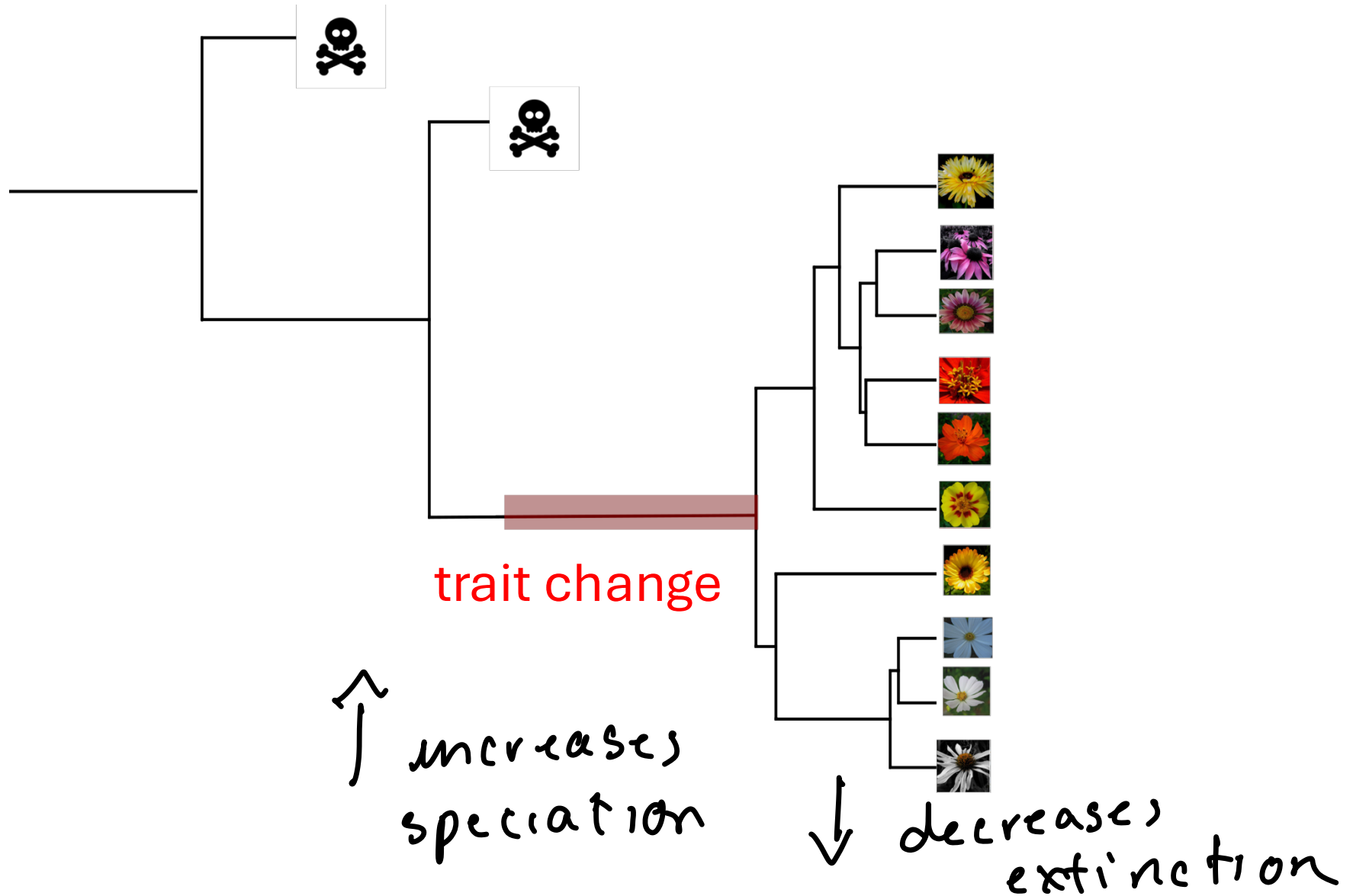


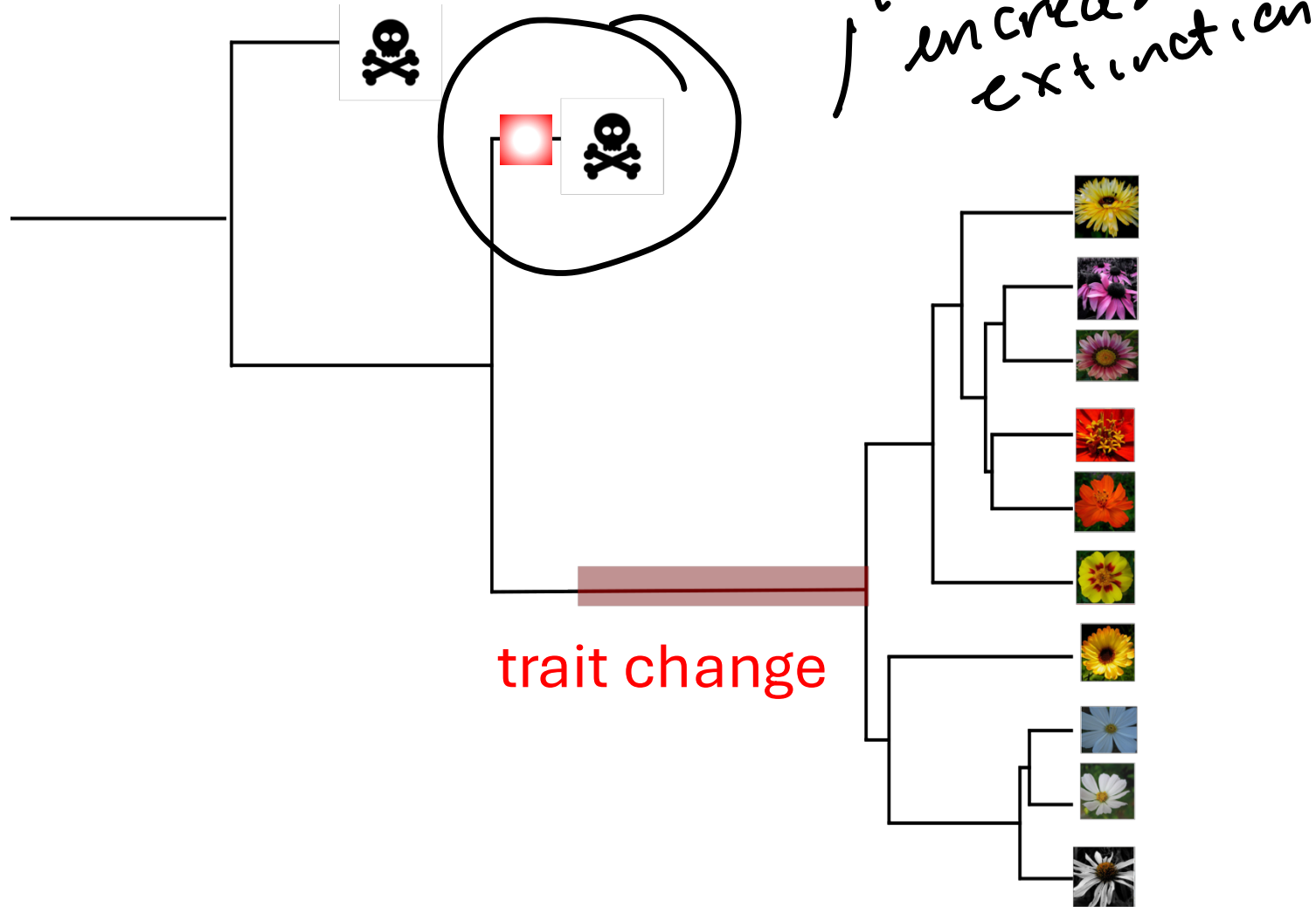
# State-dependent diversification models

