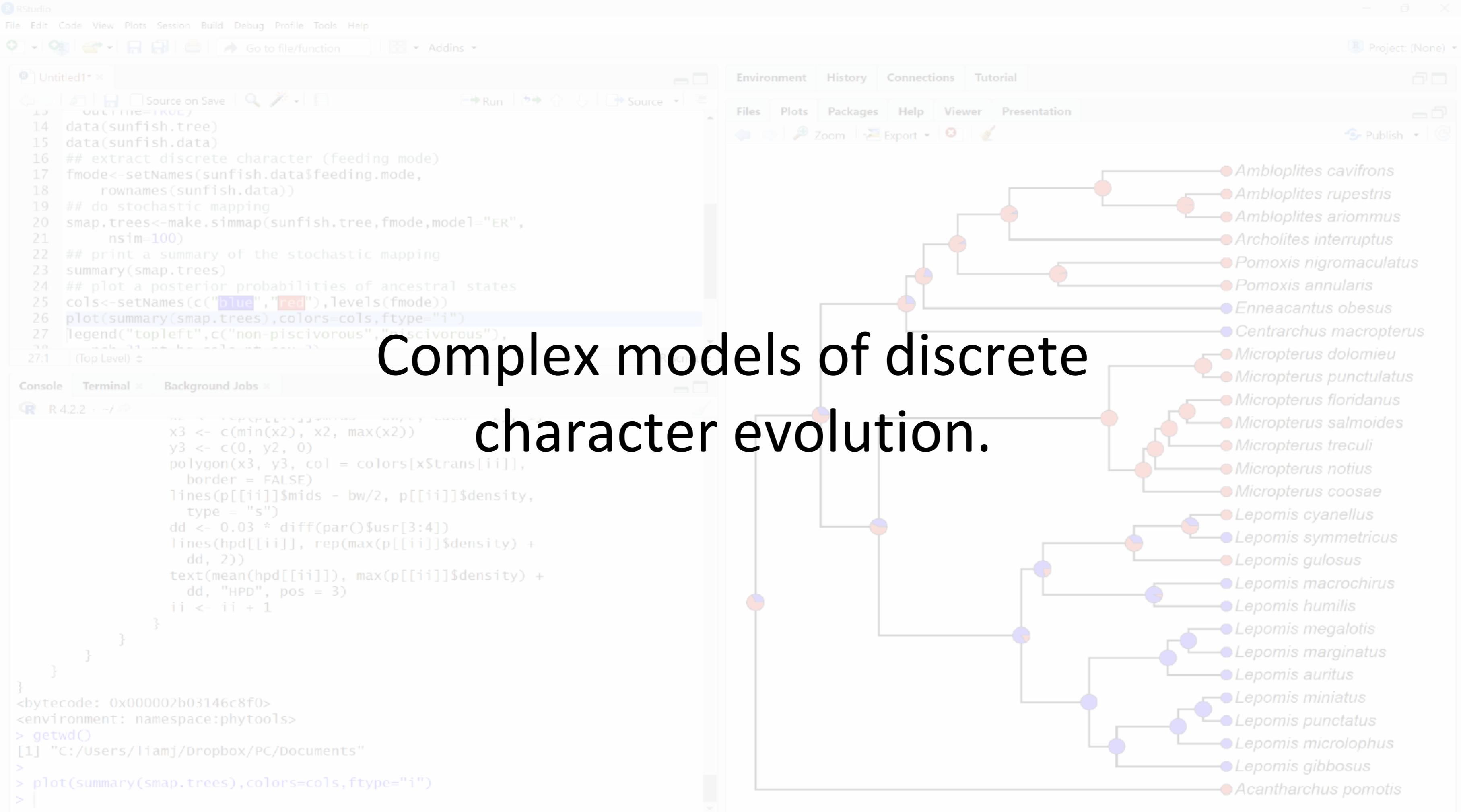
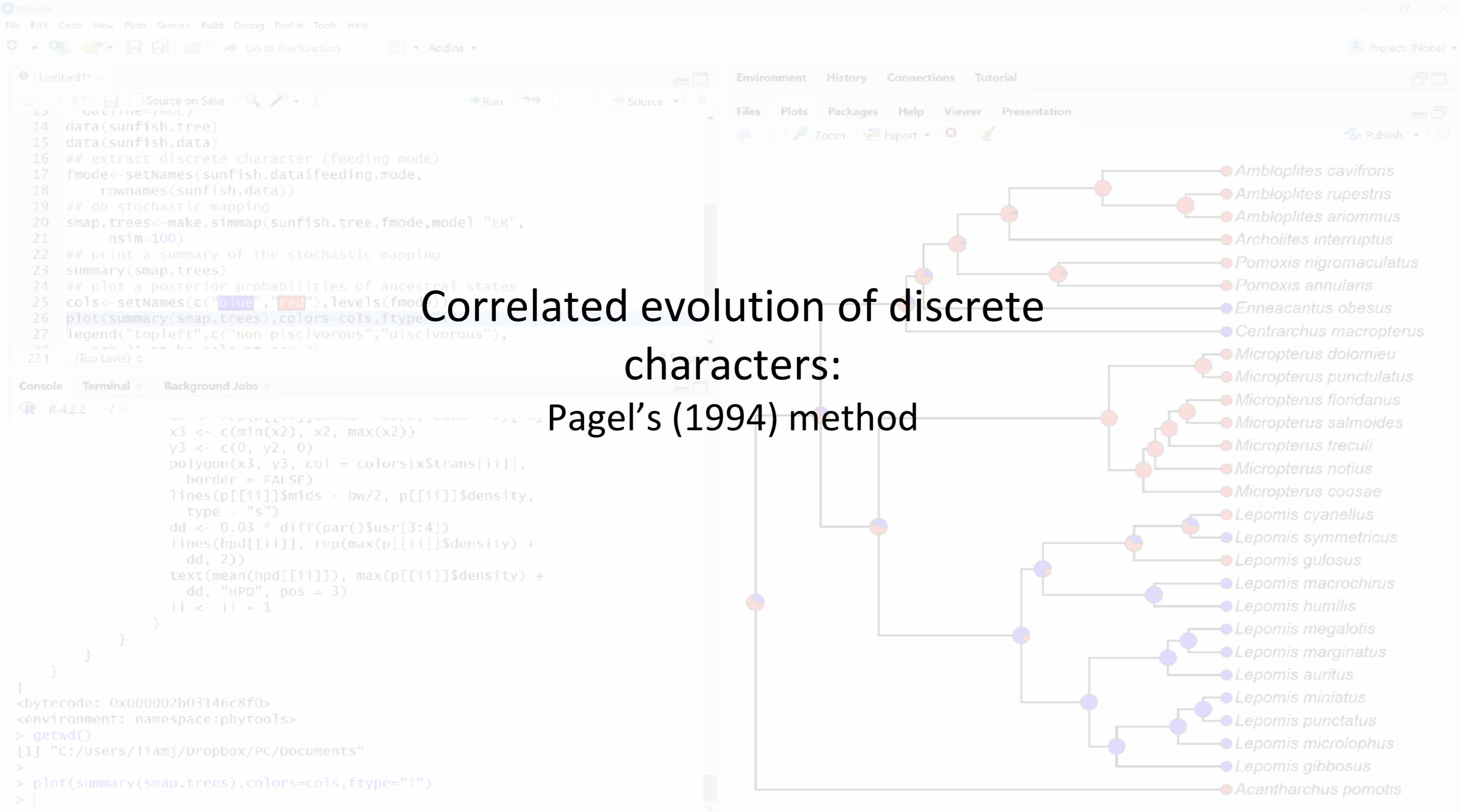


# Models that vary... through time and space

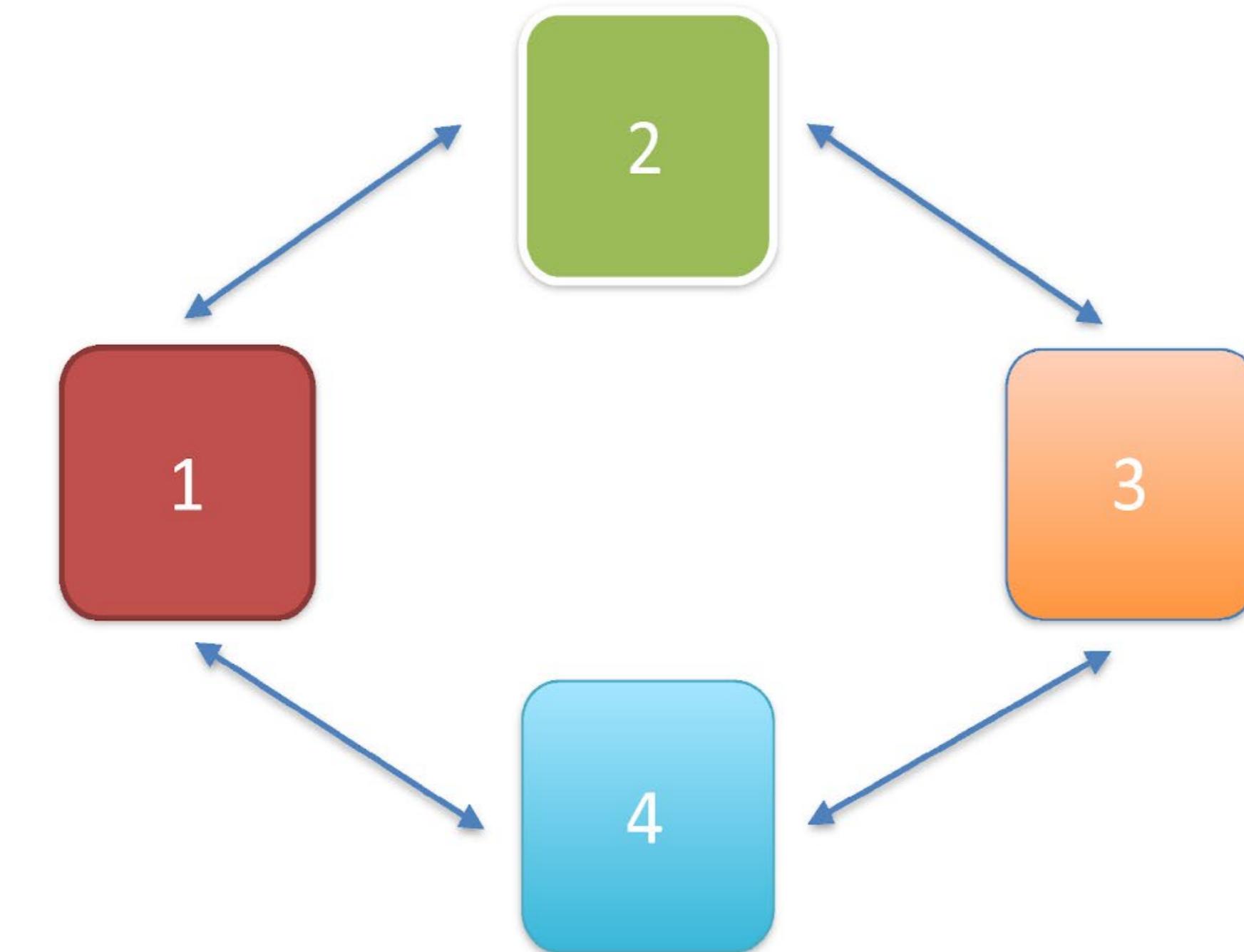


**Strange things are afoot at the Circle-K.**



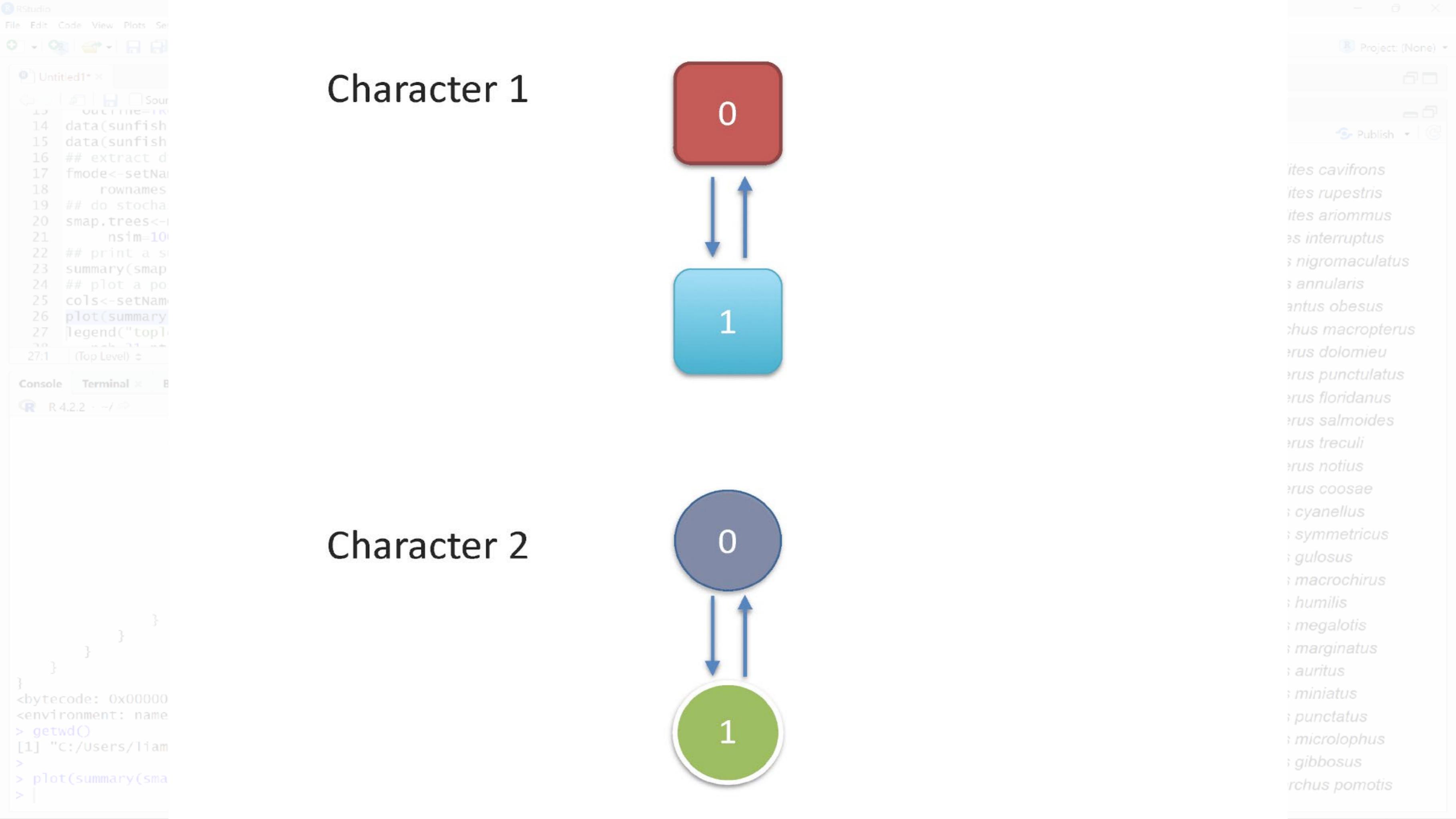


# Discrete trait evolution



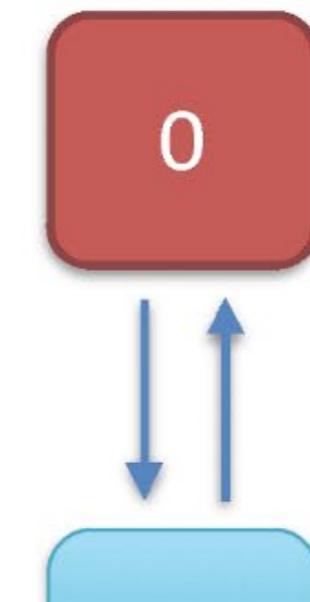
# Do discrete traits evolve in a correlated fashion?

- Markov model:
  - Instantaneous rate of change
  - Estimate transition rates between traits
  - Compare 2 models:
    1. Independent model
    2. Dependent model



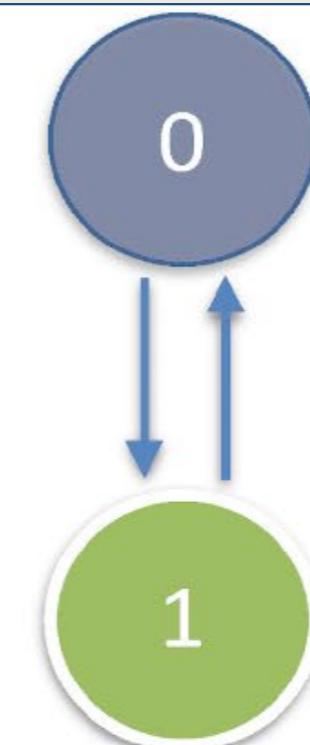
```
RStudio  
File Edit Code View Plots Session Help  
Untitled1 *  
Source Editor  
14 data(sunfish)  
15 data(sunfish)  
16 ## extract data  
17 fmode<-setNA  
18 rownames  
19 ## do stochastic  
20 smap.trees<-i  
21 nsim=100  
22 ## print a summary  
23 summary(smap)  
24 ## plot a phylogenetic tree  
25 cols<-setNames  
26 plot(summary(smap),  
27 legend("top"))  
28 sunfish >#>  
27:1 (Top Level) <br>  
Console Terminal R 4.2.2 · ~ / ~  
<bytecode: 0x0000000000000000>  
<environment: name空间>  
> getwd()  
[1] "C:/Users/liam"  
> plot(summary(smap))
```

