

IMBALANCED DIVERSIFICATION SUSTAIN THE RISE, DECLINE AND FALL OF CLADES

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How is biodiversity generated and maintained?

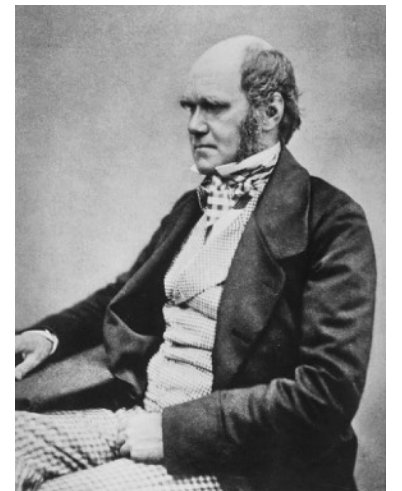


ON
THE ORIGIN OF SPECIES
BY MEANS OF NATURAL SELECTION,
OR THE
PRESERVATION OF FAVOURED RACES IN THE STRUGGLE
FOR LIFE.

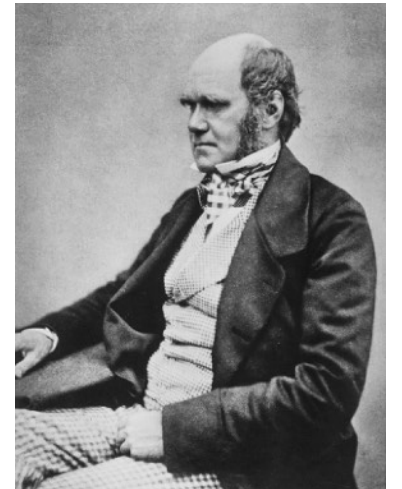
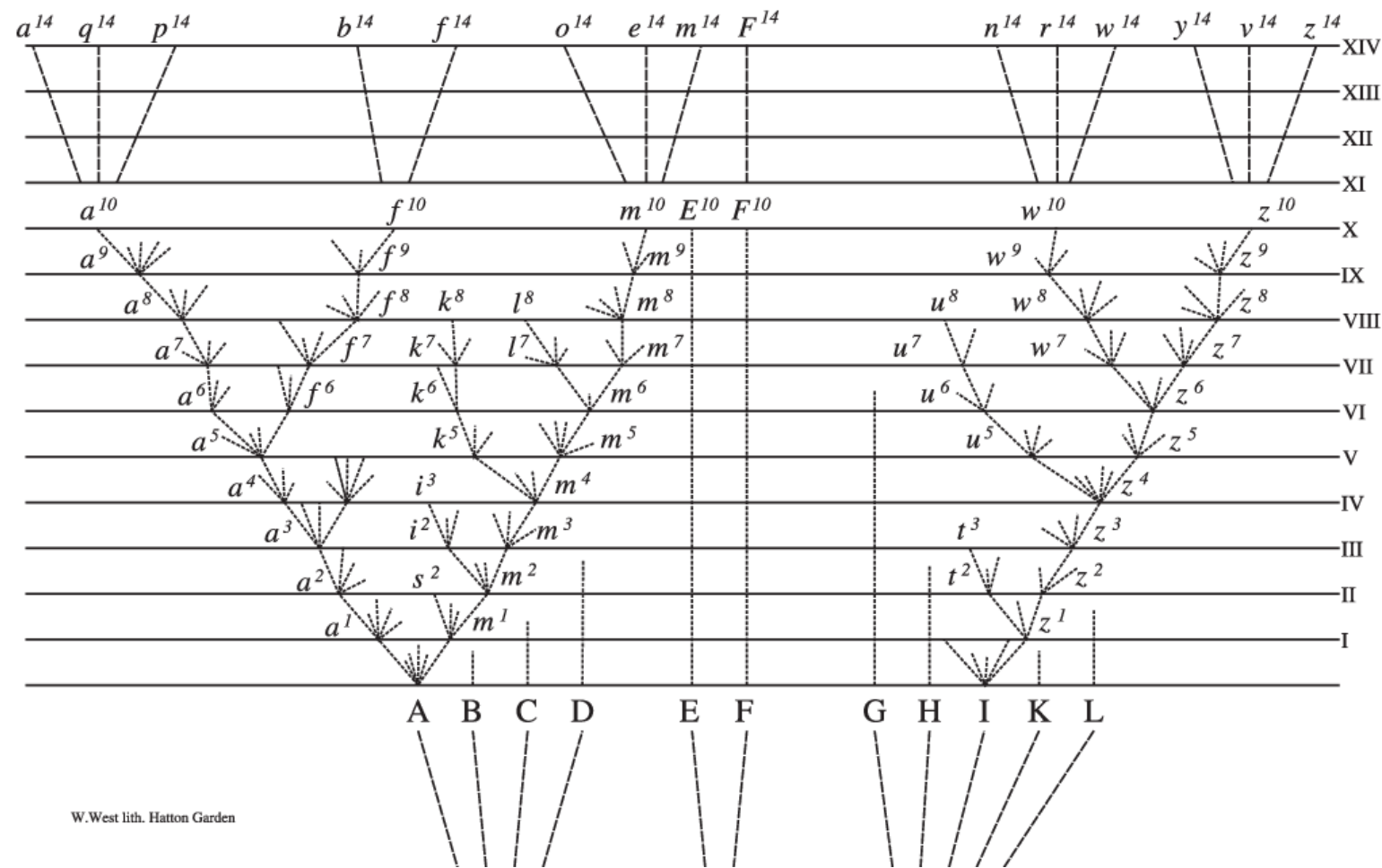
By CHARLES DARWIN, M.A.,
FELLOW OF THE ROYAL, GEOLOGICAL, LINNEAN, ETC., SOCIETIES;
AUTHOR OF 'JOURNAL OF RESEARCHES DURING H. M. S. BEAGLE'S VOYAGE
ROUND THE WORLD.'

LONDON:
JOHN MURRAY, ALBEMARLE STREET.
1859.

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THE 'UNIFORMITARIANISM' OF GRADUALISM



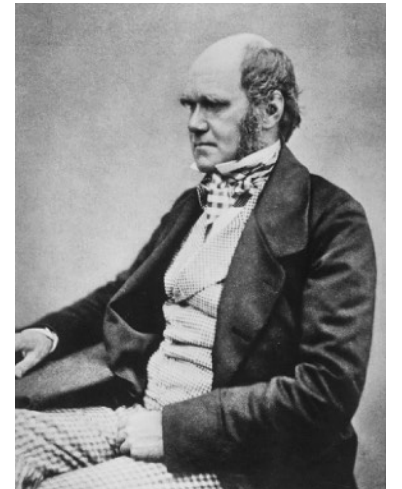
"...natural selection is daily and hourly scrutinising [...] at the improvement of each organic being [...]. **We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages.**"

"The **amount of organic change** in the fossils [...] probably serves as a **fair measure of the lapse of actual time.**"

C. R. Darwin (1859)

'ABOMINABLE MYSTERIES'

to H. Frank comes back in to the
beginning of ^{next} month from
Waring, whom he has been
working pretty hard on various
subjects & producing lectures,
lectures & so on.
I have just read Bell's
& says. It is pretty bold. The
rapid development, as far as
we can judge, of ^{all} the
higher plants ^{within recent geological times} is an abominable
mystery. Certainly it is
a great step if we could
believe that ^{the higher} plants at first
could live at a high
level; but still it is apparently



"The **rapid** development as far as we can judge of all the higher plants within recent geological times is an **abominable mystery**".

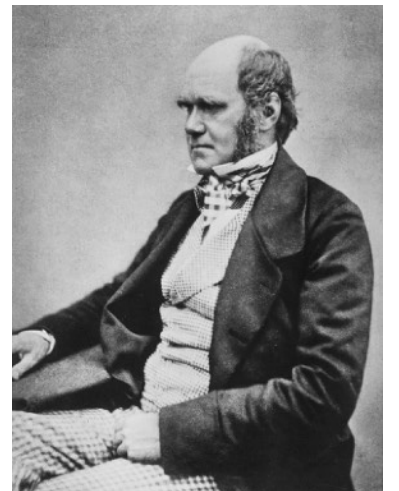
C. R. Darwin to J. Hooker (1879)

~300,000 extant Angiosperms (younger) vs ~1000 extant Gymnosperms (older).

'GHOST CONTINENTS'

“Nothing is more extraordinary [...] than the **apparently very sudden or abrupt development of the higher plants**. I have sometimes speculated whether there did not exist somewhere during long ages an **extremely isolated continent**, perhaps near **the South Pole**.”

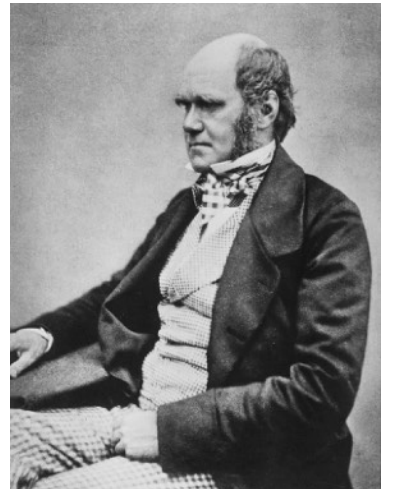
C. R. Darwin to J. Hooker (1881)



'ON THE IMPERFECTION OF THE GEOLOGICAL RECORD'

"If then the **geological record be as imperfect as I believe it to be [...]** the main objections to the theory of natural selection are greatly diminished or disappear."

C. R. Darwin (1859)





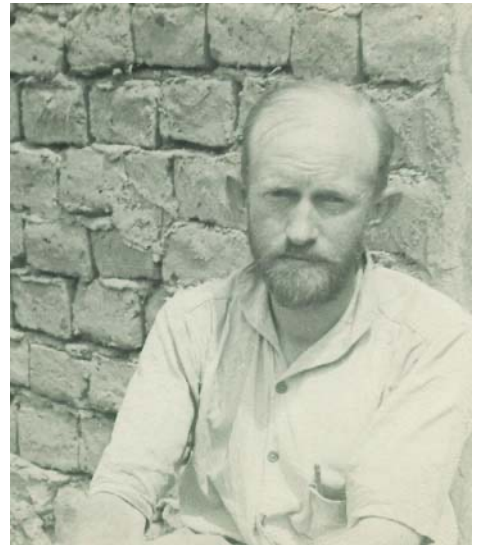
TEMPO TO INFER MODE

Tempo and Mode in Evolution

George Gaylord Simpson

A Columbia Classic in Evolution

*With a new introduction by
George Gaylord Simpson*

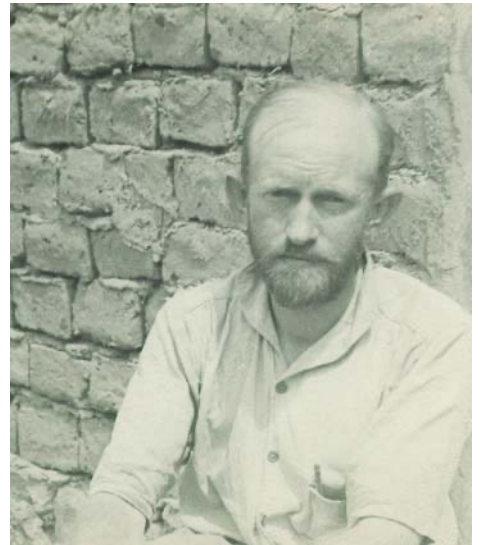


PALAEONTOLOGY'S BRAVADO

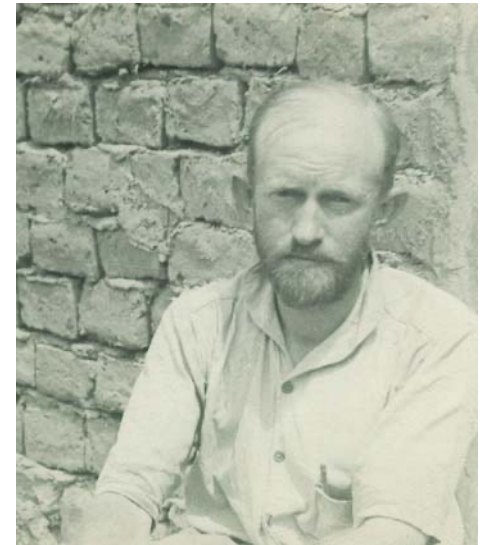
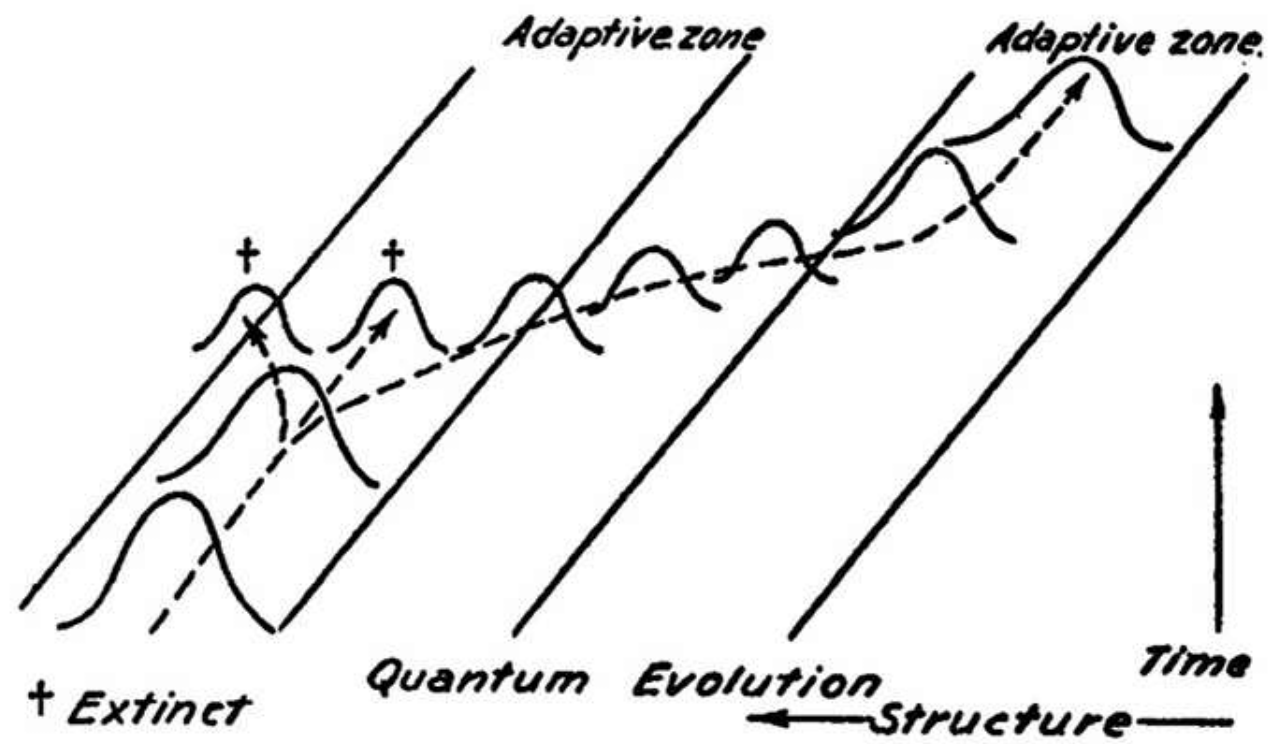
“They [experimental biologists] may reveal what happens to a hundred rats in the course of ten years under fixed and simple conditions, but not **what happened to a billion rats in the course of ten million years under the fluctuating conditions of earth history.**

Obviously, the latter problem is much more important.”

G.G. Simpson (1944)

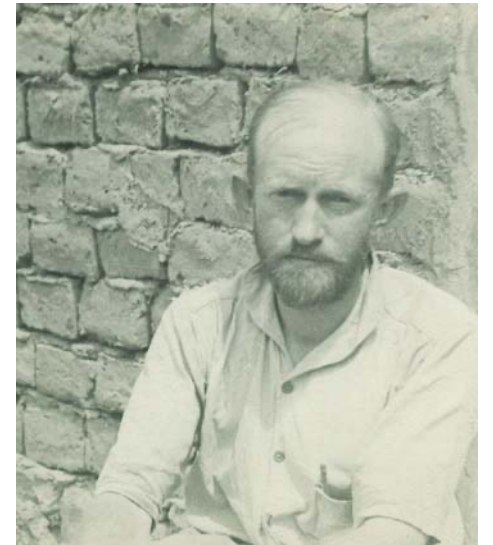
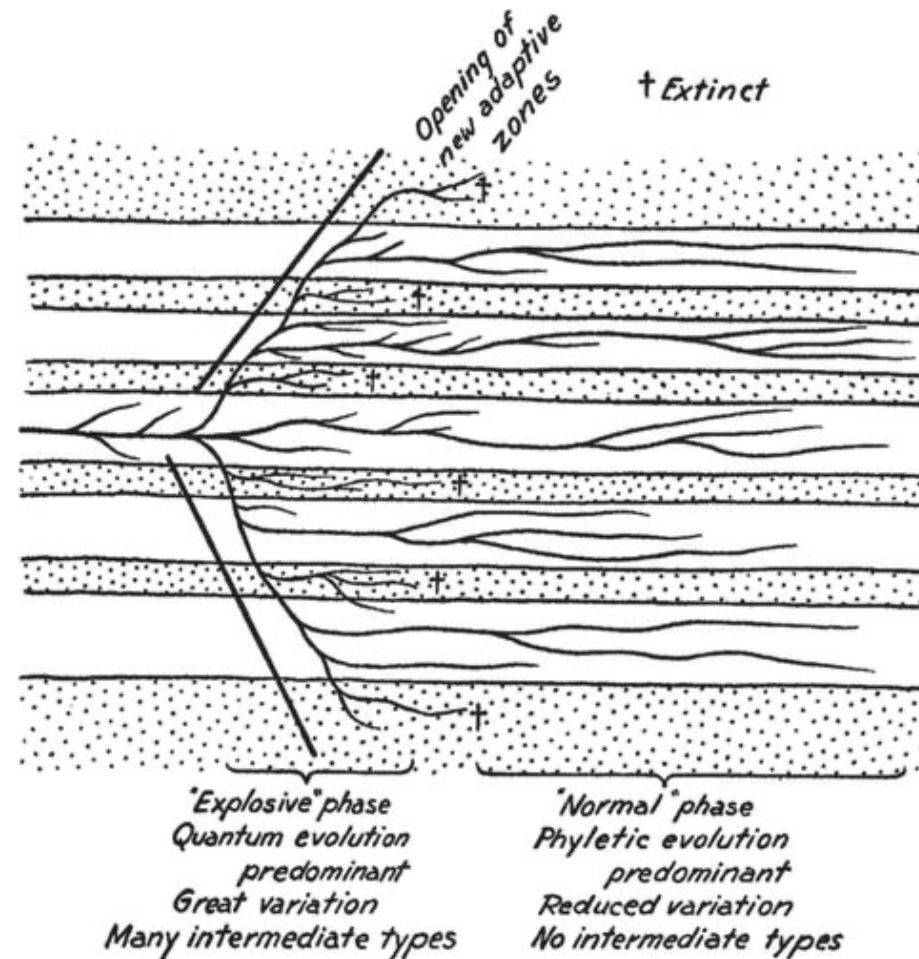


'QUANTUM EVOLUTION'



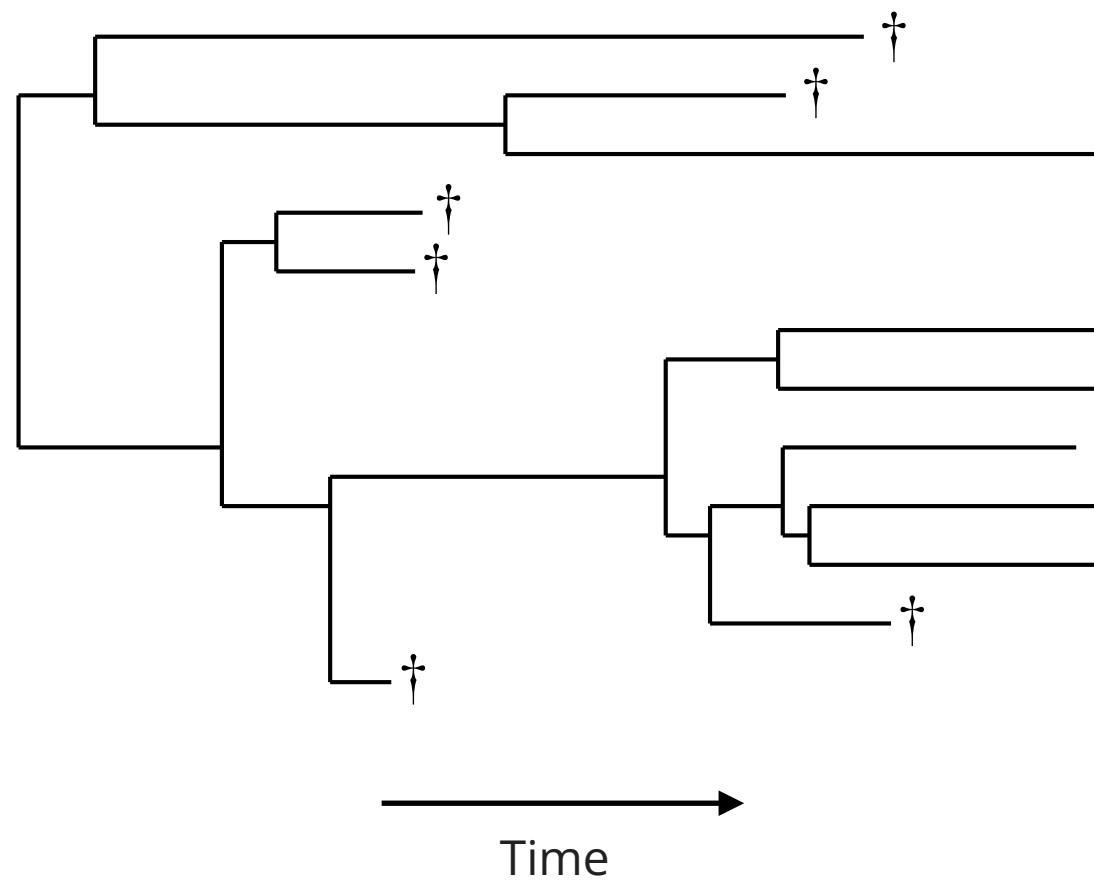
CLADE-LEVEL PROCESSES

Fast diversification result from colonisation of new adaptive zones: the **opening of ecological opportunities** (e.g., key innovations) that materialise at the **clade level**.



“Much of life’s diversity originated from adaptive radiations”.

