

# Bayesian Phylogenetic Inference using RevBayes:

**Diversification Rate Estimation**

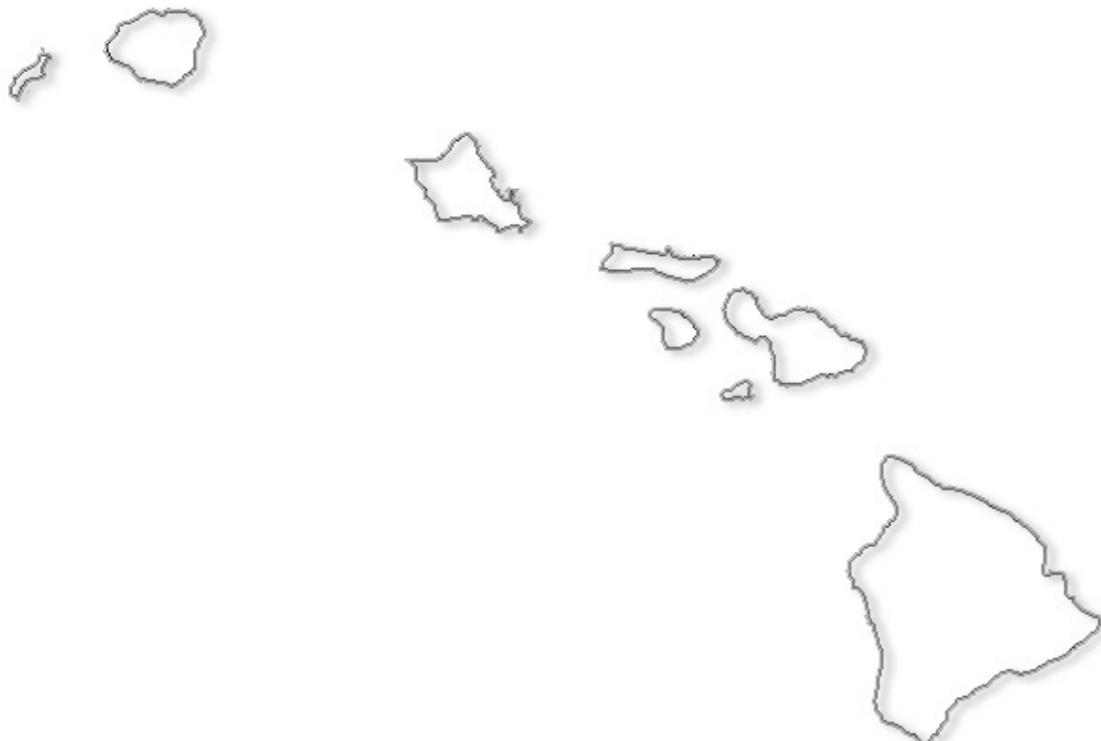
**Sebastian Höhna**

Division of Evolutionary Biology  
Ludwig-Maximilians Universität, München



# Patterns of diversification

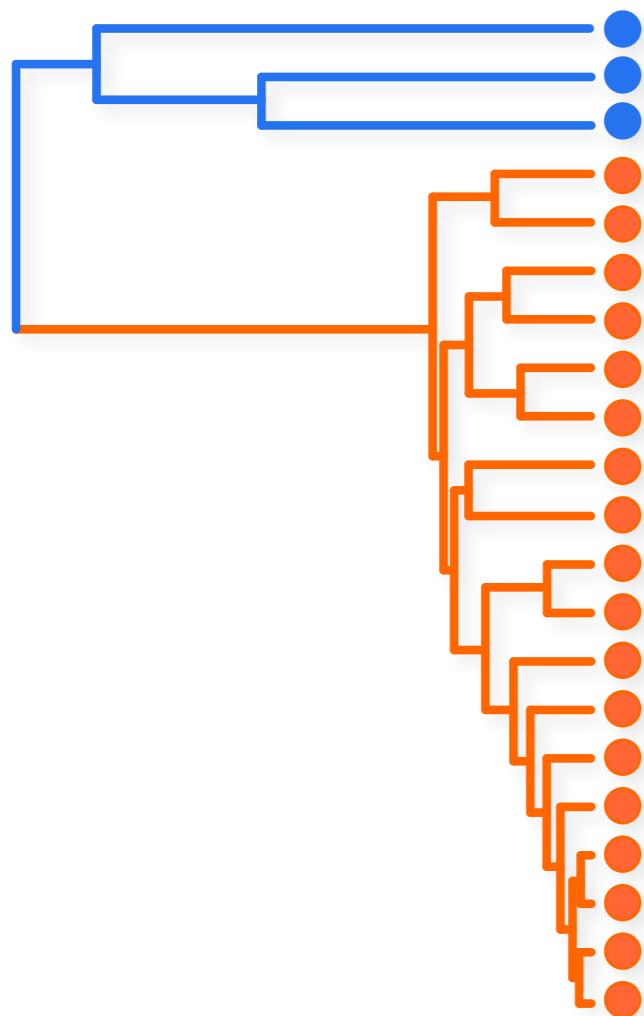
- adaptive radiation



Hawaiian silverswords

# Patterns of diversification

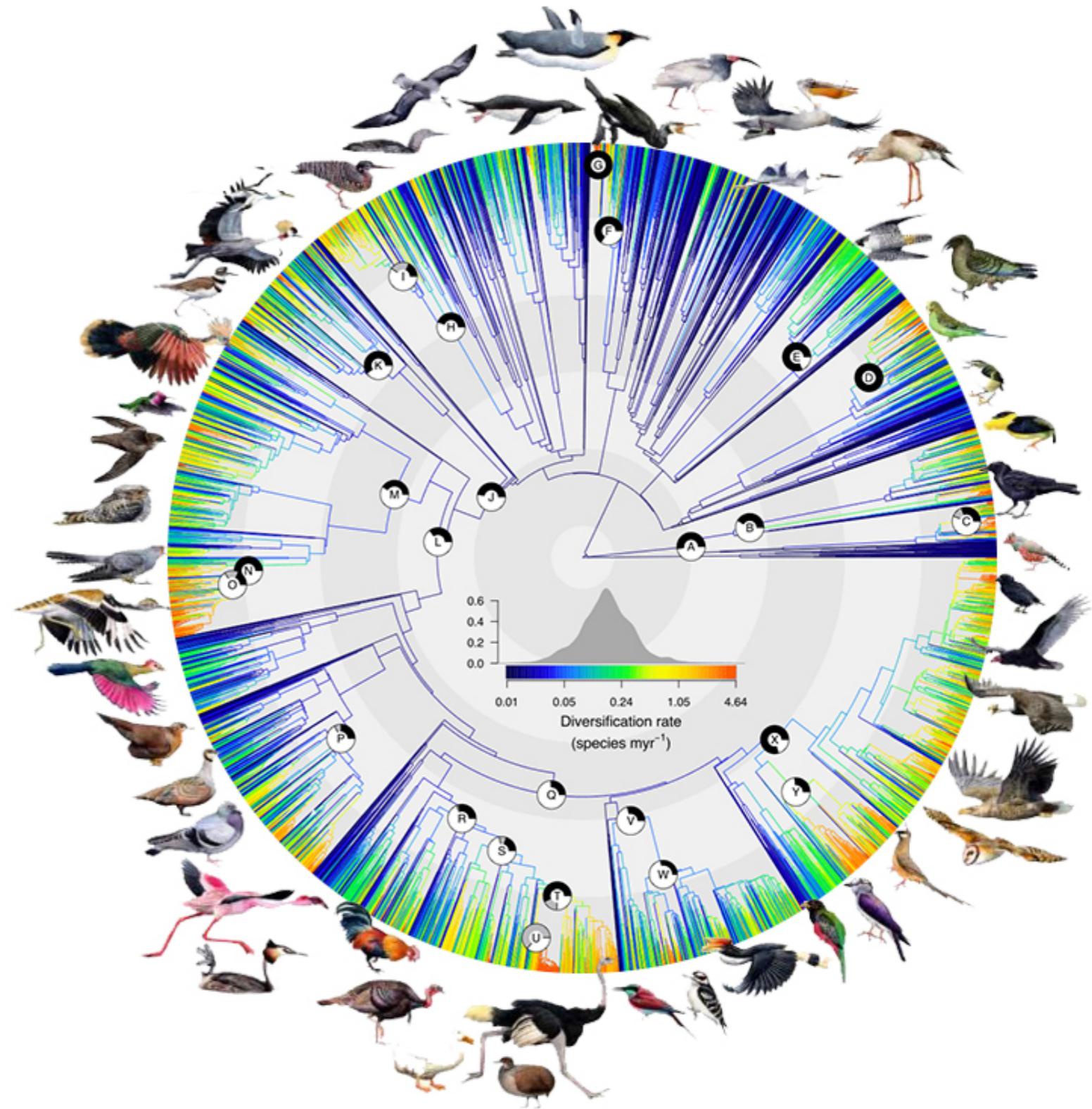
- adaptive radiation
  - key innovation



# Nectar spurs in columbines

# Patterns of diversification

- adaptive radiation
- key innovation
- diversity dependence



Global deceleration in birds

# Patterns of diversification

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- adaptive radiation
- key innovation
- diversity dependence
- mass extinction



K-Pg bolide impact

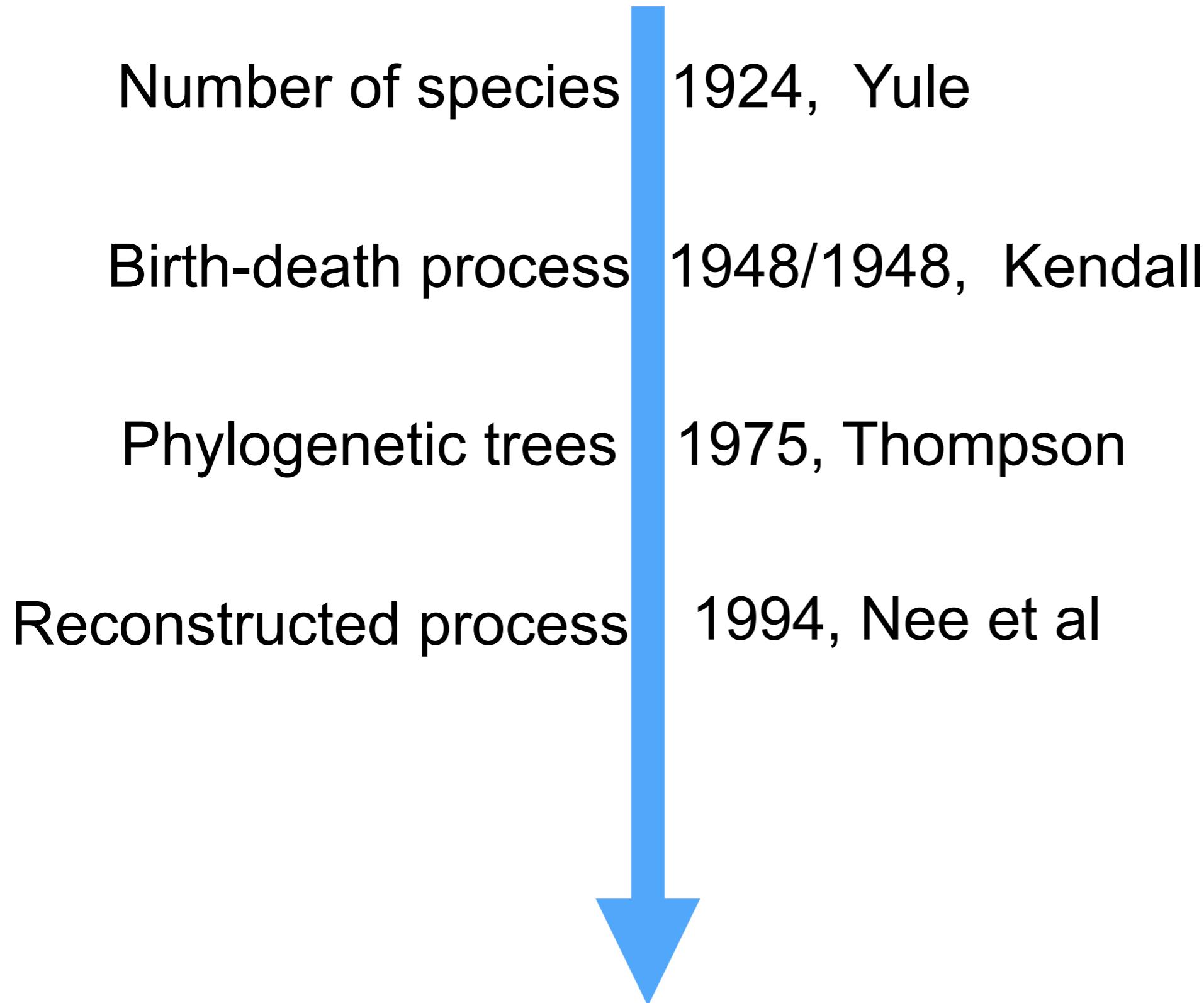
# Outline

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1. Constant diversification rates.
2. Diversification rates through time
3. Branch-specific diversification rates
4. Character-dependent diversification rates

# A brief history

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# Birth-Death Process

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| Origin (single species)

# Birth-Death Process

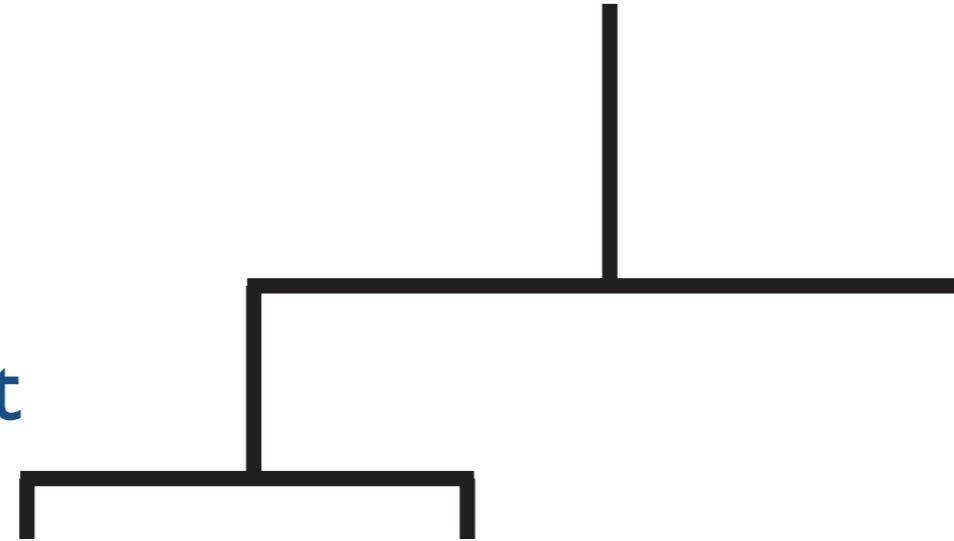
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# Birth-Death Process

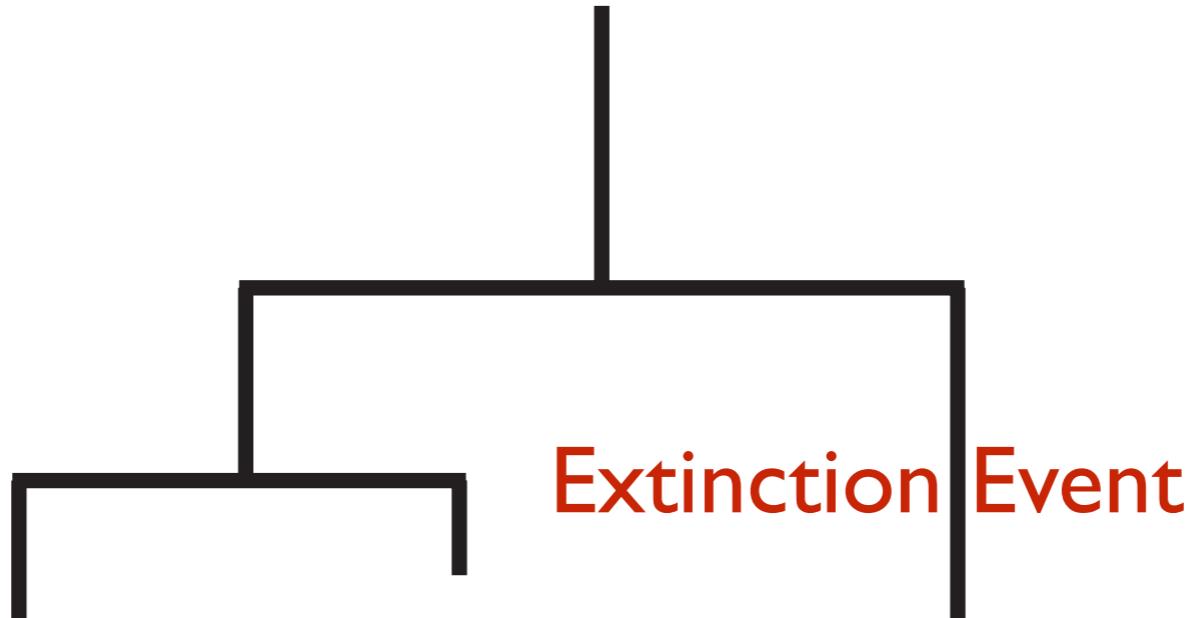
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Speciation Event



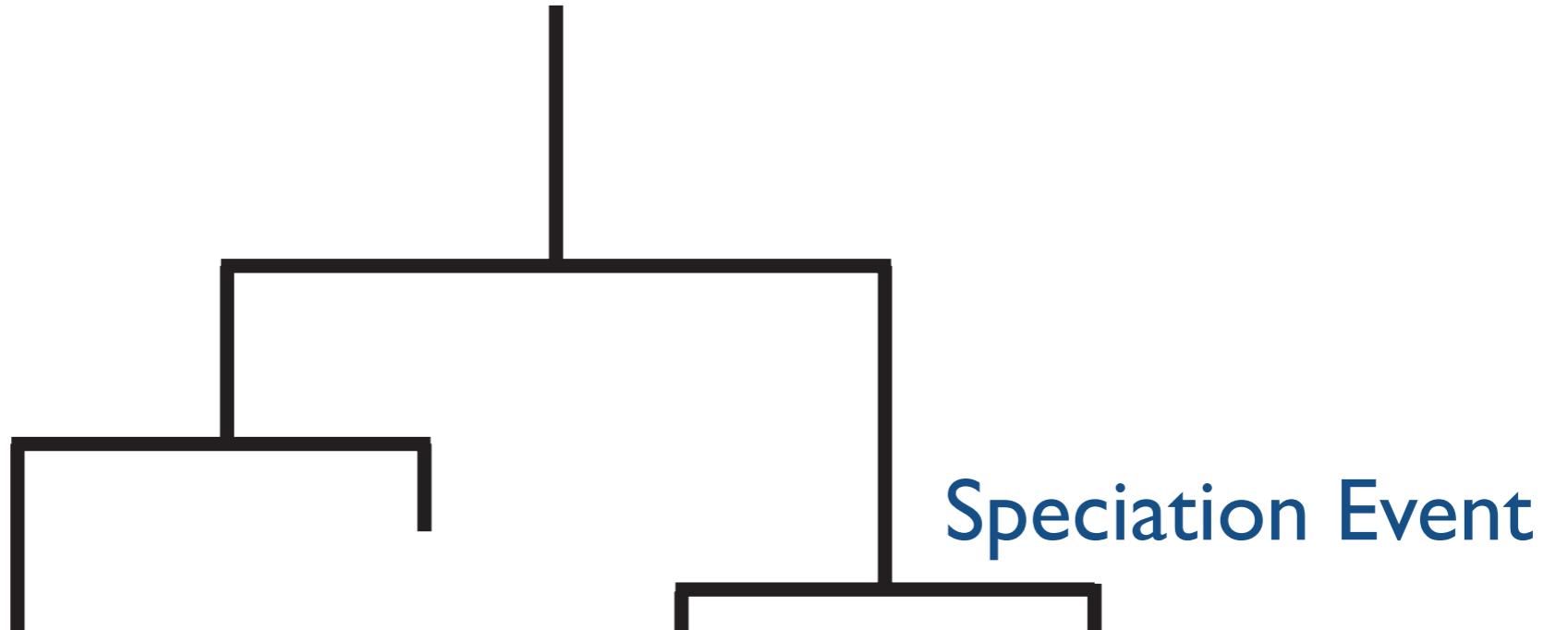
# Birth-Death Process

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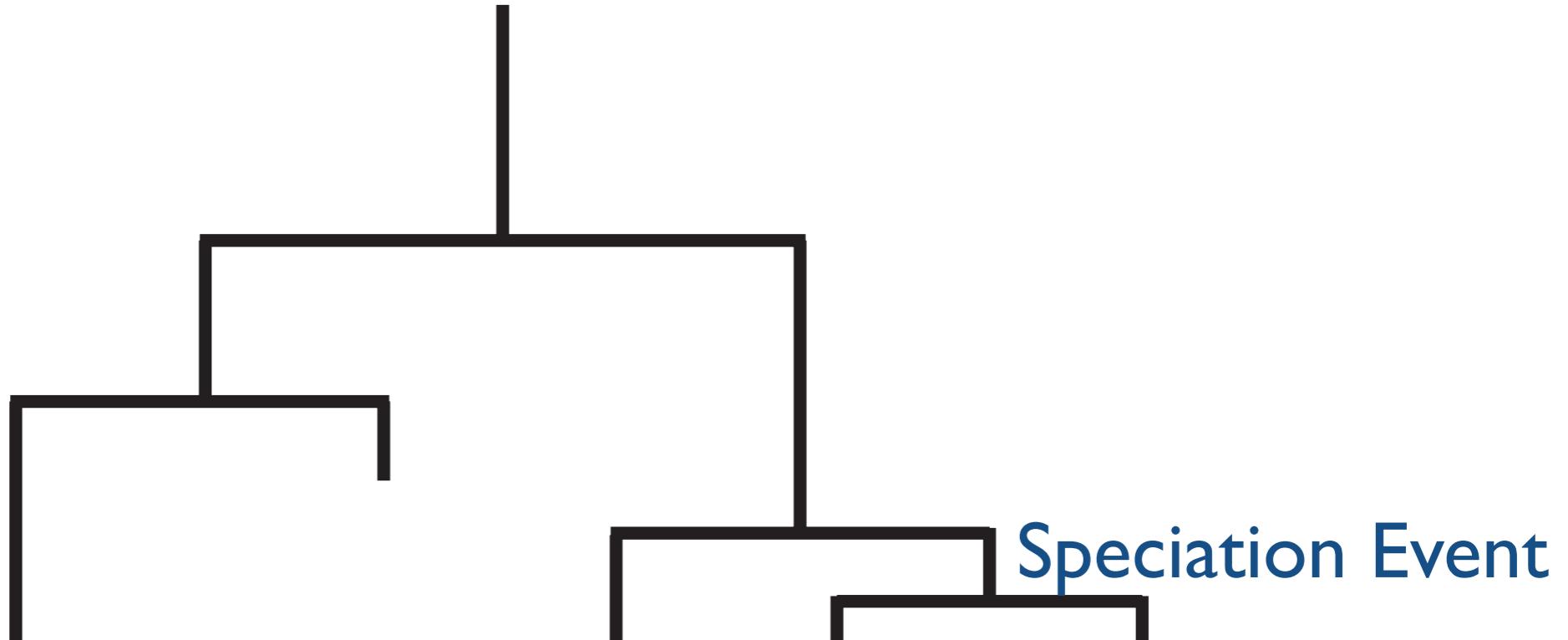
# Birth-Death Process

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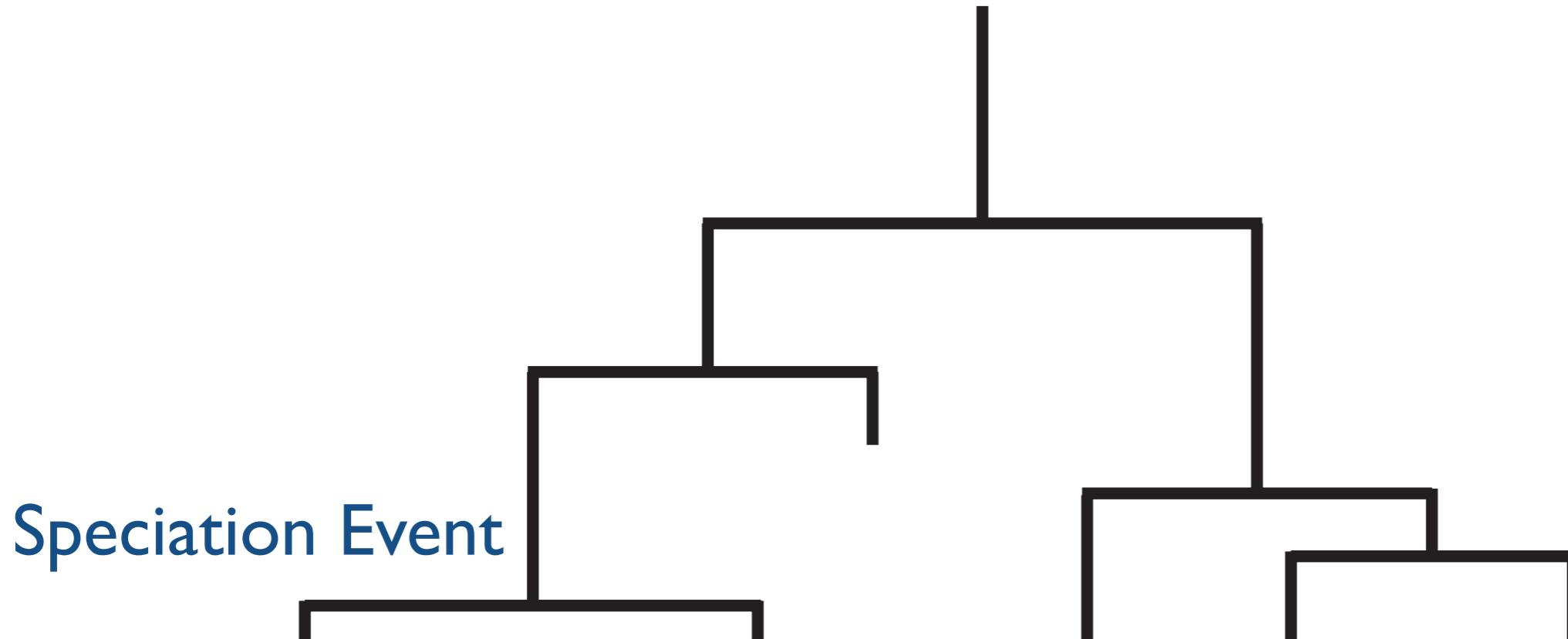
# Birth-Death Process

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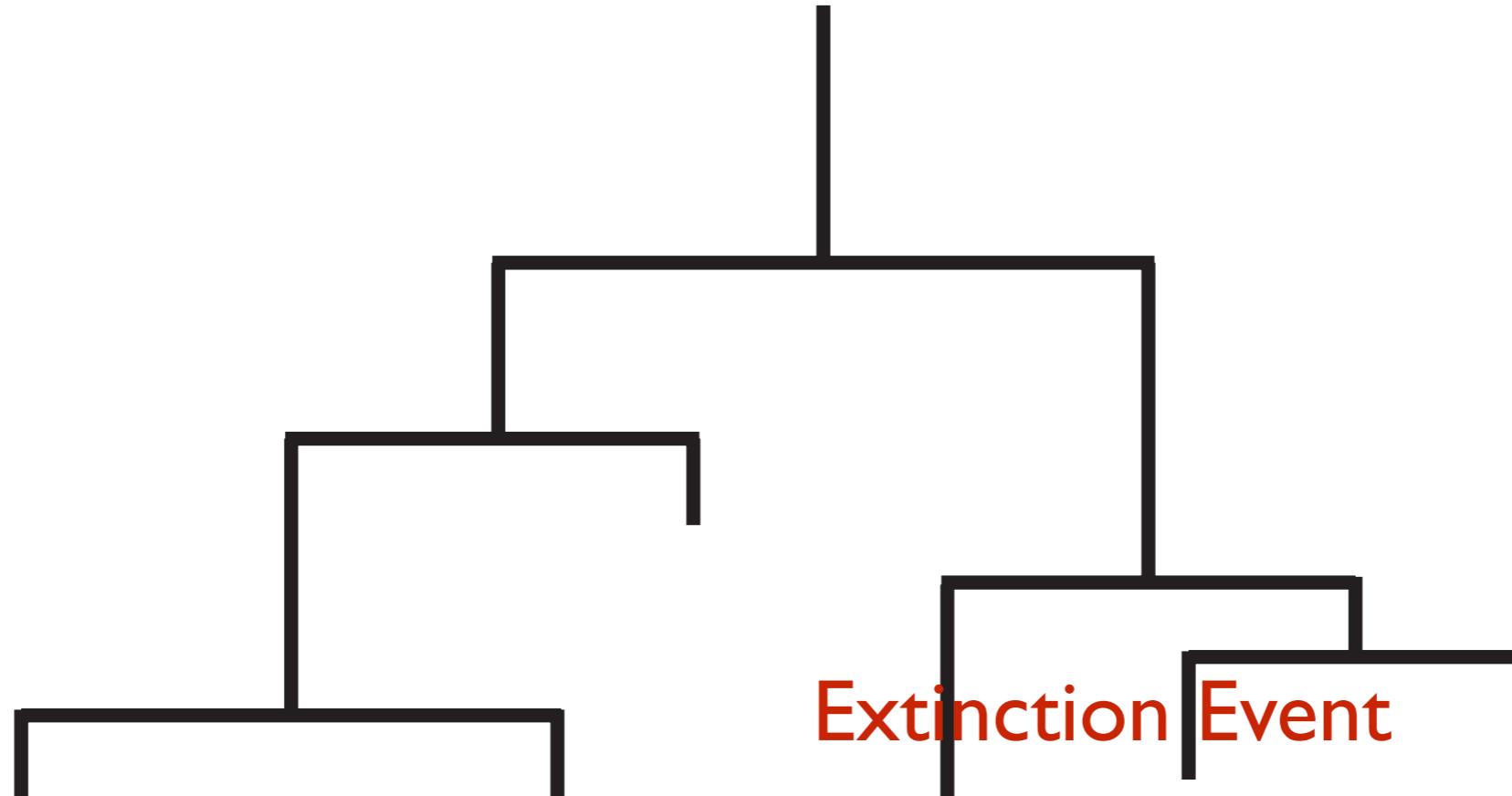
# Birth-Death Process

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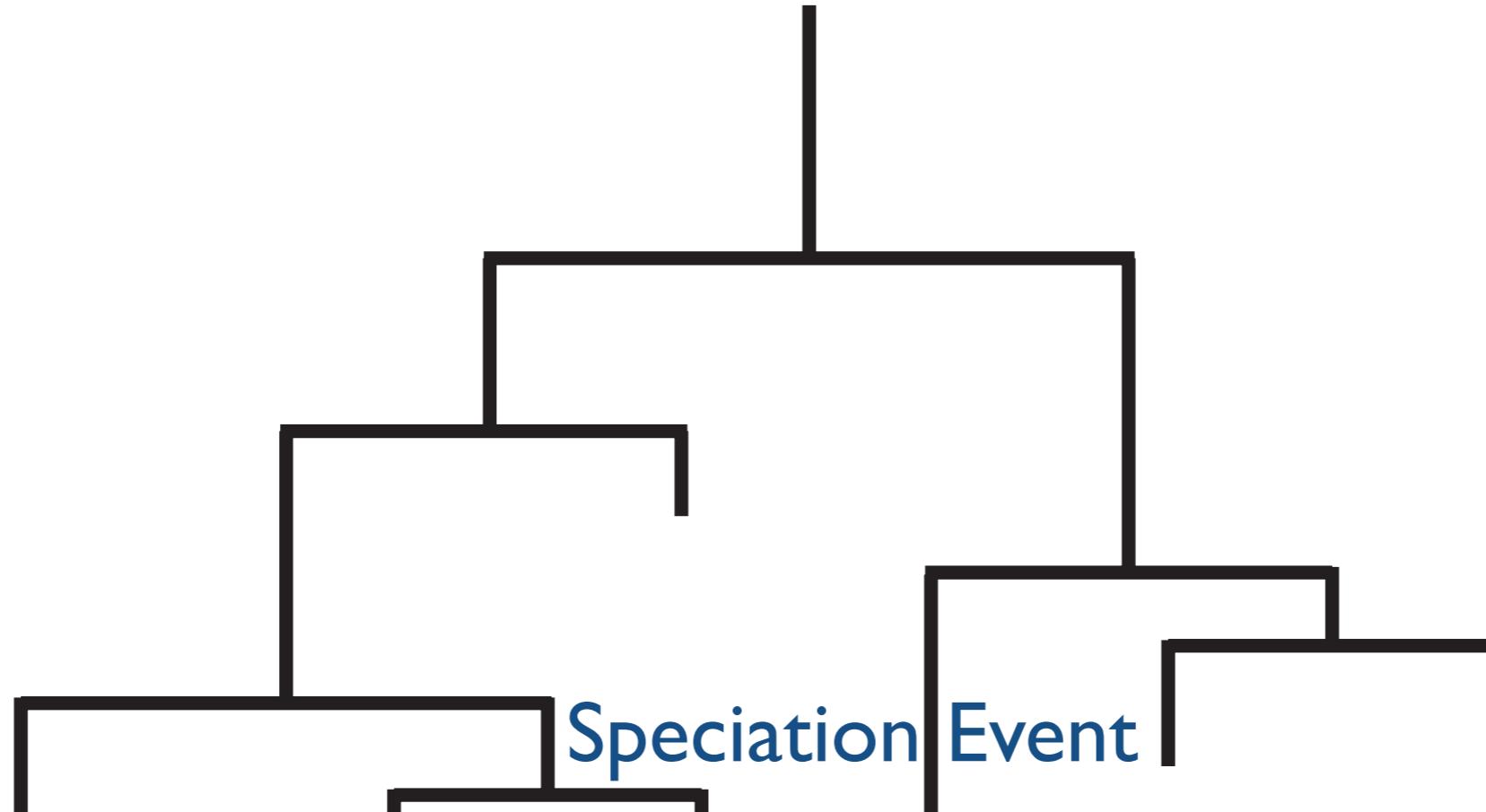
# Birth-Death Process

