



rijksuniversiteit  
groningen

# MODELING MACRO-EVOLUTIONARY PROCESSES

## Biological Diversity Models

---



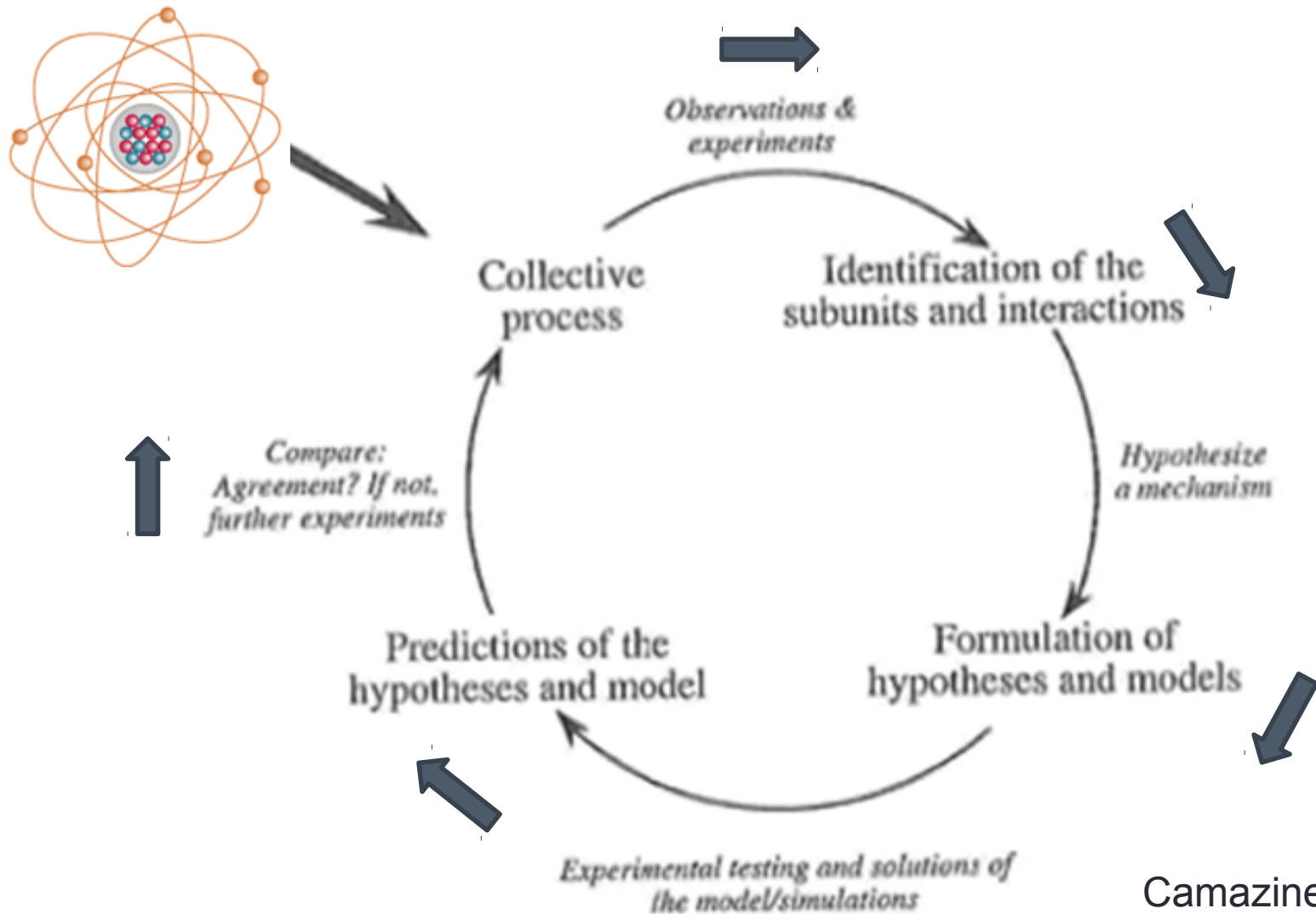
Freek de Haas  
19/2/2014

Supervisor  
Rampal Etienne

# Presentation Lay-Out

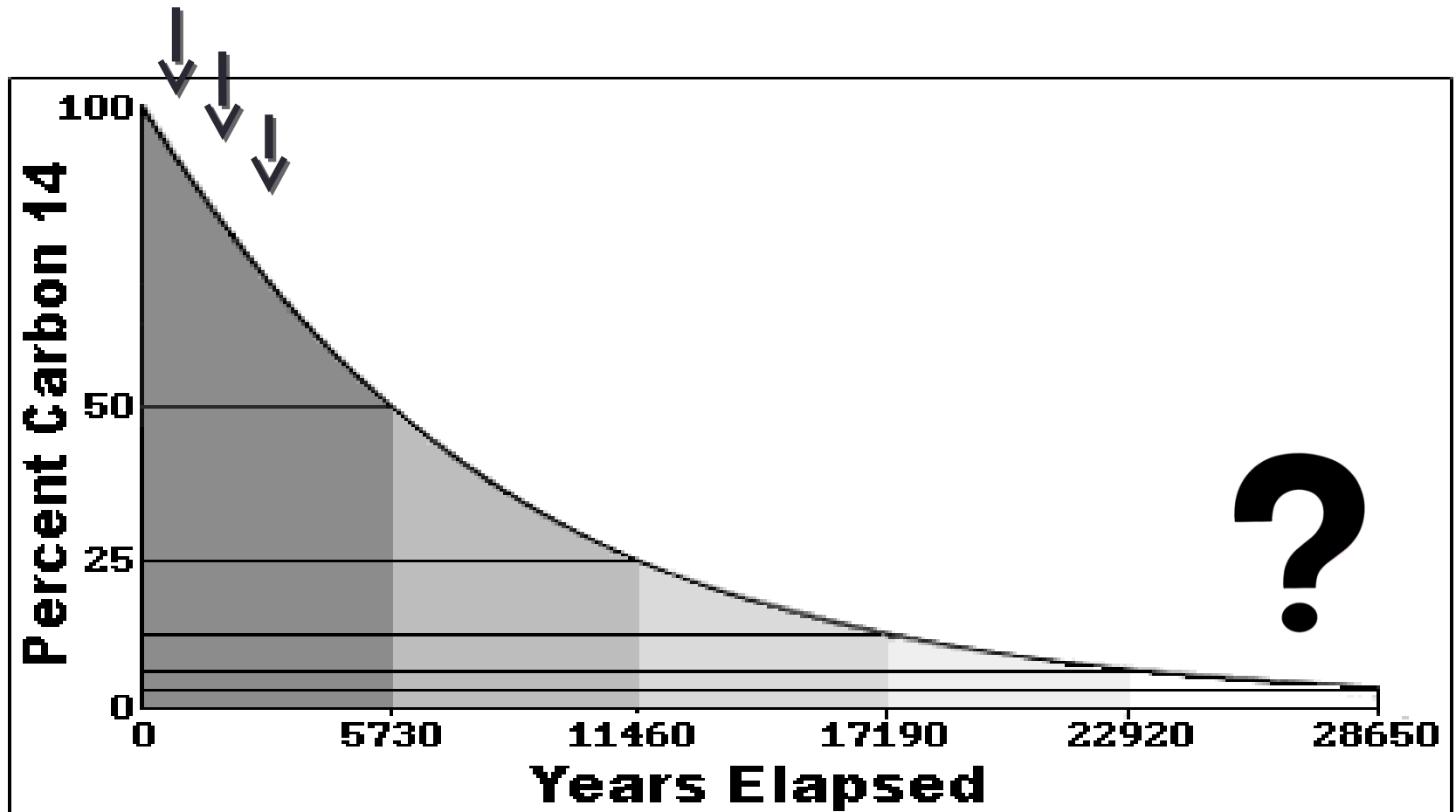
- Modeling empirical data
  - Assumptions
- Modeling biological diversity
  - Empirical Data
  - Model
- Discuss Papers
  - Overview: Daniel Moen and Helene Morlon
  - Etienne et al; 2012
  - Etienne & Rosindell; 2011

# Modeling Cycle



Camazine et al; 2002

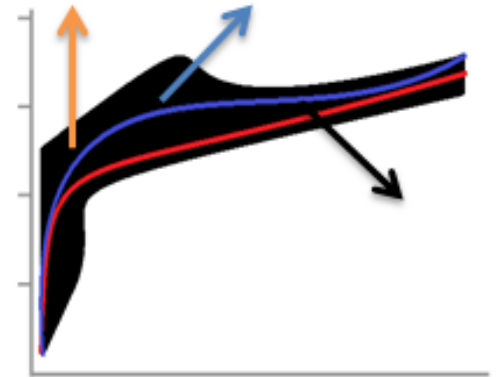
# Model & Assumptions



Constant radioactive decay over time?

# Use of models & degrees of freedom

- Multiple factors
- More flexibility
- More variables ➡ prediction power
- Degrees of freedom



## Akaike information criterion

$$AIC = 2k - 2 \ln(L)$$



df



maximized  
likelihood

*Preferred model is minimum AIC value*



**KEEP  
CALM  
AND USE  
OCCAM'S  
RAZOR**

# Biological Diversity



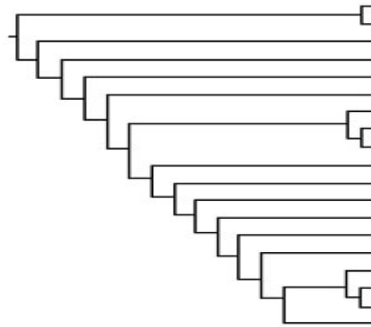
Response Variable

# Relevance

Speciation Rate  
(Parameter estimation)



