

**Macroevolution Part II:
Allopatric Speciation**

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Looks Can Be Deceiving!

- These meadowlarks *look* very similar yet they are **not** the same species.
- By contrast, these brittle stars *look very different* from one another, but they are the same species.

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Definition of Species

- A species is a group of interbreeding organisms that produce *viable*, fertile offspring in nature.
- Members of a species will interbreed with one another but not other organisms outside of the species. (At least most of the time!)

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Macroevolution vs. Microevolution

- Macroevolution is evolution on a scale of separated gene pools.
- Macroevolutionary studies focus on change that occurs at or above the level of species, in contrast with microevolution, which refers to smaller evolutionary changes (typically described as changes in allele frequencies) within a species or population.

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Asexual Species

Asexual Species

Even though asexual groups do not exchange genes, they do form recognizable groups.

Most have evolved from a sexual species. Only those whose phenotype is best adapted to the environment, will continue to survive. However, it makes them less adapted to environmental change.

Dandelions are asexual. The pollen is sterile and the egg is diploid.

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Ring Species

- A **ring species** is a connected series of *neighboring populations*, each of which can interbreed with closely sited related populations, but for which there exist at least two "end" populations in the series.
- These end populations are too distantly related to interbreed, though there is a potential gene flow between each "linked" species.
- Such non-breeding, though genetically connected, "end" populations may coexist in the same region thus closing a "ring".

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Ring Species

- Ensatina escholtzi* is a salamander ring species that has a range along the coast and inside range of California.
- All along this range, the salamanders interbreed, but the salamanders on the ends of the ring do not interbreed.
- Their groupings are called *subspecies*.

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Ring Species

- The blue zones represent where interbreeding is occurring.
- So are there is gene flow all along the salamander's range, yet the ends of the rings do not interbreed. Are they the same species?

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Ring species: exciting, and tricky

A ring species is a series of **geographically neighboring populations** that are **linked** together.

Members of adjacent groups are **interbreed**. This would make them **the same species**, despite some differences.

Members of populations near the ends of the sequence **do not interbreed**. This would make them **separate species**.

In mathematics: If $A = B$, and $B = C$ then $A = C$

But in a ring species: $A = B, B = C, C = D, D = E$ but $A \neq E$

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Limited Interbreeding

- Each *Canis* species will interbreed with the domestic dog but not readily with one another.
- This is true, even when given the opportunity to do so. Thus, they are *not* the same species since they *do not* interbreed in nature.

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Limited Interbreeding

- Tigers and lions will interbreed in captivity, but they do *not* interbreed in nature.
- Lions form groups or prides and live in the grasslands.
- Tigers are more solitary and live in the forests.
- Tiglon are products of male tigers and female lions.
- Ligers are the opposite cross.

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Cladogenesis vs. Anagenesis

I. Anagenesis- is the accumulation of changes in one species that leads to another species. It is the lineage of a species. Over time a species may accumulate enough changes that it is considered a species that differs from the ancestral species.

II. Cladogenesis- is the *budding* of one or more new species from an ancestral species that continues to exist. This results in biological diversity.

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Allopatric vs. Sympatric Speciation

Allopatric speciation- Speciation occurs because a given group has been separated from the parent group, usually because of a geographic separation as time goes by.

Sympatric speciation-speciation occurs even though the two groups are still living in the same area.

(a) Allopatric speciation (b) Sympatric speciation

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Allopatric Speciation

- First, geographic isolation occurs. This is an extrinsic isolating mechanism.
- The two populations must become isolated geographically from one another.
- If the groups become sympatric again one of two things result...

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Allopatric Speciation

- They become separate species, as evidenced by the fact they can no longer interbreed.
- They can still interbreed, thus they remain the same species.

Islands produce some of the most profound examples of speciation due to geographic isolation.

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Why does speciation occur after geographic isolation?

- The population that left the original group will have a different allelic make-up than the original species, thus experiencing the "founder effect".
- The two groups will continue to experience different mutations.
- The two groups will now experience genetic drift and different selection pressures due to living in separate and perhaps different environments.

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Adaptive Radiation

- The classic adaptive radiation example involves the finches of the Galapagos Islands.
- There are 14 different species of finches and 13 main islands, 3 smaller islands, and 107 rocks and islets.

