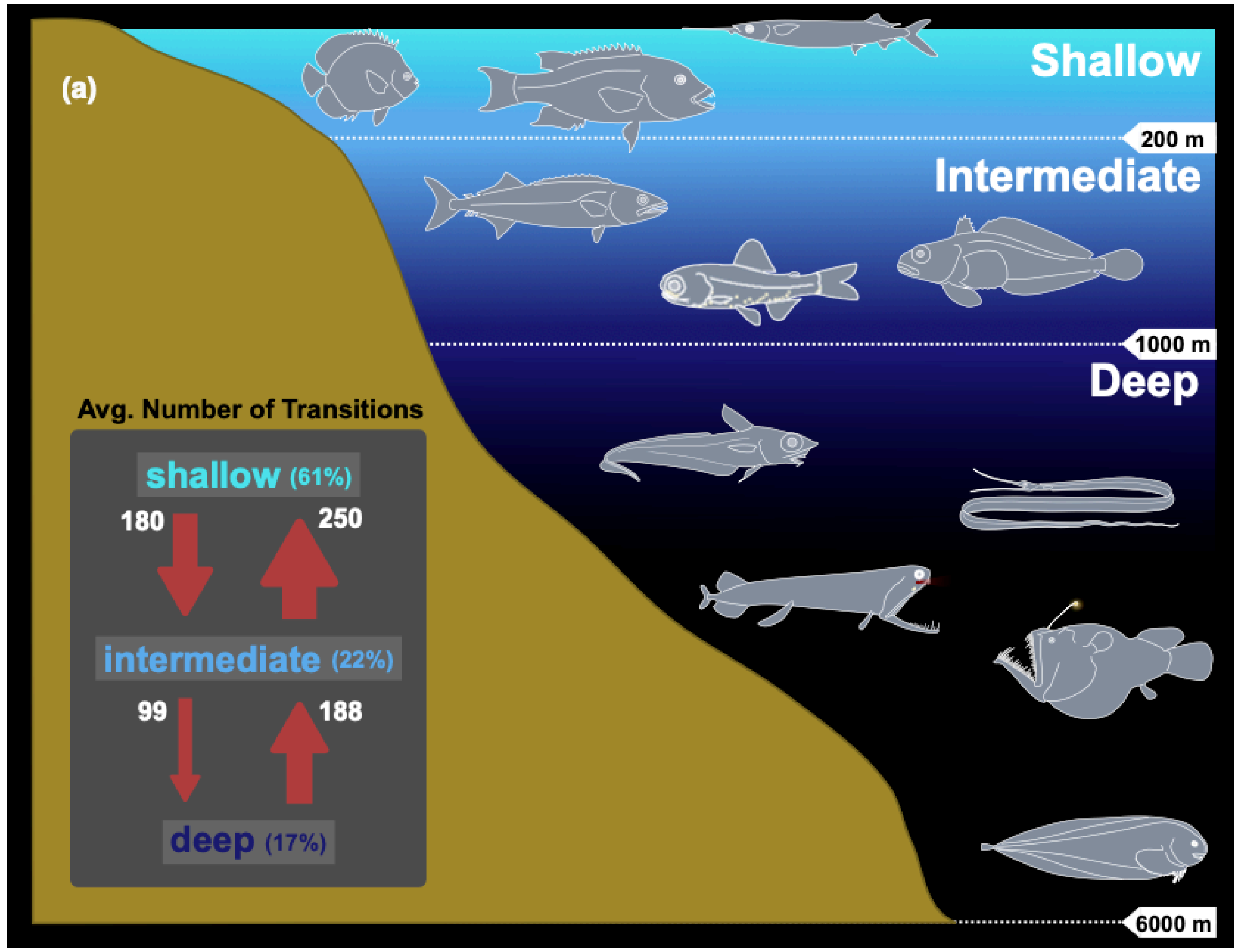
Introduction to trait evolution
(on phylogenies)

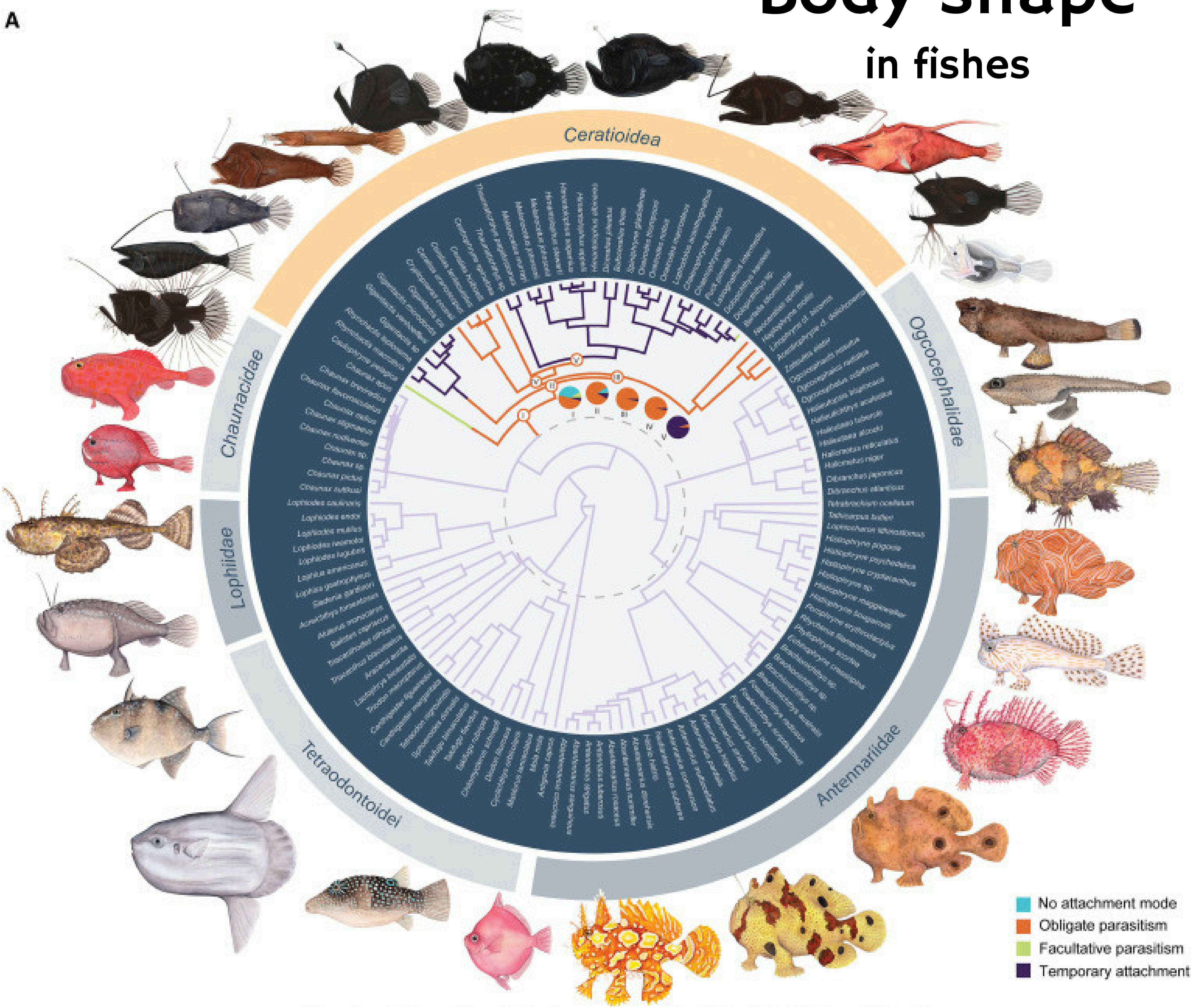
TRAIT DIVERSITY IS ONE OF THE MOST STRIKING PATTERNS IN NATURE:



Martinez et al. 2021 Ecol. Lett.

Body shape

in fishes

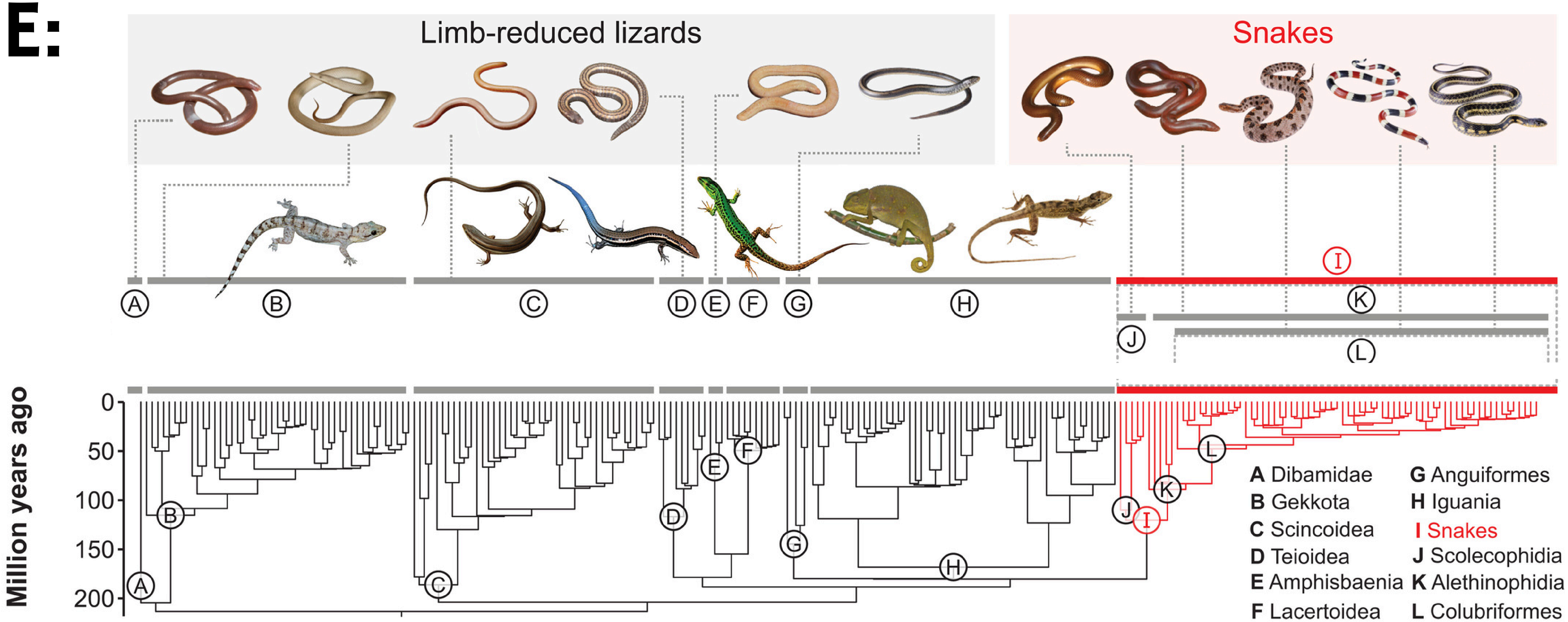


Bownstein et al. 2024 Curr. Biol.

TRAIT DIVERSITY IS ONE OF THE MOST STRIKING PATTERNS IN NATURE:

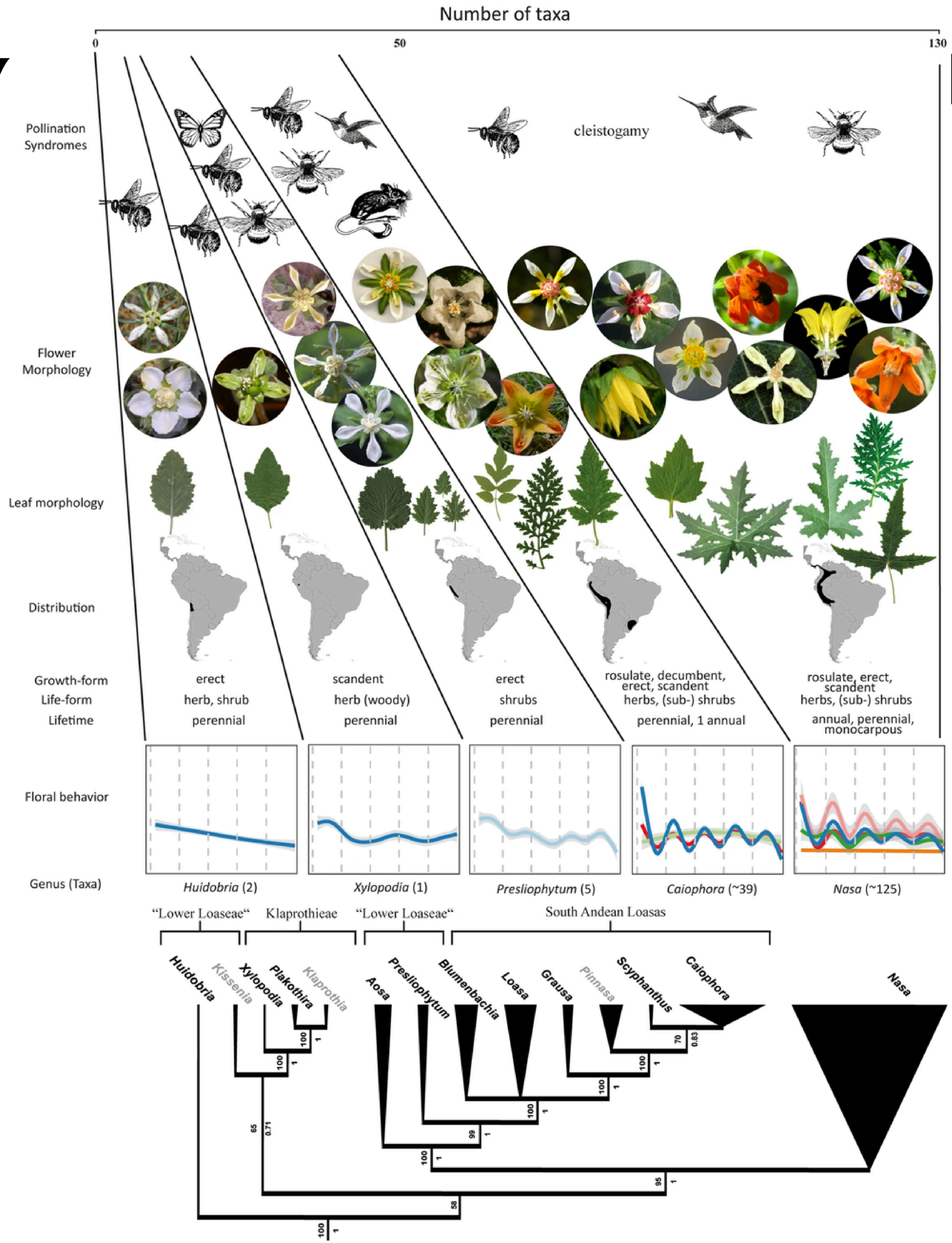
Limb reduction

in lizards & snakes



Title et al. 2024 Science

TRAIT DIVERSITY IS ONE OF THE MOST STRIKING PATTERNS IN NATURE:



Morphological diversity

in flowers

Henning et al. 2018 Scie. Reports.

Why does trait diversity vary across space?
Why does trait diversity vary across time?
Why does trait diversity vary across lineages?

↓

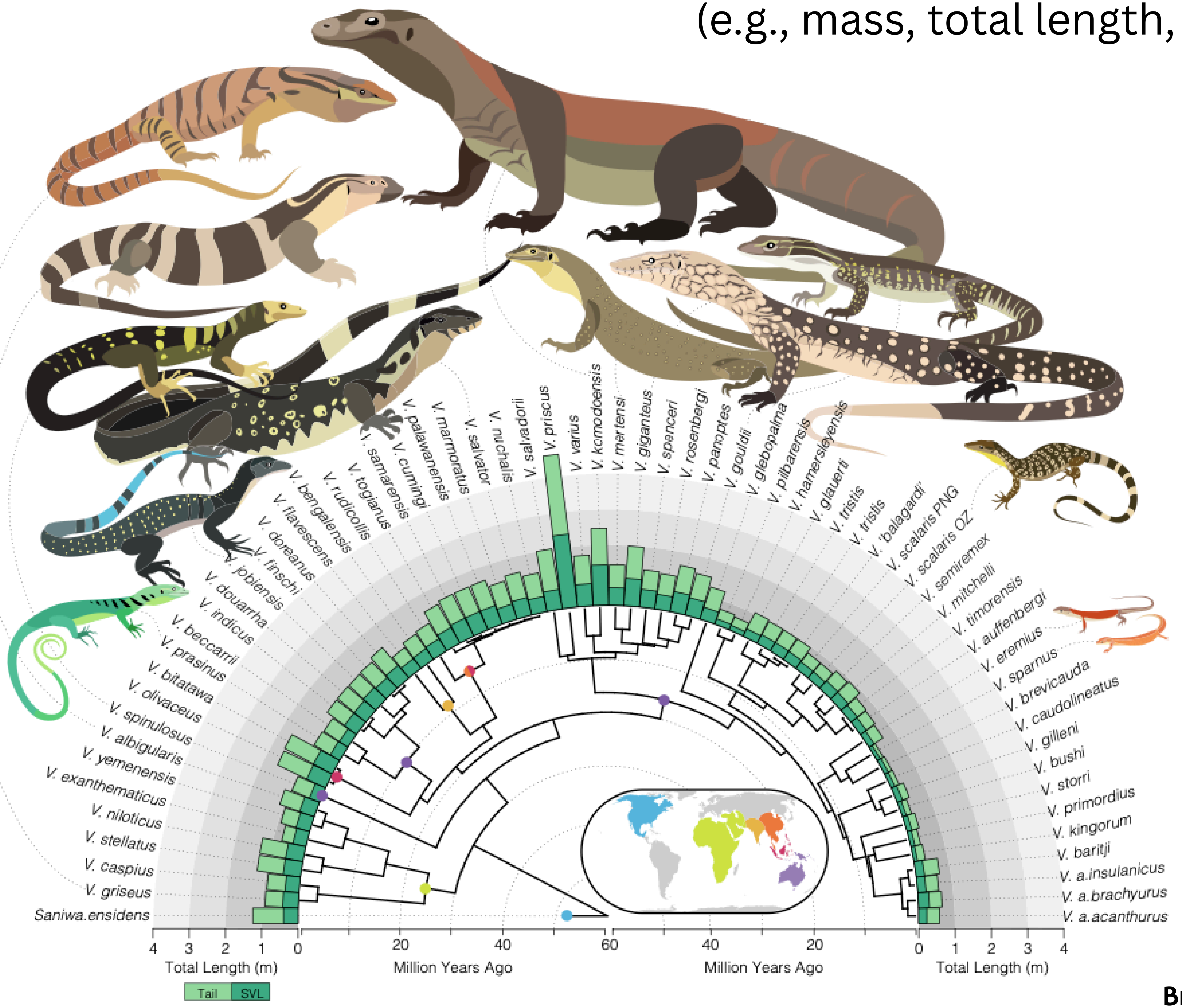
What shapes trait diversity?

What is a trait?

A trait is any measurable or observable feature of an organism that can vary among individuals or species and can be studied in an evolutionary framework.

MORPHOLOGICAL traits

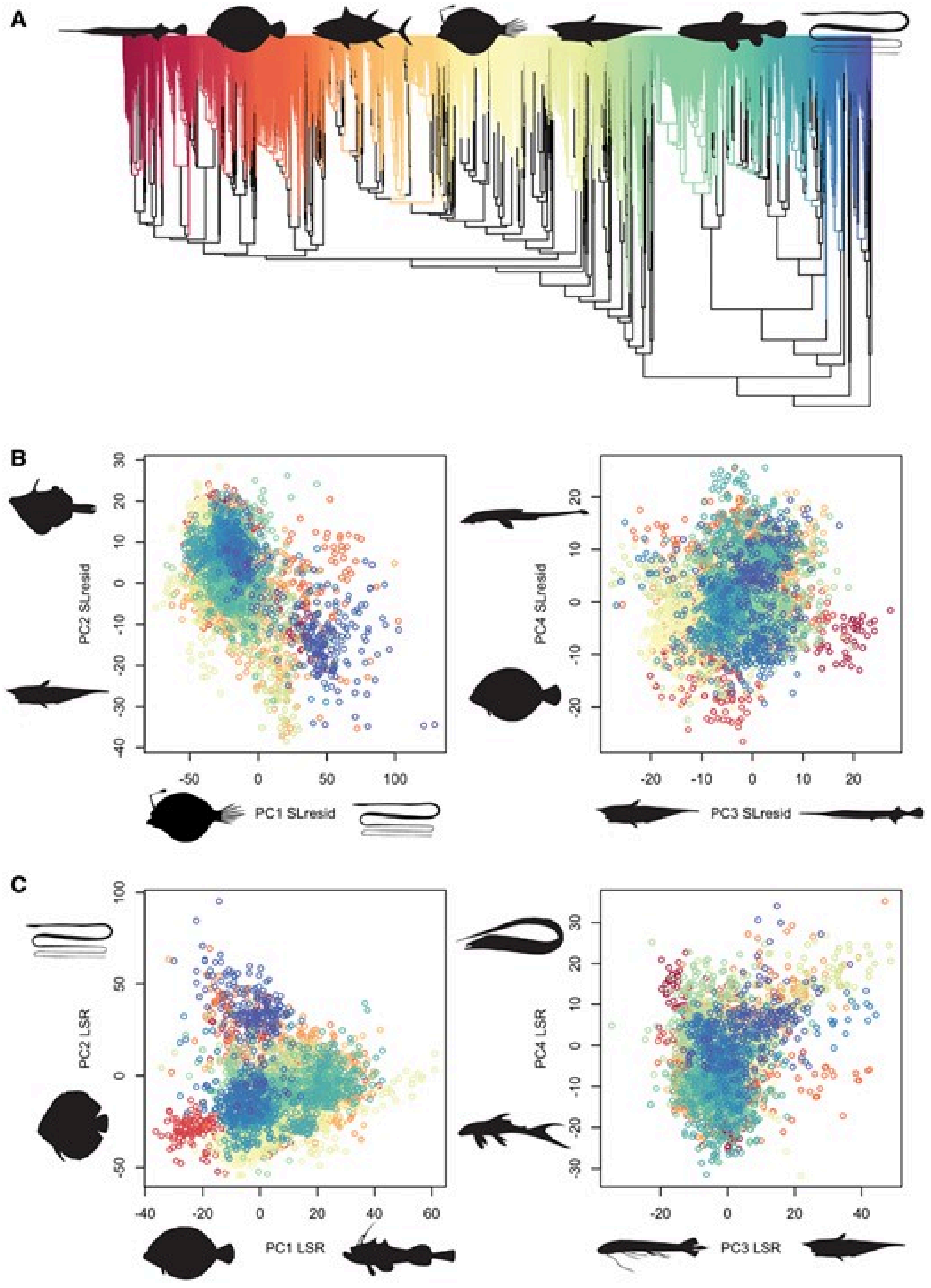
Body size
(e.g., mass, total length, snout-vent length)



