

# Markov Chains in Diversification

Introduction to state-dependent diversification



NSF-DEB 2323170



Rosana Zenil-Ferguson  
Assistant Professor, University of Kentucky  
SSB Brekout Meeting 2026

# Download slides and files

---

<https://roszenil.github.io/mytutorials>

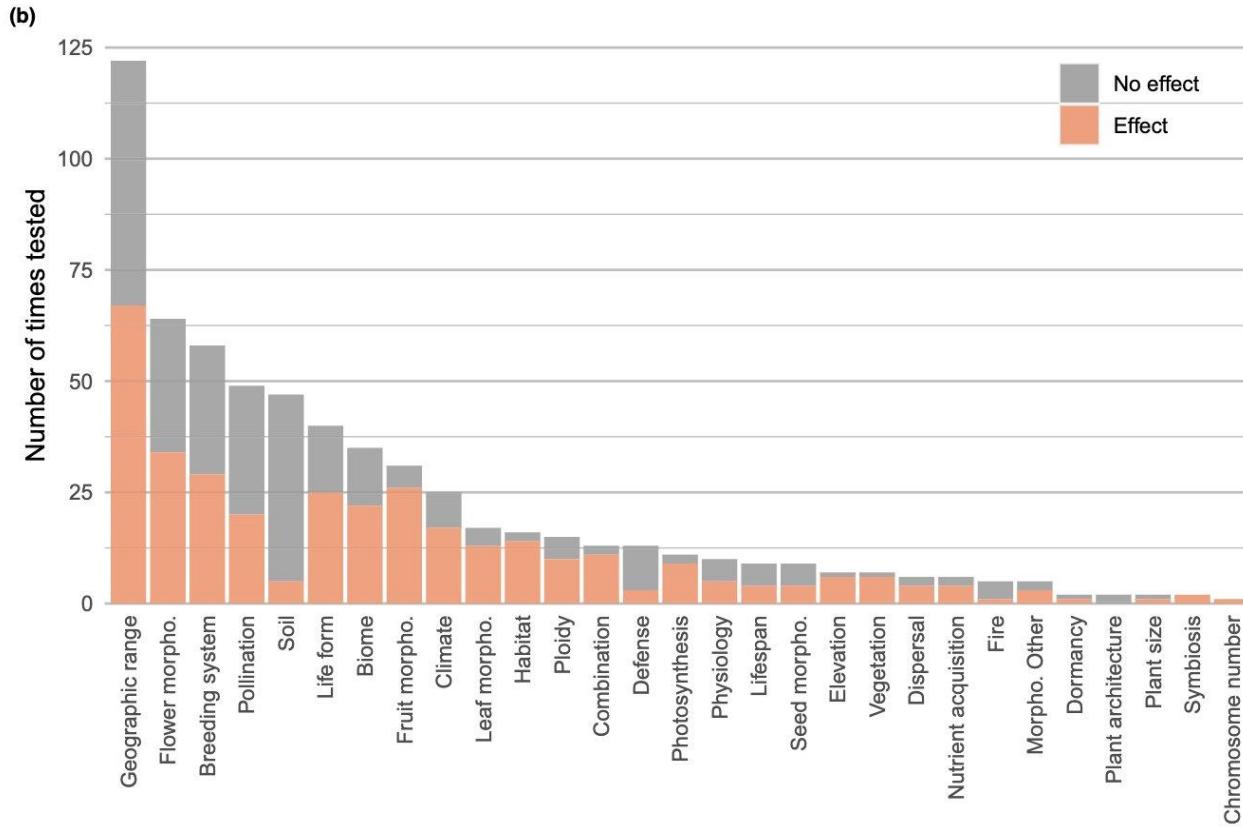


There are  
400,000  
vascular plants  
in the planet.

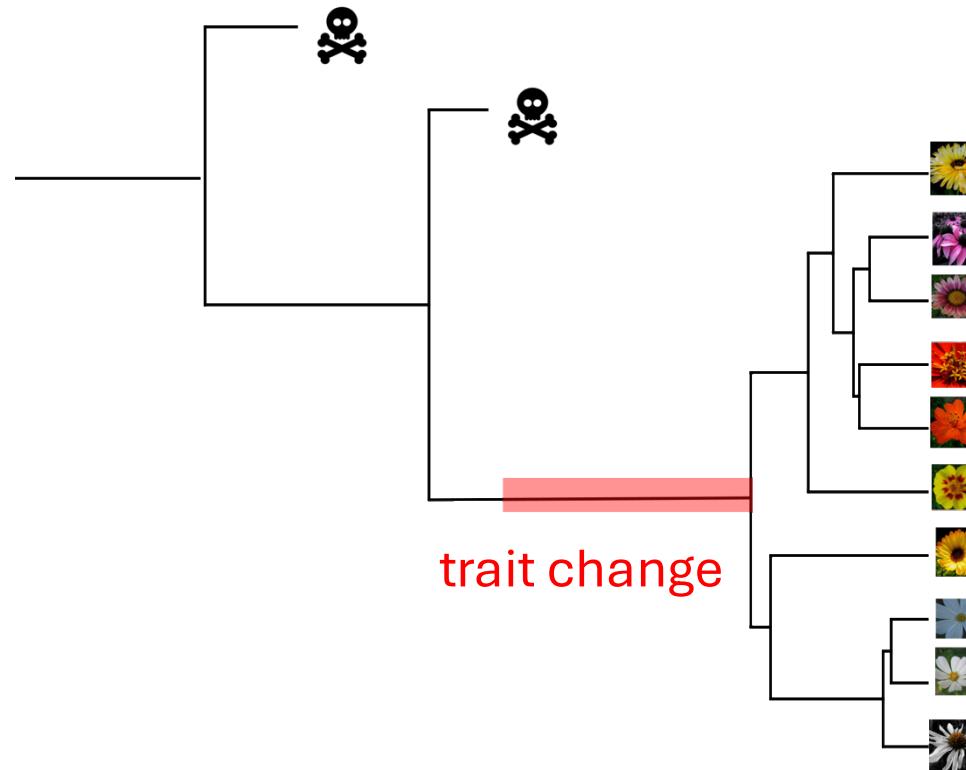


Volcanoes photography: Maria Costantini 2021  
Plant photography: RZF and Carrie Tribble

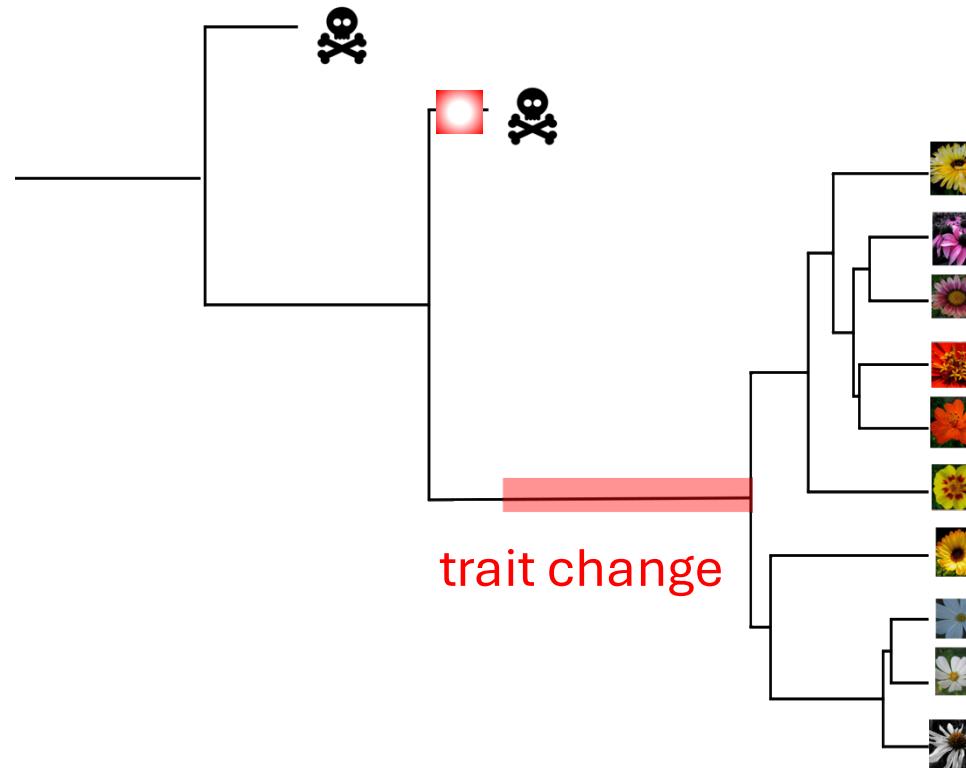
152 studies linking plant traits to speciation and extinction using state-dependent diversification



