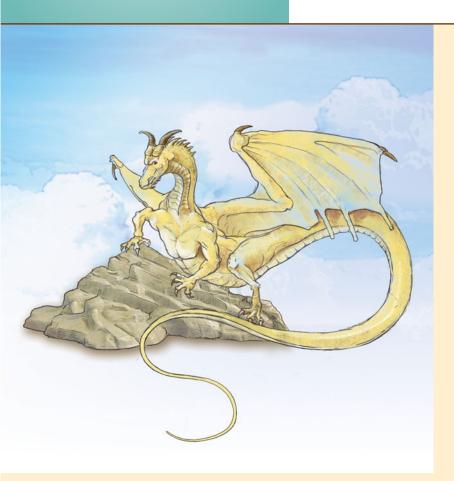
O H A P H E B

Biological Diversity and Biological Invasions



Yellow dragon disease—huanglongbing in Chinese, "citrus greening" in the United States, represented in China by this iconic symbol for the disease, is a growing threat worldwide to citrus crops. The reason this is a threat has to do with patterns of biodiversity and how people interface with these.

LEARNING OBJECTIVES

Biological diversity has become one of the "hot-button" environmental topics—there is a lot of news about endangered species, loss of biodiversity, and its causes. This chapter provides a basic scientific introduction that will help you understand the background to this news, the causes of and solutions to species loss, and the problems that arise when we move species around the globe. Interest in the variety of life on Earth is not new; people have long wondered how the amazing diversity of living things on Earth came to be. This diversity has developed through biological evolution and is affected by interactions among species and by the environment. After reading this chapter, you should understand . . .

- How biological evolution works—how mutation, natural selection, migration, and genetic drift lead to evolution of new species;
- Why people value biological diversity;
- How people affect biological diversity: by eliminating, reducing, or altering habitats; harvesting; introducing new species where they had not lived before; and polluting the environment;
- When and how biological diversity is important to ecosystems—how it may affect biological production, energy flow, chemical cycling, and other ecosystem processes;
- What major environmental problems are associated with biological diversity;
- Why so many species have been able to evolve and persist;
- The concepts of the ecological niche and habitat;
- The theory of island biogeography;
- How species invade new habitats, and when this can be beneficial and when harmful.

CASE STUDY

Citrus Greening

In 2005 a tiny fruit fly that carries and disperses a bacterial disease of citrus plants arrived in the United States from China (Figure 8.1). This disease, known as "citrus greening" or Chinese huanglongbing (yellow dragon disease) had been extending its range and had reached India, many African countries, and Brazil (Figure 8.2). Wherever the fly and the bacteria have gone, citrus crops have failed. The bacteria interfere with the flow of organic compounds in the phloem (the living part of the plant's bark). The larvae of the fruit fly sucks juices from the tree, inadvertently injecting the bacteria. Winds blow the adult flies from one tree to another, making control of the fly difficult. According to the U.S. Department of Agriculture (USDA), citrus greening is the most severe new threat to citrus plants in the United States and might end commercial orange production in Florida. Many Florida

counties are under a quarantine that prevents citrus plants from being moved from one area to another.¹

Introductions of new species into new habitats have occurred as long as life has existed on Earth. And beginning with the earliest human travelers, our ancestors have moved species around the world, sometimes on purpose, sometimes unknowingly. Polynesians brought crops, pigs, and many other animals and plants from one Pacific Island to another as they migrated and settled widely before A.D. 1000. The intentional spread of crop plants around the world has been one of the primary reasons that our species has been able to survive in so many habitats and has grown to such a huge number. But if invasion by species is as old as life, and often beneficial to people, why is it also the source of so many environmental problems? The answers lie in this chapter.



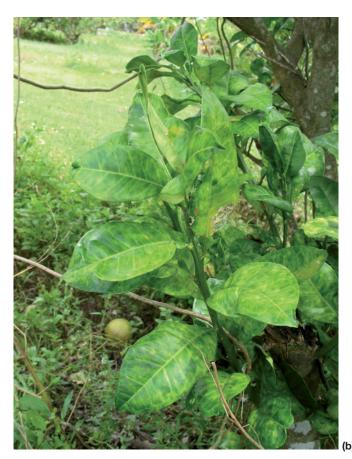


FIGURE 8.1 (a) Larvae of Diaphorina citri, the tiny fly that spreads citrus greening bacteria (Candidatus Liberibacter asiaticus); (b) the disease yellows leaves, turns fruit greenish brown, and eventually kills the tree.

(a

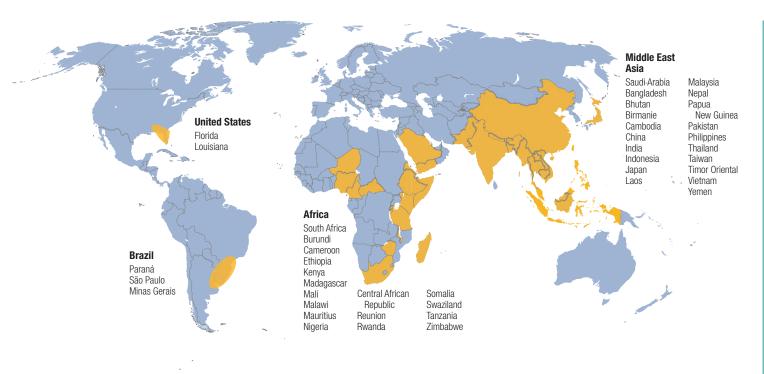


FIGURE 8.2 Where citrus greening has spread from its origin in China. The yellow shows the disease locations. (Source: USDA.)

8.1 What Is Biological **Diversity?**

Biological diversity refers to the variety of life-forms, commonly expressed as the number of species or the number of genetic types in an area. (We remind you of the definitions of population and species in Chapter 4: A population is a group of individuals of the same species living in the same area or interbreeding and sharing genetic information. A species is all individuals that are capable of interbreeding. A species is made up of populations.)

Conservation of biological diversity gets lots of attention these days. One day we hear about polar bears on the news, the next day something about wolves or salmon or elephants or whales. What should we do to protect these species that mean so much to people? What do we need to do about biological diversity in general—all the life-forms, whether people enjoy them or not? And is this a scientific issue or not? Is it even partially scientific?

That's what this chapter is about. It introduces the scientific concepts concerning biological diversity, explains the aspects of biological diversity that have a scientific base, distinguishes the scientific aspects from the

nonscientific ones, and thereby provides a basis for you to evaluate the biodiversity issues you read about.

Why Do People Value Biodiversity?

Before we discuss the scientific basis of biodiversity and the role of science in its conservation, we should consider why people value it. There are nine primary reasons: utilitarian; public-service; ecological; moral; theological; aesthetic; recreational; spiritual; and creative.²

Utilitarian means that a species or group of species provides a product that is of direct value to people. Publicservice means that nature and its diversity provide some service, such as taking up carbon dioxide or pollinating flowers, that is essential or valuable to human life and would be expensive or impossible to do ourselves. Ecological refers to the fact that species have roles in their ecosystems, and that some of these are necessary for the persistence of their ecosystems, perhaps even for the persistence of all life. Scientific research tells us which species have such ecosystem roles. The moral reason for valuing biodiversity is the belief that species have a right to exist, independent of their value to people. The theological reason refers to the fact that some religions value nature and its diversity, and a person who subscribes to that religion supports this belief.

The last four reasons for valuing nature and its diversity—aesthetic, recreational, spiritual, and creative—have to do with the intangible (nonmaterial) ways that nature and its diversity benefit people (see Figure 8.3). These four are often lumped together, but we separate them here. *Aesthetic* refers to the beauty of nature, including the variety of life. *Recreational* is self-explanatory—people enjoy getting out into nature, not just because it is beautiful to look at but because it provides us with healthful activities that we enjoy. *Spiritual* describes the way contact with nature and its diversity often moves people, an uplifting often perceived as a religious experience. *Creative* refers to the fact that artists, writers, and musicians find stimulation for their creativity in nature and its diversity.

Science helps us determine what are utilitarian, publicservice, and ecosystem functions of biological diversity, and scientific research can lead to new utilitarian benefits



FIGURE 8.3 People have long loved the diversity of life. Here, a late-15th-century Dutch medieval tapestry, *The Hunting of the Unicorn* (now housed in The Cloisters, part of the New York City's Metropolitan Museum of Art), celebrates the great diversity of life. Except for the mythological unicorn, all the plants and animals shown, including frogs and insects, are familiar to naturalists today and are depicted with great accuracy.

from biological diversity. For example, medical research led to the discovery and development of paclitaxel (trade name Taxol), a chemical found in the Pacific yew and now used widely in chemotherapy treatment of certain cancers. (Ironically, this discovery led at first to the harvest of this endangered tree species, creating an environmental controversy until the compound could be made artificially.)

The rise of the scientific and industrial age brought a great change in the way that people valued nature. Long ago, for example, when travel through mountains was arduous, people struggling to cross them were probably not particularly interested in the scenic vistas. But around the time of the Romantic poets, travel through the Alps became easier, and suddenly poets began to appreciate the "terrible joy" of mountain scenery. Thus scientific knowledge indirectly influences the nonmaterial ways that people value biological diversity.

8.2 Biological Diversity Basics

Biological diversity involves the following concepts:

- *Genetic diversity*: the total number of genetic characteristics of a specific species, subspecies, or group of species. In terms of genetic engineering and our new understanding of DNA, this could mean the total basepair sequences in DNA; the total number of genes, active or not; or the total number of active genes.
- *Habitat diversity*: the different kinds of habitats in a given unit area.
- Species diversity, which in turn has three qualities:
 species richness—the total number of species;
 species evenness—the relative abundance of species; and
 species dominance—the most abundant species.

