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1 Evolutionary Thinking

Introduction (Lecture)

- ▷ Essential questions of evolutionary biology:
 - Why do organisms look so different?
 - Why develop elaborate sexual traits?
 - Why do organisms senesce?
- ▷ Evolution is mainly an historical science and thus must rely on other methods of reconstructing the past or making inferences about evolutionary forces.
- ▷ **Proximate**: a question about a mechanistic cause; provides an immediate explanation about **how** a mechanistic cause functions.
- ▷ **Ultimate**: **why**, or the reason, a trait or organism is the way it is; an evolutionary explanation.
- ▷ Example of proximate vs ultimate in Galapagos finches:
 - Proximate: developmental growth factor is increased/decreased in some birds.
 - Ultimate: different habits are selected on breaks that maximize food gathering ability.
- ▷ Evolutionary biology's approach to answering questions:
 - **Empirical data**: **observation** studies, experiments; the *comparative method*.
 - **Theory**: **predictions** that use models and mathematical reasoning which can be **tested** with empirical data.
- ▷ Overview of the components of evolution by natural selection:
 - Genetic variation exists, via mutations.
 - Mutations are heritable.
 - There is an advantage to survival and/or reproduction from the mutation.
 - Individuals with the advantage in survival/reproduction are selected for.

10 Studying Adaptation

Hypothesis Testing: Oxpeckers Reconsidered

- ▷ **Adaption:** a trait, or a suite of traits, that increases the fitness of its possessor.
- ▷ No hypothesis for the adaptive value of a trait should be accepted simply because of its plausibility.
- ▷ Oxpeckers and impalas traditionally were thought to have a mutually beneficial existence; oxpeckers ate ticks and impalas provided a safe environment.
- ▷ Experiments on cattle were done to test whether this observation was true:
 - Results show red-billed oxpeckers have no effect tick loads of cattle.
 - Red-billed oxpeckers maintained open wounds, even enlarging existing wounds to feed on the cattle's blood.
 - Red-billed oxpeckers removed hosts' earwax; whether this is good or bad is unclear.
 - Even these results must remain in question, as cattle are not the native host for the birds.
- ▷ Other important points to remember:
 - Differences among populations or species are not always adaptive.
 - Not every trait is adaptive.
 - Not every adaptation is perfect, often the adaptation just happened to work well enough or by chance better than other adaptations.

Experimental Design

- ▷ Defining and testing effective control groups is critical.
- ▷ Treatments of controls and experimental measures must be handled as close to exactly alike as possible.
- ▷ Randomization is a key technique for equalizing miscellaneous effects and a tool to avoid bias.
- ▷ Reproduction is essential in order to help remove potential outlier effects.
 - Allows for greater understanding of precision, accuracy, and variation by providing more data for statistical tests.

4 Evolutionary Trees

How to Read an Evolutionary Tree

- ▷ **Phylogeny**: aka evolutionary tree or phylogenetic tree, is a diagram showing the history of divergence and evolutionary change. Essentially, it's the **genealogical relationships** of organisms based on descent with modification.
 - **Taxa**: the units you are analyzing, e.g. certain species or DNA sequences.
 - **Character**: a feature or trait present among the taxa of interest, e.g. teeth of mammals or nucleotides of DNA sequences.
 - *Character state(s)*: an **alternative condition** of a character, which are able to evolve one to another, e.g. pointed/flat teeth of mammals.
 - **Ancestral character**: a trait that was **possessed by the common ancestor**.
 - **Derived character**: a trait the was **not possessed by the common ancestor** and instead **evolved** in at least one of the descendants.
 - **Synapomorphy**: derived character state shared by **two or more** taxa and used to define a clade of taxa.
 - **Autapomorphy**: derived character state in only **one** taxon.
 - **Outgroup**: a taxon or taxa that are used to root the phylogeny or determine ancestral character states.
 - **Ingroup**: the set of taxa that are the focus of the phylogeny.
 - **Nodes**: points at which the tree splits; represents mutations, speciation events, or **character changes**.
 - **Anagenesis**: descent with modification, but **no speciation**.
 - **Cladogenesis**: **speciation**, origin of clades.
 - **Clade**: also known as a **monophyletic group**, an ancestor and **all** of its descendants.
 - **Paraphyletic group**: a group of organisms consisting of an ancestor and **some** of its descendants.
 - **Sister**: a taxa or clade that are most closely related to each other; they **share the most recent** common ancestor.
- ▷ **Homology**: similarity due to common descent; **continuity** of a trait, character, or character state through time.
 - *Homologous trait*: found in a taxa that inherited the trait from a common ancestor.