# Macroevolutionary consequences of trait change



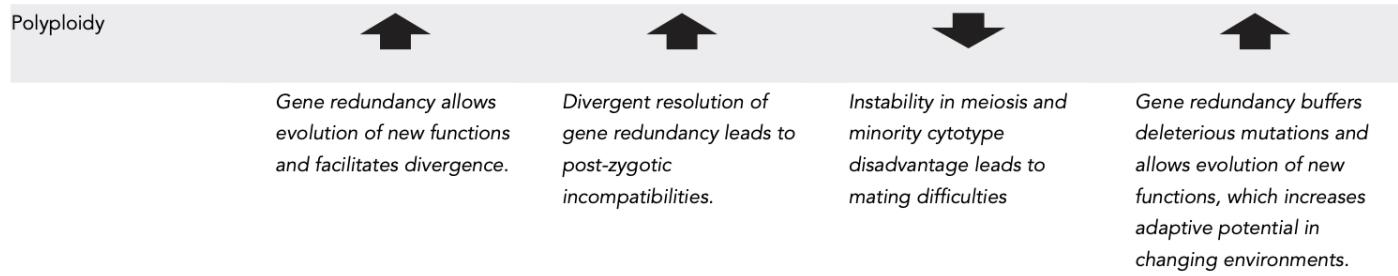
# Macroevolutionary consequences of trait change



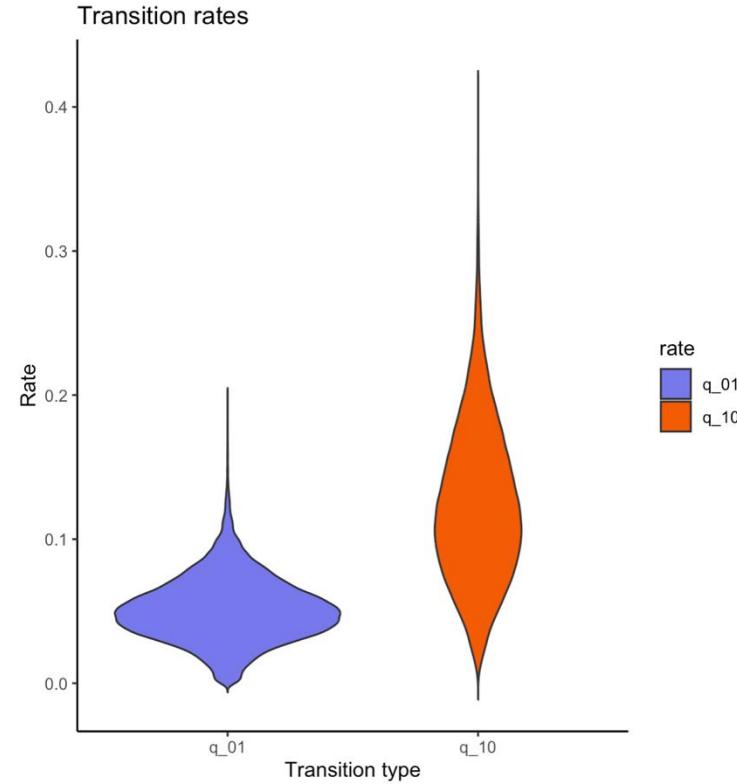
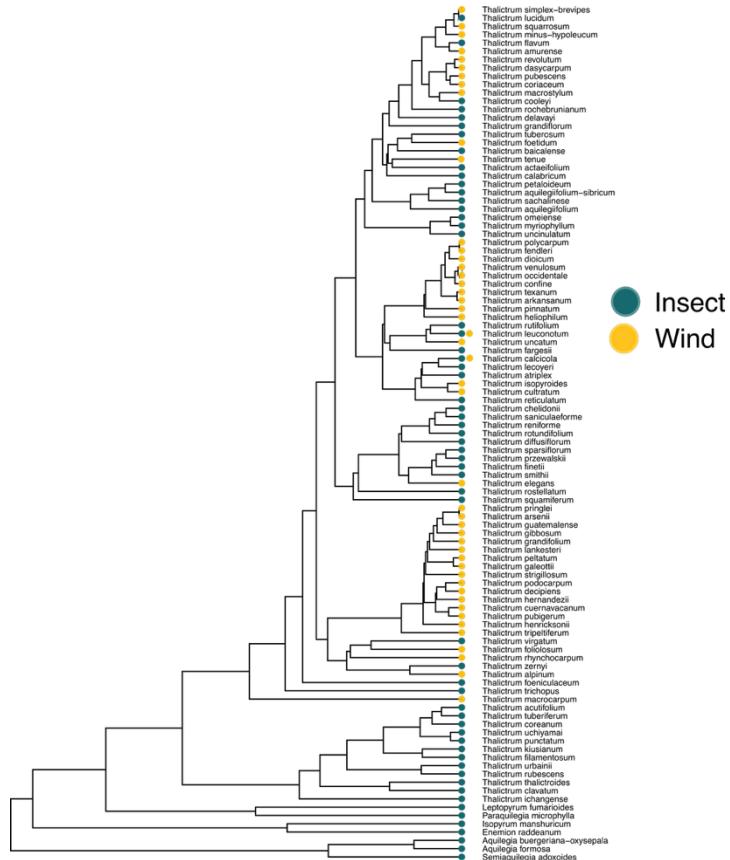
## Perspective

# Opposing effects of plant traits on diversification

Bruce Anderson,<sup>1,\*</sup> John Pannell,<sup>2</sup> Sylvain Billiard,<sup>3</sup> Concetta Burgarella,<sup>4</sup> Hugo de Boer,<sup>5</sup> Mathilde Dufay,<sup>6</sup> Andrew J. Helmstetter,<sup>7</sup> Marcos Méndez,<sup>8</sup> Sarah P. Otto,<sup>9</sup> Denis Roze,<sup>10</sup> Hervé Sauquet,<sup>11,12</sup> Daniel Schoen,<sup>13</sup> Jürg Schönenberger,<sup>14</sup> Mario Vallejo-Marin,<sup>15</sup> Rosana Zenil-Ferguson,<sup>16</sup> Jos Käfer,<sup>17,\*</sup> and Sylvain Glémén<sup>15,18,\*</sup>

