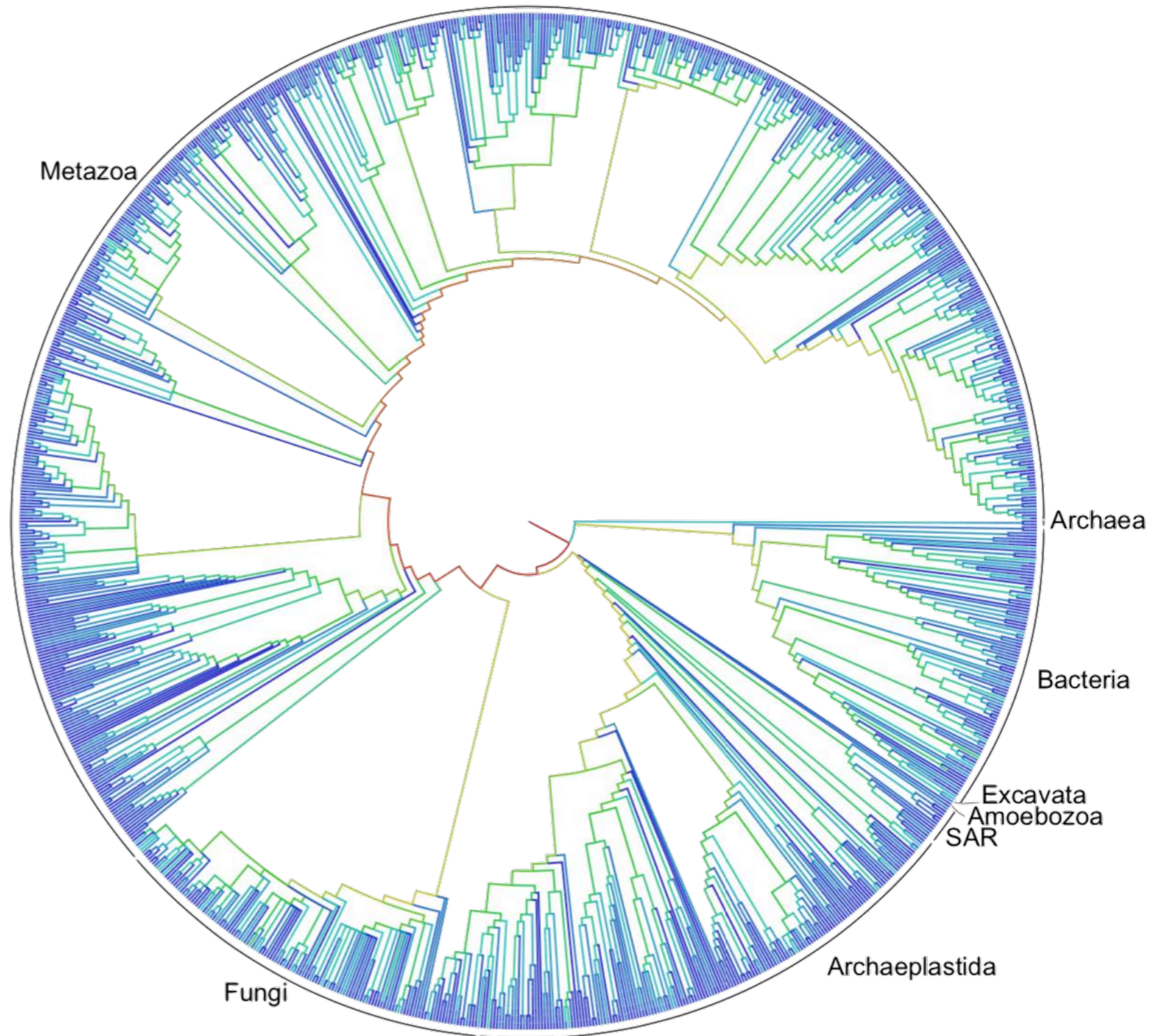# Diversification Rate Variation in the Tree of Life

The Tree of Life

What are the processes governing the patterns of species diversity in the tree of life?

Open Tree of Life Synthetic Tree from Hinchliff et al. (PNAS 2015)

Taxonomic Diversity

We observe variation in species richness across the tree of life

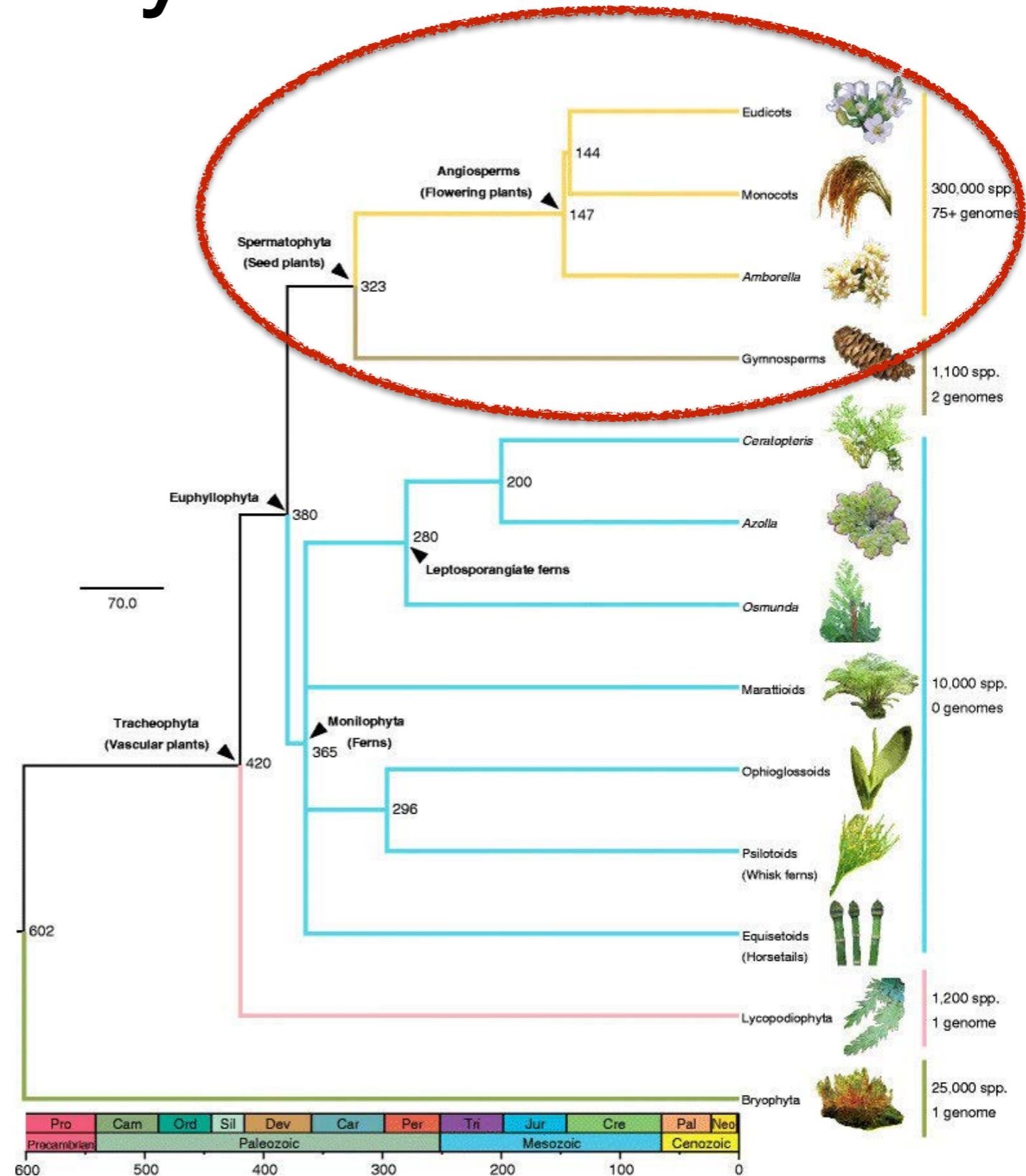**Relative diversity of extant animals**

Major protostome phyla

Major non-protostome phyla

Insects

Chelicerates

Crustaceans

Myriapods

Arthropoda

Nematoda

Mollusca

Platyhelminthes

Annelida

Chordata

Echinodermata

Cnidaria

Porifera

Other invertebrates

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© Alex Wild
alexanderwild.com

Taxonomic Diversity

Why are there ~300,000 Angiosperm species and only ~1,100 Gymnosperms?
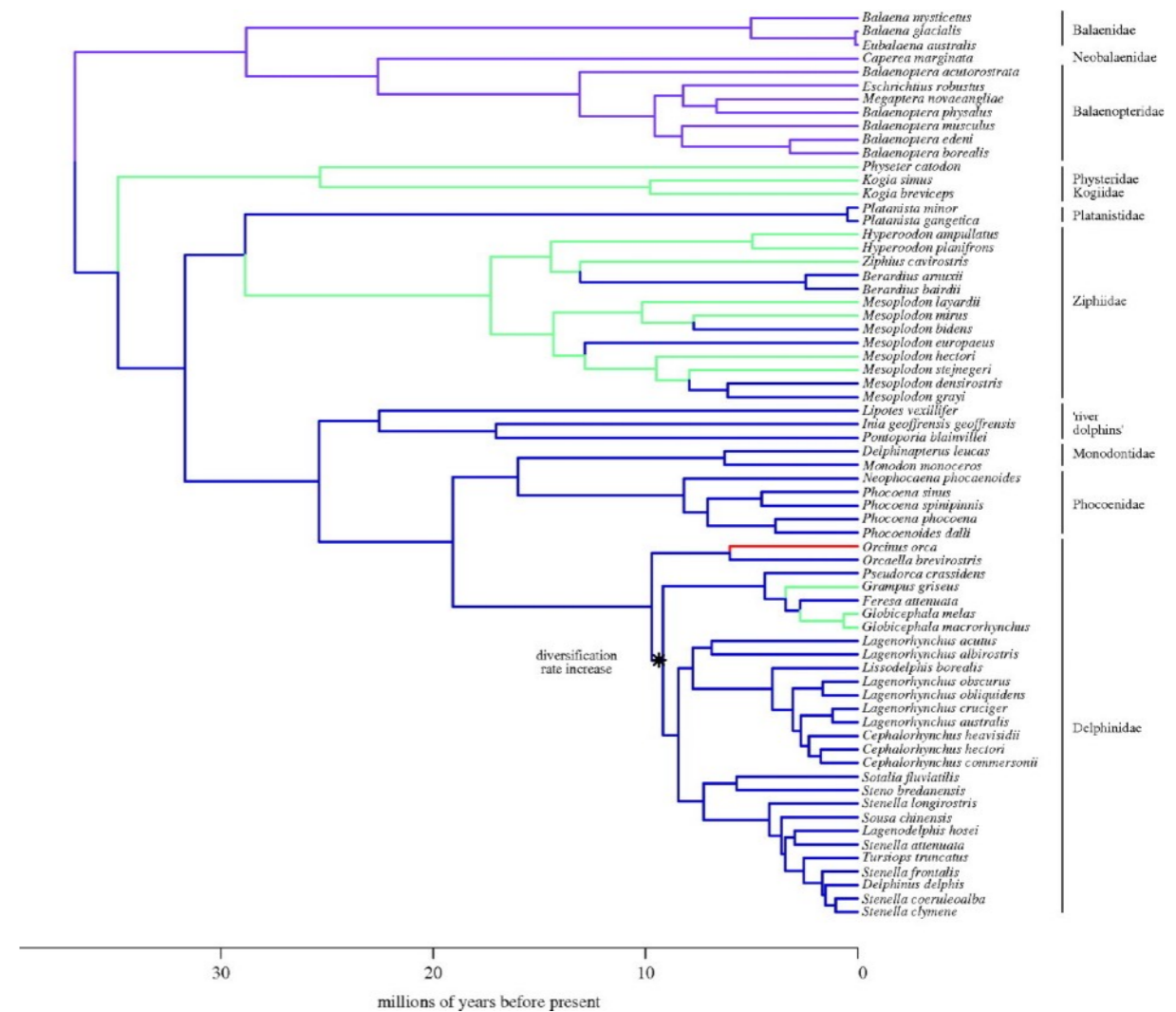
(figure from Sessa et al. 2014)

