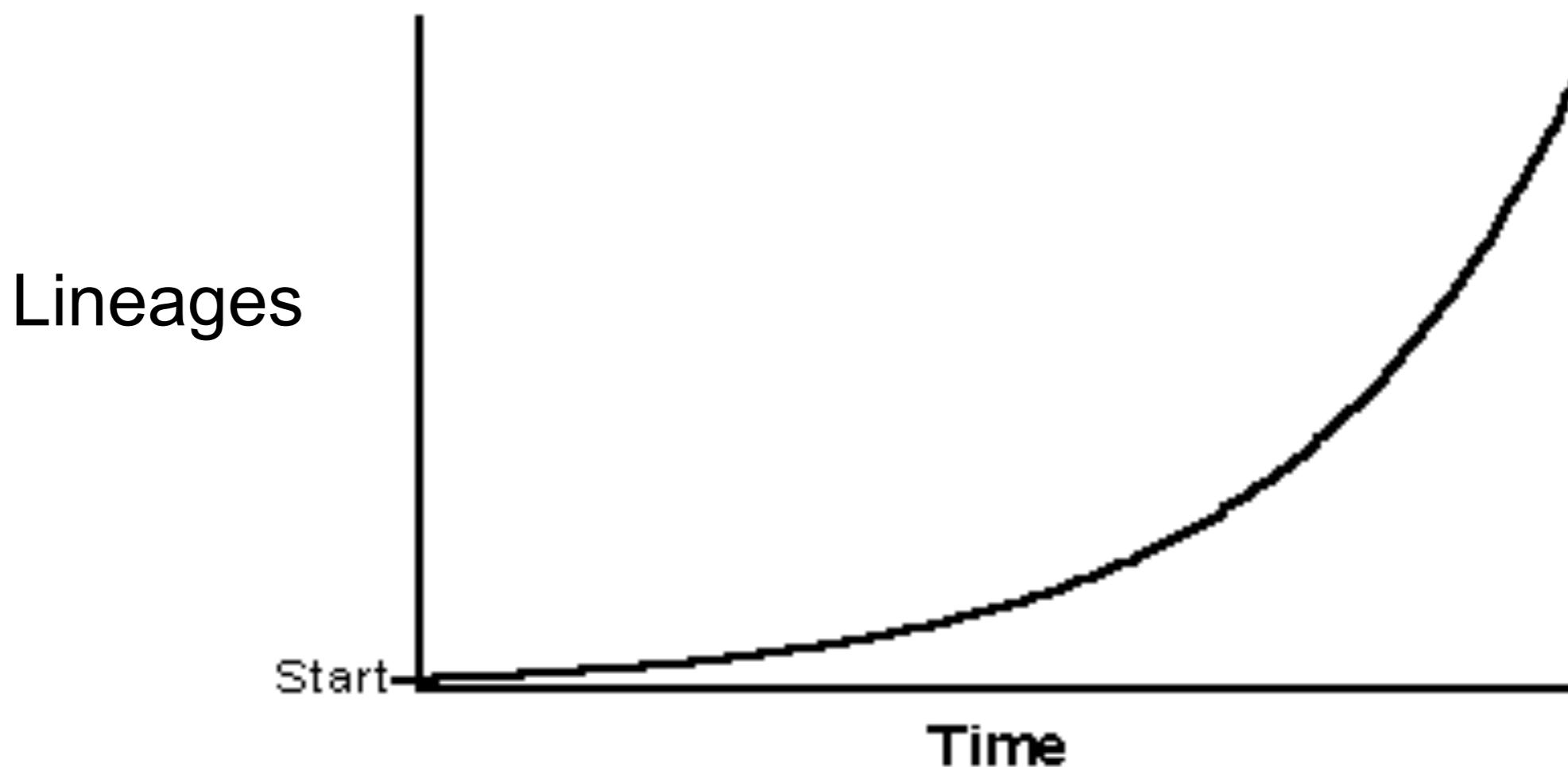


# Diversification models



# Birth-death model

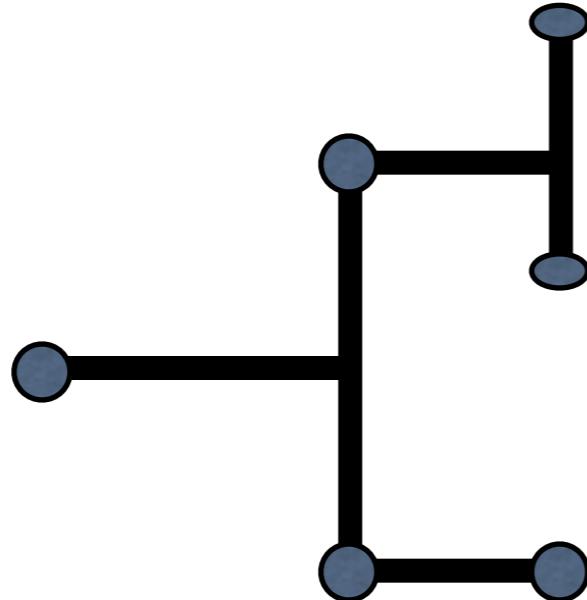
- Assumptions:
  - Speciation and extinction occur randomly
  - Each lineage has an equal and constant rate of speciation,  $b$ , and extinction,  $d$

# 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

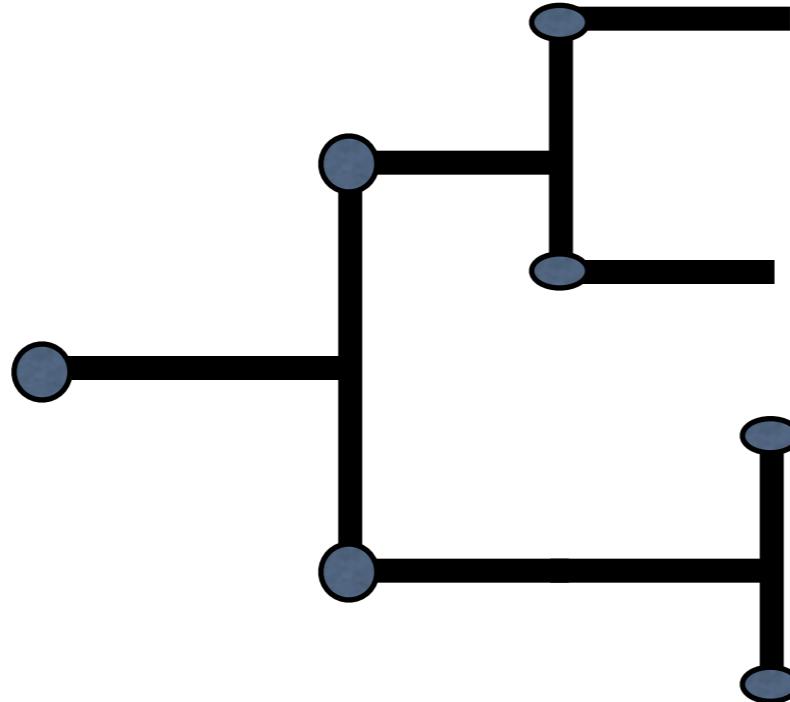
# Diversification Model

- Model: birth-death
- Every lineage has constant probability of:
  - speciation ( $\lambda$ )
  - extinction ( $\mu$ )



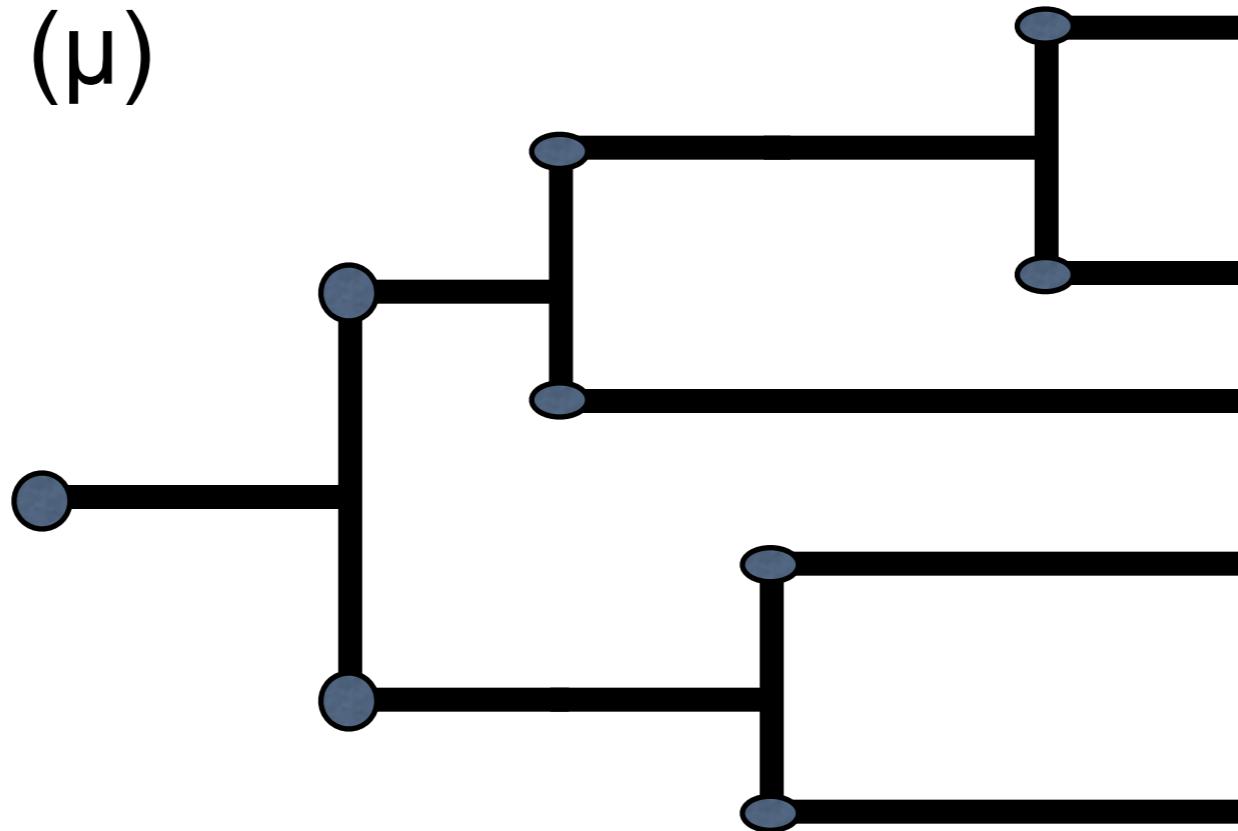
# Diversification Model

- Model: birth-death
- Every lineage has constant probability of:
  - speciation ( $\lambda$ )
  - extinction ( $\mu$ )



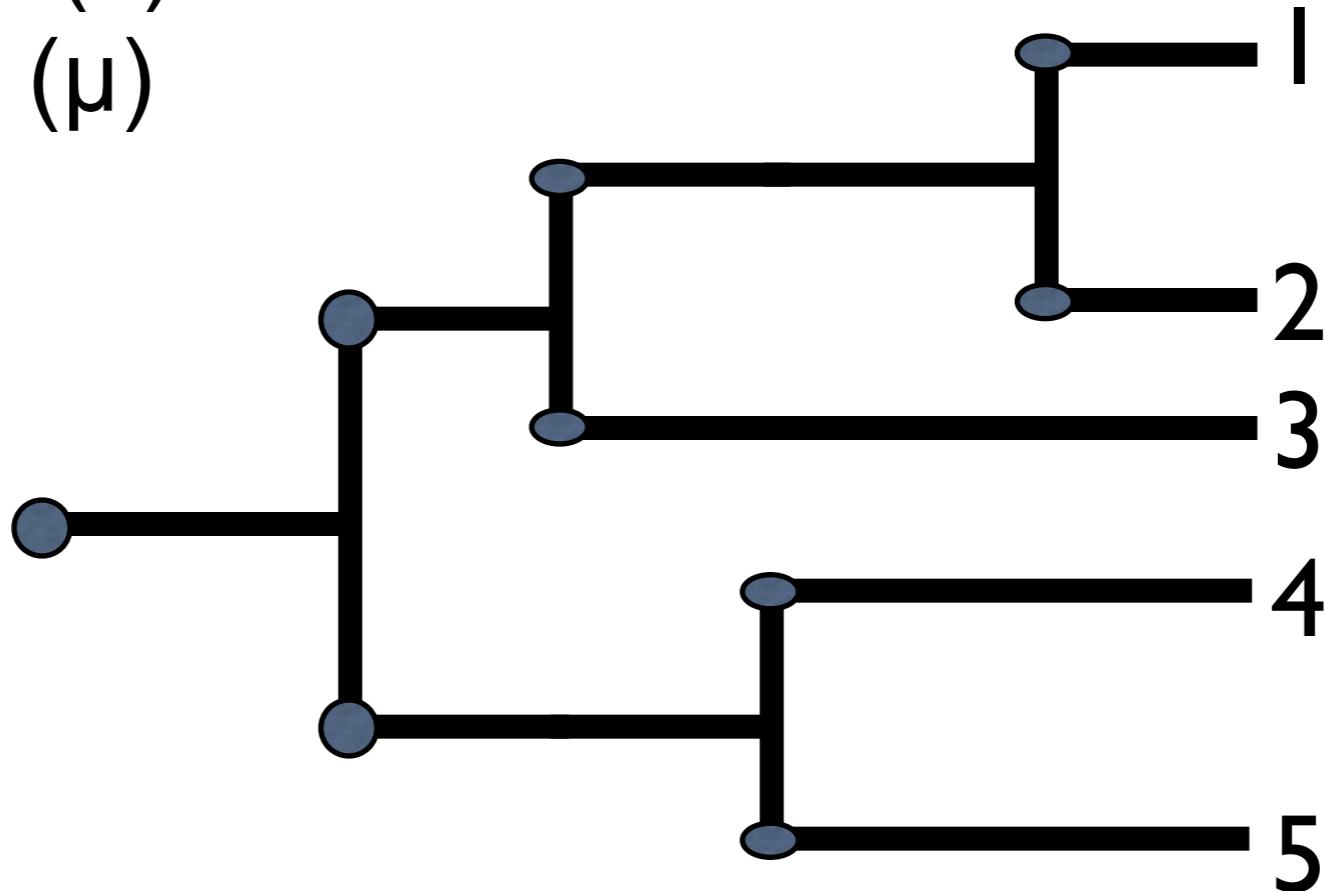
# Diversification Model

- Model: birth-death
- Every lineage has constant probability of:
  - speciation ( $\lambda$ )
  - extinction ( $\mu$ )



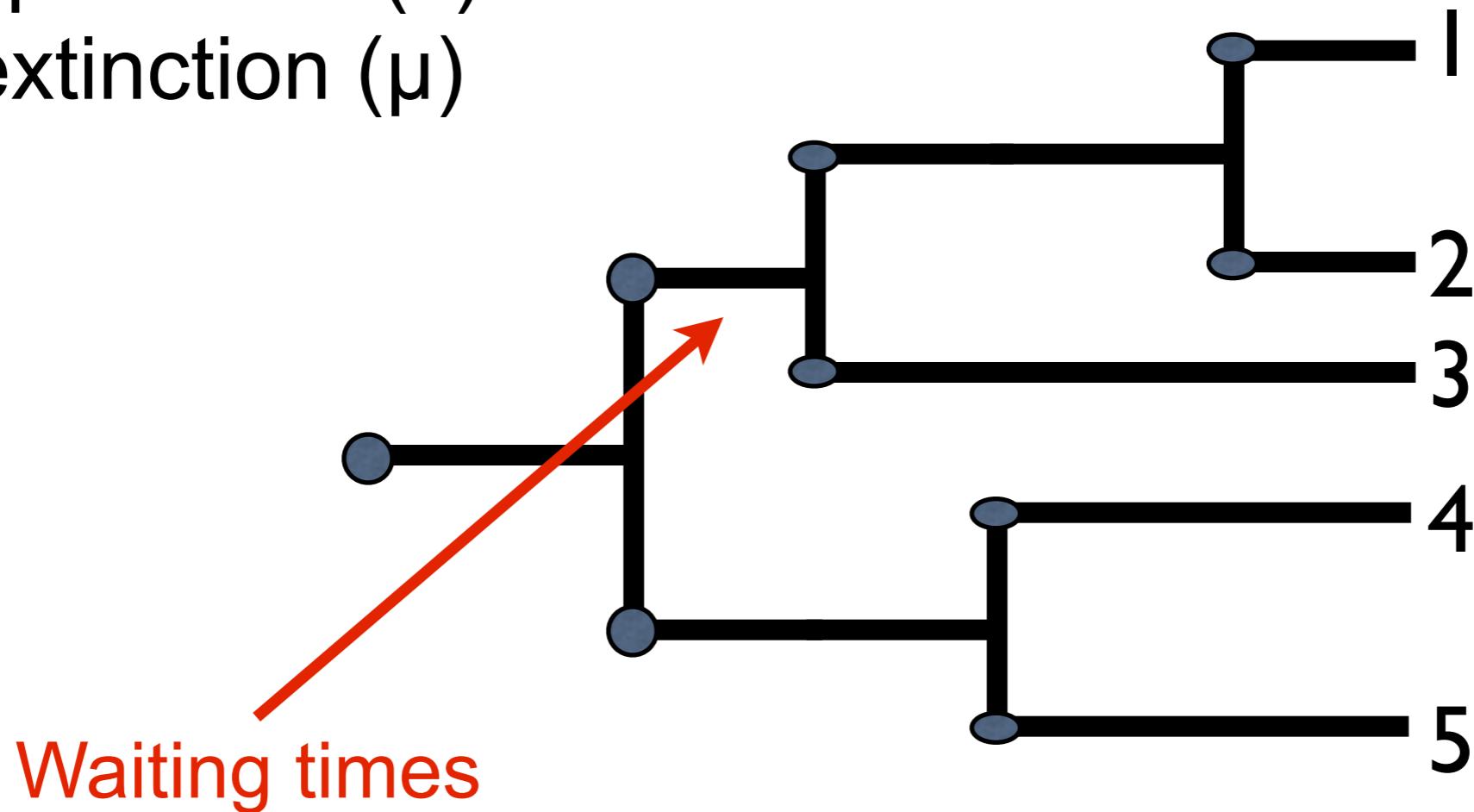
# Diversification Model

- Model: birth-death
- Every lineage has constant probability of:
  - speciation ( $\lambda$ )
  - extinction ( $\mu$ )



