Lecture III – Species and Speciation – Dr. Kopeny

Delivered 1/25 (evening), and 1/28

What Species Are and How They Arise

Sketches of four species of Galapagos Finches from Darwin’s “Journal of Researches”

Large Ground Finch  Medium Ground Finch

Small Tree Finch  Warbler Finch

A page from “On the Origin of Species” (Darwin 1859)

The divergent pattern of evolution  Related lineages tend to “evolve away” from each other, producing a tree-like pattern. Darwin proposed a process underlying this pattern; competition between closely related lineages
Outline of Topics

I. Species Concepts
- Morphological species concept
- Biological species concept

II. Speciation in sexually reproducing lineages: Origin of new species from existing ones
- Basic Elements of Speciation
  - interrupted gene flow among subunits of a species
  - evolutionary processes that proceed within those subunits
- Allopatric speciation
- Sympatric speciation

III. If a new species persists, processes by which that occurs

The fossil record reveals two patterns of speciation
- **Anagenesis** (phyletic speciation):
  - Accumulation of heritable changes in a population associated with speciation

- **Cladogenesis** (branching speciation):
  - New species arises from a population that buds from a parent species
  - Basis for biological diversity

Speciation: Origin of New Species from Existing Species (after Campbell 2000)
Species Concepts

*Morphological Species Concept*
- Group of individuals united by similarities that distinguish them from all other individuals.
- Aristotle, Carolus Linnaeus…

*Biological Species Concept*
- Groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such populations
- Theodosius Dobzhansky, Ernst Mayr (1940)...

**Biological Species Concept: elements and issues**

*...actually or potentially interbreeding...*
- regard geographically separated populations as same species if presumed to be capable of interbreeding
- Concept is restricted in its generality, in that it does not apply to asexually reproducing species

*...natural populations...*
- species may be interbred in captivity, but that is irrelevant to evolutionary processes underlying speciation and the biological species concept in nature
II. Speciation: Processes by which new species arise

### Basic Elements of Speciation

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<tr>
<th>Barrier to Gene Flow</th>
<th>Genetic Differentiation</th>
<th>Reproduction Isolation</th>
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</table>

- **Population to Gene Flow**: Established
- **Populations diverge genetically but are still reproductively compatible**
- **Interbreeding population (parent species)**
- **Sexual incompatibility is established**
- **Daughter species A**
- **Daughter species B**

(after Purves 1999)
Gene flow is interrupted

Agents of evolutionary change variously operate on the isolated gene pools
  • Selection (\rightarrow \text{Adaptation})
  • Mutation, Migration (gene flow), Drift
  • Non-random mating

Degree of reproductive isolation evolves

After repatriation, reinforcement of reproductive isolation by natural selection

Reproductive isolation may be a consequence of independent evolution

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**Two Modes (processes) of Speciation**

**Allopatric Speciation**

• Etymology: “allo-patric” = “different-country”
• Gene pools isolated via geographic separation
• Prevalent mechanism of speciation in animals

**Sympatric Speciation**

• Etymology: “sym-patric” = “same-country”
• Gene pools isolated via process other than geographic separation
  • via polyploidy, particularly in plants
  • via behavior, ecology and to a lesser extent polyploidy in animals
• Common in plants (\geq 70\% of species via sympatric speciation)
• Growing understanding of this process as it applies to animals
Peripheral Isolates may be predisposed to (Allopatric) Speciation

Peripheral Isolate; small, isolated population at edge of species’ range

- Environment, and therefore selection pressures may differ substantially compared to parent population
- Gene pool likely to show incipient differentiation
- Genetic drift will drive random changes in genetic structure

(Freeman and Herron 1998)
Founder Events (dispersal, in the example to follow)
May Lead to Speciation

Ten species of Darwin's Finches from Isla Santa Cruz, each with different bill size and feeding habits.
Dispersion model for evolution of Darwin’s Finches

- Founding population inhabits San Cristobal
- Period of dispersals and differentiation
- Secondary contact; immigrants from Santa Cruz are reproductively isolated from the ancestral stock on San Cristobal
- The consequence of repeated speciation events, such as is thought to have occurred with Darwin’s finches, is referred to as Adaptive Radiation; Emergence of numerous species from common ancestor

Model for speciation and adaptive radiation on island chains

- Dispersal and colonization
- Adaptation of colonizing population to environment on colonized island
- Genetic differentiation underlies phenotypic adaptations
- If, following repatriation of ancestral and descendant lineages, those lineages are reproductively isolated, we recognize those lineages as distinct species
Hypothetical Example of Allopatric Speciation by Vicariance

A single species is distributed over a broad range.

Sea level rises and isolates species. Populations adapt to differing environments on opposite sides of the barrier.

If the barrier to breeding is removed, the populations may recolonize the intervening area and mingle, but do not interbreed.

