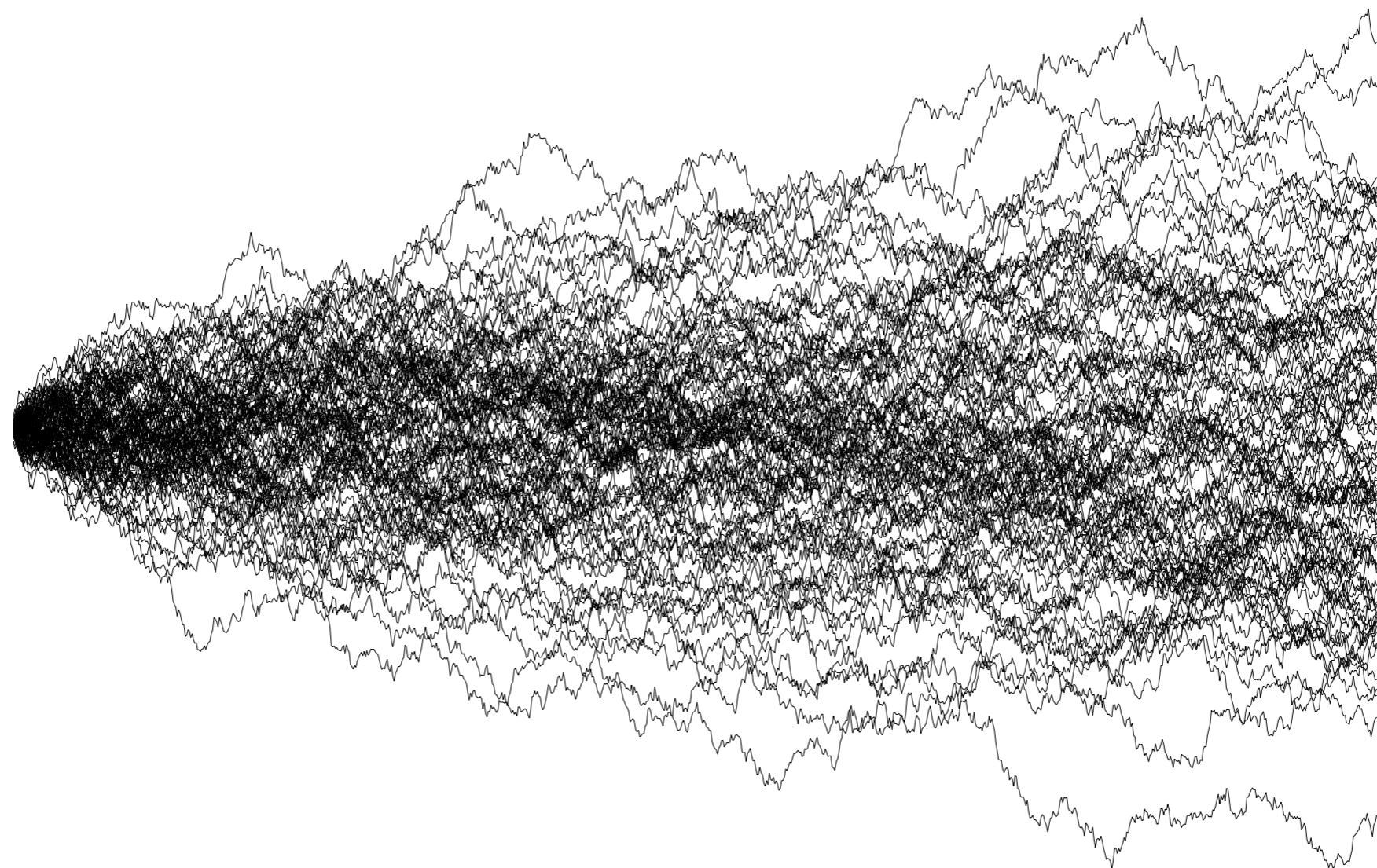


Comparative methods:  
modeling continuous  
and discrete character  
evolution

# Brownian Motion



# **What is Brownian motion?**

# Brownian Motion: The Model

- Describes a “random walk” of evolution for continuously-valued characters

# Three Facts Describe Brownian Motion

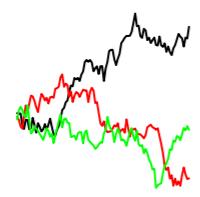
- No trend
- Successive steps independent
- Expected values follow normal distribution where variance depends on rate and time

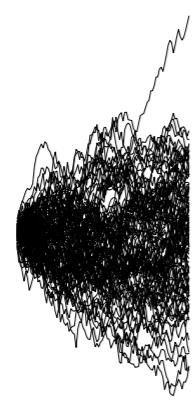
# Parameters of BM

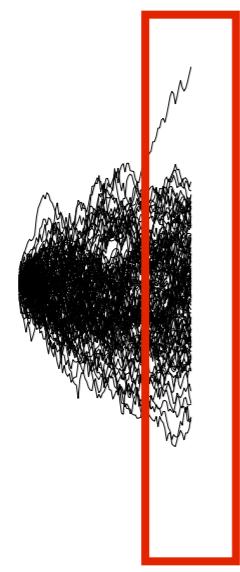
- Brownian motion models have two parameters:
  - $\Theta$ , the starting value;  $W(0) = \Theta$
  - $\sigma^2$ , the rate parameter

