Characters and Diversification
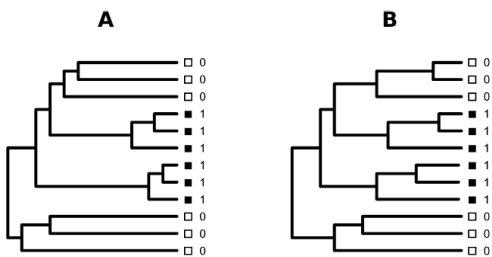
April 16, 2009

A   **B**

Fig. 1. Hypothetical phylogenies with a candidate key innovation (black boxes, state 1). Absence of the trait, state 0, is denoted by open boxes. The relative durations of terminal branches suggest that the character covaries with diversification rate in (A) but not in (B).
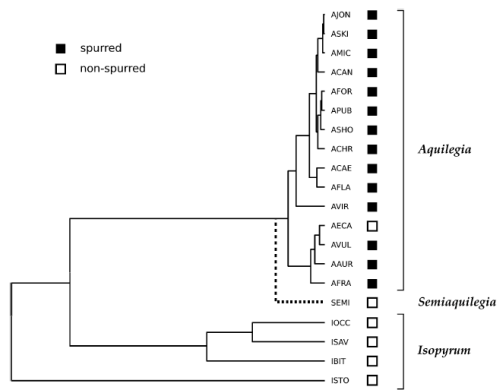

Fɪɢ. 4. ITS phylogeny of *Aquilegia* and *Isopyrum* showing one of approximately 10,000 trees sampled by Markov chain Monte Carlo under the assumption of a molecular clock. The hypothesized key innovation, floral nectar spurs, is designated by black boxes. The approximate position of *Semiaquilegia*, not included in this analysis but found by Hodges and Arnold (1995) to be the sister group of *Aquilegia*, is shown by the dotted line.
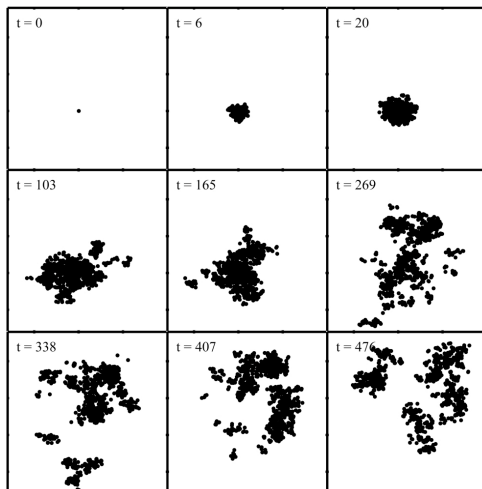
Outline

- Combining models for diversification and character evolution

- Older approaches to the problem

- BiSSE

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Combining models

- Lineage diversification: birth-death models
- Character evolution: Brownian motion
- Combine these two: Branching random walks

| t = 0 | t = 6 | t = 20 |
| t = 103 | t = 165 | t = 269 |
| t = 338 | t = 407 | t = 476 |

Pie and Weitz 2005

Moving beyond the "null"

- Is there a relationship between characters and lineage diversification
- For example, might some trait values be associated with higher rates of net diversification?
- Testing key innovations, etc.

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Diversity of Sister Clades
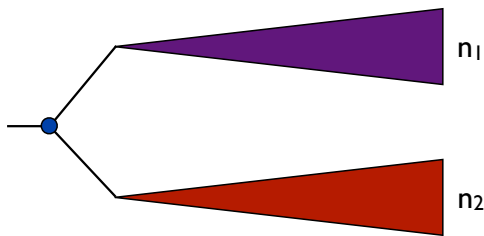
What is the expected distribution for n_1 and n_2 under BD?

