

Evolution lecture #13 -- **Speciation** -- Dec. 5<sup>th</sup>, 2008

487-506 (ch. 24) **in 8th ed.**

472-480 (ch. 24) **in 7th ed.**

## • Summary of topics

- Describe the **biological species concept** and understand its limitations; be aware of **other species concepts, especially the phylogenetic species concept**
- Understand different mechanisms of **reproductive isolation**
- Contrast **allopatric** and **sympatric** modes of speciation
- Describe examples of **species clusters** in connection to concepts of niche, adaptive radiation, and convergent evolution

## • Species concepts

### Why classify organisms?

All societies classify local plants and animals because they are important to them. We want to eat some; we want to exploit some; we want to avoid eating others; and we want to avoid being eaten or harmed by still others.

In Europe, the age of exploration and especially the discovery of North and South America created the need to classify a huge number of new organisms, some of which were very similar to what was known in Europe and others of which were completely different. Linnaeus was the first to successfully devise a system of classifying all organisms and be able to accommodate new types.

Now, one of the main reasons to refine our methods of classification is to understand and preserve natural diversity.

**Species:** A basic "kind" of organism; designated through a concept most appropriate to the group of interest, often limited by criteria available to diagnose membership in and boundaries of this group. This is a very controversial topic -- there are many competing species concepts (more than 20!). For our purposes, these four are sufficient to discuss:

- The **typological species concept** (sometimes known as the **morphological species concept**) groups organisms into species based on a common morphology, or body plan. This was the concept of the ancient Greeks up through Linnaeus, but still may be used today (e.g., by historical biologists such as paleontologists who have morphology and want to estimate time of presence in the fossil record).

Linnaeus's definition was that a species is a group of organisms that share important characters, and are dissimilar enough to in these essential characters from other groups be regarded as distinct.

The emphasis is on morphology rather than behavior or environment because much of the classification was and still is done with preserved specimens.

The morphological definition works in many cases. Traditional societies, which depend on their environment for food, recognize different species. Western scientists usually agree with their distinctions although they usually recognize more species.

- The **biological species concept**, explicated by Mayr (1942), is widely used in biology for sexually reproducing organisms (Fig. 24.4 (8th); Fig. 24.3 (7th)). Here a species consists of members of a group of populations that interbreed, or potentially interbreed, with each other under natural conditions. The biological species concept hinges on reproductive isolation with each species isolated by factors (barriers) that prevent interbreeding, thereby blocking genetic mixing with other "types".

Even though the BSC is widely accepted, it cannot always be used in practice.

In one location, it is usually possible to tell which groups are interbreeding, so identifying species is not too difficult, at least to people very familiar with particular groups. Sometimes, close observation will allow splitting of species previous thought to be a single species.

In groups in different areas or groups known only from specimens or fossils, it is usually impossible to know whether interbreeding would occur. In that case, the extent of morphological variation between species within a region is used as a guide so say whether groups in different areas are species, subspecies, geographic races. It is ultimately a subjective judgment and, as in all such situations, people defend vigorously their own interpretations. *Ensatina* is an example. If the intermediates were now known, the ends would be good species. Two species of birds (yellow and red tailed flickers) were thought to be good species. When one of them expanded its range, they hybridized, so they are now subspecies of one species. If you accept that species have evolved, then you should expect a whole spectrum of intermediate cases to exist, making it impossible to say exactly how different two species are.

- The **phenetic species concept**, which views species of clusters of similar organisms whether based on molecular or morphological data, is widely used in biology in cases where researchers think the biological species concept doesn't apply. It is applied for example in bacteria and in many plants that may be either asexual or else engage in widespread hybridization. Researchers who favor this approach often think that ecological factors and stabilizing selection are more important for keeping species separate than barriers to interbreeding.

One problem with a morphological definition is that it is difficult to say how different two groups have to look in order to be called different species, or how similar they have to look to be put in the same species.

Another problem with the morphological definition is that males and females might be classified as different species, although they will not be if their reproductive biology is known. In practice, the phenetic species concept tries to take into account such variation. Even though people can look very different, we are all in the same species.

New genetic data may help, but the logic is the same as for morphological characters. The difference will be that you do not need specialists in the morphology of each group, once a standard of difference is agreed upon.

- The **phylogenetic species concept** is the most recently developed and looks at species from the standpoint of cladistics. Like cladistic taxa at other ranks, species are defined by the splitting of lineages (cladogenesis) through time. In this approach a species is the smallest monophyletic group recognized in a classification. All types of criteria are used as potential synapomorphies to determine evolutionary relationships (i.e., build a cladogram) of individual organisms.

Patterns of interbreeding, ecology, and selection can be mapped onto the cladogram, so to a large extent this concept encompasses the important aspects of the previous two.