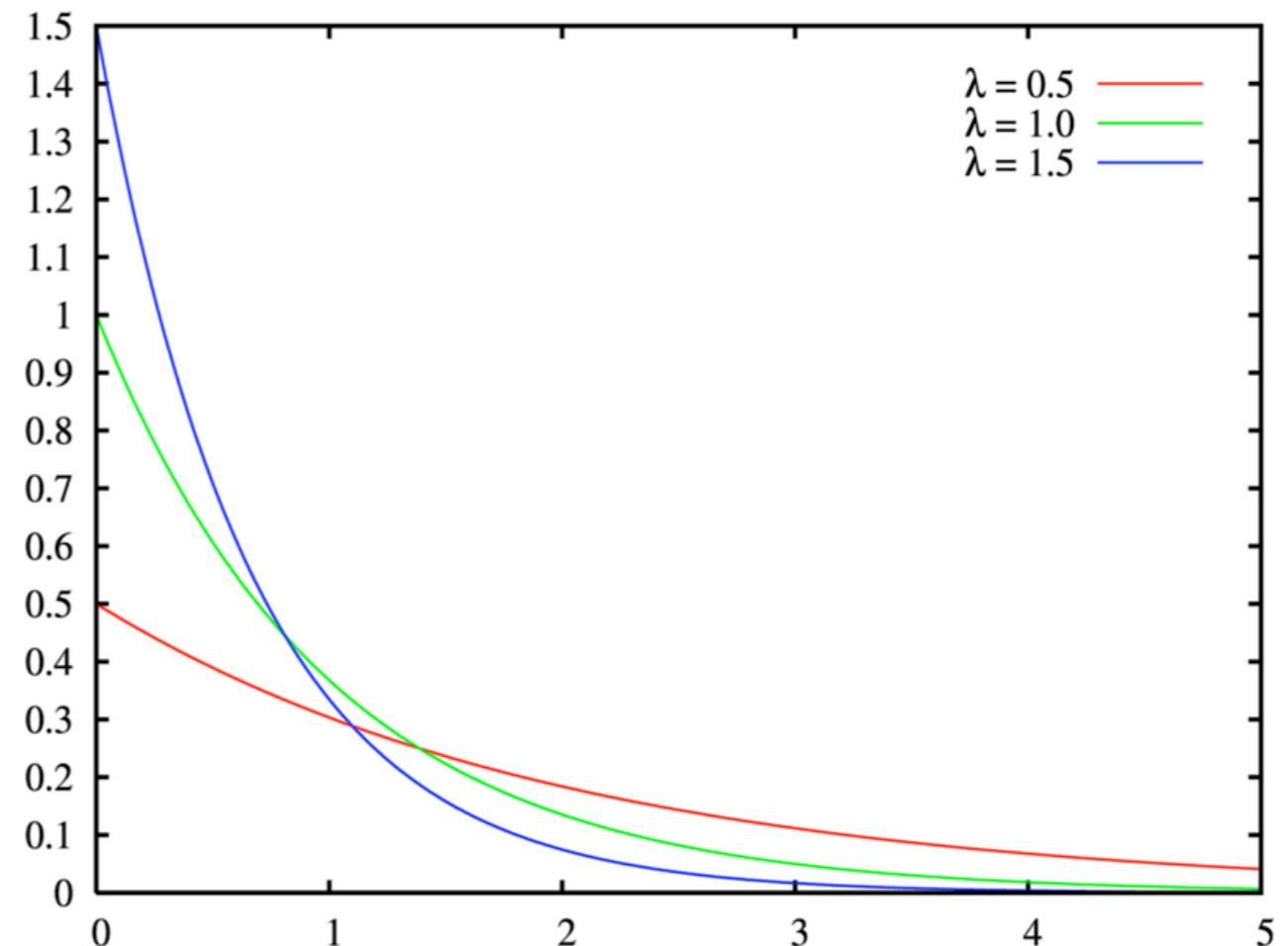
# Diversification Model

- Model: birth-death
- Every lineage has constant probability of:
  - speciation ( $\lambda$ )
  - extinction ( $\mu$ )



# Waiting times

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



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

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

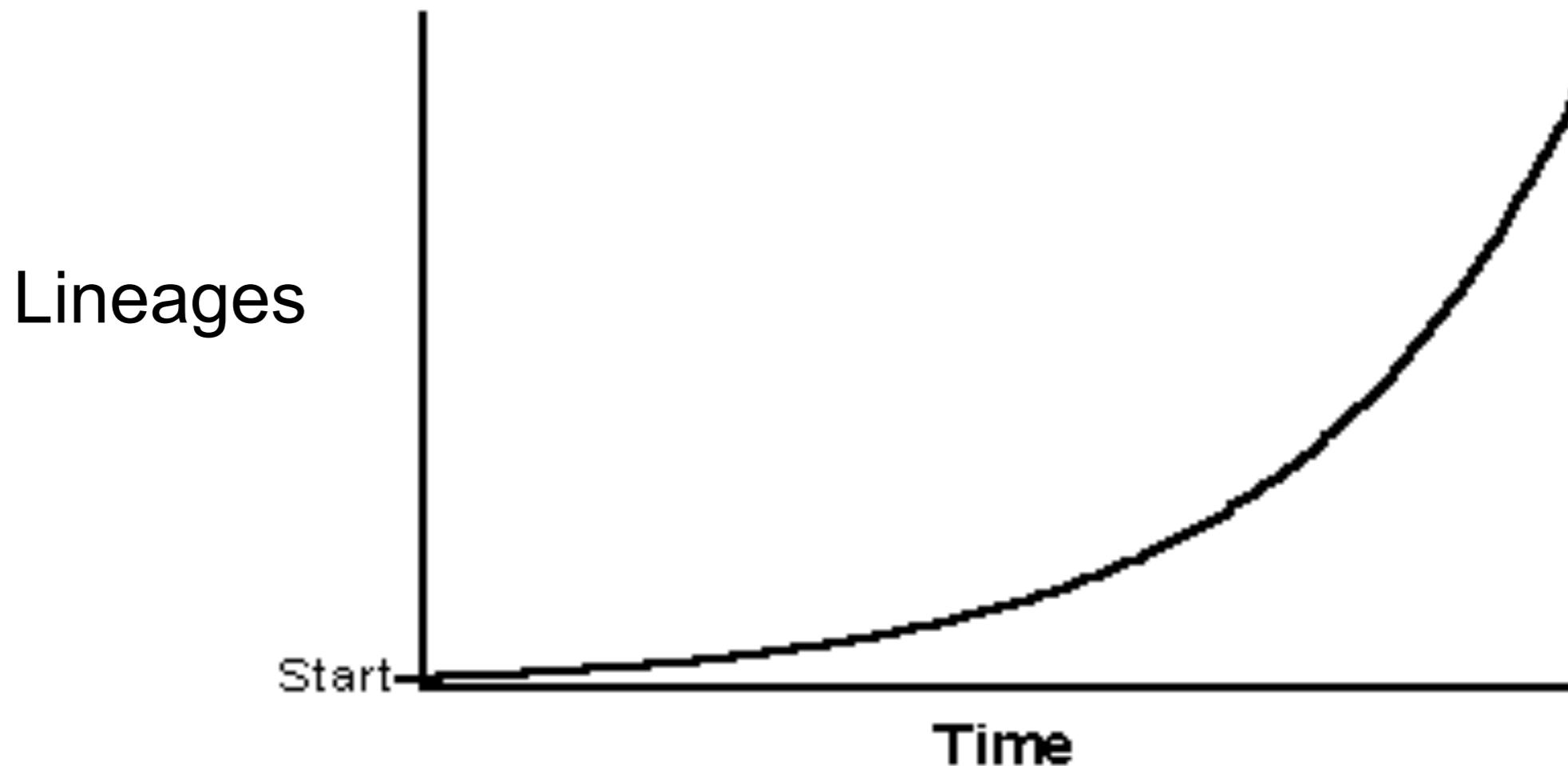
$b$  = birth rate

$d$  = death rate

$t$  = time

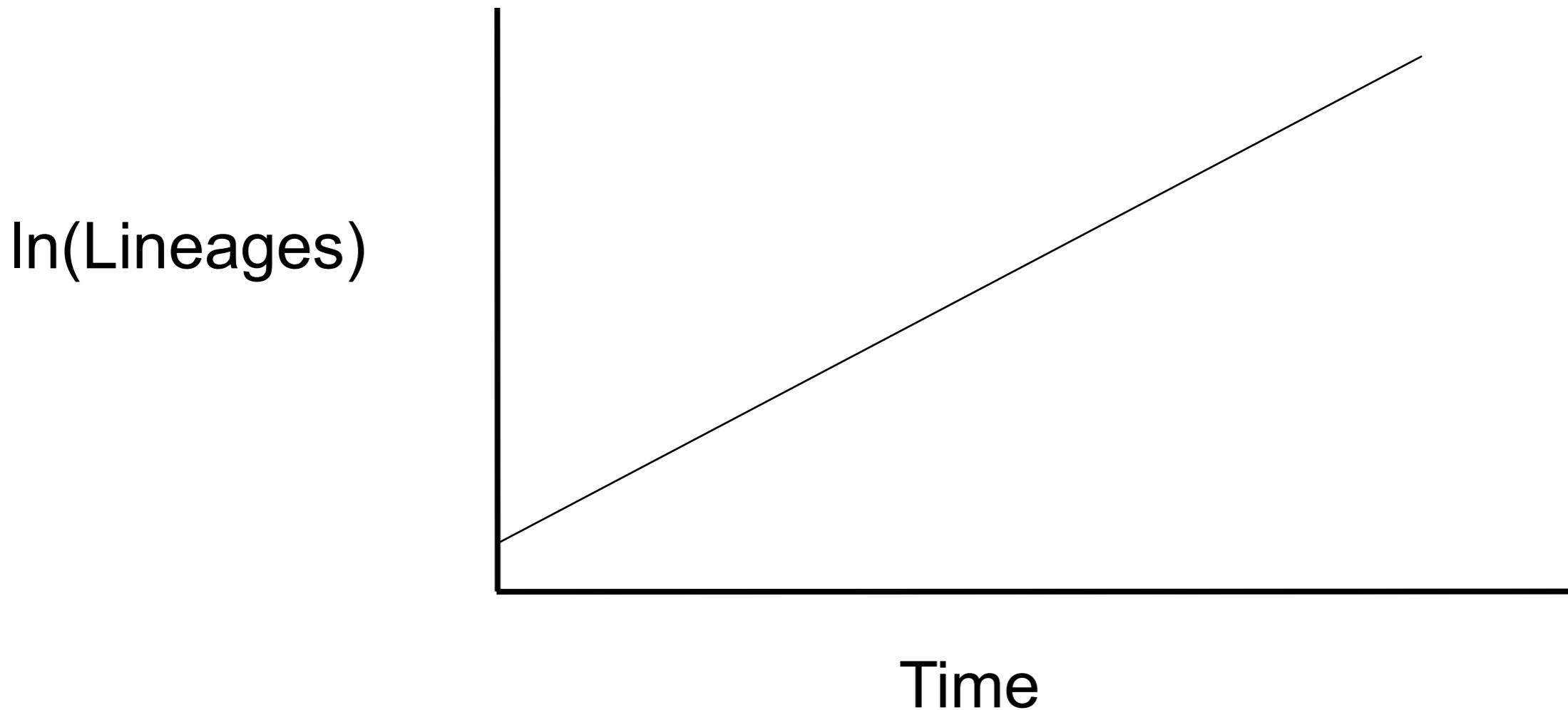
# Species Accumulation

- Expected number of species increases exponentially with  $\lambda - \mu$



# Diversification Model

- Expected number of species increases exponentially with  $\lambda - \mu$

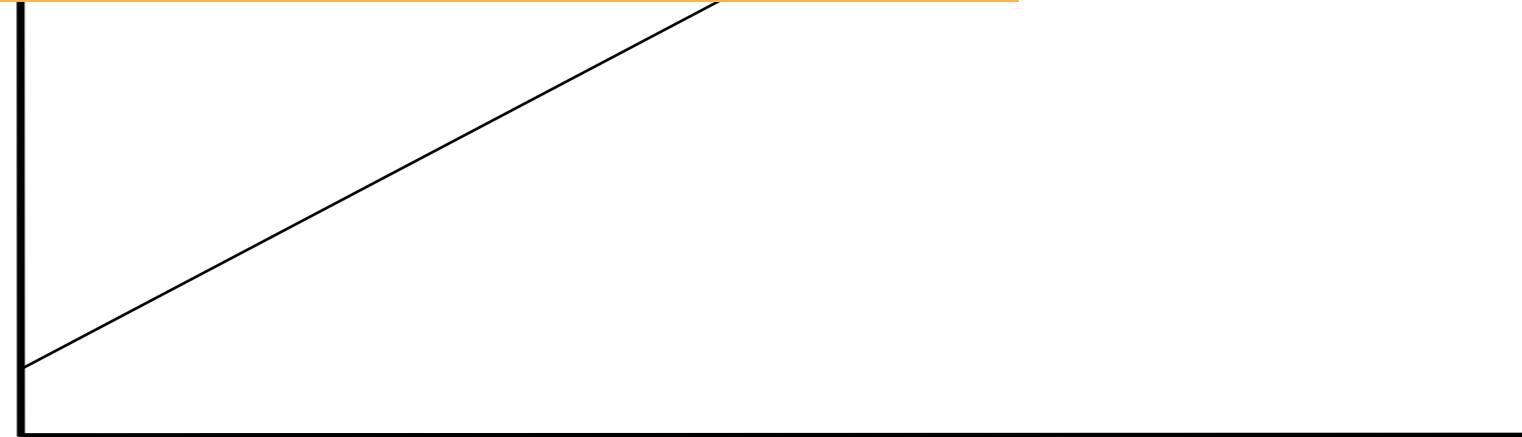


# Diversification Model

- Expected number of species increases exponentially with  $\lambda - \mu$

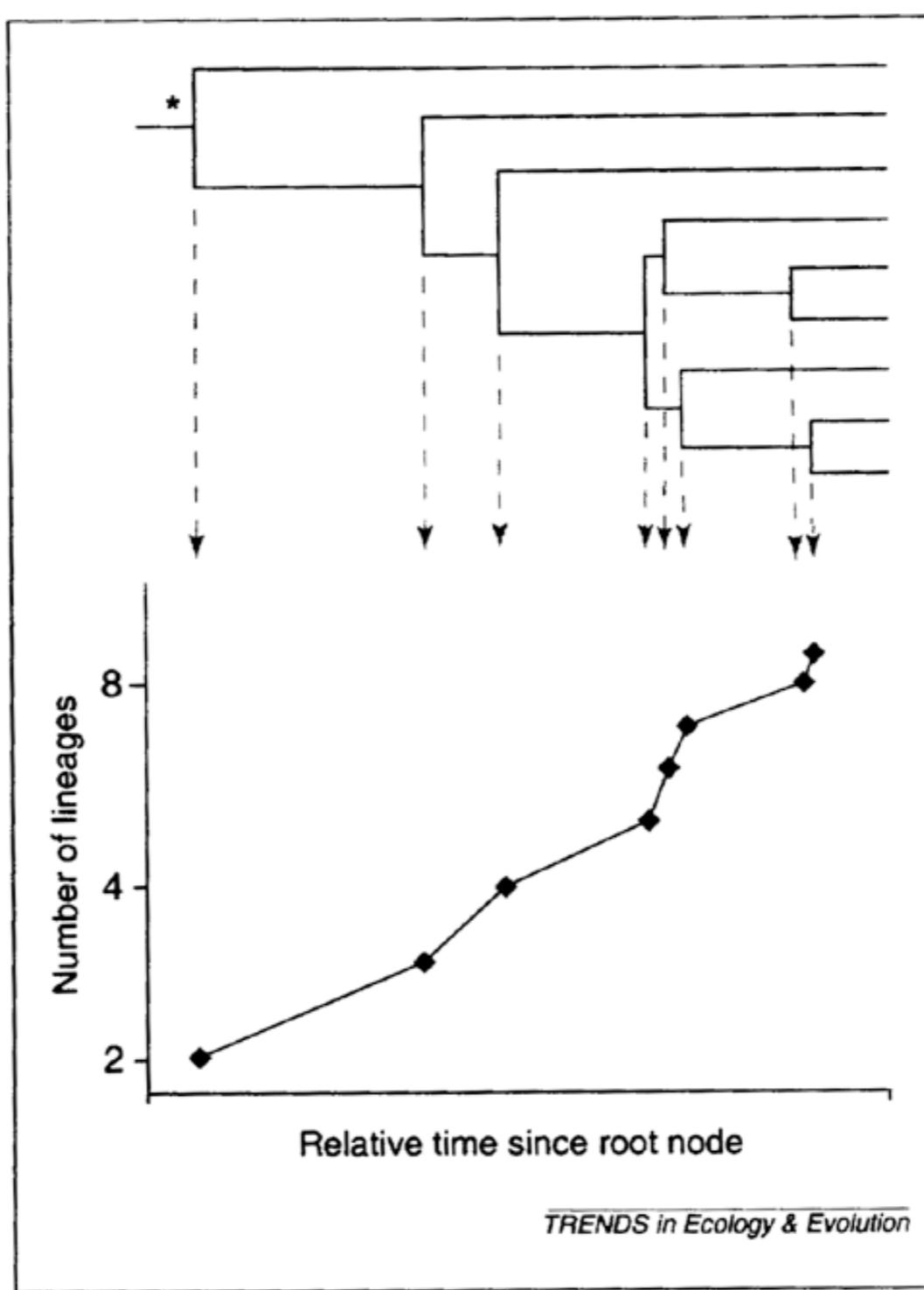
$\ln(\text{Lineages})$

What if we just  
have the  
phylogeny?

