What is Evolution
Systematics often divided into two areas: phylogenetics or pattern and biosystematics or process.

Genetic Variation within Species
Evolution requires source of genetic variation and a driving force.
Genetic variation within species is the rule - human selection or natural selection or random events involved.

Capsicum - pepper
Claytonia - spring beauty
Genetic Variation within Species
Evolution requires source of genetic variation and a driving force

Variation seen in flowers, pollinators, light regimes, moisture regimes, chromosome number

Genetic Variation within Species
• Modern genetic tools indicate substantial genetic variation within and among populations of species – raw material for natural selection or random events to act upon

Genetic Variation within Species
• three American botanists documented this linkage with their studies on a variety of plant species in California during 1940-1950s

Genetic Variation within Species
Natural selection - mechanism by which populations become modified in response to the environment

Adaptation - adjustment of the population to the environment

Genetic Variation within Species
Hypopitys monotropa - pinesap

Genetic Variation within Species
Claytonia - spring beauty
Genetic Variation within Species

- used a reciprocal transplant design by setting up common garden sites across an elevation gradient from coastal California, through the Coast Range, and up and over the Sierra Nevada

Clausen, Keck & Heisey’s California Transect Study Sites

Coastal California, near Big Sur

Coast Ranges, inland from Big Sur

Foothills of the Sierra Nevada

Timberline, east side of Sierra Nevada

Common garden at Stanford

Common garden at Mather

Genetic Variation within Species

- *Achillea lanulosa* exhibits clinal phenotypic variation in natural populations across the elevational gradient in the Sierra Nevada

Genetic Variation within Species

- populations exhibit marked lowering of fitness and adaptation when placed at other sites — clinal genotypic variation or the formation of ecotypes

Evolution requires source of genetic variation and a driving force

Random Events - gene frequencies may fluctuate despite natural selection owing to random sampling of genes - genetic drift, founder events

2019

or dispersal to Area "B"

2020

or Area "A"
Genetic Variation within Species
Evolution requires source of genetic variation and a driving force

Random Events - gene frequencies may fluctuate despite natural selection owing to random sampling of genes - genetic drift, founder events
- effect is greatest in small, isolated populations on "islands" - e.g., cloud forest peaks in central Panama
- widespread lower elevation Lisianthus skinneri (●) and isolated cloud forest taxa (●)

Genetic Variation within Species
Evolution requires source of genetic variation and a driving force

Random Events - gene frequencies may fluctuate despite natural selection owing to random sampling of genes - genetic drift, founder events

Speciation
Cladogenesis - formation of new species
- anagenesis - evolution within a species lineage — (Darwin’s modification)
- cladogenesis - evolution to form new species lineages or speciation — (Darwin’s descent)

How to Define Species?
Cladogenesis - formation of new species
How do you define species?
Ernst Mayr
- difficult, due to continuum of evolutionary processes and products
- emphasis on reproductive isolating mechanisms

Biological Species Definitions
Species represent groups of populations reproductively isolated from one another
Reproductive Isolation
Many kinds of isolating mechanisms

Ecological or habitat isolation

- species adapted to harsh, heavy metal serpentine soils in California ecologically separated from crossing with those that do not

*Ceanothus* (California lilac) on Catalina Island

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Reproductive Isolation
Seasonal or temporal isolation - different times of reproduction

- Pinus radiata
  - Monterey pine
- Pinus muricata
  - Bishop pine

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Reproductive Isolation
Mechanical isolation - variation in floral form prevents interspecies pollen movement

- pollen placement or floral form in pseudocopulatory orchids

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Reproductive Isolation
Mechanical isolation - variation in floral form prevents interspecies pollen movement

- two western U.S. monkeyflowers *Mimulus cardinalis* and *M. lewisii* — a pair of recently speciated species — are isolated in nature due to different modes of pollination
Reproductive Isolation

Mechanical isolation - variation in floral form prevents interspecies pollen movement

Mimulus cardinalis

• few genes generated the floral differences that maintain reproductive isolation - however, species can readily hybridize in the greenhouse