- ▷ **Homoplasy:** or analogous, similarity in the characters or traits in different taxa due to convergent evolution, parallelism, or reversal, but **not due to common descent**.
 - **Convergent evolution:** similar traits due to selective forces and **not shared ancestry**.
 - **Parallelism:** convergent evolution in **recently diverged** taxa.
 - **Reversal:** derived traits or character states that revert to the ancestral form.

Inferring Phylogenetic Trees

- ▷ **Parsimony:** relationships that require the **smallest number of character changes** are most likely to be correct.
 - Based on shared and **derived** traits(synapomorphies).
 - Reconstruction using parsimony:
 1. Code characters.
 2. Make up a taxon×character matrix.
 3. Search for synapomorphies, and the shortest tree.
 - Outgroups can help polarize (ancestral vs derived) the characters.
 - **Treelength:** a measure of evolutionary change using parsimony.
 - Shortest tree length produces most parsimonious tree.
 - Length determined by number of synapomorphies.
 - Homoplasious characters increase tree length.
- ▷ **Distance Methods:** converts a sequence alignment to genetic distances between pairs of sequences.
 - Branch length is proportional to genetic differences.
- ▷ **Maximum likelihood:** a method of estimating the parameters of a probability distribution by **maximizing a likelihood function**.
 - One of the more dominant means of statistical inference.
 - **Likelihood:** measure of goodness of fit of a statistical model to a sample of data for given values of the unknown parameters.
 - $P(D|H)$; probability(P), Data(D), Hypothesis(H)
 - **Bayesian:** uses the likelihood function to create a quantity called the *posterior probability* of trees using a model of evolution based on prior probabilities in order to produce the most likely tree.

- **Bootstrapping:** creating a value that indicates how many times out of 100 (normally) that the same branch was observed when repeating the phylogenetic reconstruction on re-sampled (pseudoreplicated) set of data.

6 Mechanisms of Evolutionary Change

Hardy-Weinberg Equilibrium

- ▷ **Population:** a group of interbreeding individuals and their offspring.
- ▷ **Gene pool:** the set of all genes, or genetic information, in any population.
- ▷ **Genotypic frequency:** number of individuals with a given genotype divided by the total number of individuals in the population.
 - The proportion (i.e., $0 < f < 1$) of genotypes in a population.
- ▷ **Allele frequencies:** relative frequency of an allele at a particular locus in a population.
 - **Locus:** a fixed position on a chromosome where a particular gene or genetic marker is.
 - Monoploids: frequency of an allele is the result of the number of copies of the allele divided by sample size.
 - $p = i/N$
 - p : frequency | i : copies of alleles | N : sample size
 - Diploids: frequency of alleles within three possible genotypes at a locus with two alleles.
 - $p = f(AA) + \frac{1}{2}f(AB)$ frequency of A-allele
 - $q = f(BB) + \frac{1}{2}f(AB)$ frequency of B-allele
 - Allele frequency can always be calculated from genotype frequency, whereas the reverse requires the *Hardy-Weinberg principle* of random mating apply.
- ▷ **Hardy-Weinberg principle:** allele and genotype frequencies in a population will remain constant in the absence of evolutionary influences.
 - Allele frequencies do not change from one generation to the next.
 - Genotypic frequencies after one generation of random mating:

$$p^2 + 2pq + q^2$$
 - Evolutionary influences: genetic drift, mate choice, assortative mating, natural selection, sexual selection, mutation, gene flow, meiotic drive, genetic hitchhiking, population bottleneck, founder effect, and inbreeding.
 - *Most of these influences will be discussed later.*

Selection

- ▷ **Fitness:** success at which a organism produces fertile offspring.
- ▷ **Competition:** an interaction between organism in which the fitness of one is lowered by the presence of another.
- ▷ **Selection:** the act on a heritable phenotypic trait due to competition.
 - Can be members of the same of different species.
 - Not always directional and adaptive, instead selection pressure is applied and removes the less fit variants.
 - Can be classified in different ways, such as effect on a trait, on genetic diversity, by life cycle, by unit of selection, or by the resource in competition.
 - Most effective on large populations.

