What are the chances?

50:50 chance that the coin will turn up heads. If you flip two coins, you may come up with two heads, two tails, or one head and one tail. Only one of these possibilities gives the theoretical 50:50 ratio. To come closer to the statistical probability of flipping 50% heads and 50% tails, you would need to flip many coins at the same time. The more coins you flip, the more likely it is that you will end up with 50% of all the coins showing heads and the other 50% showing tails. The number of coins flipped is important. The same is true of gene frequencies. The smaller the population, the more likely it is that random events will alter the gene pool—that is, the more likely it is that genetic drift will occur.

Finally, *genes are not all equally likely to be passed to the next generation*. It is important to understand that genes differ in their value to the species. Some genes result in characteristics that are important to survival and reproductive success. Other genes reduce the likelihood of survival and reproduction. For instance, many animals have cryptic color patterns that make them difficult to see. The genes that determine the cryptic color pattern would be selected for (favored), because animals that are difficult to see are not killed and eaten as often as those that are easy to see. Recall that albinism is the inability to produce pigment, so that the individual's color is white. White animals are conspicuous, so we might expect them to be discovered more easily by predators (figure 13.12). Because not all genes have equal value, natural selection will operate and some genes will be more likely to be passed on to the next generation.

(a)

(b)

FIGURE 13.12 Albino Animals Are More Conspicuous
Pythons rely on camouflage coloring to help them catch prey. This albino form *(a)* is more likely to be spotted than a member of the species with normal coloration *(b)*.

Using the Hardy-Weinberg Concept to Show Allele-Frequency Change

We can return to our original example of alleles *A* and *a* to determine how natural selection based on differences in survival can result in allele-frequency changes in only one generation. Again, assume that the parent generation has the following genotype frequencies: *AA* = 36%, *Aa* = 48%, and *aa* = 16%, with a total population of 100,000 individuals. Suppose that 50% of the individuals having at least one *A* allele do not reproduce because they are more susceptible to disease. The parent population of 100,000 would have 36,000 individuals with the *AA* genotype, 48,000 with the *Aa* genotype, and 16,000 with the *aa* genotype. Because only 50% of those with an *A* allele reproduce, only 18,000 *AA* individuals and 24,000 *Aa* individuals will reproduce. All 16,000 of the *aa* individuals will reproduce, however. Thus, there is a total reproducing population of only 58,000 individuals out of the entire original population of 100,000. What percentage of *A* and *a* will go into the gametes produced by these 58,000 individuals?

The percentage of *A*-containing gametes produced by the reproducing population will be 31% from the *AA* parents and 20.7% from the *Aa* parents (table 13.2). The frequency of the *A* allele in the gametes is 51.7% (31% + 20.7%). The percentage of *a*-containing gametes is 48.3% (20.7% from the *Aa* parents plus 27.6% from the *aa* parents). The original parental allele frequencies were *A* = 60% and *a* = 40%. These have changed to *A* = 51.7% and *a* = 48.3%. More individuals in the population will have

TABLE 13.2 Differential Reproduction

The percentage of each genotype in the offspring differs from the percentage of each genotype in the original population as a result of differential reproduction.

Original Frequency of Genotypes	Total Number of Individuals Within a Population of 100,000 with Each Genotype	Number of Each Genotype Not Reproducing Subtracted from the Total	Total of Each Genotype in the Reproducing Population of 58,000 Following Selection	New Percentage of Each Genotype in the Reproducing Population
AA = 36%	36,000	36,000 −18,000 = 18,000	18,000	$\frac{18{,}000}{58{,}000}$ = 31.0%
Aa = 48%	48,000	48,000 −24,000 = 24,000	24,000	$\frac{24{,}000}{58{,}000}$ = 41.4%
aa = 16%	16,000	16,000 − 0 = 16,000	16,000	$\frac{16{,}000}{58{,}000}$ = 27.6%
100%	100,000		58,000	100.0%

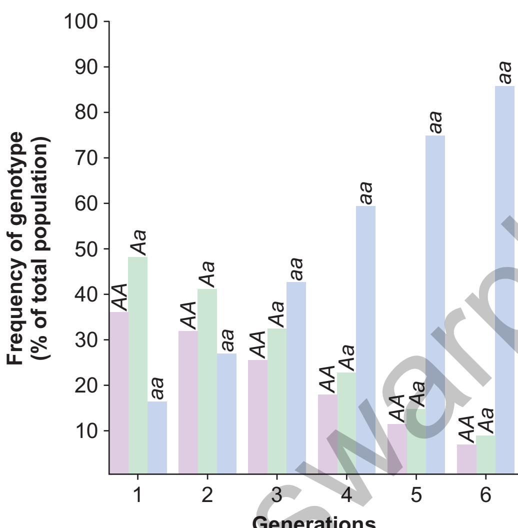


FIGURE 13.13 Changing Allele Frequency
If 50% of all individuals with the genotypes *AA* and *Aa* do not reproduce in each generation, the frequency of the *a* allele will increase, whereas the frequency of the *A* allele will decrease. Consequently, the *aa* genotype will increase in frequency, whereas that of the *AA* and *Aa* genotypes will decrease.

the *aa* genotype, and fewer will have the *AA* and *Aa* genotypes.

If this process continued for several generations, the allele frequency would continue to shift until the *A* allele became rare in the population (figure 13.13). This is natural selection in action. Differential reproduction rates have changed the frequency of the *A* and *a* alleles in this population.

13.9 CONCEPT REVIEW

17. A gene pool has equal numbers of alleles *B* and *b*. Half of the *B* alleles mutate to *b* alleles in the original generation. What will the allele frequencies be in the next generation?
18. Hardy-Weinberg is a theoretical concept that describes gene frequencies. List five reasons why the conditions of the Hardy-Weinberg concept are rarely met.
19. The smaller the population, the more likely it is that random changes will influence gene frequencies. Why is this true?

13.10 A Summary of the Causes of Evolutionary Change

At the beginning of this chapter, evolution was described as a change in allele frequency over time. It is clear that several mechanisms operate to bring about this change. Mutations can either change one allele into another or introduce an entirely new piece of genetic information into the population. Immigration can introduce new genetic information if the entering organisms have genetic information that was not in the population previously. Emigration and death remove genes from the gene pool. Natural selection systematically filters some genes from the population, allowing other genes to remain and become more common. The primary mechanisms involved in natural selection are differences in death rates, reproductive rates, and the rate at which individuals are selected as mates (figure 13.14). In addition, gene frequencies are more easily

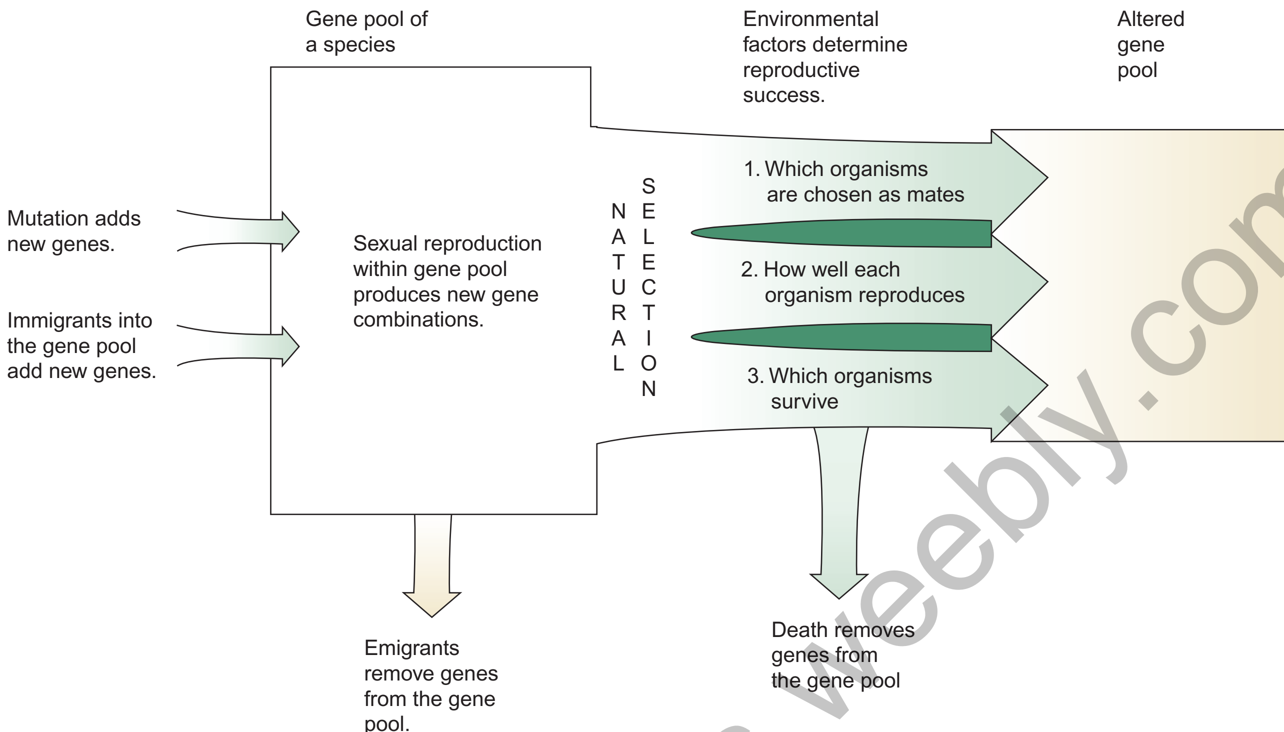


FIGURE 13.14 Processes That Influence Evolution
Several processes cause gene frequencies to change. New genetic information enters populations through immigration and mutation. Genetic information leaves populations through emigration and death. Natural selection operates within populations through death, mate selection, and rates of reproduction. Genetic drift can also result in evolutionary change but is not shown in this diagram.

changed in small populations, because events such as death, immigration, emigration, and mutation can have a greater impact on a small population than on a large population.

13.10 CONCEPT REVIEW

20. Why is each of the following important for an understanding of evolution: mutation, migration, sexual reproduction, selective agents, and population size?

Summary

At one time, people thought that all organisms were unchangeable. Lamarck suggested that change does occur and thought that acquired characteristics could be passed from generation to generation. Darwin and Wallace proposed the theory of natural selection as the mechanism that drives evolution. All populations of sexually reproducing organisms naturally exhibit genetic diversity among individuals as a result of mutation and the genetic recombination resulting from meiosis and fertilization. The genetic differences are reflected in phenotypic differences among individuals. These genetic differences are important in changing environments, because natural selection must have genetic diversity to select from. Natural selection by the environment results in better-suited organisms having greater numbers of offspring than those that are less well off genetically. Not all genes are equally expressed. Some express themselves only during specific periods in the life of an organism, and some are recessive alleles that show themselves only when in the homozygous state. Characteristics that are acquired during the life of an individual and are not determined by genes cannot be raw material for natural selection. Sexual selection occurs when specific individuals are chosen as mates to the exclusion of others. In addition to natural selection and sexual selection, genetic drift in small populations can lead to evolutionary change.

Selecting agents change the gene frequencies of the population if the conditions of the Hardy-Weinberg concept are violated. The conditions required for the Hardy-Weinberg equilibrium are random mating, no mutations, no migration, large population size, and no selective advantage for any genes. These conditions are met only rarely, however, so that, after generations of time, the genes of the more favored individuals will make up a greater proportion of the gene pool. The process of natural selection allows the maintenance of a species in its environment, even as the environment changes.

Key Terms

Use the interactive flash cards on the ***Concepts in Biology,*** *14/e website to help you learn the meaning of these terms.*

acquired characteristics 269
directional selection 280
disruptive selection 281
evolution 268
expressivity 276
fitness 272
genetic recombination 275
Hardy-Weinberg concept 282
penetrance 276
selecting agents 272
sexual selection 279
spontaneous mutations 275
stabilizing selection 280
theory of natural selection 270

Basic Review

1. Which of the following is not true?
   a. All organisms produce more offspring than can survive.
   b. All organisms of the same species are exactly alike.
   c. Among organisms, there is a constant struggle for survival.
   d. Individuals that possess favorable characteristics for their environment have a higher rate of survival and produce more offspring.
2. _____ characteristics are traits gained during an organism's life and not determined genetically.
   a. Genetic
   b. Acquired
   c. Sexual
   d. Dominant
3. Who proposed the theory of natural selection?
   a. Darwin and Wallace
   b. Buffon
   c. Lamarck
   d. Hardy and Weinberg
4. _____ is the success of an organism in passing on its gene to the next generation, compared with other members of its population.
5. _____ occurs within animal populations when some individuals are chosen as mates more frequently than others.
   a. Stabilizing selection
   b. Disruptive selection
   c. Sexual selection
   d. Normative selection
6. _____ is how often an allele expresses itself when present.
   a. Expressivity
   b. Dominance
   c. Fitness
   d. Penetrance
7. Specific environmental factors that favor certain characteristics are called
   a. selecting agents.
   b. hurricanes.
   c. mutations.
   d. disruptive factors.
8. _____ _____ is a significant change in the frequency of an allele that is not the result of natural selection.
9. The conditions necessary for gene frequencies to remain constant include all the following except
   a. mating must be completely random.
   b. mutations must not occur.
   c. the migration of individual organisms into and out of the population must not occur.
   d. the population must be very small.
10. _____ occurs when there are minor differences in allele frequency between populations of the same species, as when genetic differences between subspecies are examined.
11. Natural selection can take place when genetic differences exist among individuals in a population and these differences affect the overall health or _____.
12. _____-evolution has taken place when the percentage of dark peppered moths in a population increases as a result of allele-frequency changes.
13. A change in allele _____ can result from changes resulting from rapid periods of climate warming.
14. _____ diseases were thought to be controlled but have become common in recent years.
    a. Reemerging infectious
    b. Genetic abnormalities
    c. Recurring infectious
    d. Incidental
15. A high _____ _____ tends to offset the high _____ _____ and population size remains stable.

Answers
1. b 2. b 3. a 4. Fitness 5. c 6. d 7. a 8. Genetic drift 9. d 10. Microevolution 11. fitness 12. Micro- 13. frequency 14. a 15. death rate/reproductive rate

Thinking Critically

Microevolution and Sexually Transmitted Diseases
Penicillin was introduced as an antibiotic in the early 1940s. Since that time, it has been found to be effective against the bacteria that cause gonorrhea, a sexually transmitted disease. The drug acts on dividing bacterial cells by preventing the formation of a new protective cell wall. Without the wall, the bacteria can be killed by normal body defenses. As time passed, a new strain of this disease-causing bacterium developed. This bacterium produces an enzyme that metabolizes penicillin. How can gonorrhea be controlled now that this organism is resistant to penicillin? How did a resistant strain develop? Include the following in your consideration: DNA, enzymes, selecting agents, and gene-frequency changes.

CHAPTER 14

The Formation of Species and Evolutionary Change

Another Piece of the Human Evolution Puzzle Unearthed

The newest fossil may reveal more information about our origins.

CHAPTER OUTLINE

Just where would you expect to find a 47-million-year-old primate fossil? Africa, of course! But not this time. "Ida" (*Darwinius masillae*) was found in Messel Pit, a pit created by an oil shale mining operation in Germany in 1983, and not by a professional paleontologist, but an amateur collector. Fossil exploration began after the mining operation was completed and the pit was authorized to become a garbage dump. Ida was kept in a private collection for 25 years before she was acquired by the Natural History Museum of the University of Oslo for scientific study.

Ida is the most complete primate skeleton known in the fossil record. She has a complete skeleton, a soft body outline, and food in her digestive tract. Preliminary evidence reveals that she lived during the Eocene Epoch, after the extinction of dinosaurs and when primates split into two major groups: prosimians and anthropoids. The region was experiencing continental drift and just beginning to take on features we would recognize as Germany's landscape today. During the Eocene, many modern plants and animals were evolving in a subtropical, jungle-like environment. Evolutionarily, Ida and her relatives are thought to have been the evolutionary base of the anthropoid branch that led to monkeys, apes, and humans.

Ida lacks traits found in lemurs, such as a grooming claw on the second toe of the foot, a fused row of teeth in the middle of her lower jaw (known as a toothcomb), and claws. Her more advanced traits include the presence of fingernails, forward-facing eyes (allowing her to have 3-D vision and the ability to judge distance), and teeth similar to those of monkeys. Ida also has a talus bone in her feet. This bone allows her entire weight to be transmitted to the foot, an important feature in bipedal animals.

- **What role have fossils played in understanding species evolution?**
- **What factors are important to the formation of a new species?**
- **What do scientists know about the evolution of humans?**

Background Check

Concepts you should already understand to get the most out of this chapter:

- The fundamentals of meiosis, genes, and alleles (chapter 10)
- Traits that make a population a species (chapter 12)
- The role natural selection plays in evolution (chapter 13)

14.1 Evolutionary Patterns at the Species Level

Chapter 13 focused on the concept of microevolution—that is, minor differences in allele frequency between populations of the same species, as when genetic differences between subspecies are examined. This chapter focuses on macroevolution, the major differences that have occurred over long periods that have resulted in so much genetic change that new kinds of species are produced. Furthermore, the present situation is not the end of the evolutionary process because evolution is still occurring today. Recall from chapter 12 that a species is a population of organisms whose members have the potential to interbreed naturally and to produce fertile offspring but *do not* interbreed with other groups. This inability of a species to generate fertile offspring after breeding with other more genetically different organisms is a key to understanding how a new species can originate from a preexisting ancestral species.

California condor

There are three key ideas within this definition. First, a species is a population of organisms. An individual is not a species. An individual can only be a member of a group that is a species. The human species, *Homo sapiens,* consists of over 7 billion individuals, whereas the endangered California condor species, *Gymnogyps californianus,* currently consists of about 322 individuals, 179 of which live in the wild.

Second, the definition takes into consideration the ability of individuals within the group to produce fertile offspring. Obviously, not every individual can be checked to see if it is capable of mating with any other individual that is similar to it, so we must make some judgment calls. Can most individuals within the population interbreed to produce fertile offspring? Although all humans are of the same species, some individuals are sterile and cannot reproduce. However, we don't exclude them from the human species because of this. If they were not sterile, they would have the potential to interbreed. Although humans normally choose mating partners from their own local ethnic groups, humans from all parts of the world are potentially capable of interbreeding. This is known to be true because of the large number of instances of reproduction involving people of different ethnic backgrounds. The same is true for many other species that have local subpopulations but have a wide geographic distribution.

Third, the species concept also takes into account an organism's evolutionary history. A species is a group of organisms that shares a common ancestor with other species, but is set off from those others by having newer, genetically unique traits.

So how do we know if two populations really do belong to the same species?

Gene Flow

One way to find out if two populations belong to the same species is to investigate *gene flow*. **Gene flow** is the movement of genes from one generation to the next as a result of reproduction or from one region to another by migration. Two or more populations that demonstrate gene flow among them constitute a single species. On the other hand, two or more populations that do not have gene flow through reproduction, when given the opportunity, are generally considered to be different species. Some examples will clarify this working definition.

Donkeys (also called asses) and horses are thought to be two different species, even though they can be mated and produce offspring, called mules (figure 14.1). Because mules are nearly always sterile and do not produce offspring, this is not considered to be gene flow, so donkeys and horses are considered separate species. Similarly, lions and tigers can be mated in zoos to produce offspring. However, this does not happen in nature, so gene flow does not occur naturally; thus, they are also considered two separate species.

Liger

Genetic Similarity

Another way to find out if two organisms belong to different species is to determine their degree of genetic similarity. Advances in molecular genetics have allowed scientists to examine the sequence of bases in the genes present in individuals from a variety of populations. Those that have a great deal of similarity in their nitrogenous base sequences are assumed to have resulted from populations that have exchanged genes through sexual reproduction in the recent past. If there are significant differences, the two populations have probably not exchanged genes recently and are more likely to be members of separate species. There is no universal rule that states the smallest allowable genetic difference between two species. For example, genetic similarity between two South American field

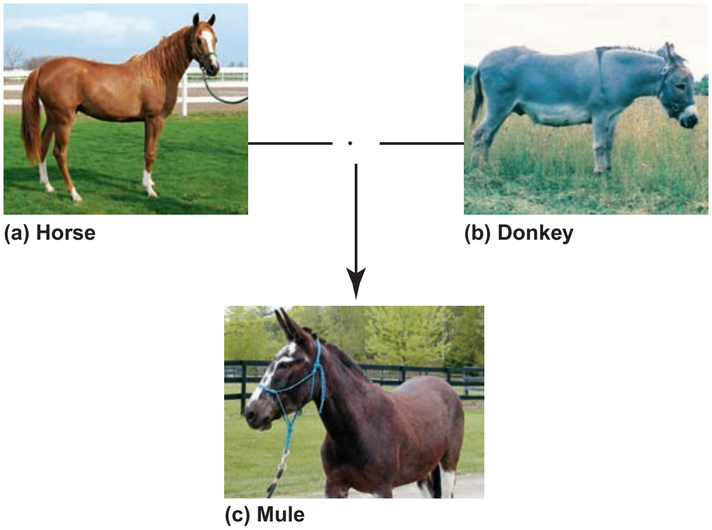


FIGURE 14.1 Hybrid Sterility
Even though they do not do so in nature, *(a)* horses *(Equus caballus)* and *(b)* donkeys *(Equus asinus)* can be mated. The offspring produced by mating a female horse with a male donkey is called a *(c)* mule *(Equus asinus* x *caballus)* and is sterile. Because all mules are sterile, the horse and the donkey are considered to be of different species.

mice, *Akodon dolores* and *A. molinae,* have been analyzed to determine if they are, in fact, members of the same species located in different geographic regions. Experts examining the genetic differences concluded that they are the same species but different geographic subspecies. The interpretation of the results obtained by examining genetic differences still requires the judgment of experts. Although this technique is probably not the ultimate method to settle every dispute related to the identification of species, it is an important tool.

14.1 CONCEPT REVIEW

1. How is the concept of gene flow related to the species concept?
2. Why aren't mules considered a species?

14.2 How New Species Originate

Speciation is the process of generating new species. When biologists look at the evolutionary history of living things, they see that new species have arisen continuously for as long as life has been on Earth. *Fossils* are often used as evidence of the past evolution of organisms. A **fossil** is any evidence of an organism of a past geologic age, such as a preserved skeleton or body imprint. The fossil record shows that huge numbers of new species have originated and that most species have gone extinct. Two mechanisms are probably responsible for the vast majority of speciation events: geographic isolation, and polyploidy (instant speciation).

Speciation by Geographic Isolation

Geographic isolation occurs when a portion of a species becomes totally cut off from the rest of the gene pool by geographic distance. In order for geographic isolation to lead to speciation, the following steps are necessary: (1) *population isolation* of a subpopulation of a species; (2) *genetic divergence*—that is, a change in the allele frequencies of the isolated subpopulation compared to the rest of the species; and (3) *reproductive isolation* of the new species from its parent species.

Population Isolation

There are at least three ways that populations can become geographically isolated (figure 14.2). First, the *colonization of a distant area* by one or only a few individuals can lead to

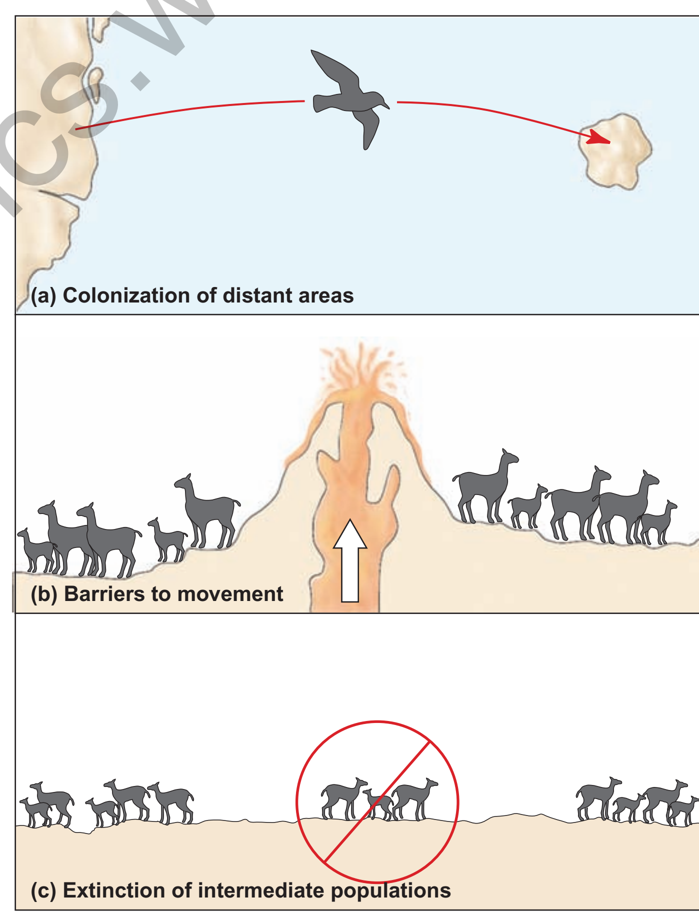


FIGURE 14.2 Geographically Isolated Populations
(a) The colonization of distant areas by one or a few individuals can cut off a population far from the center of their home population. *(b)* Barriers to movement can split an ancestral population into two isolated groups. *(c)* Extinction of intermediate populations can leave the remaining populations reproductively isolated from one another.

the establishment of a population far from the center of their home population. If these colonies are so far from their home populations that there is no gene flow between them, they are genetically isolated.

Second, speciation occurs if a *geographic barrier* totally isolates a subpopulation from the rest of the species. The uplifting of mountains, the rerouting of rivers, and the formation of deserts may separate one portion of a gene pool from another. For example, two kinds of squirrels are found on opposite sides of the Grand Canyon. The canyon is a barrier that prevents interbreeding among members of the two populations. Some people consider the two types of squirrels to be separate species; others consider them to be different, isolated sub-populations of the same species. Even small changes can cause geographic isolation in species that have little ability to move. A fallen tree, a plowed field, or even a new freeway may effectively isolate populations within such species. Snails in two valleys separated by a high ridge have been found to be closely related but different species. The snails cannot get from one valley to the next because of the height and climatic differences presented by the ridge.

Third, the *extinction of intermediate populations* can leave the remaining populations reproductively isolated from one another for periods that are long enough for them to develop into separate species. For example, the *range* of an organism is the geographic area over which a species can be found. As a species expands its range, some intermediate populations may go extinct so that portions of the original population become separated from the rest. Thus, many species are made up of several, smaller populations that display characteristics significantly different from those of other local populations. Many of these differences are adaptations to local environmental conditions. If the smaller subpopulation in the middle becomes extinct, the distance between the more extreme isolated populations may be too great for gene flow to occur.

Genetic Divergence

Genetic divergence is necessary for new species to develop. Differences in environments and natural selection play very important roles in the process of forming new species. Following separation from the main portion of the gene pool by geographic isolation, the organisms within a small, local population are likely to experience different environmental conditions. If, for example, a mountain range has separated a species into two populations, one population may receive more rain or more sunlight than the other. These environmental differences act as natural selecting agents on the two gene pools and, over a long period of time, account for different genetic combinations in the two places. Furthermore, different mutations may occur in the two isolated populations, and each may generate unique combinations of genes as a result of sexual reproduction. This is particularly true if one of the populations is very small. As a result, the two populations may show differences in color, height, enzyme production, time of seed germination, or many other genetic characteristics. Over a long period of time, the genetic differences that accumulate may result in subspecies that are significantly modified structurally, physiologically, or behaviorally. In some cases the changes may be so great that new species result.

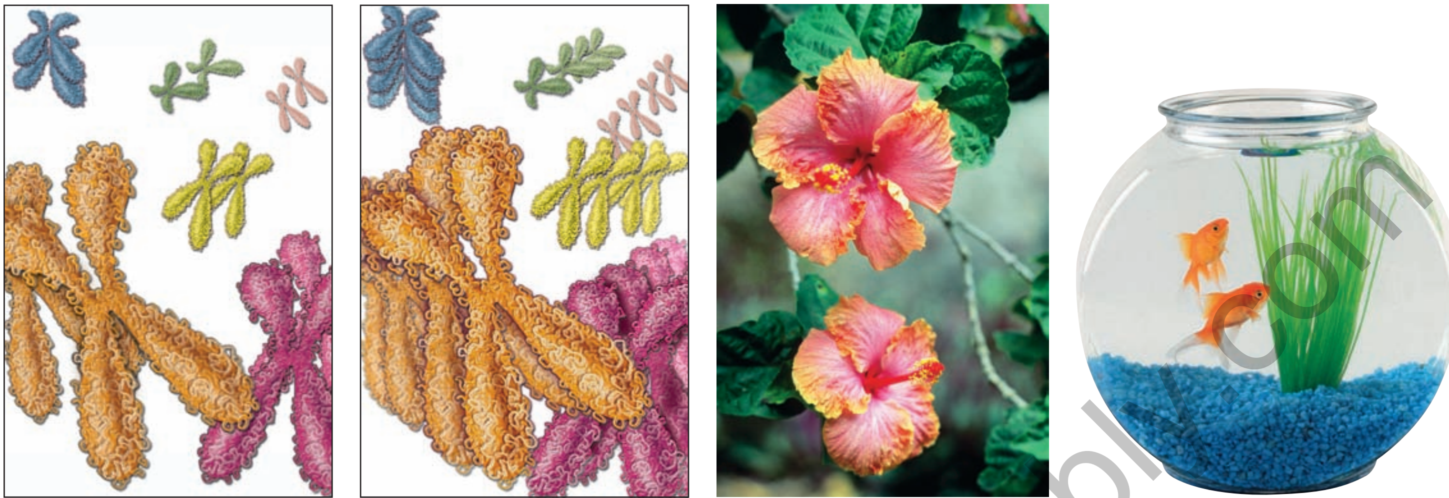
Reproductive Isolation

Reproductive isolation, or *genetic isolation,* has occurred if the genetic differences between the two populations have become so great that reproduction cannot occur between members of the two populations if they are brought together. At this point, speciation has occurred. In other words, the process of speciation can begin with the geographic isolation of a portion of the species, but new species are generated only if isolated populations become separate from one another *genetically* and gene flow is not reestablished if the geographic barrier is removed.

Polyploidy: Instant Speciation

Another important mechanism known to generate new species is polyploidy. **Polyploidy** is a condition of having multiple sets of chromosomes, rather than the normal haploid or diploid number. The increase in the number of chromosomes can result from abnormal mitosis or meiosis in which the chromosomes do not separate properly. For example, if a cell had the normal diploid chromosome number of 6 ($2n = 6$), and the cell went through mitosis but did not divide into two cells, it would then contain 12 chromosomes. It is also possible that a new polyploid species could result from crosses between two species followed by a doubling of the chromosome number (figure 14.3). Because the number of chromosomes of the polyploidy is different from that of the parent, successful reproduction between the polyploid and the parent is usually not possible. This is because meiosis would result in gametes that had chromosome numbers different from those of the original parent organism. In one step, the polyploid could be isolated reproductively from its original species.

A single polyploid plant does not constitute a new species. However, because most plants can reproduce asexually, they can create an entire population of organisms that have the same polyploid chromosome number. The members of this population would probably be able to undergo normal meiosis and would be capable of sexual reproduction among themselves. In effect, a new species can be created within a couple of generations. Some groups of plants, such as the grasses, may have 50% of their species produced as a result of polyploidy. Many economically important species are polyploids. Cotton, potatoes, sugarcane, broccoli, wheat, and many garden flowers are examples. Although it is rare in animals, polyploidy is found in some insects, fishes, amphibians, and reptiles. Certain lizards have only female individuals and lay eggs, which develop into additional females. Various species of these lizards appear to have developed by polyploidy. To date, the only mammal found to be polyploid is a rat (*Tympanoctomys barrerae*) found in Argentina and is tetraploid, $4n = 204$.



