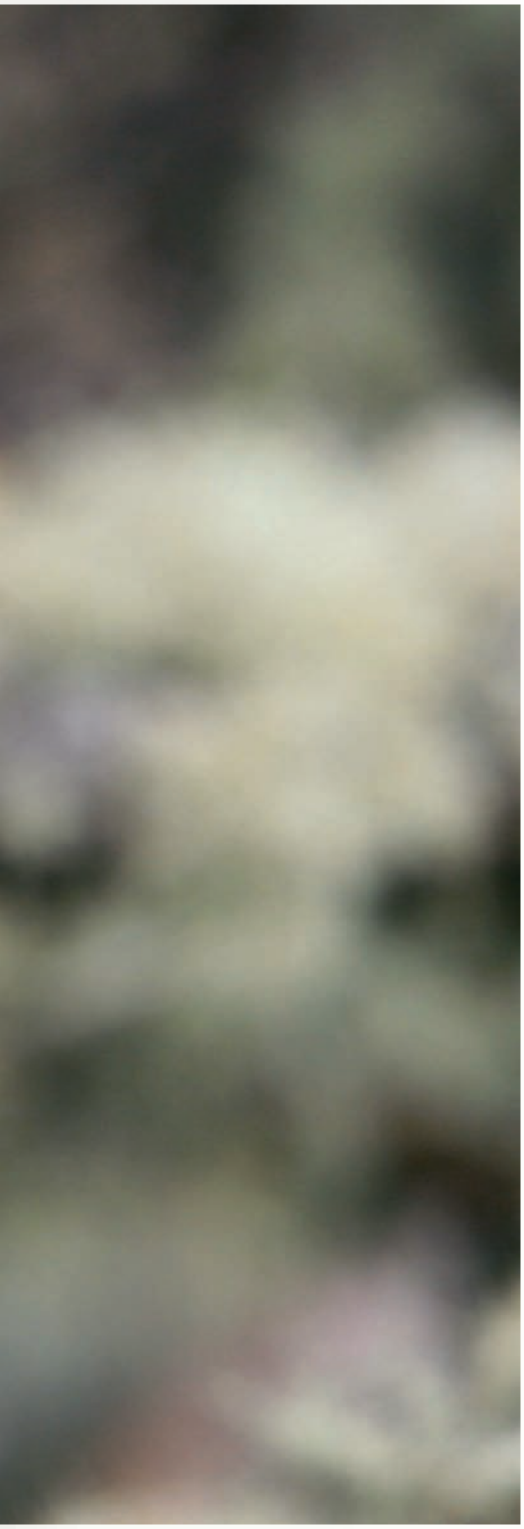
Neospiza wilkinsii **bunting, with a large bill, on the Tristan da Cunha archipelago. Tristan da Cunha is an isolated series of islands in the South Atlantic ocean.**



CHAPTER 3

Natural Selection, Speciation, and Extinction

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In 2007 Peter Ryan and his South African colleagues described the parallel colonization of finches on two small islands in the Tristan da Cunha archipelago in the South Atlantic Ocean. Tristan is one of the world's most isolated island systems, lying midway between South America and the tip of South Africa. Of the three islands, two of them, Inaccessible and Nightingale, had been relatively untouched by humans and their associated pests, mice and rats. Both these islands had two species of *Neospiza* buntings that had evolved from finch tanagers blown there from South America across 3,000 km of ocean. Such long-distance dispersal is likely very rare. Ryan and colleagues discovered that each island had a small-billed seed generalist and a large-billed seed specialist, matching the availability of seeds on each island. Generalists eat a variety of seeds from different plant species. Specialists feed on seeds of just one plant species. Additional genetic evidence suggested that one small-billed and one large-billed species had evolved independently on each island. This mechanism was supported rather than the prevailing and simpler hypothesis that a large-billed species evolved on one island and a small-billed species evolved on another island, and subsequent dispersal of both species between islands formed different species of small-billed and large-billed *Neospiza* on each island. This work showed how the formation of species does not always occur via the simplest route but may involve more circuitous pathways.

As we discussed in Chapter 2, Charles Darwin and Alfred Wallace independently proposed the theory of evolution by natural selection. According to this theory, a struggle for existence results in the selective survival of individuals that have inherited genotypes that confer greater reproductive success. In this chapter we see how natural selection can follow four different patterns: directional, stabilizing, balancing, and disruptive. Given enough time, disruptive selection can lead to **speciation**, the formation of new species. There are many definitions of what constitutes a species. We will examine the species concept and the two main mechanisms of speciation, allopatric and sympatric speciation. New species arise from older species, but they may also go extinct after various lengths of time. In order to understand patterns of species origination and extinction, we will briefly examine the history of life on Earth and the pattern of species origination and extinction. Conservation biologists have a strong interest in determining where and how species are going extinct. In the last part of the chapter we address the current extinction crisis and the current factors endangering life on Earth.

3.1 Natural Selection Can Follow One of Four Different Pathways

At its simplest, natural selection will tend to lead to an increase in the frequency of the allele that confers the highest fitness in a given environment. In some cases, however, selection will act to maintain a number of alleles in a population, especially if the relative fitness of different alleles changes on a spatial or temporal scale. Here we describe four different patterns of natural selection: directional, stabilizing, balancing, and disruptive.

3.1.1 Directional selection favors phenotypes at one extreme

Directional selection favors individuals at one extreme of a phenotypic distribution that have greater reproductive success in a particular environment. One way in which directional selection may arise is that a new allele may be introduced into a population by mutation, and the new allele may confer a higher fitness in individuals that carry it (**Figure 3.1**).

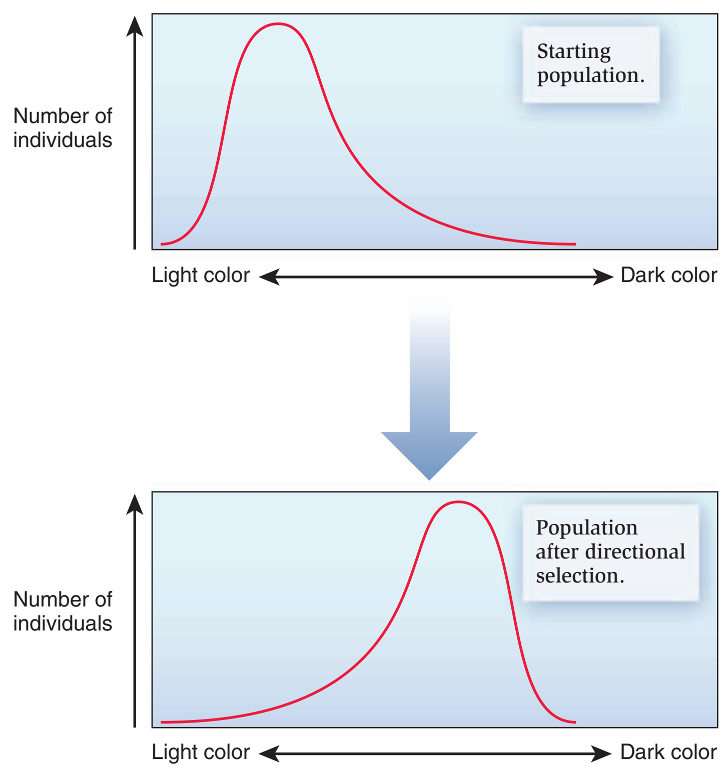

Figure 3.1 Graphical representation of directional selection. This pattern of selection selects for a darker phenotype that confers higher fitness in, for example, a polluted environment as with the peppered moth, *Biston betularia*.

In Chapter 2 we saw how darker color conferred greater fitness to peppered moths in polluted environments. If the homozygote carrying the favored allele has the highest fitness value, directional selection may cause this favored allele to eventually become predominant in the population.

Figure 3.2 The study site and study organism of the Grants' work on natural selection. **(a)** Daphne Major, a small island in the Galápagos. **(b)** The medium ground finch, *Geospiza fortis.*

Another example of directional selection was provided by Peter and Rosemary Grant's study of natural selection in Galápagos finches. The Grants focused much of their work on one of the Galápagos Islands known as Daphne Major (**Figure 3.2a**). This small island (0.3 km^2) has a resident population of the medium ground finch, *Geospiza fortis* (**Figure 3.2b**). The medium ground finch has a relatively small crushing beak, allowing it to feed on small, tender seeds. The Grants quantified beak size among the medium ground finches of Daphne Major by carefully measuring beak depth, a measure of the beak from top to bottom. They compared the beak sizes of parents and offspring by examining broods over many years. The depth of the beak was inherited by offspring from parents, regardless of environmental conditions, indicating that differences in beak sizes are due to genetic differences in the population. This means that beak depth is a heritable trait. In the wet year of 1976, the plants of Daphne Major produced an abundance of small seeds that finches could easily eat. In 1977 a drought occurred and plants produced few of the smaller seeds and only larger drier seeds, which are harder to crush, were readily available. As a result, birds with larger beaks were more likely to survive, because they were better at breaking open the large seeds. In the year after the drought, the average beak depth of birds in the population increased by almost 10% (**Figure 3.3**).

3.1.2 Stabilizing selection favors intermediate phenotypes

Stabilizing selection favors the survival of individuals with intermediate phenotypes. The extreme values of a trait are selected against. An example of stabilizing selection involves

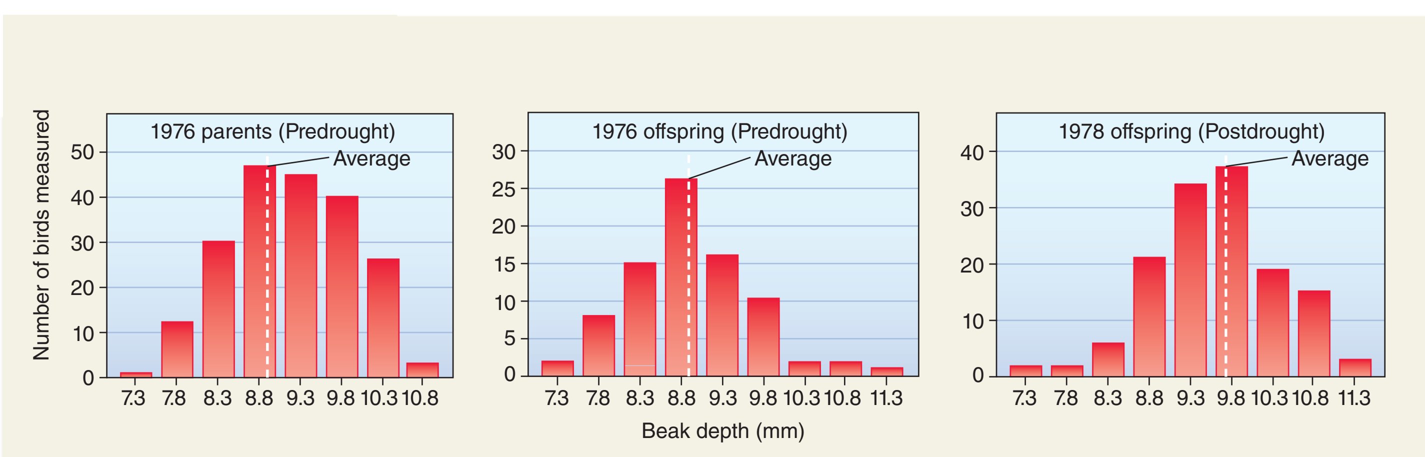

Figure 3.3 Variation in the beak size of the medium ground finch, *G. fortis,* on Daphne Major in 1976 and 1978. Beak size increased almost 10% the year following the drought.

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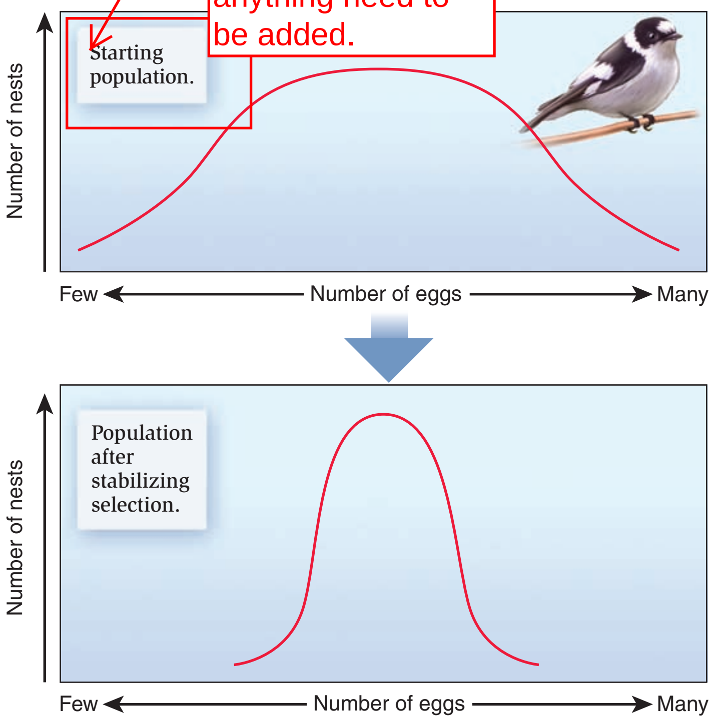


Figure 3.4 Graphical representation of stabilizing selection. Here the extremes of a phenotypic distribution are selected against while individuals with intermediate traits are favored. These graphs illustrate stabilizing selection in clutch size of birds.

clutch size (the number of eggs laid) in animals. British ornithologist David Lack suggested that birds that lay too many or too few eggs per nest have lower fitness values than do those that lay an intermediate number of eggs (**Figure 3.4**). Laying too many eggs is disadvantageous because many chicks die due to an inadequate supply of food. In addition, the parent's survival may be reduced because of the strain of trying to feed a large brood. On the other hand, having too few offspring results in the contribution of relatively few individuals to the next generation. Therefore, an intermediate clutch size is favored.

3.1.3 Balancing selection promotes genetic diversity

Balancing selection is a type of natural selection that maintains genetic diversity in a population. In balancing selection, two or more alleles are kept in balance and therefore are maintained in a population over the course of many generations. Balancing selection does not favor one particular

Feature Investigation

John Losey and Colleagues Demonstrated That Balancing Selection by Opposite Patterns of Parasitism and Predation Can Maintain Different-Colored Forms of Aphids

In frequency-dependent selection, the fitness of a genotype changes when its frequency changes. In other words, rare individuals have a different fitness from common individuals. John Losey and colleagues (1997) showed how the existence of both green and red color forms or morphs of the pea aphid, *Acyrthosiphon pisum,* were maintained by the action of natural enemies. This situation is known as a **balanced polymorphism**, where two or more alleles or morphs are maintained in a population. Aphids parasitized by the wasp *Aphidius ervi* become mummified; that is, they turn a golden brown and become immobile, stuck to their host plant. Aphids may also be eaten by ladybird beetles, *Coccinella septempunctata.* Green morphs suffered higher rates of parasitism than red morphs, whereas red morphs were more likely to be attacked by ladybird predators than were green morphs. Therefore, when parasitism rates were high relative to predation rates, the population of red morphs increased relative to green morphs, whereas the converse was true when predation rates were relatively high (**Figure 3.A**).

ECOLOGICAL INQUIRY

If the parasitism rates on the different-colored morphs were reversed, what would happen in the field?

HYPOTHESIS The action of parasitoids and predators maintains a color polymorphism in the pea aphid, *Acyrthosiphon pisum*.

STARTING LOCATION Alfalfa fields in south central Wisconsin, USA.

