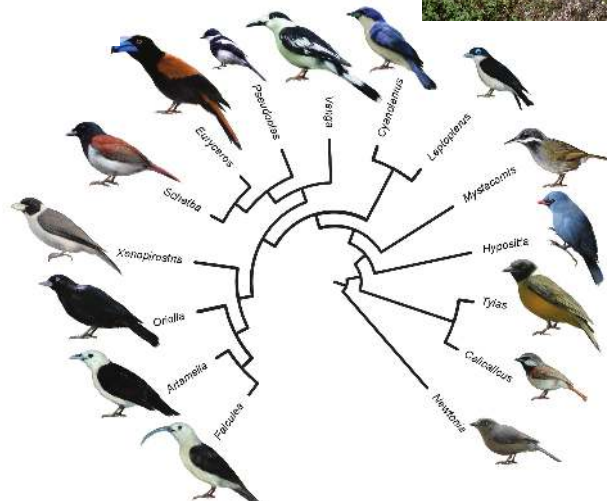
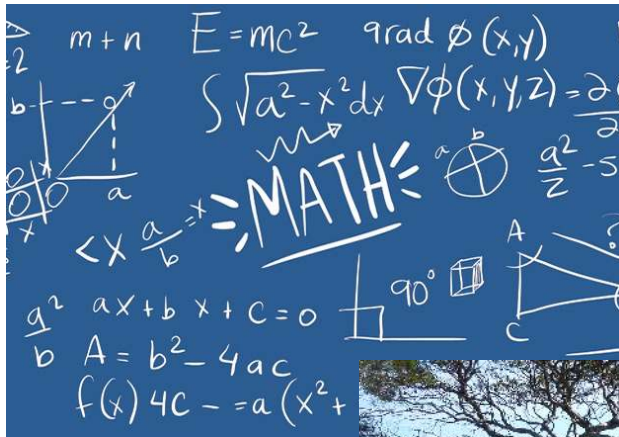


Hélène Morlon



Beast2

Bayesian evolutionary analysis by sampling trees

Cesky Krumlov

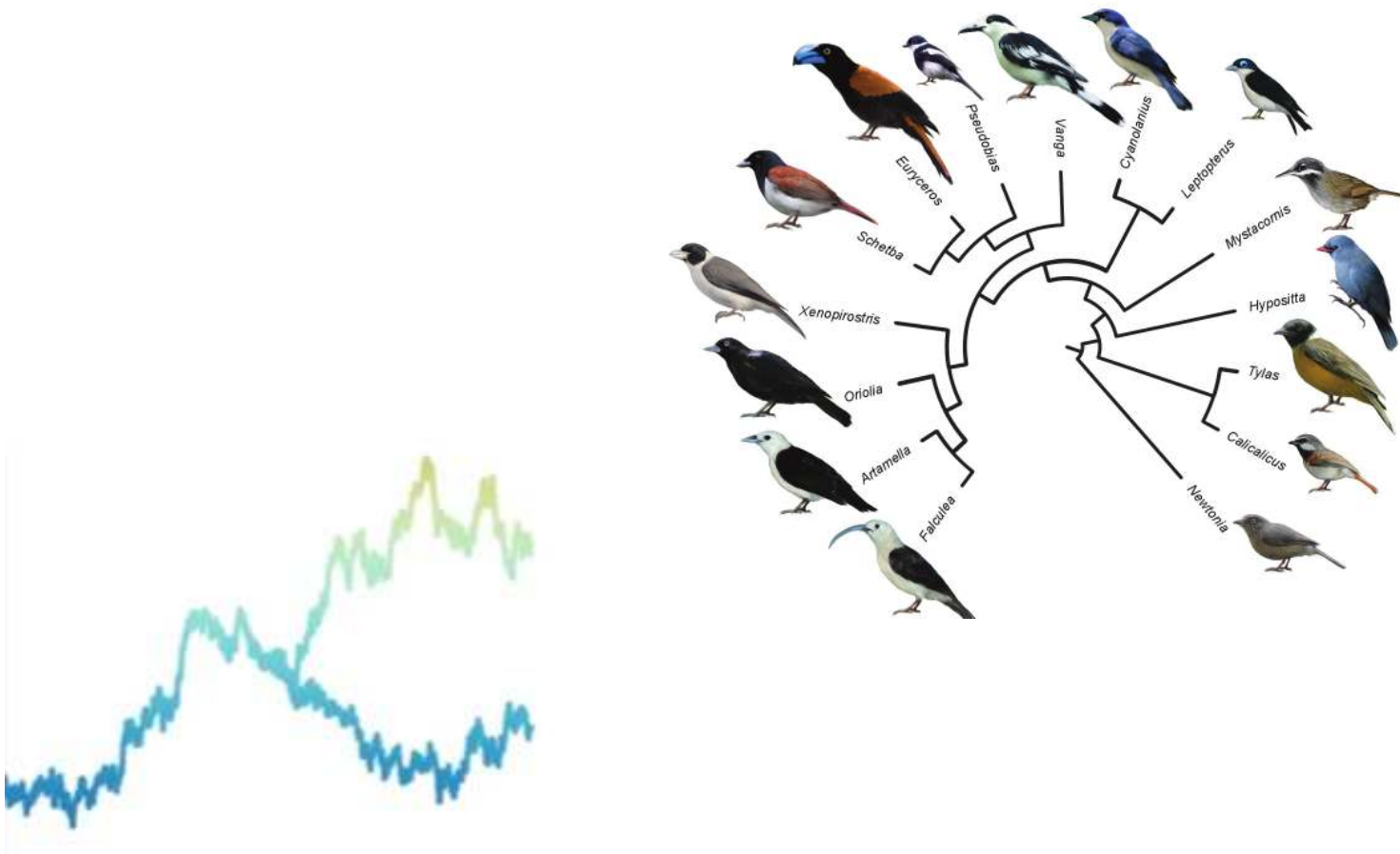


Joëlle Barido-Sottani

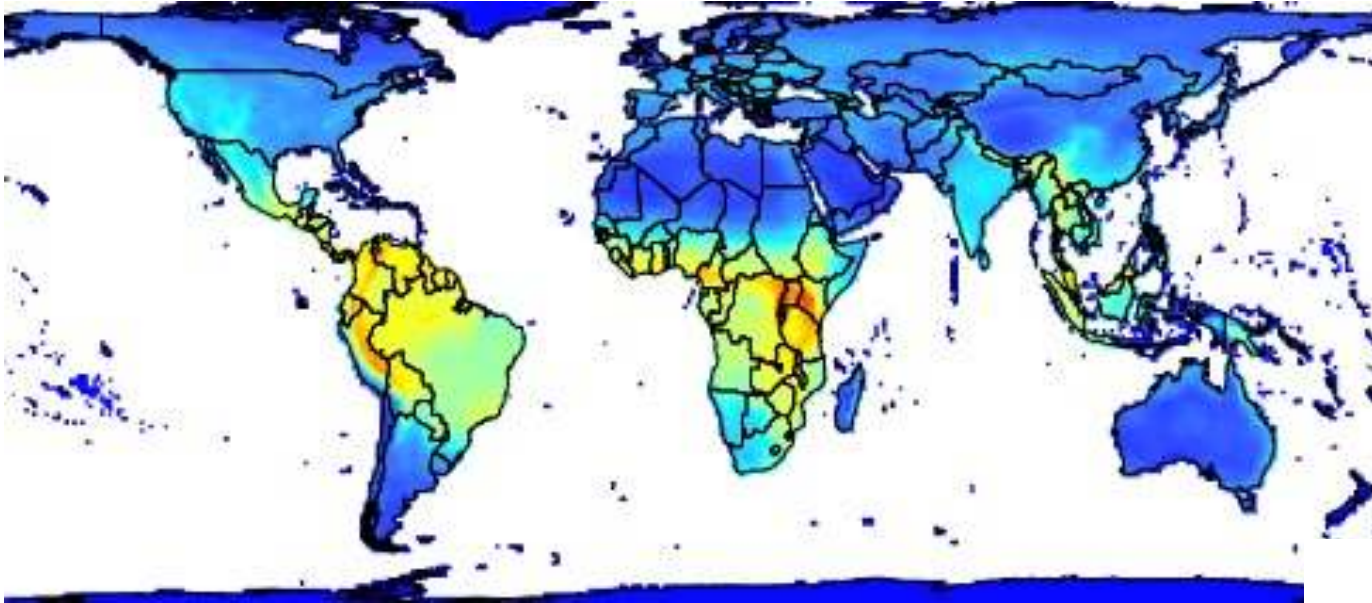


Mahwash Jamy

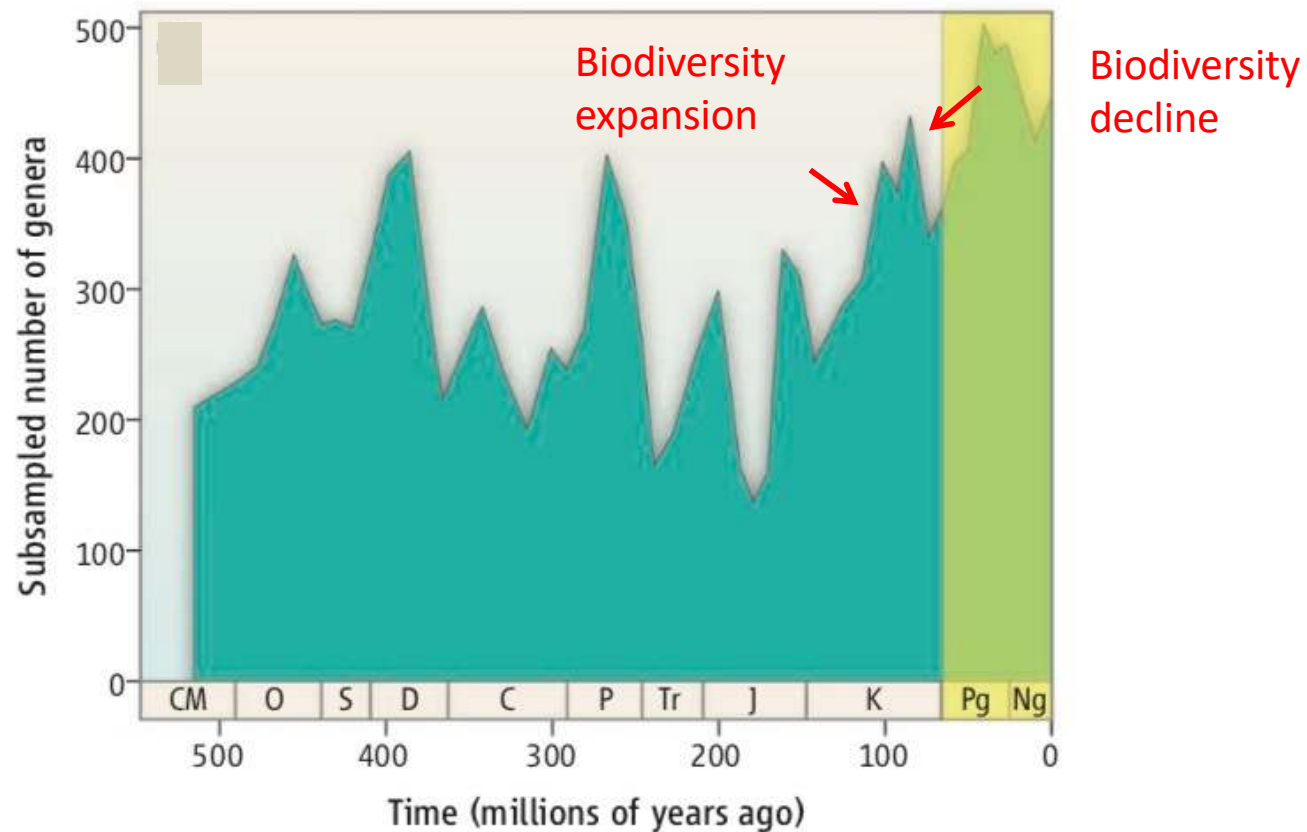
Trait evolution on trees, phenotypic and species diversification



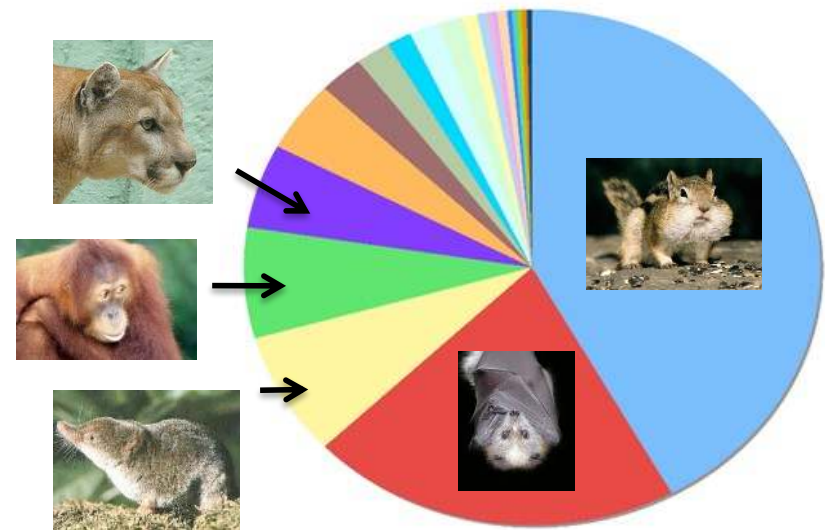
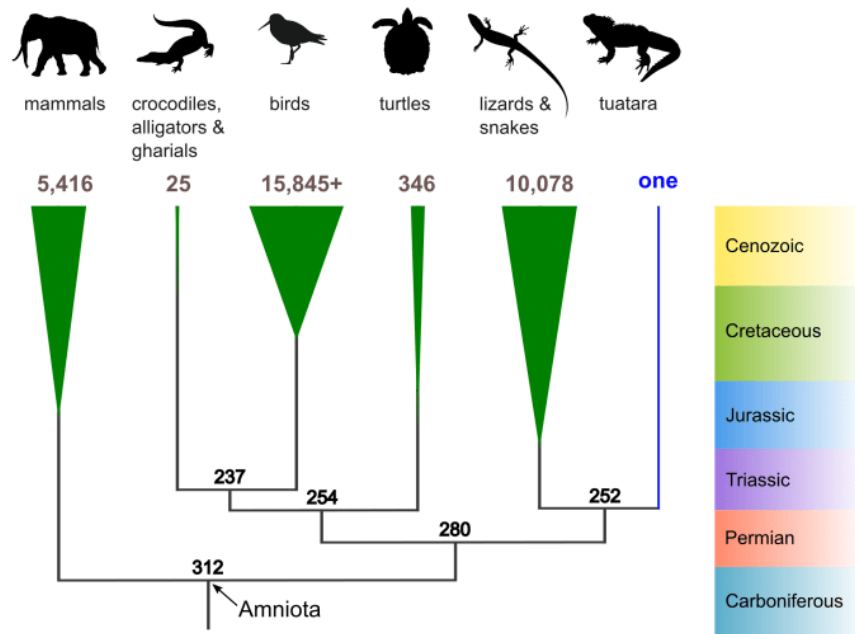
What are the processes that generate biodiversity as we see it around us today?



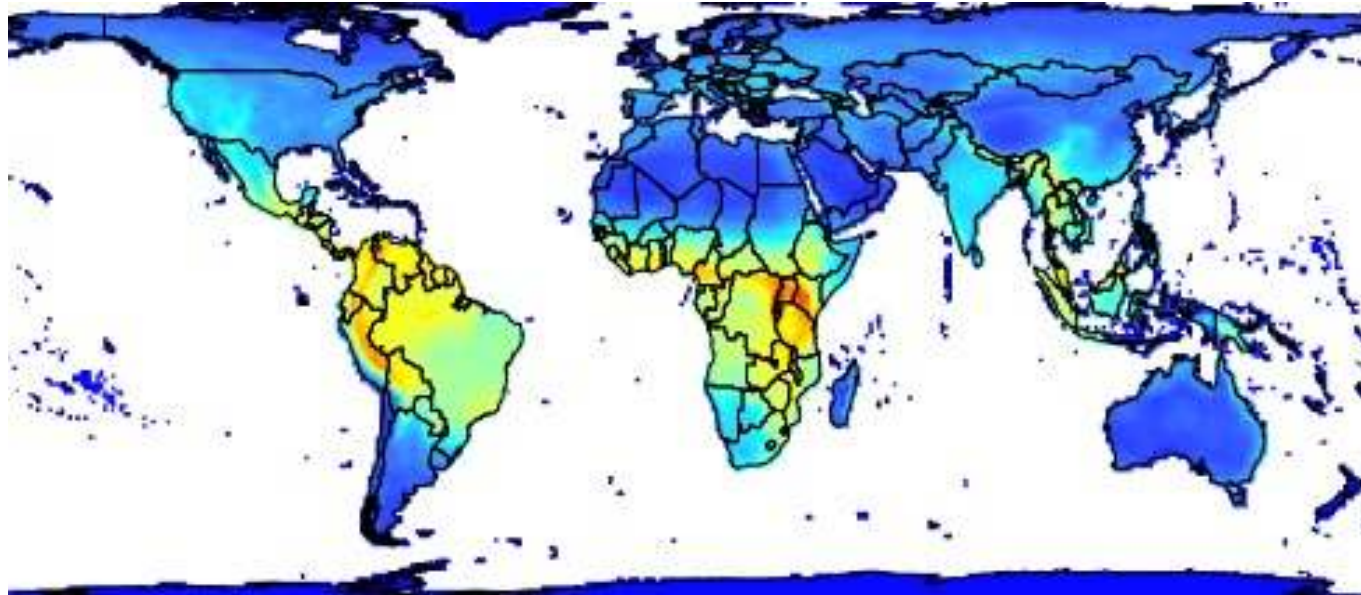
Present-day biodiversity is the result of historical events of speciation and extinction



The balance between speciation and extinction events explain why some species groups are much more species rich than others



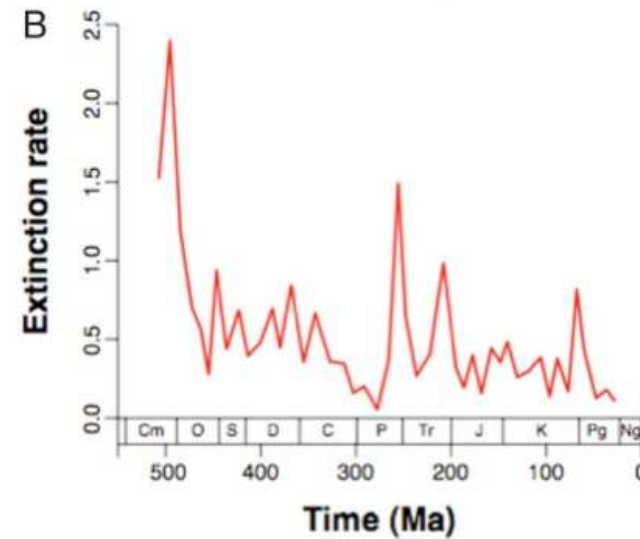
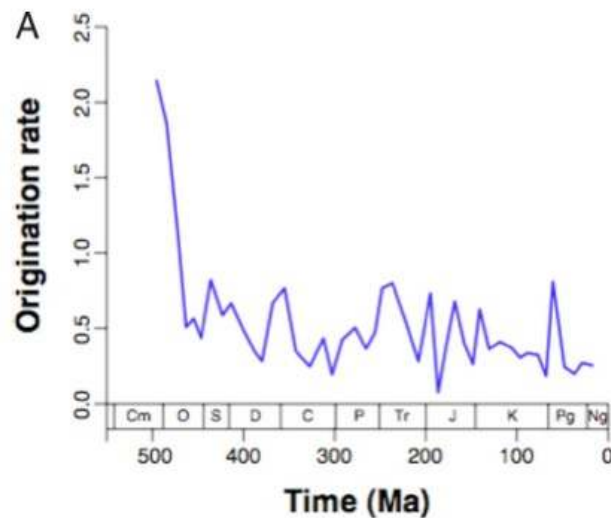
The balance between speciation, extinction and dispersal events explain why some regions of the planet are much more species rich than others



**How can we study species diversification
(speciation & extinction) using empirical
data?**

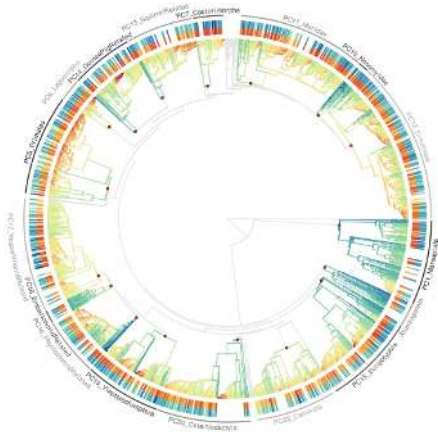
How can we study species diversification (speciation and extinction) using empirical data?

The fossil record

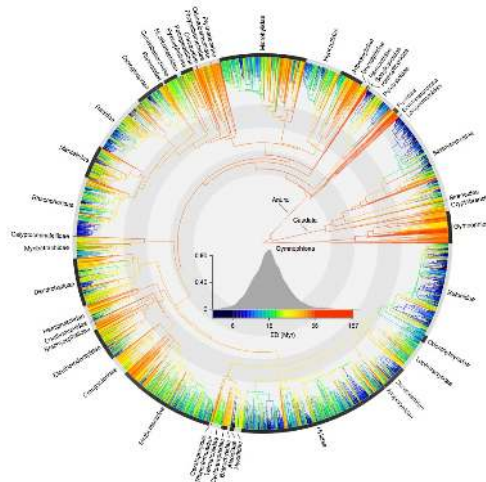


Alroy *PNAS* 2008

Studying species diversification from the phylogenetic trees of present-day species



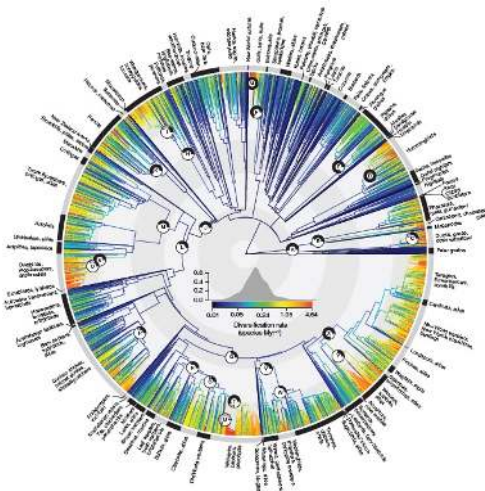
6 000 mammal species
Upham *et al.* PloSB 2019



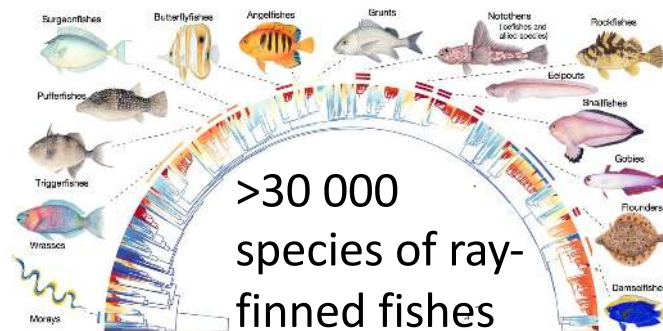
> 7 000 amphibian species
Jetz & Pyron *Nat Ecol Evol* 2018



