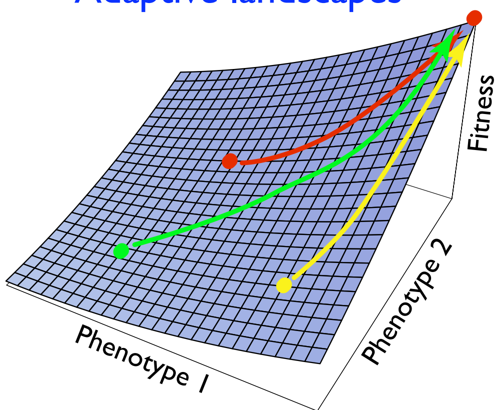
Speciation

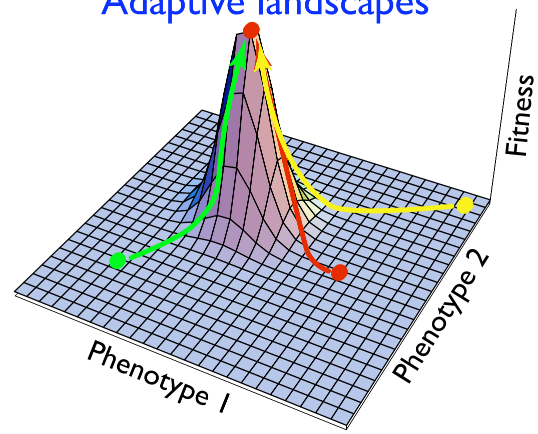
Adaptive landscapes



Selection will tend to move populations in the direction of increased fitness.

Speciation

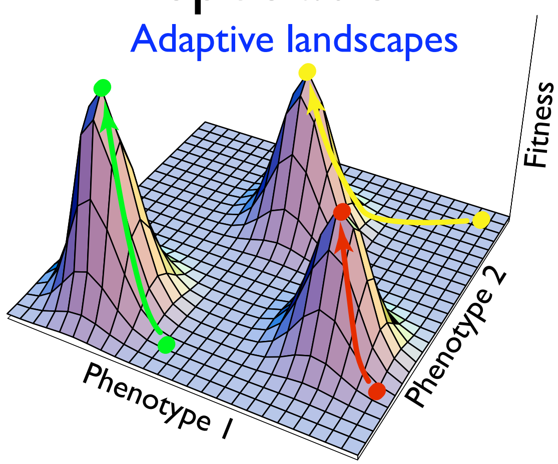
Adaptive landscapes



Selection isn't always directional: sometimes there is an optimal phenotype (or set of phenotypes).

Speciation

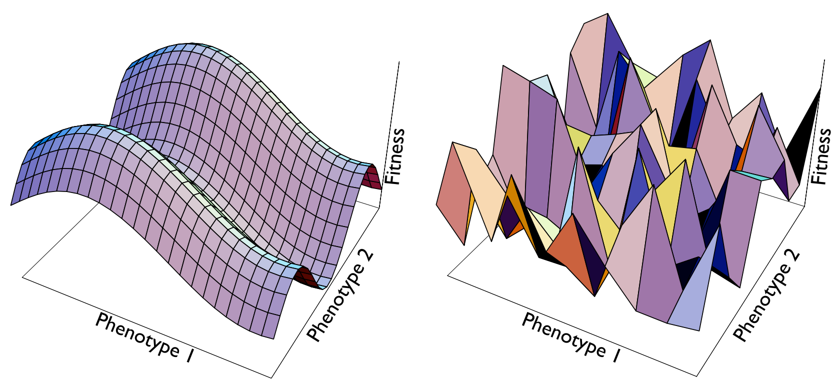
Adaptive landscapes



Sometimes there may be more than one optimum.

Speciation

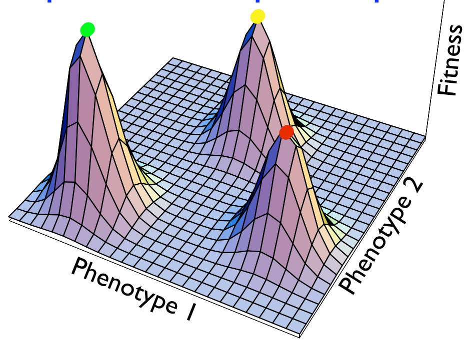
Adaptive landscapes



Adaptive landscapes might take any form imaginable.

