"PRINCIPLES OF PHYLOGENETICS: ECOLOGY AND EVOLUTION"

Integrative Biology 200 Spring 2020
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March 30th 2020**. Phylogenetics and Adaptation**

A. *Adaptation:* Based on the observation that an organism often matches its environment. Darwin & many Darwinians thought that all structures must be adaptive for something. But, this has come under severe challenge in recent years. Not all structures and functions are adaptive. Some matches between organism and environment are accidental, or the causality is reverse (i.e., the structure came first, function came later). In fact, there are very few completely worked-out examples of adaptations.

What is to be explained?

- What is the evolutionary history of trait x that we see in one or more lineages (whether homology or homoplasy) and what are the processes influencing the evolution of that trait?
- Is natural selection the primary evolutionary process leading to the ‘fit’ of organisms to their environment?
- Why are some traits more prevalent than other traits across a lineage: number of origins vs. trait-dependent diversification rates (speciation - extinction)? Is the organism-level the only level at which adaptation can happen?

Some high points in the earlier history of the adaptation debate:

1950s -- Modern Synthesis of Genetics (Dobzhansky), Paleontology (Simpson), and Systematics (Mayr, Grant)

1960s -- Rise of evolutionary ecology – synthesis of ecology with strong adaptationism via optimality theory, with little to no history; leads to Sociobiology in the 70s

1972 -- Eldredge and Gould – punctuated equilibrium – argue that Modern Synthesis can’t explain pervasive observation of stasis in fossil record; Gould focuses on development and constraint as explanations, Eldredge more on ecology and importance of migration to minimize selective pressure.

1979 -- Gould and Lewontin – Spandrels – general critique of adaptationist program and call for rigorous hypothesis testing of alternatives for the ‘fit’ between organism and environment .

1980’s -- Debate on whether macroevolution can be explained by microevolutionary processes; 82: Gould and Vrba: exaptation: when trait arises before current function; 84 Sober: “The Nature of Selection” a philosophical critique of natural selection theory; 85 Janzen: ‘On ecological fitting’, *Oikos* – little noticed paper, mirrors Eldredge’s ideas.

1990's on -- Development of quantitative comparative methods, some of which we are covering in this class.

B. *Constraints* (why is phenospace filled in a clumped manner?)

Physical (possible vs. impossible; not historically contingent)

-- size (e.g., fluid flow, compressive strength. elasticity)
-- coiling
-- branching
-- properties of biological materials

Developmental (historically contingent biases in generation of phenotypes)
-- inherent homeostasis because of gene interactions
-- biases among possible trajectories of character change
-- not all phenotype changes are equally likely in development

Environmental (direct action on the phenotype by the environment)
-- phenotypic plasticity

Adaptive (selection among alternative, realized , heritable variants)
-- stabilizing selection
-- note the real possibility of developmental selection in modular organisms (e.g., among multiple embryos in one seed or among branches on a tree); results in what can be called "metapopulation genetics"
-- selection for or against plasticity

C. *Definition of adaptation* in a formal sense requires fulfillment of four different criteria (Mishler 1998, pp. 285-306 in J. Lovett Doust and L. Lovett Doust (eds.), *Plant Reproductive Ecology*) :

1. **Engineering**. Structure must indeed function in hypothesized sense. Requires functional tests.

2. **Heritability**. Differences between organisms must be passed on to offspring, at least probabilistically. Requires heritability tests (parent-offspring correlations; common garden studies).

3. **Natural Selection.** Difference in fitness must occur because of differences in the hypothesized adaptation (in common environment -- see over). Requires fitness tests.

4. **Phylogeny**. Hypothesized adaptive state must have evolved in the context of the hypothesized cause. Think in terms of problem (e.g., environmental change) and solution (adaptation). Requires phylogenetic tests.

-- Only something that passes all these tests is a **adaptation**. If it passes tests 1-3 it could be called an **aptation**. If it then fails test 4 it could be called as **exaptation**. (see: Gould, S.J. and E.S. Vrba 1982. Exaptation--a missing term in the science of form. *Paleobiology* 8:4-15).