2.2 Million species
on a single tree

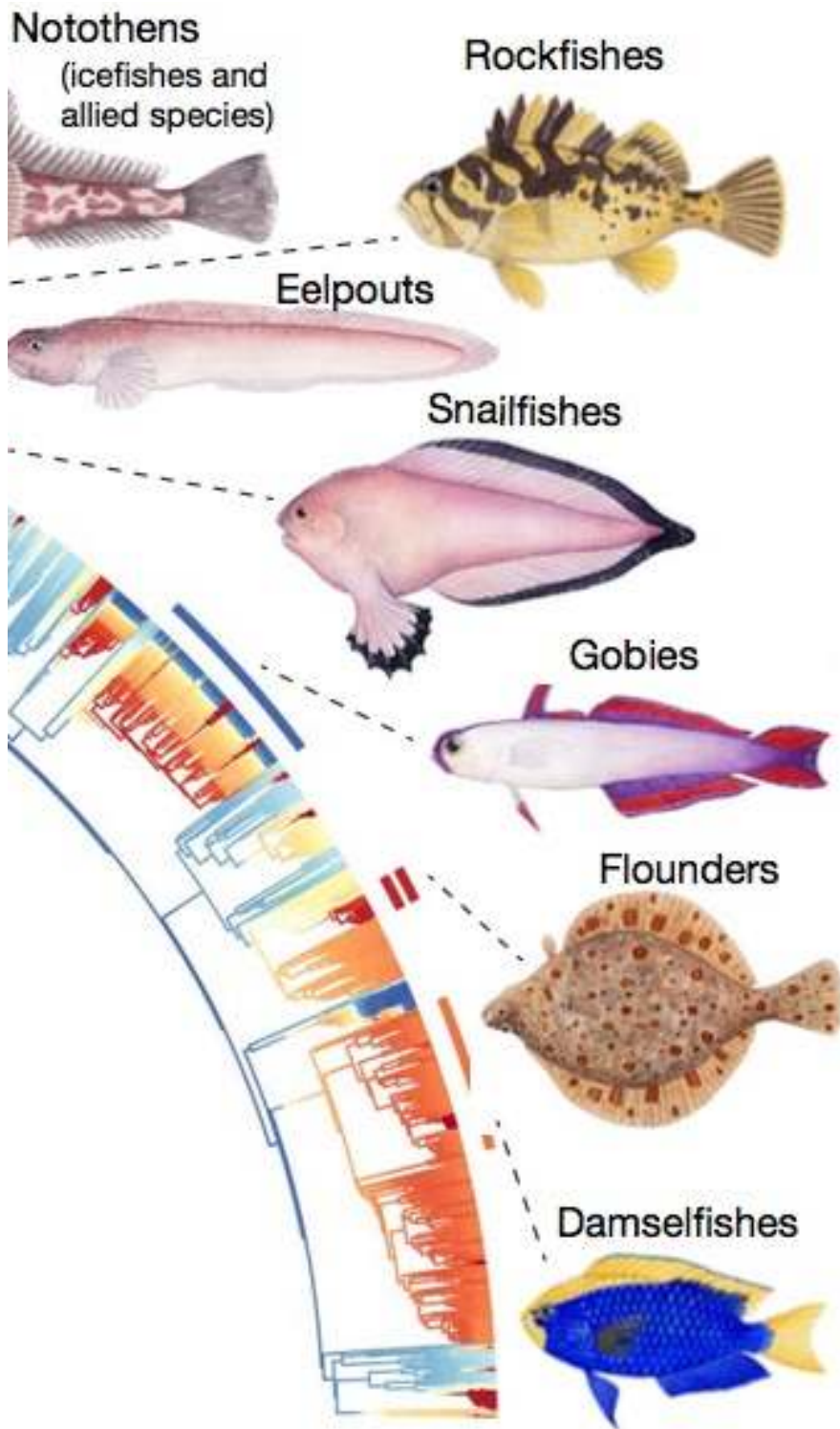


10 000 bird species
Jetz *et al.* Nature 2012

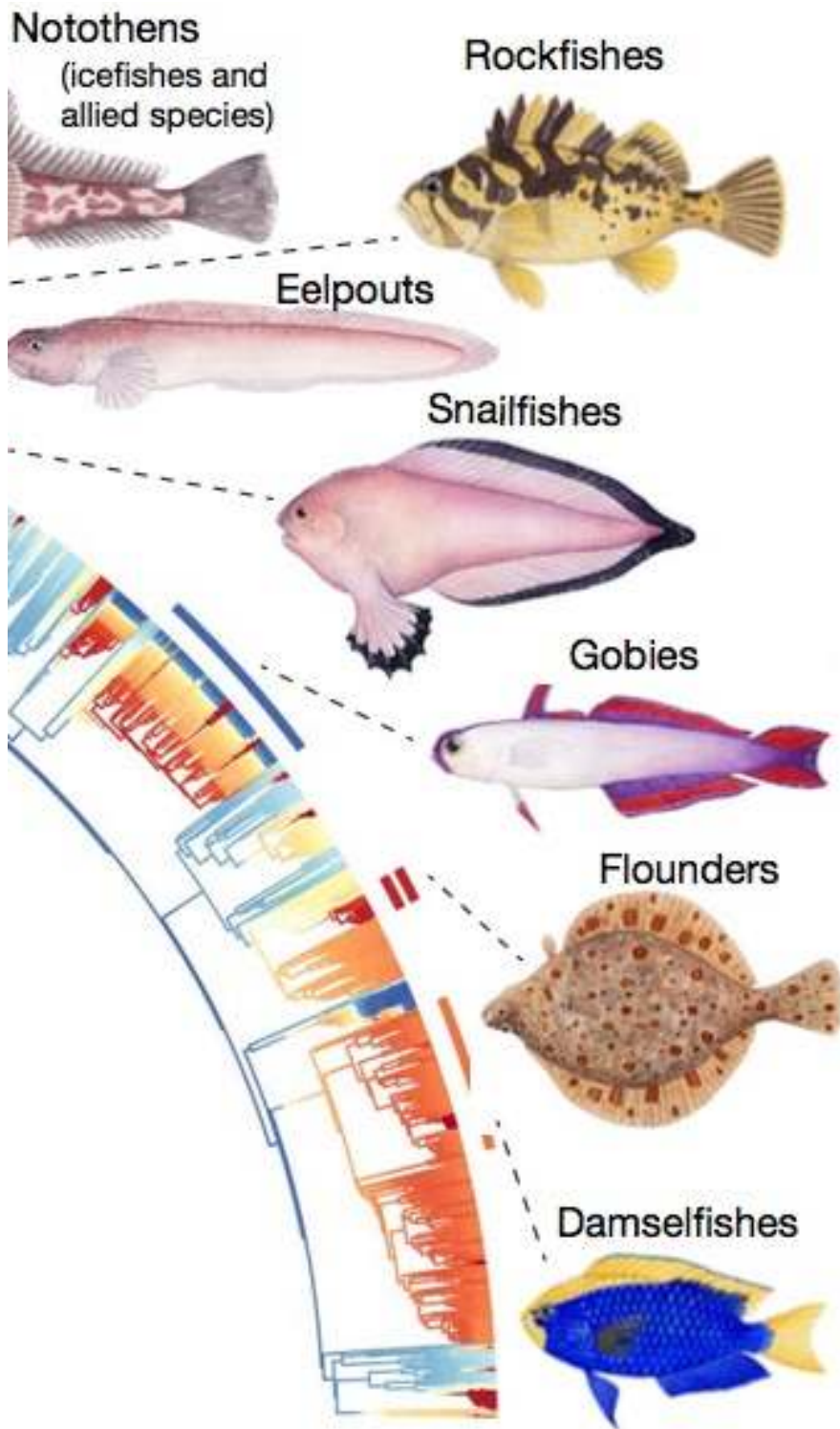


>30 000
species of ray-
finned fishes
Rabosky *et al.* Nature 2018

**Ultrametric and dated
phylogenies** : an hypothesis
of the order and timing of
divergences between
ancestral lineages that led to
present-day species



In what follows, we consider
the (dated) phylogenetic tree
as **data**

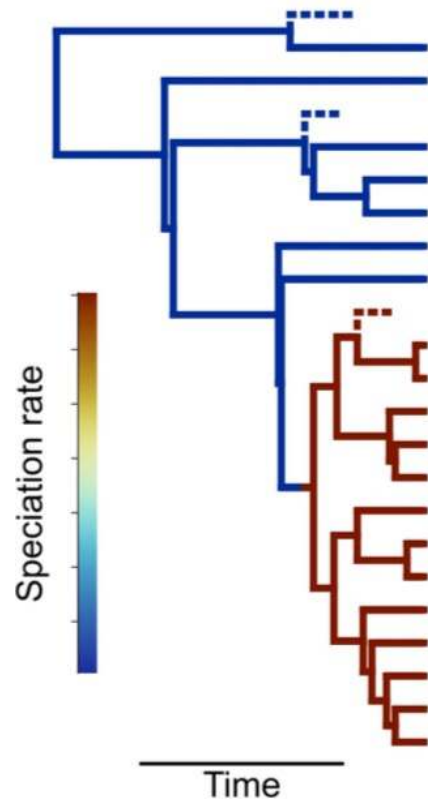


Keep listing even
if the only thing
you are
interested in is
inferring the tree!

Phylogenetic approaches for studying diversification

Develop **diversification models** AND **statistical inference approaches** that allow adjusting the models to **phylogenetic trees** to **test alternative hypotheses about diversification** and **estimate speciation and extinction rates**

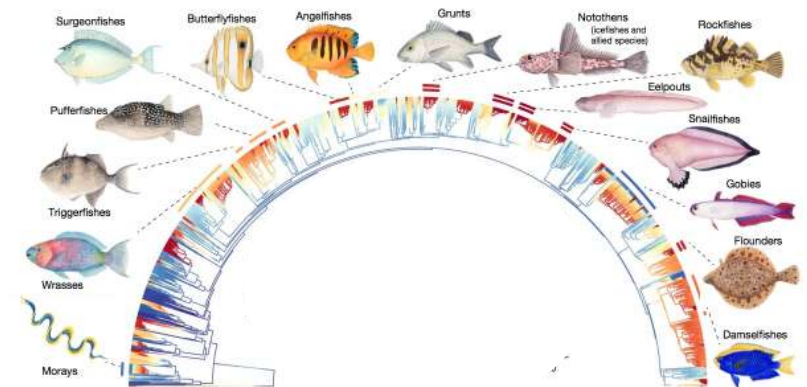
Diversification model



Statistical inference



Phylogenetic tree

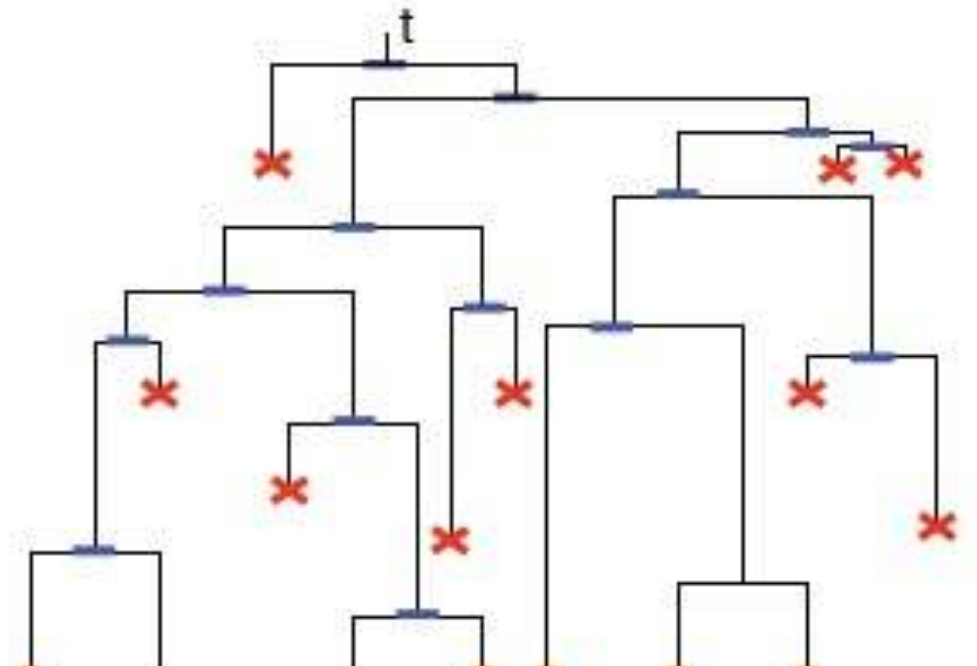


Hypothesis testing
Estimation of speciation and extinction rates

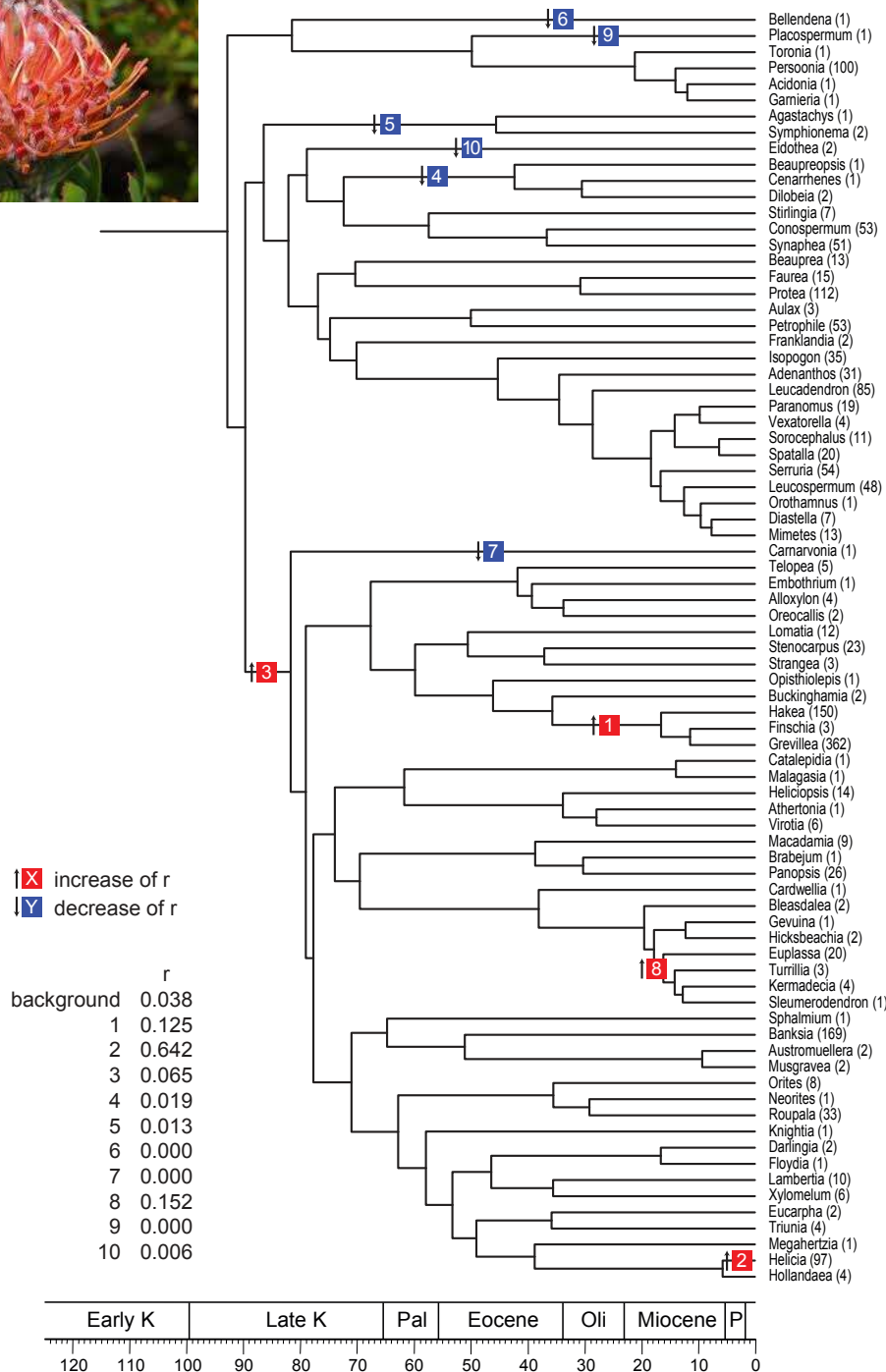
Birth-death model for the analysis of diversification

We model the evolution of a given clade (group of species that contains a common ancestor and all its descendants) with stochastic birth-death models:

- the clade starts with a single ancestor at time T
- species give rise to new species with the **per lineage per unit time rate of speciation** λ , and they go extinct with the **per lineage per unit time rate of extinction** μ



Here a lineage corresponds to a species



Estimating diversification from the age and size of a clade

In the absence of extinction
(pure birth, Yule model)

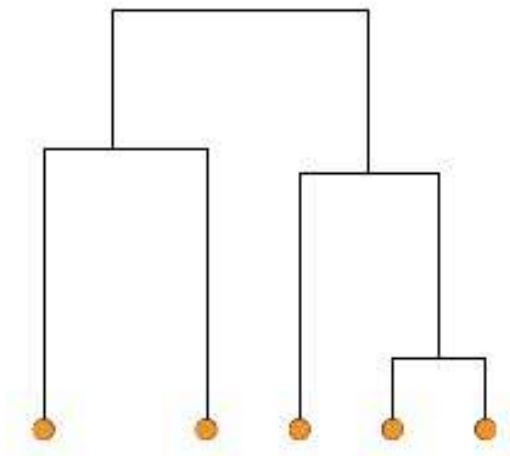
$$\hat{\lambda} = \frac{\log(n)}{T}$$

With extinction
(birth-death model)

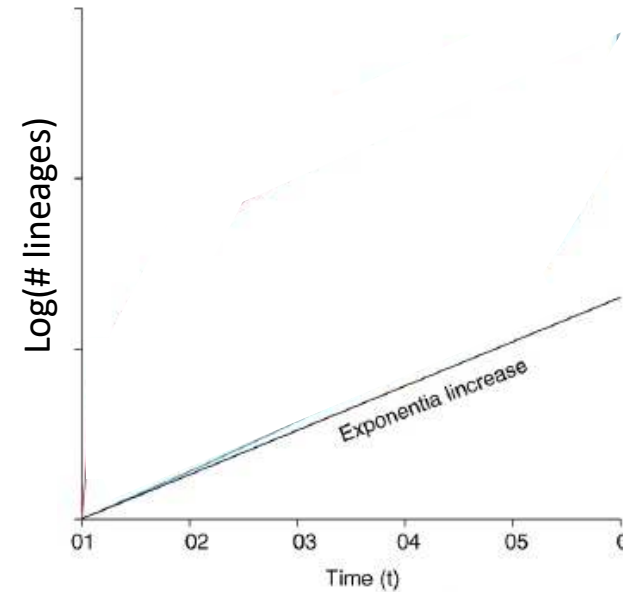
$$\hat{r} = \frac{1}{T} \log(n(1 - \varepsilon) + \varepsilon) \quad \varepsilon = \frac{\mu}{\lambda}$$

↑
 $r = \lambda - \mu$

Estimating diversification using Lineage Through Time plots (LTT)

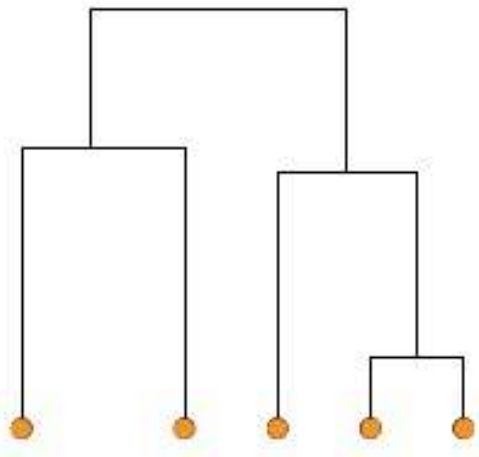


Phylogenetic tree of present-day
species

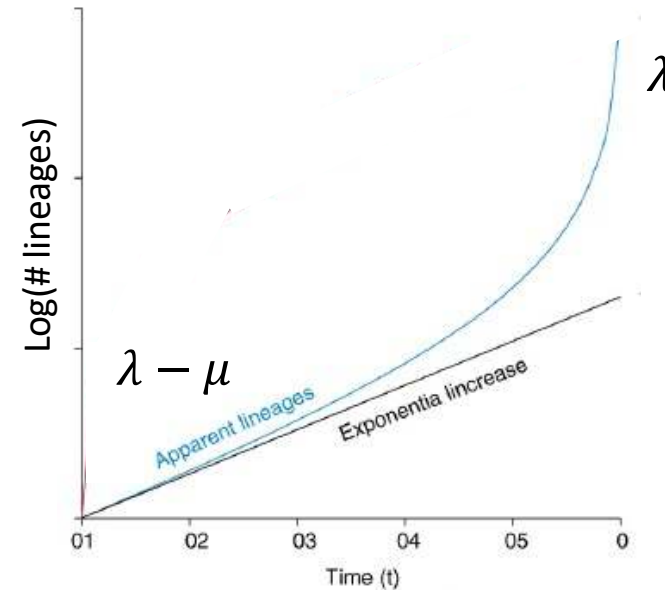


In the absence of extinction, an estimate of the speciation rate is given by the slope of the Lineage Through Time plot

Estimating diversification using Lineage Through Time plots (LTT)



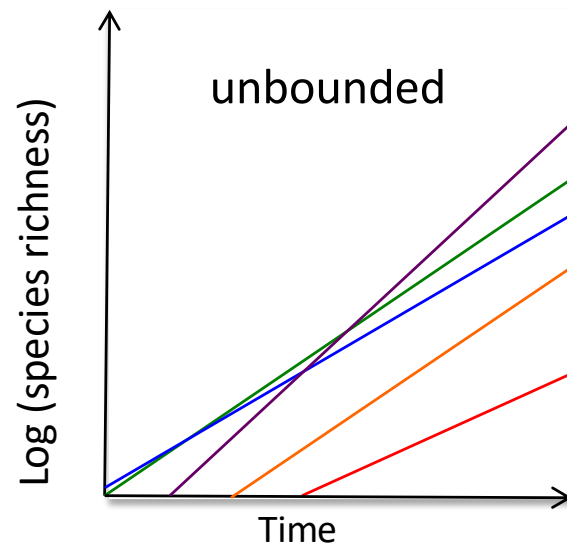
Phylogenetic tree of present-day species



With extinction, the Lineage Through Time plot is characterized by an acceleration towards the present known as « the pull of the present »

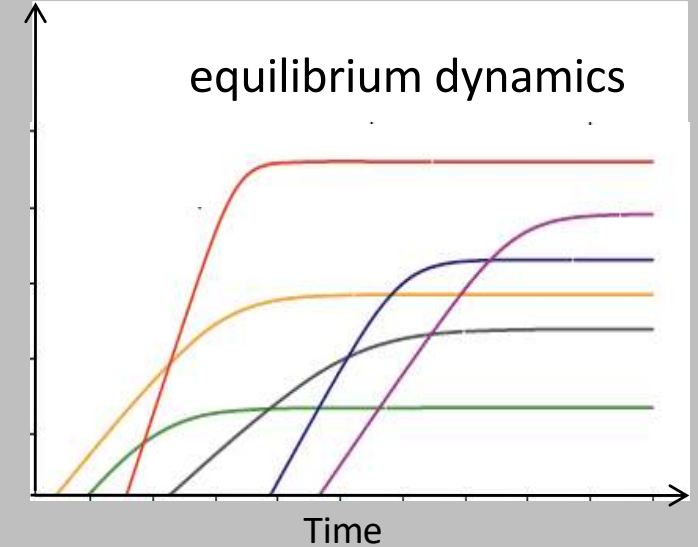
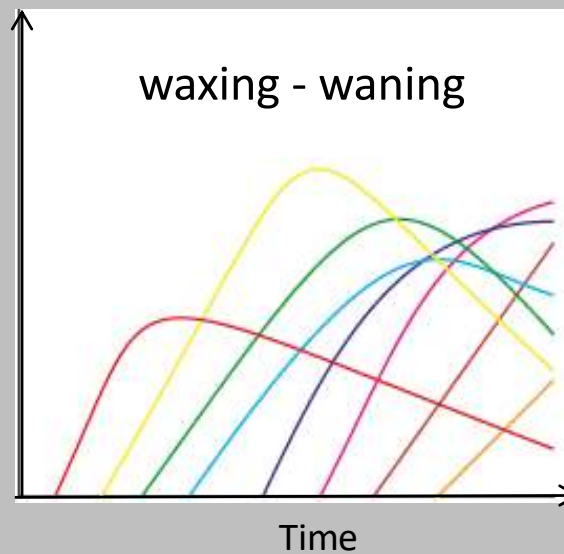
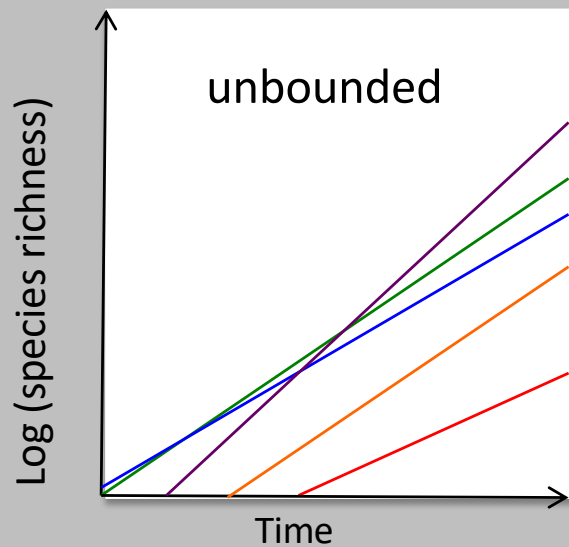
The slope towards the present provides an estimate of the speciation rate, the slope in the past provides an estimate of the net diversification rate.

All the above methods assume speciation and extinction rates are constant through time and homogeneous across lineages

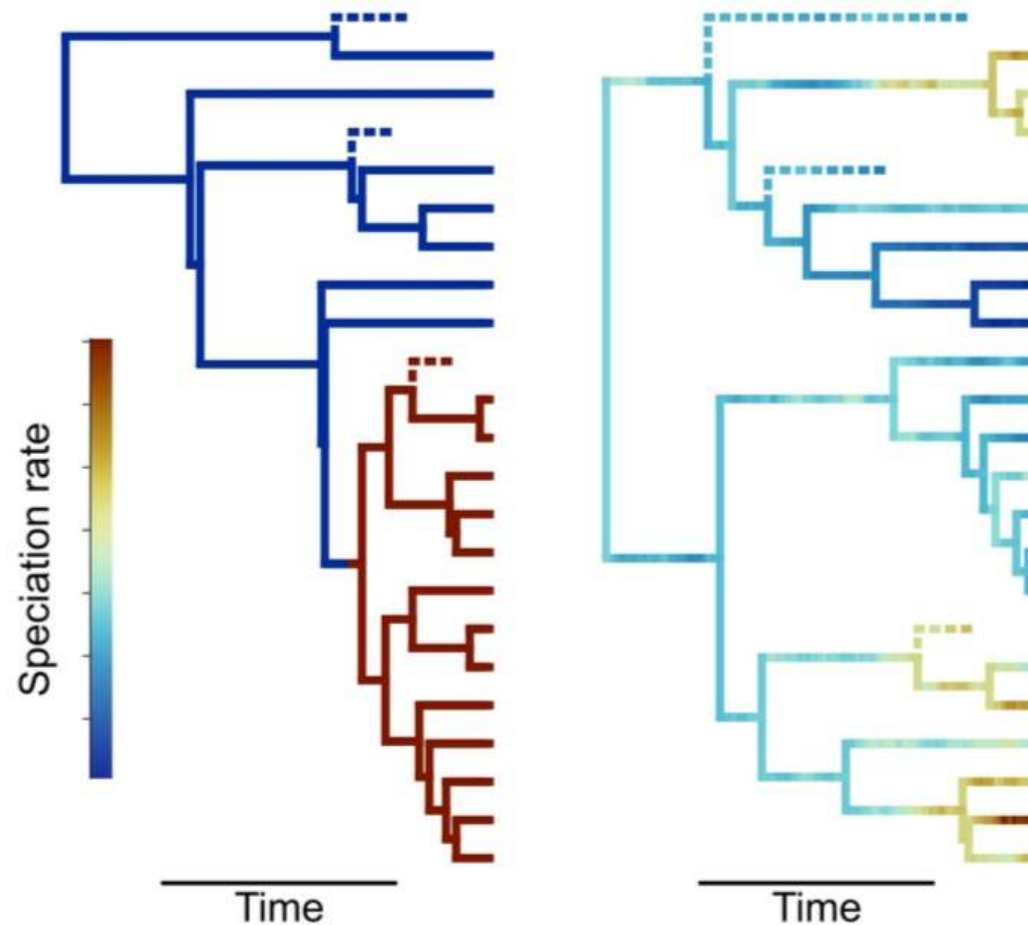


What if biodiversity dynamics are not unbounded?

