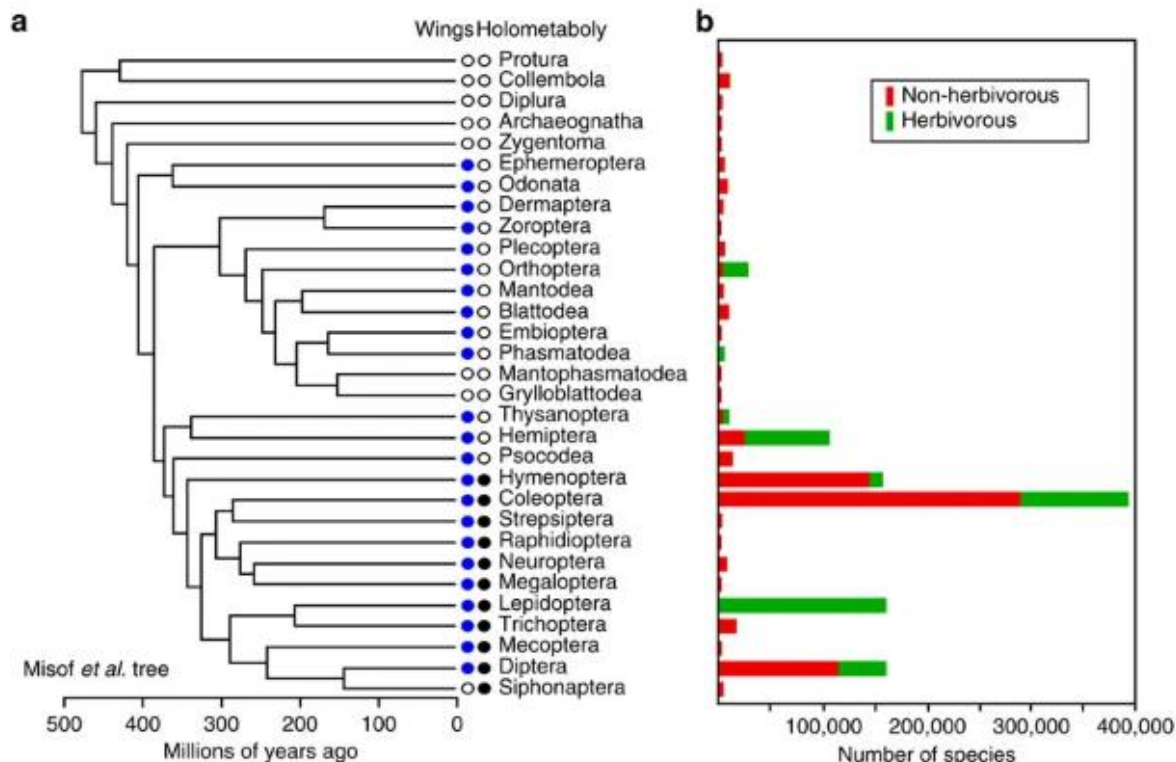


Diversification & SSE models

Trait-dependent diversification

One approach: Estimate net div in a bunch of clades, estimate trait (prop/freq) in same clades, see if correlated (w/PGLS)

