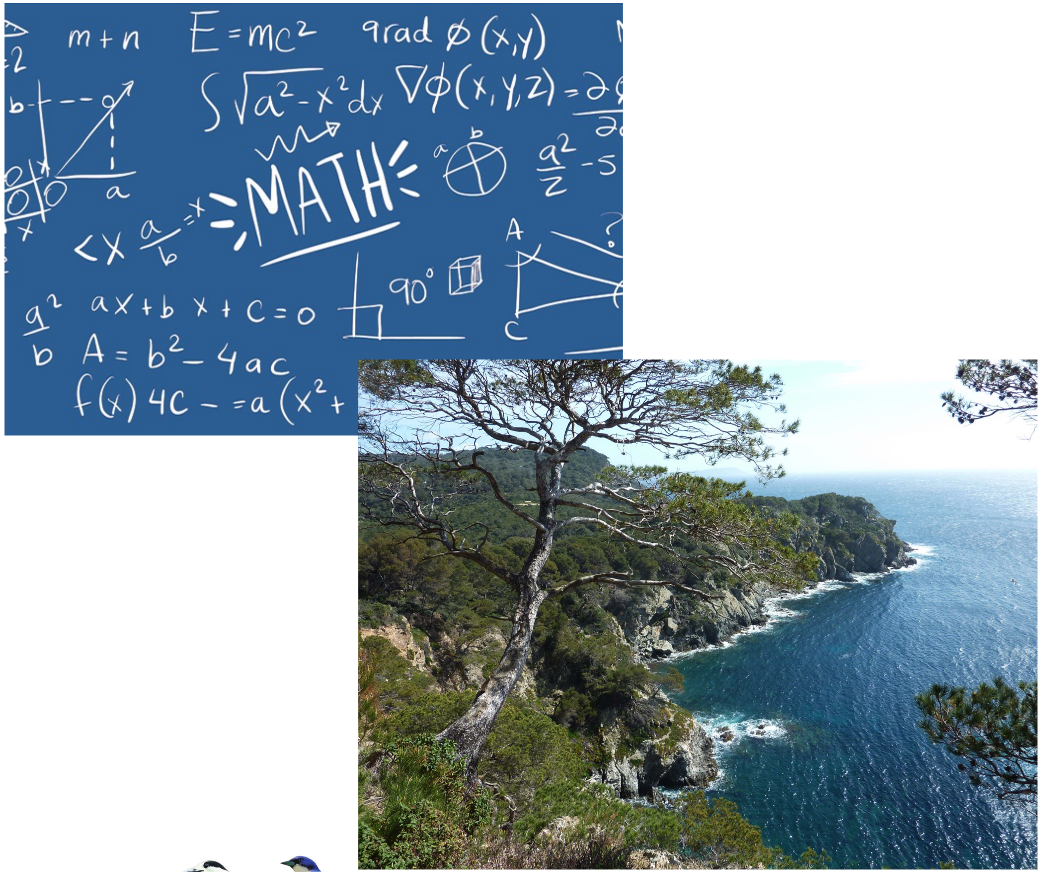
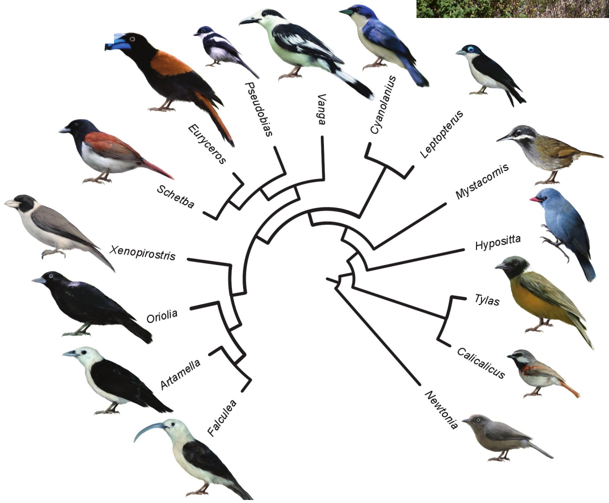
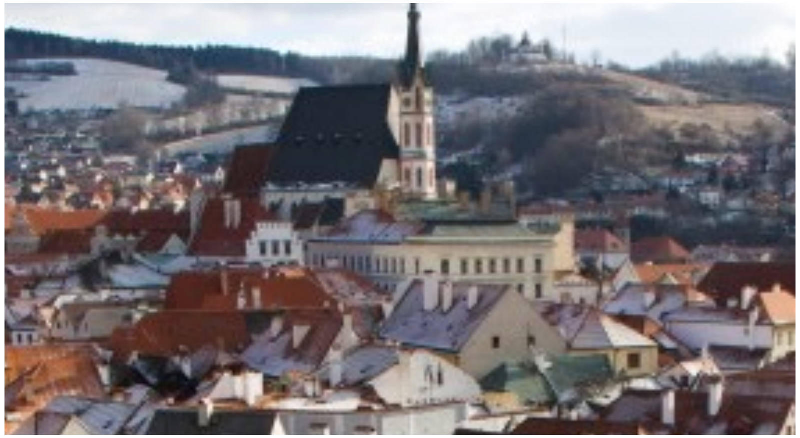
Hélène Morlon





Cesky Krumlov



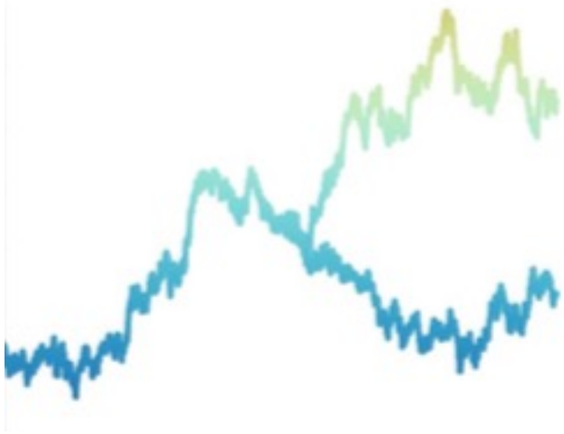
Joëlle Barido-Sottani

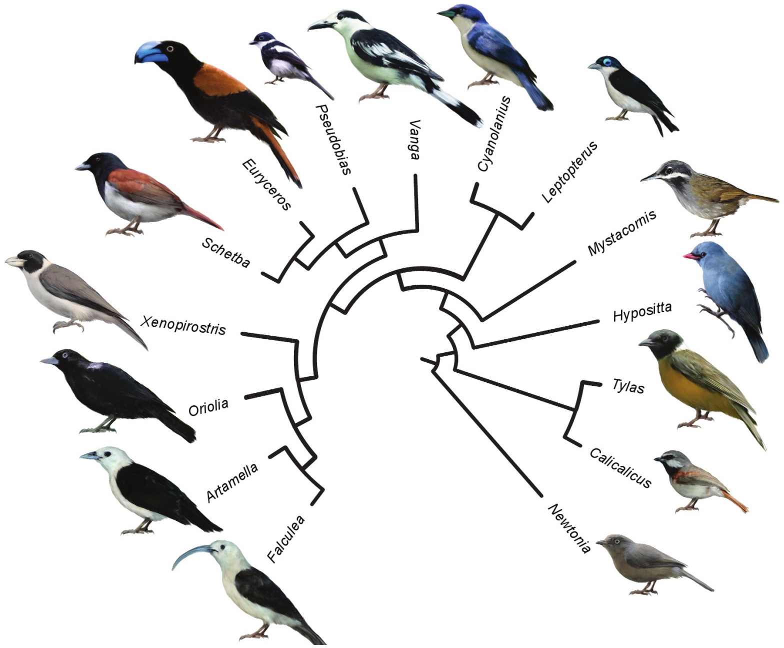
Mahwash Jamy

Beast2

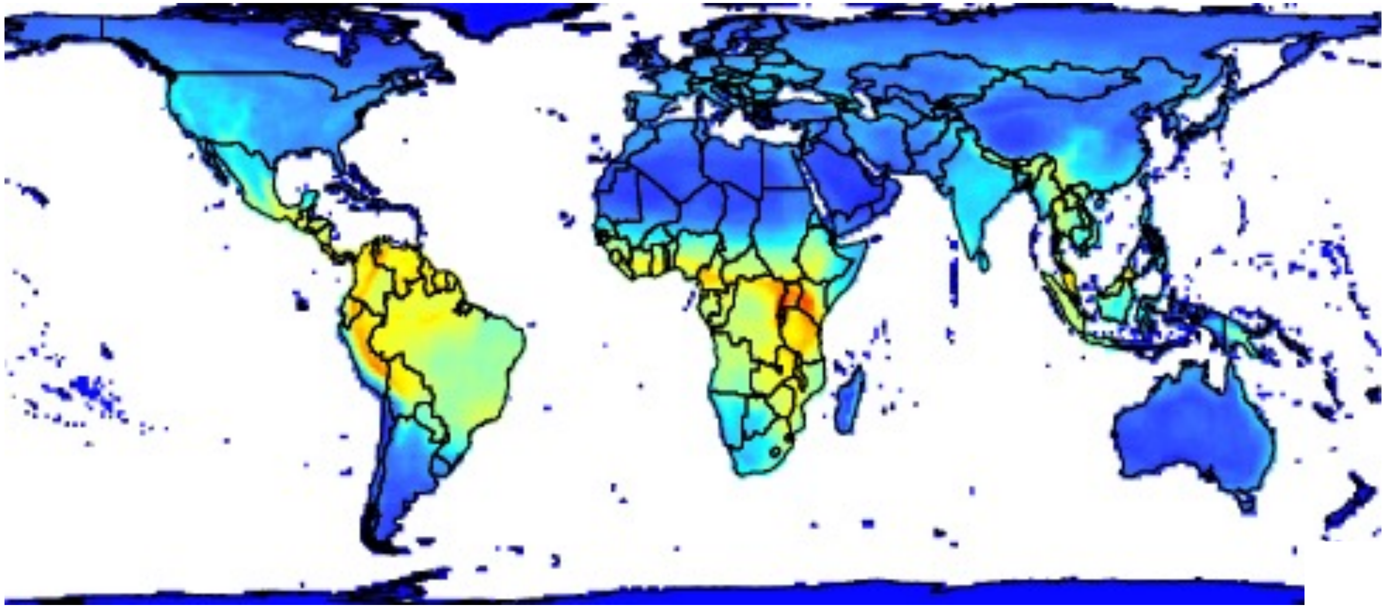
Bayesian evolutionary analysis by sampling trees

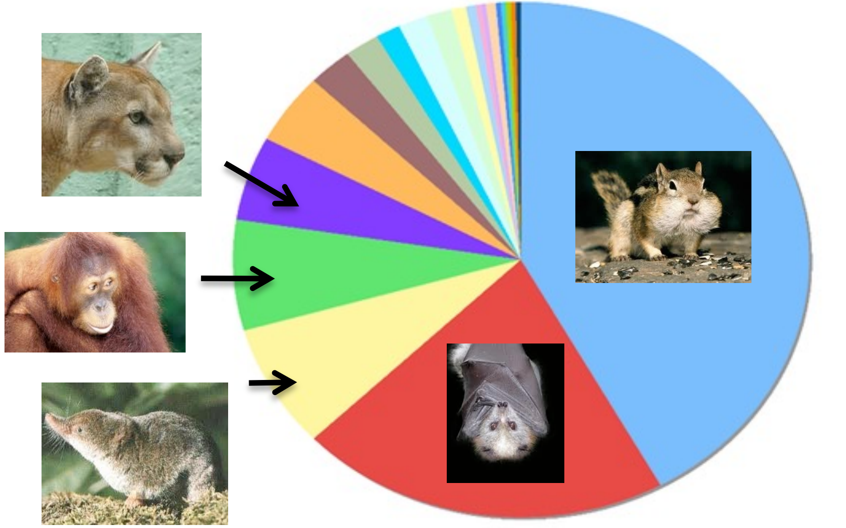
Trait evolution on trees, phenotypic and species diversification



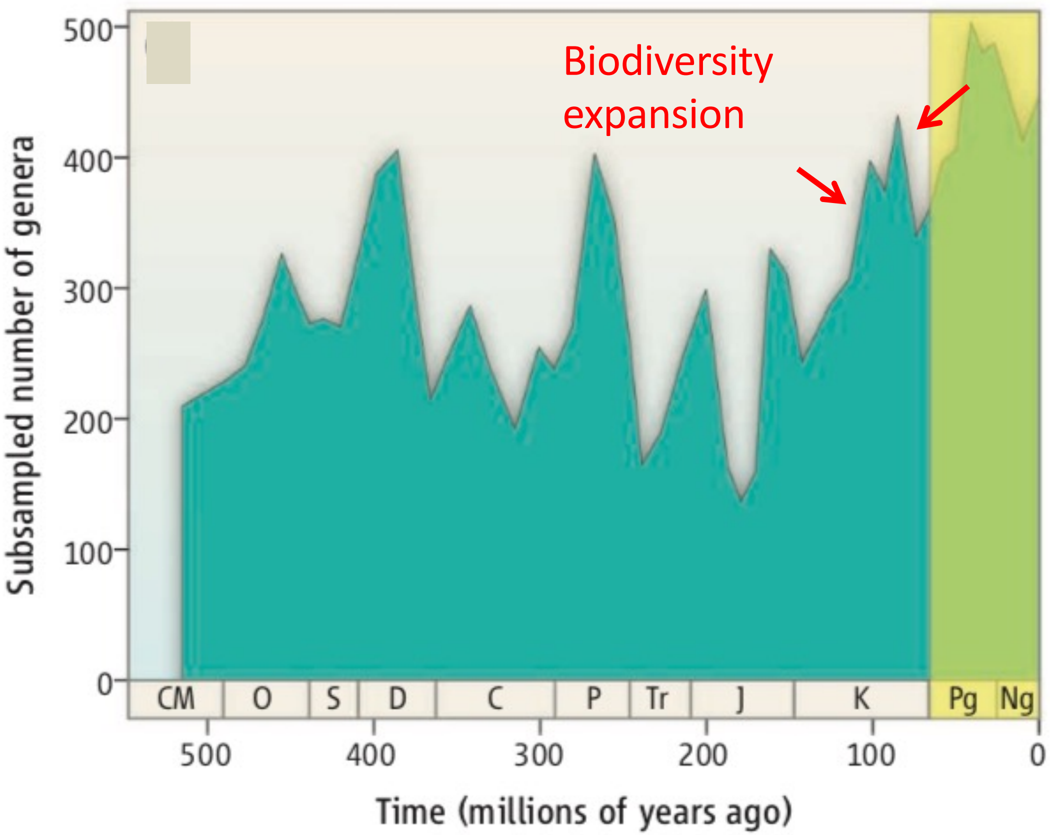


What are the processes that generate biodiversity as we see it around us today?





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

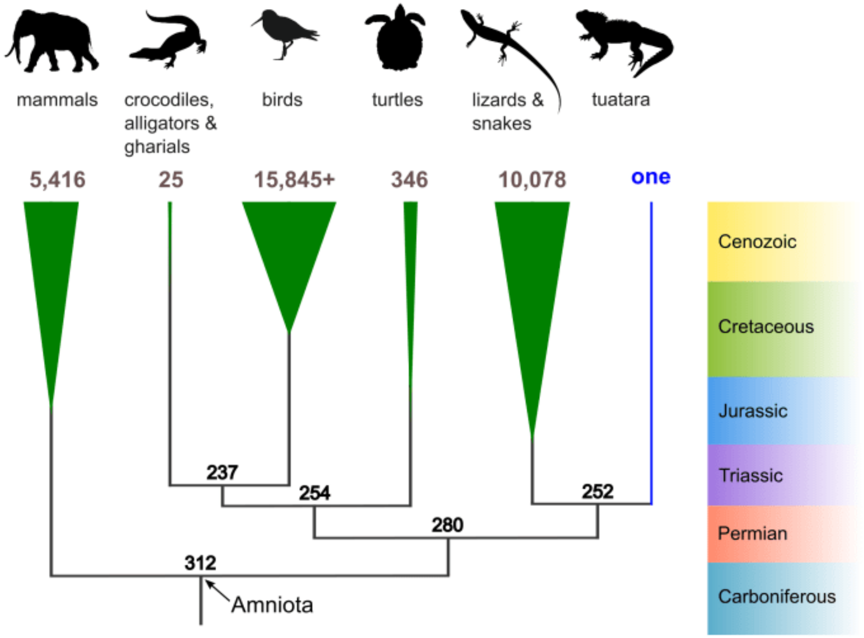


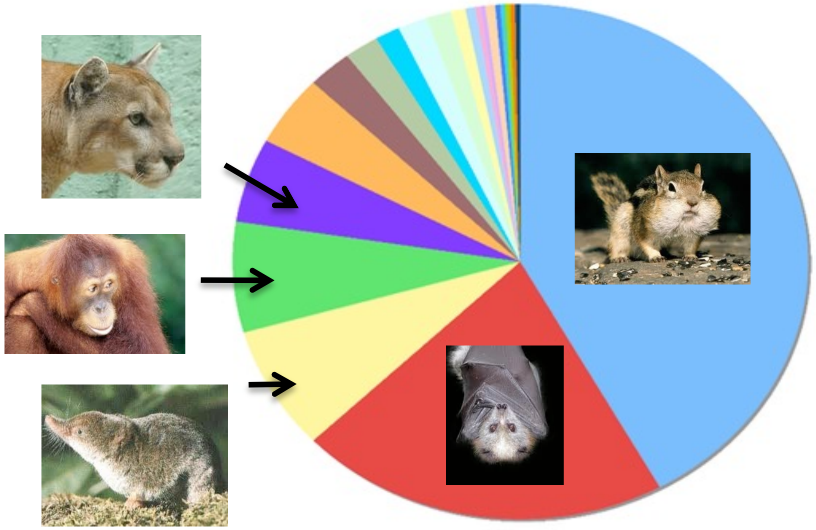
Biodiversity expansion

Biodiversity decline

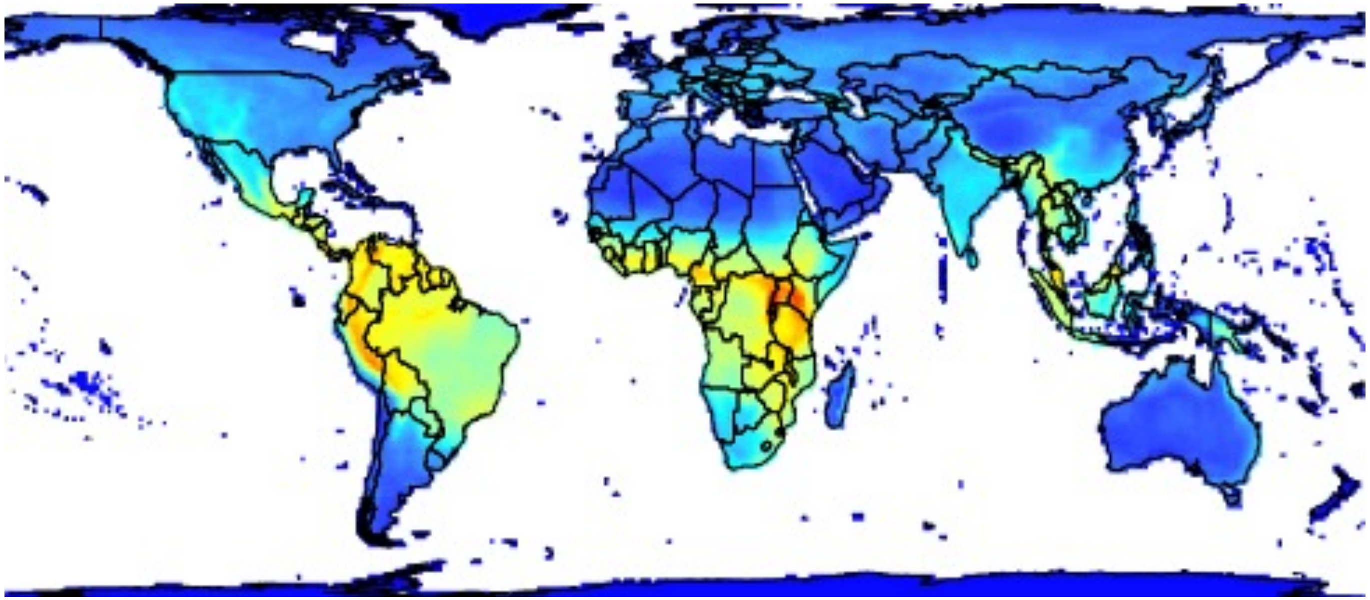
Marshall *et al.* Science 2010

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





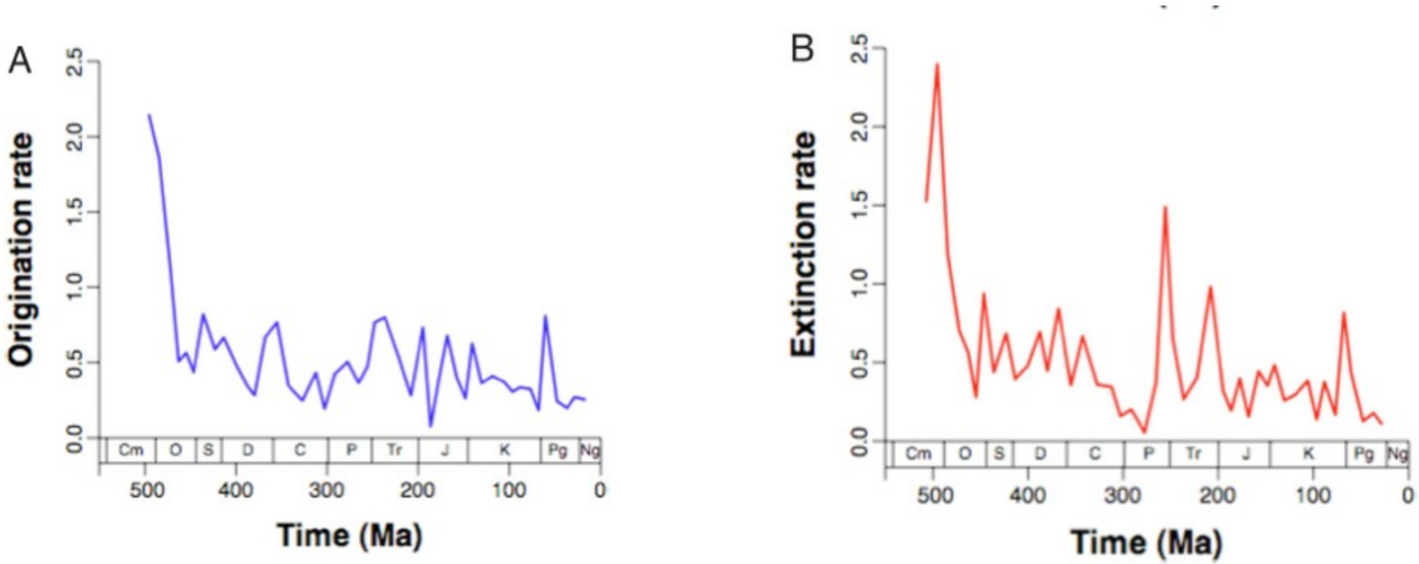
The balance between speciation, extinction and dispersal events explain why some regions of the planet are much more species rich than others



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

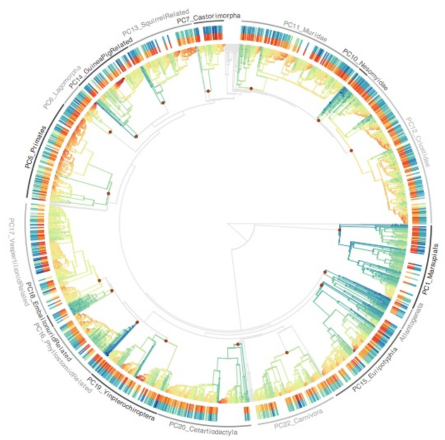
How can we study species diversification (speciation and extinction) using empirical data?