BIODIVERSITY IS THE RESULT OF A DIVERSIFICATION PROCESS



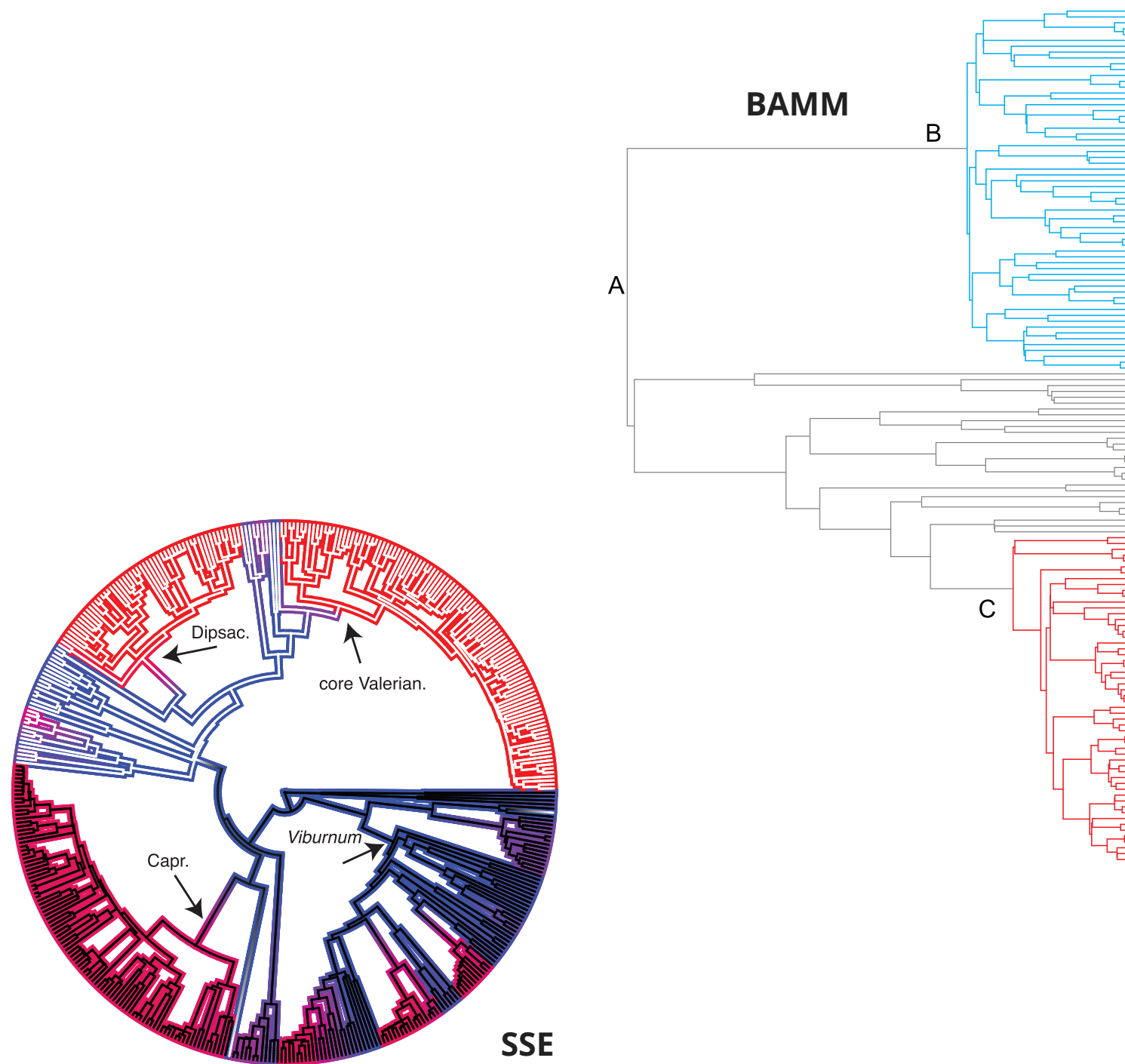
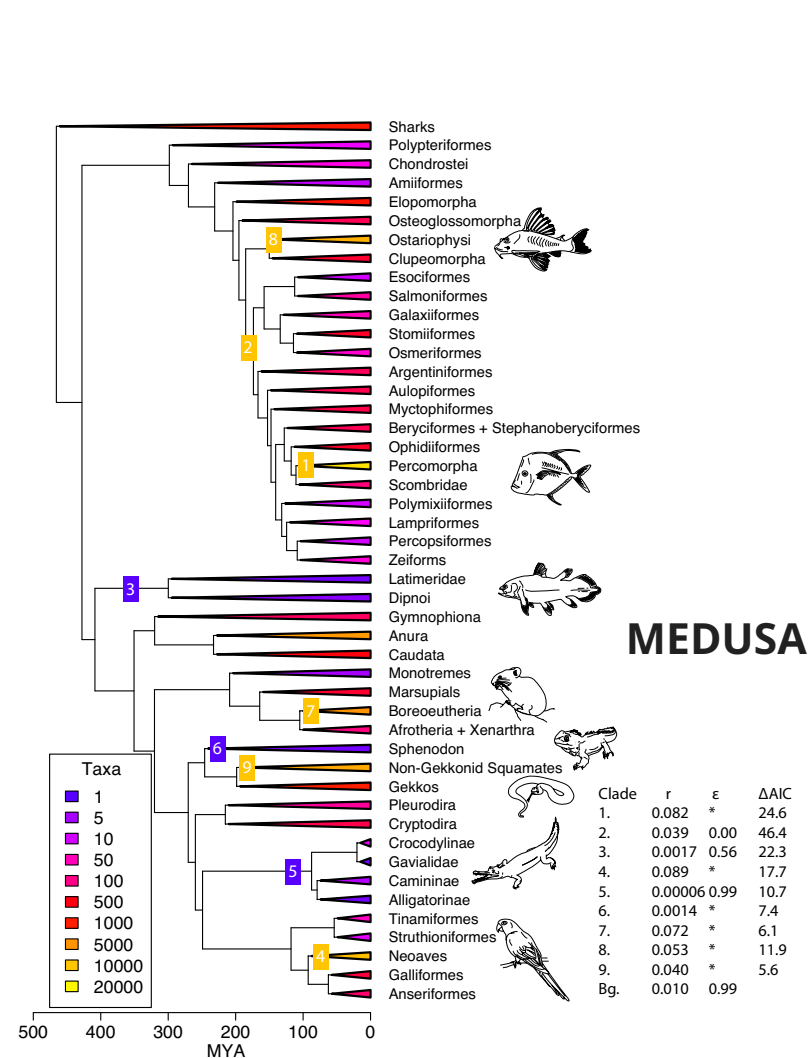
Birth-death models

λ (Speciation rate)

μ (Extinction rate)

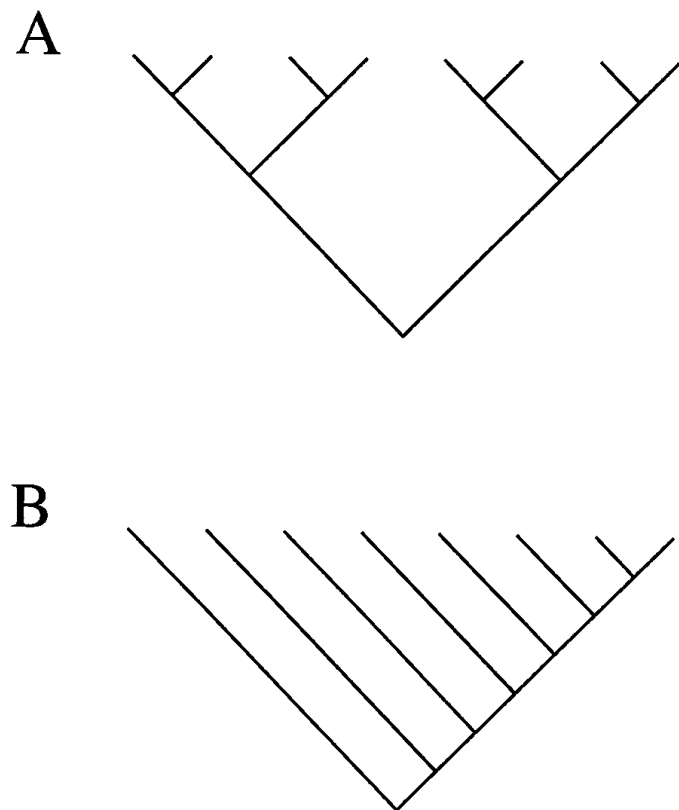
PROCESS-BASED MODELS ASSUME CLADE-LEVEL VARIATION

Few major discrete shifts following ‘ecological opportunities’
(e.g., key innovations, geographical colonization)

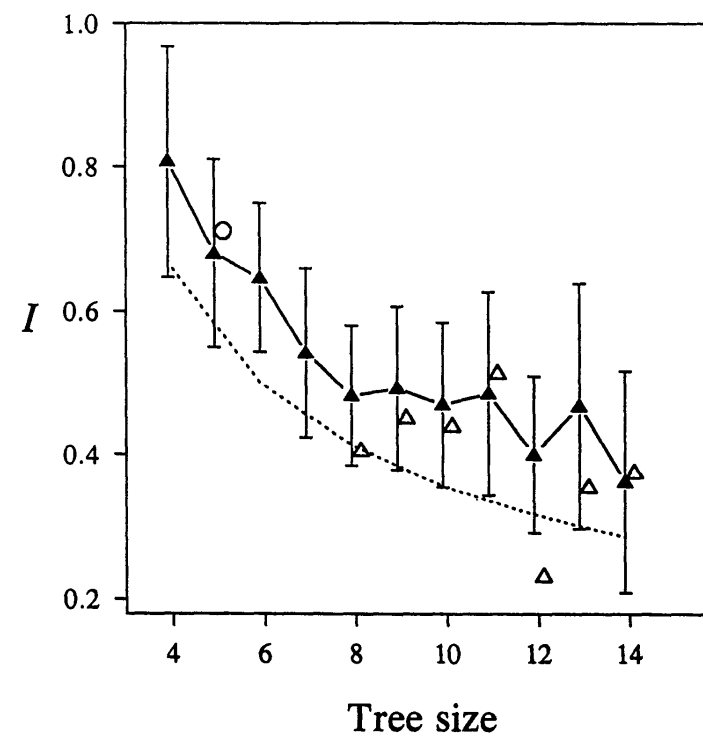


THE FORGOTTEN TREE IMBALANCE

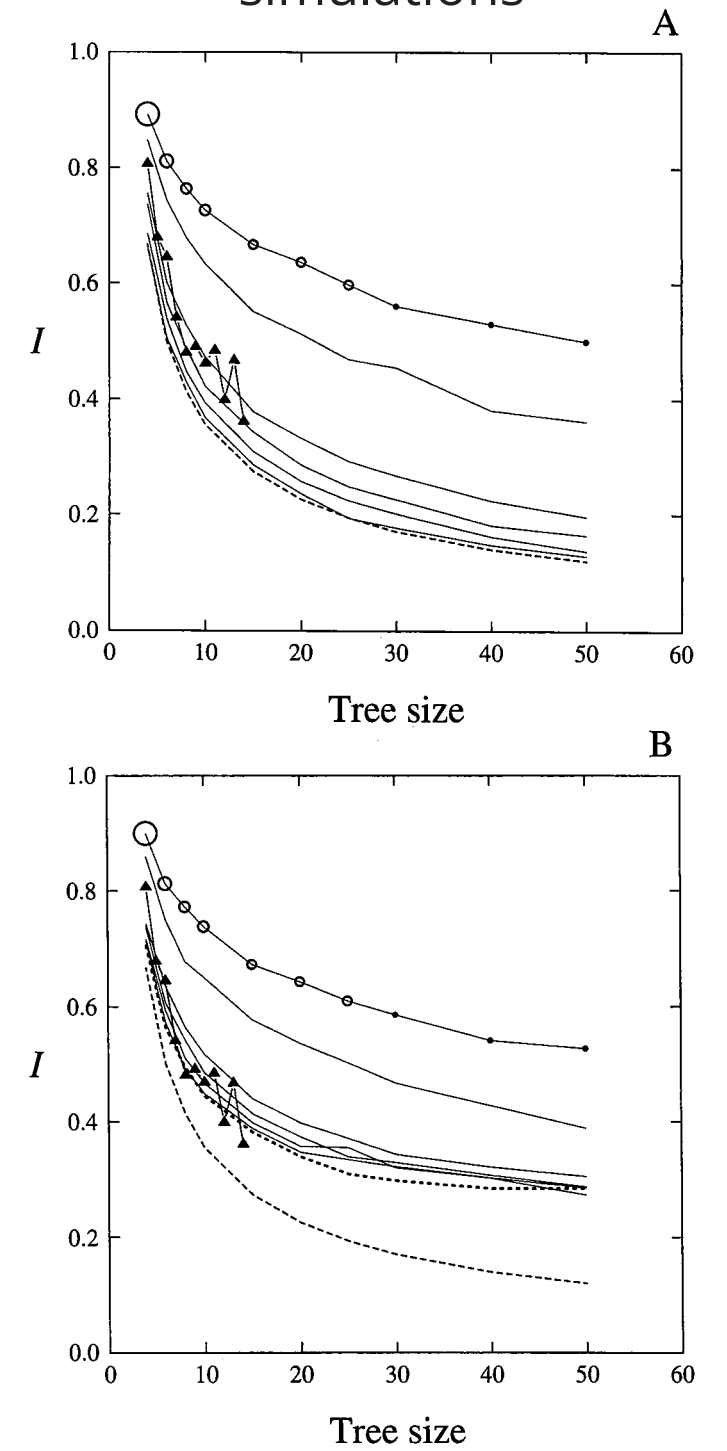
Imbalance



Imbalance in
empirical trees



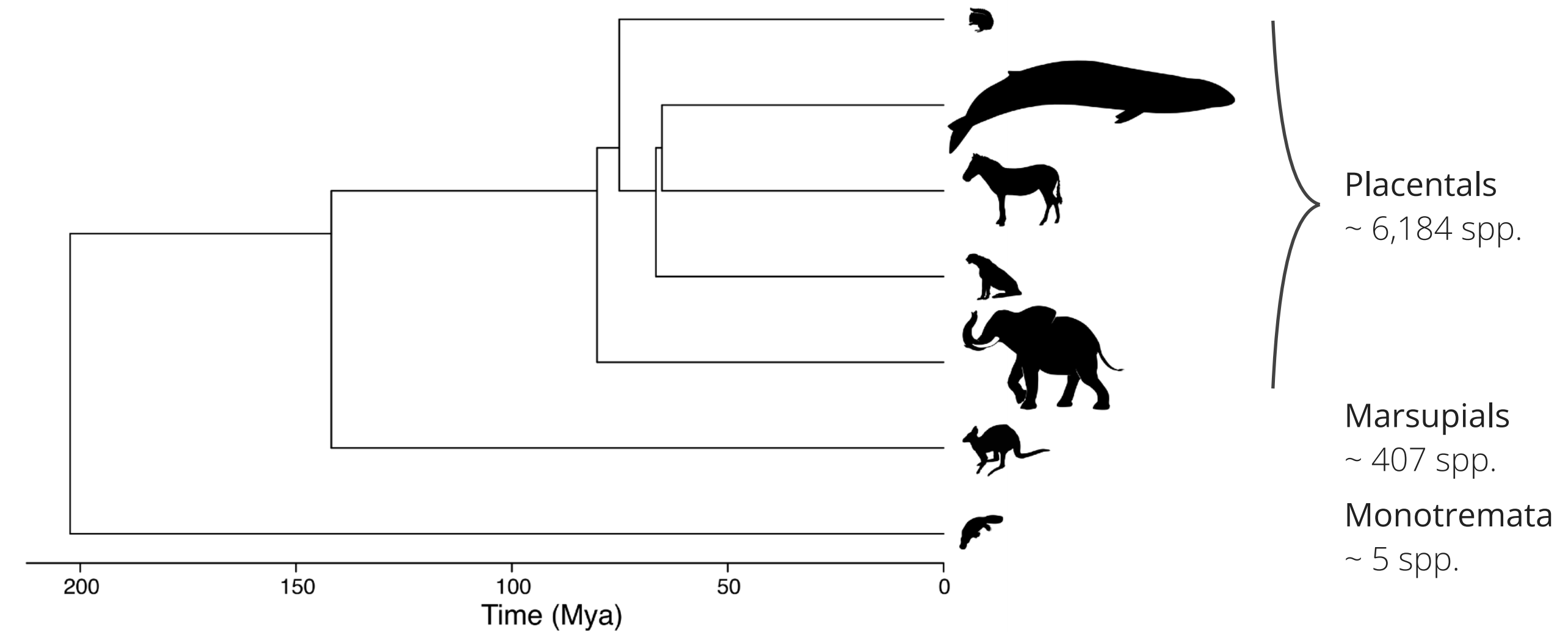
Imbalance in
simulations



TREE IMBALANCE

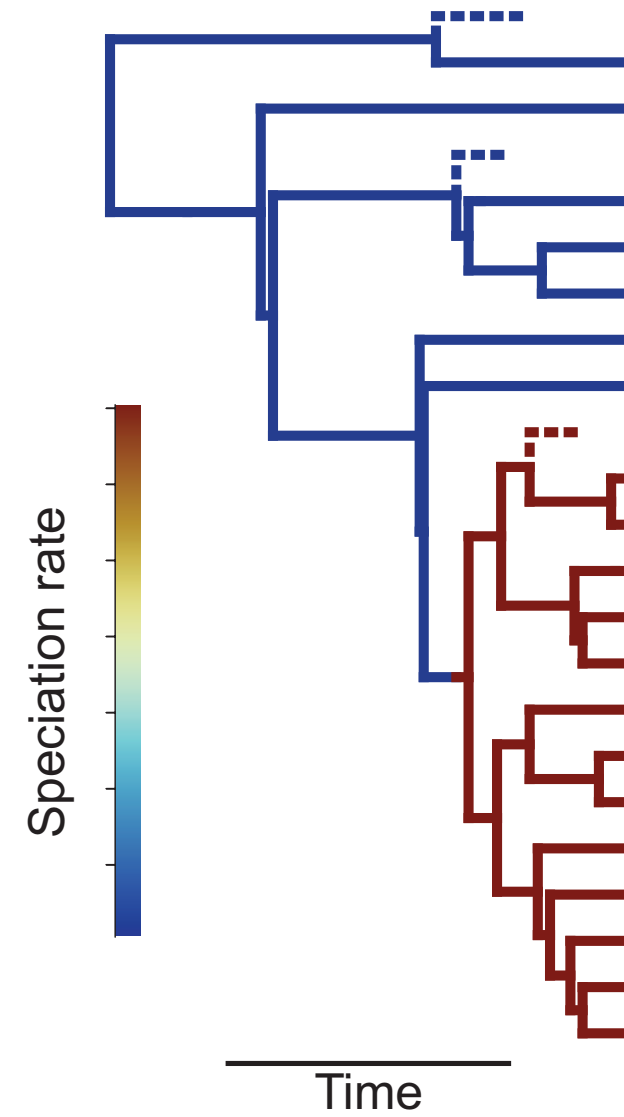
A **less predictable** interplay of species ecologies with their environment:

Contingent diversification dynamics.



ALTERNATIVE PARADIGMS

A Punctuated diversification rate shifts



$\Phi(\lambda(t), \mu(t), t)$ Probability of a lineage at time $\mathbf{t}$ going extinct by the present.

$$\begin{aligned}
 \Phi(\lambda_0, \mu_0, t + \delta t) = & \\
 & \mu_0 \delta t + \\
 & (1 - \mu_0 \delta t) \times \lambda_0 \delta t \times \\
 & \left[\iint \frac{1}{2\pi\sigma_\lambda\sigma_\mu\delta t} \exp\left(\frac{(\ln(\lambda_1) - \ln(\lambda_0))^2}{2\sigma_\lambda\sqrt{\delta t}} + \frac{(\ln(\mu_1) - \ln(\mu_0))^2}{2\sigma_\mu\sqrt{\delta t}}\right) \Phi(\lambda_1, \mu_1, t) d\lambda_1 d\mu_1 \right]^2 + \quad (3) \\
 & (1 - \mu_0 \delta t) \times (1 - \lambda_0 \delta t) \times \\
 & \iint \frac{1}{2\pi\sigma_\lambda\sigma_\mu\delta t} \exp\left(\frac{(\ln(\lambda_1) - \ln(\lambda_0))^2}{2\sigma_\lambda\sqrt{\delta t}} + \frac{(\ln(\mu_1) - \ln(\mu_0))^2}{2\sigma_\mu\sqrt{\delta t}}\right) \Phi(\lambda_1, \mu_1, t) d\lambda_1 d\mu_1.
 \end{aligned}$$

BAYESIAN DATA AUGMENTATION

The **BDD** model remains (in)famously **intractable**.

Bayesian data augmentation to estimate the posterior distribution.

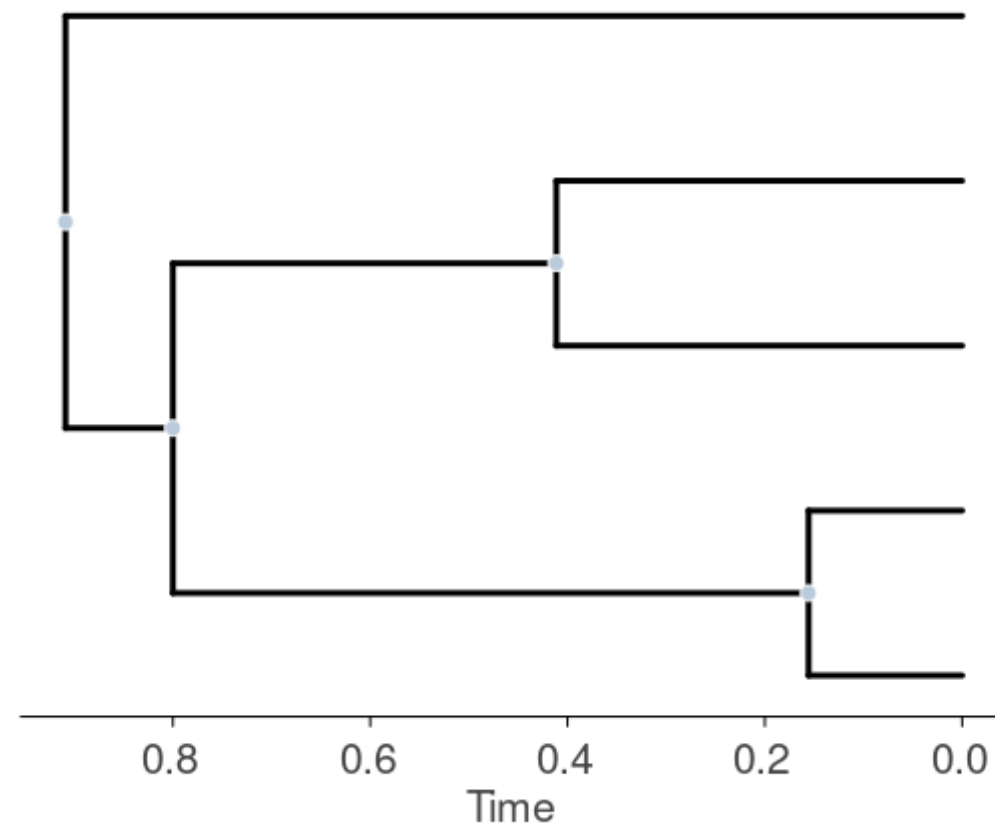
$$p(\theta | o)$$
$$p(\theta | o) = \int_A p(\theta | o, a) p(a | o) da$$

θ = parameters

o = observed data

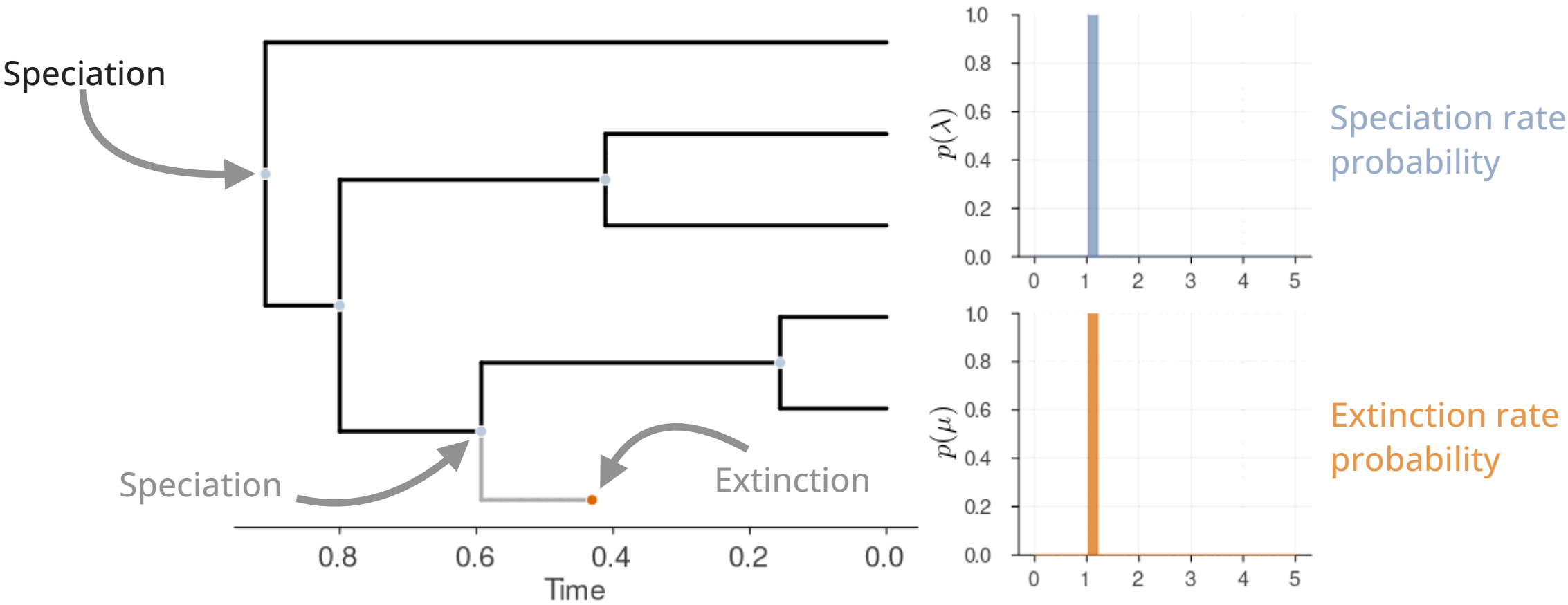
a = augmented data

BAYESIAN DATA AUGMENTATION OF CONSTANT BIRTH-DEATH

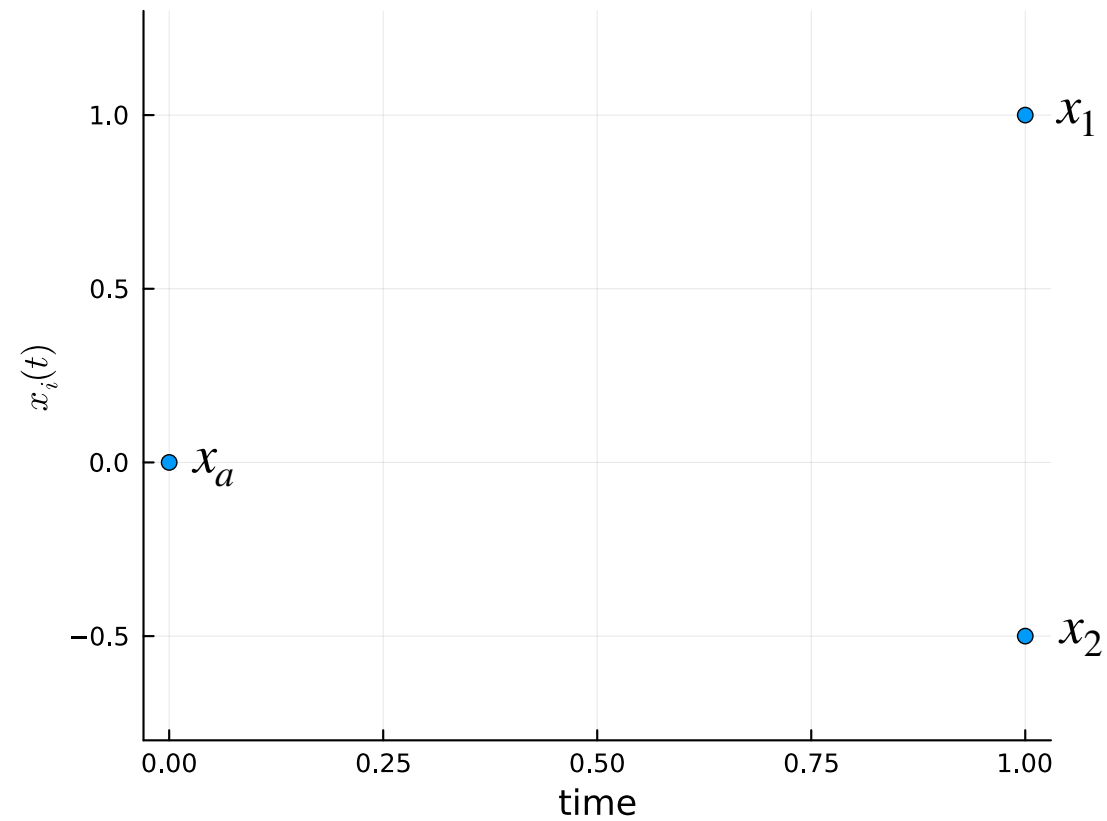


What are the past
rates of **speciation**
and **extinction**?

