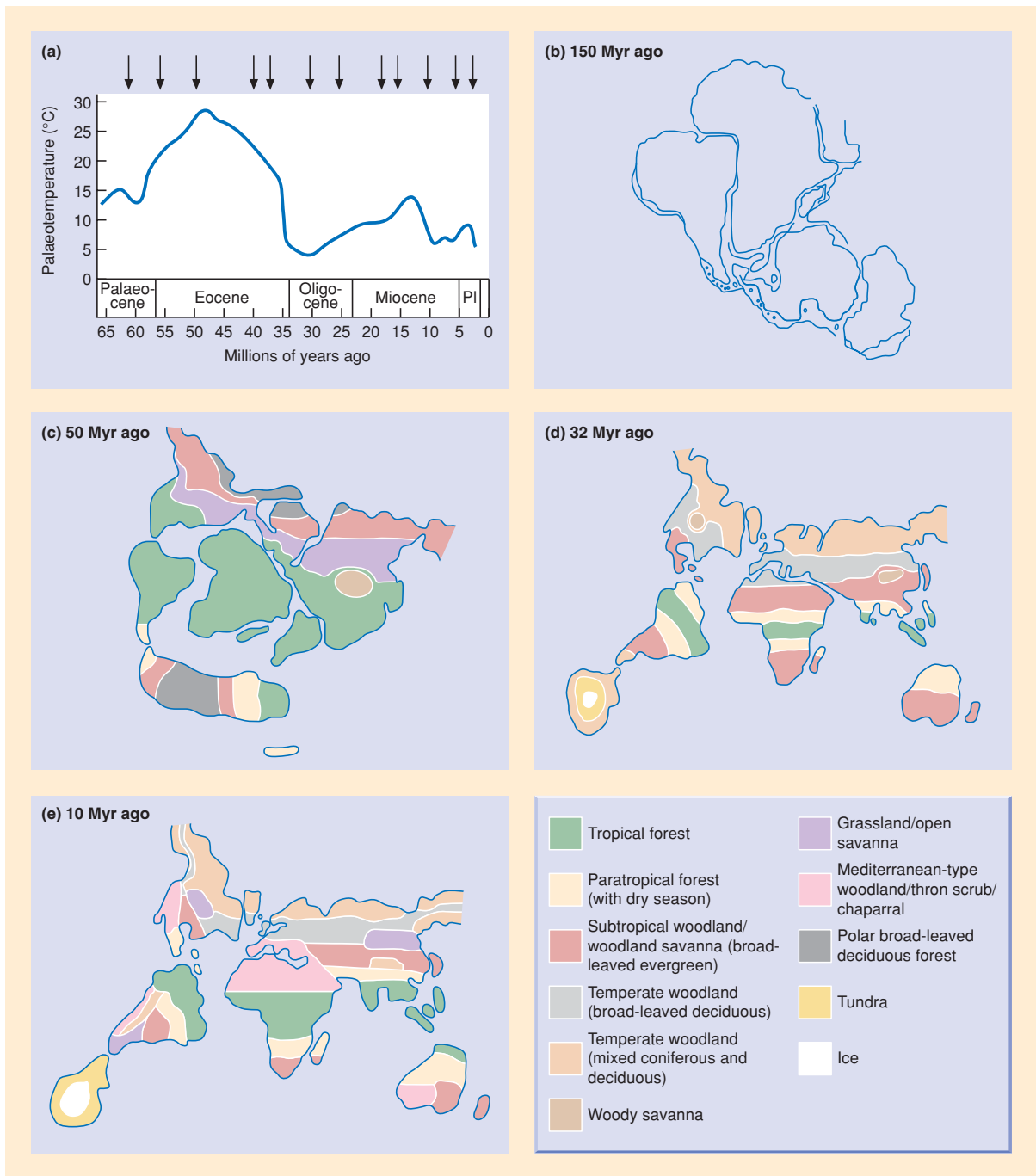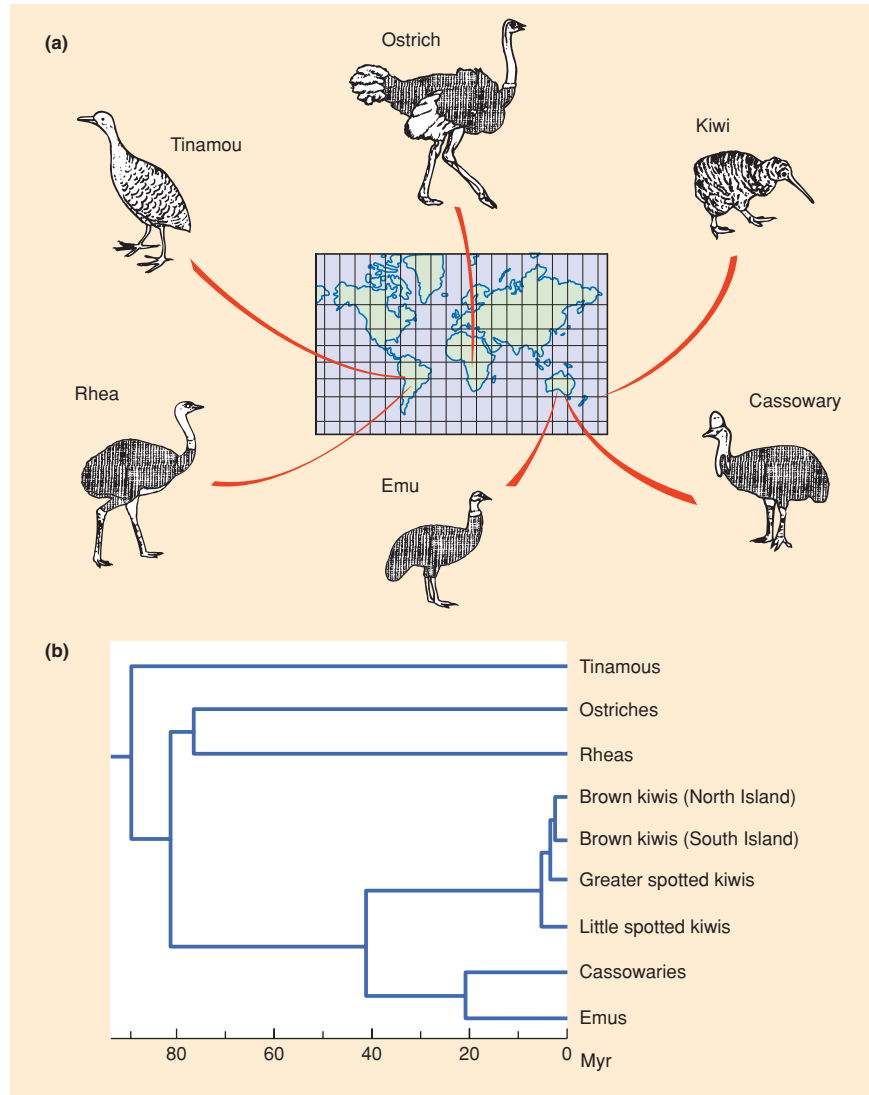
Figure 2.19
(a) Changes in temperature in the North Sea over the past 65 million years. During this period there were large changes in sea level that allowed the dispersal of both plants and animals between land masses. (b–e) Continental drift. (b) The ancient supercontinent of Gondwanaland began to break up about 150 million years ago. (c) About 50 million years ago (early Middle Eocene) recognizable bands of distinctive vegetation had developed, and (d) by 32 million years ago (early Oligocene) these had become more sharply defined. (e) By 10 million years ago (early Miocene) much of the present geography of the continents had become established but with dramatically different climates and vegetation from today: the position of the Antarctic ice cap is highly schematic. (After Norton & Sclater, 1979; Janis, 1993; and other sources.)

