

# Outline

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- Pure-birth model: lineage through time plots,  $\gamma$  statistic and lineage diversification index
- Constant birth-death model: estimating speciation and extinction rates from molecular phylogenies
- Complex models: clade-dependent, time-dependent (incl. diversity-dependent) & trait-dependent models

# Models of lineage diversification

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- Yule or pure birth (pb)
- Constant birth-death (bd)
- Clade dependent
- Time dependent (more complex, non-constant)

# Methods for detecting shifts in diversification rate across clades

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- MEDUSA (Alfaro et al., 2009)



Modeling Evolutionary Diversification Using Stepwise AIC

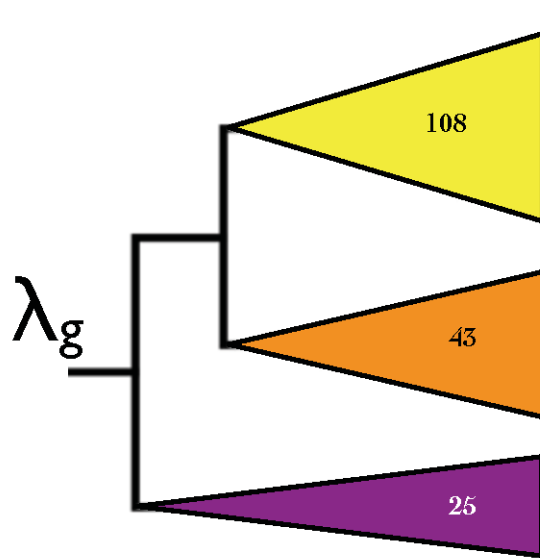
# MEDUSA: rate shifts across clades

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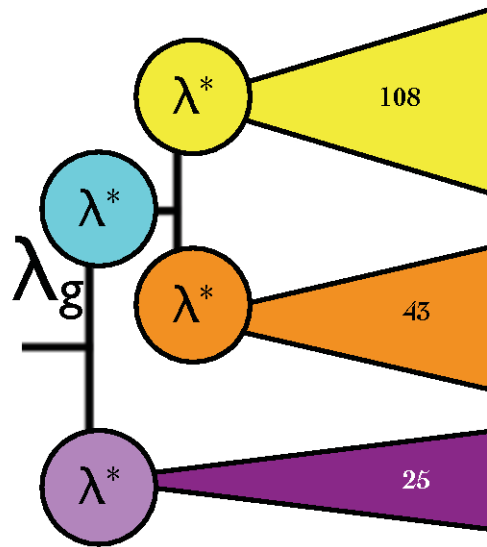
- Explaining the uneven distribution of species richness across clades is a longstanding challenge in evolutionary biology
- MEDUSA: a likelihood, stepwise approach based upon the Akaike information criterion for detecting multiple shifts in diversification rates
- It can use incompletely resolved phylogenies

# MEDUSA: sequential AIC

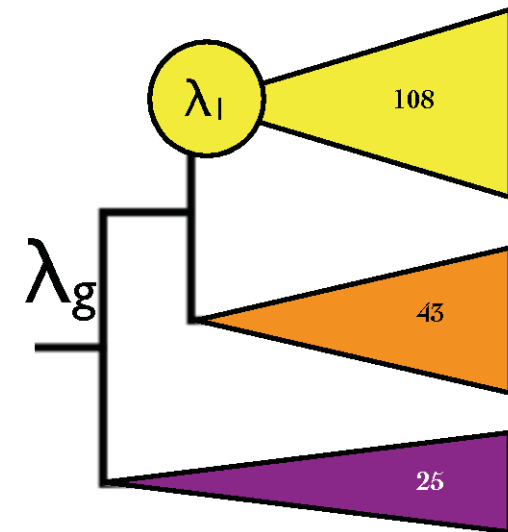
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1.  $\lambda$  for whole tree



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

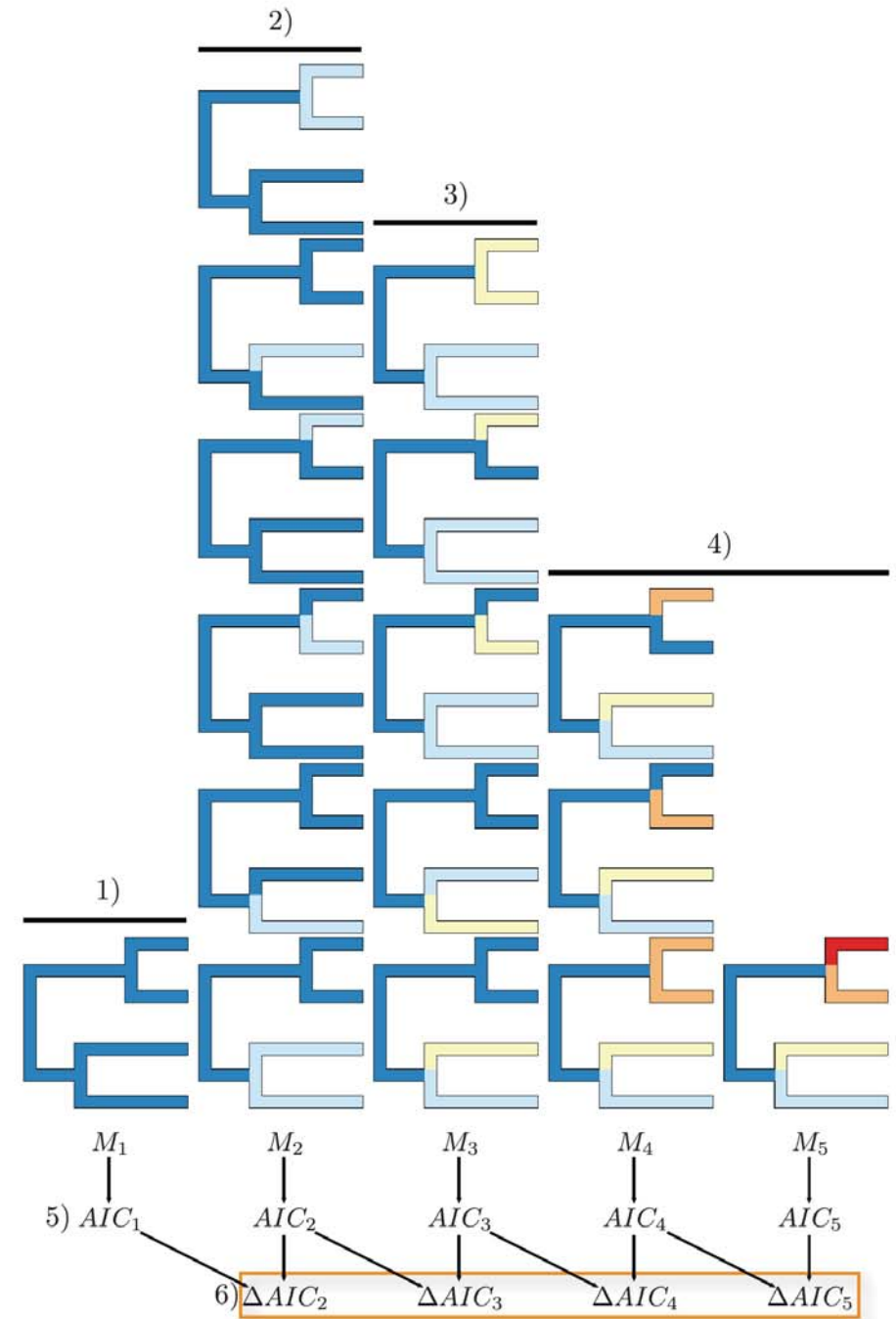


3. if  $\Delta AIC$  of best new  $\lambda$  and  $\lambda_g > 4$ ,  
retain rate & repeat

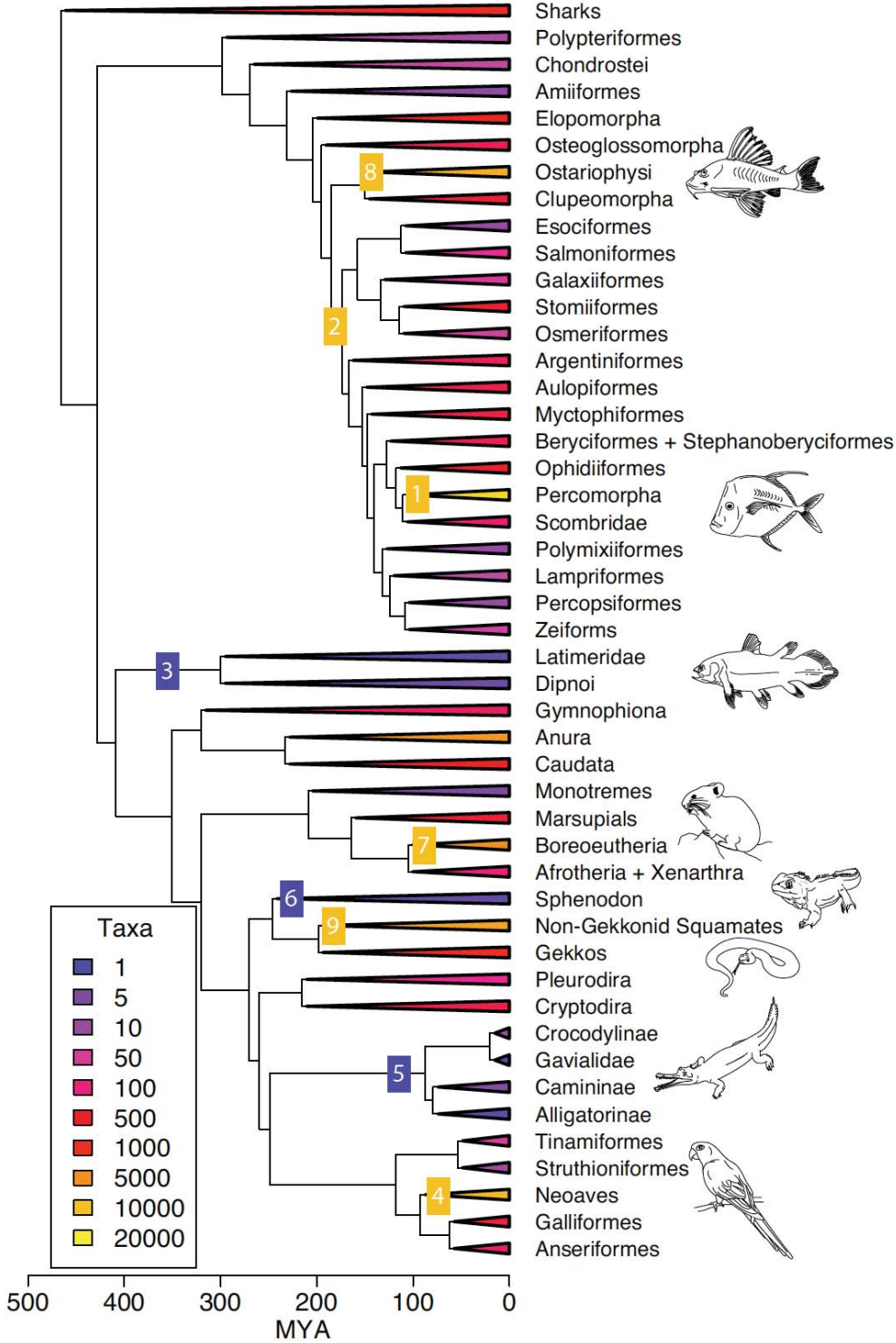
# MEDUSA: Sequential AIC Model Fitting

## Algorithm

- 1) Fit a one-rate model to the data.
- 2) Fit “every” two-rate model to the data.
- 3) Fit “every” three-rate model that contains the best two-rate model.
- 4) Keep fitting increasingly complex models.
- 5) Compute the AIC score for the best model in each level of model complexity.
- 6) Starting with the one-rate model, accept the next-most-complex model if the improvement in model fit is “good enough.”



