What is Evolution

Darwin himself never uses the word "evolution" in *Origin of Species*.

He calls the process "descent with modification".
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

*Claytonia* - spring beauty
Genetic Variation within Species

Evolution requires source of **genetic variation** and a **driving force**

**Natural selection** - mechanism by which populations become modified in response to the environment

**Adaptation** - adjustment of the population to the environment

*Claytonia - spring beauty*
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.

Figure 3: Distribution of chloroplast rps2 haplotypes of Monotropa hypopitys. Pie chart sizes are approximately proportional to sample size, with the smallest circles representing $n = 1$ and the largest representing $n = 8$. The inset shows the phylogenetic relationships between the 42 haplotypes. Open diamonds represent missing haplotypes and small black circles represent unique haplotypes, i.e. those found in a single individual. The population of origin of each unique haplotype is indicated.

Hypopitys monotropa - pinesap
Genetic Variation within Species

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

• their work on the *Achillea millefolium* (yarrow) and *Potentilla glandulosa* (sticky cinquefoil) complexes are the best known
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
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
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

2018
or Area “A”

2019
or dispersal to Area “B”
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
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

- widespread lower elevation *Lisianthius skinneri* (♦) and isolated cloud forest taxa (♦)
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?

- difficult, due to continuum of evolutionary processes and products
- emphasis on reproductive isolating mechanisms

Ernst Mayr

Biological Species Definitions

Species represent groups of populations reproductively & potentially reproductively isolated from other such groups
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
Reproductive Isolation

Seasonal or temporal isolation - different times of reproduction

*Pinus radiata*  
Monterey pine

*Pinus muricata*  
Bishop pine

Pollen Dispersal

- Feb
- Mar
- Apr

Wet years

Dry years
Reproductive Isolation

Mechanical isolation - variation in floral form prevents interspecies pollen movement

- pollen placement or floral form in pseudocopulatory orchids
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 - $F_1$ sterility

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

A. *C. biloba*  
B. *C. lingulata*  

California
Reproductive Isolation

$F_2$ breakdown - $F_1$ 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 small

- **Sympatric speciation**
  - ranges overlap significantly
  - gene flow is not prevented by geography

- geographical
- catastrophic or quantum – will not talk about
- diploid hybrid (homoploid)
- polyploid
Models of Speciation

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• allopatric speciation refers to lineage splitting facilitated by complete geographical separation

• called the geographical or conventional model of speciation — it is the best documented and most important
Geographic Speciation

- ‘dumb-bell’ model: ancestral species forms two new species by division

- peripheral isolate model: 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.
Geographic Speciation

“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

- peripheral isolate model: new species forms at edge of retained ancestral species
Geographic Speciation

- Tepuis in Venezuela - continental "islands"
- Hawaiian Islands - oceanic "islands"
- Vernal pools in California - "islands" in Central Valley
Two types of sympatric speciation where gene flow is not prevented by geography are:

(1) diploid or homoploid hybrid speciation

(2) allopolyloid speciation
Homoploid Hybrid Speciation

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

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

*Solanum raphanifolium*
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
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
- DNA says no! not a hybrid species
Homoploid Hybrid Speciation

• but supports example #2

• *P. clevelandii* is a diploid 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)
- Allopolyploid is **fertile** and reproductively isolated from both parental species
Polyploid Speciation

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 the goat’s-beards in North America.

*Tragopogon* - goat’s beard

Pam & Doug Soltis
Even more recent speciation has occurred in the goat’s-beards in North America.

*Tragopogon* - goat’s beard

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

The frequency of polyploid speciation in vascular plants

Troy E. Wood, Naoki Takebayashi, Michael S. Barker, Itay Mayrose, Philip B. Greenspoon, and Loren H. Rieseberg

2009

- Asterids: 106,150 species, 35.05 ± 1% incidence, 12.45 ± 1% frequency
- Rosids: 58,700 species, 31.91 ± 2% incidence, 20.63 ± 2% frequency
- Basal Eudicots: 24,950 species, 37.24 ± 2% incidence, 14.11 ± 2% frequency
- Higher Monocots: 28,150 species, 46.58 ± 2% incidence, 21.43 ± 5% frequency
- Basal Monocots: 33,160 species, 29.94 ± 2% incidence, 25.74 ± 4% frequency
- Basal Angiosperms: 9,250 species, 37.57 ± 6% incidence, 1.64 ± 2% frequency
- Gymnosperms: 830 species, 4.04 ± 3% incidence, -- ± -- frequency
- Leptospor. Ferns: 11,000 species, 32.86 ± 2% incidence, 34.01 ± 4% frequency
- Eusporangiate Ferns: 380 species, 24.00 ± 7% incidence, 19.36 ± 7% frequency
- Lycophytes: 1,200 species, 33.61 ± 10% incidence, 30.77 ± 9% frequency

Divergence Times (millions of years)
Polyploid Speciation

Ancestral polyploidy events in seed plants and angiosperms.

Polyploid Speciation

Ancestral polyploidy events in seed plants and angiosperms.
Polyploid Speciation

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