Biological Evolution: Modes of Speciation

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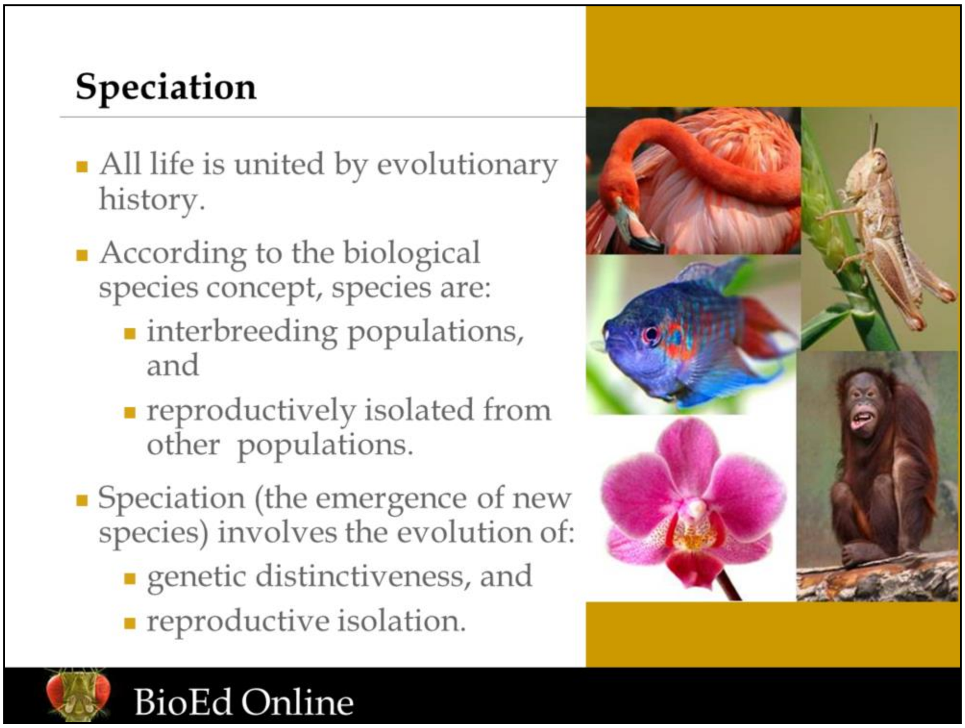

Speciation

With the 1859 publication of *On the Origin of Species*, Charles Darwin put forth the idea that all species have descended, with modification, from a common population of ancestors. All life on earth is therefore united by evolutionary history. This idea, which also is credited to Alfred Wallace, revolutionized scientific thought and is the cornerstone of modern evolutionary theory. However, what Darwin didn't fully understand, what he called the "mystery of mysteries," is how new species arise. We now know that there are many modes, mechanisms, and evolutionary forces that play a role in the formation of new species.

To understand **speciation** (the formation of new species) we must first have an idea of what species are. Many different definitions have been proposed; none of them are universally applicable and all of them are useful in particular contexts. At present, one of the most widely used definitions of species is based on the biological species concept. This definition is appropriate for our discussion of speciation because it not only defines species, but it also emphasizes the process by which species arise. The biological species concept states that "species are groups of interbreeding natural populations that are reproductively isolated from other such groups." Reproductive isolation refers to biological differences between two populations that impede or greatly reduce gene exchange between them. Most biologists recognize that some gene flow occurs between populations and do not require complete reproductive isolation in order to recognize a population as a distinct species. The study of speciation can therefore be thought of as the study of how a population evolves genetic distinctiveness and becomes reproductively separate from other populations.

