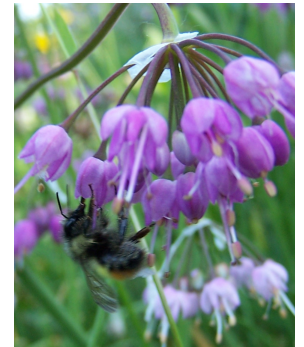# *Inferring the past for traits that alter speciation and extinction rates*

Sally Otto

Wayne Maddison   Rich FitzJohn

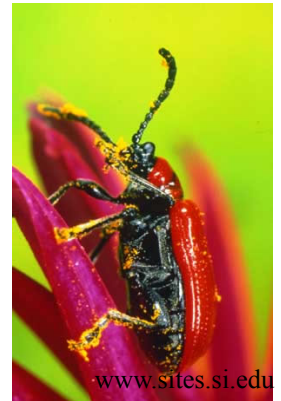Peter Midford

University of British Columbia

Comparative analyses

* *Impact of a trait on speciation and extinction*

- *Herbivory in insects (Mitter et al. 1988)*

- *Defense mechanisms in plants (Farrell et al. 1991)*

- *Floral symmetry (Sargent 2004)*

- *Tropical/temperate distribution (Weir and Schluter 2007)*

Comparative analyses
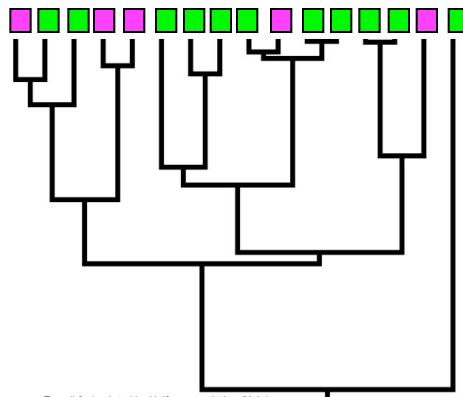
* Trait transitions and ancestral states

- _Gain/loss of migratory behavior (Kondo and Omland 2007)_

- _Biogeographic range (Ree and Smith 2008)_

- _Ancestral state of vivipary in mangroves (Shi et al 2005)_

Comparative analyses

* But what if an evolving trait influences the rate of speciation and extinction?

- Diversification rates will vary over a phylogeny

Comparative analyses

* But what if an evolving trait influences the rate of speciation and extinction?

- Diversification rates will vary over a phylogeny

Sister-species analysis

Comparative analyses

* But what if an evolving trait influences the rate of speciation and extinction?

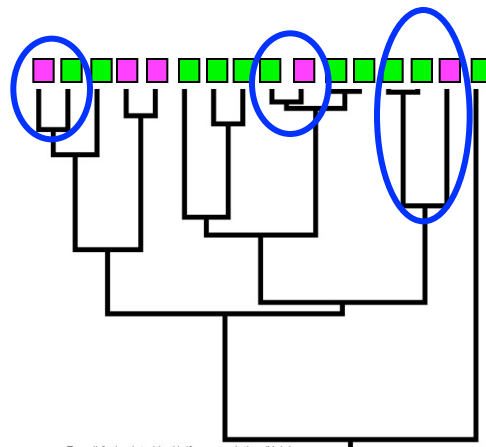*- Diversification rates will vary over a phylogeny*
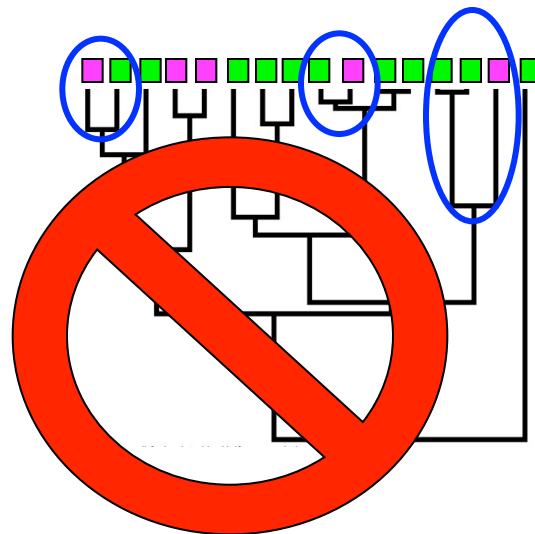

Sister-species analysis

Comparative analyses

But what if an evolving trait influences the rate of speciation and extinction?

- Diversification rates will vary over a phylogeny

Sister-species analysis

Cannot assess whether higher diversification is due to increased speciation, decreased extinction, or both.

Comparative analyses

* But what if an evolving trait influences the rate of speciation and extinction?

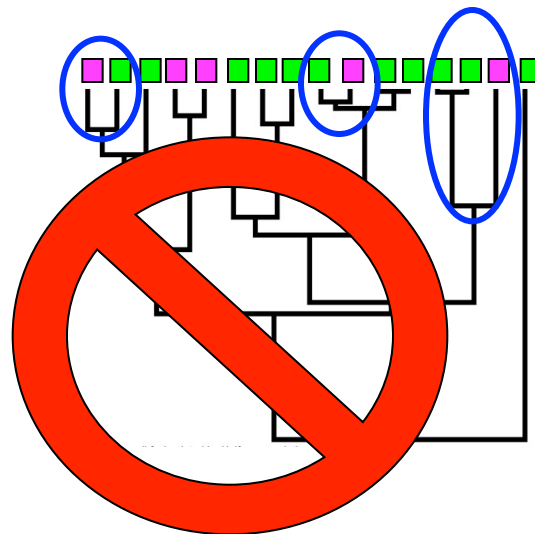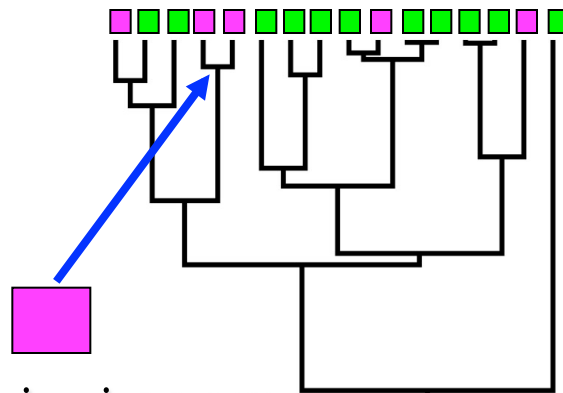   *- Diversification rates will vary over a phylogeny*

    - Trait inference may be misled

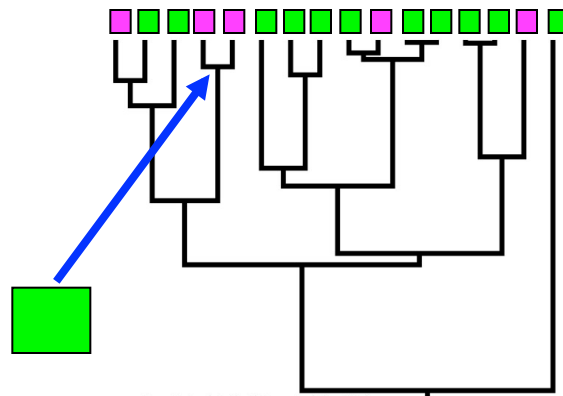*<u>Ancestral reconstruction:</u>*
No effects on speciation/extinction

Comparative analyses

* But what if an evolving trait influences the rate of speciation and extinction?
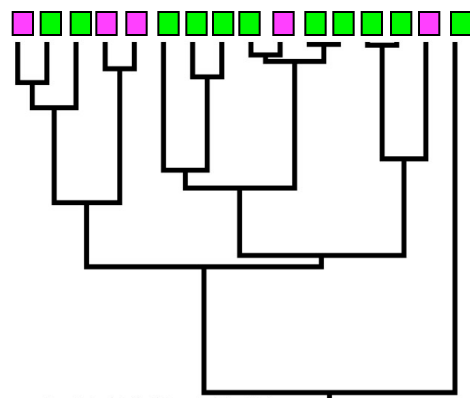
    - Diversification rates will vary over a phylogeny

    - Trait inference may be misled
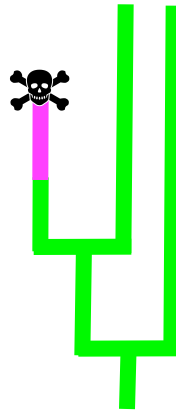

Ancestral reconstruction:
If species with purple trait
are prone to extinction

We have been developing likelihood methods to infer parameters of interest given a phylogeny and the states of present-day species.
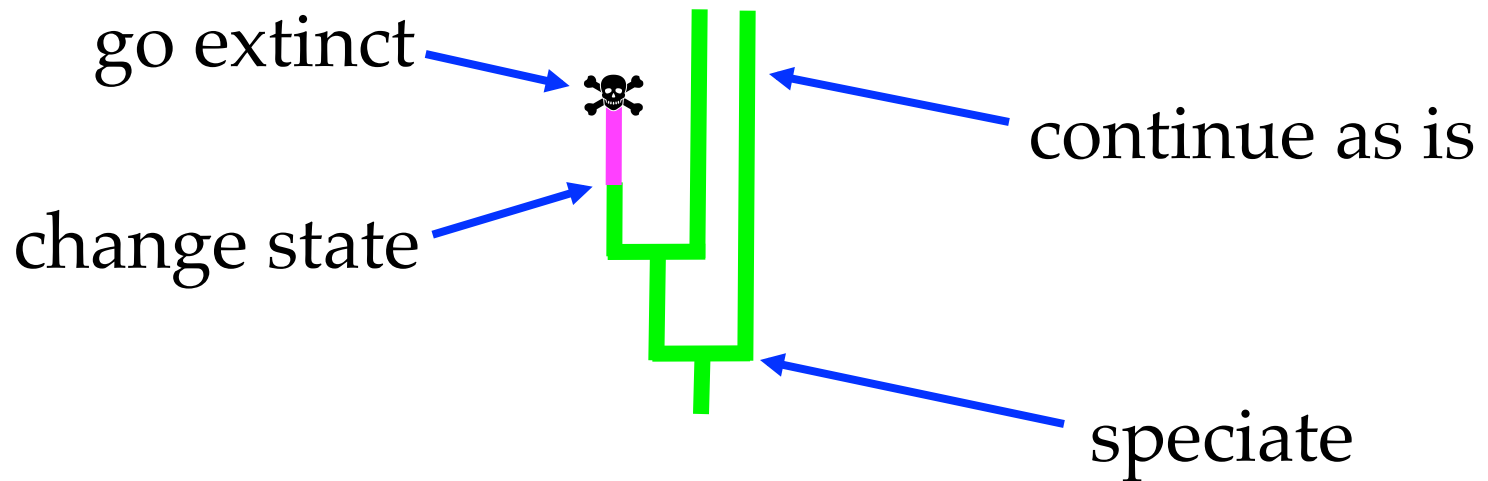
At time *t*, a lineage exists in state 0 (■) or state 1 (■)