Extrapolate &  
Correlations



Fossil vs. Molecular

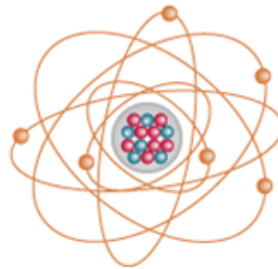


# Empirical data



- Molecular data
  - DNA comparison

- Fossil records
  - Radiocarbon dating

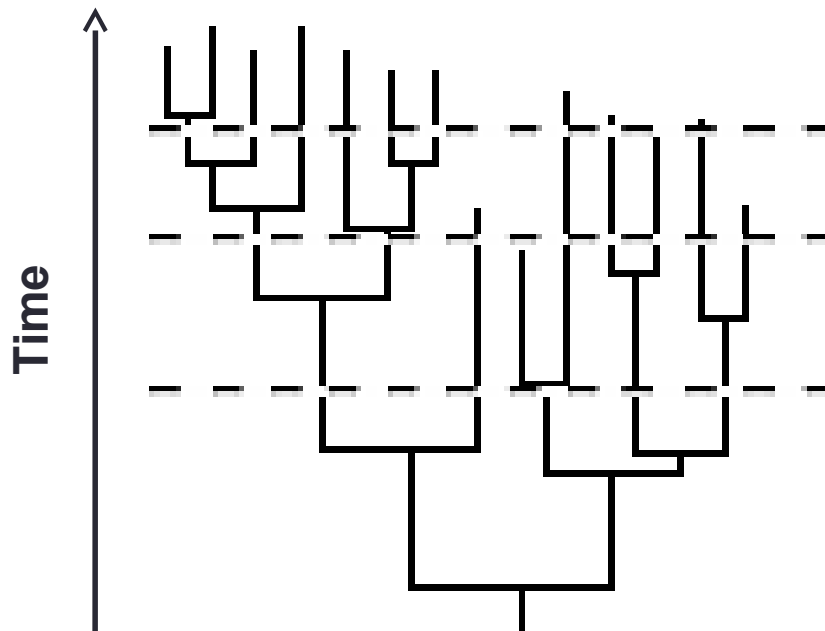


**EMPIRICAL  
DATA ?**



# Phylogeny model

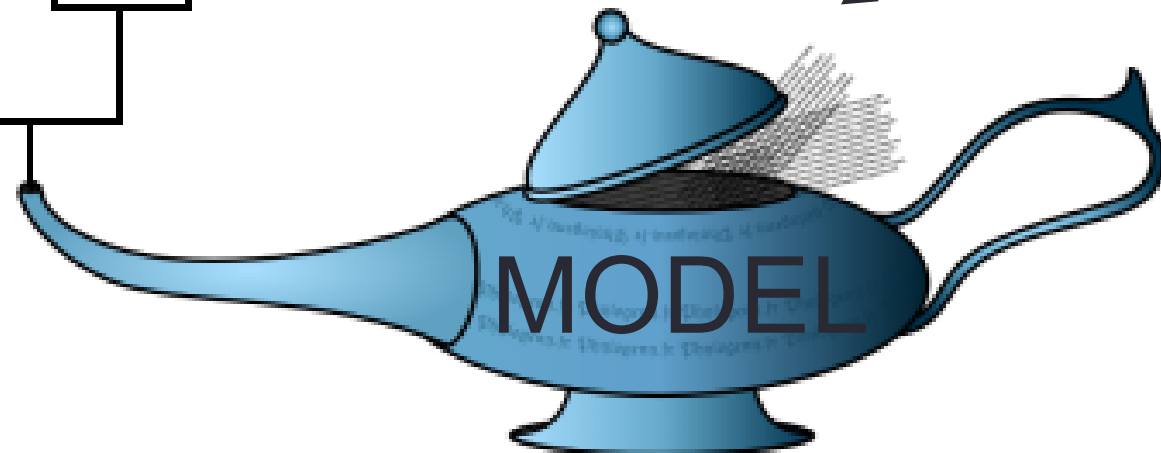
**OUTPUT**



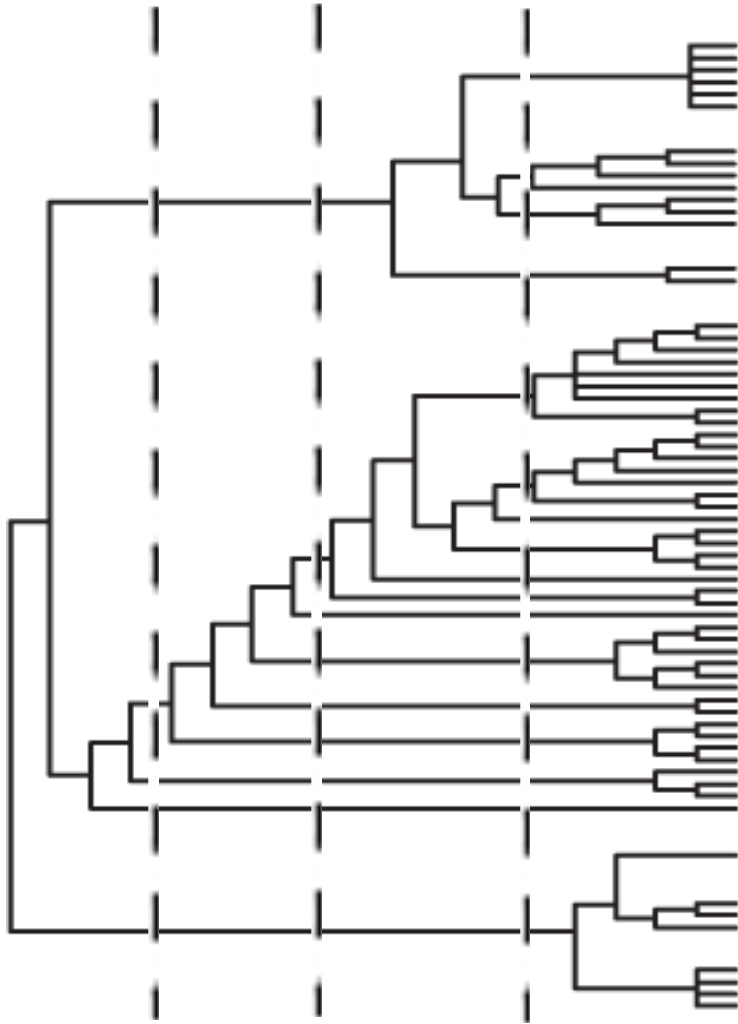
**INPUT**

Variables:

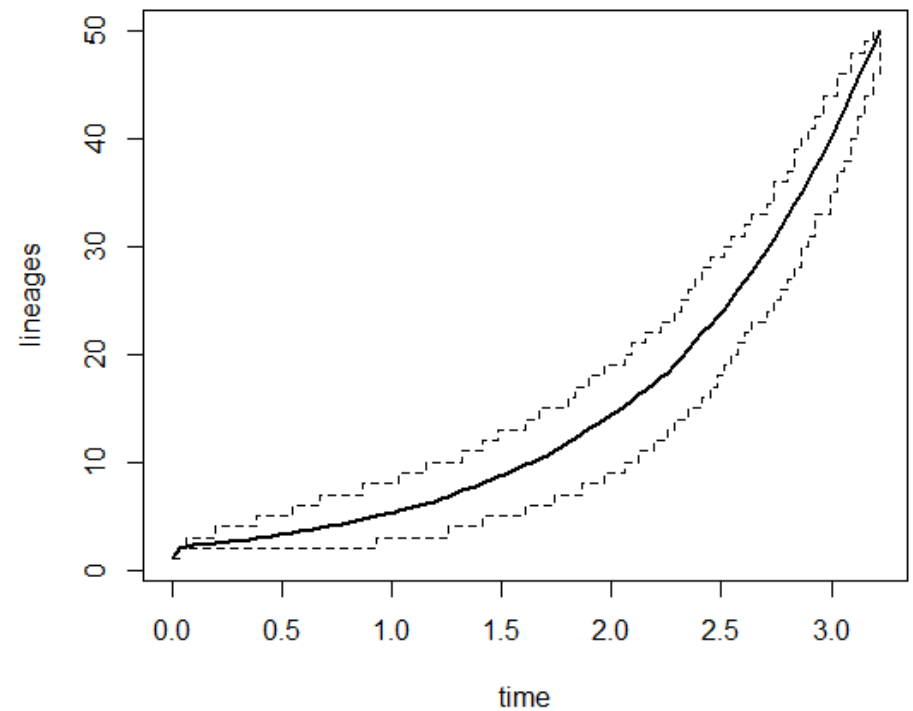
- Speciation
- Extinction
- etc



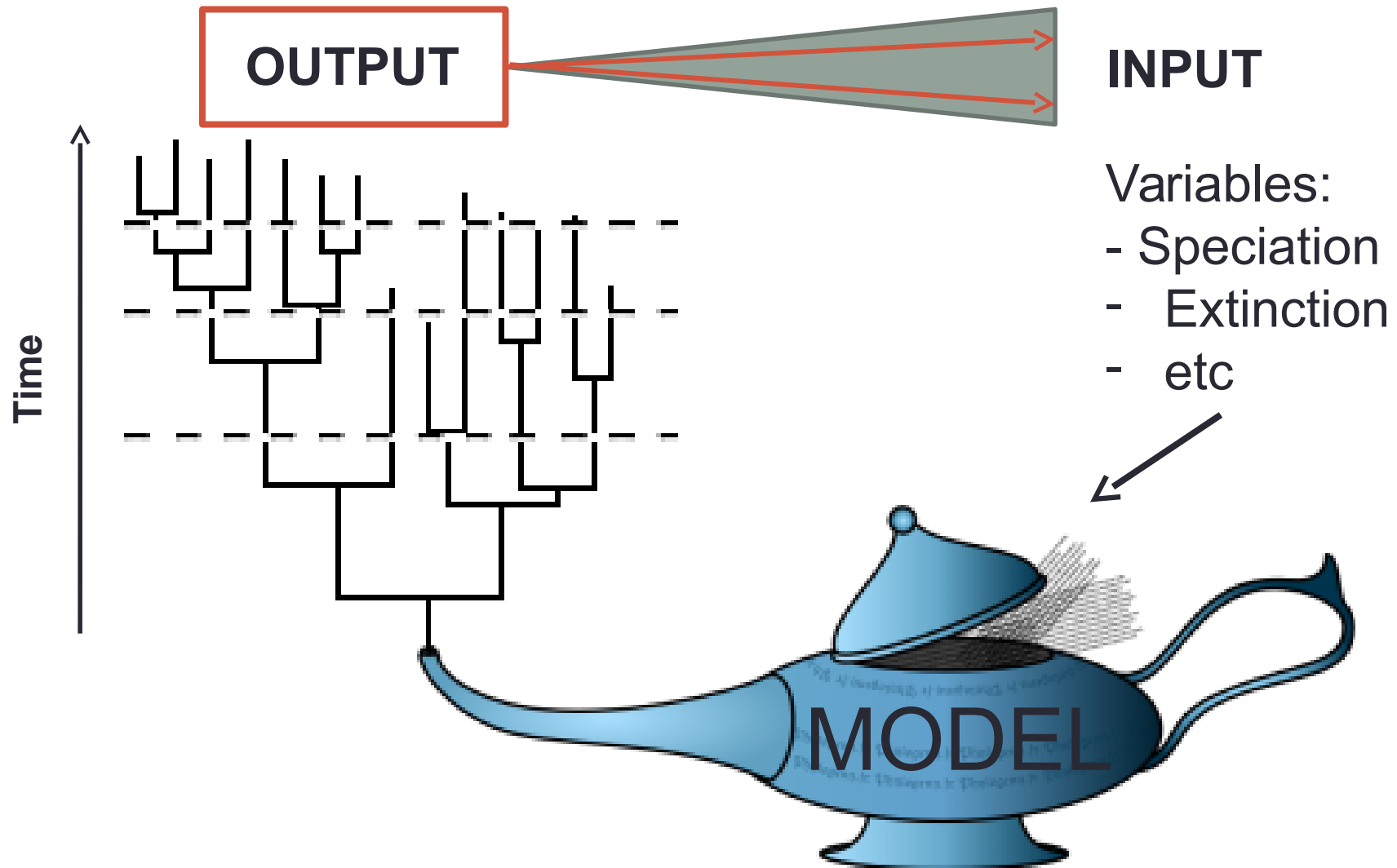
# Model Assumptions & Predictions



Lineages Through Time



# Phylogeny model

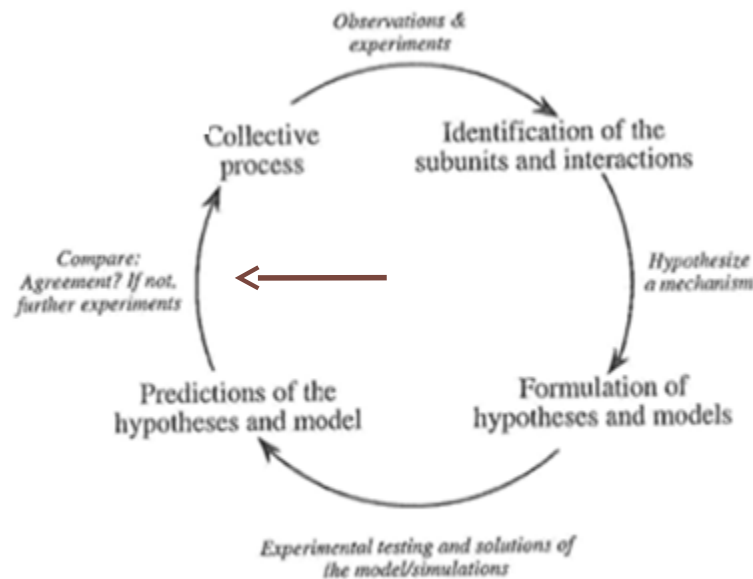


# Evaluation

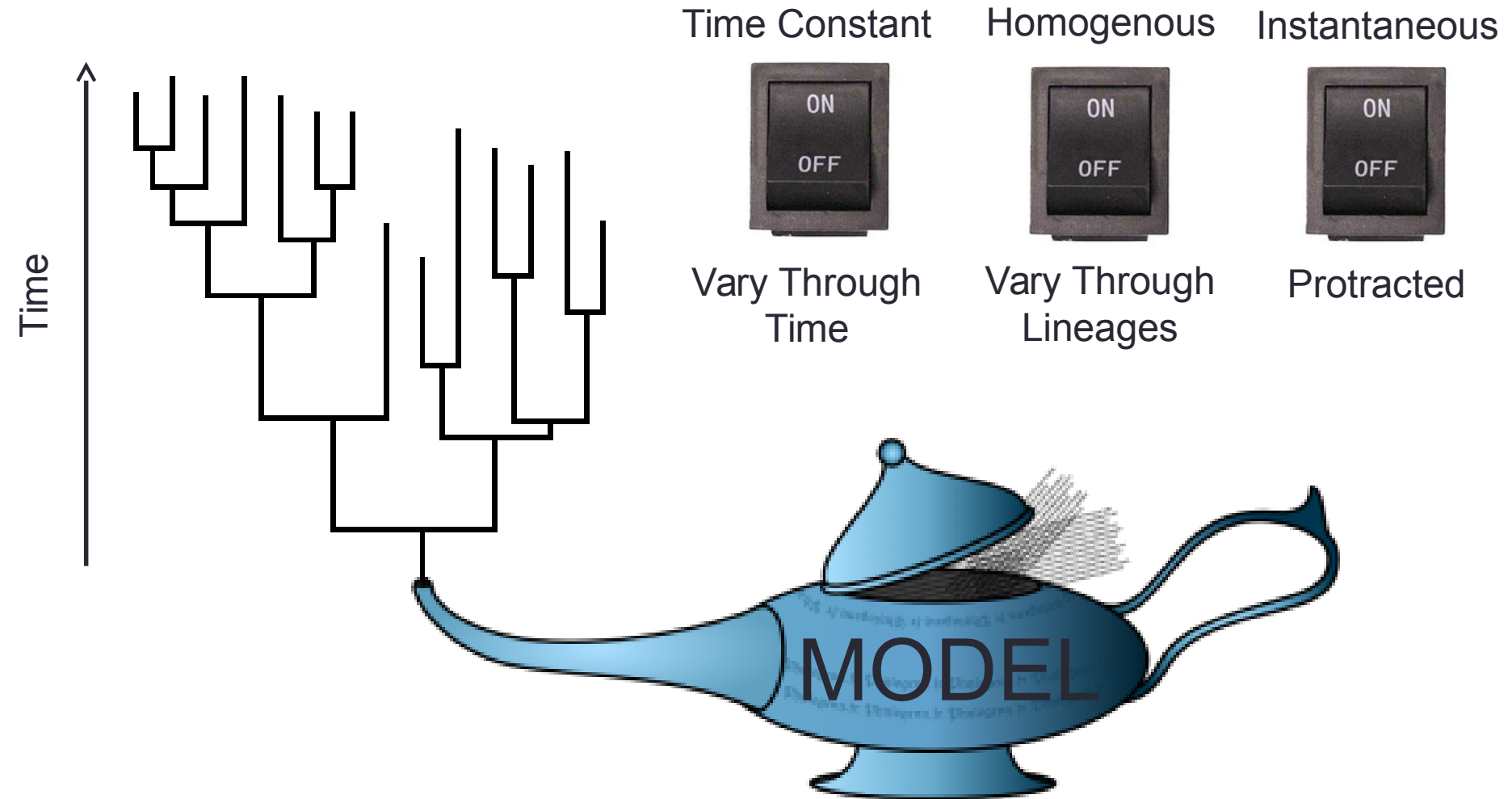
Empirical phylogenies



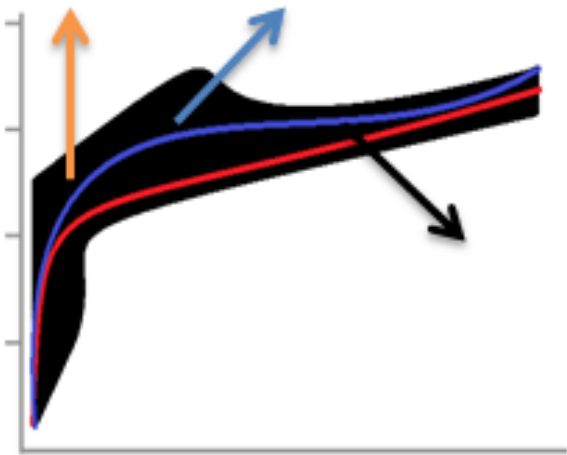
Modeled Phylogenies



# Different Parameters Speciation



# Different Parameters Speciation



- Pure birth models
- Birth-death models
- Density dependent
- Time-dependent
- Protracted speciation
- Waxing & Waning
- Etc...

Time Constant



Vary Through  
Time

Homogenous



Vary Through  
Lineages

Instantaneous



Protracted

## Changing the model

- Find a reason and change the model
- Change the model and find a reason



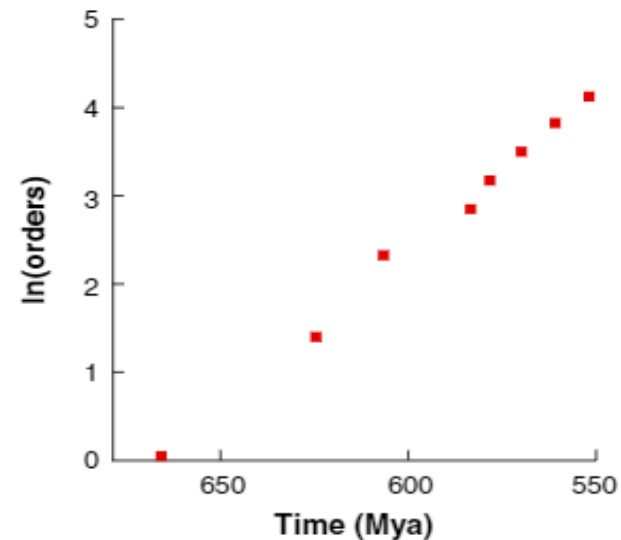
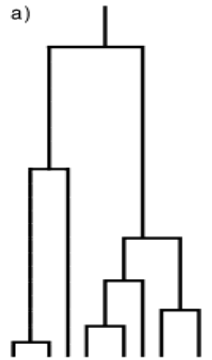
# Pure Birth Model

## Assumptions Model

- Only Speciation drives Biological Diversity
- Common Ancestor
- Speciation is constant over time

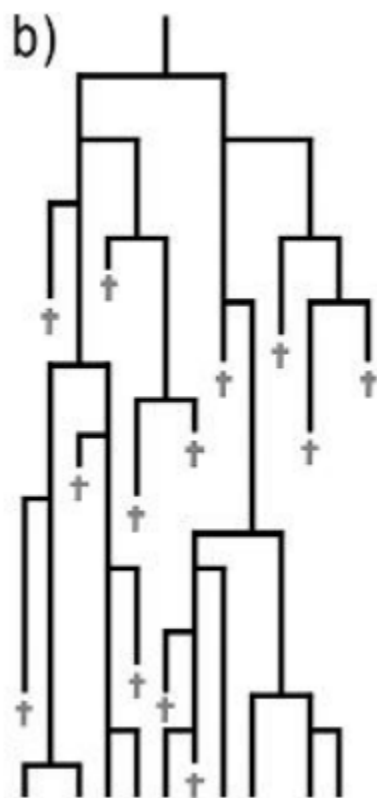
$$N(t) = N(0)e^{bt}$$

- $N(0)$  – Nr of species at time 0
- $b$  – P[speciation event]



# Birth-Death Model

- $H_0$  model
- Birth rate ( $b$ )  $\rightarrow b - d$



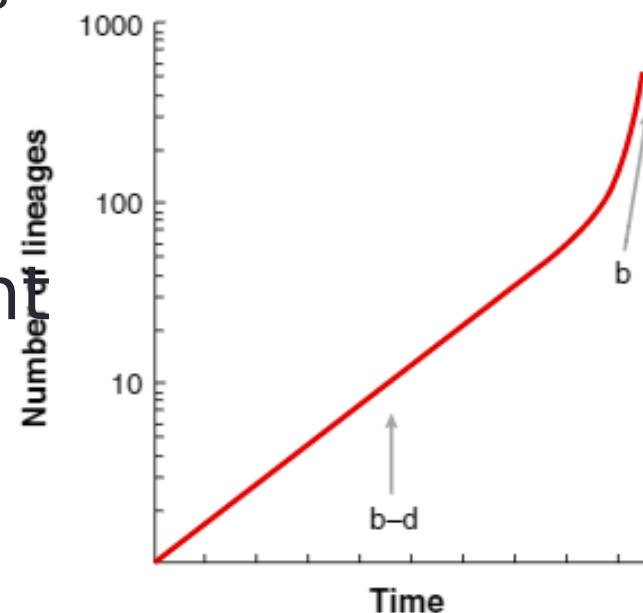
Molecular Phylogenies



Pull of the Present



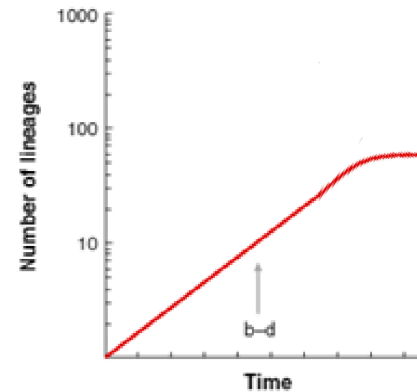
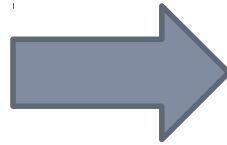
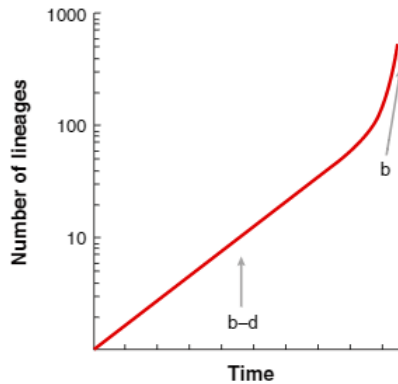
Extinction rate