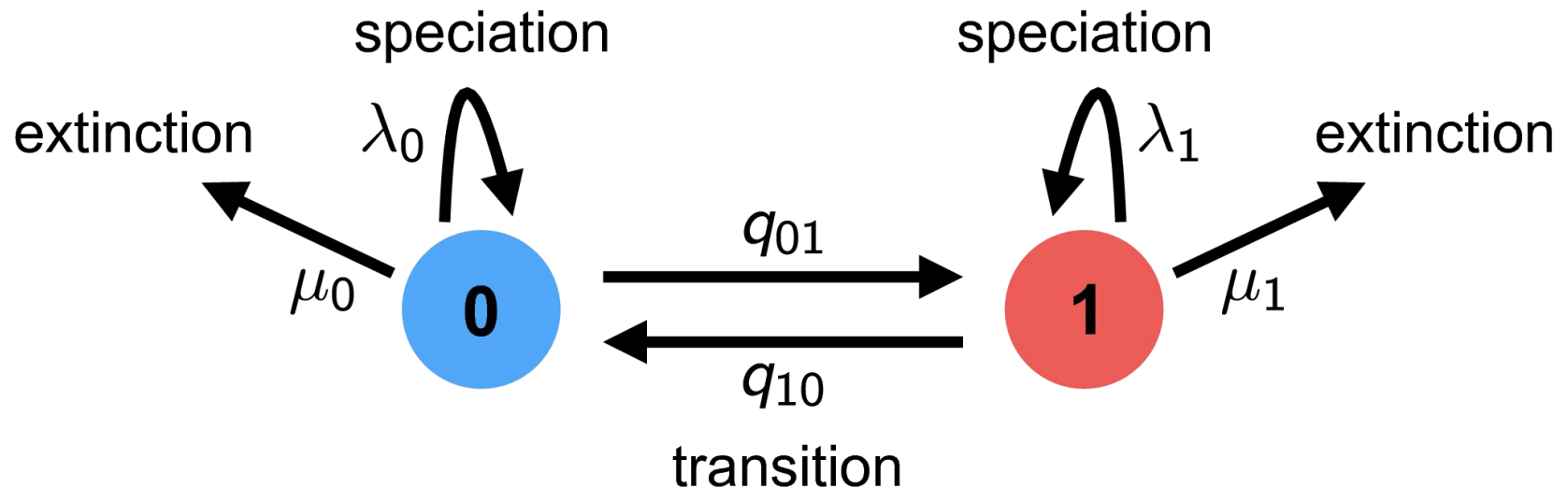
Figure 1: Phylogenies of insect orders and distributions of species richness and herbivory and other traits among clades.



Trait-dependent Diversification

Species Selection (sometimes species sorting)

-- Controversial?!? Not anymore!



Why important?

Ancestral state reconstructions *biased* with trait-dependent diversification!
(Maddison 2007)

