

# SPECIATION

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## OVERVIEW

Speciation is the origin of new species. Generally, this entails one species changing over time and eventually becoming two species. It consists of the evolution of biological barriers to gene flow (reproductive isolation) between two populations of the same species. As a field of scientific investigation, it links the fields of macroevolution and microevolution, including the fields of genetics, ecology, behavior and biogeography. It is currently one of the most active and exciting areas of evolutionary biology.

## WHAT IS A SPECIES?

This seemingly simple question has actually been very hard to answer. Defining the term species has been problematic for evolutionary biologists for decades. The difficulty in determining what, exactly, a species is, arises because *speciation is a continuous, ongoing process*. Often, there is a continuum of variation between populations and species. Our perspective is analogous to a photograph; when we examine populations today, we see only a snapshot, a single moment in the lifetime of a species. When, in that gradual continuum populations of one species are genetically different enough to merit the distinction of being separate species is not always clear.

Still, biologists have attempted to tackle this question and obtain a meaningful definition of a species. A **species concept** is a way of defining a species, and a recent reviewer found 24 different species concepts that have been proposed over the past century. The most famous, and the one that most biologists use today, is the *biological species concept*, which states that *species are groups of actually or potentially interbreeding populations, which are **reproductively isolated** from other such groups*. In other words, *speciation is the evolution of reproductive isolation* between two groups. Operationally, this definition works well for most animals. However, it has limitations: it does not always work with plants, and it cannot be applied to extinct species (e.g. fossils) or asexually reproducing species (e.g. bacteria).

## WHAT CAUSES SPECIATION?

*Speciation, or the evolution of reproductive isolation, occurs as a by-product of genetic changes that accumulate between two previously interbreeding populations of the same species.* For example, let us start with two populations of the same species that do not differ genetically. Initially, an individual from population A is able to successfully breed with an individual from population B. As these populations evolve, they each gradually accumulate genetic changes that are different from the other populations' genetic changes. In other words, the two populations genetically **diverge** from each other. These changes can be due to different selection pressures because of different environments, or because of genetic drift/founder events.

At some point in this process, some of these genetic changes cause the two populations to become reproductively isolated from each other. In other words, these genetic changes no longer allow an individual from population A to successfully breed with an individual from population B. They prevent gene flow between populations. These specific genetic differences that confer reproductive isolation are called **reproductive isolating mechanisms**.

There are several different types of reproductive isolating mechanisms, which are classified according to when in the life cycle of the organism isolation occurs (see Table 1 for a summary). Isolation can occur before fertilization (**prezygotic barriers**) or after fertilization (**postzygotic barriers**).

Prezygotic isolation can occur either before mating occurs (pre mating barriers) or after mating occurs (post mating barriers). One type of pre mating prezygotic isolation occurs when potential mates from the two populations do not meet, either because they are separated in time (**temporal isolation**) or in space (**habitat isolation**). Temporal isolation can occur if individuals in two different populations mate at different times of the day or in different seasons, or even years (e.g. species of periodical cicadas mate either every 7 years or every 13 years). Habitat isolation occurs, for example, when herbivorous insects from two populations feed and mate on different host plants. Another type of pre mating prezygotic isolation occurs when individuals from two populations meet, but they do not mate (**behavioral or sexual isolation**). This occurs, for example, when courtship behaviors differ between individuals of two populations (e.g. songs in birds, pheromones in moths, light displays in fireflies, etc.).

Table 1: Reproductive Isolating Mechanisms

**Prezygotic Barriers**

- pre mating
  - habitat isolation
  - temporal isolation
  - behavioral isolation
- post mating
  - mechanical isolation
  - gametic isolation

**Postzygotic Barriers**

- hybrid inviability
- hybrid sterility
- hybrid breakdown

One type of postmating prezygotic isolation occurs when mating actually takes place, but male gametes are not actually transferred to the female (**mechanical isolation**). This happens when there is an anatomical incompatibility between individuals from two populations. For example, the floral anatomy of some plant species prevents some pollinators that visit the plant from actually transferring pollen. In this case, mating (pollination) occurs, but the male gametes (pollen) are not able to reach the eggs. A

second type of postmating prezygotic isolation occurs after mating taking places, male gametes are actually transferred, but the egg is not fertilized (**gametic isolation**). This can be an important isolating mechanism in externally reproducing species that send out their gametes en masse. Sea urchins, for example, release their gametes into the water column. In reproductively isolated species, male and female gametes actually meet, but the sperm does not fertilize the egg. Another example of this would be when pollen from a plant of one species lands on the stigma of a plant from another species, and a pollen tube is not completely formed. In both of these cases, a genetic mismatch between the gametes prevents successful fertilization.

