Chapter 14 - The Origin of Species

The fossil record chronicles 2 patterns of speciation:

1. **Anagenesis (or Phyletic Evolution)**

Transformation of an unbranched lineage of organisms to a state different enough from the ancestors to be classified as a new species

2. **Cladogenesis (or Branching Evolution)**

The formation of one or more new species from a parental species that continues to exist
The most common pattern of speciation
Only this form of speciation promotes biological diversity (increase in species number)

What is a Species?

Species is a latin word meaning "kind" or "appearance"

Species have traditionally been described on the basis of their physical form or morphology
Species defined by anatomical features are called **morphospecies**

Variation within a species creates practical problems of species recognition using phenotypic characters

Species Concepts

Morphospecies Concept

Species traditionally have been described and identified on the basis of morphological criteria, a classification system which is commonly referred to as the **morphological** or **typological species concept**

Morphological species were customarily described from an examination of a few individuals that were collected from a single locality
Species traditionally had been defined by reference to a morphological type

With the advent of world travel, it became apparent that what appeared to be distinct morphological species at the local level were merely one in a series of morphologically intergrading populations on a broader geographic scale
As a consequence, the emphasis shifted from characterizing individuals from local populations to describing what Mayr referred to as populational systems

The Biological Species Concept

The BSC defines species in terms of interbreeding
Mayr defined species as follows: “species are groups of interbreeding natural populations that are reproductively isolated from other such groups”

It is important because it places the taxonomy of natural species within the conceptual scheme of population genetics
e.g., a community of interbreeding organisms is, in population genetic terms, a gene pool (total aggregate of genes in a population)

Inconsistencies between Morphological and Biological Concepts

Members of a species are by no means all uniform - biological species are **polytypic -** they have many (or perhaps no) morphological types

It is possible for a species to differ reproductively but not morphologically
These kinds of species are called **sibling species**

Problems with the BSC

Although biologists have and continue to use this approach, it can raise some special concerns when working with **fossils**
Also, the criterion of interbreeding is useless for asexual populations

The Ecological Species Concept

The exploited by the members of a species form that species ecological niche
The **ecological species concept** defines a species as a set of organisms exploiting a single niche (set of resources and habitats)

Speciation

We can analyze speciation as a three-step process: 1) an initial step that isolates populations; 2) a second step that results in the divergence of characteristics between populations; 3) a final step that results in reproductive isolation (re-enforcement)

1. Mechanisms of Isolation

The speciation process begins when populations become isolated and gene flow is reduced
One of the classical models of speciation is related to this phenomenon is **allopatric speciation -** the formation of a new species in isolated geographical areas

Populations can become isolated through dispersal and colonization
Populations can also become geographically isolated as the result of splitting of a populations's former range into 2 or more isolated patches (e.g., formation of mountains ranges, river formation, drying and the subsequent fragmentation of forests, lava flows, etc.)

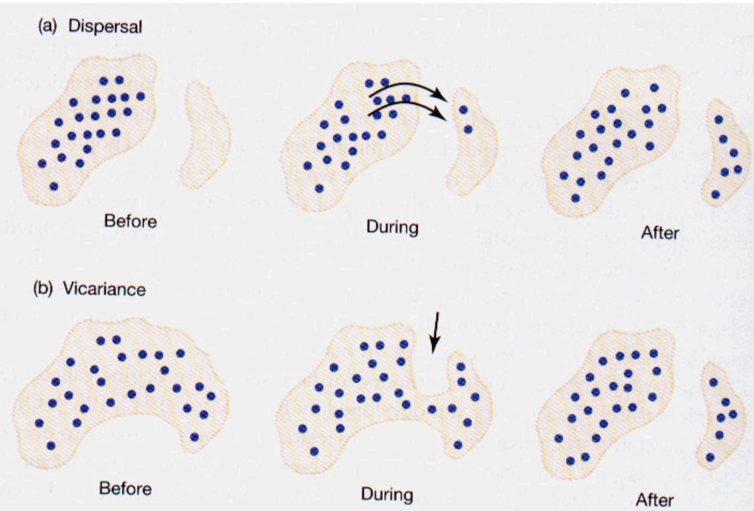

Figure 12.5 Isolation by dispersal and vicariance In the diagram of dispersal (a), the arrows indicate movement of individuals. In the diagram of vicariance (b), the arrows indicate an encroaching physical feature such as a river, glacier, lava flow, or new habitat.