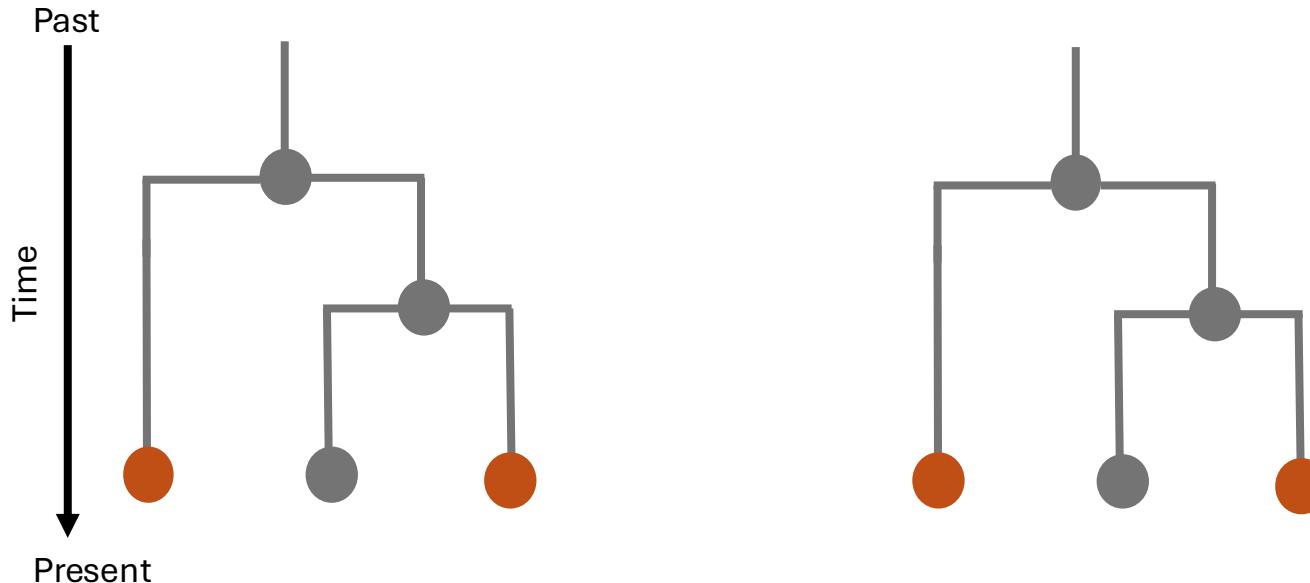


# Under a Mk2 we estimated for our data



# Trait evolution is biased without understanding the role of speciation and extinction events

---

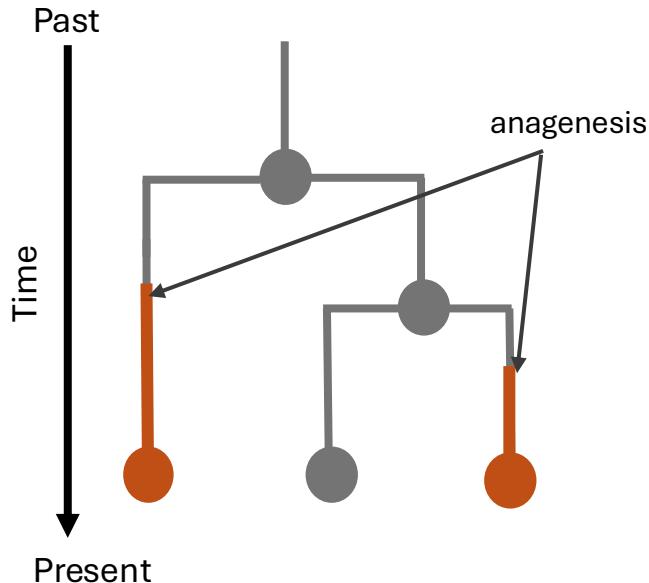


Maddison. 2006. *Sys Bio.*

**Considering speciation and extinction is necessary to decrease biases  
in ancestral reconstruction and estimates of transition rates**

# Trait evolution is biased without understanding the role of speciation and extinction events

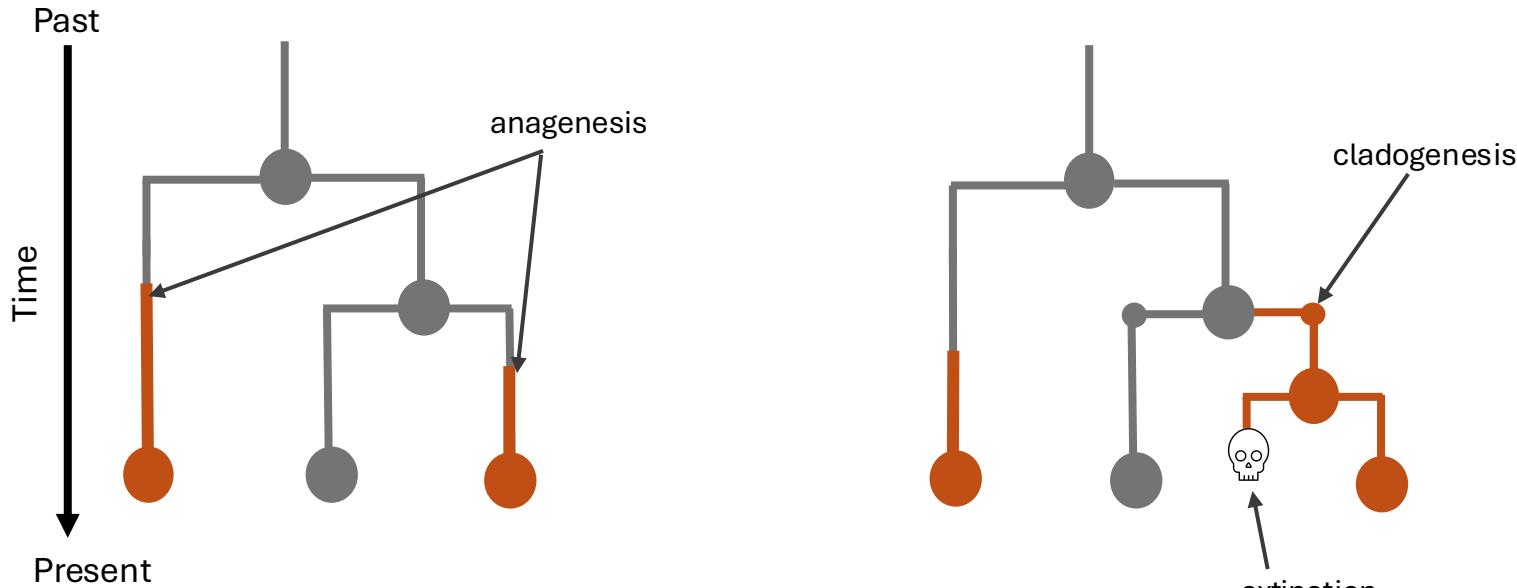
---



Maddison. 2006. *Sys Bio.*

**Considering speciation and extinction is necessary to decrease biases  
in ancestral reconstruction and estimates of transition rates**

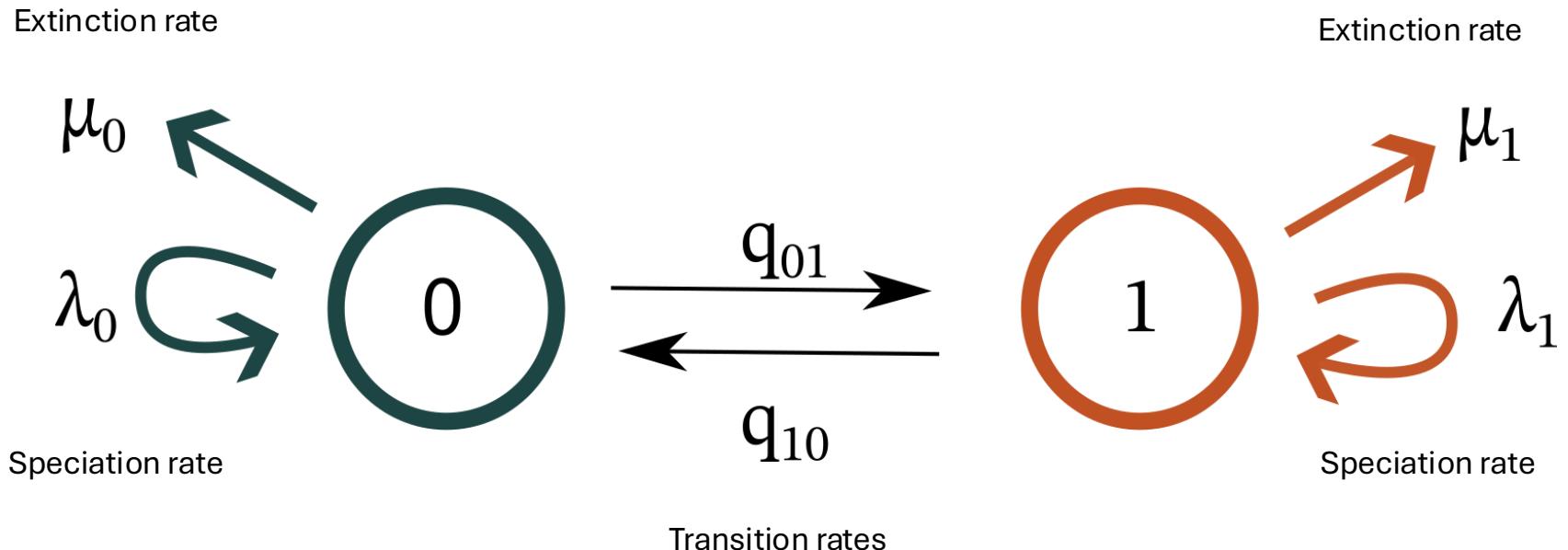
# Trait evolution is biased without understanding the role of speciation and extinction events



Maddison. 2006. *Sys Bio.*

**Considering speciation and extinction is necessary to decrease biases  
in ancestral reconstruction and estimates of transition rates**