Brennan et al. 2021 Evolution

MORPHOLOGICAL traits

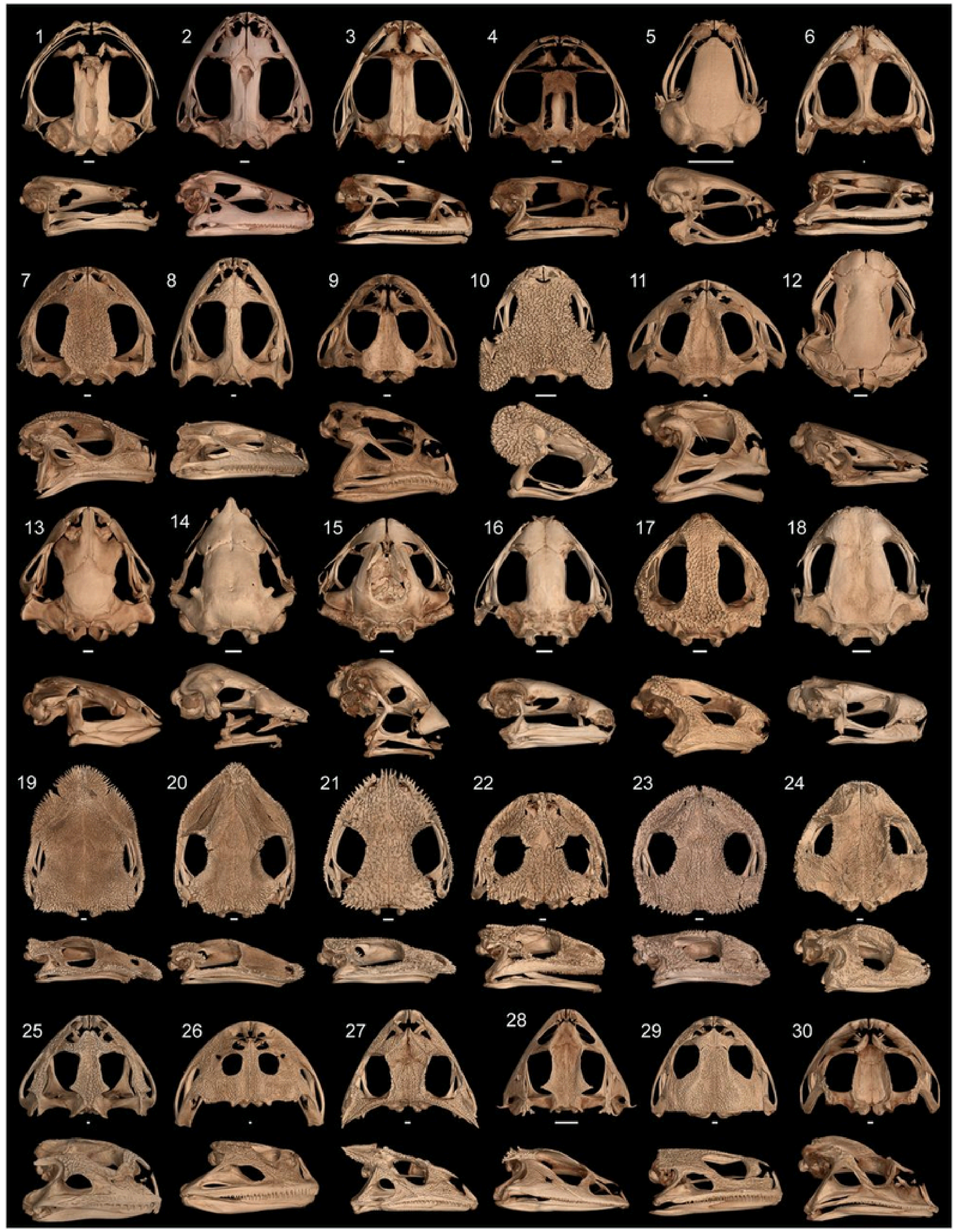
Shape

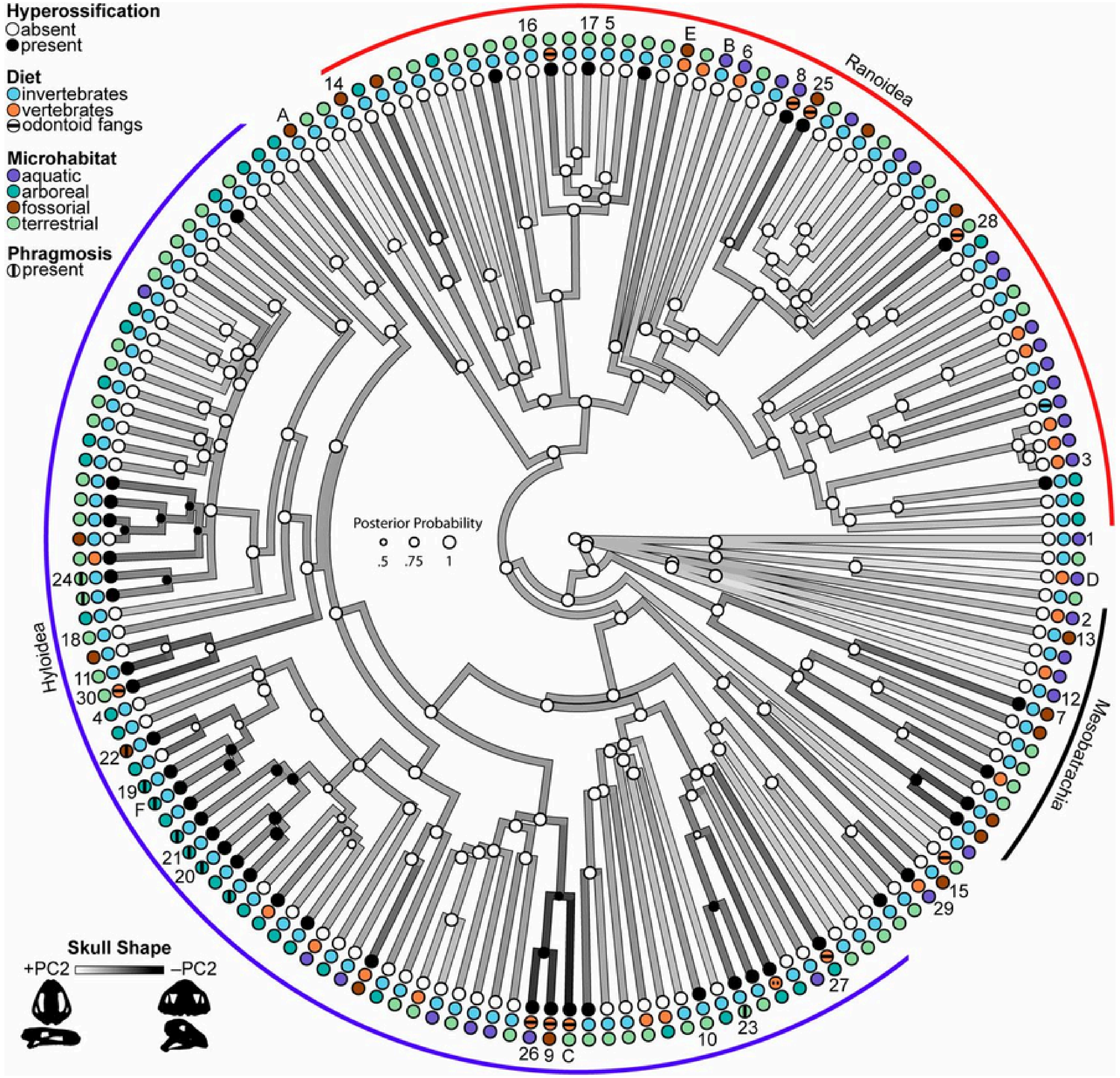


Price et al. 2019 ICB

MORPHOLOGICAL traits

Shape

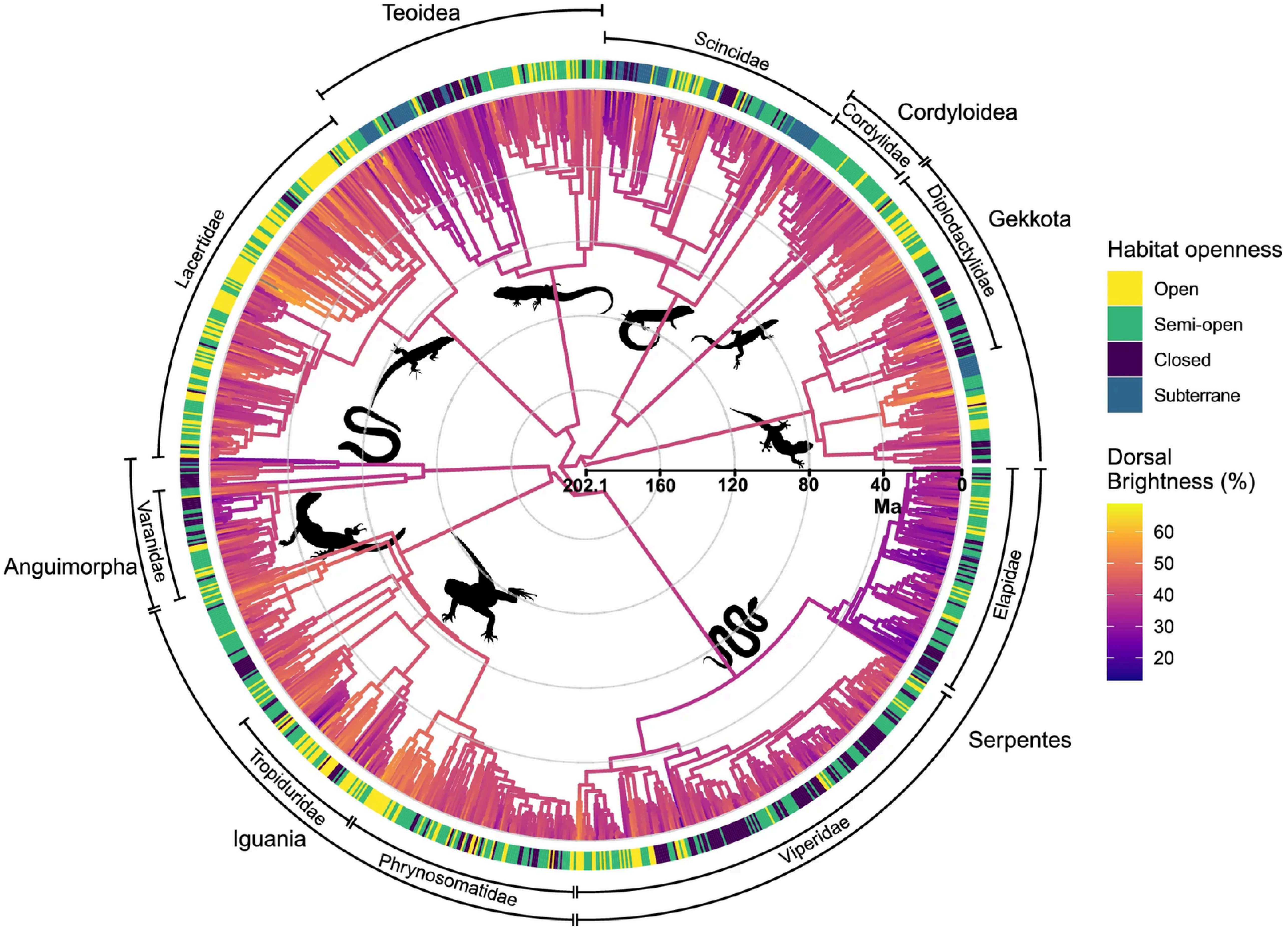




Paluh et al. 2020 PNAS

MORPHOLOGICAL traits

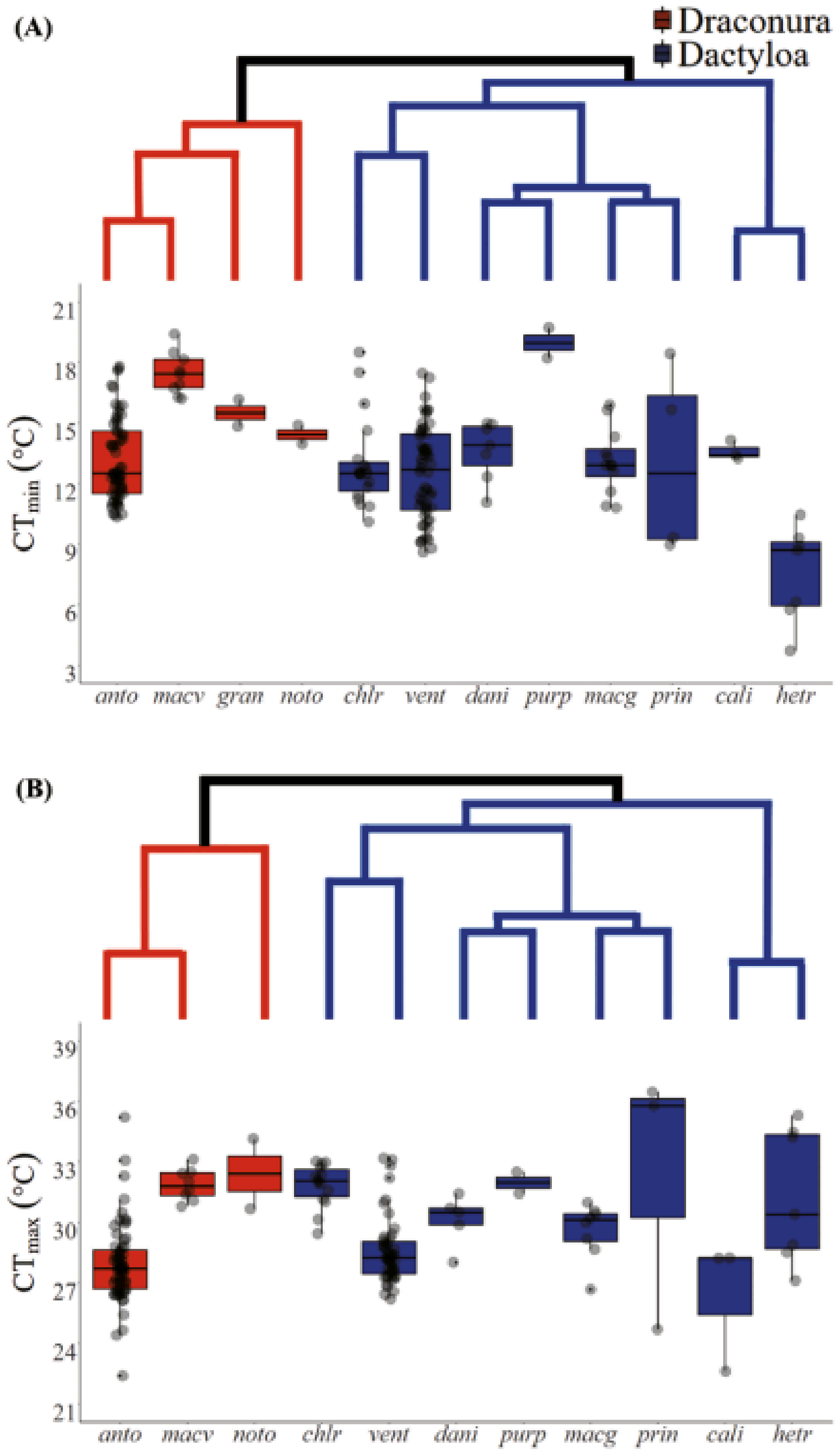
Color



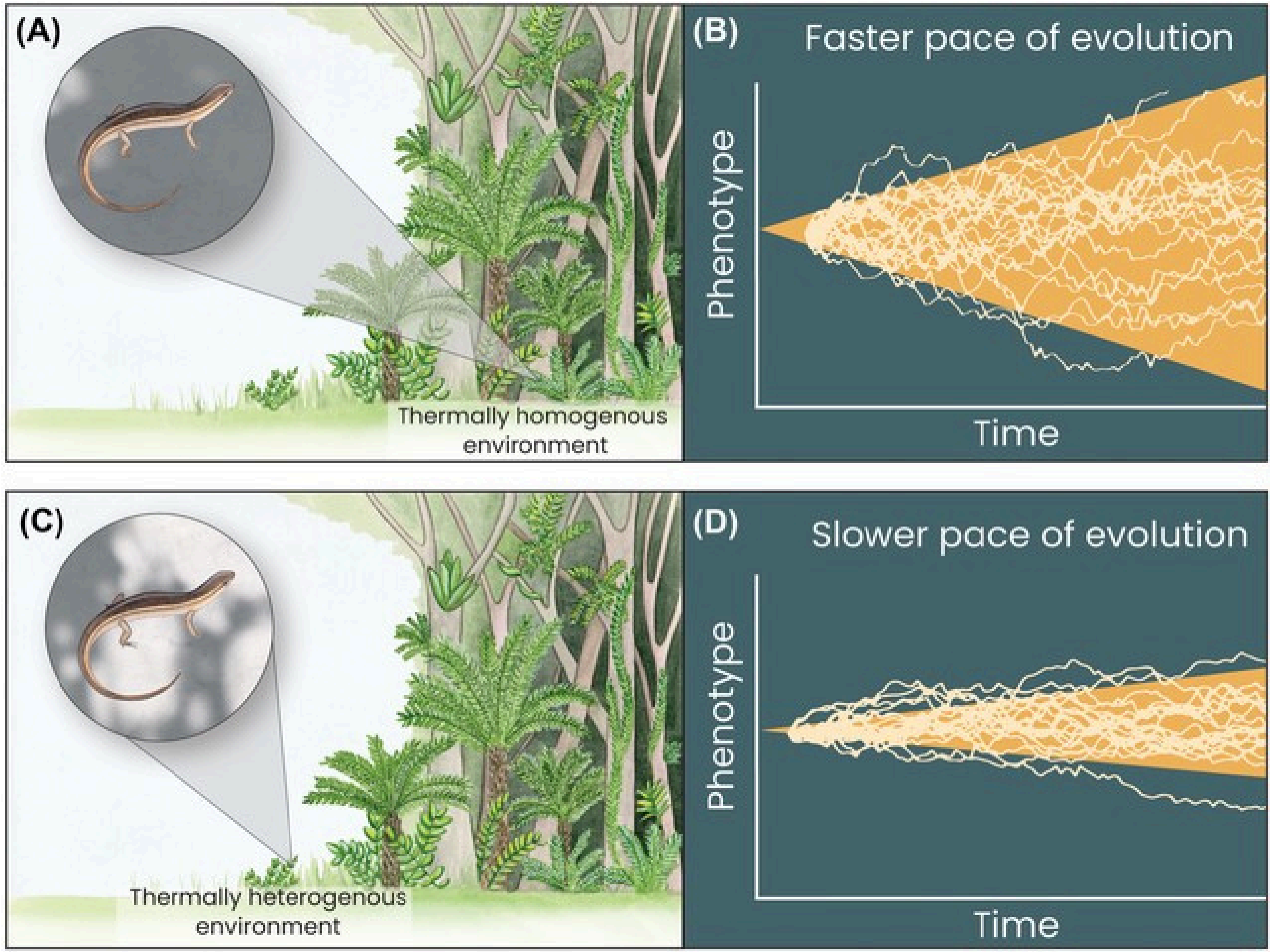
Goldenberg et al. 2024 Nat Comm

PHYSIOLOGICAL traits

Thermal tolerance limits



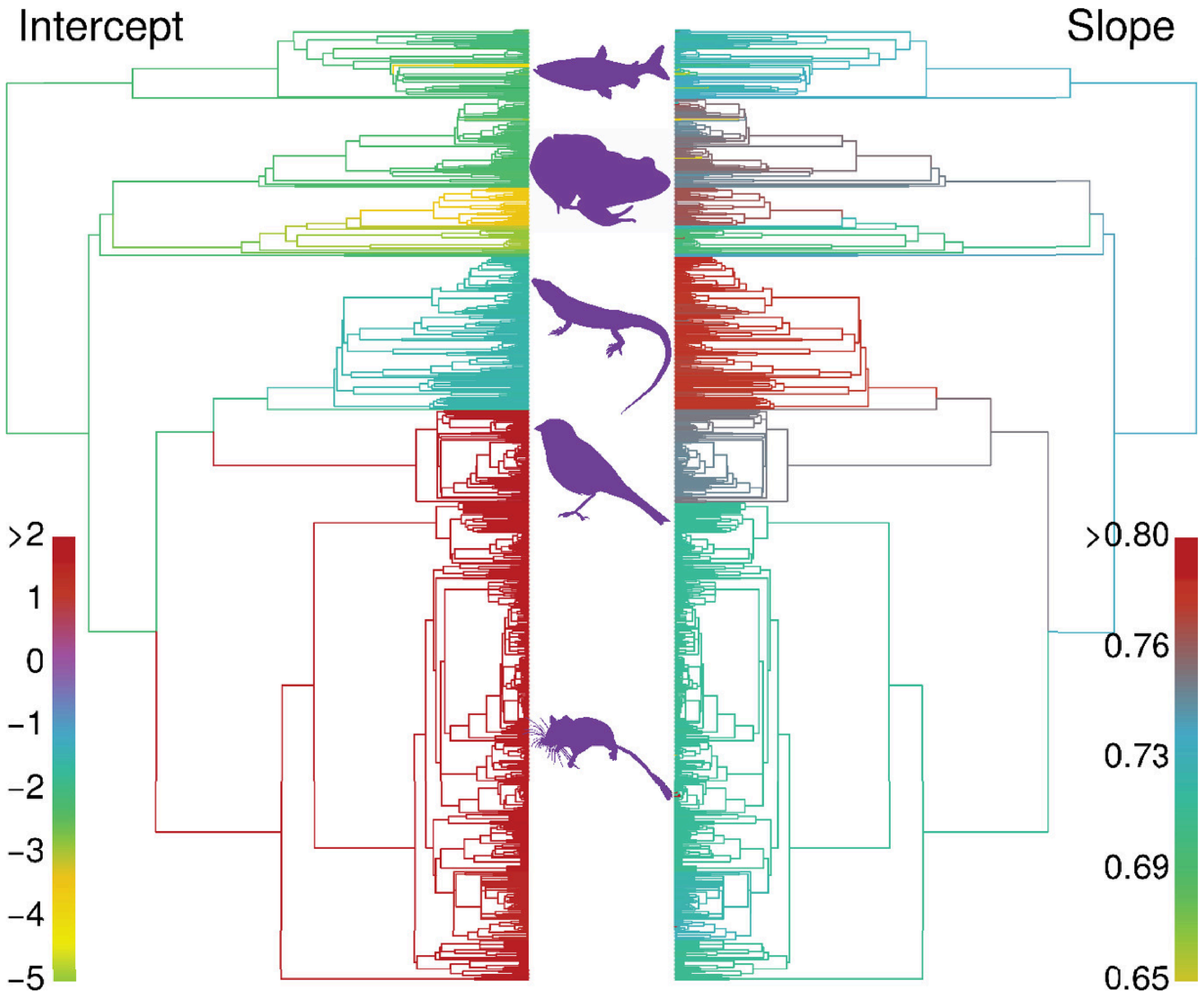
Salazar et al. 2024 Evolution



Muñoz 2022 Evolution

PHYSIOLOGICAL traits

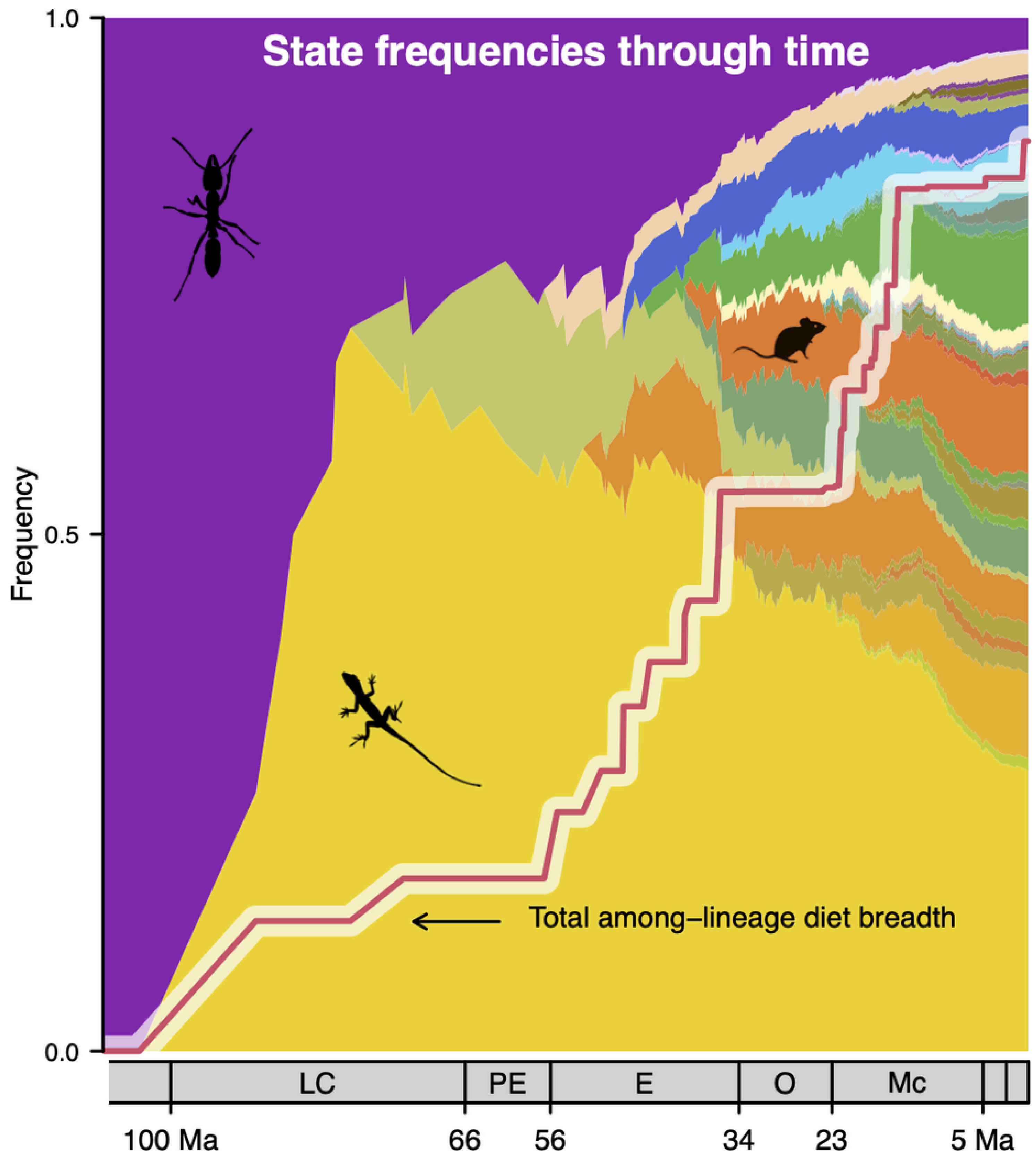
Metabolic rates

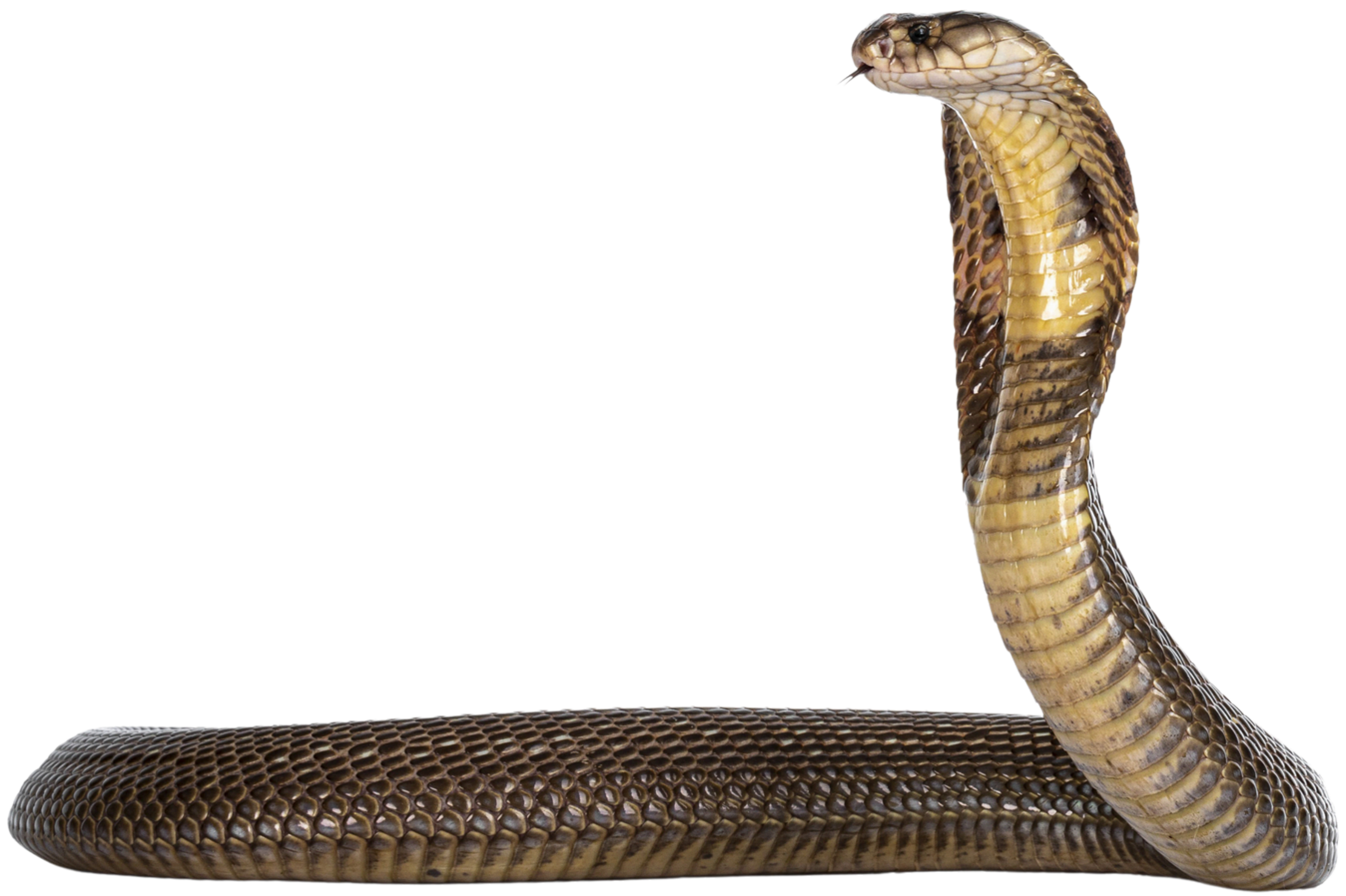


Uyeda et al. 2017 Am Nat

ECOLOGICAL traits

Diet

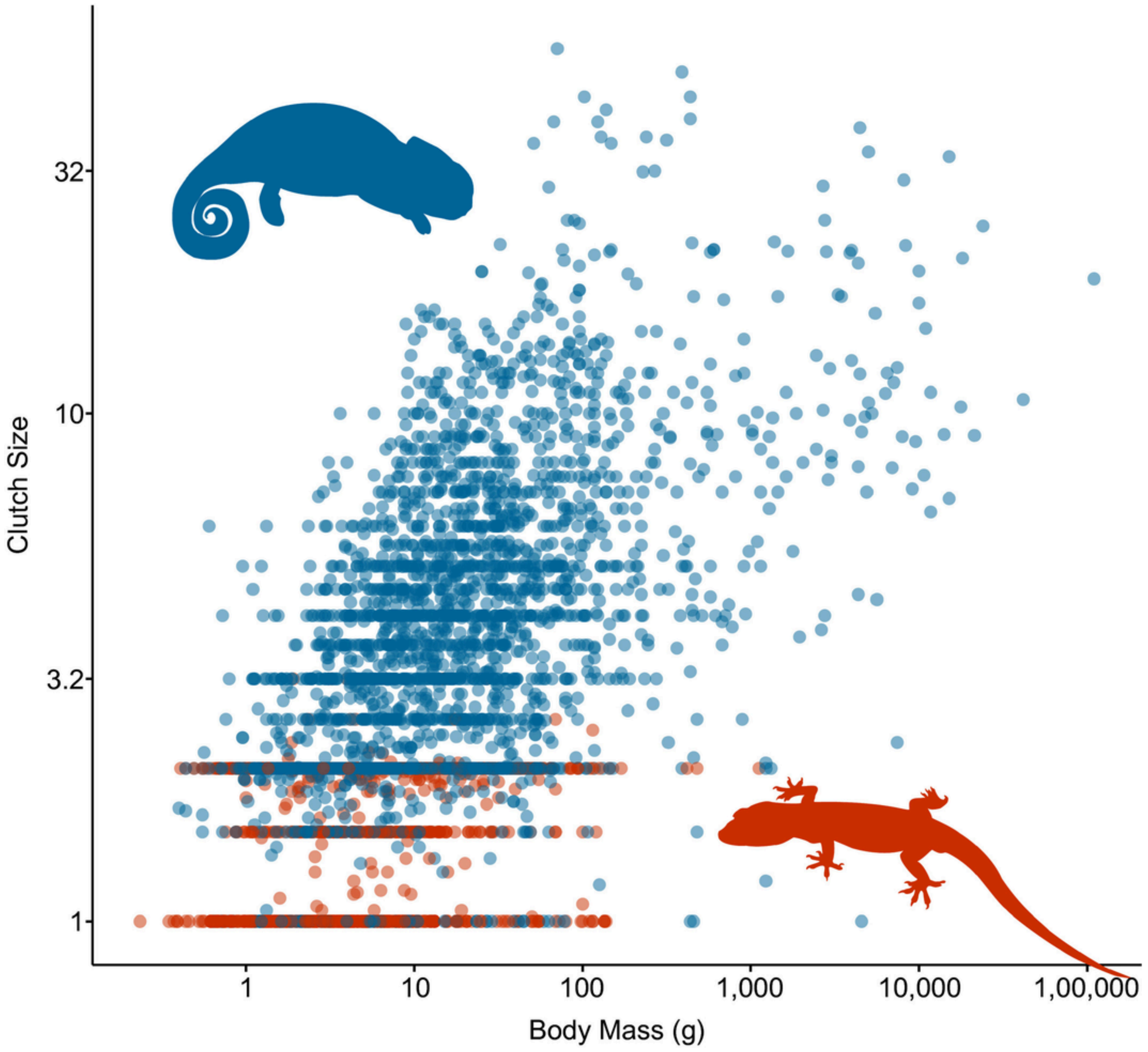


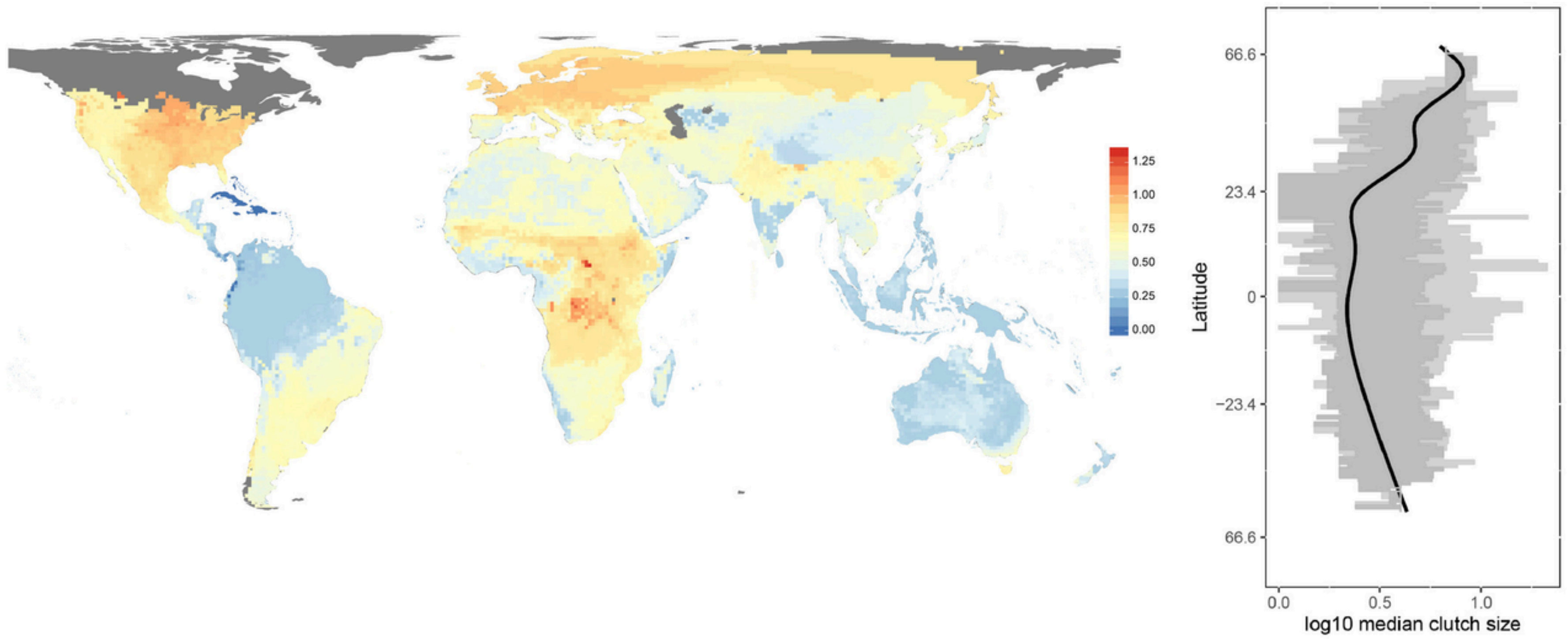


Grundler and Rabosky 2021 Plos Biology

LIFE-HISTORY traits

Clutch size

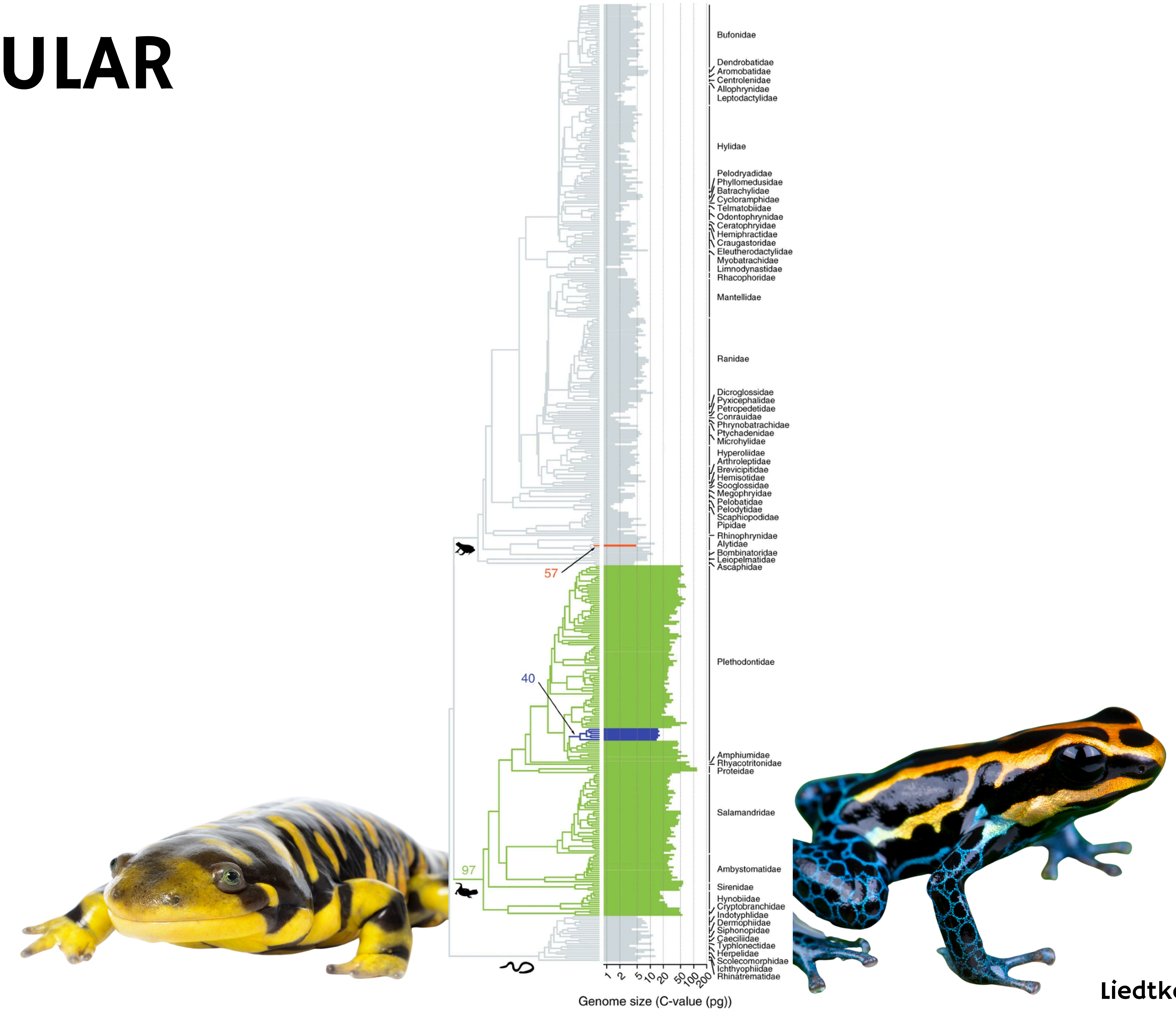




Meiri et al. 2020 Global Ecol. Biogeo.

