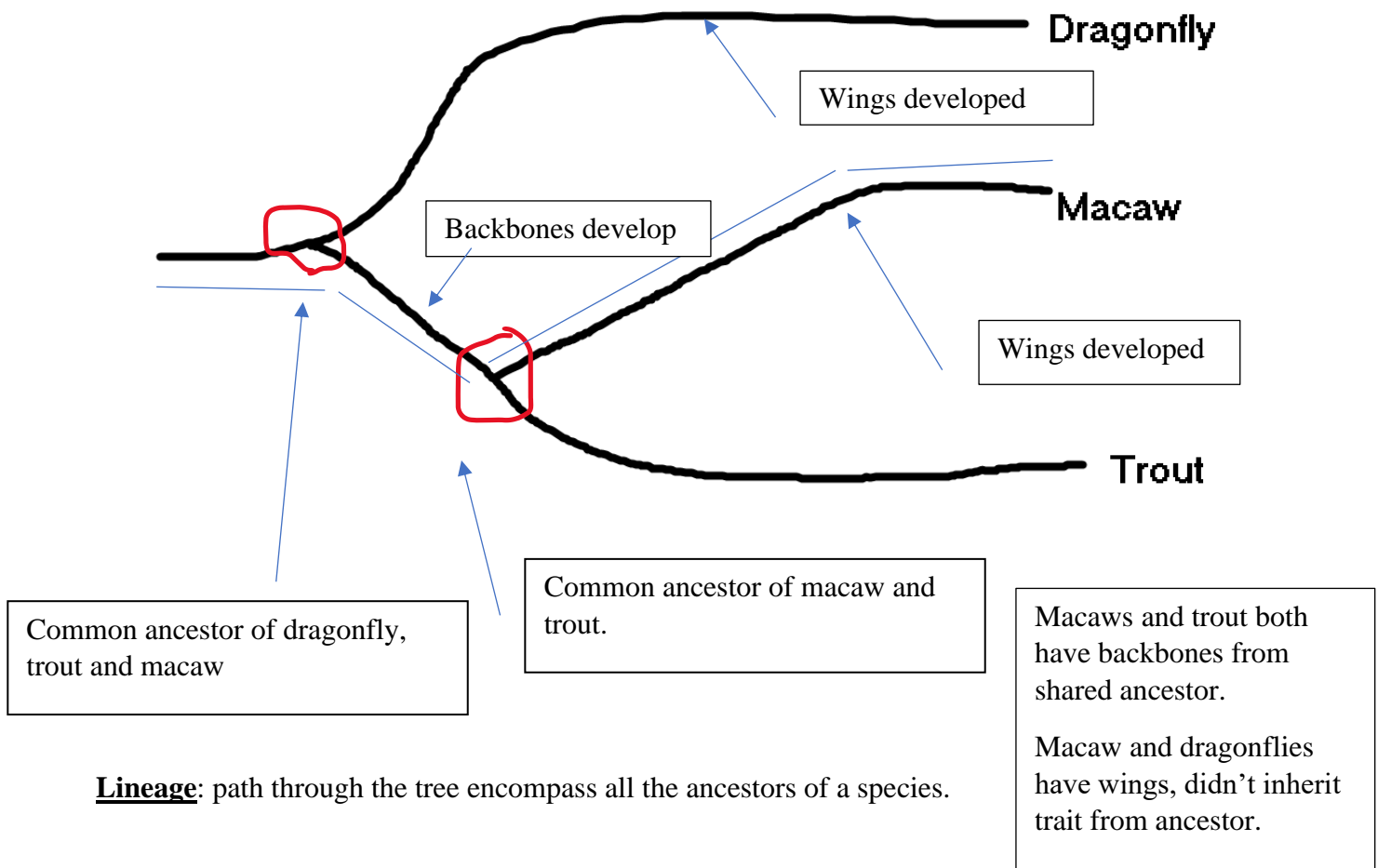


## Evolution

- Adapting to an environment
- Mutations —> new versions of genes
- Survival of the fittest
- Scientific explanation of biodiversity
- Species that share the same origin become different as they adapt to new environments
- Gradual change over time

**Trait/Character:** Something you can measure about an organism.

Time ->



**Lineage:** path through the tree encompass all the ancestors of a species.

Wings independently developed for macaws and dragonflies.