# Character 1

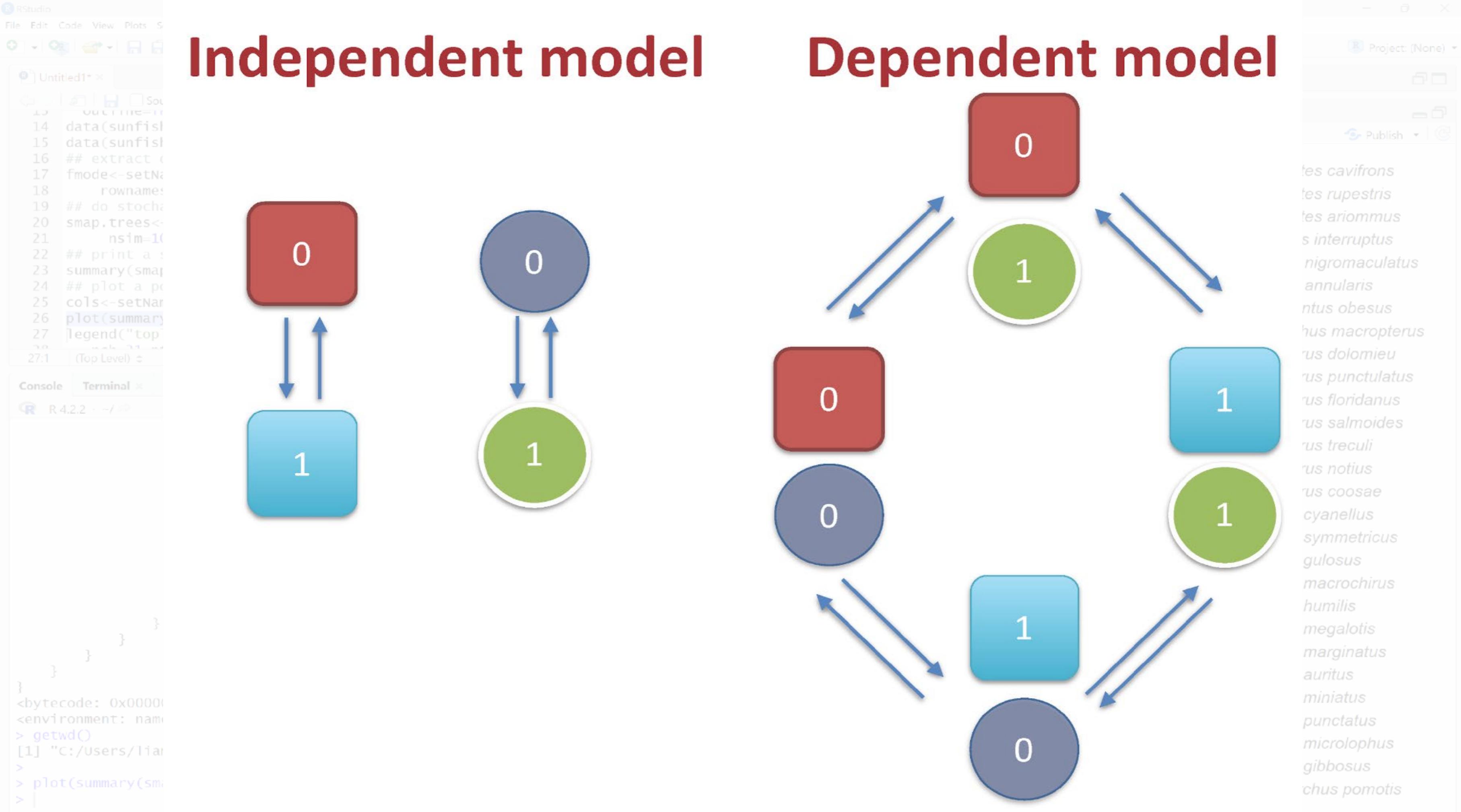


**When character 1 changes, does that affect the evolution of character 2?**

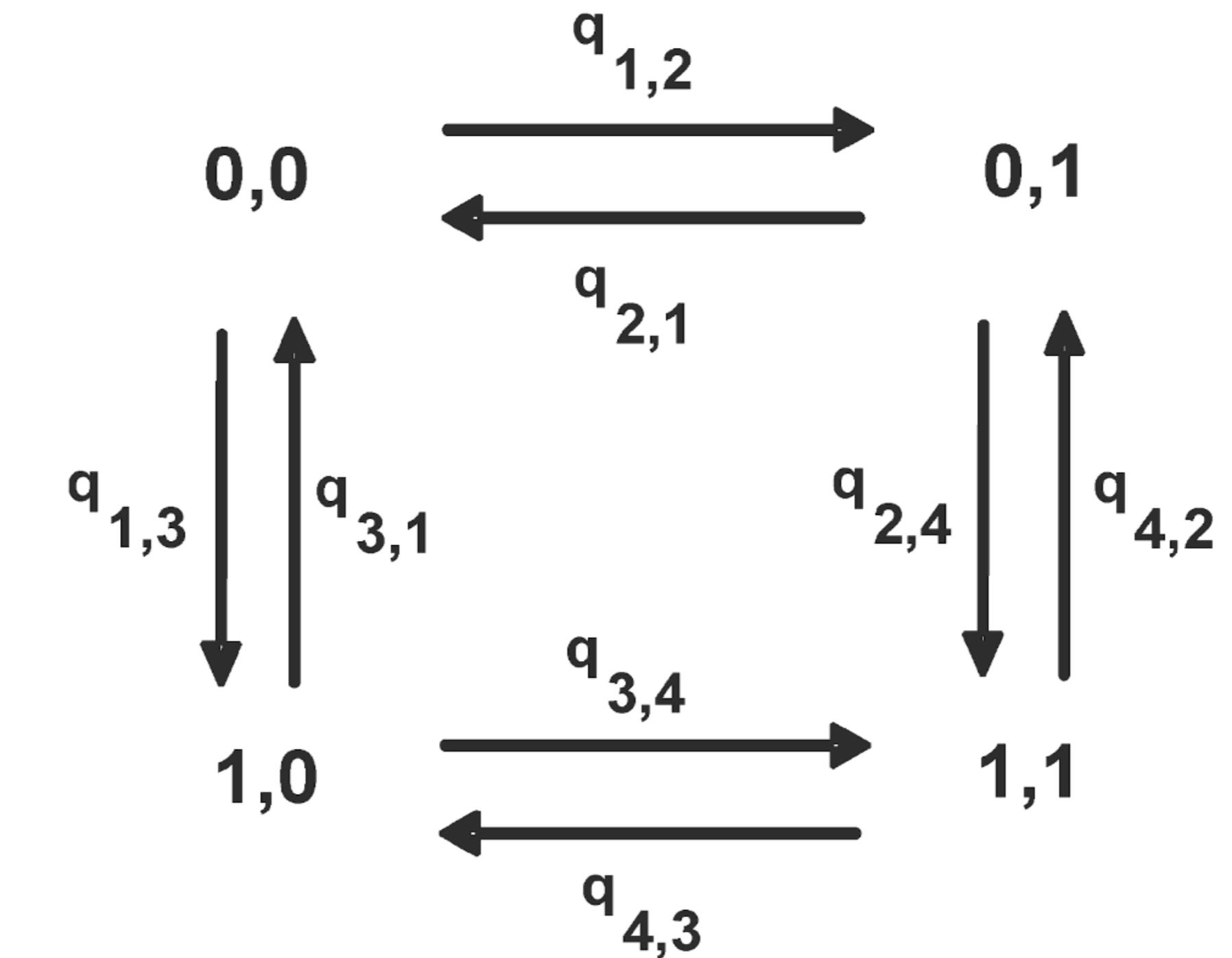
# Character 2



*ites cavifrons  
ites rupestris  
ites ariommus  
es interruptus  
s nigromaculatus  
s annularis  
antus obesus  
chus macropterus  
erus dolomieu  
erus punctulatus  
erus floridanus  
erus salmoides  
erus treculii  
erus notius  
erus coosae  
cyanellus  
symmetricus  
gulosus  
macrochirus  
humilis  
megalotis  
marginatus  
auritus  
miniatus  
punctatus  
microlophus  
gibbosus  
rhus pomotis*



# Model of correlated evolution

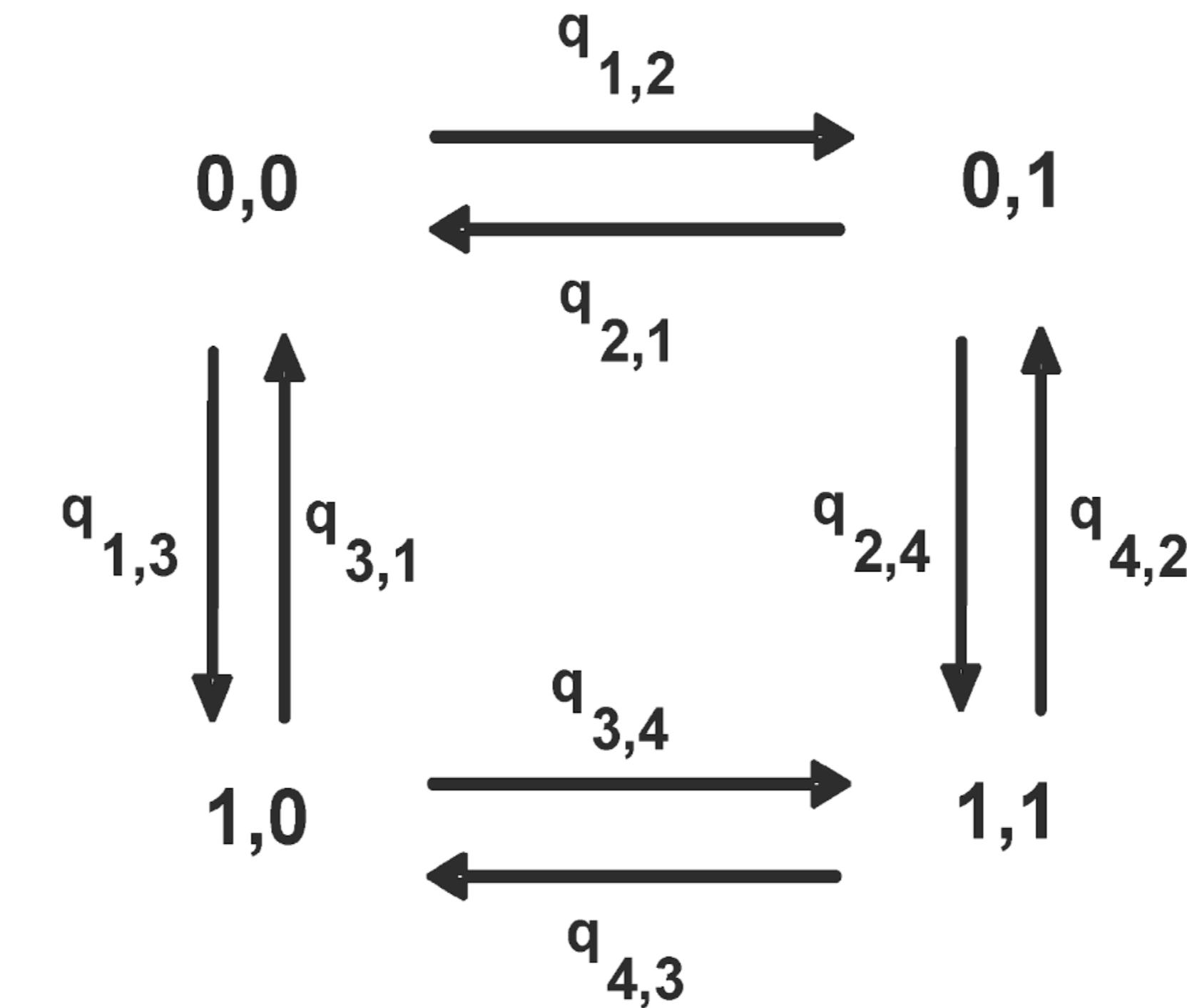


# Correlated evolution of discrete traits

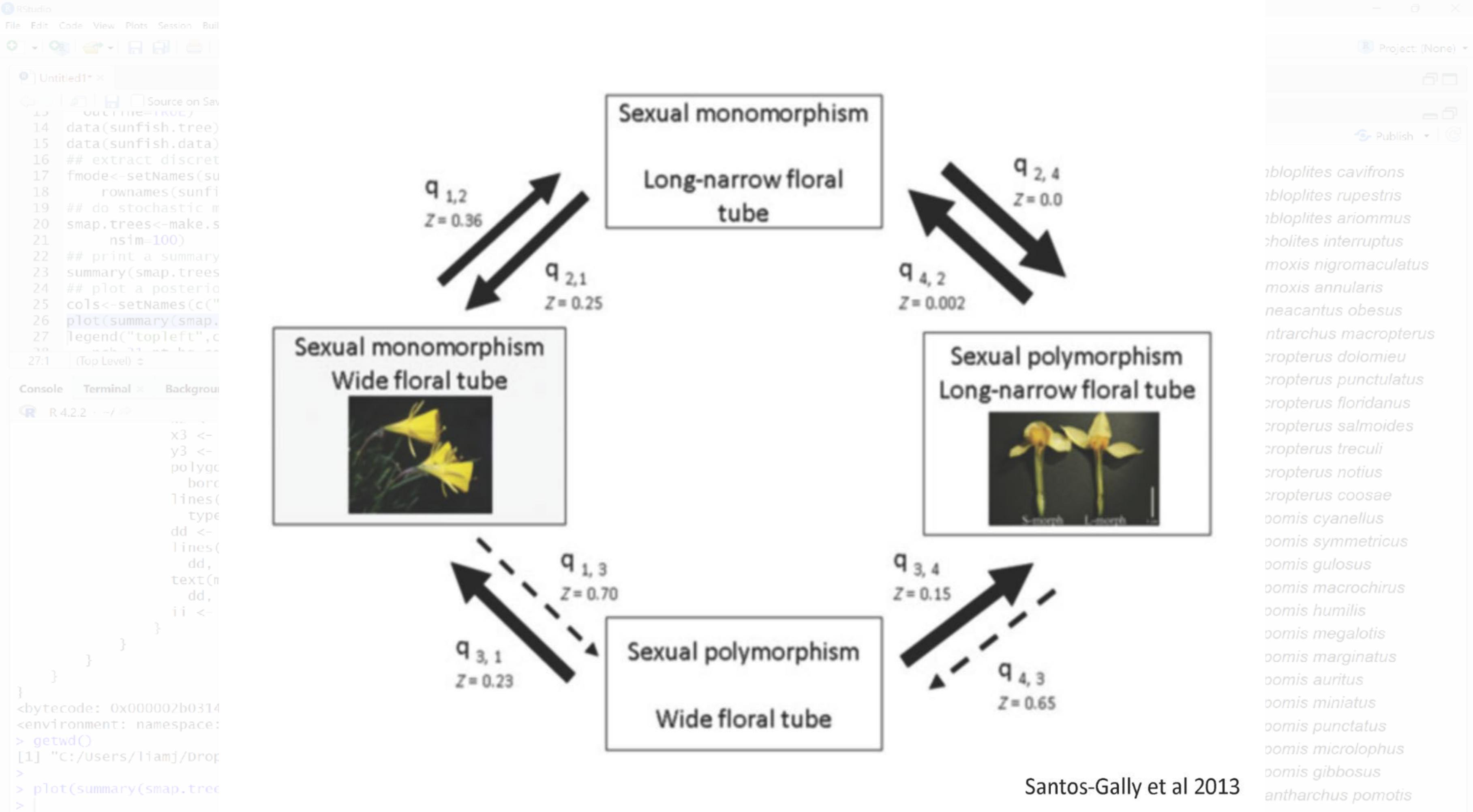
- Compare the fit of both models
- Maximum likelihood gives estimate of “goodness of fit”
- Can compare models with a Log-likelihoods ratio test