There are three types of postzygotic isolating mechanisms. In the first type, mating occurs, a zygote is formed, but the hybrid has reduced viability (**hybrid inviability**). In other words, hybrids do not survive long enough to reproduce. The other type of postzygotic isolation occurs when hybrids are viable, but they have reduced fertility (**hybrid sterility**). A classic example is the mule, which is the result of a cross between a donkey and a horse. Mules are viable, healthy animals, but they are always sterile (i.e. they are unable to successfully reproduce). The third type of postzygotic isolation occurs when hybrids are viable and fertile, but the offspring of the hybrids are inviable or sterile (**hybrid breakdown**). In all of these postzygotic examples, individuals from the two populations will mate with each other, and the gametes fuse, but the genetic material in each of the gametes differs enough that the combinations of alleles are not compatible.

## HOW DOES SPECIATION OCCUR?

There are several different ways in which the evolution of reproductive isolation is thought to occur. These can, however, be generalized into a series of events, or steps.

### The “Steps” in a speciation event:

**Step 1: gene flow between two populations is interrupted**

(populations become genetically isolated from each other)

**Step 2: genetic differences gradually accumulate between the two populations**

(populations diverge genetically)

**Step 3: reproductive isolation evolves as a consequence of this divergence**

(a reproductive isolating mechanism evolves)

The main difference between the different models of speciation is in the first step, or how the populations become genetically isolated from each other (see below).

### Allopatric Model of Speciation

The **allopatric model of speciation** is thought to be the most prevalent mode of speciation in animals. In this model, *gene flow between two populations is interrupted by a physical or geographic barrier* (step 1). The two populations are physically separated from each other, and individuals from the two populations cannot, therefore, mate. This type of isolation occurs, for example, when a geological process splits a large population into several physically isolated populations (a river forms a canyon, a land bridge forms and isolates marine organisms on either side, a mountain range forms, a glaciation event fragments patches of previously contiguous habitats, etc.). Alternatively, colonization events can isolate a new population from its parent population; for example, when a few individuals disperse from a mainland and colonize an island.

In each of these situations, populations become physically separated from each other. Individuals from one population can no longer mate with individuals from the other population—there is no gene flow between them. Within each of these populations genetic changes occur. The genetic changes that accumulate in one population will be different from the

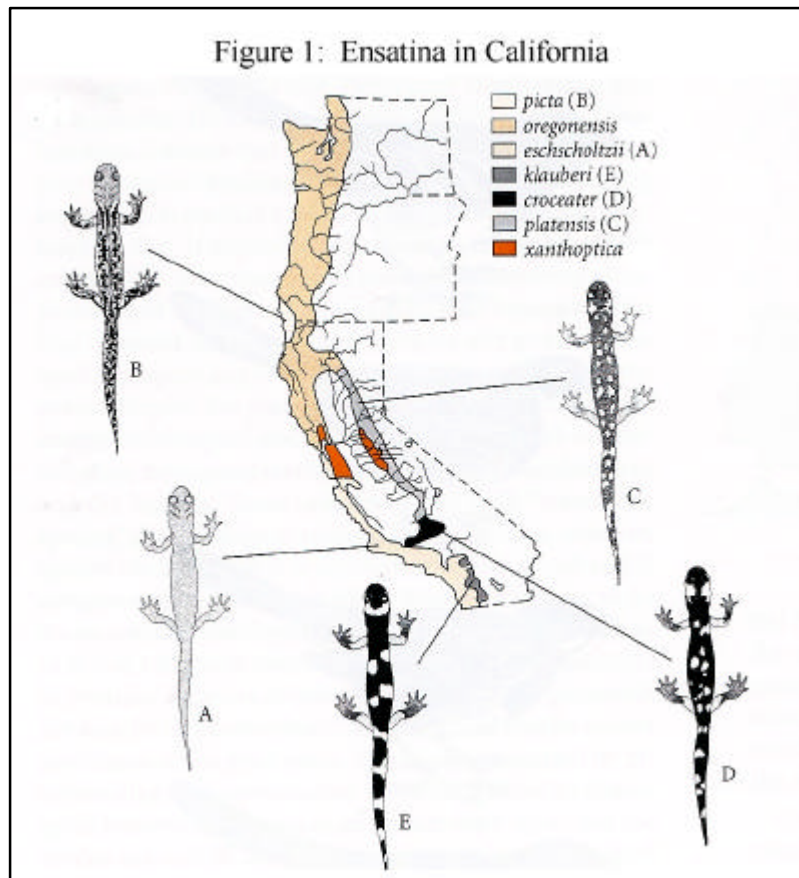
genetic changes accumulated in the other population: the populations will genetically diverge (step 2). *The reasons the physically isolated populations will genetically diverge are genetic drift, and differences in natural selection between the two populations.* Genetic drift acts on all populations, and can be especially strong in small populations, as you would find with a fragmented larger population, or in a small founding population. Furthermore, natural selection may differ between the two populations if they differ in habitat type (especially in newly colonized areas). The populations may also experience different types of changes in their environment.