BAYESIAN DATA AUGMENTATION OF CONSTANT BIRTH-DEATH



BAYESIAN DATA AUGMENTATION OF DIFFUSION

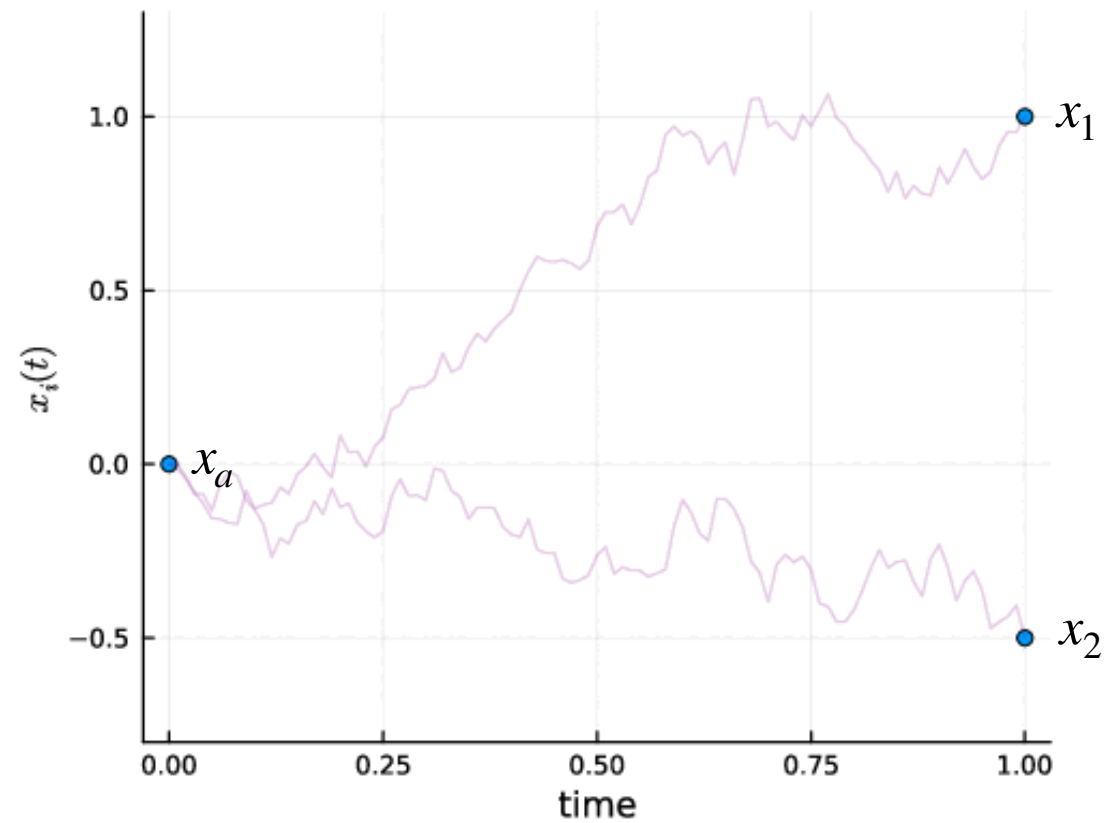


$$x_1 \sim N(x_a, \sigma^2 t)$$

$$x_2 \sim N(x_a, \sigma^2 t)$$

$\sigma^2 = \text{diffusion rate}$

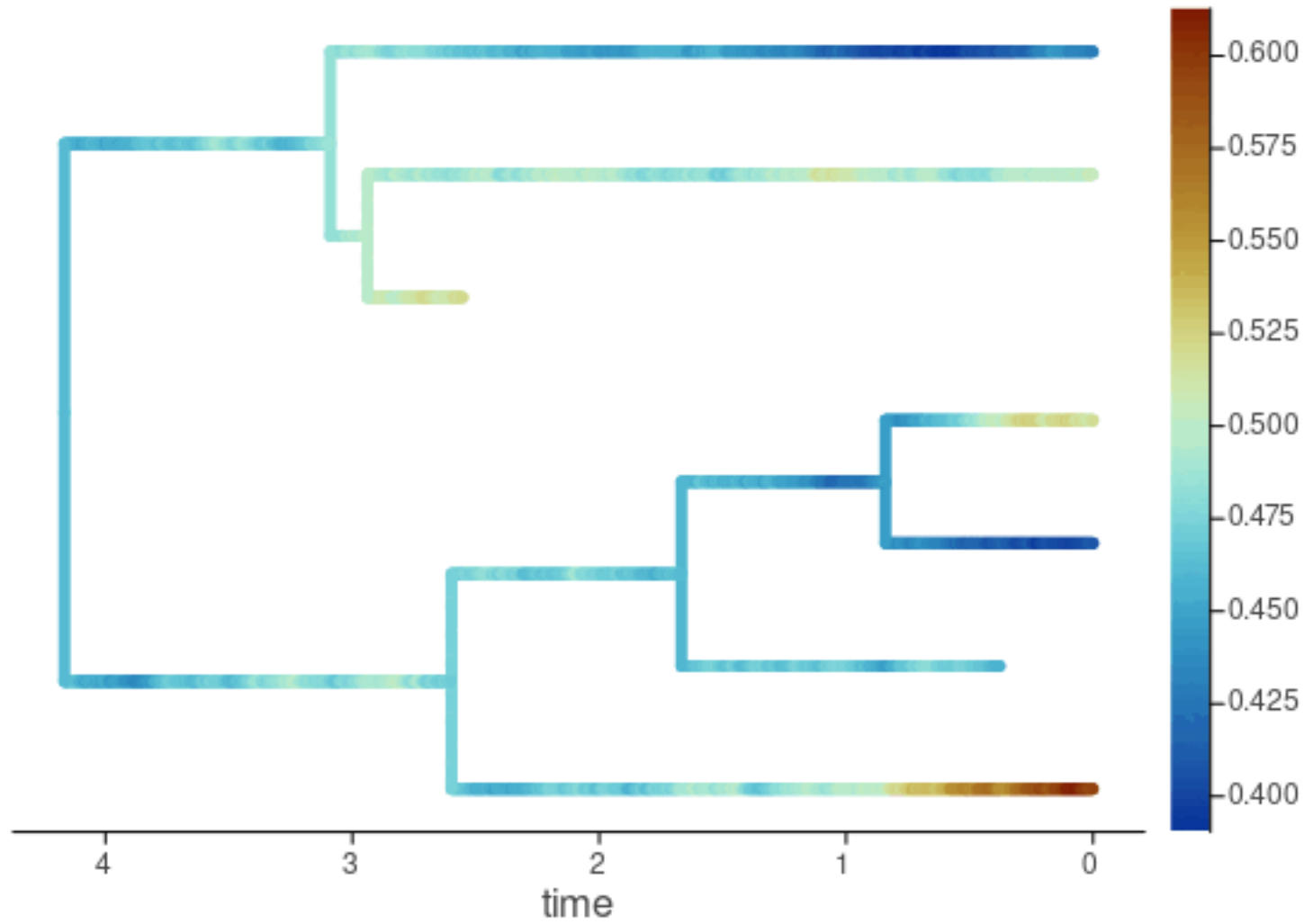
BAYESIAN DATA AUGMENTATION OF DIFFUSION



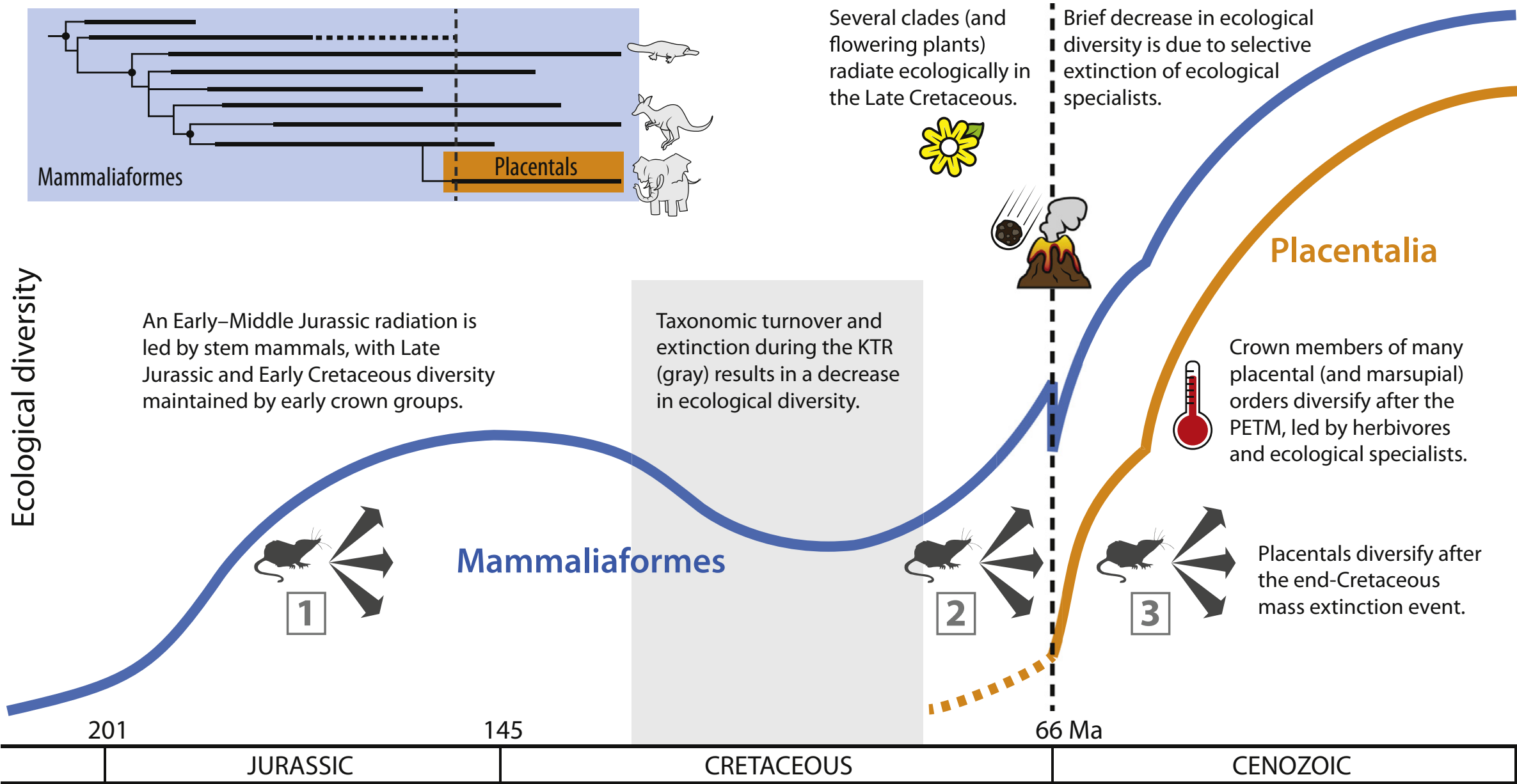
$$\int_X \prod_i^{n-1} x_{i+1} \sim N\left(x_i, \sigma^2 \frac{t}{n-1}\right) dx$$

σ^2 = diffusion rate

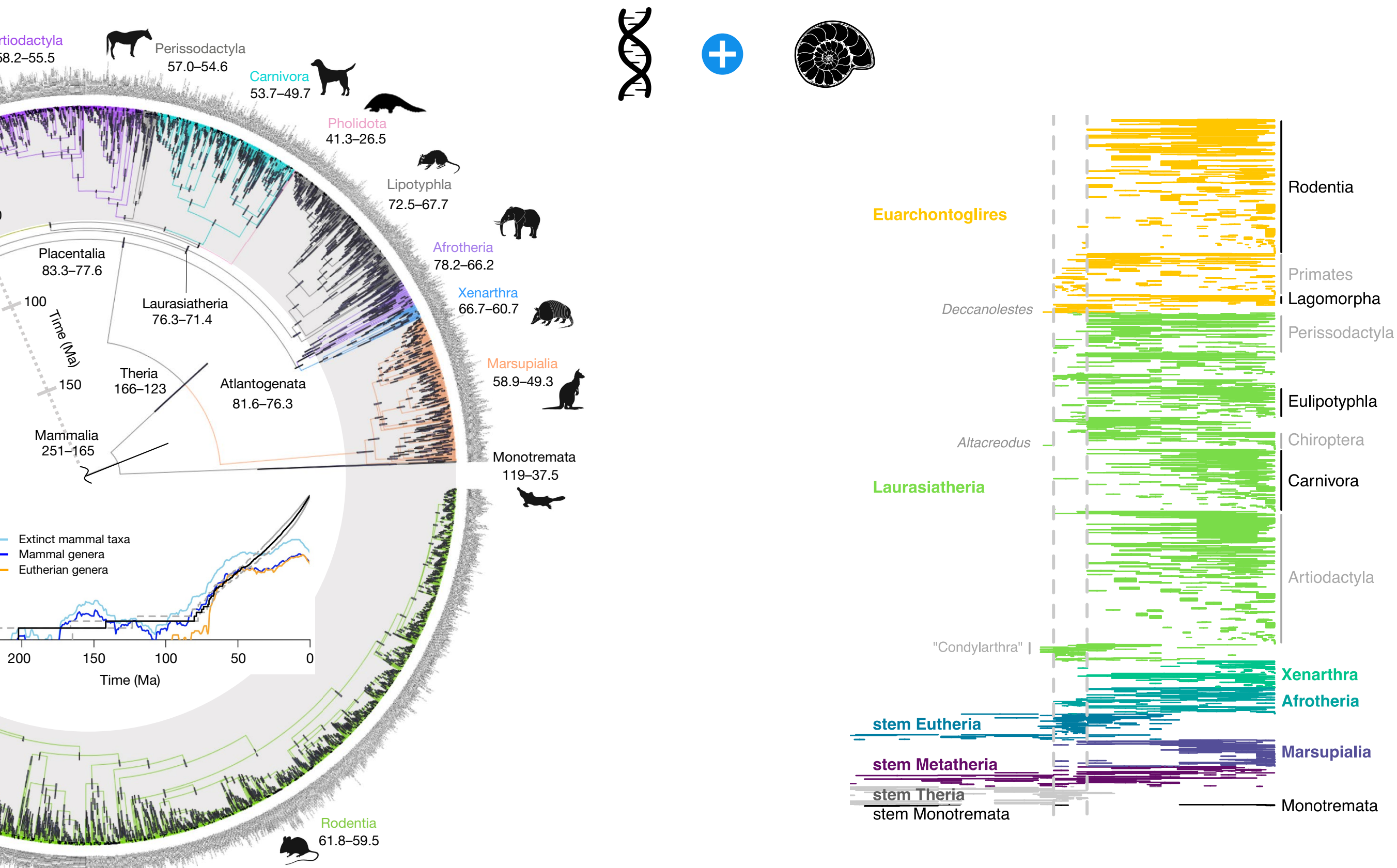
BAYESIAN DATA AUGMENTATION OF **BDD**



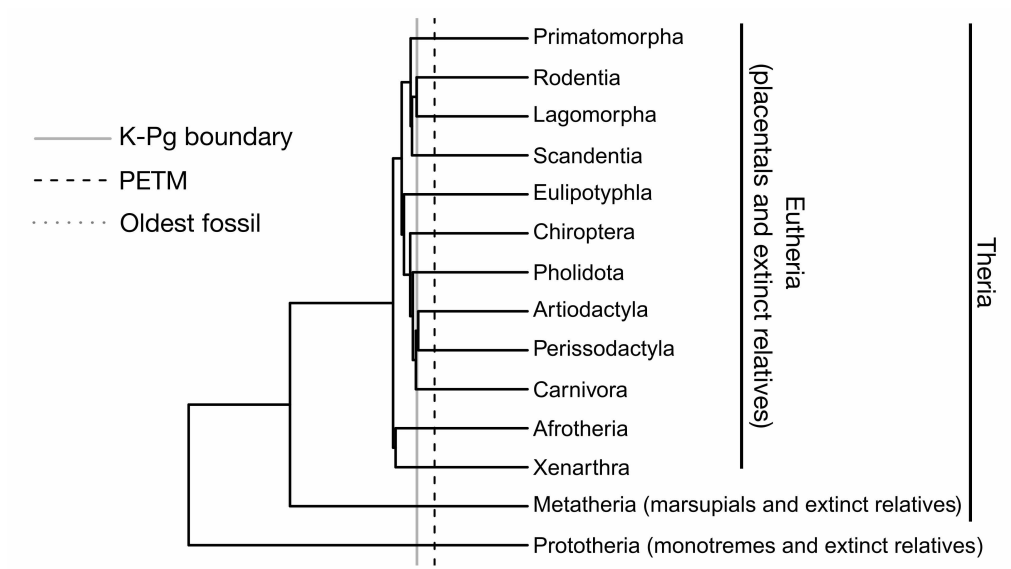
MAMMAL RADIATION



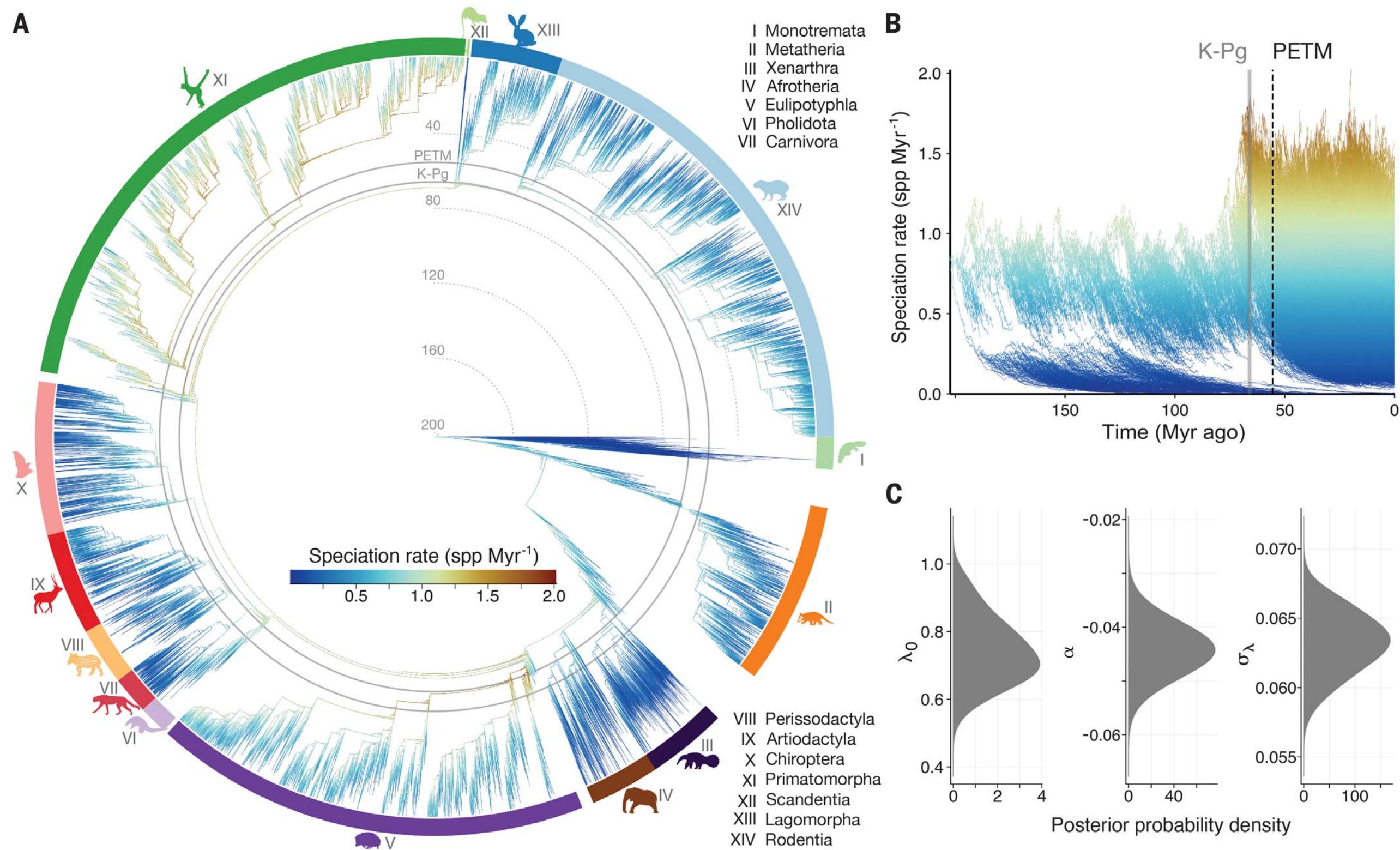
COMBINING PALEO- AND NEONTOLOGICAL INFORMATION