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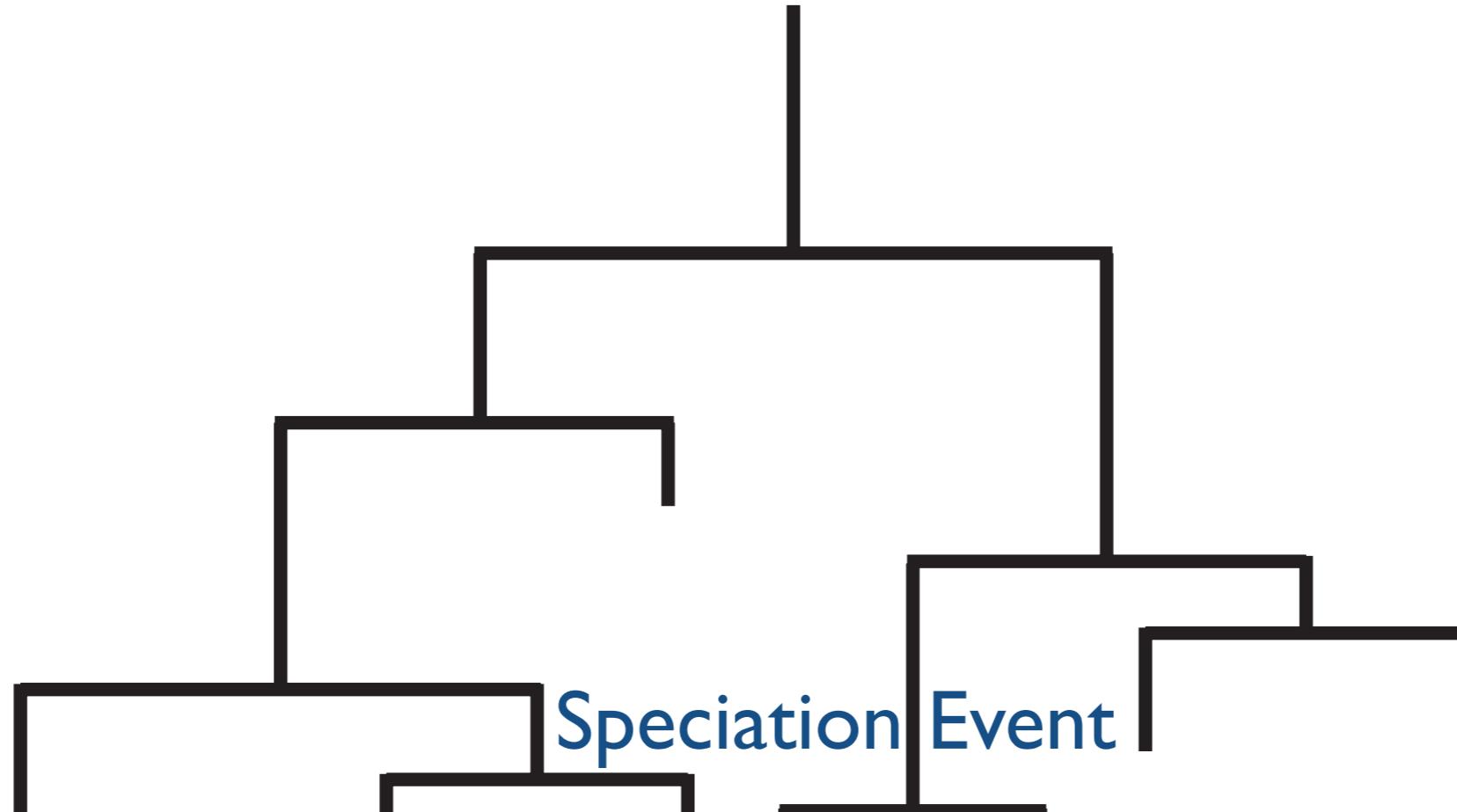
# Birth-Death Process

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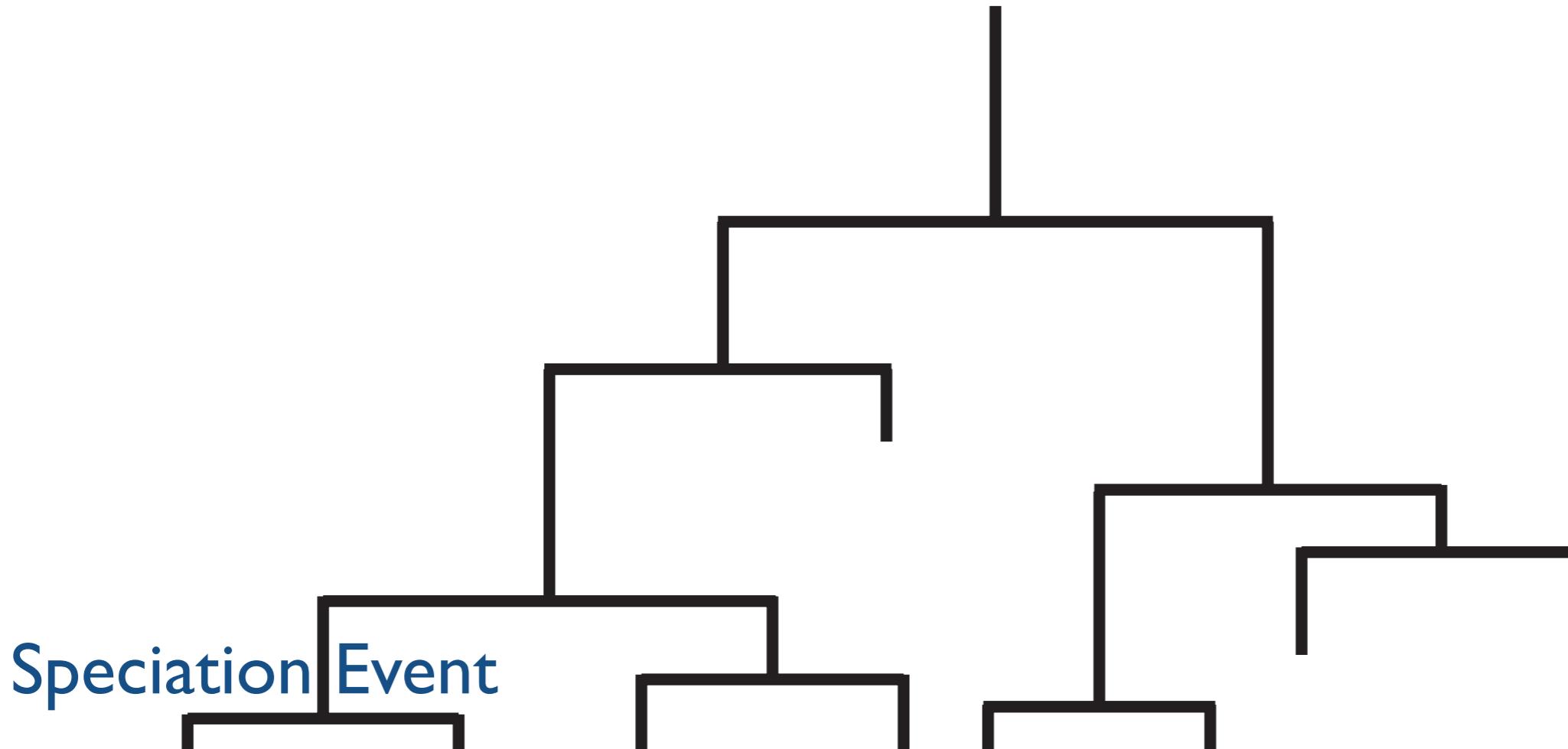


# Birth-Death Process

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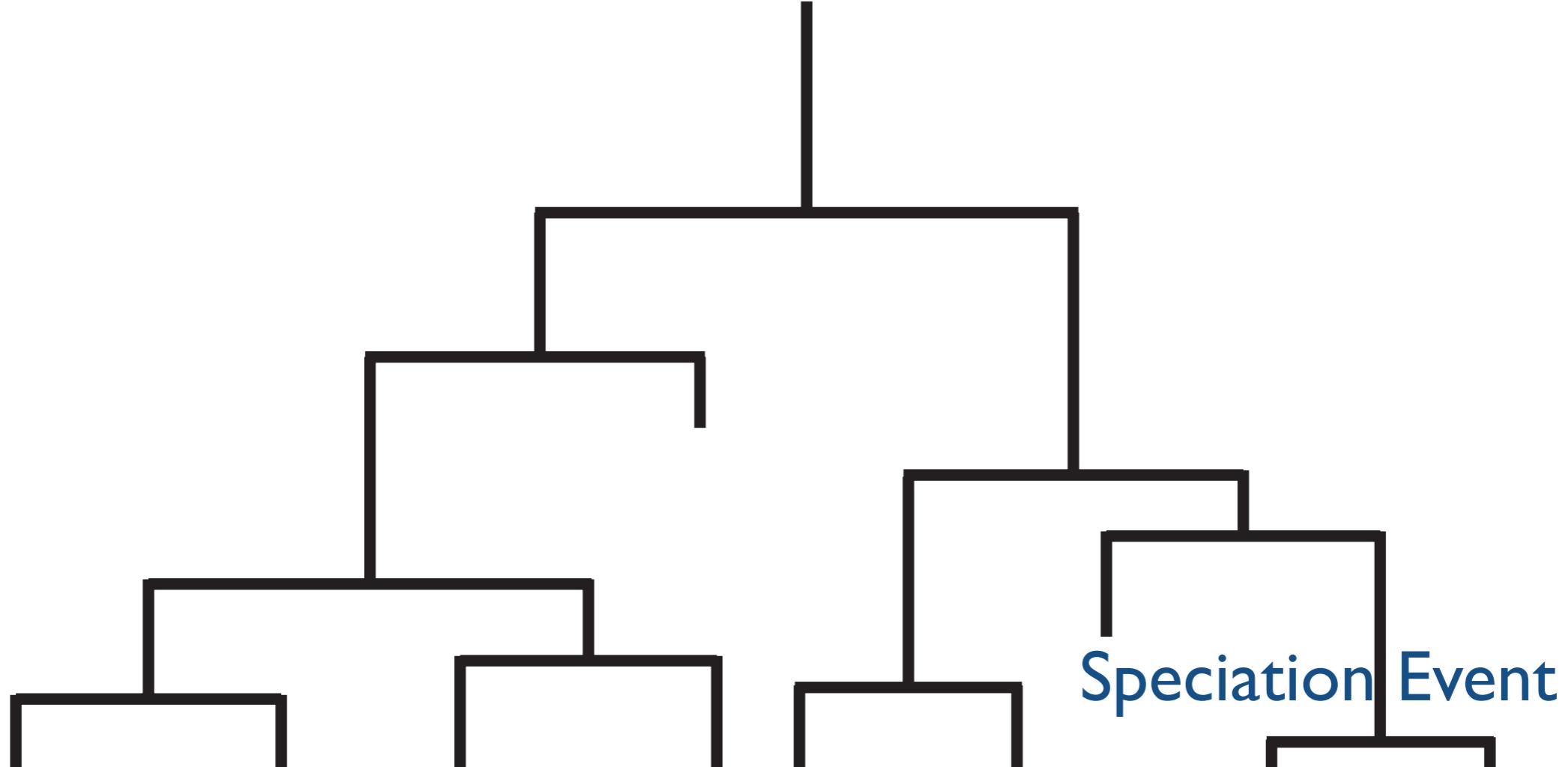


# Birth-Death Process

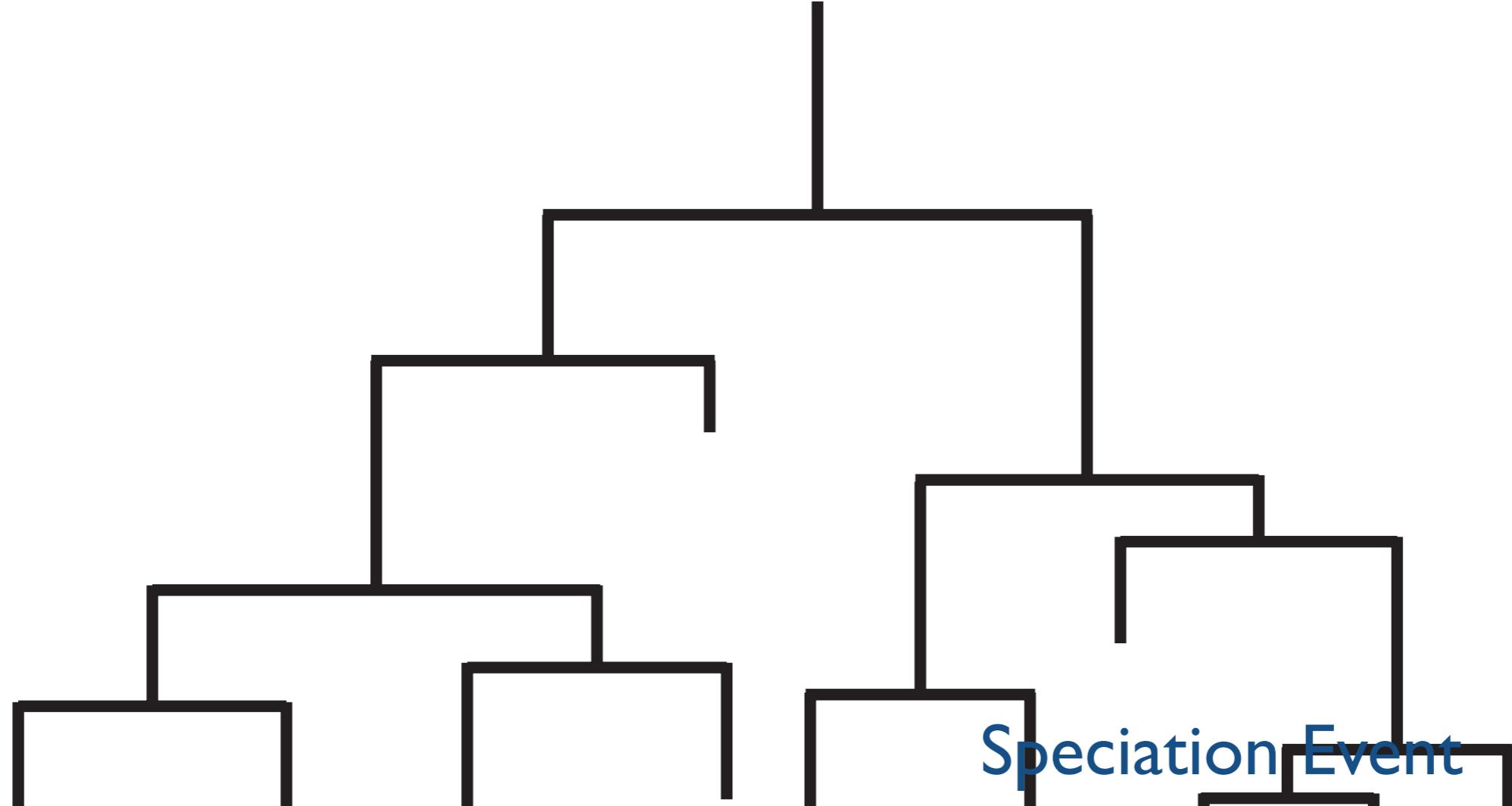


# Birth-Death Process

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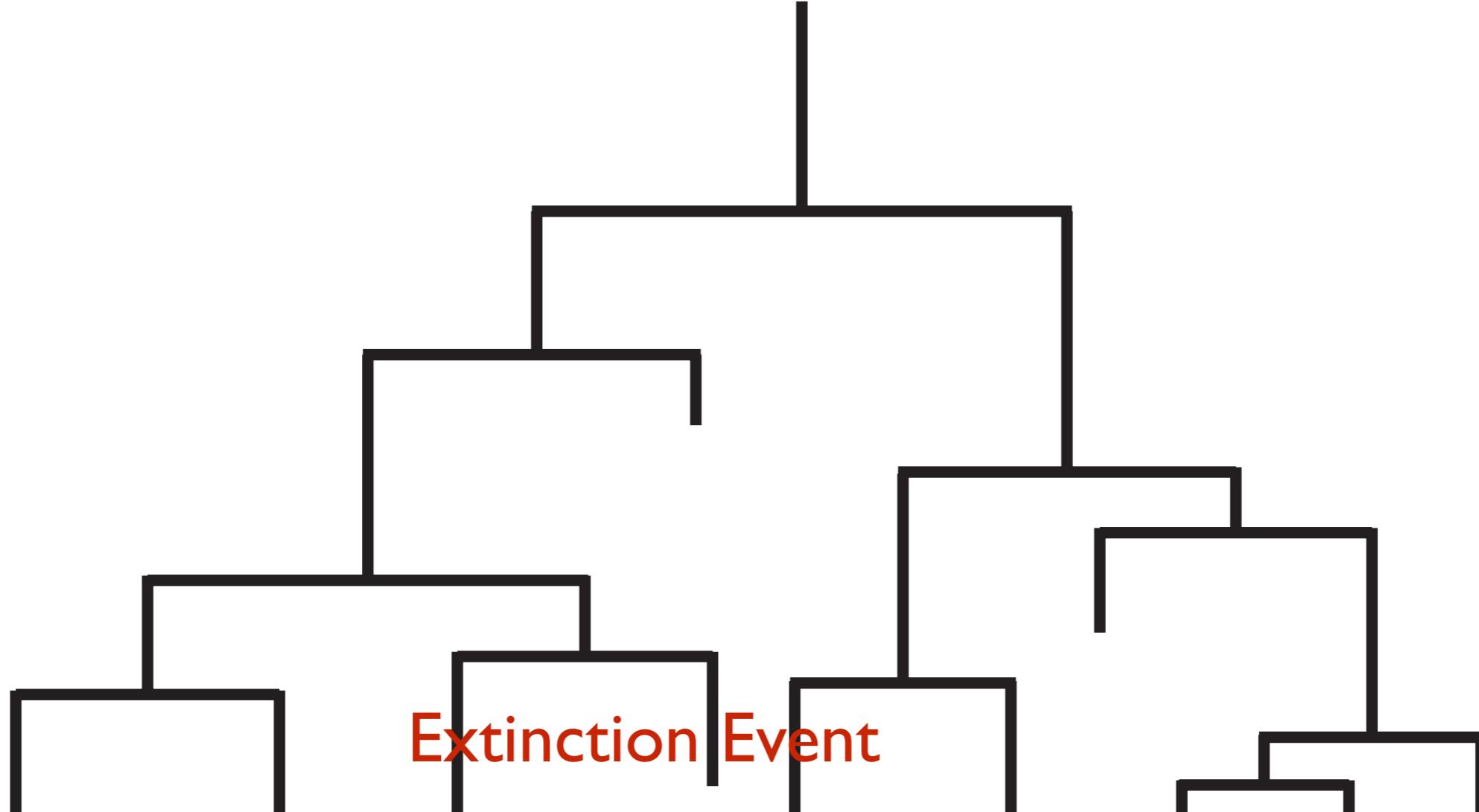


# Birth-Death Process



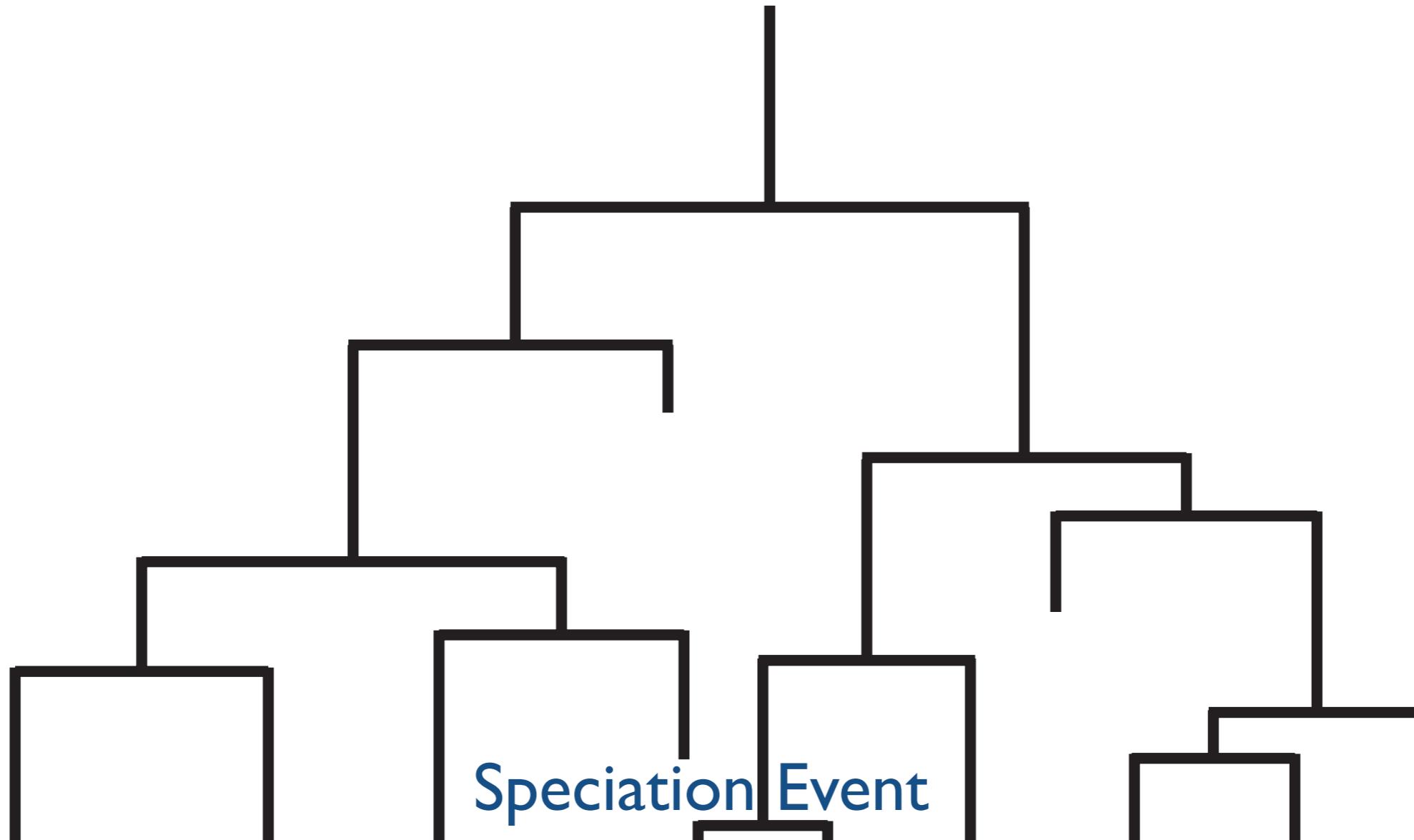
# Birth-Death Process

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# Birth-Death Process

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# Birth-Death Process

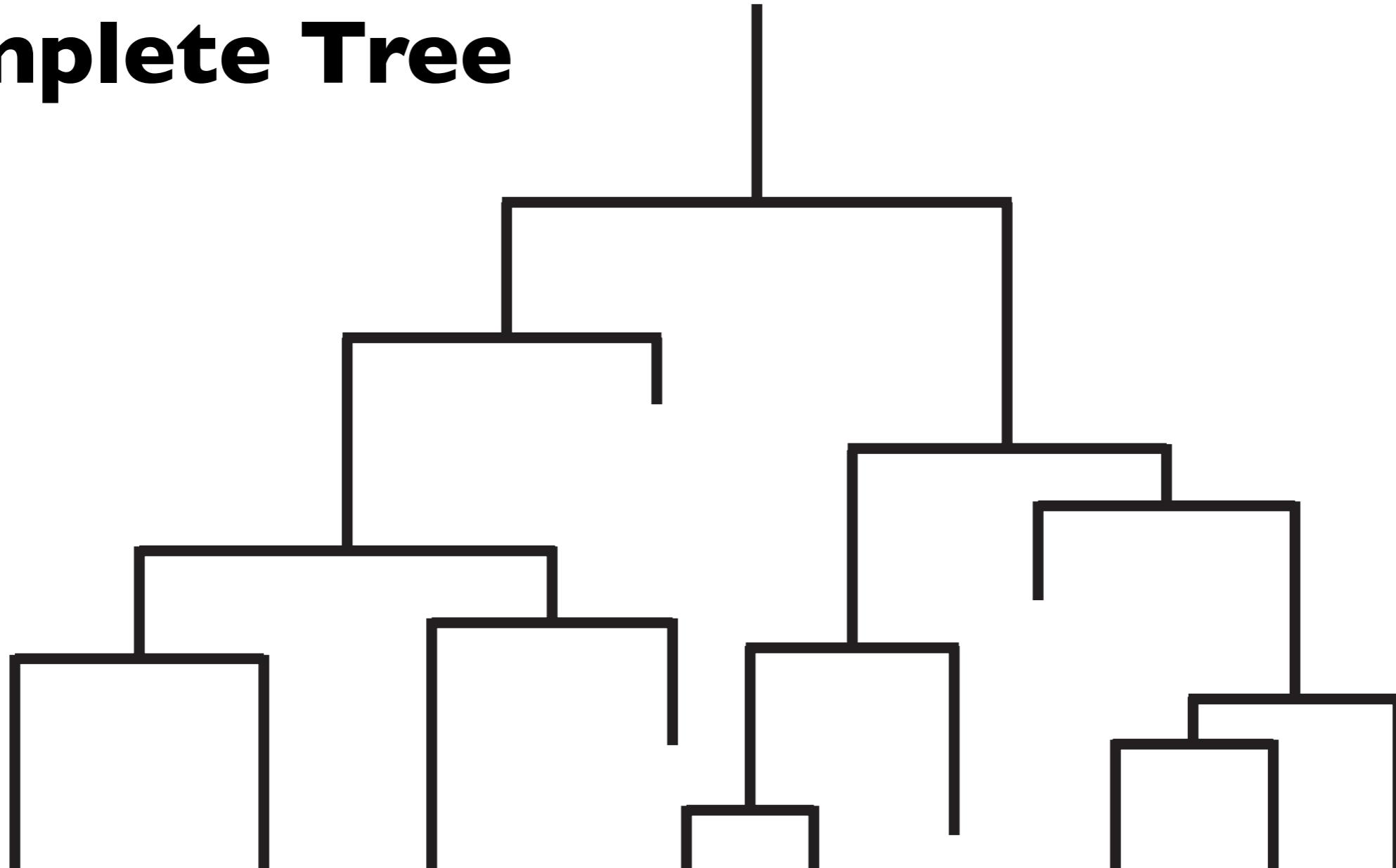
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# Birth-Death Process

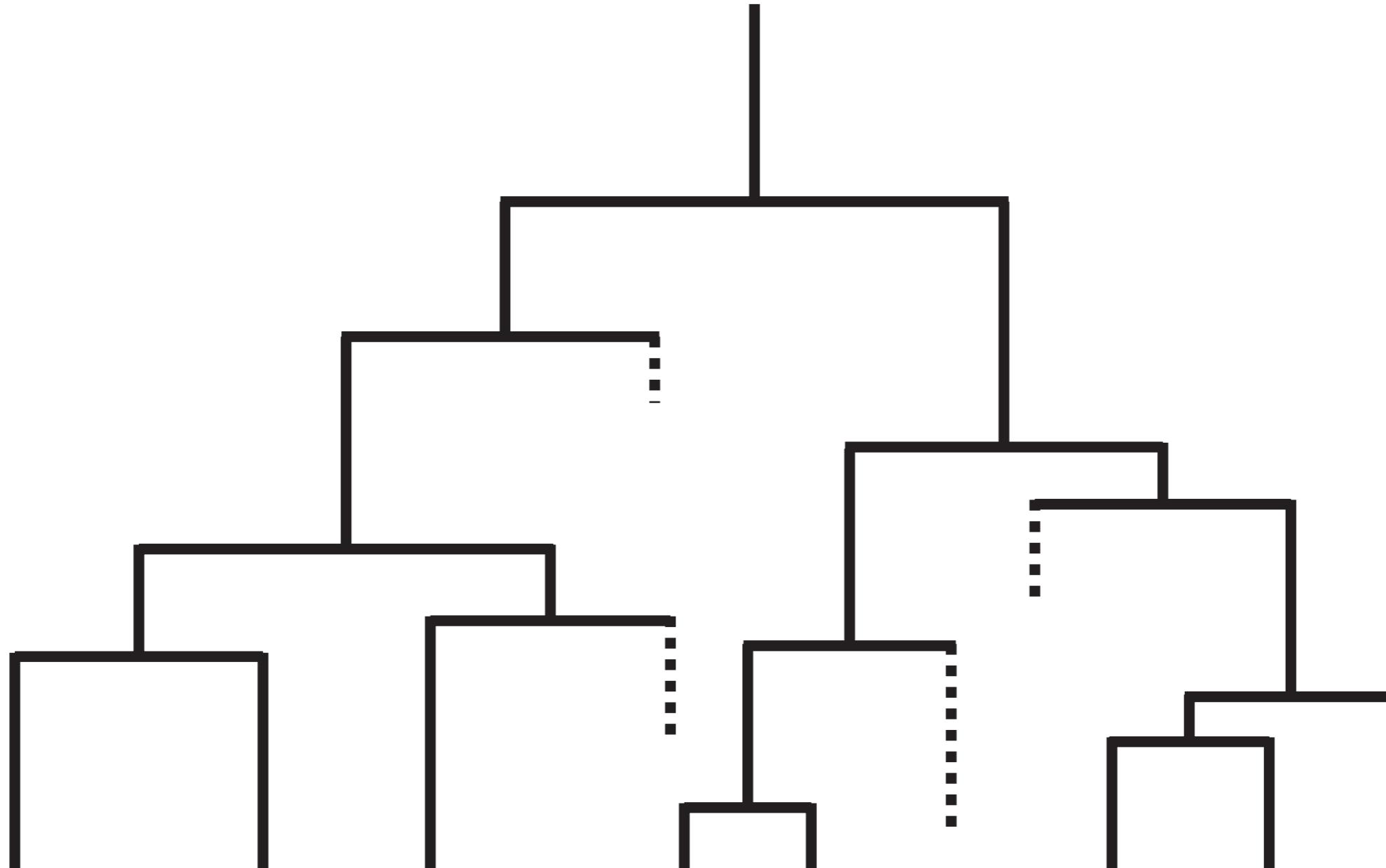
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**Complete Tree**



# Birth-Death Process

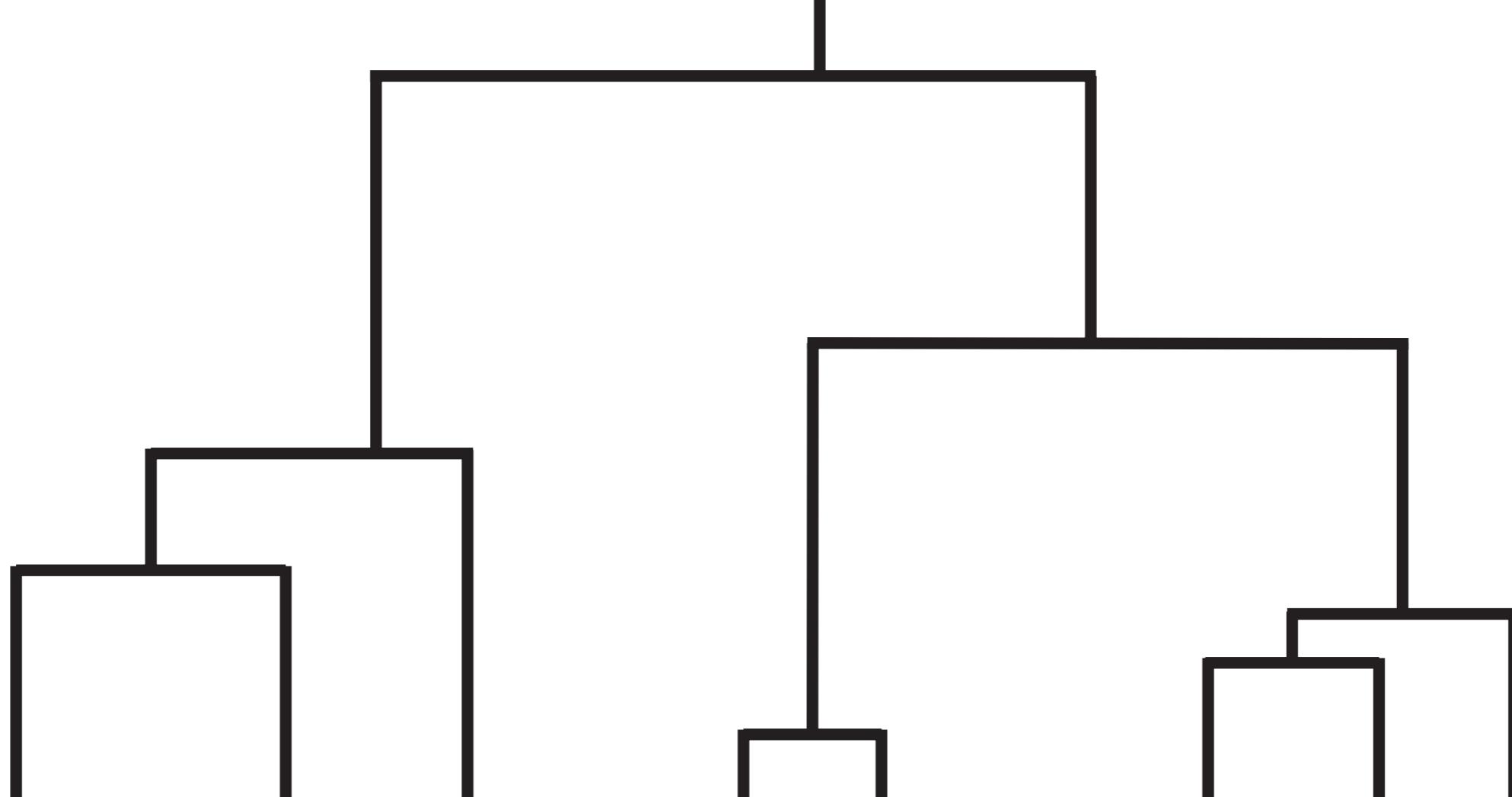
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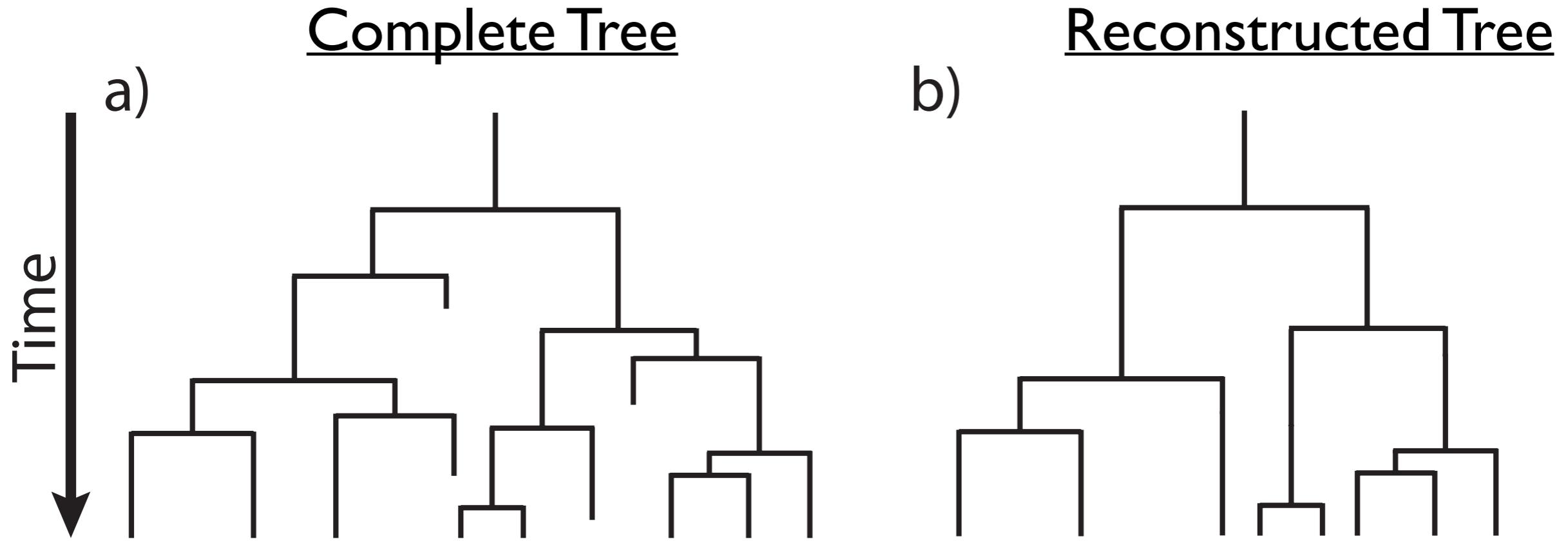
# Birth-Death Process

