UNIVERSITY OF WATERLOO

BIOL 359: Evolution 1 - Mechanisms
Review Notes

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Module 1 - Introduction

Terminology

- **Fact:** observation that has been repeatedly confirmed and all practical purposes is accepted as True - never final
- **Hypothesis:** tentative statement about natural world
    - The deduction and prediction can be tested
        - If verified: hypothesis is correct
        - If not: hypothesis abandoned or need modification
- **Law:** a descriptive generalization about how some aspect of natural world behaves under specified circumstances
- **Theory:** a well substantiated explanation of some aspect of natural world that incorporate facts, laws, and tested hypothesis
    - The ultimate goal of SCI

Evolution is a scientific fact as well as a scientific theory

History of Evolution

- Closely connected with important development of geology
    - Catastrophism
    - Principle of Uniformitarianism
    - Lamarckism - based on inheritance of acquired characteristics

~500 BCE: **Anaximander** (6th century BCE, ancient Greek)

- Species come from water,human and other animals descended from fish

~400 BCE: **Empedocles** (5th century BCE, ancient Greek)

- Body parts were joined together as random and only some combinations were fit for survival

~300 BCE: **Plato** (423 - 347 BCE)

- Idealism
    - All natural phenomena are imperfect representations of a true essence of an ideal unseen world

~300 BCE: **Aristotle** (384 - 322 BCE)

- Species are organized on a “Scale Nature” (scala naturae)
    - Least (barely animated organism) - Most perfect (human)

1735: **Carolus Linnaeus** (1707 - 1778)

- Father of taxonomy --> published works in Systema Naturae

1809: **Jean Baptiste Lamarck** (1744 - 1829)

- Species change overtime -> evolve into different species
- By inheritance of characters acquired during lifetime (wrong wrong wrong)
    - Lamarckism / Lamarckian Evolution

1794: **Erasmus Darwin** (1731 - 1802)

- Book "Law of Organic Life"
- Species also evolved and are descendents of earlier life-forms
- He (grandfather of Charles Darwin) does not have evidence for this

1801: **Georges Cuvier** (1769 - 1832)

- Father of comparative anatomy and paleontology
- Proponent of **Catastrophism**
    - Earth's physical features had been modelled by major catastrophes that were the result of forces that are no longer in operation today
    - Arose as a result of trying to reconcile geological history with the Bible's age of Earth

1785: **James Hutton** (1726 - 1797)

- Father of modern geology
- Principle of **Uniformitarianism**
    - Earth has always changed in uniform ways and that the present is the key to the past --> geological process is the same in time

1830: **Charles Lyell** (1793 - 1875)

- Published book called **Principle of Geology**
    - Supported uniformitarianism, ended catastrophism

1859: **Chales Darwin** (1809 - 1882)

- Surveying on Galapagos Island, South Africa
- Different species on the island lead to species change over time
    - Species evolve and change over time
    - Struggled with numerous things (including Lamarckism) --> but he thinks that Lamarckism might be wrong!
- Natural selection --> "On the Origin of Species"

1858: **Alfred Russel Wallace** (1823 - 1913)

- Worked on Pacific with the same conclusion as Darwin
- Papers: “On the Tendency of Species to Form Varieties” and “On the Perpetuation of Varieties and Species by Natural Means of Selection”

Modern Synthesis marks the shift from simply documenting evolution to understanding the mechanism of evolution --> selection is based on genetic variation

Module 2 - Evidence for Evolution

Evolution:

- descent with modification
- a change in population allele frequency

Homology:

- Similarity resulting from common ancestry, despite differences in function
- ex: human and cats --> both have 4 limbs

Analogy:

- Similarity in function, but not having the same evolutionary origin
- ex: bird and insect wings

Selective breeding

- 200+ dogs with different traits
- Domestication of Dogs
    - Dogs are descendants of wolves (canis lupus)

<u>Non-human-induced Evolutionary change</u>

- **Microevolution:** <u>small</u> evolutionary changes within species or population
- **Speciation:** the <u>splitting</u> and <u>divergence</u> of lineages. An ancestral species can give rise to two or more descendent or daughter species
- **Macroevolution:** larger phenotypic changes sufficient to place an organism in a different higher level taxon (eg., phylum).
- Over time, microevolution resulted in both speciation and macroevolutionary differences

<u>Direct observation of evolutionary changes</u>

- **Incipient Species**
    - Two populations that have nearly completed the process of becoming separate species
    - Eg. <u>Apple maggot fly</u> (Rhagoletis pomonella)
        - First in hawthorn trees, then moved to apple tree (imported later) because apple tree ripen earlier than hawthorn

Vestigial Structures

- Body parts that are useless / rudimentary in one or more organism, but have an important function in related organisms
- Darwin: evidence of evolution - one evolved form another due to different needs

Evidence from Lab Experiments

- Smaller organisms - faster generation for experiment
- Garner important insight about evolution and mechanisms
    - Proved speciation using virus and bacteria

Evidence from Natural Population

- Observe different stages of speciation

Species

- Difficult to define, controversial, difficult to make def. that encapsulates the tremendous biological diversity - different species concepts
- **The Biological Species Concept**
    - Species are groups of interbreeding natural populations that are reproductively isolated from other such groups (E. Mayr.)
    - reproductive isolation --> key operational criterion
    - Can only be applied to species that are sexually reproducing
    - Not a universal definition
    - Evidence for evolution in natural population
    - If evolution occurs we should be able to look at natural populations and observe different stages on the way to reproductive isolation
        1. Single variable population
        2. Distinguishable but interbreeding subpopulation
        3. Different populations with limited interbreeding
        4. Reproductively isolated -> species

Evidence from Extinction and Fossil Record

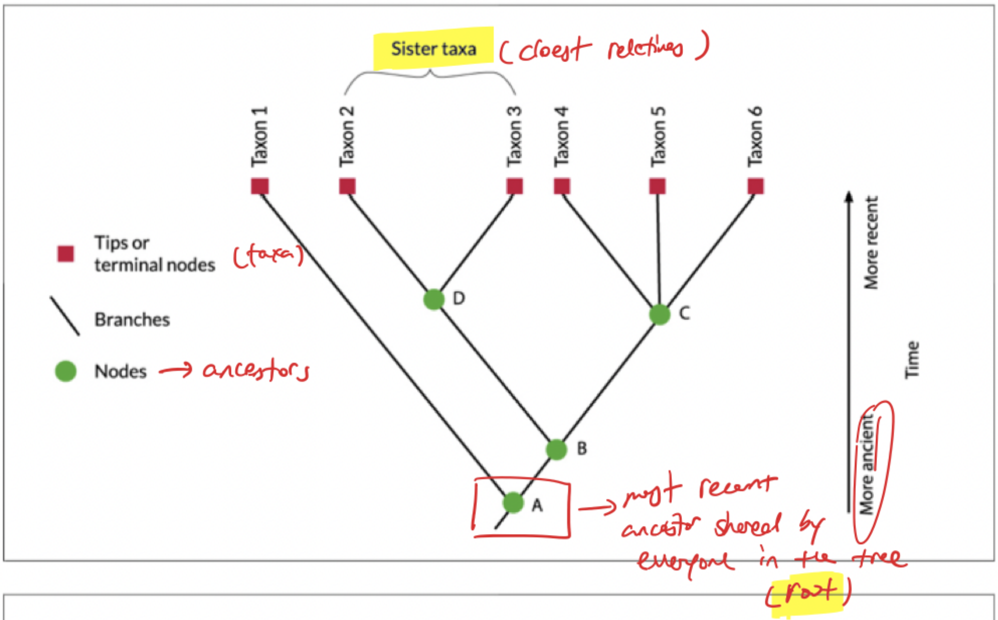
The Fossil Record

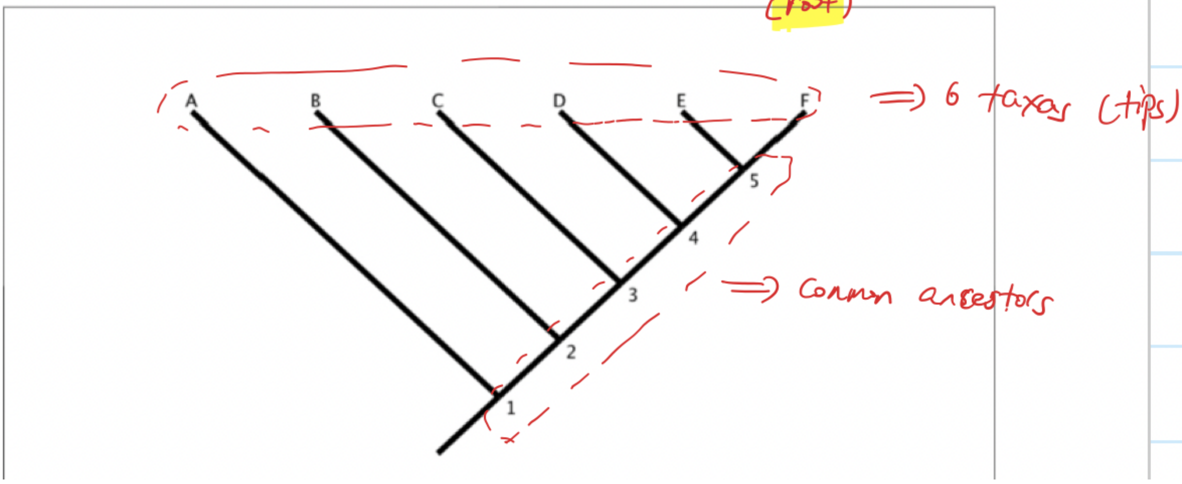
- The entire collection of fossils that we have globally
- **Paleontology** is the study of fossils
- In 1801, Georges Cuvier published a list of 23 extinct species --> before that, people do not believe that species can go extinct
- Eg. Irish Elk Fossil: proved not moose, but are large species that is hard to miss by humans --> can only go extinct

- <u>Null hypothesis</u>: evolution has not occured. -> we should see the same organism in the fossil compared to that exists today
- <u>Alternate hypothesis</u>: evolution has occurred. -> see changes in the organisms according to fossil record, show strong geographic patterns with respect to the similarity of organisms in the fossil record and those exist today
    - **The Law of Succession**
        - Fossils in a given geographic region are more closely related to the extant fauna of that region than they are organisms in a different geographic region

<u>Phylogenetic Tree</u>

- Study of ancestor - descendent relationship --> only a hypothesis
- **Taxa**: tips or terminal nodes
- **Root**: the most recent ancestor shared by everyone in the tree
- Slanted cladogram vs. rectangular



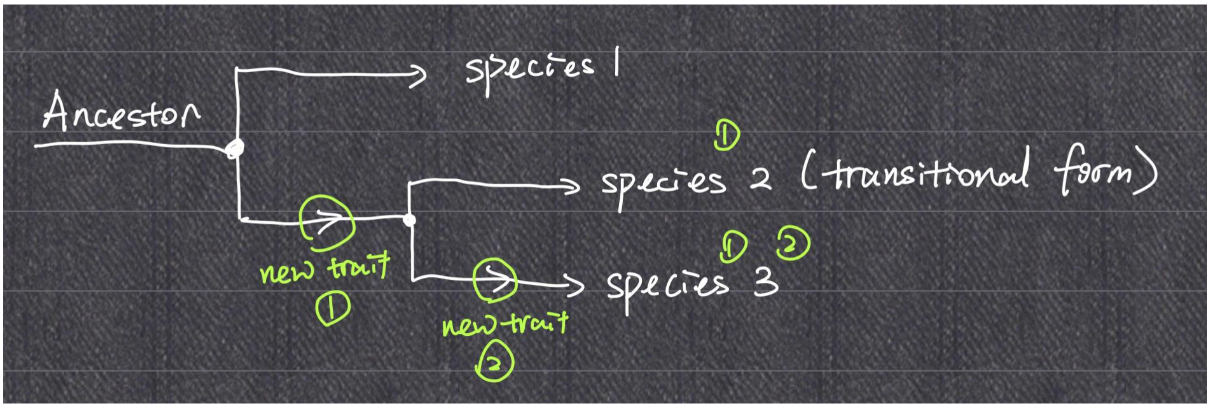


*You can rotate by 180 degree and do not change ancestor relationship

*Do not look at the order at which taxa appears, Look at branching order --> find the most recent common ancestor and compare

<u>Transitional forms</u>

- fossil/living record with organism that are an **intermediate** or a **mixture** between the species



Species 2 is the transitional form of species 1 to 3

* not necessary of ancestor - descendent, but rather just all 3 evolves from a common ancestor but evolve differently --> they can all exist today together

Homology

- Remarkable similarities between the fetus of multiple species (snake, chicken, possum, cat, bat, human)
- Tail on human fetus - evidence of evolution
- Eg. Male Hernias:
    - A problem resulting from a developmental homology
    - Gonad at similar position as fish (very high up)
    - descending down, leaving weak points in abdomen --> caused hernia later

Age of Earth

- Only long age can generate such huge diversity of life from a single ancestor
- Idea of **special creation** (~6000 years old - Archbishop Ussher)
- **Uniformitarianism**: the idea that geological forces that we see operating today are the same as those that operated in the past --> earth has to be very old
- Used **relative dating** - chronological dating --> no exact dates
    - prior to radioactive dating, geologists cannot put an exact age on Earth
- **Principle of Superposition** - younger geological layers sit on top of older ones
- **Principle of Original Horizontality** - lava and sedimentary rocks were originally laid down in a horizontal position - detect by **radiological dating** - put in exact age order

Correlation of Data sets

- The combination of <u>geological data</u> sets with <u>biological data sets</u> and fossils provides us with very powerful evidence for evolution and it also allows us to trace the history of file on Earth
- **Plate Tectonics**
    - Central geological principle since 1960s
    - Can determine how continents have moved over time (via **continental drift**)
- Example: Ostrich ratites was found at Gondwana (150 mya)
    - Gondwana breaks up --> Ratites speciated as continents move apart (20 mya)

Module 3 - Introduction to Natural Selection

Natural selection:
the difference in the survival and reproduction of phenotypes, which leads to differences in their contribution to the next generation, resulting in a change in the frequency of heritable phenotypic variations in populations over time.