Introduction to phylogenetic comparative methods

# 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 Glémin<sup>15,18,\*</sup>

Polyploidy



*Gene redundancy allows evolution of new functions and facilitates divergence.*



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

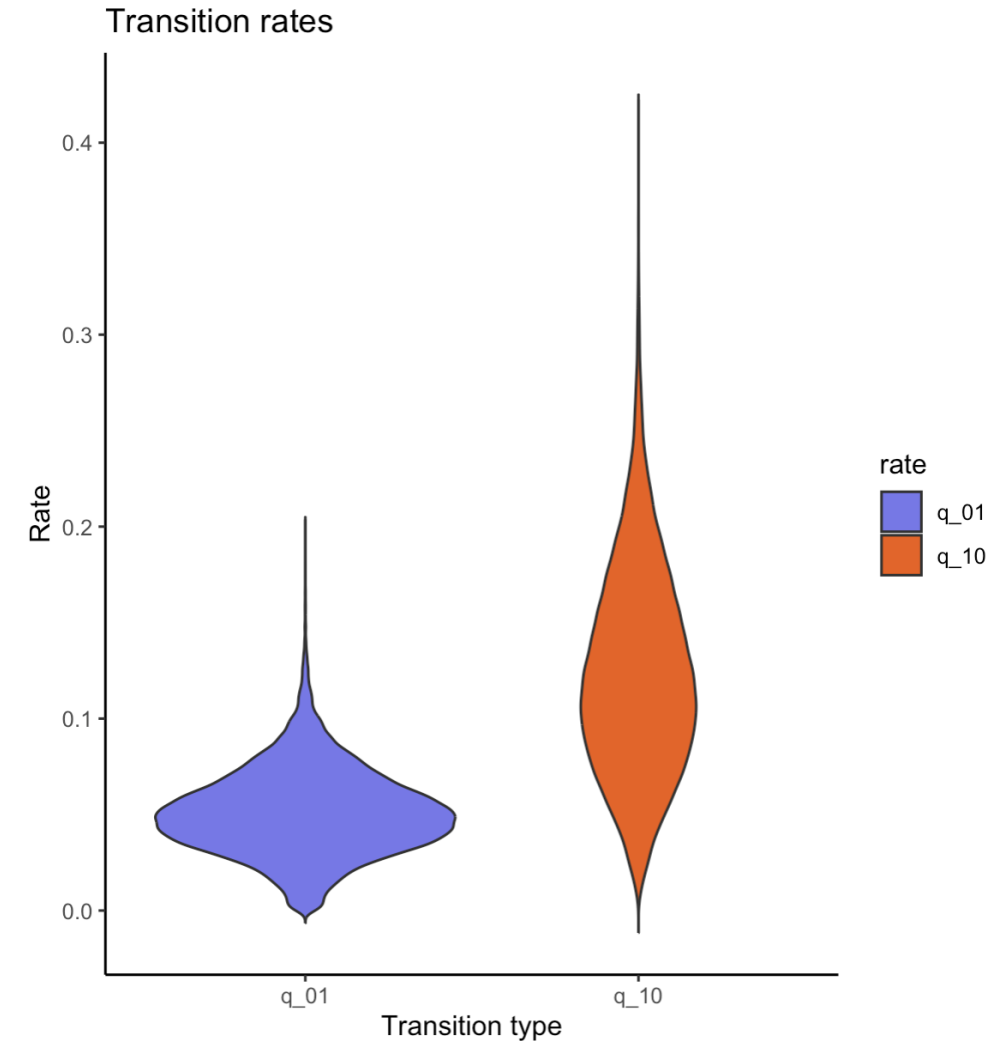