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## Reconstructed Tree

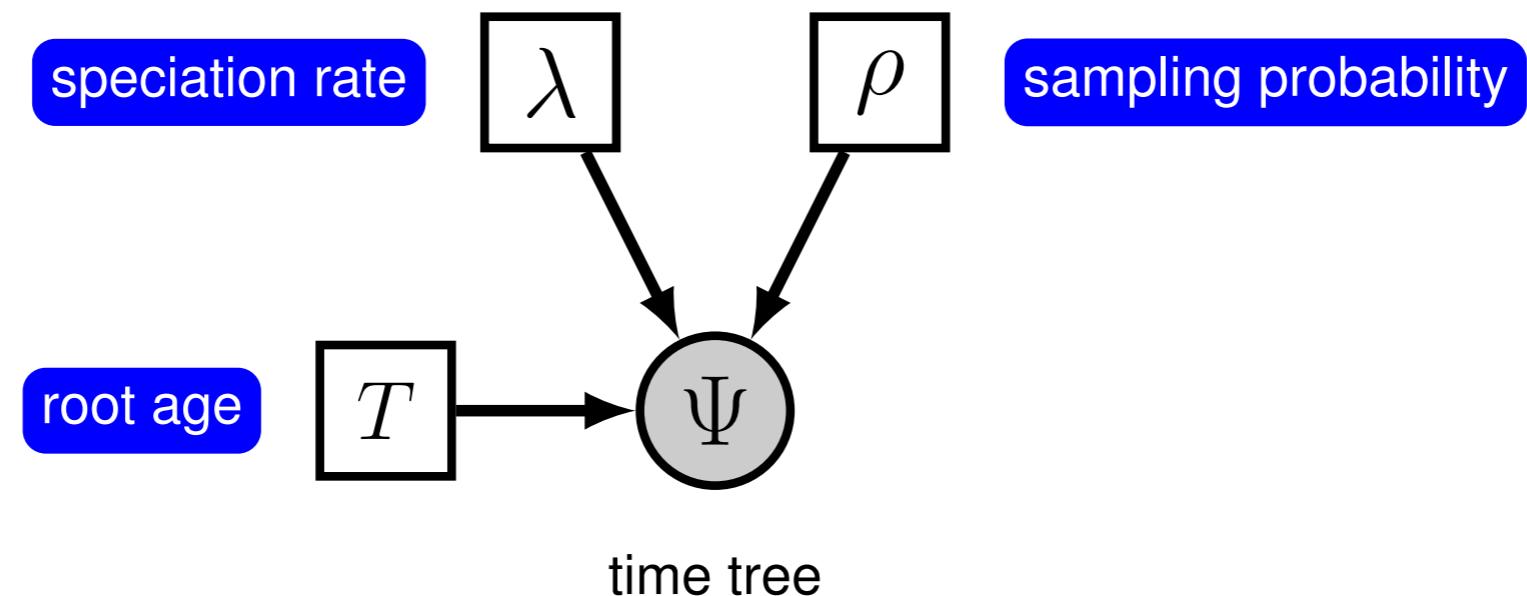


# Birth-Death Process

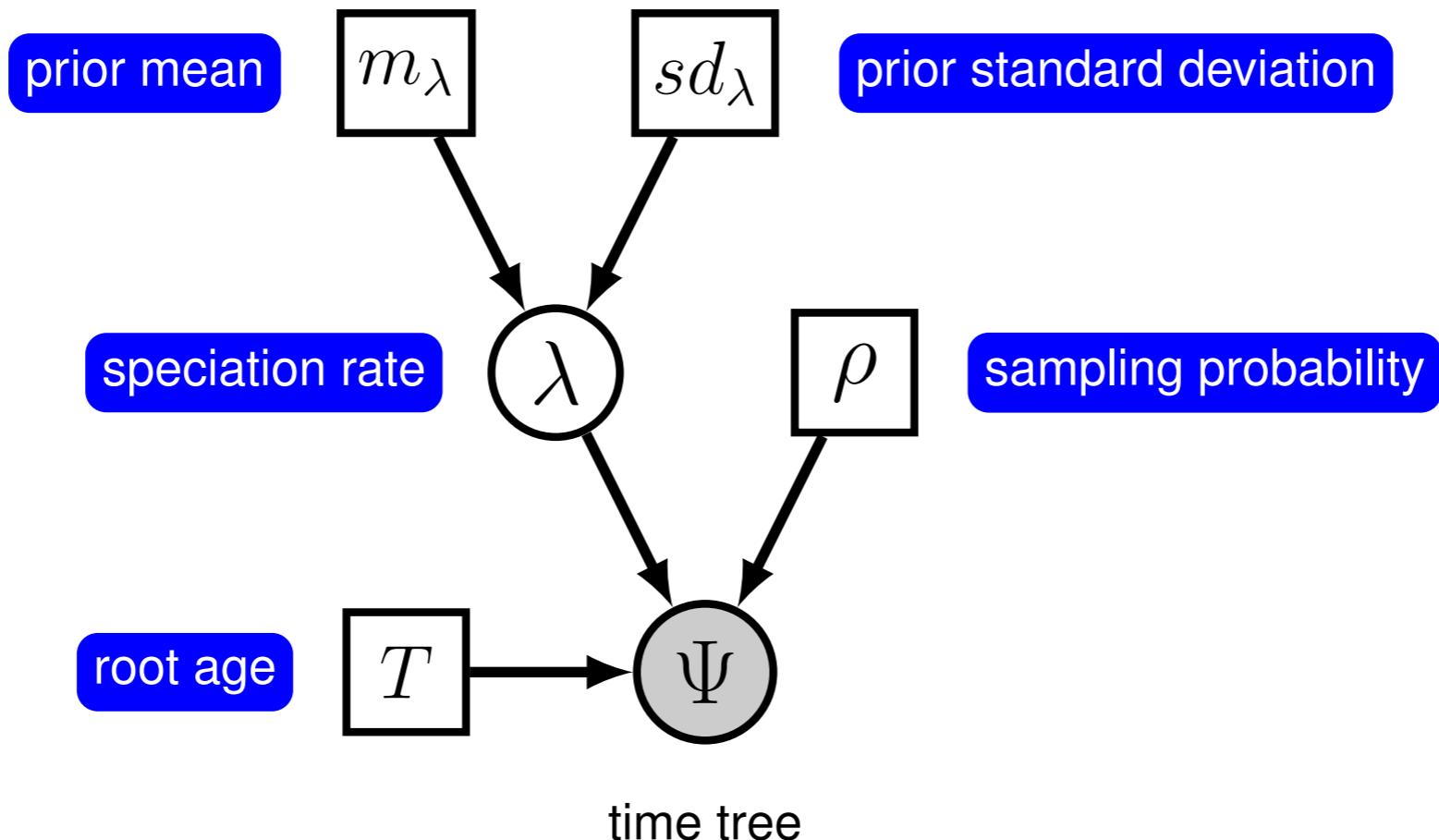


- A species gives birth to exactly one new species with rate  $\lambda(t)$
- A species dies with rate  $\mu(t)$
- Only extant species can be observed/sampled.

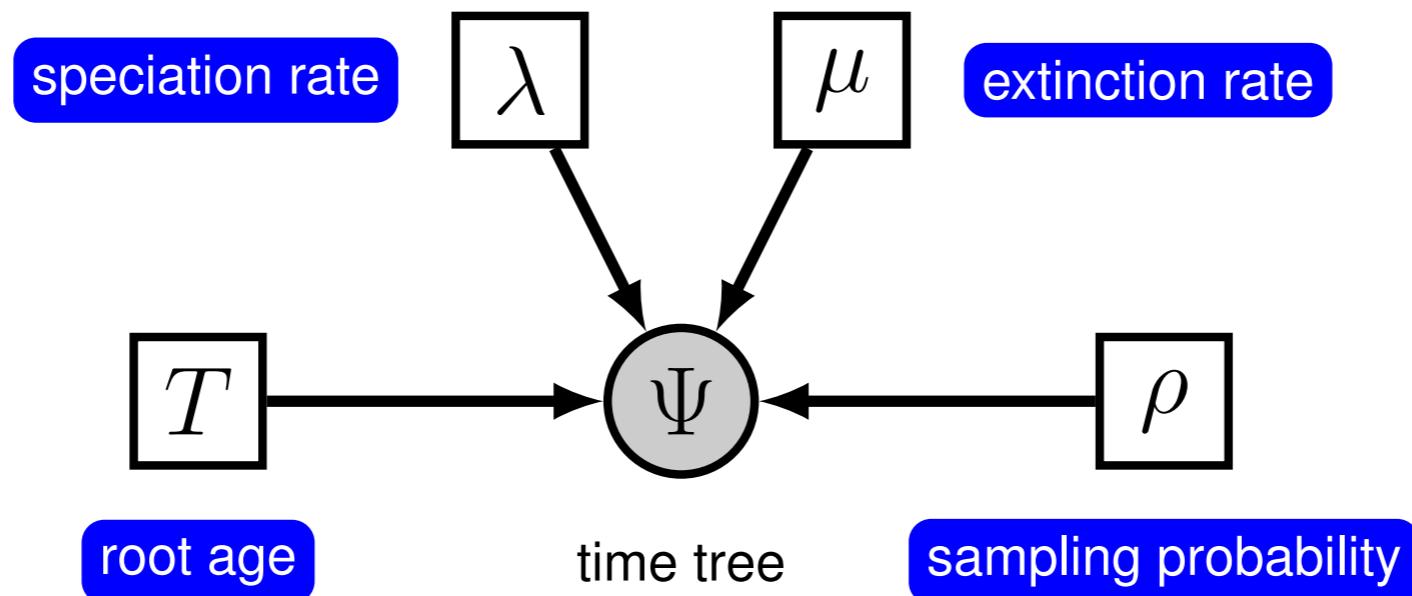
# Simple pure-birth (Yule) model



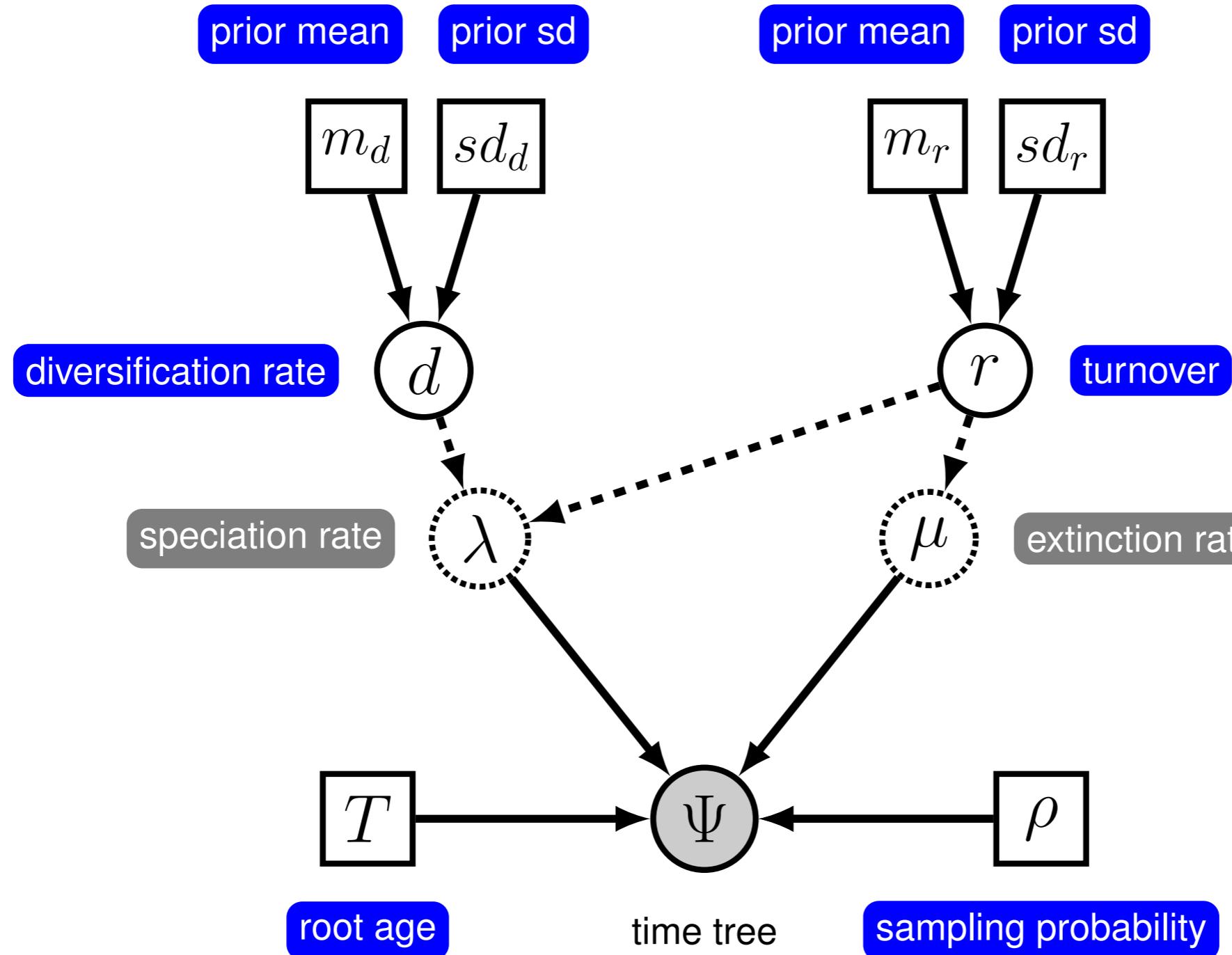
# Pure-birth (Yule) model with prior



# Simple Birth-Death Model



# Birth-Death Model with Prior



# Parameterization and interpretation

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1)	Speciation rate	$\lambda$
	Extinction rate	$\mu$
2)	Net-diversification rate:	$\lambda - \mu$
	Turnover rate	$\mu$
3)	Net-diversification rate:	$\lambda - \mu$
	Relative extinction rate	$\frac{\mu}{\lambda}$
4)	Speciation rate	$\lambda$
	Relative extinction rate	$\frac{\mu}{\lambda}$

# Parameterization and interpretation

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Speciation rate

$$\lambda$$

Extinction rate

$$\mu$$

- + Natural parameterization of the birth-death process
- Extinction rate might be larger than speciation rate
- Difficult to estimate parameters

# Parameterization and interpretation

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Net-diversification rate:  $\lambda - \mu$

Turnover rate  $\mu$

+ Good prior information about net-diversification:

$$E[\lambda - \mu] = \ln\left(\frac{N}{2}\right) / T$$

+ Extinction rate can be enforced to be smaller than speciation

+ Biological interpretation of turnover rate

# Parameterization and interpretation

---

Net-diversification rate:  $\lambda - \mu$

Relative extinction rate  $\frac{\mu}{\lambda}$

+ Good prior information about net-diversification:

$$E[\lambda - \mu] = \ln\left(\frac{N}{2}\right) / T$$

+ Extinction rate can be enforced to be smaller than speciation

+ Simple prior on turnover rate (Beta distribution)

- Weird induced priors on parameters

# Parameterization and interpretation

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Speciation rate

$$\lambda$$

Relative extinction rate

$$\frac{\mu}{\lambda}$$

- + Extinction rate can be enforced to be smaller than speciation
- + Simple prior on turnover rate (Beta distribution)
- Difficult to specify prior on speciation rate

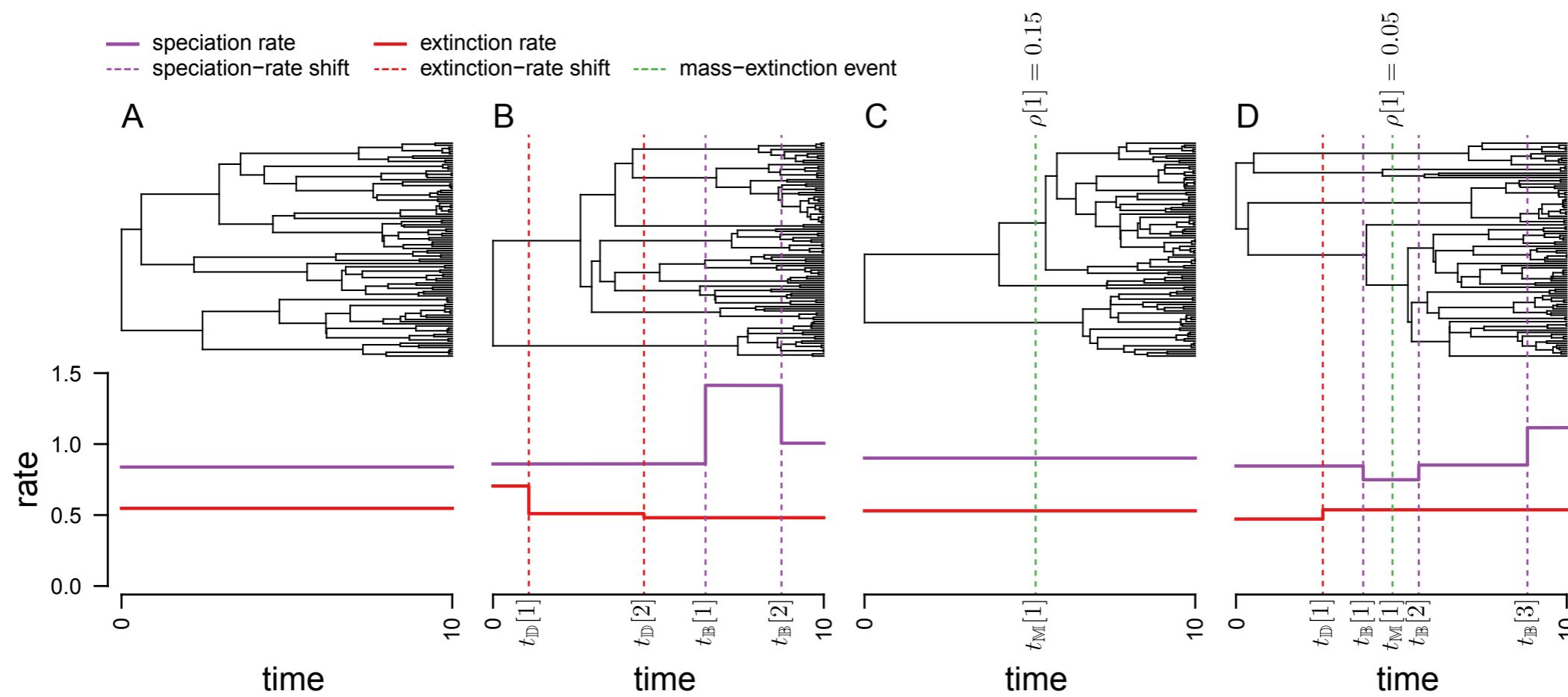
# Outline

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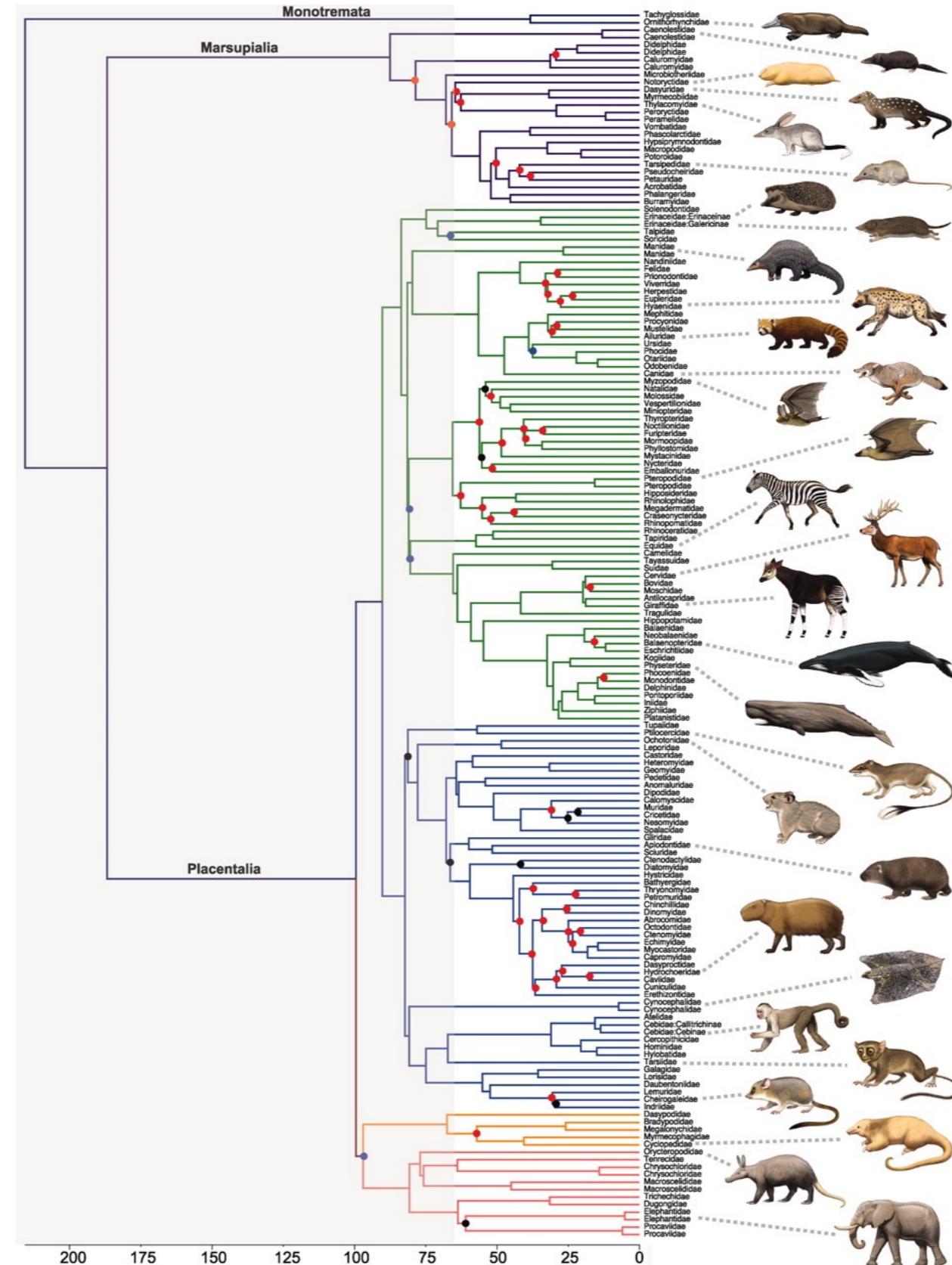
1. Constant diversification rates.
2. Diversification rates through time
3. Branch-specific diversification rates
4. Character-dependent diversification rates

# Diversification Rate Through Time

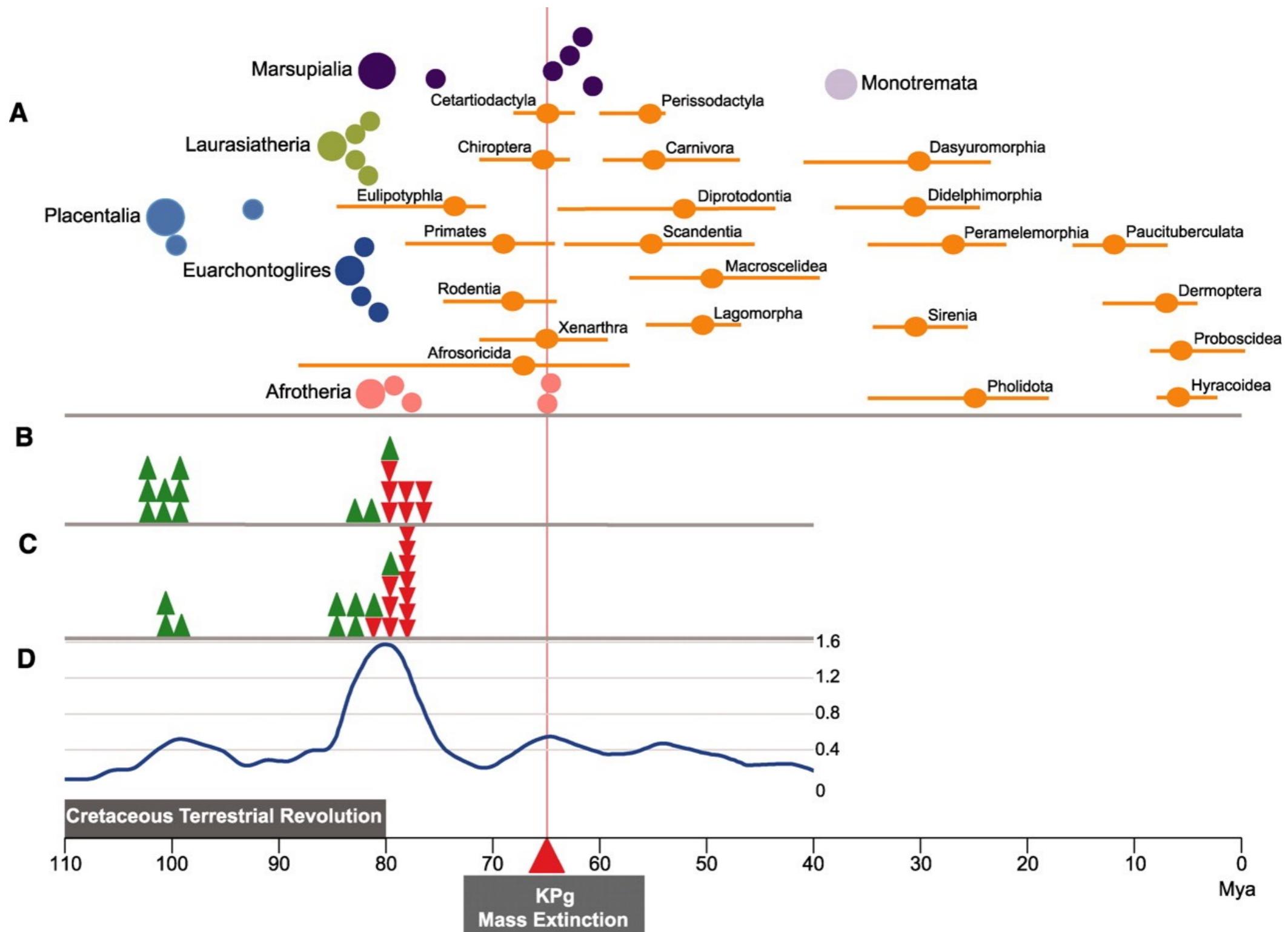
- I. Rate increase & decrease (gradual vs episodic)
2. Correlation to environmental factors



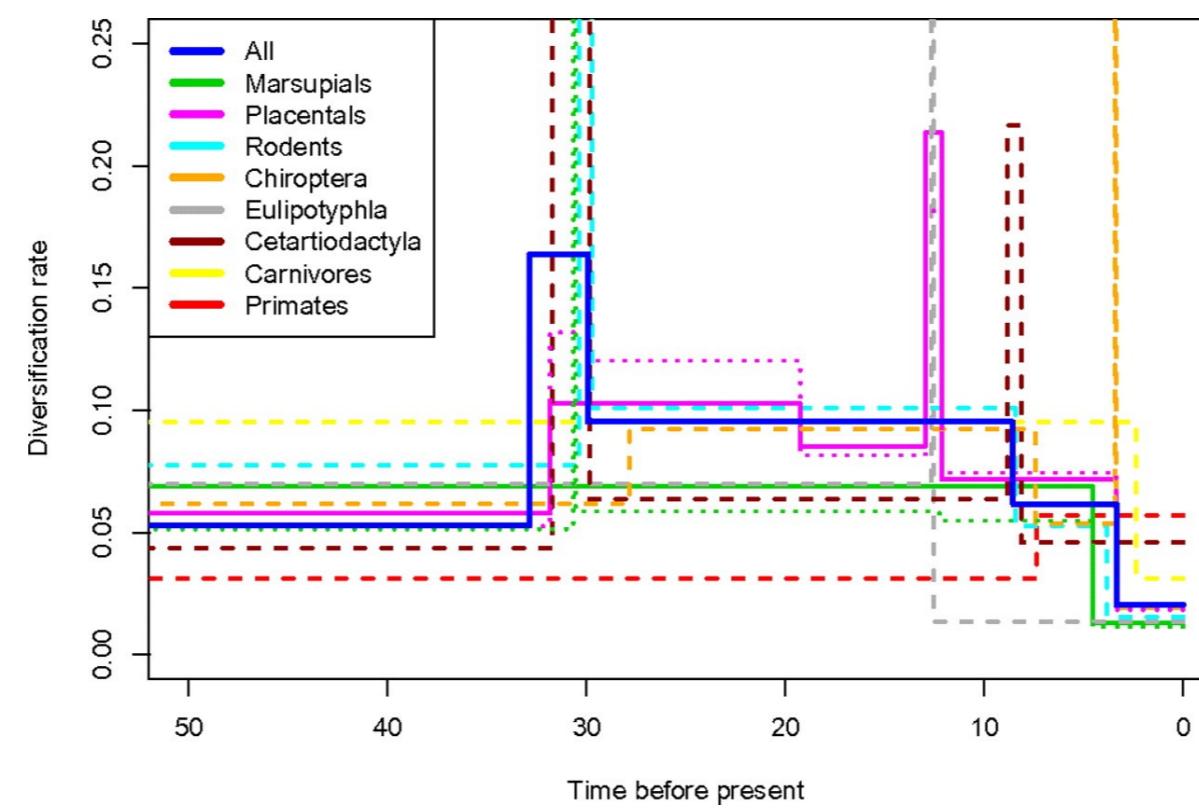
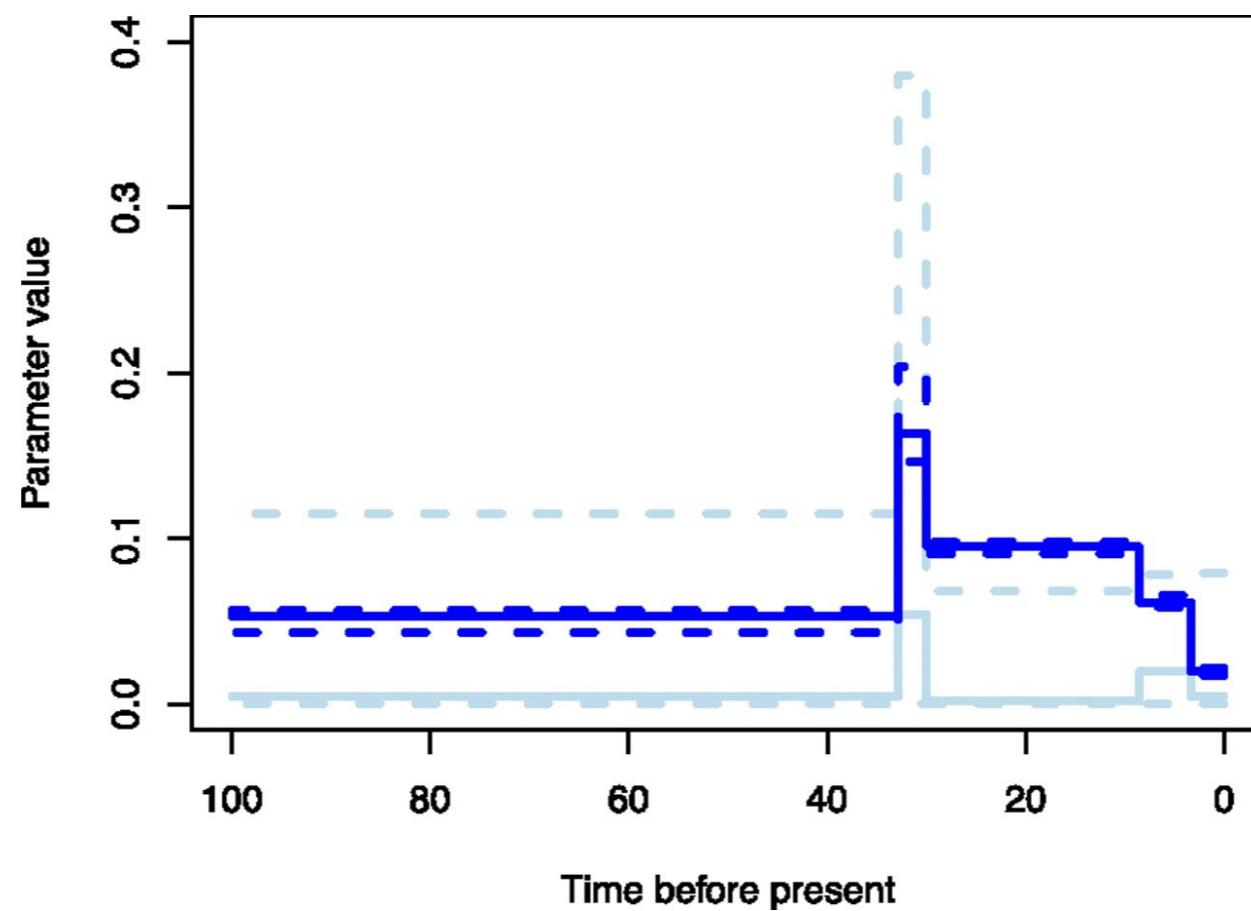
# Diversification rates in mammals by Meredith et al (2011)



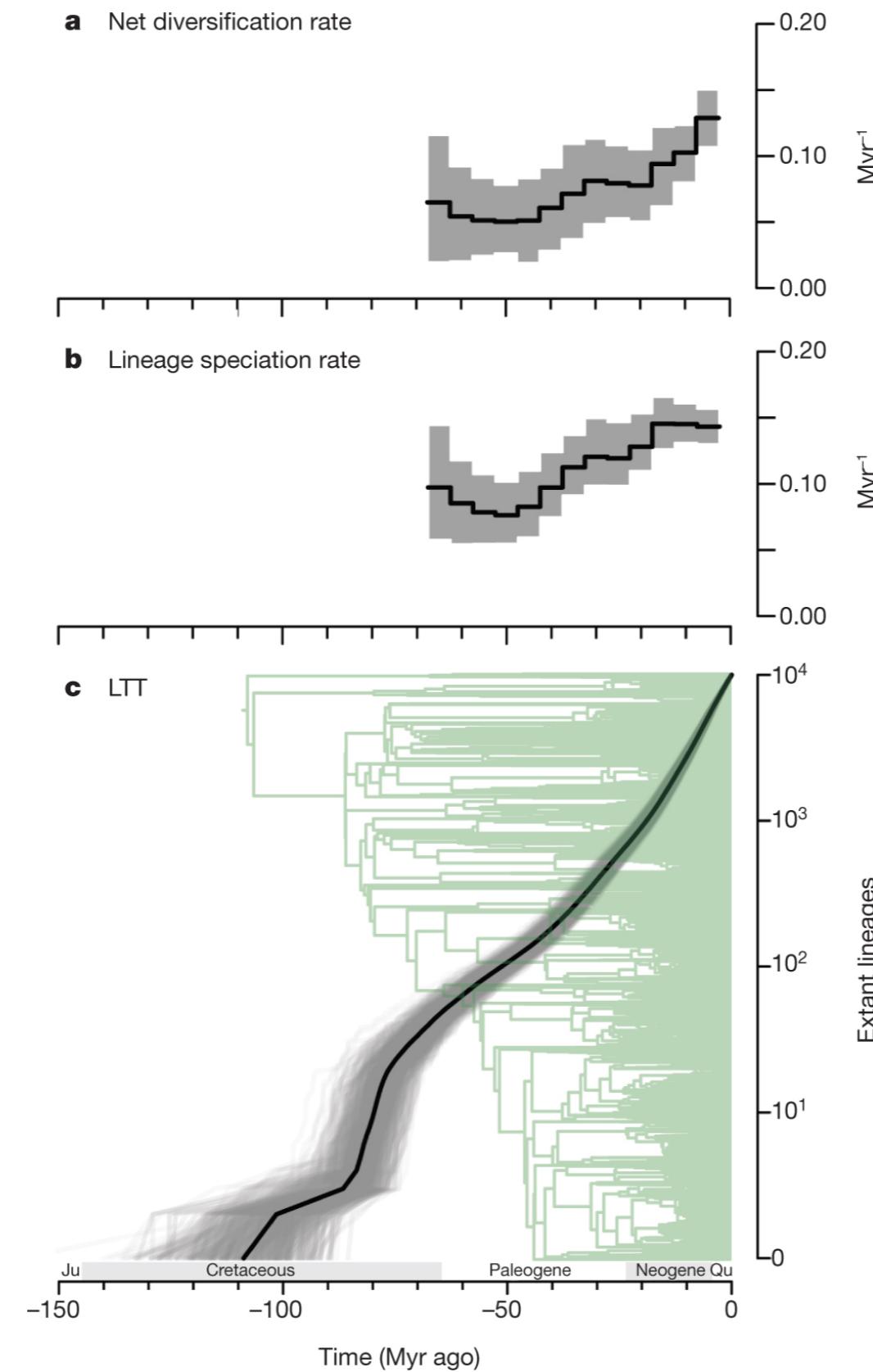
# Diversification rates in mammals by Meredith et al (2011)