**Homologous trait:** A trait that is shared between two species because both species inherited it from their common (shared) ancestor.

Ex: backbone in trout/macaw. Wings in macaw/hummingbird.

**Convergent trait**: A trait that is shared between two species because it evolved multiple times. The trait arose independently in both lineages.

Ex: wings in macaw/dragonfly

## Evolution is a pattern and a process

Pattern:

Descent with modification and divergence

As lineages evolve over time, they tend to:

1. Become more similar to modern species
2. Become more different from one another
3. Become more different from the common ancestor of the group.
4. Diversify into more and more species.

Process (i.e., mechanism):

- Random processes such as mutation and genetic drift.
- Natural selection (not random).

Together, these evolutionary processes produce the pattern of descent with modification.

### Limits on Population Growth

Factors affecting survival:

- Predation
- Starvation (competition or lack of food)
- Emigration
- Habitat loss (e.g., housing developments)
- Pathogens/parasites
- Fire, flood, drought

Factors affecting reproduction:

- Insufficient habitat
- Pollutants

In real populations, more offspring are born than can survive and reproduce.

In every species, in every generation, MANY individuals die before they can reproduce

### Variation

Do all individuals have an equal chance at surviving and reproducing? They do not.

Natural selection happens whenever there is variation in a trait that affects survival and/or reproduction.

Natural Selection: Occurs when a particular version of a trait makes the individuals who have it more likely to reproduce

### **Heritability**

- Are some of these traits HERITABLE (genetic)?
- Examples of traits in humans:
  - Heritable:
    - Hair color
    - Eye color
    - Skin color
  - Non-heritable:
    - Having a tattoo
    - Knowledge
    - Hobbies
    - Strength

Evolution: Change in a population's heritable traits or gene pool over time.

Evolution by natural selection happens whenever there is variation in a heritable trait that affects survival and/or reproduction.

Darwin's argument for natural selection:

Observation #1: Members of a population often vary in their inherited traits.

Observation #2: All species can produce more offspring than their environment can support, and many of these offspring fail to survive and reproduce.

Inference #1: Individuals whose inherited traits give them a higher probability of surviving and reproducing in a given environment tend to leave more offspring than other individuals.

Inference #2: The unequal ability of individuals to survive and reproduce will lead to the accumulation of favorable traits in the population over generations. (Evolution by natural selection; Adaptation.)

Darwin's Theory of Evolution

Pattern: Descent with modification and divergence

Process (mechanism):

These ideas came later

- Random processes such as mutation and genetic drift
- Natural selection (not random)

-How did Darwin come up with these ideas?

### **Conventional Wisdom in England and Europe at the time**

- Each species were thought to have been created individually by God via “special creation.”
- Most scholars accepted that the earth was older than 6000 years, but it was unclear how old (a few million years?)
- Paleontologists were finding fossils and documenting extinctions and changes over time.
- Hints at the pattern (change over time), but not the process (natural selection).

Principle of Succession: Living organisms look similar to the fossils in their region. This is because they are descended from those ancestors, with modification.

<u>Observation</u>	<u>Darwin later figured out:</u>
Slots and armadillos: Modern species in a region resemble ancient species in that same region: Principle of succession.	Species are similar across time in a region because modern species are descended with modification from local ancestors. Also: species go extinct.
Seashells in the Andes Mountains, rising coastline: Earth changes slowly. Earth is old.	There have been enough time for many tree branchings (divergence) to create an enormous tree of life and all of modern biodiversity.
Galapagos tortoises: Different environments correspond to different body shapes. Each shape is well matched to its environment	Different selection pressures on each island produced different local adaptations via natural selection. Result: new branches of the tree.

