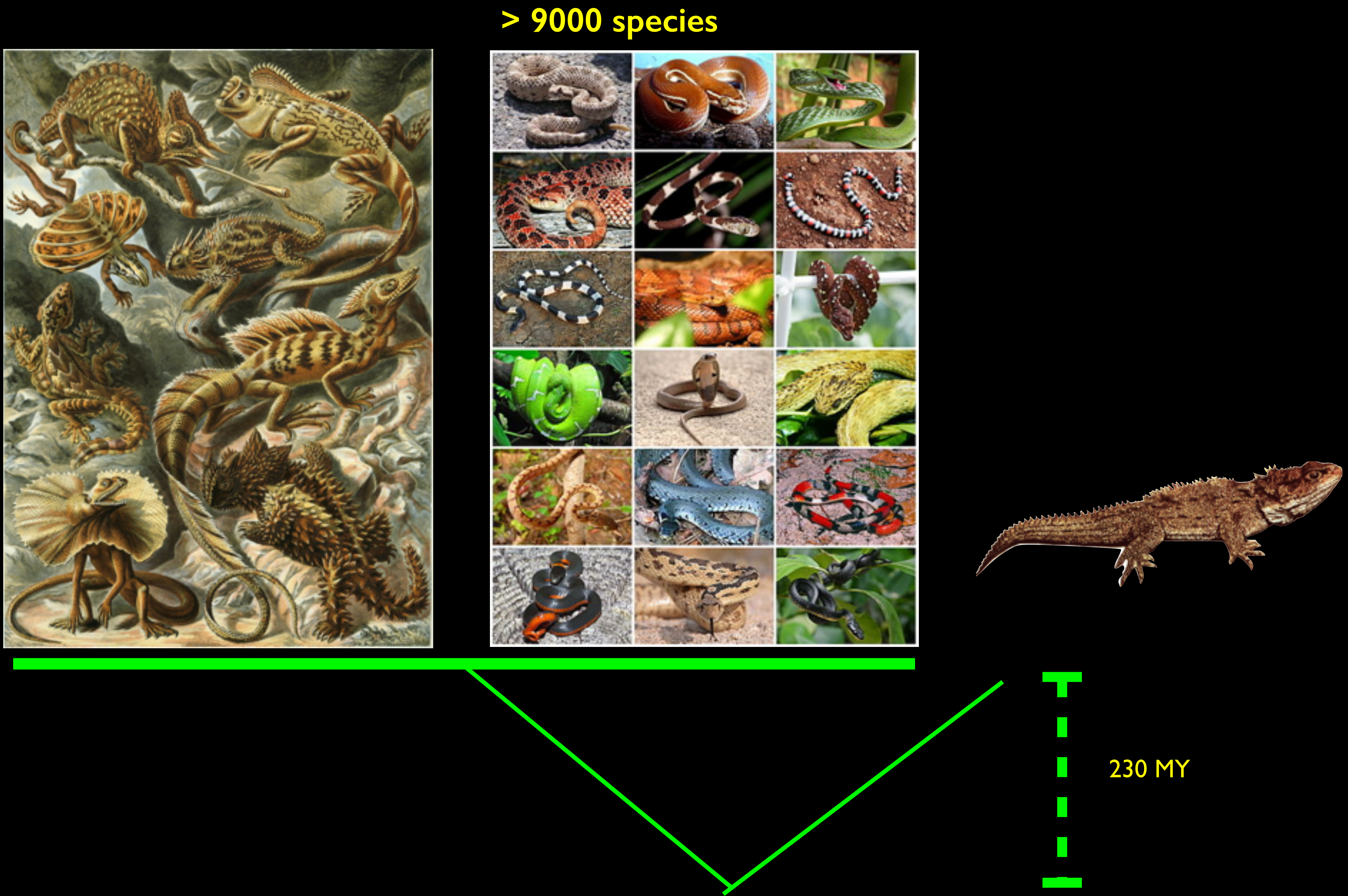
Diversification models

THE FUNDAMENTAL PATTERN OF BIODIVERSITY: UNEVENNESS




TUATARA
Y U NO SPECIATE
imgflip.com

ECOLOGICAL ADAPTIVE RADIATION THEORY

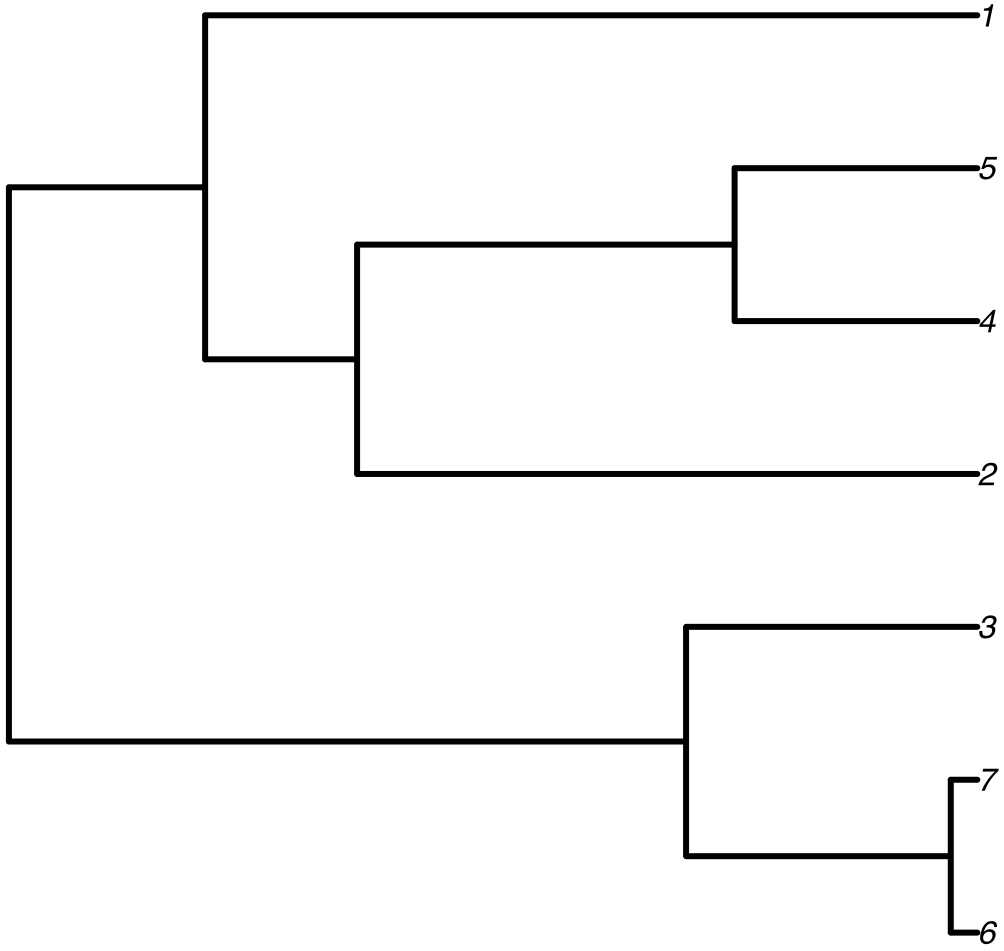
- innovation + ecological opportunity = rapid diversification

- ++speciation & ++disparification

Schluter 2000

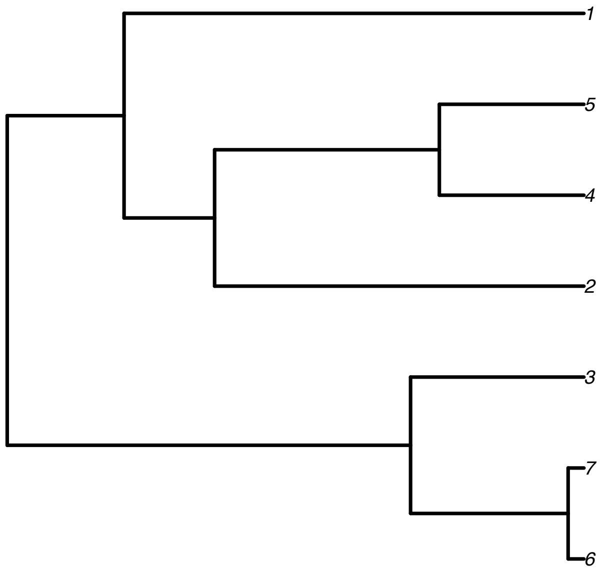
Pure Birth model

- each lineage has a constant probability of speciating, b
- b = birth rate
- $N(t) = N(0)e^{bt}$

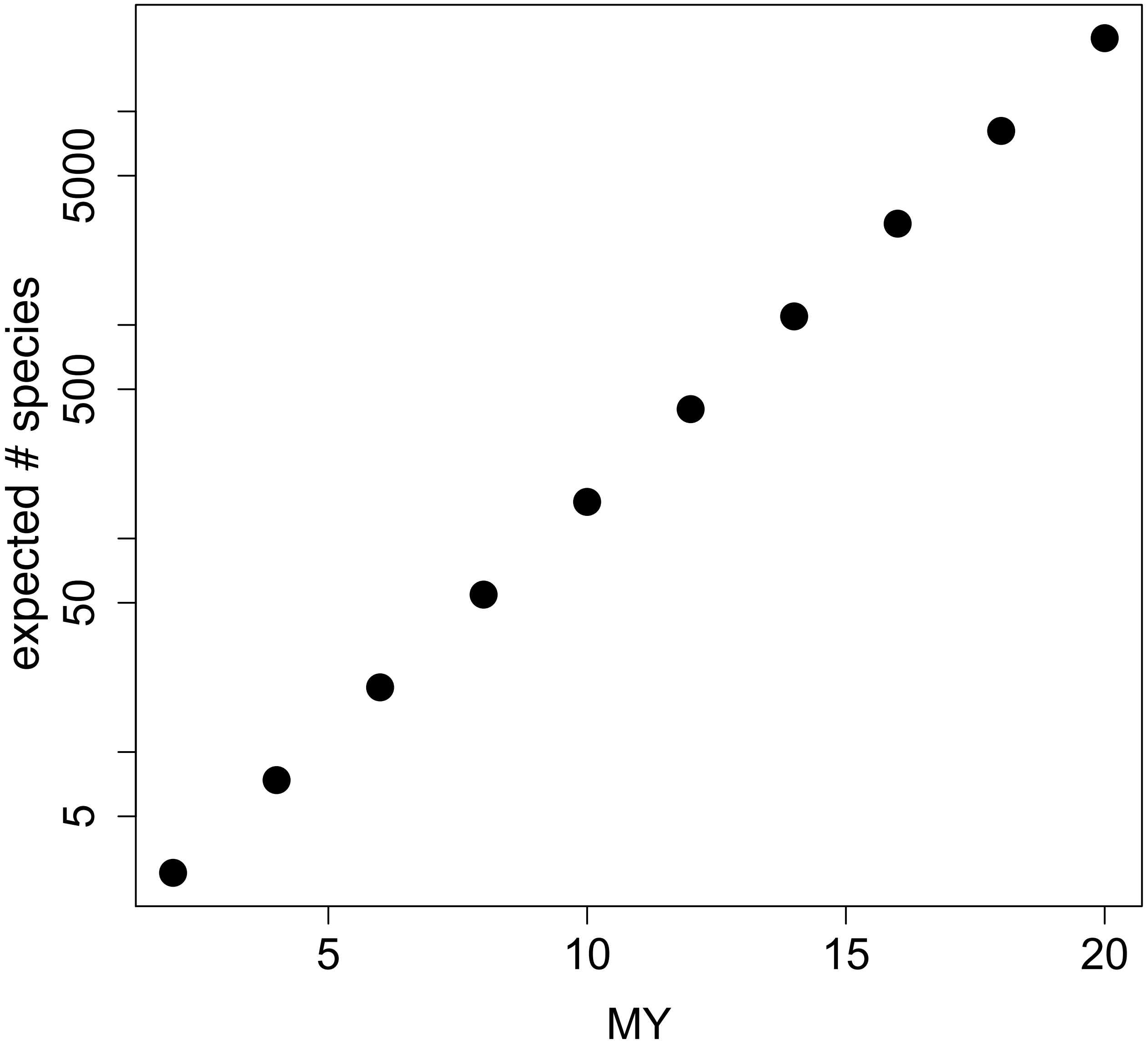


*Raup, D. 1975. Taxonomic survivorship curves and Van Valen's law. Paleobiology 1:82-96.

expectations



- $N(t) = N(0)e^{bt}$
- lineages accumulate exponentially (why?)

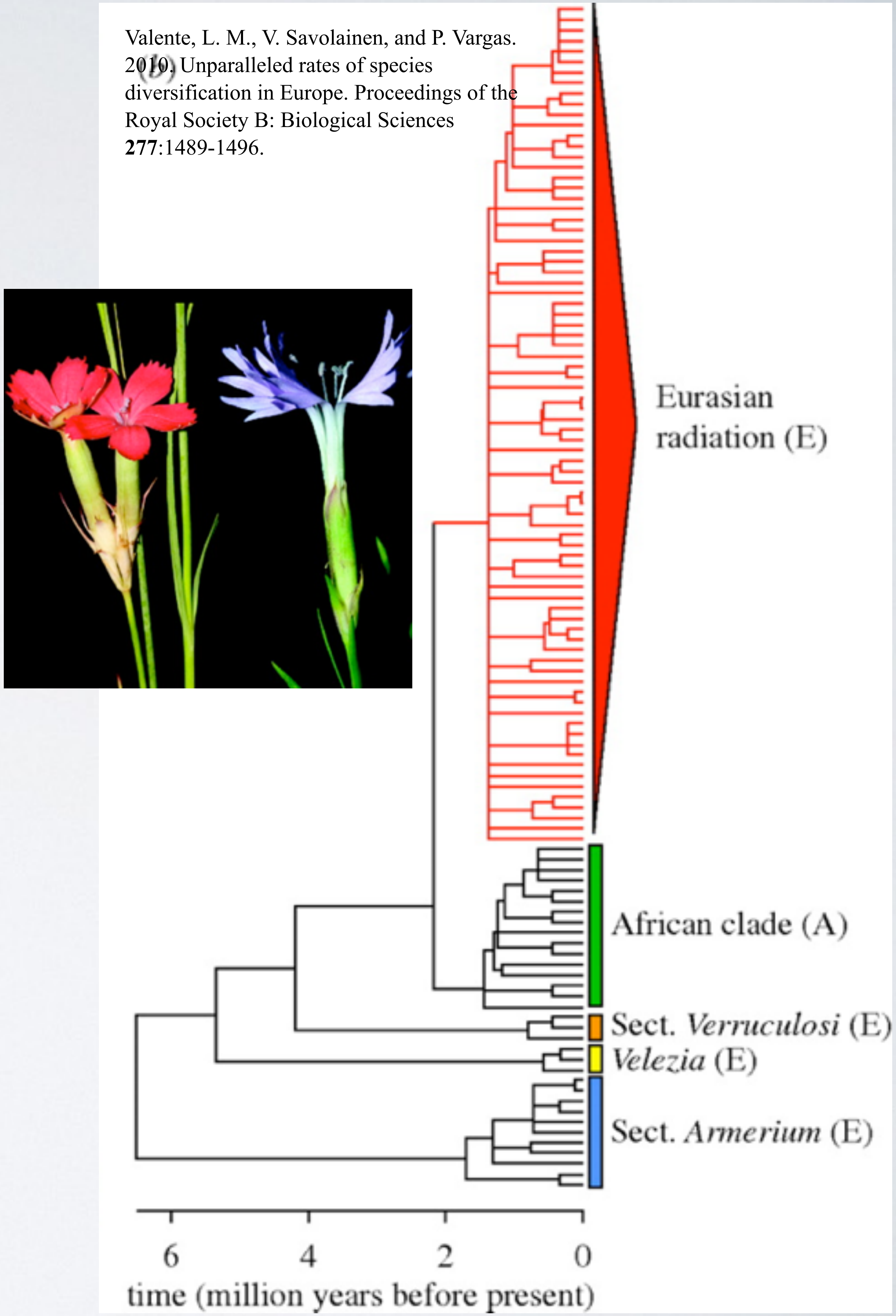


FUN WITH THE PURE BIRTH MODEL

- Carnation birth rate =b 7.6 species/my

- how many carnations will there be in 10 million years?

- what does this tell you about the pure birth model?



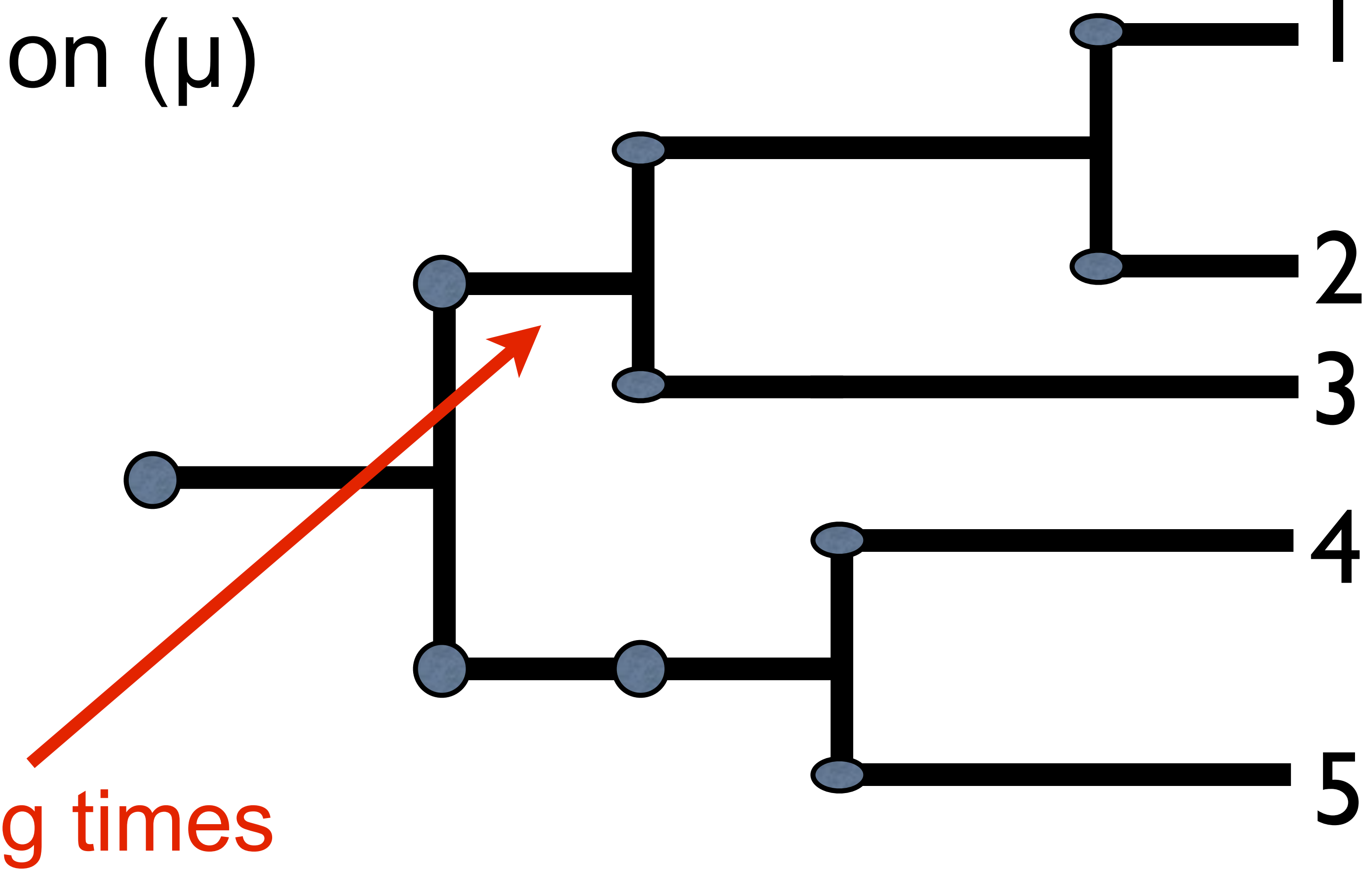
Valente, L. M., V. Savolainen, and P. Vargas. 2010. Unparalleled rates of species diversification in Europe. Proceedings of the Royal Society B: Biological Sciences **277**:1489-1496.

an improvement: the birth-death model

- Assumptions:
  - Speciation and extinction occur randomly
  - Each lineage has an equal and constant rate of speciation, *b*, and extinction, *d*

Diversification Model

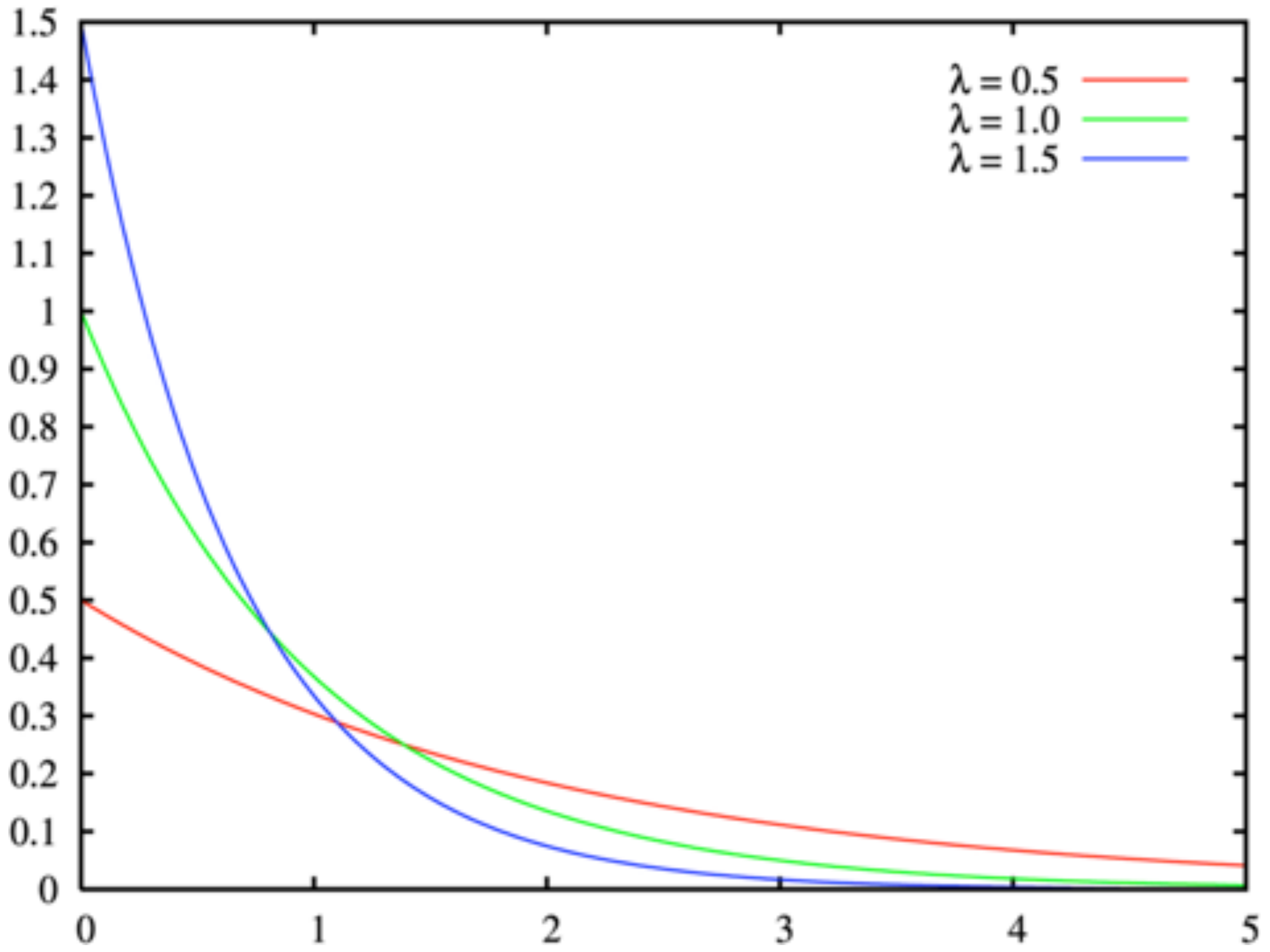
- Model: birth-death
- Every lineage has constant probability of:
  - –speciation (λ)
  - –extinction (μ)