To understand the differences between species richness, species evenness, and species dominance, imagine two ecological communities, each with 10 species and 100 individuals, as illustrated in Figure 8.4. In the first community (Figure 8.4a), 82 individuals belong to a single species, and the remaining nine species are represented by two individuals each. In the second community (Figure 8.4b), all the species are equally abundant; each therefore has 10 individuals. Which community is more diverse?

At first, one might think that the two communities have the same species diversity because they have the same number of species. However, if you walked through both communities, the second would appear more diverse. In the first community, most of the time you would see individuals only of the dominant species (elephants in Figure 8.4a); you probably wouldn't see many of the other species at all.

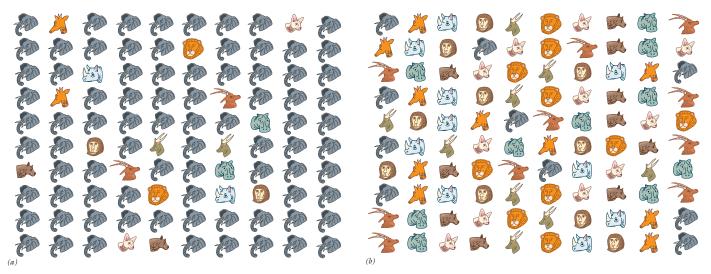


FIGURE 8.4 Diagram illustrating the difference between species evenness, which is the relative abundance of each species, and species richness, which is the total number of species. Figures (a) and (b) have the same number of species but different relative abundances. Lay a ruler across each diagram and count the number of species the edge crosses. Do this several times, and determine how many species are diagram (a) and diagram (b). See text for explanation of results.

The first community would appear to have relatively little diversity until it was subjected to careful study, whereas in the second community even a casual visitor would see many of the species in a short time. You can test the probability of encountering a new species in either community by laying a ruler down in any direction on Figures 8.4a and 8.4b and counting the number of species that it touches.

As this example suggests, merely counting the number of species is not enough to describe biological diversity. Species diversity has to do with the relative chance of seeing species as much as it has to do with the actual number present. Ecologists refer to the total number of species in an area as **species richness**, the relative abundance of species as species evenness, and the most abundant species as dominant.

The Number of Species on Earth

Many species have come and gone on Earth. But how many exist today? Some 1.5 million species have been named, but available estimates suggest there may be almost 3 million (Table 8.1), and some biologists believe the number will turn out to be much, much larger. No one knows the exact number because new species are discovered all the time, especially in little-explored areas such as tropical savannas and rain forests.

For example, in the spring of 2008, an expedition sponsored by Conservation International and led by scientists from Brazilian universities discovered 14 new species in or near Serra Geral do Tocantins Ecological Station, a 716,000-hectare (1.77-million-acre) protected area in the Cerrado, a remote tropical savanna region of Brazil,

said to be one of the world's most biodiverse areas. They found eight new fish, three new reptiles, one new amphibian, one new mammal, and one new bird.

In Laos, a new bird, the barefaced bulbul, was discovered in 2009 (Figure 8.5) and five new mammals have been discovered since 1992: (1) the spindle-horned oryx (which is not only a new species but also represents a previously unknown genus); (2) the small black muntjak; (3) the giant muntjak (the muntjak, also known as "barking deer," is a small deer; the giant muntjak is so called because it has large antlers); (4) the striped hare (whose nearest relative lives in Sumatra); and (5) a new species of civet cat. That such a small country with a long history of human occupancy would have so many mammal species previously unknown to science—and some of these were not all that small—suggests how little we still know about the total biological diversity on Earth. But as scientists we must act from what we know, so in this book we will focus on the 1.5 million species identified and named so far (see Table 8.1).

All living organisms are classified into groups called taxa, usually on the basis of their evolutionary relationships or similarity of characteristics. (Carl Linnaeus, a Swedish physician and biologist, who lived from 1707 to 1778, was the originator of the classification system and played a crucial role in working all this out. He explained this system in his book Systema Naturae.)

The hierarchy of these groups (from largest and most inclusive to smallest and least inclusive) begins with a domain or kingdom. In the recent past, scientists classified life into five kingdoms: animals, plants, fungi, protists, and bacteria. Recent evidence from the

Table 8.1 NUMBER OF SPECIES BY MAJOR FORMS OF LIFE AND BY NUMBER OF ANIMAL SPECIES (FOR A DETAILED LIST OF SPECIES BY TAXONOMIC GROUP, SEE APPENDIX.)

A. NUMBER OF SPECIES BY MAJOR FORMS OF LIFE

		ESTIMATED NUMBER	
LIFE-FORM	EXAMPLE	MINIMUM	MAXIMUM
Monera/Bacteria	Bacteria	4,800	10,000
ungi	Yeast	71,760	116,260
_ichens	Old man's beard	13,500	13,500
Prostista/Protoctist	Ameba	80,710	194,760
Plantae	Maple tree	478,365	529,705
Animalia	Honeybee	873,084	1,870,019
Total		1,522,219	2,734,244
B. NUMBER OF ANIM	MAL SPECIES		
ANIMALS			
nsecta	Honeybees	668,050	1,060,550
Chondrichthyes	Sharks, rays, etc.	750	850
Osteichthyes	Bony fish	20,000	30,000
Amphibia	Amphibians	200	4,800
Reptilia	Reptiles	5,000	7,000
Aves	Birds	8,600	9,000
Mammalia	Mammals	4,000	5,000

fossil record and studies in molecular biology suggest that it may be more appropriate to describe life as existing in three major domains, one called Eukaryota or



FIGURE 8.5 The barefaced bulbul, discovered in Laos in 2009, shows us once again that there are still species of animals and plants unknown to science.

Eukarya, which includes animals, plants, fungi, and protists (mostly single-celled organisms); Bacteria; and Archaea.³ As you learned in Chapter 6, Eukarya cells include a nucleus and other small, organized features called organelles; Bacteria and Archaea do not. (Archaea used to be classified among Bacteria, but they have substantial molecular differences that suggest ancient divergence in heritage—see Chapter 6, Figure 6.7.)

The plant kingdom is made up of divisions, whereas the animal kingdom is made up of phyla (singular: phylum). A phylum or division is, in turn, made up of classes, which are made up of orders, which are made up of families, which are made up of genera (singular: genus), which are made up of species.

Some argue that the most important thing about biological diversity is the total number of species, and that the primary goal of biological conservation should be to maintain that number at its current known maximum. An interesting and important point to take away from Table 8.1 is that most of the species on Earth are insects (somewhere between 668,000 and more than 1 million) and

plants (somewhere between 480,000 and 530,000), and also that there are many species of fungi (about 100,000) and protists (about 80,000 to almost 200,000). In contrast, our own kind, the kind of animals most celebrated on television and in movies, mammals, number a meager 4,000 to 5,000, about the same as reptiles. When it comes to numbers of species on Earth, our kind doesn't seem to matter much—we amount to about half a percent of all animals. If the total number in a species were the only gauge of a species' importance, we wouldn't matter.

8.3 Biological Evolution

The first big question about biological diversity is: How did it all come about? Before modern science, the diversity of life and the adaptations of living things to their environment seemed too amazing to have come about by chance. The great Roman philosopher and writer Cicero put it succinctly: "Who cannot wonder at this harmony of things, at this symphony of nature which seems to will the well-being of the world?" He concluded that "everything in the world is marvelously ordered by divine providence and wisdom for the safety and protection of us all."4 The only possible explanation seemed to be that this diversity was created by God (or gods).

With the rise of modern science, however, other explanations became possible. In the 19th century, Charles Darwin found an explanation that became known as biological evolution. **Biological evolution** refers to the change in inherited characteristics of a population from generation to generation. It can result in new species—populations that can no longer reproduce with members of the original species but can (and at least occasionally do) reproduce with each other. Along with self-reproduction, biological evolution is one of the features that distinguish life from everything else in the universe. (The others are carbon-based, organic-compound-based, self-replicating systems.)

The word *evolution* in the term *biological evolution* has a special meaning. Outside biology, evolution is used broadly to mean the history and development of something. For example, book reviewers talk about the evolution of a novel's plot, meaning how the story unfolds. Geologists talk about the evolution of Earth, which simply means Earth's history and the geologic changes that have occurred over that history. Within biology, however, the term has a more specialized meaning. Biological evolution is a one-way process: Once a species is extinct, it is gone forever. You can run a machine, such as a mechanical grandfather clock, forward and backward, but when a new species evolves, it cannot evolve backward into its parents.

Our understanding of evolution today owes a lot to the modern science of molecular biology and the practice of genetic engineering, which are creating a revolution in

how we think about and deal with species. At present, scientists have essentially the complete DNA code for a number of species, including the bacterium Haemophilus influenzae; the malaria parasite; its carrier the malaria mosquito; the fruit fly (*Drosophila*); a nematode *C. elegans*, (a very small worm that lives in water); yeast; a small weed plant, thale cress (Arabidopsis thaliana); and ourselves humans. Scientists focused on these species either because they are of great interest to us or because they are relatively easy to study, having either few base pairs (the nematode worm) or having already well-known genetic characteristics (the fruit fly).

According to the theory of biological evolution, new species arise as a result of competition for resources and the differences among individuals in their adaptations to environmental conditions. Since the environment continually changes, which individuals are best adapted changes too. As Darwin wrote, "Can it be doubted, from the struggle each individual has to obtain subsistence, that any minute variation in structure, habits, or instincts, adapting that individual better to the new [environmental] conditions, would tell upon its vigor and health? In the struggle it would have a better chance of surviving; and those of its offspring that inherited the variation, be it ever so slight, would also have a better chance."

Sounds plausible, but how does this evolution occur? Through four processes: mutation, natural selection, migration, and genetic drift.

