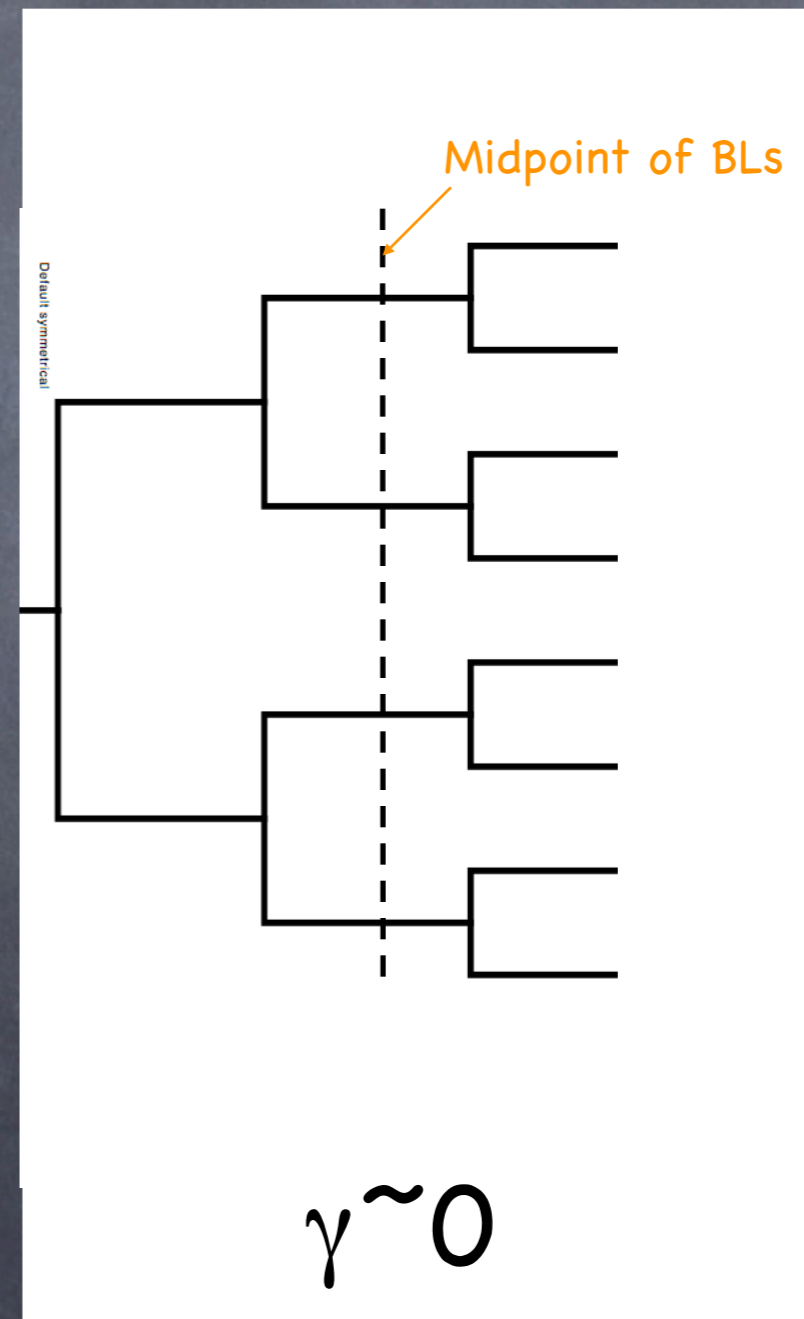


Testing for Rapid Radiation Over Clade History Using the Gamma Statistic

- Did a clade 'adaptively radiate'?
- Expect initial diversification to be fast
- Pybus and Harvey (2001)* proposed a test for rate shift across the tree

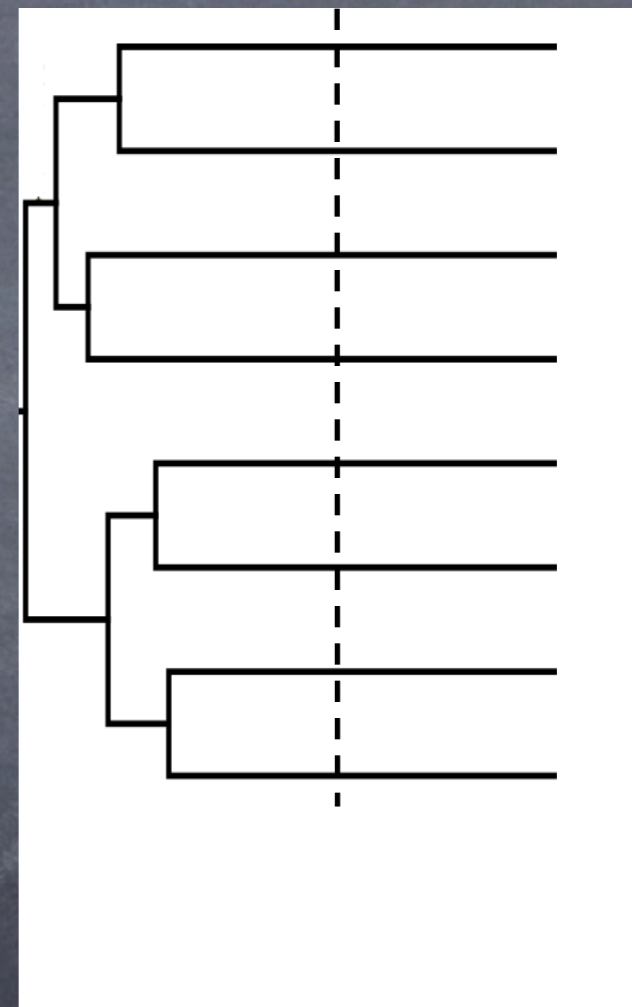
The gamma statistic

- a tree branching under a constant-rates model should have a balance of node depths around the midpoint of the tree
- γ describes this distance



Early branching

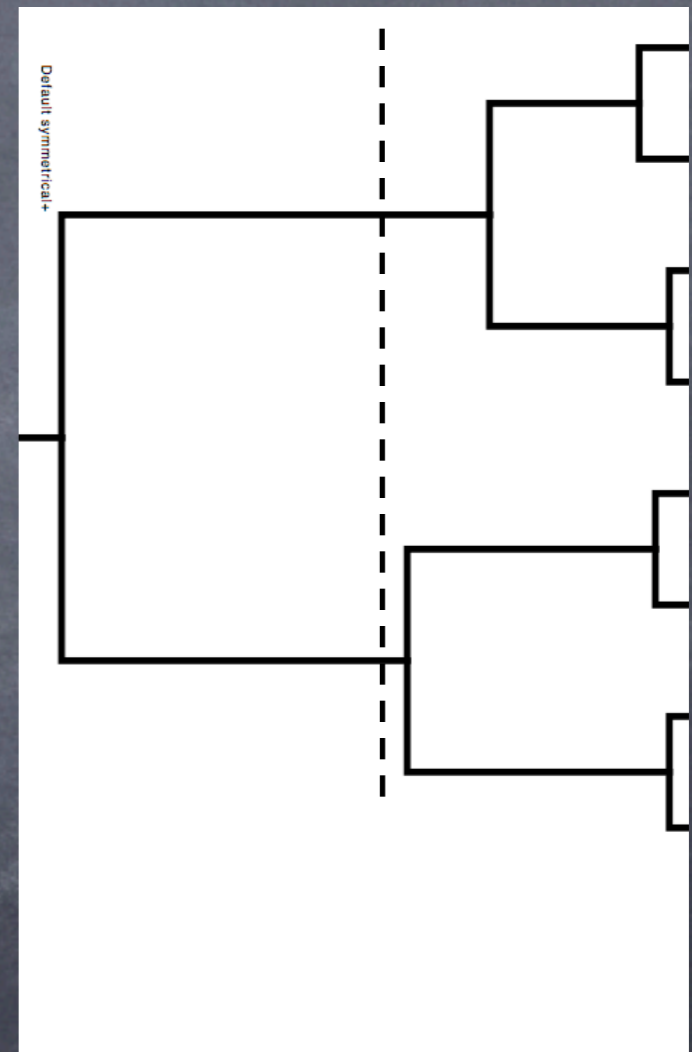
- rapid, early diversification will create an imbalance of young nodes
- this will be reflected by a $-\gamma$
- evidence for adaptive radiation



