1. Review of the biological barriers that limit gene flow between populations and species.

2. Back to Darwin’s problem:
   - Q: How do these biological barriers (reproductive isolating mechanisms) evolve in a population?

3. Some phylogenetic foundations

4. Extrinsic barriers & modes of speciation: allopatry, parapatry, peripatry, & sympathy

5. Modes of speciation: allopatry, parapatry, & sympathy

6. Sexual selection (maybe)
So, how do genetic barriers to gene flow evolve?

How could these two populations have diverged from each other in the first place?

- If the ancestral population (#1) carried only A1 alleles, the low fitness of A1A2 individuals would have prevented A2 alleles from increasing in frequency & thus forming a reproductively incompatible population.
- The same would be true for a population (#2) starting with only the A2 allele.

**Answer:** There must be some pre-existing EXTRINSIC barriers to gene flow so that the populations can diverge through (1) selection &/or (2) drift.

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**Speciation: Part 2**

1. Back to Darwin’s problem:
   - Q: How can such biological barriers evolve in a population?
   - A: It’s REALLY hard if there is unrestricted gene flow.
   - There must be some EXTRINSIC barriers that limit gene flow between members of a population, so that lineages can diverge (by selection & drift) and evolve INTRINSIC genetic (PRE- AND POST-ZYGOTIC) barriers to further exchange.

2. Some phylogenetic foundations

3. Extrinsic barriers & modes of speciation: allopatry, parapatry, peripatry, & sympathy

4. Sexual selection (Time permitting)

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**Like your genealogy, evolution is a branching process...**

So, what's the answer??????
PHYLOGENETIC TREE (or phylogeny): a graphical depiction of the history of relationships among a group of organisms.

- **SPECIATION** causes the tree to branch.
- **EXTINCTION** causes the loss of branches (or lineages).

**How to Read a Phylogenetic Tree**

- The common ancestor for the group is called the root of the tree.
- The splits in branches are called nodes, and indicate a division of one lineage into two.
- The positions of the nodes on the time scale (if present) indicate the times of the corresponding speciation events.

**More important tree terminology…**

- **Monophyletic clade**: a taxonomic group that includes ALL of the taxa/species descended from a specific common ancestor.
- **Paraphyletic clade**: a taxonomic group that excludes some of the descendants from a specific common ancestor.
- **Polyphyletic clade**: a taxonomic group that does not contain the most recent common ancestor of its members.

**Turtles + Snakes & Lizards + Crocodiles + Birds = MONOPHYLETIC REPTILIA**
Speciation: Part 2

1. Finish up analysis of the biological barriers that limit gene flow between populations and species.
2. Back to Darwin's problem:
   - **Q**: How can such biological barriers evolve in a population?
     - In other words, how can a trait that reduces reproductive opportunities be favored by natural selection?
   - **A**: It's hard (or impossible) if there is unrestricted gene flow.
     - There must be some barriers that limit gene flow between members of a population, so that lineages can diverge (by selection & or drift) and evolve genetic reproductive barriers.
3. Some phylogenetic foundations
4. Extrinsic barriers to gene flow & modes of speciation: allopatry (vicariance + dispersal), parapatry, & sympathy
5. Sexual selection (Time permitting)

The central problem for speciation:

- How can two reproductively incompatible populations (SPECIES) be formed without intermediates of low fitness?
  - Somehow, EXTRINSIC limits to gene flow have to be erected before populations can accumulate the genetic barriers that confer reproductive incompatibility (reproductive isolation) can evolve
- There are 3 basic geographic modes or settings in which reproductive isolation could evolve:
  1. Allopatry (allopatric speciation)
     a) vicariance
     b) peripatric dispersal/ founder effect
  2. Parapatry (parapatric speciation)
  3. Sympatry (sympatric speciation)
**Geographic Modes of Speciation**

1. **Allopatric Speciation:**
   - A physical barrier subdivides a species range into 2 or more populations that no longer freely exchange genes.
   - The barrier could be a river, mountain range, peninsula, deep water, ocean current, glacier, or any kind of impassable habitat.
   - Events that divide a species range are called **VICARIANT** events.

2. Once vicariance has occurred, the separated populations can independently accumulate genetic differences either through
   - (1) diversifying selection or (2) genetic drift (or both).

3. **Litmus test of speciation:** when populations come into **SECONDARY CONTACT**, are they reproductively isolated? (i.e., are they genetically incompatible?)
   - In other words, what happens when ________ is re-established?

**A Major Marine Vicariant Event:**

- The rise of the Isthmus of Panama (3-5 MYA) shut off gene flow between the Pacific Ocean & Caribbean Sea (**EVENT**).
- The Isthmus separated previously connected populations of snapping shrimp, so there is no longer any gene flow.