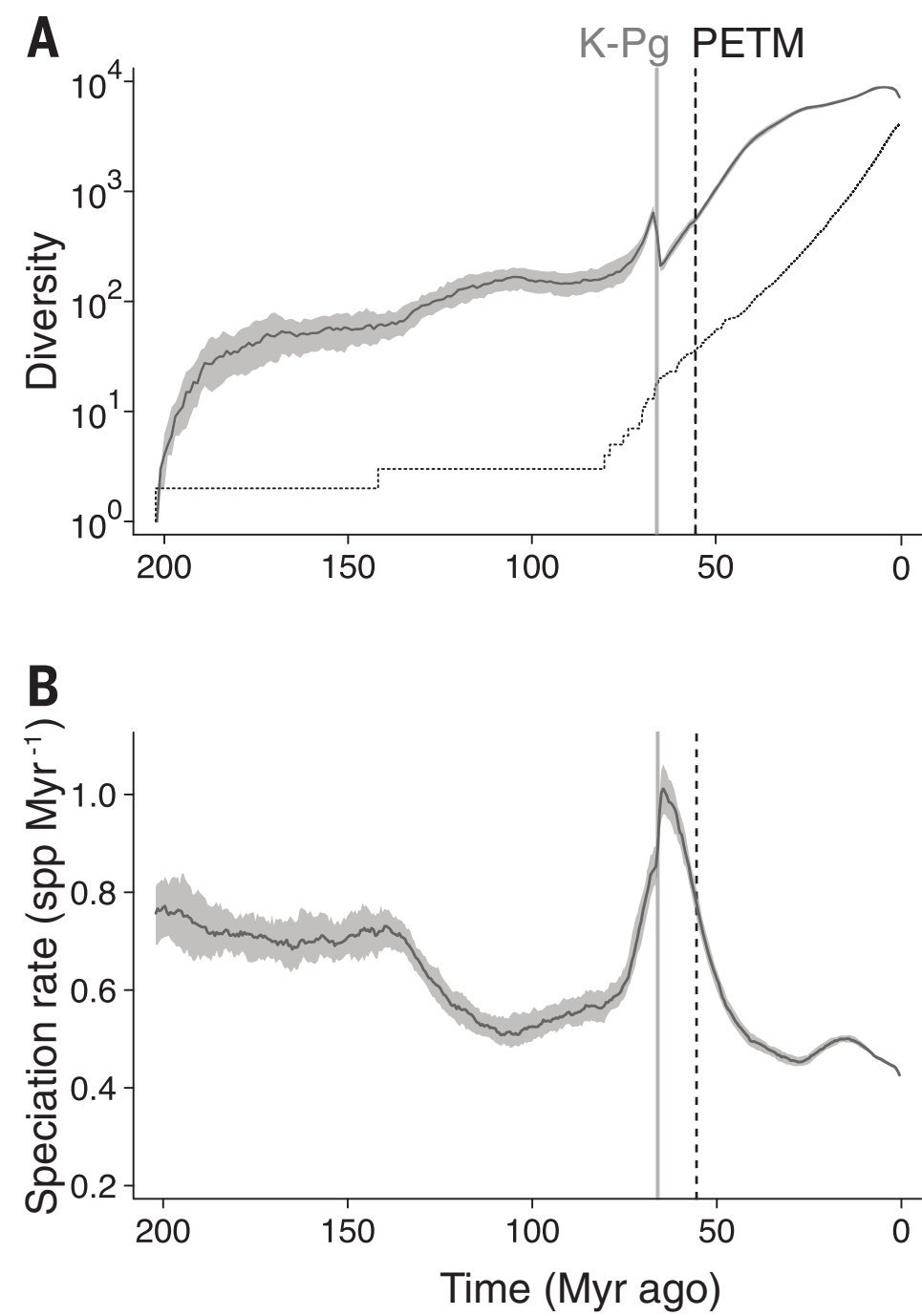
PALEO-EXTINCTION CURVES



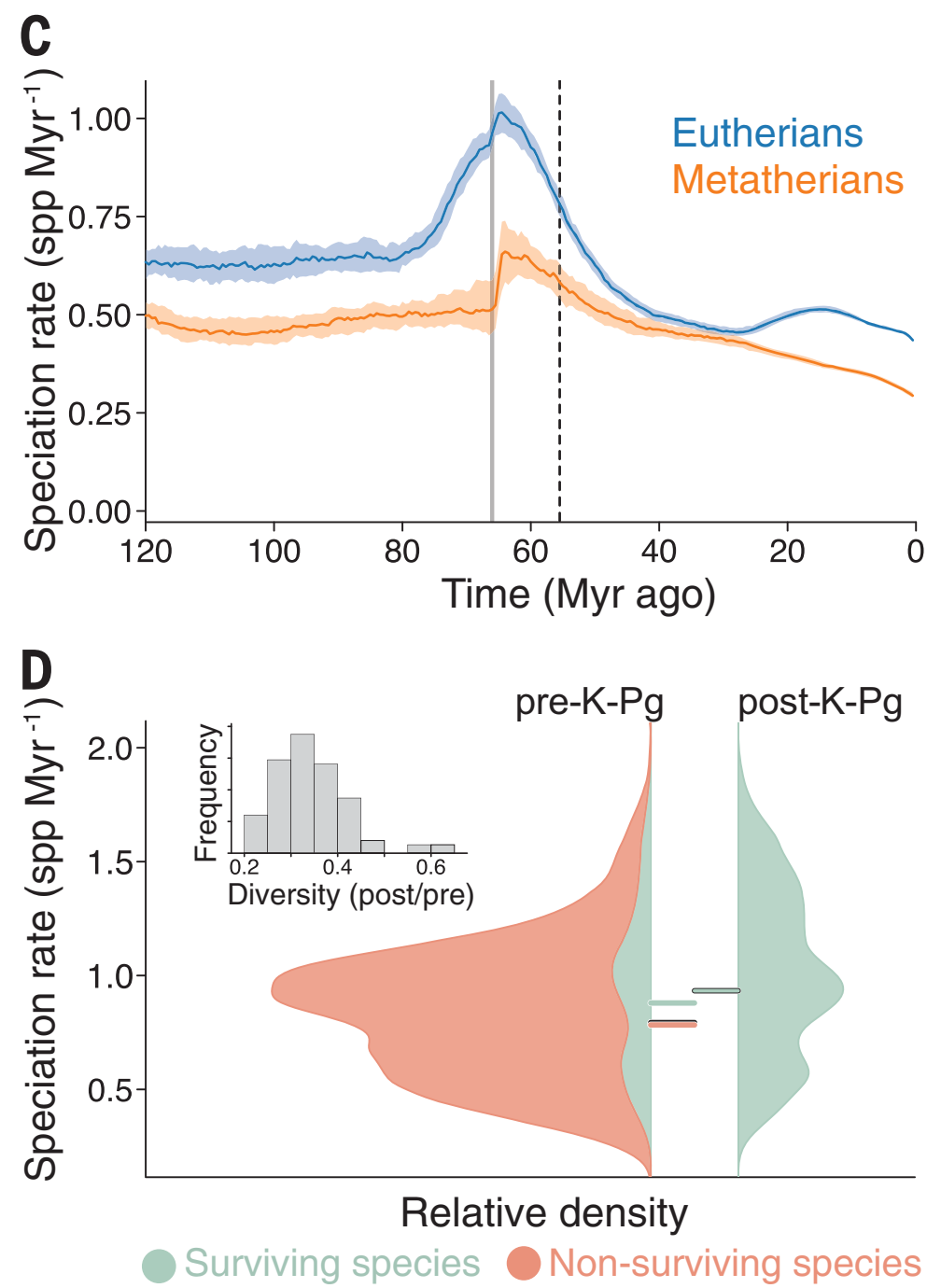
SPECIATION RATE HETEROGENEITY



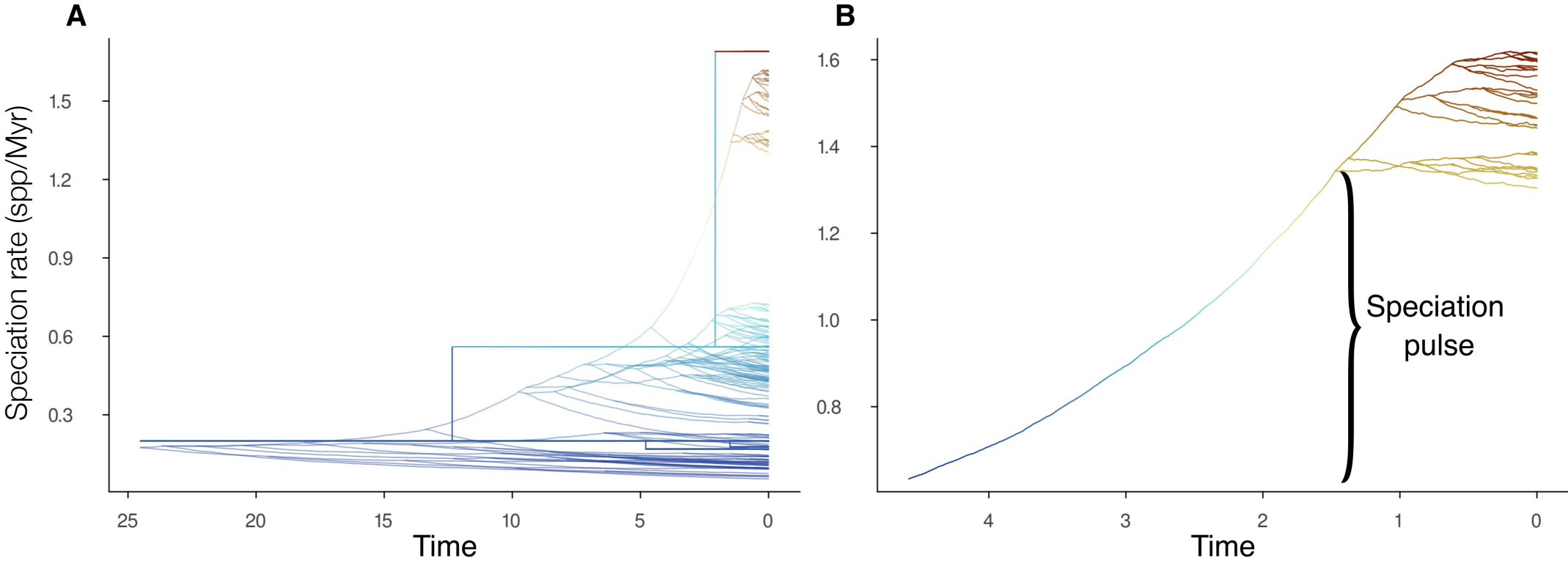
MAMMAL DIVERSITY AND SPECIATION ALONG TIME



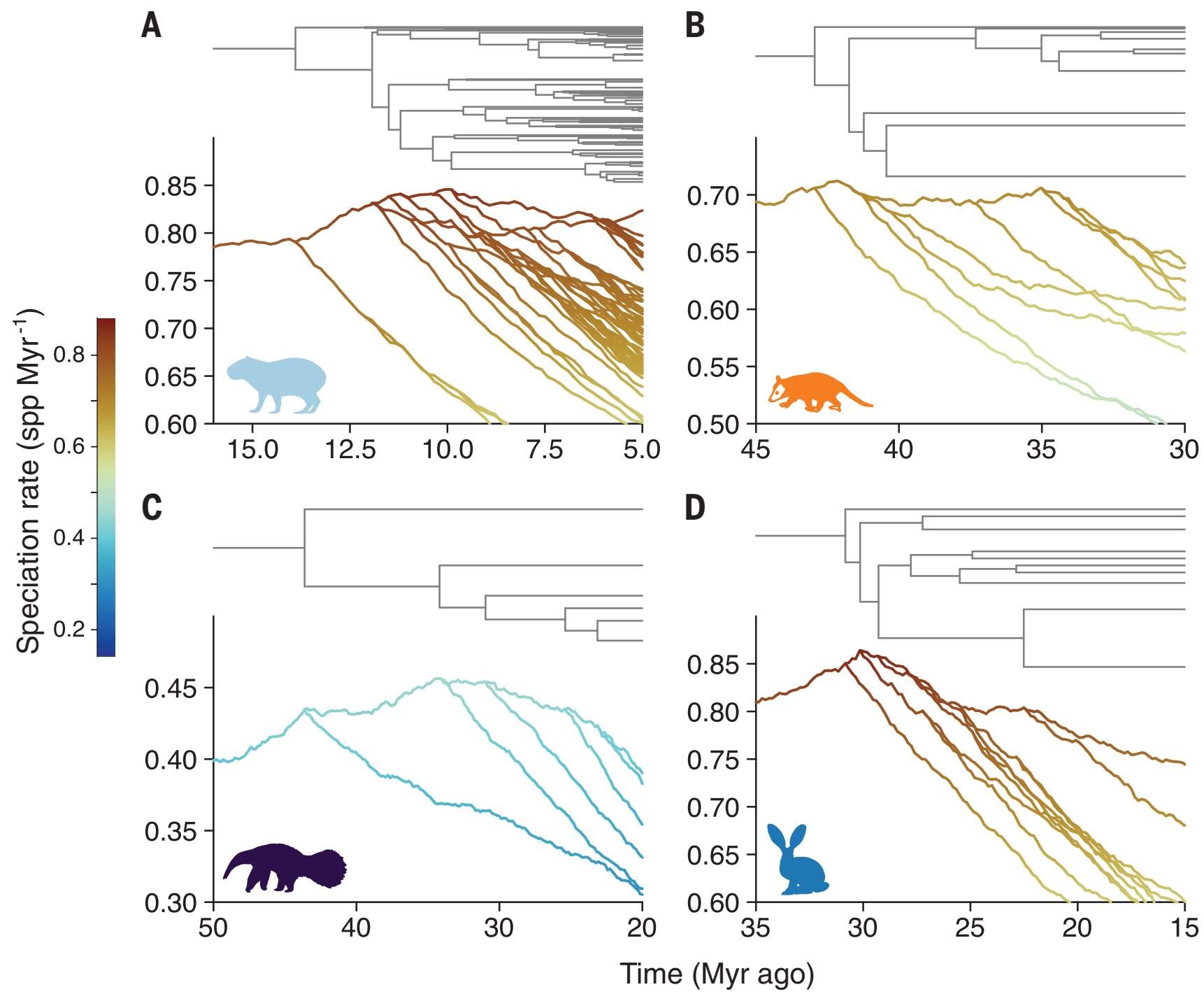
FILTERING OF SLOWLY-SPECIATING LINEAGES



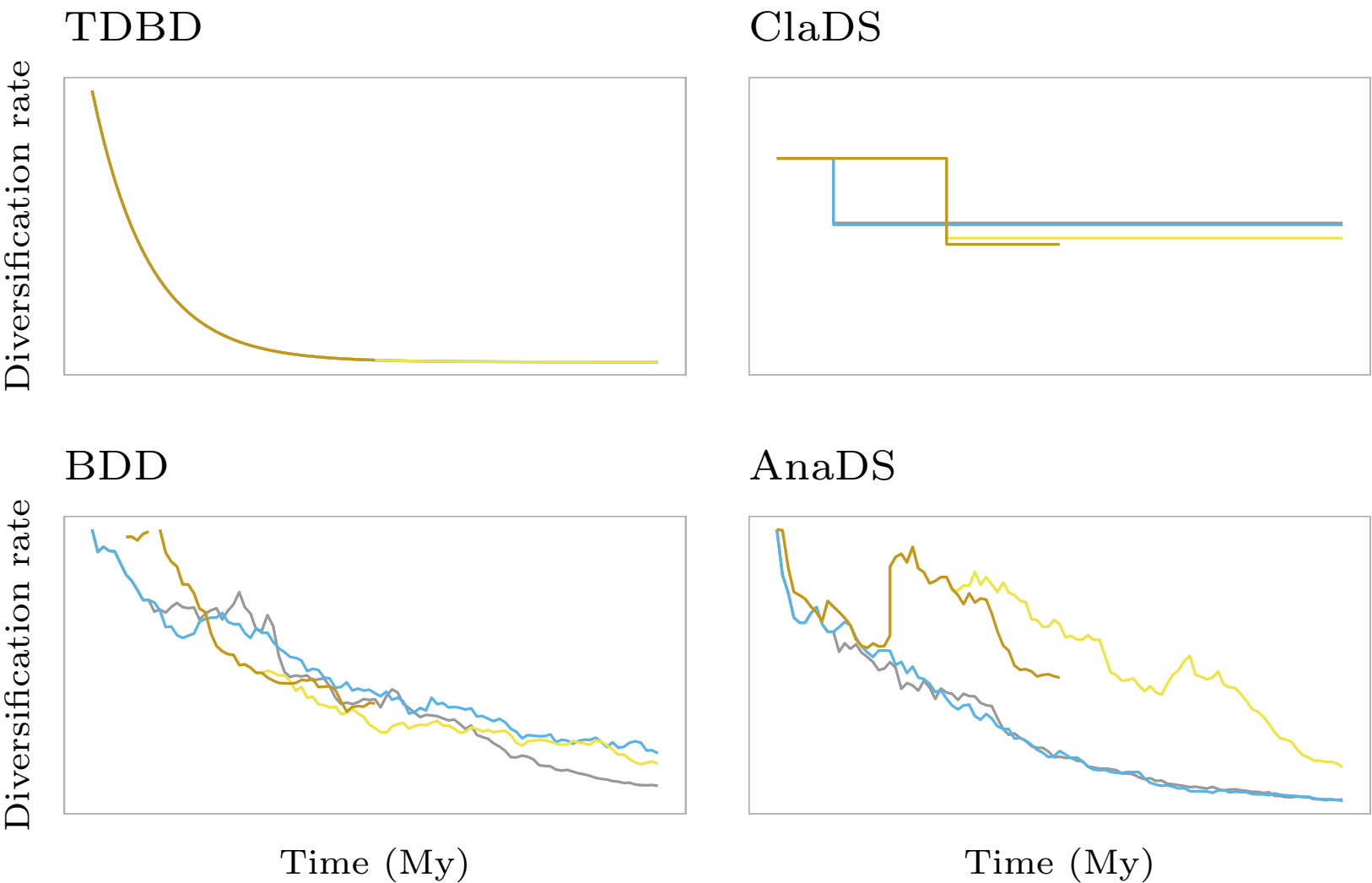
CLADE-LEVEL DYNAMICS?



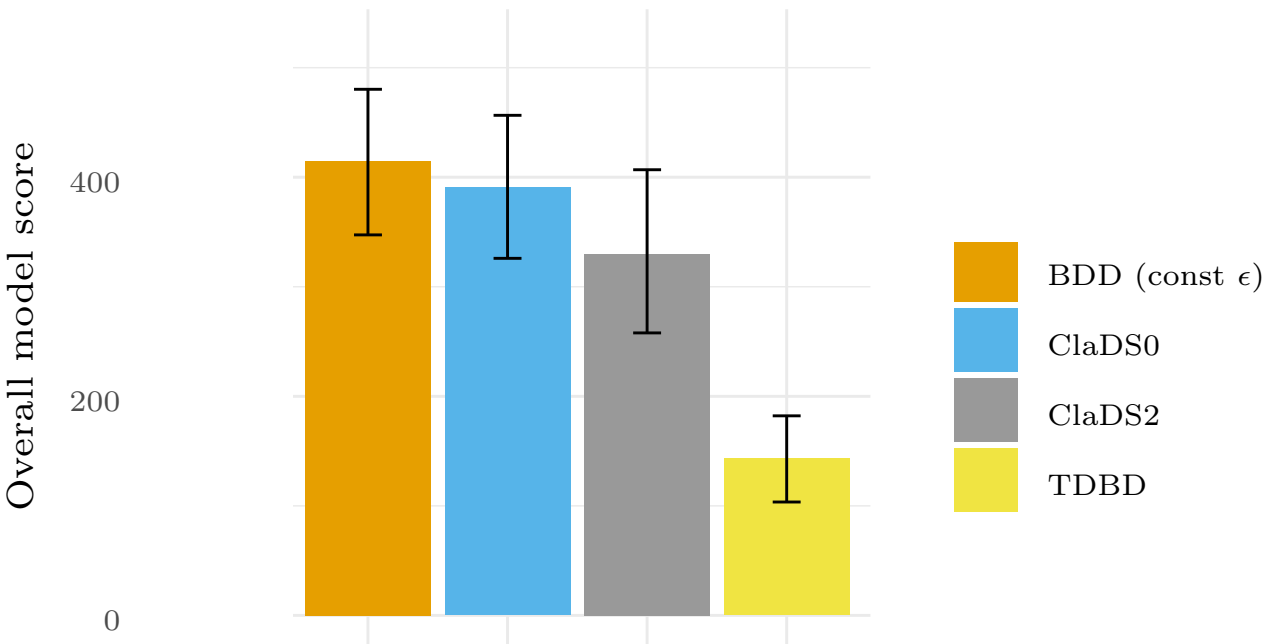
IMBALANCED SPECIATION PULSES



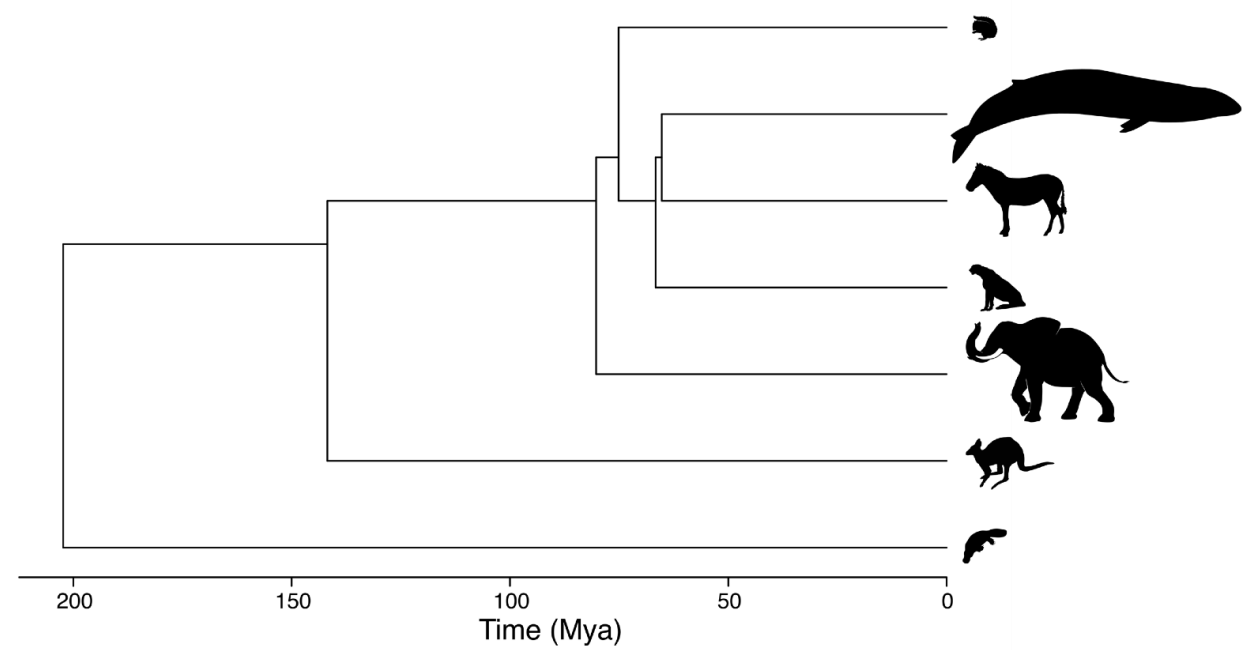
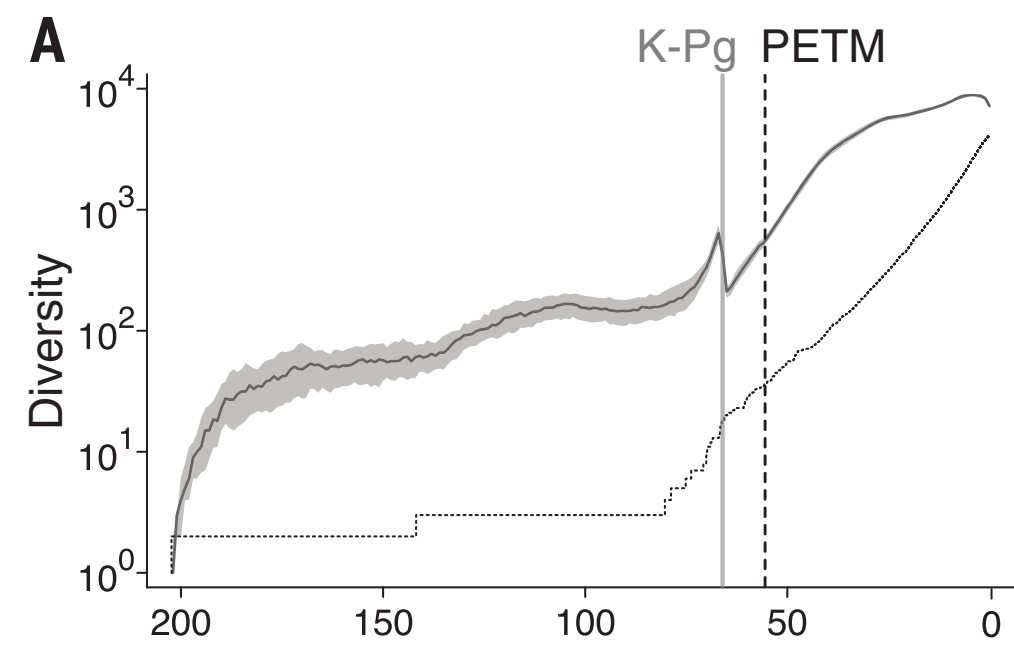
SUPPORT FOR BDD OVER CLADE-WIDE SHIFTS