Geographic Isolation via Dispersal and Colonization

This often occurs as the result of founder events – when individuals of a population disperse to new habitats or islands
One consequence of founder events is that colonizing individuals are isolated from the original ancestral population

The isolated founding population experiences drift and differences in mutation and selection as the result of being in different environments
In the process of adapting to different environments, the populations genetically differentiated

Example: Hawaiian Drosophila

Hawaii contains a diverse assemblage of drosophilids – they occur in a variety of habitats, ranging from sea level to mountains to dry scrub forest habitats to tropical rainforests
They also utilize a variety of different food sources
Many of the Hawaiian *Drosophila* are endemic to particular islands of the archipelago
And the leading hypothesis for their diversification is the founder effect

Based on the manner in which the islands were formed, the founder event hypothesis makes two predictions: 1) closely related species should be found on adjacent islands; 2) phylogenetic relations among the flies should correspond to the manner in which the islands were formed

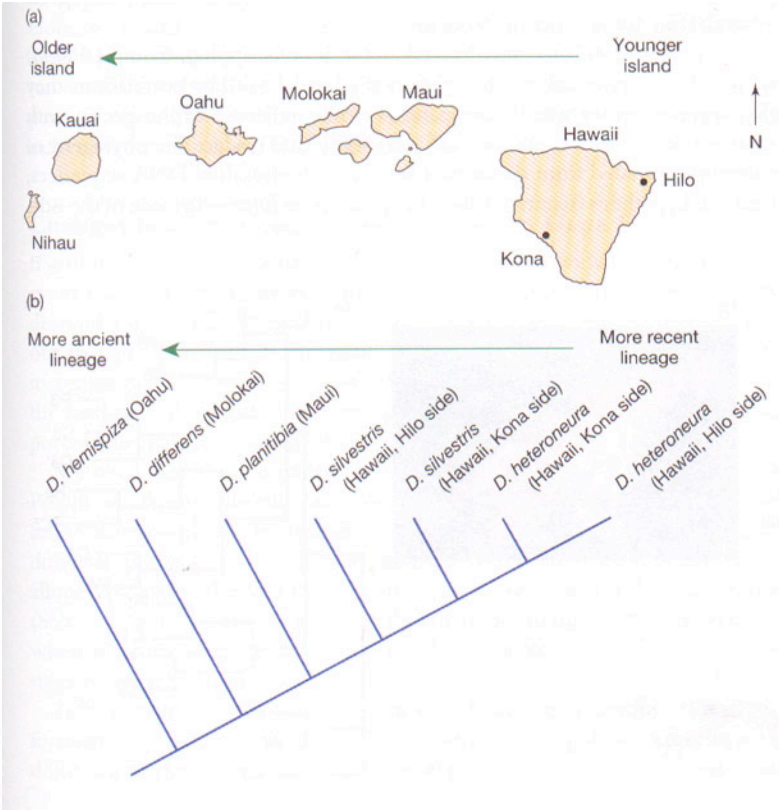

Figure 12.7 Evidence for speciation by dispersal and colonization events (a) The Hawaiian islands are part of an archipelago that stretches from the island of Hawaii to the Emperor Seamounts near Siberia. The youngest landform in the chain is the island of Hawaii, which still has active volcanoes. (b) *Drosophila silvestris, D. heteroneura, D. planitibia,* and *D. differens* are a closely related group. Note that the older-to-younger sequence of branches on the phylogeny shown here corresponds to the older-younger sequence of island formation shown in part (a). This pattern is consistent with the hypothesis that at least some of the speciation events in this group were the result of island hopping. (The phylogeny was estimated from data on sequence divergence in mitochondrial DNA; see DeSalle and Giddings 1986.)

Changes in Chromosomes as a Barrier to Gene Flow

Chromosomal mutations that lead to polyploidization can result in (instant) reproductive isolation between populations because if the incompatibilities between gametes with different number of chromosomes
This phenomenon is particularly prominent in plants

Symaptric Speciation

Sympatric speciation by polyploidy was discovered in the 1900s by the Dutch botanist Hugo de Vries

Sympatric speciation refers to reproductive isolation and the formation of new species in the absence of geographic separation

2. Mechanisms of Divergence

The Role of Genetic Drift

One of the major effects of drift with a population includes the random fixation and random loss of alleles is populations
And genetic drift is most pronounced in small populations
Most species are thought to have originated as a consequence of low population sizes (during colonization events, in peripheral populations, etc.)

The Role of Natural Selection

Good evidence of the importance of NS has come from research on the apple maggot fly, *Rhagoletis pomonella*
The fly traditionally has parasitized hawthorne fruit trees
These flies have more recently become parasitic with apple trees; probably when they were introduced from Europe some 300 years ago

Researchers were interested in determining whether the flies that parasitize these two host species were distinct species
Has NS based on host preference for different food created different races of flies?

It appears that rather than being isolated by dispersal or vicariance, the flies are isolated on different host species
In experiments where individuals are given a choice of host plants, flies show a strong preference for their original host type
Because mating occurs on the plant, host preference results in strong nonrandom mating

It appears that selection has favored distinct habitat preferences in apple and hawthorn flies.

