

3. Rates of extinction of higher taxa

Fig 24.23 taxonomic survival curves: frequency vs. duration (longevity)

What should we expect? **a)** extinction probability should **decrease** with time, if evolution is **progressive**, i.e., organisms in taxa that survive longer are better adapted; **b)** extinction rates should **increase**, if evolution is **escalatory**, as older taxa lose evolutionary flexibility; **c)** extinction rates remain relatively constant over time.

van Valen (1974): noted a generally log linear decline for fish, reptiles, mammals, suggesting possibility **c**: longer-lived taxa do not appear to have any higher or lower likelihood of surviving than others. To explain these data, van Valen proposed **the Red Queen** hypothesis, based on idea of coevolution among members of biotic communities: instead of evolving to some optimal state, organisms must continually evolve *in response to the adaptations* of their competitors, prey or predators/parasites (the Red Queen had to run as fast as she could just to stay in place).

Stenseth & Maynard Smith formalized a framework that included a Red Queen scenario as just 1 of 4 possibilities. They defined the **Lag load** as the relative differential between the fitness an optimum phenotype would produce, and the actual species fitness ($L = (w_{opt} - w_{bar}) / w_{opt}$). The farther a species falls behind its evolutionary antagonists, the higher the lag load, and the higher the intensity of selection.

2 of the 4 possibilities are either unlikely (species #s in community continue to increase indefinitely) or uninteresting: S & MS noted that higher **mean** values of **L** (for the community) were associated with higher likelihood of extinction for many or all members of community. The other 2 seem biologically interesting. A **stationary mode** is attained if species can attain mutual optimality **mean L** ≈ 0 , thus each species has **L** ≈ 0 (these can be perturbed by abiotic factors). The Red Queen represents a dynamic equilibrium, where all species involved maintain lag loads that do not differ radically. Selection pushes each to evolve in response to the others, but optima are not achieved because of the coevolutionary responses.

Can't easily test RQ because both constant & varying extinction rates can produce log-linear relationships. If RQ is responsible for most extinctions, a plot of extinction probabilities vs. absolute time should result in a line with 0 slope (e.g., test between mass extinction events). van Valen 1985 found such a relationship, but Raup & Boyajian did not (20,000 genera across wide taxonomic diversity of marine organisms).

A. Evolutionary Rates

the BIG question: do macroevolutionary patterns need special explanations for the mechanisms, or are microevolutionary processes sufficient ?

Character change - phylogenetic rates → highly variable from trait to trait

$$r = \frac{\ln x_2 - \ln x_1}{t_2 - t_1}$$
 a darwin is a change by a factor of e (2.718) in a million years
(when back-transformed 1d = 100% change per

MY)

$$H = \frac{\left(\frac{x_2}{\sigma_p}\right) - \left(\frac{x_1}{\sigma_p}\right)}{g}$$
 a haldane records the rate of change in

s.d.'s/generation

Most rates of morphological change for fossils are quite slow and are reported in millidarwins (1/1000) representative rates:

ceratopsian dinosaur body size, smallest to largest - 6 *md* (6%/MY);

horse teeth: 45 - 104 *md* on average for 4 traits (ranges from -74 to 339)

house sparrow in North America in last 100 years: 50 - 300 darwins for skeletal

traits **Artificial selection**: 12 - 200,000 darwins; .006 - .030 haldanes

Kinnison & Hendry (2001): Distribution of evolutionary rates approx log-normal, many slow, few fast rates. Rates tended to decrease with time.

Long-term selection intensities (*haldanes*) were on average lower than instantaneous measures in natural pops: intensities of selection typically measured in nature are rarely maintained for long.

“macroevolutionary transitions may ultimately arise through microevolution occasionally 'writ large' but are perhaps temporally characterized by microevolution 'writ in fits and starts'.”

Gingerich (2001): $H = 0.2$ standard deviations per generation on the time scale of the evolutionary process – “All evidence indicates that the evolutionary process is much more dynamic than we generally recognize.” “However, it appears virtually stationary on longer time scales.”

The results from artificial selection and colonization clearly show that micro-evolutionary forces are quite powerful; **other mechanisms are not required.**

In fact, Lande has shown that many patterns of evolutionary change in the fossil record could have been produced by drift given the very long time periods measured. Neither of these conclusions *mean that other factors don't play a role.*

In early evolutionary thought and even up to the 1940's there were proponents of *macromutation* or *saltational* change as driving forces - e.g., Richard Goldschmidt, who argued that macroevolution was a result of major chromosomal changes.

At various times these arguments were either refuted or shown to be unnecessary to explain observed patterns. The majority of evolutionists believed evolution to be a slow, steady process governed by microevolutionary forces.

In 1972, Niles Eldredge and Stephen Jay Gould argued that a careful examination of the fossil record showed very few smooth evolutionary transitions, but instead the more common pattern is for new species or morphological types to appear abruptly, persist relatively unchanged for awhile and then go extinct.

They contrasted two models of evolutionary change:

1. **Phyletic gradualism** (Darwin & the Synthesists)

a) new species arise by transformation of ancestral populations into modified descendants

-b) transformation is slow and even

c) transformation involves most or all of the ancestral population

d) and over most or all of the ancestral range

with

2. **Punctuated equilibria**

a) new species arise via splitting of lineages

b) they develop rapidly

c) from a small sub-population at the edge of the ancestral species range

d) Between speciation events, there are extended periods of no change - **stasis**

A Key distinction: punctuated equilibria predicts that evolutionary change will be concentrated at the time of speciation events; no prediction for PG.

Although polarized as alternatives these are actually two endpoints on a continuum.

What patterns exist? Both are apparent in fossil record (see text for examples)

Data required: a complete stratigraphic record (i.e. without gaps) and from a large # of specimens