Speciation

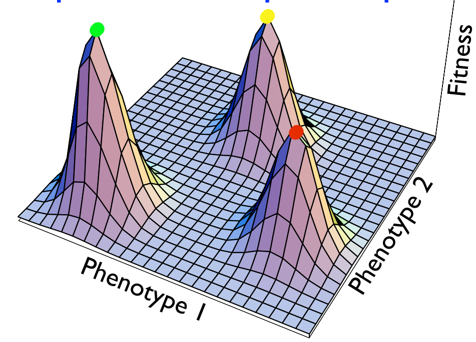
Adaptive landscapes & species



"...the living world is not a formless mass of randomly combining genes and traits, but a great array...of gene combinations, which are clustered on a large but finite number of adaptive peaks." – Theodosius Dobzhansky (1951)

Speciation

Adaptive landscapes & species



Why do living organisms cluster into discrete species?

What are the processes at work that lead to the origin of discrete species?

Speciation

General classification of processes

Mayr (1963) classified speciation processes as:

- Gradual speciation
  - Allopatric speciation (with geographic isolation)
    - Vicariant speciation (following the appearance of a barrier)
    - Peripatric speciation (by evolution in an isolated colony)
  - Parapatric speciation (with contiguous but non-overlapping distributions)
  - Sympatric speciation (with overlapping distributions)

Speciation

General classification of processes

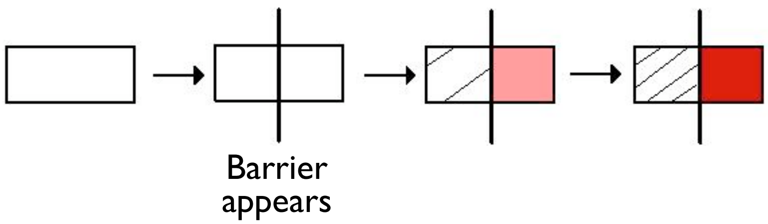
Mayr (1963) classified speciation processes as:

- Instantaneous speciation
  - Single genetic mutations
  - Cytological changes
    - Chromosome rearrangements
    - Polyploidy
- Hybridization (producing new reproductively isolated species)

(We'll concentrate on gradual processes)

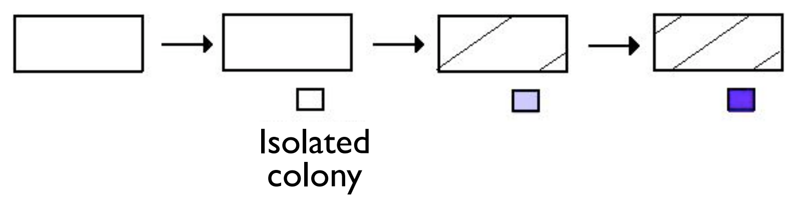
Speciation

Allopatric speciation – Vicariant speciation



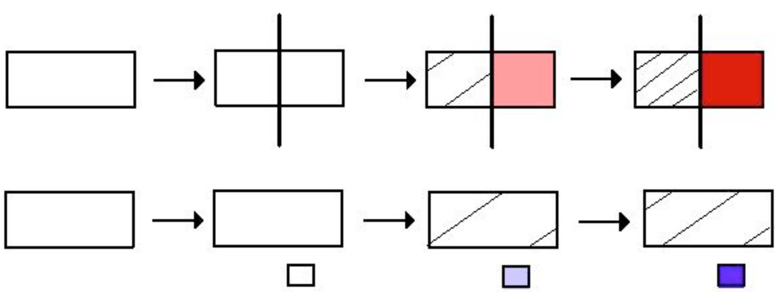
Speciation

Allopatric speciation – Peripatric speciation



Speciation

Allopatric speciation

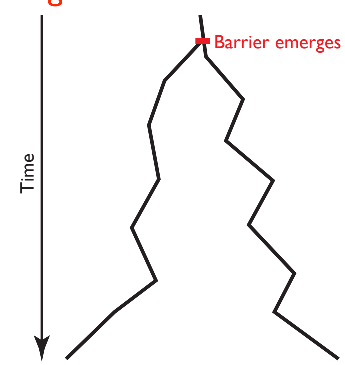


The extrinsic barrier halts gene flow between the isolated populations.