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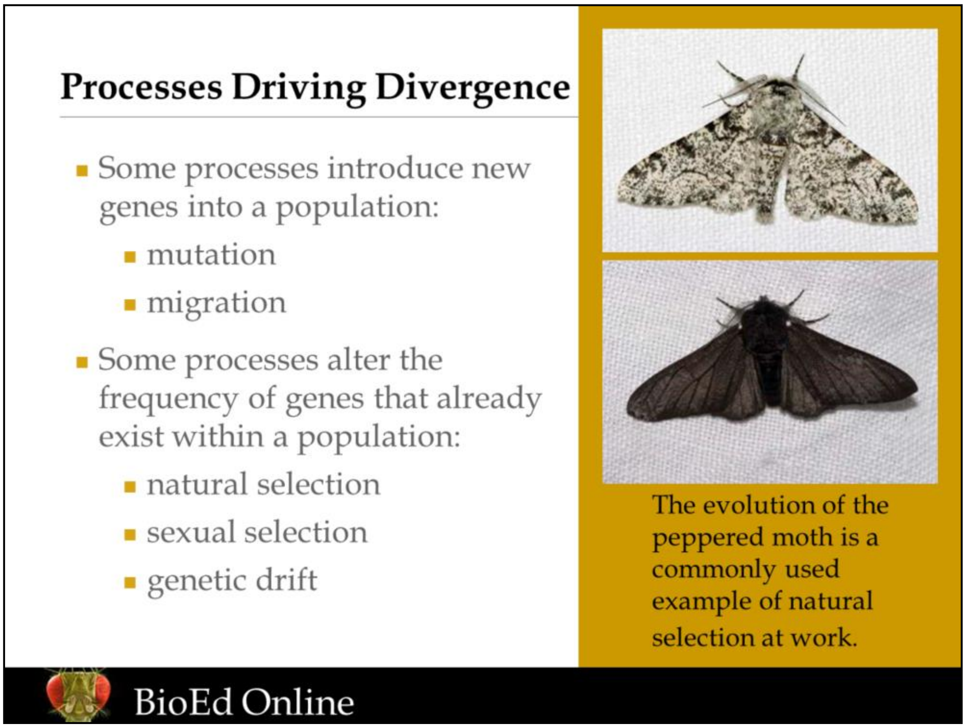

Processes Driving Divergence

Genetic distinctiveness arises through processes that introduce new alleles and genes into a population (mutation and migration) and processes that alter the frequencies of genes that already exist within a population (natural selection, sexual selection, and genetic drift).

A **mutation** is a random change in an organism's genetic material. Heritable mutations (those that are carried by the gametes) can introduce new alleles and genes into a population and, therefore, provide raw material for the evolutionary process.

Migration, or the movement of organisms from one place to another, can also cause changes in the gene pools of different populations. Through migration, new alleles can be introduced or taken away from a population, or the frequencies of alleles and genotypes in a population can be altered.

Through **natural selection**, heritable traits (and the alleles that confer those traits) that are beneficial to reproductive success become more common in a population while those that are disadvantageous become increasingly rare.

Sexual selection is a special form of selection that leads to the development of sexual dimorphic traits (traits that differ between the sexes). Through sexual selection, alleles that confer an advantage in the ability to obtain mates become more common in a population.

Genetic drift refers to changes in a population's allele frequencies that occur due to chance. In general, the smaller the population, the greater the impact of genetic drift.

These processes, which drive evolution and speciation, can be reviewed in the *BioEd Online* presentation entitled "Biological Evolution." In addition, information about different species concepts, as well as mechanisms of reproductive isolation, can be found in the presentation "Species Concepts."

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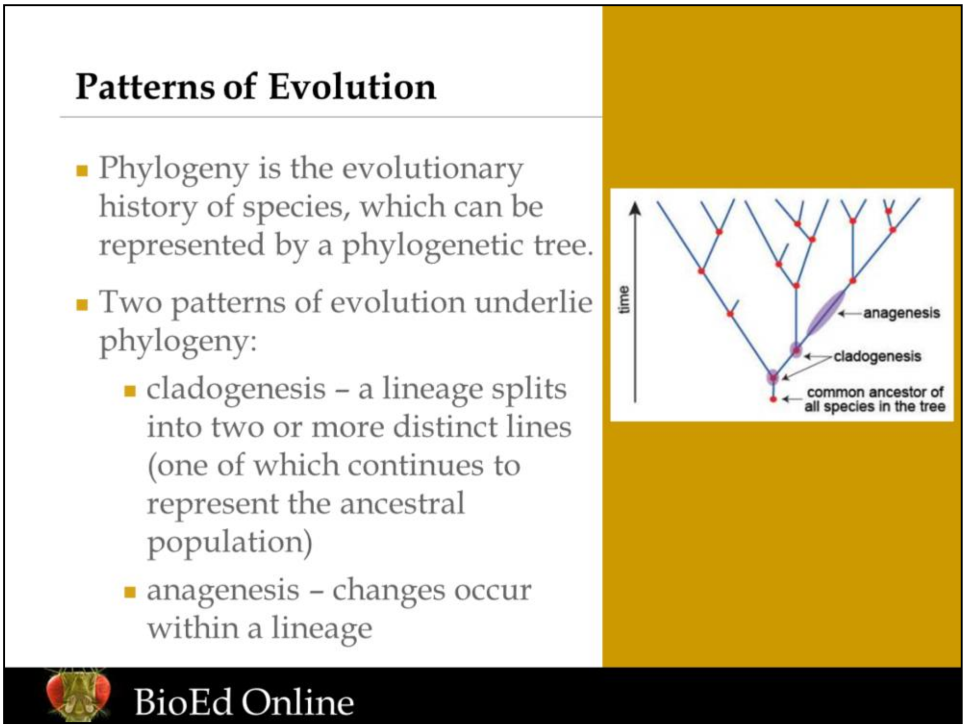

