# Diversification & SSE models

# Why care about diversification?

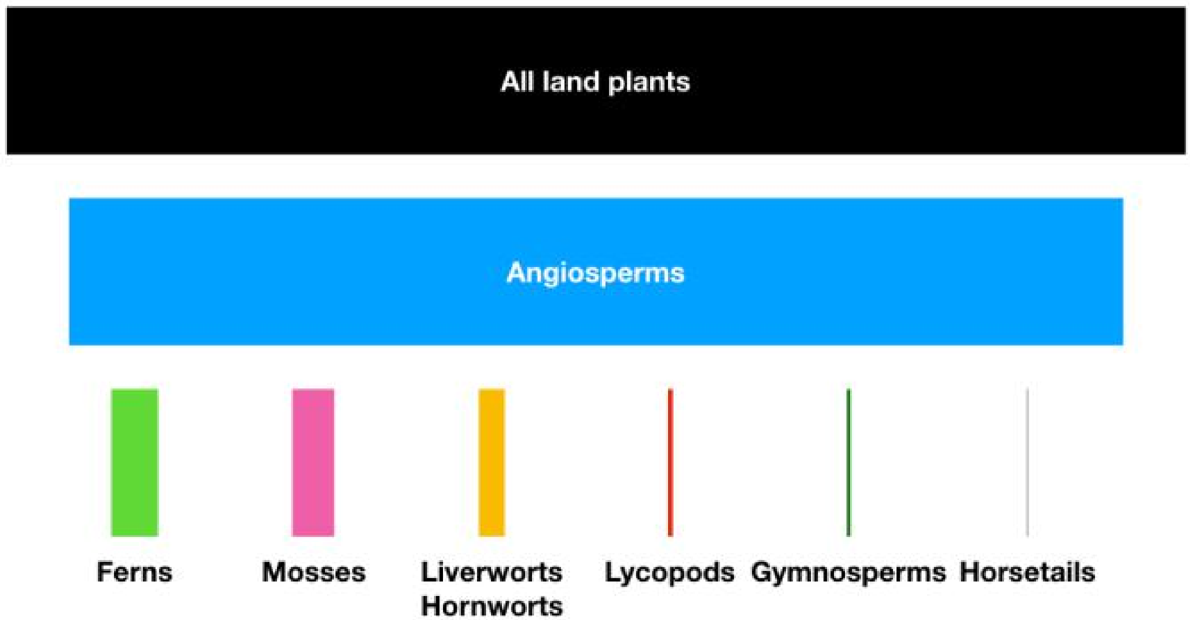



Figure 10.1. Diversity of major groups of embryophytes (land plants); bar areas are proportional to species diversity of each clade. Angiosperms, including some 250,000 species, comprise more than 90% of species of land plants. Figure modified from Crepet and Niklas (2009)

(Harmon, *Phylogenetic comparative methods*)

# Birth-Death model

Poisson process (like CTMC models) - but events = Speciation/Extinction rather than substitution