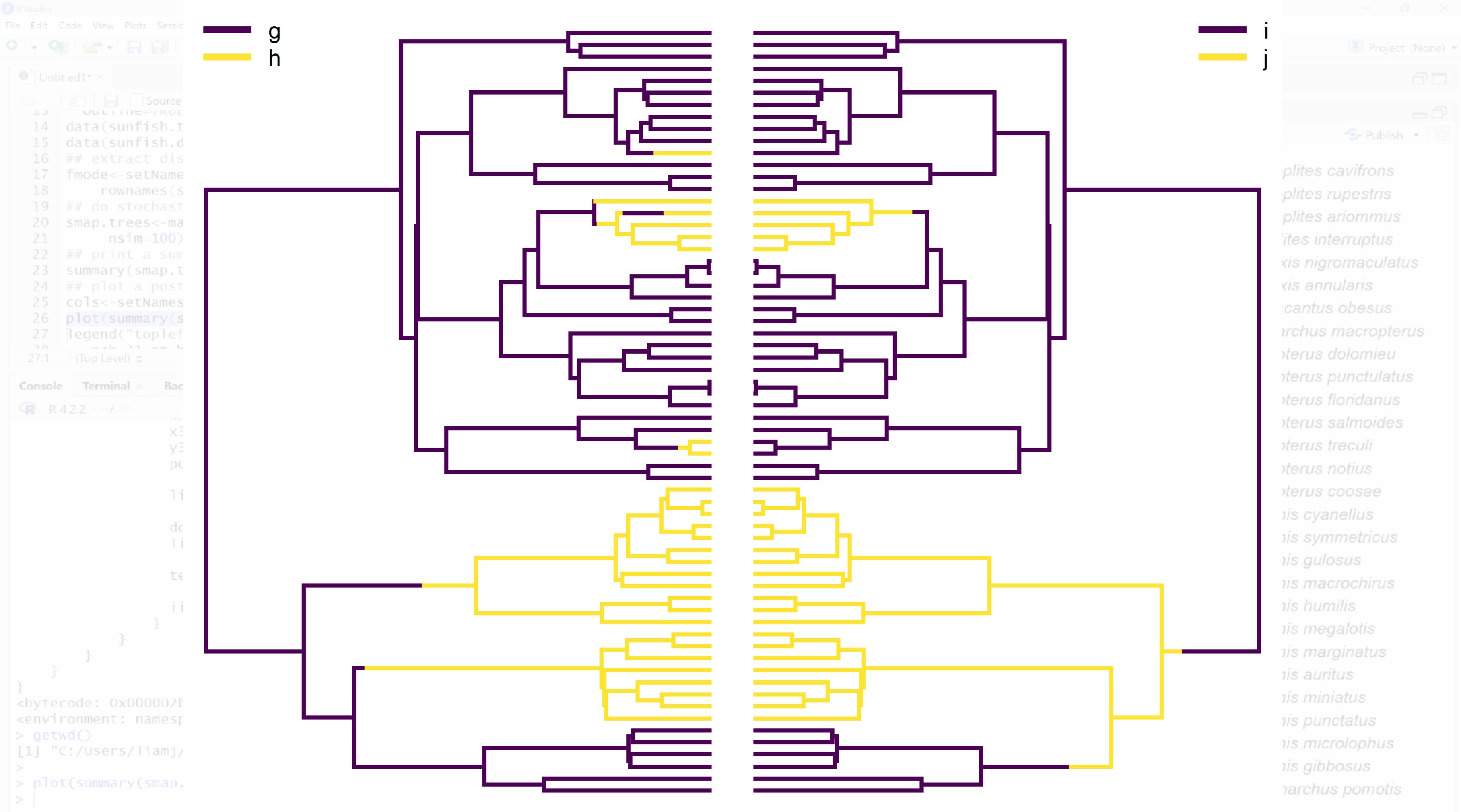


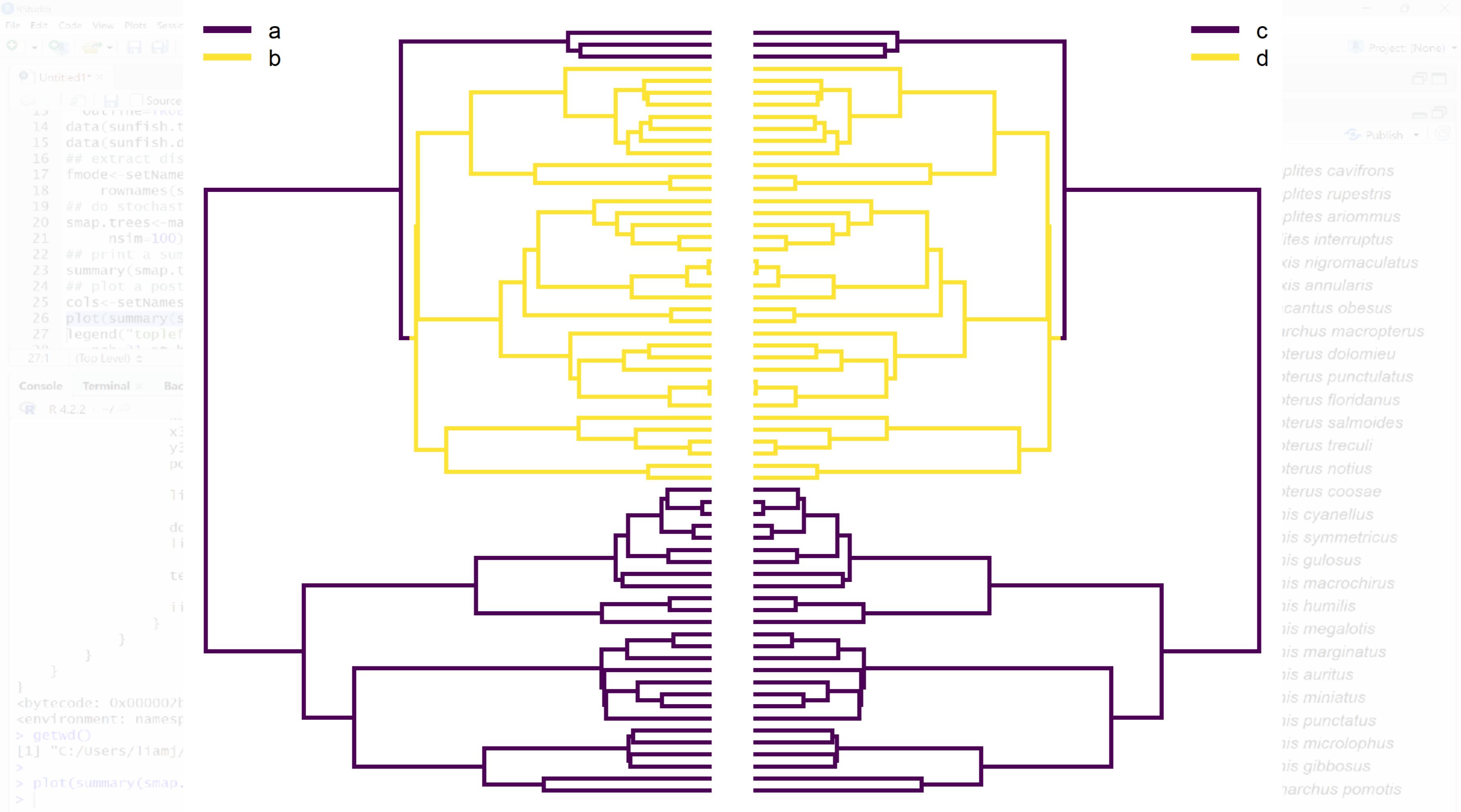
# Model of correlated evolution

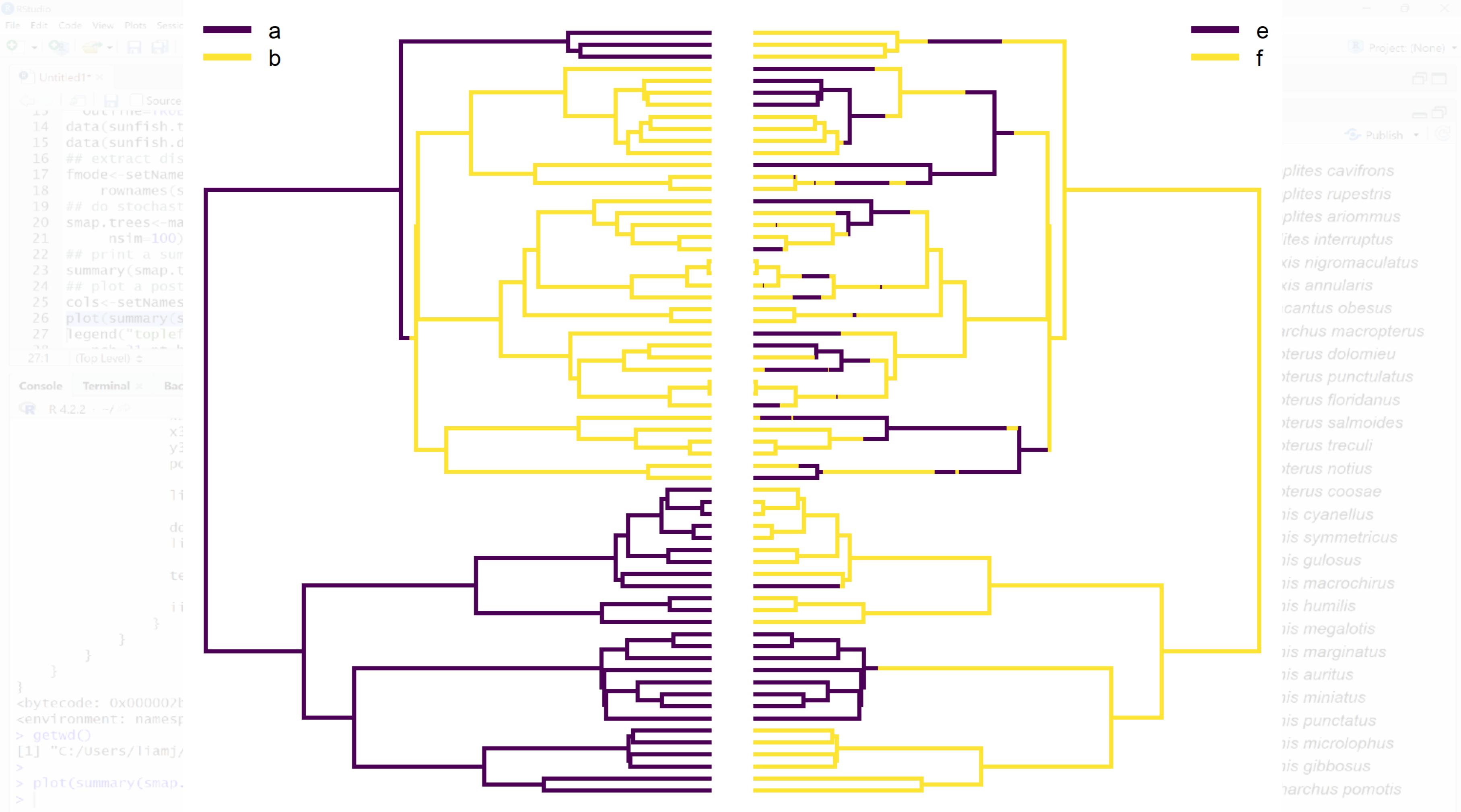


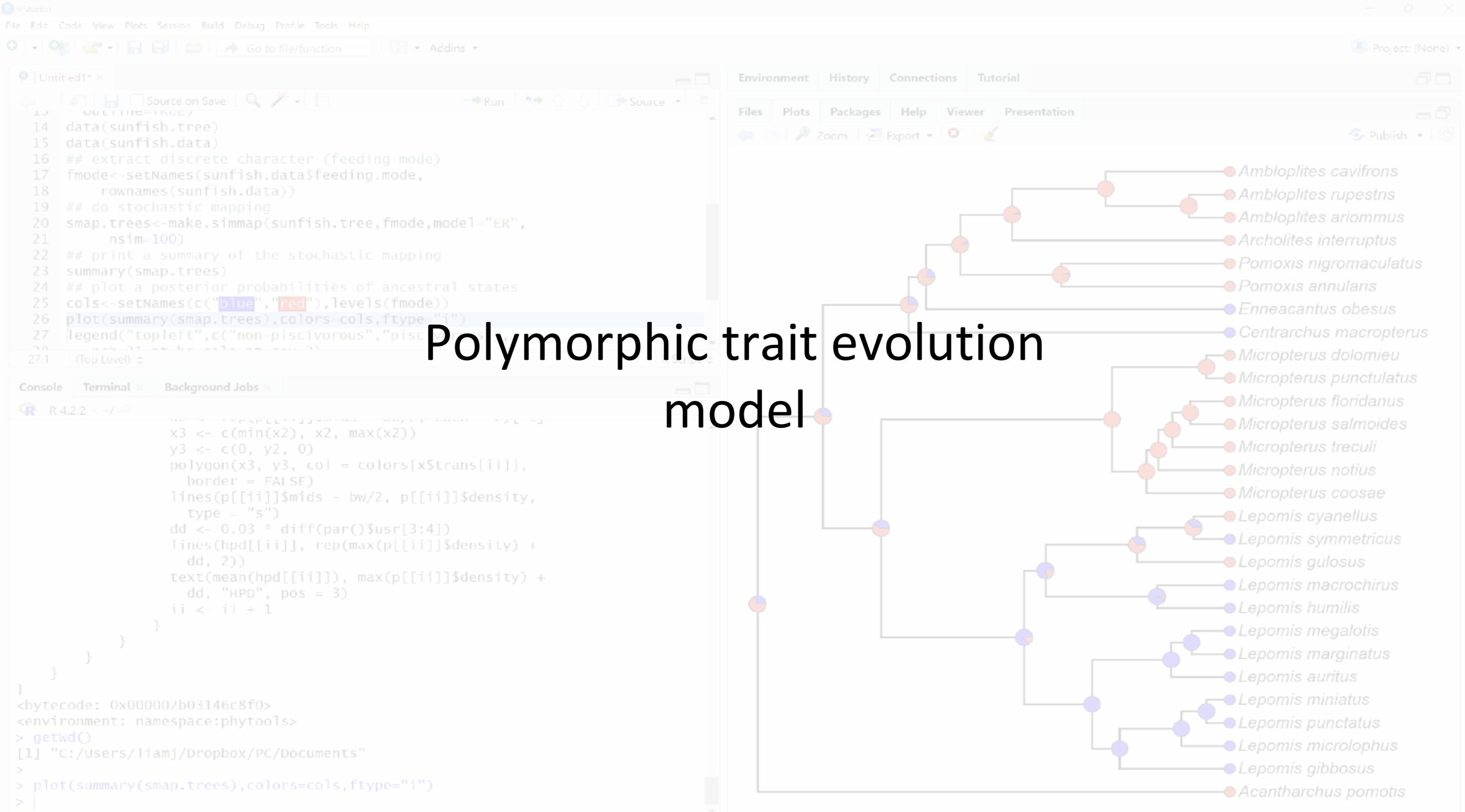
*nbloplites cavifrons*  
*nbloplites rupestris*  
*nbloplites ariommus*  
*cholites interruptus*  
*omoxis nigromaculatus*  
*omoxis annularis*  
*ineacanthus obesus*  
*entrarchus macropterus*  
*icropterus dolomieu*  
*icropterus punctulatus*  
*icropterus floridanus*  
*icropterus salmoides*  
*icropterus treculii*  
*icropterus notius*  
*icropterus coosae*  
*ipomis cyanellus*  
*ipomis symmetricus*  
*ipomis gulosus*  
*ipomis macrochirus*  
*ipomis humilis*  
*ipomis megalotis*  
*ipomis marginatus*  
*ipomis auritus*  
*ipomis miniatus*  
*ipomis punctatus*  
*ipomis microlophus*  
*ipomis gibbosus*  
*cantharchus pomotis*