Waiting times

Waiting times

- Under a birth-death model, the time intervals between successive events are always drawn from exponential distributions



$$f(x;\lambda) = \begin{cases} \lambda e^{-\lambda x} & , \; x \ge 0, \\ 0 & , \; x < 0. \end{cases}$$

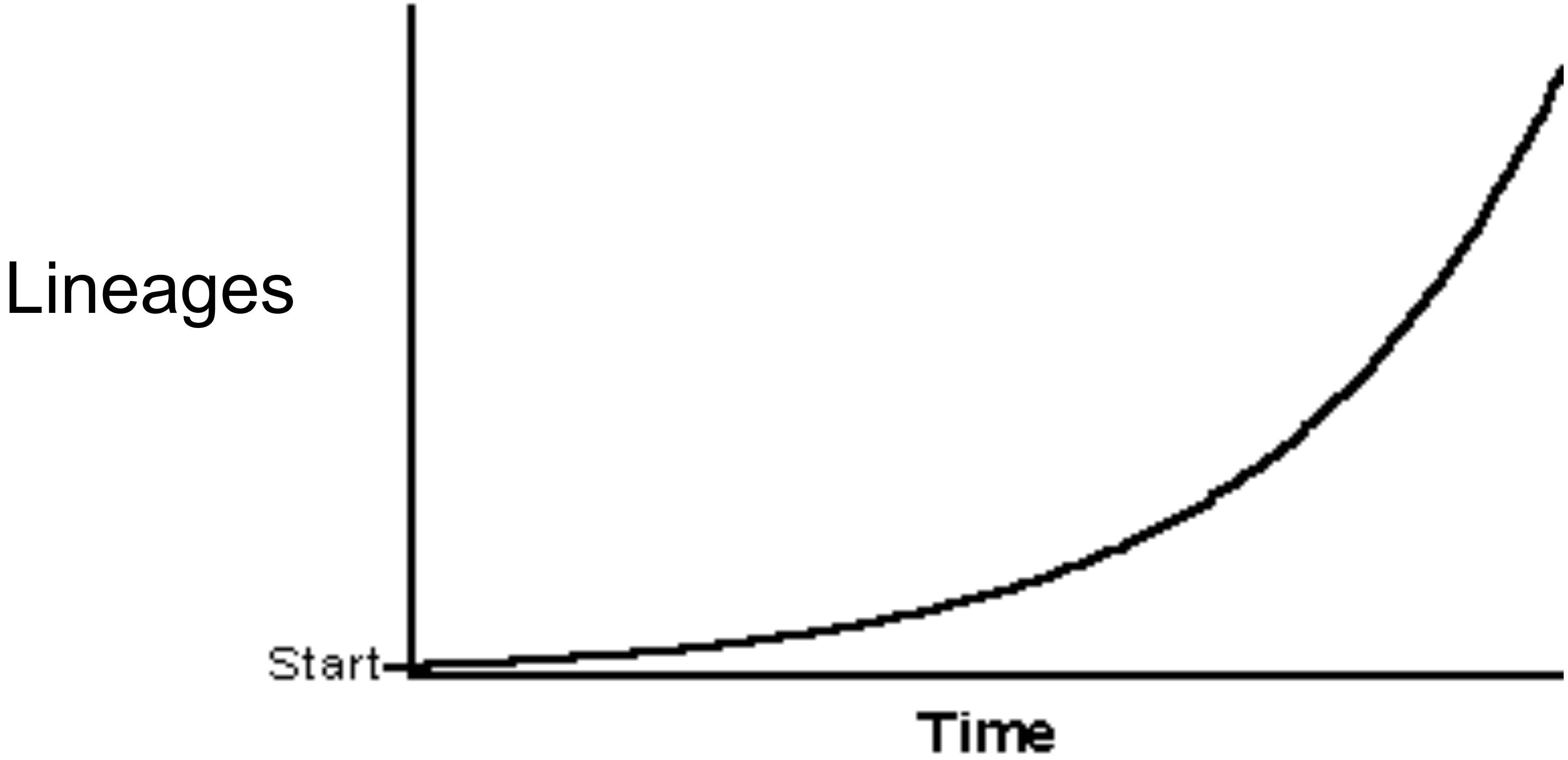
Expected species diversity under a birth-death model:

$$E[N_t] = N_o e^{(b-d)t}$$

N_t = species diversity after time t
N_o = starting species diversity
b = birth rate
d = death rate
t = time

Species Accumulation

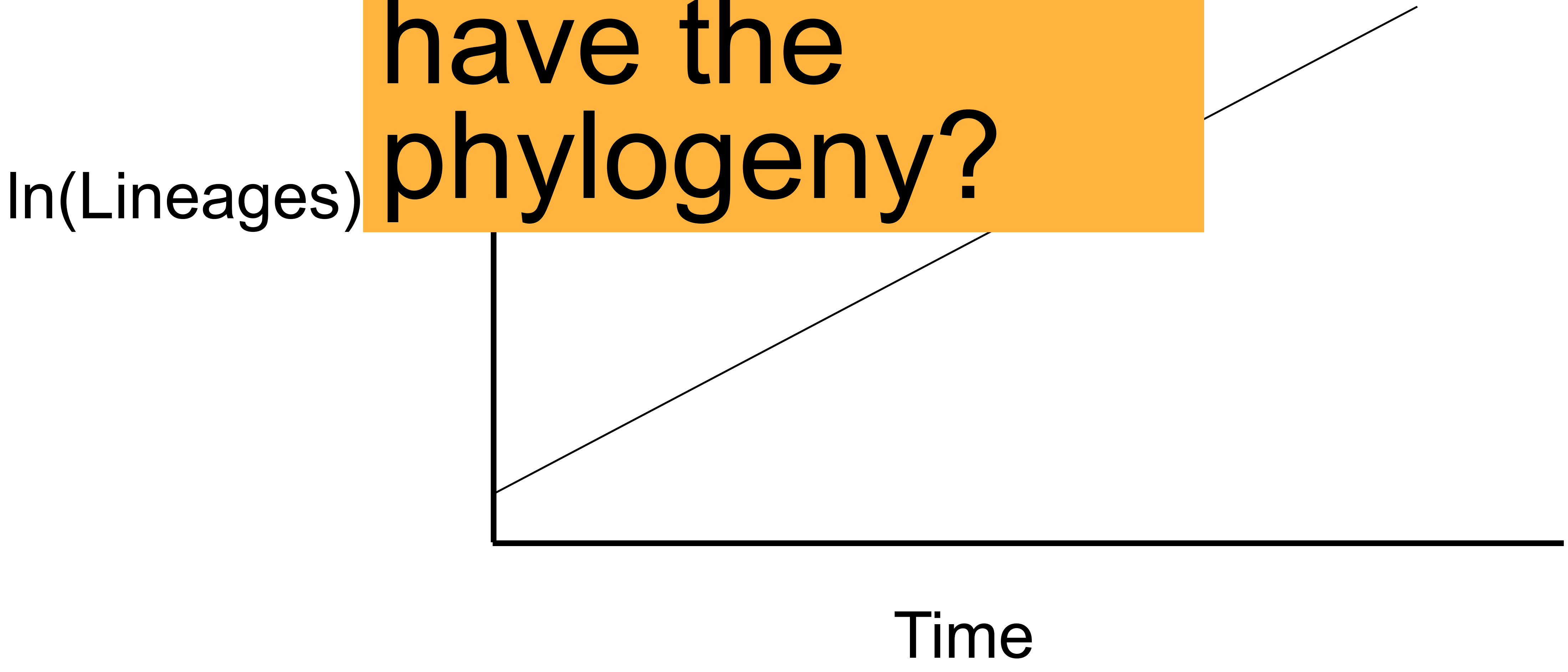
- Expected number of species increases exponentially with λ-μ



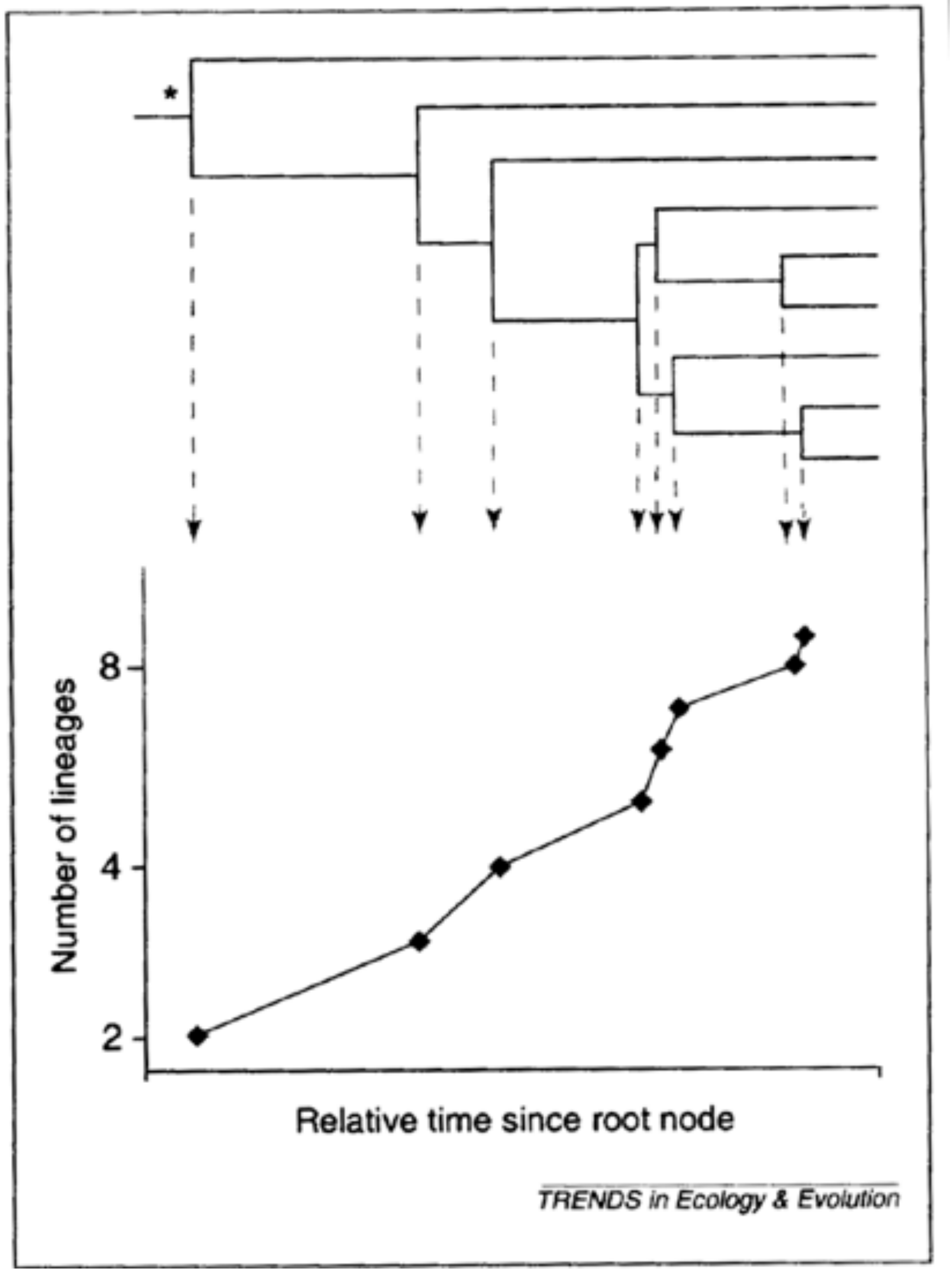
Diversification Model

- Expected number of species increases exponentially with λ-μ

What if we just have the phylogeny?

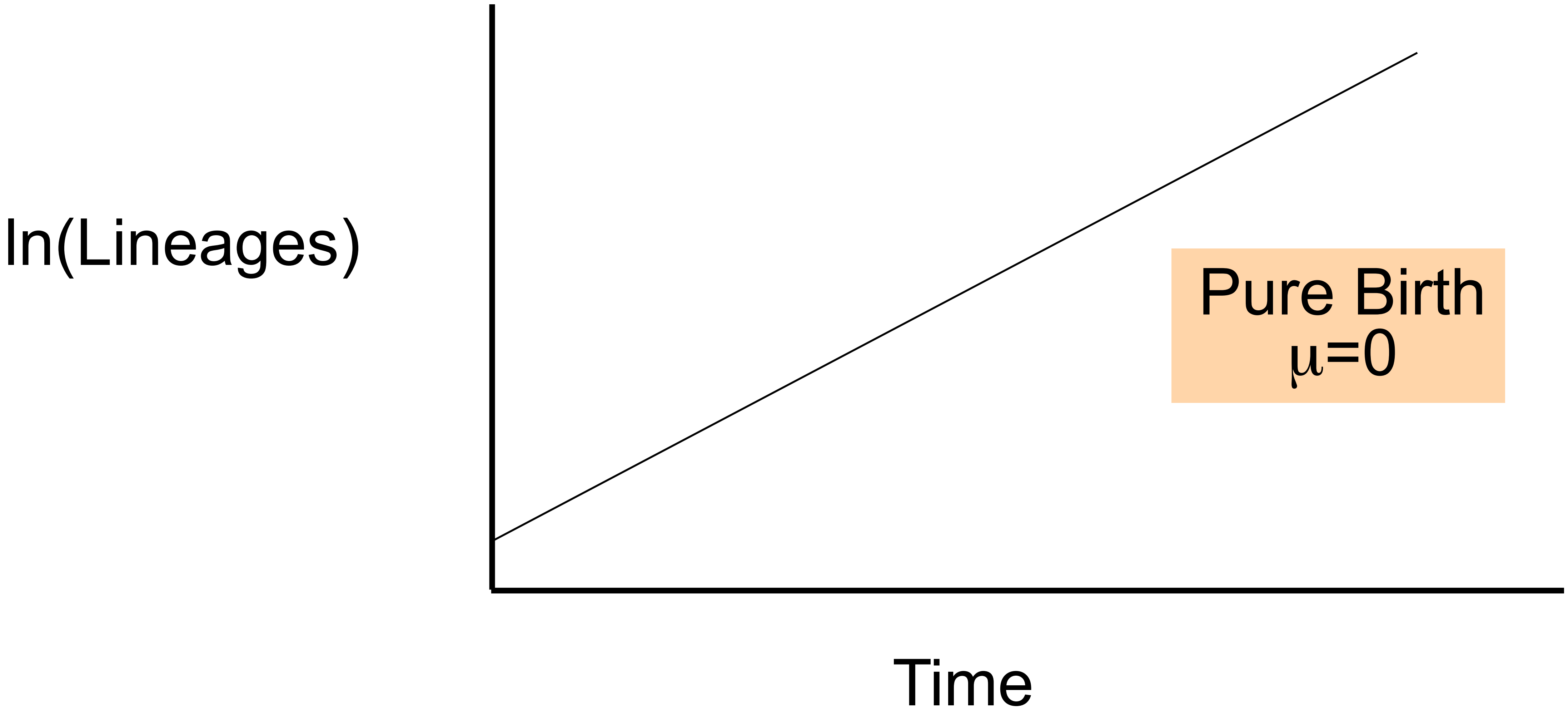


Lineage-through-time



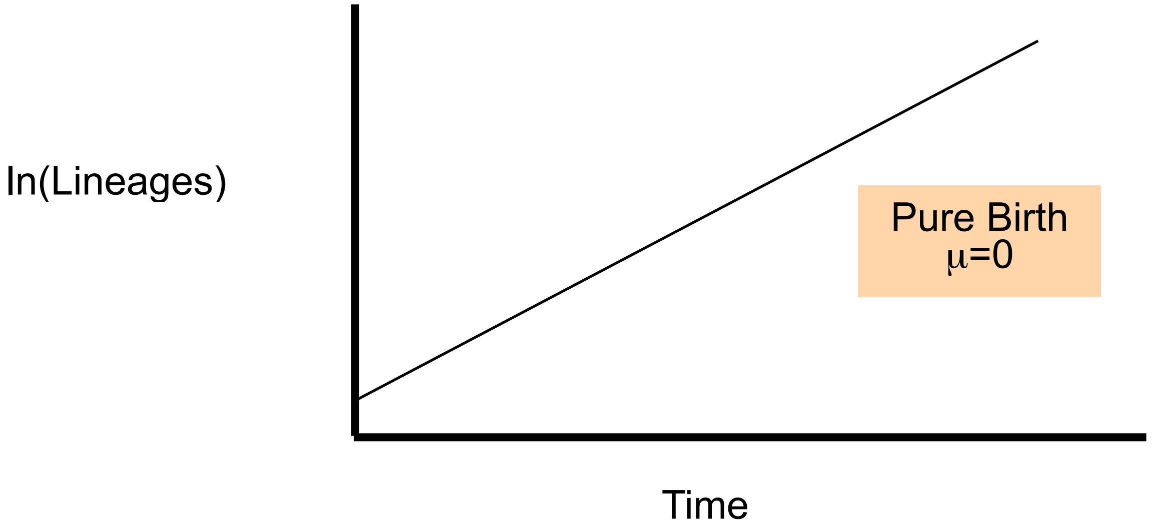
TRENDS in Ecology & Evolution

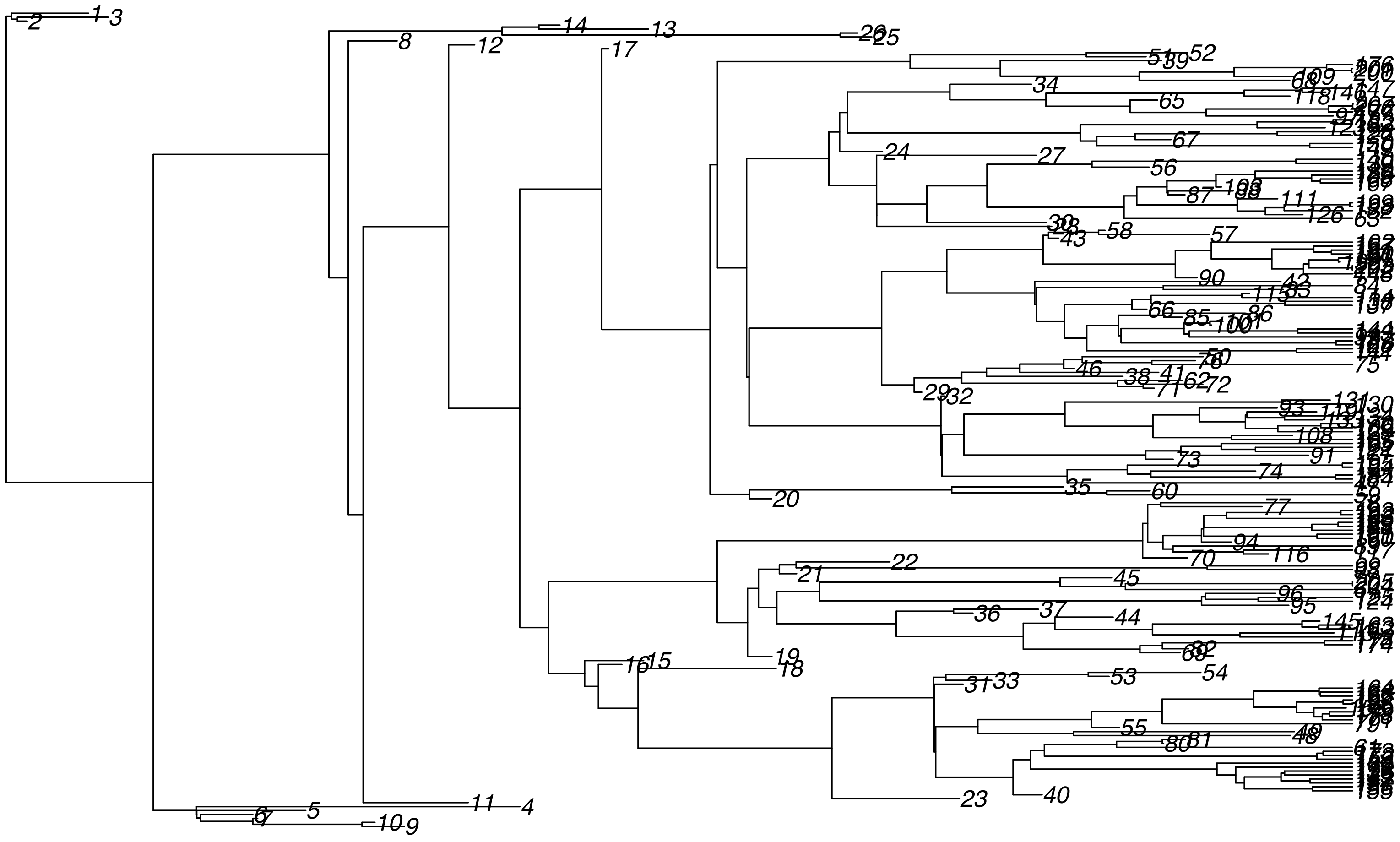
LTT Plot



Think about extinction

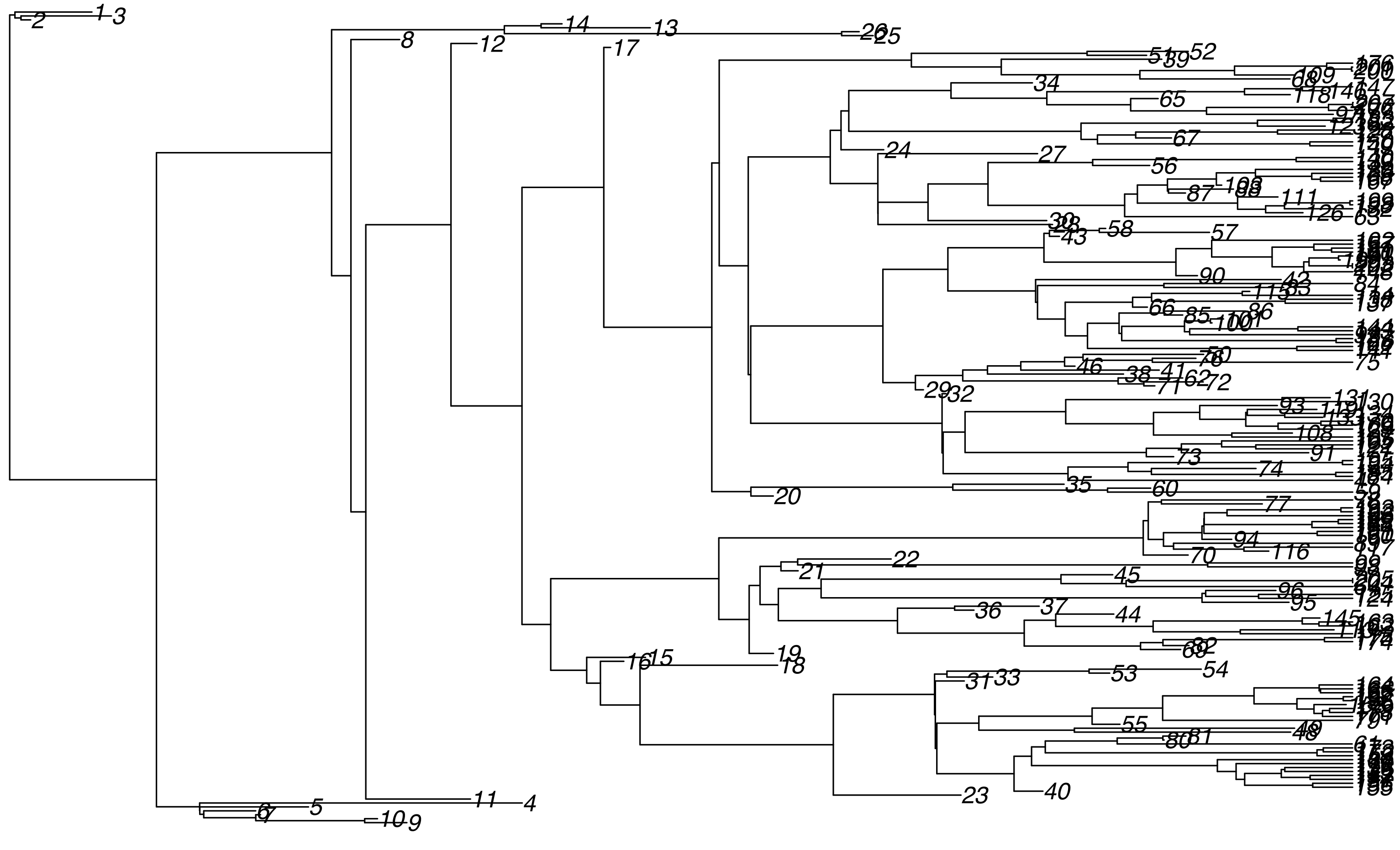
- how should extinction affect the rate of species accumulation in a phylogeny? why?
- can we infer extinction from phylogenetic data?