(Figure 2.20a). The presence of the ostrich in Africa, the emu in Australia, and the very similar rhea in South America could scarcely be explained by dispersal of some common flightless ancestor. Now, techniques of molecular biology make it possible to analyze the time at which the various flightless birds started their evolutionary divergence (Figure 2.20b). The tinamous seem to have been the first to diverge and became evolutionarily separate from the rest, the *ratites*. Australasia next became separated from the other southern continents, and from the latter, the ancestral stocks of ostriches and rheas were subsequently separated when the Atlantic opened up between Africa and South America. Back in Australasia, the Tasman Sea opened up about 80 million years ago and ancestors of the kiwi are thought to have made their way, by island hopping, about 40 million years ago across to New Zealand, where divergence into the present

(a) (b) (c)
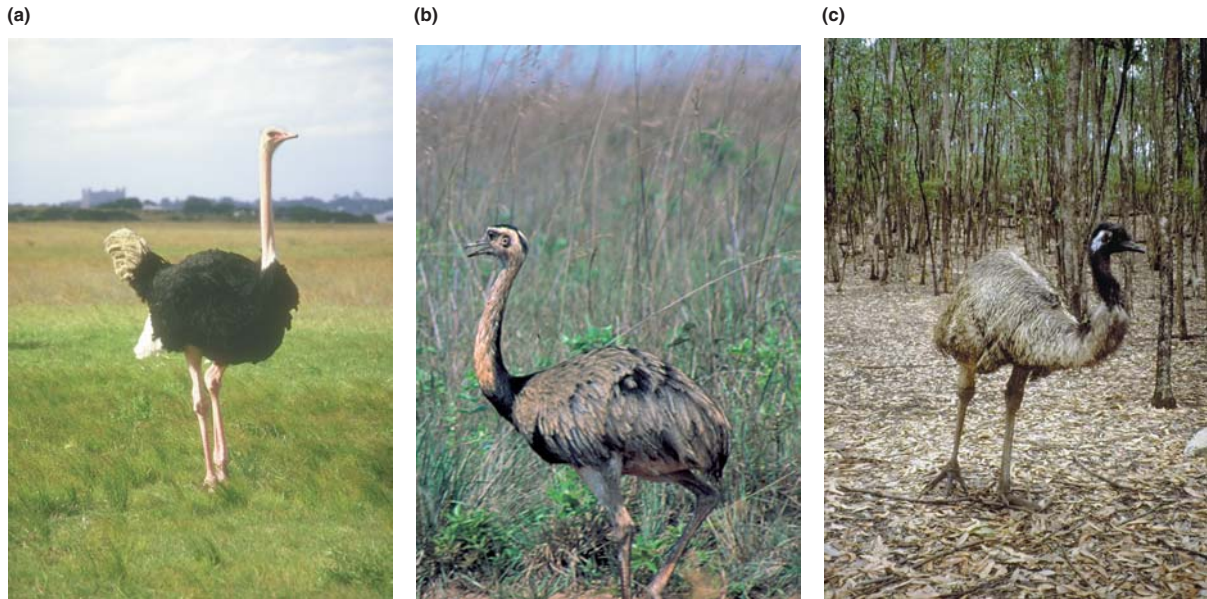
Large flightless birds are found in three major continents. (a) The ostrich (*Struthio camelus*) is African and commonly occurs together with herds of zebra and antelope in savanna or steppe grasslands. (b) The rhea (*Rhea americana*) is found in similar grasslands in South America (e.g., Brazil and Argentina), commonly together with herds of deer and guanocos (© Walt Anderson, Visuals Unlimited). (c) The emu (*Dromaius novaehollandiae*) inhabits equivalent habitats in Australia. Many other species of these very large, mainly herbivorous birds have been sought after by humans for food and have become extinct. The presence of these evolutionarily related and ecologically similar species in three widely separated continents is explained by the drifting apart of the continents from the time (150 million years ago) when they were portions of the primitive continent of Gondwanaland (see Figure 2.19).

species happened relatively recently. The unraveling of this particular example implies the early evolution of the property of flightlessness and only subsequently the isolation of the different types between the emerging continents.

2.7 Interpreting the Results of Evolution: Convergent and Parallel Evolution

Flightlessness did not evolve independently on the different continents. However, there are many examples of organisms that have evolved in isolation from each other and then converged on remarkably similar forms or behavior. Such similarity is particularly striking when similar roles are played by structures that have quite different evolutionary origins—that is, when the structures are *analogous* (similar in superficial form or function) but not *homologous* (derived from an equivalent structure in a common ancestry). When this occurs, it is termed *convergent evolution*. Bird and bat wings are a classic example (Figure 2.21).

convergent evolution

Such convergence is direct evidence of the power of evolutionary forces to shape the same form from quite different starting material. The French geneticist Jacob said that evolution was like "tinkering". It did not create ideal forms from ideal beginnings —rather it tinkered together what it could from what was available at the time (a good tinker can make a saucepan from a bicycle or a bicycle from saucepans).