Components of Natural Selection

- Living things produce more offspring than can be supported
- There is a constant struggle for existence
- Individuals in a population vary in their phenotypes
- Some of this variation is heritable (based in genotypes)
- Those individuals best adapted to current conditions are most likely to survive and reproduce themselves
- If these adaptations are heritable, they will be passed on to their offspring

Natural selection acts on phenotypes, yet

- Evolution only occurs if there is a change in **allele frequency**
- Therefore natural selection is driven by changes in **evolutionary fitness** among individuals
  - Individual's contribution to the next generation, in terms of number of offspring
    - increased number offspring = increased evolutionary fitness --> measure of **reproductive success**

Three components (selective elements) that contribute to the individual's evolutionary fitness

- **Viability or mortality selection** - an individual's ability to survive and reach reproductive age (age of maturation)
- **Sexual selection** - an individual's ability to procure a mate (mating success)
- **Fecundity selection** - family size, usually measured as # female gametes (eggs) per reproductive event
  - Excess fecundity --> the struggle for existence

Indirect fitness

- any impact that **an individual has on the survival and reproduction of relatives**

- Eg. kin selection; altruism

Adaptation

- A trait or characteristic that increases an individual's fitness, in comparison to individuals that do not possess that trait
- Natural selection results in adaptive evolution --> increase the population's fitness (but not all evolution is adaptive)

Darwin's Four Postulates

1. Individuals within species are **phenotypically variable**
2. Some of these variations are **heritable** (have a genetic bases)
3. In every generation, **more offspring are produced than survive**, some are more successful at survival and reproduction than others
4. The survival and reproduction of individuals is **not random**. Those who reproduce, or reproduce the most are those with the most favourable variations (aka. adaptation) and are naturally selected

Eg. Beach mice

- Disruptive selection: lighter fur color survive while darker fur color 被吃掉了

Not only about survival of the fittest, it is also about the contribution to next generation

Natural Selection in Action

1. Natural selection is dynamic
    - Phenotypes favoured in one generation might be different than that of the subsequent generation
2. Natural selection does not produce any new variation
    - it acted on heritable phenotypic variation already present in the population, and altered the frequency of different heritable phenotypic variants

Heritability

- key component of natural selection
- proportion of trait variation in a population that is attributable to genotypes as opposed to environmentally induced differences
- range between 0 and 1
- slope of a parent/offspring regression line for a given trait estimates the heritability of that trait

***Natural selection does not produce new trait, but mutation and recombination can

How Natural Selection Operates

- Natural selection acts on **individuals** but consequences occur in **populations**
    - It is just a statistical process that changes the statistical property of the population
- Natural selection acts on **phenotypes** but evolution consists of **changes in allele frequencies**
- Natural selection produces **nothing new**
    - something new arises only when it is in conjunction with mutation --> if beneficial, natural selection acts on it and increases it frequency
- Natural selection is **backlooking**
    - Always one generation behind
        - 2nd generation is better adapted to their parents' condition that their parents
    - can't prepare for the future --> can't pre-adapt
- Evolution is **NOT perfect**
    - **Antagonistic selection**
        - When any of the three selective elements (viability, sexual, and/or fecundity) of fitness act in opposite to each other
        - One of the reasons why natural selection does not lead to perfectly adapted organism
- Natural selection is **non-random**
    - a specific subset of the population successfully reproduce
    - Some evolutionary forces are random (mutation), but not natural selection (which is also an evolutionary force)
- Natural selection is **NOT progressive** and has **NO objective**
    - it is always behind!
- Natural selection acts on **individuals** but not a group of individuals
    - natural selection **does not** act for the good of the species
        - each individual just wants more resource to reproduce and survive

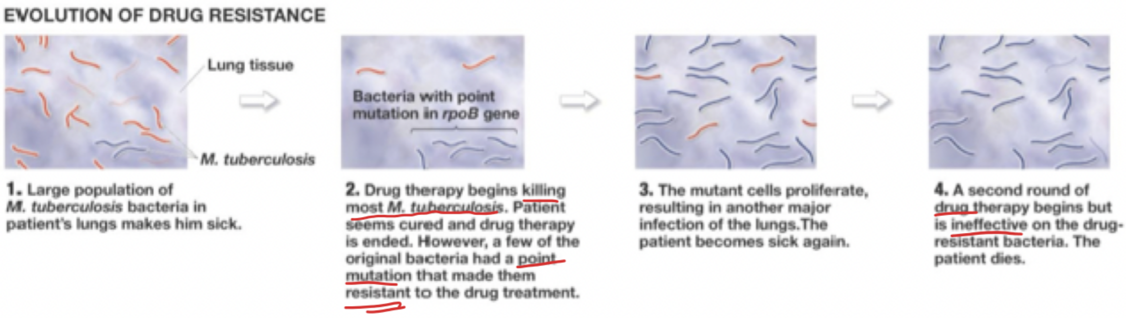
Human Induced Selection Regions in Natural Selection

- By human management policies - might be disadvantageous

- We can impose selective regimes on population with measurable consequences
- Example: Horns sizes of rams at Ram Mountain Alberta

<u>The Evolution of Bacterial Resistance to Antibiotics</u>

- Tuberculosis



Module 4 - Variation and mutation

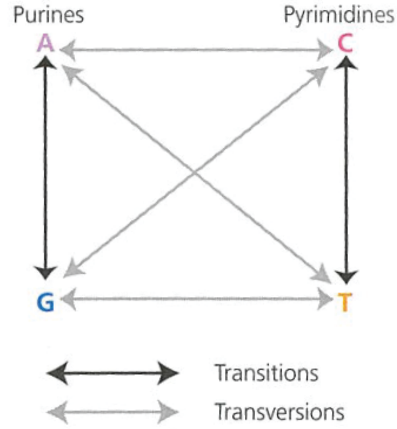
- **Genetic Variation:** individuals can possess different phenotypes as a result of genetic differences (different genotypes)
- **Environmental Variation:** individuals can possess different phenotypes as a result of exposure to different environments, despite identical genotypes
  - Resulted in: **Phenotypic plasticity:** genetically identical individuals can have different phenotypes in different environmental conditions
- **Genotype by Environment Interactions:** interaction of their genotypes with the environment possess different phenotypes
- **Reaction norm:** the pattern or range of phenotypes that the same genotype can possess as a result of different environments

Topic 2: DNA, point mutation, and Indels

- **Premutation** - DNA alterations still susceptible to repair
- **Point mutation** - substitution of one base for another
- **Transition** - substitution of a purine for a purine, pyrimidine for a pyrimidine
- **Transversion** - substitution of a purine for a pyrimidine, or vice versa
- **Synonymous (silent) substitution** - mutation that does not alter the encoded protein
  - Still be non-neutral, due to different supply of tRNAs
    - Most organisms only use one or a couple of codons for a given amino acid - **codon bias**
- **Non-synonymous (replacement) substitution** - mutation that change the amino acid specified by a codon
- **Nonsense mutation** - a mutation that introduces a premature stop codon

Transversion is 2x likely to happen than transitions

- Transition : transversion among DNA sequence > 10:1
  - Transversion is more likely to be detected by proofreading and DNA repair system

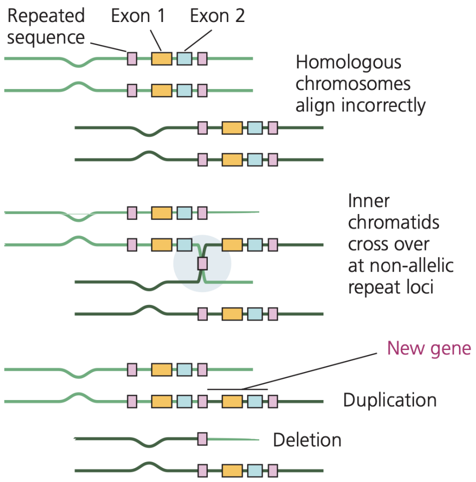


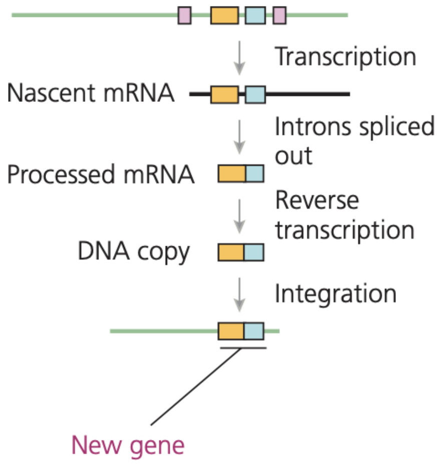
Indel

- <u>Insertion</u> or <u>deletion</u> of one or more nucleotides in a DNA sequence
- Frequently resulted in **frameshift** - often deleterious

Topic 3: New gene formation and chromosome mutation

- **Gene duplication**
    - Result of unequal crossover during meiosis (left)
    - Or as a consequence of **retroduplication** / **retroposition** (right)





- Result in the formation of **multigene families**
    - Eg. Human globin genes or major histocompatibility complex
- **Chromosomal mutations**
    - <u>Inversions</u> - affect gene order and recombination
    - <u>Polyploidization events</u> - duplication of entire genomes
        - Facilitate adaptation and speciation

Topic 4: Mutation Rates and Fitness Effects

- Rate can <u>vary</u> among different organisms and genes
    - Depends on how we measure mutations (generation or year)
        - We usually measure in generations to facilitate meaningful comparisons amongst different organisms
- Vary as a result of the fidelity of polymerase, and the effectiveness of their proofreading and mismatch repair mechanism
    - Mismatch repair works more effectively on regions that are coding and frequently transcribed

        - Varying mutation rate across genome

Point mutations and indels result in new alleles, which have associated fitness effects:

- **Neutral Mutations -** have no effect on fitness
- **Deleterious Mutations -** reduce the fitness of an individual
- **Beneficial Mutations (or advantageous) -** increase the fitness of an individual
- **Lethal Mutations -** deleterious mutations that result in an organism's death before it can reproduce

- Deleterious and lethal mutations are more common than beneficial mutations
- Mutation rate is a heritable trait
    - Mutation in DNA polymerase or gene responsible for mismatch repair can affect the rate
    - Can increase mutation rate by 1000x
- High mutation rates are:
    - Beneficial in a novel environment in which individuals are poorly adapted
    - Deleterious if individuals are well-adapted

Module 5: Population genetics

Topic 1: Measuring Genetic Variation

- **The Classical Hypothesis (wrong wrong)**
    - populations contain very little variation
    - selection maintains a single best allele at any locus
    - heterozygotes are rare
        - as a result of rare deleterious mutations that are quickly eliminated by selection
- **The Balance Hypothesis**
    - individuals are heterozygous at many loci
    - balancing selection maintains lots of genetic variability within populations
- **Balancing selection**
    - any form of selection that results in the maintenance of genetic variation (allelic diversity) in natural populations
- **Population heterozygosity (H)**
    - Heterozygotes / total number of individuals

Measuring genetic variation: <u>protein electrophoresis</u>

- Need to determine individual's genotypes
- Old: **Protein electrophoresis**
    - <u>Amino acid variation</u> - DNA variation with silent mutations
    - 1960-1970 - Revealed substantial genetic variation in all kinds of organisms
        - Strong support for balance hypothesis
        - Variation at DNA level is even greater
- Now: **Direct DNA sequencing**

The high genetic variability resulted in a new debate

- **The selectionist hypothesis**
    - Balancing selection results in the maintenance of high genetic variability (heterozygotes usually have higher fitness)
- **The neutral hypothesis (true true)**
    - Most alleles in natural populations are neutral, and do not affect fitness
- Debate resulted in development of the **neutral theory of molecular evolution**

Calculating **diploid genotype frequencies**

- Genotype frequency = # individuals of genotype in question / N

Calculating **allele frequencies**

- Allele frequency = sum of allele # of genotype in homo and hetero / 2N

Topic 2. The Hardy-Weinberg Principle

- HW principle
  - Bedrock of population genetics
  - How allele and genotype frequencies behave in natural populations if no external forces are acting on them, and the population is waiting randomly
  - Model of random mating in the absence of evolutionary mechanisms
  - Predict genotype frequencies from allele frequencies
    - Serve as starting point / null hypothesis in population genetic studies

Panmictic population

- Randomly mating = each gender has equal probability of mating

Modelling Random Mating

- Assumptions: genotype frequencies are the same among males and females and the population is infinitely large in a panmictic population
- **Random mating** = random union of gametes
- Modeling random mating - probability that two allele unite
  - The probability of A gamete unite with A gamete: p2
  - The probability of A gamete unite with B gamete: pq
  - The probability of B gamete unite with A gamete: pq
  - The probability of B gamete unite with B gamete: q2
- **Expected genotype frequency (HW proportions)** among offspring:

p2+2pq+q2 = 1

HW principle

- Provides a null model to predict genotype frequencies from allele frequencies in the absence of evolutionary forces, and non-random mating
- Important points:
  1. If a population is out of HW equilibrium - takes a single generation of random mating to restore HW equilibrium
  2. If there are no violations of its assumptions, the HW principle shows that genotype and allele frequencies will not change from one generation to the next

Topic 3. Testing hypothesis using the HW principle

1. Start point of natural population investigation
2. Genotype individuals in a population, then estimate allele frequencies from observed genotypes
3. Calculate expected genotype numbers assuming the population is in HW equilibrium
4. If observed genotype numbers are different than those expected, something interesting occured in the population

Chi square of fit test

- HW principle provides a Null Hypothesis, used for test Alternate Hypothesis
- X2 = sum of (obs-exp)^2 / exp
    - Always put numbers not frequencies
- Degree of freedom
    - = number of classes of data (different genotypes, K) - 1 - number of parameters estimated from the data
    - DF = 1, X2 = 3.84
    - 2, 5.99
    - 3, 7.82
    - 4, 9.49
- Calculated X2 < critical X2, do not reject null hypothesis -> in HW equilibrium
- Calculated X2 > critical X2, reject null hypothesis -> out of HW equilibrium

HW disequilibirum

- When genotype frequencies are not equal to the expected pq
- HWd will always result as a consequence of **heterozygote deficit (less than expected)** or **heterozygote excess (more than expected)**
    - **Heterozygosity** = # of heterozygote / total number of individuals
- Both evolutionary and non-evolutionary forces can result in HWd

Topic 4. Selection and HW principle

- Evolutionary forces:
    - Genetic drift, natural selection, migration, mutation
- Evolution: change in population allele frequencies
    - NOT genotype frequencies!!!

