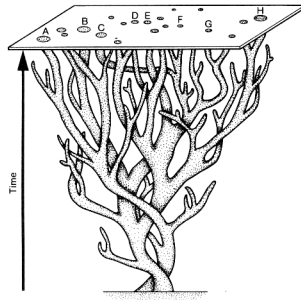


We can only experience species as “snapshots” in time



**Another way to think about it:**

“Species are the cross-sections of branches on the tree of life.”

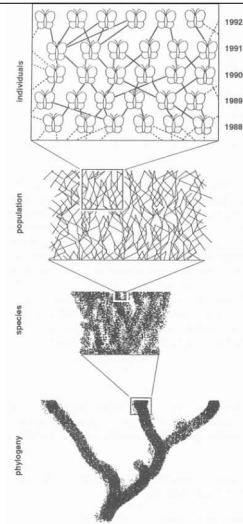
What would it look like if we could zoom in on the branches of a phylogenetic tree?

**Reticulate genealogy**

How does reticulate genealogy (within a species) become **divergent genealogy**?

or in other words,

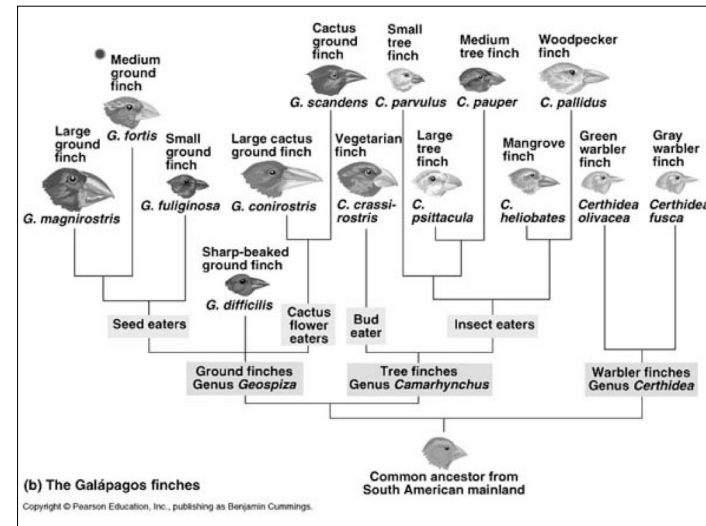
**How does speciation occur?**



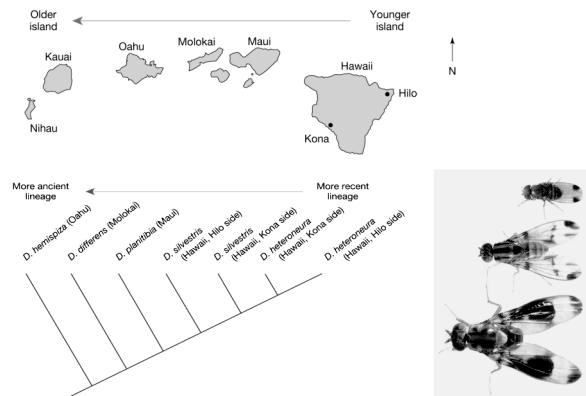
Speciation: the divergence of an ancestral species into two separate species lineages

Results over time from several factors, including:

- spatial subdivision
- limited dispersal and migration
- genetic drift
- natural selection



## Geographic Speciation of Hawaiian *Drosophila*

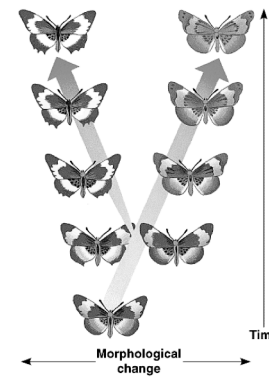


## How species evolve from other species: the short answer

- Speciation is the outcome of isolation and divergence.
  - Isolation is created by reductions in gene flow.
  - Divergence is created when mutation, genetic drift, and selection act on populations separately.