# MEDUSA: rate shifts across vertebrate clades



■ Slow-downs  
■ Speed-ups

# MEDUSA: caveats

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- Type I (false discovery) error rate as identified by simulations
- Can provide biased parameter estimates
- Assumes rates rate constancy through time



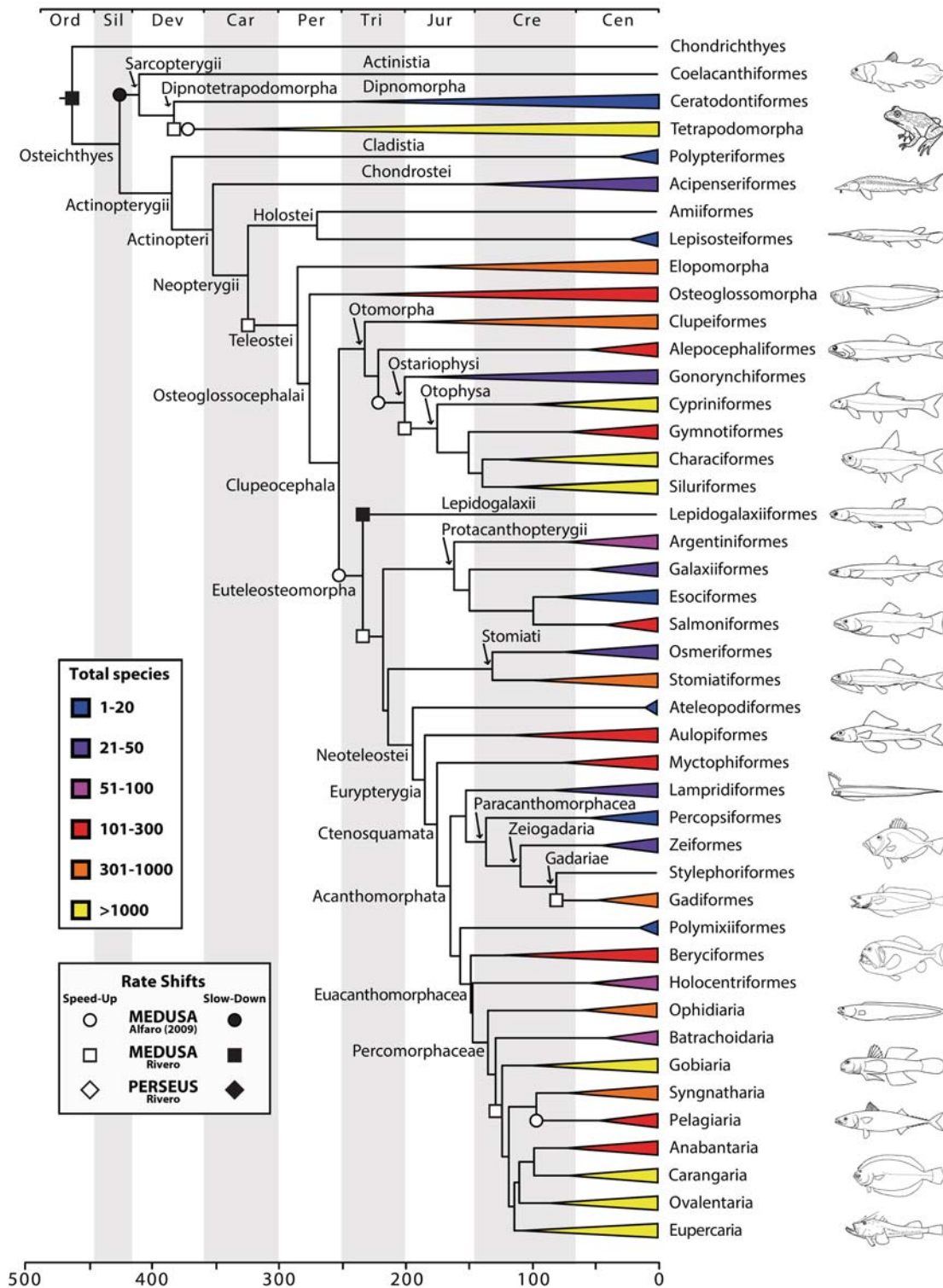
# PERSEUS

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*May & Moore (in prep)*

# PERSEUS vs MEDUSA in fishes

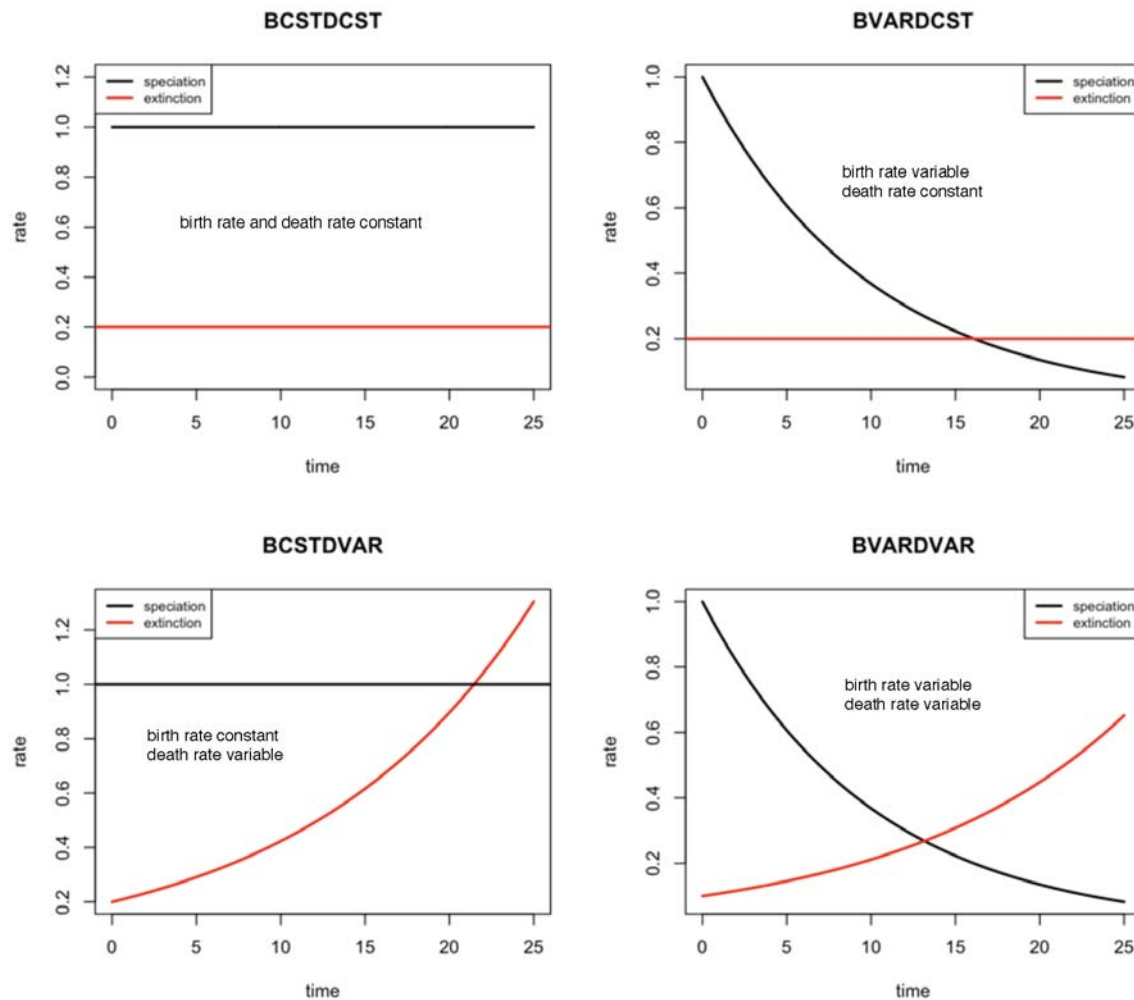


# Models of lineage diversification

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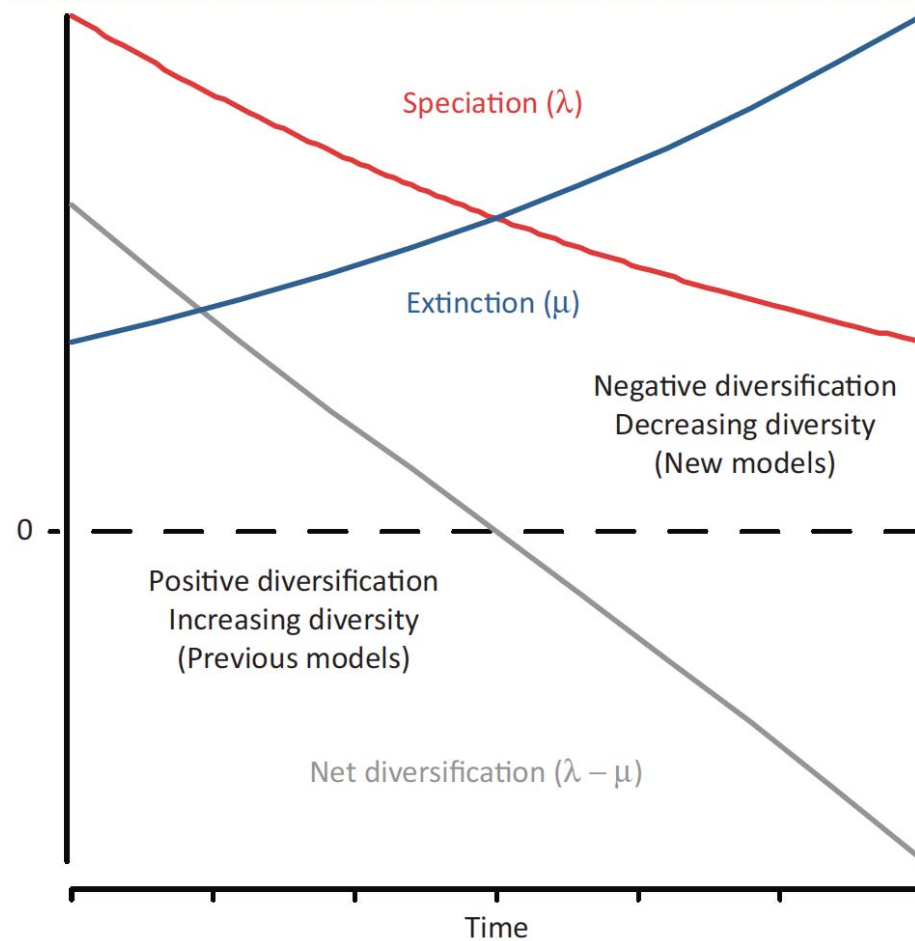
- Yule or pure birth (pb)
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- Clade dependent
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# Complex scenarios that relax the assumption of rate constancy through time



# Time-dependent rates of diversification

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# Time-dependent rates of diversification

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- Model time-dependent rates of diversification; i.e., account for periods of both expansion and contraction in diversity
- Relax the assumption of rate constancy
- Many reasons why the null assumption of (diversification) rate constancy through time may be violated:

# Time-dependent rates of diversification

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- Model time-dependent rates of diversification; i.e., account for periods of both expansion and contraction in diversity
- Relax the assumption of rate constancy
- Many reasons why the null assumption of (diversification) rate constancy through time may be violated:
  - Diversity dependence
  - Mass extinction (promote high rates of diversification)
  - Changing environmental conditions

