What is a Species?

- The smallest evolutionarily independent unit

Evolutionary independence occurs when mutation, selection, gene flow, and drift operate on populations separately. Species form a boundary to the spread of alleles (gene flow).

I. Biological Species Concept

- Evolutionary independence is indicated by reproductive isolation in this case
- If populations living at the same time do not hybridize or fail to produce fertile offspring when they do, they are separate species
- This definition has been around the longest and makes sense but…..

Problems:

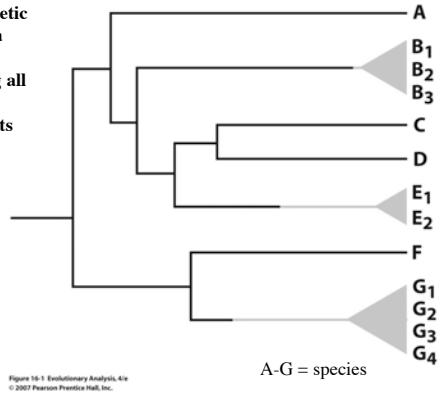
1. What if populations normally never meet?
2. Can't be used for fossils
3. Doesn't work with asexual organisms
   1. Gene flow causes speciation in bacteria
4. Difficult to apply to plants where hybridization between divergent populations is routine

II. Phyologenetic Species Concept

- Systematists prefer this one which focuses on **monophyly**
- A **monophyletic** group is a group of taxa that contain all known descendents of a common ancestor

(a taxon is any named group of organisms; population, species, genus, order, etc)

Monophyletic Groups: a group containing all known descendents of a single common ancestor



A-G = species

Makes sense because….

1. Traits can only distinguish populations on a phylogeny if they've diverged genetically and morphologically (implies no gene flow)
- Applies to fossils and asexual organisms just as well
- It's testable: species are named based on statistically significant differences

The trouble is….

- It takes significant time, money, and analysis to estimate phylogenies well so few have been established
- Also this method would easily double the number of named species---yikes!

III. Morphospecies Concept

- Paleontologists define species based on morphological differences of fossils
- When tests of reproductive isolation or phylogenies are lacking---they usually are---this works for everything
- So the advantage is it is highly applicable

The trouble is…

- It's very subjective and can be arbitrary
- With fossils there are no colors or soft tissues available, or behavioral information---when these things are unknown, the species is called **cryptic**, they might appear similar but may not be if more info were available

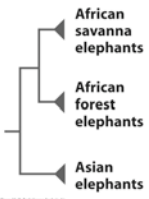
An example of how these concepts are applied…

- Diversification of Marine Copepods
  - *Eurytemora affinis*-many populations found in most temperate coastal waters considered all one species
  - DNA analysis to develop phylogenies showed 8 different species
  - Are they evolving in response to the different environments? their prey and predators?

African Elephants

Thought to be 2 elephant species: Asian and African

- Turns out savannah and forest dwelling African elephants are morphologically different
- DNA sequences suggests they're 2 species
- Important consequences for conservation

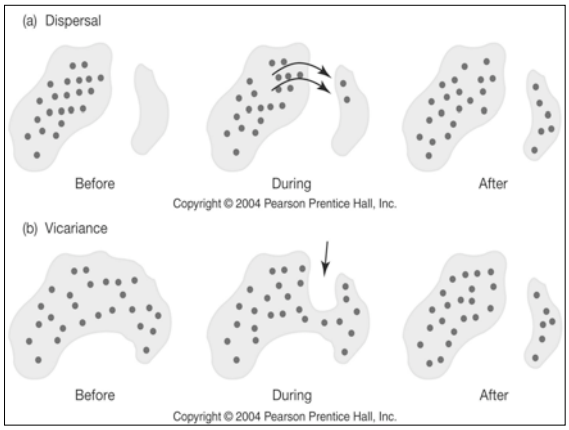


Mechanisms of Speciation

1. Two populations are isolated from each other
2. There is a divergence of traits such as mating systems or habitat use
3. Reproductive isolation evolves even when populations are re-introduced (secondary contact)

I. Physical Isolation as a Barrier to Gene Flow

- **Allopatric Model**-population is physically separated and diverges
  - **Erie water snakes: dispersal**
  - **An existing range is split: vicariance**
    - **(river, glacier, lava flow, highway)**