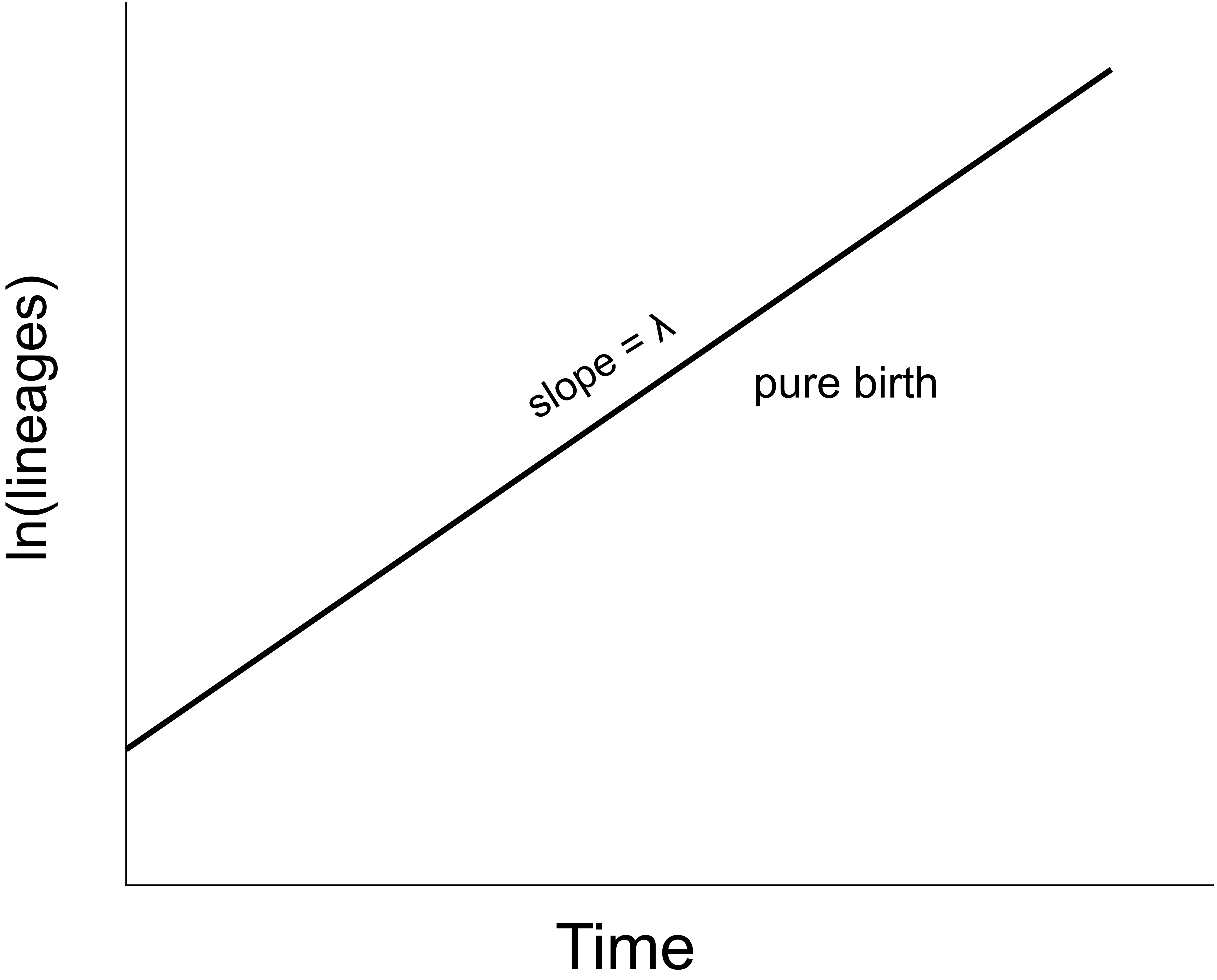


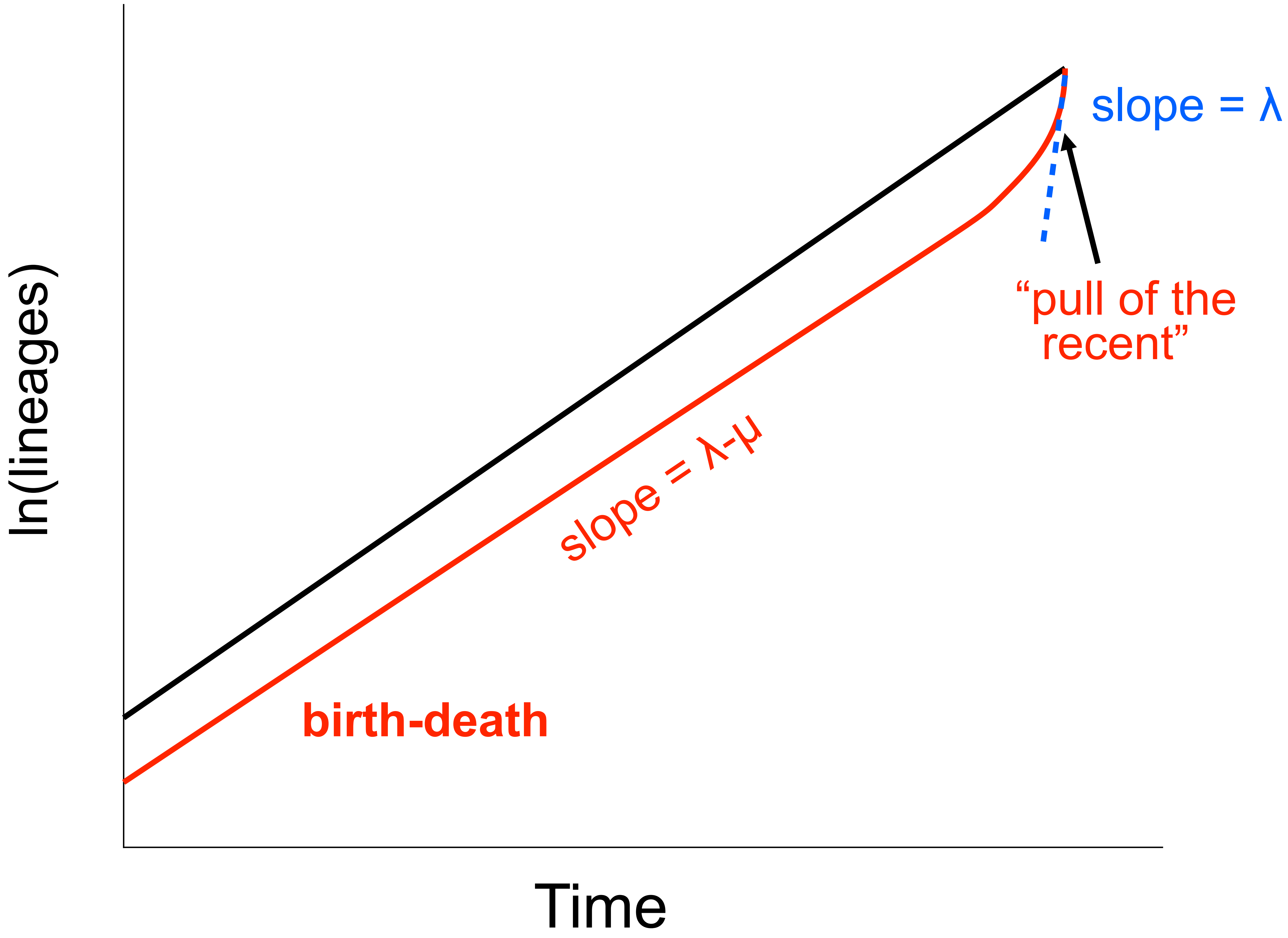


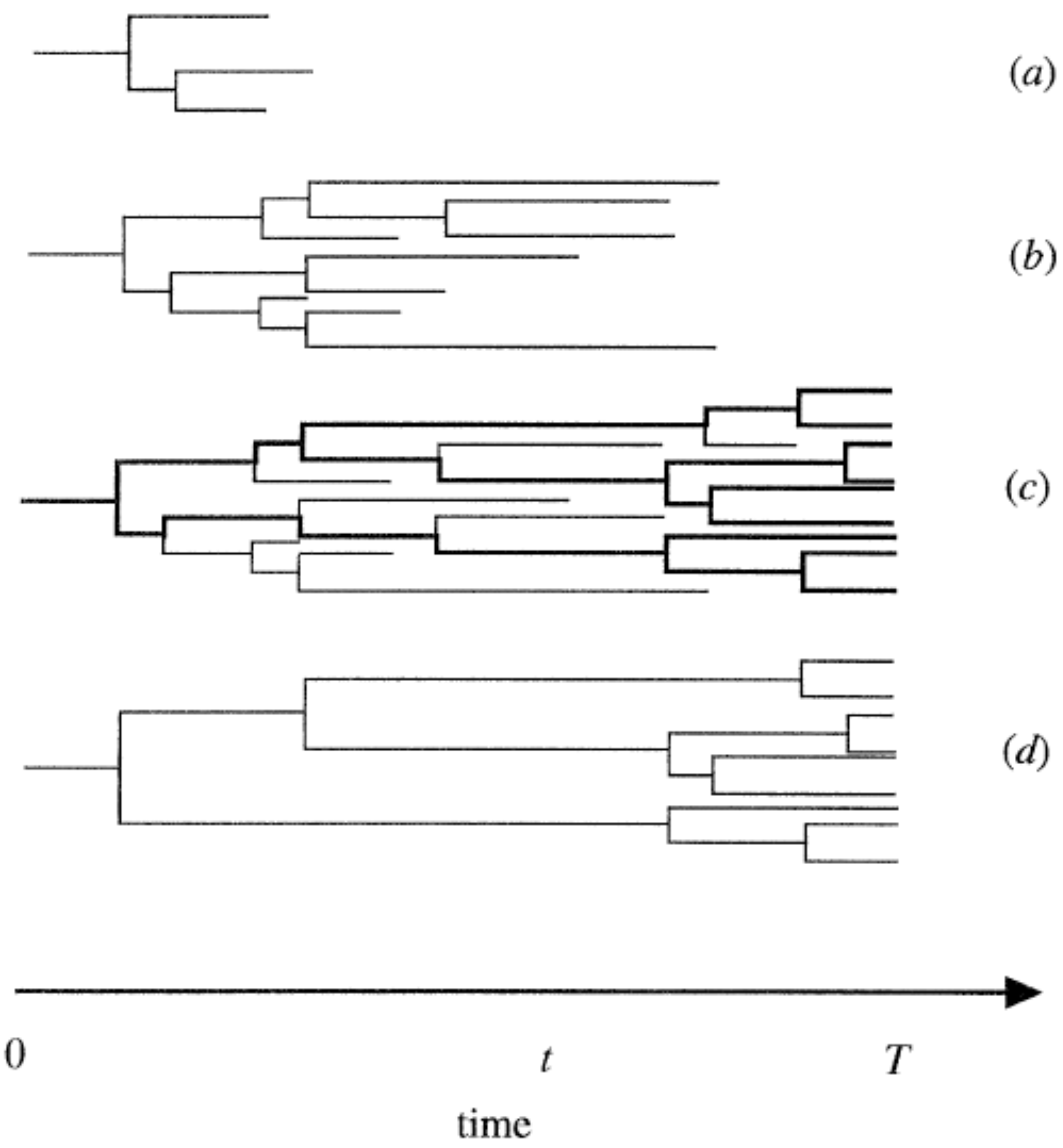
Extinction

- Can leave an imprint on present-day phylogenies
- Older lineages are more likely to have gone extinct than younger ones