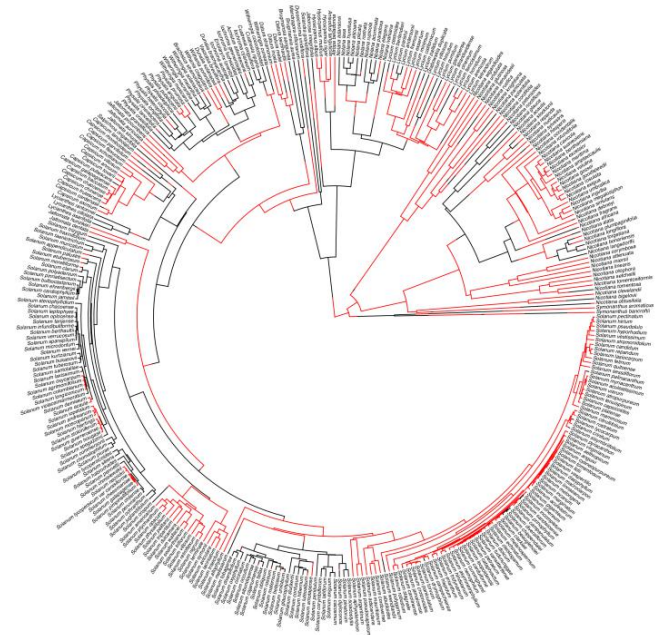
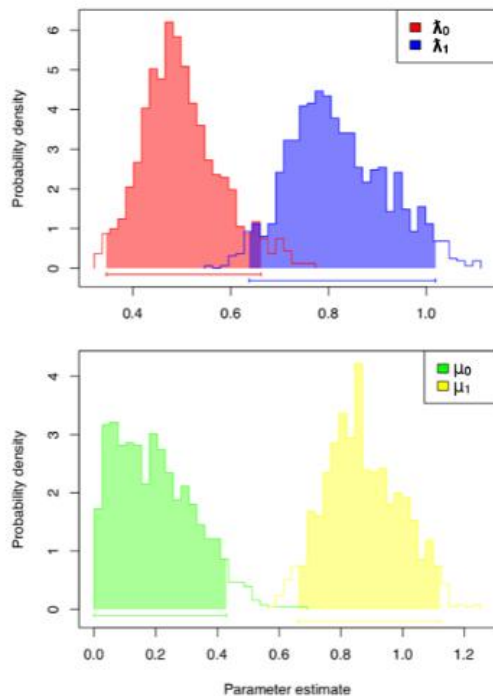
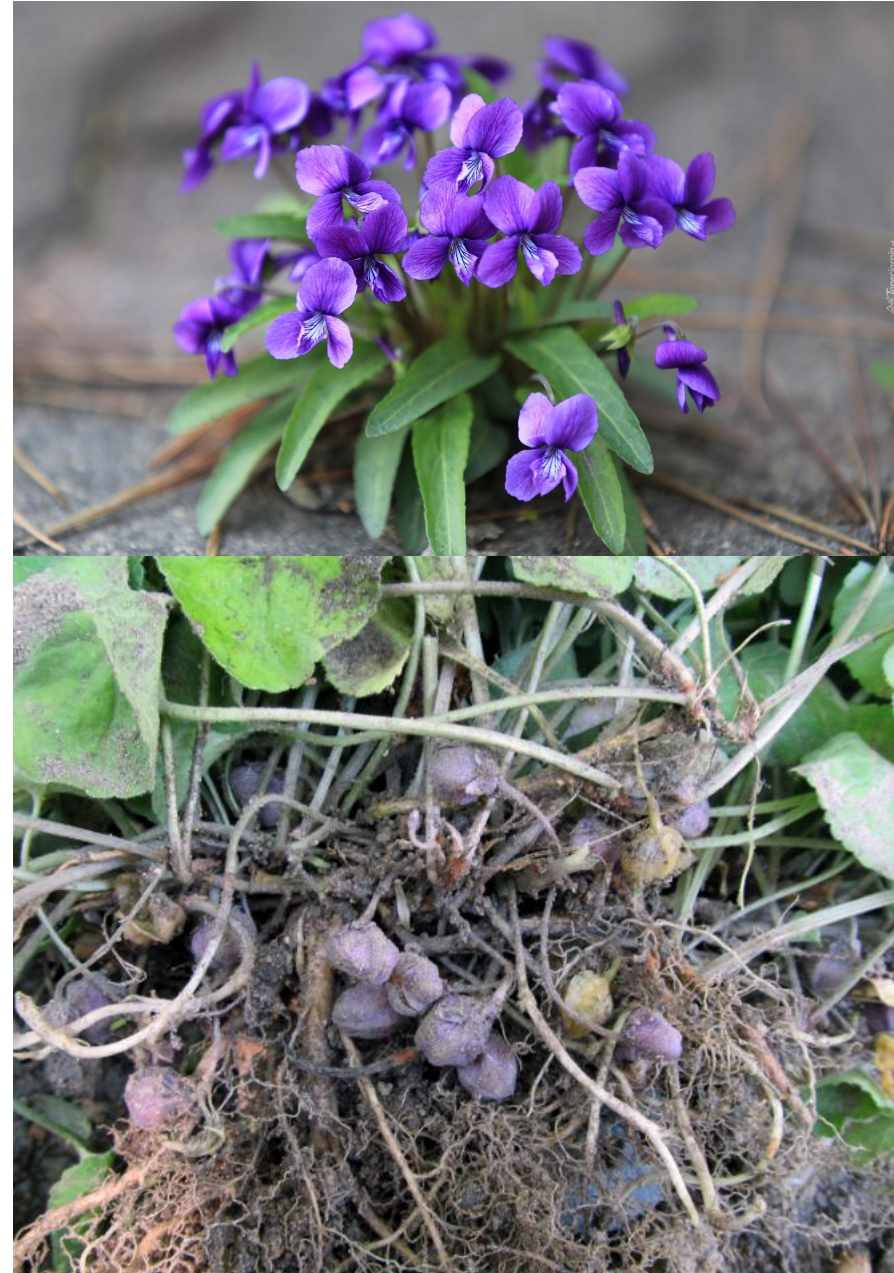