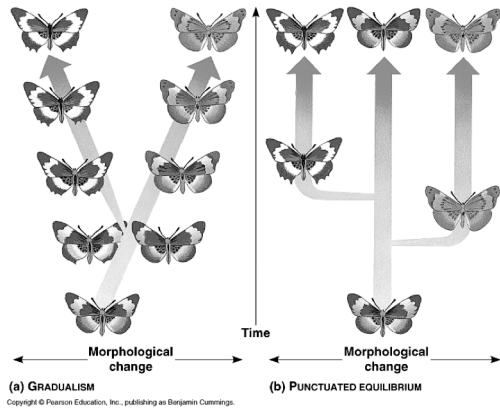
## Speciation tempo: can be gradual or punctuated

Figure 24.13 Two models for the tempo of speciation



## Speciation tempo: can be gradual or punctuated

Figure 24.13 Two models for the tempo of speciation



In sexual organisms, speciation requires the evolution of one or more isolating mechanisms (geographic, temporal, ecological, behavioral, mechanical, biochemical, developmental, etc.)

### Two alternative modes of speciation:

Allopatric speciation (or geographic speciation)

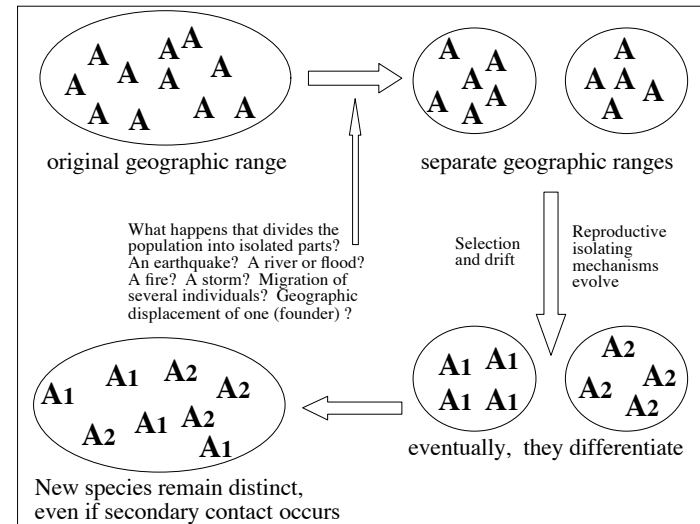
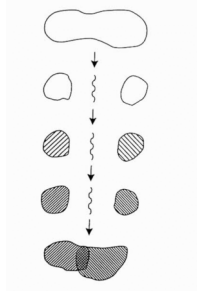
Occurs when an original population becomes geographically divided, and the ranges of the daughter populations do not overlap

Sympatric speciation (including allochronic speciation)

Occurs when isolating mechanisms evolve in the same area, without geographical separation

## Allopatric Speciation

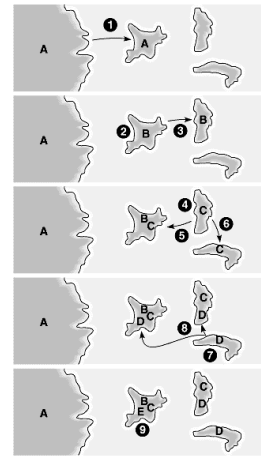
- The simplest and most common mechanism of speciation is allopatric speciation: two groups of one species become isolated geographically, and this isolation is maintained long enough for selection and drift to cause divergence into two new species



Adaptive radiations on island chains (e.g. finches, honeycreepers, etc.) are most likely histories of sequential allopatric speciation

Evidence?

In birds, no two sister species coexist on any *isolated* island



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## Allopatric Speciation

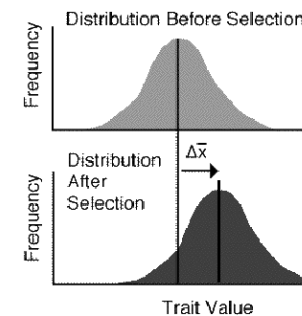
- Geographical barriers: mountains, oceans, rivers. A few members of a species manage to cross by a rare chance event.
- This is the mechanism by which Darwin's finches evolved into separate species in the Galapagos islands. Only very rarely can birds cross the ocean to get to other islands.
- Or, the barrier develops slowly as conditions change: the gradual formation of the Grand Canyon split a population into 2 isolated groups, that have diverged into separate species, the Kaibab and Albert squirrels.