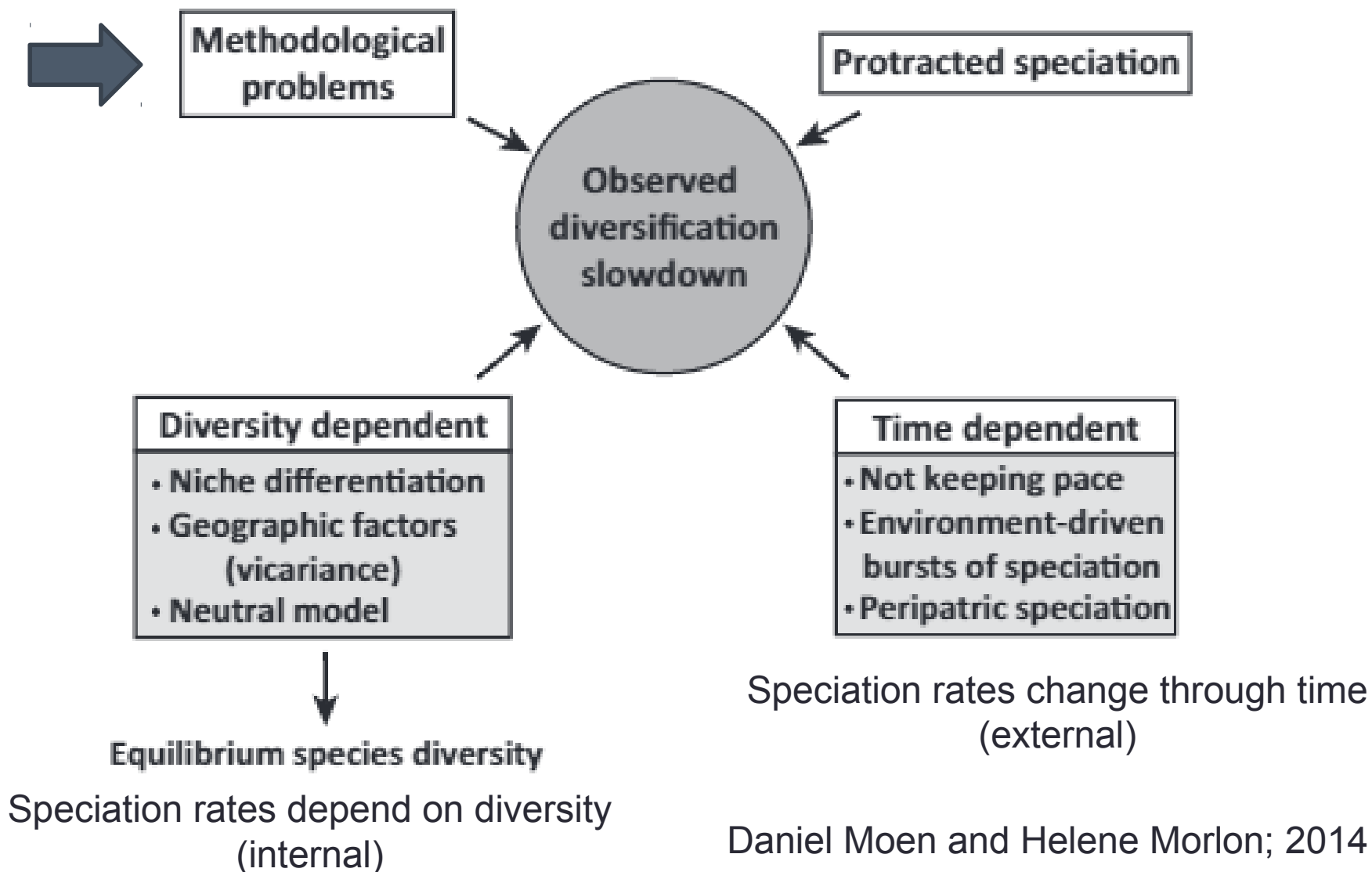
# Empirical Data

- Molecular empirical data is not in line with “pull of the present”
- Most show a slow down of diversification towards the present



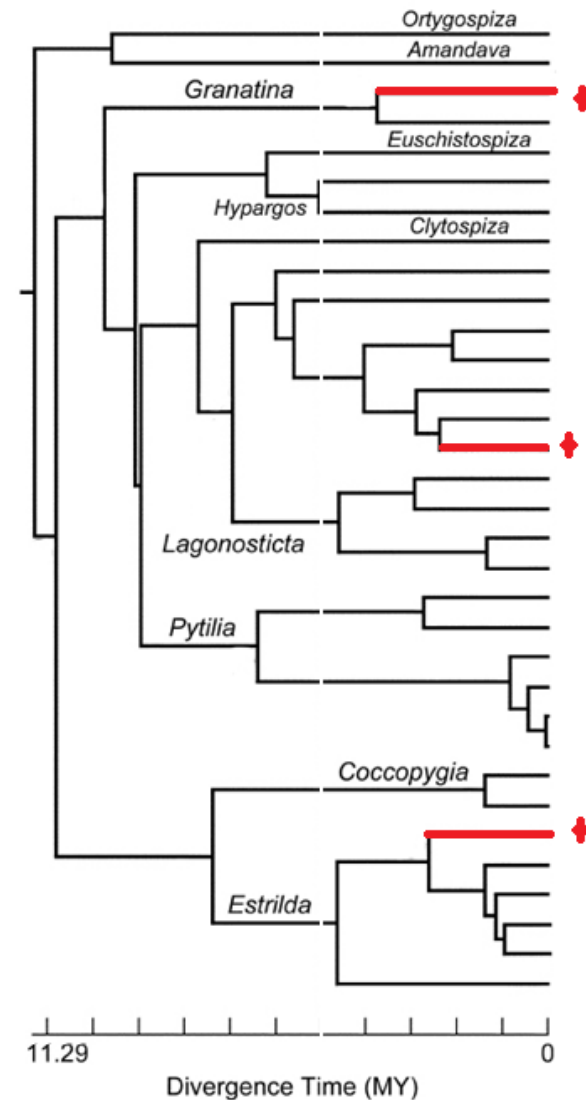
- Extinction = 0 / Speciation goes down
- Not in line with the fossil records

# Diversification Slowdown



# Methodological Biases

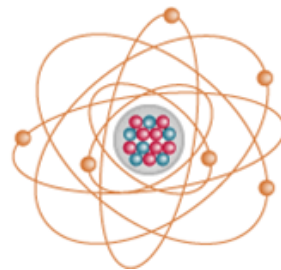
- Empirical
  - Taxonomic sampling



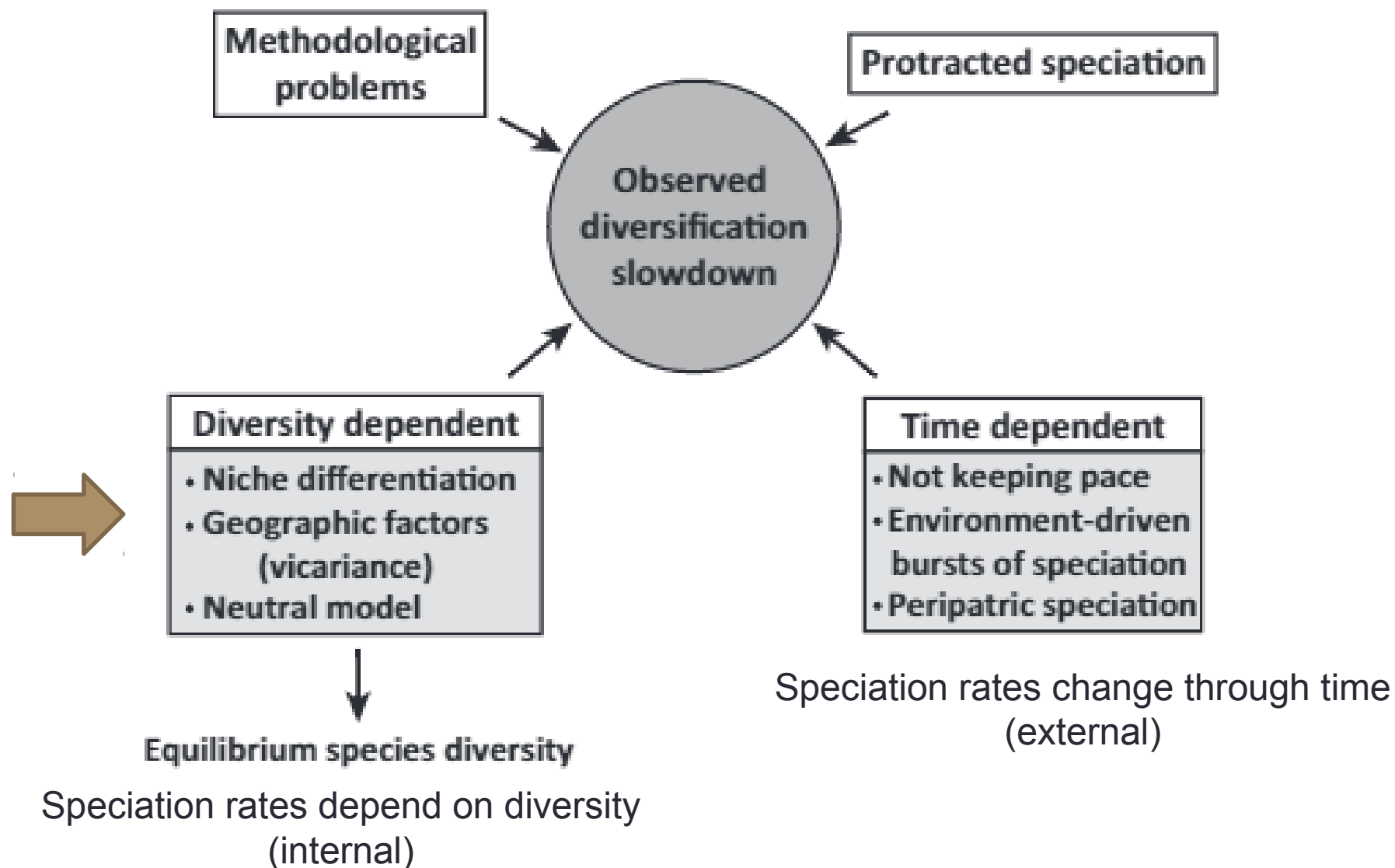
# Methodological Biases

- Empirical
    - Taxonomic sampling
      - Large phylogenies can show slowdowns by chance
- 

- Model
  - Inaccurate estimation from DNA sequences
    - Scaling molecular branch lengths into units of time



# Diversification Slowdown

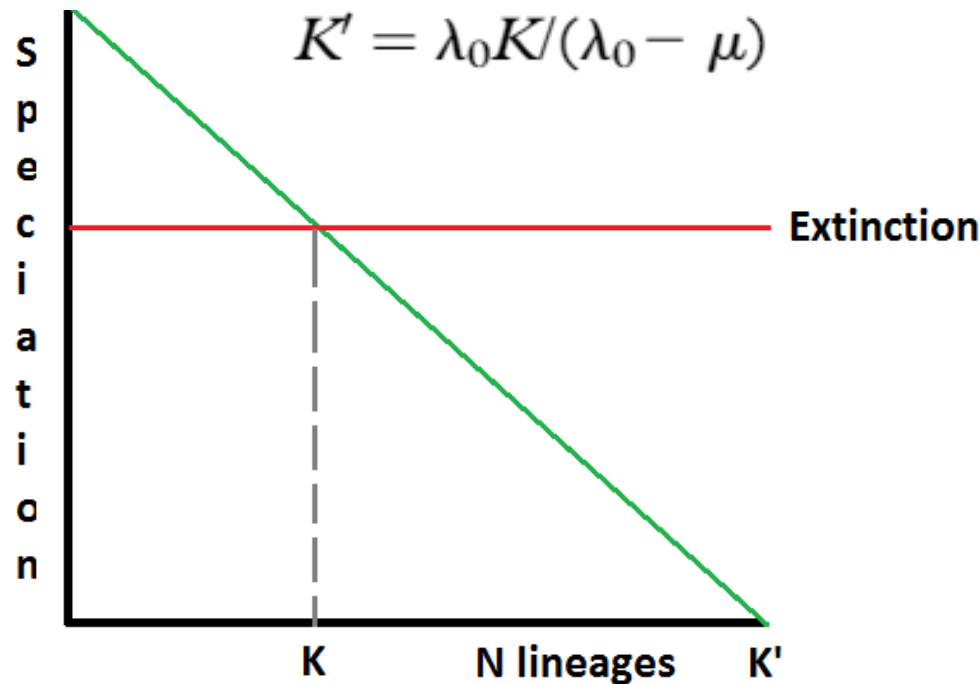


# Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record (Etienne et al; 2012)

Birth-Death Model

$$\lambda_n = \max\left(0, \lambda_0 \left(1 - \frac{n}{K'}\right)\right) \quad \text{and} \quad \mu_n = \mu$$

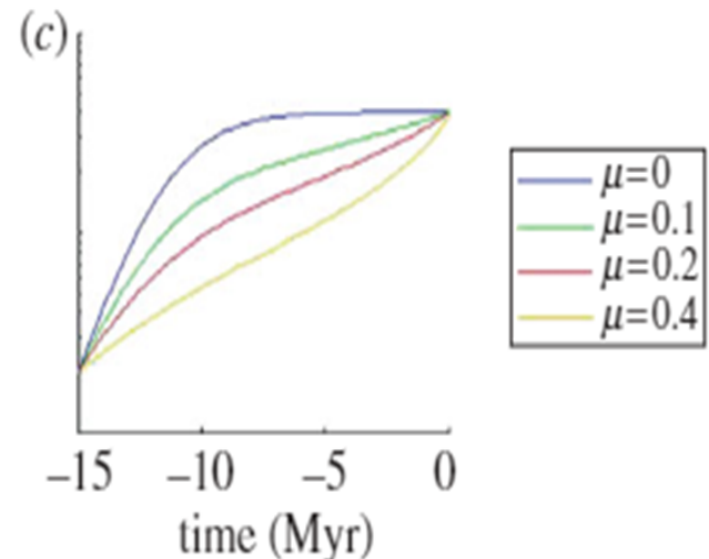
$$K' = \lambda_0 K / (\lambda_0 - \mu)$$