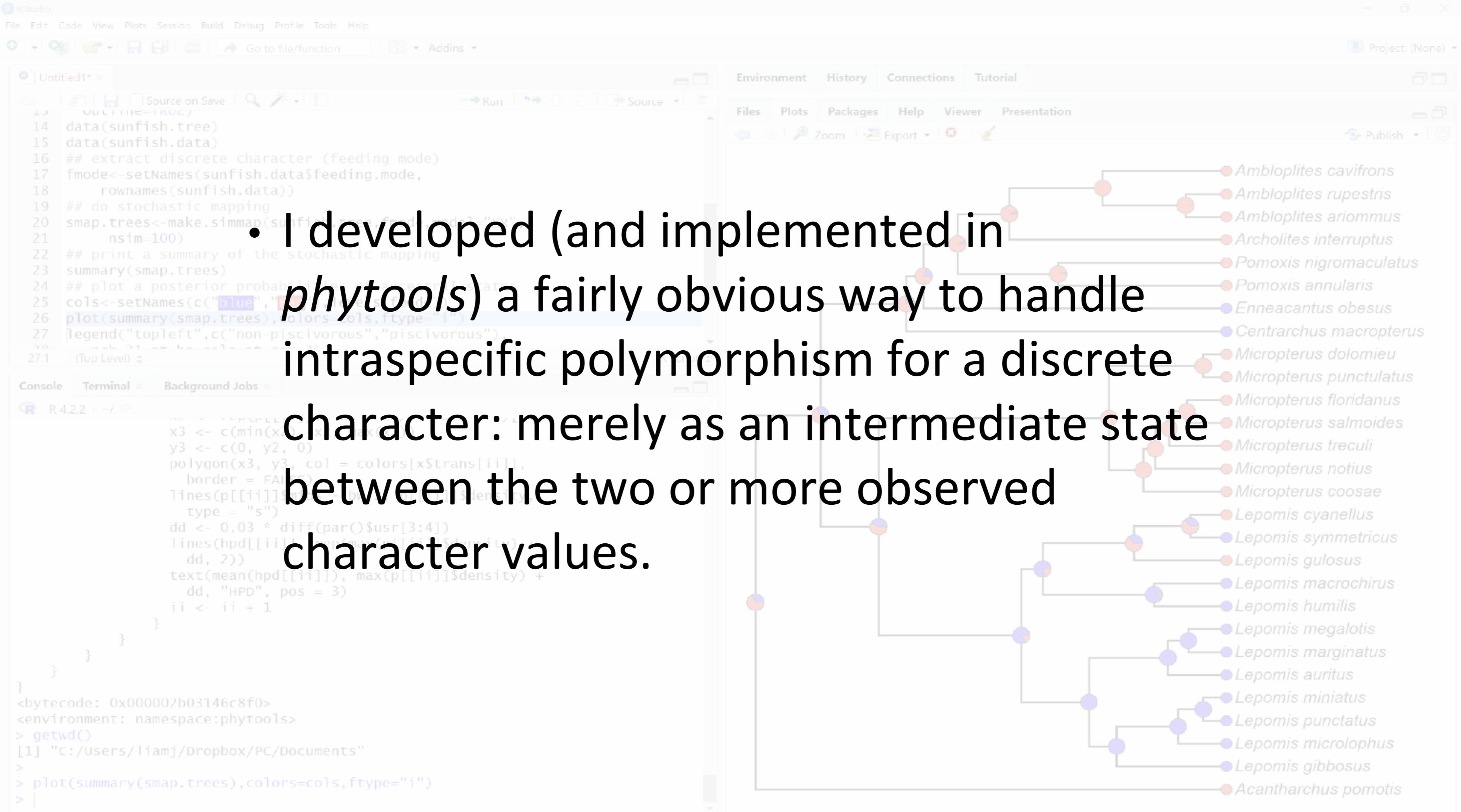








# Polymorphic trait evolution model



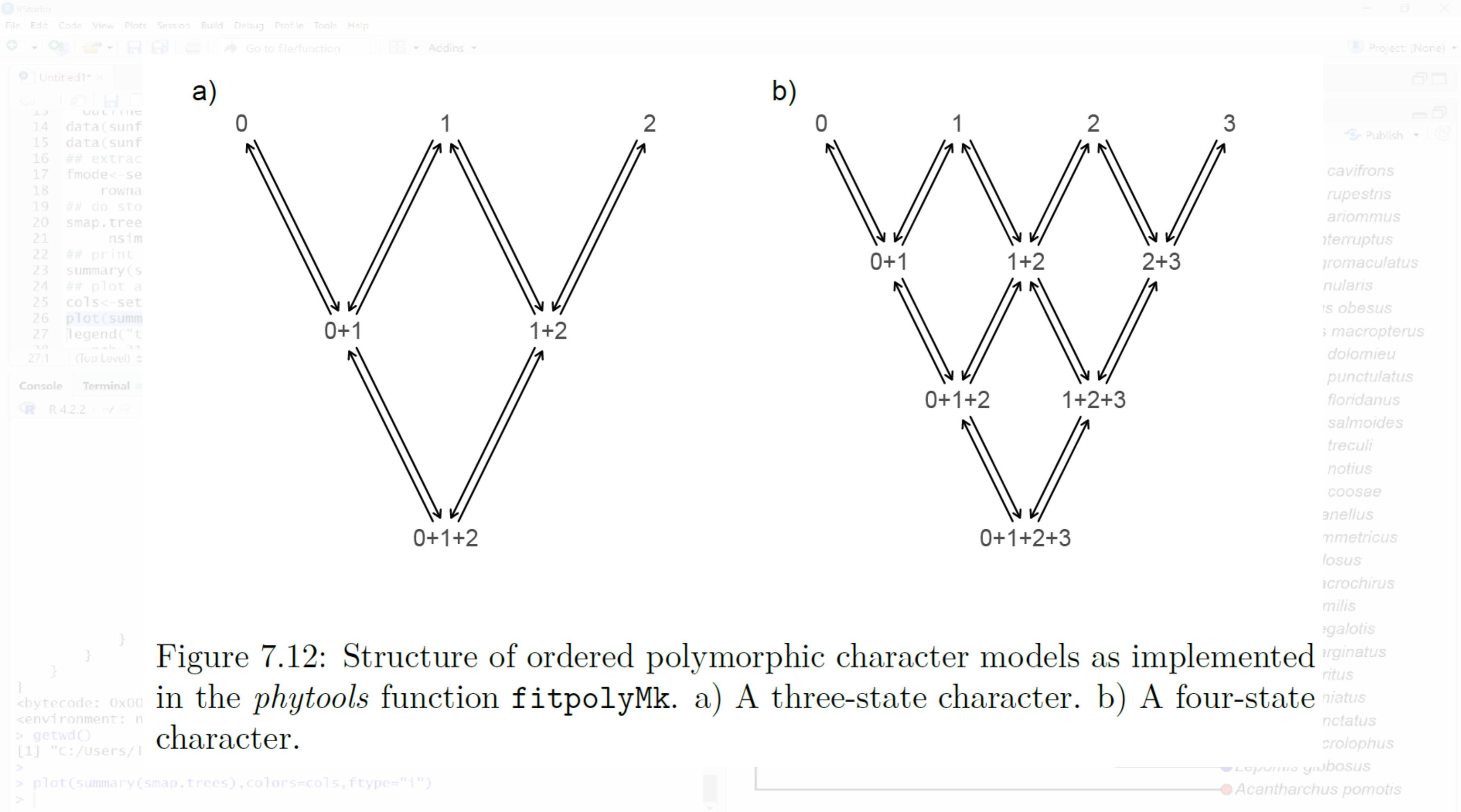
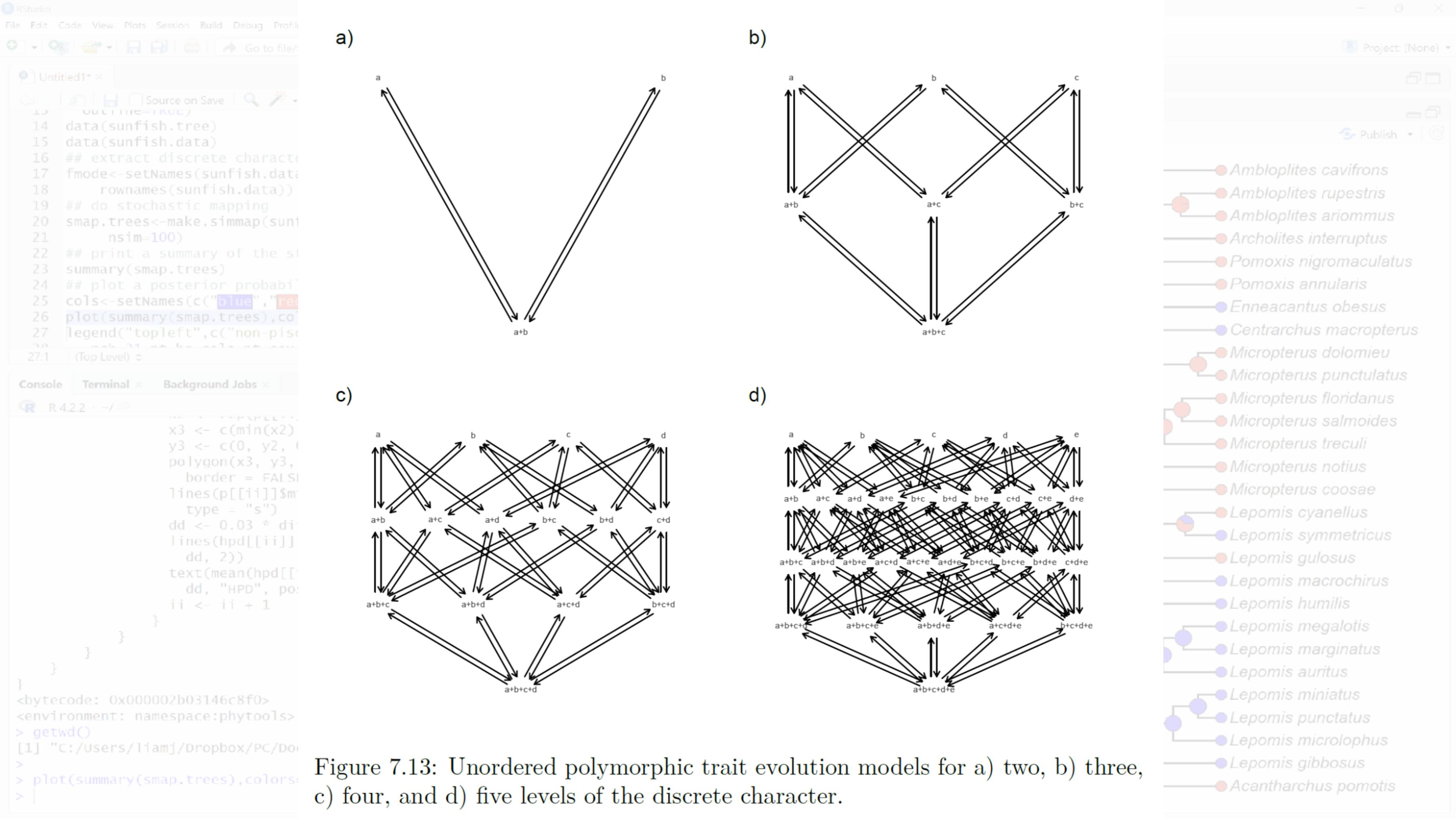
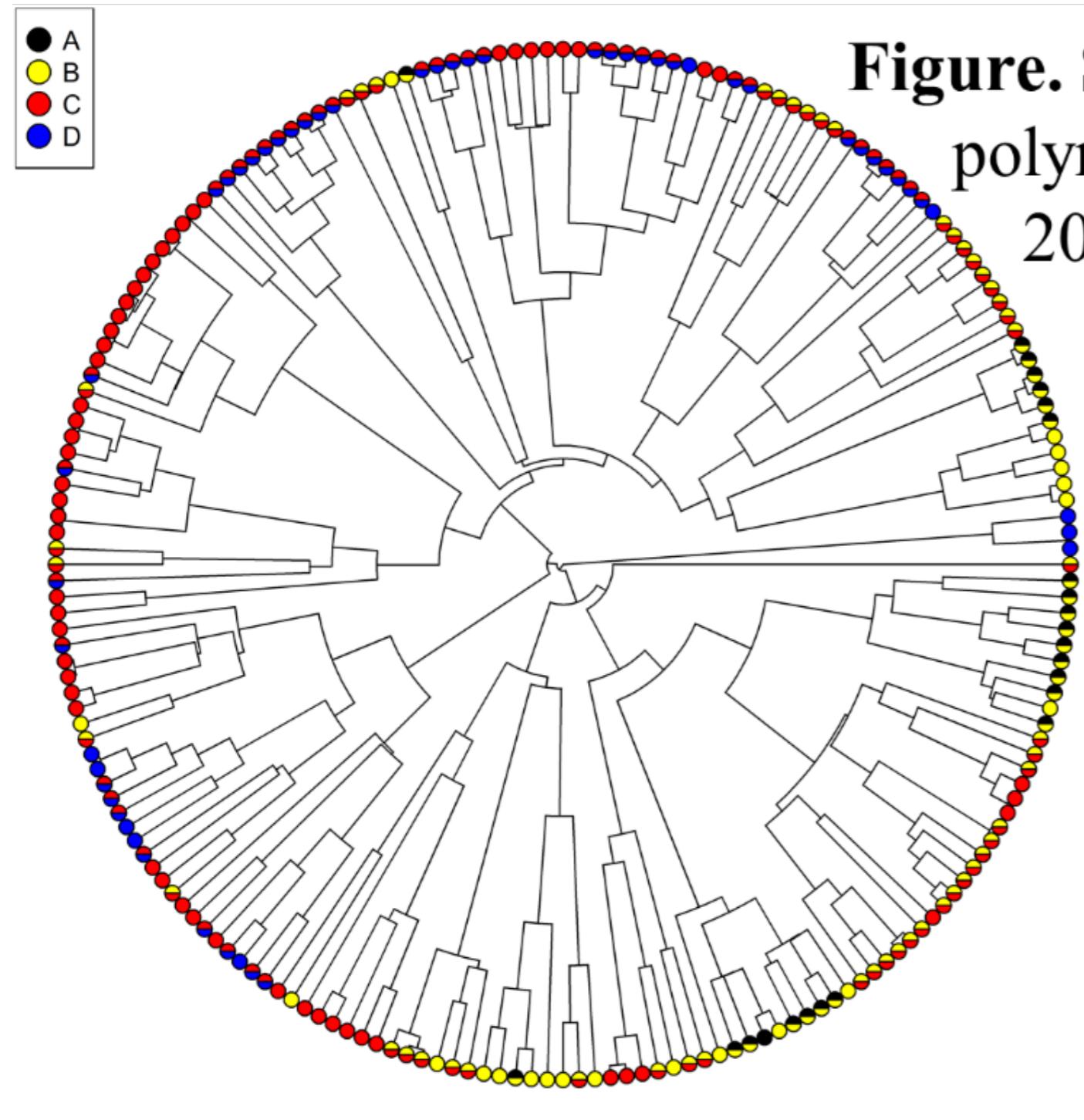


Figure 7.12: Structure of ordered polymorphic character models as implemented in the *phytools* function **fitpolyMk**. a) A three-state character. b) A four-state character.



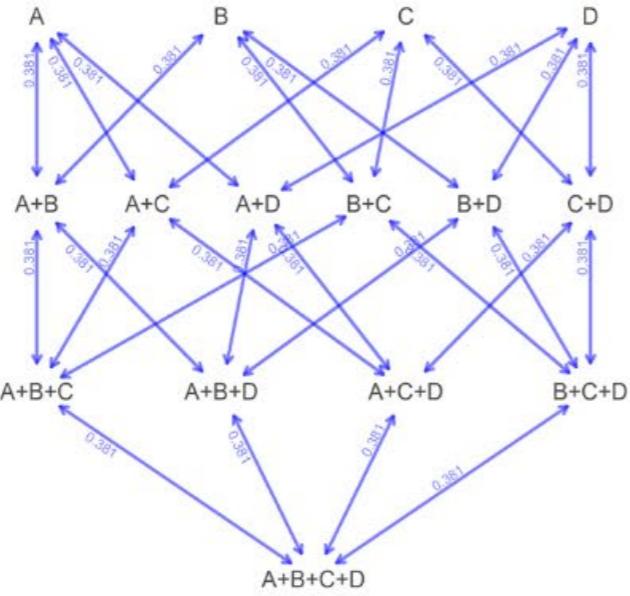


**Figure.** Simulated four-state polymorphic character mapped on a 200-taxon phylogeny.

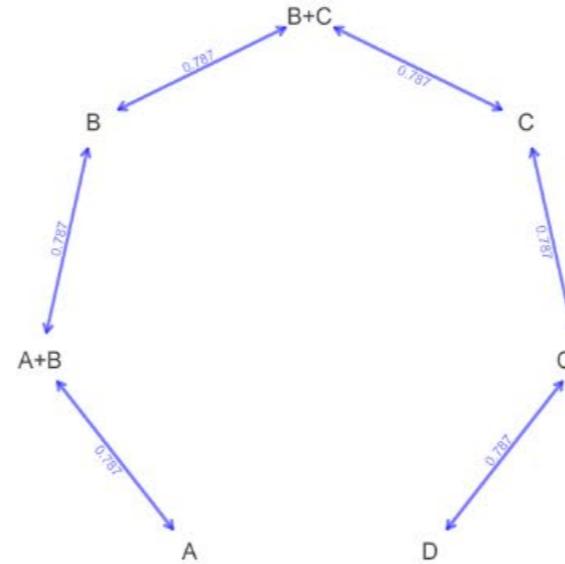
**Table.** Model comparison of ordered & unordered ‘ER’ & ‘transient’ transition models.

transition model	ordered	$\log(L)$	$k$	AIC
ER	no	-213.1	1	428.2
ER	yes	-175.4	1	352.9
transient	no	-205.8	2	415.7
transient	yes	<b>-174.2</b>	<b>2</b>	<b>352.5</b>

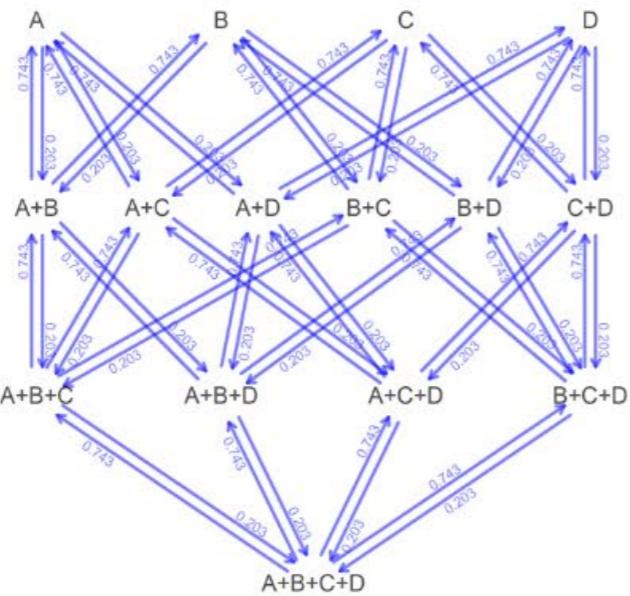
a) Fitted 'ER' unordered model



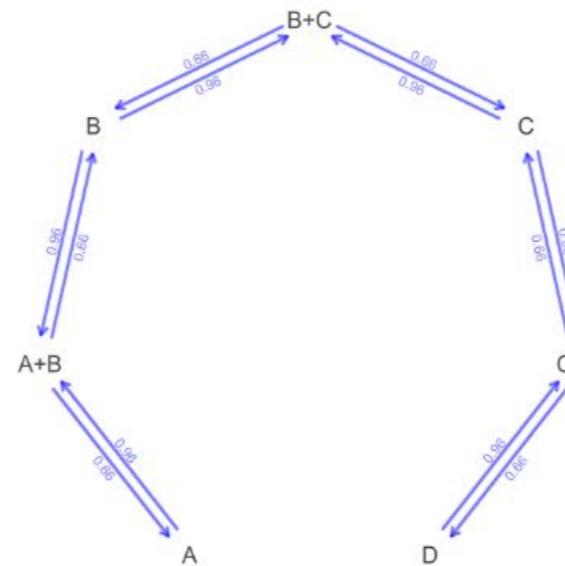
b) Fitted 'ER' ordered model



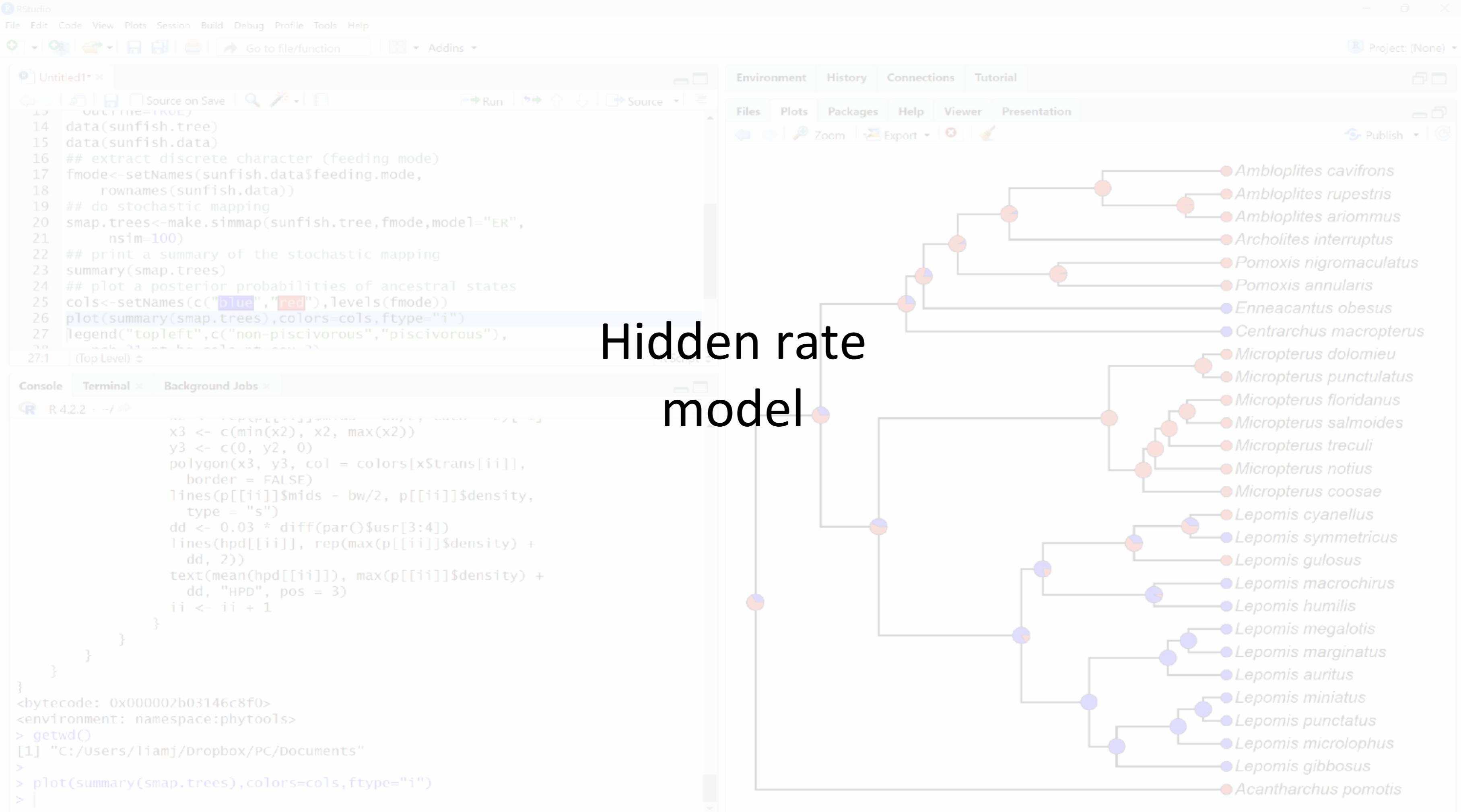
b) Fitted 'transient' unordered model



c) Fitted 'transient' ordered model



**Figure.** Plotted transition models between polymorphic states. Models in the left column assume that character evolution is unordered. Models in the bottom row (the ‘transient’ model) assumes that the acquisition of polymorphism occurs at a different rate from its loss. All models assume that transitions between any pair of states must occur through an intermediate polymorphic condition.



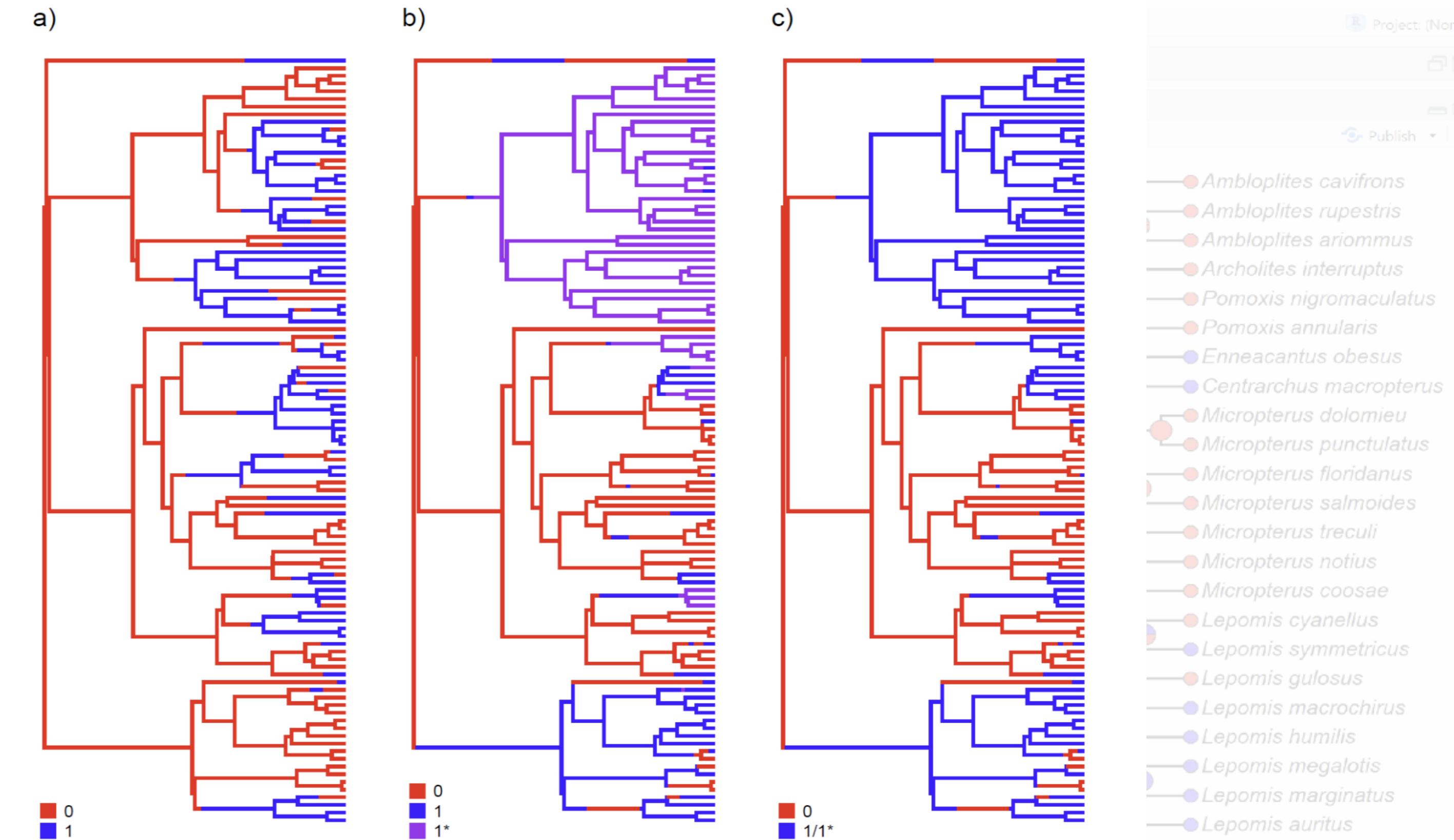


Figure 7.7: Simulation under: a) A constant-rate Mk model. b) A hidden-rates model, but in which the hidden-state is shown (purple branches). c) The same as b), but in which the hidden-state is no longer shown.

