

Markov Chains in Diversification

Introduction to state-dependent diversification



NSF-DEB 2323170



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SSB Brekout Meeting 2026

Download slides and files

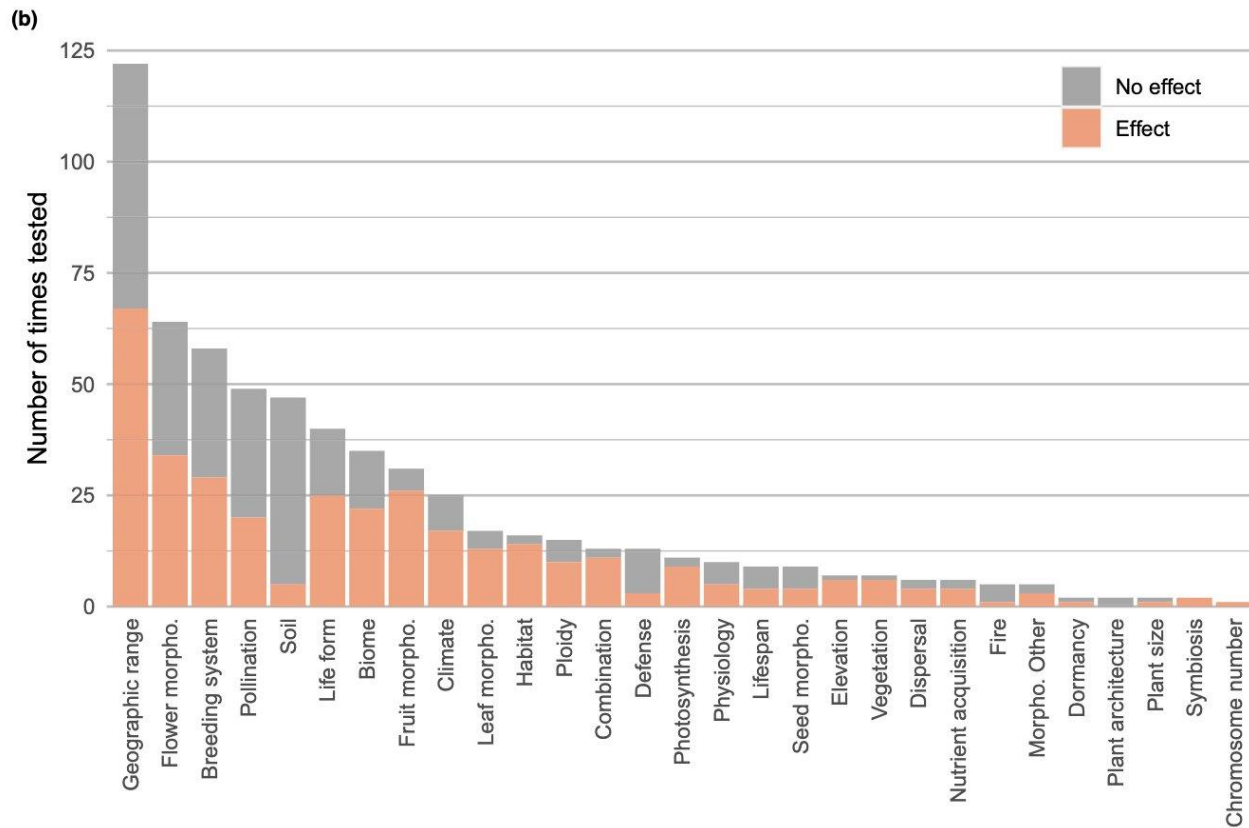
<https://roszenil.github.io/mytutorials>



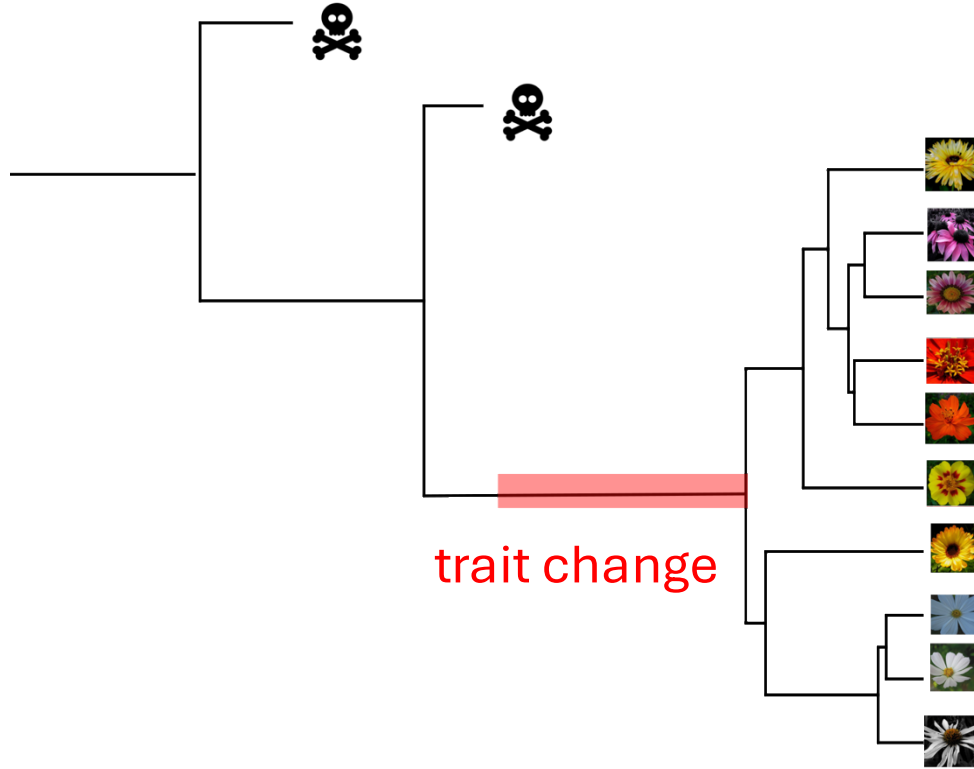
There are
400,000
vascular plants
in the planet.



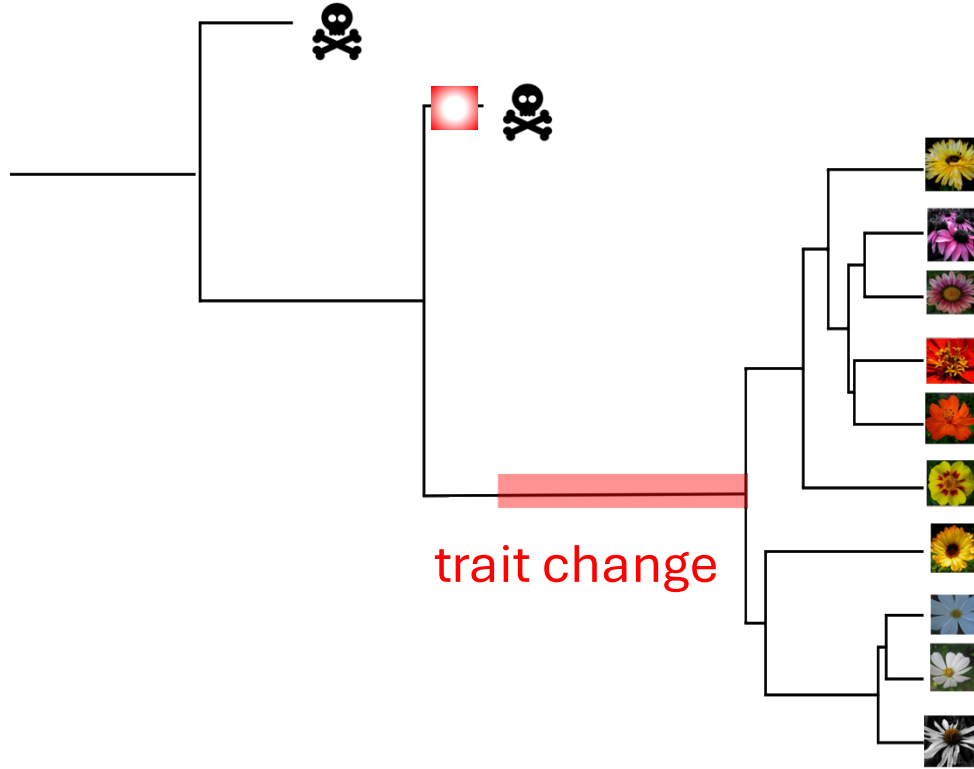
152 studies linking plant traits to speciation and extinction using state-dependent diversification



Macroevolutionary consequences of trait change



Macroevolutionary consequences of trait change



Perspective

Opposing effects of plant
traits on diversification

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

Polyploidy



Gene redundancy allows evolution of new functions and facilitates divergence.