What would be the consequences for terrestrial organisms?
Vicariant (allopatric) speciation in snapping shrimp

- 7 sister species pairs have their sister species on the opposite side of the Isthmus (they hate to mate with each other)
- 3 instances of within ocean basin speciation

What's the Genetic Basis of Reproductive Isolation in Snapping Shrimp?

Duh...they got rhythm!

Snap Fu

Geographic Modes of Speciation

Allopatric speciation: Vicariance
- Allopatric speciation: Peripatric/Founder effect
- Parapatric speciation
- Sympatric speciation
Dispersal-mediated/______ effect/peripatric speciation

Hawaiian “picture-wing” fruit flies (Drosophila)

- There are at least 106 species of picture-wing Drosophila that are ENDEMIC (live only there) to the Hawaiian Islands.
- The oldest emergent Hawaiian Islands are younger than 5.6 million years.
- How did so many species evolve in so little time?
- How did >100 displays diversify?

Hot spots & the formation of the Hawaiian Archipelago

The phylogeny of Hawaiian Drosophila mirrors the order of appearance of the islands.

- More ancient lineage
- More recent lineage

So, dispersal by a few individuals to a new island explains between island speciation
But what about the 30-100 species that live on each island?

Lava flows & ________ (vegetated islands) formation on the Big Island of Hawaii

Once you’ve gotten to a _____, it’s a mean world out there.

Most species of Hawaiian Drosophila are confined to a single _____

THE PARTY LINE ON ALLOPATRIC SPECIATION...

1. _____________ speciation is basically caused by disruptive/ diversifying natural selection
   * Once gene flow is interrupted between 2 populations, environmental differences between the habitats occupied by each population cause the evolution of genetic differences that create either pre- or post-zygotic incompatibility
   * Most of the reproductive isolation evolves while the populations are allopatric, so that if & when the populations come back into sympathy, they are substantially isolated.
   * In other words, “SPECIATION IS A BY-PRODUCT OF THE DIVERGENT SELECTION THAT OCCURRED DURING ALLOPATRY.”

2. Founder effect/peripatric speciation may be driven by genetic drift (especially in small, newly founded populations), along with diversifying selection.

(1) Founder effects/genetic drift + (2) diversifying selection (slightly different habitats on different kipukas) are important for the evolution of new species within an island
What happens when 2 formerly allopatric subpopulations come into contact?

1. They may have diverged so much that they have evolved strong pre- or post-reproductive genetic barriers to gene flow.
   - THERE ARE NOW 2 SPECIES WHERE THERE ONCE WAS 1

2. They may not have genetically diverged enough to be reproductively incompatible.
   - They readily hybridize & eventually merge into a single population.

3. They hybridize, BUT HYBRIDS HAVE LOWER FITNESS THAN EITHER PARENTAL POPULATION.
   - Selection should act to reduce matings (PRE-ZYGOTIC BARRIERS) between the parental populations.
   - This process is called _______________.

Evidence for reinforcement after secondary contact of populations in *Drosophila* (fruit fly) species

- For a given level of genetic divergence, SYMPATRIC sister species have MUCH higher levels of pre-zygotic isolation than ALLOPATRIC pairs of sister species.
- Reinforcement "selection" increases reproductive isolation and reduces gene flow between recently diverged species that have come into secondary contact.

Geographic Modes of Speciation

- **Allopatric speciation:** Vicariance
- **Allopatric speciation:** Peripatric/Founder effect
- **Parapatric speciation**
- **Sympatric speciation**

- Barrier removed or new species disperse over it, re-establishing sympathy
- Range expansion re-establishes sympathy
- Range expansion leads to sympathy
- Genetic differences result in reproductive isolation
Parapatric speciation in pasture grasses (Agrostis tenuis)

• "Para" means "______", so PARApratic populations have adjacent, but non-overlapping borders.
• By definition, there is no obvious geographic barrier to gene flow.
• So, how can reproductive isolation evolve?

• Answer? Dramatic environmental discontinuities match distributions of 2 populations.
  • One population is well-adapted to the environment on one side of the discontinuity
  • The other population is better adapted to the other environment
  • Migrants from one population to the other will be selected _________
  • If the disadvantage is big enough, then barriers to gene flow can evolve & reproductive isolation occurs.

Geographic Modes of Speciation

<table>
<thead>
<tr>
<th>Allopatric speciation: Vicariance</th>
<th>Allopatric speciation: Peripatric/founder effect</th>
<th>Parapatric speciation</th>
<th>Sympatric speciation</th>
</tr>
</thead>
<tbody>
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<td>Barrier removed or new species disperse over it, re-establishing sympatry</td>
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<td>genetic differences result in reproductive isolation</td>
</tr>
</tbody>
</table>

Sympatric speciation in crater lake cichlids

1. Sympatric "populations" have completely overlapping ranges.
2. By definition, there is no obvious geographic barrier to gene flow.
3. PROBLEM: When you see 2 species that are currently sympatric, you need to ask whether they evolved reproductive isolation in sympatry OR...
   • Did the species evolve reproductive isolation in _________, then subsequently become _________.