	Conceptual level	Experimental level
1	Assess rate of predation of different aphid color morphs by ladybird beetles.	A single adult *C. septempunctata* beetle was released on caged alfalfa plants with 15 adults of each color morph for 4 hours. This experiment was replicated 27 times. The number of survivors was recorded. The predation rate was higher on red morphs, 0.91 aphids eaten per hour, than on green morphs, 0.73 aphids eaten per hour.
2	Determine whether parasitism is different on different color morphs	Sample 5 alfalfa fields on 5 days in the summer and dissect a total of 643 aphids for *Aphidius ervi* larvae. Parasitism rates were 53% on green morphs and 42% on red morphs.
3	Assess densities of aphids, parasitoids, and predators in the field.	12 alfalfa fields were sampled roughly every 6 days throughout the summer. In each field, aphid density and color were recorded on 100 stems in 8 locations within the field. Twelve 3-minute walking scans were also made throughout each field to count parasitoids (*A. ervi*) and predators (*C. septempunctata*).

4 **THE DATA** The data show that in the field, red aphid morphs are more common where parasitoids are abundant and green morphs predominate where predators are more common.

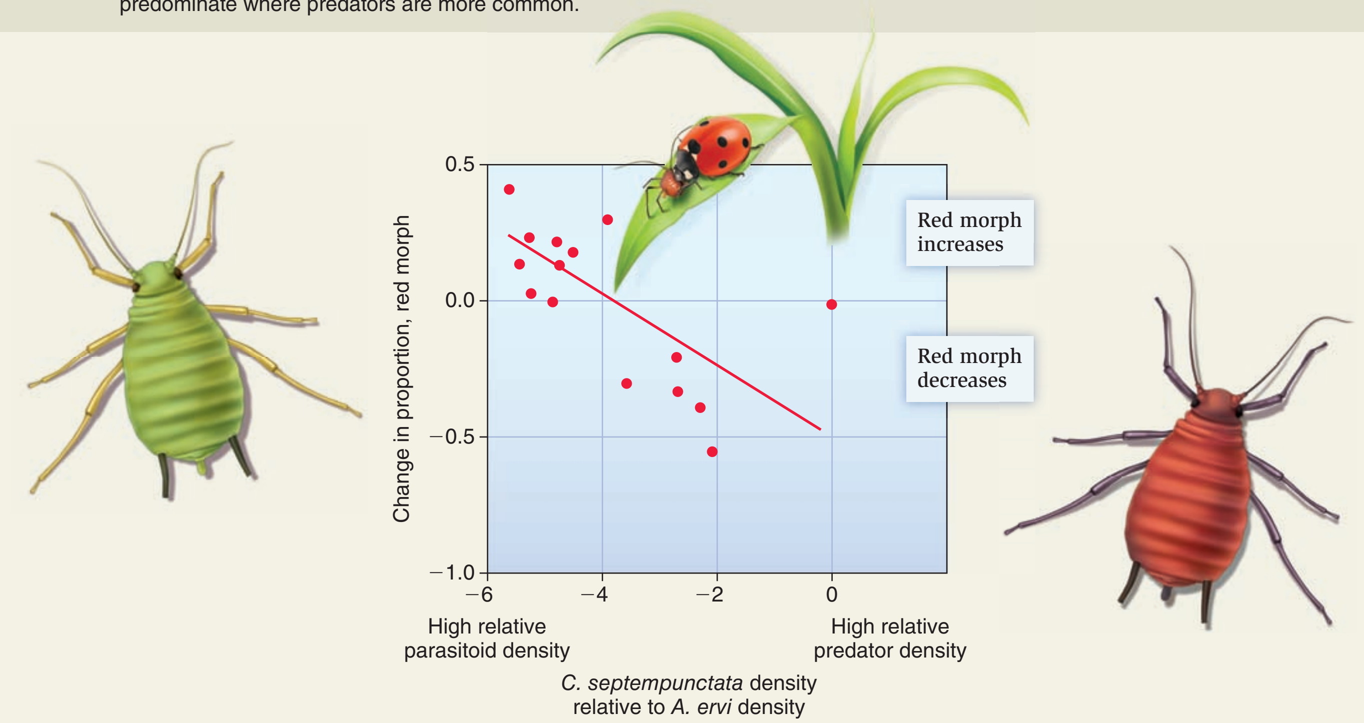


Figure 3.A The effects of natural enemies on aphid color morphs.

allele in the population. Population geneticists have identified two common pathways along which balancing selection can occur. The first is heterozygote advantage and the second is frequency-dependent selection.

A classic example of heterozygote advantage involves the sickle-cell allele of the human β-globin gene. A homozygous individual with two copies of this allele has sickle-cell disease, a hereditary disease that damages blood cells (refer back to Figure 2.8). The sickle-cell homozygote has a lower fitness than a homozygote with two copies of the normal and more common β-globin allele. However, in areas where malaria is endemic, the heterozygote has the highest level of fitness. Compared with normal homozygotes, heterozygotes have a 10–15% better chance of survival if infected by the malarial parasite, *Plasmodium falciparum*. Therefore, the sickle-cell allele is maintained in populations where malaria is prevalent, even though the allele is detrimental in the homozygous state.

Frequency-dependent selection is another mechanism that causes balancing selection (see **Feature Investigation**). In frequency-dependent selection, the fitness of one phenotype is dependent on its frequency relative to other phenotypes in the population. For example, many species of invertebrates exist as different-colored forms, identical in all respects except color. Visually searching predators often develop a search image for one color form, usually the more common form. The prey then proliferates in the rarer form until this form itself becomes more common.

3.1.4 Disruptive selection favors the survival of two phenotypes

Disruptive selection favors the survival of individuals at both extremes of a range, rather than the intermediate. It is similar but not identical to balancing selection, where individuals of average trait values are favored against those of extreme trait values. The fitness values of one genotype are higher in one environment, while the fitness values of the other genotype are higher in another environment. Janis Antonovics and Anthony Bradshaw (1970) provided an example of disruptive selection in colonial bentgrass, *Agrostis tenuis*. In certain locations where this grass is found, such as South Wales, isolated places contain high levels of heavy metals such as copper from mining. Such pollution has selected for mutant strains that show tolerance to copper. This genetic change enables the plants to grow on copper-contaminated soil but tends to inhibit growth on a normal, uncontaminated soil. This results in metal-resistant plants growing on contaminated sites that are close to normal plants growing on uncontaminated land (**Figure 3.5**).

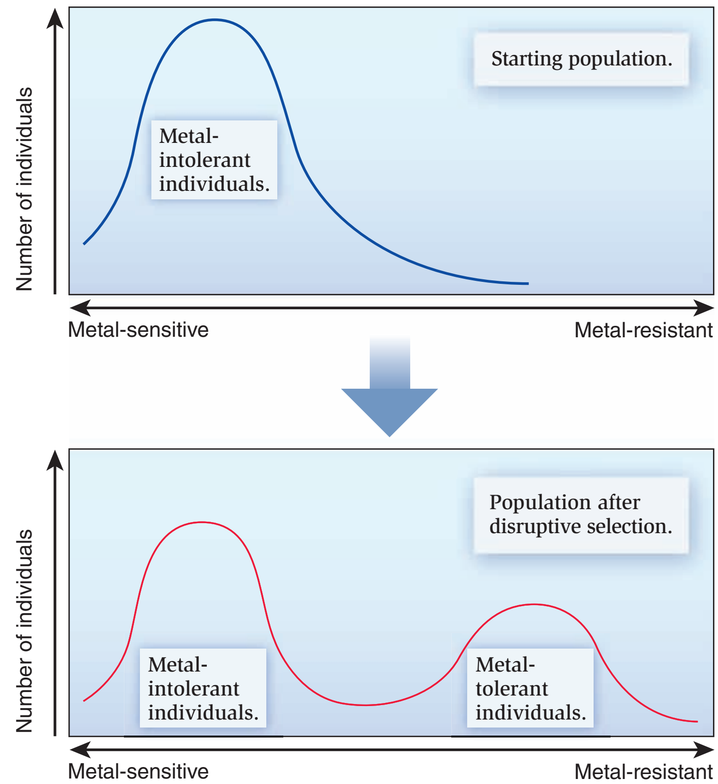


Figure 3.5 Graphical representation of disruptive selection. In this example, the normal wild-type colonial bentgrass, *Agrostis tenuis*, is intolerant to metals in the soil. A mutation creates a metal-tolerant variety, which can grow in soils contaminated with metals from mining operations.

Check Your Understanding

3.1 What were the results of the Grants' study of *Geospiza fortis* finches in the Galápagos following the drought of 1977 and how did this work impact the theory of natural selection?

3.2 Speciation Occurs Where Genetically Distinct Groups Separate into Species

Over a long enough time span, disruptive selection can result in speciation. Here we describe two alternative mechanisms by which speciation occurs: allopatric speciation and sympatric speciation. But first we discuss the species concept. In any

Table 3.1 Four Different Species Concepts.

Species Concept	Description
Biological	Species are separate if they are unable to interbreed and produce fertile offspring.
Phylogenetic	Differences in physical characteristics (morphology) or molecular characteristics are used to distinguish species.
Evolutionary	Phylogenetic trees and analyses of ancestry serve to differentiate species.
Ecological	Species separate based on their use of different ecological niches and their presence in different habitats and environments.

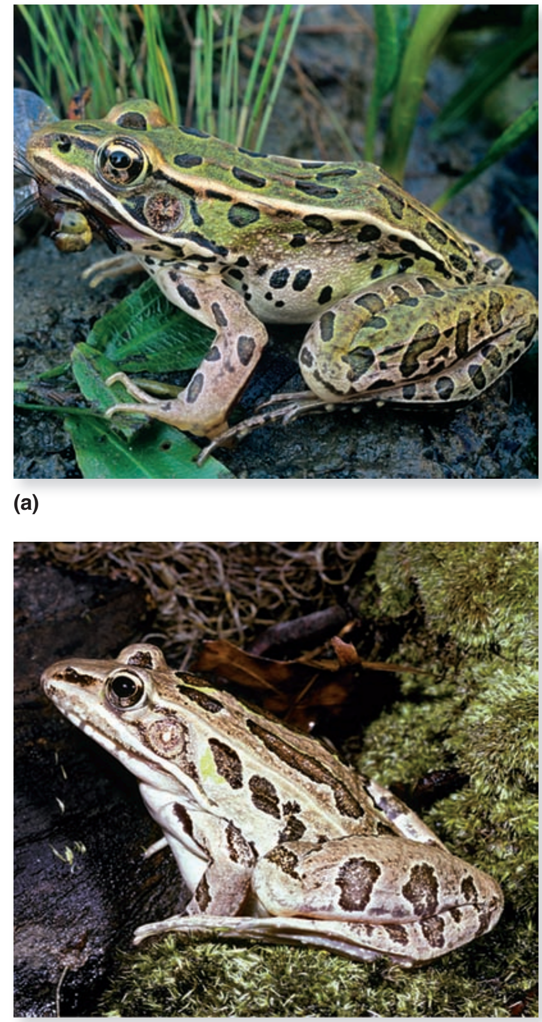
discussion of speciation, it is valuable to have a good working concept of species. While one might think this is a simple matter, there are over 20 species concepts, each with its own advantages and disadvantages.

3.2.1 There are many definitions of what constitutes a species

There is considerable debate about what constitutes a species. We will consider four of the more widely accepted species concepts, the biological, phylogenetic, evolutionary, and ecological species concepts (**Table 3.1**).

Biological species concept

Perhaps the best-known species concept is the **biological species concept** of Ernst Mayr (1942), who defined species as "groups of populations that can actually or potentially exchange genes with one another and that are reproductively isolated from other such groups." The biological species concept defines species in terms of interbreeding. It has been used to distinguish morphologically similar yet reproductively isolated species, such as the northern leopard frog, *Rana pipiens,* and the southern leopard frog, *R. utricularia* (**Figure 3.6**).



(a)

(b)

Figure 3.6 **The biological species concept.** The northern leopard frog, *Rana pipiens* **(a)**, and the southern leopard frog, *R. utricularia* **(b)**, appear very similar but are reproductively isolated from each other.

Despite its advantages, the biological species concept suffers from at least three disadvantages. First, for many species with widely separate ranges, we have no idea if the reproductive isolation is by distance only or whether there is some species-isolating mechanism. Second, especially in plants, individuals called hybrids often form when parents from two different species are crossed with each other and the resultant progeny develop. This greatly blurs species distinctions. Oak trees provide a particularly good example of confusion in species definitions. Oaks often form reproductively viable hybrid populations. That is, oaks from different species interbreed and their offspring are themselves viable, capable of reproducing with other oaks. For this reason, one might question whether the parental species should be called species at all. For example, *Quercus alba* and *Q. stellata* form natural hybrids with 11 other oak species in the eastern United States. It could be argued, humorously, that if these oaks cannot tell each other apart, why should biologists impose different names on them? Ecologists have noted many examples of viable hybrid formation when historically isolated species

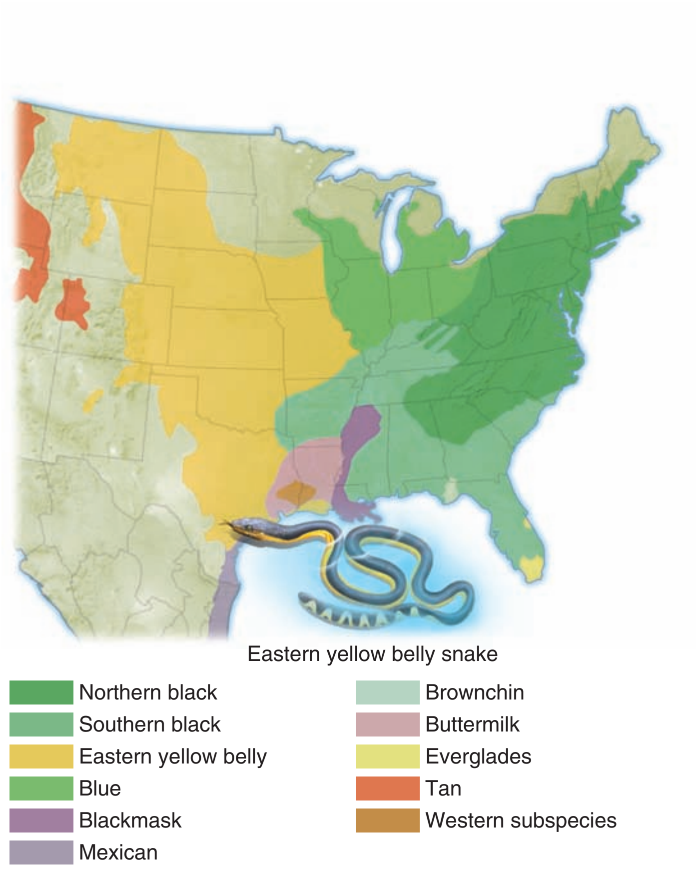


Figure 3.7 Difficulties with the phylogenetic species concept. The subspecies of the black racer, *Coluber constrictor,* appear different yet are members of the same species. (Modified from Conant, 1975.)

ECOLOGICAL INQUIRY

What would happen if you attempted to breed the blue and western yellow-bellied races of the black racer?

are brought into contact through climate change, landscape transformation, or transport beyond their historic boundaries (see **Global Insight**). Third, the biological species concept cannot be applied to asexually reproducing species, such as bacteria and some plants and fungi, or to extinct species.