Divergent resolution of gene redundancy leads to post-zygotic incompatibilities.

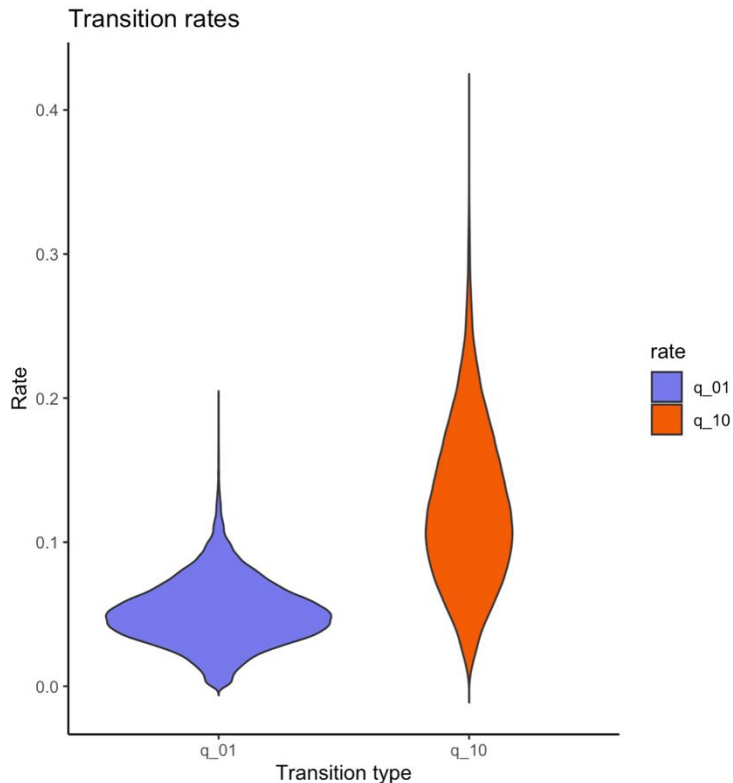
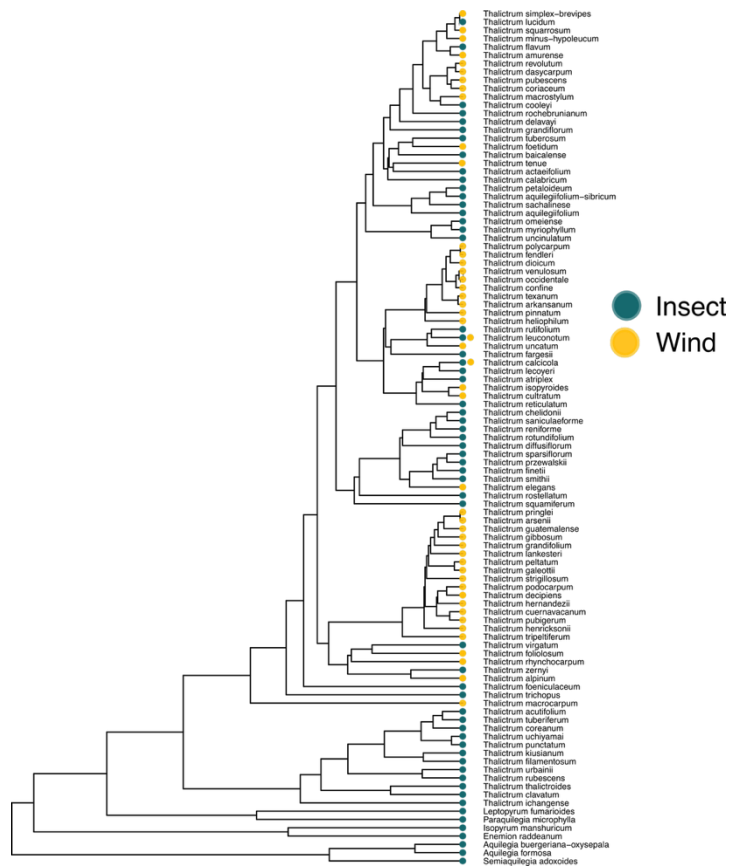


Instability in meiosis and minority cytotype disadvantage leads to mating difficulties

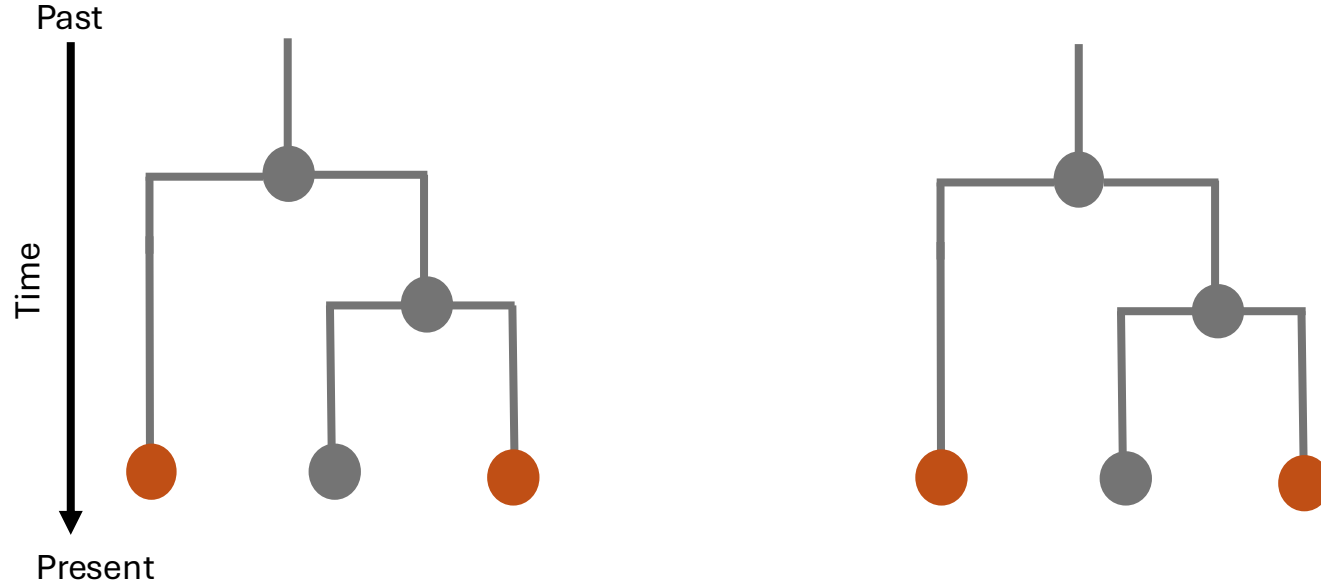


Gene redundancy buffers deleterious mutations and allows evolution of new functions, which increases adaptive potential in changing environments.

Under a Mk2 we estimated for our data



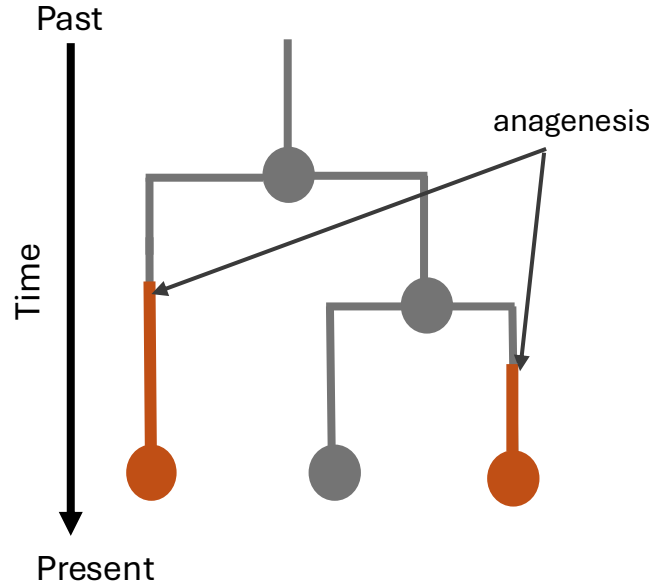
Trait evolution is biased without understanding the role of speciation and extinction events



Maddison. 2006. *Sys Bio*.