Speciation

Allopatric speciation

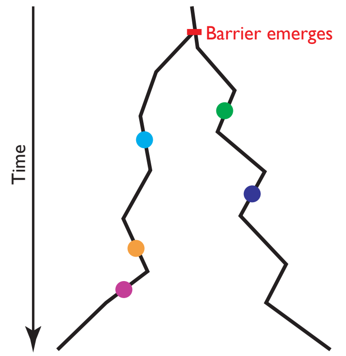
Without gene flow, each population follows an independent evolutionary trajectory, accumulating genetic changes through drift and/or selection.



Speciation

Allopatric speciation

For these changes to lead to speciation, the genetic changes in one population must be incompatible with the genetic changes in the other population.



Speciation

Allopatric speciation

As populations accumulate changes over time (R), the number of possible ways in which an incompatibility can occur rises at least as fast as R^2: the more changes occur in one population, the more possible ways in which a genetic incompatibility could occur with the second population.

Once genetic incompatibilities have arisen between two separately evolving populations, the populations are no longer able to cross and produce fertile offspring.

⇨ Speciation.

Speciation

Allopatric speciation

The genetic changes that accumulate in the two populations may be caused by natural selection, sexual selection, or by random genetic drift.

Which forces would you expect to be faster?

Which forces would you expect to be relatively more important in peripatric speciation?

Speciation

Allopatric speciation – example

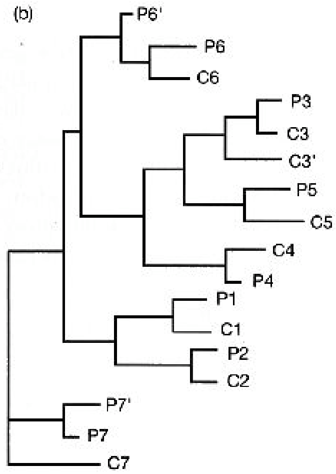
About 3 million years ago, North and South America merged, forming a land bridge (the Isthmus of Panama) and isolating the marine communities of the Carribean and Pacific.

Knowlton et al (1993) studied snapping shrimp from seven pairs of similar species on either side of the isthmus.

Speciation

Allopatric speciation – example

A phylogeny of the seven pairs indicated that each of the species was most closely related to a similar looking species from the other coast.



Speciation

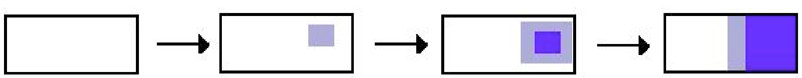
Allopatric speciation – example

Mating experiments in the lab indicated that, in each case, the sister species from the Carribean and from the Pacific failed to produce viable offspring.

The formation of the land bridge between North and South America led to the isolation of populations on either side. With gene flow cut off, the populations diverged, leading to new species in 7/7 cases.

Speciation

Parapatric speciation



Without a geographic barrier, gene flow may swamp out genetic differences that arise within a population.

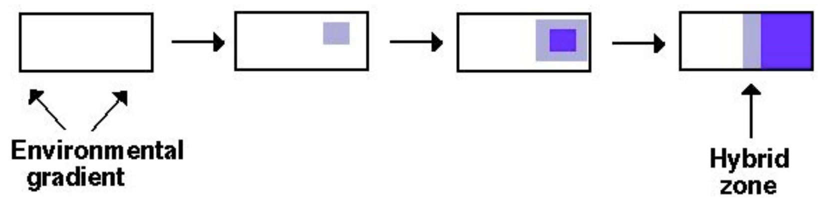
If, however, the population is distributed over space and:

- little gene flow occurs between distant locations and
- there is an environmental gradient favoring different genetic combinations in different places,

selection may be strong enough to maintain genetic differences, creating a genetic cline.