Darwin found that:

- Islands with sparse, tall vegetation had tortoises with bumpy shells and long legs/necks
  - Islands with dense, low-growing vegetation had tortoises with smooth, domed shells and short legs/necks
  - Islands with intermediate vegetation had intermediate tortoises
- Each Galapagos tortoise population was a good fit for the vegetation of its particular island.

Darwin studied how organisms dispersed

>How could a plant or animal colonize a new island?

Darwin conducted experiments.

>Conclusion: Plants and animals could disperse on their own.

This allowed for plants and animals to disperse across oceans and colonize new volcanic islands.

Adaptive Radiation: The diversification of species originating from a common ancestor to fill a wide variety of ecological niches.

Local adaption to different environments contributes to divergence between populations and the origin of new species.

When this happens repeatedly in one lineage, the results,

Selection can transform one form into many.

Result: many strains or species all descended from a single common ancestor.

All organisms evolved from a common ancestor via descent with modification and divergence

Inspiration:

- Adaptive radiations
- Local adaption
- Biogeography

How Darwin's ideas were received:

- a. Descent with modification from a common ancestor: Widely accepted soon after publication.
- b. Natural selection: Universally rejected for 50-60 years.

Why was the idea of natural selection rejected?

1. Seemed to reject religious belief of divine purpose.
2. Scholars thought the Earth wasn't old enough for natural selection to create the diversity we see today
3. No understanding of inheritance; it wasn't clear how traits were passed down to descendants.

How were those arguments countered?

**Better understanding that the earth is really old.**

Discovery of radioactivity and radiometric dating.

Current estimates: ~4.6 billion years old.

**Better understanding of genetics**

Modern Synthesis: Bringing Darwinian evolution and genetics together in the 1930s.

Result: population genetics (coming soon).

Microevolution:

- Short times scales
- Changes in the gene pool
- Mutation, gene flow, genetic drift, natural selection

Examples: soapberry bugs, house sparrows, beak size change in ground finches, antibiotic resistance.

Evidence: watching it happen, comparing museum specimens with living organisms, etc.

Macroevolution:

- Long time scales
- Major changes in traits
- Origin of new species

Examples: evolution of whales, adaptive radiation of Galapagos finch species.

Evidence: geology, fossils, and DNA/traits of living organisms.

The double-ended arrow means that there is often no clear-cut distinction between microevolution and macroevolution.

#### I. The Fossil Record

Fossil: Any trace of an organism that lived in the past.

-Plant and animal remains in sediments can become fossilized.

Principle of stratigraphy: more recent fossils tend to be in younger layers, and older fossils tend to be in older, deeper layers.

Do Species go Extinct?

The discovery of the Irish elk helped demonstrate that they do.

Largest deer that ever lived. Largest antlers of any animal.

1812: Cuvier studied the Irish elk and found it was different from any extinct animal.

He also described mastodons and other fossil vertebrates.

Conclusion: Extinctions have happened. Life does change over time.

#### II. Vestigial structure:

A functionless\*, reduced structure in one species that has an important function in other, related species and was functional in their common ancestor.

Vestigial eyes in cave dwelling vertebrates

- a. Mexican tetra
- b. Blind cave tetra

“Nothing in biology makes sense except in the light of evolution.” -Dobzhansky

Human vestigial structures:

- Human goose bumps: muscles attached to hair follicles contract, makes hair “stand on end.”
  - When do you get goosebumps? When cold and scared.
  - Useful for hairy mammals:
    - Traps air for thermoregulation
    - Makes animal look bigger
 Not so useful in humans.
- Wisdom teeth
- Appendix
- Tailbone

Homology: Tetrapod forelimbs have the same basic skeletal structure despite different functions because all of these are modifications of a shared ancestral form.

### **Why is homology so interesting?**

Developmental homology: Inherited similarities during development, despite differences in adults

Vertebrate embryos: All have pharyngeal pouches (similar to gill slits of fishes).

