

"PRINCIPLES OF PHYLOGENETICS: ECOLOGY AND EVOLUTION"

Integrative Biology 200B

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Adaptation: Based on the observation that organism matches 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 much later). In fact, there are very few completely worked-out examples of adaptations.

A. Definition of adaptation in a formal sense requires fulfillment of four different criteria:

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).

B. 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:

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

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: Brandon, R. N. 1990. *Adaptation and Environment*. Princeton University Press).

C. 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)

- inherent homeostasis because of gene interactions
- biases among possible trajectories of character change
- not all changes are equally likely

Adaptive (selection among alternative realized variants)

- stabilizing selection
- note the real possibility of developmental selection in modular organisms.
- selection for or against plasticity