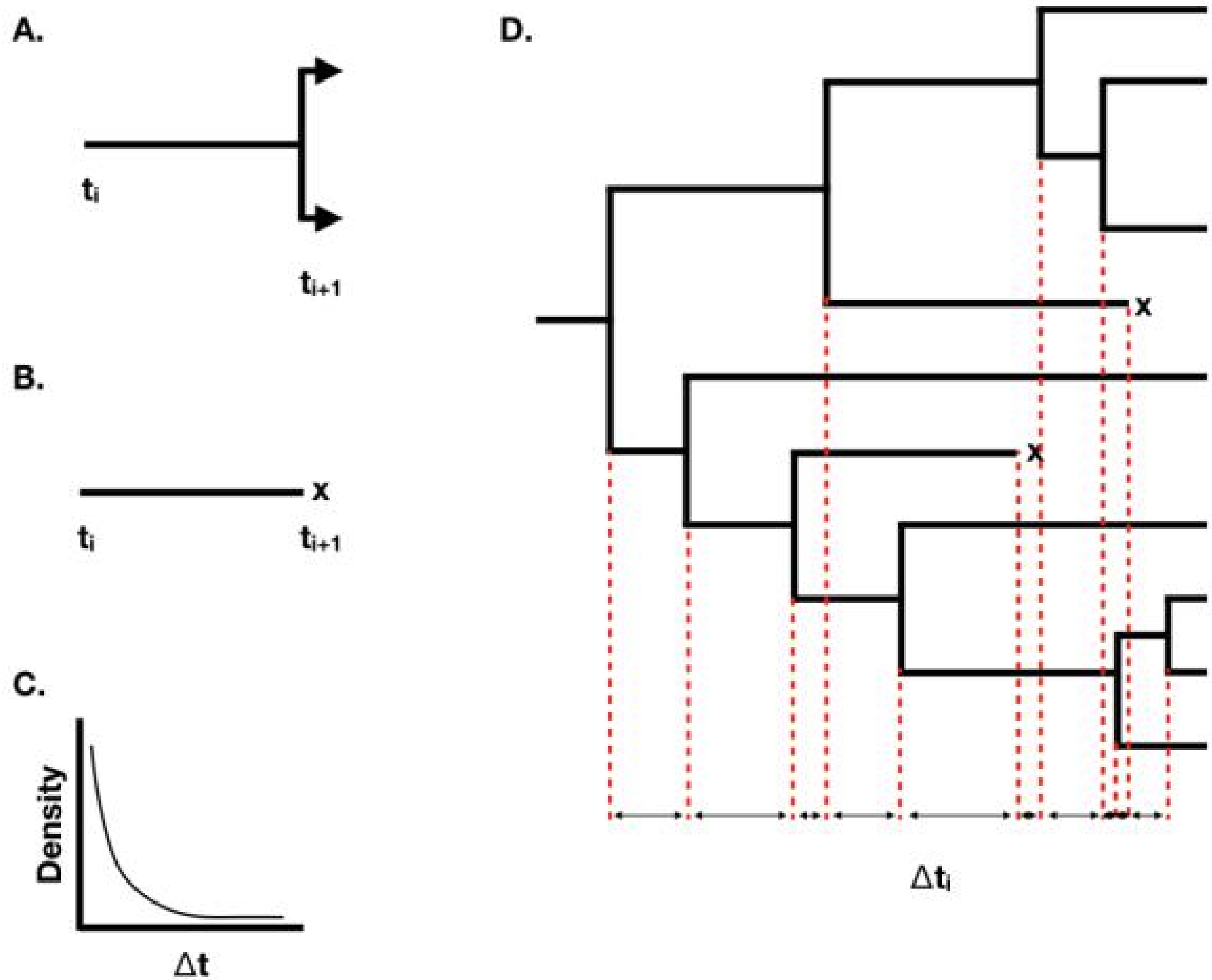
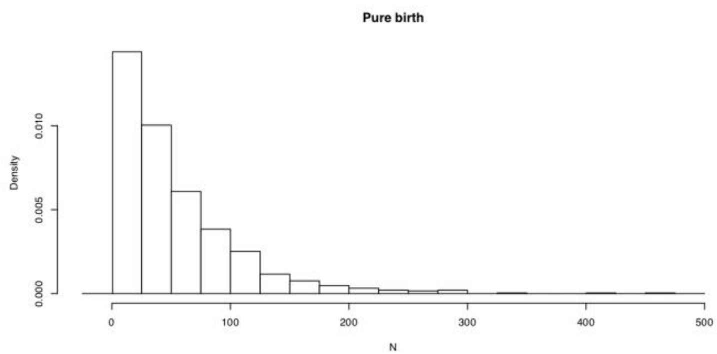
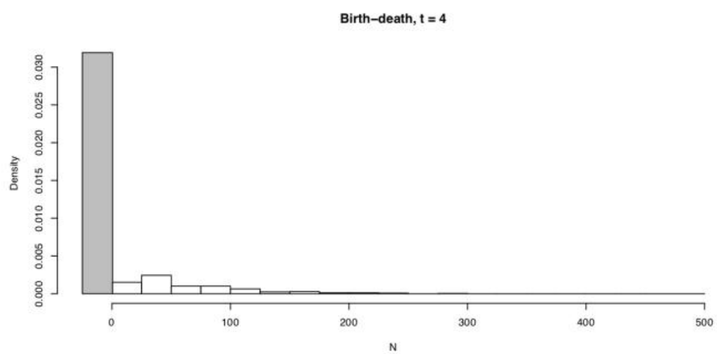
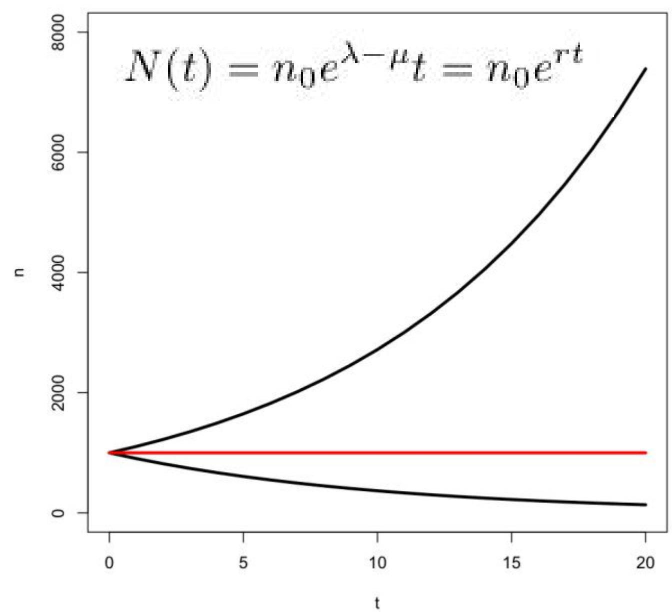



Figure 10.2. Illustration of the basic properties of birth-death models. A. Waiting time to a speciation event; B. Waiting time to an extinction event; C. Exponential distribution of waiting times until the next event; D. A birth-death tree with waiting times, with x denoting extinct taxa.

(Harmon, *Phylogenetic comparative methods*)




**The Dub's view** @DaBauz · Feb 13

You're such a #LIAR4Atheism! Show me where I - "...new species can't arise once every 3 years..."! You, and your #IDIOTS4Atheism friends, @curvemudgen, @ExMissionary & @Wearetheleavers... 1 / 3

cc - @pseudacris & @OregonState

3

**The Dub's view**
@DaBauz

Follow

Replying to @DaBauz @pseudacris and 45 others

The #ToE says - "...evolutionary change takes about one million years" - bit.ly/2BstLUz - and Mr. (possibly Professor) Josef Uyeda seems to agree. Using 1m years, per species, we'd need...

WAIT FOR IT...

WAIT FOR IT...

5*10^15 - Five Quadrillion years... HA!