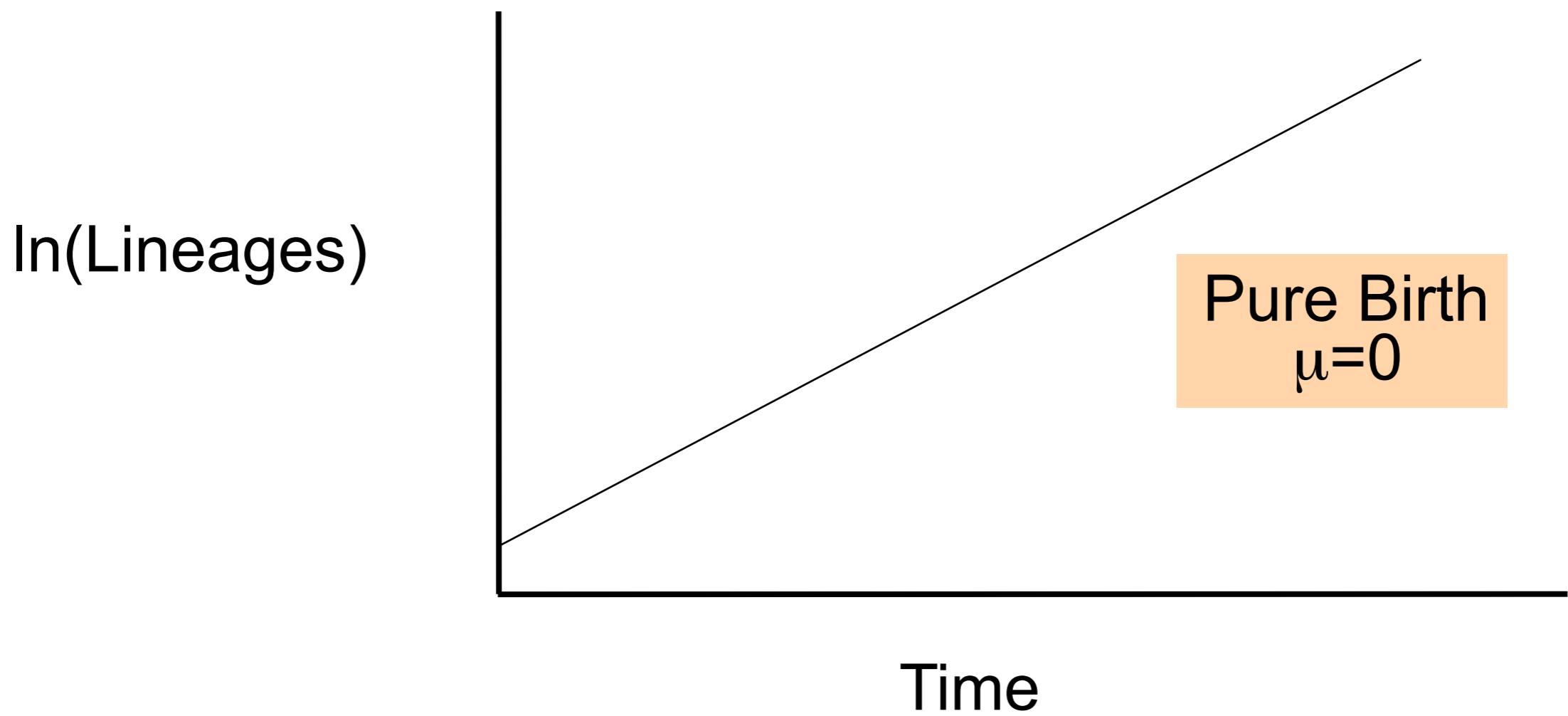


Time

# Lineage-through-time

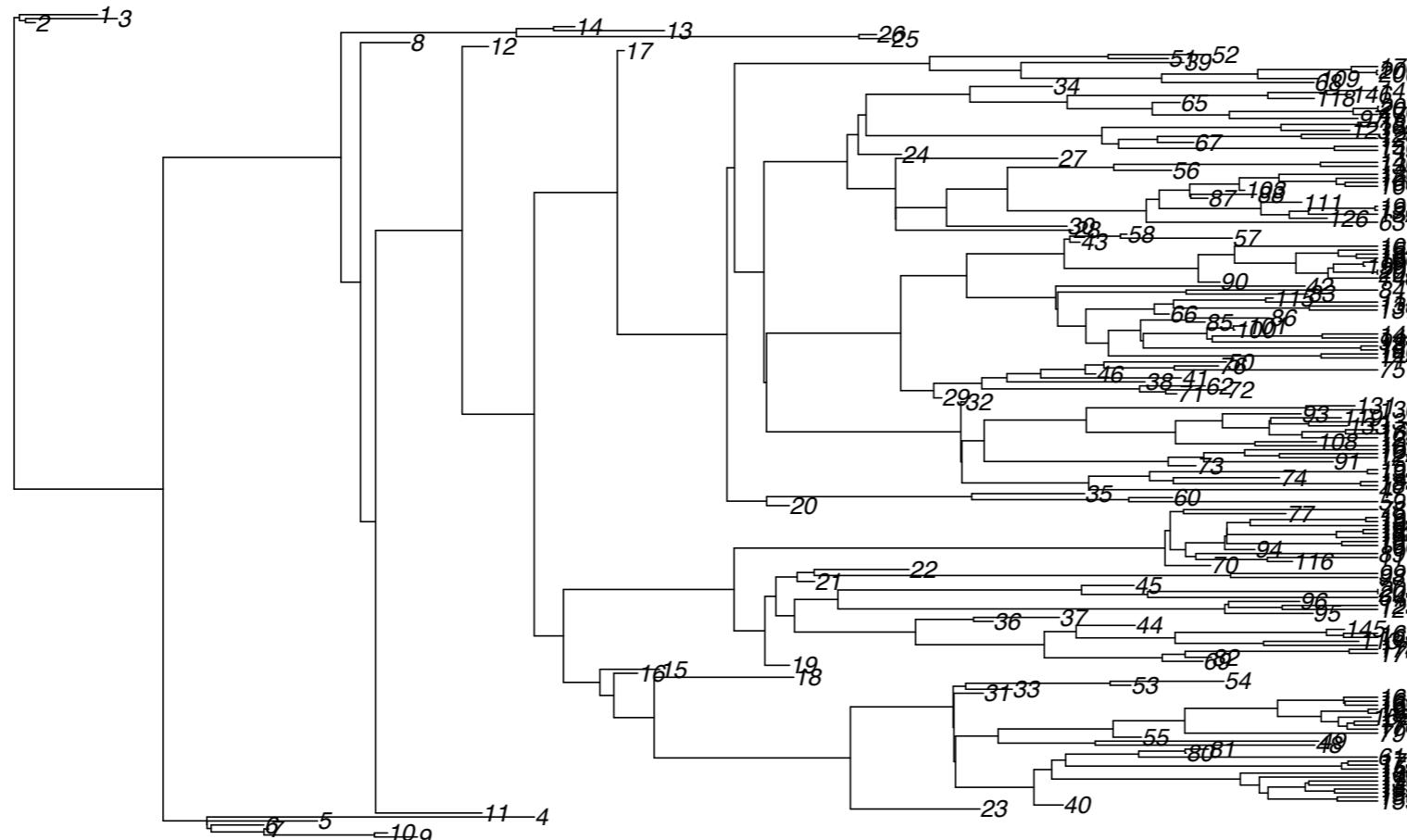


# LTT Plot

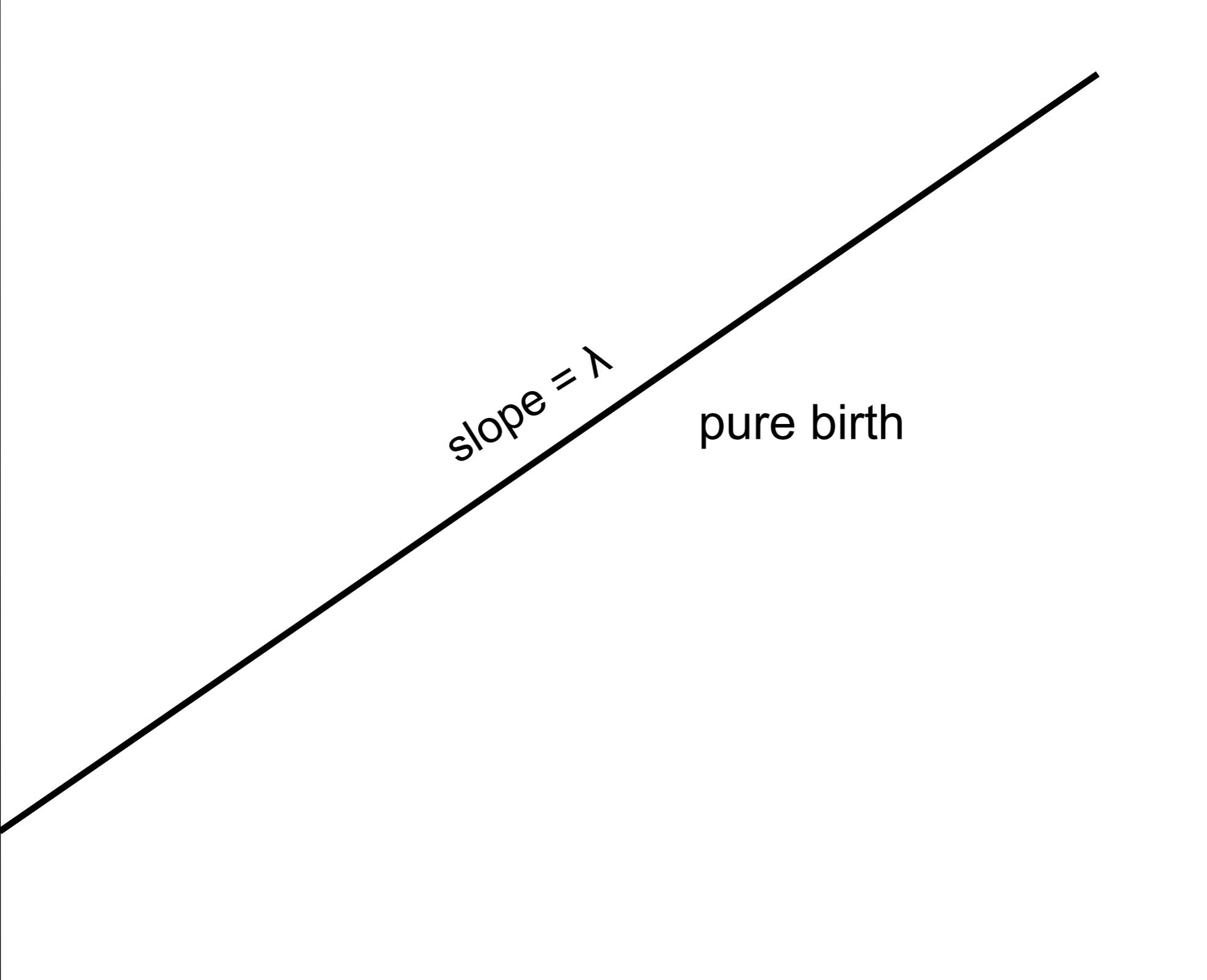


# Extinction

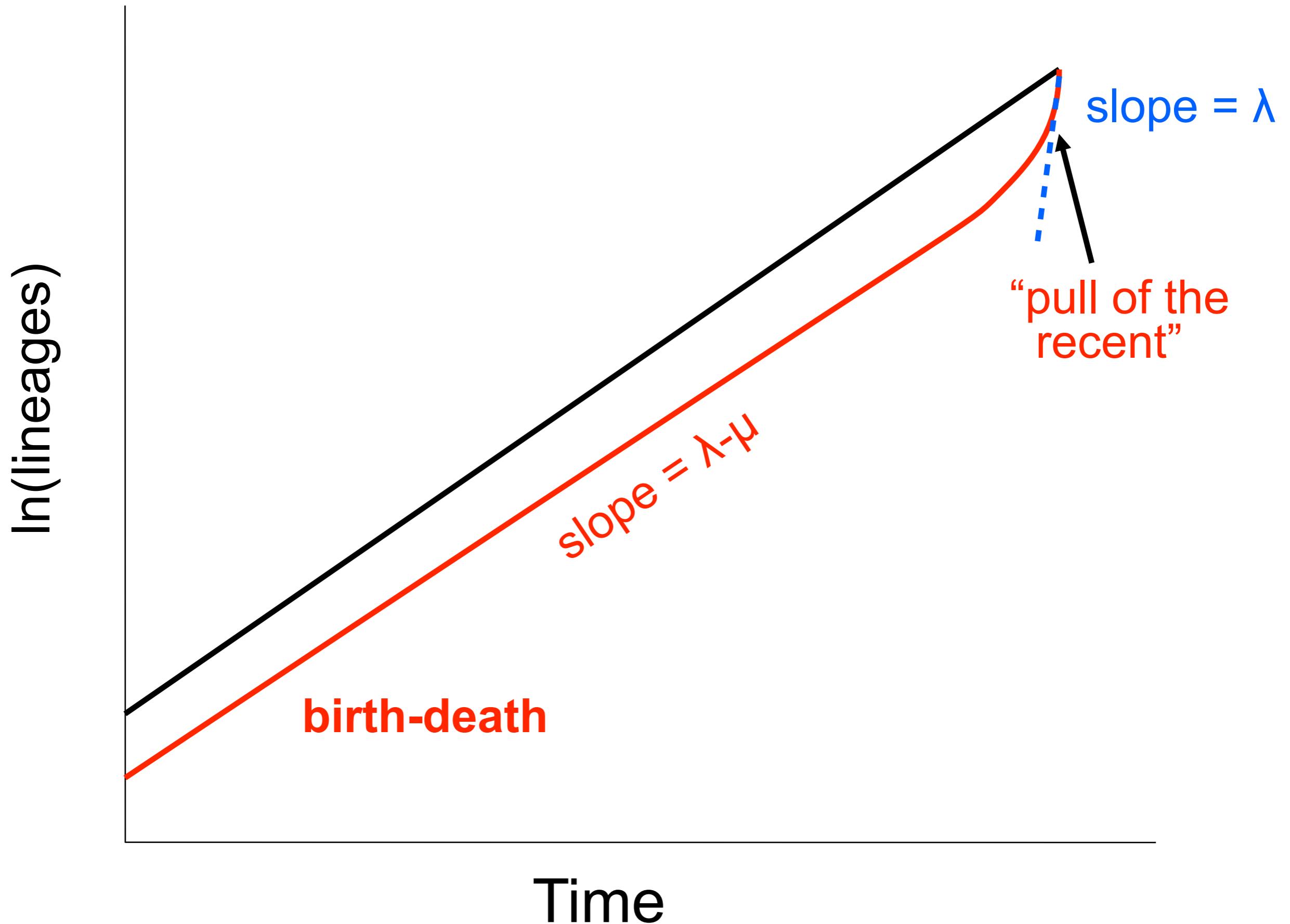
- Can leave an imprint on present-day phylogenies
- Older lineages are more likely to have gone extinct than younger ones