D. *Levels of selection*.

-- There are two different hierarchies that need to be considered in evolutionary biology, **interactors** and **replicators**.

-- Natural selection explained:
replicator -- any entity that passes its structure on with high fidelity
lineage -- a sequence of ancestor/descendent replicators
interactor -- an entity that interacts with other entities such that replication is differential

Evolution by natural selection is:

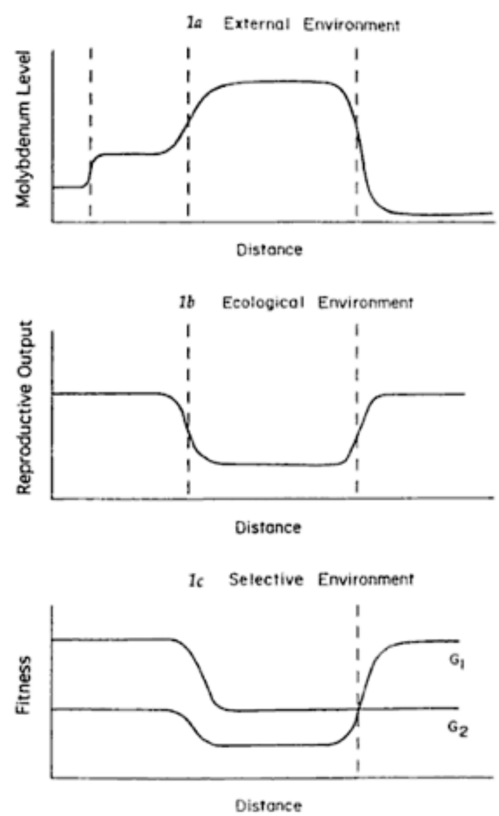
1. heritable variation in a trait (the *adaptation*) causing...
2. differential reproductive success of one replicator lineage over others...
3. due to competition among interactors within a common environment.

-- Finding the correct level at which interaction or replication is occurring requires application of the principle of **screening off**. This concept is due to Salmon 1971 (*Statistical Explanation and Statistical Relevance*. Pittsburgh University Press). If *A* makes *B* statistically irrelevant with respect to the outcome *E* (but not vice-versa), then *A* screens off *B*. In equation form:

$$P(E, A|B) = P(E,A) \neq P(E,B)$$

This makes intuitive sense: proximate causes screen off remote causes.

-- The process of evolution by natural selection requires consideration of the environment and the concept of **norm of reaction** (Schmalhausen, 1949, *Factors of evolution: the theory of stabilizing selection*). To be considered a single process, it must be occurring in a single **selective environment**. This selective environment is a special part of the overall environment, a region of phenotypic space where the fitness differences between interactors are maintained (see also: Brandon, R. N. 1990. *Adaptation and Environment*. Princeton University Press).

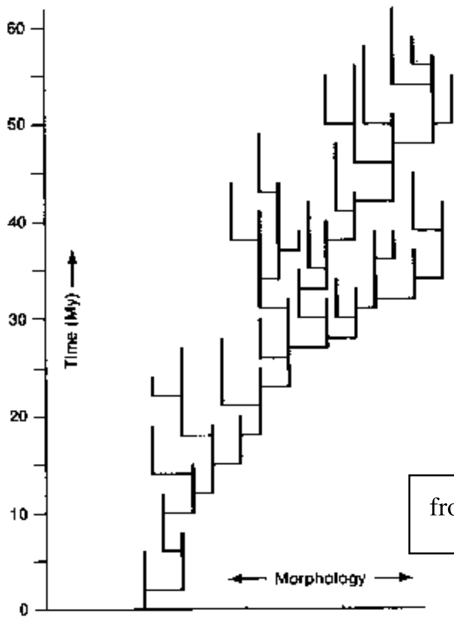


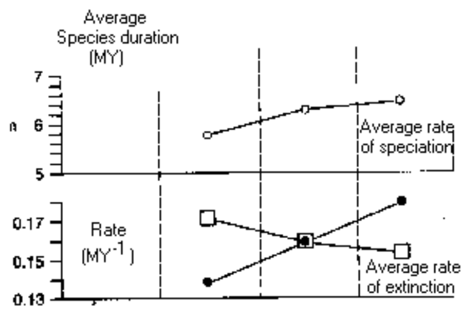
from: *Concepts and methods in evolutionary biology*, by Robert N. Brandon, 1996.

