

### MACROEVOLUTION

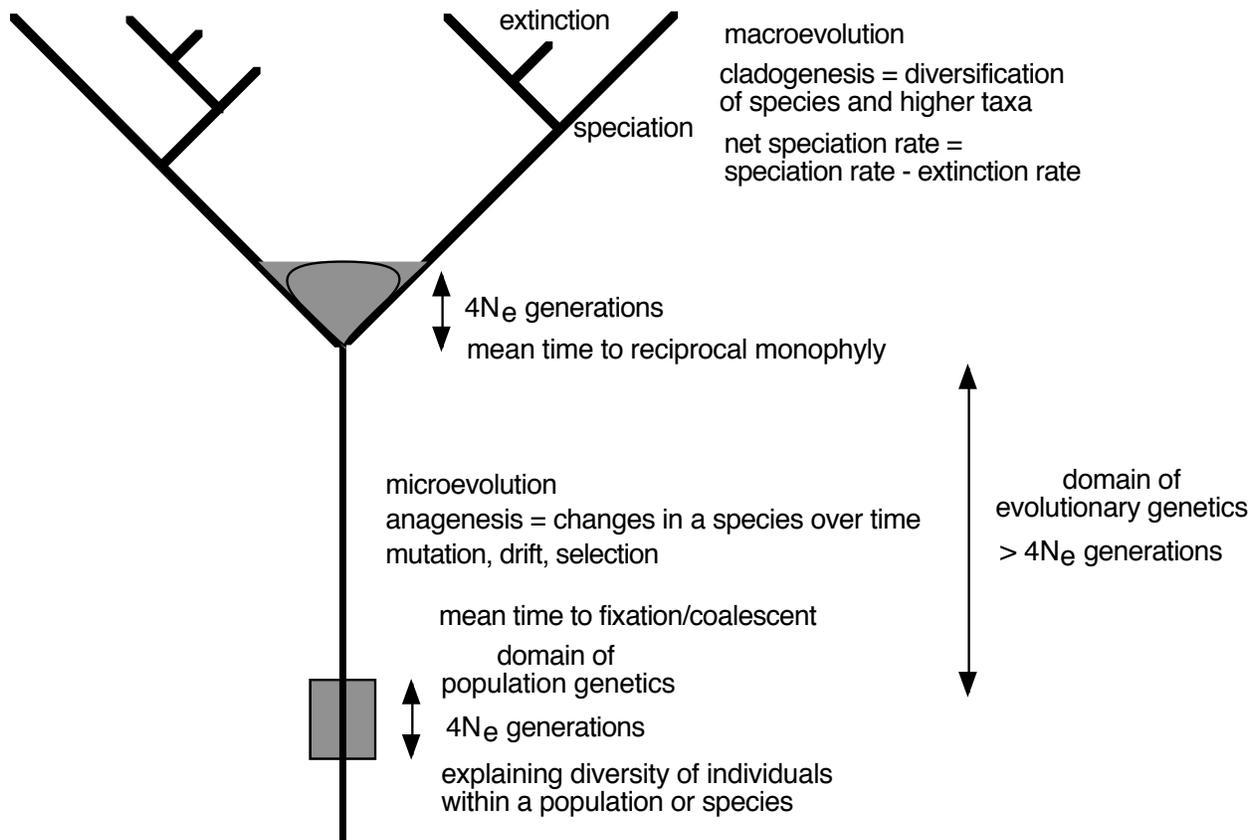
Vague term. Most definitions focus on various aspects of the evolution of taxa at or above the species level, as opposed to individuals within species.

Differentiation between macro- and microevolution seems to have arisen in the course of discussions about

1. whether macroevolutionary changes could be explained in terms of changes in genes within species (answered by Modern Synthesis), and
2. of gradualism vs. saltational evolution (whether big phenotypic changes arise as an accumulation of small changes, or in single jumps).

Also much interest in comparative diversity of species within higher taxa and the relationship of differences in diversity to the traits that differentiate those higher taxa.