INTERNAL FEEDBACK

$$\lambda_0 - n\left(\frac{\lambda_0}{K'}\right)$$

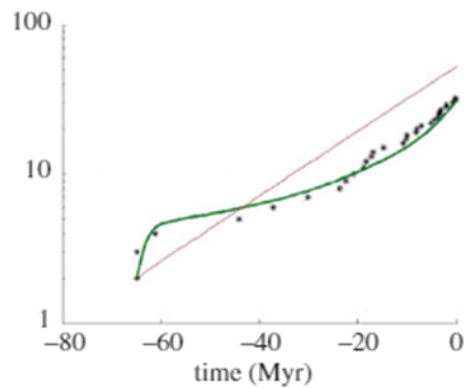
$$K' = \lambda_0 * \frac{K}{(\lambda_0 - \mu)}$$



# Empirical Data

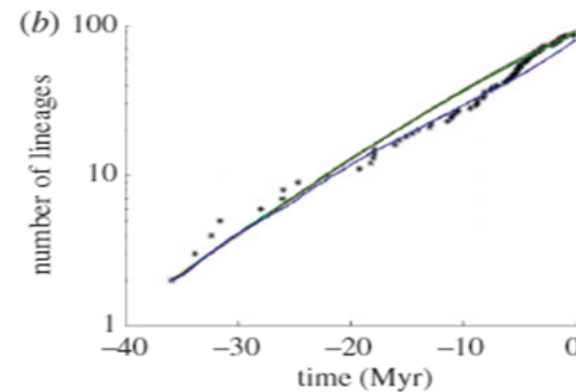
## Foraminifera

Foraminifera

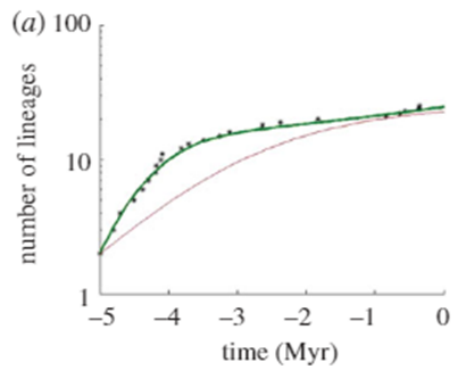


## Cetacea

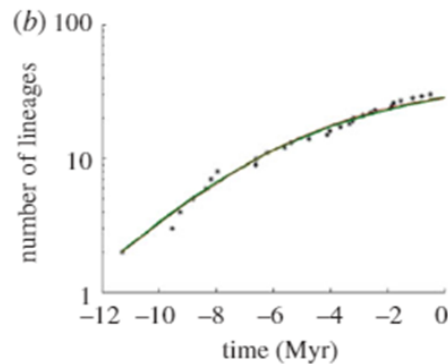
Cetacea



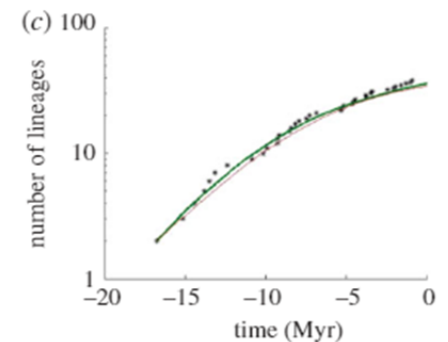
## Dendroica Warblers



## *Glutinosus*

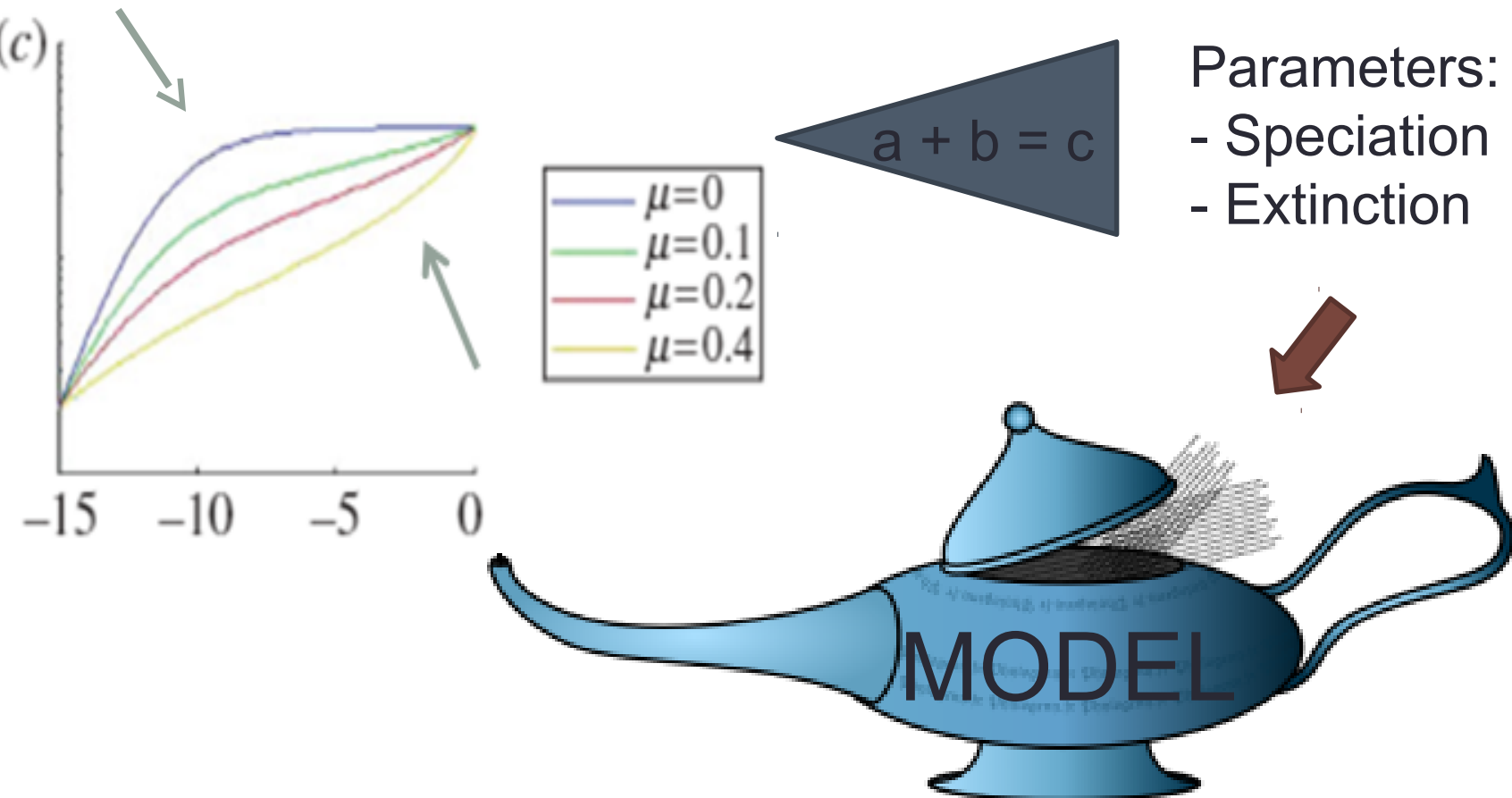


## *Heliconius*



# Hidden Markov Model

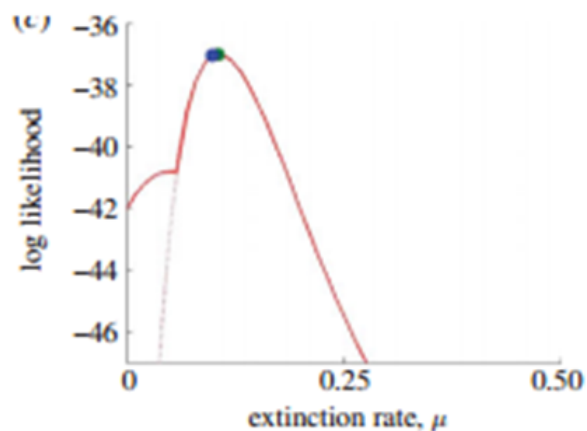
- Likelihood computation -> Hidden Markov Model
  - Compute likelihood of phylogeny for different parameters