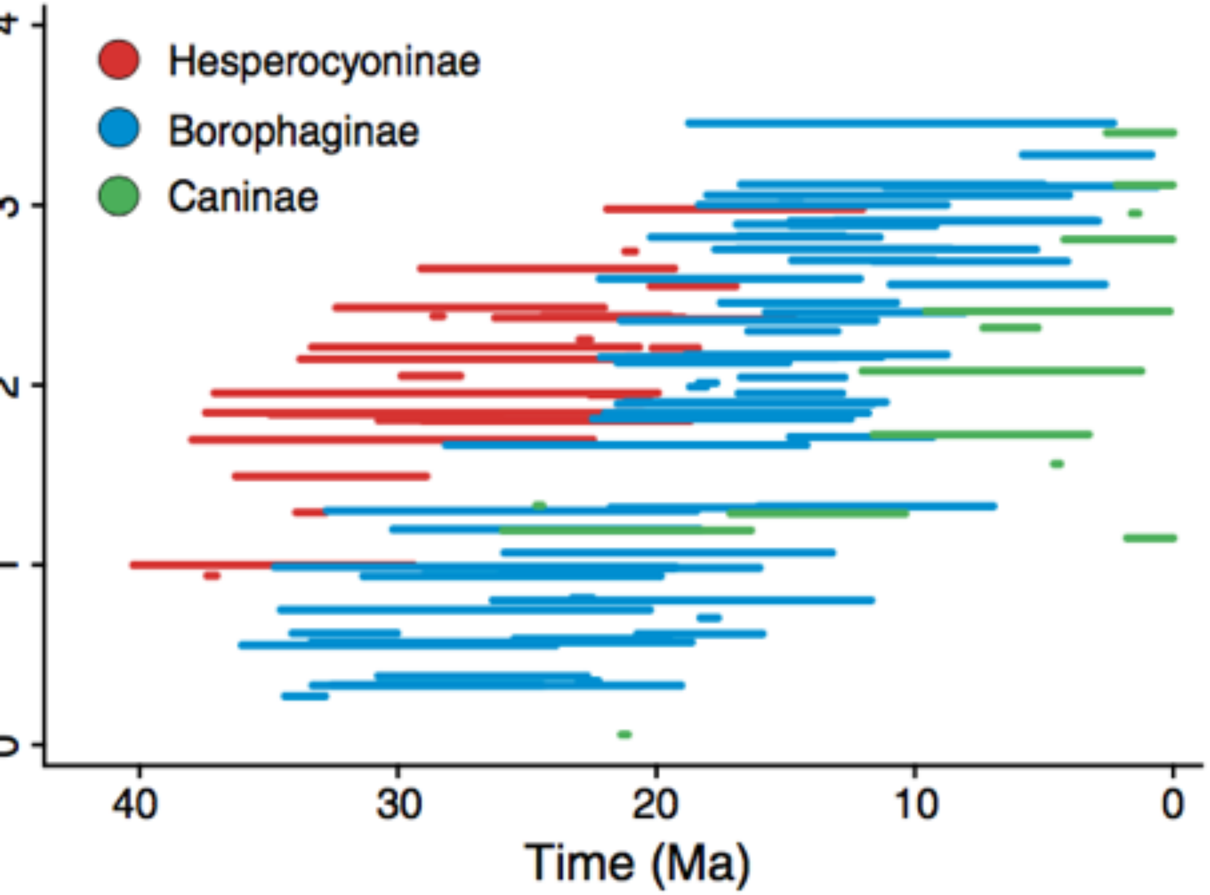


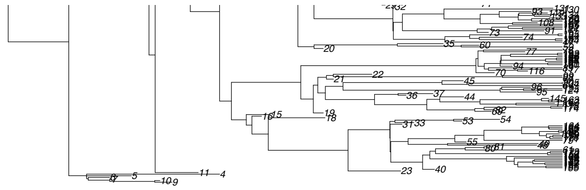

ln(lineages)
slope = λ
pure birth
Time

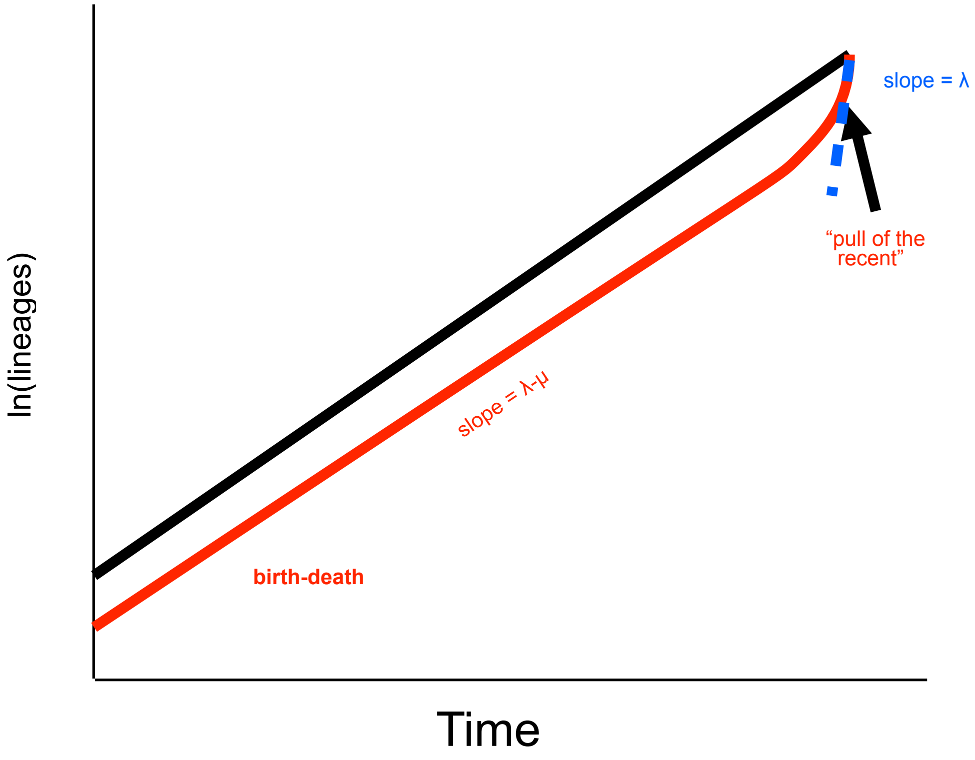

ln(lineages)
Time
slope = λ
"pull of the recent"
slope = λ-μ
birth-death

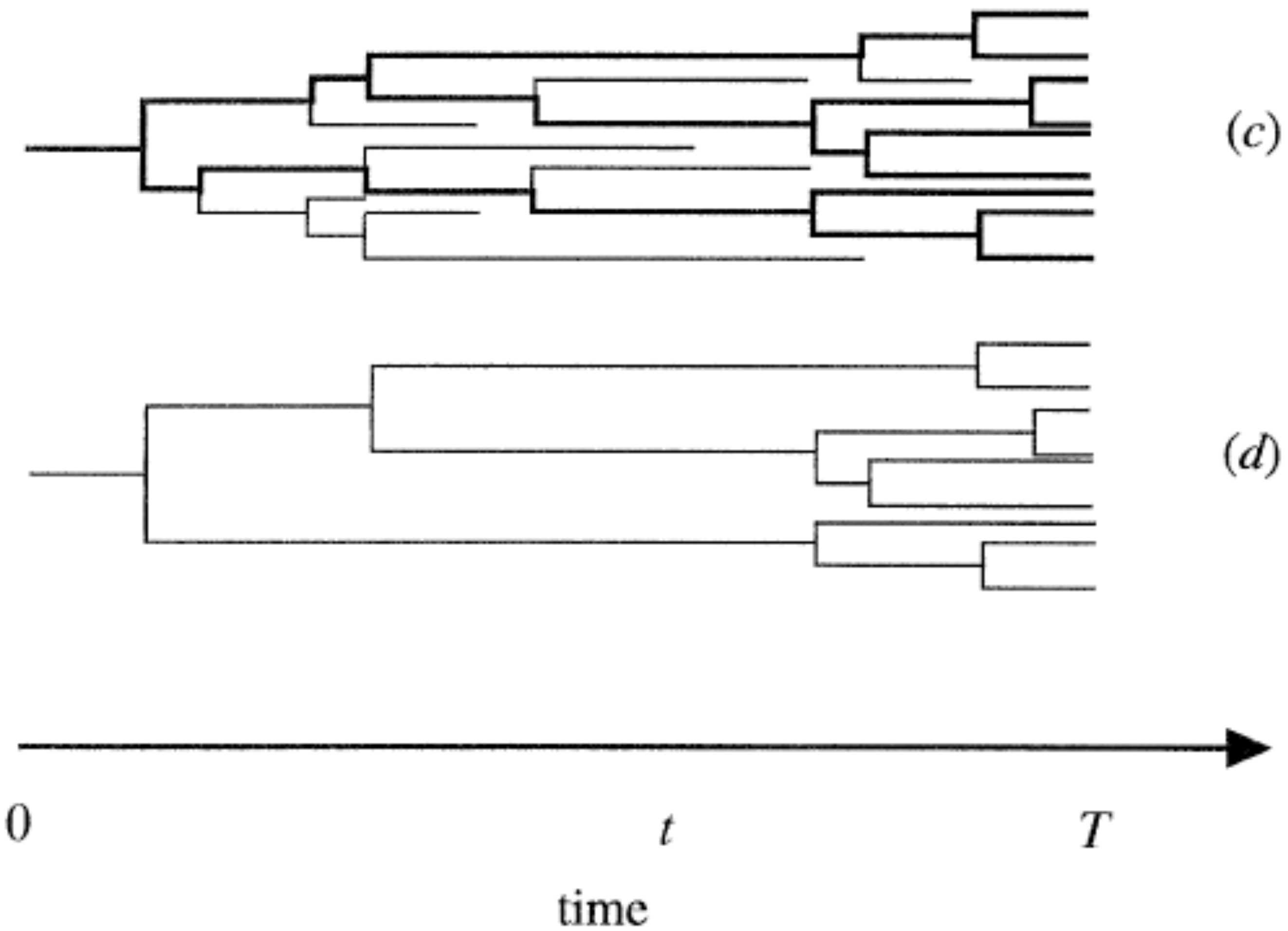

(a)
(b)
(c)
(d)
0
t
T
time

fossil versus molecular signature of extinction

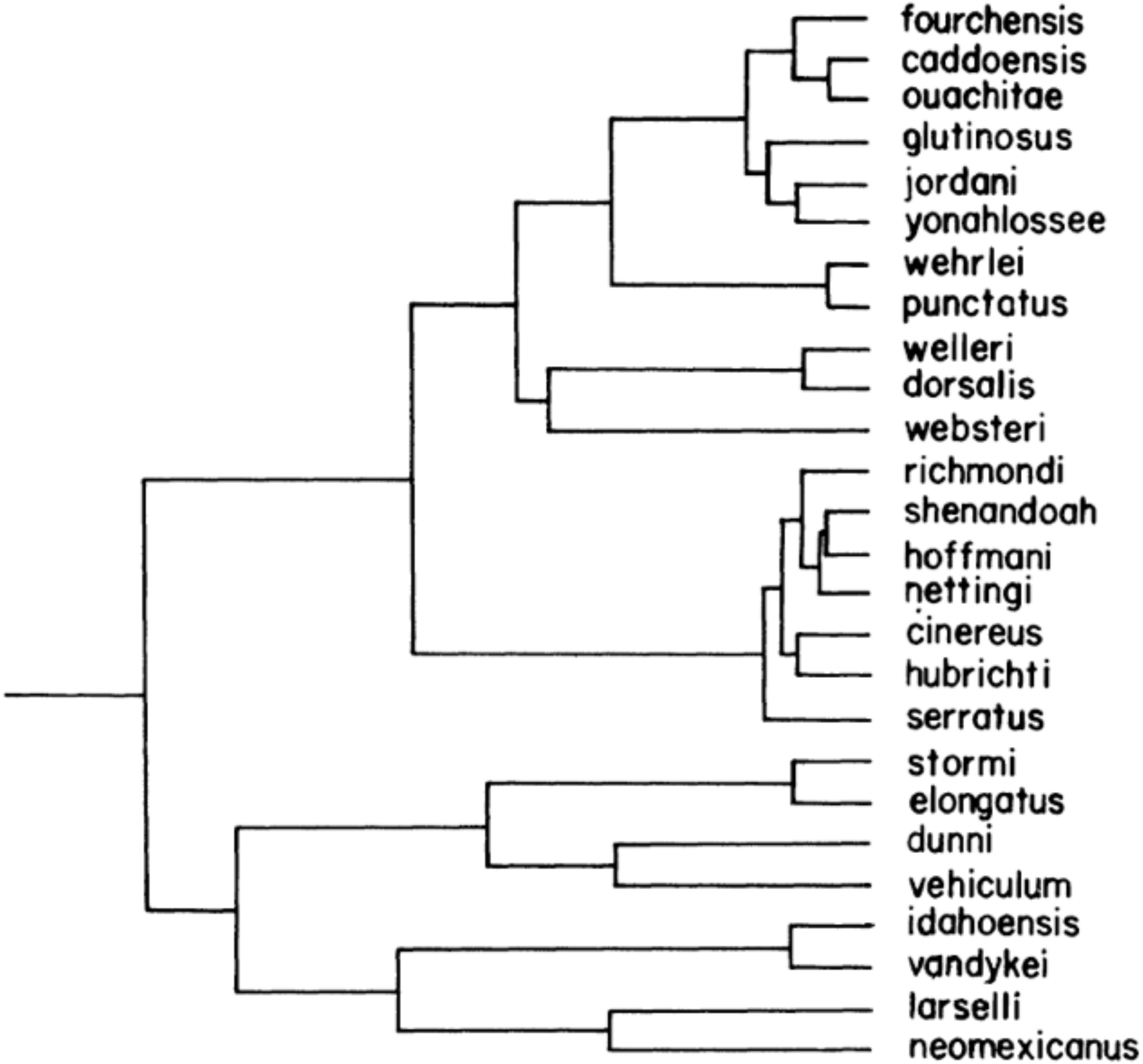






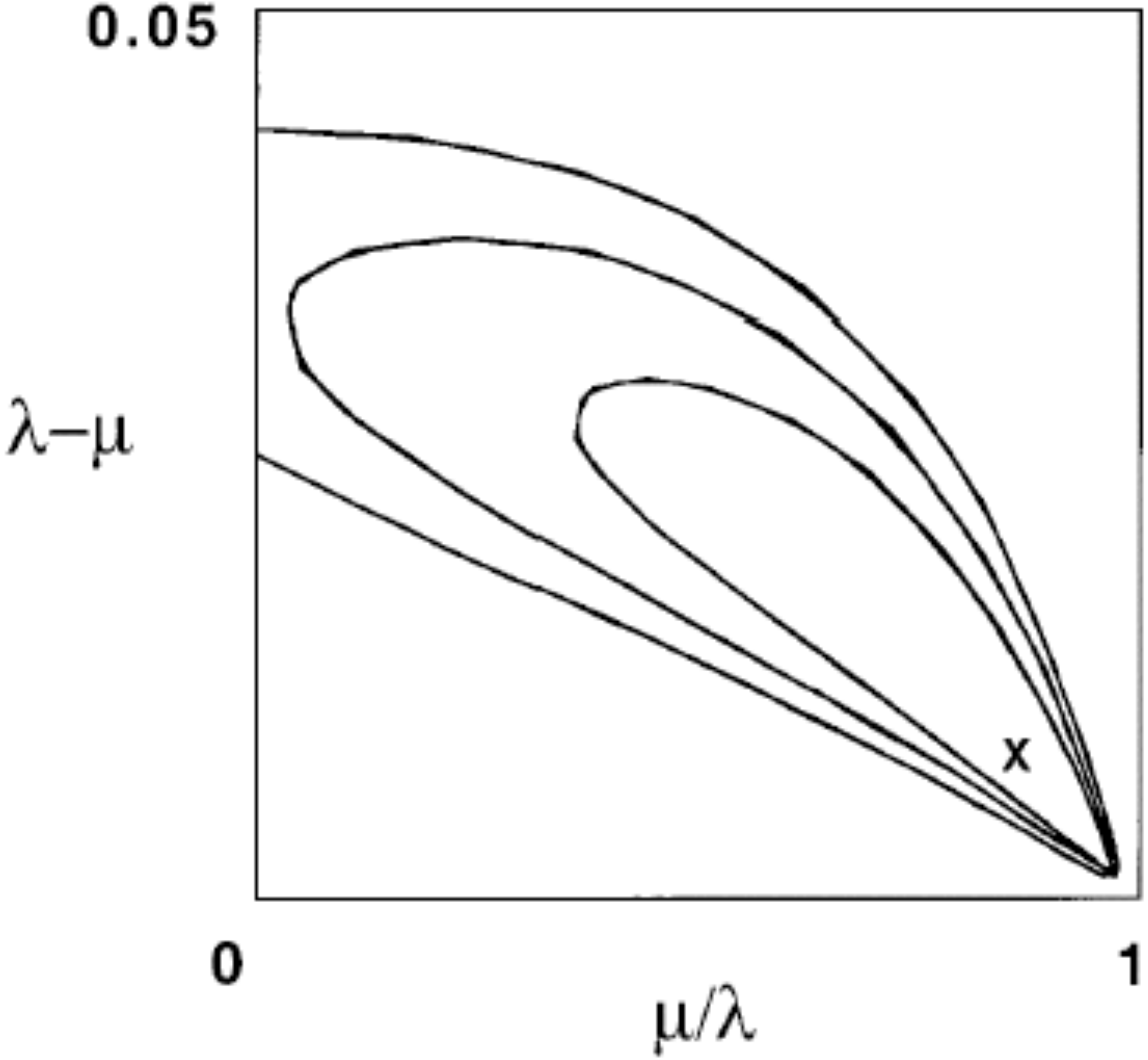


Plethodontid salamanders



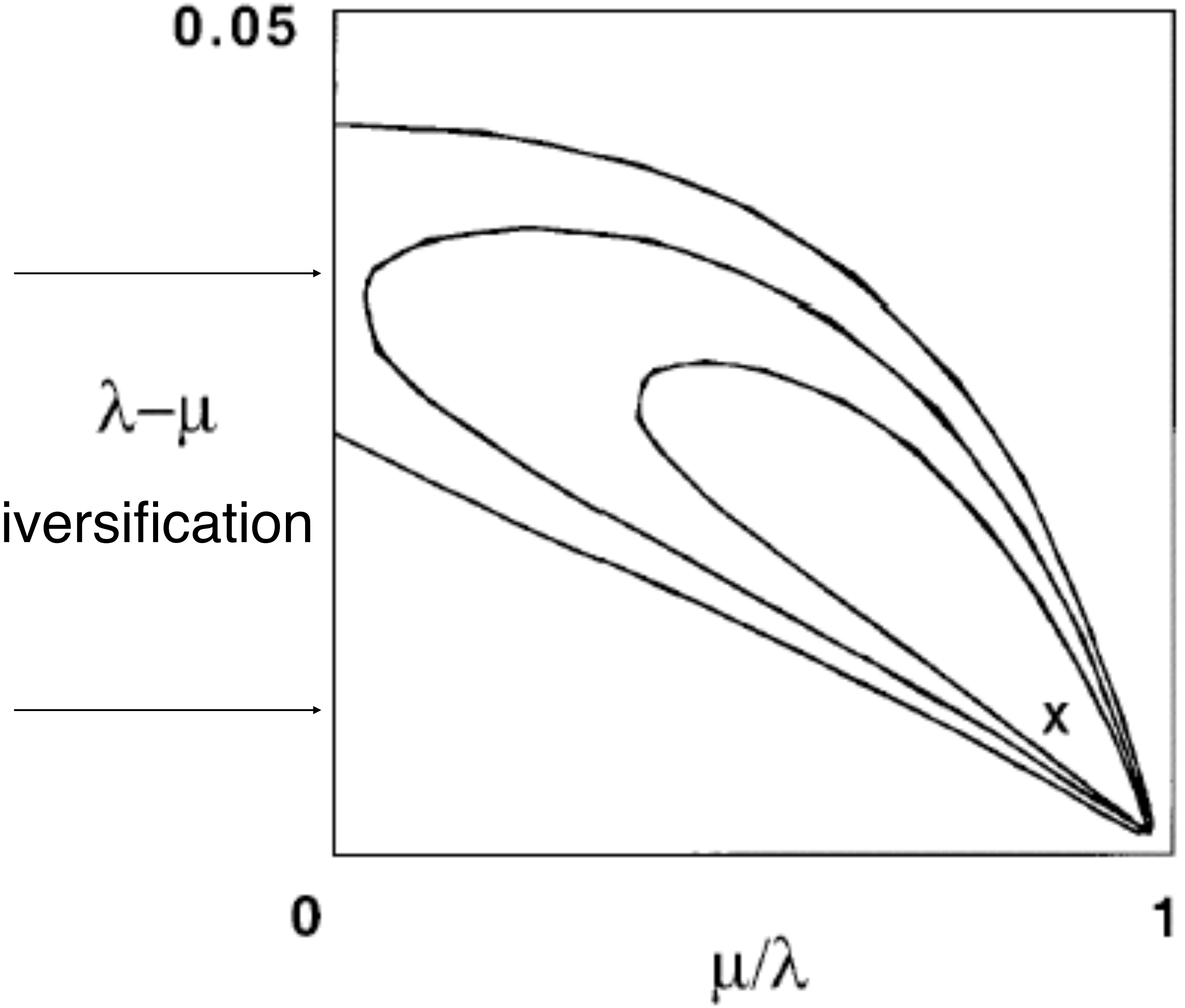
(Highton and Larson 1979)

Plethodontid salamanders



from Nee 2001

Plethodontid salamanders



net diversification

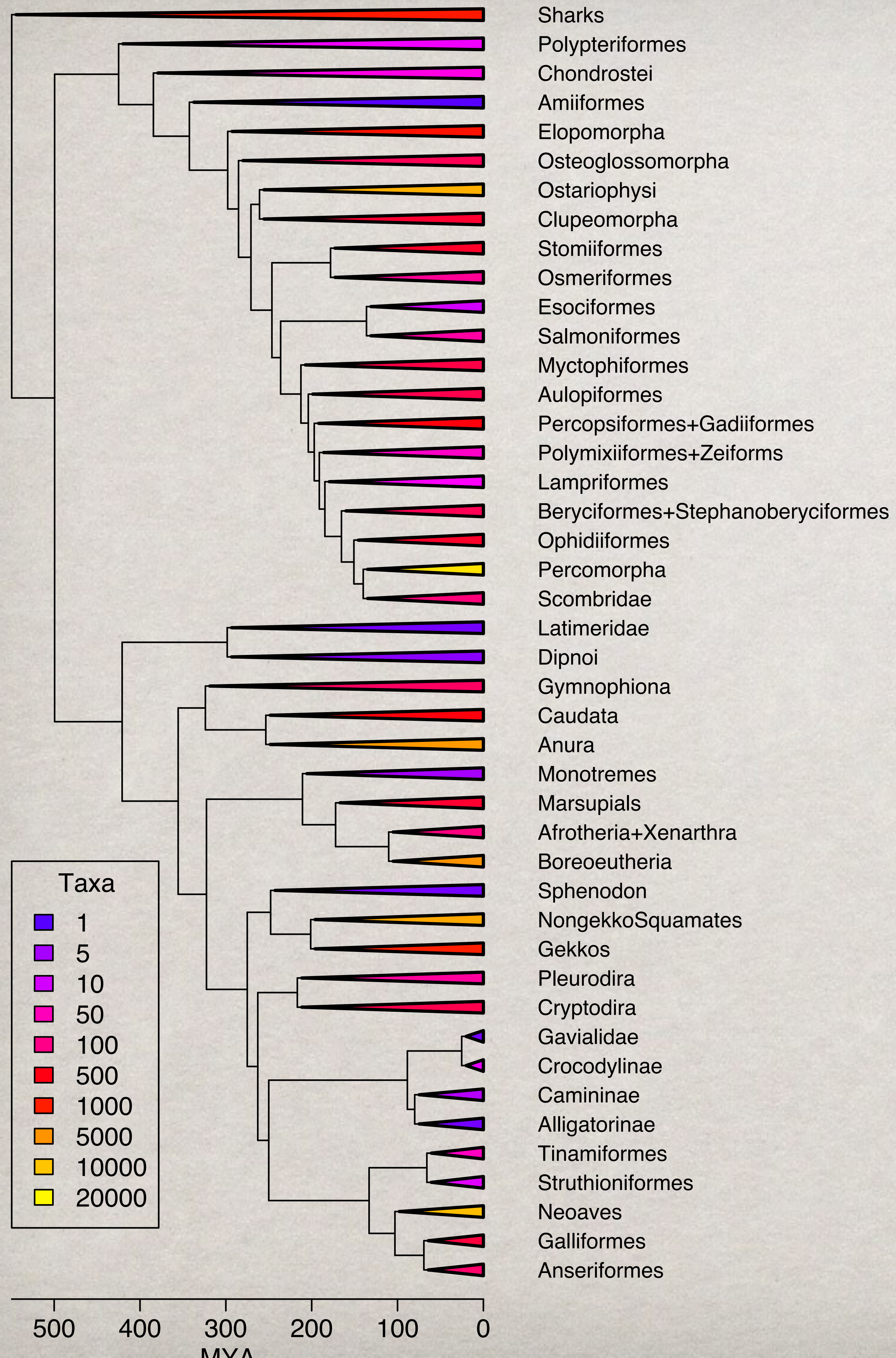
turnover

from Nee 2001

We can use ML or Bayesian methods
to analyze data, estimate parameters, and
carry out model selection

Models have grown in sophistication since Nee 2001

How Fast Did Gnathostomes Diversify?



1. λ_G = [log(n) - log 2]/t

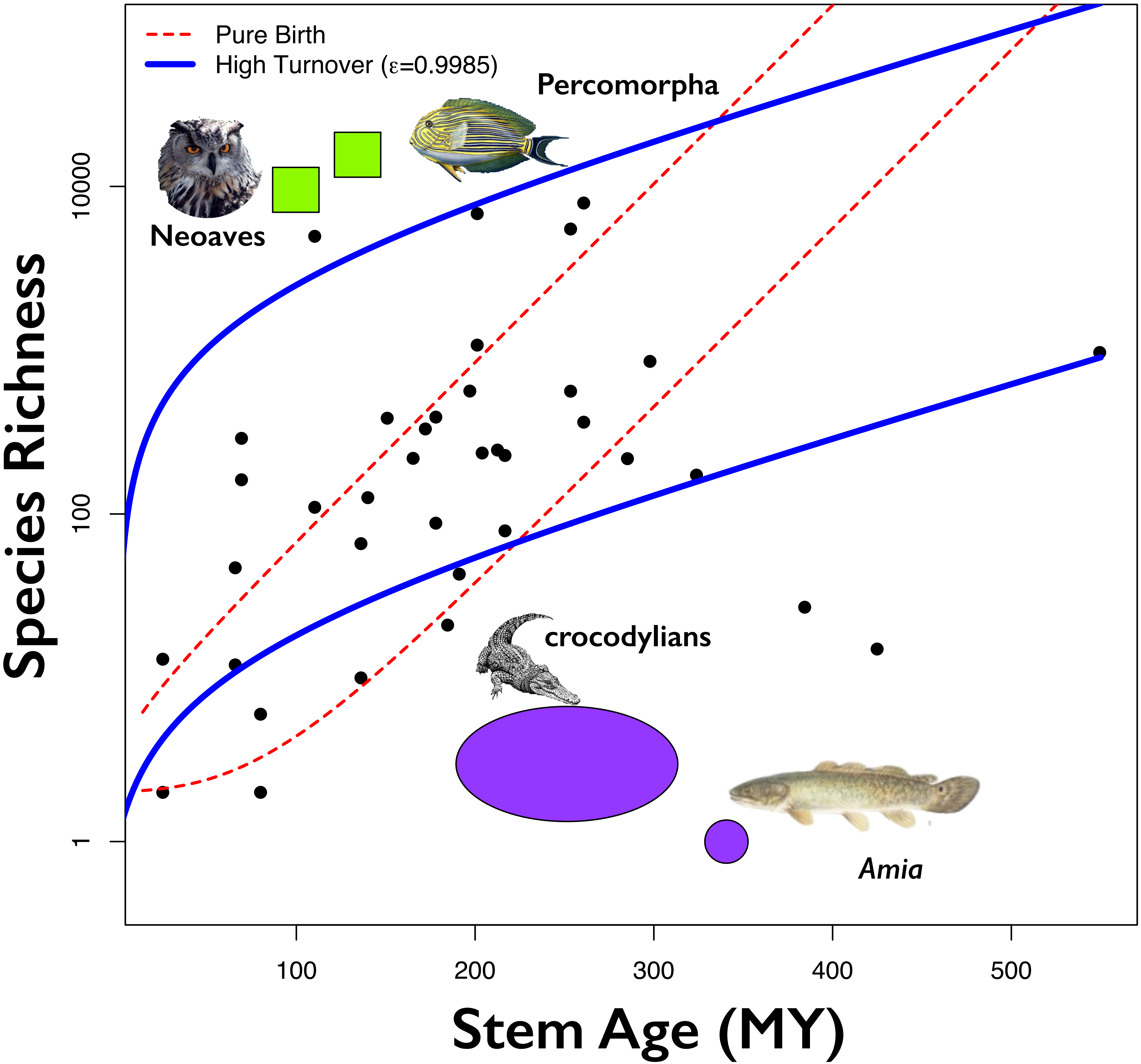
n = 57,859 species

t = 549 mya

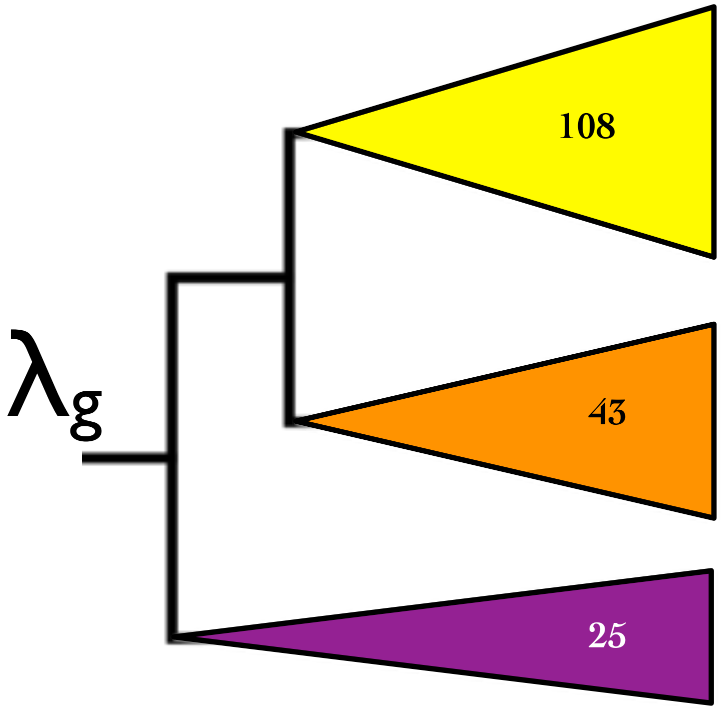
$$\lambda_G = \frac{\ln(n) - \ln(2)}{t}$$

$$\lambda_G = \frac{\ln(57859) - \ln(2)}{549}$$

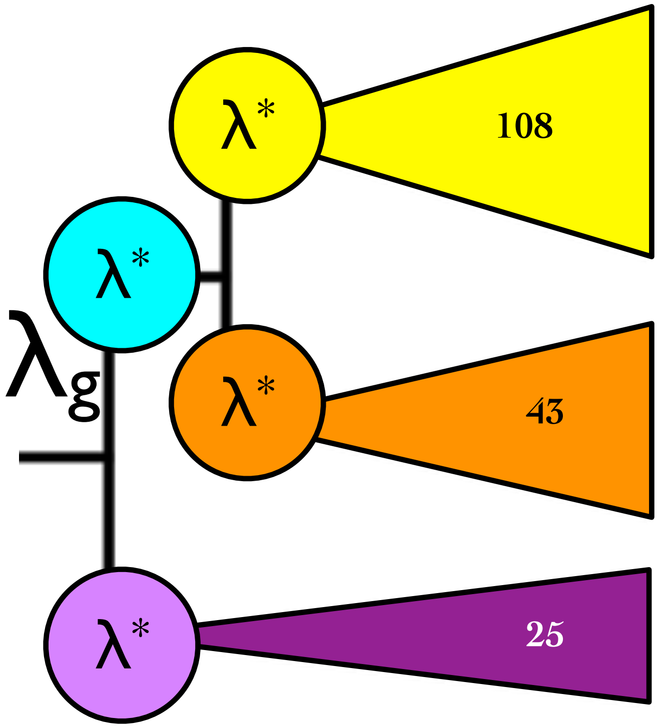
$\lambda_G = 0.019$



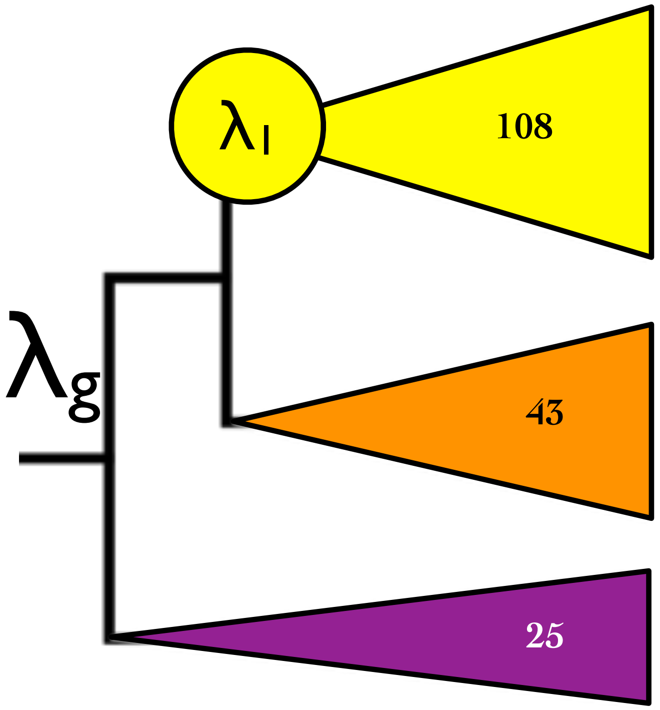
Pure Birth
High Turnover (ε=0.9985)
Percomorpha
Neoaves
crocodylians
Amia
10000
100
1
100
200
300
400
500
Species Richness
Stem Age (MY)