My perspective:



### Gradualism vs. Saltational Evolution

E.g. of saltation in origin of new species:

Origin of new species by polyploidization: (Futuyma pp. 504-508)

- Rare in animals; most are asexual and therefore new species.

- Common in plants, especially grasses: 7% of speciation events in ferns; 2%-4% of speciation events in angiosperms.
- Usually allopolyploids.
- Often occupy new niches.

Origin of new species by hybridization: (Futuyma pp. 508-509)

Loren Rieseberg: sunflowers *Helianthus annuus* X *H. petiolaris* (crosses semisterile) → *H. anomalus*, *H. deserticola*, *H. paradoxus*.

- reproductively isolated
- adapted to different environments
- multiple origins
- *H. annuus* X *H. petiolaris* hybrids reproduced in lab

### Punctuated Equilibrium

Rapid morphological evolution during speciation events with intervening long periods of slow evolution.

Based on fossil record, but controversial.

Does not require saltational speciation because rapid evolution periods may last many generations.

### Species Diversity

Phylogenetic approach: consider species as lineages.

Parameters of model are rates of speciation and extinction.

Species diversity determined by rate of speciation – rate of extinction = net speciation rate.

These lectures mostly concerned with two questions:

- (1) Do specific alternative traits affect diversity, i.e. rates of speciation and extinction?
- (2) How do we measure rates of speciation and extinction in a lineage?

First question can be hard to answer. Best to use comparative method.

Compare randomly selected groups of same age. Problems:

- Selecting groups of the same age requires appropriately accurate fossil record, biogeographic record, or molecular clock.
- Some taxa may share a high speciation rate due to a trait that they inherited from a common ancestor, i.e. they are not independent tests of the hypothesis.
- There may be a high level of noise due to variation in confounding variables that affect speciation rates.

Better to compare sister-groups. Advantages:

- Know they are of same age, requires only accurate phylogeny.
- All differences between sister groups arose since they split.

Some results:

- Phytophagous insects are more speciose in 11 / 13 sister-group comparisons; highly significant.

- Plants with resin canals are more speciose.
- Darwin: sexual selection by female choice increases rate of reproductive isolation and hence speciation. Tested and verified by Barraclough et al. using sexual dichromatism as proxy for female mate choice.
- Flowering plants and passerine birds show positive relationship between rate of molecular evolution and rate of speciation.

Limitations sister-group comparisons:

- Don't address speciation and extinction rates separately.
- Can't investigate changes in speciation and extinction rates over time.
- Can't investigate differences between lineages that aren't sister-groups.

Now being done by analyzing molecular phylogenetic trees.

Theory of generalized birth-death processes. At species level, birth and death of lineages correspond to speciation and extinction.

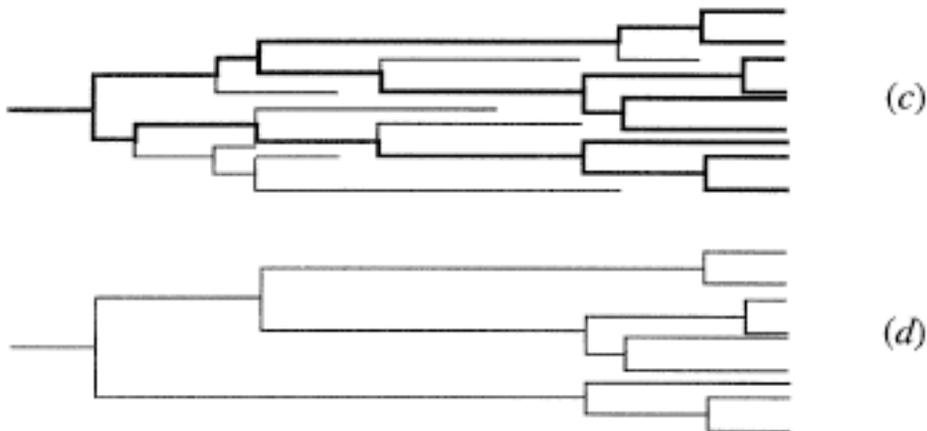
Sean Nee, Paul Harvey, et al. at Oxford:

Constant rate birth-death model: at any point in time, every lineage has same  $b$  = probability of branching and  $d$  = probability of extinction.

