would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotic.

In a larger sense, evolution is not goal directed. Species do not become "better" over time. They simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species, despite the commonness of this kind of language in popular discourse. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a nondirectional way. A trait that fits in one environment at one time may well be fatal at some point in the future. This holds equally well for insect and human species.

## **18.2 Formation of New Species**

By the end of this section, you will be able to do the following:

- Define species and describe how scientists identify species as different
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Explain allopatric and sympatric speciation
- Describe adaptive radiation

Although all life on earth shares various genetic similarities, only certain organisms combine genetic information by sexual reproduction and have offspring that can then successfully reproduce. Scientists call such organisms members of the same biological species.

### **Species and the Ability to Reproduce**

A **species** is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics, which develop from their DNA. The closer relationship two organisms share, the more DNA they have in common, just like people and their families. People's DNA is likely to be more like their father or mother's DNA than their cousin or grandparent's DNA. Organisms of the same species have the highest level of DNA alignment and therefore share characteristics and behaviors that lead to successful reproduction.

Species' appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce (Figure 18.9).







Figure 18.9 The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo. (credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin)

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group (Figure 18.10). If humans were to artificially intervene and fertilize a bald eagle's egg with an African fish eagle's sperm and a chick did hatch, that offspring, called a **hybrid** (a cross between two species), would probably be infertile—unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even

though hybridization may take place, the two species still remain separate.



Figure 18.10 The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species. (credit a: modification of work by Nigel Wedge; credit b: modification of work by U.S. Fish and Wildlife Service)

Populations of species share a gene pool: a collection of all the gene variants in the species. Again, the basis to any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only pass to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will pass on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to pass on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually-reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role for genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

### **Speciation**

The biological definition of species, which works for sexually reproducing organisms, is a group of actual or potential interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species this rule generally holds. The presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration in *On the Origin of Species* (Figure 18.11a). Compare this illustration to the diagram of elephant evolution (Figure 18.11), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.

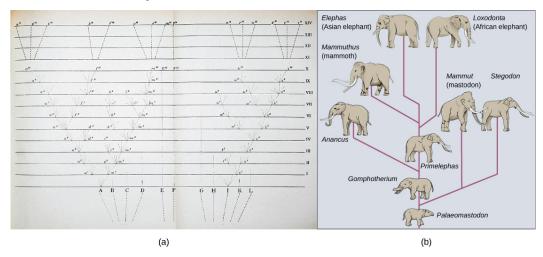


Figure 18.11 The only illustration in Darwin's *On the Origin of Species* is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that today illustrate the relationships of species. (b) Modern elephants

evolved from the Palaeomastodon, a species that lived in Egypt 35-50 million years ago.

For speciation to occur, two new populations must form from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation** (allo-="other"; -patric = "homeland") involves geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (sym-="same"; -patric = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why more than two species might not form at one time except that it is less likely and we can conceptualize multiple events as single splits occurring close in time.

### **Allopatric Speciation**

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across a species' range, is relatively free because individuals can move and then mate with individuals in their new location. Thus, an allele's frequency at one end of a distribution will be similar to the allele's frequency at the other end. When populations become geographically discontinuous, it prevents alleles' free-flow. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become increasingly different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion creating a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the organism's biology and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow. However, if a new lake divided two rodent populations continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories: dispersal and vicariance. **Dispersal** is when a few members of a species move to a new geographical area, and **vicariance** is when a natural situation arises to physically divide organisms.

Scientists have documented numerous cases of allopatric speciation taking place. For example, along the west coast of the United States, two separate spotted owl subspecies exist. The northern spotted owl has genetic and phenotypic differences from its close relative: the Mexican spotted owl, which lives in the south (Figure 18.12).



**Mexican Spotted Owl** 

Figure 18.12 The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke)

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south. The types of organisms in each ecosystem differ, as do their behaviors and habits. Also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

#### **Adaptive Radiation**

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. We call this **adaptive radiation** because many adaptations evolve from a single point of origin; thus, causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, the founder species, numerous species have evolved, including the six in Figure 18.13.

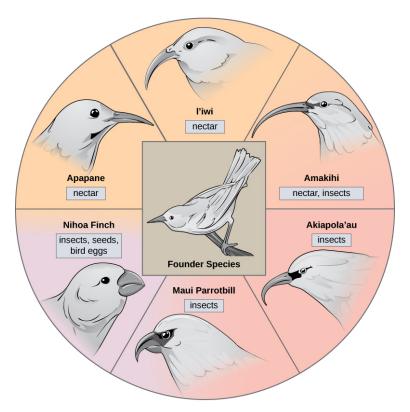


Figure 18.13 The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

Notice the differences in the species' beaks in Figure 18.13. Evolution in response to natural selection based on specific food sources in each new habitat led to evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

## LINK TO LEARNING

Watch this video (http://openstax.org/l/bird evolution) to see how scientists use evidence to understand how birds evolved.

## **Sympatric Speciation**

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. We call the process of speciation within the same space sympatric. The prefix "sym" means same, so "sympatric" means "same homeland" in contrast to "allopatric" meaning "other homeland." Scientists have proposed and studied many mechanisms.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition that we call **aneuploidy** (Figure 18.14).

# **WISUAL CONNECTION**

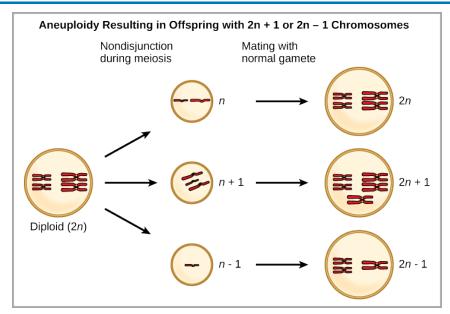


Figure 18.14 Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In this example, the resulting offspring will have 2n+1 or 2n-1 chromosomes.