Taxonomic Diversity
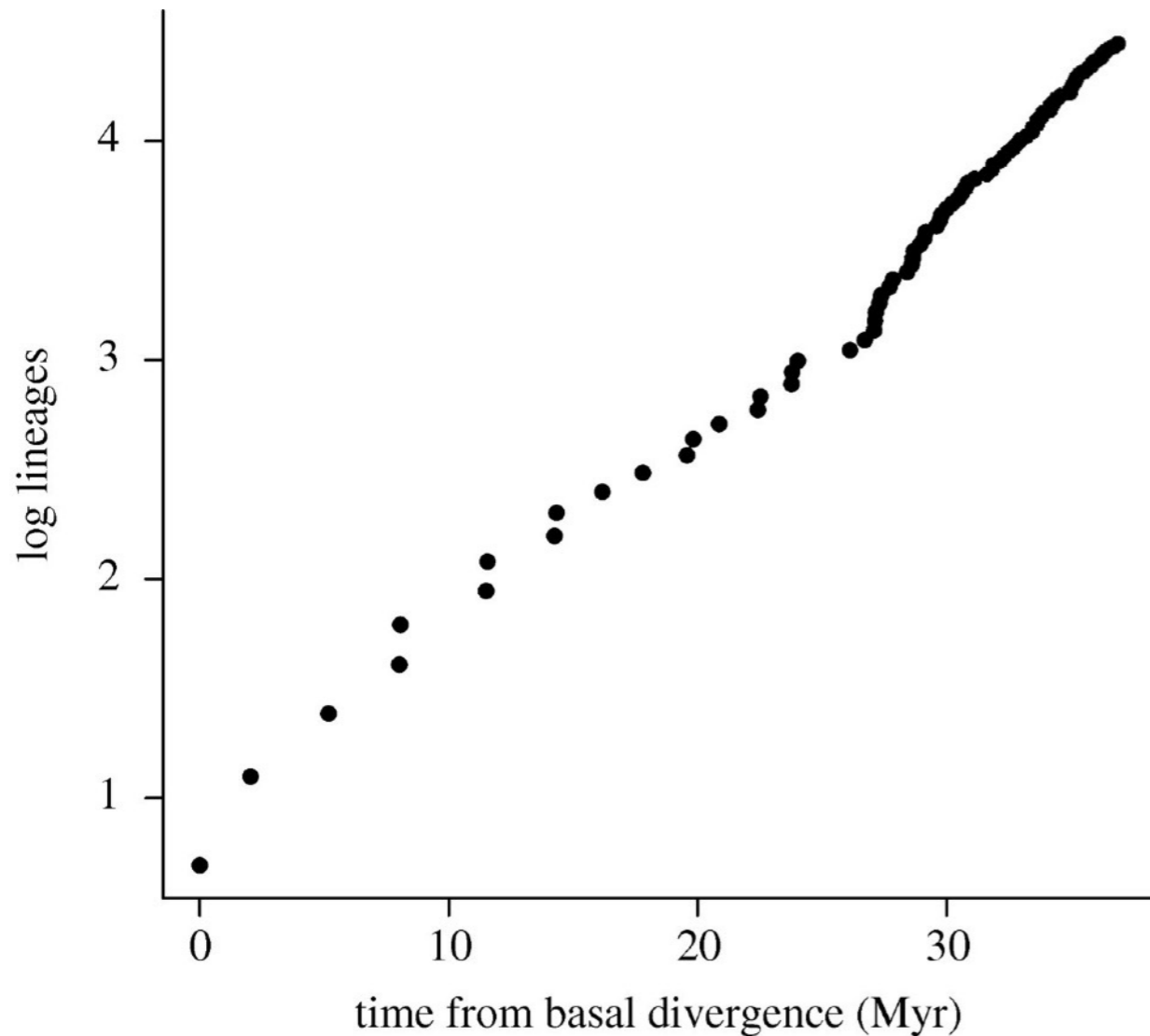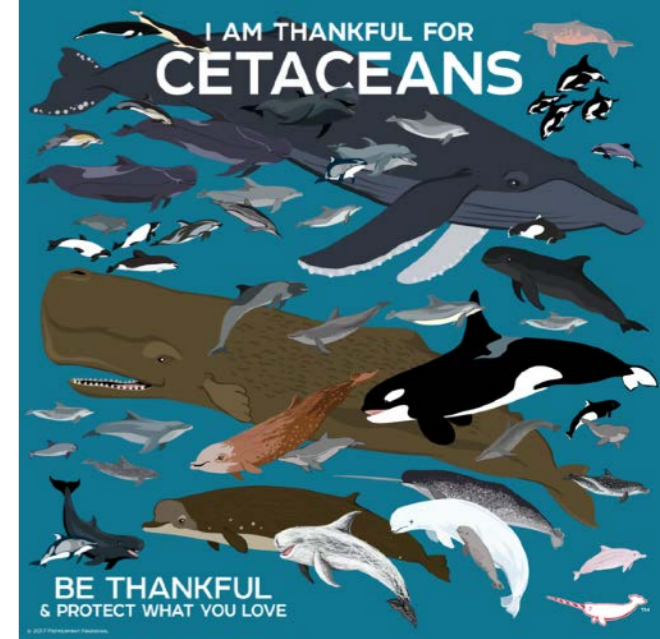

TABLE V.—*Chrysomelidæ* : observed and calculated numbers of genera of each size.

Number of species in genus.	Number of genera.	
	Observed.	Calculated.
1	215	214·9
2	90	85·6
3	38	48·9
4	35	32·6
5	21	23·8
6	16	18·3
7	15	14·7
8	14	12·2
9 to 11	28	27·0
12 to 14	20	18·6
15 to 20	30	24·9
21 to 30	32	25·0
31 to 40	13	15·9
41 to 50	14	11·4
51 to 75	17	18·5
76 to 100	13	11·1
101 to 150 ...	7	12·3*
151 upwards ...	9	11·3*
Total ...	627	627·0

* The frequency of genera of 101 species and upwards was subdivided by extrapolation.
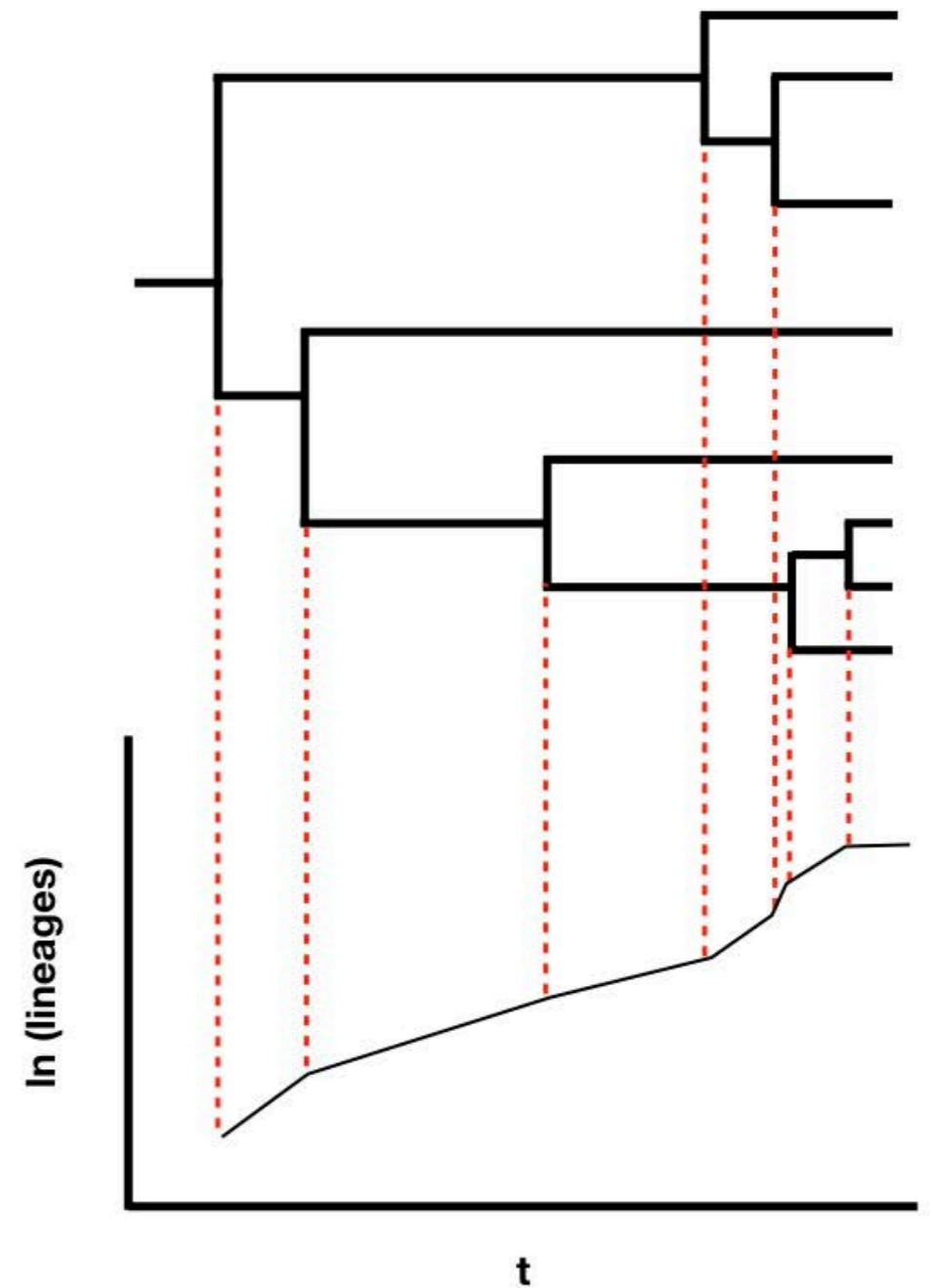
(table from Yule 1924)