Eventually, the populations may come back together, called **secondary contact**, with the renewed potential for gene flow. If the two populations have not genetically diverged enough, then there may be successful interbreeding among individuals from the two populations. In this case, speciation has not occurred, and the two populations will eventually merge. The genetic divergence that had occurred before secondary contact will disappear as individuals from the two populations interbreed. On the other hand, *if the two populations have genetically diverged enough so that hybrids, if there are any, are sterile or inviable, then speciation has occurred*, and the populations have evolved into two completely isolated species (step 3).

If only postzygotic isolation has occurred (i.e. hybrids are inviable or sterile and thus have a lower fitness than non-hybrids), then there may be selection pressure for the evolution of premating isolation. There will be selection, for example, for behavioral isolation. In other words, since their offspring will be viable and fertile, the individuals that are able to choose mates only from their own population will have a reproductive advantage over individuals that choose mates from either population. This selection for traits that prevent hybridization is called **reinforcement**.

Several types of geographic patterns in species distribution provide evidence of allopatric speciation. For example, geographic populations of the same species are often genetically different from each other, and these differences are most pronounced when gene flow between the populations is reduced by a physical barrier (e.g. populations on islands). In addition, geographic populations of the same species show some degree of reproductive isolation (both prezygotic and postzygotic) when tested in the laboratory. Note that reproductive isolation is not an “all or nothing” phenomenon—it varies from complete interbreeding to some interbreeding to no interbreeding at all.

**Ring species** also provide evidence that speciation has occurred allopatrically. Ring species consist of a chain of interbreeding populations that surround some physical barrier, like a mountain range or a desert valley, with the terminal two populations unable to successfully interbreed. It is inferred that originally there was a single population at one end of the barrier, and gradually, individuals from this original population dispersed along both sides of the barrier. These populations on either side of the barrier were geographically, and thus genetically, isolated from each other. Genetic changes gradually accumulated in populations on both sides of



the barrier. Eventually, members of the populations on both sides had expanded their range enough so that the populations had eventually extended all the way around the barrier. These terminal populations then made secondary contact. These two populations had been isolated long enough, and diverged enough that individuals from the two sides of the barrier were no longer able to successfully interbreed. The *Ensatina* salamanders in California are one example of this phenomenon (Figure 1)<sup>1</sup>. In this figure, individuals from all adjacent populations can interbreed, with the exception of individuals from populations A and E, which are reproductively isolated from each other.

## Sympatric Model of Speciation

<sup>1</sup> This figure was modified from Futuyma 1998.

Another type of speciation is **sympatric speciation**. The main difference between sympatric and allopatric speciation is in how gene flow is interrupted (step 1). In allopatric speciation, two populations are physically separated from each other; individuals from the two populations are genetically isolated from each other because there is a physical barrier between them that does not allow them to interbreed. ***In sympatric speciation, however, the populations are not physically or geographically isolated from each other; they live in the same place.*** Gene flow between the two populations is interrupted through mechanisms other than simply being physically separated. One model of sympatric speciation is by *ecological isolation*. This occurs when there is disruptive selection for resource use, and when mating occurs exclusively on the resource. This is thought to occur, for example, when in an herbivorous insect species there are individuals with one of two distinct phenotypes: preference for host plant A and preference for host plant B, such as *Rhagoletis* flies.

*Rhagoletis* flies are native to North America. Their original, native host plants are hawthorn trees. Apple trees were introduced in North America more than 300 years ago, and they grow in the same habitats as hawthorns. Now, some flies use apple trees instead of hawthorns as their host plants. Experiments have shown that flies have a strong genetic preference for the tree (apple or hawthorn) on which they were found, and that mating takes place on the host plant. Because flies specialized for apples may never encounter/mate with flies specialized for hawthorns, this is a situation in which sympatric speciation can occur. Has it? Are the flies on apples genetically distinct from the flies on hawthorns? It turns out that flies that use apples are genetically different from the flies that use hawthorns. Even though these two populations are found in the same areas, they are isolated enough ecologically that genetic divergence has occurred, and they are considered incipient species (i.e. they are currently partially reproductively isolated).