By Effect on a Trait

- **Stabilizing selection:** the simplest case in which selection acts to hold a trait at a stable optimum.
 - Reduces the individuals in the tails of the trait's distribution, reducing variation.
- **Directional selection:** favours extreme values of a trait.
 - Directional selection on a continuous trait changes the average value of the trait in the population.
 - Can reduce variation in the population, generally not by large amounts though.
- **Disruptive selection (diversifying selection):** acts during transition periods when current mode is sub-optimal, but alters trait in more than one direction.
 - **Univariate:** when the trait is both quantitatively favoured in either direction and can lead to speciation.
 - Generally **increases the variance** on continuous traits.
 - May be more common than generally recognized.
- All three increases the mean fitness of the population.

By Effect on Genetic Diversity

- **Purifying selection:** aka negative selection; acts to remove genetic variation from the population.
- **de novo mutation:** introduces new variation and opposes negative selection.
- **Balancing selection:** acts to maintain genetic variation, even in absence of *de novo* mutation by frequency-dependent selection.
 - **Frequency-dependent selection:** fitness that depends of the phenotypic or genotypic **composition** of a population.
 - **Positive:** fitness **increases** as frequency of the trait **increases**.
 - **Negative:** fitness **decreases** as the frequency of the trait **increases**.
 - **Overdominance**, aka *heterozygote advantage*: when a combination of alleles confers a selective advantage over individuals with one allele.
 - **Underdominance**, aka *heterozygote disadvantage*: when the heterozygote has lower fitness than either homozygote.

By Life Cycle Stage

- **Viability selection:** aka *survival selection*: increases probability of survival.
 - Can act to improve probability of survival before and after reproduction.
- **Fecundity selection:** increases the rate of reproduction given survival.
 - May be split into sub-components including sexual selection, gametic selection, gamete viability, compatability selection, and zygote formation.

Mutation

- ▷ **Mutation:** alteration in the nucleotide sequence of the genome of an organism.
 - May not produce discernible phenotypic changes.
 - The ultimate source of genetic variation.
 - Have several types of changes, from no effect, to small changes, or complete loss of function.

Large-Scale Structural Mutations

- **Gene duplications**, *aka amplifications*: repetition of a chromosomal segment or attachment of extra piece of chromosome to another, leading to multiple copies of chromosomal regions.
- Deletions of large chromosomal regions.
- **Fusion genes**: mutations that join previously separated genes into one new distinct gene.
- **Chromosomal rearrangement**: large scale changes in structure of chromosomes, leading to speciation in isolated, inbred populations. Includes:
 - **Chromosomal translocations**: interchange of genetic parts from nonhomologous chromosomes.
 - **Chromosomal inversions**: reversing the orientation of a chromosomal segment.
 - Non-homologous chromosomal crossover.
 - **Interstitial deletions**: inverse of fusion genes; removes a segment of DNA joining distant genes.
- **Loss of heterozygosity**: loss of one allele, by deletion or genetic recombination, in a organism that previously had two different alleles.

Small-Scale Mutations

- **Point mutation**: a single nucleotide base change, that can result in a variety of effects.
- **Insertions**: add one or more extra nucleotides into the DNA.
 - Usually caused by transposable elements, or errors during replication or repeating elements.
 - Can cause *reading frame shift*, possibly effecting how many codons are read, and thus altering the gene product.
- **Deletions**: remove one or more nucleotides from the DNA.
 - Also can cause a reading frame shift like insertions.
 - Generally irreversible.
- **Substitutions**: exchange of a single nucleotide for another.
 - Often classified as transitions or transversions.
 - Generally a purine (A-G) for a purine, or a pyrimidine (C-T) for a pyrimidine.
 - Can be reversed by another point mutation.