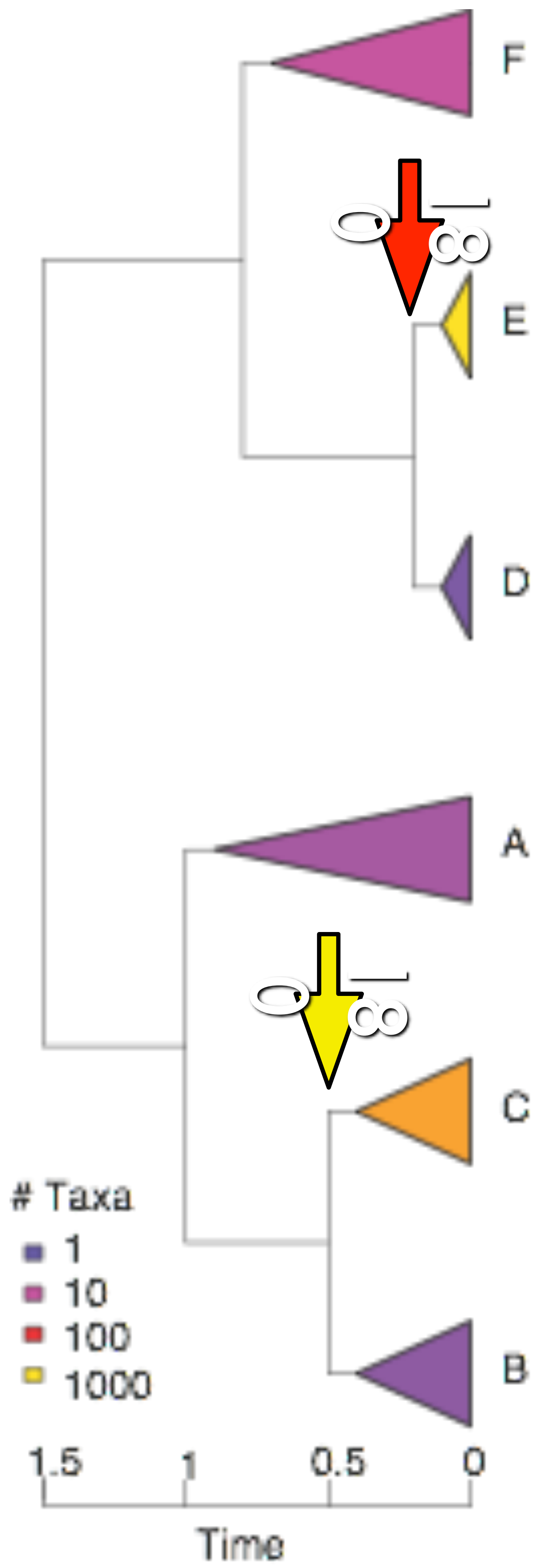
1. λ for whole tree

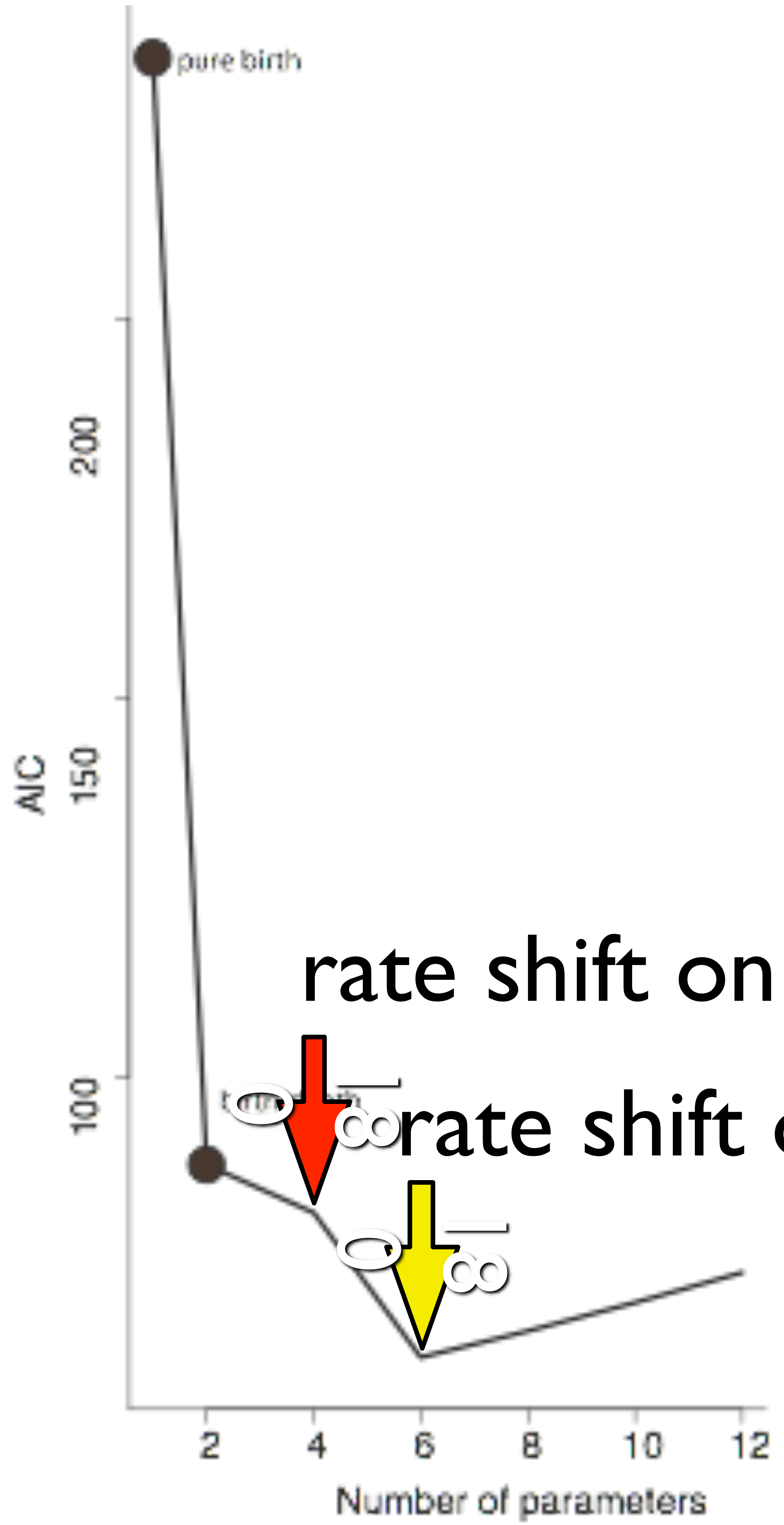


2. allow λ to change on each branch



3. if ΔAIC of best new λ and $\lambda_g > 4$,
retain rate & repeat





rate shift on E

rate shift on C

What Can MEDUSA Do For You?

MEDUSA

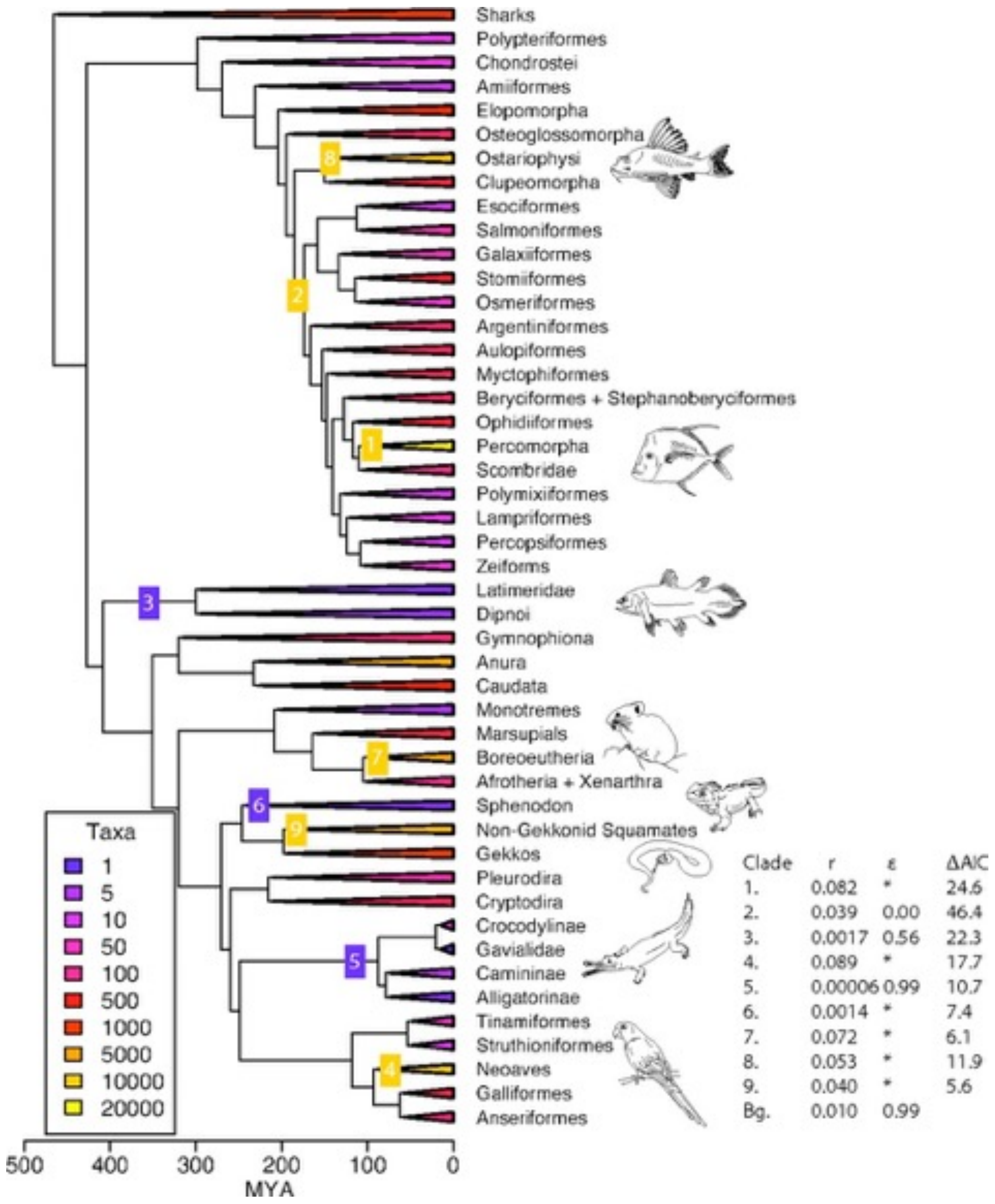
- Learn about diversification dynamics through fitting <u>piecewise</u> models of birth (λ) and death (μ)
  - Where have rates changed?
  - By what magnitude?
  - Why do clades differ in size?

r = net diversification rate

= λ - μ

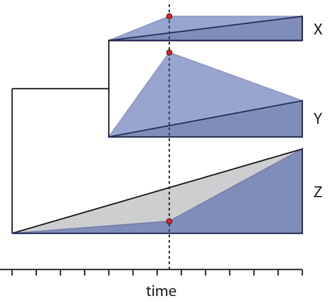
ε = extinction fraction

= μ / λ



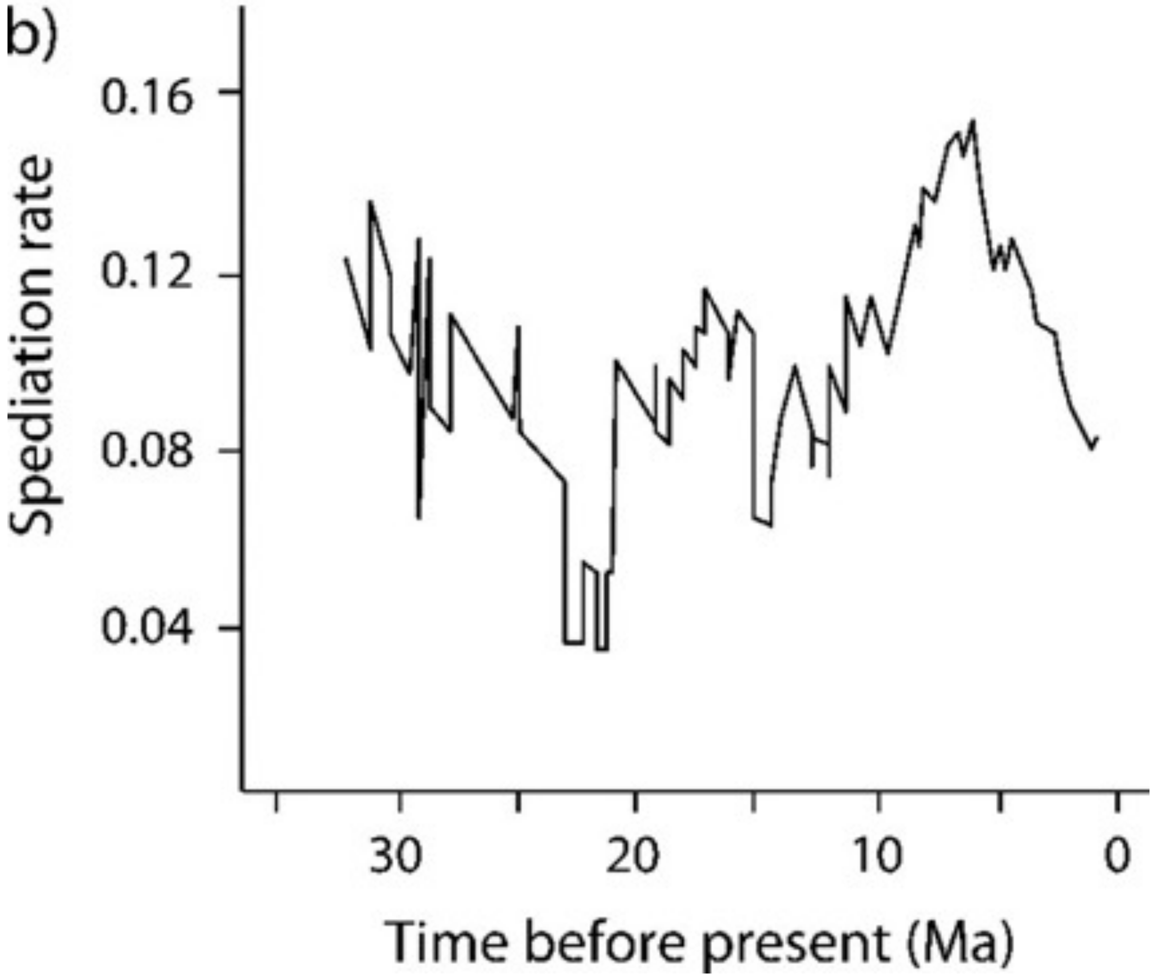
Clade	r	ε	ΔAIC
1.	0.082	*	24.6
2.	0.039	0.00	46.4
3.	0.0017	0.56	22.3
4.	0.089	*	17.7
5.	0.00006	0.99	10.7
6.	0.0014	*	7.4
7.	0.072	*	6.1
8.	0.053	*	11.9
9.	0.040	*	5.6
Bg.	0.010	0.99	

Alfaro et al. 2009 PNAS

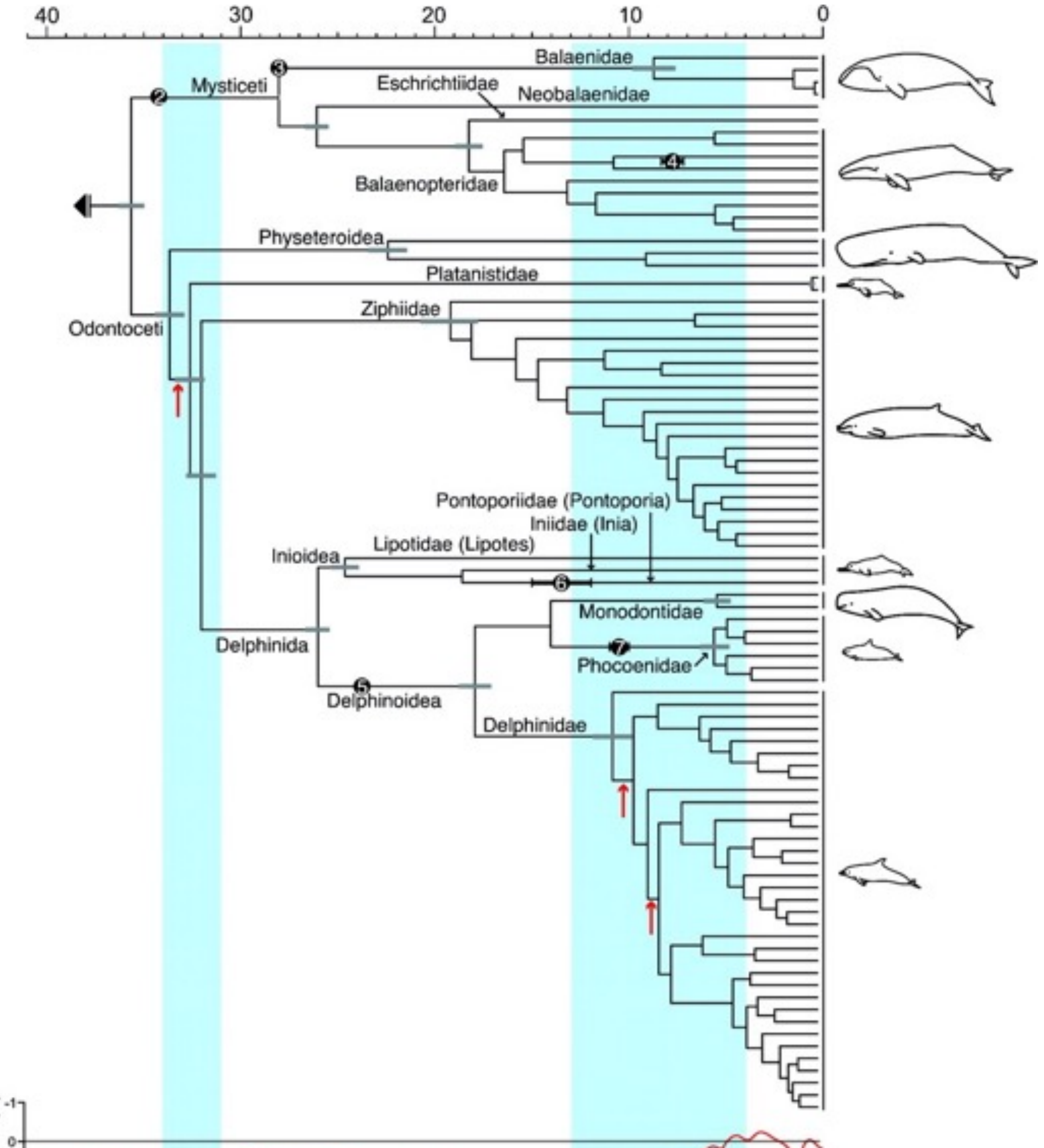


More recent models allow for diversity dependence

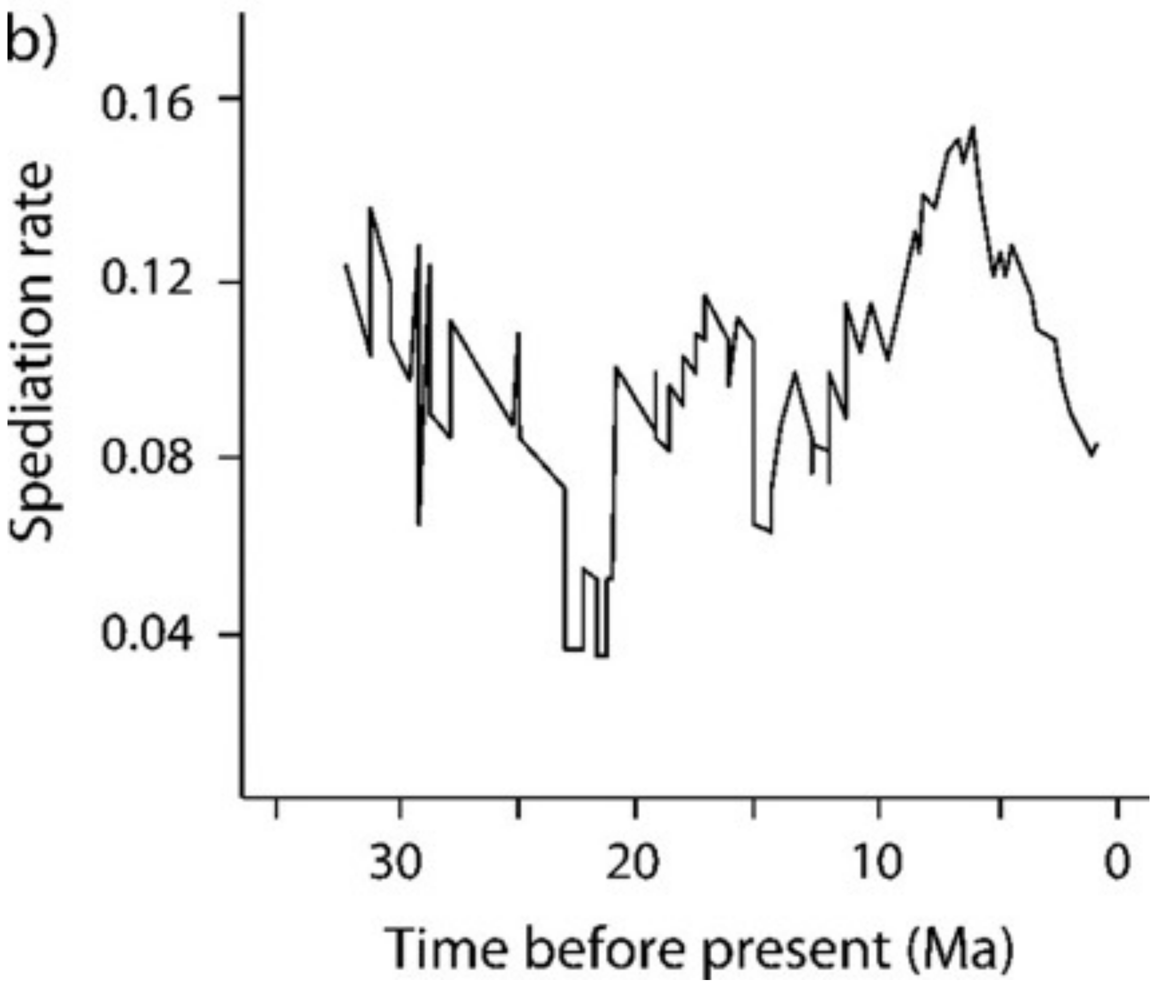
BAMM, RPANDA, and trait independent diversification



