Bio 1M: Speciation (complete)

1 How are species defined?

- Conceptually, we define species as "evolutionary units":
  - Individuals within a species are evolving together
  - Individuals of different species evolve independently
- It is difficult to make this conceptual definition into a practical definition
  - **Answer:** i.e., one that we can apply to decide how to group organisms into species
  - Life is complex

1.1 Biological species concept

- Biological species are defined by reproductive isolation
- Different biological species either:
  - Don't breed in nature
  - Breed but fail to produce offspring
  - Produce **inviable** offspring – offspring do not develop to adulthood
  - Produce **sterile** offspring – offspring that cannot themselves reproduce

Mechanisms of isolation

- Mechanisms of isolation are often divided into two classes:
  - **Prezygotic** isolation refers to any mechanism that prevents successful mating
  - **Postzygotic** isolation refers to any mechanism that prevents offspring from producing offspring of their own
  - "Zygote" means a cell formed by the fusion of a sperm and an egg

Mechanism examples

- Pre- or post-?
  - Different malaria parasites breed inside different hosts
  - Different species of doves can nest together, but eggs fail to hatch or chicks fail to grow
  - The offspring of horses and donkeys grow up to be healthy, infertile adults
  - Sea urchin eggs cannot be penetrated by sperm from other species
  - Species of pine trees release and receive pollen and different times of year

Pre- vs. post-zygotic mechanisms

- Which should be adaptively favored?
  - **Answer:** Pre-zygotic mechanisms mean less wasted effort
  - **Answer:** When post-zygotic isolation is happening, there will be natural selection for pre-zygotic isolation
  - **Answer:** Example: it takes a lot of resources for a horse to birth and raise a mule, but there is no long-term fitness benefit
    - **Answer:** This is presumably why horses rarely mate with donkeys

Disadvantages of the biological species concept

- **Answer:** Doesn't apply to asexual species
- **Answer:** Not practical for extinct species
- **Answer:** May be hard to evaluate
  - **Answer:** What if two populations rarely come into contact because of geographic distance?
- *Comment:* Rings of populations

1.2 Morphological species concept

- Morphological species are defined to be different if they **look** different
  - Useful for working with fossils, or very diverse groups (e.g., insects)
  - A lot of expertise and experience guides morphospecies decisions
- Disadvantages?
  - **Answer:** Subjective, prone to disagreements
  - **Answer:** There are groups that look very similar but can't produce viable offspring
  - **Answer:** Not clear how definition relates to our conceptual definition of evolutionary units

1.3 Ecological species concept

- An ecological species is a set of related organisms occupying the same ecological **niche**
  - Exploit similar resources
  - Tolerate similar environments
  - Face similar natural enemies
- Commonly used for small things, particularly small asexual things

1.4 Phylogenetic species concept

- A phylogenetic species is a monophyletic group of *populations*
  - Must not be divisible into smaller species
- A **monophyletic group** is a group *defined by* a single common ancestor
  - All descendants of the ancestor must be in the group

Phylogenetic species concept

- Advantages
  - Well defined (as long as you know what a population is)
  - Broadly applicable
- Disadvantages
  - Hard to estimate phylogenies
  - Requires a lot of information about populations
- Believers in the phylogenetic species concept recognize a *lot* of species

Defining species

- Defining species formally can be very tricky
  - No one way is agreed to be the best
- Usually we know more or less what we mean by a species, though

Generating species

- We believe new species are generated from old species
- One species can gradually evolve into another
  - We can't say exactly when the switch occurs
- Species can also **diverge**: one species splits into two species
  - Divergence is the origin of **diversity**

How do species split?

- Genetic isolation
- Genetic divergence
- Which comes first?
  - **Answer:** Usually isolation: with too much gene flow populations can't diverge
  - **Answer:** There is often a loop: isolation allows divergence, which causes natural selection for more isolation

2 Species divergence in allopatry

- **Allopatry** refers to organisms living apart from each other
- If two populations are isolated from each other, we would expect that they might diverge. Why?
  - **Answer:** Genetic drift
  - **Answer:** Natural selection
    - **Answer:** Different environments, or different adaptive mutations
- How can two populations of the same species be isolated from each other?