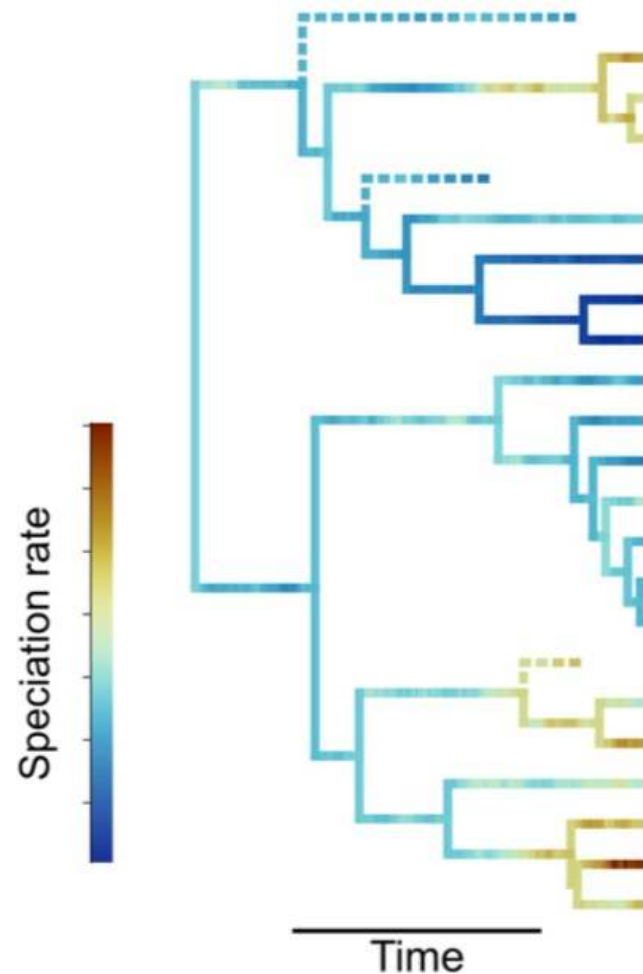
What if we want to test the support of different visions of how the evolution of diversity proceeds?



**What if we rates are not homogeneous across lineages
and we want to test the support of different visions of
how rate variation occurs?**



**Intuitively, the distribution of branching times informs
on temporal variation in speciation and extinction rates,
topology informs on rate variation across lineages**

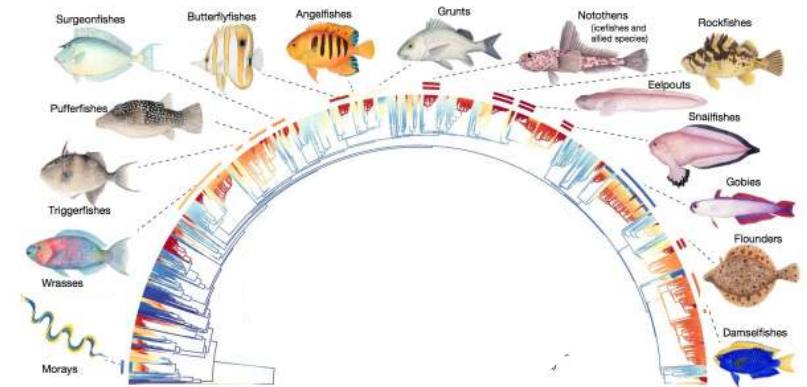
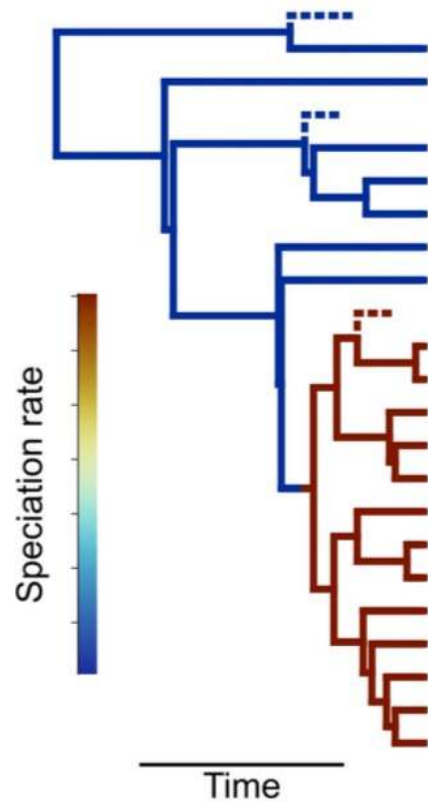


Statistical Inference

Diversification model



Phylogenetic tree



Hypothesis testing
Estimation of speciation and extinction rates

Likelihood-based inference

Given a parametric model (a model defined with one or several free parameters θ), we want to find the values of the parameters that most likely produced the data that is actually observed.

The likelihood function is defined as: $L_{\mathbf{x}}(\theta) = f_{\theta}(\mathbf{x})$ where $f_{\theta}(\mathbf{x})$ is the probability of observing a realization $\mathbf{x}$ under the model for parameters fixed at the value θ

The maximum likelihood estimate of θ is the value of θ that maximize $L_{\mathbf{x}}(\theta)$ with $\mathbf{x}$ the observed data

Likelihood-based inference

Given a family of parametric models, we want to find the model that most likely produced the data that is actually observed.

Step 1: we fit each model to the data, meaning that for each model, we find the set of parameters that maximize $L_x(\theta)$, and we record the value of the maximum likelihood.

Step 2: we compare the values of the likelihood associated to each model.

case #1: the different models have the same number of parameters -> the model with highest likelihood is selected

case #2: the models are nested (the more complex model can be transformed into the simpler model by imposing a set of constraints on the parameters) -> sequential likelihood ratio tests are used to select the 'best' model. The null hypothesis H_0 is that θ is in a specified subset Θ_0 of the parameter space Θ . The likelihood ratio is defined as:

$$\Lambda(x) = \frac{\sup\{L(\theta | x) : \theta \in \Theta_0\}}{\sup\{L(\theta | x) : \theta \in \Theta\}}$$

Wilk's theorem: under H_0 , $-2\log(\Lambda)$ is asymptotically chi-squared distributed with degrees of freedom the difference of dimensionality of Θ and Θ_0 . H_0 is rejected if $-2\log(\Lambda)$ is greater than the chi-squared value at the desired statistical significance.

Likelihood-based inference

Step 2: we compare the values of the likelihood associated to each model.

case #1: the different models have the same number of parameters

case #2: the models are nested

case #3: the models are not nested -> we compute the Akaike Information Criterion (AIC) of each model. The AIC is defined as $AIC = 2k - 2\ln(L)$ where k is the number of free parameters in the model and L is the maximum likelihood value. The model with minimum AIC value is preferred. AIC is a way to avoid overfitting by penalizing parameter-rich models

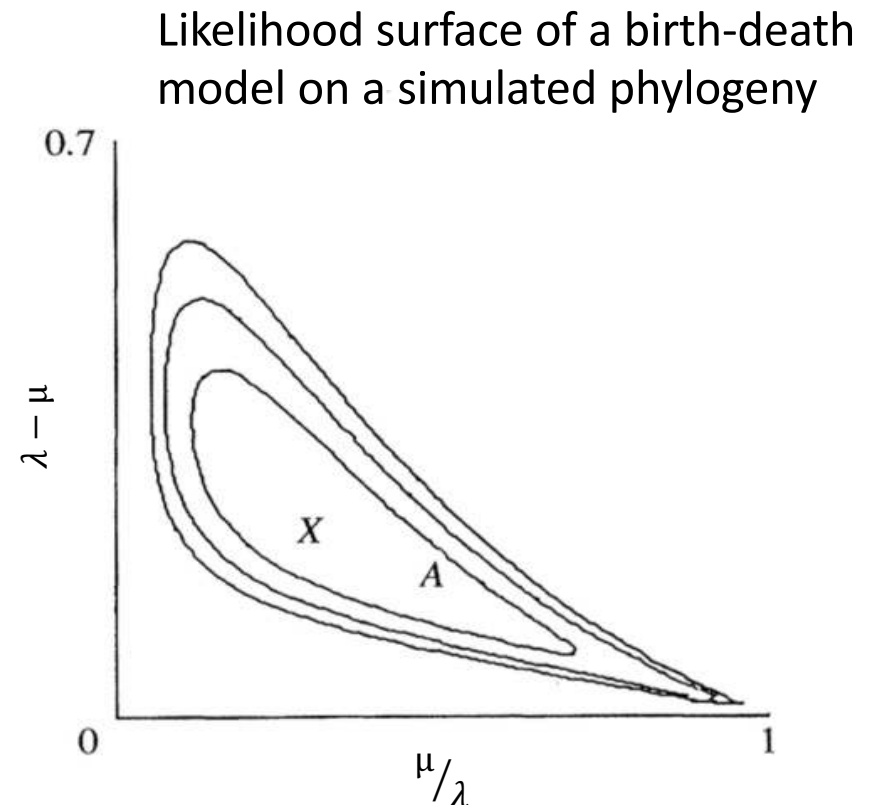
Given an empirical phylogeny, we can compare the statistical support of different diversification models, and estimate parameters of these models, i.e. λ and μ , using likelihood-based statistical inference

The likelihood is defined as

$$\mathcal{L}_x(\theta) = f_\theta(x)$$

where $f_\theta(x)$ is the probability of observing x under the model for parameters θ

The ML estimate is the parameter θ that maximizes $\mathcal{L}_x(\theta)$



Examples

(with a focus on developments from my research group)

Ecology Letters, (2014)

doi: 10.1111/ele.12251

REVIEW AND SYNTHESIS

Phylogenetic approaches for studying diversification

Hélène Morlon*

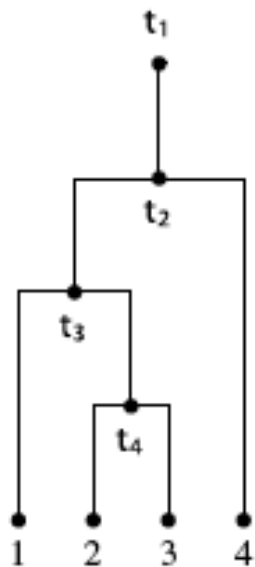
Abstract

Estimating rates of speciation and extinction, and understanding how and why they vary over evolutionary time, geographical space and species groups, is a key to understanding how ecologi-

Likelihood of a phylogeny of extant species under the birth-death process

stem age t_1
 speciation rate λ
 extinction rate μ

+ λ and μ can vary over time
 sampling probability f



sampling probability

probability that a lineage survives from t_1 to t_2 and leaves no descendant in the sample

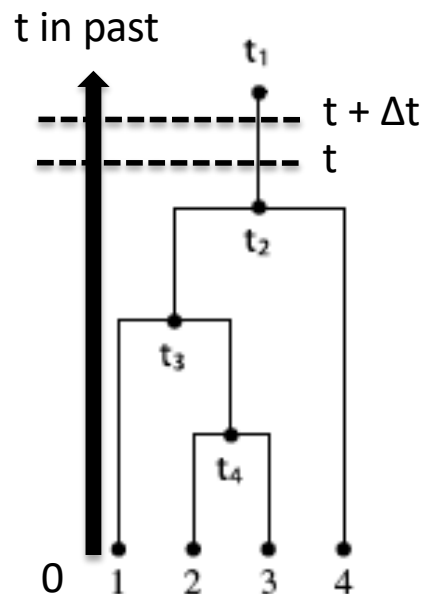
$$\mathcal{L}(t_1, \dots, t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^n \lambda(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)},$$

speciation rate at time t_i

probability that a lineage alive at time t_1 has no descendant in the sample

Likelihood of a phylogeny of extant species under the birth-death process

birth-death model



stem age t_1

speciation rate λ

extinction rate μ

+

λ and μ can vary over time

sampling fraction f

$\Phi(t) = \mathbb{P}\{\text{a lineage is not in the sample} | \text{it was alive at the time } t\}$

$$\begin{aligned} \Phi(t + \Delta t) &= \mu(t)\Delta t \\ &+ (1 - \mu(t)\Delta t)\lambda(t)\Phi^2(t) \\ &+ (1 - \mu(t)\Delta t)(1 - \lambda(t)\Delta t)\Phi(t) \\ &+ o(\Delta t). \end{aligned}$$

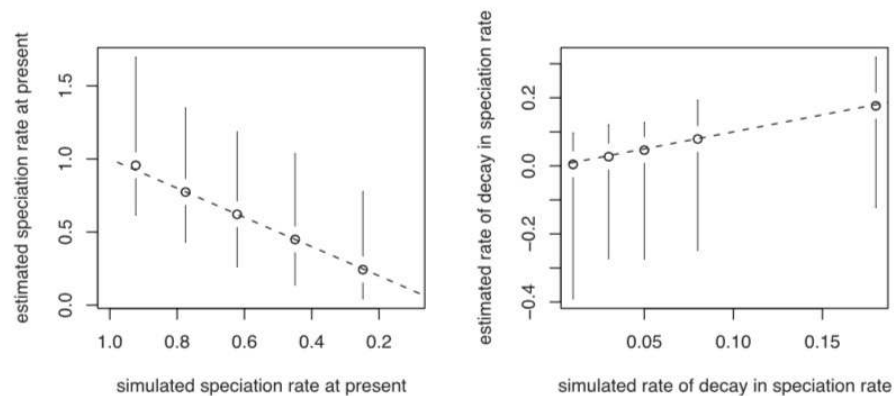
$\Delta t \rightarrow 0$

$$\frac{d\Phi}{dt} = \mu(t) - (\lambda(t) + \mu(t))\Phi(t) + \lambda(t)\Phi^2(t)$$

$$\Phi(t) = 1 - \frac{e^{\int_0^t \lambda(u) - \mu(u) du}}{\frac{1}{f} + \int_0^t e^{\int_0^s \lambda(u) - \mu(u) du} \lambda(s) ds}$$

Unbiased parameter estimates

Exponential decay of speciation rate,
constant extinction



Exponential increase of extinction rate,
constant speciation

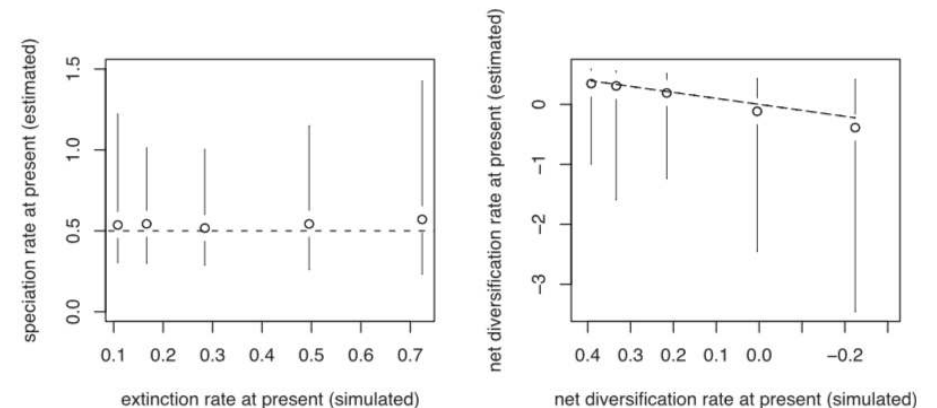
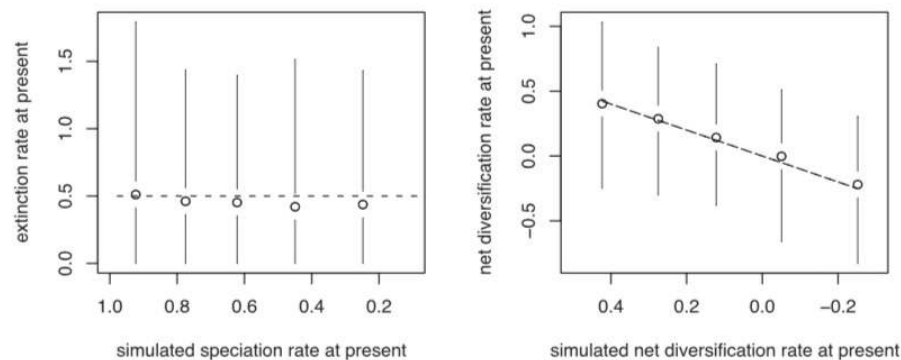
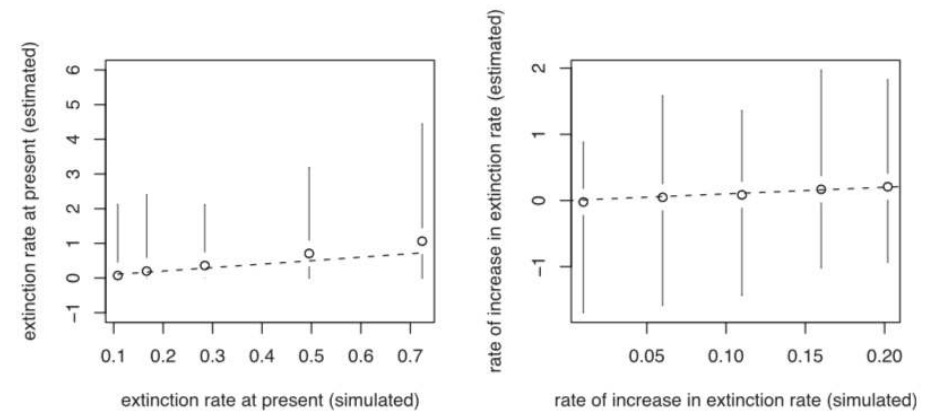


Illustration: the diversification of cetaceans

We can test the statistical support of models where diversification rates “shift” at the base of major families

Support for a 4-shift rate model in the cetacean phylogeny

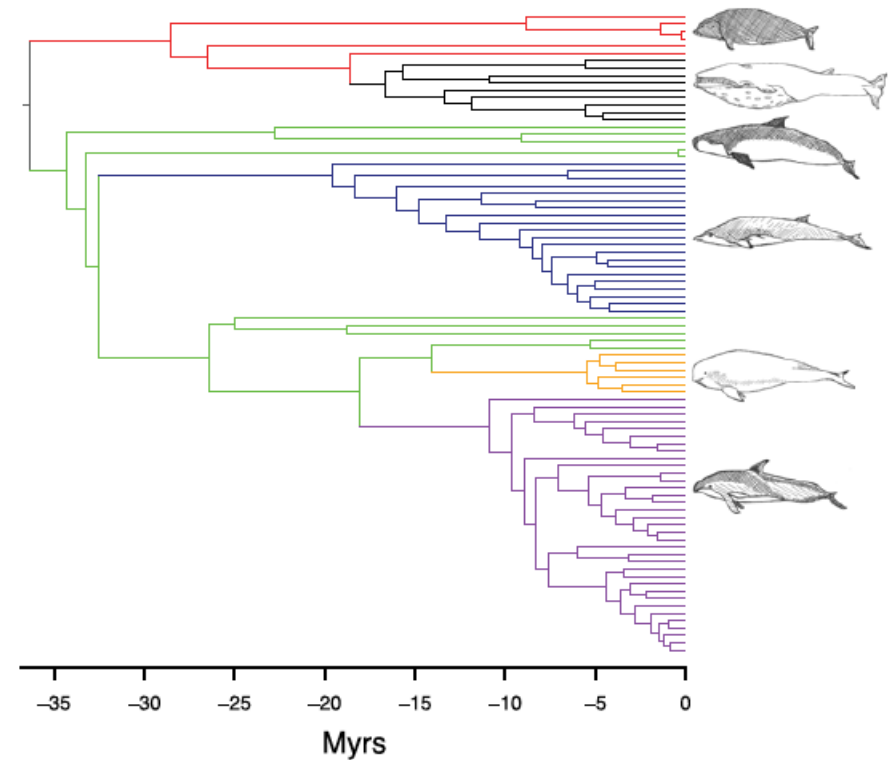
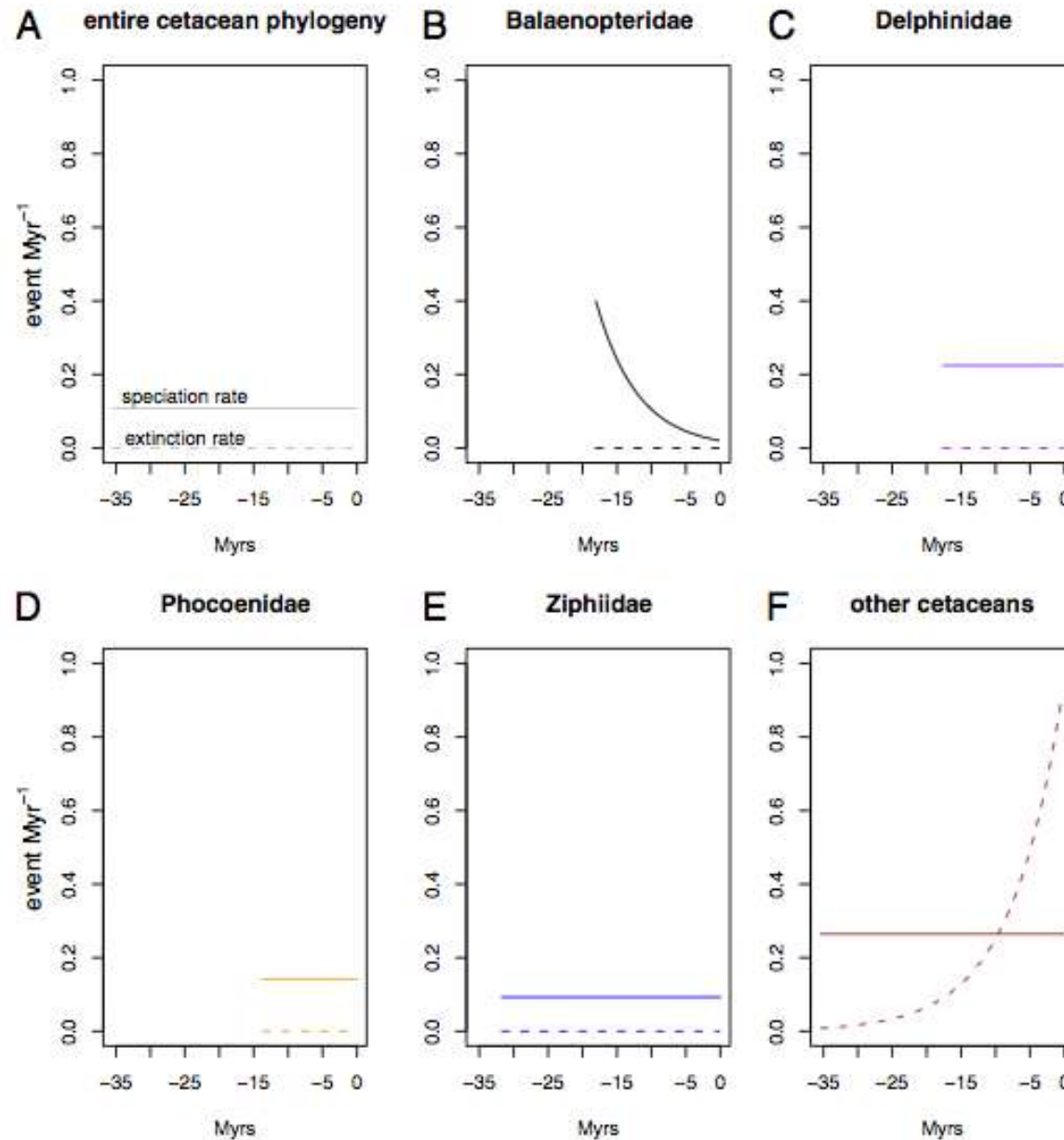


