Phylogenetics

Phylodynamics models I

RL-V3 MPP

Rachel Warnock

29.04.2025

Schedule available online

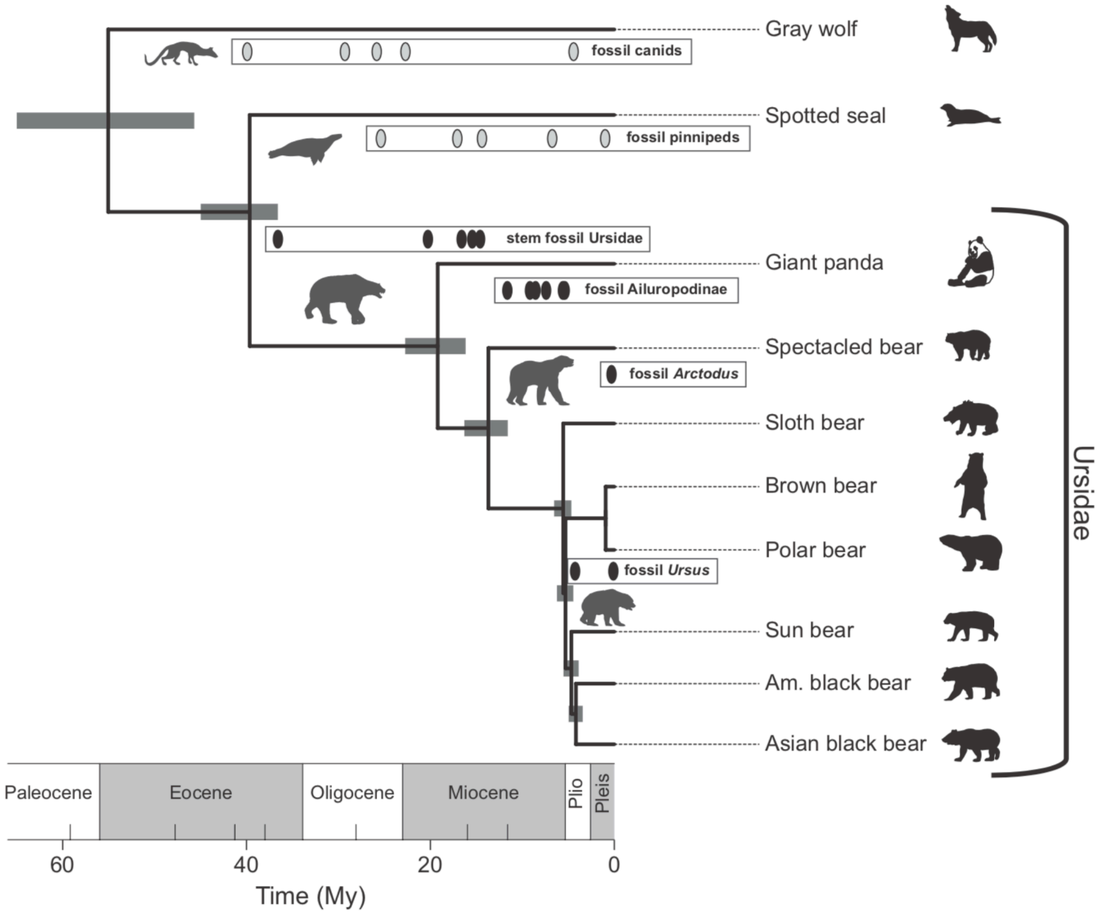
https://phylogenetics-fau.netlify.app/schedule_part_2

No lecture next week (06.05)

But we can meet after the hypothesis testing presentations 09.05 to discuss projects