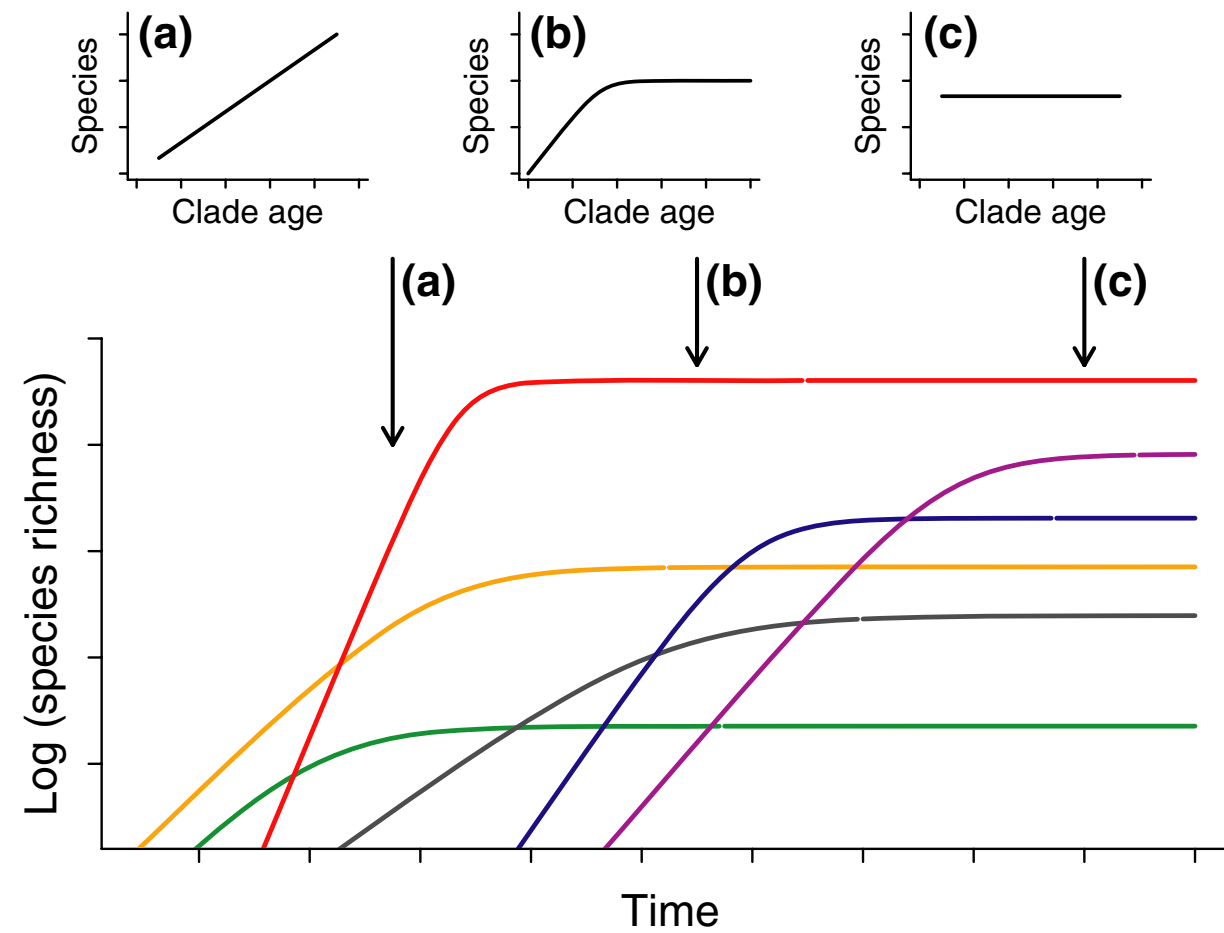
Viktor Senderov



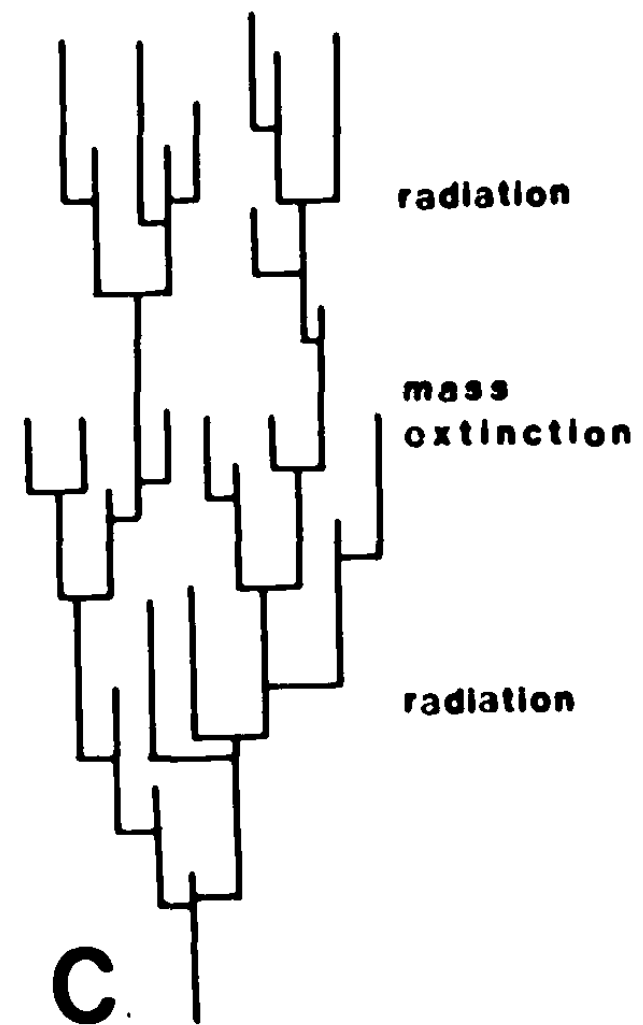
NEONTOLOGICAL TREES



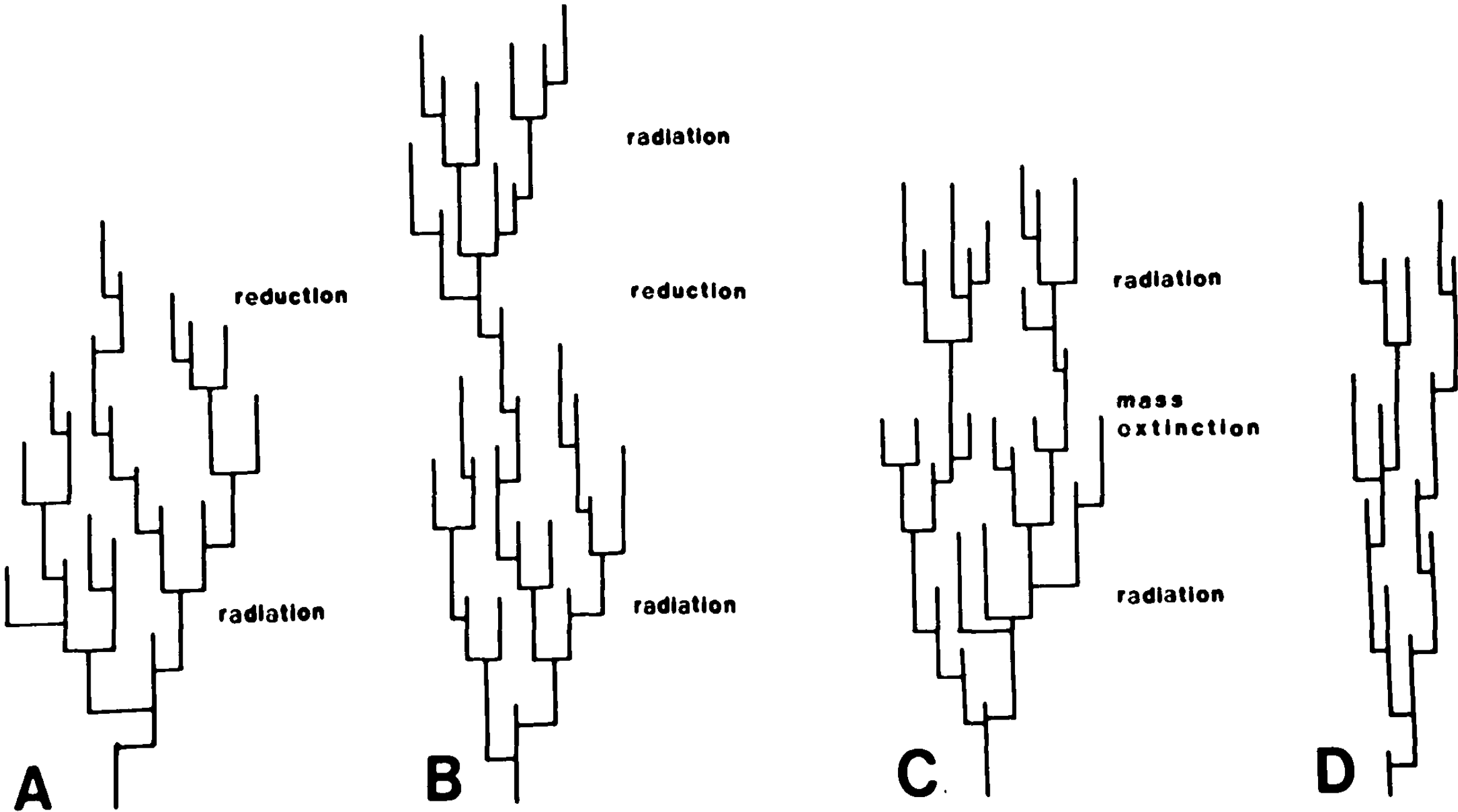
NEONTOLOGICAL BIAS



In **extant-only phylogenies**, diversity seems to always increase or stabilise: used as evidence for '**adaptive radiations**' and '**ecological limits**'.



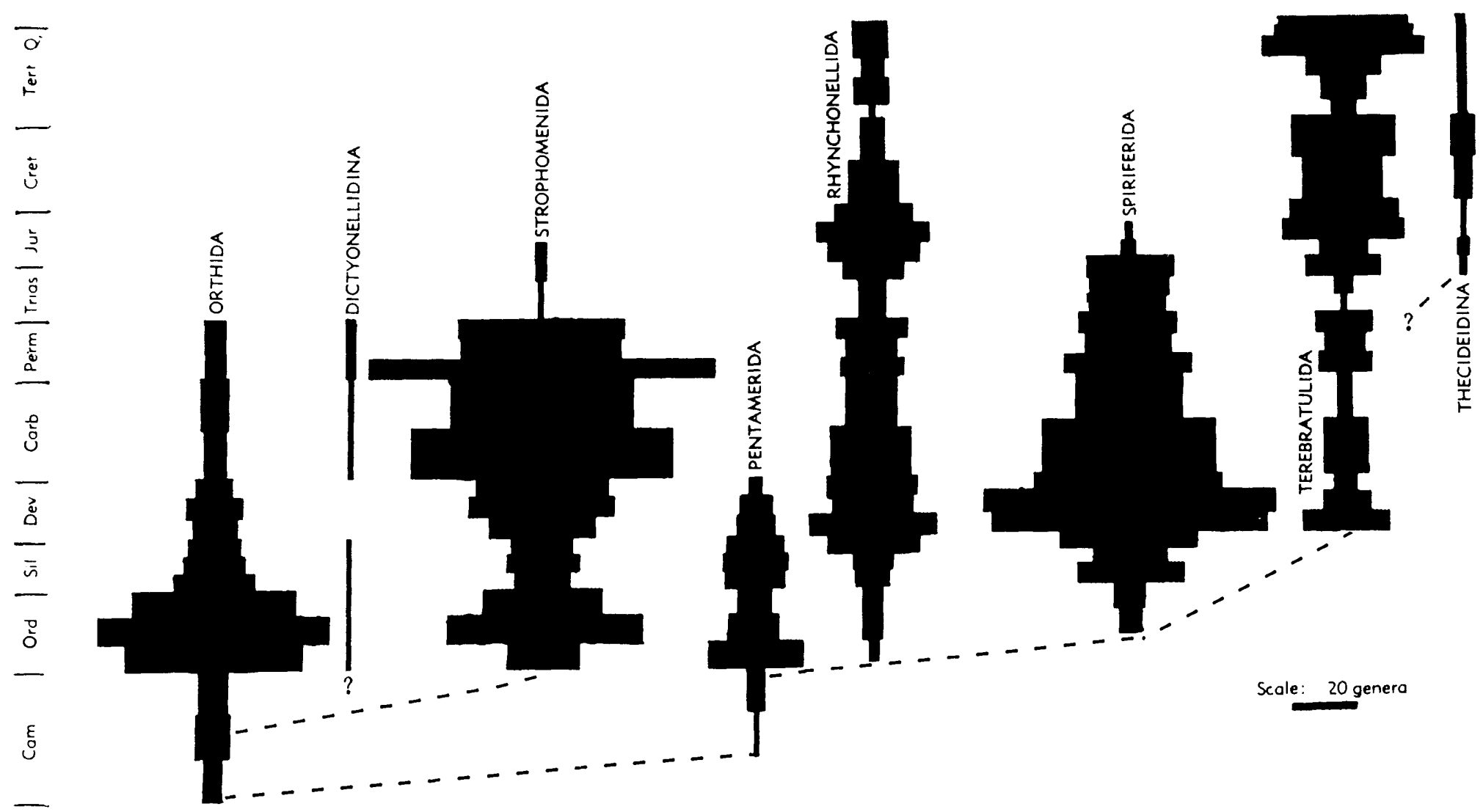
CLADES RISE, DECLINE AND FALL



A MORE COMPREHENSIVE UNDERSTANDING
OF THE ORIGIN AND MAINTENANCE OF BIODIVERSITY:
THE RISE, DECLINE AND FALL OF CLADES

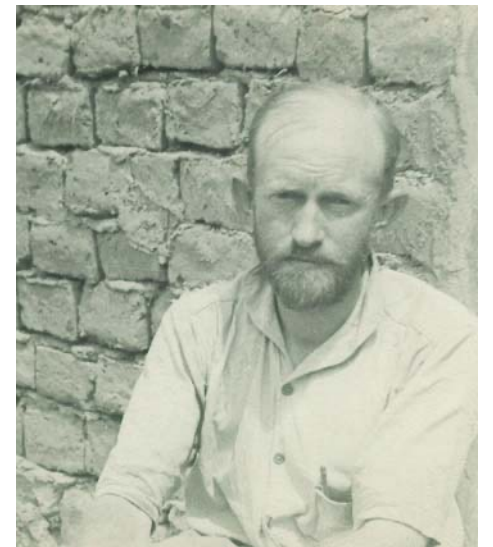
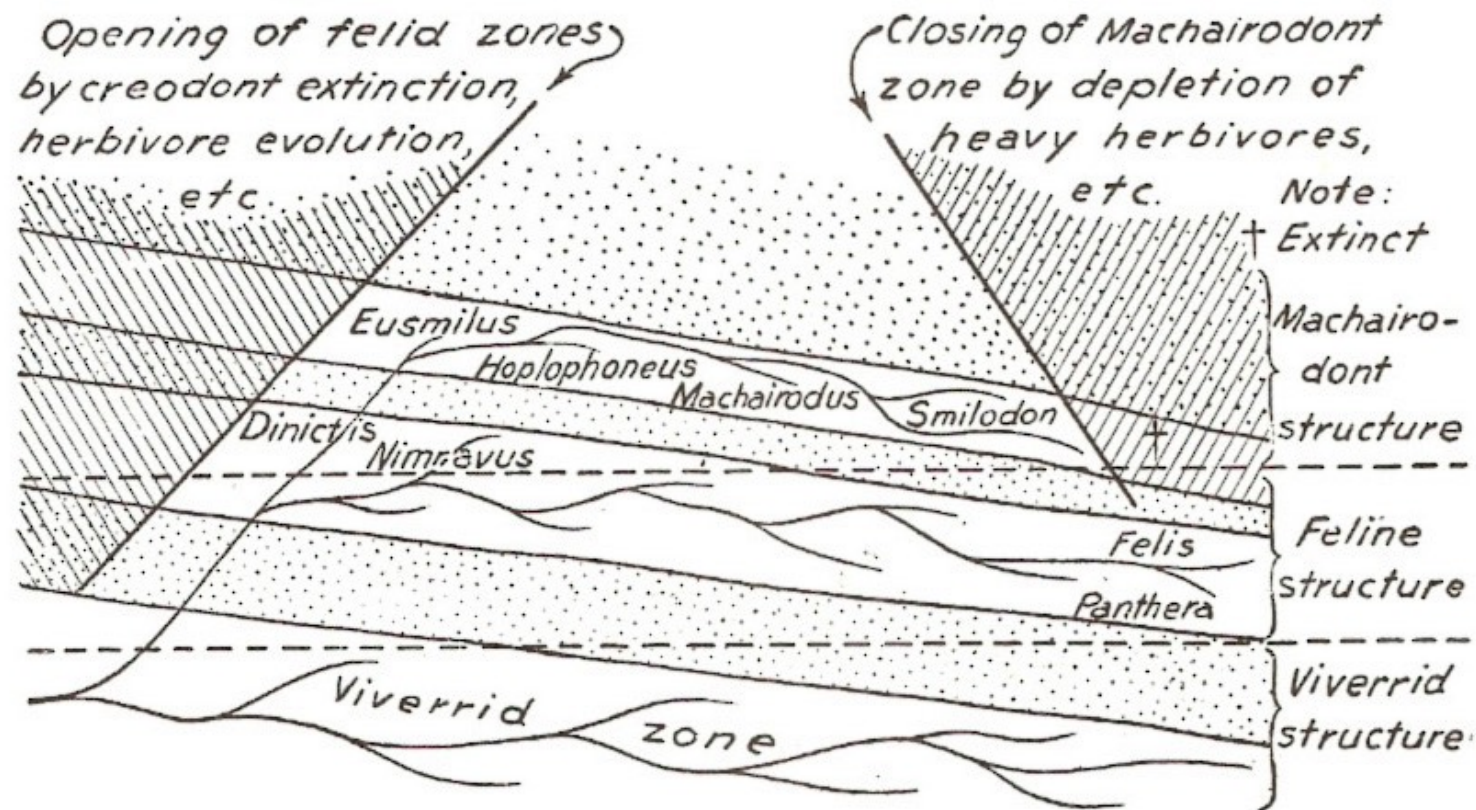
Photograph by Sebastião Salgado

DIVERSITY TRAJECTORIES: RISE, DECLINE AND FALL

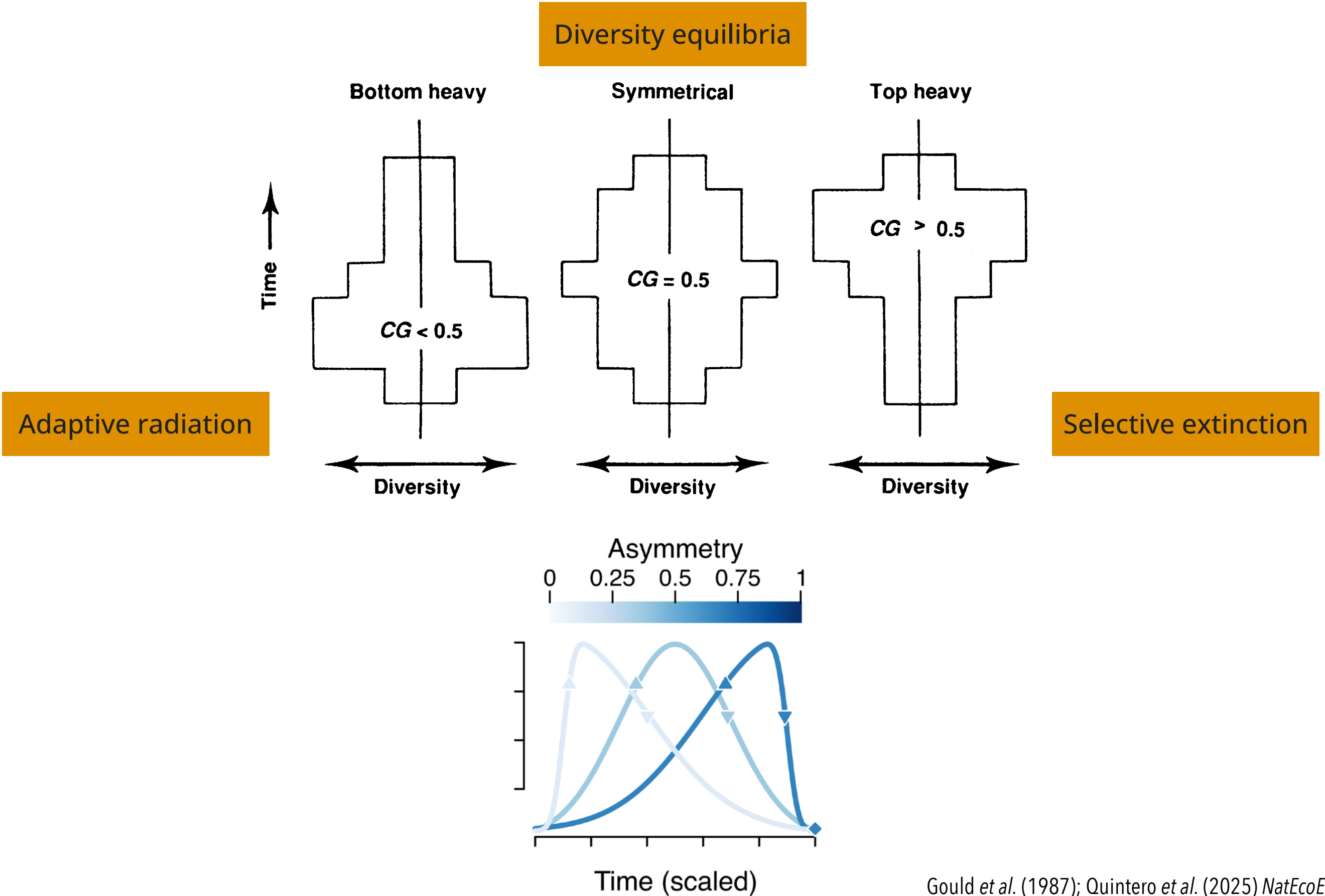


CLADE-LEVEL PROCESSES

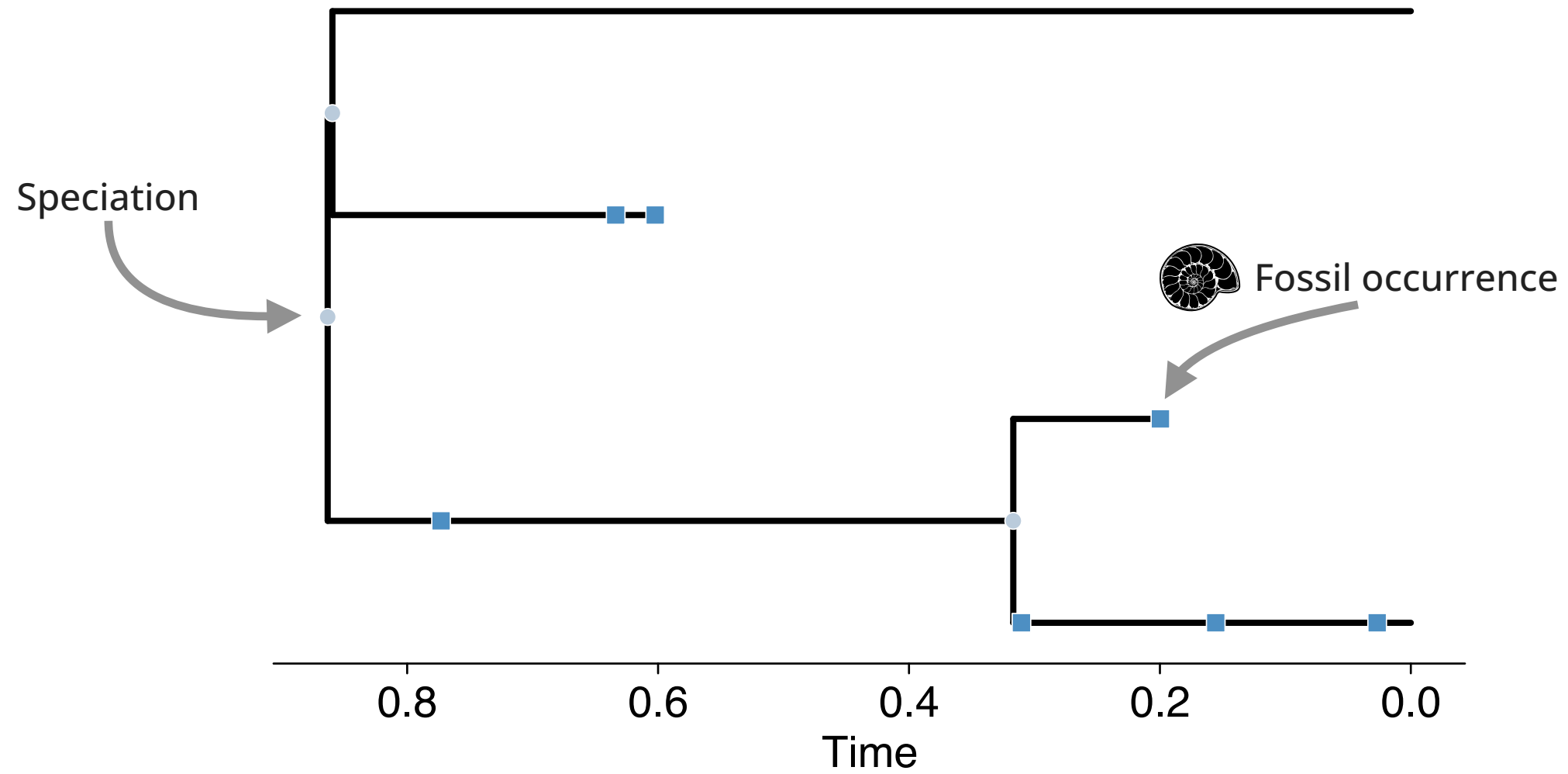
Diversity stagnates and decreases through **filling (diversity-dependence)** or **closing of 'adaptive zones'**.