# Diversity-dependent diversification

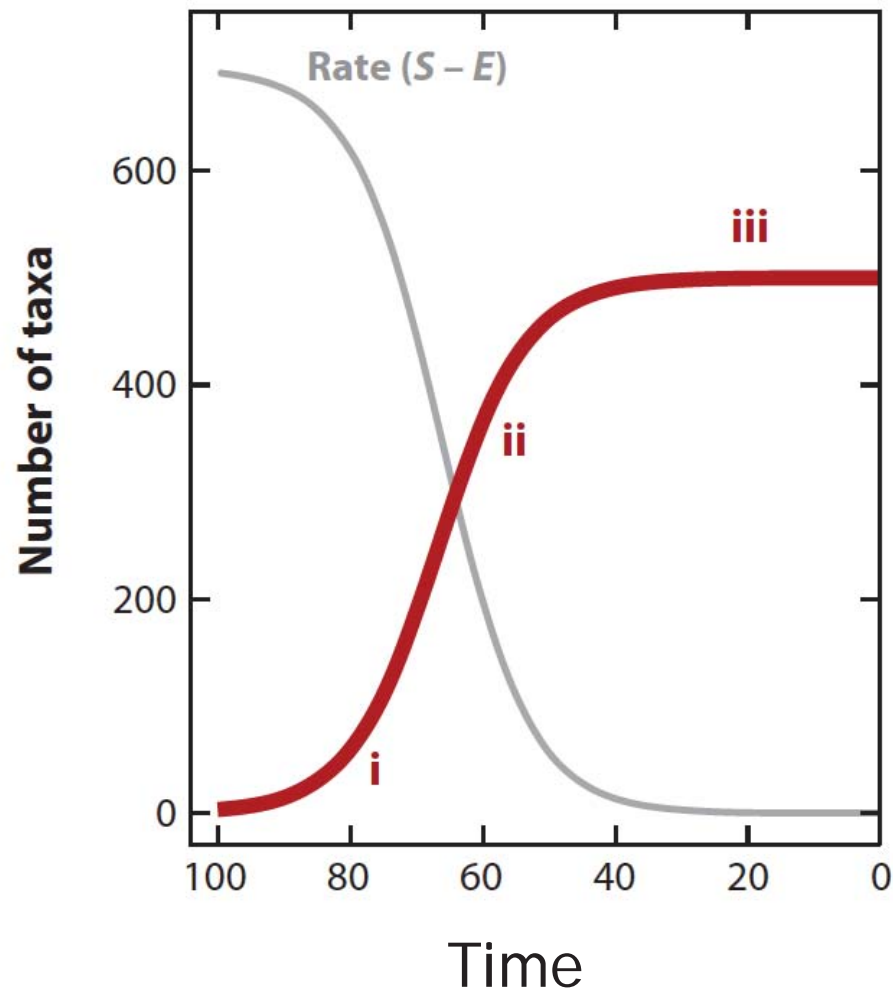
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- Also known as density-dependent diversification
- A subclass of time-dependent models
- Diversity-dependence is a process and a pattern of evolutionary diversity regulation through time
- It also reflects a process by which interspecific competition influences the dynamics of speciation and extinction

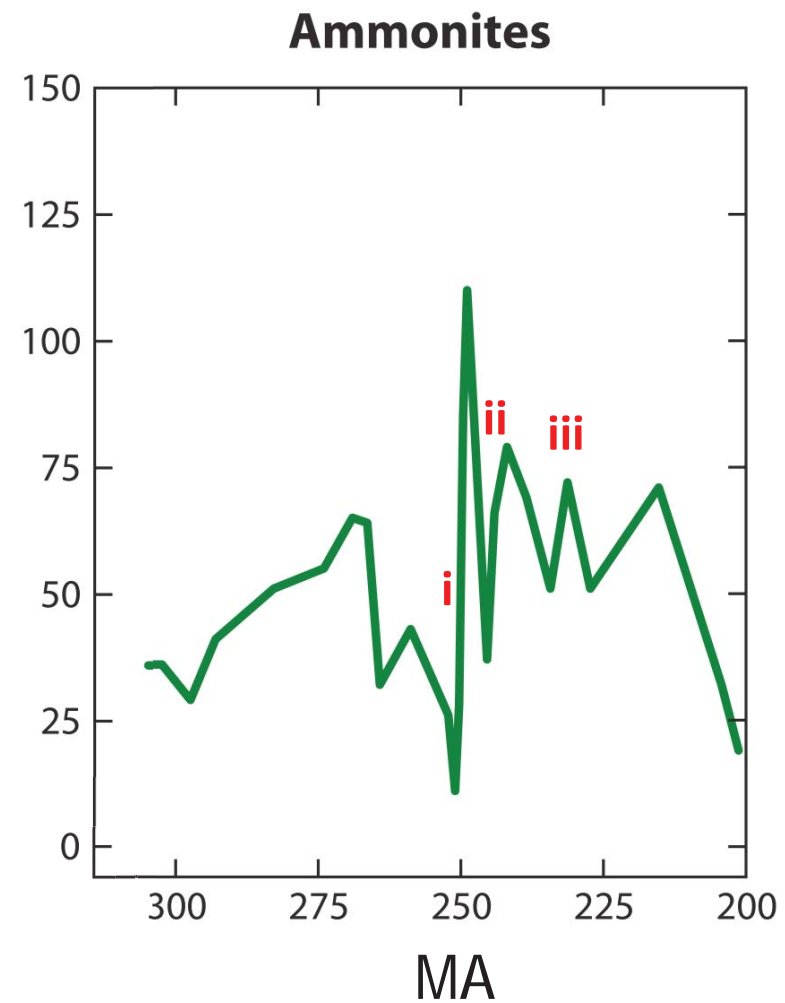
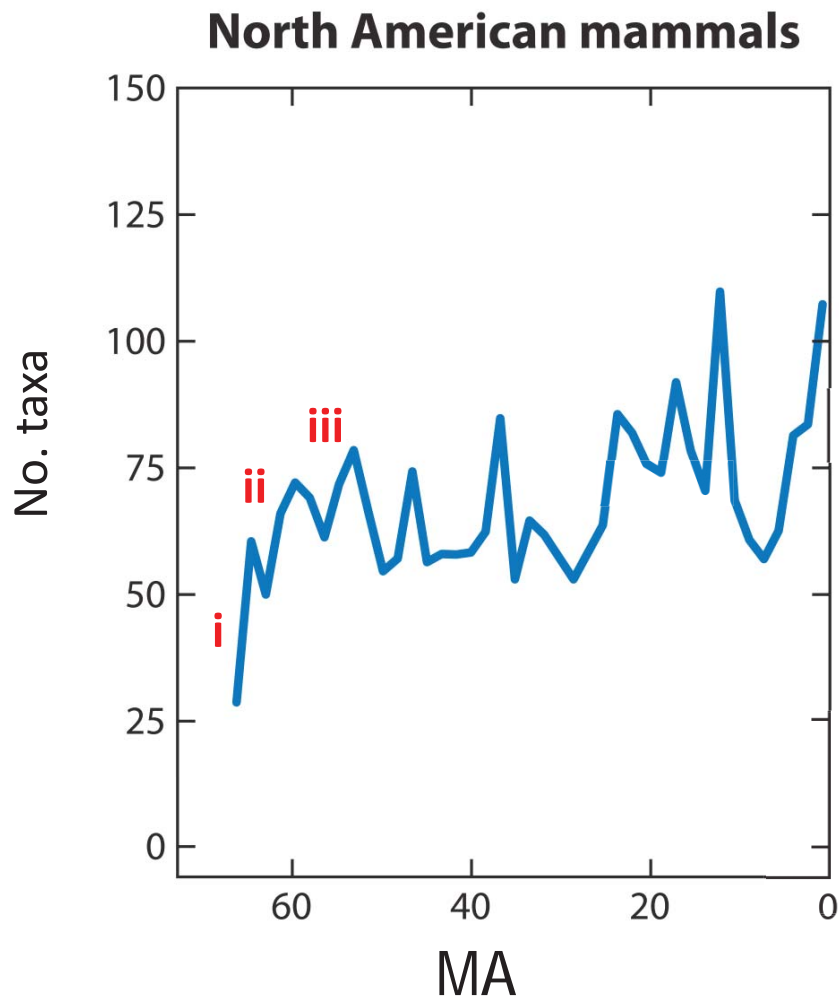


# Diversity-dependent diversification

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# Diversity-dependent diversification

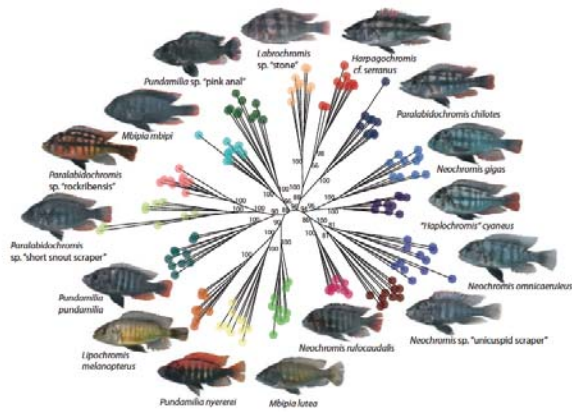


# Diversity-dependent diversification & adaptive radiation

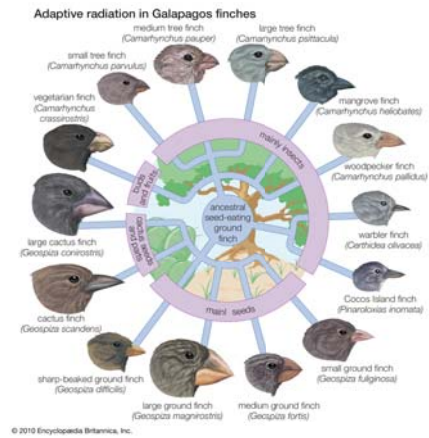
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- Adaptive radiations often occur when a lineage becomes decoupled from the normal diversity-dependent controls that regulate rates
- This release can occur in response to extrinsic ecological opportunity (colonization of novel habitats), extinction of competitors, or the evolution of intrinsic traits (key innovations).

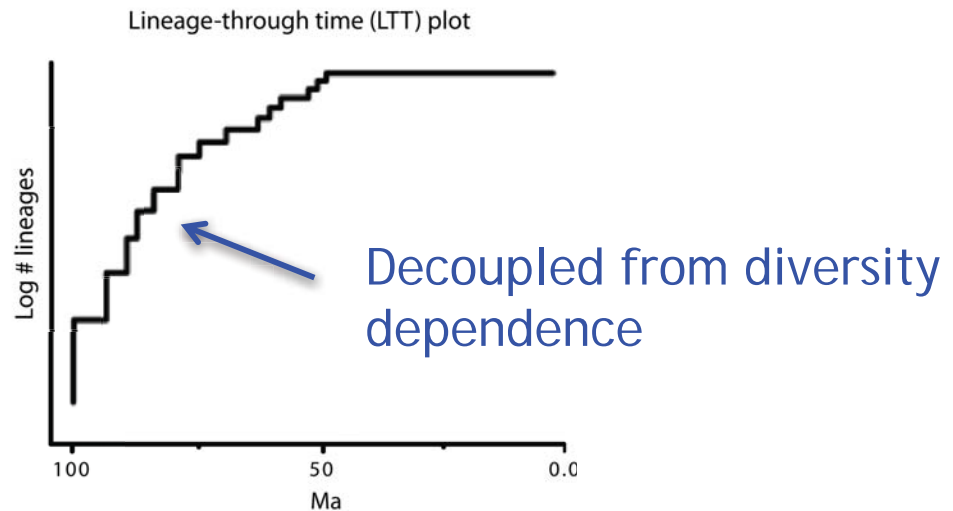
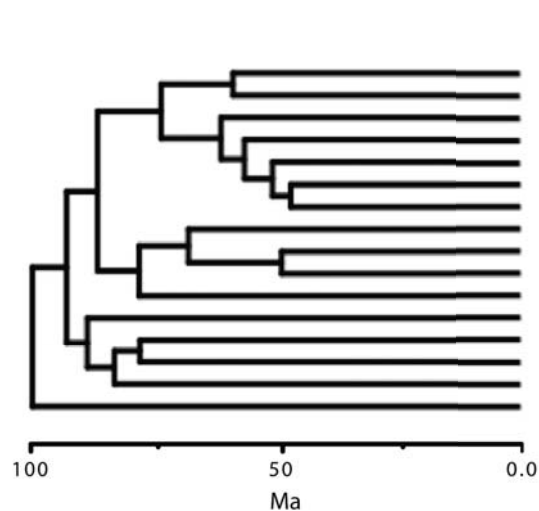
# Diversity-dependent diversification & adaptive radiation