MOLECULAR traits

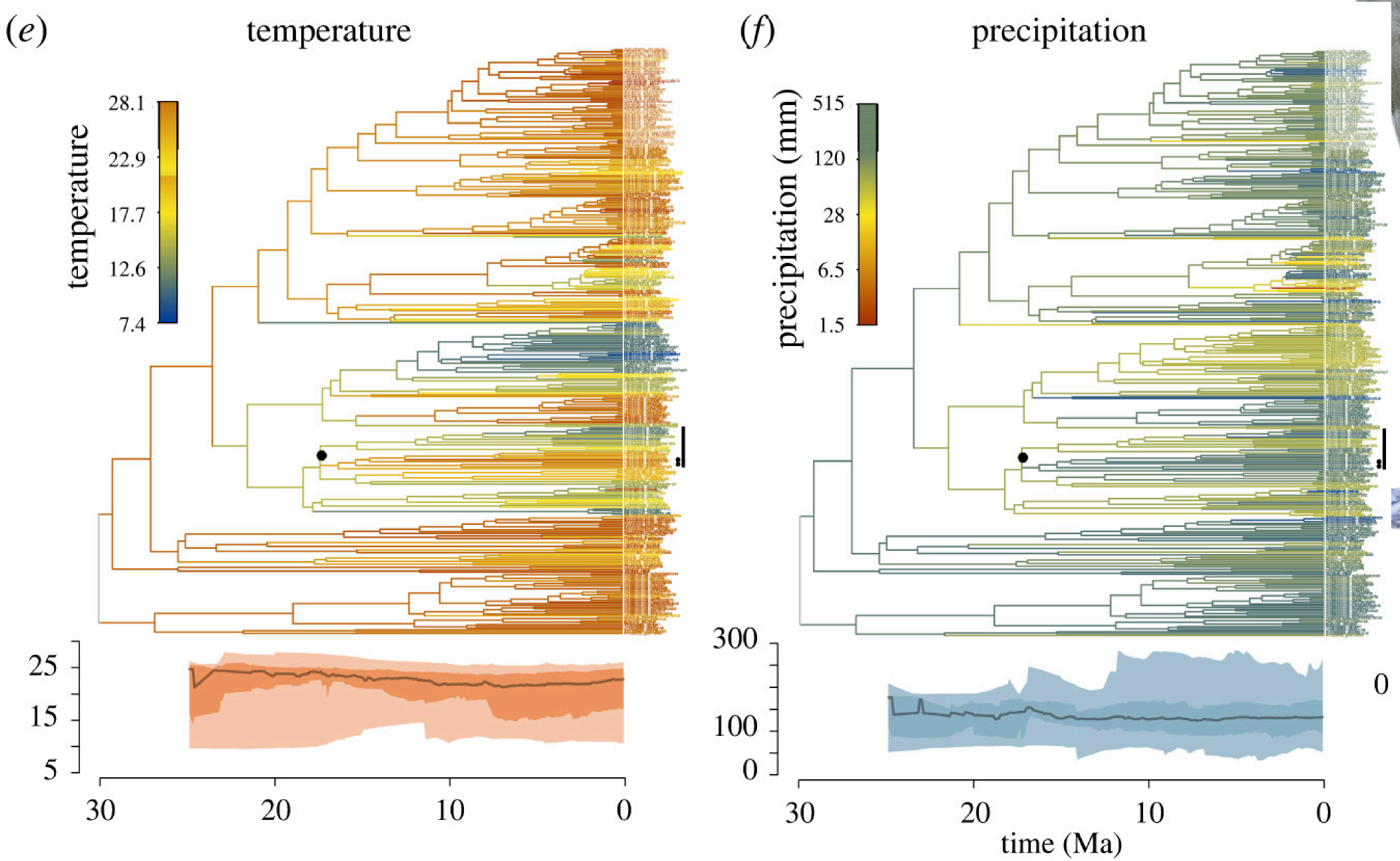
Genome size

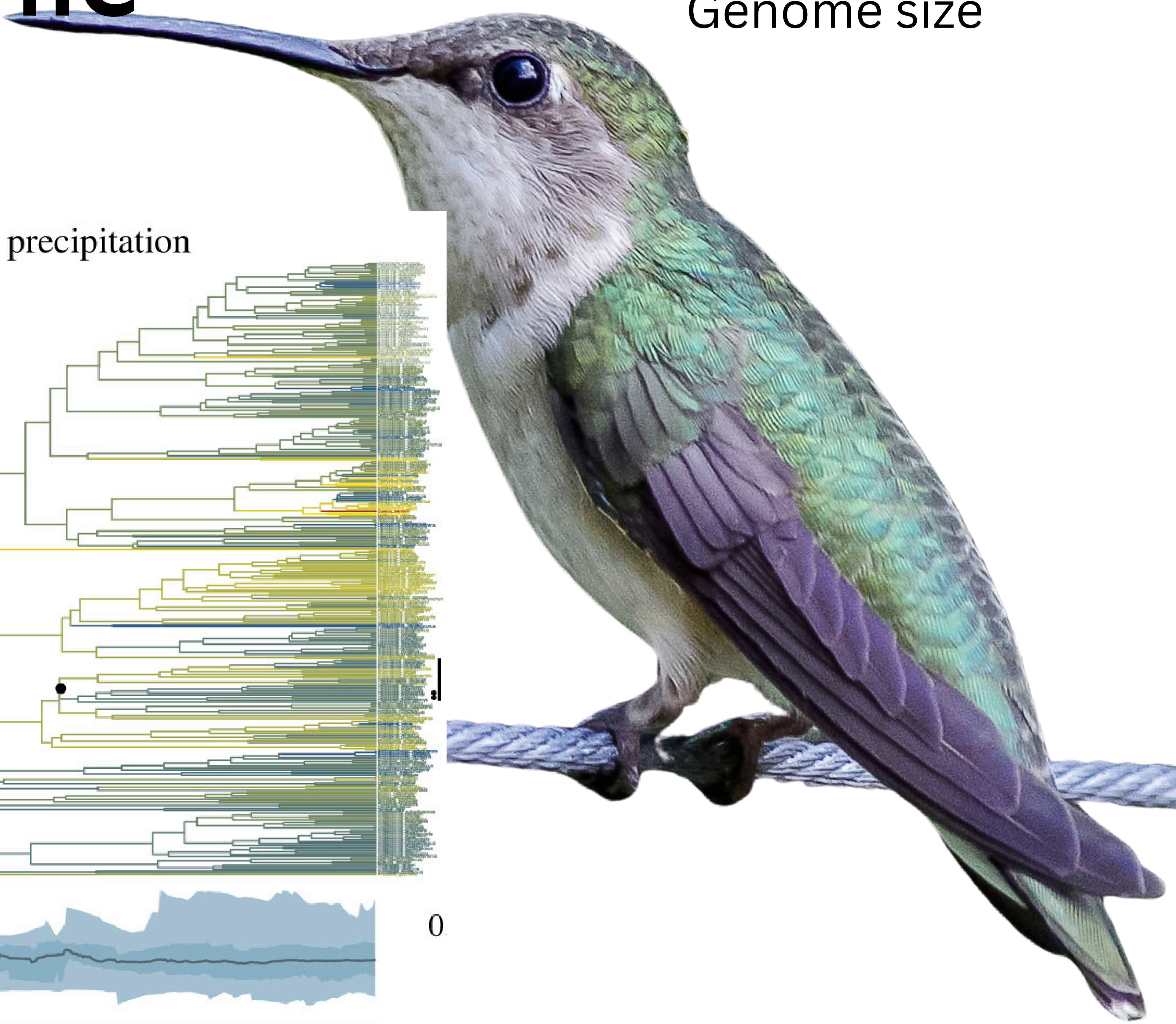


Liedtke et al. 2018 Nat Ecol Evol

CLIMATIC AND GEOGRAPHIC traits

Genome size

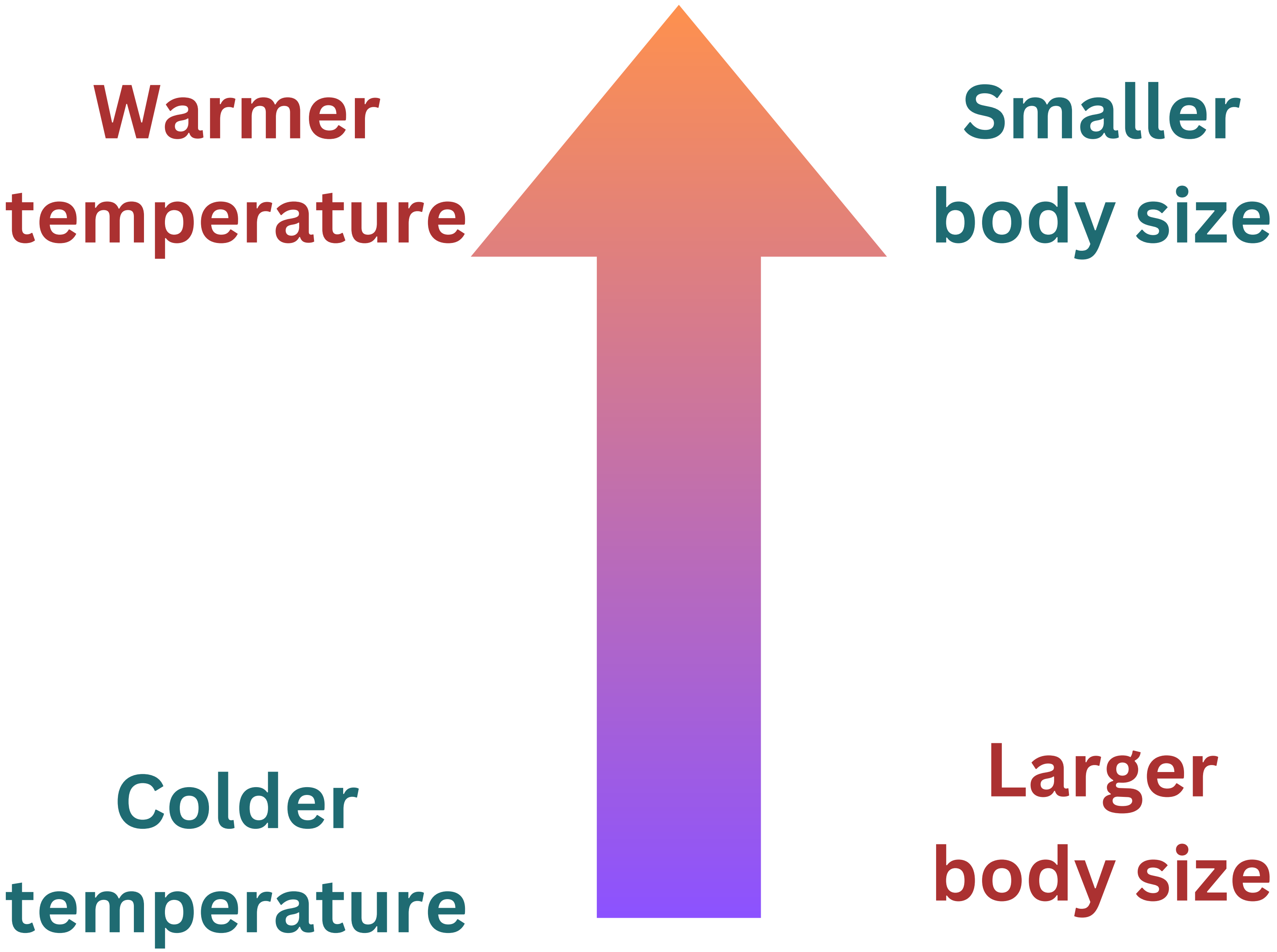




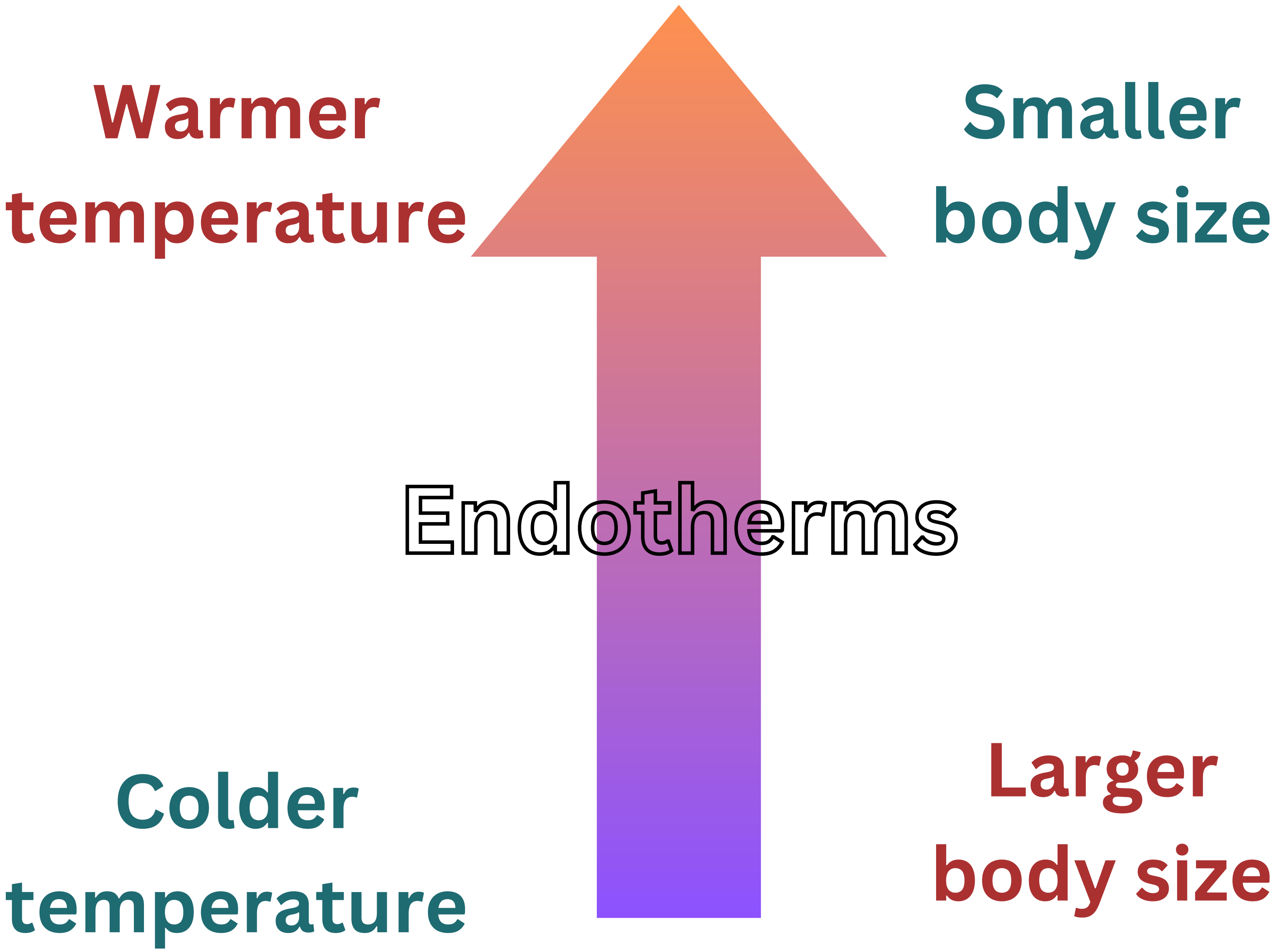
Quintero et al. 2022 Proc B

TRAIT DIVERSITY ACROSS SPACE

TRAIT DIVERSITY ACROSS SPACE
Bergmann’s Rule



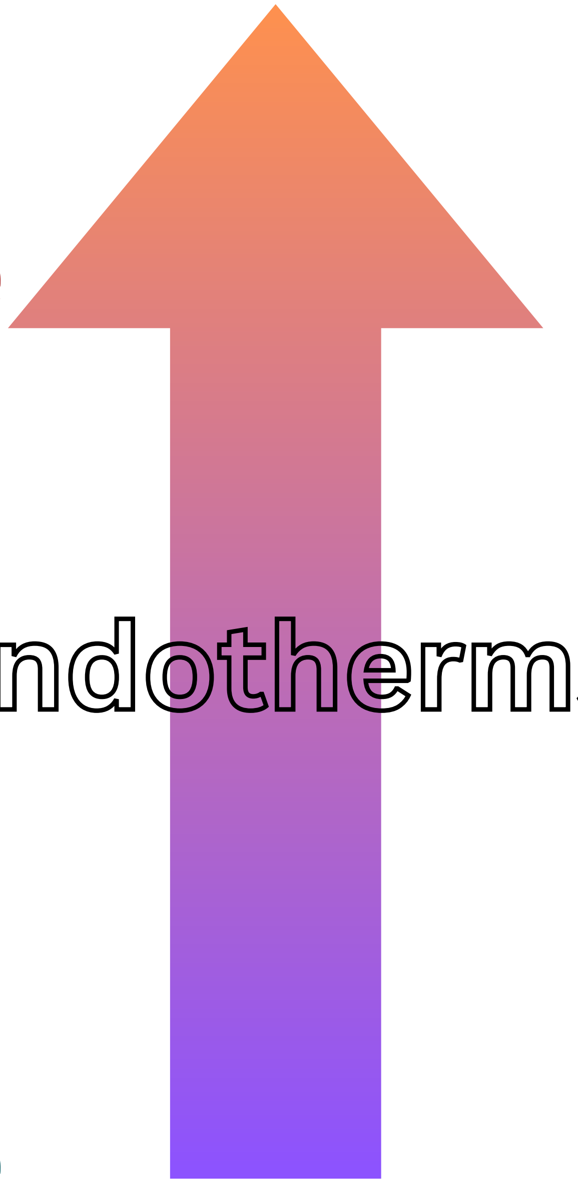
TRAIT DIVERSITY ACROSS SPACE
Bergmann’s Rule



TRAIT DIVERSITY ACROSS SPACE
Bergmann's Rule

Warmer temperature

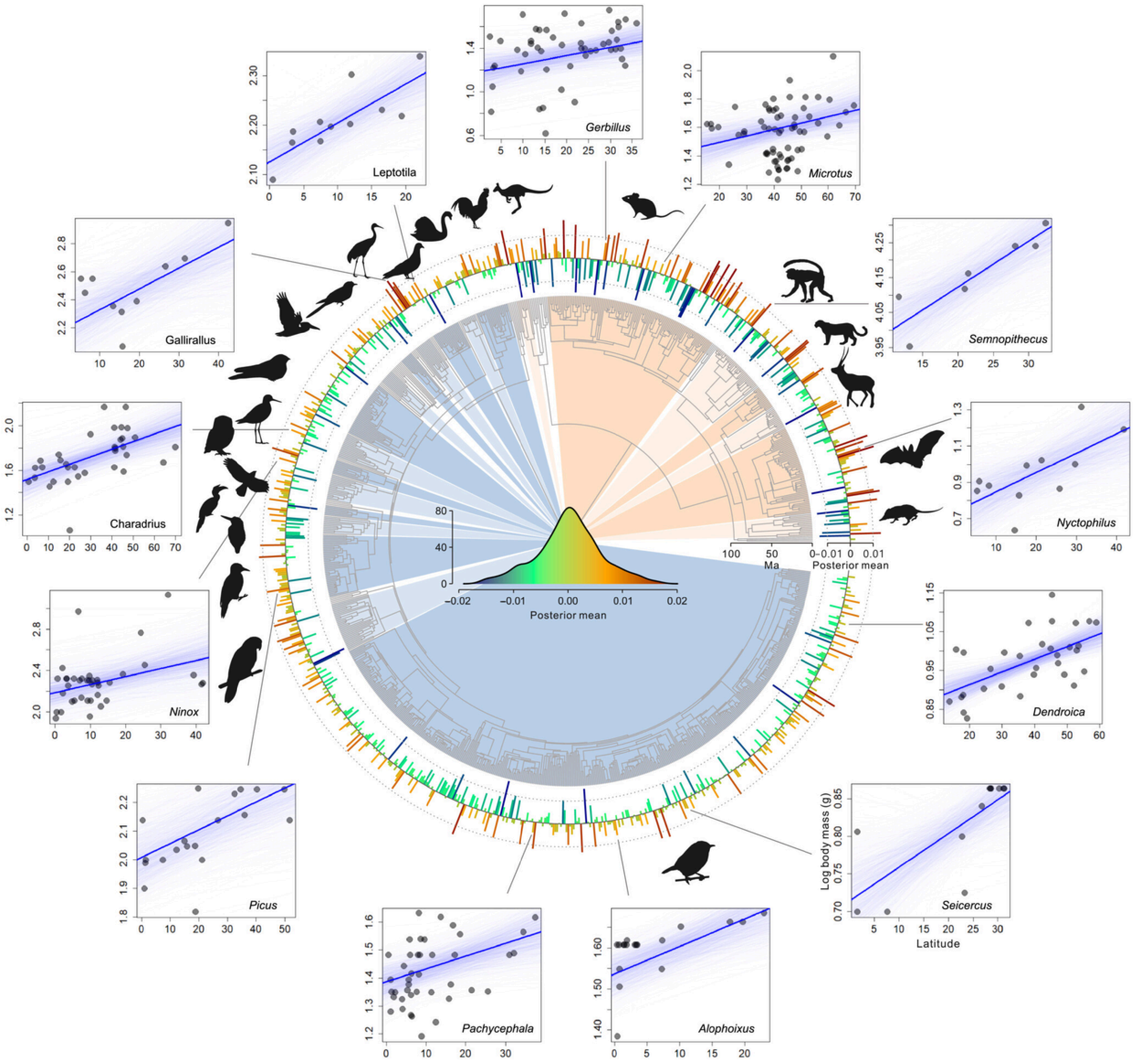
Smaller body size



Endotherms

Colder temperature

Larger body size



He et al. 2023 Global Change Biology

TRAIT DIVERSITY ACROSS SPACE

Bergmann's Rule

Wolmack and Bell 2020 JEB

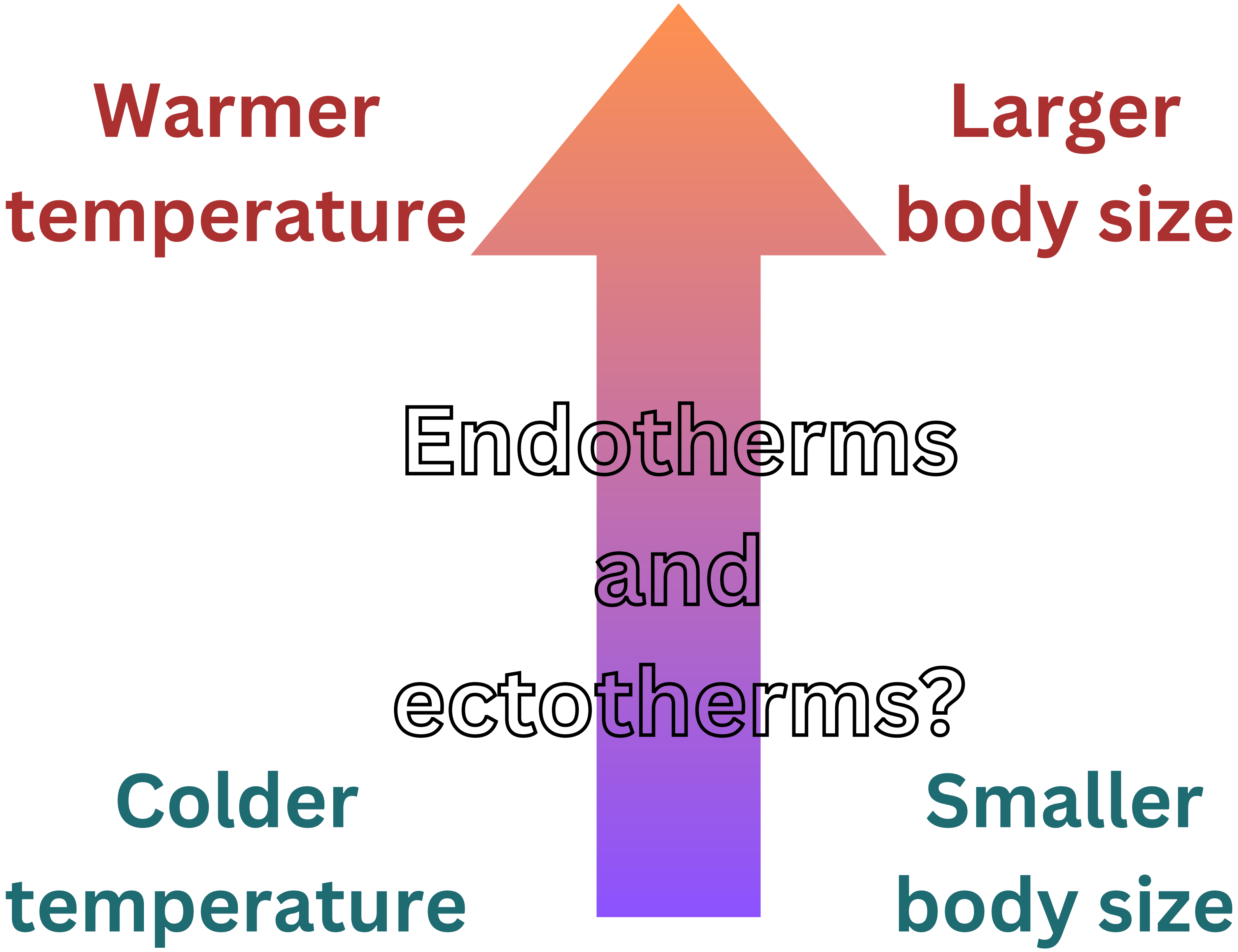
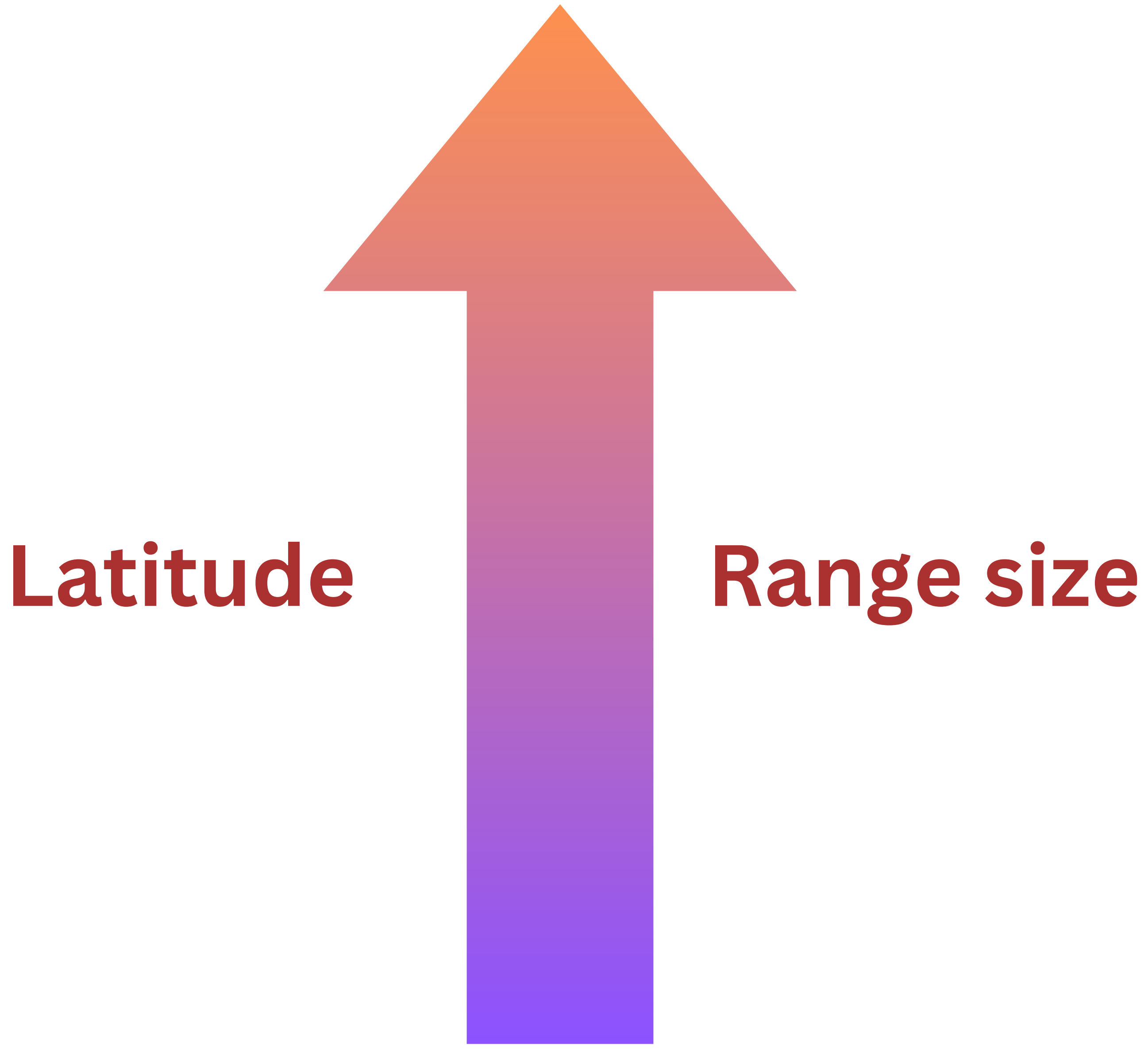


TABLE 1 Studies evaluating Bergmann's rule in extant tetrapod ectotherms

Support for Bergmann's?	Inter- or Intraspecific?	Clade	No of species	Geographic areas	Study
Yes	Inter	Anurans, urodeles, and snakes	657, 189, 1,222	Worldwide	Lindsey (1966)
	Intra	*Pseudacris triseriata* (boreal chorus frog)	1	Northern Colorado, US	Pettus & Angleton (1967)
	Intra	*Rana sylvatica* (wood frog)	1	Virginia, US	Berven (1982)
	Intra	Anurans and salamanders	16,18	Not specified	Ashton (2002)
	Intra	Turtles	23	Not specified	Ashton & Feldman (2003)
	Intra	Amphibians and turtles	34, 23	Not specified	de Queiroz & Ashton (2004)
	Intra	*Limnodynastes peronii* and *L. tasmaniensis*	2	South Australia	Schäuble (2004)
	Inter	*Liolaemus* lizards	34	South America	Cruz, Fitzgerald, Espinoza, & Schulte Ii (2005)
	Intra	*Schistometopum thomense*	1	São Tomé Island	Measey & Van Dongen (2006)
	Inter/ assemblage-based	anurans	112	Europe and North America	Olalla-Tárraga and Rodríguez (2007)
	Inter/ assemblage-based	anurans	131	Brazilian Cerrado	Olalla-Tárraga et al. (2009)
	Inter/ assemblage-based	*Plethodon* salamanders	44	eastern North America	Olalla-Tárraga et al. (2010)
	Intra	*Bufo andrewsi* (Asiatic toad)	1	western China	Liao & Lu (2012)
	Intra	*Rhinoderma darwinii* (Darwin's frog)	1	Chile	Valenzuela-Sánchez et al. (2015)
	Inter/ assemblage-based	Anurans	2,761	The Americas	Amado et al. (2019)
No	Inter	Lizards and turtles	935, 154	worldwide	Lindsey (1966)
	Intra	Squamates	83	Not specified	Ashton & Feldman (2003)
	Intra	Squamates	83	Not specified	de Queiroz & Ashton (2004)
	Intra	*Rana temporaria* (common frog)	1	Scandinavia	Laugen, Laurila, Jönsson, Söderman, & Merilä (2005)
	Inter/ assemblage-based	Urodeles	153	Europe and North America	Olalla-Tárraga and Rodríguez (2007)
	Inter	*Liolaemus* lizards	26	South America	Pincheira-Donoso et al. (2008)
	Intra and inter	Amphibians	59	United States	Adams & Church (2008)

TRAIT DIVERSITY ACROSS SPACE

Rapoport's Rule



TRAIT DIVERSITY ACROSS SPACE
Island's rule (Foster's rule)

NATURE April 18, 1964 VOL. 202

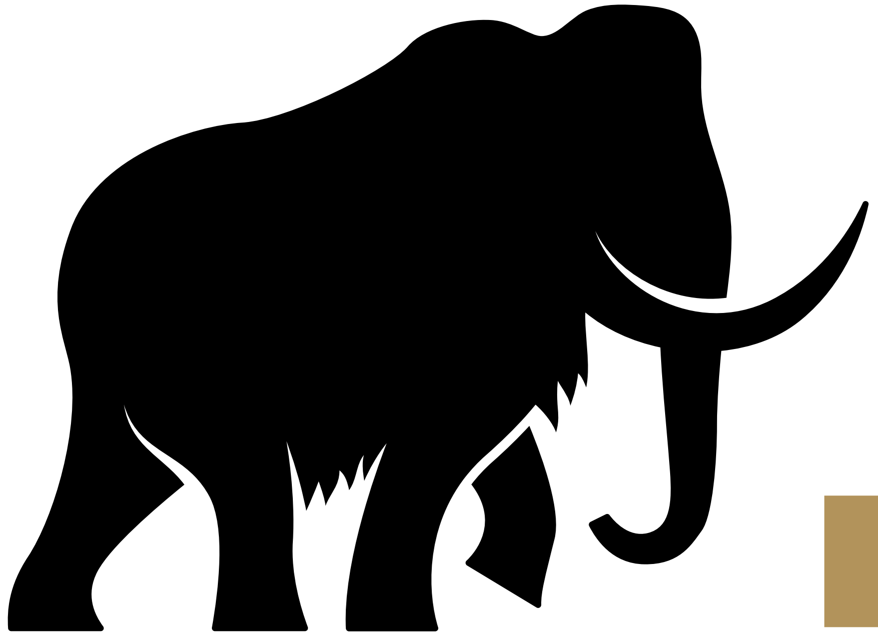
EVOLUTION OF MAMMALS ON ISLANDS

By DR. J. BRISTOL FOSTER
Department of Zoolcgy, Royal College (University of East Africa), Nairobi, Kenya