$\gamma < 0$

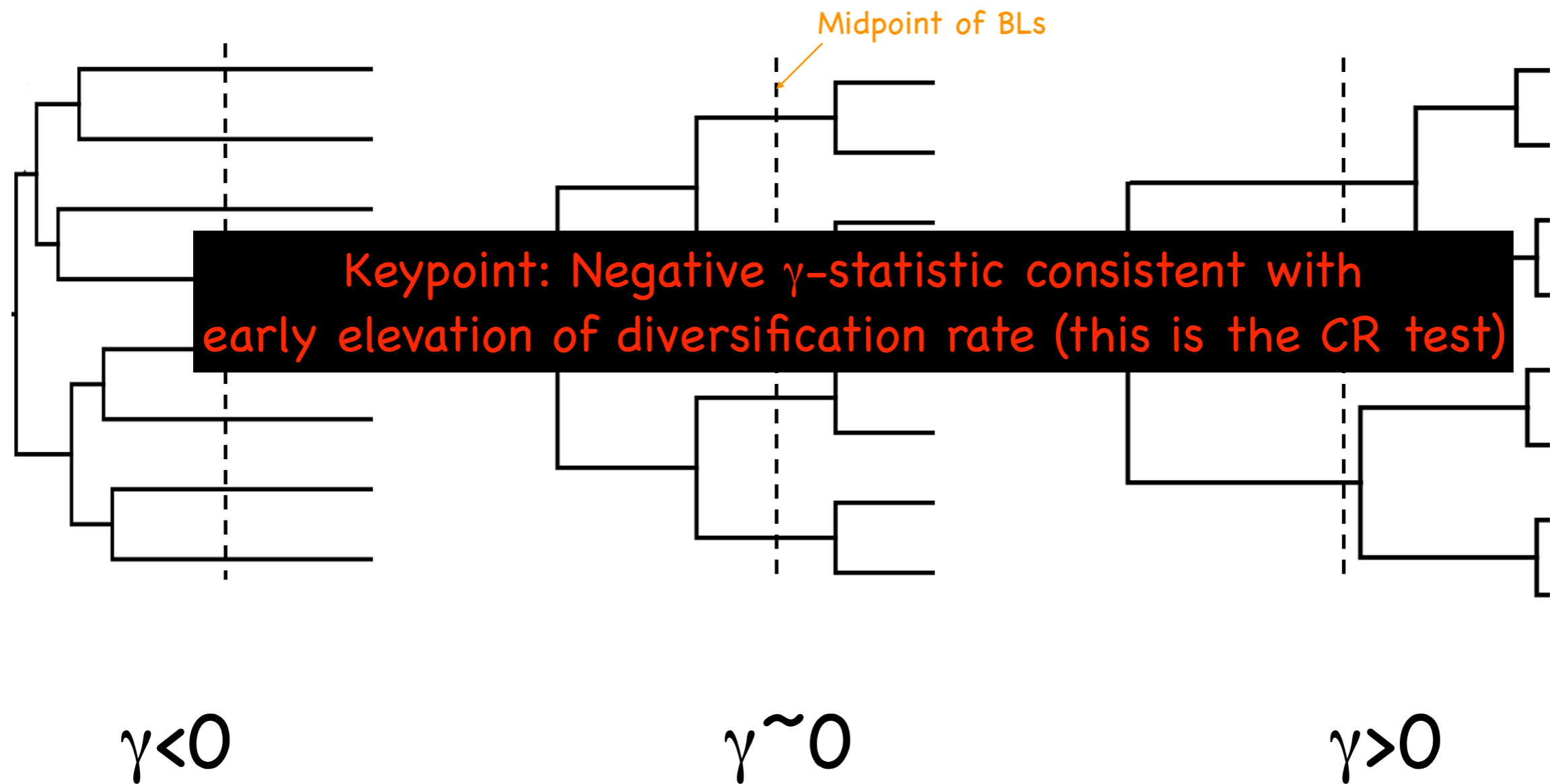
Late branching

- recent accelerated net diversification will concentrate nodes towards the tips
- could be due to increase in birth rate or decrease in death rate



$$\gamma > 0$$

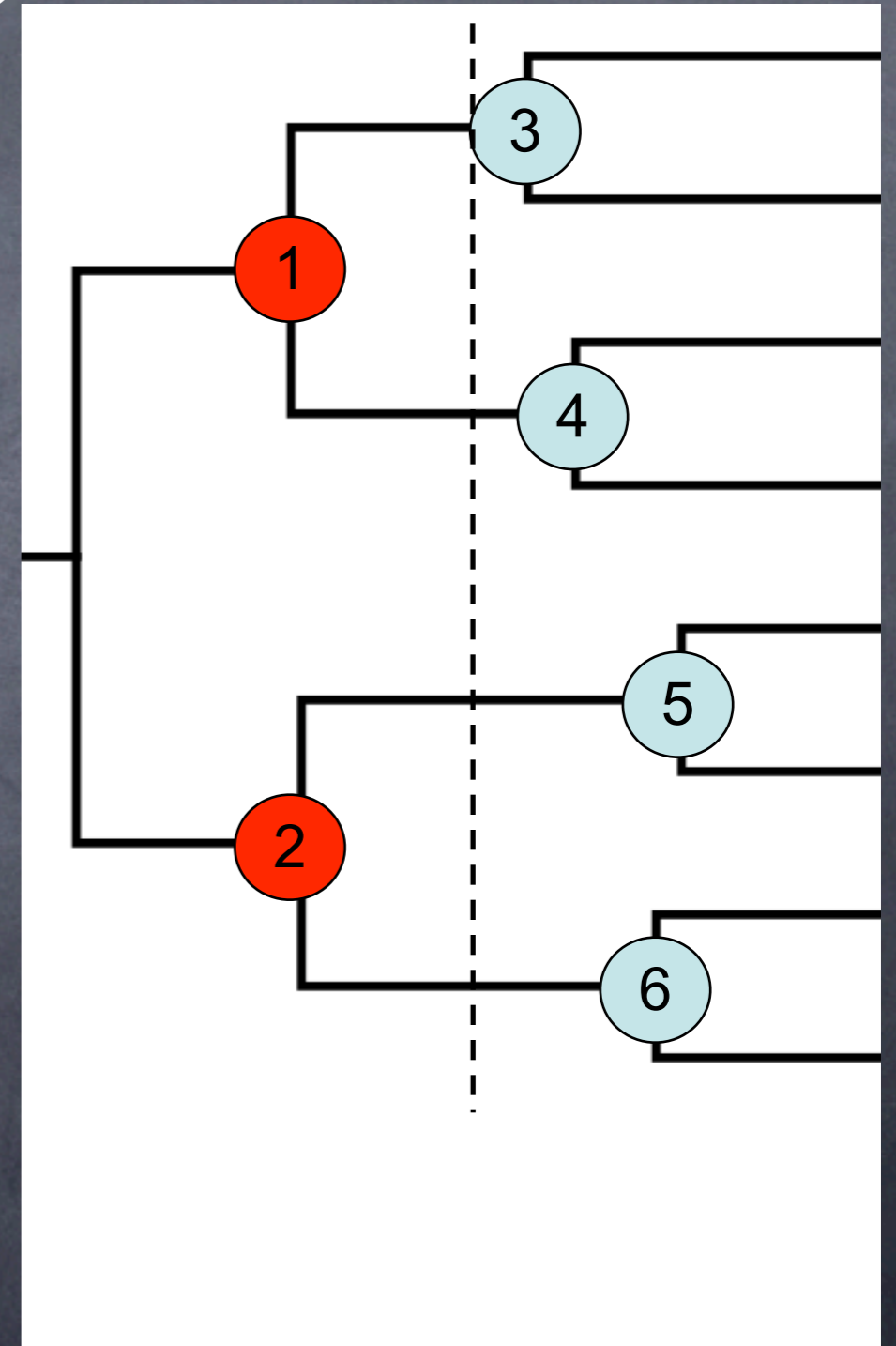
γ -statistic



if gamma is less than 2 std. deviations from mean ($\gamma \leq -1.645$), reject constant rate of diversification

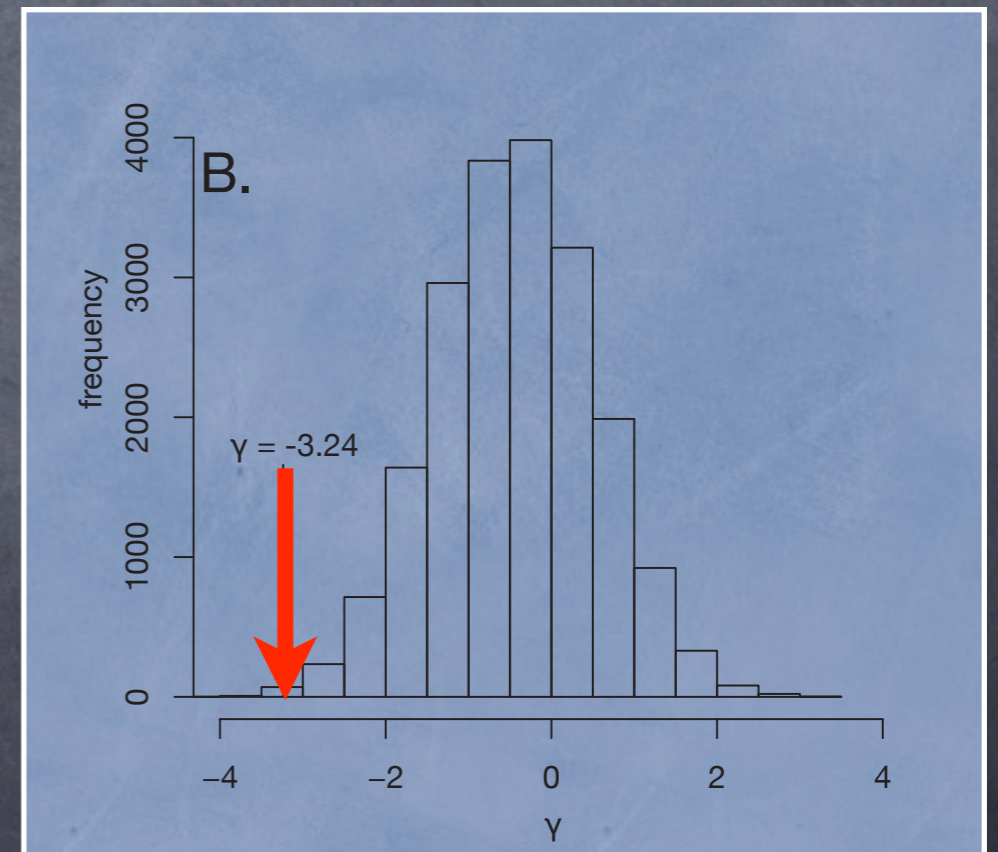
What about incomplete sampling?

- with random sampling of four taxa, what nodes would be expected to miss?
- how would this affect gamma?



