Why do we care about evolution?

1. Evolution helps us understand ourselves
   - By studying evolution, we better know our own place on a planet with 1.8 million identified species, and perhaps 10 million total species. We know that all species have evolved, and that we are not the pinnacle.
   - The context of evolution helps us know how to behave to members of our own species and to members of other species.
   - Evolution helps us understand the purpose and reasons for our physiology and anatomy.
   - Studying evolution has helped us in the field of human health because it has equipped us to fight many diseases. This is known as evolutionary medicine, a topic that will be discussed more later in the course.
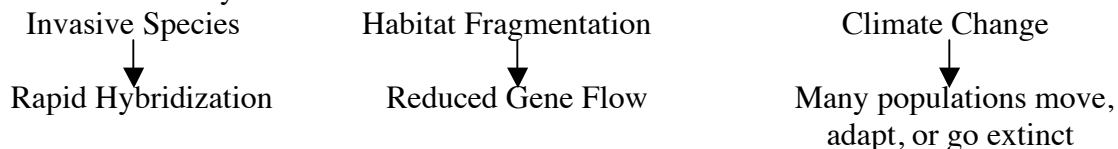   An example of evolutionary medicine is antibiotic resistance to penicillin. The drug was mass produced around 1943, and by 1947 the bacteria it was created to kill had begun to develop a resistance. The same is true of rapid evolution of the resistance of HIV to the 3TC drug today.
2. Evolution is a major part of the planet's food supply
   - The Green Revolution has led to a widespread application of monoculture crops, now including genetically modified organisms. Due to their genetic similarity, pests (weeds, insects, and pathogens) could take out entire crops.
   - Evolution comes into play as pests develop resistance to the insecticides and herbicides used to combat them.
3. Humans must acknowledge our own role in evolution
   - Humans have shaped the planet, and might be considered the greatest evolutionary force:

Invasive Species	Habitat Fragmentation	Climate Change
↓	↓	↓
Rapid Hybridization	Reduced Gene Flow	Many populations move, adapt, or go extinct

Development of the Theory of Evolution

Before Darwin, there was Aristotle and Linnaeus
- Aristotle had the idea of fixed species that were part of a great chain of being, or *scala naturae*
- This meant that all species sat somewhere along a hierarchy from slime molds to humans (at the pinnacle)
- Linnaeus developed the binomial system used today to classify organisms, though he did not work on evolution. See an example of his system of hierarchy below:
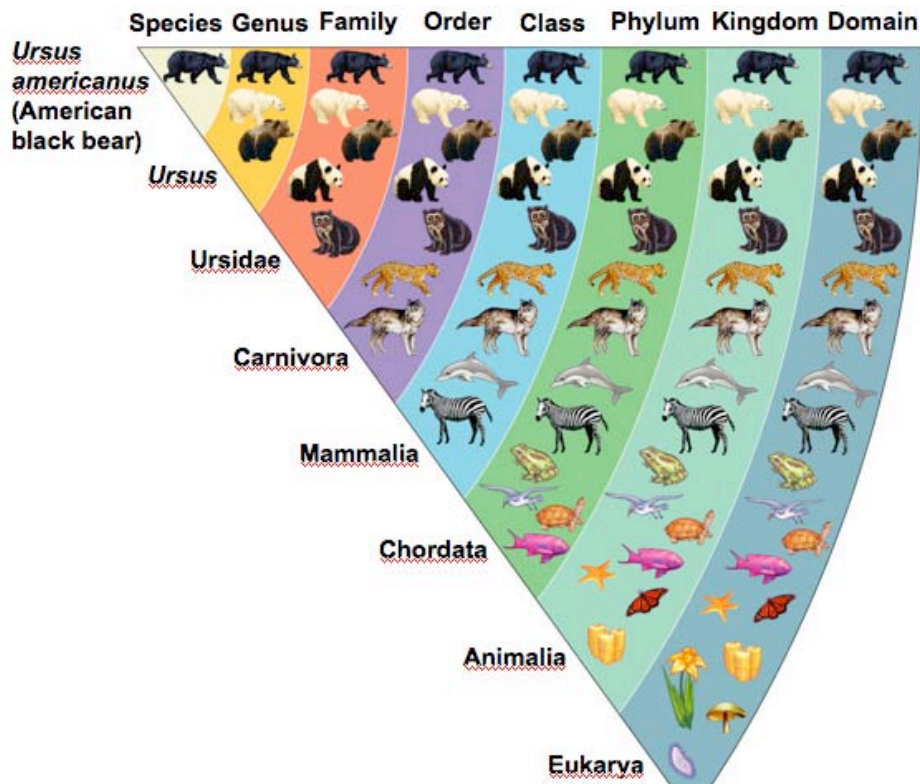
Figure 1.14 (Pg. 12, 8th edition)

Darwin and Wallace's theory of evolution was based on two big ideas: descent with modification (which was not new to the world) and natural selection as the mechanism of evolution (this was their unique contribution).
They had many influences:
- The concept of species' ability to change (Lamarck, and Erasmus Darwin)
- Biogeography, or the distribution of species across the globe (Humboldt, and Hooker)
- Taxonomic classification and hierarchy (Linnaeus)
- Population pressures and the idea that populations will run out of resources before they stop overproducing offspring (Malthus)
- Gradual geological change and uniformitarianism (Lyell)
- Well-studies fossils and extinct species (Cuvier)
- Comparative anatomy and embryology (Huxley, Owen, and Saint-Hillaire)

Personal Influences on Darwin

Time on the *HMS Beagle*
- Darwin was hired as an educated companion and naturalist for the captain of this small ship, on the recommendation of his professors
- He spent 5 years on this ship and sailed a route that was literally around the world:
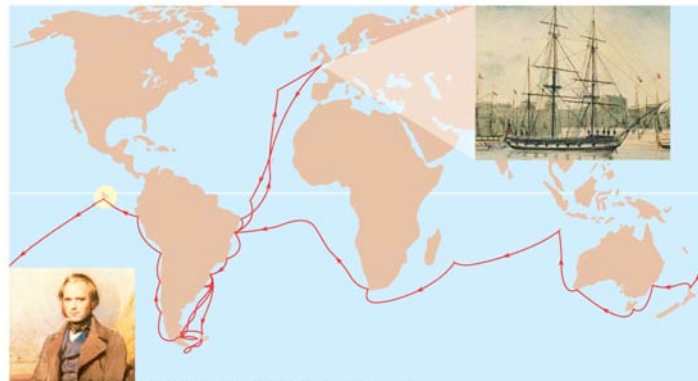
Formative experiences aboard the ship:
- His first look at tropical diversity was at a stop near Rio, Brazil, where the exuberance of biodiversity blew his mind!
- Darwin was in the Andes during a major earthquake that unearthed some fossils that he recognized as related to living species. The uplift also made him consider geologic change (Lyell's influence)
- Upon visiting islands, Darwin began to see how species changed from a common ancestor that colonized the island
Island mockingbirds that resembled a mainland ancestor:

Darwin's Finches
- He studied 14 species, about half of the species present on the Galapagos Island
- Darwin thought that the finches were many species, such as grosbeaks and blackbirds, but upon returning to England, an ornithologist pointed out to him that they were all finches
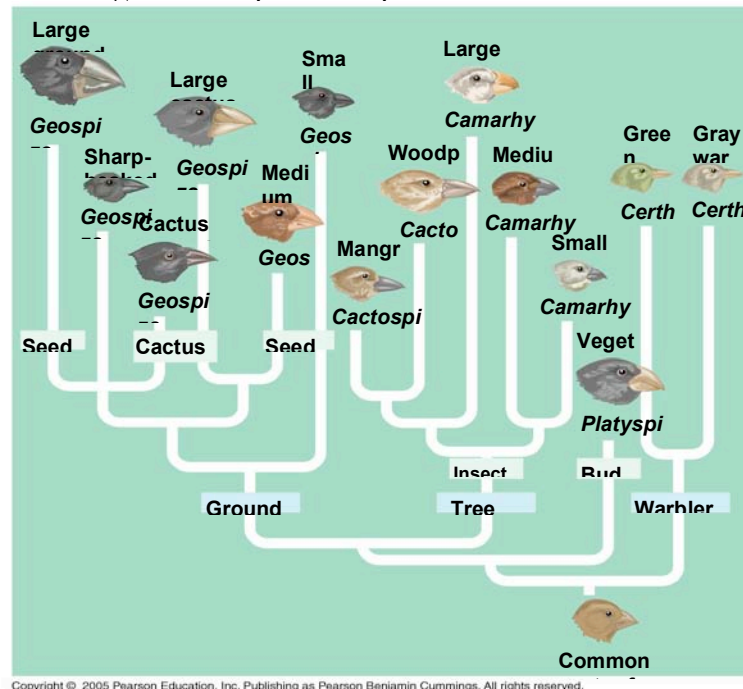- The finches are a good example of adaptive radiation

Figure 1-22: A finch classification tree (pg. 17, 8th edition)

Alfred Russel Wallace
- Unlike Darwin, Wallace came from humble backgrounds and started his work as a naturalist collecting specimens to sell to gentlemen collectors
- Went to the Amazon after Darwin had returned from his voyages on *The Beagle* and lost his entire collection due to a boat fire
- After returning to Britain, he traveled to the Indo-Malay archipelago for 8 years. While there, and shaking with Malaria, he remembered the works of Thomas Malthus (population studies) and wrote two papers that he sent back to England
- One paper outlined the Sarawak Law, or "Every species has come to existence coincident both in time and space with a pre-existing, closely related allied species"—Alfred Russel Wallace
- Wallace sent his paper on evolution by natural selection to Darwin, which immediately pushed him to publish a summary of his own work alongside Wallace's.

Natural Selection (Darwin-Wallace):

There are three conditions for natural selection:

1. **Variation:** Individuals within a population have different characteristics/traits (or **phenotypes**).
2. **Inheritance:** Offspring inherit traits from their parents. An offspring does not receive the same spectra of traits as either parent, but rather a mixture of both parents' traits.
3. **Competition:** More offspring are produced than can survive, so offspring with traits better matched to the environment will survive and reproduce more effectively than others.
4. **Natural selection** states that given these three conditions, a population will accumulate the traits that enable more successful competition.

"Origin of the species by means of natural selection" (Darwin, 1859)

Darwin used several lines of evidence:

1. **Artificial Selection** was used as an analogy for natural selection: If humans can breed animals (dogs, horses, crops) for certain traits (tiny size, speed, high yield), then it makes sense that in a natural environment, nature would "select for" the traits that allow organisms to survive and reproduce better.
2. **Biogeography:** Nested geographic distributions. Species that occur on islands are often closely related to species each other species on the nearby mainland. (Wallace also contributed a lot in terms of examples of adaptive radiation for island evolution. Repeated observations like this cemented the idea of descent with modification.)
3. **Homology:**
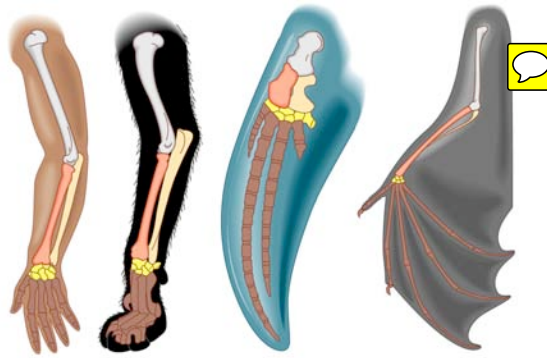
Figure 1: Homologies in mammal forelimbs
Campbell 8th edition. *Copyright © 2005 Pearson Education, Inc. Publishing as Pearson Benjamin Cummings.* (pg 463)

    a. Darwin used the example of **homologous structures**, or variations on a structure present in a common ancestor. For example, a human arm, a cat's leg, a whale's flipper, and a bat's wing all are adapted to different purposes, but share the same bone structure. This suggests one common ancestor with that common structure.

        i. Don't confuse a homology with the term "**homoplasy**" from lab, which means the opposite: similar structures/functions that originated from different ancestors and **converged**. A homoplasy can also be called an "analogous structure."

    b. Embryological homologies: developing embryos are identical at certain stages: the longer two creatures' developing embryos remain similar, the more closely related they are.

    c. Creatures have **vestigial structures** or remnants of structures that were used for one function in an ancestor, but are no longer used for that function.
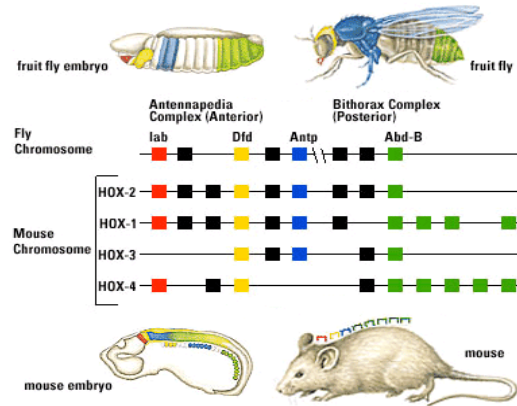
Figure 2: Hox genes controlling body segment development
Campbell 8th edition. *Copyright © 2005 Pearson Education, Inc. Publishing as Pearson Benjamin Cummings.* (pg 463)

    d.   Molecular homologies (while not available to Darwin) provide further evidence for natural selection. The genes that govern development of body sections are known, and are expressed in the same anterior to posterior sequence in embryos of mice and fruit flies. However, in each animal, the genes eventually specific different structures: they form portions of the spinal cord in the mouse, while forming the segments of the fly's body. This suggests the two animals diverged from a common ancestor with the common genes.