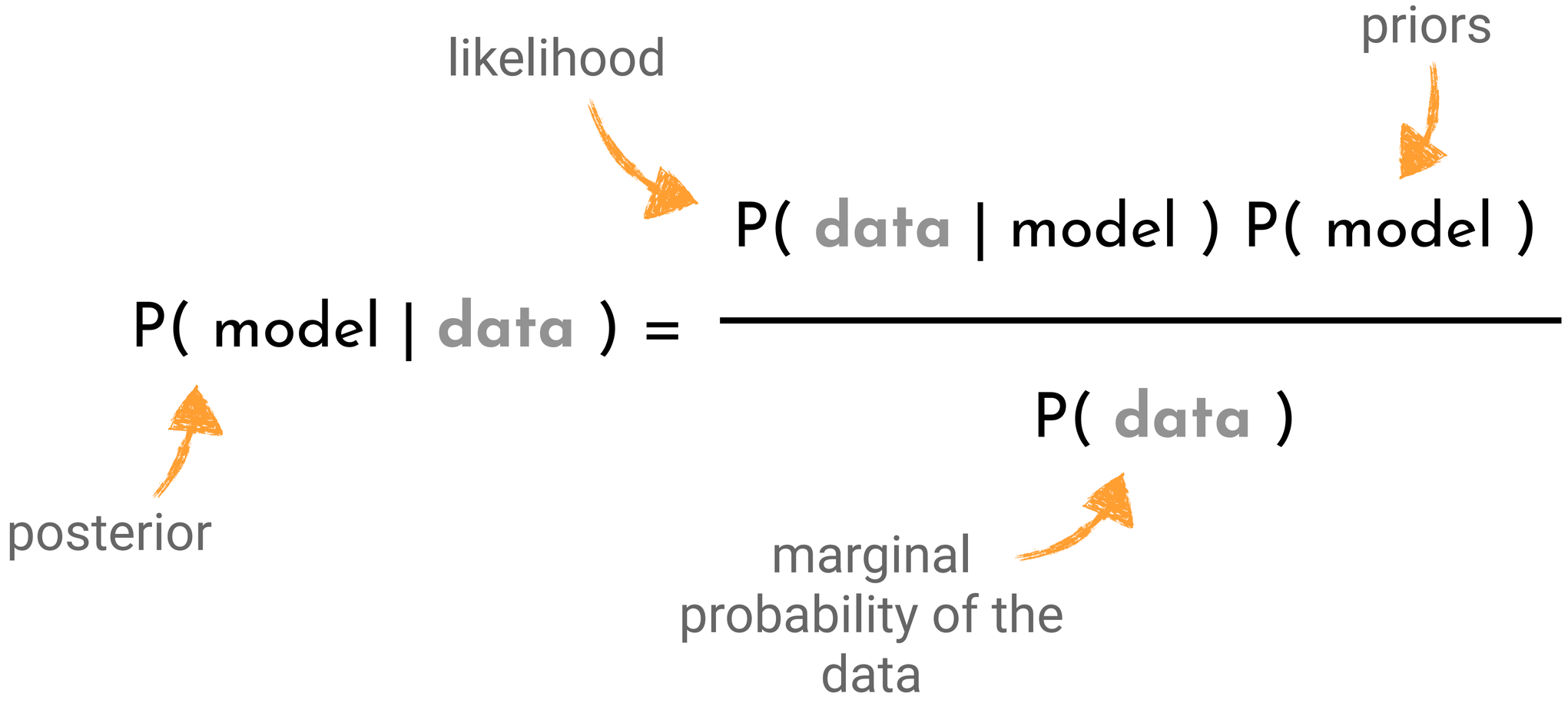
Objectives

- **Recap**: tripartite framework and the FBD process
- Diversification rate estimation and phylodynamics



The big recap:
Bayesian divergence time estimation

We use a Bayesian framework



Bayesian divergence time estimation

The data

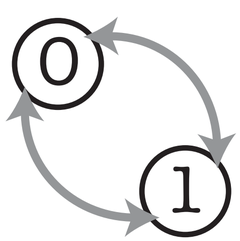
and / or

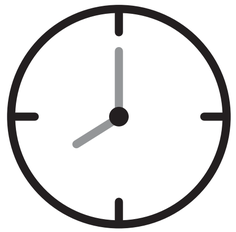
```
0101... ATTG...
1101... TTGC...
0100... ATTC...
```