In a short interval of time, the lineage might:

At time t, a lineage exists in state 0 (🟩) or state 1 (🟪)
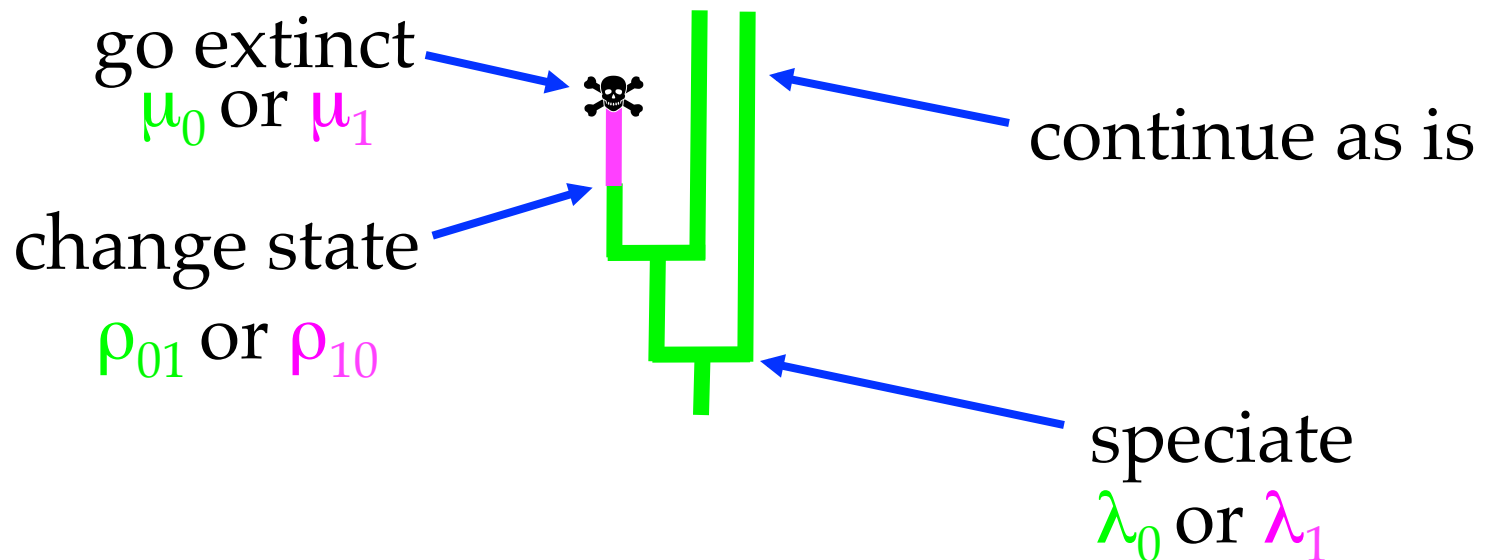
In a short interval of time, the lineage might:

go extinct

continue as is

change state

speciate

At time t, a lineage exists in state 0 (■) or state 1 (■)

In a short interval of time, the lineage might:

go extinct
μ_0 or μ_1

change state
ρ_{01} or ρ_{10}

continue as is

speciate
λ_0 or λ_1

(Forward rates)
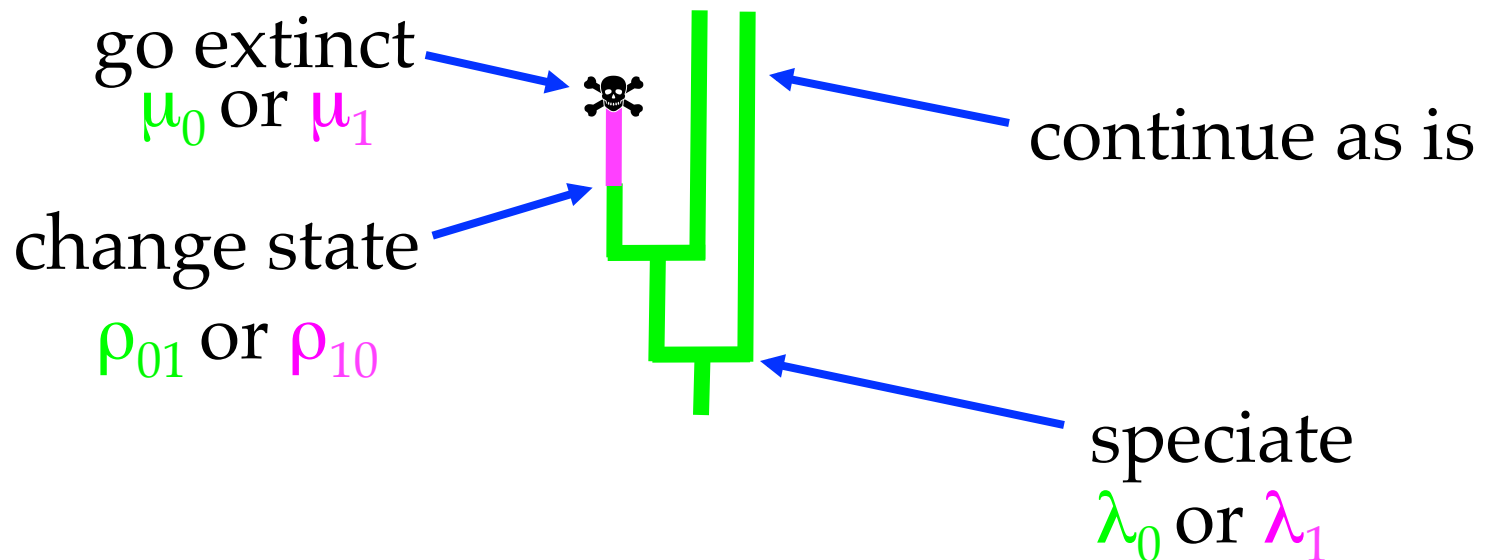
At time *t*, a lineage exists in state 0 (■) or state 1 (■)

In a short interval of time, the lineage might:

go extinct
μ_0 or μ_1

change state
ρ_{01} or ρ_{10}

continue as is

speciate
λ_0 or λ_1

For example, if species in state 1 are more prone to extinction, then $\mu_0 < \mu_1$.

BiSSE: A likelihood approach

① *Consider possible events*

No state change, No speciation

State change, No speciation

No state change, Speciation & Extinction

No state change, Speciation & Extinction

N

N

N

N

t
t+Δt

0
0

2

t
t+Δt

1
0

3

t
t+Δt

0
0

4

t
t+Δt

0
0

5

A

A

A

A
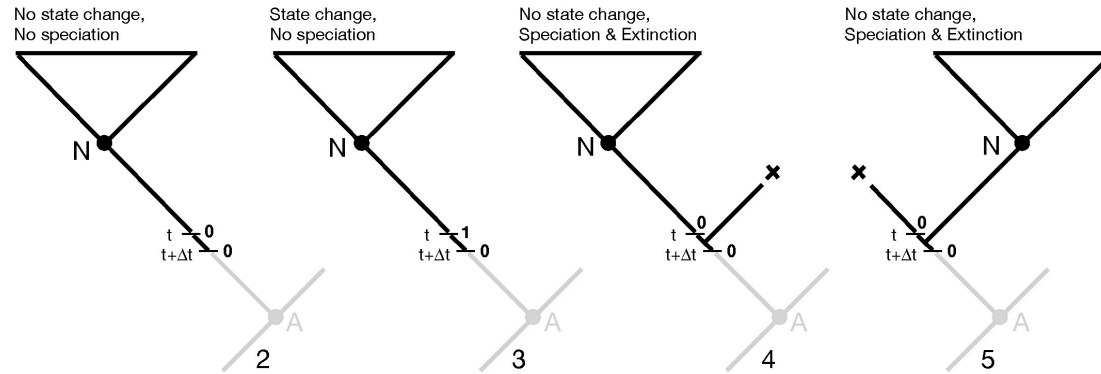
② *Derive differential equations*

Probabilities of lineage evolving as observed (D_0 and D_1):

$$\frac{\mathrm{d}D_{N0}}{\mathrm{d}t} = -\left(\lambda_0 + \mu_0 + \rho_{01}\right) D_{N0} + \rho_{01}\, D_{N1} + 2\,\lambda_0\, E_0(t)\, D_{N0}$$
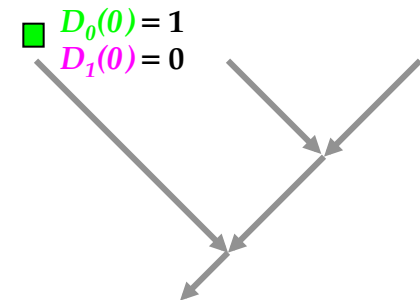
$$\frac{\mathrm{d}D_{N1}}{\mathrm{d}t} = -\left(\lambda_1 + \mu_1 + \rho_{10}\right) D_{N1} + \rho_{10}\, D_{N0} + 2\,\lambda_1\, E_1(t)\, D_{N1}$$