MCCR: The constant rates test for incompletely sampled trees*

- Complete sampling: $\gamma \leq -1.645$
- Incomplete sampling means that old nodes more likely to be recovered, biasing CR test
- Solution: MCCR test*
 - Simulate tree with n taxa
 - RANDOMLY prune missing taxa
 - Calculate the γ -statistic on pruned tree
 - Repeat
 - Calculate corrected p-value

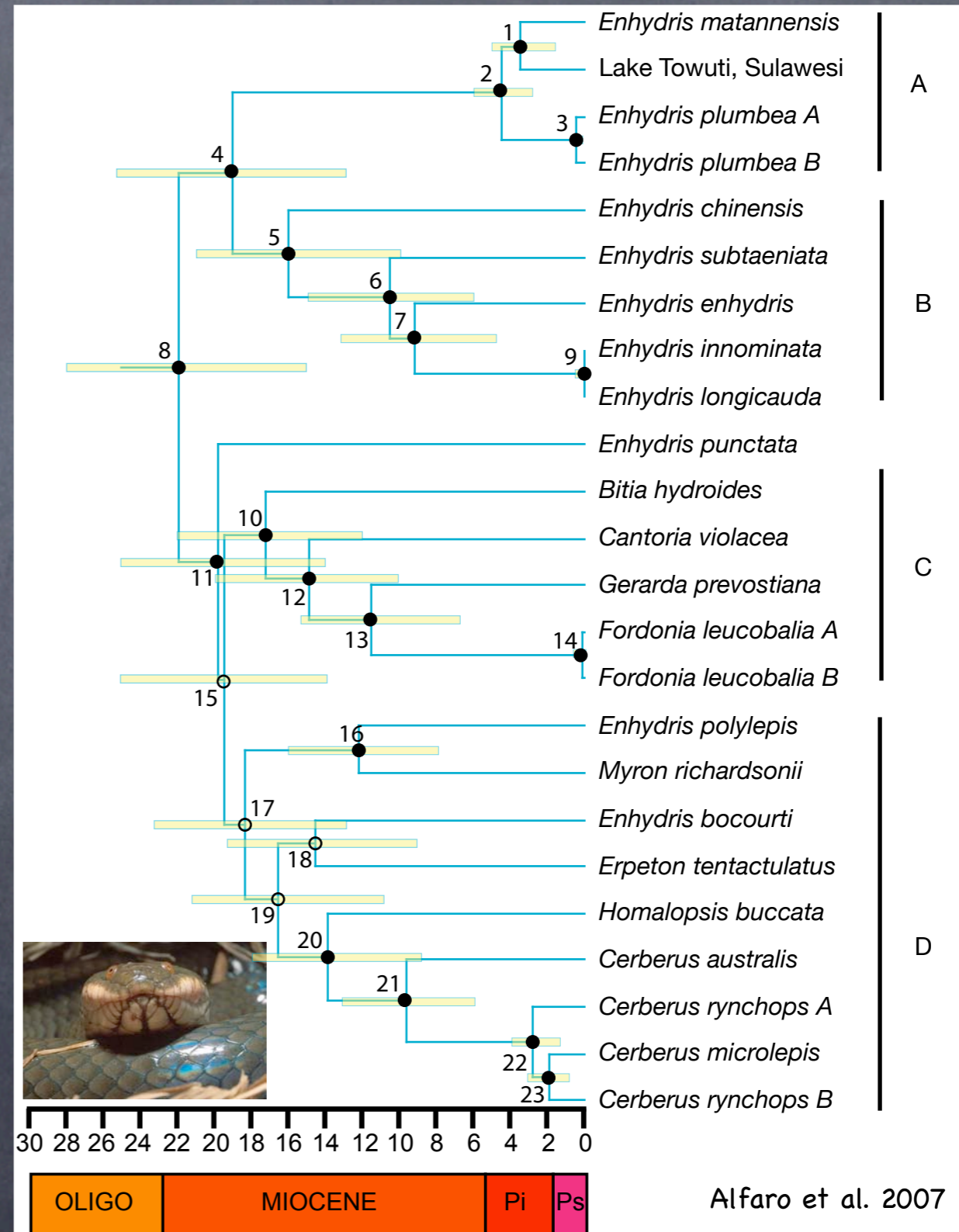
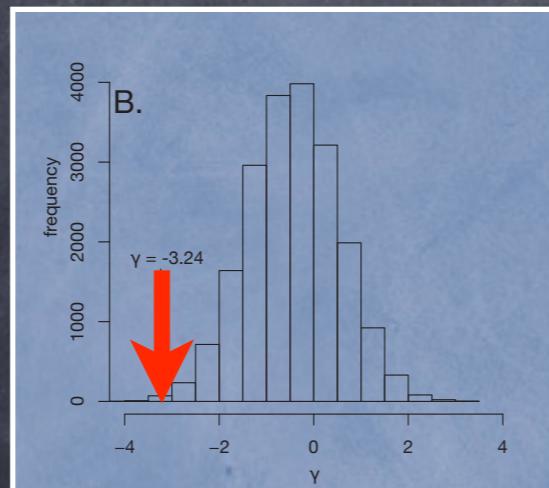


Example of Gamma Statistic: Diversification of Homalopsid Snakes

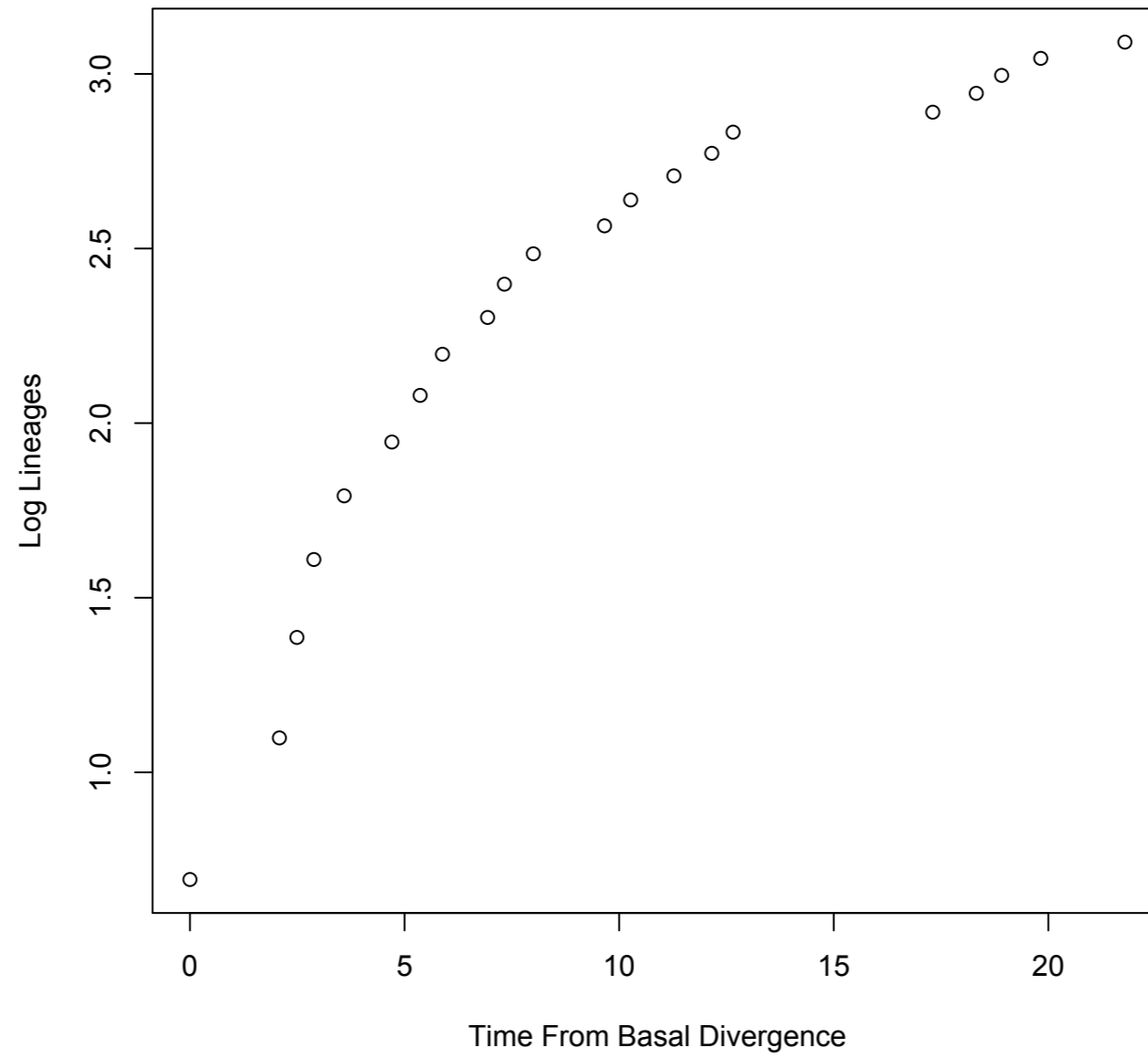
- 34 species distributed across S.E. Asia
- Aquatic to semi-aquatic

A timetree for homalopsid diversification

- Bayesian timetree using BEAST
- 4 genes (12S, 16S, cytB, C-Mos)
- 9 of 10 genera, 20 of 34 species
- MCCR test suggests rapid initial diversification ($P < 0.001$)