4. **Population pressures:** Malthus, population growth requires resources.

5. **Fossil Record:** At the time, there was a fossil record, and it was known that many of the fossilized species did not exist any longer and were organized into time series (strata).

Descent with Modification: Putting it Together

Natural selection is different from **descent with modification**. The first is the process: the second is the result. For example, the famous diagram included in the Origin of the Species shows descent with modification. From a single ancestor, you have multiple branches (**lineages**) with diverging phenotypes. Natural selection is the reason that these branches exist, rather than a solid cone of phenotypes. Not all phenotypes survive, as intermediate phenotypes less able to survive die out, creating the branching structure of the tree of life. Extinction events also lead to phenotypic gaps in the tree.
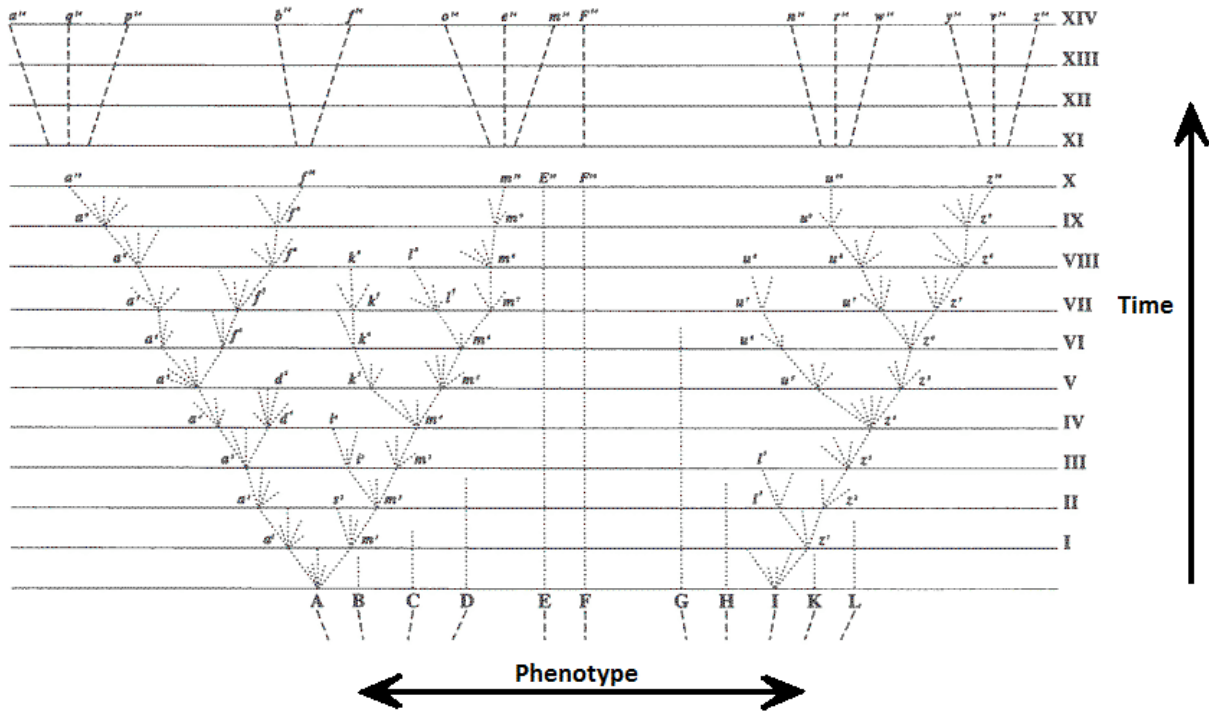
Figure 3: Darwin's Tree of Life diagram (from the Origin of the Species)

The Tree of Life

In the past, species were viewed as fixed discrete categories of beings, and were permanent and non-alterable (e.g Aristotle). Under that system, classifying all the creatures that exist is simple: you simply need to record them. If you accept that there is all this variation, however, then classifying the existing species becomes more difficult. (See Lecture 8 for more information about defining species). Currently, we use a phylogenetic hierarchy revealed by comparative DNA sequenceto define the domains of life. There are three domains: **Archaea**, **Bacteria**, and **Eukarya**. Each of these branches contain related organisms that share a common ancestor. Those domains split into further branches, repeatedly, until eventually the tips of those branches are the currently existing species, or species that have gone extinct.

Estimation & Interpretation of Phylogeny

How do we know that species are descended from a common ancestor? We use systematics, or the science of estimating phylogenies. We have a few sources of information (the dashed line indicates some DNA acquired from recent fossils):

Type of Evidence	Species it tells us about
Morphology	Extinct (fossils)
Molecules (DNA)	Extant (alive now)

Type of Evidence	What it tells us about
Fossils	Ancestral taxa
Molecular	Time / when changes occurred

Key Concepts:

A **cladogram** shows how different groups of organisms are related. A **phylogeny** shows how different groups of organisms are related and provides times that each of these organisms existed.

A **character** is a characteristic or a trait. A **character state** is what an organism has for that trait.
A **taxon** (plural is taxa) is a group (species, genera, family, order, etc.) grouped by shared, derived traits.
Taxa should be **monophyletic**: that is, all entities descended from the same common ancestor.
A **clade** is a monophyletic group, where all descended extant taxa are from a common ancestor.
A **paraphyletic group** is where either some but not all taxa are from a common ancestor (DEF below).
A **polyphyletic group** is when the taxa independently evolved analogous traits (CDEFG below).
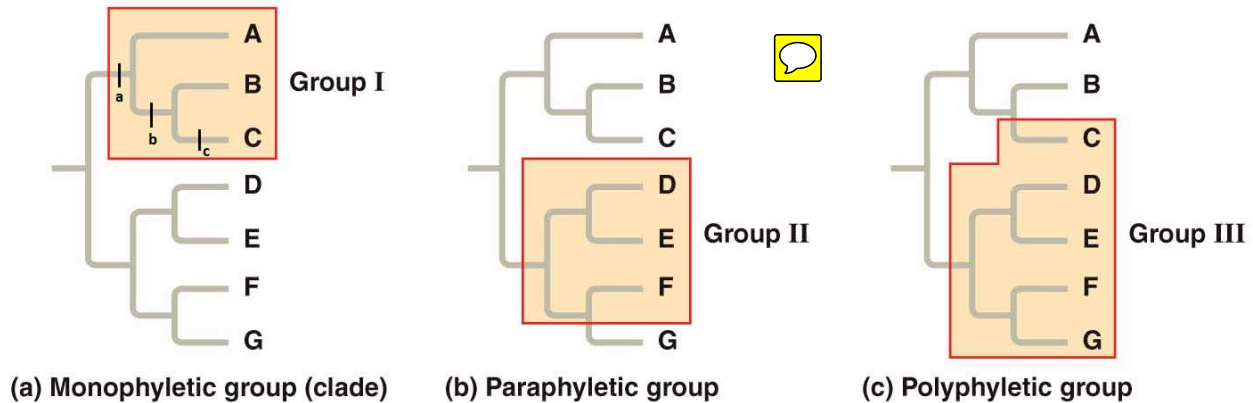
Figure 4: Different types of phyletic groups
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For groups A and B and C, trait "a" is a shared, derived trait: therefore in terms of "a", A and B and C form a clade.
If you had a branch C* coming off on the same family as F and G, then C and c* would be examples of parallel or convergent evolution. They possess the same trait (c and c*), but that trait arose independently, and those two organisms cannot form a clade.
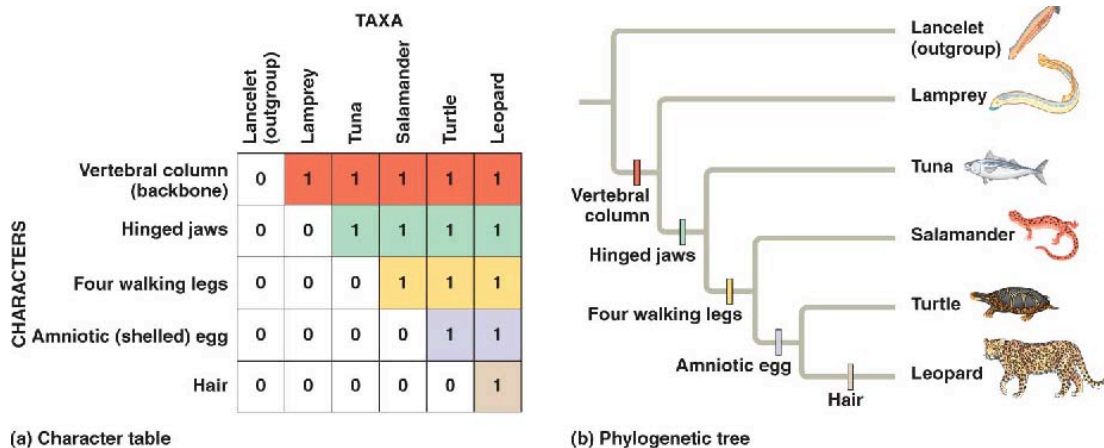

Figure 5: Character matrix and resulting cladogram
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To create a cladogram, you create a character matrix, or a table where the rows are characters and the columns are taxa. You fill in each cell with a 0 (lacks the trait) or a 1 (has the trait). From this, you should

be able to see the relationships between the organisms and create a clade, if you have enough data. (Refer to the lab for the week of March 8 – 12 for more detail.)

The concept of **parsimony** is a very important one when constructing phylogenies and cladograms. *The number of changes in a phylogeny should be minimized.*

Molecular Data Analysis

Simply because two phenotypes or character states appear identical does not mean they share a common ancestor. One way to determine relatedness is to perform phylogenetic analysis of variation in a homologous gene or stretch of DNA sequence. Given that two species had a common ancestor, you can determine the number of changes to each species' DNA relative to the common ancestor. In practice, this can be done using parsimony (as for morphological characters) or statistical methods that incorporate a model of sequence evolution to infer the tree that minimizes the amount of evolution or best fits the data.

Genetic changes accumulate over time. If the changes in the DNA sequence accumulate at a steady rate, and the rate of change can be calibrated using dated fossils on key branches, then this information can be used as a **molecular clock** to estimate the dates of divergence of other lineages. If you know the number of changes from a species to a common ancestor, and have a rate / molecular clock, then you can multiply the two numbers to find how long it took for that species to diverge from the given ancestor. This information helps scientists create the most probable phylogenies.

Molecular analysis has been instrumental in constructing the current tree of life model. Before molecular analysis of DNA, the tree of life was split into five kingdoms:
1. Prokaryotes
2. Protista
3. Fungi
4. Plants
5. Animals.