Taxonomic Diversity

In cetaceans, there was an increase in the diversification rate over the last 10 My
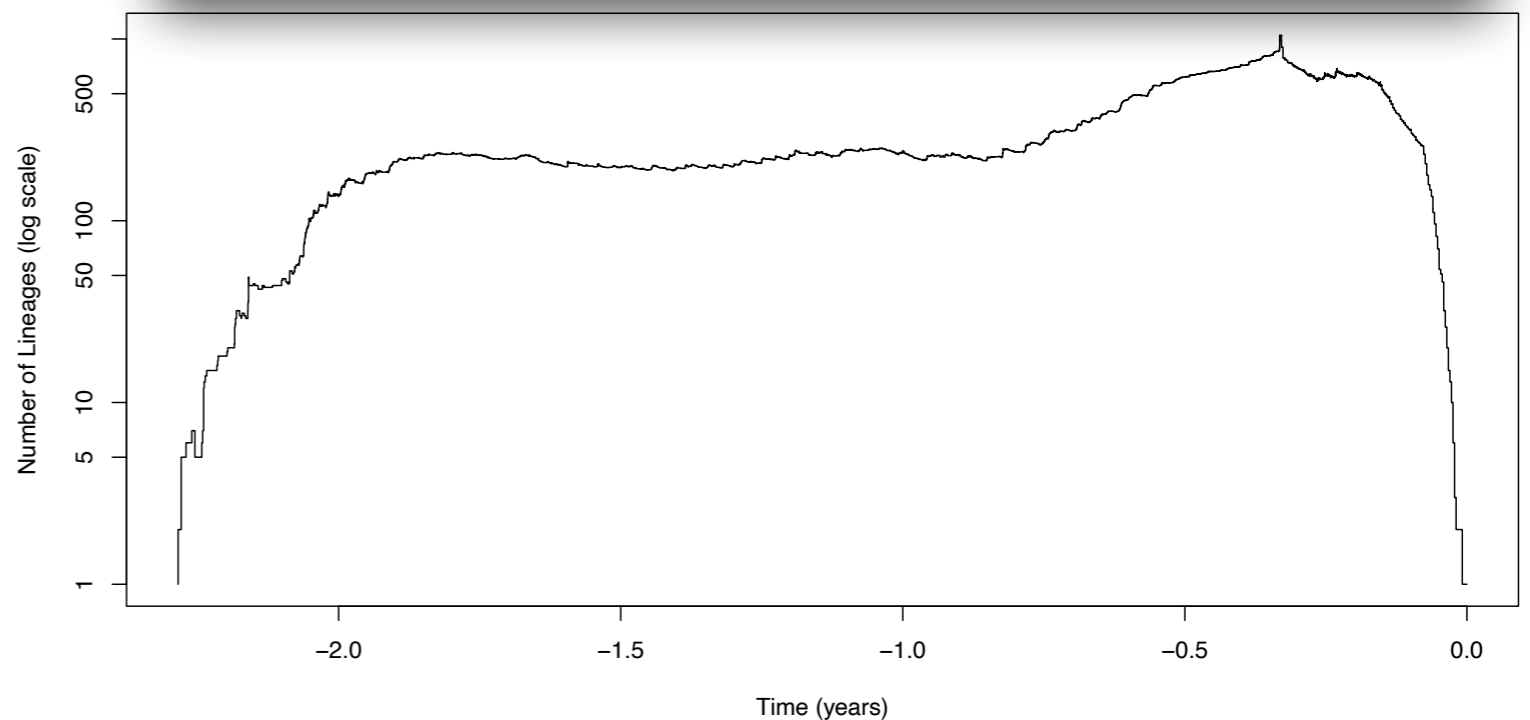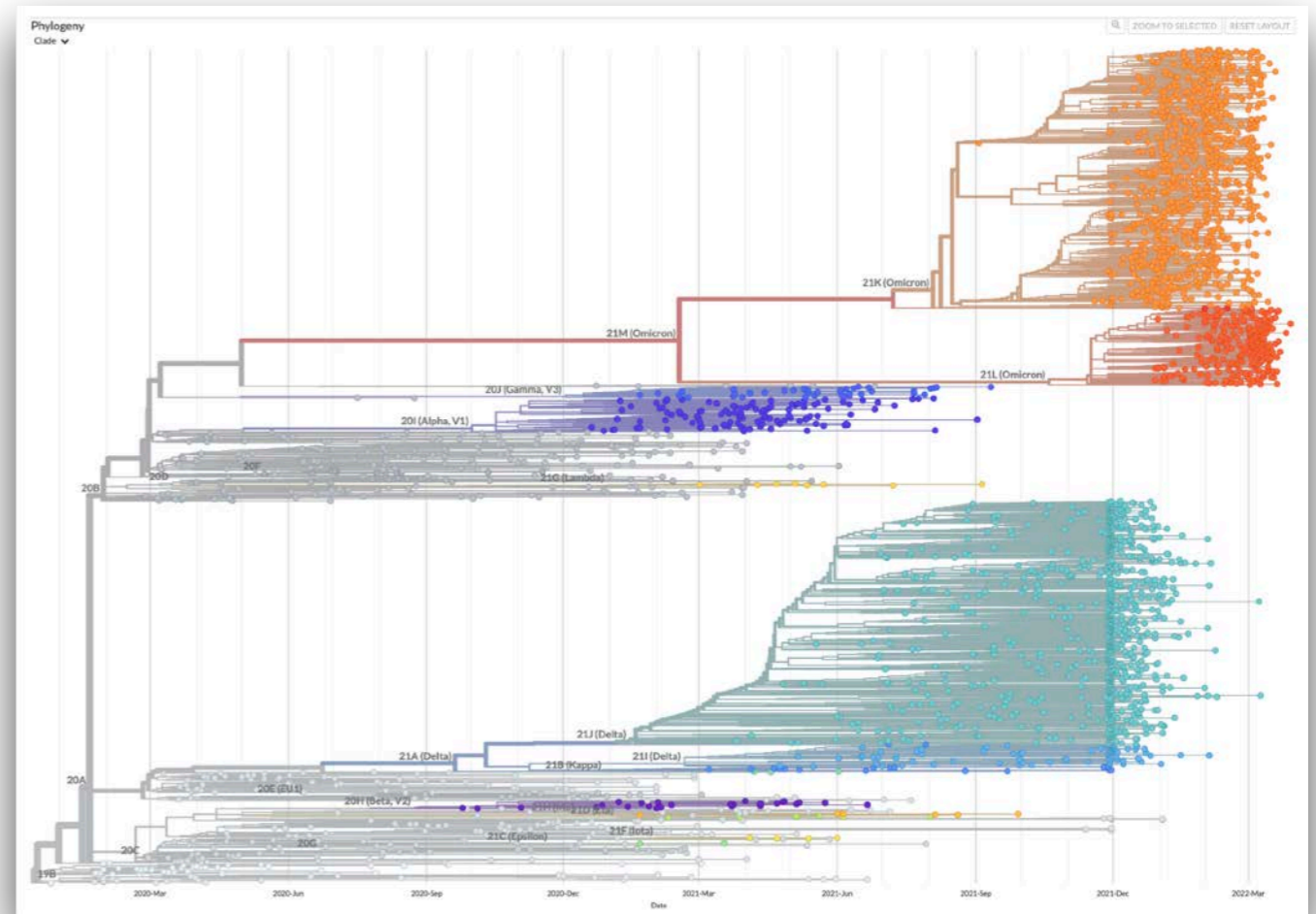
(Slater et al. 2010)

Lineages through Time

One approach to understanding patterns of cladogenesis over time is to plot the accumulation of lineages over time

(figures from Harmon 2019, Ch 10)

SARS-CoV-2 Infections Through Time

LTT plots based on phylogenies of infectious disease show the number of infections over time

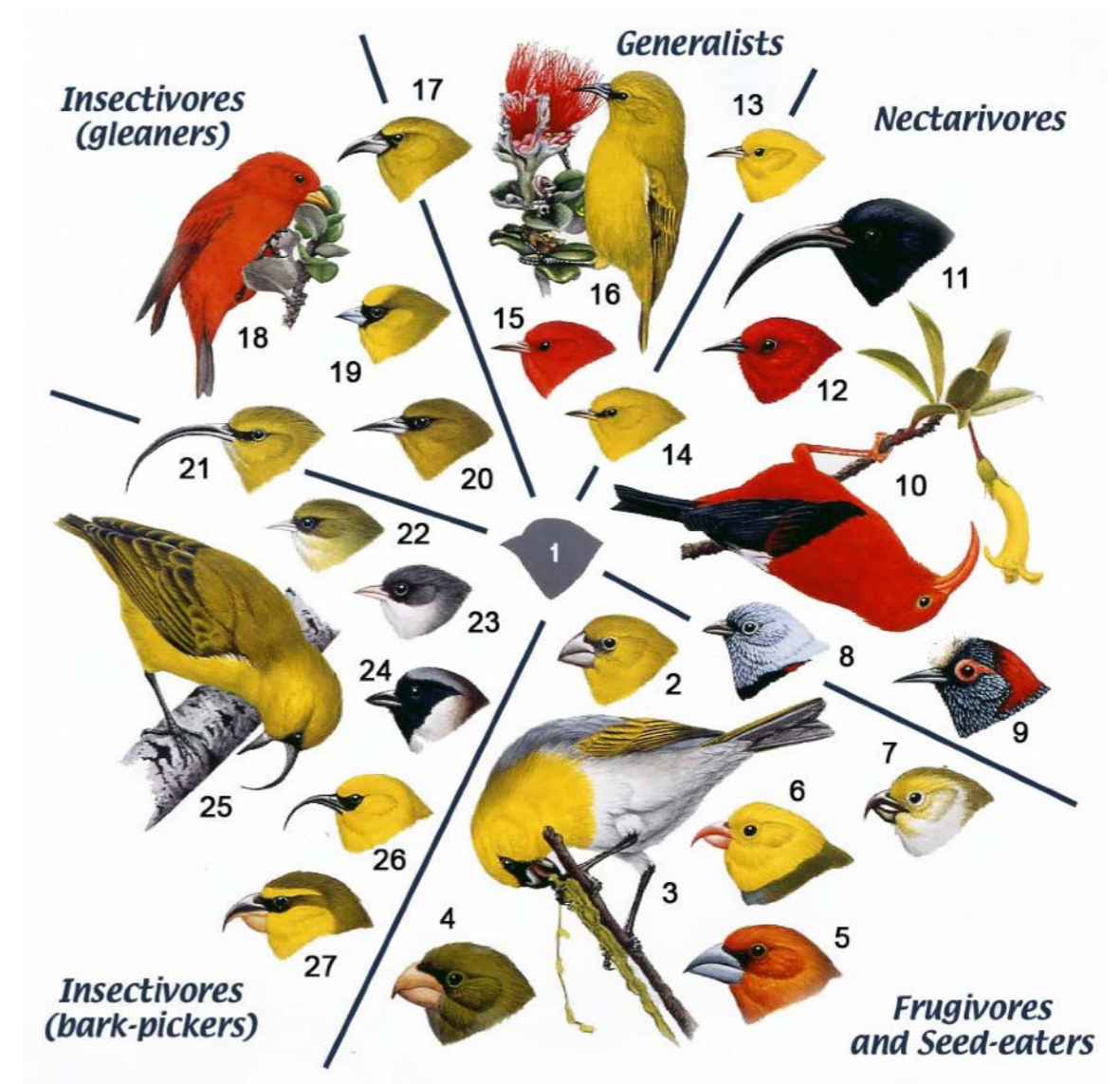(based on data from 3 April 2022 on nextstrain.org)

Diversification in Macroevolution

Evolutionary radiations

Mass extinction

Diversity dependence

Infectious disease dynamics

(figure from Losos & Mahler, 2010)

Macroevolutionary Questions

What is the average rate of diversification?

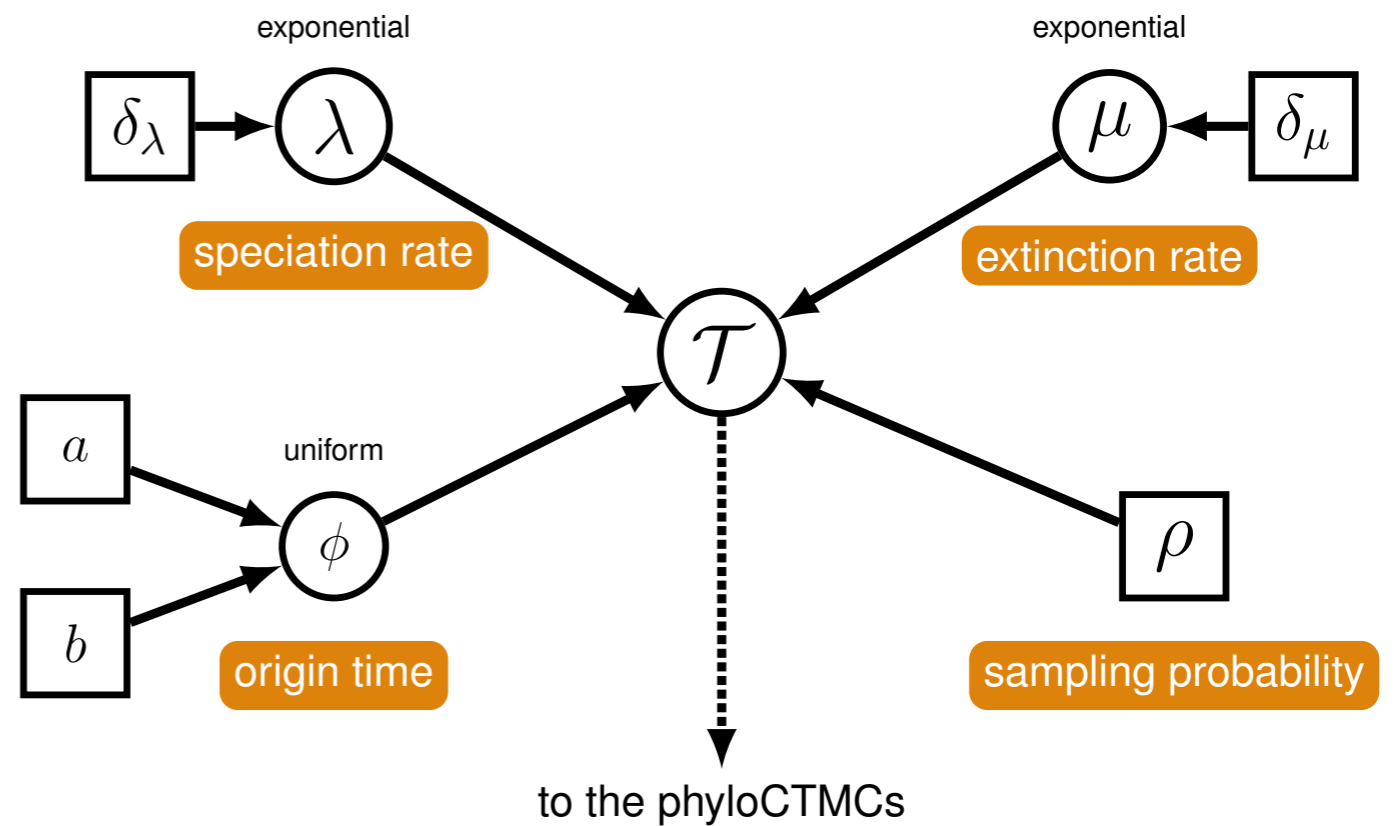Has the diversification rate rate changed over time?

Do rates of diversification vary among branches?