Figure 13.4. Data from Goldberg and Igic (2012) showing presence (red) and absence (black) of self-incompatibility among Solanaceae. Branches colored using stochastic character mapping under a model with distinct forwards and backwards rates; these reconstructions are biased if characters affect diversification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

Which is better?
How will it affect
speciation/extinction?

Self-incompatibility
(Obligate outcrossing)

Self-compatibility
(Selfing possible)



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

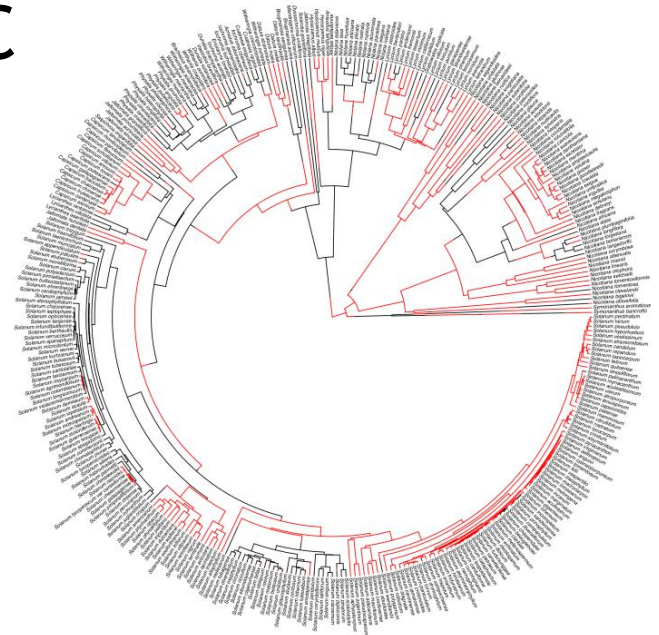
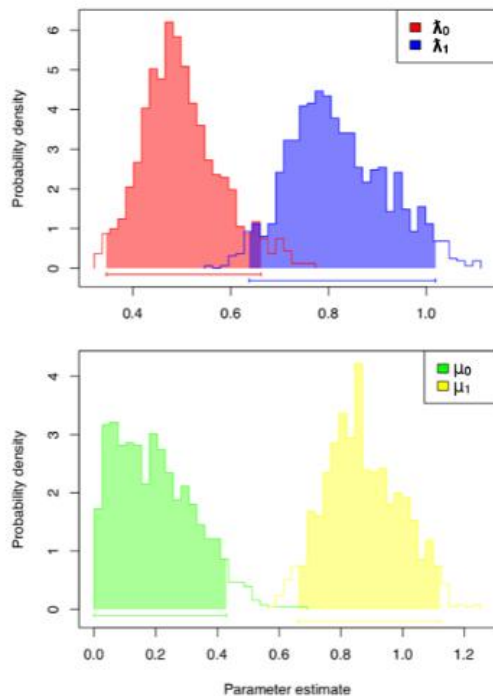


Figure 13.4. Data from Goldberg and Iqic (2012) showing presence (red) and absence (black) of self-incompatibility among Solanaceae. Branches colored using stochastic character mapping under a model with distinct forwards and backwards rates; these reconstructions are biased if characters affect diversification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

A word about Ancestral State Reconstruction...