Adaptive Radiation

Adaptive Radiation

- One would expect that each island would have only one species, however, each island has more than one species of finch and larger islands may have as many as ten.
- The process one species inhabiting a new area and evolving into several new species is called **adaptive radiation**.

The Amazing Galapagos Islands

Adaptive Radiation

- Lets suppose that finch species A, from South America migrates to an island 1.
- Finch species A would undergo speciation into finch species B due to one or more of the following:
 - The Founder effect
 - Varying selection pressures
 - Varying mutations

Adaptive Radiation

- Now let's suppose that some of the new finch species B migrate over to a second island. 2 (speciation) & 3 (migration)
- The finches in this new environment are *geographically isolated* from the other island and now will evolve into finch species C for the same three basic reasons. (Founder effect, varying selection pressures, or varying mutations.)

Adaptive Radiation

- Now *some* of the newly evolved finch species C 4 make their way to yet another new island. 5
- Guess what? Yep! Once again finch species C will evolve into finch species D (not shown yet) for the same three reasons. (Founder effect, varying selection pressures, or varying mutations.)
- But** suppose some of species C make it **back to the first island.** 6 (The plot thickens...)

Adaptive Radiation

- Obviously, species C is different from finch species B thus they can no longer interbreed back on the original island.
- Finch species C may *or* may not evolve into another species.
- If there is a niche similar to that of the second island, the selection pressure may also be similar and species C may be slow to change.
- So, both first and second islands will have species C. The third island will have a new species D.

Adaptive Radiation

- Now lastly, lets suppose that finch species D from the third island returns to the first *and* second islands. 7 & 8
- On the *second* island finch species D *does not change* because it finds a niche similar to the third island so no selection pressure is exerted upon it.

Adaptive Radiation

- Alas, the *first island* has no such niche. Now, there exists a selection pressure on finch species D causing it to evolve (character displacement) into species E. 9
- As a result, the *first island* now has **three different species of finches**. Two of which are not found on other islands (B & E). Each species has a distinct habitat with different food sources. This process is called adaptive radiation and most commonly involves islands.

The Amazing Galapagos Islands

So, NOW we understand how it is possible that each island has more than one finch species. Some islands actually have as many as 10 species. Examine the map once more.

The Amazing Finches From the Galapagos Islands

Differences are found among the beaks and feathers of the finches. Darwin found 14 different species of finches inhabiting these islands which are a result of adaptive radiation. There are finches that eat seeds, cacti, insects and other interesting foods. He also observed adaptive radiation among the tortoises and mocking birds.

The Amazing Finches From the Galapagos Islands

- Vegetarian Finch
- Warbler finch
- Large insectivorous tree finch
- Medium insectivorous tree finch
- Mangrove finch
- Small insectivorous tree finch
- Large cactus ground finch
- Cactus ground finch
- Cocos finch
- Woodpecker finch
- Large ground finch
- Sharp-beaked ground finch
- Medium ground finch
- Small ground finch

Example of Natural Selection

- During droughts in the Galapagos Islands, larger seeds are more abundant. Finches with slightly larger beaks have an advantage since they are able to crack larger seeds.
- Thus, natural selection favors finches with larger beaks. These finches are more likely to survive and pass those genes on to the next generation. A study conducted by Peter and Rosemary Grant over a 20 year period confirmed these assertions.

How Does Speciation Occur?

Individuals of different species

PREZYGOTIC BARRIERS

- Behavioral isolation: populations live in different habitats and do not meet
- Behavioral isolation: little or no sexual attraction between males and females
- Temporal isolation: mating or flowering occurs at different seasons or times of day
- Mechanical isolation: structural differences in genitalia or flowers prevent copulation or pollen transfer
- Genetic isolation: female and male gametes fail to attract each other or are unable to fuse

POSTZYGOTIC BARRIERS

- Reduced hybrid viability: hybrid offspring fail to develop or fail to reach maturity
- Reduced hybrid fertility: hybrids fail to produce functional gametes
- Hybrid breakdown: offspring of hybrids have reduced viability or fertility

Each Prezygotic and Postzygotic barrier left explains HOW speciation occurs.

Prezygotic: Ecogeographic Isolation

- Ecogeographic Isolation** – Two populations have become so specialized for survival in different environments, that once the geographical barrier is removed the two species will never again interbreed as one species. The adaptations for survival in their geographic locations prevent gene flow.