2 / 3

**Lasting evolutionary change takes about one million years**
CORVALLIS, Ore. - In research that will help address a long-running debate and apparent contradiction between short- and long-term evolutionary change, scientists have discovered that...
today.oregonstate.edu

11:01 AM - 13 Feb 2018

**1** Like

4 1

# Diversification vs. Turnover

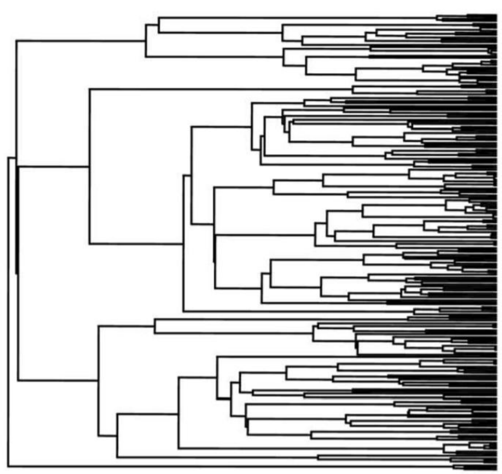
λ =Speciation rate

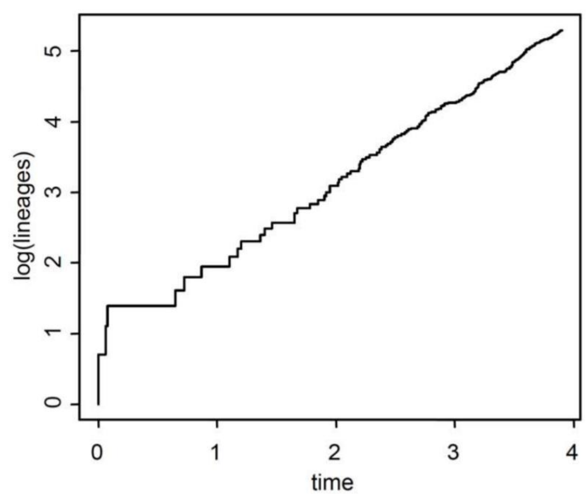
μ = Extinction rate

λ - μ = Diversification rate

μ/λ = Turnover rate

Yule process/Pure Birth model -> μ = 0






Under pure birth, lineages accrue log-linearly with time

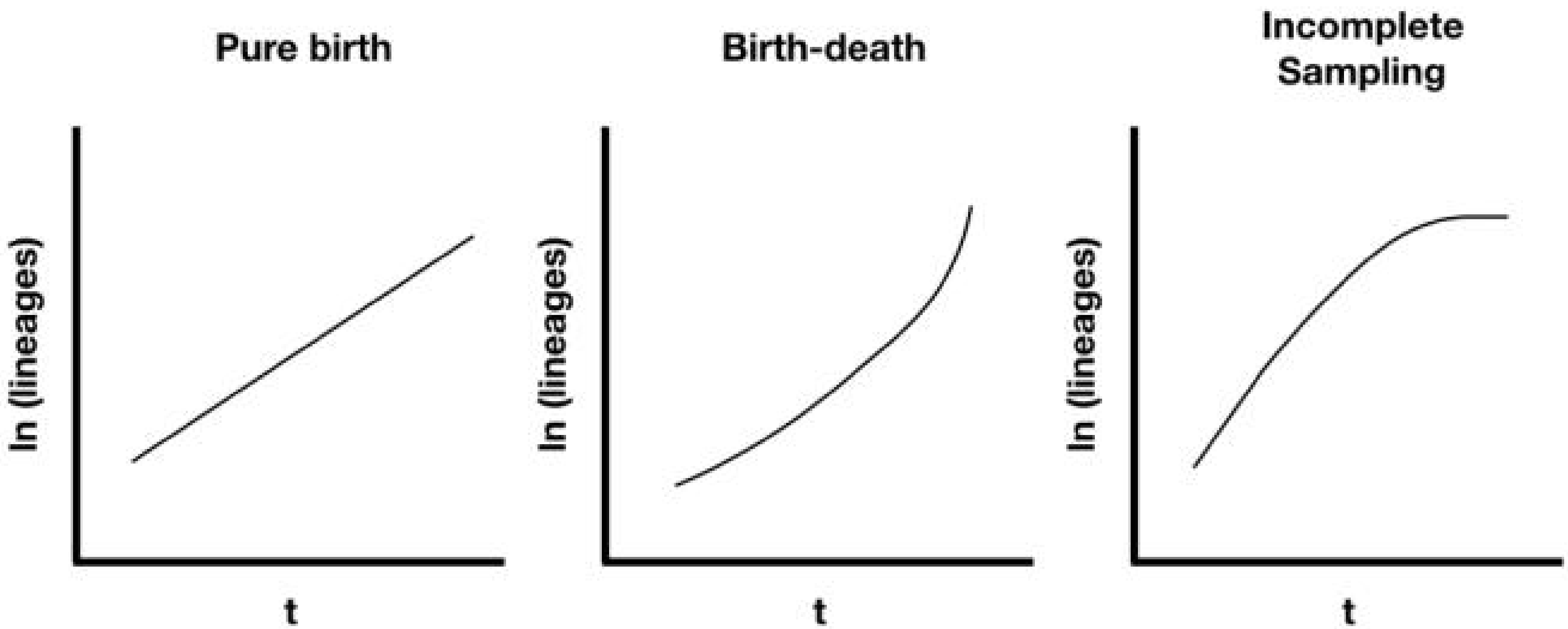
# A few notes...

Speciation and extinction correlated in nature, and in estimation

Estimating diversification and turnover often easier

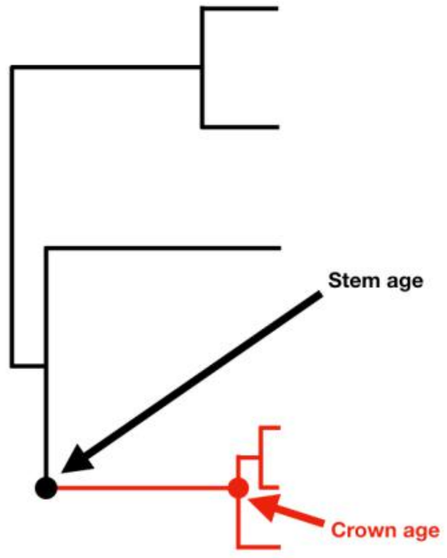
Can we even estimate extinction from extant-only data?