The Four Key Processes of Biological Evolution

Mutation

Mutations are changes in genes. Contained in the chromosomes within cells, each **gene** carries a single piece of inherited information from one generation to the next, producing a genotype, the genetic makeup that is characteristic of an individual or a group.

Genes are made up of a complex chemical compound called deoxyribonucleic acid (DNA). DNA in turn is made up of chemical building blocks that form a code, a kind of alphabet of information. The DNA alphabet consists of four letters that stand for specific nitrogencontaining compounds, called bases, which are combined in pairs: (A) adenine, (C) cytosine, (G) guanine, and (T) thymine. Each gene has a set of the four base pairs, and how these letters are combined in long strands determines the genetic "message" interpreted by a cell to produce specific compounds.

The number of base pairs that make up a strand of DNA varies. To make matters more complex, some base pairs found in DNA are nonfunctional—they are not active and do not determine any chemicals produced by the cell. Furthermore, some genes affect the activity of others, turning those other genes on or off. And creatures such as ourselves have genes that limit the number of times a cell can divide, and thus determine the individual's maximum longevity.

When a cell divides, the DNA is reproduced and each new cell gets a copy. But sometimes an error in reproduction changes the DNA and thereby changes the inherited characteristics. Such errors can arise from various causes. Sometimes an external agent comes in contact with DNA and alters it. Radiation, such as X rays and gamma rays, can break the DNA apart or change its chemical structure. Certain chemicals, also, can change DNA. So can viruses. When DNA changes in any of these ways, it is said to have undergone **mutation**.

In some cases, a cell or an offspring with a mutation cannot survive (Figure 8.6a and b). In other cases, the mutation simply adds variability to the inherited characteristics (Figure 8.6c). But in still other cases, individuals with mutations are so different from their parents that they cannot reproduce with normal offspring of their species, so a new species has been created.

Natural Selection

When there is variation within a species, some individuals may be better suited to the environment than others. (Change is not always for the better. Mutation can result in a new species whether or not that species is better adapted than its parent species to the environment.) Organisms whose biological characteristics make them better able to survive and reproduce in their environment leave more offspring than others. Their descendants form a larger proportion of the next generation and are more "fit" for the environment. This process of increasing the proportion of offspring is called **natural selection**. Which inherited characteristics lead to more offspring depends on the specific characteristics of an environment, and as the environment changes over time, the characteristics'

"fit" will also change. In summary, natural selection involves four primary factors:

- Inheritance of traits from one generation to the next and some variation in these traits—that is, genetic variability.
- Environmental variability.
- Differential reproduction (differences in numbers of offspring per individual), which varies with the environment.
- Influence of the environment on survival and reproduction.

Natural selection is illustrated in A Closer Look 8.1, which describes how the mosquitoes that carry malaria develop a resistance to DDT and how the microorganism that causes malaria develops a resistance to quinine, a treatment for the disease.

As explained before, when natural selection takes place over a long time, a number of characteristics can change. The accumulation of these changes may become so great that the present generation can no longer reproduce with individuals that have the original DNA structure, resulting in a new species.

Ironically, the *loss* of geographic isolation can also lead to a new species. This can happen when one population of a species migrates into a habitat already occupied by another population of that species, thereby changing gene frequency in that habitat. Such a change can result, for example, from the migration of seeds of flowering plants blown by wind or carried in the fur of mammals. If the seed lands in a new habitat, the environment may be different enough to favor genotypes not as favored by natural selection in the parents' habitat. Natural selection, in combination with geographic isolation and subsequent migration, can thus lead to new dominant genotypes and eventually to new species.



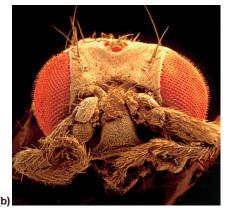




FIGURE 8.6 (a) A normal fruit fly, (b) a fruit fly with an antennae mutation, and (c) *Tradescantia*, a small flowering plant used in the study of effects of mutagens. The color of stamen hairs in the flower (pink versus clear) is the result of a single gene and changes when that gene is mutated by radiation or certain chemicals, such as ethylene chloride.



A CLOSER LOOK 8.1

Natural Selection: Mosquitoes and the Malaria Parasite

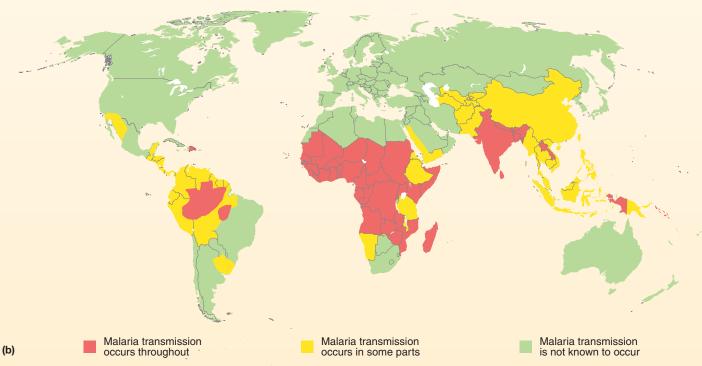
Malaria poses a great threat to 2.4 billion people—over onethird of the world's population—living in more than 90 countries, most of them in the tropics. In the United States, in 2003, Palm Beach County, Florida, experienced a small but serious malaria outbreak, and of particular concern is that the malaria was the result of bites from local mosquitoes, not brought in by travelers from nations where malaria is a continual problem. Worldwide, an estimated 300-400 million people are infected each year, and 1.1 million of them die (Figure 8.7).⁶ It is the



fourth largest cause of death of children in developing nations in Africa alone, more than 3,000 children die daily from this disease.⁷ Once thought to be caused by filth or bad air (hence the name malaria, from the Latin for "bad air"), malaria is actually caused by parasitic microbes (four species of the protozoon Plasmodium). These microbes affect and are carried by Anopheles mosquitoes, which then transfer the protozoa to people. One solution to the malaria problem, then, would be the eradication of Anopheles mosquitoes.

By the end of World War II, scientists had discovered that the pesticide DDT was extremely effective against Anopheles mosquitoes. They had also found chloroquine highly effective in killing Plasmodium parasites. (Chloroquine is an artificial derivative of quinine, a chemical from the bark of the quinine tree that was an early treatment for malaria.) In 1957 the World Health Organization (WHO) began a \$6 billion campaign to rid the world of malaria using a combination of DDT and chloroquine.

FIGURE 8.7 (a) A child with malaria and (b) where malaria primarily occurs today. [Source: (b) U.S. Centers for Disease Control, http://www.cdc.gov/Malaria/distribution_epi/distribution.htm.]



At first, the strategy seemed successful. By the mid-1960s, malaria was nearly gone or had been eliminated from 80% of the target areas. However, success was short-lived. The mosquitoes began to develop a resistance to DDT, and the protozoa became resistant to chloroquine. In many tropical areas, the incidence of malaria worsened. For example, the WHO program had reduced the number of cases in Sri Lanka from 1 million to only 17 by 1963, but by 1975, 600,000 cases had been reported, and the actual number is believed to be four times higher. Worldwide, in 2006 (most recent data available) there were 247 million cases of malaria, resulting in 881,000 deaths. The mosquitoes' resistance to DDT became widespread, and resistance of the protozoa to chloroquine was found in 80% of the 92 countries where malaria was a major killer.

The mosquitoes and the protozoa developed this resistance through natural selection. When they were exposed to DDT and chloroquine, the susceptible individuals died; they left few or no offspring, and any offspring they left were susceptible. The most resistant survived and passed their resistant genes on to their offspring. Thus, a change in the environment—the human introduction of DDT and chloroquine—caused a particular genotype to become dominant in the populations.

A practical lesson from this experience is that if we set out to eliminate a disease-causing species, we must attack it completely at the outset and destroy all the individuals before natural selection leads to resistance. But sometimes this is impossible, in part because of the natural genetic variation in the target species. Since the drug chloroquine is generally ineffective now, new drugs have been developed to treat malaria. However, these second- and third-line drugs will eventually become unsuccessful, too, as a result of the same process of biological evolution by natural selection. This process is speeded up by the ability of the *Plasmodium* to rapidly mutate. In South Africa, for example, the protozoa became resistant to mefloquine immediately after the drug became available as a treatment.

An alternative is to develop a vaccine against the *Plasmo-dium* protozoa. Biotechnology has made it possible to map the genetic structure of these malaria-causing organisms. Scientists are currently mapping the genetic structure of *P. falciparum*, the most deadly of the malaria protozoa, and expect to finish within several years. With this information, they expect to create a vaccine containing a variety of the species that is benign in human beings but produces an immune reaction. In addition, scientists are mapping the genetic structure of *Anopheles gambiae*, the carrier mosquito. This project could provide insight into genes, which could prevent development of the malaria parasite within the mosquito. In addition, it could identify genes associated with insecticide resistance and provide clues to developing a new pesticide.

Migration and Geographic Isolation

Sometimes two populations of the same species become geographically isolated from each other for a long time. During that time, the two populations may change so much that they can no longer reproduce together even when they are brought back into contact. In this case, two new species have evolved from the original species. This can happen even if the genetic changes are not more fit but simply different enough to prevent reproduction. **Migration** has been an important evolutionary process over geologic time (a period long enough for geologic changes to take place).

Darwin's visit to the Galápagos Islands gave him his most powerful insight into biological evolution. ¹⁰ He found many species of finches that were related to a single species found elsewhere. On the Galápagos, each species was adapted to a different niche. ¹¹ Darwin suggested that finches isolated from other species on the continents eventually separated into a number of groups, each adapted to a more specialized role. The process is called **adaptive radiation**. This evolution continues today, as illustrated by a recently discovered new species of finch on the Galápagos Islands (Figure 8.8).