Figure 1. Schematic representation of external (1a), ecological (1b), and selective (1c) environments. The horizontal axes all represent distance along the same spatial transect. The vertical axes represent: (1a) the amount of some arbitrarily chosen factor, here molybdenum; (1b) the reproductive output of a single genotype as it contributes to population growth; and (1c) the fitnesses of two or more genotypes. The vertical broken lines in each graph represent where the environments change. Notice how they change at different places, thus showing different scales of heterogeneity.

-- So let's now think about whether selection can act at higher levels. What conditions would have to be met for "clade selection" to occur? [This is sometimes known as "species selection," but we know species are at best just one particular level of clade!]

-- To decide whether selection is acting at a higher level involves the same criteria discussed above.

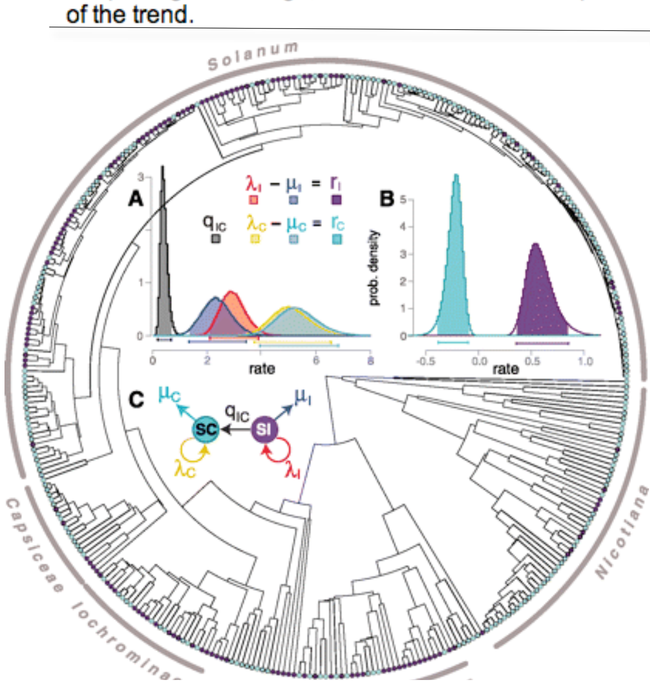




from: http://www.mun.ca/biology/scarr/Species_Selection.htm

Species Selection

Suppose that larger-bodied species lineages tend to speciate more rapidly, and that the average rate of extinction (the inverse of the species duration) is also less for larger species. Over time, this will result in a **species trend**, in which the clade becomes more speciose and each species on average larger. Careful examination of the clade shows that (*a*) speciation events that produce smaller-bodied species are equal in number to those that produce larger, and (*b*) that they contribute the same total amount of morphological change, so that the direction of speciation plays no role in the formation of the trend.



From: *Science* 22 October 2010: Vol. 330 no. 6003 pp. 493-495. "**Species Selection Maintains Self-Incompatibility**" Emma E. Goldberg, Joshua R. Kohn, Russell Lande, Kelly A. Robertson, Stephen A. Smith and Boris Igić.

Fig. 1. Maximum likelihood tree of phylogenetic relationships among 356 species of Solanaceae. Higher ranks are indicated around the perimeter of the tree. Purple and turquoise tip colors denote SI and SC extant species, respectively. The root age is 36 million years. Inset panels display posterior probability distributions and 95% credibility intervals of reconstructed rates of character evolution (the time unit is millions of years). (A) BiSSE estimates of transition, speciation, and extinction parameters ($q_{IC} << \mu_I < \lambda_I << \lambda_C < \mu_C$). (B) Net diversification rate—the difference between speciation and extinction rates—associated with each state. (C) Schematic summary of estimated rate parameters. For methods, species names, character states, and further results, see (19).