The fossil record



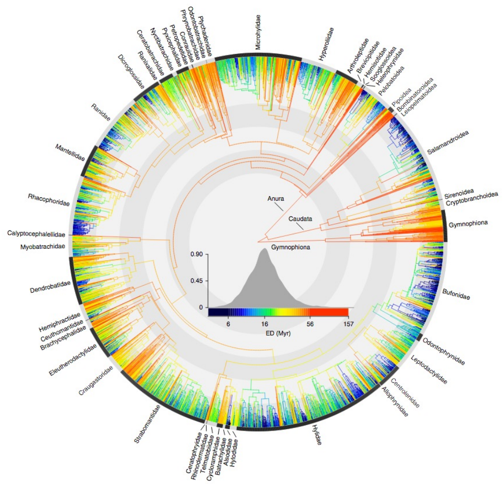
Alroy *PNAS* 2008

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



6 000 mammal species

Upham *et al. PloSB 2019*

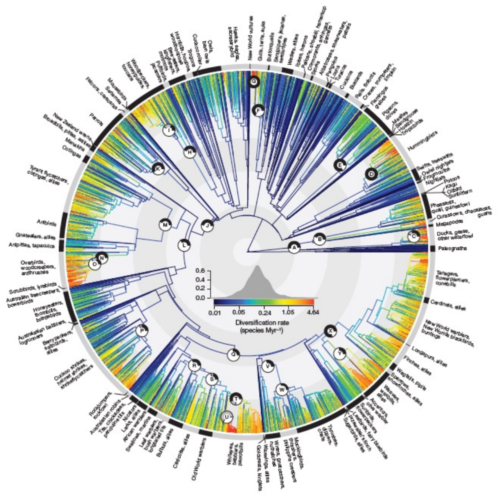


> 7 000 amphibian species

Jetz & Pyron *Nat Ecol Evol* 2018

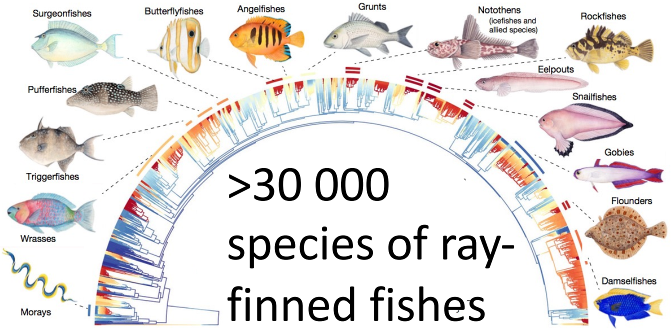
OPEN Tree of Life

2.2 Million species
on a single tree



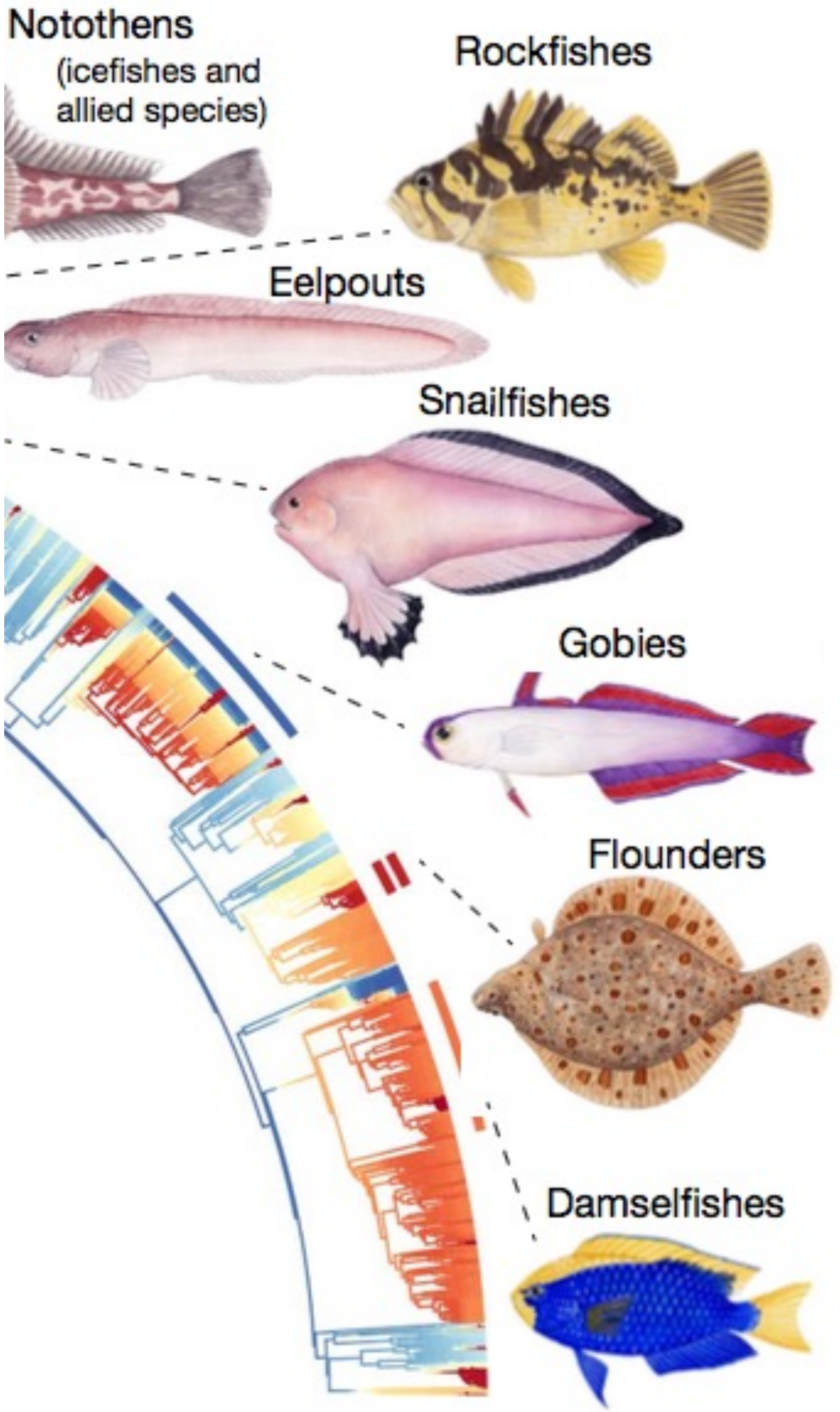
10 000 bird species

Jetz *et al. Nature* 2012

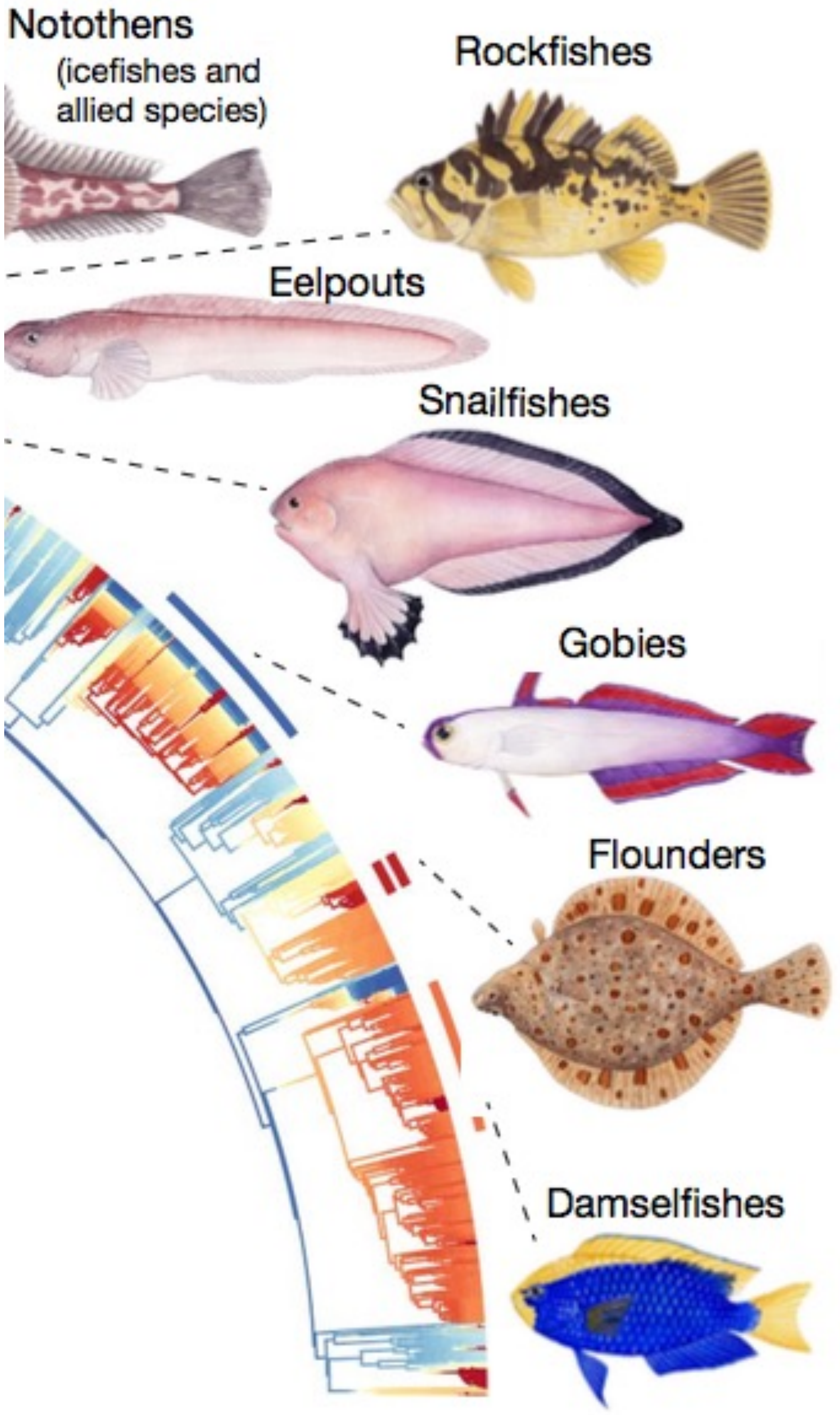


>30 000
species of ray-finned fishes

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



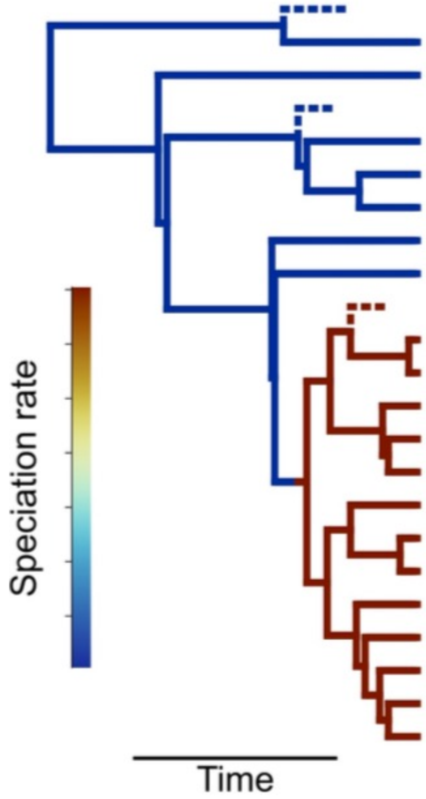
In what follows, we consider the (dated) phylogenetic tree as **data**

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

Phylogenetic approaches for studying diversification

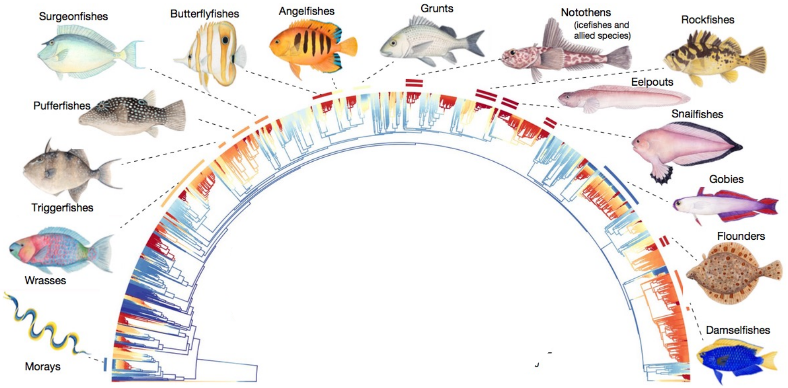
Develop **diversification models** AND **statistical inference approaches** that allow adjusting the models to **phylogenetic trees** to **test alternative hypotheses about diversification** and **estimate speciation and extinction rates**

Diversification model



Statistical inference

Phylogenetic tree

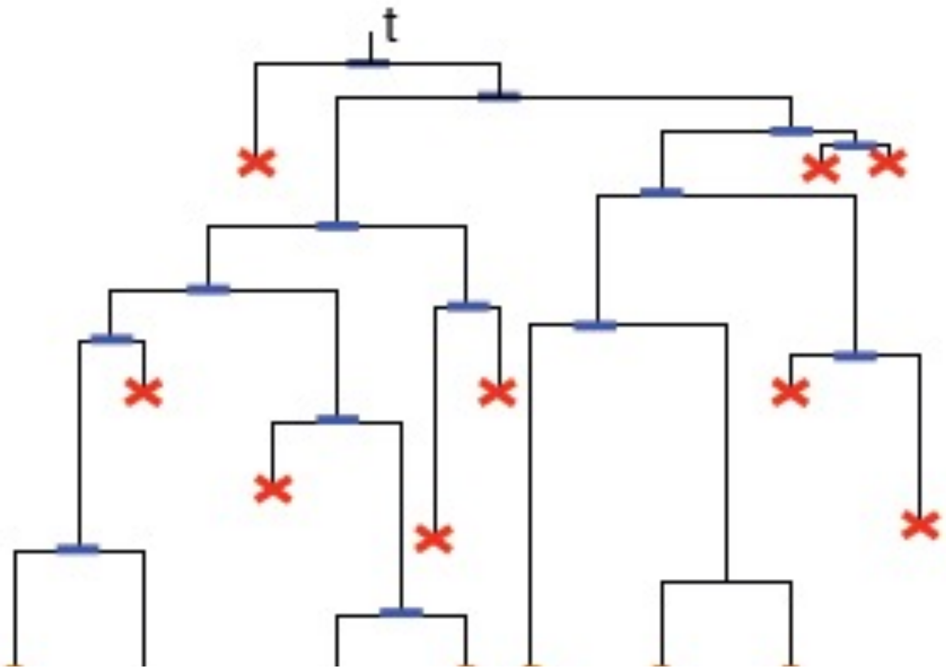


Hypothesis testing
Estimation of speciation and extinction rates

Birth-death model for the analysis of diversification

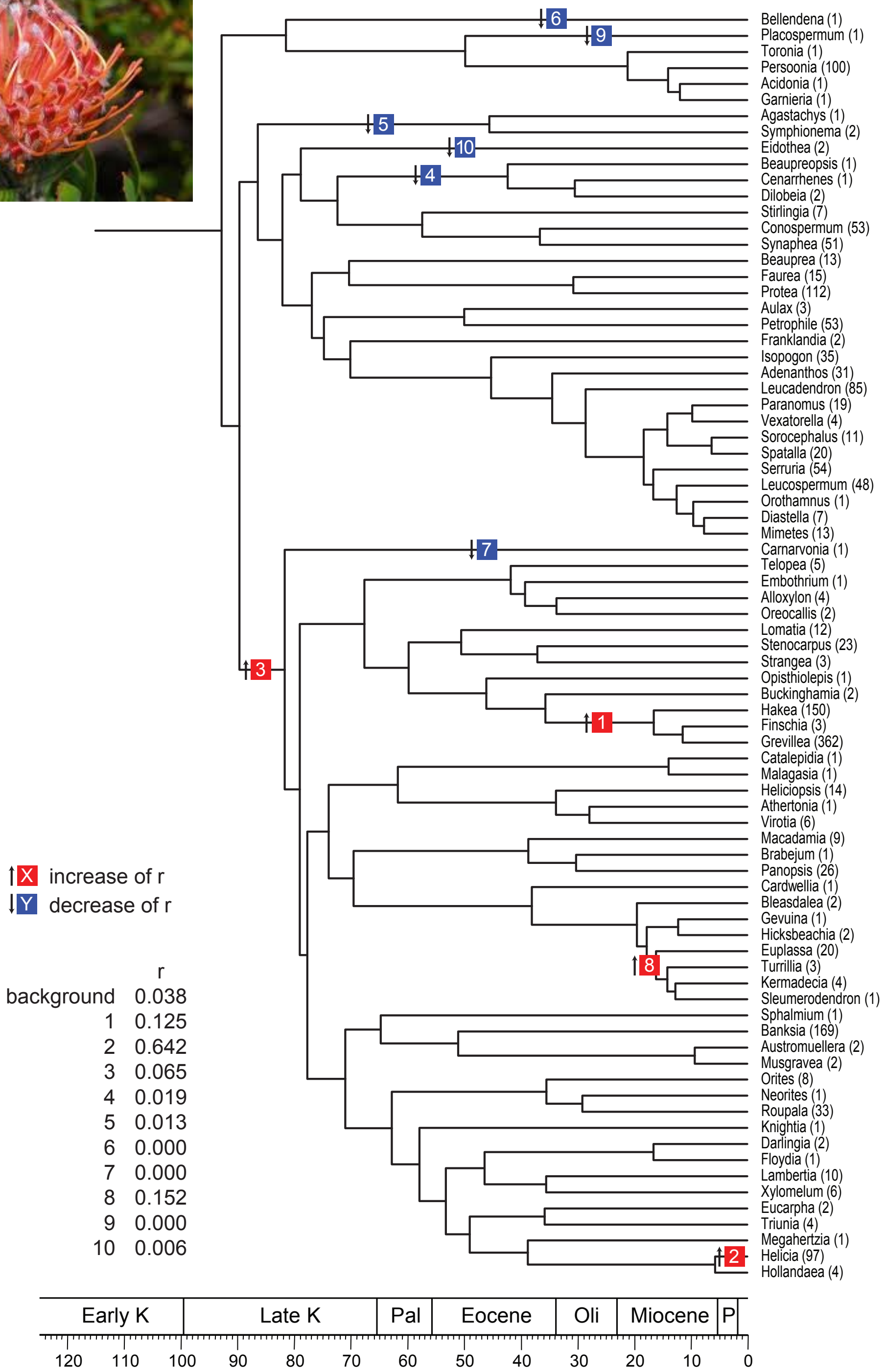
We model the evolution of a given clade (group of species that contains a common ancestor and all its descendants) with stochastic birth-death models:

- the clade starts with a single ancestor at time T
- species give rise to new speces 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



	r
background	0.038
1	0.125
2	0.642
3	0.065
4	0.019
5	0.013
6	0.000
7	0.000
8	0.152
9	0.000
10	0.006

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

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

With extinction
(birth-death model)

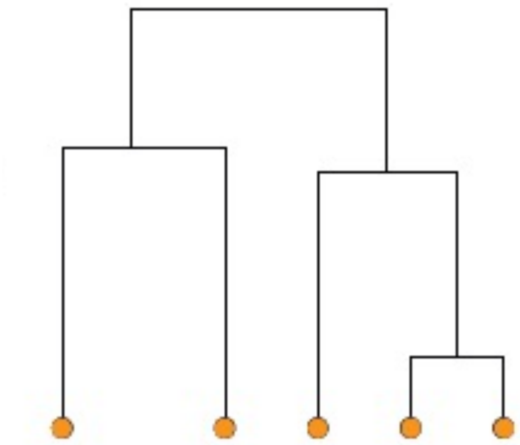
$$\hat{r} = \frac{1}{T}\log(n(1-\varepsilon)+\varepsilon) \qquad \varepsilon = \frac{\mu}{\lambda}$$

↗

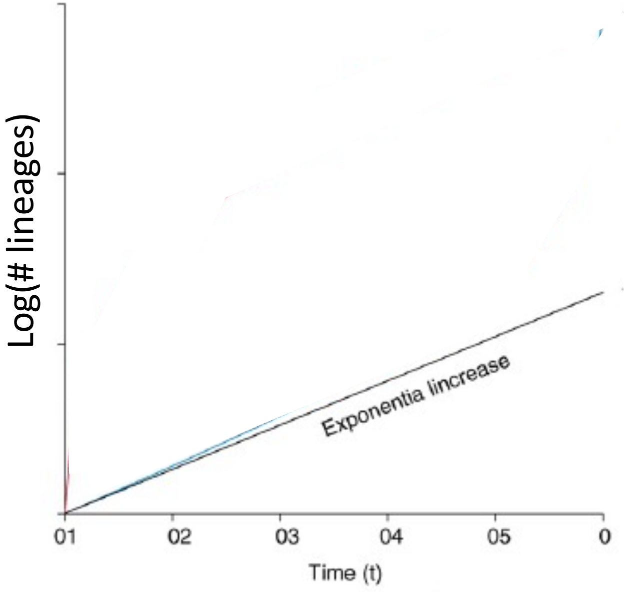
r = $\lambda - \mu$

Magallon & Sanderson *Evolution* 2001

Estimating diversification using Lineage Through Time plots (LTT)

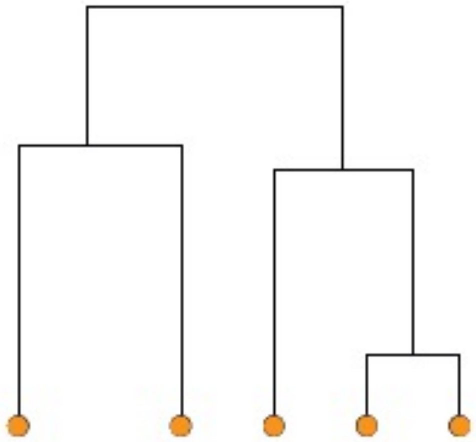


Phylogenetic tree of present-day species

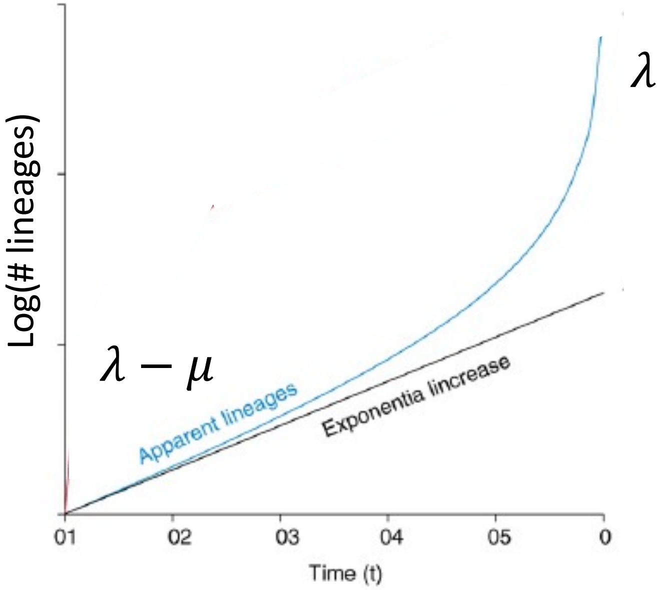


In the absence of extinction, an estimate of the speciation rate is given by the slope of the Lineage Through Time plot

Estimating diversification using Lineage Through Time plots (LTT)



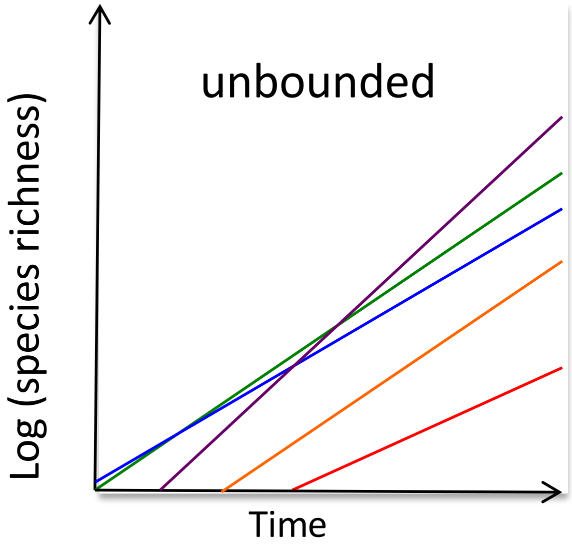
Phylogenetic tree of present-day species



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

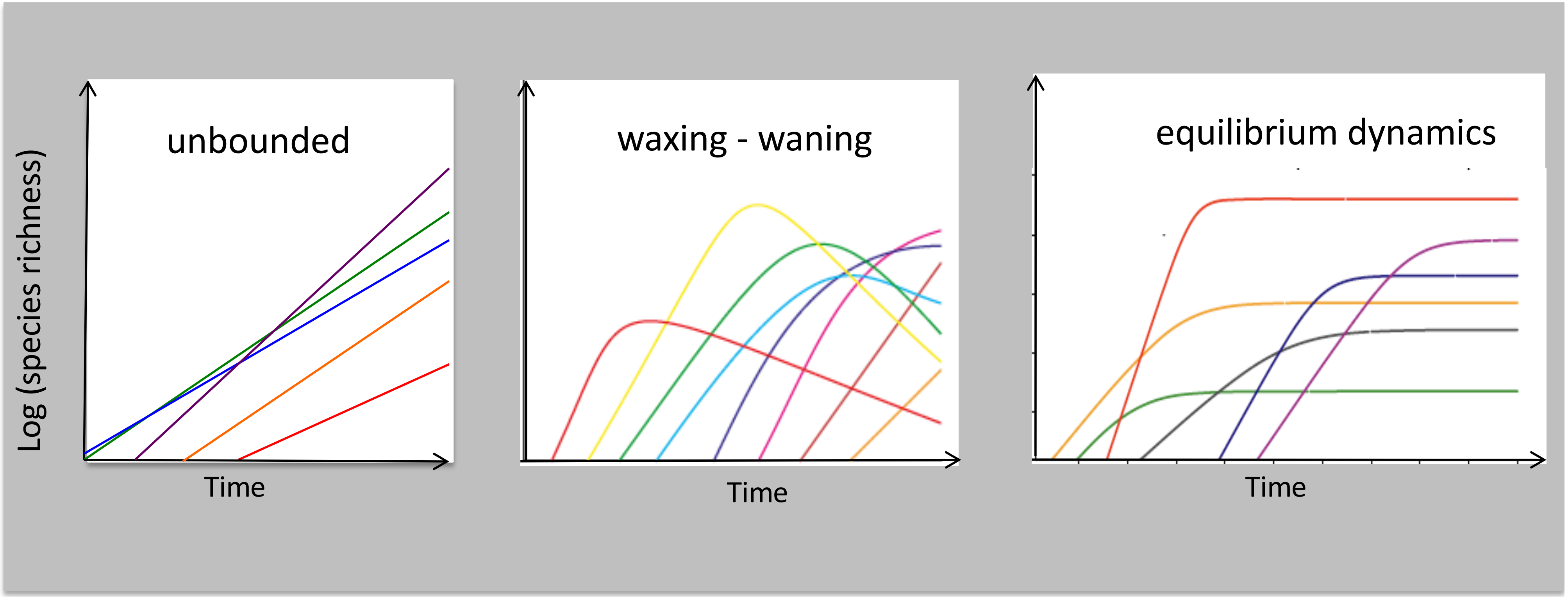
The slope towards the present provides an estimate of the speciation rate, the slope in the past provides an estimate of the net diversification rate.