Probabilities of extinction before the present (E_0 and E_1):

$$\frac{\mathrm{d}E_0}{\mathrm{d}t} = \mu_0 - \left(\mu_0 + \rho_{01} + \lambda_0\right) E_0 + \rho_{01}\, E_1 + \lambda_0\, E_0^{\,2}$$

$$\frac{\mathrm{d}E_1}{\mathrm{d}t} = \mu_1 - \left(\mu_1 + \rho_{10} + \lambda_1\right) E_1 + \rho_{10}\, E_0 + \lambda_1\, E_1^{\,2}$$

③ *Move from tree tips to root*

$D_0(0) = 1$
$D_1(0) = 0$

BiSSE: A likelihood approach
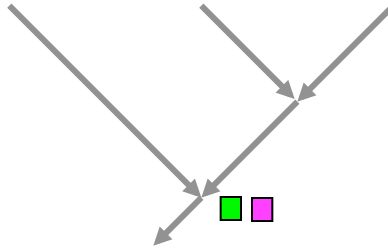
Once at the root, we sum over the root states to get an overall likelihood of observing the data (the states of present day species), given the phylogeny and the model parameters (λ_0, λ_1, μ_0, μ_1, ρ_{01}, ρ_{10}).

- Allows hypothesis testing using LRT (e.g., $\lambda_0 = \lambda_1$)
- Provides credibility intervals for parameters of interest
- Can be used in a Bayesian framework to provide posterior probability distributions
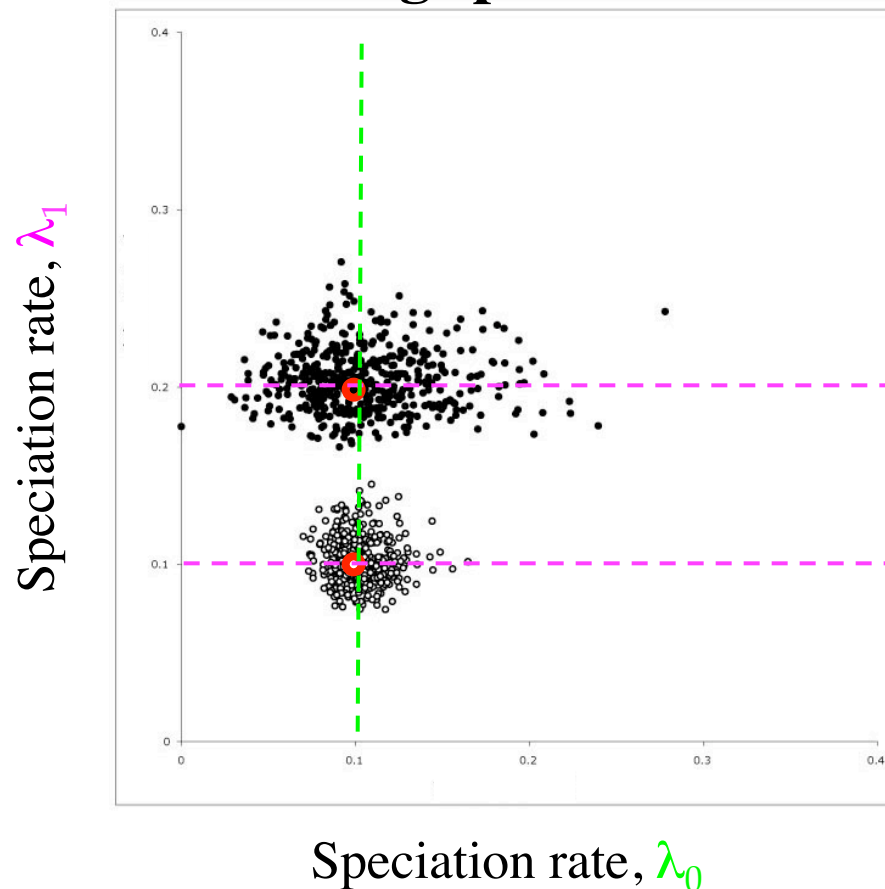
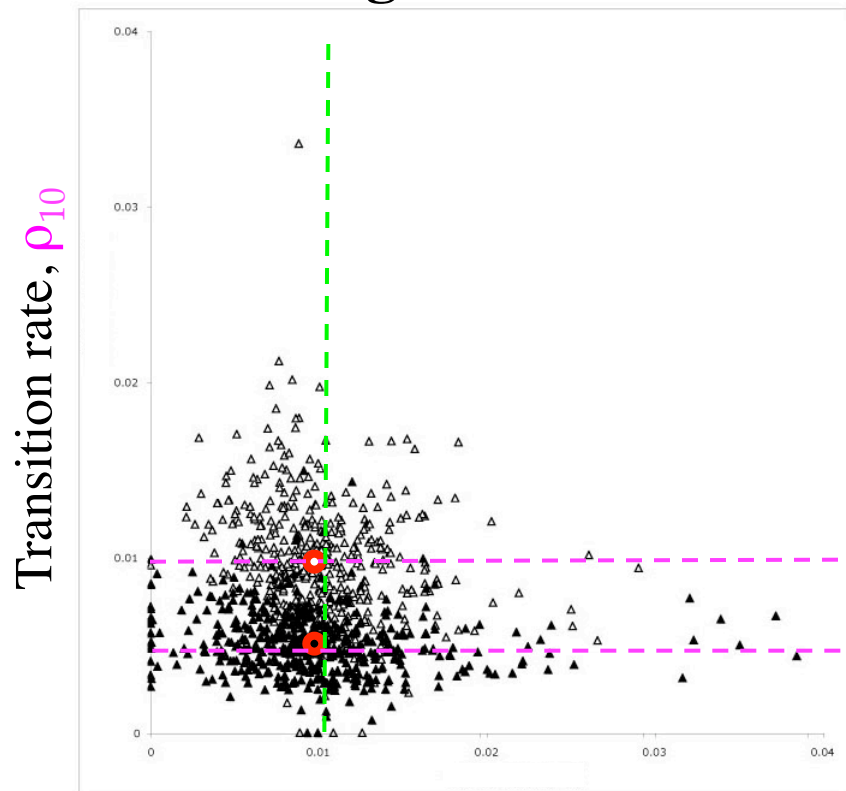## BiSSE: Binary State Speciation & Extinction

Simulation test:

- *500 taxon tree*
- *500 replicate analyses*

λ_0=0.1, λ_1=0.1 *or* 0.2,
μ_0=0.03, μ_1=0.03,
ρ_{01}=0.01, ρ_{10}=0.01

Inferring speciation rate

Speciation rate, λ_1

Speciation rate, λ_0
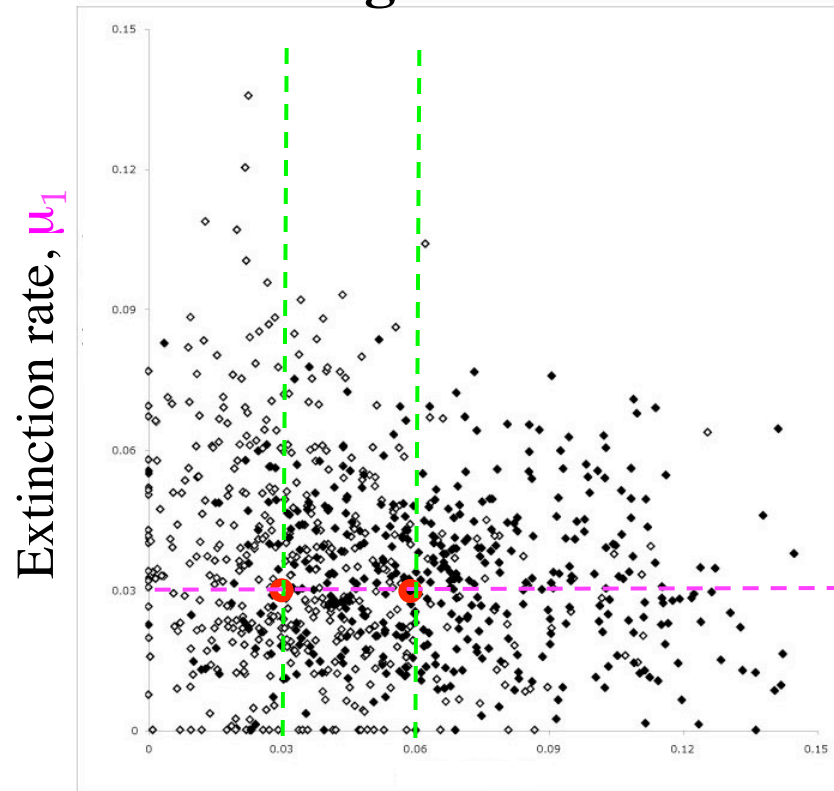
Inferring transition rates