However, molecular analysis revealed that the prokaryotes were not all related to each other. Further, the protista, fungi, plants, and animals were all more closely related to each other than to prokaryotes. Therefore, the tree of life was changed to its current configuration:
1. Archaea (former prokaryotes)
2. Bacteria (former prokaryotes)
3. Eukarya (formerly protista, fungi, plants, and animals)

After *On the Origin…*

When Darwin and Wallace jointly published their paper on natural selection, they began a new era of evolutionary study. While their work was important, they were still wrong about inheritance, a process which they believed was the result of blending of genetic factors.
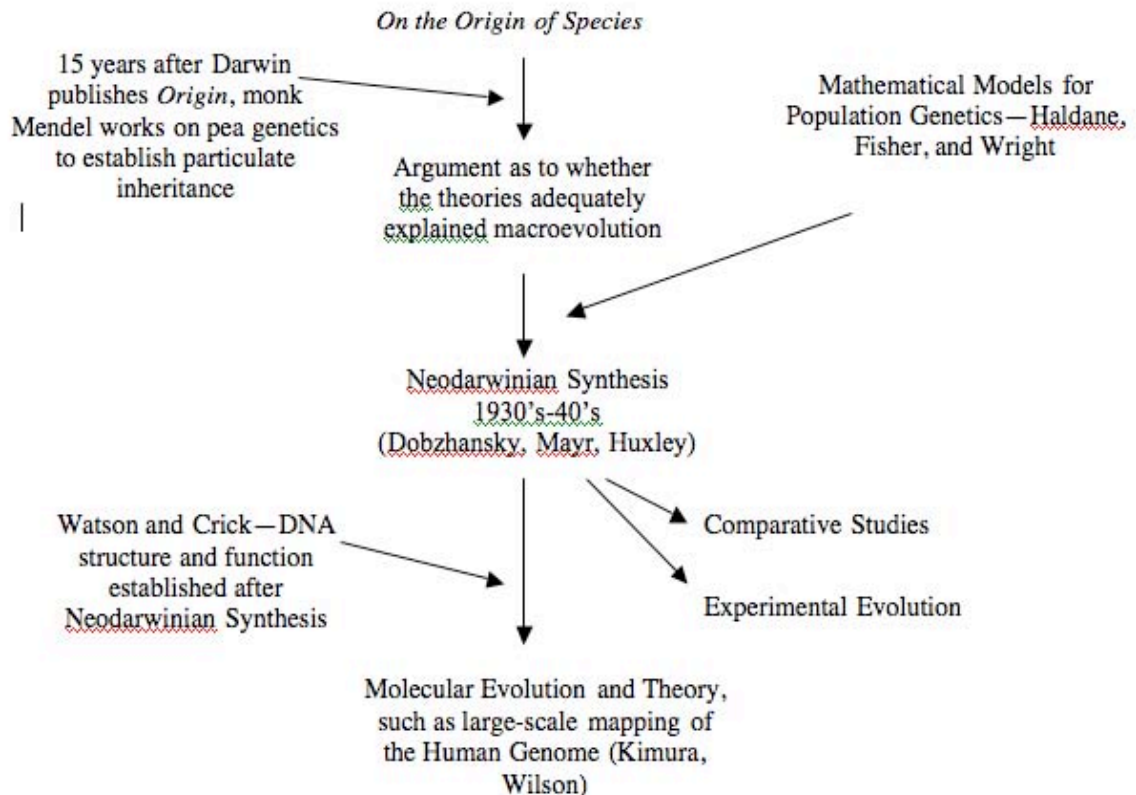
Mendel's Principles

- Alternative forms of genes, known as alleles, account for variation
- Offspring individuals inherit two copies of genes, one from each parent, in most cases (these are known as diploid organisms)
- If the possible alleles of a gene differ, one *may* be dominant (meaning that it would mask the phenotypic expression of the other allele)
- Two alleles for a heritable trait segregate during meiosis, usually independently of other traits (except for case of linked genes, which are close together on the chromosome)
- Dominant alleles mask all other phenotypes (known as recessive), but there is also the case of co-dominance—think of one red and one white flower making a pink flower, or look at the examples below
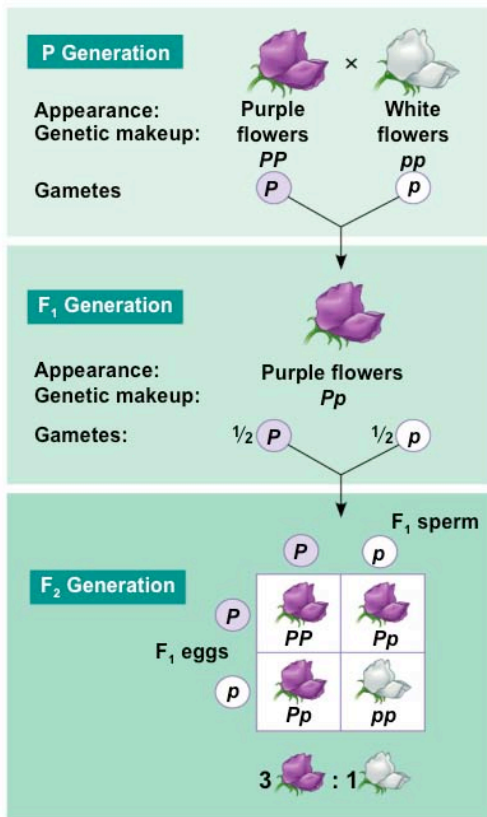
Figure 14.5 (pg. 266, 8th edition)   Figure 14.10 (pg. 272, 8th edition)
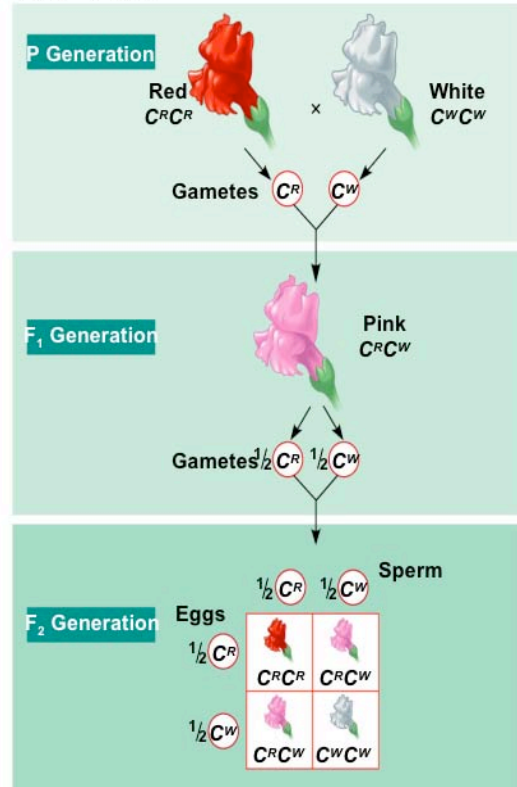
Alleles	Genotypes	Possible Phenotypes
A	AA	Dominant
	AB	Codominant Dominant
B	BB	Recessive

In this case, AA and BB are known as *homozygous* (same allele type) and AB is known as *heterozygous*.

Population Genetics

- A population, in genetic terms, is a randomly breeding group of individuals that is largely isolated from others
- Key evolutionary processes: mutation (the only source of variation), sampling processes (also known as genetic drift), the various forms of natural selection, exchange of genes through migration, and non-random mating

Mathematical Models—Hardy-Weinberg Equilibrium

Example of a natural population of flowers:

Gametes for each generation are
drawn at random from the gene pool
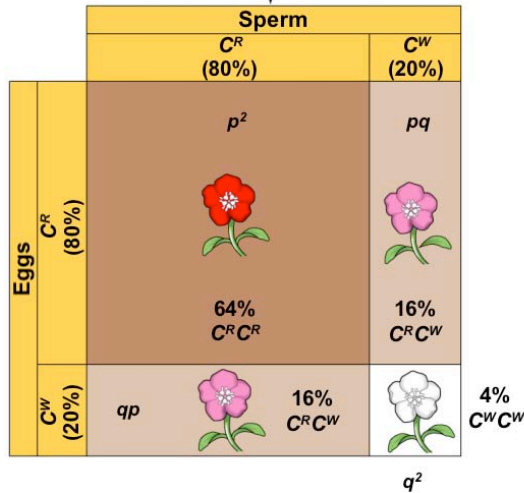of the previous generation:

80% C^R (p = 0.8)   20% C^W (q = 0.2)

Fig 23.7

Sperm	
C^R (80%)	C^W (20%)
p^2 / 64% $C^R C^R$	pq / 16% $C^R C^W$
qp / 16% $C^R C^W$	q^2 / 4% $C^W C^W$

Eggs: C^R (80%), C^W (20%)

Phenotype Frequency		Genotype Frequency	
Red Flowers	320	$C^R C^R$	0.64
Pink Flowers	160	$C^R C^W$	0.32
White Flowers	20	$C^W C^W$	0.04

Allele Frequency
p=f(C^R)=0.8
q=f(C^W)=0.2

Figure 23.7 (pg. 474, 8th edition)

Now, the general case:

general case

male gametes
f(A_1) = p   f(A_2) = q

female gametes

f(A_1) = p :
p^2 A_1A_1	pq A_1A_2
qp A_2A_1	q^2 A_2A_2

f(A_2) = q

Expected genotype frequencies

A_1A_1 = p^2

A_1A_2 = 2pq

A_2A_2 = q^2

Expected proportions:
$p^2+2pq+q^2=1$

Also, p+q=1 because there are only two possible alleles (in this case)

f(A_1) = p^2+1/2(2pq) = p(p+q) = p, meaning that the next generation will in theory have the same gene frequency as that of the parents

Conclusions from Hardy-Weinberg math: Inheritance alone does not cause the frequency allele changes of evolution

This is because Hardy-Weinberg acts on these assumptions:
- Random mating only - for this gene/trait
- No mutation or selection on population in question
- This is an isolated population with no gene flow from outside (i.e. no migration)
- This is only true for a large population with no sampling error

Based on these assumptions, we can call Hardy-Weinberg a *null hypothesis* for evolution. That means that if a population does not conform to Hardy-Weinberg Equilibrium for a certain trait, then evolution has occurred

Example of HWE as a Null Hypothesis:

Wild Oats—

Genotype Frequency

0.548	A_1A_1
0.071	A_1A_2
0.381	A_2A_2

Note that there are far fewer heterozygotes than HWE would predict. Some explanations for this would be that the wild oats do not practice non-random mating, or that heterozygotes are selected against in the environment the oats inhabit.

Hardy (Castle) Weinberg Equilibrium:

The allele frequency for any characteristic in a stable, non-evolving population will remain the same. For HWE to apply, there are three main assumptions:

1. Random mating
2. No mutation, selection, or migration.
3. A large population (no genetic drift is occurring)

Given two alleles in a population, the frequencies of each (p and q respectively) are $p^2 + 2pq + q^2$ for any population in Hardy-Weinberg Equilibrium (HWE).

This can be used as a "null model" for evolution: if the population is in Hardy-Weinberg Equilibrium, that trait is not evolving (being selected for/against). But if there are deviations, then that means that something interesting is occurring, possibly evolution.

A key result is that if an allele is rare (eg. $p < 0.1$), it occurs most often in heterozygotes rather than homozygotes – i.e. $2pq \gg p^2$

The Hardy-Weinburg Equilibrium can also be used to predict the frequency of heterozygotes in a given population, given the proportion of homozygous recessive phenotype individuals in the population. The heterozygotes are indistinguishable from the dominant homozygous individuals: however, the recessive homozygous individuals are uniquely identifiable. Therefore, q = square-root(frequency homozygous recessive). Since there are only two alleles, p = (1-q). Once you know p and q, you can solve for the frequency of heterozygotes (2pq).

Genotype	Phenotype
AA	A ($p^2 + 2pq$)
AB	
BB	B (q^2)

Frequency q = square-root of frequency of B
Frequency (AB) = 2*p*q

Example - Cystic Fibrosis:
Affected individuals in Caucasian population (homozygote recessives) = 4/10000 = 0.0004
Assuming HWE, the estimated frequency of the CF- allele = p = 0.02.
Therefore, q = 0.98
The frequency of heterozygotes is 2pq = 2*(.02)*(.98) = .0392 ~~ .04
What does this tell us? Compare the probabilities. In general, recessive alleles are more likely to be present in heterozygous individuals than in homozygous individuals.