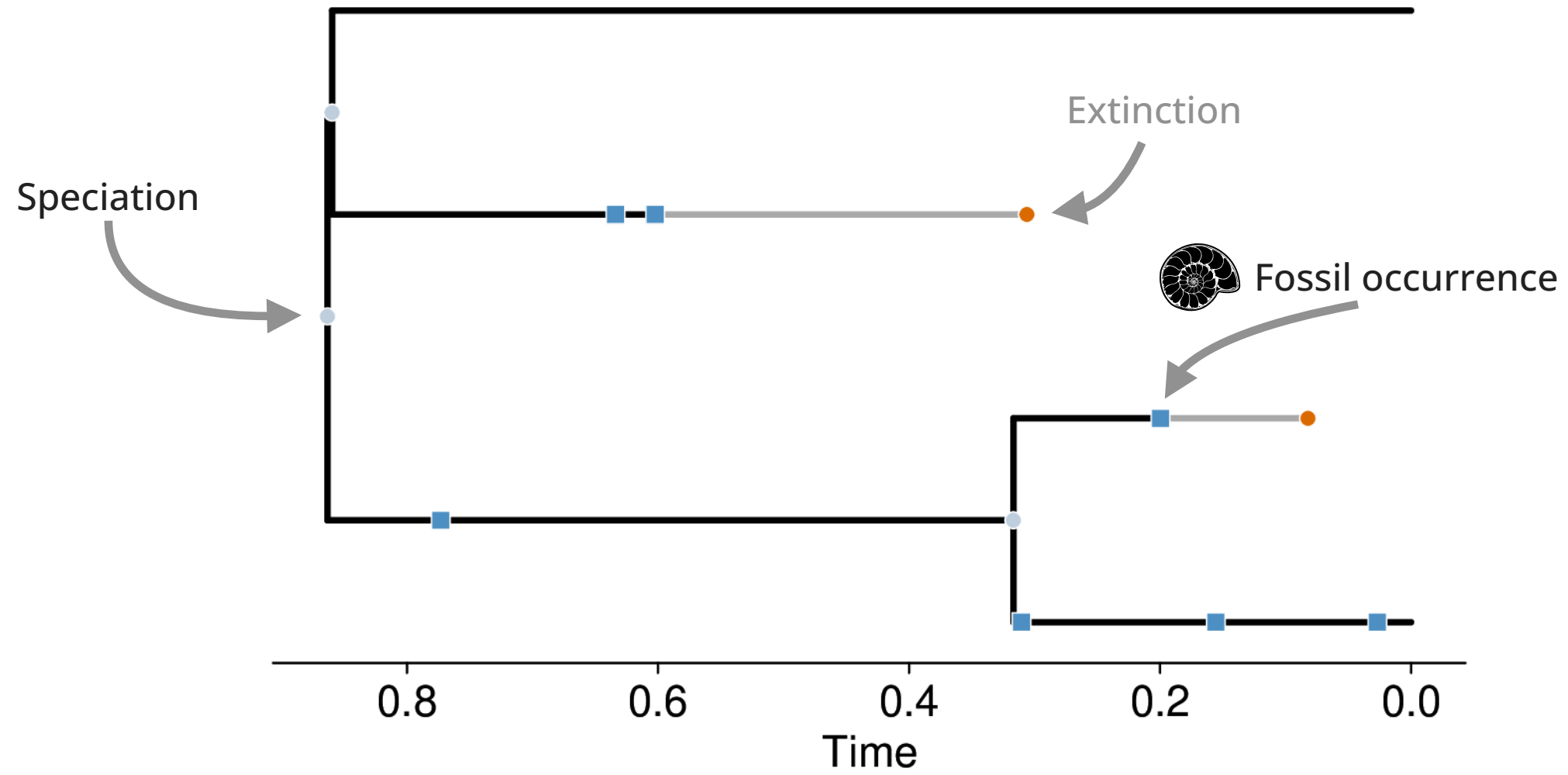
CLADE-LEVEL PROCESSES?



THE FOSSILISED BIRTH-DEATH (FBD) PROCESS

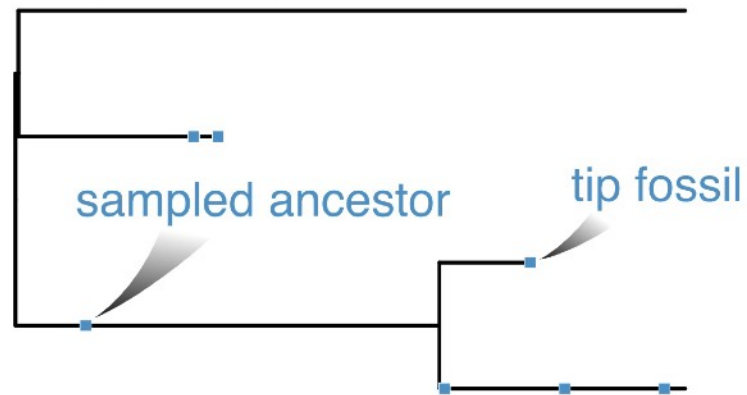


THE FOSSILISED BIRTH-DEATH (FBD) PROCESS

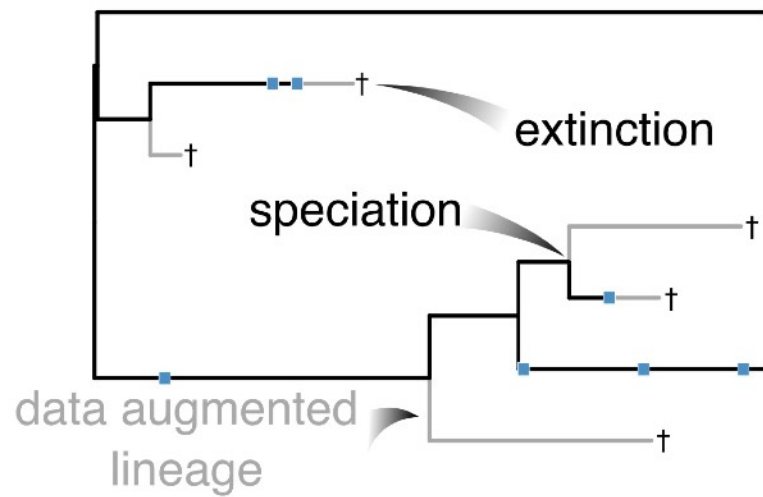


FOSSILISED BIRTH DEATH DIFFUSION

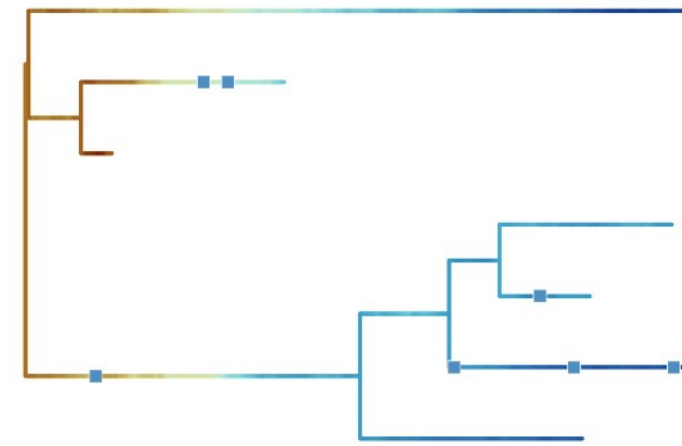
A Empirical (observed) FBD tree



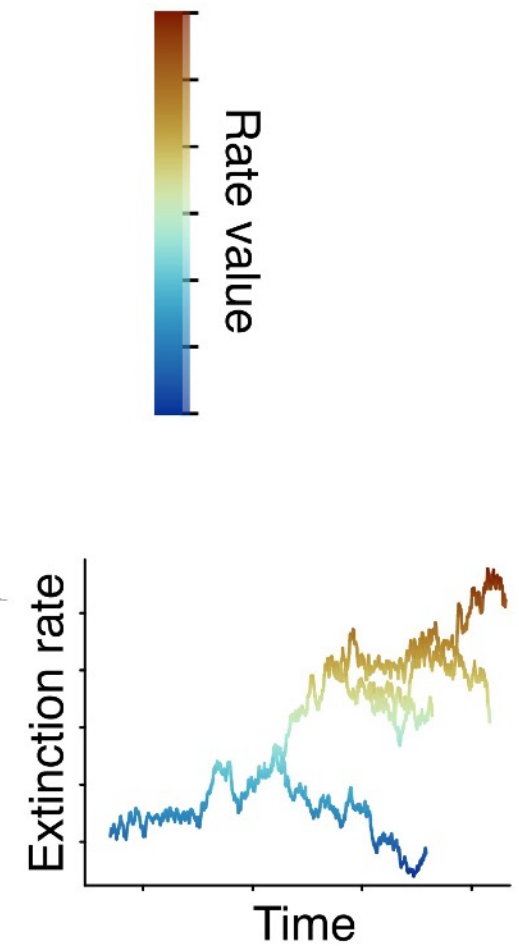
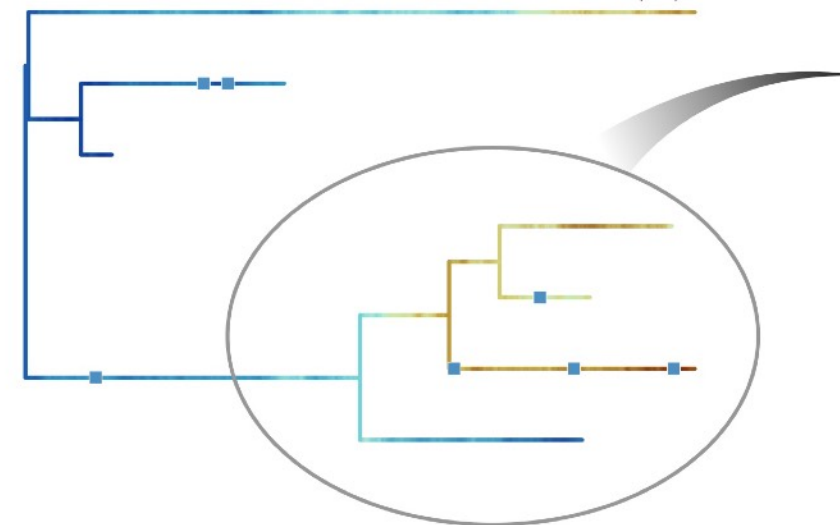
B One complete (data augmented) FBDD tree



C Latent speciation rate $\lambda(t)$



D Latent extinction rate $\mu(t)$

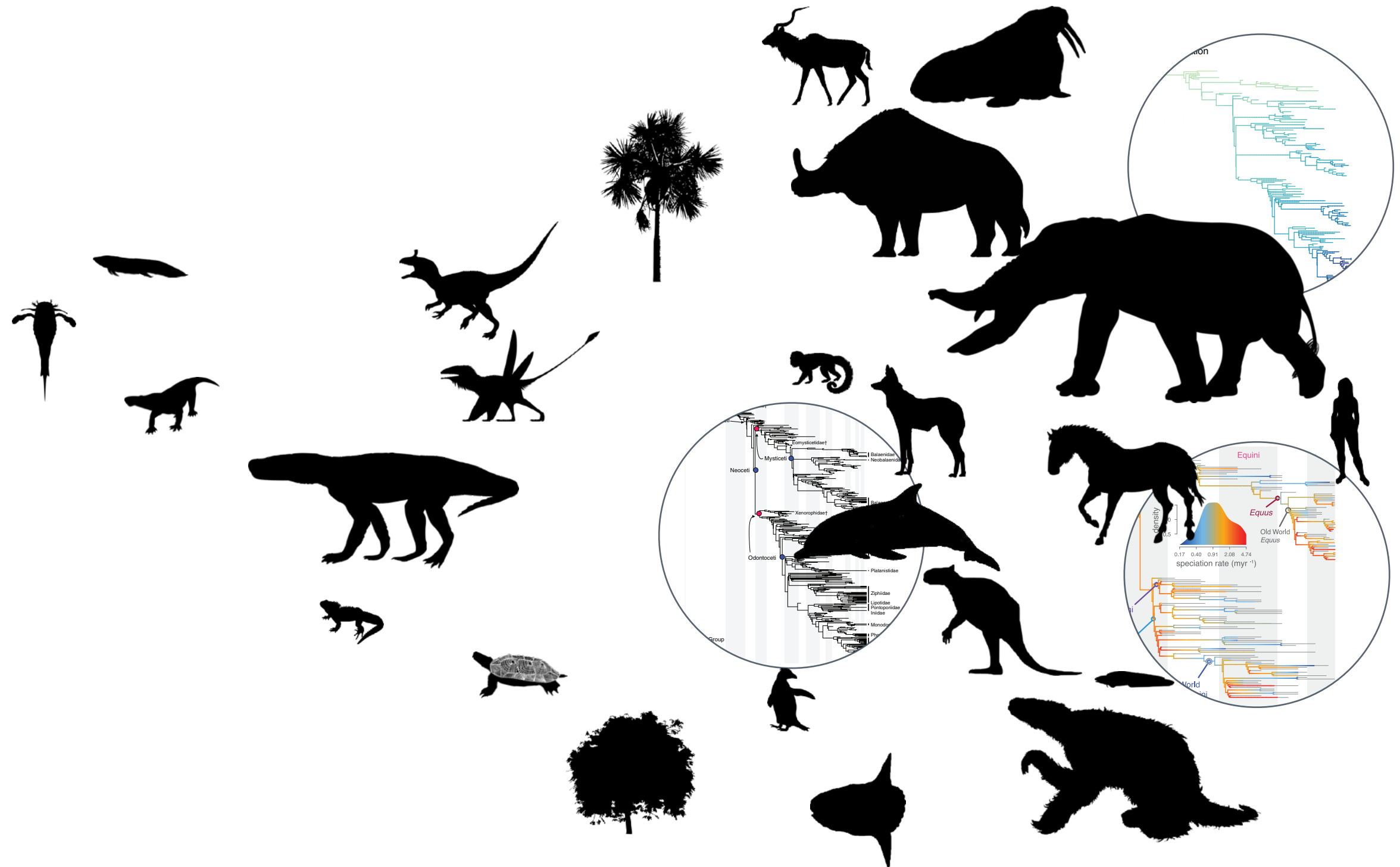


$$d\ln(\lambda_i(t)) = \alpha_\lambda dt + \sigma_\lambda dW(t)$$

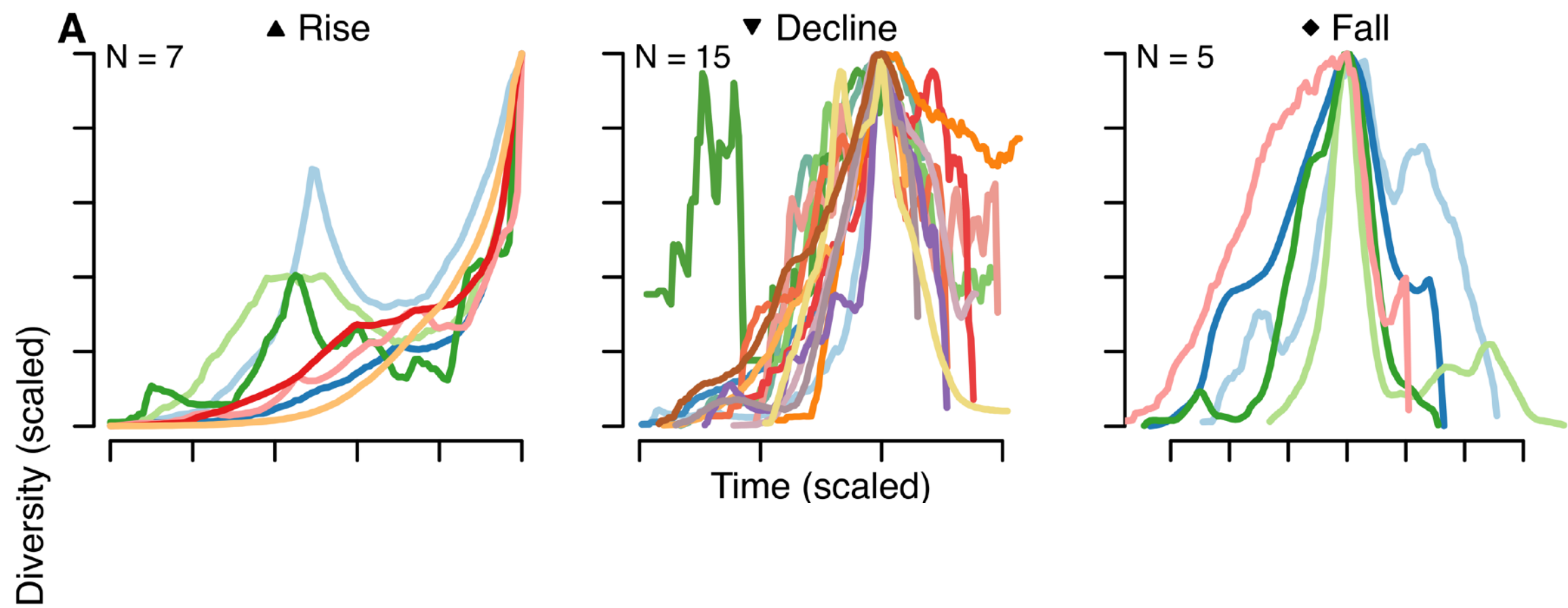
$$d\ln(\mu_i(t)) = \alpha_\mu dt + \sigma_\mu dW(t)$$

TAXONOMIC COVERAGE

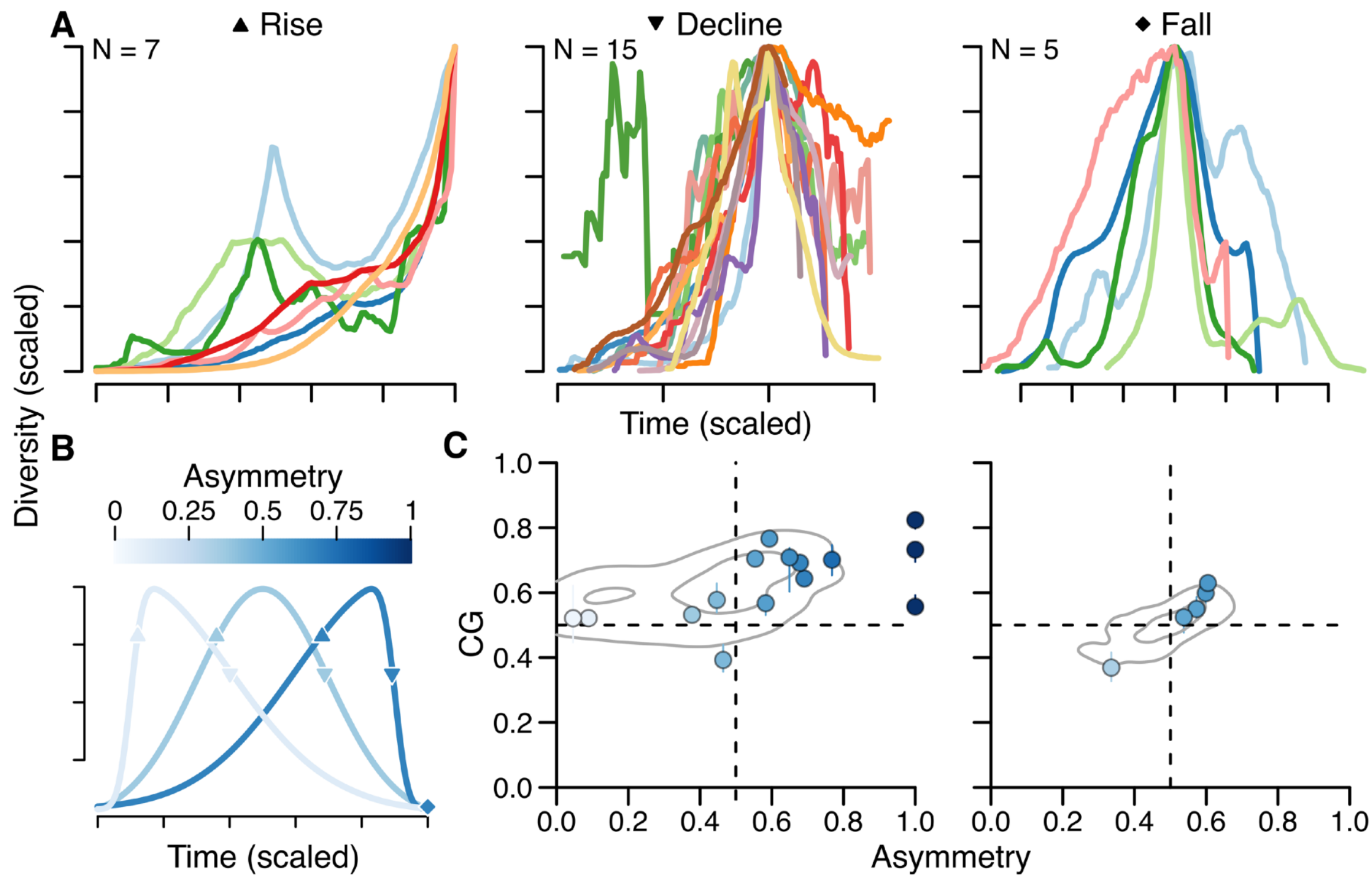
27 groups encompassing ~5500 extinct and ~3000 extant species.



