**Chapter 13  
The origin of species**

Species are independently evolving lineages

* **General lineage species concept:** species are metapopulations that exchange alleles frequently enough to comprise the same gene pool

**Phenetic characters**

* Make sure you can distinguish between **defining** a species by phenetic characters and **recognizing** species according to phenetic characters.
* The distinction between "definition" and "recognition" is similar to the distinction between the **formal description** of a species and the **diagnosis** of a species.
* Phenetic characters are all the observable or measureable characters of an organism, including microscopic and physiological. Pretty much interchangeable with “morphological”.
* The distinction is between features which are essential, in principle, and those which are useful, in practice.  It is a distinction between an explanation of what a species *ought to be* and a description of what a species *happens to be*.
* **formal definition is the description** of a species, using phenetic characters
  + i.e. describe the difference between a rose, gardenia and a magnolia

**Some species concepts define species at a point in time; others define species through evolutionary time**

* Non-temporal species concepts
  + **Phenetic species** (definition based on clustering of **physical characters**)
  + **Typological species** (definition based on similarity to a **type specimen** or ideal type)
  + **Reproductive species** (definition based on **reproductive isolation**)
  + **Ecological species** (definition based on **niche**)
* Temporal species concept
  + **Cladistic species** (definition based on segment of **phylogenetic tree)**
  + **Evolutionary species concept** (definition based on vague "tendencies")

**The phenetic species concept**

* Phenetic species are defined as as populations distinguished by discrete clusters of phenotypic characters.
* The phenetic species concept resembles the practical criteria commonly used to describe species.  A population can be defined as a species by a group of phenetic characters sufficient to distinguish it from other populations.

Other ways to identify species

* **Biological species concept:** species are groups of interbreeding populations that are reproductively isolated from other such groups
* **Phylogenetic species concept:** smallest possible group descending from a common ancestor and recognizable by unique, derived traits

**The biological species concept**

* **Ernst Mayr**'s Biological Species Concept (**BSC**) defines species as **"groups of interbreeding natural populations that are reproductively isolated from other such groups"** is the most widely accepted definition for species.
* Most discussion of speciation has been based on this species concept.
* That is, most hypotheses concern mechanisms which establish reproductive isolation.
* In the BSC, species are unified by **gene flow** within a common **gene pool**; gene flow involves migration and interbreeding.

**Interbreeding between species is prevented by isolating mechanisms**

* **isolating mechanisms** serve to prevent interbreeding and thereby establish reproductive isolation of populations.
* Isolating mechanisms can be categorized as either **premating (prezygotic)** or **postmating (postzygotic)**.

**Isolating barriers**

* Premating isolating mechanisms prevent potential mates from two separate populations from getting together.
  + The most basic of premechanisms involve one or another variation on allopatry (geographic separation, habitat separation, seasonal or temporal separation).
  + More complicated premating mechanisms involve behavior, biomechanics, or gamete interaction to prevent gametes from coming together.

**Premating mechanisms**

* geographic separation
  + populations are geographically separated
  + (e.g. islands)
* habitat separation
  + Populations occur in different habitats in the same general region
  + (e.g. mangroves)
* seasonal or temporal separation
  + Mating or flowering occur in different seasons
  + Separation of photosynthesis and nitrogen fixing

Geographical variation

* A cline is a type of geographical variation
* Cline is the gradual change in the species’ phenotype and genotype frequencies through a series of geographically separate populations (ex: ring species)

Postmating-prezygotic barriers

* **Gametic incompatibility:** sperm or pollen from one species fails to penetrate and fertilize the egg of another species
* Postmating isolating mechanisms involve some form of genetic incompatibility, such as reduced viability or reduced fertility of hybrid individuals.
  + **Haldane's rule** notes that in species with genetic sex determination, reduced viability or fertility is much more common in the *heterogametic* sex (e.g., the sex that produces different gametes, the XY sex; in mammals the heterogametic sex is male, in birds it is females).
  + Postmating isolating mechanisms comprise a selection pressure that favors premating mechanisms, to minimize the production of less-fit offspring.