# Diversification rates in mammals by Stadler (2011)



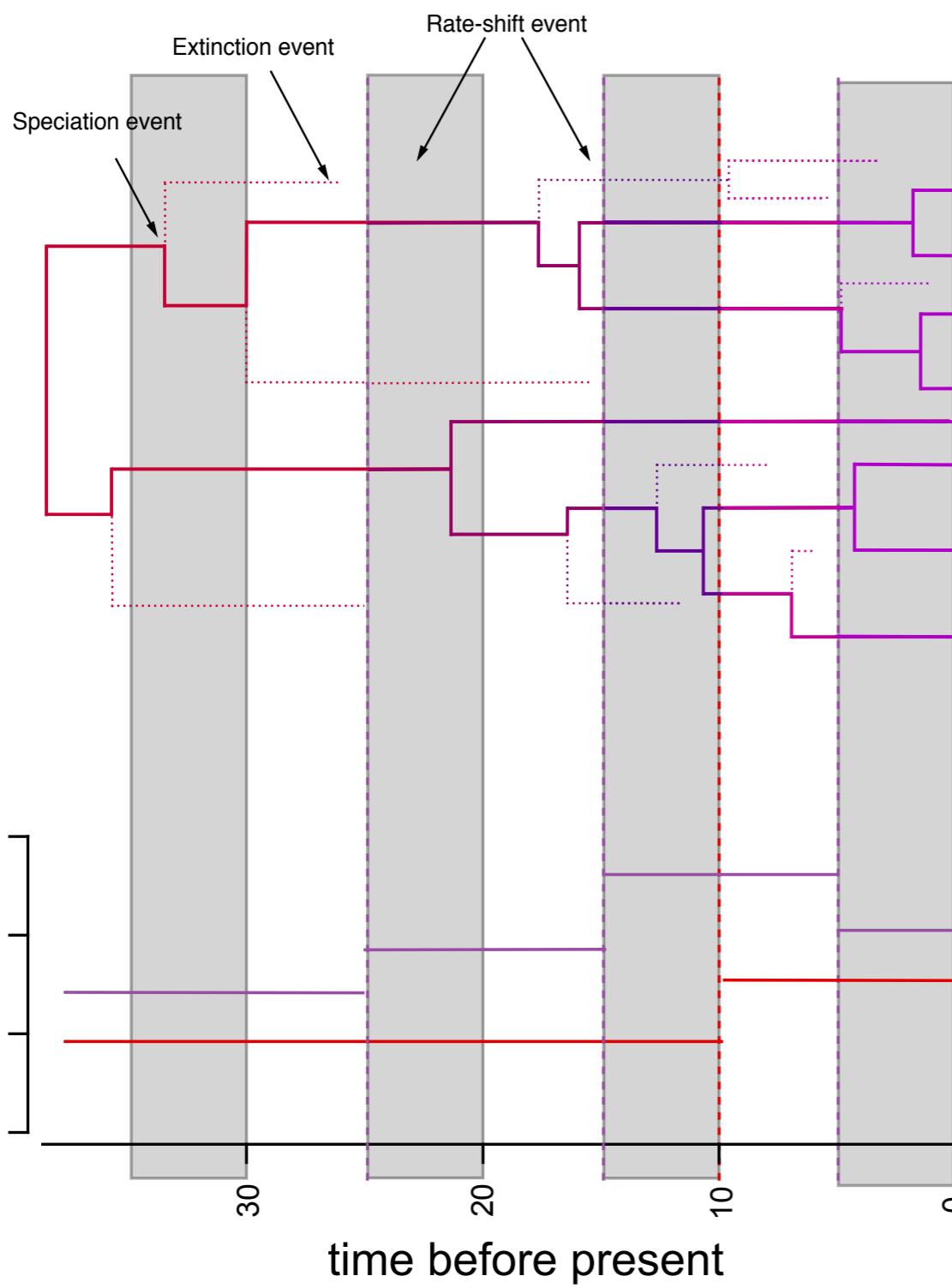
# Diversification rates in birds by Jetz et al. (2012)



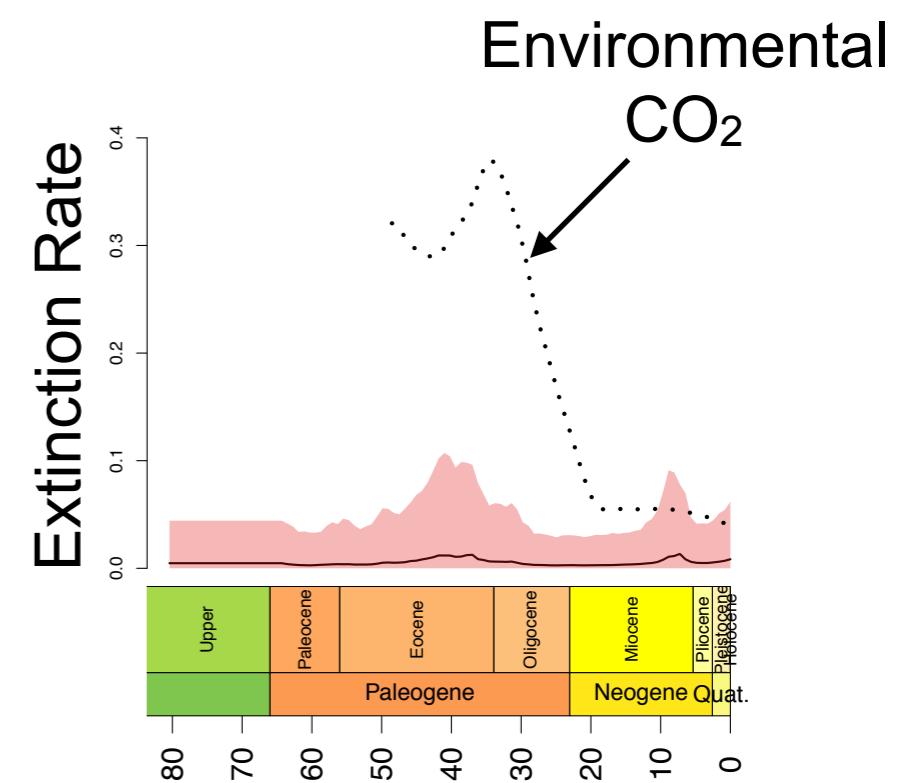
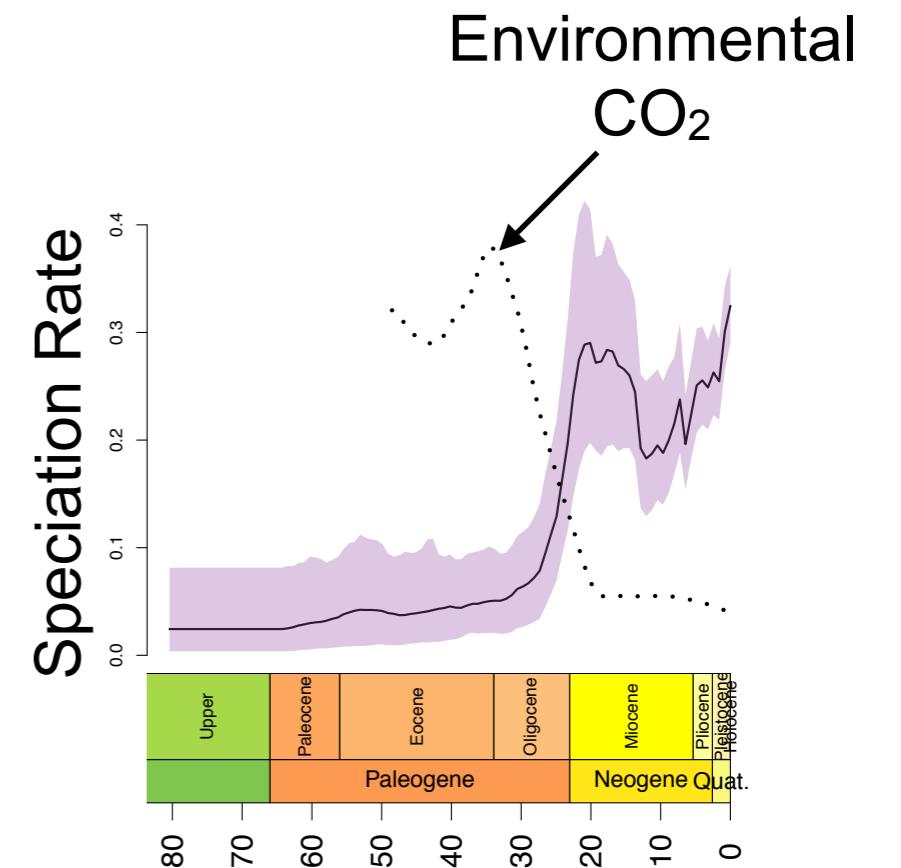
# Hypothesis: CO<sub>2</sub> is correlated with diversification rate

## Episodic birth-death process:

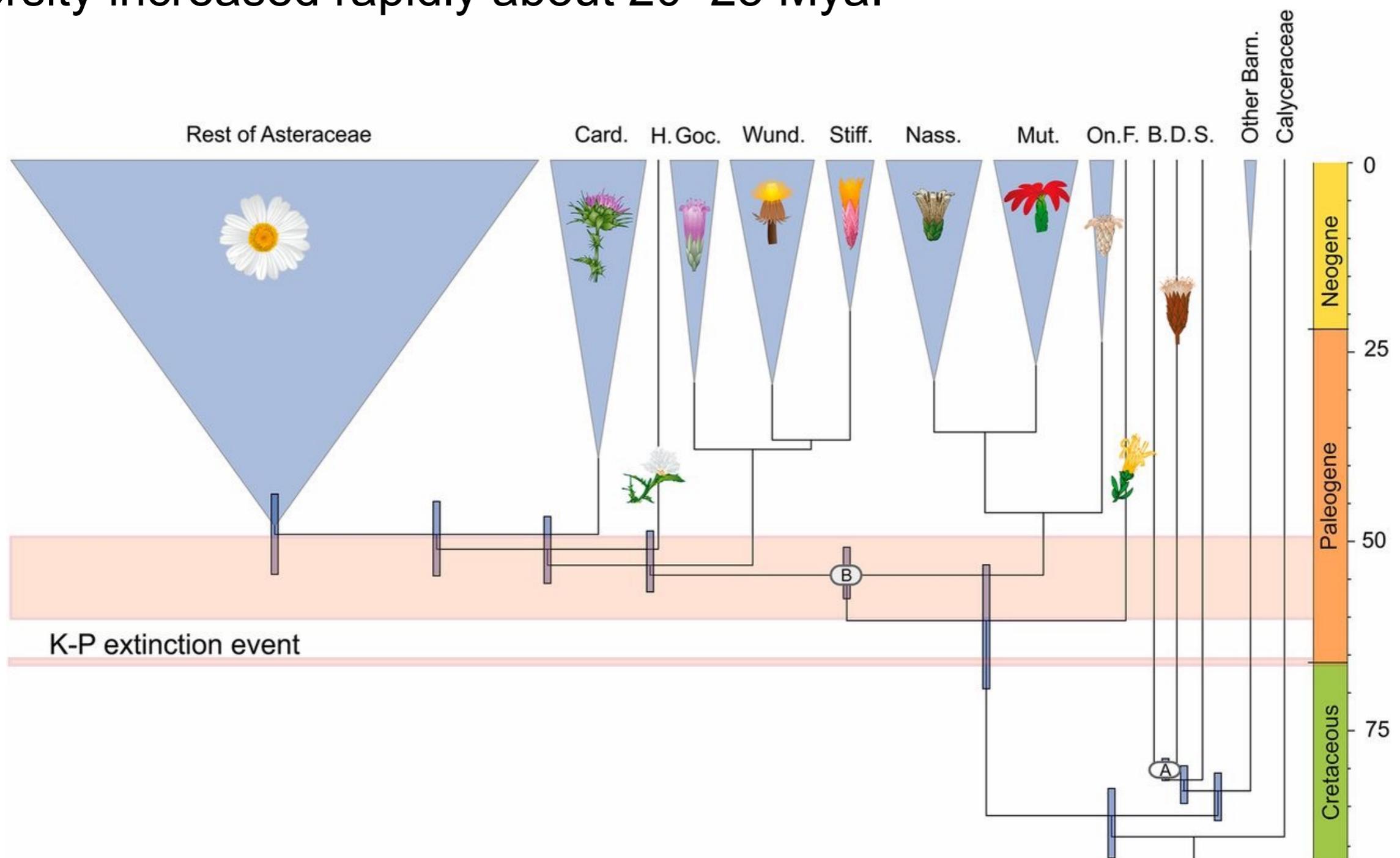
A



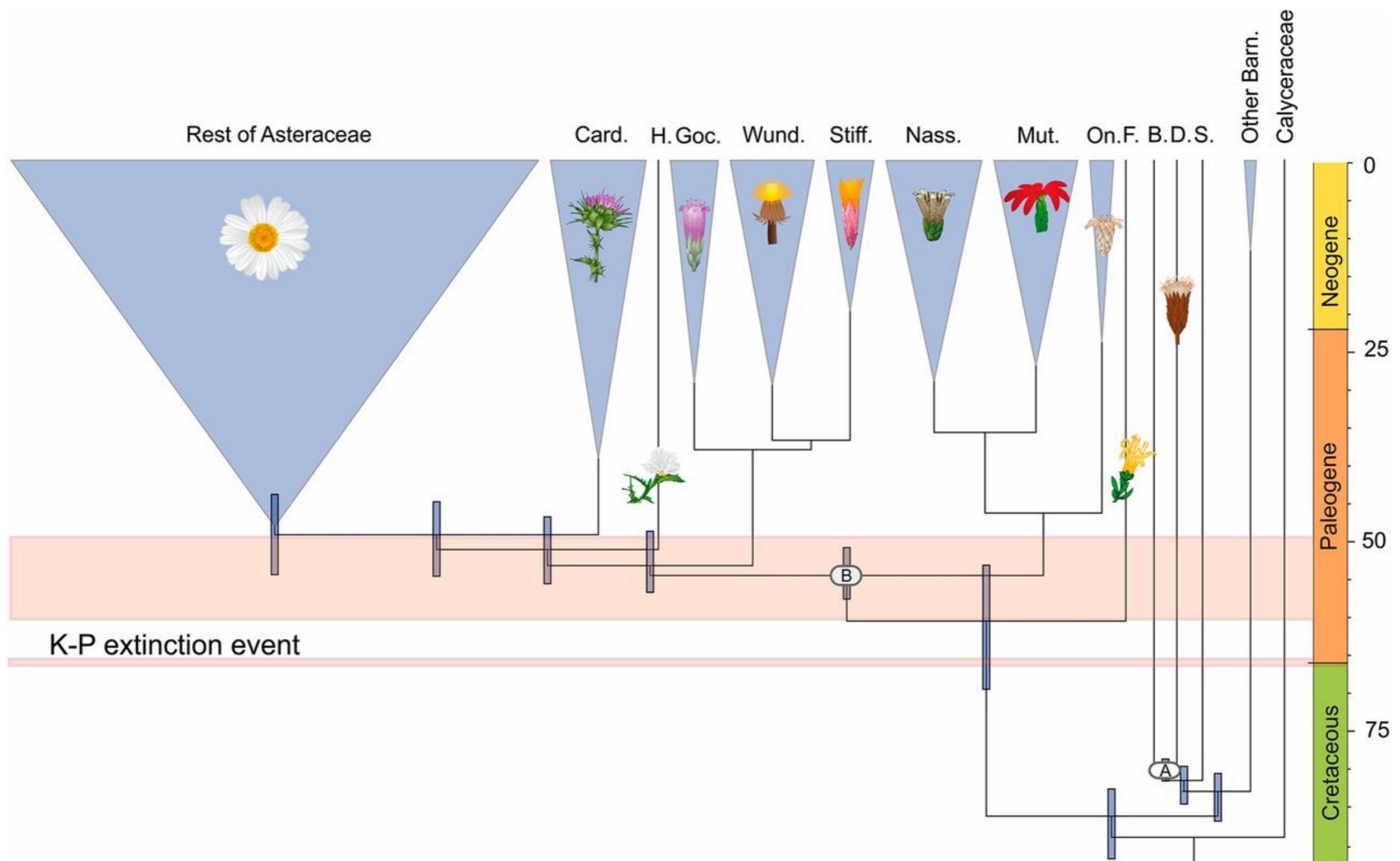
B



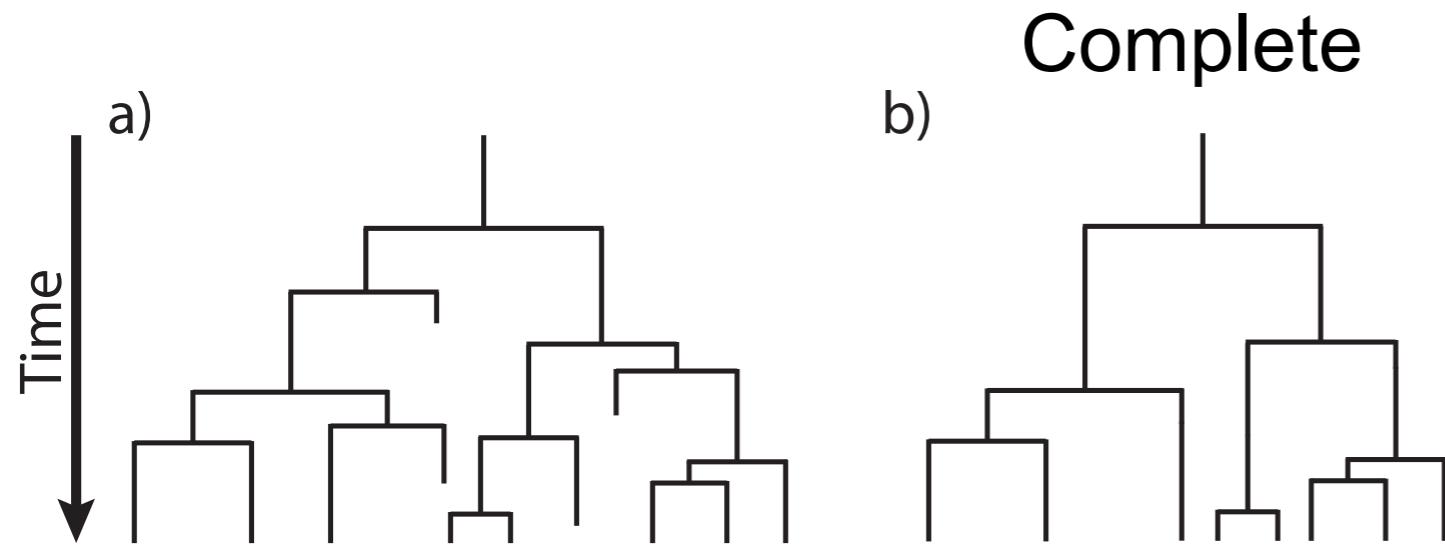
Asteraceae is one of the largest (plant) families: >23,000 species.  
Very few fossils from the Cretaceous known.  
Diversity increased rapidly about 20–25 Mya.



Estimated dated super tree with ~2200 species.  
Only 10% of taxa sampled.



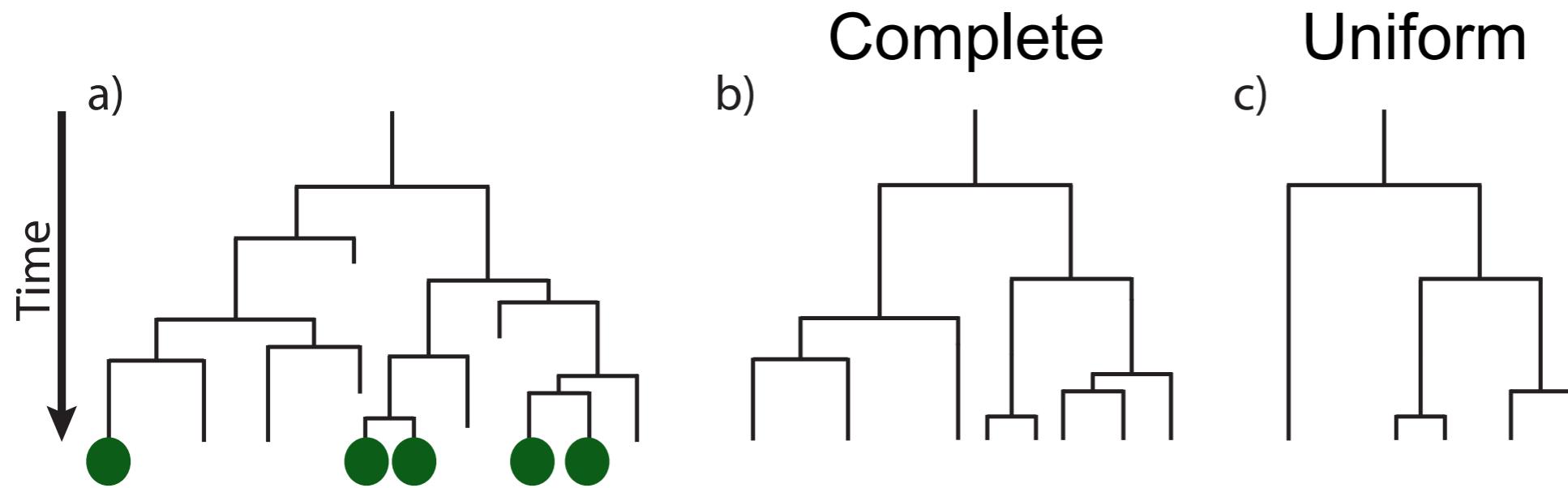
# Incomplete taxon sampling



Complete taxon sampling:

All extant taxa are included.

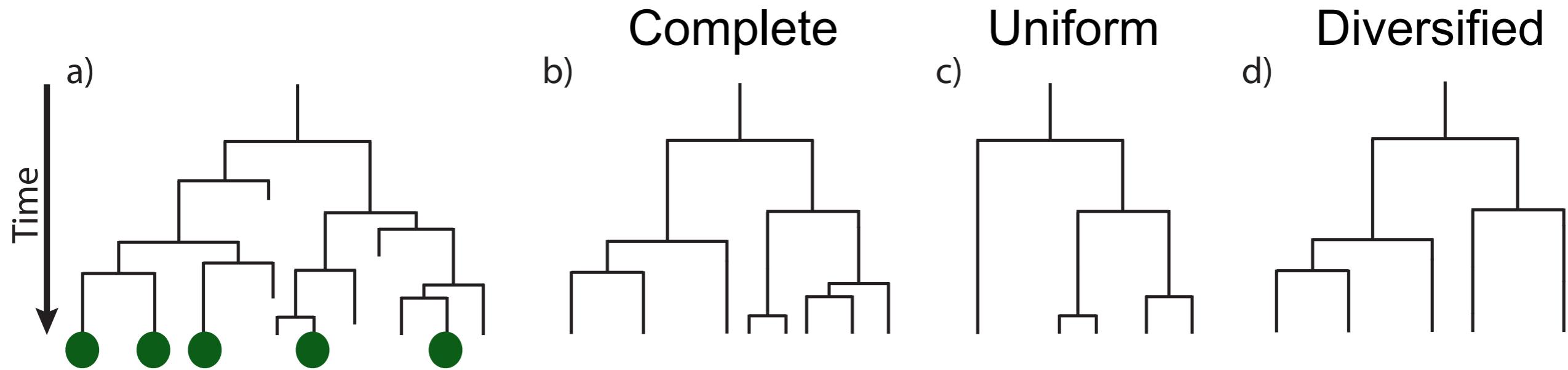
# Incomplete taxon sampling



Uniform taxon sampling:

Each extant taxon has the same probability to be included.

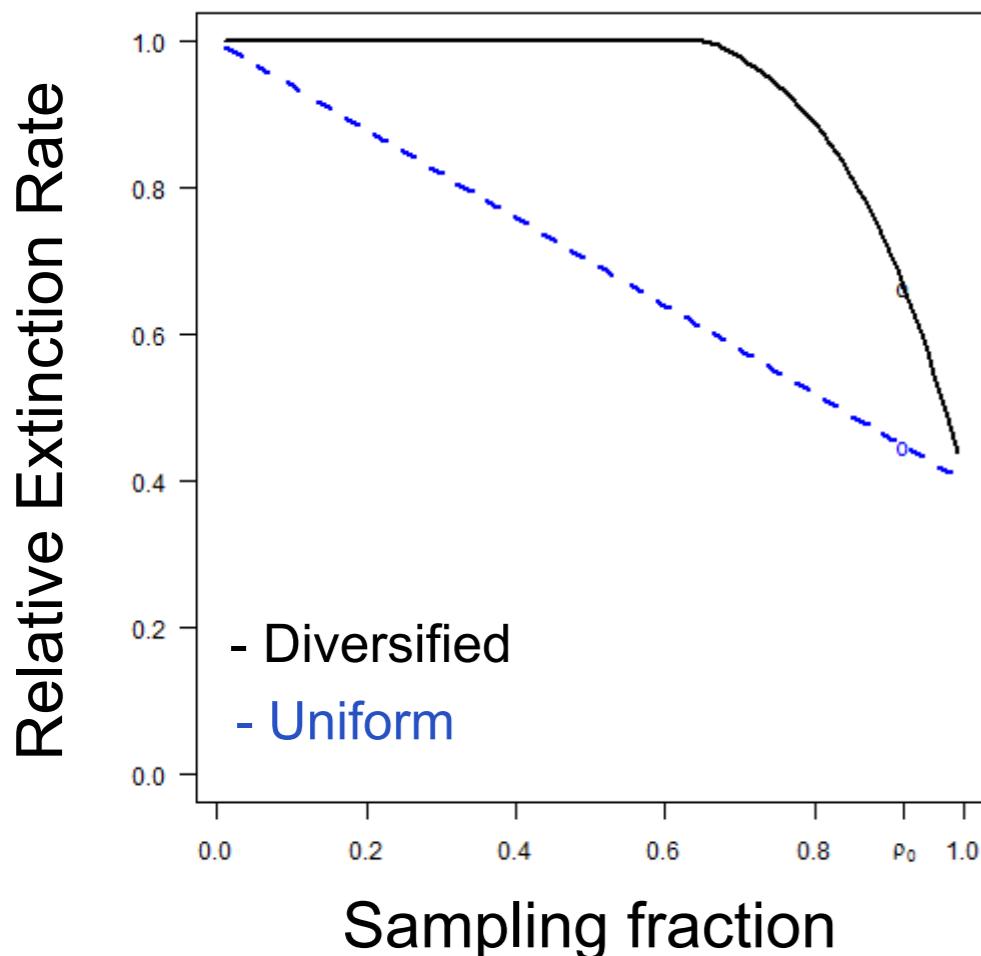
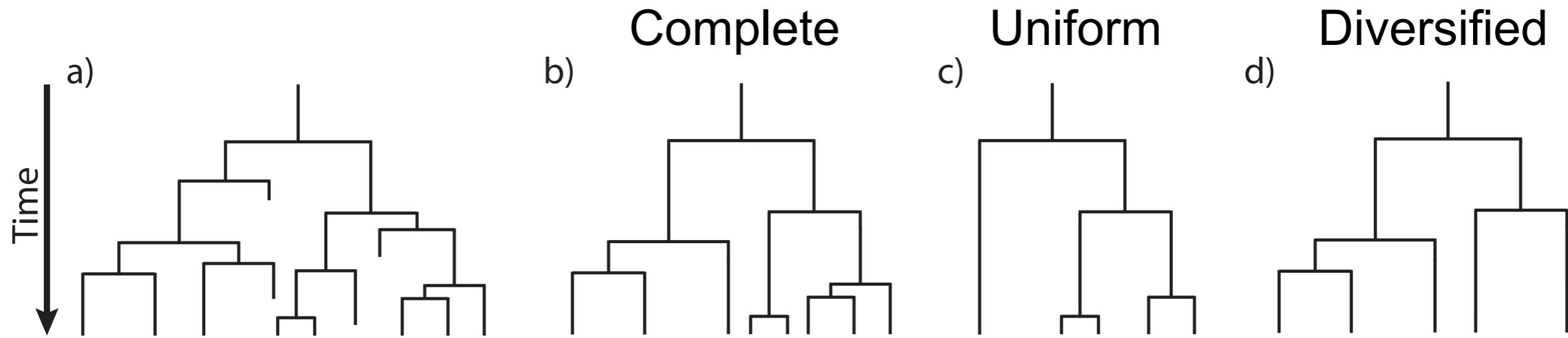
# Incomplete taxon sampling



Diversified taxon sampling:

Only one taxon per group (e.g., genus) is included.

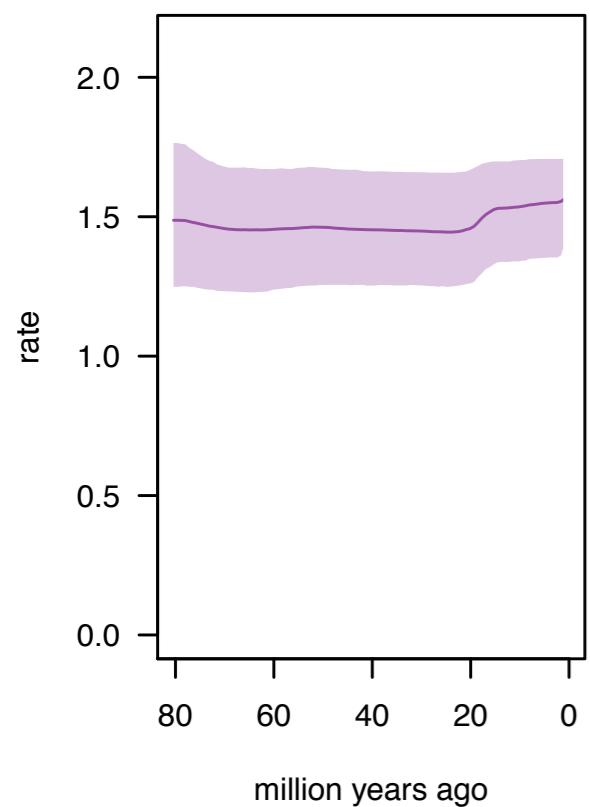
# Incomplete taxon sampling



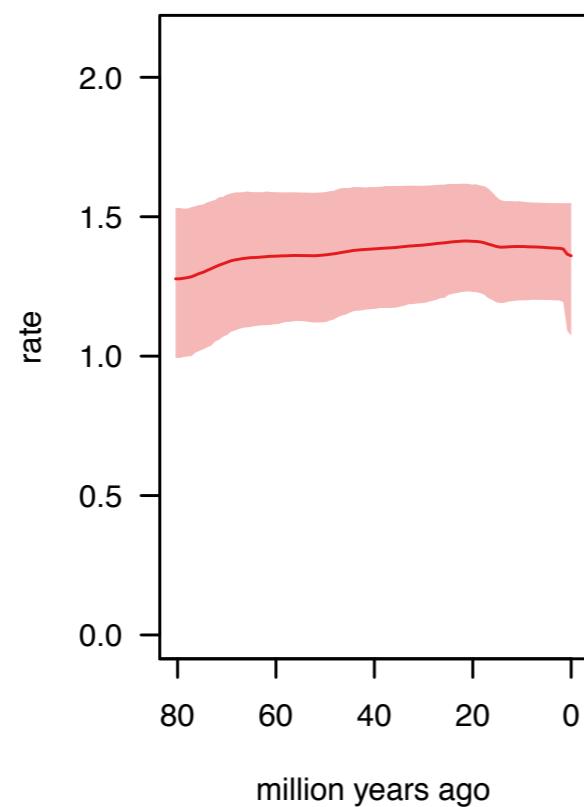
Incomplete taxon sampling  
biases diversification rate  
estimate!

# Uniform Sampling

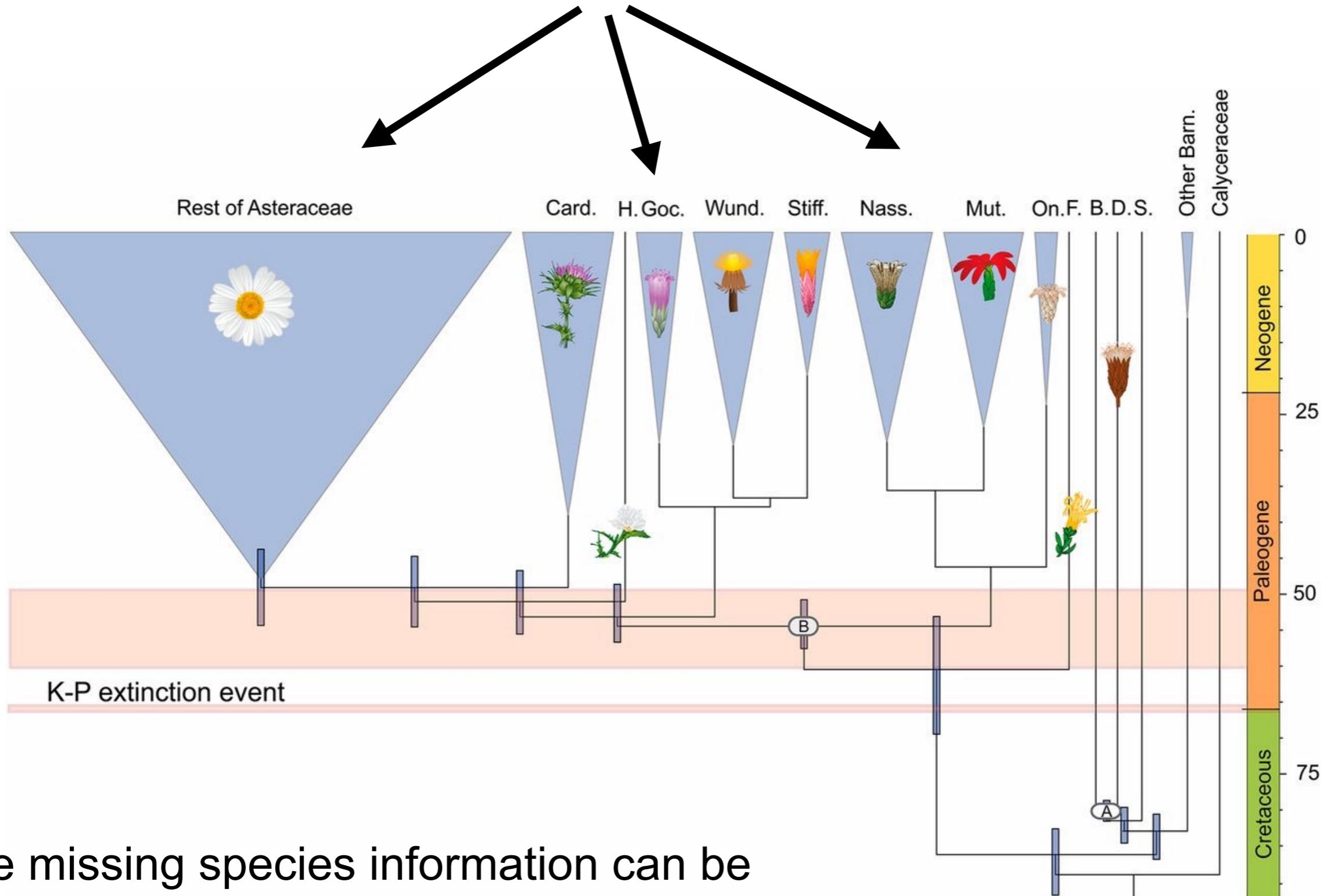
**speciation rates**



**extinction rates**

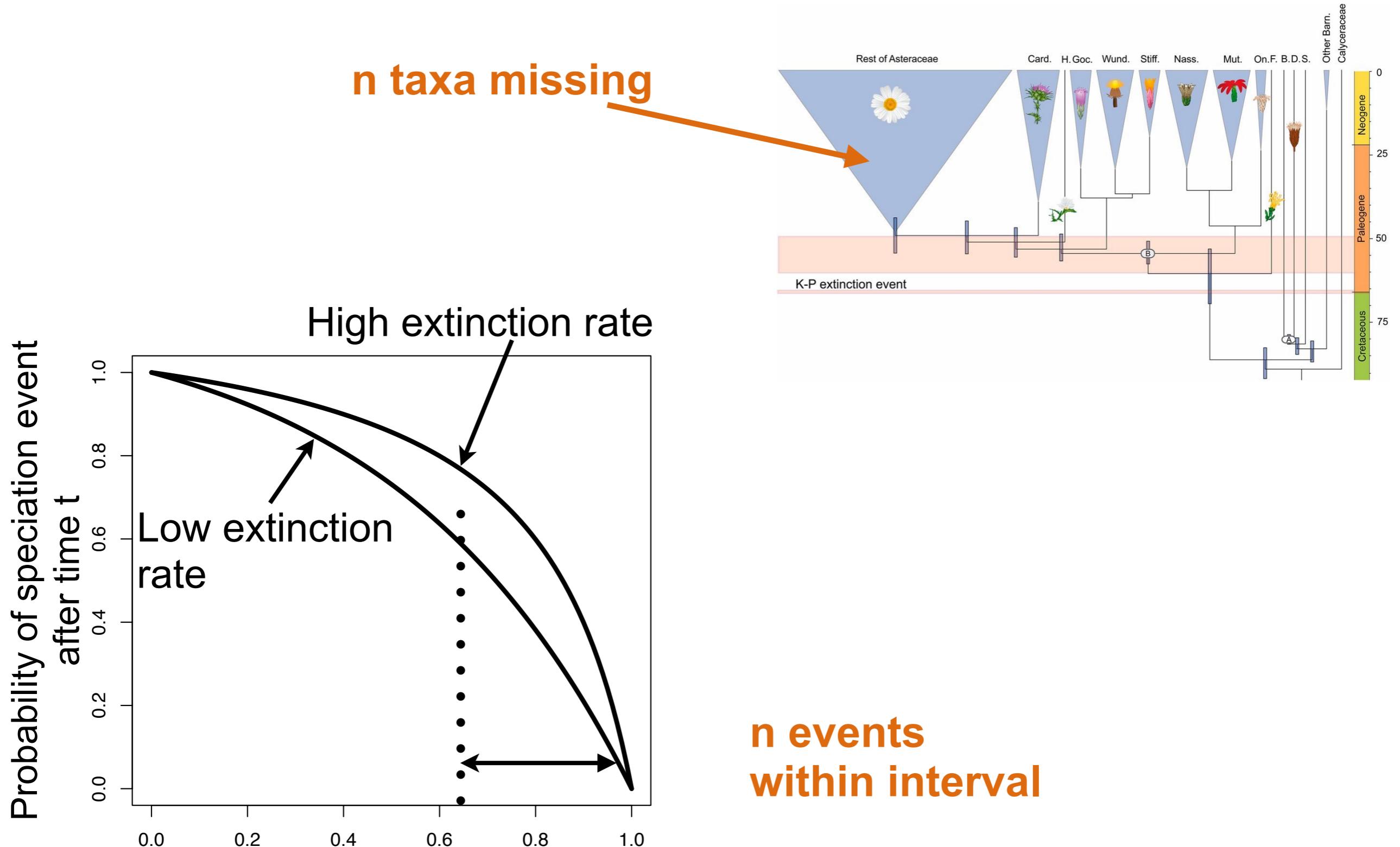


We know how many species belong to each group!