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

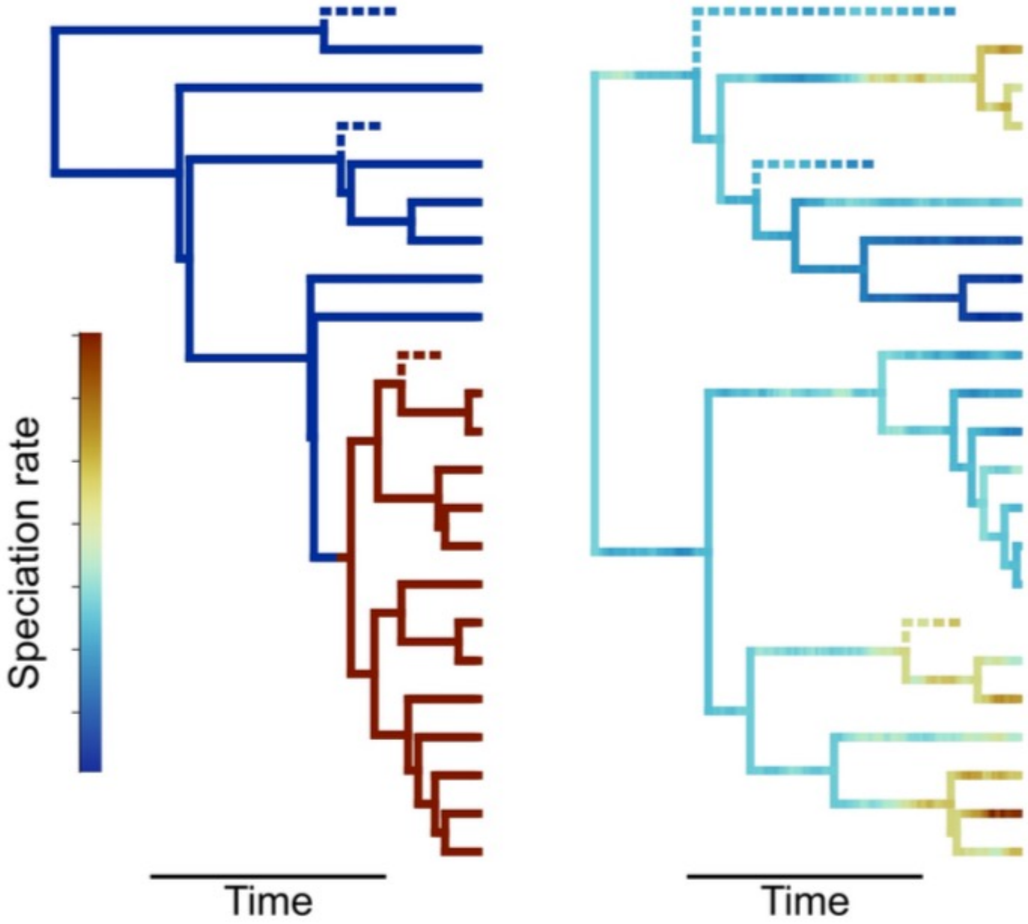


What if biodiversity dynamics are not unbounded?

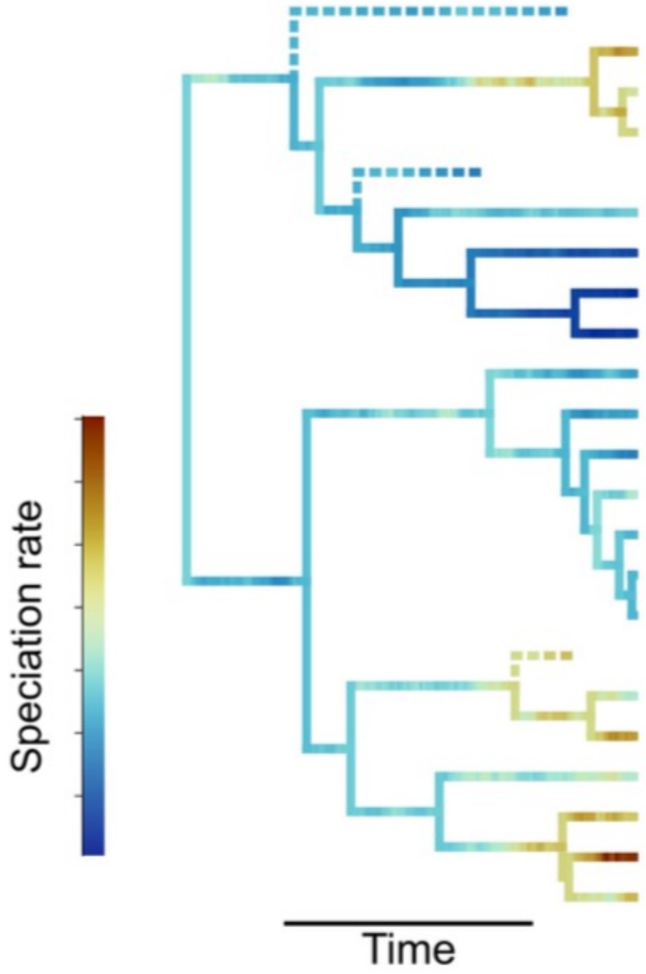
What if we want to test the support of different visions of how the evolution of diversity proceeds?



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

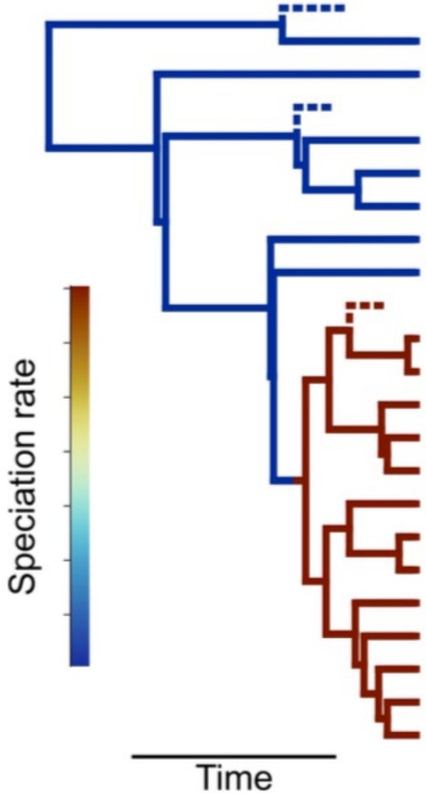


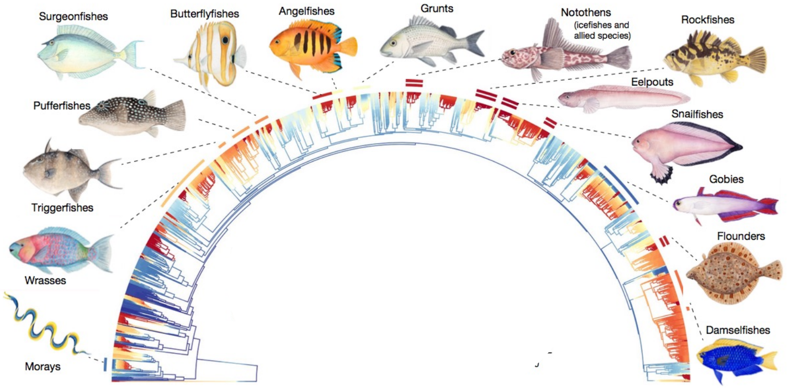
Intuitively, the distribution of branching times informs on temporal variation in speciation and extinction rates, topology informs on rate variation across lineages



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: $L_{\boldsymbol{x}}(\theta) = f_\theta(\boldsymbol{x})$ where $f_\theta(\boldsymbol{x})$ is the probabilty of observing a realization $\boldsymbol{x}$ under the model for parameters fixed at the value θ

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

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

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

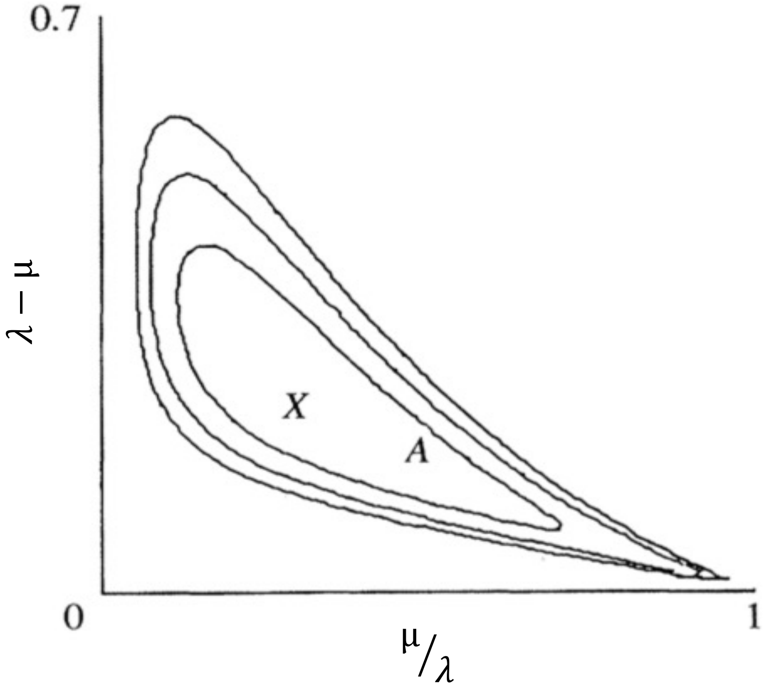
The likelihood is defined as

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

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 $\mathcal{L}_x(\theta)$

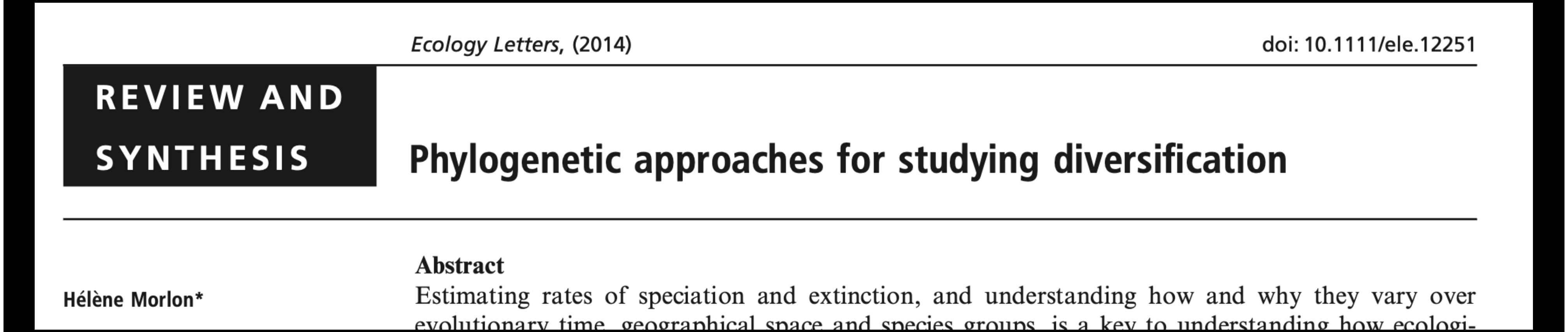
Likelihood surface of a birth-death model on a simulated phylogeny



Nee *et al.* PTB 1994

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

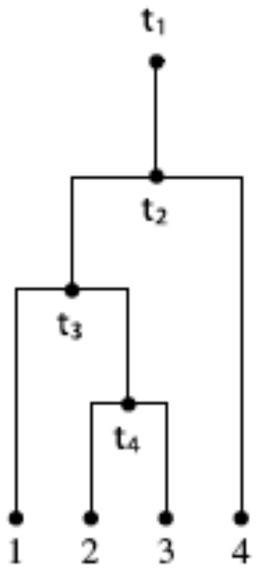
Estimating rates of speciation and extinction, and understanding how and why they vary over evolutionary time, geographical space and species groups, is a key to understanding how ecologi-

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

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

speciation rate at time t_i

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

Morlon *et al.* PNAS 2011

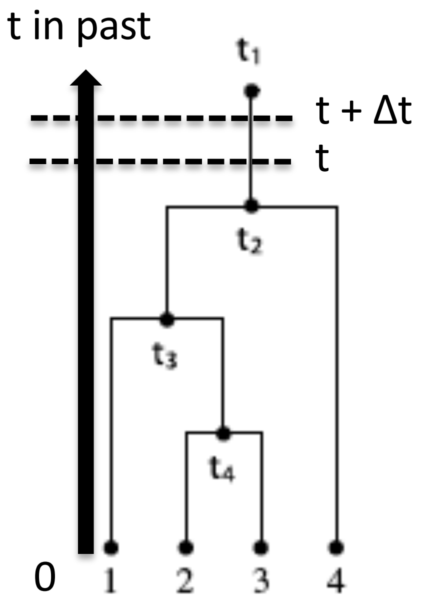
Likelihood of a phylogeny of extant species under the birth-death process

birth-death model

stem age t_1
speciation rate λ
extinction rate μ

+

λ and μ can vary over time
sampling fraction f



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

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

$\Delta t \rightarrow 0$

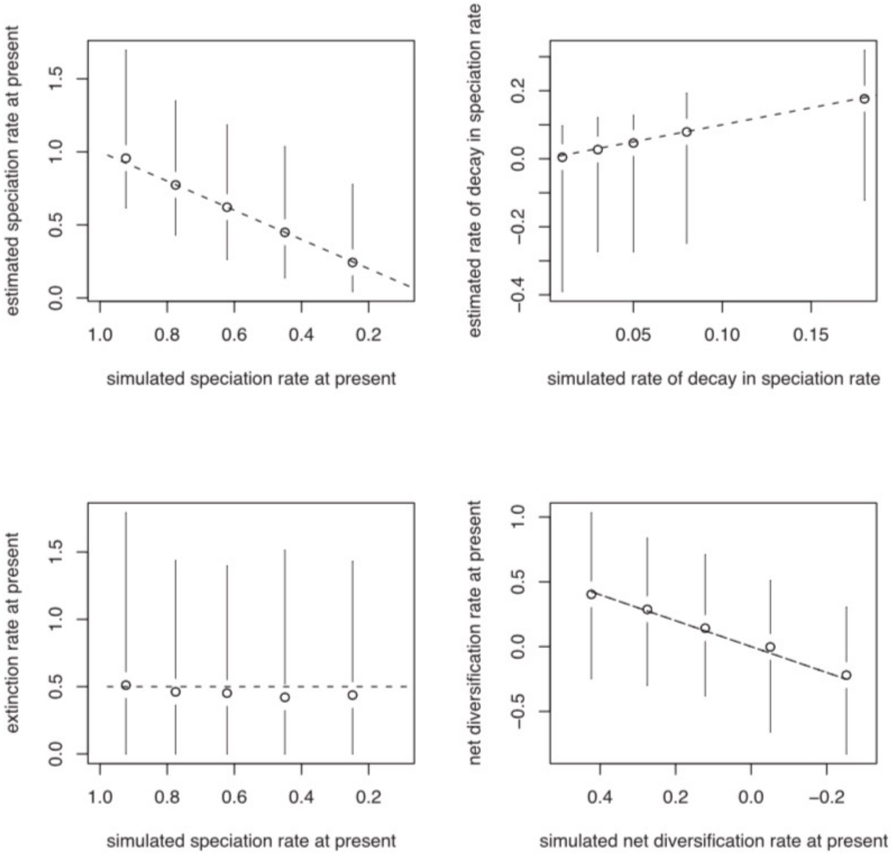
$$\frac{d\Phi}{dt} = \mu(t) - (\lambda(t)+\mu(t))\Phi(t) + \lambda(t)\Phi^2(t)$$

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

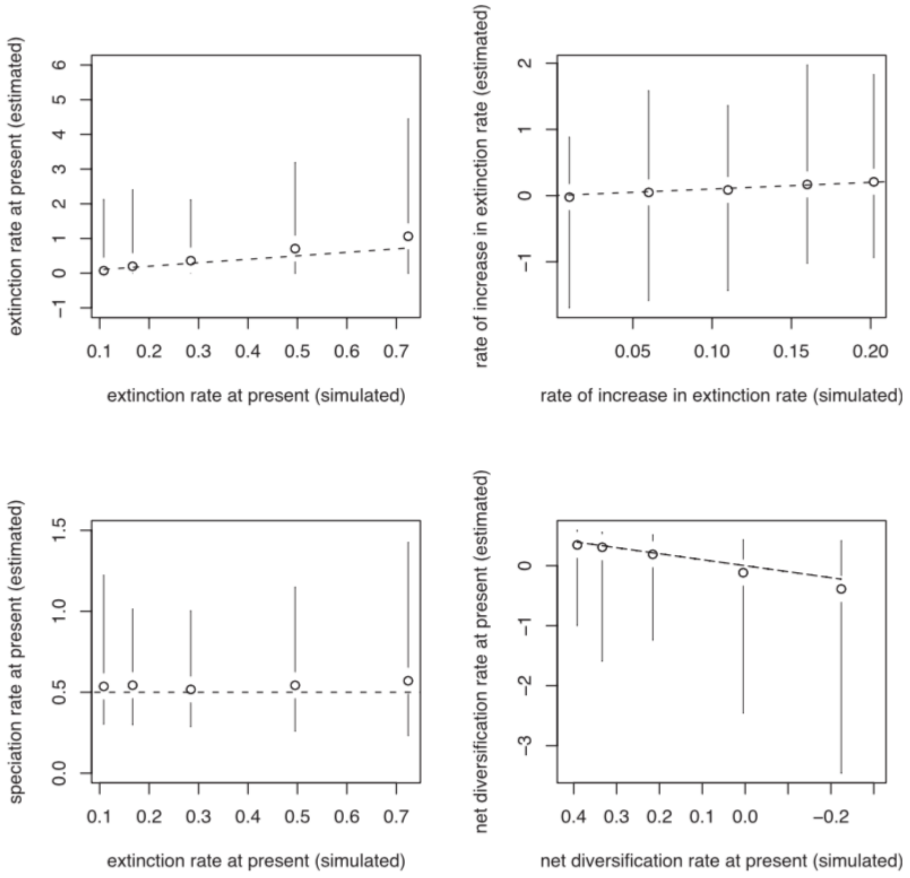
Morlon *et al.* PNAS 2011

Unbiased parameter estimates

Exponential decay of speciation rate, constant extinction



Exponential increase of extinction rate, constant speciation

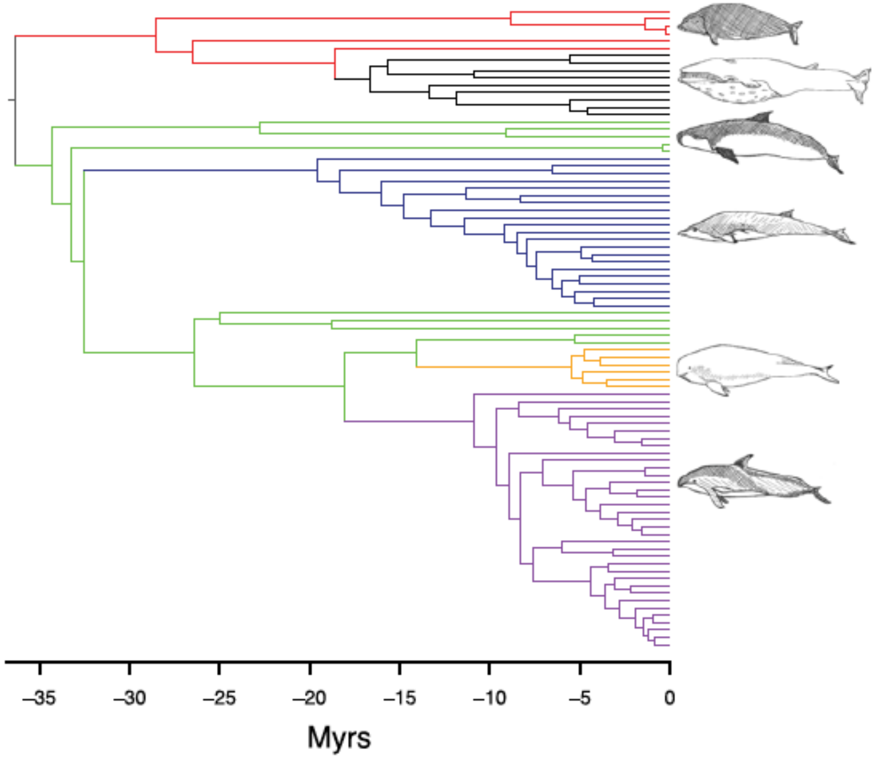


Morlon *et al.* PNAS 2011

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



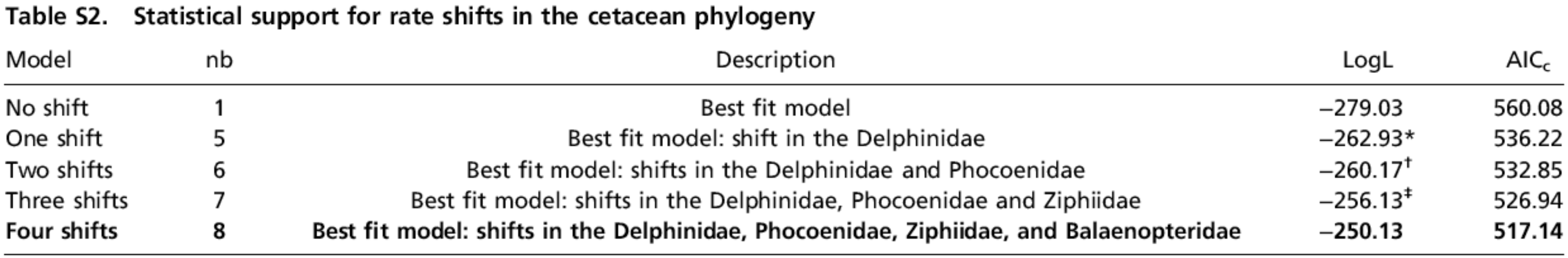
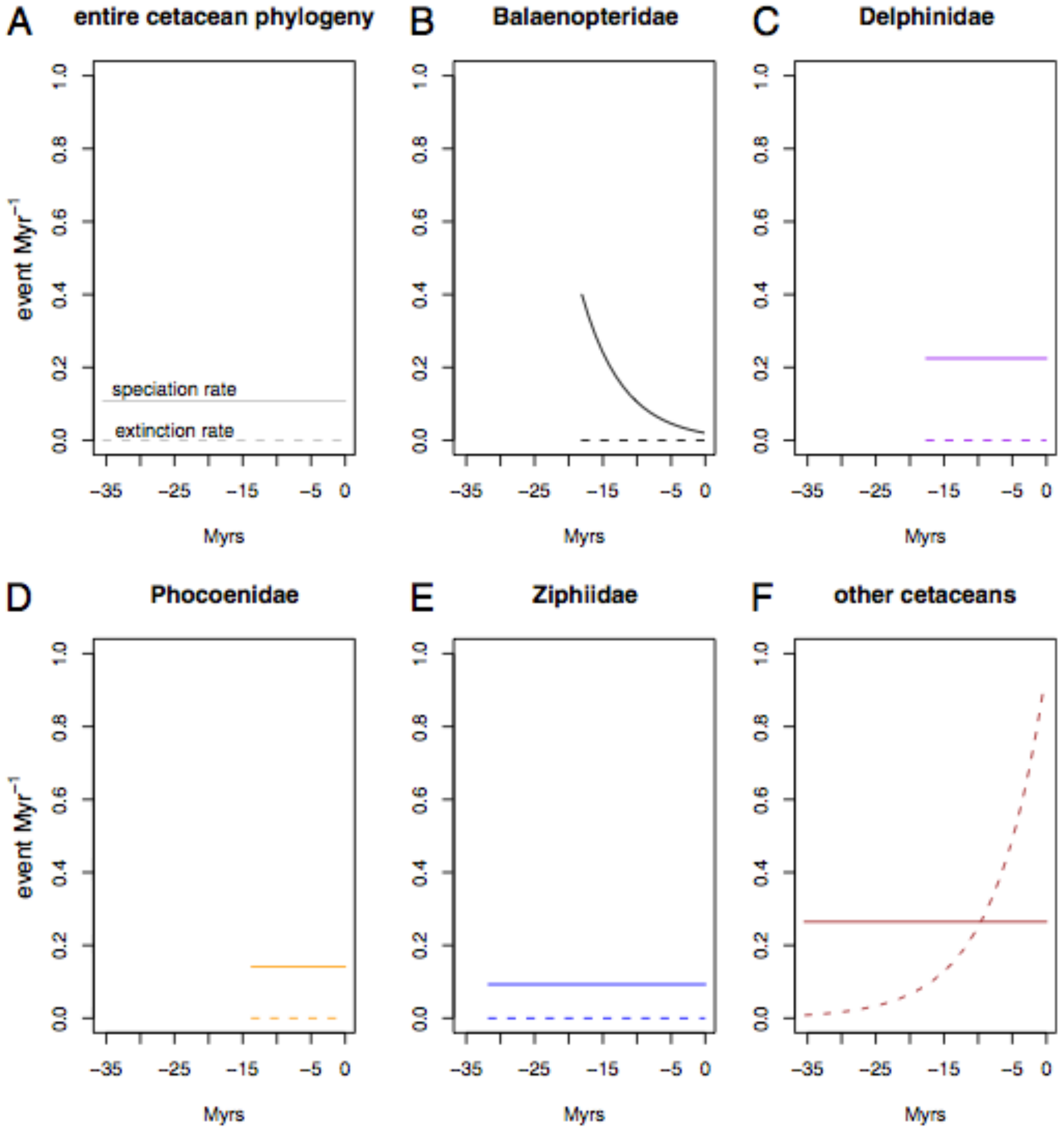