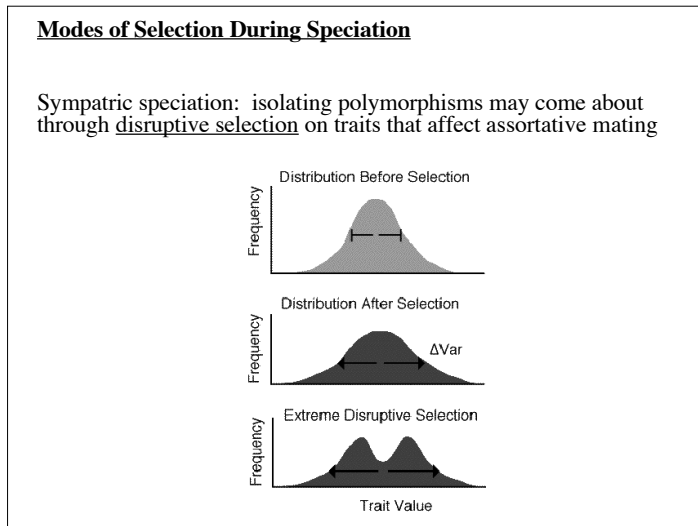
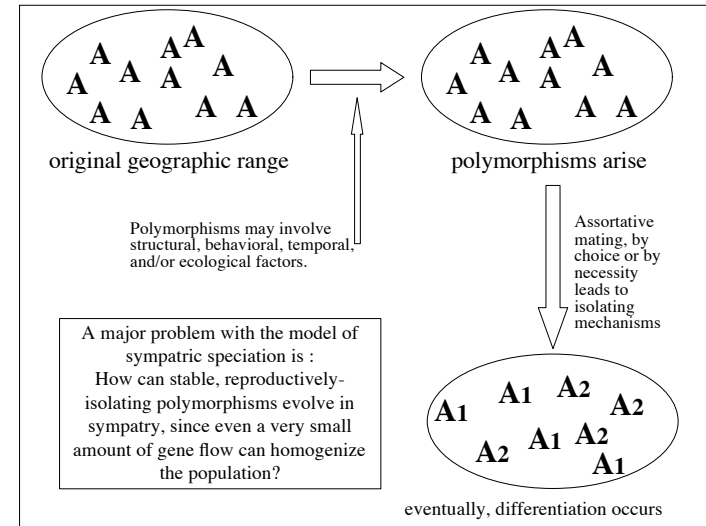
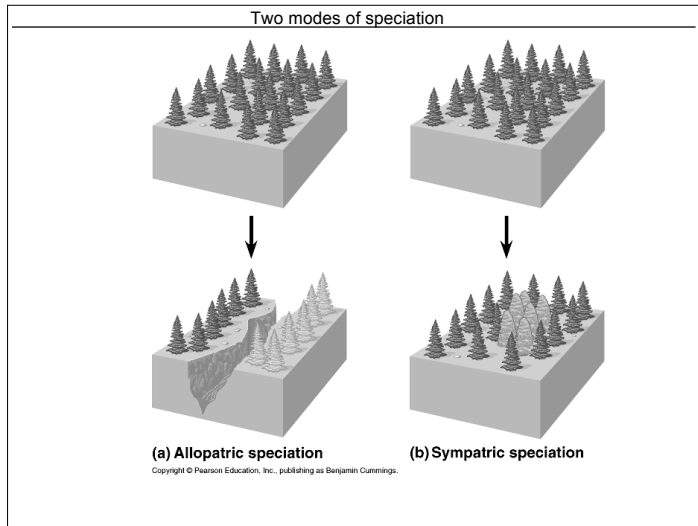
### Squirrels of the Grand Canyon