Phylogenetic species concept

Another popular definition of species is the **phylogenetic species concept**, which advocates that members of a single species are identified by a unique combination of characters. This definition incorporates the classic taxonomic view of species based on their morphological characters and, more recently, molecular features such as DNA sequences. A disadvantage of this concept is in determining how much difference between

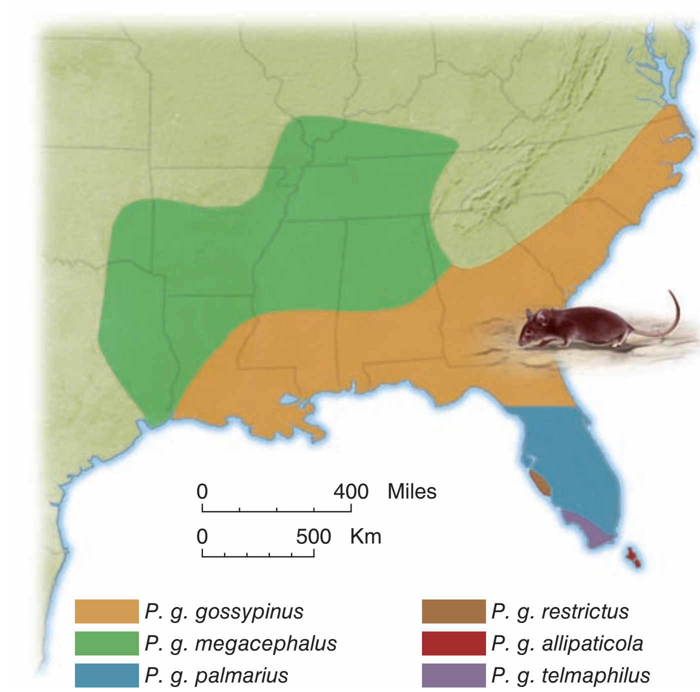


Figure 3.8 Difficulties with the phylogenetic species concept. The cotton mouse, *Peromyscus gossypinus,* exists as six subspecies. The subspecies possess slightly different coat colors and different lengths of tail and hind feet.

populations is enough to call them separate species. Many color differences in hair or feathers are controlled by a single gene. Conversely, many genetic changes have no discernible effect on the phenotype. Using this definition, many currently recognized subspecies or distinct populations would be elevated to species status. The black racer, *Coluber constrictor,* is a snake that exists as many different color forms or races throughout the United States (**Figure 3.7**). Some authorities argue that each race should be elevated to the status of a species. Similarly, the cotton mouse, *Peromyscus gossypinus,* exists as six formal subspecies in the southeastern U.S. (**Figure 3.8**).

Evolutionary species concept

George Gaylord Simpson (1961) proposed the **evolutionary species concept**, whereby a species is distinct from other lineages if it has its own evolutionary tendencies and historical fate. For example, paleontologists have charted the course of species formation in the fossil record. One of the best examples documents the evolutionary changes that led to the development of many horse species, including modern horses. Some scientists believe this is both the best definition and, at the same time, the least operational, because lineages are difficult to examine and evaluate quantitatively. Incomplete fossil records and lack of transitional forms make lineages difficult to trace.

Global Insight

Hybridization and Extinction

Introduced species can bring about a form of extinction of native flora and fauna by **hybridization**, breeding between individuals from different species. Purposeful or accidental introductions by humans or by habitat modification may bring previously isolated species together. For example, mallard ducks, *Anas platyrhynchos,* which occur throughout the Northern Hemisphere, have been introduced into many areas such as New Zealand, Hawaii, and Australia. The mallard has been implicated in the decline of the New Zealand gray duck, *A. superciliosa,* and the Hawaiian duck *A. wyvilliana* through hybridization (**Figure 3.B**). The northern American ruddy duck, *Oxyura jamaicensis,* similarly threatens Europe's rarest duck, the white-headed duck, *O. leucocephala,* which now exists only in Spain. The northern spotted owl, *Strix occidentalis,* is threatened in the Pacific Northwest by the recent invasion of the barred owl, *S. varia*. Hybrids and fertile offspring have been found.

Extinction from hybridization threatens mammals as well. Feral house cats, *Felix catus,* threaten the existence of the endangered wild cat, *F. silvestris*. In Scotland, 80% of wild cats have domestic cat traits, raising the question of at what point is an endangered species no longer a pure species. The Florida panther, *Puma concolor coryi,* a subspecies of the cougar, is listed as endangered by the U.S. Fish and Wildlife Service. Although over 100 Florida panthers now exist, most are hybrids between original Florida panthers and females captured in Texas and released in Florida in the 1990s. Some scientists question whether the Florida panther should be delisted. Hybrid plants also threaten natives with extinction. Many coastal temperate areas contain *Spartina* cordgrasses. In Britain, the native European cordgrass, *S. maritima,* hybridized with the introduced American smooth cordgrass, *S. alterniflora,* in about 1870 to form *S. anglica*. At first this hardy hybrid was seen as valuable in the fight against coastal erosion, and it was widely planted. With its dense root system and quick vegetative spread, it became invasive and displaced *S. maritima* from much of its native habitat.

(i) Mallard duck

(ii) New Zealand gray duck

(iii) Hybrid

Figure 3.B **Hybrid ducks.** **(i)** Mallard duck, *Anas platyrhynchos,* **(ii)** New Zealand gray duck, *A. superciliosa,* and **(iii)** the hybrid between them. Hybridization is threatening the New Zealand gray duck with extinction.

Ecological species concept

American biologist Leigh Van Valen (1976) proposed the **ecological species concept**, in which each species occupies a distinct ecological niche, a unique set of habitat requirements. Competition between species is likely to result in each individual species occupying a unique niche. This species concept is useful in distinguishing asexually reproducing and morphologically similar species such as bacteria.

3.2.2 The main mechanisms of speciation are allopatric speciation and sympatric speciation

Two mechanisms have been proposed to explain the process of speciation. **Allopatric speciation** (from the Greek words *allo*, meaning different and *patra*, meaning fatherland) involves spatial separation of populations by a geographical barrier. For example, nonswimming populations separated by a river may gradually diverge because there is no gene flow between them. Alternatively, aquatic species separated by the emergence of land may undergo allopatric speciation. The emergence of the isthmus of Panama about 3.5 million years ago separated porkfish in the Caribbean Sea and the Pacific Ocean (**Figure 3.9**). Since this event, the two populations have been geographically separated and have evolved into a Caribbean porkfish species, *Anisostremus virginicus*, and the Panamic porkfish, *A. taeniatus*.

The alternative to allopatric speciation is **sympatric speciation** (from the Greek word *sym*, meaning alike), which occurs when members of a species that initially occupied the same habitat within the same range diverge into two or more different species. The metal-tolerant *Agrostis tenuis* plants in Wales (see Figure 3.5) are starting to show a change in their flowering season. Over time this population may evolve into a new species that cannot interbreed with the original metal-sensitive species. A common sympatric speciation mechanism in plants involves a change in chromosome number. Plants commonly exhibit polyploidy, meaning they contain three or more sets of chromosomes. At least 30–50% of all species of ferns and flowering plants are polyploid. Such changes can result in sympatric speciation. Polyploidy is much less common in animals, but some insects and about 30 species of reptiles and amphibians are polyploids. In many groups of herbivorous insects, individual species are restricted to individual host plant species; thus, as plants speciate, each has its own unique set of herbivores. Guy Bush (1994) and others have argued that sympatric speciation has occurred frequently among herbivorous insects. Sympatric speciation may also have been common in fish. In many isolated lakes, there has been a divergence of fish species. For example, cichlid fish have been isolated in the African rift valley lakes, Lakes Victoria, Malawi, and Tanganyika, for about 10 million years, and hundreds of species have arisen from a few founding lineages.

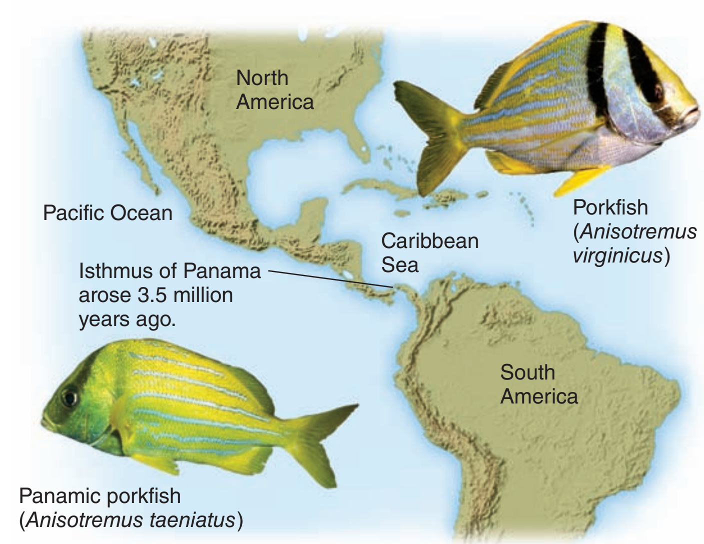


Figure 3.9 Allopatric speciation in porkfish. About 3.5 million years ago the isthmus of Panama arose, separating porkfish into two distinct populations with no opportunity for mixing. Since then, genetic changes in each population have led to the formation of two species, one in the Caribbean and one in the Pacific.

As we saw at the beginning of the chapter, recent evidence has suggested sympatric speciation among island birds in the South Atlantic as well.

Check Your Understanding

3.2 Why is sympatric speciation more common in plants than in animals?

3.3 Evolution Has Accompanied Geologic Changes on Earth

The history of life on Earth and of the associated geological changes and formation of new taxa are summarized in **Table 3.2.** Following the appearance of eukaryotes around 1.2 billion years ago, most of our current taxa, from worms to tunicates, sprang into existence in the Cambrian explosion. The Earth's physical terrestrial environment, from climatic conditions to atmospheric oxygen, changed over the millennia as first the plants and invertebrates colonized the land, then the amphibians and reptiles, and finally the mammals appeared. In this section we review the history of life on Earth, together with associated geological changes, including drifting of the continents. We then discuss how continental drift and other factors have created disjunct distributions. Finally, we discuss the classification of modern biogeographic realms.

Table 3.2 A brief history of life on Earth.

Era	Period	Millions of Years from Beginning of Period	Major Geologic Changes	Major Evolutionary Events
Cenozoic	Quaternary	2	• Cold/dry climate • Repeated glaciations in Northern Hemisphere	• Extinctions of large mammals • Rise of civilization • Evolution of *Homo*
	Tertiary	65	• Continents in approximately modern positions. India collides with Eurasia, Himalayas uplifted • Atmospheric oxygen reaches today's level of 21% • Drying and cooling trend in mid-Tertiary. Sea levels drop	• Radiation of mammals and birds • Flourishing of insects and angiosperms
Mesozoic	Cretaceous	144	• Northern continents attached • Gondwanaland drifting apart • Sea levels rise • Meteorite strikes Earth	• Mass extinctions of marine and terrestrial life, including last dinosaurs • Angiosperms become dominant over gymnosperms
	Jurassic	206	• Two large continents form, Laurasia in the north and Gondwanaland in the south • Climate warms • Oxygen drops to 13%	• First birds and angiosperms appear • Dinosaurs abundant • Gymnosperms dominant
	Triassic	251	• Pangaea begins to drift apart • Hot/wet climate • Sea levels drop below current levels	• Mammals appear • Mass extinction near end of period • Increase of reptiles, first dinosaurs • Gymnosperms become dominant
Paleozoic	Permian	286	• Continents aggregated into Pangaea, dry interior • Large glaciers form • Atmospheric oxygen reaches 30%	• Mass marine extinctions, including last trilobites • Reptiles radiate, amphibians decline • Metamorphic development in insects
	Carboniferous	360	• Climate cools • Sea levels drop dramatically to present-day levels • Oxygen levels increase dramatically	• Extensive forests of early vascular plants, especially ferns • Amphibians diversify; first reptiles • Sharks roam the seas • Radiation of early insect orders
	Devonian	409	• Major glaciation occurs	• Seed plants appear • Fishes and trilobites abundant • First amphibians and insects • Mass extinction late in period
	Silurian	439	• Two large continents form • Warm/wet climate • Sea levels rise	• Invasion of land by primitive land plants, arthropods • Jawed fish appear
	Ordovician	510	• Mostly southern or equatorial land masses • Gondwanaland moves over South Pole • Climate cools resulting in glaciation and 50-m sea level drop	• Primitive plants and fungi colonize land • Diversification of echinoderms, first jawless vertebrates • Mass extinction at end of period
	Cambrian	542	• Ozone layer forms, blocking UV radiation and permitting colonization of land • High sea levels	• Sudden appearance of most marine invertebrate phyla including crustaceans, mollusks, sponges, echinoderms, cnidarians, annelids, and tunicates
Pre-cambrian		1,200	• Oxygen levels increase	• Origins of multicellular eukaryotes, sexual reproduction evolves, increasing the rate of evolution
		3,000	• Moon is close to the Earth, causing larger and more frequent tides	• Photosynthesizing cyanobacteria evolve • Oxygen is toxic for many bacteria
		3,900	• No atmospheric oxygen	

3.3.1 Early life caused changes in atmospheric oxygen and carbon dioxide

The original composition of Earth, formed by coalescence of material from the solar nebula 4.5 billion years ago, was largely a mixture of silicates, together with iron and sulfides. The planet was so hot that the iron melted and sunk to the center. Water was not present in a free form but was bound to hydrated minerals such as mica in the Earth's crust. Water released from rocks via volcanic explosions condensed to form the hydrosphere. We have a good idea about the composition of volcanic effluents by studying their emissions, which turn out to contain 50–60% water vapor, 24% carbon dioxide, 13% sulfur, and about 6% nitrogen. The atmosphere continued to be rich in carbon dioxide with little to no oxygen until about 2.5 billion years ago. We know this because of the absence of "red beds," sedimentary rocks stained red by iron oxide, in rocks older than 2.5 billion years. As a consequence, the climate would have been hot and steamy. Before life evolved, Earth had a reducing atmosphere, and only with the evolution of photosynthetic organisms, initially algae, about 3 billion years ago did an oxidizing atmosphere begin to form (**Figure 3.10**).

The essential step in the origin of life was the formation of replicating DNA or DNA-like molecules possessing the properties now found in genes. DNA became enclosed in membranes, which provided a stable physical and chemical environment and accelerated replication. For more than half a billion years there were no recorded living things on Earth. The earliest origins of life in the fossil record appeared about 3.5 billion years ago at the beginning of the Precambrian era. Unicellular prokaryotic life-forms, such as cyanobacteria, predominated. In these early days, atmospheric conditions were anaerobic, and fermentation provided most of the energy, but this process was inefficient and left most of the carbon compounds untapped. With the appearance of the first eukaryotes, about 2 billion years ago, chromosomes, meiosis, and sexual reproduction evolved. The long period needed for the action of prokaryotes and primitive eukaryotes to build up an oxygen layer through photosynthesis may explain the 2-billion-year gap between the origin of life and the appearance of multicelled aerobically respiring animals, metazoans. At the same time, the buildup of oxygen led to the formation of an ozone layer that shielded life from the harmful effects of radiation. The buildup of oxygen concomitantly led to the demise of many of the early anaerobic organisms. As we will see throughout this book, environmental conditions greatly affect the abundance and diversity of life.

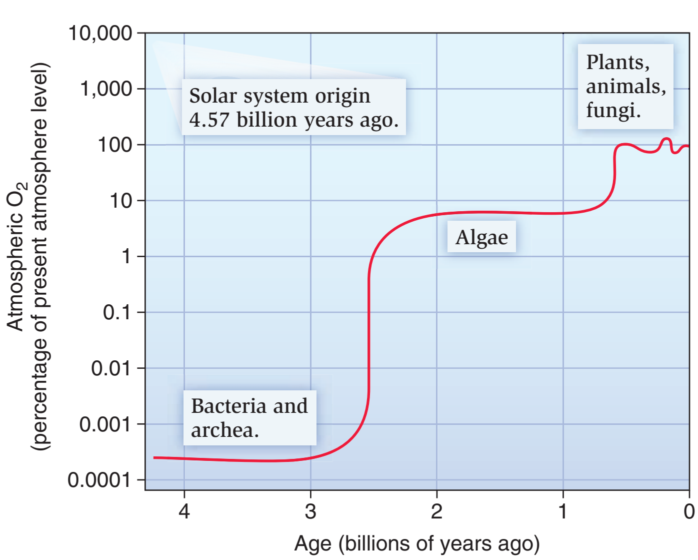


Figure 3.10 Changes in atmospheric oxygen over the Earth's history. (After Kump, 2008.)