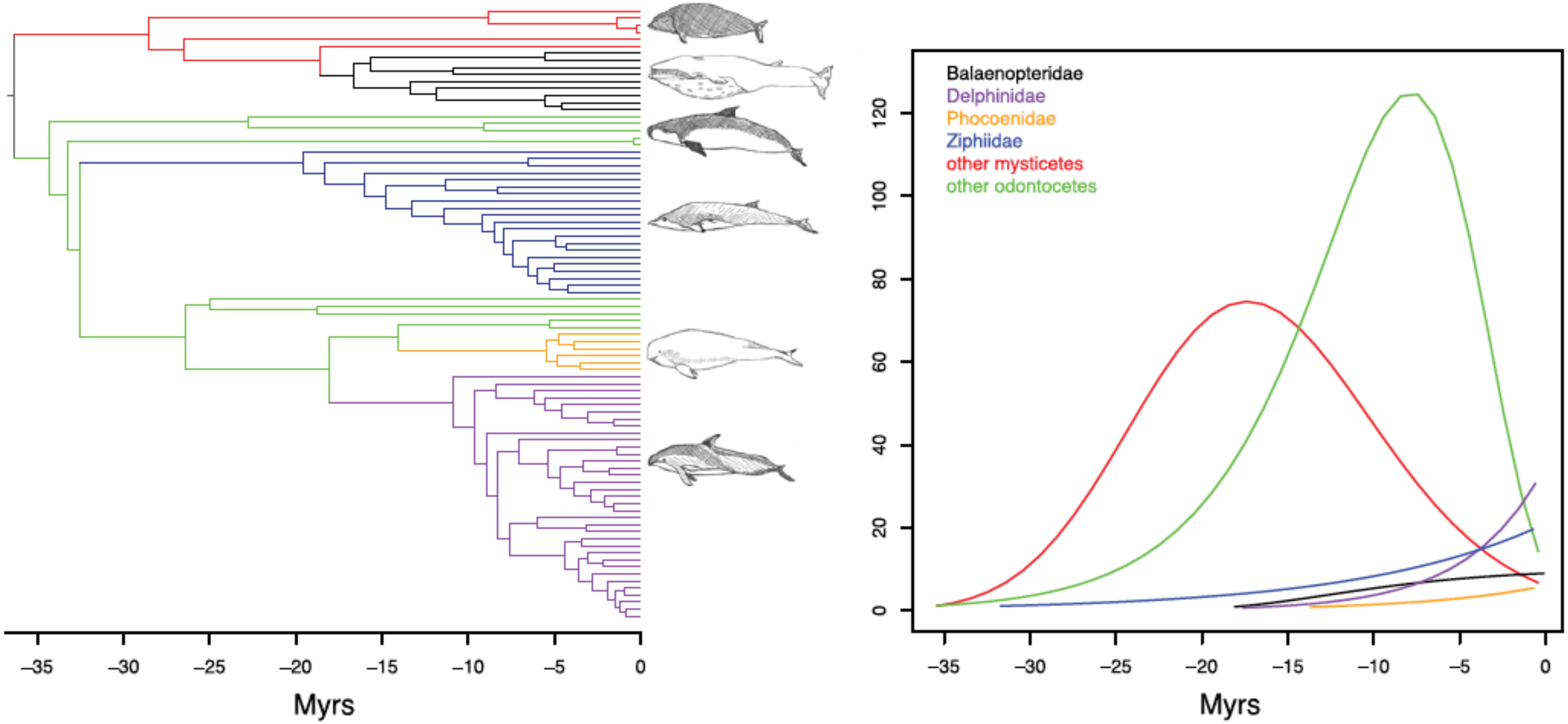
Table S2. Statistical support for rate shifts in the cetacean phylogeny

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

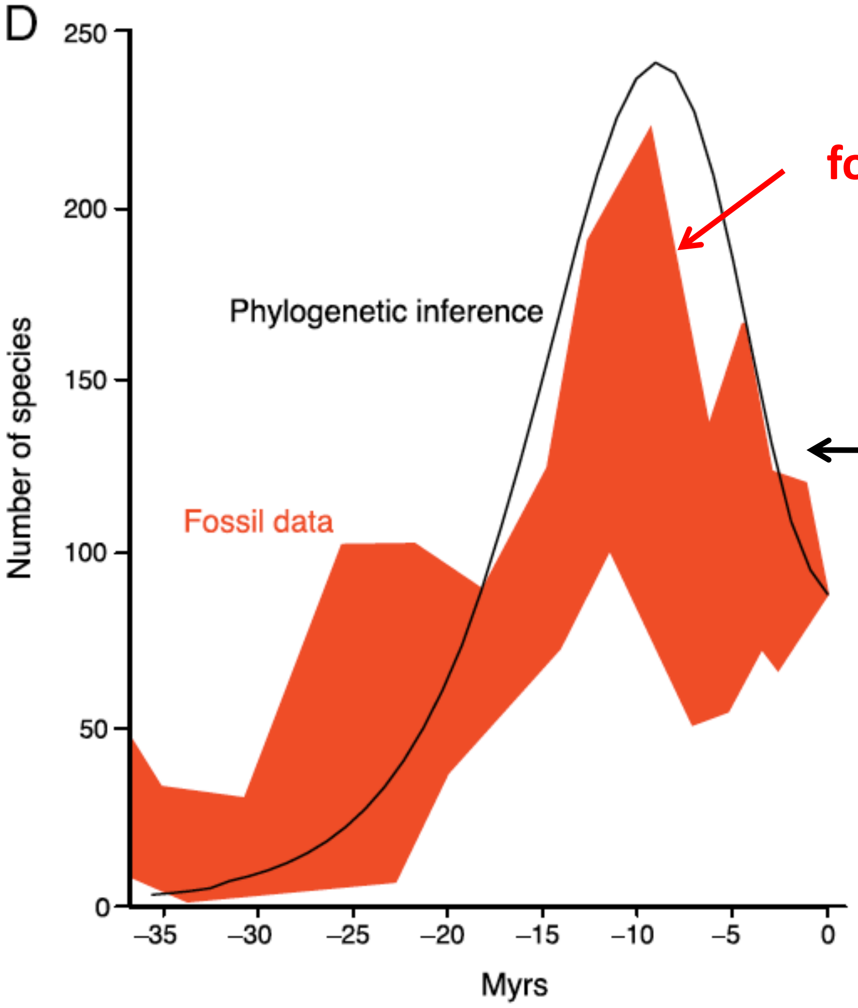


Resulting estimates of diversity through time : boom-then-bust diversity dynamics



Morlon *et al. PNAS* 2011

The resulting diversity curve is consistent with the fossil record



fossil record

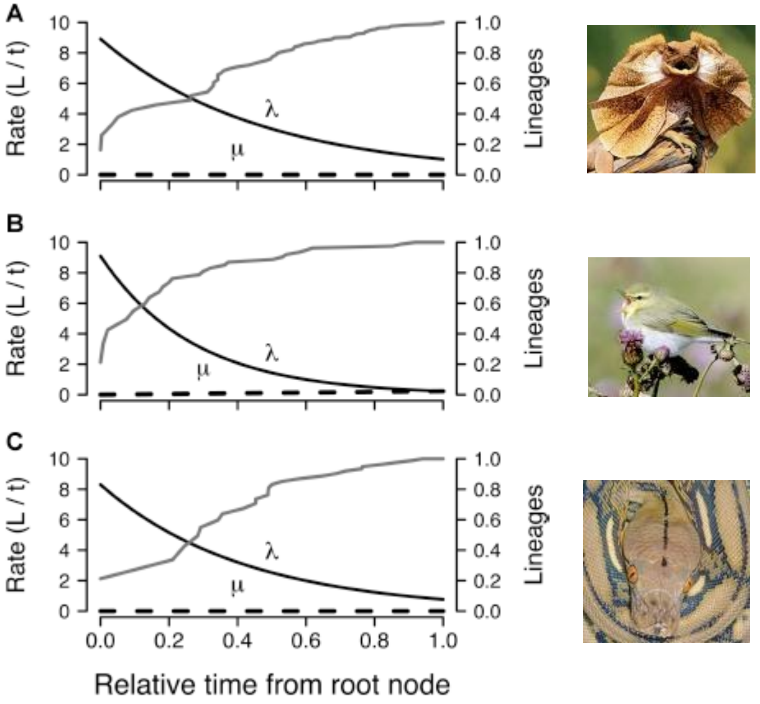
phylogenetic inference, obtained by summing individual diversity curves

Morlon *et al. PNAS* 2011

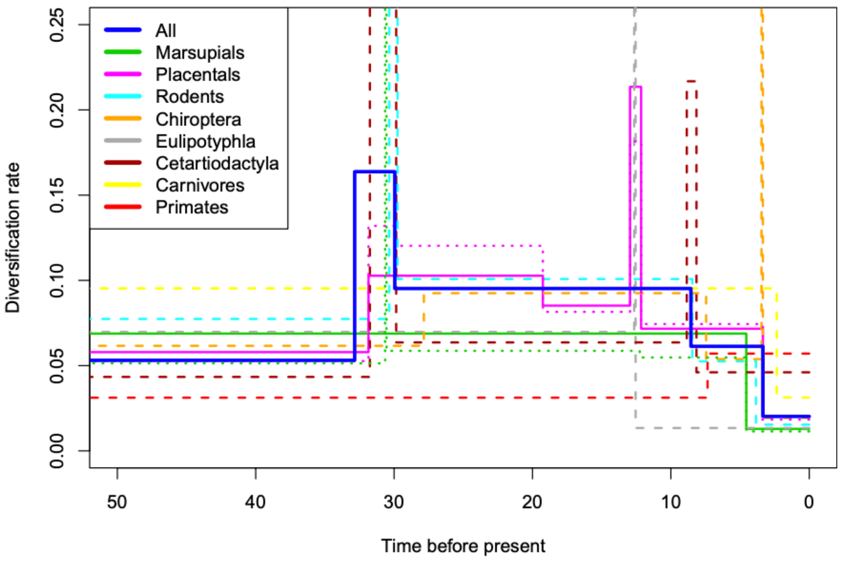
Do rates of species diversification vary through time? How?

Speciation rates often decline through time

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

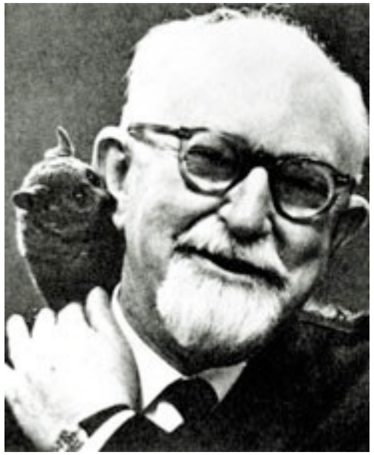


Rabosky & Lovette Evolution 2008



Stadler *et al.* PNAS 2011

Why do rates of species diversification vary through time?

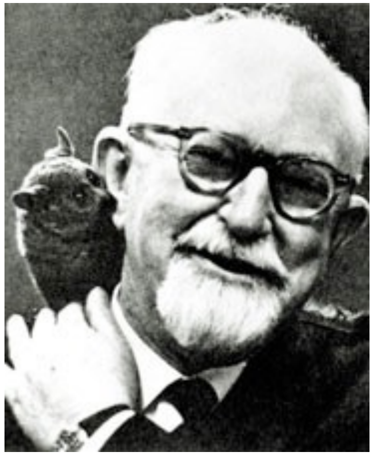


George Gaylord Simpson

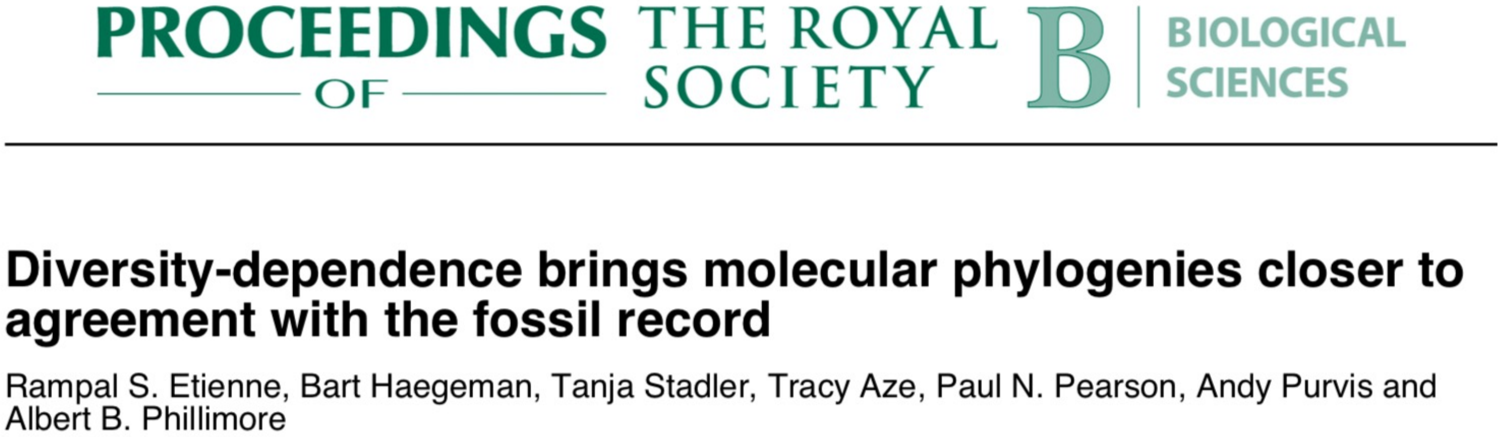
Most diversity of life on Earth arises from adaptive radiations, the fast diversification of ecological traits in a rapidly speciating group of organisms

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.

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



George Gaylord Simpson



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

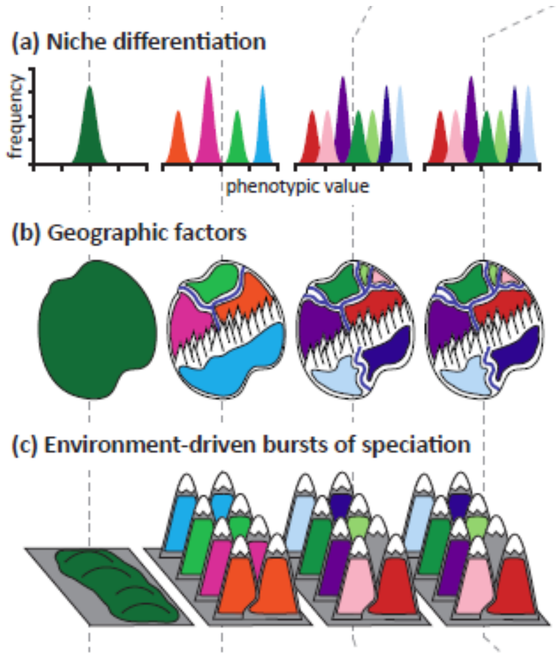
$$\lambda_n = \max\left(0, \lambda_0 - (\lambda_0 - \mu)\frac{n}{K}\right) \quad \text{and} \quad \mu_n = \mu$$

Maximum number of species

Opinion CellPress

Why does diversification slow down?

Daniel Moen and Hélène Morlon

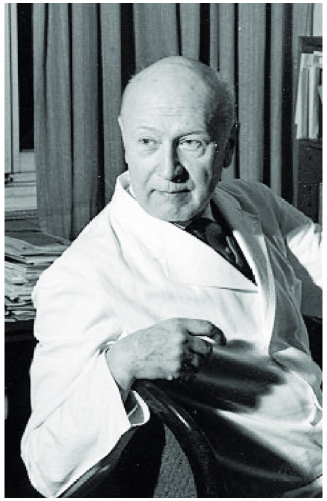


Trends Ecol Evol 2014

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

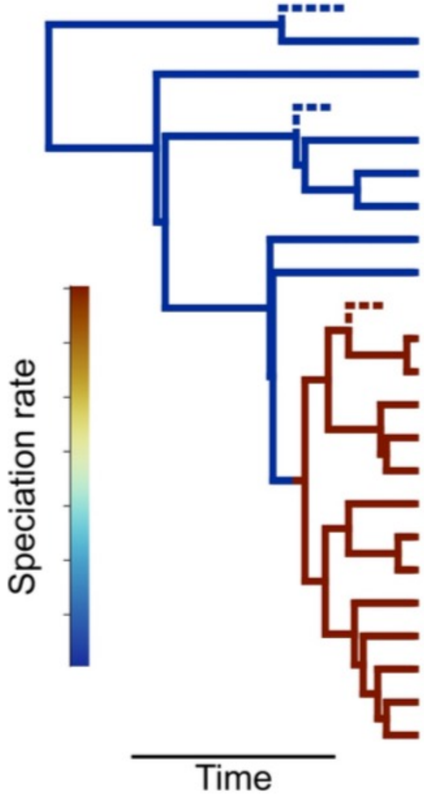
Metabolic activity is faster under warm climates, potentially increasing the action of free radicals and increasing mutation rates

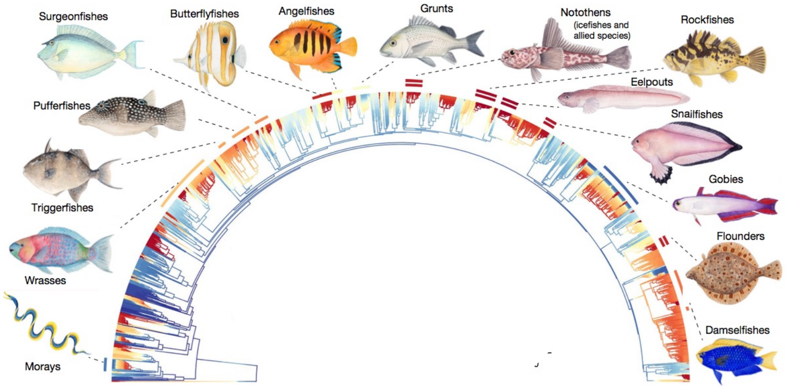
Warmer climates are often associated with increased climatic stability and productivity, which could promote speciation

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

Statistical Inference

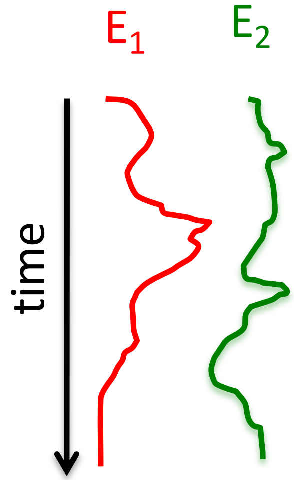
Diversification model ⟷ Phylogenetic tree





Hypothesis testing
using likelihood comparison

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



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

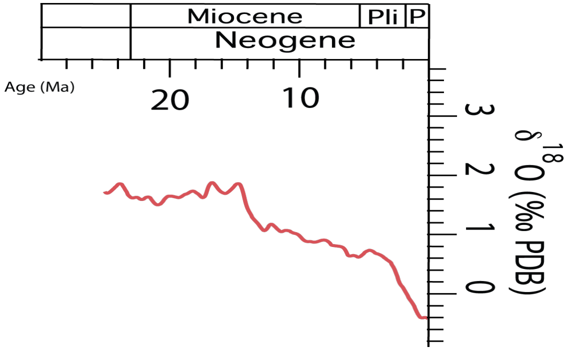
$$\tilde{\mu}(t) = \mu(t, E_1(t), E_2(t), \ldots, E_k(t))$$

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

Condamine *et al.* Eco Lett 2013
Lewitus *et al.* Syst Bio 2018

Did past climatic changes affect diversification rates? How?

218 phylogenies of tetrapod families

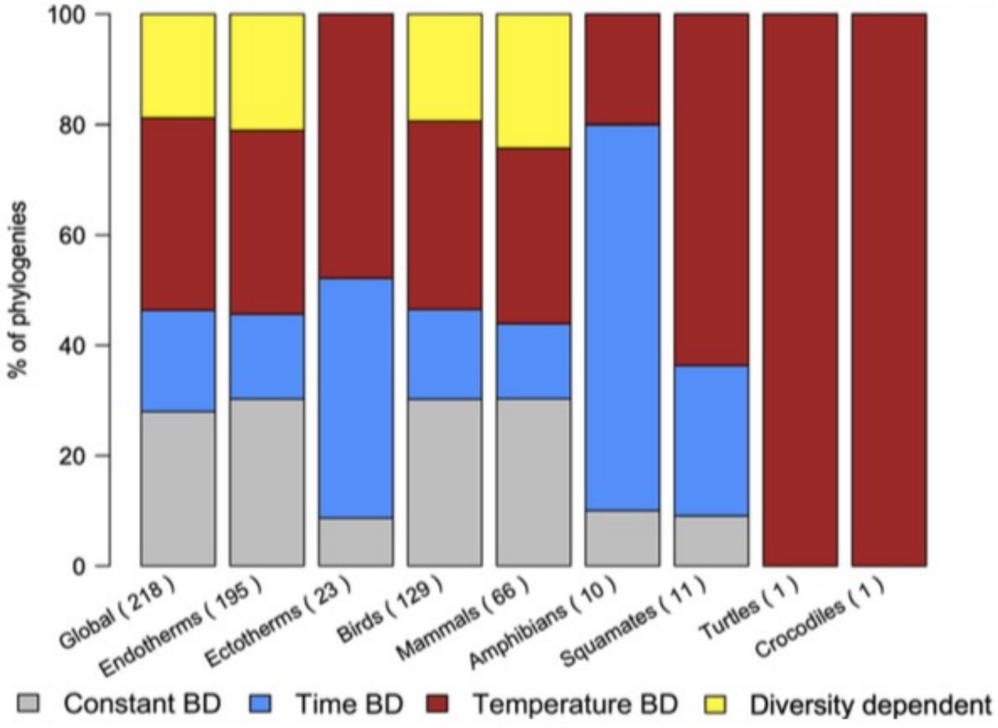


Zachos *et al.* 2008

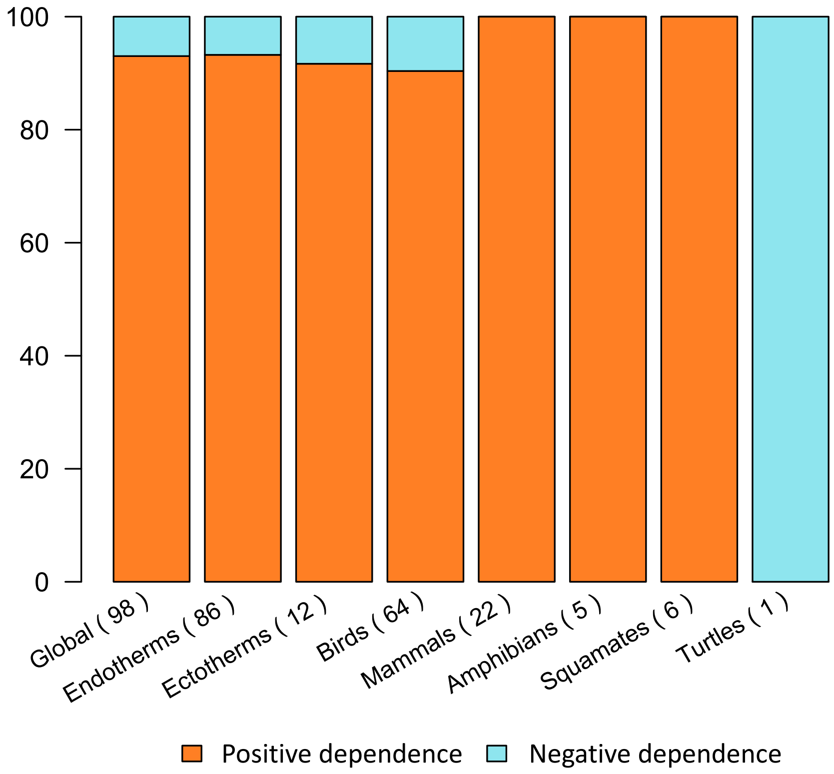
Comparison of 22 models including constant rate diversification models, models with time-varying rates, diversity-dependent rates, and temperature-dependent models

Condamine *et al.* Eco Lett 2019

Speciation rates often vary with temperature

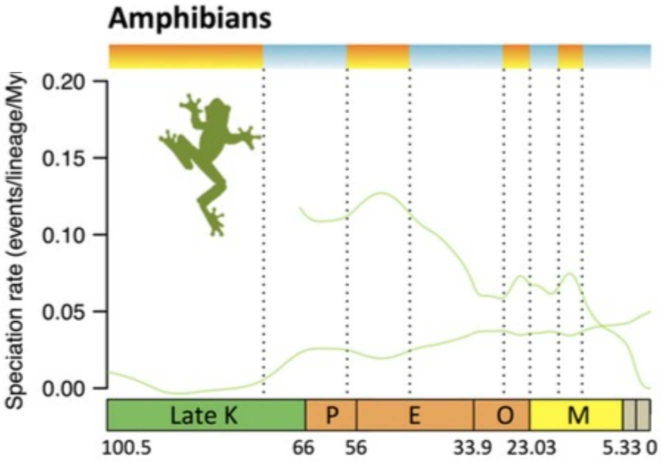


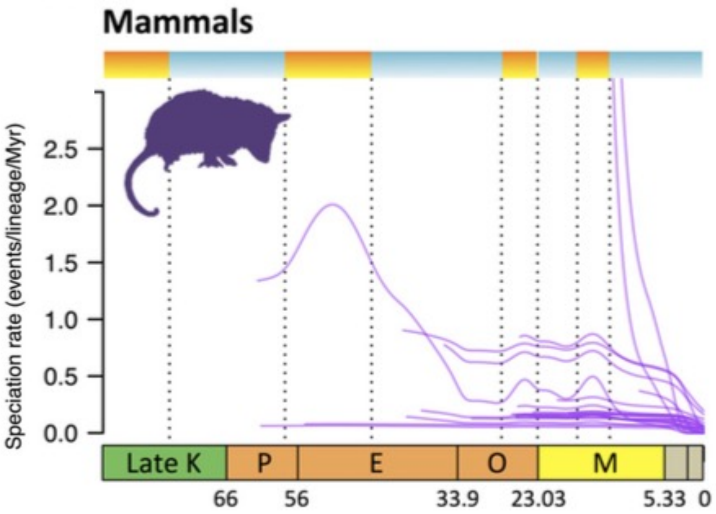
Speciation rates are higher during warm geological periods