African cichlids



Galapagos Finches



# Other methods for detecting shifts in diversification rate through time

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- TreePar: maximum likelihood estimation of temporal shifts in diversification rate (Stadler, 2011)
- TESS: Bayesian inference of temporal shifts in diversification rate (Höhna, 2014)

# Other methods for detecting shifts in diversification rate through time

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- Model time-dependent rates of diversification; i.e., account for periods of both expansion and contraction in diversity. Can use incompletely sampled trees.
  - TreePar: maximum likelihood estimation of temporal shifts in diversification rate (Stadler, 2011)
  - TESS: Bayesian inference of temporal shifts in diversification rate (Höhna, 2014)

# TreePar: ML estimates of temporal shifts

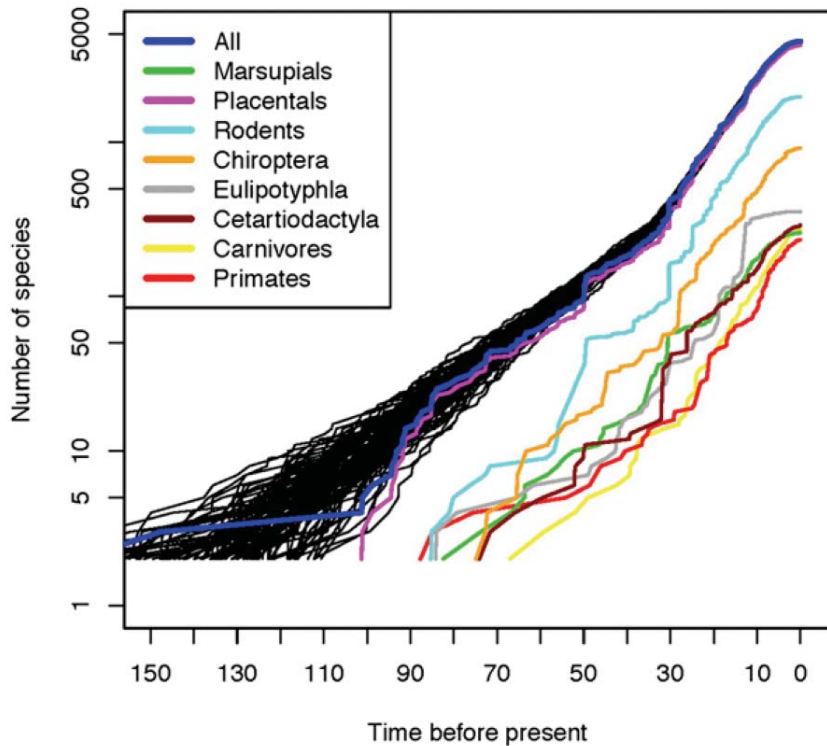
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- Time-dependent birth-death process
- Likelihood

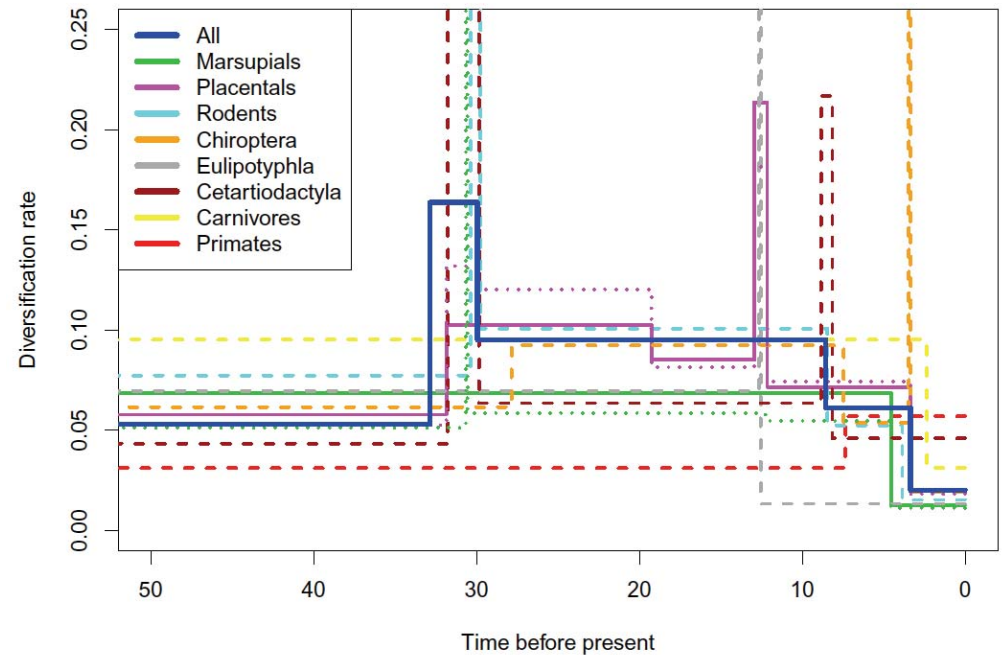
$$\begin{aligned} f[\mathcal{T} | t_{\text{mrca}} = x_1] &= f[\mathcal{T}_{\text{or}}^{\text{L}} | t_{\text{or}} = x_1, S] f[\mathcal{T}_{\text{or}}^{\text{L}} | t_{\text{or}} = x_1, S] \\ &= \frac{f[\mathcal{T}_{\text{or}}^{\text{L}}, S | t_{\text{or}} = x_1] f[\mathcal{T}_{\text{or}}^{\text{L}}, S | t_{\text{or}} = x_1]}{(f[S | t_{\text{or}} = x_1])^2} \\ &= \frac{f[\mathcal{T}_{\text{or}}^{\text{L}} | t_{\text{or}} = x_1] f[\mathcal{T}_{\text{or}}^{\text{L}} | t_{\text{or}} = x_1]}{(1 - \rho_0^{l(x_1)}(x_1))^2}. \end{aligned}$$

# TreePar: ML estimates of temporal shifts

Standard LTT plots



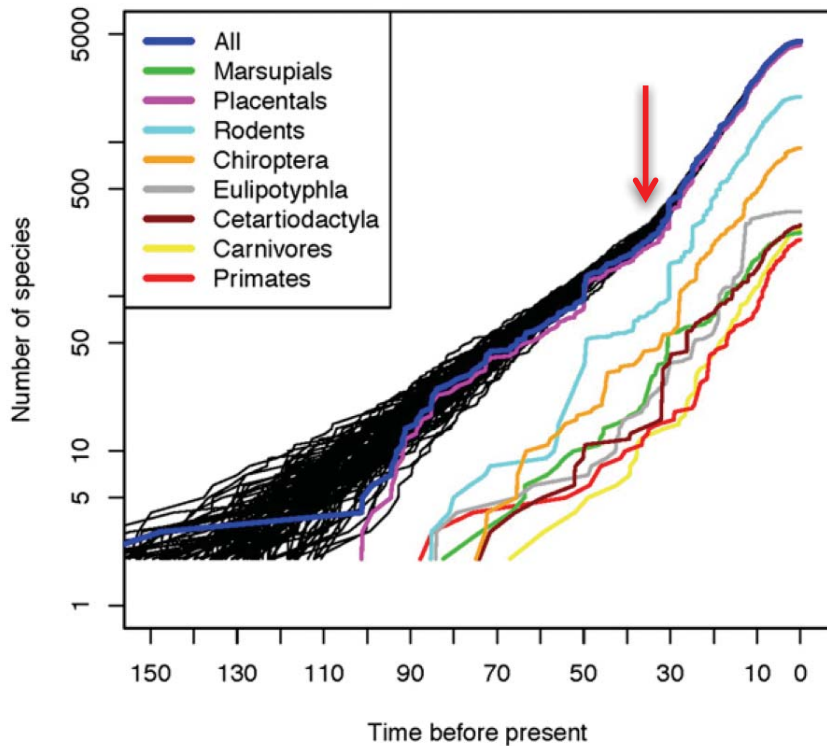
TreePar  
(rate-through-time plots)