Transition rate, ρ_{10}

Transition rate, ρ_{01}

λ_0=0.1, λ_1=0.1,
μ_0 =0.03, μ_1=0.03,
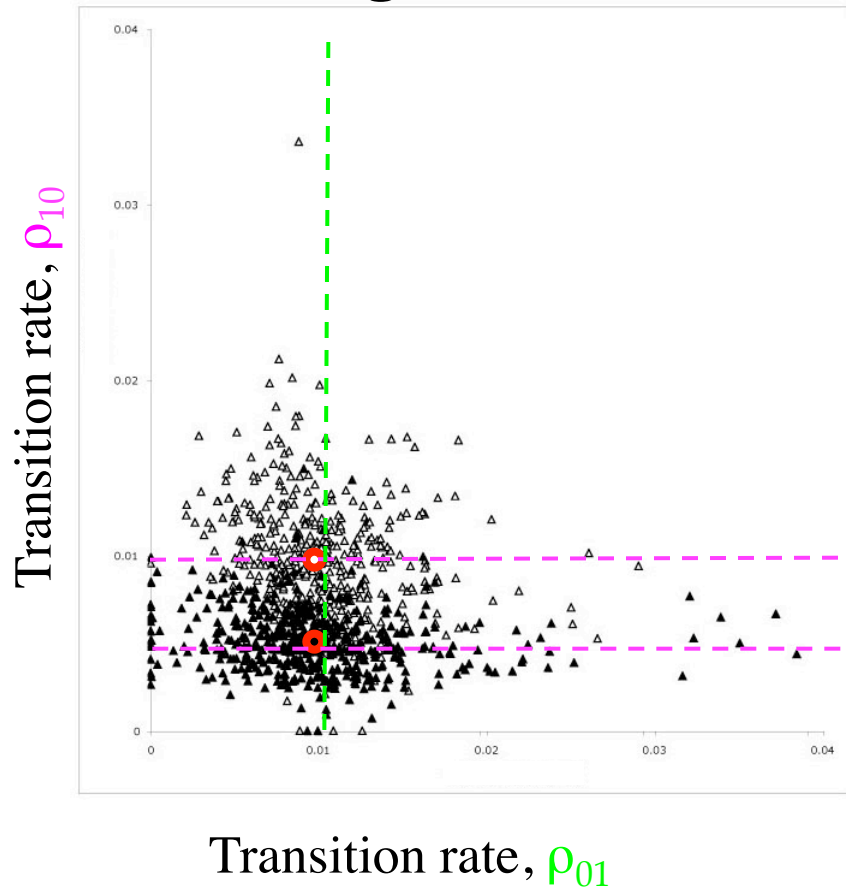ρ_{01}=0.01, ρ_{10}=0.01 *or* 0.02

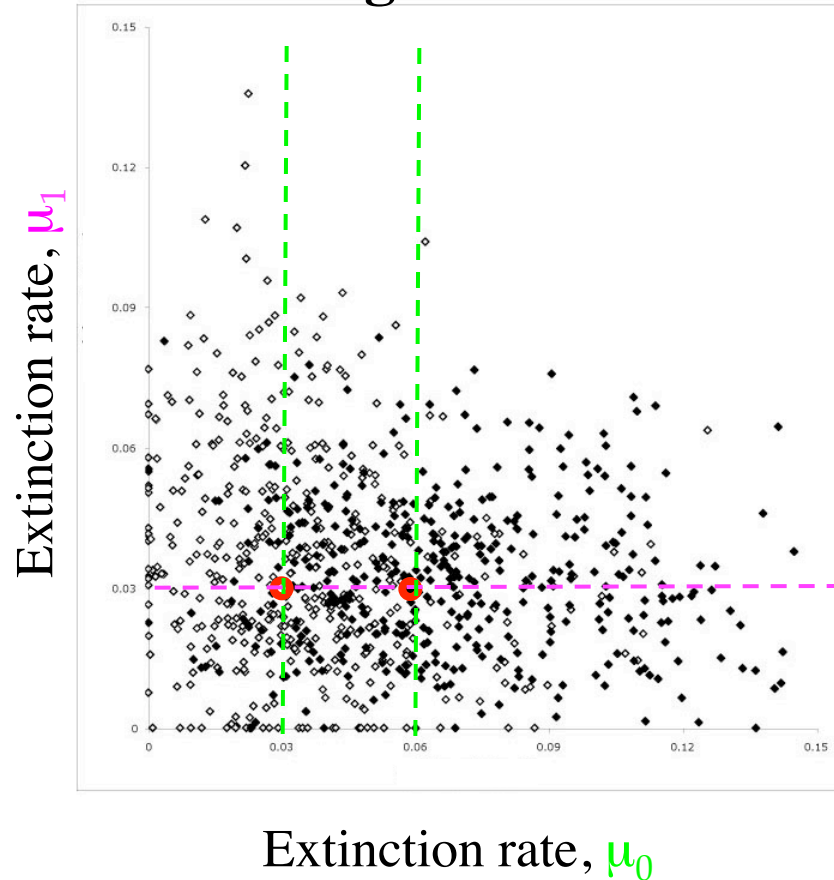**Inferring extinction rate**

Extinction rate, μ_1

Extinction rate, μ_0

λ_0=0.1, λ_1=0.1,
μ_0 =0.03 *or* 0.06, μ_1=0.03,
ρ_{01}=0.01, ρ_{10}=0.01

Inferring transition rates

Transition rate, ρ_{01}

Inferring extinction rate

Extinction rate, μ_0

Extinction rates harder to estimate:
- Fewer events
- Absence of evidence

BiSSE:

- Allows researchers to disentangle speciation/extinction
- Analyzes trait evolution and diversification jointly
- Available in Mesquite and R*
- Requires full phylogenetic information

Maddison, Midford, and Otto (2007)
Systematic Biology 56: 701-710

*http://www.zoology.ubc.ca/prog/diversitree/

BiSSE:

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FitzJohn, Maddison, and Otto (2009)
Syst. Biol. 58: 595-611

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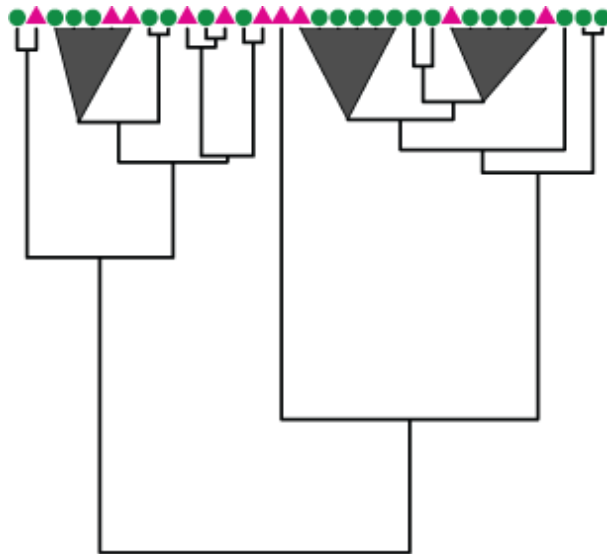
Accounting for
unresolved clades

Accounting for unresolved clades:

• Method 1: If a fraction, f_0 or f_1, of present-day species have been sampled *and* if this sampling is random, we can adjust the initial conditions in the likelihood calculations.

• Method 2: If there are unresolved clades (e.g., all the members of a genus), we can splice together:

Birth-death process
BiSSE

$$\vec{x}(t_1) = \exp\left(\mathbf{Q}(t_2 - t_1)\right)\vec{x}(t_2)$$
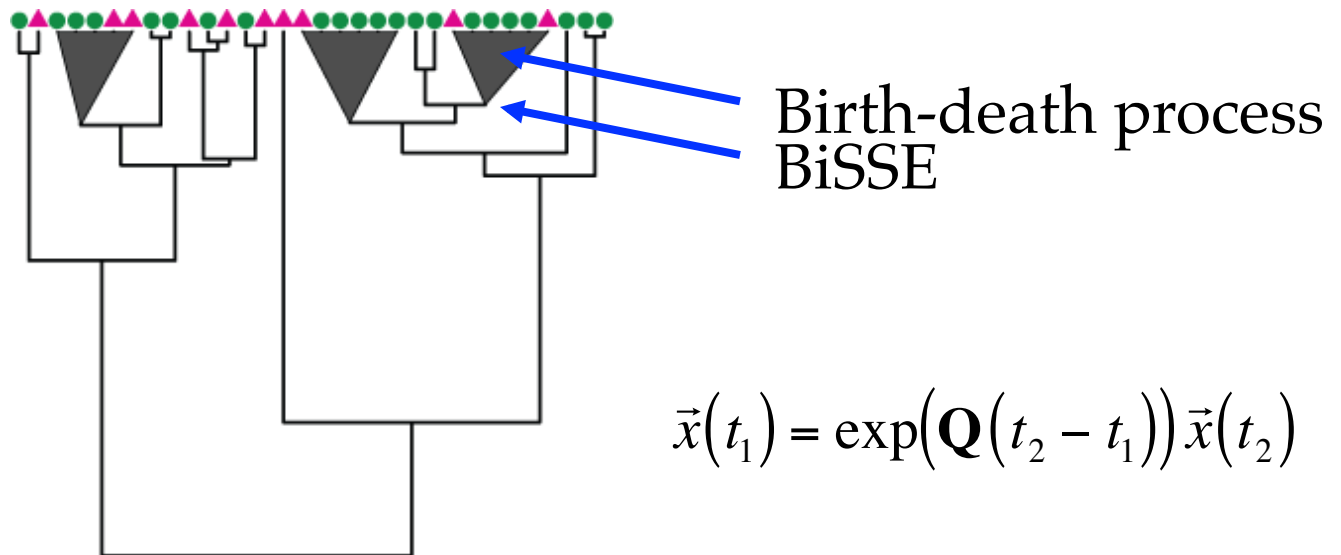
Power & Accuracy
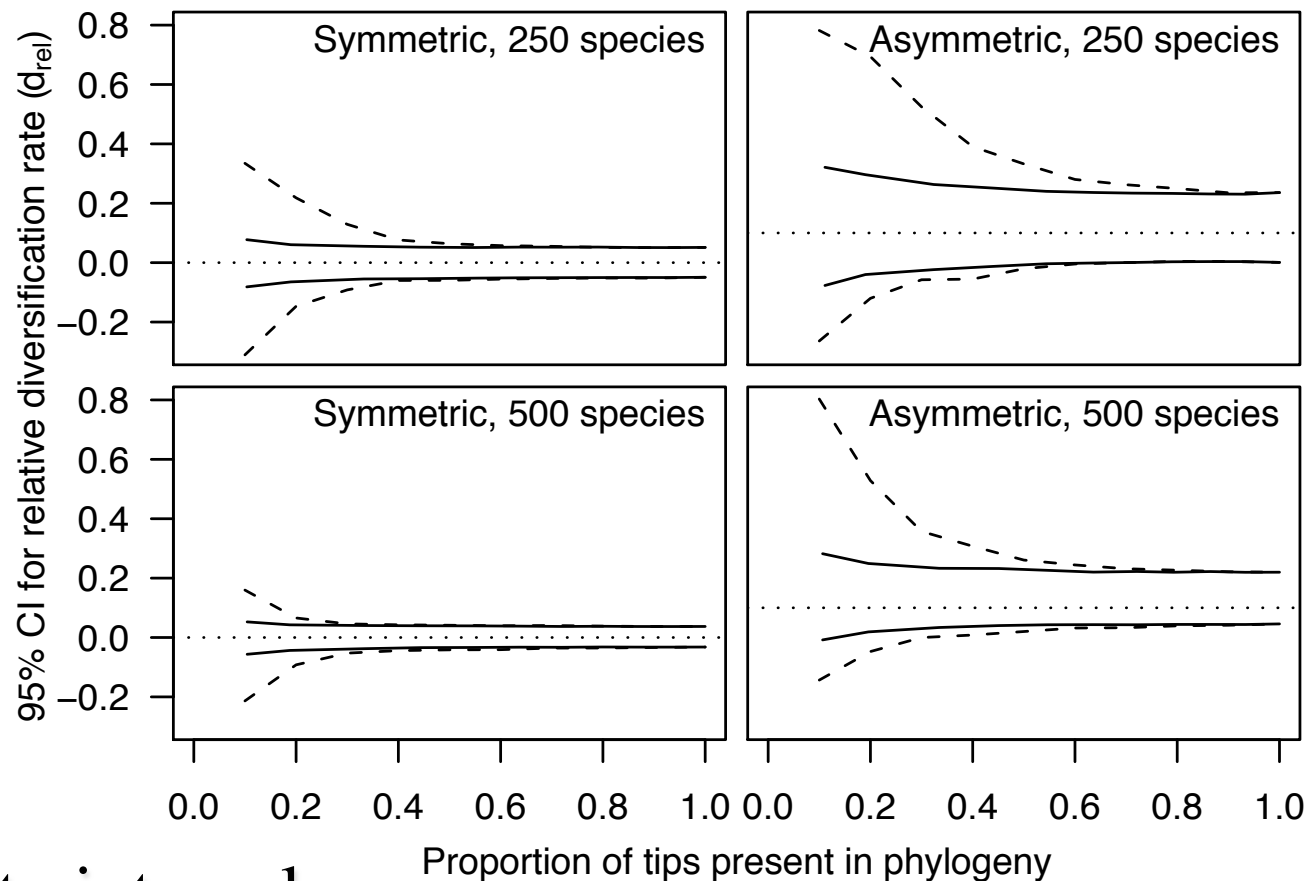
95% Credibility intervals
- Method 1: Dashed curves
- Method 2: Solid curves