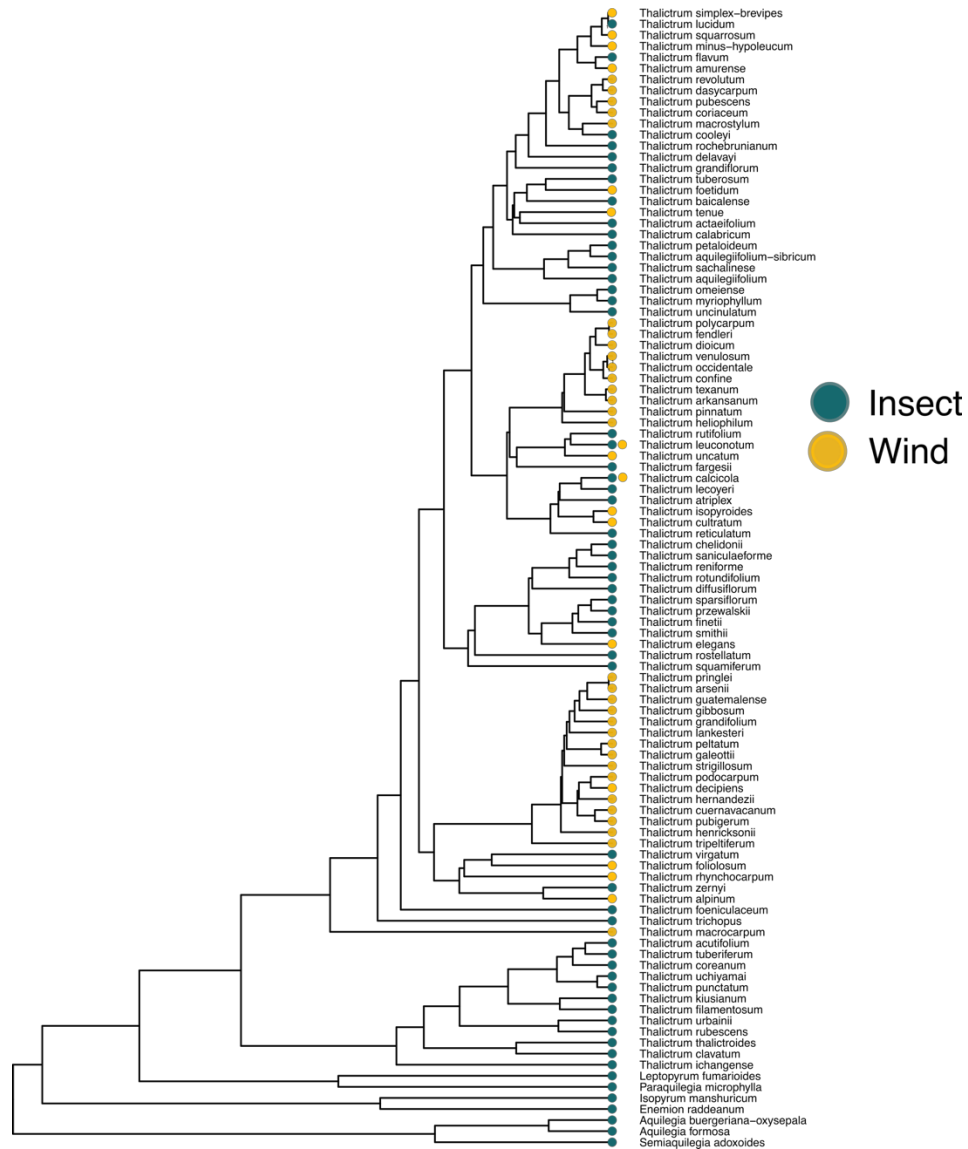


*Instability in meiosis and minority cytotype disadvantage leads to mating difficulties*



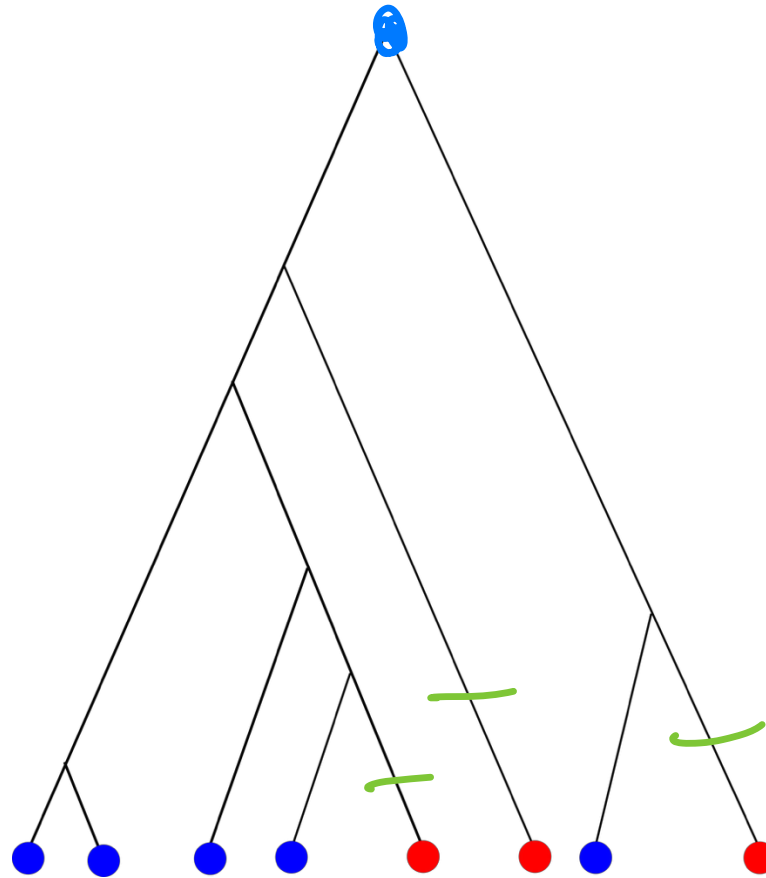
*Gene redundancy buffers deleterious mutations and allows evolution of new functions, which increases adaptive potential in changing environments.*