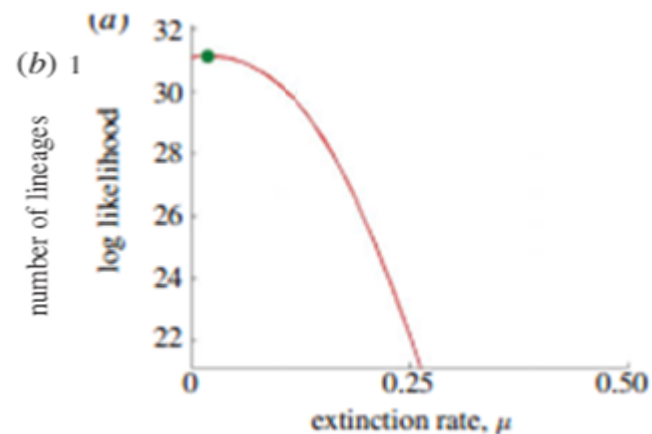


# Likelihood Extinction Rate

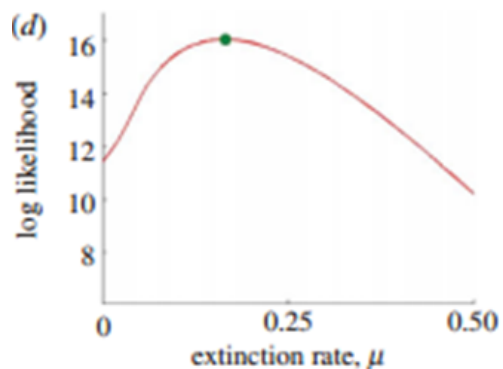
Foraminifera



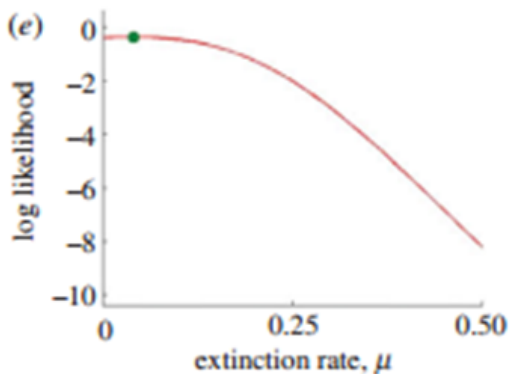
Cetacea



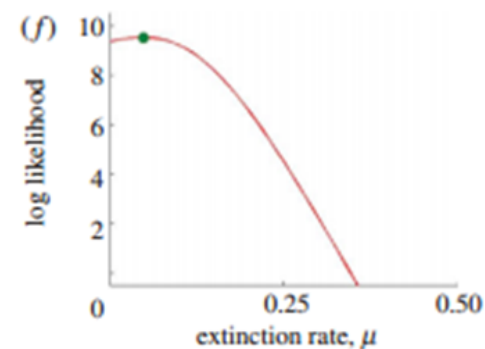
Dendroica Warblers



*Glutinosus*

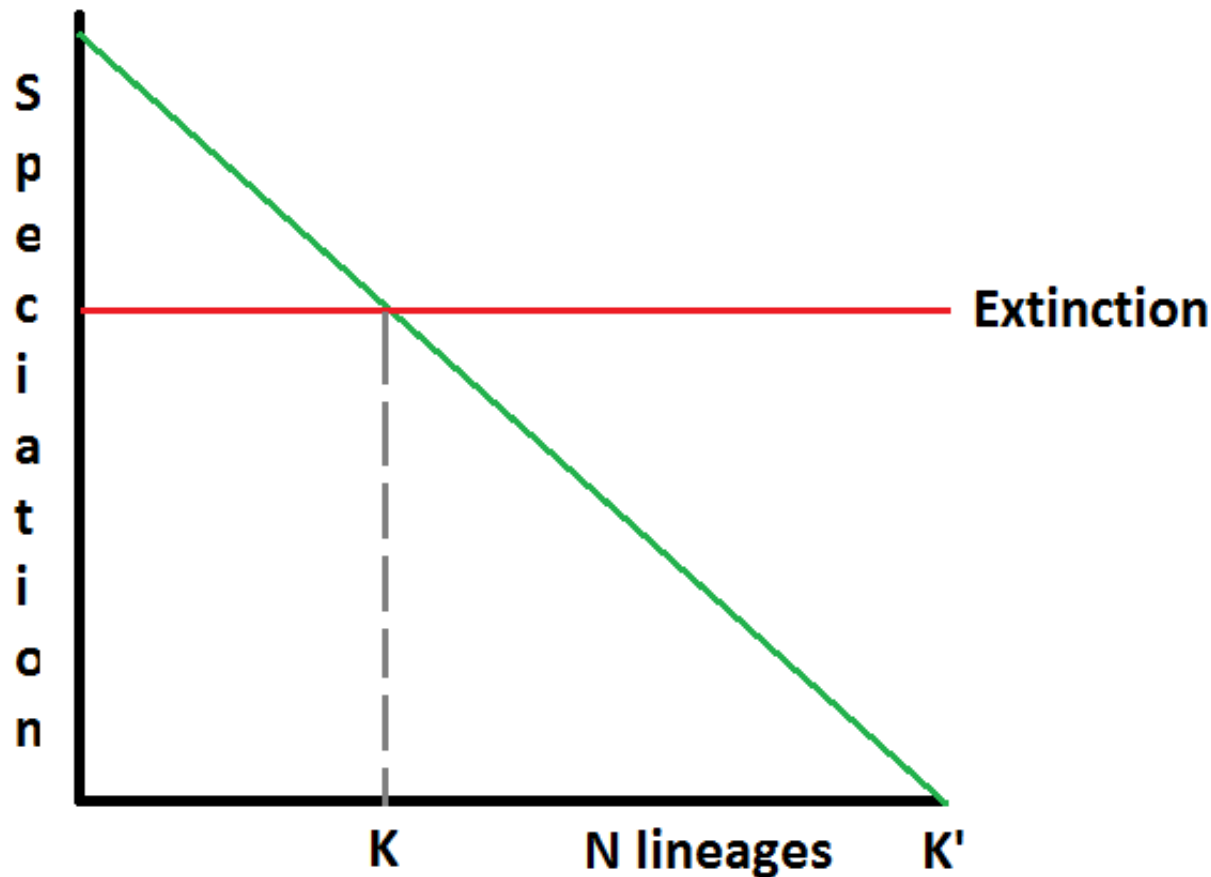


*Heliconius*



# Likelihood Speciation Rate

Likelihood of extinction  $\sim$  Likelihood of speciation

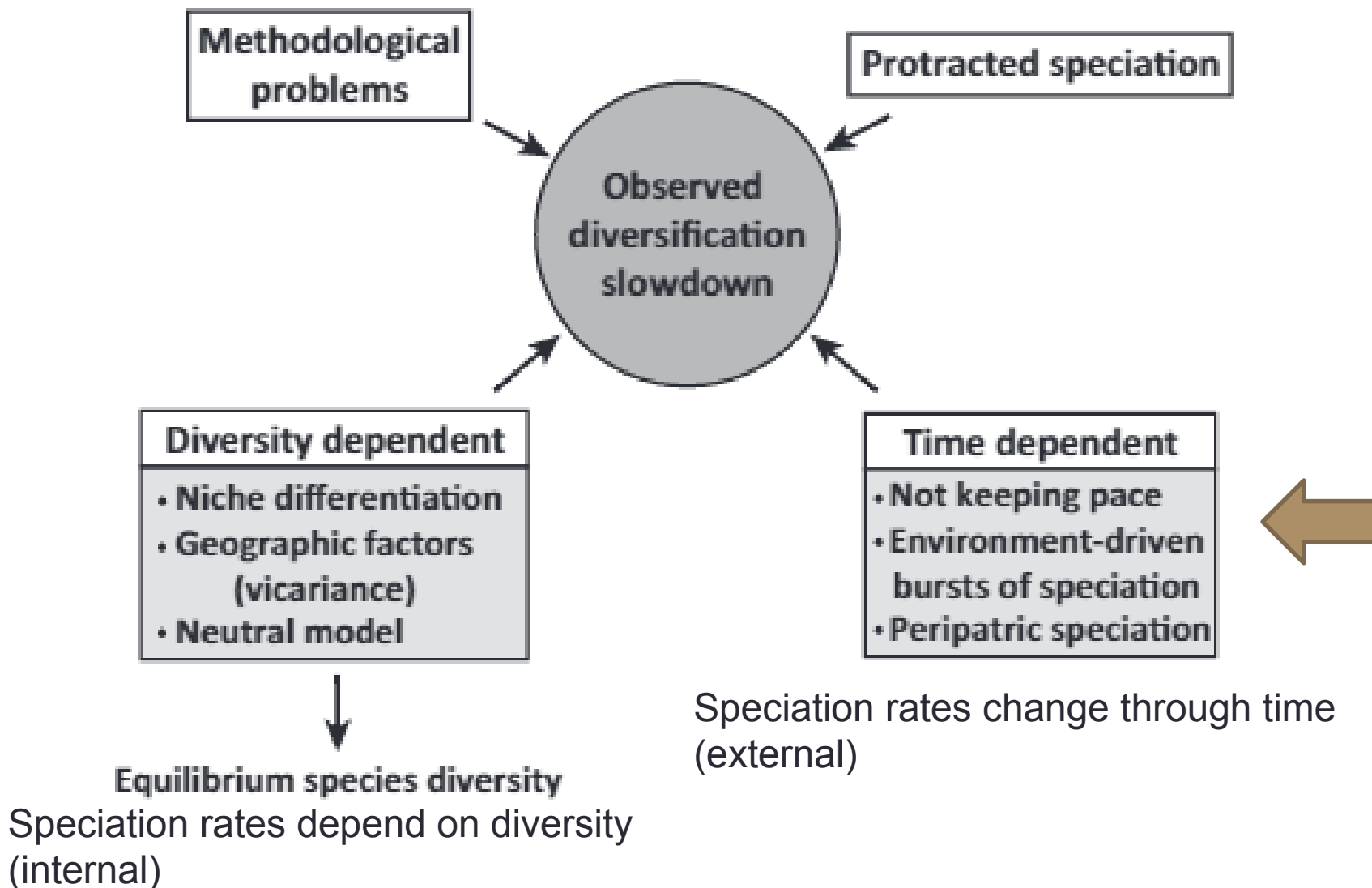


# Discussion

- Parameters are in line with fossil records
  - Extinction in model
- Better fit to the data
- Ezard et al. used complete fossil phylogeny Foraminifera (extinct & extant), estimate similar extinction rates.

- Diversity Dependent Models
  - New species - New niches?
- Mechanisms are still unclear
- Diversification slowdown at present
  - K reached always at present?
- Meta-analysis of early burst 2 out of 88

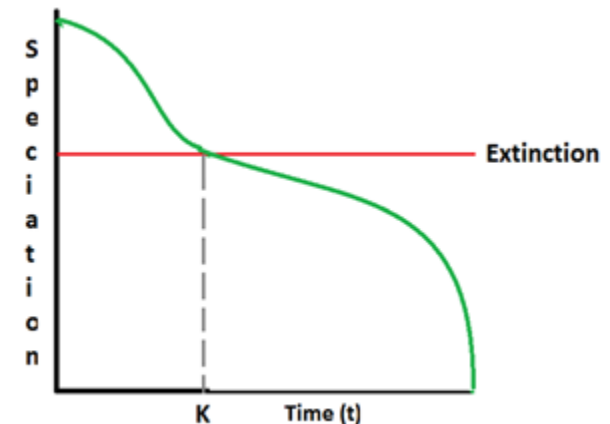
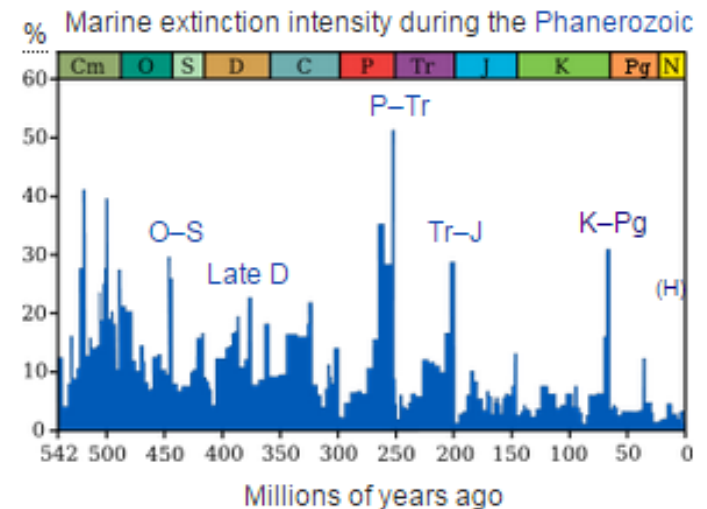
# Diversification Slowdown



# Time dependent model

## Environmental drivers

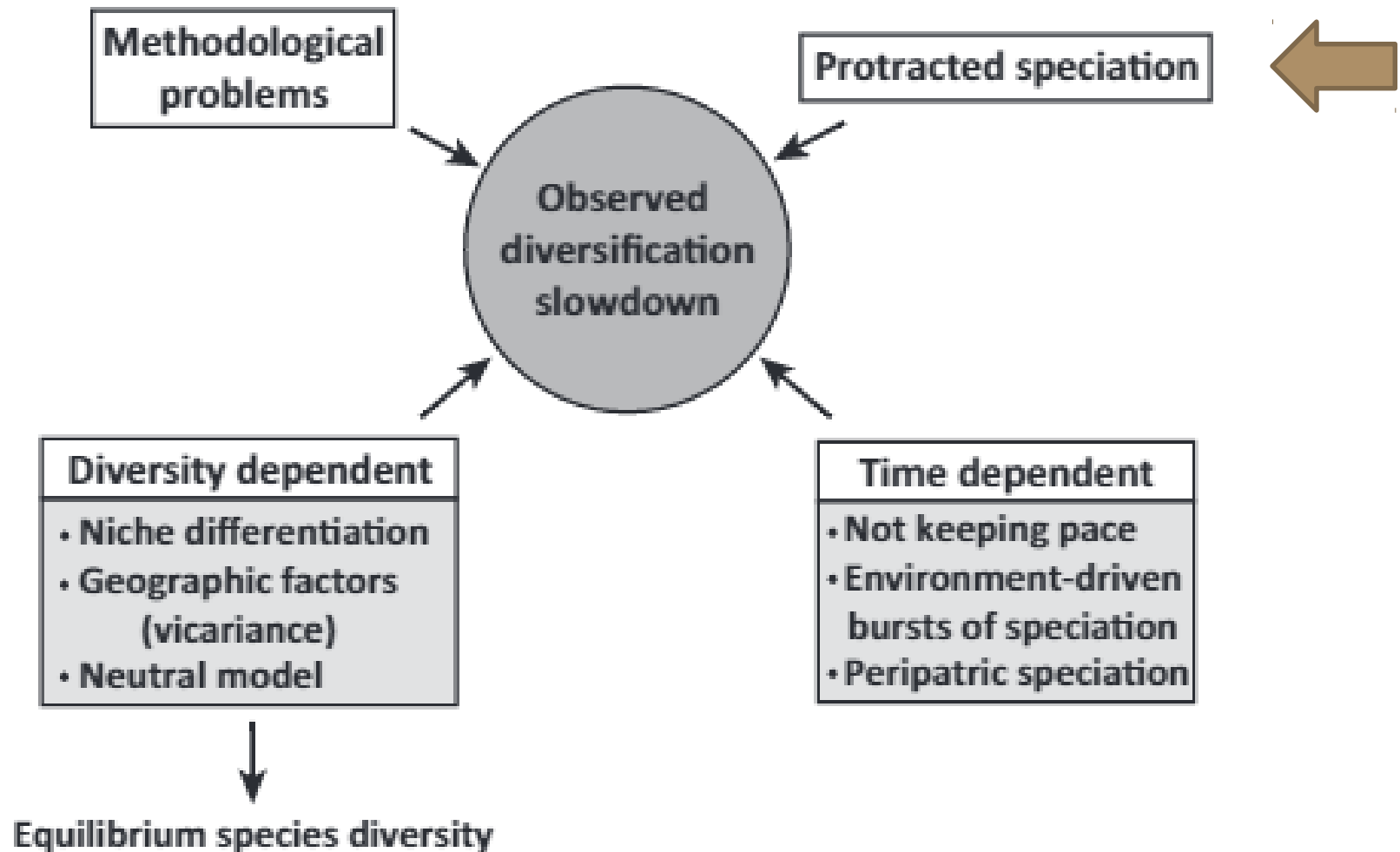
- Abiotic
  - Geographical
  - Climatic
- Biotic
  - Access to food
  - Predator intensity