More recently and more accessible to most visitors, we can find adapative radiation on the Hawaiian Islands, where a finchlike ancestor evolved into several



FIGURE 8.8 One of Darwin's finches. Charles Darwin's observations of the adaptive radiation of finches on the Galápagos Islands was a key to the development of the theory of biological evolution. This evolution continues today. In 1982 a finch new to the islands, a large ground finch, migrated there. Over the years since then, the beak of a smaller, native ground species of finch has been evolving to become larger, apparently in response to competition from the new arrival. Today, the offspring of the native ground finch have on average longer beaks than their ancestors'. This is said to be the first time such a response has been observed in progress on the islands.

species, including fruit and seed eaters, insect eaters, and nectar eaters, each with a beak adapted for its specific food (Figure 8.9).12

Genetic Drift

Genetic drift refers to changes in the frequency of a gene in a population due not to mutation, selection, or migration, but simply to chance. One way this happens is through the **founder effect**. The founder effect occurs when a small number of individuals are isolated from a larger population; they may have much less genetic variation than the original species (and usually do), and the characteristics that the isolated population has will be affected by chance. In the founder effect and genetic drift, individuals may not be better adapted to the environment—in fact, they may be more poorly adapted or neutrally adapted. Genetic drift can occur in any small population and may present conservation problems when it is by chance isolated from the main population.

For example, bighorn sheep live in the mountains of the southwestern deserts of the United States and Mexico.

In the summer, these sheep feed high up in the mountains, where it is cooler, wetter, and greener. Before high-density European settlement of the region, the sheep could move freely and sometimes migrated from one mountain to another by descending into the valleys and crossing them in the winter. In this way, large numbers of sheep interbred. With the development of cattle ranches and other human activities, many populations of bighorn sheep could no longer migrate among the mountains by crossing the valleys. These sheep became isolated in very small groups commonly, a dozen or so-and chance may play a large role in what inherited characteristics remain in the population.

This happened to a population of bighorn sheep on Tiburón Island in Mexico, which was reduced to 20 animals in 1975 but increased greatly to 650 by 1999. Because of the large recovery, this population has been used to repopulate other bighorn sheep habitats in northern Mexico. But a study of the DNA shows that the genetic variability is much less than in other populations in Arizona. Scientists who studied this population suggest that

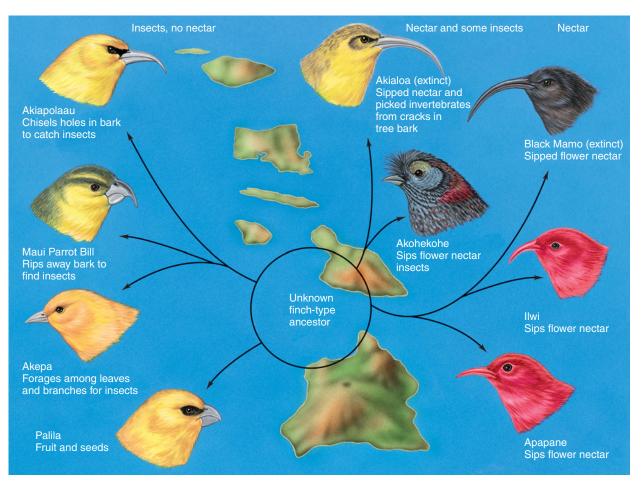


FIGURE 8.9 Evolutionary divergence among honeycreepers in Hawaii. Sixteen species of birds, each with a beak specialized for its food, evolved from a single ancestor. Nine of the species are shown here. The species evolved to fit ecological niches that, on the North American continent, had been filled by other species not closely related to the ancestor. (Source: From C.B. Cox, I.N. Healey, and P.D. Moore, Biogeography [New York: Halsted, 1973].)

individuals from other isolated bighorn sheep populations should be added to any new transplants to help restore some of the greater genetic variation of the past.¹³

Biological Evolution as a Strange Kind of Game

Biological evolution is so different from other processes that it is worthwhile to spend some extra time exploring the topic. There are no simple rules that species must follow to win or even just to stay in the game of life. Sometimes when we try to manage species, we assume that evolution will follow simple rules. But species play tricks on us; they adapt or fail to adapt over time in ways that we did not anticipate. Such unexpected outcomes result from our failure to fully understand how species have evolved in relation to their ecological situations. Nevertheless, we continue to hope and plan as if life and its environment will follow simple rules. This is true even for the most recent work in genetic engineering.

Complexity is a feature of evolution. Species have evolved many intricate and amazing adaptations that have allowed them to persist. It is essential to realize that these adaptations have evolved not in isolation but in the context of relationships to other organisms and to the environment. The environment sets up a situation within which evolution, by natural selection, takes place. The great ecologist G.E. Hutchinson referred to this interaction in the title of one of his books, The Ecological Theater and the Evolutionary Play. Here, the ecological situation—the condition of the environment and other species—is the theater and the scenery within which natural selection occurs, and natural selection results in a story of evolution played out in that theater—over the history of life on Earth. 14 These features of evolution are another reason that life and ecosystems are not simple, linear, steady-state systems (see Chapter 3).

In summary, the theory of biological evolution tells us the following about biodiversity:

- Since species have evolved and do evolve, and since some species are also always becoming extinct, biological diversity is always changing, and which species are present in any one location can change over time.
- Adaptation has no rigid rules; species adapt in response to environmental conditions, and complexity is a part of nature. We cannot expect threats to one species to necessarily be threats to another.
- Species and populations do become geographically isolated from time to time, and undergo the founder effect and genetic drift.
- Species are always evolving and adapting to environmental change. One way they get into trouble—become endangered—is when they do not evolve fast enough to keep up with the environment.

8.4 Competition and Ecological Niches

Why there are so many species on Earth has become a key question since the rise of modern ecological and evolutionary sciences. In the next sections we discuss the answers. They partly have to do with how species interact. Speaking most generally, they interact in three ways: competition, in which the outcome is negative for both; symbiosis, in which the interaction benefits both participants; and predation—parasitism, in which the outcome benefits one and is detrimental to the other.

The Competitive Exclusion Principle

The **competitive exclusion principle** supports those who argue that there should be only a few species. It states that *two species with exactly the same requirements cannot coexist in exactly the same habitat*. Garrett Hardin expressed the idea most succinctly: "Complete competitors cannot coexist." ¹⁵

This is illustrated by the introduction of the American gray squirrel into Great Britain. It was introduced intentionally because some people thought it was attractive and would be a pleasant addition to the landscape. About a dozen attempts were made, the first perhaps as early as 1830 (Figure 8.10). By the 1920s, the American gray squirrel was well established in Great Britain, and in the 1940s and 1950s its numbers expanded greatly. It competes with the native red squirrel and is winning—there are now about 2.5 million gray squirrels in Great Britain, and only 140,000 red squirrels, most them in Scotland, where the gray squirrel is less abundant. The two species have almost exactly the same habitat requirements.

One reason for the shift in the balance of these species may be that in the winter the main source of food for red squirrels is hazelnuts, while gray squirrels prefer acorns. Thus, red squirrels have a competitive advantage in areas with hazelnuts, and gray squirrels have the advantage in oak forests. When gray squirrels were introduced, oaks were the dominant mature trees in Great Britain; about 40% of the trees planted were oaks. But that is not the case today. This difference in food preference may allow the coexistence of the two, or perhaps not.

The competitive exclusion principle suggests that there should be very few species. We know from our discussions of ecosystems (Chapter 5) that food webs have at least four levels—producers, herbivores, carnivores, and decomposers. Suppose we allowed for several more levels of carnivores, so that the average food web had six levels. Since there are about 20 major kinds of ecosystems, one would guess that the total number of winners on Earth would be only 6×20 , or 120 species.





(a) British red squirrel, which is being outcompeted by the (b) American gray squirrel introduced into Great Britain.

Being a little more realistic, we could take into account adaptations to major differences in climate and other environmental aspects within kinds of ecosystems. Perhaps we could specify 100 environmental categories: cold and dry; cold and wet; warm and dry; warm and wet; and so forth. Even so, we would expect that within each environmental category, competitive exclusion would result in the survival of only a few species. Allowing six species per major environmental category would result in only 600 species.

That just isn't the case. How did so many different species survive, and how do so many coexist? Part of the answer lies in the different ways in which organisms interact, and part of the answer lies with the idea of the ecological niche.

Niches: How Species Coexist

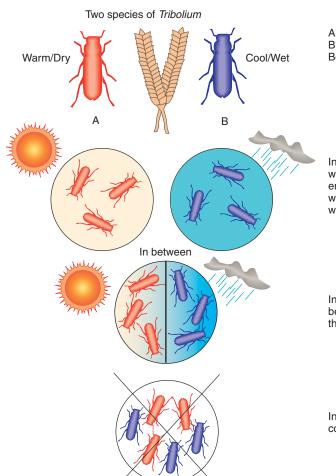
The **ecological niche** concept explains how so many species can coexist, and this concept is introduced most easily by experiments done with a small, common insect the flour beetle (*Tribolium*), which, as its name suggests, lives on wheat flour. Flour beetles make good experimental subjects because they require only small containers of wheat flour to live and are easy to grow (in fact, too easy; if you don't store your flour at home properly, you will find these little beetles happily eating in it).

The flour beetle experiments work like this: A specified number of beetles of two species are placed in small containers of flour-each container with the same number of beetles of each species. The containers are then maintained at various temperature and moisture levelssome are cool and wet, others warm and dry. Periodically, the beetles in each container are counted. This is very easy. The experimenter just puts the flour through a sieve that lets the flour through but not the beetles. Then the experimenter counts the number of beetles of each species and puts the beetles back in their container to eat, grow, and reproduce for another interval. Eventually, one species always wins—some of its individuals continue to live in the container while the other species goes extinct. So far, it would seem that there should be only one species of *Tribo*lium. But which species survives depends on temperature and moisture. One species does better when it is cold and wet, the other when it is warm and dry (Figure 8.11).