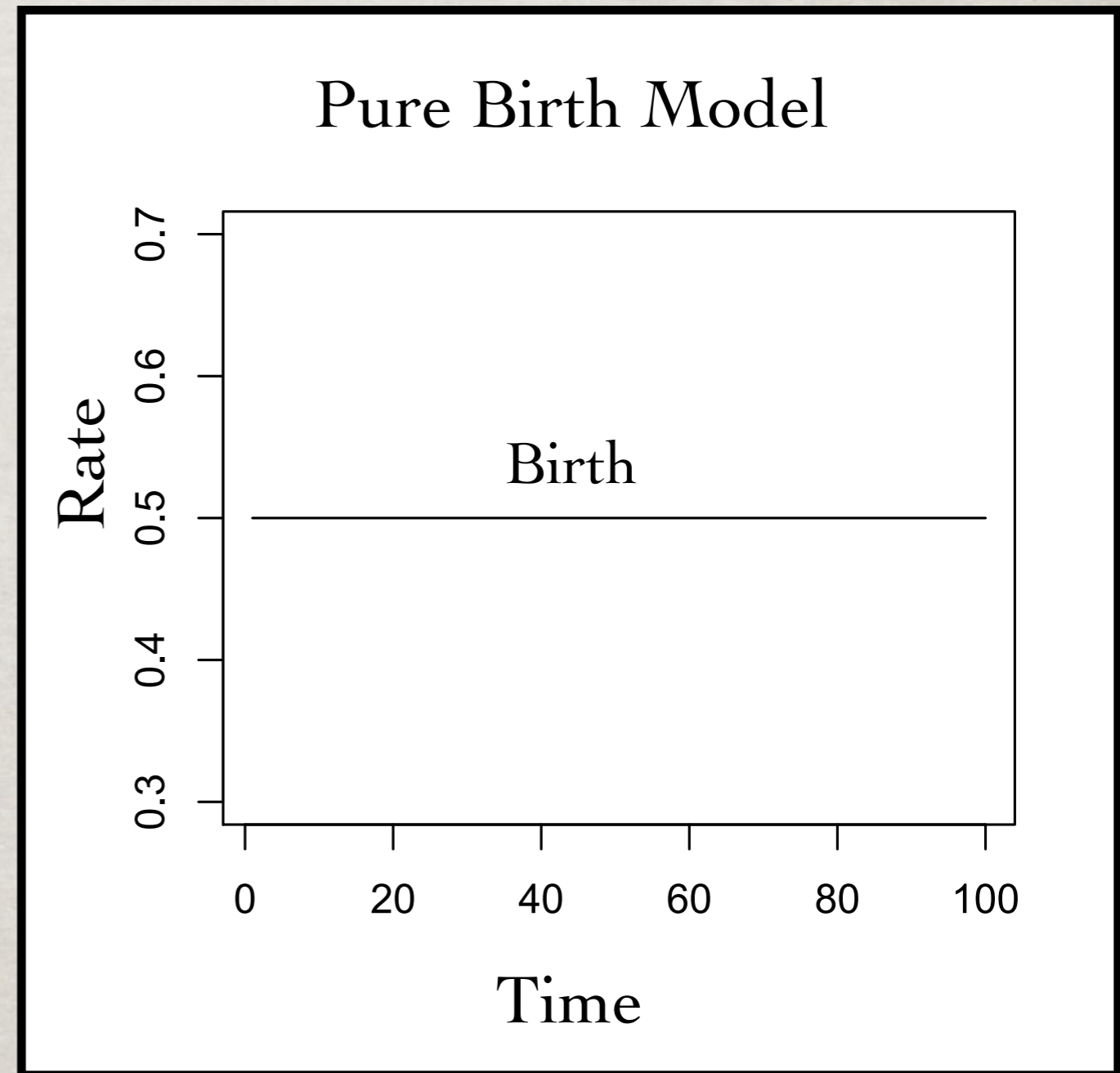
Log-Lineages Through Time



MODELS OF DIVERSIFICATION: CONSTANT-RATE MODELS

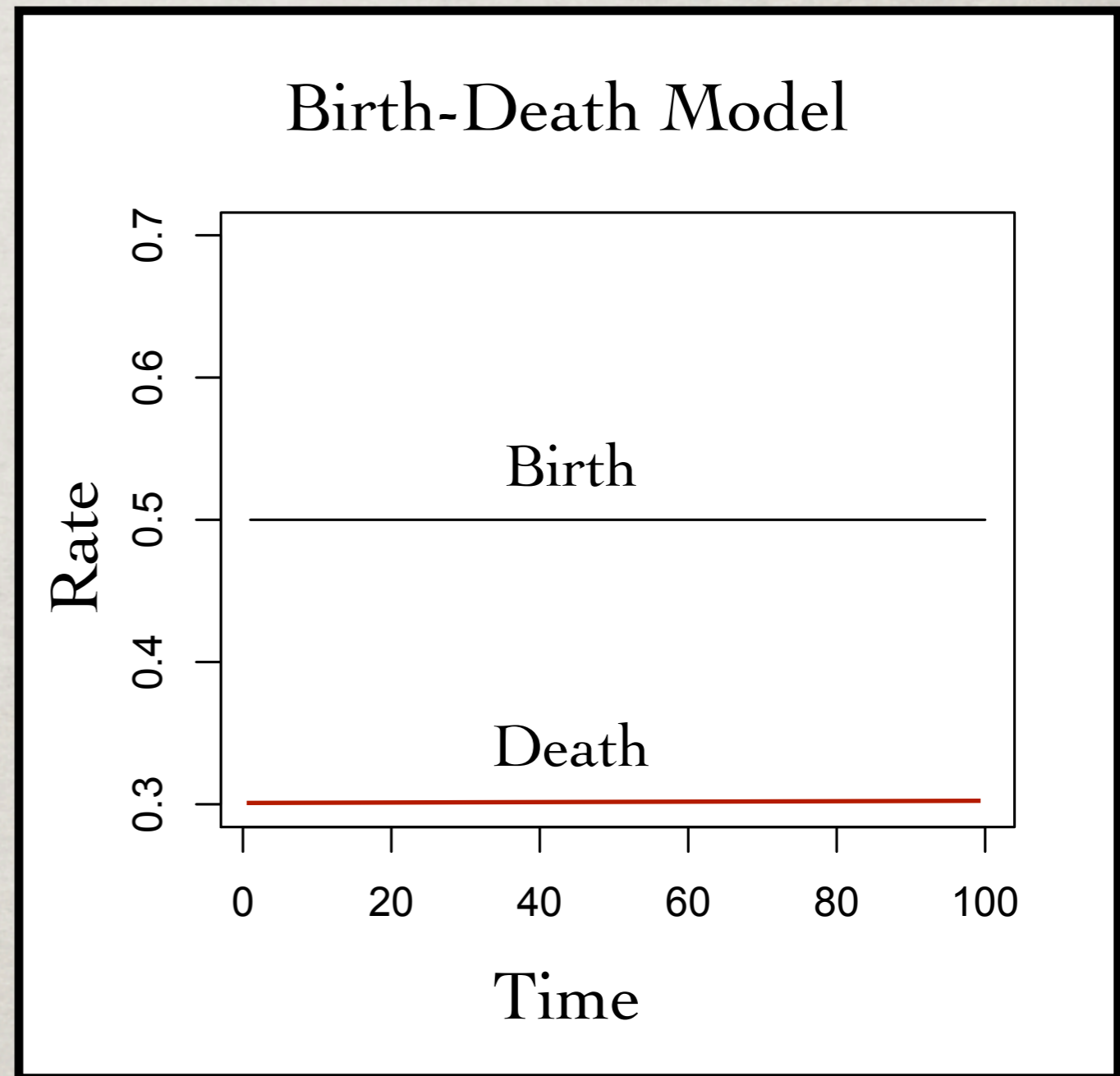
- ☼ Pure birth (PB)