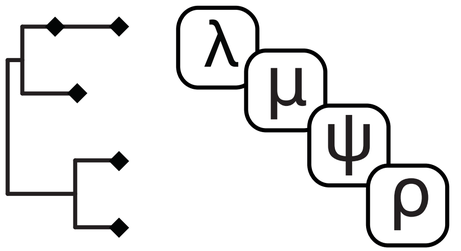
phylogenetics characters

sample ages

3 model components







substitution model

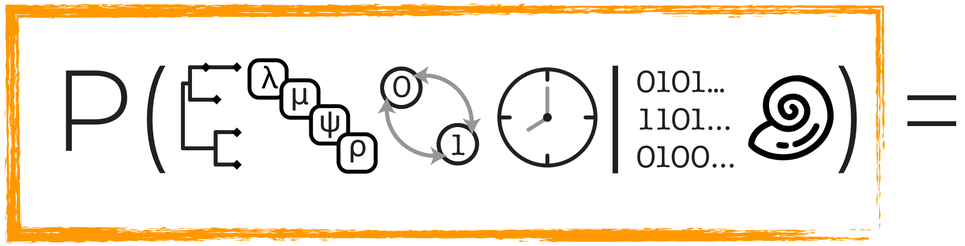
clock model

tree and tree model

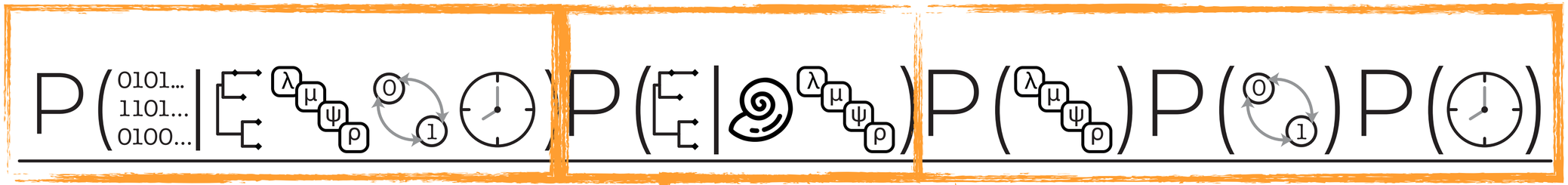
Understanding the tripartite approach to Bayesian divergence time estimation
Warnock, Wright. (2020)

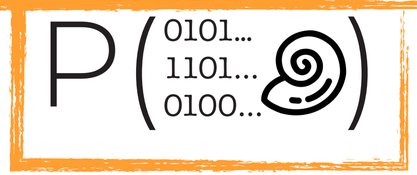
Bayesian divergence time estimation

posterior



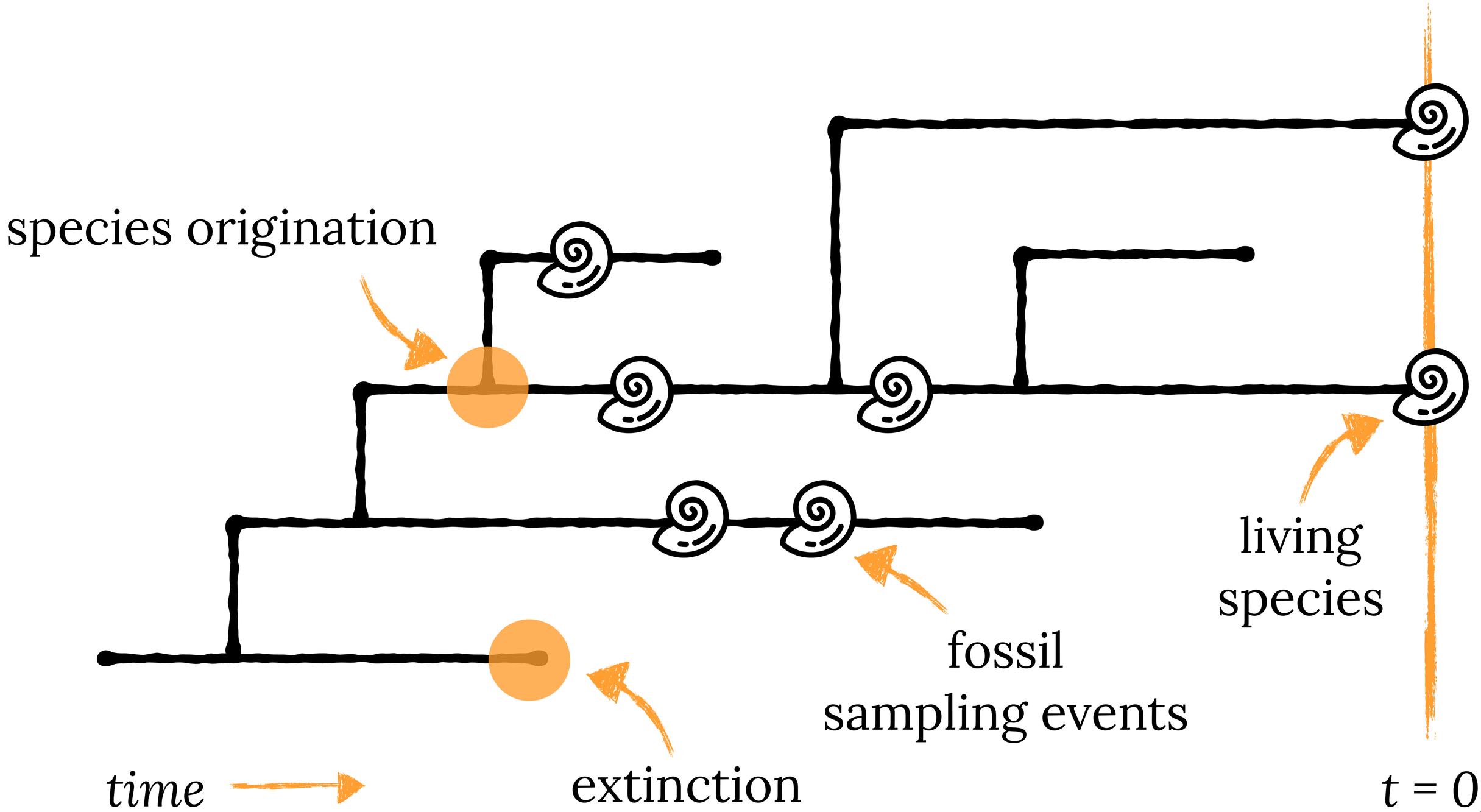
likelihood | probability of the time tree | priors