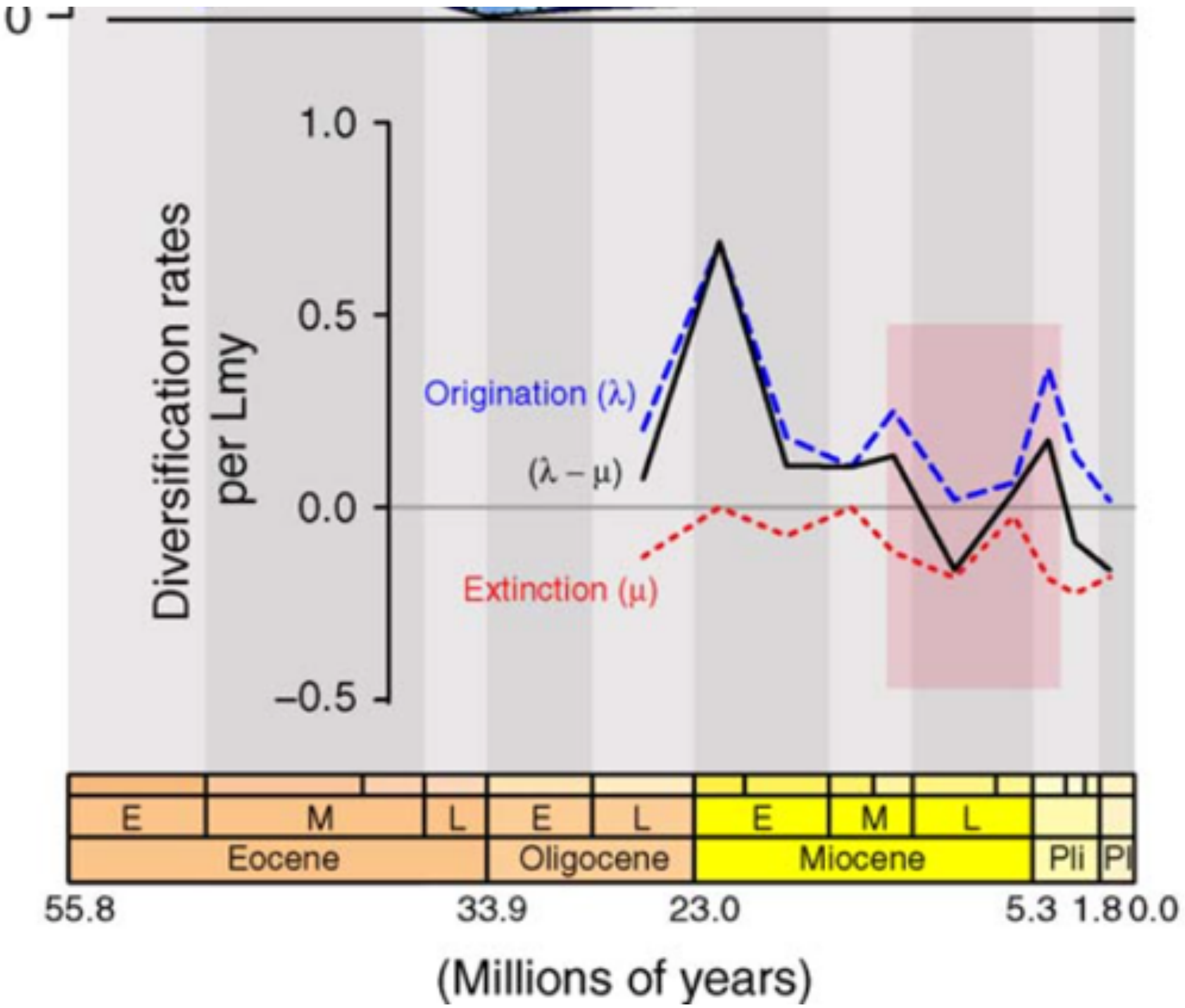
Steeman et al 2009



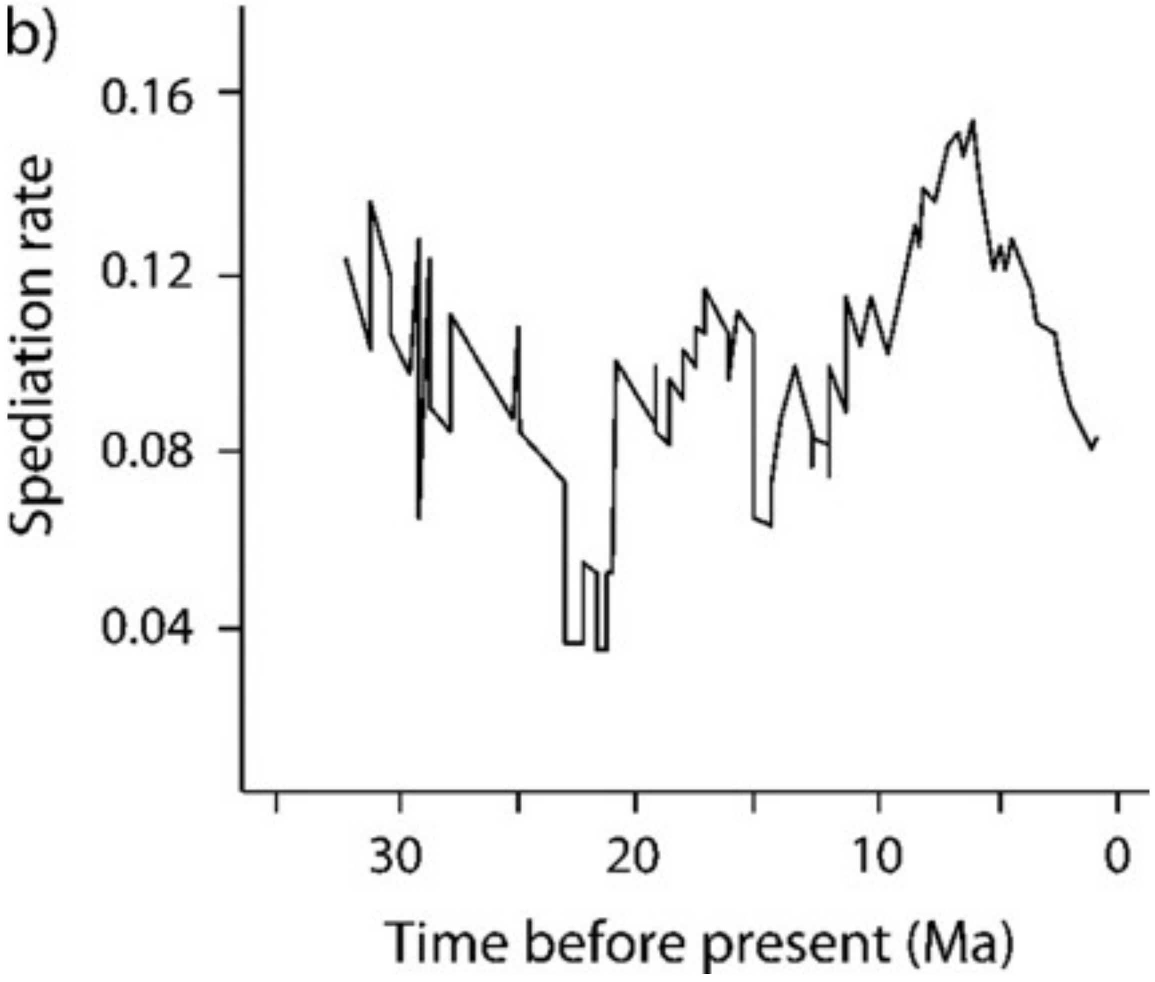
BAMM, RPANDA, and trait independent diversification



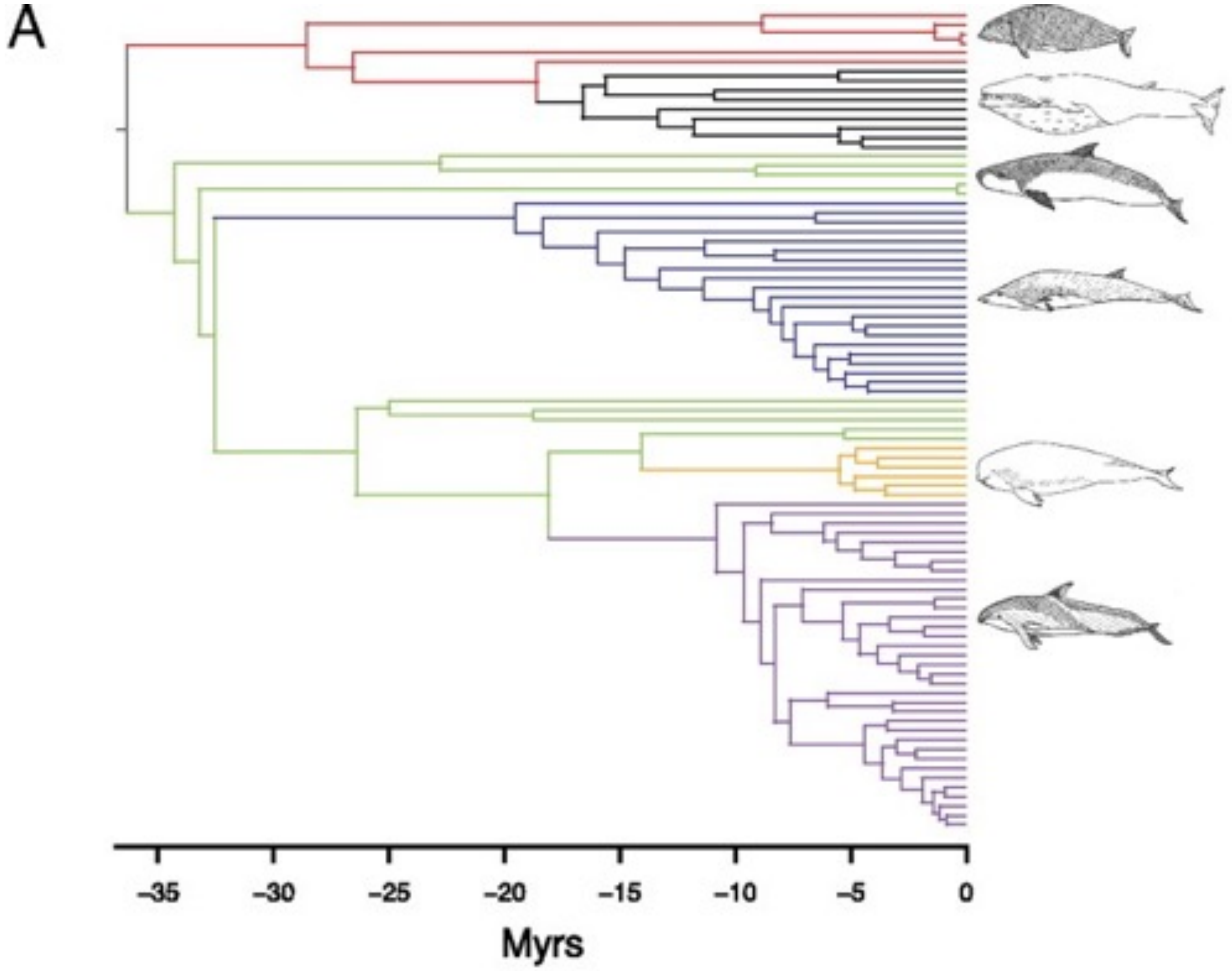
Steeman et al 2009



BAMM, RPANDA, and trait independent diversification

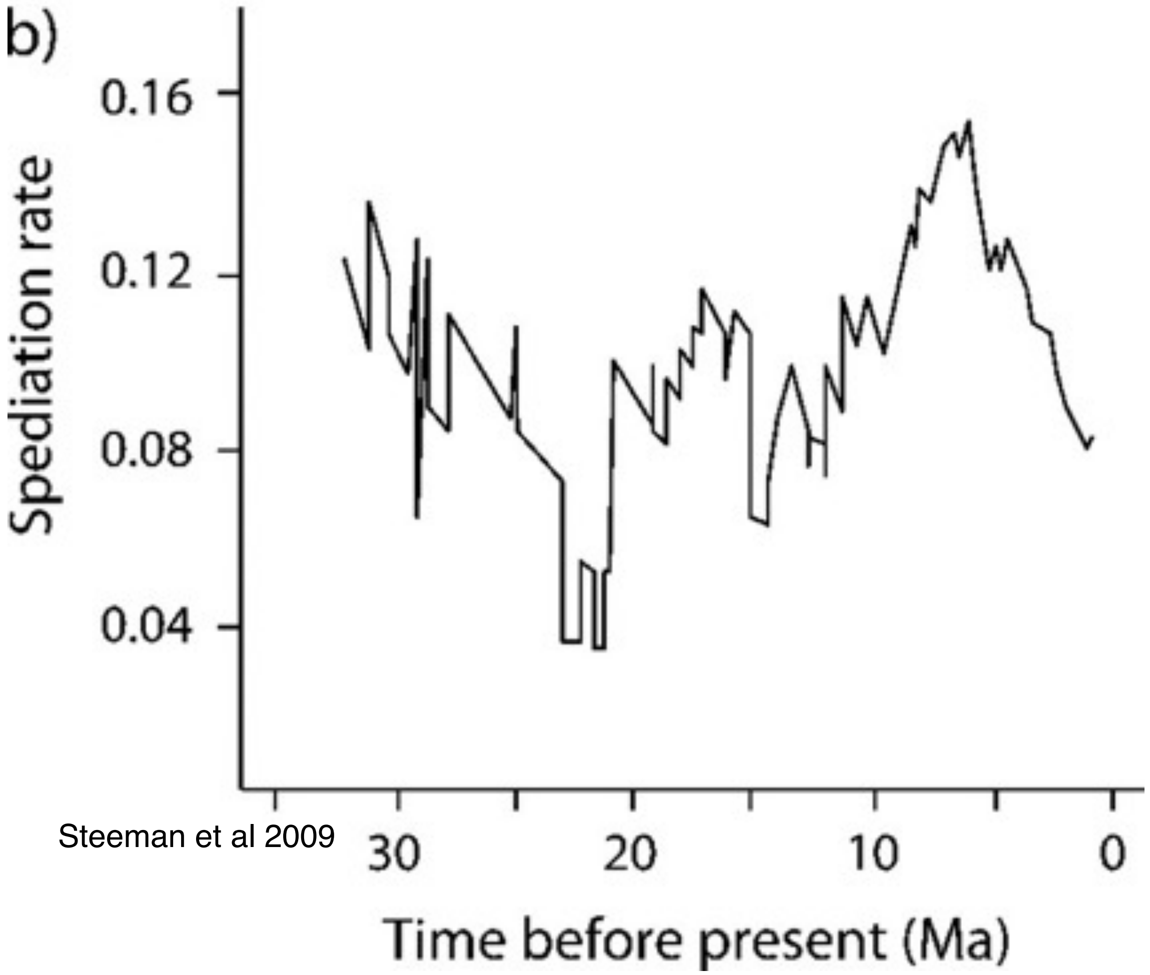


Steeman et al 2009

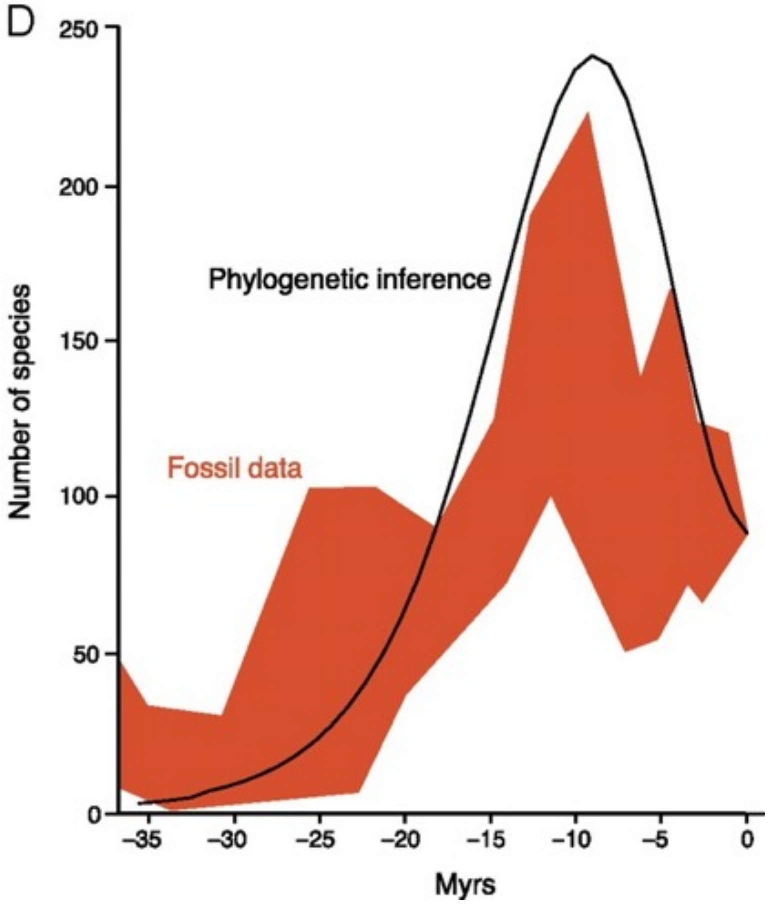


Morlon et al 2010

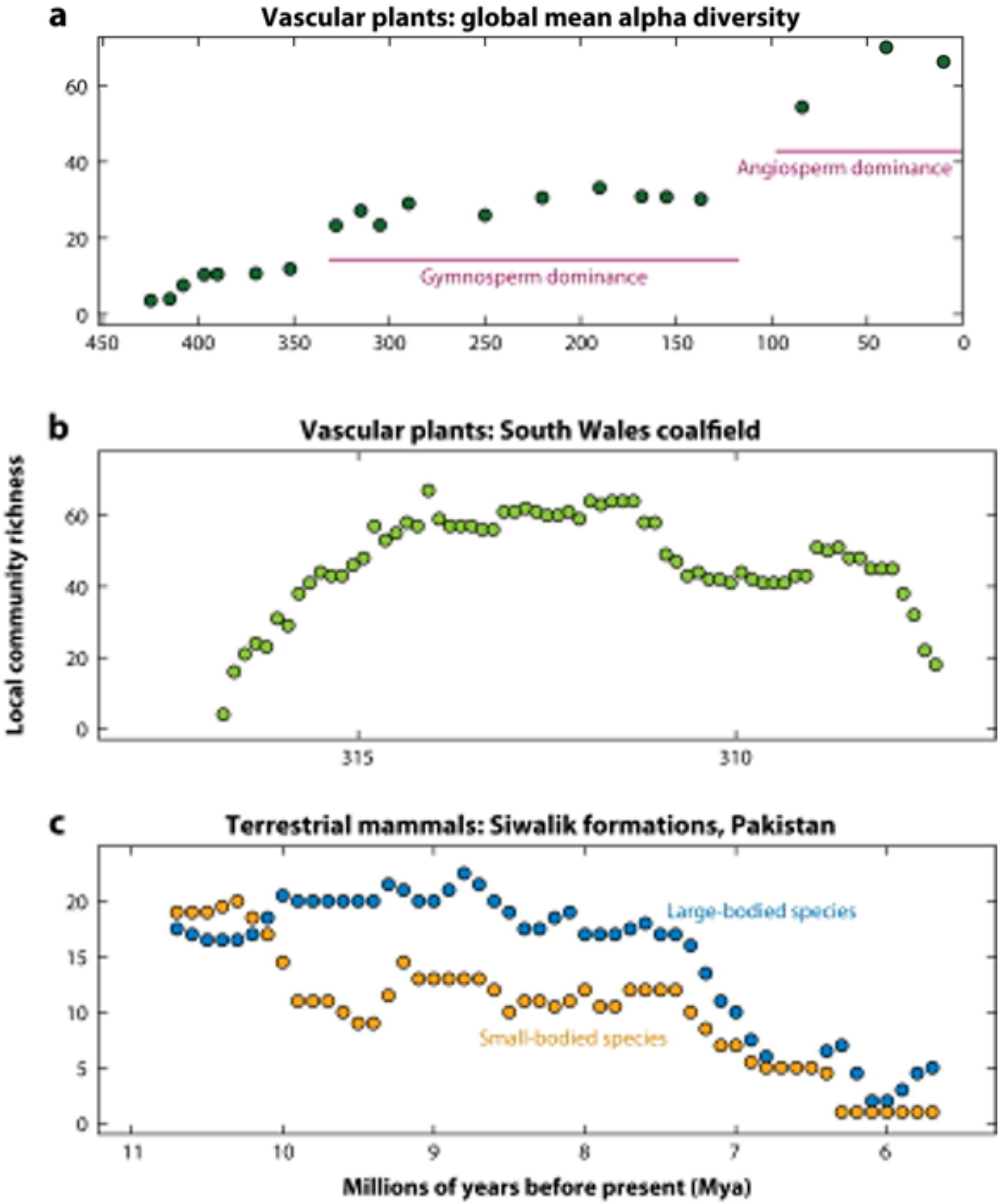
BAMM, RPANDA, and trait independent diversification



Steeman et al 2009



Morlon et al 2010

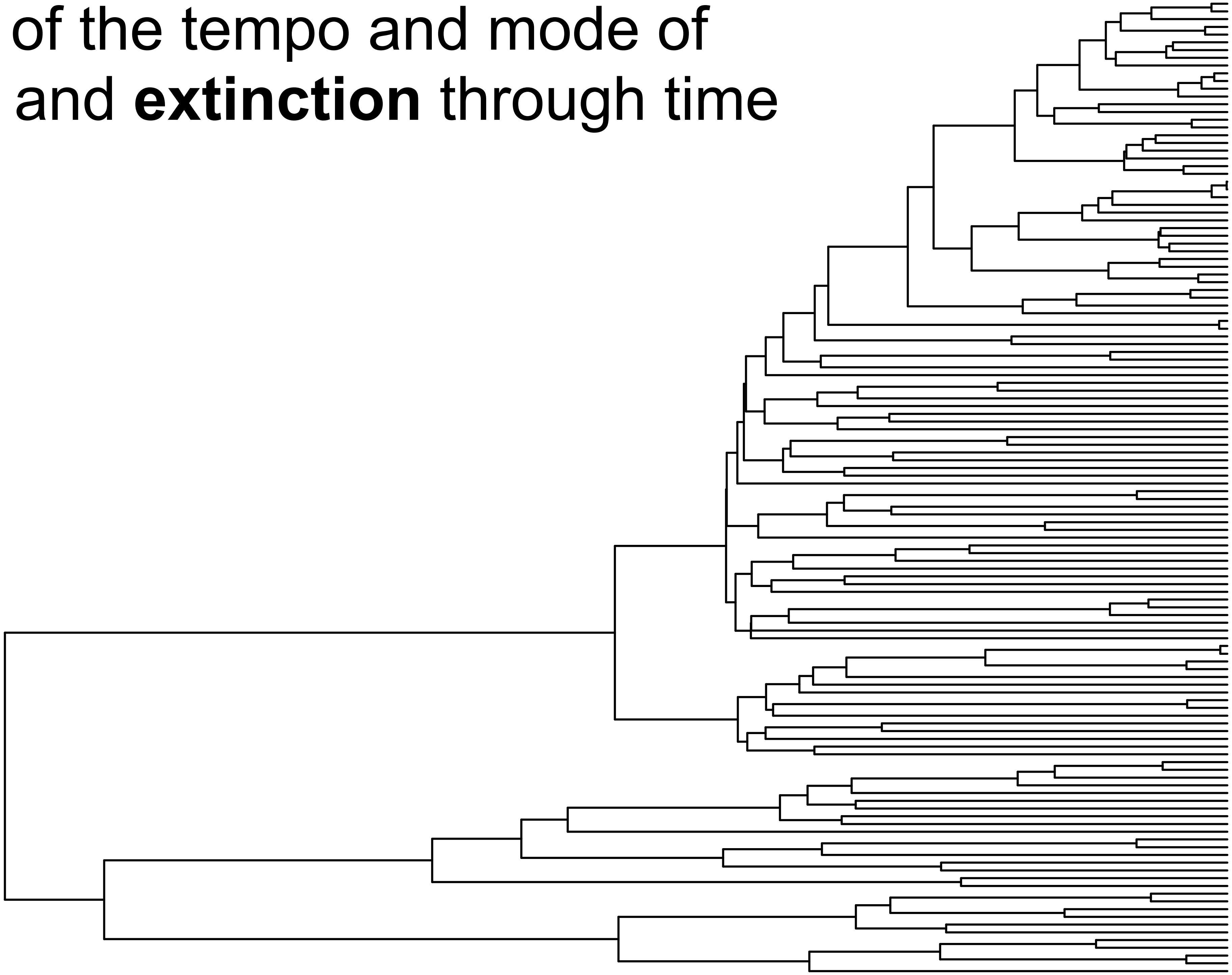


Rabosky DL. 2013.
Annu. Rev. Ecol. Evol. Syst. 44:481–502

does it matter if we study diversity without assuming controls on richness?