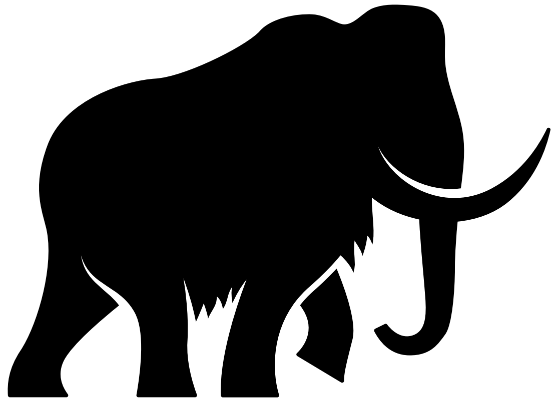
A NEW EVOLUTIONARY LAW

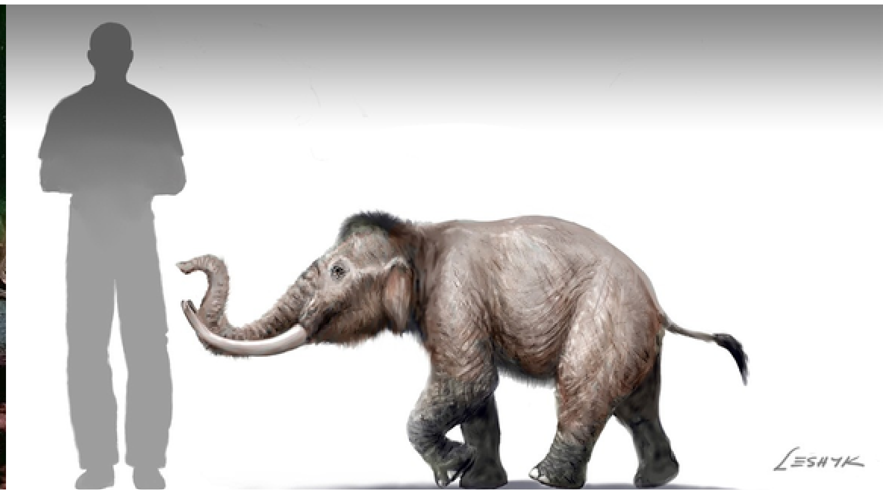
Leigh Van Valen
Department of Biology
The University of Chicago
Chicago, Illinois 60637

TRAIT DIVERSITY ACROSS SPACE
Island's rule (Foster's rule)



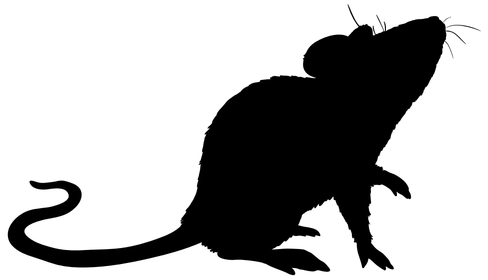
(island dwarfism)





Continent

island



Continent

island

(island gigantism)

TRAIT DIVERSITY ACROSS SPACE
Island's rule (Foster's rule)

Journal of Biogeography (*J. Biogeogr.*) (2005) **32**, 1683–1699

SPECIAL PAPER

Body size evolution in insular vertebrates: generality of the island rule

Mark V. Lomolino*

PROCEEDINGS OF THE ROYAL SOCIETY B

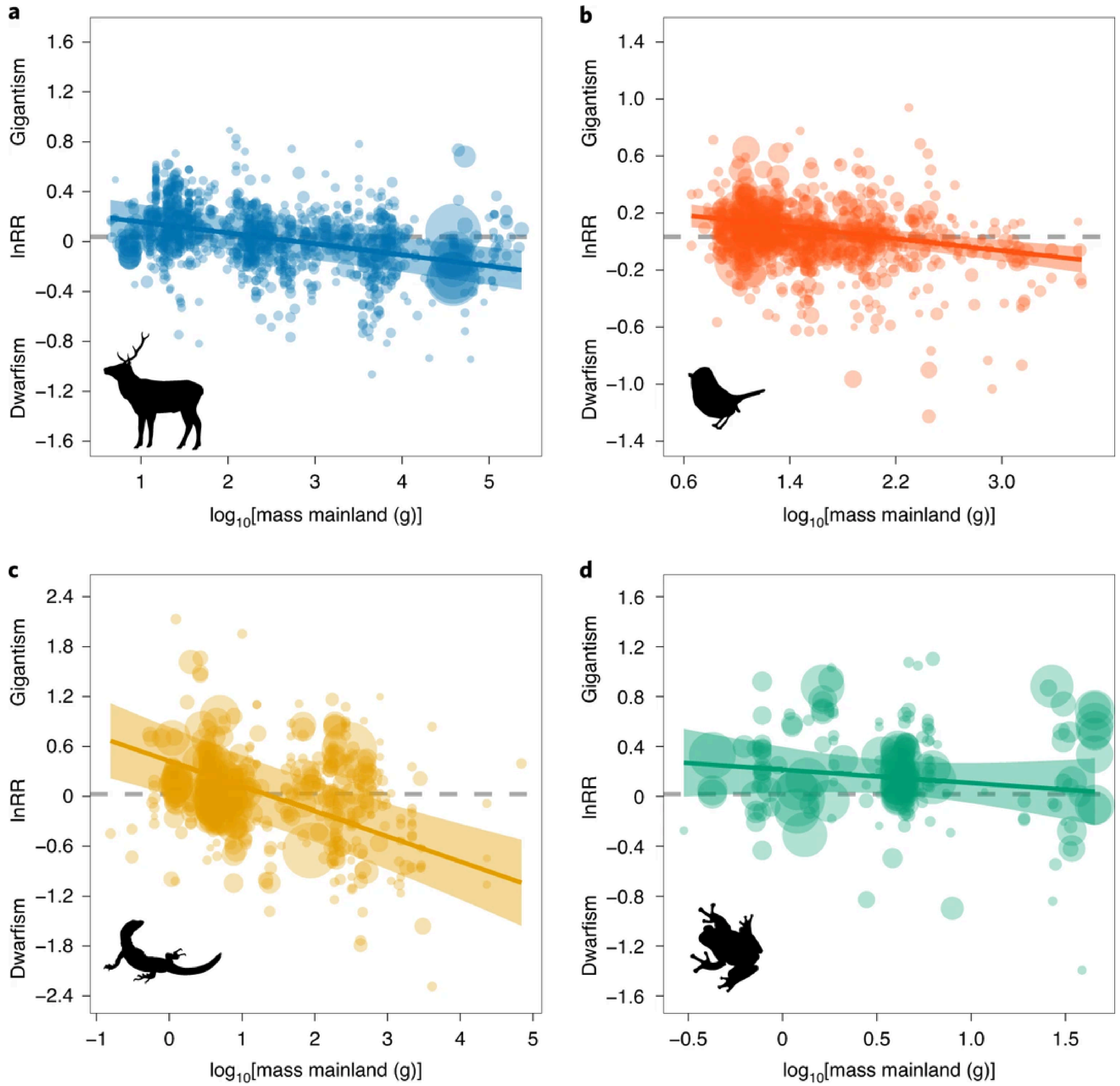
Proc. R. Soc. B (2008) **275**, 141–148
doi:10.1098/rspb.2007.1056
Published online 7 November 2007

The island rule: made to be broken?

Shai Meiri[1,*], Natalie Cooper[2,3] and Andy Purvis[2]

[1]*NERC Centre for Population Biology, and* [2]*Division of Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*
[3]*Institute of Zoology, Zoological Society of London Regents Park, London NW1 4RY, UK*

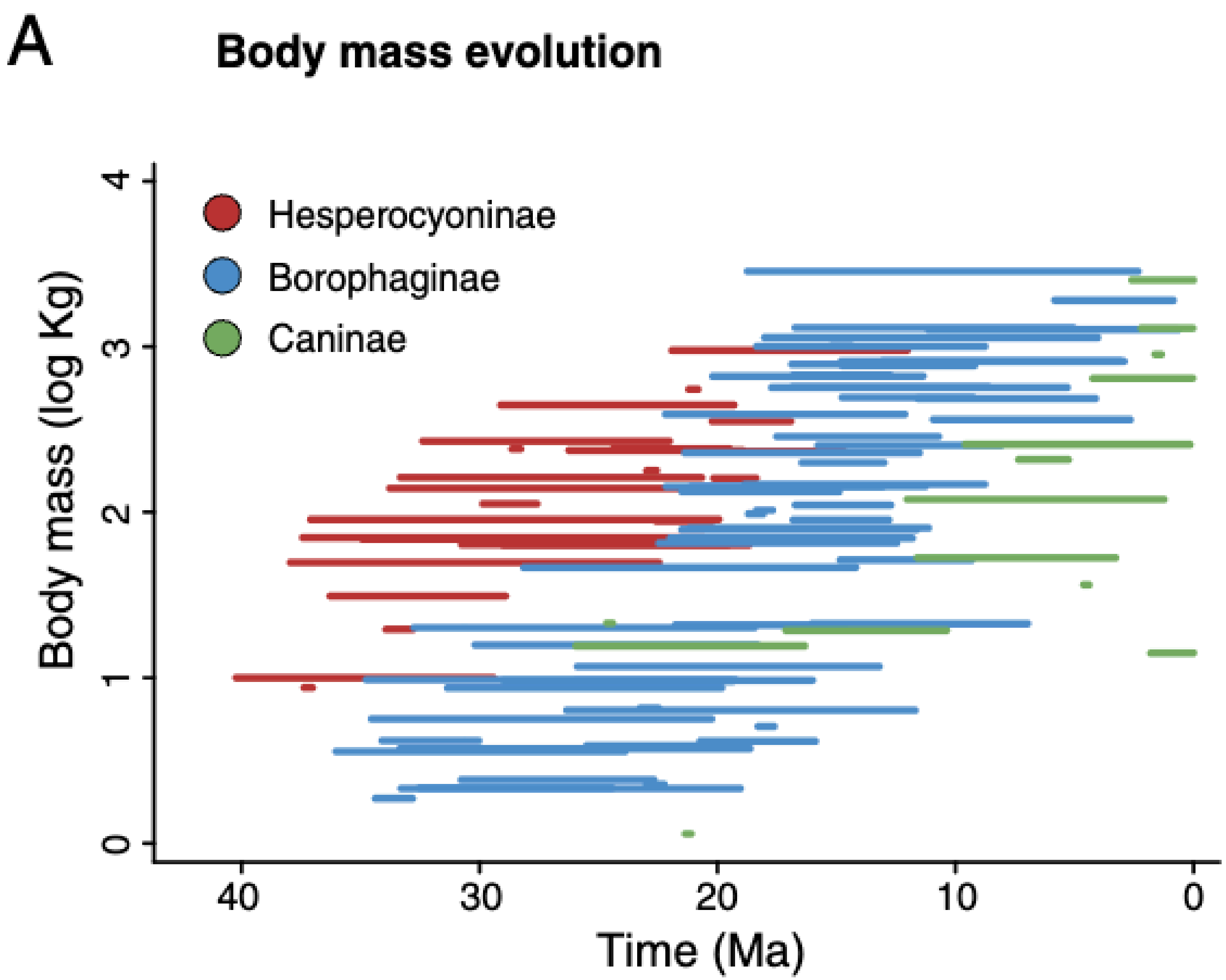
TRAIT DIVERSITY ACROSS SPACE
Island’s rule (Foster’s rule)