Are diversification rates correlated with a particular morphological trait?
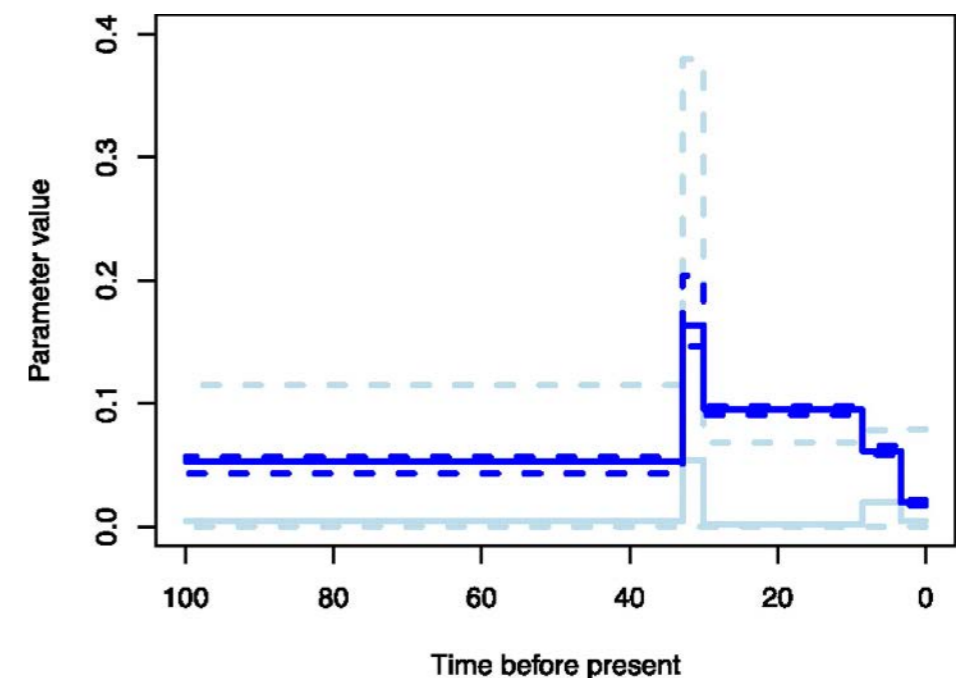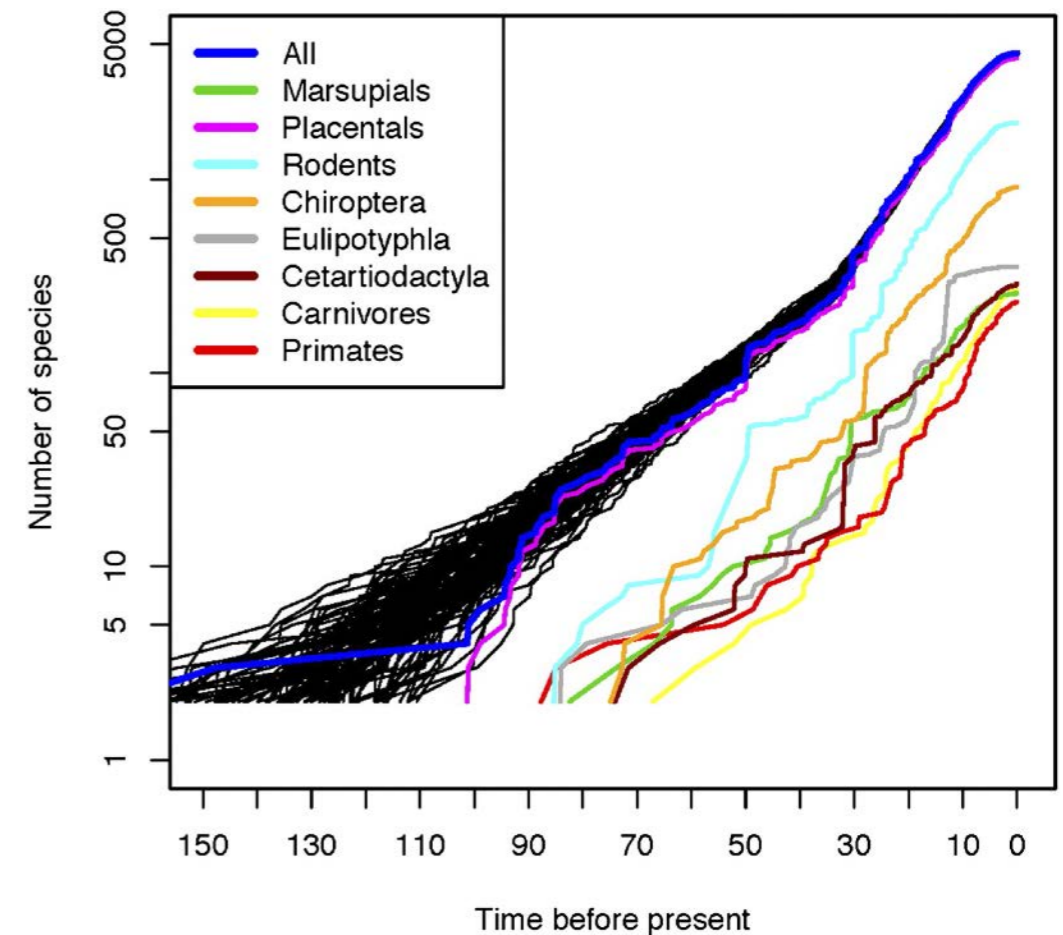
The Birth-Death Process

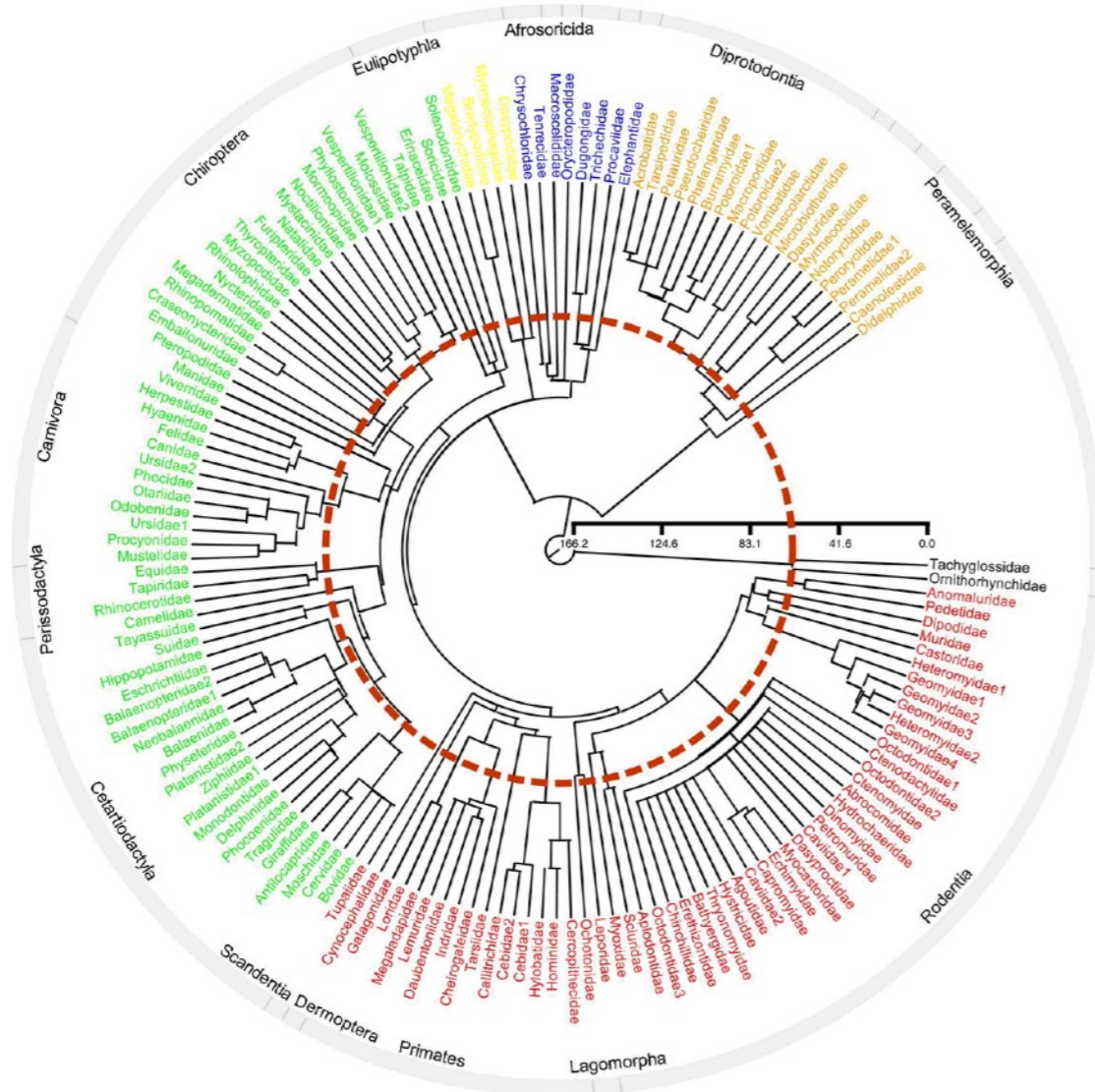At any point in time a lineage can speciate at rate **λ** or go extinct with a rate of **μ**

Conditions on a probability of sampling a tip **ρ**, and the origin time of the process **φ**

How do rates change over time?

Did mammalian diversification rates accelerate after the K/T extinction?

(figures from Stadler, 2011)

How do rates vary among branches?

(figures from Varga et al., 2019)

Lineage-Specific Speciation & Extinction Rates

Estimating rates of diversification among branches is a very difficult problem

Many models & methods have been proposed

(McGuire et al, 2014)

(Jetz et al, 2012)

(Condamine et al, 2016)

(Kissling 2017)

Lineage-Specific Speciation & Extinction Rates

Recently, these methods have been the focus of controversy

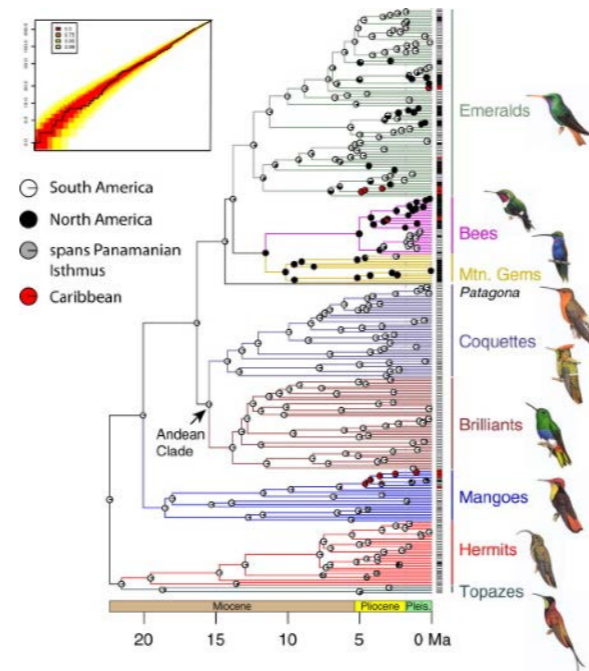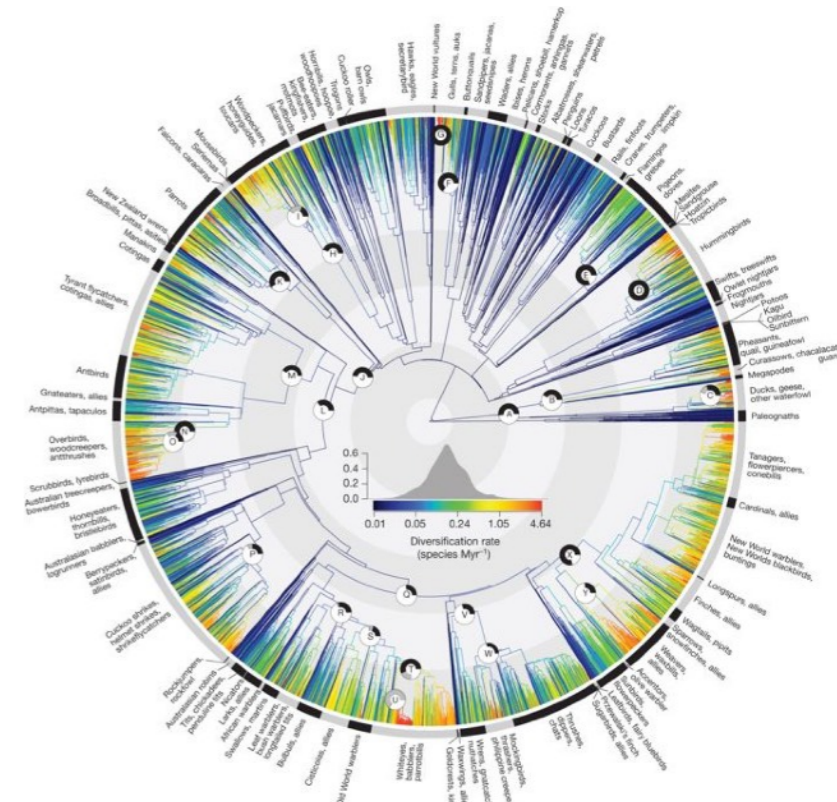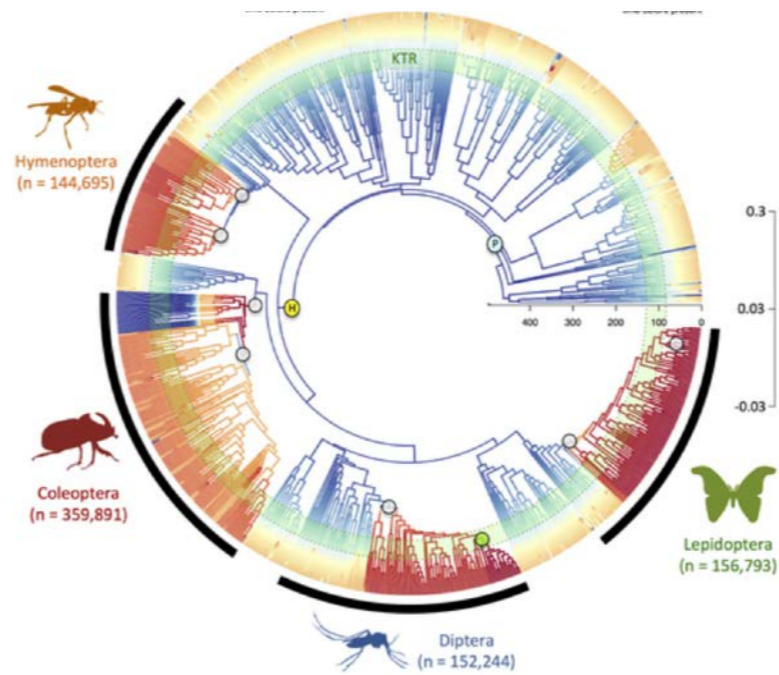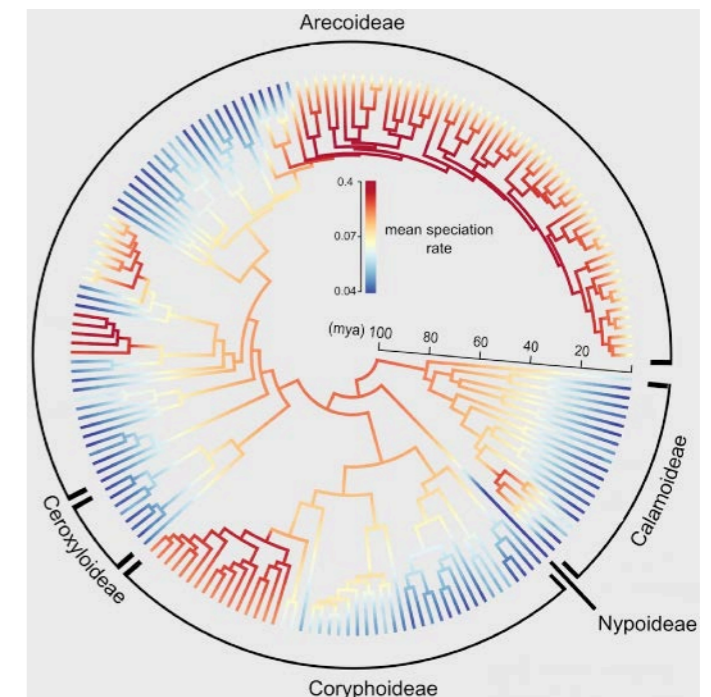### How Well Can We Detect Lineage-Specific Diversification-Rate Shifts? A Simulation Study of Sequential AIC Methods