(a) (b) (c) (d)

FIGURE 14.3 Polyploidy
(a) The chromosome number of this diploid cell is $2n = 12$. *(b)* What happens when it undergoes polyploidy and doubles its chromosome count—that is, $4n = 24$. Polyploidy has been found in many kinds of plants including grasses and ferns. *(c)* Hibiscus plants (*Hibiscus rosa-sinensis*), and *(d)* many varieties of goldfish (*Carassius auratus*).

Other Speciation Mechanisms

Speciation can also occur without geographic isolation or polyploidy. Any process that can result in the reproductive isolation of a portion of a species can lead to the possibility of speciation. For example, within populations, some individuals may breed or flower at a somewhat different time of the year. If the difference in reproductive time is genetically based, different breeding populations could be established that could eventually lead to speciation. Among animals, variations in the genetically determined behaviors related to courtship and mating could effectively separate one species into two or more separate breeding populations. In plants, genetically determined incompatibility of the pollen of one population of flowering plants with the flowers of other populations of the same species could lead to separate species. Although there are many examples of these kinds of speciation mechanisms, geographic isolation and polyploidy are considered the primary mechanisms for speciation.

14.2 CONCEPT REVIEW

3. How does speciation differ from the formation of subspecies?
4. Can you always tell by looking at two organisms whether or not they belong to the same species?
5. Why is geographic isolation important in the process of speciation?
6. How does a polyploid organism differ from a haploid or diploid organism?
7. List the series of events necessary for speciation to occur.

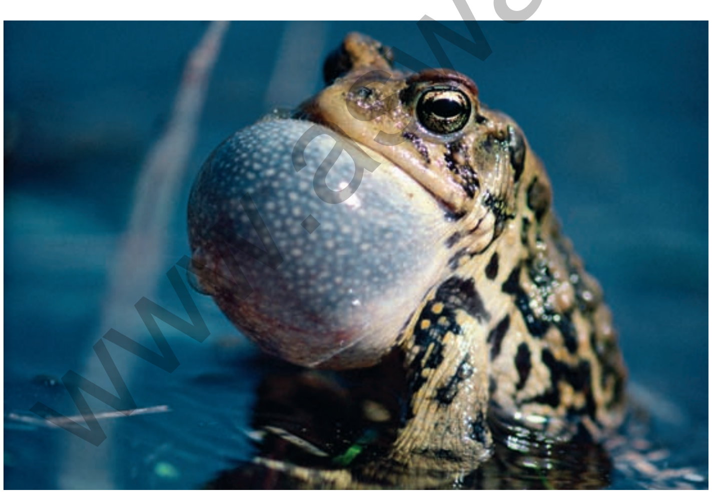
14.3 The Maintenance of Reproductive Isolation Between Species

For a new species to continue to exist, it must reproduce and continue to remain genetically isolated from other, similar species. The speciation process involves the development of **reproductive,** or **genetic, isolating mechanisms.** These mechanisms prevent matings between members of two different species and, therefore, help maintain distinct species. There are several mechanisms for maintaining reproductive (genetic) isolation:

1. **Habitat preference,** or **ecological, isolating mechanisms,** occur when two species do not have the opportunity to interbreed because they typically live in different ecological settings. For example, in central Mexico, two species of robin-sized birds, called *towhees*, live in the same general region. However, the collared towhee lives on the mountainsides in the pine forest, whereas the spotted towhee is found at lower elevations in oak forests. Geography presents no barriers to these birds. They are capable of flying to each other's habitats, but they do not. Therefore, they are reproductively isolated because of the habitats they prefer. Similarly, areas with wet soil have different species of plants than nearby areas with drier soils.
2. **Seasonal isolating mechanisms** (differences in the time of year at which reproduction takes place) are effective genetic isolating mechanisms. Some plants flower only in the spring, whereas other species that are closely related flower in midsummer or fall; therefore, the two species are not very likely to pollinate one another. Among insects, there are examples of similar spacing of the reproductive periods of closely related species, so that they do not overlap.

3. **Behavioral isolating mechanisms** occur when inborn behavior patterns prevent breeding between species. The mating calls of frogs and crickets are highly specific. The sound pattern produced by the males is species-specific and invites only females of the same species to engage in mating. The females have a built-in response to the particular species-specific call and mate only with those that produce the correct call. The courtship behavior of birds involves both sound and visual signals that are species-specific. For example, groups of male prairie chickens gather on meadows shortly before dawn in the early summer and begin their dances. The air sacs on both sides of the neck are inflated, so that the brightly colored skin is exposed. Their feet move up and down very rapidly and their wings are spread out and quiver slightly (figure 14.4). This combination of sight and sound is attractive to females. When the females arrive, the males compete for the opportunity to mate with them. Other, related species of birds conduct their own similar, but distinct, courtship displays. The differences among the dances are great enough that a female can recognize the dance of a male of her own species. Behavioral isolating mechanisms such as these occur among other types of animals as well. The strutting of a peacock, the fin display of a beta (Siamese fighting) fish, and the flashing light patterns of "lightning bugs"/"fireflies" (they are actually beetles) of various species are all examples of behaviors that help individuals identify members of their own species and prevent different species from interbreeding (figure 14.5).
4. **Mechanical,** or **morphological, isolating mechanisms** involve differences in the structure of organisms. The specific shapes of the structures involved in reproduction may prevent different species from interbreeding. Among insects, the structure of the penis and the reciprocal structures of the female fit like a lock and key; therefore, breeding between different species is very difficult. Similarly, the shapes of flowers may permit only certain animals to carry pollen from one flower to the next.
5. **Biochemical isolating mechanisms** occur when molecular incompatibility prevents successful mating. A vast number of biochemical activities take place around the union of egg and sperm. Molecules on the outside of the egg or sperm may trigger events that prevent their union if they are not from the same species. Among plants, biochemical interactions between the pollen and the receiving flower prevent the germination of the pollen grain and, therefore, prevent sexual reproduction between two closely related species.
6. **Hybrid inviability,** or **infertility, mechanisms** prevents the offspring of two different species from continuing to

FIGURE 14.4 Courtship Behavior (Behavioral Isolating Mechanism)
The dancing of a male prairie chicken attracts female prairie chickens, but not females of other species. This behavior tends to keep prairie chickens reproductively isolated from other species.



(a) Species-specific sounds

(b) Species-specific displays

FIGURE 14.5 Animal Communication—Identifying Members of Their Own Species
Most animals use specific behaviors to communicate with others of the same species. *(a)* The trilling of a male American toad is specific to its species and is different from that of males of other species. *(b)* The visual displays of this orange octopus communicate to others of the same species.

reproduce. This can occur in three ways: (a) the embryos of such a mating may not develop properly and die; (b) if offspring are produced, they die before they can reproduce; or (c) such hybrids may be sterile or have greatly reduced fertility (review figure 14.1).

14.3 CONCEPT REVIEW

8. Describe three kinds of reproductive isolating mechanisms that prevent interbreeding between different species.
9. Give an example of seasonal isolating mechanisms, habitat preference, and behavioral isolating mechanisms.

14.4 Evolutionary Patterns Above the Species Level

A species is the smallest irreversible unit of evolution. Because the exact conditions present when a species came into being will never exist again, it is highly unlikely that it will evolve back into an earlier stage in its development. Furthermore, because species are reproductively isolated from one another, they usually do not combine with other species to make something new; they can only diverge further. When life in the past is compared with our current diversity of life, many different evolutionary patterns emerge.

Divergent Evolution

Divergent evolution is a basic evolutionary pattern in which individual speciation events cause successive branches in the evolution of a group of organisms. This basic pattern is well illustrated by the evolution of the horse, shown in figure 14.6 Each of the many branches of the evolutionary history of the horse began with a speciation event that separated one species into two species as each separately adapted to local conditions. Changes in the environment from moist forests to drier grasslands would have set the stage for change. The modern horse, with its large size, single toe on each foot, and teeth designed for grinding grasses, is thought to be the result of accumulated genetic changes beginning from a small, dog-sized animal with four toes on its front feet, three toes on its hind feet, and teeth designed for chewing leaves and small twigs. Even though we know much about

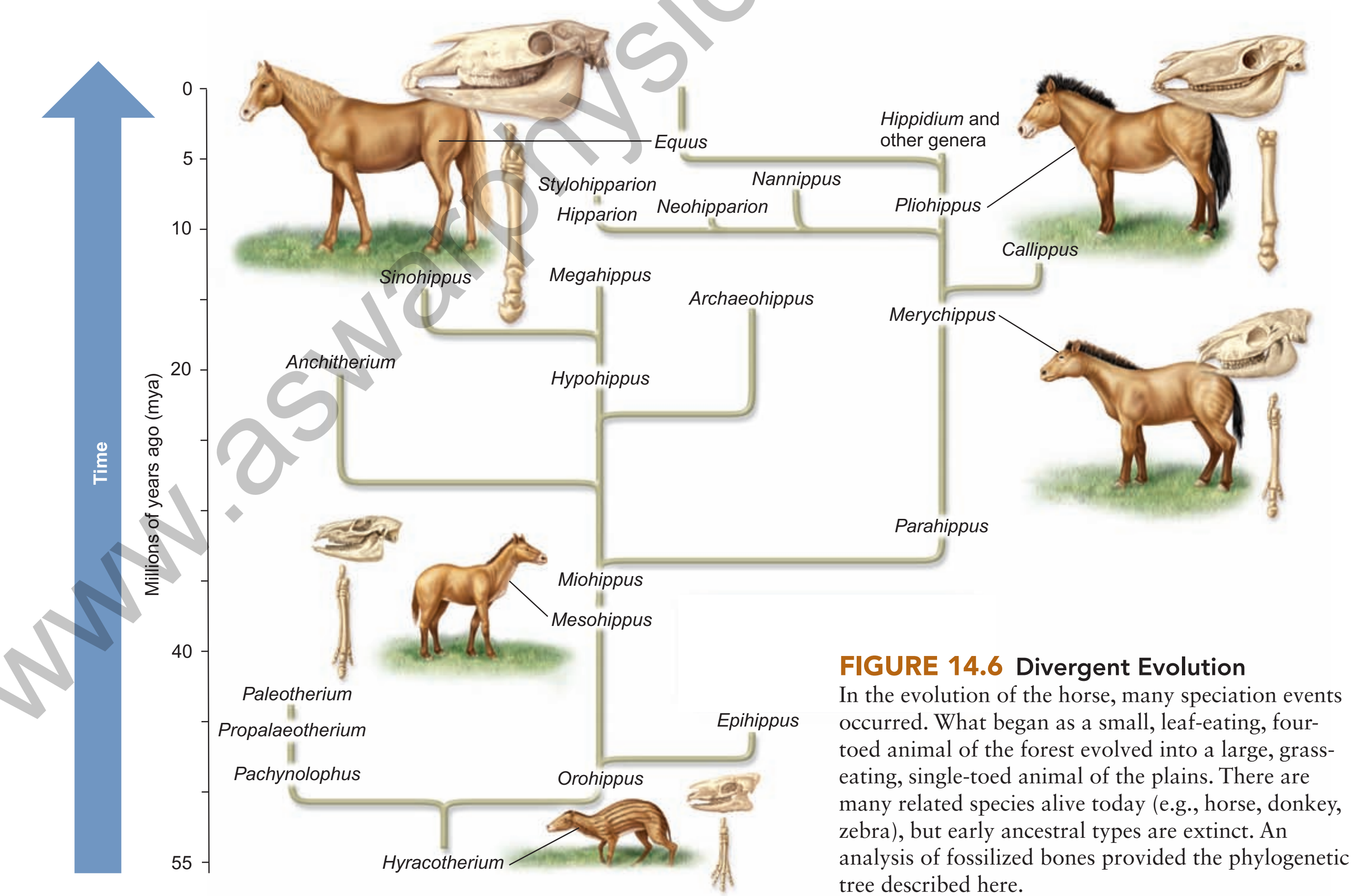


FIGURE 14.6 Divergent Evolution
In the evolution of the horse, many speciation events occurred. What began as a small, leaf-eating, four-toed animal of the forest evolved into a large, grass-eating, single-toed animal of the plains. There are many related species alive today (e.g., horse, donkey, zebra), but early ancestral types are extinct. An analysis of fossilized bones provided the phylogenetic tree described here.

evolution, there are still many gaps that need to be filled before we have a complete evolutionary history of any organism (Outlooks 14.1).

Extinction

Extinction is the loss of a species. It is a common pattern in the evolution of organisms. Notice in figure 14.6 that most of the species that developed during the evolution of the horse are extinct. Only members of the genus *Equus* remain. This is typical. Most of the species that have ever existed are extinct. Estimates of extinction are around 99%; that is, 99% or more of all the species that ever existed are extinct. Given this high rate of extinction, we can picture current species of organisms as the product of much evolutionary experimentation. This is not the complete picture, though. Recall from chapter 13 that organisms are continually being subjected to selection pressures that lead to a high degree of adaptation to a particular set of environmental conditions. Organisms become more and more specialized. However, the environment does not remain constant; it often changes in such a way that the species that were originally present are unable to adapt to the new set of conditions. The early ancestors of the modern horse were well adapted to a moist tropical environment, but, when the climate became drier, most were no longer able to survive. Only some kinds had the genes necessary to lead to the development of modern horses and their relatives.

Furthermore, many extinct species were very successful organisms for millions of years. They were not failures for their time but simply did not survive to the present. It is also important to realize that many currently existing organisms will eventually become extinct—perhaps even *Homo sapiens*. Thus, the basic evolutionary pattern is one of divergence with a great deal of extinction. Although divergence and extinction are dominant themes in the evolution of life, adaptive radiation and convergent evolution are two other important evolutionary patterns.

Adaptive Radiation

Adaptive radiation is an evolutionary pattern characterized by a rapid increase in the number of kinds of closely related species. Adaptive radiation results in an evolutionary explosion of new species from a common ancestor. There are basically two situations thought to favor adaptive radiation. One is a condition in which an organism invades a previously unexploited environment. For example, at one time, there were no animals on the landmasses of the Earth. The amphibians were the first vertebrate animals able to spend part of their lives on land. Fossil evidence shows that a variety of amphibians evolved rapidly and exploited several kinds of lifestyles.

Another good example of adaptive radiation is found among the finches of the Galápagos Islands, located 1,000 kilometers west of Ecuador in the Pacific Ocean. These birds were first studied by Charles Darwin. Because these islands are volcanic and arose from the ocean floor, it is assumed that they have always been isolated from South America and originally lacked finches and other land-based birds. It is thought that one kind of finch arrived from South America to colonize the islands and that adaptive radiation from the common ancestor resulted in the many kinds of finches found on the islands today (figure 14.7). Although the islands are close to one another, they are quite diverse. Some are dry and treeless, some have moist forests, and others have intermediate conditions. Conditions were ideal for several speciation events. Because the islands were separated from one another,

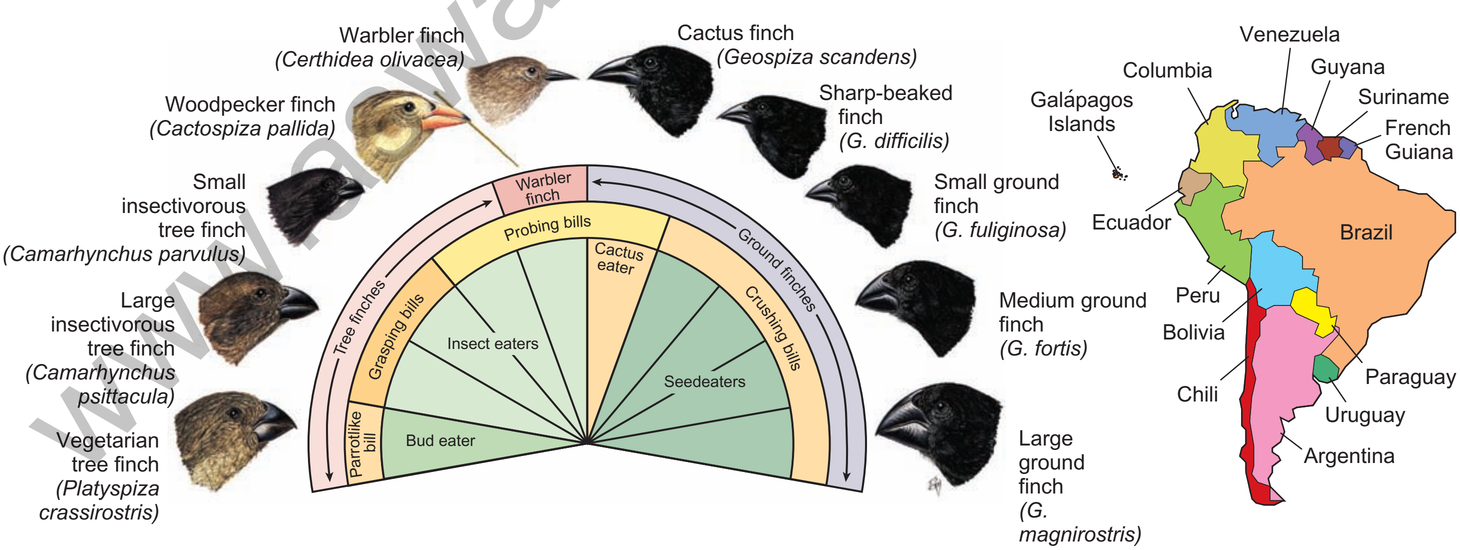


FIGURE 14.7 Adaptive Radiation
When Darwin discovered the finches of the Galápagos Islands, he thought they might all have derived from one common ancestor that arrived on these relatively isolated islands. If they were the only birds to inhabit the islands, they could have evolved very rapidly into the many types shown here. The drawings show the specializations of beaks for different kinds of food.

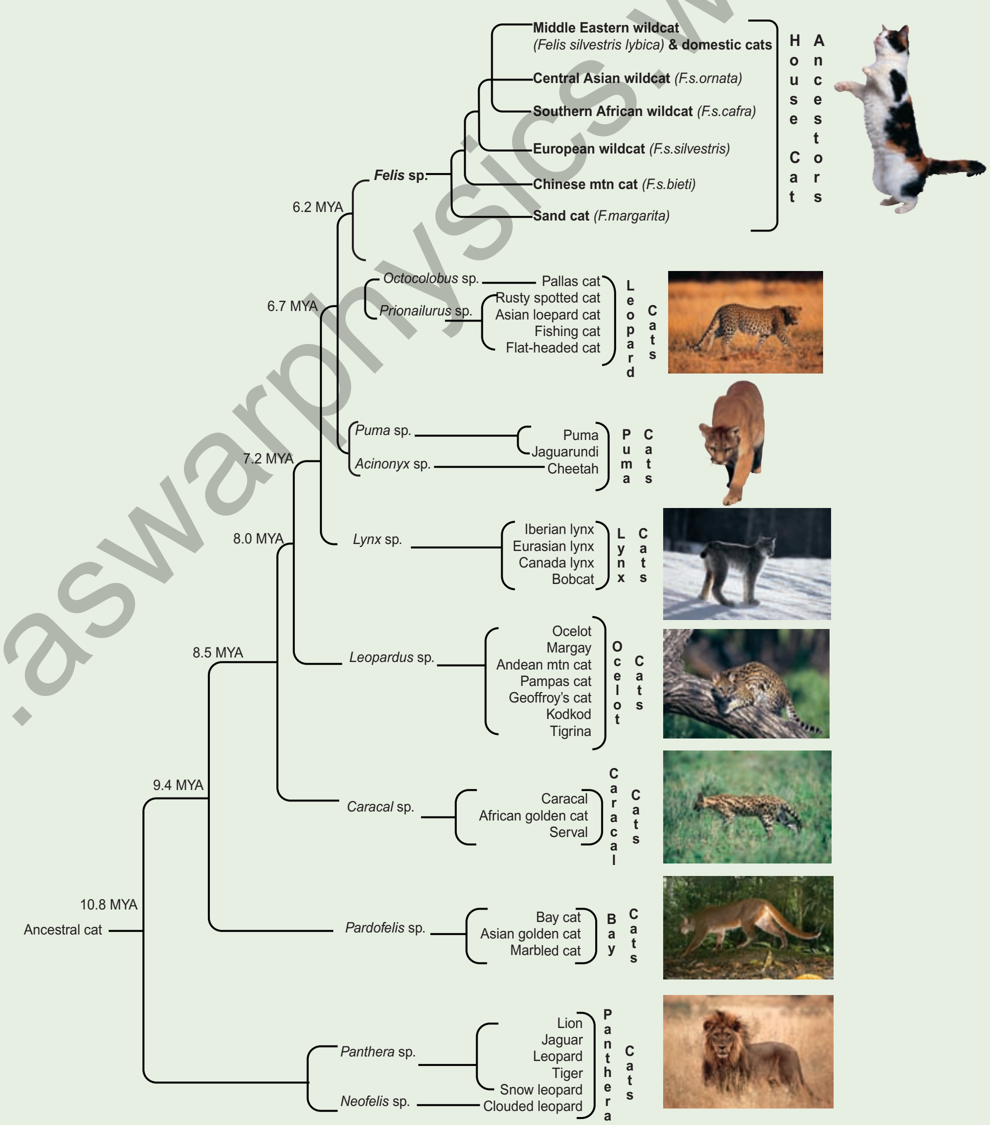
OUTLOOKS 14.1

Evolution and Domesticated Cats

The evolutionary history of the domestic cat (*Felis silvestris lybica*) has been unclear because of incomplete fossil records. However, an international team sampling both mitochondrial DNA and the DNA from both X and Y sex chromosomes has finally come up with an evolutionary tree for felines. The group proposes that about 11 million years ago, a single, ancestral feline-like species migrated from Asia throughout the world except Australia.

Researchers believe that 10 to 3 million years ago (MYA) land bridges between continents were created when sea levels fell. The common ancestor to all of today's cats probably migrated south to Africa from Asia. The cats also moved north crossing the Bering land bridge (as wide as 1,000 miles) to North America and migrated to South America by the Panamanian land bridge. When sea levels rose, they covered the land bridges and cut off cat species from their original groups. These isolated subpopulations genetically drifted apart, each adapting to its unique environment. When the subpopulations had the chance of coming back together, they were no longer able to interbreed and, at that point, found themselves to be different species. Ancestral felines, originally a Eurasian genus, successfully migrated throughout the globe because they encountered little or no competition from other carnivores. They continue to be one of the most successful of carnivore families.

Traditionally, domestication was thought to have occurred about 3,600 years ago in Egypt. Archeological evidence in Egyptian hieroglyphics portrays cats, and bones of cats have been found buried with humans in tombs. However, more recent archeological and genetic evidence strongly suggests that cats were domesticated about 9,500 years ago in the Fertile Crescent, the Middle East. Today, this region includes Egypt, Israel, the West Bank, Gaza strip, and Lebanon; and parts of Jordan, Syria, Iraq, southeastern Turkey, and southwestern Iran and Kuwait.



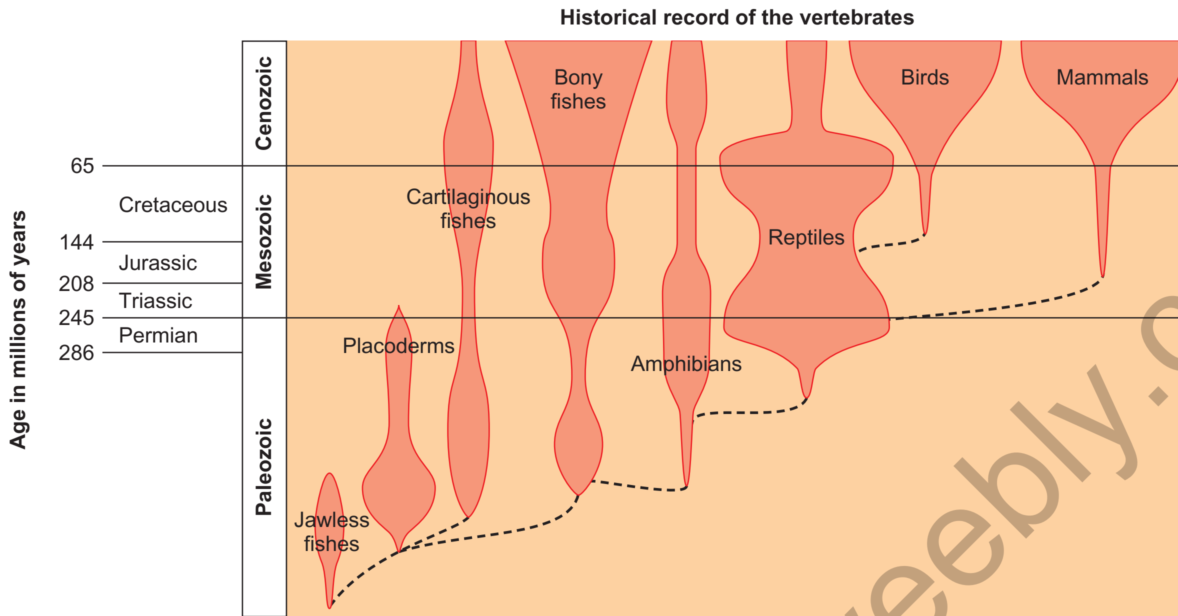


FIGURE 14.8 Adaptive Radiation in Terrestrial Vertebrates
The amphibians were the first vertebrates to live on land. They were replaced by the reptiles, which were better adapted to land. The reptiles, in turn, were replaced by the adaptive radiation of birds and mammals. (Note: The width of the colored bars indicates the number of species present.)

the element of geographic isolation was present. Because environmental conditions on the islands were quite different, particular characteristics in the resident birds would have been favored. Furthermore, the absence of other kinds of birds meant that there were many lifestyles that had not been exploited.

In the absence of competition, some of these finches took roles normally filled by other kinds of birds elsewhere in the world. Although finches are normally seed-eating birds, some of the Galápagos finches became warblerlike insect-eaters, others became leaf-eaters, and one uses a cactus spine as a tool to probe for insects.

The second situation that can favor adaptive radiation is one in which a type of organism evolves a new set of characteristics that enables it to displace organisms that previously filled specific roles in the environment. For example, although amphibians were the first vertebrates to occupy land, they lived only near freshwater, where they would not dry out and could lay eggs, which developed in the water. They were replaced by reptiles with such characteristics as dry skin, which prevented the loss of water, and an egg that could develop on land. The adaptive radiation of reptiles was extensive. They invaded most terrestrial settings and even evolved forms that flew and lived in the sea. With the extinction of dinosaurs and many other reptiles, birds and mammals went through a similar radiation. Perhaps the development of homeothermism (the ability to maintain a constant body temperature) had something to do with the success of birds and mammals. Figure 14.8 shows the radiations that occurred within the vertebrate group. The number of species of bony fishes has increased as the number of other kinds of fishes (jawless fishes, placoderms, cartilaginous fishes) declined and the number of species of birds and mammals has increased as the number of reptiles and amphibians decreased.

Convergent Evolution

Convergent evolution is an interesting evolutionary pattern that involves the development of similar characteristics in organisms of widely different evolutionary backgrounds. This pattern often leads people to misinterpret the evolutionary history of organisms. For example, many kinds of plants that live in desert situations have sharp, pointed structures, such as spines or thorns, and lack leaves during much of the year. Superficially, the sharp, pointed structures may resemble one another to a remarkable degree but may have a completely different evolutionary history. Some of these structures are modified twigs, others are modified leaves, and still others are modifications of the surface of the stem. The presence of sharp, pointed structures and the absence of leaves are adaptations to a desert type of environment: The thorns and spines discourage herbivores and the absence of leaves reduces water loss.

Another example is animals that survive by catching insects while flying. Bats, swallows, and dragonflies all obtain food in this manner. They have wings, good eyesight or hearing to locate flying insects, and great agility and speed in flight, but they are evolved from quite different ancestors (figure 14.9). At first glance, they may appear very similar

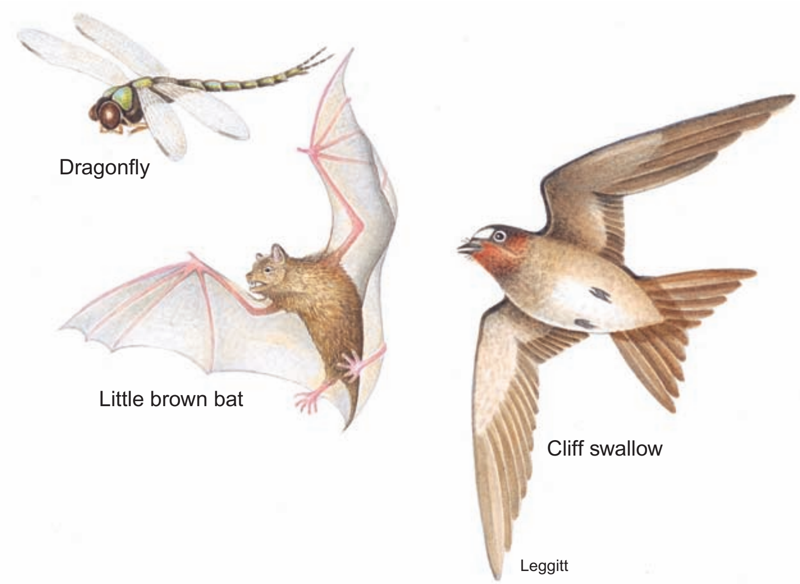


FIGURE 14.9 Convergent Evolution
All of these animals have evolved wings as a method of movement and capture insects for food as they fly. However, flight originated independently in each of them.

and perhaps closely related, but a detailed study of their wings and other structures shows that they are different kinds of animals. They have simply converged in structure, the type of food they eat, and their method of obtaining food. Likewise, whales, sharks, and the barracuda appear to be similar—they all have a streamlined shape, which aids in rapid movement through the water; a dorsal fin, which helps prevent rolling; fins or flippers for steering; and a large tail, which provides power for swimming. However, they are quite different kinds of animals that happen to live in the open ocean, where they pursue other animals as prey. Their structural similarities are adaptations to being fast-swimming predators.

Homologous or Analogous Structures

To help evolutionary biologists distinguish between structures that are the result of convergent evolution and those that are not, they try to determine if the structures evolved from a common ancestor. **Homologous structures** are structures in different species that have been derived from a common ancestral structure. Thus, the wing of a bat, the front leg of a horse, and the arm of a human show the same basic pattern of bones, but they are extreme modifications of the same basic evolutionary structure (figure 14.10). On the other hand, structures that have the same function (such as the wing of a butterfly and the wing of a bird) but different evolutionary backgrounds are called **analogous structures** and are the result of convergent evolution (review figure 14.9).

14.4 CONCEPT REVIEW

10. Describe convergent evolution and adaptive radiation.
11. What are the two dominant evolutionary patterns?
12. How are analogous and homologous structures different?