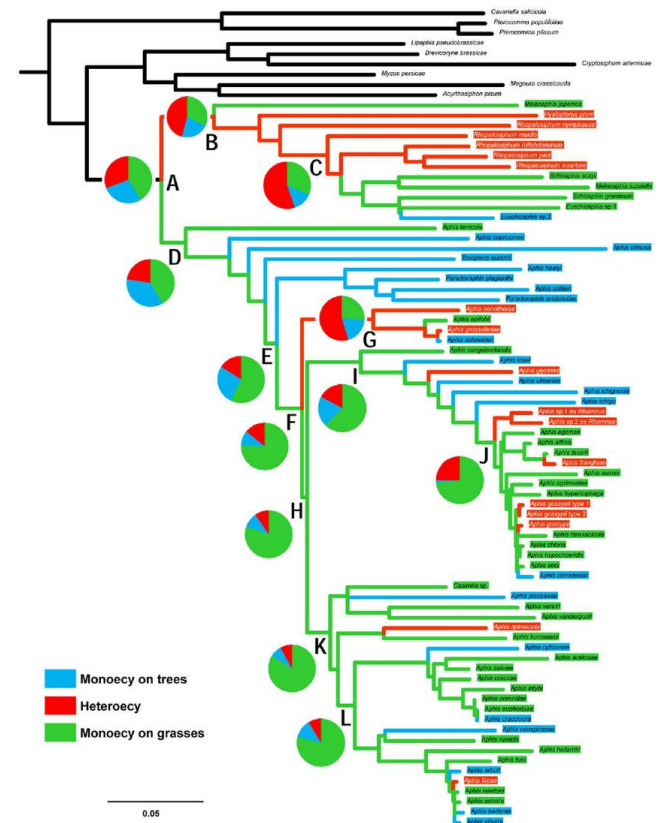
Whether under BM/OU/CTMC etc.

ML: Assumes ML param. are known without error, uncertainty is assuming you know the true model without error

Since we are always uncertain about the model, we should always assume more uncertainty

Can be even worse: BM vs. BM with a trend
CI for ancestral state under BM vs.
BM w/trend?

Darwinian uncertainty principle



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)

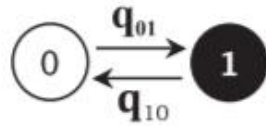
BiSSE-ness/ClaSSE: Cladogenetic SSE

Hidden-state models that account for background heterogeneity:

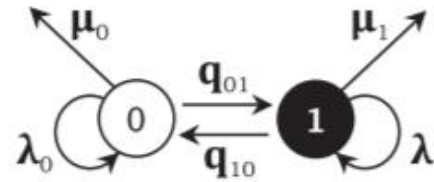
HiSSE: Hidden-State SSE (Solution to problem pointed out by Rabosky and Goldberg)