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

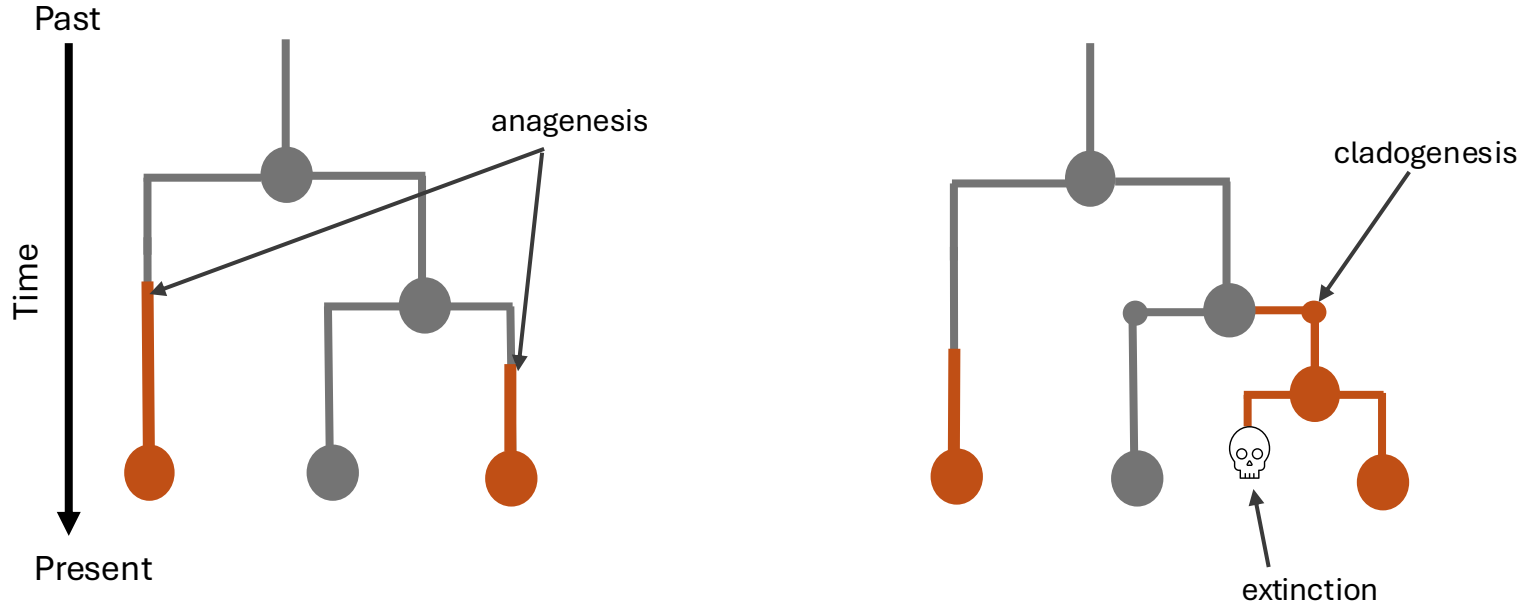
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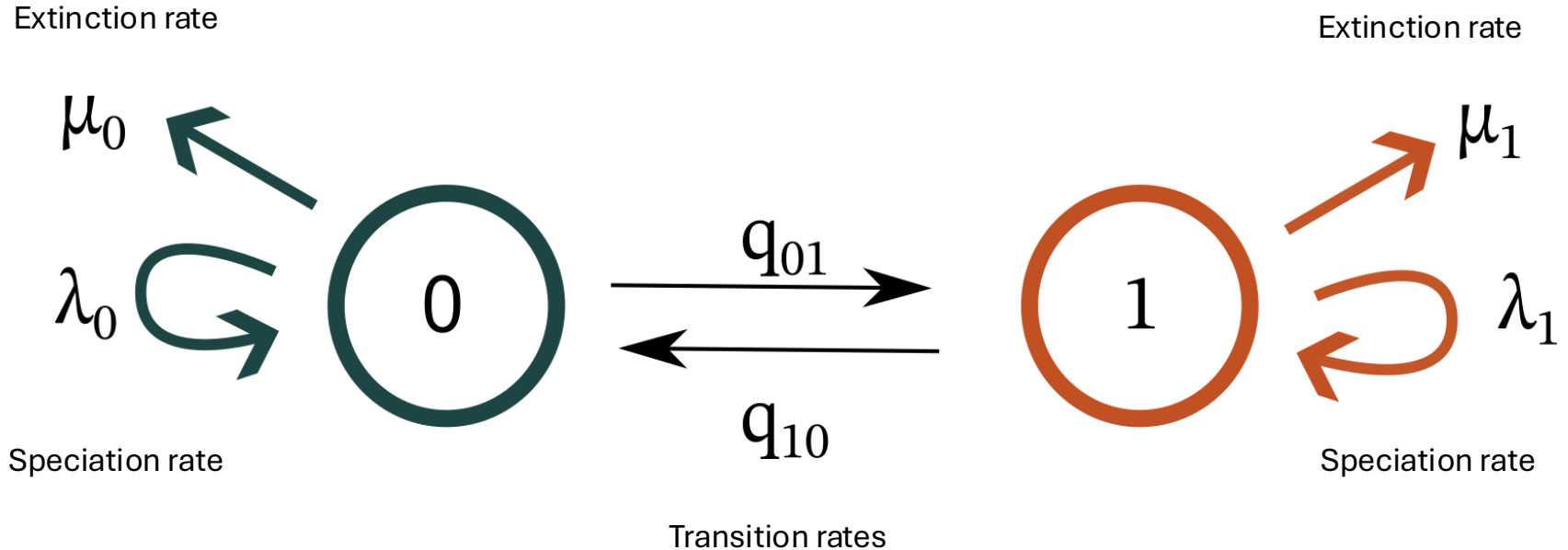
Trait evolution is biased without understanding the role of speciation and extinction events



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)



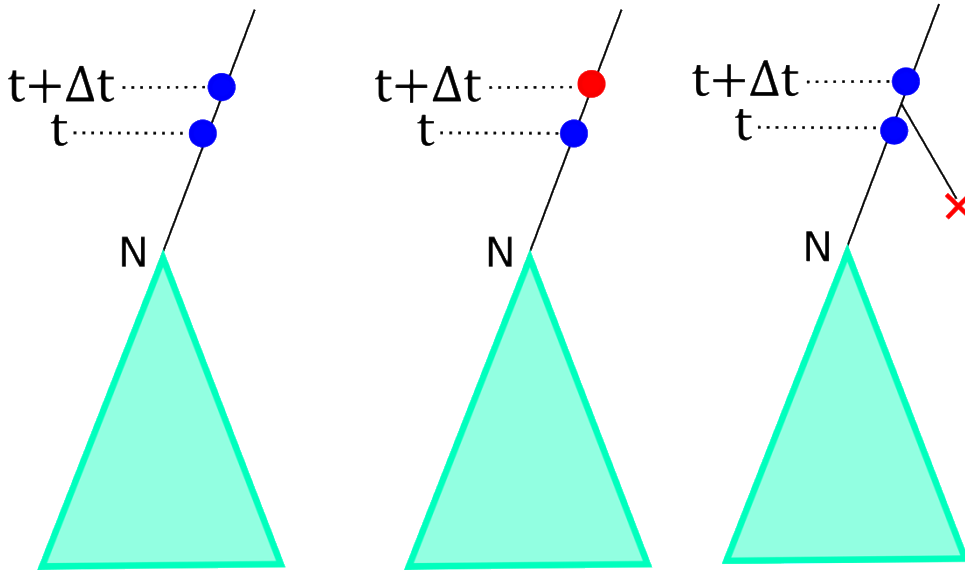


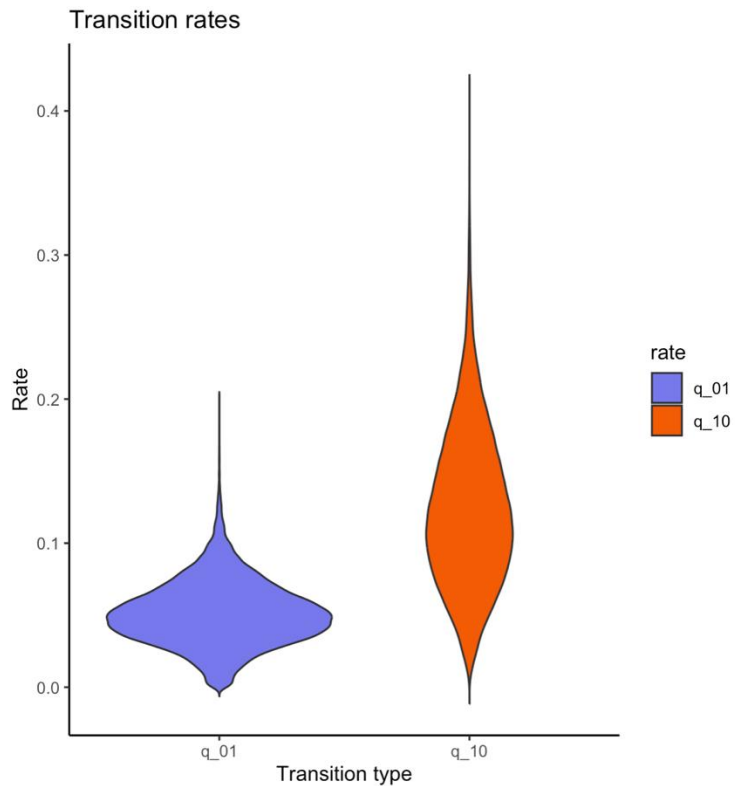
SCAN ME

Phyloseminar
Dra. Sally Otto
BiSSE
developer

How do we specify a Q-matrix for this?