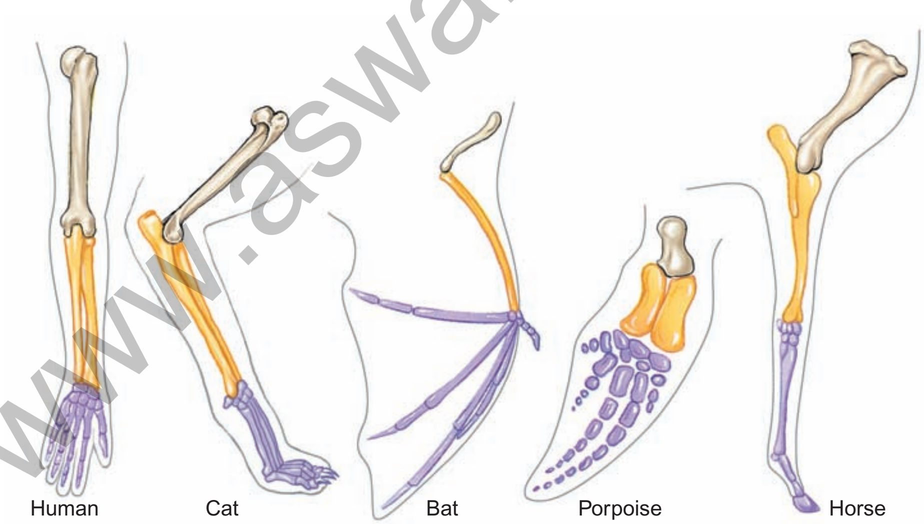


FIGURE 14.10 Maintaining Traits Through Time—Homologous Structures
Although these body parts are considerably different in structure and function, the same bones are present in the forelimbs of humans, cats, bats, porpoises, and horses.

14.5 Rates of Evolution

Although it is commonly thought that evolutionary change takes long periods of time, rates of evolution can vary greatly. Remember that natural selection is driven by the environment. If the environment is changing rapidly, changes in organisms should be rapid. Periods of rapid environmental change also result in extensive episodes of extinction. During some periods in the history of the Earth when little environmental change was taking place, the rate of evolutionary change was probably slow. Nevertheless, when we talk about evolutionary time, we are generally thinking in thousands or millions of years. Although both of these time periods are long compared with the human life span, the difference between thousands of years and millions of years in the evolutionary time scale is still significant.

The fossil record shows many examples of gradual changes in the physical features of organisms over time. For example, the extinct humanoid fossil *Homo erectus* shows a gradual increase in the size of the skull, a reduction in the size of the jaw, and the development of a chin over about a million years. The accumulation of these changes could result in such extensive change from the original species that we would consider the current organism to be a different species from its ancestor. (Many believe that *Homo erectus* became modern humans, *Homo sapiens*.) This is such a common feature of the evolutionary record that biologists refer to this kind of evolutionary change as *gradualism* (figure 14.11a).

Gradualism is a model for evolutionary change that evolution occurred slowly by accumulating small changes over a long period of time. Charles Darwin's view of evolution was based on gradual changes in the features of specific species he observed in his studies of geology and natural history. However, as early as the 1940s, some biologists began to challenge gradualism as the only model for evolutionary change. They pointed out that the fossils of some species were virtually unchanged over millions of years. If gradualism were the only explanation for how species evolved, then gradual changes in the fossil record of a species would always be found. Furthermore, some organisms appear suddenly in the fossil record and show rapid change from the time they first appeared. There are many modern examples of rapid evolutionary change; the development of pesticide resistance in insects and antibiotic resistance in various bacteria has occurred recently.

In 1972, two biologists, Niles Eldredge of the American Museum of Natural History and Stephen Jay Gould of Harvard University, proposed a very different idea. **Punctuated equilibrium** is their hypothesis that evolution occurs in spurts of rapid change, followed by long periods with little evolutionary change (figure 14.11b). The punctuated equilibrium concept is a companion hypothesis to gradualism and suggests a different way of achieving evolutionary change. Punctuated equilibrium proposes that, rather than one species slowly accumulating changes to become a different descendant species, there is a rapid evolution of several closely related species from isolated populations. This would produce a number of species that would compete with one another as the environment changed. Many of these species would become extinct and the fossil record would show change.

Another way to look at gradualism and punctuated equilibrium is to assume that both occur. It is clear from the fossil record that there were periods in the past when there was very rapid evolutionary change, compared with other times. Also, some environments, such as the ocean, have been relatively stable, whereas others, such as the terrestrial environment, have changed significantly. Many marine organisms have remained unchanged for hundreds of millions of years, but there has been great change in the kinds of terrestrial organisms in the past few million years. Thus, it is possible that both gradualism and punctuated equilibrium have operated. The important contribution of punctuated equilibrium is that there can be alternative ways of interpreting the fossil record and that the pace of evolution can be quite variable. However, both approaches take into account the importance of genetic diversity as the raw material for evolution and the mechanism of natural selection as the process of determining which gene combinations fit the environment. The gradualists point to the fossil record as proof that evolution is a slow, steady process. Those who support punctuated equilibrium point to the gaps in the fossil record as evidence that rapid change occurs.

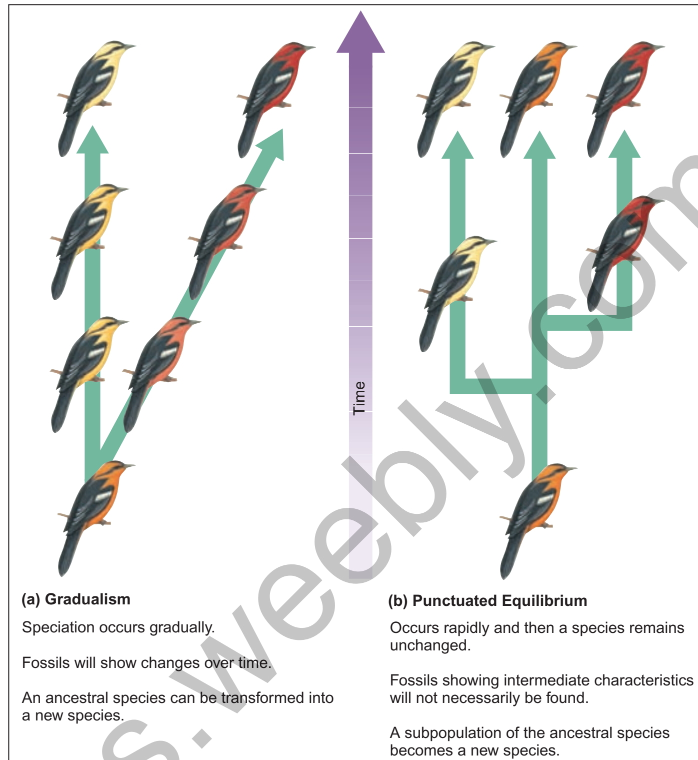


FIGURE 14.11 Gradualism vs. Punctuated Equilibrium
(a) Gradualism is the evolution of new species from the accumulation of a series of small changes over a long period of time. *(b)* Punctuated equilibrium is the evolution of new species from a large number of changes in a short period of time.

14.5 CONCEPT REVIEW

13. What is the difference between gradualism and punctuated equilibrium?

14.6 The Tentative Nature of the Evolutionary History of Organisms

Tracing the evolutionary history of an organism back to its origins is a very difficult task, because most of its ancestors no longer exist. Scientists act as "time detectives" when they study fossils of extinct organisms but must keep in mind that the fossil record is incomplete and provides only limited information about the biology of the organism represented in that record. However, new fossils are always being discovered.

There are three reasons that the fossil record is incomplete. First, the likelihood that an organism will become a fossil is low. Most organisms die and decompose, leaving no trace of their existence. (Today, road-killed opossums are not likely to become fossils because they will be eaten by scavengers, repeatedly run over, or decompose by the roadside.) Second, in order to form a fossil, the dead organism must be covered by sediments, dehydrated, or preserved in some other way.

Several factors increase the likelihood that an organism will be found in the fossil record:

- The presence of hard body parts resist decomposition.
- Marine organisms can be covered by sediment on the bottom.
- Fossils of more recent organisms are less likely to have been destroyed by geological forces.
- Fossils of large organisms are easier to find.
- Organisms that were extremely common are more likely to show up in the fossil record.

For example, trilobites are very common in the fossil record. They were relatively large marine organisms, with hard body parts, that were extremely abundant. However, fossils of soft-bodied, extremely ancient, wormlike organisms are rare.

Third, the discovery of fossils is often accidental. It is impossible to search through all the layers of sedimentary rock on the entire surface of the Earth. Therefore, scientists will continue to find new fossils that will extend the known information about ancient life into the foreseeable future. But there can be no question that evolution occurred in the past and continues to occur today (How Science Works 14.1).

Scientists may know a lot about the structure of the bones and teeth or the stems and leaves of an extinct ancestor from fossils but know almost nothing about its behavior, physiology, and natural history. Biologists must use a great deal of indirect evidence to piece together the series of evolutionary steps that led to a current species.

14.6 CONCEPT REVIEW

14. Why is it difficult to determine the evolutionary history of a species?

14.7 Human Evolution

There is intense curiosity about how our species (*Homo sapiens*) came to be, and the evolution of the human species remains an interesting and hot topic. Human beings are classified as mammals belonging to a group known as primates. Primates are thought to have come into existence approximately 66 million years ago. They include animals with enlarged, complex brains; five digits, with nails, on the hands and feet; and hands and feet adapted for grasping. Their bodies, except those of humans, are covered with hair. There are two groups of primates, the prosimians—lemurs and tarsiers—and the anthropoids—monkeys, apes, and humans (figure 14.12).

You cannot shake hands with any other species belonging to the genus *Homo*. All other versions of our close evolutionary relatives are extinct. This makes it difficult to visualize our evolutionary development. Therefore we tend to think we are not subject to the laws of nature. However, humans show genetic diversity, experience mutations, and are subject to the same evolutionary forces as other organisms.

Scientists use several kinds of evidence to try to sort out our evolutionary history. Fossils of various kinds of prehuman and ancient human ancestors have been found, but many of these are only fragments of skeletons, which are difficult to interpret and are hard to date. Stone tools of various kinds have also been found that are associated with prehuman and early human sites. Finally, other aspects of the culture of our ancestors have been found in burial sites, including cave paintings and ceremonial objects. Various methods have been used to date these findings. When fossils are examined, anthropologists can identify differences in the structures of bones that are consistent with changes in species. Based on the amount of change they see and the ages of the fossils, scientists make judgments about the species to which the fossil belongs.

As new discoveries are made, experts' opinions will change, and our evolutionary history may become clearer as old ideas are replaced. Scientists must also review and make changes in the terminology they use to refer to our ancestors. The term *hominin* now refers to humans and their humanlike ancestors, whereas previously the term *hominid* was used. The term *hominid* now refers to the broader group that includes all humanlike organisms plus the great apes—gorillas, orangutans, chimpanzees, and bonobos. When you read material about this topic, you will need to determine how the terms are being used. Although there is no clear picture of how humans evolved, the fossil record shows that humans are a relatively recent addition to the forms of life. Members of the genus *Homo* are believed to have evolved at least 2.2 million to 2.5 million years ago (Table 14.1).

HOW SCIENCE WORKS 14.1

Accumulating Evidence for Evolution

The theory of evolution has become the major unifying theory of the biological sciences. Those in medicine understand the dangers of mutations, the similarity in function of the same organ in related species, and the way in which the environment can interfere with the preprogrammed process of embryological development. Agricultural science has demonstrated the importance of selecting specific genetically determined characteristics for passage into new varieties of crop plants and animals. The concepts of mutation, selection, and evolution are so fundamental to an understanding of what happens in biology that we often forget to take note of the many kinds of observations that support the theory of evolution. The following list describes some of the more important pieces of evidence that support the idea that evolution has been a major force in shaping the nature of living things.

1. Species and populations are not genetically fixed. Change occurs in individuals and populations.
   a. Mutations cause slight changes in the genetic makeup of an individual organism.
   b. Different populations of the same species show adaptations suitable for their local conditions.
   c. Changes in the characteristics displayed by species can be linked to environmental changes.
   d. The selective breeding of domesticated plants and animals indicates that the shape, color, behavior, metabolism, and many other characteristics of organisms can be selected for.
   e. The extinction of poorly adapted species is common.
2. All evidence suggests that, once embarked on a particular evolutionary road, structures, behaviors, or physiological processes are not abandoned, only modified. New organisms are formed by the modification of ancestral species, not by major changes. The following list supports the concept that evolution proceeds by the modification of previously existing structures and processes, rather than by catastrophic change.
   a. All species use the same DNA code.
   b. All species use the same left-handed (levorotary) amino acid building blocks.
   c. It is difficult to eliminate a body part when it is part of a developmental process controlled by genes. A vestigial structure is an organ that is functionless and generally reduced in size. It resembles the fully functioning organs found in related organisms. Structures such as the human appendix, whale pelvic bones, and human tailbone are vestigial structures and evidence of genetic material from previous stages in evolution.
   d. The embryological development of related animals is similar, regardless of the peculiarities of adult anatomy. All vertebrate embryos have an early stage that contains gill-like structures.
   e. Species of organisms that are known to be closely related show greater similarity in their DNA than do those that are distantly related.

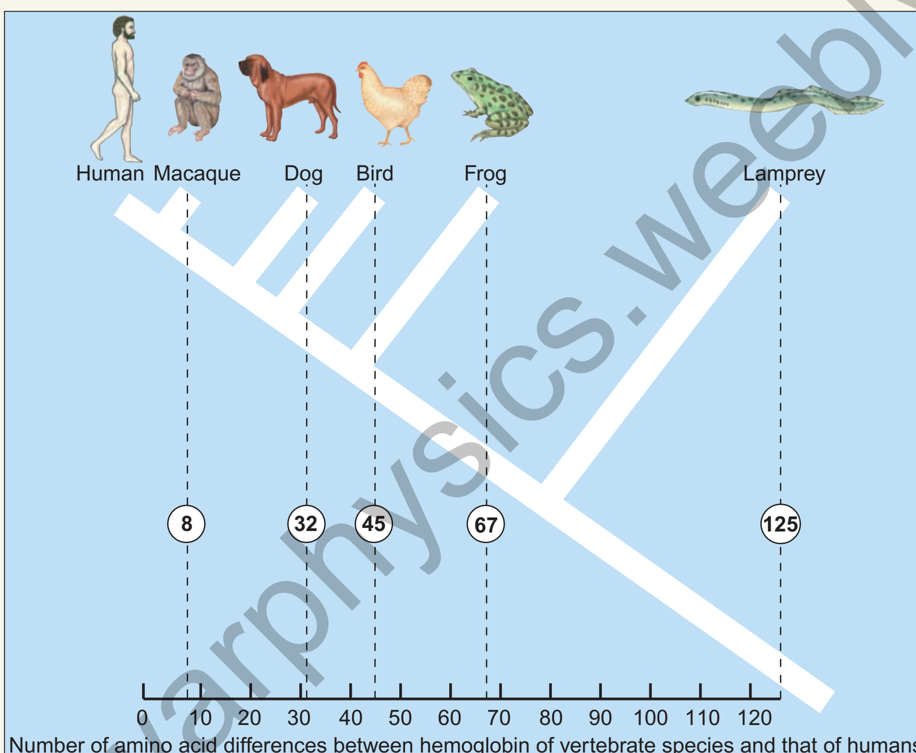
Fossil of sequoia twig

3. Several aspects of the fossil record support the concept of evolution.
   a. The nature of the Earth has changed significantly over time.
   b. The fossil record shows vast changes in the kinds of organisms present on Earth. New species appear and most go extinct. This is evidence that living things change in response to changes in their environment.
   c. The fossils found in old rocks do not reappear in younger rocks. Once an organism goes extinct, it does not reappear, but new organisms arise that are modifications of previous organisms.

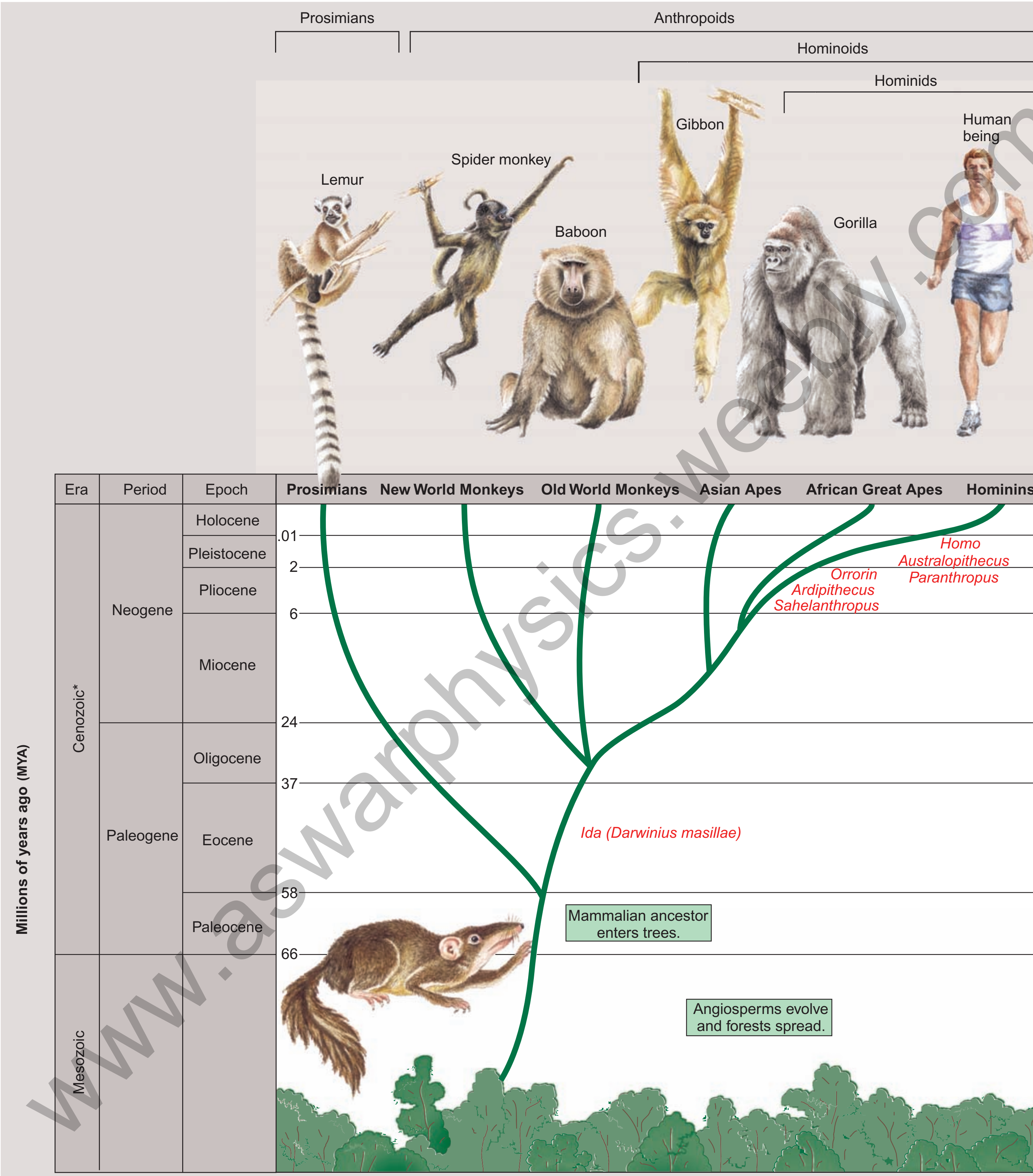
***Archaeopteryx*, fossil skeleton with feathers**

HOW SCIENCE WORKS 14.1 (*Continued*)

4. New techniques and discoveries invariably support the theory of evolution.
   a. The recognition that the Earth was formed billions of years ago supports the slow development of new kinds of organisms.
   b. The recognition that the continents of the Earth have separated helps explain why organisms on Australia are so different from those elsewhere.
   c. The discovery of DNA and how it works helps explain mutation and demonstrates the genetic similarity of closely related species.
   d. Similarities in protein structure can indicate the degree of relatedness among organisms. For example, the greater the evolutionary distance from humans, the greater is the number of amino acid differences in the vertebrate hemoglobin polypeptide.



1. There is a great deal of fossil evidence that several species of the genera *Australopithecus* and *Paranthropus* were common in Africa beginning at about 4 million years ago. These organisms walked upright and are often referred to collectively as australopiths.
2. Based on fossil evidence, it appears that the climate of Africa was becoming drier during much of the time during which the evolution of humans was occurring.
3. The earliest *Australopithecus* fossils are from about 4.2 million years ago. Earlier fossils, such as *Ardipithecus* (which could have included a number of species), *Orrorin*, and *Sahelanthropus* may be ancestral to the genus *Australopithecus*. *Ardipithecus* would most likely be a "distant cousin" to human beings rather than a direct ancestor. *Australopithecus* and *Paranthropus* were herbivores and walked upright. Their fossils and those of earlier organisms, such as *Ardipithecus*, *Orrorin*, and *Sahelanthropus*, are found only in Africa.
4. The australopiths were sexually dimorphic, with the males much larger than the females, and they had relatively small brains (a cranial capacity of 530 cm^3 or less—about the size of a standard softball).
5. Several species of the genus *Homo* became prominent in Africa beginning at about 2.2 million years ago and appear to have made a change from a primarily herbivorous diet to a carnivorous or omnivorous diet.
6. All members of the genus *Homo* have relatively large brains compared with the australopiths. The cranial capacity ranges from about 650 cm^3 for early fossils of *Homo* to about 1,450 cm^3 for modern humans. These organisms are also associated with various degrees of



*Many authorities divide the Cenozoic era into the Tertiary period (contains Paleocene, Eocene, Oligocene, Miocene, and Pliocene) and the Quaternary period (contains Pleistocene and Holocene).

FIGURE 14.12 **Where We Are on the Primate Tree**
As new evidence is uncovered, scientists reconsider how that information best fits into the hypothesis on the evolution of humans. As the pieces of the puzzle are reexamined and rearranged, we see a clearer picture of where human beings fit in the scheme of life.

TABLE 14.1 Primate Classification—Order to Subfamily

Classification Category	Name	Members
Order	Primates (*Primates*)	Prosimians, tarsiers, monkeys, gibbons, orangutans, gorillas, chimps, humans
Suborder	Anthropoidea (*Anthropoid*)	Tarsiers, monkeys, gibbons, orangutans, gorillas, chimpanzee, humans
Superfamily	Hominoidea (*Hominoid*)	Gibbons, orangutans, gorillas, chimps, humans
Family	Hominidae (*Hominid*)	Orangutans, gorillas, chimps, humans
Subfamily	Homininae (*Hominin*)	Humans and direct ancestors

stone tool construction and use. Some of the australopiths may also have constructed stone tools.

7. The fossils of australopiths, several early species of *Homo*, and the fossils of earlier organisms such as *Ardipithecus, Orrorin,* and *Sahelanthropus* are found only in Africa. Fossils of several later species of the genus *Homo* have larger brains and are found in Africa, Europe, and Asia but not in Australia or the Americas. Only *Homo sapiens* is found in Australia and the Americas.
8. Since the fossils of *Homo* species found in Asia and Europe are generally younger than the early *Homo* species found in Africa, it is assumed that species of *Homo* migrated from Africa to Europe and Asia from Africa.
9. Differences in size between males and females are less prominent in the members of the genus *Homo,* so perhaps there were fewer sexual differences in activities than with the australopiths.

When scientists put all these bits of information together, they constructed the following scenario for the likely evolution of our species. Rather than humans evolving from a chimpanzee-like ancestor, chimps and humans evolved from a common primate ancestor. Early primates, ancestors to modern monkeys, chimpanzees, and apes, were adapted to living in forested areas, where their grasping hands, opposable thumbs, big toes, and wide range of shoulder movement, allow them to move freely in the trees. As the climate became drier, grasslands replaced the forests. Early hominins were adapted to drier conditions. Walking upright was probably an adaptation to these conditions. Most later hominins had large brains and used tools. A recent find, however, illustrates just how tentative the understanding of human evolution really is.

The discovery of fossils of a small human—known as the "hobbit"—in the sediments of a cave on an Indonesian island in 2003 has led to much speculation about a possible new species of *Homo*; *Homo floresiensis*. The fossils were dated to about 18,000 years ago. There has been much discussion among scientists about the significance of this discovery. Some feel that the small size indicates a developmental abnormality and that the remains could be that of an abnormally small *H. sapiens*. Others suggest that there are many examples of island animals that show small size and that these fossils were adapted to island conditions. Research continues and a more complete understanding will develop as more information is gathered. Like other human relatives, *H. floresiensis* is extinct. Therefore, *the sole surviving member of our evolutionary line is* Homo sapiens. We are now going to look at several organisms important to understanding the evolution of human beings.

The Genus *Ardipithecus*

Ardipithecus ramidus lived in woodlands and was able to walk upright when on the ground as well as navigate on branches of trees. The fossils from the best-studied site have been aged at about 4.4 million years ago. Studies of these fossils indicate that *Ardipithecus ramidus* was about 120 cm (4 ft) tall when standing, weighed about 50 kg (110 lb), and had a brain capacity of less than 400 cm^3. It was able to walk and run on its hindlimbs but had an opposable big toe and was able to climb and walk on the tops of branches on all fours. Males and females were about the same size. They ate a variety of plant and animal materials in their woodland habitat.

The Genera *Australopithecus* and *Paranthropus*

Both *Australopithecus* and *Paranthropus* are important evolutionary links in understanding our evolutionary past. Various species of *Australopithecus* and *Paranthropus* were present in Africa from about 4.4 million years ago until about 1 million years ago. Various members of these two extinct genera are often referred to as australopiths. *Australopithecus* is the genus to which the famed 3.2 million-year-old "Lucy" belongs, together with a 3.3 million-year-old *A. afarensis*, dubbed "Lucy's baby." Lucy's baby, Selam, is estimated to have been about 3 years of age when she died and is the most complete hominin skeleton ever found. There are few fossils of these early humanlike organisms, however, and many fossils are fragments of organisms. This has led to much speculation and argument among experts about the specific position each fossil has in the evolutionary history of humans. However, from examinations of the fossil bones of the leg, pelvis, and foot, it is apparent that the australopiths were relatively short (males, 1.5 meters or less; females, about 1.1 meters) and stocky and walked upright, as humans do. They had relatively small brains (cranial capacity 530 cm^3 or less—about the size of a standard softball).

An upright posture had several advantages in a world that was becoming drier. It allowed for more rapid movement over long distances and the ability to see longer distances, and it reduced the amount of heat gained from the sun. In addition, upright posture freed the arms for other uses, such as carrying and manipulating objects and using tools. The various species of *Australopithecus* and *Paranthropus* shared these characteristics and, based on the structure of their skulls, jaws, and teeth, appear to have been herbivores with relatively small brains.

The Genus *Homo*

About 2.5 million years ago, the first members of the genus *Homo* appeared on the scene. There is considerable disagreement about how many species there were, but *Homo habilis* is one of the earliest. *H. habilis* had a larger brain (650 cm^3) and smaller teeth than the australopiths and made much more use of stone tools. Some experts feel that it was a direct descendant of *Australopithecus africanus*. Many experts feel that *H. habilis* persisted until about 1.44 million years ago. *H. habilis* made use of group activities, tools, and higher intelligence to take over the kills made by other carnivores. The higher-quality diet would have supported the metabolic needs of the larger brain.

About 1.8 million years ago, *Homo ergaster* appeared. It was much larger, up to 1.6 meters tall, than *H. habilis,* which was about 1.3 meters tall and had a much larger brain (a cranial capacity of 850 cm^3). A little later, a similar species (*Homo erectus*) appeared in the fossil record and for awhile, coexisted with *H. habilis*. Some consider *H. ergaster* and *H. erectus* to be variations of the same species. Along with their larger brains and body size, *H. ergaster* and *H. erectus* are distinguished from earlier species by their extensive use of stone tools. Hand axes were manufactured and used to cut the flesh of prey and crush the bones to obtain the fatty marrow. These organisms appear to have been predators, whereas *H. habilis* was a scavenger. The use of meat as food allows animals to move about more freely, because appropriate food is available almost everywhere. By contrast, herbivores are often confined to places that have foods appropriate to their use: fruits for fruit eaters, grass for grazers, forests for browsers, and so on. In fact, fossils of *H. erectus* have been found in the Middle East and Asia, as well as Africa. Most experts feel that *H. erectus* originated in Africa and migrated through the Middle East to Asia.

At about 800,000 years ago, another hominin, classified as *Homo heidelbergensis,* appeared in the fossil record. Since fossils of this species are found in Africa, Europe, and Asia, it appears that they constitute a second wave of migration of early *Homo* from Africa to other parts of the world. Both *H. erectus* and *H. heidelbergensis* disappeared from the fossil record as two new species (*Homo neanderthalensis* and *Homo sapiens*) become common.

The Neandertals were primarily found in Europe and adjoining parts of Asia and were not found in Africa. Since Neandertals were common in Europe, many people feel Neandertals are descendants of *H. heidelbergensis,* which also was common in Europe and preceded Neandertals (How Science Works 14.2).

Two Points of View on the Origin of *Homo sapiens*

Homo sapiens is found throughout the world and is now the only species remaining of a long line of ancestors. Two theories seek to explain the origin of *Homo sapiens*. One theory, known as the **out-of-Africa hypothesis,** states that modern humans (*Homo sapiens*) originated in Africa, as did several other similar species (figure 14.13). They migrated

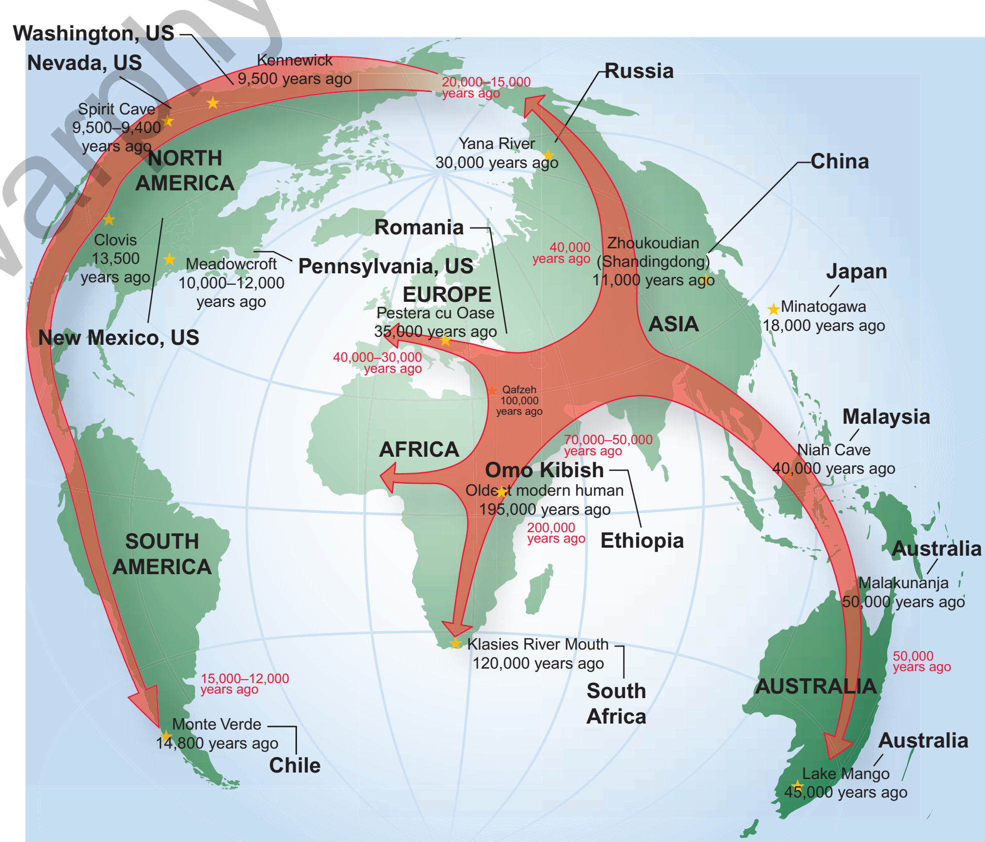


FIGURE 14.13 Out-of Africa Hypothesis
Most scientists favor this explanation on the origin and dispersal of *Homo sapiens* that arose in Africa about 200,000 years ago. The first to leave ventured out some 70,000 to 50,000 years ago, reaching Asia and Australia about 50,000 years ago. Speculation is that they moved into the Americas about 20,000 to 15,000 years ago taking advantage of low sea levels and a land bridge that connect Siberia to Alaska.