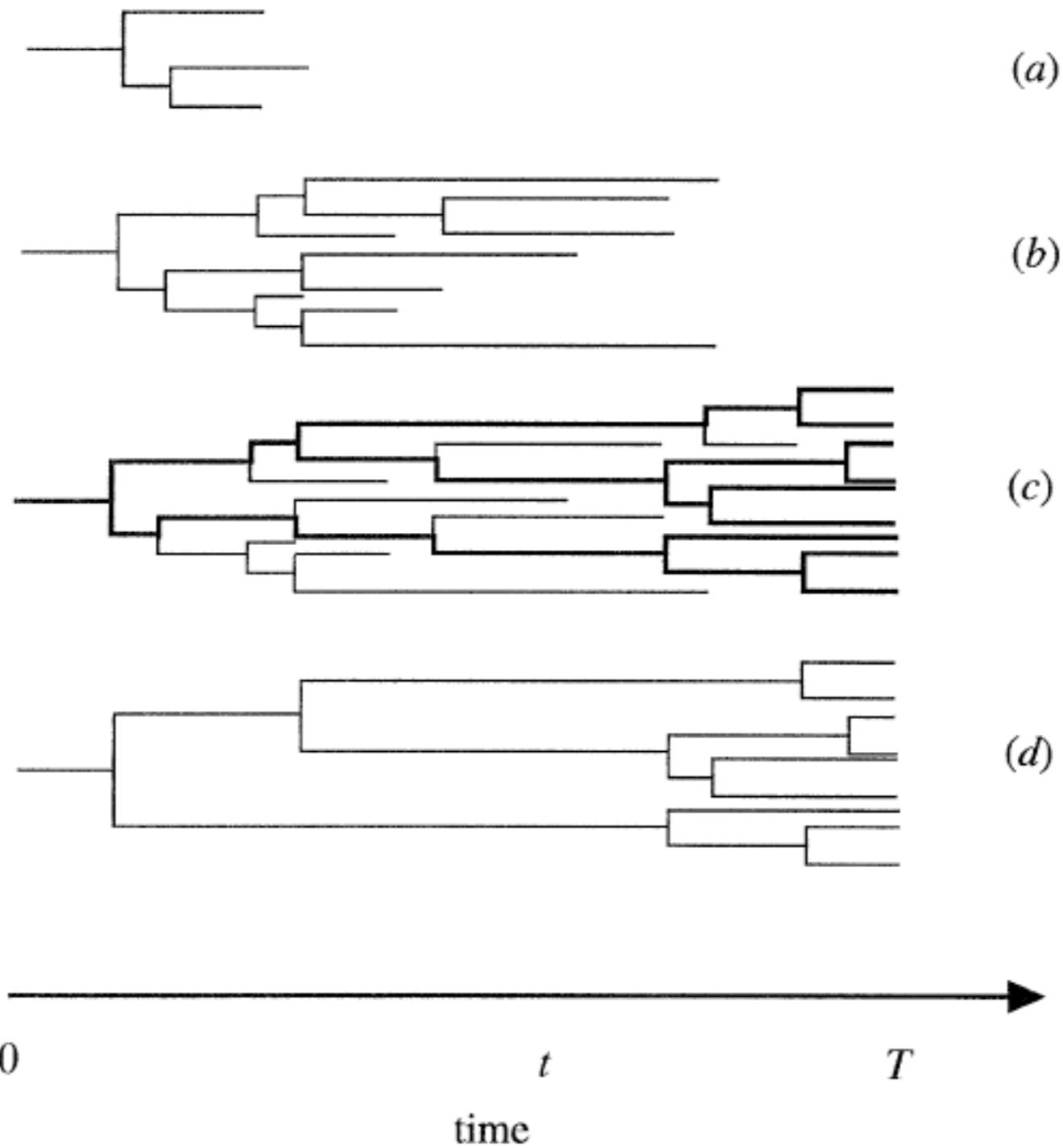


$\ln(\text{lineages})$

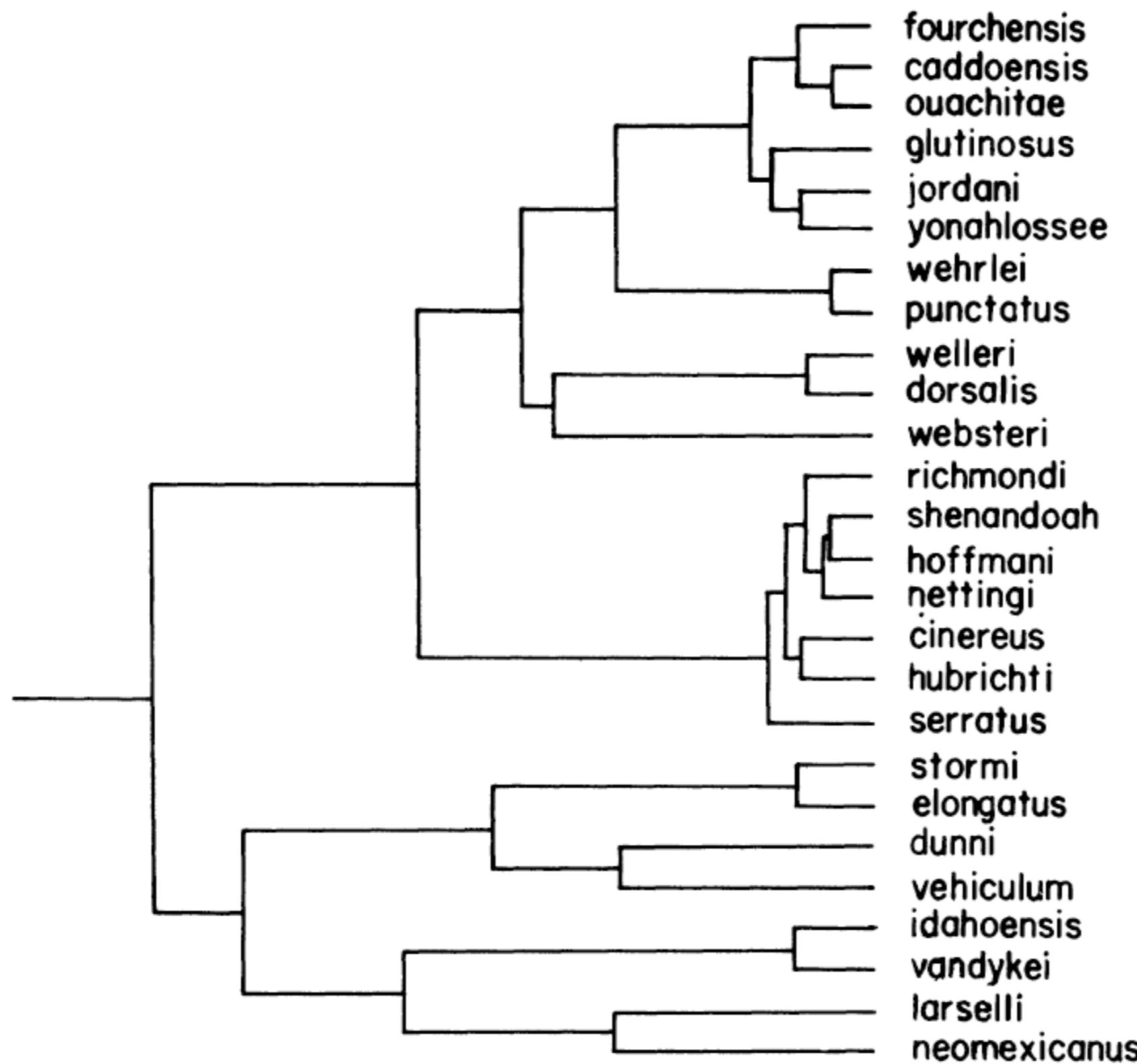


Time

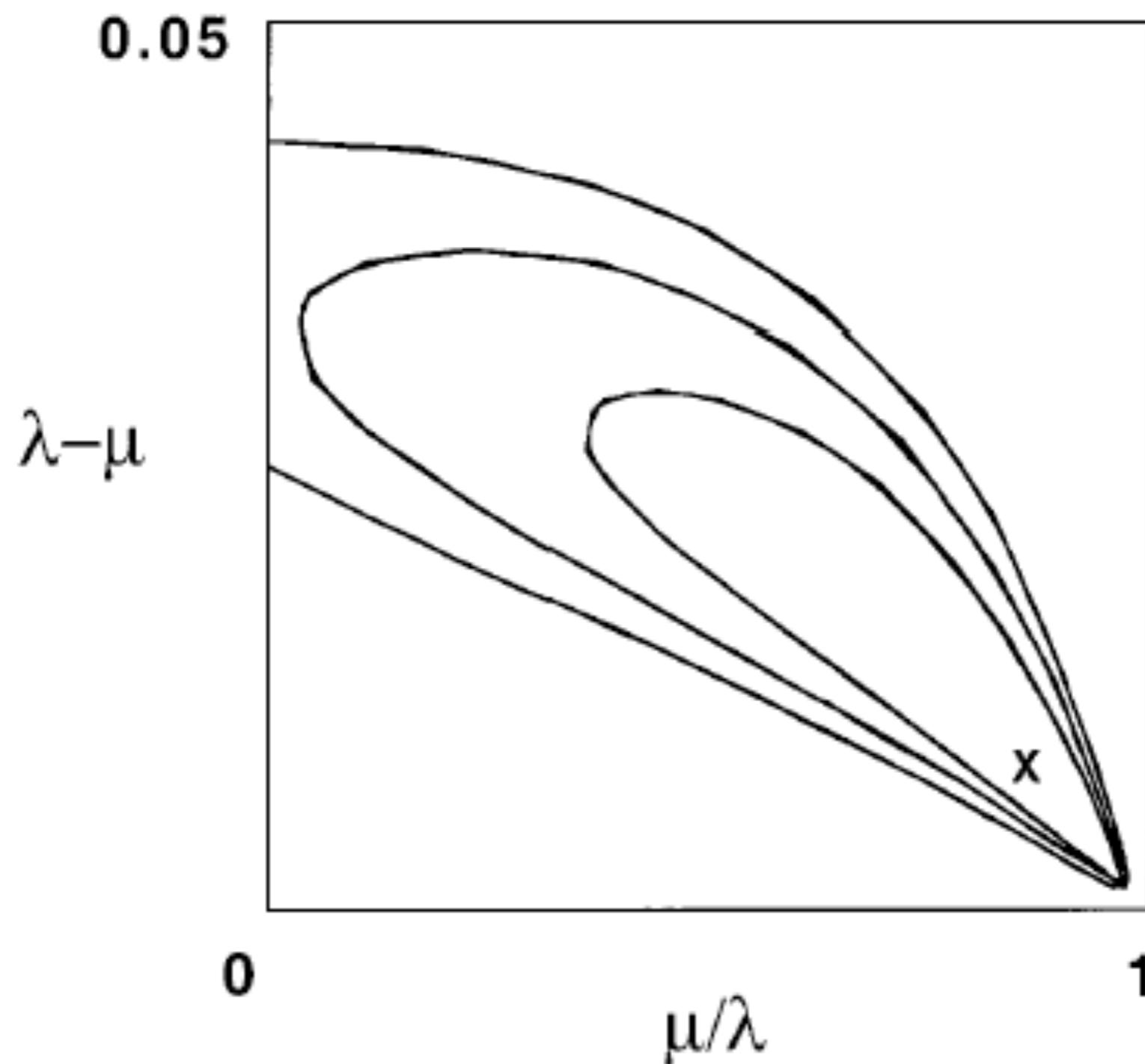




# Plethodontid salamanders

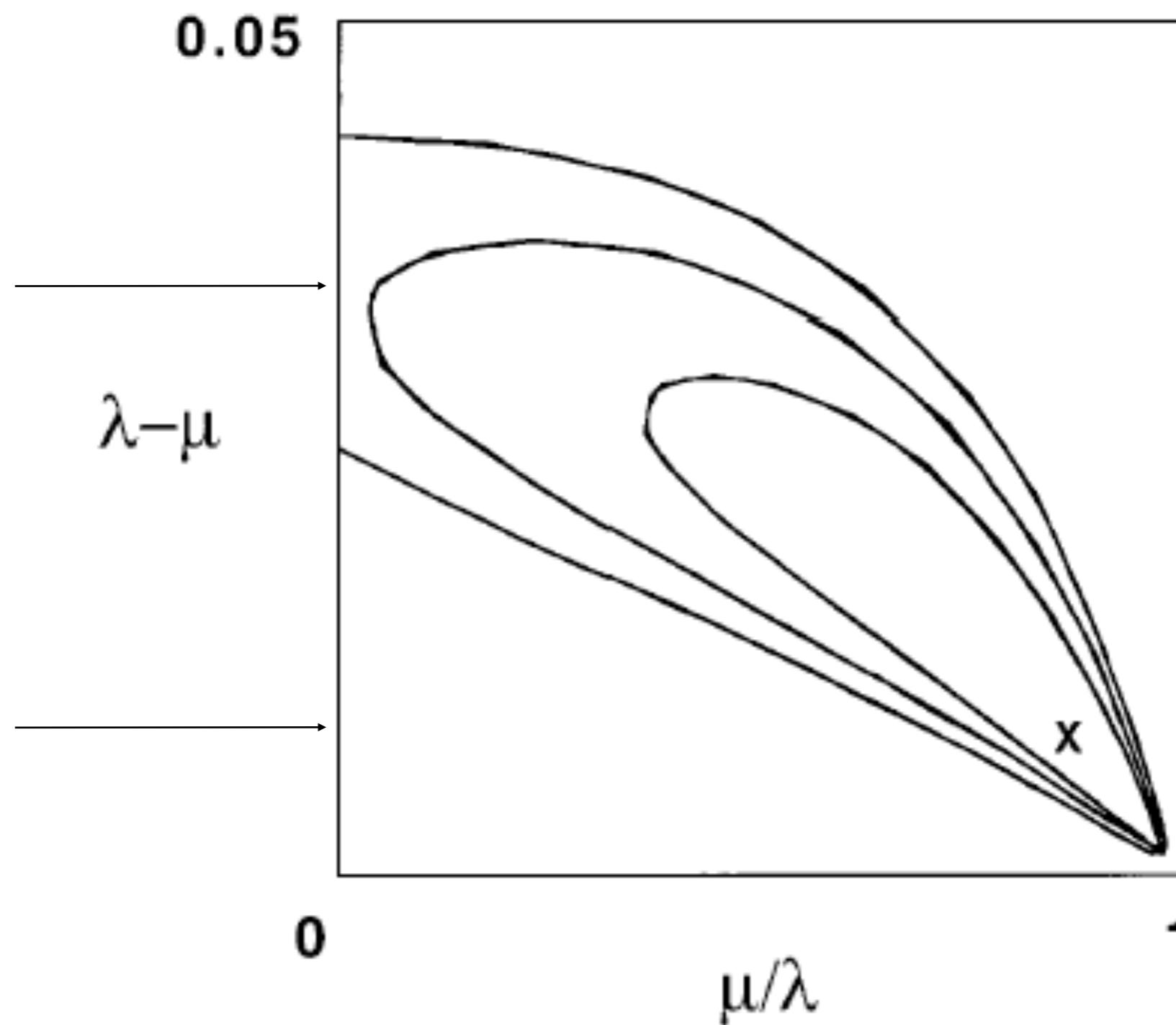


# Plethodontid salamanders



from Nee 2001

# Plethodontid salamanders



from Nee 2001

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

# Testing for slowdowns

- Pybus and Harvey gamma statistic
- Diversity-dependent models

# Trait-dependent diversification models

- We can use BiSSE (and related) models to test for a relationship between traits and diversification rates
- For example, do speciation rates depend on character state?

Character-  
independent  
model

vs.

Character-  
dependent  
model

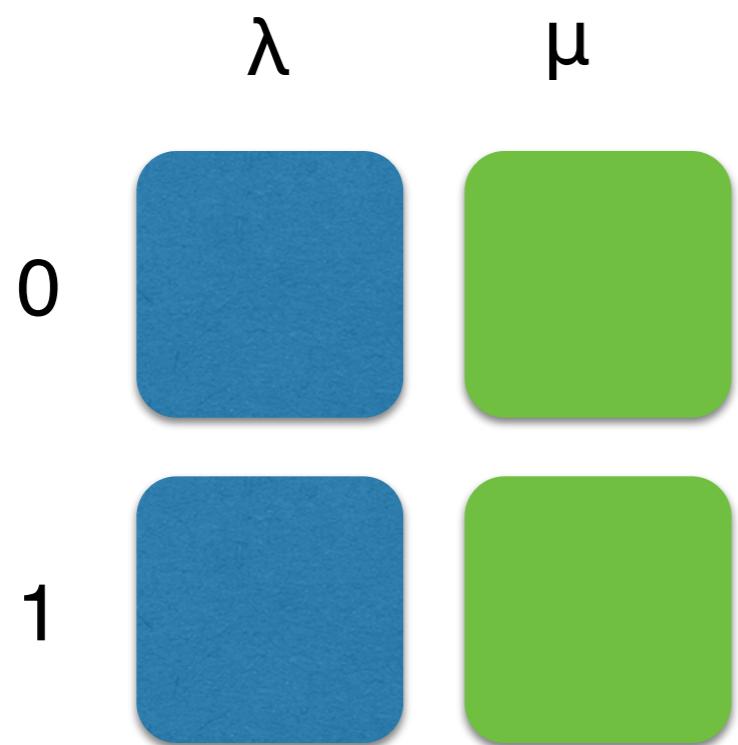
Character-  
independent  
model

vs.