Benítez-López et al. 2021 Nat Eco Evo

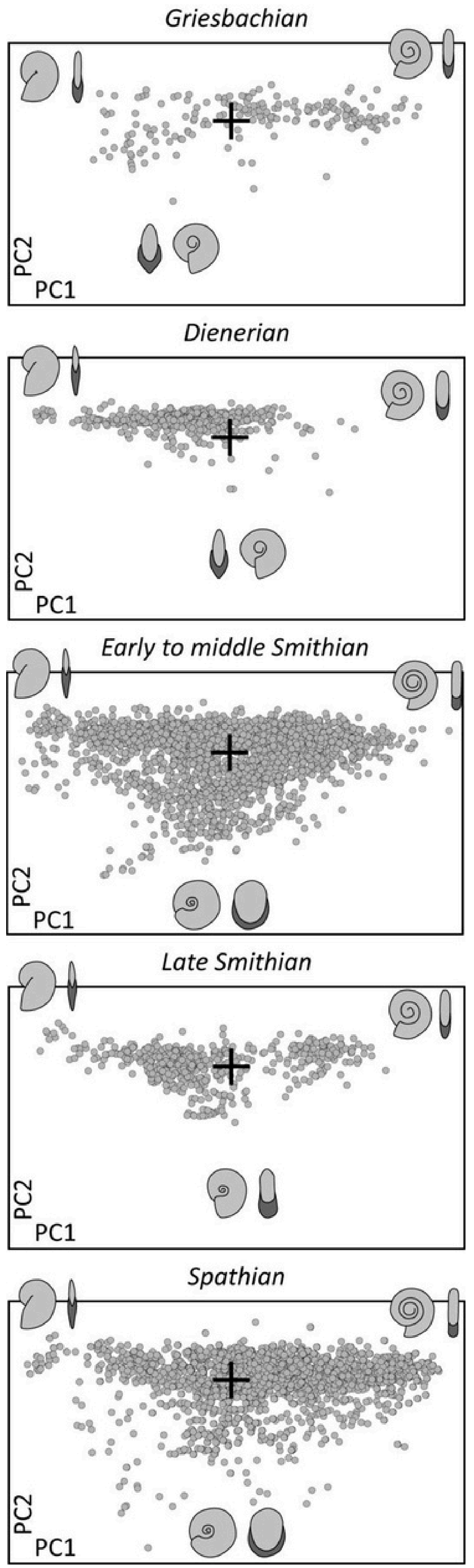
TRAIT DIVERSITY ACROSS TIME

TRAIT DIVERSITY ACROSS TIME



Silvestro et al. 2015 PNAS

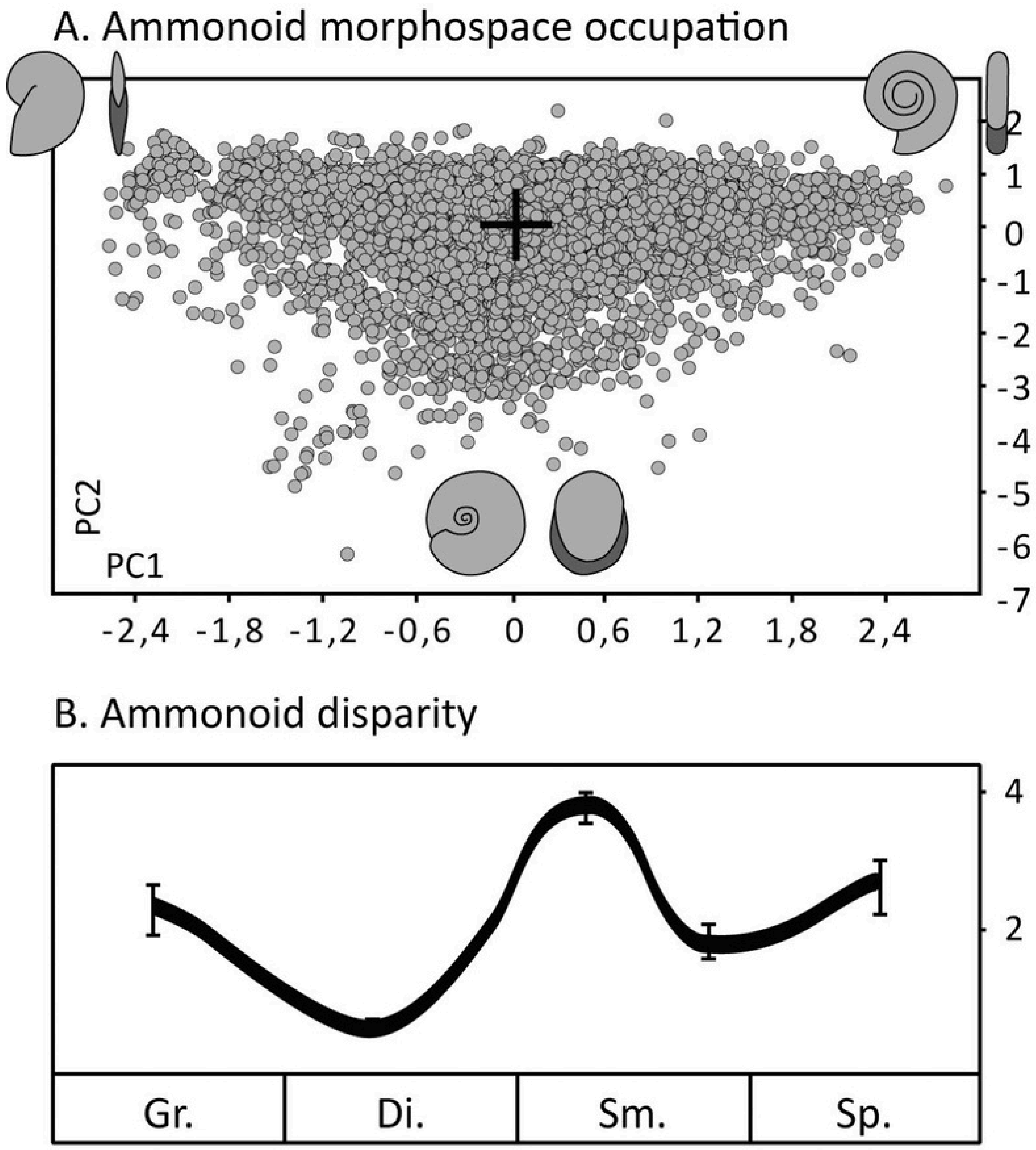
TRAIT DIVERSITY ACROSS TIME

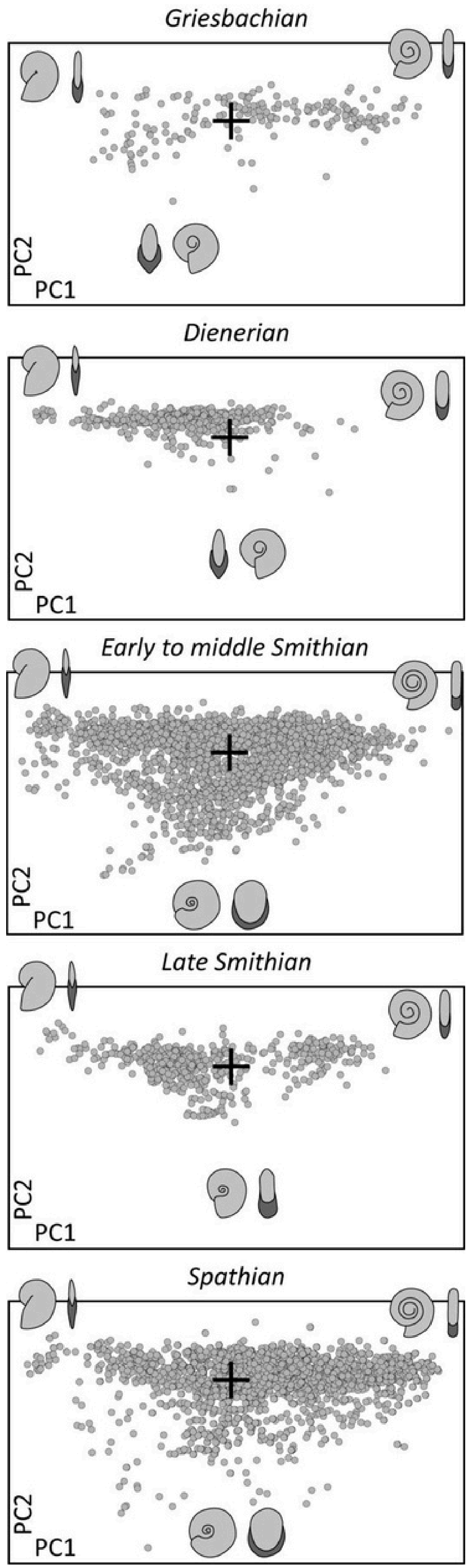


Extinction event

Brosse et al. 2013 JGS

TRAIT DIVERSITY ACROSS TIME

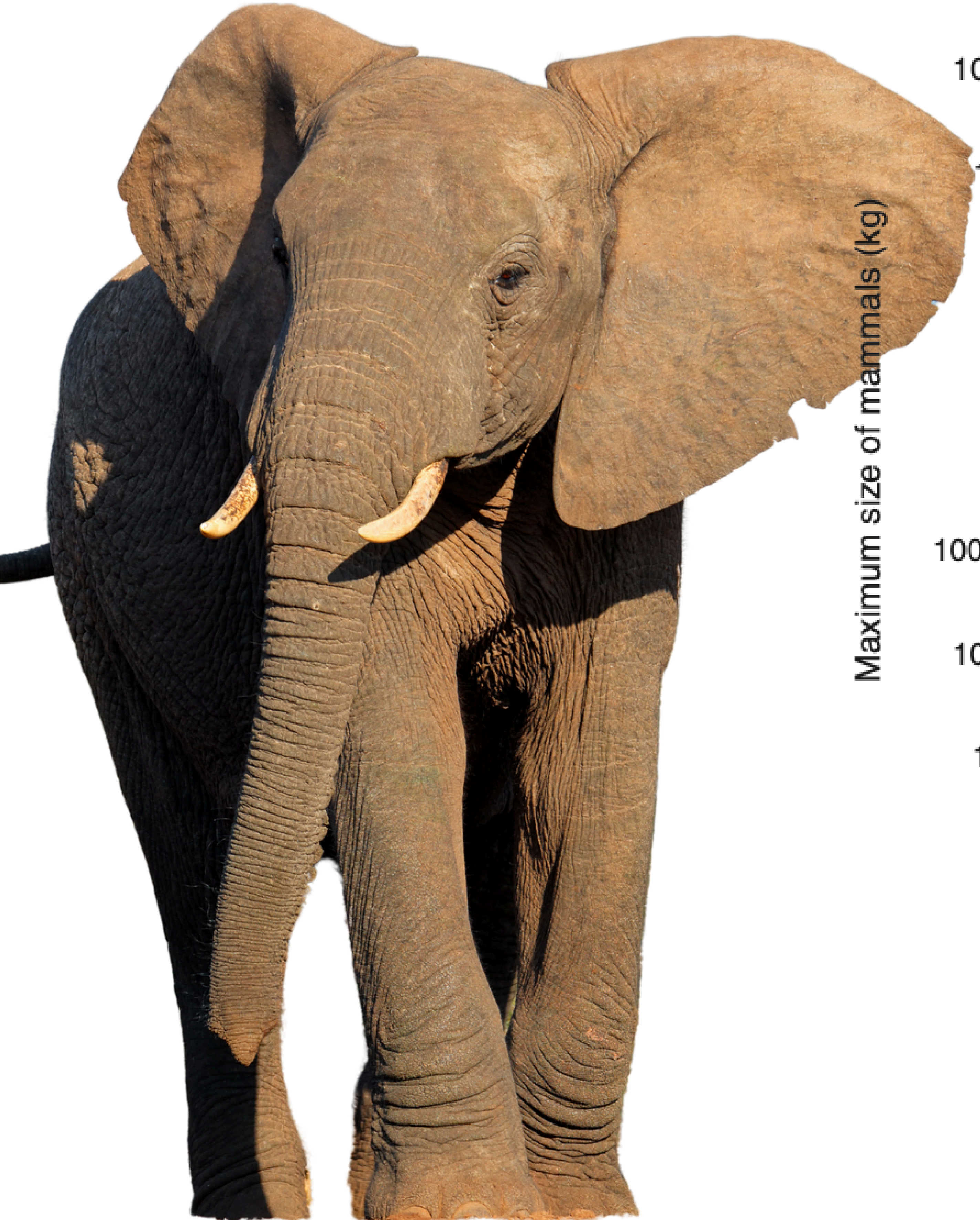


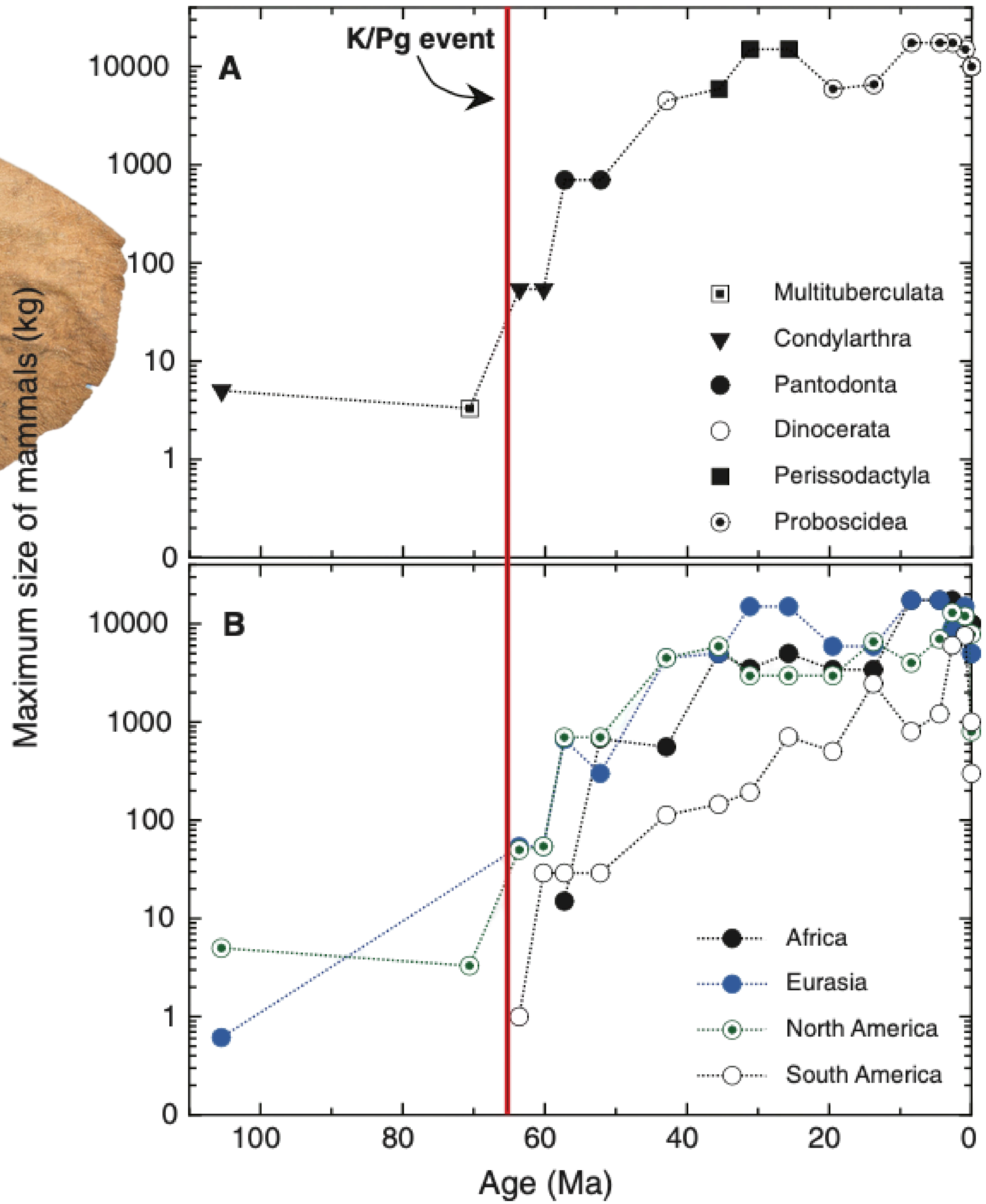


Extinction event

Brosse et al. 2013 JGS

TRAIT DIVERSITY ACROSS TIME

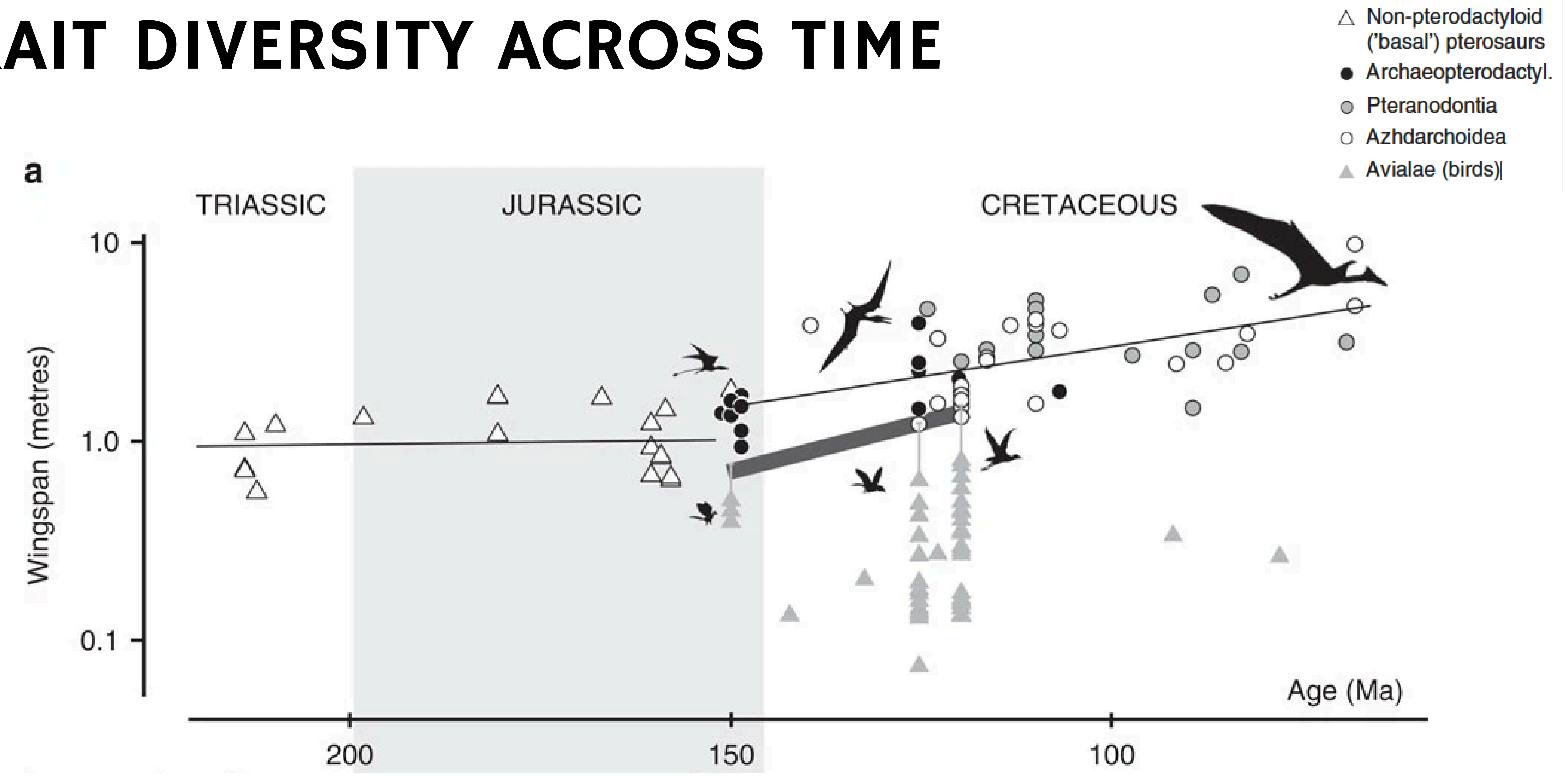




Smith et al. 2010 Science

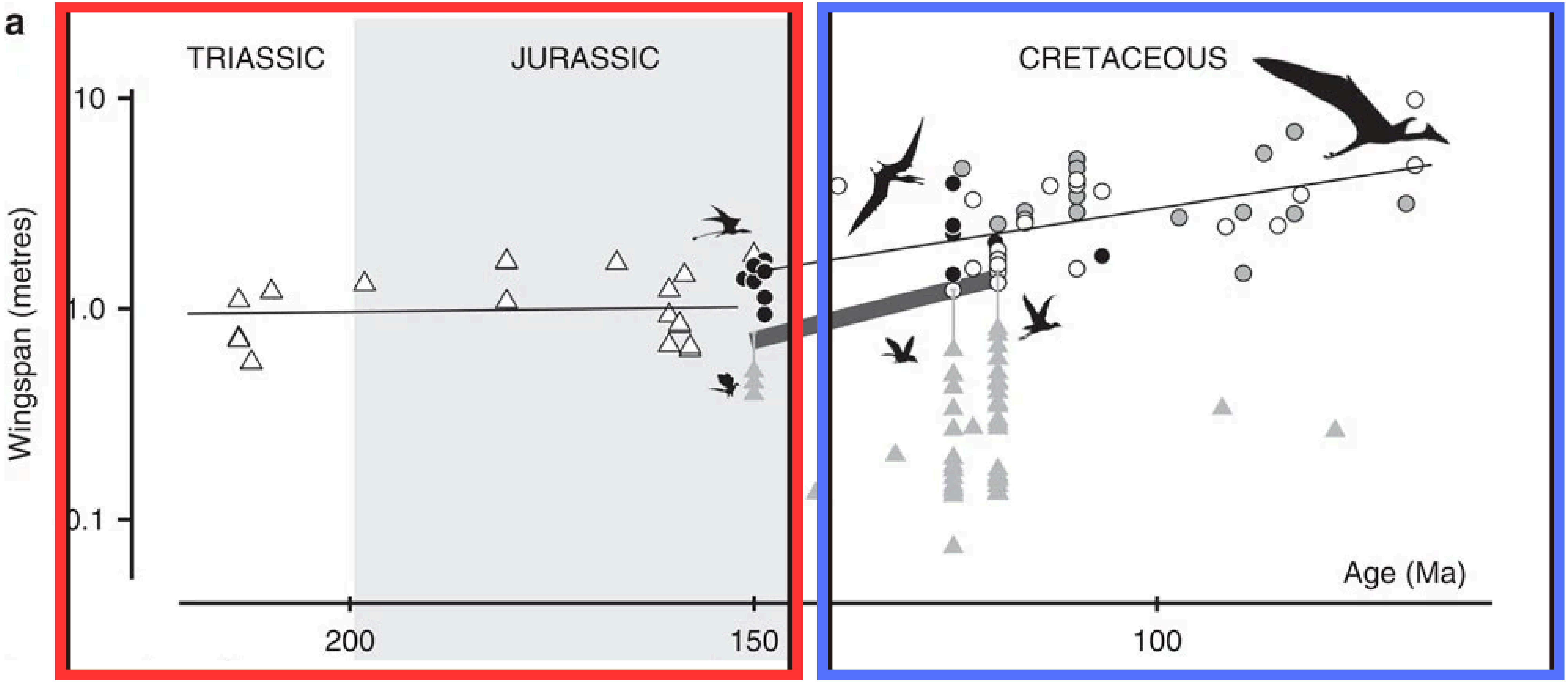
Cope's rule

TRAIT DIVERSITY ACROSS TIME



Benson et al. 2014 Nat Comm

TRAIT DIVERSITY ACROSS TIME



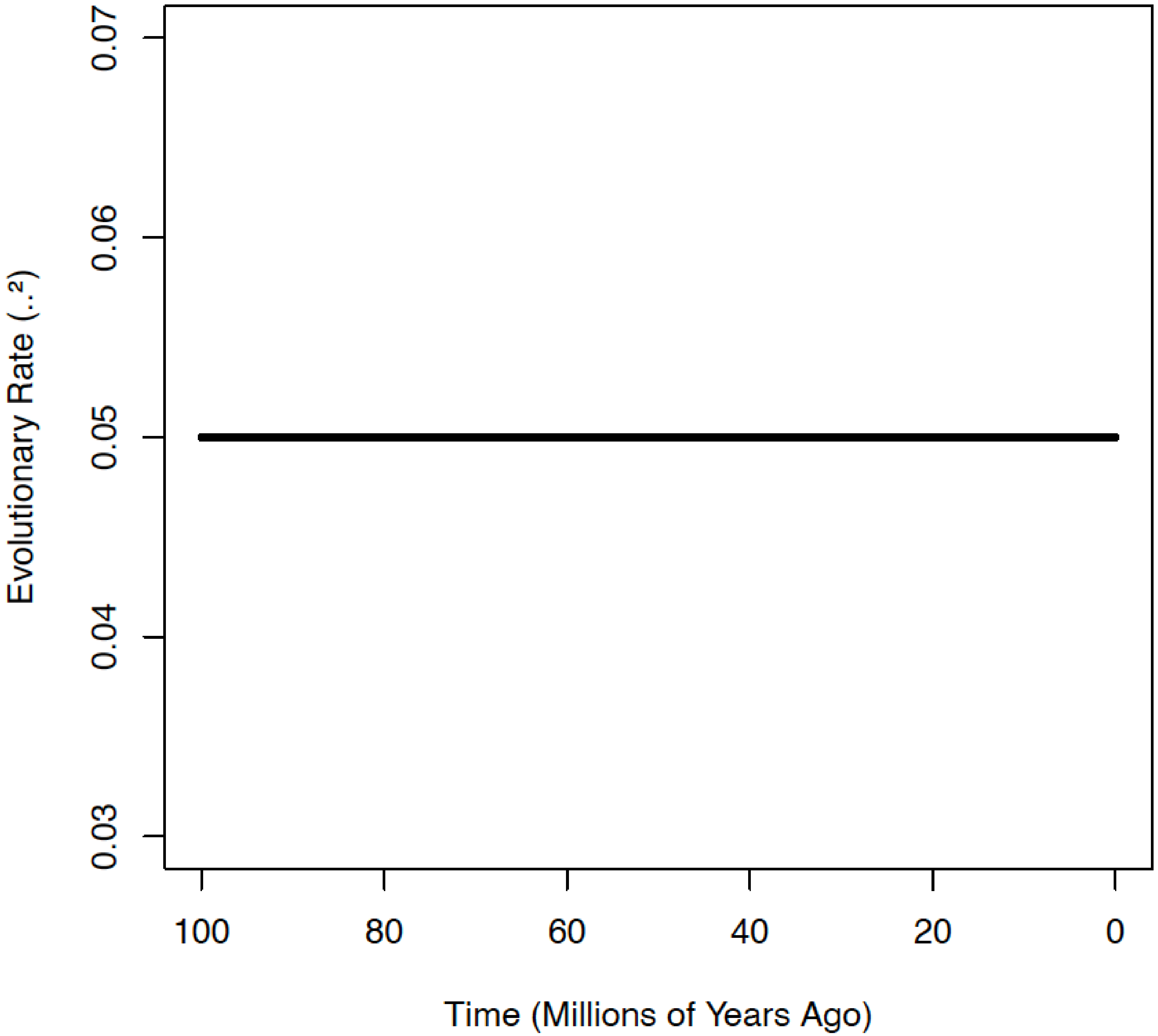
The trajectories of morphological evolution in a group can change over time.

Benson et al. 2014 Nat Comm

TRAIT DIVERSITY ACROSS TIME

Brownian motion:

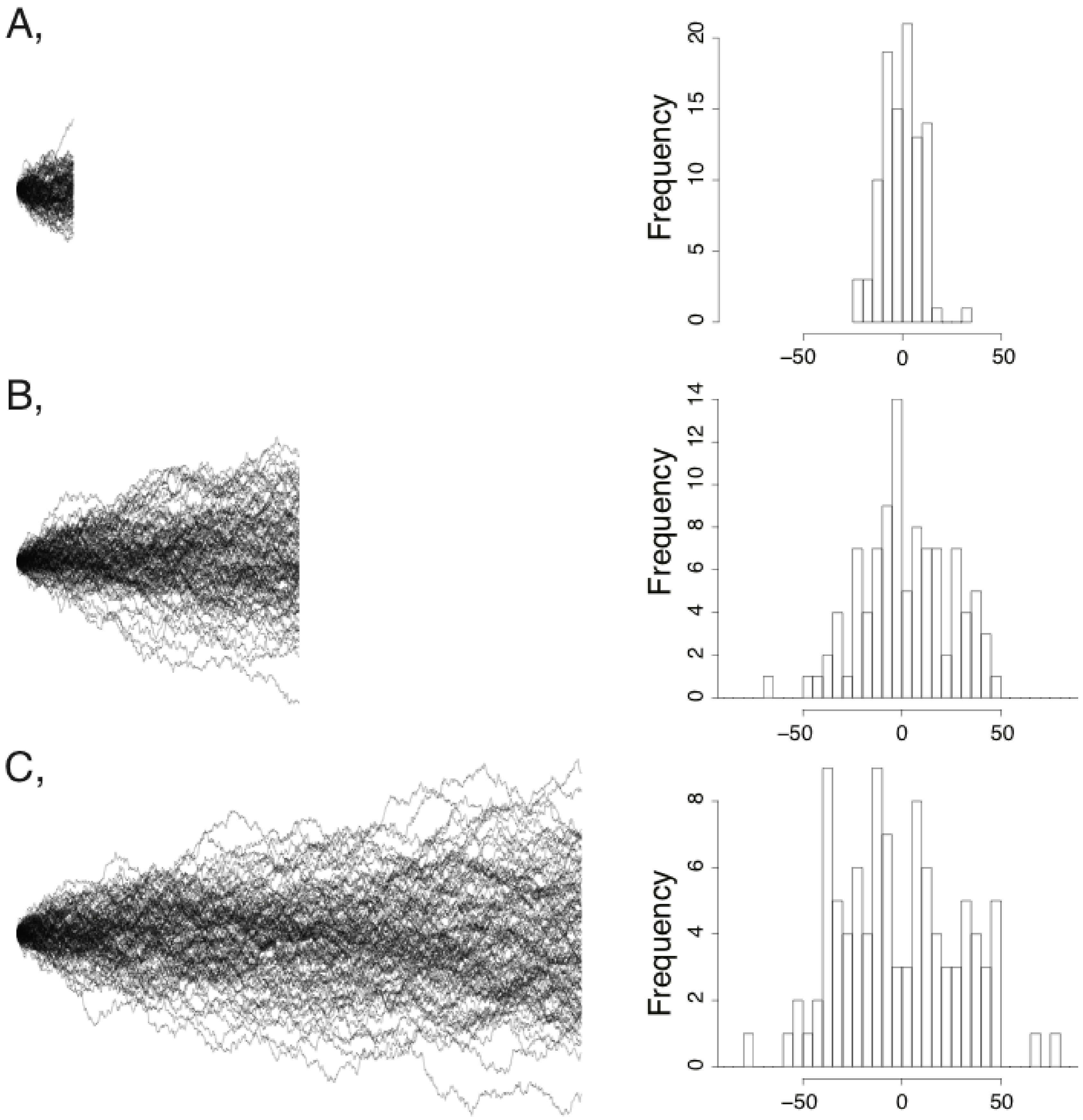
$$dX(t) = \sigma^2 * t$$



TRAIT DIVERSITY ACROSS TIME

Brownian motion:

$$dX(t) = \sigma^2 * t$$



www.lukejharmon.github.io

TRAIT DIVERSITY ACROSS TIME

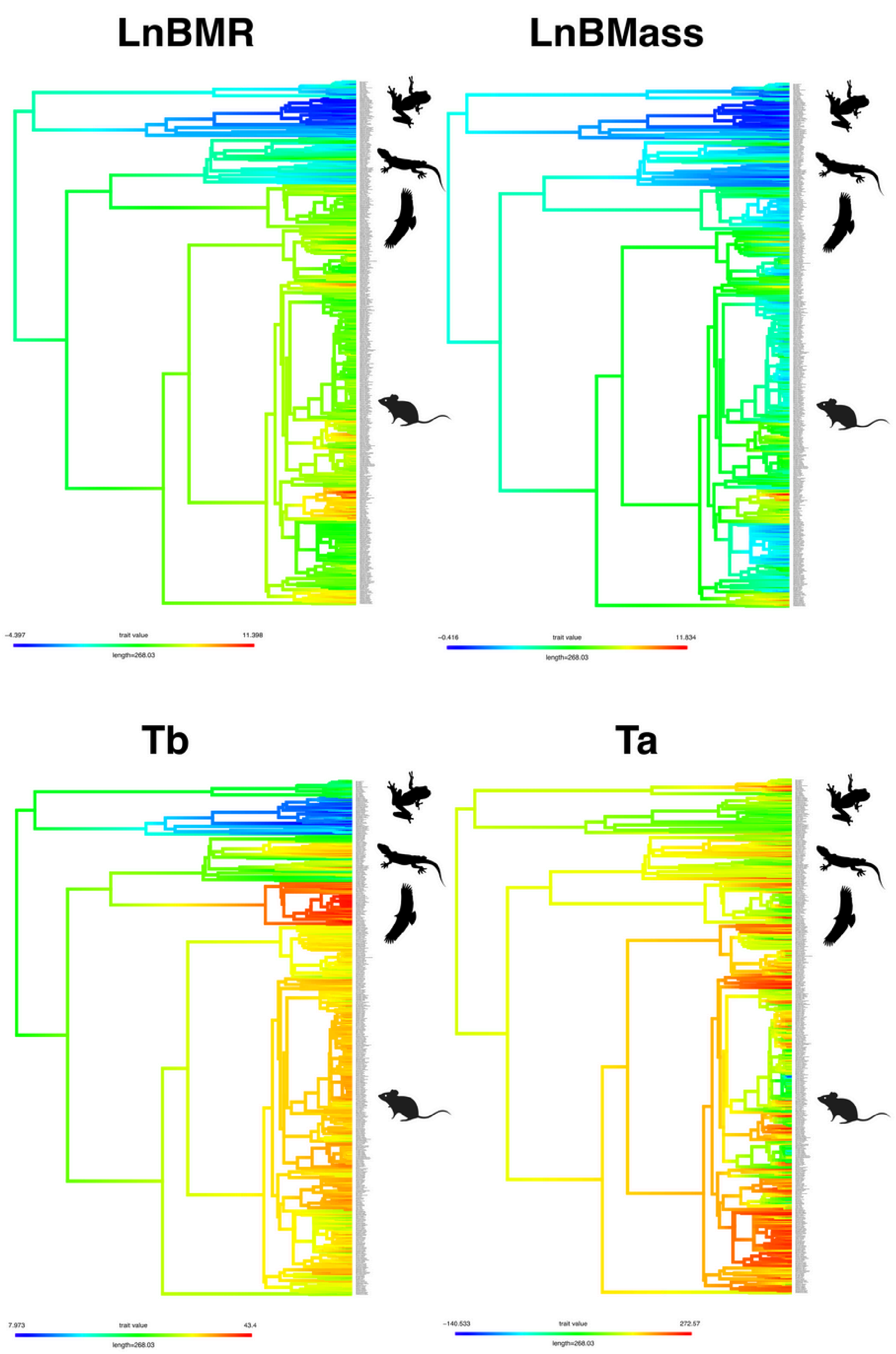
Brownian motion:

Ancestral character reconstruction

Given a set of trait values at the tips, what might the traits of their ancestors have looked like?

- Uncertainity increases deeper in the tree

- Without fossil data, ancestral state estimates are likely to be uncertain



Reconstructions made using "fastAnc()" in phytools R package

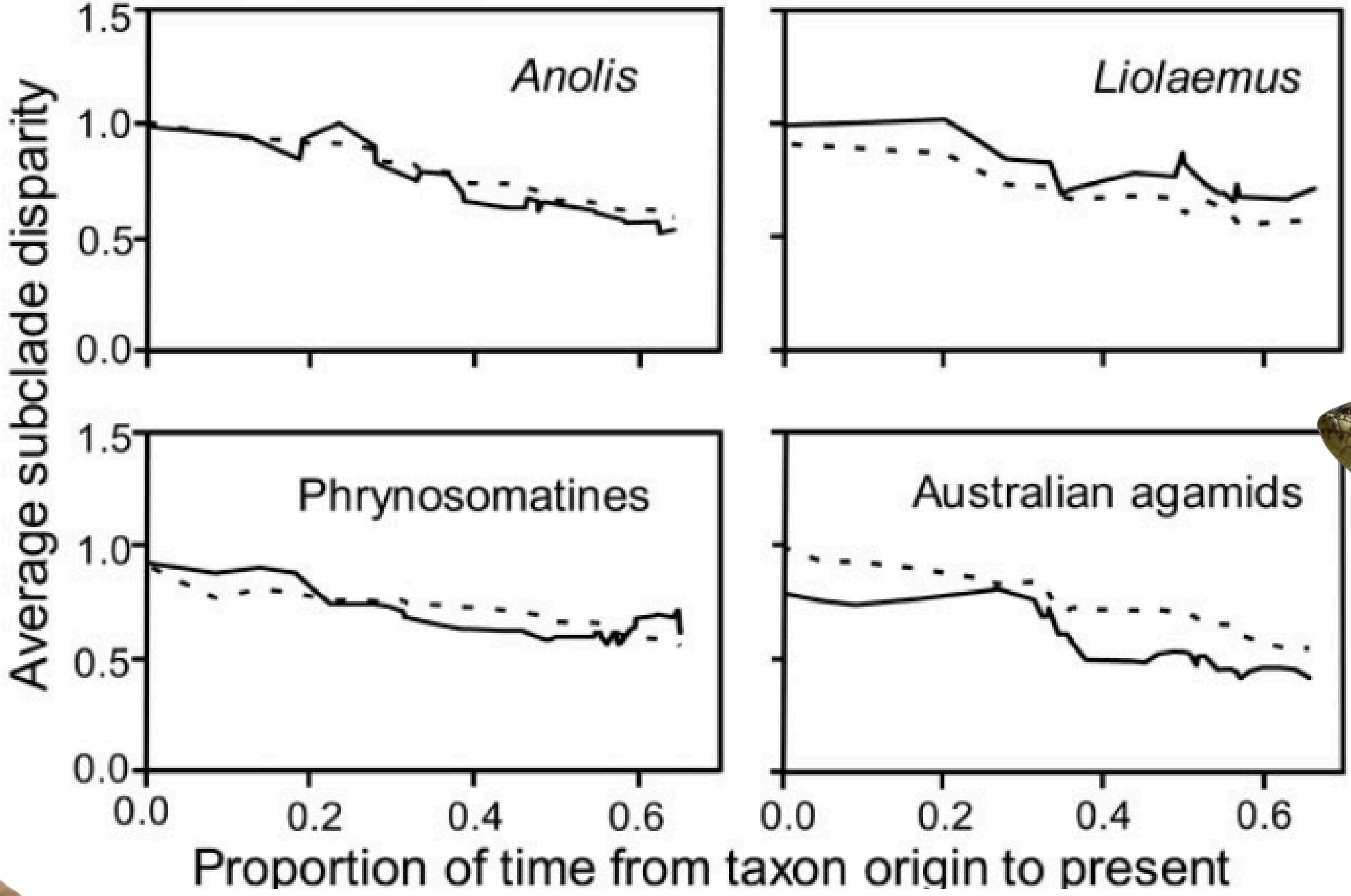
TRAIT DIVERSITY ACROSS TIME

Brownian motion:

Diversity through time plots (DTT)

Tempo and Mode of Evolutionary Radiation in Iguanian Lizards

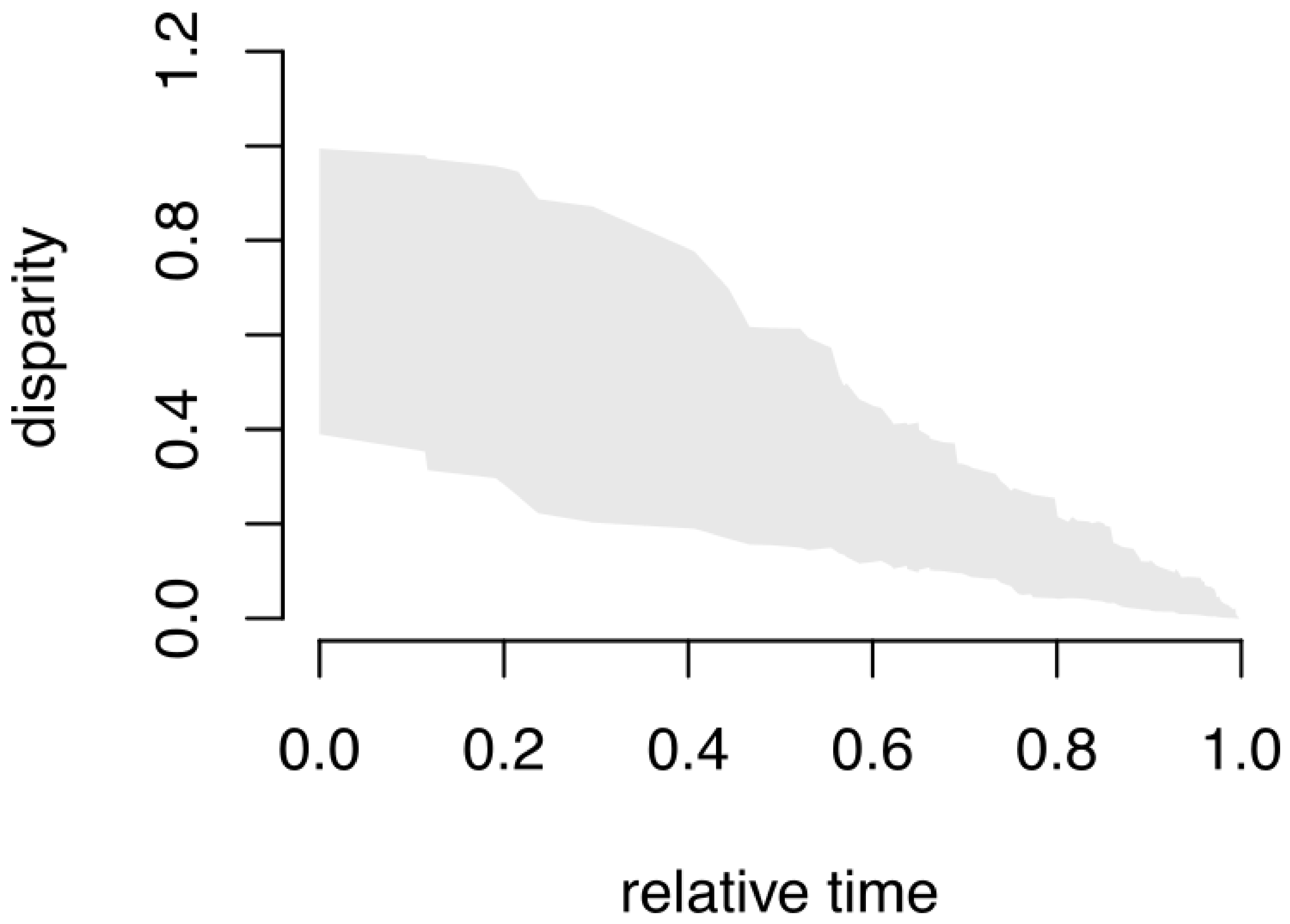
Luke J. Harmon,* James A. Schulte II,† Allan Larson, Jonathan B. Losos



TRAIT DIVERSITY ACROSS TIME

Brownian motion:

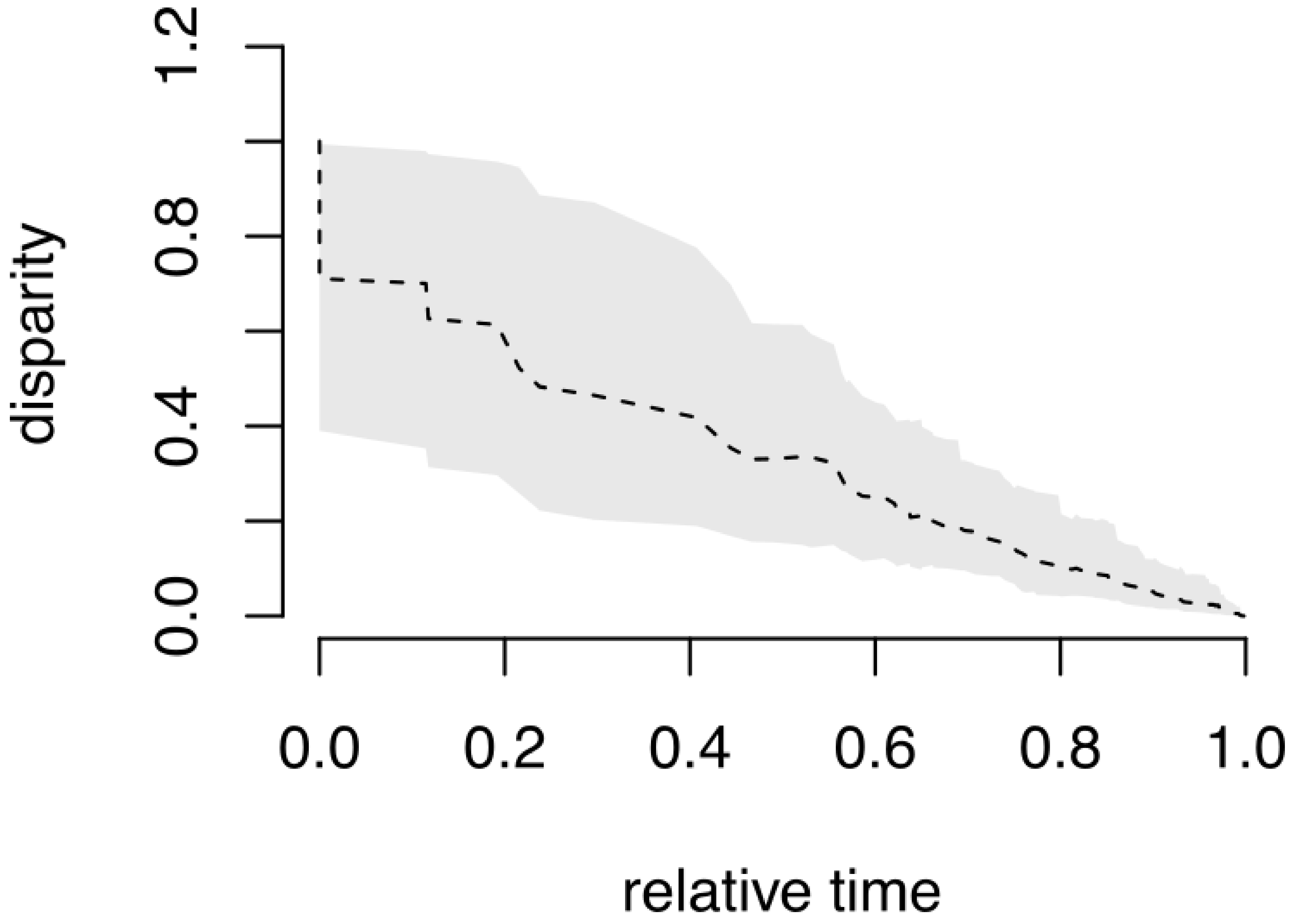
Diversity through time plots (DTT)



TRAIT DIVERSITY ACROSS TIME

Brownian motion:

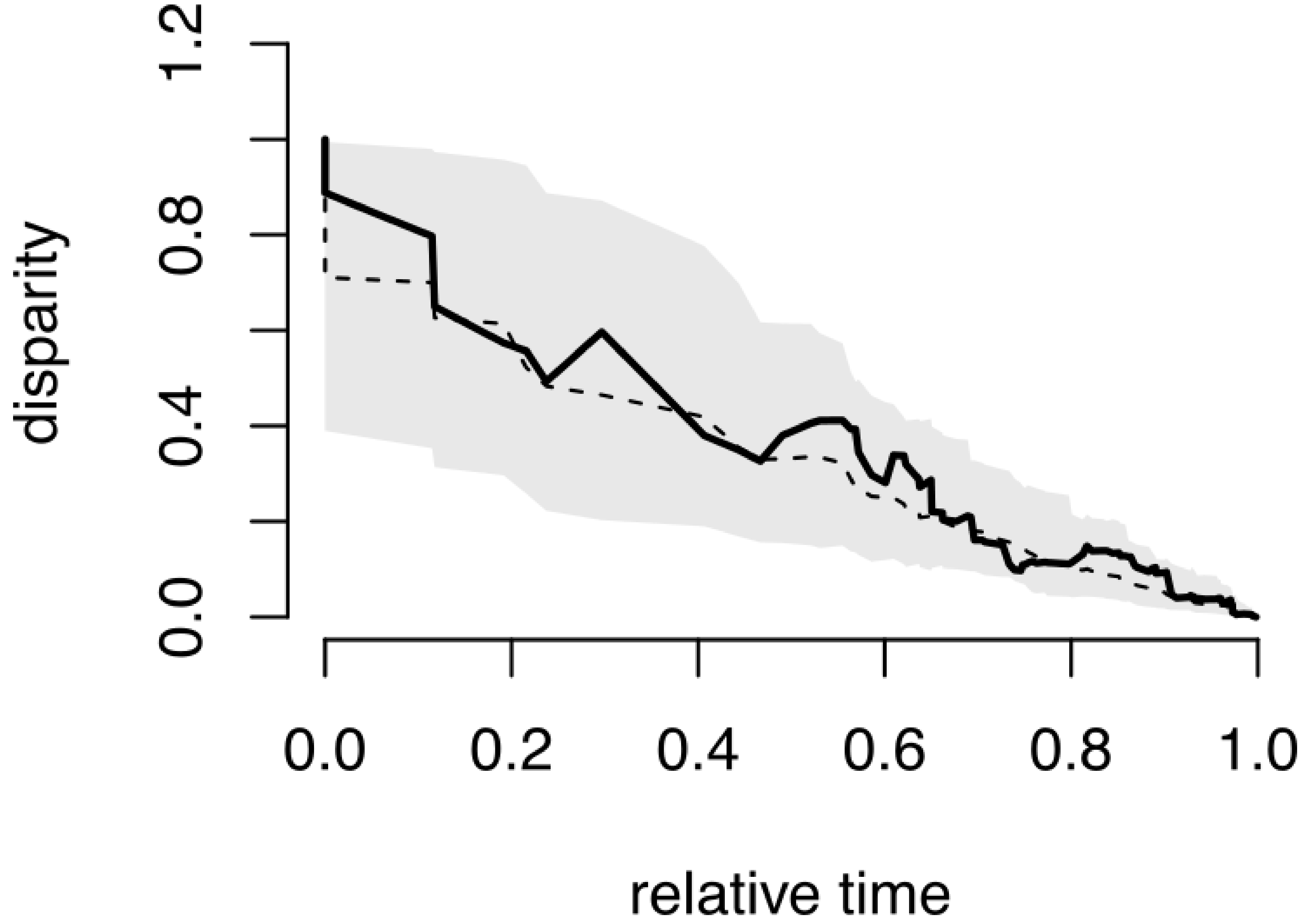
Diversity through time plots (DTT)



TRAIT DIVERSITY ACROSS TIME

Brownian motion:

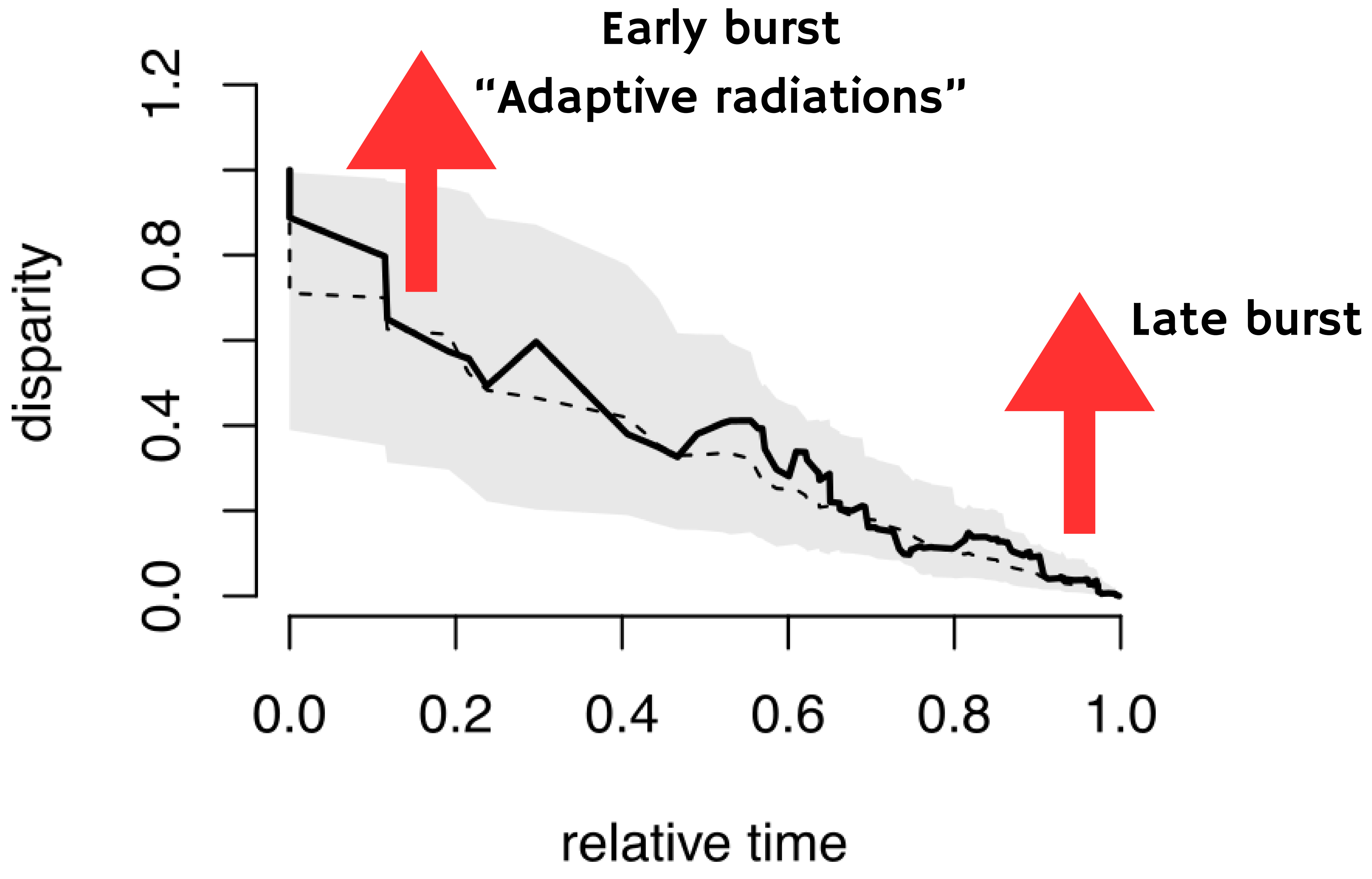
Diversity through time plots (DTT)