HOW SCIENCE WORKS 14.2

Neandertals—*Homo neanderthalensis* or *Homo sapiens*??

An ongoing controversy surrounds the relationship between the Neandertals and other forms of prehistoric humans. One position is that the Neandertals were a small, separate race or subspecies of human that lived in Europe and western Asia from more than 350,000 years ago to about 30,000 years ago. They could have interbred with other humans and may have disappeared because their subspecies was eliminated by interbreeding with more populous, more successful groups. (Many small, remote tribes have been lost as distinct cultural and genetic entities in the same way in recent history.) Others maintain that the Neandertals showed such great difference from other early humans that they must have been a different species and became extinct because they could not compete with more successful *Homo sapiens* immigrants from Africa. (The names of these ancient people typically are derived from the place where the fossils were first discovered. For example, the Neandertals were first found in the Neander Valley of Germany, and the Cro-Magnons, considered to be modern *Homo sapiens*, were initially found in the Cro-Magnon caves in France.)

The use of molecular genetic technology has shed some light on the relationship of the Neandertals to other kinds of humans. Examination of the mitochondrial DNA obtained from the bones of a Neandertal individual reveals that there are significant differences between the Neandertals and other kinds of early humans. This greatly strengthens the argument that the Neandertals were a separate species, *Homo neanderthalensis*.

In 2006, U.S. and German scientists began a two-year project to decipher Neandertals' genetic code. They used samples from a 38,000-year-old Neandertal fossil. They filtered out non-Neandertal DNA that had contaminated the samples following the death of the Neandertal individual. The hope is that this investigation will reveal the genetic differences in cognitive abilities (the process of being aware, knowing, thinking, learning, and judging) between *Homo neanderthalensis* and *H. sapiens*. To date, they have evidence suggesting that Neandertals and modern humans may have interbred, most likely *H. sapiens* fathering children with *H. neanderthalensis* females. Using the latest biotech techniques, scientists have found Neandertal and human genomes are between 99.5% and 99.9% identical. Some researchers believe that the most recent common ancestor of the two human species (*H. sapiens* and *H. neanderthalensis*) lived about 800,000 years ago. Others believe a more recent divergence time, about 465,000 to 569,000 years ago.

Homo neanderthalensis

from Africa to Asia and Europe and displaced species such as *H. erectus* and *H. heidelbergensis*, which had previously migrated into these areas. The other theory, known as the **multiregional hypothesis,** states that *H. erectus* evolved into *H. sapiens*. During a period of about 1.7 million years, fossils of *Homo erectus* showed a progressive increase in the size of the cranial capacity and reduction in the size of the jaw, so it is difficult to distinguish *H. erectus* from *H. heidelbergensis* and *H. heidelbergensis* from *H. sapiens*. Proponents of this hypothesis believe that *H. heidelbergensis* is not a distinct species but, rather, an intermediate between the earlier *H. erectus* and *H. sapiens*. According to this theory, various subgroups of *H. erectus* existed throughout Africa, Asia, and Europe and interbreeding among the various groups gave rise to the various races of humans we see today.

Another continuing puzzle is the relationship of *Homo sapiens* to the Neandertals. Some people consider the Neandertals to be a subgroup of *Homo sapiens* specially adapted to life in the harsh conditions found in postglacial Europe. Others consider them to be a separate species, *Homo neanderthalensis*. The Neandertals were muscular, had a larger brain capacity than modern humans, and had many elements of culture, including burials. The cause of their disappearance from the fossil record at about 25,000 years ago remains a mystery. Perhaps a change to a warmer climate was responsible. Perhaps contact with *Homo sapiens* resulted in their elimination either through hostile interactions or interbreeding with *H. sapiens*, resulting in their absorption into the larger *H. sapiens* population.

Large numbers of fossils of prehistoric humans have been found in all parts of the world. Many of these show evidence of a collective group memory, called *culture*. Cave paintings, carvings in wood and bone, tools of various kinds, and burials are examples. These are also evidence of a capacity to think and invent, as well as "free time" to devote to things other than gathering food and other necessities of life. We may never know how we came to be, but

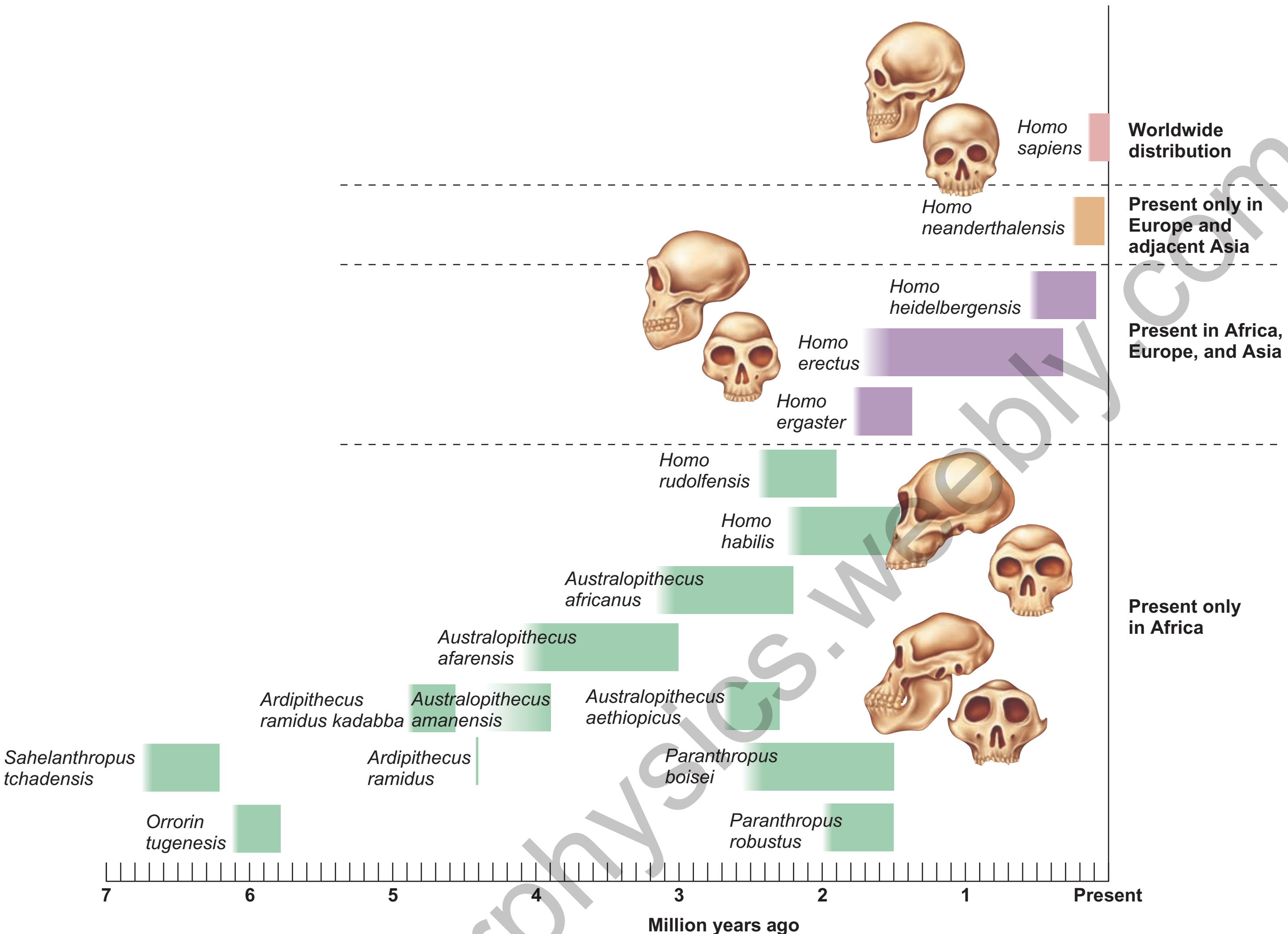


FIGURE 14.14 Human Evolution
This diagram shows the various organisms thought to be relatives of humans. The bars represent approximate times the species are thought to have existed. Notice that (1) all species are extinct today except for modern humans, (2) several species of organisms coexisted for extensive periods, (3) all the older species are found only in Africa, and (4) more recent species of *Homo* are found in Europe and Asia, as well as Africa.

we will always be curious and will continue to search and speculate about our beginnings. Figure 14.14 summarizes the current knowledge of the historical record of humans and their relatives.

14.7 CONCEPT REVIEW

15. List three differences between australopiths and members of the genus *Homo*.
16. Compare the out-of-Africa hypothesis with the multiregional hypothesis of the origin of *Homo sapiens*.
17. Diagram the relationship among anthropoids, hominoids, and hominids.

Summary

Populations are usually genetically diverse. Mutations, meiosis, and sexual reproduction tend to introduce genetic diversity into a population. Organisms with wide geographic distribution often show different gene frequencies in different parts of their range. A species is a group of organisms that can interbreed to produce fertile offspring. The process of speciation usually involves the geographic separation of the species into two or more isolated populations. While they are separated, natural selection operates and each population adapts to its environment. If this generates enough change, the two populations may become so different that they cannot interbreed. Similar organisms that have recently evolved into separate species normally have genetic (reproductive) isolating mechanisms to prevent interbreeding. Some of these are habitat preference, seasonal isolating mechanisms, and behavioral isolating mechanisms. Many plants and some animals have a special way of generating new species by increasing their chromosome numbers as a result of abnormal mitosis or meiosis. Organisms that have multiple sets of chromosomes are called polyploids.

Evolution is basically a divergent process on which other patterns can be superimposed. Adaptive radiation is a very rapid divergent evolution; convergent evolution involves the development of superficial similarities among widely different organisms. The rate at which evolution has occurred probably varies. The fossil record shows periods of rapid change interspersed with periods of little change. This has caused some to look for mechanisms that could cause the sudden appearance of large numbers of new species in the fossil record, which challenge the traditional idea of slow, steady change accumulating enough differences to cause a new species to be formed. The early evolution of humans has been difficult to piece together because of the fragmentary evidence. Beginning about 4.4 million years ago, the earliest forms of *Australopithecus* and *Paranthropus* showed upright posture and other humanlike characteristics. The structure of the jaw and teeth indicates that the various kinds of australopiths were herbivores. *Homo habilis* had a larger brain and appears to have been a scavenger. Several other species of the genus *Homo* arose in Africa. These forms appear to have been carnivores. Some of these migrated to Europe and Asia. The origin of *Homo sapiens* is in dispute. It may have arisen in Africa and migrated throughout the world or evolved from earlier ancestors found throughout Africa, Asia, and Europe.

Key Terms

*Use the interactive flash cards on the **Concepts in Biology**, 14/e website to help you learn the meaning of these terms.*

adaptive radiation 296
analogous structures 299
behavioral isolating mechanisms 294
biochemical isolating mechanisms 294
convergent evolution 298
divergent evolution 295
extinction 296
fossil 291
gene flow 290
geographic isolation 291
gradualism 300
habitat preference (ecological isolating mechanisms) 293
homologous structures 299
hybrid inviability (infertility mechanisms) 294
mechanical (morphological) isolating mechanisms 294
multiregional hypothesis 307
out-of-Africa hypothesis 306
polyploidy 292
punctuated equilibrium 300
reproductive (genetic) isolating mechanisms 293
seasonal isolating mechanisms 293
speciation 291

Basic Review

1. _____ _____ is the movement of genes from one generation to the next as a result of reproduction or from one region to another by migration.
2. A(n) _____ is any remains of an organism of a past geologic age, such as a preserved skeleton or body imprint.
3. Which of the following steps are not necessary for speciation to occur?
   a. geographic isolation
   b. genetic divergence
   c. reproductive isolation
   d. hybrid viability
4. The _____ of an organism is the geographic area over which a species can be found.
   a. range
   b. region
   c. pasture
   d. geographic location
5. If individuals from separate populations overcome the geographic barrier, they may not have accumulated enough _____ to prevent reproductive success.
   a. mutations
   b. genetic differences
   c. barriers
   d. sexual differences
6. _____ is a condition of having multiple sets of chromosomes, rather than the normal haploid or diploid number.
7. Differences in the time of the year at which reproduction takes place are called
   a. geographic isolating mechanisms.
   b. hybrid isolating mechanisms.
   c. seasonal isolating mechanisms.
   d. physical isolating mechanisms.
8. A _____ is a group of organisms that shares a common ancestor with other species, but is set off from those others by having newer, genetically unique traits.

9. The term _____ is now used to refer to humans and their humanlike ancestors.
   a. *hominid*
   b. *anthropoid*
   c. *hominoid*
   d. *hominin*
10. The scientific name for modern human beings is
   a. *Homo habilis*.
   b. *Homo neanderthalensis*.
   c. *H. erectus*.
   d. *Homo sapiens*.
11. Fossil of which small human found in Indonesia are speculated to be a new species of *Homo?*
   a. the "hobbit"
   b. Ida
   c. *Australopithecus* sp.
   d. *Paranthropus* sp.
12. Genetic _____ is a change in the allele frequencies of the isolated subpopulation compared to the rest of the species.
13. The _____ _____ concept is a companion hypothesis to gradualism and suggests a different way of achieving evolutionary change.
14. Which factor will not increase the likelihood that an organism is found in the fossil record?
   a. The soft body parts decompose.
   b. Marine organisms can be covered by sediment on the bottom.
   c. Fossils of more recent organisms are less likely to have been destroyed by geological forces.
   d. Fossils of large organisms are easier to find.
15. _____ structures are similar structures in different species that have been derived from a common ancestor.

Answers
1. Gene flow 2. fossil 3. d 4. a 5. b 6. Polyploidy 7. c 8. species 9. d 10. d 11. a 12. divergence 13. punctuated equilibrium 14. a 15. Homologous

Thinking Critically

Speciation Has Many Dimensions
Explain how all of the following are related to the process of speciation: mutation, natural selection, meiosis, geographic isolation, fossils, continental drift, and gene pool.

CHAPTER 15

Ecosystem Dynamics

The Flow of Energy and Matter

CHAPTER OUTLINE

Fertilizer on Lawns Causes Water Pollution

You may be able to help solve the problem.

In urban areas, lawn care is big business. Millions of dollars are spent annually for fertilizer and pesticides and landscape services to maintain lawns. It is estimated that 15–30% of the fertilizer applied to lawns is washed from the soil and ends up in local streams, ponds, and lakes. Most fertilizers contain nitrogen, phosphorus, and potassium. Of these three components, phosphorus is the most detrimental to aquatic ecosystems because it stimulates the growth of algae and aquatic plants that foul the water and make it unappealing for recreational purposes. Furthermore, in the winter the algae and plants die and decay. The bacteria that bring about their decomposition use oxygen from the water and often lower the oxygen level of the water so much that aquatic animals die from a lack of oxygen.

In order to control pollution of local water bodies in urban areas, the State of Minnesota ("Land of 10,000 Lakes") has passed a law that prohibits the use of phosphorus in fertilizer that is to be applied to lawns. This ban does not extend to agriculture.

- **Can lawns be maintained without the use of fertilizer?**
- **Why does phosphorus stimulate the growth of algae and aquatic plants more than nitrogen?**
- **In order to improve local water quality, would you vote to restrict the use of fertilizer on lawns?**

Background Check

Concepts you should already know to get the most out of this chapter:
- What energy is and how it is related to matter (chapter 2)
- How the atoms of various elements differ in structure (chapter 2)

15.1 What Is Ecology?

People often use the terms *ecology* and *environment* as if they meant the same thing. Students, homeowners, politicians, planners, and union leaders speak of "environmental issues" and "ecological concerns." They speak of products that are "green" or "environmentally friendly" and activities that will do "ecological damage." However, scientists use the terms *ecology* and *environment* in a more restricted way.

Ecology is the branch of biology that studies the relationships between organisms and their environments. This is a very simple definition for a very complex branch of science. Throughout the next four chapters, we will explore many of the aspects of this interesting topic. Because the word *environment* is included in this definition of *ecology,* it is important to have a clear understanding of how an ecologist uses the term. Most ecologists define the word **environment** very broadly as anything that affects an organism during its lifetime. These environmental influences can be divided into two broad categories: biotic environmental factors and abiotic environmental factors.

The field of environmental science is related to ecology. While environmental science is based on ecology, it is an applied science that looks at the impact of humans on their surroundings. Thus, politics, social interactions, economics, and other aspects of human behavior are important aspects of environmental science.

Biotic and Abiotic Environmental Factors

Biotic factors are living things that affect an organism. You are affected by many different biotic factors. Your classmates, disease organisms, the food you eat, and the trees you seek for shade are all biotic factors. **Abiotic factors** are nonliving things that affect an organism. Common abiotic factors are wind, rain, the composition of the atmosphere, minerals in the soil, sunlight, temperature, and elevation above sea level (figure 15.1).

Characterizing the environment of an organism is a complex and challenging process. There are many things to be considered, and everything seems to be influenced or modified by other factors. For example, consider a fish in a stream; many environmental factors are important to its life. The temperature of the water is extremely important as an abiotic factor, but the temperature may be influenced by the presence of trees (biotic factor) along the stream bank that shade the stream and prevent the Sun from heating it. Obviously, the kind and number of food organisms in the stream are important biotic factors as well. The type of material that makes up the stream bottom—mud, sand, or gravel—and the amount of oxygen

(a) Biotic factor (nesting material and tree)

(b) Abiotic factor (wind-driven snow)

FIGURE 15.1 Biotic and Abiotic Environmental Factors
(a) The sticks and branches bald eagles use to build their nest are part of their biotic environment. The pine tree in which this nest is built is also part of the eagle's biotic environment. *(b)* The irregular shape of the tree is the result of wind, an abiotic factor that tends to sandblast one side of the tree and prevent limb growth on that side.

dissolved in the water are other important abiotic factors, both of which are related to how rapidly the water is flowing.

Similarly, a plant is influenced by many factors during its lifetime. The types and amounts of minerals in the soil, the amount of sunlight hitting the plant, and the amount of rainfall are important abiotic factors. The animals that eat the plant and the fungi that cause disease are important biotic factors. Each item on this list can be further subdivided. For instance, because plants obtain water from the soil, rainfall is studied in plant ecology. But even the study of rainfall is not simple. In some places, it rains only during one part of the year; in other places, it rains throughout the year. Some places experience hard, driving rains, whereas others experience long, misty showers. The kind of rainfall affects how much water soaks into the ground—heavy rains tend to run off into streams and be carried away, whereas gentle rain tends to sink into the soil.

Levels of Organization in Ecology

Ecologists study ecological relationships at several levels of organization. Some ecologists focus on what happens to individual organisms and how they interact with their surroundings. Others are interested in groups of organisms of the same species, called **populations,** and how they change. Interacting populations of different species are called **communities,** and community ecologists are interested in how various kinds of organisms interact in a specific location. The highest level of ecological organization is the **ecosystem,** which consists of all the interacting organisms in an area and their interactions with their abiotic surroundings. Figure 15.2 shows how these levels of organization are related to one another.

Understanding the ecological relationships of any species of organism involves the accumulation of large amounts of detailed information about the organism and how it interacts

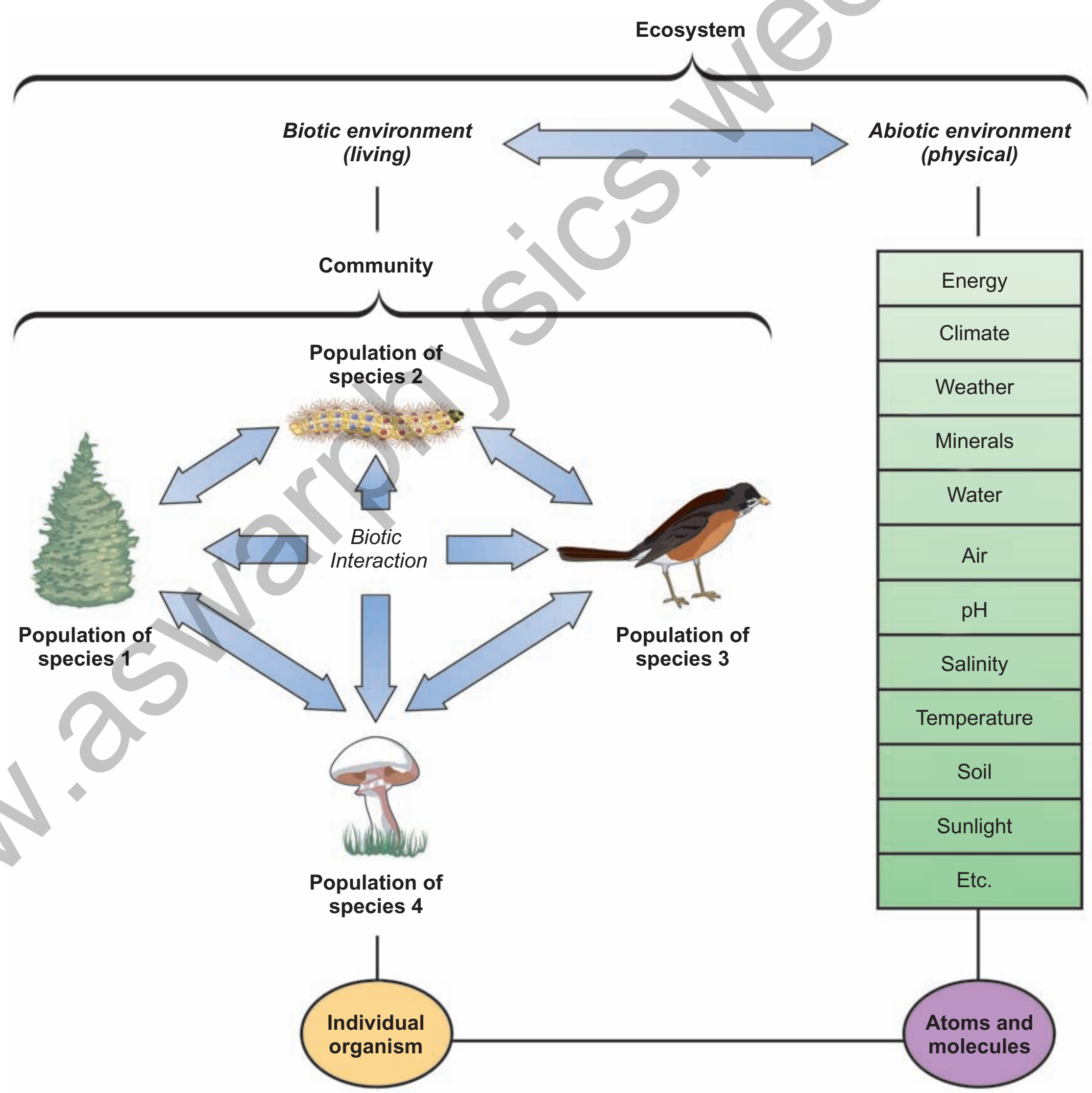


FIGURE 15.2 Levels of Organization in Ecology
Ecology is the branch of biology that studies the interactions between organisms and their environments. This study can take place at several levels, from the broad ecosystem level through community interactions to population studies and the study of individual organisms. Ecology also involves the study of the physical environment, which makes up the nonliving parts of an ecosystem.

with its surroundings. Although this task may seem impossible, ecologists recognize three broad concepts that help simplify the task:

1. Each organism is part of one or more food chains.
2. The organisms in food chains can be separated into functional units called *trophic levels* based on how they obtain energy.
3. It is possible to trace the flow of energy and matter through ecosystems.

15.1 CONCEPT REVIEW

1. List three abiotic factors in the environment of a fish.
2. List three biotic factors in the environment of a songbird.
3. How do an ecosystem, a population, and a community differ?

15.2 Trophic Levels and Food Chains

One of the broad concepts of ecology is that organisms fit into categories, based on how they satisfy their energy requirements. There is a pattern in the way energy moves through an ecosystem. In general, energy flows from the Sun to plants and from plants to animals. However, there are recognizable steps in this flow of energy. Each stage in the flow of energy through an ecosystem is known as a **trophic level.** The series of organisms feeding on one another is known as a **food chain** (figure 15.3).

Producers

Producers are organisms that trap sunlight and use it to produce organic molecules from inorganic molecules through the process of photosynthesis. Green plants and other photosynthetic organisms, such as algae and cyanobacteria, in effect, convert sunlight energy into the energy contained within the chemical bonds of organic compounds. Because producers are the first step in the flow of energy, they occupy the *first trophic level.*

Consumers

Only producers are capable of using sunlight to make organic molecules. All other organisms are directly or indirectly dependent on the organic molecules generated at the producer trophic level to meet their energy needs. Because these organisms must consume organic matter as a source of energy, they are called **consumers.** Consumers can be subdivided into several categories, based on how they obtain food.

Herbivores are animals that obtain energy by eating plants. Because herbivores obtain their energy from eating

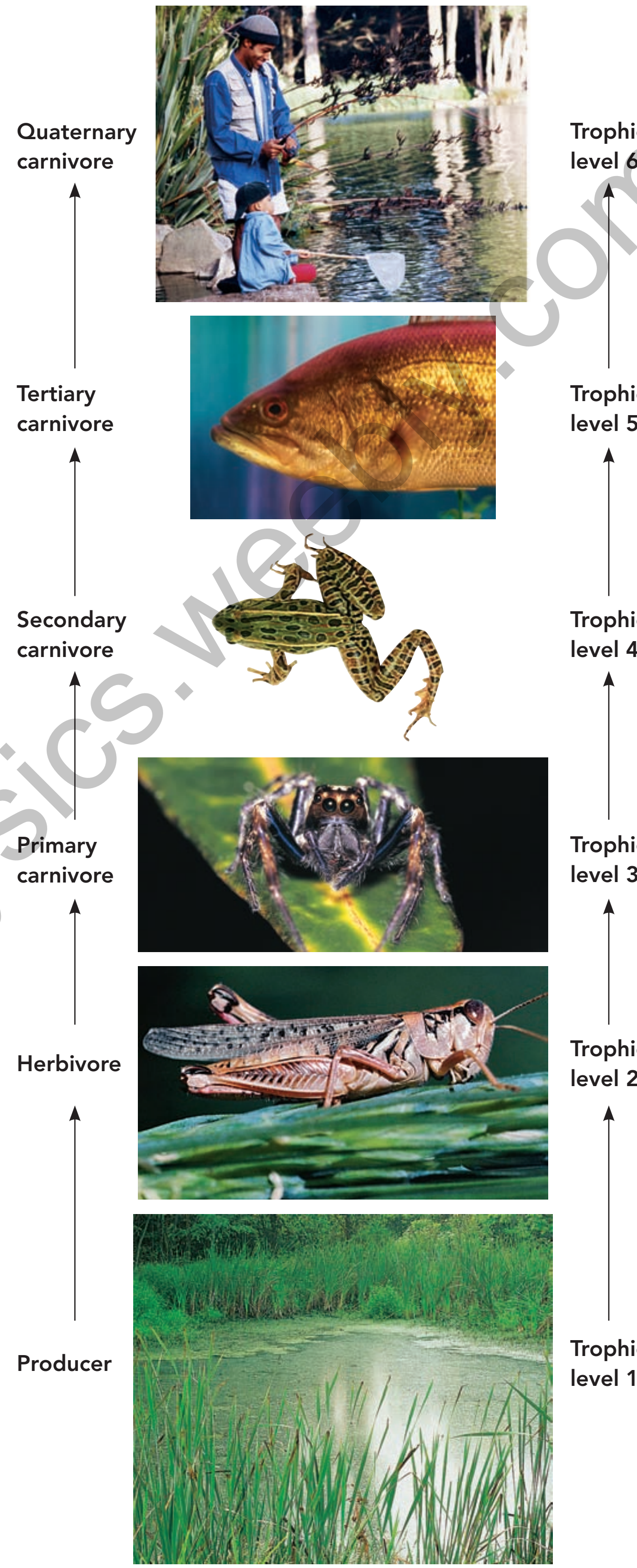


FIGURE 15.3 Trophic Levels in a Food Chain
As one organism feeds on another organism, energy flows from one trophic level to the next. This illustration shows six trophic levels.

plants, they are also called **primary consumers**, and they occupy the *second trophic level*.

Carnivores are animals that eat other animals. They are also referred to as **secondary consumers.** Carnivores can be subdivided into different trophic levels, depending on what animals they eat. Animals that feed on herbivores occupy the *third trophic level* and are known as **primary carnivores.** Animals that feed on the primary carnivores are known as **secondary carnivores,** and they occupy the *fourth trophic level*. For example, a human may eat a fish that ate a frog that ate a spider that ate an insect that consumed plants for food.

Omnivores are animals that have generalized food habits and act as carnivores sometimes and herbivores other times. They are classified into different trophic levels depending on what they are eating at the moment. Most humans are omnivores.

Decomposers

Decomposers are a special category of consumers that obtain energy when they decompose the organic matter of dead organisms and the waste products of living organisms. Decomposers are usually not assigned to a trophic level, because they break down the organic matter produced by all trophic levels. Furthermore, the decomposer category includes a wide variety of organisms, such as bacteria, fungi, and other microorganisms, that feed on one another. Thus, there are food chains of decomposers.

Decomposers efficiently convert nonliving organic matter into simple inorganic molecules, which producers can reuse in the process of trapping energy. Thus, decomposers are very important components of ecosystems that cause materials to be recycled. As long as the Sun supplies the energy, elements are cycled repeatedly through ecosystems. Table 15.1 summarizes the categories of organisms within an ecosystem. Outlooks 15.1 describes changes in food chains that result from the introduction of exotic, invasive species.

15.2 CONCEPT REVIEW

4. Describe two ways that decomposers differ from herbivores.
5. Name an organism that occupies each of the following trophic levels: the producer trophic level, the second trophic level, and the third trophic level.
6. How does each of the following organisms satisfy its energy needs: decomposer, plant, herbivore, omnivore, carnivore?

15.3 Energy Flow Through Ecosystems

The ancient Egyptians constructed elaborate tombs we call *pyramids*. The broad base of the pyramid is necessary to support the upper levels of the structure, which narrows to a point at the top. The same kind of relationship exists for the various trophic levels of ecosystems. Biologists have adopted this pyramid model as a way to think about how ecosystems are organized. Most ecosystems have large quantities of producers, small quantities of herbivores, and still smaller quantities of carnivores. Because this is so common, ecologists have sought reasons to explain the relationship.