Which is most likely to survive, offspring with 2n+1 chromosomes or offspring with 2n-1 chromosomes?

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition that we call **autopolyploidy** (Figure 18.15). The prefix "auto-" means "self," so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

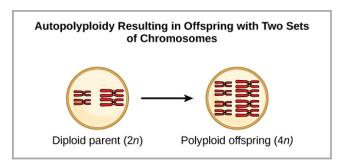
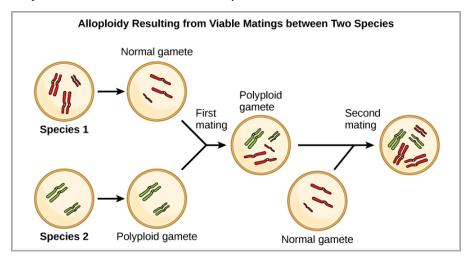


Figure 18.15 Autopolyploidy results when mitosis is not followed by cytokinesis.

For example, if a plant species with 2n = 6 produces autopolyploid gametes that are also diploid (2n = 6, when they should be n = 3), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes that this plant species produces. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with 4n that we call a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring that we call an **allopolyploid**. The prefix "allo-" means "other" (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. Figure 18.16 illustrates one possible way an allopolyploid can form. Notice how it takes two

generations, or two reproductive acts, before the viable fertile hybrid results.



**Figure 18.16** Alloploidy results when two species mate to produce viable offspring. In this example, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations that we describe here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

### **Reproductive Isolation**

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were brought together, mating would be less likely, but if mating occurred, offspring would be nonviable or infertile. Many types of diverging characters may affect the **reproductive isolation**, the ability to interbreed, of the two populations.

Reproductive isolation can take place in a variety of ways. Scientists organize them into two groups: prezygotic barriers and postzygotic barriers. Recall that a zygote is a fertilized egg: the first cell of an organism's development that reproduces sexually. Therefore, a **prezygotic barrier** is a mechanism that blocks reproduction from taking place. This includes barriers that prevent fertilization when organisms attempt reproduction. A **postzygotic barrier** occurs after zygote formation. This includes organisms that don't survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, which we call **temporal isolation**, can act as a form of reproductive isolation. For example, two frog species inhabit the same area, but one reproduces from January to March; whereas, the other reproduces from March to May (Figure 18.17).



Figure 18.17 These two related frog species exhibit temporal reproductive isolation. (a) *Rana aurora* breeds earlier in the year than (b) *Rana boylii*. (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi)

In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the same species' other populations. We call this situation **habitat isolation**. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, natural selection forces, mutation, and genetic drift will likely result in the two groups diverging (Figure 18.18).

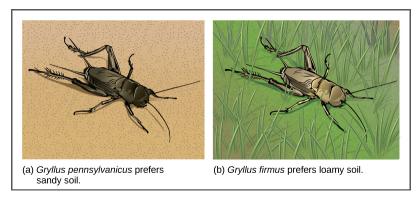


Figure 18.18 Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, and the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

**Behavioral isolation** occurs when the presence or absence of a specific behavior prevents reproduction. For example, male fireflies use specific light patterns to attract females. Various firefly species display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place. We call this a **gametic barrier**. Similarly, in some cases closely related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together. (Figure 18.19).

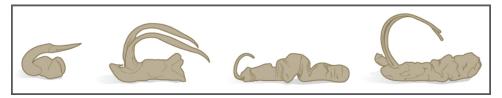


Figure 18.19 The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from cross-pollinating with a different species (Figure 18.20).

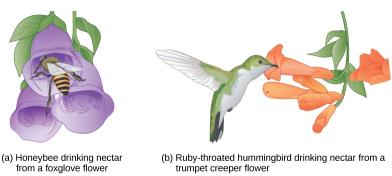


Figure 18.20 Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by hummingbirds.

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. We call this **hybrid inviability** because the hybrid organisms simply are not viable. In another postzygotic situation, reproduction leads to hybrid birth and growth that is sterile. Therefore, the organisms are unable to reproduce offspring of their own. We call this hybrid sterility.

#### **Habitat Influence on Speciation**

Sympatric speciation may also take place in ways other than polyploidy. For example, consider a fish species that lives in a lake. As the population grows, competition for food increases. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that other fish did not use. What if this new food source was located at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number, but also over a short period of time. Figure 18.21 shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.

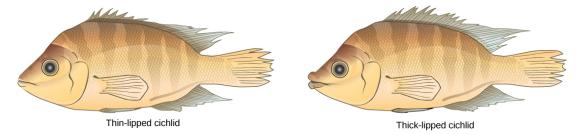


Figure 18.21 Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that a single population of cichlid fish populated the lake only 100 years ago. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.

## 18.3 Reconnection and Speciation Rates

By the end of this section, you will be able to do the following:

- Describe pathways of species evolution in hybrid zones
- Explain the two major theories on rates of speciation

Speciation occurs over a span of evolutionary time, so when a new species arises, there is a transition period during which the closely related species continue to interact.

### Reconnection

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual with whom they are capable of breeding. We call an area where two closely related species continue to interact and reproduce, forming hybrids a **hybrid zone**. Over time, the hybrid zone may change depending on the fitness of the hybrids and the reproductive barriers (Figure 18.22). If the hybrids are less fit than the parents, speciation reinforcement occurs, and the species continue to diverge until they can no longer mate and produce viable offspring. If reproductive barriers weaken, fusion occurs and the two species become one. Barriers remain the same if hybrids are fit and reproductive: stability may occur and hybridization continues.