Use as null model to test hypotheses about diversification.

Focus on processes where at least one lineage survives to present day ((c) below).

Prune all branches that don't survive to present day → ideal tree ((d) below).



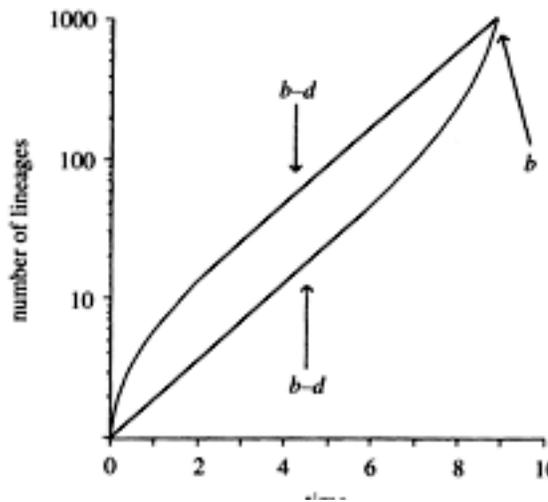
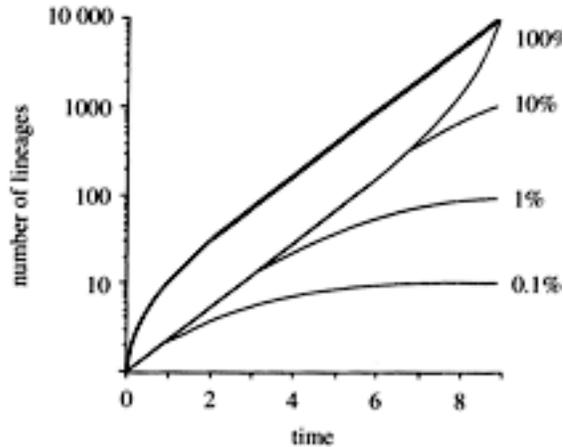


Figure 3. The theoretically expected growth in the number of lineages through time for an actual (top line) and a reconstructed phylogeny growing according to a constant rate birth-death process. The slopes of both curves are  $b-d$ , the speciation rate minus the extinction rate, over most of the history of the clade, and the slope of the reconstructed phylogeny asymptotically approaches the speciation rate towards the present day. The two curves pull apart further the greater the ratio of the extinction rate to the speciation rate.

Observed upturn at the end is because most recently derived lineages haven't had time to go extinct. Strength of the upturn depends on  $d/b$ .

A decrease in rate of increase of number of species toward the present may mean

- decrease in speciation rate
- increase in extinction rate (might be accompanied by an upturn in number vs. time curve near present)
- incomplete sampling



Phylogeny based on sample sizes of varying percentages of entire population.

Can get maximum likelihood (ML) estimates of  $b$  and  $d$ . If null model of constant  $b$  and  $d$  is rejected, test alternatives:

- (1) Are deviations from null model due to incomplete sampling?
- (2) Are birth and death rates constant over time? Over lineages?

Some results:

Pybus & Harvey 2000 *Proc.R.Soc.Lond.B* 267,2267-2272

1. MtDNA sequences from 27/70 extant species of *Sorex* shrews.

Molecular clock not rejected.

Rejected equal rates across lineages, due to one clade.

When that clade was removed, could not reject constant  $b$  and  $d$ .

2. mtDNA from 24/27 North American *Dendroica* wood warbler species

Speciation rate not constant among lineages, due to outgroup.

Speciation rate also declining through time.

Primates:

South American *Platyrrhini*: constant  $b$  and  $d$  not rejected

Madagascar *Strepsirhini*: constant  $b$  and  $d$  rejected, possibly because restricted area of Madagascar caused density-dependent cladogenesis.