Speciation

Parapatric speciation



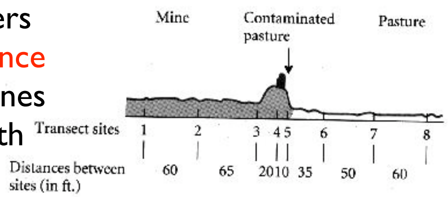
If the habitat changes fairly abruptly, there may be a sharp border between different types: a hybrid zone.

Over time, the hybrid zone may shrink or remain stable.

Speciation

Parapatric speciation – Example

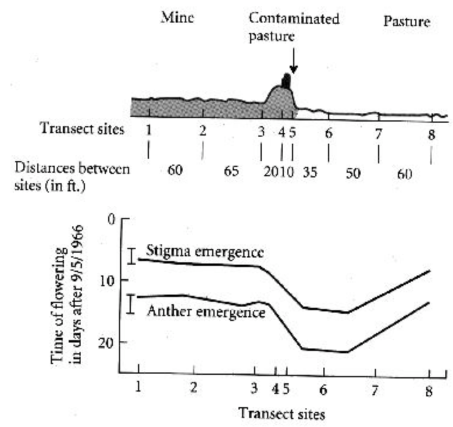
Antonovics and co-workers studied heavy metal tolerance in grasses growing near mines on land contaminated with lead and zinc.



Plants from the grass species *Anthoxanthum odoratum* were tolerant near the mine but remained intolerant at distant sites.

Speciation

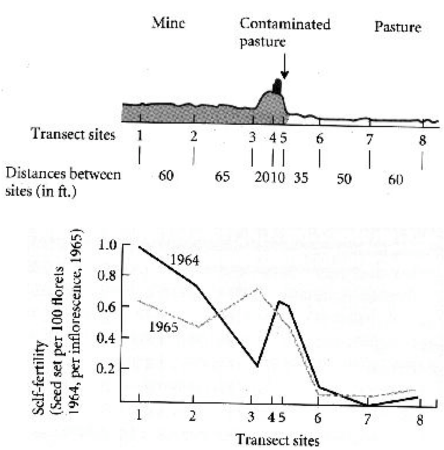
Parapatric speciation – Example



Heavy metal tolerance was not the only difference observed; flowering time also differed along the transect.

Speciation

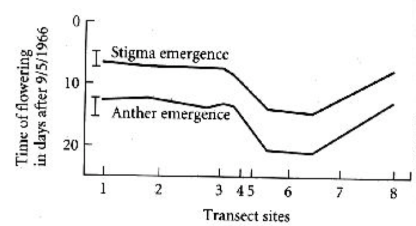
Parapatric speciation – Example

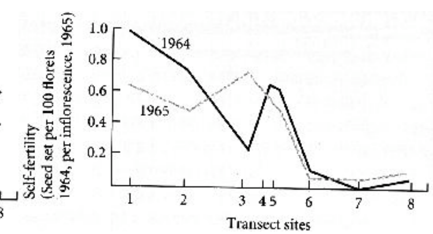


Selfing rates were also higher near the mine.

Speciation

Parapatric speciation – Example





The divergence in flowering time and increased selfing rates have reduced gene flow between tolerant and non-tolerant grasses and increased the reproductive isolation of grasses near the mine.

Speciation

Parapatric speciation

In this case, heavy metal tolerance has evolved recently, during which time the species has always had a continuous distribution.

Therefore, parapatric speciation processes can be inferred. In most other cases, however, it is difficult to know whether a species that is currently parapatric may have been previously allopatric.

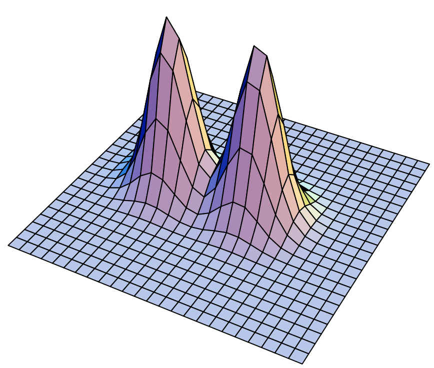
Speciation

Sympatric speciation

Sympatric speciation is the most controversial of all the modes of speciation, since divergence must occur in the face of high levels of genetic exchange.