Impact on Protein Sequence

- Effect of mutation depends heavily on where it occurs, particularly in a coding or non-coding region.
- Regulator sequences, e.g. promoters, enhancers, silencers, can alter gene expression but are less likely to alter protein sequence.
- **Frameshift mutation:** caused by insertion or deletion of nucleotides that is not divisible by three, resulting in a different translation from the original.
- **Synonymous substitution:** a codon replacement with another that codes for same amino acid.
 - **Silent substitution:** no phenotypic difference after a synonymous substitution.
- **Nonsynonymous substitution:** a codon replacement that codes for a different amino acid.
 - **Missense mutation:** codon replacement that renders the resulting protein nonfunctional.
 - **Nonsense mutation:** codon replacement that results in a premature stop codon that produces a truncated and often nonfunctional protein.

Migration

- ▷ **Gene flow:** movement of alleles, or genetic variation, between populations.
 - If the rate of gene flow is high enough, then two populations are considered to have equivalent allele frequencies and thus a single population.
 - Constrains speciation by combining gene pools of the groups.
 - May result in the addition of novel genetic variants in the gene pool.
- ▷ Gene flow is expected to be lower in species that:
 - have low mobility or dispersal.
 - occur in fragmented habitats.
 - have long distances between populations.
 - have small population sizes.
- ▷ **Allopatric speciation:** when gene flow is blocked by **physical** barriers that inhibit gene flow.
- ▷ **Sympatric speciation:** result of gene flow that is blocked due to **non-physical** barriers that inhibit gene flow.

Genetic Drift

- ▷ **Genetic drift:** the change in the **allele frequencies** in a population due to **random sampling**.
 - Not influenced by environmental factors.
- ▷ May cause certain gene variants to become fixed or lost by chance.
- ▷ Generally drives populations towards genetic uniformity over time, **decreasing heterozygosity**.
- ▷ Only mutation or gene flow can introduce new alleles, which acts against genetic drift.
- ▷ **Founder effect:** result of sampling error which has an increased likelihood on populations with low numbers.
 - By chance certain alleles can be dominant when they otherwise wouldn't be in a new founding population.
 - Often acts to drastically increase rate of genetic drift.
- ▷ **Genetic bottleneck:** a sharp reduction in the size of population due to environmental events.
 - Can essentially cause a founder effect, though it's not a new population.

Coalescent Theory

- **Coalescent theory:** how gene variants sampled from a population may have **originated** from a common ancestor.
 - Assumes no recombination, no natural selection, no gene flow in the simplest case.
- Aims to look backward in time by merging alleles into a single ancestral copy according to a random process in coalescence events.
- Many theoretical genealogies are made in order to compare to observed data in order to test assumptions about demographic history of a population.
 - Used to make inference about population genetic parameters, such as migration, population size, and recombination.
- **Coalescent time:** number of preceding generations where the coalescence took place, not calendar time.
 - Estimation of the time can be made multiplied by $2N_e$ with the average time between generations.
 - Time to coalescence for a pair of alleles at a locus is **dependent** on population size.

- Formula: $P_c(t) = \left(1 - \frac{1}{2N_e}\right)^{t-1} \left(\frac{1}{2N_e}\right)$
- Can also be used to model the amount of variation in DNA sequences expected from genetic drift and mutation.

Molecular Evolution

- ▷ **Molecular evolution:** the process of change in the sequence composition of cellular molecules across generations.
- ▷ **Polymorphism:** occurrence of two or more clearly different morphs, or alternative phenotypes, in the population of a species.
 - **Substitution:** when alleles become fixed or lost in a population and polymorphism is ended.
 - Substitution rate (k): $k = sN\mu$
 - s = probability of fixation.
 - $N\mu$ = mutation rate of population.

Recombination

- **Recombination:** the process that results in genetic exchange between chromosomes or chromosomal regions.
 - Can also cause mutations due to misalignment after recombination.
 - **Gene repair:** a type of recombination that is the product of DNA repair that corrects damage using a homologous template.
 - Often responsible for homogenizing sequences of duplicate genes over long periods of time, which reduces nucleotide divergence.
- **Genetic hitchhiking:** change in allele frequency not because of natural selection, but due to proximity to a gene undergoing selective sweep.
 - **Selective sweep:** a beneficial mutation that increases frequency and generally becomes fixed.