- **Fixed (or fixation):** when an evolutionary mechanism results in an allele moving to a frequency of 1, we say that the population has become fixed for that allele, or moved to fixation for that allele.
- **Heterozygote superiority (good):** when (in a two allele system, e.g. 3 possible genotypes), the heterozygote has the highest fitness. Heterozygote superiority is a form of balancing selection.
- **Heterozygote inferiority (bad):** when (in a two allele system, e.g. 3 possible genotypes), the heterozygote has lowest fitness.

The **impact of selection on allele and genotype frequencies** depends on:

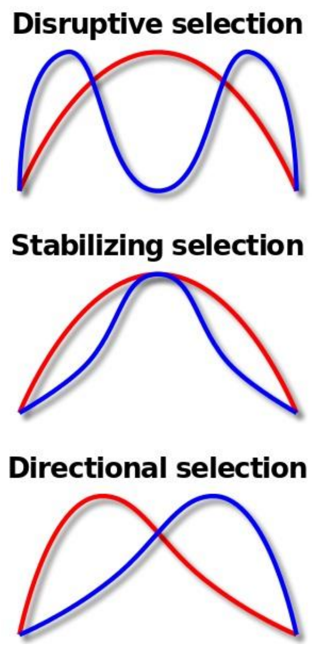
- **Alleles are <u>common or rare</u>**
    - Common: high frequency, <u>dramatic change</u> of allele frequencies in the next generation if selected out
    - Rare: low frequency, <u>similar</u> allele frequencies in the next generation
- **Alleles are <u>dominant or recessive</u>**
    - <u>Deleterious recessive alleles</u> will <u>escape</u> natural selection when hide in <u>heterozygous</u>
        - Reason of deleterious recessive allele persist in population at low frequency
        - Eg. flour beetle - lethal recessive, l hind in heterozygote
            - Selection cannot remove l allele
- **<u>Fitness</u> of different genotype**
    - Fitness of heterozygotes
        - Dominant and recessive alleles: the fitness of heterozygotes is the same as the dominant homo
        - Fitness can be between that of the two homozygotes (codominant)
        - Fitness can be superior or inferior to that of either homozygote
            - Superiority (overdominance) and inferiority (underdominance) can produce interesting outcomes
            - Eg. superiority of drosophila melanogaster
                - One homo is variable and another homo is not
                - In this case, recessive allele at higher frequency

Selection in HW population:

- HW Assume: all individuals survive at equal rates and contribute equally to the next generation
- Selection - individual with a particular phenotype have greater survival and reproduction than other phenotype
    - Phenotype have a genetic basis
- In nature, differences in survival rates are not large enough to make a big impact over a single generation
    - But smaller changes accumulate over generations

1. Selection can change allele frequencies - evolutionary force or mechanism
2. Can also change population genotype frequencies
3. Change genotype and allele frequencies - cause HWd with heterozygote excess or deficit (**cannot** use HW to calculate genotype frequencies, even if the allele frequencies are the same)

Topic 5. Modes of selection on Quantitative traits



- Quantitative trait is a phenotypic characteristic that varies continuously as opposed to directly and involves multiple loci
- **Disruptive selection (2 sides)** - little / no change of the mean, increase the variants of traits
- **Stabilizing selection (middle)** - little / no change of the mean, reduce variants
- **Directional selection (1 side)** - shift population, inc/dec the mean and reduce variants

Eg. Goldenrod Gall - stabilizing selection

- Middle size - avoid parasite and birds

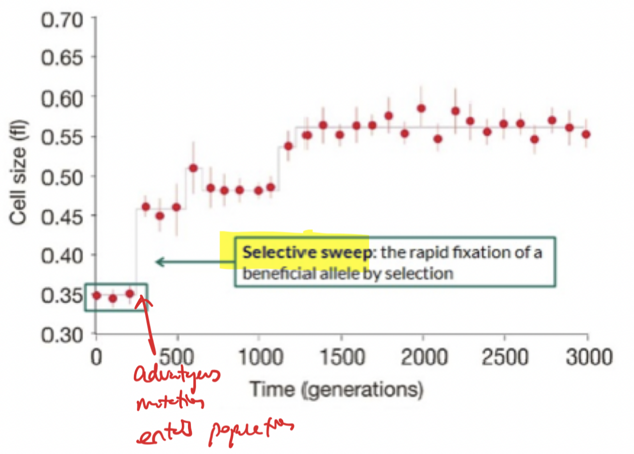
- Directional and stabilizing are common, disruptive is more rare (may be more common than thought)
- Directional and stabilizing reduce phenotypic variation and are common → why do we still see genetic variation?

1. Populations are not in evolutionary equilibrium with respect to directional or stabilizing selection

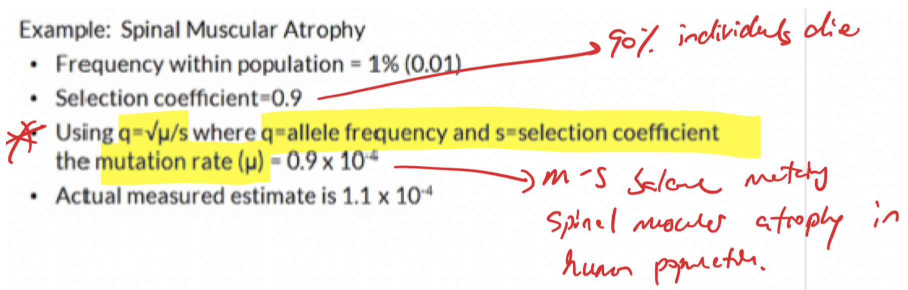
2. In most populations, there is a balance between mutation and selection
3. Disruptive selection may be more common than thought

Topic 6. Mutation and the HW principle

- Mutation: source of all population genetic variation
    - Germline mutations occurred during gametogenesis
- Mutation charges allele frequencies slightly, but does not cause HWd
    - Very stable from generation to generation
        - Only has minor impact over very long period of time or numerous generations
- **Selective sweep**
    - The rapid fixation of a new advantageous mutation by selection



- **Mutation-selection balance**
    - Selection remove deleterious mutations but mutation reintroduce them
    - The equilibrium allele frequency established when the mutation rate of a deleterious allele into a population is equal to the rate of its removal by selection
    - This is another reason why deleterious alleles can persist in populations
    - Eg. spinal muscular atrophy



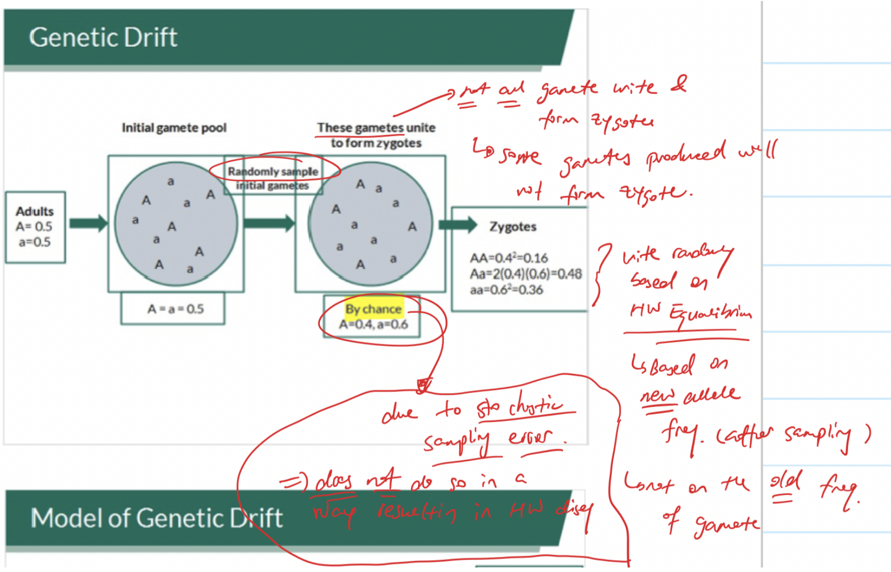
Topic 7. Migration and the HW principle

- **Migration**: movement of alleles into (or among) populations, and is typically referred to as gene flow
- Rate of gene flow among populations will be part dependent on the dispensal capabilities of the organism (bird vs snake)
- Migration can change allele frequencies, result in HWd
    - Evolutionary force that can potentially act against selection, or work with selection and aid the fixation of a beneficial allele
    - Resulted in heterozygote deficit or excesses, or makes them more similar to each other in terms of allele frequencies
    - Not necessarily result in HWd depends on circumstances (eg. A1 migrate into A1 population)
- Migration and Homogenization
    - All populations gradually converge to equilibrium
        - All have the same average allele frequencies
- FST
    - **The fixation index,** the measure of how much populations differ in allele frequencies at a locus, or quantifies genetic variability among populations
    - FST = 0, all population have identical allele frequencies
    - FST = 1, no alleles are shared among populations
    - Migration reduces the value of FST -> make them similar

Topic 8. Genetic drift and HW principle

1. Natural selection is a non-random mechanism of evolution
2. Mutation is a random mechanism
3. Migration can be either random or non-random

- **Genetic drift**
    - Change population allele frequency from one generation to the next in a completely unpredictable and random manner (stochastic mechanism of evolution)
    - Does not result in HWd -> does not change allele frequency
- Generates a random sample of the gametes produced by the previous generation, and drift is the sampling error spread across the generations



Topic 9. The Nature and consequences of genetic drift

- Genetic drift results from <u>sampling error during the gamete phase</u> of an organism's life cycle
    - <u>Very powerful</u> when the population is <u>small</u>
        - Greatly impact on allele frequency from one generation to the next
        - <u>GD overpower natural selection</u>
            - Random fixation of deleterious and advantages alleles
    - <u>Weak</u> & non-existent when population size is <u>large</u>
    - <u>Won't cause HWd</u> because allele frequency will be stable in the next generation
    - Cause allele frequencies to wander over generations:
        1. Alleles drift to fixation (a.f. 1) or loss (a.f. 0)
        2. **Allelic diversity in a population decreases** -> the frequency of heterozygotes decreases over time

- **Genetic drift**: results in divergence of allele frequency of population
    - Increase value of FST
- **Migration**: homogenizes allele frequency of population
    - Decrease value of FST

- **Founder effect**
  - Allelic sampling error that occurs when a group of individuals from a population colonize a new area, and start a new generation
  - The new generation can differ in allele frequencies in comparison to the source population due to sampling error and chance
- **Population bottleneck**
  - A sharp reduction in population size that can alter allele frequency as a result of sampling error
- Both founder effect and population bottleneck can result in HWd
  - Cause heterozygote deficit and excesses
  - One round of random mating -> restore HW equilibrium

The probability of fixation

- Probability of one allele or another to go into fixation
- 约等于allele frequency

Topic 10. Non-random mating

- Indirectly affect evolution, not an evolutionary mechanism (but have important evolutionary consequences in conjunction with selection)
  - Does not change allele frequencies, but change genotype frequencies
    - Creates heterozygote deficit or excess (HWd)
  - Including inbreeding, outbreeding, positive assortative mating, negative assortative mating
- **Inbreeding**
  - mating among closely related individuals and results in deviation from HW equilibrium as a result of heterozygote deficits (HWd)
  - **Self-fertilization** - strongest form of inbreeding
  - **Inbreeding depression**
    - Reduction in the average fitness among individuals within a population due to inbreeding
- **Outbreeding**
  - opposite of inbreeding
  - higher incidence of mating among distantly related individuals than expected in a randomly mating population
  - causes HW disequilibrium with heterozygote **excesses**, but it does not change allele frequencies, and on its own is not a mechanism of evolution.

- **Assortative mating**
    - **Positive assortative mating:** When individuals with similar phenotypes mate, e.g. large individuals only mate with other large individuals
    - **Negative assortative mating:** When individuals with dissimilar phenotypes mate, e,g. small individuals only mate with large individuals at a higher frequency than occurs in a randomly mating panmictic population.
    - Either cause HWd with heterozygote deficits (positive) or excesses (negative), but **only** at those loci involved in the traits (in and out affect all loci)
    - Assortative mating **does not** change allele frequencies on its own
    - Positive assortative mating + **disruptive selection** -> important component in speciation

Topic 11. Population genetics and conservation

1. Genetic drift will be strong, and will reduce heterozygosity by randomly fixing alleles, removing variation and **adaptive potential**.
2. Drift can overpower natural selection, and randomly fix deleterious alleles.
3. The probability of mating among close relatives **increases** in small populations, resulting in inbreeding depression.