3.3.2 The evolution of multicellular organisms also accompanied atmospheric changes

We have a more detailed knowledge of atmospheric conditions and the history of life on Earth from about 600 million years ago (**Figure 3.11**). At about 530 million years ago, the

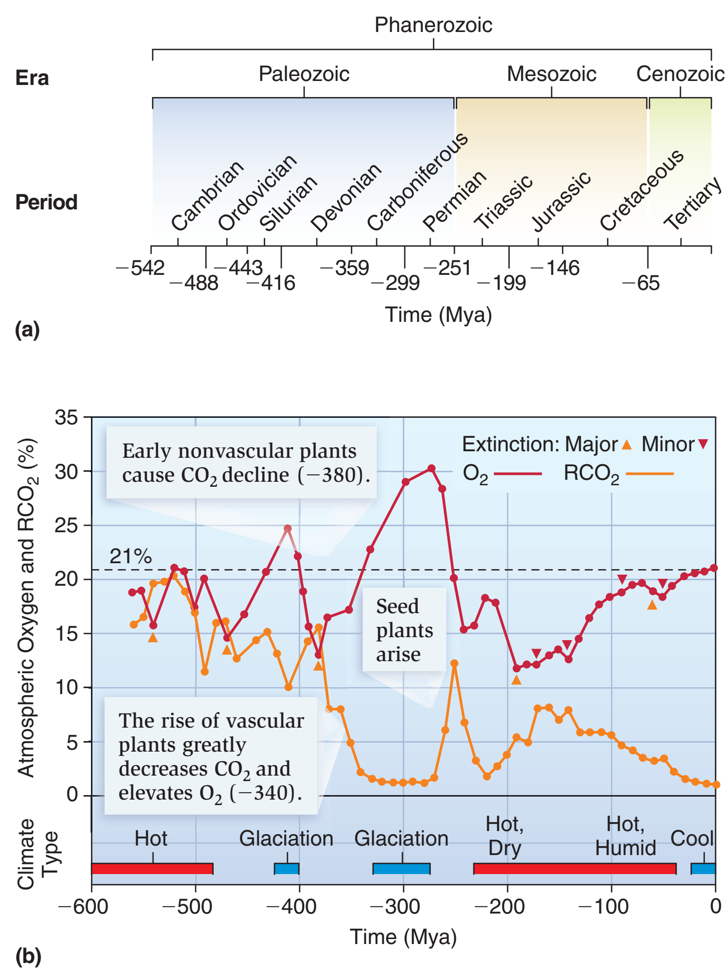


Figure 3.11 Changes in atmospheric oxygen and carbon dioxide since the Cambrian explosion. RCO_2 is a multiplier for current atmospheric CO_2 levels. (After Ward, 2006.)

Cambrian explosion marked the appearance of most of our current marine invertebrate phyla—sponges, cnidarians, annelids, mollusks, crustaceans, echinoderms, and tunicates. Most organisms were soft-bodied and large. Without skeletons for muscle attachment, their movements would have been slow. They survived partly because no predators with jaws existed to prey on them. The appearance of skeletons permitted more diverse lifestyles and body forms. Among these early taxa are the now-extinct trilobites, whose closest living relative is the horseshoe crab, *Limulus polyphemus* (**Figure 3.12**).

During the Ordovician, the first chordates, jawless fish, were recorded. Also in the Ordovician, the first evidence of terrestrial life appeared as primitive plants and fungi colonized the land. As terrestrial vegetation formed and decayed, organic soils began to form. In the Silurian, the first jawed fish appeared, and arthropods and vascular plants invaded terrestrial habitats. In the Devonian, marine invertebrates, especially trilobites and corals, continued to diversify, and the first bony fishes appeared in the fossil record. The Devonian is sometimes known as the "age of fishes." Devonian fish were often heavily armored to defend against predation, in contrast with modern fish, which emphasize speed. The relatively high oxygen levels promoted large marine arthropod predators, the longest up to 10 feet long. Environment permitting, there is a tendency for animals to become larger over evolutionary time. This tendency is known as Cope's rule, after the 19th-century paleontologist Edward Cope, who suggested that large size protects against predation. Amphibians appeared at the end of the Devonian, as did the first insects, undoubtedly connected with the proliferation of land plants such as bryophytes. The amphibians would have been sluggish. Their salamander-like gait compressed the chest and lungs, making it difficult to breath and walk at the same time. Breaths were taken between steps, limiting periods of high activity. The proliferation of land plants caused carbon dioxide to decline and oxygen levels to increase.

Figure 3.12 **A living fossil.** The horseshoe crab, *Limulus polyphemus,* has existed unchanged for hundreds of millions of years. It is the nearest surviving relative of the trilobites. Most live in water off the coasts of eastern North America and Southeast Asia, but every spring they appear along the coasts to mate and lay eggs.

In the Carboniferous period, insects radiated. The reptiles arose, and the amphibians radiated briefly. Huge, lumbering 5-m amphibians appeared, quite unlike the small forms present today. The extensive forests of this period gave rise to today's rich coal beds and greatly increased atmospheric oxygen. Vascular plants were the first to use lignin for skeletal support. Carboniferous trees grew huge but had relatively shallow roots and fell over quite easily. However, bacteria that could decompose wood had not yet evolved, so the trees did not easily decompose. They lay on the ground and gradually became covered with sediment, and their reduced carbon would be buried. The lack of decomposition also allowed oxygen levels to rise. Some insects, such as dragonflies with 1-m wingspans, became very large, fueled by 30% oxygen levels. The lack of carbon dioxide cooled the planet and there were ice caps at each pole, with extensive glaciers reaching out from the mountains. Forest fires burned frequently and hot, but swampy conditions helped limit the fires' effects.

During the Permian period, the continents had aggregated into one central landmass, called Pangaea. Reptiles and insects underwent extensive radiation, and the amphibia suffered mass extinctions. Perhaps the most remarkable feature of this period, however, was the vast extinction of marine invertebrates, including the last of the trilobites and plankton, corals, and benthic invertebrates, on a scale that commonly implies some worldwide catastrophe. At the end of the Permian, oxygen levels dropped and carbon dioxide levels rose, increasing global temperatures and causing hot, dry conditions. Seed plants arose at this time, but plant life became scarce.

During the Mesozoic era, beginning 251 million years ago, Pangaea started to split up into a southern continent, Gondwanaland, and a northern one, Laurasia. By the end of the era Gondwanaland had formed South America, Africa, Australia, Antarctica, and India, which later drifted north, and Laurasia had begun to split into Eurasia and North America. The land now called the Sahara Desert was probably located near the South Pole 450 million years ago and has since passed through every major climatic zone. Now still drifting northward at 1–2 cm per year, the Sahara will move north 1° in the next 5–10 million years, and the climate and vegetation will change accordingly.

Following the Permian extinctions, marine invertebrates and reptiles began to diversify in the first Mesozoic period, the Triassic. Gymnosperms became large and dominant, and large herbivorous dinosaurs fed upon them. Early mammals also appeared. Oxygen levels dropped to 13%. By the Jurassic period, dinosaurs dominated the terrestrial vertebrate fossil records, and the first birds appeared. Peter Ward (2006) argues that both dinosaurs and birds developed extensive air sacs,

Figure 3.13 **Dilophosaurus.** Fossils of this predatory dinosaur, which was 6 m (20 ft) long, have been found in Arizona.

ECOLOGICAL INQUIRY

What caused the extinction of the dinosaurs?

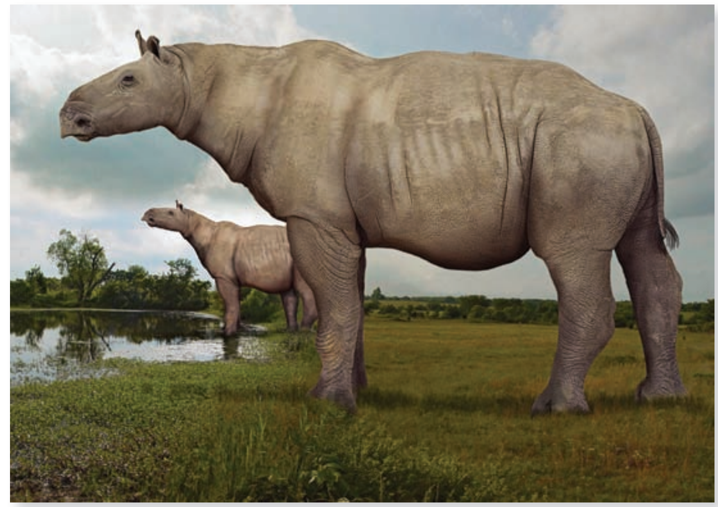


Figure 3.14 **Artist's rendition of *Paraceratherium,* a rhinoceros-like mammal.** At 5.5 m (18 ft) tall, it was the largest land mammal ever known, even larger than mammoths.

extending the lungs and countercurrent blood flow. This highly efficient system was a wonderful adaptation for low atmospheric oxygen. Even today birds can fly over mountaintops, actively using flight muscles, despite low oxygen. The whole of the Mesozoic is generally known as the "age of reptiles." Turtles and crocodilians had appeared, and giant predatory dinosaurs stalked the Earth, preying on the herbivorous species (**Figure 3.13**). Advanced insect orders such as Diptera (flies) and Hymenoptera (wasps) were also evolving in conjunction with the first flowering plants, angiosperms. By the Cretaceous, dinosaurs had become extinct, as had many other animal groups, including, once again, much marine life, such as ammonites and planktonic Foraminifera. This extinction was, after the Permian, the second greatest extinction in the history of life. The explanation considered most likely is that a severe change took place, probably a cooling of the climate. What brought this climatic change about is the subject of much debate, with meteorite collisions featuring prominently. On land, all vertebrates larger than about 25 kg seem to have gone extinct, but extinction was virtually undetectable in fish.

In the early part of the Cenozoic era, most of the modern orders of birds and mammals arose, and the angiosperms and insects continued to diversify. By the middle of the Tertiary period, the world's forests were dominated by angiosperms. The continents arrived at their present positions early in the era but were connected and disconnected as the sea levels rose and fell. For example, during the early and late Cenozoic, Central America formed a series of islands between North and South America. Substantial numbers of vertebrate genera evolved in the Tertiary. During this time there existed *Paraceratherium,* an extinct rhinoceros. At 18 feet high at the shoulder, it is the largest land mammal known, weighing about 30 metric tons (**Figure 3.14**). Modern elephants rarely weigh more than 10 tons. Though the elephants evolved into a great diversity of forms, only three species survive today.

In the Quaternary period beginning about 2 million years ago, there were four ice ages, separated by warmer interglacial periods. During the ice ages, mammals adapted to cold conditions came southward, reindeer and arctic fox roamed in England, and musk ox ranged in the southern United States. Conversely, in the interglacial periods, species spread northward from the Tropics. Lions are known from northern England and the hippopotamus from the River Thames. During the glacial periods, some species that had moved south during the interglacial periods became restricted to isolated pockets of cool habitat, such as mountaintops, as the climate warmed. The most important extinctions at this time were of large mammals and ground birds, the so-called megafauna. For example, in North America, *Megatherium,* the giant 18-foot ground sloth, became extinct about 11,000 years ago. By 13,000 years ago, early humans had crossed the Bering land bridge into the New World, and these extinctions almost certainly were the first of many extinctions caused by human hunters.

3.3.3 Modern distribution patterns of plants and animals have been influenced by continental drift

The arrangement of the seas and landmasses on Earth has changed enormously over time as a result of **continental drift**, the slow movement of the Earth's surface plates. The present-day Earth consists of a molten mass overlain by a solid crust about 100 km thick. This crust is not a single continuous piece but is broken into about 14 irregular pieces, called tectonic plates (**Figure 3.15**). As the molten material below rises along

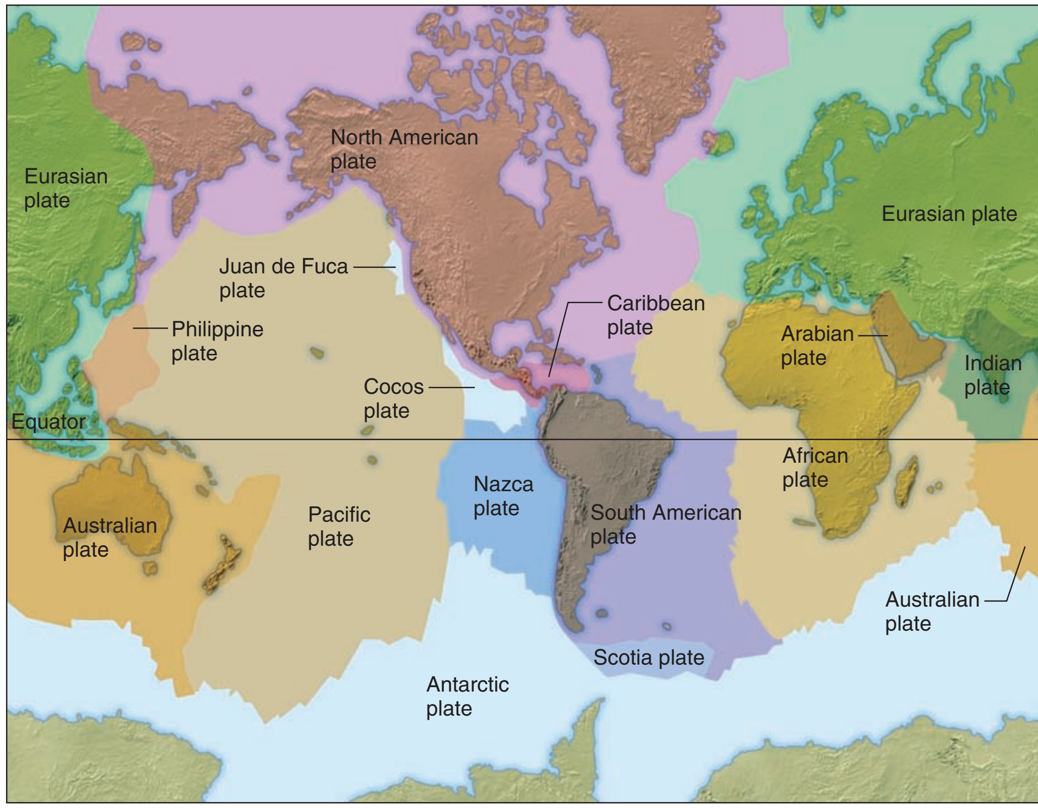


Figure 3.15 Global tectonic plates. There are about 14 major rigid slabs, called tectonic plates, that form the current surface of the Earth.

the cracks between the plates, it pushes them aside and cools to form new edges to the plates. The irregular, tumbled edges of these plates are the mid-oceanic ridges. As the plates are pushed aside, their opposite edges meet. Where they meet, one edge is forced under the other, a phenomenon called subduction (**Figure 3.16**). In subduction zones, mountain chains may be formed. Continental drift was first proposed by a German

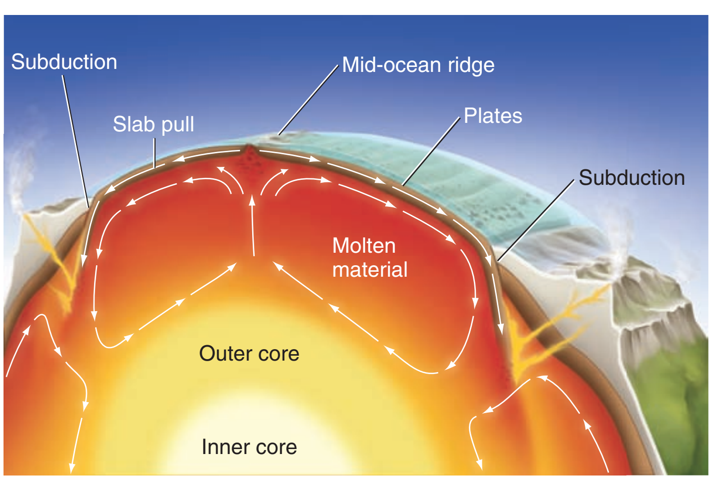


Figure 3.16 Tectonic plates shift due to the movement of molten material. A continent moves as the tectonic plate beneath it gradually shifts position.

meteorologist, Alfred A. Wegener, in 1912 and has since been supported by a variety of geological and biological evidence.