EXTERNAL FEEDBACK

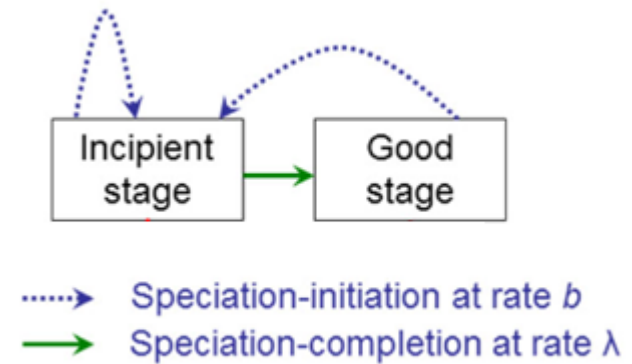
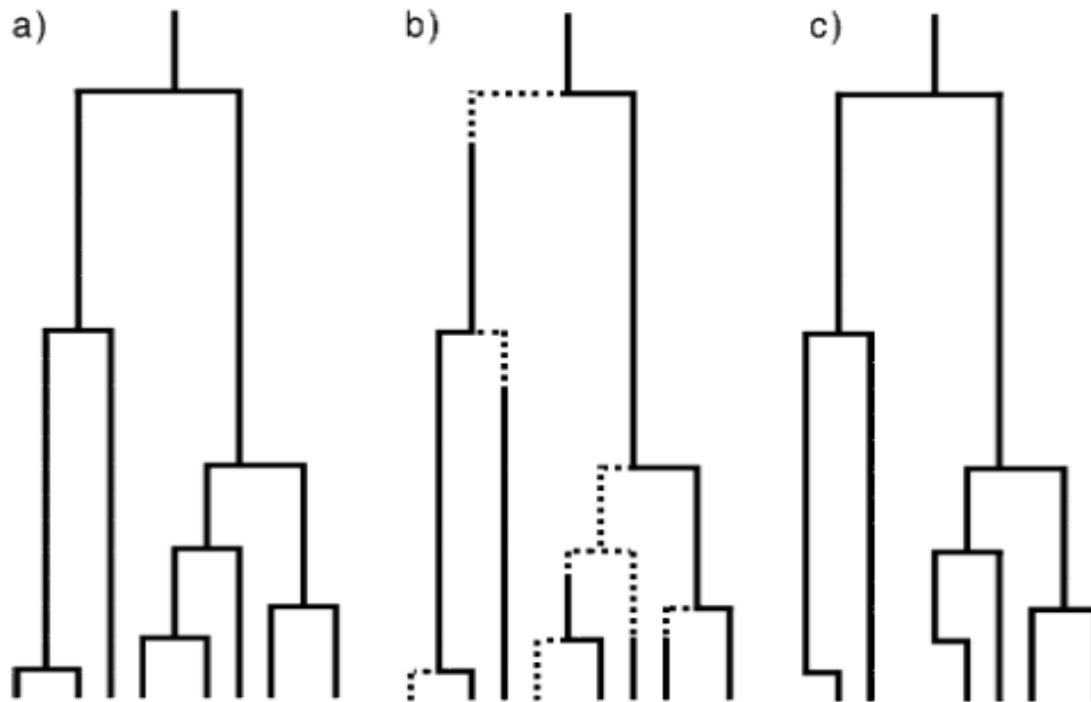
Diversification slowdowns

# Diversification Slowdown



# Protracted Speciation

Pure Birth Model (no extinction)

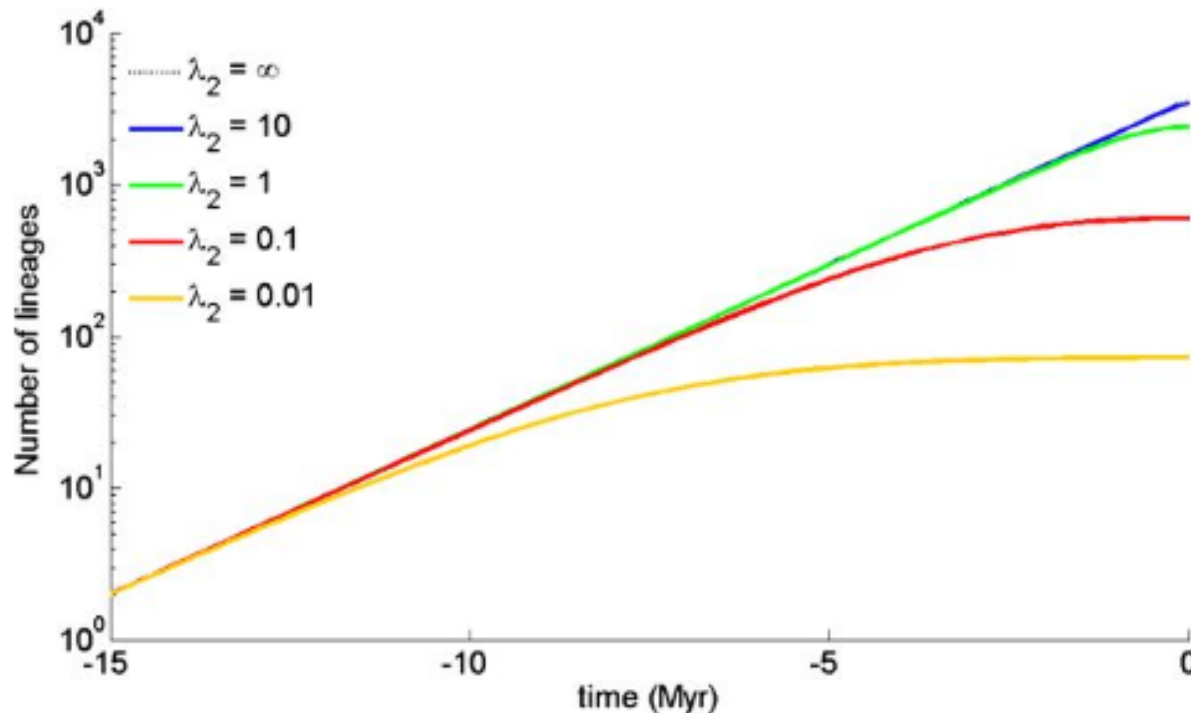


# Protracted Speciation Model - E

$\lambda_1$  = speciation rate

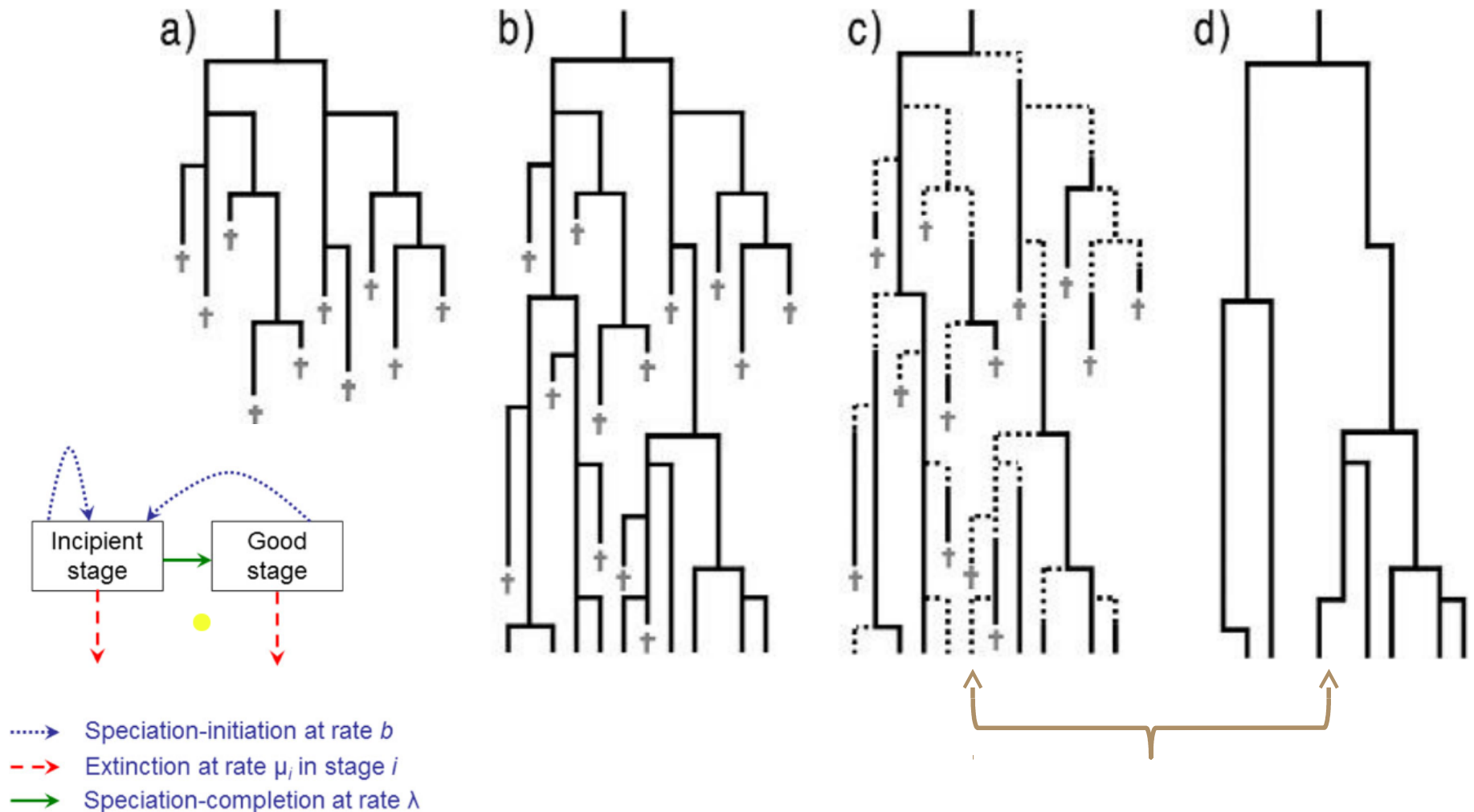
$\lambda_2$  = "good" speciation rate

$$\mathbb{E}[L; t, T] = N_g(0) \left( \exp(\lambda_1 t) - \frac{e^{(\lambda_1 t)} - e^{(-\lambda_2 t)}}{1 + \frac{\lambda_2}{\lambda_1} e^{(\lambda_1 + \lambda_2)(T-t)}} \right)$$