- **Genetic rescue**
    - Inc average population fitness as a result of the restoration of genetic diversity
    - Achieved by the deliberate introduction of individuals into a population suffering the ill effects of small population size, from a population with greater level of allelic diversity
- **Linkage corridors**
    - Connect fragmented and isolated habitats
        - Create a single larger habitat -> reduce the negative evolutionary effects by small population size

Module 6 Phylogeny

Topic 1. Introduction to Phylogeny

- **Phylogeny** - is a hypothesis of ancestor-descendant relationships
- **Phylogenetic tree** - is a graphical summary of a phylogeny
- **Phylogenetics** - is the study of ancestor-descendant relationships.
    - The objective of phylogeneticists is to construct phylogenies
        - Provides explanations of the diversity seen in the natural world
        - Based on morphological, physiological, and molecular data
        - Today, usually using DNA sequence data

Topic 2. Important Phylogenetic Terms

- **Monophyletic group / clade**
    - a group that includes all of the descendants of a common ancestor
    - Can have monophyletic groups within a monophyletic group
    - Taxonomists based their classification on monophyletic groups
- **Non-monophyletic Group**
    - **Paraphyletic**
        - A group that includes some, but not all of the descendants of a common ancestor
        - Ex: reptiles are a paraphyletic group of sauropsida
    - **Polyphyletic**
        - Assemblages of taxa that have been erroneously grouped together on the basis of homoplasious characters (eg. vultures)
        - Grouped together but do not share a common ancestor

Topic 3. DNA sequences and distance measurements

Distance measures: Models of DNA Sequence Change

- We must first align our sequences such that homogeneous positions are adjacent to each other
- Then, we estimate # of base pair differences, b/w each pair of sequences

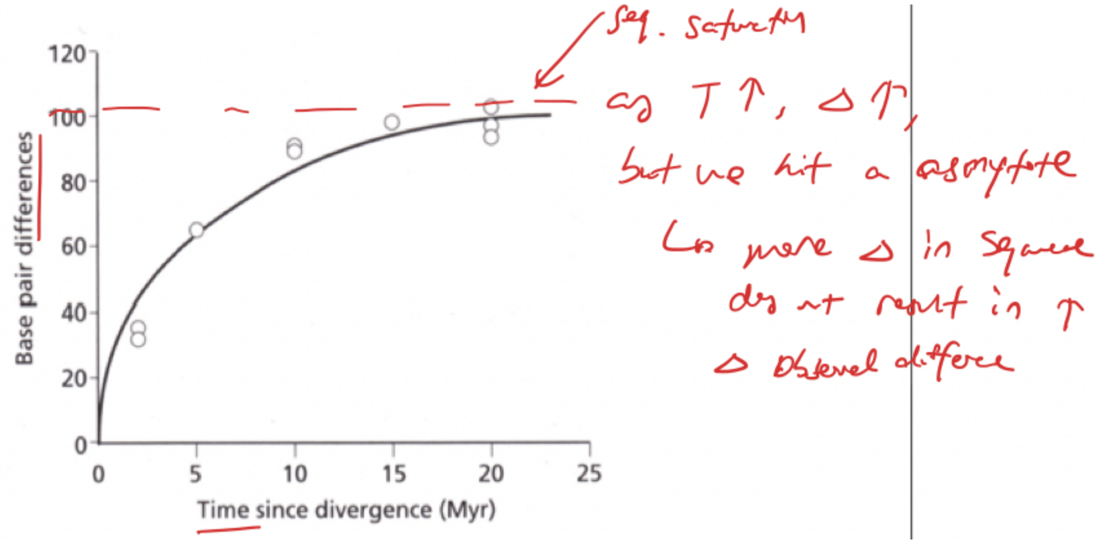
Nucleotide Sequence Divergence (d)

- P-distance / proposition of differences
- Equal to the # of differences over sequence length
    - Often expressed as %
        - d = (numbers of differences / sequence length) *100%
- Does not account for the evolutionary process of sequence divergence

- No consideration on how the difference arose

Multiple Hits & Models of Sequence Change

- Account for multiple substitutions at sequence positions
- Multiple hits and their effects
    - Single substitution → 1 change, 1 difference
    - Multiple substitutions → 2 changes, 1 difference
    - Coincidental substitution → 2 changes, 1 difference
    - Parallel substitution → 2 changes, no difference
    - Convergent substitution → 3 changes, no difference
    - Back substitution / reversal → 2 changes, no difference
- Multiple hits result in **sequence saturation**
    - Sequence saturation occurs when nucleotide changes between two DNA sequences no longer result in an increase of the observed number of nucleotide differences between those sequences
    - As a result, we need to correct for multiple hits



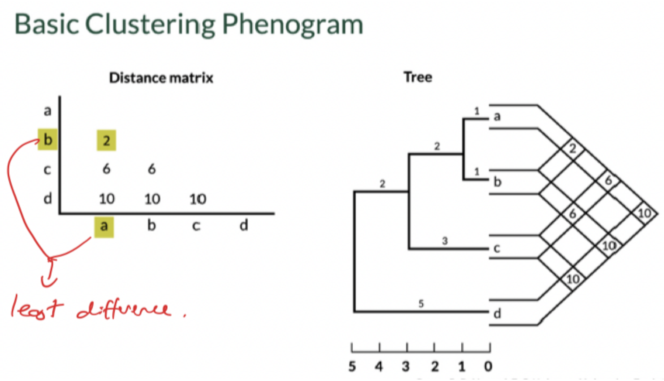
- **Methods to correct multiple hits: Models of sequence evolution**
    - The simplest: **Jukes and Cantor Model (JC Model)**
        - d = 3/4ln(1-4/3p)
            - p = observed proportion of differences between two sequences (eg. the p-distance)
        - Assumptions:
            - 1). Nucleotide frequencies are equal. Eg. A=G=C=T
            - 2). The probability of substitution between all nucleotides is equal. Eg. frequency of transitions = transversions

- 3). Rates of change at all positions are equal. Eg. third position codon changes at the same rate as first and second
- This model is not very realistic but is appropriate when the number of differences between sequences is small (proportion of differences < 4%)
  - very bad for more distant taxa
  - reason: assumptions are not always correct (ex: transition is more likely to happen than transversion)
    - as a result, transition reaches saturation quicker due to its more common occurrence

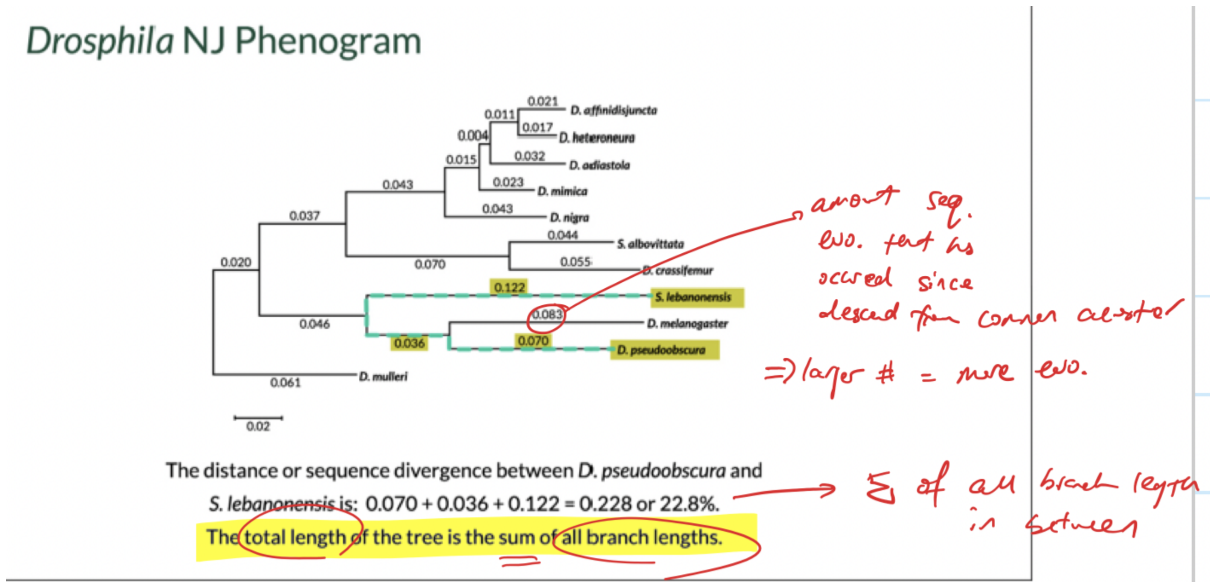
- **Kimura's two parameter model (K2P)**
  - d = 1/2ln[1/1-2p-Q]+1/4ln[1/(1-2Q)]
    - p is observed proportion of transitional differences
    - Q is the observed proportion of transversional differences
  - account for the more commonplace of transitional differences
    - other assumptions are the same as JC model
- **The General Time Reversible Model (GTR)**
  - Contains 6 rate categories
    - Ex: G <-> T; C <-> T etc. → each forward rate is the same as reverse
  - More complex but more realistic
  - Useful when the difference is substantial (ie: p-distance > 0.04)

Topic 4. Phylogenetics I

- **Clustering methods**
  - The simplest way of constructing phylogenies using DNA sequences
  - First, use a model of sequence evolution to estimate the distances between all of the taxa or species that we are studying
    - Utilize a matrix of pairwise distances or similarity values between all possible things (ex: pairs of taxa, sequence, population, etc.)
    - Use the matrix in conjunction with a clustering algorithm to produce a **bifurcating tree (aka. a phenogram)**

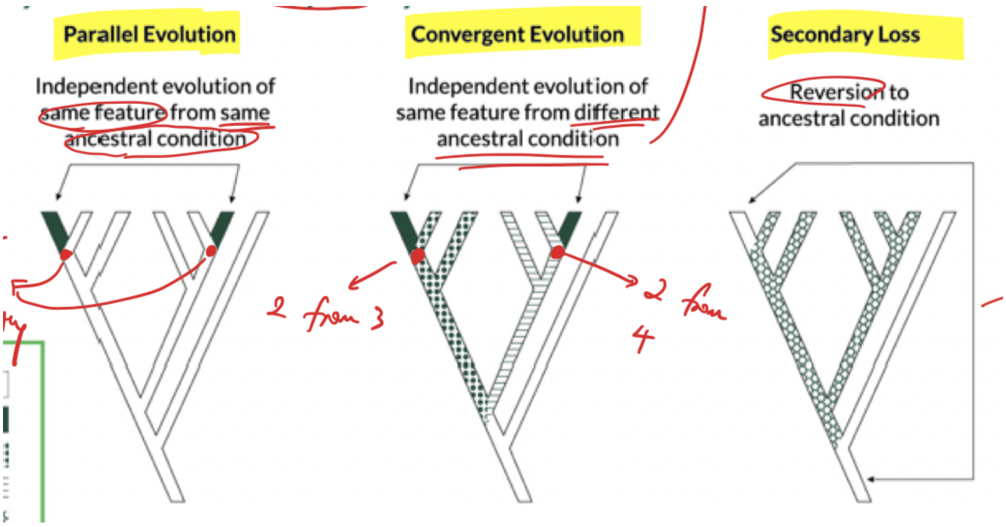


- **Neighbouring-Joining (NJ)**
    - most common clustering algorithm
        - Advantage: Fast and easy
        - Disadvantage: produce a single tree only (out of many possible trees)
            - offer no evaluation of other possible trees
    - works by minimizing the total length of the tree (or the sum of all branch lengths)
    - **Distance matrix** can consist of sequence distances estimated (produced by the model of sequence evolution)
    - Distance / Sequence Divergence
        - sum of all branch lengths in between



Topic 5. Phylogenetic Characters, Homology, and Homoplasy

- **Phylogenetic Characters**
    - **Character**
        - Any attribute of an organism that can provide us with insights into the history or shared ancestry
    - In molecular phylogenies:
        - Characters = nucleotide positions in a gene sequence
        - Each position can possess four character states: ACTG
- **Homology / Synapomorphy**
    - A character state that is shared between two DNA sequences or taxa may be so because they inherited it from a common ancestor
- **Homoplasy**
    - Have shared character because they evolved independently
        - Enemy of phylogenetic reconstruction → result in polyphyletic group
    - Occur because
        - **Parallel evolution**
            - Independent evolution of the same feature from the same ancestral conditions (eg. Stickle Back Fish)
        - **Convergent evolution**
            - Independent evolution of the same feature from different ancestral conditions (eg. vulture → a polyphyletic group)
        - **Secondary loss**
            - Reversion to the ancestral condition
    - Multiple hits are the principle source of homoplasy
        - When sequence researches saturation, more homoplasy will be resulted due to multiple hits



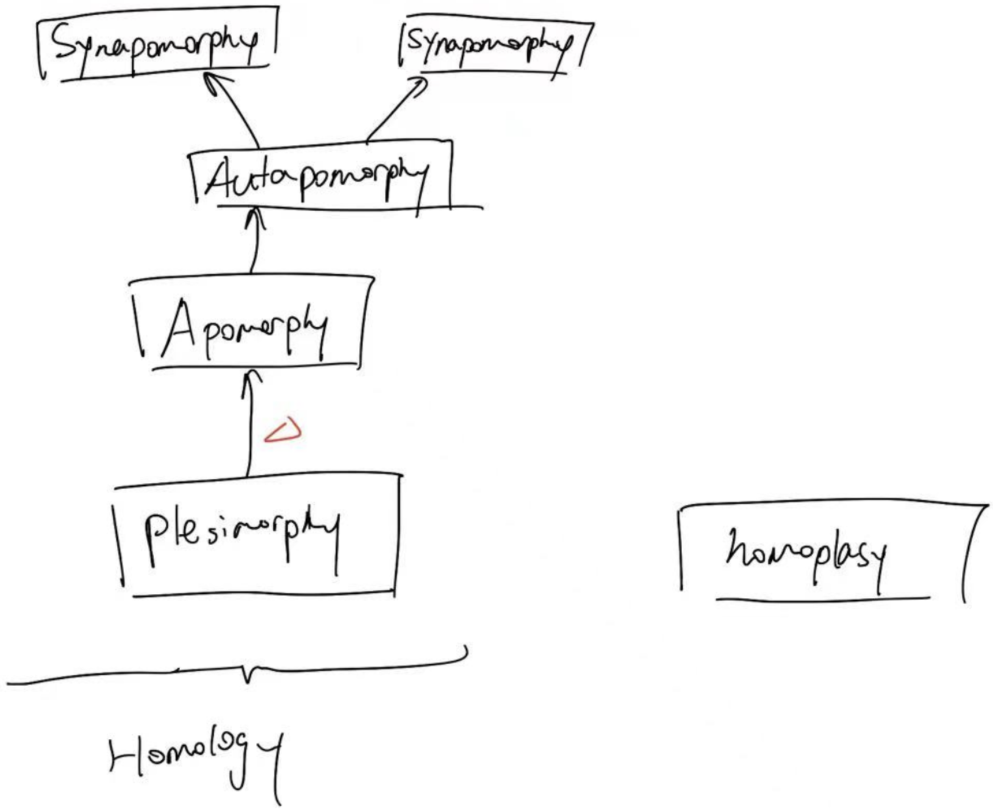
- **Analogy (non-homology)**
    - Similar function but due to different evolution
        - Ex: sharks and whales' fins

Topic 6 Phylogenetic Methods II

- **Optimality Criteria**
    - Sophisticated methods of phylogenetic reconstruction
    - two types:
        - **Frequency probability methods** (maximum likelihood and Bayesian methods)
        - **Parsimony** (also called cladistics)
- **Plesiomorphy:** refers to the ancestral character state
- **Apomorphy / derived state:** a character state different from the ancestral state
    - **Synapomorphy**: a derived character state (apomorphy) that is **shared** by two or more taxa due to inheritance from a common ancestor
        - these character states are *phylogenetically informative using the parsimony or cladistic criterion*
        - Construct monophyletic groups by using synapomorphies (and by avoiding homoplasies)
    - **Autapomorphy:** a uniquely derived character state.
- All synapomorphies are homologies, but not all homologies are synapomorphies
    - Homology can be the result of both plesiomorphy and synapomorphy
- Synapomorphies evolve from autapomorphies
    - Synapomorphies are autapomorphies shared by more than one taxa
- **Parsimony / Cladistics**

- **The Principle of Parsimony**
    - Simple explanations are preferred to more complicated explanations
        - Fewer evolutionary steps are better than more evolutionary steps
        - Construct the tree with the least number of evolutionary steps
- Constructing Trees
    - **Ingroup**
        - the group of organisms for which we wish to develop an understanding of relationships
    - **Outgroup**
        - a taxon or an organism which is NOT part of the ingroup but also NOT too distantly related to our ingroup organisms
        - used to polarize or infer the direction of character change.
            - The character state possessed by the outgroup is defined as being **ancestral or plesiomorphic a priori.**
    - Most serious mistake: use an outgroup that is actually a part of the ingroup
        - Result in really erroneous phylogenetic relationships
- Steps to construct a tree
    - 1. Consider all possible ways to arrange the ingroup
    - 2. Evaluate each synapomorphy using principle of parsimony
        - Evaluate the # of steps required to produce the change
    - 3. Repeat for all hypothesis → find the one with the fewest number of total steps
- As number of taxa increases, number of trees

- Determine homology vs. homoplasy
    - Cannot tell the differences between those two by just looking at one character
    - Solution: we use a large number of characters


Synapomorphy
Synapomorphy
Autapomorphy
Apomorphy
plesiomorphy
homoplasy
Homology

Module 7 Adaptation

Topic 1 Studying Adaptation

- Adaptation
    - a trait that increases the fitness of an individual in comparison to individuals that don't possess the trait
- In order to demonstrate that a trait is adaptive, we require evidence
    - gathering that evidence can be challenging. It requires us to carefully develop and test hypotheses
- Hypothesis testing lies at the core of evolutionary biology, and science in general.
    - All hypotheses must be tested.
    - While untested hypotheses may be interesting and intriguing, they do not constitute evidence.
- Sometimes the adaptive value of a trait might seem readily apparent, but until the hypothesis of adaptive value is tested and confirmed, it is not supported by evidence.