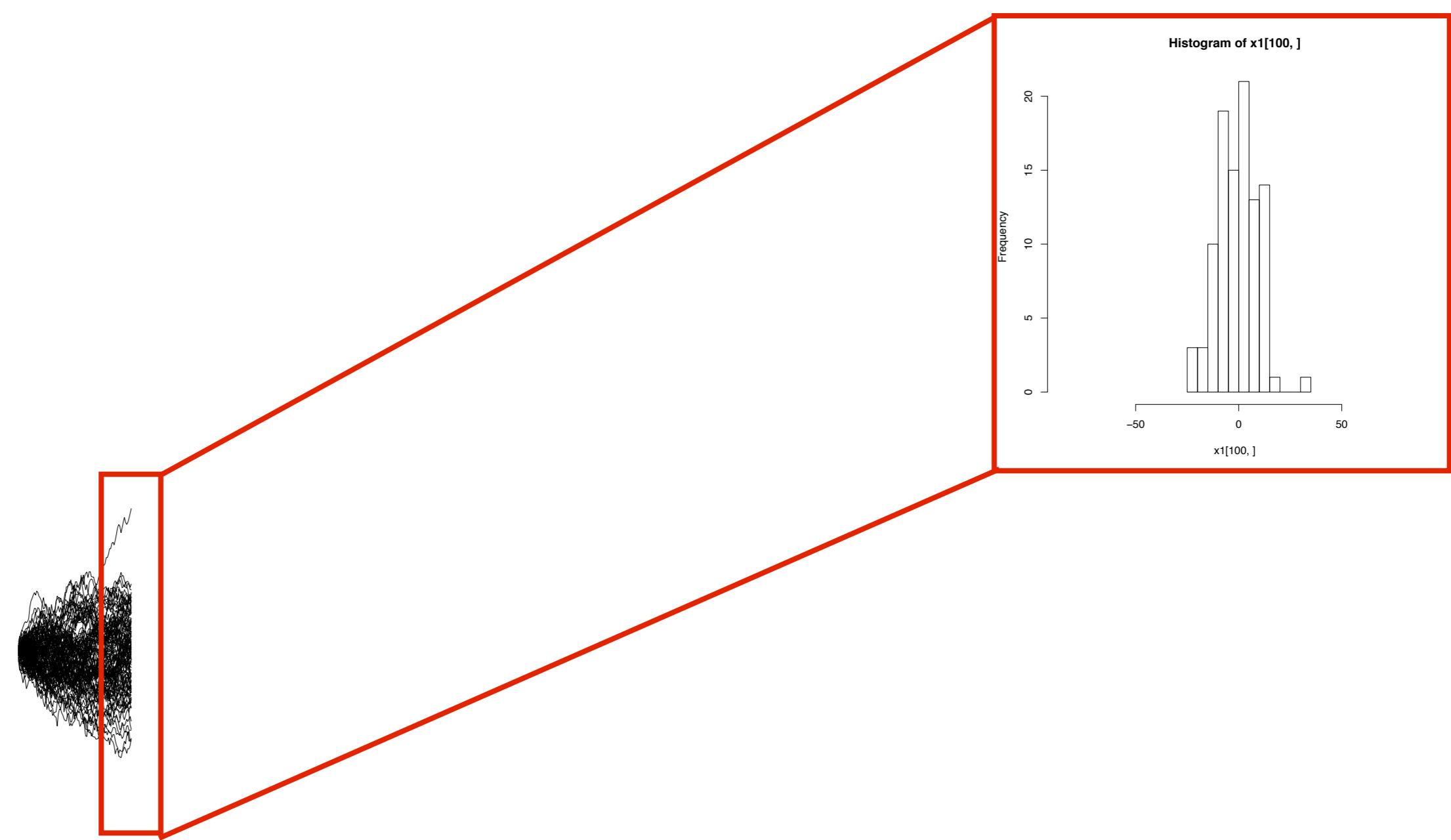




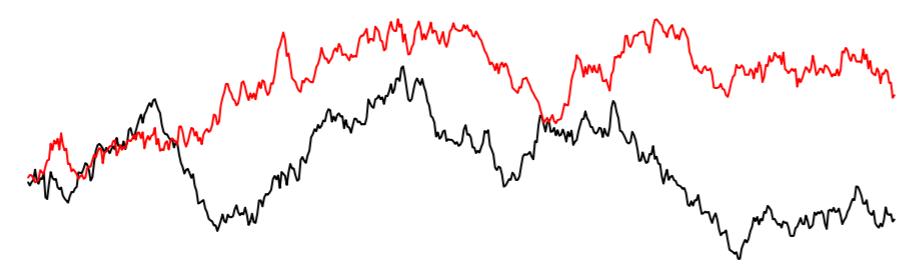


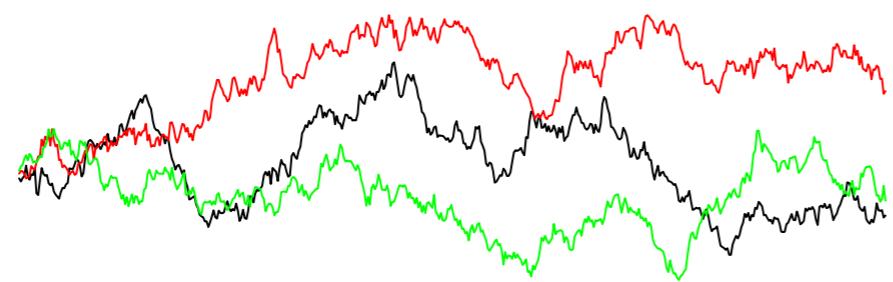


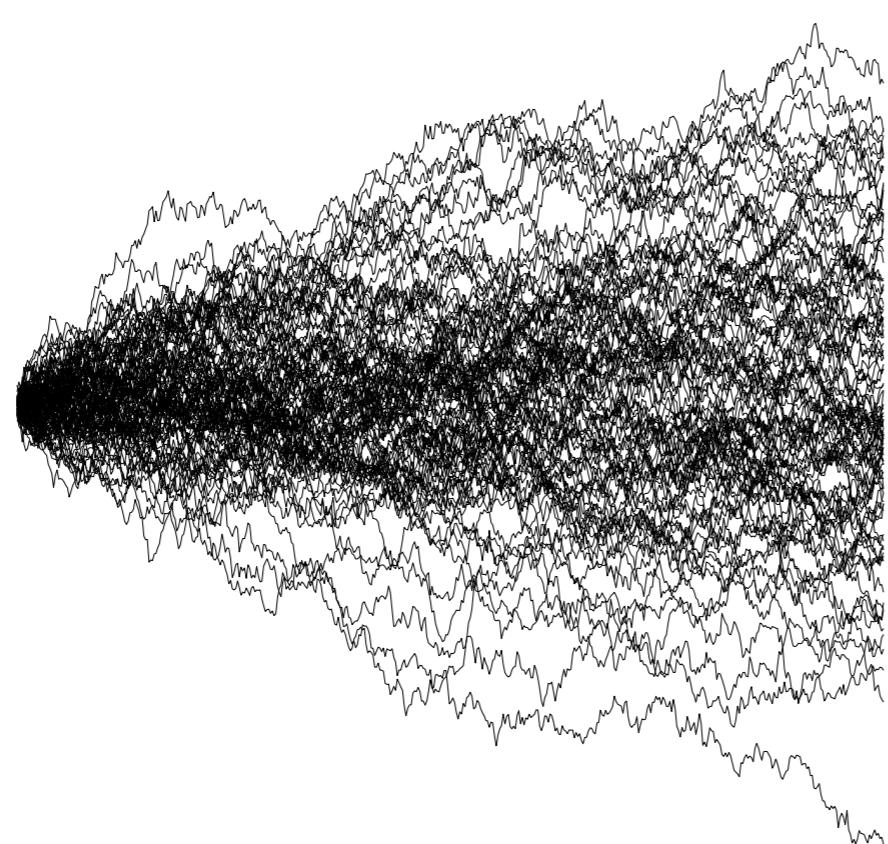


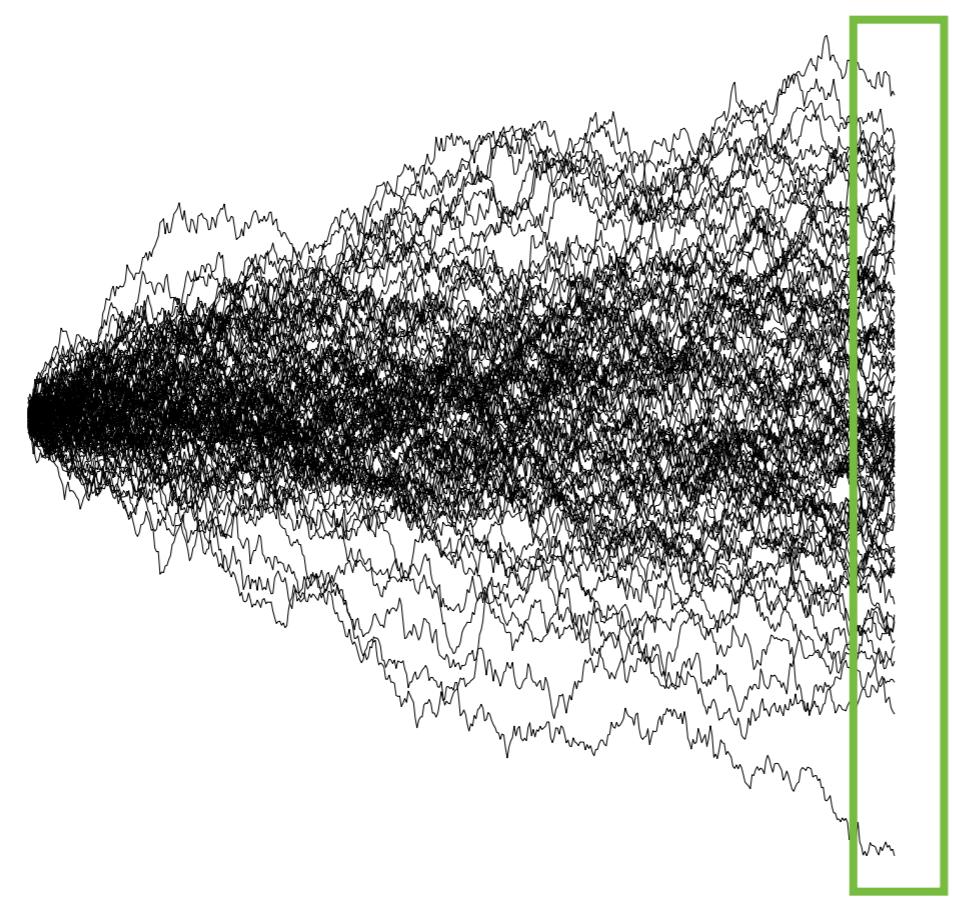




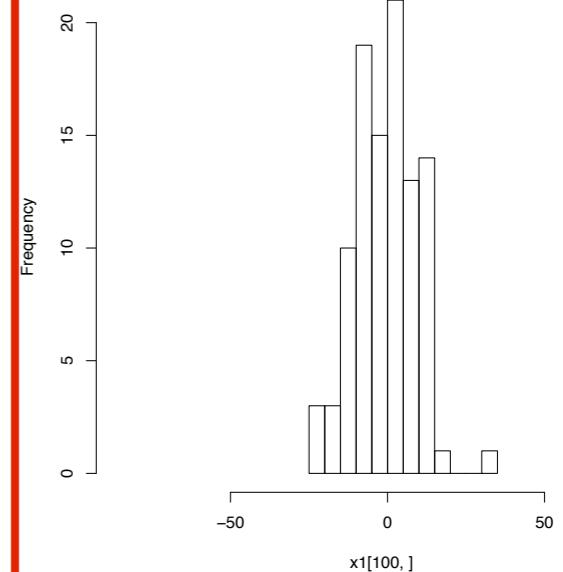




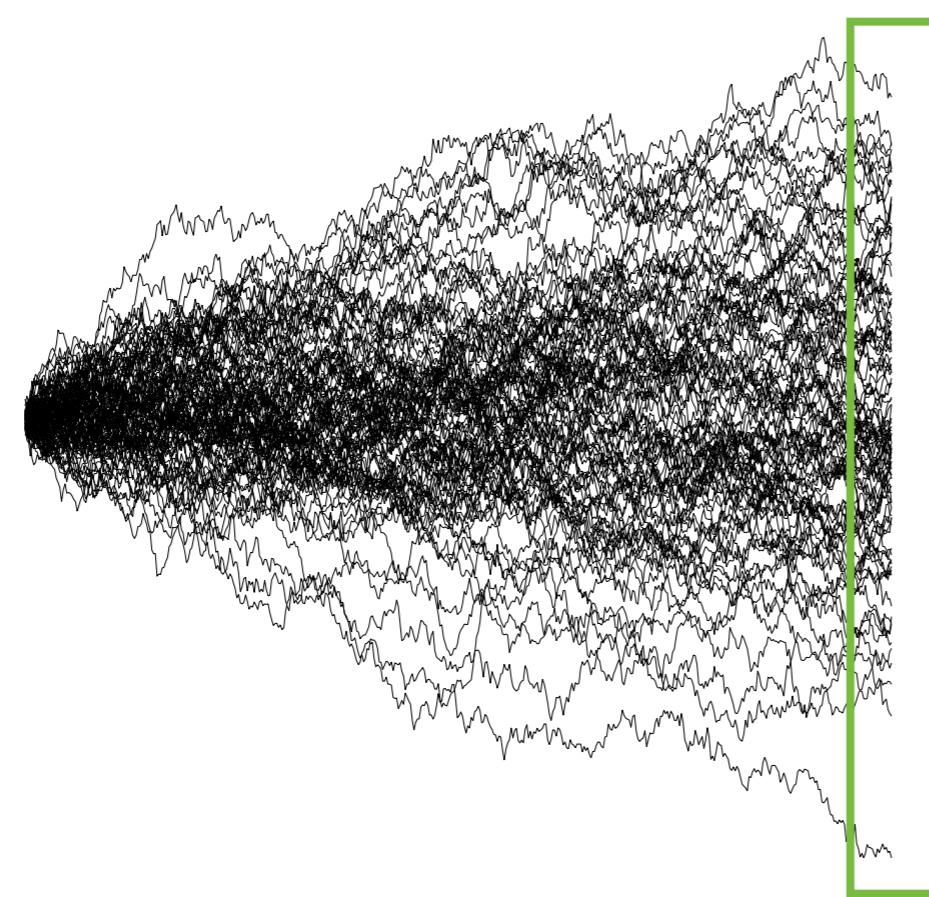
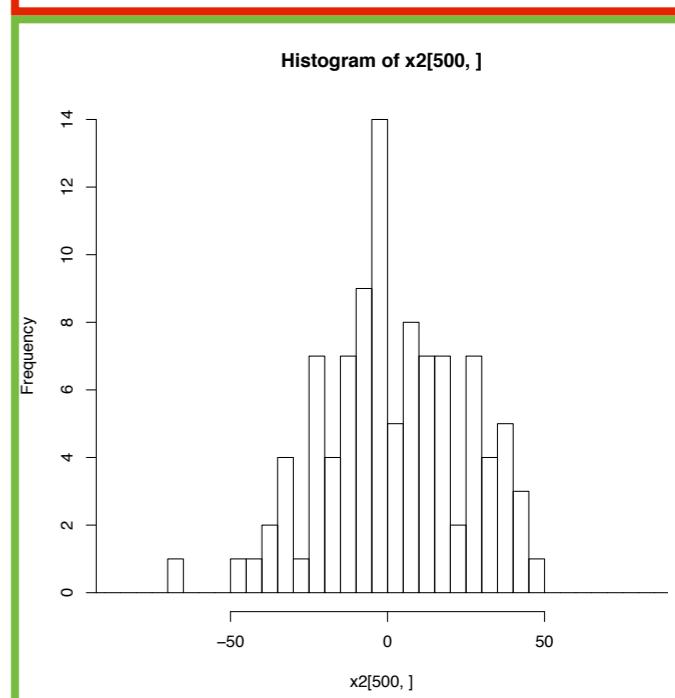