# Under a Mk2 we estimated for our data

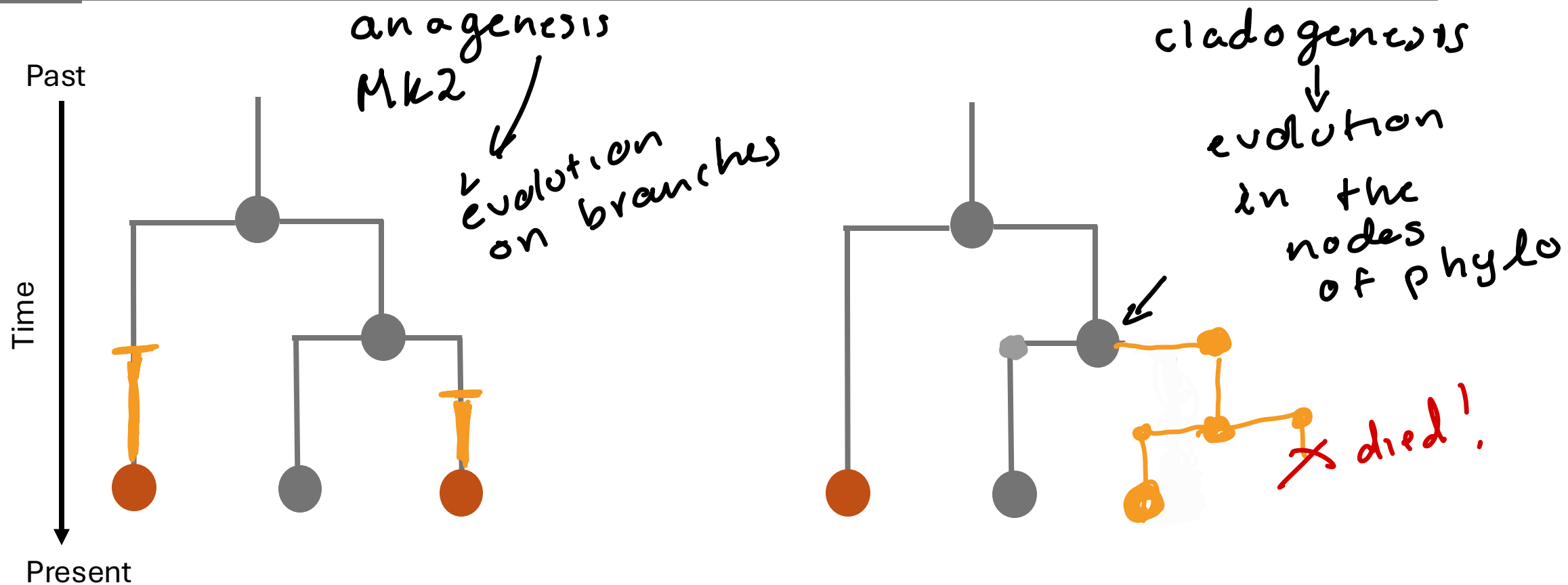


## Stop and think

Where and how many transitions happened in this phylogeny?