Postzygotic barriers

* Hybrids are produced but have low fitness
  + Hybrid inviability
  + Hybrid sterility
  + Ecological inviability
  + Behavioral sterility

**Recognition species concept**

* The recognition species concept places emphasis not on reproductive isolation per se but on mechanisms for recognizing suitable mates.
* In this concept, a species is defined by mutual recognition of suitable mates among the members of a population.
* **Specific mate recognition system** is the term given to a method of recognizing mates that is shared by all the members of a population.
* In this concept, mate recognition is causal for the origin of species, while reproductive isolation is a secondary consequence of mate recognition.
* The recognition species concept is thus associated with a more specific hypothesis concerning speciation than is the more general biological species concept.

**Ecological species concept**

* The ecological species concept places on emphasis on **niche** or **adaptive zone** rather than reproductive isolation.
* This concept draws support from two phenomena.
  + In the phenomenon called **competitive exclusion**, two or more species cannot occupy the same niche.  Either one will be better and beat out the other one in competition, or (in the unlikely event that they are exactly equal) chance drift in relative population size will eventually eliminate one or the other.
  + In the phenomenon called **character displacement**, similar species which share a common resource will diverge from one another.  This effectively divides the shared niche and reduces competition.

**Pluralistic species concept**

* Whether or not a pluralistic species concept is the best choice is related to the question of how many different ways there are for speciation to occur.
* If species can form by adaptive splitting within a population, *and* by specific mate recognition systems, *and* by incidental reproductive isolation (i.e., allopatry), *and* by reorganization of genomic architecture, then a pluralistic concept might be appropriate.
* But a pluralistic concept raises the question, is there anything *essentially* the same in the various accounts?  If so, shouldn't that "essence" define species?  And, if not, is the concept of species meaningful?

**Causes of Speciation**

* **Geographic Isolation**
  + Scientists think that geographic isolation is a common way for the process of speciation to begin: rivers change course, mountains rise, continents drift, organisms migrate, and what was once a continuous population is divided into two or more smaller populations.
  + It doesn’t even need to be a physical barrier like a river that separates two or more groups of organisms—it might just be unfavorable habitat between the two populations that keeps them from mating with one another.
* **Reduction of Gene Flow**
  + However, speciation might also happen in a population with no specific extrinsic barrier to gene flow. Imagine a situation in which a population extends over a broad geographic range, and mating throughout the population is not random. Individuals in the far west would have zero chance of mating with individuals in the far eastern end of the range. So we have reduced gene flow, but not total isolation.

**Modes of Speciation**

* The key to speciation is the evolution of genetic differences between the incipient species.
* For a lineage to split once and for all, the two incipient species must have genetic differences that are expressed in some way that causes matings between them to either not happen or to be unsuccessful.
* These need not be huge genetic differences. A small change in the timing, location, or rituals of mating could be enough. But still, some difference is necessary. This change might evolve by natural selection or genetic drift.

**Allopatric Speciation**

* (allo = other, patric = place)
* Allopatric speciation is just a fancy name for speciation by geographic isolation, discussed earlier.
* In this mode of speciation, something extrinsic to the organisms prevents two or more groups from mating with each other regularly, eventually causing that lineage to speciate. Isolation might occur because of great distance or a physical barrier, such as a desert or river.
* Allopatric speciation can occur even if the barrier is a little “porous,” that is, even if a few individuals can cross the barrier to mate with members of the other group.
* In order for a speciation even to be considered “allopatric,” gene flow between the soon-to-be species must be greatly reduced—but it doesn’t have to be reduced completely to zero.

**Peripatric Speciation**

* Peripatric speciation is a special version of the allopatric speciation mode and happens when one of the isolated populations has very few individuals.
* (peri = near, patric = place)  
  a small population isolated at the edge of a larger population
  + Double disaster: Not only are the island fruit flies geographically isolated from their mainland relatives, but only a few larvae have survived the harrowing journey to end up colonizing the island.
  + Rare genes survive: These few survivors just by chance carry some genes that are rare in the mainland population. One of these rare genes happens to cause a slight variation in the mating dance. Another causes a slight difference in the shape of male genitalia. This is an example of the founder effect.
* In peripatric speciation, small population size would make full-blown speciation a more likely result of the geographic isolation because genetic drift acts more quickly in small populations. Genetic drift, and perhaps strong selective pressures, would cause rapid genetic change in the small population. This genetic change could lead to speciation.
* The essential characteristic of this mode is that genetic drift plays a role in speciation. There are likely many cases where a population is split into two unequally-sized populations and they become separate species. However, it is very difficult for us to tell after the fact what role genetic drift played in the divergence of the two populations—so gathering evidence to support or refute this mode is challenging.