TRAIT DIVERSITY ACROSS TIME

Brownian motion:

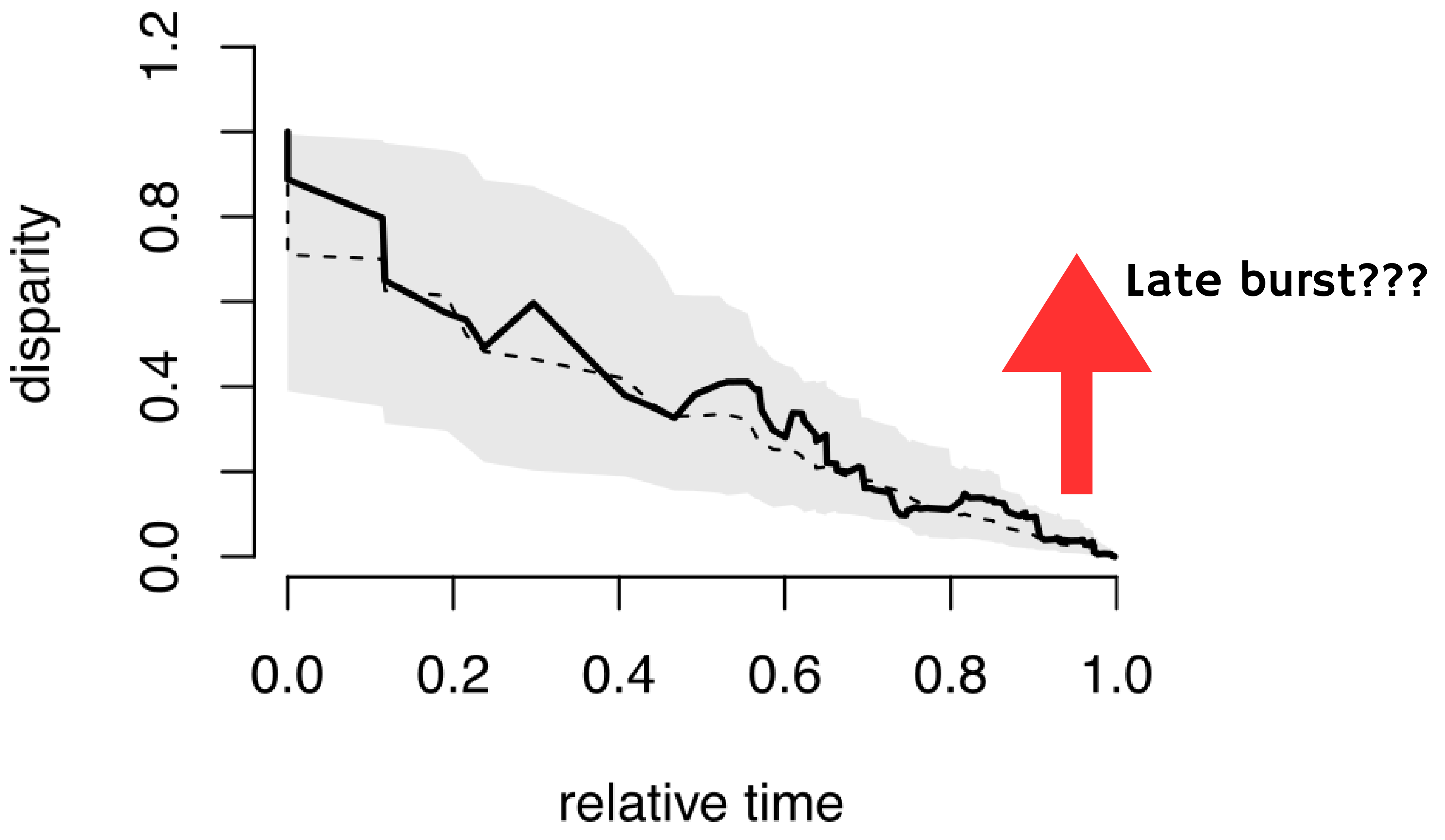
Diversity through time plots (DTT)

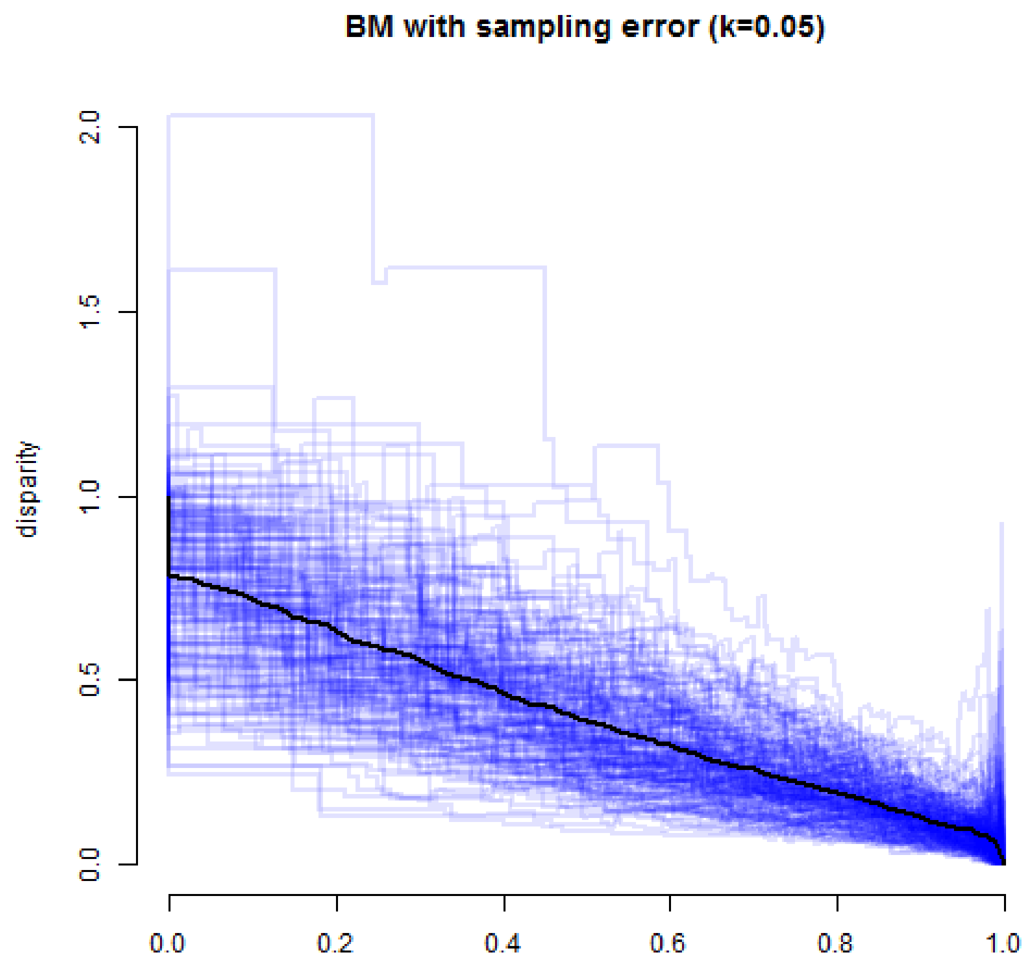


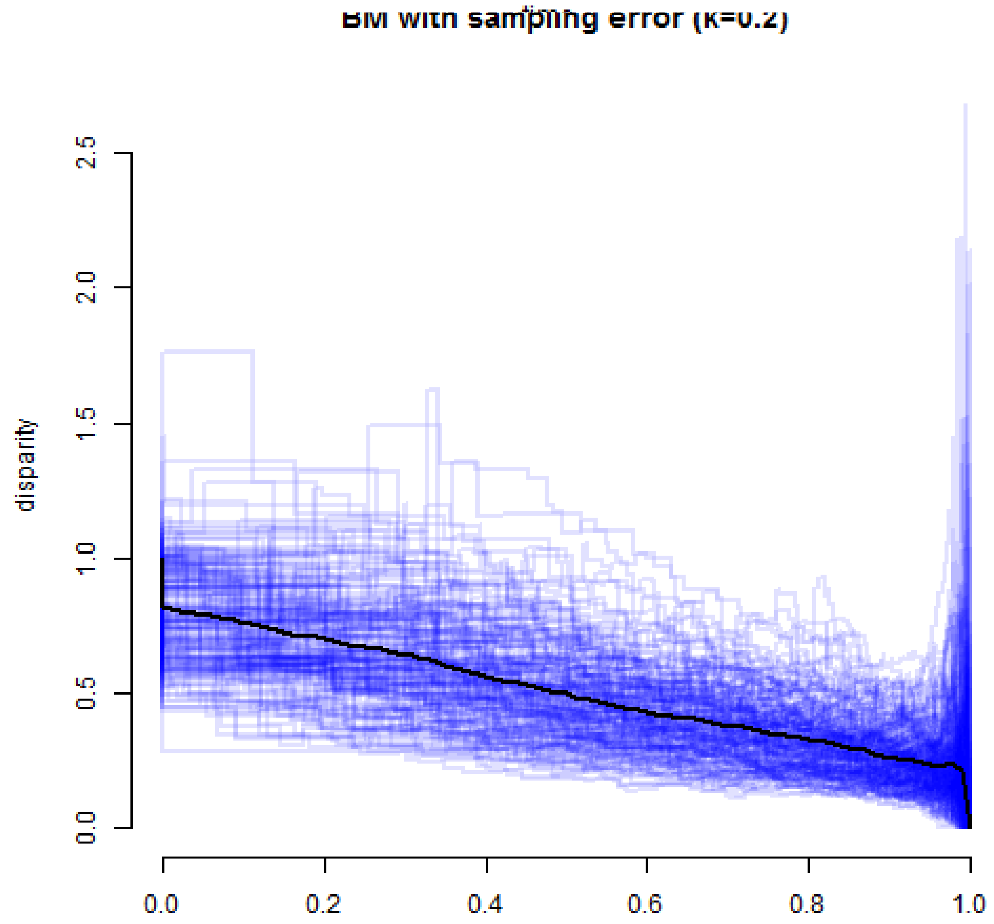
TRAIT DIVERSITY ACROSS TIME

Brownian motion:

Diversity through time plots (DTT)





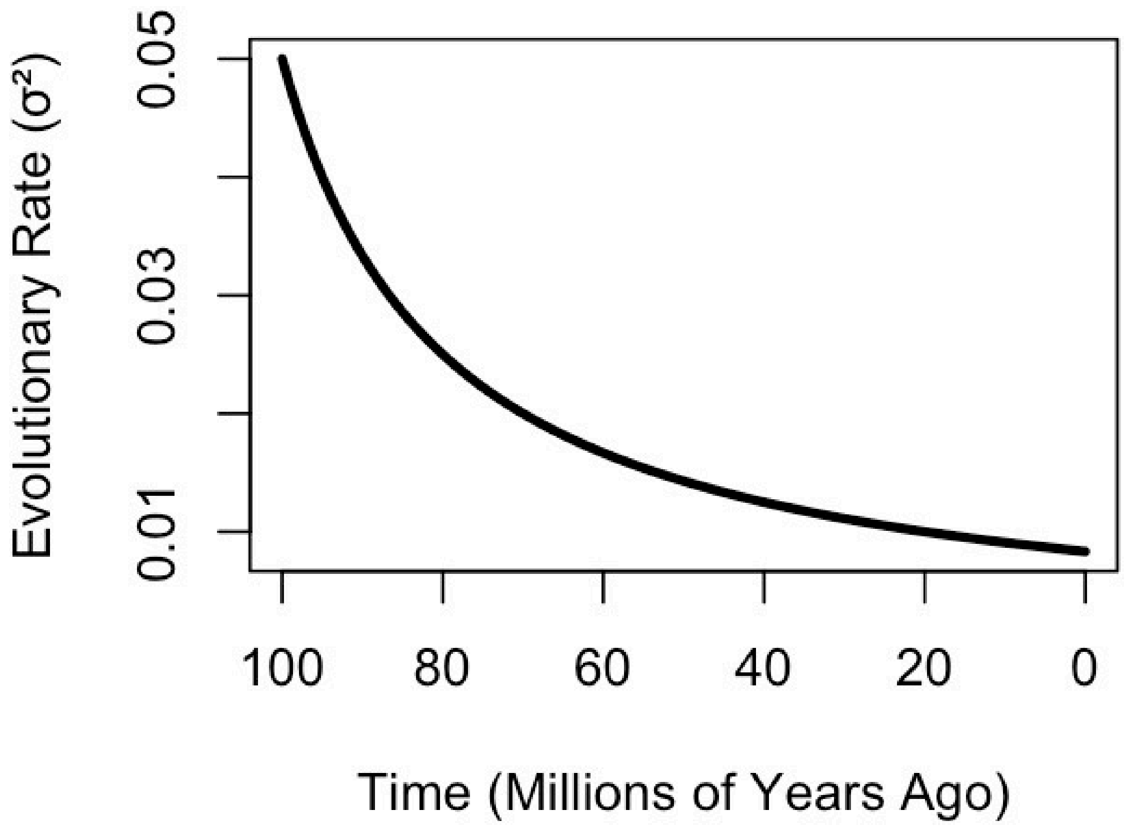


http://blog.phytools.org

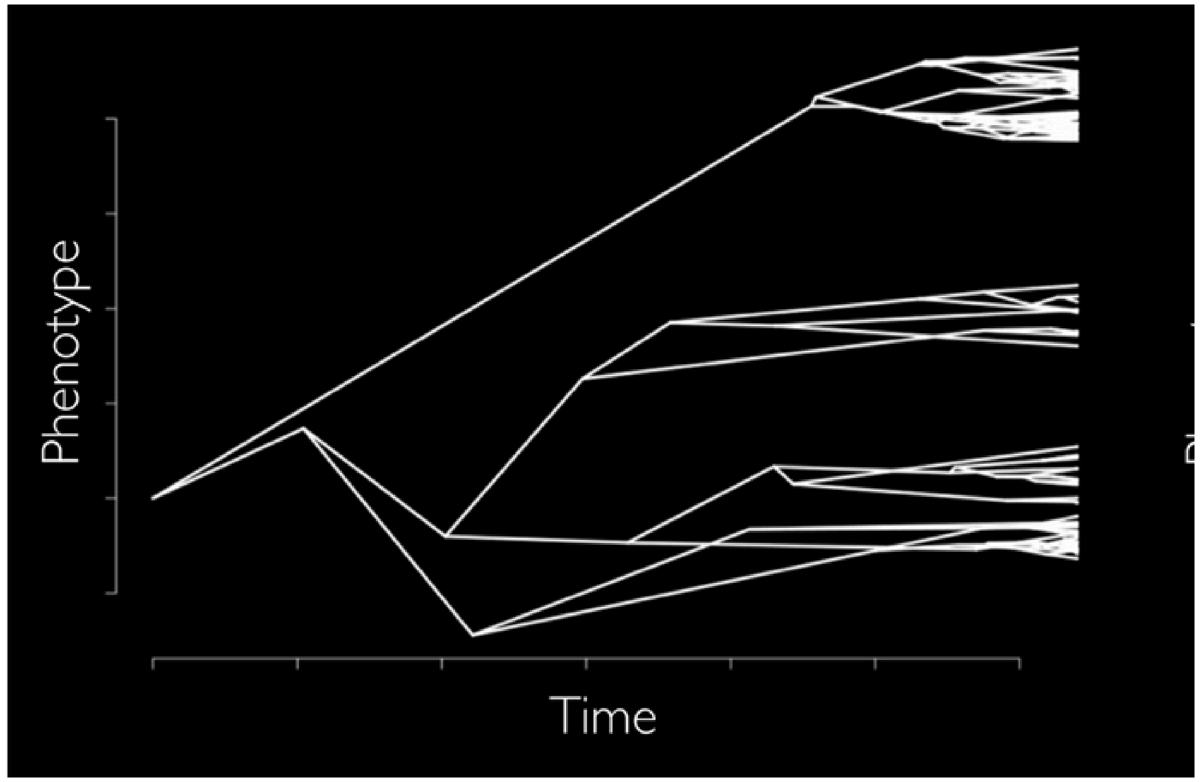
TRAIT DIVERSITY ACROSS TIME

*We will work with these models during the tutorial.

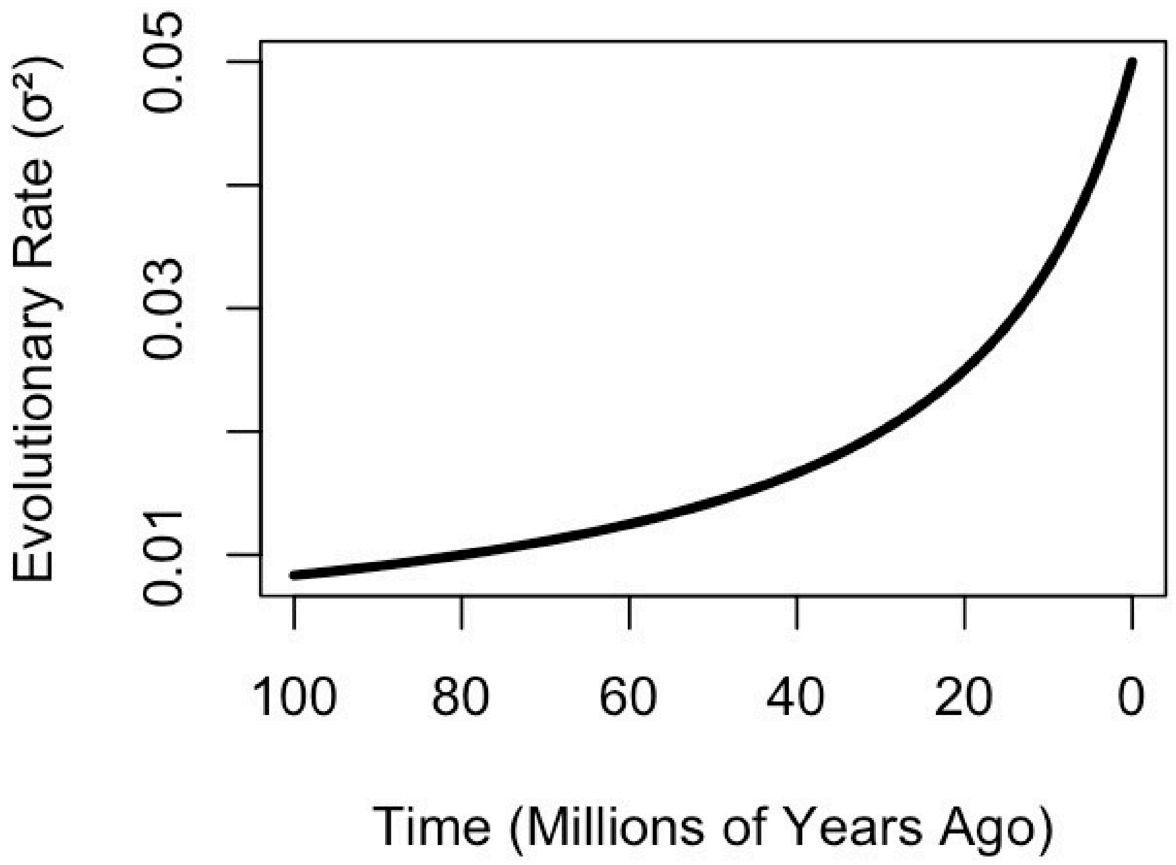
Early Burst



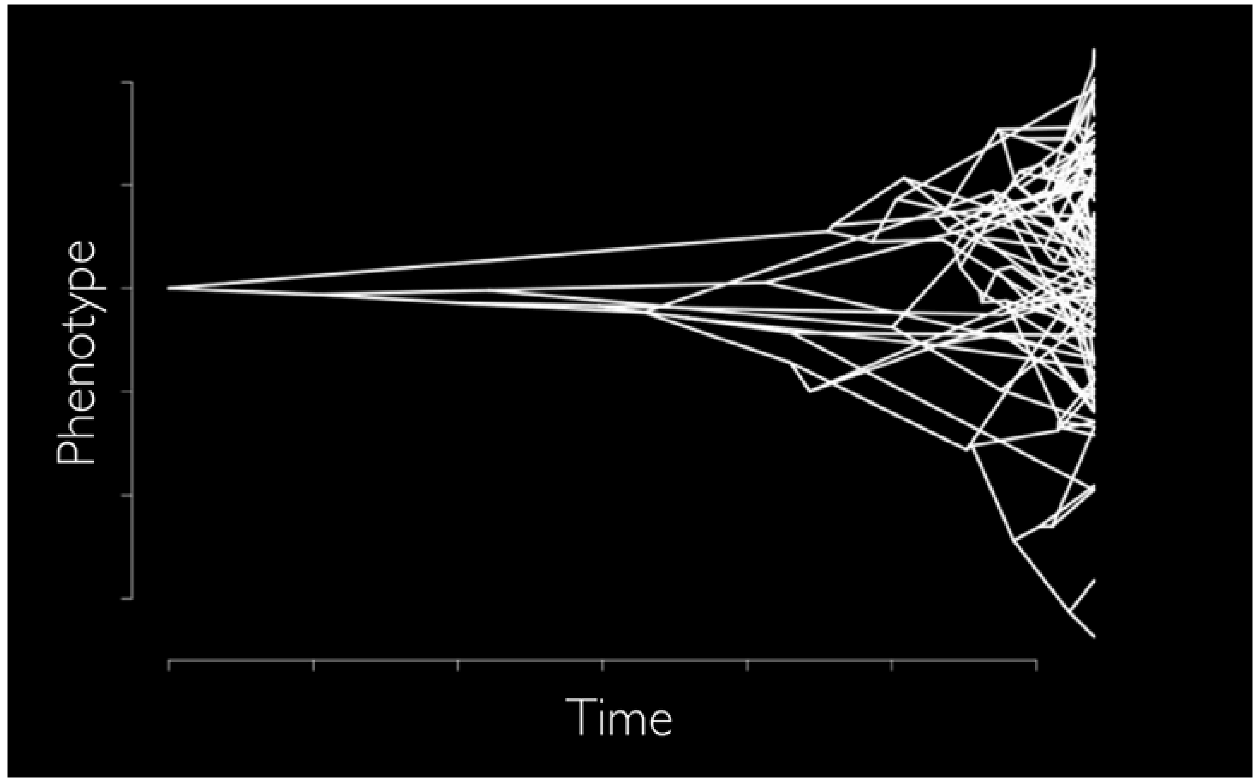
- Expansion into new adaptive zones
- New geographic areas



"Late Burst"



- Lineages takes time to explore new resources
- First stages of an early burst

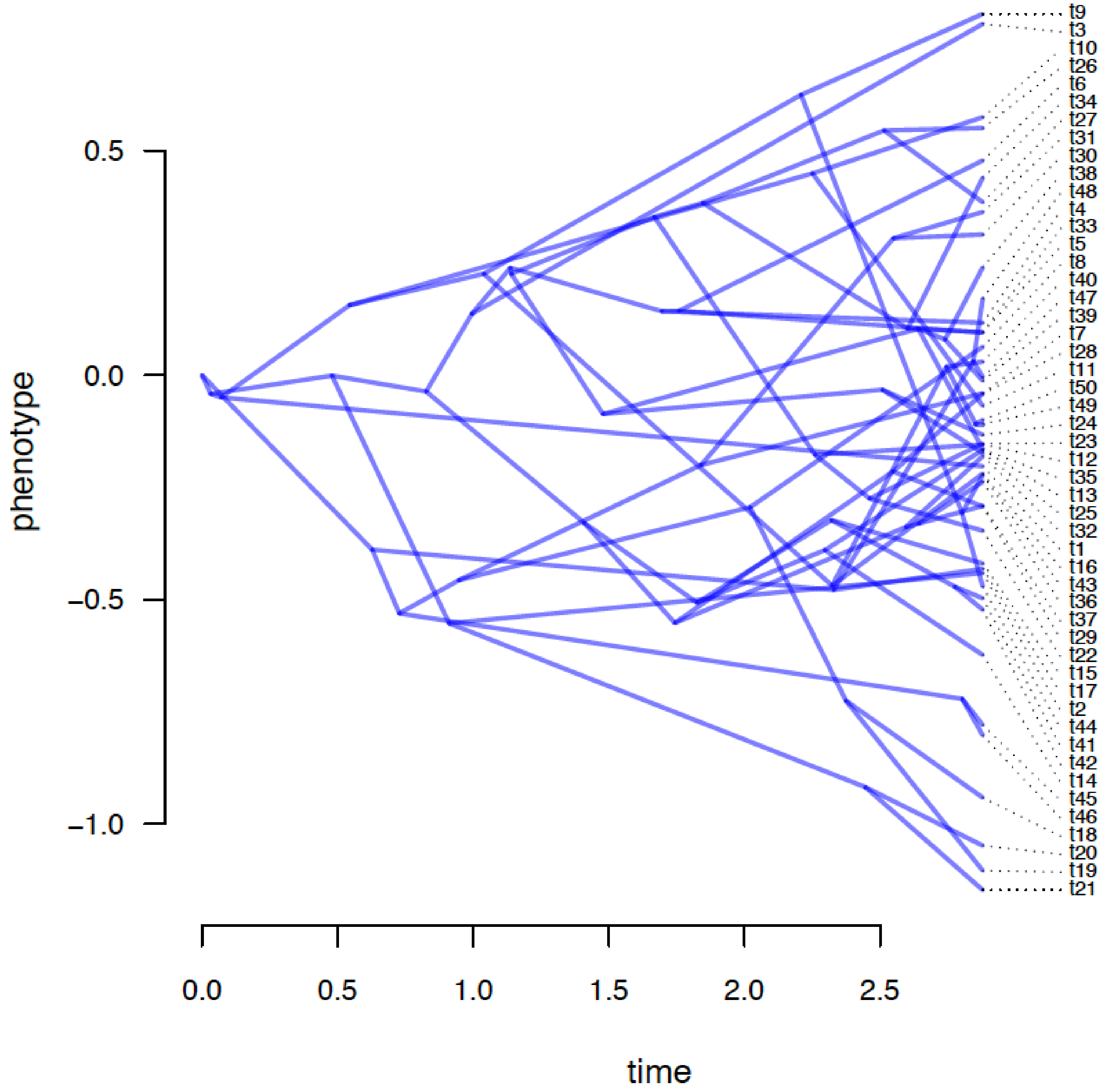


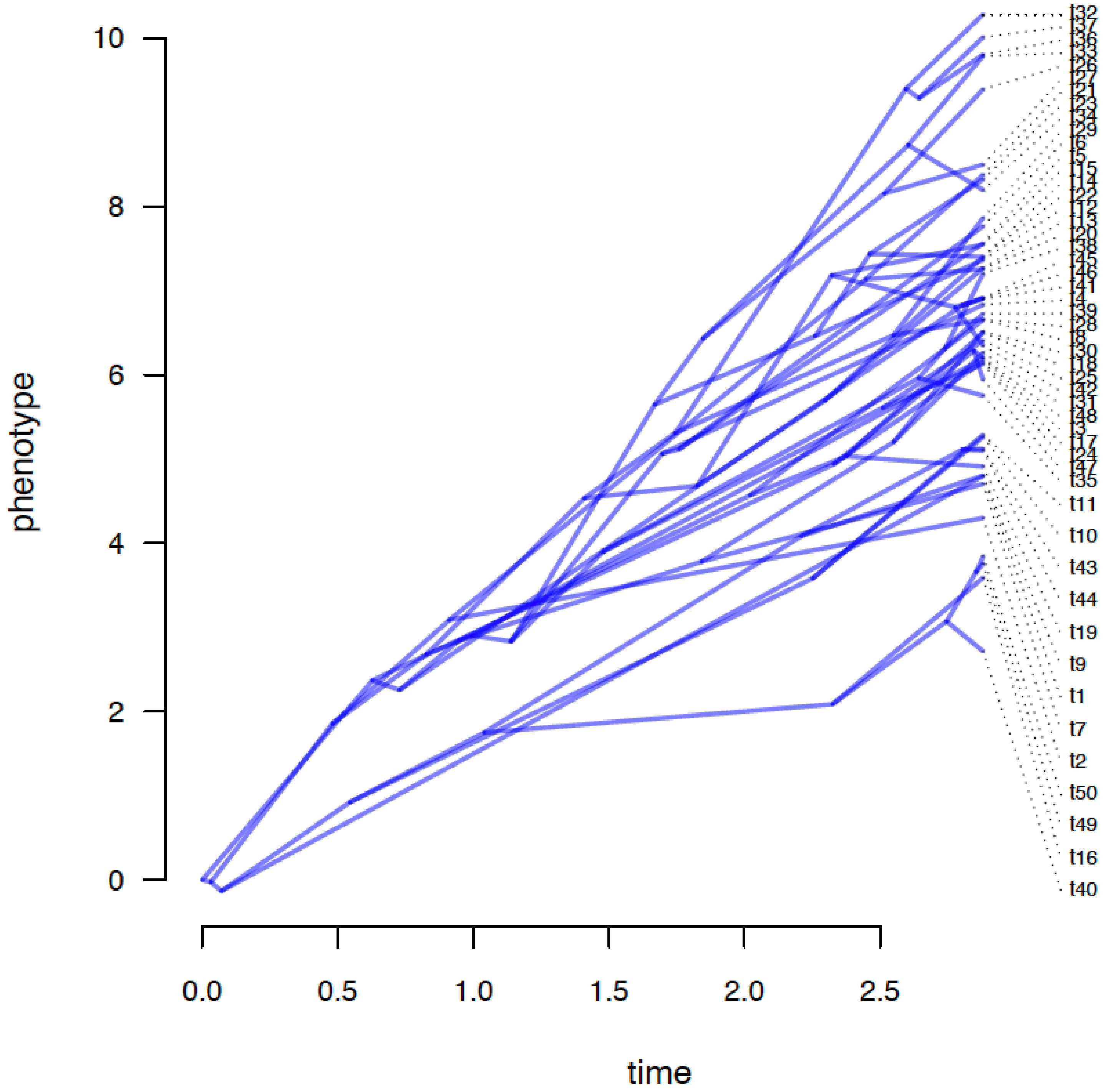
Others?

TRAIT DIVERSITY ACROSS TIME

*We will work with these models during the tutorial.

Brownian evolution with a trend





- Changing environments, or expanding ecological opportunities (e.g., cope's rule!)

TRAIT DIVERSITY ACROSS TIME

Phylogenetic signal

TRAIT DIVERSITY ACROSS TIME

Phylogenetic signal

What is it?

The tendency for related species to resemble each other more than expected by chance.

TRAIT DIVERSITY ACROSS TIME

Phylogenetic signal

What is it?

The tendency for related species to resemble each other more than expected by chance.

High signal = traits are "conserved" and reflect shared ancestry.

Low signal = traits evolve more rapidly or convergently, decoupled from phylogeny.