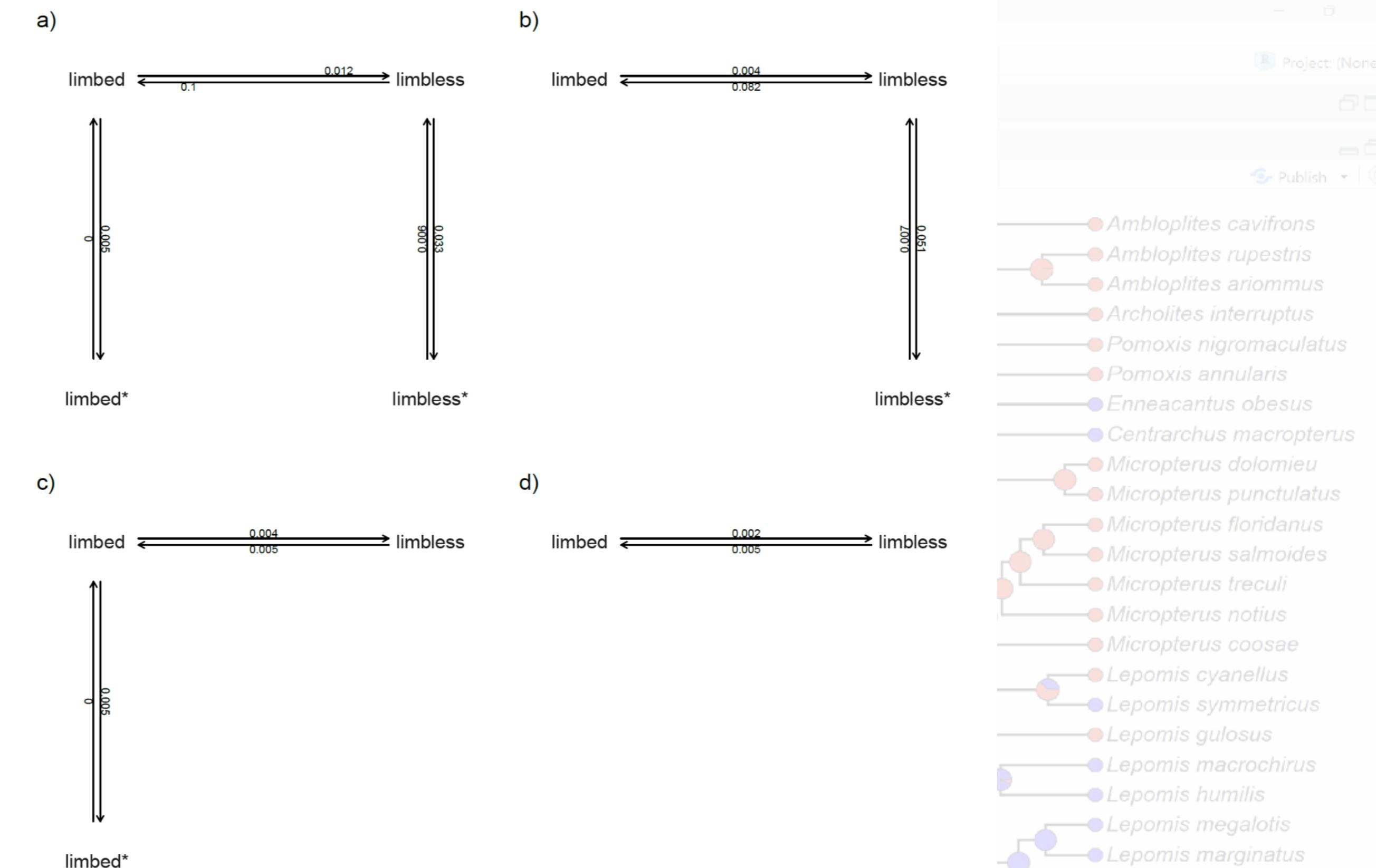


Figure 7.8: Fitted hidden-rate models for data for limbs vs. limblessness in 119 species of squamate reptiles. a) Hidden-rate model in which each of the two binary states had a single hidden rate. b) Hidden-rate model with a hidden rate for *limbless* but not *limbs*. c) The converse of b). d) Fitted Mk ARD model.

# What about continuous characters?



**Trunk – crown anoles:**

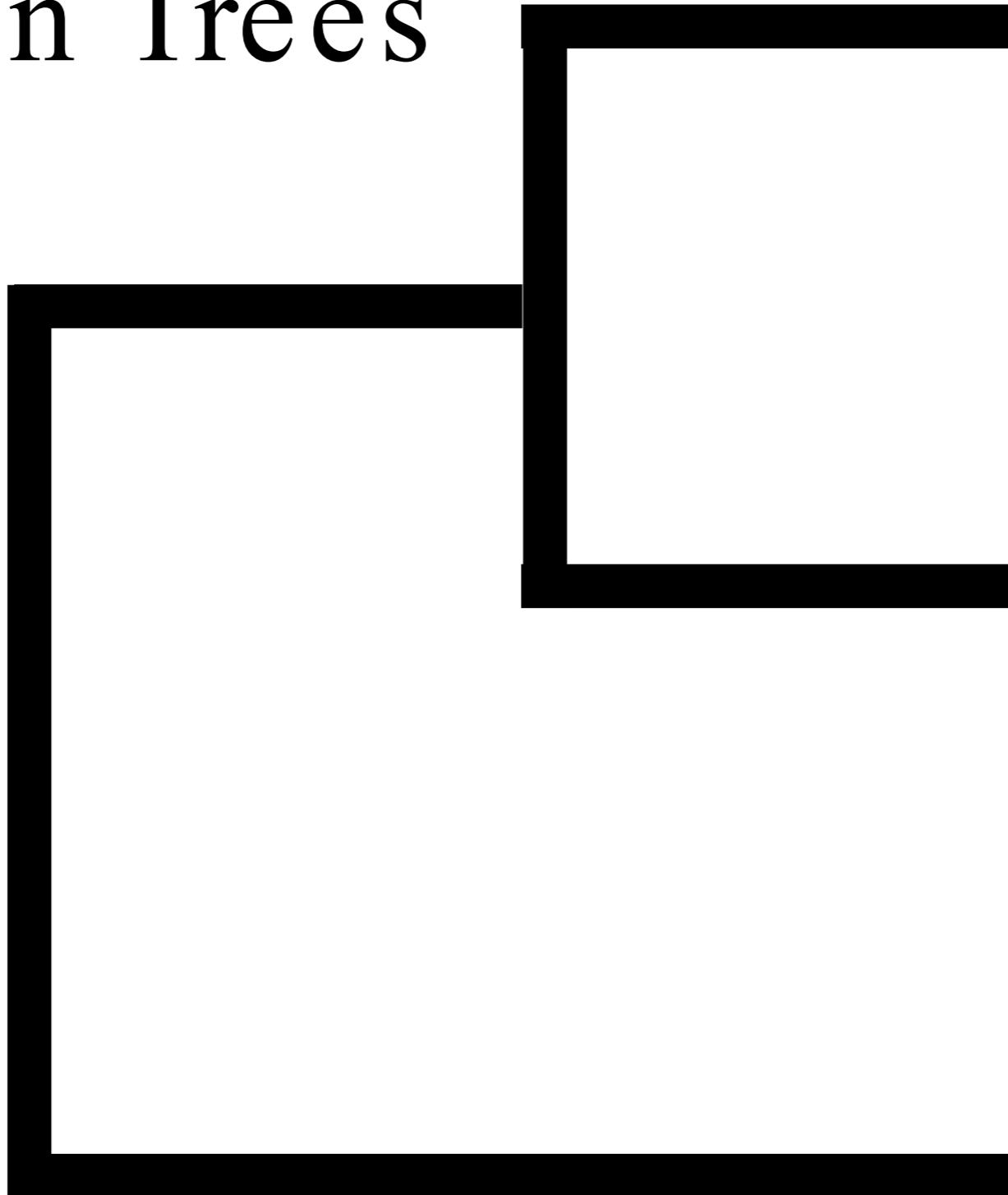
*A. allisoni* (Cuba) and *A. chlorocyanus*  
(Hispaniola)

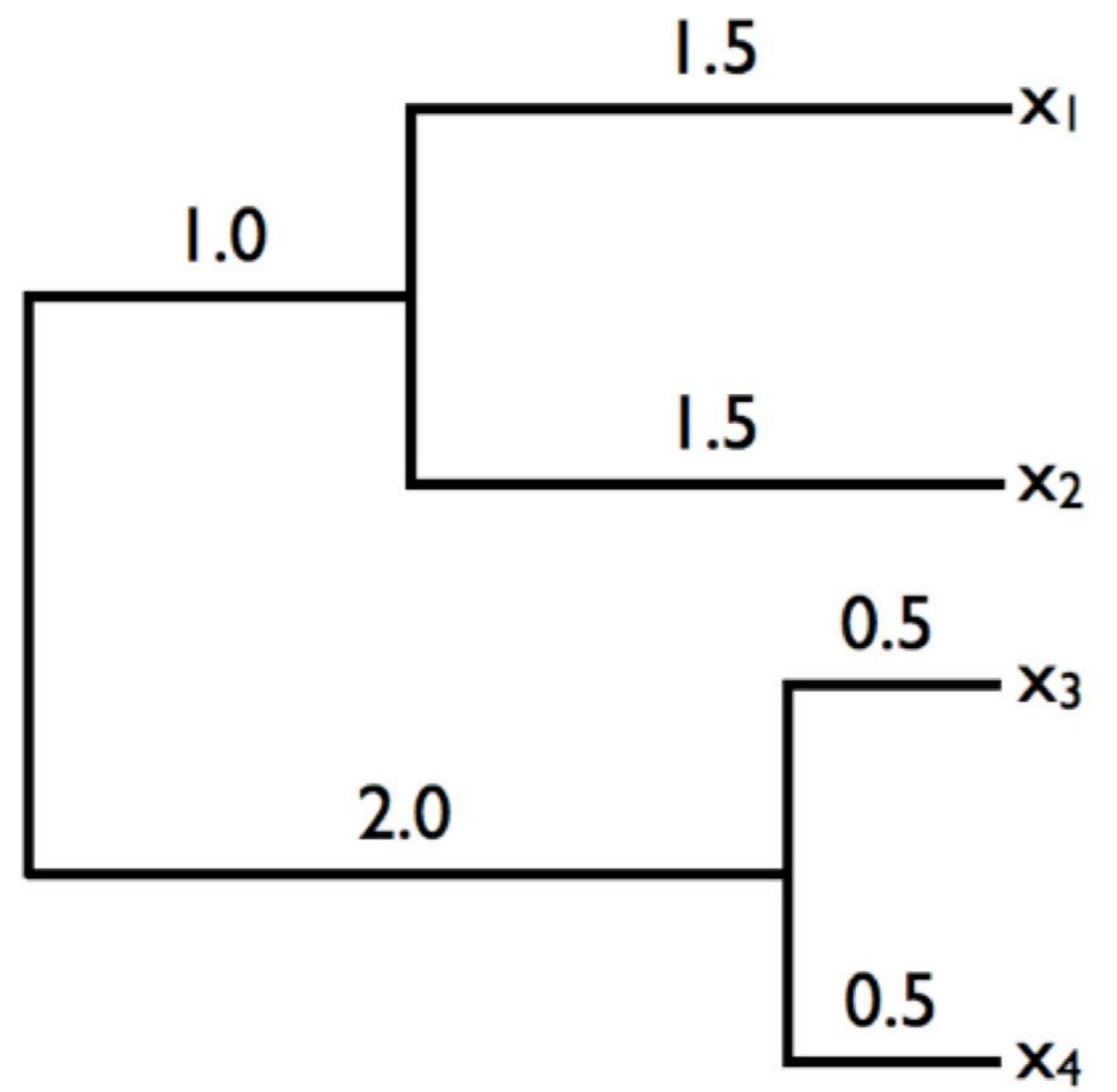


**Twig anoles:**

*A. valencienni* (Jamaica) and *A. insolitus* (Hispaniola)

# Models of evolution on Trees





$C =$

$$\begin{bmatrix} 2.5 & 1.0 & 0 & 0 \\ 1.0 & 2.5 & 0 & 0 \\ 0 & 0 & 2.5 & 2.0 \\ 0 & 0 & 2.0 & 2.5 \end{bmatrix}$$

# "Common" Models for Phenotypic Evolution

Brownian Motion (BM)

Early Burst (EB)

Ornstein-Uhlenbeck (OU)

# Brownian Motion (BM)

Brownian motion model with a constant rate of evolution

Two parameters: starting value ( $z_0$ ) and rate ( $\sigma^2$ )

# Early Burst Model (EB)

Rate of evolution slows through time

Highest rate at the root of the tree

Three parameters: starting value ( $z_0$ ),  
starting rate ( $\sigma^2_0$ ), and rate change ( $r$ )

$$r(t) = \sigma_0^2 e^{rt}$$

$$\overleftarrow{\overrightarrow{s_{ij}}}$$

$$V_{ij} = \int_0^{s_{ij}} \sigma_0^2 e^{rt} dt = \sigma_0^2 \frac{e^{rs_{ij}} - 1}{r}$$

# Ornstein-Uhlenbeck Model (OU)

Evolution has a tendency to move towards some medial value

“Brownian motion with a spring”

Three parameters: starting value ( $z_0$ ), rate ( $\sigma^2$ ), and constraint parameter ( $\alpha$ )

$$V_{ij} = \frac{\sigma^2}{\alpha} e^{-2\alpha(T-s_{ij})} (1 - e^{-2\alpha s_{ij}})$$

$$\overleftarrow{\overrightarrow{s_{ij}}}$$

$$\overleftarrow{\overrightarrow{T = \text{total tree depth}}}$$

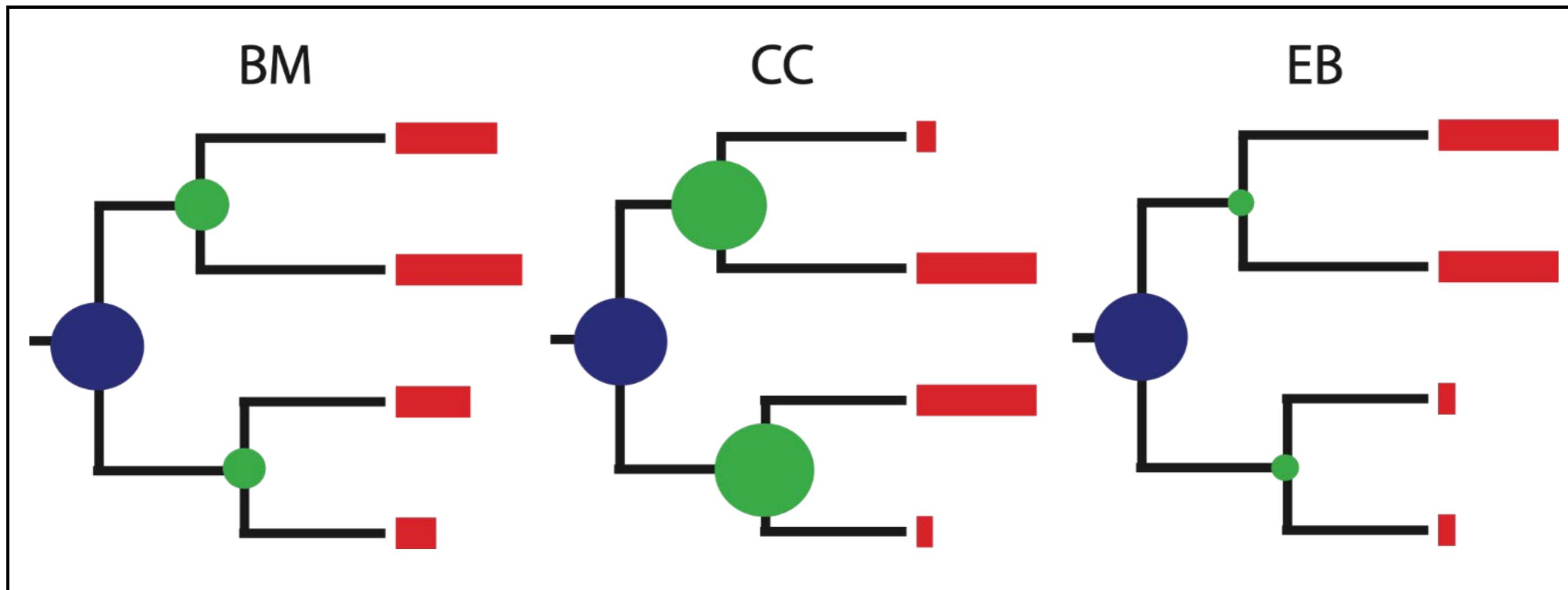
# Why these three?

BM is assumed by almost all phylogenetic comparative methods

EB corresponds to one idea of adaptive radiation

OU may capture the importance of constraints on evolution

How do we tell these  
models apart?