Topic 2 The approaches to studying adaptation

- Keep in mind:
    1. Differences among populations are not always adaptations
        a. Eg. neutral differences fixed by genetic drift
    2. Not every trait is adaptive
        a. Eg. vestigial structure
    3. Not every adaptation is perfect
        a. Eg. antagonistic selection
- Methods to study adaptation
    - **Experimental studies**
        - Mores powerful
        - Carefully control conditions so we can investigate a single effect and learn about what potentially could cause it
    - **Observational studies**
        - When experimental studies are not possible
        - Lead us into very important insights
    - **Comparative studies**
        - Require an understanding of phylogeny among the organisms being considered

- Correlation and causation

- Correlation does not imply causation
- Yet, the existence of a correlation can be used to test the hypothesis, given that we have made a prediction prior

Topic 3 Phenotypic Plasticity and Adaptation

- Phenotypes arise as a consequence of genotypes and their interactions with the environment
- **Phenotypic plasticity**
    - Identical genotypes can result in different phenotypes in different environments
    - Some studies suggested that the plasticity itself is an adaptive trait

Topic 4 What can hinder adaptation

- Natural selection is the primary agent of adaptive evolution, with mutation providing the raw material for it to act on

- Two evolutionary mechanisms both either help or hinder natural selection in the adaptive process:
    - **Genetic drift** (and other types of sampling error such as population bottlenecks)
        - When population size is small, genetic drift can be powerful and fix deleterious alleles that selection is acting to remove.
        - Genetic drift is entirely random and unpredictable, and could also potentially work alongside selection and aid the fixation of a beneficial allele.
    - **Migration**
        - Eg. migration hindering selection with Lake Erie water snakes
- Two additional factors that can hinder adaptation
    - **Trade-off**
        - a compromise between one trait and another, which cannot be avoided
    - **Constraint**
        - a factor that tends to retard the rate of adaptive evolution, or prevent a population from optimizing a trait
        - 3 types
            - **Functional / Developmental constraint**

- Ex: Fuchsia exoticate
- **Genetic constraint**
    - Ex: the beetle venus Ophraella
- **Ecological constraints**
    - Ex: Body and feather lice in doves

Module 8 Evolution and Sexual Reproduction

Topic 1: Asexual Reproduction and the Two-Fold Cost of Sex

Sexual reproduction comes with enormous costs and risks

- Asexual reproduction produces a huge numerical advantage
- Also, many organisms (including some vertebrates) are capable of asexual reproduction
    - Ex: eukaryotes such as volvox and hydra
- Big Q: is sexual reproduction associated with an increased fitness among offspring?

Parthenogenesis - virgin birth (no male contribution) (ex: aphids)

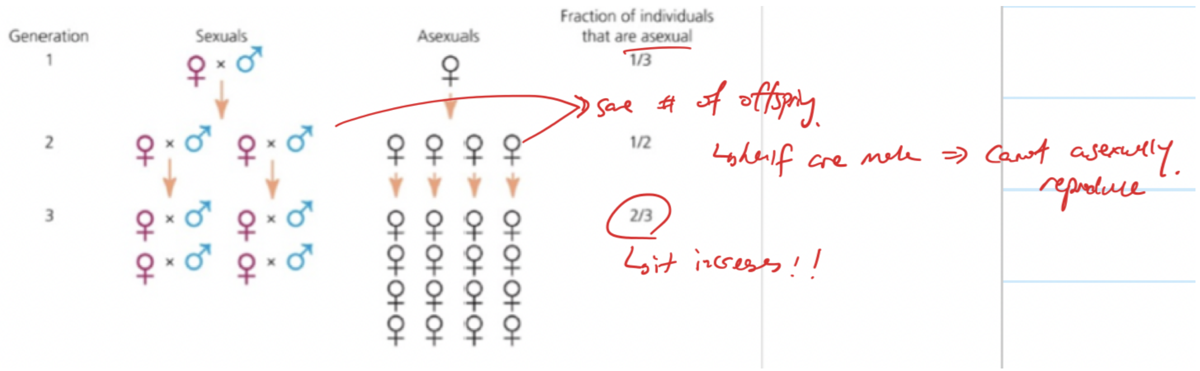
- **Obligate Parthenogenesis**
    - Entire species consists of females only, which reproduce by making identical clones of themselves
- **Cyclical Parthenogenesis**
    - Populations consist of females that reproduce clonally throughout most of the year, but at certain times males are produced, and sexual reproduction occurs
        - Usually, males are produced upon environmental cues (such as harsh conditions)

Hermaphrodite (Hermaphrodism, Androgyne)

- Organisms that have both male and female sex organs (gonads), and are capable of self-fertilization
    - Still a form of sexual reproduction b/c gametes are still formed via meiosis
- Offspring of hermaphrodites are genetically less diverse than the offspring of individuals that outcross

Why does sex exist?

- Null model by Maynard Smith, with two assumptions
    - A female's reproductive mode does not affect the number of offspring she can make
    - A female's reproductive mode does not affect the probability that her offspring will survive
- Parthenogenetic females produce only females; sexual females produce a mixture of males and females in equal ratio
- Result: a **two-fold cost** of sexual reproduction
    - There must be benefits to sex, given that asexual females can reproduce at a much greater rate



- In practise
    - Male provide parental care → affect number of offspring
        - Eg wolves and many birds
    - Do descendants produced by sexual reproduction have higher fitness?
        - Might affect the probability that the offspring will survive

What does sex boil down to?

- Mating between different individuals results in new combinations of genes in the offspring
- Recombination and crossing over in the process of meiosis during gametogenesis → new genetic variant

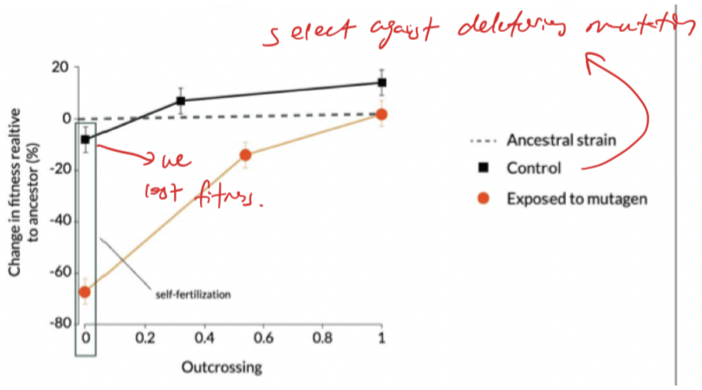
Together → genetically diverse offspring and allow the purging (removal) of deleterious mutations

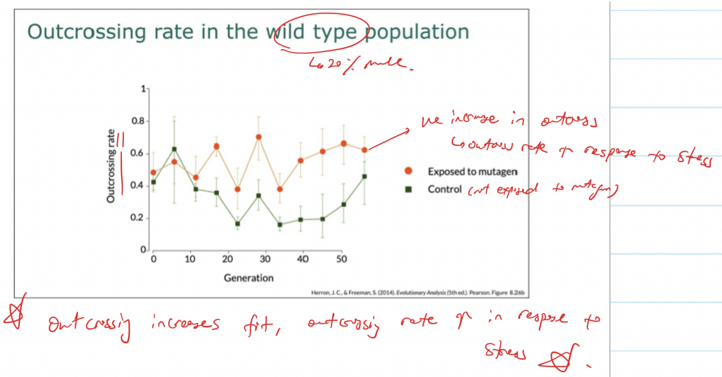
Topic 2 The effect of sex

Model Organism for Evolutionary Biology: **Caenorhabditis elegans → experimental**

- It is about 1 millimetre long, very easy to culture, has fast generation times (about 3 days), and its genome is well characterized
- The first multicellular organism → entire genome sequenced
- Can be easily genetically altered to produce strains with very useful experimental properties
- The "normal" or wild type strain is **hermaphroditic**, consisting of self-fertilizing hermaphrodites, as well as males, the latter of which can constitute as high as about 20% of the population
    - The hermaphrodites (both male and female gonads) predominantly reproduce by self-fertilization, but can also outcross with males
- The hermaphrodites do not outcross with other hermaphrodites
- Self-fertilization is still a form of sexual reproduction → chromosomal crossing over and recombination occur during gametogenesis

- Offspring of self-fertilization are genetically less diverse than normal sexual reproduction involving outcrossing
    - Loss of diversity resulting from mating between different individuals.
- Wild type can be genetically altered to create additional strain
    - allow us to explore the fitness effects of outcrossing in the offspring
    - Introduce a mutagen to introduce deleterious mutations in the genome
- **Experiment Results**
    - Outcross can maintain / increase fitness → can be beneficial in stressful environment
    - Outcrossing rate in wild type increases as a response to stress





Muller's ratchet

- The process by which obligately asexual species are doomed to accumulate deleterious mutations

Genetic load

- Defined as the reduction in average population fitness resulting from the total number of deleterious mutations in a population

Topic 3 Recombination

Mendel's Laws

- First Law: Random segregation
    - Alleles at a single locus segregate randomly
    - Offspring have 50% chance of inheriting each of a parent's alleles
        - Basis of hardy-weinberg principle
- Second Law: Independent segregation
    - Alleles at different loci segregate independently
        - Inheritance of alleles at locus A is independent of the inheritance of locus B
        - A is randomly associated with B
- Violate Mendel's second Law = Linkage Disequilibrium

Linkage disequilibrium / Gametic Disequilibrium

- constitutes a violation of Mendel's second law.
- Non-random associations between alleles at different loci.
- arise when different loci are situated close together on the same chromosome
    - inherited as a single unit, not segregating independently
- This will result in less genetic diversity in offspring.
- can also be caused by selection, migration and genetic drift.
- **recombination** (during meiosis) breaks up linked genes, and breaks down linkage disequilibrium

Crossing over and recombination during gametogenesis have two important effects:

- It breaks down linkage disequilibrium
- It increases genetic diversity in offspring by creating new combinations of alleles

The effect of recombination on gene combination

- Sexual recombination creates new combinations of alleles and destroys existing combinations
- Always have at least some of the favourable genotypes → for natural selection to act on
- Sex creates new gene combinations that **may be** more fit than previously existing ones

Topic 4 Sex, Evolutionary Arms Race, and Red Queen Hypothesis

Coevolution

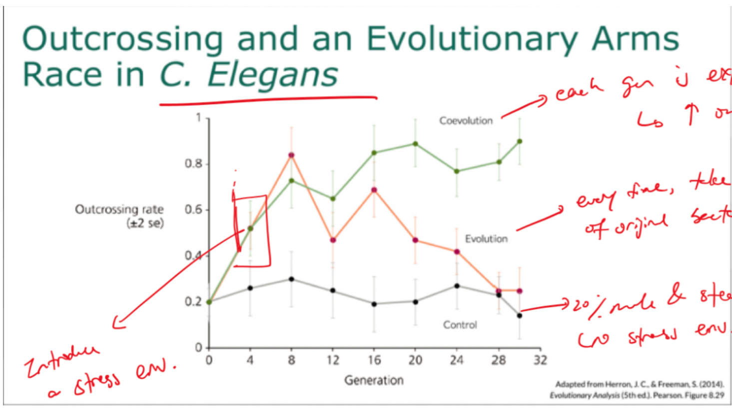
- 2 or more species evolve in response to each other
    - Ex: host/parasite and predator/prey

Evolutionary Arms Race

- Both must continuously evolve better → competing with the other

Red Queen Hypothesis

- An evolutionary advance by the pathogen results in an evolutionary advance in its host, and vice versa
- Each species must continually evolve in a perpetual arms race to keep up with the other
- Sex is adaptive in such circumstances because it provides new and/or different allelic combinations across loci
    - In a new stress condition
        - Coevolution has an increasing outcrossing rate as the environment is constantly changing → locked in the arms race
        - Evolution has an increasing then decreasing outcrossing rate as it finds the most optimal condition
        - Control has a constant outcrossing rate as there is no stress



Module 9 Sexual Selection

Topic 1 Introduction to Sexual Selection

- The measure of fitness - reproductive success (contribute to the next generation)
    - Survival or mortality selection
    - Mating success or sexual selection
    - Family size or fecundity selection
- Eg. Peacock
    - Male peacock are more beautiful
        - More obvious for predators
        - Does not contribute to survival, and if it does, why doesn't peahen have it? → Can't be explained by viability selection
- **Sexual Dimorphism**
    - <u>Phenotypic differences</u> between males and females
    - Can't be explained by viability selection
        - If a trait results in increased probability of survival, why wouldn't both sexes possess it?
- **Sexual Selection**
    - Differential reproductive success resulting from <u>different abilities to procure a mate</u> → Darvin's greatest contribution to evolutionary biology
    - **Parental investment**
        - Refers to the energy, time and resources devoted to mating, gestating, and caring for offspring
        - Typically much greater for females → eggs are expensive, sperm are cheap
            - Daily female egg production requires 3X the energy needed for daily basal metabolism
            - Daily male sperm production requires 4/1000 of the energy needed for daily basal metabolism
    - **Asymmetric limits** on **reproductive potential**
        - Usually (not always) female make greater parental investment → reproductive success is limited by number of eggs they produce and rear
            - 90% of mammals, males provide no parental care
        - Reproductive success in males is potentially enormous as they can essentially produce an infinite quantity of sperm