Neutral Theory

- **Neutral theory of molecular evolution:** most evolutionary changes occur at the molecular level.
- Most variation is due to random genetic drift of mutant alleles that are selectively neutral.
- Compatible with phenotypic evolution, as phenotypes are driven by molecular changes.
- Most mutations are neutral with respect to fitness.
- A minority of mutation are advantageous.
- Substitution rate predicted to be neutral, equal to per-individual mutation rate, **independent** of population size.
- K_A/K_S test used to determin direction selection based on evolutionary history.
 - K_A : number of nonsynonymous substitutions (replacement).
 - K_S : number of synonymous substitutions (silent).
 - $K_A > K_S$ signals for **diversifying selection**.
 - $K_A < K_S$ signals for **purifying selection**.

Molecular Clocks

- **Molecular clocks:** the average rate at which species' genomes accumulates **neutral mutations** over time.
 - A linear rate is often easy to establish.
 - Used to measure evolutionary divergence.

Nonrandom Mating

- ▷ **Inbreeding:** production of offspring from closely genetically related individuals.
 - Results in homozygosity, which can increase chances of offspring being affected by deleterious or recessive traits.
 - **Inbreeding depression:** the reduced fitness in a given population due to inbreeding.
 - Usually caused by population bottlenecks or the founder effect.
 - Can also result in purging of deleterious alleles through purifying selection.
 - Can allow for the expression of advantageous phenotypes, which if outweighs the disadvantages, then could potentially lead to speciation.
 - **Coefficient of inbreeding:** the probability that two alleles at any locus in an individual are identical by descent.
 - Nonrandom mating does not alter allele frequencies and not a mechanism of evolution.
 - Can alter the frequencies of genotypes, changing the distribution of phenotypes in a population, which can alter patterns of natural selection.
- ▷ **Assortative mating:** mating based on phenotypic factors.
 - Can play a role in sympatric speciation.
 - A form of sexual selection.
 - Can be either positive or negative, selecting for similar or different phenotypes respectively.

8 Evolution at Multiple Loci

Linkage Equilibrium and Disequilibrium

- ▷ **Linkage equilibrium:** when the genotype of a chromosome at one locus is **independent** of its genotype at another locus.
- ▷ **Linkage disequilibrium:** the non-random association of alleles at different loci in a given population.
 - Occurs when frequency of the association between loci's different alleles is higher or lower than expected.
- ▷ **Haplotype:** a group of alleles in an organism that are inherited together from a single parent.
 - Used to mean the collection of specific alleles that represent a phenotype and likely to be conserved.
 - Also can be used to mean a set of linked single-nucleotide polymorphism alleles that are associated statistically.
- ▷ Factors that influences disequilibrium: selection, rate or genetic recombination, mutation rate, genetic drift, system of mating, population structure.
 - Understanding linkage disequilibrium in a genome can be a powerful signal of the population genetic processes that structure it.
 - Selection, genetic drift, assortative mating, and population admixture act to **create disequilibrium**.
 - Recombination and outbreeding act to **reduce disequilibrium**.
- ▷ Level of linkage disequilibrium can between A and B can be quantified by the **coefficient of linkage disequilibrium**, D_{AB} .
 - Formula: $D_{AB} = P_{AB} - P_A P_B$
 - P_{AB} : the frequency with which both occur together on same gamete, or the frequency of the AB haplotype.
 - $P_A P_B$: product of the probabilities give the probability they occur together.
 - When there is a difference, the magnitude of the coefficient rises, indicating linkage disequilibrium.
 - Strong recent selection can be indicated by linkage disequilibrium of alleles located next to neutral alleles.