Convergent evolution: the wings of birds are analogous (not homologous). They are structurally different—the bird wing is supported by digit number 2 and is covered with feathers; the bat wing is supported by digits 2–5 and is covered with skin. (After Ridley, 1993.)
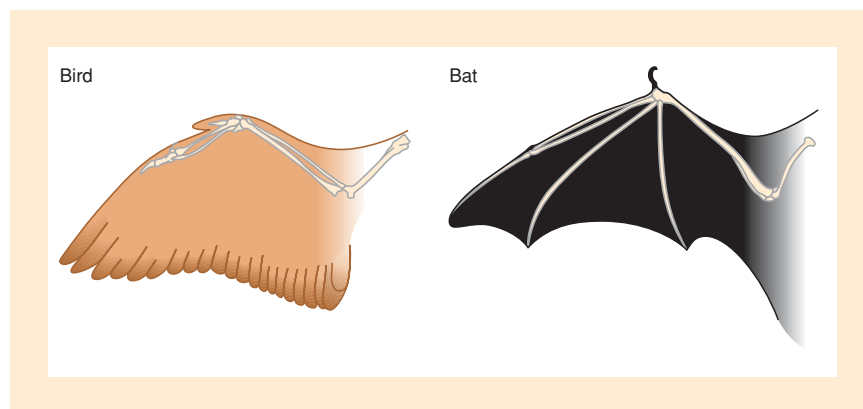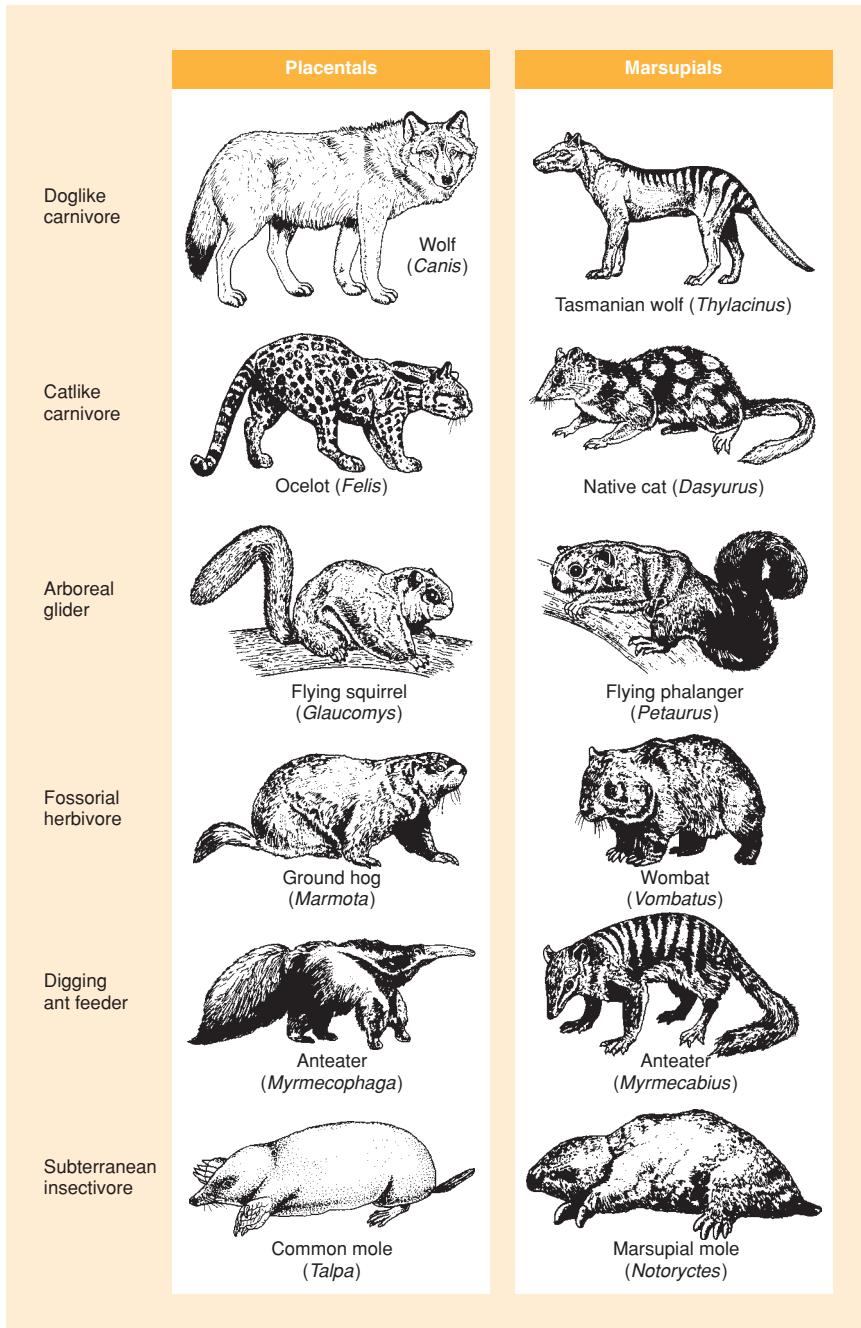