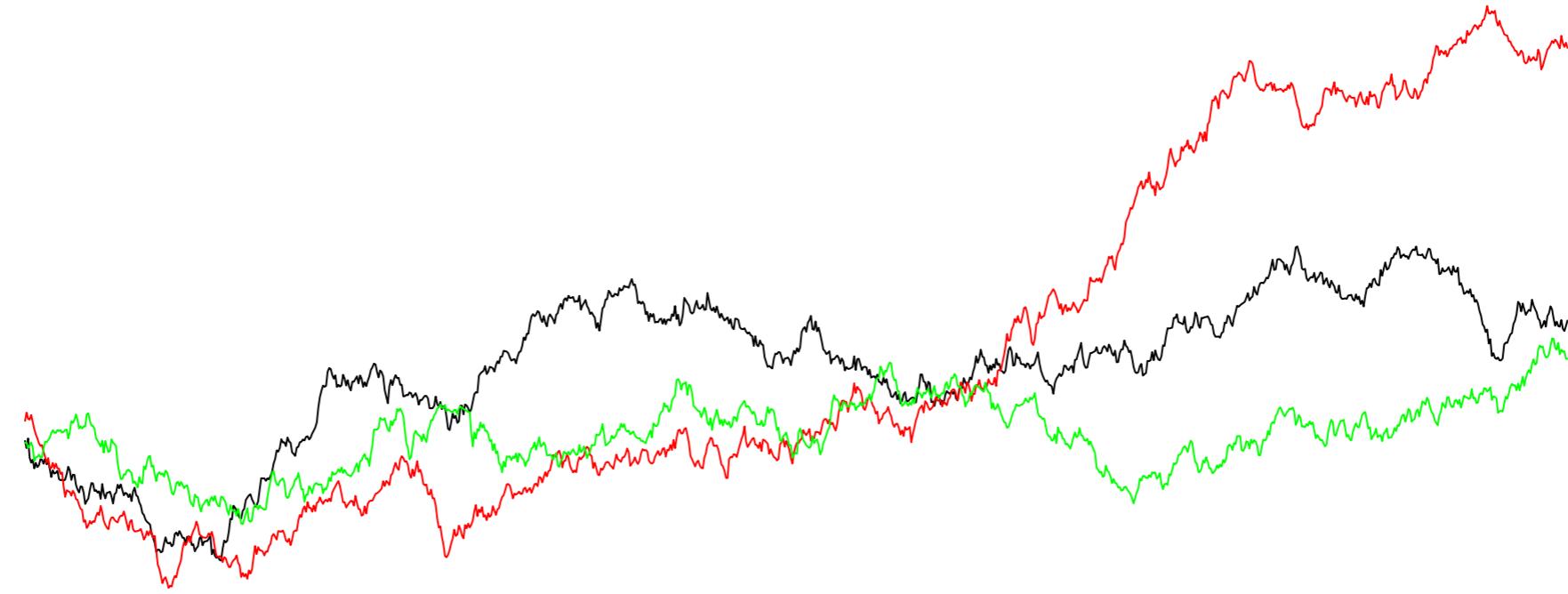


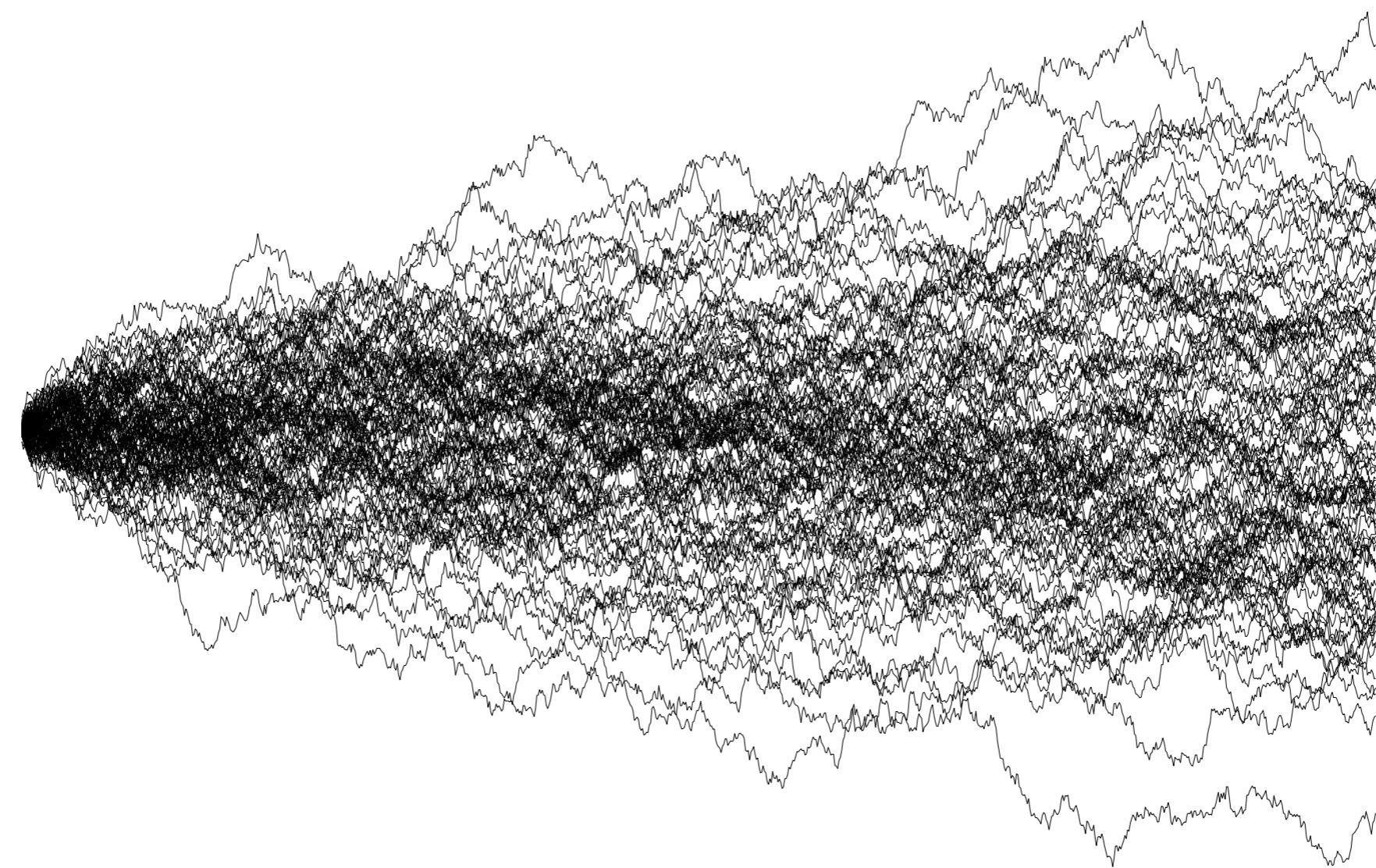
Histogram of  $x1[100, ]$

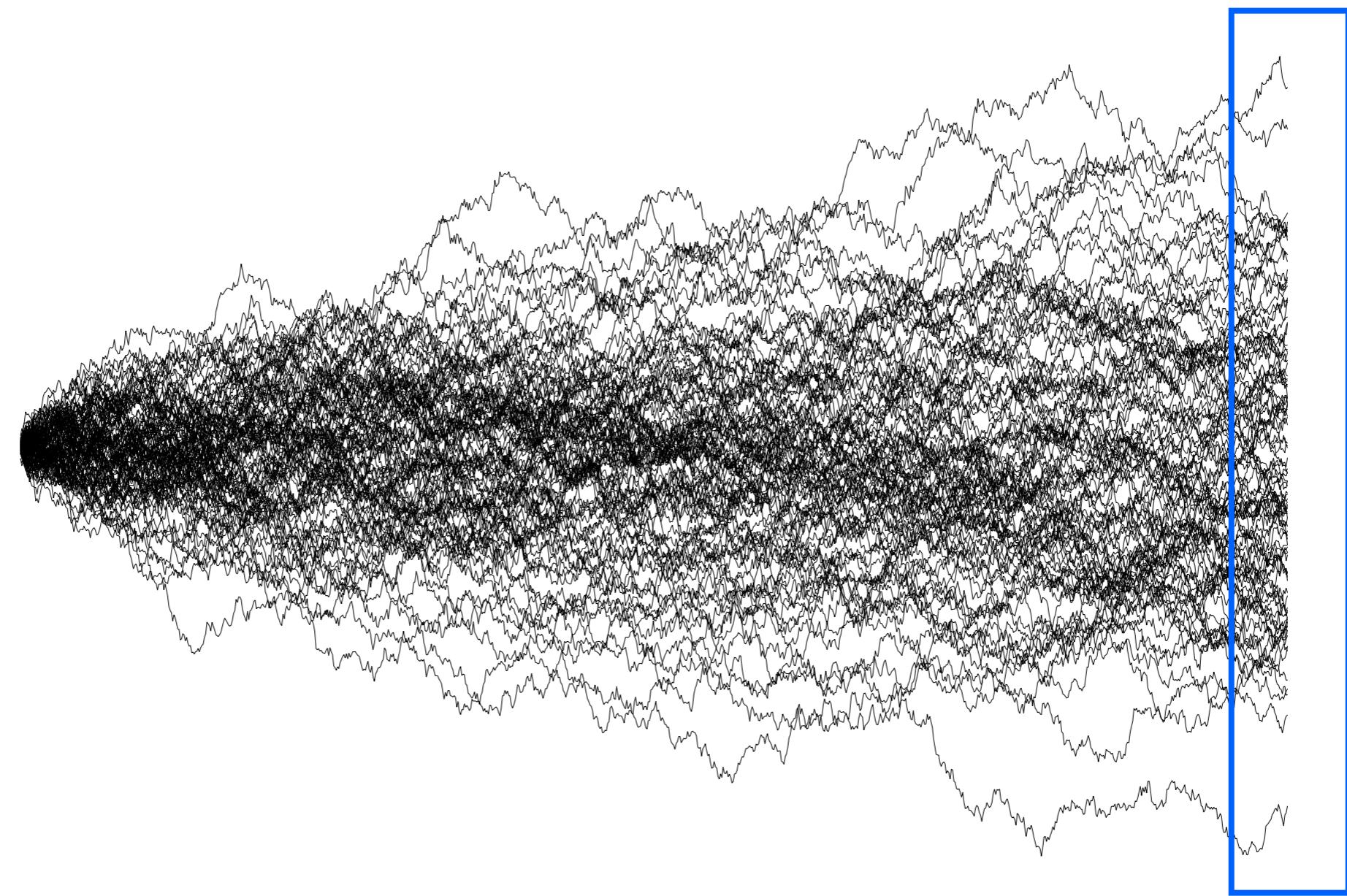


Histogram of  $x2[500, ]$

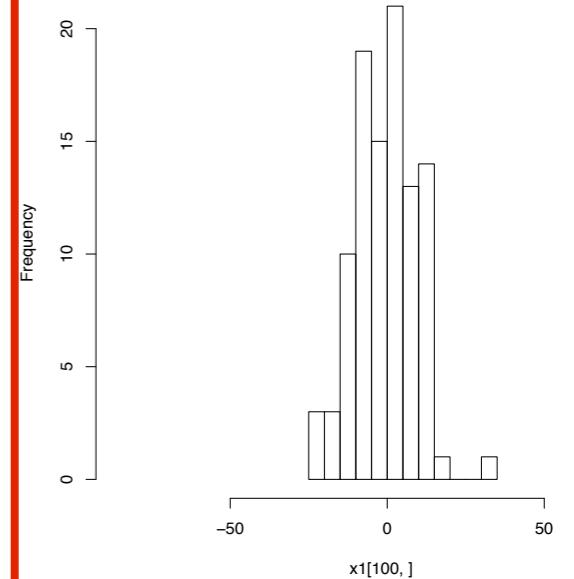




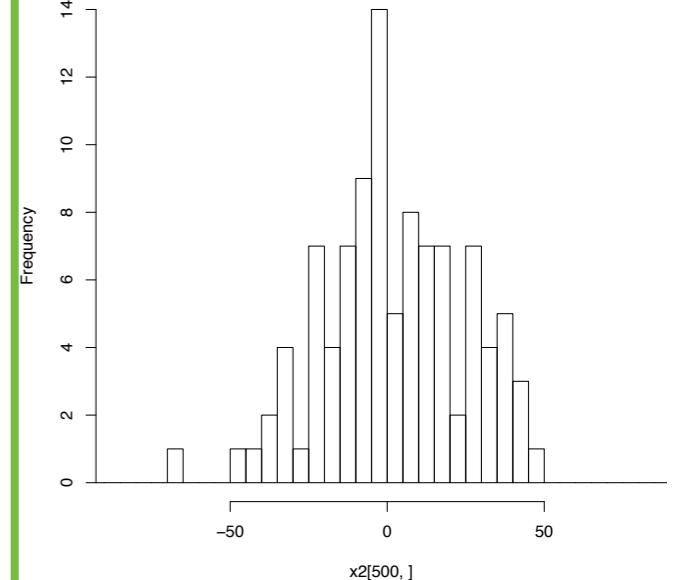




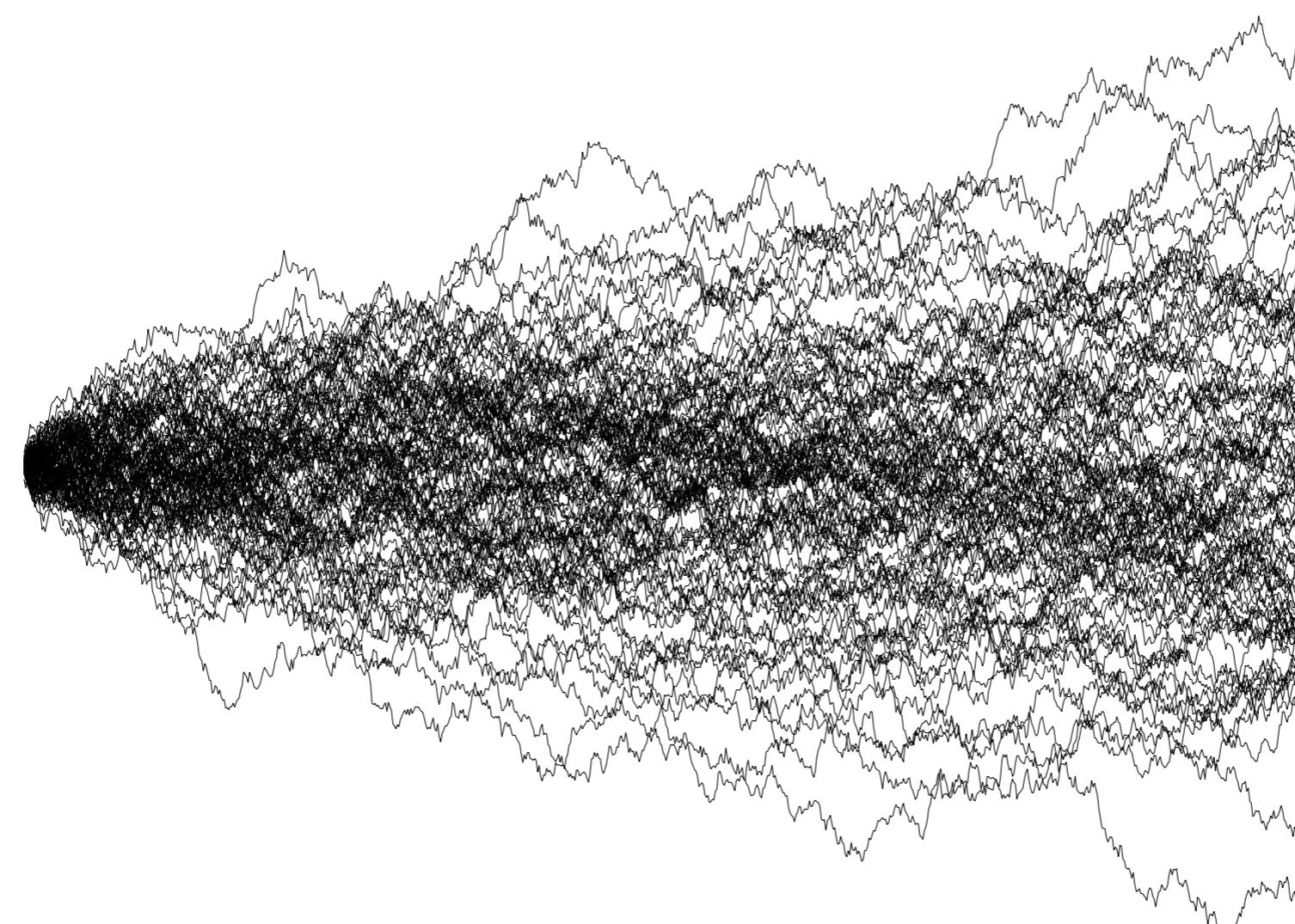
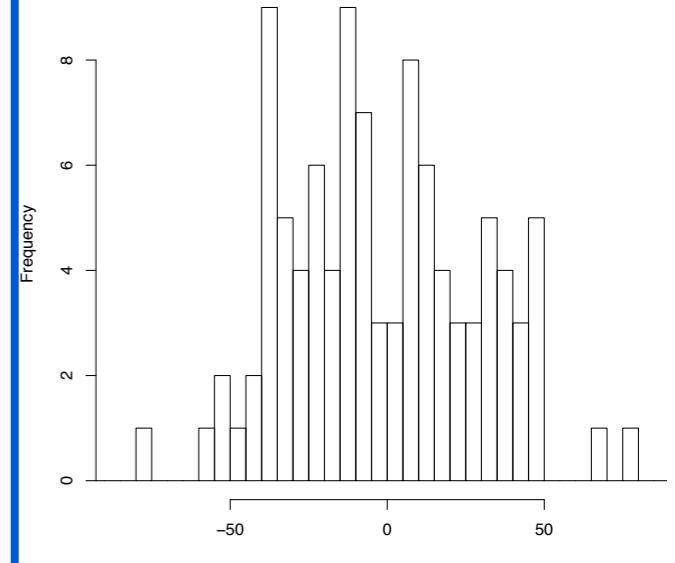
Histogram of  $x1[100, ]$



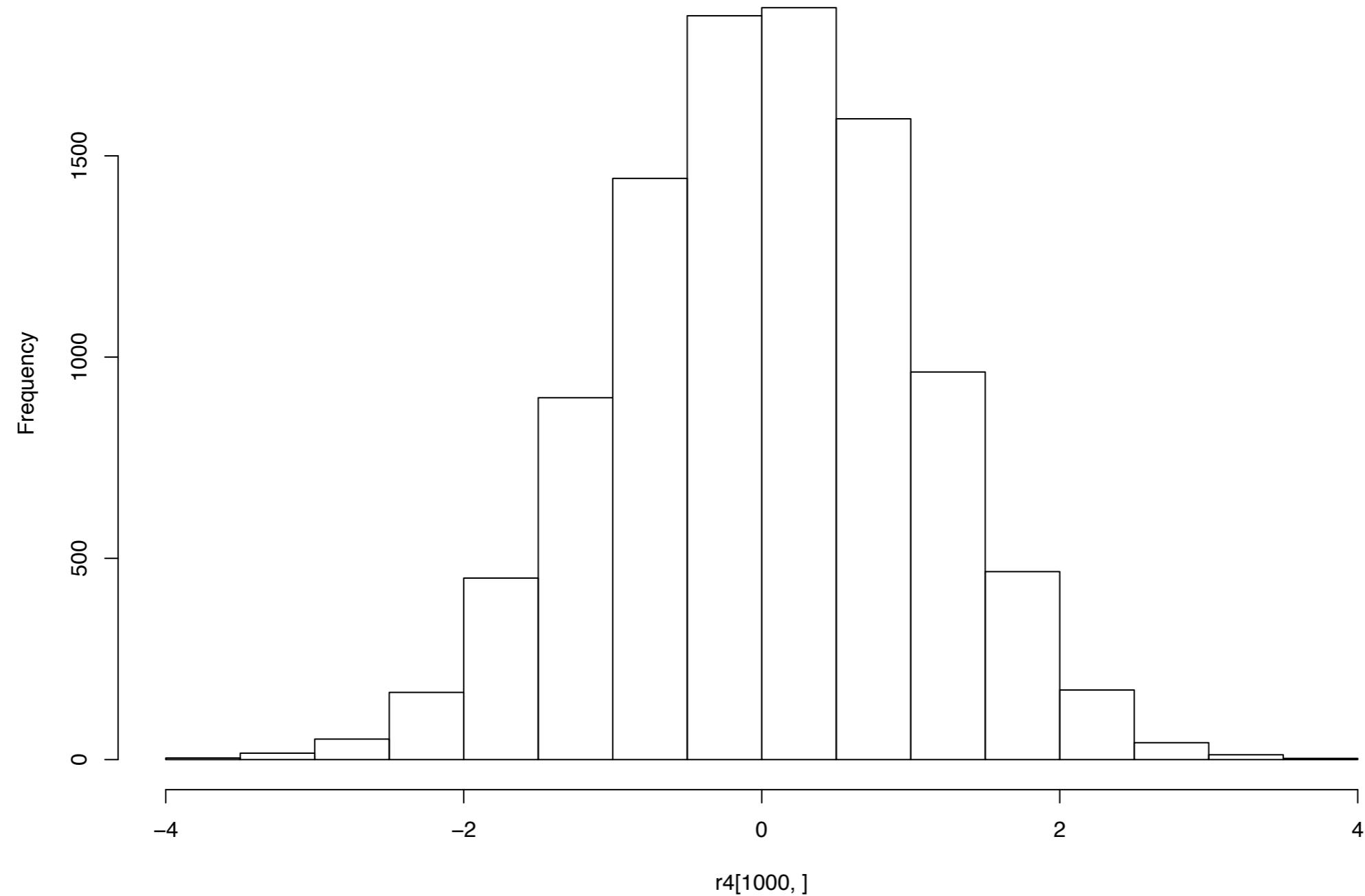
Histogram of  $x2[500, ]$

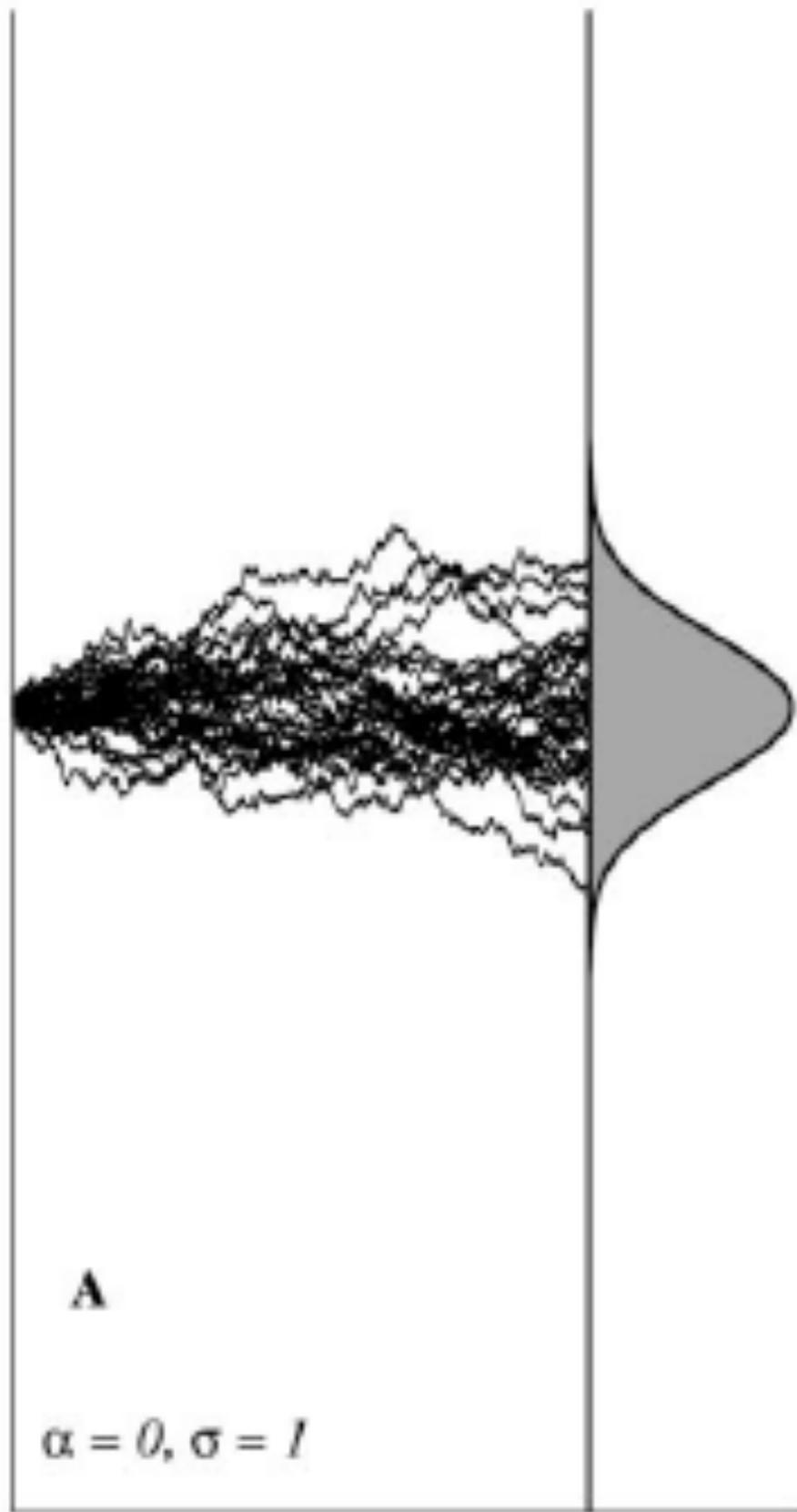


Histogram of  $x3[1000, ]$



**Histogram of r4[1000, ]**





**Why use this model  
for trait evolution?**

# Brownian Motion

- BM can be used to describe motion that results from the combination of a large number of independent weak forces
- Adding many small independent variables result in normal distributions, no matter the original distribution (Central limit theorem)

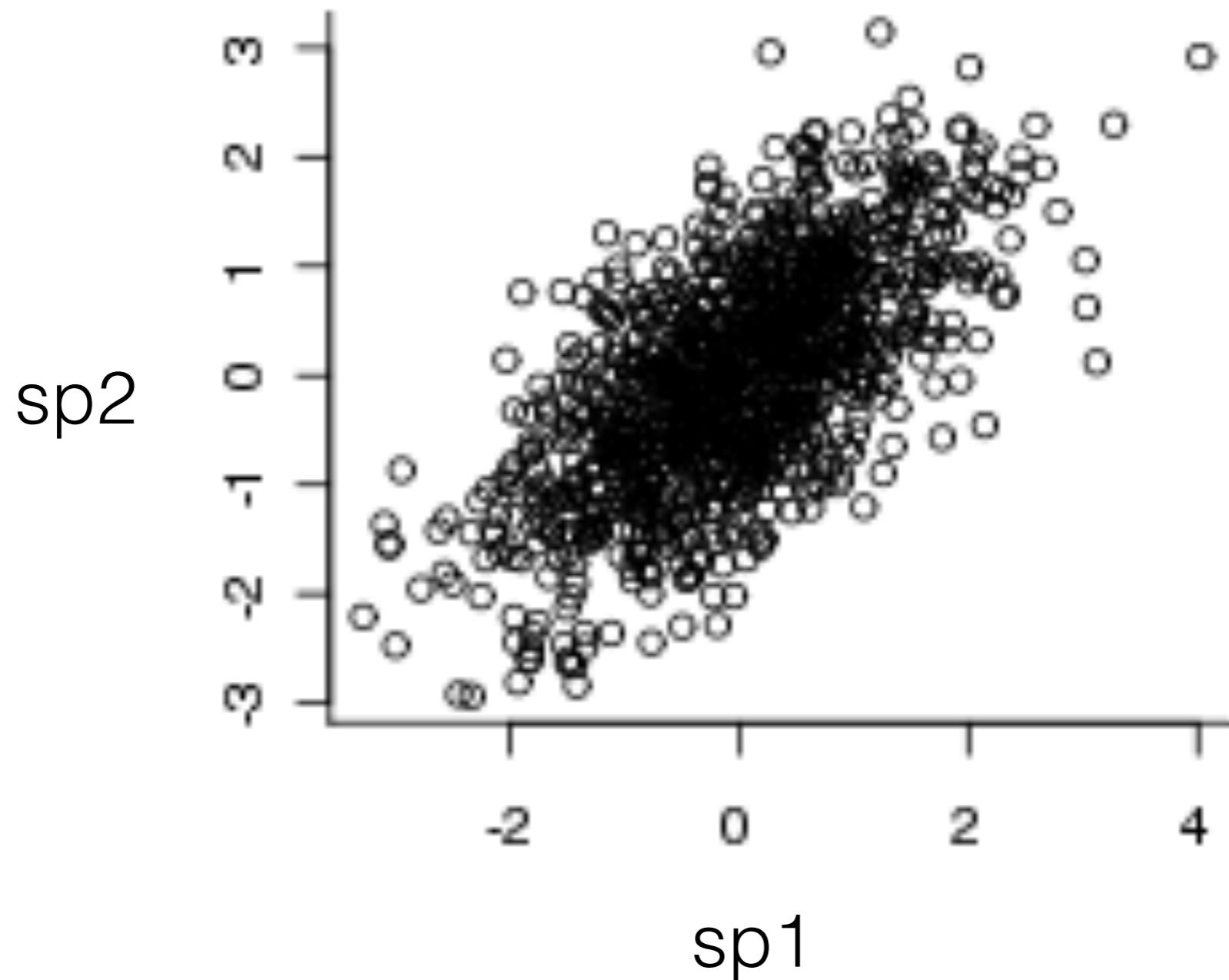
# Evolution might approximate BM...