- Male reproductive success is limited by the number of mates that they can obtain due to their higher reproductive potential

Topic 2. Asymmetric Limits on reproductive success

- When one parent (usually female) has a higher cost of investment in offspring
  - Contribution to the next generation will be limited by energy
- The parent (usually male) with the lower cost of investment in offspring
  - Contribution to the next generation will be limited by the number of mates
- EX: **Pipefish**
  - Reversed → female can produce eggs at a faster rate than male can rear
    - Female's reproductive success is proportional to the number of mates more than male
- Asymmetry in reproductive potential predicts that differences in mating behaviour will exist between two sexes
  - Males: usually be **competitive** (combat, sperm competition, infanticide)
    - **strong** sexual selection
  - Females: usually be **selective**, or choosy
    - **weak** sexual selection
- **Intrasexual selection**
  - interactions between members of the same sex
    - Ex: males fight for females
- **Intersexual selection**
  - interactions between members of opposite sexes
    - Ex: males grow feathers to attract females

Topic 3. Sexual selection on males - male-male competition

- In many species, armour and weaponry only occur on males
  - **Direct combat** is a common form of male-male competition for mates
    - Favours the evolution of weaponry and large body size in males
  - EX: Iguanas
    - Average body size is above the point where survival is optimal (where males can maintain body sizes for 2 different years)
    - Antagonist selection → viability vs. sexual
- Other type of male-male competition:
  - Sperm competition
    - When >= 2 males fertilize the same egg

- **Infanticide**
    - In order to replace the original sexual partner
    - EX: Infanticide is responsible for 10% of mortality among lions
    - EX: Gelada Baboons
        - **Bruce Effect** → pregnancy termination in the presence of unfamiliar males

Topic 4. Sexual selection on Males - Female Choice

- Males are not able to control females themselves (eg. gelada baboons), or resources and habitats required by females
- Males will advertise for mates, and females will choose a male based on the quality of advertisement
    - Result: evolution of elaborate calling, singing and courtship displays, embellished morphological feature and extravagant colouration (peacock)
- **Evolution of female preference**
    - Explanation #1: female preference can be arbitrary
        - **Run-away selection**
            - When correlated responses carry further and further away from equilibrium line → evolution of trait that is very maladaptive with respect to viability
                - Move away from optimal line from viability
    - Explanation #2: responding to males as a result of a pre-existing sensory bias
        - makes them susceptible to certain sensations that mimic cues in their environment
        - Ex: water mite Neumania papillator
    - Explanation #3: preference may result in acquisition of resources
        - In some species, males provide food, parental care, protection and other benefits that help female and her offspring
        - Female can distinguish males that provide high-quality resources from those don't, will garner a fitness benefit
            - **Nuptial Gift**
                - a nutritional gift given by one partner in some animal's sexual practices → to improve the reproductive fitness of the donor
            - Ex: Widow spider
                - Eat male as a gift → **sexual cannibalism**

- Ex: The Hanging Fly
    - 吃饭骗炮
- Explanation #4: by being picky and choosing only the highest quality males, females may get better genes for their offspring
    - Ex: grey tree frogs

Topic 5 Sexual Selection on females

- **Polygyny**
    - Males frequently mate with more than one female
- **Polyandry**
    - Females can mate with more than one males
    - Widespread in nature
- Selection on Female
    - Male is picky and choosy

Topic 6 Sexual Selection and Sexual Dimorphism in Humans

- Difficult to address since methods described in the module cannot be used on humans
- Yet, attempts have been made using proxy data

Module 10 Introduction to Kin Selection

Topic 1. Introduction to Behavior and Hamilton's Rule

- **Actor**
  - An individual carrying out an action / behaviour
- **Recipient**
  - An individual on the receiving end of the behaviour
- **Mutually Beneficial (双赢)**
  - A behaviour resulting in fitness benefits for: both the actor and recipient
- **Selfish (损人利己)**
  - A behaviour resulting in a fitness benefit for the actor, but a fitness reduction for the recipient
- **Spite (傻子)**
  - A behaviour resulting in fitness reductions for both the actor and the recipient
- **Altruistic (活菩萨)**
  - A behaviour resulting in a fitness benefit for the recipient, but a fitness reduction for the actor
  - Paradox of Darwinism → how can the altruistic alleles spread?
    - Increase survival and fitness of an actor's close relatives even if there is decreased fitness for the actor carrying out the behaviour
  - Direct fitness + indirect fitness = inclusive fitness (total fitness)
    - **Direct fitness**
      - An individual's direct contribution to the next generation by reproduction (# of offspring contributed)
    - **Indirect fitness**
      - Arises from additional reproduction by relatives that results from an actor's actions (eg. assistance)
        - It is additional reproduction that would NOT have been achieved without assistance provided by the actor
    - The selection for and spread of alleles that increase indirect fitness is **Kin Selection**
  - **Coefficient of Relatedness (r)**
    - Half-siblings = ¼; full siblings = ½; cousins: ⅛
    - Probability of each individual receiving same half of the genome
      - **Identical by descent (IBD)**

    - **Hamilton's Rule**

- An allele for altruistic behaviour will spread if
  - **(B x r) - C > 0**
    - B = benefit to the recipient (# of surviving offsprings)
    - C = cost to the actor (# of surviving offsprings)
    - r = coefficient of relatedness
- Altruistic allele is more likely to spread if behaviour is amongst relatives with higher r

Topic 2 Hamilton's Rule in Action

- Ex: Prairie dogs and squirrels
- Ex: White-Fronted Bee-Eaters
  - Many will stay and help at nest during what should really be their own first breeding season → location for nesting is in short supply
    - Help those with high r
  - Die within 6 months starvation
- Ex: Wood Mouse Altruistic Sperm
  - Sperms form a hock to connect with each other and form a train → reduces enzyme usage and swim faster
  - Break up before meeting the egg
    - Sacrifice a lot of sperms in the process, yet increase the chance for those who are not sacrificed (with r = 0.5)
- Hamilton's rule also shows that the adaptive value of spiteful behaviour
  - Cost to actor is low
  - Damage to recipient is high
  - r is low

Module 11 Species Concepts and Speciation

Topic 1 Species Concepts

- Definition of species is contentious → due to the extraordinary biodiversity and problems with the establishment of practical criteria for recognizing evolutionary independence
    - 3 major definitions
- **Typological or morphological species concept**
    - **Type specimen**
        - A single individual (usually) that represents the entire species
    - Individuals are considered to belong to the same species <u>if they look like or morphologically agree with the "Type" of the species</u>
        - However, many species show a continuum of <u>morphological variation</u>
    - Still used today → there is an attempt to select defining characters that have a <u>genetic basis</u>
    - There are clearly written rules for naming and renaming taxa (Botanical code, Zoological code, etc.)
    - Problems
        - **Cryptic species:** species that cannot be distinguished on the basis of their morphological characteristics
            - look pretty much identical but genetically different
        - **Phenotypic Plasticity**: morphological variation that does not have a genetic basis → <u>Environmentally-induced morphological differences</u>
    - Yet, a lot species that are recognized today is based on the morphological method
- **Biological Species Concept**
    - Species are groups of interbreeding natural populations that are reproductively isolated from other such groups
        - Individuals within a species resemble each other due to gene flow, resulting from <u>interbreeding</u>
    - Evolutionary criteria is **reproductive isolation** and **interbreeding**
    - Legal definition used in US Endangered Species
    - Problems
        - Asexual Taxa and Fossil Taxa
        - Hybridization
        - Can sometimes be impractical for **reproductive compatibility trials**

- **Hybridization**
    - Intrahybridization → hybridize b/w different lineages within the same species
    - Interhybridizaiton → Hybridize between 2 different species
        - EX: Grizzy + Polar Bears
        - EX: Lake Trout + Speckled Trout
- **Phylogenetic Species Concept**
    - Species consists of a population or group of populations that share a <u>common evolutionary history</u> over the course of time
    - **Species are monophyletic groups**: taxa that contain all of the known descendants of a single common ancestor
    - Populations must have been <u>evolutionarily independent</u> long enough for diagnostic traits to appear
    - Problems
        - Species might have been separated long before they can be recognized as monophyletic groups → underestimate the biodiversity
        - Species often show geographical clusters → phylogenetic groups within a species that occupied different geographical locations
            - Might over-splitting the taxes into species

Topic 2. Applying Species Concept

- EX: marine phytoplankton and skates
- EX: Cryptic species: *Hyalella azteca*
    - 7 species monophyletic groups in total
        - Under estimate species diversity → requires experiment to test reproductive isolation

Biological vs. Phylogenetic

- Means to test the hypothesis
- **Biological Species Concept**
    - Commonly applied to natural populations but is <u>difficult test</u>
    - Cannot be applied to species that <u>hybridize freely</u> or <u>reproduce asexually</u>
    - Cannot be applied to <u>extinct species</u>
- **Phylogenetic Species Concept**
    - Can be applied to both living and extinct species
    - Is applicable to species that reproduce asexually or sexually

        - Based on evolutionary independence, can be applied without direct observation of species

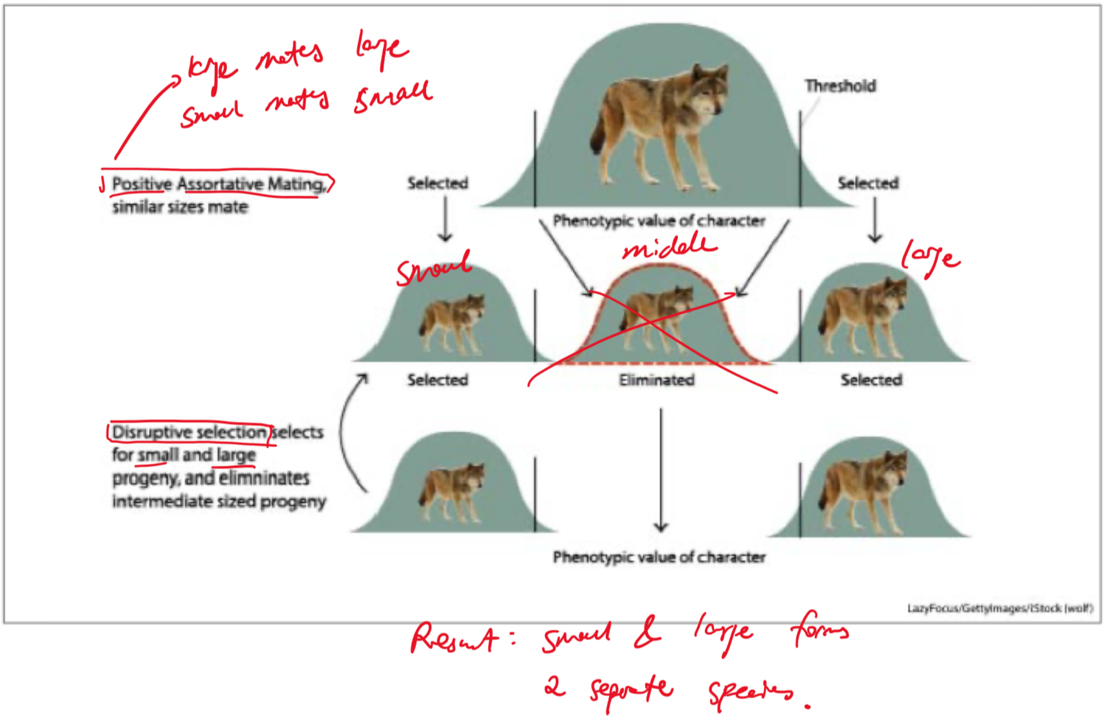
- About 2 million known species
- Most are identified by morphological species concept
- Estimate from 1 to 10 billion or greater
- We only recognized a fraction of the species that inhabit the planet

Topic 3. Isolating Mechanism

- **Allopatric divergence and speciation**
    - Most common isolating mechanism
    - The process of speciation frequently begins with the physical isolation of populations → cessation of gene flow between them
    - **Allopatric**: physical separation of populations; can result from two process:
        - **Dispersal**
            - A few members of a species move to a new geographical area
        - **Vicariance**
            - when a natural situation (such as formation of river or valley) physically divide organisms
- Other isolating mechanisms
    - **Polyploidization events** & **other chromosomal changes**
        - common in plants
    - **Temporal isolation**
        - become isolated in time

Topic 4. The Process of Divergence

- Once the populations become allopatrically isolated…
    - Mutation, genetic drift, and selection (the most important when in concert with mutation) drives divergence allopatrically isolated populations
- **Sympatric speciation**
    - Sympatric → in the same place
    - Divergence and speciation that occurs in the **absence of physical isolating barriers** (no barrier for gene flow → once thought impossible)
    - Involves positive assortative mating and disruptive selection



- Ex. hawthorn and apple maggot fly
    - **Incipient species** between apple and hawthorn
        - two populations that have nearly completed the process of becoming separate species, on the basis of the biological species concept.
    - Hybrids have lower fitness → disruptive selection;
      same type of flies mate → positive assortative mating
    - Result: sympatric speciation
        - Usually begins with **resource polymorphism**
            - Utilization of different foods or hosts among the nascent (new) lineage
- Allopatric divergence and speciation are far more common than sympatric speciation.
    - Once populations are physically isolated…
        - selection can drive divergence in response to different habitats and environments (eg. yellow monkeyflower)
        - sexual selection and mating preferences can also drive divergence (eg. Hawaiian crickets)
        - Environmental and mating preferences can also act in concert
        - Speciation by sensory drive (eg. cichlid fishes)