Prezygotic: Ecogeographic Isolation

- The *Plantus occidentalis* (sycamore tree) is found in the eastern United States and the *Plantus orientalis* (oriental plane tree) is found in the Mediterranean area.
- They can form fertile hybrids when artificially crossed but are so different from one another that neither tree can survive in the other's habitat.

Sycamore Tree Oriental Plane Tree

Prezygotic: Habitat Isolation

Bufo woodhousei and *Bufo americanus*

Habitat isolation- two species have developed a preference for two different habitats. Even if the species become sympatric, the probability that they will meet and mate is low.

Example: *Bufo woodhousei* and *Bufo americanus* are two closely related toads. *B. woodhousei* prefers to reproduce in the quiet water of a stream whereas *B. americanus* prefers to reproduce in shallow rain-pools. As a result, they remain separate species.

Prezygotic: Seasonal Isolation

Seasonal isolation- the two species have developed different times of the year to mate.

Example: There are four species of frogs from the genus, *Rana*, each of these frogs mates at different times of the year so that if they are sympatric, no interbreeding occurs.

Prezygotic: Behavioral Isolation

Behavioral isolation- If courtship behavior changes during separation, then sympatric mating will not occur and two new species are formed.

Example: Twelve fiddler crab species inhabit a certain beach in Panama. Males of each species have distinctive mating displays which include waving claws, elevating the body, and moving around the burrow.

Prezygotic: Mechanical Isolation

Mechanical isolation- There is a physical or biological structure that prevents mating. For example differences in the size or fit of genitalia may not allow mating. This can be found in certain snails, insects and plants.

Example: The *Bradybaena* shown are two different species of snails because the shells spiral in opposite directions, thus they are unable to mate with one another.

Prezygotic: Gametic Isolation

Gametic Isolation: The gametes are shed simultaneously but something physical or chemical prevents the sperm from fertilizing the egg.

Example: Many sea urchin species shed their gametes at the same time, but remain evolutionarily distinct.

The formation of hybrid zygotes is prevented because the surface proteins of the ovule (the "lock") and sperm, or male gametes (the "keys") of different species do not fit together.

Postzygotic: Developmental Isolation

The next isolating mechanisms are postzygotic meaning the zygote is indeed formed. Energy and resources are wasted in producing gametes and subsequent zygote production, yet no offspring.

Developmental isolation- If fertilization occurs, the development of the embryo can be irregular and is thus spontaneously aborted.

Example: Sheep belong to the genus *Ovis* and have 54 chromosomes, while goats belong to the genus *Capra* and have 60 chromosomes. When goats and sheep mate, they produce embryos that die prior to birth.

Postzygotic: Hybrid Inviability

Hybrid inviability- A hybrid is produced, but often does not make it to reproductive age because it is weak, irregular, etc.

Example: When tobacco hybrids are successful, they often form tumors. These tumors are located in their vegetative parts. Often no flowering occurs, thus no reproduction occurs.

Postzygotic- Hybrid Sterility

Hybrid sterility- some hybrids produce superior offspring but the offspring are sterile.

Example: A mule is the result of female horse crossed with a male donkey. Mules are sterile, thus there is no potential for gene flow. In terms of evolution it is a dead end. The horse is on the left, the donkey is in the center and the mule is on the right.

Postzygotic: Selective Hybrid Elimination

Selective hybrid elimination or hybrid breakdown occurs if two species are sympatric and can hybridize, and their offspring can reproduce.

One of the following two things will happen:

- The hybrids are as viable or as fit as the parents and gene flow will occur and the two species will become one again.
- The hybrids are weaker or have lower fitness than the parents and will be selected against.

Postzygotic: Selective Hybrid Elimination

- Natural selection will select for those individuals that will mate with their own species and the hybrids will die out. The competition between the two species will cause character displacement.
- Example: the offspring of rice hybrid are not as fit as the parents. Crosses between the purebred parents will be favored.

Summary of Prezygotic Barriers

When allopatric speciation occurs, usually more than one isolation mechanism also occurs and more than one trait will change between the two populations.

Summary of Postzygotic Barriers

Postzygotic barriers keep two populations distinct, thus they are no longer the same species and can no longer **interbreed** to produce **viable, fertile, offspring** in nature. Again, when two population are allopatric and changes occur, most likely more than one of the 10 barriers will occur in the population leading to speciation.

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