parallel evolution

Further examples show *parallels* in the evolutionary pathways of ancestrally related groups occurring after they were isolated from each other. The classic example is provided by the placental and marsupial mammals. Marsupials arrived on what would become the Australian continent in the Cretaceous period (around 90 million years ago; see Figure 2.19), when the only other mammals present were the curious egg-laying monotremes (now represented only by the spiny anteaters and the duck-billed platypus). An evolutionary process of radiation then occurred among the Australian marsupials that in many ways accurately paralleled what was occurring among the placental mammals on other continents (Figure 2.22). It is hard to escape the view that the environments of placentals and marsupials contained ecological pigeonholes (niches) into which the evolutionary process has neatly "fitted" ecological equivalents. In contrast to convergent evolution, however, the marsupials and placentals started to diversify from a common ancestral line, and both inherited a common set of potentials and constraints.

interpreting the match between organisms and their environment

When we marvel at the diversity of complex specializations by which organisms match their varied environments there is a temptation to regard each case as an example of evolved perfection. But there is nothing in the process of evolution by natural selection that implies perfection. For example, no population of organisms can contain all the possible genetic variants that might exist and might influence fitness. The evolutionary process works on the genetic variation that is available. It favors only those forms that are fittest *from among the range of variety available*, and this may be a very restricted choice. The very essence of natural selection is that organisms come to match their environments by being "the fittest available" or "the fittest yet"—they are not "the best imaginable".

It is particularly important to realize that past events on the Earth can have profound repercussions on the present. Our world has not been constructed by taking each organism in turn, testing it against each environment, and molding it so that every organism finds its perfect place. It is a world in which organisms live where they do for reasons that are often, at least in part, accidents of history. Moreover the ancestors of the organisms that we see around us lived in environments that were profoundly different from those of the present. Evolving organisms are not free agents—some of the features acquired by their ancestors hang like millstones around their necks, limiting and constraining where they can now live and what they might become. It is very easy

Placentals	Marsupials

Doglike carnivore

Wolf (*Canis*)

Tasmanian wolf (*Thylacinus*)

Catlike carnivore

Ocelot (*Felis*)

Native cat (*Dasyurus*)

Arboreal glider

Flying squirrel (*Glaucomys*)

Flying phalanger (*Petaurus*)

Fossorial herbivore

Ground hog (*Marmota*)

Wombat (*Vombatus*)

Digging ant feeder

Anteater (*Myrmecophaga*)

Anteater (*Myrmecabius*)

Subterranean insectivore

Common mole (*Talpa*)

Marsupial mole (*Notoryctes*)

to wonder and marvel at how beautifully the properties of fish fit them to live in water —but just as important to emphasize that these same properties prevent them from living on land. Indeed it was the few that chanced to escape from their ancestral watery home that started the evolutionary lines that diversified into the dinosaurs and mammals.

Summary

The force of natural selection

Life is represented on Earth by a diversity of specialist species, each of which is absent from almost everywhere. Early interest in this diversity mainly existed among explorers and collectors, and the idea that the diversity had arisen by evolution from earlier ancestors over geological time was not seriously discussed until the first half of the 19th century. Charles Darwin and Alfred Russell Wallace (strongly influenced by having read Malthus's *An Essay on the Principle of Population*) independently proposed that natural selection constituted a force that would drive a process of evolution. The theory of natural selection is an ecological theory. The reproductive potential of living organisms leads them inescapably to compete for limited resources. Success in this competition is measured by leaving more descendants than others to subsequent generations. When these ancestors differ in properties that are heritable, the character of populations will necessarily change over time and evolution will happen.