Character-  
dependent  
model

Diversification rate

Character State

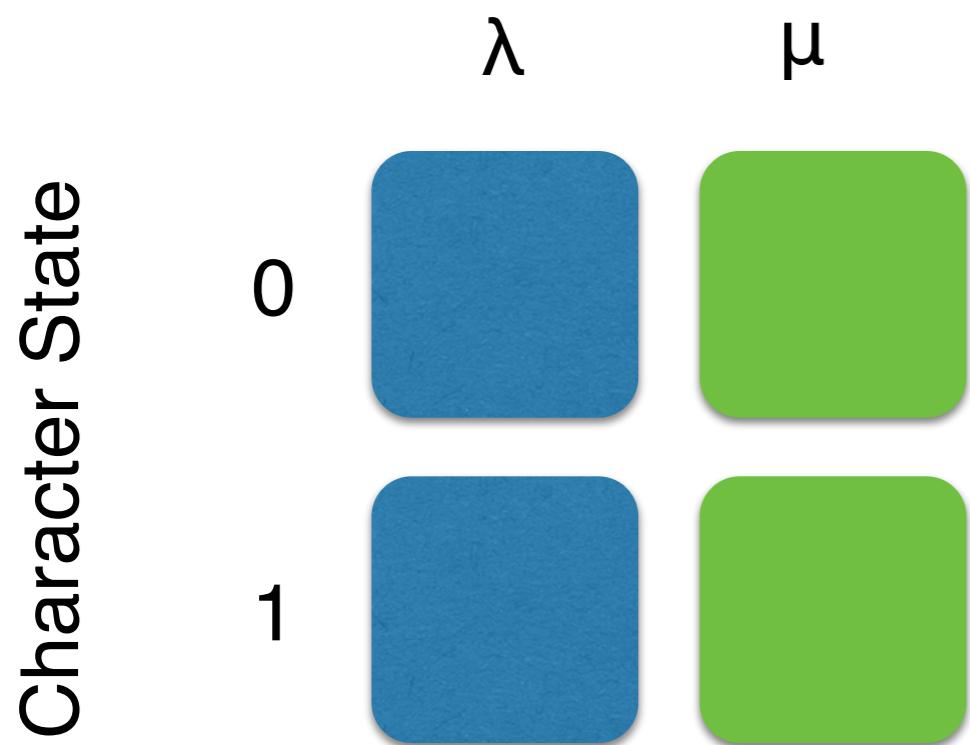


# Character-independent model

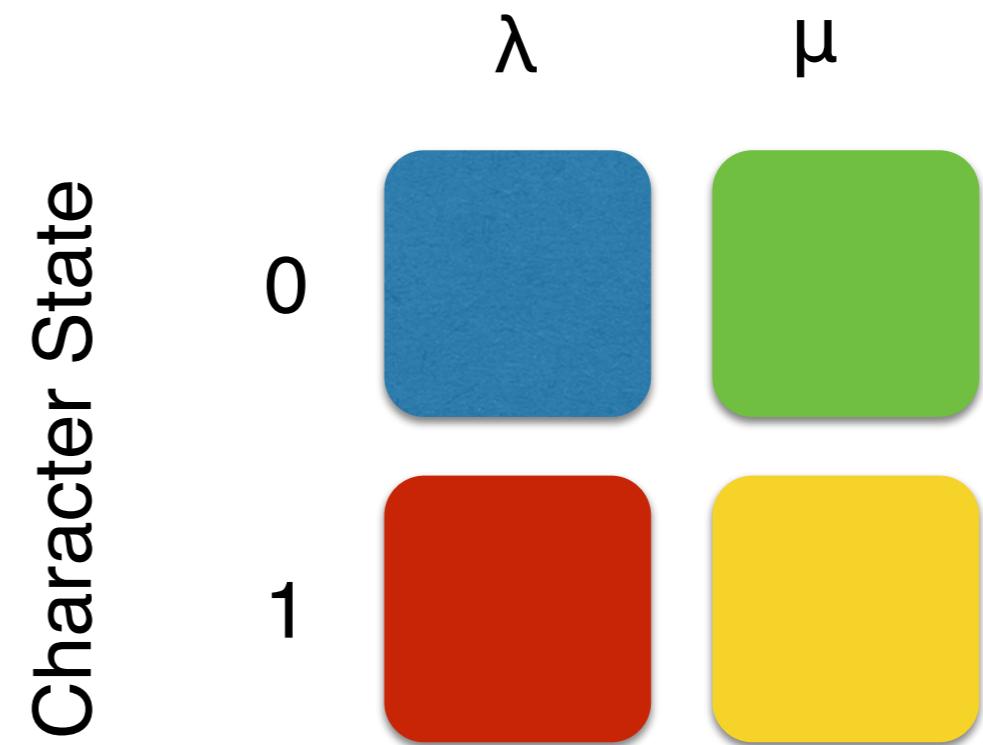
vs.

# Character-dependent model

Diversification rate



Diversification rate



# BiSSE Family

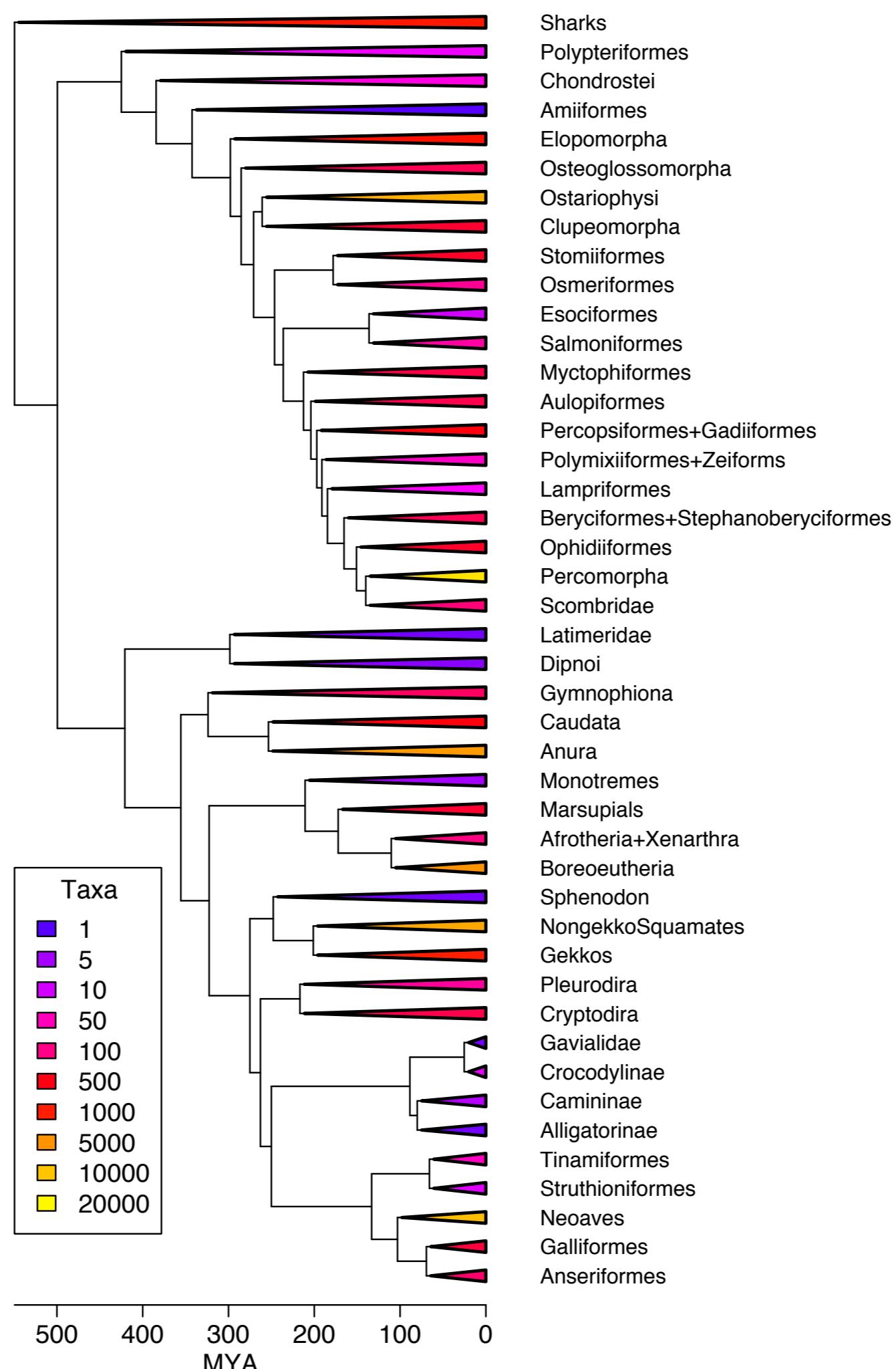
- BiSSE - binary character
- MuSSE - multi-state character
- ClaSSE - cladogenesis
- GeoSSE - geography
- QuaSSE - quantitative character

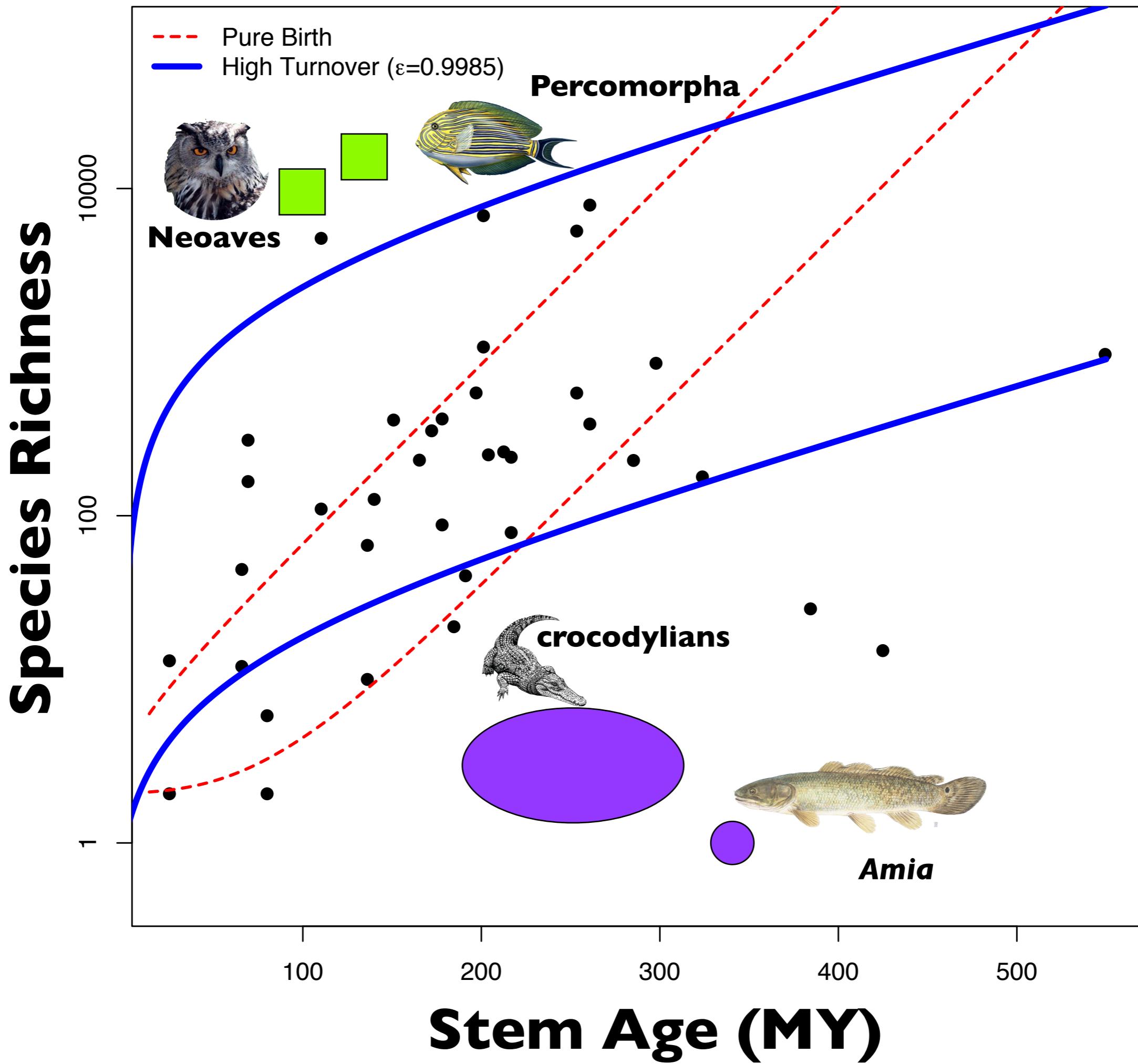


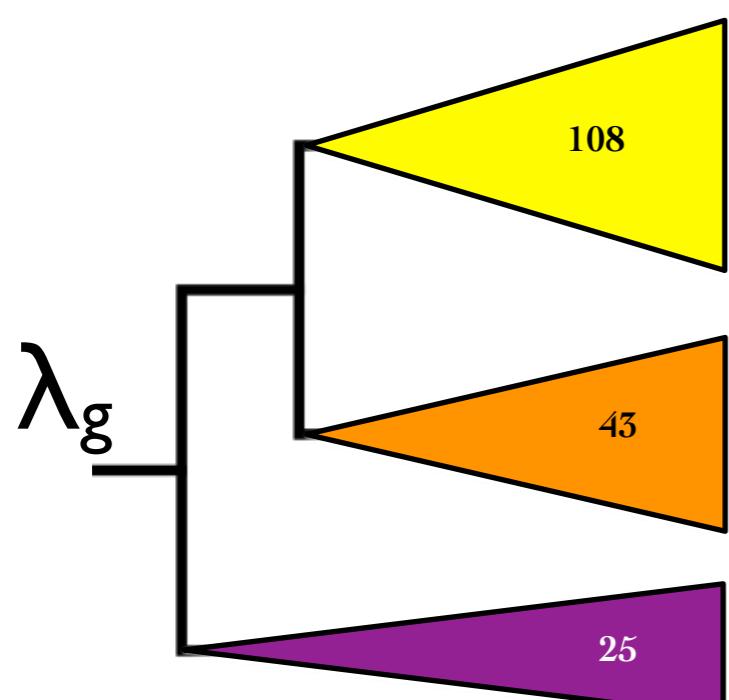
Beyond birth and death

Models have grown in sophistication  
since Nee 2001...