- ☼ Death = 0



MODELS OF DIVERSIFICATION: CONSTANT-RATE MODELS

- ✿ Birth-Death (BD)
- ✿ Birth & Death constant

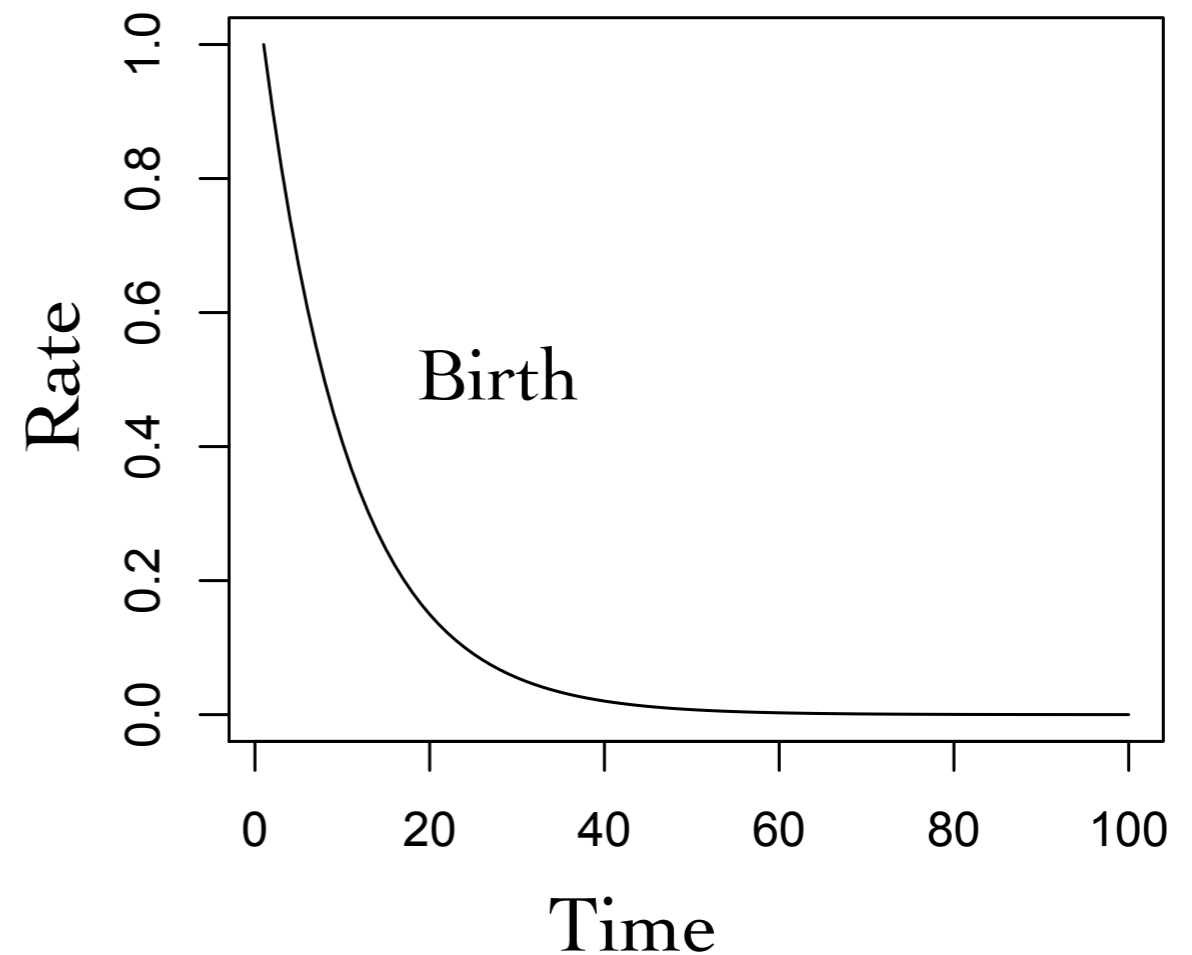


RATE-VARIABLE MODELS: DENSITY-DEPENDENT

- ☼ Density-dependent: Exponential

- ☼ $R(t) = R_0 * (N(t))^{-x}$

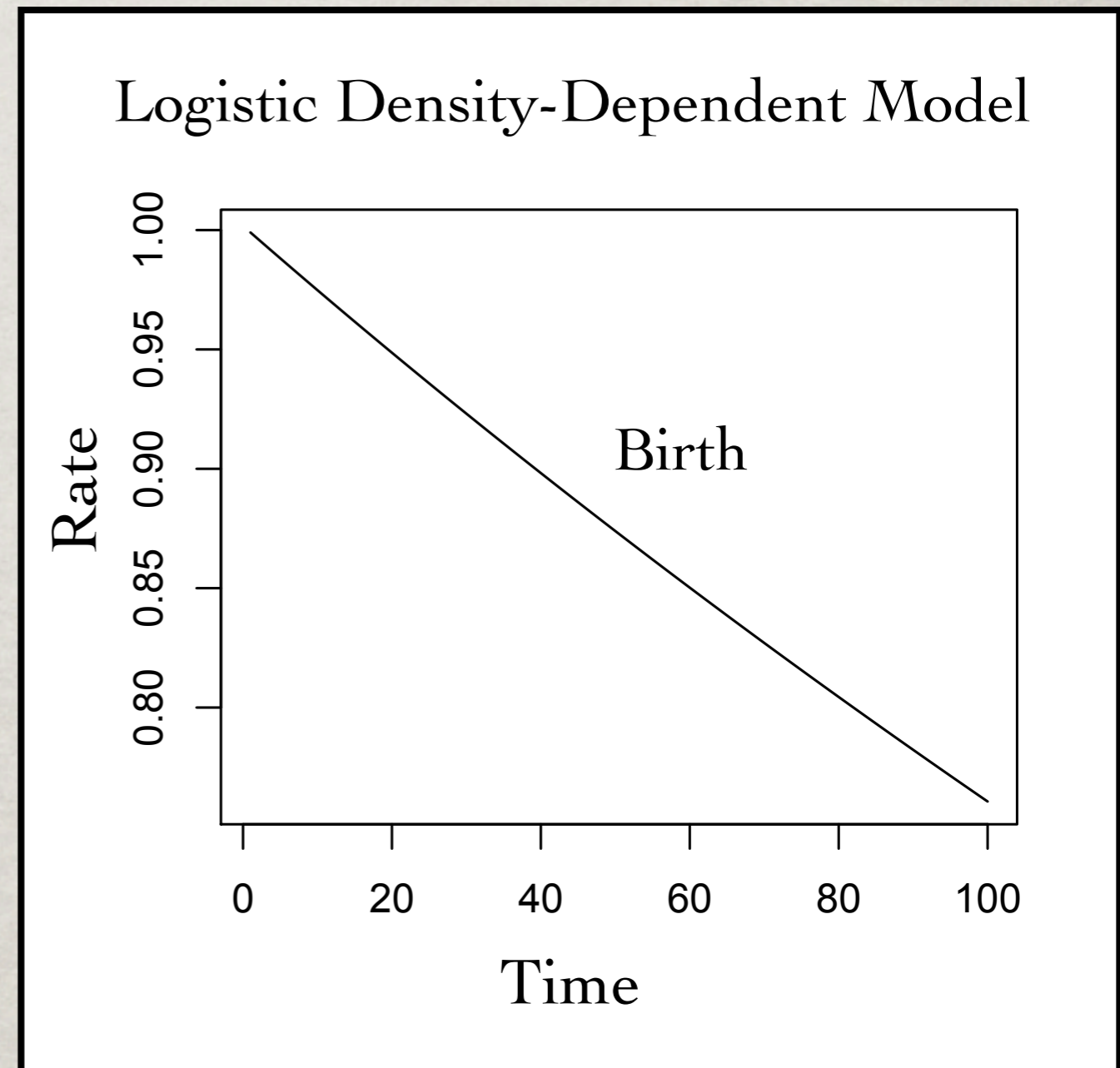
Exponential Density-Dependent Model



RATE-VARIABLE MODELS: DENSITY-DEPENDENT

✿ Density-dependent: Logistic

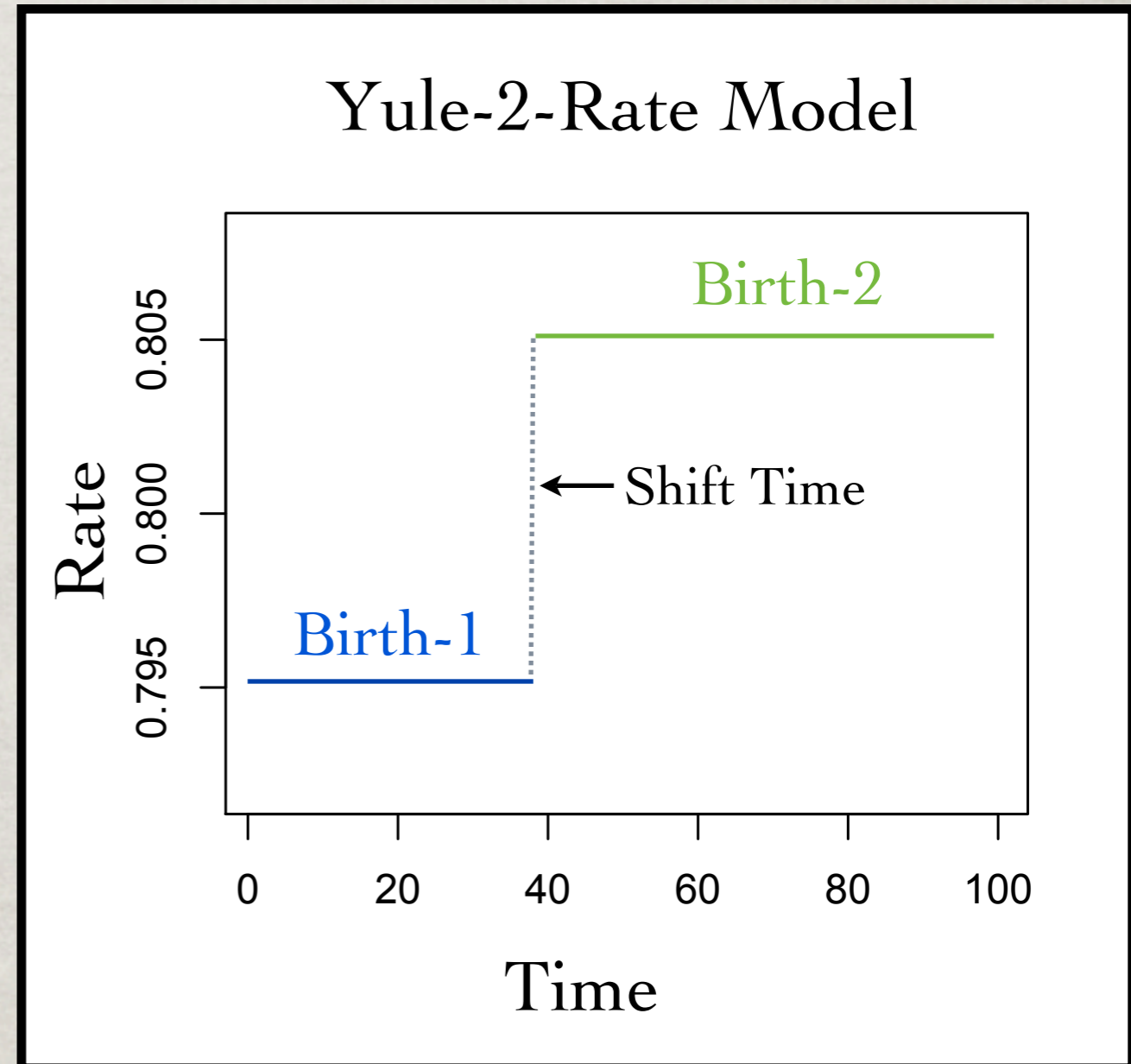
✿ $R(t) = R_0 * (1 - N(t)/K)$



MODELS OF DIVERSIFICATION: VARIABLE-RATE MODELS

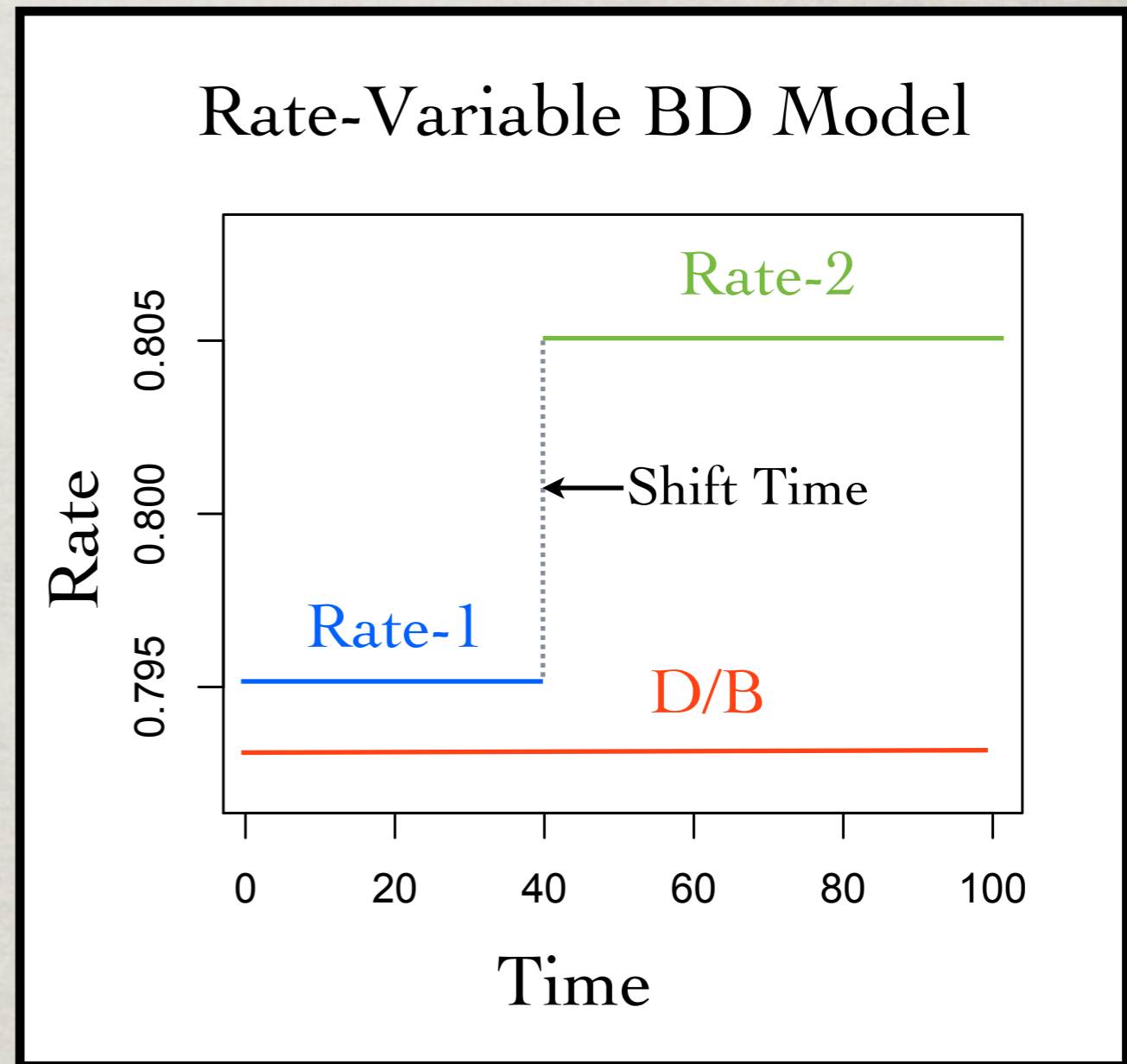
- ✻ Yule-2-Rate (Y2R)