Laws of Thermodynamics

Two fundamental physical laws of energy are important when looking at ecological systems from an energy point of view. The first law of thermodynamics states that energy is neither created nor destroyed. That means that we should be able to describe the amounts of energy in each trophic level and follow energy as it flows through successive trophic levels. The second law of thermodynamics states that, when energy is converted from one form to another, some energy escapes to the surroundings as heat. This means that, as

TABLE 15.1 Categories in an Ecosystem

Category	Description	Examples
Producers	Organisms that convert simple inorganic compounds in to complex organic compounds by photosynthesis	Trees, flowers, grasses, ferns, mosses, algae, cyanobacteria
Consumers	Organisms that rely on other organisms as food, animals that eat plants or other animals	
Herbivore	Eats plants	Deer, goose, cricket, vegetarian human, many snails
Carnivore	Eats meat	Wolf, pike, dragonfly
Omnivore	Eats plants and meat	Rat, most humans
Scavenger	Eats food left by others	Coyote, skunk, vulture, crayfish
Parasite	Lives in or on another organism, using it for food	Tick, tapeworm, many insects
Decomposer	Returns organic compounds to inorganic compounds, is an important component in recycling	Bacteria, fungi

OUTLOOKS 15.1

Changes in the Food Chain of the Great Lakes

Many kinds of human activity aid the distribution of species from one place to another. Today there are over 100 exotic species in the Great Lakes. Some, such as smelt, brown trout, and several species of salmon, were purposely introduced. However, most exotic species entered accidentally as a result of human activity.

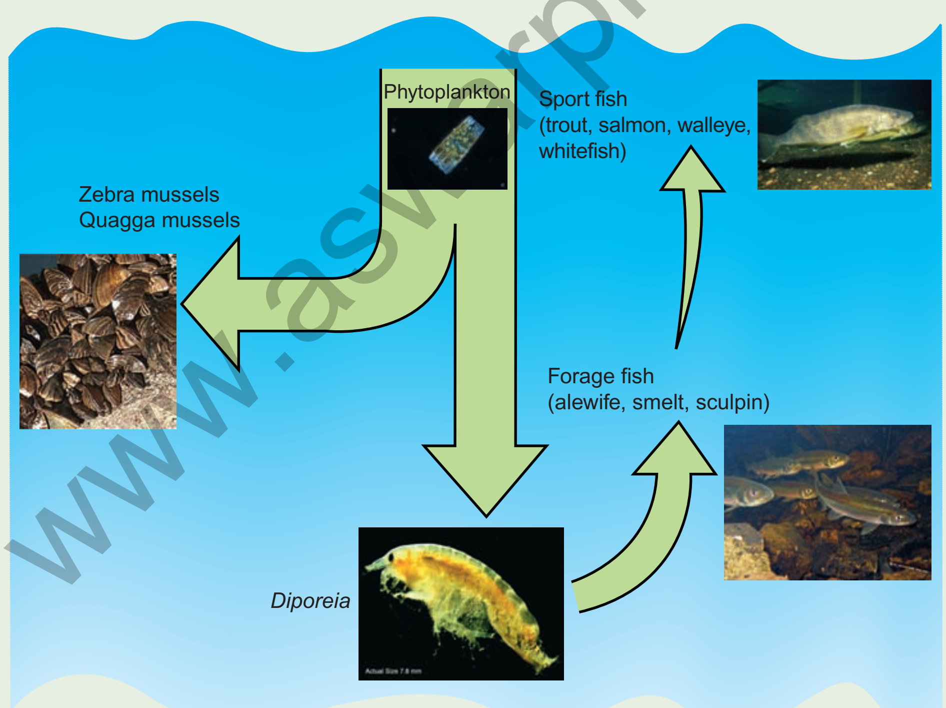
Prior to the construction of locks and canals, the Great Lakes were effectively isolated from invasion of exotic fish and other species by Niagara Falls. Beginning in the early 1800s, the construction of canals allowed small ships to get around the falls. This also allowed some fish species such as the sea lamprey and alewife to enter the Great Lakes. The completion of the St. Lawrence Seaway in 1959 allowed ocean-going ships to enter the Great Lakes. Because of the practice of using water as ballast, ocean-going vessels are a particularly effective means of introducing species. They pump water into their holds to provide ballast when they do not have a full load of cargo. (Ballast adds weight to empty ships to make their travel safer.) Ballast water is pumped out when cargo is added. Since these vessels may add water as ballast in Europe and empty it in the Great Lakes, it is highly likely that organisms will be transported to the Great Lakes from European waters. Some of these exotic species have caused profound changes in the food chain of the Great Lakes.

The introduction of the zebra and quagga mussels is correlated with several changes in the food web of the Great Lakes. Both mussels reproduce rapidly and attach themselves to any hard surface, including other mussels. They are very efficient filter feeders that remove organic matter and small organisms from the water. Measurements of the abundance of diatoms and other tiny algae show that they have declined greatly—up to 90% in some areas where zebra or quagga mussels are common. There has been a corresponding increase in the clarity of the water. In many places, people can see objects two times deeper than they could in the past.

Diporeia is a bottom-dwelling crustacean that feeds on organic matter. Populations of *Diporeia* have declined by 70% in many places in the Great Lakes. Many feel that this decline is the result of a reduction in their food sources, which are being removed from the water by zebra and quagga mussels. Since *Diporeia* is a major food organism for many kinds of bottom-feeding fish, there has been a ripple effect through the food chain. Recently, whitefish that rely on *Diporeia* as a food source have shown a decline in body condition. Other bottom-feeding fish that eat *Diporeia* serve as a food source for larger predator fish and there have been recent declines in the populations and health of some of these predator fish.

Another phenomenon that is correlated with the increase in zebra and quagga mussels is an increased frequency of toxic algal blooms in the Great Lakes. Although there are no clear answers to why this is occurring, two suggested links have been tied to mussels. The clarity of the water may be encouraging the growth of the toxic algae or the mussels may be selectively rejecting toxic algae as food, while consuming the nontoxic algae. Thus, the toxic algae have a competitive advantage.

Finally, wherever zebra or quagga mussels are common, species of native mussels and clams have declined. There may be several reasons for this correlation. First, the zebra and quagga mussels are in direct competition with the native species of mussels and clams. Zebra and quagga mussels are very efficient at removing food from the water and may be out-competing the native species for food. Secondly, since zebra and quagga mussels attach to any hard surface, they attach to native clams, essentially burying them.



A new threat to the Great Lakes involves the potential for exotic Asian carp (bighead and silver carp) to enter through a canal system that connects Lake Michigan at Chicago to the Mississippi River. These and other species of carp were introduced into commercial fish ponds in the southern United States. However, they soon escaped and entered the Mississippi River and have migrated upstream and could easily enter Lake Michigan. Both bighead and silver carp are filter-feeders that consume up to 40% of their body weight in plankton per day. They could have a further impact on the base of the Great Lakes food web, which has already been greatly modified by zebra and quagga mussels.

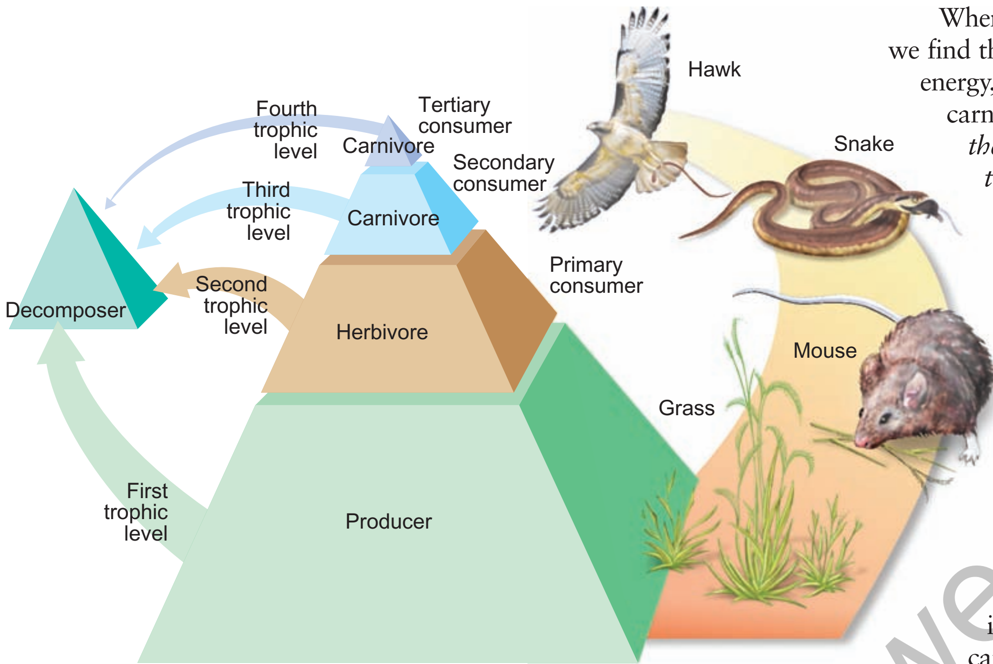


FIGURE 15.4 Energy and Trophic Levels
The producer trophic level has the greatest amount of energy and matter. At each successive trophic level, there is less energy and matter.

energy passes from one trophic level to the next, there is a reduction in the amount of energy in living things and an increase in the amount of heat in their surroundings (figure 15.4).

Think of any energy-converting machine; a certain amount of energy enters the machine and a certain amount of work is done. However, it also releases a great deal of heat energy. For example, an automobile engine must have a cooling system to get rid of the heat energy produced. Similarly, electrical energy is used in an incandescent lightbulb to produce light, but the bulb also produces large amounts of heat. Although living systems are somewhat different, they follow the same energy rules.

The Pyramid of Energy

The energy within an ecosystem can be measured in several ways. One simple way is to collect all the organisms present at any trophic level and burn them. For example, all the plants in a small field (producer trophic level) can be harvested and burned. The number of calories of heat produced by burning is equivalent to the energy content of the organic material collected. Similarly, all the herbivores in the second trophic level could be collected and burned. Then you could compare the amount of heat generated by producers and herbivores and get an idea of how much energy is lost as you go from the producer to the herbivore trophic level.

Another way of determining the energy present is to measure the rate of photosynthesis and respiration of a group of producers. The difference between the rates of respiration and photosynthesis is the amount of energy trapped in the living material of the plants.

When we examine a wide variety of ecosystems, we find that the producer trophic level has the most energy, the herbivore trophic level has less, and the carnivore trophic level has the least. *In general, there is about a 90% loss of energy from one trophic level to the next higher level.* Actual measurements vary from one ecosystem to another. Some may lose as much as 99%, whereas other, more efficient systems may lose only 70%, but 90% is a good rule of thumb. This loss in energy content at the second and subsequent trophic levels is primarily due to the second law of thermodynamics. (Whenever energy is converted from one form to another, some energy is lost to the surroundings as heat.)

In addition to the loss of energy as a result of the second law of thermodynamics, there is an additional loss involved in the capture and processing of food material by herbivores and carnivores. Although herbivores don't need to chase their food, they do need to travel to where food is available, then gather, chew, digest, and metabolize it (figure 15.5). All of these processes require energy. Just as the herbivore trophic level experiences a 90% loss in energy content, the higher trophic levels of primary carnivores, secondary carnivores, and tertiary carnivores also experience a 90% reduction in the energy available to them. Figure 15.6 shows the flow of energy through an ecosystem.

The Pyramid of Numbers

Because it is difficult to measure the amount of energy at any one trophic level of an ecosystem, scientists often use other methods to quantify trophic levels. One method is simply to count the number of organisms at each trophic level. This

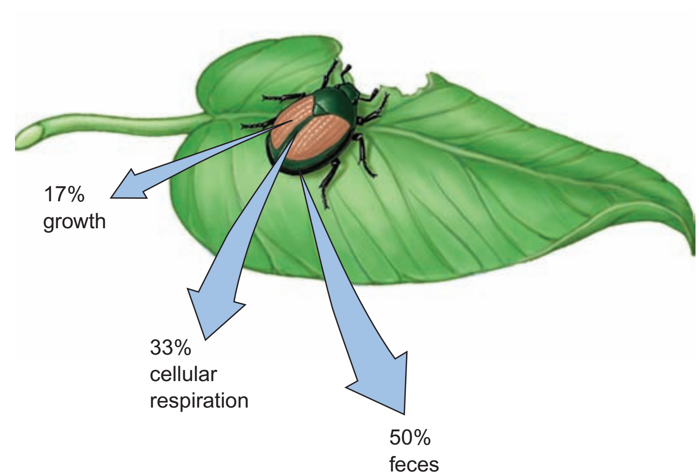


FIGURE 15.5 Energy Losses in an Herbivore
When an insect eats a plant to obtain energy, only a small amount is actually converted to new biological tissue in the insect.

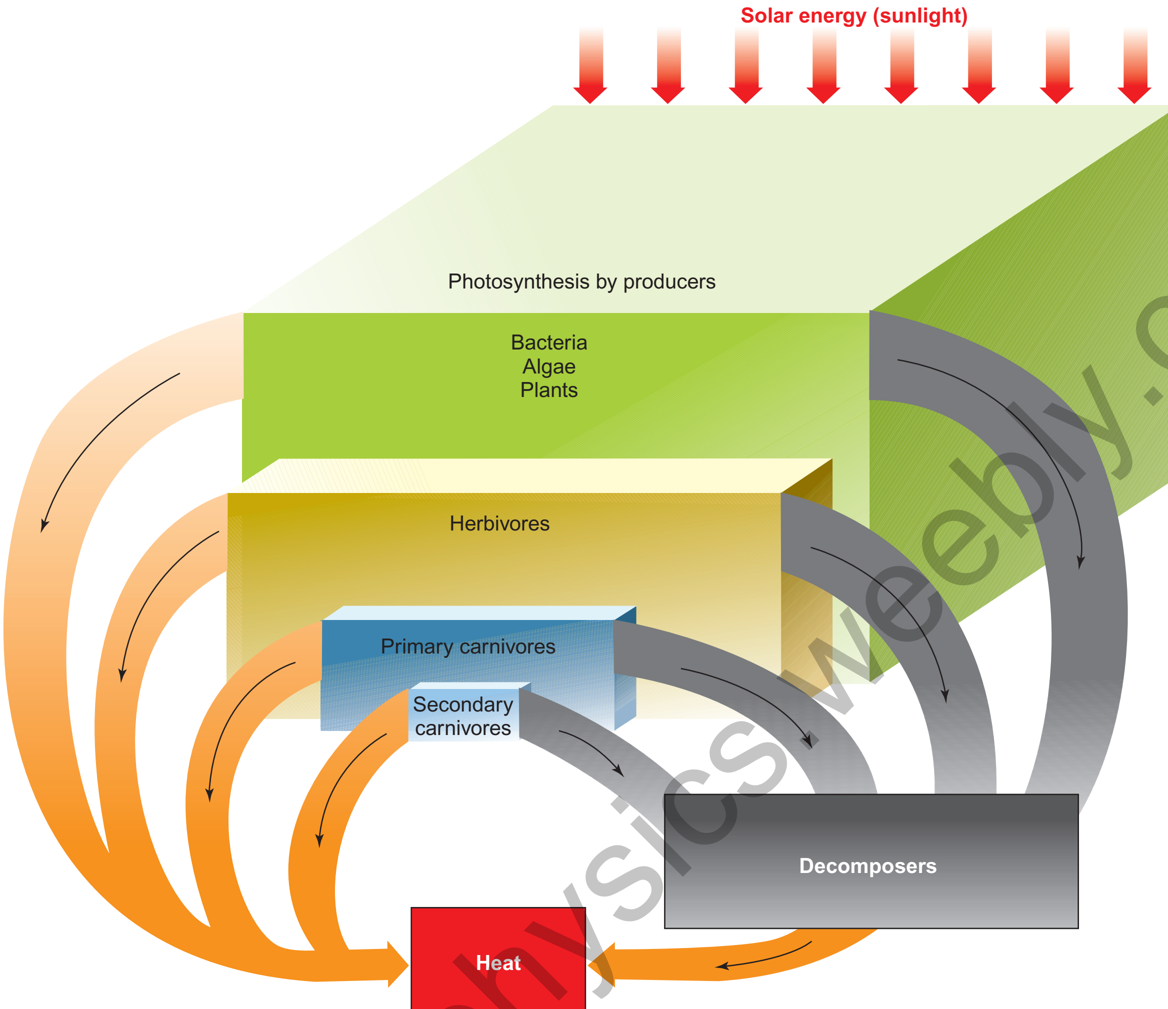


FIGURE 15.6 Energy Flow Through an Ecosystem
Energy from the Sun is captured by organisms that carry on photosynthesis. These are the producers at the first trophic level. As energy flows from one trophic level to the next, approximately 90% of it is lost. This means that the amount of energy at the producer level must be 10 times larger than the amount of energy at the herbivore level. Ultimately, all the energy used by organisms is released to the surroundings as heat.

generally gives the same pyramid relationship, called a *pyramid of numbers* (figure 15.7). This is not a very good method to use if the organisms at the different trophic levels are of greatly differing sizes. For example, if you counted all the small insects feeding on the leaves of one large tree, you would actually get an inverted pyramid.

The Pyramid of Biomass

One way to overcome some of the problems associated with simply counting organisms is to measure the *biomass* at each trophic level. **Biomass** is the amount of living material present; it is usually determined by collecting all the organisms at one trophic level and measuring their dry weight. This eliminates the size-difference problem associated with a pyramid of numbers, because all the organisms at each trophic level are combined and weighed. The *pyramid of biomass* also shows the typical 90% loss at each trophic level.

Although a pyramid of biomass is better than a pyramid of numbers in measuring some ecosystems, it has some shortcomings. Some organisms tend to accumulate biomass over long periods of time, whereas others do not. Many trees live for hundreds of years; their primary consumers, insects, generally live only 1 year. Likewise, a whale is a long-lived animal, whereas its food organisms are relatively short-lived. Figure 15.8 shows two pyramids of biomass.

15.3 CONCEPT REVIEW

7. What is the second law of thermodynamics? Why is it important for understanding energy relationships in ecosystems?
8. Why is the biomass of the herbivore trophic level larger than the biomass of the carnivore trophic level?
9. List an advantage and a disdvantage to using each of the following for characterizing relationships among organisms in an ecosystem: pyramid of energy, pyramid of biomass, and pyramid of numbers.

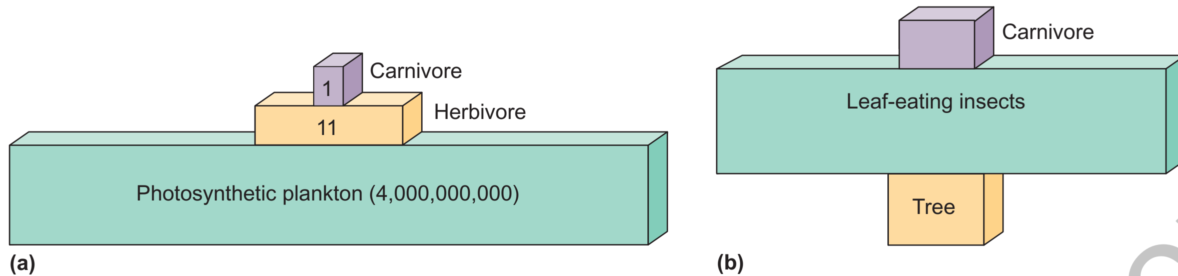


FIGURE 15.7 Pyramid of Numbers
One of the easiest ways to quantify the various trophic levels in an ecosystem is to count the number of individuals in a small portion of the ecosystem. As long as all the organisms are of similar size and live about the same length of time, this method gives a good picture of how the trophic levels are related. *(a)* The relationship among photosynthetic plankton in the ocean, the herbivores that eat them, and the carnivores that eat the herbivores is a good example. However, if the organisms at one trophic level are much larger or live much longer than those at other levels, the picture of the relationship may be distorted. *(b)* This is the relationship between forest trees and the insects that feed on them. This pyramid of numbers is inverted.

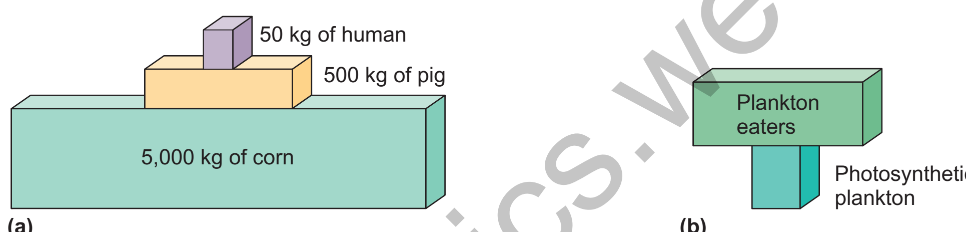


FIGURE 15.8 Pyramid of Biomass
Biomass is determined by collecting and weighing all the organisms in a small portion of an ecosystem. *(a)* This method of quantifying trophic levels eliminates the problem of different-sized organisms at different trophic levels. However, it does not always give a clear picture of the relationship among trophic levels if the organisms have widely different lengths of life. *(b)* For example, in aquatic ecosystems, many of the small producers divide several times per day. The tiny animals (zooplankton) that feed on them live much longer and tend to accumulate biomass over time. The single-celled algae produce much more living material but are eaten as fast as they are produced and, so, do not accumulate a large biomass.

15.4 The Cycling of Materials in Ecosystems—Biogeochemical Cycles

Except for small amounts of matter added to the Earth from cosmic dust and meteorites, the amount of matter that makes up the Earth is essentially constant. However, energy comes to the Earth in a continuous stream as sunlight, and even this is ultimately returned to space as heat energy. It is this flow of energy that drives all biological processes. Living systems use this energy to assemble organic matter and continue life through growth and reproduction. Because the amount of matter on Earth does not change, the existing atoms must be continually reused as organisms grow, reproduce, and die. In this recycling process, photosynthesis is involved in combining inorganic molecules to form the organic compounds of living things. The process of respiration by all organisms breaks down organic molecules to inorganic molecules. Decomposer organisms are particularly important in breaking down the organic remains of waste products and dead organisms. If there were no way of recycling this organic matter back into its inorganic forms, organic material would build up as the bodies of dead organisms.

Deposits of organic material do build up if decomposers are prevented from doing their job. This occurred millions of years ago, when the present deposits of coal, oil, and natural gas were formed. Today, new organic deposits are forming in swamps and bogs where acid conditions or lack of oxygen prevent decomposers from breaking down submerged vegetation.

One way to get an appreciation of how various kinds of organisms interact to cycle materials is to look at a specific kind of atom and follow its progress through an ecosystem. Carbon, nitrogen, oxygen, hydrogen, phosphorus, and many other atoms are found in all living things and are recycled when an organism dies.

The Carbon Cycle

All living things are composed of organic molecules that contain atoms of the element carbon. The **carbon cycle** includes the processes and pathways involved in capturing inorganic carbon-containing molecules, converting them into organic

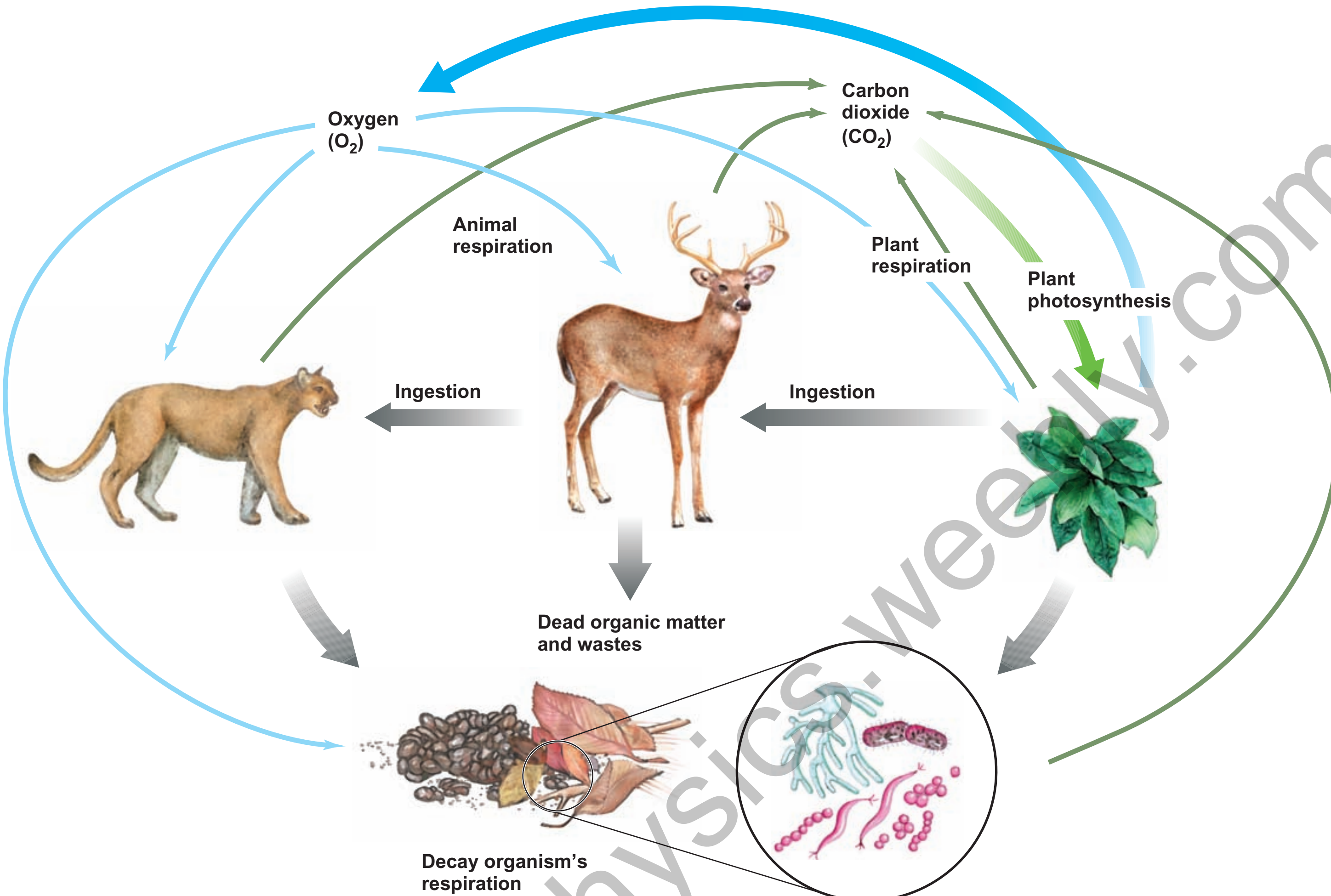


FIGURE 15.9 The Carbon Cycle
Carbon atoms are cycled through ecosystems. Carbon dioxide (green arrows) produced by respiration is the source of the carbon that plants incorporate into organic molecules when they carry on photosynthesis. These carbon-containing organic molecules—carbohydrates, fats, and proteins—(black arrows) are passed to animals when they eat plants and other animals. Organic molecules in waste products or dead organisms are consumed by decomposers. In the process, decomposers break down organic molecules into inorganic molecules. All organisms (plants, animals, and decomposers) return carbon atoms to the atmosphere as carbon dioxide when they carry on cellular respiration. Oxygen (blue arrows) is being cycled at the same time that carbon is. The oxygen is released during photosynthesis and taken up during cellular respiration.

molecules that are used by organisms, and the ultimate release of inorganic carbon molecules back to the abiotic environment (figure 15.9).

The same carbon atoms are used over and over again. In fact, you are not exactly the same person today that you were yesterday. Some of your carbon atoms are different. Furthermore, those carbon atoms have been involved in many other kinds of living things over the past several billion years. Some of them were temporary residents in dinosaurs, extinct trees, or insects, but at this instant, they are part of you. Other organic molecules have become part of fossil fuels.

1. **The Role of Producers**

Carbon and oxygen combine to form the molecule carbon dioxide (CO_2), which is present in small quantities as a gas in the atmosphere and dissolved in water. During photosynthesis, carbon dioxide from the atmosphere is taken into the leaves of plants where it is combined with hydrogen from water molecules (H_2O), which are absorbed from the soil by the roots and transported to the leaves. Many kinds of aquatic organisms such as algae and some bacteria also perform photosynthesis but absorb carbon dioxide and water molecules from the water in which they live. (Actually about 50% of photosynthetic activity on Earth takes place in the oceans due to the activity of algae and photosynthetic bacteria.)

The energy needed to perform photosynthesis is provided by sunlight. As a result of photosynthesis, complex organic molecules such as carbohydrates (sugars) are formed. Producer organisms use these sugars to provide themselves with energy and to make other kinds of organic molecules needed for growth and reproduction. At the same time that carbon is being incorporated into organic molecules, oxygen molecules (O_2) are released into the atmosphere or water—because during the process of photosynthesis, water molecules are split to provide hydrogen atoms necessary to manufacture carbohydrate molecules.

2. **The Role of Consumers**
   Herbivores can use the complex organic molecules of producers as food. When an herbivore eats plants or algae, the complex organic molecules in their food are broken down into simpler organic molecular building blocks, such as simple sugars, amino acids, glycerol, and fatty acids, which then can be reassembled into the specific organic molecules that are part of the herbivore's chemical structure. Thus, the atoms in the herbivore's body can be traced back to the plants it ate. Nearly all organisms also carry on the process of respiration, in which oxygen from the atmosphere is used to break down organic molecules into carbon dioxide and water. Much of the chemical-bond energy released by respiration is lost as heat, but the remainder is used by the herbivore for movement, growth, and other activities.

   In similar fashion, when an herbivore is eaten by a carnivore, some of the carbon-containing molecules of the herbivore become incorporated into the body of the carnivore. The remaining organic molecules are broken down in the process of respiration to obtain energy, and carbon dioxide and water are released.

3. **The Role of Decomposers**
   The organic molecules contained in animal waste products and dead organisms are acted upon by decomposers that use these organic materials as a source of food. The decay process of decomposers involves respiration and releases carbon dioxide and water so that organic molecules are typically recycled. (Many human-made organic compounds—plastics, industrial chemicals, and pesticides—are not readily broken down by decomposers.) How Science Works 15.1 describes how human alteration of the carbon cycle has affected climate.

The Hydrologic Cycle

Water molecules are the most common molecules in living things. Because all the metabolic reactions that occur in organisms take place in a watery environment, within cells or body parts, water is essential to life. During photosynthesis, the hydrogen atoms (H) from water molecules (H_2O) are added to carbon atoms to make carbohydrates and other organic molecules. At the same time, the oxygen atoms in water molecules are released as oxygen molecules (O_2). The movement of water molecules can be traced as a hydrologic cycle (figure 15.10).

Most of the forces that cause water to be cycled do not involve organisms but, rather, are the result of normal physical and geologic processes. Because of the kinetic energy possessed by water molecules, at normal Earth temperatures liquid water evaporates into the atmosphere as water vapor. This can occur wherever water is present; it evaporates from lakes, rivers, soil, and the surfaces of organisms. Because the oceans contain most of the world's water, an extremely large amount of water enters the atmosphere from the oceans.

Water molecules also enter the atmosphere as a result of *transpiration* by plants. **Transpiration** is a process whereby water is lost from leaves through small openings called stomates. The water that is lost is absorbed from the soil into roots and transported from the roots to leaves, where it is used in photosynthesis or evaporates. This movement of water carries nutrients to the leaves, and the evaporation of the water from the leaves assists in the movement of water upward in the stem. Thus, transpired water can be moved from deep layers of the soil to the atmosphere.

Once the water molecules are in the atmosphere, they are moved along with other atmospheric gases by prevailing wind patterns. If warm, moist air encounters cooler temperatures, which often happens over landmasses, the water vapor condenses into droplets and falls as rain or snow. When the precipitation falls on land, some of it runs off the surface, some of it evaporates, and some penetrates into the soil. The water that runs off the surface makes its way through streams and rivers to the ocean. The water in the soil may be taken up by plants and transpired into the atmosphere, or it may become groundwater. Much of the groundwater eventually makes its way into lakes and streams and ultimately arrives at the ocean, from which it originated.