Probability of a split at one node

$$Pr[(k,n-k)] = \begin{cases} \dfrac{2}{n-1} & k \neq n-k \\ \\ \dfrac{1}{n-1} & k = n-k \end{cases}$$

* Under any ERM model, including BD

Sister-clade Comparisons

- Compare pairs of sister clades, where one clade has the trait of interest and the other does not

- Under ERM, either clade is equally likely to be the larger of the two

- Use binomial test to evaluate significance

Binomial Probability
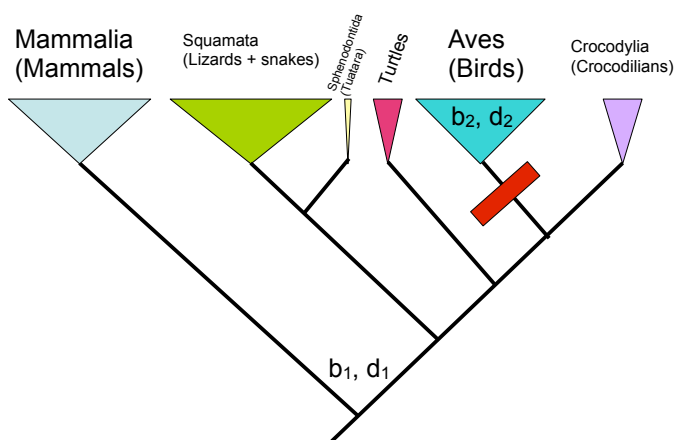
$$Pr(x) = \binom{n}{x} p^x (1-p)^{n-x}$$

x = number of "successes"
n = number of trials (sister pairs)
p = 0.5 (Pr[success] under H_o)

ML test of multiple rates

- Compare models where some parts of the tree have distinct speciation and/or extinction rates

- If you have likelihoods and the number of parameters, you can compare these models

Mammalia (Mammals) · Squamata (Lizards + snakes) · Sphenodontida (Tuatara) · Turtles · Aves (Birds) · Crocodylia (Crocodilians)

b_2, d_2

b_1, d_1

Model 1: b_1, d_1
lnL = -124.5

Model 2: b_1, d_1, b_2, d_2
lnL = -114.1

Compare with likelihood ratio test or AIC
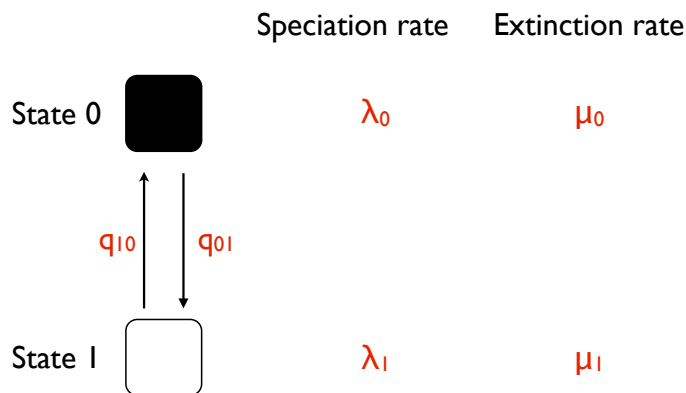
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BiSSE

- Binary state speciation and extinction
- Maddison et al. 2007

The BiSSE Model

		Speciation rate	Extinction rate
State 0		λ_0	μ_0
State 1		λ_1	μ_1

q_{10} q_{01}

Fitting the BiSSE model

t
$t+\Delta t$
N
A

Assume: $D_{N0}(t)$ and $D_{N1}(t)$
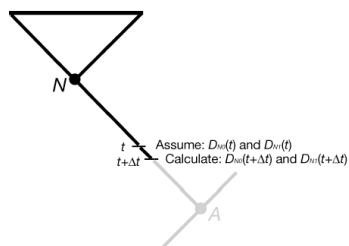Calculate: $D_{N0}(t+\Delta t)$ and $D_{N1}(t+\Delta t)$