# Lineage through time plots



# Estimating diversification

Net diversification methods using clade age & diversity (can be used on unresolved trees)



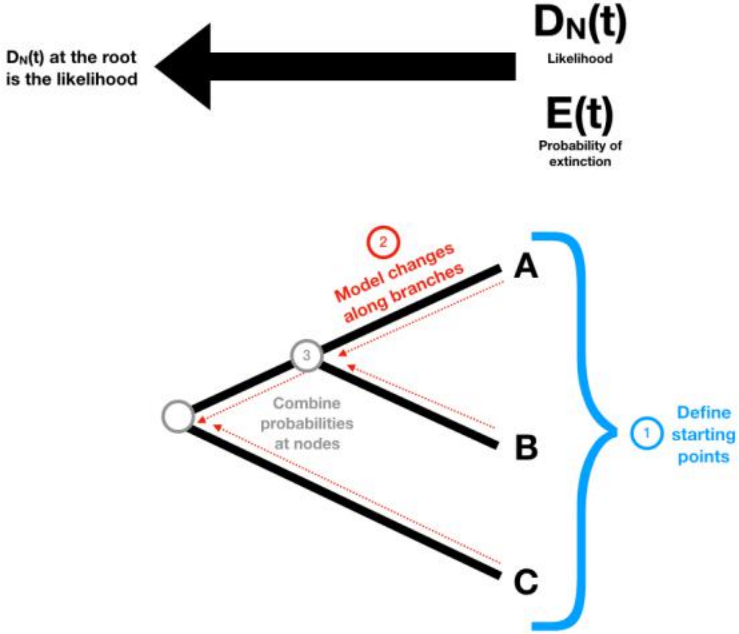

$$\hat{r} = \frac{ln(n)}{t_{stem}}$$

$$\hat{r} = \frac{ln(n) - ln(2)}{t_{crown}}$$

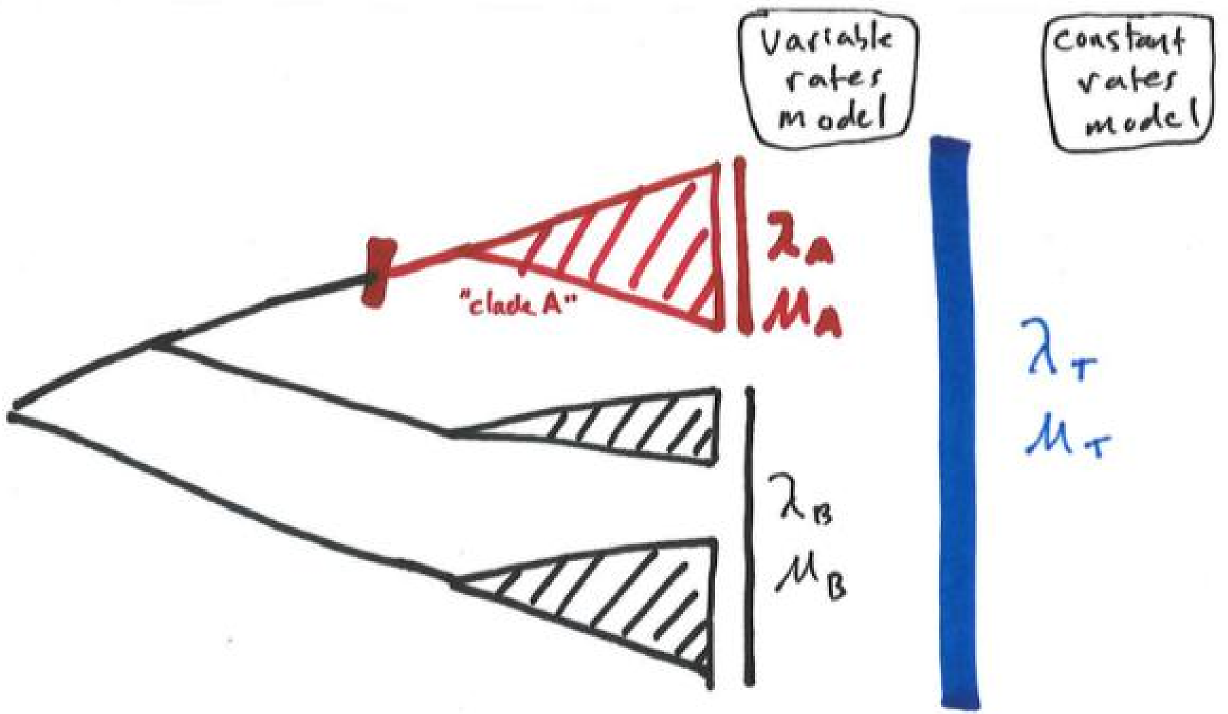
Magallon & Sanderson, 2001

# Estimating diversification

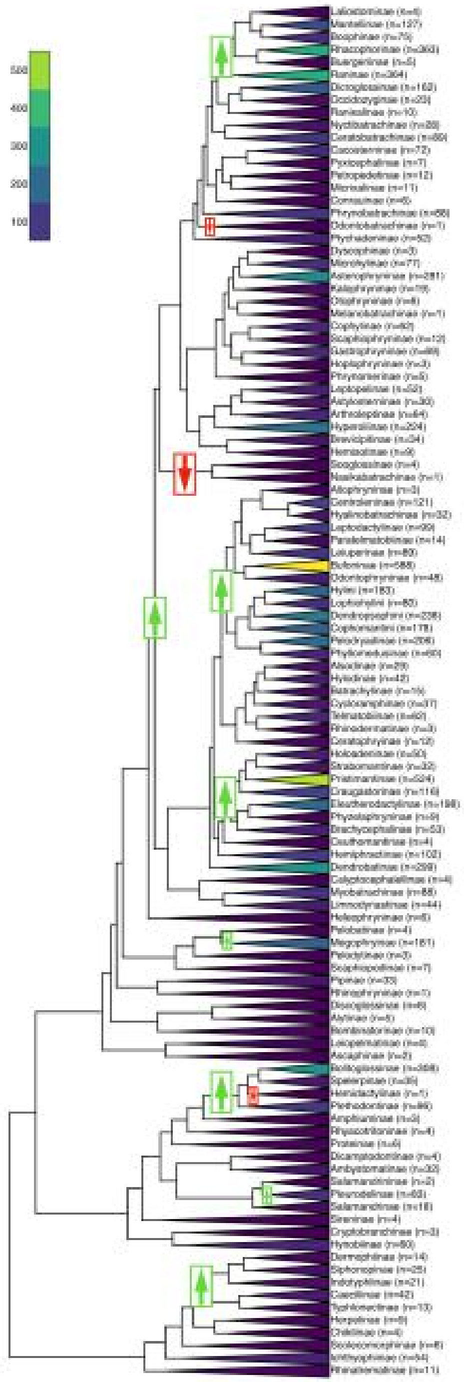
Using the distribution of branch lengths/waiting times (requires whole tree or partial tree and assumptions about sampling)



# Modeling heterogeneity in diversification




Hypothesis testing



"Phylogenetic Natural History" methods