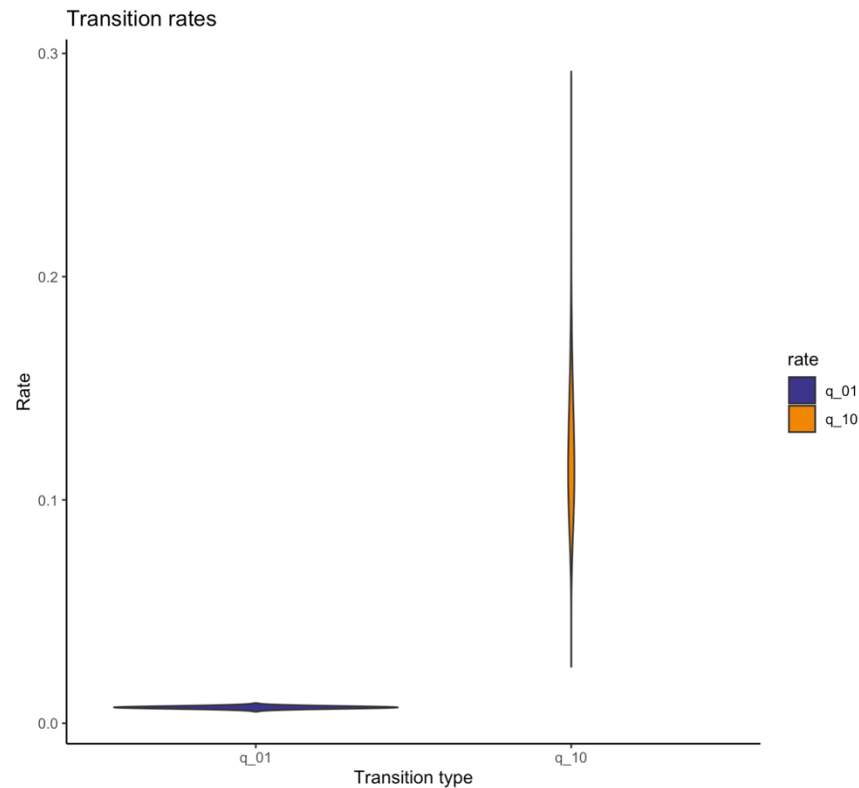
Stochastic differential equations (Kolmogorov-Forward)





Mk2

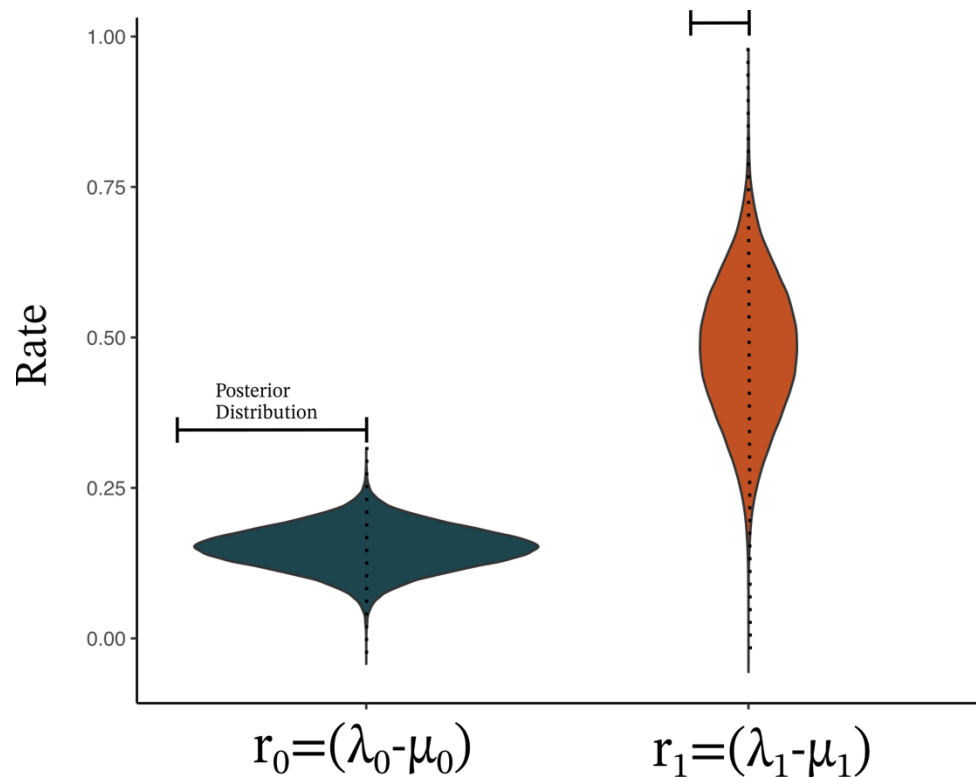
Equal transitions back and
forth from pollination



BiSSE

Easier to transition from
Wind to Insect but uncertain

Checking for differences in diversification correlated to a discrete trait



Net diversification rate (r) =
Speciation rate (λ) – Extinction rate (μ)

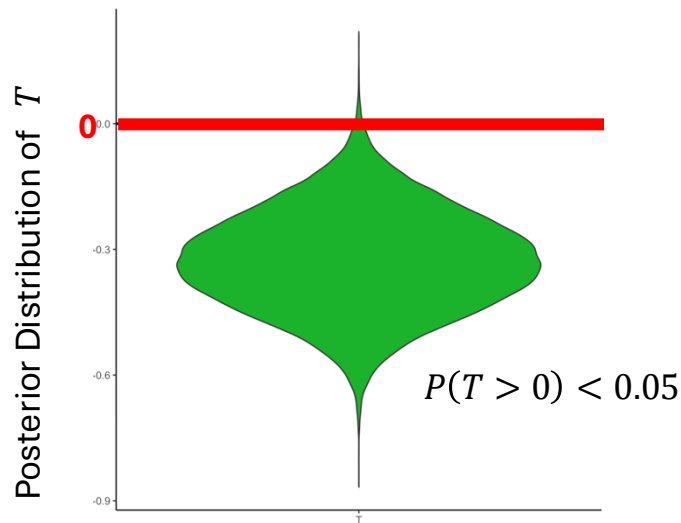
**Is it probable
that they are different?**

Developing a hypothesis testing framework to find differences in net diversification

$$H_0: r_0 = r_1$$



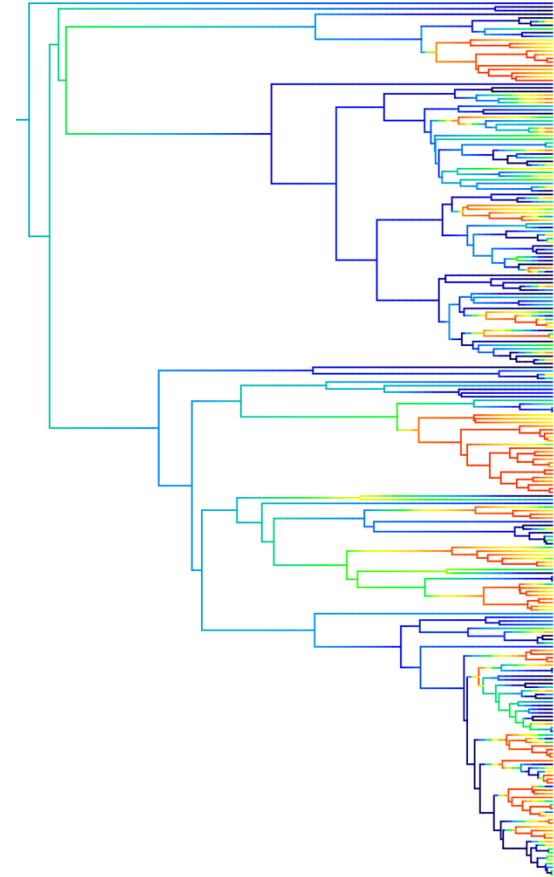
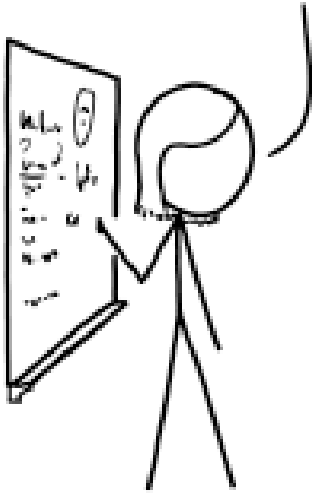
$$\text{Test statistic } T = r_0 - r_1$$