Curiously, when conditions are in between, sometimes one species wins and sometimes the other, seemingly randomly; but invariably one persists while the second becomes extinct. So the competitive exclusion principle holds for these beetles. Both species can survive in a complex environment—one that has cold and wet habitats as well as warm and dry habitats. In no location, however, do the species coexist.

The little beetles provide us with the key to the coexistence of many species. Species that require the same resources can coexist by using those resources under different environmental conditions. So it is habitat *complexity* that allows complete competitors—and not-so-complete competitors—to coexist because they avoid competing with each other.17

The flour beetles are said to have the same ecologically functional niche, which means they have the same profession—eating flour. But they have different habitats. Where a species lives is its habitat, but what it does for a living (its profession) is its ecological niche. 18 Suppose you have a neighbor who drives a school bus. Where your neighbor lives and works—your town—is his habitat. What your neighbor does—drive a bus—is his niche. Similarly, if someone says, "Here comes a wolf," you think not only of a creature that inhabits the northern forests (its habitat) but also of a predator that feeds on large mammals (its niche).



(a)

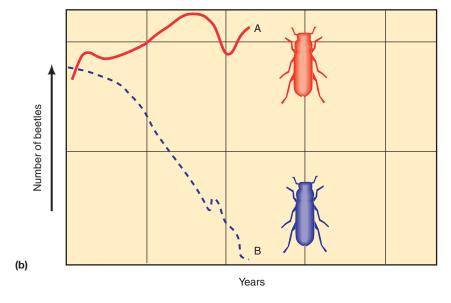
A: Likes warm, dry conditions B: Likes cool, wet conditions Both: Like to eat wheat

In a *uniform* environment, one will win out over the other. If the environment is warm and dry, A will win; if it is cool and wet, B will win.

periment with flour beetles. Two species of flour beetles are placed in small containers of flour. Each container is kept at a specified temperature and humidity. Periodically, the flour is sifted, and the beetles are counted and then returned to their containers. Which species persists is observed and recorded. (a) The general process illustrating competitive exclusion in these species; (b) results of a specific, typical experiment under warm, dry conditions.

In a mixed environment, the beetles will use separate parts of the habitat.

In either case, the beetles do not coexist.



Understanding the niche of a species is useful in assessing the impact of land development or changes in land use. Will the change remove an essential requirement for some species' niche? A new highway that makes car travel easier might eliminate your neighbor's bus route (an essential part of his habitat) and thereby eliminate his pro-

fession (or niche). Other things could also eliminate this niche. Suppose a new school were built and all the children could now walk to school. A school bus driver would not be needed; this niche would no longer exist in your town. In the same way, cutting a forest may drive away prey and eliminate the wolf's niche.

Measuring Niches

An ecological niche is often described and measured as the set of all environmental conditions under which a species can persist and carry out its life functions. ¹⁹ It is illustrated by the distribution of two species of flatworm that live on the bottom of freshwater streams. A study of two species of these small worms in Great Britain found that

some streams contained one species, some the other, and still others both. 17

The stream waters are cold at their source in the mountains and become progressively warmer as they flow downstream. Each species of flatworm occurs within a

specific range of water temperatures. In streams where species A occurs alone, it is found from 6° to 17°C (42.8°-62.6°F) (Figure 8.12a). Where species B occurs alone, it is found from 6° to 23°C (42.8°–73.4°F) (Figure 8.12b). When they occur in the same stream, their temperature ranges are much narrower. Species A lives in the upstream sections, where the temperature ranges from 6° to 14°C (42.8°-57.2°F), and species B lives in the warmer downstream areas, where temperatures range from 14° to 23°C (57.2°-73.4°F) (Figure 8.12c).

The temperature range in which species A occurs when it has no competition from B is called its fundamental temperature niche. The set of conditions under which it persists in the presence of B is called its realized temperature niche. The flatworms show that species divide up their habitat so that they use resources from different parts of it. Of course, temperature is only one aspect of the environment. Flatworms also have requirements relating to the acidity of the water and other factors. We could create graphs for each of these factors, showing the range within which A and B occurred. The collection of all those graphs would constitute the complete Hutchinsonian description of the niche of a species.

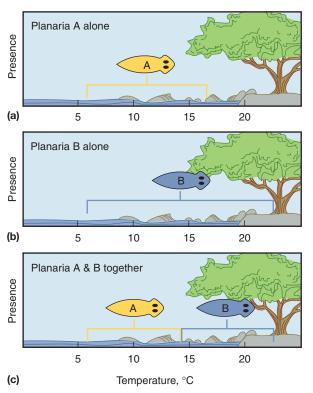


FIGURE 8.12 Fundamental and realized niches: The occurrence of freshwater flatworms in cold mountain streams in Great Britain. (a) The presence of species A in relation to temperature in streams where it occurs alone. (b) The presence of species B in relation to temperature in streams where it occurs alone. (c) The temperature range of both species in streams where they occur together. Inspect the three graphs: What is the effect of each species on the other?

A Practical Implication

From the discussion of the competitive exclusion principle and the ecological niche, we learn something important about the conservation of species: If we want to conserve a species in its native habitat, we must make sure that all the requirements of its niche are present. Conservation of endangered species is more than a matter of putting many individuals of that species into an area. All the life requirements for that species must also be present—we have to conserve not only a population but also its habitat and its niche.

8.5 Symbiosis

Our discussion up to this point might leave the impression that species interact mainly through competitionby interfering with one another. But symbiosis is also important. This term is derived from a Greek word meaning "living together." In ecology, symbiosis describes a relationship between two organisms that is beneficial to both and enhances each organism's chances of persisting. Each partner in symbiosis is called a symbiont.

Symbiosis is widespread and common; most animals and plants have symbiotic relationships with other species. We, too, have symbionts-microbiologists tell us that about 10% of our body weight is actually the weight of symbiotic microorganisms that live in our intestines. They help our digestion, and we provide a habitat that supplies all their needs; both we and they benefit. We become aware of this intestinal community when it changes—for example, when we take antibiotics that kill some of these organisms, changing the balance of that community, or when we travel to a foreign country and ingest new strains of bacteria. Then we suffer a wellknown traveler's malady, gastrointestinal upset.

Another important kind of symbiotic interaction occurs between certain mammals and bacteria. A reindeer on the northern tundra may appear to be alone but carries with it many companions. Like domestic cattle, the reindeer is a ruminant, with a four-chambered stomach (Figure 8.13) teeming with microbes (a billion per cubic centimeter). In this partially closed environment, the respiration of microorganisms uses up the oxygen ingested by the reindeer while eating. Other microorganisms digest cellulose, take nitrogen from the air in the stomach, and make proteins. The bacterial species that digest the parts of the vegetation that the reindeer cannot digest itself (in particular, the cellulose and lignins of cell walls in woody tissue) require a peculiar environment: They can survive only in an environment without oxygen. One of the few places on Earth's surface where such an environment exists is the inside of a ruminant's stomach.²⁰ The bacteria and the reindeer are symbionts,

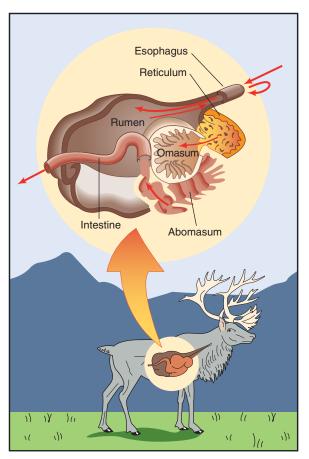


FIGURE 8.13 The stomach of a reindeer illustrates complex symbiotic relationships. For example, in the rumen, bacteria digest woody tissue the reindeer could not otherwise digest. The result is food for the reindeer and food and a home for the bacteria, which could not survive in the local environment outside.

each providing what the other needs, and neither could survive without the other. They are therefore called **ob**ligate symbionts.

Crop plants illustrate another kind of symbiosis. Plants depend on animals to spread their seeds and have evolved symbiotic relationships with them. That's why fruits are so eatable; it's a way for plants to get their seeds spread, as Henry David Thoreau discussed in his book Faith in a Seed.

A Broader View of Symbiosis

So far we have discussed symbiosis in terms of physiological relationships between organisms of different species. But symbiosis is much broader, and includes social and behavioral relationships that benefit both populations. Consider, for example, dogs and wolves. Wolves avoid human beings and have long been feared and disliked by many peoples, but dogs have done very well because of the behavioral connection with people. Being friendly, helpful, and companionable to people has made dogs very abundant. This is another kind of symbiosis.

A Practical Implication

We can see that symbiosis promotes biological diversity, and that if we want to save a species from extinction, we must save not only its habitat and niche but also its symbionts. This suggests another important point that will become more and more evident in later chapters: The attempt to save a single species almost invariably leads us to conserve a group of species, not just a single species or a particular physical habitat.

8.6 Predation and Parasitism

Predation-parasitism is the third way in which species interact. In ecology, a predator-parasite relation is one that benefits one individual (the predator or parasite) and is negative for the other (the prey or host). Predation is when an organism (a predator) feeds on other live organisms (prey), usually of another species. Parasitism is when one organism (the parasite) lives on or within another (the host) and depends on it for existence but makes no useful contribution to it and may in fact harm it.

Predation can increase the diversity of prey species. Think again about the competitive exclusion principle. Suppose two species are competing in the same habitat and have the same requirements. One will win out. But if a predator feeds on the more abundant species, it can keep that prey species from overwhelming the other. Both might persist, whereas without the predator only one would. For example, some studies have shown that a moderately grazed pasture has more species of plants than an ungrazed one. The same seems to be true for natural grasslands and savannas. Without grazers and browsers, then, African grasslands and savannas might have fewer species of plants.