Patterns of Evolution

In *On the Origin of Species*, Darwin wrote that all species, whether living or extinct, form a great "Tree of Life," now commonly referred to as a phylogenetic tree. A phylogenetic tree graphically represents the evolutionary history (phylogeny) of species, groups of related species, or other taxonomic groups. A branch point of the tree represents divergence of one or more new populations from a parent population. In some phylogenetic representations, the branch length is proportional to the predicted evolutionary time between branching events. These branches and nodes represent two different patterns of evolution: cladogenesis and anagenesis.

Cladogenesis, also known as branching evolution, is the evolutionary pattern by which a new group splits from a parent group. Because this results in an increase in the total number of existing taxa, cladogenesis is responsible for the diversity of organisms seen in nature. In contrast, anagenesis, also known as phyletic evolution, results in the linear transformation of a population. There is no branching of the phylogenetic tree and no increase in the total number of species. Instead, anagenesis causes two species that split from the same parent species diverge more and more from one another over time.

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Image Reference:

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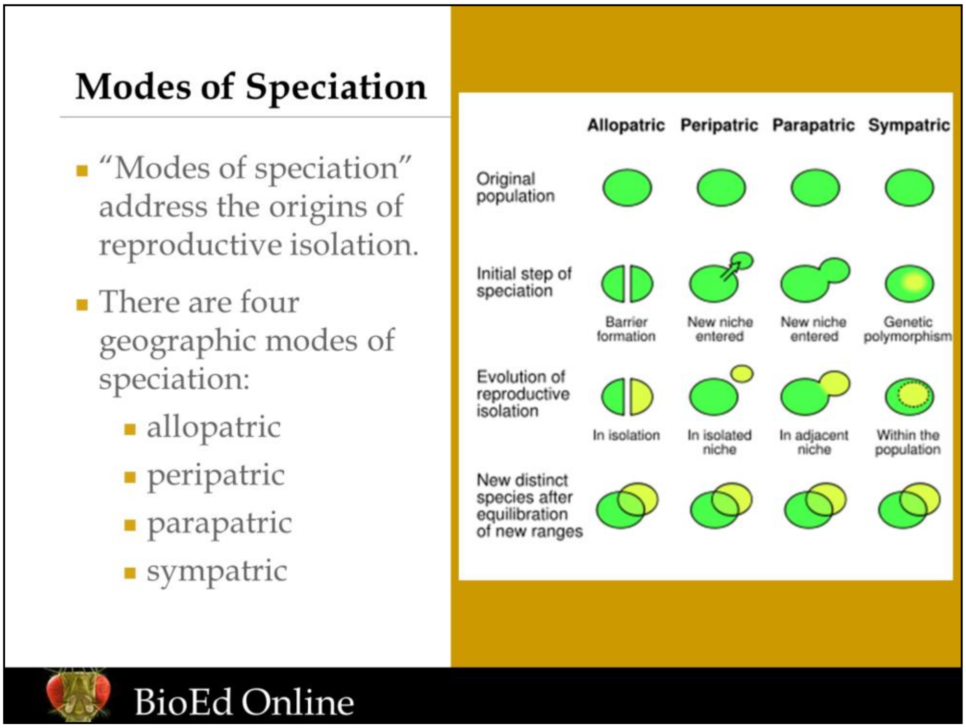

Modes of Speciation

Many biologists interpret "species" as the fundamental unit into which populations of organisms can be classified. However, what is considered to constitute a species varies by taxonomic group as well as the purpose for which this classification is being used. The biological species concept, which defines species as interbreeding populations that are reproductively isolated from other populations, is a useful definition, particularly for thinking about how many species of sexually reproducing animals and plants arise.

There are four geographic modes of speciation that are based on the extent to which the incipient species (populations that are in the process of forming distinct species) are geographically isolated from one another. Allopatric speciation occurs in populations that became separated by a geographic barrier. Peripatric speciation, also known as founder effect speciation, is a special type of allopatric speciation. It occurs when a small population becomes isolated from its parent species. Parapatric speciation arises between neighboring populations that share small zones of contact and exhibit modest gene exchange. Sympatric speciation occurs within a single, freely interbreeding population, and is believed to occur only rarely. These modes were first described for animals and also are useful for distinguishing patterns of speciation in plants.