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

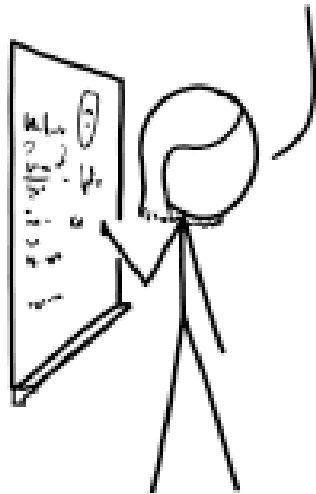
Null hypothesis of BiSSE

$$H_0: r_0 = r_1$$



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

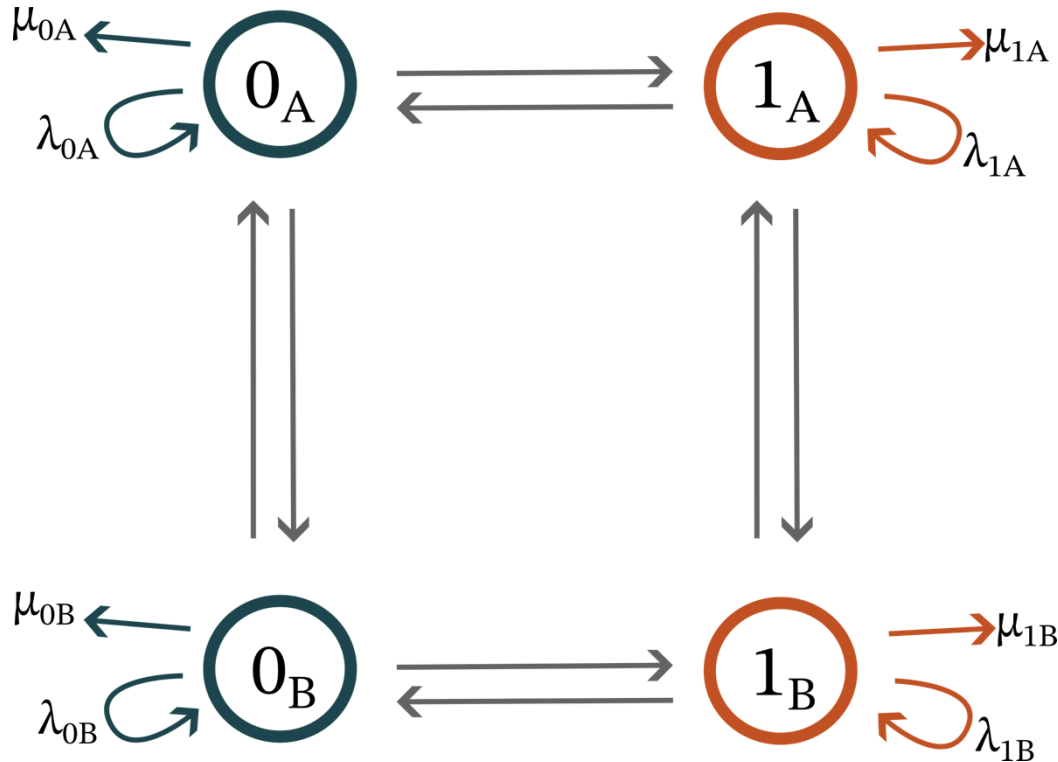


Hidden states
A and B
represent other
unmeasured sources
of diversification

HiSSE

- 4 speciations
- 4 extinctions
- 8 transition rates

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

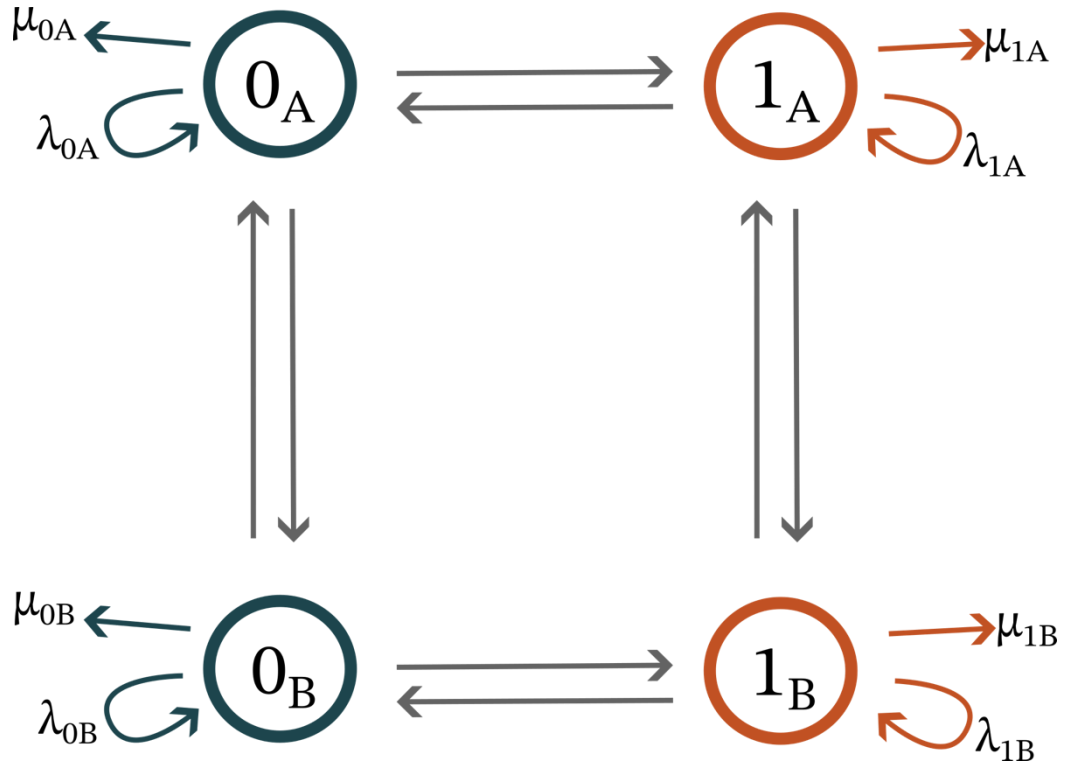


Hidden states
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HiSSE

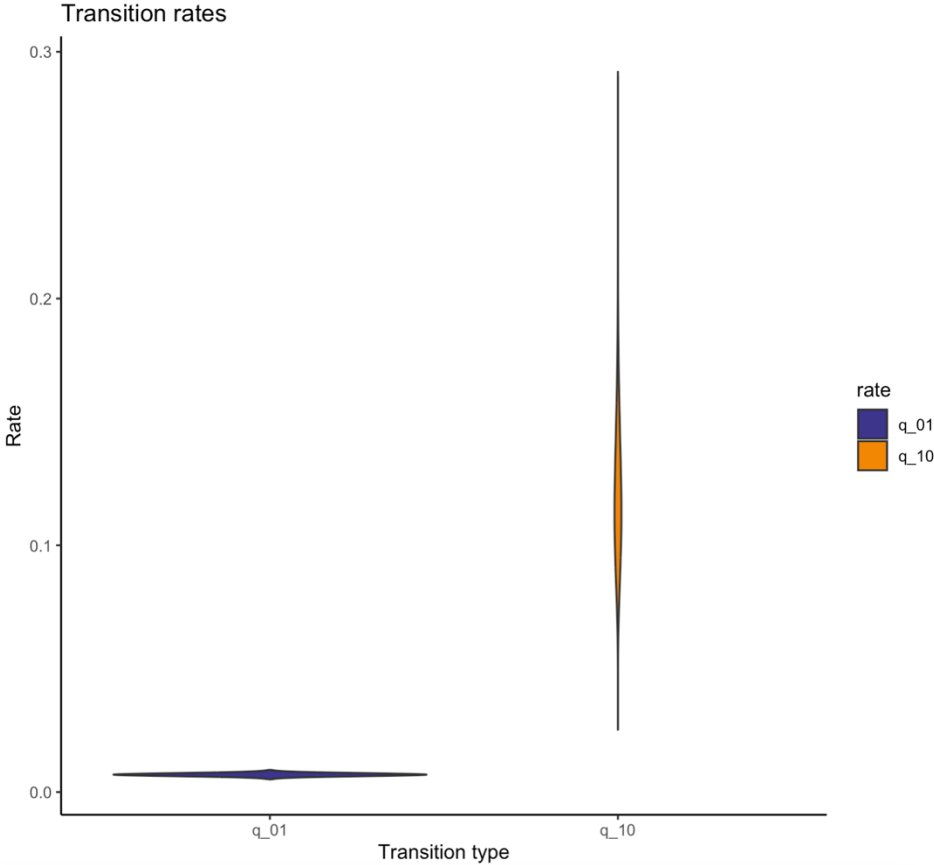
- 4 speciations
- 4 extinctions
- 8 transition rates