Phylogenetic estimates of macroevolutionary rates

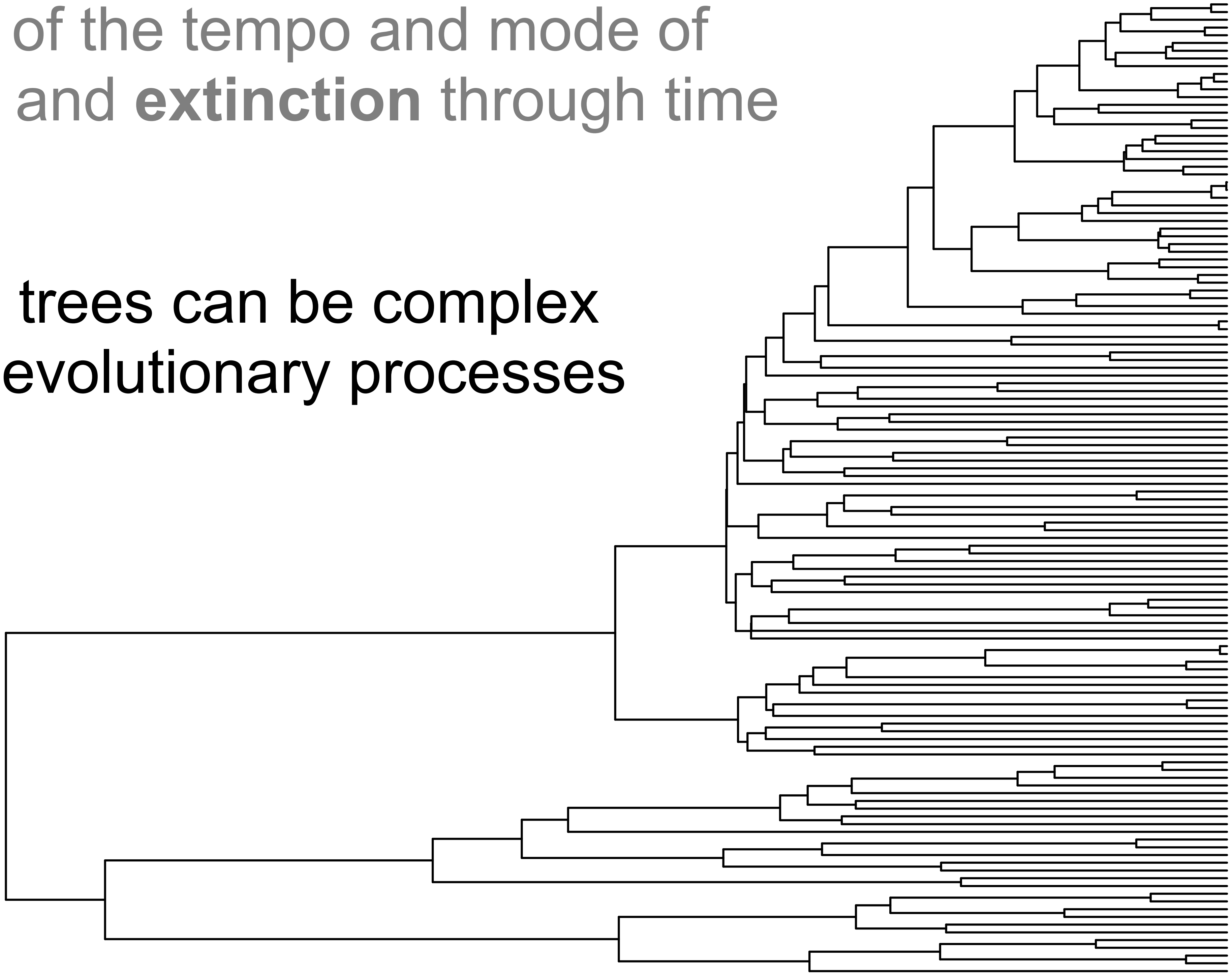
A record of the tempo and mode of **speciation** and **extinction** through time



Phylogenetic estimates of macroevolutionary rates

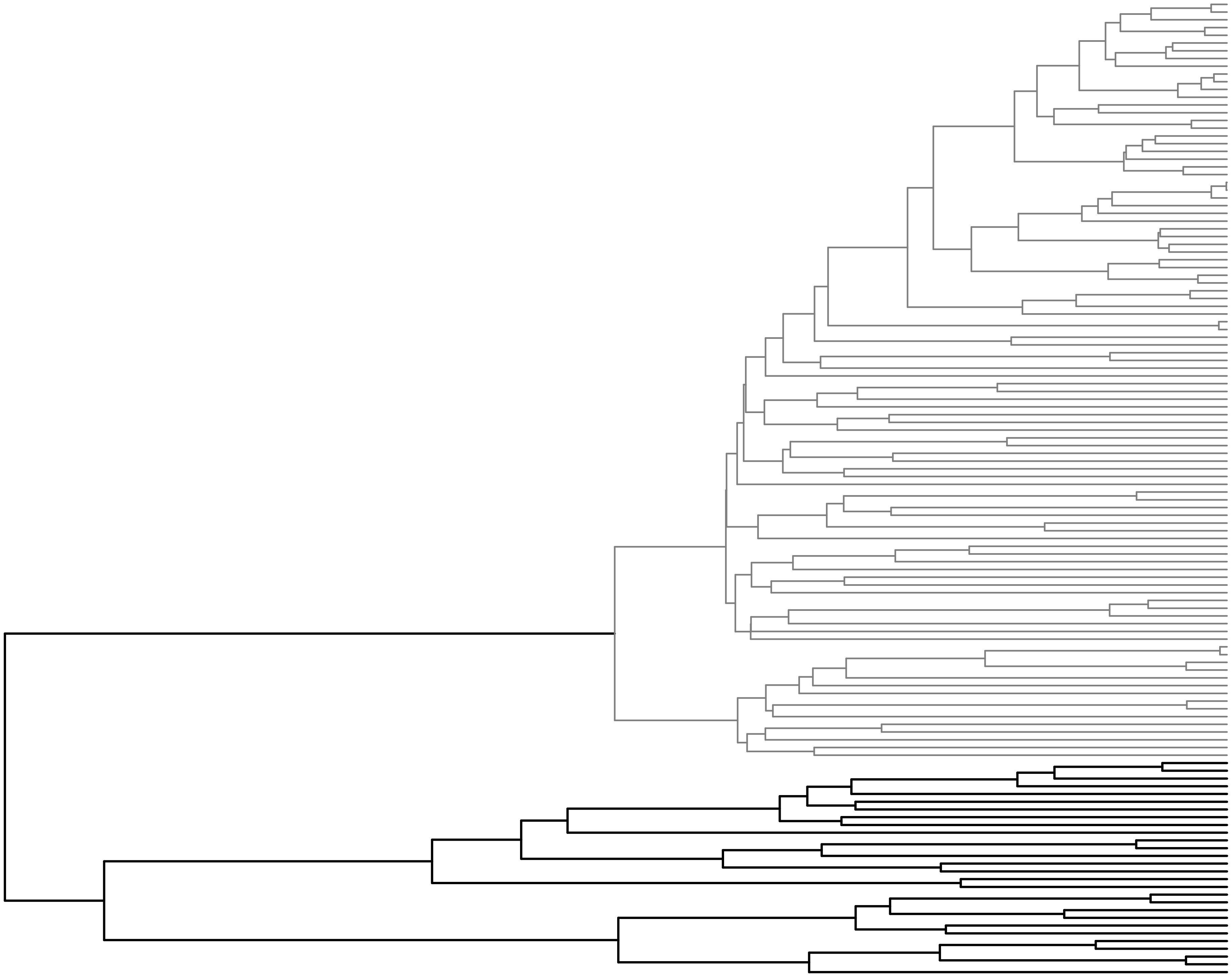
A record of the tempo and mode of **speciation** and **extinction** through time

...but large trees can be complex mixtures of evolutionary processes

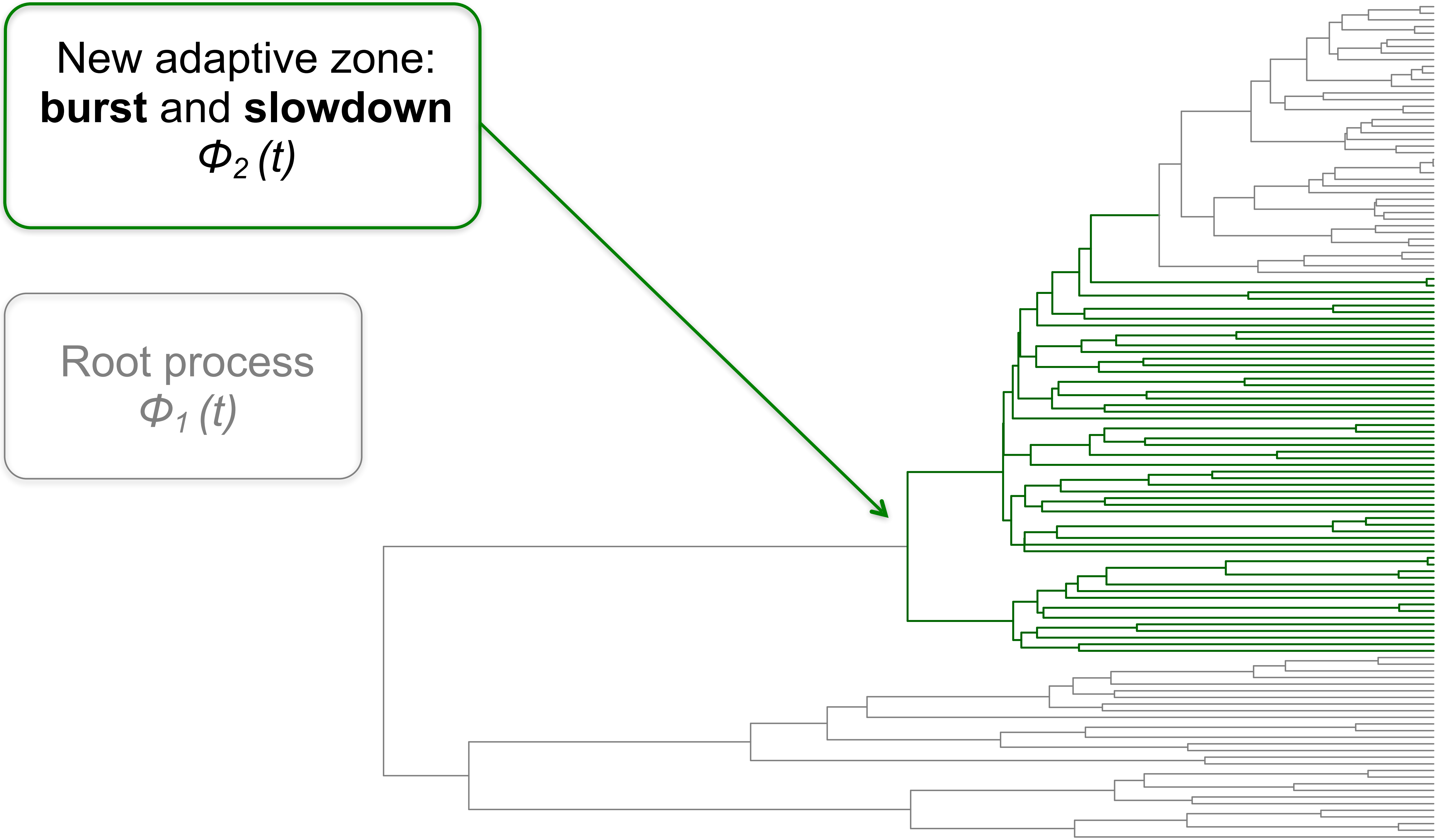


Phylogenetic estimates of macroevolutionary rates

Root process
$\Phi_1(t)$



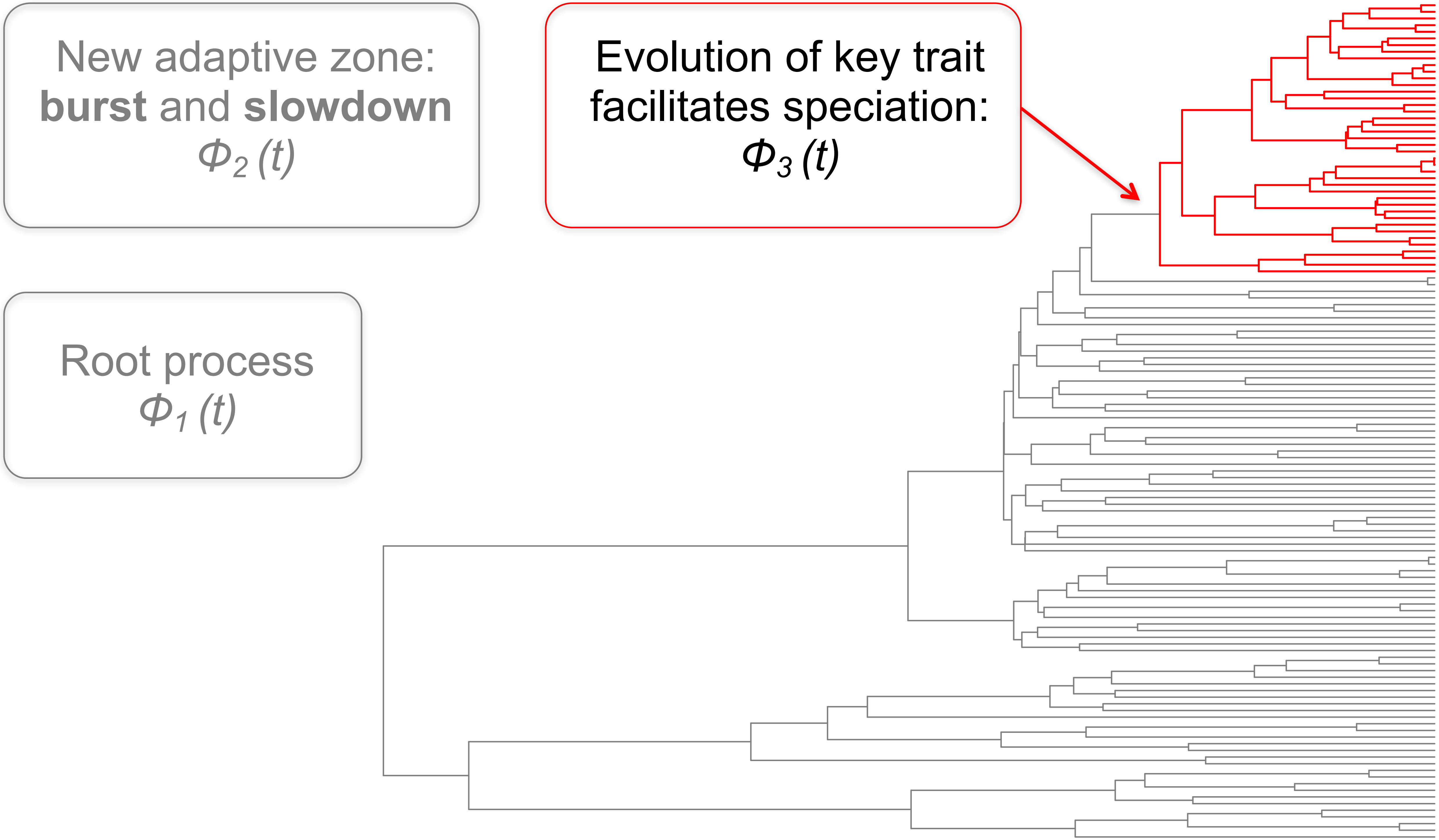
Phylogenetic estimates of macroevolutionary rates



New adaptive zone:
burst and **slowdown**
$\Phi_2(t)$

Root process
$\Phi_1(t)$

Phylogenetic estimates of macroevolutionary rates



New adaptive zone:
burst and **slowdown**
$\Phi_2(t)$

Evolution of key trait facilitates speciation:
$\Phi_3(t)$

Root process
$\Phi_1(t)$

BAMM: Bayesian Analysis of Macroevolutionary Mixtures

What are the evolutionary processes that have shaped a phylogenetic tree?

BAMM: Bayesian Analysis of Macroevolutionary Mixtures

What are the evolutionary processes that have shaped a phylogenetic tree?

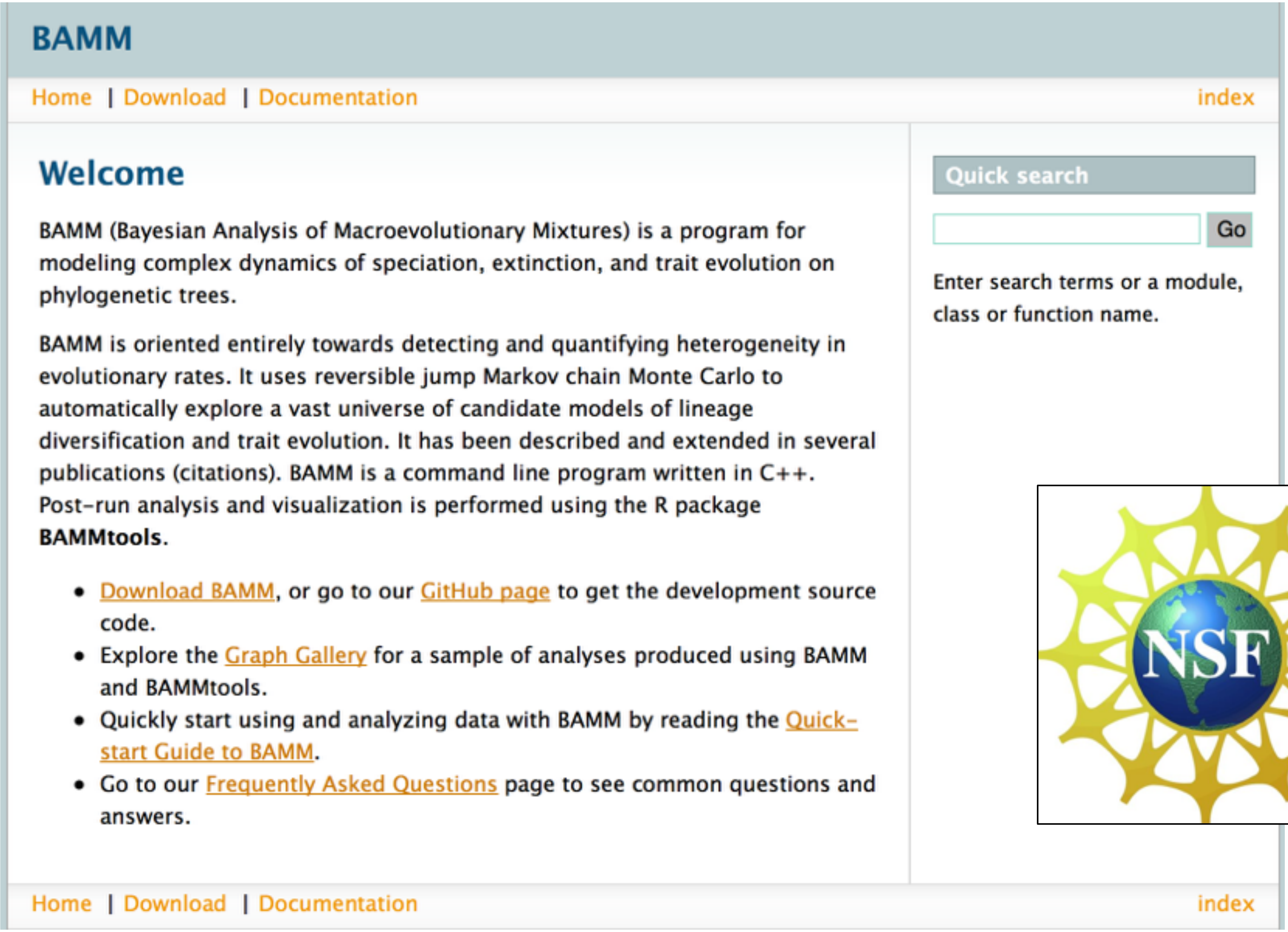
BAMM uses **transdimensional MCMC** to automatically detect:

- Key innovations
- Explosive radiations
- Diversity-dependence and rate variation through time

Estimates of distributions of evolutionary rates
at ***every point in time*** *on* ***every branch***

Rabosky, PLoS ONE, *2014*

http://bamm-project.org/



Enter search terms or a module, class or function name.

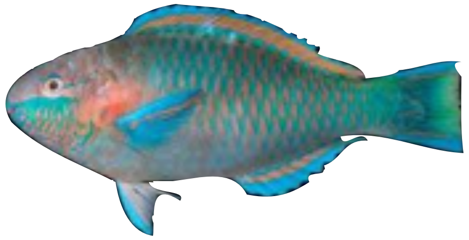
Welcome

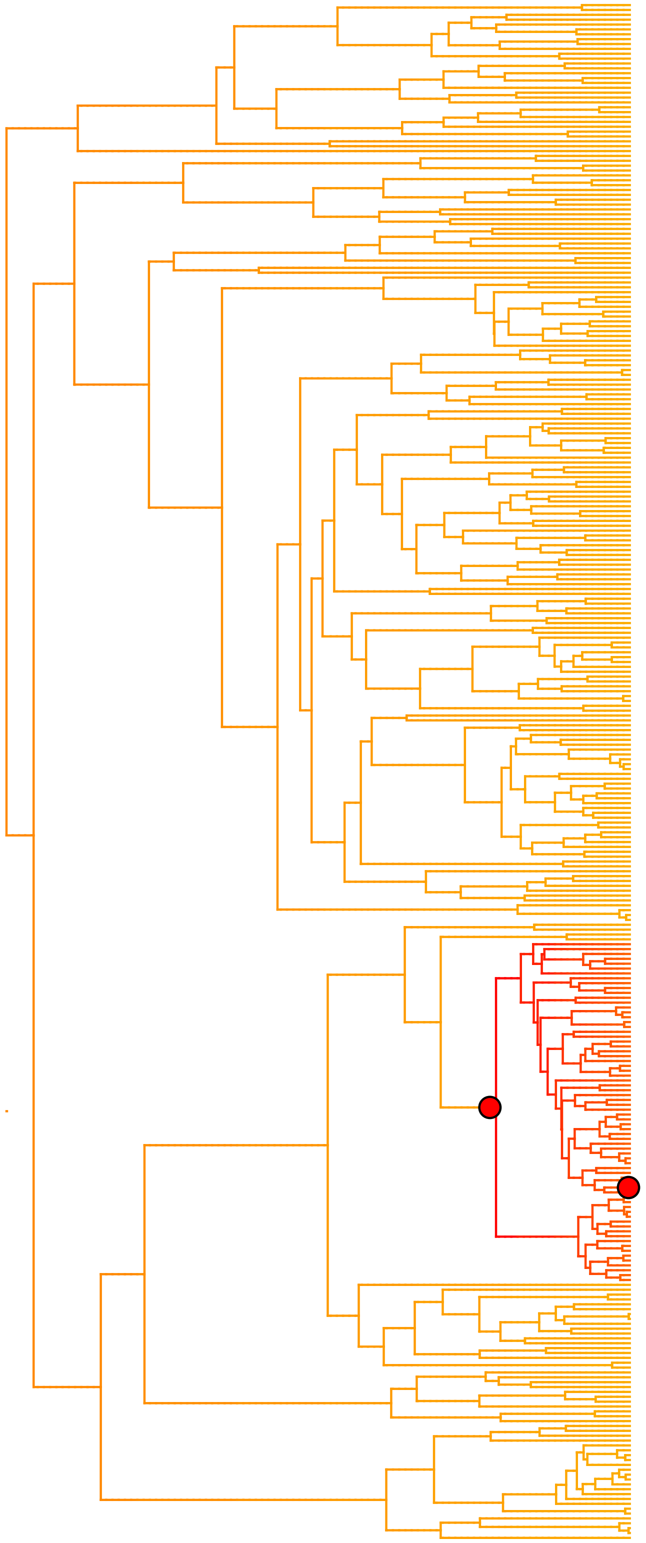
BAMM (Bayesian Analysis of Macroevolutionary Mixtures) is a program for modeling complex dynamics of speciation, extinction, and trait evolution on phylogenetic trees.