FIGURE 1. Calculation of the probabilities (D) of the observed tree and character states, along a branch of the tree. We assume that we know the D's for time t on the branch and attempt to calculate them for time $t+\Delta t$.
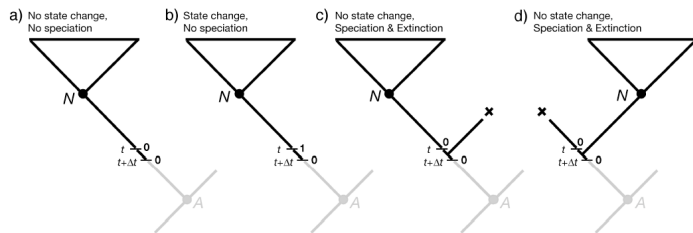
FIGURE 2. Alternative scenarios by which a lineage with state 0 at time $t+\Delta t$ on the branch might yield clade descended from node N but no other living descendants.
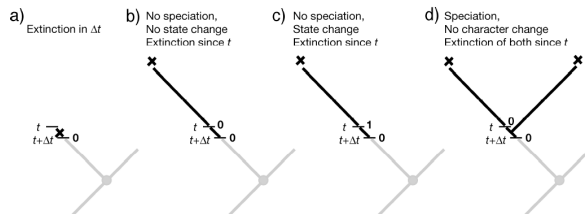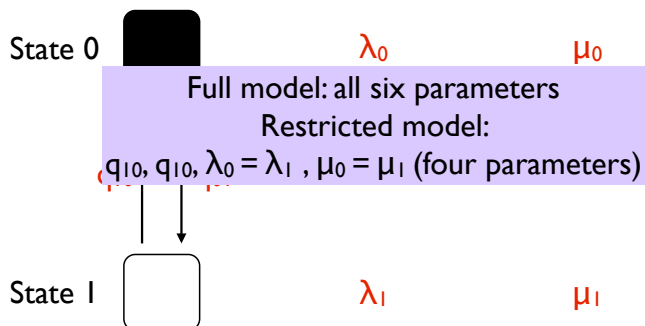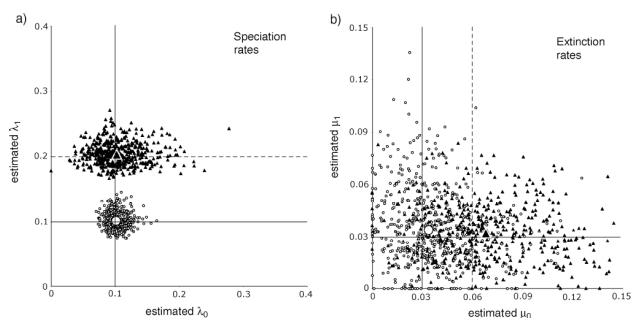

FIGURE 3. Alternative scenarios by which a lineage at time t with state 0 might go extinct.

The BiSSE Model

	Speciation rate	Extinction rate
State 0	λ_0	μ_0
State 1	λ_1	μ_1

Full model: all six parameters
Restricted model:
$q_{10}, q_{10}, \lambda_0 = \lambda_1 , \mu_0 = \mu_1$ (four parameters)
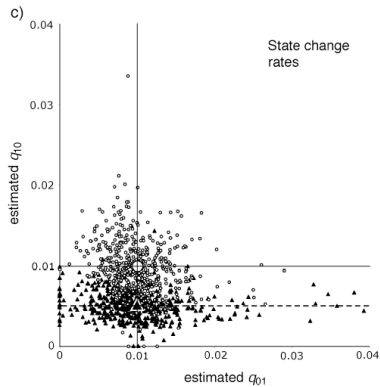
How well does BiSSE work?

How well does BiSSE work?

Summary: BiSSE

- Requires accurate tree, trait data for all living species

- Assumes diversification under variable rate birth-death model

- Can test whether certain character states affect speciation, extinction, or both

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