TRAIT DIVERSITY ACROSS TIME

Phylogenetic signal

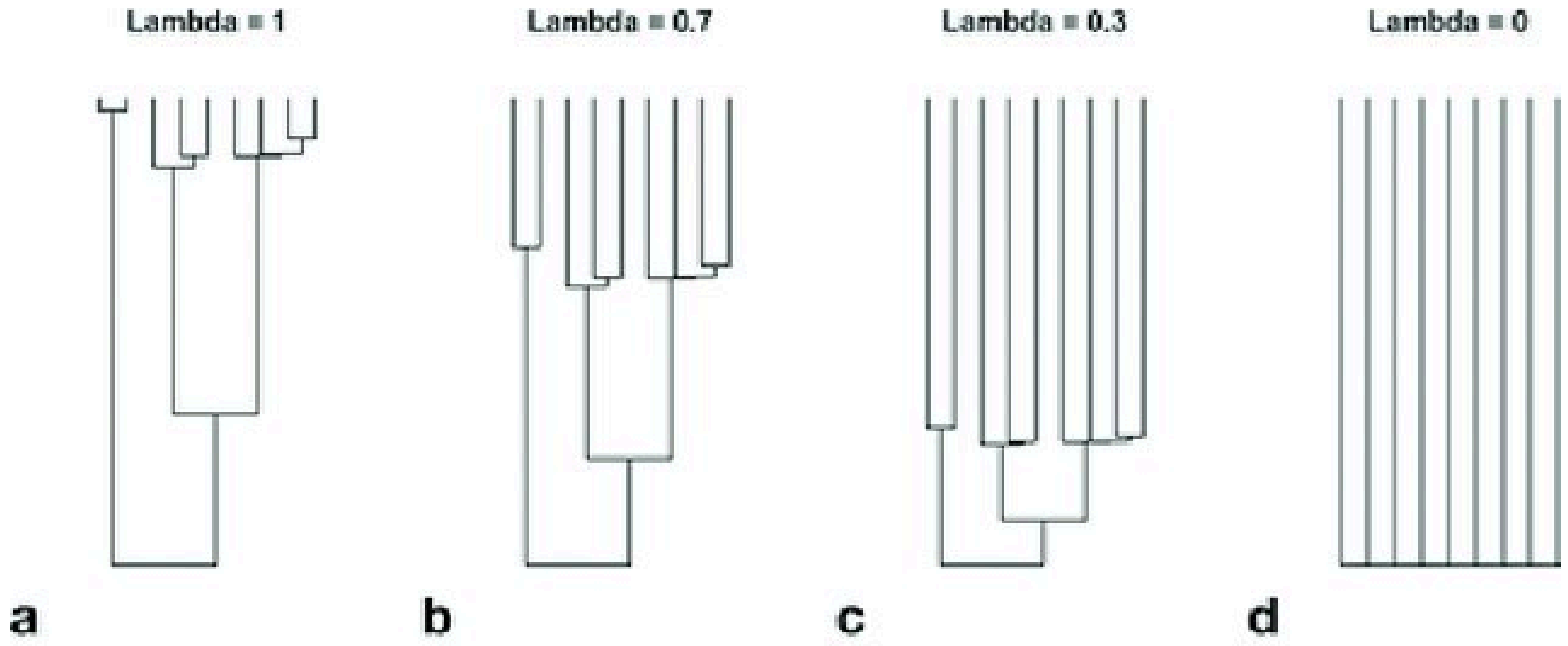
Pagel's lambda

Quantifies phylogenetic signal by scaling internal branches to reflect how much shared ancestry explains trait similarity.

λ = 1: trait variation follows Brownian motion.

λ = 0: traits vary independently of phylogeny

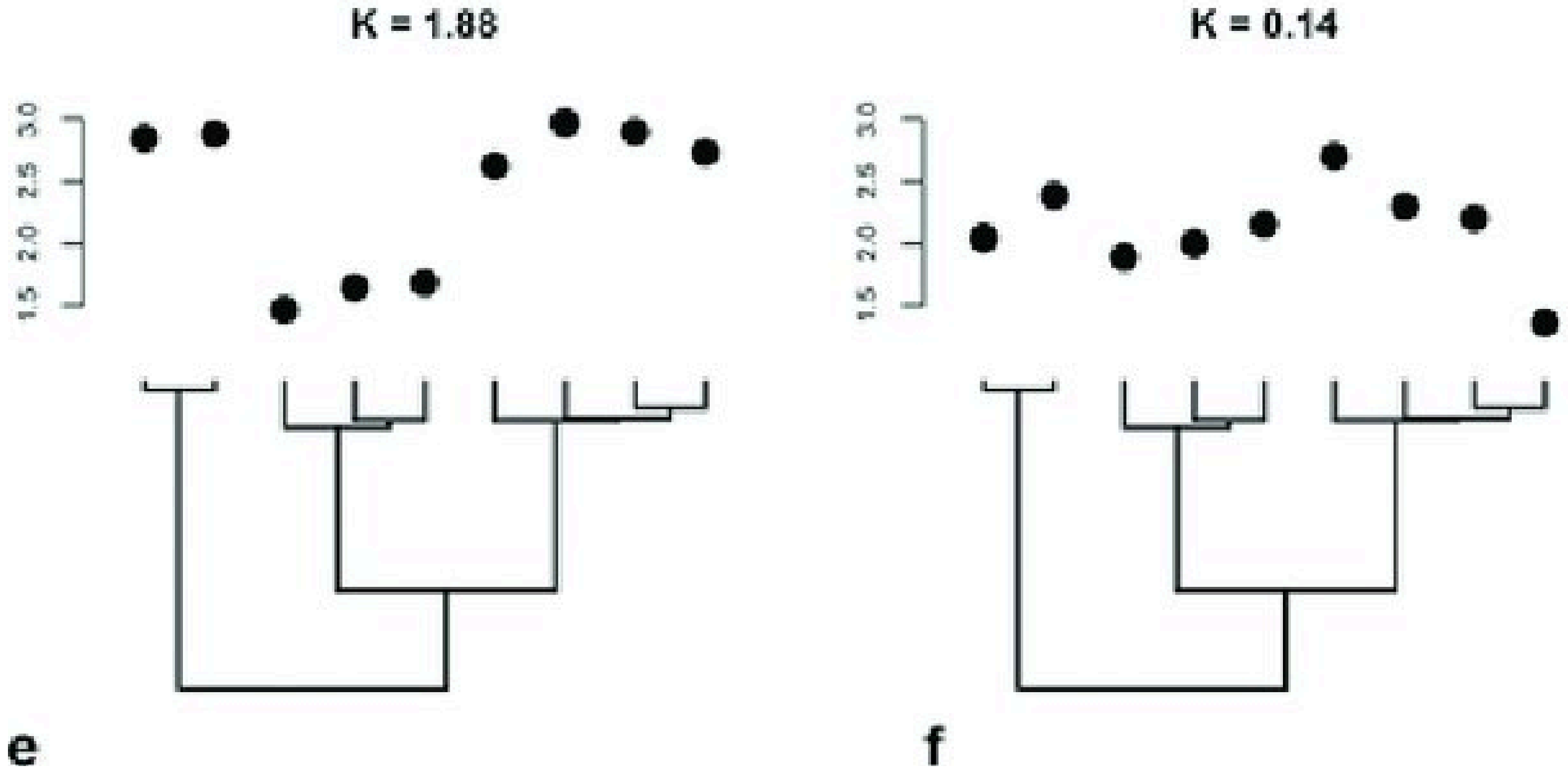
Pagel 1999. Nature.



Meireles et al. 2020. Chapter 7 in Remote Sensing in Plant Diversity.

TRAIT DIVERSITY ACROSS TIME

Phylogenetic signal



Meireles et al. 2020. Chapter 7 in Remote Sensing in Plant Diversity.

Blomberg's K

Measures how strongly trait values cluster within clades.

K > 1: closely related species are more similar than expected (strong phylogenetic signal)

K < 1: trait values are more randomly distributed (weak signal)

Blomberg et al. 2003 Evolution.

TRAIT DIVERSITY ACROSS TIME

Phylogenetic signal

Limitations

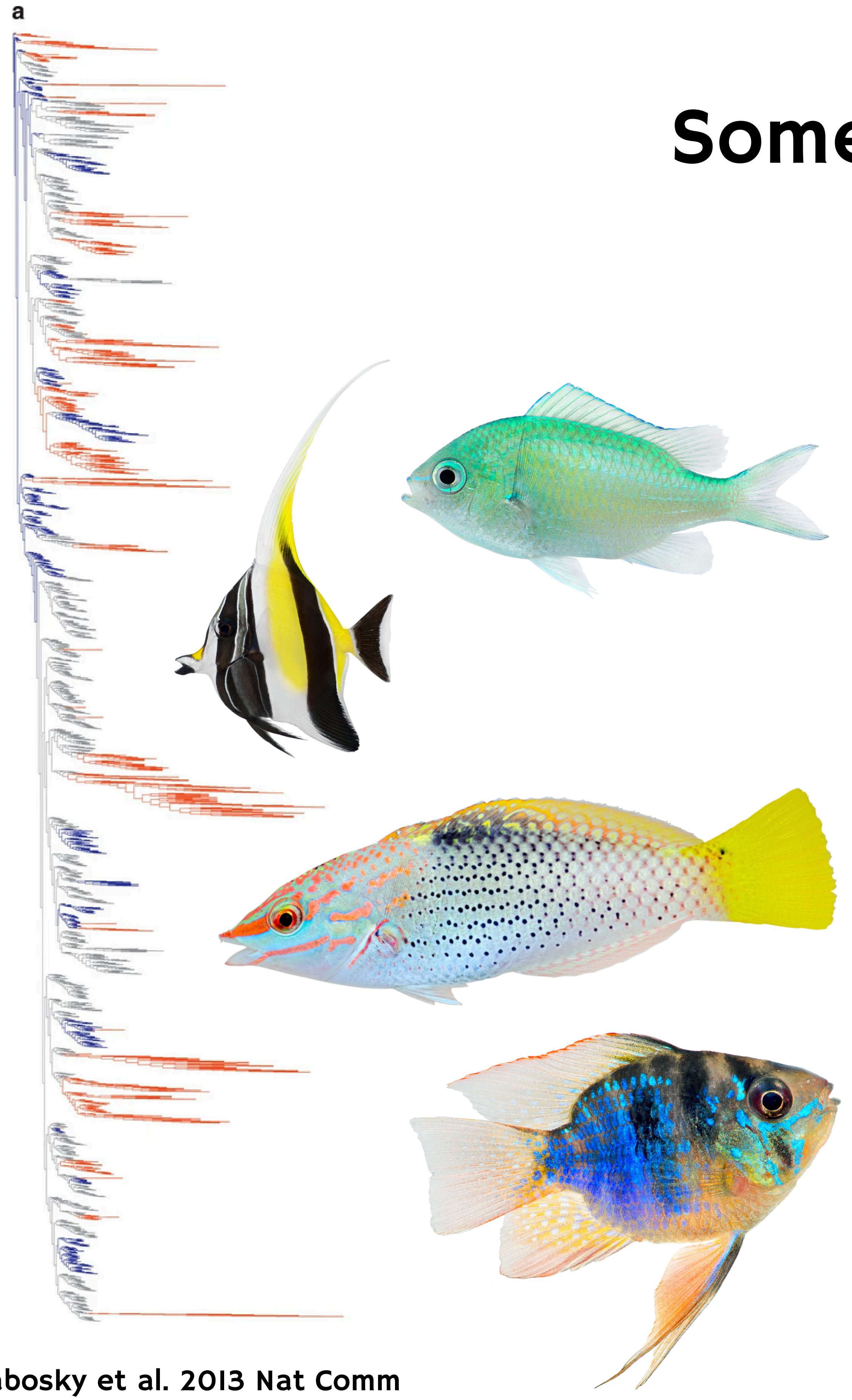
Pagel's λ and Blomberg's K assume a single evolutionary process across the tree.

If evolutionary rates vary among clades, the global signal estimate can be diluted or misleading.

TRAIT DIVERSITY ACROSS LINEAGES

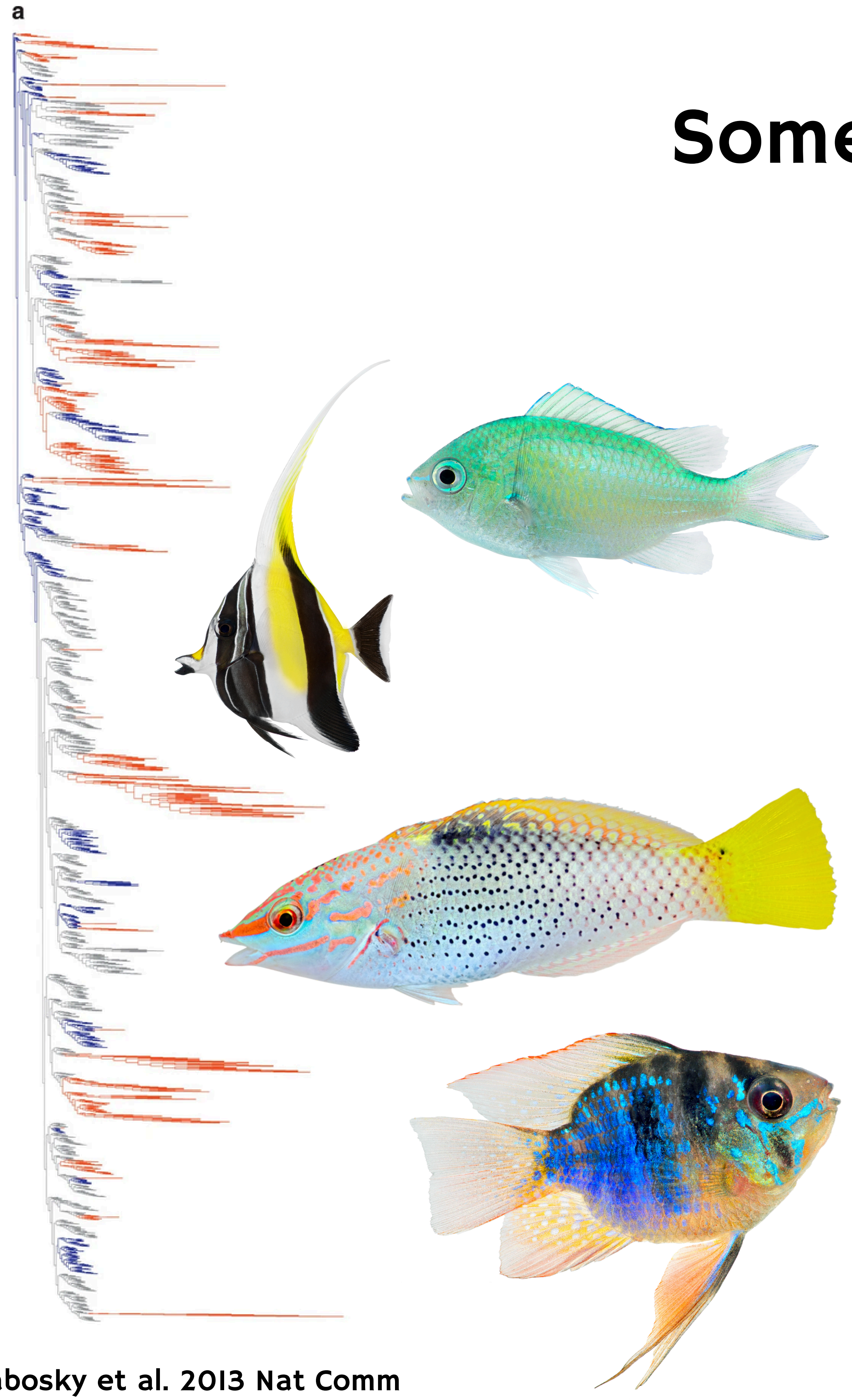
TRAIT DIVERSITY ACROSS LINEAGES

Some lineages evolve rapidly, others barely change.



Rabosky et al. 2013 Nat Comm

TRAIT DIVERSITY ACROSS LINEAGES



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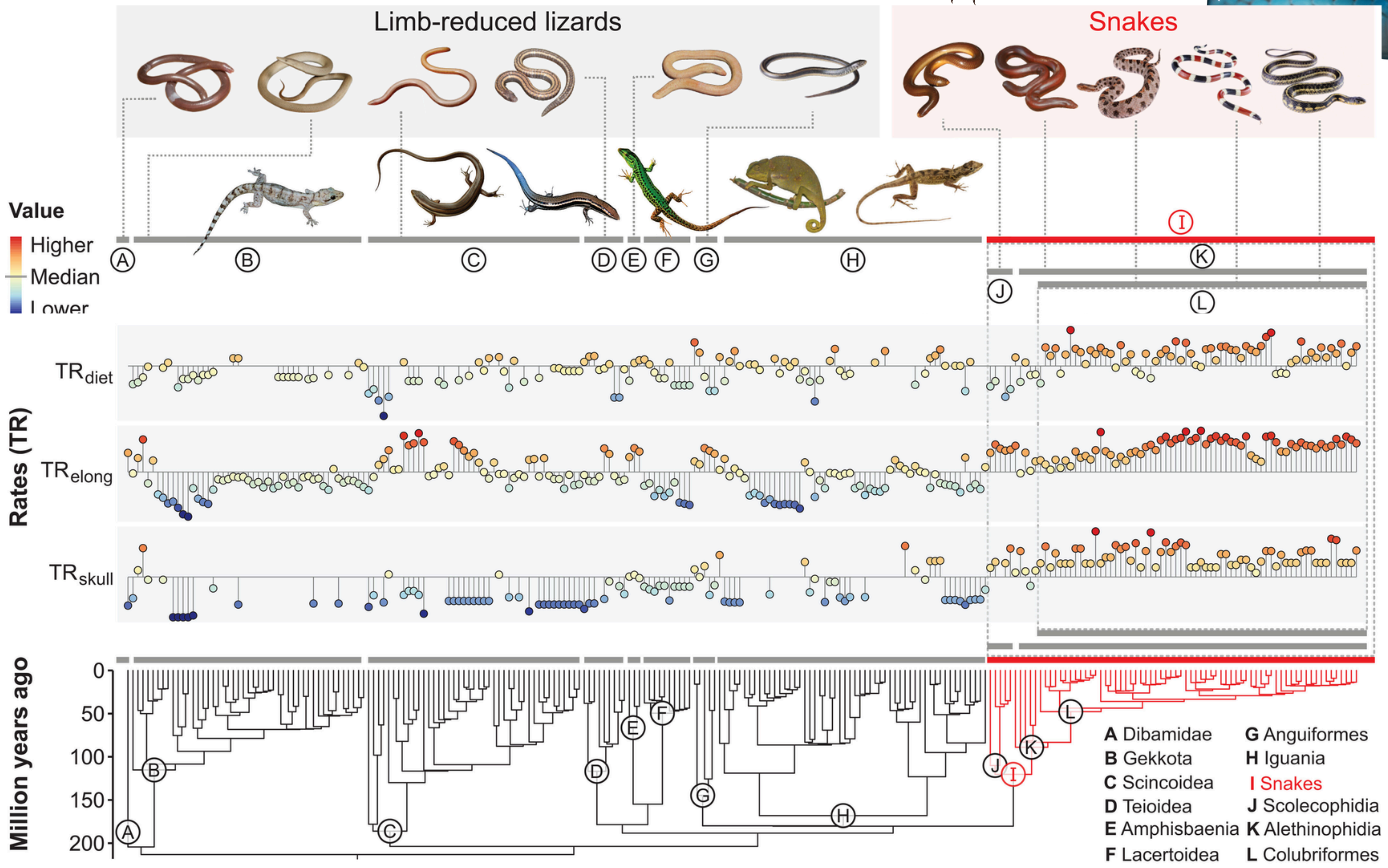
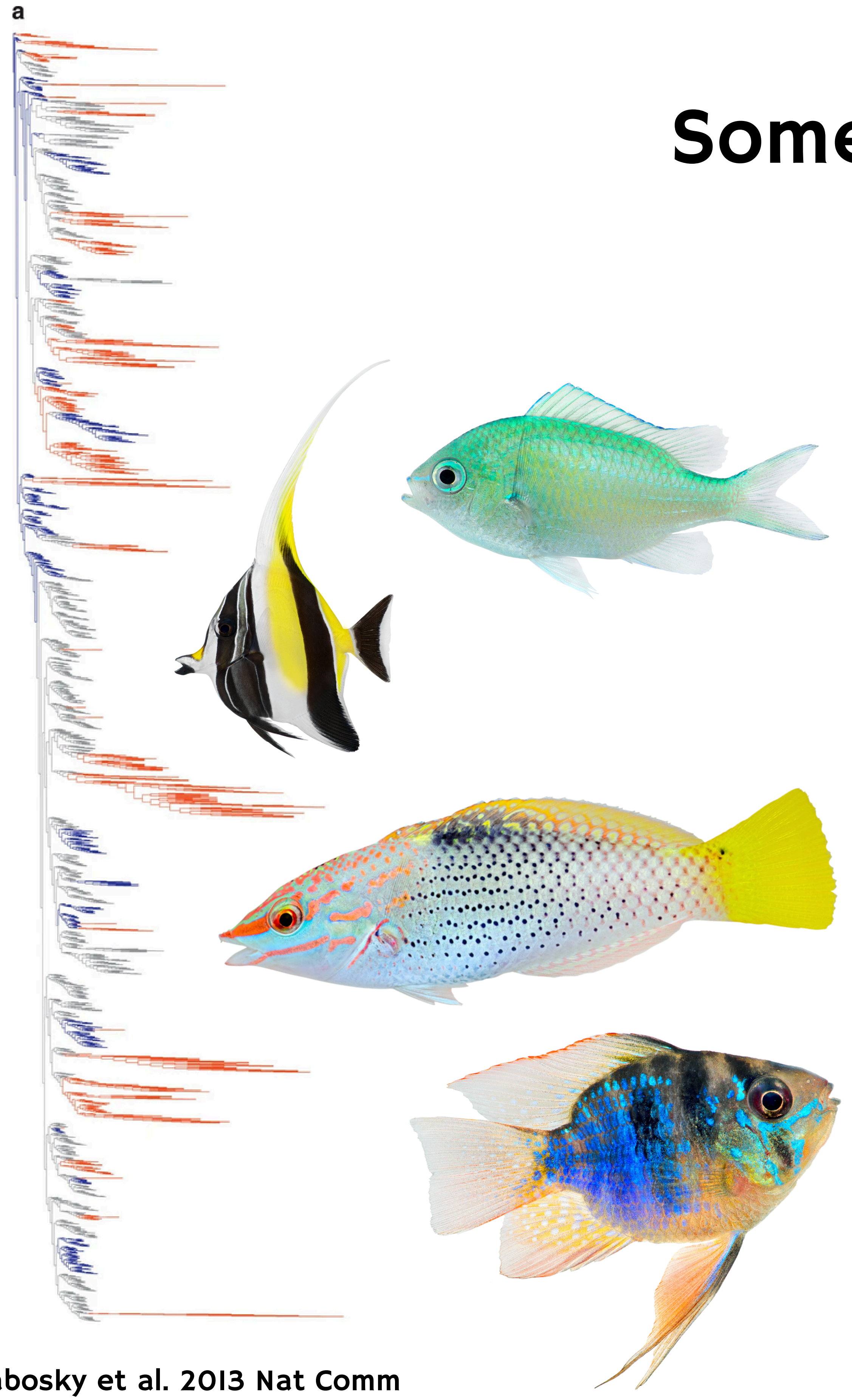


Rabosky et al. 2013 Nat Comm

Title et al. 2024 Science

TRAIT DIVERSITY ACROSS LINEAGES



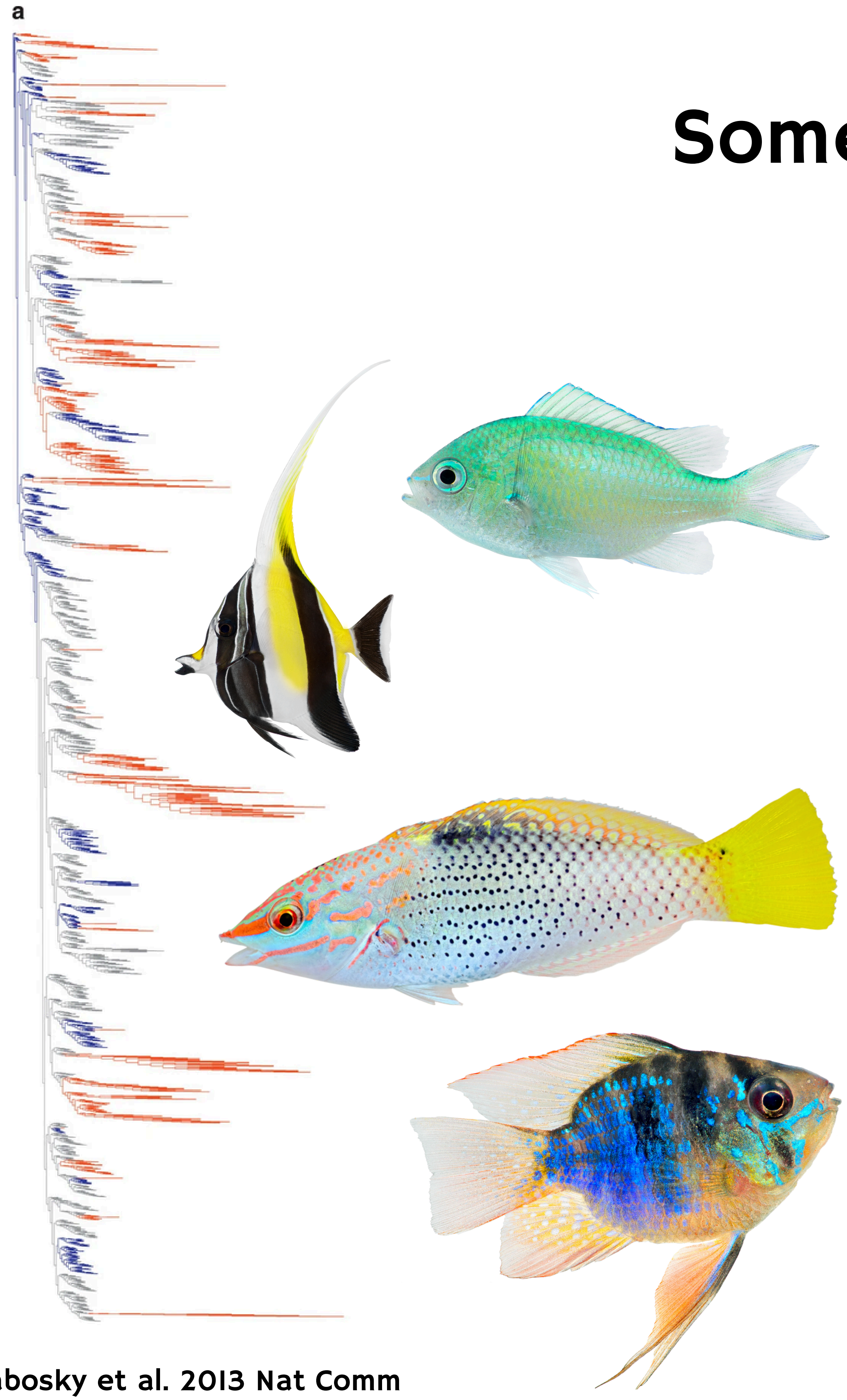
Rabosky et al. 2013 Nat Comm

Some lineages evolve rapidly, others barely change.

Rate heterogeneity

- Ecological opportunity
- Release from constraints
- Differences in life-history

TRAIT DIVERSITY ACROSS LINEAGES



Rabosky et al. 2013 Nat Comm

Some lineages evolve rapidly, others barely change.

Rate heterogeneity

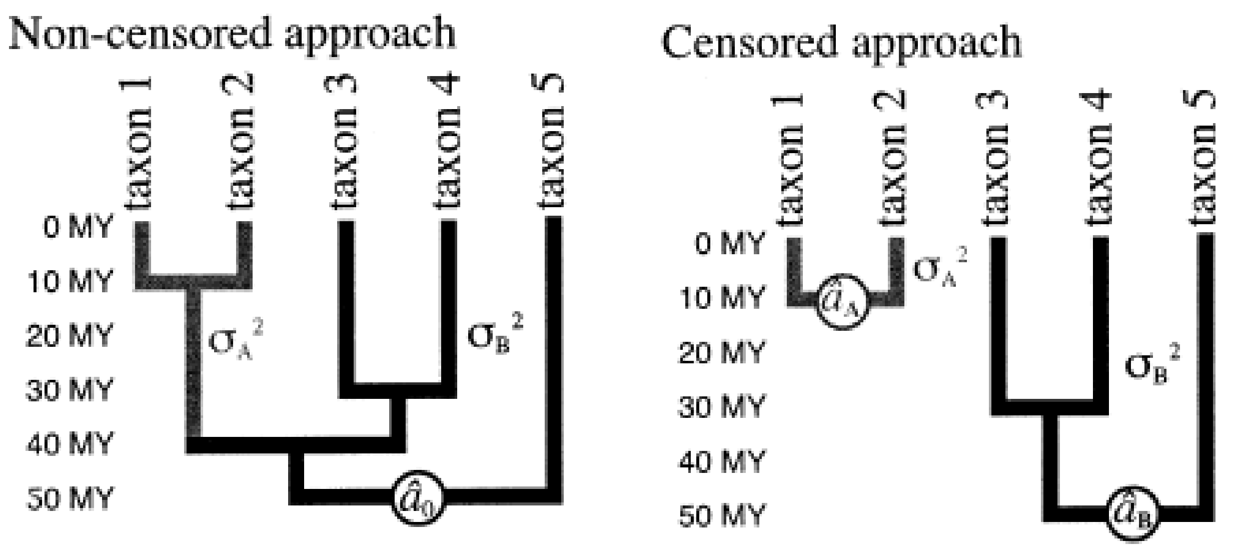
- Ecological opportunity
- Release from constraints
- Differences in life-history

Let's relax the assumption of a "single rate"

TRAIT DIVERSITY ACROSS LINEAGES

$dX(t) = \sigma^2 * t$

A Brownian motion model allowing the rate of evolution (σ2) to differ in different lineages.



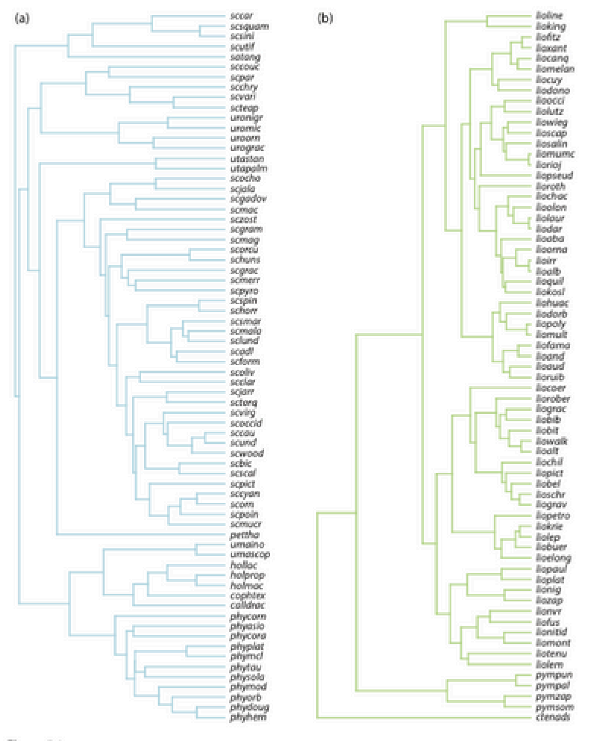
Within clades

Evolution, 60(5), 2006, pp. 922–933

TESTING FOR DIFFERENT RATES OF CONTINUOUS TRAIT EVOLUTION USING LIKELIHOOD

Brian C. O'Meara,[1] Cécile Ané,[2] Michael J. Sanderson,[3,4] and Peter C. Wainwright[3,5]

Between clades

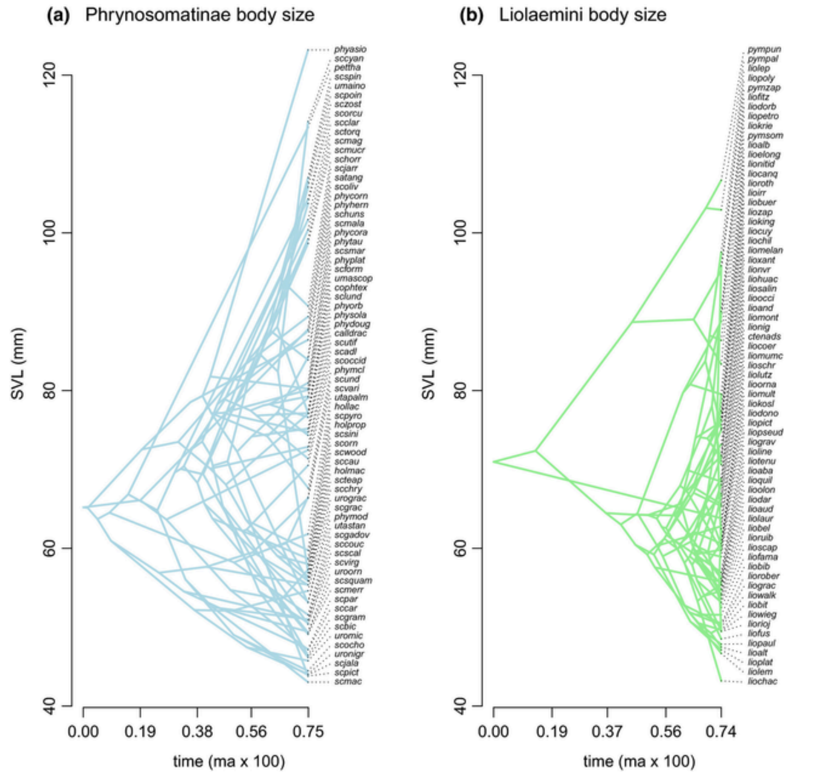


RESEARCH ARTICLE

Methods in Ecology and Evolution BRITISH ECOLOGICAL SOCIETY

Comparing evolutionary rates between trees, clades and traits

Liam J. Revell[1,2] | Laura E. González-Valenzuela[3] | Alejandro Alfonso[3] | Luisa A. Castellanos-García[3] | Carlos E. Guarnizo[3] | Andrew J. Crawford[3]



TRAIT DIVERSITY ACROSS LINEAGES

A Brownian motion model allowing the rate of evolution ($\sigma 2$) to differ in different lineages. But where are these changes?