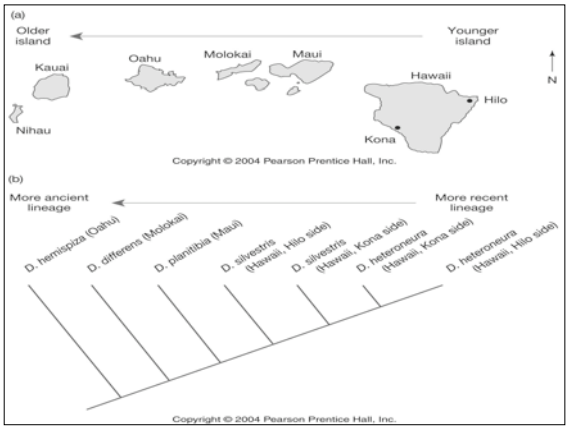
A. Isolation by Dispersal: Endemic Hawaiian Flies

- 500 named species with ~350 more to go
- Every conceivable habitat, food source, shape, color, courtship displays, etc

How did this happen?

Founder Hypothesis

- A few organisms or even one pregnant female winds up in a novel habitat, isolated from her population, and divergence ensues
- For Hawaii, this makes two predictions:
  - Closely related species should be found on adjacent islands
  - At least some sequences of branching events should correspond to the sequence in which the islands were formed



Isolation by Vicariance: S. American Snapping Shrimp

- Isthmus of Panama closed about 3 million years ago, separating the marine animals on the Atlantic and Pacific sides
- There are 7 pairs of sister species of snapping shrimp in this area, with one of each pair on either side of Central America
- DNA sequences confirmed their close relationships although some pairs were more closely related than others---why??

2. Polyploidy as a Barrier to Gene Flow

- It's not necessary for populations to be physically isolated for speciation
- Polyploid plants can't breed with diploid ones, and even flower shape and timing tend to be different so pollinators tend not to pollinate one with the other
- 70% of angiosperms and 95% of ferns/ mosses have polyploidy in the lineages

I. Genetic Drift

- Thought to be the key to the second step of speciation
  - Most pronounced in small populations and most species are thought to have originated with small population sizes
  - The isolated population is a small random sample of the original and drift leads to random loss and fixing of new and old alleles---ie divergence

But……

- In **bottlenecking**---when a population is reduced to a small size for a short time--- only the very rare alleles are lost to drift; the population has to stay small for a long time for dramatic allele changes
- Humans have introduced hundreds of small populations to new habitats and no known speciations have occurred

2. Natural Selection

- If a population occupies a novel habitat or uses a novel resource, natural selection can create new species without drift

The Apple Maggot Fly

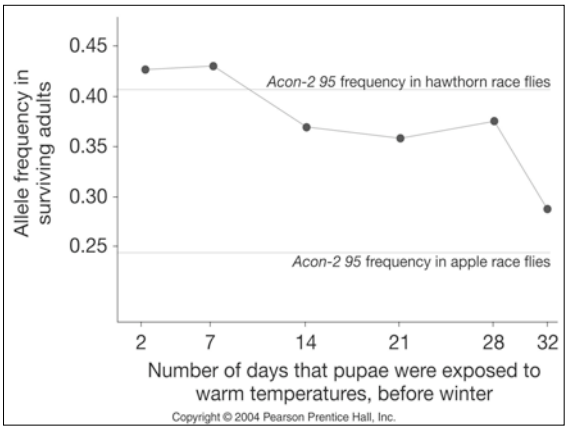
- Historical habitat was native North American hawthorne trees
- Started showing up in apples in the mid-1800's
- Apple trees were introduced to North America about 300 years ago

So are the apple preferring flies a distinct population, selected apart by food preference?