Deviations from Hardy-Weinberg Equilibrium

Inbreeding - How does it affect a population?
Inbreeding is when two relatives produce offspring. Since the inbreeders are related, it's more likely than random mating that for one characteristic they will have matching alleles. This includes recessive alleles. Therefore, the frequency of homozygotes increases (as the genes the offspring receives from both related parents are more likely to be the same) and the frequency of heterozygotes decreases. Consider the following case of self-fertilization, an extreme form of inbreeding:
AA * AA   Homozygote frequency increases
AB * AB   Heterozygote frequency decreases as AB*AB produces both homozygotes and heterozygotes
BB * BB   Homozygote frequency increases

Note that inbreeding changes the proportion of genotypes (increasing homozygotes) but does not in itself change allele frequencies

Small Population Sizes: Genetic Drift
In a small population, the sampling of gametes and fertilization to create zygotes causes random error in allele frequencies. This results in a deviation from the Hardy-Weinberg Equilibrium. This deviation is larger at small sample sizes and smaller at large sample sizes. Think of it like tossing coins - the average result for tossing two coins might be 100% heads. The average for tossing four coins might be 75% heads. But if you take a sample of 10,000 coin tosses, then you are more likely to be close to 50% heads. The direction of this change is random: the dominant or recessive allele might be over or under represented in the next generation relative to the predicted HWE values.
This effect is called **genetic drift**, or that the amplitude of allele frequency fluctuation from one generation to the next increases in small populations. In a small population, genetic drift can result in a loss of variation across the entire genome over time. This even can result in a loss of **polymorphism** (alternate alleles) and driving the frequency of one allele to 1.
How is this relevant to evolution? The fluctuation of allele frequencies in a small isolated population might lead to novel genetic combinations that would not be possibly merely through selection. There are several different situations, which are described below. Alternatively, genetic drift may just reduce genetic diversity **(evolutionary potential)**.

Small Population Sizes: Population Bottlenecks
A **population bottleneck** occurs when a population undergoes a severe decrease in size. The effect of genetic drift on this new population is much higher than on the previous population. The new population will be much reduced in genetic diversity: consider the diagram below. Of a population with equal proportions of blue, yellow, and white marbles amongst a population numbering in the 100s, the new population has 5 blue marbles, 1 white marble, and no yellow marbles. This rapid change in allele frequencies could lead to divergence and a new species forming.
Note that a population bottleneck does not involve migration (that's comes later). The most likely causes of a population bottleneck are disease, habitat loss, overharvesting leading to insufficient resources, or climate change.
An example is the prairie chickens of the Illinois plains. Their habitat loss resulted in many smaller populations, rather than a large unified population. The smaller population sizes led to a decrease in diversity and a decrease in the viability (i.e. the number of hatching chicks).
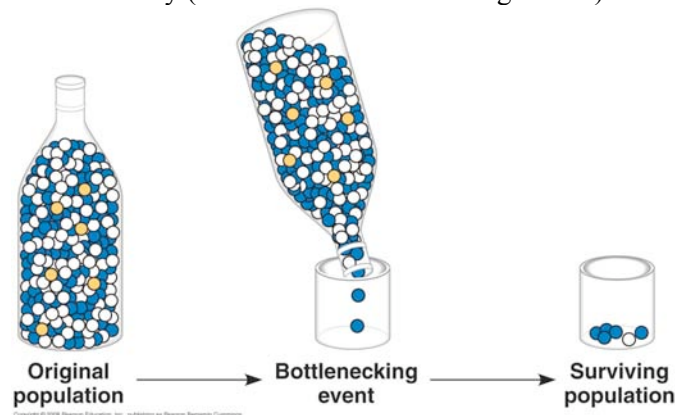

Figure 1: Population Bottlenecks
Campbell 8th edition. *Copyright © 2008 Pearson Education Inc., publishing as Pearson Benjamin Cummings.* (Pg 477)

Small Population Sizes: Founder Events
In this case, a small population of a species moves to a new habitat. The effects are mostly similar to population bottlenecks (reduced genetic diversity in the new population, rapid change in allele frequency, high potential for divergence and speciation) with the exception that there would be more selection occurring due to the new habitat.
An example would be human colonization. African *Homo sapiens* have the most genetic diversity of any human species, while Europe, Asia, and the Americas have lower genetic diversity. This implies that the wellspring of the human species is in Africa (where the original population with high genetic diversity resided/resides), and the other populations are descendants of smaller migrating populations with lower genetic diversity. (This is what is termed the "Out of Africa" theory of human evolution.)
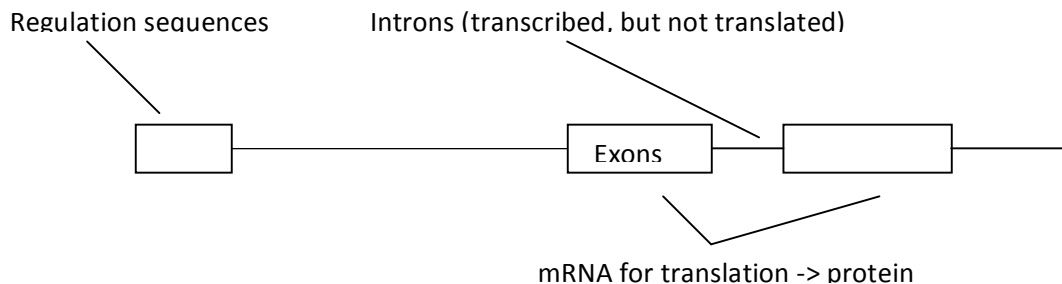
Mutation

The ultimate source of variation in the genome. The process through which DNA is replicated in meiosis is not perfect, and it can produce errors. There are an average of 1 in a hundred million nucleotide-copying errors per base pair gamete per generation – doesn't sound like much, but the human genome is 3 billion nucleotides long. Therefore, each time the human genome is replicated, it has an average of 30 mutations.
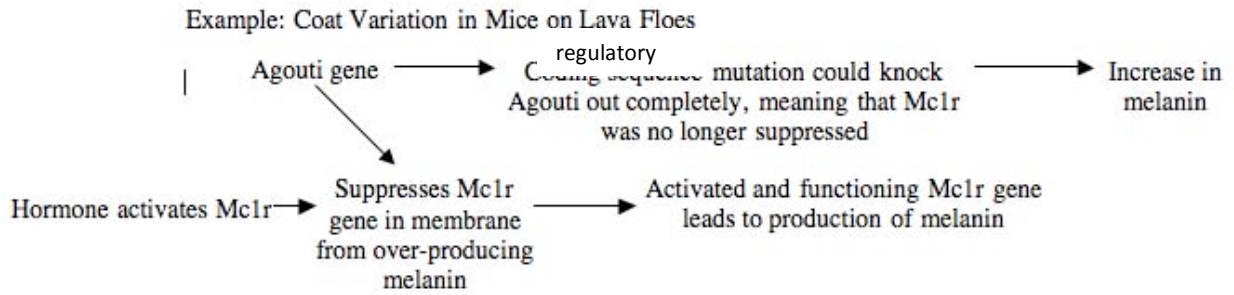
Mutations can arise in either a **somatic** cell line or in the **germ line**. Somatic cells are the cells that make up your body, so mutations in those cells are not passed on to the next generation. Mutations in the germ line, or in gametes, are passed on, so they are the mutations we talk about here.

These errors can be in one of four forms:
1. **Point mutation:** an alteration in the nucleotide coding sequence. For example, from a CTT/GAA sequence, a copy with a point-mutation might read CAT/GTA.
2. **Gene regulation:** a region controlling gene regulation and expression is altered.
3. **Gene copy number error**: a gene is copied more than it should be, so that the copy has multiple copies of the same gene.
4. **Chromosome number and structure**: during meiosis, a gamete receives too many or two few chromosomes, or a chromosome is damaged. Examples include Trisomy 21 (Down's syndrome) and plant polyploidy, when a plant can have nuclei with genetic material at 2N, 4N, 6N, etc...

Regulation sequences   Introns (transcribed, but not translated)

Exons

mRNA for translation -> protein

Note on basic genetic principles: Definitions of basic genetic terms such as DNA, nucleotide, gene regulation, gene expression, chromosome, etc. were not and will not be covered in lecture. If this material is foreign, you can look them up in the textbook. In Campbell 8th edition, most of the material should be within chapters 15-18. Use the table of contents and the index to find whatever specific material you need clarified.

Example: Coat Variation in Mice on Lava Floes

| Agouti gene → Coding sequence mutation could knock Agouti out completely, meaning that Mc1r was no longer suppressed → Increase in melanin

regulatory

Hormone activates Mc1r → Suppresses Mc1r gene in membrane from over-producing melanin → Activated and functioning Mc1r gene leads to production of melanin

- ==Agouti's presence is based on two genes, and both would need to be knocked out to completely stop suppression of Mc1r (recessive)==
- Some mutations could increase expression of Agouti, which would lead to a very light colored mouse (paler than normal)
- Mc1r can have dominant mutations that increase the sensitivity to the activation hormone, thus further increasing the production of melanin

Migration

- In evolutionary terms, migration is defined as movement that will result in gene flow, or the movement of genes from one place to another

Roles in Evolution

- Spreads "successful" mutation from one population to another through migration of individuals from place of birth to place of reproduction
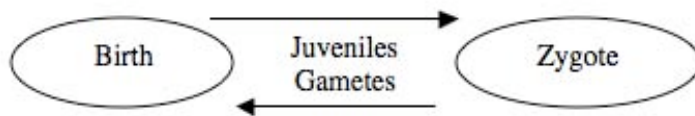
- Opposes the effects of genetic drift (divergence among populations) because it keeps genes flowing throughout; also opposes local selection
- With migration, two populations' allele frequencies come closer to equilibrium

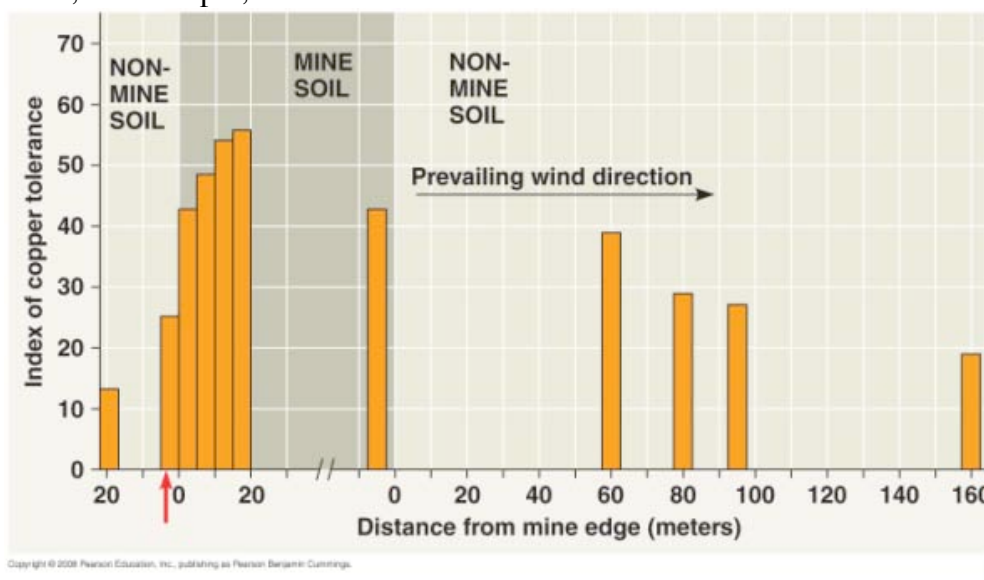Take, for example, a contaminated mine area:

Figure 23.12 (pg. 479, 8th edition)

- A species of grass lives in both the mine soil and non-mine soil
- In the mine soil, there is local selection for copper tolerance and on the non-mine soil, there is selection against copper tolerance because it is disadvantageous to have that trait in the absence of copper
- In the contaminated soil, the frequency of the tolerance allele would be close to 1 (theoretically) whereas the frequency of the tolerance allele in the non-contaminated grass would be close to zero
- However, due to wind migration of pollen, the distribution is different than predicted. By taking a transect sample across the mine and non-mine soil, a cline can be created:
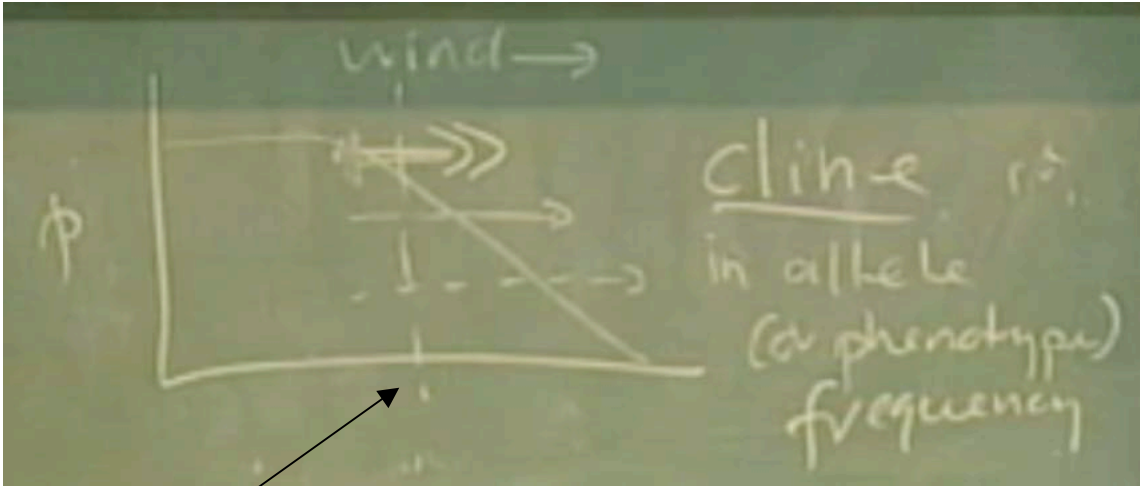
Here, the center line represents the divide between the contaminated and non-contaminated soil. P is the frequency of the phenotype for copper tolerance.