The breakup of a supercontinental landmass into constituent continents and the eventual re-formation of a supercontinent is probably a cyclical event, with a distinct periodicity. As we noted earlier, the most recent of these supercontinents was Pangaea (meaning "all lands" in Greek), which subsequently broke up into Laurasia in the Northern Hemisphere and Gondwanaland in the Southern Hemisphere. These landmasses continued to break up into the present-day continents and drift farther apart (**Figure 3.17**).

Wegener's hypothesis about continental drift was based on several lines of evidence. The first was the remarkable fit of the South American and African continents, as part of Gondwanaland, shown in **Figure 3.18.** Furthermore, Wegener noted that the occurrence of matching plant and animal fossils in South America, Africa, India, Antarctica, and Australia was best explained by continental drift. Many of these fossils were of large land animals, such as the Triassic reptiles *Lystrosaurus* and *Cynognathus,* that could not have easily dispersed among continents, or of plants whose seeds were not likely to be dispersed far by wind, such as the fossil fern *Glossopteris.* Also, the discovery of abundant fossils in Antarctica was proof that this presently frozen land must have been situated much closer to temperate areas in earlier geological times.

The distribution of the essentially flightless bird family, the ratites, in the Southern Hemisphere is also the result of continental drift. The common ancestor of these birds

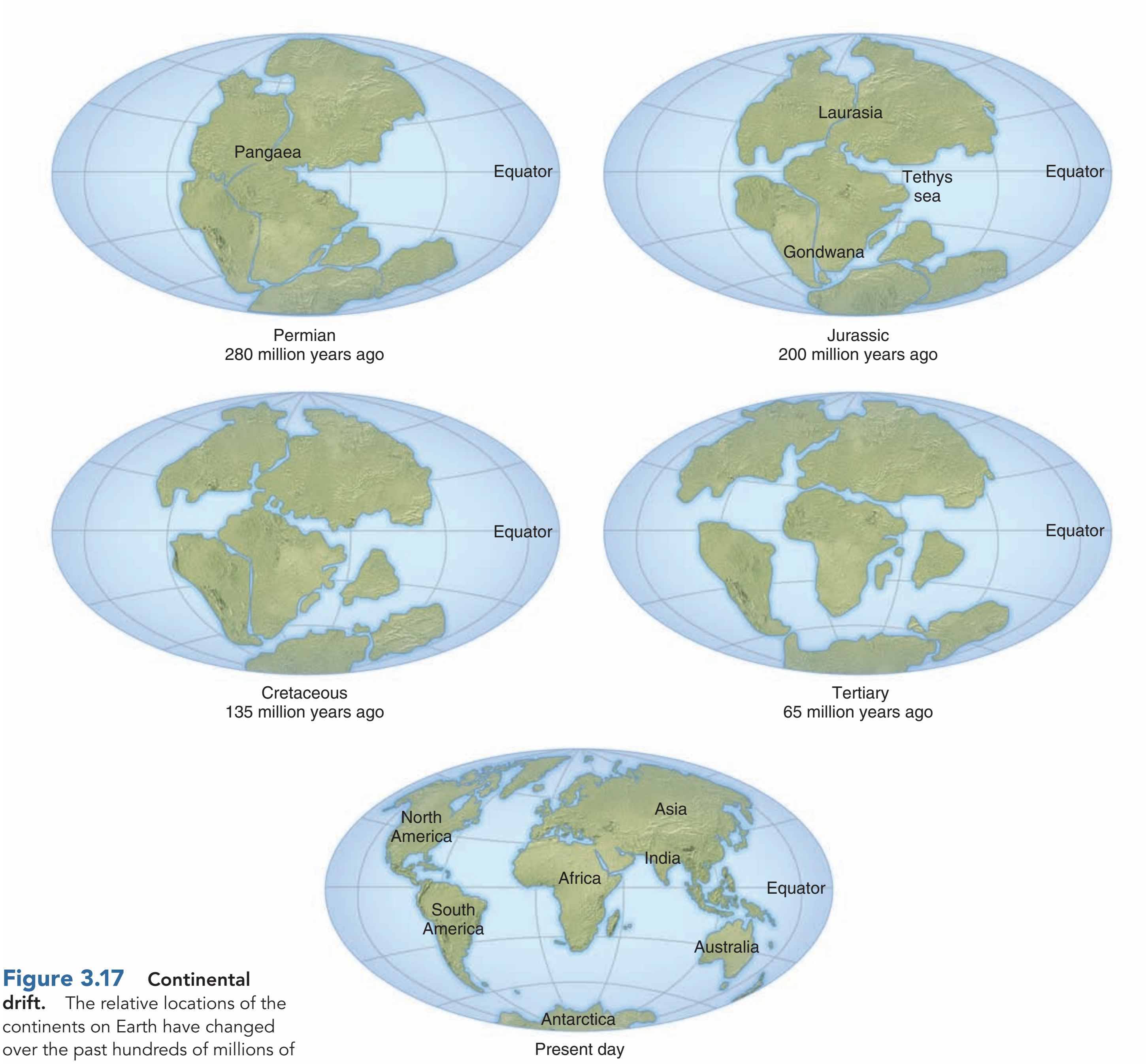


Figure 3.17 Continental drift. The relative locations of the continents on Earth have changed over the past hundreds of millions of years.

occurred in Gondwanaland. As Gondwanaland split apart, genera evolved separately in each continent, so that today we have ostriches in Africa, emus in Australia, and rheas in South America. Similarly, the southern beech trees of the genus *Nothofagus* have widely separate distributions in the Southern Hemisphere (**Figure 3.19**). The southern beech nuts have limited powers of dispersal and are not thought to be capable of germinating after long-distance ocean travel. However, trees produce abundant pollen that is found in many fossil records throughout Gondwanaland. Taken together, present-day and fossil records suggest a Gondwanaland ancestor.

Continental drift is not the only mechanism that creates disjunct distributions. The distributions of many present-day species are relics of once much broader distributions. For example, there are currently four living species of tapir, three in Central and South America and one in Malaysia (**Figure 3.20**). Fossil records reveal a much more widespread distribution over much of Europe, Asia, and North America. The oldest fossils come from Europe, making it likely that this was the center of origin of tapirs. Dispersal resulted in a more widespread distribution. Cooling climate resulted in the demise of tapirs in all areas except the tropical locations.

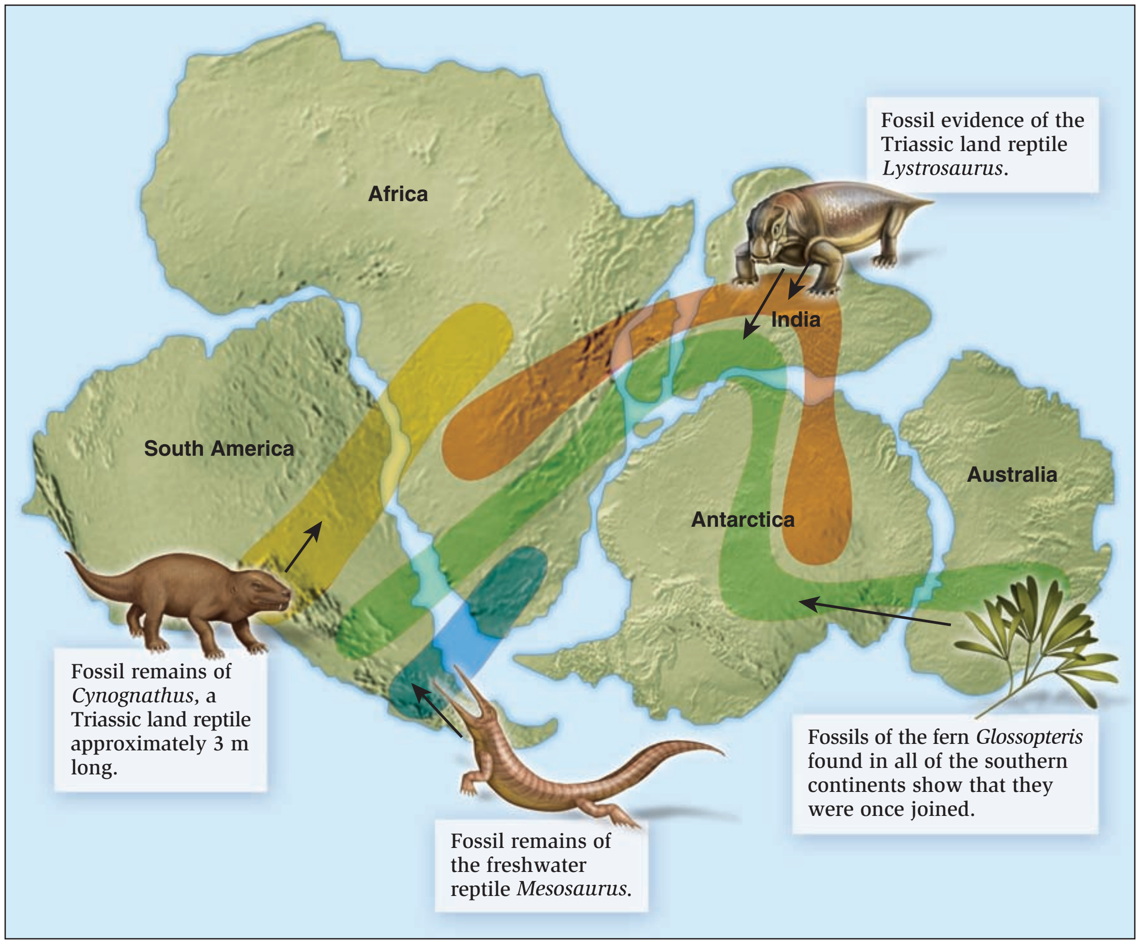


Figure 3.18 **The location of fossil plants and animals on present-day continents can be explained by continental drift.** The fossil remains of dinosaurs and ancient plants are spread across regions of South America, Africa, India, Antarctica, and Australia, which were once united as Gondwanaland.

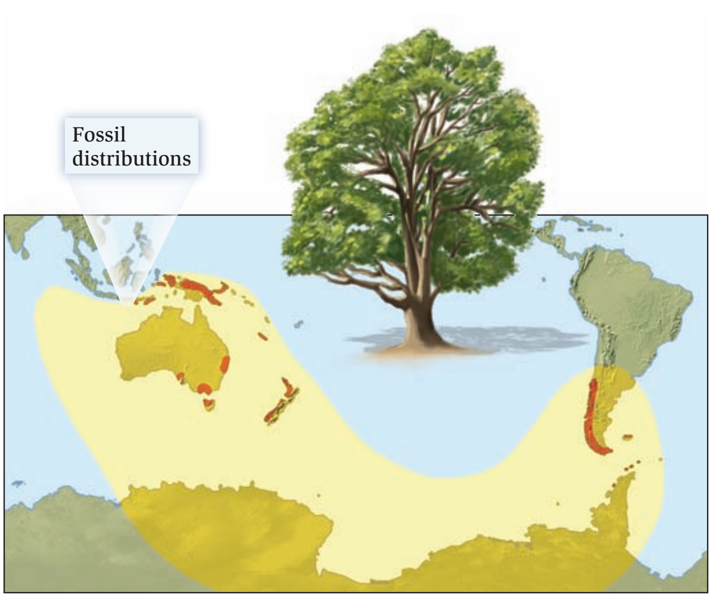


Figure 3.19 **The distribution of *Nothofagus* trees.** Present-day (dark) and fossil distributions (yellow shading) suggest a Gondwanaland ancestor. (After Heads, 2006.)

Another well-known example of a disjunct distribution is the restricted distribution of monotremes and marsupials. These animals were once plentiful all over North America and Europe. They spread into the rest of the world, including South America and Australia, at the end of the Cretaceous period when, although the continents were separated, land bridges existed between them. Later, placental mammals evolved in North America and displaced the marsupials there, apart from a few species such as the opossum. However, placental mammals could not invade Australia because the land bridge by then was broken.

The Elephantidae and Camelidae also have disjunct distributions. Elephants evolved in Africa and subsequently dispersed on foot through Eurasia and across the Bering land bridge from Siberia to North America, where many are found as fossils. They subsequently became extinct everywhere except Africa and India. Camels evolved in North America and made the reverse trek across the Bering bridge into Eurasia; they also crossed into South America via the Central

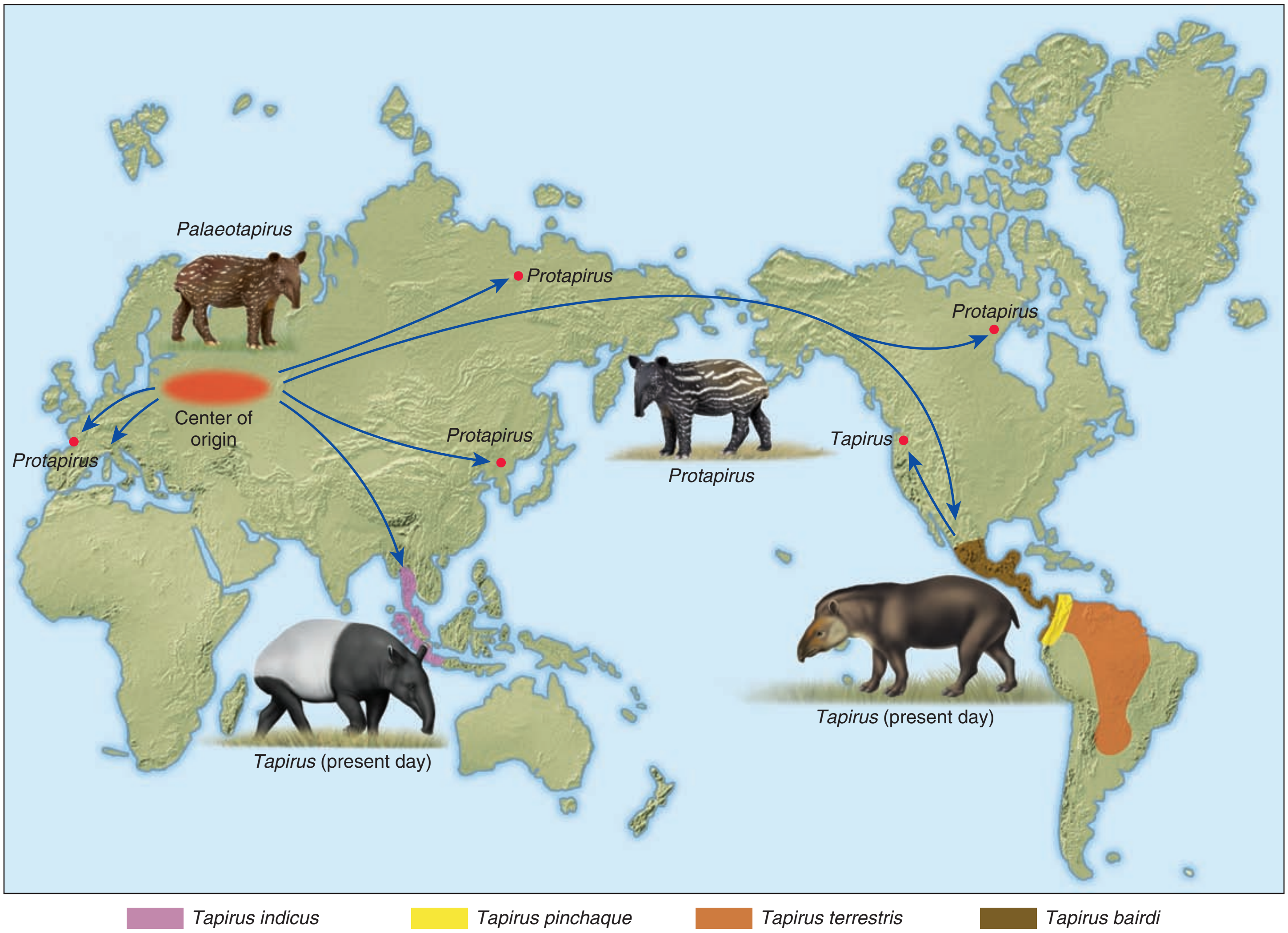


Figure 3.20 Tapir distribution. There are four living tapir species, three in Central and South America and one in Malaysia. Fossil evidence suggests a European origin of the ancestral *Paleotapirus* and a dispersal of later-evolving *Protapirus.* A more widespread distribution followed with tapirs dying out in other regions (marked with a red dot), possibly due to climate change. (After Rodriquez de la Fuente, 1975.)