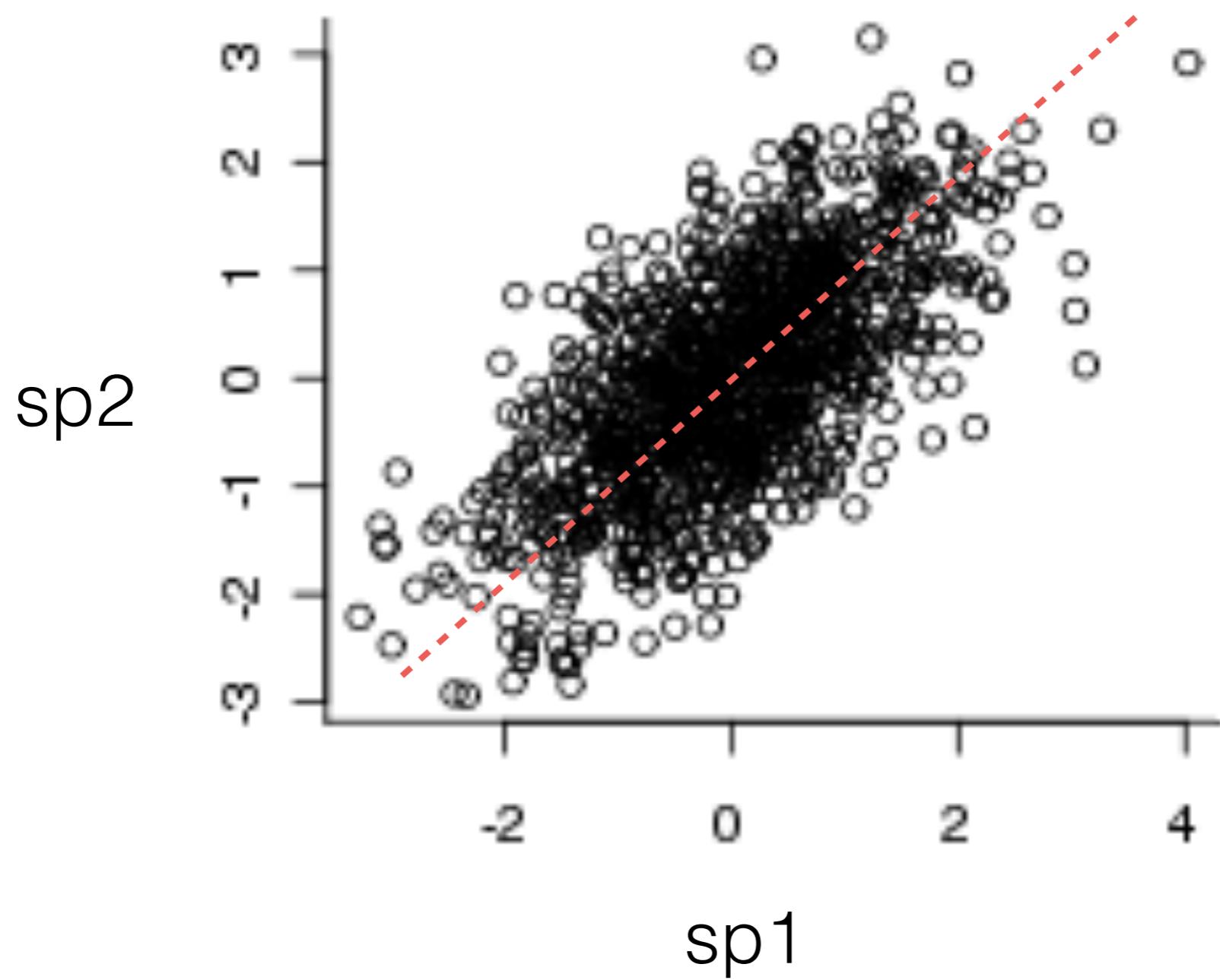
- Genetic drift
- Random punctuated change
- Selection that is weak relative to the time interval considered
- Selection that changes randomly through time

Why are close relatives similar  
to one another?

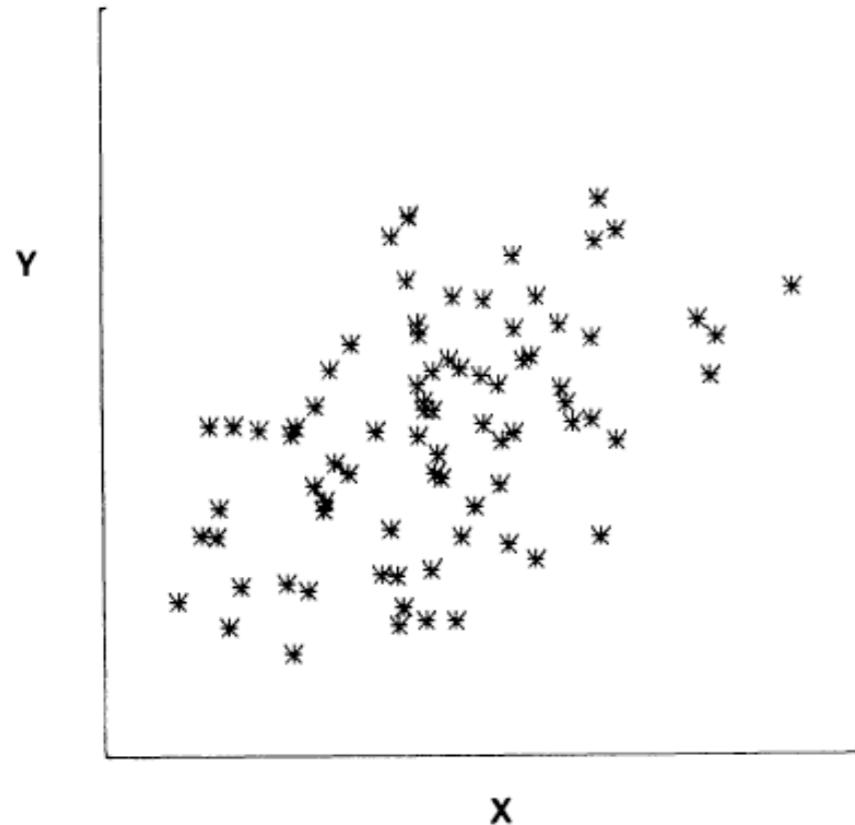
Species covary because they  
descend from a common ancestor

# Comparisons of traits between two species

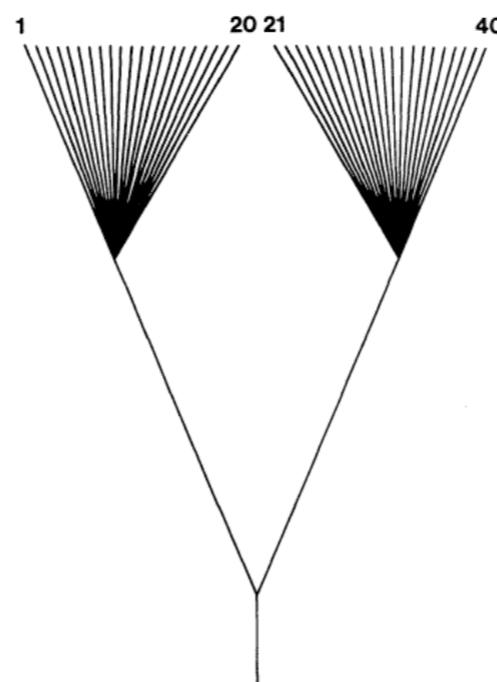
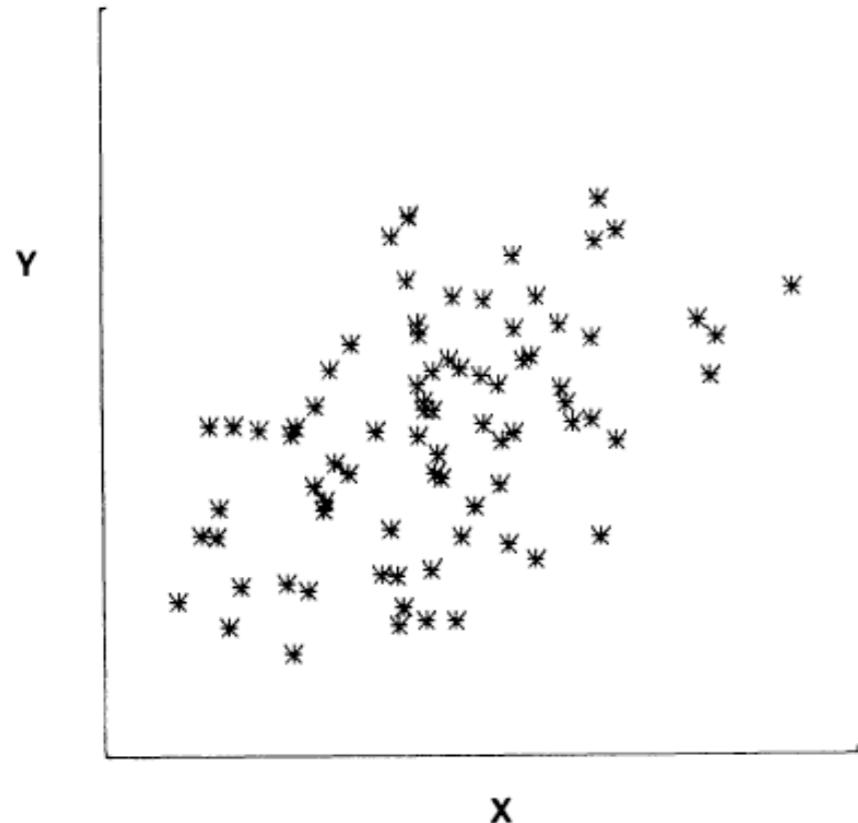




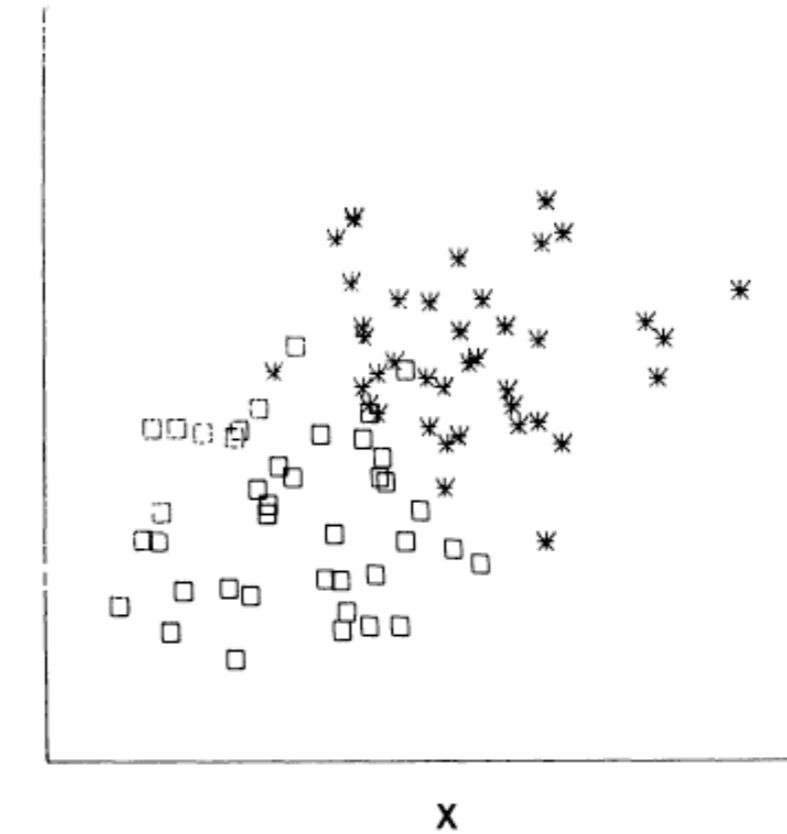
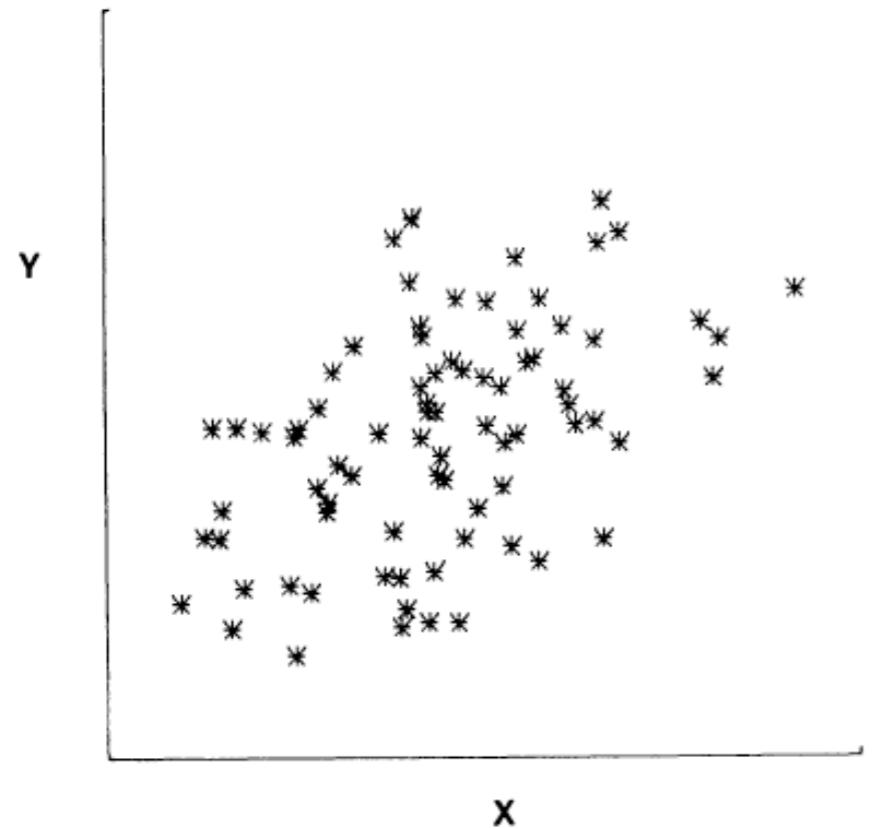
# Felsenstein’s “Worst Case”



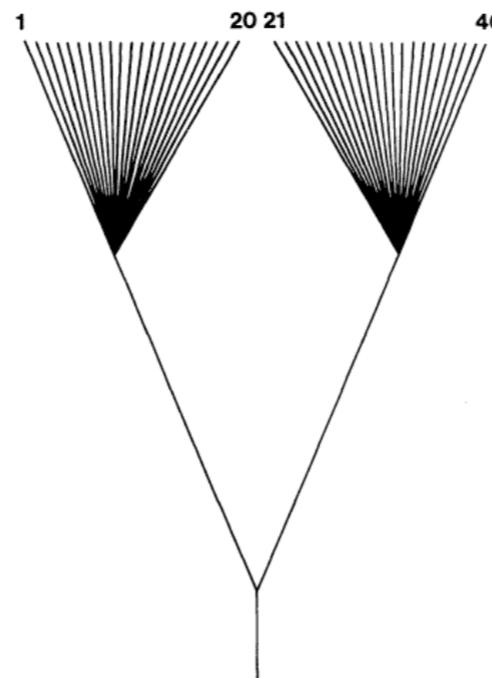
# Felsenstein's “Worst Case”



# Felsenstein's “Worst Case”

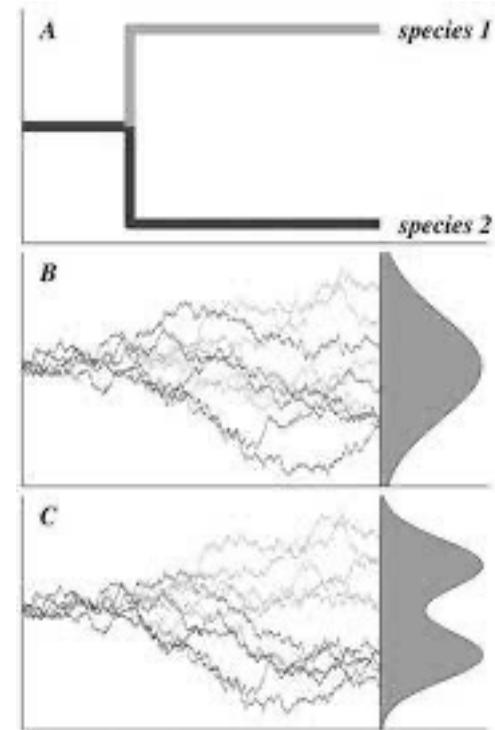


If we don't account  
for relatedness

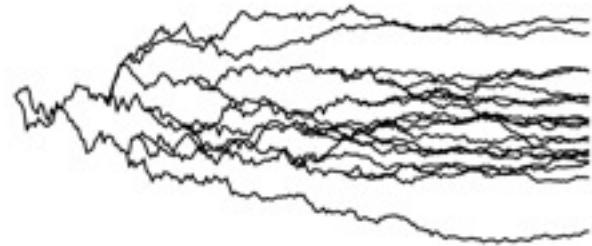


# Extensions of Brownian motion models

- Ornstein Uhlenbeck (OU) model
  - stabilizing selection in which the trait is drawn towards a fitness optimum
    - Each species might have different optimum
- Early Burst model
  - Time varying model where after split variance is higher

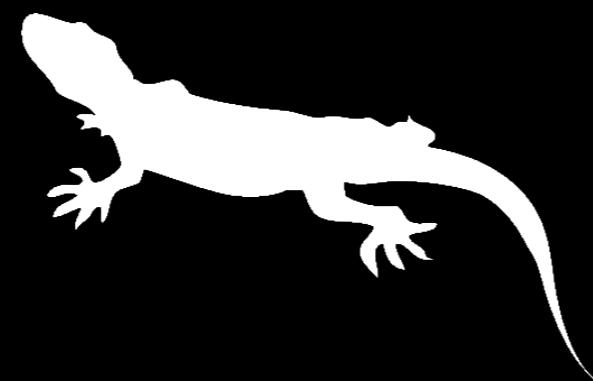


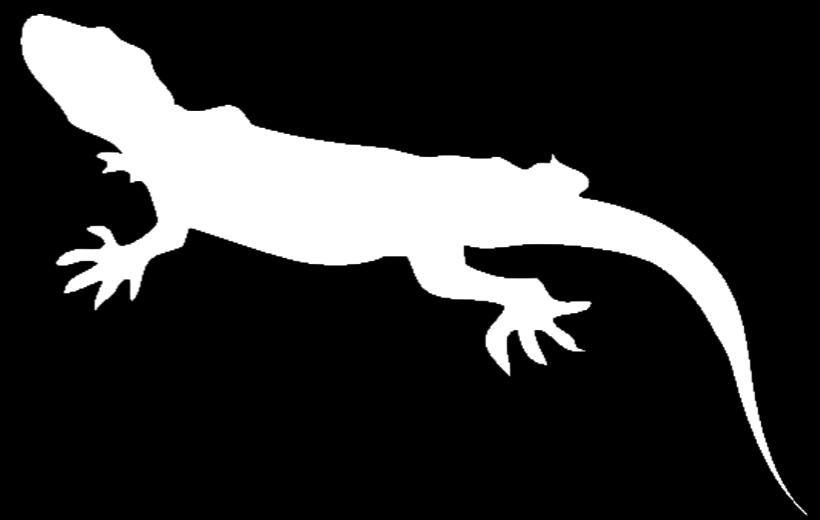
Early Burst

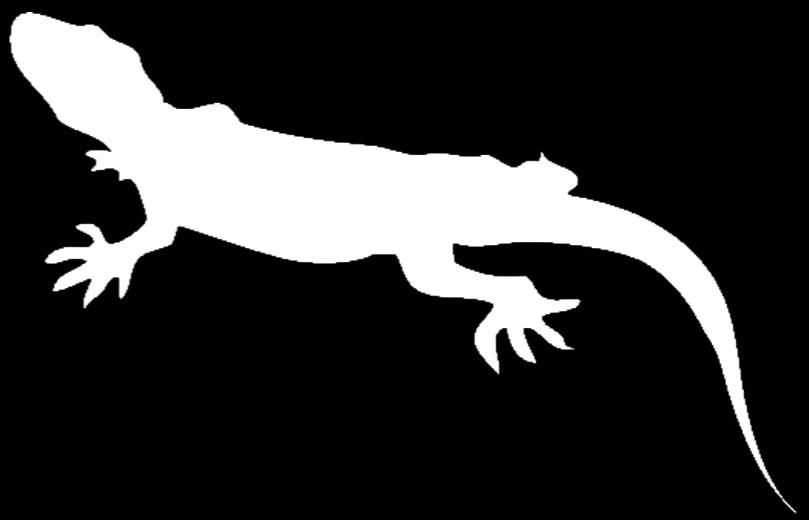


# Evolution of discrete characters

How do we model the process  
by which squamates  
(snakes and lizards)  
lose their limbs?