A Practical Implication

Predators and parasites influence diversity and can increase it.

8.7 How Geography and Geology Affect **Biological Diversity**

Species are not uniformly distributed over the Earth's surface; diversity varies greatly from place to place. For instance, suppose you were to go outside and count all the species in a field or any open space near where you are reading this book (that would be a good way to begin to learn for yourself about biodiversity). The number of species you found would depend on where you are. If you live

in northern Alaska or Canada, Scandinavia, or Siberia, you would probably find a significantly smaller number of species than if you live in the tropical areas of Brazil, Indonesia, or central Africa. Variation in diversity is partially a question of latitude—in general, greater diversity occurs at lower latitudes. Diversity also varies within local areas. If you count species in the relatively sparse environment of an abandoned city lot, for example, you will find quite a different number than if you count species in an old, long-undisturbed forest.

The species and ecosystems that occur on the land change with soil type and topography: slope, aspect (the direction the slope faces), elevation, and nearness to a drainage basin. These factors influence the number and kinds of plants, and the kinds of plants in turn influence the number and kinds of animals.

Such a change in species can be seen with changes in elevation in mountainous areas like the Grand Canyon and the nearby San Francisco Mountains of Arizona (Figure 8.14). Although such patterns are easiest to see in vegetation, they occur for all organisms.

Some habitats harbor few species because they are stressful to life, as a comparison of vegetation in two areas of Africa illustrates. In eastern and southern Africa, well-drained, sandy soils support diverse vegetation, including many species of *Acacia* and *Combretum* trees, as well as many grasses. In contrast, woodlands on the very heavy clay soils of wet areas near rivers, such as the Sengwa River in Zimbabwe, consist almost exclusively of a single species called *Mopane*. Very heavy clay soils store water and prevent most oxygen from reaching roots. As a result, only tree species with very shallow roots survive.

Moderate environmental disturbance can also increase diversity. For example, fire is a common disturbance in many forests and grasslands. Occasional light fires produce a mosaic of recently burned and unburned areas. These patches favor different kinds of species and increase overall diversity. Table 8.2 shows some of the major influences on biodiversity. Of course, people also affect diversity. In general, urbanization, industrialization, and agriculture decrease diversity, reducing the number of habitats and simplifying habitats. (See, for example, the effects of agriculture on habitats, discussed in Chapter 11.) In addition, we intentionally favor specific species and manipulate populations for our own purposes—for example, when a person plants a lawn or when a farmer plants a single crop over a large area.

Most people don't think of cities as having any beneficial effects on biological diversity. Indeed, the development of cities tends to reduce biological diversity. This is partly because cities have typically been located at good sites for travel, such as along rivers or near oceans, where biological diversity is often high. However, in recent years we have begun to realize that cities can contribute in important ways to the conservation of biological diversity.

Wallace's Realms: Biotic Provinces

As we noted, biological diversity differs among continents, in terms of both total species diversity and the particular species that occur. This large-scale difference has long fascinated naturalists and travelers, many of whom have discovered strange, new (for them) animals and plants as they have traveled between continents. In 1876 the great

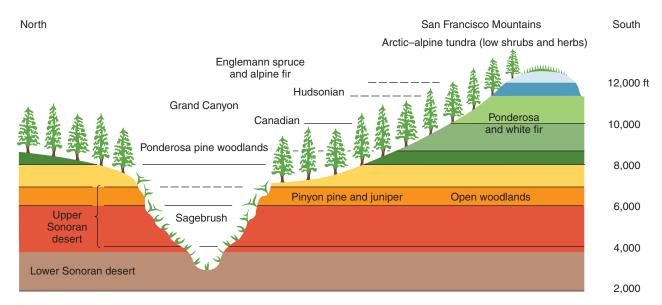


FIGURE 8.14 Change in the relative abundance of a species over an area or a distance is referred to as an ecological gradient. Such a change can be seen with changes in elevation in mountainous areas. The altitudinal zones of vegetation in the Grand Canyon of Arizona and the nearby San Francisco Mountains are shown. (Source: From C.B. Hunt, Natural Regions of the United States and Canada [San Francisco: W.H. Freeman, 1974].)

Table 8.2 SOME MAJOR FACTORS THAT INCREASE AND DECREASE BIOLOGICAL DIVERSITY

A. FACTORS THAT TEND TO INCREASE DIVERSITY

- 1. A physically diverse habitat
- 2. Moderate amounts of disturbance (such as fire or storm in a forest or a sudden flow of water from a storm into a pond).
- 3. A small variation in environmental conditions (temperature, precipitation, nutrient supply, etc.).
- 4. High diversity at one trophic level increases the diversity at another trophic level. (Many kinds of trees provide habitats for many kinds of birds and insects.)
- 5. An environment highly modified by life (e.g., a rich organic soil).
- 6. Middle stages of succession.
- 7. Evolution.

B. FACTORS THAT TEND TO DECREASE DIVERSITY

- 1. Environmental stress.
- 2. Extreme environments (conditions near the limit of what living things can withstand).
- 3. A severe limitation in the supply of an essential resource.
- 4. Extreme amounts of disturbance.
- 5. Recent introduction of exotic species (species from other areas).
- 6. Geographic isolation (being on a real or ecological island).

British biologist Alfred Russel Wallace (co-discoverer of the theory of biological evolution with Charles Darwin) suggested that the world could be divided into six biogeographic regions on the basis of fundamental features of the animals found in those areas. ²¹ He referred to these regions as realms and named them Nearctic (North America), Neotropical (Central and South America), Palaearctic (Europe, northern Asia, and northern Africa), Ethiopian (central and southern Africa), Oriental (the Indian subcontinent and Malaysia), and Australian. These have become known as Wallace's realms (Figure 8.15). Recognition of these worldwide patterns in animal species was the first step in understanding **biogeography**—the geographic distribution of species.

In each major biogeographic area (Wallace's realm), certain families of animals are dominant, and animals of these families fill the ecological niches. Animals filling a particular ecological niche in one realm are of different genetic stock from those filling the same niche in the other realms. For example, bison and pronghorn antelope are among the large mammalian herbivores in North America. Rodents such as the capybara fill the same niches in South America, and kangaroos fill them in Australia. In central and southern Africa, many species, including giraffes and antelopes, fill these niches.

This is the basic concept of Wallace's realms, and it is still considered valid and has been extended to all life-forms, ²²

including plants (Figure 8.15b)²³ and invertebrates. These realms are now referred to as "biotic provinces."²⁴ A **biotic province** is a region inhabited by a characteristic set of taxa (species, families, orders), bounded by barriers that prevent the spread of those distinctive kinds of life to other regions and the immigration of foreign species.¹⁰ So in a biotic province, organisms share a common genetic heritage but may live in a variety of environments as long as they are genetically isolated from other regions.

Biotic provinces came about because of continental drift, which is caused by plate tectonics and has periodically joined and separated the continents (see the discussion in Chapter 6).²⁵ The unification (joining) of continents enabled organisms to enter new habitats and allowed genetic mixing. Continental separation led to genetic isolation and the evolution of new species.

This at least partially explains why introducing species from one part of the Earth to another can cause problems. Within a realm, species are more likely to be related and to have evolved and adapted in the same place for a long time. But when people bring home a species from far away, they are likely to be introducing a species that is unrelated, or only distantly related, to native species. This new and unrelated "exotic" species has not evolved and adapted in the presence of the home species, so ecological and evolutionary adjustments are yet to take place. Sometimes an introduction brings in a superior competitor.

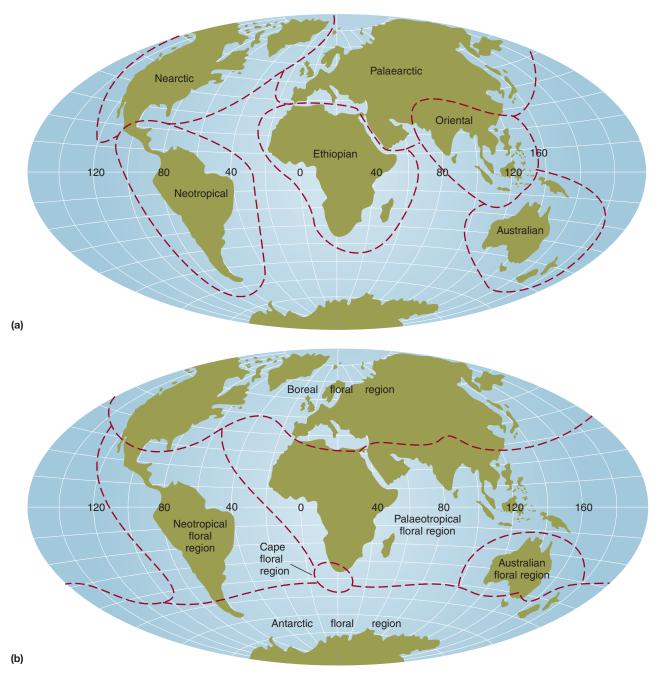


FIGURE 8.15 Wallace's (Biogeographic) Realms (a) for animals and (b) for plants are based on genetic factors. Within each realm, the vertebrates are in general more closely related to each other than to vertebrates filling similar niches in other realms; similarly, plants within a realm are more closely related to each other than to plants of other realms.

Biomes

A biome is a kind of ecosystem, such as a desert, a tropical rain forest, or a grassland. The same biome can occur on different continents because similar environments provide similar opportunities for life and similar constraints. As a result, similar environments lead to the evolution of organisms similar in form and function (but not necessarily in genetic heritage or internal makeup) and similar ecosystems. This is known as the rule of climatic similarity. The close relationship between environment and kinds of life-forms is shown in Figure 8.16.