Bayesian - BAMM (But see controversies)

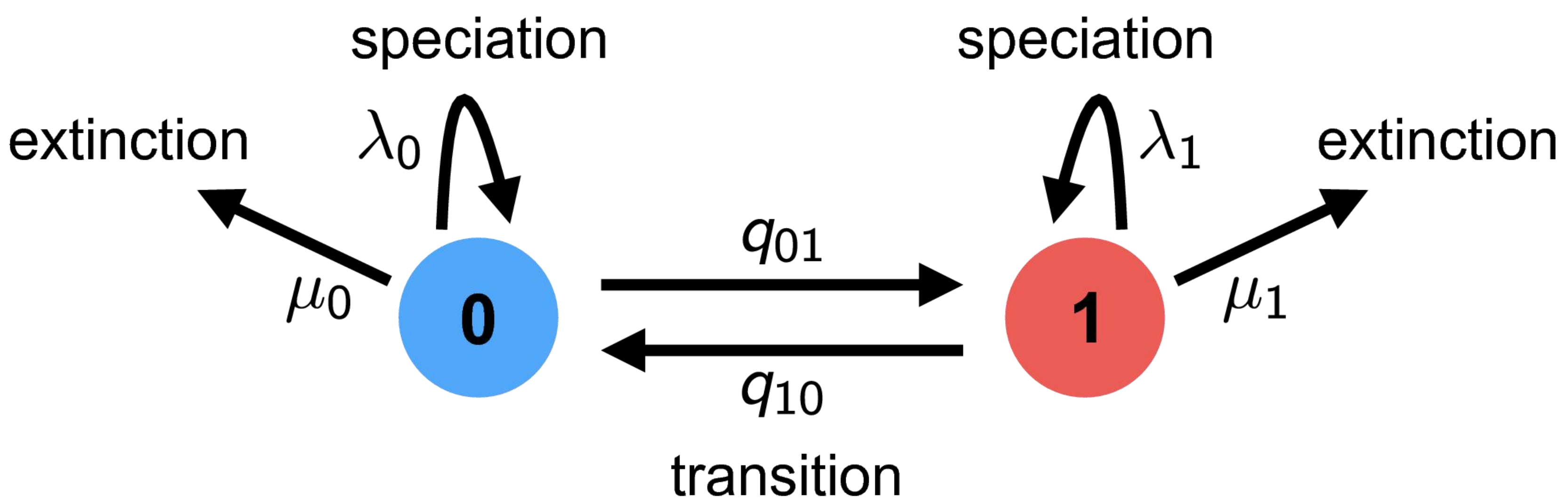
Likelihood (Stepwise AIC) - MEDUSA (but see problems with stepwise AIC)

# Other active areas of research:

- Incorporating fossils & sampling
- Diversity-dependent diversification
- Time-varying diversification
- Protracted Speciation
- Neutral theory (Hubbell) from ecology
- Trait-dependent diversification

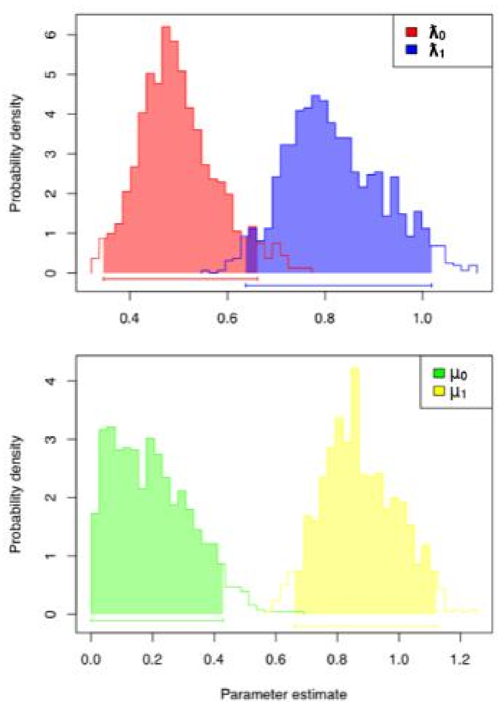
# Trait-dependent Diversification

*Species Selection (sometimes species sorting)*



# Why important?

Ancestral state reconstructions *biased* with trait-dependent diversification!