TRAIT DIVERSITY ACROSS LINEAGES

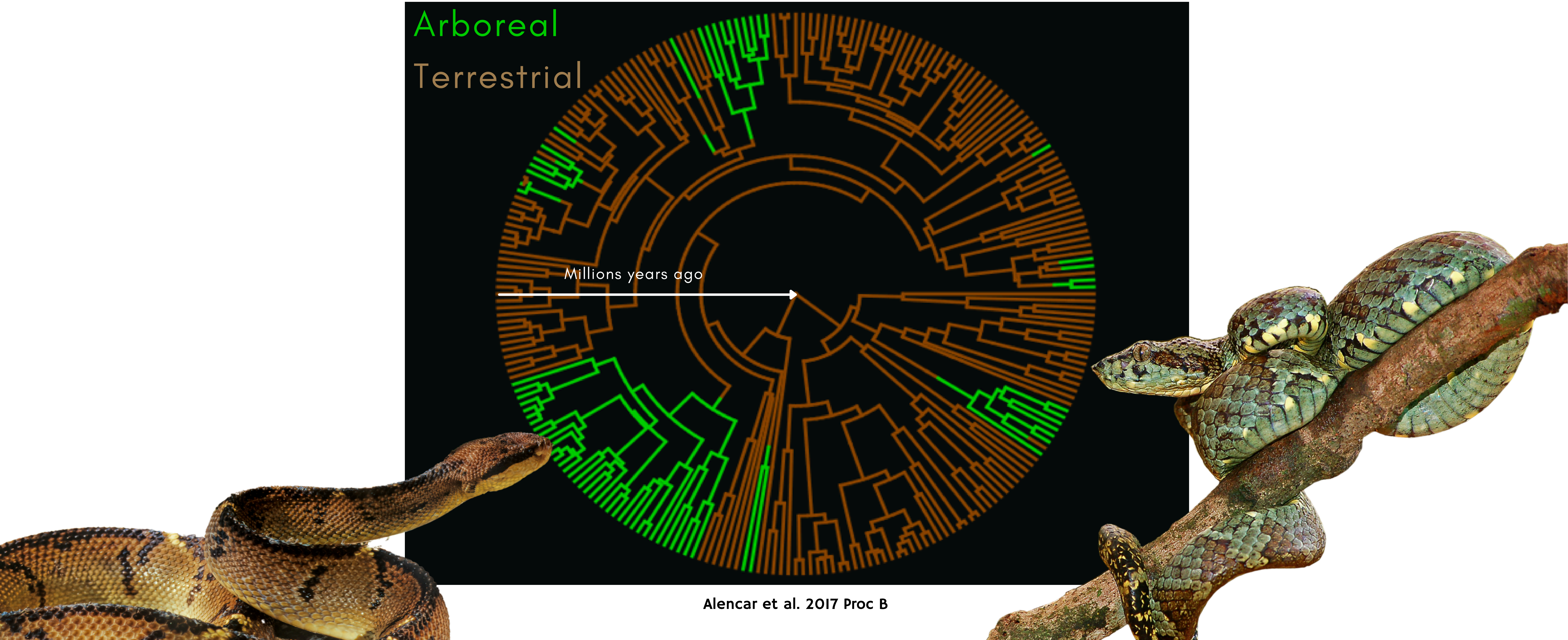
A Brownian motion model allowing the rate of evolution ($\sigma 2$) to differ in different lineages. But where are these changes?

1) Using a priori "regimes"

2) Data-driven approaches

TRAIT DIVERSITY ACROSS LINEAGES

Using a priori “regimes”



Alencar et al. 2017 Proc B

TRAIT DIVERSITY ACROSS LINEAGES

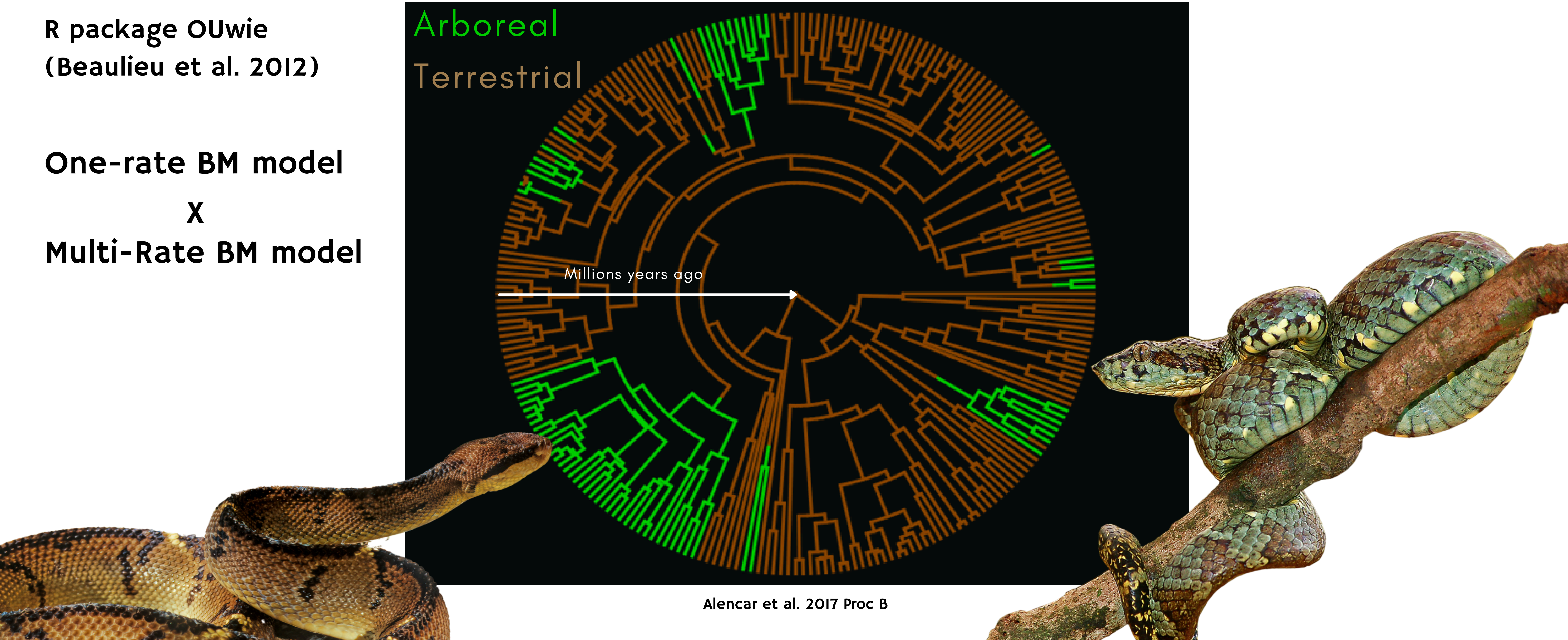
Using a priori “regimes”

R package OUwie
(Beaulieu et al. 2012)

One-rate BM model

X

Multi-Rate BM model



Alencar et al. 2017 Proc B

TRAIT DIVERSITY ACROSS LINEAGES

Using a priori “regimes”

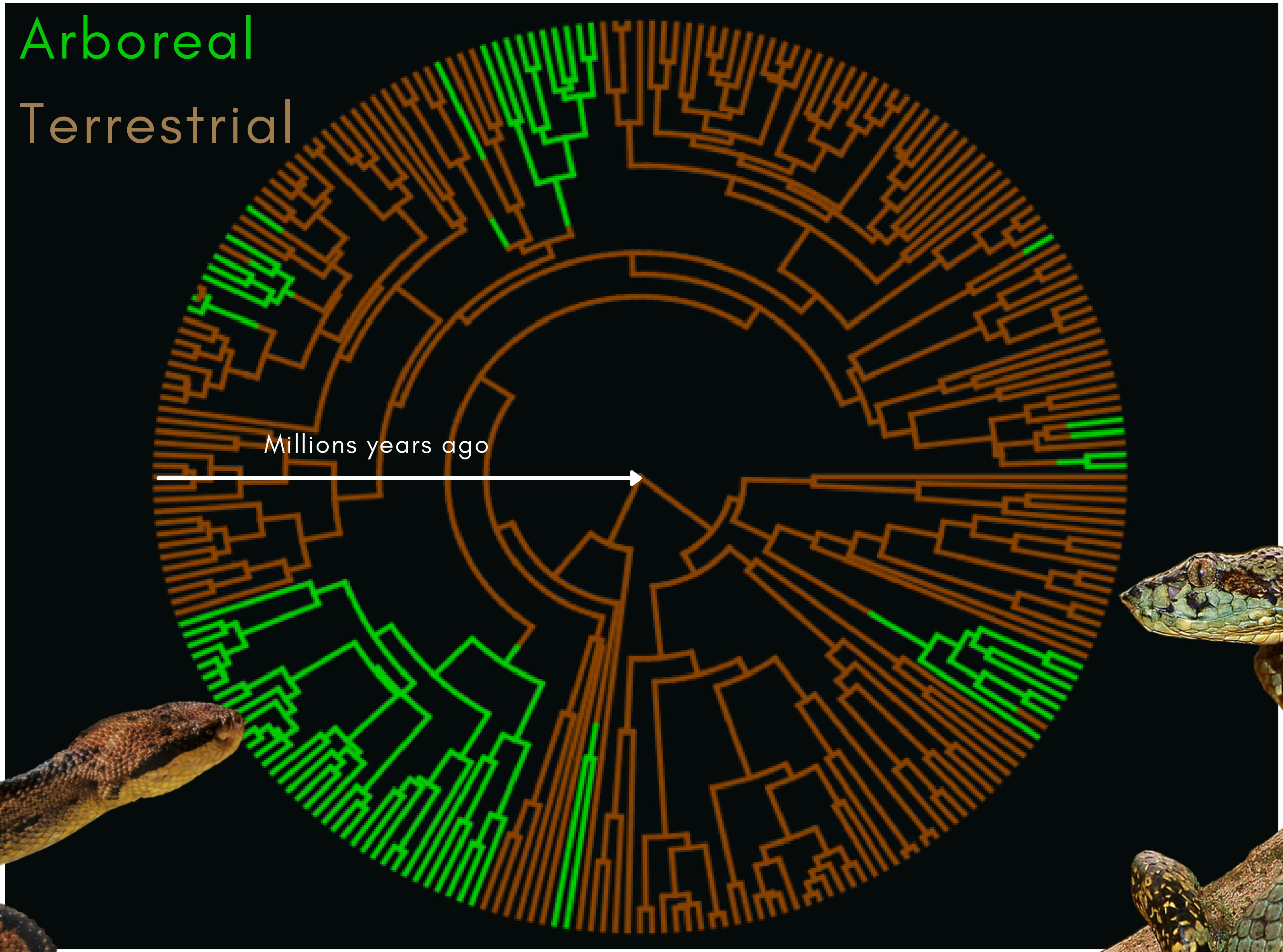
R package OUwie
(Beaulieu et al. 2012)

One-rate BM model

X

Multi-Rate BM model

Body size, body circumference, tail length...



Alencar et al. 2017 Proc B

TRAIT DIVERSITY ACROSS LINEAGES

Using a priori "regimes"

Terrestrial vipers have higher rates.

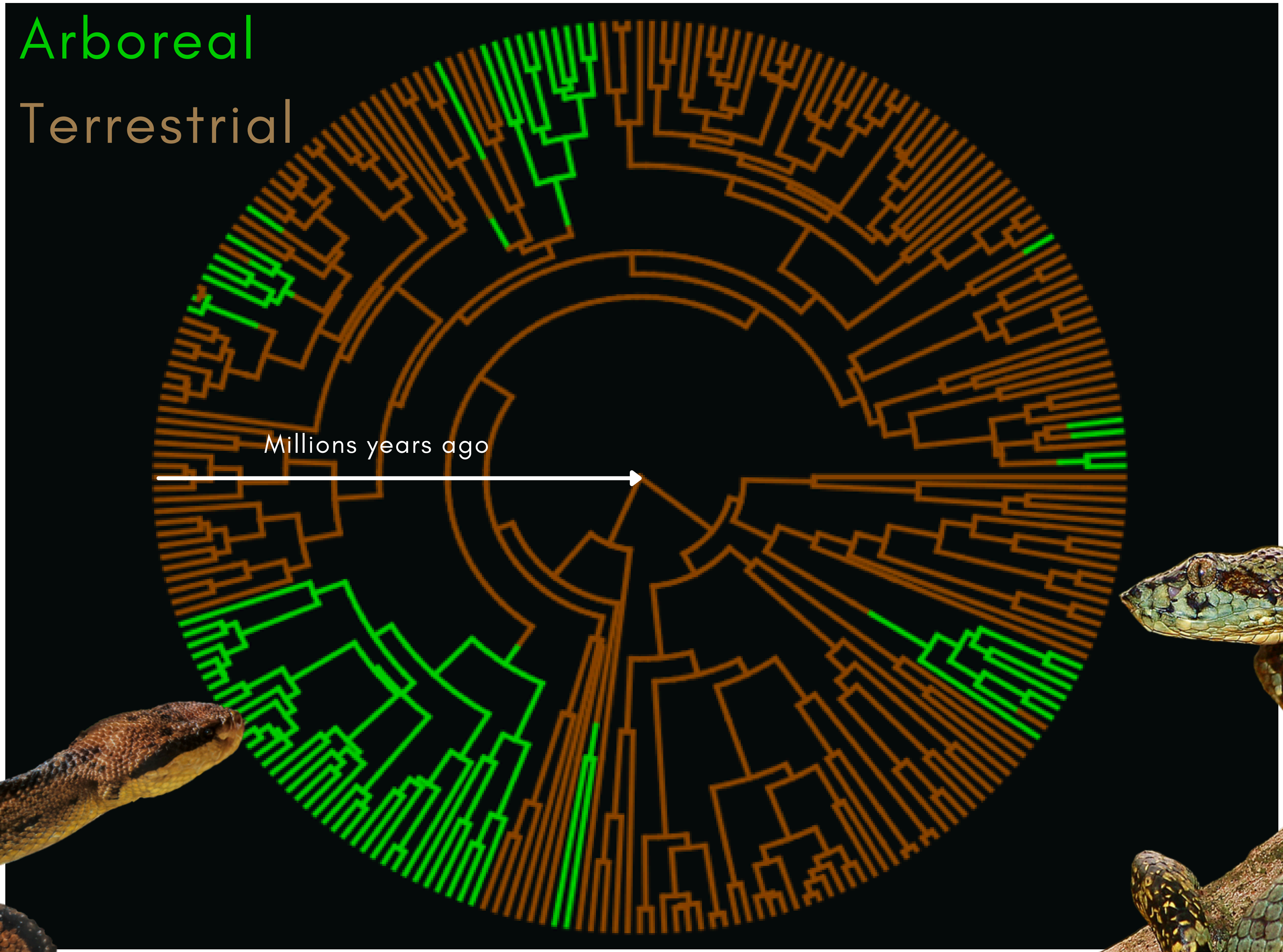
R package OUwie
(Beaulieu et al. 2012)

One-rate BM model

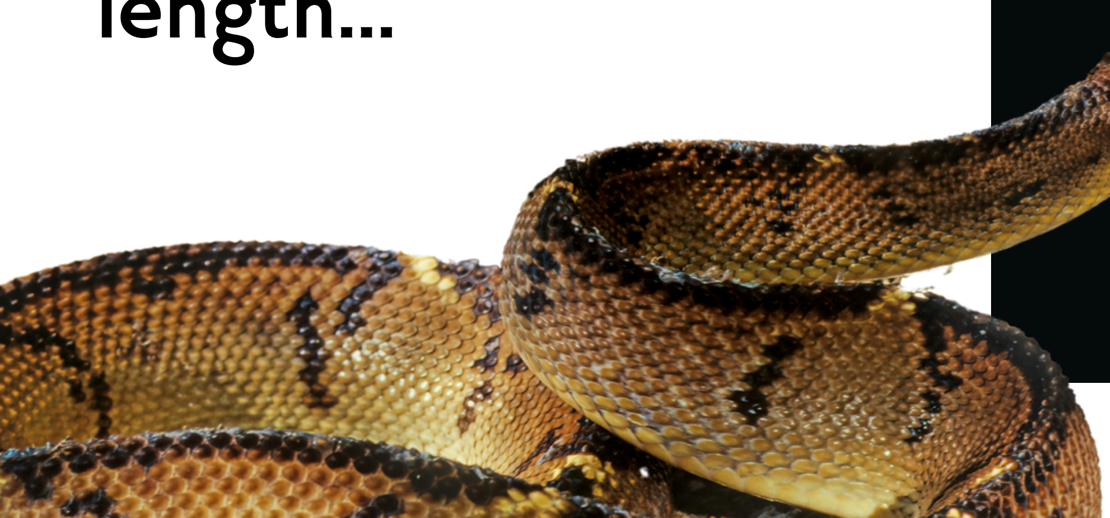
X

Multi-Rate BM model

Body size, body circumference, tail length...



Alencar et al. 2017 Proc B



TRAIT DIVERSITY ACROSS LINEAGES

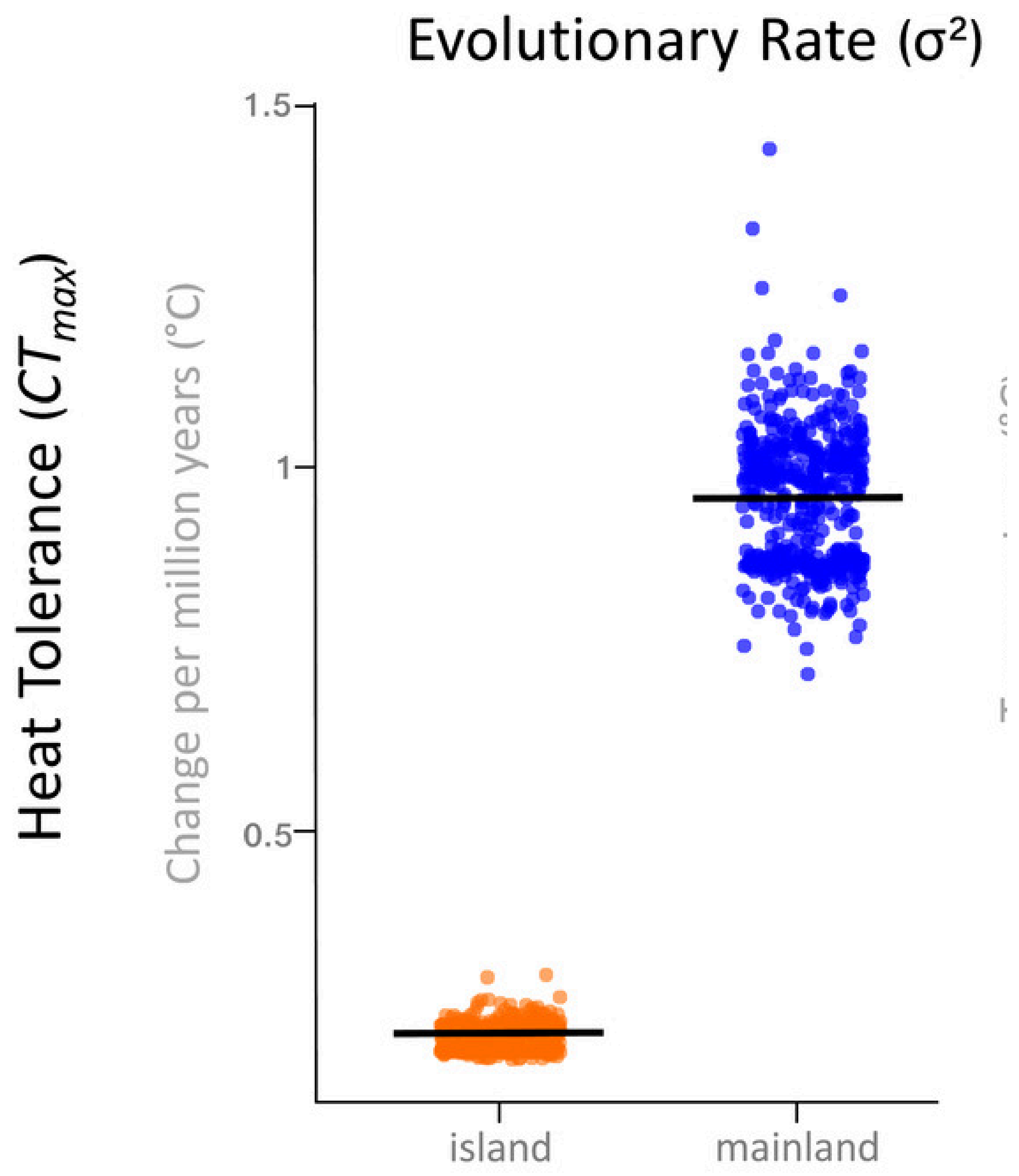
Using a priori "regimes"

Island x Mainland

Anoles

Salazar et al. 2019 Evolution

Heat tolerance in mainlad anoles diversify faster than in islands.



TRAIT DIVERSITY ACROSS LINEAGES

Data-driven approaches

BAMM

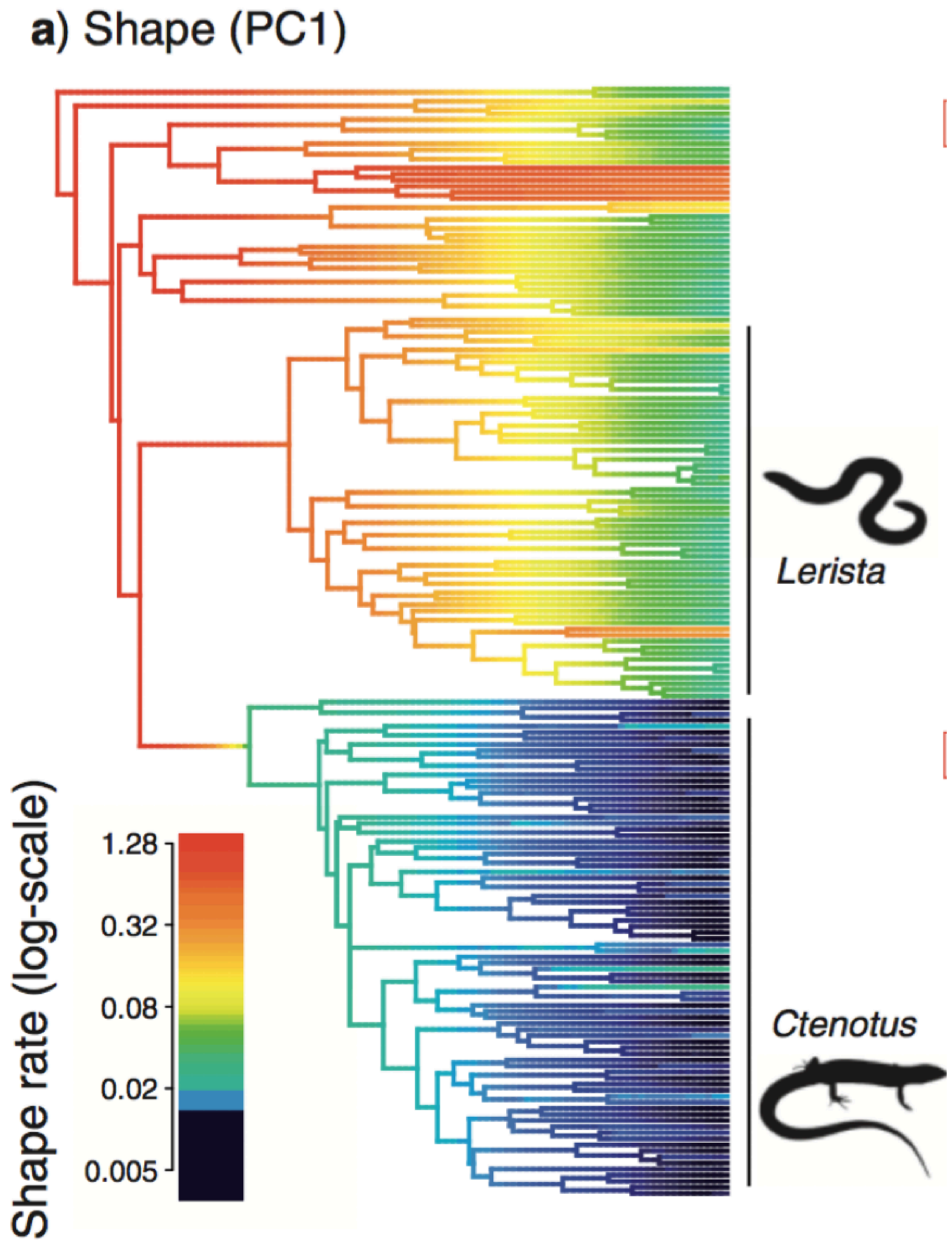
(Bayesian Analysis of Macroevolutionary Mixtures)

Rabosky 2014 PlosOne, Rabosky et al. 2013, 2014

Automatically explore candidate models of lineage diversification and trait evolution.

C++ and R

http://bamm-project.org



Rabosky et al. 2014 Syst Bio

TRAIT DIVERSITY ACROSS LINEAGES

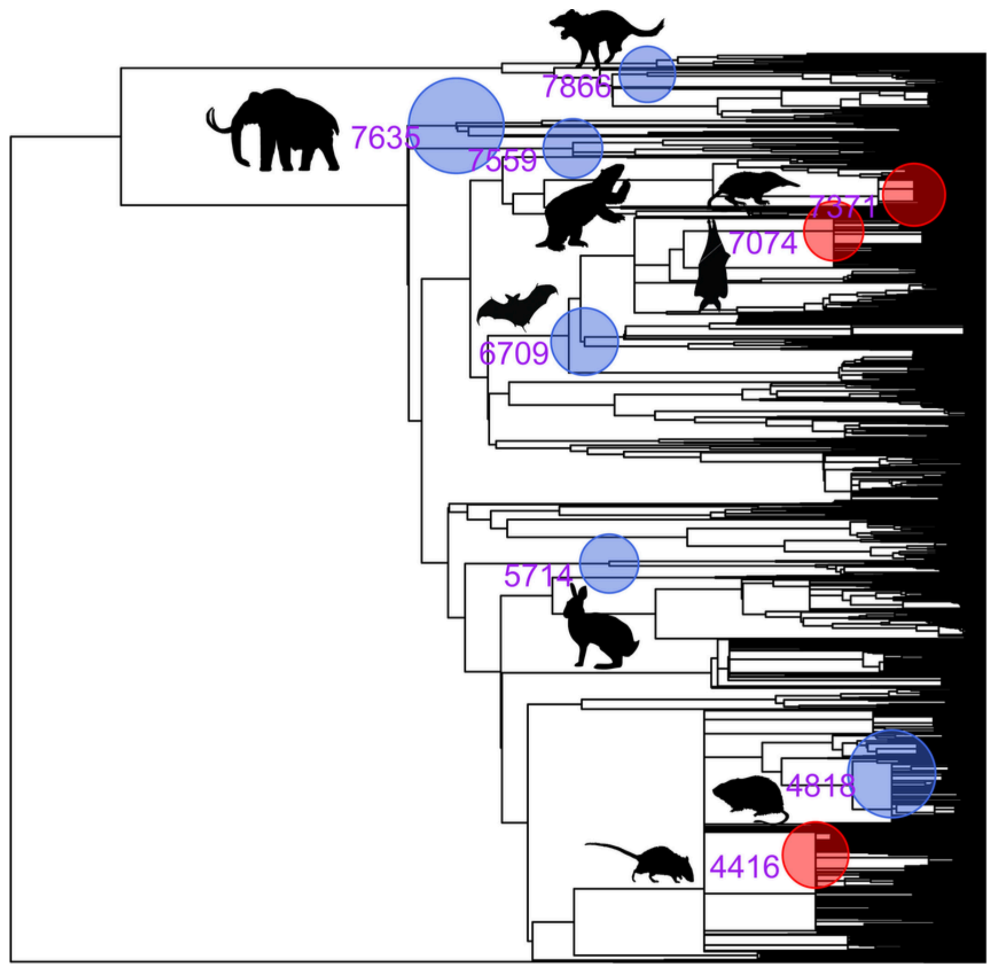
Data-driven approaches

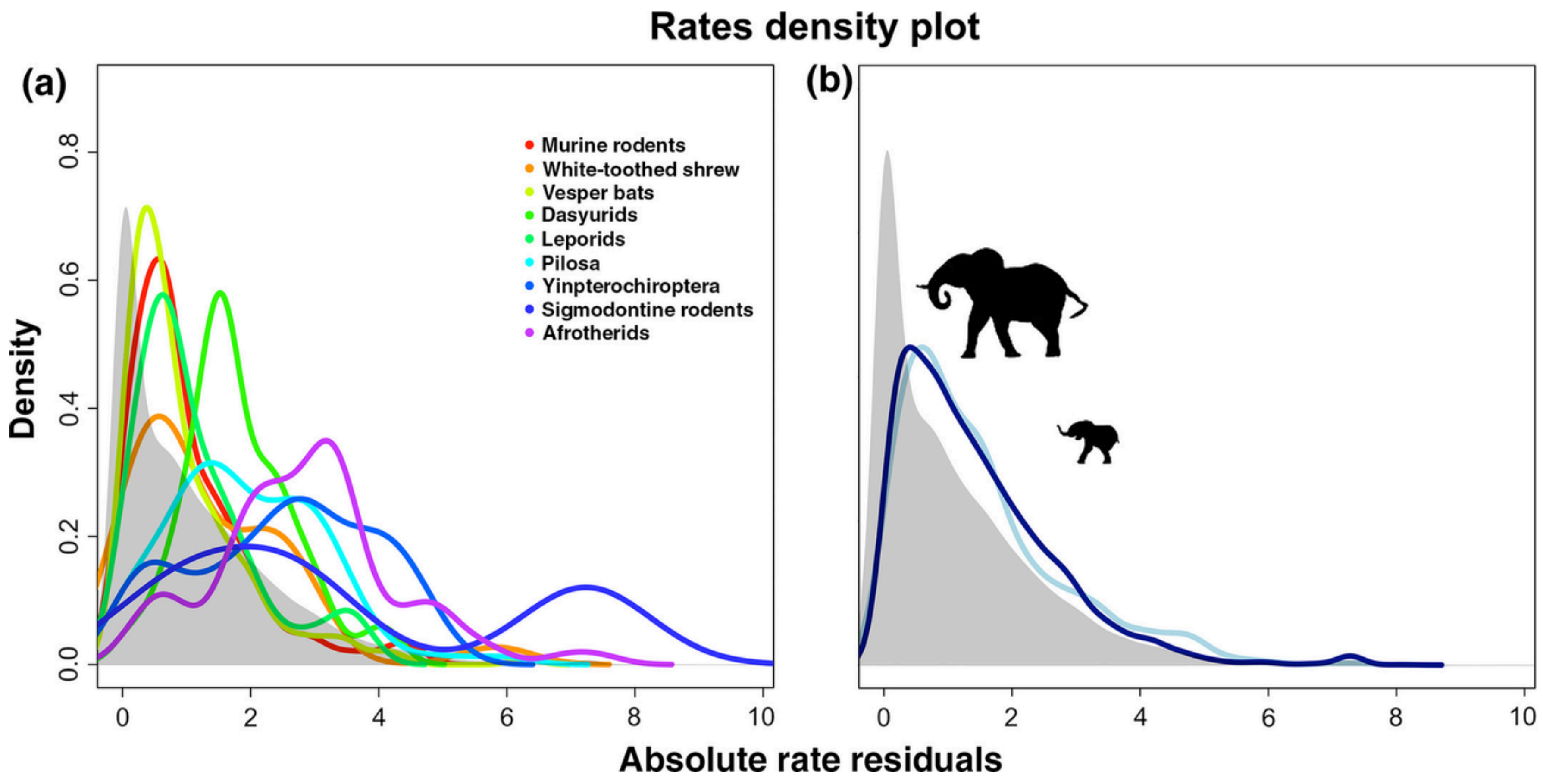
RRphylo

Castiglione et al. 2018 MEE

Uses ridge regression to estimate rate changes across branches

R package





Tutorial time!