American isthmus. They have since become extinct everywhere except Asia, North Africa, and South America.

Alfred Russel Wallace was one of the earliest scientists to realize that certain plant and animal taxa were restricted to certain geographic areas of the Earth, called biogeographic realms. For example, the distribution patterns of guinea pigs, anteaters, and many other groups are confined to Central and South America, from central Mexico southward. The whole area was distinct enough for Wallace to proclaim it the "neotropical realm." Wallace went on to divide the world's biota into six major realms, or zoogeographic regions. The most recent analyses divide the world into 11 major realms, with the Neotropical, Madagascan, and Australian being the most distinct (**Figure 3.21**).

Biogeographic realms correspond largely to continents but more exactly to areas bounded by major barriers to dispersal, like the Himalayas and the Sahara Desert. Within these realms, areas of similar climates are often inhabited by species with similar appearance and habits but from different taxonomic groups. For example, the kangaroo rats of North American deserts, the jerboas of central Asian deserts, and the hopping mice of Australian deserts look similar and occupy similar hot, arid environments, but they arise from different lineages, belonging to the families Heteromyidae, Dipodidae, and Muridae, respectively. This phenomenon, called **convergent evolution,** has led to the emergence in each realm of herbivores and predators that have evolved from different taxonomic ancestors (**Figure 3.22**).

In some cases individuals have been able to disperse from the area where the group originally evolved. This kind of dispersal is obviously easier for birds and insects, which have the power of flight, or for aquatic organisms, which can drift with the tide. Cattle egrets, *Bubulcus ibis,* crossed the South Atlantic from Africa to northern South America in the late

Figure 3.21 **The world's major zoogeographic realms.** Note that the borders do not always demarcate continents, but reflect major barriers to dispersal such as deserts, mountain ranges, or oceans. Eleven broad-scale realms are named. Color differences depict the relative phylogenetic differences between realms. The Panamanian and Neotropical realms are very similar, whereas the Australia and Madagascan realms are quite distinct. (After Holt et al., 2013)

1800s, possibly with the assistance of humans. Since then they have spread widely in South America and the United States. Humans, of course, have succeeded in transporting many species, such as rats, rabbits, sparrows, and starlings, outside their native ranges.

Check Your Understanding

3.3 The giant anteater, *Myrmecophaga tridactyla,* of South America, and the Echidna, *Tachyglossus aculeatus,* of Australia look similar. Both have long snouts and eat ants, yet they are only distantly related. Explain how this is possible.

3.4 Many Patterns Exist in the Formation and Extinction of Species

Because the environment is constantly changing, new species evolve and others go extinct. Species become extinct when all individuals die without producing progeny. They disappear in a different sense when a species' lineage is transformed over evolutionary time or divides into two or more separate lineages. This is called pseudoextinction. The relative frequency of true extinction and pseudoextinction in evolutionary history is not yet known. Species extinction is a natural process. Fossil records show that the vast majority of species that have ever existed are now extinct. Leigh Van Valen (1976) described the evolutionary history of life as a continual race with no winners, only losers. He termed this view the **Red Queen hypothesis,** named for the red queen in Lewis Carroll's *Through the Looking Glass* who said to Alice, "It takes all the running you can do to keep in the same place." The analogy was that, in an ever-changing world, species must continually evolve and change in order not to go extinct. In this section we ask, What are the rates of formation of new species and the rates of extinction of old ones? Where are extinctions highest globally? We can possibly use this information to decrease rates of extinction.

3.4.1 Species formation may be gradual or sporadic

The rate of evolutionary change and species formation is not constant, though the tempo of evolutionary change is often debated. The concept of **gradualism** proposes that new species evolve continuously over long periods of time (**Figure 3.23a**). The idea of gradualism suggests that large phenotypic differences that produce new species are the result of long periods of small genetic changes that accumulate over time. Such gradual transitions are relatively rare in the fossil record. Instead, fossils of new species appear relatively rapidly and with few transitional types. Stephen Jay Gould and Niles Eldredge (1977) championed the idea of **punctuated equilibrium,** which suggests that the tempo of evolution is more sporadic (**Figure 3.23b**). According to this concept,

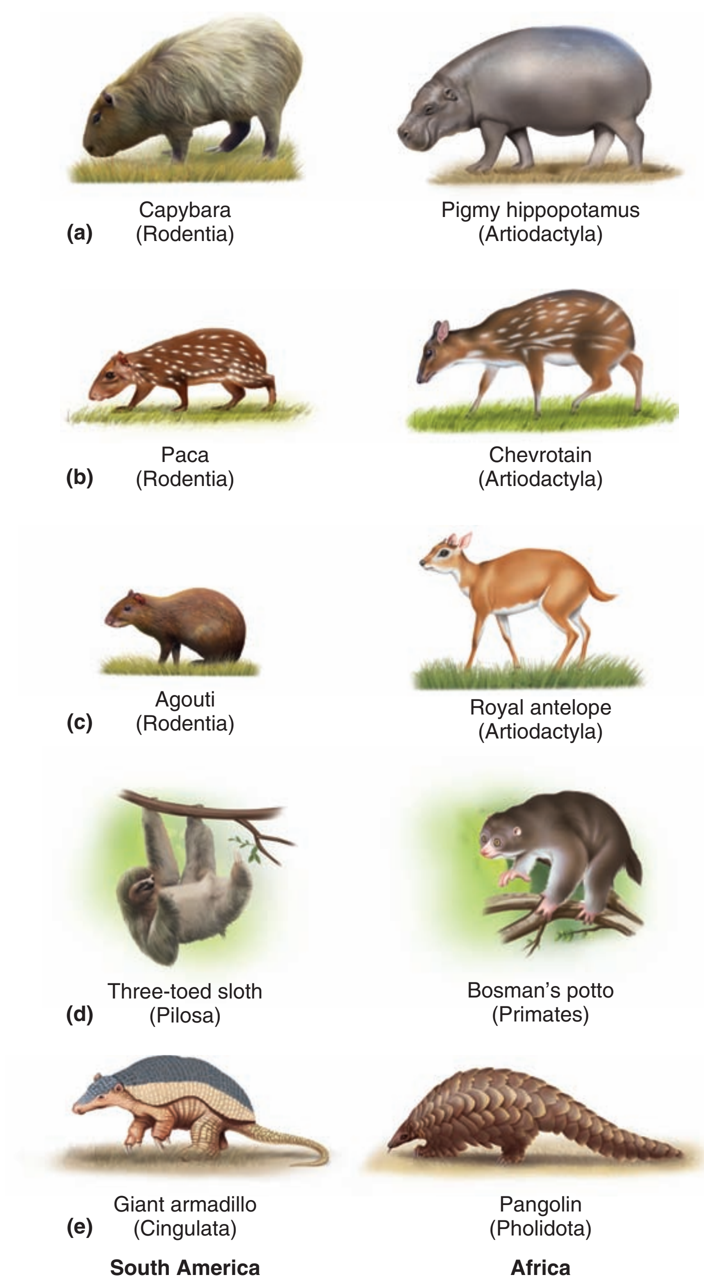


Figure 3.22 Convergent evolution between tropical rain forest mammals of South America and Africa. Common names and orders are shown, illustrating how similar-looking species have very different taxonomic affiliations.

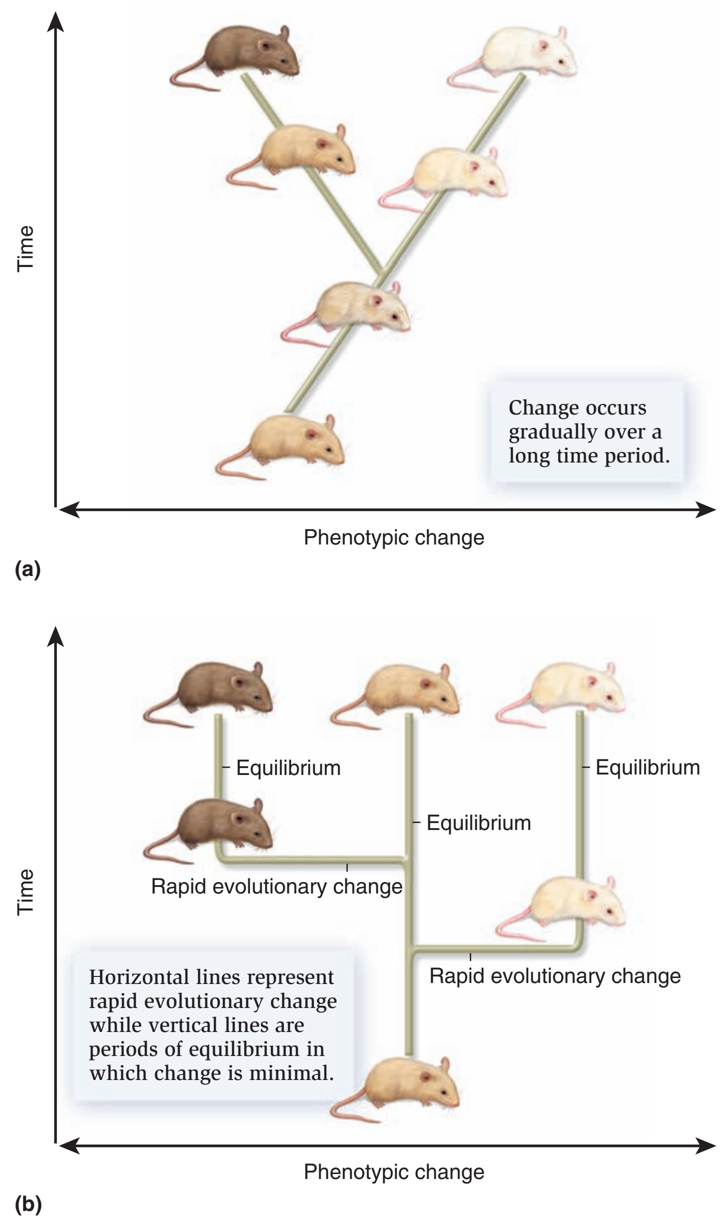


Figure 3.23 The pace of speciation. **(a)** Gradualism depicts evolution as a gradual change in phenotype from accumulated small genetic changes. **(b)** Punctuated equilibrium depicts evolution as occurring during relatively long periods of stasis punctuated by periods of relatively rapid evolutionary change.

species remain relatively unchanged for long periods of time and are at equilibrium with their environment. These long periods of stasis are punctuated by relatively rapid periods of change. This concept is supported by the fact that fossils of new species usually appear suddenly, with few transitional types. Proponents of gradualism brush off this phenomenon as simply an inadequacy of the fossil record, but advocates of punctuated equilibrium argue that the fossil record accurately represents what happens in nature and that new species do appear suddenly. This process is too quick for the slow process of fossilization to reflect accurately. According to the idea of punctuated equilibrium, most evolution occurs not as "ladders," in which one species slowly turns into another and in turn into another, but as "bushes," where species arise relatively quickly and where only a few active tips survive in the long term.

How rapidly does speciation occur? The answer differs for different organisms. American and Eurasian sycamore trees, *Platanus occidentalis* and *P. orientalis,* have been isolated for at least 20 million years, yet still form fertile hybrids.

The selective forces on these two continents have obviously not been sufficient to cause reproductive isolation between these ecologically general species. However, several genera of mammals, including polar bears, *Ursus maritimus,* and *Microtus* voles, do appear to have originated relatively recently, roughly 200,000 years ago in the Quaternary period. Lake Nabugabo in Africa has been isolated from Lake Victoria for less than 4,000 years, yet it contains five species of fish that are found nowhere else on Earth. Again in Hawaii, at least five species of *Hedylepta* moth feed exclusively on bananas, which were introduced by the Polynesians only some 1,000 years ago.

3.4.2 Patterns of extinction are evident from the fossil record

For many taxa, five major mass extinction events appear in the geological record: one in each of the Ordovician, Devonian, Permian, Triassic, and Cretaceous periods. The causes of these extinctions have been much debated. The Ordovician extinction appears correlated with a huge global glaciation. The Permian was the largest recorded extinction for both fishes, 44% of families disappearing, and tetrapods, 58% of families disappearing. For the Permian extinction, geologically rapid changes in climate, continental drift, and volcanic activity are probably the most important causes, though a meteor strike has also been implicated. The causes of the Triassic and Devonian extinctions are not well known. Luis Alvarez and his colleagues (1980) at the University of California, Berkeley, suggested that the Cretaceous extinction may also have been associated with a single catastrophic event such as a meteor strike. The resultant dust cloud presumably blocked solar radiation, resulting in rapid global cooling and causing extinction of plants and animals alike. Groups that had little capacity for temperature regulation became extinct. Taxa with life history stages that were resistant to brief but intense cold, such as seed plants, insects, and endothermic birds and mammals, suffered fewer extinctions. The late Cretaceous extinction was far more significant for tetrapods than for other groups, with 75% of species in the fossil record disappearing at this time. Affected taxa were mainly confined to three major groups: the dinosaurs, plesiosaurs, and pterosaurs.

It is important to realize that extinction is the rule rather than the exception. Because the average species lives 5–10 million years in the fossil record, and the duration of the fossil record is 600 million years, the Earth's current number of plant and animal species represents about 1–2% of species that have ever lived. Leigh Van Valen (1973) suggested that over evolutionary time, the probability of the extinction of a genus or family is independent of the duration of its existence. Old lineages do not die out more readily than younger ones. On the other hand, past adaptations of species provide little preadaptation to extraordinary periodic conditions. There is some evidence that the survivors of mass extinctions tended to be the more ecologically generalist, having a broad diet and existing in a wide variety of habitats. Generalists also tend to have a greater breadth of geographic distribution, which appears to be important in enhancing survival.