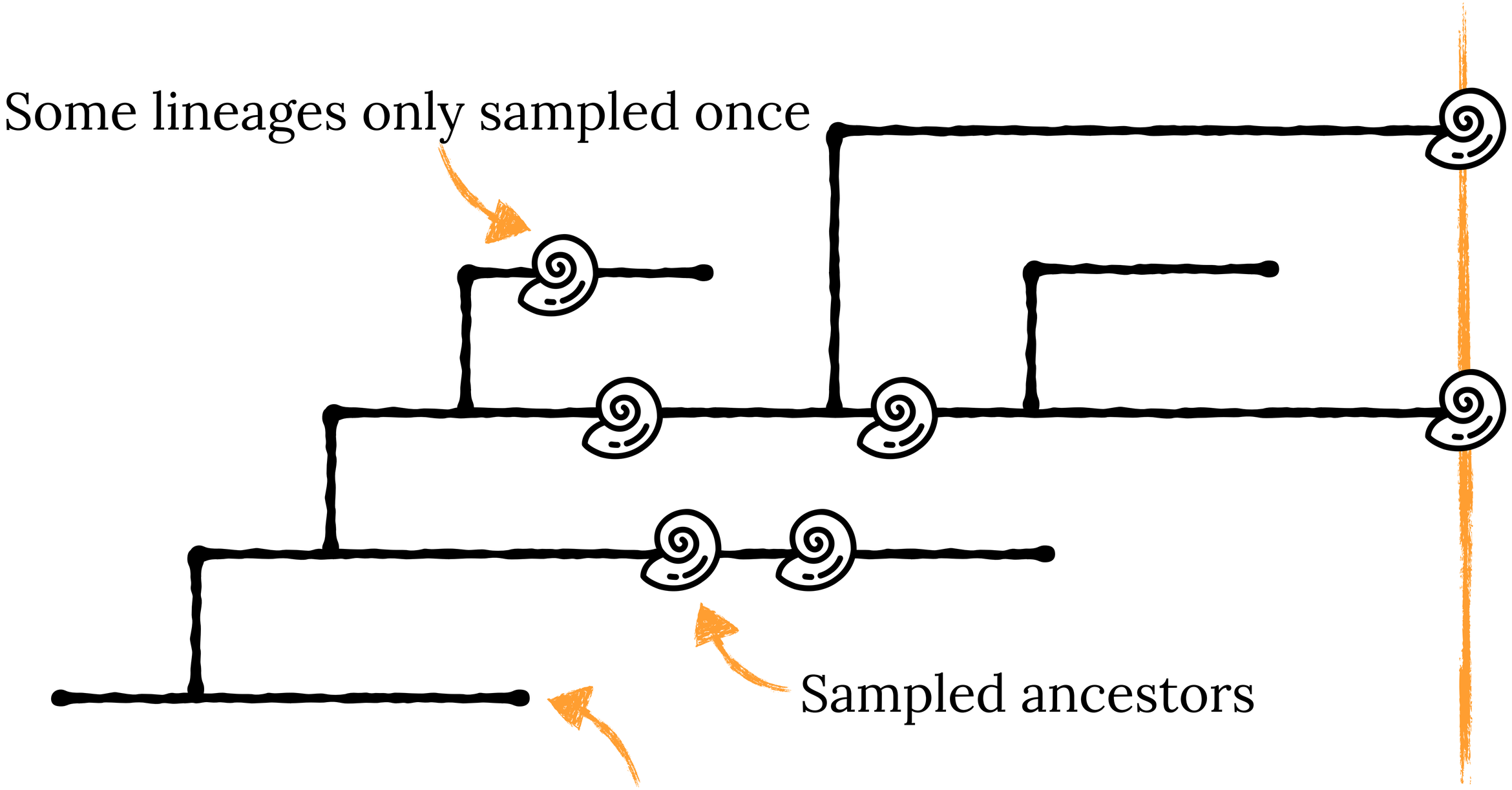




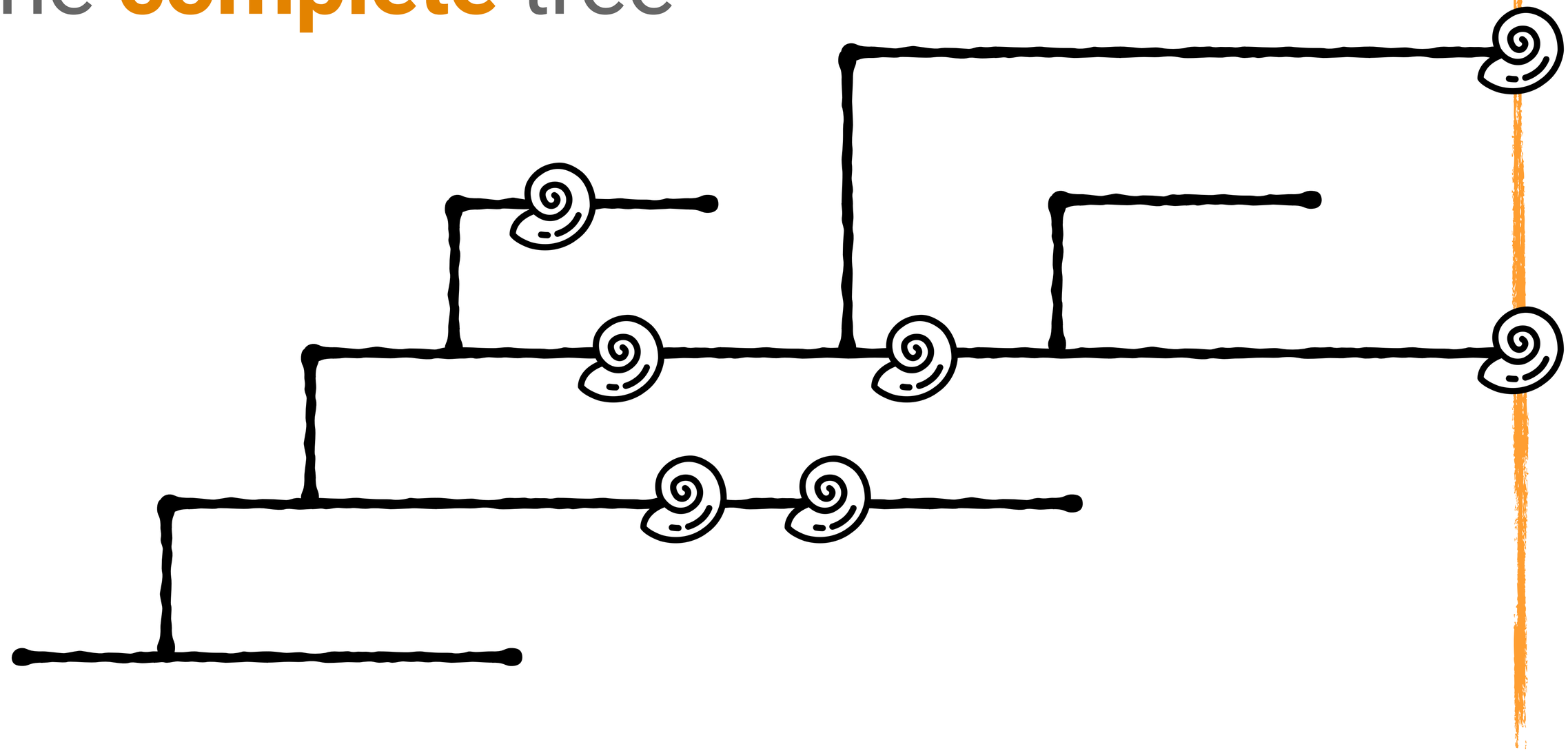
marginal pr of the data

The fossilised birth-death process


species origination
living species
fossil sampling events
extinction
time
t = 0


Some lineages only sampled once
Sampled ancestors
Some lineages go completely unsampled
$t = 0$