- ✻ Death = 0



MODELS OF DIVERSIFICATION: VARIABLE-RATE MODELS

- ☼ Rate-variable BD (RVBD)
- ☼ Death/Birth is constant



MODEL SCORES

Model	LH	dAIC	Rate 1	Rate 2	Shift Time
PB	75.73	12.07	0.153	NA	NA
BD	75.73	14.07	0.153	NA	NA
DDL	79.07	7.4	0.236	NA	NA
DDX	77.58	10.37	0.352	NA	NA
Y2R	83.77	0	0.177	0.036	1.127
RVBD	83.77	2.0	0.177	0.036	1.127

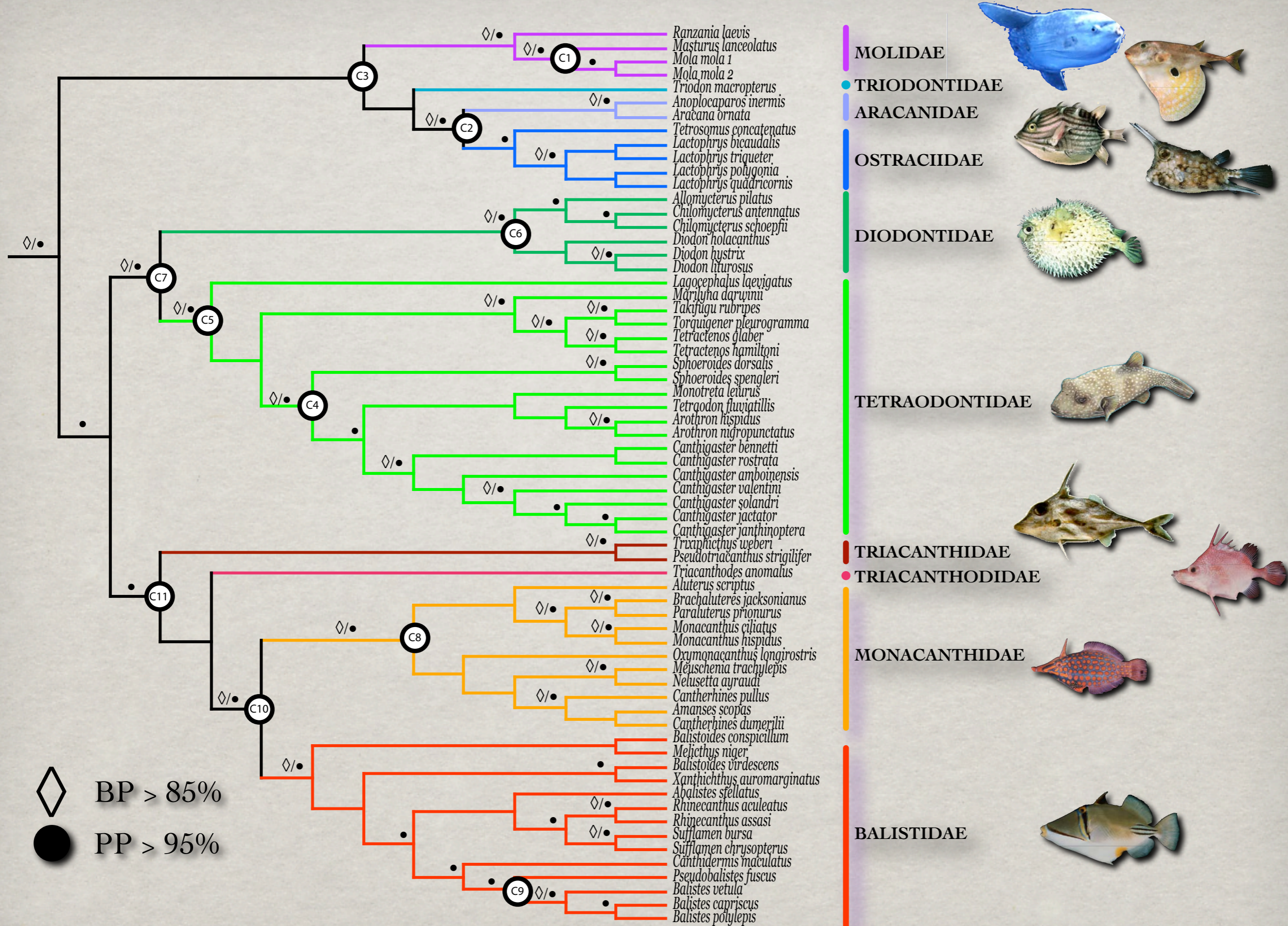
density-dependent models rejected for rockfish

HOW CAN WE TEST FOR UNEQUAL RATES OF DIVERSIFICATION?

- ✿ Construct a timetree
- ✿ Calculate rates
- ✿ Test for significant differences using comparative methods

STEP 1: MOLECULAR PHYLOGENY

- ✿ Molecular sequence data from three loci *Rag1*, *12S*, *16S* (Holcroft, 2005, plus additional data)
- ✿ Sampled 86 ingroup taxa including members of all extant families
- ✿ Bayesian analysis using *MrBayes*, 1×10^7 generations, multiple independent runs