- Genetically the flies are statistically different, so they are distinct populations even though they look identical
- They show strong habitat preference for apples or hawthornes and since that's where they mate, they only crossbreed 6% of the time
- This limits gene flow so natural selection could be working separately on the two

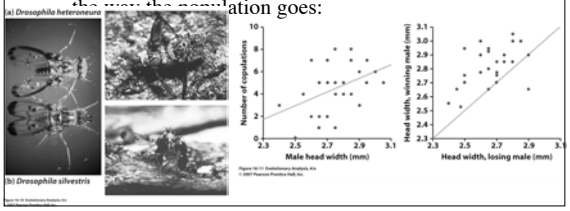
In addition…

- Hawthorne larvae have to withstand colder temperatures because hawthornes ripen later in the year. Is this driving divergence also?
- Researchers exposed hawthorne larvae to 1-5 weeks of warm weather followed by a brief "winter" and then "spring"



3. Sexual Selection

- This can trigger rapid divergence because it affects gene flow directly
- If female flies suddenly prefer wide heads, that's the way the population goes:



Secondary Contact

- This is when populations that have diverged come back together
- Hybridization can occur and there are 3 possible outcomes:
  - Thriving hybrids can erase the divergence
  - If the hybrids have new characteristics they may become a 3rd species
  - Hybrids may have reduced fitness and thus little effect

1. Reinforcement

- Hybrids should theoretically be less fit
  - natural selection hasn't been working to adapt them to their environment
  - Combination of new mating systems may not be able to communicate to mate
  - Heterozygote alleles from diverged parents may not work well together

  This should reinforce the divergence of the parents and finalize speciation

Reinforcement Hypothesis

- When closely related species come into contact and hybridize, a mechanism that prevents hybridization should evolve:
  - **Pre-zygotic isolation**: anything that prevents fertilization from occurring between populations
  - **Post-zygotic isolation**-hybrid offspring are sterile

2. Hybridization

- If hybrids prosper….
  - Creation of a new species-if hybrids occupy a different habitat than the parents and do better there than the parents
  - Hybrid zones-a region where interbreeding between diverged populations occurs and hybrid offspring are frequent

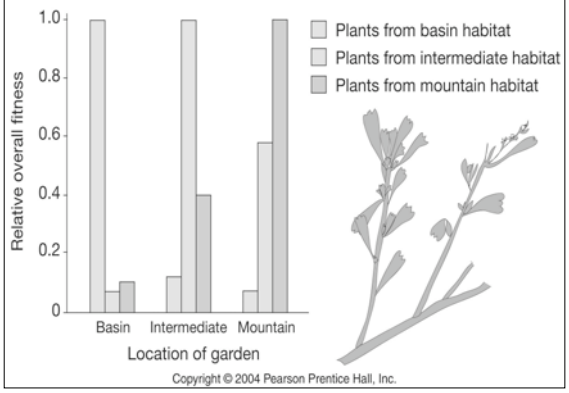
Table 16.3 Outcomes of secondary contact and hybridization

When populations hybridize after diverging in allopatry, several different outcomes are possible. The type of hybrid zone formed and the eventual outcome depend on the relative fitness of hybrid individuals.

Fitness of hybrids	Hybrid zone	Eventual outcome
Lower than parental forms	Relatively narrow and short lived	Reinforcement (differentiation between parental populations increases)
Equal to parental forms	Relatively wide and long lived	Parental populations coalesce (differentiation between parental populations decreases)
Higher than parental forms	Depends on whether fitness advantage occurs in ecotone or new habitat	Stable hybrid zone or formation of new species

Table 16-3 Evolutionary Analysis, 4/e

Two sub-species of Sagebrush



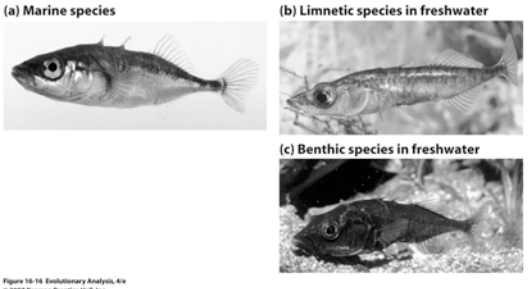


Figure 16-16 Evolutionary Analysis, 4/e

Threespine Sticklebacks

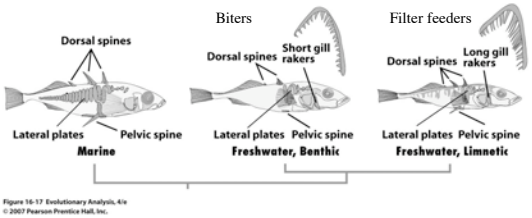


Figure 16-17 Evolutionary Analysis, 4/e

Freshwater species can hybridize but the hybrids are less fit than either parent. It's also rare because females choose mates based on body size and color.