3.4.3 Current patterns of extinction have been influenced by humans

As we noted in Chapter 1, it is indisputable that humans are the cause of accelerated extinction rates on Earth. Early anthropogenically caused extinctions were mostly due to hunting. As a result, the most widespread extinctions in the Quaternary period involved the so-called megafauna—mammals, birds, and reptiles over 44 kg in body size. The arrival of humans on previously isolated continents, around 40,000 years ago in the case of Australia and 15,000 years ago, or possibly earlier, for North and South America, coincides with large-scale extinctions in certain taxa. Australia lost nearly all its species of very large mammals, giant snakes, and reptiles, and nearly half its large flightless birds around this time. Similarly, North America lost 73% and South America 80% of their genera of large mammals around the time of the arrival of the first humans. The probable cause was hunting, but the fact that climate changed at around this same time leaves the door open for natural changes as a contributing cause of these extinctions. Many taxa were lost in Alaska and northern Asia, where human populations were never large, suggesting that in these cases climate change was the major cause.

However, the rates of extinctions on islands in the more recent past confirm the devastating effects of humans. The Polynesians, who colonized Hawaii in the 4th and 5th centuries C.E., appear to have been responsible for exterminating over 2,000 bird species, including around 50 of the 100 or so endemic species. Introduced predators, such as rats, aided in these extinctions. A similar impact probably was felt in New Zealand, which was colonized some 500 years later than Hawaii. There, an entire avian megafauna, consisting of 15 species of huge land birds, was exterminated by the end of the 18th century by the Maoris. This extinction was probably accomplished through a combination of direct hunting, large-scale habitat destruction through burning, and introduced dogs and rats. Only the smaller kiwis survived.

3.4.4 Extinction rates are higher on islands than on the mainland

Certain generalized patterns of extinction emerge on examination of the data. One of the strongest of these is the preponderance of extinctions on islands versus continental areas. While islands often have greater overall numbers of recorded extinctions (**Figure 3.24**), there are also lower numbers of species on islands than on continents, making the percentage of taxa extinct on islands even greater than on continents. The reason for high extinction rates on islands are many and varied. Many island species effectively consist of single

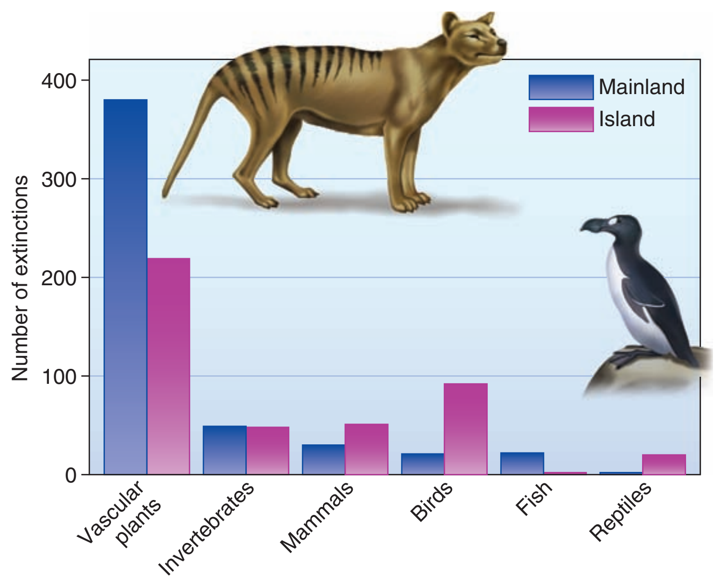


Figure 3.24 **Recorded extinctions, from 1600 to the present, on continents and islands.**

ECOLOGICAL INQUIRY

Why do so many extinctions occur on islands?

populations. Adverse factors are thus likely to affect the entire species and bring about its extinction. In support of this idea, extinction rates of land birds of the Pacific islands tend to decrease with increasing island area (**Figure 3.25**). Also, species on islands may have evolved in the absence of terrestrial predators and may often be flightless. They may also have reduced reproductive rates. Finally, many island species were so tame and ecologically naive that when humans invaded,

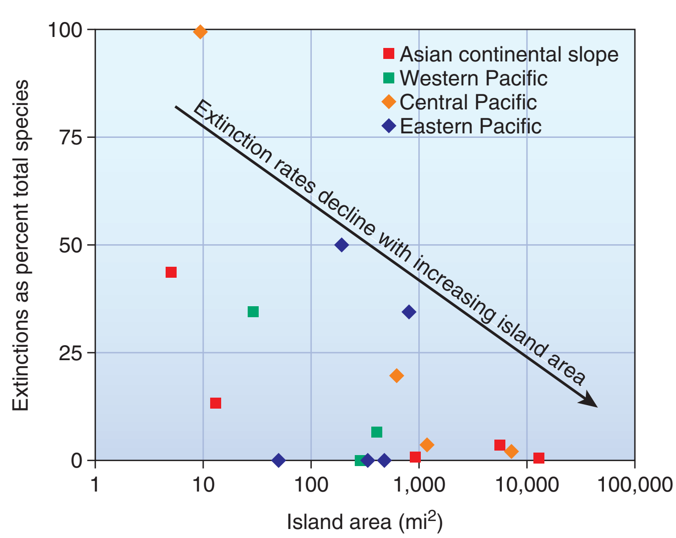


Figure 3.25 **Extinction rates of Pacific island land birds.** Extinction rates tend to decrease with increasing land area. (After Greenway, 1967.)

they were easily killed. On Chiloe Island, off the coast of Chile, Darwin found the foxes so tame that he collected the species by hitting it over the head with his hammer. It was later named Darwin's fox (*Pseudalopex fulvipes*). Tameness, flightlessness, and reduced reproductive rates appear to be major contributory factors to species extinction, especially when novel predators are introduced.

3.4.5 Extinctions are most commonly caused by introduced species and habitat destruction

Introduced species and habitat destruction by humans have been the major factors involved in extinctions worldwide. In the United States these causes have been implicated in 38% and 36%, respectively, of known causes of extinctions (**Figure 3.26a**). Hunting and overcollecting also contribute significantly, causing 23% of extinctions. However, causes differ slightly for different taxa. Hunting and introduced species are much more important for mammals than for other animals (**Figure 3.26b**). For aquatic species, such as mollusks, habitat destruction, including pollution, has accounted for the majority of extinctions (**Figure 3.26c**).

The effects of introduced species can be assigned to competition, predation, or disease and parasitism. Competition may exterminate local populations, but it has less frequently been shown to extirpate entire populations of rare species. For predation there have been many recorded cases of extinction. James Brown (1989) noted that introduced predators such as rats, cats, and mongooses have accounted for at least 43.4% of recorded extinctions of birds on islands. Parasitism and disease by introduced organisms is also important in causing extinctions. As noted in Chapter 1, avian malaria in Hawaii, facilitated by the introduction of mosquitoes, is thought to have killed 50% of local Hawaiian bird species. Similarly, the American chestnut tree, *Castanea dentata,* and European and American elm trees, *Ulmus procera* and *U. americana* respectively, have been severely decreased in numbers by introduced plant diseases, though none of these has yet become extinct.

Check Your Understanding

3.4 Why might length of evolutionary existence not guarantee future success to a lineage?

3.5 Degree of Endangerment Varies by Taxa, Geographic Location, and Species Characteristics

Knowing why species have gone extinct in the past helps us to recognize the problems that are likely to threaten species with extinction today. At least 20% of vertebrates are threatened with extinction, but the figure is much higher for amphibians (**Table 3.3**). Within the mammals some orders seem to have

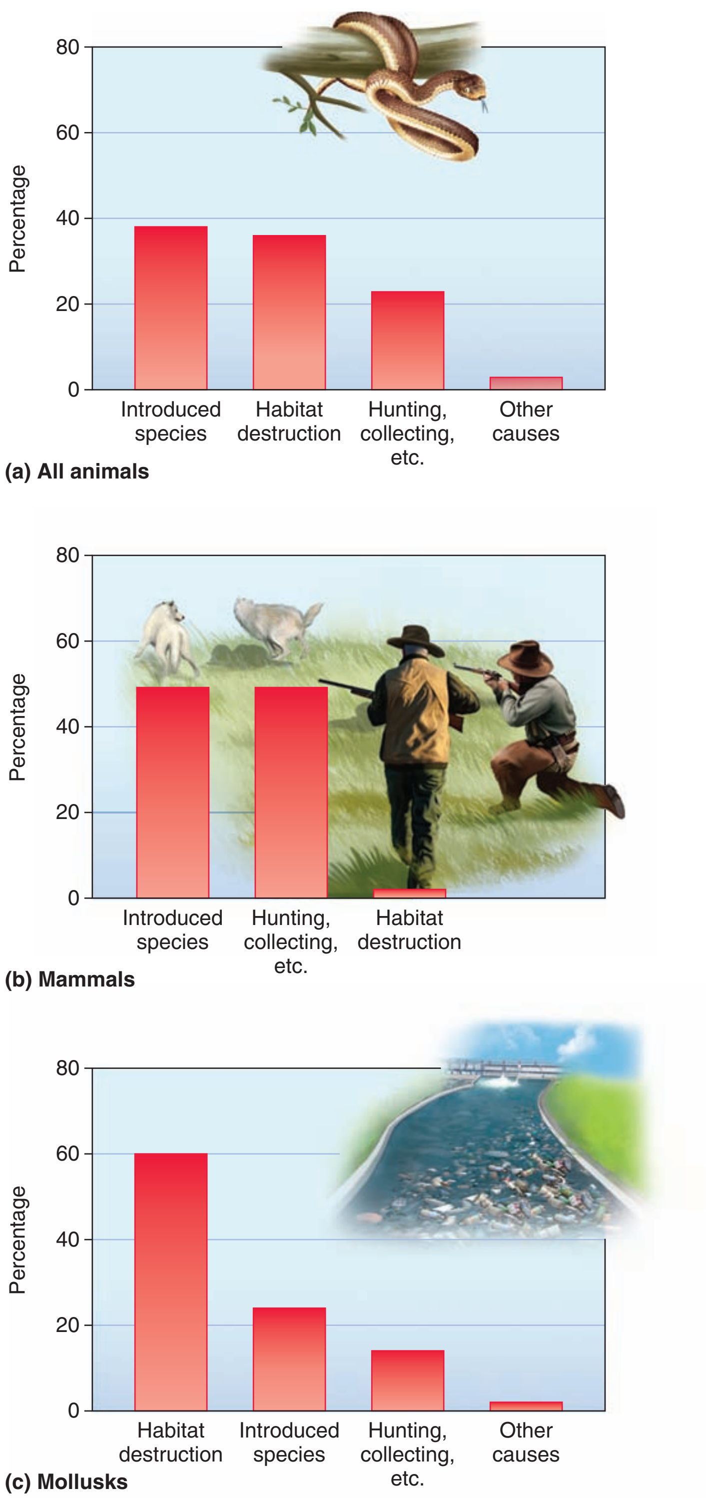


Figure 3.26 **Causes of animal extinctions in the United States, 1600–1980.** **(a)** Causes of historical extinctions in all animals. **(b)** Causes of historical extinctions in mammals. **(c)** Causes of historical extinctions in mollusks.

ECOLOGICAL INQUIRY

Why is habitat destruction so much more important for mollusks than for other taxa?

a disproportionately high number of endangered species. For example, manatees and dugongs have four out of five species threatened. Members of the horses, primates, antelopes, and carnivores, are also highly threatened with 79%, 38%, 35%, and 28%, respectively, of their constituent species listed. Although these latter four orders combined contain only a little over 20% of the world's mammal species, they account for just over half of the endangered species. Vertebrates are probably more vulnerable to extinction than invertebrates, because they are much larger and require more resources and larger ranges. Most of the causal factors currently threatening species are anthropogenic in nature, and data from the United States show that current threats are similar to the causes of extinction, with habitat destruction, invasive species, pollution, and direct exploitation the most important (refer back to Figure 1.6).

3.5.1 Endangered species are not evenly distributed among geographical areas

Ecologists have determined which geopolitical areas contain the most endangered species (**Table 3.4**). Ecuador and the United States have the highest number of endangered species. This is in part due to relatively thorough biological inventories, and the fact that both countries are rich in species. The majority of threatened mammals occur in mainly tropical countries, with the highest numbers recorded from Indonesia (146), India (89), China (83), Brazil (73), and Mexico (72). Such countries may have large numbers of endangered mammals simply because they have more mammals in general; therefore, if the same percentage were threatened with extinction in each country, a country having a larger number of mammals to begin with would have a higher number endangered.

We can obtain some idea of the number of endangered species a country might be expected to have by graphically plotting the number of endangered mammal species against that country's area (**Figure 3.27**). Bigger countries should have more mammal species than smaller ones and so should have more endangered species. The line describes the relationships between area and number of endangered mammal species. Indonesia in particular has more endangered mammals in relation to country area than would be predicted statistically (points above the line), whereas the United States, for example, has fewer (points below the line). It may come as a surprise to find that the United States heads the list (Table 3.4) in terms of the numbers of endangered fishes and invertebrates, but this is probably because other countries have not inventoried such species as thoroughly.

In the United States the greatest numbers of endangered species occur in Hawaii, southern California, southern Appalachia, and the southeastern coastal states. Many endangered species are restricted to very small areas. For example, Andy Dobson and colleagues (1997) discovered that 48% of endangered plants and 40% of endangered arthropods are restricted to a single county.

Table 3.3 Numbers of threatened vertebrate species, by taxon, according to the IUCN, as of 2007.

	Number of described species	Number of species evaluated by 2007	Number of threatened species in 2007	Percentage threatened in 2007, as % of species described	Percentage threatened in 2007, as % of species evaluated
Mammals	5,416	4,863	1,094	20%	22%
Birds	9,956	9,956	1,217	12%	12%
Reptiles	8,240	1,385	422	5%	30%
Amphibians	6,199	5,915	1,808	29%	31%
Fishes	30,000	3,119	1,201	4%	39%
TOTAL	**59,811**	**25,238**	**5,742**	**10%**	**23%**

Table 3.4 Numbers of threatened species in twelve countries with the greatest overall numbers of threatened species.

	Mammals	Birds	Reptiles	Amphibians	Fishes	Invertebrates	Plants	Total
Ecuador	33	68	10	163	15	51	1,838	2,178
United States	41	74	32	53	166	571	242	1,179
Malaysia	50	40	21	46	47	21	686	911
Indonesia	146	116	27	33	111	31	386	850
Mexico	72	59	95	198	115	40	261	840
China	83	86	31	85	60	6	446	797
Brazil	73	122	22	25	66	35	382	725
Australia	64	50	38	47	87	282	52	623
Colombia	38	87	15	209	31	2	222	604
India	89	75	25	63	39	22	247	560
Madagascar	47	35	20	55	73	32	280	542
Tanzania	34	39	5	41	137	43	240	539

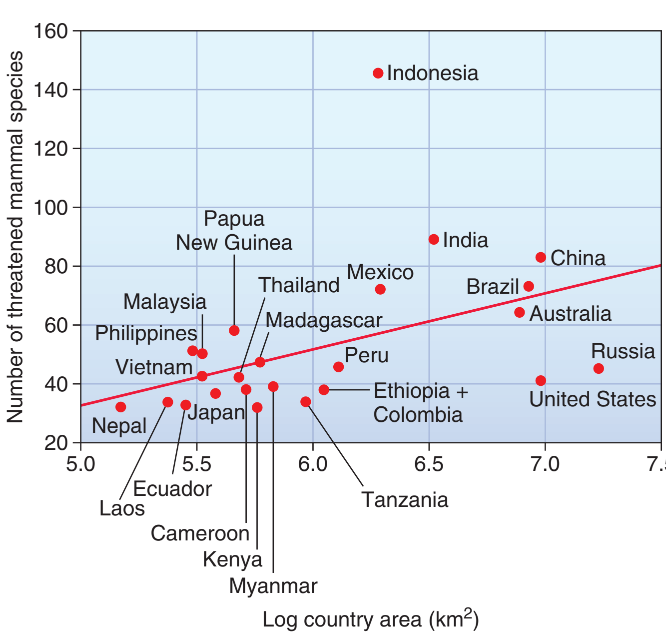


Figure 3.27 The relationship between the number of threatened species in a country and the area of that country. Data are for countries with greater than 30 species of threatened mammals. Countries with more threatened species than would be expected based on their area lie above the line, those with fewer threatened species fall below it.