Mimulus lewisii

Reproductive Isolation

Gametic incompatibility - at three levels in Heliconia

• pollen - stigma: no recognition (lipids)
• pollen tube - style: pollen tube rupture (arabinogalactan protein growth regulation)
• gamete - gamete: sperm-egg rejection

Reproductive Isolation

Hybrid sterility - F₁ sterility

• Clarkia biloba & C. lingulata - sister species, but differ in chromosome number (n=8 vs. n=9) - intersterile

Reproductive Isolation

F₂ breakdown - F₁ fertile, but subsequent generations show lethal effects

• well studied in cultivated species of cotton (Gossypium)
Models of Speciation

Speciation or Cladogenesis - most models or processes of speciation are based on biogeography ('patry' - homeland)

- Allopatric speciation
  - ranges do not touch or overlap
  - no gene flow
- Parapatric speciation
  - ranges touch but do not overlap significantly
  - gene flow usually weak
- Sympatric speciation
  - ranges overlap significantly
  - gene flow is not prevented by geography

Models of Speciation

Speciation or Cladogenesis - most models or processes of speciation are based on biogeography ('patry' - homeland)

- Allopatric speciation refers to lineage splitting facilitated by complete geographical separation
- Parapatric speciation refers to lineage splitting facilitated by significant gene flow
- Sympatric speciation refers to lineage splitting facilitated by complete gene flow

Geographic Speciation

- 'dumb-bell' model: ancestral species forms two new species by division
- peripheral isolate model: one new species forms at edge of retained ancestral species

Geographic Speciation

- freely interbreeding series of populations
- races form in response to n.s. and environmental variation
- differentiation and migration lead to geographically isolated races or subspecies
- reproductive isolation forms within or between subspecies and races
- range expansion allows new species to co-exist
Geographic Speciation

The degree of reproductive isolation among geographical sets of populations within an actively evolving species complex is often tested by crosses.

• **Peripheral isolate model**: new species forms at edge of retained ancestral species

“Island” Model of Speciation

- A rapid form of peripheral isolation and speciation involving “island” like habitats completely separated from contact
- The founder event often involves a very small subset of the original genetic pool of the ancestral species — thus differences accumulate rapidly

Sympatric Speciation

Two types of sympatric speciation where gene flow is not prevented by geography are:

1. **Diploid or homoploid hybrid speciation**
2. **Allopolyloid speciation**

- Allopatric speciation: ranges do not touch or overlap; no gene flow
- Parapatric speciation: ranges touch but do not overlap; significantly gene flow usually small
- Sympatric speciation: ranges overlap; gene flow is not prevented by geography
Homoploid Hybrid Speciation

*S. canescens* X *S. megistacoolobum* → *Solanum raphanifolium*

- **ranges overlap**
- **morphologically intermediate**
- **DNA says NO! Just an unrelated species**

Spooner, Smith, Sytsma 1991

Andrea Wolfe

Homoploid Hybrid Speciation

- **two parental species differ in habitat, floral form, pollinators**
- **P. spectabilis** is intermediate in habitat, floral form, and isolated by new pollinator

1. *P. spectabilis*
2. *P. clevelandii*
3. *P. spectabilis* is a diploid hybrid species

- but supports example #2

**DNA says no! not a hybrid species**
A very common and instantaneous form of speciation in plants (and a few animals) is allopolyploidy.

- Hybridization occurs between two species.
- Meiotic incompatibilities make hybrids sterile.
- Doubling of chromosomes occurs (polyploidy).
- Allopolyploids are fertile and reproductively isolated from both parental species.

Under human selection in the Middle East, bread wheat (Triticum aestivum) has evolved in about 11,000 years.

Two successive rounds of hybridization followed by polyploidization have given bread wheat the genomes of three diploid species — it is a hexaploid (6 sets of chromosomes, or 2 from each diploid parental species).

Even more recent speciation has occurred in goat's beard in North America.

- By early 1900s, these species had hybridized with each other and then formed two different allopolyploid (tetraploid) species.
- Three diploid (2n=12) species were introduced into North America about 200 years ago.
- These two new allopolyploid species have evolved numerous times (!) in areas where the diploid species overlap in geographical range in North America.
Polyploid Speciation