Transition Rates

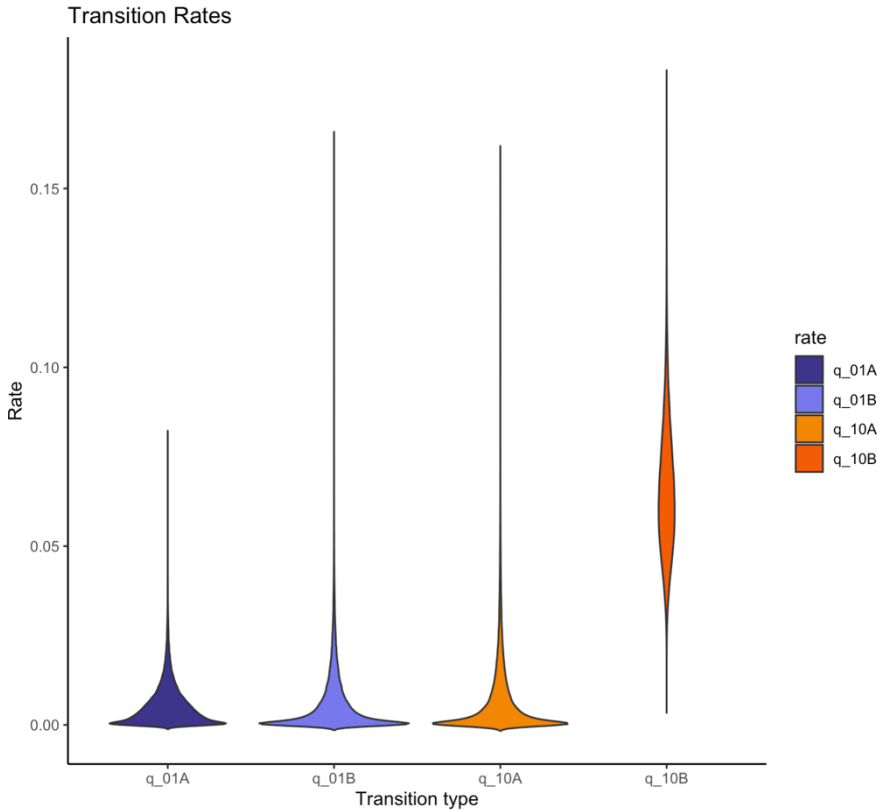


Transition rates

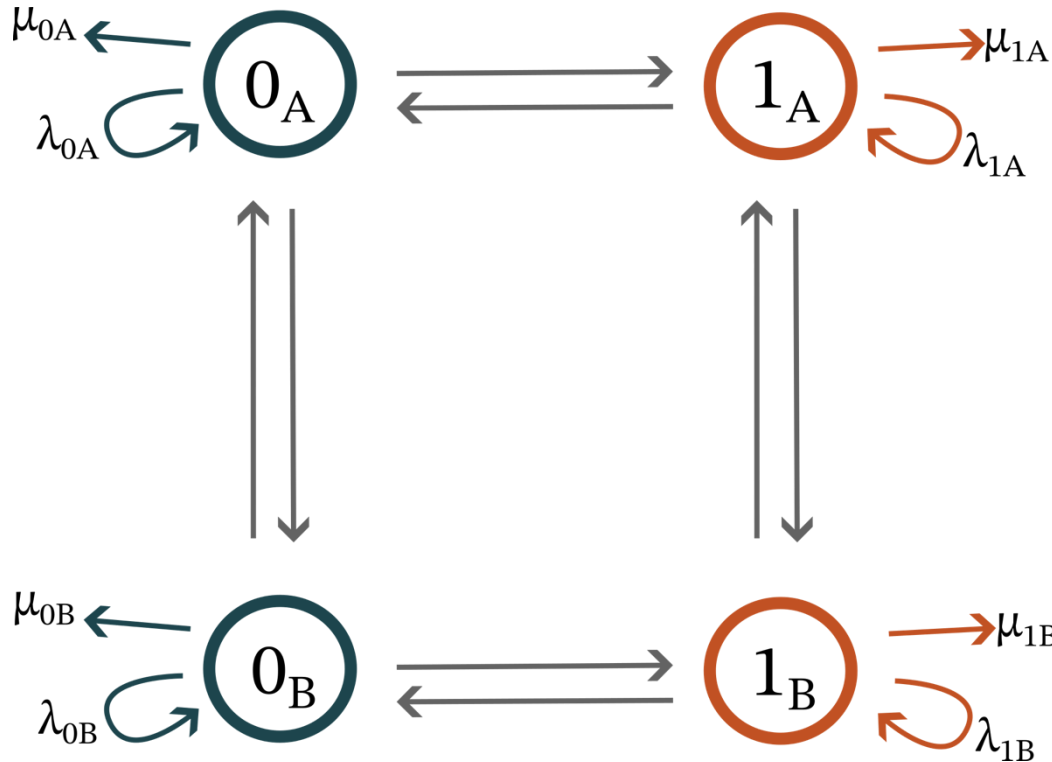
BiSSE



HiSSE



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



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

$$0 = 1$$

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

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