It has thus become apparent that things called "species" under this definition (or any other, actually) will not necessarily be comparable in terms of the process by which they arise or are maintained. Thus "speciation" means different things in different groups.

This is likely to be the species concept of the future (disclaimer: your professor is one of the authors of the phylogenetic species concept, so may be biased!). For now, however, the biological species concept still holds sway in textbooks...

## • Reproductive isolation

**reproductive isolating mechanisms:** There are many mechanisms that prevent successful reproduction between incompatible groups of organisms (Fig. 24.4 (8th); Fig. 24.4 (7th)); these are grouped into two categories:

1. **Prezygotic:** 1) habitat isolation, 2) temporal isolation, 3) behavioral isolation, 4) mechanical isolation, 5) gametic incompatibility

Anything that prevents mating and fertilization is a prezygotic mechanism.

Prezygotic mechanisms fall into two broad categories, depending on whether they could have evolved because of natural or sexual selection. Habitat isolation, that is, preferring different habitats, is likely to have evolved because of natural selection. In this case, reproductive isolation is a byproduct of changes occurring for other reasons. *Rhagoletis* fruit flies have evolved host races.

In other cases, characters associated with mating also are isolating mechanisms. Differences between species could have evolved in order to prevent hybridization. Birds of paradise provide a likely example.

In some cases, such as the time of mating, it is difficult to tell. Species could be active at different times of the day or breed at slightly different times of the year, because of food preferences or because selection favored reduced hybridization.

## **2. Postzygotic:** 1) hybrid inviability, 2) hybrid sterility, 3) hybrid breakdown

Postzygotic barriers prevent the hybrid zygote from developing into a viable, fertile adult. The mule, Fig. 24.4 is a typical example.

Reduced viability or fertility of hybrid offspring all are known to be postzygotic isolating mechanisms. Lack of ability to survive in intermediate habits is an ecological barrier. Often differences in chromosome number or arrangement of genes on chromosomes result in genetic barriers.

Prezygotic and postzygotic barriers can be seen to evolve in laboratory experiments:

A prezygotic barrier in two groups of fruit flies evolved in a laboratory experiment, Fig. 24.9 (8th); Fig. 24.7 (7th).

In some cases, such as the *Mimulus* example discussed on p. 493 (8th), p. 474 (7th), it is possible to test for the presence of prezygotic or postzygotic barriers.

## **• Geographic modes of speciation**

The formation of new species usually requires some initial reduction of gene flow, often provided by geography. There are two basic geographic modes (see also Fig 24.5 (7th and 8th)):

### **1. Allopatric speciation:** Speciation by geographically separated populations.

Either a barrier can form, separating a single species into two isolated groups, or a species can colonize a new area separated. In both cases, gene flow is reduced to zero or nearly zero. The formation of a barrier is sometimes called a vicariant event.

Geographic isolation alone is not a reproductive isolating mechanism. How large a barrier has to be depends on dispersal capacity. A river may be a barrier for a snake but not a bird. It is just common sense.

There are two important subtypes of allopatric speciation:

- I. Initial population divided into two large halves (the "dumbbell" model)
- II. Initial population divided into one large half and one small, marginal half (the peripheral isolate model)

Small newly-founded populations may evolve reproductive isolation quickly. Small population size results in substantial changes because of genetic drift alone because of a founder effect. A population arriving in a new habitat may experience new environmental conditions that lead either to rapid evolution or to extinction.

Islands or island-like habitats provide many examples of major adaptive radiations, permitted by isolation from the mainland and the many ecological opportunities (empty niches). The most rapid speciation events and the most spectacular examples of evolutionary convergence are found on islands.

Darwin's finches on the Galapagos are a good example, but all other island groups provide similar and even more dramatic examples. It appears that the outcome of natural selection is predictable to some extent. A species that enters an empty habitat will give rise to an adaptive radiation. But exactly what happens depends on other factors. On New Zealand, giant moas evolved but similar species did not evolve in Hawaii or in the Galapagos.

The refugium hypothesis: a once widespread range can be subdivided by factors such as climate change (e.g., Amazon basin) or glaciation (e.g., North America), resulting in speciation in isolated geographic pockets.

The two different types of allopatric speciation can give rise to two different macroevolutionary patterns: gradualism vs. punctuated equilibrium -- which would be associated with which?

## 2. Sympatric speciation: Speciation in populations with overlapping geographic ranges

In plants polyploidy can lead to immediate reproductive isolation. Chromosomal mutations in self-fertile plants can lead to instant speciation, as illustrated in Fig. 24.10 and 24.11 (8th), Fig. 24.9 (7th). The genus *Clarkia* provides several examples of allopolyploid and autopolyploid species. Three *Tragopogon* species were introduced from Europe in the early 1900s. By the 1950s two new polyploid species have arisen, as described in the book.