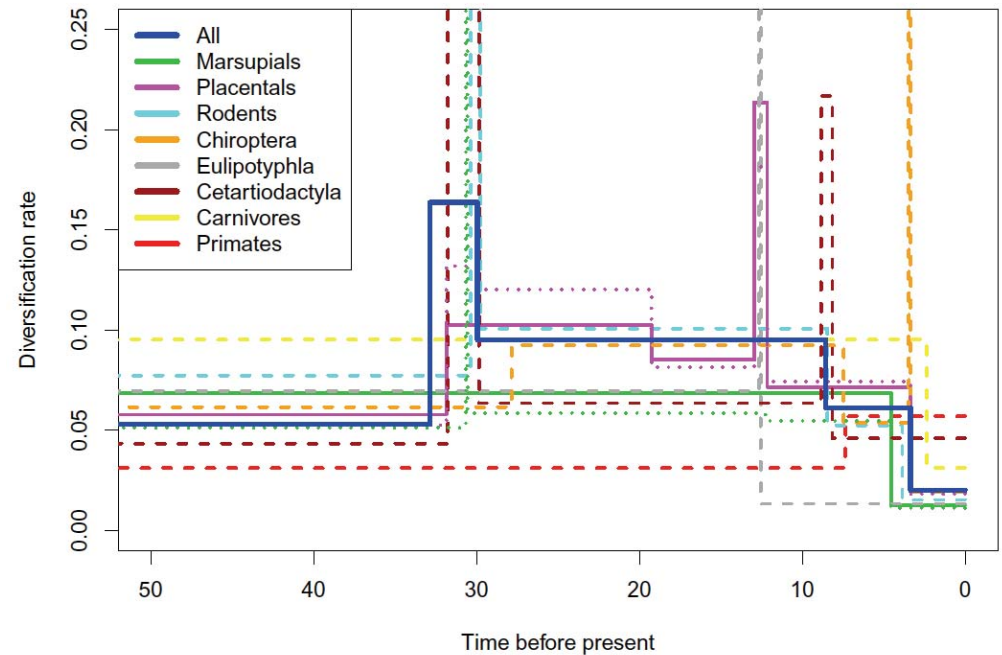


# TreePar: ML estimates of temporal shifts

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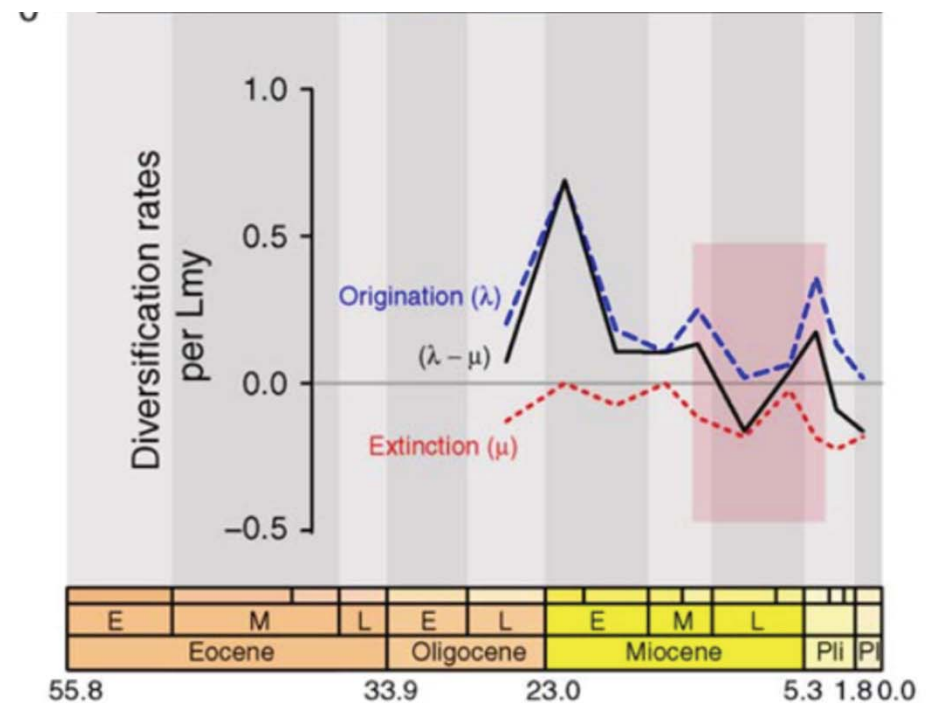
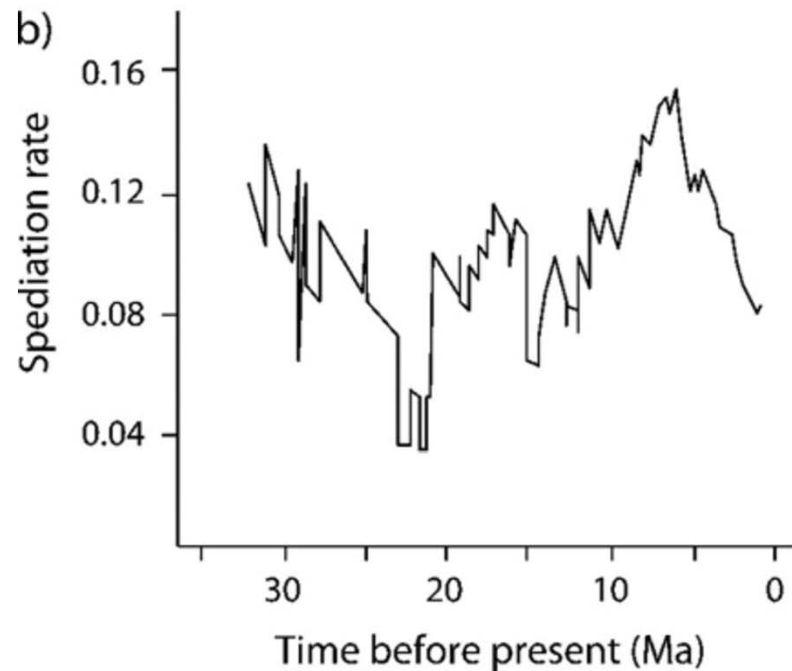


# TESS: Bayesian estimates of temporal shifts

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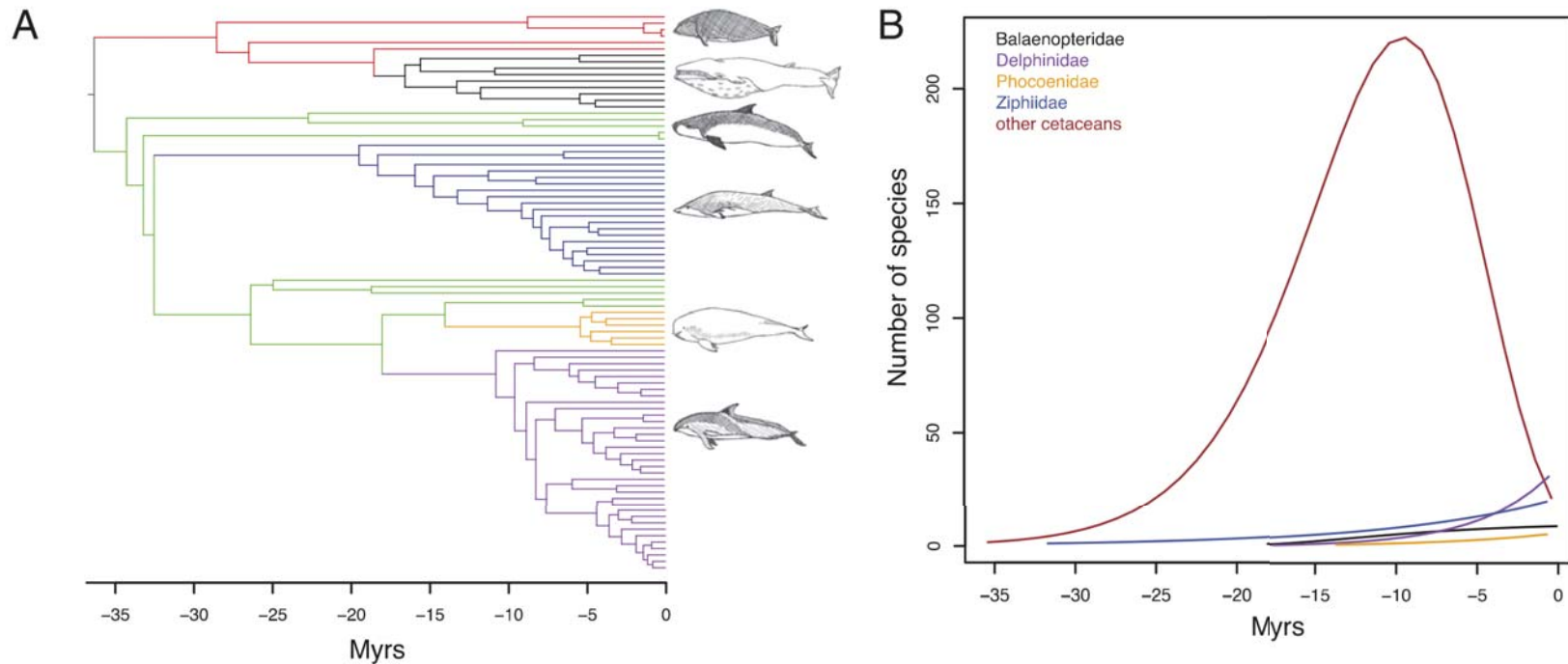
- TESS: Bayesian inference of temporal shifts in diversification rate (Höhna, 2013)
- Can account for mass-extinction events (e.g., CoMET function of TESS)

# BAMM & RPANDA – time variable (trait independent diversification)



# RPANDA – time variable (trait independent diversification)

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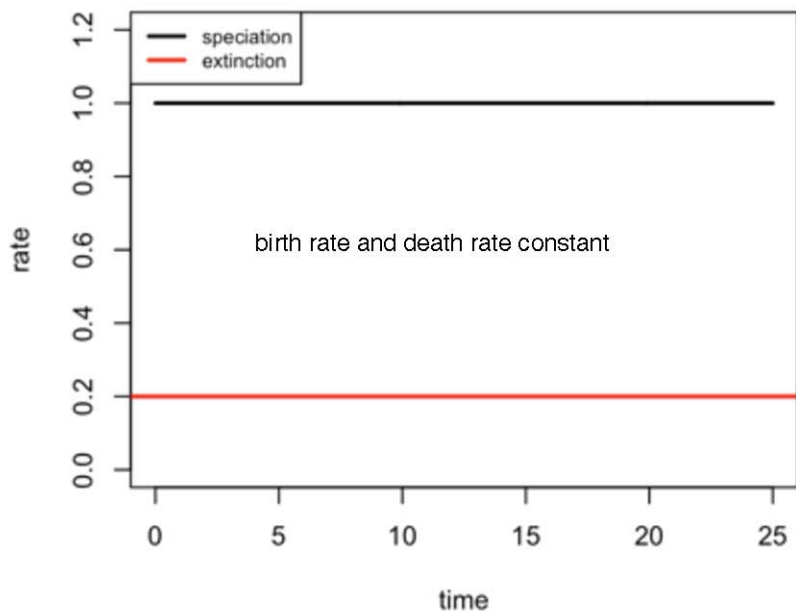


# RPANDA – time variable (trait independent diversification)

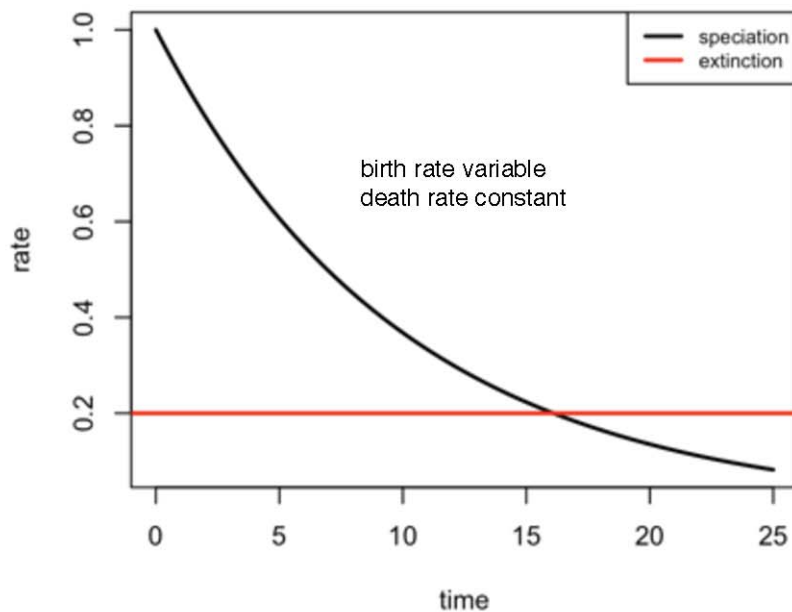
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- Allows rate to change over time and across clades
- Extinction can be higher than speciation at certain time points
- Accounts for incomplete sampling
- Requires subclades to be identified *a priori*
- Although it doesn't integrate paleontological information, it tends to give closer estimates between molecular trees and fossil occurrence data

