1. Ecological (maintenance/coexistence) vs. evolutionary (origins) explanations for species diversity

2. **THE BIOLOGICAL SPECIES CONCEPT**
   - Speciation **is** the evolution of __________ __________

3. **The Paradox:** How can selection cause the evolution of reproductive isolation?

4. From anagenesis (within-lineage/species change) to cladogenesis (lineage splitting)
   - Micro- (within lineage) vs. Macro- (among lineage) evolution

5. What is reproductive isolation? “Permanent cessation of gene flow between populations” ⇒ __________ __________

6. The mechanisms that cause reproductive isolation
   - Pre-zygotic vs. post-zygotic reproductive isolating mechanisms

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**ALL YOU NEED TO KNOW ABOUT SPECIATION!**

*The Speciation Song*

Cheryl Van Buskirk and Cameron G. Brown

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**Maintenance versus origins of species diversity**

- **MAINTENANCE OF SPECIES DIVERSITY:** How do various kinds of ecological interactions (competition, predation, parasitism, mutualism, etc.) influence the number of species in a particular place at a particular time?

**FUNCTIONAL, ECOLOGICAL, & SPECIES DIVERSITY: DARWIN'S FINCHES**
"It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by the laws acting around us."

Charles Darwin, 'On The Origin Of Species', Chapter 14

"There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."

Charles Darwin, 'On The Origin Of Species', Chapter 14

ORIGINS OF DIVERSITY

1. There are 10-50 million species of living organisms alive today.
   • Probably ~ 500,000,000 have existed; most are extinct
2. All of these species descended from a single ancestor.
3. All of these species must have arisen over the last 4.5 billion years by the repeated division of an ancestral species into two daughter species.

Lake Victoria cichlids: 100’s of species in <20,000 years

4. HOW DID ALL OF THESE NEW SPECIES FORM?

ORIGINS OF DIVERSITY:
Diversification of Galápagos finches
(1 ancestral species into 14 in <2-3 million years)

Tangled bank; schmangled bank...

"There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved."

Charles Darwin, 'On The Origin Of Species', Chapter 14

Hey Prof. Strauss... here’s what I really said, dude.

Functional Diversity
Step 1: What do we mean by "species"?

1. **BIOLOGICAL SPECIES CONCEPT**:
   - A species consists of groups of actually or potentially interbreeding natural populations that are __________ from other such groups.

   - Two individuals are members of the same species if they **BOTH CAN AND DO** produce viable AND fertile offspring in the wild.
   - In other words, they can (and do) exchange genes.

   - Two individuals are members of **DIFFERENT** species if they **DO NOT** produce viable AND fertile offspring in the wild.
   - They DO **NOT** freely exchange genes in nature.

<table>
<thead>
<tr>
<th>Zebra (male)</th>
<th>Horse (female)</th>
<th>Zorse (sterile)</th>
</tr>
</thead>
<tbody>
<tr>
<td>+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coyote</td>
<td>Grey Wolf</td>
<td>Red Wolf (fertile)</td>
</tr>
</tbody>
</table>

Disclaimer: Problems with the Biological Species Concept

1. How do we know if individuals in separate populations could actually or potentially interbreed?

2. What’s “natural”/“in the wild” (coyotes & grey wolves rarely naturally interbreed)?

3. What about extinct organisms? (you can’t get a fossil to do “it”)

4. What about organisms that don’t sexually reproduce?

Implications of the Biological Species Concept

- A species consists of groups of actually or potentially interbreeding natural populations that are **REPRODUCTIVELY ISOLATED** from other such groups.

1. Species are breeding units that are evolutionarily independent from other such breeding units.

2. **So, _________ ARE THE FUNDAMENTAL EVOLUTIONARY UNIT**
   - Individuals do **NOT** evolve.
   - Populations & species **DO** evolve.

3. Species represent separate evolutionary units/gene pools/populations that can no longer exchange genes (GENE FLOW STOPS), hence evolve independently of each other.

**YOU!**
Outta The Gene Pool

So, how does REPRODUCTIVE ISOLATION evolve?

- A species consists of groups of actually or potentially interbreeding natural populations that are **REPRODUCTIVELY ISOLATED** from other such groups.

Darwin’s explanation in a nutshell:
- **________ causes divergence among “races” so that they eventually become full-fledged species.**

1. What biological mechanism(s) limit gene flow (i.e., cause reproductive isolation) between species?
2. How can selection favor the evolution of reproductive isolation?
   - In other words, how can a trait that reduces reproductive opportunities be favored by natural selection?
It’s easiest to think about this like Darwin...
3 kinds of evolutionary changes influence the shape of phylogenetic trees:
1. the origin of new lineages by **speciation**
2. within-lineage change
   - natural selection + random processes (mutation, genetic drift)
3. the disappearance of lineages through **anagenesis**

How is **anagenesis** related to the evolution of reproductive isolation (cladogenesis)?

Mechanisms that limit genetic exchange (Reproductive isolating mechanisms)

“Speciation – the origin of two species from a common ancestral species – consists of the evolution of biological barriers to gene flow.”