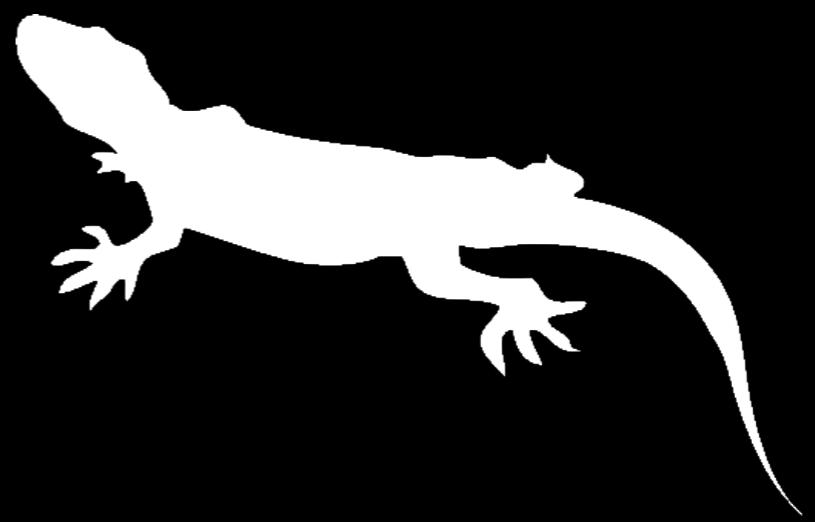
No limbs

State 0



No limbs

State 0



Limbs

State 1

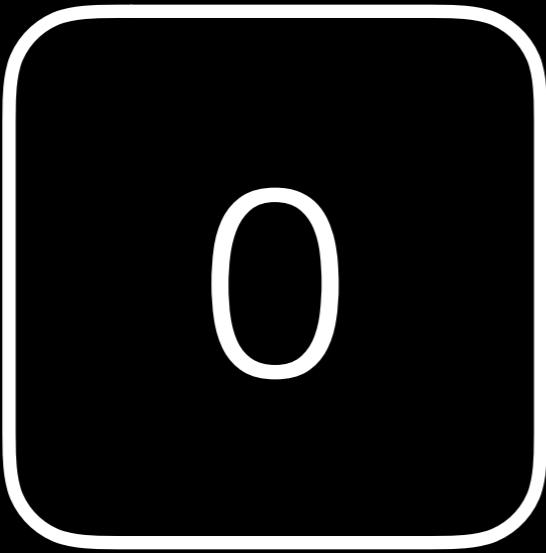
The Mk model

The Mk model

*“Markov k-state”*

0

1



0

no limbs

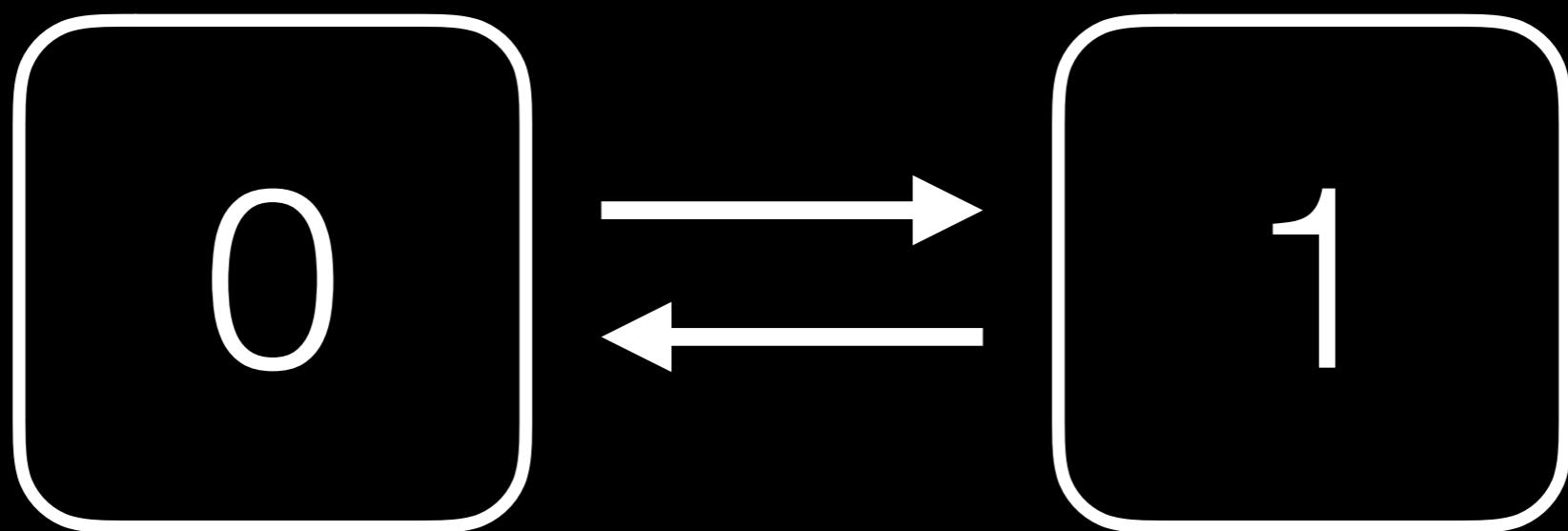


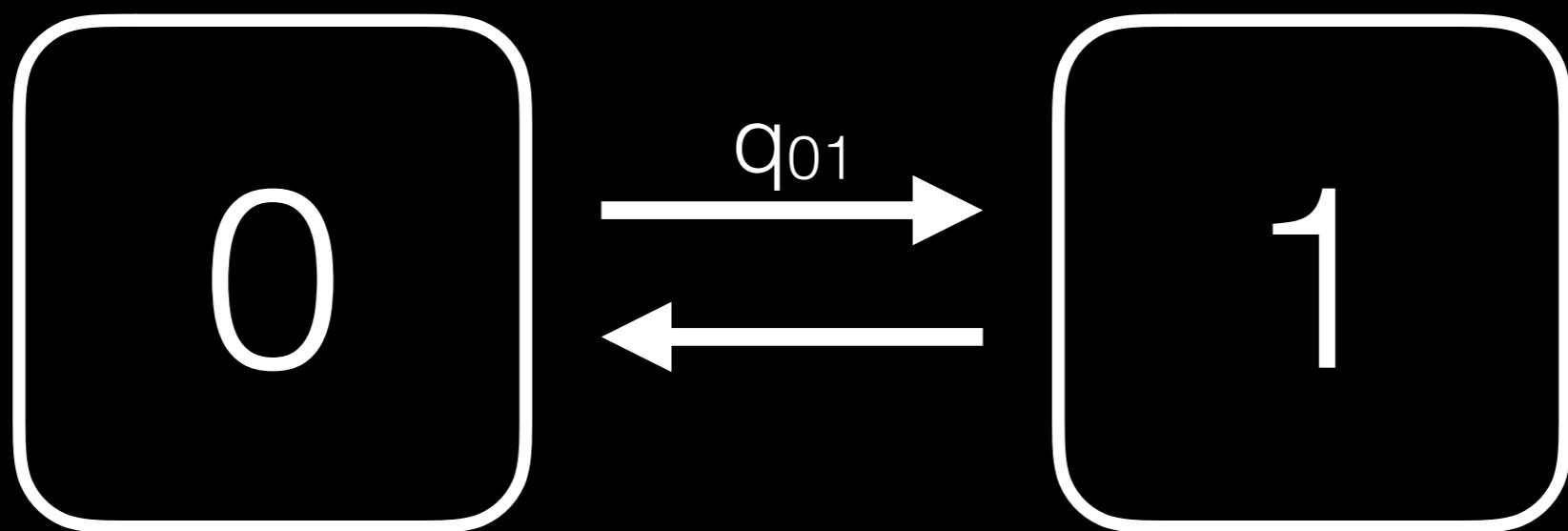
1

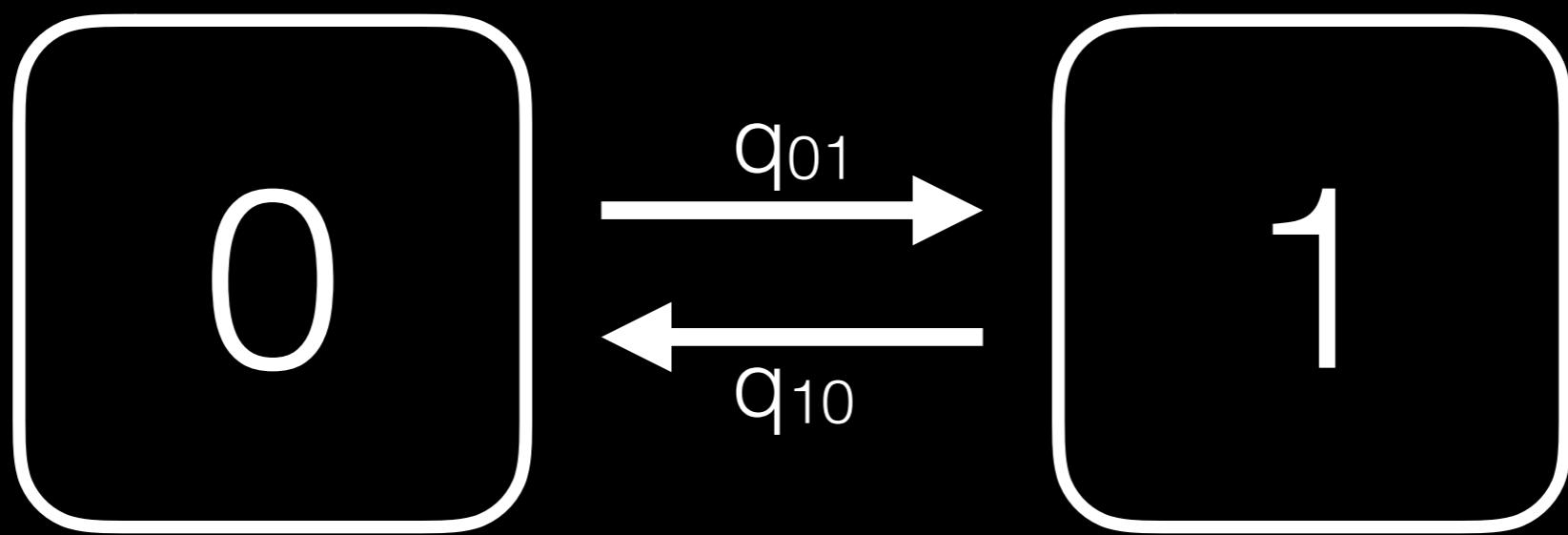
limbs

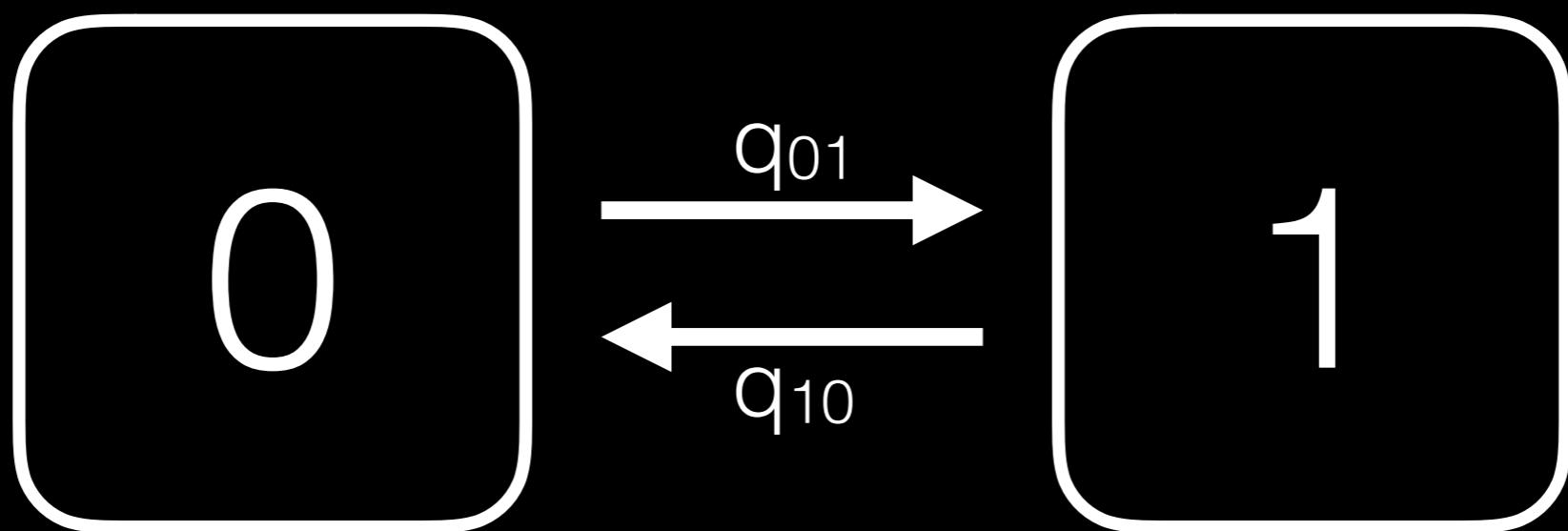
0

1









$q_{01}$  = instantaneous rate of change from 0 to 1