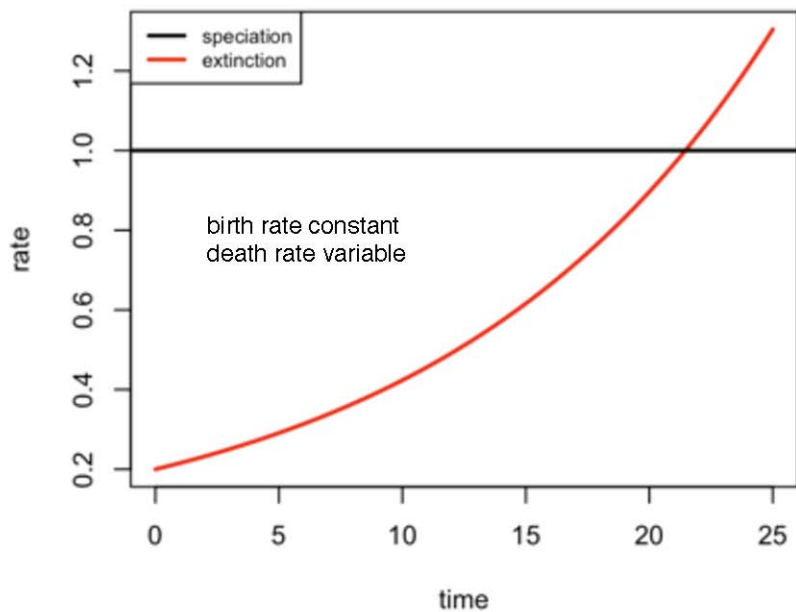
**BCSTDCST**



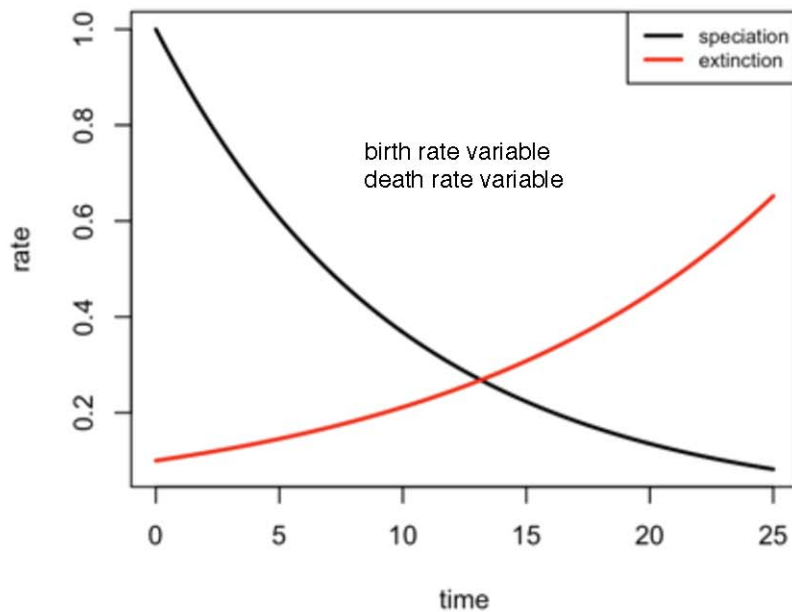
**BVARDCST**



**BCSTDVAR**

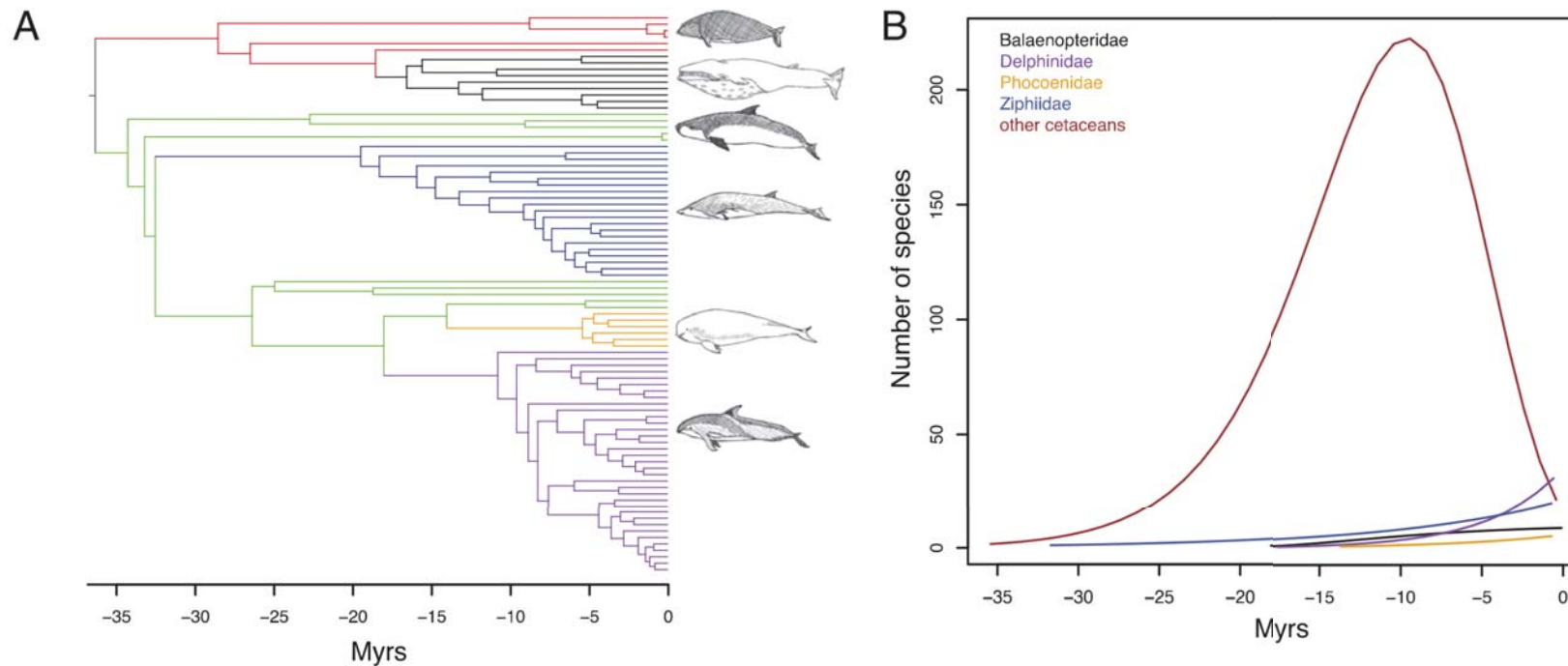


**BVARDVAR**

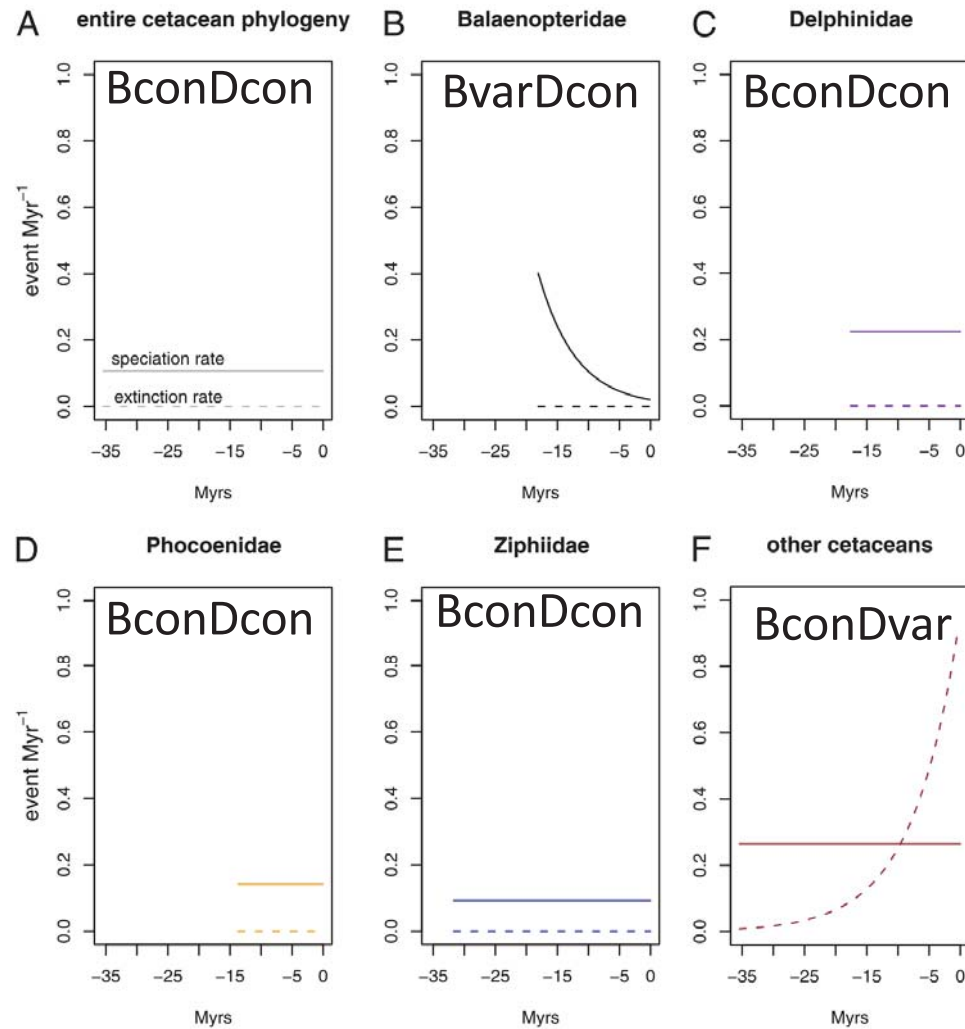


# RPANDA – time variable, trait independent diversification

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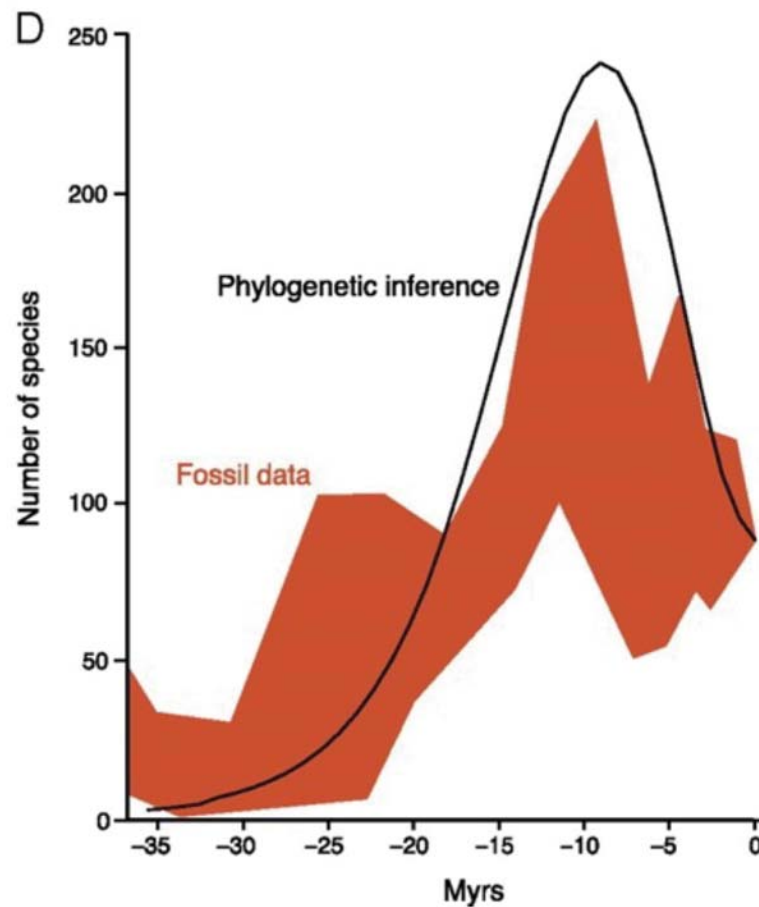
# RPANDA – time variable, trait independent diversification





# RPANDA – time variable, trait independent diversification

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# BAMM – further extension

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- Bayesian Analysis of Macroevolutionary Mixtures. Uses reversible jump MCMC. Simulates post. distr.
- Identifies rate variation in a tree - both through time and across clades
- Incorporates a wide range of complex models
- Data-driven framework - no a priori designation of clades (unlike RPANDA)