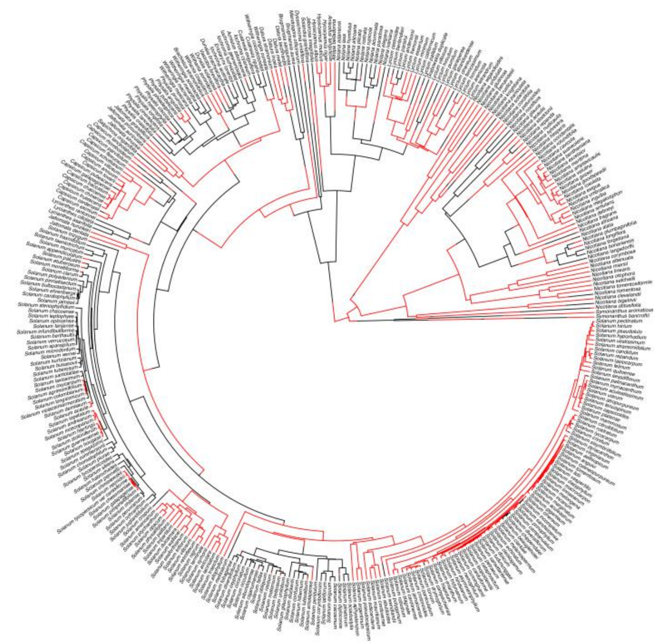



Figure 13.4. Data from Goldberg and Igic (2012) showing presence (red) and absence (black) of self-incomatibility among Solanaceae. Branches colored using stochastic character mapping under a model with distinct forwards and backwards rates; these reconstructions are biased if characters affect diversification rates.

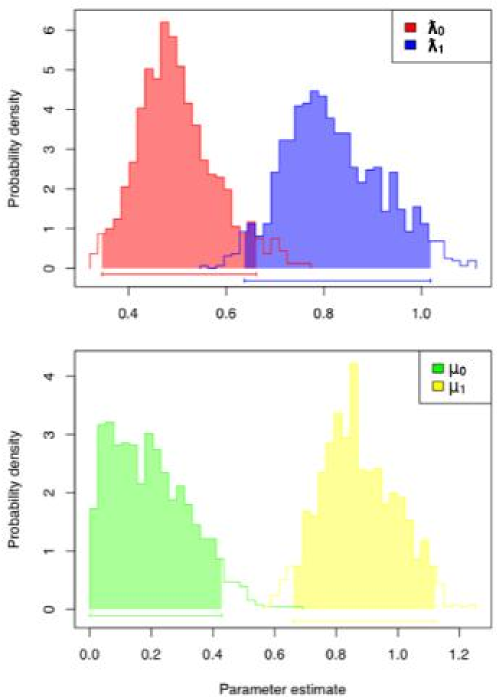
# Example:

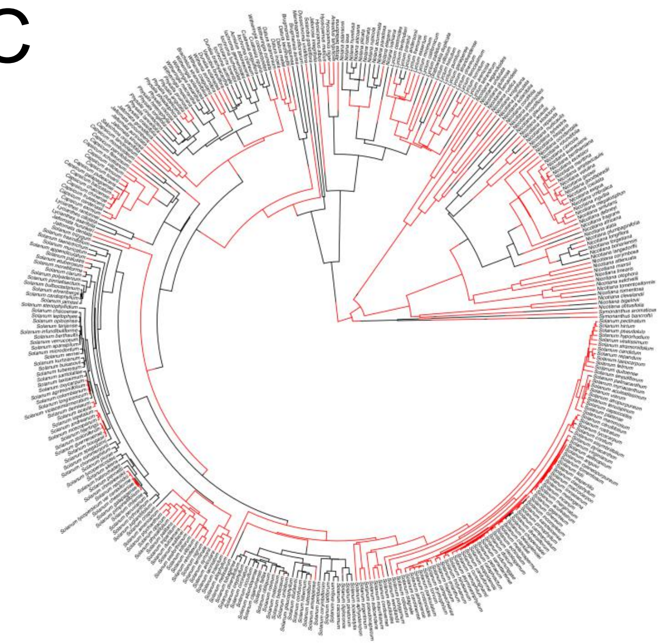
Self-incompatibility in plants: Prevents selfing

Equal distribution but...

Selfing results in higher speciation rates AND higher extinction rates

Ancestor more likely SI than SC



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# The SSE family of models

**Trait models:**

BiSSE: Binary State-dependent Speciation and Extinction (extensions for incompletely resolved trees)

MuSSE: Multiple SSE

QuaSSE: Quantitative SSE (but slow)