De Vries found that new species of the evening primrose, *Oenothera* could arise by autopolyploidy. He was one of the three people who rediscovered Mendelism. He thought he discovered a new mechanism of evolution, mutations of large effect, that overcame some of the problems with natural selection. For a few years, he was one of the most prominent evolutionary biologists in the world, until it was found that *Oenothera* had very unusual chromosomes that were not typical of other species.

Many domesticated plants are polyploid, including oats, wheat, barley, potatoes, bananas, tobacco. It is likely that polyploid individuals were used early in the domestication of plants, both because they had unusual properties and because they were reproductively isolated from their wild relatives. Polyploidy is induced today in order to create plants with new traits or combinations of traits.

Autopolyploidy vs. allopolyploidy (definitions below)

In animals, rapid speciation can occur because of differences in habitat or food preference, although polyploid species do not seem to form often in animals.

Host shifts combined with extreme habitat fidelity can lead to rapid speciation, as has occurred in fig wasps. Each species of fig has its own wasp species.

Female choice can play an important role in species differences, as illustrated by the cichlid species in Fig. 24.12 (8th), Fig. 24.10 (7th). Accidental differences in female preference can lead to rapid speciation provided that some differences in males exist.

### Some definitions:

**hybrid:** Offspring of genetically dissimilar parents (stocks, varieties, or species)

**ring species:** A situation in which two reproductively isolated populations (populations that cannot successfully reproduce) living in the same region are connected by a geographic ring of populations that can interbreed). Ring species illustrate various stages of geographic differentiation. Without the intermediate form of *Ensatina* we would call the groups at the two ends different species.

**polyploid:** An individual containing more than two sets of chromosomes (Figs. 24.10 and 24.11 (8th); Figs. 24.8 and 24.9 (7th)). There are two kinds:

**autopolyploidy** (doubling of chromosomes in one lineage)

**allopolyploidy** (doubling of chromosomes after hybridization between two lineages).

### • Is reproductive isolation a byproduct or an adaptation?

Identifying isolating barriers is often not difficult. What is difficult is deciding whether an isolating barrier evolved for selection to prevent hybridization (Wallace's view) or as an incidental consequence of other changes (Darwin's view). Darwin did not explicitly discuss reproductive isolation, but his theory of the origin of species was that species differed because they accumulated enough changes under natural selection that descendants of organisms in the same species could be recognized as members of different species.

In the modern synthesis beginning in the 1940's, more emphasis was placed on the importance of genetic isolation, meaning the cessation of gene flow, and that required the evolution of isolating barriers that would permit further differences to evolve. In some cases, it appears that

barriers such as mechanical or behavioral barriers evolved in order to prevent hybridization and permit species to differentiate.

## • Species clusters

One of the most visible manifestations of evolution is the existence of groups of closely related species that often have evolved relatively recently from a common ancestor. Also called **species flocks**. Examples are:

**Darwin's finches:** Fourteen species of finches occur on the Galapagos Islands; actually one of the species lives only on Cocos Island ~1000 km north. This group of birds provides one of the most striking and best-studied examples of evolution on the islands. The descendants of the original finches that reached the Galapagos Islands now occupy many different kinds of habitats on the islands. These habitats encompass a variety of niches comparable to those occupied by several distinct groups of mainland birds. Note the specialization of beaks, which are adapted to various food sources. (Also see Fig 22.6 in 8th or 7th edition)

**Hawaiian *Drosophila* and Silverswords:** There exists at least 1,250 species of the fly genus *Drosophila* throughout the world, and ~800 of them are found only in the Hawaiian Islands. Aside from their sheer number of species, these Hawaiian flies are unusual in morphological and behavioral traits. No comparable species of *Drosophila* are found anywhere else in the world. The native Hawaiian *Drosophila* are closely associated with the remarkable native plants (Hawaiian Silversword) of these islands and many are highly selective in both their choice of host plants for their larvae and in the part of the plant that they use. As new islands are created from fissures on the ocean floor, new species of *Drosophila* colonize and evolve on these islands.

**Cichlid fish:** Lake Victoria, one of the Great African Rift Lakes, harbors over 500 species of cichlid fish. These fish are one of the most exciting groups to study, as they provide a spectacular example of **adaptive radiation**. Scientists attribute their success and rapid evolution to the scarcity of other fish in the lake and subsequent niche differentiation, as well as the evolution of the pharyngeal jaw. There is very little genetic differentiation between cichlid species, but they exhibit a spectrum of specialized feeding habits and reproductive behaviors. The teeth and coloration in many of these species are remarkably modified for such specializations. The recent introduction of the Nile Perch contributed to the extinction of many cichlid species and continued alteration of the aquatic environment.

## Questions relating to lecture on Speciation

1. Do self-quiz questions 1-6 on page 505-506 of the textbook (8th); or 1-8 on page 489 of the textbook (7th).