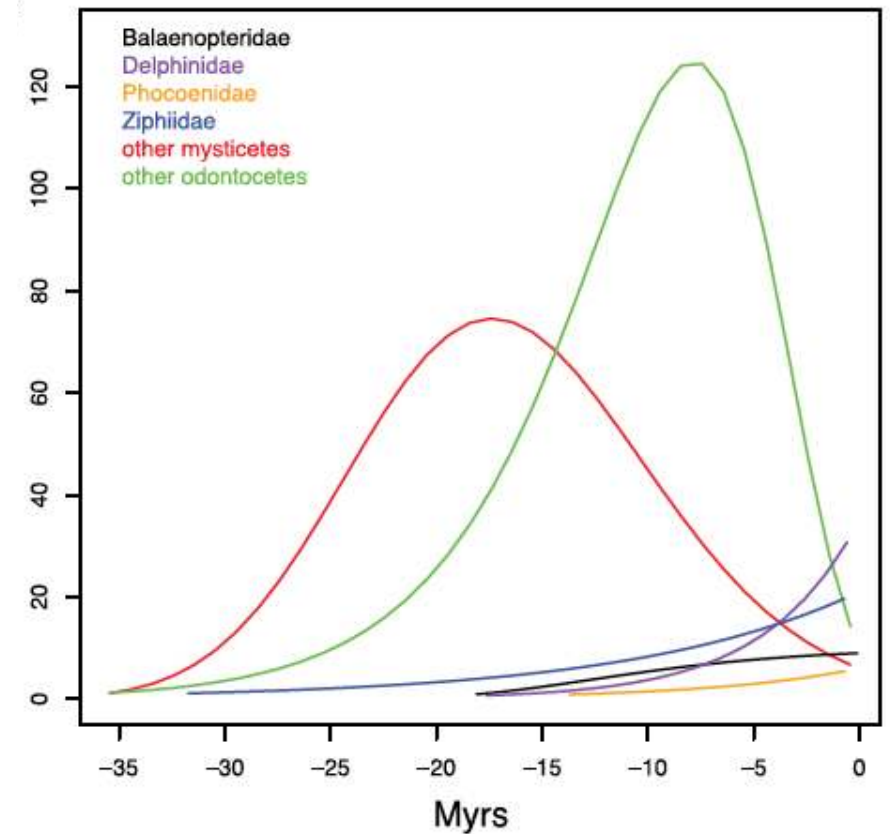
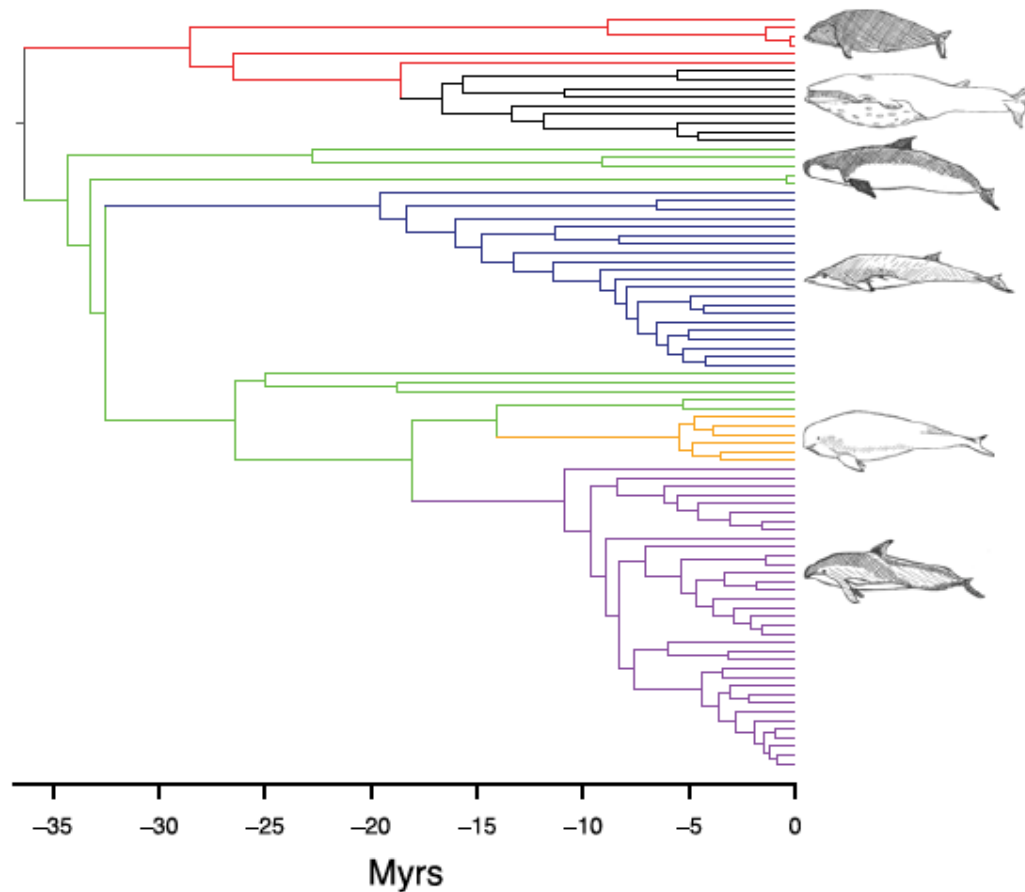
Table S2. Statistical support for rate shifts in the cetacean phylogeny

Model	nb	Description	LogL	AIC _c
No shift	1	Best fit model	-279.03	560.08
One shift	5	Best fit model: shift in the Delphinidae	-262.93*	536.22
Two shifts	6	Best fit model: shifts in the Delphinidae and Phocoenidae	-260.17 [†]	532.85
Three shifts	7	Best fit model: shifts in the Delphinidae, Phocoenidae and Ziphiidae	-256.13 [‡]	526.94
Four shifts	8	Best fit model: shifts in the Delphinidae, Phocoenidae, Ziphiidae, and Balaenopteridae	-250.13	517.14

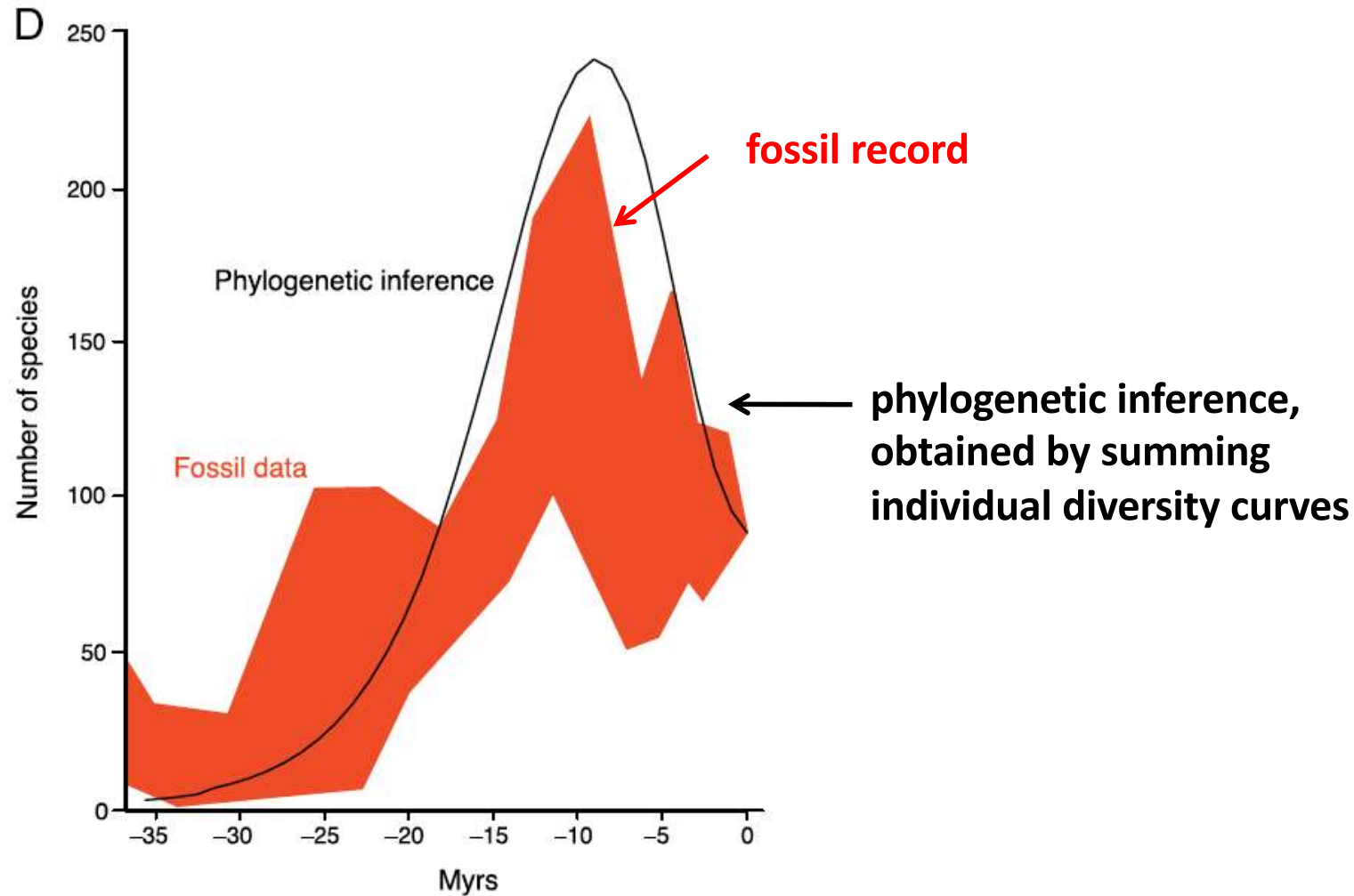
We can compute estimates of speciation and extinction rates through time



Resulting estimates of diversity through time : boom-then-bust diversity dynamics



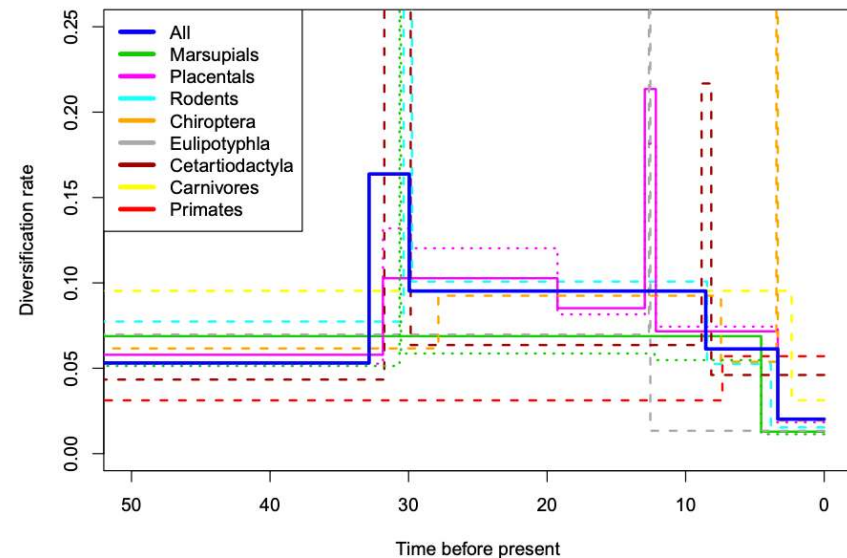
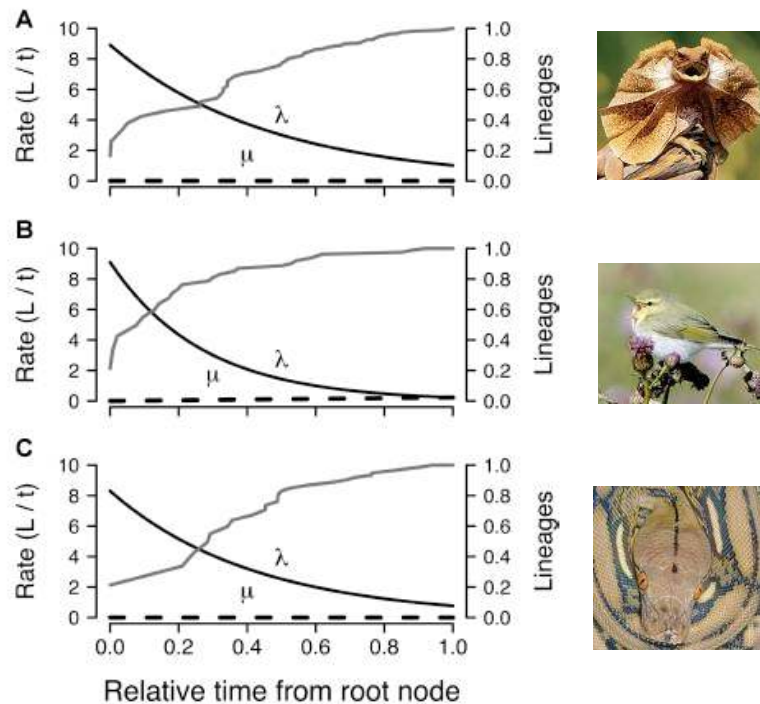
The resulting diversity curve is consistent with the fossil record



**Do rates of species diversification vary through time?
How?**

Speciation rates often decline through time

Estimates obtained by maximum-likelihood fit of birth-death models to phylogenies of present-day species



Stadler *et al.*
PNAS 2011

Rabosky & Lovette Evolution 2008

Why do rates of species diversification vary through time?



George Gaylord Simpson

Most diversity of life on Earth arises from adaptive radiations, the fast diversification of ecological traits in a rapidly speciating group of organisms

Under this hypothesis, diversification is fast in the presence of ecological opportunities, but slows down as these opportunities are exploited by an increasing number of species, generating so-called « Early burst » patterns.



George Gaylord Simpson

Diversity slowdowns linked to limited ecological opportunities and the diversity-dependent diversification model

PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record

Rampal S. Etienne, Bart Haegeman, Tanja Stadler, Tracy Aze, Paul N. Pearson, Andy Purvis and Albert B. Phillimore

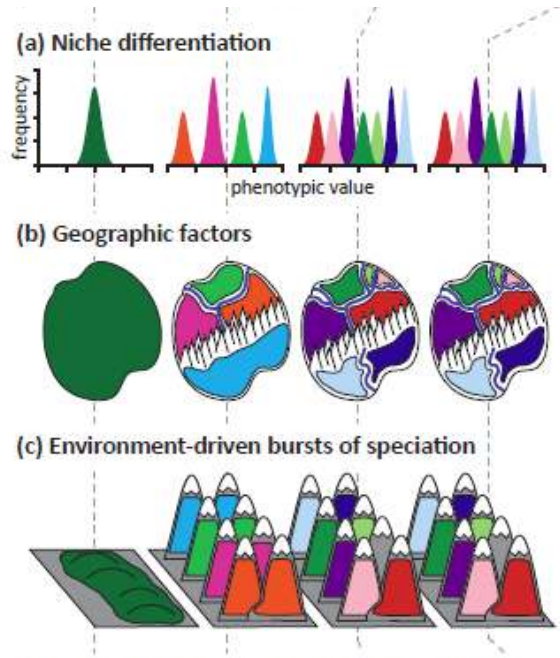
$$\lambda_n = \max\left(0, \lambda_0 - (\lambda_0 - \mu) \frac{n}{K}\right) \quad \text{and} \quad \mu_n = \mu$$



Maximum number of species

Why does diversification slow down?

Daniel Moen and H  l  ne Morlon



Trends Ecol Evol 2014

Why are diversification slowdowns observed even when species do not coexist (and therefore do not compete for ecological opportunities)?

Do interactions with closely-related species necessarily impede diversification?



The evolutionary speed hypothesis and other climate-related hypotheses

Bernhard Rensch

Warmer climates select for small-bodied species, which have fast generation times, high mutation rates, and therefore potentially higher speciation rates

Metabolic activity is faster under warm climates, potentially increasing the action of free radicals and increasing mutation rates

Warmer climates are often associated with increased climatic stability and productivity, which could promote speciation

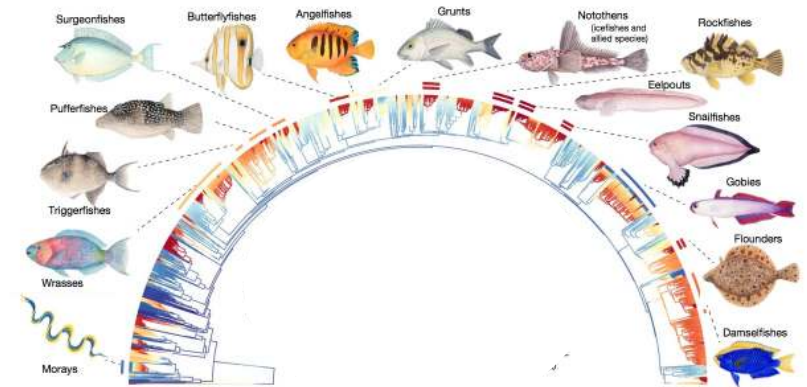
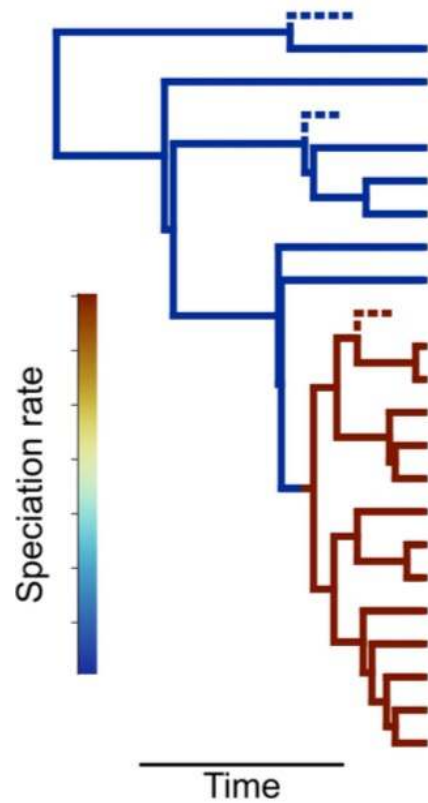
Could diversification slowdowns be related to the cooling of the Earth during the Cenozoic?

Statistical Inference

Diversification model

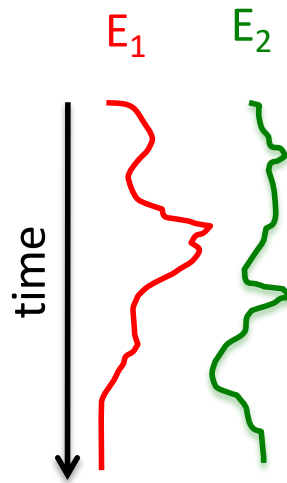


Phylogenetic tree



Hypothesis testing
using likelihood comparison

Models of diversification with rates that depend on measured (a)biotic variables



$$\tilde{\lambda}(t) = \lambda(t, E_1(t), E_2(t), \dots, E_k(t))$$

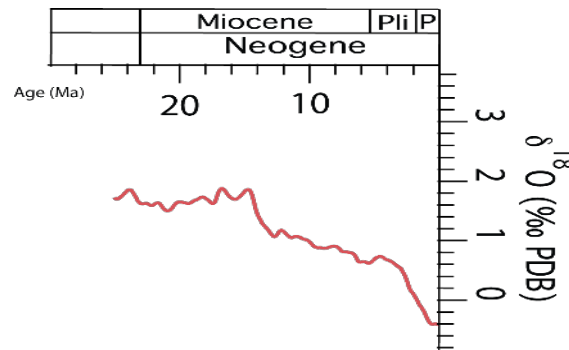
$$\tilde{\mu}(t) = \mu(t, E_1(t), E_2(t), \dots, E_k(t))$$

$$\mathcal{L}(t_1, \dots, t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^n \lambda(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)},$$

Did past climatic changes affect diversification rates?

How?

218 phylogenies of tetrapod families

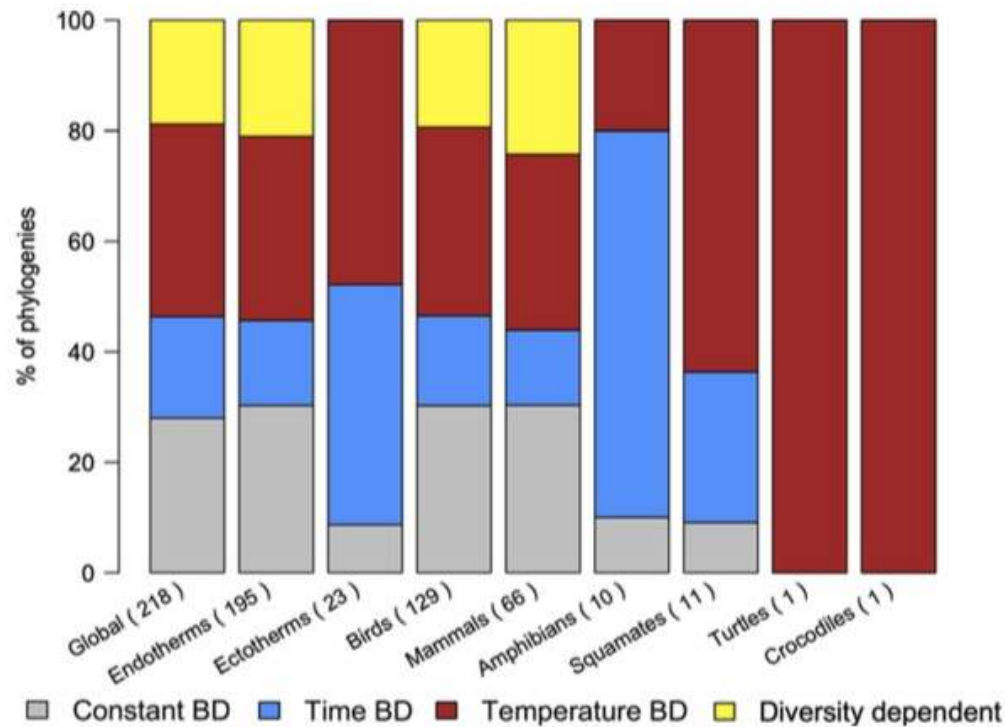


Zachos *et al.* 2008

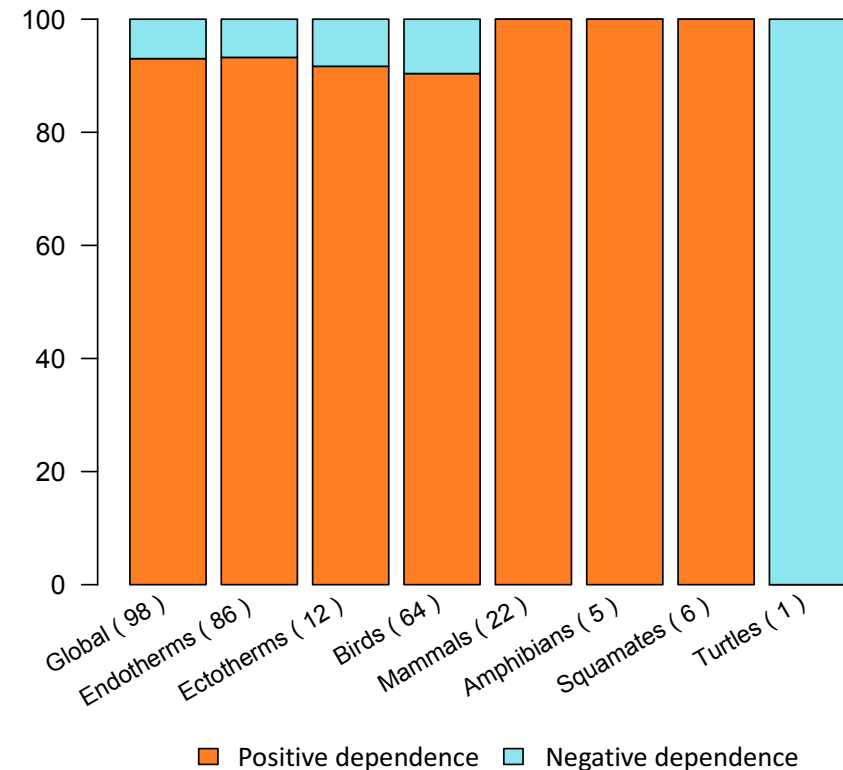
Comparison of 22 models including constant rate diversification models, models with time-varying rates, diversity-dependent rates, and temperature-dependent models

Condamine *et al.* Eco Lett 2019

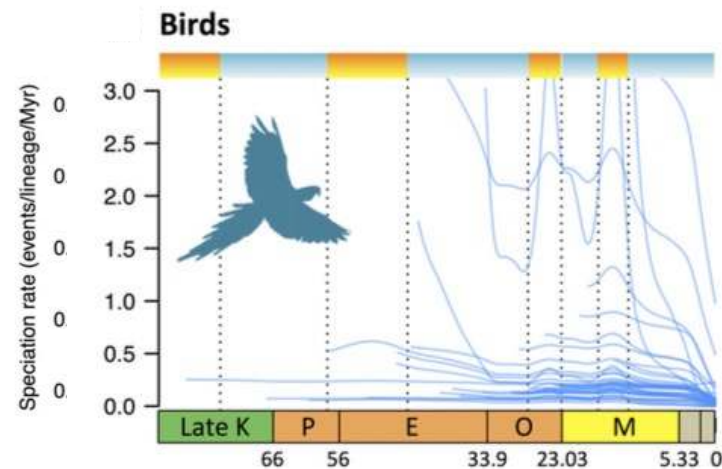
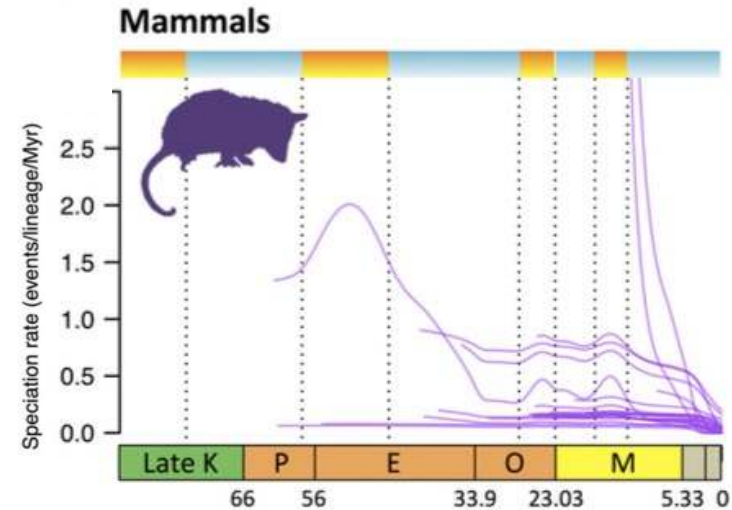
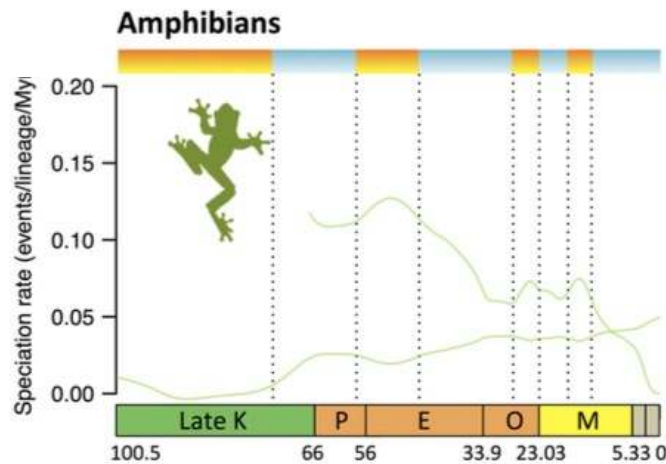
Speciation rates often vary with temperature



Speciation rates are higher during warm geological periods



Climate cooling during the Cenozoic results in a slowdown in diversification



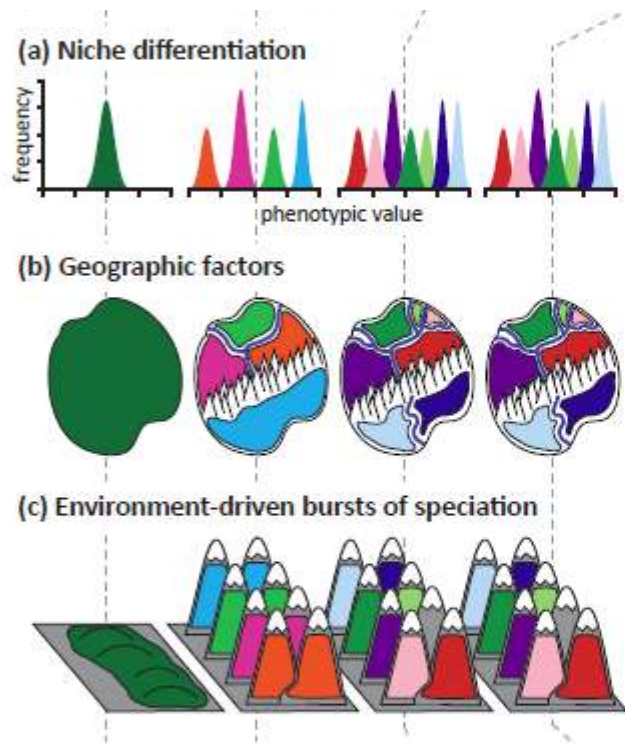
Climate cooling provides a potential alternative explanation for speciation rates slowdowns to the often invoked filling of niche space

Opinion

CellPress

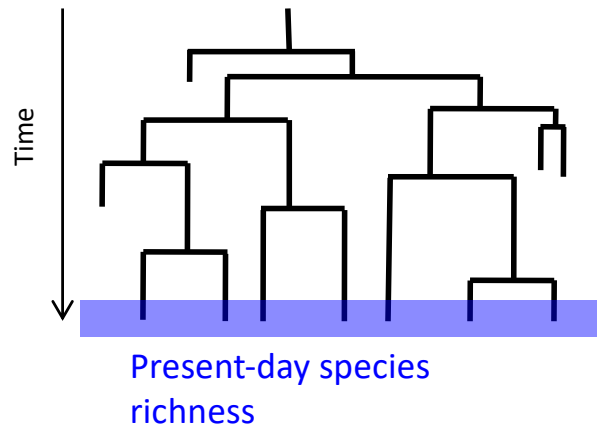
Why does diversification slow down?