# Binary state speciation and extinction model (BiSSE)



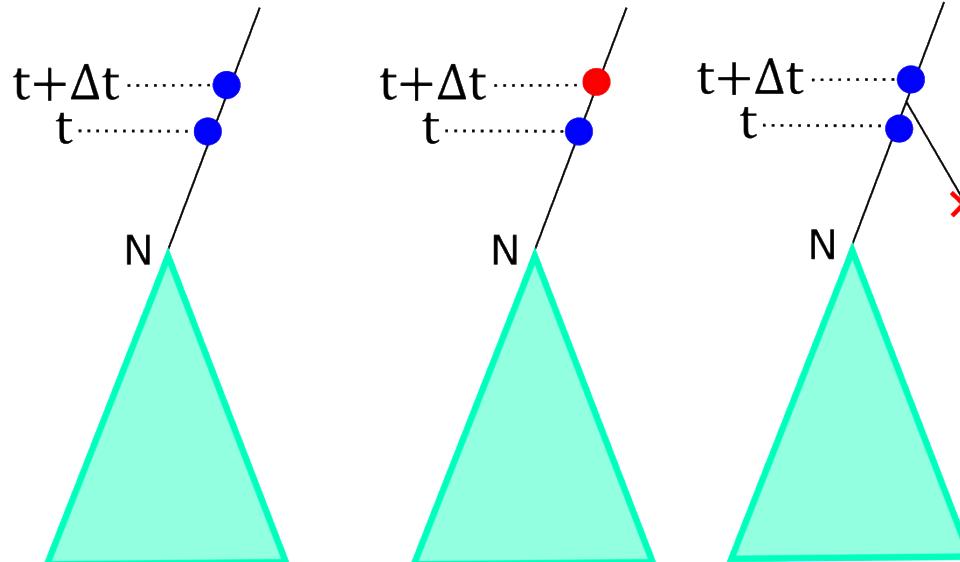


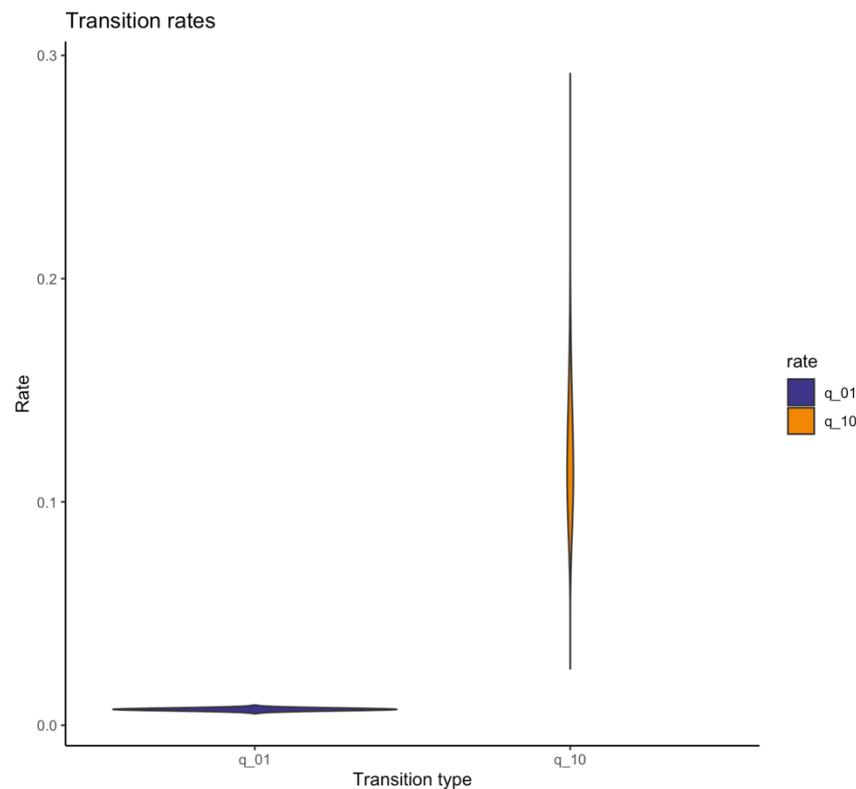
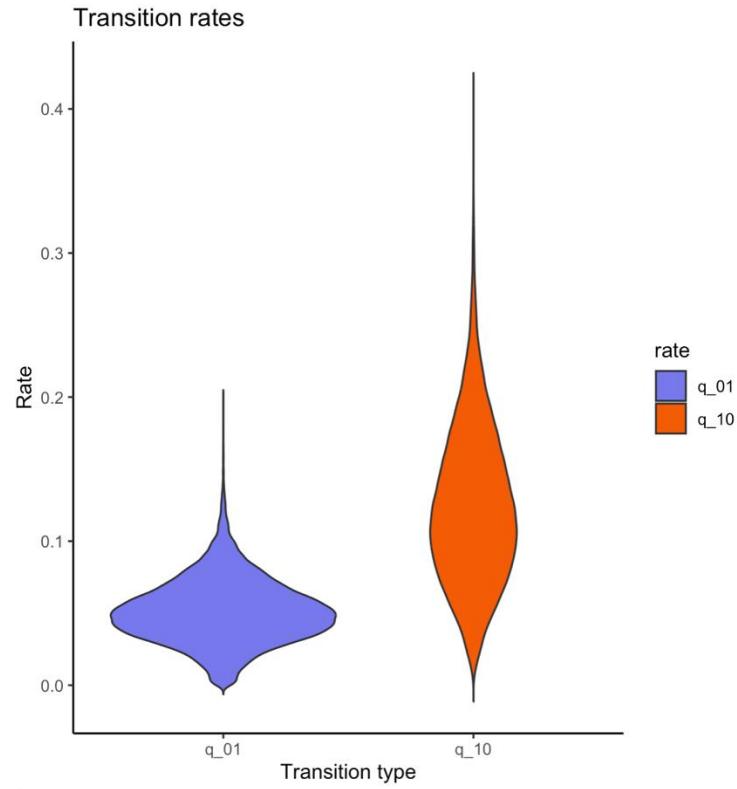
SCAN ME

Phyloseminar  
Dra. Sally Otto  
BiSSE  
developer

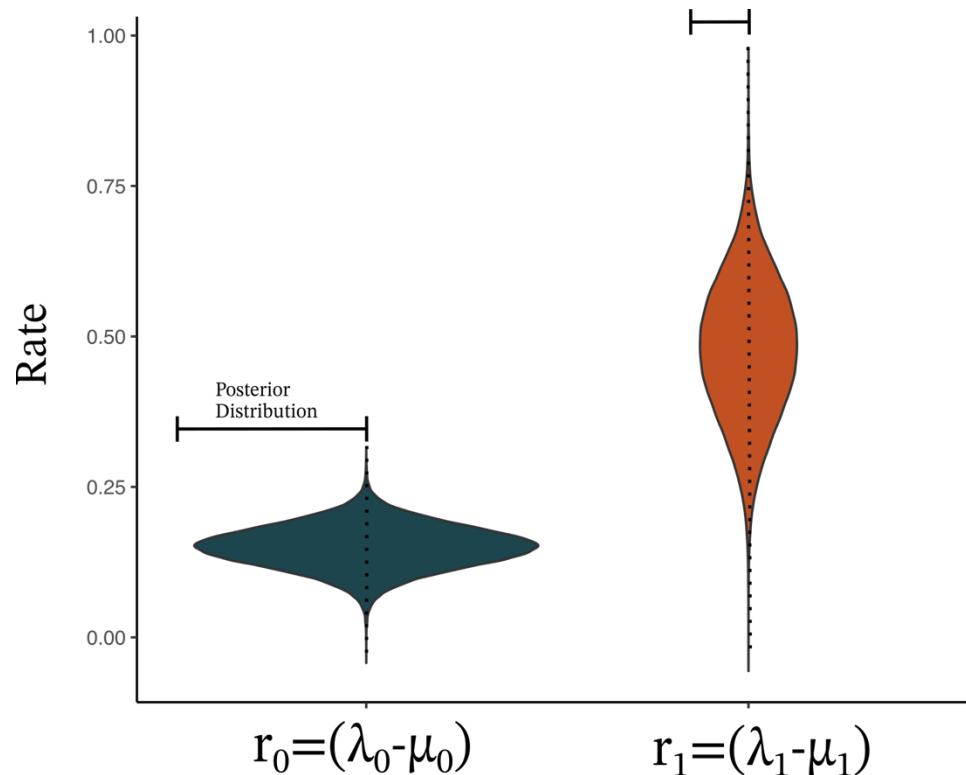
## How do we specify a Q-matrix for this?