Michael R. May ✉, Brian R. Moore   Author Notes

Systematic Biology, Volume 65, Issue 6, November 2016, Pages 1076–1084, https://doi.org /10.1093/sysbio/syw026

Critically evaluating the theory and performance of Bayesian analysis of macroevolutionary mixtures

Brian R. Moore, Sebastian Höhna, Michael R. May, Bruce Rannala, and John P. Huelsenbeck

PNAS August 23, 2016 113 (34) 9569–9574; first published August 10, 2016 https://doi.org/10.1073/pnas.1518659113

Estimating diversification rates for higher taxa: BAMM can give problematic estimates of rates and rate shifts

Andreas L. S. Meyer, John J. Wiens ✉   EVOLUTION SSE

First published: 21 October 2017 | https://doi.org/10.1111/evo.13378 | Citations: 32

Is BAMM Flawed? Theoretical and Practical Concerns in the Analysis of Multi-Rate Diversification Models

Daniel L. Rabosky ✉, Jonathan S. Mitchell, Jonathan Chang   Author Notes

Systematic Biology, Volume 66, Issue 4, July 2017, Pages 477–498, https://doi.org/10.1093 /sysbio/syx037

BAMM at the court of false equivalency: A response to Meyer and Wiens

Daniel L. Rabosky ✉   EVOLUTION SSE

First published: 12 August 2018 | https://doi.org/10.1111/evo.13566 | Citations: 13

BAMM gives misleading rate estimates in simulated and empirical datasets

Andreas L. S. Meyer, Cristian Román-Palacios, John J. Wiens ✉   EVOLUTION SSE

First published: 13 August 2018 | https://doi.org/10.1111/evo.13574 | Citations: 16

Extant timetrees are consistent with a myriad of diversification histories

nature

https://doi.org/10.1038/s41586-020-2176-1   Stilianos Louca[1,2]✉ & Matthew W. Pennell[3,4]✉

Pulled Diversification Rates, Lineages-Through-Time Plots, and Modern Macroevolutionary Modeling

Andrew J Helmstetter ✉, Sylvain Glemin, Jos Käfer, Rosana Zenil-Ferguson, Hervé Sauquet, Hugo de Boer, Léo-Paul M J Dagallier, Nathan Mazet, Eliette L Reboud, Thomas L P Couvreur ... Show more

Systematic Biology, syab083, https://doi.org/10.1093/sysbio/syab083

Inherent issues with these models mean that studies must critically evaluate rates estimated by these methods

Lineage-Specific Speciation & Extinction Rates

A model with many small shifts for estimating species-specific diversification rates

Odile Maliet ✉, Florian Hartig & Hélène Morlon

Nature Ecology & Evolution **3**, 1086–1092(2019) │ Cite this article

A Multi-Type Birth–Death model for Bayesian inference of lineage-specific birth and death rates ∂

Joëlle Barido-Sottani ✉, Timothy G Vaughan, Tanja Stadler ✉

Systematic Biology, syaa016, https://doi.org/10.1093/sysbio/syaa016

Published: 27 February 2020   **Article history ▾**

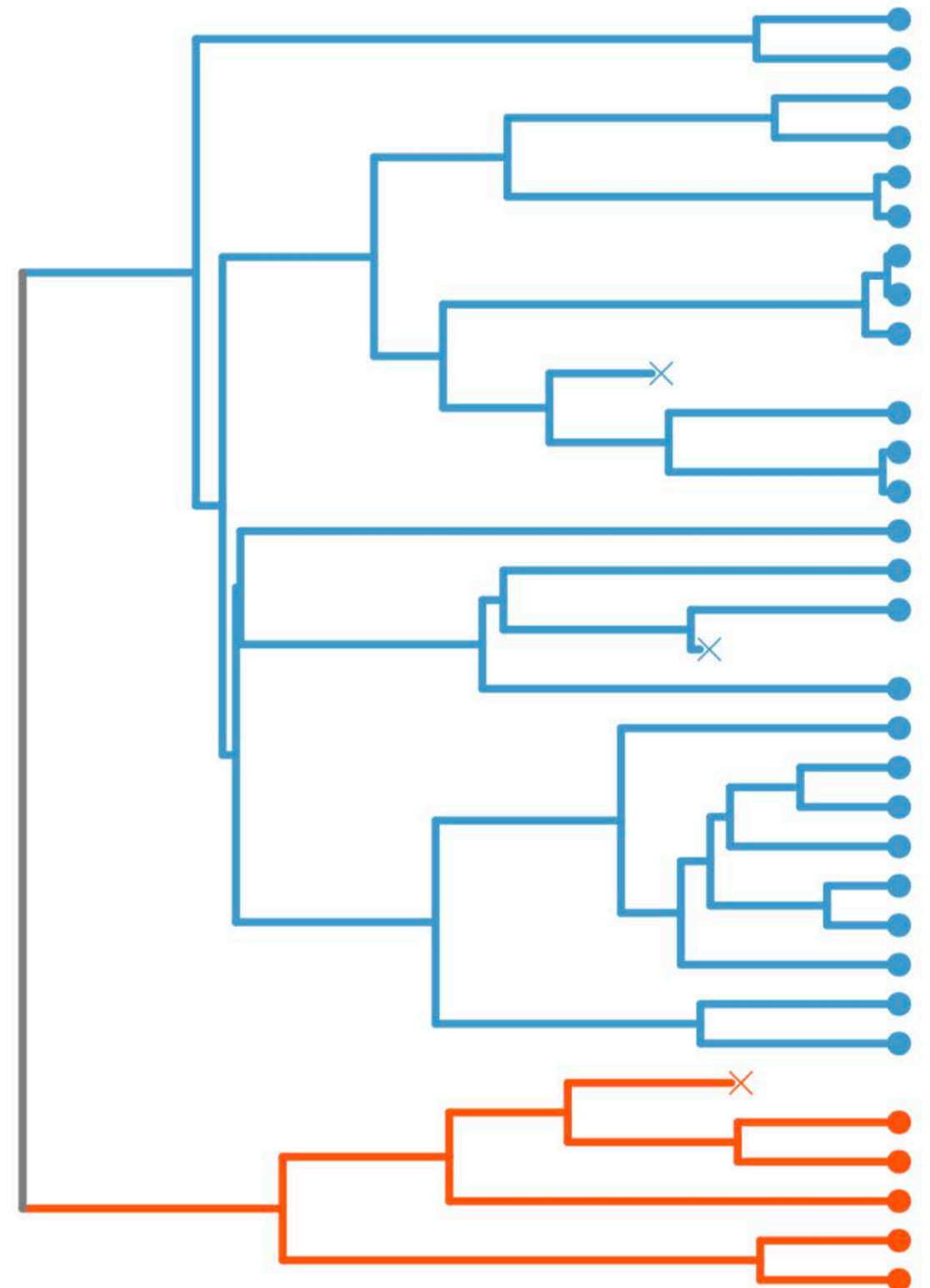## A Bayesian Approach for Estimating Branch-Specific Speciation and Extinction Rates

CSH Cold Spring Harbor Laboratory   bioRχiv
THE PREPRINT SERVER FOR BIOLOGY

Sebastian Höhna, William A. Freyman, Zachary Nolen, John P. Huelsenbeck, Michael R. May, Brian R. Moore
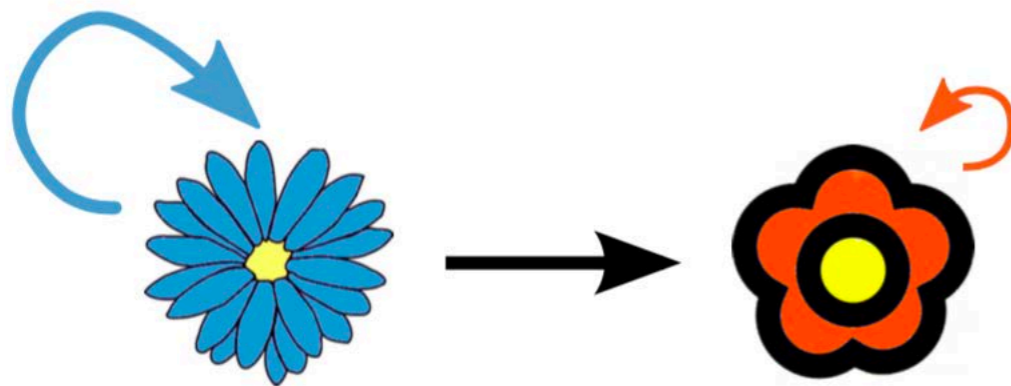
doi: https://doi.org/10.1101/555805

What if traits influence diversification?