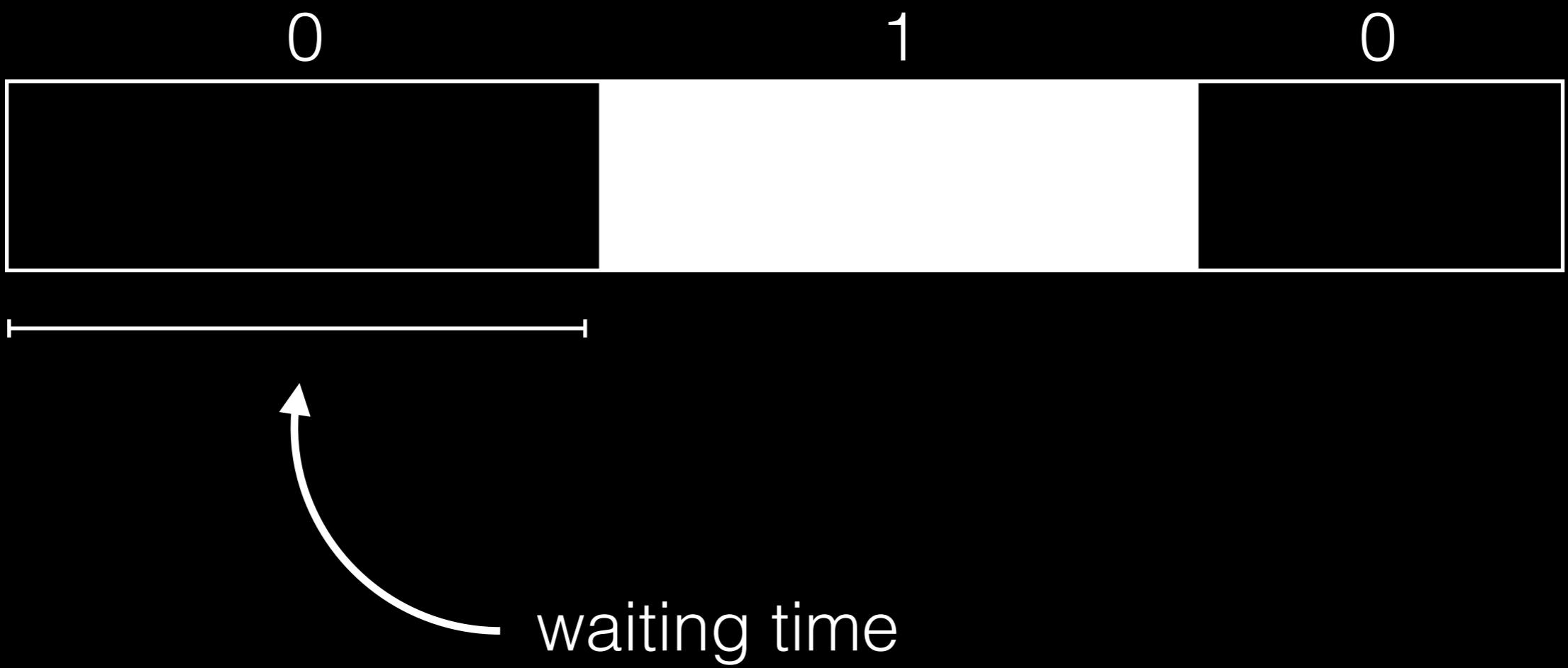


0

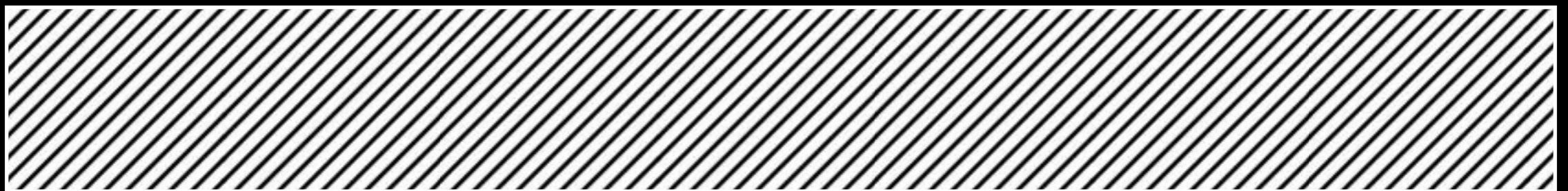
1



0



1



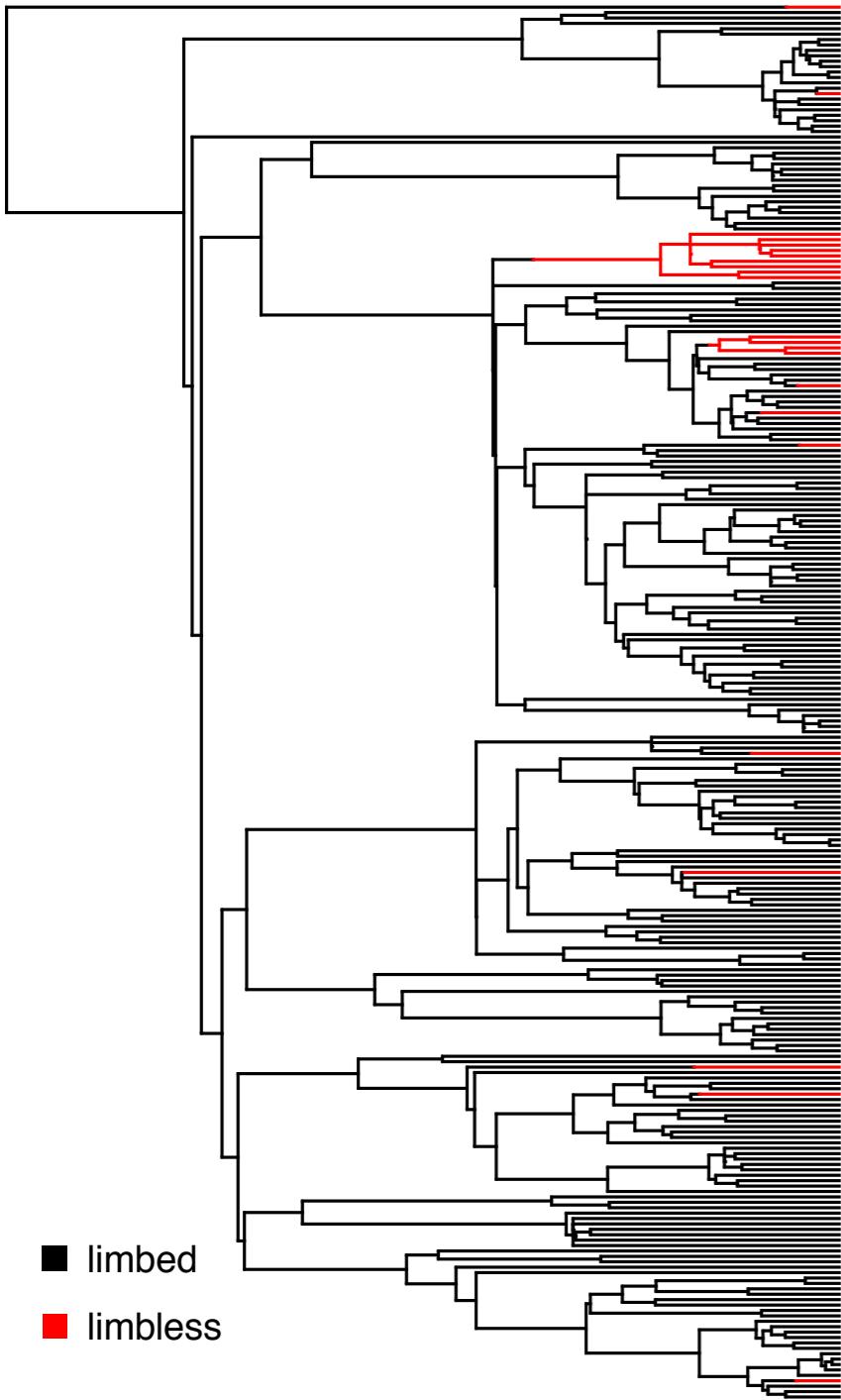
t

?

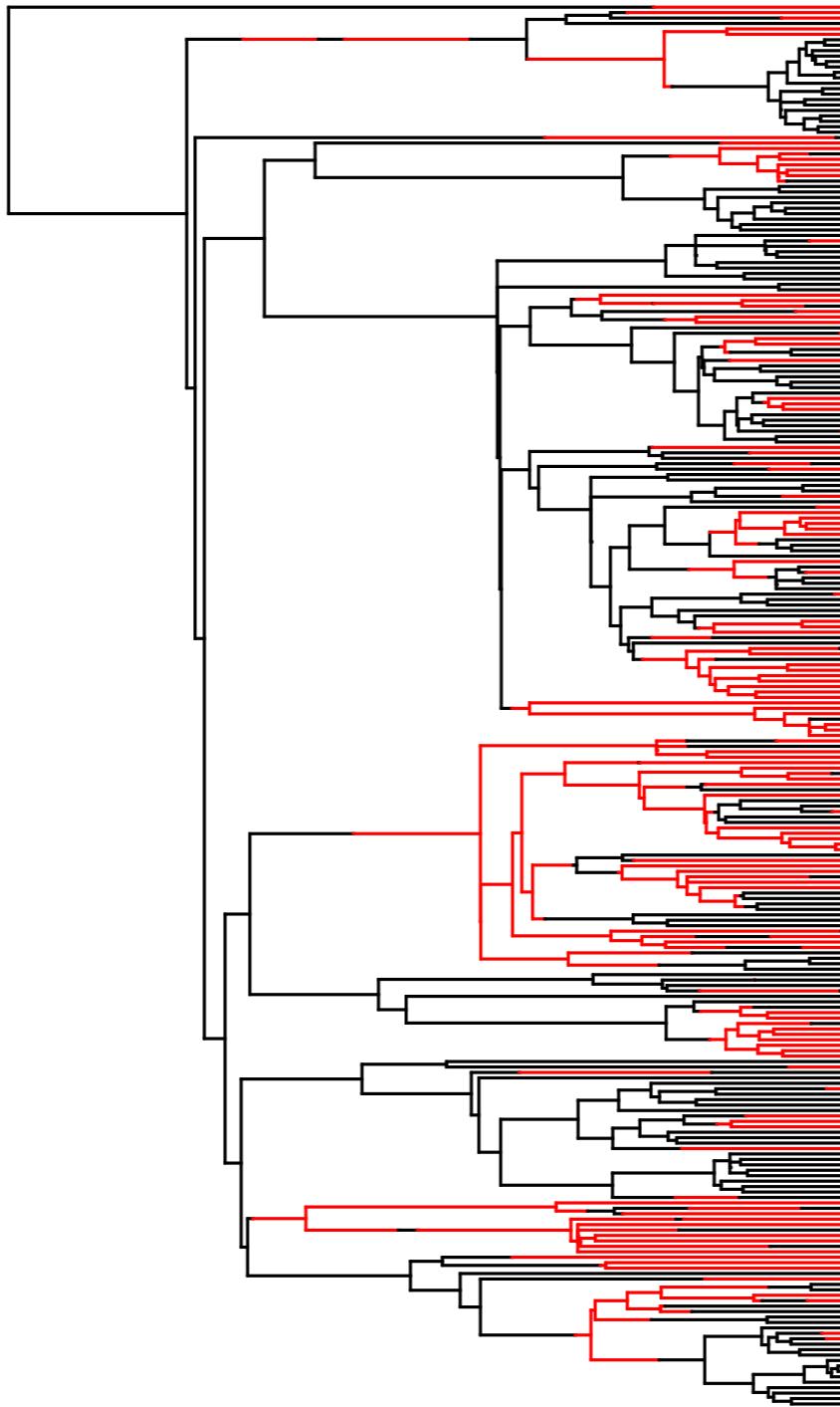
$$Q = \begin{bmatrix} -q_{01} & q_{01} \\ q_{10} & -q_{10} \end{bmatrix}$$

*The instantaneous rate matrix*

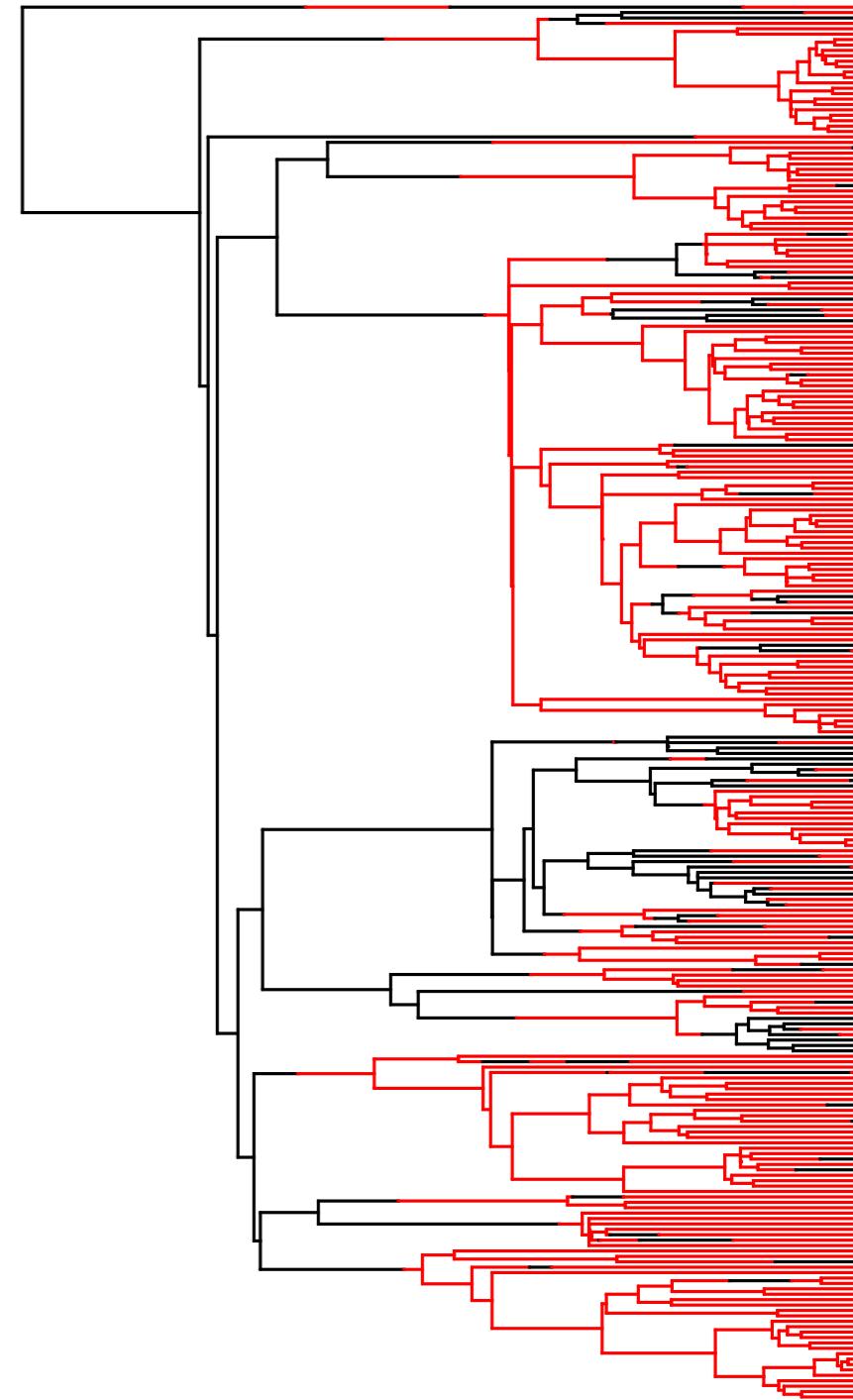
Equal rates (slow)

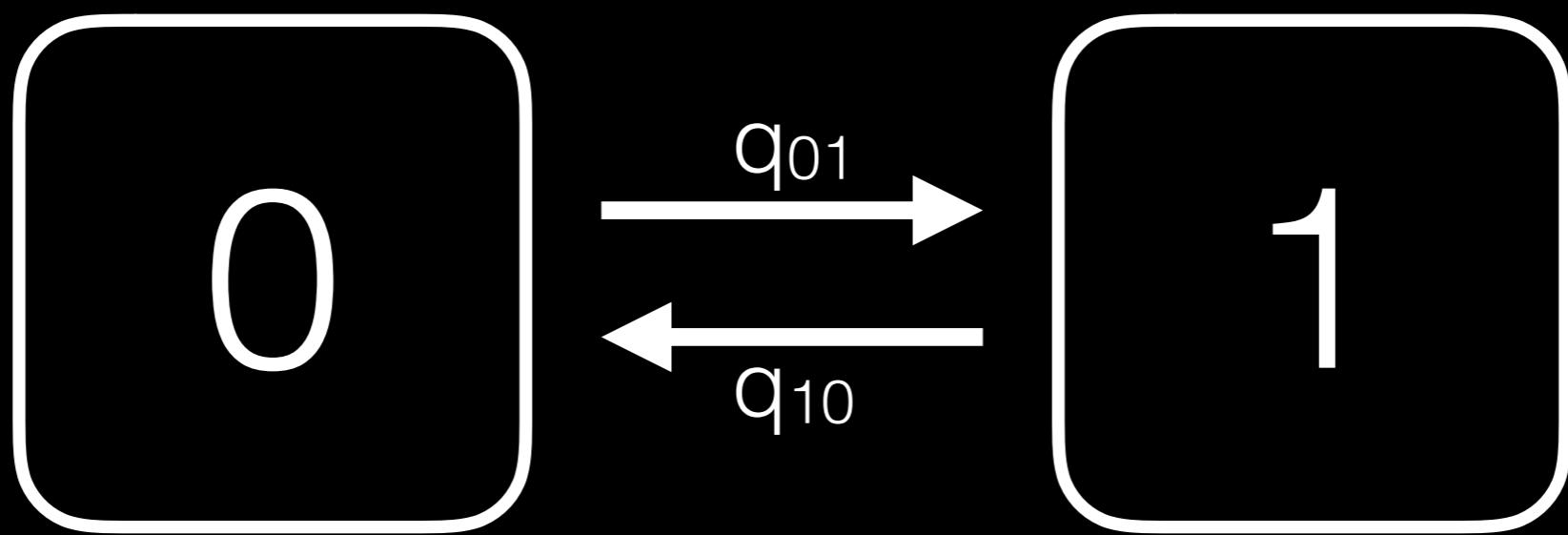


Equal rates (fast)