⇨ Phylogeny need not be complete to be able to infer parameters of interest with confidence.

Recent developments:
- Quantitative traits (QuaSSE; FitzJohn 2010)
- Multiple traits & multiple states (MuSSE; FitzJohn 2012)
- Cladogenetic & anagenetic trait shifts (BiSSE-ness; Magnuson-Ford & Otto 2012)

These methods provides a powerful method to address:
- Are rare traits rare because they increase extinction, reduce speciation, or rapidly change?
- How can we infer ancestral states when a trait affects diversification?
- Do particular habitats promote speciation?
- Do diversification rates vary over time?
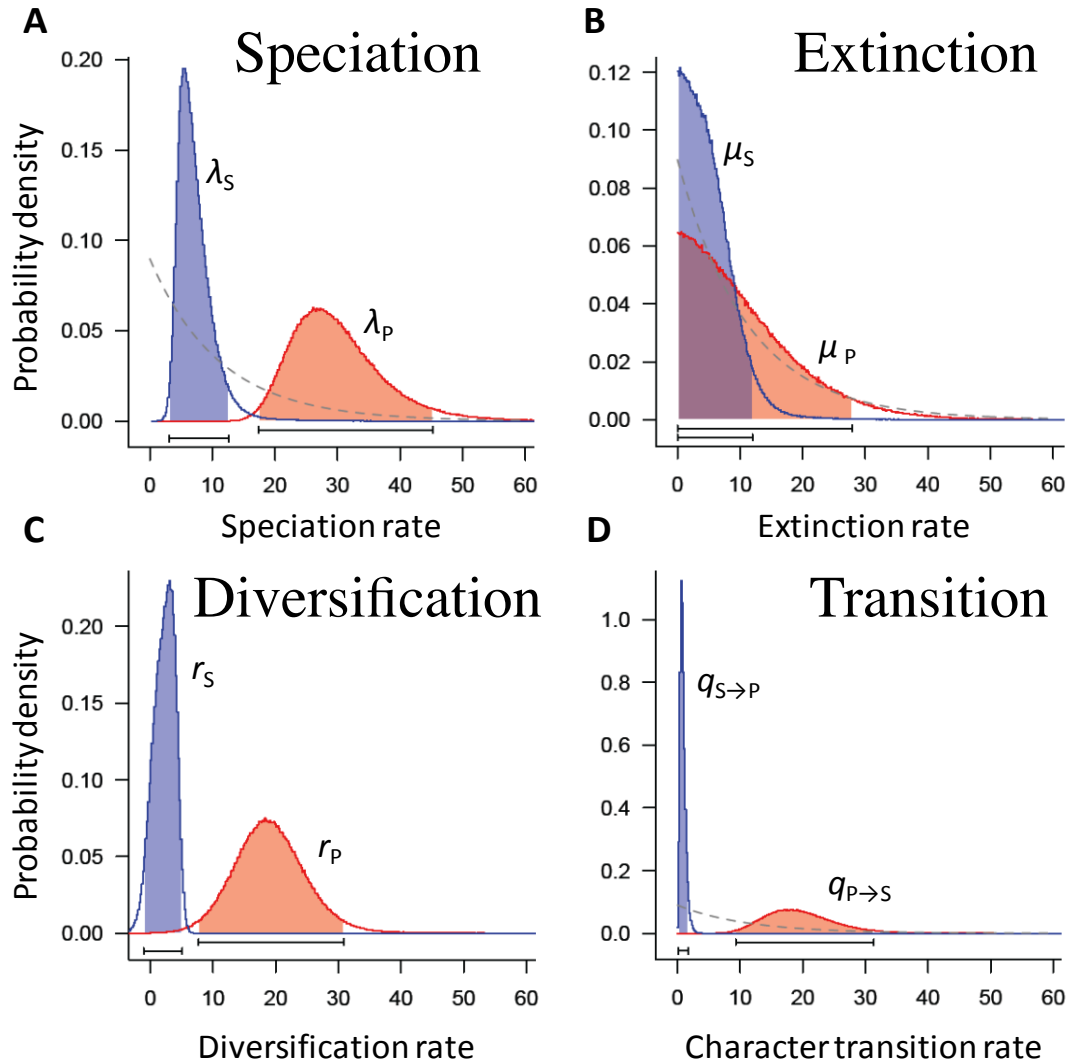
BiSSE: A likelihood approach
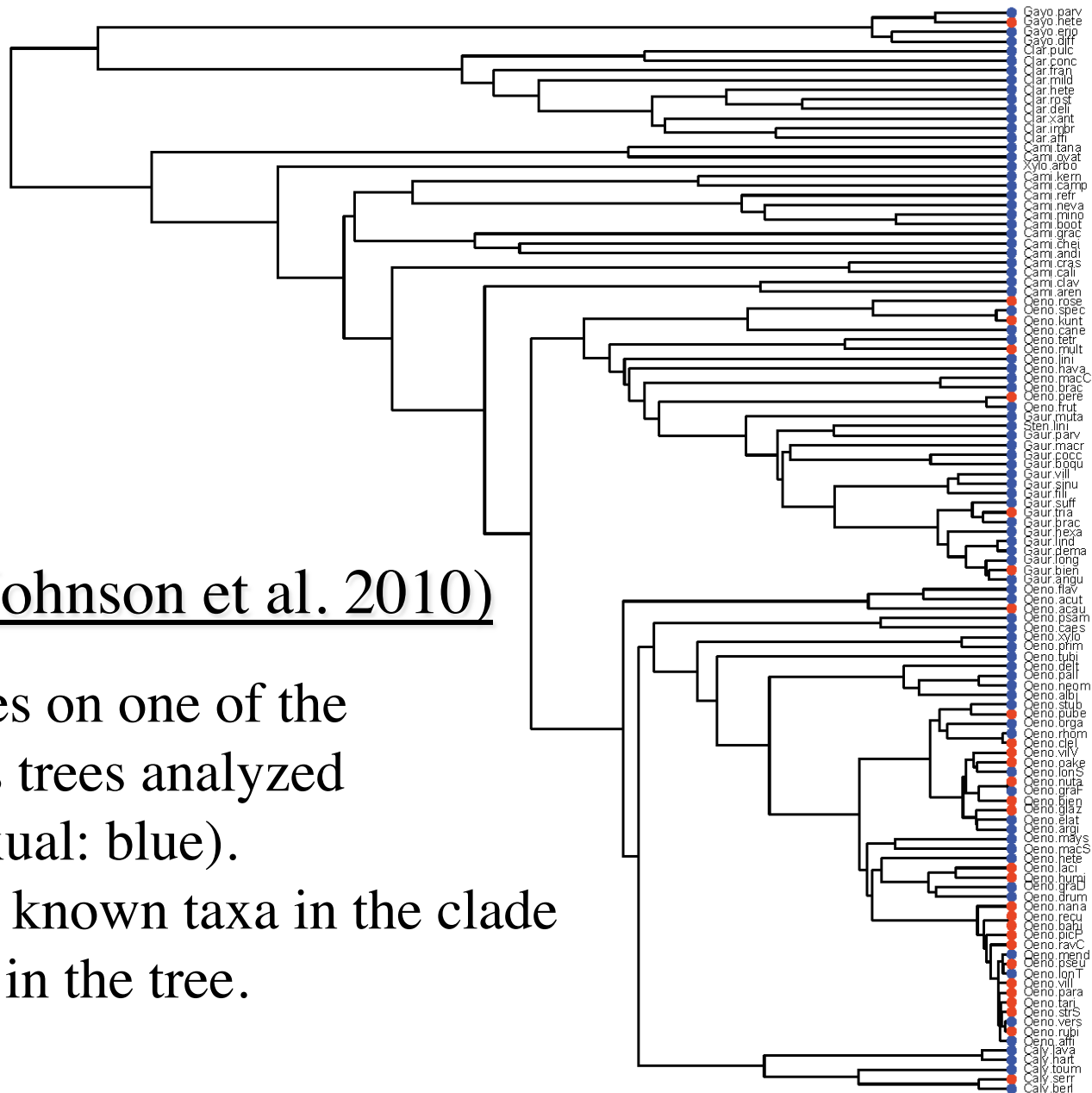
Oenothera (Johnson et al. 2010)