Most diversification studies assume that character evolution and diversification are independent

(based on slides by Emma Goldberg)

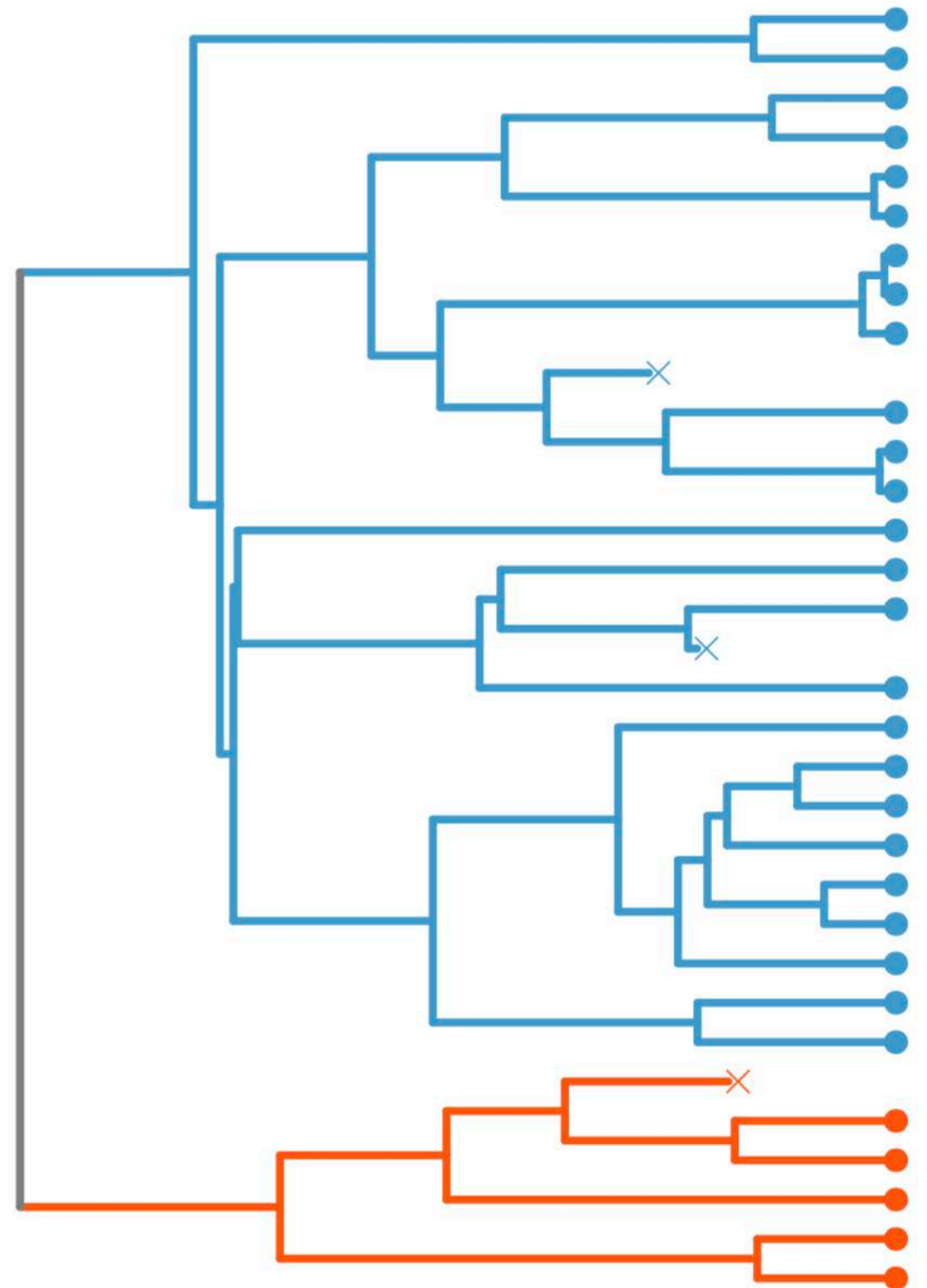# State-Dependent Diarsification

Do traits affect diversification rates?

Is the blue clade larger because blue is associated with higher speciation?
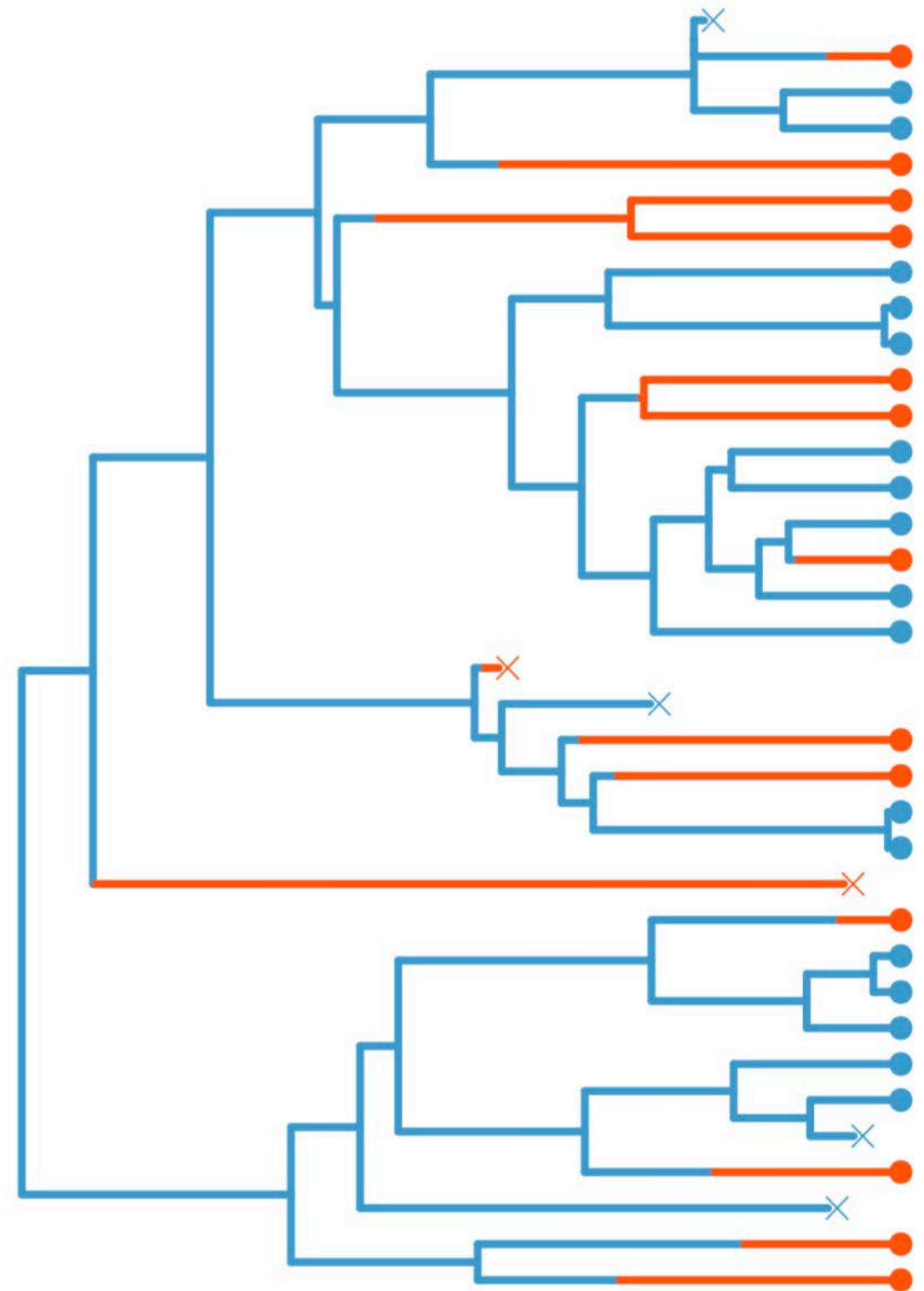
(based on slides by Emma Goldberg)

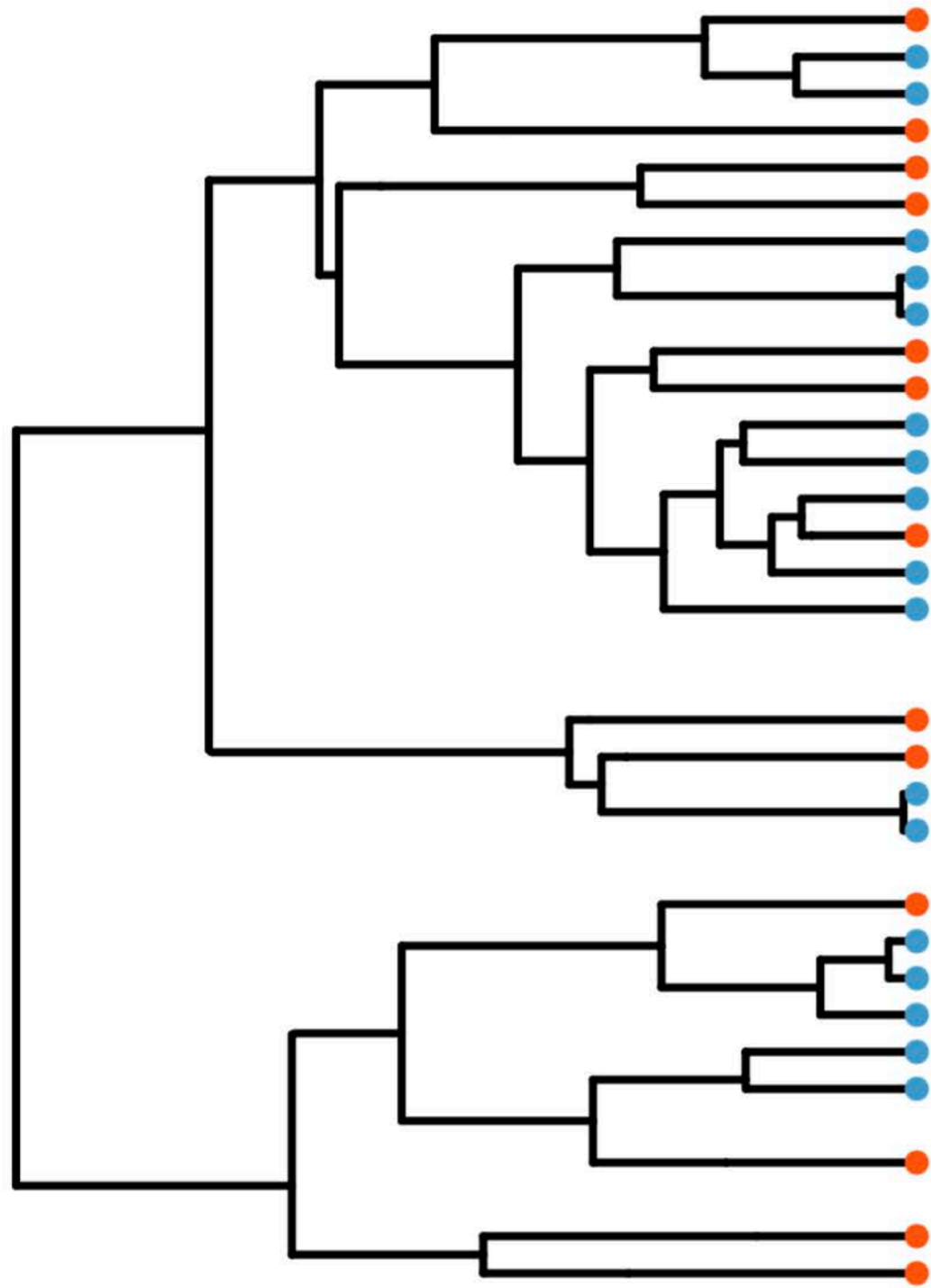# State-Dependent Diversification

Are evolving traits driving rates of speciation and extinction?

If a lineage transitions from blue to orange does its rate of diversification decrease?

(based on slides by Emma Goldberg)

State-Dependent Diversification

Without detailed information about past states and extinct species, we need powerful phylogenetic methods.

(based on slides by Emma Goldberg)

Problems with Assuming Independence

CONFOUNDING ASYMMETRIES IN EVOLUTIONARY DIVERSIFICATION AND
CHARACTER CHANGE

WAYNE P. MADDISON
Departments of Zoology and Botany and Biodiversity Research Centre, University of British Columbia,
Vancouver, British Columbia V6T 1Z4
E-mail: wmaddisn@interchange.ubc.ca

"Studies of character evolution often assume that a phylogeny's shape is determined independently of the characters, which then evolve as mere passengers along the tree's branches. However, if the characters help shape the tree, but this is not considered, biased inferences can result."

(1) If a character affects rates of speciation or extinction, then inferences about character-state transitions based on simple models can be biased

(2) If transition rates between character states are asymmetric, inferences based on sister-clade comparisons about whether a character correlates w/ diversification can be biased

Binary-State Speciation & Extinction Model (BiSSE)

BiSSE was the first model introduced to address state-dependent diversification

There are several extensions of this model: MuSSE (multi-state discrete traits), QuaSSE (continuous traits), GeoSSE (biogeography), ClaSSE (cladogenic traits), HiSSE (hidden traits)

BiSSE

BiSSE accounts for

(1) Speciation & extinction rates associated with each state

(2) Asymmetric transition rates between states

(based on slides by Emma Goldberg)

BiSSE

Each lineage is currently in state 0 or 1

Each state is associated with its own speciation and extinction rates

Binary-State Speciation & Extinction Model (BiSSE)

Estimating a Binary Character's Effect on Speciation and Extinction FREE

Wayne P. Maddison, Peter E. Midford, Sarah P. Otto

Systematic Biology, Volume 56, Issue 5, October 2007, Pages 701–710,

https://doi.org/10.1080/10635150701607033

BiSSE and related models involve a set of ordinary differential equations (ODEs) that describe how the probability of observing a descendant clade changes along a branch in the observed phylogeny.