Stochastic differential equations (Kolmogorov-Forward)





# Checking for differences in diversification correlated to a discrete trait



Net diversification rate ( $r$ ) =  
Speciation rate ( $\lambda$ ) – Extinction rate ( $\mu$ )

**Is it probable  
that they are different?**

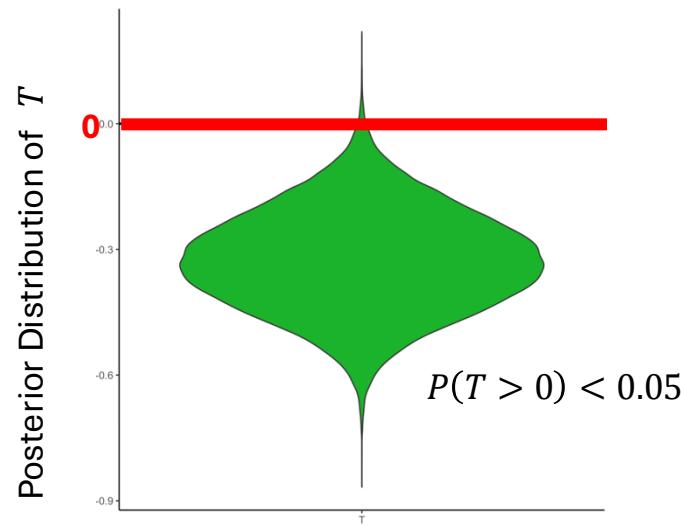
# Developing a hypothesis testing framework to find differences in net diversification

---

$$H_0: r_0 = r_1$$



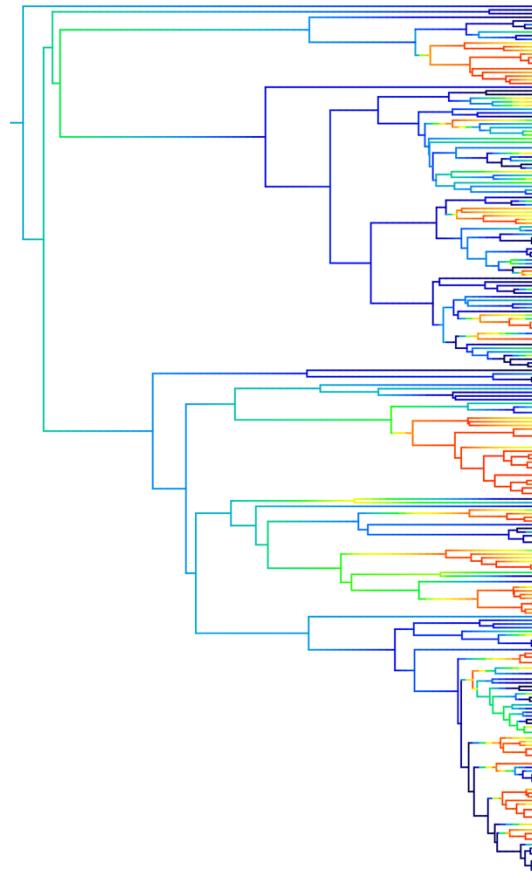
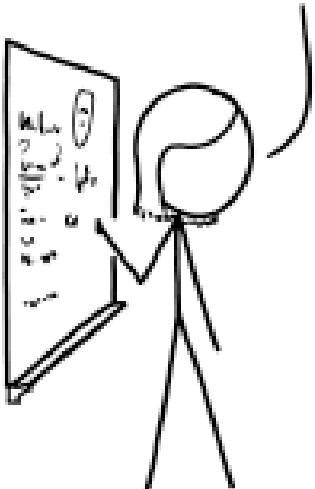
$$\text{Test statistic } T = r_0 - r_1$$



The probability that 0 and 1 being equal is less than 5%

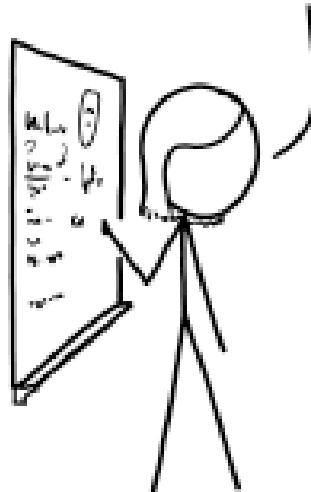
# Null hypothesis of BiSSE

$$H_0: r_0 = r_1$$



# BiSSE's Null Hypothesis is too simple

$$H_0: r_0 = r_1$$



Davis et al. 2013. *BMC Evolutionary Biology*  
Rabosky and Goldberg 2015. *Sys Bio*

Type I error 50%

Misspecification of null hypothesis

New null  $H_0$ :  
Something else can be modifying diversification other than my trait



Better model (Heterogeneity in diversification)  
HiSSE: Hidden State-dependent Speciation and Extinction

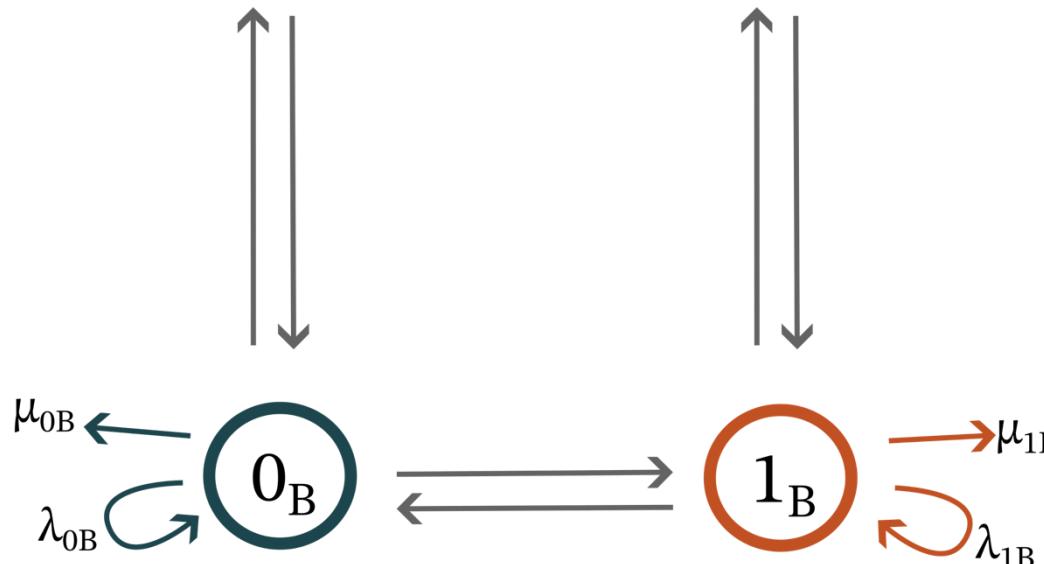
---



Hidden states  
A and B  
represent other  
unmeasured sources  
of diversification

HiSSE  
- 4 speciations  
- 4 extinctions  
- 8 transition rates

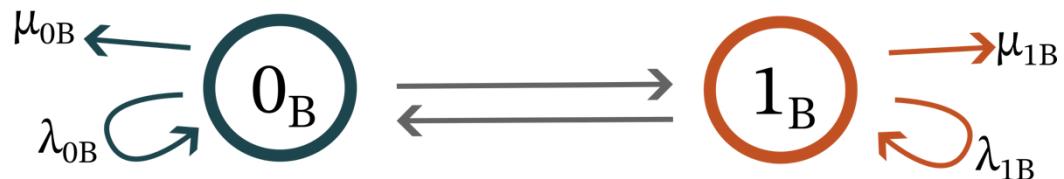
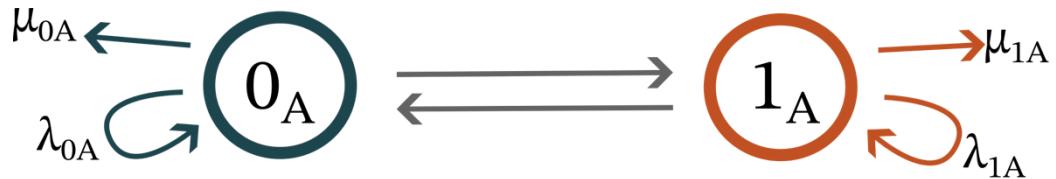
Better model (Heterogeneity in diversification)  
HiSSE: Hidden State-dependent Speciation and Extinction



Hidden states  
A and B  
represent other  
unmeasured sources  
of diversification

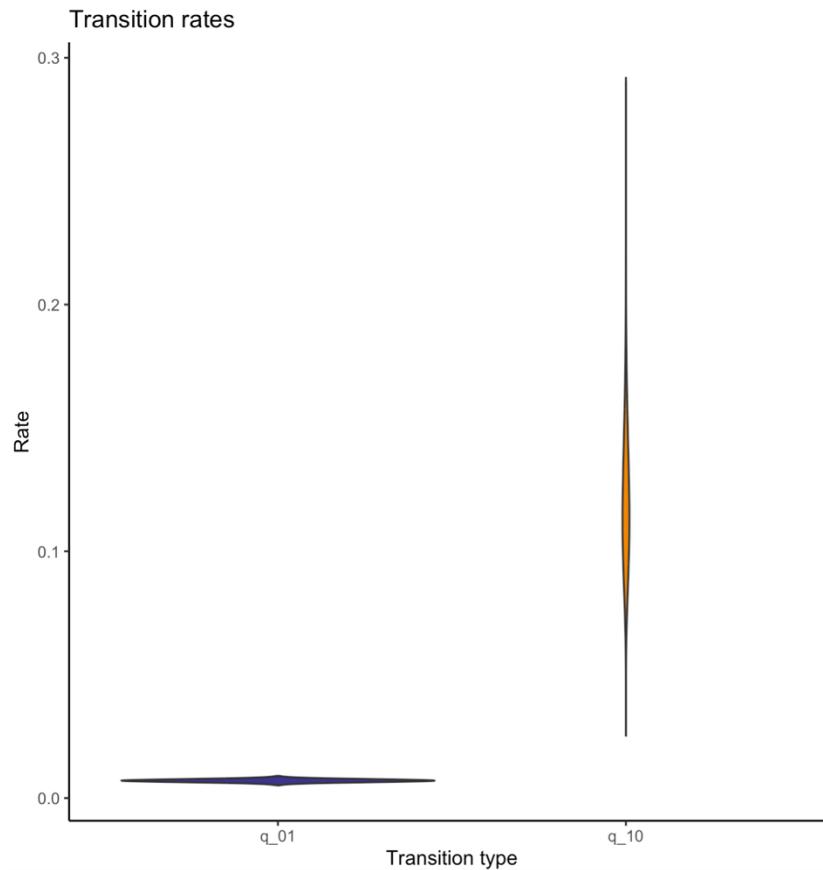
HiSSE  
- 4 speciations  
- 4 extinctions  
- 8 transition rates