Unequal rates



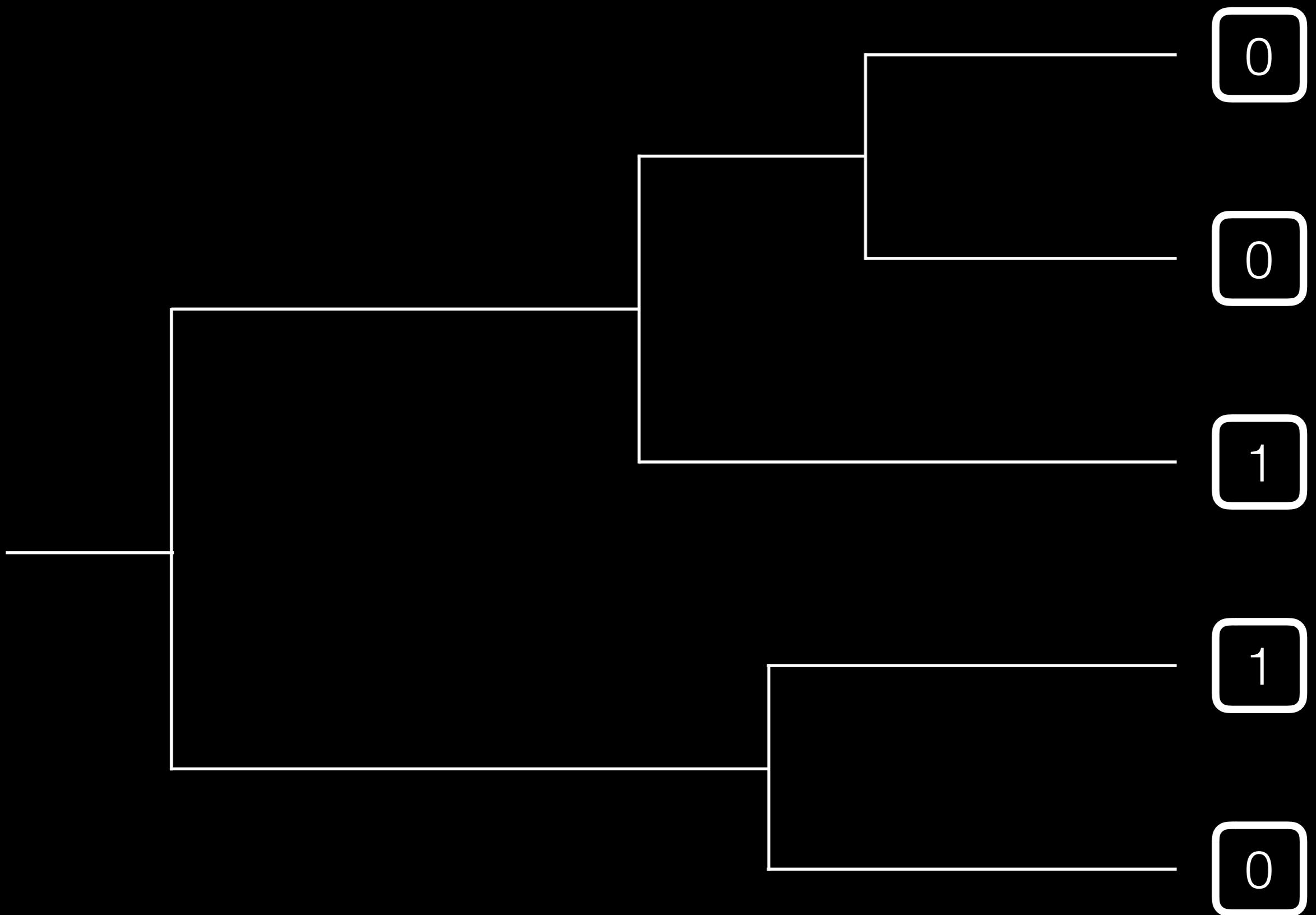


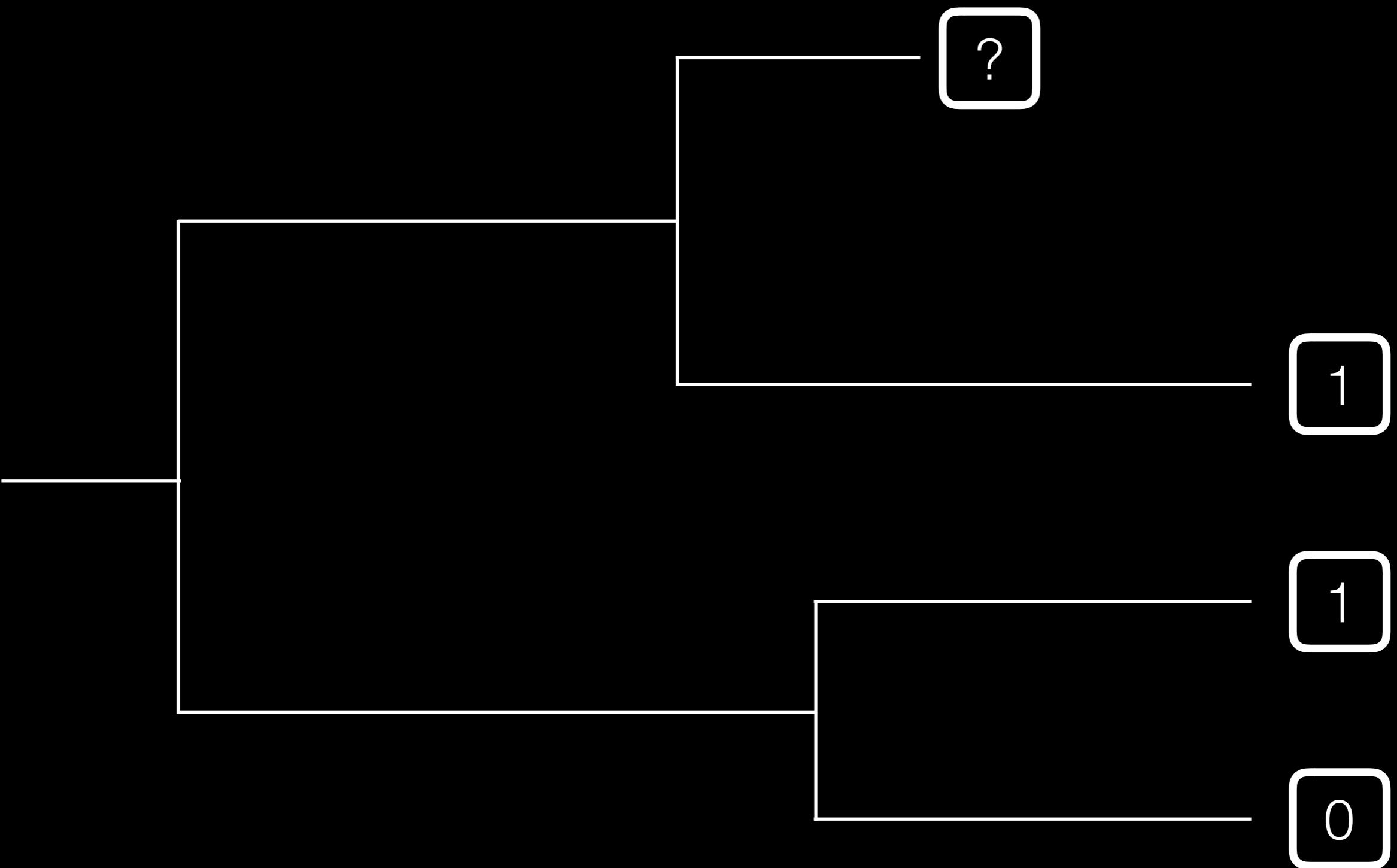
We can calculate the likelihood of the data  
given the model and tree  
using a **pruning algorithm**

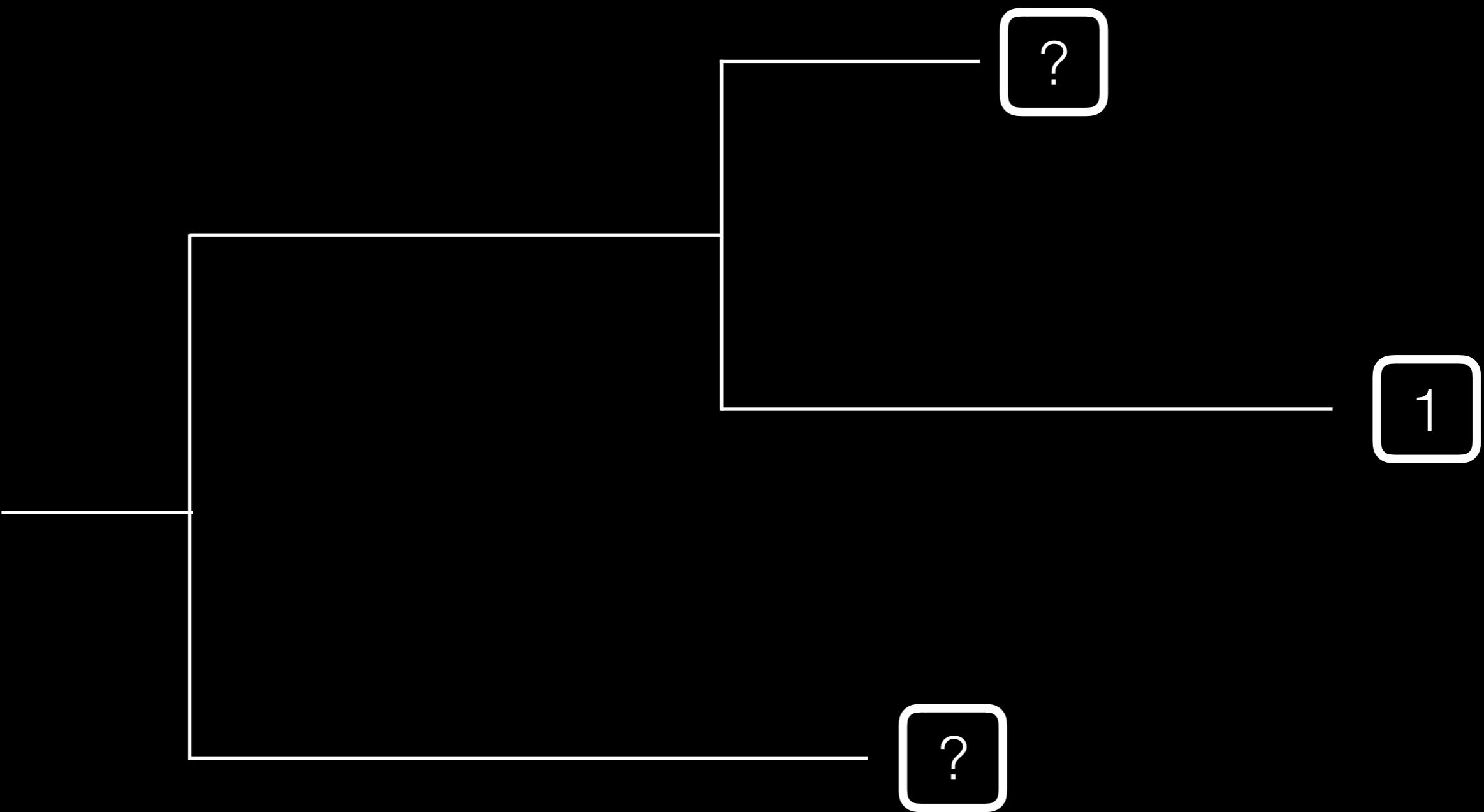
Data = Character states

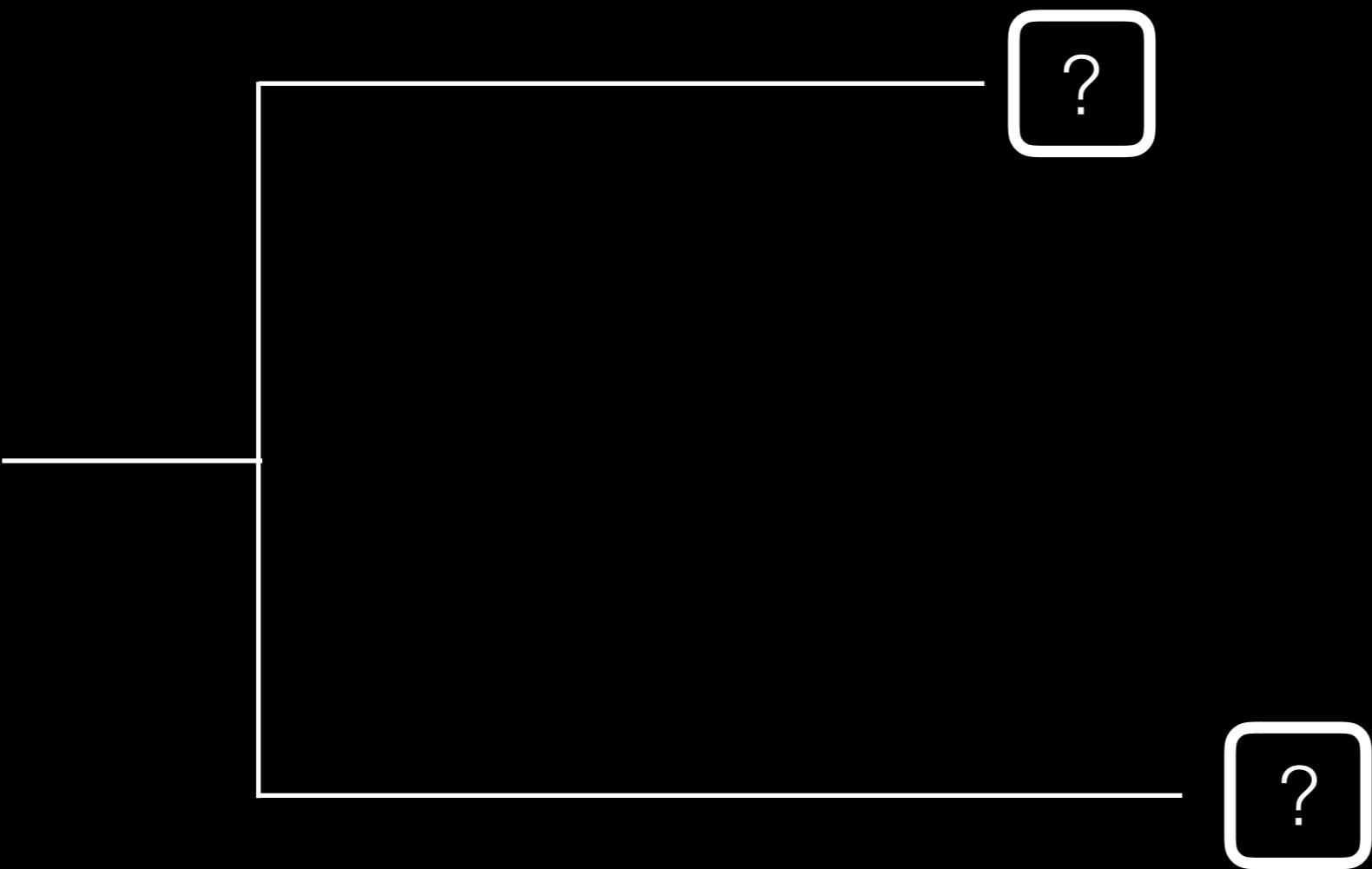
Model = Markov model

Tree = Inferred phylogenetic tree

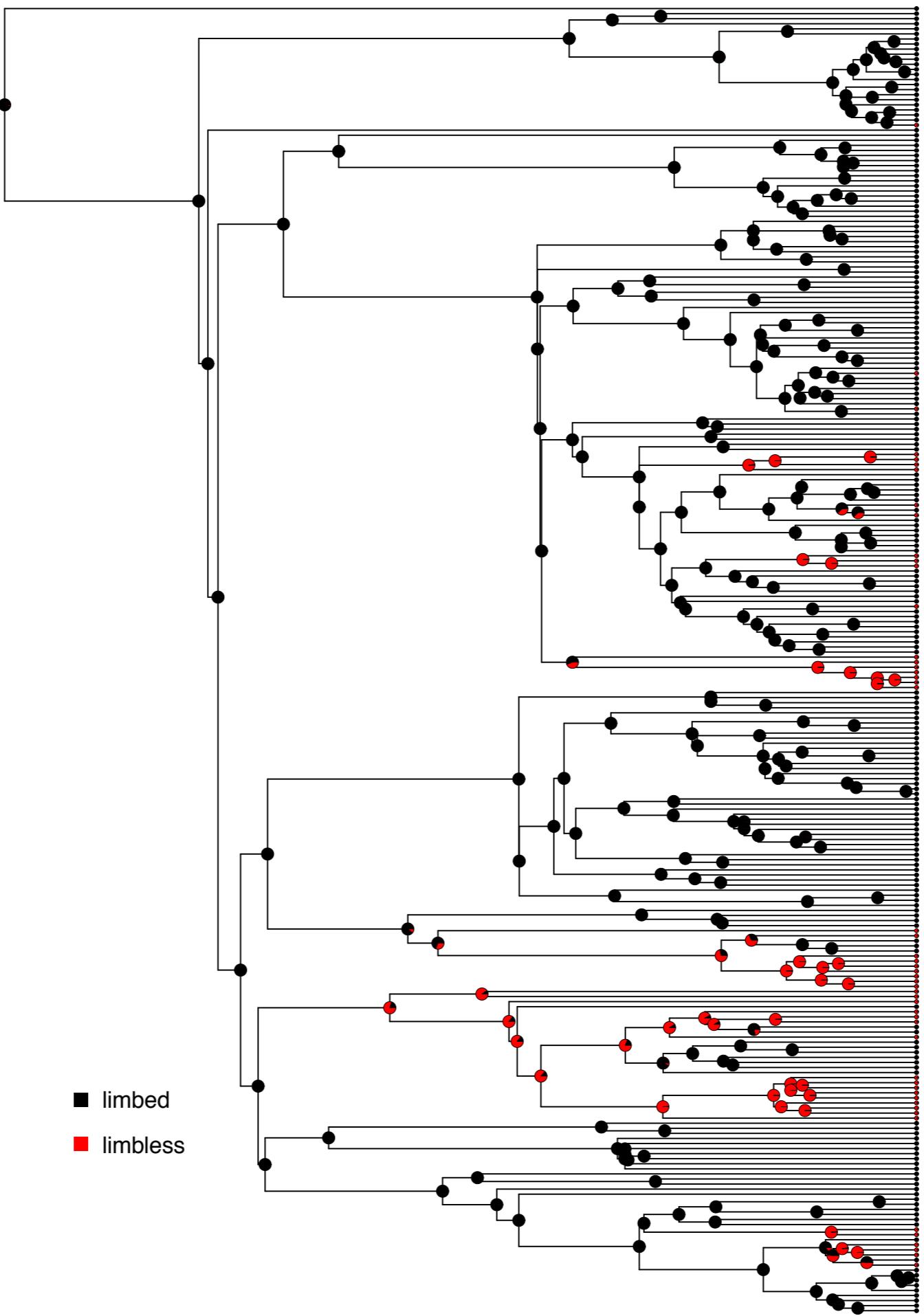










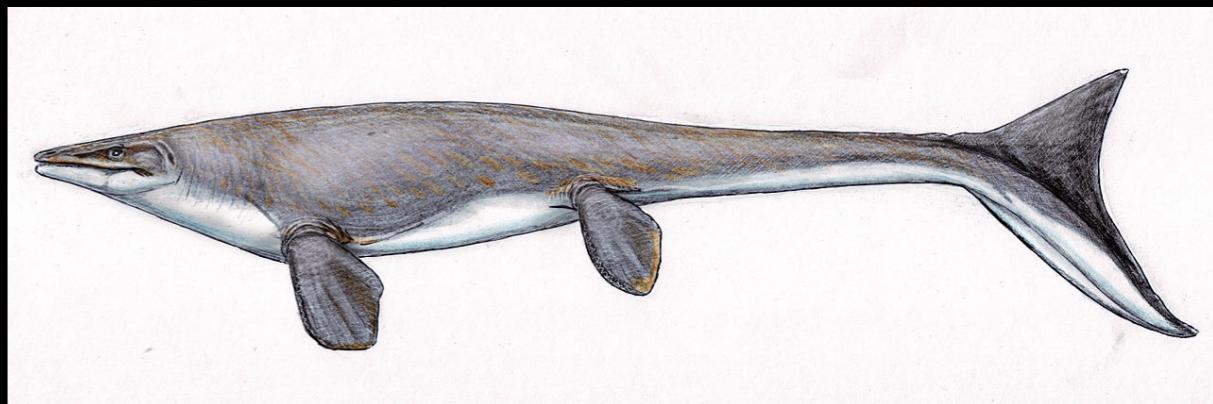
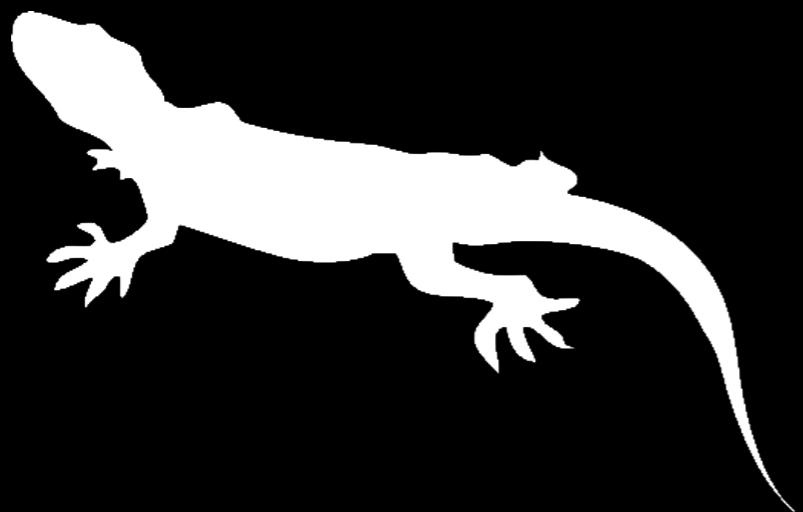