In sum, the difference between a biome and a biotic province is that a biotic province is based on who is related to whom, while a biome is based on niches and habitats. In general, species within a biotic province are

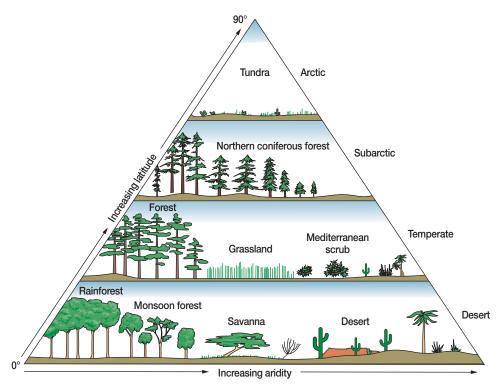


FIGURE 8.16 Simplified diagram of the relationship between precipitation and latitude and Earth's major land biomes. Here, latitude serves as an index of average temperature, so latitude can be replaced by average temperature in this diagram. (Source: Harm de Blij, Peter O. Muller, and Richard S. Williams, Physical Geography of the Global Environment. Figure 27-4, p. 293, edited by Harm de Blij, copyright 2004 by Oxford University Press. Used by permission of Oxford University Press.)

more closely related to each other than to species in other provinces. In two different biotic provinces, the same ecological niche will be filled with species that perform a specific function and may look very similar to each other but have quite different genetic ancestries. In this way, a biotic province is an evolutionary unit.

Convergent and Divergent Evolution

Plants that grow in deserts of North America and East Africa illustrate the idea of a biome (see Figure 8.17). The Joshua tree and saguaro cactus of North America and the giant Euphorbia of East and Southern Africa are tall, have succulent green stems that replace the leaves as the major sites of photosynthesis, and have spiny projections, but these plants are not closely related. The Joshua tree is a member of the agave family, the saguaro is a member of the cactus family, and the Euphorbia is a member of the spurge family. The ancestral differences between these look-alike plants can be found in their flowers, fruits, and seeds, which change the least over time and thus provide the best clues to the genetic history of a species. Geographically isolated for 180 million years, these plants have been subjected to similar climates, which imposed similar stresses and opened up similar ecological opportunities. On both continents, desert plants evolved to adapt to these stresses and potentials, and have come to look alike and prevail in like habitats. Their similar shapes result from evolution in similar desert climates, a process known as **convergent evolution**.

Another important process that influences life's geography is **divergent evolution**. In this process, a population is divided, usually by geographic barriers. Once separated into two populations, each evolves separately, but the two groups retain some characteristics in common. It is now believed that the ostrich (native to Africa), the rhea (native to South America), and the emu (native to Australia) have a common ancestor but evolved separately (Figure 8.18). In open savannas and grasslands, a large bird that can run quickly but feed efficiently on small seeds and insects has certain advantages over other organisms seeking the same food. Thus, these species maintained the same characteristics in widely separated areas. Both convergent and divergent evolution increase biological diversity.

People make use of convergent evolution when they move decorative and useful plants around the world. Cities that lie in similar climates in different parts of the world now share many of the same decorative plants. Bougainvillea, a spectacularly bright flowering shrub originally native to Southeast Asia, decorates cities as distant from each other as Los Angeles and the capital of Zimbabwe. In New York City and its outlying suburbs, Norway maple from Europe and the tree of heaven and gingko tree from China grow with native species such as sweet gum, sugar maple, and pin oak. People intentionally introduced the Asian and European trees.







FIGURE 8.17 Joshua Tree of North America and giant Euphorbia of Africa illustrate convergent evolution. Given sufficient time and similar climates in different areas, species similar in shape will tend to occur. The Joshua tree (a) and saguaro cactus (b) of North America look similar to the giant Euphorbia (c) of East Africa. But these plants are not closely related. Their similar shapes result from evolution under similar climates, a process known as convergent evolution.







FIGURE 8.18 Divergent evolution. Three large, flightless birds evolved from a common ancestor but are now found in widely separated regions: (a) the ostrich in Africa, (b) the rhea in South America, and (c) the emu in Australia.

8.8 Invasions, Invasive Species, and Island Biogeography

Ever since Darwin's voyage on *The Beagle*, which took him to the Galápagos Islands, biologists have been curious about how biological diversity can develop on islands: Do any rules govern this process? How do such invasions happen? And how is biological diversity affected by the size of and distance to a new habitat? E.O. Wilson and R. MacArthur established a theory of island biogeography that sets forth major principles about biological invasion of new habitats, ²⁶ and as it turns out, the many jokes and stories about castaways on isolated islands have a basis in fact.

- Islands have fewer species than continents.
- The two sources of new species on an island are migration from the mainland and evolution of new species in place.
- The smaller the island, the fewer the species, as can be seen in the number of reptiles and amphibians in various West Indian islands (Figure 8.20).
- The farther the island is from a mainland (continent), the fewer the species (Figure 8.19).²⁷

Clearly, the farther an island is from the mainland, the harder it will be for an organism to travel the distance, and the smaller the island, the less likely that it will be found by individuals of any species. In addition, the smaller the island, the fewer individuals it can support. Small islands tend to have fewer habitat types, and some habitats on a small island may be too small to support a population large

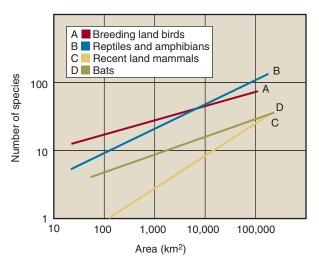


FIGURE 8.20 Islands have fewer species than do mainlands. The larger the island, the greater the number of species. This general rule is shown by a graph of the number of species of birds, reptiles and amphibians, recent land mammals, and bats for islands in the Caribbean. (Modified from B. Wilcox, ed., [Gland, Switzerland: IUCN, 1988].)

enough to have a good chance of surviving for a long time. Generally, the smaller the population, the greater its risk of extinction. It might be easily extinguished by a storm, flood, or other catastrophe or disturbance, and every species is subject to the risk of extinction by predation, disease (parasitism), competition, climatic change, or habitat alteration.

A final generalization about island biogeography is that over a long time, an island tends to maintain a rather constant number of species, which is the result of the rate at which species are added minus the rate at which they become extinct. These numbers follow the curves shown in Figure 8.20. For any island, the number of species of a particular life-form can be predicted from the island's size and distance from the mainland.

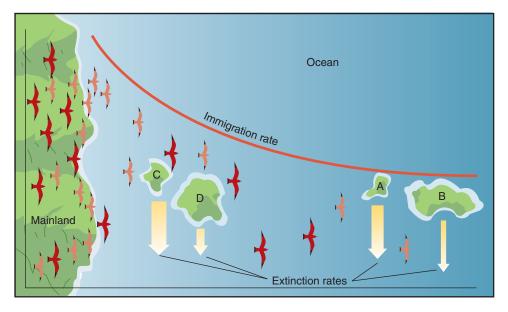


FIGURE 8.19 Idealized relation of an island's size, distance from the mainland, and number of species. The nearer an island is to the mainland, the more likely it is to be found by an individual, and thus the higher the rate of immigration. The larger the island, the larger the population it can support and the greater the chance of persistence of a species-small islands have a higher rate of extinction. The average number of species therefore depends on the rate of immigration and the rate of extinction. Thus, a small island near the mainland may have the same number of species as a large island far from the mainland. The thickness of the arrow represents the magnitude of the rate. (Source: Modified from R.H. MacArthur and E.O. Wilson, The Theory of Island Biogeography [Princeton, NJ: Princeton University Press, 19671.)

The concepts of island biogeography apply not just to real islands in an ocean but also to ecological islands. An **ecological island** is a comparatively small habitat separated from a major habitat of the same kind. For example, a pond in the Michigan woods is an ecological island relative to the Great Lakes that border Michigan. A small stand of trees within a prairie is a forest island. A city park is also an ecological island. Is a city park large enough to support a population of a particular species? To know whether it is, we can apply the concepts of island biogeography.

Biogeography and People

Benefits of Biological Invasions

We have seen that biogeography affects biological diversity. Changes in biological diversity in turn affect people and the living resources on which we depend. These effects extend from individuals to civilizations. For example, the last ice ages had dramatic effects on plants and animals and thus on human beings. Europe and Great Britain have fewer native species of trees than other temperate regions of the world. Only 30 tree species are native to Great Britain (that is, they were present prior to human settlement), although hundreds of species grow there today.

Why are there so few native species in Europe and Great Britain? Because of the combined effects of climate change and the geography of European mountain ranges. In Europe, major mountain ranges run east-west, whereas in North America and Asia the major ranges run northsouth. During the past 2 million years, Earth has experienced several episodes of continental glaciation, when glaciers several kilometers thick expanded from the Arctic over the landscape. At the same time, glaciers formed in the mountains and expanded downward. Trees in Europe, caught between the ice from the north and the ice from the mountains, had few refuges, and many species became extinct. In contrast, in North America and Asia, as the ice advanced, tree seeds could spread southward, where they became established and produced new plants. Thus, the tree species "migrated" southward and survived each episode of glaciation. 16

Since the rise of modern civilization, these ancient events have had many practical consequences. As we mentioned earlier, soon after Europeans discovered North America, they began to bring exotic North American species of trees and shrubs into Europe and Great Britain. These exotic imports were used to decorate gardens, homes, and parks and formed the basis of much of the commercial forestry in the region. For example, in the famous gardens of the Alhambra in Granada, Spain, Monterey cypress from North America are grown as hedges and cut in elaborate shapes. In Great Britain and Europe, Douglas fir and Monterey pine are important commercial timber trees today. These are only two examples of how

knowledge of biogeography—enabling people to predict what will grow where based on climatic similarity—has been used for both aesthetic and economic benefits.