Daniel Moen and H  l  ne Morlon



Trends Ecol Evol 2014

From estimates of speciation and extinction rates to estimates of past diversity



$$N(t) = N_0 e^{\int_0^t (-\lambda(s) + \mu(s)) ds}$$

speciation rate extinction rate
number of species today

Morlon *et al.* PNAS 2011

probability there were m species at time t
 given there were x species at time s
 and there are n species today

↓ ↓ ↓

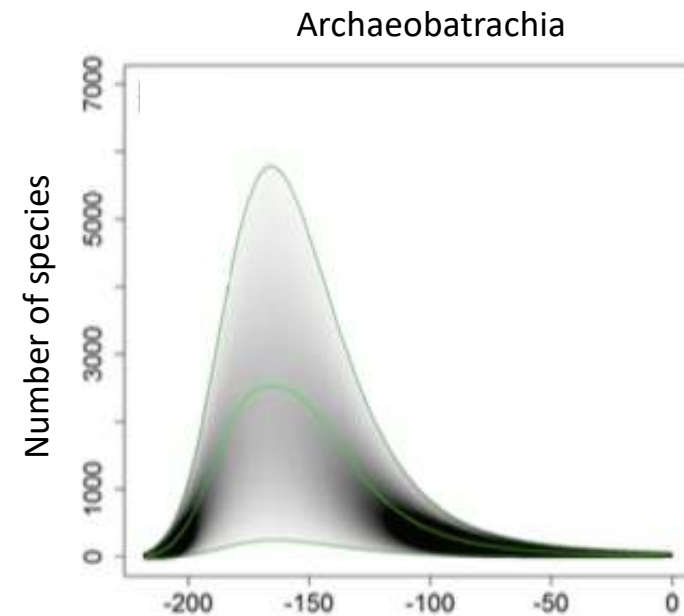
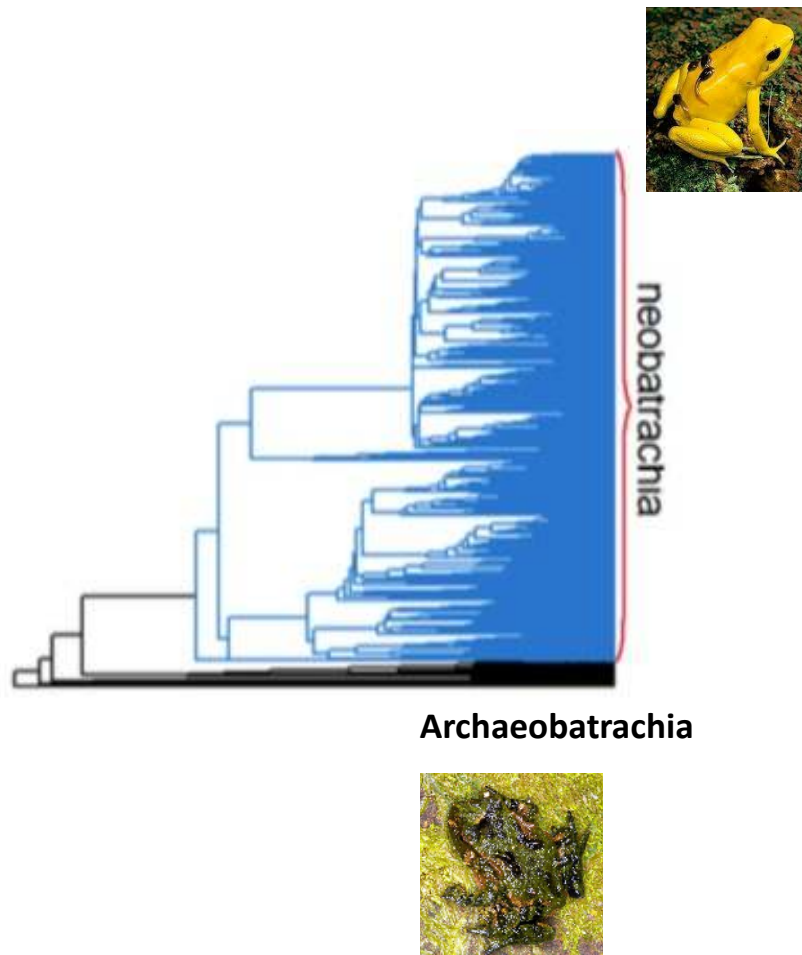
$$\mathbb{P}(N(t) = m \mid N(s) = x, N(T_{pres}) = n)$$



Olivier Billaud

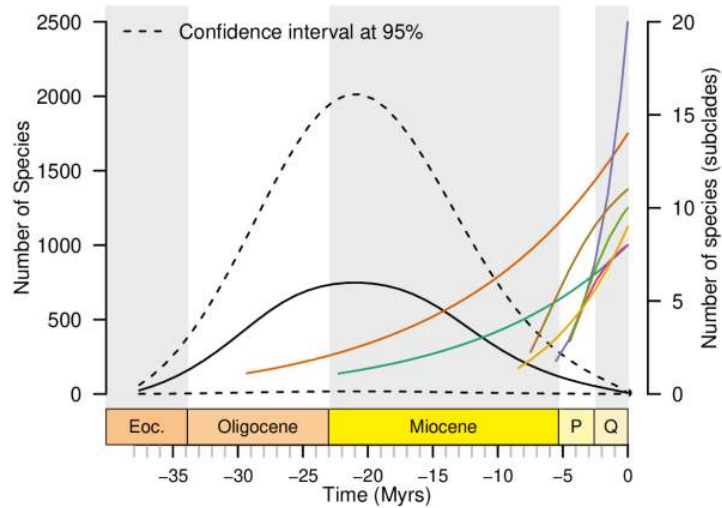
Billaud *et al.* Syst Bio 2019

Are old and species-poor groups groups that have always be poor, or are they the remnants of a diverse past?

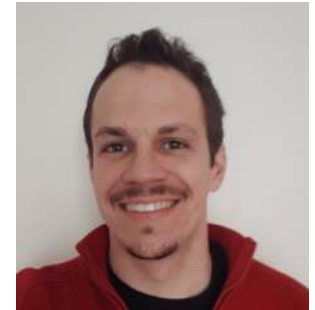


Old and poor frog families are the remnant of a diverse past

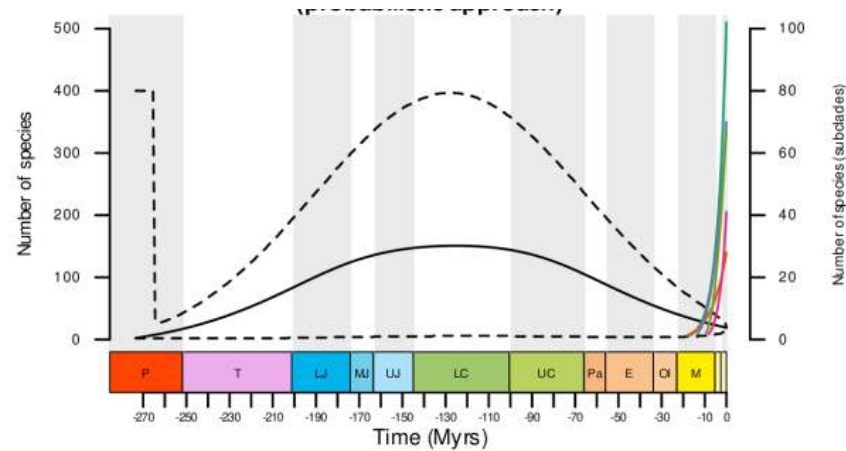
Other examples of old and poor groups that are the remnant of a diverse past



Nathan
Mazet



Pierre-Henri
Fabre



Fabien
Condamine



**Do rates of species diversification vary across lineages?
How & Why?**

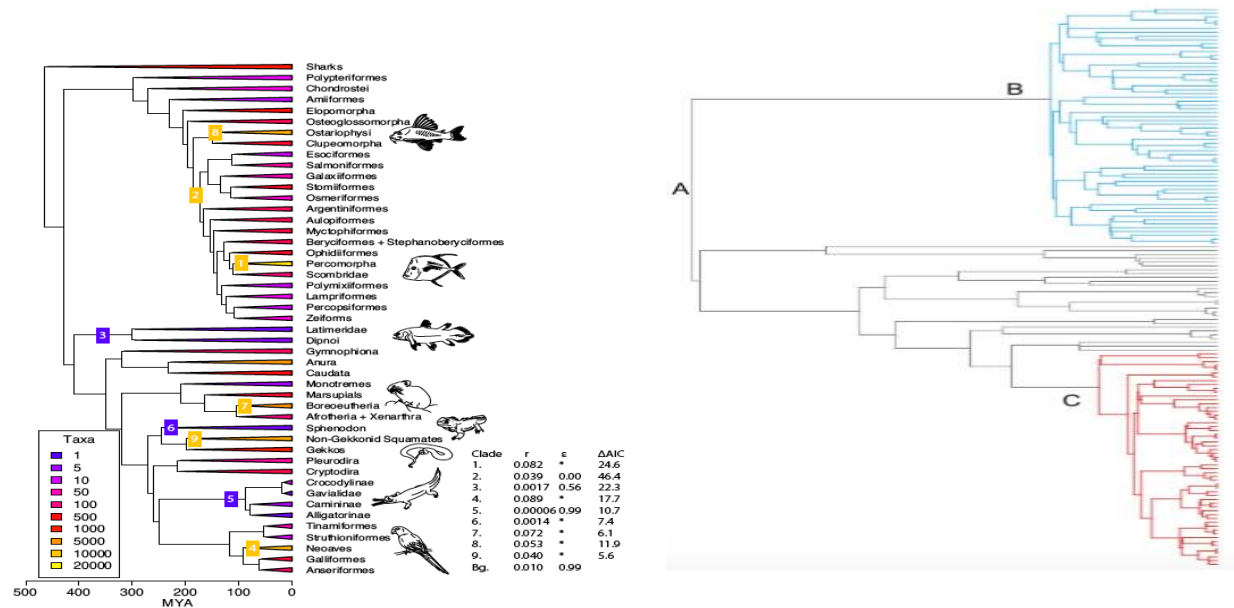


George Gaylord Simpson

Most diversity of life on Earth arises from adaptive radiations, the fast diversification of ecological traits in a rapidly speciating group of organisms

Under this hypothesis, bursts of diversification are clade-wide, linked to the rapid filling of a niche space that has been freed from other occupants (e.g. by major environmental changes) or opened by a major key innovation.

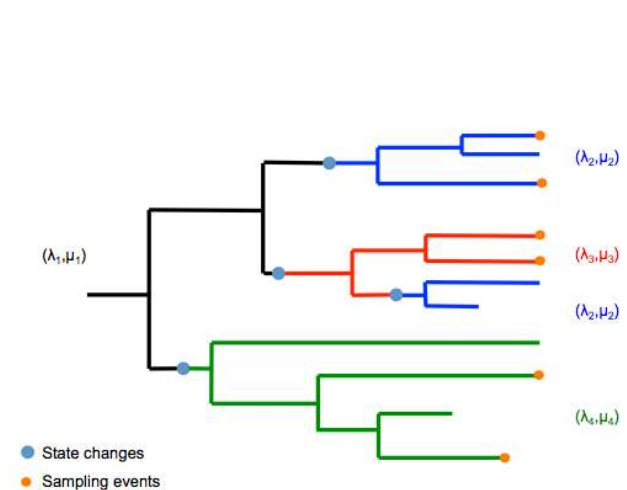
Heterogeneous birth-death models with clade-wide rate variation: few rate shifts with large effects



MEDUSA
Alfaro et al. PNAS 2009

BAMM
Rabosky PloS One 2014

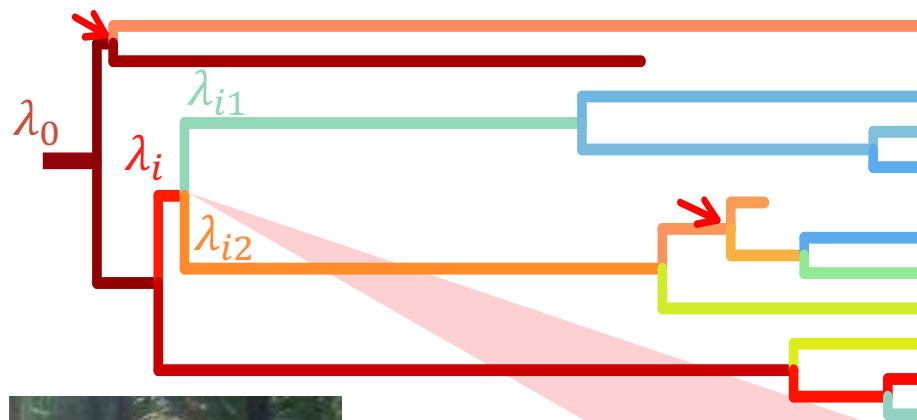
MSBD
Barido-Sottani *et al.* Syst Bio 2020



Another view of diversification

The complex interplay between species evolving ecologies and their specific spatial and environmental context results in highly dynamic diversification rates

The Cladogenetic Diversification rate Shift model (ClaDS):
a new model with lineage-specific rate variation

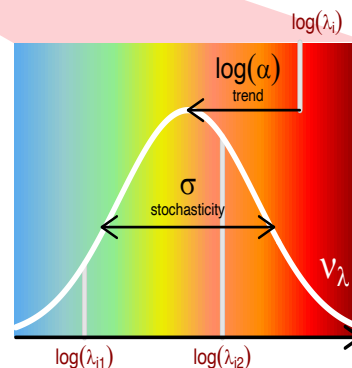


λ_0 initial speciation rate

α deterministic trend

σ^2 stochastic variation

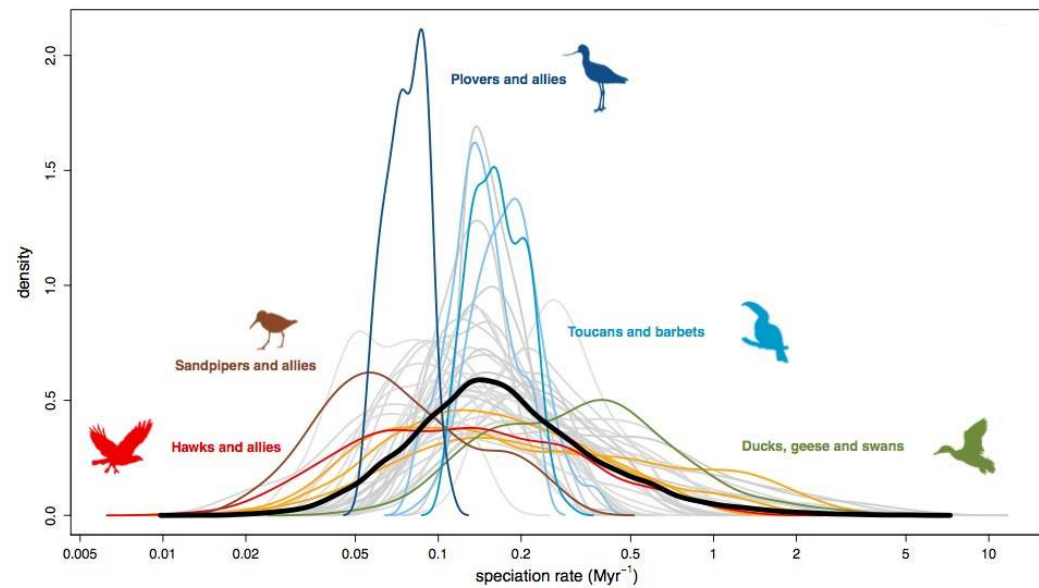
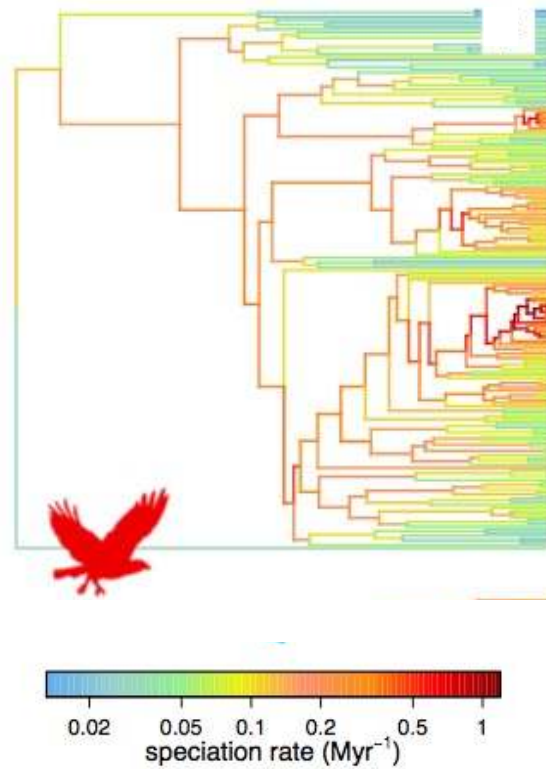
$\varepsilon = \mu_i / \lambda_i$ relative extinction rate



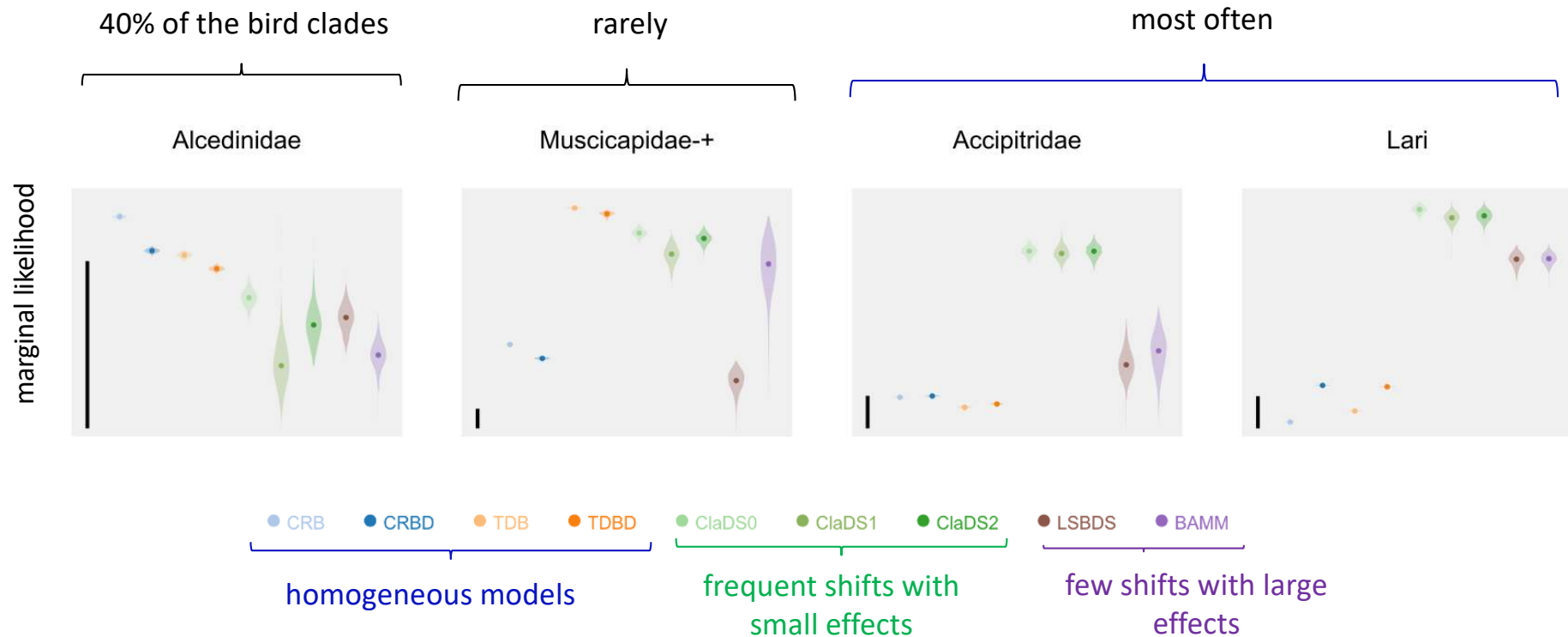
Maliet et al.