We can also fit a model with more character states



Front limbs only

State 1





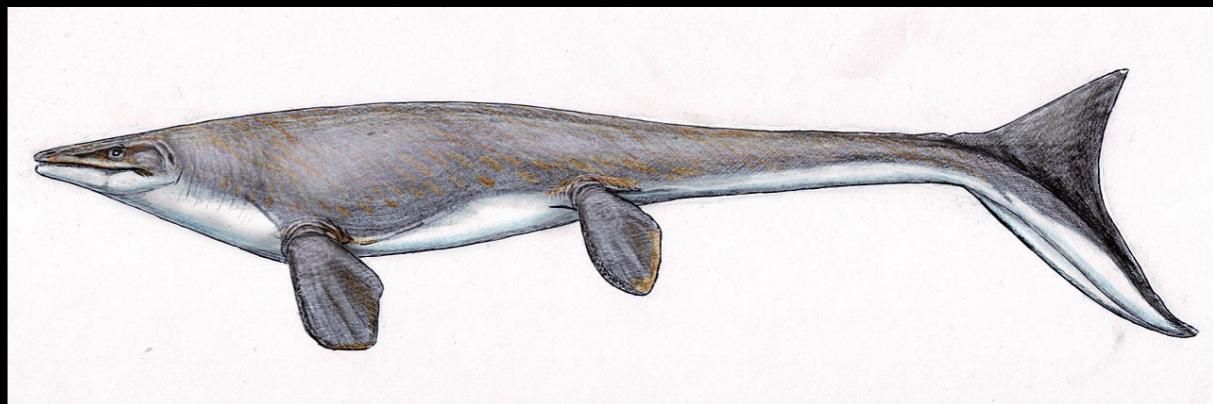
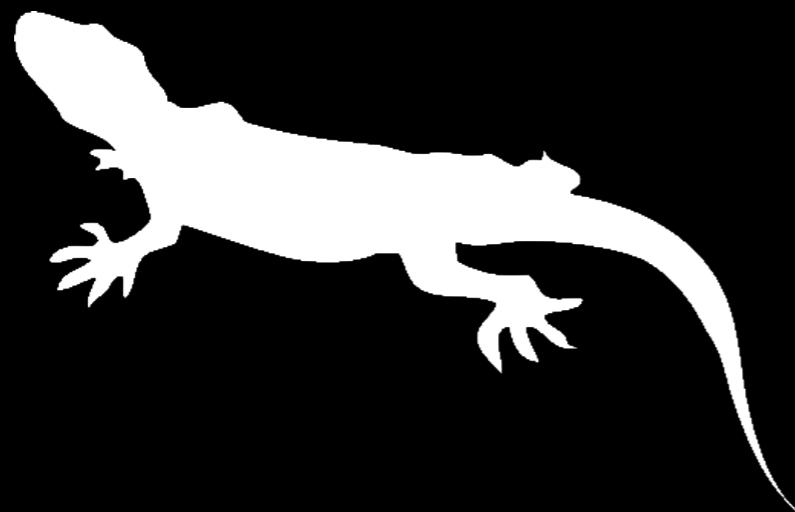
No limbs

State 0



Front limbs only

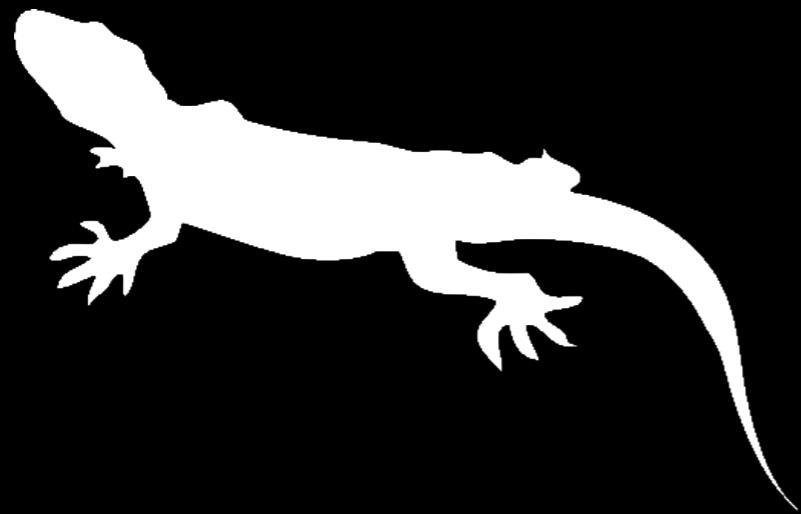
State 1





No limbs

State 0



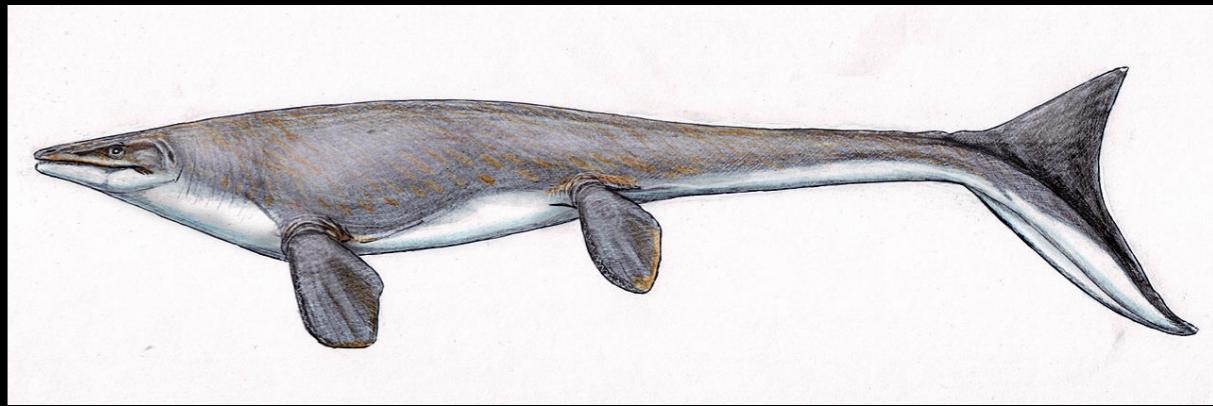
Limbs

State 2



Front limbs only

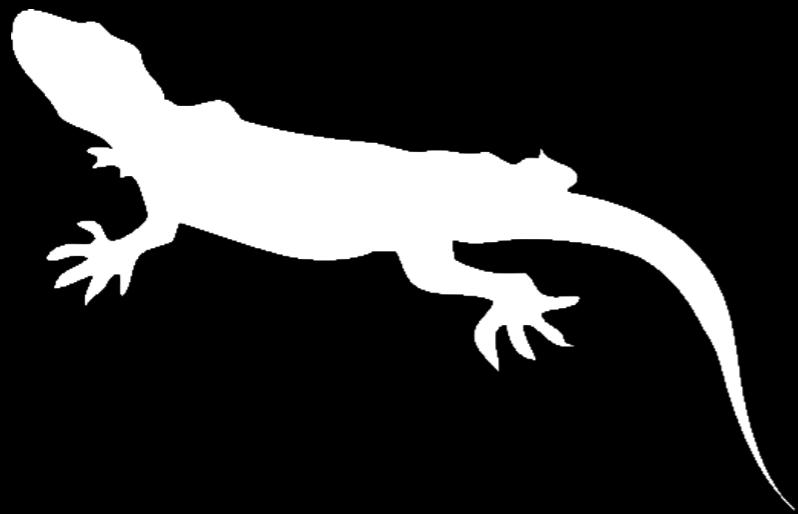
State 1





No limbs

State 0



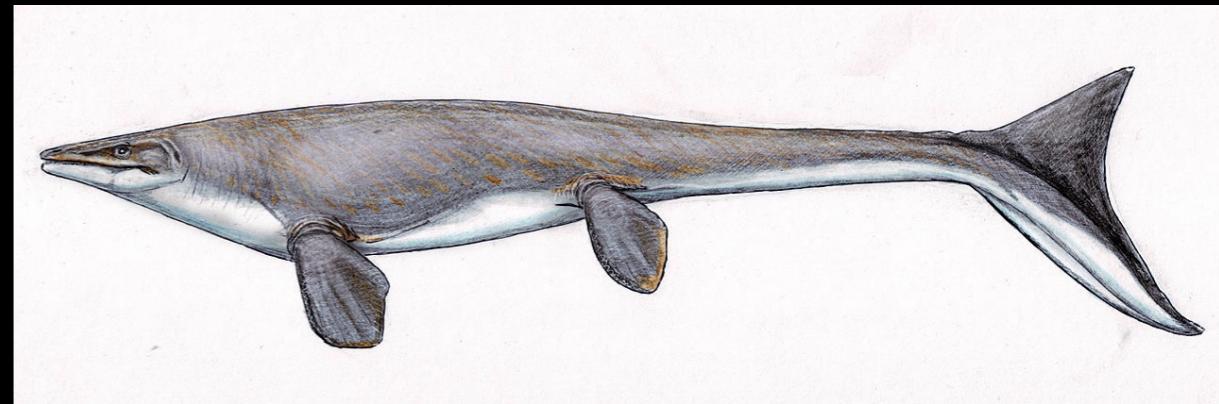
Limbs

State 2



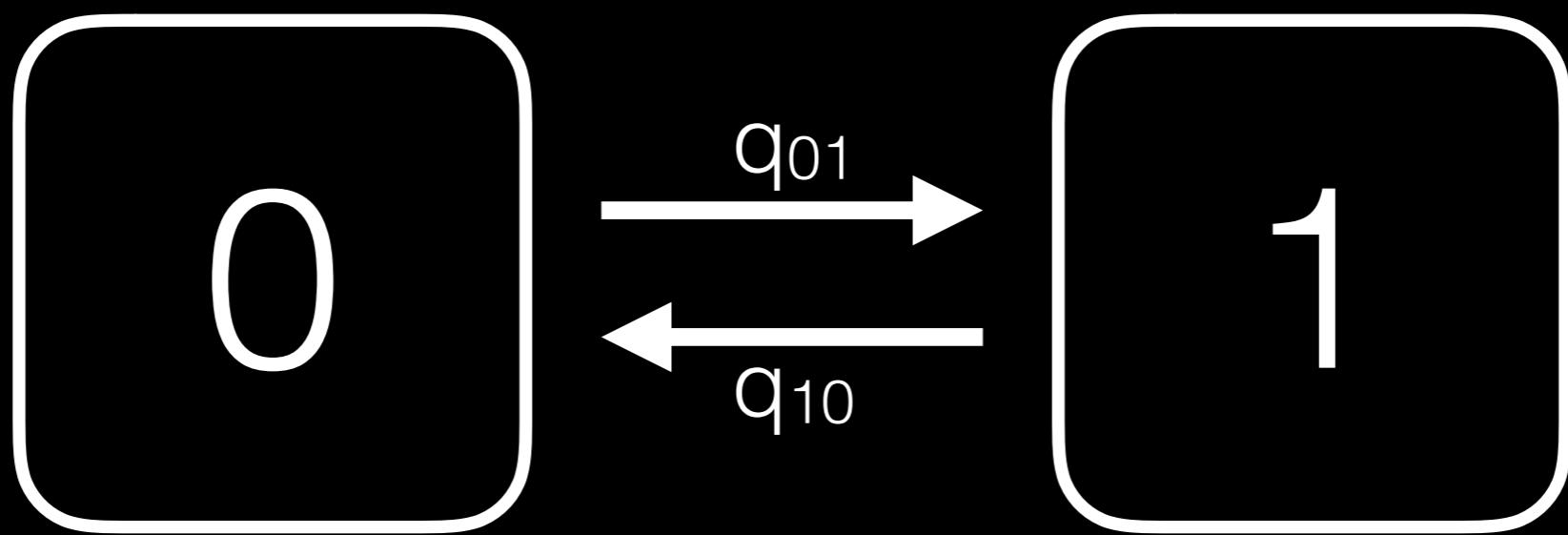
Front limbs only

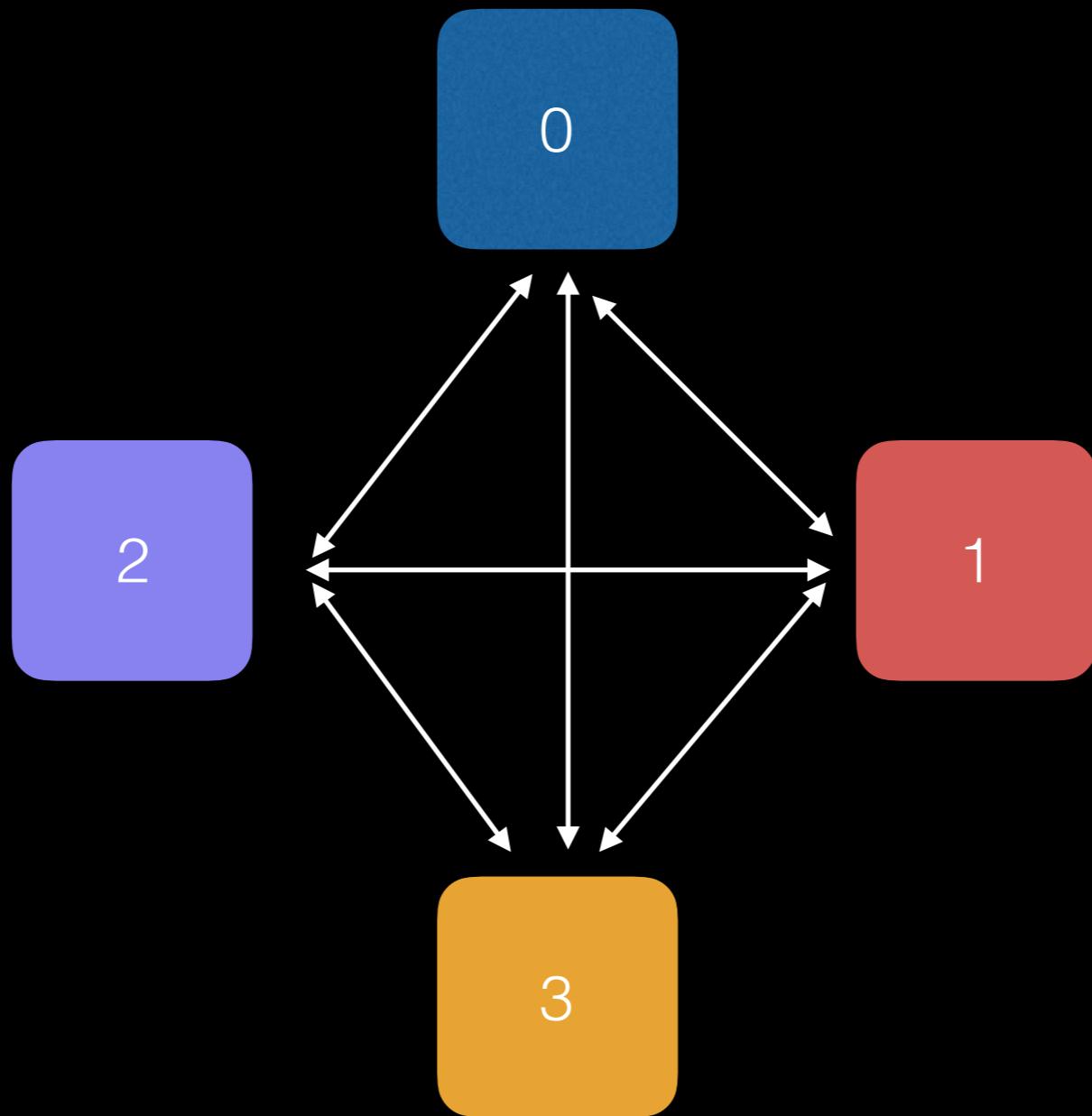
State 1



“Fins”

State 3





We can use the Mk model to test a wide variety of evolutionary hypotheses about discrete characters