# BAMM – further extension

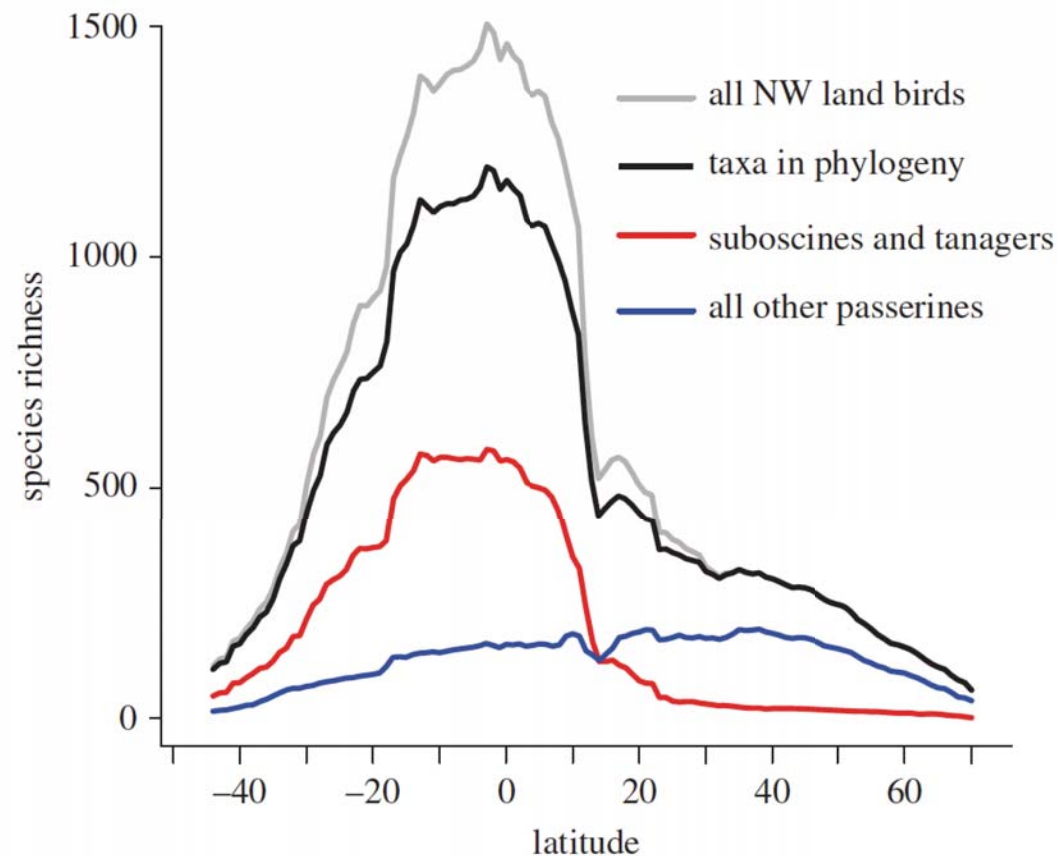
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- But it does require a prior probability on the number of diversification rate shifts. Influence of prior?
- Recent BAMM update: “number of shifts is not sensitive to the choice of model prior... BAMM rarely includes spurious shifts (<2% of all runs) when diversification models are selected using Bayes factors”

# Testing the effects of latitude on land bird diversification using BAMM

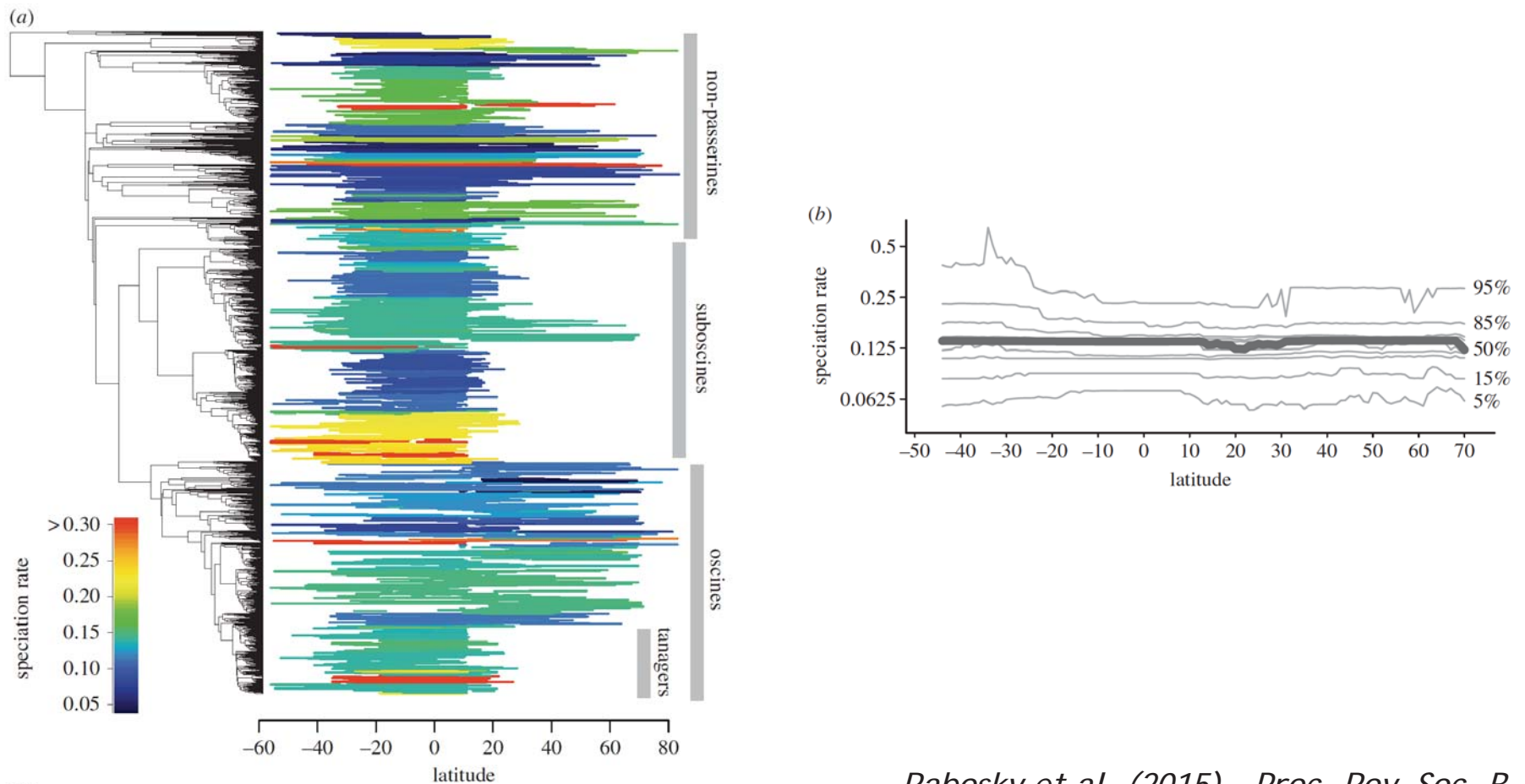
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- Do tropics promote bird speciation?



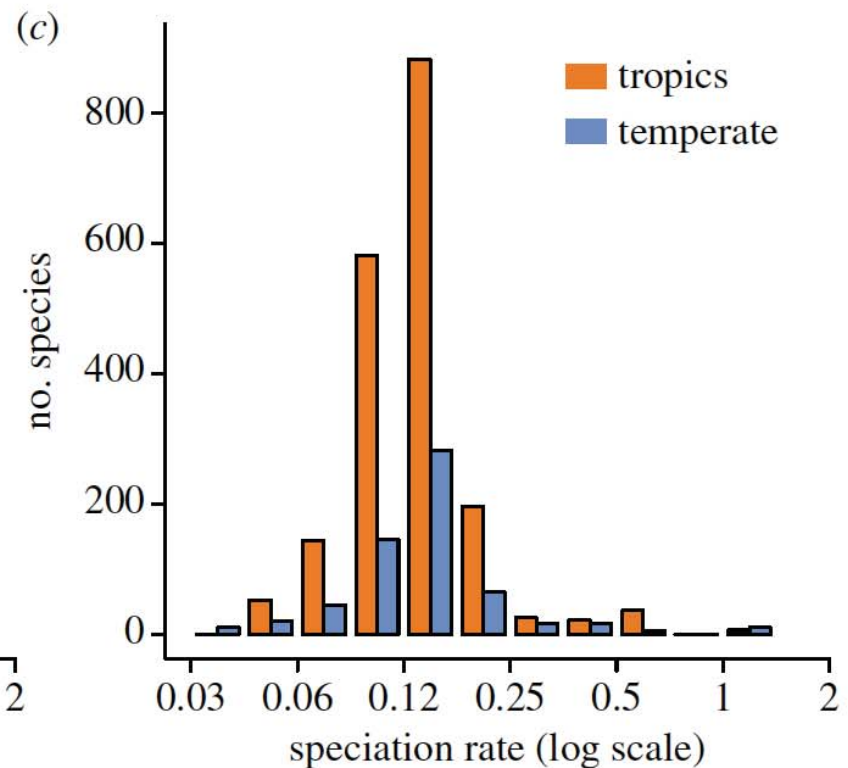
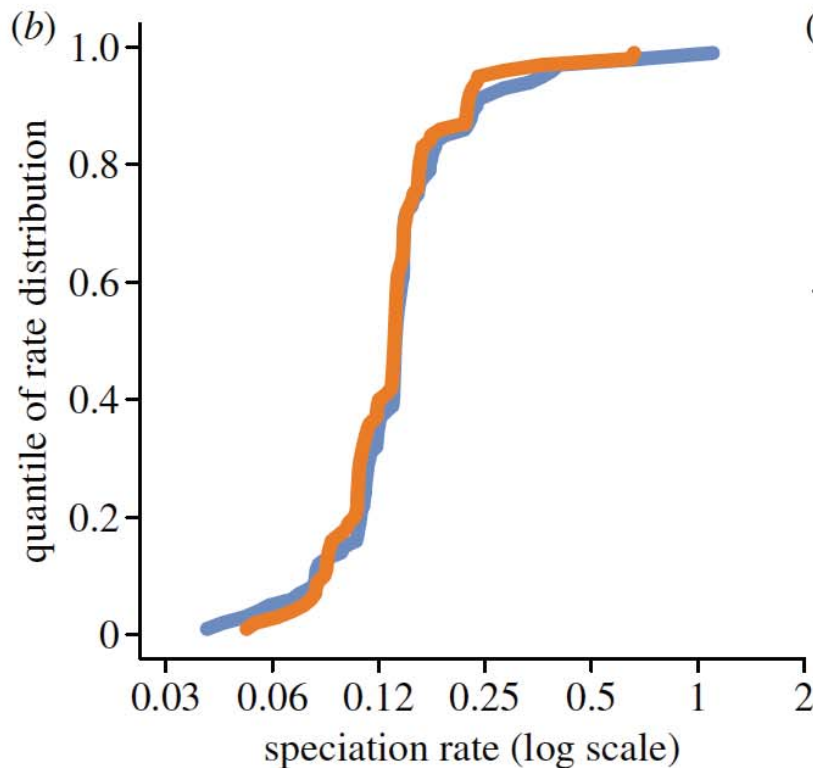
# Testing the effects of latitude on land bird diversification using BAMM

- Do tropics promote bird speciation?

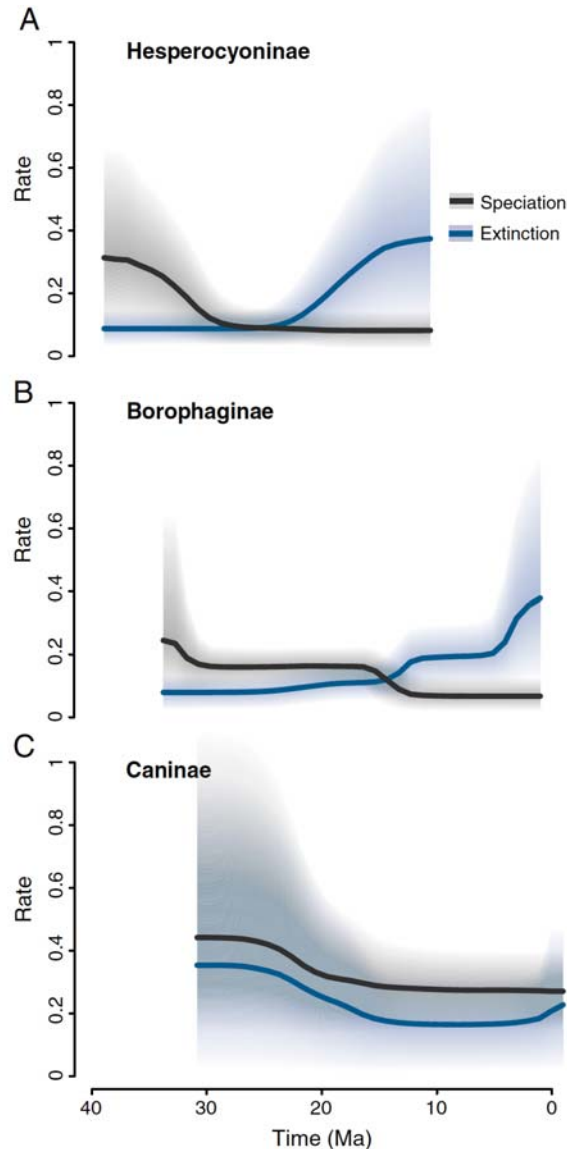


# Testing the effects of latitude on land bird diversification using BAMM

- Do tropics promote bird speciation? NO!