2.1 Dispersal

- Isolated populations of the same species can develop if some individuals **disperse** (move) to a new area and **colonize** it (establish a new population).
- Since colonizing populations are usually small, we expect founder effects and drift to be particularly important

2.2 Vicariance

- Isolated populations of the same species can develop when a population is split by a geographical or ecological barrier
- Such splits are called **vicariance** events.
  - Rivers change course, mountains appear or disappear, continents split and join
  - When temperature changes, some species may only be able to survive in "refuges", small, protected parts of their original range

Example: ratites

- The ancestors of today's ostriches, emus, etc. were isolated when the super-continent of Gondwanaland drifted apart starting about 140 million years ago

3 Species divergence in sympatry

- **Sympatry** refers to organisms living in the same geographic area
- In general, it should be hard for populations of the same species living in sympatry to diverge.

  - **Answer:** Gene flow
  - **Answer:** Competition
- Are there exceptions to this expectation?
  - **Answer:** Seed crackers?
  - **Answer:** Hawthorn flies
  - **Answer:** Soapberry bugs

3.1 Disruptive selection

Divergence by partitioning habitats

- Insects that feed on many different plants may be subject to divergent selection
  - An individual may do most of its feeding on one particular plant
- In some cases, gene flow will prevent divergence
- In other cases, individuals may mate preferentially with individuals with the same host plant, and divergence may occur

3.2 Genetic incompatibility

- Divergence can also occur when mutation causes genetic incompatibility
  - If two populations are in the same place, but can't produce fertile offspring, they are reproductively isolated
- Genetic incompatibility is less likely to produce divergence than physical separation
  - **Answer:** The populations will still compete, and one may drive the other extinct
  - **Answer:** Or, reproductive isolation and disruptive selection may work together to make divergence more likely
    - **Answer:** or less unlikely

Polyploidy

- Reproductive mistakes can occur that produce individuals with extra copies of each chromosome
- Sometimes these **polyploid** individuals survive, and can even mate
- This produces instant reproductive isolation
- It can also provide material for new genetic innovation
  - **Answer:** Two copies of each gene, so it may be possible to keep one and mutate one

4 Reuniting

- What happens when isolated populations come back into contact?
- Usually this happens when a geographic barrier disappears
  - a land bridge forms between an island and the continent
  - a river changes course

4.1 Fusion

- When two isolated populations come into contact, they may **fuse** – go back together
  - Adaptive differences may be small
  - Adaptive differences may be overwhelmed by gene flow

4.2 Reinforcement

- In some cases, hybrid offspring may have low fitness
  - **Answer:** Incompatible alleles
  - **Answer:** Disruptive selection
- In these cases we expect natural selection for traits that **reinforce** the distinction between the two species
  - They avoid mating, using coloration, timing, courtship rituals

Meadowlarks

- Eastern and Western meadowlarks have hybrid zones in the Great Plains
- Hybrids don't reproduce well
  - Probably due to incompatible alleles after evolving separately
- They have evolved to avoid inter-breeding:
  - **Answer:** They have different songs

Sticklebacks

- Closely related freshwater sticklebacks live on the bottom (benthic) or in the water column (limnetic)
- Benthic sticklebacks arrived first (from the ocean), and are highly adapted to live on the bottom
- Limnetic sticklebacks arrived later
  - **Answer:** Adapted to live in the water column
- The two groups evolved to avoiding breeding with each other
  - **Answer:** Courtship rituals

4.3 Hybrid zones

- When hybrid offspring are functional, and well-adapted to the overlap zone, there may be a zone where hybrids occur
- Not always clear when we should consider the species to be different
  - What if species B has hybrid zones with A and C but A and C don't mate in nature?

4.4 Exclusion

- One species might eliminate the other species, either by competition, or by better success in mating
  - Warblers competing for mates
  - Modern humans

4.5 New species

Sunflowers

- A cool species of sunflower
  - Resembles natural hybrids from a hybrid zone
  - Is that how it arose?
- Breeding experiments suggest that it's likely
- Why is this surprising?

- **Answer:** Rarely seems to happen
- **Answer:** If the hybrid has high fitness, why would reproductive isolation evolve?

- How did it happen?
  - **Answer:** Probably because of an unusual adaptation: the hybrids live in drier climates than either of the "parent" species

Conclusion

- The diversity we see in the world arises from speciation events; mostly by single species splitting into two
- Species splits typically involve isolation and divergence
  - Isolation can happen allopatrically or sympatrically
  - New species can also sometimes arise from hybridization between related species
- Defining species can be complicated
  - Particularly if we want definitions that include both asexual and sexual species