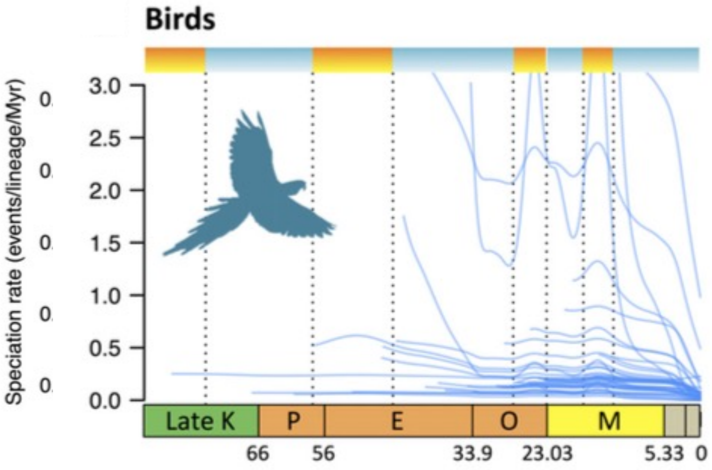


Condamine et al. Eco Lett 2019

Climate cooling during the Cenozoic results in a slowdown in diversification

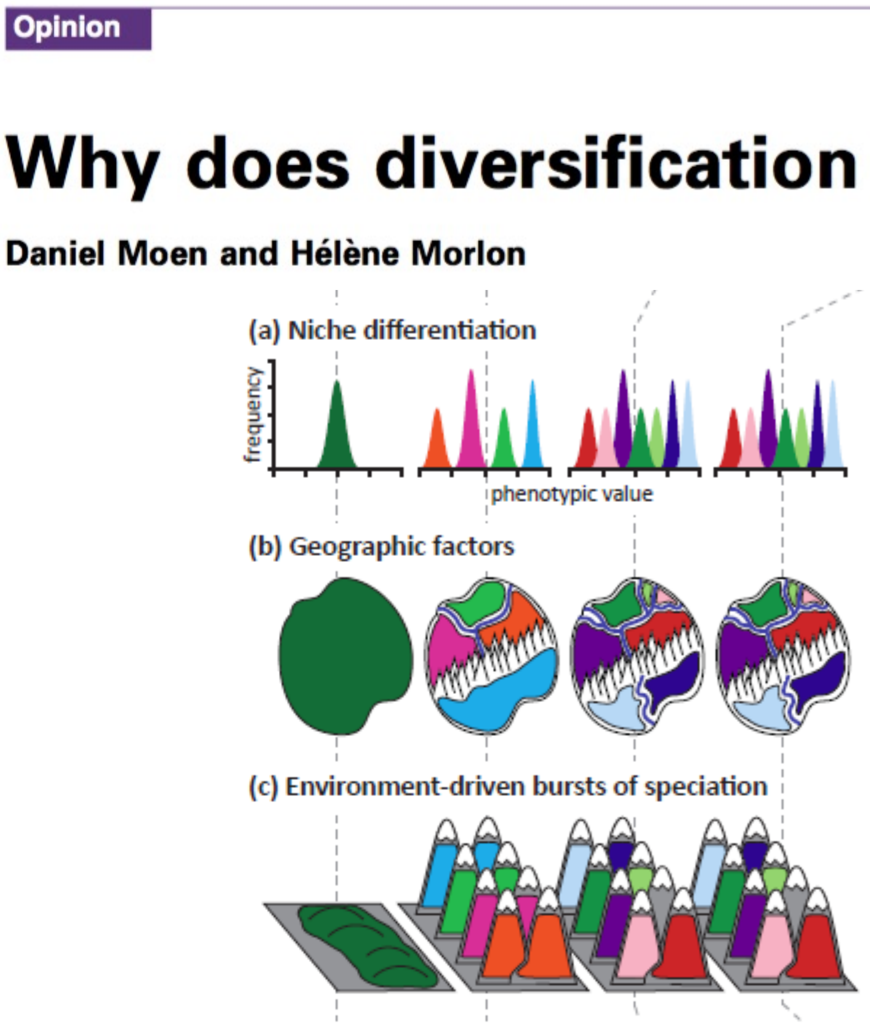






Condamine et al. Eco Lett 2019

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



Opinion

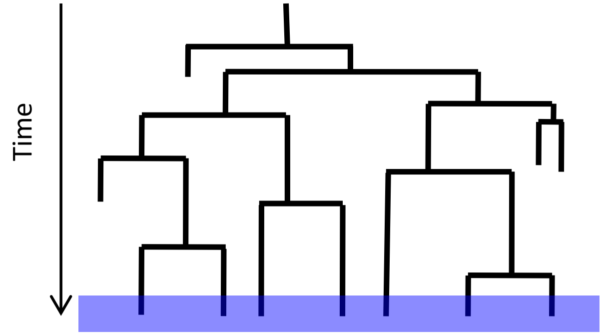
CellPress

Why does diversification slow down?

Daniel Moen and Hélène Morlon

Trends Ecol Evol 2014

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



Present-day species richness

speciation rate

extinction rate

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

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

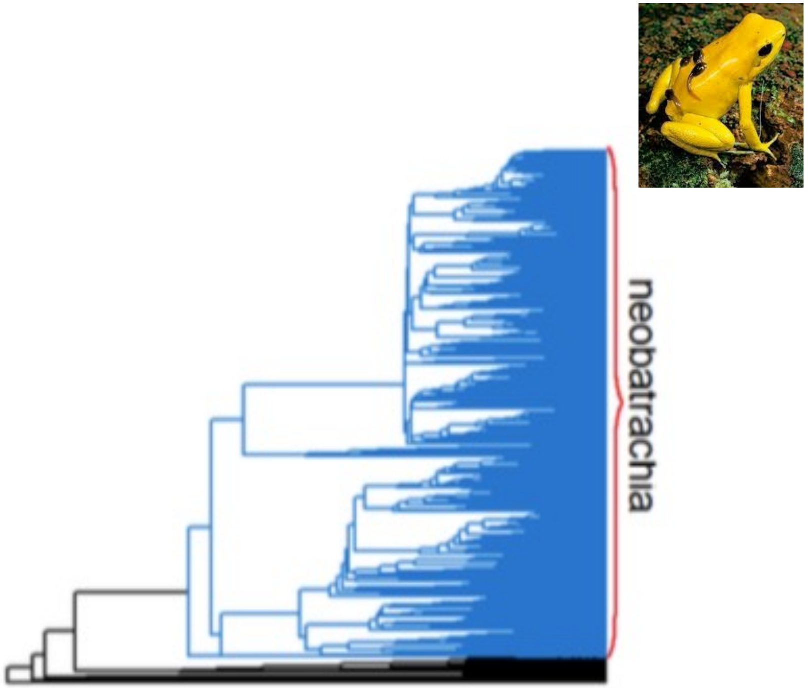
and there are n species today

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

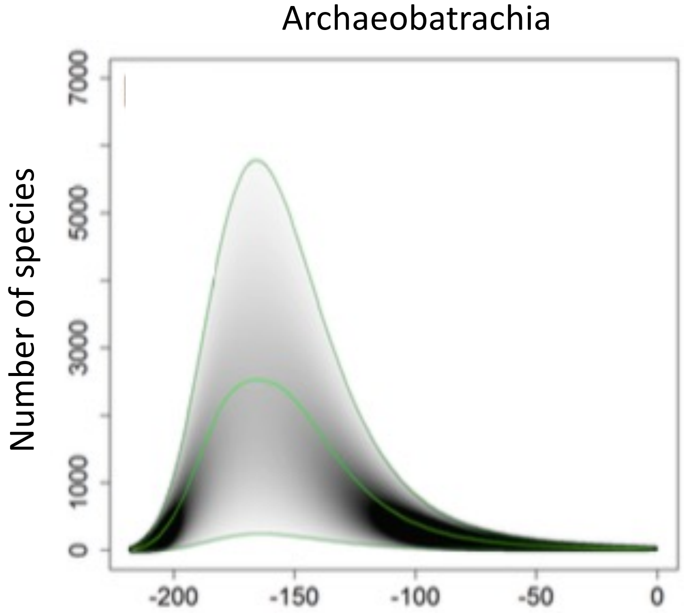
Olivier Billaud

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?



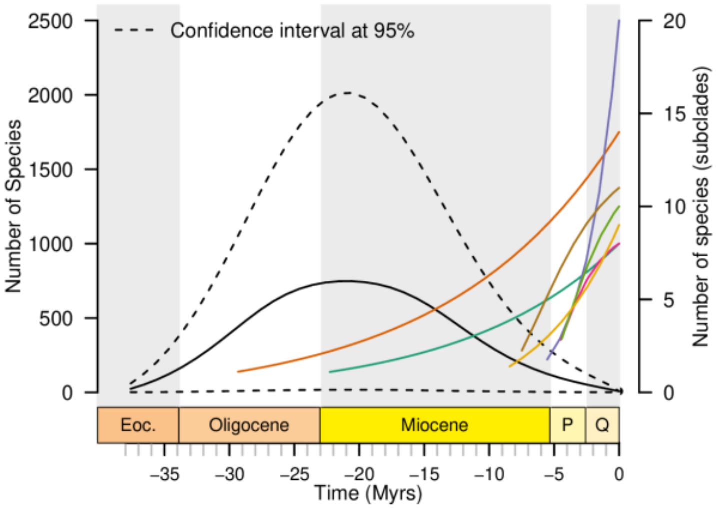
Archaeobatrachia



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

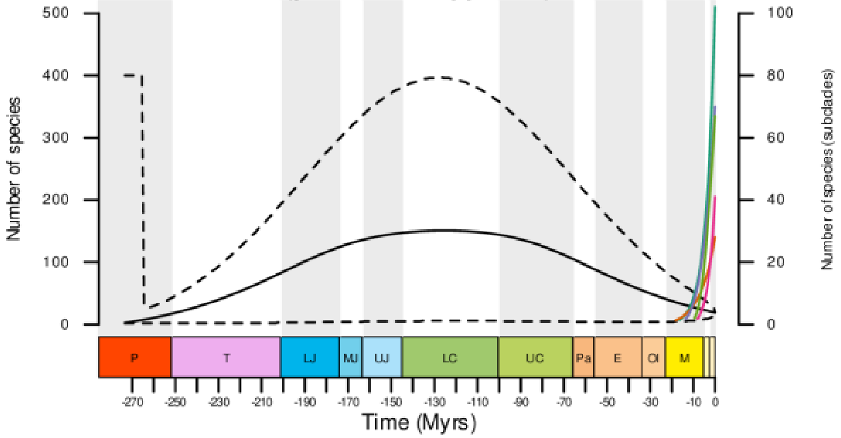
Billaud *et al.* *Syst Bio* 2019

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

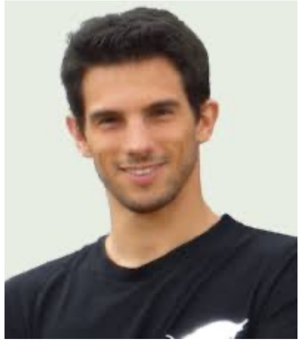


Nathan
Mazet

Pierre-Henri
Fabre

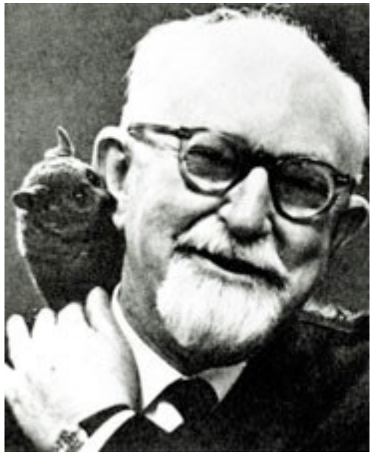


Fabien
Condamine



Mazet *et al.* Methods Ecol Evol 2023

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

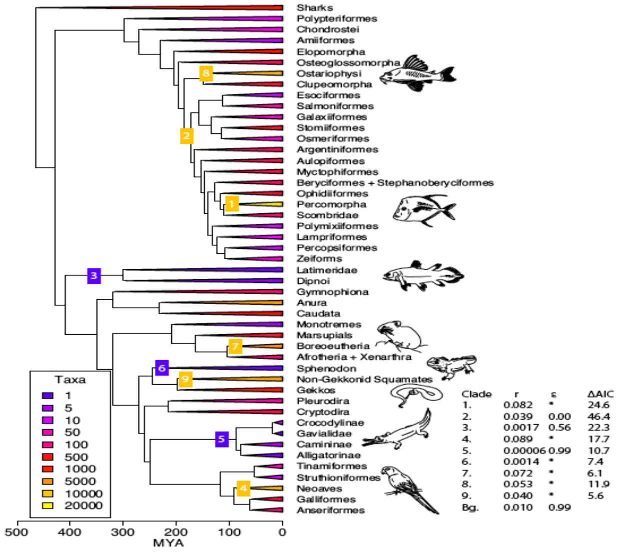


George Gaylord Simpson

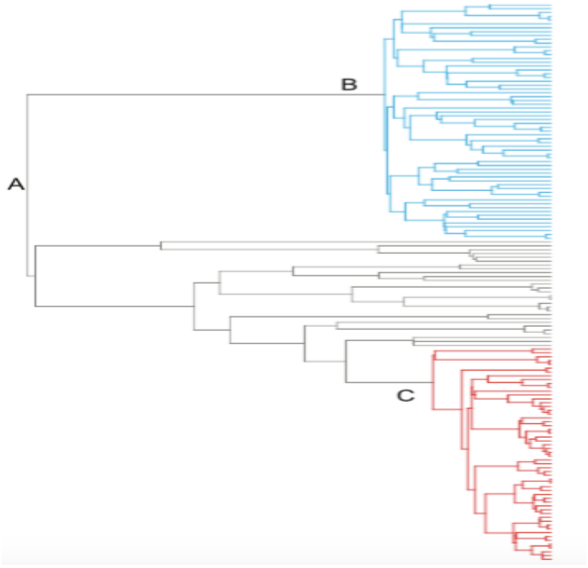
Most diversity of life on Earth arises from adaptive radiations, the fast diversification of ecological traits in a rapidly speciating group of organisms

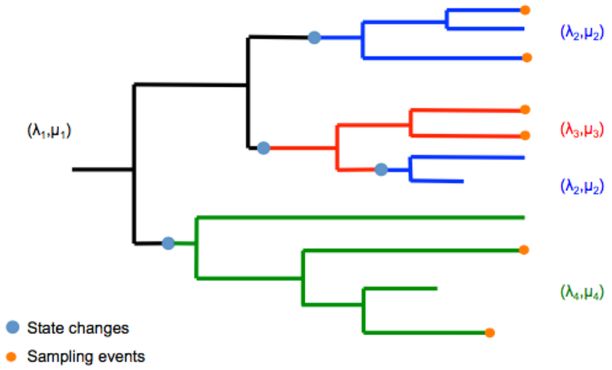
Under this hypothesis, bursts of diversification are clade-wide, linked to the rapid filling of a niche space that has been freed from other occupants (e.g. by major environmental changes) or opened by a major key innovation.

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



Clade	r	ε	ΔAIC
1.	0.082	*	24.6
2.	0.039	0.00	46.4
3.	0.0017	0.56	22.3
4.	0.089	*	17.7
5.	0.00006	0.99	10.7
6.	0.0014	*	7.4
7.	0.072	*	6.1
8.	0.053	*	11.9
9.	0.040	*	5.6
Bg.	0.010	0.99	





MEDUSA
Alfaro et al. PNAS 2009

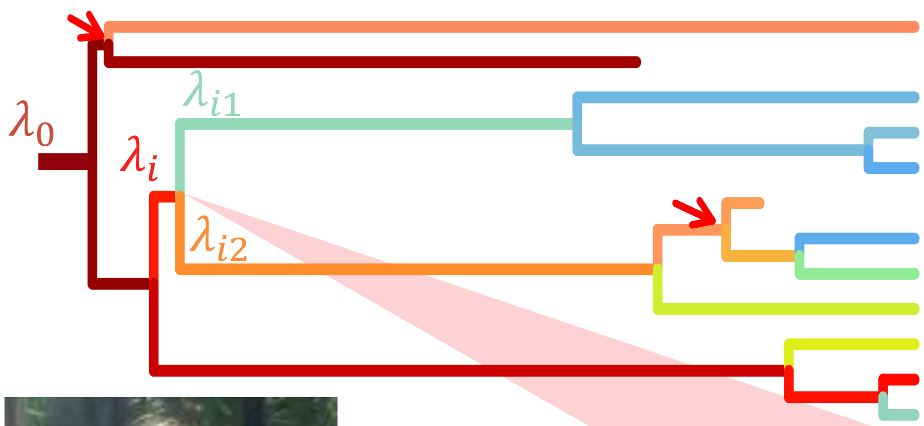
BAMM
Rabosky PloS One 2014

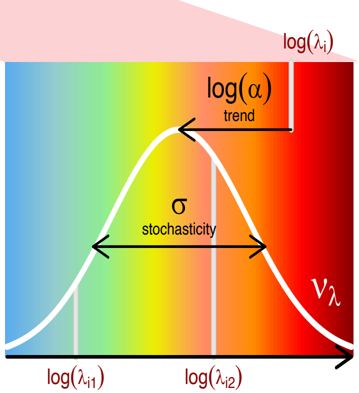
MSBD
Barido-Sottani *et al.* Syst Bio 2020

Another view of diversification

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

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

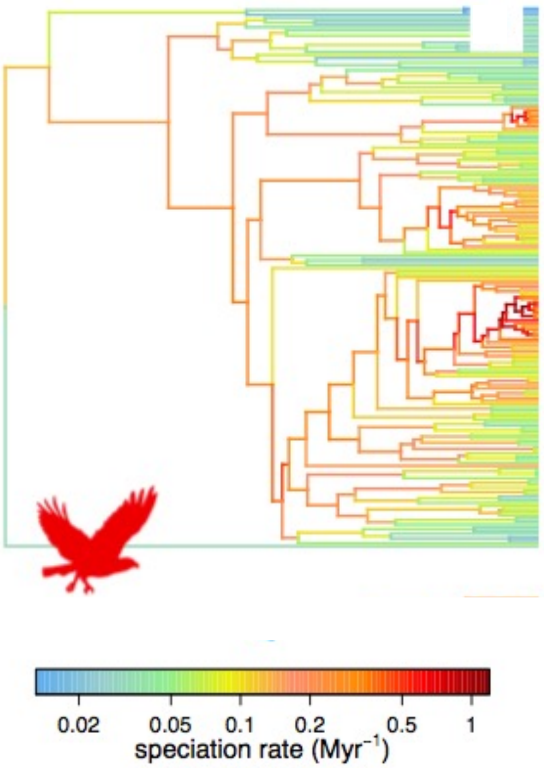


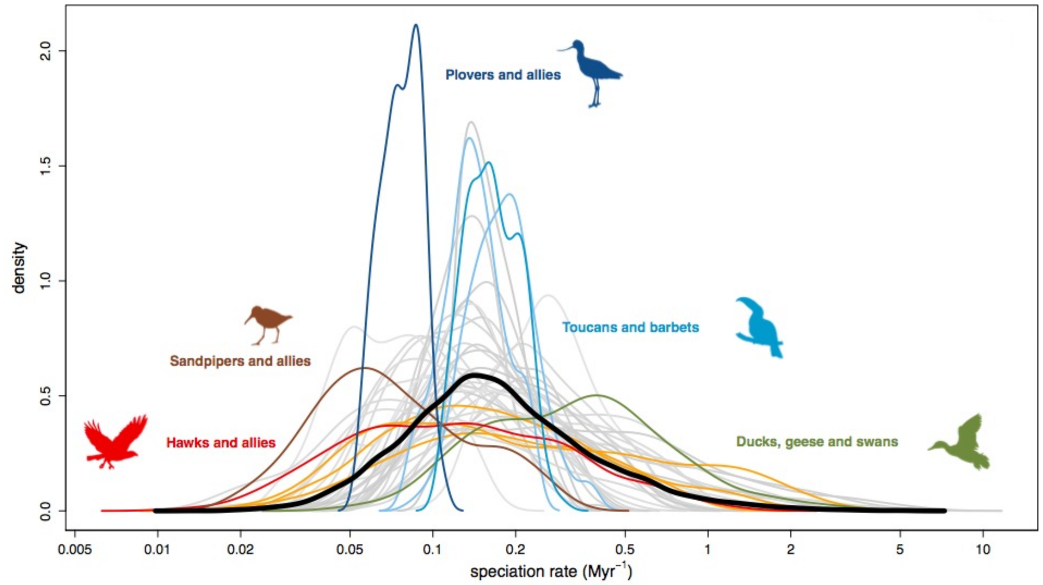


λ_0	initial speciation rate
α	deterministic trend
σ^2	stochastic variation
$\varepsilon = \mu_i / \lambda_i$	relative extinction rate

Maliet *et al.*
***Nature Ecology & Evolution* 2019**

Speciation rates vary widely across lineages





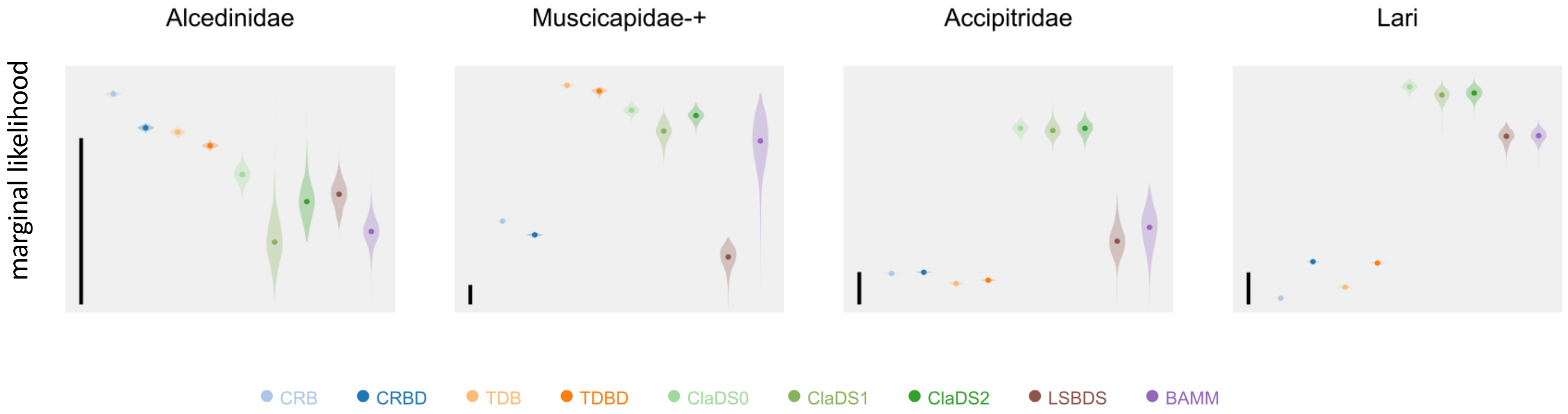
Maliet *et al.* Nature Ecol Evol 2019

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

40% of the bird clades

rarely

most often



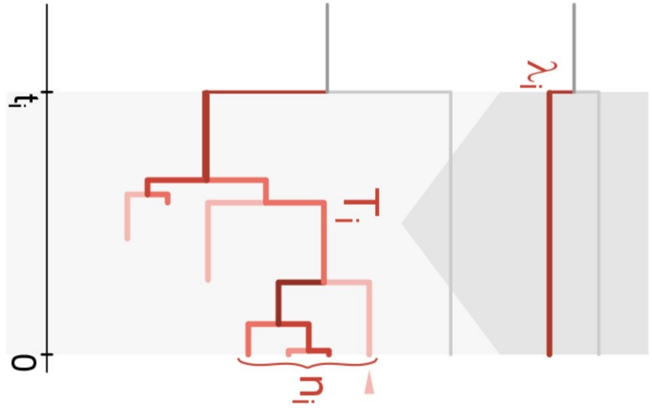
homogeneous models

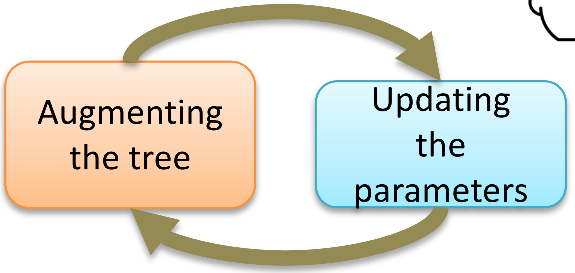
frequent shifts with small effects

few shifts with large effects

Ronquist *et al.* Comm Biol 2021

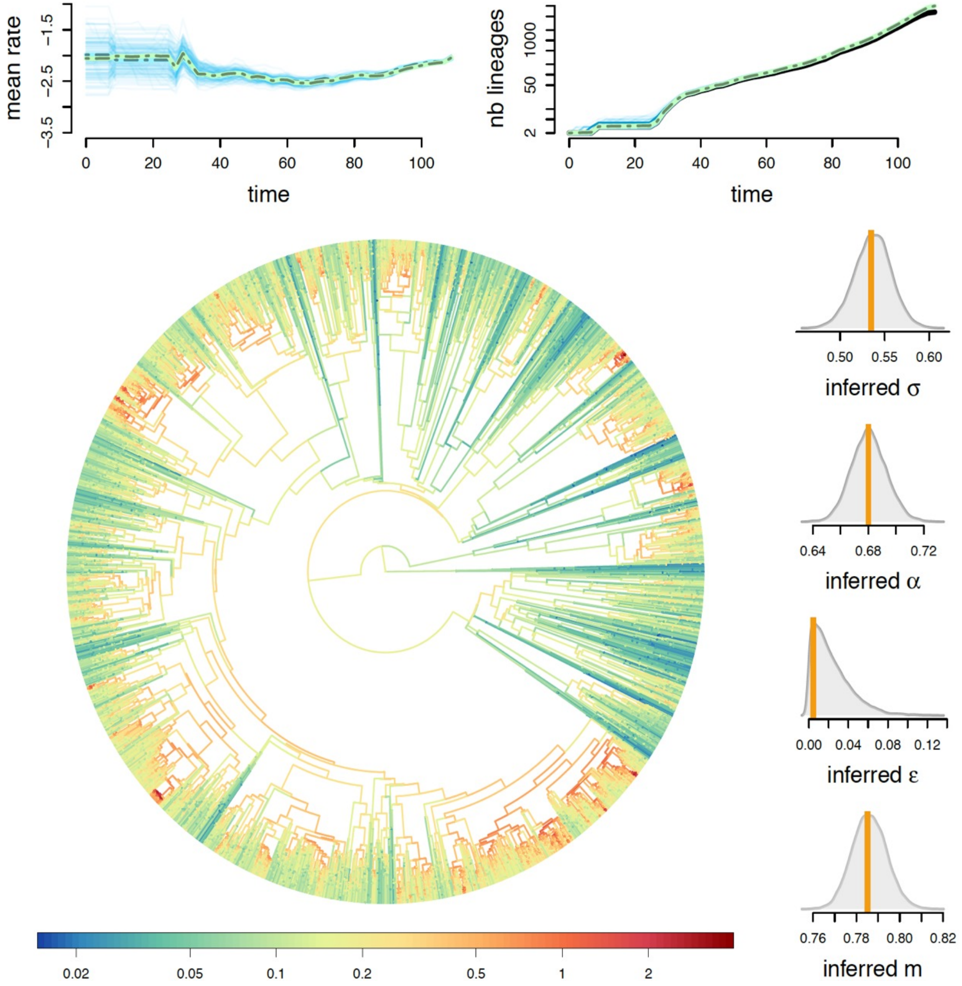
Faster and improved inference with Bayesian Data Augmentation