### Modes of Selection During Speciation

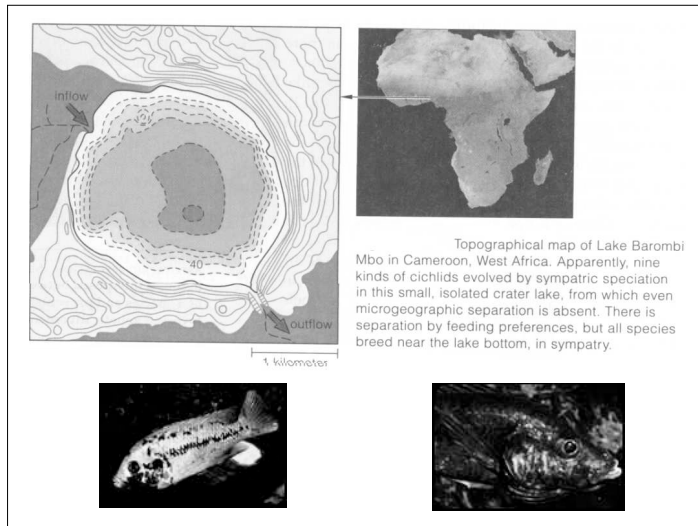
Allopatric speciation: Differentiation may occur as a result of directional selection in the separated sub-populations; however, remember that distributions also shift through random genetic drift





## Sympatric Speciation

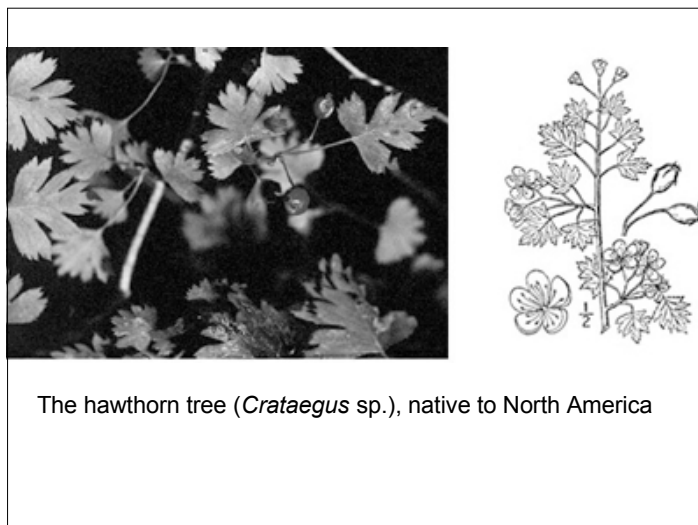
- Geographical isolation is probably the easiest way for species to form, but there are other possible mechanisms. “Sympatric speciation” means speciation that occurs within the same geographical location.
- An example: cichlid fish in Lake Barmobi Mbo in Cameroon, Africa—an isolated volcanic lake. Nine species, all more closely related to each other (by DNA evidence) than to similar fish in other lakes. The lake has no distinct geographical zones, and the fish can easily swim anywhere in it. They feed in different locations, but all breed in the same location, close to the bottom. This appears to be an example of sympatric speciation, but the mechanism is not clear.



Sympatric speciation in the apple maggot fly *Rhagoletis pomonella*



The apple maggot fly (*Rhagoletis pomonella*) is native to eastern North America. It originally bred in the large fruits of hawthorn trees.



***Rhagoletis* Reproduction is dependent on fruit**

The female fly lays fertilized eggs into the fruit. Maggots (larvae) emerge from the egg, eat and grow, and pupate where the last larval skin is retained and hardened to form the protective covering for metamorphosis. Pupating individuals develop into adult flies, emerge from the fruit, and reproduce.



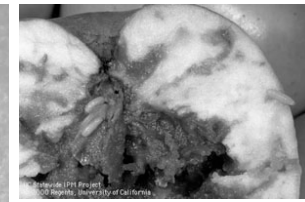
Apples: the most widely grown fruit in North America

Apples are not native to North America. They were introduced in the 17th century by European colonists.



However, apples are somewhat related to the Hawthorn plant (they are classified in the same family)

In 1864 maggot flies were first noted to infest apples grown in New York's Hudson River Valley. Maggot flies ultimately became a major pest of apples in the northeastern United States and Canada.



### Pros and Cons of Hawthorn fruits vs. Apples:

On average, apples are bigger fruits than hawthorns (70 mm vs. 12.6 mm) and provide 5.5 times more depth (based on diameter) to developing maggots than do hawthorn fruits.