BAMM is oriented entirely towards detecting and quantifying heterogeneity in evolutionary rates. It uses reversible jump Markov chain Monte Carlo to automatically explore a vast universe of candidate models of lineage diversification and trait evolution. It has been described and extended in several publications (citations). BAMM is a command line program written in C++. Post-run analysis and visualization is performed using the R package **BAMMtools**.

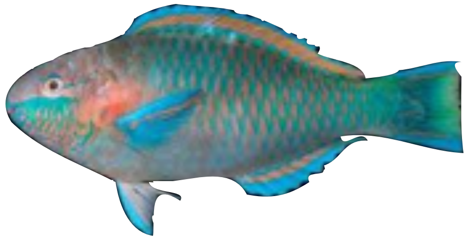
- Download BAMM, or go to our GitHub page to get the development source code.
- Explore the Graph Gallery for a sample of analyses produced using BAMM and BAMMtools.
- Quickly start using and analyzing data with BAMM by reading the Quick-start Guide to BAMM.
- Go to our Frequently Asked Questions page to see common questions and answers.

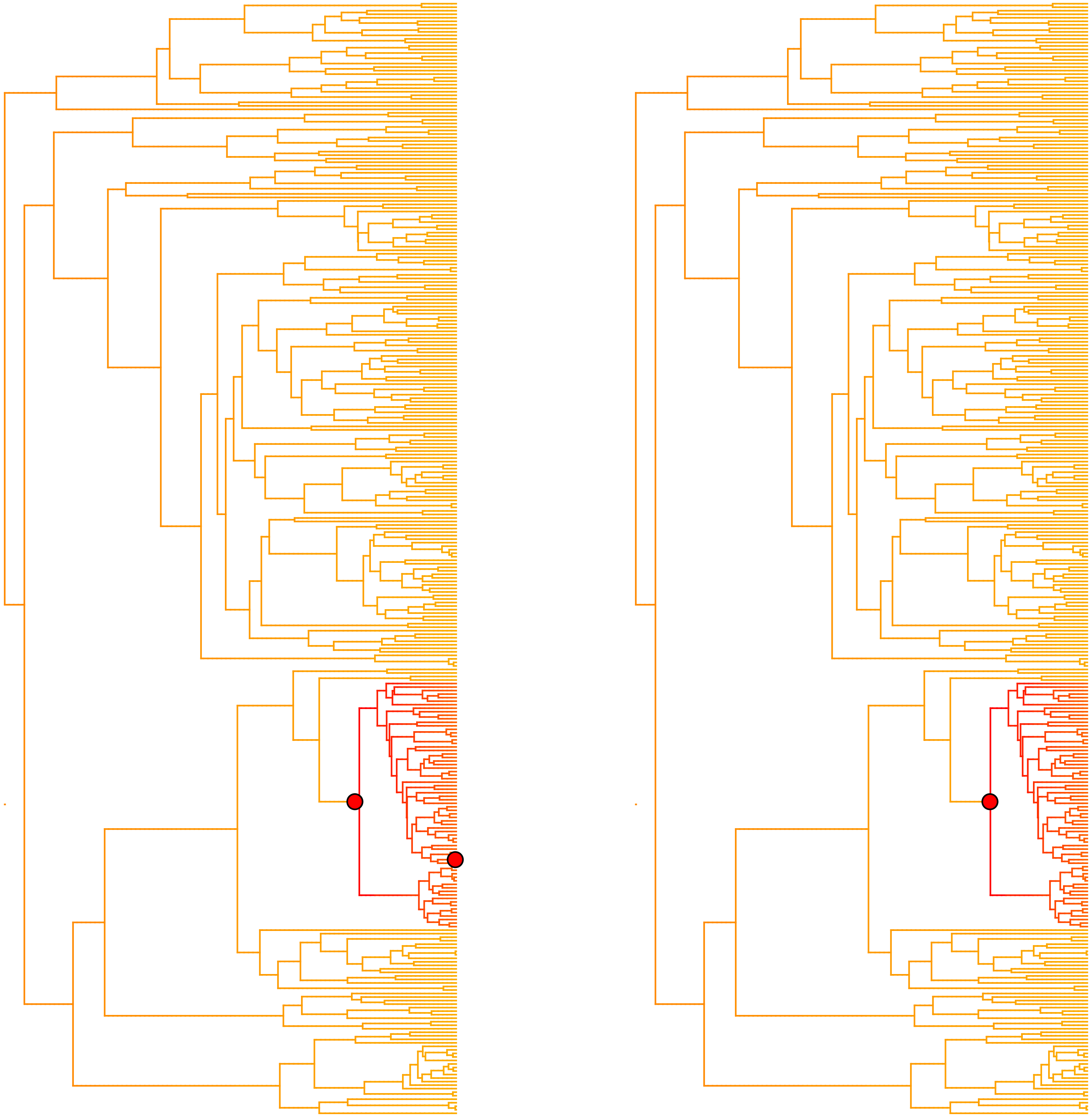
BAMM example



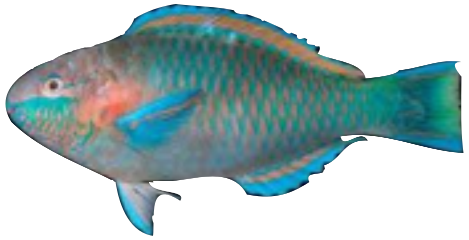


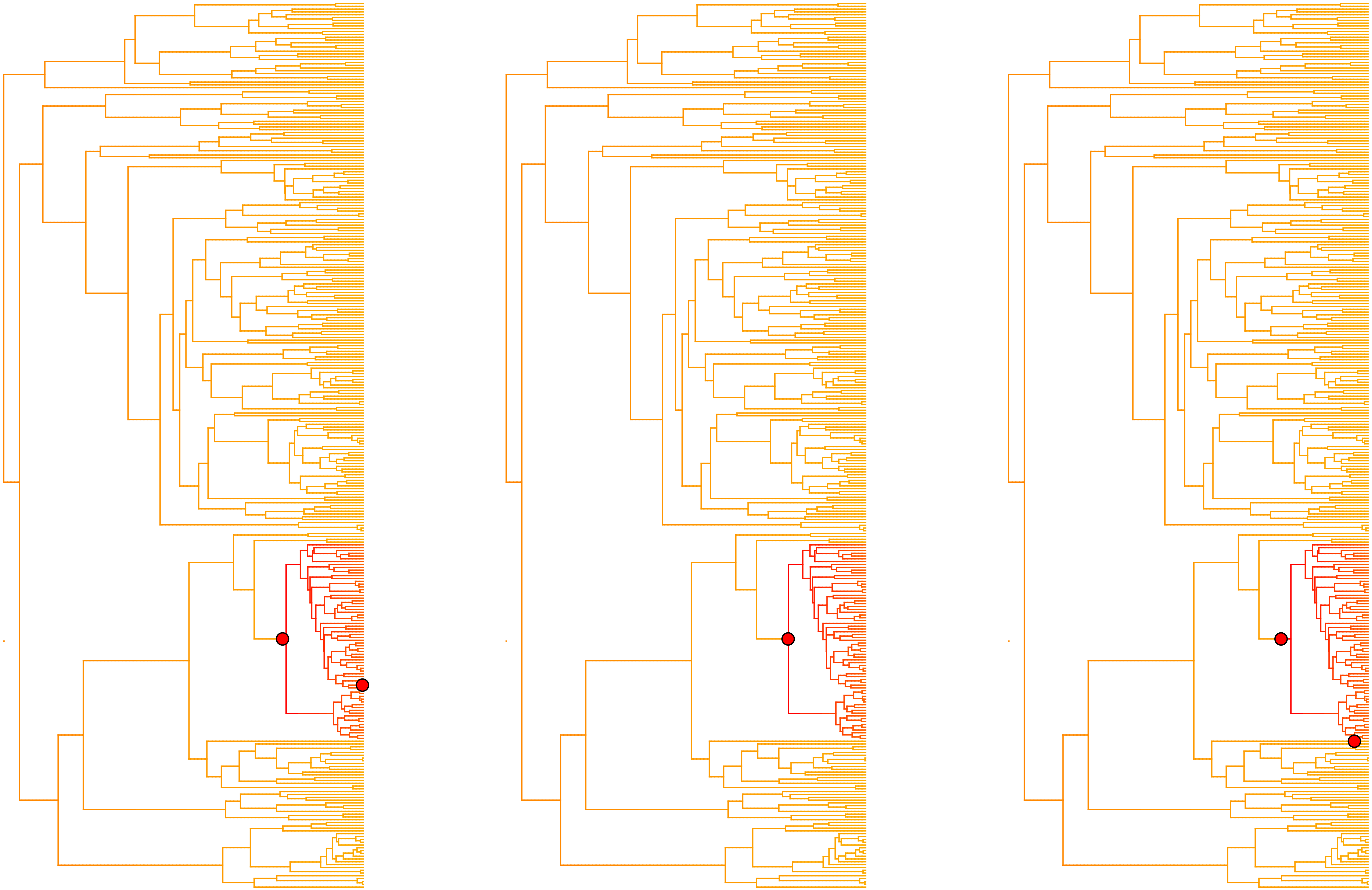
BAMM example

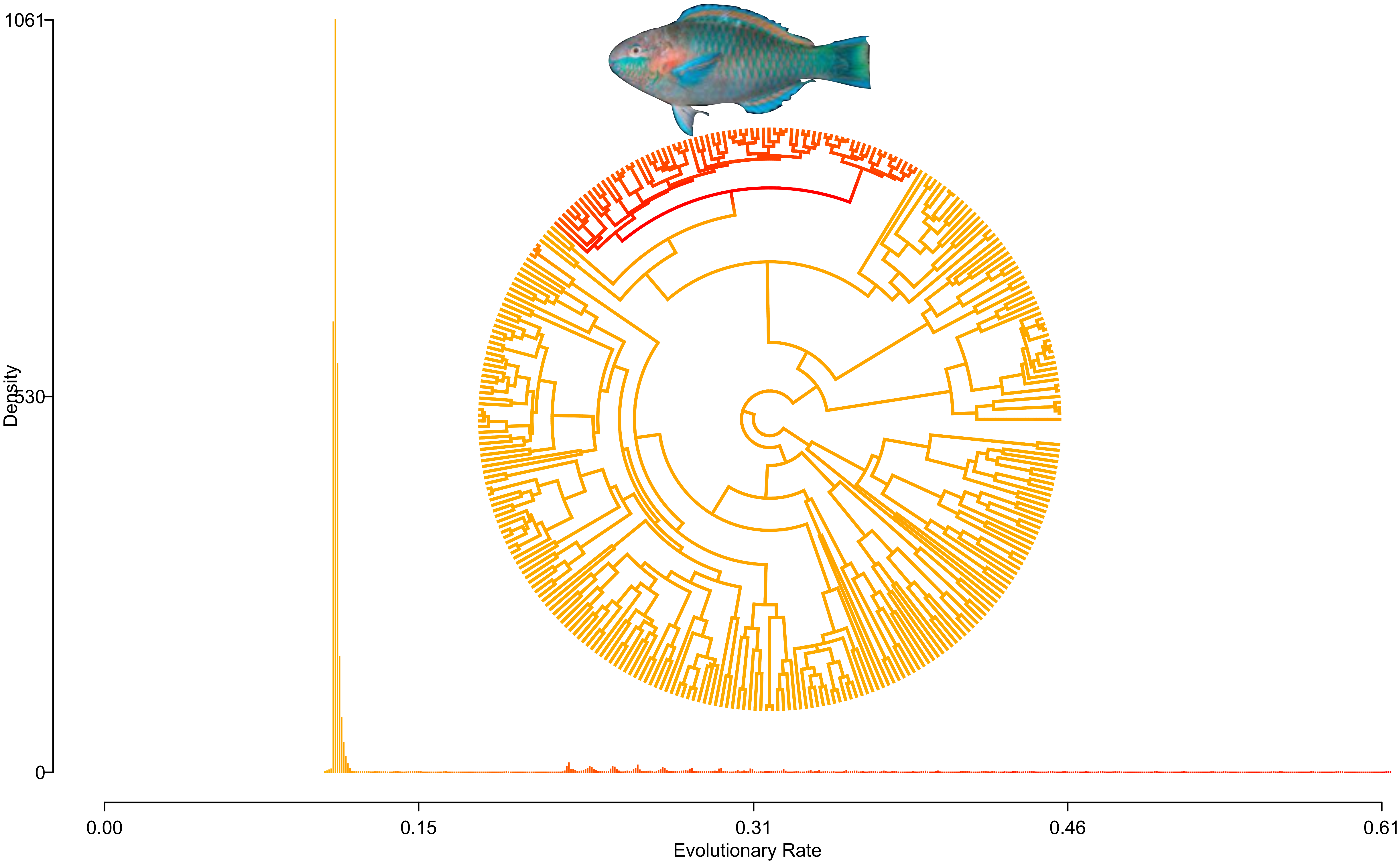


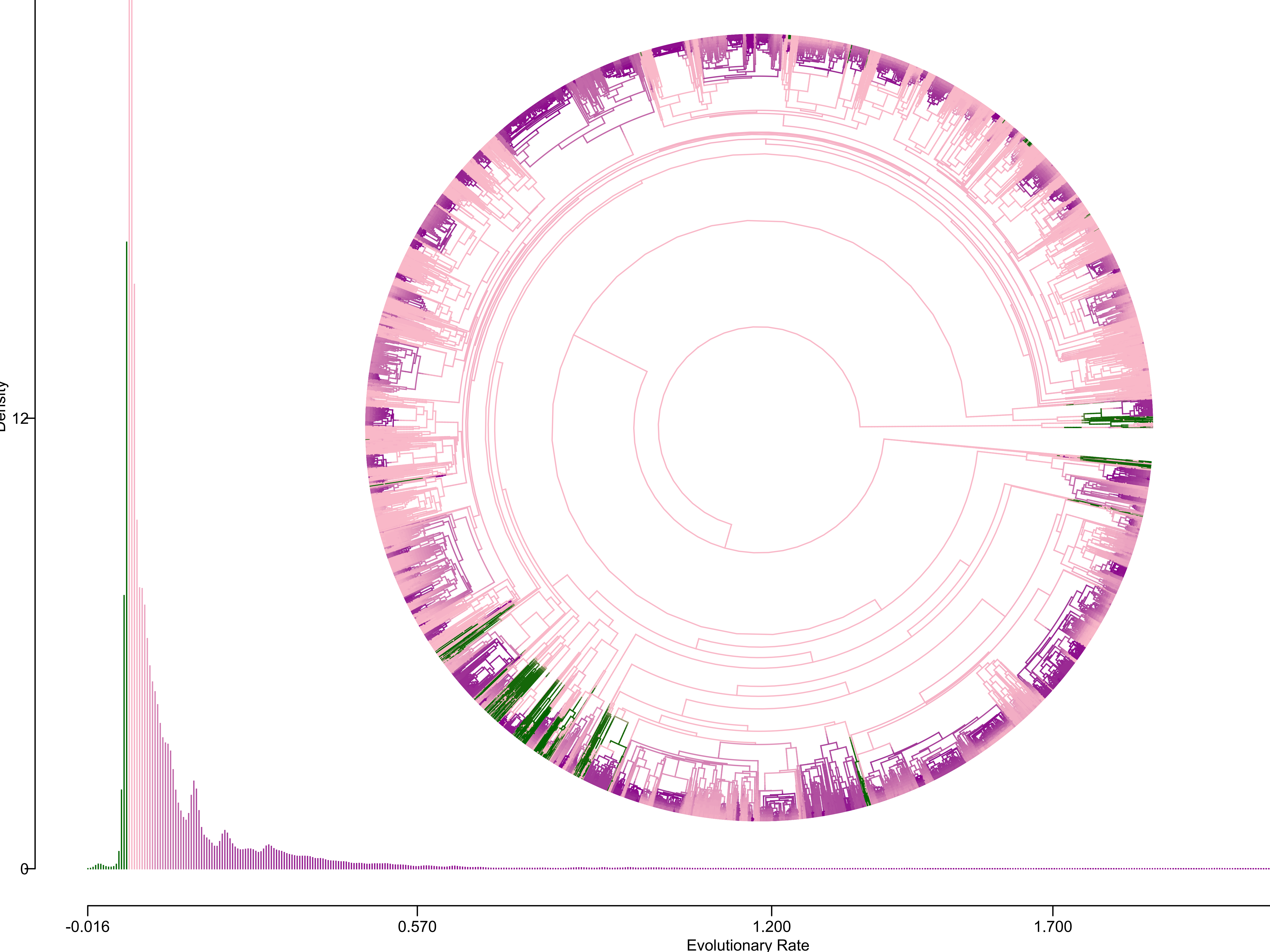


BAMM example



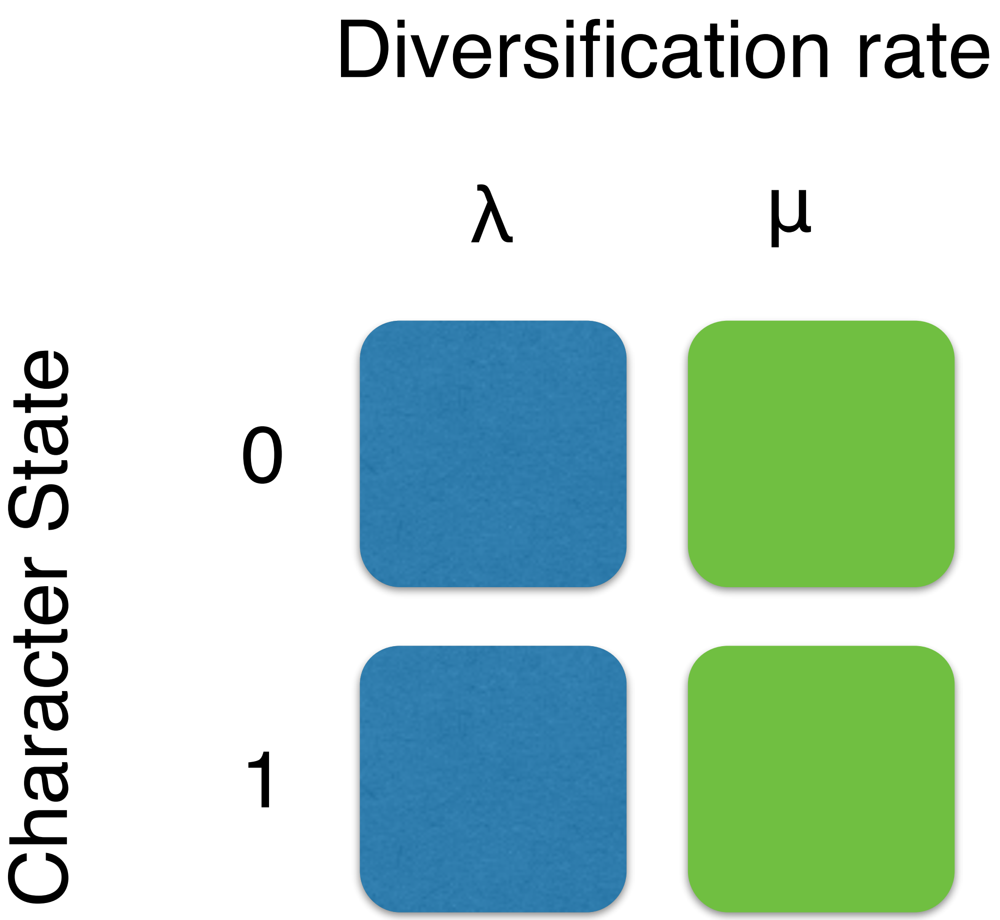



1061
530
0
Density
0.00
0.15
0.31
0.46
0.61
Evolutionary Rate


Density
12
0
-0.016
0.570
1.200
1.700
Evolutionary Rate

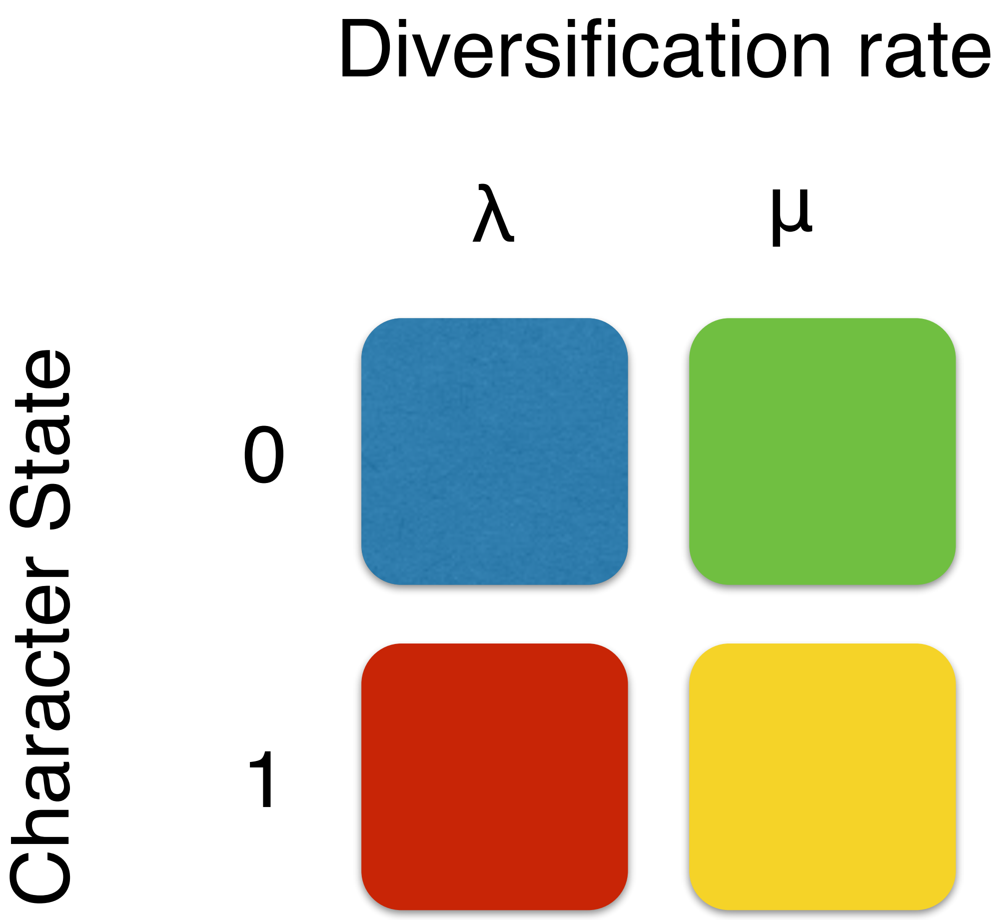
BiSSE and SSE models

Character-independent model vs. Character-dependent model



Diversification rate

Character State	λ	μ
0	🟦	🟩
1	🟦	🟩



Diversification rate

Character State	λ	μ
0	🟦	🟩
1	🟥	🟨

BiSSE Family

- BiSSE - binary character
- MuSSE - multi-state character
- ClaSSE - cladogenesis
- GeoSSE - geography
- QuaSSE - quantitative character

ERM Model

- BD is a special case of the Equal Rates Markov model (ERM)
- ERM Model assumptions
  - Markov model: next step depends only on current state
  - Equal rates: b and d are constant across lineages at any given time
  - b and/or d might change through time