Variation

	Within Populations	Among Populations
Mutation	⇧	
Genetic Drift	⇩	⇧
Gene Flow	⇧	⇩
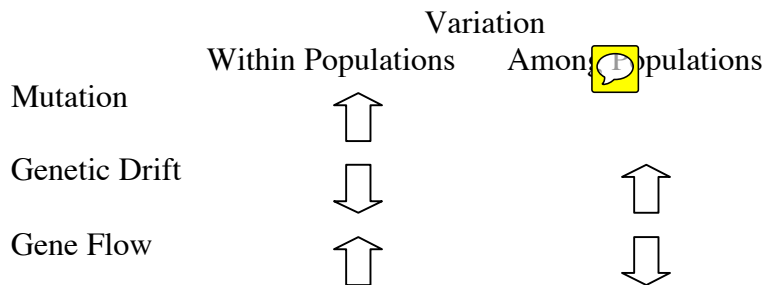
Selection (and Genetic Fitness)

- Fitness, as defined within evolutionary parameters, refers to an individual's ability to produce viable and fertile offspring (nothing to do with working out in the gym!)
- Natural selection acts through the phenotype (which is influenced by genotype) of individuals, and its effects are felt on the population
- Furthermore, selection acts on the survival/reproduction of a heritable pheno/genotype relative to others within the population
- Selection and fitness are environmentally dependent

Variation in phenotype is often continuous – eg. for height – and reflects both genetic variaition for that trait within a population, and environmental variation through its effects on development.
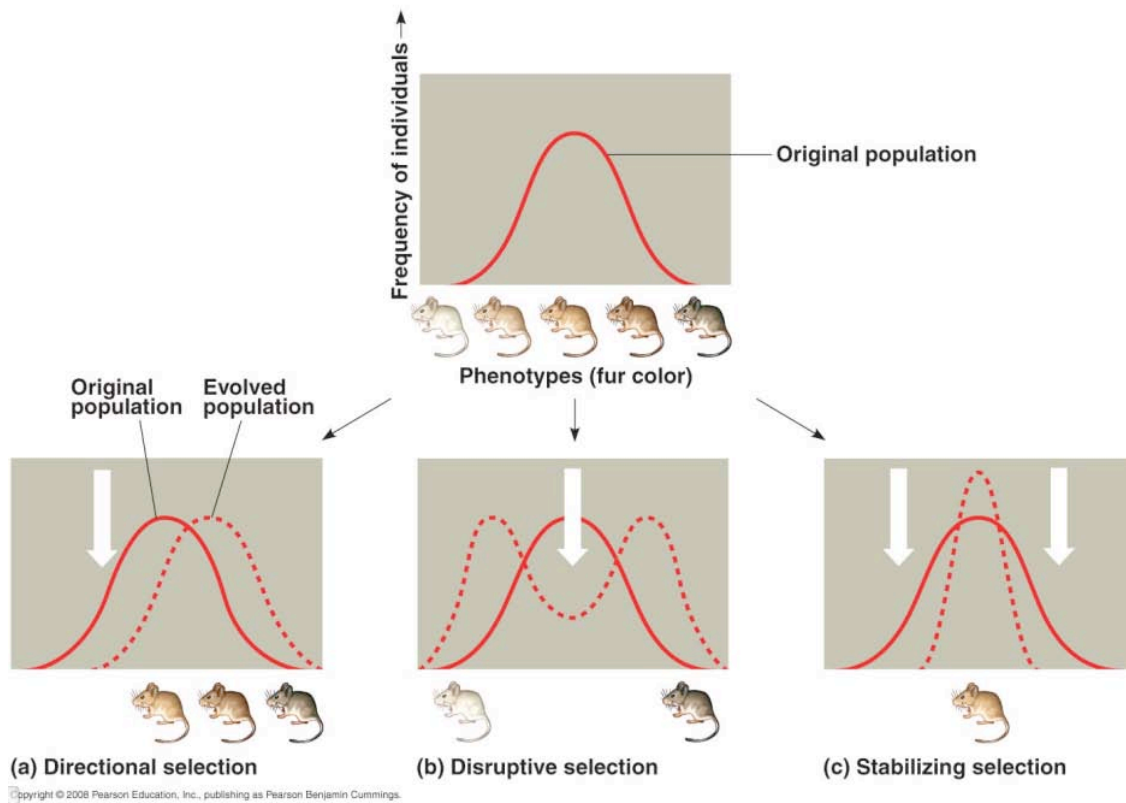
Phenotype Distribution and Evolution

Figure 23.13 (pg. 480 8th edition)

(a) Directional Selection: As shown above, individuals at the left-most end of the phenotype distribution have lower fitness &/or lower probability of surviving. As generations continue to reproduce with the same selective pressure, the curve is pushed to the right of the original because those phenotypes are more advantageous.

(b) Disruptive Selection: Individuals with intermediate phenotpytes are selected against, so individuals on each extreme survive and go on to reproduce. If the next generation reproduces randomly, the original curve will return. However, if non-random mating occurs, speciation may be the result (more on this later).

(c) Stabilizing Selection: In this case, both phenotypic extremes do not do well, so the middle phenotypic range increases in frequency. However, due to Mendelian inheritance, the generation following this selection will produce a generation similar to the original graph. However, this form of selection actively maintains genetic diversity in populations.

Sickle-Cell Anemia Example:
In the absence of malaria, genetic fitness is as follows:
$Hbb^{AA} > Hbb^{As} > Hbb^{ss}$

Hbb^{ss} denotes individuals who have malformed red blood cells, and thus have trouble transporting oxygen in the blood. This causes health problems (anaemia) that often prevent the individual from reproducing.

However, in the presence of malaria:
Hbb^{As}>Hbb^{AA}>Hbb^{ss}
This is the case because individuals with the heterozygous genotype have a slight resistance to malaria (with the s allele), but are not afflicted with Sickle-Cell Anemia

Darwin thought that evolution by natural selection was a very slow process, however it can also be very fast, only taking a few generations.

Directional Selection is when the ideal phenotype shifts from that of the original population to a phenotype more adapted to the environment. For example, light-colored mice living on a dark lava flow are more visible to predators, leading to selection for darker colored mice and a shift in the population to a darker coat color.
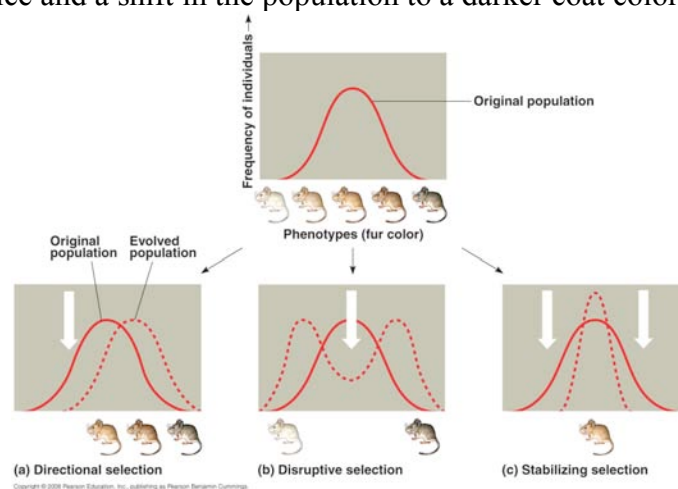

Figure 3: Different types of selection.
Campbell 8th edition. C*opyright © 2008 Pearson Education, Inc., publishing as Pearson Benjamin Cummings.* (Pg 480)

Scientists can generate **experimental evidence** using experiments with organisms that have a short life cycle, such as bacteria, yeast, and flies (Drosophila).
For example, consider guppies. Females are more attracted to male guppies with many large brightly colored spots, than to male guppies with fewer, smaller, or duller spots. However, bright colors attract predators. So, the brightly colored guppies survive less but reproduce more, while duller fish survive more but reproduce less.
Endlew and Reznick transplanted fish from a predator-filled pool at the bottom of a waterfall into the predator and guppy-free waters at the top of the waterfall. Therefore, a population of fish with drab colorations were moved into an environment with no predators. There, within generations the male fish quickly came to have more spots that

were larger and more brightly colored. This field experiment demonstrates the response of heritable phenotypes to a change in selection for a trait.
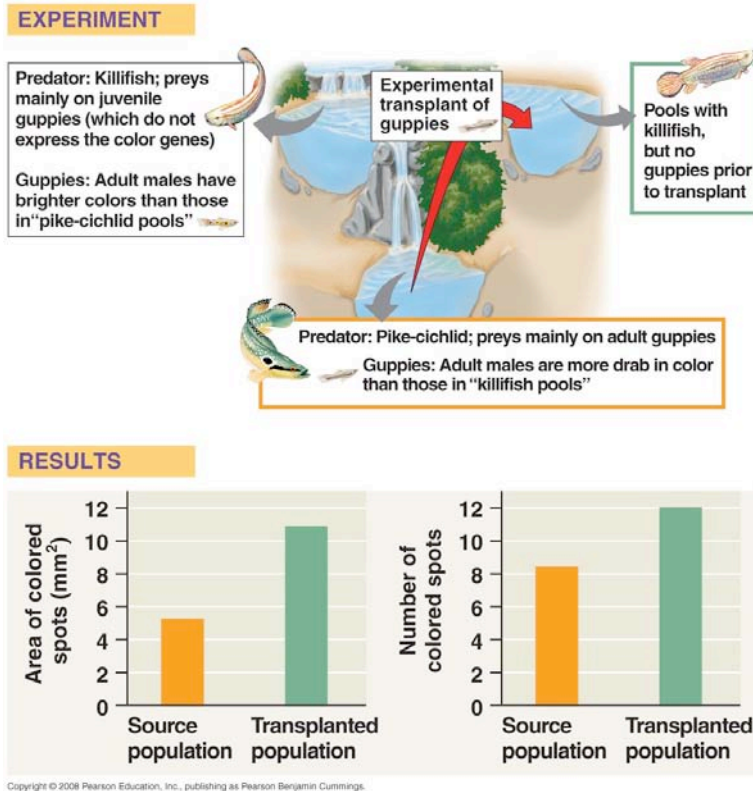
1.

Figure 1: Guppy Experiment
Campbell 8th Edition. *Copyright © 2008 Pearson Education, Inc., publishing as Pearson Benjamin Cummings* (pg 460)

Selection

Genomic Signatures are another way to see whether natural selection is operating in a population. It has become increasingly popular as the technology to do so has become more advanced and the cost of such tests has decreased markedly. A **candidate gene approach** targets genes (consider the pocket mice example: MC1R, agouti) known to cause universal effects. Contrarily, a **genome scan** sequences an entire genome and searches for regions of very low variation.