Why Invasive Species Are a Serious Problem Today

The ease and speed of long-distance travel have led to a huge rate of introductions, with invasive pests (including disease-causing microbes) arriving from all around the world both intentionally and unintentionally (Table 8.3 and Figure 8.21). Table 8.3 shows the number of plant pests intercepted by various means in 2007 by the U.S. government. The majority of interceptions—42,003—were at airports, ten times more than maritime interceptions, which before the jet age would have accounted for

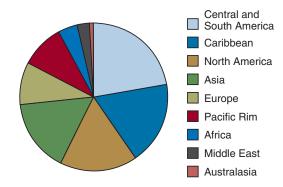


FIGURE 8.21 Where invasive pests are coming from. (Source: USDA.)

Table 8.3	REPORTABLE PLANT PEST
	INTERCEPTIONS, 2007

PLANT PEST INTERCEPTIONS	NUMBER	PERCENT
Airport	42,003	61%
Express carrier	6	0.01%
Inspection station	2,763	4.01%
Land border	14,394	20.91%
Maritime	4,518	6.56%
Other government programs	86	0.12%
Pre-departure	4,869	7.07%
Rail	16	0.02%
USPS Mail	184	0.27%
Total	68,839	100%

Source: McCullough, D. G., T. T. Works, J. F. Cavey, A. M. Liebold, and D. Marshall. 2006. Interceptions of nonindigenous-plant pests at U.S. ports of entry and border crossings over a 17-year period. *Biological Invasions* 8: 611–630.)



CRITICAL THINKING ISSUE

Polar Bears and the Reasons People Value Biodiversity

In 2008, the U.S. Endangered Species Act listed polar bears as a threatened species. Worldwide, an estimated 20,000 to 25,000 polar bears roam the Arctic, hunting ringed and bearded seals, their primary food. About 5,000 of these polar bears live within the United States. Refer back to the reasons that people value biodiversity. Read up on polar bears (we've listed some sources below) and decide which of these reasons apply to this species. In particular, consider the following questions.

Critical Thinking Questions

- 1. As a top predator, is the polar bear a necessary part of its ecosystem? (Hint: Consider the polar bear's ecological niche.)
- 2. Do the Inuit who live among polar bears value them as part of the Arctic diversity of life? (This will take some additional study on your part.)
- 3. Of the nine reasons we discussed earlier for conserving biological diversity, which ones are the primary reasons for conservation of polar bears?

Some Additional Sources of Information about **Polar Bears**

U.S. Department of Interior Ruling on the Polar Bear: http:// alaska.fws.gov/fisheries/mmm/polarbear/pdf/Polar_Bear_ Final_Rule.pdf

About Polar Bears as a Species and Their Habitat and Requirements: Polar Bears: Proceedings of the 14th Working Meeting of the IUCN/SSC Polar Bear Specialist Group, June 20-24, 2005, Seattle, Washington. Available at the International Union for the Conservation of Nature (IUCN) website: http://www.iucnredlist.org/search/details.php/22823/summ

Global Warming and Polar Bears: A.E. Derocher, Nicholas J. Lunn, and Ian Stirling, 2004, Polar bears in a warming climate. Integrative and Comparative Biology, 44:13-176.

most of them. Passenger ships arrive at fewer locations and far less frequently than do commercial aircraft today. Bear in mind that the 42,003 were just those intercepted—no doubt many passed undetected—and that these are only for pests of plants, not for such things as zebra mussels dumped into American waters from cargo ships. According to the USDA, the present situation is not completely controllable.

Another major avenue of species invasions has been the international trade in exotic pets, like the Burmese python. Many of these are released outdoors when they get to be too big and too much trouble for their owners.

The upshot of this is that we can expect the invasion of species to continue in large numbers, and some will cause problems not yet known in the United States.

SUMMARY

- Biological evolution—the change in inherited characteristics of a population from generation to generation—is responsible for the development of the many species of life on Earth. Four processes that lead to evolution are mutation, natural selection, migration, and genetic drift.
- Biological diversity involves three concepts: genetic diversity (the total number of genetic characteristics), habitat diversity (the diversity of habitats in a given unit area), and species diversity. Species diversity, in turn, involves three ideas: species richness (the total number of species), species evenness (the relative abundance of species), and species dominance (the most abundant species).
- About 1.4 million species have been identified and named. Insects and plants make up most of these species. With further explorations, especially in tropical areas, the number of identified species, especially of invertebrates and plants, will increase.
- Species engage in three basic kinds of interactions: competition, symbiosis, and predation-parasitism. Each type of interaction affects evolution, the persistence of species, and the overall diversity of life. It is important to understand that organisms have evolved together, so predator, parasite, prey, competitor, and symbiont have adjusted to one another. Human interventions frequently upset these adjustments.

- The competitive exclusion principle states that two species that have exactly the same requirements cannot coexist in exactly the same habitat; one must win. The reason more species do not die out from competition is that they have developed a particular niche and thus avoid competition.
- The number of species in a given habitat is determined by many factors, including latitude, elevation, topography, severity of the environment, and diversity of the habitat. Predation and moderate disturbances, such as fire, can actually increase the diversity of species. The number of species also varies over time. Of course, people affect diversity as well.

REEXAMINING THEMES AND ISSUES



Human



Sustainabilitv



Global **Perspective**



Urban World



People and Nature



and Values

The growth of human populations has decreased biological diversity. If the human population continues to grow, pressures will continue on endangered species, and maintaining existing biological diversity will be an ever-greater challenge.

Sustainability involves more than just having many individuals of a species. For a species to persist, its habitat must be in good condition and must provide that species' life requirements. A diversity of habitats enables more species to persist.

For several billion years, life has affected the environment on a global scale. These global effects have in turn affected biological diversity. Life added oxygen to the atmosphere and removed carbon dioxide, thereby making animal life possible.

People have rarely thought about cities as having any beneficial effects on biological diversity. However, in recent years there has been a growing realization that cities can contribute in important ways to the conservation of biological diversity. This topic will be discussed in Chapter 22.

People have always treasured the diversity of life, but we have been one of the main causes of the loss in diversity.

Perhaps no environmental issue causes more debate, is more central to arguments over values, or has greater emotional importance to people than biological diversity. Concern about specific endangered species has been at the heart of many political controversies. Resolving these conflicts and debates will require a clear understanding of the values at issue, as well as knowledge about species and their habitat requirements and the role of biological diversity in life's history on Earth.

KEY TERMS

adaptive radiation 152 biogeography 160 biological diversity 145 biological evolution 149 biome **161** biotic province 160 competitive exclusion principle 154 convergent evolution 162 divergent evolution dominant species 147

ecological island 165 ecological niche 155 founder effect 153 gene 149 genetic drift 153 genotype 149 migration 152 mutation 150 natural selection 150 obligate symbionts 158

parasitism 158 population 145 predation 158 species 145 species evenness species richness symbiont 157 symbiosis 157

STUDY QUESTIONS -

- 1. Why do introduced species often become pests?
- **2.** On which of the following planets would you expect a greater diversity of species? (a) a planet with intense tectonic activity; (b) a tectonically dead planet. (Remember that tectonics refers to the geologic processes involving the movement of tectonic plates and continents, processes that lead to mountain building and so forth.)
- 3. You are going to conduct a survey of national parks. What relationship would you expect to find between the number of species of trees and the size of each park?
- **4.** A city park manager has run out of money to buy new plants. How can the park's labor force alone be used to increase the diversity of (a) trees and (b) birds in the park?
- 5. A plague of locusts visits a farm field. Soon after, many kinds of birds arrive to feed on the locusts. What changes occur in animal dominance and diversity?

- Begin with the time before the locusts arrive and end after the birds have been present for several days.
- **6.** What will happen to total biodiversity if (a) the emperor penguin becomes extinct? (b) the grizzly bear becomes extinct?
- 7. What is the difference between a habitat and a niche?
- **8.** More than 600 species of trees grow in Costa Rica, most of them in the tropical rain forests. What might account for the coexistence of so many species with similar resource needs?
- **9.** Which of the following can lead to populations that are less adapted to the environment than were their ancestors?
 - (a) Natural selection
 - (b) Migration
 - (c) Mutation
 - (d) Genetic drift

FURTHER READING

- Botkin, D.B., No Man's Garden: Thoreau and a New Vision for Civilization and Nature (Washington, DC: Island Press, 2001). Discusses why people have valued biological diversity from both a scientific and cultural point of view.
- Charlesworth, B., and C. Charlesworth, Evolution: A Very Short Introduction (Oxford: Oxford University Press, 2003).
- Darwin, C.A., The Origin of Species by Means of Natural Selection, or the Preservation of Proved Races in the Struggle for Life (London: Murray, 1859., reprinted variously). A book that marked a revolution in the study and understanding of biotic existence.
- Dawkins, Richard, The Selfish Gene (New York: Oxford University Press; 3rd edition, 2008). Now considered a classic in the

- discussion of biological evolution for those who are not specialists in the field.
- Leveque, C., and J. Mounolou, Biodiversity (New York: John Wiley, 2003).
- Margulis, L., K.V. Schwartz, M. Dolan, K. Delisle, and C. Lyons, Diversity of Life: The Illustrated Guide to the Five Kingdoms (Sudbury, MA: Jones & Bartlett, 1999).
- Novacek, M.J. ed., The Biodiversity Crisis: Losing What Counts (An American Museum of Natural History Book. New York: New Press, 2001).
- Wacey, David, Early Life on Earth: A Practical Guide (New York: Springer, 2009). A new and thoughtful book about the beginnings of life on our planet.