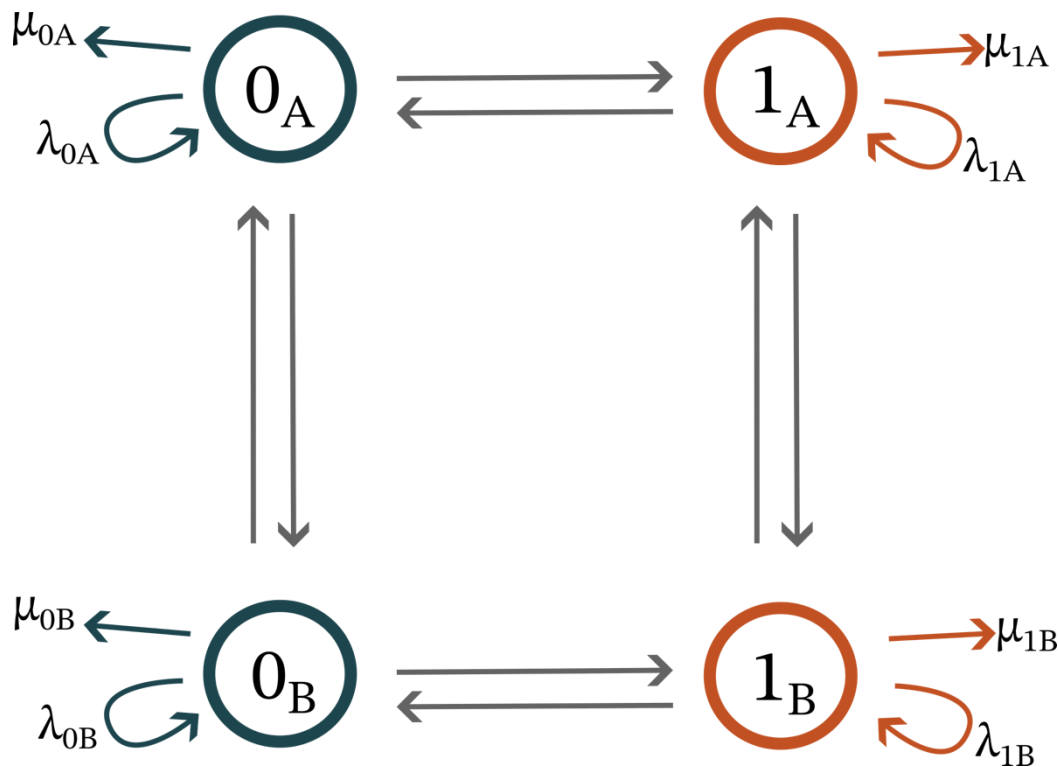
$$A \neq B$$

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

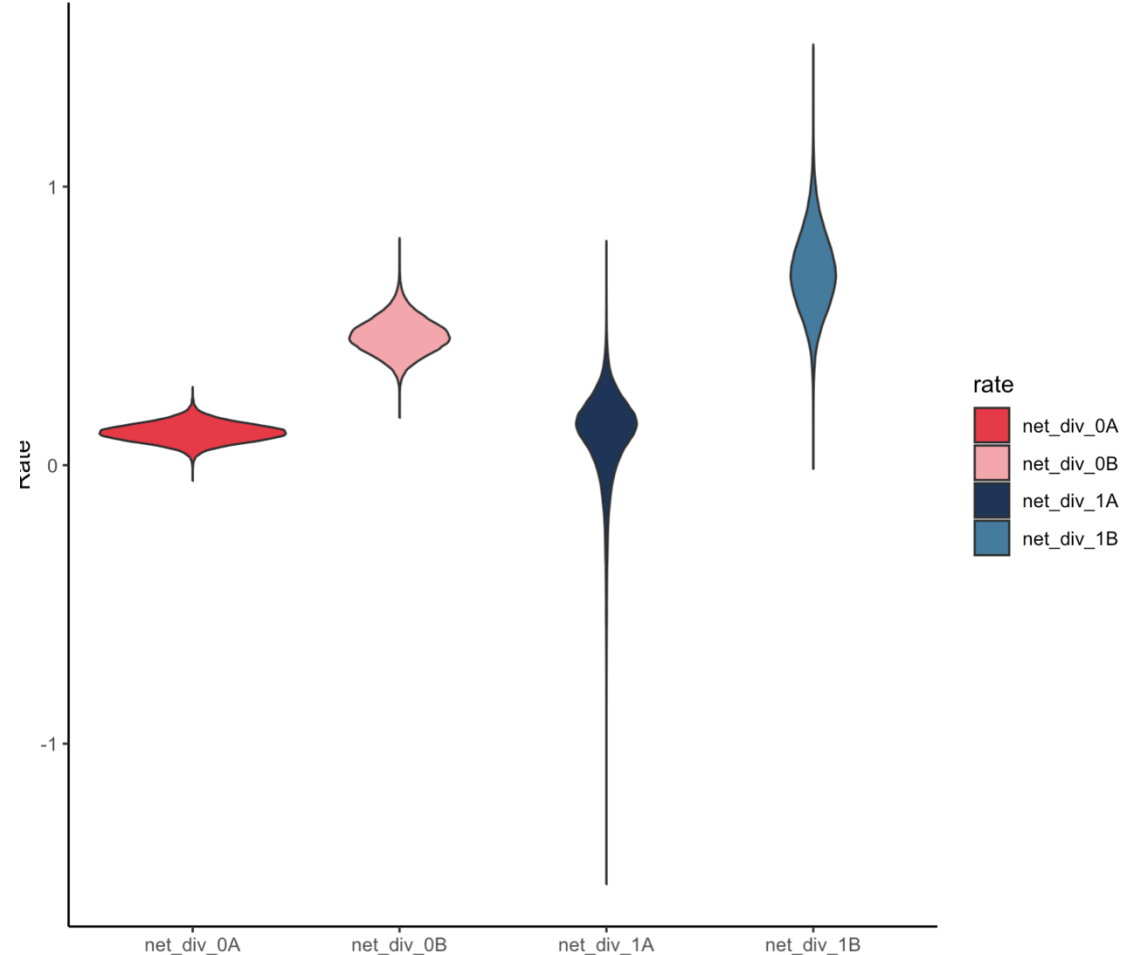
New null hypothesis:

..but diversification can
come from other factors

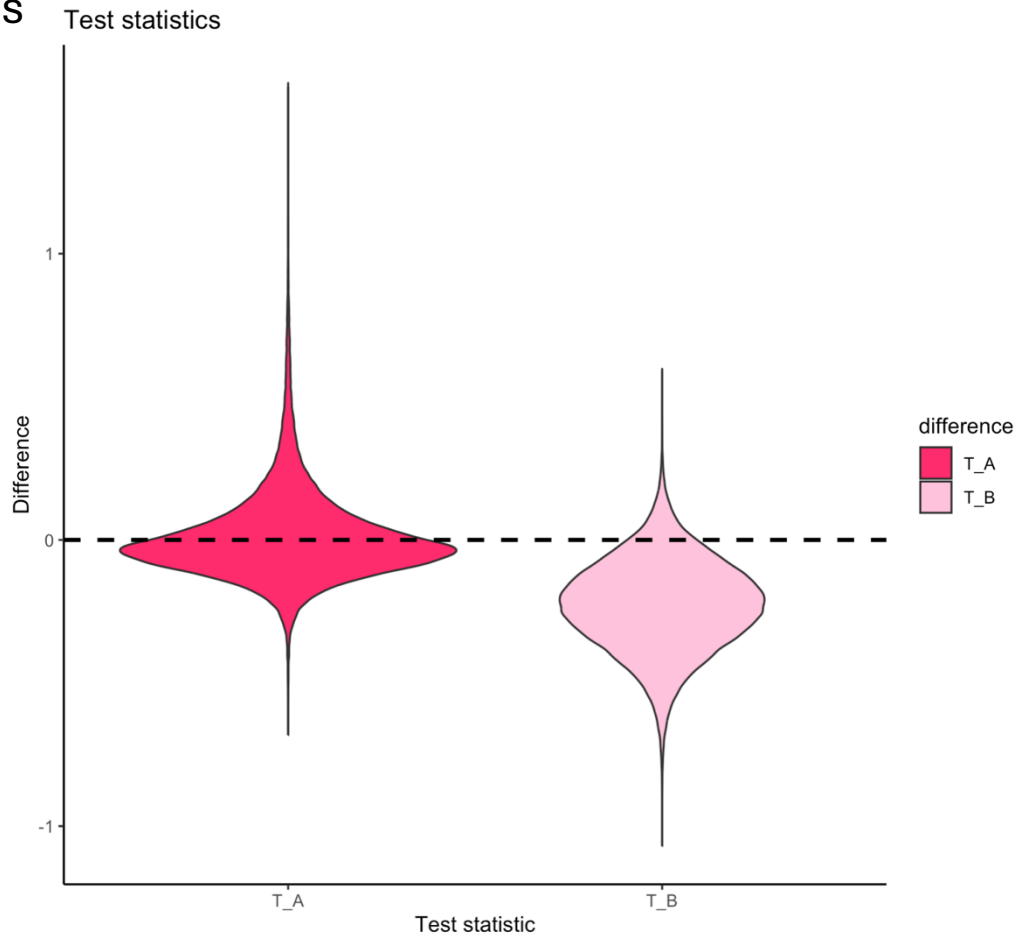
A new “model”
Character
Independent
(CID)



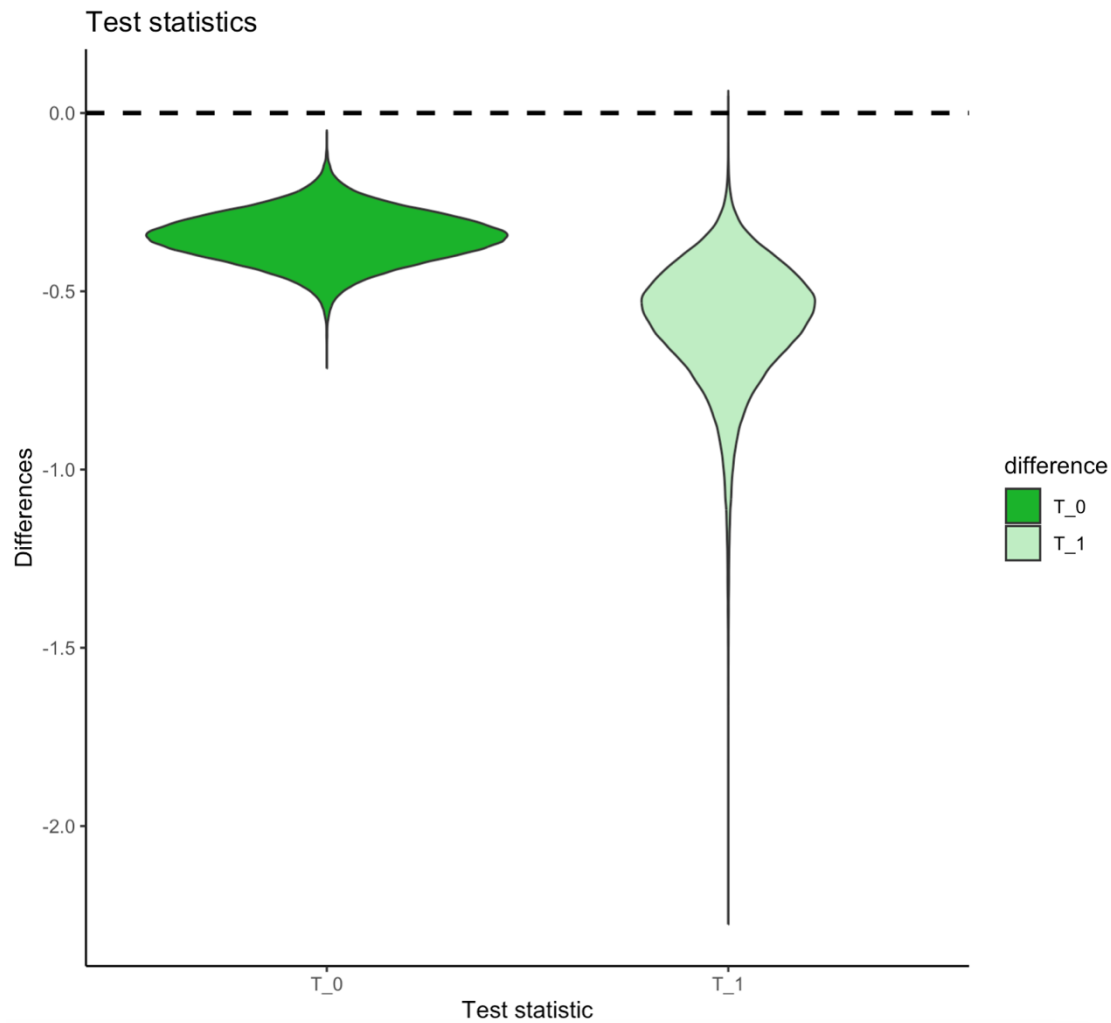
Quick conclusion?