Why would we look for regions of low variation? A gene that is not under selection will accumulate variations through the joint effects of mutation and genetic drift. However, if a new mutation is under strong and recent selection, then there will be much less variety, as the advantageous allele will increase to a frequency of 1, replacing the pre-existing (background) variation.
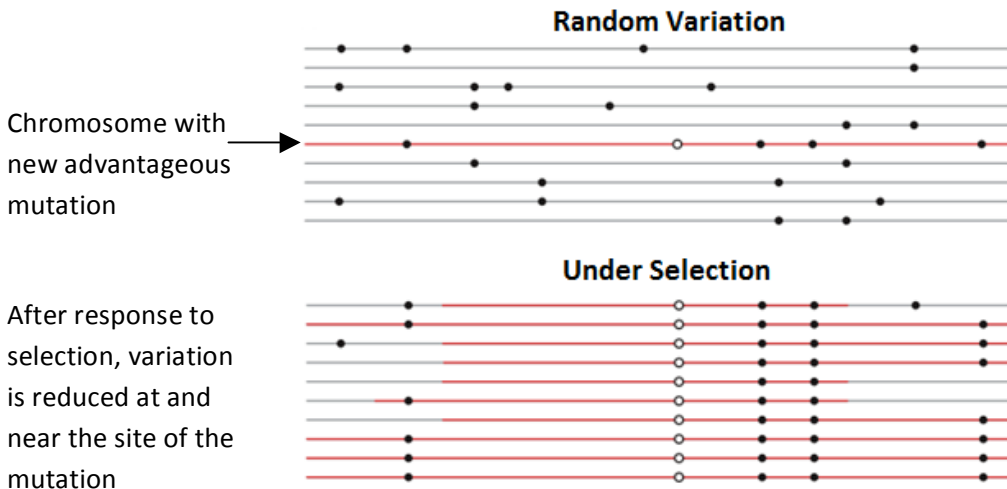
Figure 2:

For example, consider small and large breeds of dogs. All of these dogs are descended from a common ancestor that has been subject to intense artificial selection. A genome scan of small dogs revealed that all small dogs that were sequenced shared a single genetic location that exhibited very low variation. This location controlled for a growth factor: when sequenced, larger dogs did not have the same variant as small dogs. This implies that the shared inhibition of this growth factor is what makes small dogs small. (As for what makes small dogs so yappy, that's presumably still being researched.)

Coevolution

Coevolution, or reciprocal selection, is when each of two interacting species affects the fitnesses of phenotypes in the other species.
Mutualistic coevolution is when both species receive a benefit from the coevolutionary relationship. This can become an obligate (required) trait. For example, attine ants (also known as leaf-cutter ants) harvest leaves and bring them back to the ant nest, where they are digested by fungi. The fungi receives its nourishment from digesting the leaves, but the ants receive their nourishment from consuming the product produced by the fungi digesting the leaves.
Antagonistic coevolution is when one species has a negative benefit from coevolution.

Consider a host and a pathogen coevolving: the pathogen would develop surface proteins that the host cannot detect. The host's immune system would then develop sensors that could detect that pathogen. This sequence of evolutionary events has often been called an **evolutionary arms race** or a

Red Queen situation: to remain in one place (survive without being vulnerable to pathogens), you have to keep evolving new defenses.

In this case there is **frequency-dependent selection**, where the common phenotype has a reduced fitness (pathogens will easily infect individuals who all have the same immunity alleles) and the rarer phenotype has an increased fitness. This works to maintain genetic variation. (Neat note: The MHC, or major histocompatibility complex, is one of the densest genomic regions in mammals, and is responsible for our immune systems. It's very complex, and has a lot of different interacting genes.)

Another example would be a predator and its prey: predators which are more able to catch the prey will be favored, while prey that can escape from predators more often will be favored.

Alternatively, a prey species such as the Pacific newt might be very poisonous. However, its coevolved predator, the gartner snake, has the ability to detoxify the poison and prevent itself from being harmed by the poison. This coevolutionary process might continue with the newt receiving more toxic poisons, while the gartner snake would become more poison resistance.

Why have sex?

Evolutionarily, there are several strong disadvantages to sex:
1. Requires having two separate genders and expending resources on creating an entire gender (males) that waste energy by not directly producing offspring.
2. Requires that, once fully mature, individuals find a mate. This can consume a lot of time and energy that could be directly spent on offspring or survival.
3. Uses energy and entails risk.
4. By shuffling genes, sex breaks down good gene combinations.

There are alternatives to sexual reproduction. Some animals (1% of lizard species) practice **parthenogenesis**, or cloning to give birth to offspring genetically identical to the parent. Some plants have the same practice, called **apomixis.** Daphnia have a sexual-asexual system, where they reproduce asexually when the environment is favorable, and then switch to sexual reproduction when the environmental conditions are harsher.

Sexual reproduction has several advantages over asexual reproduction.
1. Produces variation through random mating, independent assortment of alleles, and recombination.
2. Recombination slows the accumulation of mutations (Mueller's ratchet)
3. Brings together good combinations of genes.
4. Produces genetically variable offspring, which:
    a. Can use more resources, and have an advantage in variable environments, in that they can adapt to changing environments more readily.
    b. Increase ability to evade pathogens and parasites. (Imagine if you have a species of clones where the only variation is due to mutations: they are going to be very vulnerable to a pathogen that is genetically adapted to that genome.)

Australian Gecko Populations
Consider *Heteronotia binoei*. These lizards reproduce parthenogenically (clonally). These clones are triploid (3N) and are all female, and arose from hybridization between different sexual morphs. The clones are genetically identical. This species of lizards has spread across a large swath of Australia. However, there will be up to 200 times as many parasites on these lizards as on other lizards, since these lizards are all genetically identical to each other (excepting mutation inherent in creating offspring). These parasites increase water loss and reduce survival rates.

Sexual Selection
Or, competition for mates or fertilization

After *On the Origin of Species*, Darwin wrote *Descent of Man*, in which he applied his theories on descent with modification to humans
- Essentially, his book covered selection in relation to sex

Here are the known systems of mating:
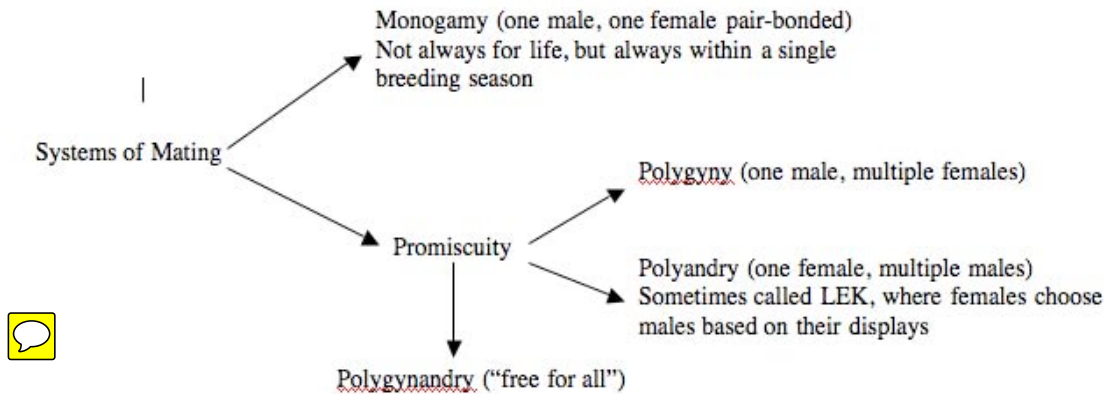
- The systems in which males must compete for females lead to extreme competition among the males (physically or competition of their sperm) and sexual dimorphism (marked differences in appearance between males and females of the same species: think of peacocks)
- Darwin hypothesized about two forms of sexual selection: intrasexual and intersexual
    1. Intrasexual includes male-male competition for females. This often results in body size sexual dimorphism, meaning that the males are much larger than females and often have adaptations to fight other males, i.e. antlers on the extinct Irish Elk)

2. Intersexual competition is the case where males must show themselves to be genetically attractive to females, such as the satin bowerbird, which decorates its nest with blue materials, such as flowers or plastic
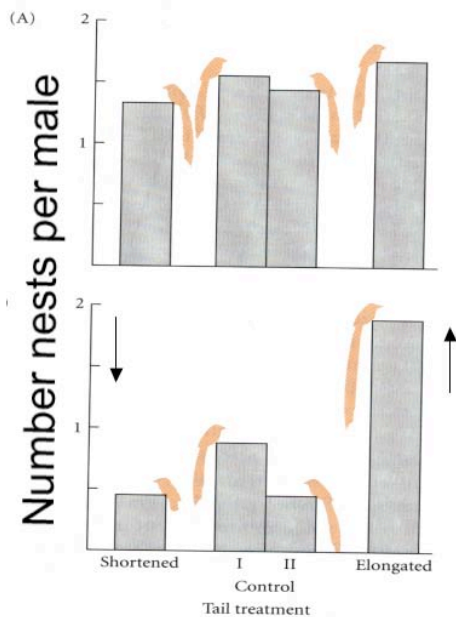
Sexual selection can be identified through experimentation, such as in the Long-Tailed Widowbird:
- In Widowbirds, longer tails are more attractive to females looking for mates
- In this study, three groups of the birds were established: a regular control group, a group in which the males' tails had been cut off/shortened, and a group in which the tails from the second group of males were glued to a set of normal males

Here are the results:

Female choice: manipulation of tail-length in male widowbirds

(A)

Number nests per male

Shortened   I   II   Elongated
Control
Tail treatment

Futuyma, Evolution, 1st Ed.

One might ask, "If longer tails mean better reproductive success, why don't males have longer tails than they naturally do?" This is where the subtle balance between natural and sexual selection. A longer tail might decrease a male's chance of survival before he is able to reproduce, thus lowering his reproductive fitness.

Back to Mating Systems:
In polygynandrous and polyandrous systems, females are promiscuous, and mate with many males. As a result, males develop sperm competition to ensure that their sperm (and genetic material) make it to the egg first
- In general, one sperm reaches one egg, but the norm is that females can ovulate multiple eggs, opening up the potential for multiple paternity as well
- Sperm often cooperate to make it to the egg first, such as aggregating to swim faster
- Fisher & Hoekstra did research on sperm aggregation in mice, and found that in sperm from a promiscuous variety of mouse, sperm from one male clumped together, yet in a monogamous variety's sperm, sperm clumped randomly, and sometimes with sperm from another species

Advantage of Multiple Mating

In species that practice multiple mating, sperm competition mediates the survival of offspring

- In the marsupial mouse Antechinus, all mating occurs within a two week period, after which all of the males die. During that period, the males mate with as many females as possible, and vice versa.
- Fisher (a different one) found that females that mated with multiple males had a higher percent of their offspring surviving:

Survival in the wild is estimated from the number of offspring that were captured at weaning. We released 100 offspring from 17 monandrous females and 139 offspring from 19 polyandrous females into the wild. Survival in captivity is calculated from the number of offspring that survived until weaning. There were 121 offspring from 18 monandrous females and 116 offspring from 18 polyandrous females in the captive experiment. Red bars indicate monandry; blue bars indicate polyandry. Data are the mean ± s.e.m.

Mean survival curves are presented for monandrous females mated to more competitive males ($n = 41$ offspring from five litters; unbroken black line) or less competitive males ($n = 80$ offspring from 13 litters; dotted black line) and polyandrous females ($n = 116$ offspring from 18 litters; blue line). The pooled curve for all 18 monandrous females that gave birth is also shown (red line).
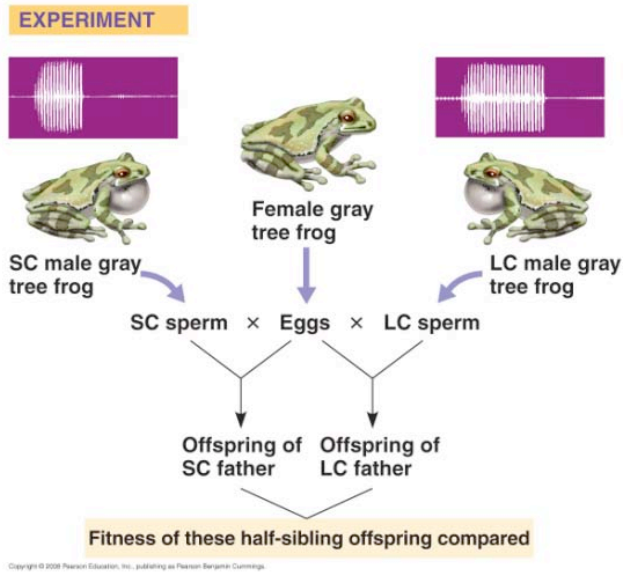
(Fisher et al. 2006 Nature 444: 89-92)

- Also, males that were able to mate multiple times had higher offspring survival rates, suggesting that their DNA was generally more fit

Why do females choose?