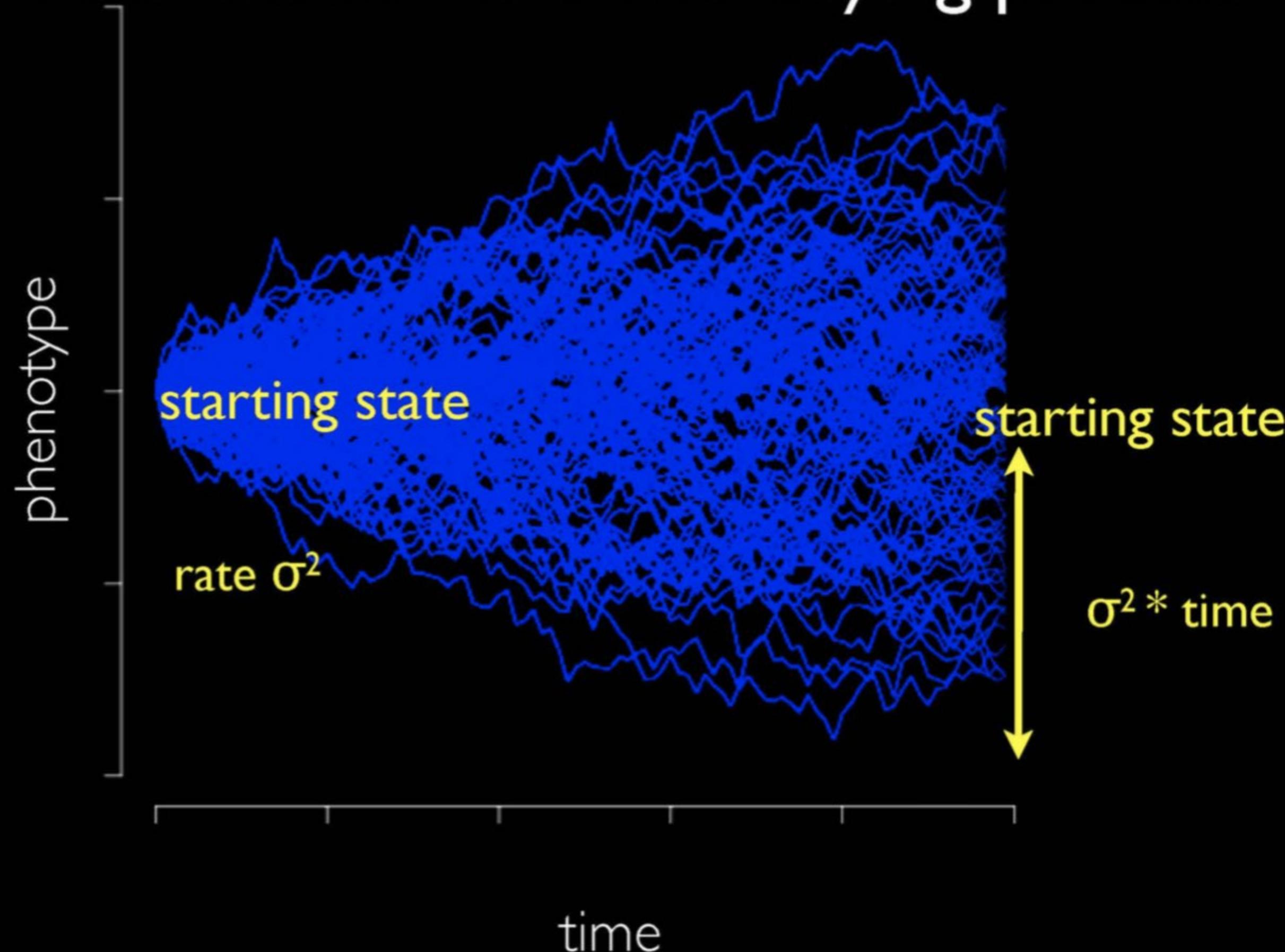
Brownian motion =  
surplus

OU =  
stabilizing  
selection

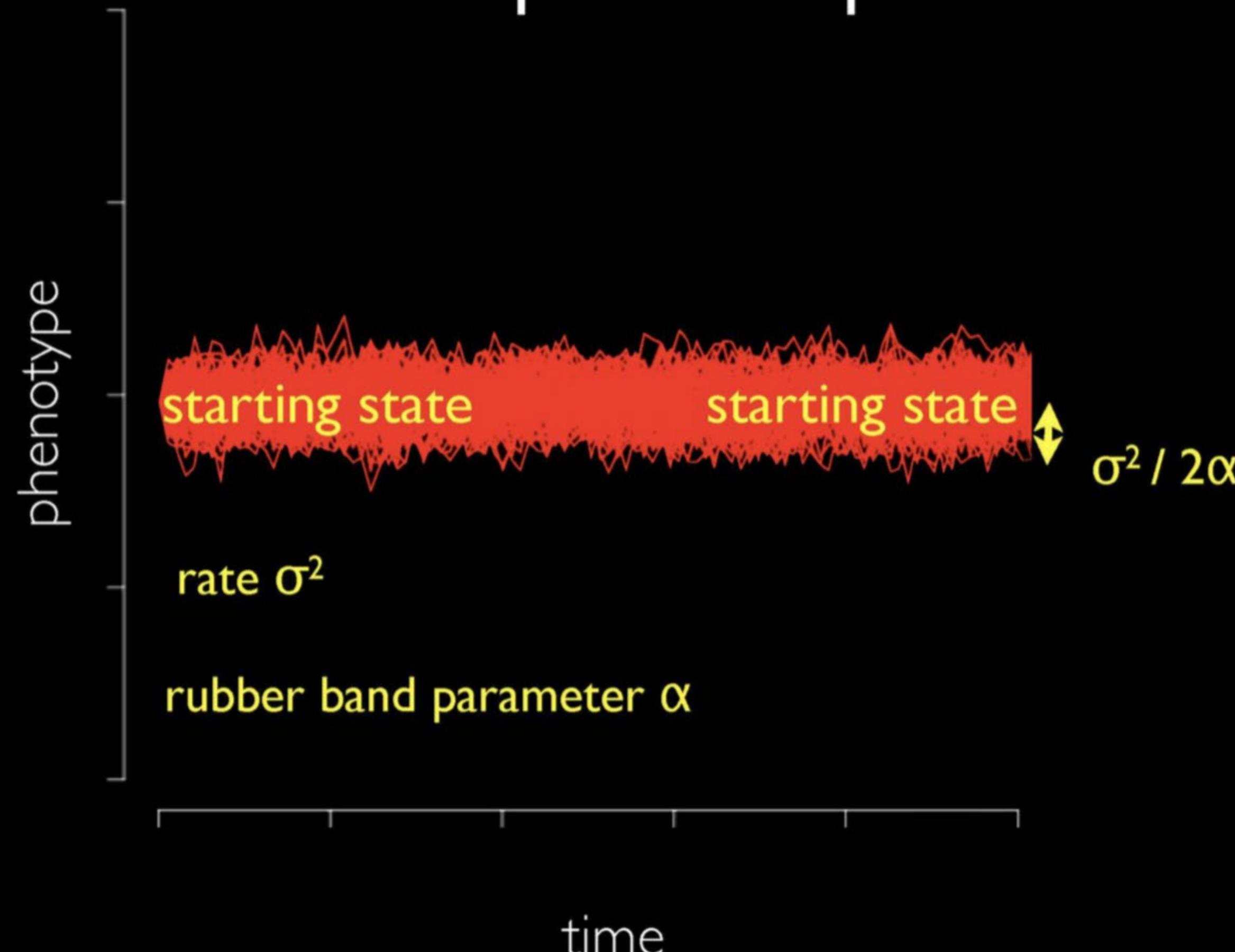
Brownian motion =  
drift or many other  
processes

OU =  
stabilizing  
selection or many  
other processes

# Brownian motion is a diversifying process



# OU is an equilibrium process

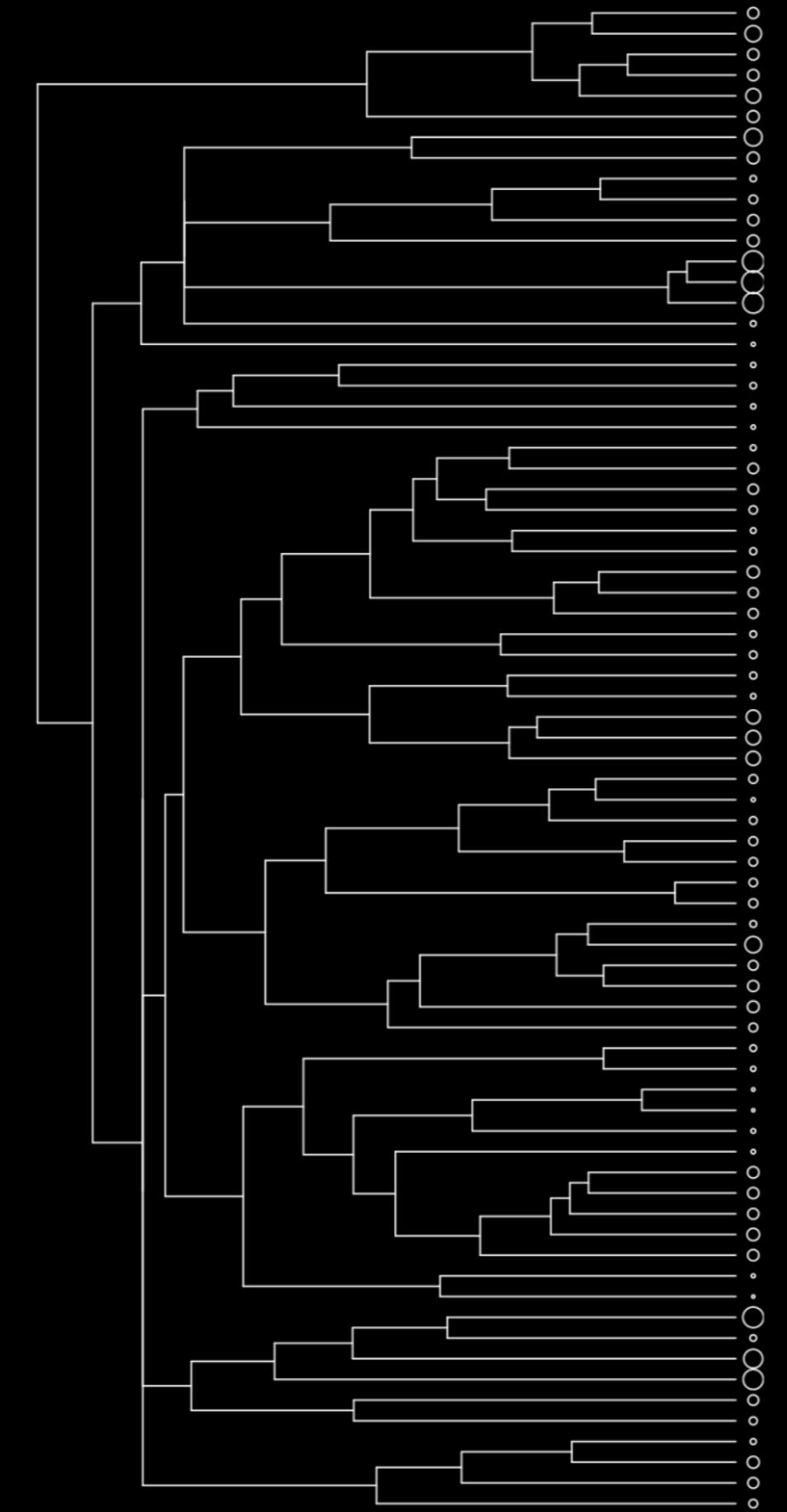


# Example: *Anolis* lizards

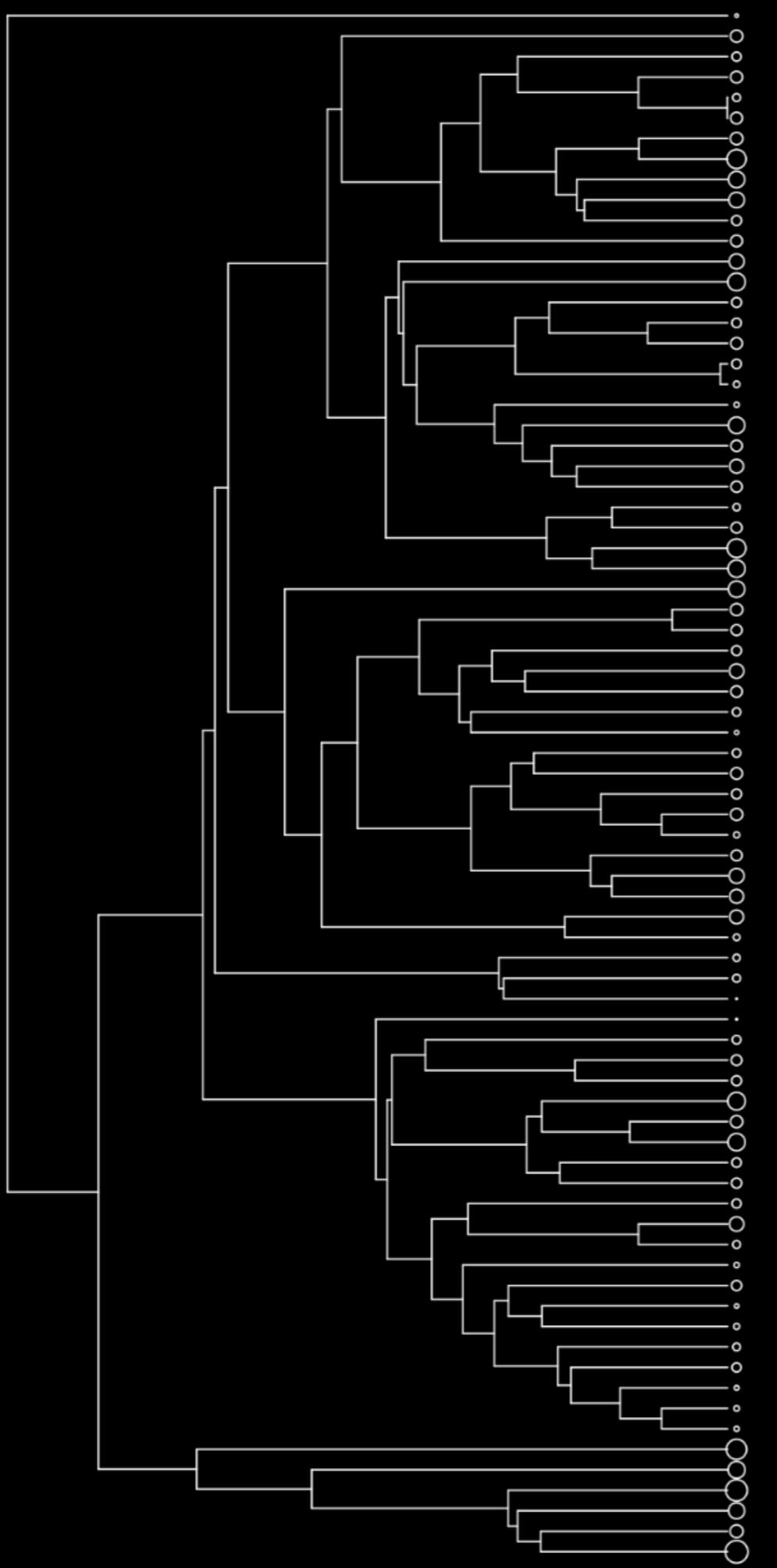
Lizards on  
Caribbean islands

Phylogenetic and  
body size data for  
73 species (out of  
~140 total)



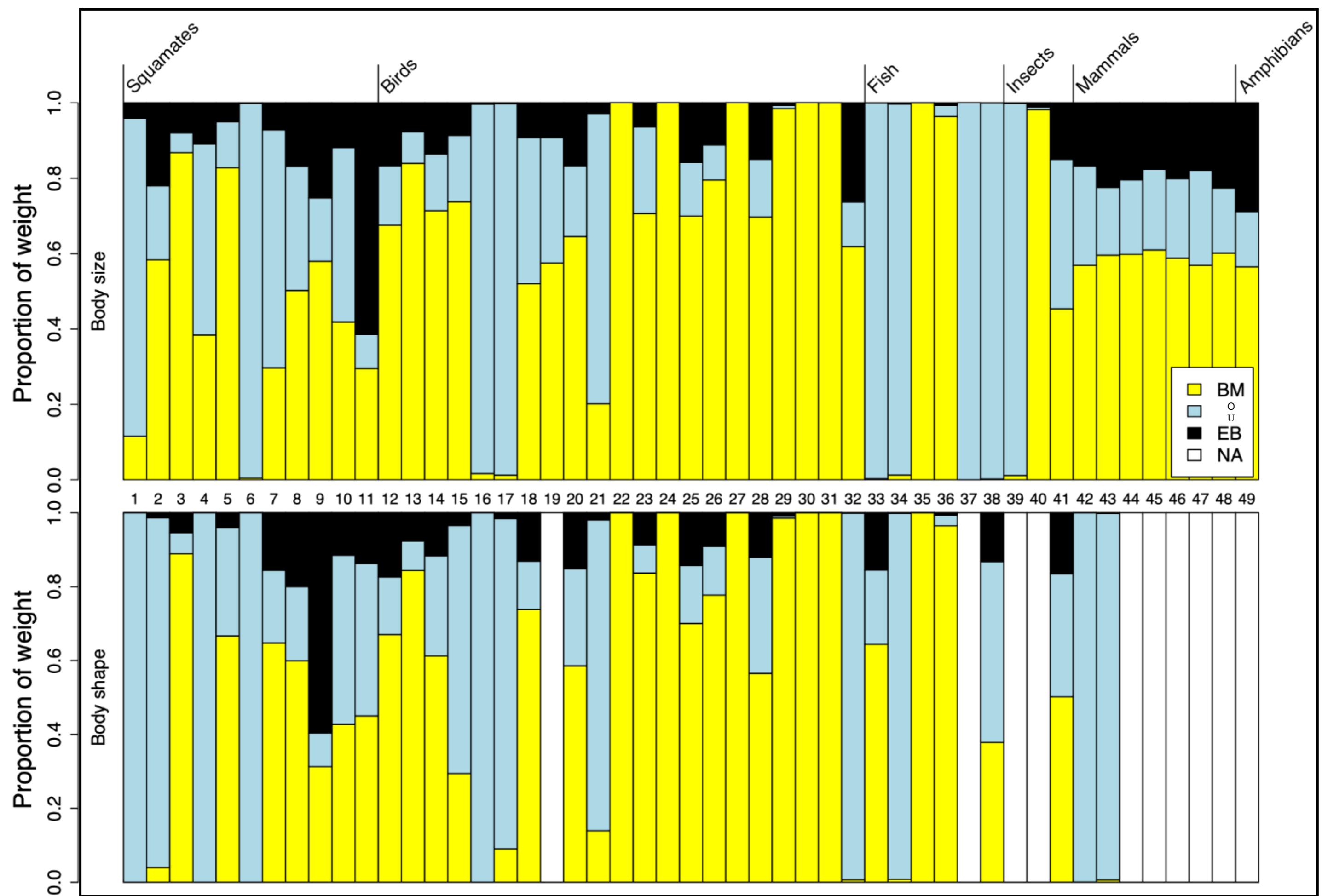


Model	Parameter estimates	InL	Akaike weight
SR	$\sigma^2 = 0.004$	-18.2	0.58
EB	$\sigma^2 = 0.006$ $r = -0.01$	-18.1	0.2
OU	$\sigma^2 = 0.004$ $\alpha = 0$	-18.2	0.22