STEP 4: COMPARE DIVERSIFICATION RATES

1. Estimate mean diversification rate of tetraodontiformes (λ_G)

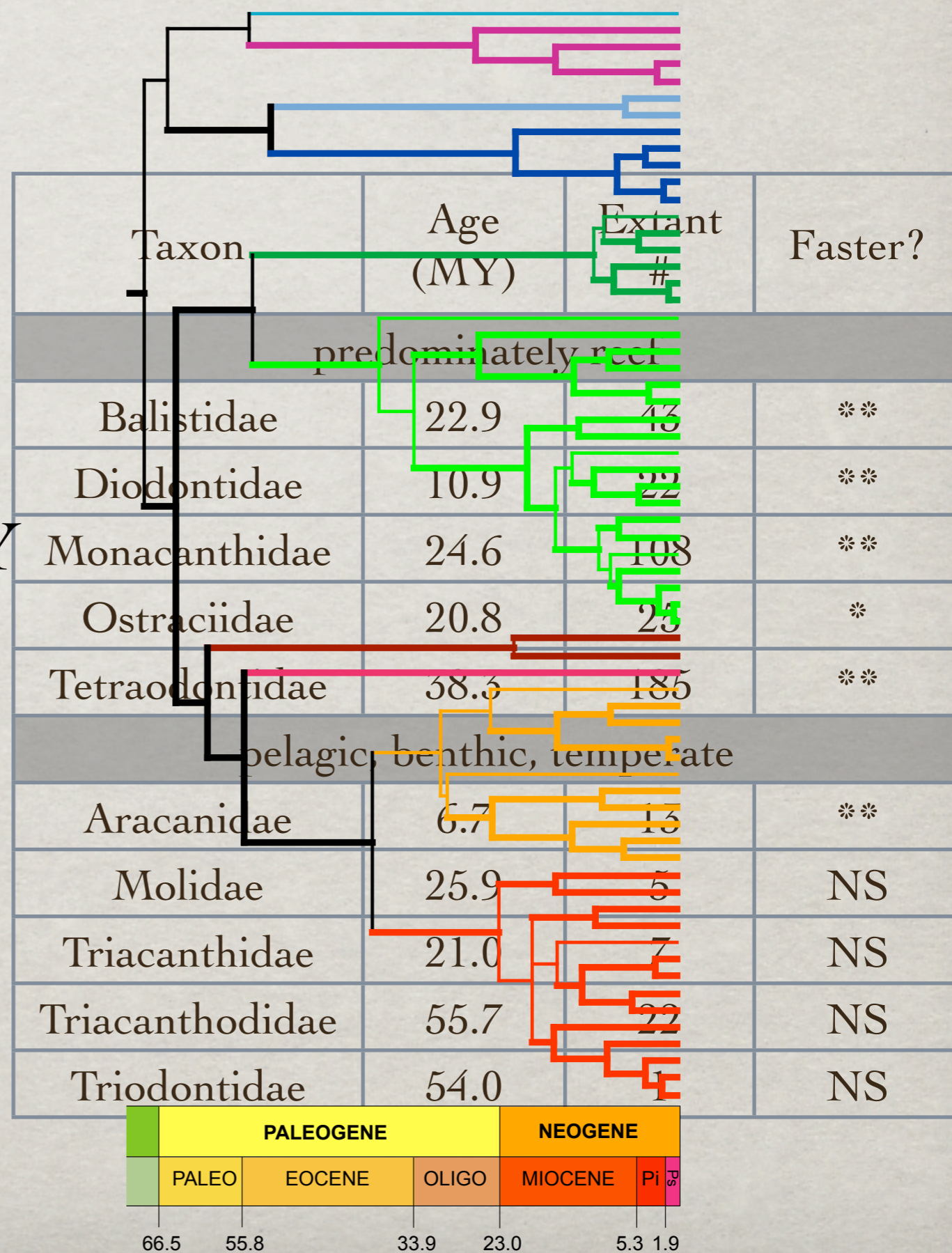
$$\lambda_G = [\ln(n) - \ln(2)]/t$$

$$= \ln(350) - \ln(2) / 70\text{MY}$$

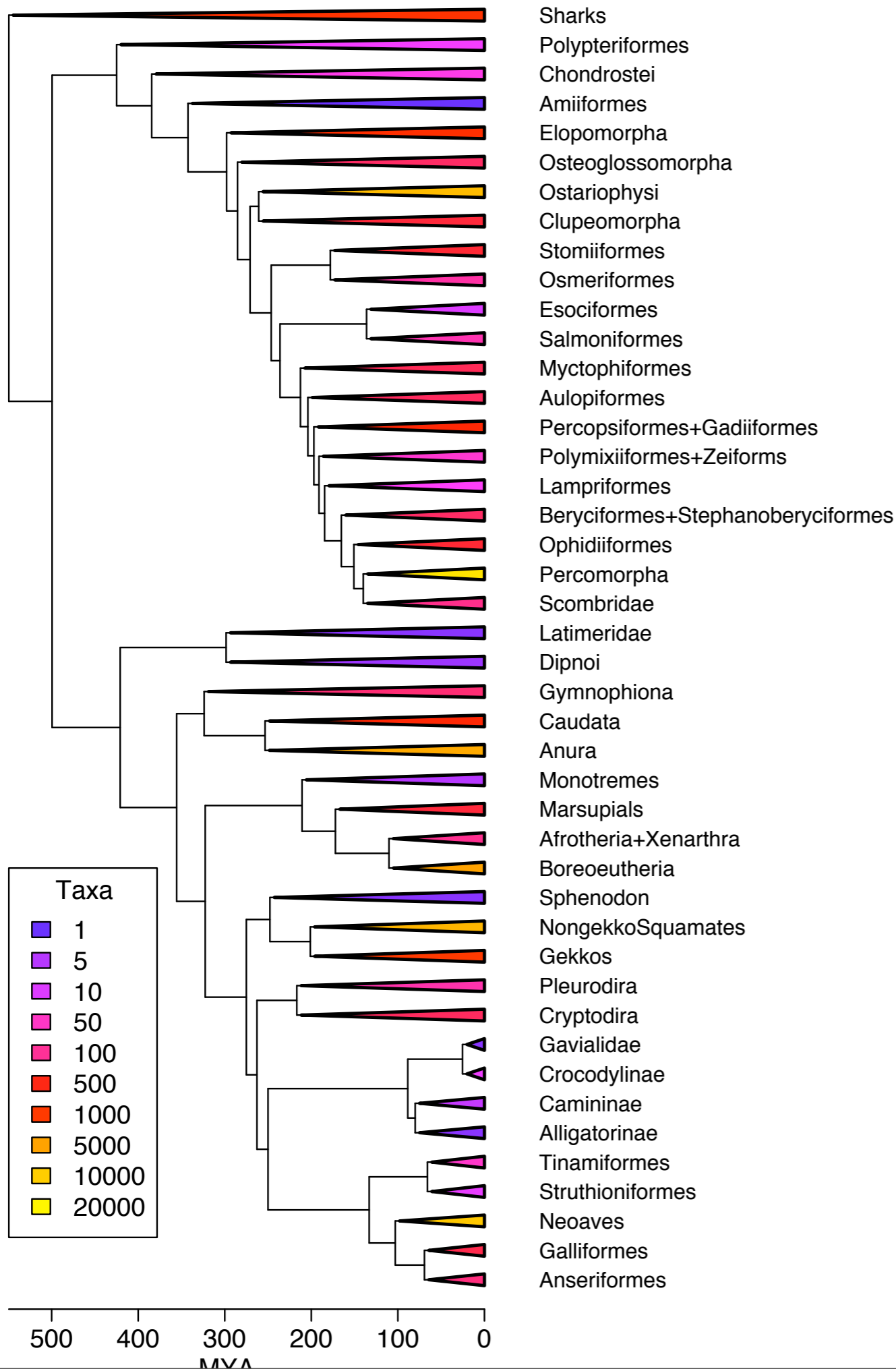
$$= \mathbf{0.07 \text{ species/MY}}$$

2. Test whether family species richness

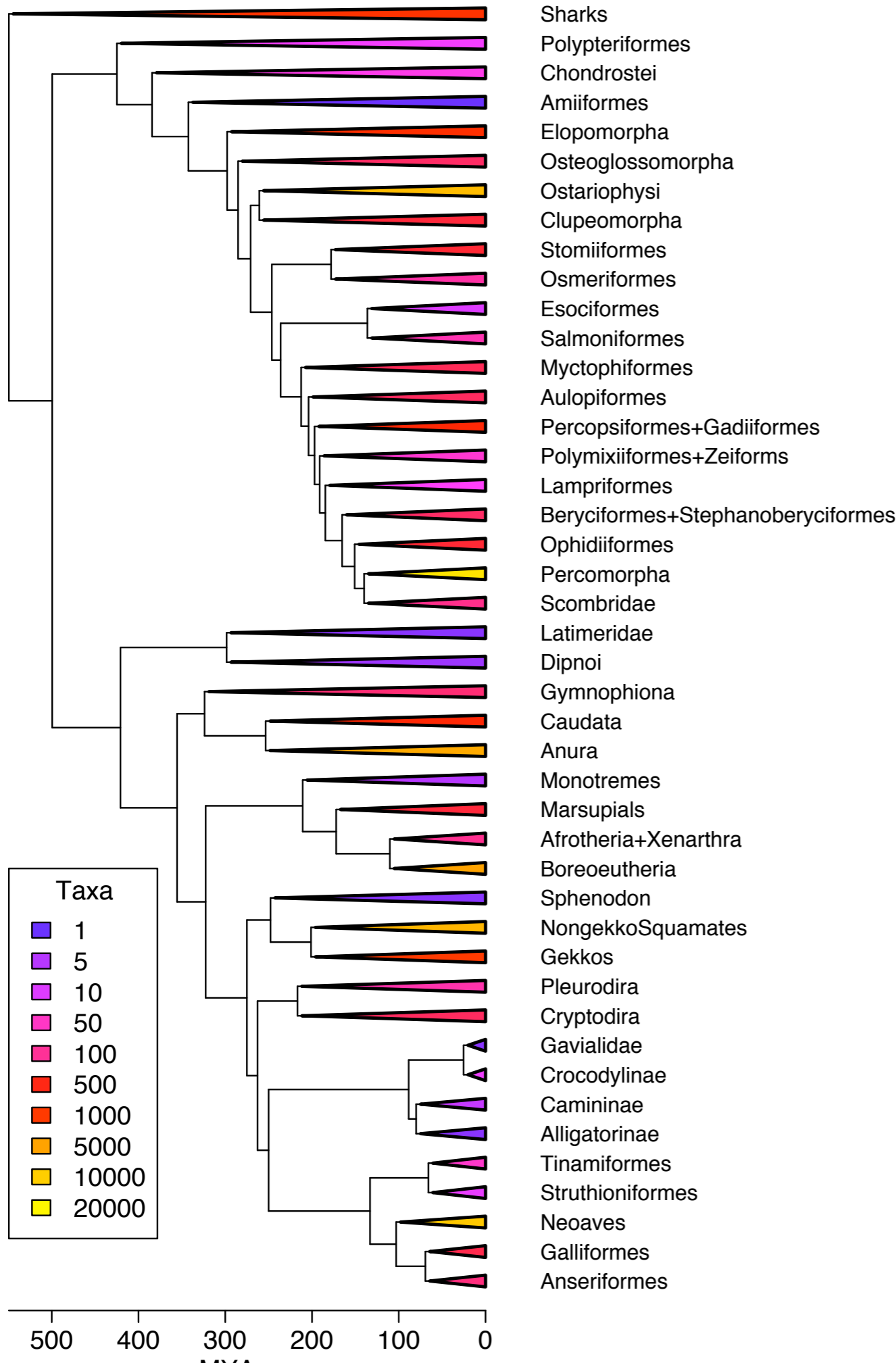
key point: species richness exceptionally high in reef groups



A Timetree for Jawed Vertebrates



- ~ 60,000 species total
- Molecular Phylogeny
 - RAG-I genbank data
 - 221 tip species
 - Relaxed molecular clock
 - 42 fossil calibrations
 - major gnathostome lineages represented