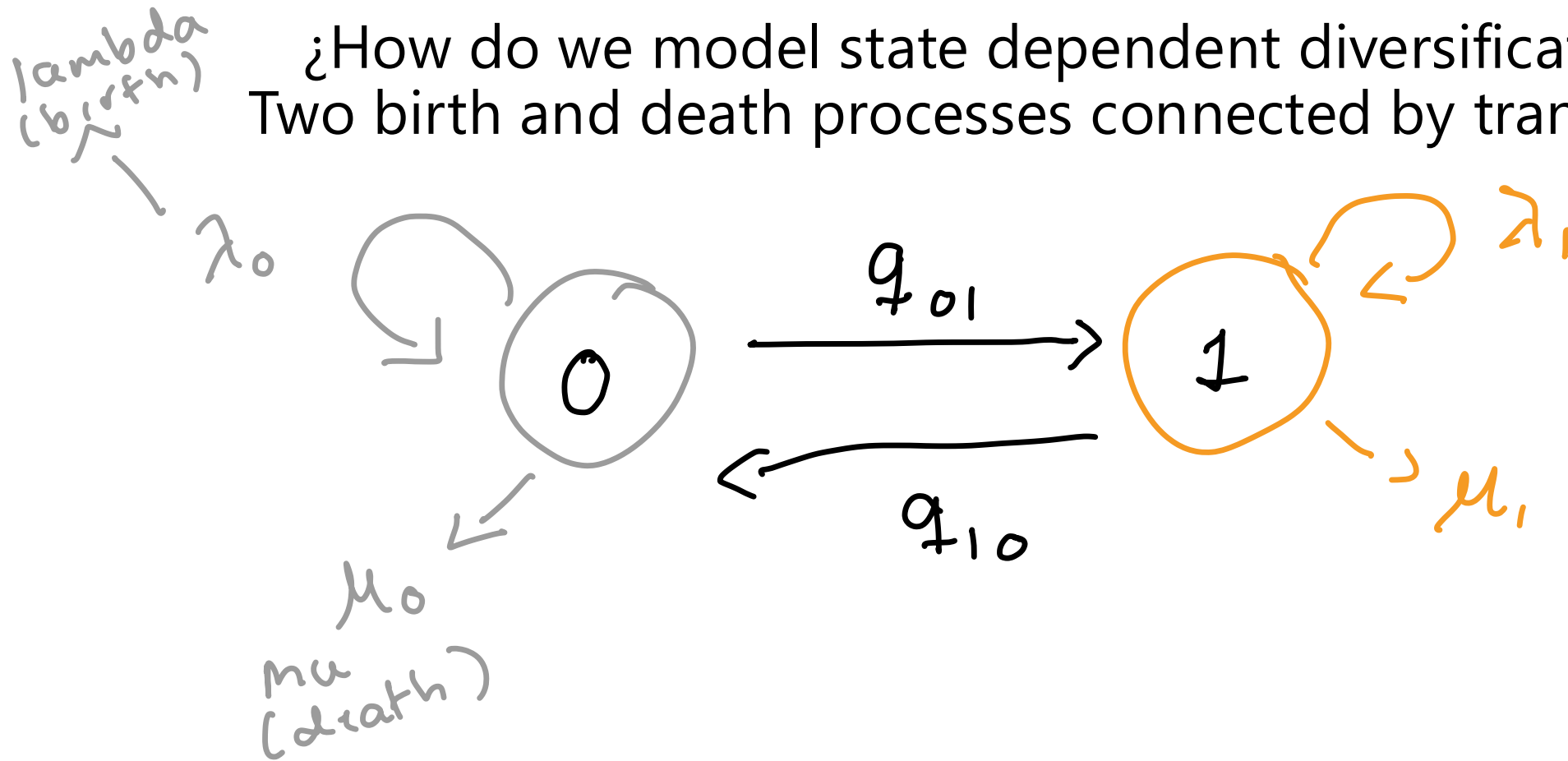
# Trait evolution is biased without understanding the role of speciation and extinction events



Maddison. 2006. *Sys Bio*.

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

¿How do we model state dependent diversification?  
Two birth and death processes connected by transitions



Phyloseminar  
Dra. Sally Otto  
BiSSE developer

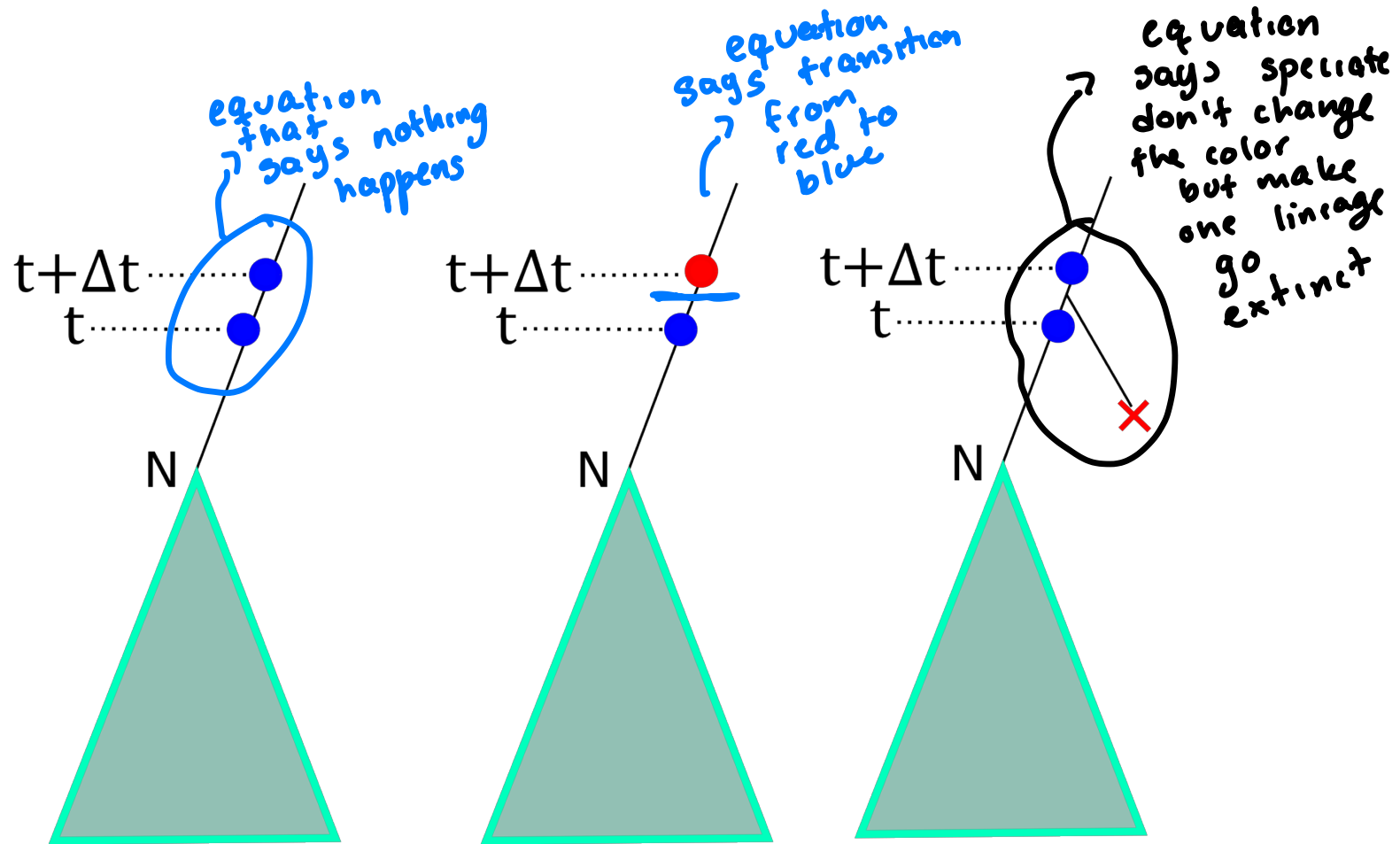
How do we specify a Q-matrix for this?