Character states on one of the
100 Mr. Bayes trees analyzed
(PTH: red; sexual: blue).
113 of the 262 known taxa in the clade
were included in the tree.

BiSSE: A likelihood approach

A — Speciation — λ_S, λ_P — Speciation rate

B — Extinction — μ_S, μ_P — Extinction rate

C — Diversification — r_S, r_P — Diversification rate

D — Transition — $q_{S\to P}$, $q_{P\to S}$ — Character transition rate

PTH (functional asexuality) was not an evolutionary dead end, exhibiting high diversification and reversion rates.

Polyploidy (Mayrose et al. 2011)
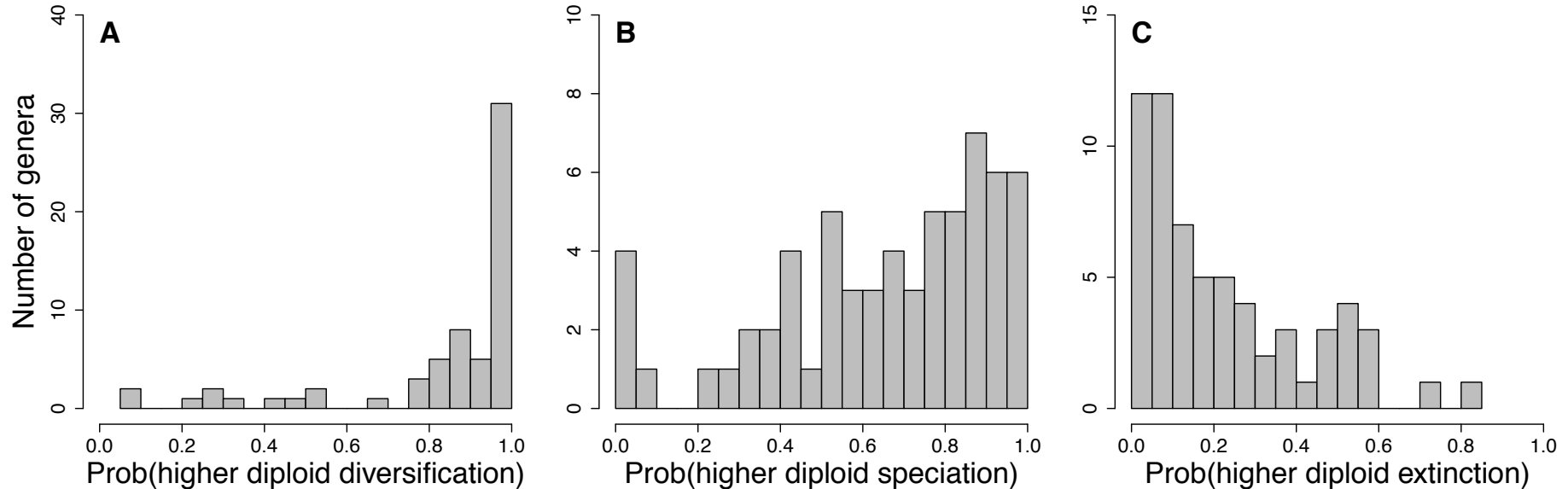
Across 63 genera of plants, diploids exhibited higher diversification, with both higher speciation rates and lower extinction rates, than polyploid clades.

<u>Within-species applications:</u>
The multi-type birth-death model may also be useful for analyzing within-species data.

• Stadler and Bonhoeffer extended the model to include sampling within species, at different time points. The model was then applied using to an HIV-1 phylogeny to determine the transmissibility for different host types (e.g., intravenous drug users vs heterosexuals).

• While the birth-death model ignores density dependence, applying the method to populations of ~constant size may still provide reasonable inferences.

Moran model simulations: Constant population size, N

Birth rate differences $(m_0 - m_1)$
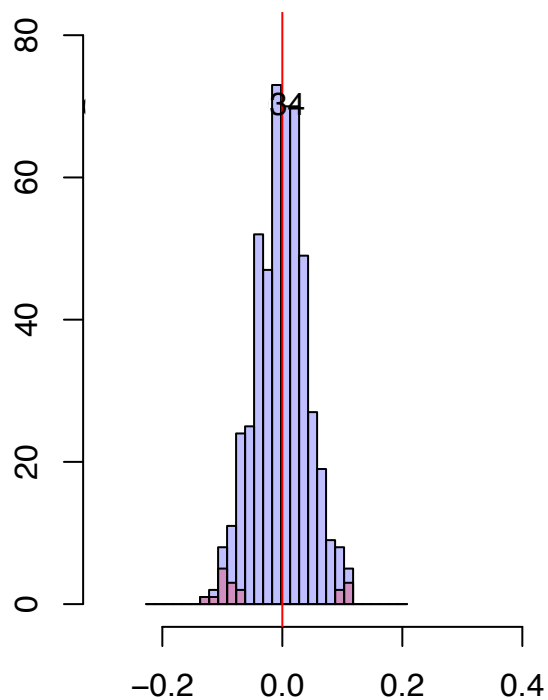
$N = 150$

True difference = 0
3.4% sig
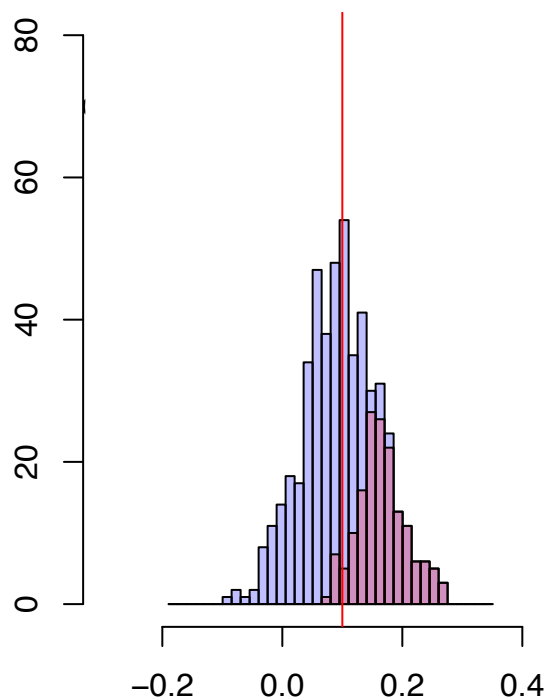
True difference = 0.1
31.6% sig

With Carl Rothfels

Acknowledgments

Collaborators:

Wayne Maddison	Itay Mayrose
Peter Midford	Shing Zhan
Rich FitzJohn	Loren Rieseberg
Marc Johnson	Mike Barker
Stacey Smith	Carl Rothfels
Mark Rausher	Karen-Magnuson Ford

UBC

Accounting for unresolved clades:

• Method 1: If a fraction, f_0 or f_1, of present-day species have been sampled *and* if this sampling is random, we can adjust the initial conditions in the likelihood calculations.