Parasitoid wasps lay eggs into the maggot's body, with the wasp larvae ultimately killing the maggot. Apple maggots are better able to escape parasitoids by living deeper in a fruit than the wasp can penetrate with its ovipositor. As a result, apple maggots bear 70% fewer parasitoid wasp eggs than do hawthorn maggots.

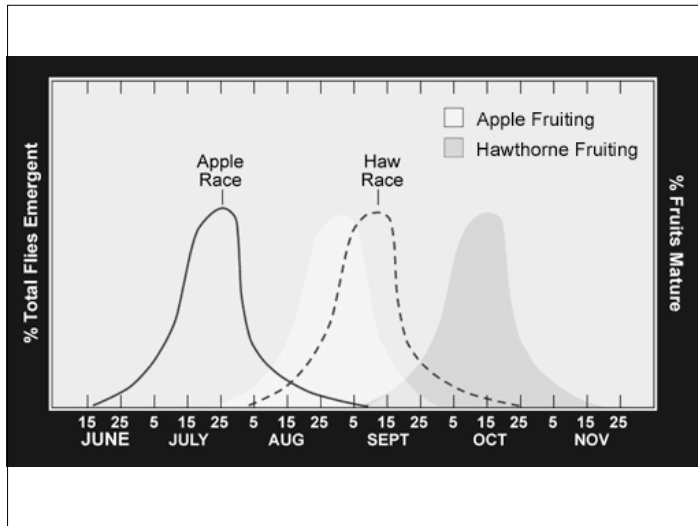
The larger fruits of apple trees provide 220 times more food (based on volume) to the growing and developing maggot than the smaller fruits of hawthorns. As a result, apple maggot flies can lay more eggs per fruit than do hawthorn maggot flies.

However, though the bigger apple provides more food (quantity), it does not provide better food (quality) to the growing maggot. The nutritional quality of hawthorn fruit is indicated by the better survival of both types of maggots in hawthorn fruits; 52% of maggot fly eggs survived in hawthorn fruits and 27% of maggot fly eggs survived in apple fruits. Caterpillars and weevils may also feed on the larger apple, reducing the quantity of food available to apple maggots.

Therefore: a **host plant shift** occurred in *Rhagoletis* within the past 300-400 years. Today, *Rhagoletis* flies use both hawthorn and apple fruits for reproduction.



So, what's the big deal?



Evolutionary consequences of the host plant shift

Because *Rhagoletis* flies mate and lay eggs on the host fruit, this fidelity to fruit type acts as a strong barrier to gene flow between the two types of maggot flies.

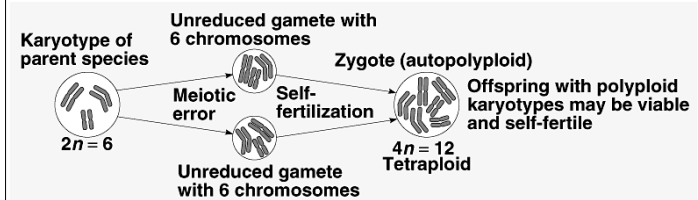
There is only a 4 to 6% hybridization rate between hawthorn maggot flies and apple maggot flies

Hawthorn and apple maggot flies are morphologically identical, but genetically distinguishable (have recognizable genetic profiles)

## Speciation by Polyploidy

- About half of all flowering plants are polyploid: more than 2 copies of each gene.
- Polyploids are initially the result of failure of cell division (mitosis or meiosis) to separate the chromosomes into 2 cells.
- New polyploids are usually sterile, or their offspring are sterile. Extra chromosomes with no homologue to pair with in meiosis leads to unbalanced (aneuploid) gametes, which will produce dead offspring.
- Triploids (3 copies of each gene) are sterile—the source of seedless fruit.
- In animals, sexual reproduction is essential every generation, so most polyploids fail to reproduce. Animals need a similarly polyploid mate to produce fertile offspring.
- But in plants, vegetative propagation is possible for many generations without sex, and in many species one plant contains both sexes. So, reproduction with a polyploid partner is easier in plants than in animals.