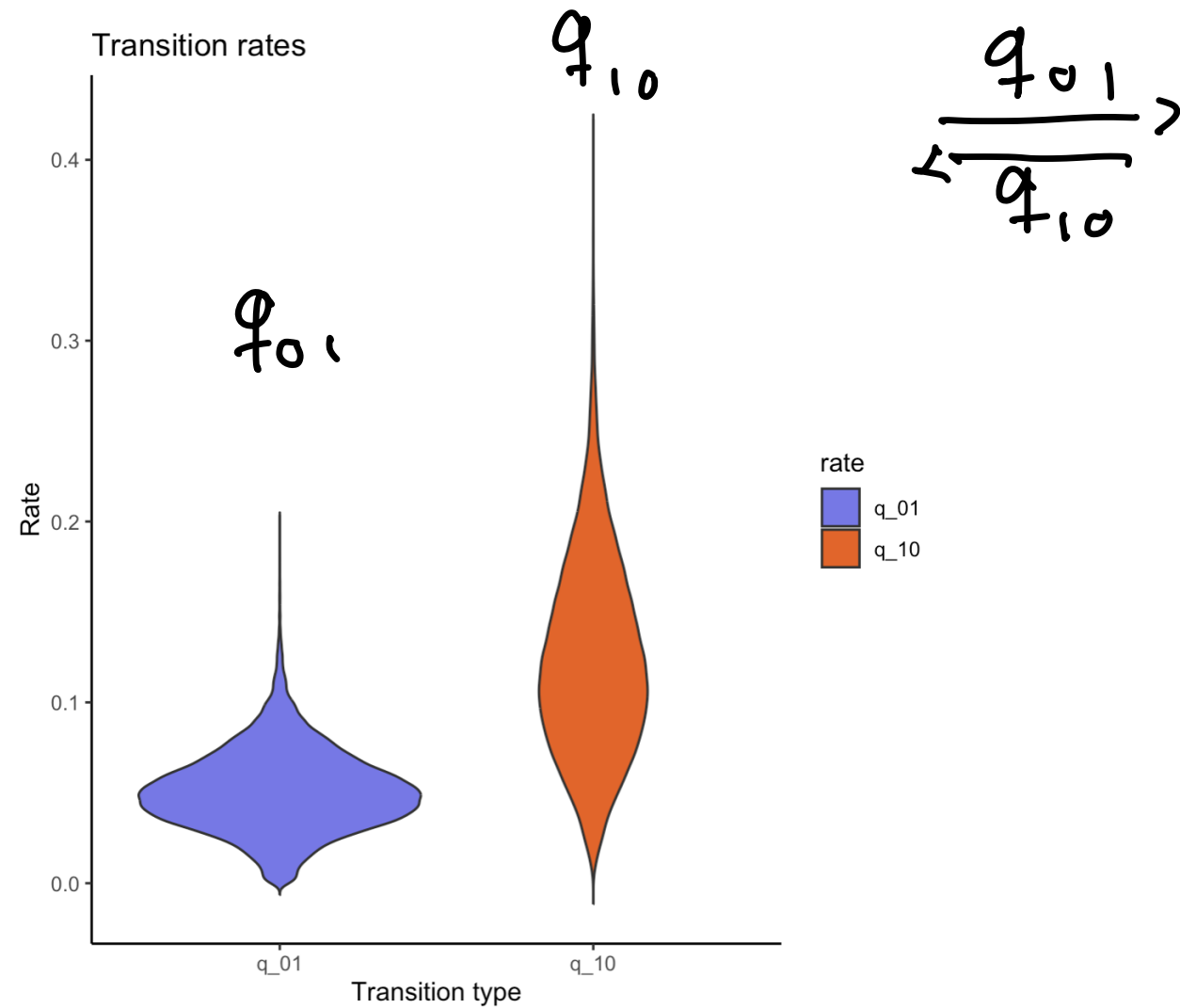
## Binary state Speciation and Extinction Model (BiSSE)