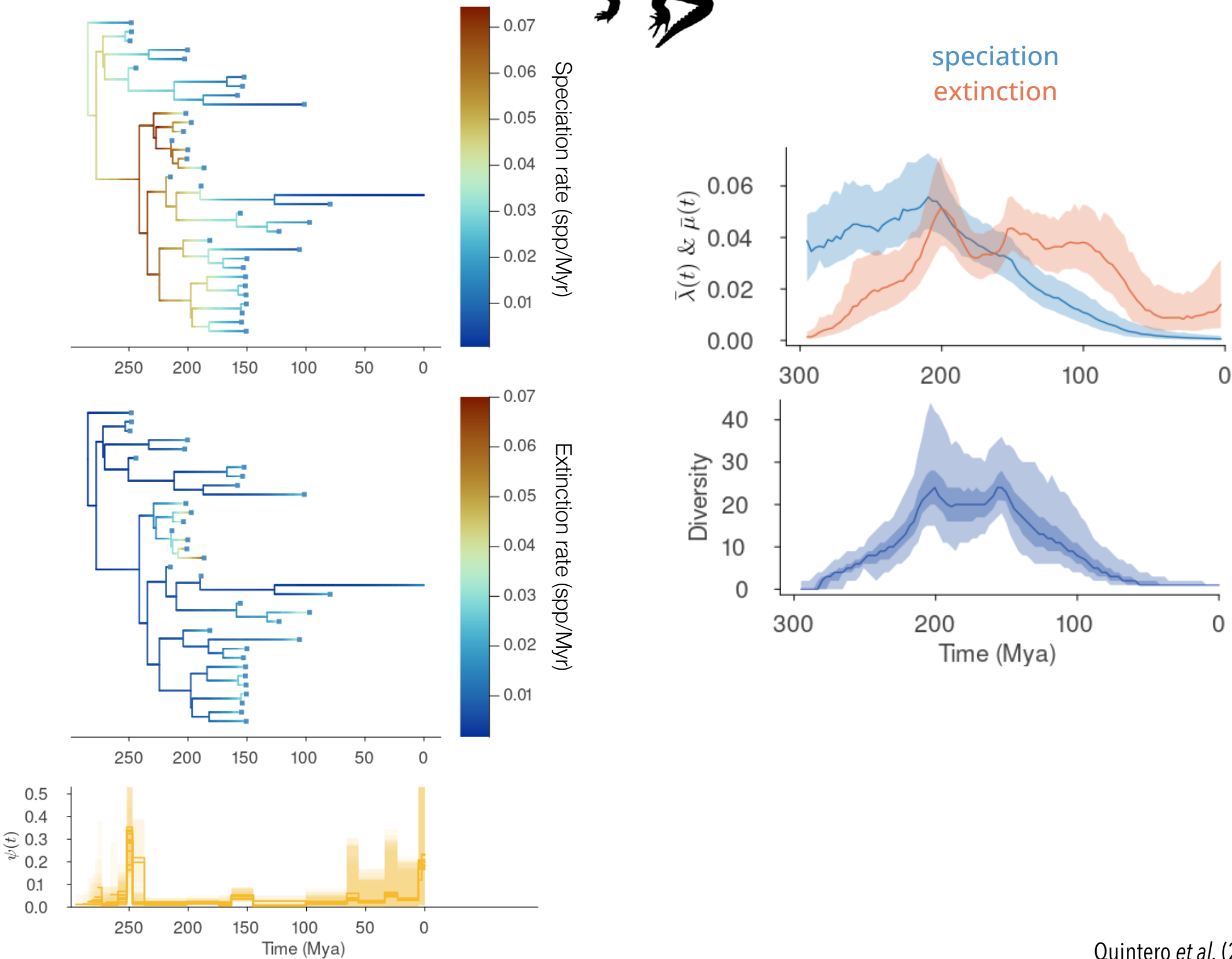
DIVERSITY CURVES



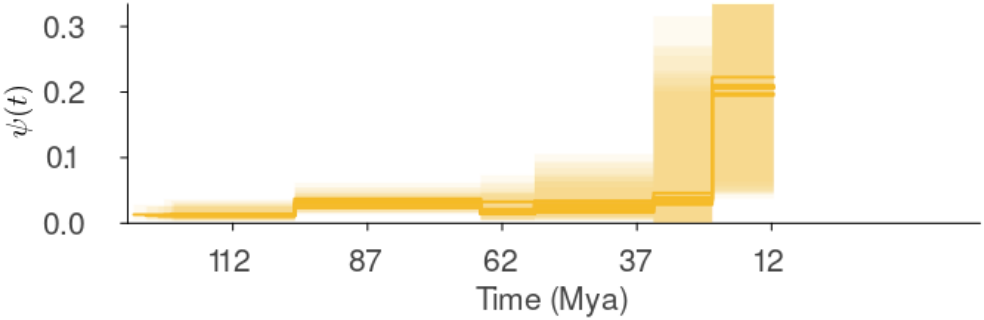
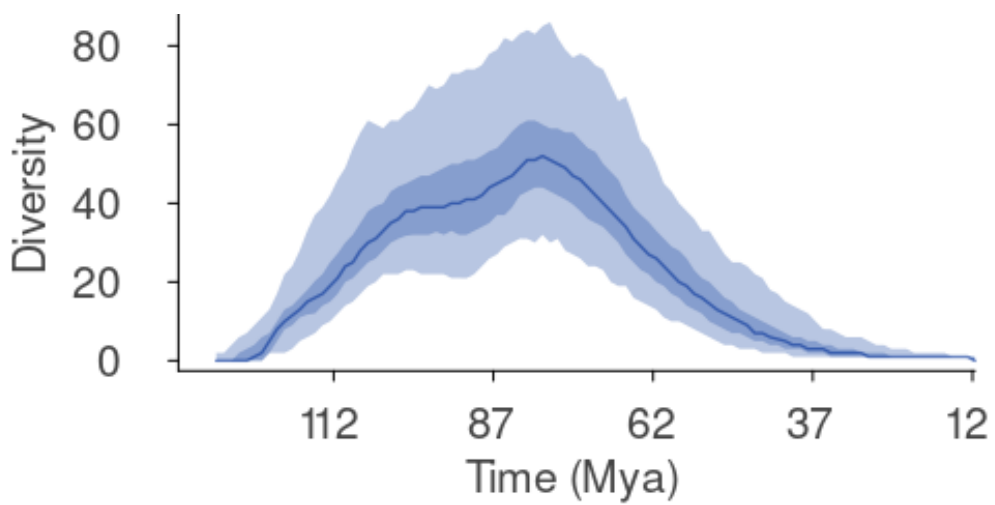
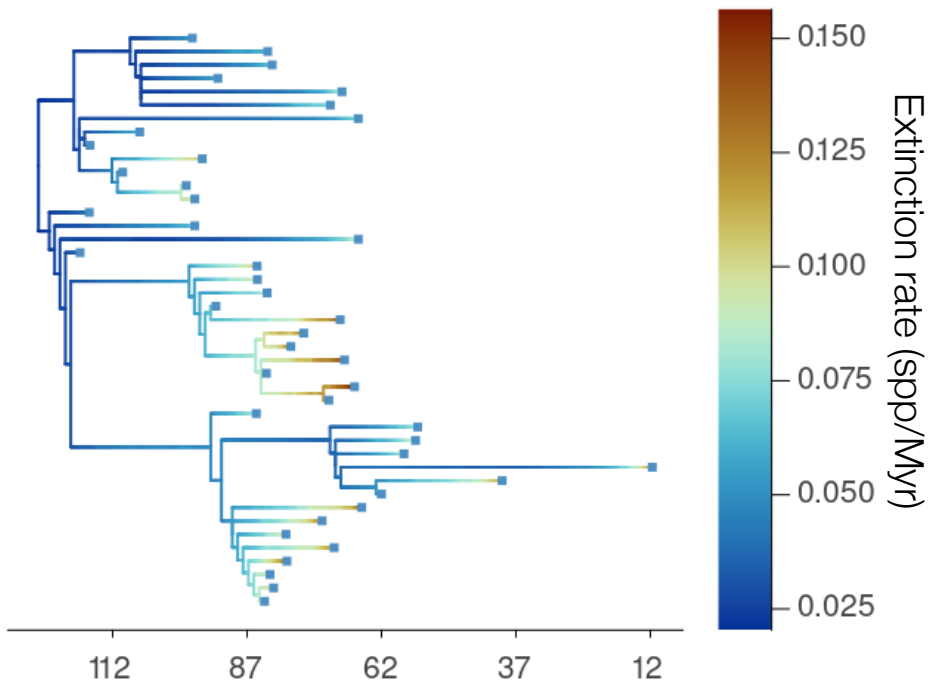
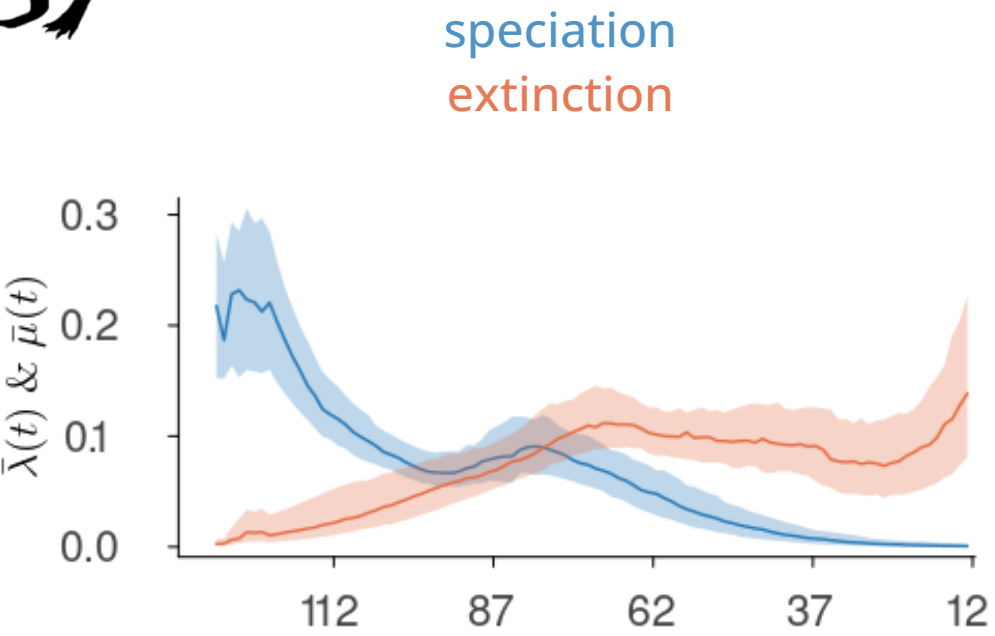
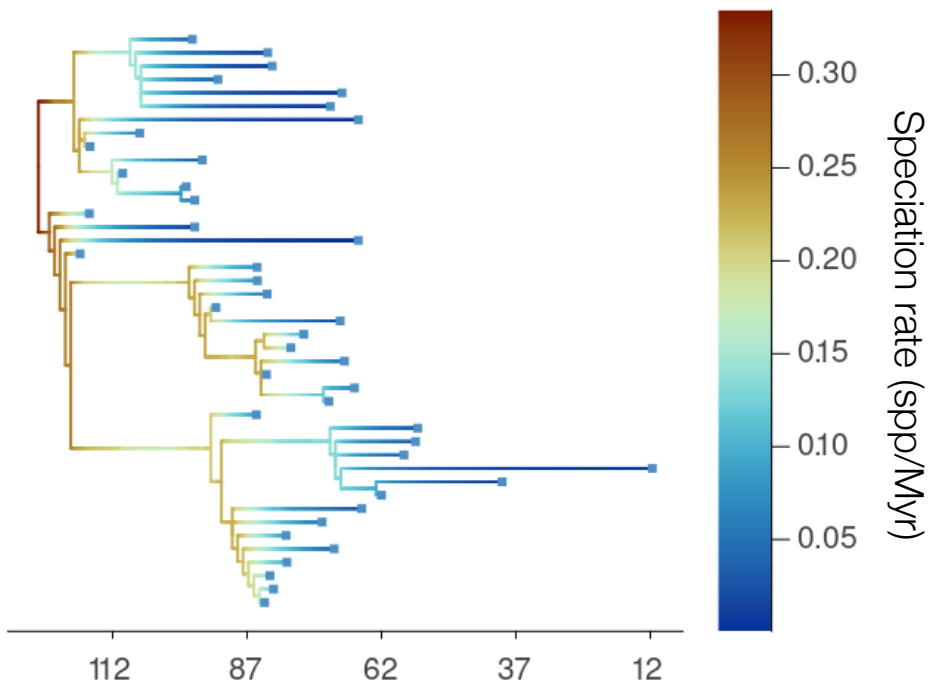
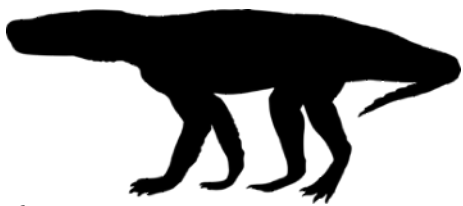
DIVERSITY CURVES