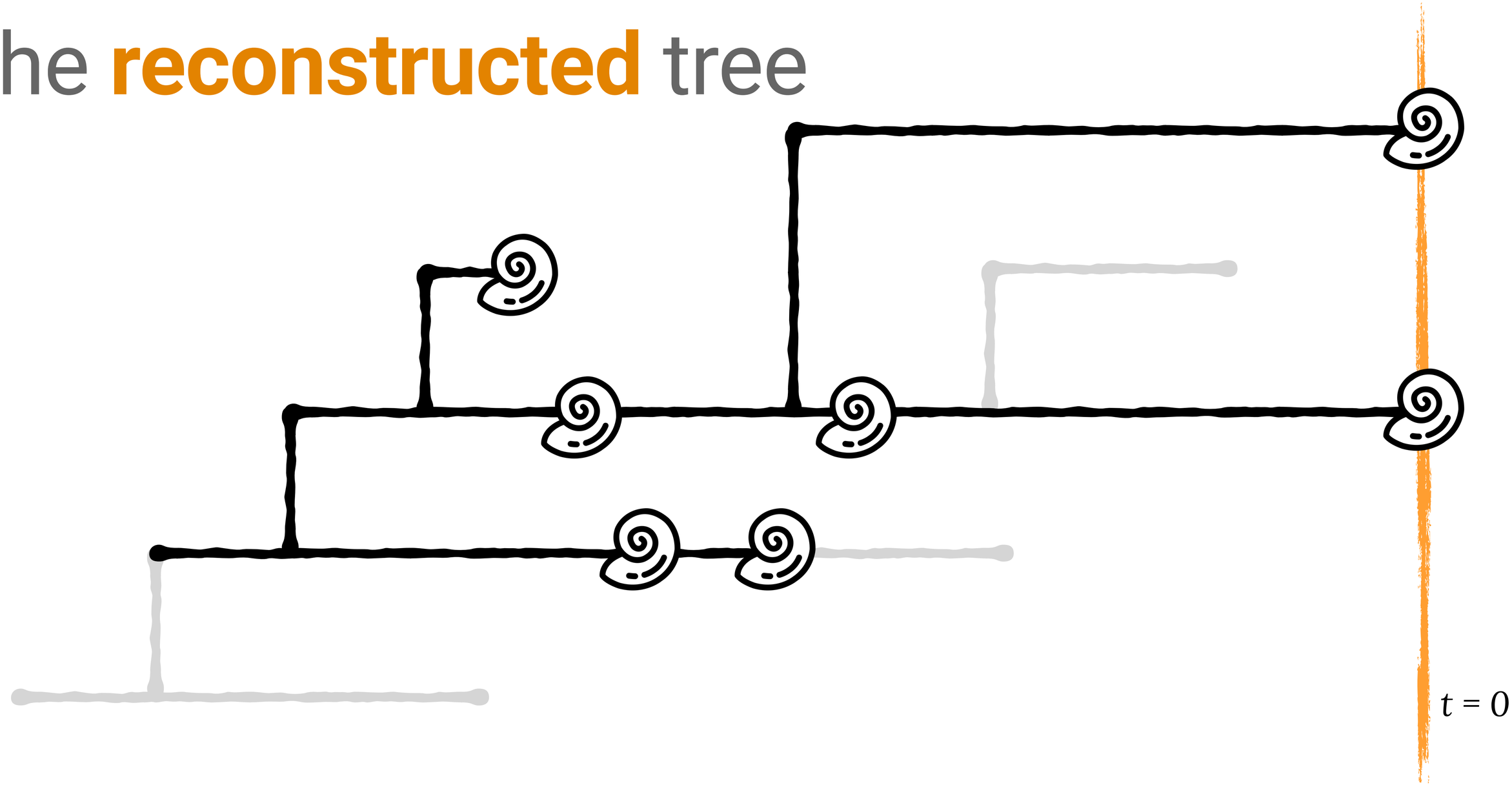
The **complete** tree