Sympatric speciation by polyploidy in plants: Autopolyploidy



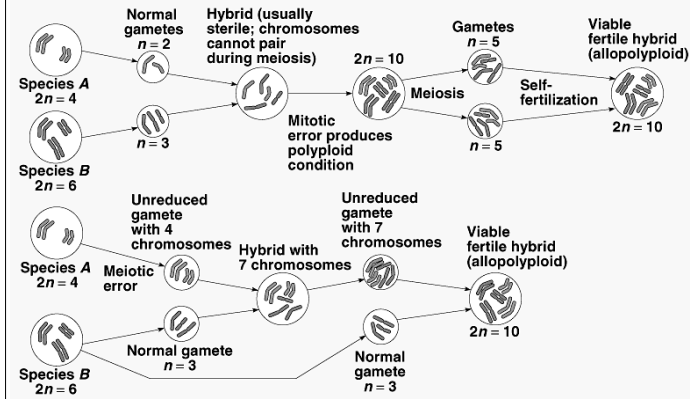
(a) Autopolyploidy

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But these new tetraploids cannot back-cross to diploid individuals; they can only form zygotes with other tetraploids.



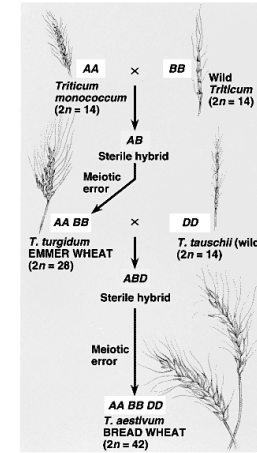
### Sympatric speciation by polyploidy in plants: Allopolyploidy



(b) Allopolyploidy

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### The evolution of wheat (*Triticum*) via allopolyploidy

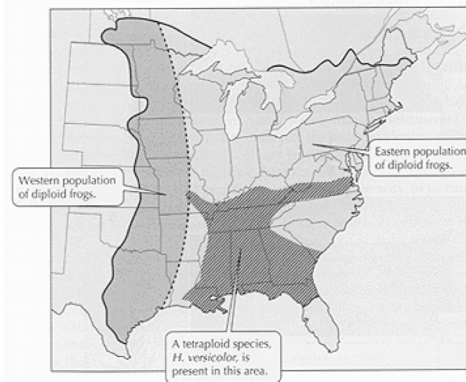


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21.3 Gray Tree Frogs Speciated by Intra-specific Hybridization The tetraploid *Hyla versicolor* resulted from hybridization between eastern and western populations of the diploid *H. chrysocelis*.



Hybridization and meiotic error can also cause Polyploidization in some animals, resulting in new species



## Hybrid Zones

- When two populations of a species are separated by a geographical barrier, they diverge genetically. Sometimes the barrier is removed and the two groups come into contact with one another. The region of contact is a "hybrid zone".
- When this happens, several possibilities exist:
- If the two groups have only diverged a little, fertile offspring will result, and the two groups will merge back into a single species. Geographical differences may exist within the species, resulting in different races or varieties, but all can interbreed freely.
- If the two groups have diverged to the point that no fertile offspring result from their matings, sexual selection should occur to deter further matings. New pre-zygotic reproductive isolation mechanisms, especially behavioral differences, arise to reinforce the division between the two species.
- This is sometimes called "parapatric speciation": 2 species forming while in contact with each other in a restricted region.

- Suppose two species form and at some later time come into contact with one another. What do you expect to happen?
- Prezygotic isolating mechanisms might minimize or prevent hybridization...
- If not, hybridization may occur, and post zygotic factors may make hybrids less viable.
- What if there's strong selection against hybrids?

## Reinforcement

If hybrids are less viable, selection can act to favor variants that are more reluctant to mate outside their own species.

Evidence: sympatric species are often more reluctant to attempt mating outside their species than are allopatric species.



- Redwing (left) and tricolored blackbirds
- In sympatry, yellow bar in Tricolored blackbird more pronounced.

## Modes of Selection After Speciation

Soon after speciation: stabilizing selection can differentiate the new species even further. This is known as Character displacement.

Character displacement (pronounced divergence of traits) stems from the competitive exclusion principle -- for species to coexist, they cannot occupy exactly the same ecological niche