**Models where something special happens at nodes:**

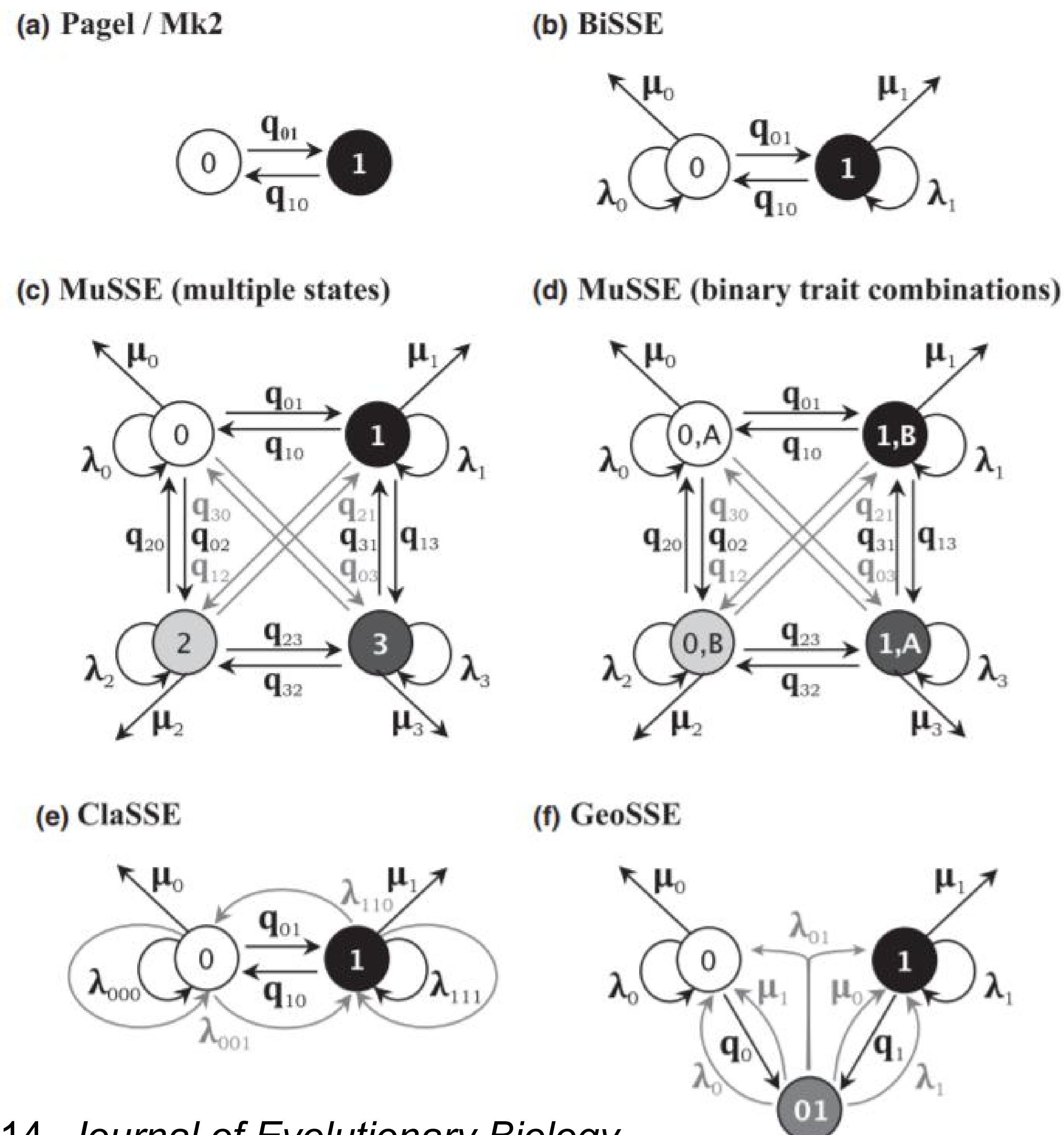
GeoSSE: Geographic SSE (DEC + SSE)

BiSSE-ness/ClaSSE: Cladogenetic SSE

**Hidden-state models that account for background heterogeneity:**

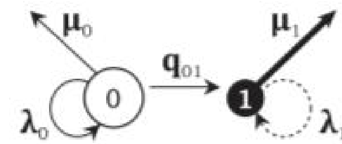
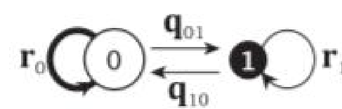
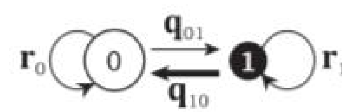
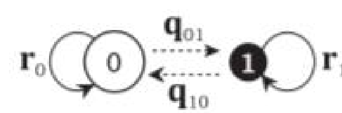
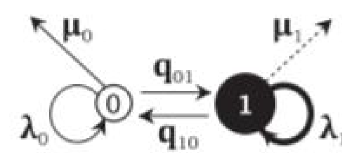
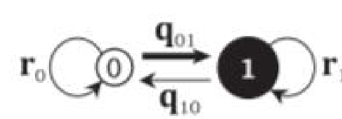
HiSSE: Hidden-State SSE (Solution to problem pointed out by Rabosky and Goldberg)

GeoHiSSE: Geographic Hidden-State SSE




Ng & Smith 2014, *Journal of Evolutionary Biology*

**Table 1** Alternative hypotheses that can be tested using BiSSE to explain disparities in clade size associated with binary traits. BiSSE simultaneously estimates rate parameters for the ancestral and derived state (0 and 1, respectively, represented as circles), each of which can be constrained for hypothesis testing: speciation ($\lambda_0$, $\lambda_1$), extinction ($\mu_0$, $\mu_1$) and transition rates ($q_{01}$, $q_{10}$). Diversification rates ($r_{0 \text{ or } 1}$) can be calculated as $r_0 = \lambda_0 - \mu_0$ and $r_1 = \lambda_1 - \mu_1$. Different hypotheses can be tested for statistical significance using either a maximum-likelihood framework, with likelihood ratio tests for nested models or Akaike information criterion, or a Bayesian framework by comparing credibility intervals from a Markov chain Monte Carlo sample of parameter values. Larger circles (for 0 or 1) indicate the state that is found in a higher proportion of extant taxa. Thicker arrows indicate higher parameter values (rates) whereas dotted arrows represent lower values. Note that these processes are not necessarily mutually exclusive.