GeoHiSSE: Geographic Hidden-State SSE

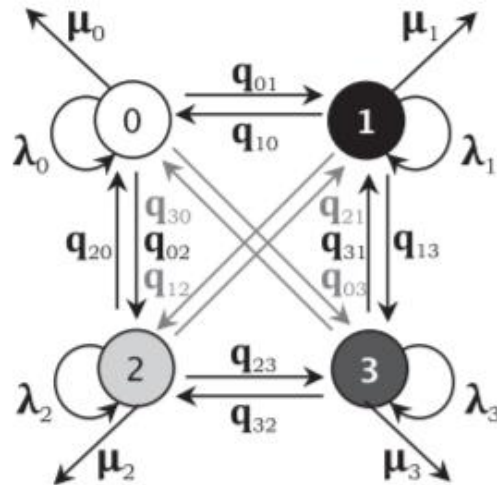
(a) Pagel / Mk2



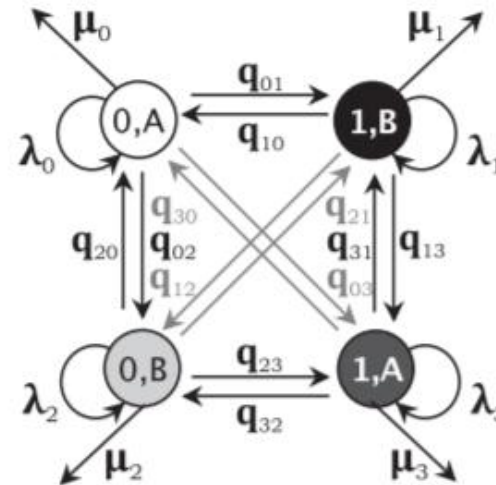
(b) BiSSE



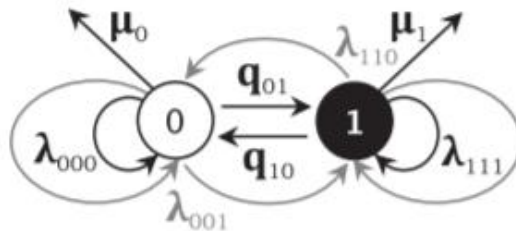
(c) MuSSE (multiple states)



(d) MuSSE (binary trait combinations)



(e) ClaSSE



(f) GeoSSE

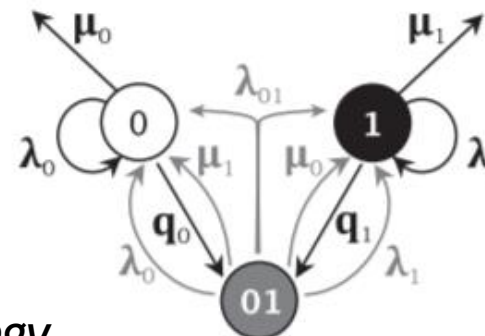


Table 1 Alternative hypotheses that can be tested using BiSSE to explain disparities in clade size associated with binary traits. BiSSE simultaneously estimates rate parameters for the ancestral and derived state (0 and 1, respectively, represented as circles), each of which can be constrained for hypothesis testing: speciation (λ_0 , λ_1), extinction (μ_0 , μ_1) and transition rates (q_{01} , q_{10}). Diversification rates (r_0 or r_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) <i>Evolutionary dead end</i> : Increased extinction rates associated with state 1 and irreversible character evolution	$\lambda_0 = \lambda_1$ or $\lambda_0 > \lambda_1$ $\mu_0 < \mu_1$ $q_{10} = 0$	
(A2) <i>Asymmetrical diversification</i> : Higher diversification rates in the ancestral state	$r_0 > r_1$ $q_{01} = q_{10}$	
(A3) <i>Asymmetrical transitions (directional evolution)</i> : Higher rate of character loss than gain	$r_0 = r_1$ $q_{01} < q_{10}$	
(A4) <i>Nonequilibrium dynamics</i> : Low transition from the ancestral state to the derived state	$r_0 = r_1$ $q_{01} = q_{10} \sim 0$	
Higher proportion of taxa with derived character state		
(B1) <i>Key innovation</i> : Increased diversification of species with state 1	$\lambda_0 < \lambda_1$ $\mu_0 = \mu_1$ or $\mu_0 > \mu_1$ $q_{01} = q_{10}$	
(B2) <i>Asymmetrical transitions (directional evolution)</i> : Higher rate of character gain than loss	$r_0 = r_1$ $q_{01} > q_{10}$	