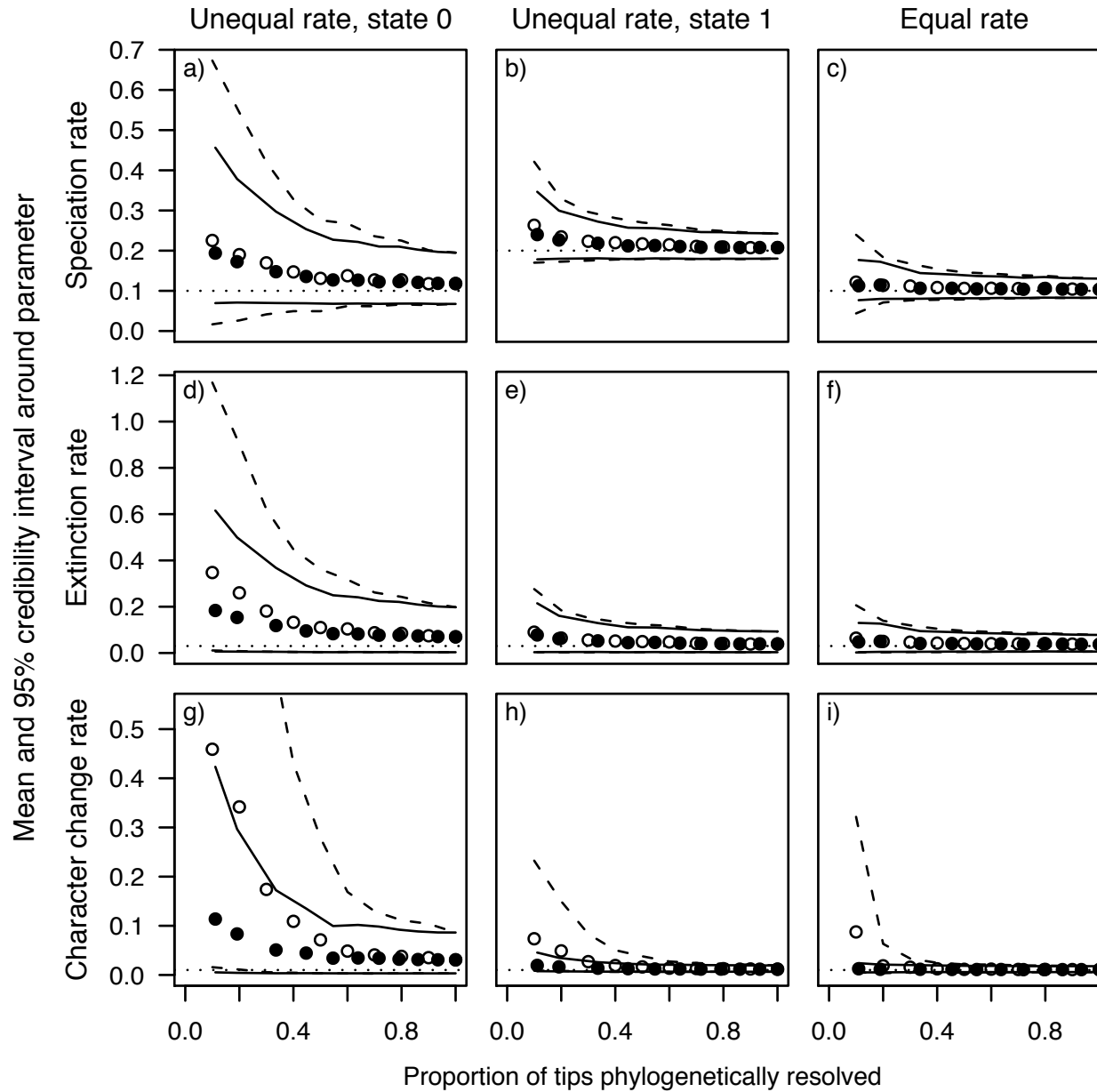• Method 2: If there are unresolved clades (e.g., all the members of a genus), we can splice together:

Full tree

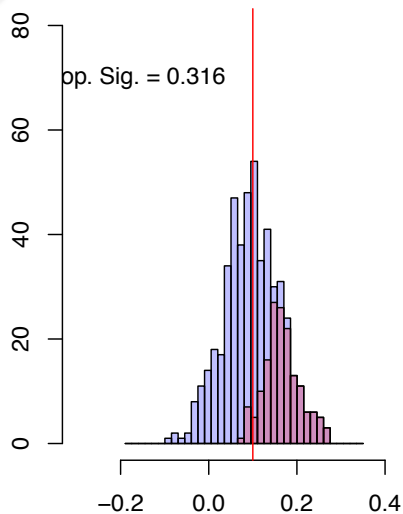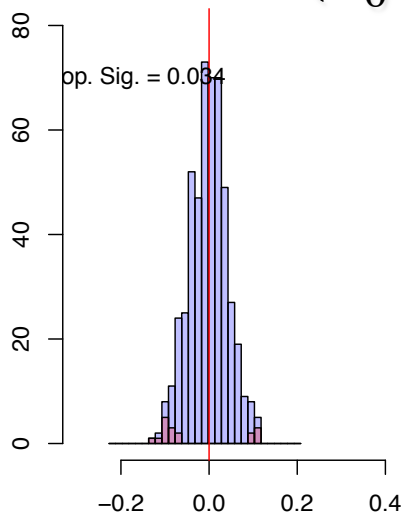15 nodes removed
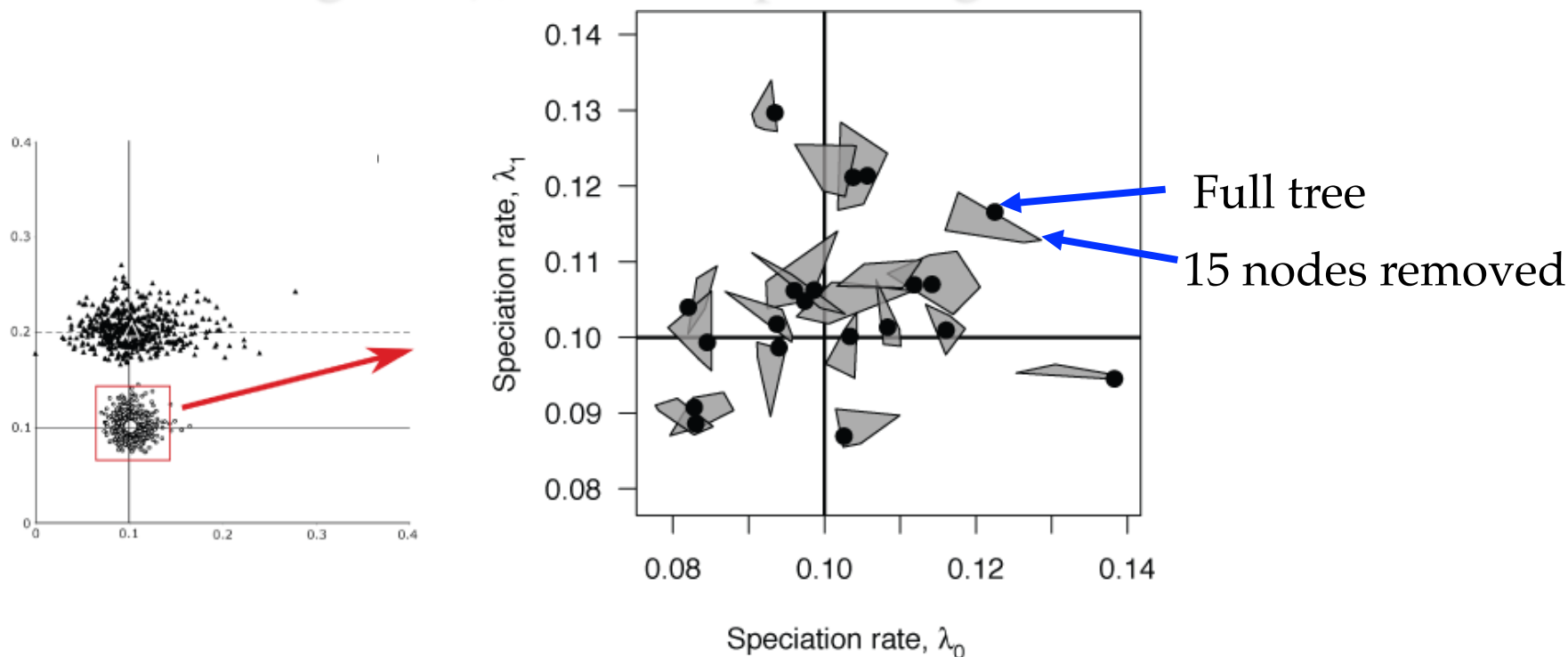
Method 1