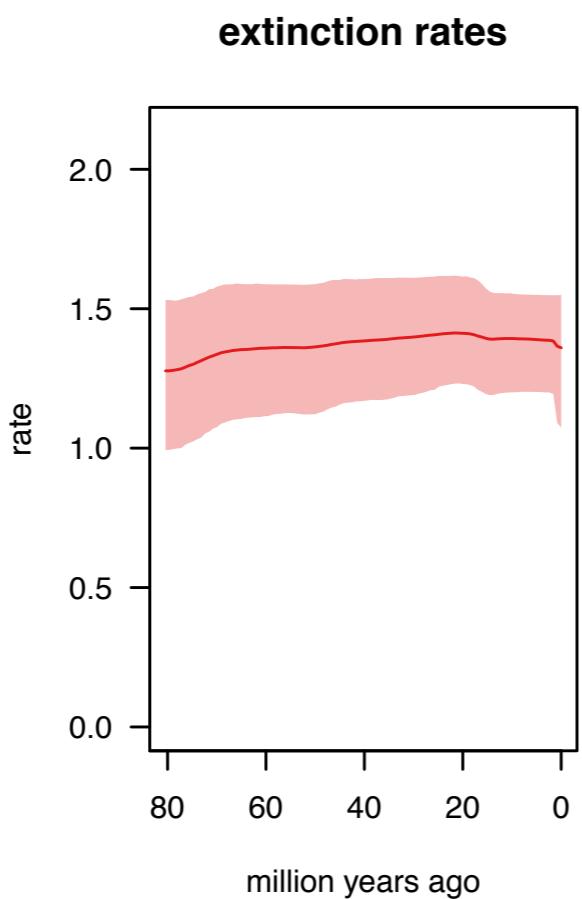
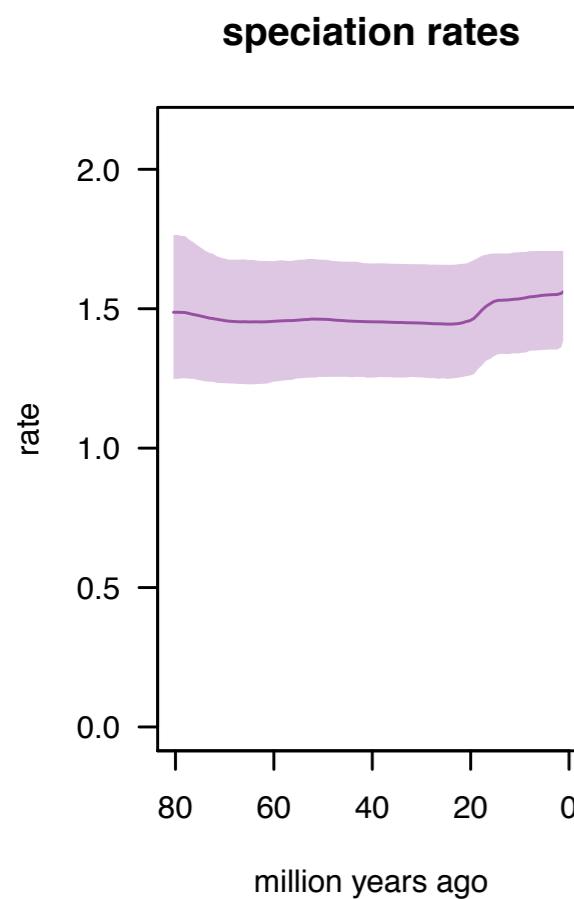


The missing species information can be used to inform diversification rate estimates.

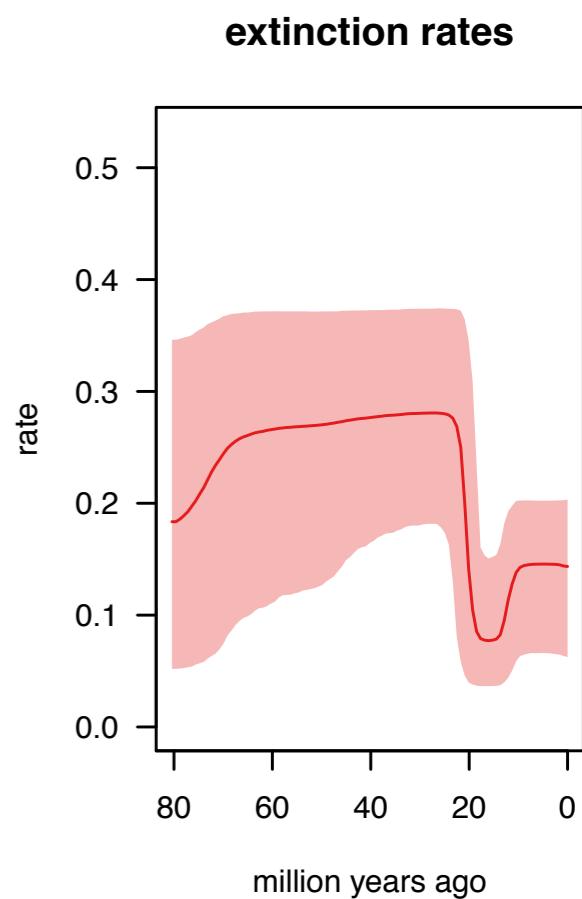
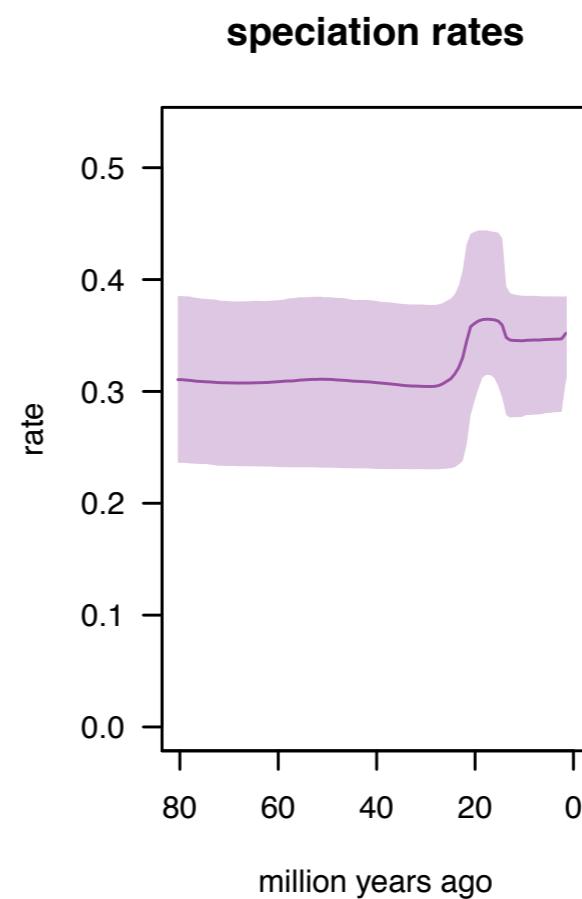
# Empirical taxon sampling

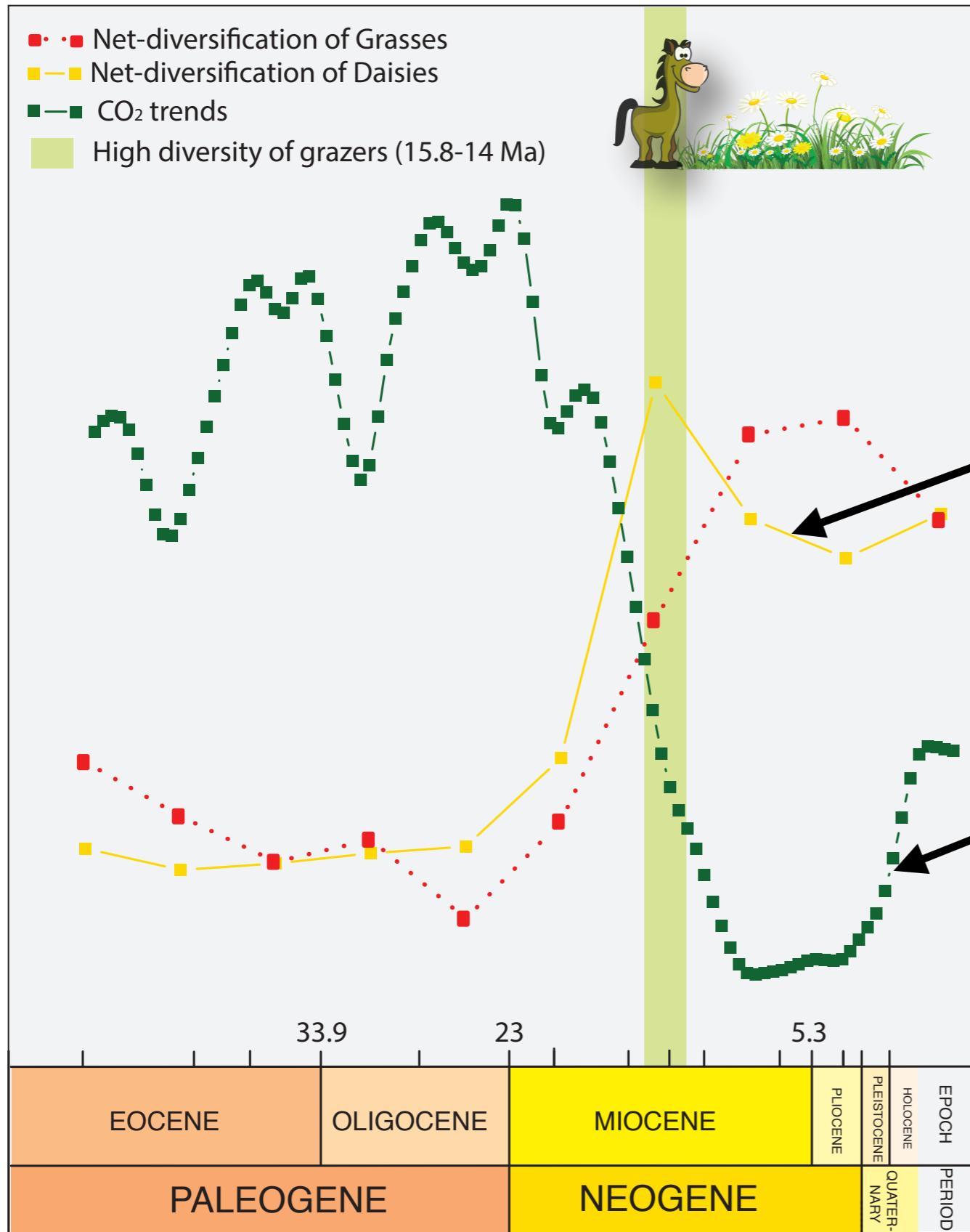


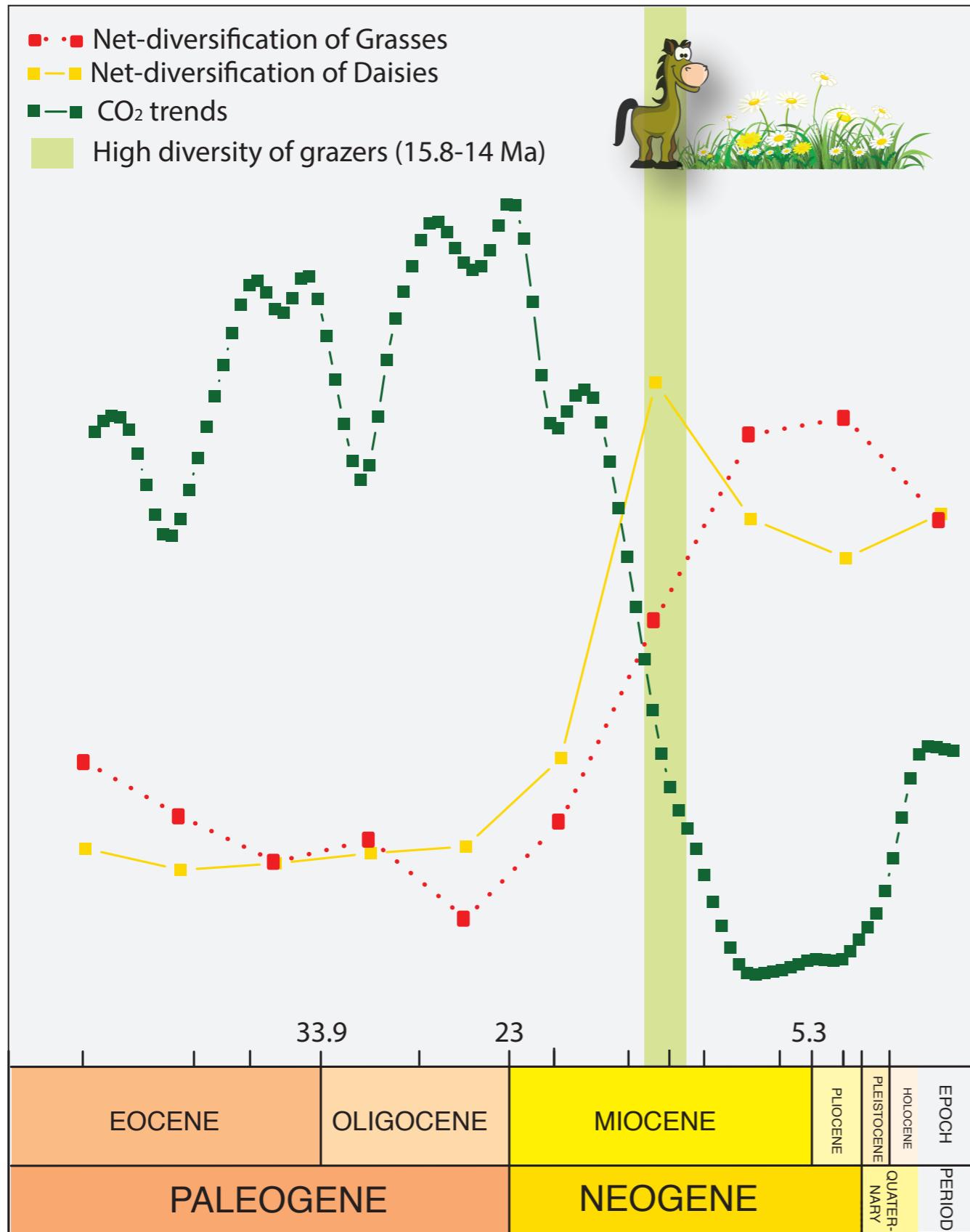
# Uniform Sampling



# Empirical Sampling







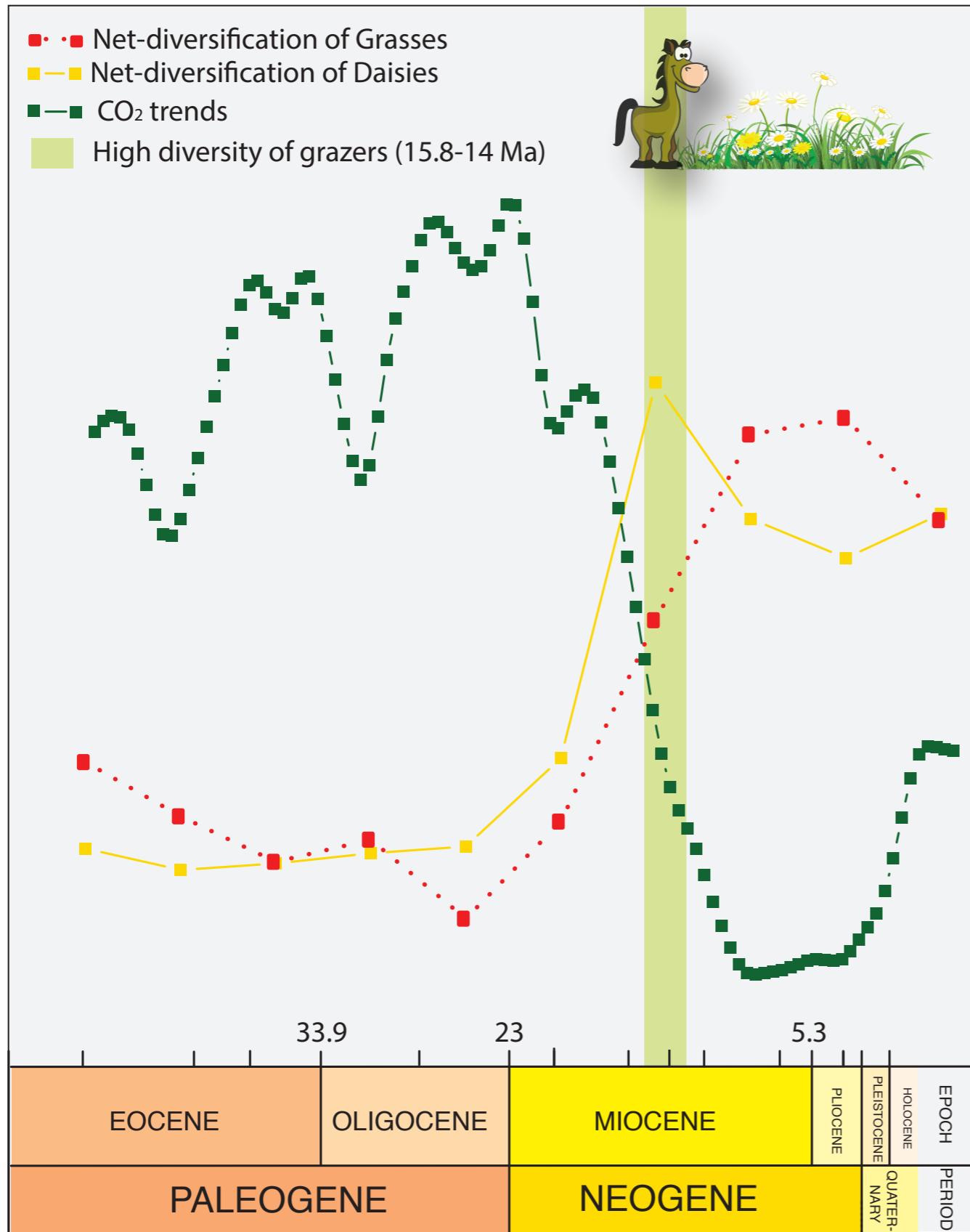
$$\lambda = \alpha_\lambda + \beta_\lambda * \text{CO}_2 + \epsilon_\lambda$$

$$\mu = \alpha_\mu + \beta_\mu * \text{CO}_2 + \epsilon_\mu$$

$\alpha$  = background rate

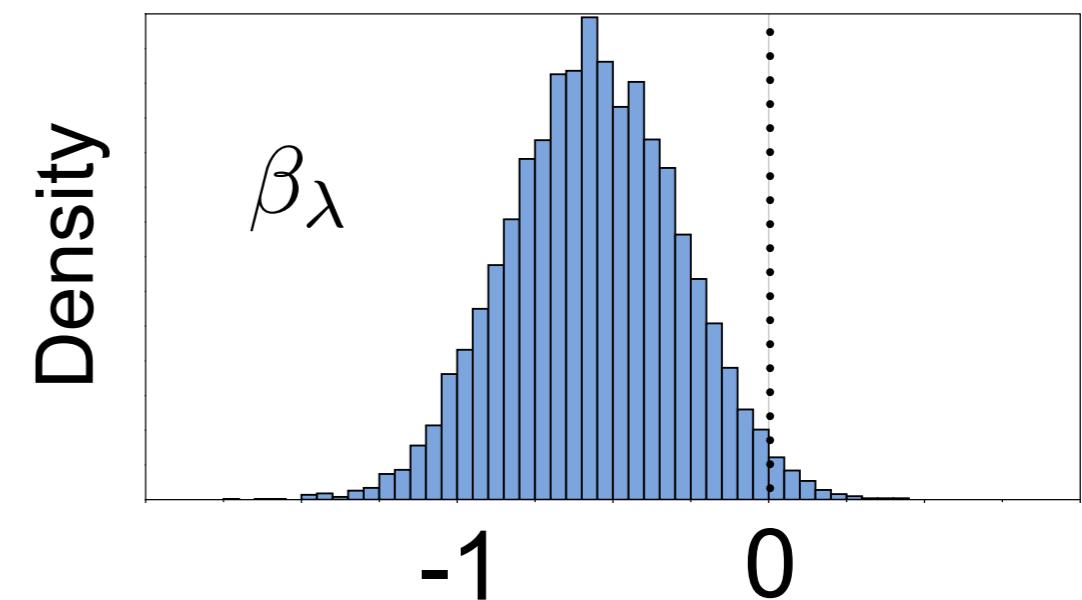
$\beta$  = regression slope

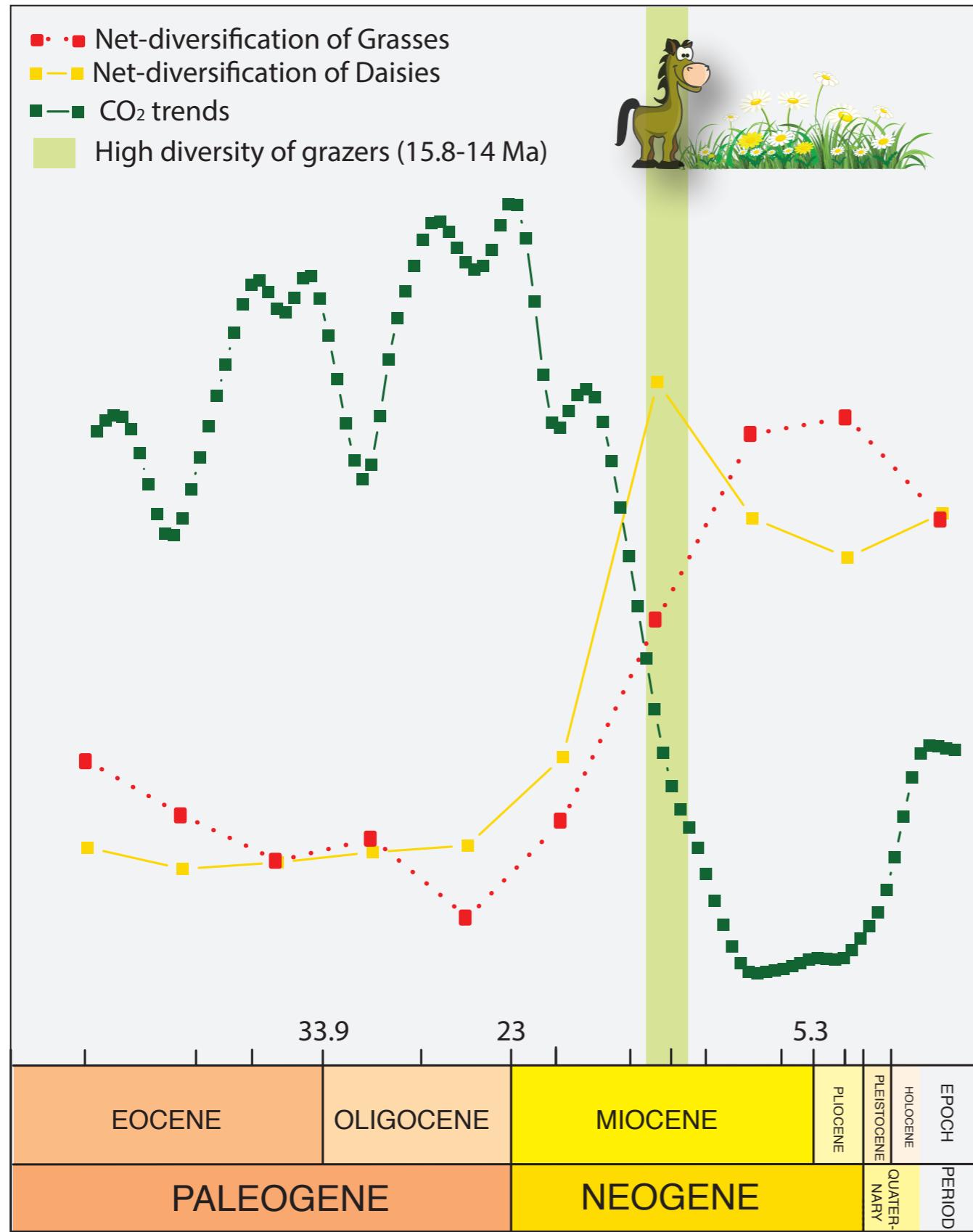
$\epsilon$  = residual



$$\lambda = \alpha_\lambda + \beta_\lambda * \text{CO}_2 + \epsilon_\lambda$$

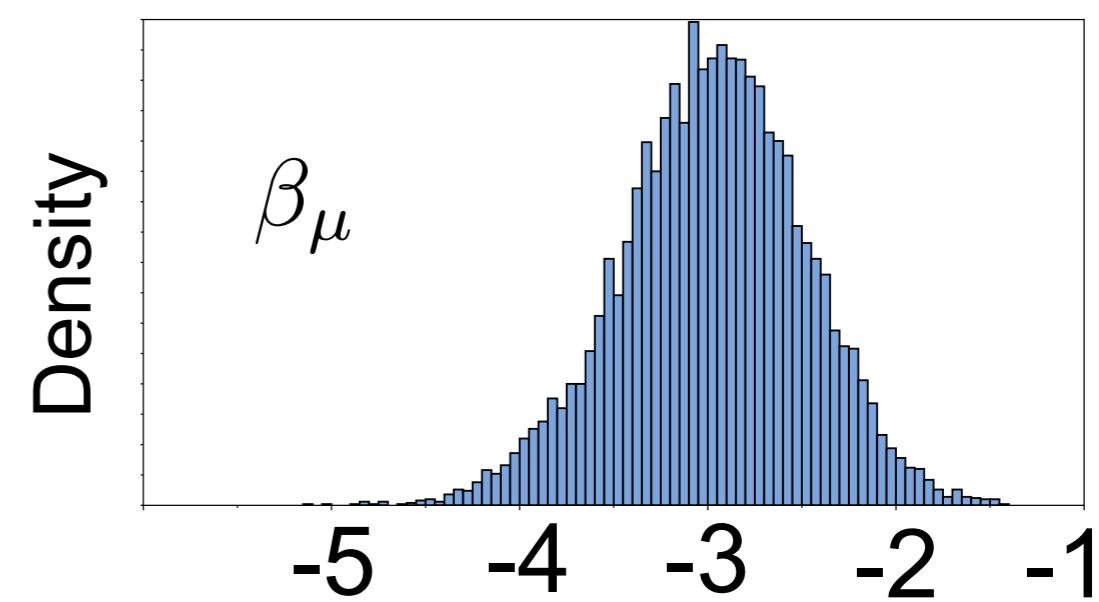
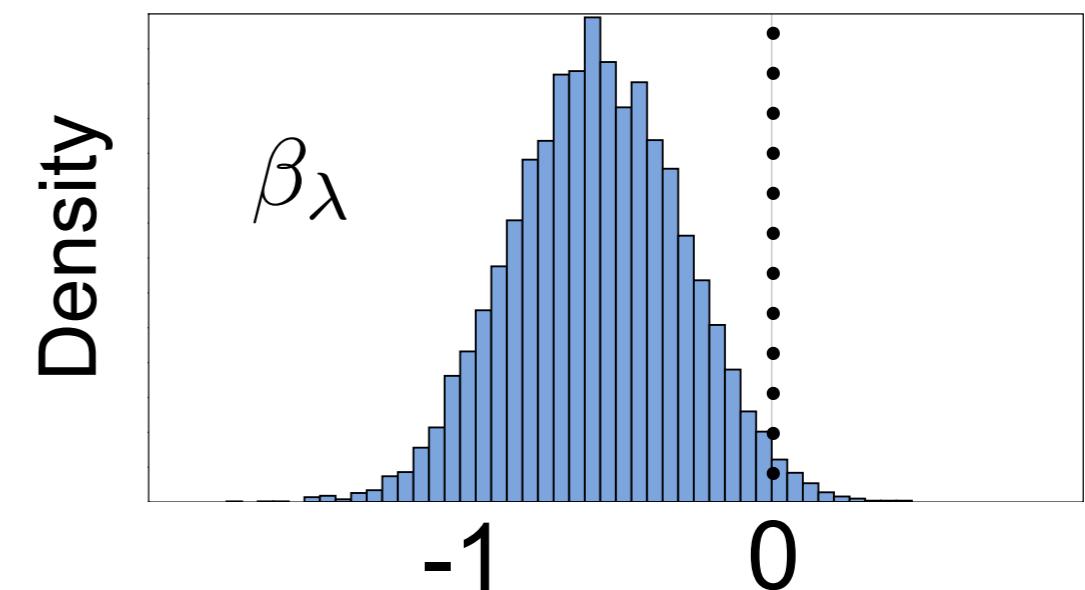
$$\mu = \alpha_\mu + \beta_\mu * \text{CO}_2 + \epsilon_\mu$$