Maddison et al. 2007. *Systematic  
Biology*



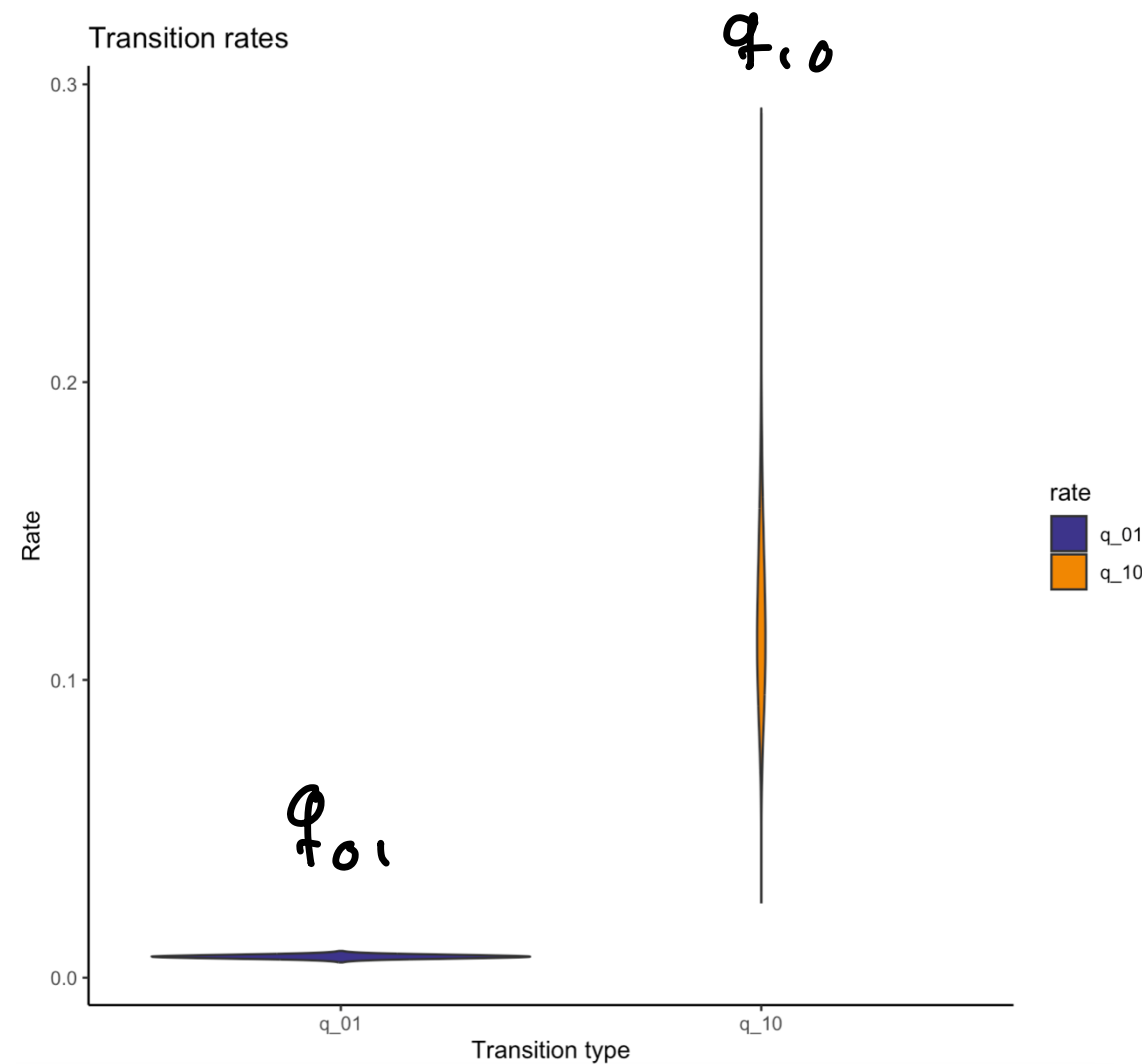
# Stochastic differential equations (Kolmogorov-Forward)





Mk2

Equal transitions back and forth from pollination



BiSSE

Easier to transition from Wind to Insect but uncertain

# What about diversification?

- Net diversification

$$r_0 = \lambda_0 - \mu_0$$

(speciation - extinction in state 0)