Augmenting the tree

Updating the parameters

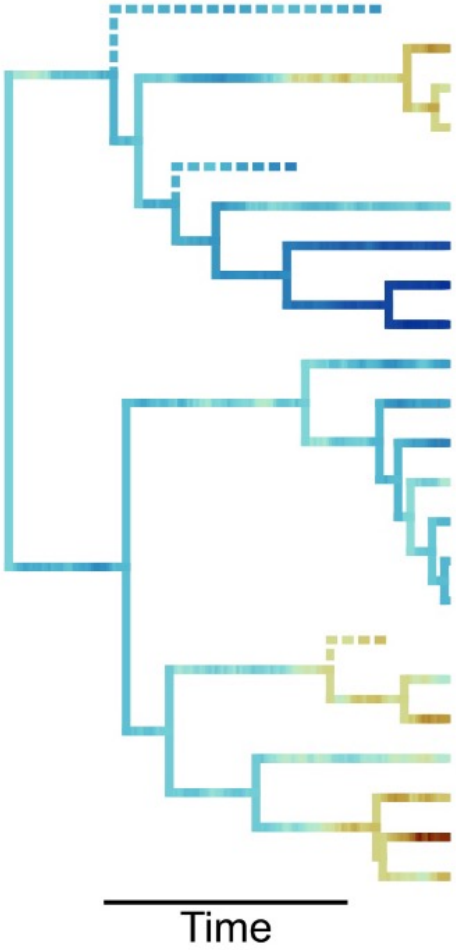


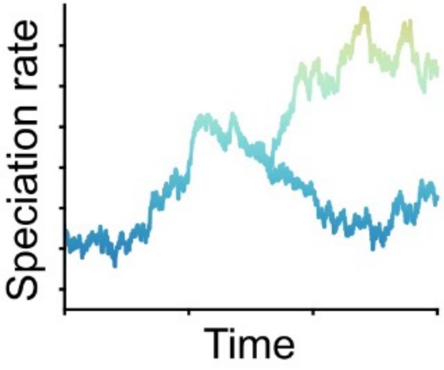
Maliet & Morlon Syst Bio 2021

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

Speciation

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





Quintero *et al.* BioRxiv 2022

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

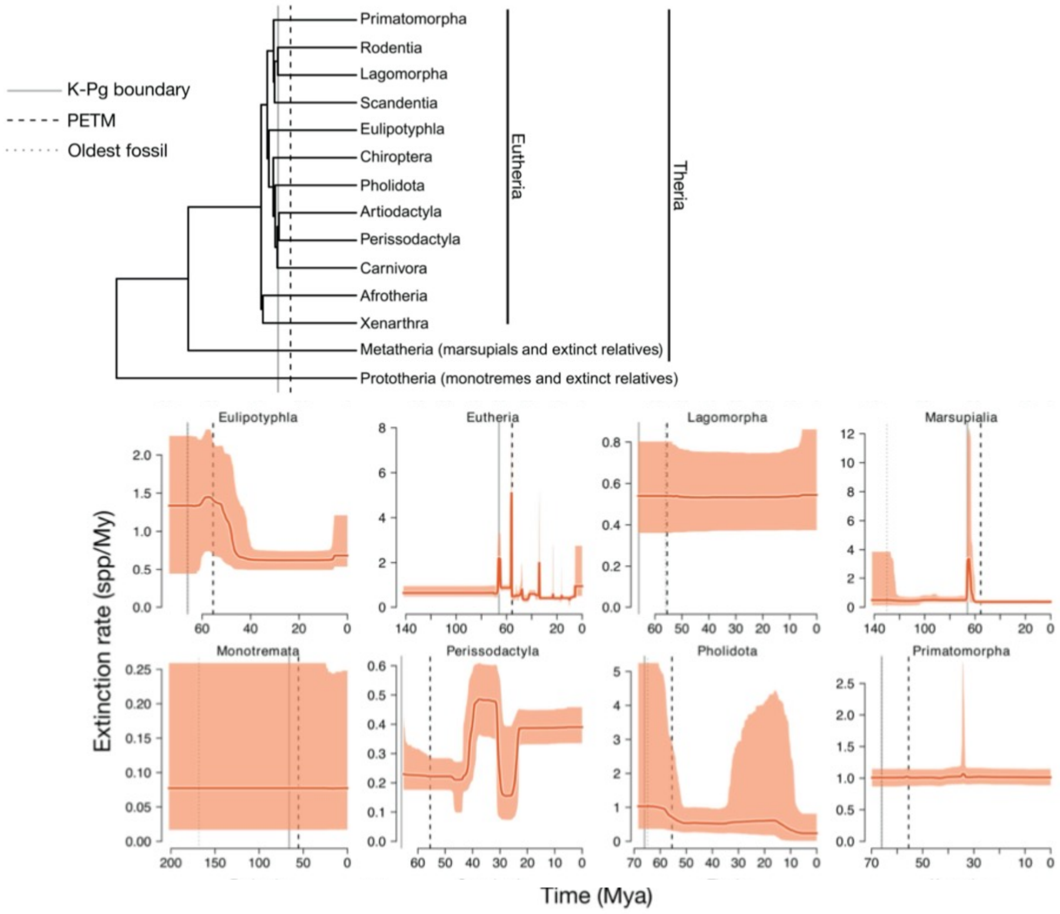
Extinction not constrained by fossil information

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

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

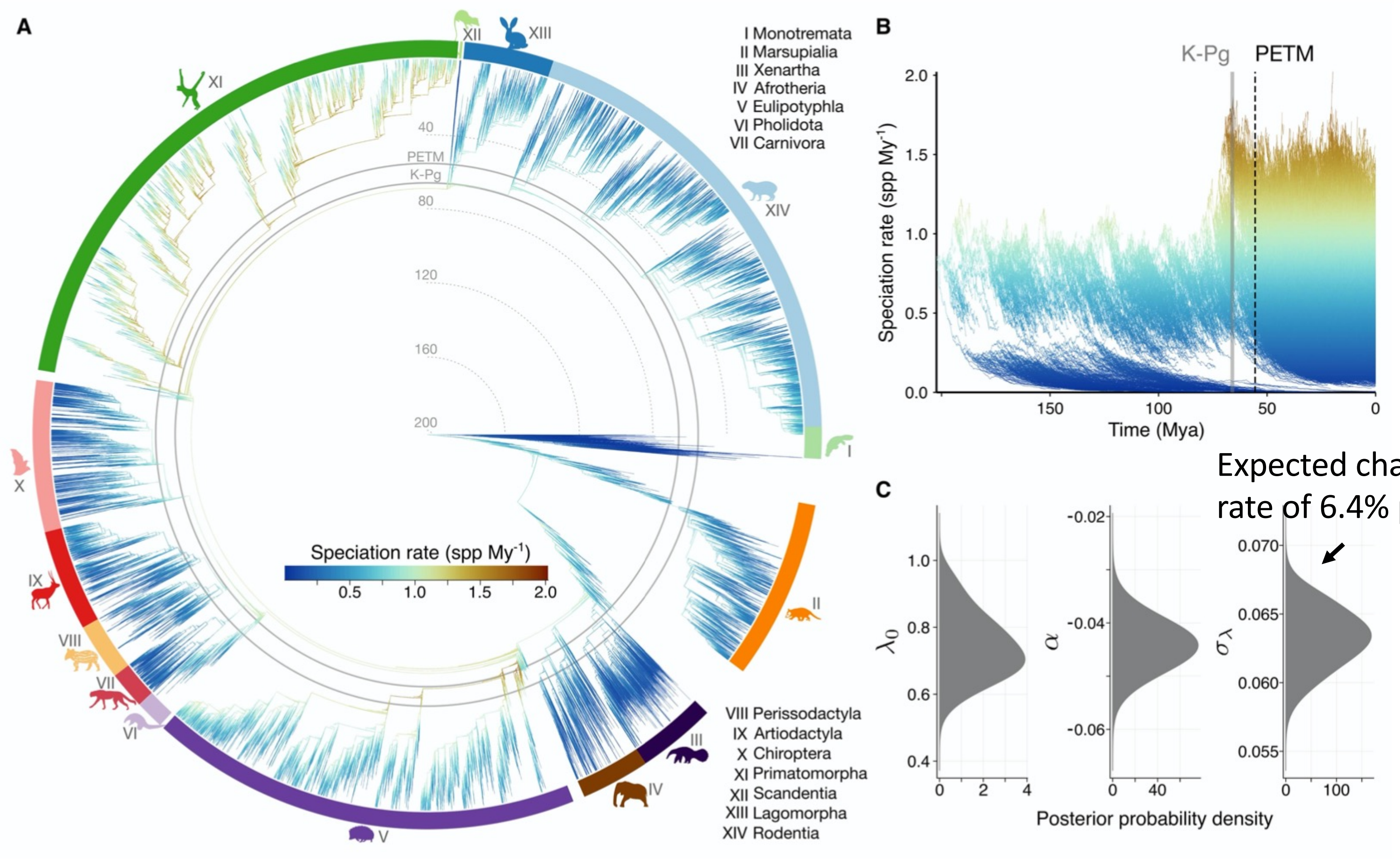
where $W(t)$ denotes the Wiener process.

Extinction constrained by fossil information



Quintero *et al.* BioRxiv 2022

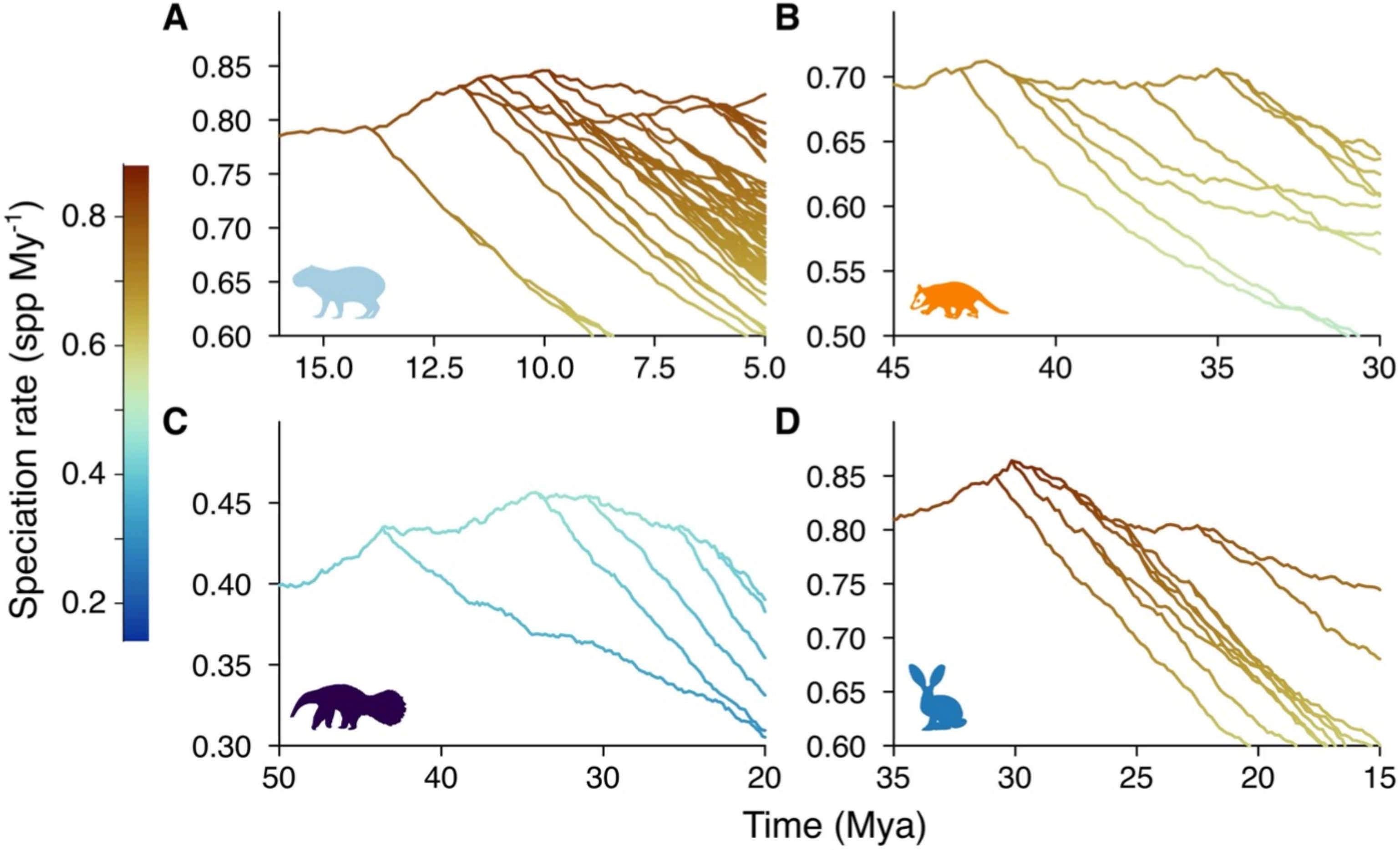
Speciation rates vary widely across lineages



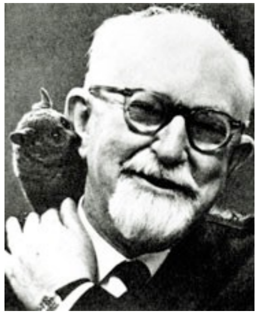
Expected change in rate of 6.4% per Myr

Quintero *et al.* BioRxiv 2022

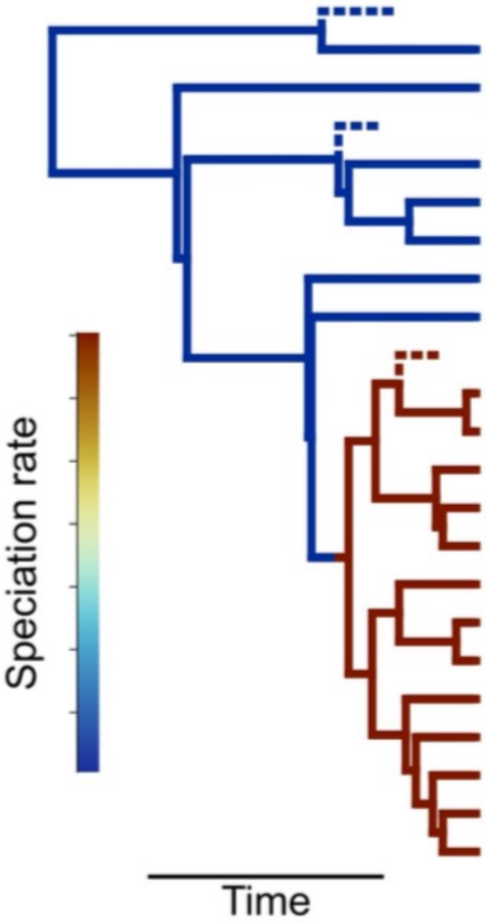
Imbalanced speciation pulses



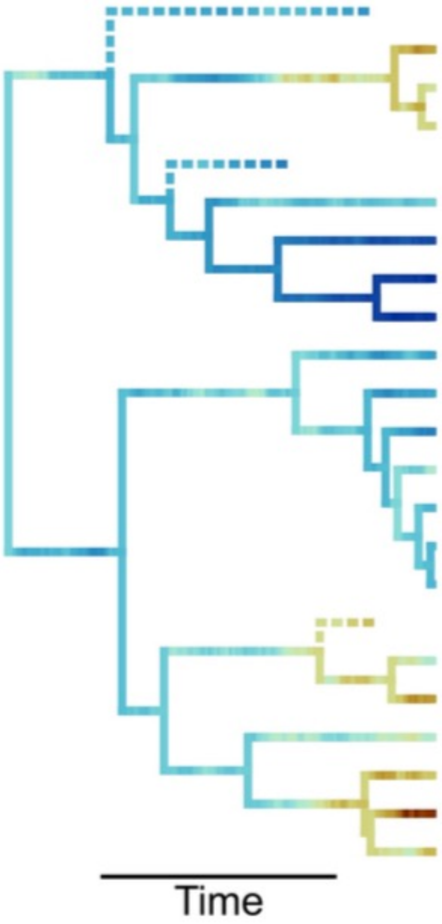
Quintero *et al.* BioRxiv 2022



Major key innovations
Adaptive radiations



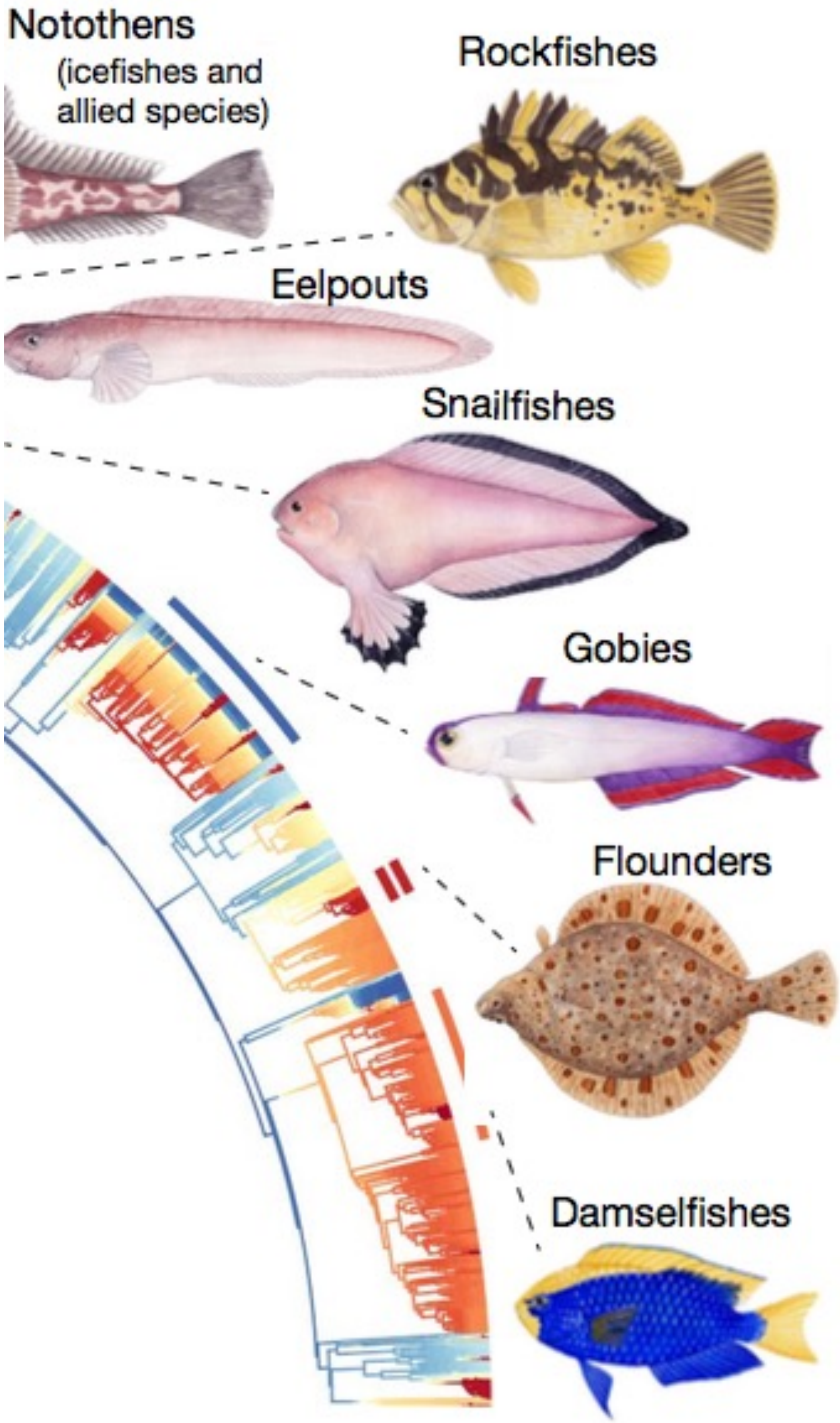
Complex interplay between species evolving ecologies and their specific spatial and environmental context



Take-home message

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

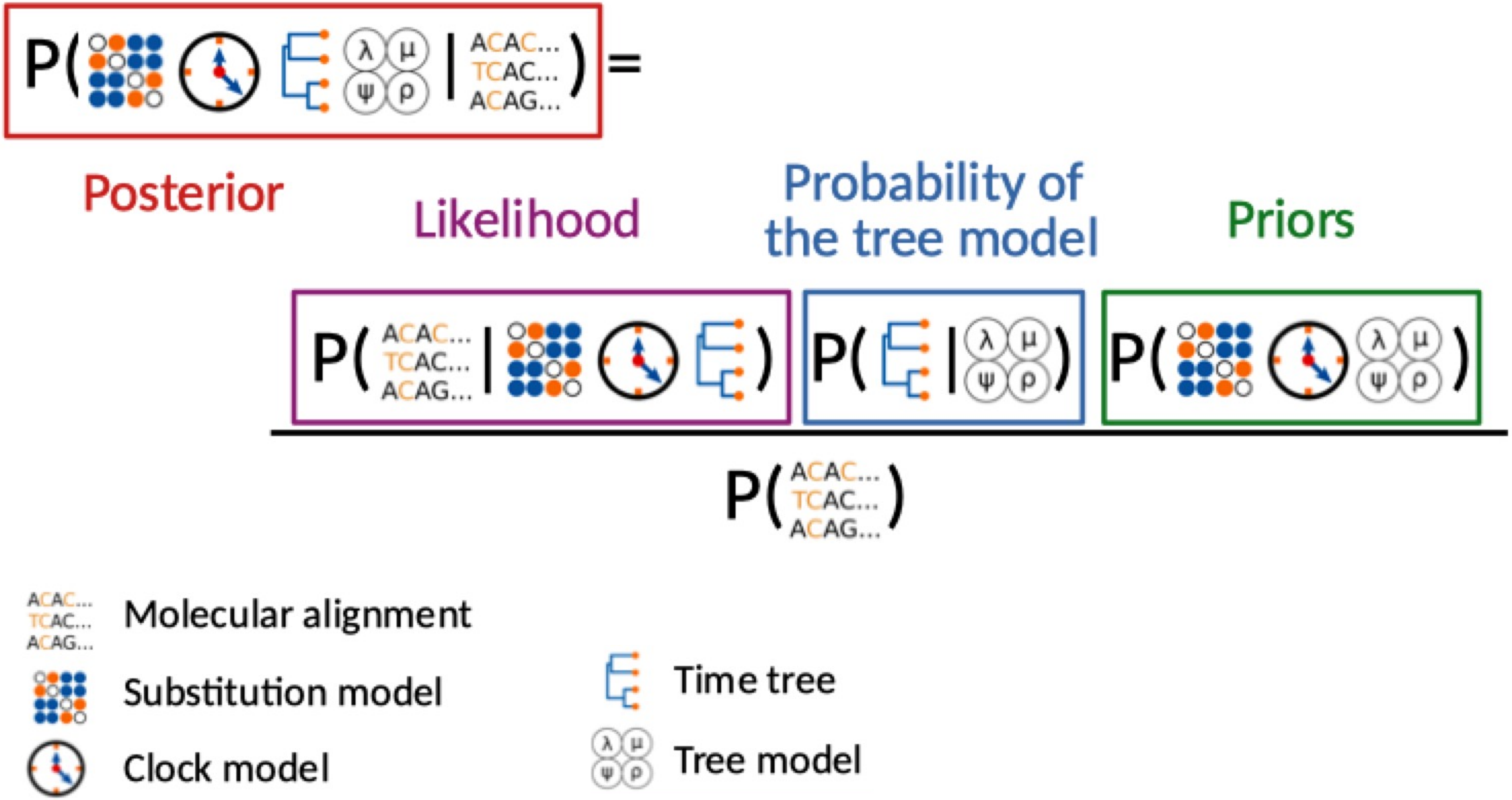
Diversification rates vary through time and across lineages



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!