Nature Ecology & Evolution 2019

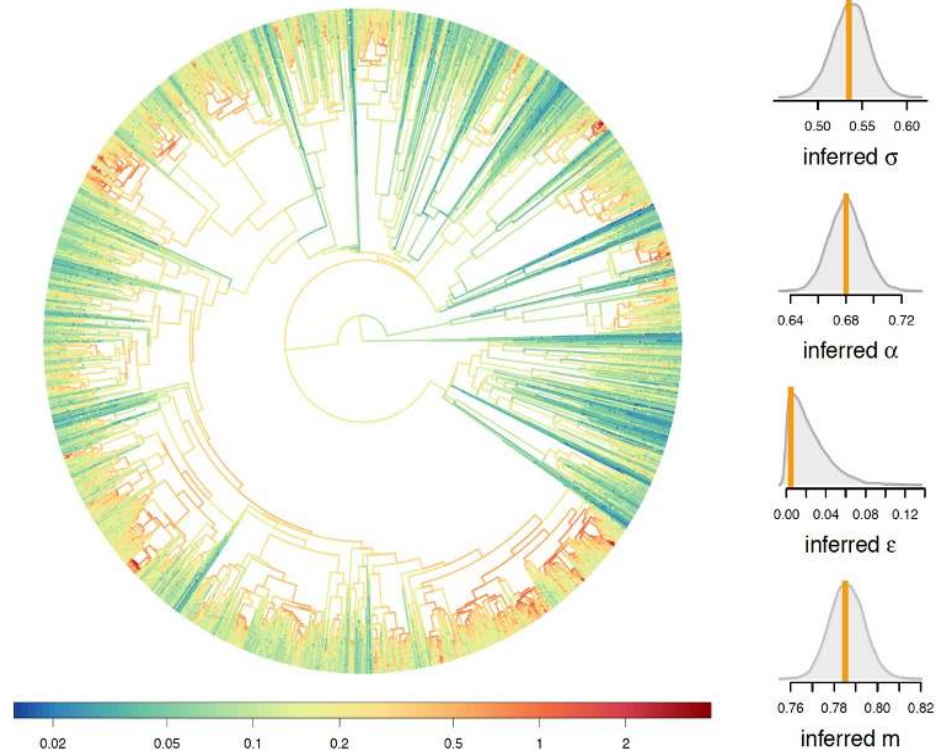
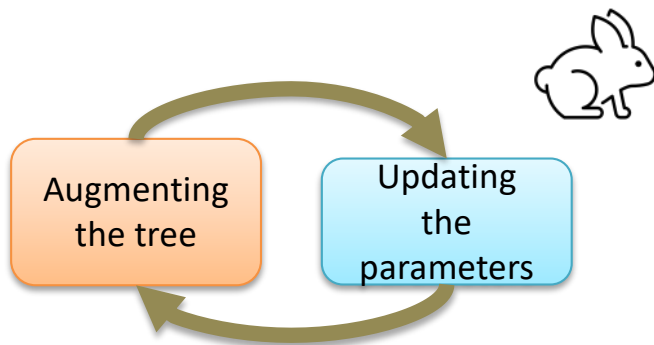
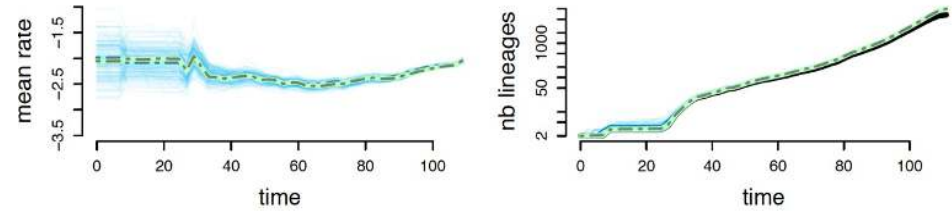
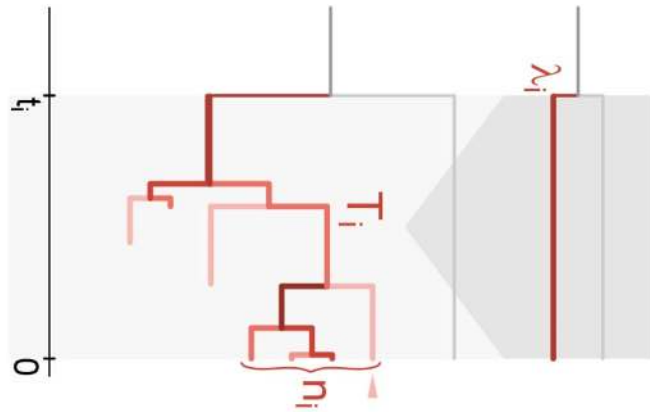
Speciation rates vary widely across lineages



Models with many small shifts are better supported than models with few large shifts



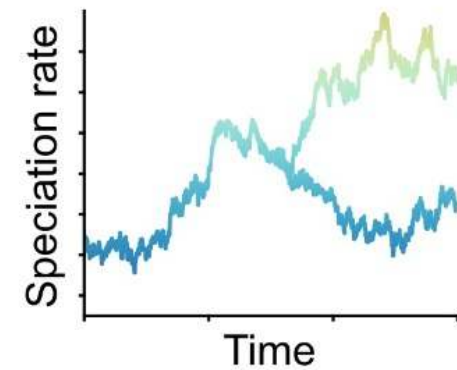
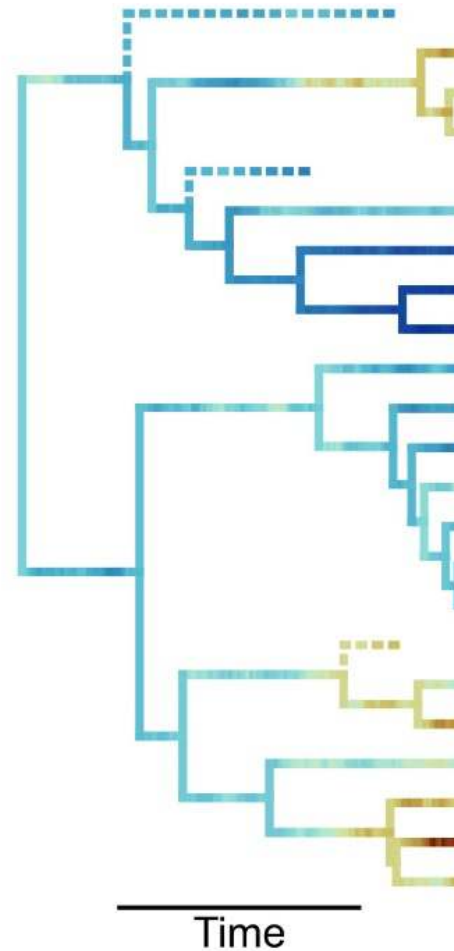
Faster and improved inference with Bayesian Data Augmentation



The Birth-Death Diffusion model (BDD): continuous diffusion of diversification rates

Speciation

$$d\ln(\lambda_i(t)) = \alpha dt + \sigma_\lambda dW(t),$$



The Birth-Death Diffusion model (BDD): continuous diffusion of diversification rates

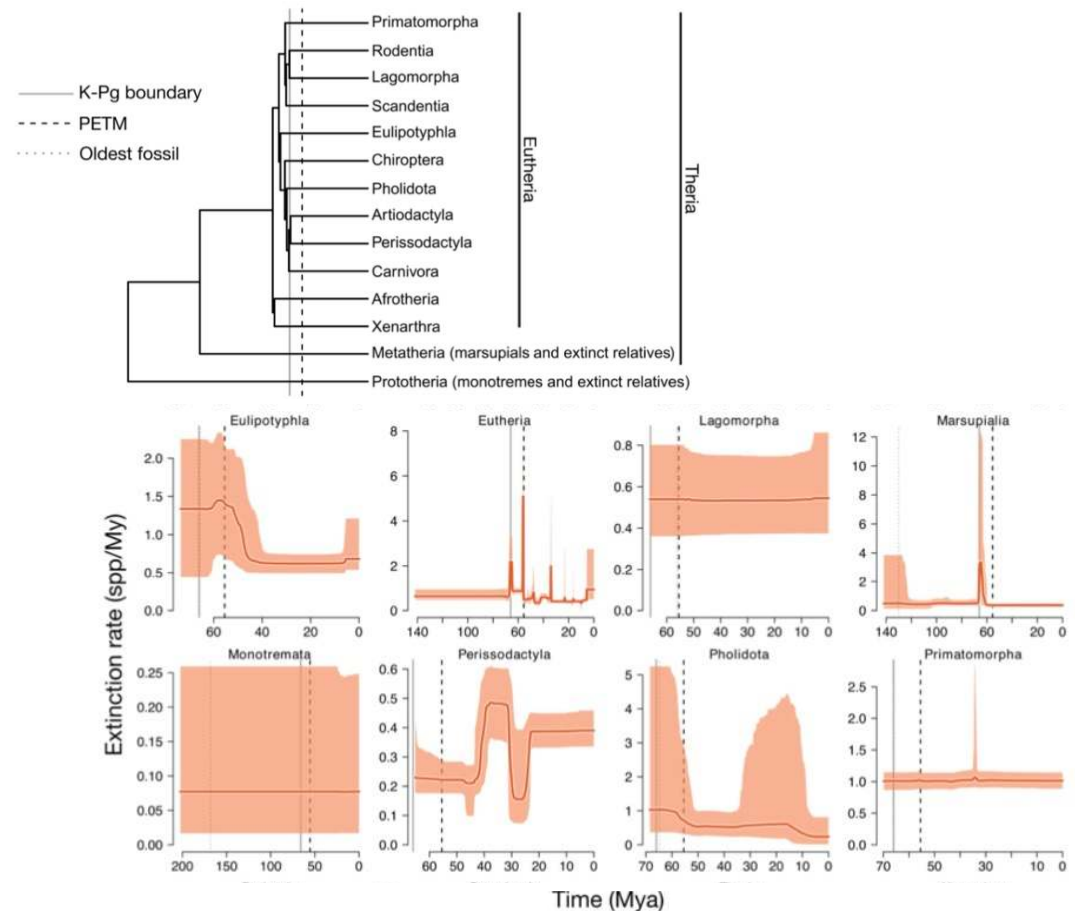
Extinction not constrained by fossil information

- No extinction
- Constant extinction
- Constant turnover
- Follows a Geometric Brownian Motion (GBM)

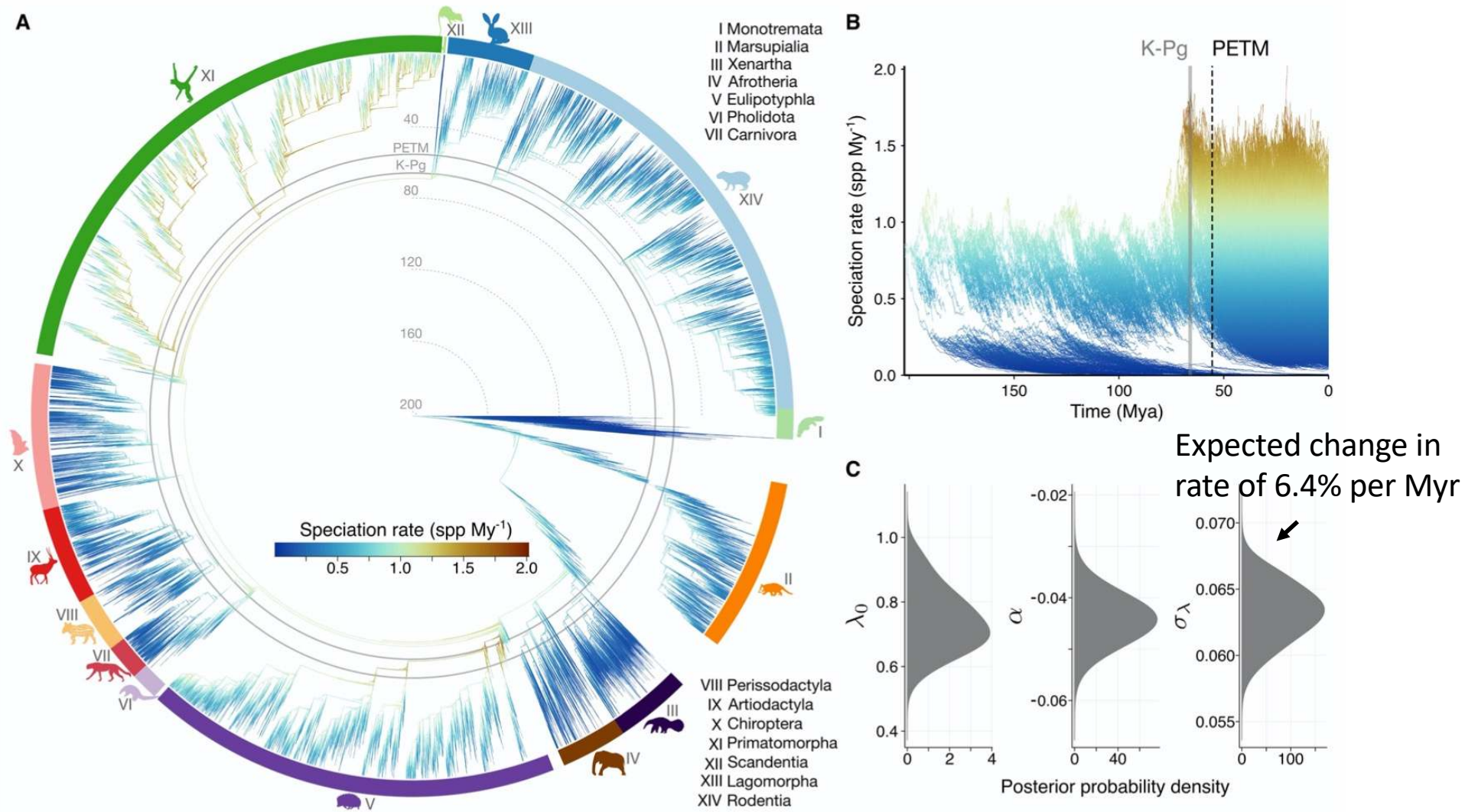
$$d\ln(\mu_i(t)) = \sigma_\mu dW(t),$$

where $W(t)$ denotes the Wiener process.

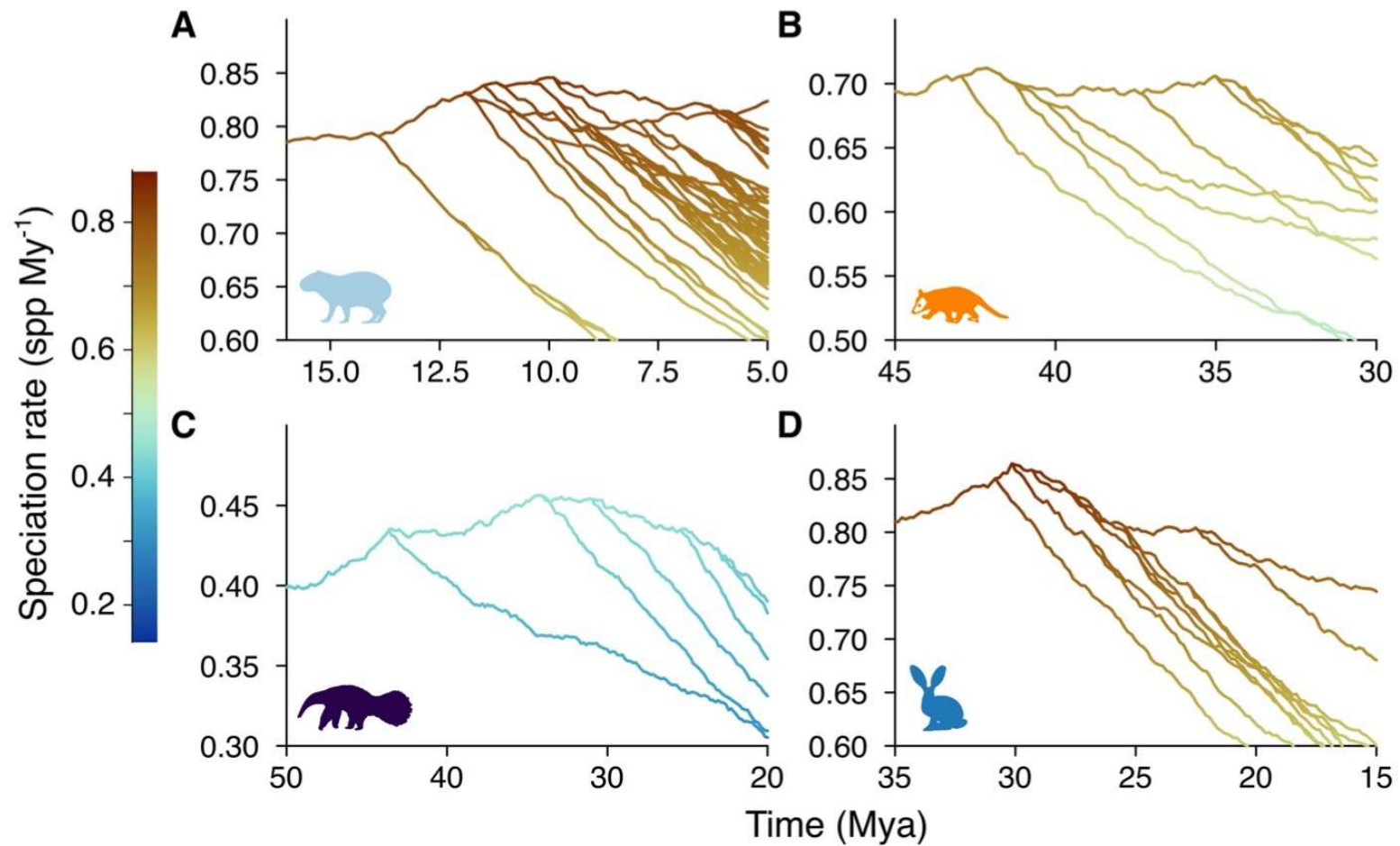
Extinction constrained by fossil information

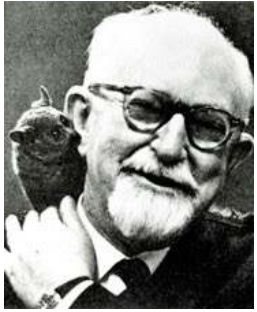


Speciation rates vary widely across lineages

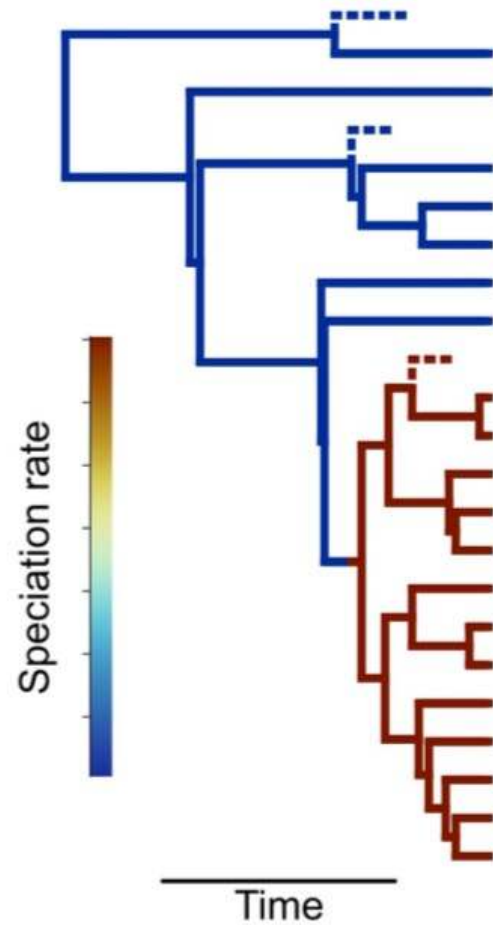


Imbalanced speciation pulses





Major key
innovations
Adaptive radiations



Complex interplay between species
evolving ecologies and their specific
spatial and environmental context

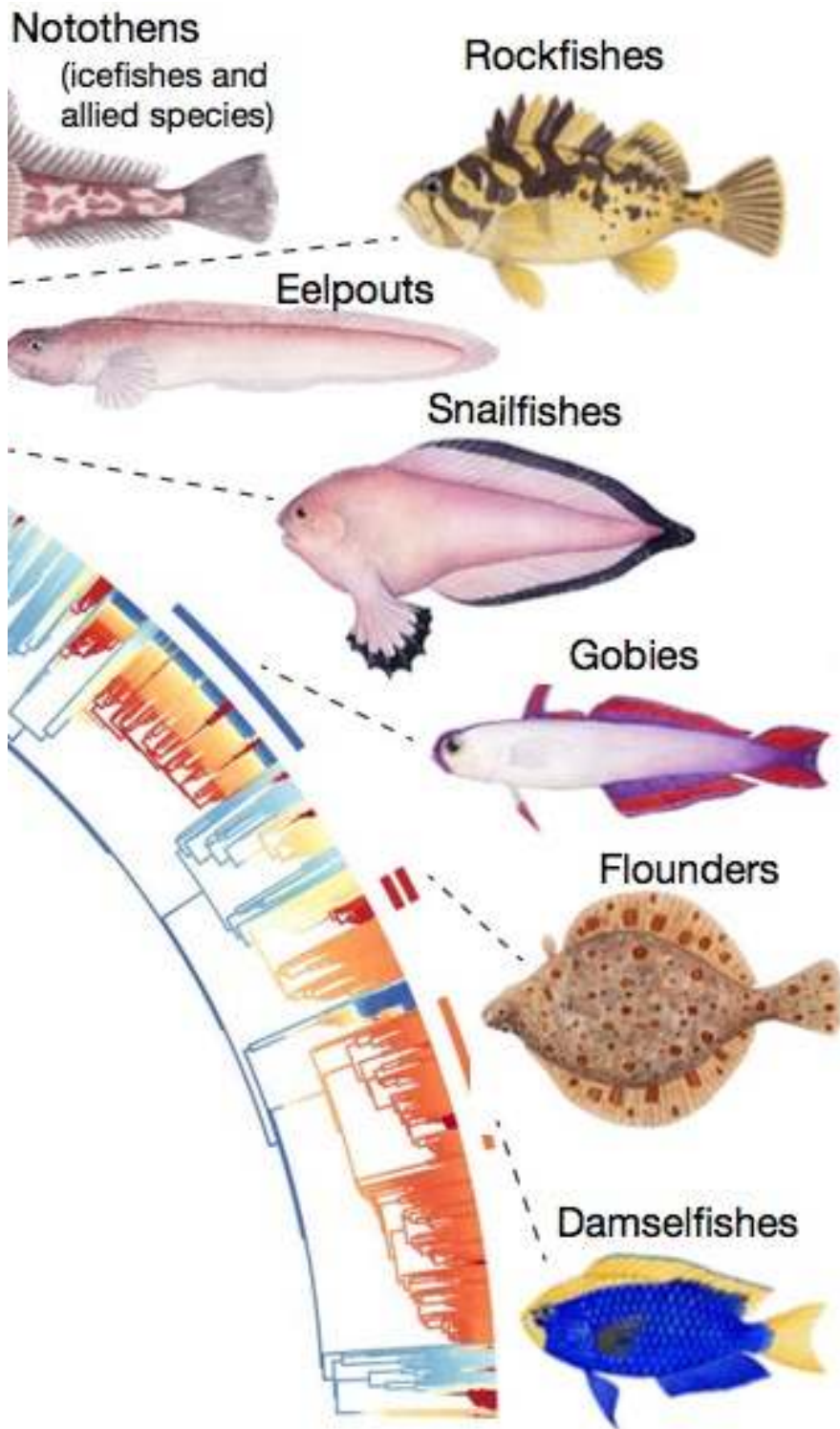


Take-home message

Applying stochastic birth-death models to empirical phylogenies is powerful for understanding modes and rates of species diversification

Diversification rates vary through time and across lineages

We have considered the
(dated) phylogenetic tree as
data



Why should you care
even if the only thing
you are interested in is
inferring the tree?

The tree model is a prior in Bayesian phylogenetic reconstruction!

$$P(\text{Molecular alignment, Substitution model, Clock model, Time tree, Tree model} \mid \text{ACAC... TCAC... ACAG...}) =$$

Posterior

Likelihood

Probability of
the tree model

Priors

$$P(\text{ACAC... TCAC... ACAG...} \mid \text{Molecular alignment, Substitution model, Clock model, Time tree})$$

$$P(\text{Time tree} \mid \text{Tree model})$$

$$P(\text{Molecular alignment, Substitution model, Clock model, Time tree, Tree model})$$

$$P(\text{ACAC... TCAC... ACAG...})$$

ACAC...
TCAC...
ACAG... Molecular alignment

 Substitution model

 Clock model

 Time tree

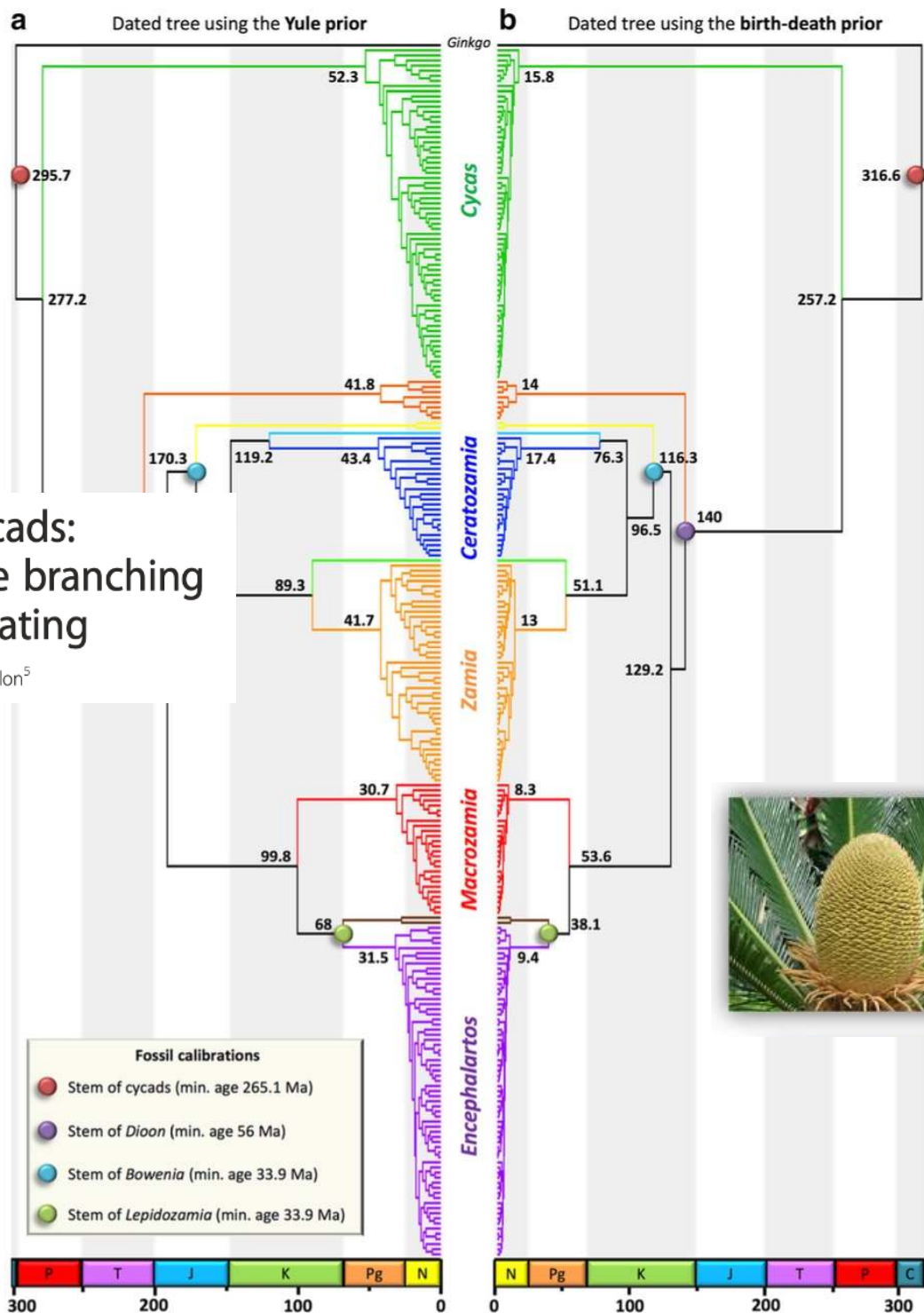
 Tree model

Using the Yule versus birth-death tree prior in phylogenetic dating

Origin and diversification of living cycads: a cautionary tale on the impact of the branching process prior in Bayesian molecular dating

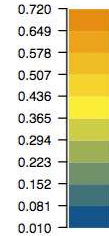
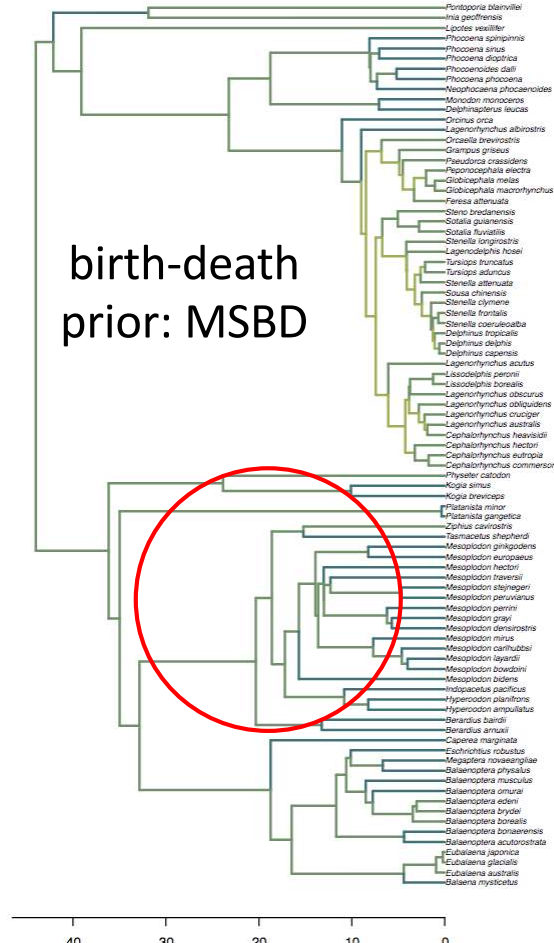
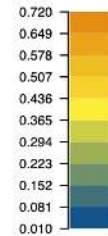
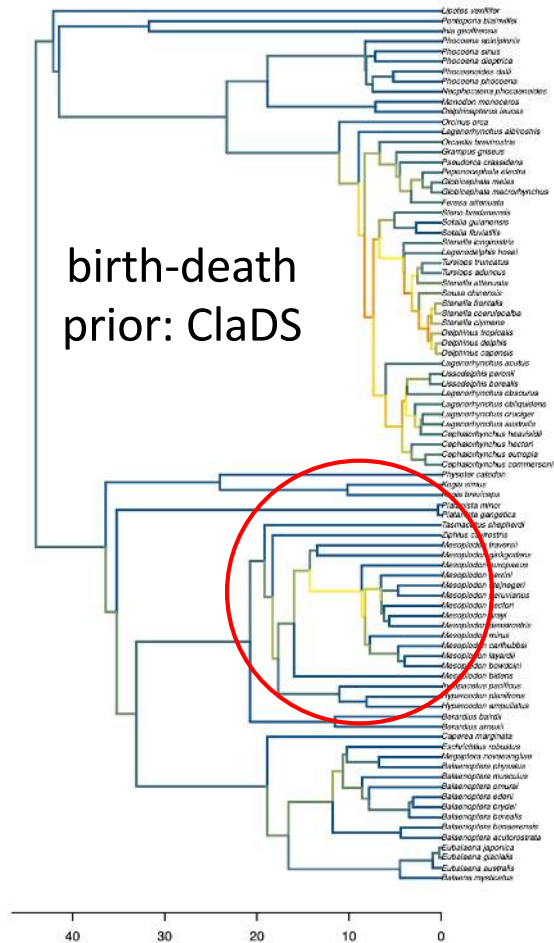
Fabien L Condamine^{1,2*}, Nathalie S Nagalingum³, Charles R Marshall⁴ and Hélène Morlon⁵

BMC Evol Biol 2015





ClaDS now integrated in BEAST2 for Bayesian full phylogenetic inference: accounting for rate heterogeneity influences phylogenetic reconstruction



Beast2

Bayesian evolutionary analysis by sampling trees

Barido-Sottani & Morlon
Syst Bio 2023

What are the factors that modulate diversification rates?