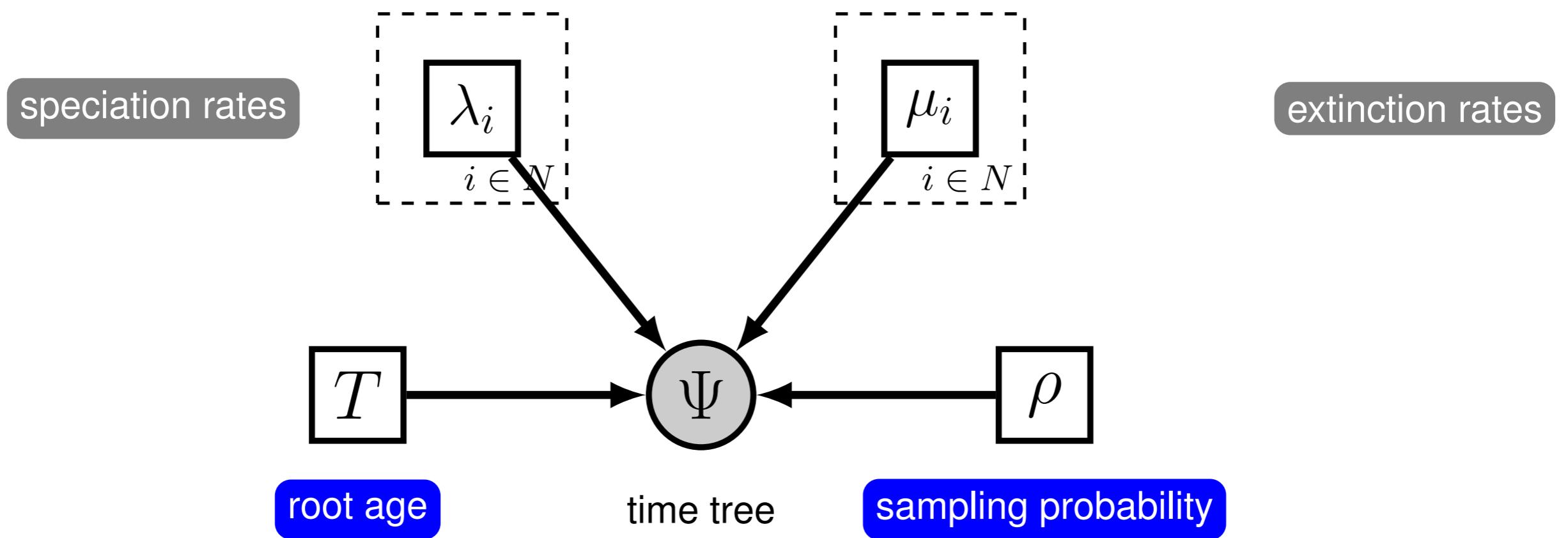


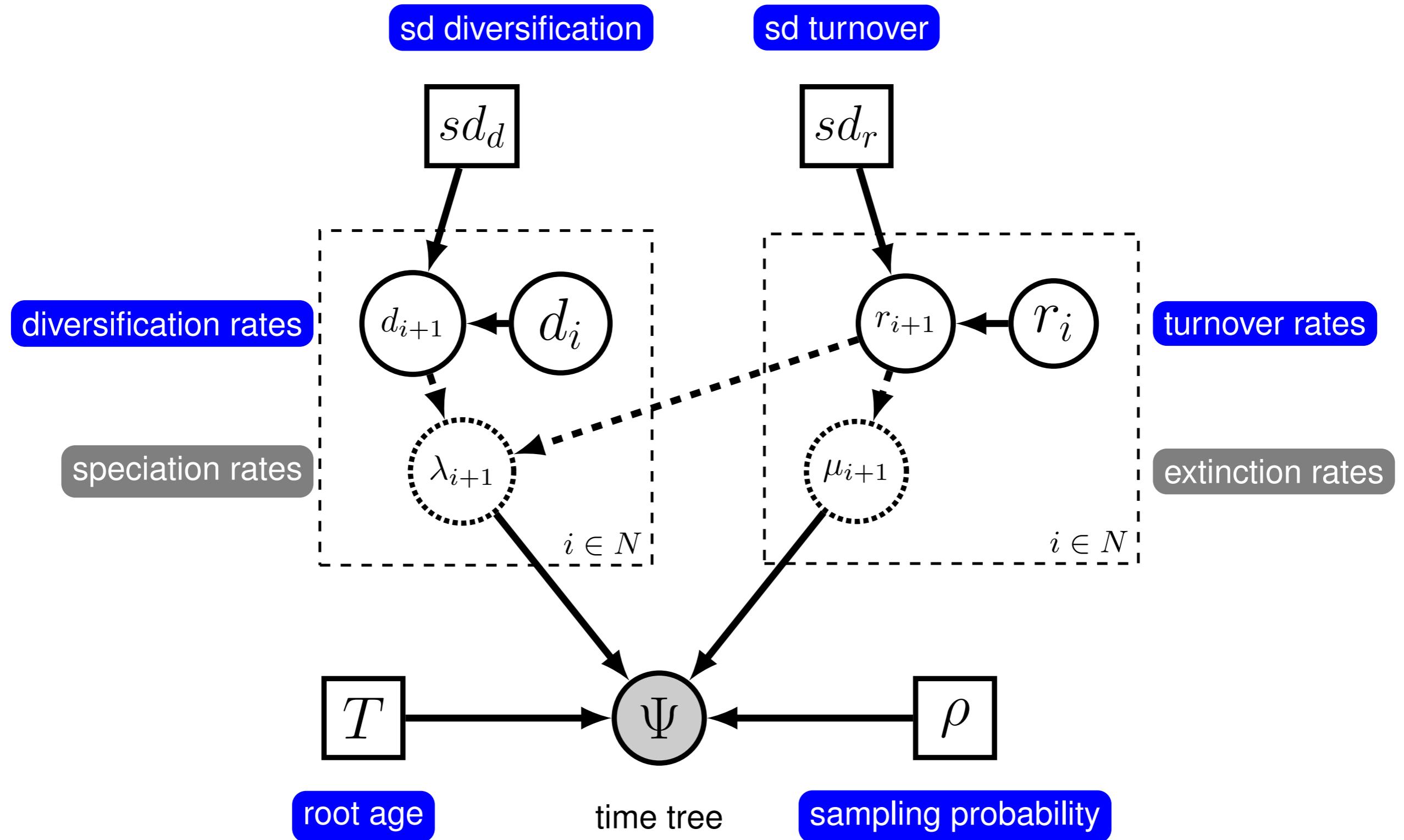


$$\lambda = \alpha_\lambda + \beta_\lambda * \text{CO}_2 + \epsilon_\lambda$$

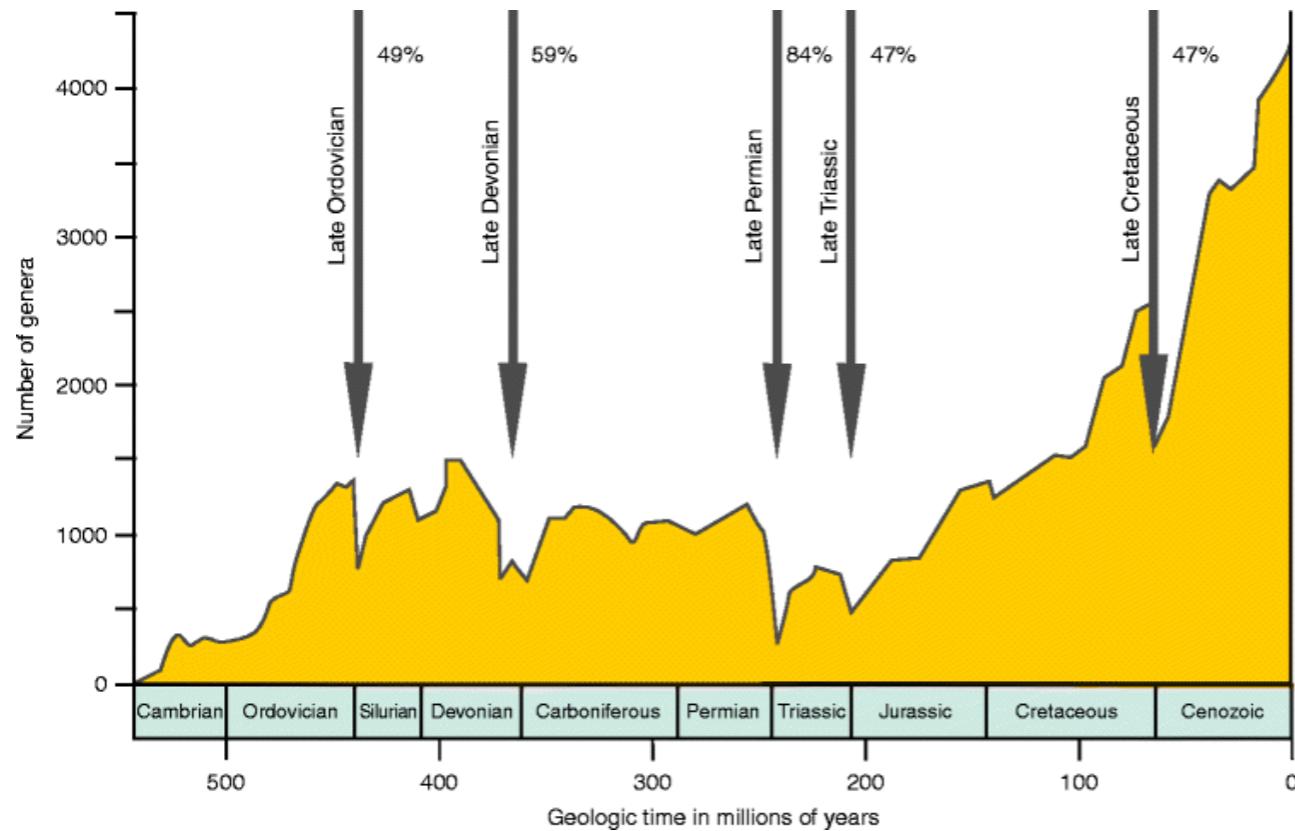
$$\mu = \alpha_\mu + \beta_\mu * \text{CO}_2 + \epsilon_\mu$$





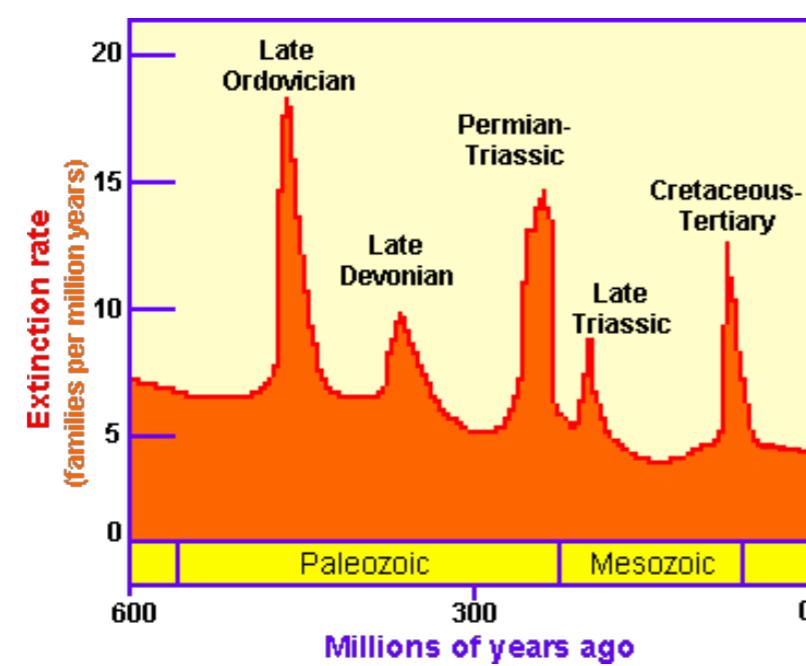


# Mass-extinction events

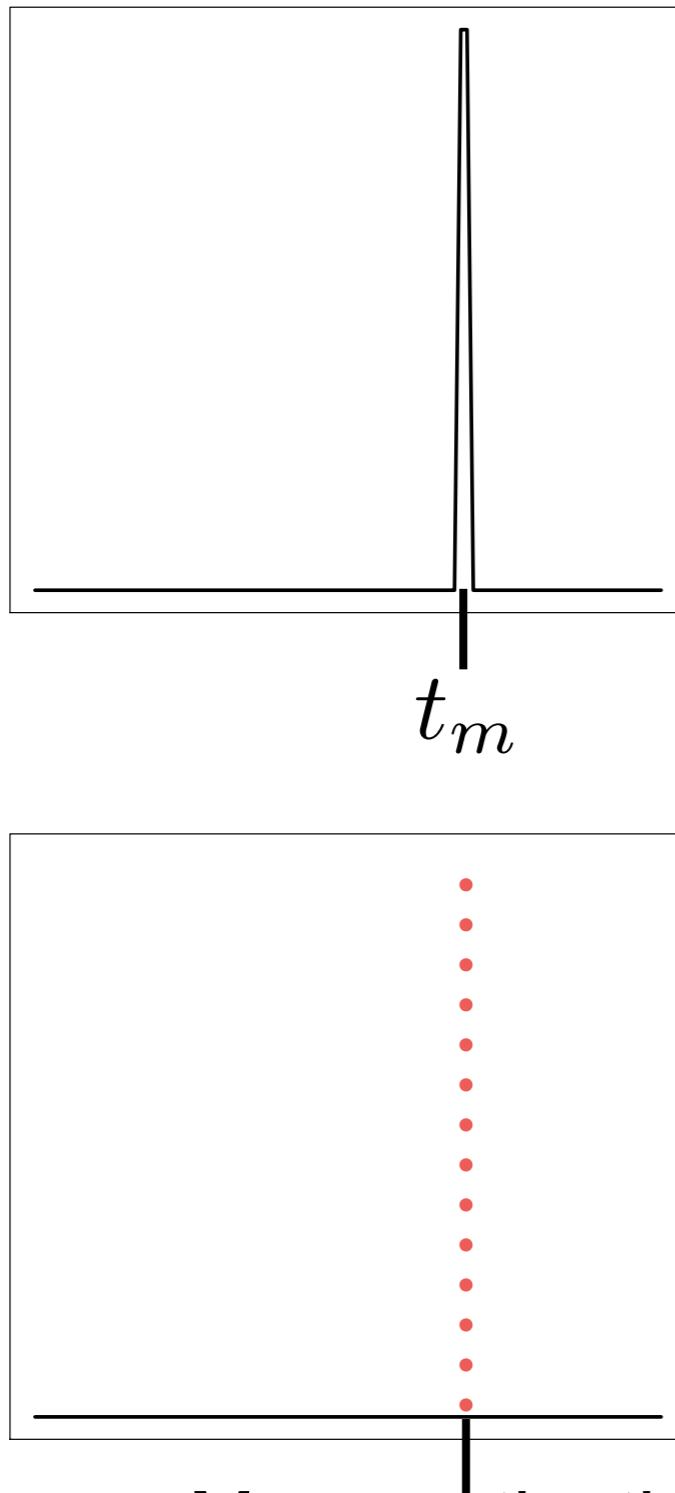


Mass-extinction events are:

- short periods of time with high extinction
- 50–75% of genera go extinct
- around 90% of species diversity goes extinction



# Modeling mass extinction



Mass-extinction events can be modeled by:

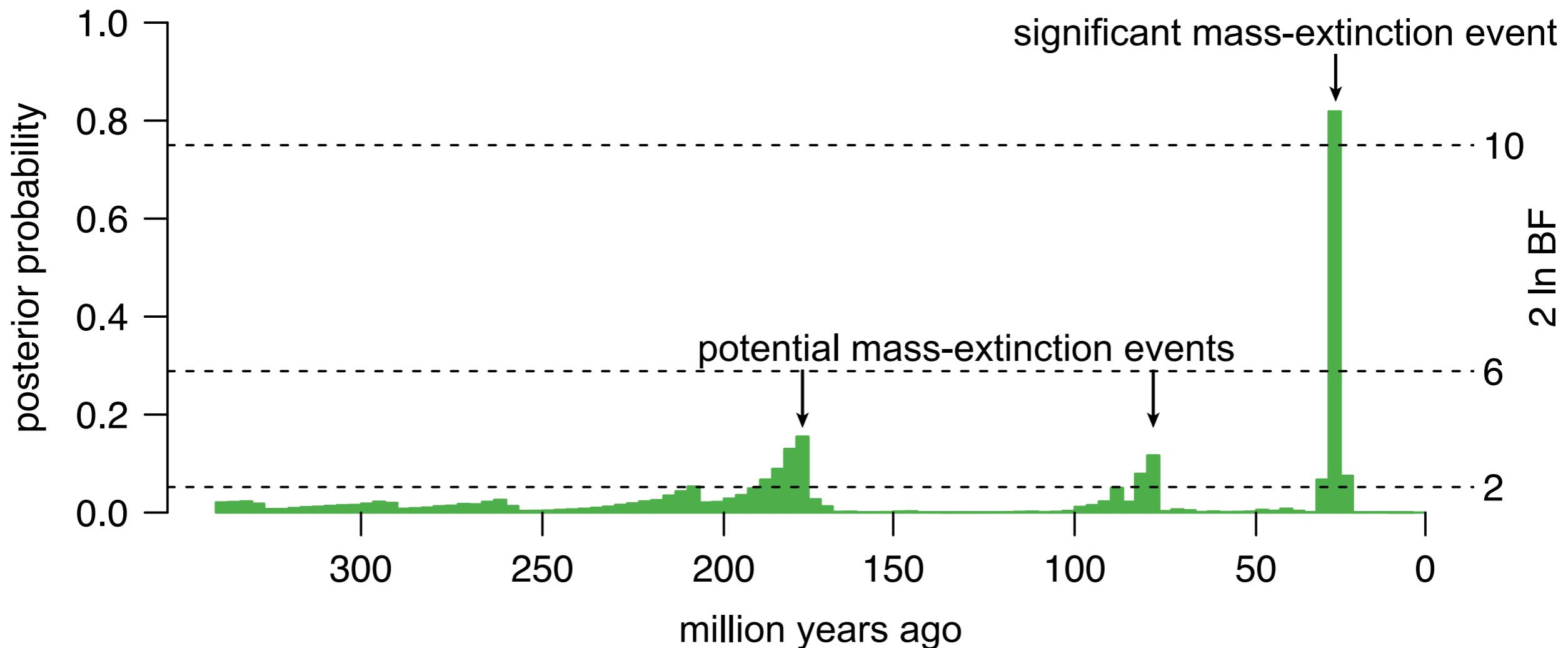
a) a short period of time with high extinction

b) an explicit mass-extinction event with a given survival probability

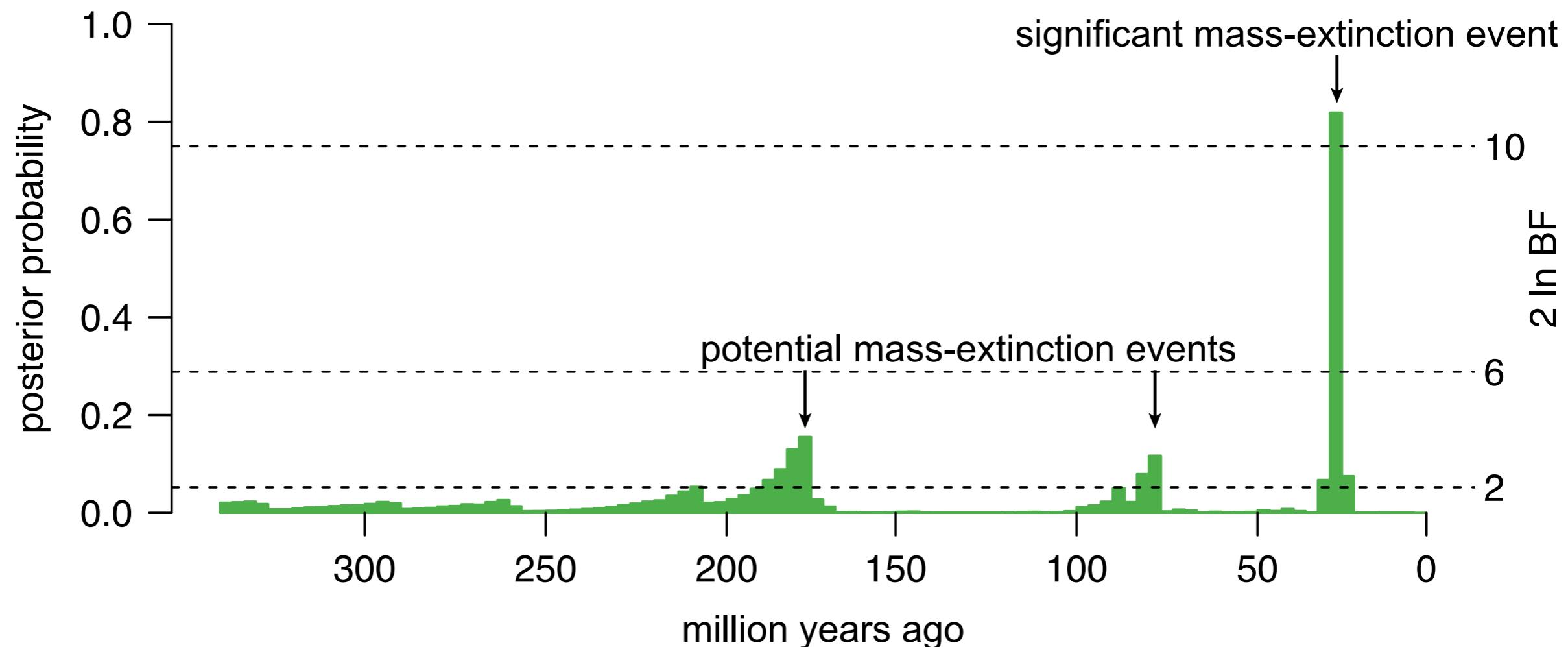
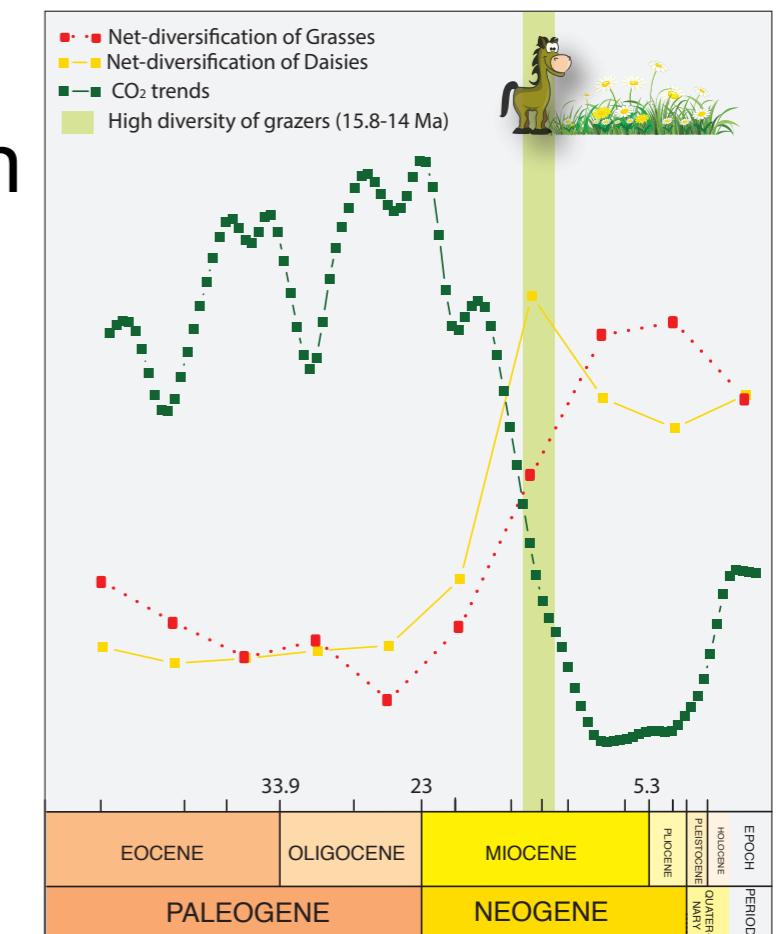
*using explicit mass extinction and biologically informed priors we can distinguish between background rate variation and mass extinctions*

# Inference of mass-extinction events in conifers

Bayes factor:  $\frac{\text{posterior mass extinction}}{\text{posterior no mass extinction}} \div \frac{\text{prior mass extinction}}{\text{prior no mass extinction}}$



- Conifers were impacted by a mass extinction about 23 Mya
- Daisies and grasses increased in diversity about 20 Mya
- Diversification rates in daisies are linked to CO<sub>2</sub>



- 
- **BREAK**

# Outline

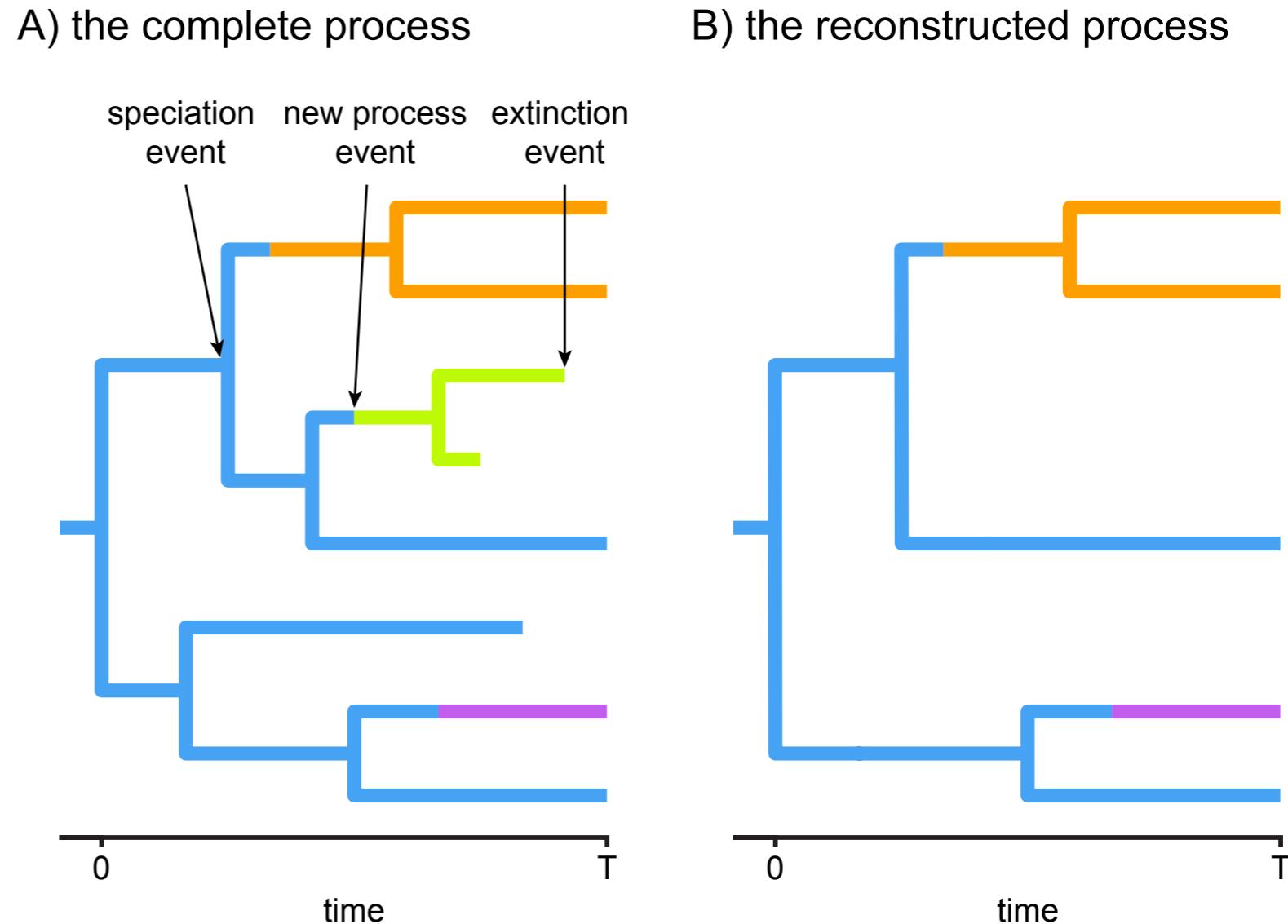
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1. Constant diversification rates.
2. Diversification rates through time
3. Branch-specific diversification rates
4. Character-dependent diversification rates

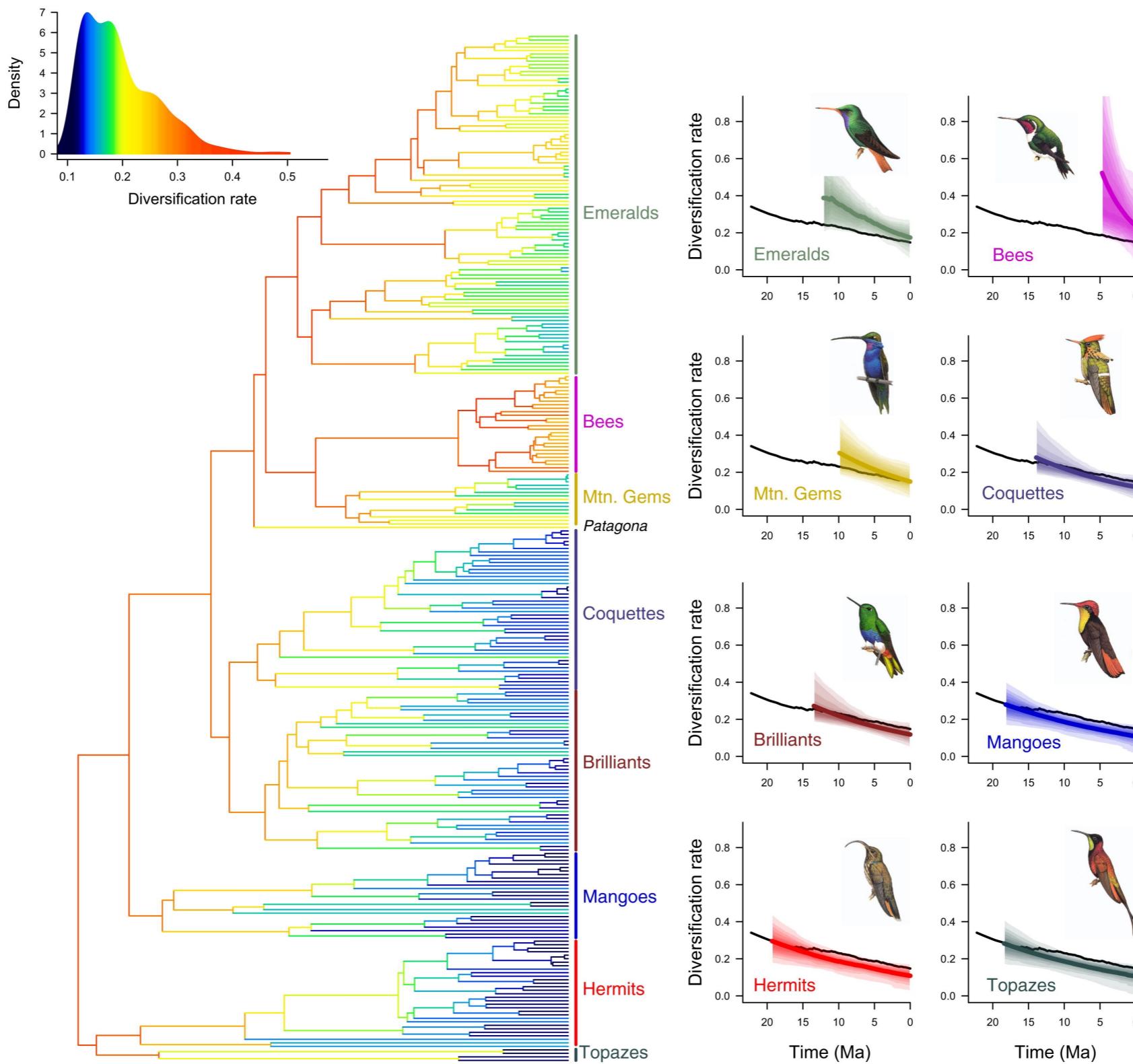
# Branch-Specific Diversification

Lineages / clades have heterogeneous diversification rates.

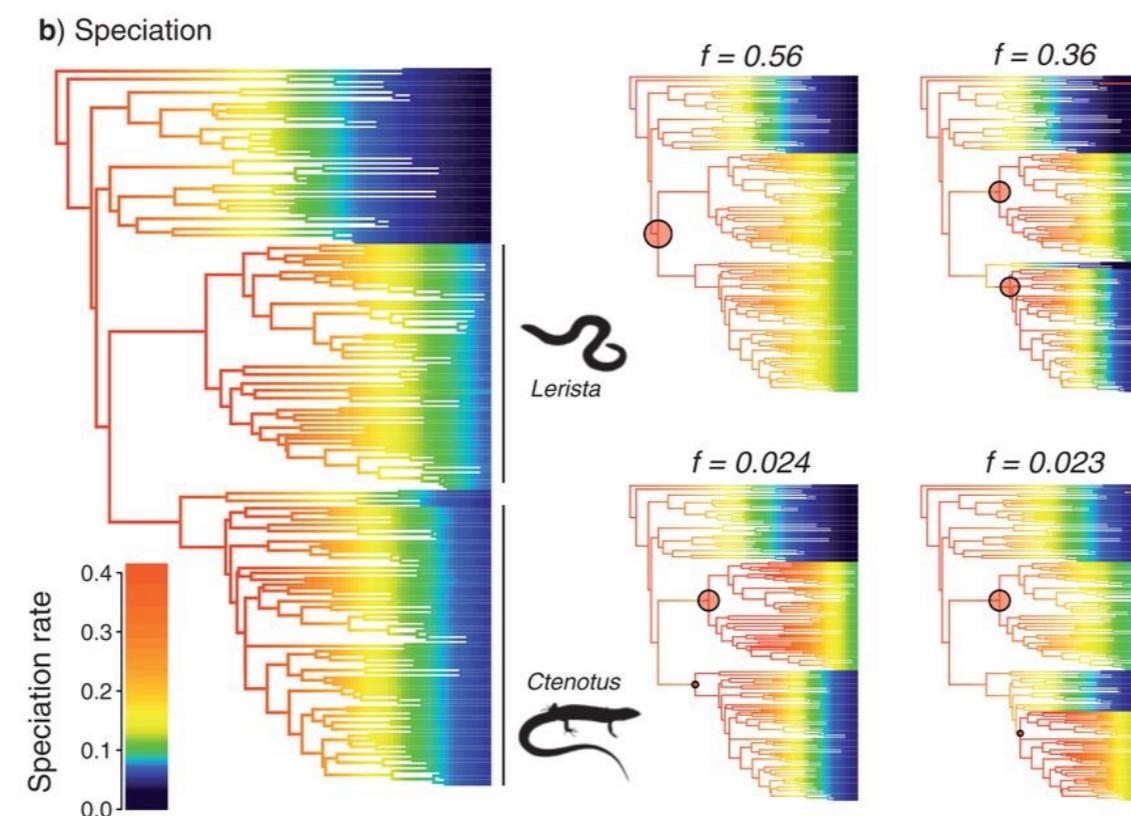
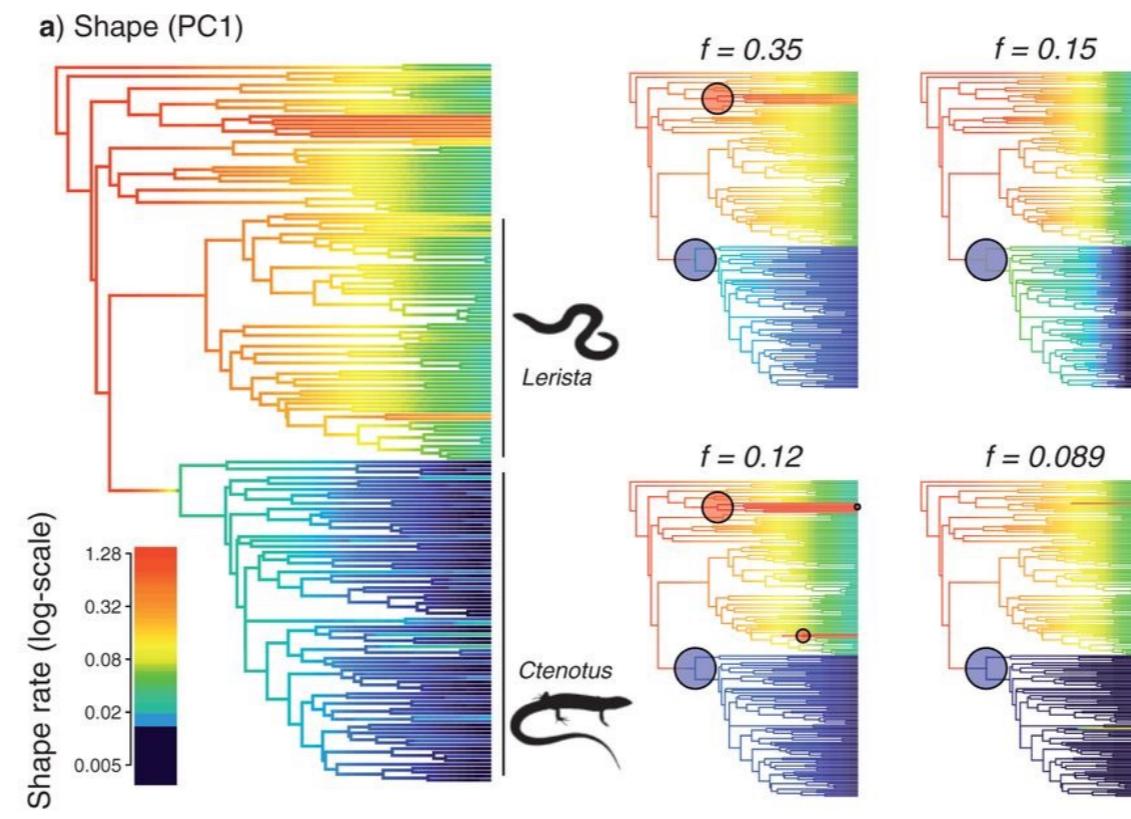
Locations of shifts are defined a priori (prior hypothesis) or estimated.