The Nitrogen Cycle

The **nitrogen cycle** involves the cycling of nitrogen atoms between the abiotic and biotic components and among the organisms in an ecosystem. Nitrogen is essential in the formation of amino acids, which are needed to form proteins, and in the formation of nitrogenous bases, which are a part of ATP and the nucleic acids, DNA and RNA. Nitrogen is found as molecules of nitrogen gas (N_2) in the atmosphere. Although nitrogen gas (N_2) makes up approximately 80% of the earth's atmosphere, it is not readily available to most organisms because the two nitrogen atoms are bound very tightly to each other and very few organisms are able to use nitrogen in this form. Since plants and other producers are at the base of nearly all food chains, they must make new nitrogen-containing molecules, such as proteins and DNA. Plants and other producers are unable to use the nitrogen in the atmosphere and must get it in the form of nitrate ($—NO_3$) or ammonia (NH_3).

1. **The Role of Nitrogen-Fixing Bacteria**
   Because atmospheric nitrogen is not usable by plants, nitrogen-containing compounds are often in short supply, and the availability of nitrogen is often a factor

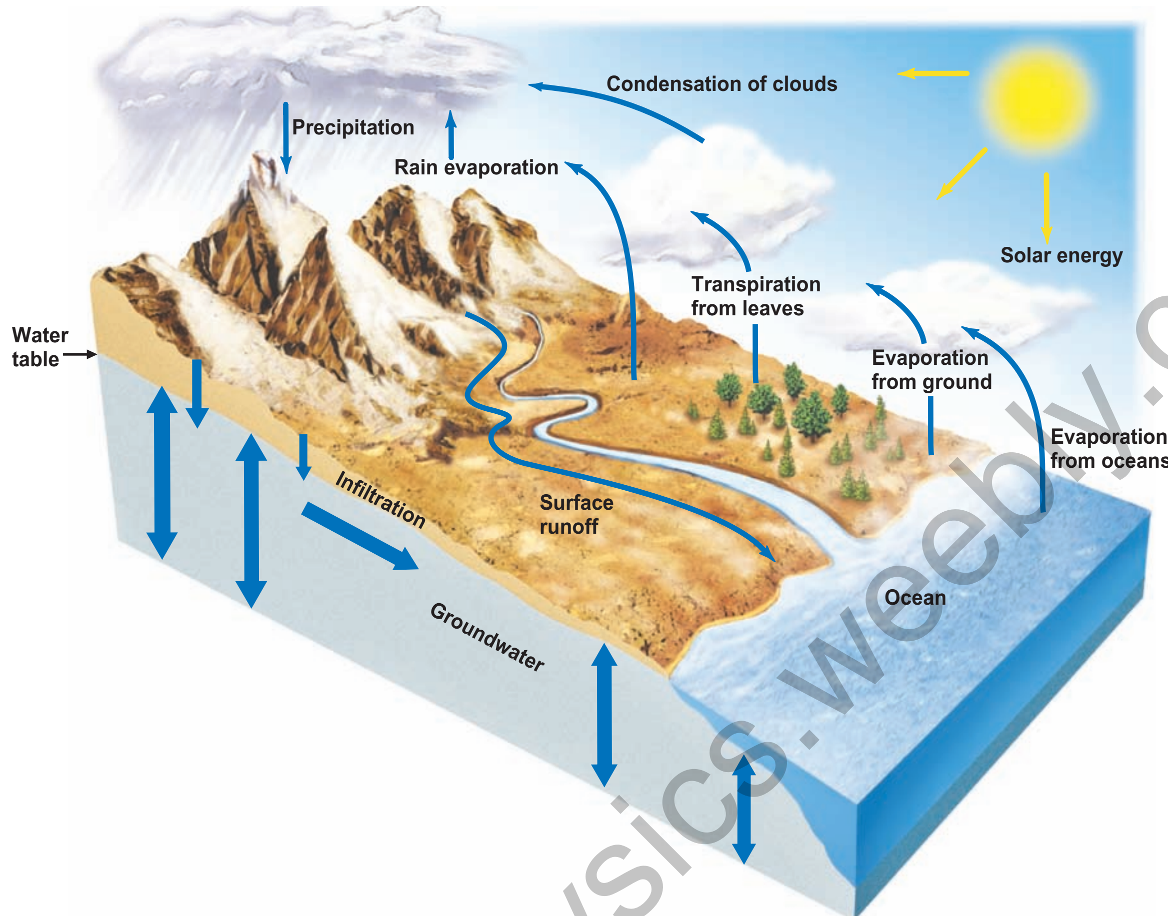


FIGURE 15.10 The Hydrologic Cycle
The cycling of water through the environment follows a simple pattern. Moisture in the atmosphere condenses into droplets, which fall to the Earth as rain or snow. Organisms use some of the water and some of it evaporates from soil and organisms, but much of it flows over the Earth as surface water or through the soil as groundwater. It eventually returns to the oceans, where it evaporates back into the atmosphere to begin the cycle again.

that limits the growth of plants. (Most aquatic ecosystems are limited by the amount of phosphorus rather than the amount of nitrogen.) Certain kinds of soil bacteria are the primary source of the nitrogen-containing molecules plants need to make proteins and DNA.

Some bacteria, called **nitrogen-fixing bacteria,** are able to convert the nitrogen gas (N_2) that enters the soil into ammonia (NH_3) that plants can use. Certain kinds of these bacteria live freely in the soil and are called **free-living nitrogen-fixing bacteria.** Others, known as **symbiotic nitrogen-fixing bacteria,** have a cooperative relationship with certain plants and live in nodules in the roots of plants such as legumes (peas, beans, and clover) and certain trees such as alders. Some grasses and evergreen trees appear to have a similar relationship with certain root fungi that seem to improve the nitrogen-fixing capacity of the plant.

2. **The Role of Producers and Consumers**
Once plants and other producers have nitrogen available in a form they can use, they can construct proteins, DNA, and other important nitrogen-containing organic molecules. When herbivores eat plants, the plant protein molecules are broken down to smaller building blocks called amino acids. These amino acids are then reassembled to form proteins typical for the herbivore. Nucleic acids and other nitrogen-containing molecules are handled similarly. During the animal's manipulation and transformation of amino acids, and some other molecules, some nitrogen is lost in the organism's waste products as ammonia, urea, or uric acid. These same processes occur when carnivores eat herbivores.
3. **The Role of Decomposers and Other Soil Bacteria**
Bacteria and other types of decay organisms are involved in the nitrogen cycle also. Dead organisms and their waste products contain molecules, such as proteins, urea, and uric acid, that contain nitrogen. Decomposers break down these nitrogen-containing organic molecules, releasing ammonia (NH_3), which can be used directly by many kinds of plants. Still other kinds of soil

HOW SCIENCE WORKS 15.1

Scientists Accumulate Knowledge About Climate Change

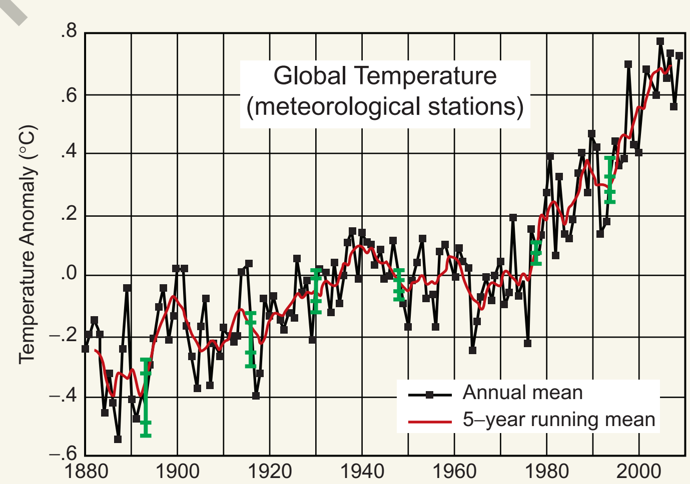
Humans have significantly altered the carbon cycle. As we burn fossil fuels, the amount of carbon dioxide in the atmosphere continually increases. Carbon dioxide allows light to enter the atmosphere but does not allow heat to exit. Because this is similar to what happens in a greenhouse, carbon dioxide and the other gases that have similar effects are called greenhouse gases. Therefore, many scientists are concerned that increased carbon dioxide levels are leading to a warming of the planet, which will cause major changes in our weather and climate.

In science, when a new discovery is made or a new issue is raised, it stimulates a large number of observations and experiments that add to the body of knowledge about the topic. Concerns about global climate change and the role that carbon dioxide plays in causing climate change have resulted in scientists studying many aspects of the problem. This has been a worldwide effort and has involved many different branches of science. This effort has resulted in critical examination of several basic assumptions about climate change, the collection of much new information, and new predictions about the consequences of global climate change.

Several significant studies include:

- Examination of gas bubbles trapped in the ice of glaciers has allowed scientists to measure the amount of carbon dioxide in the atmosphere at the time the ice formed. This provides information about carbon dioxide concentrations prior to human-caused carbon dioxide releases and allows scientists to track the rate of change.
- Long-term studies of the atmosphere at various locations throughout the world show that carbon dioxide levels are increasing.
- Measurements show that sea level is rising almost 2 millimeters per year.
- Measurements of the temperature of the Earth's atmosphere have allowed tracking of temperature. According to NASA, 10 of the warmest years on record occurred in the 12-year period between 1998 and 2009.
- Satellite images of the Arctic Ocean show reduced ice cover.
- Observations of bird migration in Europe document that birds that migrate long distances are arriving in Europe earlier in the spring.
- Many studies of the rate at which different ecosystems take up carbon dioxide have been done to determine if assumptions about the carbon dioxide trapping role of natural ecosystems are correct.
- Warming of the Arctic has resulted in less permafrost.
- Increased water temperatures have been linked to increases in the number and extent of blooms of cyanobacteria in lakes and oceans.
- Studies suggest that an increase in the level of carbon dioxide in the atmosphere could result in increased amounts of dissolved carbon dioxide in the ocean. Increased carbon dioxide will lower the pH of the ocean, which could have a negative effect on animals that make shells.
- Warming of the oceans is linked to more intense hurricanes.
- Earlier arrival of spring is linked to increased numbers and intensity of forest fires in the western United States.

The United Nations established the Intergovernmental Panel on Climate Change (IPCC)—a panel of scientists, political leaders, and economists—to analyze the large amount of information generated on the topic of climate changes. The IPCC has issued several reports about the nature, causes, and the impacts of climate change on ecosystems and culture.



Graph from NASA

bacteria, called **nitrifying bacteria,** are able to convert ammonia to nitrite ($—NO_2$), which can be converted by other bacteria to nitrate ($—NO_3$). The production of nitrate is significant because plants can use nitrate as a source of nitrogen for synthesis of nitrogen-containing organic molecules.

Finally, bacteria known as **denitrifying bacteria** are, under conditions where oxygen is absent, able to convert nitrite to nitrogen gas (N_2), which is ultimately released into the atmosphere. Atmospheric nitrogen can reenter the cycle with the aid of nitrogen-fixing bacteria.

4. **Unique Features of the Nitrogen Cycle**

Although a cyclic pattern is present in both the carbon cycle and the nitrogen cycle, the nitrogen cycle shows two significant differences. First, most of the difficult chemical conversions are made by bacteria and other microorganisms. Without the activities of bacteria, little nitrogen would be available and the world would be a very different place. Second, although nitrogen is made available to organisms by way of nitrogen-fixing bacteria and returns to the atmosphere through the actions of denitrifying bacteria, there is a secondary loop in the cycle that recycles nitrogen compounds from dead organisms and wastes directly back to producers. Figure 15.11 summarizes the roles of various organisms in the nitrogen cycle.

5. **Agriculture and the Nitrogen Cycle**
In naturally occurring soil, nitrogen is often a limiting factor of plant growth. To increase yields, farmers provide extra sources of nitrogen in several ways. Inorganic fertilizers are a primary method of increasing the nitrogen available. These fertilizers may contain ammonia, nitrate, or both.

Since the manufacture of nitrogen fertilizer requires a large amount of energy and uses natural gas as a raw material, fertilizer is expensive. Therefore, farmers use alternative methods to supply nitrogen and reduce their cost of production. Several different techniques are effective. Farmers can alternate nitrogen-yielding crops such as soybeans with nitrogen-demanding crops such as corn. Since soybeans are legumes that have symbiotic nitrogen-fixing bacteria in their roots, if soybeans are planted one year, the excess nitrogen left in the soil can be

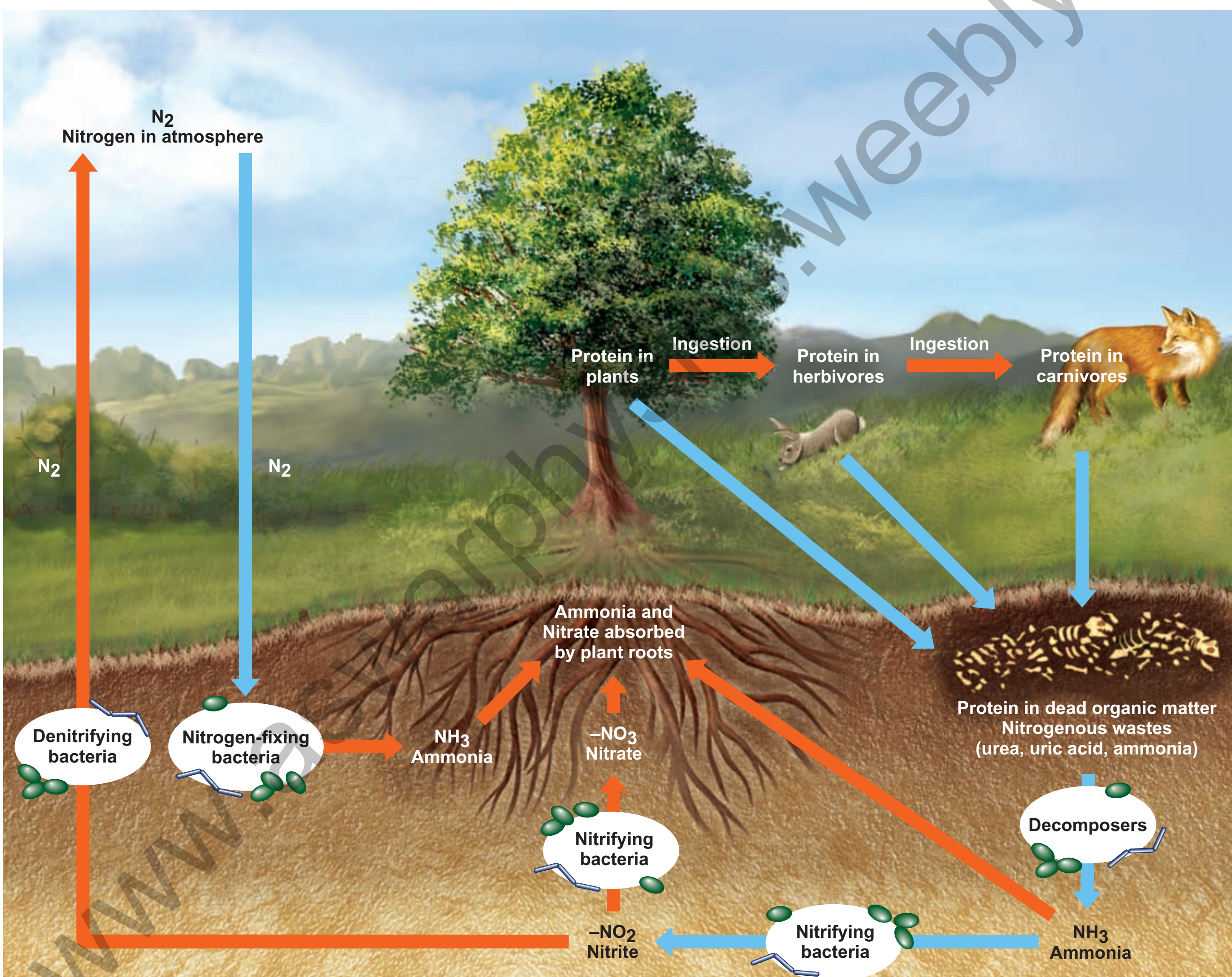


FIGURE 15.11 The Nitrogen Cycle
Nitrogen atoms are cycled through ecosystems. Atmospheric nitrogen is converted by nitrogen-fixing bacteria to nitrogen-containing compounds, which plants can use to make proteins and other compounds. Proteins are passed to other organisms when one organism is eaten by another. Dead organisms and their waste products are acted upon by decay organisms to form ammonia, which can be reused by plants and converted to other nitrogen compounds by nitrifying bacteria. Denitrifying bacteria return nitrogen as a gas to the atmosphere.

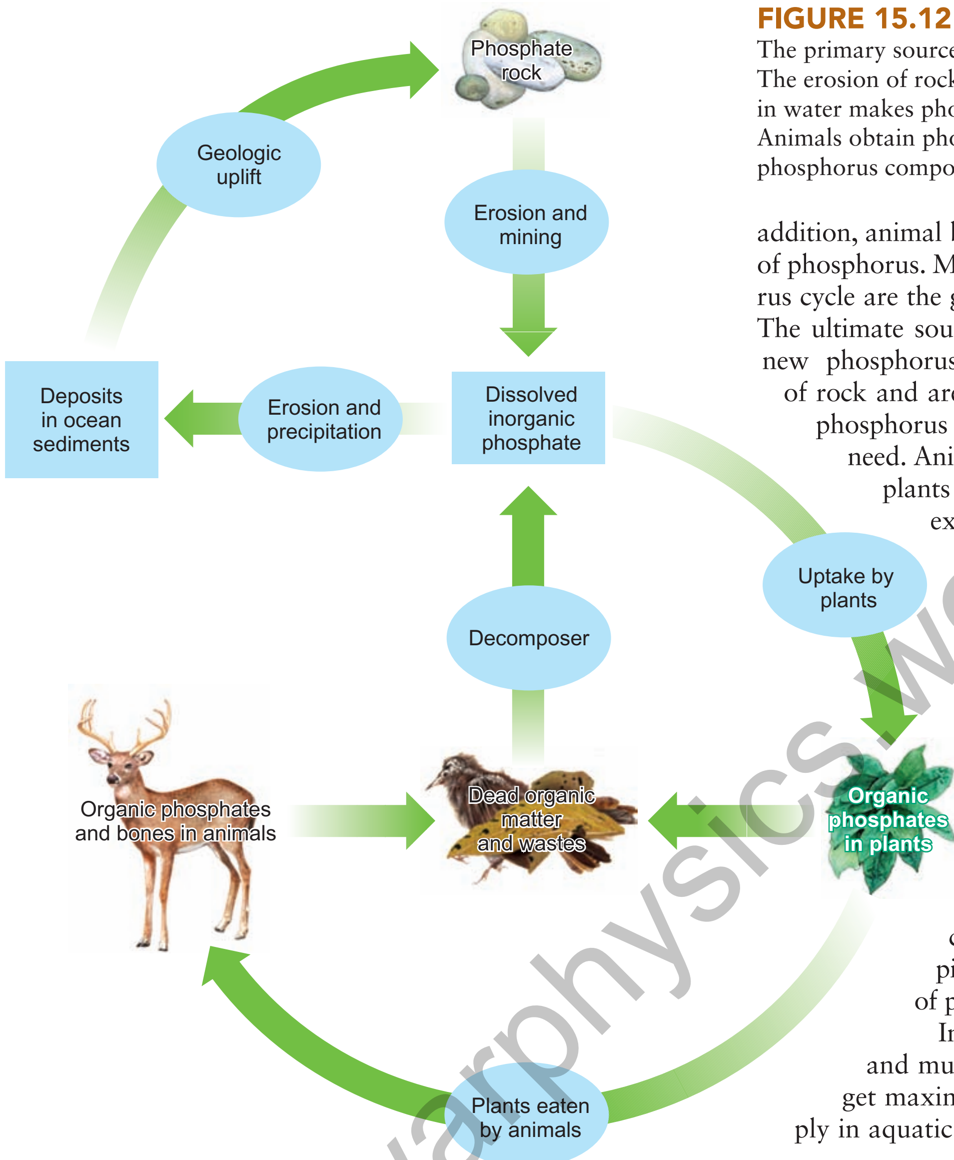


FIGURE 15.12 The Phosphorus Cycle
The primary source of phosphorus is phosphorus-containing rock. The erosion of rock and the dissolving of phosphorus compounds in water makes phosphorus available to the roots of plants. Animals obtain phosphorus in their food. Decomposers recycle phosphorus compounds back into the soil.

used by the corn plants grown the next year. Some farmers even plant alternating strips of soybeans and corn in the same field. A slightly different technique involves growing a nitrogen-fixing crop for a short period of time and then plowing the crop into the soil and letting the organic matter decompose. The ammonia released by decomposition serves as fertilizer to the crop that follows. This is often referred to as green manure. Farmers can also add nitrogen to the soil by spreading manure from animal production operations or dairy farms on the field and relying on the soil bacteria to decompose the organic matter and release the nitrogen for plant use.

The Phosphorus Cycle

Phosphorus is another atom common in the structure of living things. It is present in many important biological molecules, such as DNA, and in the membrane structure of cells. In addition, animal bones and teeth contain significant quantities of phosphorus. Most of the processes involved in the phosphorus cycle are the geologic processes of erosion and deposition. The ultimate source of phosphorus atoms is rock. In nature, new phosphorus compounds are released by the erosion of rock and are dissolved in water. Plants use the dissolved phosphorus compounds to construct the molecules they need. Animals obtain phosphorus when they consume plants or other animals. When an organism dies or excretes waste products, decomposer organisms recycle the phosphorus compounds back into the soil, where they can be reused.

Phosphorus compounds that are dissolved in water are ultimately precipitated as mineral deposits. This has occurred in the geologic past and typically has involved deposits in the oceans. Geologic processes elevate these deposits and expose them to erosion, thus making phosphorus available to organisms. Animal wastes often have significant amounts of phosphorus. In places where large numbers of seabirds or bats have congregated for hundreds of years, their droppings (called *guano*) can be a significant source of phosphorus for fertilizer (figure 15.12).

In many soils, phosphorus is in short supply and must be provided to crop plants in fertilizer to get maximum yields. Phosphorus is also in short supply in aquatic ecosystems.

Nutrient Cycles and Geologic Time

The nutrient cycles we have just discussed act on a short-term basis in which elements are continually being reused among organisms and on a long-term basis in which certain elements are tied up for long time periods and are not part of the active nutrient cycle. In our discussion of the phosphorus cycle it was mentioned that the source of phosphorus is rock. While phosphorus moves rapidly through organisms in food chains, phosphorus ions are not very soluble in water and tend to precipitate in the oceans to form sediments that eventually become rock on the ocean floor. Once this has occurred, it takes the process of geologic uplift followed by erosion to make phosphorus ions available to terrestrial ecosystems. Thus, we can think of the ocean as a place where phosphorus is removed from the active nutrient cycle (this situation is known as a *sink*).

There are also long-term aspects to the carbon cycle. Organic matter in soil and sediments are the remains of once-living organisms. Thus, these compounds constitute a sink for carbon, particularly in ecosystems in which decomposition is slow (tundra, northern forests, grasslands, swamps, marine sediments). These materials can tie up carbon for hundreds to thousands of years. Fossil fuels (coal, petroleum, and natural gas), which were also formed from the remains or organisms, are a longer-term sink that involves hundreds of millions of years. The carbon atoms in fossil fuels at one time were part of the active carbon cycle but were removed from the active cycle when the organisms accumulated without decomposing. The organisms that formed petroleum and natural gas are thought to be the remains of marine organisms that got covered by sediments. Coal was formed from the remains of plants that were buried by sediments. Once the organisms were buried, their decomposition would be slowed, and heat from the Earth and pressure from the sediments helped to transform the remains of living things into fossil fuels. The carbon atoms in fossil fuels have been locked up for hundreds of millions of years. Thus, the formation of fossil fuels was a sink for carbon atoms.

Oceans are a major carbon sink. Carbon dioxide is highly soluble in water. Many kinds of carbonate sedimentary rock are formed from the precipitation of carbonates from solution in oceans. In addition, many marine organisms form skeletons or shells of calcium carbonate. These materials accumulate on the ocean floor as sediments that over time can be converted to limestone. Limestone typically contains large numbers of fossils. The huge amount of carbonate rock is an indication that there must have been higher amounts of carbon dioxide in the Earth's atmosphere in the past.

Since fossil fuels are the remains of once-living things and living things have nitrogen as a part of protein, nitrogen that was once part of the active nitrogen cycle was removed when the fossil fuels were formed. In ecosystems in which large amounts of nonliving organic matter accumulates (swamps, humus in forests, and marine sediments), nitrogen can be tied up for relatively long time periods. In addition, some nitrogen may be tied up in sedimentary rock and, in some cases, is released with weathering. However, it appears that the major sink for nitrogen is as nitrogen in the atmosphere. Nitrogen compounds are very soluble in water, so when sedimentary rock is exposed to water, these materials are dissolved and reenter the active nitrogen cycle.

15.4 CONCEPT REVIEW

10. Trace the flow of carbon atoms through a community that contains plants, herbivores, decomposers, and parasites.
11. Describe four roles that bacteria play in the nitrogen cycle.
12. Describe the flow of water through the hydrologic cycle.
13. List three ways the carbon and nitrogen cycles are similar and three ways they differ.
14. Describe the major processes that make phosphorus available to plants.

15.5 Human Use of Ecosystems

The extent to which humans use an ecosystem is tied to its *productivity.* **Productivity** is the rate at which an ecosystem can accumulate new organic matter. Because plants are the producers, it is their activities that are most important. Ecosystems in which the conditions are the most favorable for plant growth are the most productive. Warm, moist, sunny areas with high levels of nutrients in the soil are ideal. Some areas have low productivity because one of these essential factors is missing. Deserts have low productivity because water is scarce, arctic areas because temperature is low, and the open ocean because nutrients are in short supply. Some terrestrial ecosystems, such as forests and grasslands, have high productivity. Aquatic ecosystems, such as marshes and estuaries, are highly productive, because the waters running into them are rich in the nutrients that aquatic photosynthesizers need. Furthermore, these aquatic systems are usually shallow, so that light can penetrate through most of the water column.

The Conversion of Ecosystems to Human Use

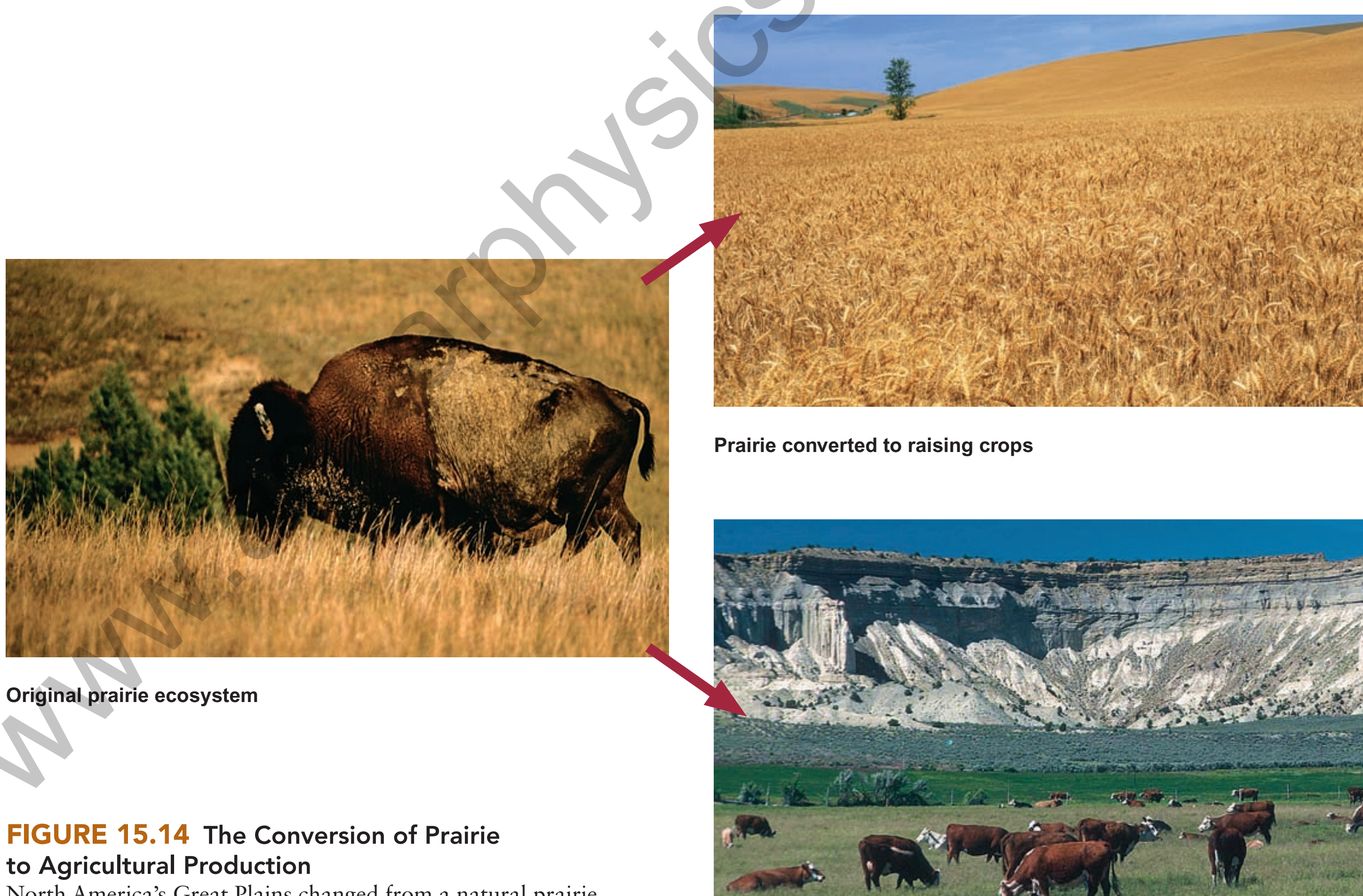
The way humans use ecosystems has changed dramatically over the past several thousand years. Initially, humans fit into ecosystems as just another consumer. These kinds of societies are known as hunter-gatherer societies because they collect food and other needed materials directly from the plants and animals that are a natural part of the ecosystem. There are still examples of peoples who live this way (figure 15.13).

However, the development of agriculture has changed how humans interact with other organisms in ecosystems. We have altered certain ecosystems substantially to increase productivity for our own purposes. In so doing, we have destroyed the original ecosystem, with all of its complexity, and have replaced it with a simpler agricultural ecosystem. In addition, many of the crops we plant are not native to the region. For example, nearly all of the Great Plains region of North America has been converted to agriculture. The original ecosystem included the Native Americans, who used buffalo and other plants and animals as a source of food. There was much grass, many buffalo, and few humans. Therefore, in the Native Americans' pyramid of energy, the base was more than ample. However, with the exploitation and settling of America, the population in North America increased at a rapid rate. The food chain (prairie grass–buffalo–human) could no longer supply the food needs of the growing population. Because wheat and corn yield more biomass for humans than the original prairie grasses could, the settlers' domestic grain and cattle replaced the prairie grass and buffalo. This was fine for the settlers, but devastating for the buffalo and Native Americans (figure 15.14). In similar fashion, the deciduous forests of the East were cut down and

FIGURE 15.13 A Hunter-Gatherer
This Australian aboriginal hunter functions as a carnivore and uses the natural ecosystem as a source of energy and materials.

burned to provide land for crops. The crops were able to provide more food than did harvesting game and plants from the forest.