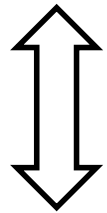


The Court Jester

Abiotic factors

climatic variation
geological context

EXTRINSIC



The Red Queen

Biotic factors

competition
mutualistic and antagonistic interactions

INTRINSIC



Species-specific traits

reproduction mode
life-history traits
dispersal capacity

What are the factors that modulate diversification rates?

Why should you care even if the only thing you are interested in is genomes?

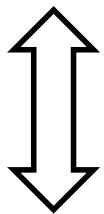


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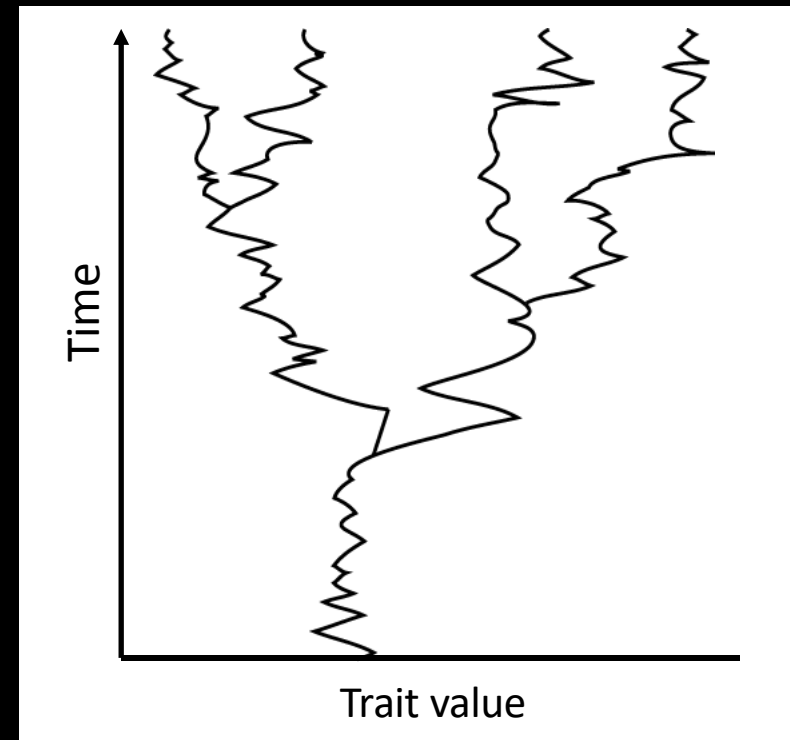
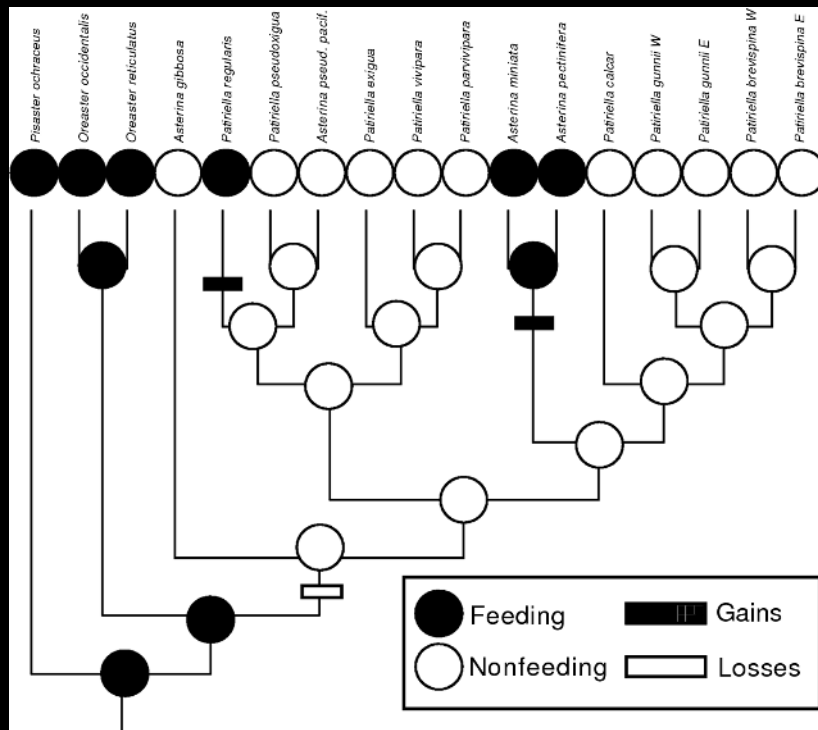


Species-specific traits

Genomic features!

Genome size, genome/gene
duplication, TEs.....

Trait evolution on trees



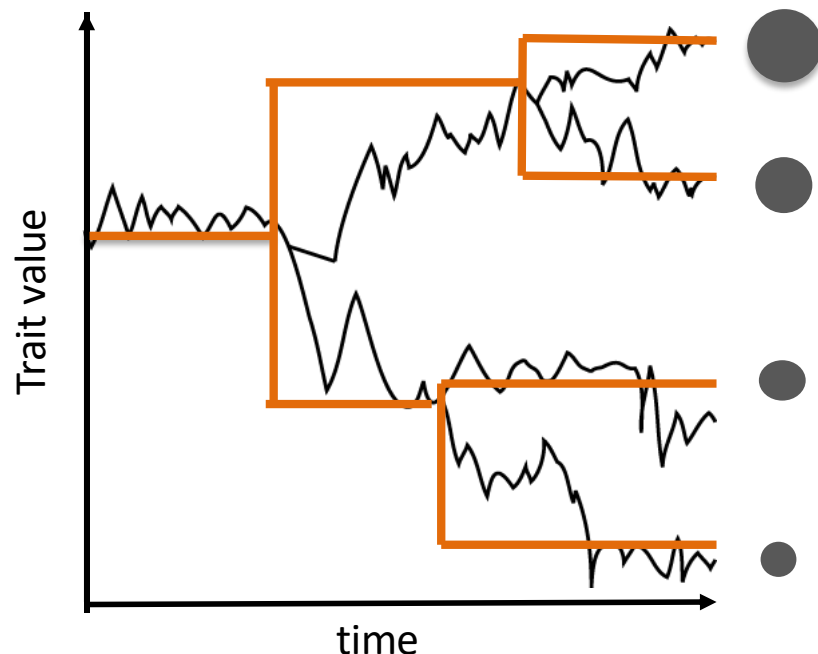
Constant rate model of phenotypic evolution

We model the evolution of a quantitative trait X on a fixed, ultrametric, bifurcating species tree with branch lengths in unit of time, assumed to be known.

Evolutionary drift

The trait evolves according to a Brownian process with rate σ

$$dX(t) = \sigma dB(t)$$



expected variance-covariance matrix

$$V_{ij} = \sigma^2 s_{ij}$$

$$L = \frac{\exp \left\{ -\frac{1}{2} [\mathbf{X} - E(\mathbf{X})]' (\mathbf{V}^{-1}) [\mathbf{X} - E(\mathbf{X})] \right\}}{\sqrt{(2\pi)^N \det(\mathbf{V})}}$$

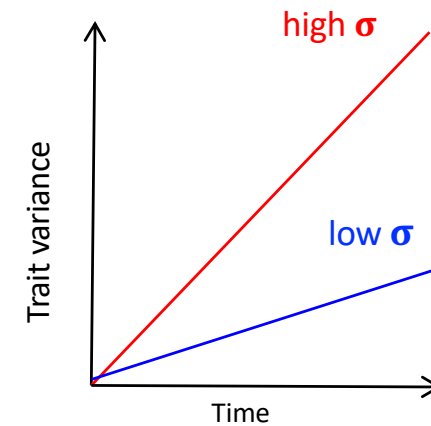
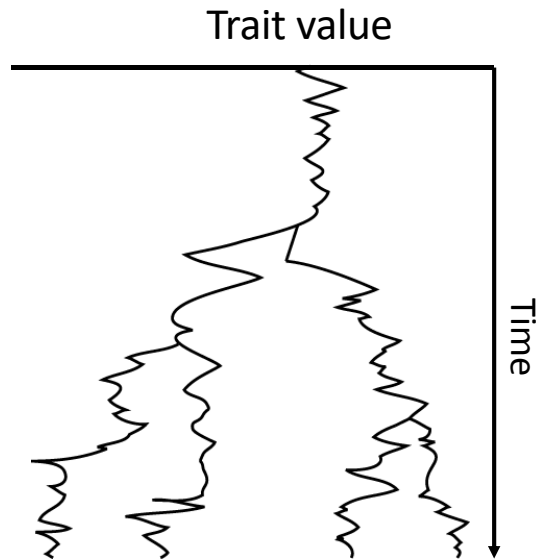
Felsenstein 1973

→ σ estimated by maximum likelihood or Bayesian inference

Current levels of phenotypic diversity result from the gradual accumulation of phenotypic variance

Rate of phenotypic
evolution

Amount of phenotypic
change in a given time unit



Stabilizing selection constrains trait evolution

Ornstein-Uhlenbeck (OU): the “rubber-band” model

$$dX(t) = \alpha[\theta - X(t)]dt + \sigma dB(t)$$

where

α = strength of "selection"

θ = adaptive optimum

Selection component

Drift (BM) component

➡ When $\alpha = 0$, this collapses to Brownian motion

expected covariance between species i and j

total height of the tree

shared evolutionary history between species i and j

$$V_{ij} = \frac{\sigma^2}{2\alpha} e^{-2\alpha(T-s_{ij})} (1 - e^{-2\alpha s_{ij}})$$

Models with a presumed effect of competition under limited ecological opportunities

$dX(t)$: change in $X(t)$ in an amount of time

The « Early Burst » model: trait evolution is fast in the initial phase of an evolutionary radiation, and slows down later on as an effect of limited ecological opportunity

$$dX(t)=\sigma(t)dB(t) \quad \text{with } \sigma^2(t) = \sigma_0^2 e^{rt} \quad \text{where } r \text{ is the rate of decline}$$

Blomberg *et al.* 2003

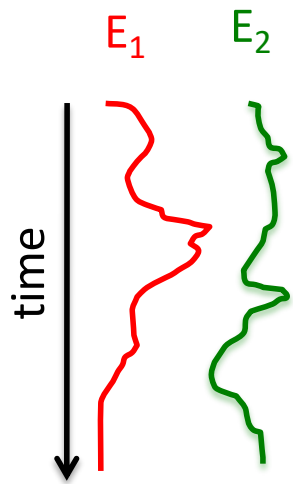
The « Diversity-dependent » model: trait evolution slows down as species pile up in a clade, therefore reducing ecological opportunity

$$dX(t)=\sigma(t)dB(t) \quad \text{with } \sigma^2(t) = \sigma_0^2 e^{bn(t)} \quad \text{where } n(t) \text{ is the number of lineages in the clade at time } t$$

Weir & Mursleen 2013



How does the (a)biotic environment modulate rates of phenotypic diversification?



$$\sigma^2(t) = f(t, E_1(t), E_2(t), \dots, E_k(t))$$



$$L = \frac{\exp \left\{ -\frac{1}{2} [\mathbf{X} - \mathbf{E}(\mathbf{X})]' (\mathbf{V}^{-1}) [\mathbf{X} - \mathbf{E}(\mathbf{X})] \right\}}{\sqrt{(2\pi)^N * \det(\mathbf{V})}}$$

$$V_{ij} = \int_0^{s_{ij}} \sigma^2(t) dt$$

Testing the effect of past climatic changes and rates of body-size evolution in mammals & birds



Ecology, 90(9), 2009, p. 2648
© 2009 by the Ecological Society of America

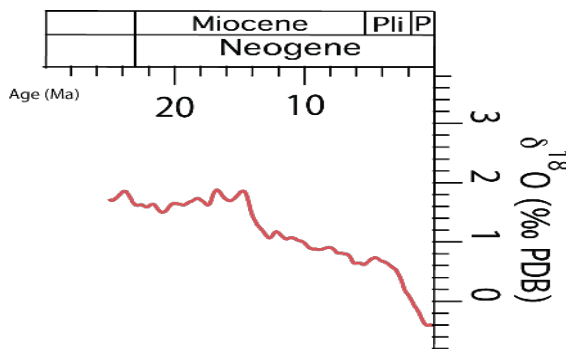
PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals

Ecological Archives E090-184



Ecology, 95(7), 2014, p. 2027
© 2014 by the Ecological Society of America

EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals



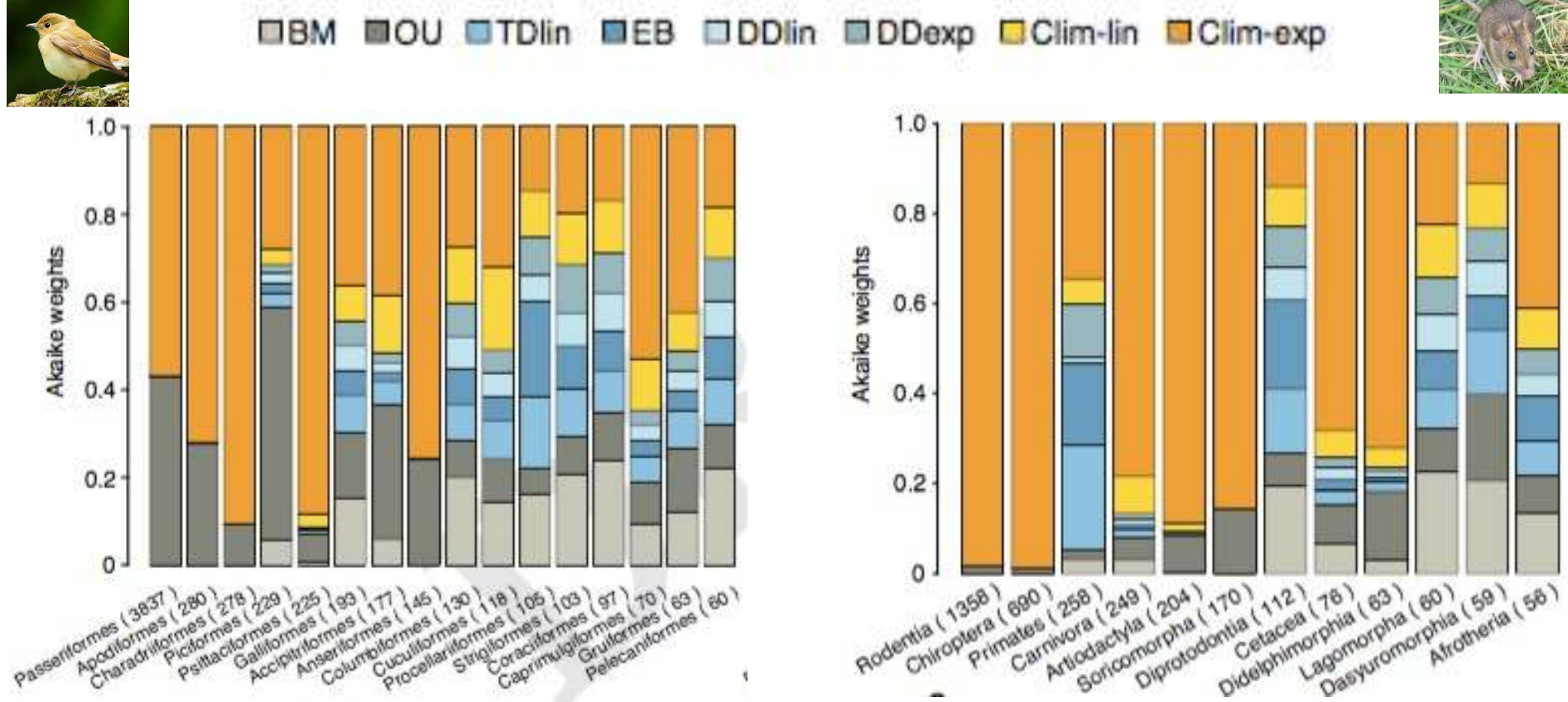
$$\sigma^2(t) = \sigma_0^2 \times e^{\beta T}$$

$$\sigma^2(t) = \sigma_0^2 + \beta T$$

Zachos *et al.* 2008

Clavel & Morlon *PNAS* 2017

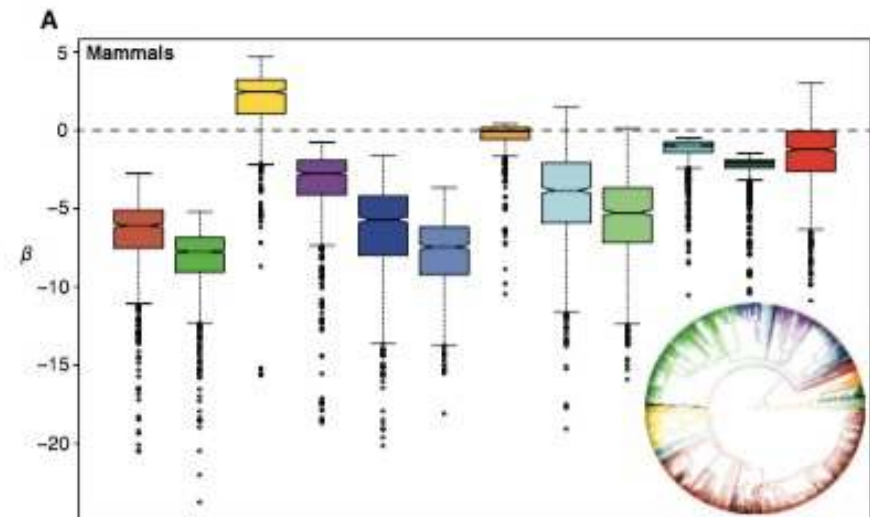
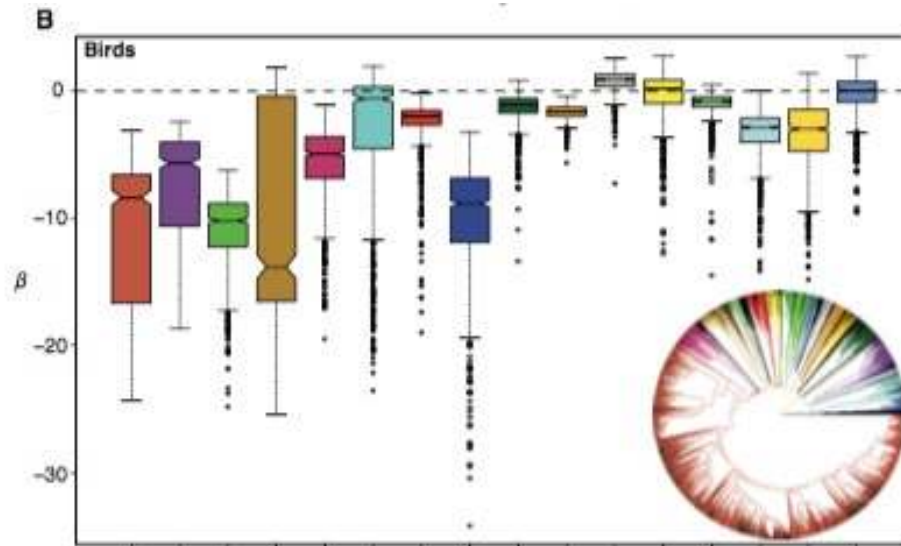
Temperature-dependent rates of phenotypic evolution is supported over 'classical' models of phenotypic evolution



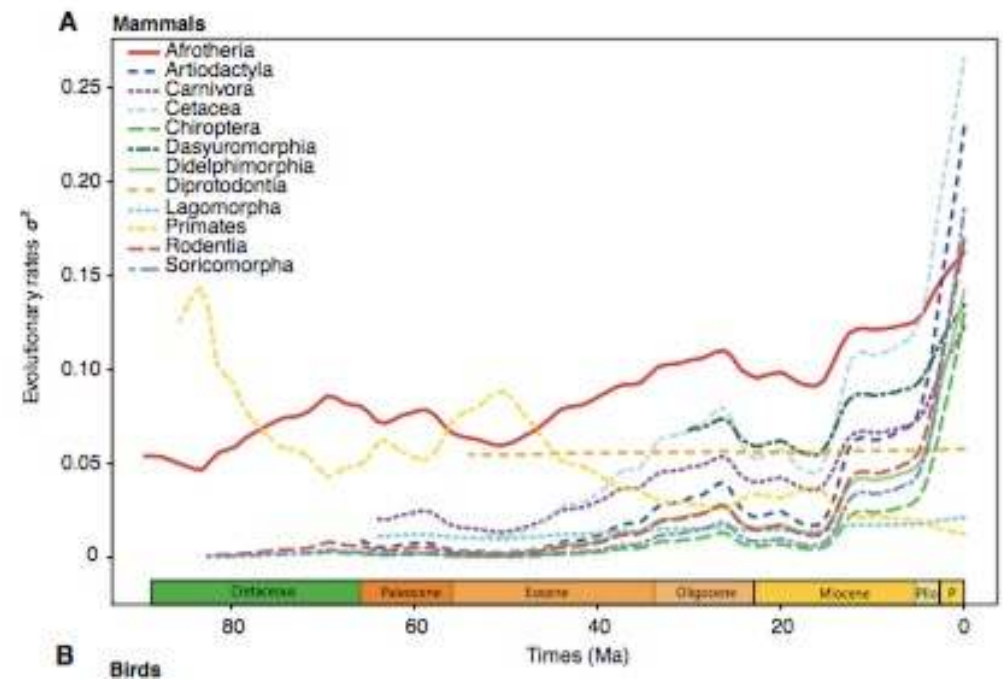
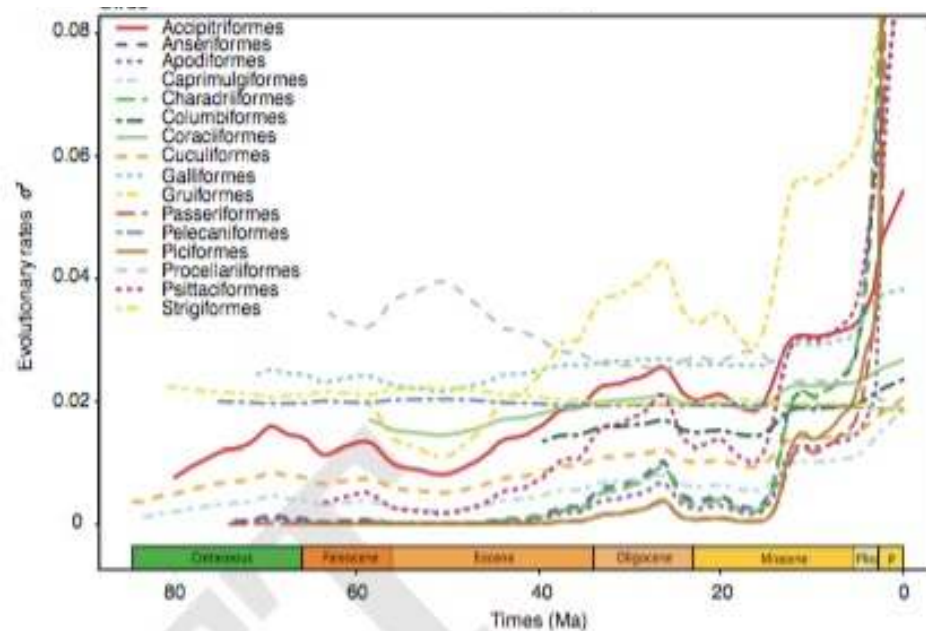
The dependence with temperature is negative
(lower rates at higher temperatures)