## Cichlids in Lake Tanganyika

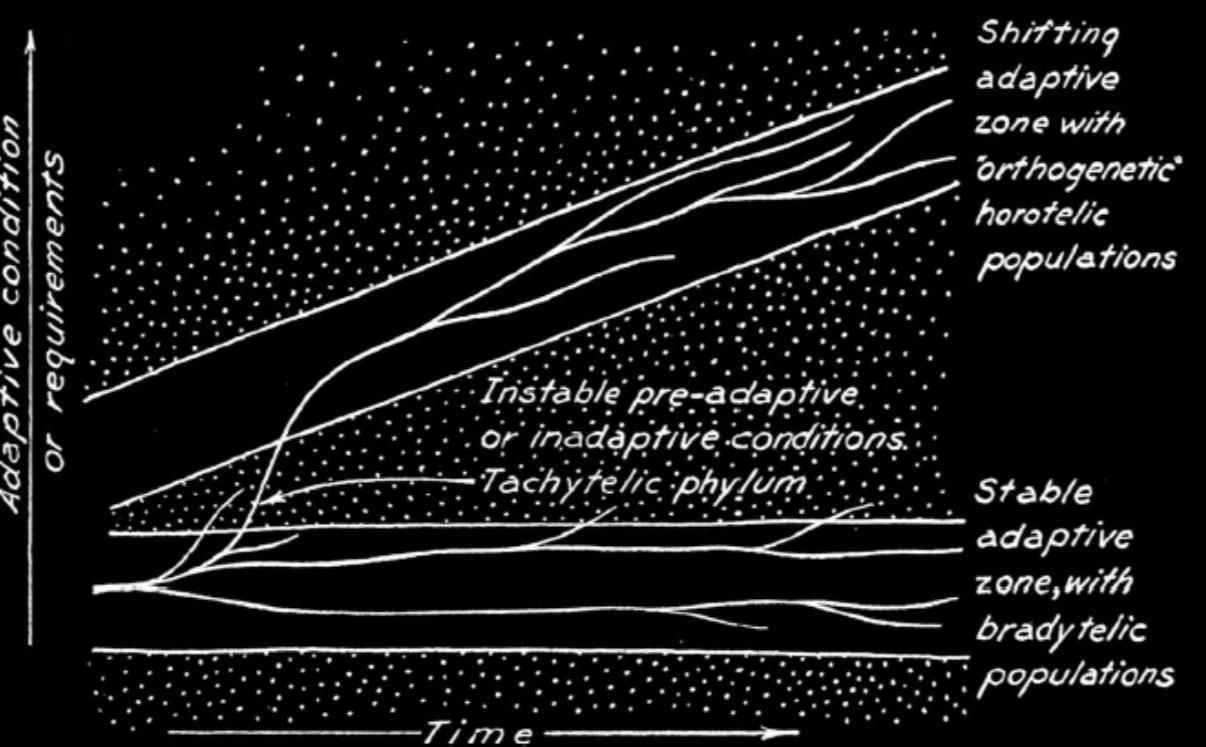
Model	Parameter estimates	InL	Akaike weight
SR	$\sigma^2 = 0.02$	-62.3	0
EB	$\sigma^2 = 0.02$ $r = 0$	-62.3	0
OU	$\sigma^2 = ...$ $\alpha = ...$	-33.3	1



# Models that vary

We can also fit models that are heterogeneous - where the model changes along branches in the tree

# Adaptive Radiation



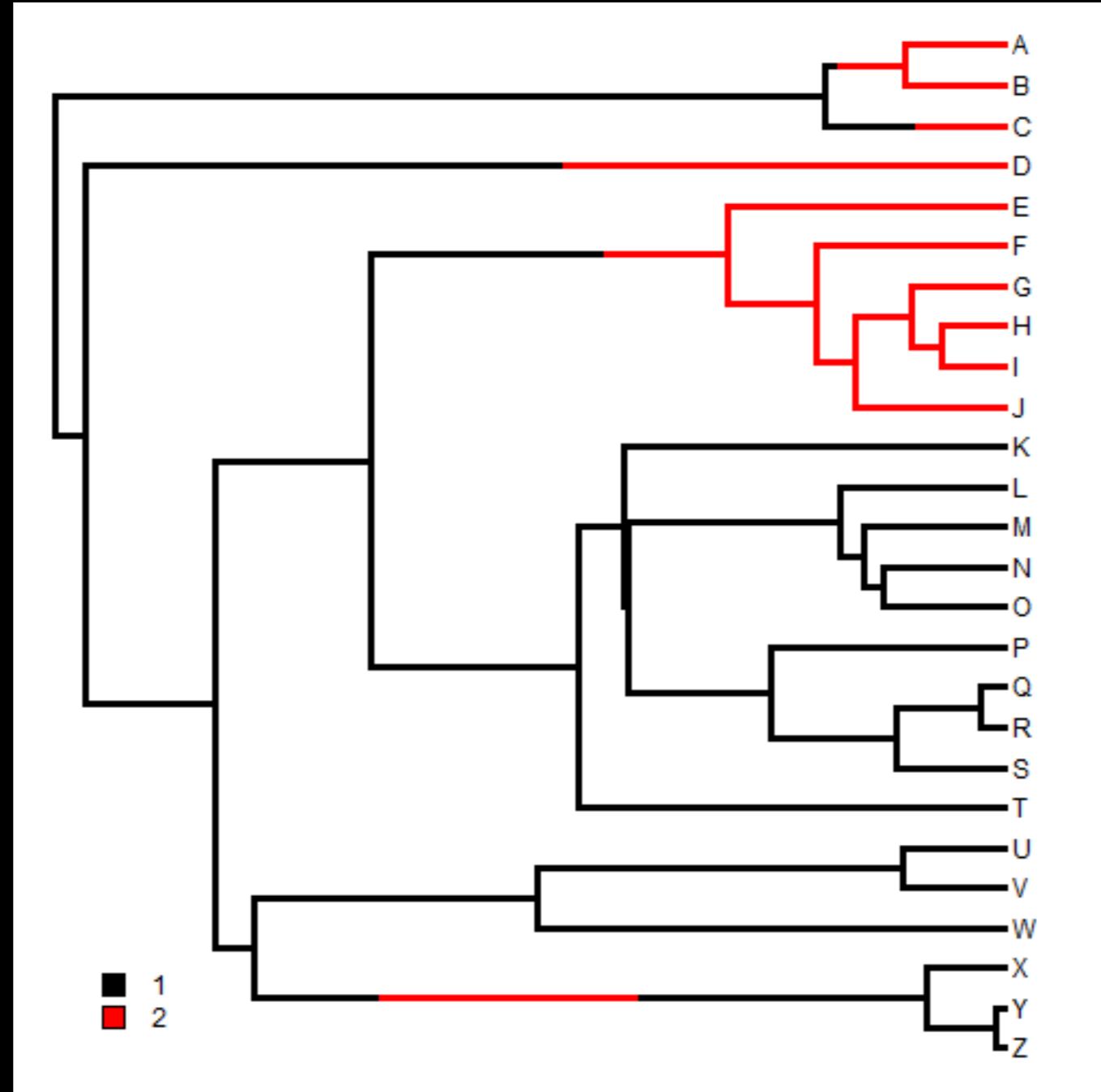
Simpson 1953

# Ways to enter a new adaptive zone, according to Simpson:

Can we detect jumps into new adaptive zones?

Do adaptive zones constrain evolutionary change?

3. Mass extinction of competitors



Is the **rate** of evolution different between  
state 1 and state 2?

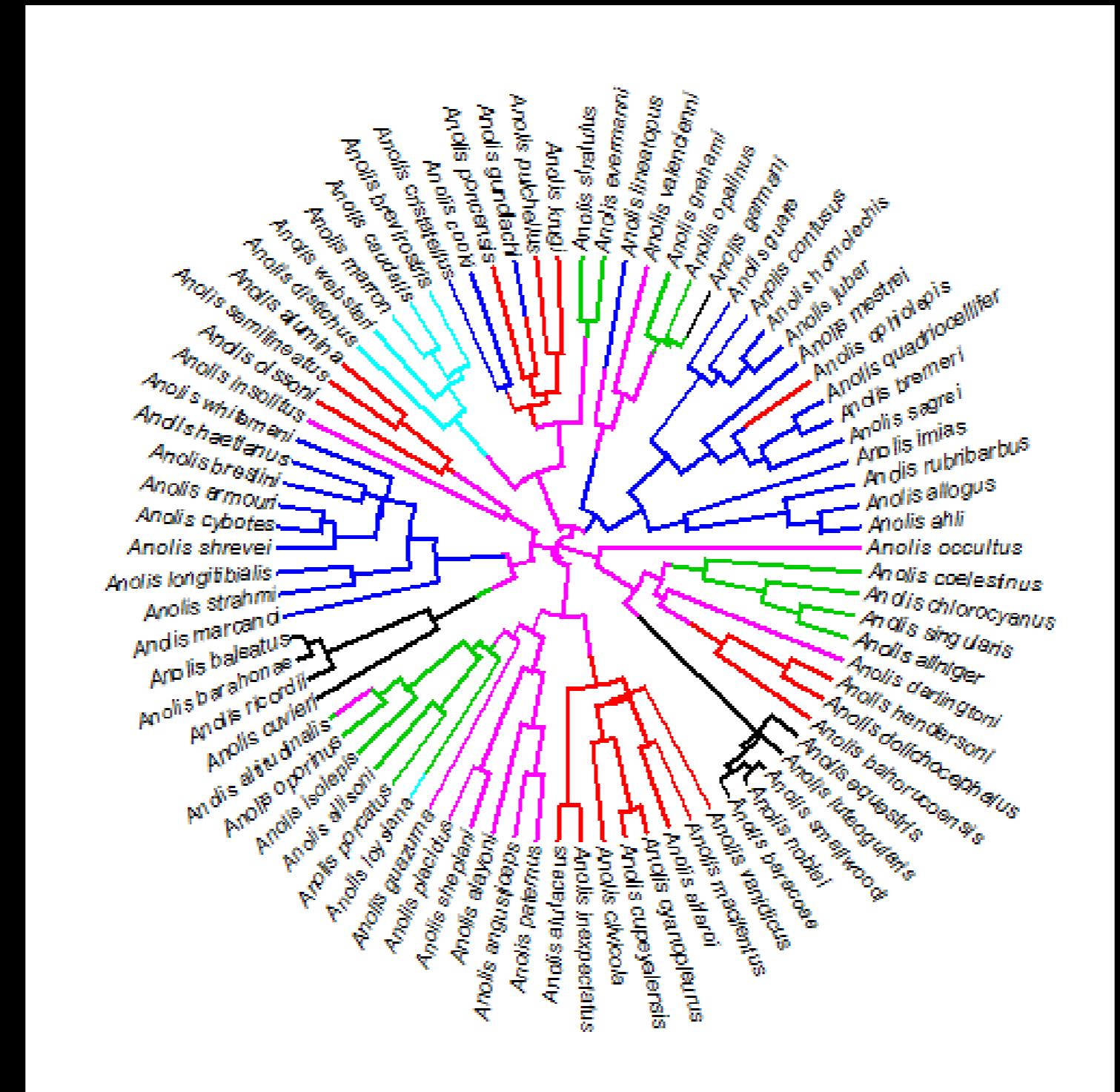
Compare the fit of a single-rate model  
to a multi-rate model

Model 1

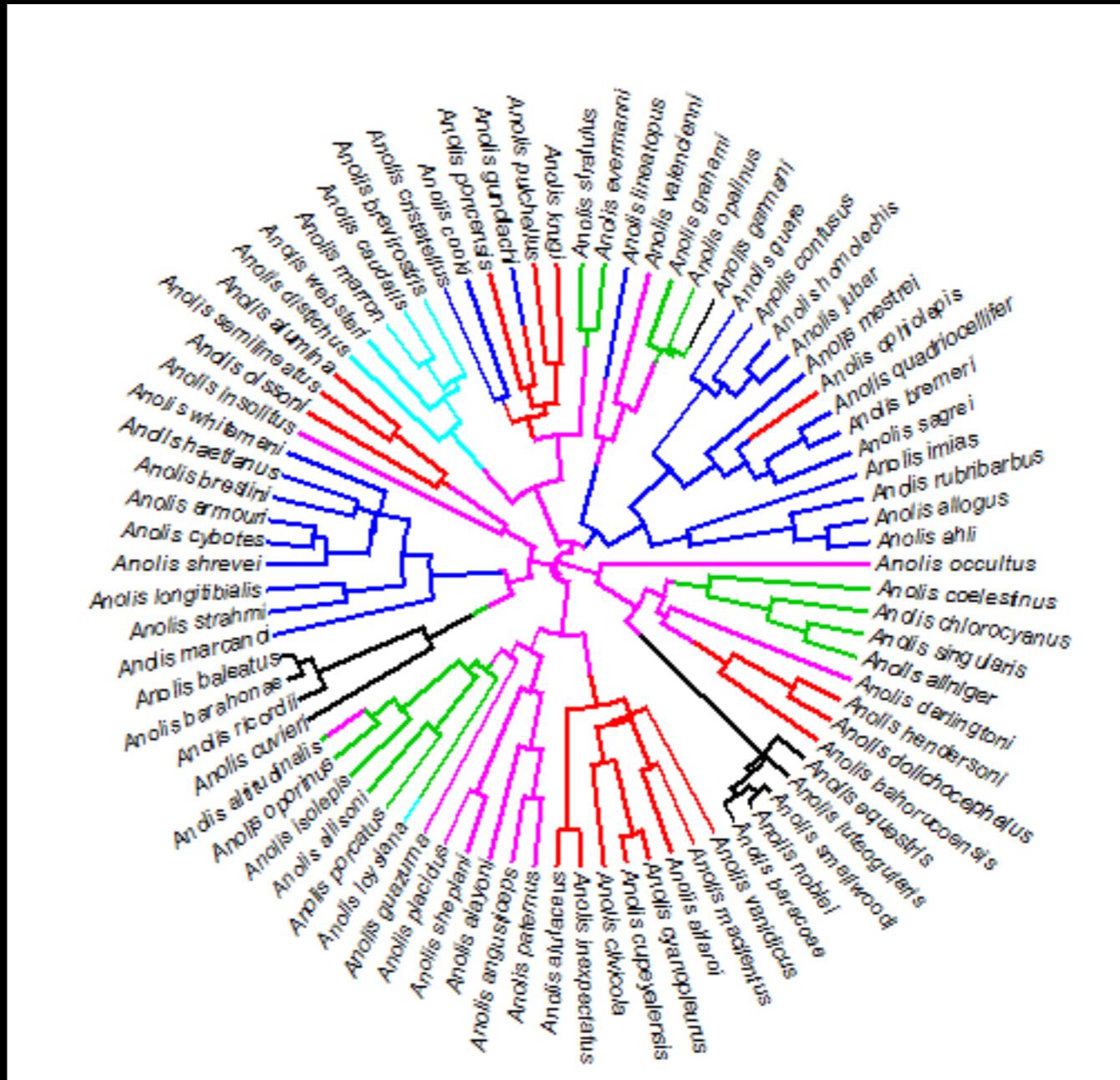
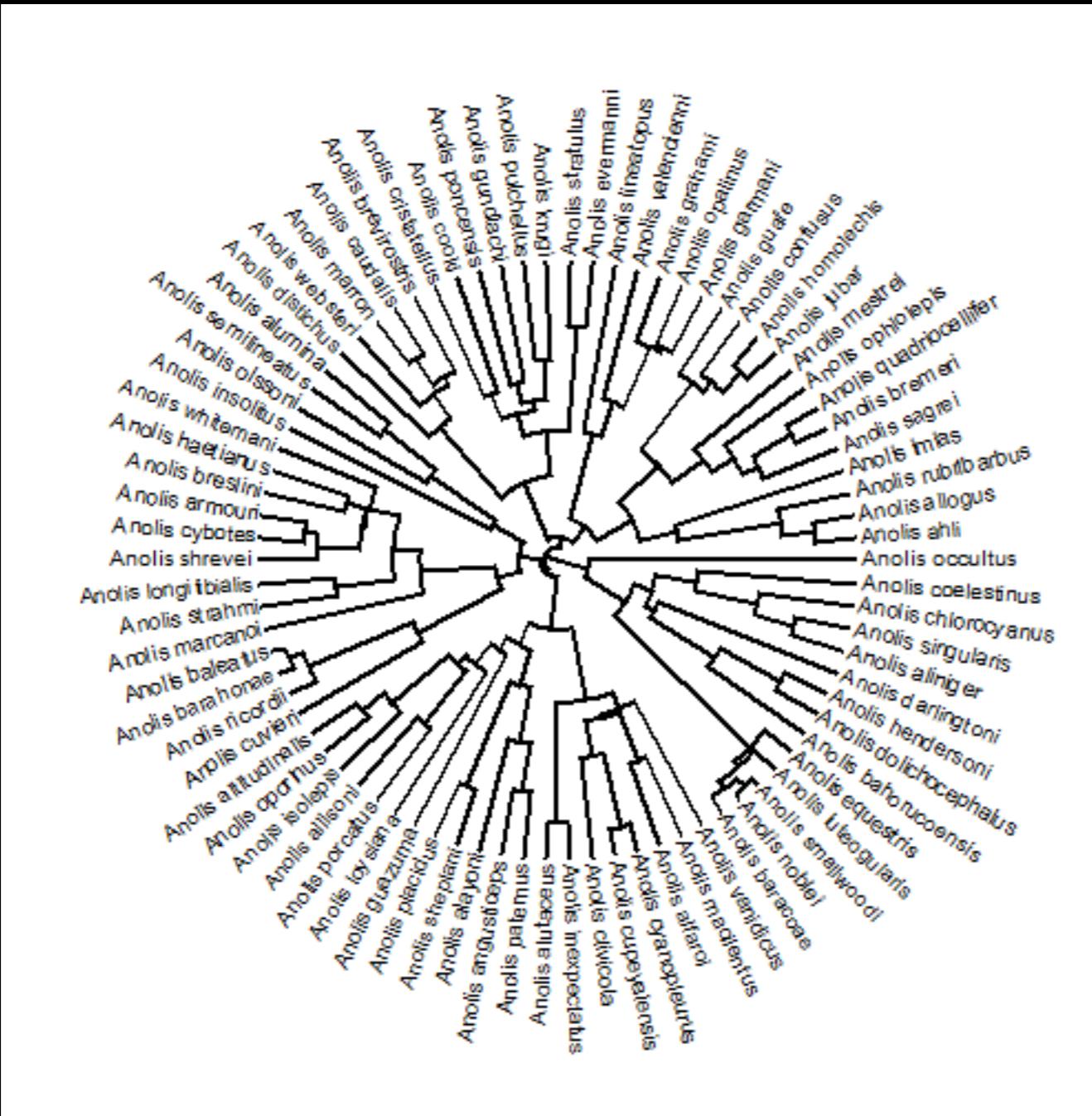
$$\sigma^2$$

Model 2

$$\begin{matrix} \sigma_1^2 \\ \sigma_2^2 \end{matrix}$$

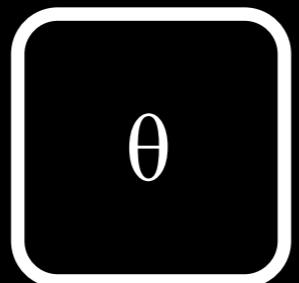


Is the evolutionary regime different between state 1 and state 2 (and so on)?