- Turnover

$$\tau_0 = \lambda_0 + \mu_0$$

- Extinction fraction

$$\frac{\mu_0}{\lambda_0 + \mu_0}$$

## How do we know BiSSE is THE ONE?

$$H_0: \lambda_0 = \lambda_1 \text{ and } \mu_0 = \mu_1$$

Original null hypothesis

- speciation equal for 0 and 1
- extinction equal for 0 and 1

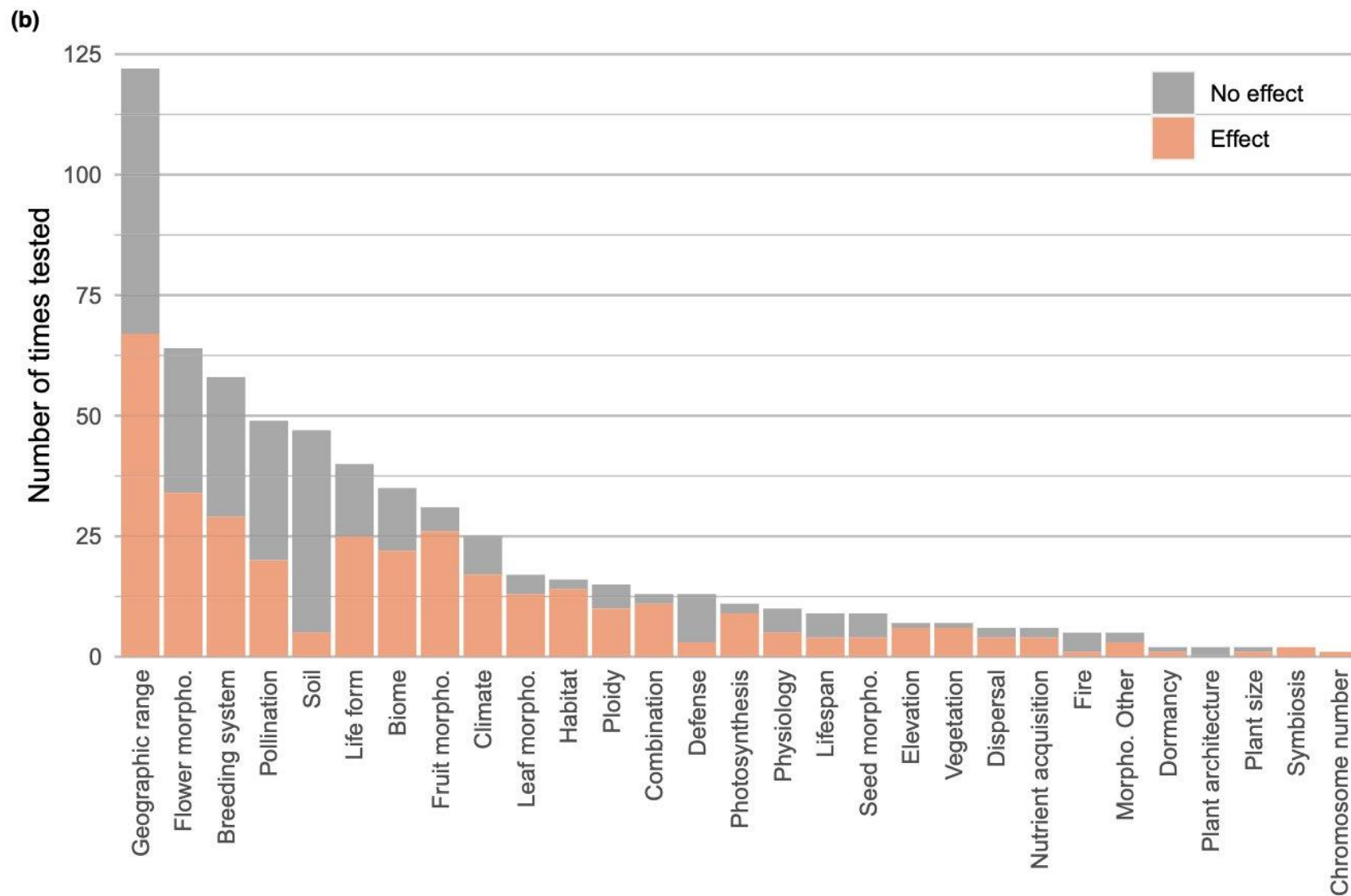
$$H_0: \underbrace{r_0 = (\lambda_0 - \mu_0) = (\lambda_1 - \mu_1) = r_1}_{r_0 = r_1}$$

OR

- net diversification equal for 0 and 1

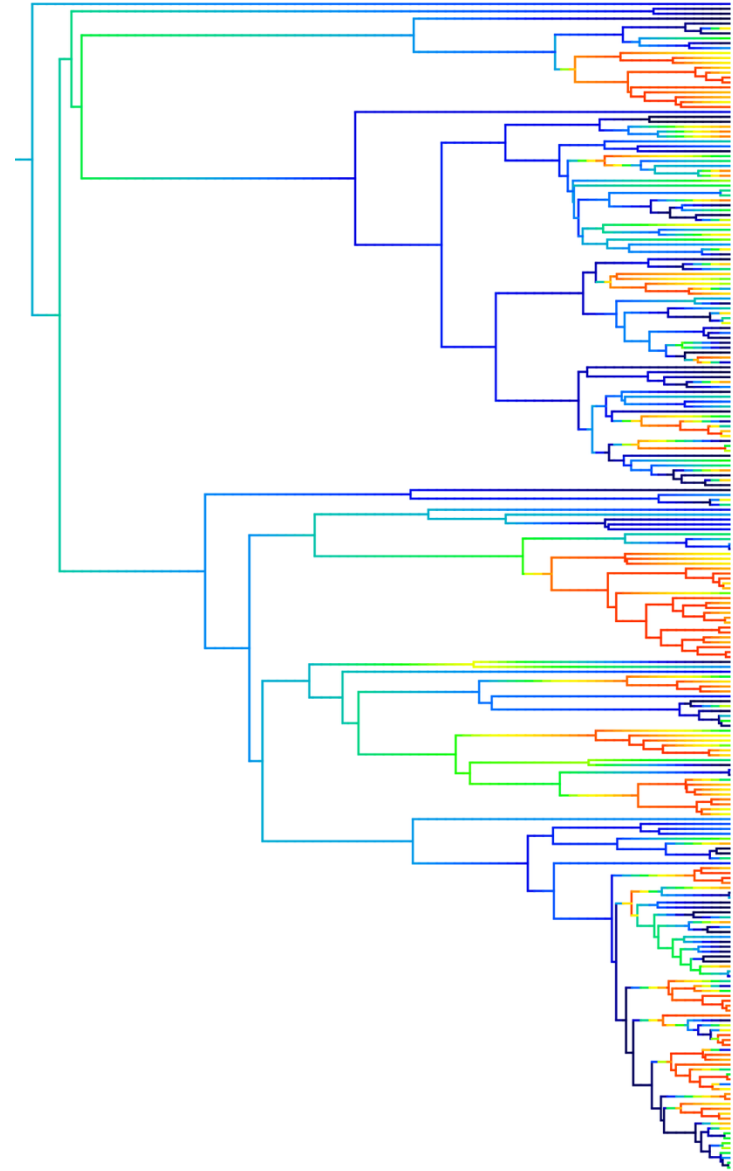
BiSSE is the alternative hypothesis

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



# Null hypothesis of BiSSE

$$H_0: r_0 = r_1$$



# BiSSE's Null Hypothesis is too simple

$$H_0: r_0 = r_1$$



# Type I error 50%

## Misspecification of null hypothesis

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

Davis et al. 2013. *BMC Evolutionary Biology*

Rabosky and Goldberg 2015. *Sys Bio*

New null hypothesis- the hidden states

$$H_0: \lambda_0 = \lambda_1 \text{ and } \mu_0 = \mu_1$$

$$H_0: r_0 = (\lambda_0 - \mu_0) = (\lambda_1 - \mu_1) = r_1$$