Method 2
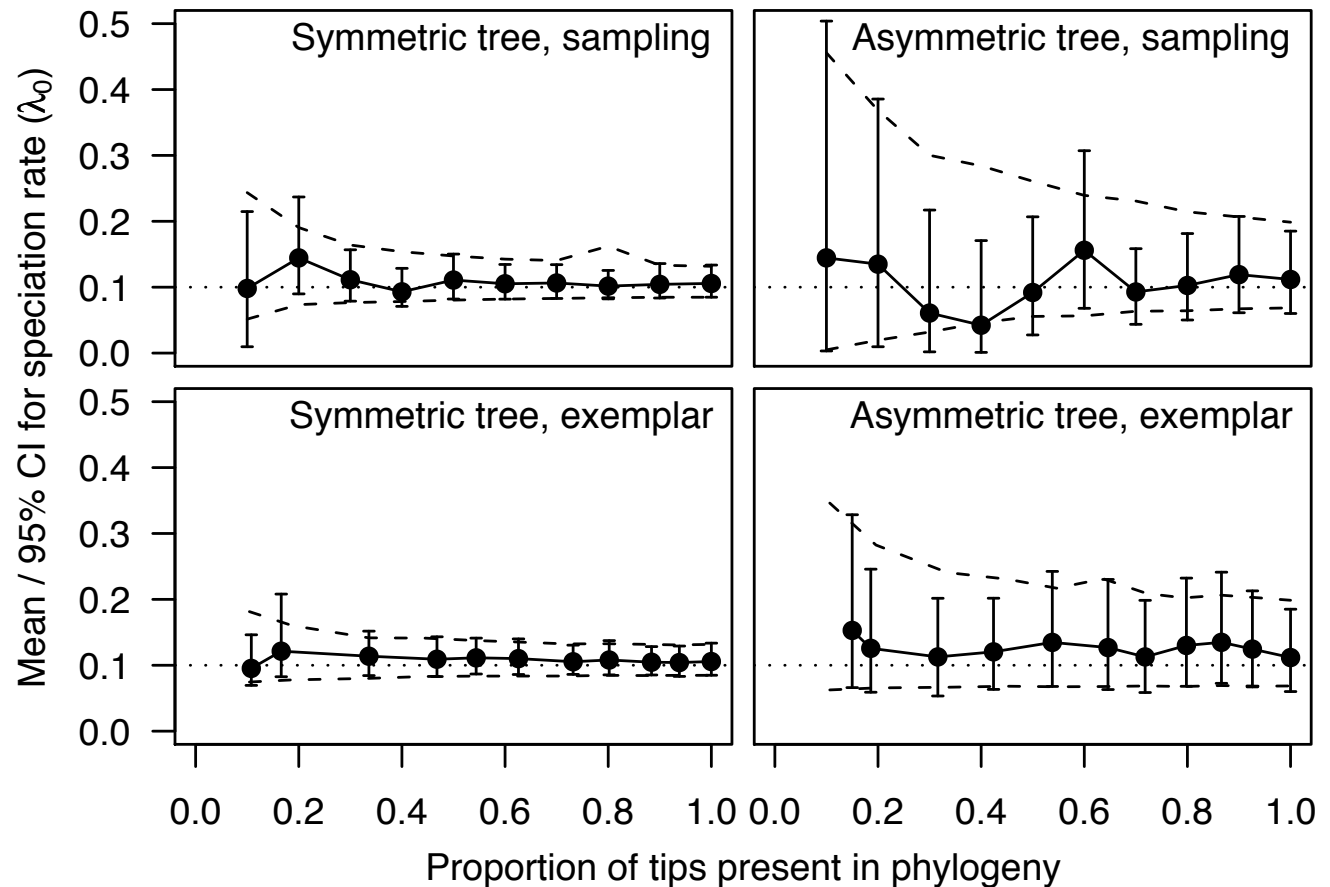
Dots and bars give point estimates and 95% credibility intervals for a single 500-species tree, sampled to varying degrees.
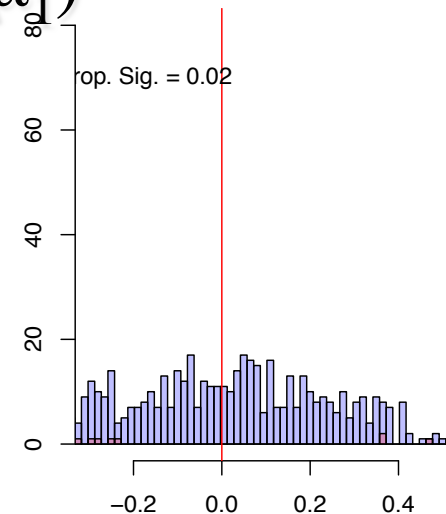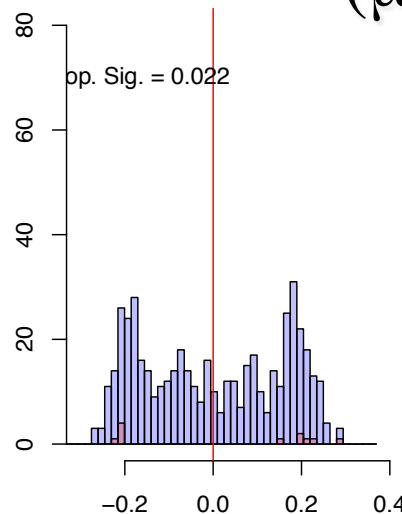
BiSSE: A likelihood approach

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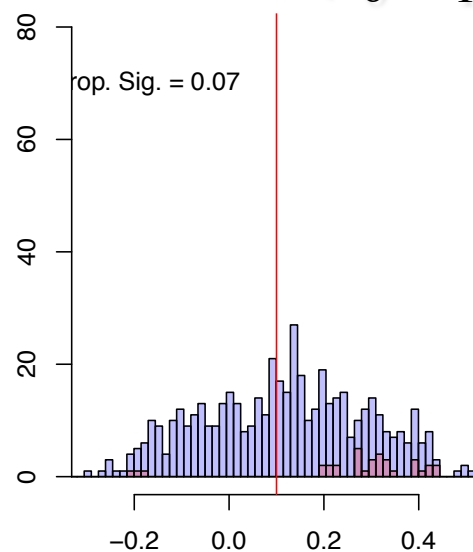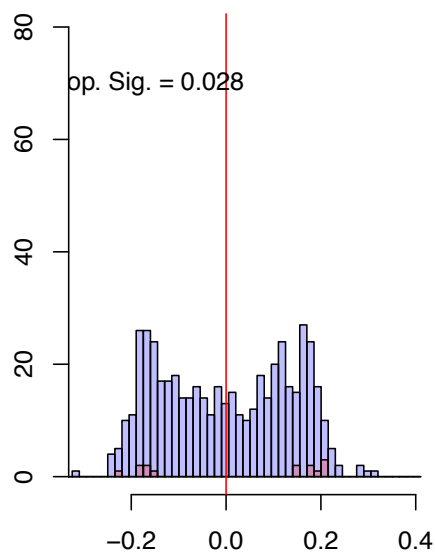

Speciation rate difference $(\lambda_0 - \lambda_1)$ — Extinction rate difference $(\mu_0 - \mu_1)$ — Difference in diversification $(r_0 - r_1)$
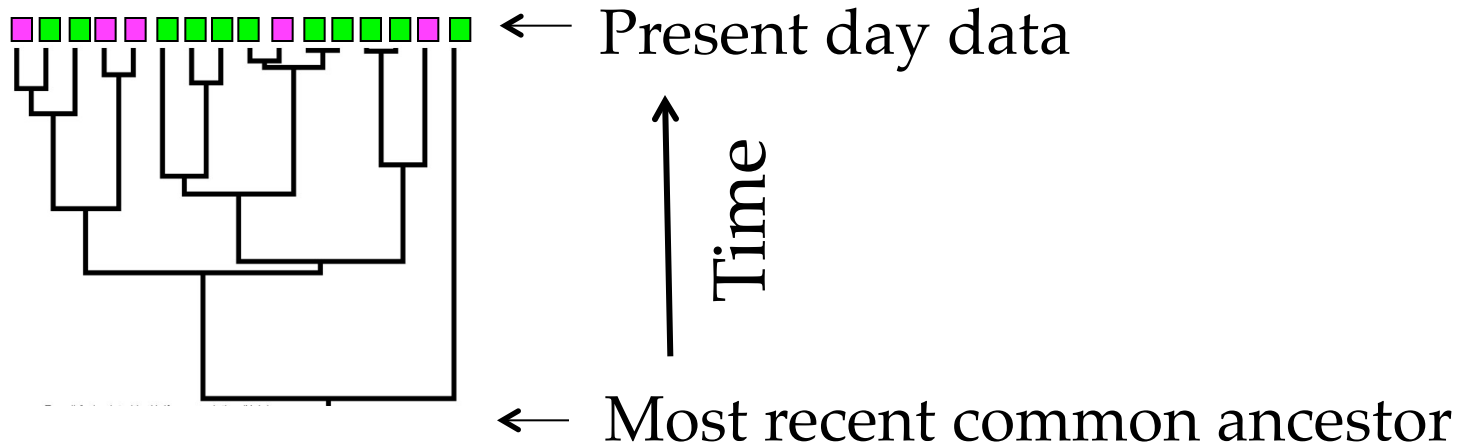
Comparative analyses

*The use of data from a number of species
to infer evolutionary parameters of interest.*

Comparative analyses

*The use of data from a number of species
to infer evolutionary parameters of interest.*

← Present day data

Time

← Most recent common ancestor

BiSSE: A likelihood approach

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Birth-death process
BiSSE
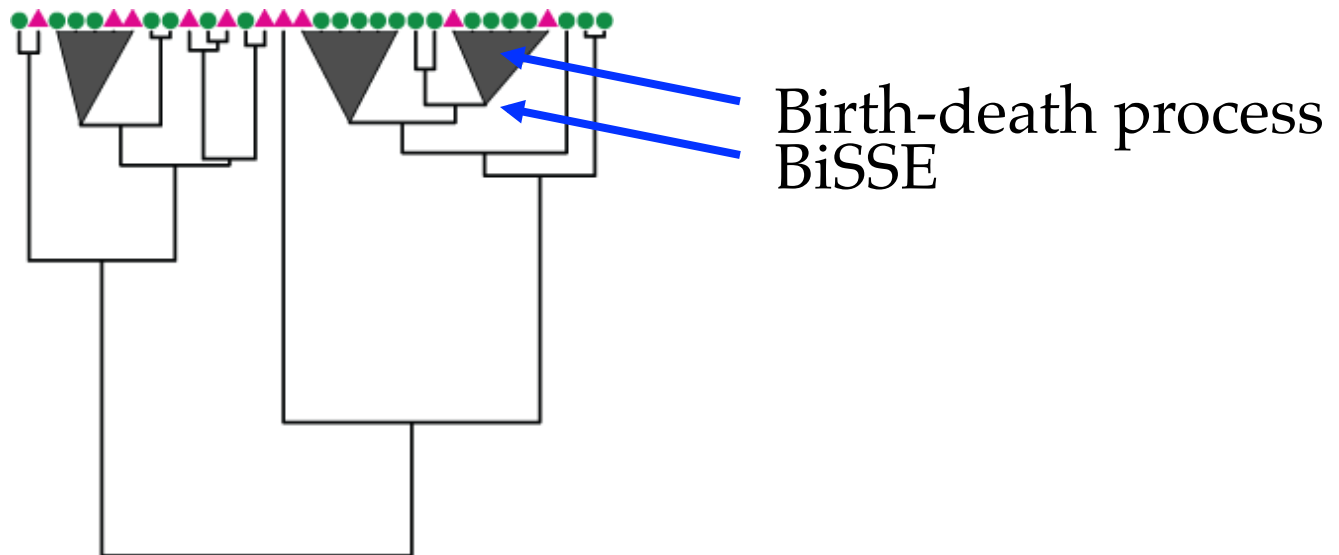
Does sexual selection influence diversification?
- Dimorphism in shorebirds (FitzJohn et al.)

Do pollinators promote speciation of colorful flowers?
- Flower color in Ipomoea (with Smith and Rausher)

Does specialization increase speciation & extinction rates?
- Resource utilization in fungi (with Binder and Hilbert)

Is asexual reproduction an evolutionary dead end?
- Mating system in Oenothera (Johnson et al)

Does polyploidization help or hinder diversification?
- An analysis of 63 genera of plants (Mayrose et al)