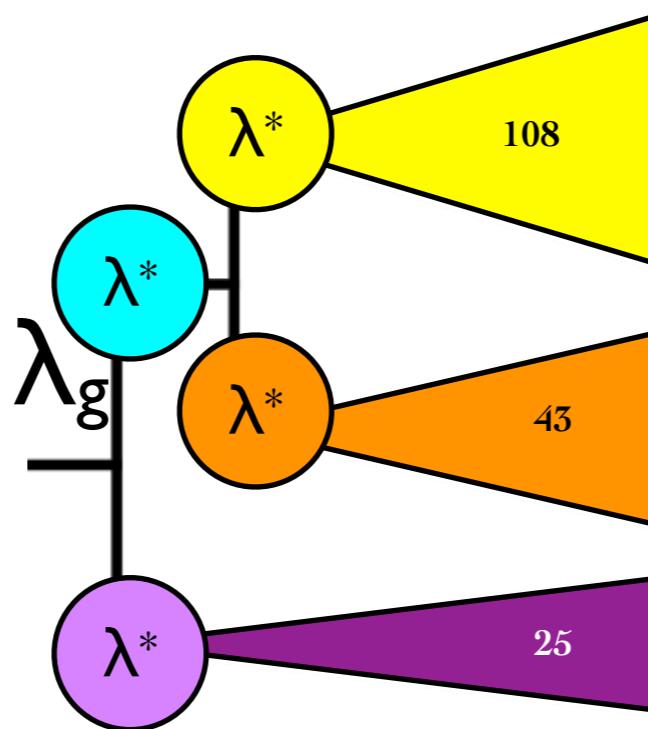
... for good reason



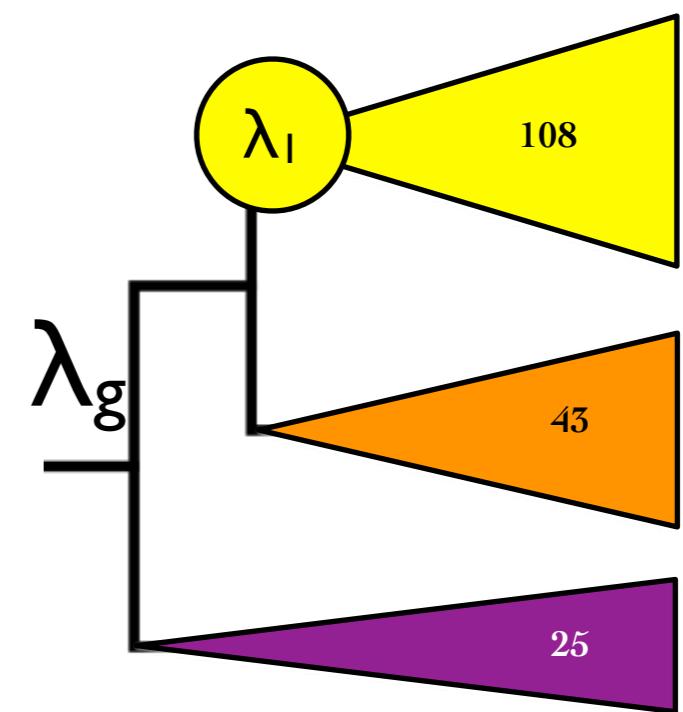




1.  $\lambda$  for whole tree



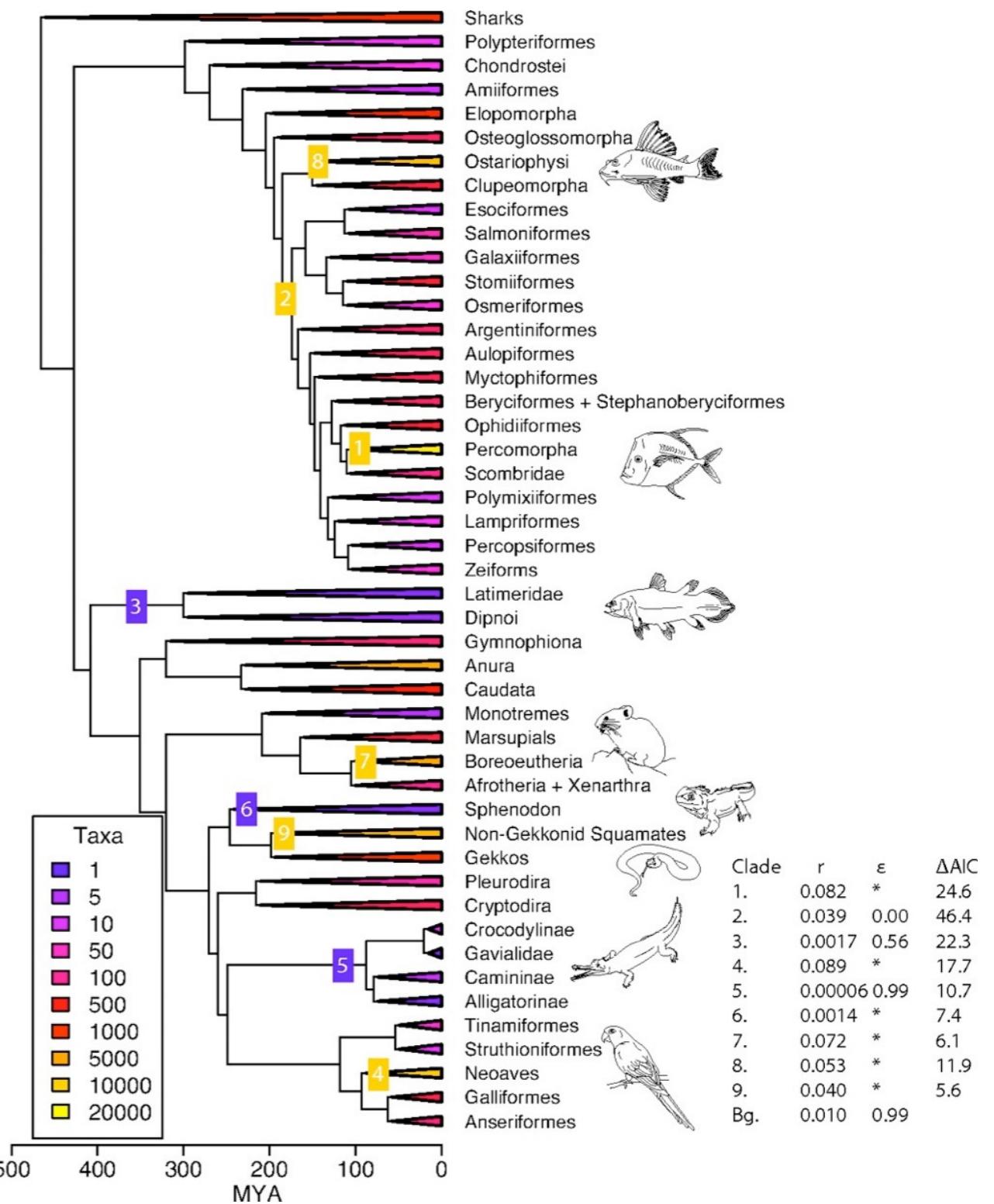
2. allow  $\lambda$  to change on each branch



3. if  $\Delta AIC$  of best new  $\lambda$  and  $\lambda_g > 4$ ,  
retain rate & repeat

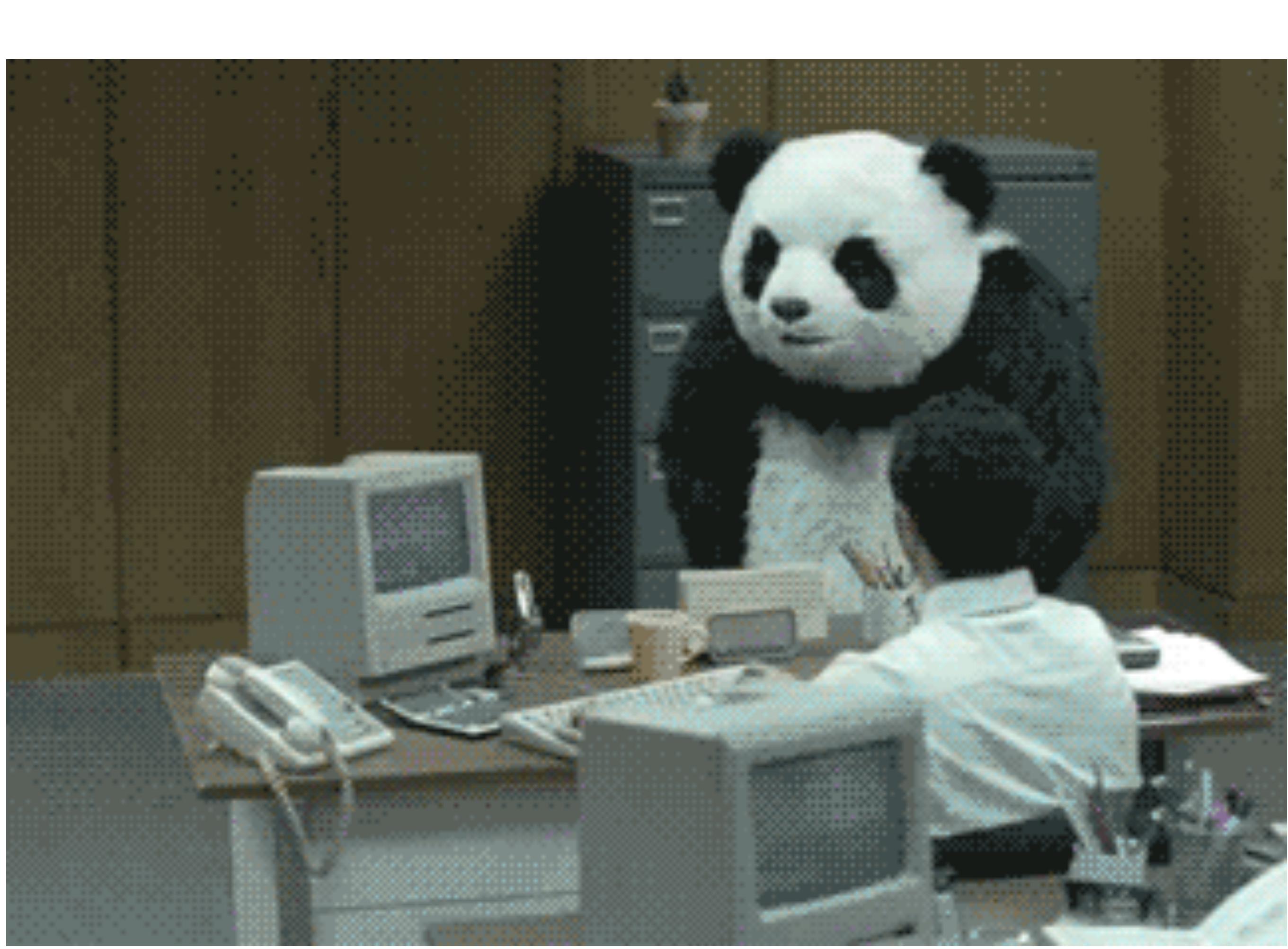
# MEDUSA

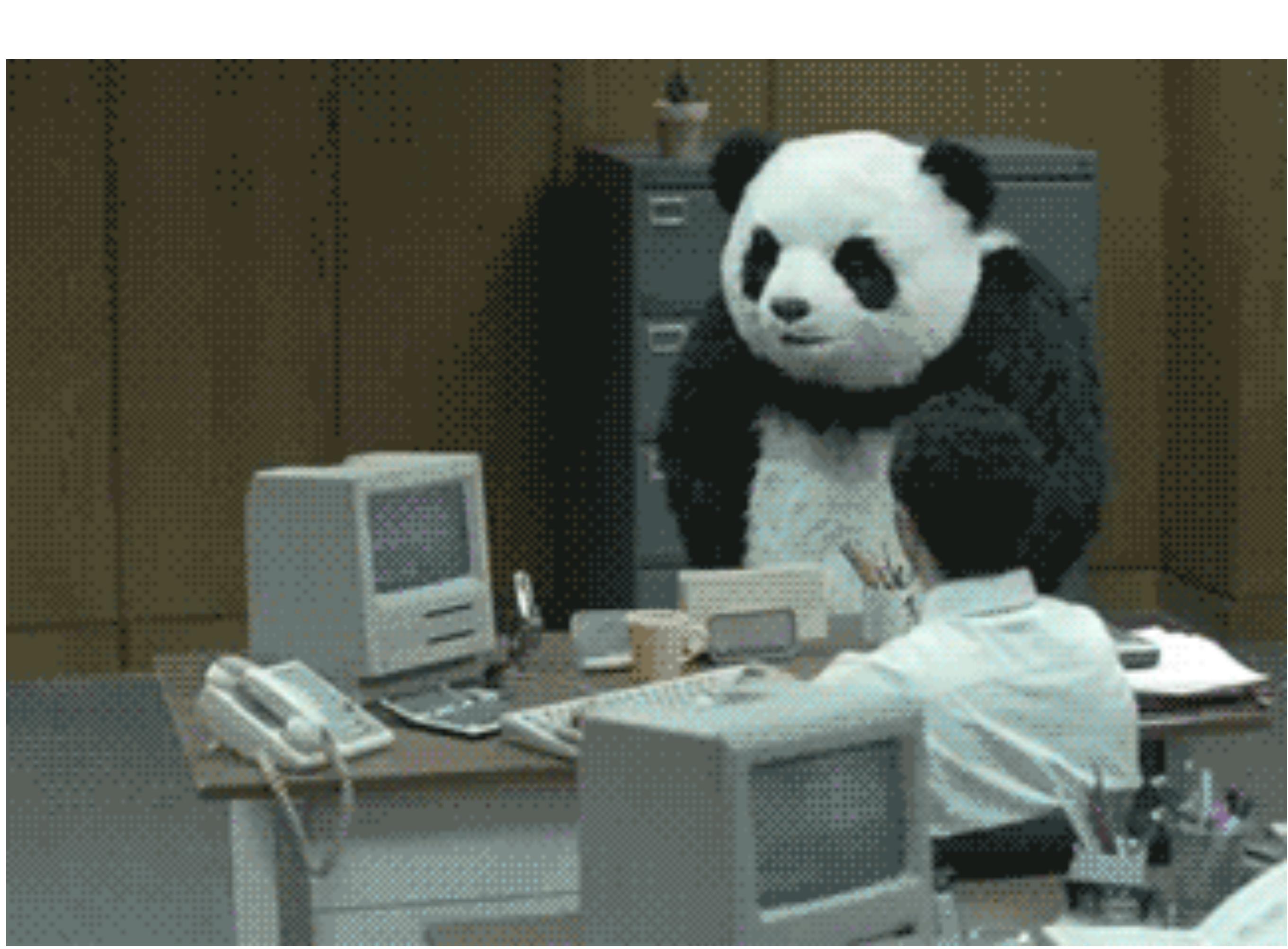
- Learn about diversification dynamics through fitting piecewise models of birth ( $\lambda$ ) and death ( $\mu$ )
  - Where have rates changed?
  - By what magnitude?
  - Why do clades differ in size?