There may be a least 3 advantages to switching to apple fruit

- Escape from parasitoids.
- Escape from intraspecific competition.
- Escape from interspecific competition.

The fitness advantages may outweigh the disadvantages of reduced larval survival and growth

The Role of Mutation

For speciation, the primary role of point mutations, gene duplications, and chromosomal inversions is to provide the raw materials for drift and selection once gene flow is reduced

Reinforcement (reproductive isolating mechanisms)

The third stage in speciation may occur if diverged populations come back into contact and have an opportunity to interbreed
There are a number of possible fates of the hybrids: 1) they may survive and interbreed with the parental populations and eliminate the divergence; 2) may have new characteristics and become a distinct population

If populations diverge sufficiently while allopatric, they may no longer be compatible
In this case, populations have developed **post-zygotic isolating mechanisms**

Selection should favor mutations in populations that would prevent mating from occurring - **prezygotic isolating mechanisms** - and that this **reinforcement** would finalize the speciation process

Post-zygotic Isolating Mechanisms

- Hybrid mortality (= inviability)
- Hybrid sterility (= infertility)
- Hybrid breakdown

Hybrid Mortality (Inviability)

The incompatibility in parental genes results in the breakdown of genetic and cellular mechanisms that regulate development
Results in the cessation of development and death before the individual reaches adulthood

Hybrid Sterility

Post-zygotic reproductive isolation in which hybrid zygotes are sterile
Therefore, they cannot reproduce and their genes cannot flow from one species to the other

Probable causes: a) abnormal development of the gonads or b) failure of parental genes to produce gametes with correct numbers of homologous chromosomes (=polyploidy)

Hybrid (F2) Breakdown

The F1 hybrids are normal, vigorous, and fertile, but the F2 contain inviable or sterile individuals (for same reasons as above)

Pre-zygotic Isolating Mechanisms

Habitat Isolation

Two species may never come into contact with one another because they occur in different habitats in the same geographical area

Temporal (Seasonal) Isolation

Potential mates do not meet because mating or cross fertilization takes place at different times of the year or different times of the day

Ethological Isolation

Populations are isolated by different and incompatible behavior before mating
e.g., incompatible special signals or courtship displays that attract mates
Also, species may come into contact with one another, but they never mate because there is no sexual attraction between males and females

Mechanical Isolation

Closely related species may attempt to mate, but fail to consummate the act because they are anatomically incompatible

Gametic Isolation

In organisms with external fertilization, male and female gametes may not be attracted to one another
In organisms with internal fertilization, although mating occurs and the gametes may meet, they do not form a zygote due to gametic mortality

Gradualism vs. Punctuated Equilibrium

The predominant view among evolutionary biologists was that there is slow, gradual change within species, and that speciation involved the gradual divergence of populations.
This is often referred to a **PHYLETIC GRADUALISM**.

In 1972 S. J. GOULD and N. ELDREDGE proposed that most species actually change little during their history, a state called stasis.
In addition, they proposed that most evolutionary changes occur at speciation; not gradual change, but sudden change.
They called this pattern **PUNCTUATED EQUILIBRIUM**.

The logical basis for phyletic gradualism*:*

There are changes within species due to natural and sexual selection.
Populations diverge and speciation occurs as different populations respond to different environments.

The logical basis for punctuated equilibrium:

Rapid Change

To explain rapid evolution at speciation Gould and Eldredge drew on the **PERIPHERAL ISOLATE** model of speciation.
This model proposes that speciation occurs in small populations separated by a barrier from other populations.

Allopatric event in Peripheral Isolates

A small population on the edge of a species range may experience extreme conditions
And may evolve rapidly - because of drift and selection
Speciation may be accompanied by a **genetic revolution -** an extensive reorganization of the gene pool

So, Gould and Eldredge argued that rapid evolution is most likely to occur in small populations.
Isolation eliminates the homogenizing influence of gene flow.
Genetic drift and selection can thus cause rapid divergence of the small, isolated population from the original population.
These small, isolated populations may diverge so much that they become different species.

Stasis

To explain stasis two ideas have been invoked: **STABILIZING SELECTION** and **EVOLUTIONARY CONSTRAINTS**.

Stabilizing selection, by favoring intermediate phenotypes, can keep a trait from changing over time - need stable environments
But, it would seem unlikely that selection will remain constant over vast periods of time since we know that environmental conditions change.
However, an organism may be buffered from large environmental changes through habitat selection.

Evolutionary constraints are factors intrinsic to the organisms that prevent it from responding to selection.
We've talked about one type of constraint already in this class, lack of genetic variation.
Also with respect to constraints - unless a trait is heritable, it will not respond to selection, and stasis will result.