| Process | Expectation | Schematic of expectation |
|---|---|---|
| Higher proportion of taxa with ancestral character state | | |
| (A1) *Evolutionary dead end*: Increased extinction rates associated with state 1 and irreversible character evolution | $\lambda_0 = \lambda_1$ or $\lambda_0 > \lambda_1$<br>$\mu_0 < \mu_1$<br>$q_{10} = 0$ |  |
| (A2) *Asymmetrical diversification*: Higher diversification rates in the ancestral state | $r_0 > r_1$<br>$q_{01} = q_{10}$ |  |
| (A3) *Asymmetrical transitions (directional evolution)*: Higher rate of character loss than gain | $r_0 = r_1$<br>$q_{01} < q_{10}$ |  |
| (A4) *Nonequilibrium dynamics*: Low transition from the ancestral state to the derived state | $r_0 = r_1$<br>$q_{01} = q_{10} \sim 0$ |  |
| Higher proportion of taxa with derived character state | | |
| (B1) *Key innovation*: Increased diversification of species with state 1 | $\lambda_0 < \lambda_1$<br>$\mu_0 = \mu_1$ or $\mu_0 > \mu_1$<br>$q_{01} = q_{10}$ |  |
| (B2) *Asymmetrical transitions (directional evolution)*: Higher rate of character gain than loss | $r_0 = r_1$<br>$q_{01} > q_{10}$ |  |

Ng & Smith 2014, *Journal of Evolutionary Biology*

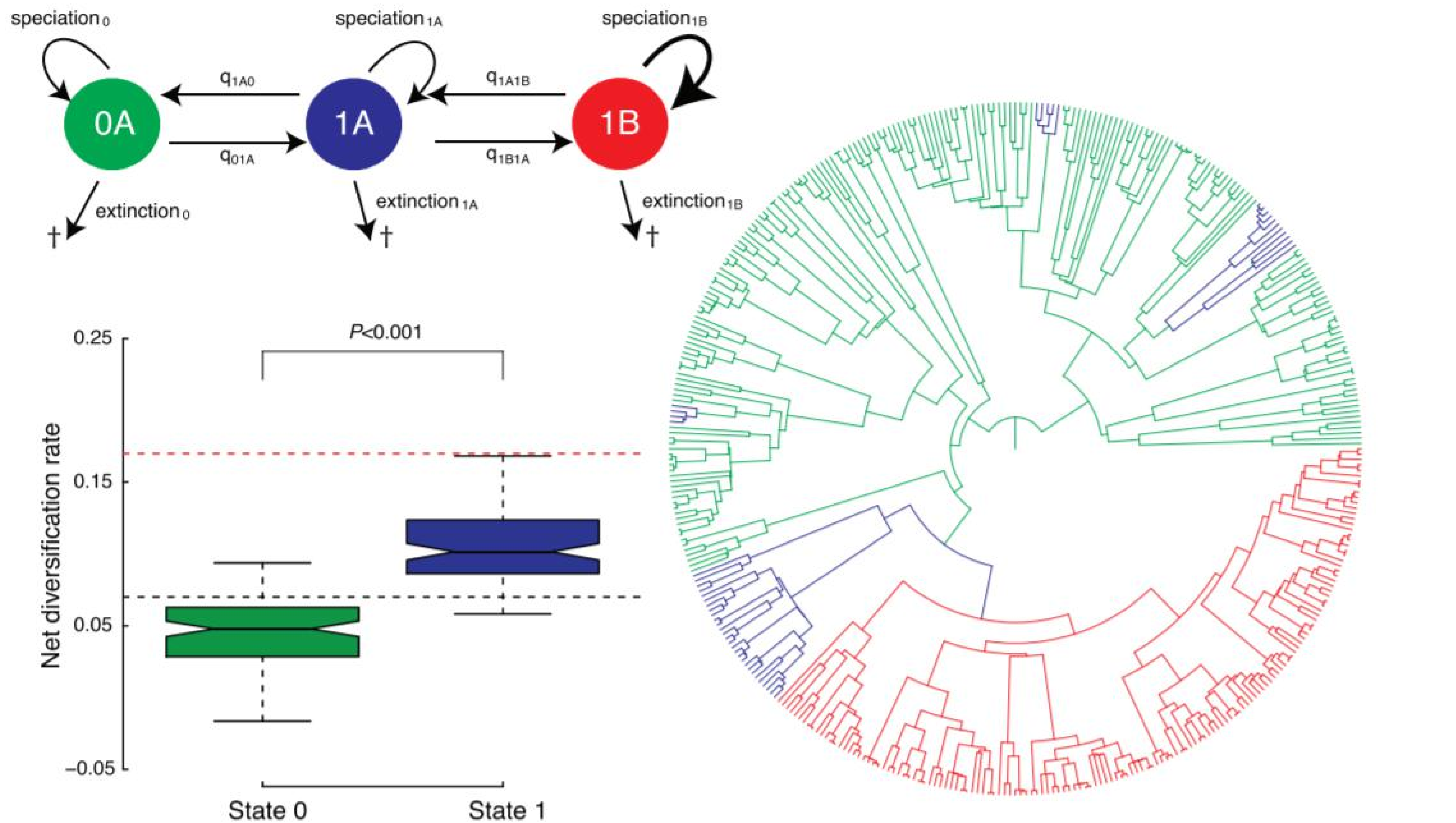



FIGURE 1. The conceptual problem with the presence of hidden states in the application of state-dependent models of speciation and extinction. Here related to state 0 and 1 is an unmeasured third variable with states *A* and *B*, and state *B* has twice the diversification rate of *A*. This trait is "hidden" because it is not observed in the tip data. If state 1 happens to be a prerequisite for evolving state *B*, all the state 0 branches will have state *A*, but some branches in state 1 will have state *A* and some will have state *B*. Thus, state 1 actually takes on two states, 1*A* when the hidden state with higher diversification rate is absent, and 1*B* when the hidden state with higher diversification rate is present. As shown in the example tree from a simulated tree and trait data, transitions to this unmeasured variable naturally produces nested shifts toward higher rates of diversification within clades comprised of species observed in state 1. When we run 100 simulations of this particular model and fit the resulting data sets in BiSSE, the model infers state 1 as being associated with a significantly higher diversification rates.

# Next time: Diversitree lab