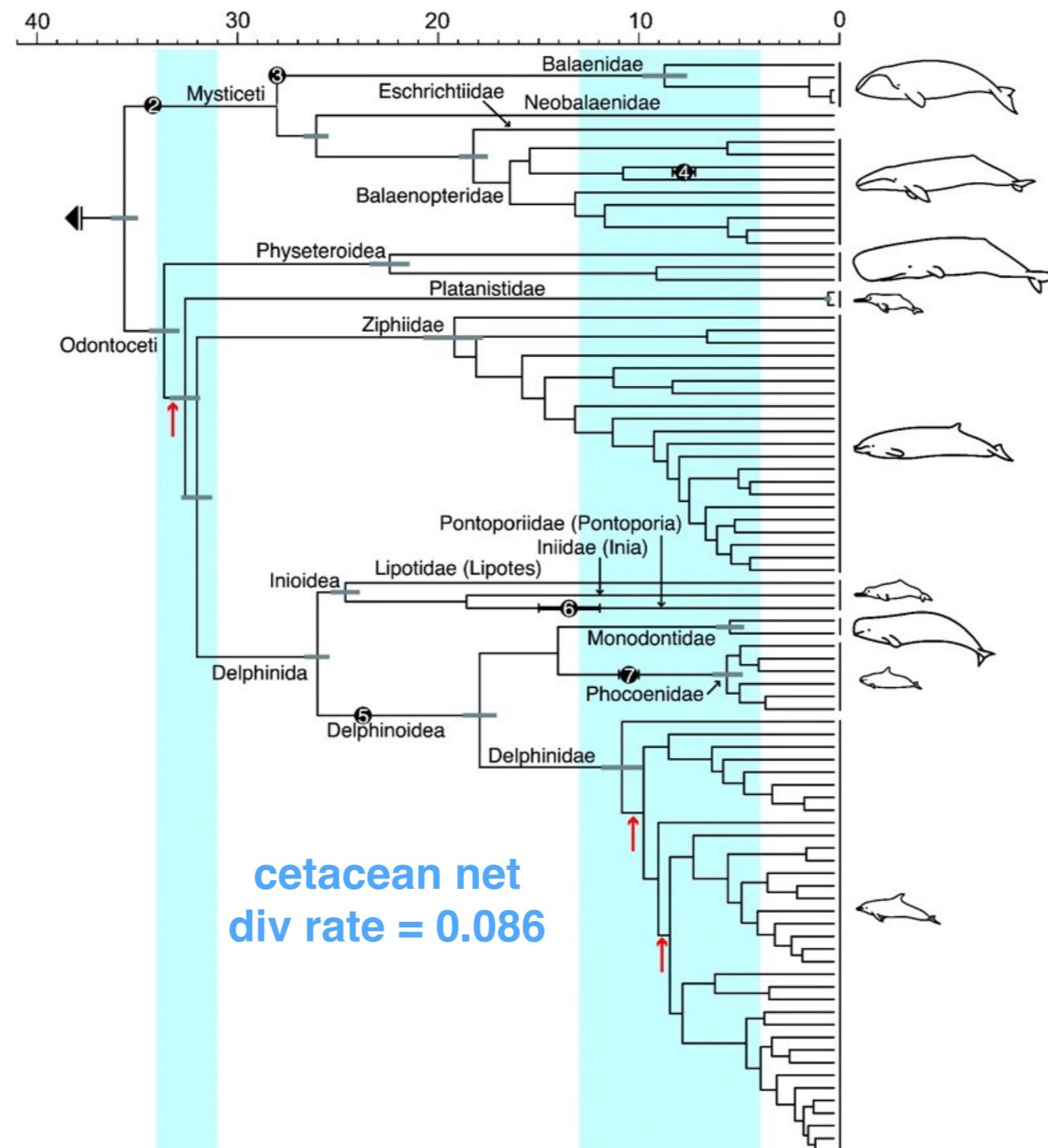
Alfaro et al. 2009 PNAS

More recent models allow for diversity dependence

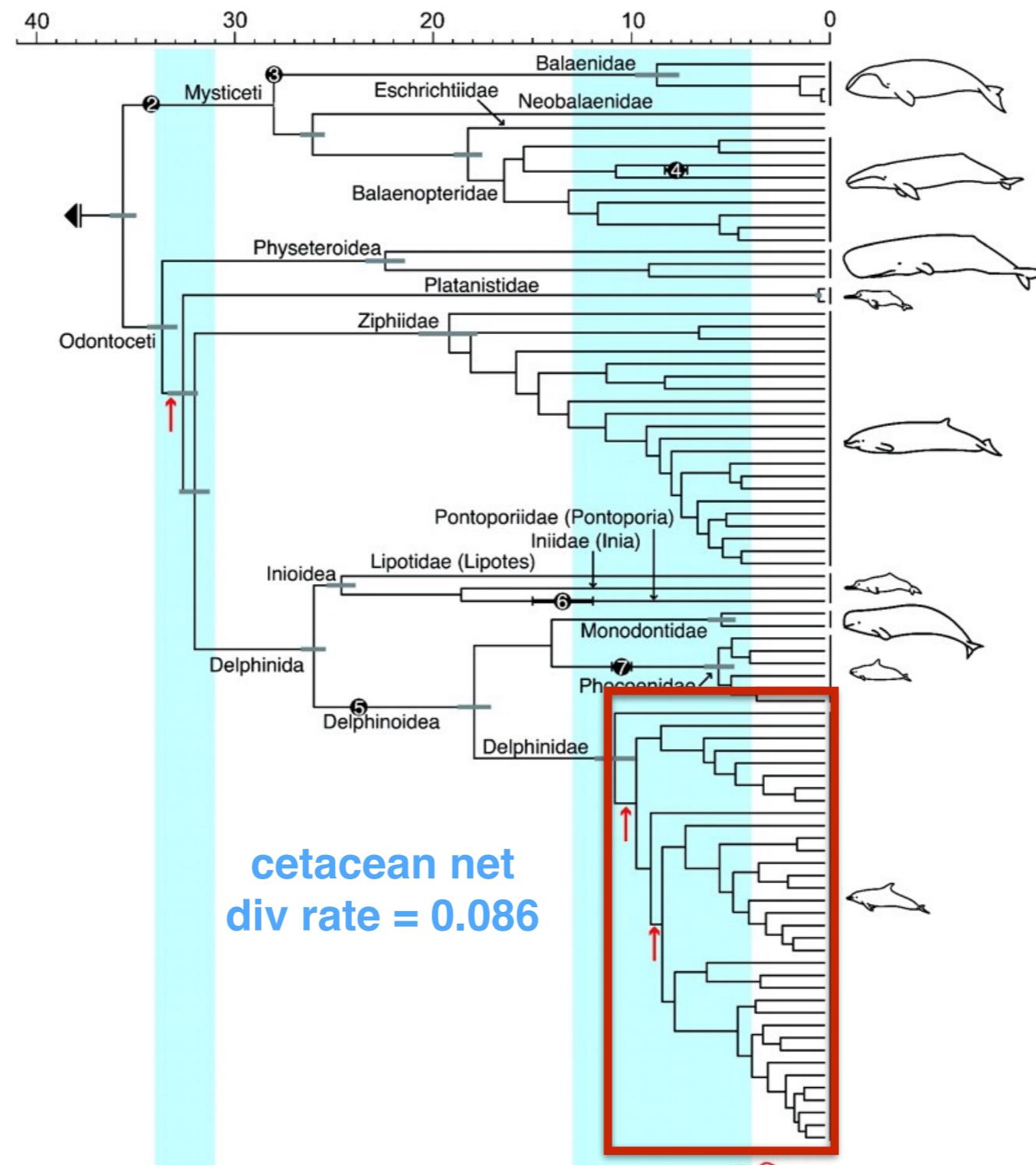




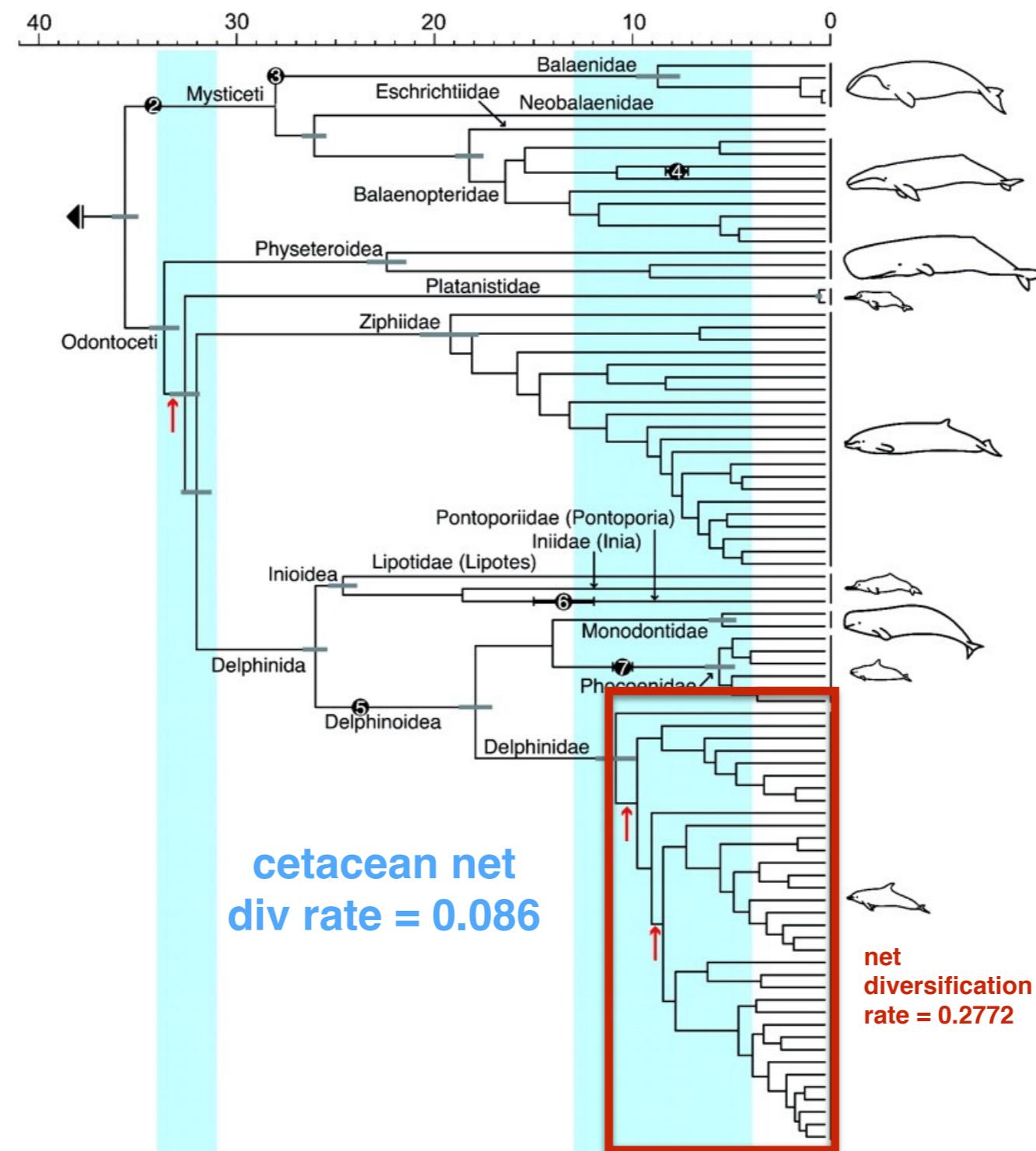
# RPANDA



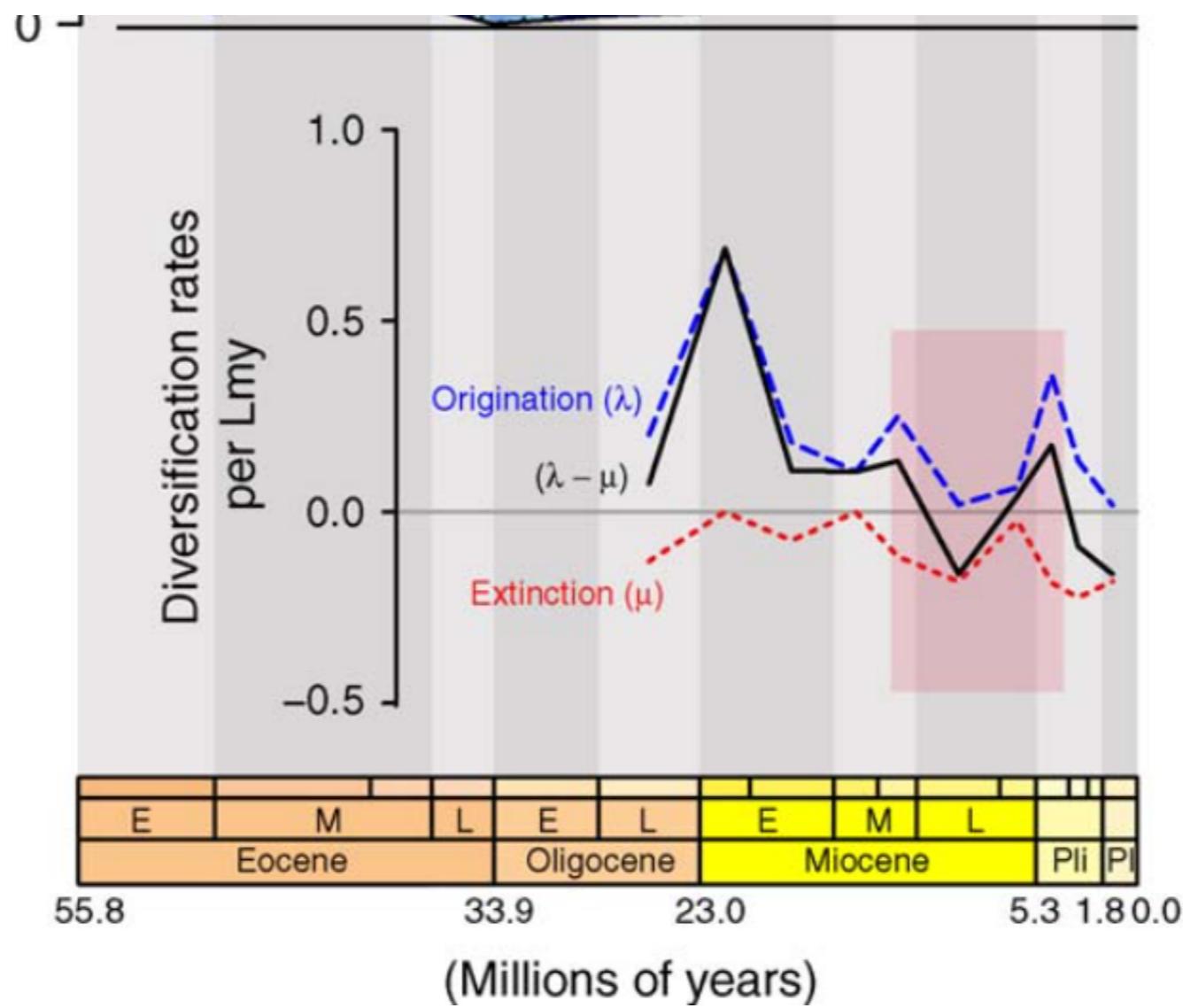
# RPANDA

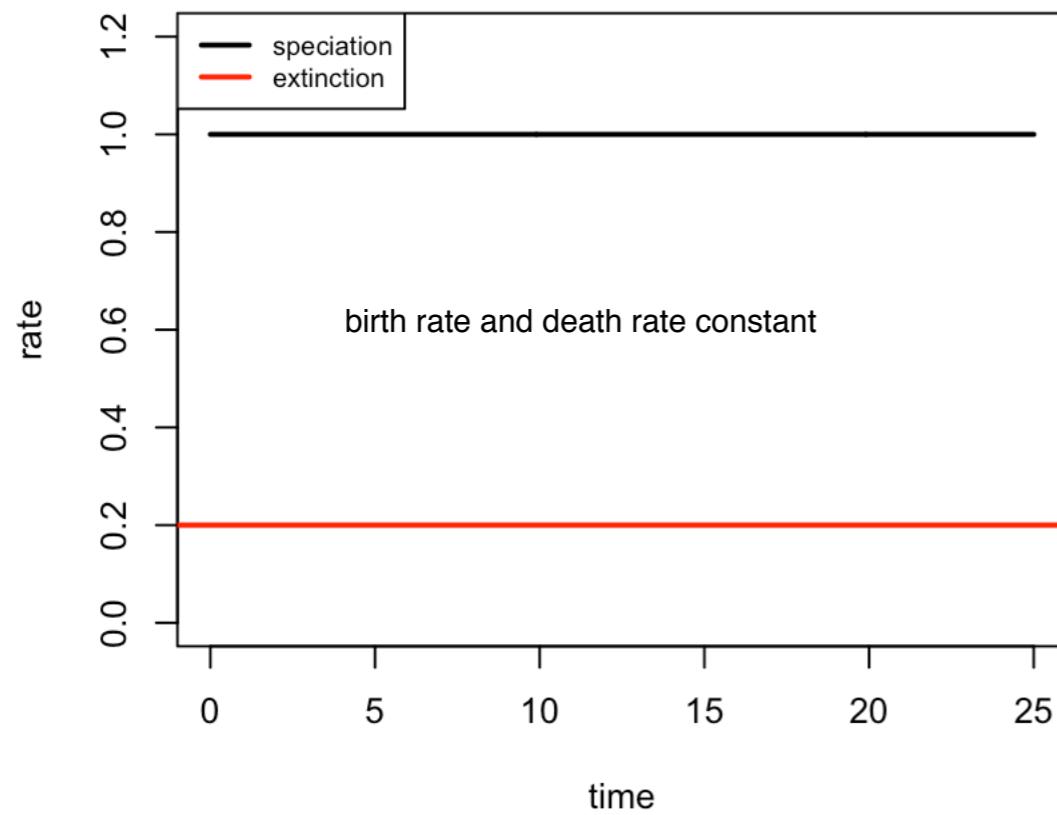
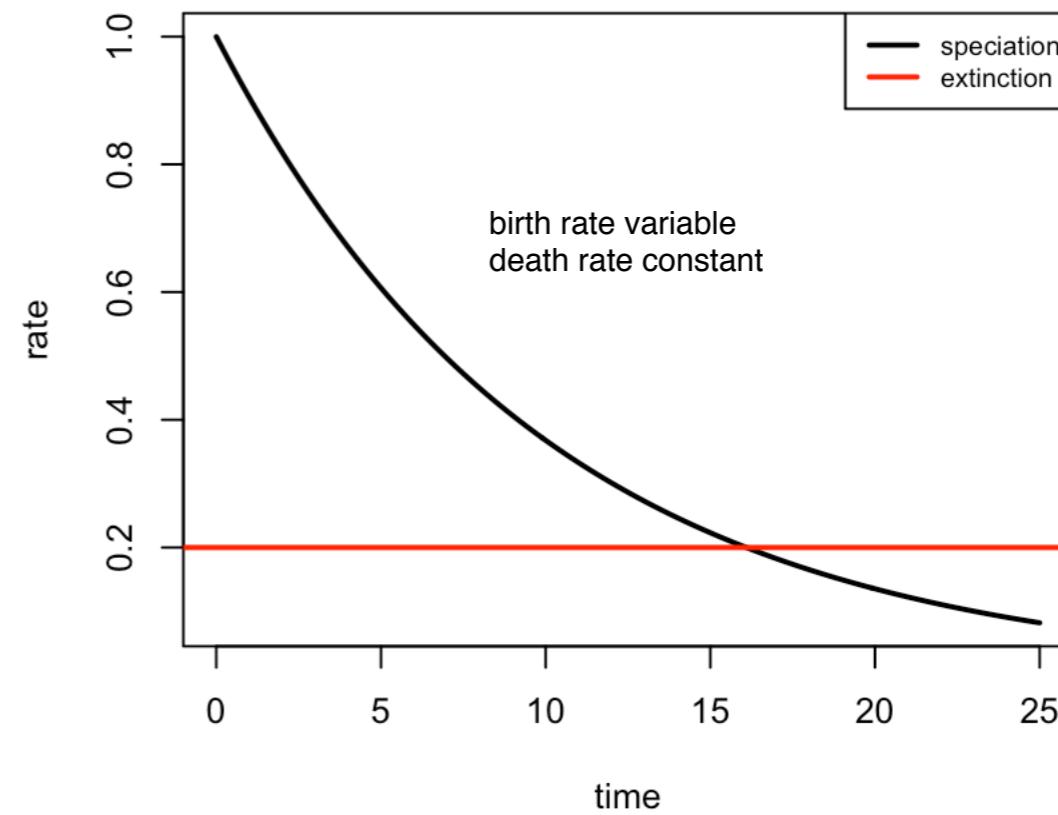
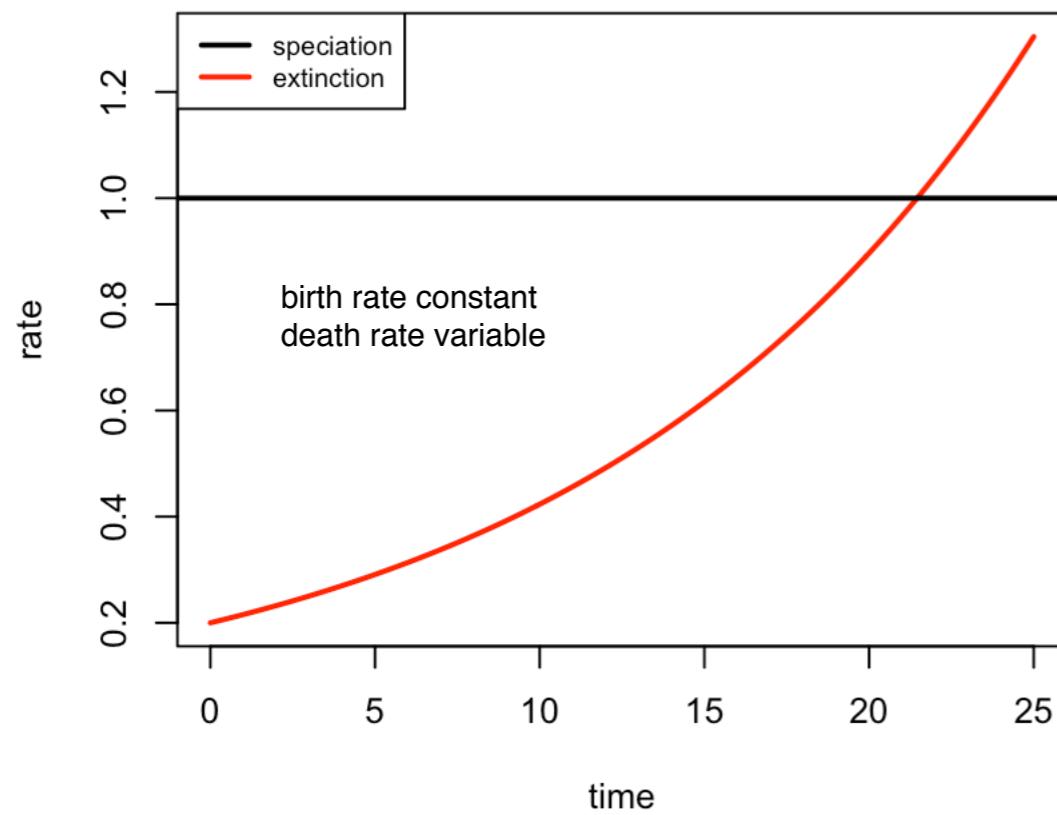
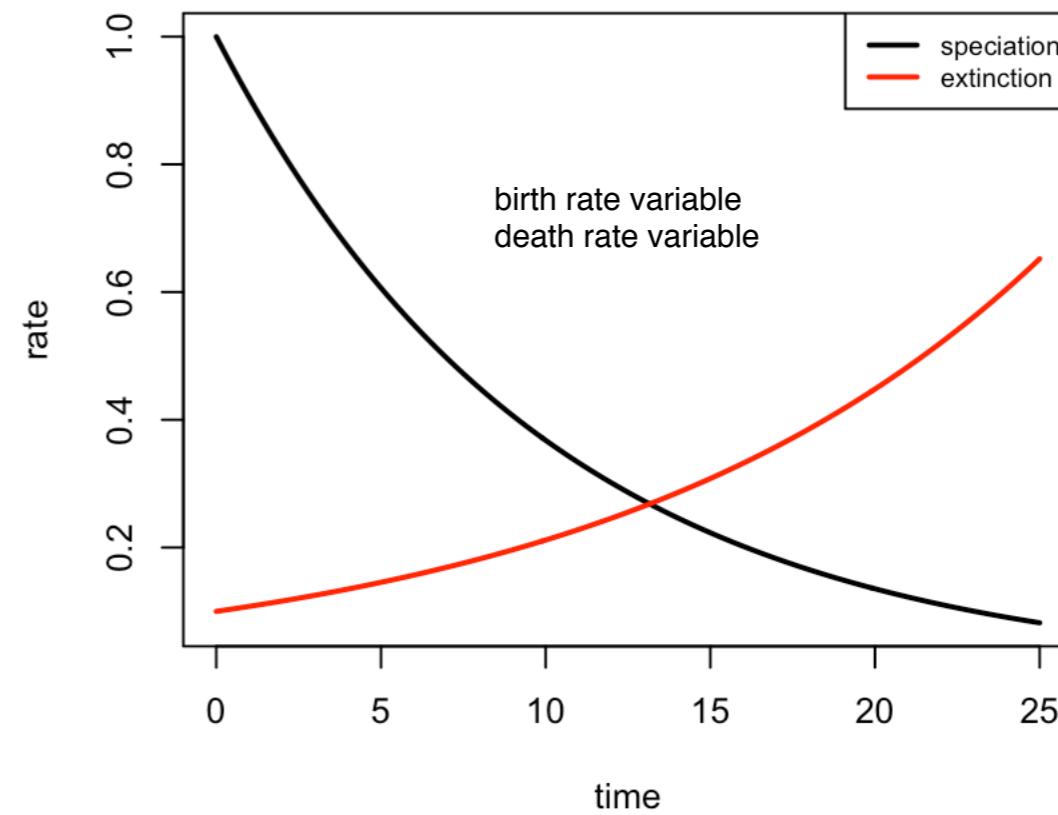