Each ODE describes how the probability of observing a clade changes through time if it is in a particular state over that time period

Self-Incompatibility (SI) in Plants

- Most plants are hermaphrodites

- Complex genetic systems have evolved to reject own pollen

- New SI systems rarely evolve. But SI is frequently lost
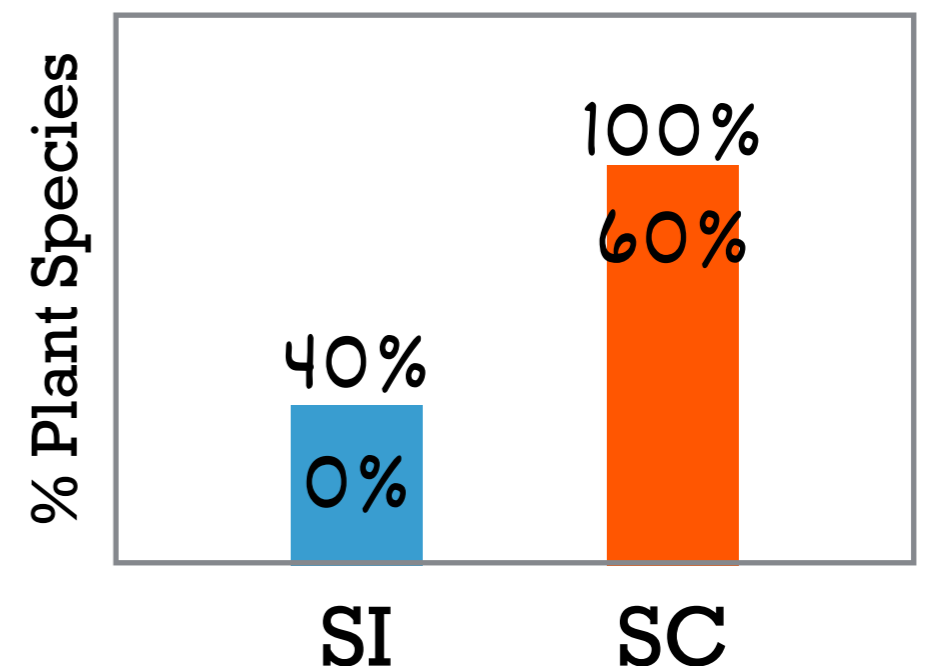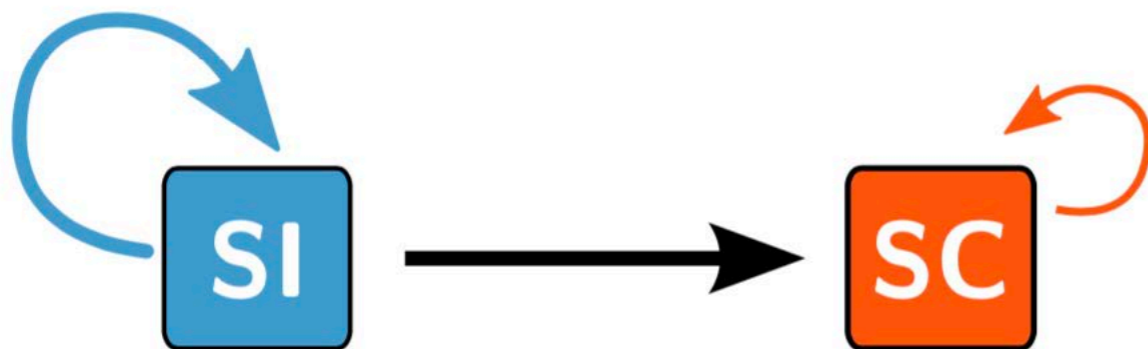
(based on slides by Emma Goldberg)
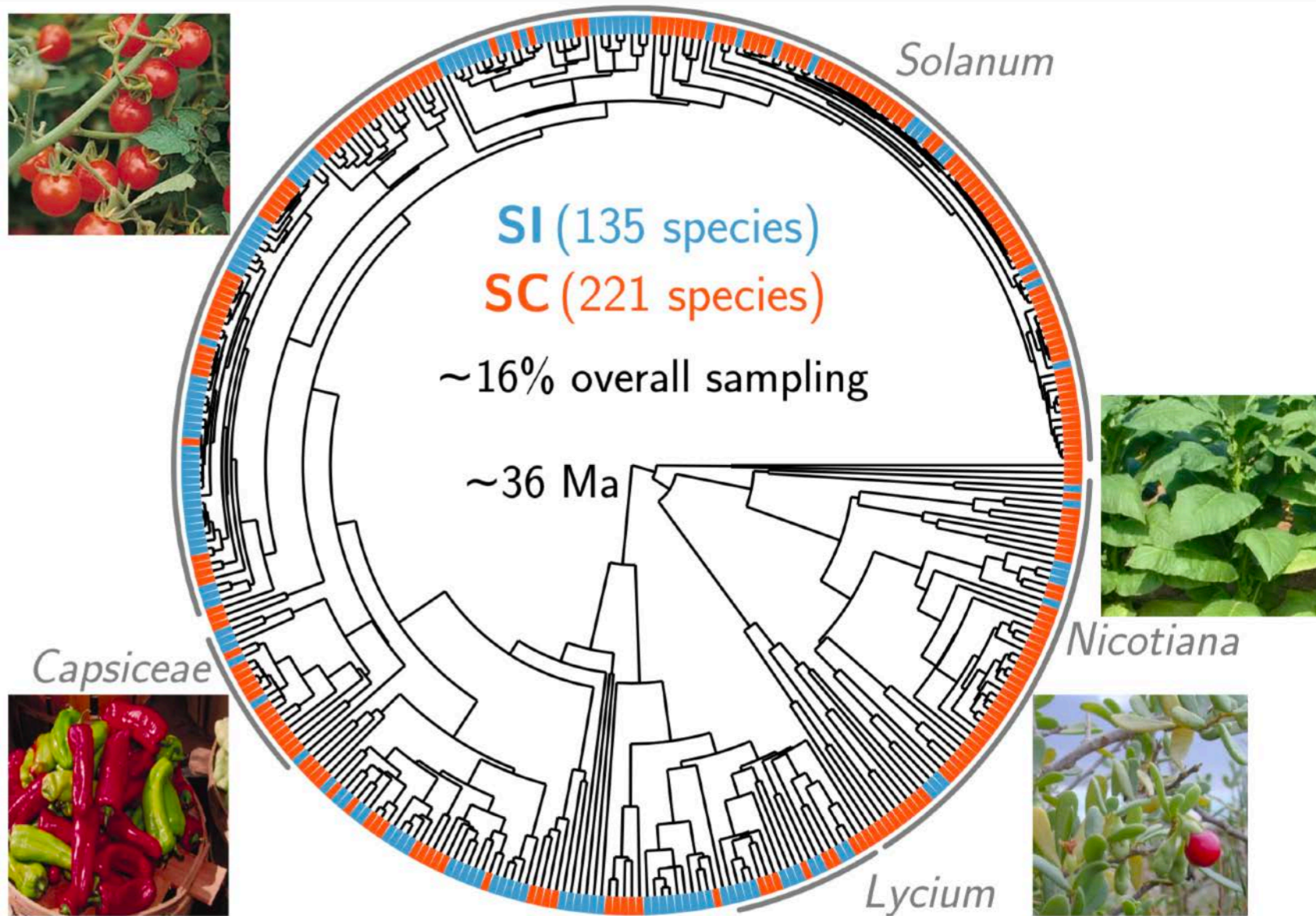
Self-Incompatibility (SI) in Plants

Does SI affect the rate of speciation?

We would expect that eventually all plant species would be self-compatible (SC)

But we observe many self-incompatible species

(based on slides by Emma Goldberg)

Self-Incompatibility (SI) in Plants

BiSSE was used to address this question in nightshades

Solanum

SI (135 species)
SC (221 species)

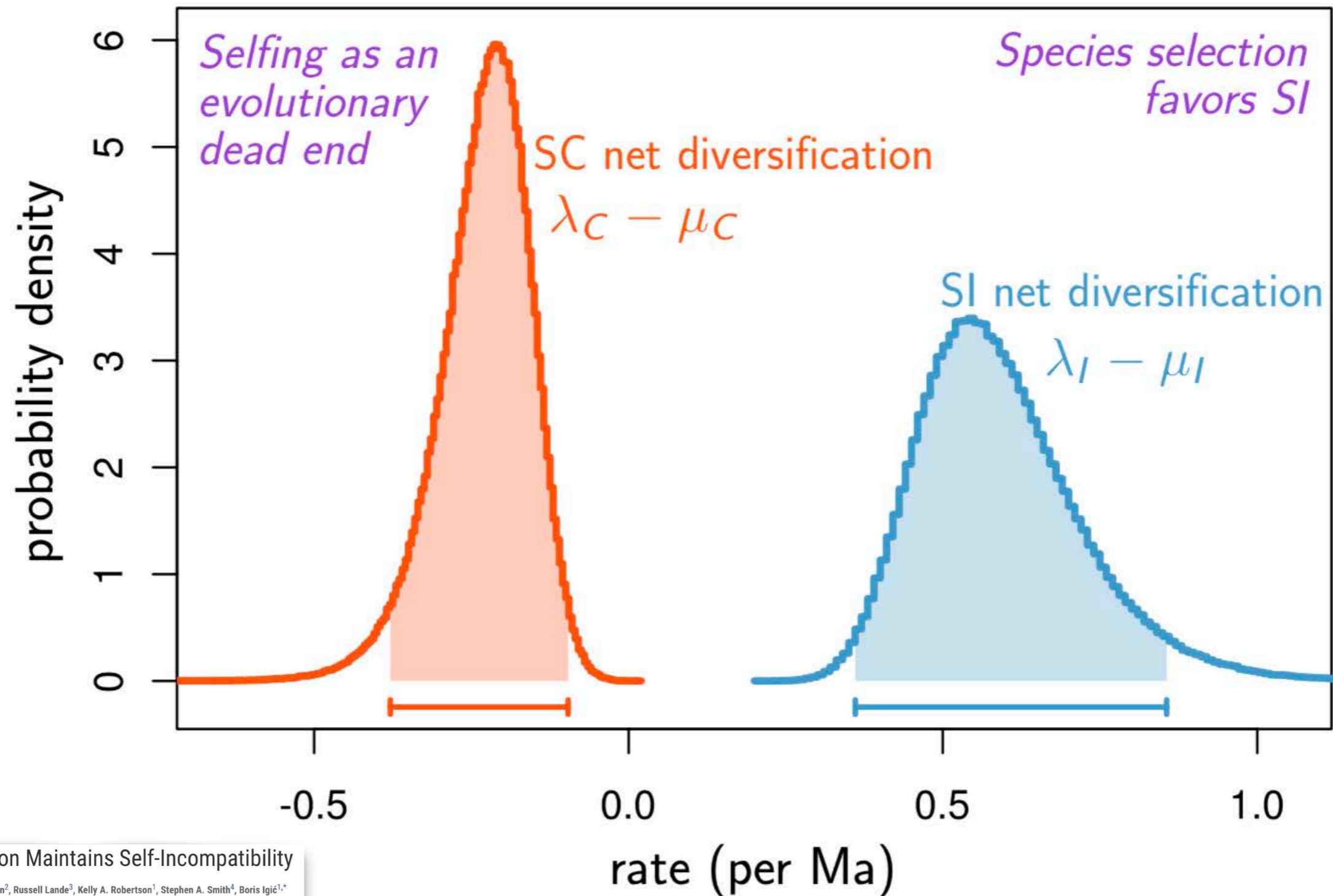~16% overall sampling

~36 Ma

Nicotiana

Capsiceae

Lycium

Species Selection Maintains Self-Incompatibility

Emma E. Goldberg[1], Joshua R. Kohn[2], Russell Lande[3], Kelly A. Robertson[1], Stephen A. Smith[4], Boris Igić[1,*]

+ See all authors and affiliations

Self-Incompatibility (SI) in Plants

Selfing as an evolutionary dead end

SC net diversification $\lambda_C - \mu_C$

Species selection favors SI

SI net diversification $\lambda_I - \mu_I$

(based on slides by Emma Goldberg)

Self-Incompatibility (SI) in Plants

In nightshades, species with functional SI diversify at a significantly higher rate than SC species

The apparent short-term advantages of SC individuals are offset by species selection, which favors outcrossing.