Range of overlap
Grand Canyon Rock Layers
Throughout the Colorado Plateau
Vertical scale has been heavily exaggerated
Angel's Window, Cape Royal, north rim

Looking northwest across the Grand Canyon, from the south rim of the in the vicinity of Hopi Point – Colorado River a mile below

Visit these two websites: http://www.edu-source.com/GCpages/CVOpage5.html
Allopatric Speciation via Vicariance: A Real Example

Harris' antelope squirrel
(Ammospermophilus harrisi)

White-tailed antelope squirrel
(Ammospermophilus leucurus)

http://animaldiversity.ummz.umich.edu/accounts/ammospermophilus/a_harrisi.html

Today: complete lecture 3 and begin lecture 4
Conclude lecture on speciation

Begin Lecture 4. Macroevolution
Variation in speciation rates (ch 22:420-422)
Evolutionary radiations (ch 22: 422-423)
The significance of speciation (ch 22; 423-424)
Rates of Evolutionary change (ch 20: 390-392)
Patterns of evolutionary change (ch 20: 392-393)
The future of evolution (ch 20; 393-394)
Allopatric Speciation: Important Considerations

• Inference for the importance of allopatric speciation in animals;
• The effectiveness of a geographic barrier to impede or eliminate gene flow depends on the locomotion and other characteristics of individuals
• We consider speciation to have ensued if and when two gene pools have diverged to the point that, should secondary contact occur, the individuals of each are reproductively isolated from each other; can no longer interbreed and produce fertile offspring.

Sympatric Speciation

New species evolves within geographic range of parent species
• Common in plants, via polyploidy

Hugo DeVries with new species of primrose, Oenothera gigas
Recall the breach between “Mendelism” and “Darwinism”…

**Sympatric Speciation in Plants via Polyploidy**

**Polyploidy** Chromosome complement with one or more extra sets of chromosomes; an increase in the number of chromosomes

There are two distinct mechanisms by which polyploid species of plants arise

<table>
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<tr>
<th>• Autopolyploid Species</th>
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<tbody>
<tr>
<td>• Autopolyploid species arise from single parent species</td>
<td>• Allopolyploid species arises through interbreeding of two different species</td>
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<tr>
<td>• Can arise through a meiotic error -- a non-disjunction event that constitutes a mutation -- results in gametes with one or more extra sets of chromosomes compared to chromosome complement in normal gametes</td>
<td>• A number of different routes to allopolyploidy are known – all involve arriving at a chromosome complement that is functional in terms of meiotic reduction division</td>
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<td></td>
<td>• Regarded as being much more common than autopolyploidy</td>
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![Diagram](image-url)
Example of Autopolyplpody through nondisjunction and self-fertilization

Meiotic nondisjunction of a diploid (2n) cell results in gamete with unreduced chromosome number of 6.

Self-fertilization, as depicted below, by such an in individual gives rise to a new species; individuals are capable of sexual reproduction with complete set of homologous chromosomes –required for successful meiosis.

Examples of Allopolyploidy
Modern Bread Wheat is a Hexaploid Plant that probably originated about 8000 years ago as a spontaneous hybrid of a cultivated wheat and a wild grass (Campbell 2000)

**Sympatric Speciation in Animals**

- Animals may become reproductively isolated if genetic factors cause them to depend on different resources than parent population
- (Polyploid speciation in animals is rare)
- Mechanisms not well-understood, but probably not common
Mouth-brooding Cichlids surrounded by swarms of fry in Lake Tanganyika. Young are periodically released to feed but gathered up into parents mouth at first sign of danger.

Non-Random mating in a polymorphic species may have led to sympatric speciation the Genus Pundamilia in Lake Victoria

two closely related species of Cichlids in the genus Pundamilia Reproductively isolated in nature and in captivity under natural light conditions – females only choose conspecific males.

Under monochromatic orange light, males look similar (presumably) to females – and females mate indiscriminantly with males of either species

Inference from experiment that speciation occurred relatively recently and that color is the main, perhaps only "reproductive barrier"

Four species of Haplochromis cichlids in Lake Victoria that occupy different ecological niches, although they are similar in appearance.
Reproductive Isolation; Prezygotic and Postzygotic Barriers that Isolate Gene Pools of Biological Species

• As an incipient new species diverge behaviorally, physiologically, morphologically from the parent species, those very differences may preclude the two from reproducing successfully; i.e., the two may become "good biological species", or not!!

• **Reproductive barriers**: Evolved traits that preclude production of fertile, viable hybrid offspring
  
  • Prezygotic Barriers: reproductive isolating mechanisms that operate before fertilization, some before mating
    
    Spatial, temporal, mechanical and gametic isolation
  
  • Postzygotic Barriers: reproductive isolating mechanisms that operate after fertilization
    
    Problems with hybrids – including developmental abnormalities, infertility and low viability

• In "hybrid zones" or "areas of secondary contact" where hybridization takes place, if there is selection against hybrids, we may expect evolution of stronger prezygotic barriers (demonstrated in some laboratory populations, not well-supported in observations of natural populations)
**Habitat Isolation.** Populations live in different habitats and do not meet

**Temporal Isolation.** Mating or flowering occurs at different seasons or times of day

**Behavioral Isolation.** Little or no sexual attraction between males and females
Spatial Isolation = Habitat or Ecological Isolation

Behavioral Isolation-- Blue-footed Boobies on Galapagos Islands
Distinct songs help prevent interbreeding among these sibling species

What can we say about “speciation” when areas of secondary contact exist where hybrids do not have reduced fitness?

The yellow-rumped warbler diverged into two distinct races: Eastern populations were separated from Western ones during the Wisconsin glaciation, and probably came into secondary contact about 7500 years ago. Populations are reproductively isolated over most areas of secondary contact, except in some regions in the Canadian Rockies, where hybrids do not have reduced fitness; yellow-rumped genes are introgressing west, and Myrtle genes are migrating east.