- **Secondary Contact**

        - Lineages that have diverged allopatrically come back into contact
        - Result depends on whether they can mate and form offspring, and the fitness of those offspring
    - **Reproductive Isolation**
        - **Premating** (Prezygotic) - prevent zygote forming
            - Ecological isolation
            - Behavioural isolation - different mating behaviour
            - Mechanical isolation - sex organs not compatible
        - **Postmating** (Posyzygotic) - zygote forms but it dies or is sterile
            - Zygotic, embryonic or larval mortality (low viability)
            - Hybrid inviability
            - Hybrid sterility (can't reproduce offspring: 骡子)
        - **Hybridization**
            - Can occur when recently diverged species come back into contact
        - **Hybrid zones**
            - Geographic contact zone where interbreeding occurs and the frequency of hybrids can be high

Three major generalized outcomes of hybridization

1. Hybrids have <u>lower fitness</u> than parental lineages
    a. **reinforcement and character displacement**, and a short-lived hybrid zone
        i. <u>Reinforcement</u>: involves assortative mating → evolution of isolating mechanisms that prevent hybridization
        ii. <u>Character displacement</u>: involves disruptive selection → increases differences between the two parental lineages
        iii. EX: hybrid inferiority by mice (Mus musculus) → eventually back crosses to non-hybrid
2. Hybrids have <u>equal fitness</u> to parental species
    a. **introgressive hybridization**: two lineages will interbreed and merge back into a single lineage
    b. EX: black duck and mallard duck → FST decreased between two species → genetically similar
3. Hybrids have <u>higher fitness</u> than the parental lineages
    a. The hybrids can displace both parental species, or possibly form a new species
    b. EX: hybrid superiority → lobster (Orconectes rusticus/propinquus)

- New Species by Hybridization
    - **Polyploid hybrid speciation**
        - Whole genome duplications impose post-zygotic barriers
    - **Homoploid hybrid speciation**
        - Hybrid forward with no whole genome duplication and no increase in ploidy
- Factors that drive diversification
    - **External** (ecological/environmental) factors
        - Ex. lizard → island size may determine speciation rate and how they change over time
    - **Endogenous** factors (intrinsic properties of organisms themselves)
        - Lineage-specific phenotypes
        - EX: Toads → attained phenotypic characters that enabled them to expand their ranges
    - EX: **adaptive radiations**
        - When one or a few lineages colonize an environment with few other organisms and many vacant ecological niches as well as unexploited resources
        - Result in rapid burst of diversification
            - Formation of many new species from one or a few ancestors
        - Often involves resource polymorphisms as a starting point

Module 12 Biogeography

Topic 1. The Biogeographical Impact of a Major Geological Event

Biogeography

- study of spatial (geographic) patterns of biodiversity → how and why organisms came to possess their geographic distributions
- focused on the geographic distributions of organisms (including species, and higher level taxa all the way from genus to phylum) in both the present and past
- Biogeography has several different sub-disciplines
    - **Zoogeography** - animal biogeography
    - **Phytogeography** - plant biogeography
    - **Historical Biogeography -** the reconstruction of the origin, dispersal and extinction of taxa, and entire biotas
    - **Phylogeography -** the branch of biogeography that considers the principles and processes that control the geographic distributions of genetic lineages, particularly within species, and among very closely related species
- Biogeographic patterns result from two processes
    - **Dispersal**: The movement of organisms away from their point of origin.
    - **Vicariance**: The splitting of floras and faunas (or populations) as a result of the formation of a physical barrier.
- **Panamanian Isthmus**
    - Formation of the great American interchange → caused by Plate tectonics (proposed by Alfred Wegner)
    - Consequence A: More migration (dispersal) from North America to South America → somewhat one sided
        - Hypothesis
            - North American fauna consists of better migrators
            - Better survivors
            - Better competitors
        - Difficult to determine with organisms that do not fossilize
    - Consequence B: Marine Vicariance
        - **Geminates**
            - Sister species that diverged → as consequence of formation of barrier
            - Many are found on both sides

- **Law of Germinate species (Jordan's Law)**
    - Given any species in any region, the <u>nearest related species</u> is not to be found in the same region, nor in a remote region, but in a neighbouring district separated from the first by a barrier of some sort or at least by a belt of country the breadth of which gives the effect of a barrier

    Geminates (sister species) across the Isthmus of Panama include:

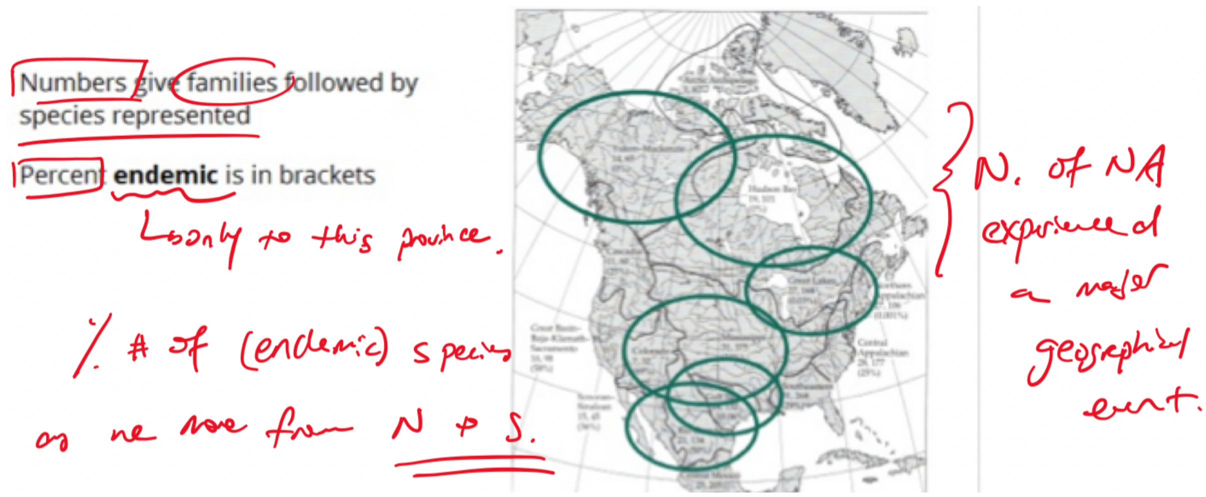
    - Fishes
    - Crabs
    - Sea Urchins
    - Shrimp
    - Gastropods (Snails)
    - Isopods (crustaceans)
    - Ostracods (crustaceans)

    - EX: Snapping shrimp germinate on Pacific and Caribbean
        - Nancy Knowlton sequenced shrimp's mitochondria → determine average rate of Gene sequences divergence with reference to the age of Panamanian Isthmus → molecular clock
            - 1.4% sequence divergence / million years

- Different Impact of formation of Panamanian Isthmus:
    - Terrestrial ecosystem: Dispersal
    - Marine ecosystem: Vicariance

Topic 2. Biogeographic Patterns and Provinces

- <u>Biogeographic Provinces</u> (Alfred Wallace and Charles Darwin)
    - possess unique floral (plants) and faunal (animals) assemblages
- Numbers in province: families followed by species represented
- Percent **endemic** is in brackets → only to this province
    - % of endemic species increases as we move from north to south
        - south has the most endemic species



Re-colonization of Northern North American Aquatic Habitats After the Pleistocene Glaciations

- Major Glacial Refugia separates species in five area → Beringia, Pacific, Missourian, Missisipian
- Isolation + Mutation + Selection + Drift = Allopatric Divergence
    - Some cases → speciation; but more cases → different lineages of the same species
- Proglacial Lakes
    - **Aquatic Dispersal Corridors**
        - Glacier melt → connect lakes → connect isolated species to return to NNA
    - **Aquatic Dispersal Capabilities**
        - Species with strong dispersal recolonize NNA to greater extent

Phylogeography

- Study of the <u>geographic distribution of genetic variation within species</u>
- Conducted by <u>sequencing the DNA</u> of representatives of a species over its geographic range
- Provide important insights into the process of <u>allopatric divergence</u> and also into <u>the way in which species recolonize North America</u> once the glaciers began receding
- Ex. Phylogeographic pattern in Arctic Charr and Lake Trout based on glacial refugia
- Phylogeographic provided us:
    - important insights into the process of allopatric divergence and dispersal patterns that species have undergone.
    - different species or different taxa have been affected by the same vicariance events (eg. Pleistocene glaciations), in very, very similar ways.

- Today, phylogeography is a very important component of biogeography

The latitudinal gradient in species diversity

- Larger numbers of species as we move from north to south.
    - not unique to fish. It occurs in mammals, birds, insects, and just about every other group of organisms, including plants and trees on the planet.
- Recognized by Darwin and Wallace.
    - species diversity increases as we move from the Earth's poles to the Earth's equator
- EX: NA Animal Mammal Diversity Gradient
    - The contour lines: the number of mammal species present in different regions
    - fewer species in the north and increase species as move south → same pattern in all organisms
- EX: Central America rainforest
    - Central American rainforests 100-4000 species of trees per hectare
    - Further north into eastern North America have about 10-30 species of trees per hectare
    - even further north into the Canadian Boreal forest have 1-5 species per hectare
- However, there is <u>another very interesting pattern</u> nested within the Diversity Latitudinal Gradient
    - fish provinces of North America → <u>percentage of endemics</u>
        - all or the vast majority of species within North provinces also occur in other provinces → relatively low endemic number
        - But, more southerly provinces → percentage of endemics within provinces <u>increases</u>.
            - So in the south, there are many more species that occur in one <u>province and only</u>
- **Rapoport's Rule**
    - <u>Geographic range of species in the north tends to be larger than the geographic range of species in the south</u>
        - the range or the area occupied by species tends to increase with increasing latitude
        - As we move from the equator to the poles, <u>the range or area occupied by species increases</u>

- species at more northerly latitudes have better dispersal abilities than species at more southerly latitudes

- WHY?
  - No perfect explanation
  - Three different factors:
    - **Historical factors**: such as the Pleistocene glaciations
    - **Ecological factors**: including climate and the amount of incident solar radiation which affects primary production
    - **Evolutionary factors**: the rate of speciation and the rate of extinction
      - some studies have indicated that rates of speciation are actually higher in northerly latitudes such as the Arctic than they are in more southerly latitudes in certain groups of organisms

Module 13 The history of Life

Topic 1 Origin of Life

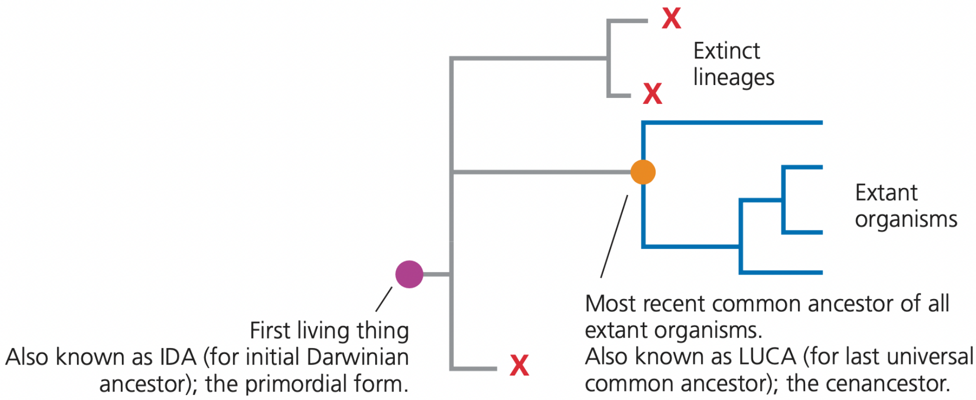
Evolutionary definition of life

- Life is that which possesses a genotype and a phenotype, and is capable of evolution by natural selection

Hard to determine earth first life form → Rock dating & chemical clues: destroyed and subducted

Earth's first life form

- Primordial form and sometimes as **the initial Darwinian ancestor, or IDA**
- Is not the same as the common ancestor of all extant organisms, or **cenancestor**, also known as the **last universal common ancestor (LUCA)**
    - Cenancestor was very likely a community of organisms that exchanged DNA, and had already been evolving for a long period of time, not a single organism
- We cannot use traits that exist today to make inferences about the initial Darwinian ancestor



RNA first

- RNA was involved in early life-forms is its role in the machinery cells use for replication and metabolism → ribosome → RNA in ribosome that catalyze the protein synthesis
- Biological currency: ribonucleoside triphosphates, such as ATP and GTP
- Electron-transfer cofactors: NAD, FAD, SAM
- Experimental Evolution of RNA
    - RNA has the capacity to store heritable information that can be propagated.
    - RNA molecules in solution can possess features of living organisms that allow them to evolve
    - The RNAs most likely to survive from one generation to the next are the ones that are most efficient at catalyzing phosphoester bonds.