Associated with modern agriculture is the use of fertilizer and other agricultural chemicals. Fertilizers usually contain nitrogen, phosphorus, and potassium compounds. The numbers on a fertilizer bag indicate the percentage of each in the fertilizer. For example, a 6-24-24 fertilizer has 6% nitrogen, 24% phosphorus, and 24% potassium compounds. In addition to nitrogen, phosphorus, and potassium, other elements including calcium, magnesium, sulfur, boron, copper, and zinc are cycled within ecosystems. In an agricultural ecosystem, these elements are removed when the crop is harvested. Therefore, farmers must not only return the nitrogen, phosphorus, and potassium to the soil but also analyze for other, less-prominent elements and add them to their fertilizer mixture. Aquatic ecosystems are also sensitive to nutrient levels. High levels of nitrates or phosphorus compounds often result in the rapid growth of aquatic producers. In aquaculture, such as that used to raise catfish, fertilizer is added to the body of water to stimulate the production of



Original prairie ecosystem

Prairie converted to raising crops

Prairie converted to grazing livestock

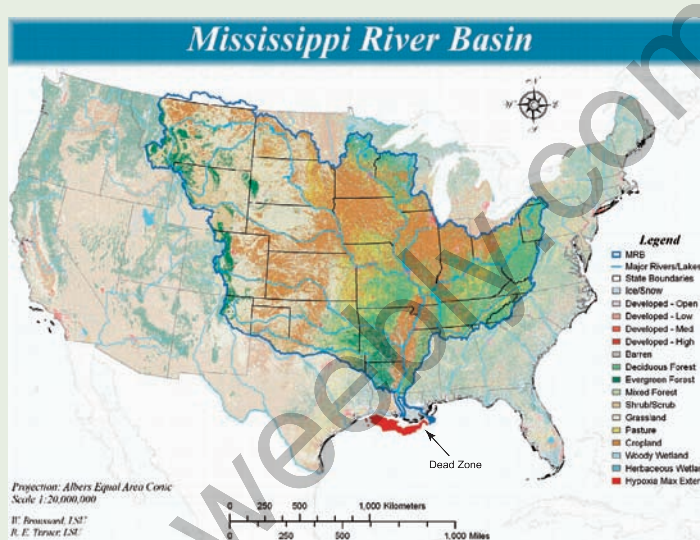
FIGURE 15.14 The Conversion of Prairie to Agricultural Production
North America's Great Plains changed from a natural prairie ecosystem to an agricultural ecosystem either for raising crops or for grazing livestock.

OUTLOOKS 15.2

Dead Zones

Dead zones are regions of the ocean bottom that have little or no oxygen dissolved in the water. Throughout the world there are about 400 such zones; most located near the mouths of rivers. Two things contribute to the development of dead zones: poor mixing of the water in the area and an input of nutrients from rivers. Rivers carry nutrients from the lands they drain and the nutrients stimulate the growth of phytoplankton (microscopic, single-celled, photosynthetic organisms) in the upper regions of the water column. When these organisms die they sink to the bottom where bacteria bring about their decay. The bacteria use oxygen from the water in the decay process and the amount of oxygen falls. As the oxygen level falls, animals are stressed. Those that are able to swim or crawl leave the area, and those that cannot, die. The result is an area on the ocean floor that is devoid of life.

Dead zones typically develop in the summer months when the water is warm. The combination of warm water and abundant nutrients results in rapid growth of phytoplankton. It appears that the primary source of the excess nutrients is related to the way humans use the land drained by rivers. Fertilizer from agriculture and lawns runs off the land into streams and rivers. Animal waste from cattle feedlots, hog farms, and chicken-raising facilities is often spread on land as fertilizer and washes into streams and rivers. Other animal waste enters streams as a result of poorly designed containment lagoons that fail. Nutrients from human wastes can also enter from sewage treatment plants. All of these sources of nutrients contribute to the problem. A major dead zone develops every year in the Gulf of Mexico near the mouth of the Mississippi River. Most years the area affected is about the size of the state of New Jersey.



Approximate dead zone in the Gulf of Mexico.

The problem is not just of concern to those worried about the environmental impact. It is important economically, since large dead zones impact commercial and recreational fishing.

algae, which is the base of most aquatic food chains (see Outlooks 15.2).

Many ecosystems, particularly the drier grasslands, cannot support the raising of crops. However, they can still be used as grazing land to raise livestock. Like the raising of crops, grazing often significantly alters the original grassland ecosystem. Some attempts have been made to harvest native species of animals from grasslands, but the primary species raised on grasslands are domesticated cattle, sheep, and goats. The substitution of the domesticated animals displaces the animals that are native to the area and alters the kinds of plants present, particularly if too many animals are allowed to graze.

Even aquatic ecosystems have been significantly altered by human activity. The Food and Agriculture Organization of the United Nations states that nearly all the fisheries of the world are being fished at capacity or overfished. Overfishing in many areas of the ocean has resulted in the loss of some important commercial species. For example, the codfishing industry along the East Coast of North America has been destroyed by overfishing.

The Energy Pyramid and Human Nutrition

Anywhere in the world the human population increases, natural ecosystems are replaced with agricultural ecosystems. In many parts of the world, the human demand for food is so large that it can be met only if humans occupy the herbivore trophic level, rather than the carnivore trophic level. Humans are omnivores able to eat both plants and animals as food, so they have a choice. However, as the size of the human population increases, it cannot afford the 90% loss that occurs when plants are fed to animals that are in turn eaten by humans. In much of the less-developed world, the primary food is grain; therefore, the people are already at the herbivore level. It is only in the developed countries that people can afford to eat large quantities of meat. This is true from both an energy point of view and a monetary point of view. Meat, fish, poultry and other sources of animal protein are more expensive than grains. (Most of the corn raised in the United States is used as cattle feed). Figure 15.15 shows a pyramid of biomass having a producer base of 100 kilograms of grain. The second trophic level has only 10 kilograms of cattle because of the 90% energy loss typical when energy is transferred from one trophic level to the next. The consumers at the third trophic level—humans, in this case—experience a similar 90% loss. Therefore, only 1 kilogram of humans can be sustained by the two-step energy transfer. There has been a 99% loss in energy: 100 kilograms of grain are necessary to sustain 1 kilogram of humans. Because much of the world's population is already feeding at the second trophic level, we cannot expect food production to increase to the extent that we could feed 10 times as many people as exist today.

It is difficult for most people to fulfill all their nutritional needs by eating only grains. Although protein is available from plants, the concentration is greater from animal sources and people who rely primarily on plants for food often experience protein deficiency. People in major parts of Africa and Asia have diets that are deficient in both calories and protein. These people have very little food, and what food they do have is mainly from plant sources. These are also the parts of the world where human population growth is the most rapid. In other words, these people are poorly nourished, and as the population increases they will probably experience greater calorie and protein deficiency. It is important to realize that currently there is enough food in the world to feed everyone, but it is not distributed equitably for a variety of reasons. The primary reasons for starvation are political and economic. Wars and civil unrest disrupt the normal food-raising process. People leave their homes and migrate to areas unfamiliar to them. Poor people and poor countries cannot afford to buy food from the countries that have a surplus.

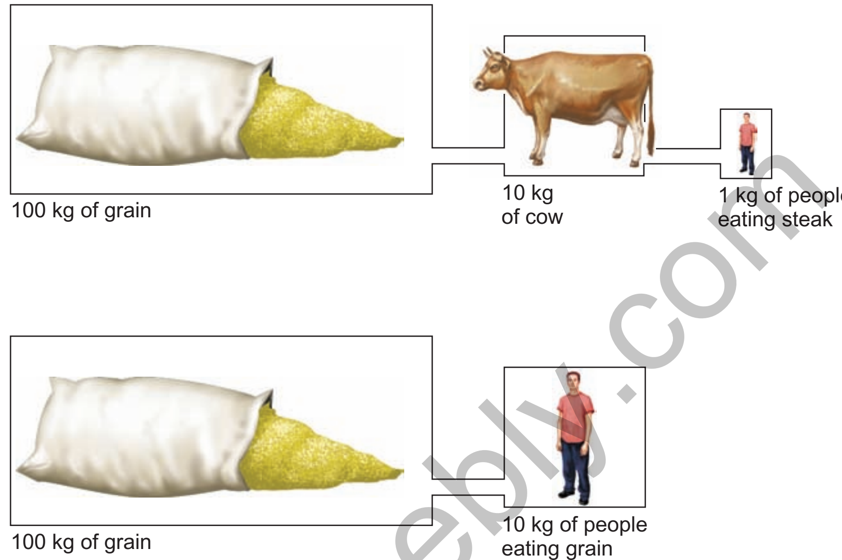


FIGURE 15.15 Human Pyramids of Biomass
Because approximately 90% of the energy is lost as energy passes from one trophic level to the next, more people can be supported if they eat producers directly than if they feed on herbivores. Much of the less-developed world is in this position today. Rice, corn, wheat, and other producers provide most of the food for the world's people.

15.4 CONCEPT REVIEW

15. Explain why poor people in countries with limited food must eat primarily grains. Explain this from both an economic and ecological point of view.
16. Define the term *productivity*.
17. What is the primary reason for humans destroying natural ecosystems like prairies and deciduous forests?

Summary

Ecology is the study of how organisms interact with their environment. The environment consists of biotic and abiotic components, which are interrelated in an ecosystem. All ecosystems must have a constant input of energy from the Sun. Producer organisms are capable of trapping the Sun's energy, through photosynthesis, and converting it into the energy in biomass. Consumers (herbivores, carnivores, and omnivores) eat other organisms. Herbivores feed on producers and are, in turn, eaten by carnivores, which may be eaten by other carnivores. Each level in the food chain is known as a trophic level. Other kinds of organisms involved in food chains are omnivores, which eat both plant and animal food, and decomposers, which break down dead organic matter and waste products.

All ecosystems have a large producer base with successively smaller amounts of energy at the herbivore, primary carnivore, and secondary carnivore trophic levels. This is because, each time energy passes from one trophic level to the next, about 90% of the energy is lost from the ecosystem.

The amount of matter in the world does not change but, rather, is recycled. The carbon cycle involves the processes of photosynthesis and respiration in the cycling of carbon through ecosystems. Water is essential to living things, most of the cycling of water involves the physical processes of evaporation and condensation. The nitrogen cycle relies on the activities of nitrogen-fixing bacteria, nitrifying bacteria, and decomposers to cycle nitrogen through ecosystems. The phosphorus cycle involves the deposition of phosphorus-containing compounds into oceans and the geologic processes of uplift and erosion to make phosphorus available to organisms.

Humans use ecosystems to provide themselves with necessary food and raw materials. As the human population increases, most people will be living as herbivores at the second trophic level, because they cannot afford to lose 90% of the energy by first feeding it to an herbivore, which they then eat. Humans have converted most productive ecosystems to agricultural production and continue to seek more agricultural land as populations increase.

Key Terms

*Use the interactive flash cards on the **Concepts in Biology, 14/e** website to help you learn the meaning of these terms.*

abiotic factors 312
biomass 318
biotic factors 312
carbon cycle 319
carnivores 315
community 313
consumers 314
decomposers 315
denitrifying bacteria 323
ecology 312
ecosystem 313
environment 312
food chain 314
free-living nitrogen-fixing bacteria 322
herbivores 314
nitrifying bacteria 323
nitrogen cycle 321
nitrogen-fixing bacteria 322
omnivores 315
population 313
primary carnivores 315
primary consumers 315
producers 314
productivity 326
secondary carnivores 315
secondary consumers 315
symbiotic nitrogen-fixing bacteria 322
transpiration 321
trophic level 314

Basic Review

1. Which one of the following is an abiotic factor?
   a. a nest in a tree
   b. the water in a pond
   c. the producers in an ecosystem
   d. the fish in a pond
2. Which one of the following categories of organisms has the largest total energy and biomass?
   a. eagles, which eat fish
   b. herbivores, which eat plants
   c. organisms that carry on photosynthesis
   d. fish that eat insects
3. The carbon that plants need for photosynthesis comes from _____.
4. Symbiotic nitrogen-fixing bacteria
   a. live in association with the roots of certain plants.
   b. convert ammonia to nitrate.
   c. are found in the atmosphere.
   d. are rare.
5. The process of absorbing water from the soil and releasing it from leaves is called _____.
6. In the phosphorus cycle, phosphorus enters plants through the roots. (T/F)
7. When energy flows from one trophic level to the next, about _____ percent of the energy is lost.
8. An herbivore is at the second trophic level. (T/F)
9. Nitrogen is important in which one of the following organic molecules?
   a. sugars
   b. fats
   c. water
   d. proteins
10. Decomposers break down organic matter and release _____ and _____.
11. Which one of the following is a producer?
    a. earthworm
    b. algae
    c. yeast
    d. fungus
12. Which of the following populations in an ecosystem would have the highest biomass?
    a. insect-eating birds
    b. fish-eating birds
    c. fungi
    d. plants
13. A vegetarian is at the _____ trophic level.
14. Which of the following is the largest conceptual unit?
    a. ecosystem
    b. community
    c. decomposers
    d. producers
15. Humans have altered most ecosystems of the world. (T/F)

Answers
1. b 2. c 3. carbon dioxide 4. a 5. transpiration 6. T 7. 90% 8. T 9. d 10. carbon dioxide and water. 11. b 12. d 13. herbivore 14. a 15. T

Thinking Critically

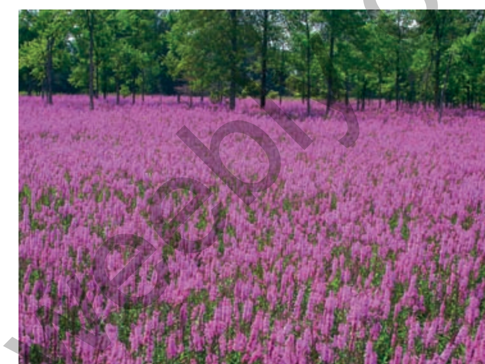
Understanding Interrelationships
Construct a diagram on a piece of paper that includes the following items to show their levels of interaction. Which is the most important item? Which items are dependent on others?

People are starving.
Commercial fertilizer production requires temperatures of 900°C.
Geneticists have developed plants that grow very rapidly and require high amounts of nitrogen to germinate during the normal growing season.
Fossil fuels are stored organic matter.
The rate of the nitrogen cycle depends on the activity of bacteria.
The sun is expected to last for several million years.
Crop rotation is becoming a thing of the past.
The clearing of forests for agriculture changes the weather in the area.

CHAPTER 16

Community Interactions

CHAPTER OUTLINE



Alien Invasion

Scientists concerned about survival of native plants.

Yard and garden centers often sell plant species that are not native to the area in which you live. Furthermore, homeowners often want unusual plants that are particularly colorful or have other striking characteristics. Some of these exotic plants are invasive. They have characteristics such as fruits or seeds that are easily spread from place to place. When this occurs, the exotic plant may become a pest because it competes with local native plants and replaces them, causing local extinctions of native species.

In the United States, there are many examples of exotic invasive species. Glossy buckthorn and autumn olive have replaced understory species in forests of the Northeast. Tamarisk (salt cedar) has become a dominant species along rivers in the Southwest. Brazilian pepper and *Melaleuca* have become major problems in south Florida. Kudzu (a vine) and water hyacinth have become significant problems in areas of the South. Purple loosestrife (see photo) has taken over wetlands in many areas of the northern parts of the United States and southern parts of Canada.

- **What are the invasive exotic species found in your area?**
- **Why do some exotic species spread so rapidly?**
- **Should the kinds of plants you select to plant in your yard be regulated by state laws and/or local ordinances?**

Background Check

Concepts you should already know to get the most out of this chapter:
- The nature of food chains (chapter 15)
- The role of natural selection in shaping the evolution of organisms (chapter 13)

16.1 The Nature of Communities

Scientists approach the study of ecological interactions in different ways. For example, in chapter 15, we looked at ecological relationships from the point of view of ecosystems and the way energy and matter flow through them. But we can also study relationships at the community level and focus on the kinds of interactions that take place among organisms. Recall that a community consists of all the populations of different kinds of organisms that interact in a particular location.

Defining Community Boundaries

One of the first things a community ecologist must do is determine the boundaries of the community to be studied. A small pond is an example of a community with easily determined natural boundaries (figure 16.1). The water's edge naturally defines the limits of this community. We would expect to find certain animals and plants living in the pond, such as fish, frogs, snails, insects, algae, pondweeds, bacteria, and fungi. But you might ask at this point, What about the plants and animals that live at the water's edge? Are they part of the pond community? Or what about great blue herons that catch fish and frogs in the pond but build nests atop some tall trees away from the pond? Or should we include in this community the ducks that spend the night but fly off to feed elsewhere during the day? Should the deer that comes to the pond to drink at dusk be included? What originally seemed to be a clear example of a community has become less clear-cut.

The point of this discussion is that all community boundaries are artificial. However, defining boundaries—even if they are artificial—is important, because it allows us to focus on the changes that occur in a particular area, recognize patterns and trends, and make predictions.

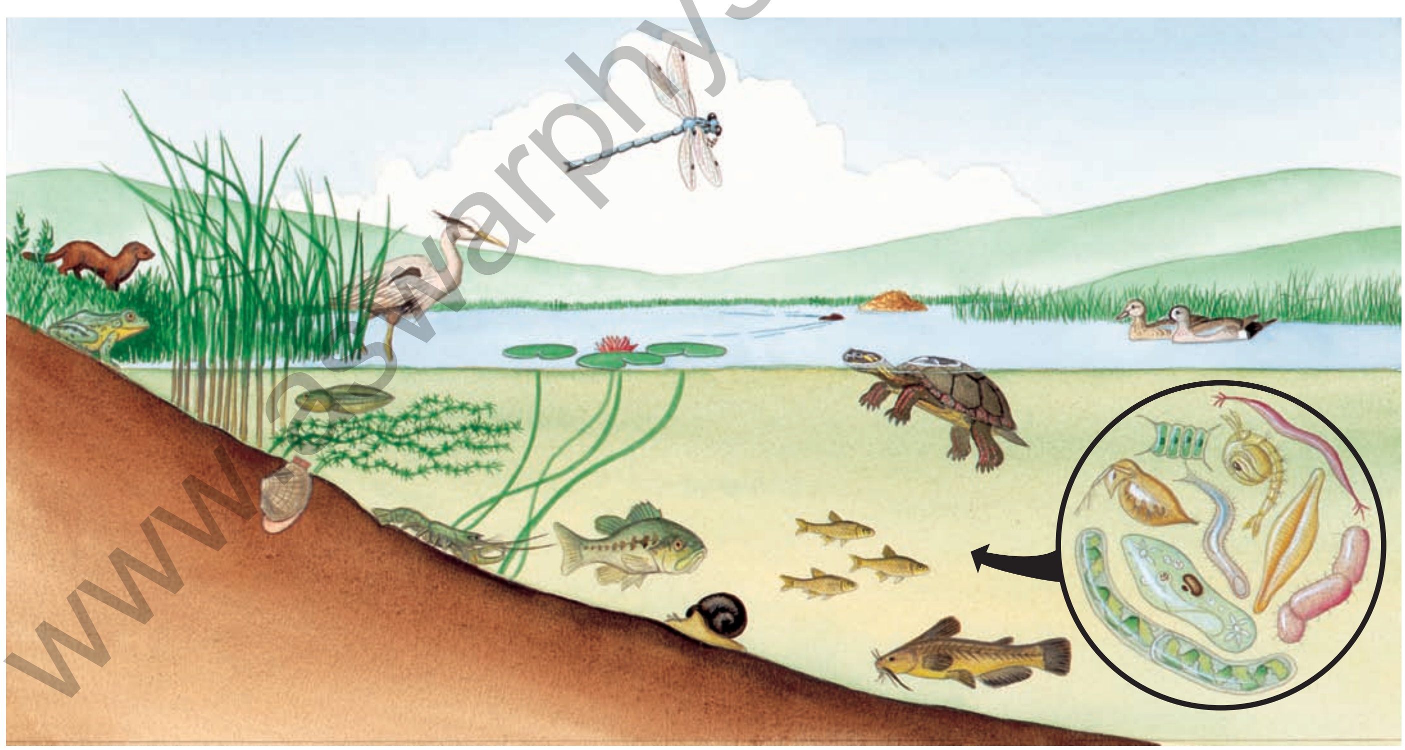


FIGURE 16.1 A Pond Community
Although a pond seems an easy community to characterize, it interacts extensively with the surrounding land-based communities. Some of the organisms associated with a pond community are always present in the water (e.g., fish, pondweeds, clams); others occasionally venture from the water to the surrounding land (e.g., frogs, dragonflies, turtles, muskrats); still others are occasional or rare visitors (e.g., minks, heron, ducks).

Complexity and Stability

Each community has a particular combination of producers, consumers, and decomposers, which interact in many ways. Within the community, each species is a specialist in certain aspects of community function. One of the ways that organisms interact is by feeding on one another. Most organisms in a community participate in several food chains. When we recognize that many food chains in an area overlap, we see a pattern of interactions we can call a **food web** (figure 16.2).

One of the common features of such a complex set of interrelationships is that natural communities are relatively stable. This stability allows us to identify and name various kinds of communities. In fact, there is a relationship between

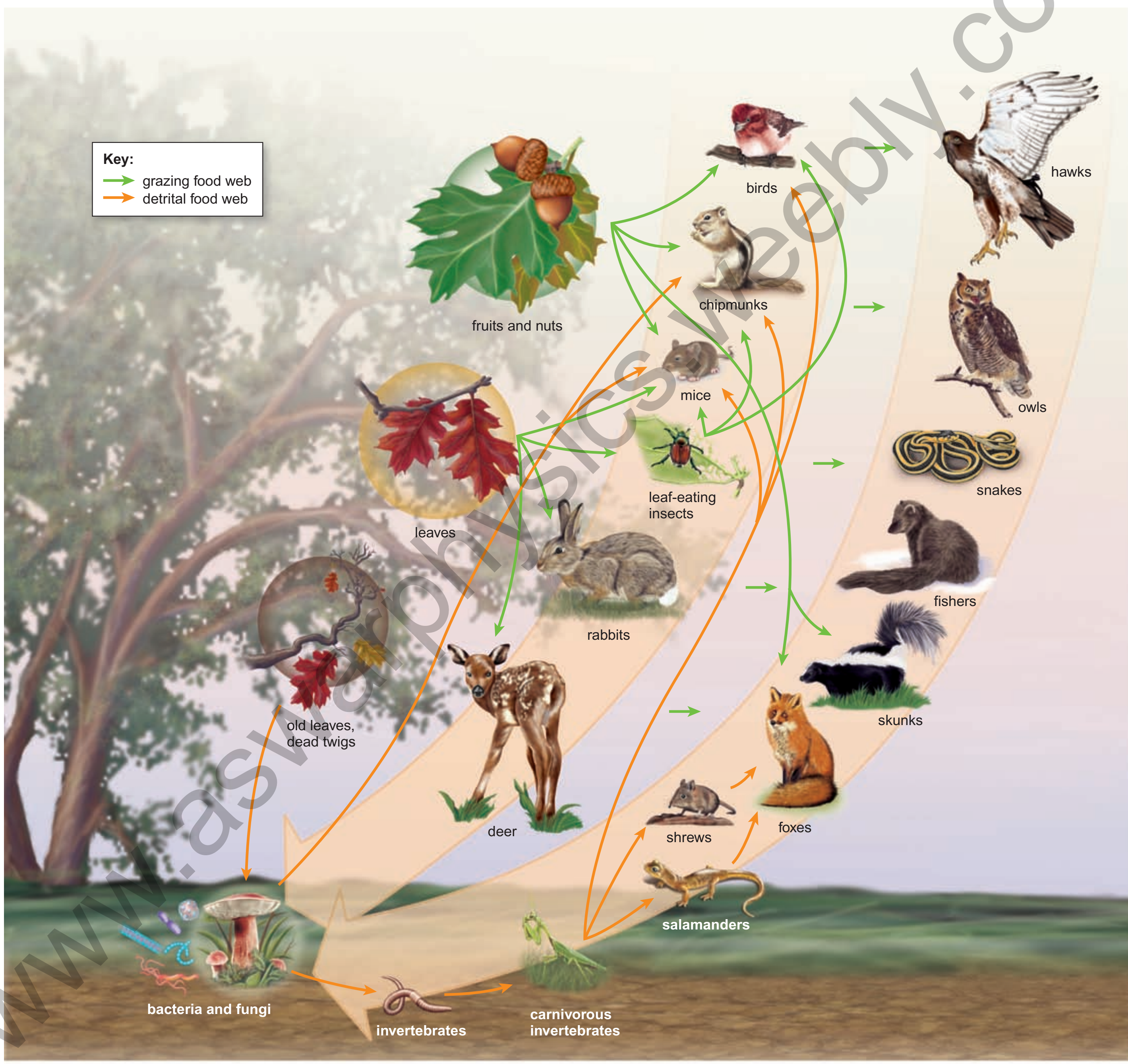


FIGURE 16.2 A Food Web
As organisms feed on one another they establish a web of relationships known as a food web. This illustration shows the interactions between grazing and detrital food webs. In grazing food webs, photosynthesis by plants provides the energy for grazing animals that eat plants, which in turn provide energy for carnivores. Since all organisms die, they ultimately become part of a detrital food web in which dead organic matter and waste products supply the energy for a series of bacteria, fungi, and animals.

the degree of complexity and the stability of a community. Complex communities with many kinds of organisms interacting in numerous ways tend to be more stable than those that have few organisms and interactions. In other words, over hundreds of years, you would see the same kinds of organisms living in a woodlot, prairie, or ponderosa pine forest. On the other hand, many human-influenced communities are very unstable. Agricultural ecosystems tend to have very few kinds of organisms and cannot maintain themselves without human involvement.

Communities Are Dynamic

Although many kinds of communities are stable, that does not mean that there is no activity going on within the community. For example, while the human body is relatively stable, its stability results from the constant activity of various organs. Although at the broad level communities may appear to be unchanging, there is much change occurring among the organisms present. Producers are capturing sunlight, herbivores are eating plants, carnivores are eating animals, and decomposers are recycling materials. Populations of many organisms may rise and fall as well.

However, if the numbers of a particular kind of organism in a community increase or decrease significantly, some adjustment usually occurs in the populations of other organisms within the community. For example, the populations of many kinds of small mammals (mice, voles, lemmings, and so on) vary from year to year. If there are few small mammals to eat, the populations of their predators decrease. In addition, predators switch to different prey species, affecting other parts of the community.

16.1 CONCEPT REVIEW

1. Why is a food web better than a food chain as a way to describe a community?
2. As the number of insects declines in the autumn as the leaves fall from trees and the grass stops growing, what would you expect to happen to bird populations?

16.2 Niche and Habitat

One of the ways scientists learn how communities work is by focusing on the activities and impacts of certain species. Each organism has a role to play and is involved in a complex set of interactions with other organisms.

The Niche Concept

The **niche** of an organism is its specific functional role in its community. A complete description of an organism's niche involves a detailed understanding of the impacts an organism has on its biotic and abiotic surroundings, as well as all the factors that affect the organism. Therefore, a complete description of the niche of an organism is probably impossible. If we look hard enough, we discover something new we didn't understand before.

For example, the niche of an earthworm includes how an earthworm is affected by abiotic factors such as the size of soil particles, soil texture, moisture, pH, and temperature. Its niche also includes biotic factors such as parasites that infect earthworms; birds, moles, and shrews that eat earthworms; dead plant material that earthworms use for food, and anglers who use worms as bait (figure 16.3). In addition, earthworms perform several important functions in their communities. They (1) transport minerals and nutrients from deeper soil layers to the surface, (2) bury seeds, (3) incorporate organic matter into the soil, and (4) create burrows, which allow air and water to penetrate the soil more easily. And this entire discussion represents only a limited sample of all the aspects of an earthworm's niche.

Some organisms have rather broad niches; others, with very specialized requirements and limited roles to play, have niches that are quite narrow. The opossum (figure 16.4a) is an animal with a very broad niche. It eats a wide variety of plant and animal foods, can adjust to a wide variety of climates, is used as food by many kinds of carnivores (including humans), and produces large numbers of offspring. By contrast, the koala of Australia (figure 16.4b) has a very narrow niche. It can live only in areas of Australia that have specific species of *Eucalyptus* trees, because it only eats the leaves of these trees. Furthermore, it cannot tolerate low temperatures and does not produce many offspring. As you might guess, the opossum is expanding its range, and the koala is endangered in much of its range.

Because an organism's niche includes a complex set of interactions with its surroundings, it is often easy to overlook important roles played by some organisms. For example, Europeans introduced cattle into Australia where there had previously been no large, hoofed mammals. When this was done, no one thought about the effects of cow manure on the biotic community or the significance of *dung beetles*. In parts of the world where dung beetles exist, they rapidly colonize fresh dung and cause it to be broken down. Although there were dung beetles in Australia, they were adapted to feeding on the dung of native marsupials and did not colonize cow dung. Therefore, in areas of Australia where cattle were raised, a significant amount of land became covered with accumulated cow dung. This reduced the area where grass could grow and reduced productivity. The problem was eventually solved by the importation of several species of dung beetles from Africa and Europe, where large, hoofed mammals are common. The dung beetles made use of what the cattle did not digest, returning it to a form that plants could recycle more easily into plant biomass.

