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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 islands 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.
- ▷ **Molecular clocks:** the average rate at which species' genomes accumulate mutations over time.
 - Generally a linear rate.
 - Used to measure evolutionary divergence.

6 Mendelian Genetics I

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.

By Effect on a Trait

- **Stablizing selection:** the simplies case in which selection acts to hold a trait at a stable optimum.
- **Directional selection:** favours extreme values of a trait.
- **Disruptive 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.

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.

Mutation



7 Mendelian Genetics II

Migration



Genetic Drift



Molecular Evolution



Nonrandom Mating



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