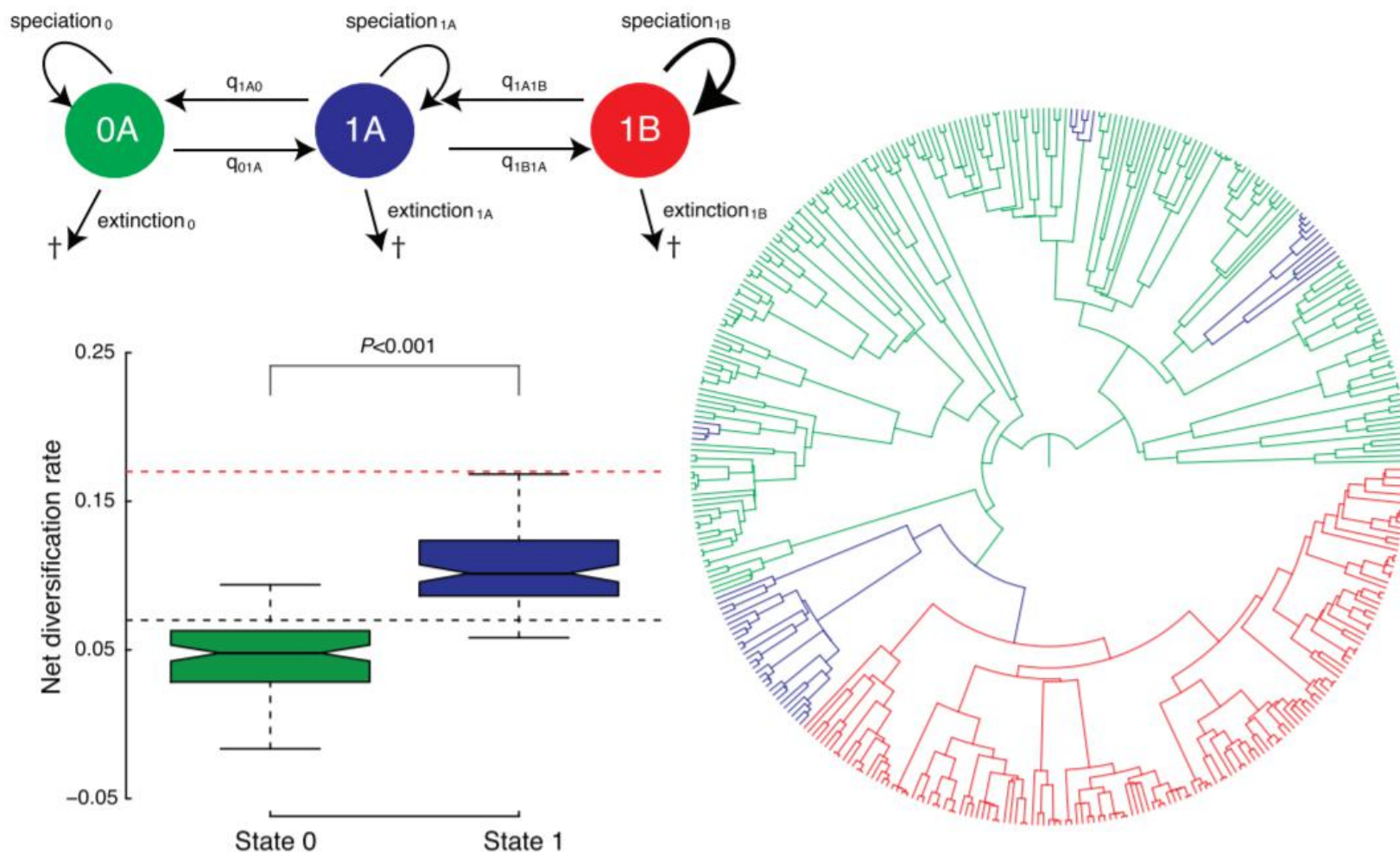


FIGURE 1. The conceptual problem with the presence of hidden states in the application of state-dependent models of speciation and extinction. Here related to state 0 and 1 is an unmeasured third variable with states A and B, and state B has twice the diversification rate of A. This trait is “hidden” 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, 1A when the hidden state with higher diversification rate is absent, and 1B 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.

Diversitree lab