Recombination's Effect on Linkage Disequilibrium

- Linkage disequilibrium (D) will converge to zero depending of the magnitude of the recombination rate (c) between two loci the absence of natural selection, inbreeding, and genetic drift.
- The smaller the distance between the two loci, the smaller the rate of convergence of D to zero.
- Genetic recombination tends to randomize genotypes, thus it tends to reduce frequency of overrepresented chromosome haplotypes and increases underrepresented haplotypes.
- In short, recombination reduces linkage disequilibrium.

Adaptive Significance of Sex

- ▷ **Parthenogenesis:** a natural form of **asexual reproduction** in which growth and development of embryos occur without fertilization.
- ▷

9 Quantitative Genetics

The Nature of Quantitative Traits

- ▷ **Quantitative genetics:** deals with phenotypes that vary continuously due to multilocus traits and environmental factors.
 - Allows for the prediction of how a population will respond to selection, even when we do not know the genetic basis of the trait.
- ▷ **Qualitative traits:** discrete traits that can be assigned individual categories by observation of simple genetic test.
- ▷ **Quantitative traits:** continuous traits determined by the combined influence of the genotype at multiple loci and the environment; the focus of quantitative genetics.
 - Study of continuous distribution requires many other statistical methods such as the effect size, mean, and variance, to link phenotypes to genotypes.

Heritable Variation

- ▷ **Heritability:** the degree of **variation** in a phenotypic trait in a population that is due to genetic variation between individuals in that population.
- ▷ **Phenotypic variance (V_P):** the genetic variance (V_G) combined with the environmental variance (V_E).
 - $V_P = V_G + V_E + V_{GE}$
 - V_{GE} represents variance associated with **intereaction** of genetic and environmental factors.

Genetic Variance

- **Additive genetic variance (V_A):** how much the phenotypic trait is influenced by traits that show an additive effect on the quantitative traits.
 - Measures the magnitude to which individual phenotypic differences can be predicted due to additive effects of allelic substitutions.
 - The greater the additive genetic variation for the trait, the greater is response to selection can be.
- **Dominance genetic variance (V_D):** associated with the dominant gene actions which cover the influence of the recessive alleles at the particular locus.
- **Epistasis (V_I):** occurs due to statistical interaction among loci, i.e., gene-by-gene modification.

- $V_G = V_A + V_D + V_I$
- ▷ **Broad-sense heritability (H^2):** all genetic contributions to a populations phenotypic variance, including additive, dominant, and epistatic, and maternal/paternal effects.
 - $H^2 = \frac{V_G}{V_P}$
- ▷ **Narrow-sense heritability (h^2):** proportion of the total phenotypic variance that is due to the additive effects of genes.
 - $h^2 = \frac{V_A}{V_P}$
 - Allows prediction of how a population will respond to selection.
 - The greater the additive genetic variation for the trait, the greater its response to selection can be.

Estimating Heritability

- Heritability is often estimated by measuring correlations between parents and offspring.
- **Midparent:** the average of the trait value between parents.
 - The mother's value often has a scaling value applied to help account for developmental sex differences.
- **Midoffspring:** the average value of a trait among offspring.
- Correlations are determined through a line of best fit.
 - Heritability of the trait is measured between 0 and 1 determined by the slope of the best fit line plotted against midparent and midoffspring values.
 - Using a method of **least-squares linear regression**, which minimizes the sum of the squared vertical distances between points, the heritability slope represents **narrow-sense heritability**.
- If a trait is heritable, monozygotic twins will resemble each other more than dizygotic twins.

Predicting Evolutionary Responses

- **Selection differential (S)**: the difference between the mean of the selected individuals (\bar{x}) and the mean of the entire population (μ)
 - $S = \bar{x} - \mu$
 - Can be used to create a statical selection gradient, which is used to represent the strength of selection.
- **Breeder's equation**: evolutionary response (R) can be predicted using narrow-sense heritability and the selection differential.
 - $R = h^2 S$
 - The greater the heritability and selection differential, the greater the response to selection.
- When characters are genetically correlated, selection for one can drag the other along through genetic hitchhiking.
- Selection on the alleles at any single locus affecting a quantitative is often very weak; substantial genetic variation may persist at equilibrium between mutation and selection.
- Low heritability often represents populations effected by strong selection, as selection removes variation.
- Higher heritability represents high variance within the population.

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