Phylogenies are essential for distinguishing between...
1. true sympatric speciation versus
2. secondary sympatry following divergence in allopatry.
Sympatric speciation in crater lake cichlids

Barombi Mbo in western Cameroon

- Small, 4 km²
- Drained by one river
- Very stable

Barombi Mbo contains 11 endemic species of cichlids
Species vary markedly in mating coloration and feeding behavior

Sympatric speciation in crater lake cichlids

- Barombi Mbo contains 11 endemic species of cichlids
- Species vary markedly in mating coloration and feeding behavior

Scenario 1: Allopatric origins & repeated colonizations of the lake

River

Red species migrates into lake & diverges into new species

River

Lake

Green species diverges into new species

Lake

River

Green species migrates into lake

Conclusion: River/Lake sister-species pairs suggest __________ origins

Scenario 2: Sympatric speciation within the lake following a single initial colonization of the lake

Green species migrates into lake

Blue species gives rise to white

Green species gives rise to blue

Conclusion: Lake-lake sister-species groups suggest __________ origins

The cichlids in Barombi Mbo are monophyletic

Pungu macarenii
Konia eisenrautii
Konia dikume
Sarotherodon linnelli
Sarotherodon caroli
Sarotherodon steinbachii
Myaka myaka
Sarotherodon lobbergerii
Stomatepis mariae
Stomatepis pindu
Stomatepis mongo
Sarotherodon galilaeus

Conclusion: The 11 species of Barombi Mbo cichlids diverged in __________.
Sympatric speciation in crater lake cichlids: How did reproductive isolation evolve?

1. Genetic variants within a population preferentially use specific microhabitats (or consume different prey) that select for different traits.
2. These contrasting microhabitat differences may subdivide the population, selecting against individuals that mate with variants specialized on alternative microhabitats.
3. But there would have to be essentially no gene flow between microhabitats.
   - This could happen if a species had very little dispersal potential (not the case in cichlids)
   - Or, a species could exhibit very strong preferences to mate with like phenotypes ⇒ **POSITIVE ASSORTATIVE MATING**

ECOLOGY MEETS EVOLUTION: MULTIPLE NICHE POLYMORPHISM

Are the cichlids in Barombi Mbo really monophyletic?

<table>
<thead>
<tr>
<th>Pungu maculatus</th>
<th>Konis efretradi</th>
<th>Konis dikum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sarotherodon (finetili)</td>
<td>Sarotherodon caroli</td>
<td>Sarotherodon steindachsi</td>
</tr>
<tr>
<td>Myola myska</td>
<td>Sarotherodon lalibergeri</td>
<td>Stomatepis manae</td>
</tr>
<tr>
<td>Stomatepis pindu</td>
<td>Stomatepis mango</td>
<td>Sarotherodon geiliius</td>
</tr>
</tbody>
</table>

**LAKE SPECIES:** Are they really 1 monophyletic clade?

RIVER SPECIES

Conclusion: There has been repeated gene flow from river species into Barombi Mbo fish

But, it's complicated:

A new study shows that there has been ongoing gene flow from river to lake species (but not a lot!)

Later: a little gene flow

Blue species gives rise to white

Green species migrates into lake

Green species gives rise to blue

Sexual Selection & Pre-zygotic Isolation

1. **Females generally make a MUCH greater investment in their young than do the males that father them.**
   - At a minimum, eggs are usually thousands of times bigger than sperm
   - Females often invest far more than males in parental care
2. **Sex ratios in almost all species with separate sexes are 1:1**
3. **Therefore, males will usually compete for females, especially when a single male can mate with multiple females.**
4. **In turn...**
   - Selection for males to acquire mates should be strong
   - Selection for females to select the best mate available should also be strong.

Sexual selection: selection for traits that are solely concerned with increasing MATING success
Two kinds of sexual selection...

1. **Intrasexual selection:**
   - Selection involving the ability of one sex (usually males) to compete directly with each other for mating opportunities.
   - **Example:** Northern elephant seals

2. **Intersexual selection:**
   - Selection favoring traits in one sex that attract the other.
   - **Examples:** Peafowl & NASCAR fans

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**Intersexual selection: evolution of long tails in widowbirds**

- Males with lengthened tails attracted more females.
- Long tails indicate the health and vigor of the male.
  - So, females that pick males with longer tails are likely to “give” his GOOD GENES to their offspring.

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**Intersexual selection, female mate choice and speciation**

- Darwin noted that elaborate secondary sexual traits tended to occur in groups that had lots of species.
- Does sexual selection for ornamentation cause groups to speciate?