3.5.2 Vulnerability to extinction can be linked to species characteristics

In order to further predict what types of human influences are critical in the extinction of wild species, it is useful to have some knowledge of the species traits that may be correlated with high levels of extinction. At least seven species characteristics have been proposed as factors affecting a species' sensitivity to extinction (**Figure 3.28**).

1. *Rarity.* Generally, rare species are more prone to extinction than common ones. This is not as intuitive as might first be thought. For example, a very common species might be very susceptible to even the slightest change in climate. A rare species, although it may exist at very low numbers, may be more resistant to climatic change and thus more persistent in evolutionary time as, for example, global warming proceeds. But what is rarity? Again, this is not as obvious as one might think. Deborah Rabinowitz (1981) showed that "rarity" itself may depend on different factors. A species is often termed rare if it is found only in one geographic area or one habitat type, regardless of its density there. A species that is widespread, but at very low density, can also be regarded as rare. Conservation by habitat management is much easier, and more likely to succeed, for species restricted to one area or habitat type than for widely distributed but rare species.
2. *Dispersal ability.* Species that are capable of migrating between fragments of habitat, such as between mainland areas and islands, may be more resistant to extinction. Even if a population goes extinct in one area, it may be "rescued" by immigrating individuals from another population.
3. *Degree of specialization.* It is often thought that organisms that are specialists are more likely to go extinct. For example, organisms that feed on only one type of plant, such as pandas, which feed on only a species of bamboo, are at a relatively high risk of extinction. Animals that have a broader diet may be able to switch from one food type to another in the event of habitat loss and are thus less prone to extinction. Plants that can live in only one soil type may be more prone to extinction.
4. *Population variability.* Species with relatively stable populations may be less prone to extinction than others. For example, some species, especially those in northern forests, show pronounced cycles. Lemmings reach very high numbers in some years, and the population crashes in others. It is thought that such species might be more likely to become extinct than others.
5. *Feeding level (animals only).* Animals feeding higher up the food chain usually have small populations (look ahead to Chapter 25). For example, birds of prey or predatory mammals number far fewer than their prey species, and, as noted earlier, rare species may be more vulnerable to extinction.
6. *Life span.* Species with naturally short life spans may be more likely to become extinct. Imagine two species of birds, one of which lives for 70 or 80 years and begins breeding at year 10, like a parrot, and the other, which is about the same size but begins breeding at age 2 or 3 and lives only to the age of 7 or 8 years, like an American robin. In the event of habitat degradation, the parrot, with its 80-year life span, may be able to "weather the storm" of a fragmented habitat for 10 years without breeding. The parrot can begin breeding again when the habitat becomes favorable. Species with naturally short life spans are not well able to wait out unfavorable periods.
7. *Reproductive ability.* Species that can reproduce and breed quickly may be more likely to recover after severe population declines than those that cannot. Thus, it is thought that those organisms with a high rate of increase, especially small organisms, like bacteria, insects, and rodents, are less likely to go extinct than larger species like elephants, whales, and redwood trees. For example, the passenger pigeon laid only one egg per year, and this low reproductive rate probably contributed to its demise.

We must decrease habitat destruction, reduce hunting, and prevent the release of exotic species in order to minimize threats to endangered species and increase their chance for survival. To identify species at risk for extinction before they reach endangered status, we must understand many aspects of their biology, including their abundance, how widely distributed they are, how specialized they are, and their reproductive rate and life span. The behavior of a species can also affect its reproductive ability and abundance, and therefore its susceptibility to extinction. In Chapter 4 we will explore the behavior of individuals and the life history strategies of organisms.

Check Your Understanding

3.5 How is it that a rare species that is confined to a small geographic area may be less prone to extinction than a more widespread species?

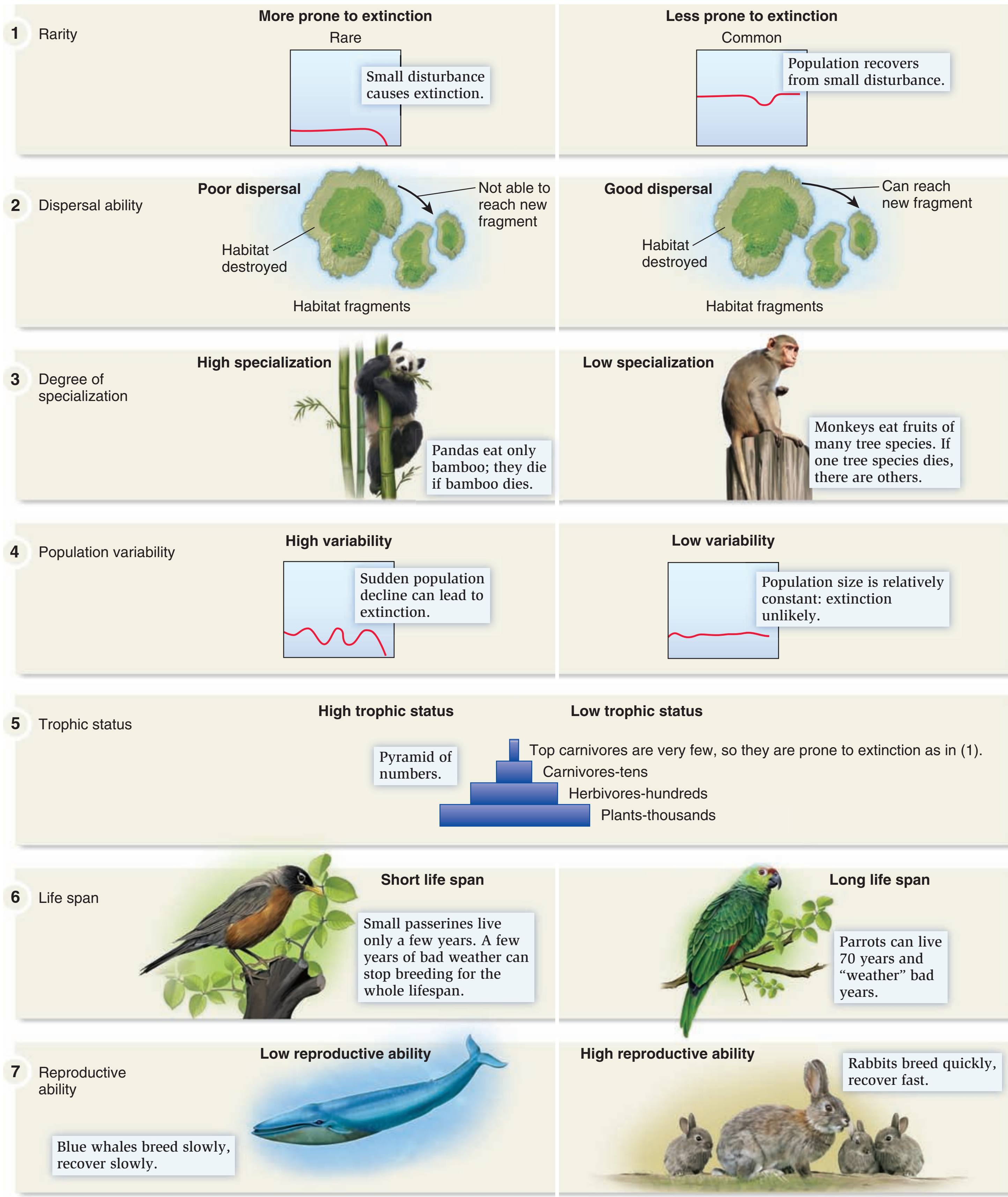


Figure 3.28 **Species characteristics that make them more or less prone to extinction.**

ECOLOGICAL INQUIRY

What defines a species' rarity?

SUMMARY

3.1 Natural Selection Can Follow One of Four Different Pathways

- Natural selection can follow one of four different paths: directional, stabilizing, balancing, and disruptive.
- Directional selection favors individuals at one end of a phenotypic distribution that have greater reproductive success in a particular environment (Figures 3.1–3.3).
- Stabilizing selection favors the survival of individuals with intermediate phenotypes, such as birds with intermediate clutch sizes (Figure 3.4).
- Balancing selection favors the maintenance of two or more morphs in a particular population (such as different colors of aphids), creating a situation known as a balanced polymorphism (Figure 3.A).
- Disruptive selection favors the existence of two or more genotypes that produce different phenotypes, as seen in different forms of plants that can survive in contaminated or uncontaminated soil (Figure 3.5).

3.2 Speciation Occurs Where Genetically Distinct Groups Separate into Species

- Among the four most important species concepts are the biological, phylogenetic, evolutionary, and ecological species concepts (Table 3.1).
- Biological species consist of groups of populations that are reproductively isolated from other such groups. This concept is useful for distinguishing morphologically similar species such as frogs (Figures 3.6).
- Phylogenetic species are identified by a unique combination of morphological or molecular features. Accepting the phylogenetic species concept would greatly increase the numbers of species on Earth, because many races of animals, such as black racers and deer mice, would be elevated to the status of species (Figures 3.7, 3.8).
- Evolutionary species have distinct historical lineages, and ecological species occupy different ecological niches.
- Hybridization between invasive and native species is threatening native species with extinction (Figure 3.B).
- Two main mechanisms explain the process of speciation, allopatric speciation and sympatric speciation.
- Allopatric speciation involves spatial separation of populations by a geographical barrier (Figure 3.9).
- Sympatric speciation involves separation of populations within the same habitat. In polyploidy, one species evolves into two species via changes in chromosome number. Insect populations may become reproductively isolated on different host plants, and other animals may become isolated in different habitats.

3.3 Evolution Has Accompanied Geologic Changes on Earth

- The history of life involves the appearance of unicellular organisms nearly 4 billion years ago and multicellular organisms about 1.2 billion years ago, both in the Precambrian era (Table 3.2). The evolution of life was accompanied by changes in atmospheric oxygen and carbon dioxide levels (Figures 3.10, 3.11).
- There was a tremendous increase in the number of invertebrate taxa on Earth in the Cambrian period, at the beginning of the Paleozoic era. Vertebrates appeared in abundance by the Ordovician period. Many millions of species have since gone extinct, while others, such as the horseshoe crab, appear relatively unchanged over hundreds of millions of years (Figure 3.12).
- The whole of the Mesozoic era is known as the age of reptiles, when giant dinosaurs roamed the Earth (Figure 3.13).
- Although mammals appeared early in the Mesozoic era, they did not flourish until the Cenozoic era, when huge species of elephant and rhinoceros were present (Figure 3.14).
- The surface of the Earth is not static but changes as underlying tectonic plates move (Figures 3.15, 3.16).
- The formation of a supercontinent and its breakup into constituent continents is probably a cyclical event; the latest supercontinent is known as Pangaea (Figure 3.17).
- Fossil records show that many species once occupied Gondwanaland, a southern supercontinent encompassing present-day South America, Africa, India, Australia, and Antarctica (Figure 3.18).
- Continental drift has affected the distribution patterns of life on Earth and has caused many disjunct distribution patterns (Figure 3.19). Range collapse has also caused disjunct distribution patterns (Figure 3.20).
- Distinct biogeographic realms with distinct flora and fauna are recognized in different parts of the world (Figure 3.21).
- Convergent evolution has led to the emergence of similar-looking floras and faunas in different realms where environmental conditions are similar (Figure 3.22).

3.4 Many Patterns Exist in the Formation and Extinction of Species

- The rate of evolutionary change may be gradual for some lineages, but for others it may show long periods of stasis punctuated by relatively quick periods of change (Figure 3.23).
- Over evolutionary time, many species have undergone periodic mass extinctions from causes as varied as global glaciations to meteor strikes.
- Humans have caused greatly accelerated extinction rates around the world. Some trends in extinction are evident.

- Extinction rates are higher on islands than the mainland (Figure 3.24) and higher on smaller islands than larger ones (Figure 3.25).
- The major causes of extinction in the past were habitat destruction, introduced species, and hunting or overcollecting (Figure 3.26).
- Most vertebrates have been evaluated as to their endangerment status, and amphibians are the most threatened taxa (Table 3.3).
- Most of the causal factors threatening species are anthropogenic in nature and are similar to the causes of extinction. The major threat is habitat loss and modification.

3.5 **Degree of Endangerment Varies by Taxa, Geographic Location, and Species Characteristics**

- Ecologists have determined which countries contain the most endangered species (Table 3.4).
- Some countries may have large numbers of endangered species simply because they have a large area and contain many species (Figure 3.27).
- At least seven species characteristics have been proposed to affect species sensitivity to extinction: rarity, dispersal ability, degree of specialization, population variability, feeding level, life span, and reproductive ability (Figure 3.28).

TEST YOURSELF

1. The birth weights of human babies generally lie in the range of 3–4 kg (6–9 lb). Mothers cannot deliver much bigger babies, and small babies tend to have increased mortality. This is an example of:
  a. Genetic drift
  b. Disruptive selection
  c. Directional selection
  d. Stabilizing selection
  e. Sexual selection

2. The biological species concept is based on species':
  a. Unique morphological characteristics
  b. Reproductive isolation
  c. Unique morphological and molecular characteristics
  d. Evolutionary lineage
  e. Unique ecological niche

3. In what geological period did most phyla on Earth arise?
  a. Cambrian
  b. Ordovician
  c. Silurian
  d. Carboniferous
  e. Permian

4. The original supercontinental landmass present 280 million years ago was called:
  a. Gondwanaland
  b. Pangaea
  c. Laurasia
  d. Tethys
  e. MesoAmerica

5. The gradual movement of the Earth's landmasses across the surface of the world is known as:
  a. Glaciation
  b. Continental drift
  c. Biogeography
  d. Convergent evolution
  e. Range collapse

6. The biogeographic realm that incorporates South America is known as:
  a. Palearctic
  b. Nearctic
  c. Ethiopian
  d. Silurian
  e. Neotropical

7. Most recorded extinctions have been caused by:
  a. Introduced species
  b. Habitat destruction
  c. Hunting and overcollection
  d. a and b equally
  e. a, b, and c equally

8. Elimination of native species by introduced species has been commonly caused by:
  a. Competition
  b. Predation
  c. Parasitism and disease
  d. a and b
  e. b and c

9. As a percentage of prescribed species, which taxa is currently threatened most with extinction?
  a. Mammals
  b. Birds
  c. Reptiles
  d. Amphibians
  e. Fishes

10. Which of the following characteristics increase a species' sensitivity to extinction?
  a. Increased rarity
  b. Increased life span
  c. Increased reproductive ability
  d. Increased dispersal ability
  e. Decreased population variability

CONCEPTUAL QUESTIONS

1. Explain the difference between directional, stabilizing, balancing, and disruptive selection.
2. Describe the advantages and disadvantages of the biological, phylogenetic, evolutionary, and ecological species concepts.
3. How can geographic isolation lead to speciation?
4. What factors can cause disjunct distribution patterns of plants and animals on Earth?
5. Explain the concepts of gradualism and punctuated equilibrium, which address the speed at which evolution occurs.

DATA ANALYSIS

The frequency of the melanic form of *Biston betularia* near industrial centers of Michigan in 1959–1962 was 533 of 598 individuals. Clean air legislation was initiated in the United States in 1963. In 1994–1995, the frequency of melanics was 11 of 60 moths. Calculate the percentage of melanics in both instances and explain what happened.

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