# Fossil vs. molecular signature of extinction



PyRate - A Bayesian method for estimating speciation and extinction rates from fossil occurrence data (without molecular trees)

# Fossil vs. molecular signature of extinction: Tetraodontiformes as case study

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10 extant families  
(all with fossils)

12 extinct families

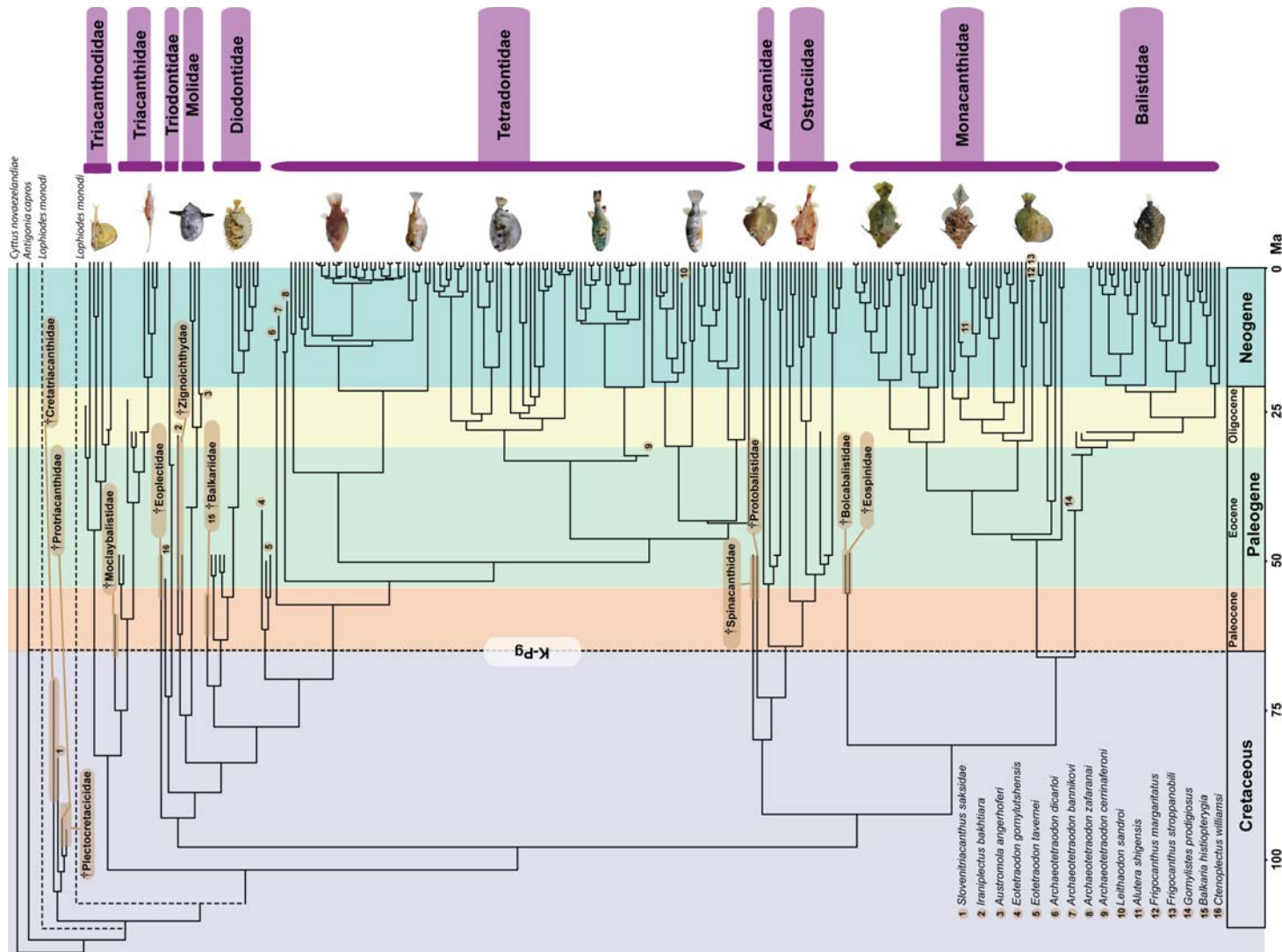
440 extant spp.

>66 fossil spp.

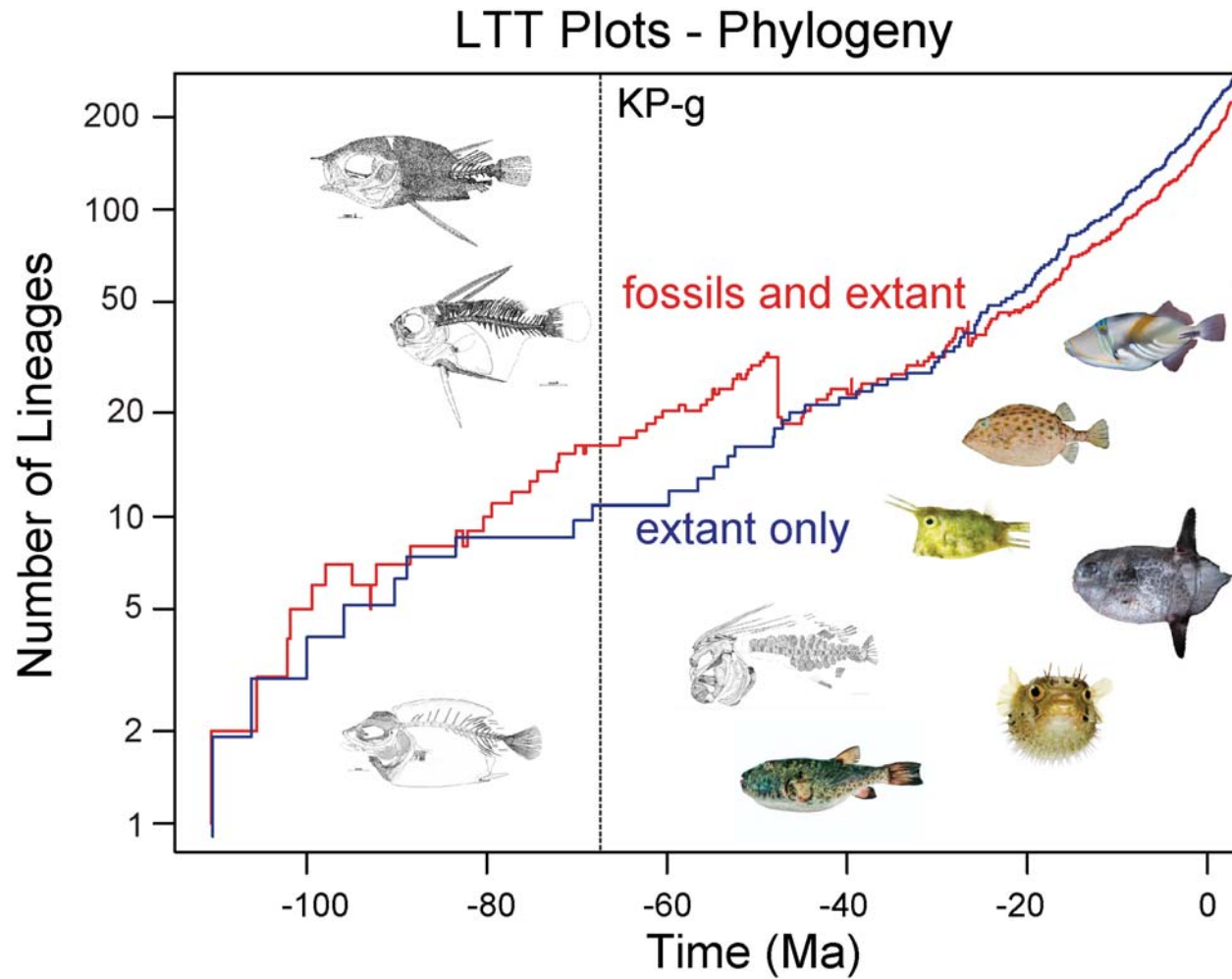
130 fossil occur.



# Fossil vs. molecular signature of extinction: Tetraodontiformes as case study



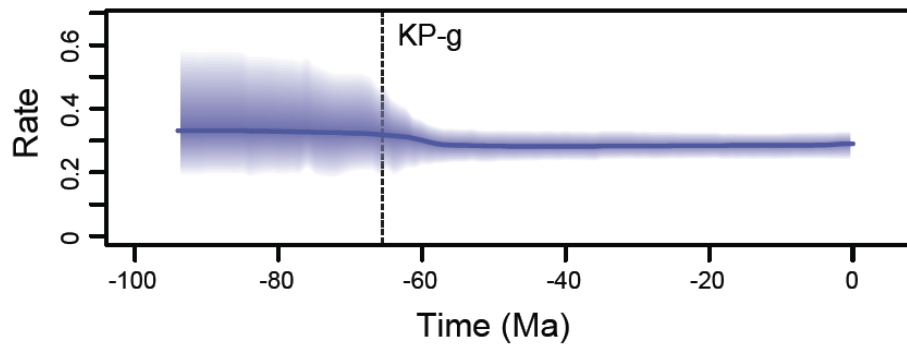
# Diversification analyses



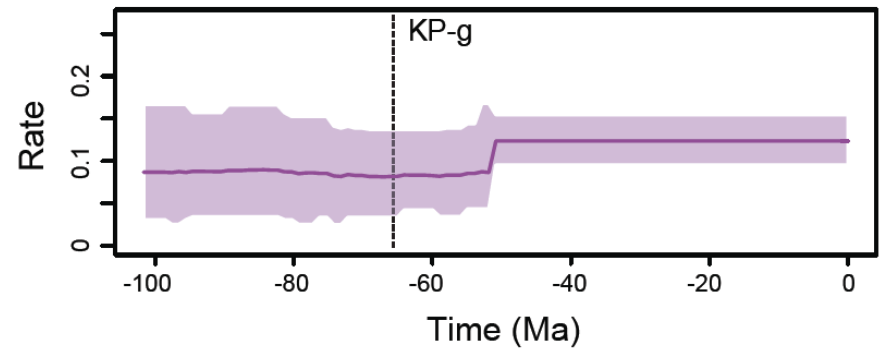
# Diversification analyses: rate through time plots

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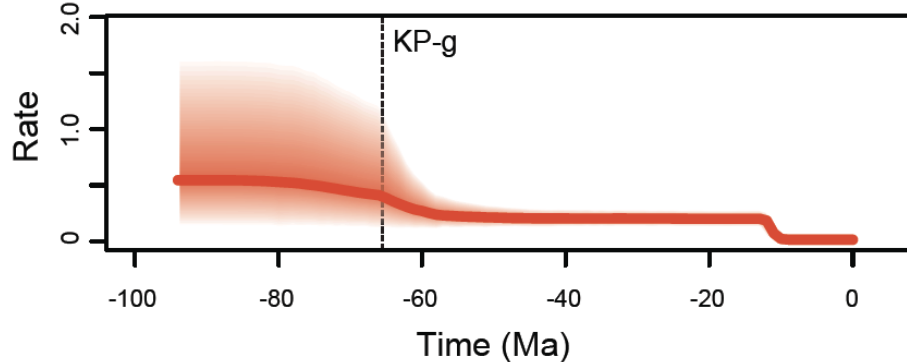
Fossil occurrences (PyRate)



Molecular phylogeny (TESS)



Extinction - Fossil Record



Extinction - Molecular Phylogeny