**Sympatric Speciation**

* Unlike the previous modes, sympatric speciation does not require large-scale geographic distance to reduce gene flow between parts of a population. How could a randomly mating population reduce gene flow and speciate?
* (sym = same, patric = place)
* Merely exploiting a new niche may automatically reduce gene flow with individuals exploiting the other niche. This may occasionally happen when, for example, herbivorous insects try out a new host plant.
* For example, 200 years ago, the ancestors of apple maggot flies laid their eggs only on hawthorns—but today, these flies lay eggs on hawthorns (which are native to America) and domestic apples (which were introduced to America by immigrants). Females generally choose to lay their eggs on the type of fruit they grew up in, and males tend to look for mates on the type of fruit they grew up in.
* So hawthorn flies generally end up mating with other hawthorn flies and apple flies generally end up mating with other apple flies. This means that gene flow between parts of the population that mate on different types of fruit is reduced. This host shift from hawthorns to apples may be the first step toward sympatric speciation—in fewer than 200 years, some genetic differences between these two groups of flies have evolved.

**Parapatric Speciation**

* In parapatric speciation there is no specific extrinsic barrier to gene flow. The population is continuous, but nonetheless, the population does not mate randomly. Individuals are more likely to mate with their geographic neighbors than with individuals in a different part of the population’s range. In this mode, divergence may happen because of reduced gene flow within the population and varying selection pressures across the population’s range.
* (para = beside, patric = place)  
  a continuously distributed population
* We may be observing the first steps of parapatric speciation in the grass species *Anthoxanthum odoratum*
* Some of these plants live near mines where the soil has become contaminated with heavy metals. The plants around the mines have experienced natural selection for genotypes that are tolerant of heavy metals. Meanwhile, neighboring plants that don’t live in polluted soil have not undergone selection for this trait.
* The two types of plants are close enough that tolerant and non-tolerant individuals could potentially fertilize each other—so they seem to meet the first requirement of parapatric speciation, that of a continuous population. However, the two types of plants have evolved different flowering times. This change could be the first step in cutting off gene flow entirely between the two groups.
* Although continuously distributed, different flowering times have begun to reduce gene flow between metal-tolerant plants and metal-intolerant plants.
* Parapatric speciation begins with the evolution of a hybrid zone
  + The transition across which allele frequencies change may be broad or narrow.
    - A broad transition, extending across much of the total range, is called cline.
    - A narrow transition is called a hybrid zone or stepped cline.
  + The width of a hybrid zone depends on hybrid fitness and on gene flow.
    - The zone will be narrower with less migration (or lower rate of gene flow) and/or with lower fitness for heterozygotes.
    - The zone will be wider with more migration (higher rate of gene flow) or with higher fitness for heterozygotes.

**Evidence for Speciation**

* In the summer of 1995, at least 15 iguanas survived Hurricane Marilyn on a raft of uprooted trees. They rode the high seas for a month before colonizing the Caribbean island, Anguilla. These few individuals were perhaps the first of their species, *Iguana iguana*, to reach the island. If there were other intrepid *Iguana iguana* colonizers of Anguilla, they died out before humans could record their presence.
* Evolutionary biologists would love to know what happens next: will the colonizing iguanas die out, will they survive and change only slightly, or will they become reproductively isolated from other *Iguana iguana* and become a new species? We could be watching the first steps of an allopatric speciation event, but in such a short time we can’t be sure.

Bacterial species often defined by specific adaptations

Horizontal gene transfer makes classification difficult

Ultimately, species concepts are human artifacts

* Methods for recognizing species continue to improve
* Remember, the definition is arbitrary..it is done for our convenience…the organisms couldn’t care!