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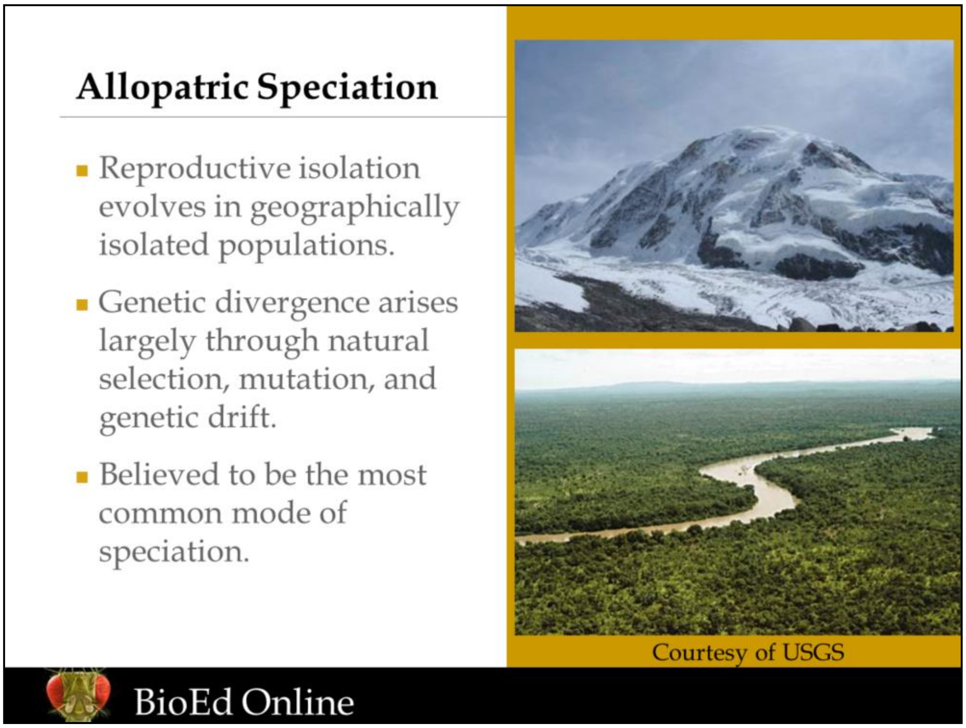

Allopatric Speciation

Allopatric speciation is the evolution of reproductive isolation in populations that are separated by geographic barriers. What constitutes a geographic barrier is not strictly defined, rather, it can be understood as any environmental factor that prevents or dramatically reduces gene flow between two populations. Thus, while geographic barriers most commonly result from large-scale climatic and geological events (mountain formation, glaciation, continental drift), they can also result from strict habitat preferences that "microgeographically" isolate populations.

Geographic isolation prevents gene flow among previously interbreeding populations and allows them to evolve independently. This almost inevitably leads to divergence between the two populations over time as distinct evolutionary changes accumulate: different mutations arise in the different populations, genetic drift fixes different genes in the populations, and the populations undergo different adaptive changes in response to natural selection. Over time, the two populations may become reproductively incompatible or isolated, essentially as a by-product of the genetic divergence of other traits. Eventually, the two (initially identical) species will no longer interbreed, even if they are brought back into contact with one another under natural conditions. Allopatric speciation is considered to be the most common of the known modes of speciation.

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Peripatric Speciation

- Reproductive isolation evolves in a small population, isolated from its parent population.
- Also known as founder effect speciation.
- Genetic divergence arises largely through genetic drift and natural selection.
- Proposed explanation for the rapid speciation of Hawaiian *Drosophila.*

Hawaiian fruit fly
Drosophila setosimentum

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Peripatric Speciation

Peripatric speciation is a type of allopatric speciation. In both of these geographic modes of speciation, a single population becomes divided into two independent populations that can no longer interbreed because they are separated by some physical barrier. Because of the separation, the two populations evolve independently and eventually become reproductively incompatible. The distinction between allopatric and peripatric speciation is the relative sizes of the populations involved. In allopatric speciation, a population is separated into two relatively large independent populations. In contrast, in peripatric speciation, only a small fraction of the original population becomes geographically isolated. Peripatric speciation originally was known as founder effect speciation because it can occur when a few individuals (the founders) colonize a new habitat, such as an island, thereby establishing a new population away from the parent population.