All have tails.

### **Evidence of homology:**

Molecular homology: Similarities among organisms at the molecular level.

Genetic code: In nearly all organisms, the same codons (nucleotide triplets) specify the same amino acids.

Many genes are also homologous (e.g., huntingtin in humans and fruit flies).

>Why is it worthwhile to test medicines on rats?

Homology is why there's such a thing as a lab rat.

It's why the National Institutes of Health funds research on fruit flies, mice, frogs, yeast, bacteria.

- Homologous anatomy (mice, frogs, rats)
  - Homologous genes
  - Homologous biochemistry
- Learning about these species teaches us about humans because we share many homologous traits with them.

The development of antibiotic resistance is observable evolution in action.

1. The bacteria vary in their response to drug
2. Some bacteria have higher survival
3. Can pass that trait to offspring

4. Bacteria population becomes resistant; it has evolved.

### III. IDK

Lipsum

- IV. Direct observation of changes (microevolution)

### **Evolution of pesticide resistance**

Field application of chemicals designed to kill all individuals creates strong selection for resistant genotypes.

Overuse of insecticides has caused many cases of evolved resistance in insects.

### **Genetic Drift:**

Allele: A variant of a gene.

Genetic drift is a random process that changes the frequencies of alleles in a population due to random sampling effects.

There is randomness in:

- Which individuals have more offspring.
- Which alleles get passed on in a particular egg/sperm.

Cumulatively, this randomness changes allele frequencies over time. The effect is slow in large populations.

### **Review**

- Gene: a small region of a chromosome that codes for a molecule (usually a protein) which performs a function for the cell.
- Allele: alternative forms of a gene (D1 or D2, B or b, etc.)
- Diploid: Having 2 copies of each gene.
- Genotype: The alleles an individual has for a gene (e.g., Bb)
- Population: Group of interbreeding individuals

Allele frequency: proportion of all the copies of a given gene that are a particular allele.

### **Measuring (Micro)Evolution**

Microevolution: Change in allele frequencies over time.

### **How can we tell when that is happening at a particular gene?**

Calculate what the expected genetic makeup of the population would be if it were **NOT** evolving at that gene (**i.e., under the null model**). Compare that to the observed (real) population.



If observed genotype counts – null model expected genotype counts: there is **no measurable evolution** and mating is random.

If observed genotype counts are different from expected: the population may be evolving. The differences can give us some clues about how.

If a population is not measurably evolving and is mating randomly its gene pool is in **Hardy-Weinberg Equilibrium (HWE)**. HWE is the null model here.

A population is in HWE at a particular gene if all these conditions are met:

- No genetic drift (i.e., a very large population)
- No natural selection
- No gene flow/migration
- No new mutation
- Random mating (no inbreeding, etc.)

If any of these conditions are NOT met, that can change the genotype frequencies in the population.

The point of HWE calculations is to find out if any of these processes are happening.

**Steps for calculating whether a population is in HWE for a particular gene:**

1. Calculate the allele frequencies.
2. Predict the EXPECTED genotype frequencies under HWE.
3. Calculate EXPECTED genotype counts.
4. Do a statistical test to decide if OBSERVED and EXPECTED genotype counts are significantly different.

If OBSERVED and EXPECTED genotype counts are similar:

- The population is said to be in “equilibrium:” it is not evolving and mating is random

If OBSERVED counts are significantly different from EXPECTED:

- The population is not in equilibrium, and may be evolving and/or mating nonrandom.
- The differences may give us hints about how.

Population is in HWE if the observed population is similar to the expected. Calculated with  $\chi^2$  Goodness of Fit Test. I don't know the significant value.

You are studying a population of weasels on an island.

The weasels' tails vary in length.

You have previously determined that tail length in this population is determined by a single gene, Tail:

TT genotype: long tail

Tt genotype: medium tail

tt genotype: short tail.