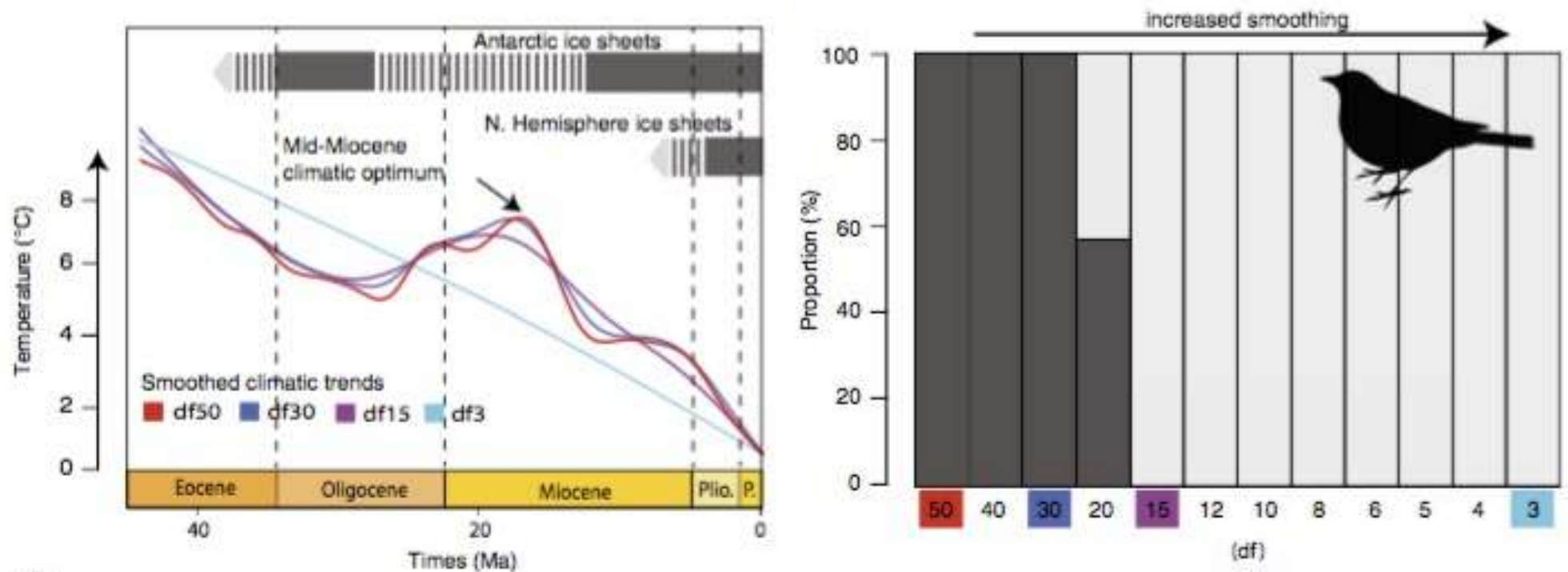
$$\sigma^2(t) = \sigma_0^2 \times e^{\beta T}$$



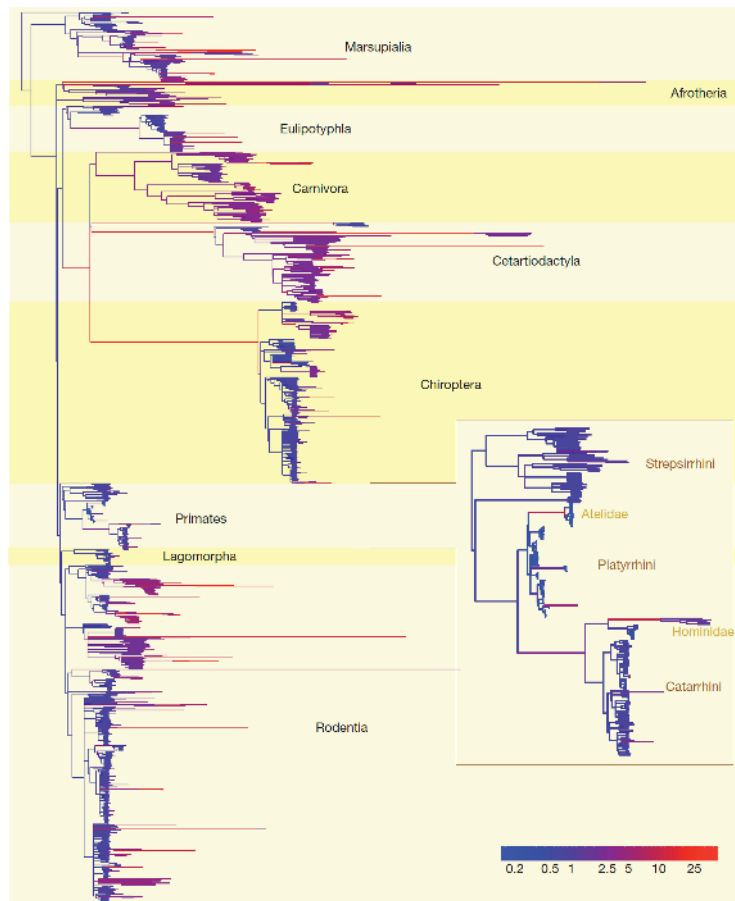
This results in an increase in evolutionary rates over the Cenozoic



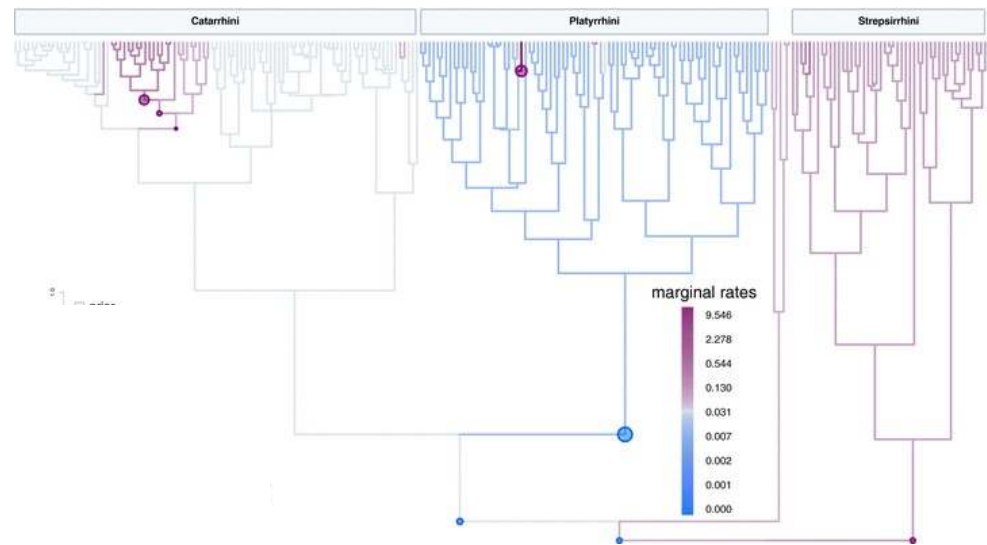
Loss of support for the climatic model when the temperature curve is smoothed suggests that support for the climatic model is real



Rates of phenotypic evolution vary across lineages



Venditti et al. Nature 2011



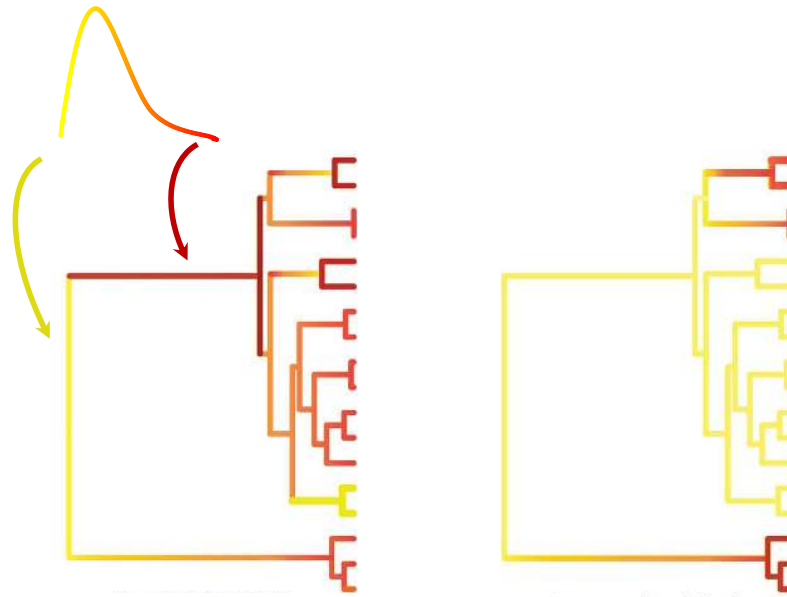
Eastman et al. Evolution 2011

Models with “local clocks” – few shifts with large effects

Models of phenotypic evolution with uncorrelated or correlated clocks



Julien Clavel



Many rate shifts with small effects

Models of phenotypic evolution with many shifts & small effects are best supported



Body-size evolution in mammals

punctuated
auto-correlated
independent
auto-correlated + jumps

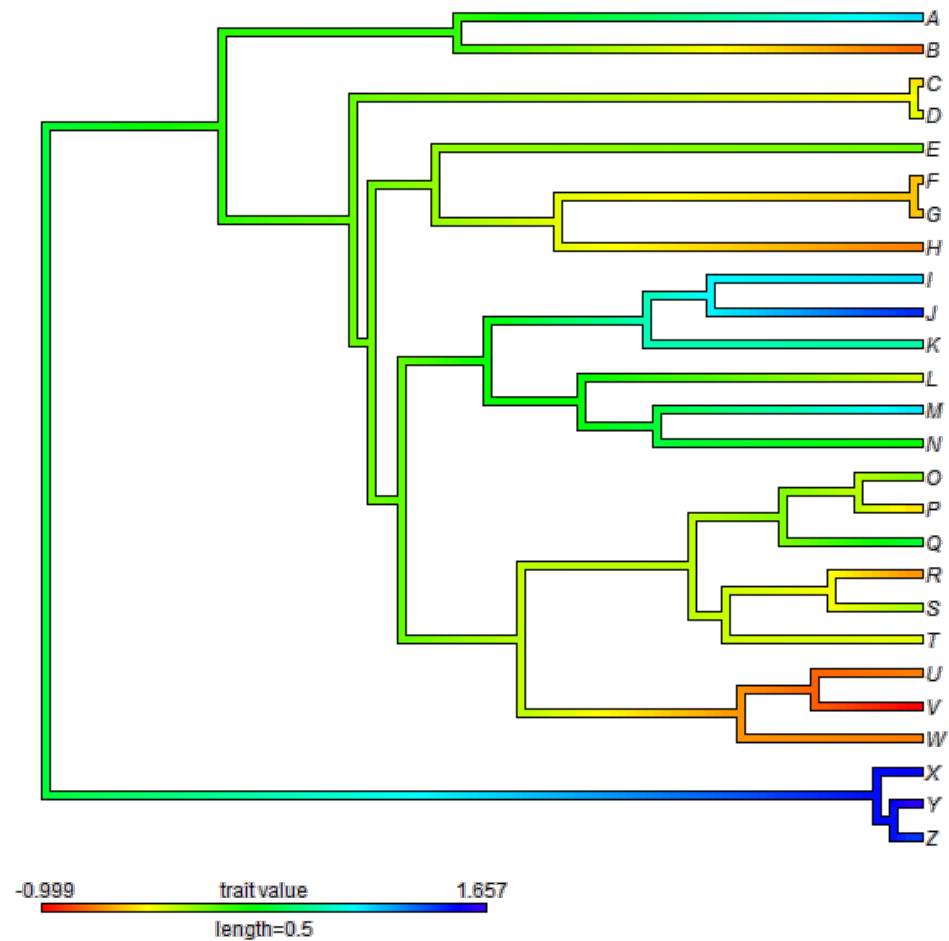
	Bovidae	Cercopithecidae	Cricetidae	Dasyuridae	Didelphidae	Heteromyidae	Muridae	Phyllostomidae	Pteropodidae	Sciuridae	Soricidae	Vespertilionidae
# of spp	118	79	327	53	50	51	228	111	96	123	119	157
BMJN	3 **	3.4 **	2.1 *	11.2 ***	2.5 *	3.6 **	13.3 ***	1.1 *	3.1 **	2.6 *	2.9 *	3.8 **
BMNIG	4.6 **	4.6 **	2.1 *	12.3 ***	3.6 **	4.6 **	14.6 ***	2 *	4.5 **	7.2 ***	4.7 **	5 ***
CIR	0	0	5.4 ***	0	0.9 .	0.5 .	1.6 *	0 .	17.4 ***	4.6 **	3 *	2.9 *
GBM	3.1 **	0.1 .	0.1 .	1.9 *	0.2 .	1.2 *	0	0.7 .	0	5.5 ***	0	3.9 **
LN	3.7 **	2.6 *	3.2 **	5.9 ***	0	0	6.7 ***	0	1.5 *	6.2 ***	1.7 *	0
SVBMJN	1.7 *	0.6 .	NA	4.4 **	0.7 .	2 *	1.9 *	0.6 .	1.9 *	0	0.8 .	2.2 *
SVBMNIG	2.3 *	2.5 *	0	6.1 ***	2 *	3 *	2.2 *	1.1 *	2.9 *	4.8 **	2.4 *	3.7 **
SVBMJN-CIR	1 .	1.6 *	8.6 ***	4.9 **	1.9 *	1.9 *	1.7 *	2 *	14.9 ***	NA	4.2 **	4.7 **
SVBMNIG-CIR	1.4 *	NA	NA	5.2 ***	3.4 **	2.6 *	7.6 ***	NA	16.6 ***	6.7 ***	NA	NA

Bayes factor support (Kass & Raftery 1995)

***	overwhelming support
**	strong support
*	positive support
.	hardly worth mentioning
	Best model

Clavel et al. in prep.

Models of phenotypic evolution allow estimating ancestral trait values



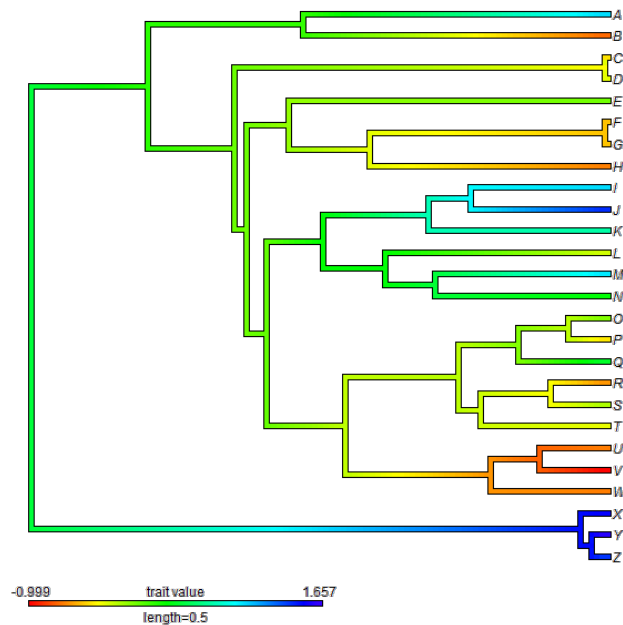
What are the factors that modulate diversification rates?

INTRINSIC

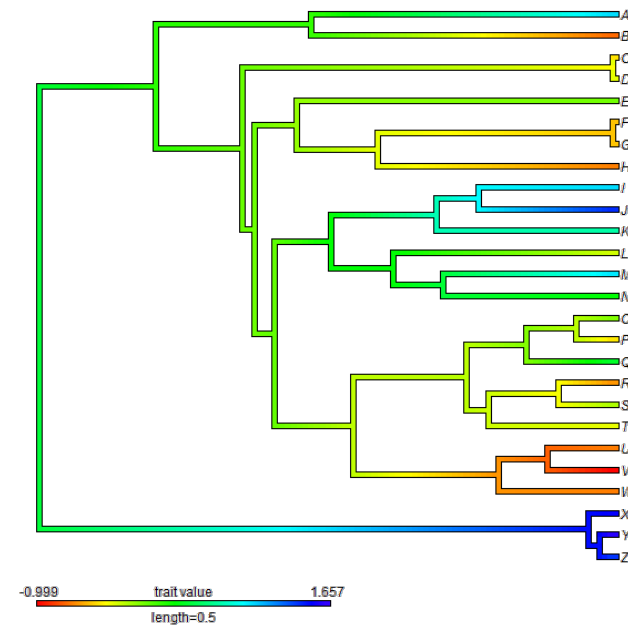


Species-specific traits
reproduction mode
life-history traits
dispersal capacity

Diversification rate estimates



Trait value estimates



Test for correlation while accounting for shared history!

What are the factors that modulate diversification rates?

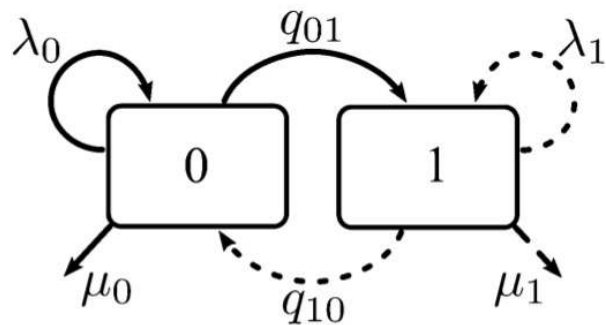
INTRINSIC



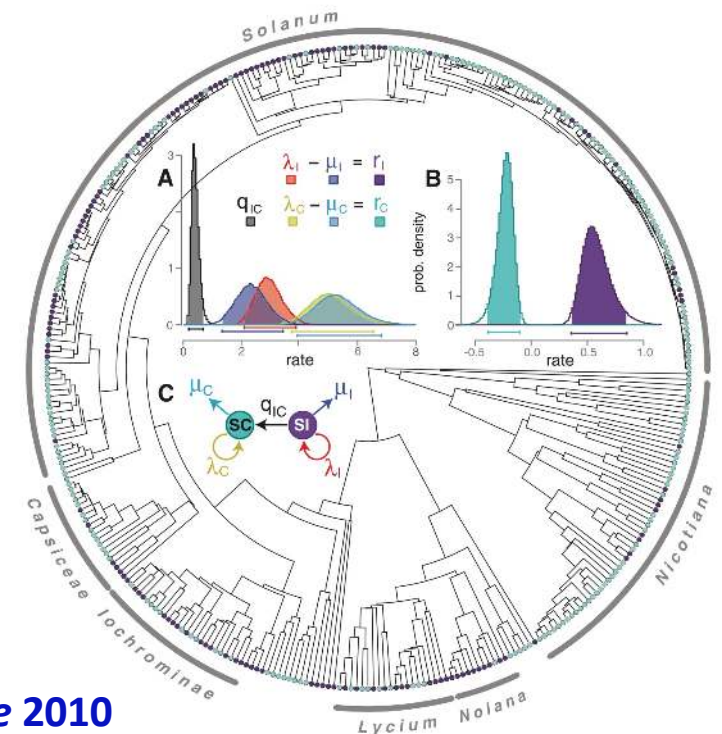
Species-specific traits
reproduction mode
life-history traits
dispersal capacity

State-dependent Speciation-Extinction (SSE) models

Transitions to selfing happen frequently, but
self-incompatible species have higher net
diversification rates



Maddison *et al.* Syst Bio 2004,
Fitzjohn *et al.* Syst Bio 2010,
Goldberg *et al.* Syst Bio 2011,
etc...



Goldberg *et al.* Science 2010

These tools are implemented in the well-documented, user-friendly packages RPANDA, jPANDA, BEAST2 and Tapestry

Methods in Ecology and Evolution



Methods in Ecology and Evolution 2016, 7, 589–597

doi: 10.1111/2041-210X.12526

APPLICATION

RPANDA: an R package for macroevolutionary analyses on phylogenetic trees

Hélène Morlon^{1*}, Eric Lewitus¹, Fabien L. Condamine², Marc Manceau¹, Julien Clavel¹ and Jonathan Drury¹



Beast2

Bayesian evolutionary analysis by sampling trees



Methods in Ecology and Evolution



Methods in Ecology and Evolution 2015, 6, 1311–1319

doi: 10.1111/2041-210X.12420

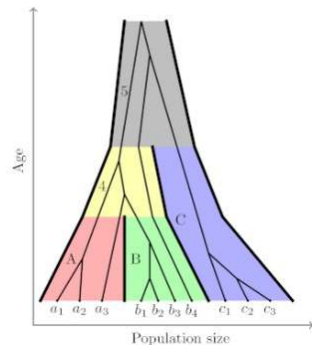
APPLICATION

mvmORPH: an R package for fitting multivariate evolutionary models to morphometric data

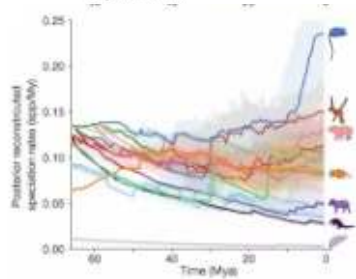
Julien Clavel^{1,2*}, Gilles Escarguel² and Gildas Merceron³



UNDERSTANDING MACROEVOLUTIONARY DYNAMICS USING RPANDA AND JPANDA



BAYESIAN PHYLOGENETIC INFERENCE WITH BEAST2



INTRODUCTION TO PROBABILISTIC INFERENCE OF PHYLOGENETIC COMPARATIVE METHODS (PCM) USING JULIA



MODELLING AND ANALYSING MULTIVARIATE TRAIT EVOLUTION USING MVMORPH

Conclusion

**Stochastic models are powerful for understanding modes
and rates of species and phenotypic diversification**

**This is fundamental for understanding current
biodiversity patterns**

**But also for phylogenetic inference, and for
understanding how genome evolution influences
biodiversity dynamics**



Fabien Condamine



Joëlle Barido-Sottani



Jonathan Rolland



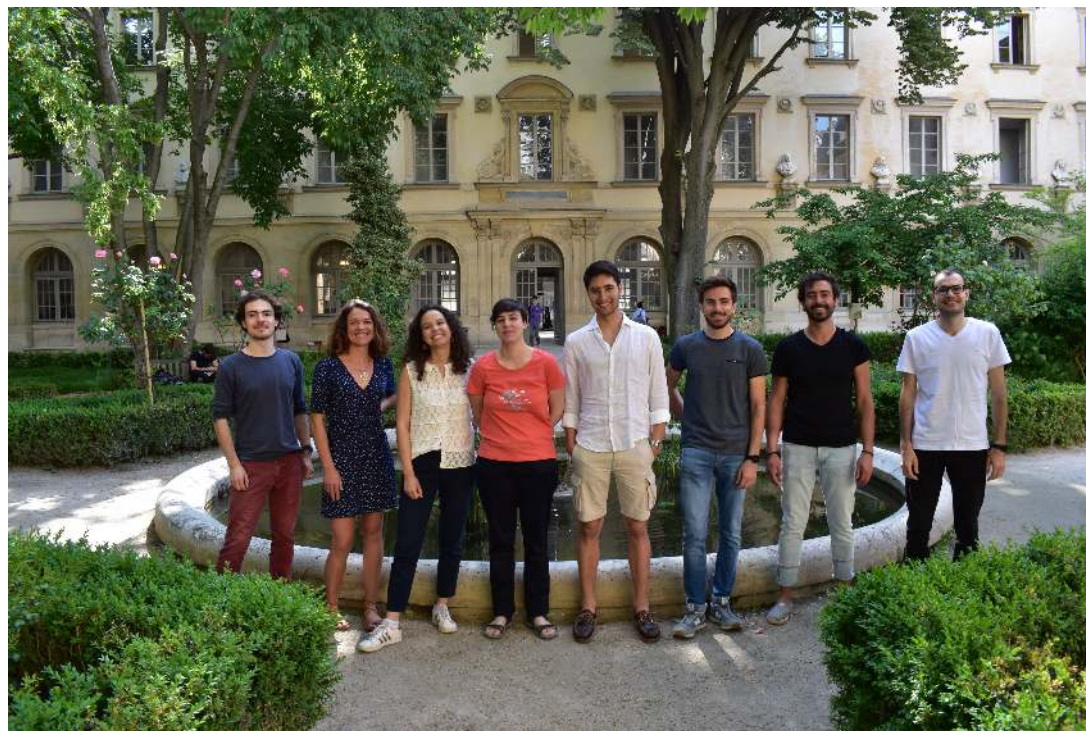
Ignacio Quintero



Odile Maliet



Dan Moen



Julien Clavel



Olivier Billaud



Nathan Mazet

THANKS! AGENCE NATIONALE DE LA RECHERCHE **ANR** **erc**
PANDA