Darwin had seen the power of human selection to change the character of domestic animals and plants and he recognized the parallel in natural selection. But there is one big difference: humans select for what they want in the future, but natural selection is a result of events in the past—it has no intentions and no aim.

Natural selection in action

We can see natural selection in action within species in the variation within species over their geographic range, and even over very short distances where we can detect powerful selective forces in action and recognize ecologically specialized races within species (*ecotypes*). Transplanting plants and animals between habitats reveals tightly specialized matches between organisms and their environments. The evolutionary responses of animals and plants to pollution demonstrate the speed of evolutionary change, as do experiments on the effects of predators on the evolution of their prey. The evolution of specialization can be interpreted as matching organisms more accurately with their environment or as forcing them into ever tighter straitjackets of form and behavior.

The origin of species

Natural selection does not normally lead to the origin of species unless it is coupled with the reproductive isolation of populations from each other—as occurs, for example, on islands and is illustrated by the finches of the Galapagos Islands. *Biospecies* are recognized when they have diverged enough to prevent them from forming fertile hybrids if and when they meet.

Climatic change and continental drift

Much of what we see in the present distribution of organisms is not so much a precise, local-evolved match to present environments as a fingerprint left by the hand of history. Changes in climate, particularly during the ice ages of the Pleistocene, bear a lot of the responsibility for the present patterns of the distribution of plants and animals. On a longer timescale, many distributions make sense only once we realize that while major evolutionary developments were occurring, populations were being split and separated, and land areas were moving across climatic zones.

Parallel and convergent evolution

Evidence of the power of ecological forces to shape the direction of evolution comes from *parallel evolution* (in which populations long isolated from common ancestors have followed similar patterns of diversification) and from *convergent evolution* (in which populations evolving from very different ancestors have converged on very similar forms and behaviors).

Review Questions

1 ▲ What do you consider to be the essential distinction between *natural selection* and evolution?

2 What was the contribution of Malthus to Darwin's and Wallace's ideas about evolution?

3 Why is "the survival of the fittest" an unsatisfactory description of natural selection?

4 What is the essential difference between natural selection and the selection practiced by plant and animal breeders?

5 What are *reciprocal transplants*? Why are they so useful in ecological studies?

6 Is sexual selection, as practiced by female guppies in choosing gaudy males, different from or just part of natural selection?

7 In what ways do the results of natural selection by parasites and predators differ from selection by physical conditions of the environment?

8 What is it about the Galapagos finches that has made them such ideal material for the study of evolution?

9 What is the difference between convergent and parallel evolution?

10 ▲ The process of evolution can be interpreted as optimizing the fit between organisms and their environment or as narrowing and constraining what they can do. Discuss whether there is a conflict between these interpretations.

▲ = Challenge Question

Web Research Questions

1 The words "ecology", "ecologist", "ecological", and so on have spread from the science of ecology to the press, to pressure groups, and to the general public. Survey and describe briefly the range of meanings these words are now being given and by whom. Some have suggested that the words have been hijacked and misused: do you see any evidence of that? Does it/would it matter if they were?

2 Discuss the pros and cons of long-term ecological research, using the Hubbard Brook Experimental Forest study as an example. This program is run by the Institute of Ecosystem Studies (IES). To get some idea of the scale of long-term ecosystem studies find out roughly how many scientists and related staff work at the IES. The Hubbard Brook Experimental Forest is one of a number of long-term ecological research (LTER) sites in North America. Compare and contrast the objectives of the Hubbard Brook study with three of the other sites. Should all long-term ecological programs go on indefinitely? If not, what criteria would you suggest to determine whether and when a long-term program should be terminated?

3 Like museums, the traditional role of zoos was to make a public display of the diversity of nature. Is this still the case? Or has the conservation of endangered species come to assume more importance? Visit the websites of local zoos, and others around the world, and discuss the relative roles of display and conservation in the different institutions. Describe the variety of endangered species that zoos are working with.