You trap some weasels from all over the island, take blood samples, and genotype them at the Tail gene. Is this population in HWE at the Tail gene, based on your sample genotypes?

Genotype	Total # of individuals (observed genotype counts)	Expected genotype frequencies under HWE (predicted)	HWE Expected genotype counts	$\chi^2$ contribution (term)
TT	100	$P^2 = (0.65)^2 = 0.42$	$(0.42)200 = 84$	$\frac{(100-84)^2}{84} = 3.05$
Tt	60	$2pq = 2(0.65)(0.35) = 0.46$	$(0.46)200 = 92$	$\frac{(60-92)^2}{92} = 11.13$
tt	40	$q^2 = (0.35)^2 = 0.12$	$(0.12)200 = 24$	$\frac{(40-24)^2}{24} = 10.67$
Total # of individuals	200			
Total # of alleles	400			

$$\frac{(O-E)^2}{E}$$

TT: Observed > Expected  
Tt: observed < Expected  
tt: observed > Expected

To calculate allele frequencies:

$$\text{Frequency of T allele} = P = \frac{2(\# \text{ of TT weasels}) + \# \text{ of Tt weasels}}{\text{Total \# of alleles}}$$

$$= \frac{2(100) + 60}{400} = \boxed{0.65}$$

Frequency of t allele = ?

Clicker question...

$$= \frac{2(\# \text{ of tt weasels}) + \# \text{ of Tt weasels}}{\text{total \# of alleles}}$$

$$= \frac{2(40) + 60}{400} = \boxed{0.35}$$

check:  $p + q = 1$ ? yes

$$\chi^2 = \sum_i \frac{(O_i - E_i)^2}{E_i}$$

$O_i$  = The observed count of genotype  $i$   
 $E_i$  = The expected " " "

Summation:  
Add them up!

TT:

$$\begin{array}{ccc} 3.05 & + & 11.13 & + & 10.67 & = & \boxed{24.85} \\ \text{TT} & & \text{Tt} & & \text{tt} & & \end{array}$$

$$\chi^2 \text{ significance cutoff: } \boxed{3.841}$$

$$\chi^2 \geq 3.841 ? \text{ YES!}$$

Then: reject H<sub>0</sub>!

## Genetic drift

Changes in the frequency of alleles due to random sampling effects.

Drift is a random process that can change allele frequencies, but effects are only noticeable in one generation if the population is very small.

In practice: genetic drift affects populations over time, but does not cause statistically significant departures from HWE.

Genetic drift...

... happens in every generation, in every population.

... is slow in medium/large populations.

...reduces genetic variation over time as alleles are fixed or lost.

...changes allele frequencies at random.

...can interfere with selection, which changes allele frequencies in a consistent direction.

### **How do populations become small?**

Genetic bottleneck: a sudden change that drastically and randomly reduces the size.

- Reduces genetic diversity
- Often changes allele frequencies by chance.

Founder effect: A small number of individuals start a new population. The allele frequencies in the new population are usually different from the source population by chance.

### **Gene flow**

- Transfer of alleles into/out of a population as a result of the movement of fertile individuals (emigration/immigration) or their gametes (e.g., pollen).

Gene flow can:

- Alter allele frequencies in populations
- Reduce genetic differences among populations
- Counteract the loss of genetic variation caused by drift.

### **Mutation:**

The source of all genetic variation, but a slow process.

Under normal circumstances, mutation is too small an effect to produce a statistically significant departure from HWE.

>important but small effect.

### **Non-random mating:**

Can produce excess homozygotes or heterozygotes.

- Assortative mating: like mates with like
  - Identical alleles are paired up as homozygotes
- Disassortative mating: like mates with unlike.
  - Different alleles are paired up as heterozygotes.

Non-random mating example: Disassortative mating produces a population with extra heterozygotes.

Find HLA genotypes for college students.

Male college students sleep in t-shirts.

Female college students rate t-shirt odor.