# RPANDA



# RPANDA

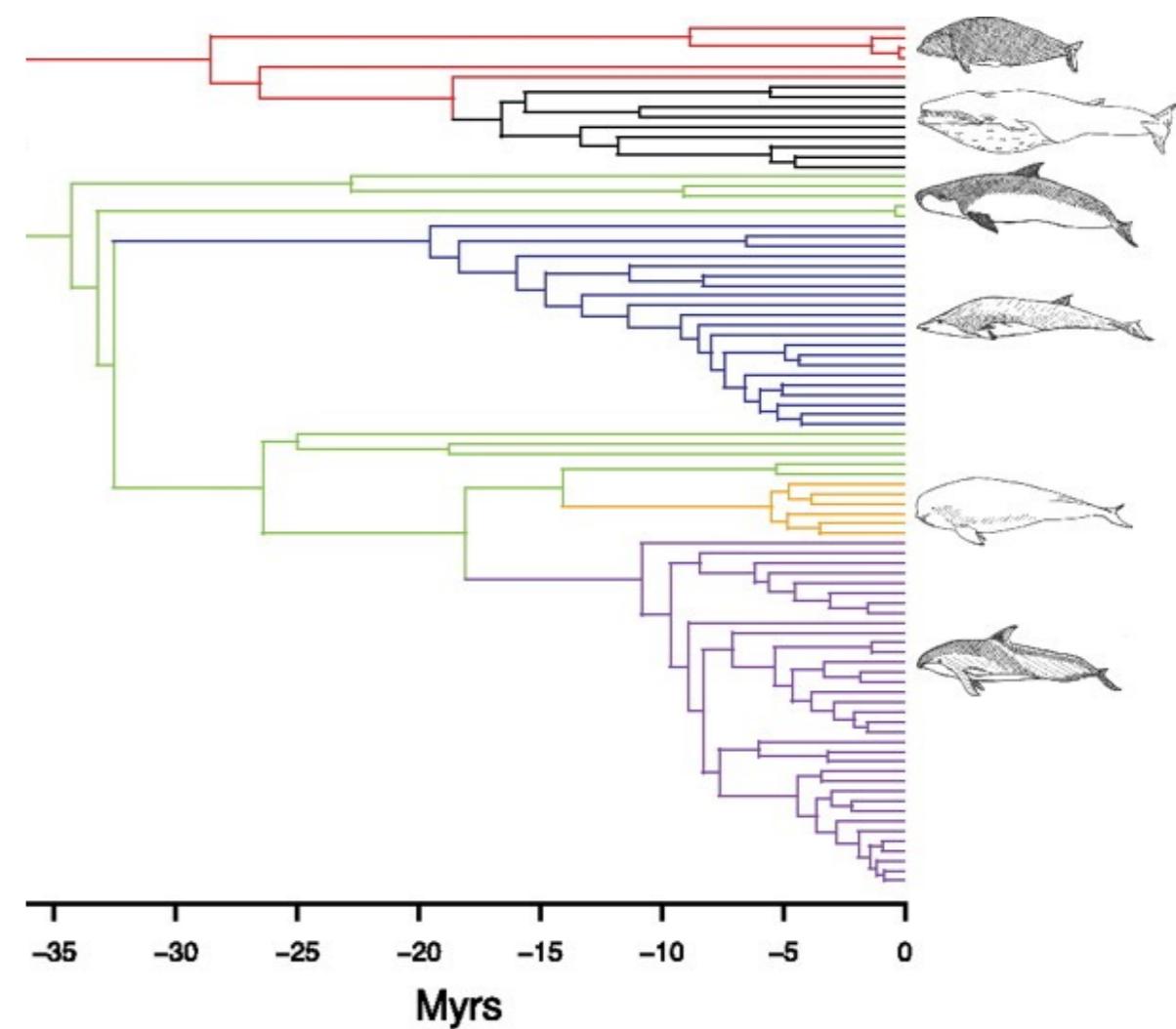
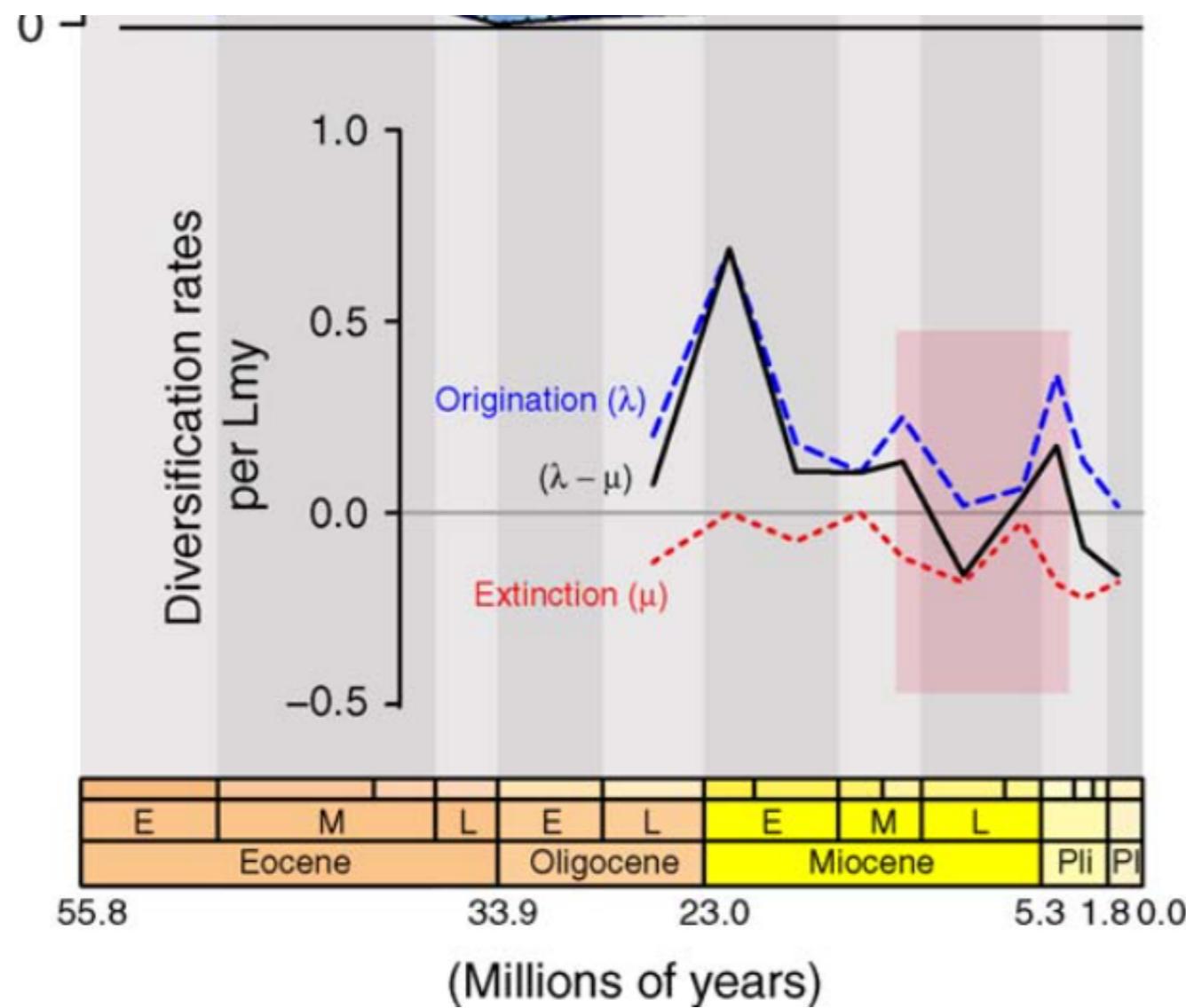


**BCSTDCST****BVARDCST****BCSTDVAR****BVARDVAR**

# Time-varying models in RPANDA

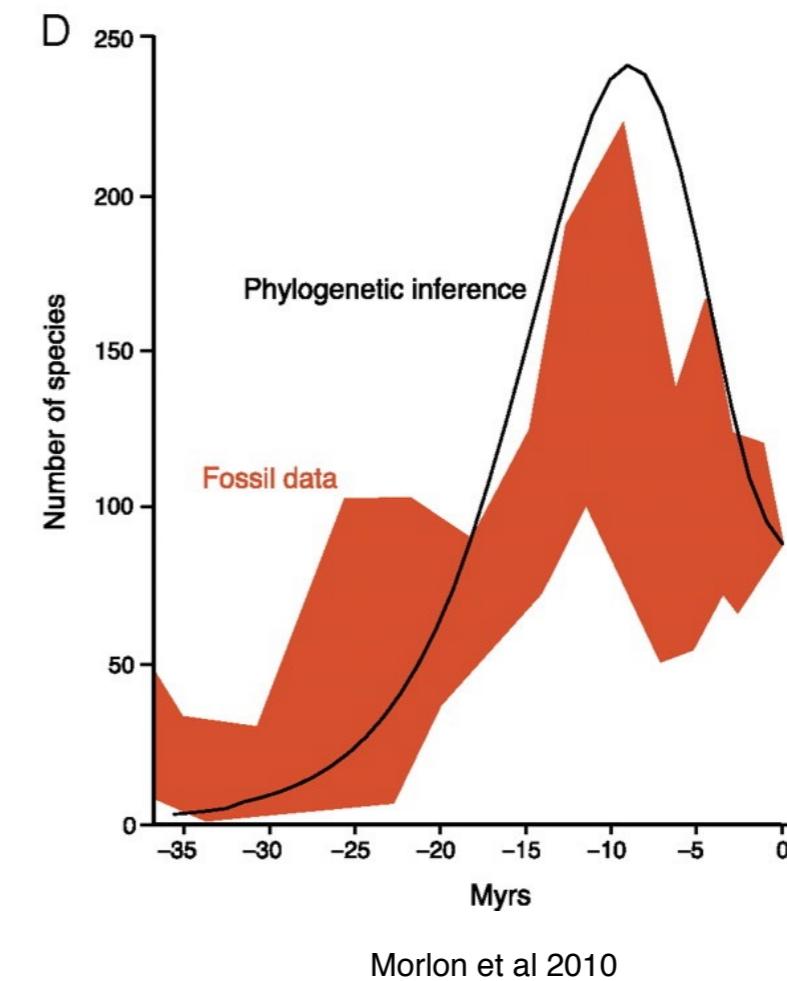
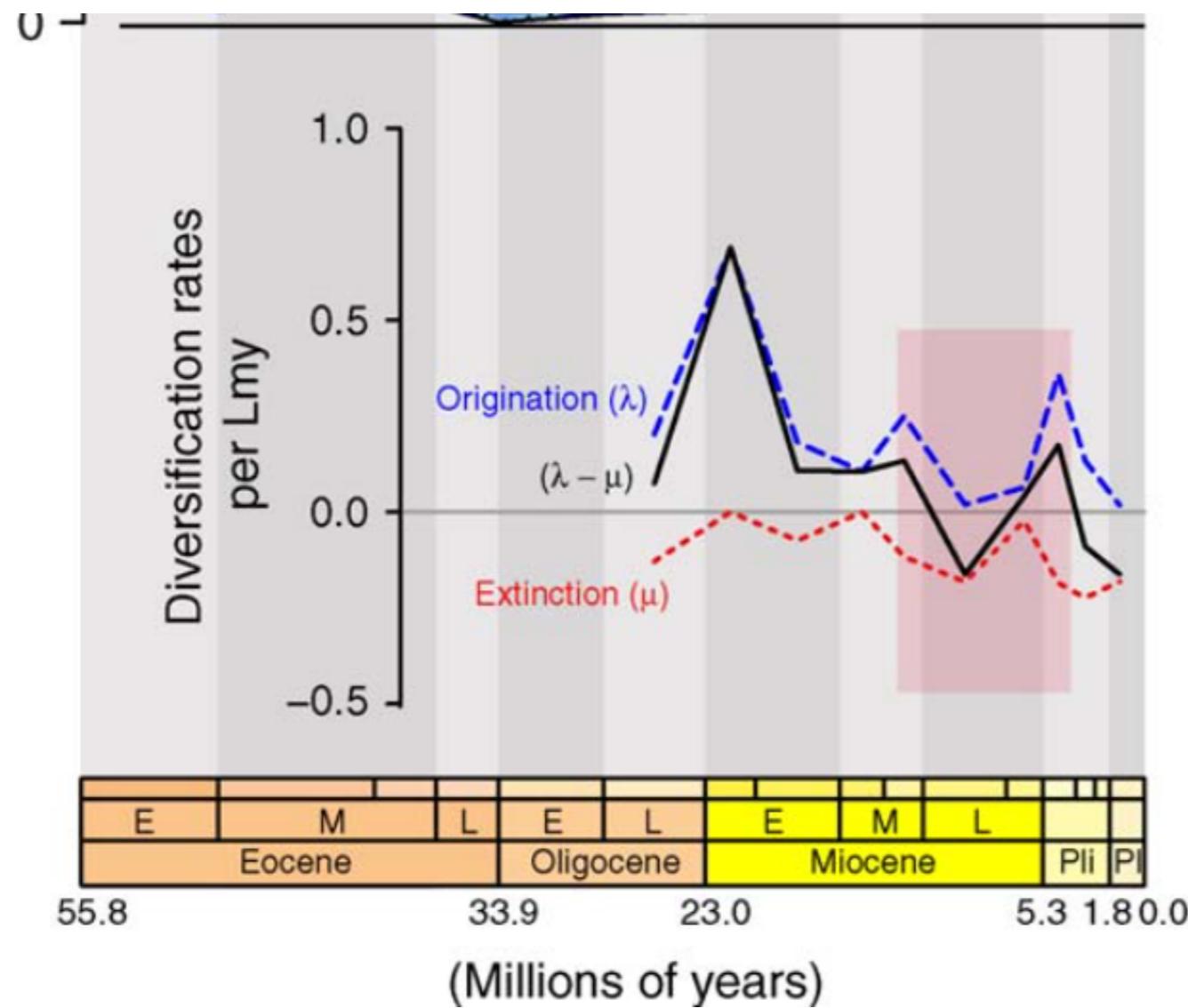
- allow rates to change with time over a tree
- extinction can be higher than speciation
- requires subclades to be identified a-priori

# RPANDA



Morlon et al 2010

# RPANDA



# BAMM

- general model:  
speciation variable,  
extinction constant
- allows tree to have as  
many diversification  
regimes as the data  
require (similar to  
MEDUSA but with a  
more flexible model)
- integrates over all  
reasonable fits of this  
multi regime model to  
any particular tree