The null hypothesis that evolutionary biologists employ is the **Oparin-Haldane mode**

- created a lasting image of life arising in an aqueous environment brimming with biologi- cal building blocks. This was Darwin's "warm little pond"
- this view remains as sort of a null model against which deviations can be tested, much like the Hardy–Weinberg equilibrium principle in population genetics
- Pg 655 section 17.2
- **Stanley Miller's Experiment**
    - sent an electrical charge through a flask of a chemical solution of methane, ammonia, hydrogen and water. This created organic compounds including amino acids
- **3 stages**
    - First, non-biological processes synthesized organic molecules, such as amino acids and nucleotides, that would later serve as the building blocks of life.
    - Second, the organic building blocks in the prebiotic soup were assembled into biological polymers, such as proteins and nucleic acids.
    - Finally, some combination of biological polymers were assembled into a self-replicating organism that fed off of the existing organic molecules

Panspermia hypothesis

- only shifts the problem of the origin of life to a different location in the universe, and does nothing to solve it

Topic 2 The Last Universal Common Ancestor (or Cenancestor) and the Tree of Life
(17.4 pg 663 to 675)

1. we need a gene possessed by all representatives of life that is not loaded with homoplasious characters
    a. What gene is this? - small-subunit ribosomal RNA
2. What do we use as an outgroup → Bacteria?
    a. Three domains of life - Bacteria, Archaea, Eucarya
    b. what node on the tree of life represents the last universal common ancestor most left node
    c. horizontal gene transfer - **the non-sexual movement of genetic information between genomes**. Incoming DNA or RNA can replace existing genes, or can introduce new genes into a genome
        - Give up the idea of finding a single LUCA → indeed a community of LUCA
    d. difficulties for phylogeny construction

        - Chief among the surprises from whole-life phylogenies is that organisms appear to have swapped their genes more readily than anyone suspected
        - This means that the phylogenies of genes may be different from the phylogenies of the organisms that harbor them [?]
    e. evidence for the last universal common ancestor being a community as opposed to a single organism
        - Horizontal gene transfer

Topic 3: Fossils and the Fossil Record, the Ediacaran Biota the Cambrian Explosion and Major Animal Transformations

- Fossils and the process of fossilization, yet they are biased...
    - **Geographic bias**
        - as a consequence of the fact that fossilization is more likely to occur in freshwater, marine or very wet terrestrial habitats
    - **Taxonomic bias**
        - certain types of organisms, those with hard chitinous, bone, or calcareous body parts are more likely to fossilize than other, soft-bodied organisms
    - **Temporal bias**
        - older fossils are more likely to have been lost by plate subduction and other geological processes than more recent fossils
- The Ediacaran Fauna
    - come to represent an **important development in the evolution of life on Earth**, because they immediately predate the explosion of life-forms at the beginning of the **Cambrian Period** 541 million years ago
- **Cambrian Explosion** → the spectacular <u>diversification of animal life</u> beginning about 540 million years ago
- pg. 691-705
    - Four categories of fossil
        - **Amber and freezing**
        - **Permineralization and replacement**
        - **Natural molds and casts** → filled up
        - **Trace fossils** → footprint, body fossil, traces behaviours
    - Briefly explain formation of fossil
    - morphological characteristics of the Ediacaran and Burgess Shale faunas

- **Ediacaran**
    - exhibited a vast range of morphological characteristics. Size ranged from millimetres to metres; complexity from "blob-like" to intricate; rigidity from sturdy and resistant to jelly-soft. Almost all forms of symmetry were present
- **Burgess Shale faunas**
    - large, bilaterally symmetric animals with well-developed segmentation
    - soft-body

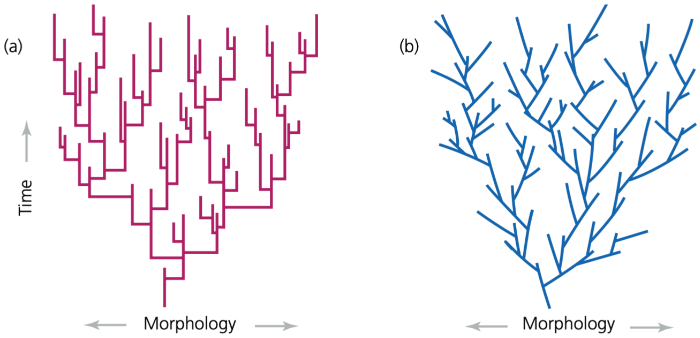
- leading hypothesis concerning the change in environmental conditions that triggered the Cambrian Explosion
    - The leading hypothesis about the cause of the Cambrian explosion involves a mass extinction of Ediacaran fauna and an increase in atmospheric oxygen → larger size
- Fish-tetrapod transition
    - Loss of fin → trans into limb
- Dinosaur-bird transition
    - Growth of theropod feathers
- Reptile-mammal transition
    - Reduce the size of the ear?
- Importance of transitional forms
    - help scientists bridge gaps in the tree of life
    - A growing collection of transitional fossils documents the evolution of feathers in theropod dinosaurs. The earliest feathers belonged to animals that could not fly, prompting a variety of hypotheses about the initial functions of feathers and the evolution of flight

Topic 4: Extinction

- Two Types: 18.4 pg 709
    - **Mass Extinction Event**
        - over 60% of the living species went extinct in the span of a million years
    - **Background Extinction**
        - occurred at normal rates
- Vast majority of organisms that have inhabited the Earth are extinct
- extinction creates opportunity → dinosaurs restricted the size of mammals as mouse and squirrel
- 5 five mass extinction events since the Cambrian Explosion
    - Most recent: K-Pg Extinction on Event

Topic 5: Punctuated Equilibrium vs. Phyletic Gradualism

- **Punctuated equilibrium**
    - Much of evolution is characterized by rapid bursts of morphological change, followed by periods of stasis, with little or no morphological change
- **Phyletic gradualism**
    - morphological evolution proceeds with slow, steady incremental change
- Both sides were correct → evidence indicates that both patterns of morphological evolution are apparent, and important.
- 719-724 figure 18.33



Gradualism vs. punctuated equilibrium was the focus of a great debate in evolutionary biology, which stimulated much investigation and thought, but both patterns are apparent in nature

Module 14 Human Evolution

Topic 1: Our Relationship with the Great Apes

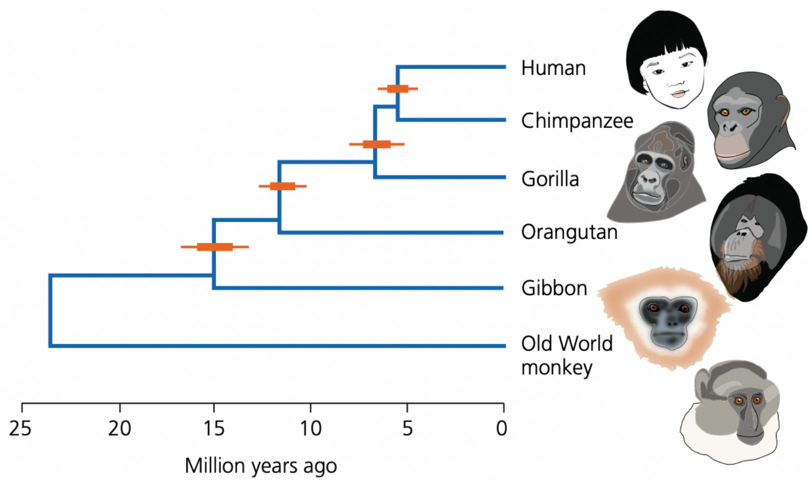
- Homo sapien belong to a clade (monophyletic group) referred to as the **Great Apes** (family Hominidae) that includes ourselves, orangutans, gorillas, and two species of chimpanzees: the common chimpanzee (Pan troglodytes) and the bonobo (Pan paniscus).
- The **African Great Apes** (subfamily Homininae) include humans, gorillas and the two species of chimpanzees.
- Most analyses revealed a close association of humans and chimpanzees, some identified gorillas are sister taxon to humans
    - The difficulty in settling this problem stemmed from a process known as **incomplete lineage sorting**.
        - arises as a result of the way that ancestral genetic variation is partitioned among species that have diverged relatively recently.
        - Its net result is that phylogenies produced by the analysis of individual genes might not always reflect the actual phylogeny of the species.
            - Solve by: analyze many genes, so that the consensus among them will converge on the actual phylogeny of the species, and phylogenetic artefacts produced by incomplete lineage sorting in some genes will be "swamped out"
            - Phylogenetic evidence derived from both molecular and morphological data now conclusively shows that our closest living relatives are the chimpanzees
            - Humans did not evolve from either species of chimpanzee as they exist today, but rather, we share a common ancestor with them, which we began to diverge from between 5 and 7 million years ago
                - That common ancestor was different from us, as well as the two extant species of chimps
- Be certain that you can draw a phylogenetic tree showing the relationships among the great apes (family Hominidae, see above), and that you can list some of the synapomorphies that identify the African Great Apes (subfamily Homininae) as a clade (see page 771). Also, be sure to understand what is meant by knuckle-walking, and its phylogenetic distribution among species within the subfamily Homininae (African Great Apes).

Topic 2: The Recent Ancestry of Humans

- Difficulty: new fossils are continuously being discovered, and fossils are almost never perfect
    - Even a very good fossil may consist of only a partial skeleton,
        - In many cases: part of a jaw or a few pelvic bones found
        - This results in sometimes heated debates over interpretation
    - Complicated by the fact that different taxonomists have applied different names to the same fossils, resulting in myriad different names throughout the scientific literature.
    - Combined, all factors create a highly complex background on which an understanding of human evolution must be based.
        - However, we can simplify things somewhat by creating a broad contextual sequence on which to frame our recent evolutionary past:
        - looked at as a series of overlapping phases of evolution, as opposed to discrete stages

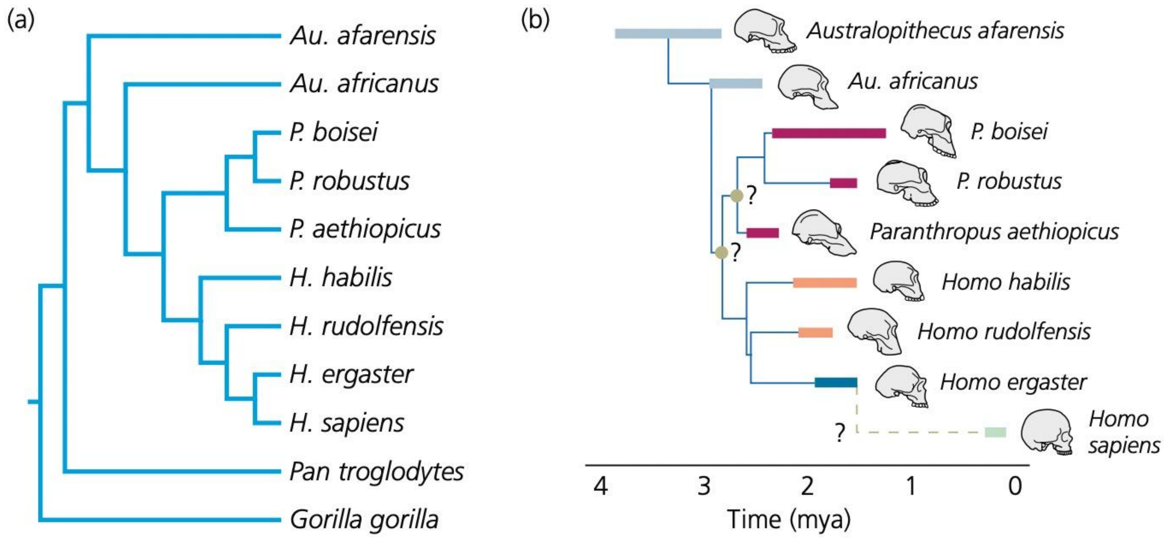
Knuckle-walking ancestor of Humans and Chimpanzees → Bipedal (upright) locomotion → increasing brain size → complex tool use/language → modern brain size

- (homo sapien, chimpanzee), gorilla → morphological analysis



- Hominin
- Major genera: ***Sahelanthropus, Australopithecus***, and ***Homo***
- Co-exist hominin lineage***: Homo floresiensis*** (hobbit man) and ***Homo neanderthalensis*** (shorter but more robust and stronger)

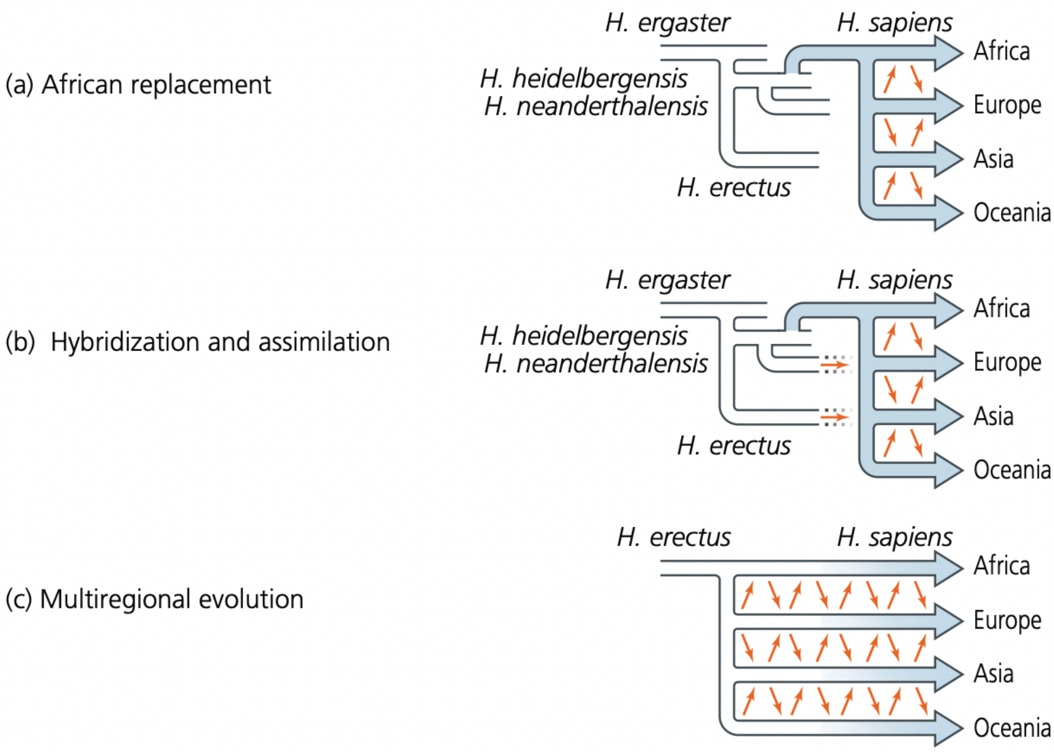
- We also interbred with another different group of hominins, the Denisovans, who also interbred with the Neanderthals
- ***Homo naledi (335,000 and 236,000 years ago)***: had same brain size as *Australopithecus*, but had other features in common with the genus *Homo*, such as hand and foot morphology, cranial architecture, and reduced tooth and jaw size



- The hominin fossil record is sufficiently detailed to allow us to conclude that *Homo sapiens* is the sole survivor among a diversity of species.

Topic 3: The Origin of Modern Humans

- **African replacement hypothesis** (in the past referred to as the out of Africa hypothesis)
    - *Homo sapiens* migrated out of Africa to Europe, Asia and elsewhere, and replaced *Homo erectus, Homo neanderthalensis* and other lineages with no interbreeding
- **Hybridization and assimilation hypothesis**.
    - migrated out of Africa, and then replaced earlier forms of the genus *Homo* in Europe and Asia, but with much interbreeding and hybridization between them
- **Multiregional hypothesis**
    - *Homo sapiens* simultaneously evolved throughout Europe, Asia, and Africa, but gene flow among the different regions was sufficient to keep *H. sapiens* glued together as a single species
- **Leaky replacement hypothesis**
    - evidence supports something intermediate between the first and second hypothesis



- Reich and colleagues estimate that 2.5% of the genome of non-African modern humans is derived from Neandertals, and that an additional 4.8% of the genome of Melanesians comes from Denisovans. This result refutes the African replacement model. It is consistent with a scenario between replacement and hybridization and assimilation. Pääbo describes the picture suggested by genomic analysis as “leaky replacement”