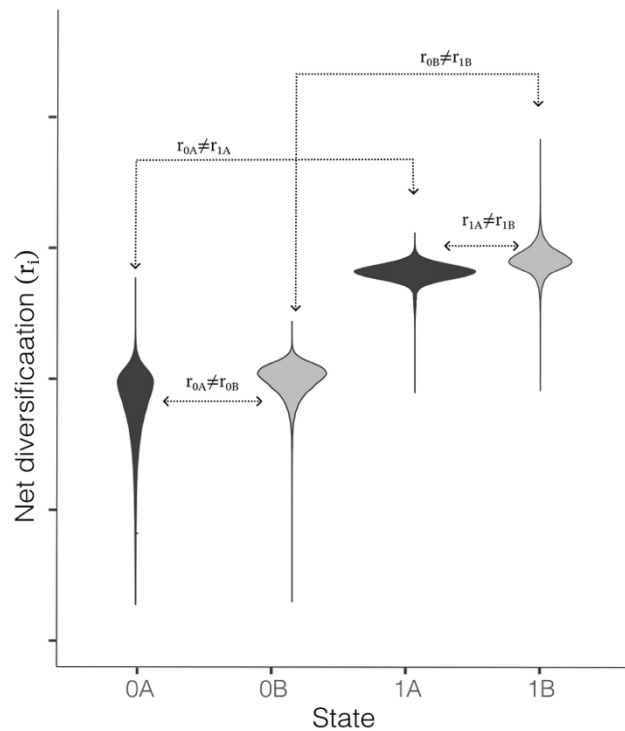
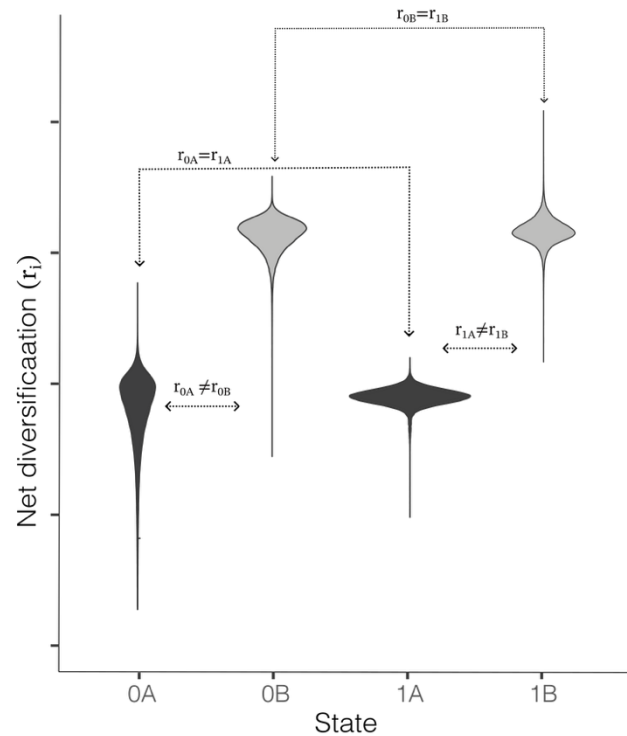


Differences of net diversifications
between 0 and 1.



Differences of net diversifications between A and B



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

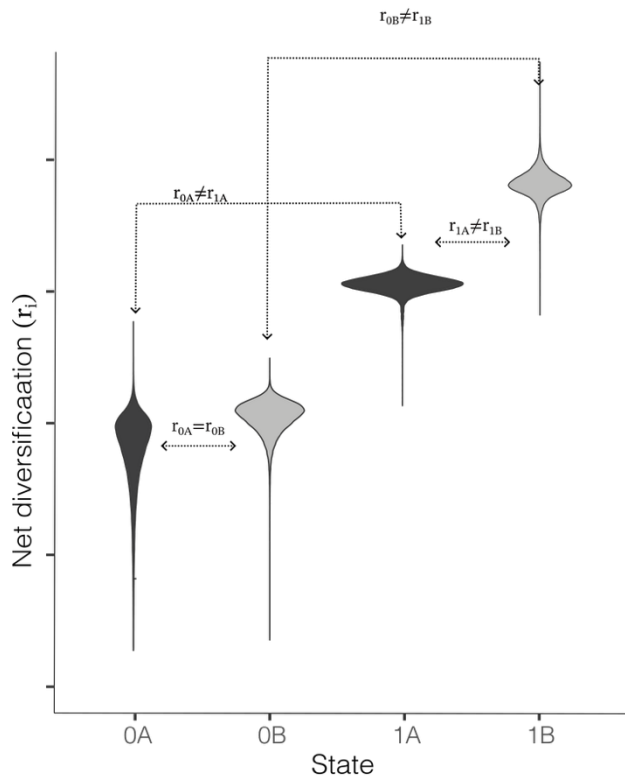
■	Unnecessary comparison
=	Equal rates with probability >5%
≠	Different rates with probability >5%

r_{0A}	r_{0B}	r_{1A}	r_{1B}	
■	=	≠	■	r_{0A}
	■	■	≠	r_{0B}
		■	=	r_{1A}
			■	r_{1B}

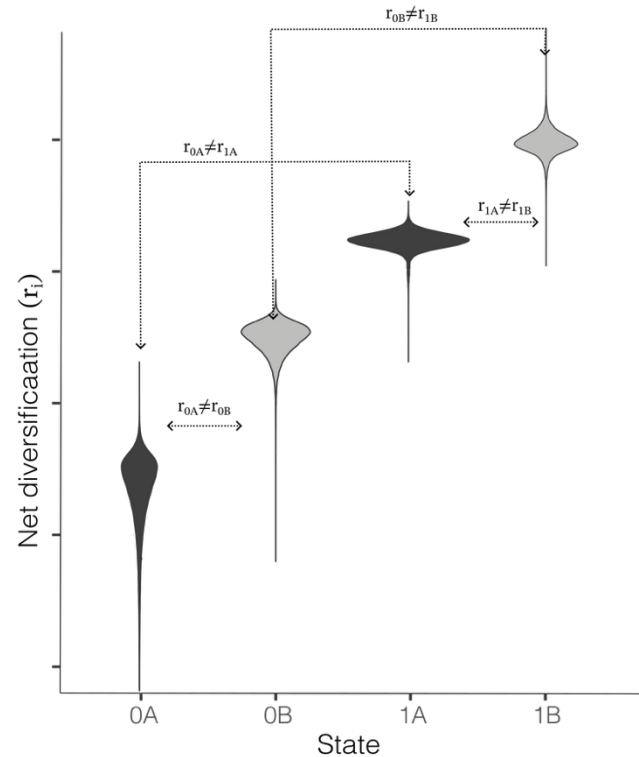
r_{0A}	r_{0B}	r_{1A}	r_{1B}	
■	≠	=	■	r_{0A}
	■	■	=	r_{0B}
		■	≠	r_{1A}
			■	r_{1B}

Interpreting results from HiSSE posteriors

(C) Gray zone



(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_{0B}
		■	≠	r_{1A}
			■	r_{1B}

r_{0A}	r_{0B}	r_{1A}	r_{1B}	
■	≠	≠	■	r_{0A}
	■	■	≠	r_{0B}
		■	≠	r_{1A}
			■	r_{1B}