$$I. \lambda_G = [\log(n) - \log 2]/t$$

$n = 57,859$ species

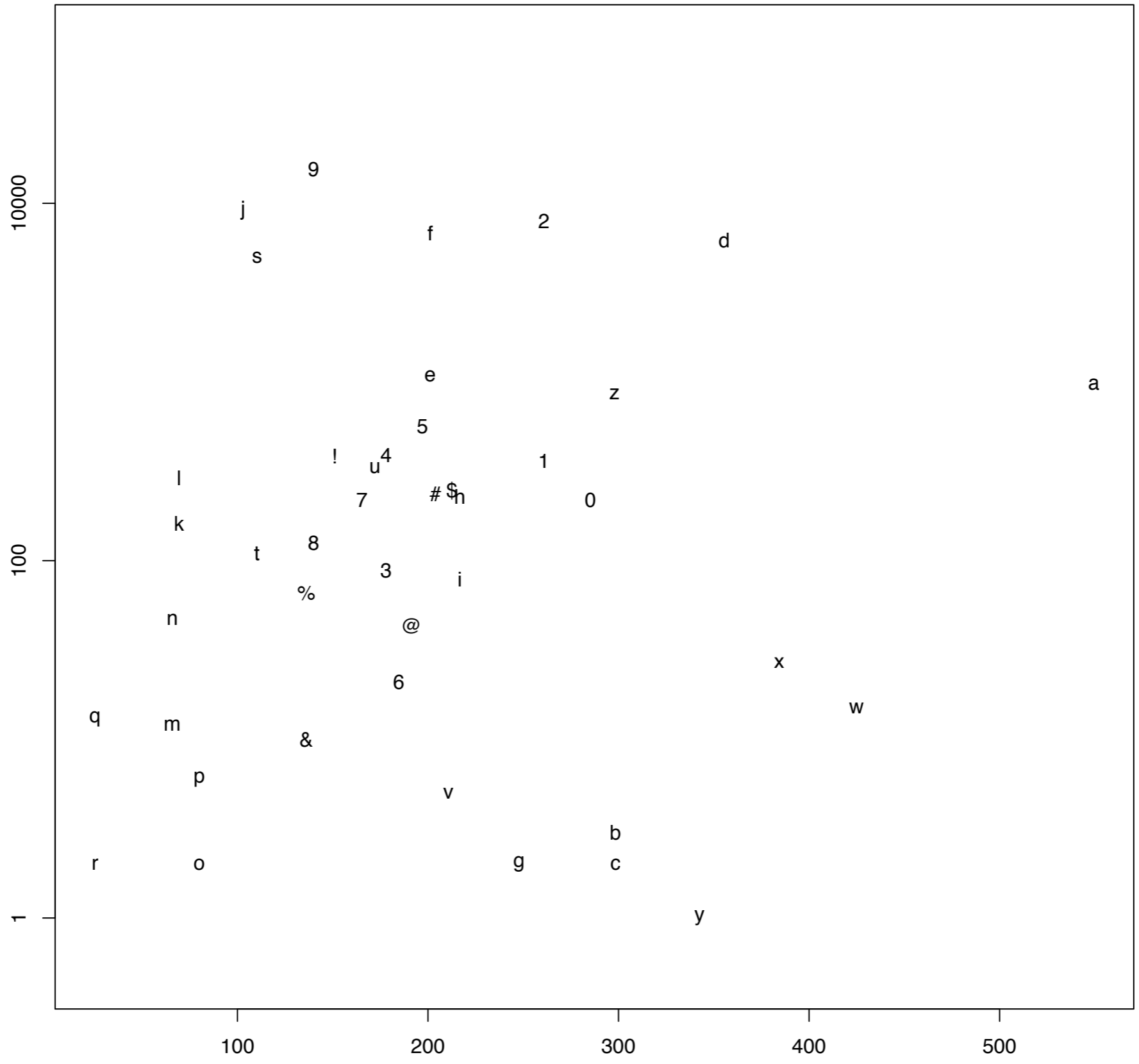
$t = 549$ mya

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

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

$$\lambda_G = 0.019$$

Species Richness

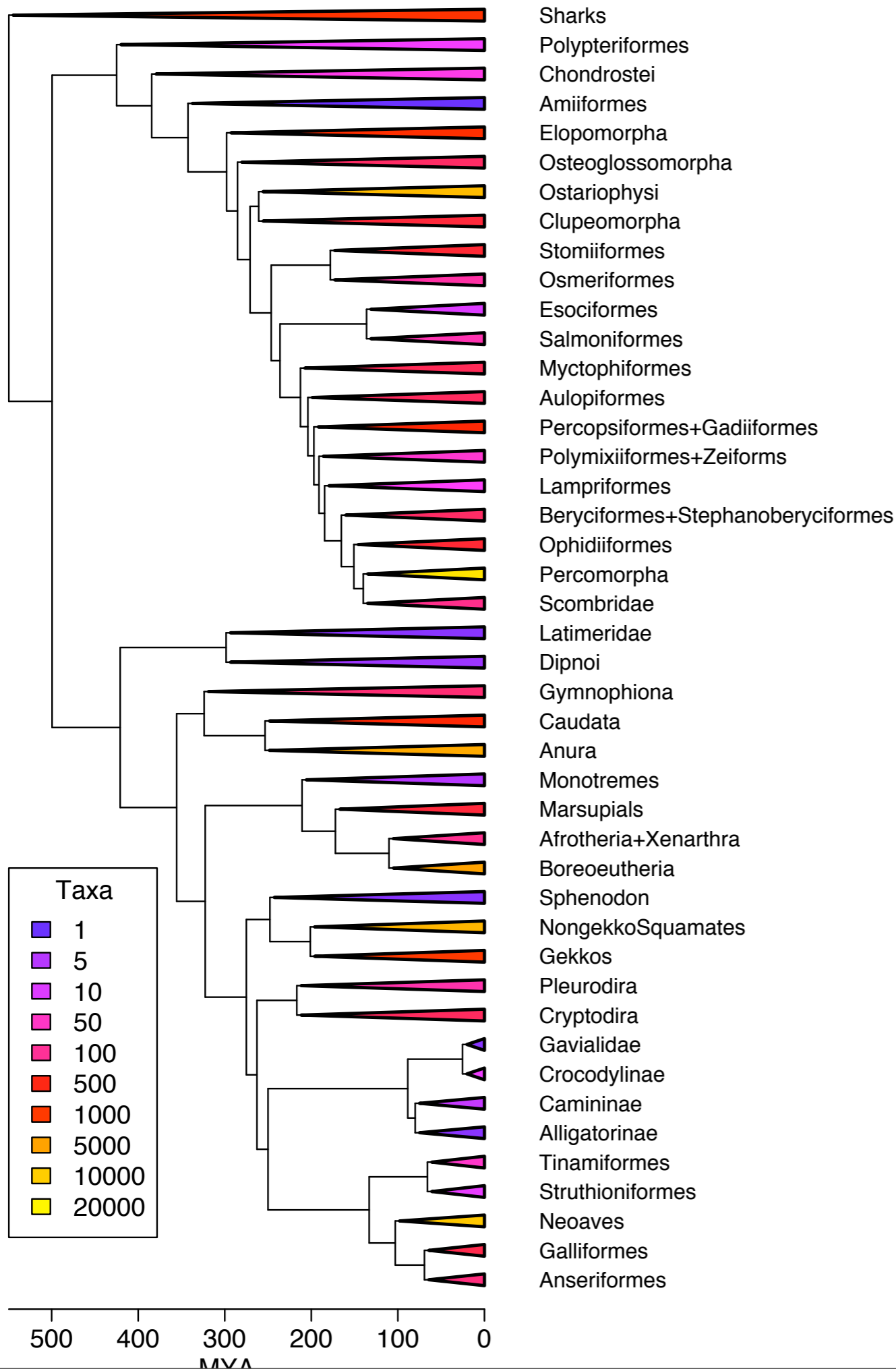


Stem Age (MY)

Thanks!!!

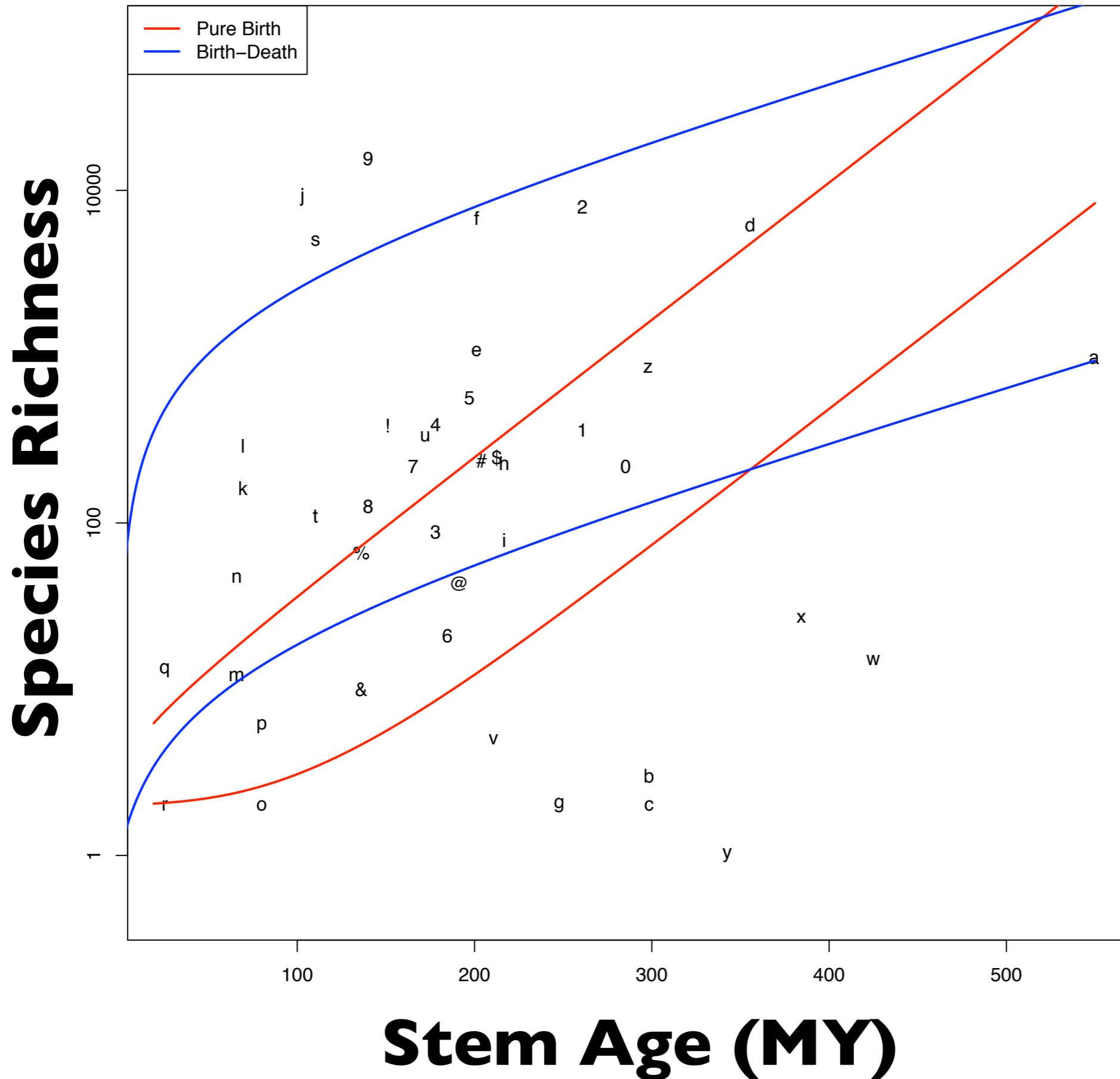
- we will send course materials out--make sure you gave us your email
- please send comments and feedback with 'FEEDBACK' in the header to michaelalfaro@ucla.edu

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key point: high turnover rates in gnathostomes



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