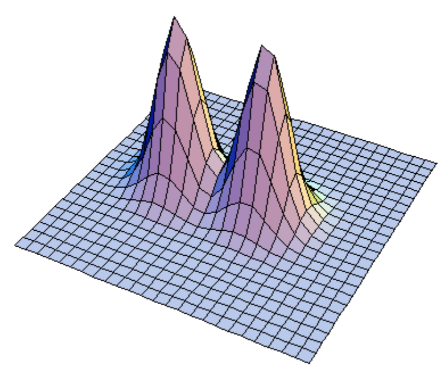
Speciation

Sympatric speciation



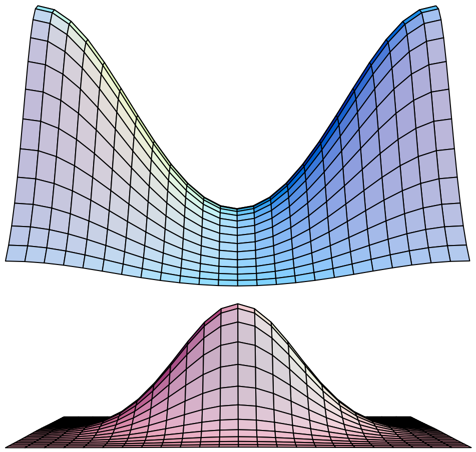
Speciation

Sympatric speciation



Speciation

Sympatric speciation

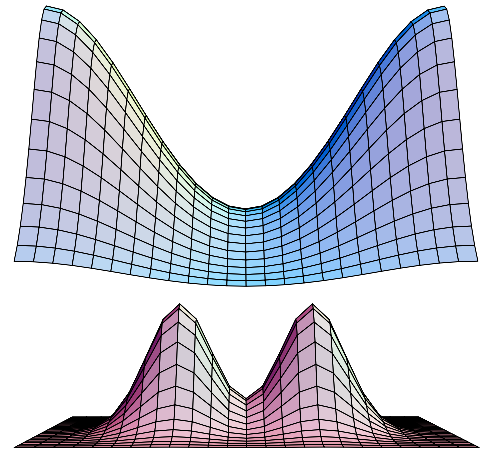


Adaptive landscape

Phenotypic distribution
Pre-selection

Speciation

Sympatric speciation

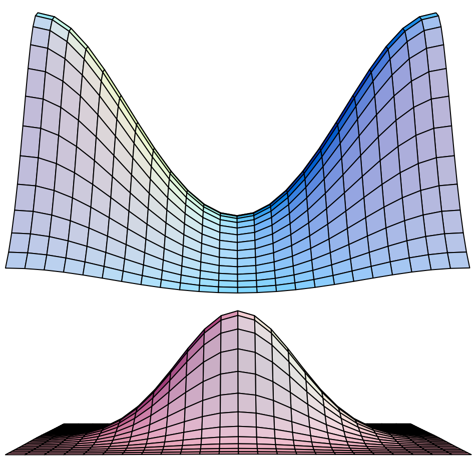


Adaptive landscape

Phenotypic distribution
Post-selection

Speciation

Sympatric speciation



Adaptive landscape

Phenotypic distribution
After random mating

Speciation

Sympatric speciation

If the extreme phenotypes in a population have the highest fitness (disruptive selection), the population will not split apart if mating is random.

If, however, genes arise that cause extreme individuals to assortatively mate (mate with similar types), then more extreme offspring can be produced:

The problem with this idea is that it is difficult for assortative mating to evolve in a way that is coupled with the trait subject to disruptive selection.

Speciation

Sympatric speciation

A second, more likely way is if the traits themselves lead to assortative mating.

For example, if the traits involve utilizing different resources and mating tends to happen around resources, then individuals with extreme traits will naturally mate with similar individuals.