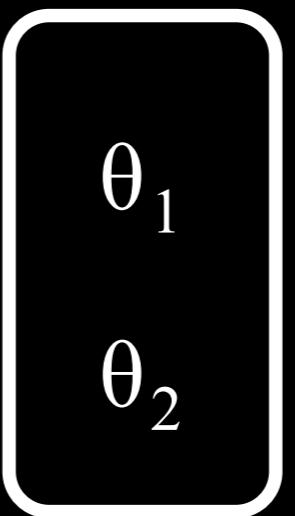


Compare the fit of a single-regime model  
to a multi-regime model

Model 1



Model 2



More complicated  
tools

rjMCMC

# split move

$$(\alpha_1 \alpha_1 \alpha_1 \alpha_1 \alpha_1 \alpha_2 \alpha_2 \alpha_2 \alpha_2 \alpha_2) \quad k = 2$$

# split move

$$(\alpha_3 \alpha_3 \alpha_3 \alpha_1 \alpha_1 \alpha_2 \alpha_2 \alpha_2 \alpha_2) \quad k = 3$$

# merge move

$$(\alpha_3 \ \alpha_3 \ \alpha_3 \ \alpha_1 \ \alpha_1 \ \alpha_1 \ \alpha_1 \ \alpha_1 \ \alpha_1 \ \alpha_1) \quad k = 2$$

Through a series of split and merge  
moves

we can fit multi-rate models to  
comparative data

ORIGINAL ARTICLE

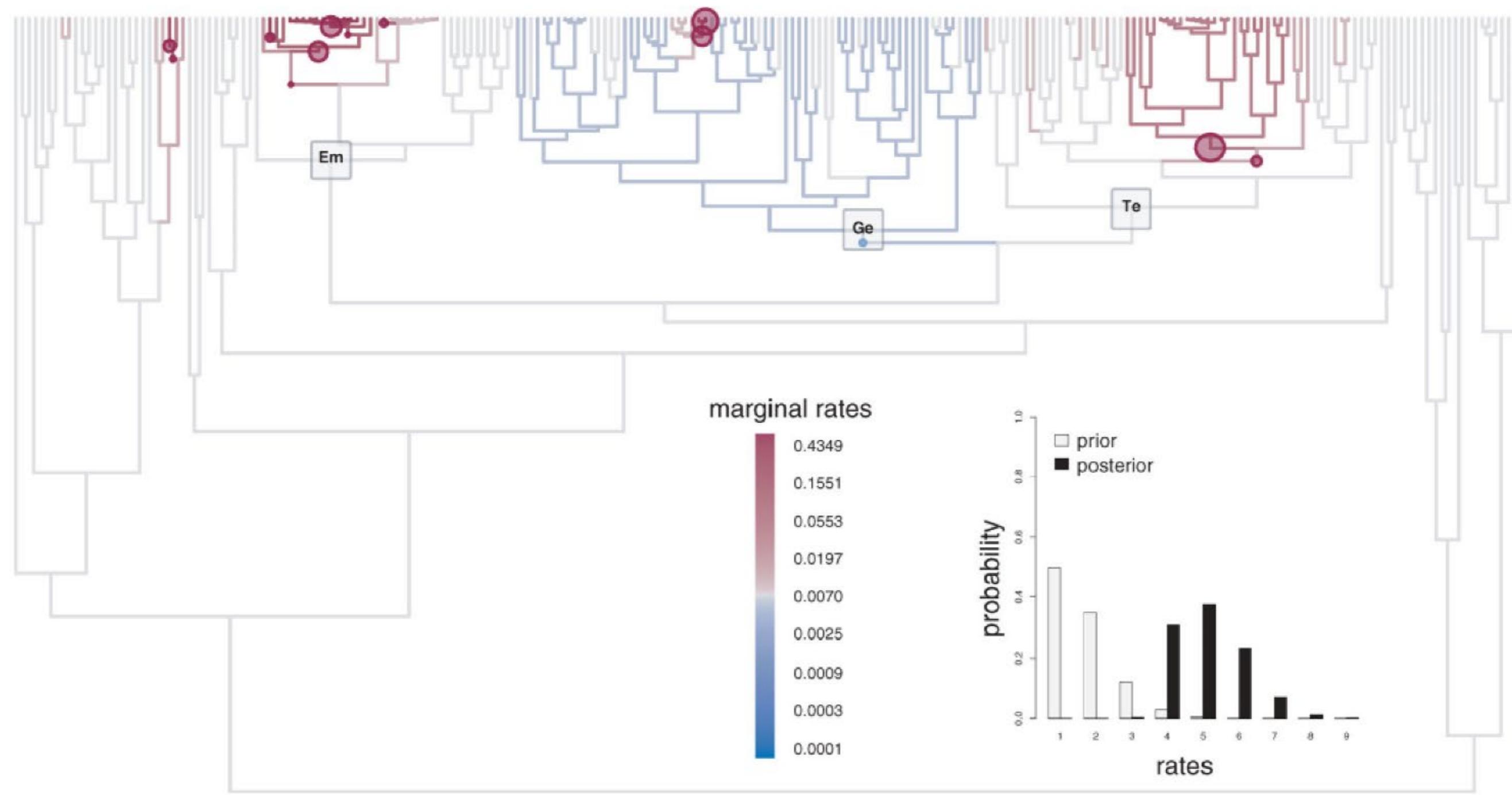
doi:10.1111/j.1558-5646.2011.01401.x

# A NOVEL COMPARATIVE METHOD FOR IDENTIFYING SHIFTS IN THE RATE OF CHARACTER EVOLUTION ON TREES

Jonathan M. Eastman,<sup>1,2</sup> Michael E. Alfaro,<sup>3,4</sup> Paul Joyce,<sup>5,6</sup> Andrew L. Hipp,<sup>7,8,9</sup> and Luke J. Harmon<sup>10,11</sup>

3578

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*Evolution* 65-12: 3578–3589



AUTEUR = changes in the *rate of evolution*  
a long branches in a phylogeny

AUTEUR “jump- b m ”

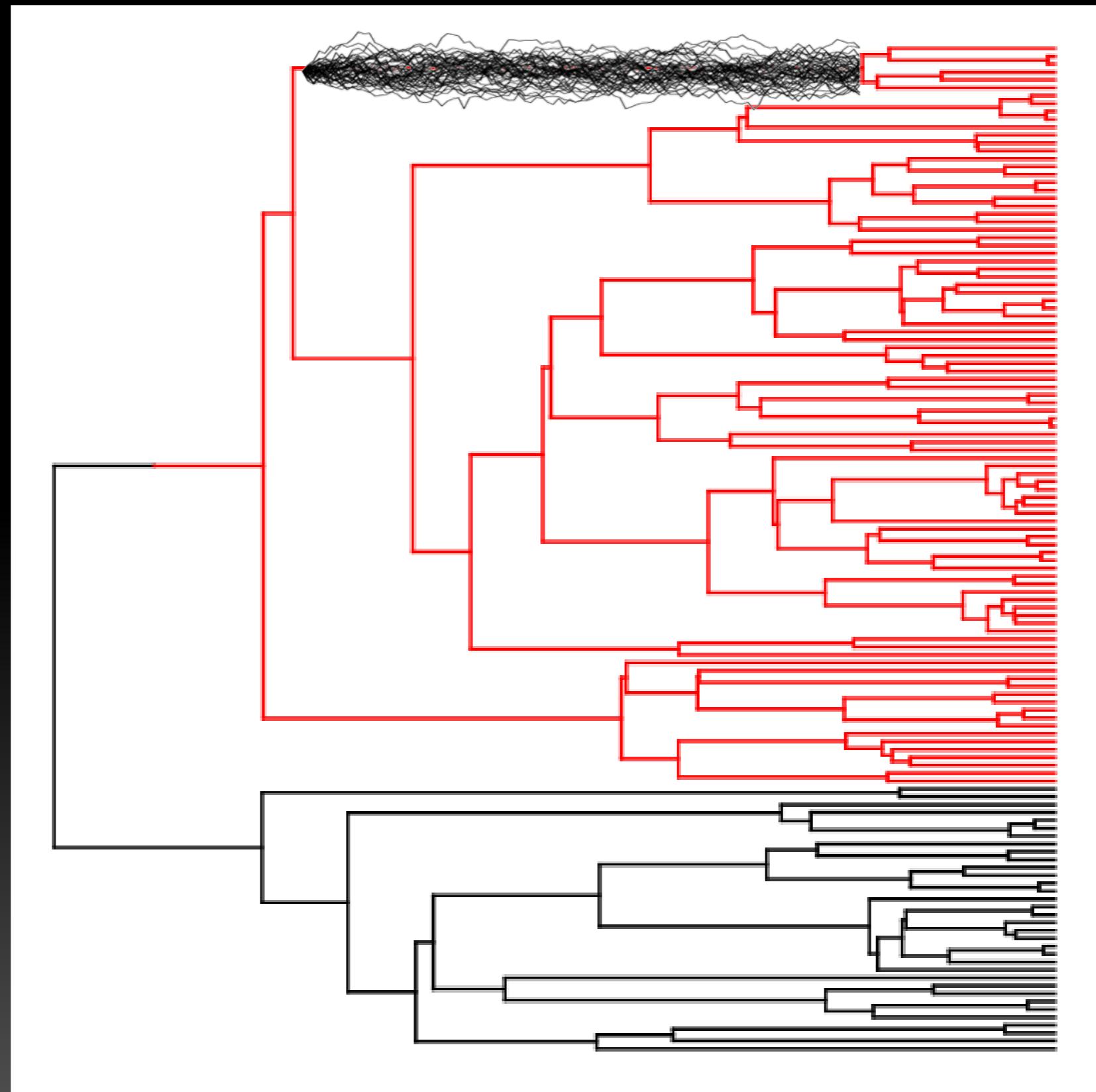
*evolutionary jumps*

a long branches in a phylogeny

AUTEUR “rbm”

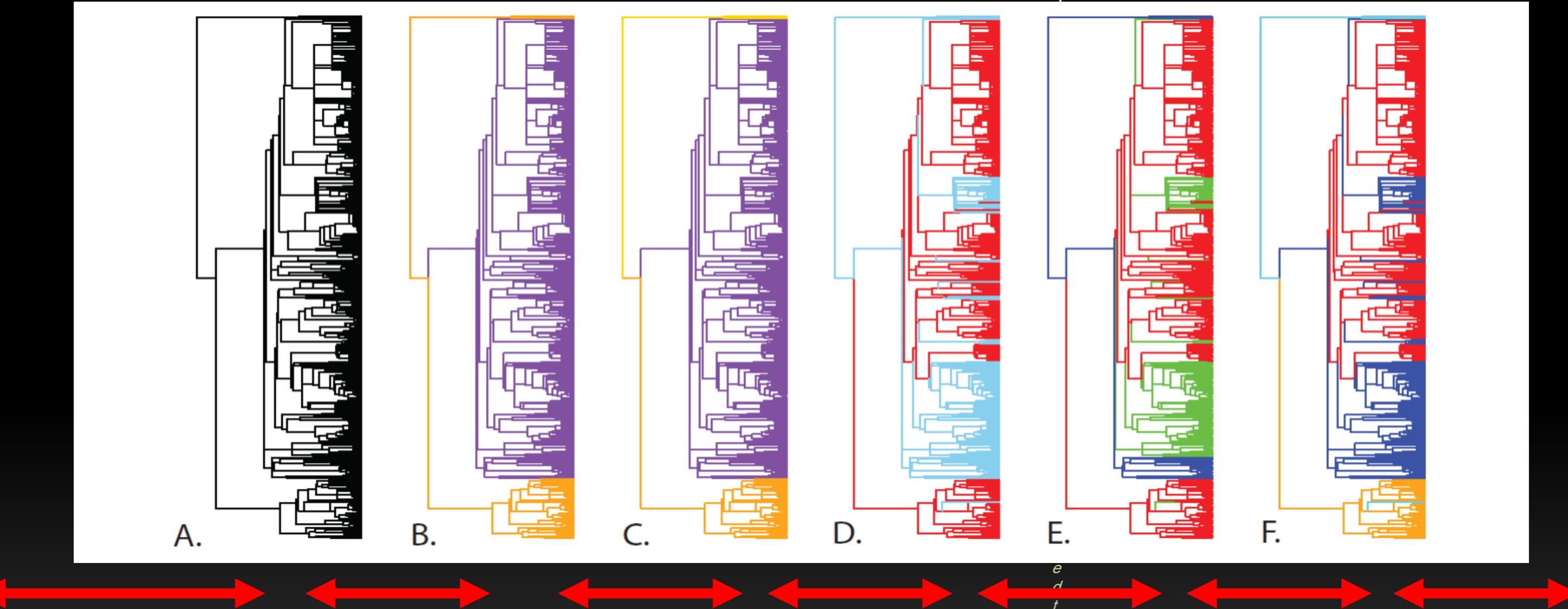
*evolutionary rate shifts*  
a long branches in a phylogeny

Do adaptive  
zones constrain  
evolutionary  
change?





m  
p  
O  
U  
M  
o  
1



# Convergent evolution in anoles



**Trunk – crown anoles:**

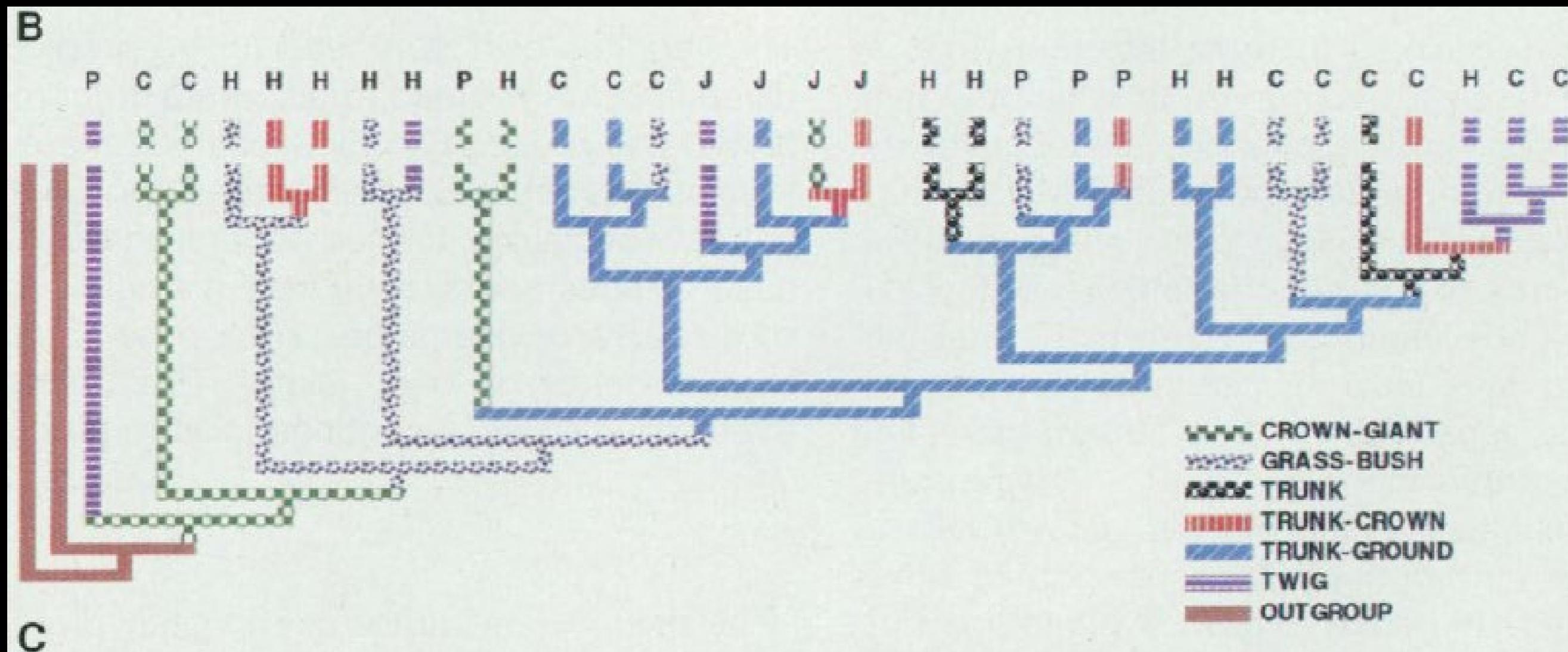
*A. allisoni* (Cuba) and *A. chlorocyanus*  
(Hispaniola)



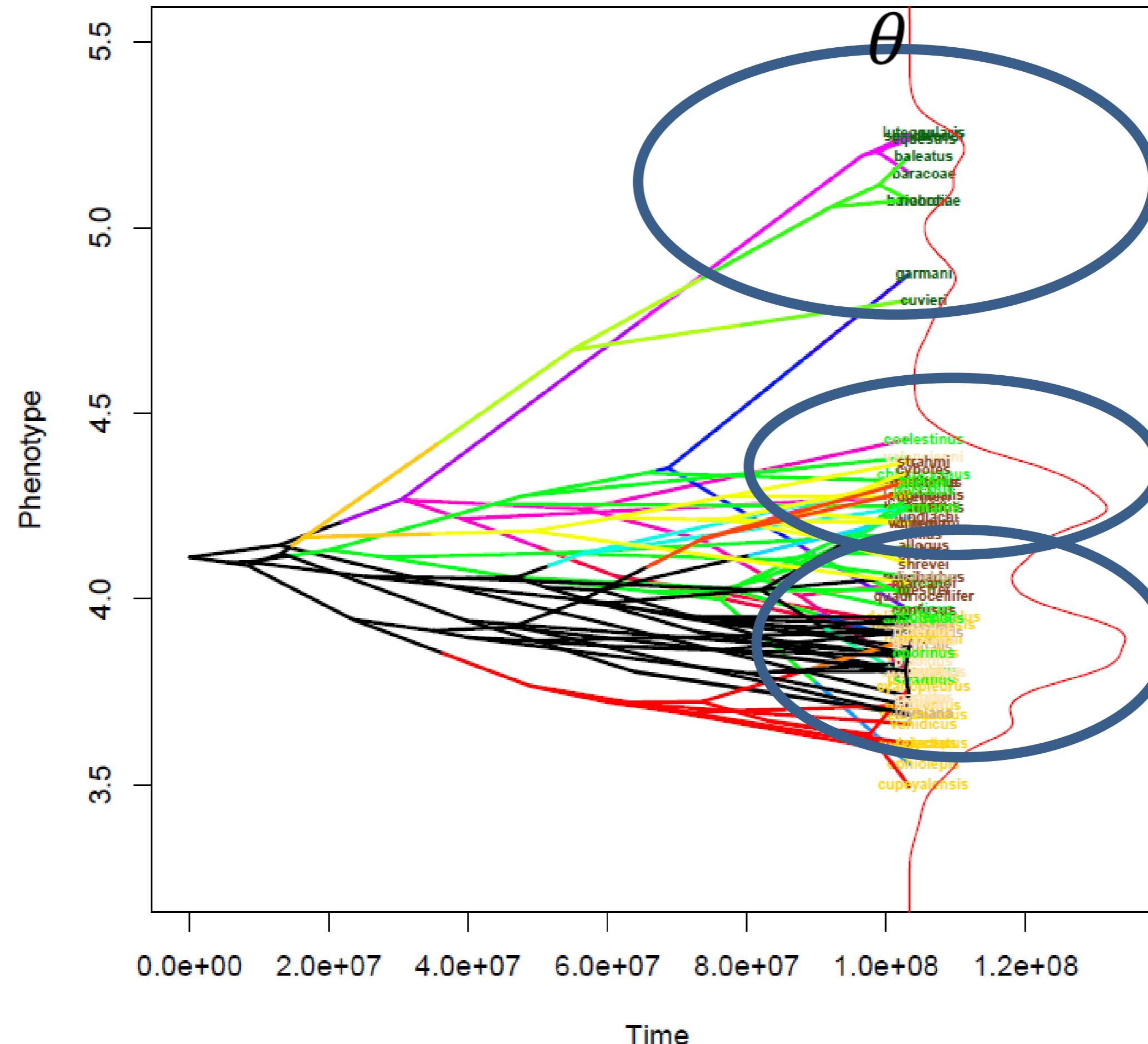
**Twig anoles:**

*A. valencienni* (Jamaica) and *A. insolitus* (Hispaniola)

# Convergent evolution in anoles



Losos et al. 1998





changes in *adaptive zones*  
a long branches in a phylogeny

Method	Base model	Addition	Notes
AUTEUR “rbm”	BM	Multiple rates	Similar to BAMM
Auteur “jump-BM”	BM	Jumps	Levy walk
Auteur “jump-rbm”	BM	Multiple rates and jumps	Untested!
BAYOU	OU	Multiple peaks	Like Surface, but Bayesian

## Other similar methods:

Surface

OUwie

BAMM