1. **Pre-zygotic**: prevent gametes from uniting to form zygotes
   - Spatial/geographical isolation
   - Ecological isolation
   - Temporal isolation
   - Behavioral isolation
   - Mechanical isolation
   - Gametic incompatibility

2. **Post-zygotic**: act after fertilization has occurred
   - Hybrid inviability
   - Hybrid sterility
   - Hybrid breakdown

Geographic barriers, cladogenesis, & speciation: Antelope *Ground* Squirrels across the Grand Canyon

The two species look and behave alike, but their chromosomes are different:
- Their offspring are viable, but infertile.

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**Allopatric versus Sympatric Distributions**

- PATRIC (disjunct)
- PATRIC (overlapping)

**Pre-zygotic Barriers: Spatial or Geographic Isolation**

1. If two species live in different places between which there is little dispersal (i.e., gene flow), they may never have the opportunity to mate and exchange genes (reproductive isolation).
   - Species with non-overlapping distributions are ______________

2. For species with weak dispersal abilities, a very short distance or small spatial barrier could be sufficient to render them allopatric.

3. Conversely, for organisms like birds or marine invertebrates, capable of moving long distances, allopatry may involve long distances or major barriers.

**Pre-zygotic Barriers: Ecological Isolation in Sticklebacks**

- If two species utilize different habitats, even if their ranges overlap (__________), they can be ecologically isolated.
  - This would make mating encounters rare.
  - Even if the two species were reproductively compatible, they never actually mate, so they are reproductively isolated.

**Benthic 3-spine stickleback**
- live & build nests on lake bottoms

**Limnetic 3-spine stickleback**
- live in the water column
- build nests in shallows
Pre-zygotic Barriers: ________ Isolation

- Species that breed at different times of the day, at different seasons, or in different years, cannot mate and are reproductively isolated.
- Periodic cicadas emerge on 13 and 17-year cycles; they are separated by 4 years so even if they were inter-fertile, they don't interbreed.

Biological barriers that limit gene flow
(aka Reproductive Isolating Mechanisms)

“Speciation – the origin of two species from a common ancestral species – consists of the evolution of biological barriers to gene flow.”

Doug Futuyma (2005)

1. **PRE-ZYGOTIC:** prevent gametes from uniting to form zygotes
   - Spatial/geographical isolation (ALLOPATRY)
   - Ecological isolation (3-spine sticklebacks: benthic vs limnetic)
   - Temporal isolation (periodic cicadas)
   - Behavioral isolation
   - Mechanical isolation
   - Gametic incompatibility

2. **POST-ZYGOTIC:** act after fertilization has occurred
   - Hybrid inviability
   - Hybrid sterility
   - Hybrid breakdown

Pre-zygotic Barriers: Behavioral Isolation

- Many organisms recognize members of their own species using highly specific...
  1. courtship behaviors
  2. songs (birds, insects)
  3. chemical signals
  4. visual signals
- Male fireflies attract females of their own species (conspecifics) with species-specific set of flashes and flying patterns
Species-specific flashing & mate attraction in *Photinus* fireflies

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Pre-zygotic Barriers: _________ Isolation

- No matter how hard males & females try to mate, they are so mismatched anatomically that they cannot consummate the act.

Pre-zygotic Barriers: _________ Incompatibility

- Even if mating is successful, gametes do not fuse to form a zygote.
- This form of reproductive isolating mechanism is especially important for...
  1. organisms that spawn their gametes into water.
  2. wind-pollinated plants that "spawn" their pollen into the air.
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**Post-zygotic Barriers: Hybrid Inviability**
- Mating occurs, zygotes are formed, but because of genetic incompatibilities during development, the hybrid zygote dies before an adult develops.

*Figs: Rana sylvatica (wood frog) × Rana pipiens (leopard frog)*

- Sp. 1 x Sp. 2 ⇒ NO F₁ Hybrids (Inviable)

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**Post-zygotic Barriers: ________ Sterility**
- Hybrid zygotes develop into adults, but the adults usually do not form viable gametes.
  - Genes cannot move from one species into another: they’re “trapped” in the hybrids

*Figs: Zebra × Horse × Zorse (sterile)*

- Sp. 1 x Sp. 2 ⇒ F₁ Hybrid (Sterile)

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**Post-zygotic Barriers: Hybrid Breakdown**
- FERTILE hybrids form between two species.
  - But these hybrids have low fitness, or their offspring are often sterile (even if F₂'s are produced)
    - So, the barrier to gene flow occurs one step further down the mating scheme (compared to hybrid sterility)

*Figs: Mallard × China Duck × Challard/Chuck?*

- Sp. 1 x Sp. 2 ⇒ F₁ Viable but reduced fitness

*Can mate w/either parental species
Will produce viable offspring
But females won't mate w/them*
Biological barriers that limit gene flow (aka Reproductive Isolating Mechanisms)

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   ✓ Hybrid inviability
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Up next...

1. Back to Darwin's problem: how can reproductive isolation evolve?
2. Some phylogenetic foundations
3. Modes of speciation: allopatry, parapatry, peripatry, & sympatry
4. Rates of speciation