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

Substitution model

Clock model

Time tree

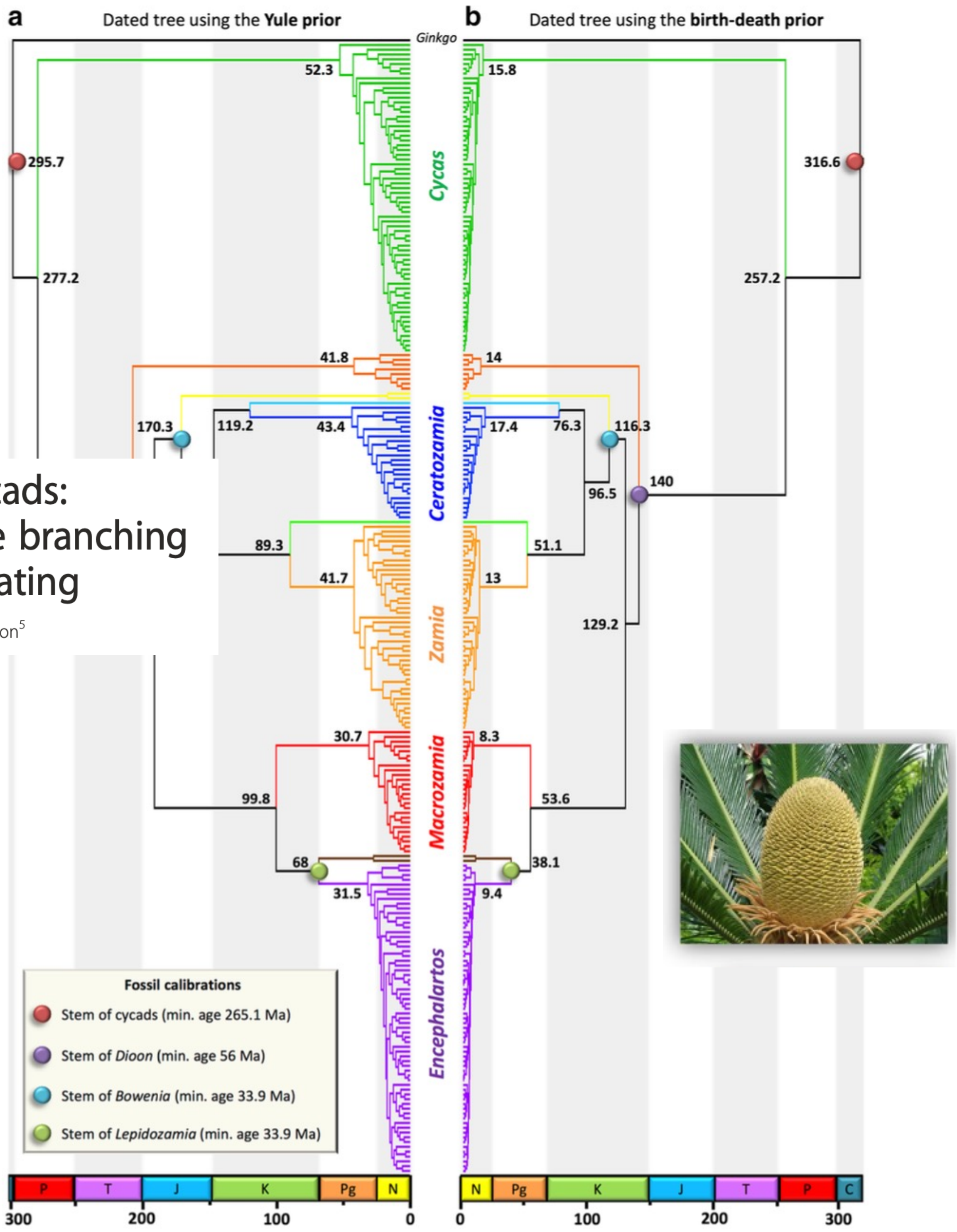
Tree model

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

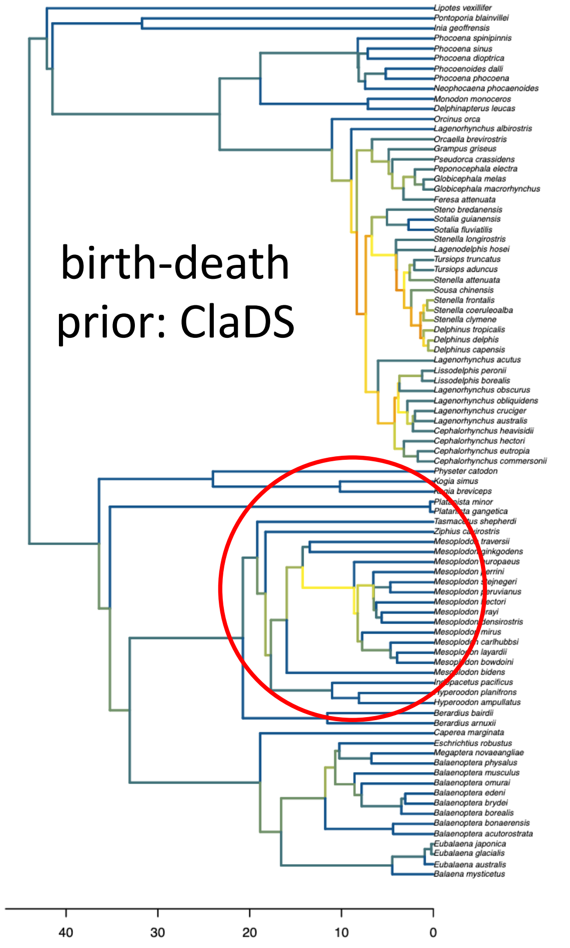
Origin and diversification of living cycads: a cautionary tale on the impact of the branching process prior in Bayesian molecular dating

Fabien L Condamine[1,2*], Nathalie S Nagalingum[3], Charles R Marshall[4] and Hélène Morlon[5]

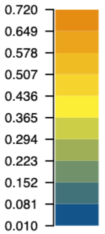
BMC Evol Biol 2015

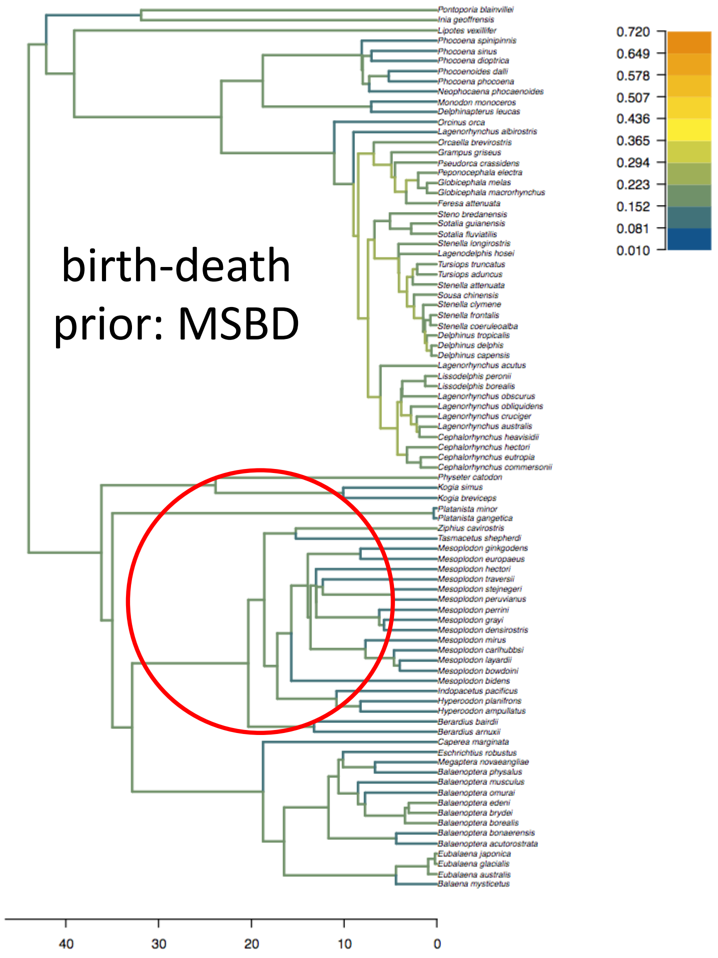


ClaDS now integrated in BEAST2 for Bayesian full phylogenetic inference: accounting for rate heterogeneity influences phylogenetic reconstruction

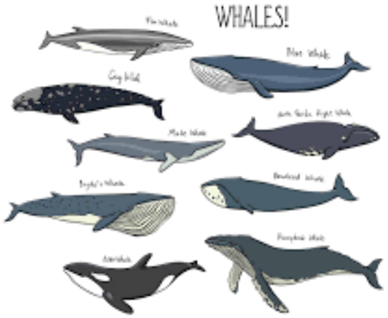


birth-death prior: ClaDS





birth-death prior: MSBD



Beast2

Bayesian evolutionary analysis by sampling trees

Barido-Sottani & Morlon
Syst Bio 2023

What are the factors that modulate diversification rates?

EXTRINSIC

The Court Jester

Abiotic factors
climatic variation
geological context

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?

The Court Jester

Abiotic factors
climatic variation
geological context

EXTRINSIC

The Red Queen

Biotic factors
competition
mutualistic and antagonistic interactions

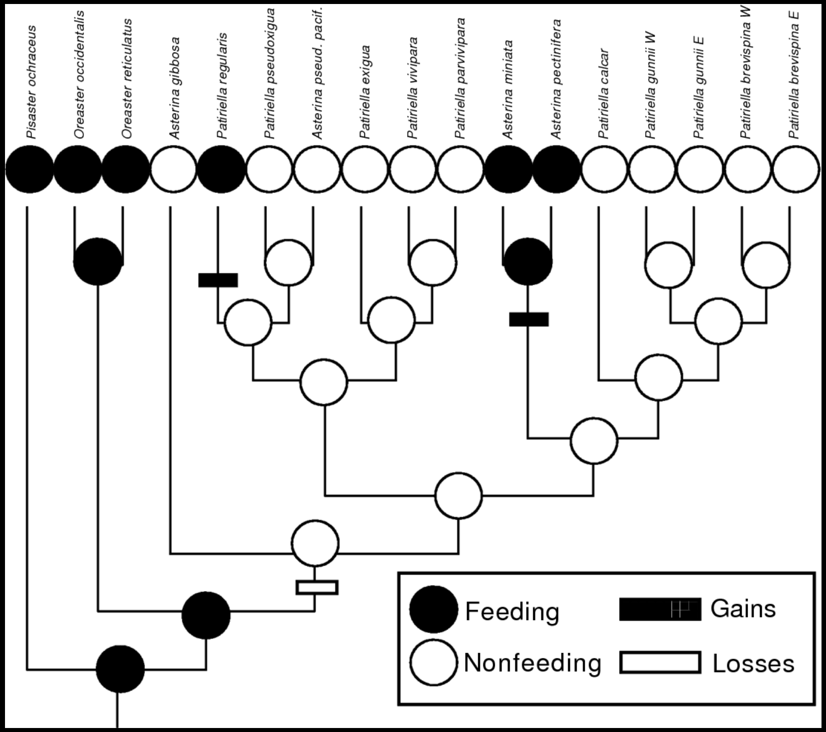
INTRINSIC

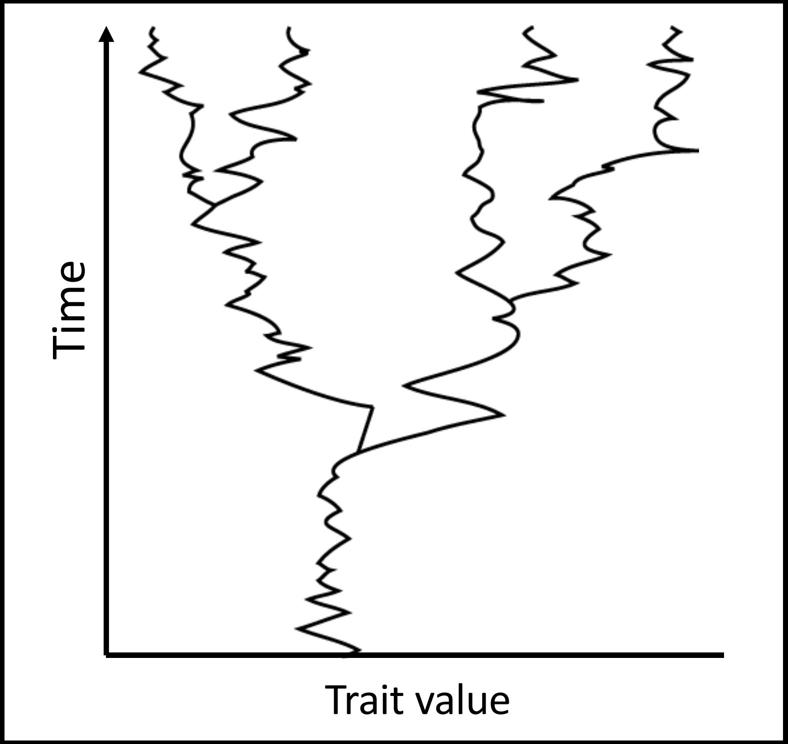
Species-specific traits

Genomic features!

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

Trait evolution on trees





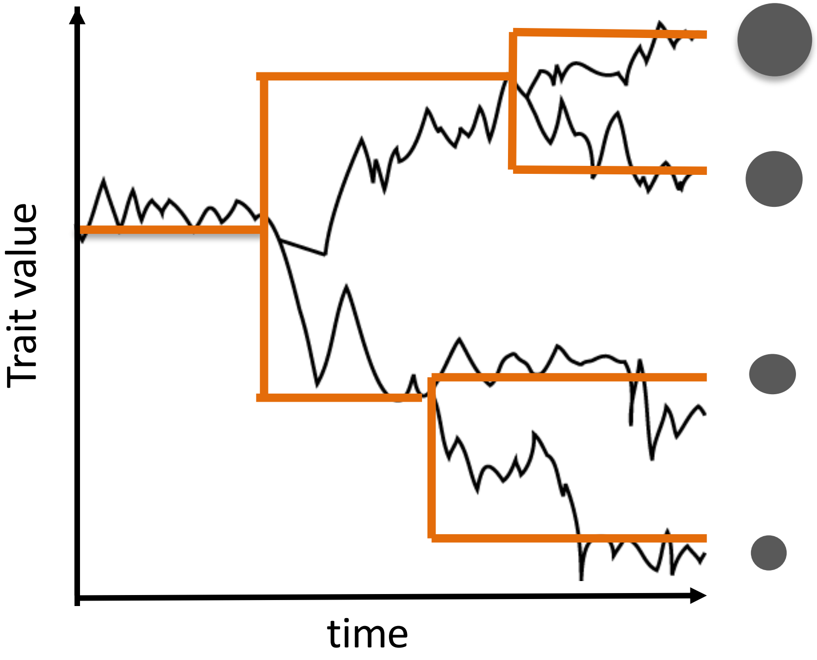
Constant rate model of phenotypic evolution

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

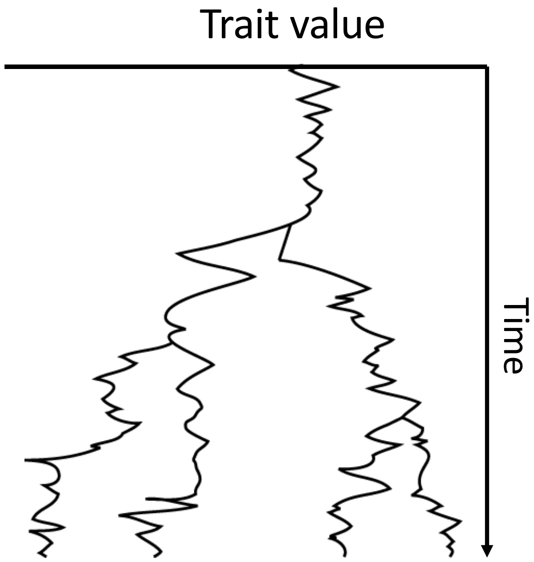
$$V_{ij} = \boldsymbol{\sigma}^2 s_{ij}$$

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

Felsenstein 1973

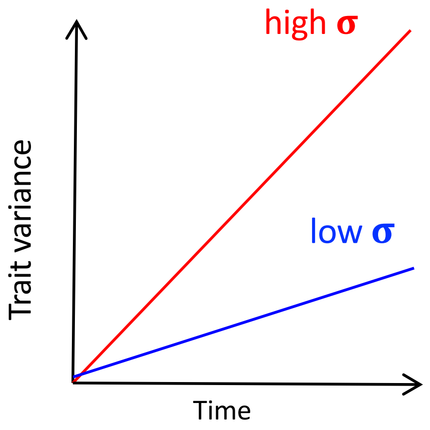
→ σ estimated by maximum likelihood or Bayesian inference

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

$$dX(t) = \underbrace{\boxed{\alpha[\theta\text{-}X(t)]dt}}_{\text{Selection component}} + \underbrace{\boxed{\sigma dB(t)}}_{\text{Drift (BM) component}}$$

where

$\alpha =$ strength of "selection"

$\theta =$ adaptive optimum

When $\boldsymbol{\alpha = 0}$, 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

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

Hansen & Martins 1996, Butler & King 2004

Models with a presumed effect of competition under limited ecological opportunities

$\boldsymbol{dX(t)}$ **: change in $\boldsymbol{X(t)}$ 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

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

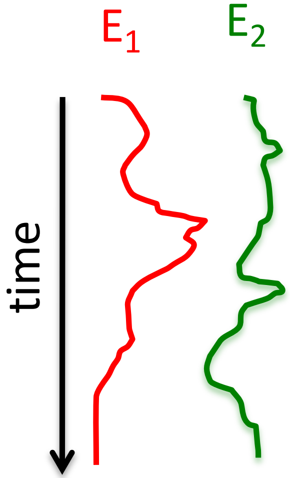
Blomberg *et al.* 2003

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

$dX(t)=\sigma(t)dB(t)$ with $\sigma^2(t) = {\sigma_0}^2 e^{bn(t)}$ where $n(t)$ 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?



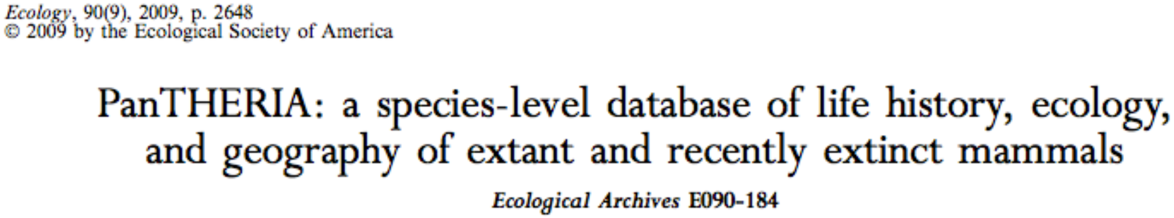
$$\sigma^2(t) = f\left(t, E_1(t), E_2(t), \ldots, E_k(t)\right)$$

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

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

Clavel & Morlon *PNAS* 2017

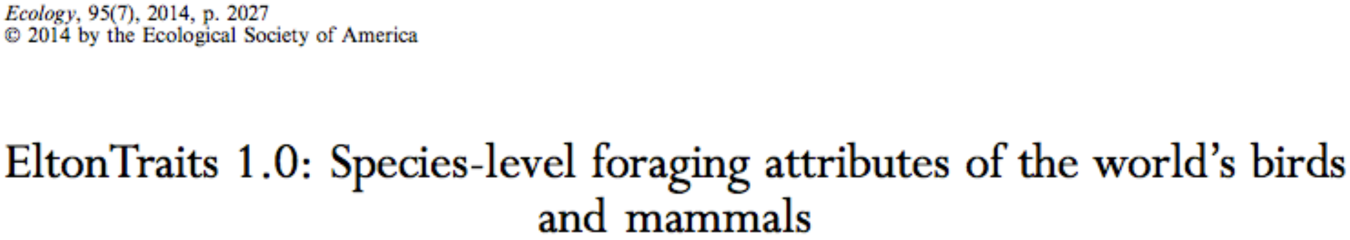
Testing the effect of past climatic changes and rates of body-size evolution in mammals & birds



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

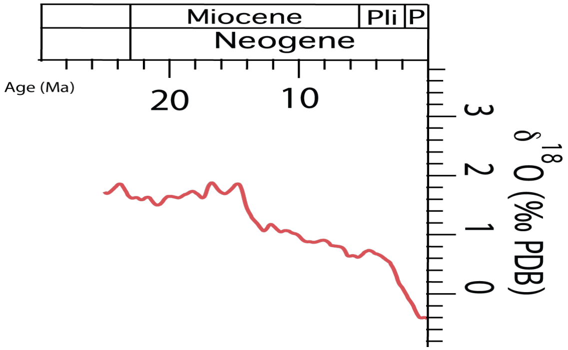
PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals

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



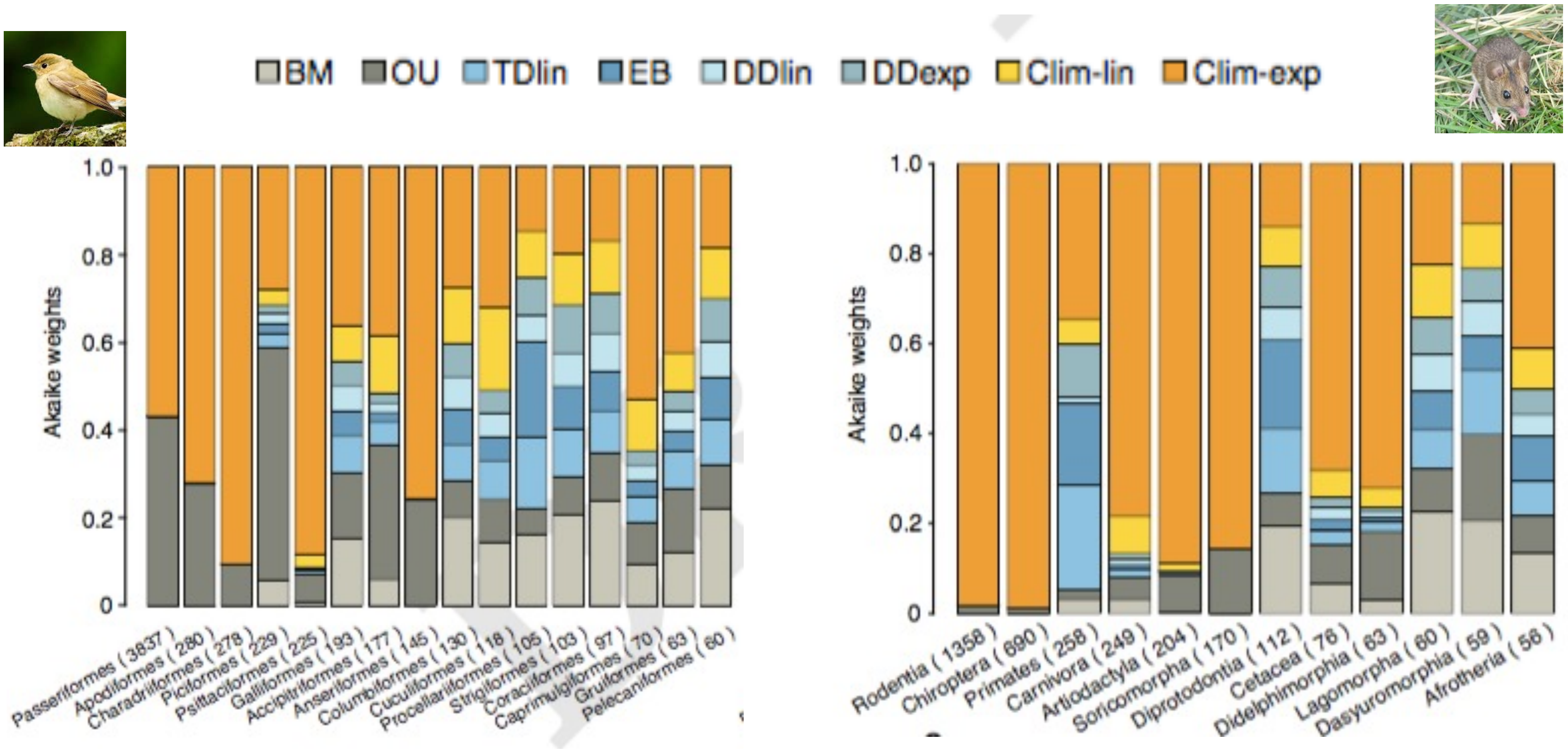
Zachos *et al.* 2008

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

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

Clavel & Morlon *PNAS* 2017

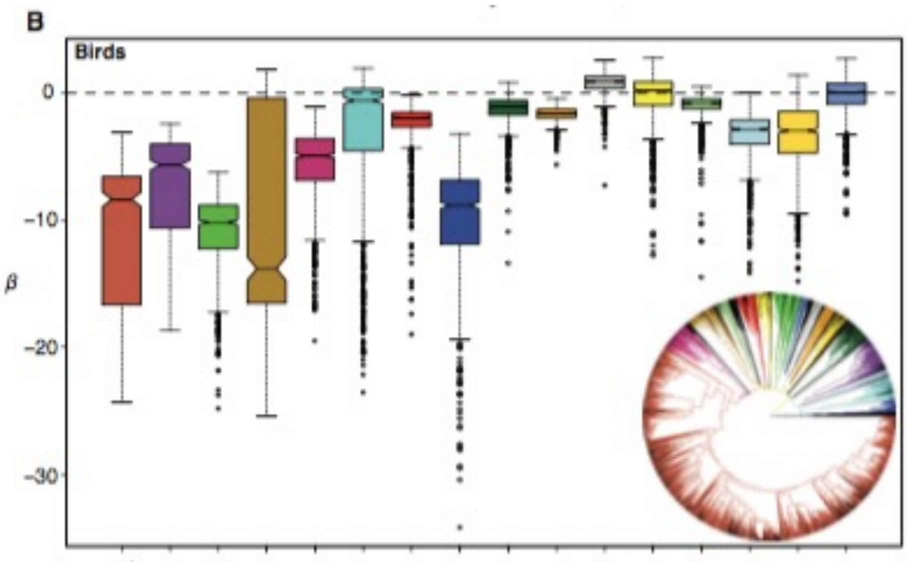
Temperature-dependent rates of phenotypic evolution is supported over 'classical' models of phenotypic evolution