## Transition Rates

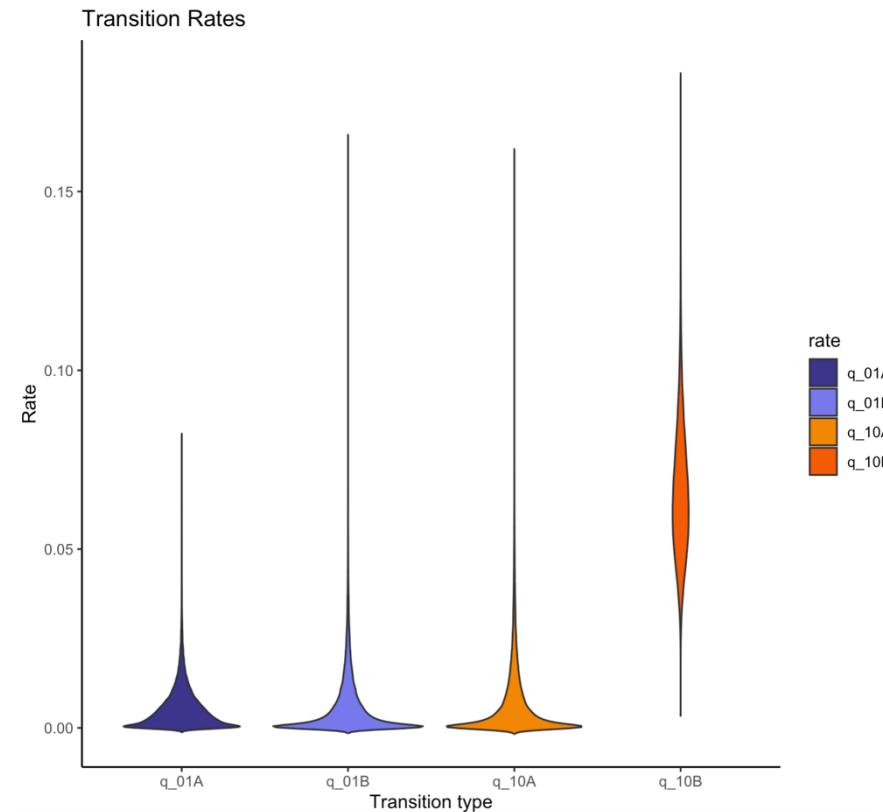


# Transition rates

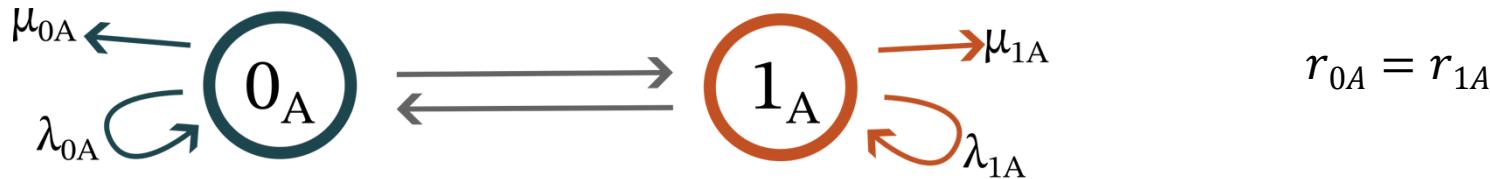
BiSSE



HiSSE



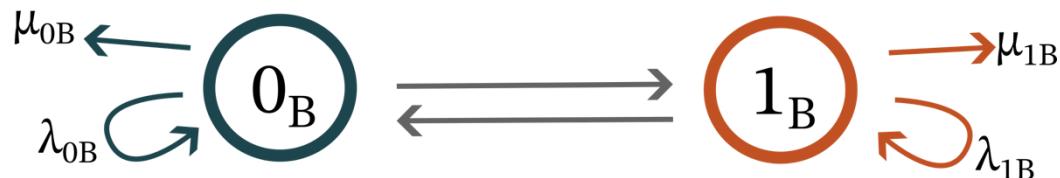
New null hypothesis: Diversification does not come from main trait...



$$r_{0A} = r_{1A}$$



$$0 = 1$$



$$r_{0B} = r_{1B}$$

$$r_{0A} \neq r_{0B}$$

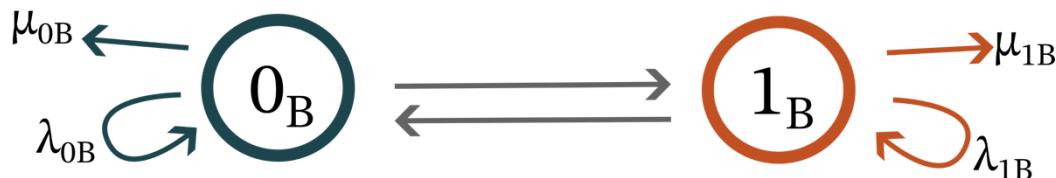
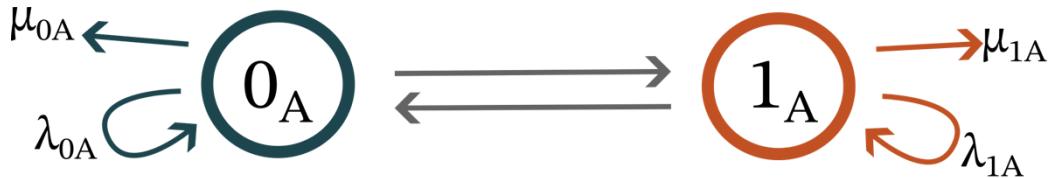
$$A \neq B$$

$$r_{1A} \neq r_{1B}$$

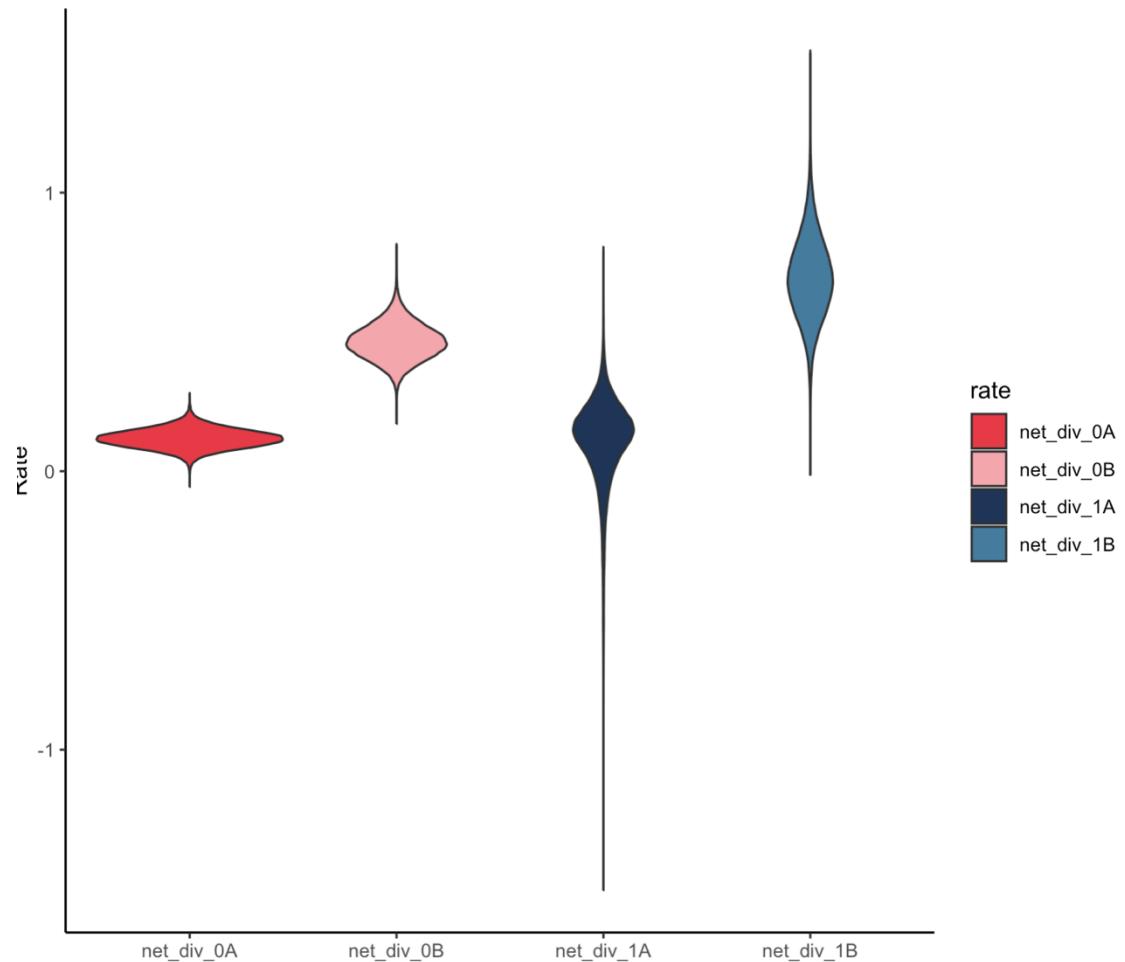
New null hypothesis:

..but diversification can come from other factors

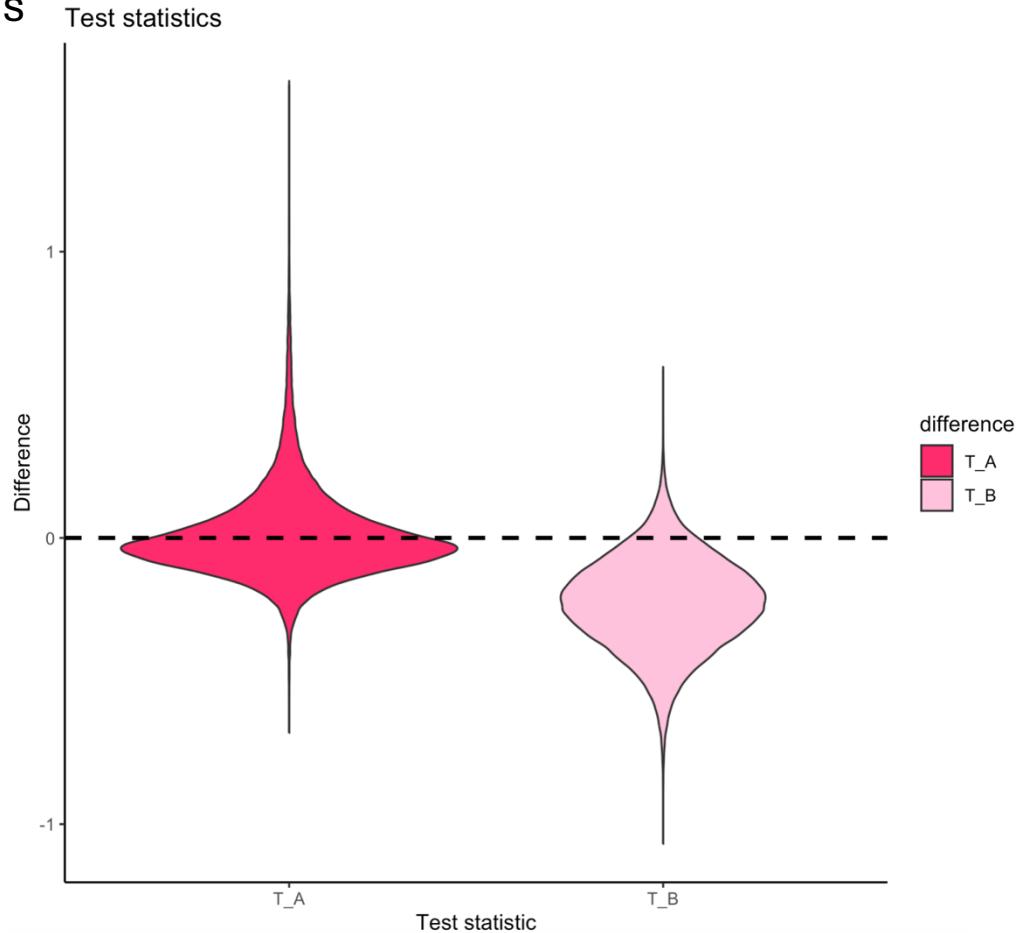
A new “model”  
Character  
Independent  
(CID)



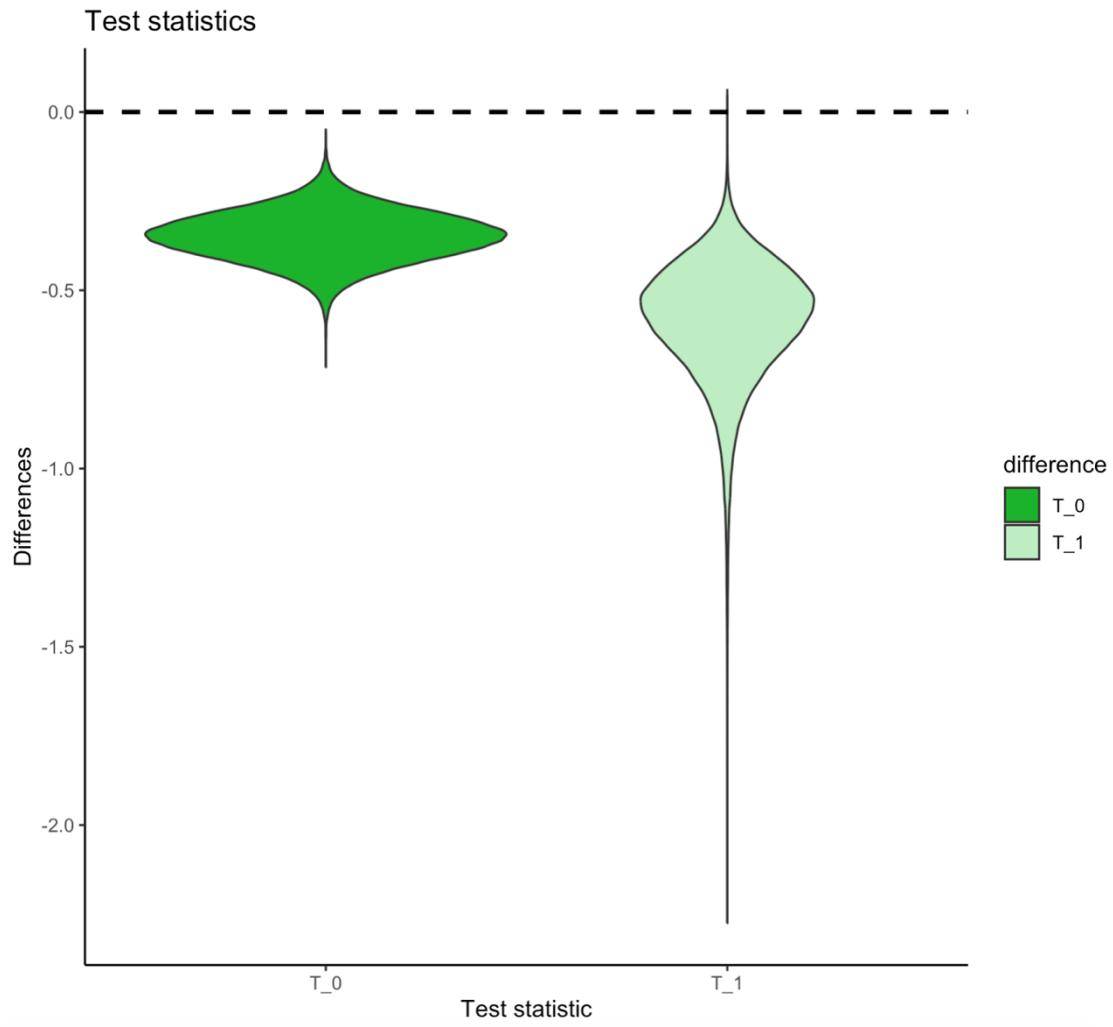
## Quick conclusion?



Differences of net diversifications  
between 0 and 1.