Over time, if sufficiently strong assortative mating evolves, sympatric speciation will be the result.

Speciation

Sympatric speciation – example

The classic case of sympatric speciation is that of the apple maggot fly, *Rhagoletis pomonella*.

Hawthorns were the original host plant of *Rhagoletis pomonella* until about 150 years ago, when the fly was observed on cultivated apple trees (introduced to the Americas).

The apple maggot fly is now widespread in the northeastern US and causes millions of dollars of damage each year to apple crops.

Speciation

Sympatric speciation – example

Rhagoletis courts, mates, and lays eggs on its preferred host plant.

Individuals that prefer apples consequently tend to mate with other individuals who prefer apples.

Since the host shift, flies that prefer hawthorns and apples have diverged genetically.

Feder et al (1988, 1990) found statistically significant differences in allele frequencies at six loci, differences that allow the two populations to be identified.

Speciation

Sympatric speciation – example

Changes in the timing of mating have also occurred: mating on apples occurs ~ 3 weeks earlier.

Overall, matings between hawthorn and apple flies has been reduced to only ~6% and the two are now considered incipient species.

Speciation

Reproductive isolation mechanisms

The exact mechanisms by which reproductive isolation is accomplished vary but fall into two main classes:

- Premating (or prezygotic) isolating mechanisms: Mating and/or fertilization are prevented.
  - e.g.: changes in habitat preferences, changes in timing of reproduction, physical incompatibilities, changes in mating preferences or mating behaviors.
- Postmating (or zygotic) isolating mechanisms: Mating occurs but hybrid offspring are inviable, infertile, or produce inviable/infertile offspring.

Speciation

Reproductive isolation mechanisms

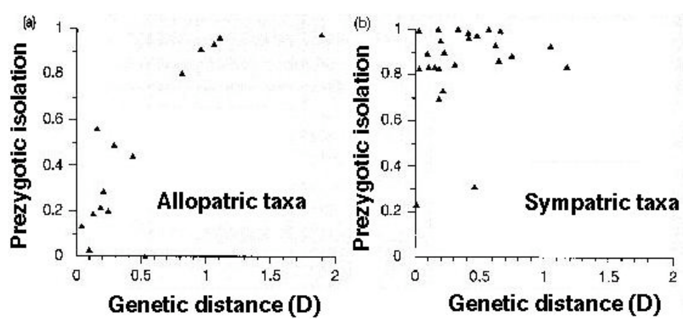
Where would you expect premating isolation to play more of a role:

allopatric speciation?

or sympatric speciation?

Speciation

Reproductive isolation mechanisms



Coyne & Orr (1997) found that premating isolation appeared earlier in sympatric *Drosophila* species pairs than in allopatric pairs.

Speciation

Reproductive isolation mechanisms

Which should evolve first in sympatric species pairs:

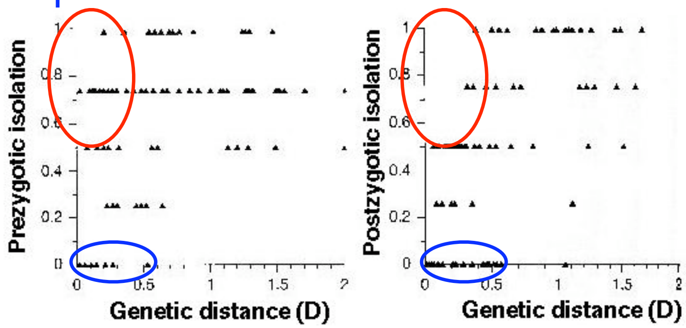
premating isolation,

or postmating isolation?

What about in allopatric pairs?

Speciation

Reproductive isolation mechanisms



Prezygotic isolation evolves earlier in the speciation process, primarily due to the rapid mating isolation that evolves between sympatric species pairs.

Speciation

Which mode of speciation is most important?

Although examples of each mode of speciation are known, it remains unclear how frequently each occur.

Because of the special circumstances required for parapatric and sympatric speciation, many evolutionary biologists suspect that allopatric speciation is responsible for the vast majority of speciation events.