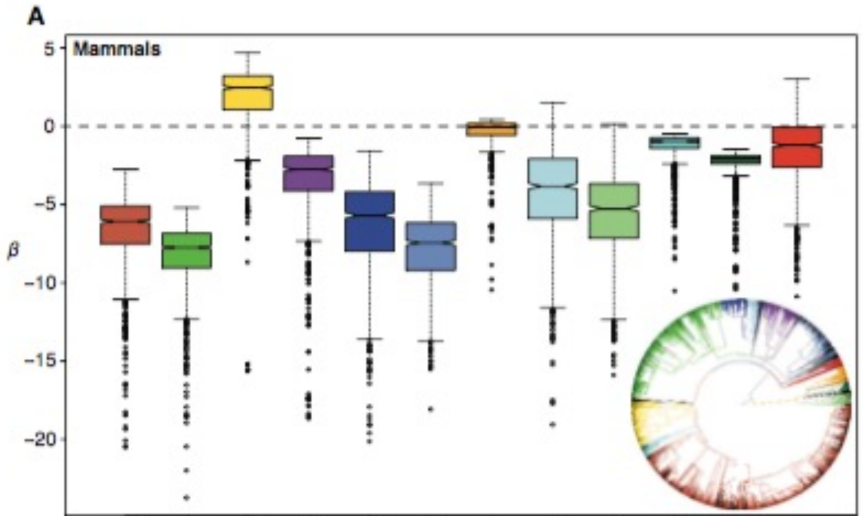


Clavel & Morlon *PNAS* 2017

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

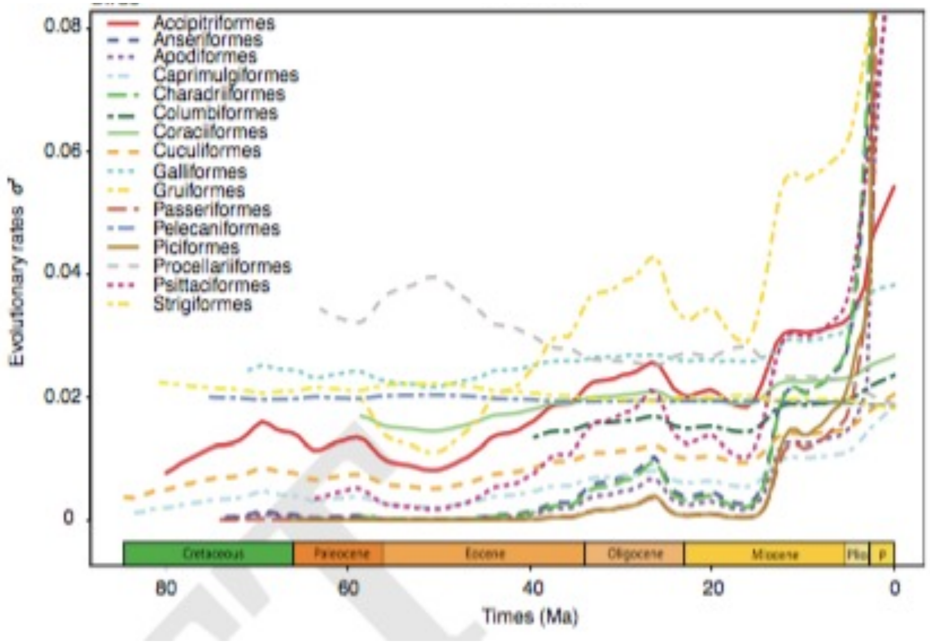
$$\sigma^2(t) = \sigma_0^2 \times e^{\beta T}$$

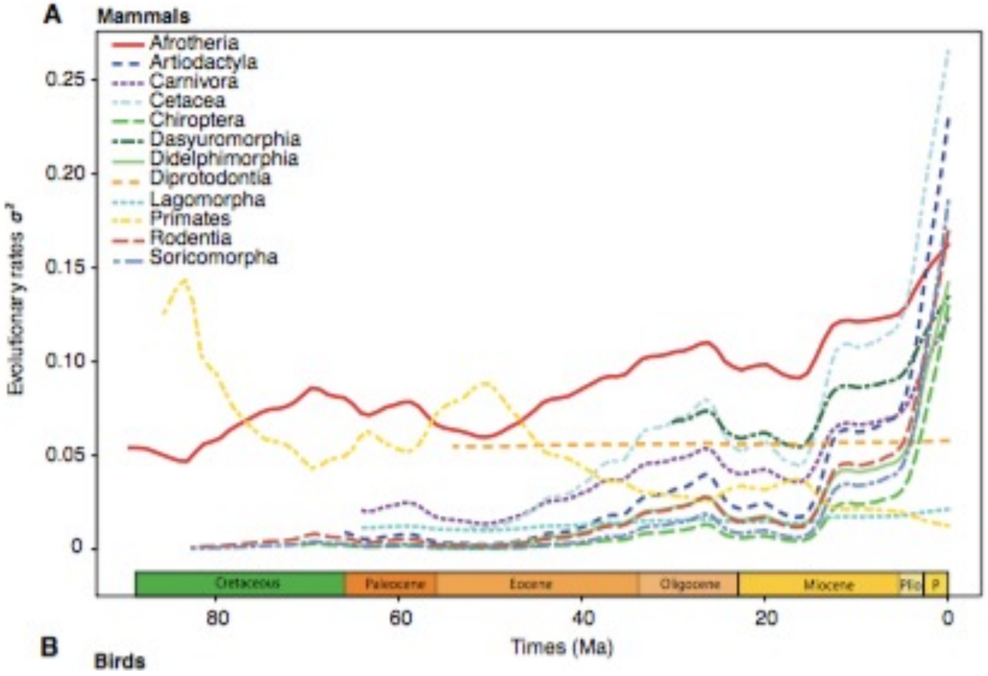




Clavel & Morlon *PNAS* 2017

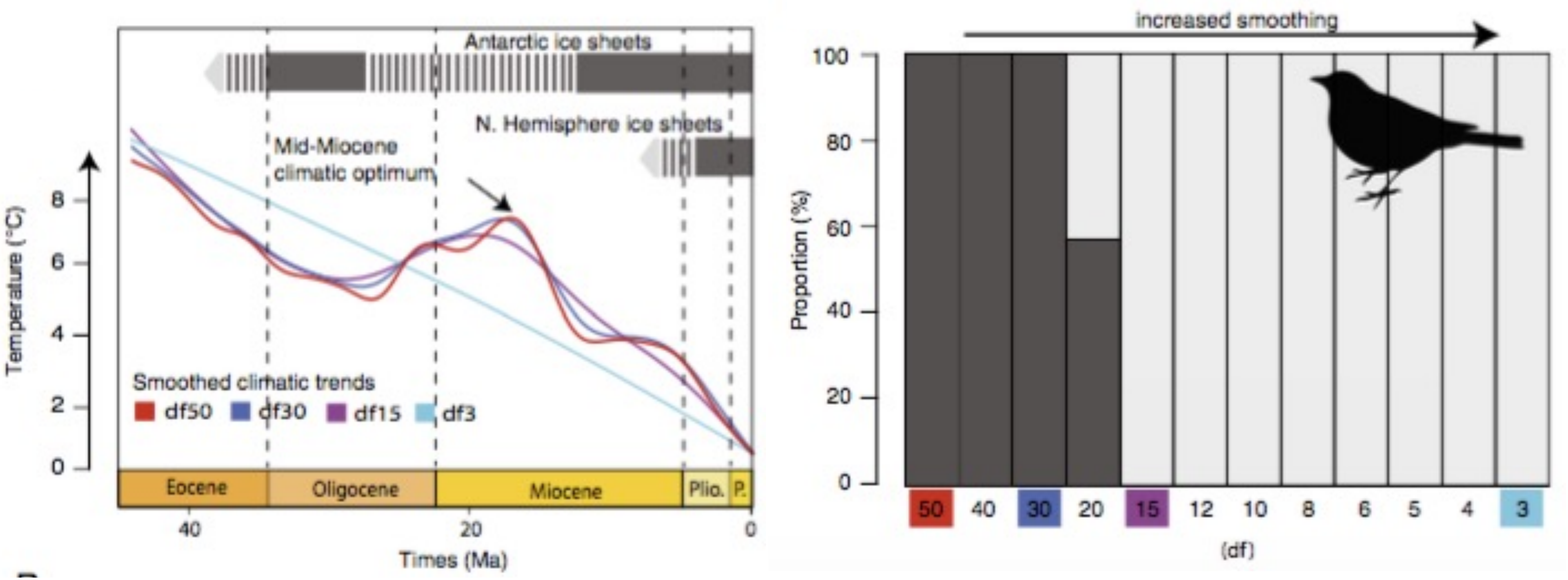
This results in an increase in evolutionary rates over the Cenozoic





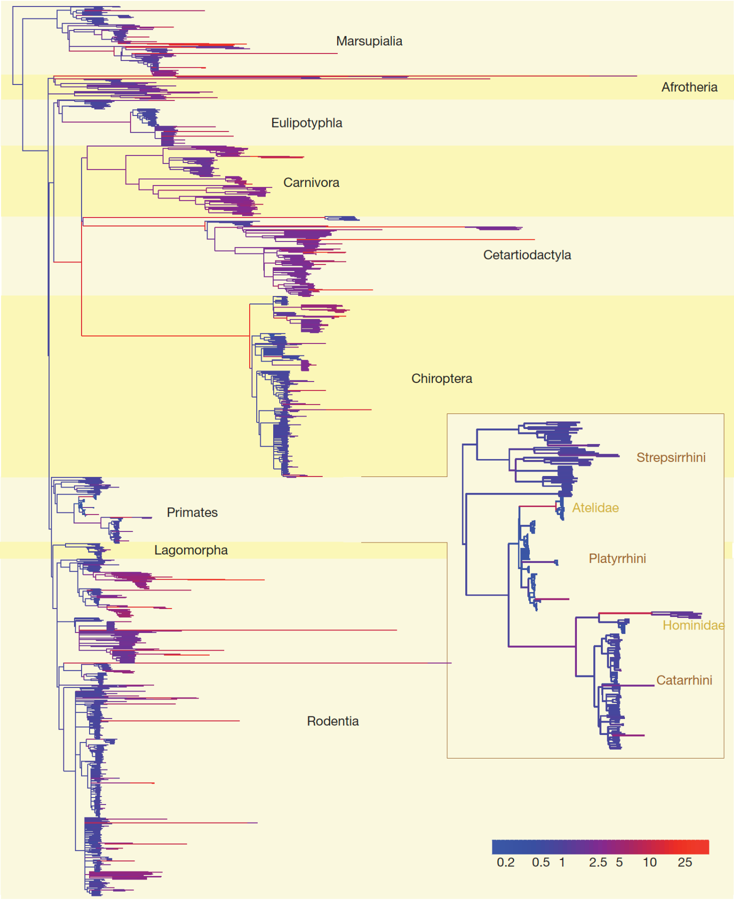
Clavel & Morlon *PNAS* 2017

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

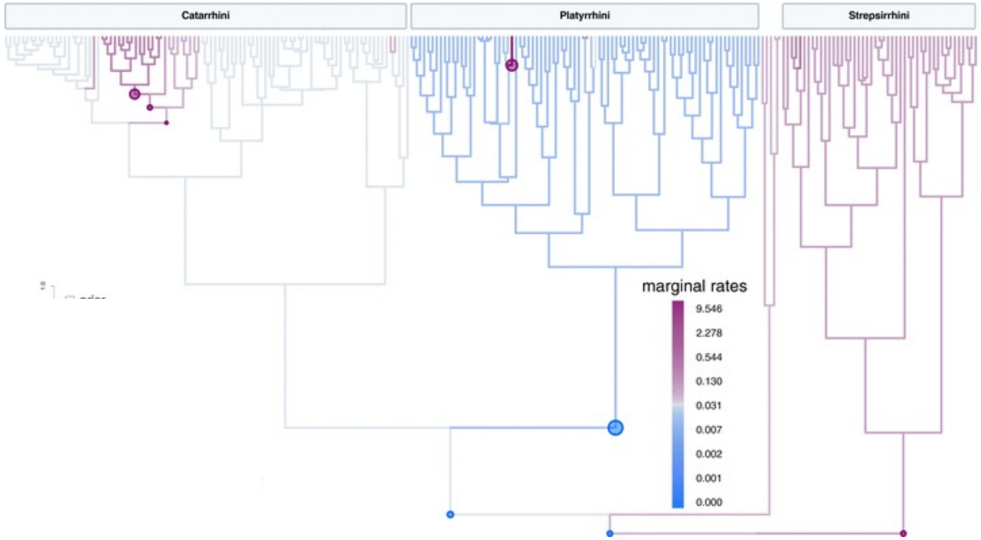


Clavel & Morlon *PNAS* 2017

Rates of phenotypic evolution vary across lineages



Venditti *et al. Nature* 2011



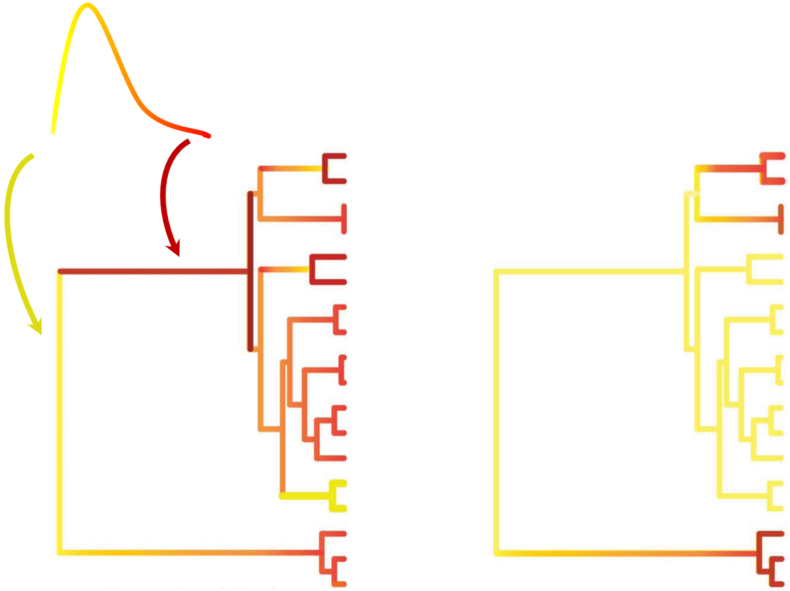
Eastman *et al. Evolution* 2011

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

Models of phenotypic evolution with uncorrelated or correlated clocks

LEHNA

Julien Clavel

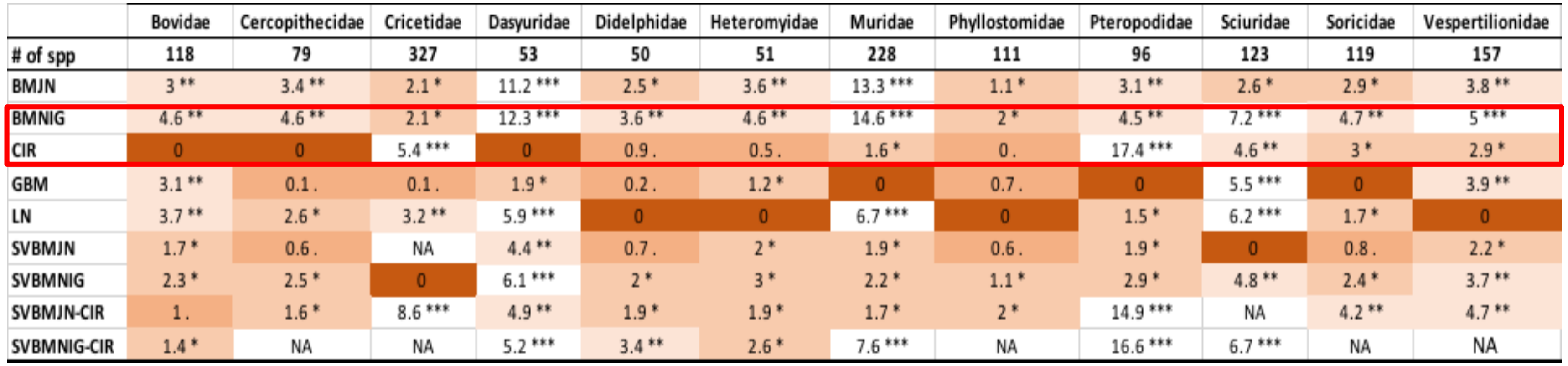


Many rate shifts with small effects

Clavel et al. in prep.

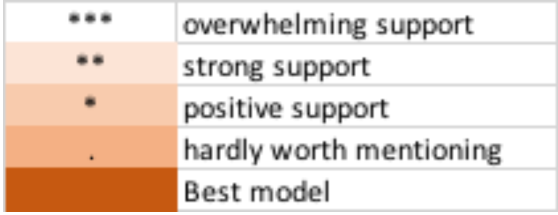
Models of phenotypic evolution with many shifts & small effects are best supported

Body-size evolution in mammals



		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**
punctuated	**BMJN**	3 **	3.4 **	2.1 *	11.2 ***	2.5 *	3.6 **	13.3 ***	1.1 *	3.1 **	2.6 *	2.9 *	3.8 **
auto-correlated	**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 *
independent	**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
auto-correlated + jumps	**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

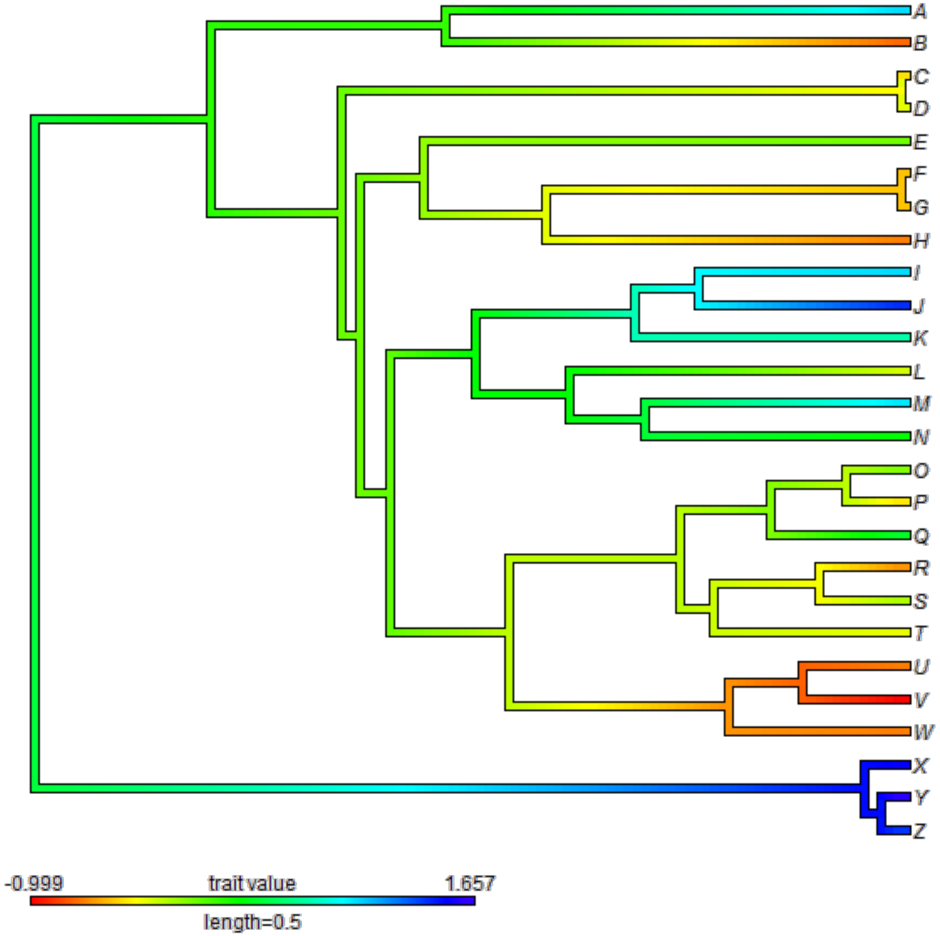
Bayes factor support (Kass & Raftery 1995)



***	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

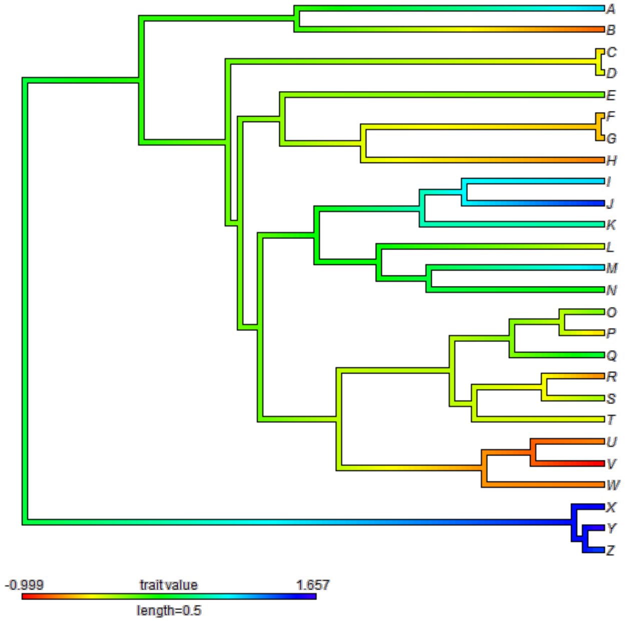


What are the factors that modulate diversification rates?

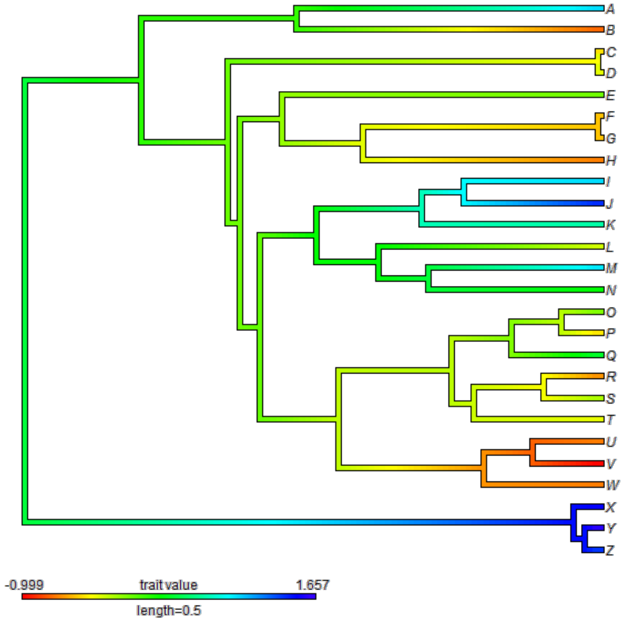
INTRINSIC

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

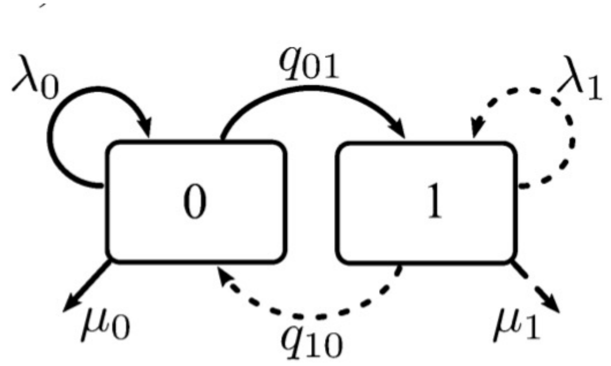
Species-specific traits

reproduction mode

life-history traits

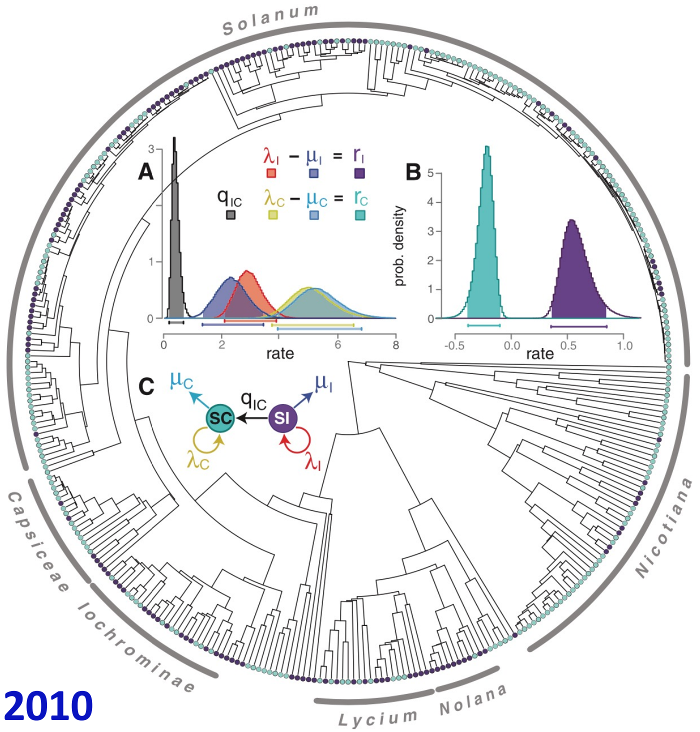
dispersal capacity

State-dependent Speciation-Extinction (SSE) models



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

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



Goldberg *et al. Science* 2010

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

Methods in Ecology and Evolution

British Ecological Society

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 Lewitus[1], Fabien L. Condamine[2], Marc Manceau[1], Julien Clavel[1] and Jonathan Drury[1]

Beast2

Bayesian evolutionary analysis by sampling trees

julia

github
SOCIAL CODING

Methods in Ecology and Evolution

British Ecological Society

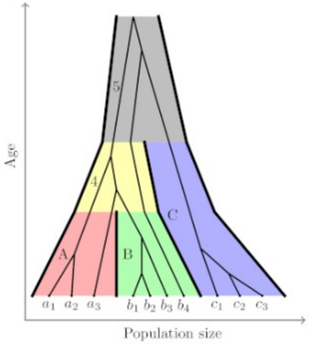
Methods in Ecology and Evolution 2015, **6**, 1311–1319 doi: 10.1111/2041-210X.12420

APPLICATION

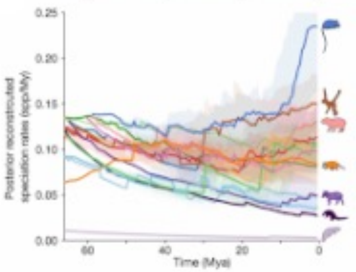
mvMORPH: an R package for fitting multivariate evolutionary models to morphometric data

Julien Clavel[1,2]*, Gilles Escarguel[2] and Gildas Merceron[3] https://www.transmittingscience.com/

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

THANKS!


Fabien Condamine


Joëlle Barido-Sottani


Jonathan Rolland


Ignacio Quintero


Odile Maliet


Dan Moen


Julien Clavel


Olivier Billaud


Nathan Mazet