SI (135 species)
SC (221 species)
~16% overall sampling
~36 Ma

Solanum
Nicotiana
Lycium
Capsiceae

Species Selection Maintains Self-Incompatibility

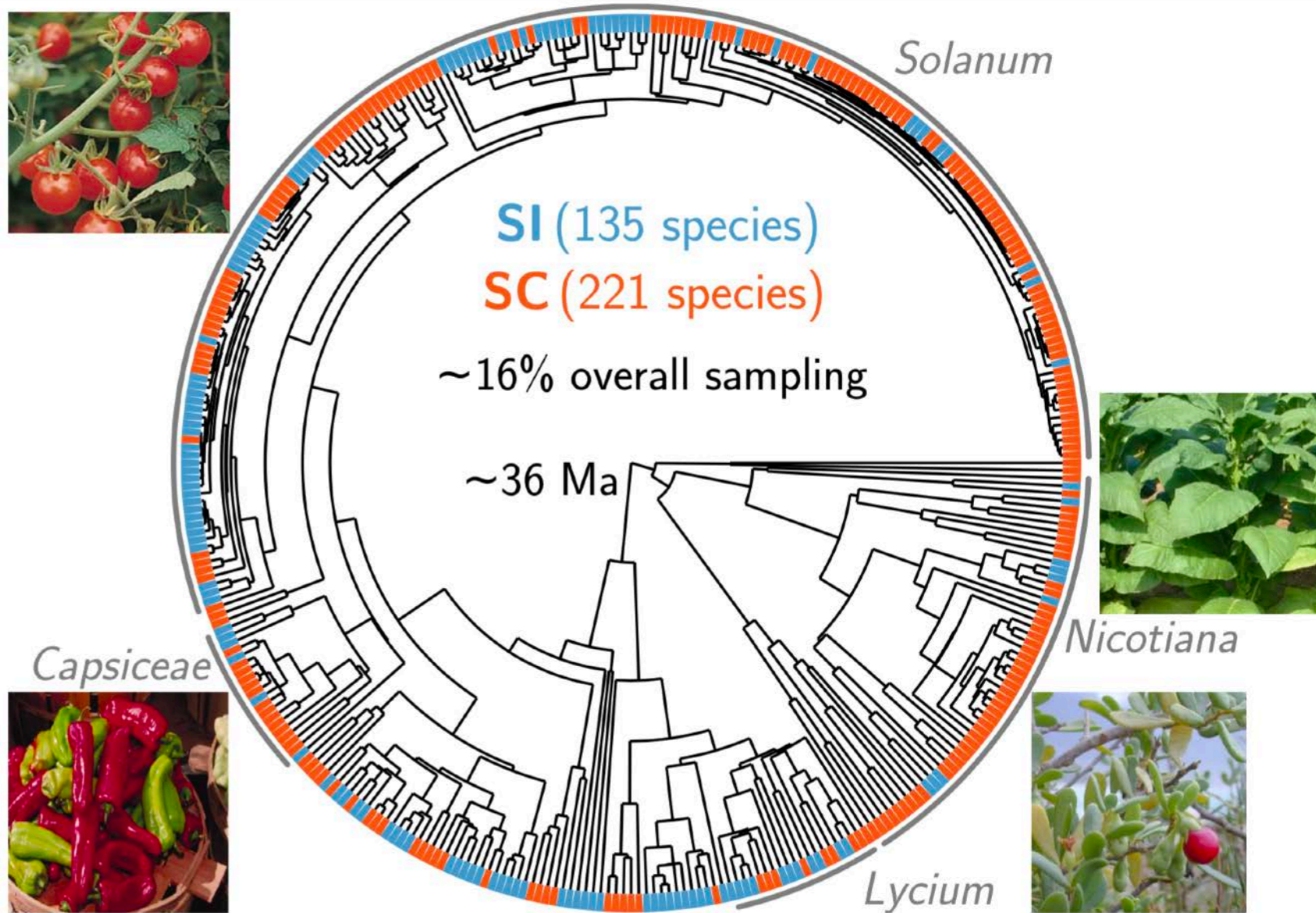Emma E. Goldberg[1], Joshua R. Kohn[2], Russell Lande[3], Kelly A. Robertson[1], Stephen A. Smith[4], Boris Igić[1,*]

+ See all authors and affiliations

Potential Pitfalls

The Unsolved Challenge to Phylogenetic Correlation Tests for Categorical Characters FREE

Wayne P. Maddison ✉, Richard G. FitzJohn   Author Notes

Systematic Biology, Volume 64, Issue 1, January 2015, Pages 127–136,
https://doi.org/10.1093/sysbio/syu070

Model Inadequacy and Mistaken Inferences of Trait-Dependent Speciation FREE

Daniel L. Rabosky ✉, Emma E. Goldberg   Author Notes

Systematic Biology, Volume 64, Issue 2, March 2015, Pages 340–355,
https://doi.org/10.1093/sysbio/syu131

BiSSE has been shown to be prone to falsely identifying a positive association when diversification rate shifts are correlated with a character not included in the model

Hidden-State Dependent Speciation & Extinction

Detecting Hidden Diversification Shifts in Models of Trait–Dependent Speciation and Extinction FREE
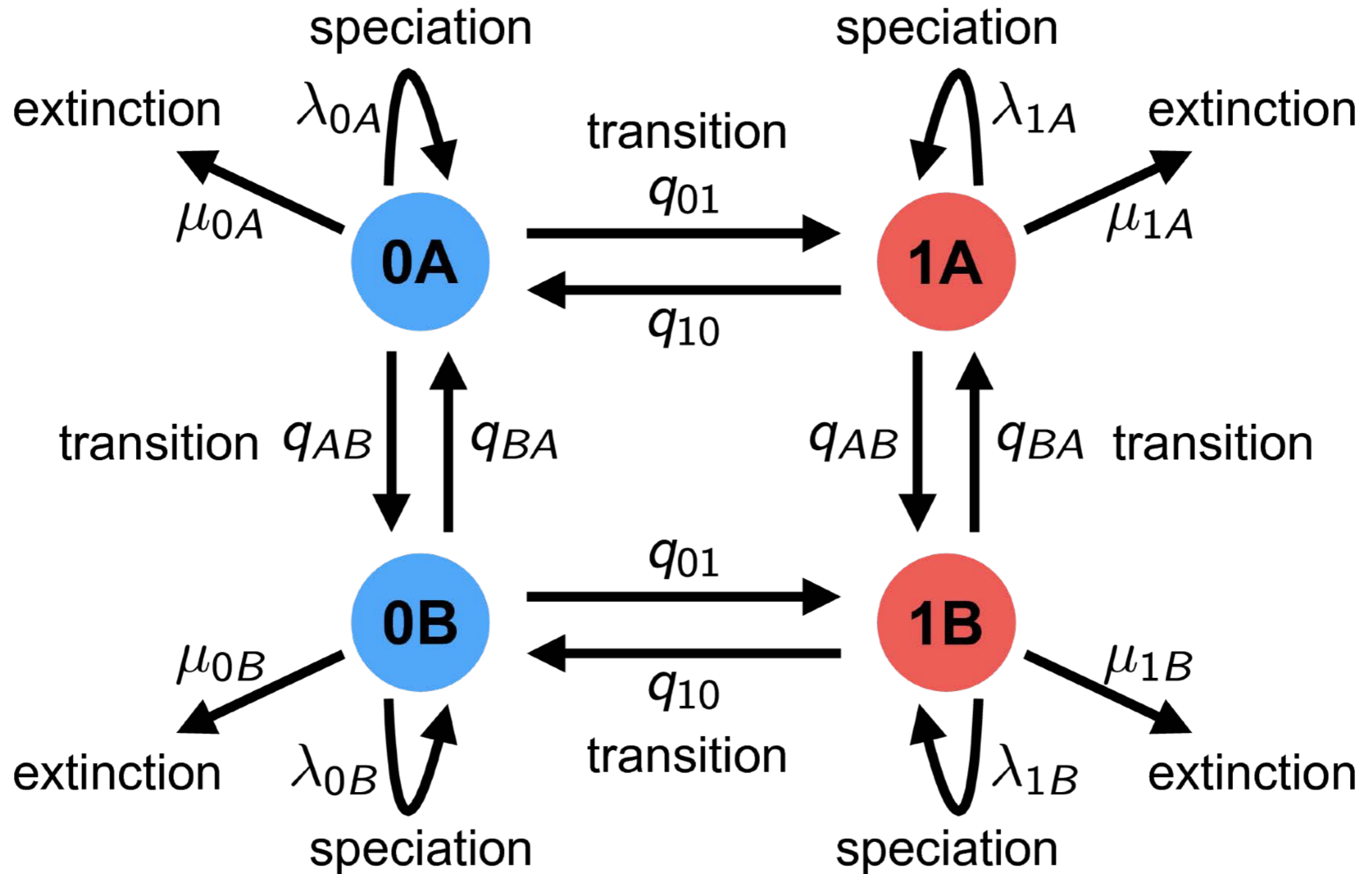
Jeremy M. Beaulieu ✉, Brian C. O'Meara   Author Notes

Systematic Biology, Volume 65, Issue 4, July 2016, Pages 583–601,
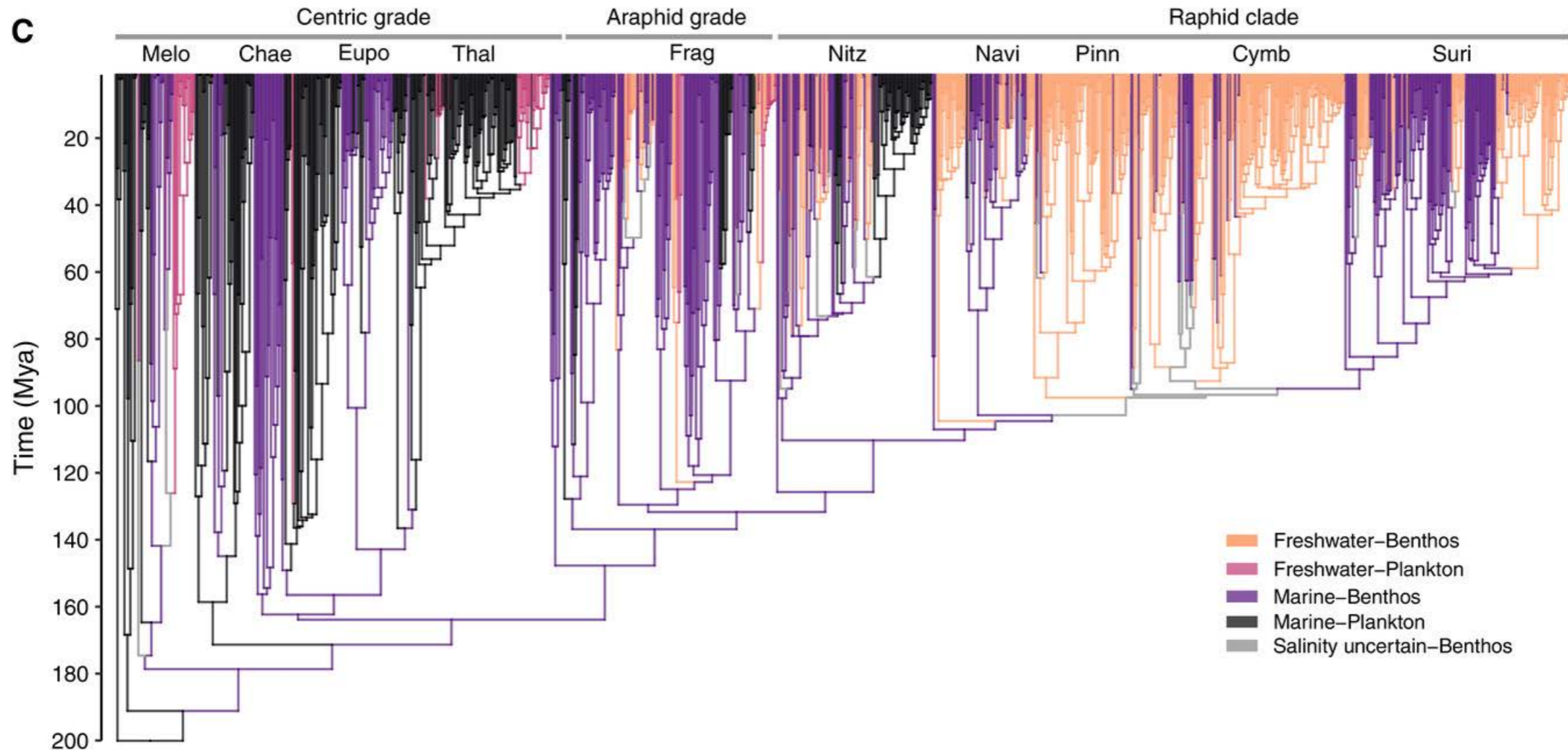
https://doi.org/10.1093/sysbio/syw022

Incorporating a 2nd, unobserved character can reduce the possibility of falsely associating the observed character with diversification

Changes in the unobserved character's state represent <u>background</u> diversification rate shifts that are uncorrelated with the observed character

HiSSE Model

Diversification in Diatoms

Diatoms diversify and turn over faster in freshwater than marine environments*

Teofil Nakov ✉, Jeremy M. Beaulieu, Andrew J. Alverson

First published:20 August 2019 | https://doi.org/10.1111/evo.13832 | Citations: 1

Thursday: BiSSE & HiSSE Tutorial

Please read: Harmon (2019), Ch. 13
-Characters and diversification rates
https://lukejharmon.github.io/pcm/chapter13_chardiv