The same genetic forces drive the evolution of reproductive isolation in both allopatric and peripatric speciation: mutation, natural selection, and genetic drift. However, in peripatric speciation, evolution may occur on a faster time scale because small populations are more susceptible to the random effects of genetic drift. In addition, it is likely that there will be a period of rapid selection and adaptation if the colonists' new habitat is substantially different from their original environment. For example, the founder effect has been used to explain the rapid speciation of Hawaiian fruit flies (*Drosophila*). Approximately 500 species of *Drosophila* currently inhabit the Hawaiian archipelago, and all are believed to have descended from a common ancestor that reached the island of Kauai (the oldest of the volcanic islands) over five million years ago. Some believe that as new Hawaiian islands formed as a result of volcanic activity, they were colonized by small groups of *Drosophila* from the older islands. Because these founders represented only a fraction of the genetic variability present in the parent species, it is likely that genetic drift played a large role in the evolution of genetic distinctiveness between species of Hawaiian *Drosophila*. In addition, the founders evolved through the process of natural selection to adapt to aspects of the new environment, such as the endemic plant hosts.

The founder effect has been invoked in the speciation events of the Hawaiian *Drosophila* because so many species were formed in such a relatively short time; the standard allopatric model does not predict that several hundred speciation events should occur in only a few million years. However, the importance of the founder-induced speciation is debated. Some have suggested that it rarely occurs, especially compared to the more standard allopatric model of speciation.

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Parapatric Speciation

- Reproductive isolation evolves in neighboring populations that share small zones of contact and exhibit modest gene exchange.
- Genetic divergence arises largely through natural selection.
- Proposed explanation for speciation of the grass *Anthoxanthum.*

Buffalo grass
Anthoxanthum odoratum

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Parapatric Speciation

Both allopatric and peripatric speciation occur when populations are physically separated and therefore do not exchange genes. In contrast, **parapatric speciation** involves the evolution of reproductive isolation within a population where gene exchange is possible because there is no physical barrier separating individuals. However, although the population is continuous, it does not interbreed randomly and the degree of gene exchange is modest. For example, if the population of a single species expands its range, some individuals may grow in new areas with distinct environmental conditions. Over time, the "subpopulation" that inhabits the new area, or a fringe region adjacent to a new area, has potential to become genetically distinct from the rest of the population as it adapts to the new environmental conditions. As genetic differences accumulate, gene flow between the incipient species may slow. Eventually, if selection pressures are strong enough, reproductive isolation will evolve and the subpopulation will become a new species.

One of the best documented examples of parapatric speciation involves the evolution of tolerance to heavy metals in the subpopulation of grass *Anthoxanthum odoratum.* Populations of *A. odorantum* growing in close proximity to abandoned mines were observed to have diverged from neighboring populations as a result of selection pressure for heavy metal tolerance. In addition to evolving tolerance to heavy metals, the new populations self–pollinate and flower at different times. These characteristics reproductively isolate the heavy–metal tolerant populations.

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Sympatric Speciation

- Reproductive isolation evolves within a single, freely interbreeding population.
- Genetic divergence arises largely through diversifying selection and polyploidy.
- Proposed explanation for speciation of *Rhagoletis.*
- The most controversial of the geographic modes of speciation.

Common hawthorn flowers
Crataegus monogyna

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Sympatric Speciation

In **sympatric speciation**, reproductive isolation is said to arise within a single, freely, and randomly interbreeding population in the absence of any spatial segregation. Thus, gene flow is initially restricted by biological features of organisms rather than by geography or distance. Because even low levels of gene exchange can swamp out the build up of genetic differentiation that is required for speciation, the occurrence of sympatric speciation is highly debated and controversial. Models of sympatric speciation propose various evolutionary forces and processes as the driving force behind the genetic divergence required for reproductive isolation in sympatry, including diversifying selection (a form of natural selection) and polyploidy (when multiple, duplicate copies of the genome are present within individuals).

When populations inhabit environments with multiple resources and microhabitats, some individuals may possess traits or characteristics that allow them to use one of the resources and/or microhabitats more efficiently. Over time, diversifying selection can cause the population to split into genetically distinct groups that are adapted to discreet niches or the use of different resources within the environment. If selection pressures are strong enough to overcome gene exchange in the population, speciation can occur in sympatry.