- There is a <u>direct benefit</u> to the female's own fitness, such as a female pairing with a male who controls a better territory with better resources that she can share by mating with him

- There is an <u>indirect benefit</u> to the female's offspring, rather than the female herself

- This gives rise to the "Good Genes" Hypothesis, which states that males able to convince females to mate with them based on their physical traits are better adapted to the environment, as will be their offspring

- An example of an experimental test of the good genes hypothesis concerns Gray Tree Frogs:

Note that females prefer males with long calls:

EXPERIMENT

SC male gray tree frog

Female gray tree frog

LC male gray tree frog

SC sperm × Eggs × LC sperm

Offspring of SC father   Offspring of LC father

Fitness of these half-sibling offspring compared

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RESULTS

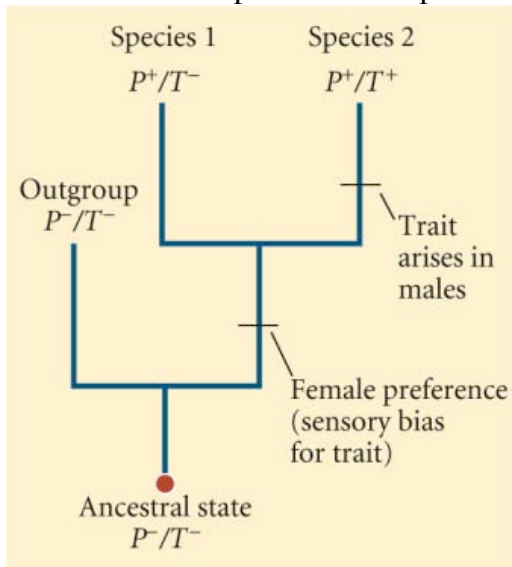| Fitness Measure	1995	1996
Larval growth	NSD	LC better
Larval survival	LC better	NSD
Time to metamorphosis	LC better (shorter)	LC better (shorter)

NSD = no significant difference; LC better = offspring of LC males superior to offspring of SC males.

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Males with longer calls had more successful offspring

Figure 23.16 (pg. 482, 8th edition)

Males can also exploit females' pre-existing preferences:

Species 1
P^+/T^-

Species 2
P^+/T^+

Outgroup
P^-/T^-

Trait arises in males

Female preference (sensory bias for trait)

Ancestral state
P^-/T^-

EVOLUTION 2e, Figure 15.22

P+ indicates that females have the preference
P- indicates no preference

T+ indicates that males have the trait preferred by females
T- indicates that males do not have the trait preferred by females

Altruism

How can we explain the evolution of **altruism**, or behavior that promotes an individual to make sacrifices to help others? For example, if a bird sees a predator and gives an alarm call to alert other birds to the danger, that action makes the bird more visible to the predator and increases the chance the predator will target it.

Altruism will be favored if it increases the fitness of close relatives who share your genes by descent. However, the degree of altruism varies with the degree of relatedness: consider full siblings and first cousins.

      A full sibling shares 50% of your genes (relatedness factor r = 0.5)

      A first cousin shares 12.5% of your genes (relatedness factor r = 0.125)

Therefore: "I would not lay down my life for a brother, but would do so for 2 brothers or 8 cousins" (Haldane). Haldane says this as a way to show how relatedness affects how many genes would be passing. For example, 2 brothers* ½ relatedness = 1. However, 8 first cousins * 0.125 relatedness = 1.

This concept was further formalized by Hamilton into **Kin-Selection Theory**, which explains when altruism will be beneficial in an <u>inclusive fitness</u> sense. Altruism will be favored if r*B > C, where r is relatedness, B is benefit to the recipient of altruism, and C is the cost to you.

      For example, consider ground squirrels. They give alarm calls when predators are near: however, it turns out the female squirrels are the only gender to give an alarm call. Further, females reside in the same territory from infanthood to adulthood, while males disperse. Therefore, all the females in one area will be related, and by giving alarm calls that female is providing a survival benefit to all the nearby females she is related to.

      Another example is the tuco-tuco. These burrowing creatures have litters, so there are lots of babies. They also practice communal nursing of young: but again, it is a group of sisters who communally nurse their babies.

      A final example is when turkeys form male coalitions to assist each other in mating competition. Why would a group of male turkeys ally themselves together? All the turkeys in a coalition are closely related (r ~ 0.5 = brothers): thus, by helping one of their group to mate, they are indirectly propagating their own shared genes.

Speciation: The Mystery of Mysteries

                 speciation

Microevolution ————————▶ Macroevolution

(Populations)   (Clades)
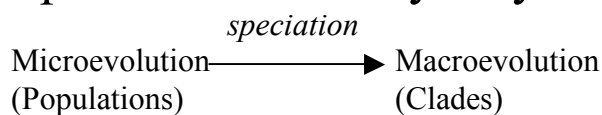
We have reviewed the major processes governing evolution within and among populations **(microevolution)**. These processes are the same that govern the evolution of new species, or **macroevolution**.

That said, what is a **species**?

1. **Typological species concept:** Species were considered to be fixed entities, or a "thought of god." Naturalists and philosophers from Aristotle through Linnaeus took this view, and

cataloguing the extent of nature was merely describing all of these fixed forms which were created along with the Earth.

2. **Evolutionary species concept:** Charles Darwin did not see species as qualitatively different from other varieties: instead, a species concept is an arbitrary category humans use to define the variation in form they see. In general, we think of species as independently evolving lineages – the general lineage concept. Different formations differ in emphasis, but are consistent with this idea:

   a. **Discontinuous species concept:** *Proposed by Darwin.* Descent with modification, combined with extinction, allows us to consider species as organisms with discontinuous phenotypes. Thus species are defined by their morphological distinctiveness, and in practice most species can be defined by taxonomists.

   b. **Phylogenetic species concept:** *Proposed by Systematists.* By looking at characters and their ancestry, you can describe a group's as shared-derived, monophyletic, etc. Thus you <u>diagnose</u> a species based on shared, derived traits relative to other sets of populations and species.

   c. **Biological species concept:** *Proposed by NeoDarwinists.* Emphasizes **reproductive isolation**, examining groups of populations reproductively isolated from others.

Forms of Reproductive Isolation

Even though these are presented as prezygotic and postzygotic, keep in mind they are not in any kind of set sequence, especially if referring to the textbook for Figure 24.4

Prezygotic Isolation occurs before mating and fertilization and prevents the formation of a zygote.

1. **Habitat:** Two sexually compatible species might dwell in different habitats and thus be reproductively isolated simply because they never meet. Consider a lake, and insects living right under the surface water, and another divergent species living just above the lake floor.

2. **Timing:** Two sexually compatible species might not have mating seasons that correspond with each other, or might not occupy the same range at the same time.

3. **Behavior:** A species behavior might prevent it from mating with another species – for example, many birds have specific mating rituals. If these are not performed correctly, then mating will not occur.

4. **Mechanical:** Two species reproductive organs just might not fit. Two species might also mate together successfully, but the female's ova will not recognize and accept the sperm (it will not have the correct surface proteins) – this is called **gamete recognition.**

Postzygotic Isolation refers to factors affecting reproductive success of hybrids.

1. **Viability:** The hybrid may have deleterious traits, or just be not well adapted to the environment.

2. **Fertility:** The hybrid may be viable, but may be sterile or unable to reproduce.

Reproductive isolation, trait differences etc. generally increase with the amount of time since the separation of two populations. Considering the **general lineage concept**, longer isolated lineages will be easier to diagnose by any method and different approaches will mostly agree. But recently separated lineages are often in a "grey zone", where different criteria or emphases (e.g. phylogenetic vs biological species) give different results. This is because there is no necessary sequence of events or extent of change that defines a species. In many ways this demonstrates that species arise via microevolutionary change, the cornerstone of Darwin's long argument.

Biology 1B—Evolution Lecture 9 - Speciation Processes
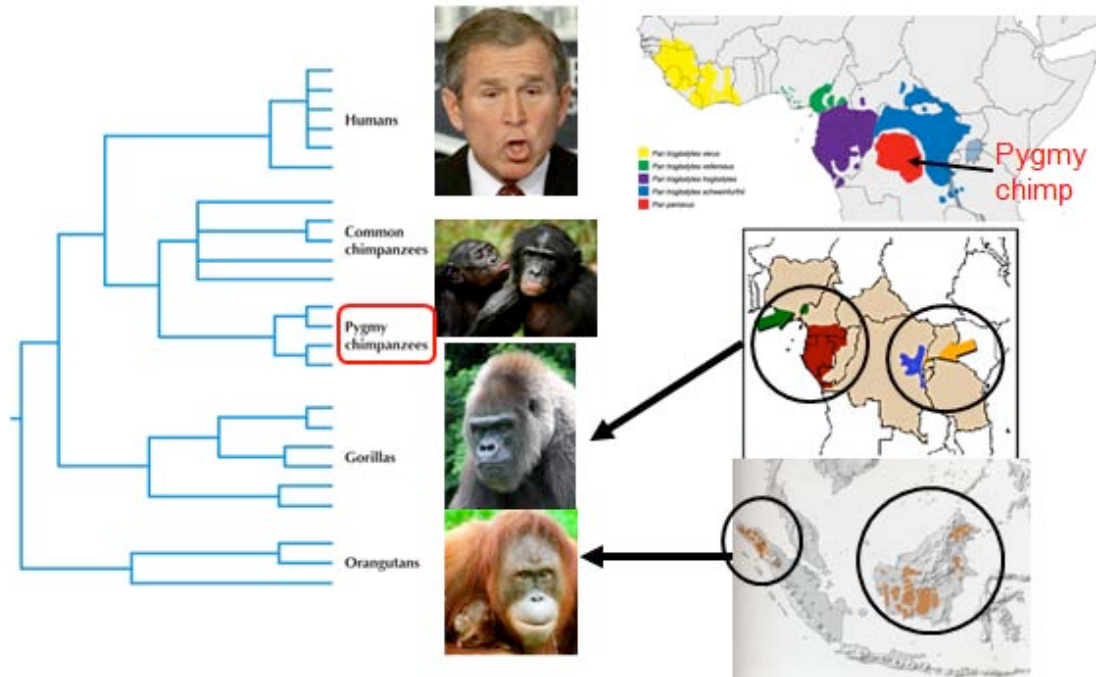
Species identification - the grey zone…

Figure 1

Consider this cladogram. Let's examine it with all three species concepts:

For each species, we can identify them and their sub-species phylogenetically using molecular analysis of their genomes. Examining them using a discontinuities species model also returns much the same result.

However, in terms of the biological species concept, we don't know for some of these species or subspecies. There are common and pygmy chimpanzees separated by a river: should we still call them a single species? Or since they are experiencing habitat reproductive isolation, are they two species? What about Bornean v Sumatran orangutans, or east vs west African gorillas?

Ensatina eschscholtzii – a ring species

- Salamanders that mimic newts with an orange stripe (in the Bay Area)
- Their geographic range covers much of California, excluding the Central Valley:

k-e overlap; hybrids

k-e overlap; no hybrids
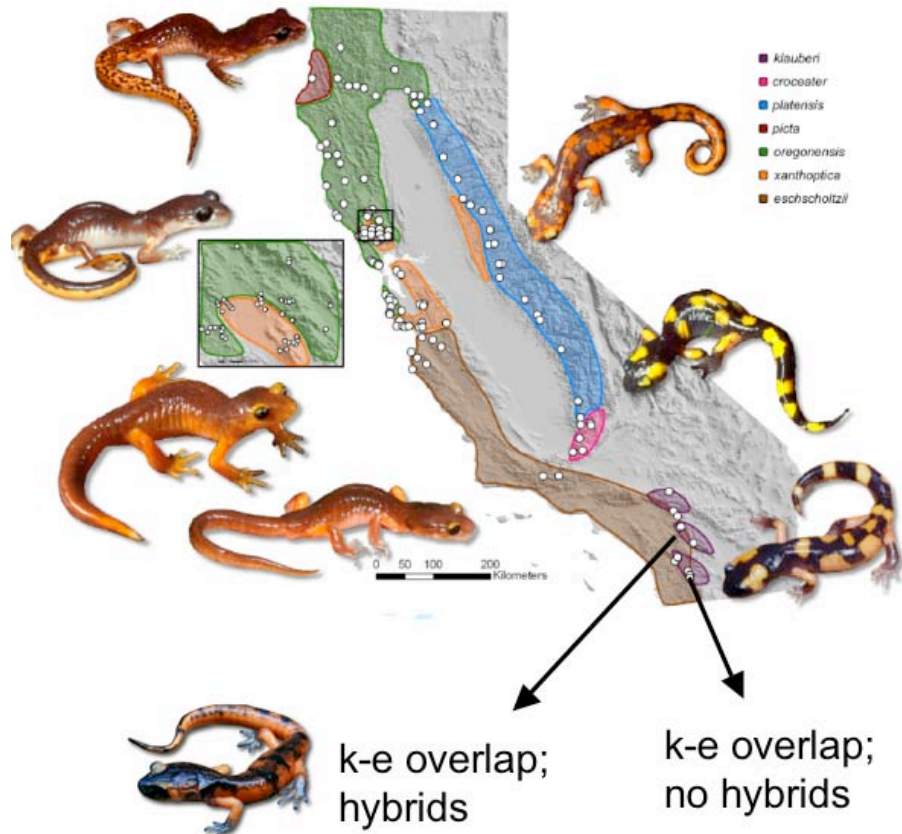
- The ancestral range was in the redwood forests of the north, but they have migrated independently along the west coast and the Sierra Nevadas
- There are gradual transitions along the coasts: on the west, the salamanders are plain and cryptic; on the east, they are disrupted (disruptive against leaf litter background), blotched, and highly colored
- In the foothills of the Sierra Nevada, there is a hybrid zone where the coastal form and Sierra form have come back together
- In the mountains behind San Diego, the plain and blotched overlap with no interbreeding. Yet, just to the north at Palomar, they overlap and form hybrids.
- Could be considered a "ring species" because they make a loop of gradual transitions
- Current taxonomy is that there is one species with 7 sub-species, but they could be classified as having two species or 11+ species if a phylogenetic concept is used
- Since these species are in the process of evolving, there is much gray area between populations, causing classification problems
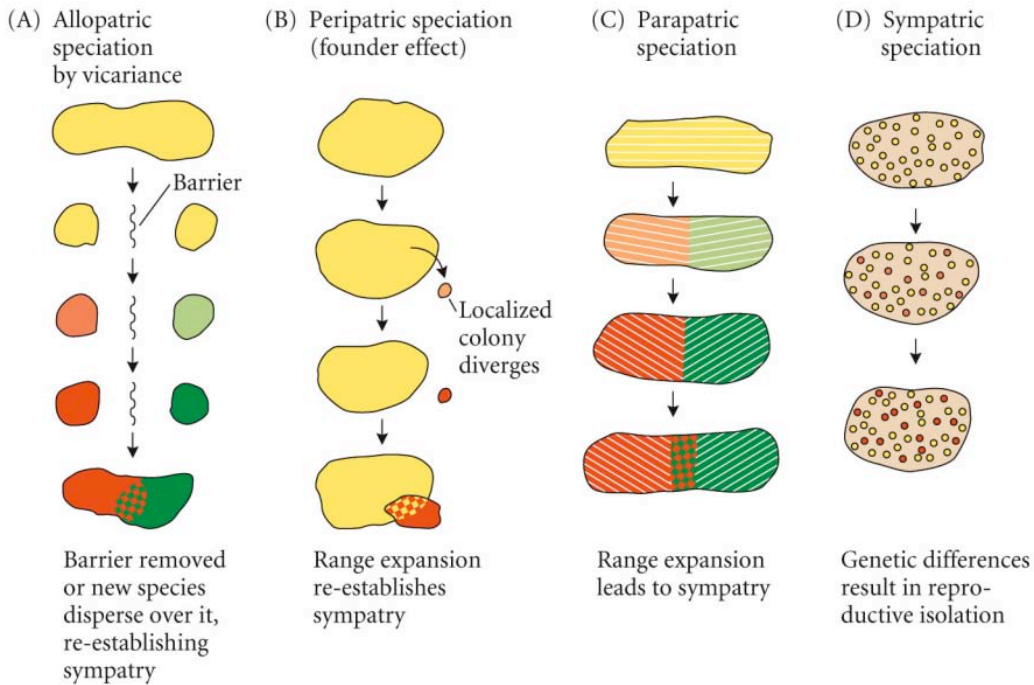
Speciation processes

Recall that:

Disruptive Selection increases population divergence

Genetic Drift increases population divergence

Migration decreases random mating and divergence

(A) Allopatric speciation by vicariance

(B) Peripatric speciation (founder effect)

(C) Parapatric speciation

(D) Sympatric speciation

Barrier

Localized colony diverges

Barrier removed or new species disperse over it, re-establishing sympatry

Range expansion re-establishes sympatry

Range expansion leads to sympatry

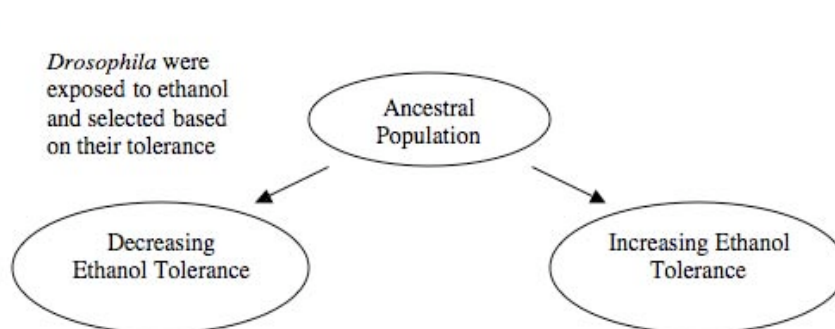Genetic differences result in repro-ductive isolation

EVOLUTION 2e, Figure 18.1   Futuyma 2005
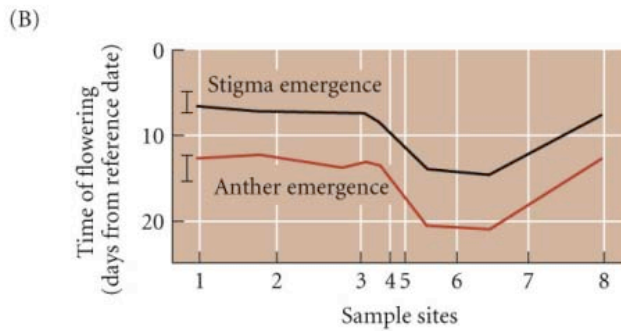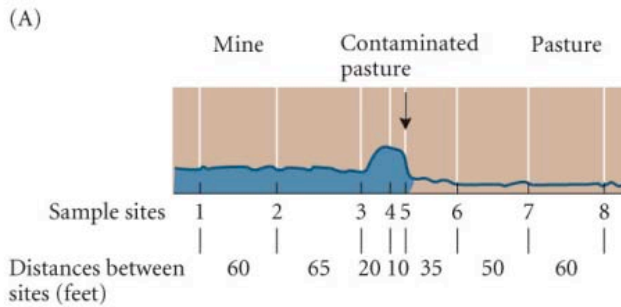
© 2009 Sinauer Associates, Inc.

Allopatric:
- A geographical barrier arises so that a population is split, and over time, the two sets of populations diverge (though drift +/or selection) such that they are reproductively isolated and perhaps ecologically distinct when they come back together
- This is the dominant form of speciation
- Enhanced with divergent selection
- Example: tiny tropical frogs on adjacent mountains diverge into sister species (they are each others' closest relatives). In rapidly breeding systems, this process can be tested experimentally in the lab:

Drosophila were exposed to ethanol and selected based on their tolerance

Ancestral Population

Decreasing Ethanol Tolerance

Increasing Ethanol Tolerance

- When the two groups of flies were brought back together, there was some reproductive isolation (in as short a time as 5 years—something Darwin would have found unbelievable)

Parapatric:
- Lacks a concrete boundary like allopatric speciation…instead it occurs in adjacent diverging populations with some potential for gene flow across the boundary
- Needs divergent (disruptive selection) and non-random mating to function as a mechanism of speciation
- Recall the grasses living on adjacent mine sites in which phenotype frequency changed based on the grasses' respective habitats:

(A)

Mine   Contaminated   Pasture
        pasture

Sample sites   1   2   3 45   6   7   8

Distances between   60   65   20 10 35   50   60
sites (feet)

(B)

Time of flowering (days from reference date)

Stigma emergence

Anther emergence

Sample sites

> Here, the grasses shift in mating (creating non-random mating because each habitat's grass mates at a different time)
>
> The mine site grasses flower earlier and have an increased rate of self-fertilization (temporal isolation). There is also the post-zygotic isolation of the fitness of the mine grass versus the non-mine grass.

(C)

Self-fertility (percent)

1964

1965

Sample sites
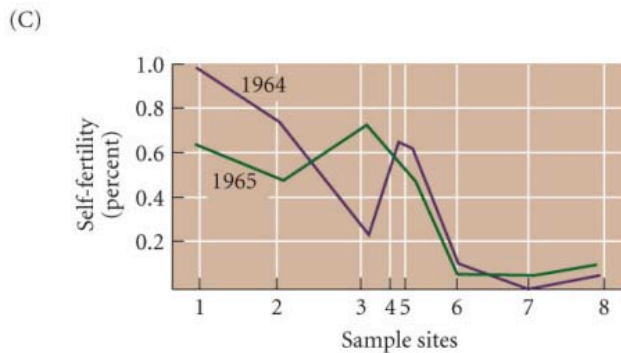
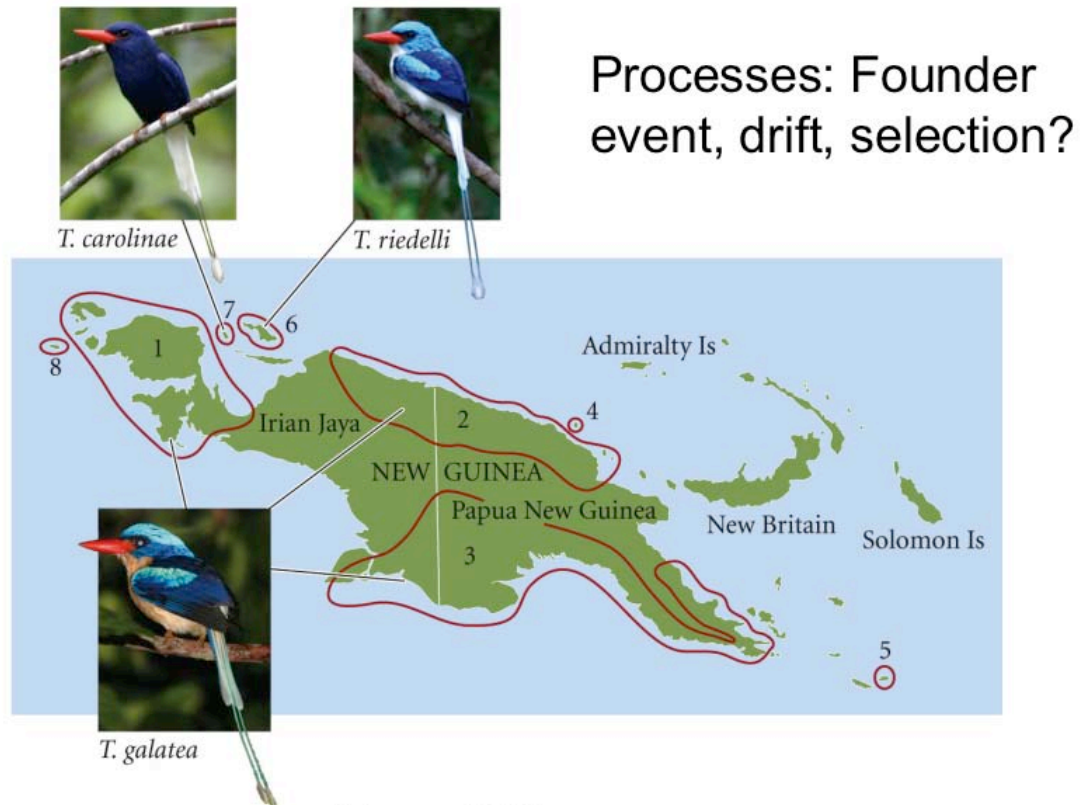**EVOLUTION 2e, Figure 18.20**

Sympatric:
- Though these populations are overlapping spatially, divergent selection is at work with pre-zygotic isolation as a necessary side effect
- Non-random mating must arise, and it does in the form of the groups isolated by disruptive selection mating only with members of their own groups
- Example: Lord Howe palms on Islands near Australia with sister species of palms that differ in important ecological characteristics (i.e. soil types)

- Different sister species on different soil types flower at different times, reproductively isolating themselves
- Difficult to say because it takes more time and more active avoidance of gene flow

Peripatric:
- May particularly apply to islands because it refers to a Founder-like speciation in which a small group of individuals (colonial group) breaks off from a large population (continental group)
- The novel environment of the island gives rise to divergent selection
- Example: the Paradise-Kingfishers of New Guinea

Processes: Founder event, drift, selection?

T. carolinae

T. riedelli

T. galatea

EVOLUTION 2e, Figure 18.17   Futuyma 2005

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