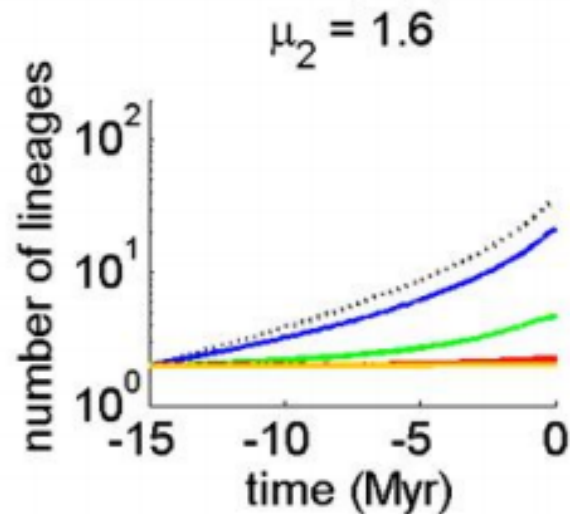
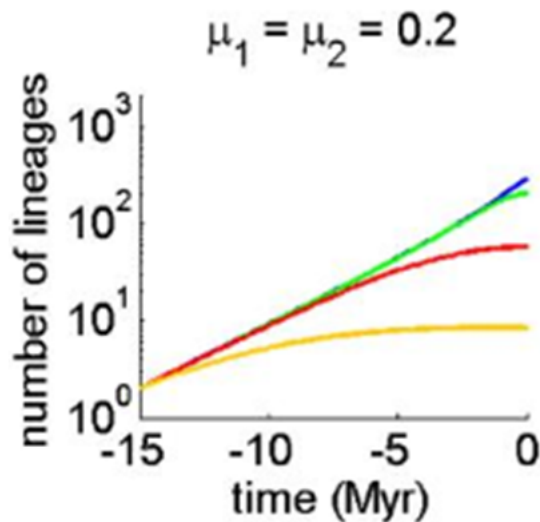
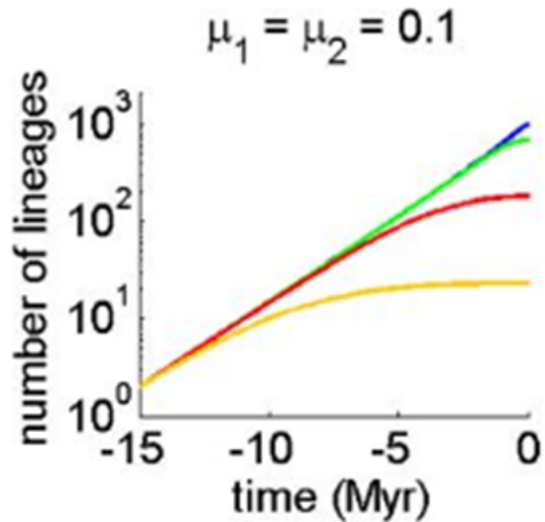
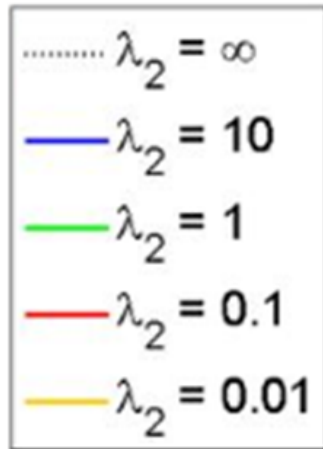




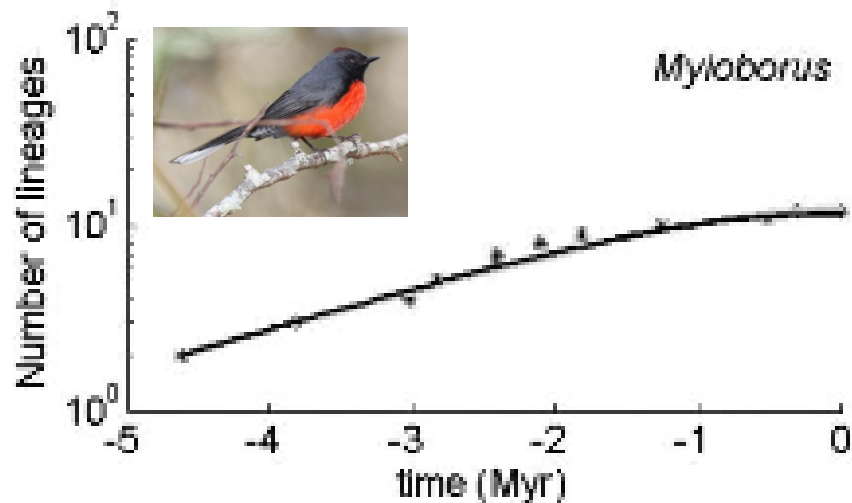
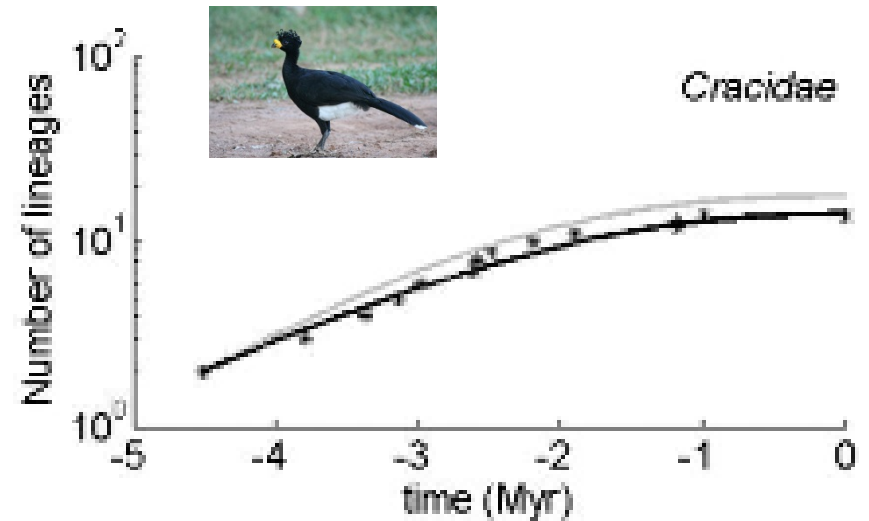
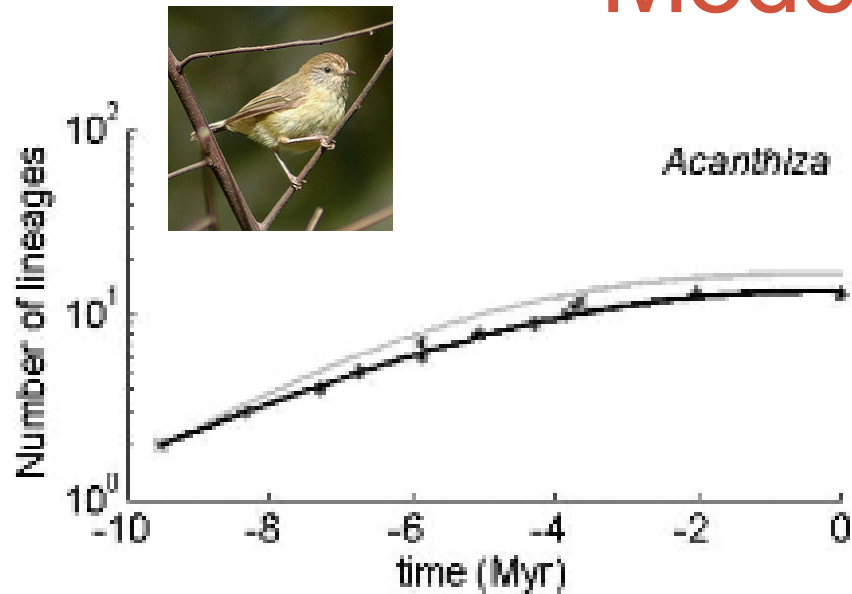
# Protracted Speciation Model + E



# Protracted Speciation Model + E



# Model Fitting



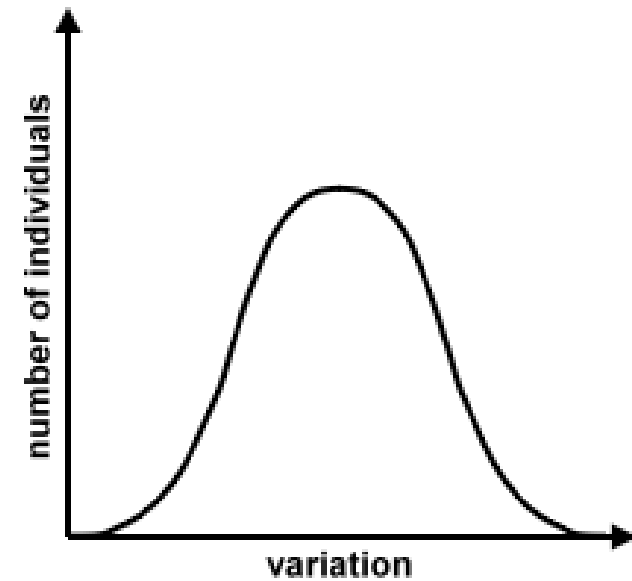
# Discussion

- Explain slowdowns
- Predict more imbalanced trees  $\lambda_3 < \lambda_1$
- Not by chance slowdown in present
- Speciation takes time – Extinction takes time

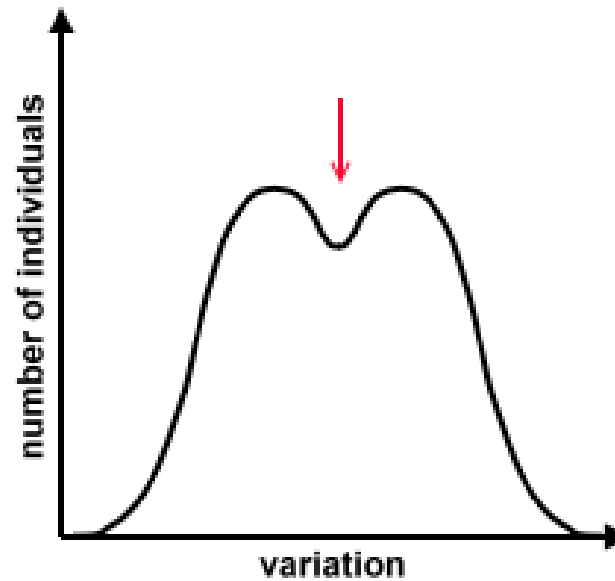
- Parameter estimation not accurate
  - speciation vs extinction <- Analytically

# New model

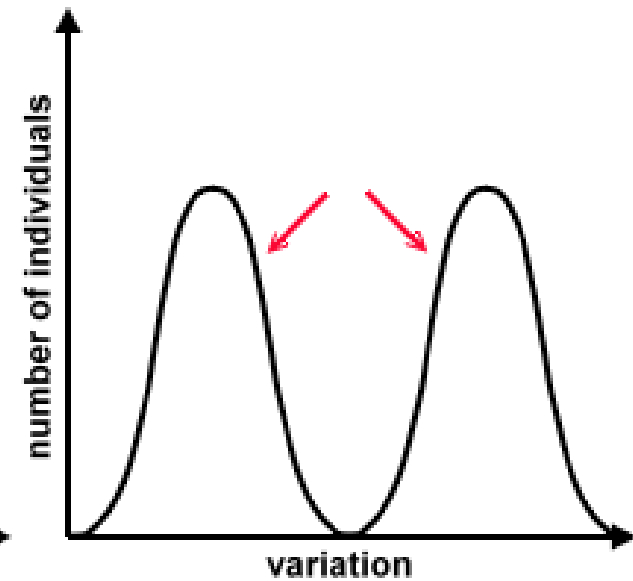
Normal Distribution



Normal selected against



Potential Speciation



Questions?