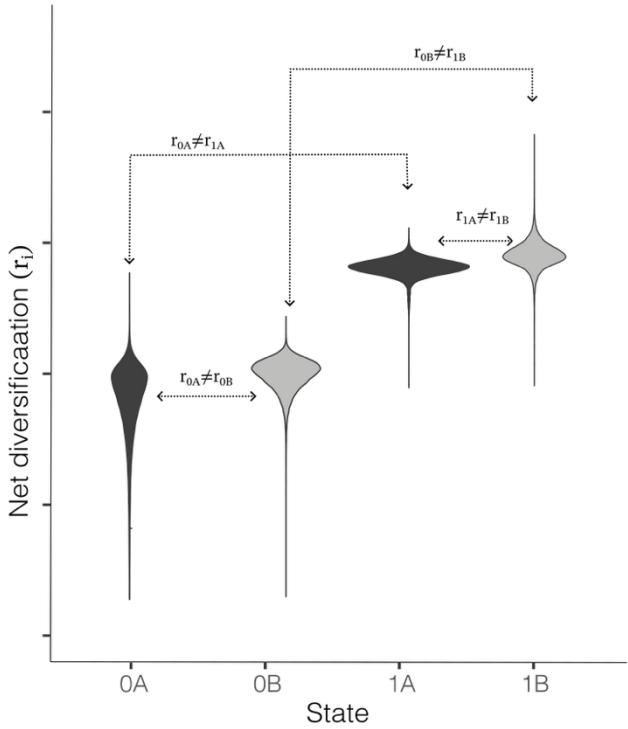
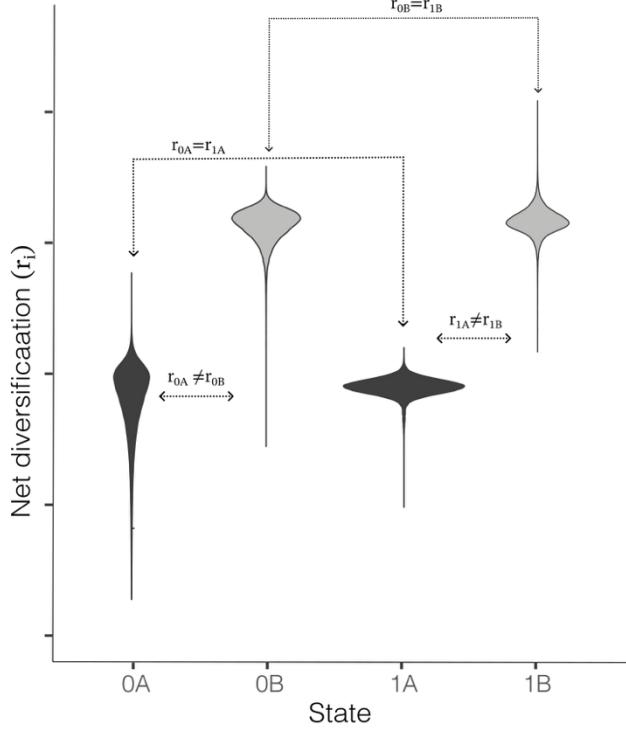


## Differences of net diversifications between A and B



**(A) BiSSE**

# Interpreting results from HiSSE posteriors

**(B) CID-2****(F) Rate comparisons**

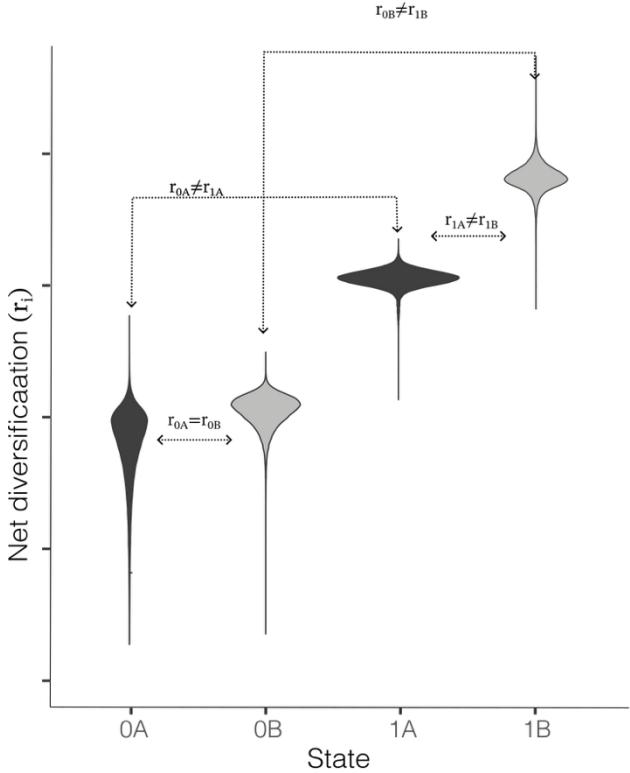
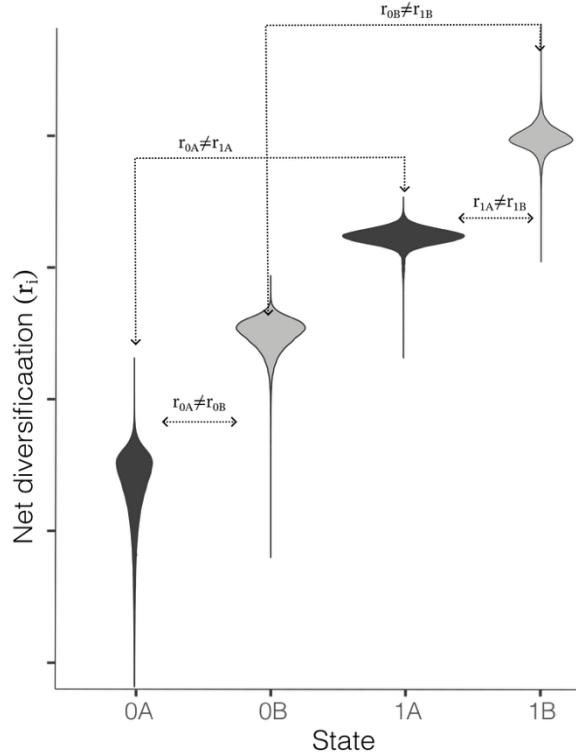
- Unnecessary comparison
- Equal rates with probability >5%
- ≠ Different rates with probability >5%

|          | $r_{0A}$ | $r_{0B}$ | $r_{1A}$ | $r_{1B}$ |          |
|----------|----------|----------|----------|----------|----------|
| $r_{0A}$ | ■        | —        | ≠        | ■        | $r_{0A}$ |
| $r_{0B}$ | ■        | ■        | ■        | ≠        | $r_{0B}$ |
| $r_{1A}$ | ■        | —        | ■        | ■        | $r_{1A}$ |
| $r_{1B}$ | ■        | ■        | ■        | ■        | $r_{1B}$ |

|          | $r_{0A}$ | $r_{0B}$ | $r_{1A}$ | $r_{1B}$ |          |
|----------|----------|----------|----------|----------|----------|
| $r_{0A}$ | ■        | ≠        | —        | ■        | $r_{0A}$ |
| $r_{0B}$ | ■        | ■        | ■        | —        | $r_{0B}$ |
| $r_{1A}$ | ■        | ■        | —        | ■        | $r_{1A}$ |
| $r_{1B}$ | ■        | ■        | ■        | ■        | $r_{1B}$ |

**(C) Gray zone**

# Interpreting results from HiSSE posteriors

**(D) HiSSE****(F) Rate comparisons**

- Unnecessary comparison
- ▬ Equal rates with probability >5%
- ≠ Different rates with probability >5%

|          | $r_{0A}$ | $r_{0B}$ | $r_{1A}$ | $r_{1B}$ |          |
|----------|----------|----------|----------|----------|----------|
| $r_{0A}$ | ■        | ▬        | ≠        | ■        | $r_{0A}$ |
| $r_{0B}$ | ■        | ■        | ■        | ≠        | $r_{0B}$ |
| $r_{1A}$ | ■        | ▬        | ■        | ≠        | $r_{1A}$ |
| $r_{1B}$ | ■        | ▬        | ≠        | ■        | $r_{1B}$ |

|          | $r_{0A}$ | $r_{0B}$ | $r_{1A}$ | $r_{1B}$ |          |
|----------|----------|----------|----------|----------|----------|
| $r_{0A}$ | ■        | ≠        | ≠        | ■        | $r_{0A}$ |
| $r_{0B}$ | ■        | ■        | ■        | ≠        | $r_{0B}$ |
| $r_{1A}$ | ■        | ▬        | ■        | ≠        | $r_{1A}$ |
| $r_{1B}$ | ■        | ▬        | ≠        | ■        | $r_{1B}$ |