Recall that: Evolution by natural selection happens when there is VARIATION in a HERITABLE characteristic that affects SURVIVAL AND/OR REPRODUCTION.

This is experimentally testable.

Some examples you've learned about where all three conditions were verified:

- Rock pocket mice (coat color)
- Galapagos ground finch (beak size)
- Guppies (bright coloration)

Modes of selection

**1. Directional**

An extreme phenotype is the most fit.

**2. Stabilizing**

An intermediate phenotype is the most fit

**3. Disruptive**

Both extremes phenotypes are most fit.

Examples: Black-bellied seed cracker

Two factors have been weakening stabilizing selection on birth weight

- Better medical care at and immediately following birth has improved outcomes for many babies.

**Disruptive Selection:** Two extreme phenotypes are more fit than intermediate phenotypes.

A bell curve will have two bumps that deviate from the center bump of the bell curve.

**Balancing Selection:**

Maintains multiple alleles in a population.

Mechanisms:

- Heterozygote advantage
- (Negative) frequency dependent selection

**I. Overview**

A **phylogeny/phylogenetic tree** shows the evolutionary history of a species or group of species.

- Branching tree diagram.
- Shows relationships among taxa (singular: taxon)
- Uses many kinds of data (DNA, morphology, fossils)

**Phylogenetic trees are hypotheses about how evolution happened for a particular group of taxa.**

Phylogenetic tree: a nested hierarchy based on relatedness.

Linnaean classification: nested hierarchy based on similarity.

Darwin gave hierarchical classification an explanation: Similarity is often due to shared ancestry.

A series of evolutionary splits produces a nested hierarchy, just as historical (Linnaean) classification does.

Evolution produces a phylogeny (evolutionary tree) based on relatedness. The tree often resembles historical classification by similarity, but not always.

Example of misleading similarity: crocodiles and lizards:

Usually, organisms that look more alike are more closely related, so classification by similarity usually matches the real history of evolution, but there are exceptions.

Birds and crocodiles are more closely related (share a more recent common ancestor) than crocodiles and lizards are.

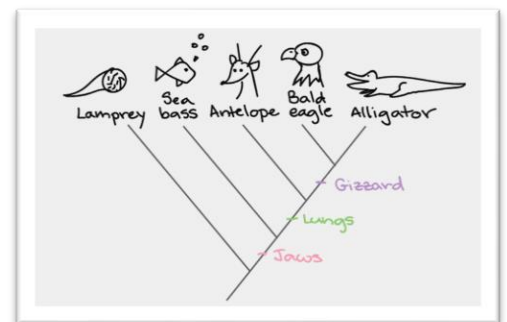
How to read a phylogenetic tree:

**Branch point:** represents the common ancestor of two lineages.

**Taxon** (plural: taxa): A named level in the hierarchy.

**Root:** The most recent common ancestor of all the taxa shown.

**Time:** goes from root to tips.



**Sister taxa:** share an immediate common ancestor and are each other's closest relatives on the tree.

**Branching pattern (topology):** informative

**Branch Length:** may or may not be informative.

Branch tips can be arranged all sorts of ways, but these three trees are all equivalent. Just look for the branchpoints in relation to the tips. Rewriting them with parentheses or sets can help.

A phylogenetic tree is a hypothesis about how evolution occurred. Therefore there is

**Monophyletic group (synonym: clade):** Contains an ancestor and all its descendants

**Non-monophyletic group:** Contains an ancestor and some, but not all, of its descendants OR Contains taxa but not all of their shared ancestors.

### III. How to build a phylogenetic tree

Measure as many characters (traits) as possible: morphological, behavioral, genetic, etc.

Score the characters: which species have which characters? Mark character transitions as possible trees.

Choose the most parsimonious tree.

Parsimony is the principle that the tree with the fewest evolutionary changes (i.e., the fewest character transitions) is most likely to be correct.

It is based on the assumption that change is rarer than staying the same: that is, a trait evolving once is more likely than the trait evolving twice. Thus, the simplest explanation for a shared character is shared ancestry.