A different type of sympatric speciation occurs in plants. Many plant species are thought to have originated through sympatric speciation, through a process known as polyploidy. *Polyploidy occurs when there is an accident in cell division that results in extra sets of chromosomes.* There are two types of polyploidy; the first is autopolyploidy, which is a failure of division in meiosis that results in double the number of chromosomes (e.g.  $4n$ , called tetraploidy). Tetraploids can self-pollinate or mate with other tetraploids, but not with individuals of either of their diploid parent species. The more common type of polyploidy is

allopolyploidy, in which individuals from two distinct species interbreed and combine chromosomes. It is thought that speciation by allopolyploidy<sup>2</sup> accounts for 25 – 50% of all plant species. Evidence for speciation by polyploidy comes from natural polyploid species that have been experimentally reproduced in the laboratory. For example, the mint *Galeopsis tetrahit* was hypothesized to have originated from hybridization between two species: *G. pubescens* and *G. speciosa*. Workers were able to experimentally reproduce *G. tetrahit* that resembled natural *G. tetrahit* and was able to successfully interbreed with it.

## GENETICS OF SPECIATION

Currently, one of the big topics in research on speciation is the genetics of speciation. For example, what types of genetic characters confer reproductive isolation? A simple example of this can be seen in the *Rhagoletis* system. As mentioned above, the population on apples has diverged genetically from the population on hawthorns. At least some of the genetic divergence between these two populations is in a character that confers reproductive isolation: length of diapause (Smith 1988). Insects often diapause (go dormant) during the winter. Length of diapause is a genetically influenced character that often evolves to match the arrival of fruits on the host plant. In this case, apple fruits mature earlier in the summer than hawthorn fruits (although there is overlap in the timing of fruit production). It turns out that apple flies end their diapause earlier than hawthorn flies, and this genetic divergence in length of diapause may lead to temporal isolation—reproductive isolation due to differences in timing of mating.

The many examples of the genetics of reproductive isolation that have been studied so far indicate that prezygotic isolation is often caused by divergence in ordinary traits, such as length of diapause, courtship behavior, size of sexual organs, and sex pheromones. Postzygotic isolation is a bit more complicated, and includes complex genetic interactions, such as epistasis (Orr 2001).

## Resource List

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<sup>2</sup> Incidentally, this technique of speciation by hybridization is used by horticulturalists to create new species of irises, orchids, and many other cultivated plants.

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## LESSONS ABOUT SPECIATION

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To investigate the species question, there is a lesson at Access Excellence, called **“Studying Species by Examining the Evolution of the Canidae Family.”**

[[[www.accessexcellence.org/AE/AEPC/WWC/1995/canidae.html](http://www.accessexcellence.org/AE/AEPC/WWC/1995/canidae.html)]] This is a reading activity and writing assignment that helps the students to explore the relationship between the gray wolf and the domesticated dog. With the given information, students write an essay arguing either that these two groups are the same species, or that they are two separate species.

To begin a discussion of geographic isolation and speciation, check out AE’s lesson: **“Australian Mammals: Evolutionary Development as a Result of Geographic Isolation.”**

[[[www.accessexcellence.org/AE/AEPC/WWC/1995/australia.html](http://www.accessexcellence.org/AE/AEPC/WWC/1995/australia.html)]] This activity explores the unique fauna of Australia, and attempts to get the students to think about why they are so different (i.e. geographic isolation).

Offner (1994) [[link to reference cited page]] discusses ways to use chromosomal rearrangements to talk about speciation. She uses several examples of speciation events that may have been precipitated by chromosomal rearrangements (e.g. humans and chimpanzees, giant pandas and bears).

There are two lessons on speciation, per se. The first is **“Island Biogeography and Evolution,”** which can be found at Evolution and the Nature of Sciences Institutes [[[www.indiana.edu/~ensiweb/lessons/island.html](http://www.indiana.edu/~ensiweb/lessons/island.html)]] or at the University of California’s Museum of Paleontology. [[[www.ucmp.berkeley.edu/fosrec/Filson.html](http://www.ucmp.berkeley.edu/fosrec/Filson.html)]] In this lesson, the students are asked to determine how several species of lizards are related, using various types of real data. The other lesson on speciation **“A Step in Speciation,”** also found at the ENSI site, [[[www.indiana.edu/~ensiweb/lessons/step.sp.html](http://www.indiana.edu/~ensiweb/lessons/step.sp.html)]] explores the geographic pattern of distribution in the *Ensatina* salamander group—a ring species. The students map the distribution of the different subspecies onto a map of California, and then discuss their evolutionary relationships.

### Reference Cited:

Offner, S. 1994. Using chromosomes to teach evolution: II. Chromosomal rearrangements in speciation events. *The American Biology Teacher* 56 (2): 86 – 93.