An example of sympatric speciation resulting from diversifying selection may be found in flies of the genus *Rhagoletis*. These flies exhibit strong fidelity to the host plants in which they mate and leave their offspring to develop. Until the mid-nineteenth century, *Rhagoletis* in the northeastern United States used hawthorns exclusively as their host plant. However, when apples were introduced in some areas approximately 150 years ago, a new "race" of *Rhagoletis* appeared that inhabits apples rather than hawthorns. Because hawthorns and apples are often found in the same geographic area, the hawthorn and apple-maggot flies can exist in trees that are only yards apart. Many consider that the hawthorn flies are the parent species of the apple flies and that the speciation event was initiated by genetic variations that caused some members of the original population to be attracted to new hosts. This argues for sympatric speciation in *Rhagoletis.* However, this claim has come under debate. For example, some argue that the hawthorn and apple-maggot flies descended from distinct, independent lineages, through allopatric speciation.

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Polyploidy

- Sympatric speciation can occur through polyploidy.
- Polyploids:
  - have more than two sets of chromosomes;
  - are reproductively isolated from their non-polyploid parent species; and
  - are rare among animals but common among plants.

Grey tree frog
Hyla versicolor

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Polyploidy

While many models of sympatric speciation remain somewhat controversial among evolutionary biologists, most (if not all) agree that sympatric speciation can occur through **polyploidy**, the inheritance of more than two basic genome copies as a result of errors during cell division. Polyploids (organisms with more than two duplicate sets of chromosomes) are named according to the number of chromosome sets they have within their nuclei: a triploid has three sets of chromosomes (3n), a tetraploid has four sets (4n), etc.

Polyploid organisms are immediately reproductively isolated from their diploid parent species. For example, a failure during meiosis can cause diploid (2n) parent species to produce tetraploid (4n) offspring. However, crosses between a diploid and a tetraploid will result in inviable or sterile offspring due to abnormal chromosomal pairings during mitosis or meiosis. In fact, for the tetraploid organism to successfully reproduce, it must fertilize itself or mate with another tetraploid. Thus, polyploidy can result in instantaneous speciation in a single genetic event.

Polyploidy is very common in plant species. It is estimated that 35% of flowering plant species are polyploid. While relatively rare, polyploidy is also found in animal species, such as the frog *Hyla versicolor*, a tetraploid derived from the diploid *Hyla chrysoscelis*. Polyploidy also provides an immediate way for hybrids of otherwise incompatible parent genomes to produce fertile offspring.

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Rate of Speciation

- For many populations, the full process of speciation can take large periods of time.
- Speciation rates:
  - vary widely both between populations and within a single population over time, and
  - are influenced by a variety of factors including the size and degree of geographic isolation of a population.

Snapping shrimp
Alpheus digitalis

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Rate of Speciation

We have considered some of the modes, mechanisms and evolutionary forces that play a role in the formation of new species, but we have not addressed how long the process of speciation takes. This question is difficult to address scientifically because, although the full process of speciation can happen almost instantaneously through polyploidy, in the vast majority of cases the evolutionary changes that lead to speciation occur over large periods of time. It is therefore difficult (if not impossible) for scientists to study speciation rates directly. In theory, this problem could be at least partially resolved by studying the fossil record, which chronicles the patterns of evolutionary change over millions of years. However, the fossil record is incomplete; only a small proportion of species that have existed have been successfully preserved as fossils, and many of those fossils have either been damaged or have simply not yet been discovered.

Due to these inherent problems, scientists who are interested in understanding the pace of speciation and the factors that influence it must consider information from a variety of sources including the fossil record, anatomical studies of living organisms, and the fields of ecology and genetics. These studies suggest that a number of factors influence speciation rates including the degree to which a population is geographically isolated, the novelty and stability of the environment, the size of the population, and the amount of genetic variability that exists within the population. As a result, the rate of speciation can vary widely, both between populations and within a single population over time. Some populations of snapping shrimp (*Alpheus*) that are found on opposite sides of the Isthmus of Panama have not yet achieved full reproductive incompatibility, despite the fact that they have been separated ever since the isthmus emerged, approximately three million years ago. In contrast, it is estimated that for some species of Hawaiian *Drosophila*, speciation occurred in less than 800,000 years.

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Summary: Modes of Speciation

- Speciation occurs when a population evolves genetic distinctiveness and becomes reproductively incompatible with other populations.
- There are four geographic modes of speciation, based on the extent to which the incipient species are geographically isolated from one another: allopatric, peripatric, parapatric, and sympatric.
- The rate of speciation can vary widely both between populations and within a single population over time.

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