For a particular taxon or clade, a trait can be ancestral or derived.

**Ancestral: shared because this taxon/clade AND earlier ancestors have it.**

Derived: arose within this taxon/clade.

Example: mammal clade.

Backbone – ancestral trait for mammals.

Why ancestral? Because it arose in an ancestor that gave rise to other taxa as well as mammals.

Fur – derived trait for mammals.

Why derived? Because it is unique to the mammal clade.

Example: cat clade.

Fur = ancestral trait for cats.

Tongue bristles – derived character for cats.

#### **IV. Phylogenetics**

Example: Parasitic Wasp Species, egg laying strategies

Ectoparasite – lay eggs outside the host

Endoparasite – lay eggs inside the host

Which came first?

Hypothesis: Ectoparasitism is the ancestral state, endoparasitism is a more recent adaptation.

Morphology => Morph = shape; ology = shape/appearance of an organism.

Speciation: divergence of a lineage into multiple species

**How would you define a species?**

Biological species concept: A species is a group whose members have the potential to interbreed in nature and produce viable, fertile offspring.

Horse and a donkey are separate species. When interbreed, create mule. Mules are viable but not fertile.

**What unites the members of a biological species?**

Gene flow between populations of that species.

### **What keeps species apart?**

Reproductive isolation.

### **How does reproductive isolation occur?**

**Prezygotic barriers:** No viable zygote is formed (usually no mating at all):

- Habitat isolation (example: threespine sticklebacks)
- Temporal isolation
- Behavioral isolation
- Mechanical isolation
- Gametic isolation

**Postzygotic barriers:** Mating occurs, but the offspring are less viable and/or less fertile than their parents.

There are situations where we can't use the biological species concept...

- Mating (or lack of mating) can be hard to observe
- Extinct species (fossils don't mate!)
- Asexual populations (e.g., bacteria)

Morphological species concept: Species are defined by morphological traits alone. Used by paleontologists to define fossils. Used by others when reproductive biology is not available.

Ecological species concept: Species are defined by the ecological niches they occupy. Niches select for different adaptations, so this often overlaps with the morphological species concept.

Example: polar bears vs. grizzly bears

### **Summary: what is a species?**

There are different species concepts (definitions of species).

Studies that define species usually use multiple techniques.

\*Mating studies

\*Morphological or behavioral differences

\*Studies of genetic divergence

Identity of species/subspecies can be controversial.

More than an academic concern: The Endangered Species Act of 1973 uses Biological Species Concept.

- **How do new species arise?**



## Evolutionary processes and speciation:

When populations stop interbreeding (no more gene flow), they begin to diverge because:

- if the environments differ, each population will adapt differently to its local environment via natural selection.
  - This local adaptation is the primary reason why populations diverge.
- In addition:
  - different mutations accumulate in each population.
  - genetic drift will result in the fixation and loss of different alleles in each population.

Allopatric speciation (common)

- Step 1: Geographic separation (barrier to gene flow)
- Step 2: Each population adapts to a different local environment, leading to divergence.

Reproductive isolation occurs because populations become separated by a geographic barrier.

How?

Dispersal: A few individuals cross a barrier and start a new population. Examples: many island species.

A new barrier can split an existing population into two.

Sympatric speciation (rare)

Speciation in geographically overlapping populations.

Mechanisms of sympatric speciation:

- Polyploidy in plants
- Habitat differentiation

,

How exactly does speciation happen?

Examples of how two populations can accumulate differences that gradually lead to reproductive isolation:

- Behavior shifting gradually in each population until it creates behavioral isolation
- Diverging morphologies -> individuals don't recognize members of the other populations as belonging to their own species.
- Diverging pheromones 0> lack of mating recognition.
- Diverging cell surface proteins 0> gametic incompatibility.
- Etc.

Population thinking (instead of essentialist thinking):

Differences can accumulate gradually, making interbreeding less and less likely to succeed, until the population reach full reproductive isolation.