# Branch-specific diversification rates in hummingbirds by McGuire et al. (2014)

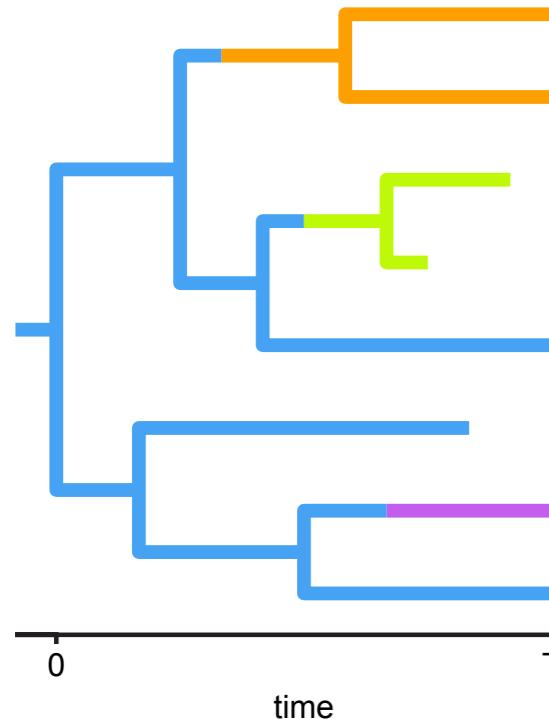


# Branch-specific diversification rates in lizards by Rabosky et al. (2014)

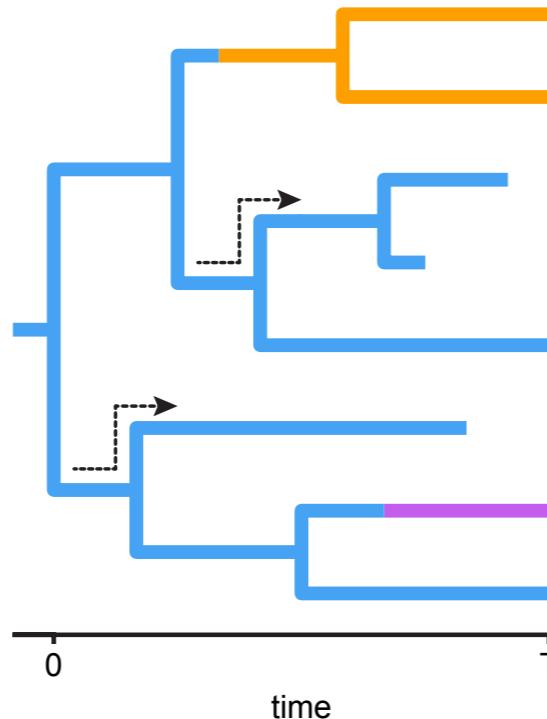


# Modeling issues in BAMM

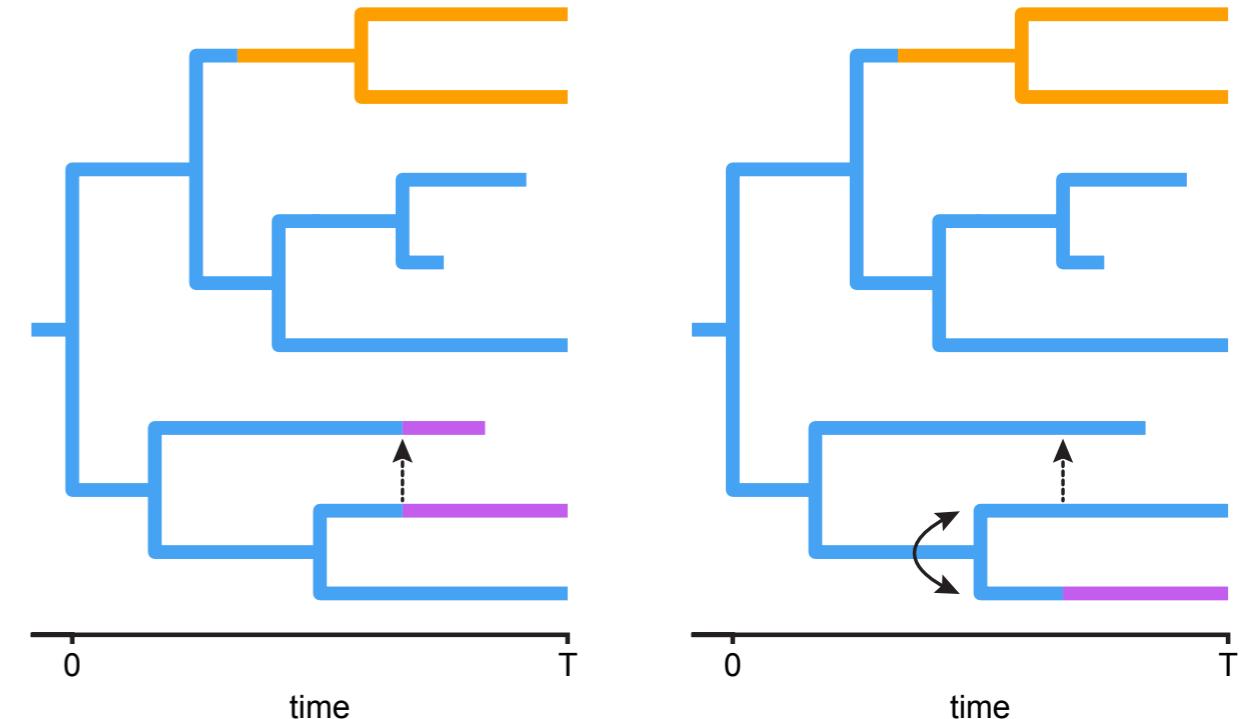
A) actual process  
(process may vary on extinct lineages)



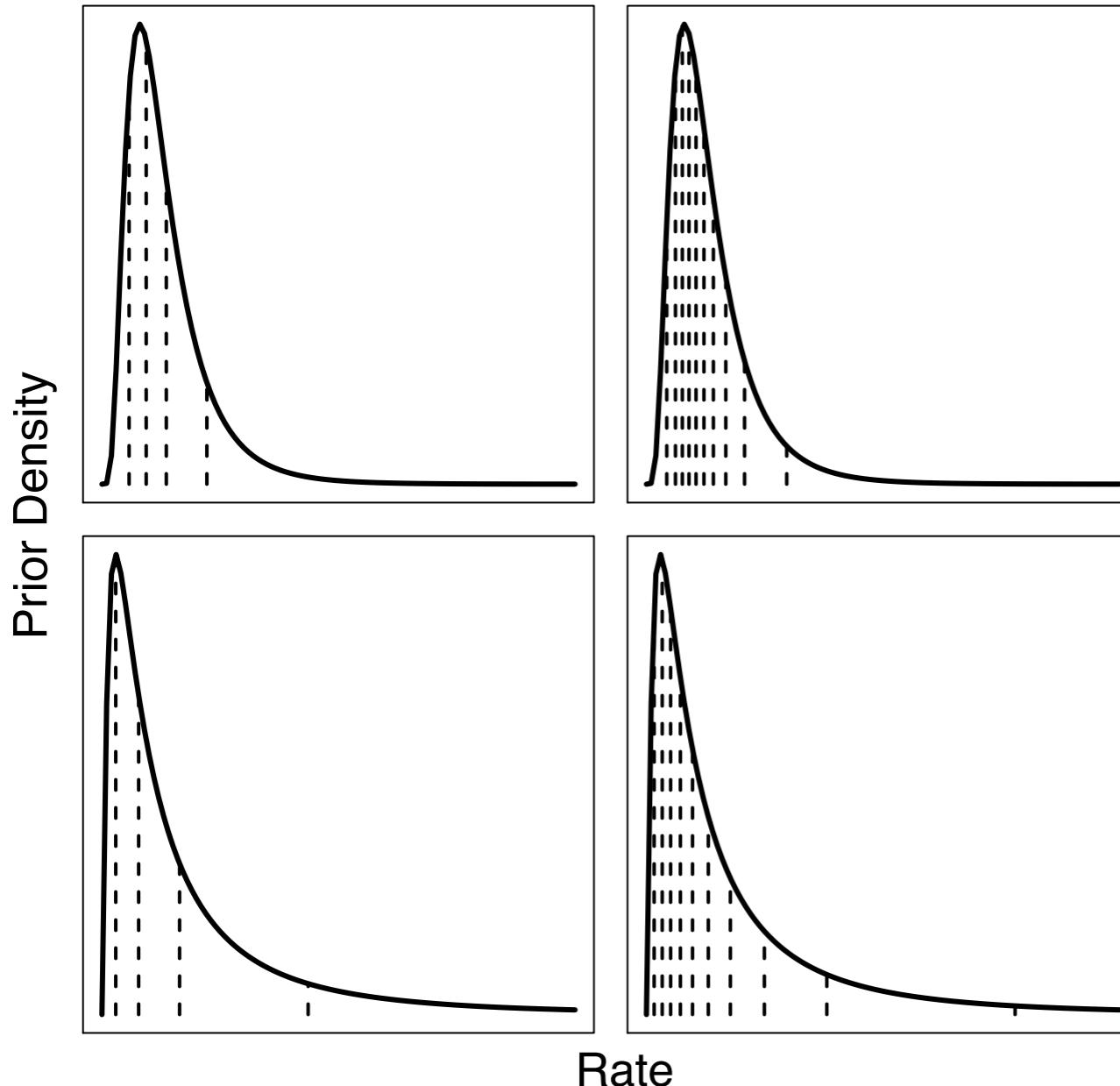
B) described process  
(extinct lineages inherit ancestral process)



C) implemented process  
(extinct lineages laterally inherit the process of the left but not the right observed branch)



# Branch-specific model in RevBayes

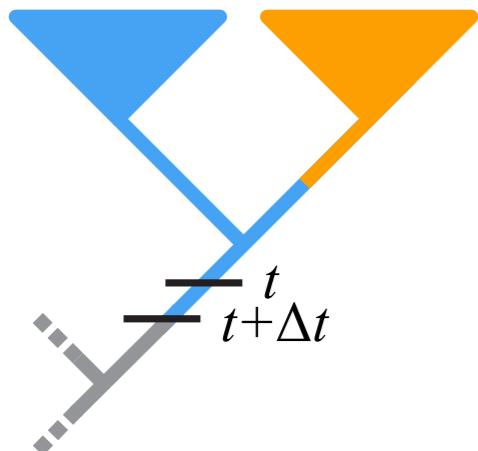


Assume there are only  $N$  discrete rate categories.

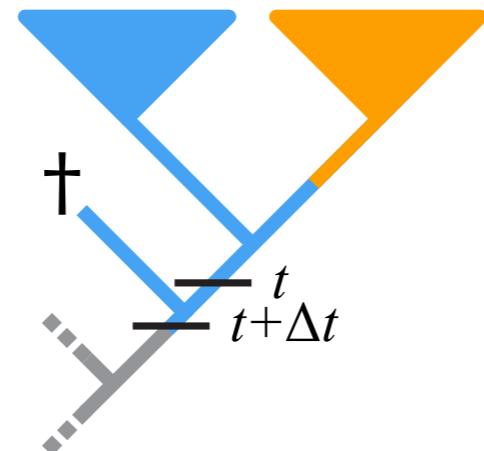
Approximate continuous distribution by  $N$  quantiles of distribution (discretization).

# Branch-specific likelihood in RevBayes

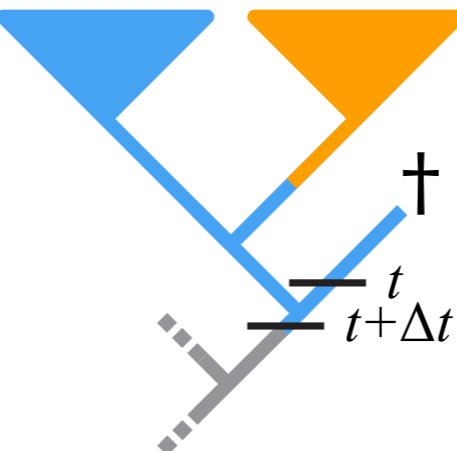
A) Scenarios for observed lineages



i. no speciation

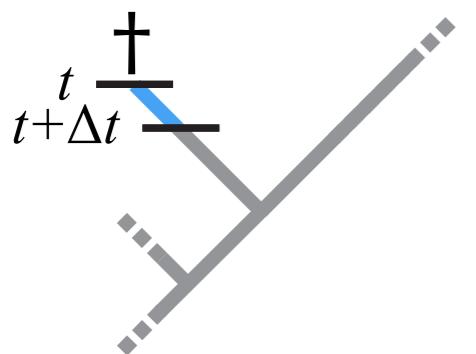


ii. speciation left branch,  
subsequent extinction

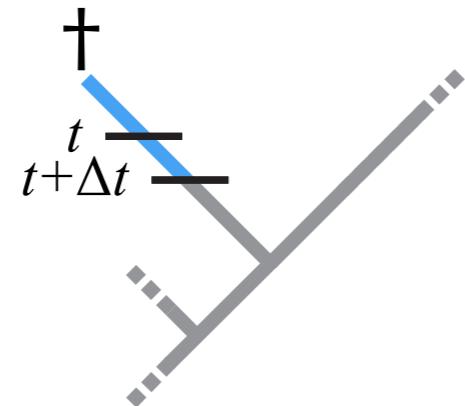


iii. speciation right branch,  
subsequent extinction

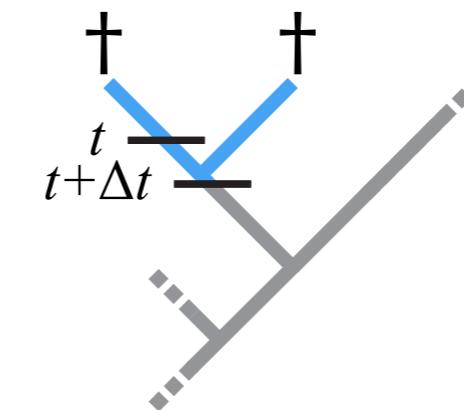
B) Scenarios for unobserved lineages



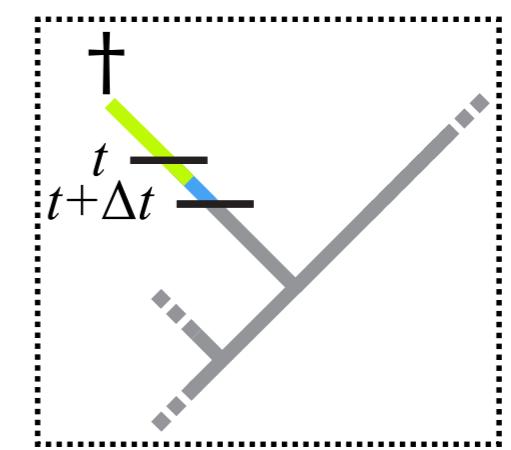
i. no rate shift,  
no speciation,  
extinction



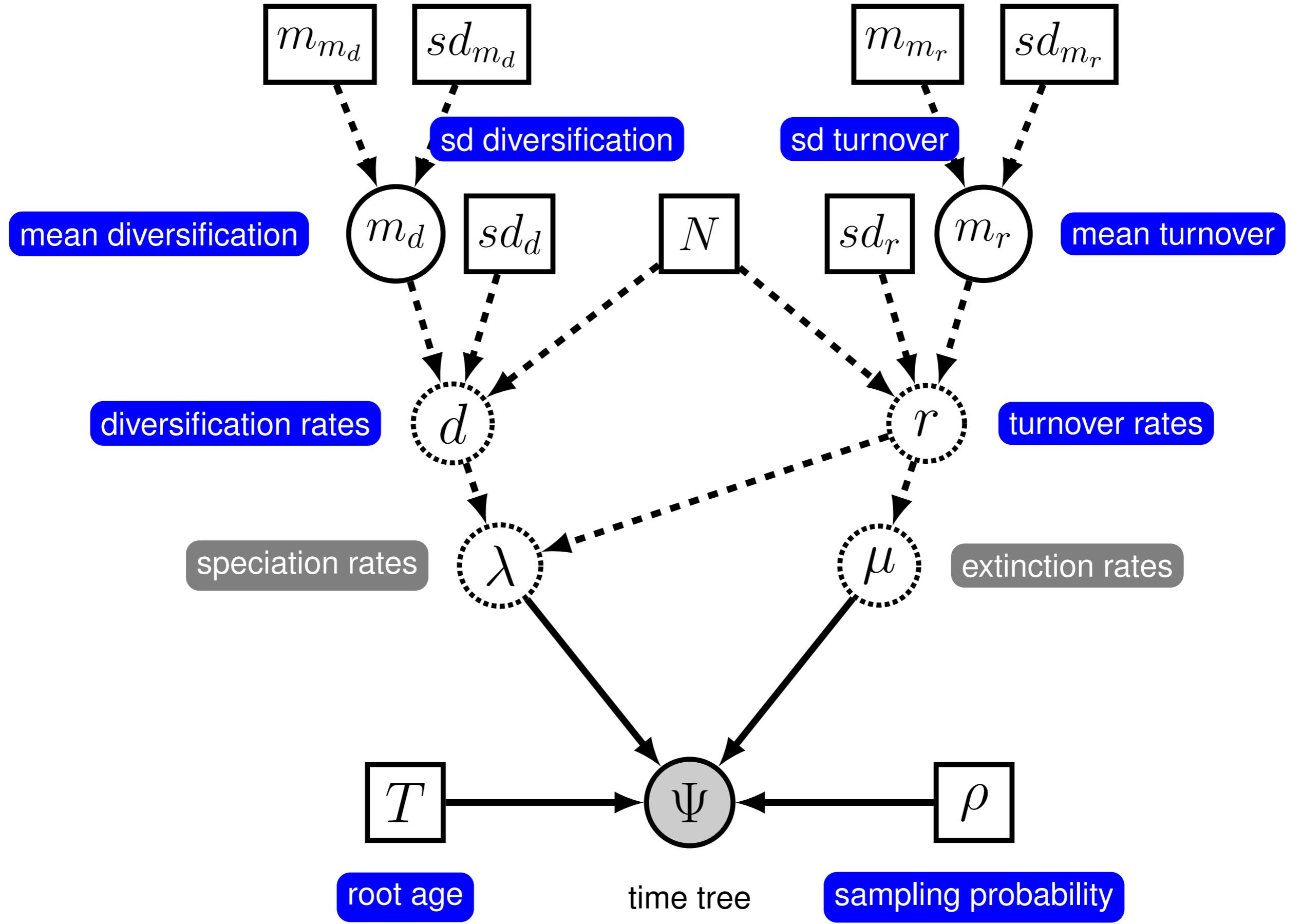
ii. no rate shift,  
no speciation,  
subsequent extinction



iii. no rate shift,  
speciation,  
subsequent extinctions



iv. rate shift,  
no speciation,  
subsequent extinction



# Outline

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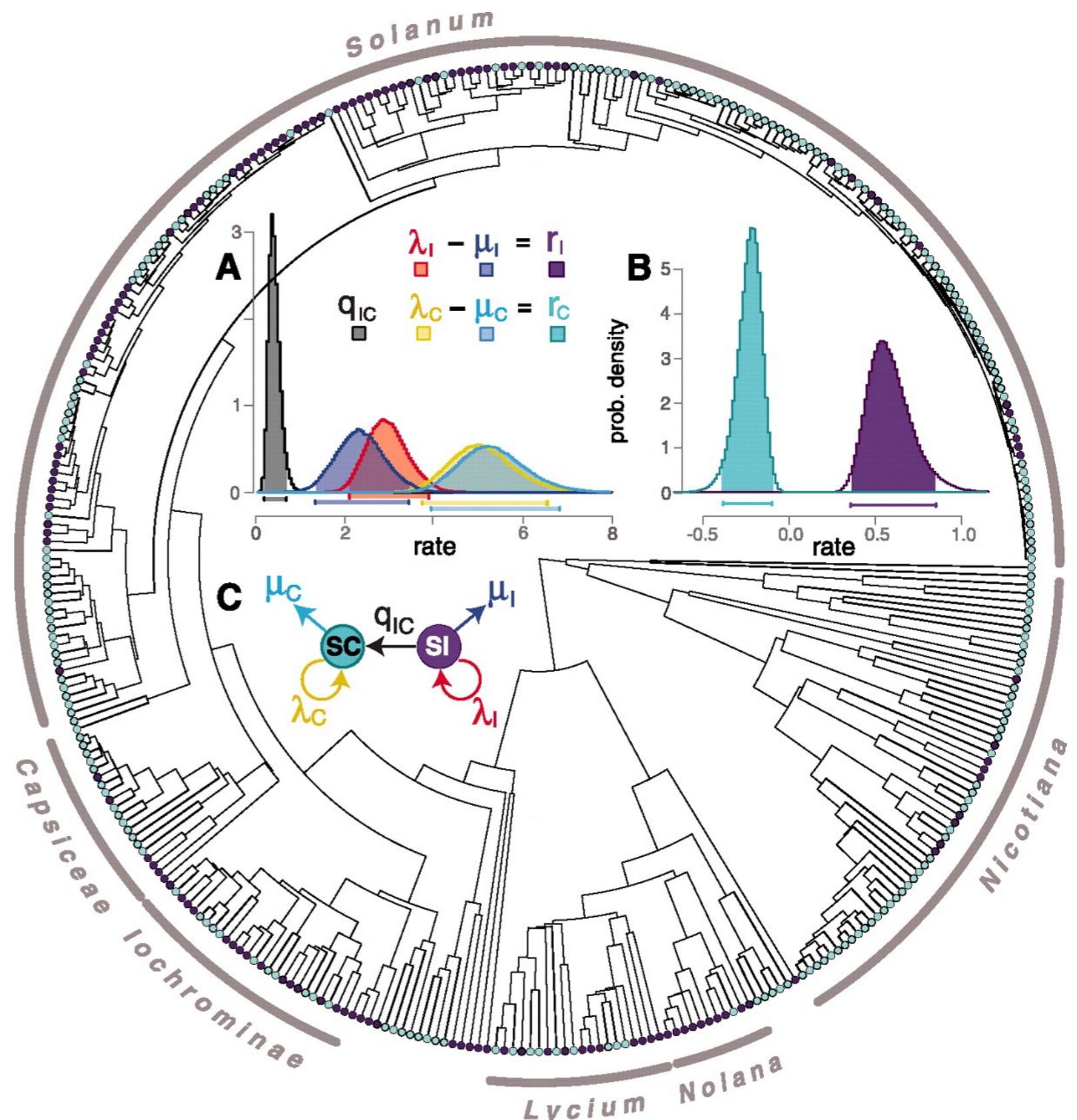
1. Constant diversification rates.
2. Diversification rates through time
3. Branch-specific diversification rates
4. Character-dependent diversification rates

# Character-Dependent Diversification

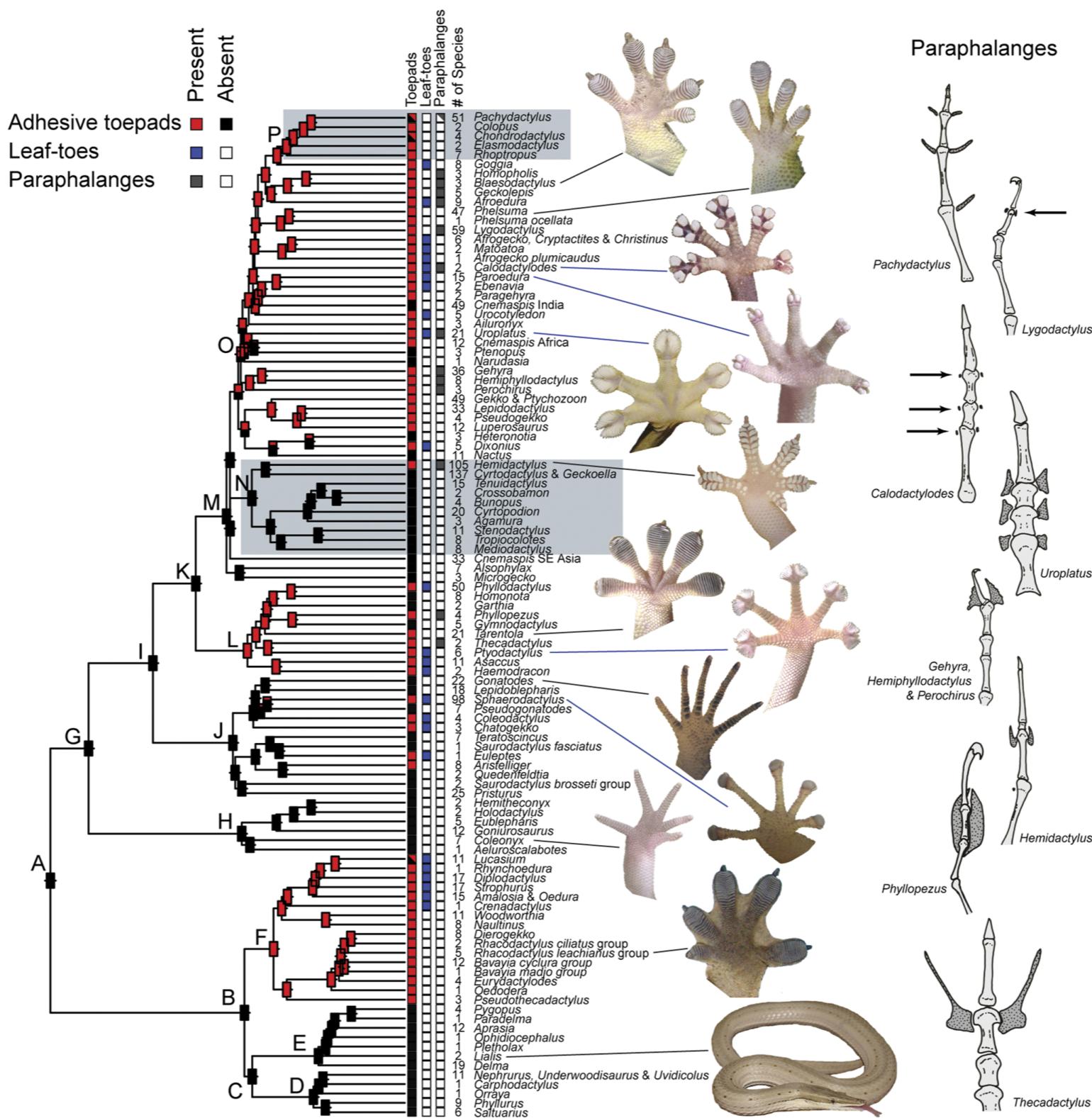
Speciation/extinction rates are dependent on character state.

Character states are only observed at tips.

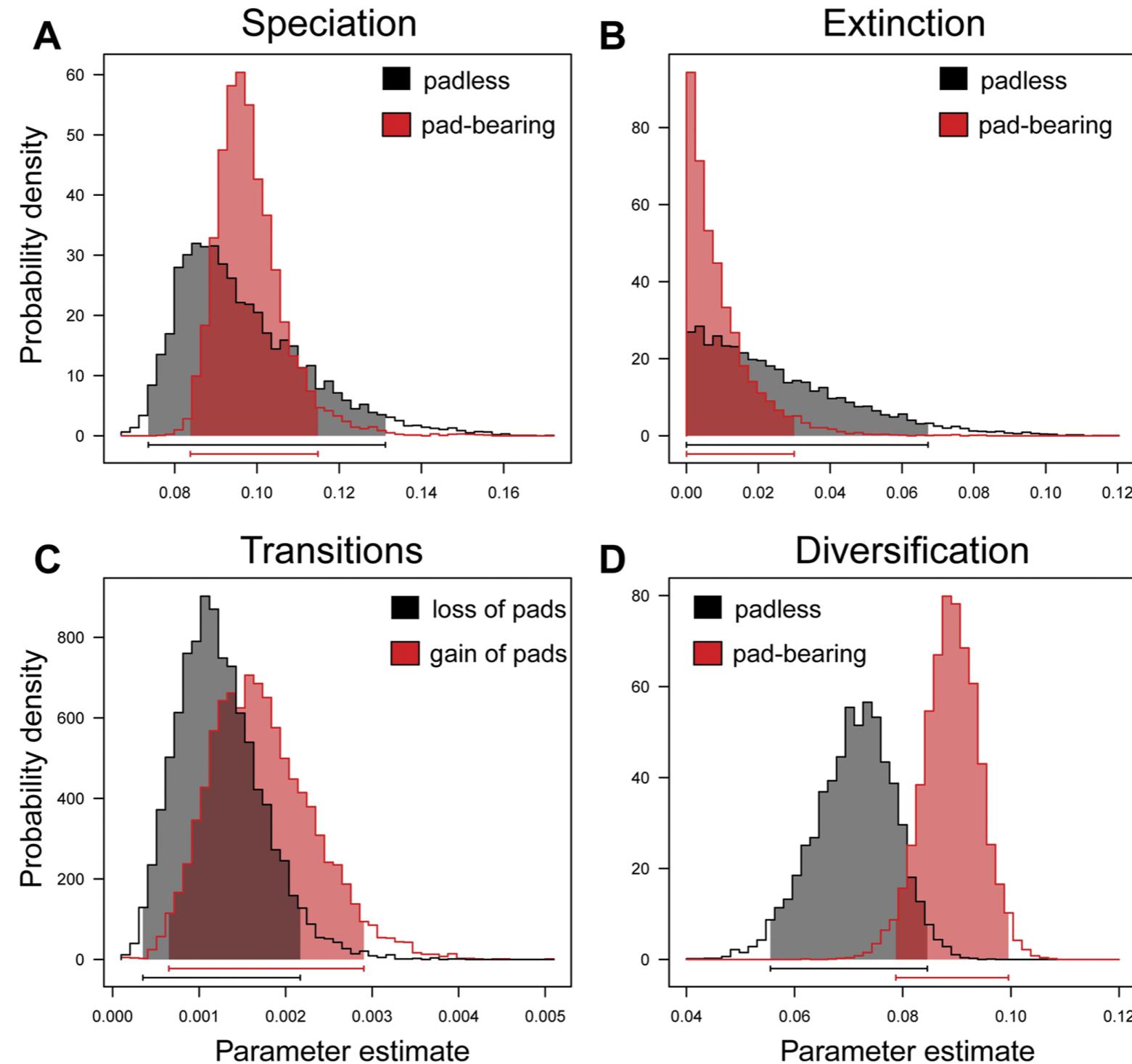
Joint model of diversification and character evolution.



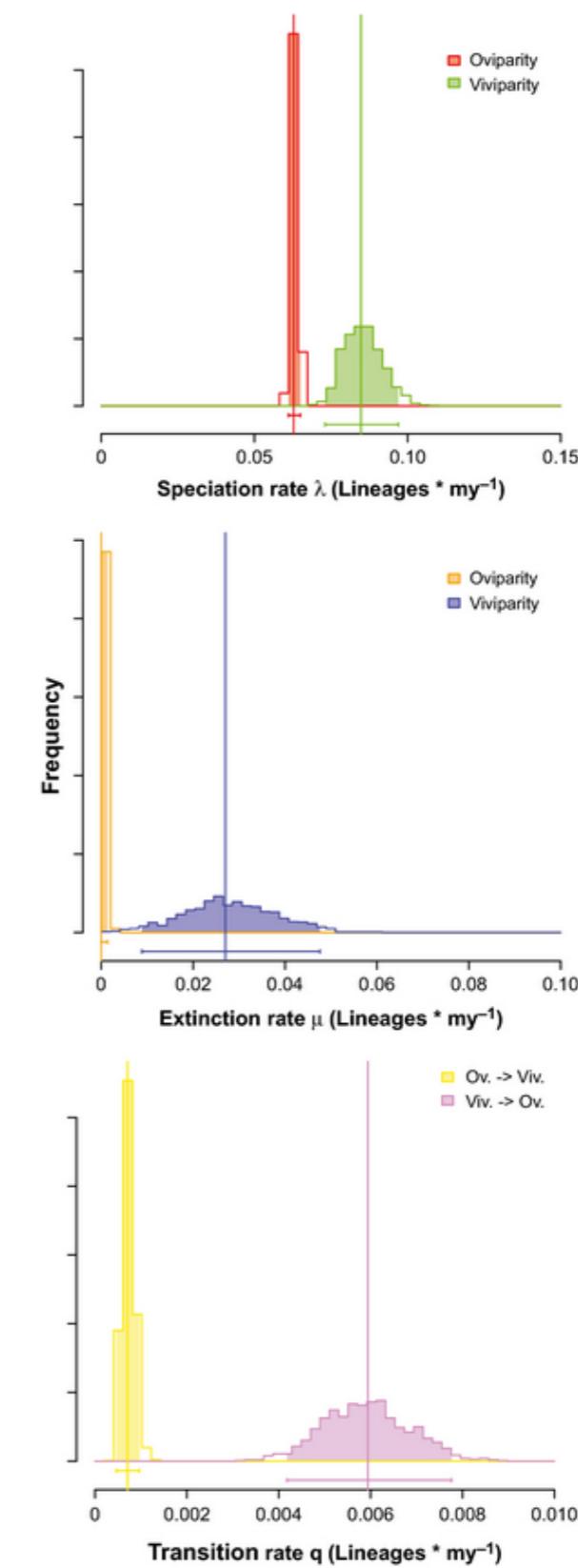
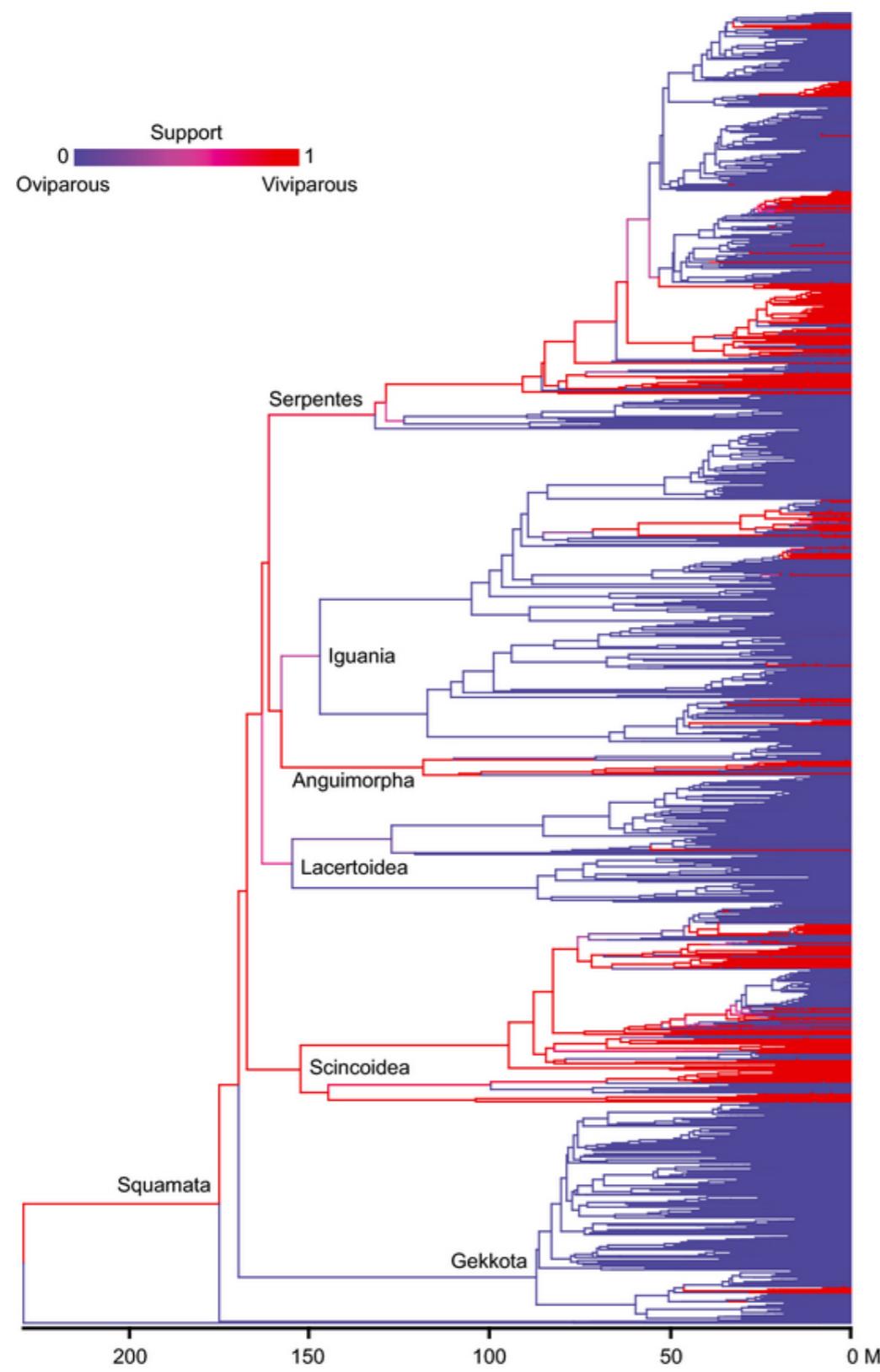
# Character-dependent diversification rates in geckos by Gamble et al. (2012)