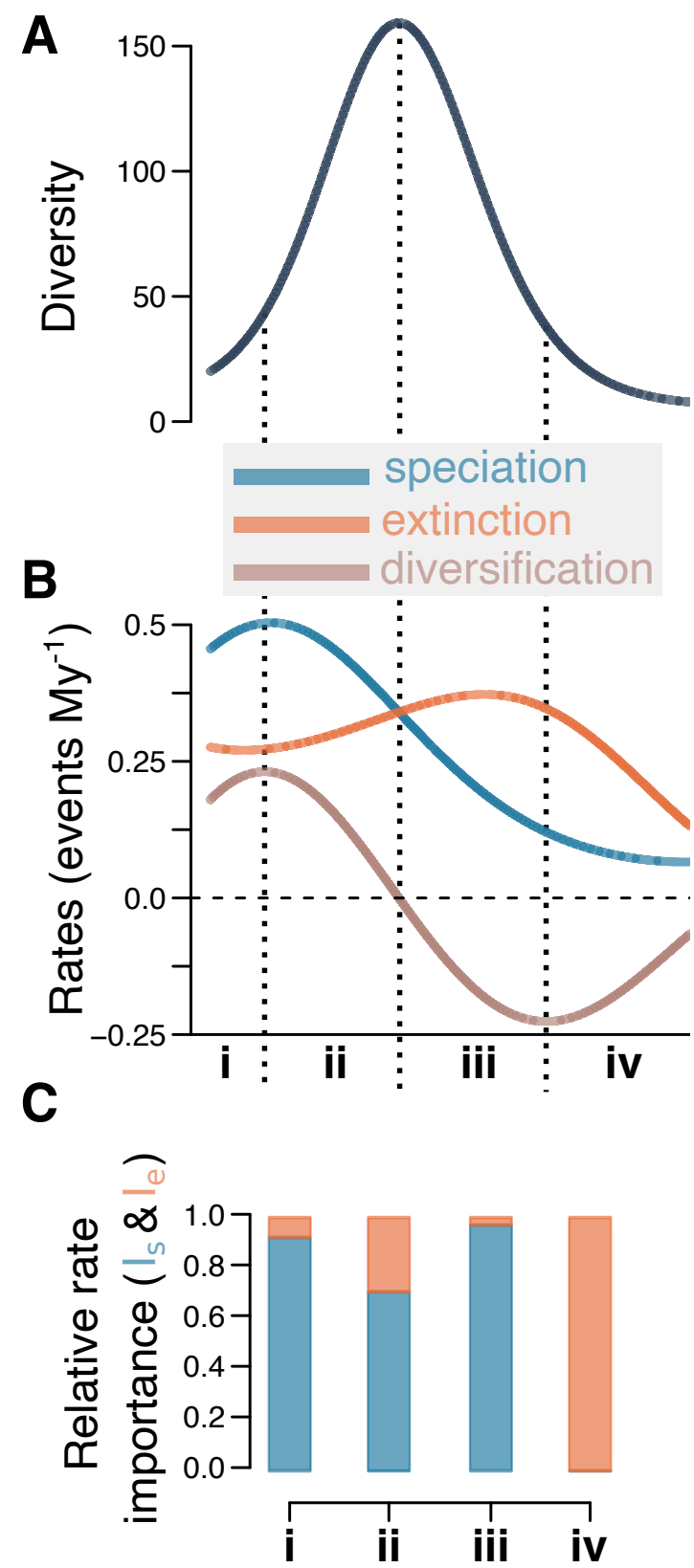
UNDERLYING DIVERSIFICATION: TUATARA



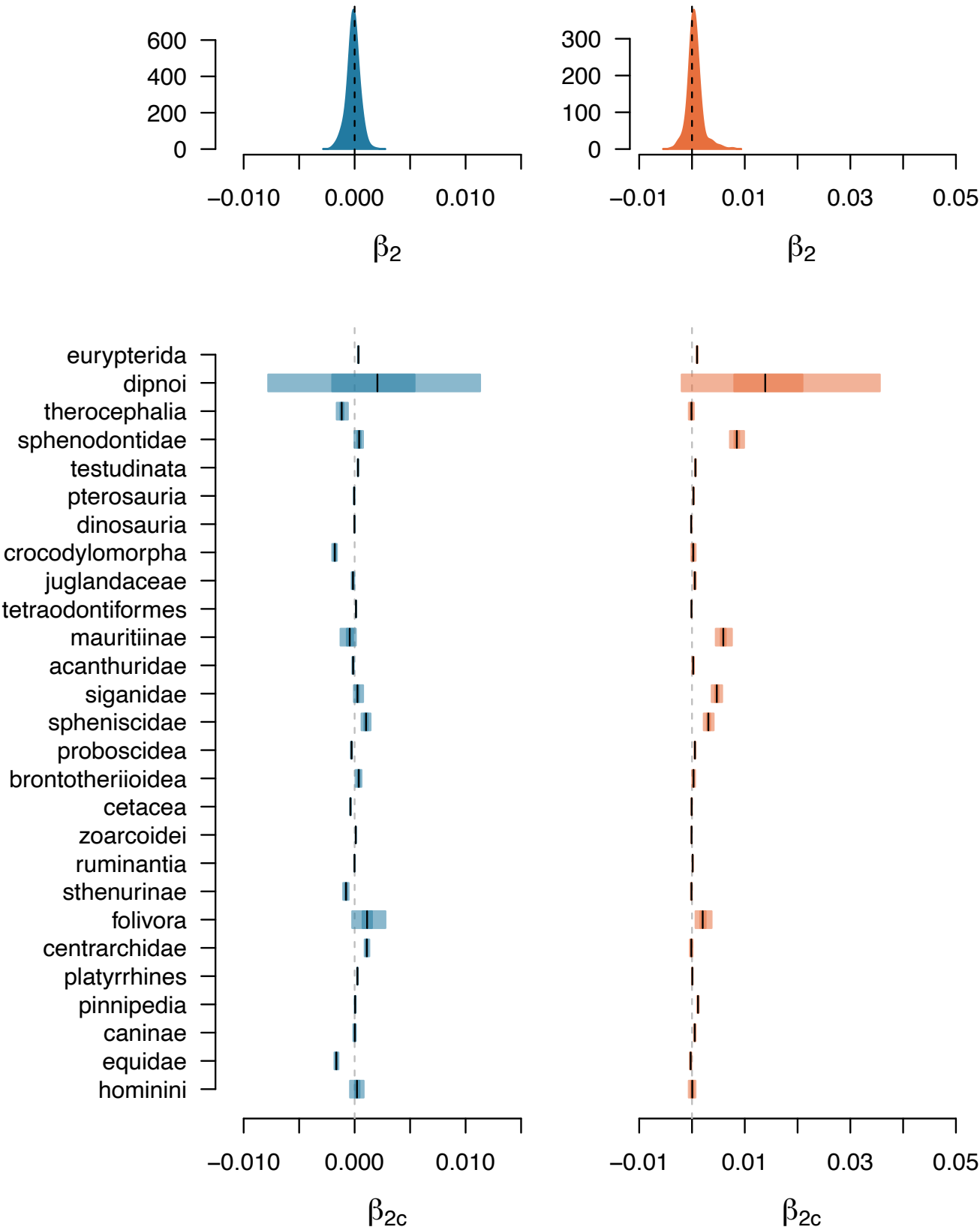
UNDERLYING DIVERSIFICATION: NOTOSUCHIA



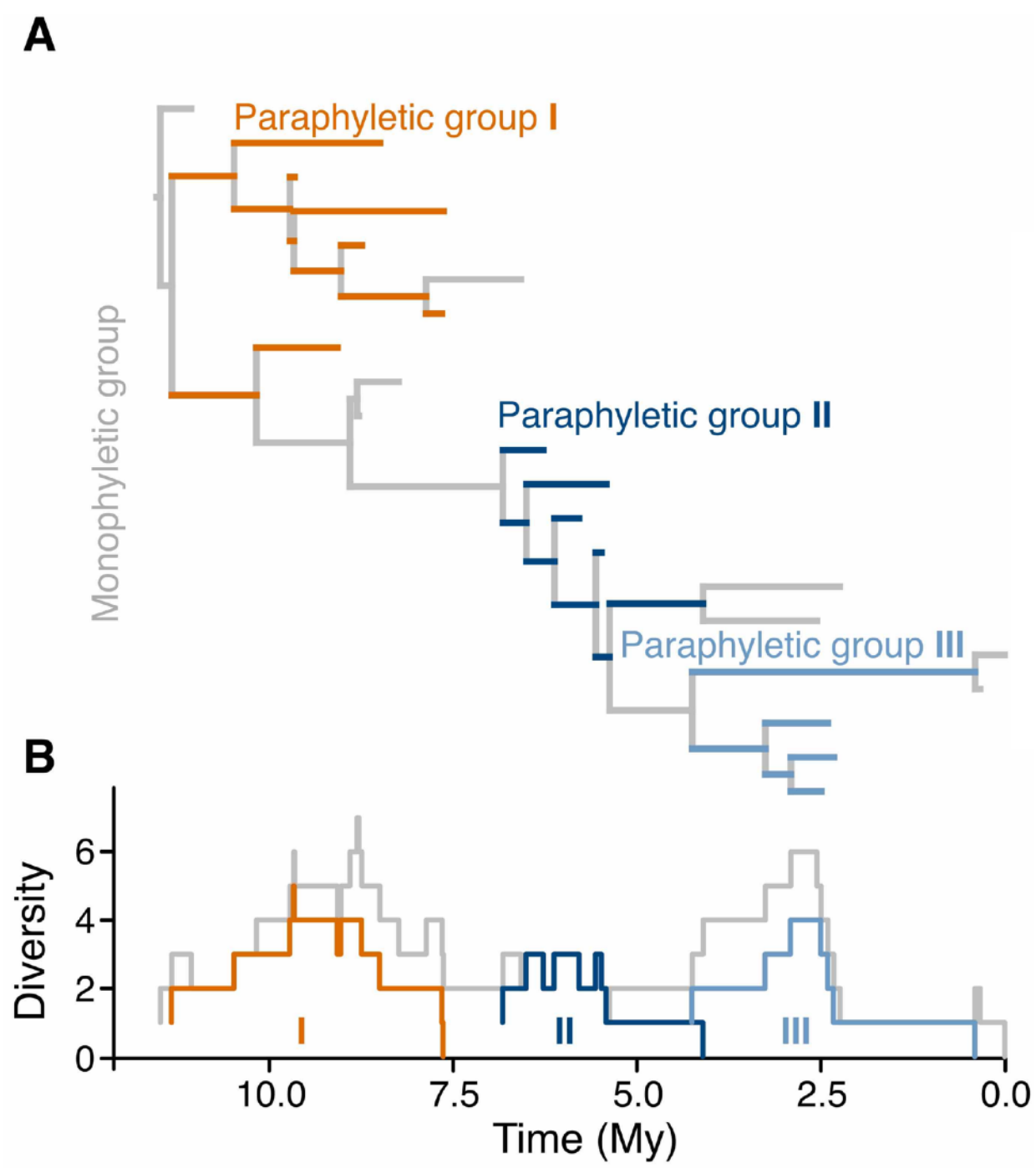
SPECIATION VS EXTINCTION IMPORTANCE



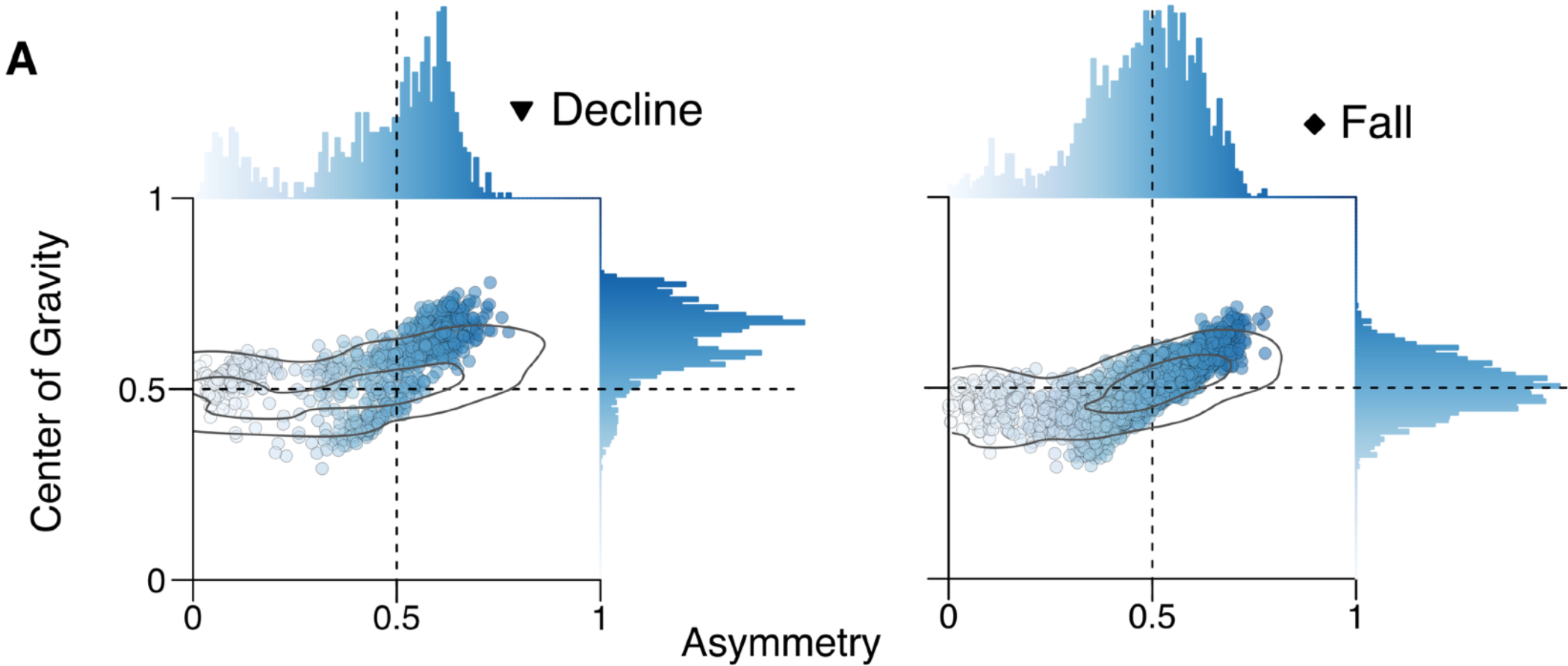
NO DIVERSITY-DEPENDENCE



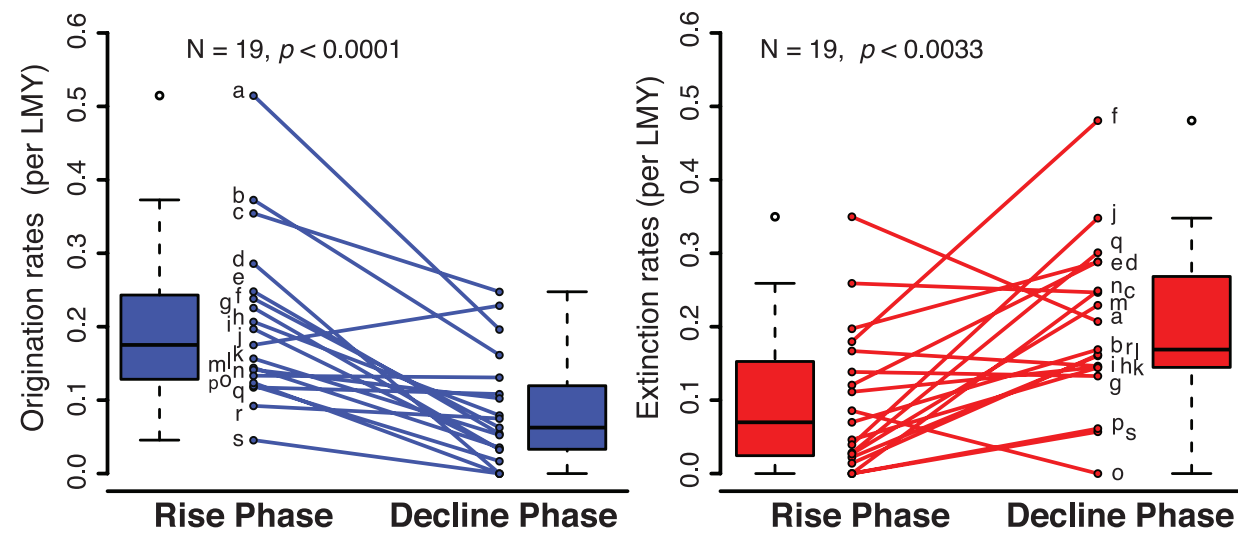
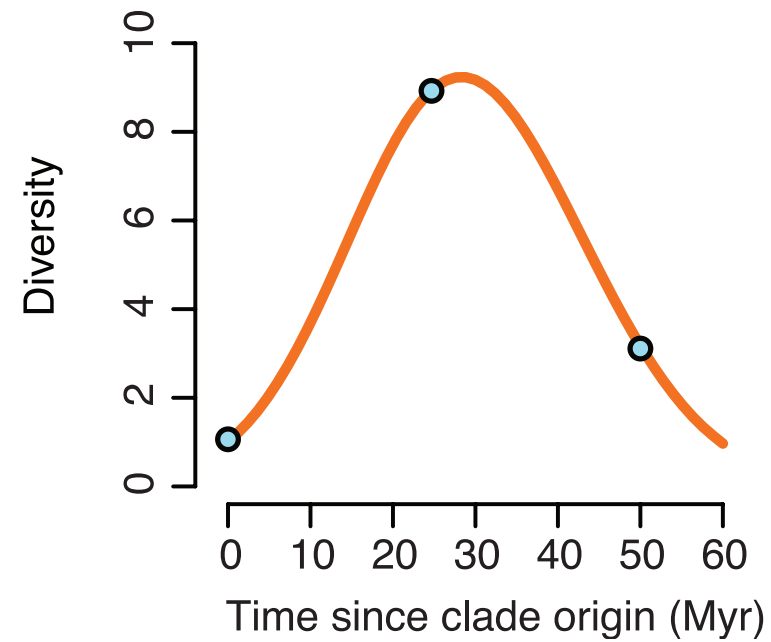
PHYLOGENETIC SCALE



SPECIATION VS EXTINCTION IMPORTANCE



WHY DO CLADES RISE AND FALL?



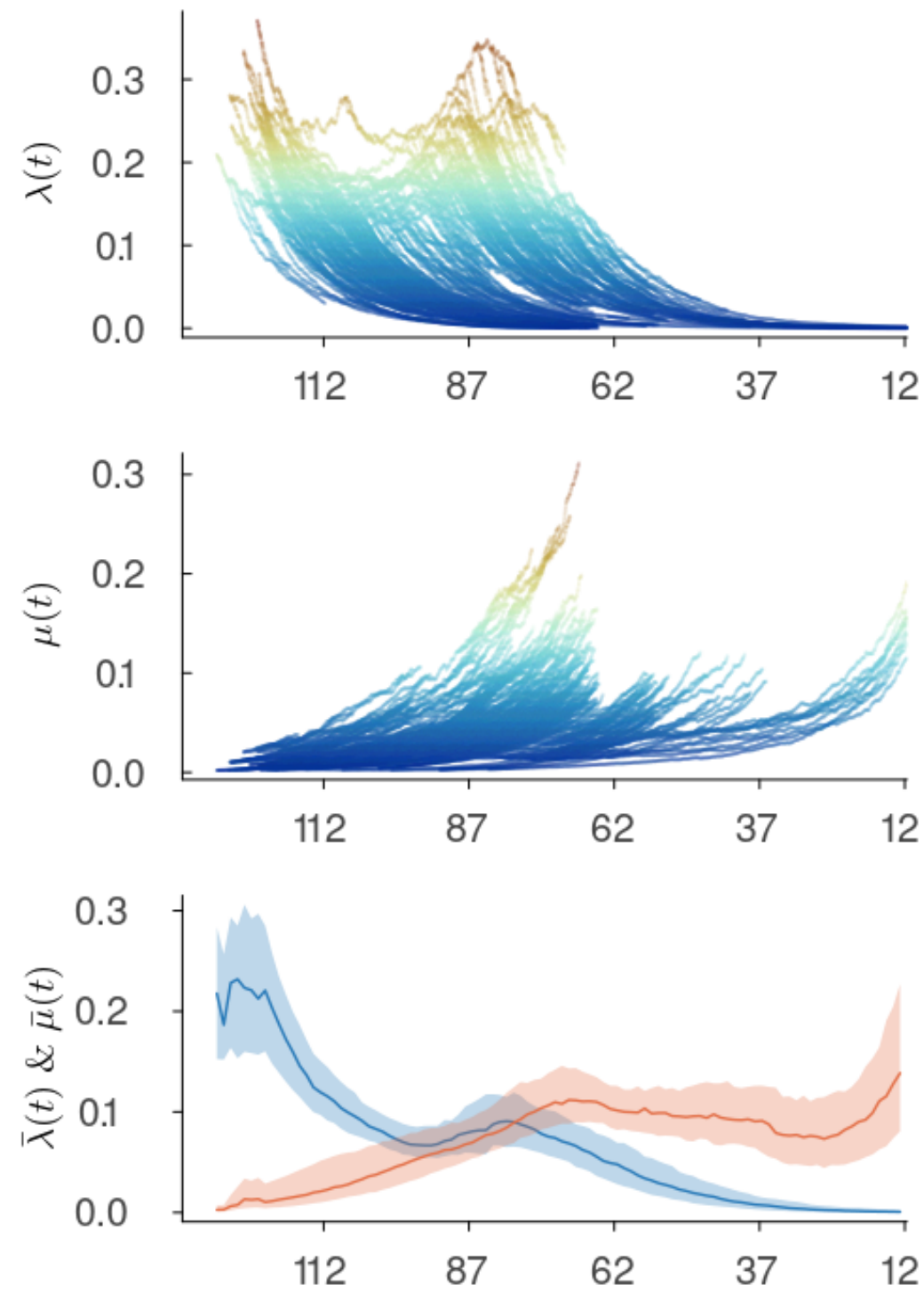
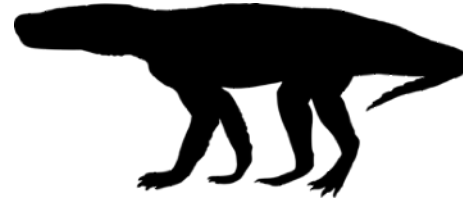
a– Antilocapridae	f– Amphicyonidae [†]	k– Tayassuidae	p– Peradectidae [†]
b– Nyctitheriidae [†]	g– Eomyidae [†]	l– Gliridae	q– Omomyidae [†]
c– Camelidae	h– Rhinocerotidae	m– Castoridae	r– Ochotonidae
d– Elephantidae	i– Equidae	n– Palaeomerycidae [†]	s– Herpetotheriidae [†]
e– Merycoidodontidae [†]	j– Hyaenidae	o– Hyracodontidae [†]	

"ENTWIVES" EFFECT

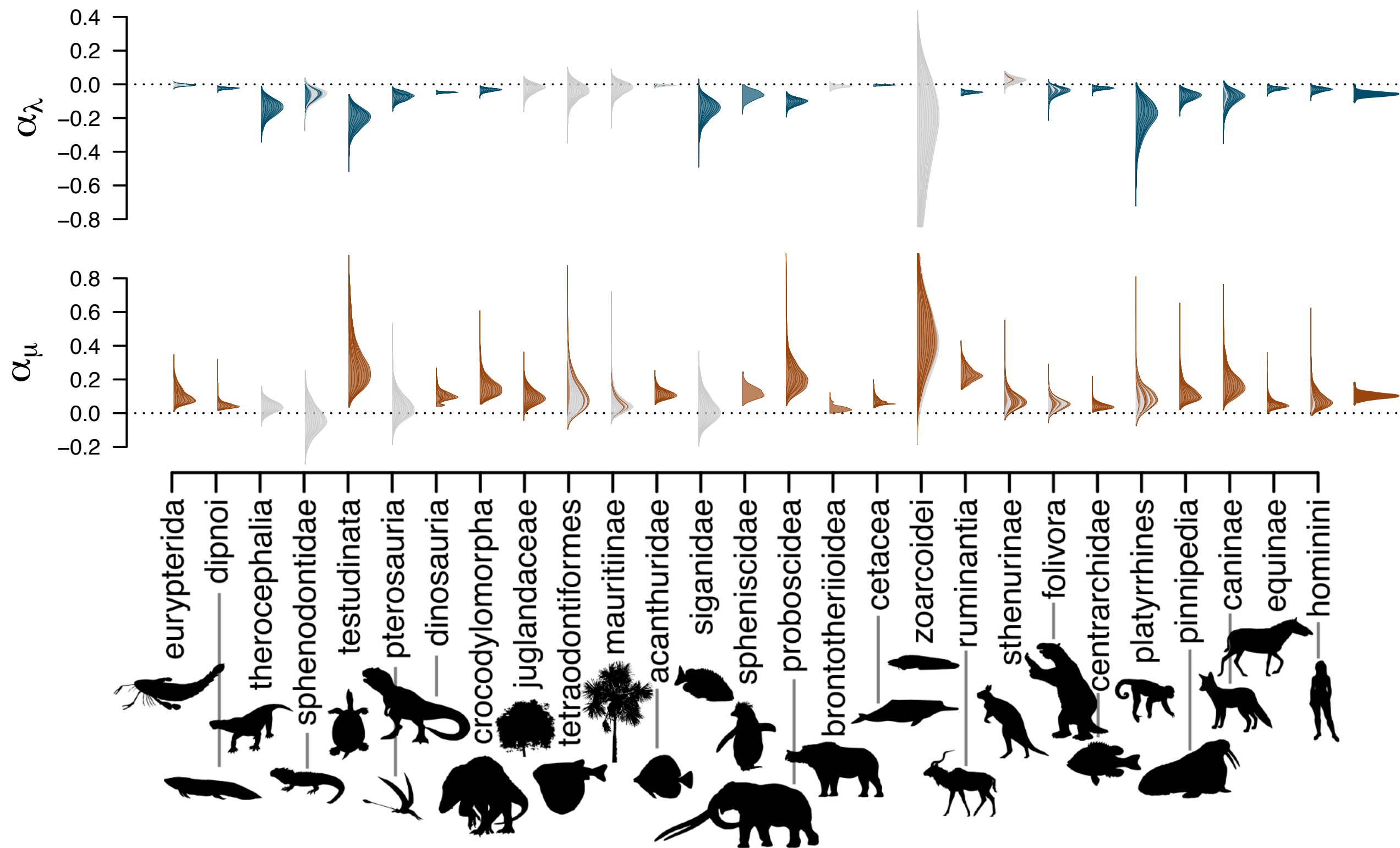
In J. R. R. Tolkien's Middle Earth [J. R. R. Tolkien, *The Lord of the Rings* (Mariner Books, Boston, 2012)], the Ents lost their wives and thus had no means of regenerating their race, hence the term the Entwives effect.



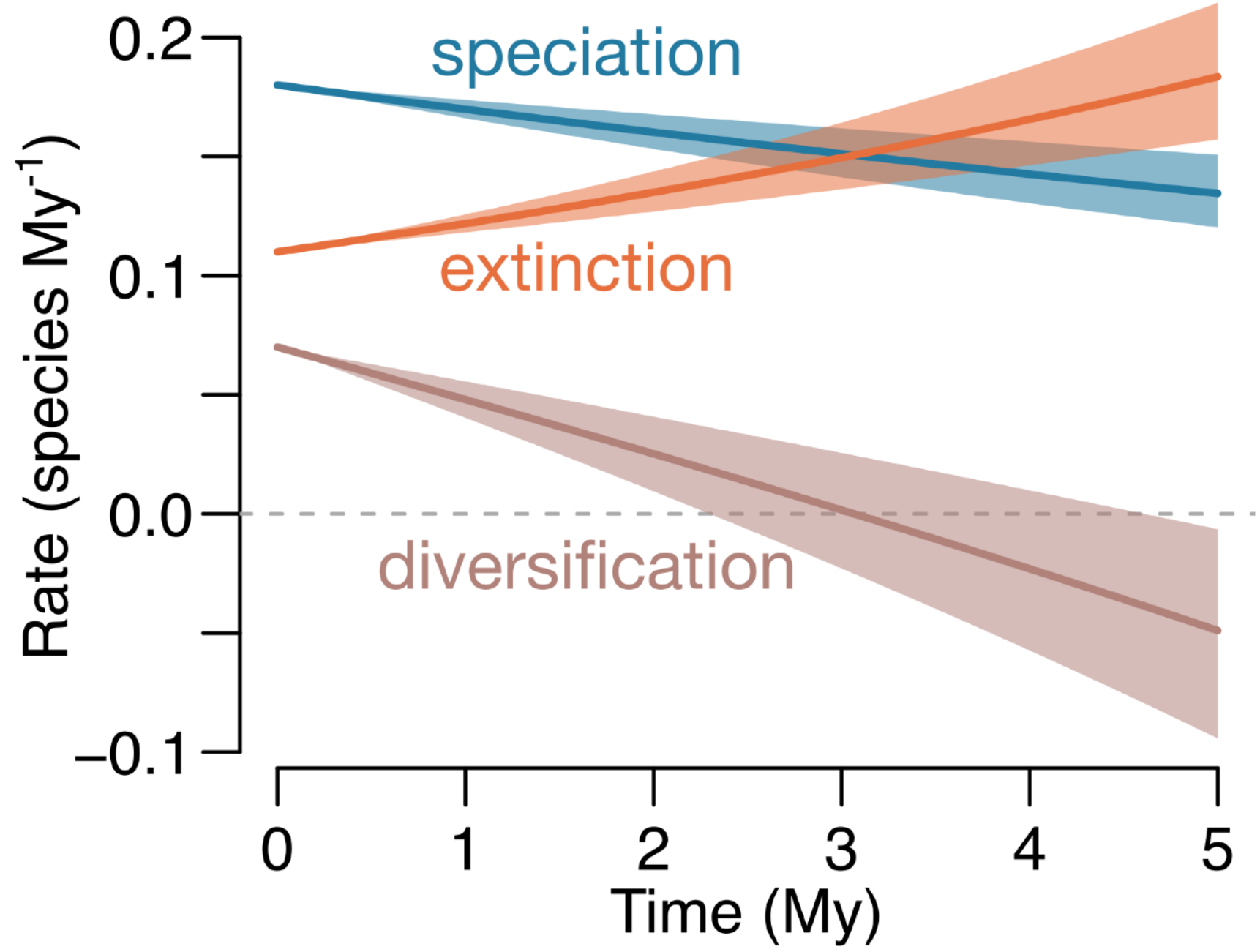
SPECIES AS INDIVIDUALS



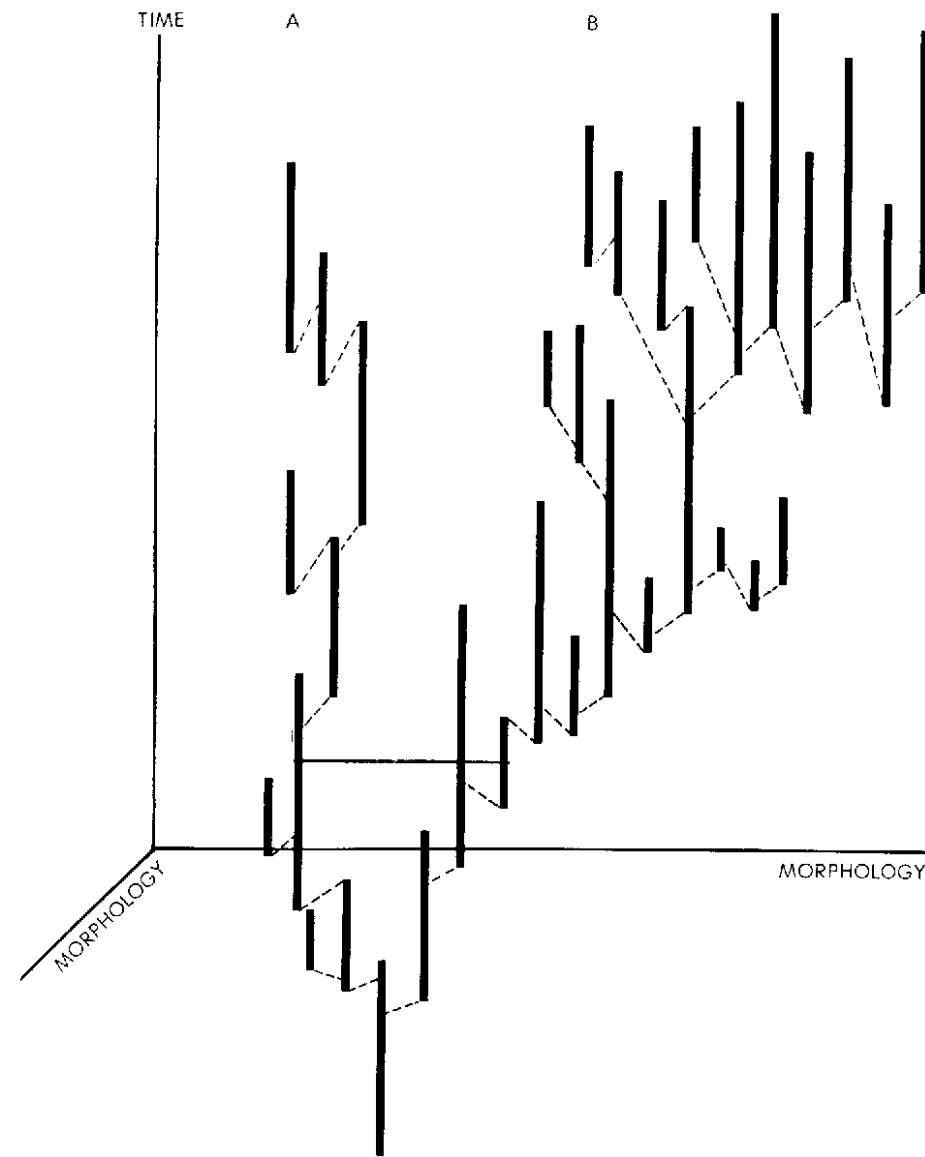
INDIVIDUAL TENDENCIES ON SPECIATION AND EXTINCTION



INSIDIOUS LOSS OF MACROEVOLUTIONARY FITNESS



AVOIDING EXTINCTION THROUGH SPECIATION



N. Eldredge &
S.J. Gould

Speciation as the main mechanism of evolutionary change.

AGE-DEPENDENT SPECIATION AND EXTINCTION

Lineages that do not speciate:

Become **stagnant** given the **homogenising and stabilising** effects of gene flow.

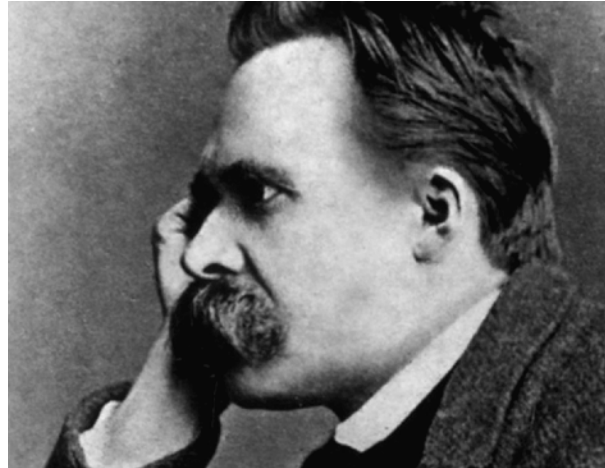


Become bested by spectating (changing) lineages and an unstable environment,
becoming maladapted.



Decrease their speciation and increase their extinction rates.

'ZARATHUSTRAN HYPOTHESIS'



The **maintenance of life** does not merely follow from conservation, but rather from **constant renovation, movement and expansion**.

"And life itself confided the secret to me: behold, it said, I am that which **must always overcome itself**."

Thus Spoke Zarathustra (1883)

SUMMARY

- I. **Reject a simple model of diversification** explained by clade-level processes, such as adaptive radiations or diversity equilibria.
- II. Suggest a more **nuanced, dynamic and unpredictable** diversification process with **species as individuals**: species traits and their specific environmental context periodically propitiate suitable conditions for speciation pulses.
- III. **Stagnation** brought about by **a lack of speciation** causes most lineages to lag behind a continuously reshaping (biotic and abiotic) environment.
- IV. The **few successful individual lineages** that depart from this general tendency **disproportionally engender biodiversity**, yet sometimes fail to compensate a general **insidious loss of macroevolutionary fitness**, leading to the **recurrent decline and fall of clades**.



Home

 GitHub   

Tapestry.jl

Unraveling the evolutionary tapestry: **Tapestry** is a **Julia** package of phylogenetic analyses of diversification, trait and biogeographic dynamics.

<https://github.com/ignacioq/Tapestry.jl>



Hélène
Morlon



Nicolas
Lartillot



Jérémy
Andréoletti



Daniele
Silvestro



THANK YOU