The Habitat Concept

The **habitat** of an organism is the kind of place or community in which it lives. Each organism has particular requirements for life and lives where the environment provides what it

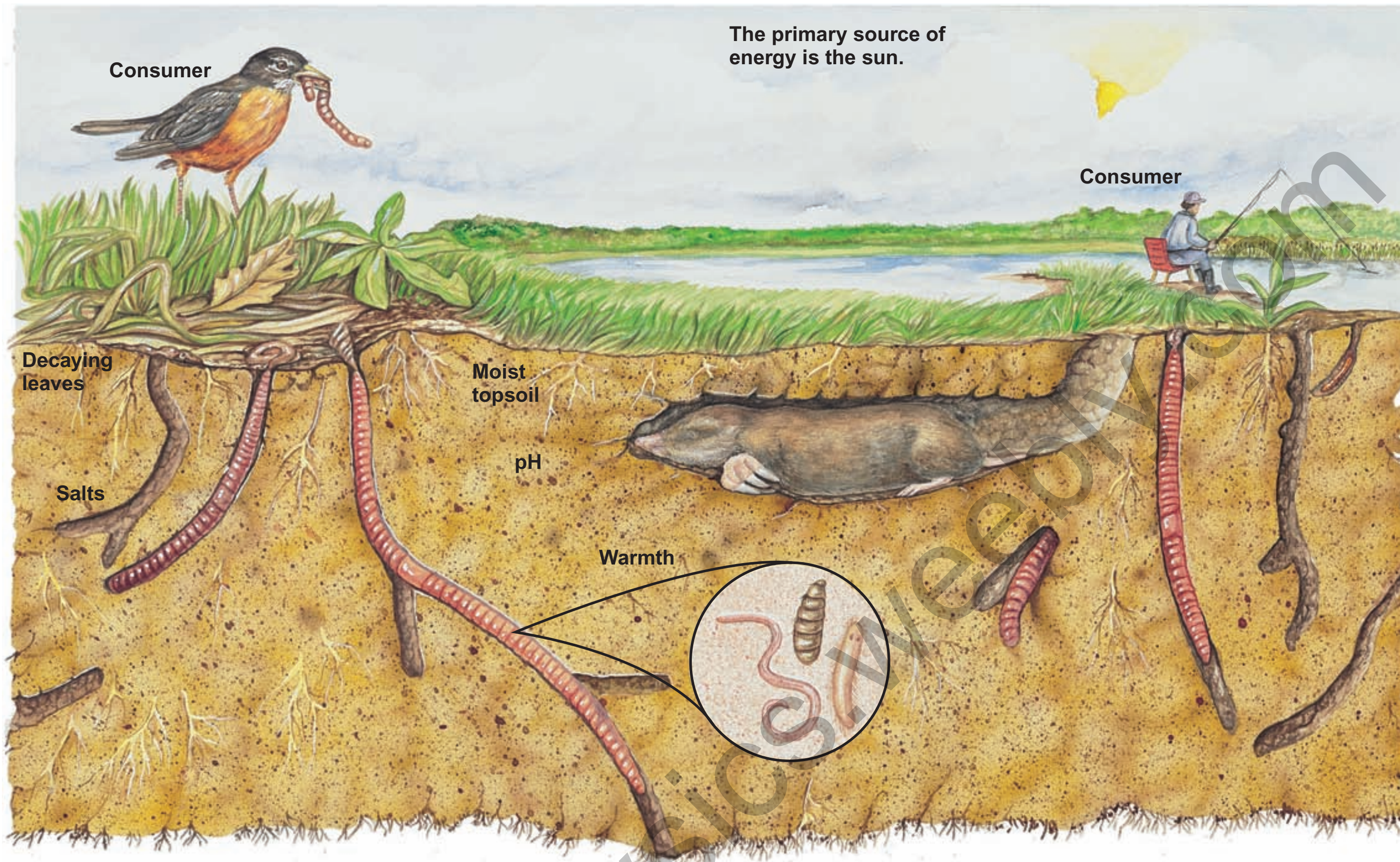


FIGURE 16.3 The Niche of an Earthworm
The niche of an earthworm involves a great many factors. It includes the fact that the earthworm is a consumer of dead organic matter, a source of food for other animals, a host to parasites, and bait for an angler. Furthermore, the earthworm loosens the soil by burrowing and "plows" the soil when it deposits materials on the surface. Additionally, the pH, texture, and moisture content of the soil have an impact on the earthworm. This is but a small part of what the niche of the earthworm includes.


(a) The opossum has a very broad niche


(b) The koala has a narrow niche

FIGURE 16.4 Broad and Narrow Niches
(a) The opossum has a very broad niche. It eats a variety of foods, is able to live in a variety of habitats, and has a large reproductive capacity. It is generally extending its range in the United States. *(b)* The koala has a narrow niche. It feeds on the leaves of only a few species of *Eucalyptus* trees, is restricted to relatively warm, forested areas, and is generally endangered in much of its habitat in Australia.

needs. Habitats are usually described in terms of a conspicuous or particularly significant feature. For example, the habitat of a prairie dog is usually described as grassland and the habitat of a tuna is described as the open ocean. The habitat of a fiddler crab is sandy ocean shores and the habitat of various kinds of cacti is the desert. It is possible to describe the habitat of the bacterium *Escherichia coli* as the gut of humans and other mammals and the habitat of a fungus as a rotting log. Organisms that have very specific places in which they live simply have more restricted habitats.

16.2 CONCEPT REVIEW

3. List 10 items that are a part of your niche.
4. What is the difference between habitat and niche?

16.3 Kinds of Organism Interactions

One of the important components of an organism's niche is the other living things with which it interacts. Some interactions are harmful to one or both of the organisms, whereas other interactions are beneficial. Ecologists have classified the kinds of interactions between organisms into broad categories.

Competition

Competition is an interaction between organisms in which both organisms are harmed to some extent. This is the most common kind of interaction among organisms. Organisms are constantly involved in competition. Competition occurs whenever two organisms need a vital resource that is in short supply (figure 16.5). The vital resource may be such things as soil nutrients, sunlight, or pollinators for plants; or food, shelter, nesting sites, water, mates, or space for animals.

Intraspecific competition takes place between members of the *same* species. It can involve a snarling tug-of-war between two dogs over a scrap of food or a silent struggle between pine seedlings for access to available light. **Interspecific competition** occurs between members of *different* species. The interaction between weeds and tomato plants in a garden is an example of interspecific competition. If the weeds are not removed, they compete with the tomatoes for available sunlight, water, and nutrients, resulting in poor growth of both the tomatoes and weeds. Similarly, there is interspecific competition among species of carnivores (e.g., hawks, owls, coyotes, foxes) for the small mammals and birds they use for food. Competition does not necessarily involve a face-to-face confrontation. For example, if a coyotes kills and eats a rodent, it has had a competitive effect on foxes, hawks, and other carnivores as well as other members of its own species, because there is now one less rodent available to be caught and eaten by others.

(a) Intraspecific competition between pine trees for light

(b) Interspecific competition between vultures and lion for food (zebra)

FIGURE 16.5 Competition
Whenever a needed resource is in limited supply, organisms compete for it. Competition between members of the same species is called *intraspecific competition*. *(a)* Intraspecific competition for sunlight among these pine trees has resulted in the tall, straight trunks. Those trees that did not grow fast enough died. Competition between different species is called *interspecific competition*. *(b)* The lion and vultures are competing for the lion's zebra kill.

Competition and Natural Selection

Competition is a powerful force for natural selection. Although competition results in harm to both organisms, there can still be winners and losers. The two organisms may not be harmed to the same extent, with the result that one gains greater access to the limited resource. Biologists have recognized that, the more similar the requirements of two species of organisms, the more intense the competition between them. This has led to the development of a general rule known as the *competitive exclusion principle*. According to the **competitive exclusion principle,** no two species of organisms can occupy the same niche at the same time. If two species of organisms do occupy the same niche, the competition will be so intense that one or more of the following processes will occur: (1) one of the two species will become extinct, (2) one will migrate to a different area where competition is less intense, or (3) the two species will evolve into slightly different niches, so that the intensity of the competition is reduced. For example, a study of the feeding habits of several kinds of warblers shows that, although they live in the same place and feed on similar organisms, their niches are slightly different, because they feed in different places on trees (figure 16.6).

Another example involves the competition of various species of flowering plants for pollinators. Some have bright red tubular flowers that are attractive to hummingbirds. Some have foul odors that attract flies or beetles. Others are open only at night and are pollinated by moths or bats. A few kinds of orchid flowers mimic female wasps and are pollinated when the male wasp tries to mate with the fake female wasp. Many flowers attract several kinds of bees, butterflies, or beetles, but the flowers open only at certain times of the day. All of these differences are niche specializations that reduce competition for pollinators.

Predation

Predation is an interaction in which one animal captures, kills, and eats another animal. The organism that is killed is the **prey,** and the one that does the killing is the **predator.** Predators benefit from the relationship because they obtain a source of food; obviously, prey organisms are harmed. Most predators are relatively large, compared to their prey, and have specific adaptations to aid them in catching prey. There are many different styles of predation. Many predators, such as leopards, lions, cheetahs, hawks, squid, sharks, and salmon, use speed and strength to capture their prey. Dragonflies, bats, and swallows use a technique that involves flying around in an area where they can capture flying insects. Predators such as frogs, many kinds of lizards, and insects (e.g., praying mantis) blend in with their surroundings and strike quickly when a prey organism happens by. Wolf spiders and jumping spiders have large eyes, which help them find prey, which they pounce on and kill. The webs of other kinds of spiders serve as nets to catch flying insects. The prey are quickly paralyzed by the spider's bite and wrapped in a tangle of silk threads (figure 16.7). Many kinds of birds, insects, and mammals simply search for slow-moving prey, such as caterpillars, grubs, aphids, slugs, snails, and similar organisms. Many kinds of marine snails and starfish are predators of other slow-moving sea creatures.

Often predators are useful to humans because they control populations of organisms that do us harm. For example, snakes eat rats and mice that eat stored grain and other agricultural products. Birds and bats eat insects that are agricultural pests.

It is even possible to think of a predator as having a beneficial effect on the prey species. Certainly, the *individual* organism that is killed is harmed, but the *population* can benefit. Predators can control the size of a prey population and thus, prevent large populations of prey organisms from

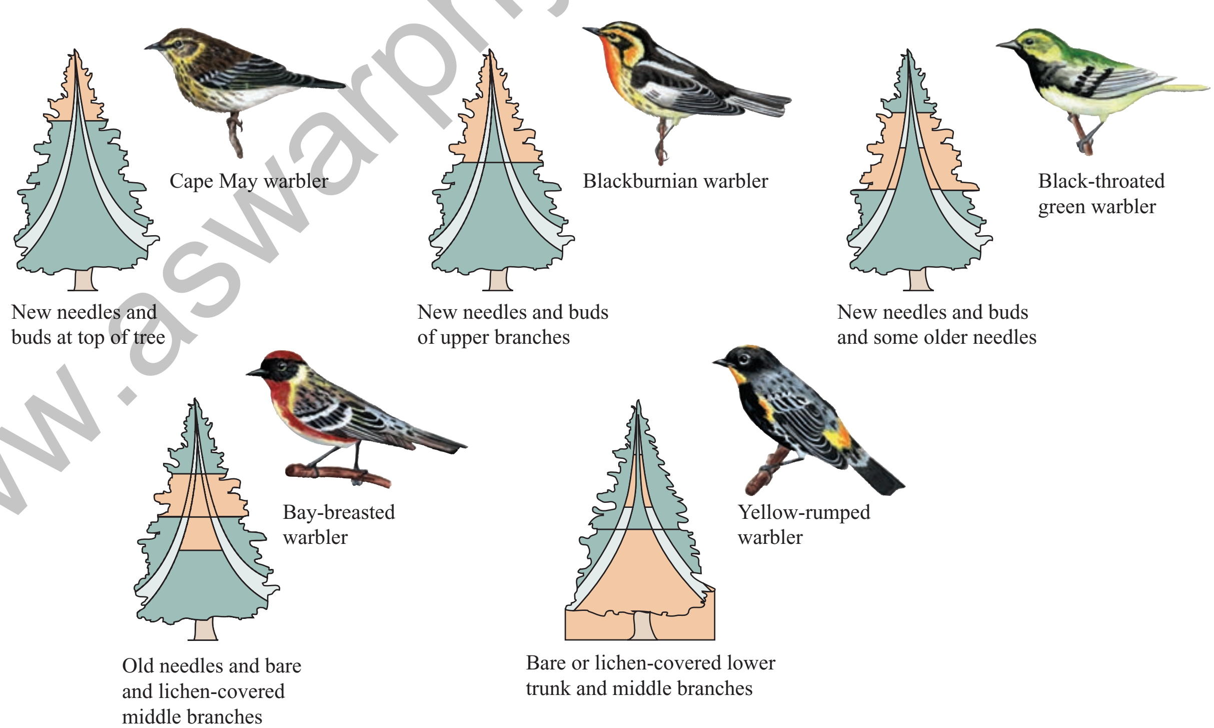


FIGURE 16.6 Niche Specialization
Although all of these warbler species have similar feeding habits, they limit the intensity of competition by feeding on different parts of the tree.

(a) Lions use speed and strength to capture their prey

(b) Chameleons use stealth and camouflage to capture prey

(c) Spiders use webs to capture prey

FIGURE 16.7 The Predator-Prey Relationship
(a) Many predators, such as lions and cheetahs, use speed and strength to capture prey. *(b)* Other predators, such as frogs and chameleons, blend in with their surroundings, lie in wait, and ambush their prey. *(c)* Some spiders use nets to capture prey. Obviously, predators benefit from the food they obtain, to the detriment of the prey.

destroying their habitat or they can reduce the likelihood of epidemic disease by eating sick or diseased individuals. Furthermore, predators act as selecting agents. The individuals that fall prey to them are likely to be less well-adapted than the ones that escape predation. Predators usually kill slow, unwary, poorly hidden, sick, or injured individuals. Thus, the genes that may have contributed to slowness, inattention, poor camouflage, illness, or the likelihood of being injured are removed from the gene pool.

Symbiotic Relationships

Symbiosis means "living together." Unfortunately, this word is used in several ways, none of which is very precise. However, the term symbiosis is usually used for interactions that involve a close physical relationship between two kinds of organisms. The three kinds of relationships discussed in the following sections—parasitism, commensalism, and mutualism—are often referred to as symbiotic relationships because they usually involve organisms that are physically connected to one another.

Parasitism

In **parasitism,** one organism lives in or on another living organism, from which it derives nourishment. The **parasite** derives benefit and harms the **host,** the organism it lives in or on. Parasites are smaller than their hosts. In general, they do not kill their host quickly but, rather, use it as a source of food for a long time. However, the parasite's activities may weaken the host so that it eventually dies. Parasitism is a very common kind of interrelationship. Nearly every category of living thing has species that are parasites. There are parasitic bacteria, fungi, protozoa, plants, fish, insects, worms, mites, and ticks. In fact, there are more species of parasites in the world than there are nonparasites.

There are many styles of parasitism. Parasites that live on the outside of their hosts are called **external parasites.** For example, ticks live on the outside of the bodies of animals, such as rats, turtles, and humans, where they suck blood and do harm to their hosts. **Internal parasites** live on the inside of their hosts. For example, tapeworms live in their hosts' intestines. Several kinds of plants are parasitic; mistletoe invades the tissues of the tree it is living on to derive its nourishment. Some flowering plants, such as beech drops and Indian pipe, lack chlorophyll and are not able to do photosynthesis. They derive their nourishment by obtaining nutrients from the roots of trees or soil fungi and grow aboveground for a short period when they flower. Indian pipe is interesting in that it is parasitic on the fungi that assist tree roots in absorbing water. The root fungi receive nourishment from the tree and the Indian pipe obtains nourishment from the fungi. So, the Indian pipe is an indirect parasite on trees (figure 16.8).

Many kinds of fungi are parasites of plants, including commercially valuable plants. Farmers spend millions of dollars each year to control fungus parasites. Many kinds of insects, worms, protozoa, bacteria, and viruses are important human parasites.

Many parasites have extremely complicated life cycles (chapter 23 discusses the life cycle of several kinds of worm parasites). In many of these life cycles, some species carry the parasite from one host to the next. Such a carrier organism is known as a **vector.** For example, the protozoan that causes malaria is carried from one human to another by certain species of mosquitos, and the bacterium *Borrelia burgdorferi,* which causes lyme disease, is carried by certain species of ticks (figure 16.9).

Special Kinds of Predation and Parasitism

Both predation and parasitism are relationships in which one member of the pair is helped and the other is harmed. But there are many kinds of common interactions in which one is harmed and the other aided that don't fit neatly into the categories of interactions dreamed up by scientists. For example, when a deer eats the leaves off a tree or a goose eats grass, they are doing harm to the plant they are eating while deriving a benefit. In essence, these herbivores are *plant predators or parasites* (figure 16.10). In aquatic habitats there are many kinds of organisms (sponges, clams, barnacles, shrimp, etc.) that live as filter-feeders. They are essentially grazers on tiny organisms in the water around them. Most consume a mixture of algae and tiny animals, but they consume the entire organism and can be considered a kind of predator. In addition, there are many animals, such as mosquitoes, biting flies, vampire bats, and ticks, that take blood meals but don't usually live permanently on the host or kill it. Are they temporary parasites or specialized predators?

(a) A tapeworm is an internal parasite

(b) A black-legged tick is an external parasite

(c) Indian pipe is a plant that is a parasite

FIGURE 16.8 The Parasite-Host Relationship
Parasites benefit from the relationship because they obtain nourishment from the host. *(a)* Tapeworms are internal parasites in the guts of their host, where they absorb food from the host's gut. *(b)* The tick is an external parasite that sucks body fluids from its host. *(c)* Indian pipe (*Monotropa uniflora*) is a flowering plant that lacks chlorophyll and is parasitic on fungi that have a mutualistic relationship with tree roots. The host in any of these three situations may not be killed directly by the relationship, but it is often weakened, becoming more vulnerable to predators and diseases.

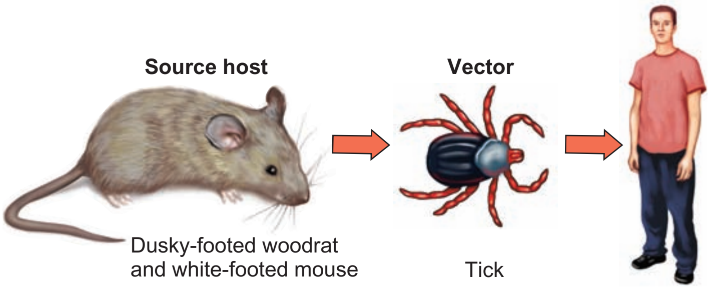


FIGURE 16.9 Lyme Disease—Hosts, Parasites, and Vectors
Lyme disease is a bacterial disease originally identified in a small number of people in the Old Lyme, Connecticut, area. Today, it is found throughout the United States and Canada. The parasite *Borrelia burgdorferi,* is a bacterium that can live in a variety of mammalian hosts (e.g., humans, mice, horses, cattle, domestic cats, and dogs). Certain ticks are vectors that suck blood from an infected animal and carry the disease to another animal when the tick feeds on it.

Finally, birds such as cowbirds and some species of European cuckoos do not build nests but, rather, lay their eggs in the nests of other species of bird, which raise these foster young rather than their own. The adult cowbird and cuckoo often remove eggs from the host nest. In addition, cowbird and cuckoo offspring typically push the hosts' eggs or young out of the nest. For these reasons, typically only the cowbird or cuckoo chick is raised by the foster parents. This kind of relationship has been called *nest parasitism.* The surrogate parents (hosts) are harmed, and the cowbird or cuckoo is aided by having others expend the energy needed to raise its young (figure 16.11).

Commensalism

Commensalism is a relationship in which one organism benefits and the other is not affected. For example, sharks often have another fish, the remora, attached to them. The remora has a sucker on the top side of its head, which allows it to attach to the shark for a free ride (figure 16.12a). Although the remora benefits from the free ride and by eating leftovers from the shark's meals, the shark does not appear to be troubled by this uninvited guest, nor does it benefit from its presence.

Another example of commensalism is the relationship between trees and epiphytic plants. **Epiphytes** are plants that live on the surface of other plants but that do not derive nourishment from them (figure 16.12b). Many kinds of plants (e.g., orchids, ferns, and mosses) use the surfaces of trees as places to live. These kinds of organisms are particularly common in tropical rainforests. Many epiphytes derive a benefit from the relationship because they are able to be located in the tops of the trees, where they receive more sunlight and moisture. The trees derive no benefit from the relationship, nor are they harmed; they simply serve as support surfaces for the epiphytes.

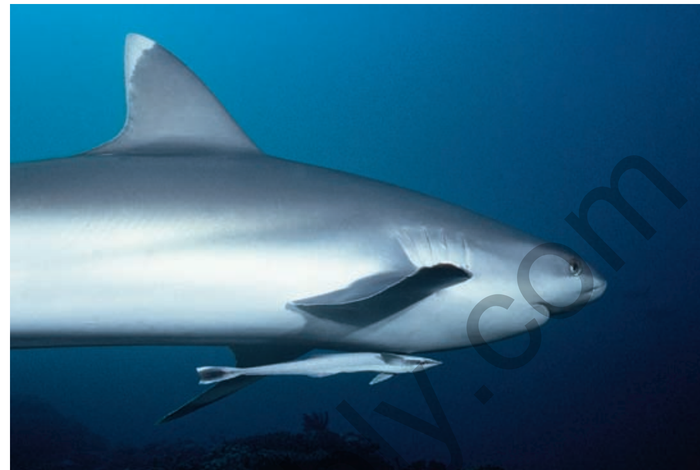
Is a monarch caterpillar eating milkweed, a parasite on milkweed?

Is a caribou eating willow, a predator on willow?

Is a mosquito sucking blood, a parasite or a specialized carnivore?

FIGURE 16.10 Special Kinds of Predation and Parasitism
Herbivores have a relationship with plants that is very similar to that of carnivores with their prey and parasites with their hosts. The herbivores are aided and the plants they feed on are harmed. Mosquitoes and other kinds of blood-sucking animals can be considered temporary parasites or predators. They do harm to the animal they feed on and benefit from the relationship.

FIGURE 16.11 Nest Parasitism
This cowbird chick in the nest is being fed by its host parent, a yellow warbler. The cowbird chick and its cowbird parents both benefit but the host is harmed because it is not raising any of its own young.



(a) A remora hitching a ride on a shark

(b) Spanish moss is an epiphyte that benefits from living on the surface of trees

FIGURE 16.12 Commensalism
In commensalism, one organism benefits and the other is not affected. *(a)* The remora shown here hitchhikes a ride on the shark. It eats scraps of food left over from the shark's messy eating habits. The shark does not seem to be hindered in any way. *(b)* The grey Spanish moss hanging on this oak tree is a good example of an epiphyte. The spanish moss does not harm the tree but benefits from using the tree surface as a place to grow.

Mutualism

Mutualism is an interrelationship in which two species live in close association with one another, and both benefit. Many kinds of animals that eat plants have a mutualistic relationship with the bacteria and protozoa that live in their guts. One of the major components of plant material is the cellulose material that makes up the cell wall. Most animals are unable to digest cellulose but rely on a collection of microorganisms in their guts to perform that function. For example, mammals such as cows, goats, camels, giraffes, and sheep have specialized portions of their guts, called a rumen, in which microorganisms live. These microbes produce enzymes, known as *cellulases,* that break down the cellulose in the food the animal eats. The microorganisms benefit because the gut provides them with a moist, warm, nourishing environment in which to live. The animals benefit because the breakdown of cellulose provides nutrients the animal could not get otherwise. Termites, plant-eating lizards, and many other kinds of herbivores have similar relationships with the bacteria and protozoa living in their digestive tracts which help them digest cellulose.

Lichens and corals exhibit a more intimate kind of mutualism. The bodies of lichens and corals are composed of the intermingled cells of two different kinds of organisms. Lichens consist of fungal cells and algal cells in a partnership; corals consist of the cells of the coral organism intermingled with algal cells. In both, the algae carry on photosynthesis and provide nutrients, and the fungus or coral provides a moist, fixed structure for the algae to live in.

Another kind of mutualistic relationship exists between flowering plants and insects. Bees and other insects visit flowers to obtain nectar from the blossoms (figure 16.13). Usually, the flowers are constructed so that the bees pick up pollen (sperm-containing packages) from the plant on their hairy bodies, which they transfer to the female part of the next flower they visit. Because bees normally visit many individual flowers of the same species for several minutes and ignore other species of flowers, they can

(a) British soldier lichen (b) Ruminants (c) Pollination

FIGURE 16.13 Mutualism
Mutualism is an interaction between two organisms in which both benefit. *(a)* The British soldier lichen in this photograph consists of a mutualistic association between a fungus and an alga. *(b)* Ruminant animals have a mutualistic relationship with the microorganisms in their gut that helps them obtain nutrients from the plants they eat. *(c)* Insects obtain nectar from plants; the plants benefit by being pollinated. (Note the yellow pollen on the bee.)

TABLE 16.1 Summary of Kinds of Organism Interactions

Kinds of Interaction	Organism 1	Organism 2	Comments
Competition	Harmed	Harmed	Usually one is harmed more than the other.
Predation	Predator benefited	Prey harmed	Predators have special adaptations for capturing prey. Prey organisms have adaptations to avoid predators.
Parasitism	Parasite benefited	Host harmed	Usually the host and parasite are in physical contact.
Commensalism	Commensal benefited	Host unaffected	Usually the host and commensal are in physical contact.
Mutualism	Benefited	Benefited	Usually the two organisms are in physical contact.

serve as pollen carriers between two flowers of the same species. Plants pollinated in this manner produce less pollen than do plants that rely on the wind to transfer pollen. This saves the plant energy, because it doesn't need to produce huge quantities of pollen. It does, however, need to transfer some of its energy savings into the production of showy flowers and nectar to attract the bees. The bees benefit from both the nectar and the pollen; they use both for food.

Some plants use birds, bats, mice, beetles, flies, and other kinds of organisms to get their pollen distributed. Each kind of flower is specialized to the kind of pollinating animal. Flowers that are pollinated by bats flower at night; and many of those that are pollinated by hummingbirds have long, tubular flowers. Table 16.1 summarizes features of these various kinds of organism interactions.

Another way in which plants and animals participate in a mutually beneficial relationship is in the production and consumption of fruit. The fruit that plants produce contains its seeds. The fruit is attractive to animals that eat it. When the seeds pass through the gut of the animal, they are typically deposited some distance from the plant that produced the fruit. Similarly animals that bury fruits typically carry the fruit away from the plant that produced it. Although they may eat some of the seeds, animals like squirrels do not find all of the fruits they buried and thus are involved in planting new plants. Therefore, animals serve as dispersal agents for the seeds of the plant. The plant encourages this activity by providing a nutritious fruit for the animal.

16.3 CONCEPT REVIEW

5. What do parasites, commensal organisms, and mutualistic organisms have in common? How are they different?
6. Describe two situations in which competition can involve combat and two that do not involve combat.
7. How is the competitive exclusion principle related to the theory of natural selection?
8. In what way are predators and parasites similar in the way they interact with other species? How do they differ in how they interact with other species?

16.4 Types of Communities

Ecologists recognize that the world can be divided into large, regional, terrestrial communities known as *biomes*. **Biomes** are communities of organisms with widespread geographic distribution that are adapted to particular climatic conditions. The primary climatic factors that determine the kinds of organisms that can live in an area are the amount and pattern of *precipitation* and the *temperature* ranges typical for the region (figure 16.14). The map in figure 16.15 shows the distribution of the major terrestrial biomes of the world.

Temperate Deciduous Forest

Temperate deciduous forest exists in the parts of the world that have moderate rainfall (75 to 130 centimeters per year) spread over the entire year and a relatively long summer growing season (130 to 260 days without frost). This biome, like other land-based biomes, is named for a major feature of the community, its dominant vegetation. The predominant plants are large trees that lose their leaves during the fall. Thus, they are called deciduous (figure 16.16). The temperate deciduous forest covers a large area from the Mississippi River to the Atlantic Coast and from Florida to southern Canada. This type of biome is also found in much of Europe and parts of eastern Asia.

Because the trees are the major producers and new leaves are produced each spring, the important primary consumers

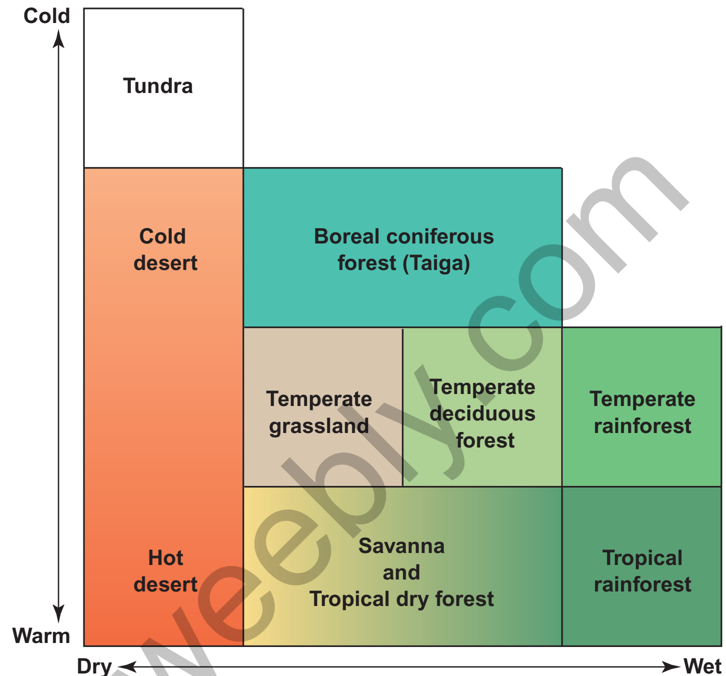


FIGURE 16.14 The Influence of Precipitation and Temperature on Vegetation
Temperature and moisture influence the kind of vegetation that can live in an area.

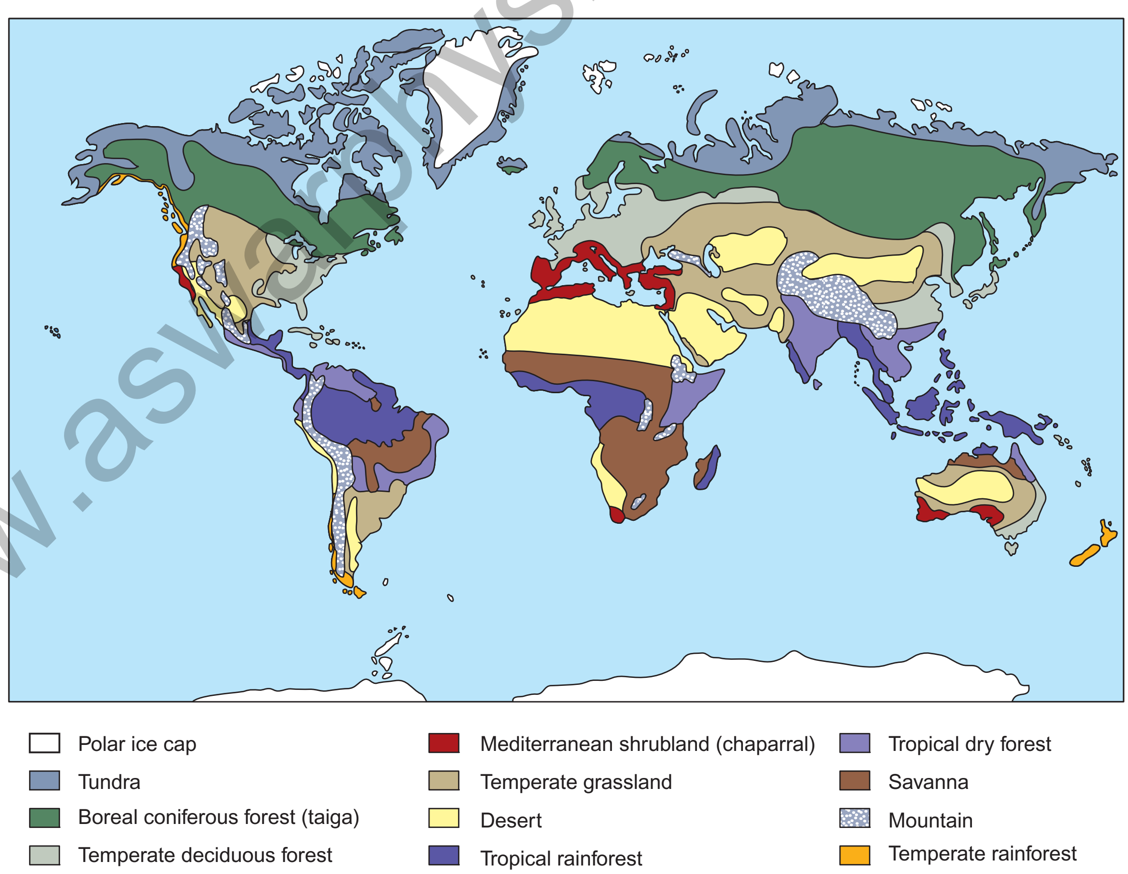


FIGURE 16.15 Biomes of the World
Major climatic differences determine the kinds of plants and animals that can live in a region. These regional communities are called biomes.