# Character-dependent diversification rates in geckos by Gamble et al. (2012)

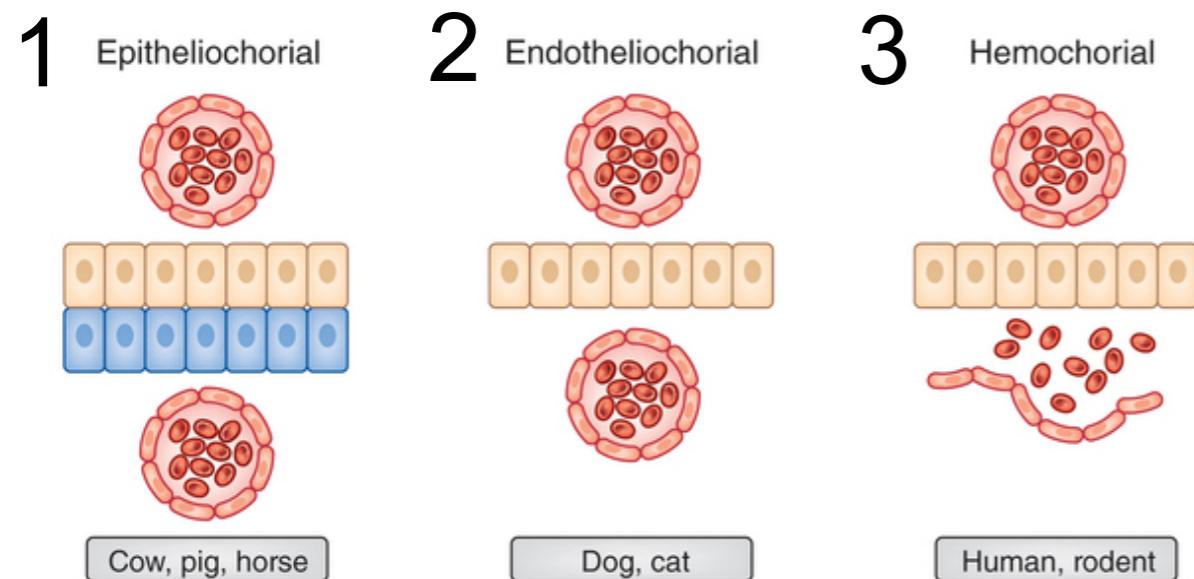


# Character-dependent diversification rates in squamates by Pyron & Burbrink (2013)

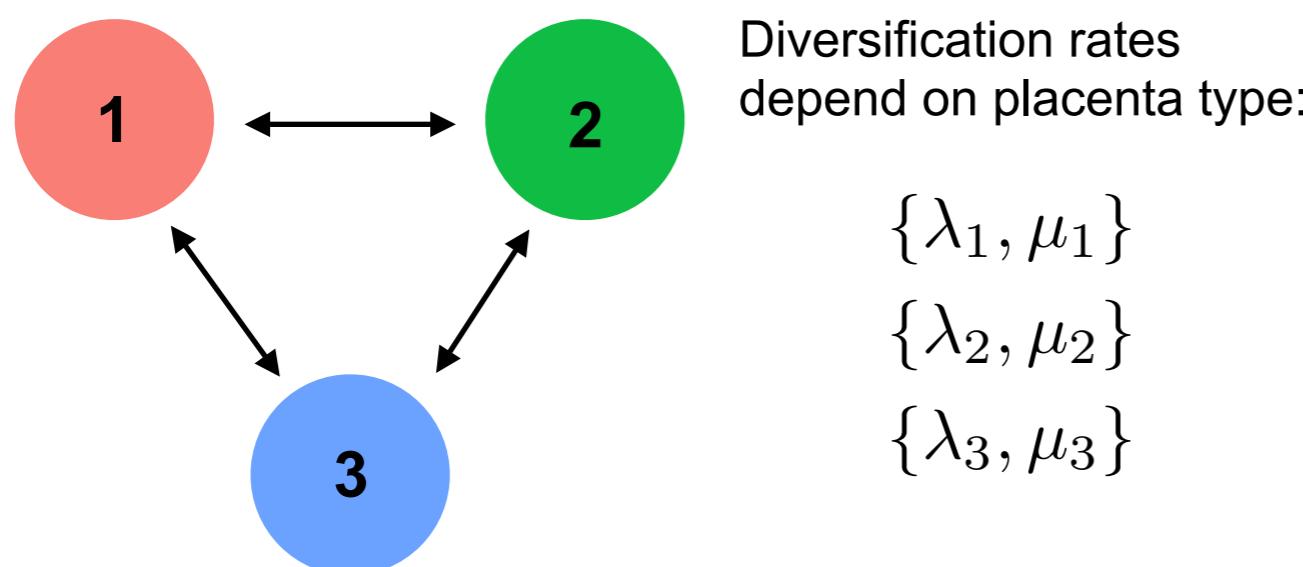


# Hypothesis: Invasiveness of placenta is correlated with speciation rate

## Placenta Types:

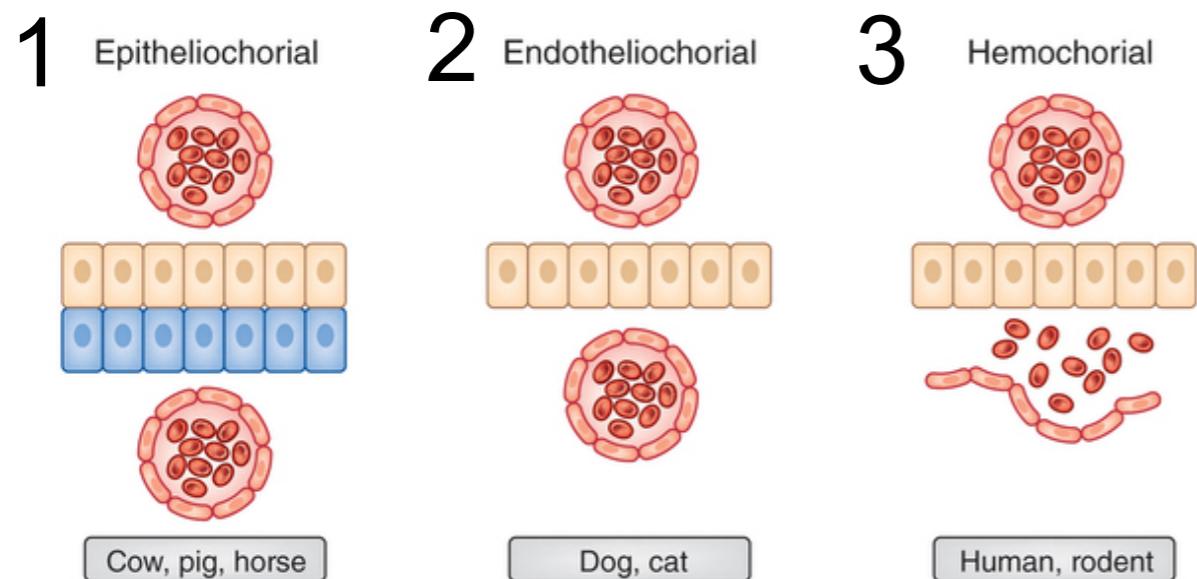


## Model:

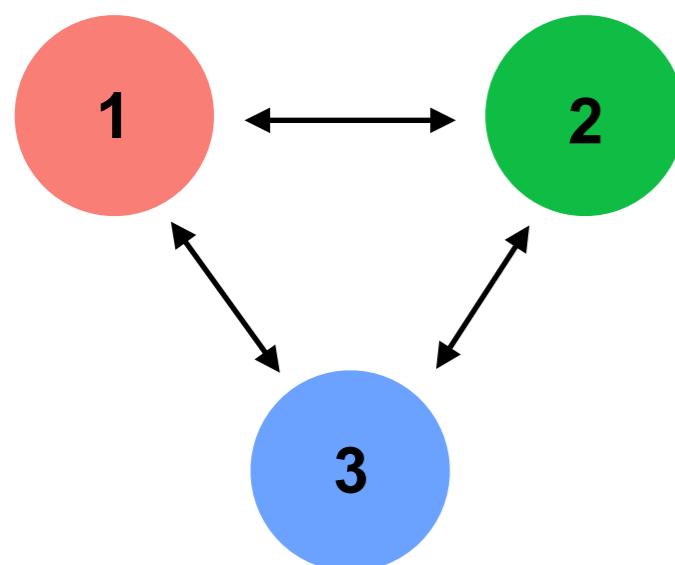


# Hypothesis: Invasiveness of placenta is correlated with speciation rate

## Placenta Types:



## Model:

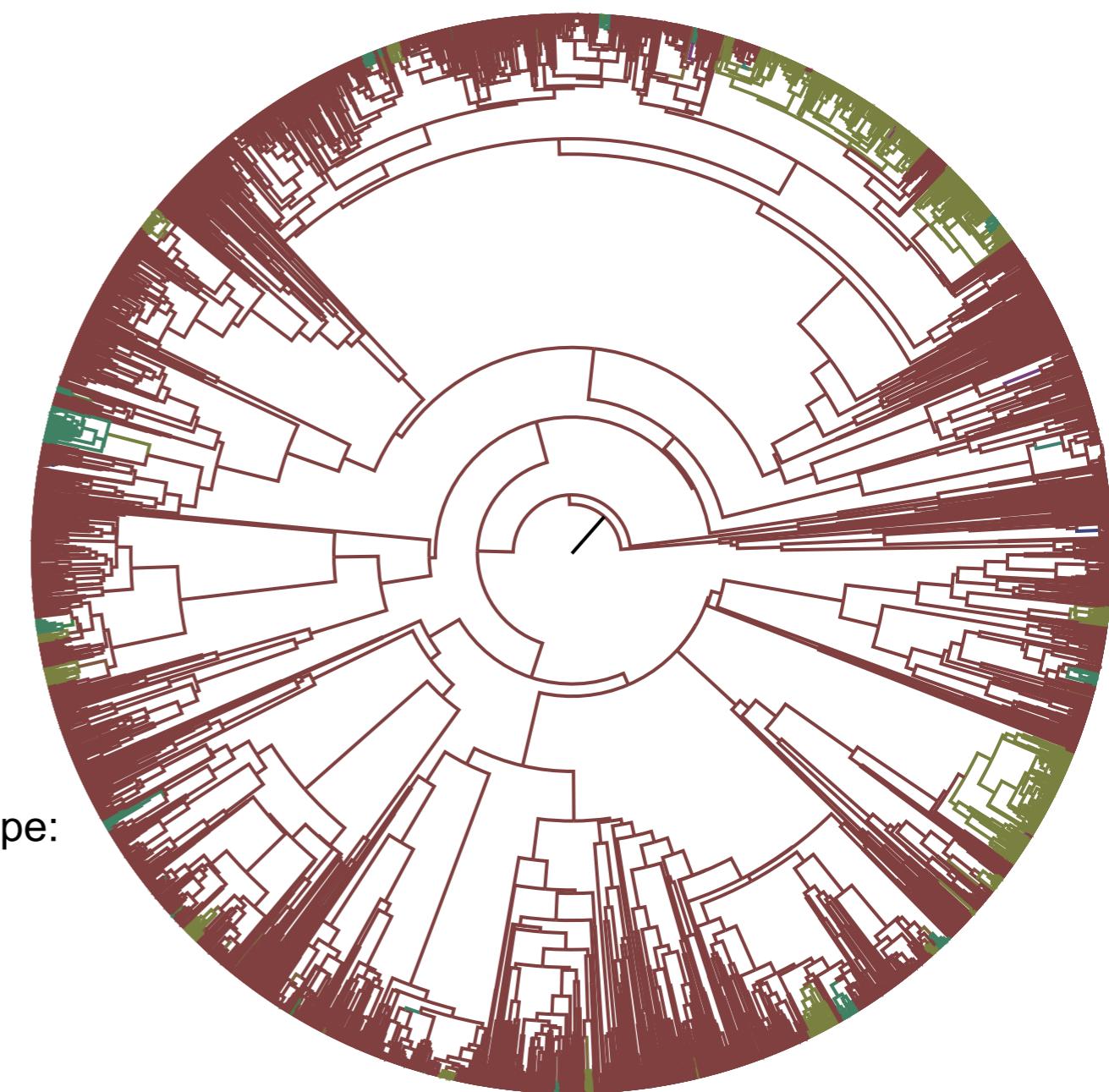


Diversification rates  
depend on placenta type:

$$\{\lambda_1, \mu_1\}$$

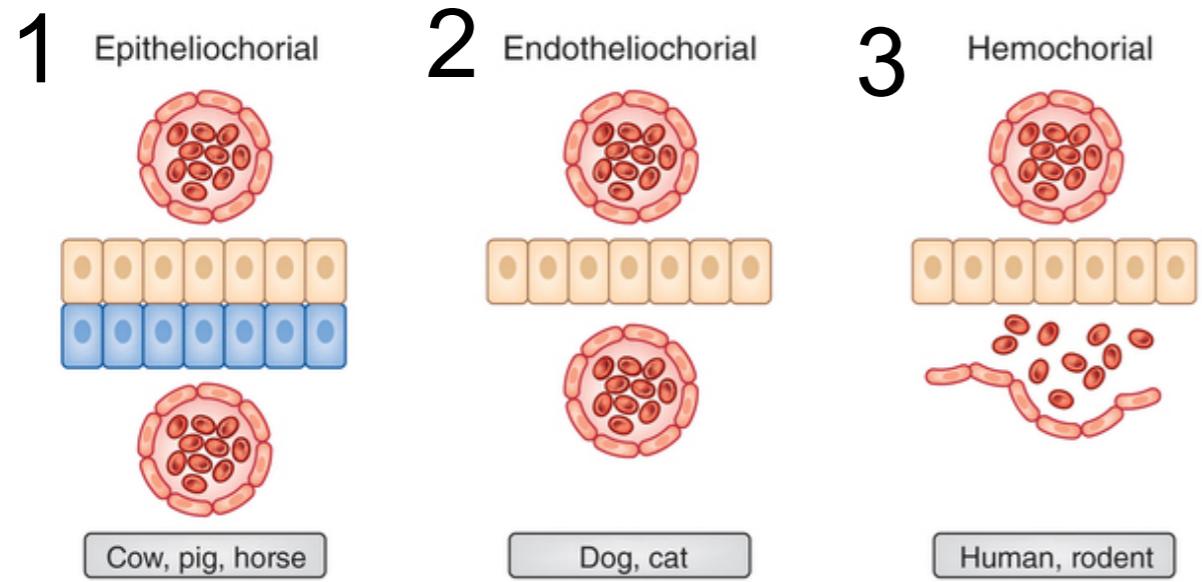
$$\{\lambda_2, \mu_2\}$$

$$\{\lambda_3, \mu_3\}$$

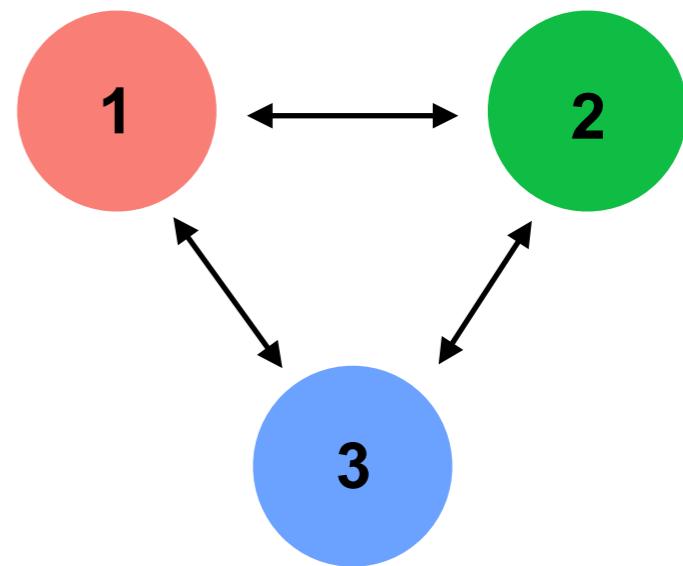


# Ancestral State Estimation

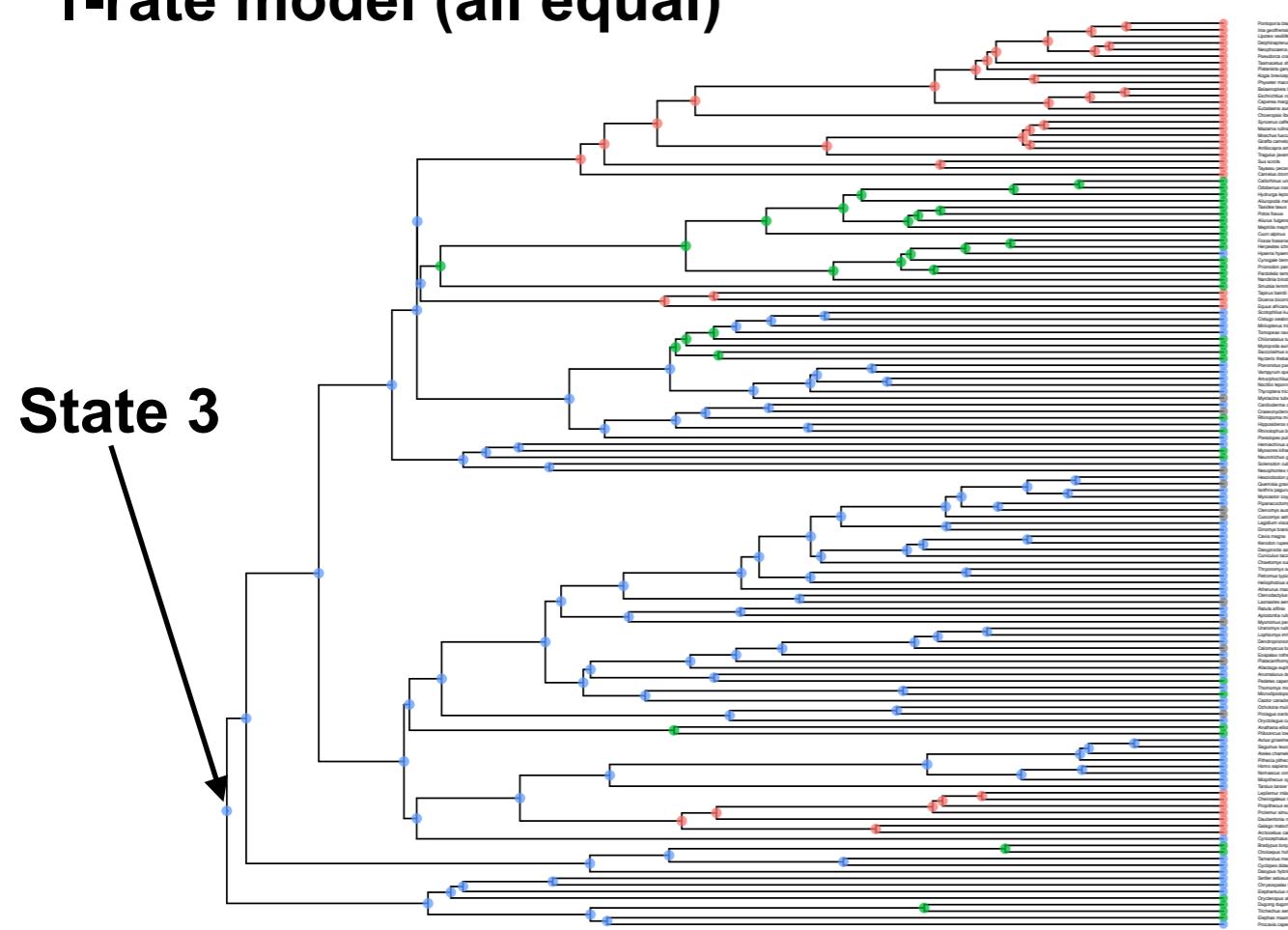
## Placenta Types:



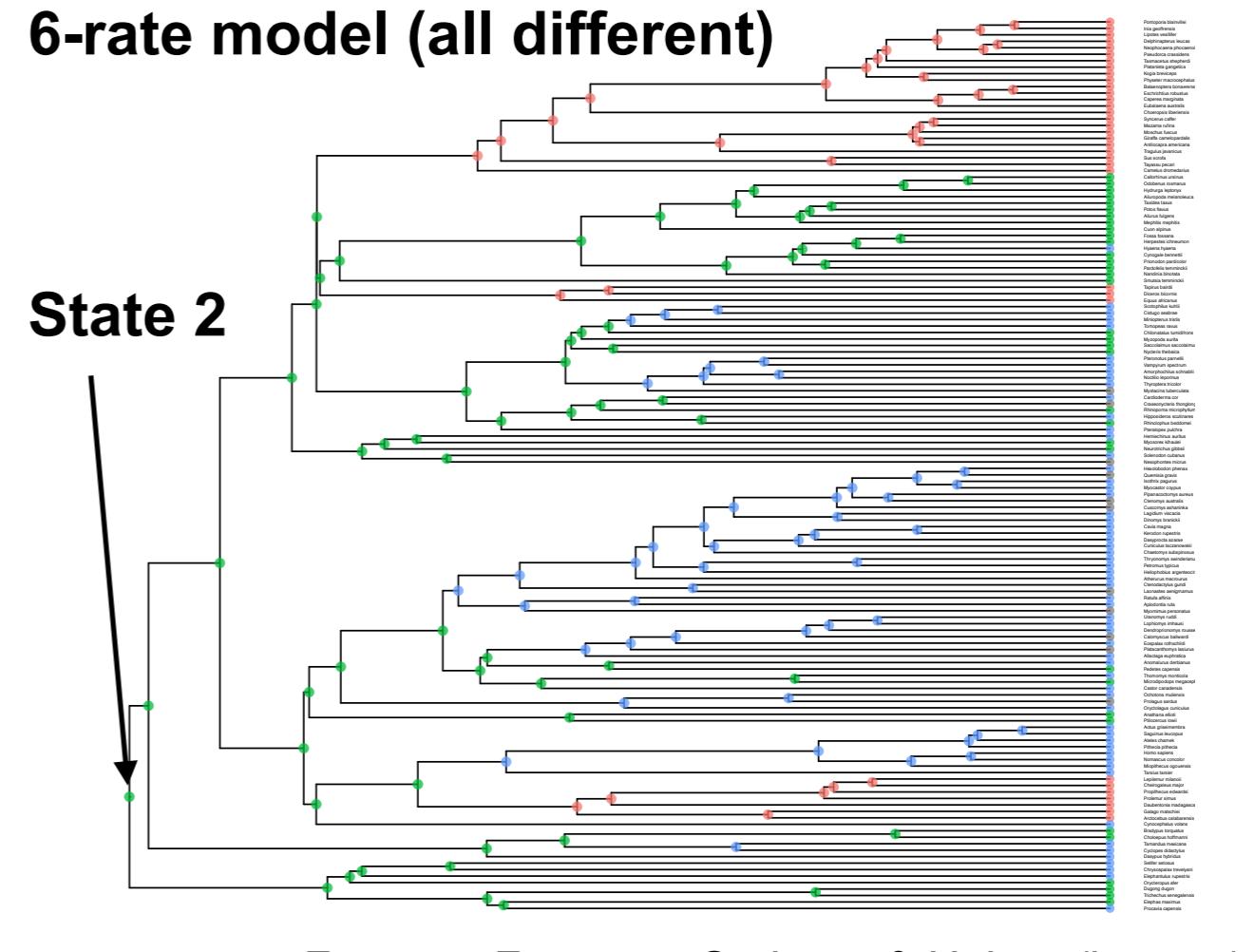
## Model:



## 1-rate model (all equal)

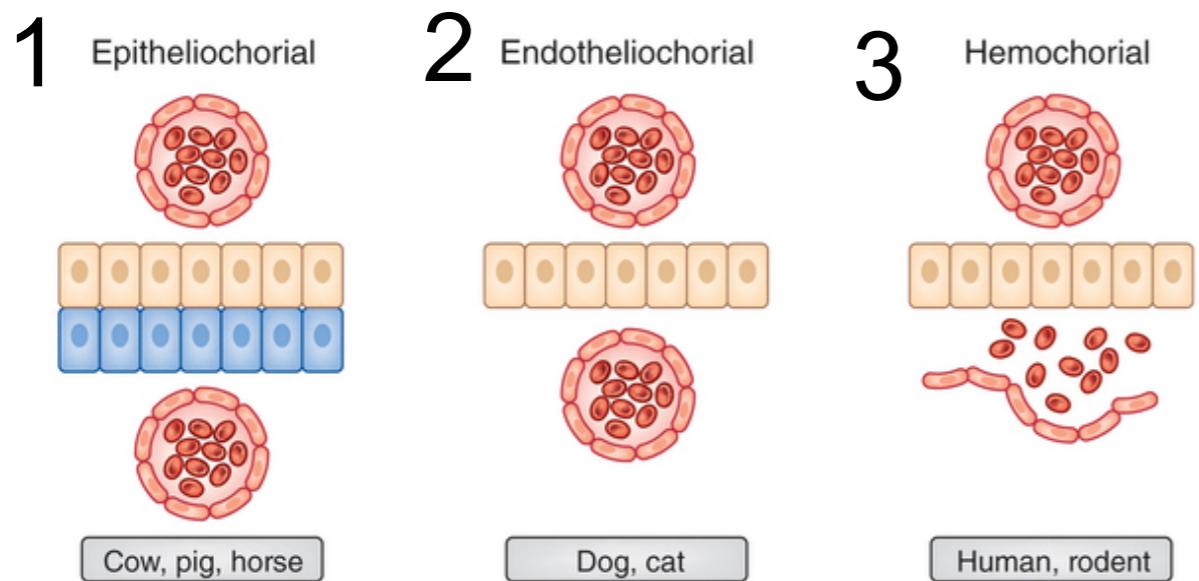


## 6-rate model (all different)

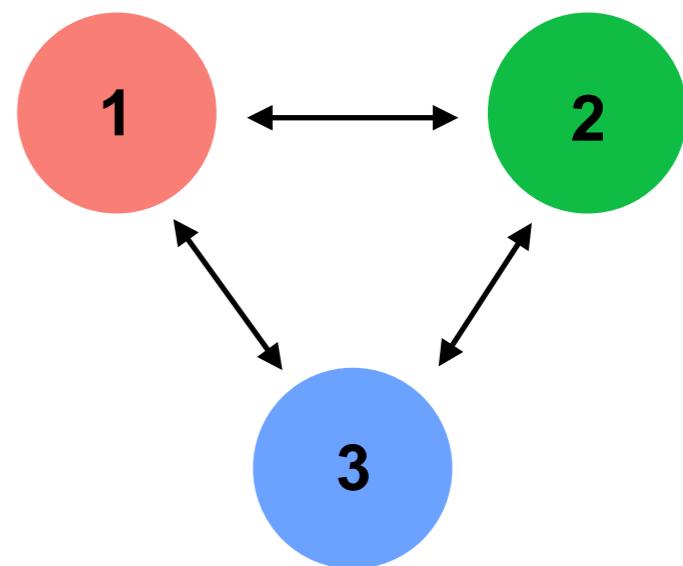


# Diversification Rate Estimation

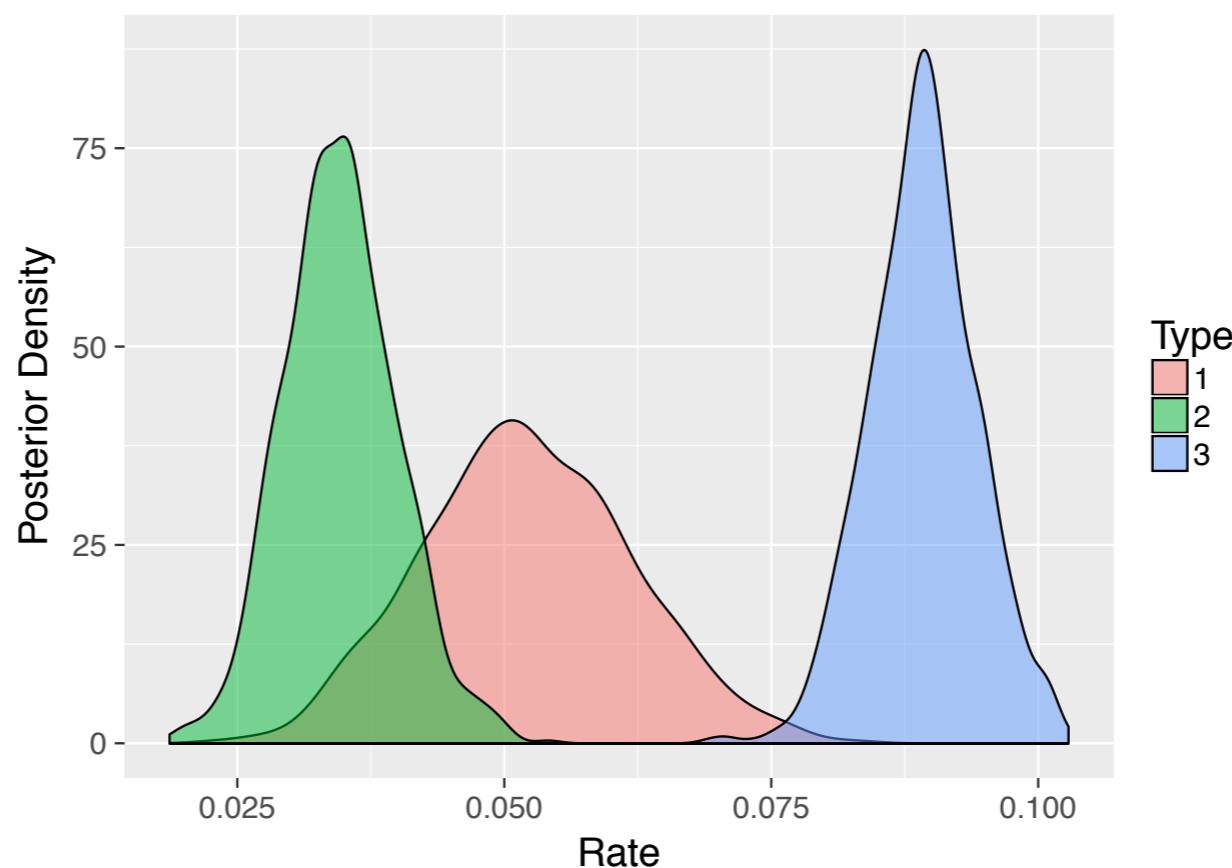
## Placenta Types:



## Model:

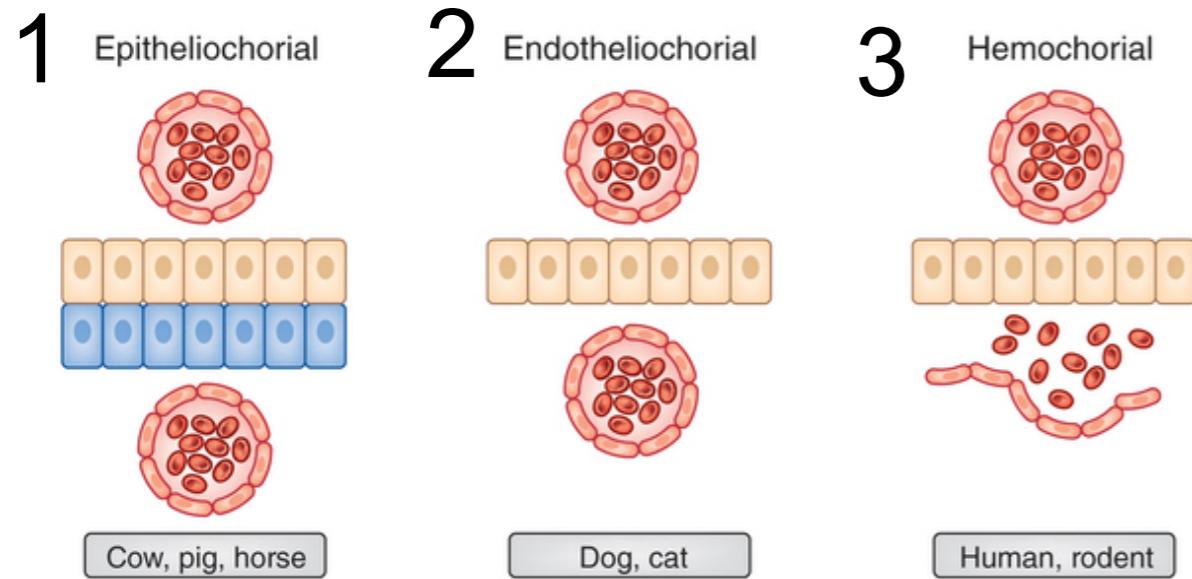


## Net-Diversification

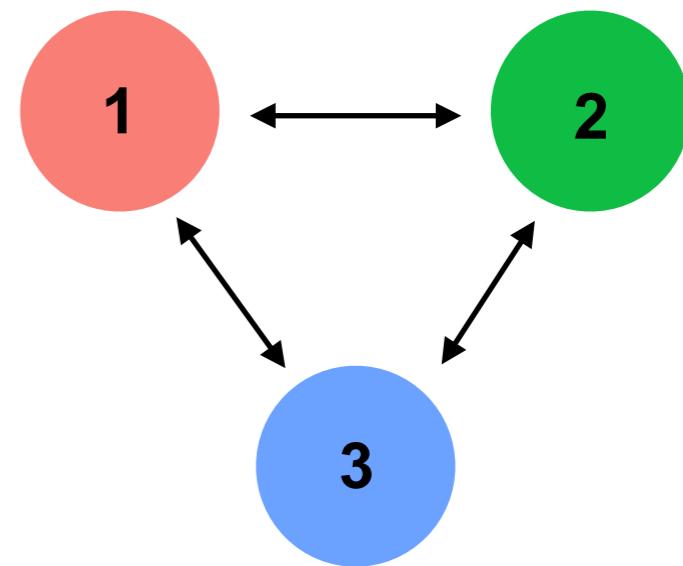


# Diversification Rate Estimation

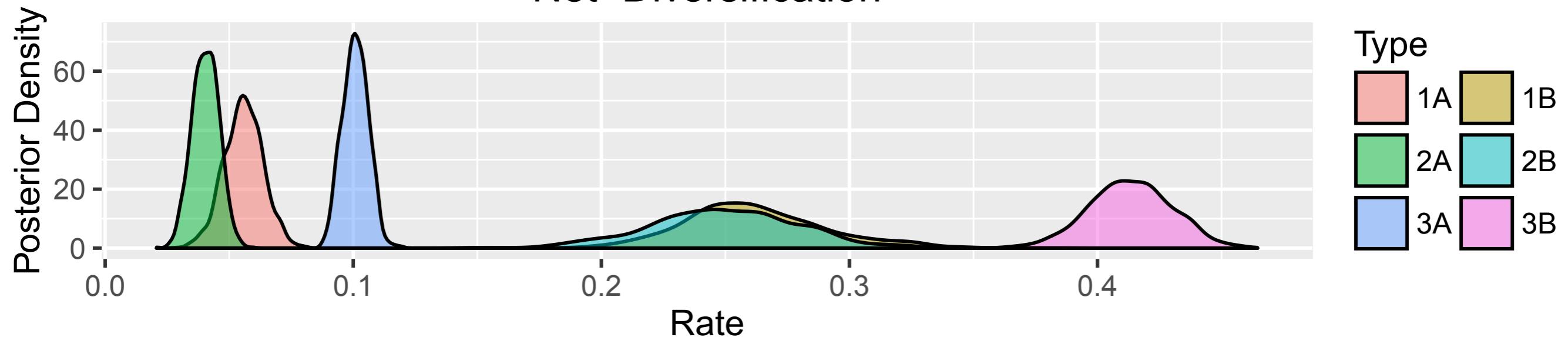
## Placenta Types:



## Model:



## Net-Diversification



# Summary: Topics of interest

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1. Constant diversification rates
2. Diversification rates through time
3. Character-dependent diversification rates
4. Branch-specific diversification rates