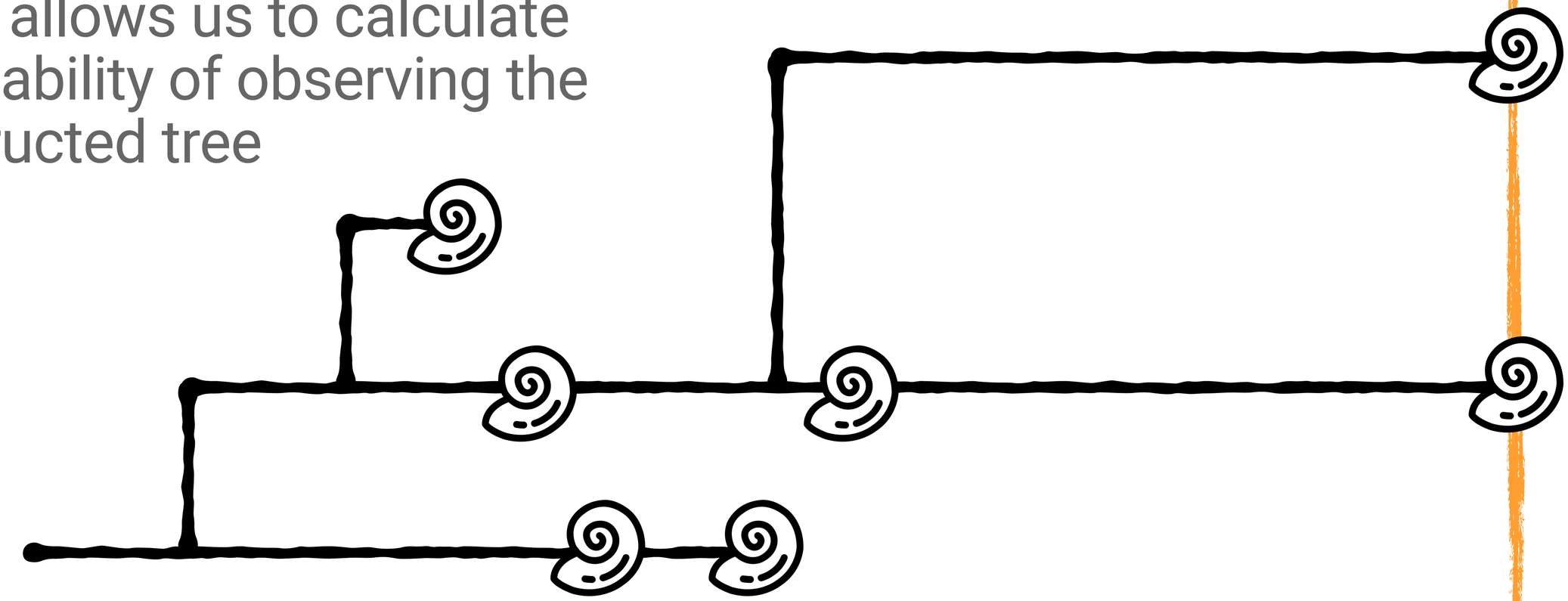
$time$ ⟶

$t = 0$

The **reconstructed** tree

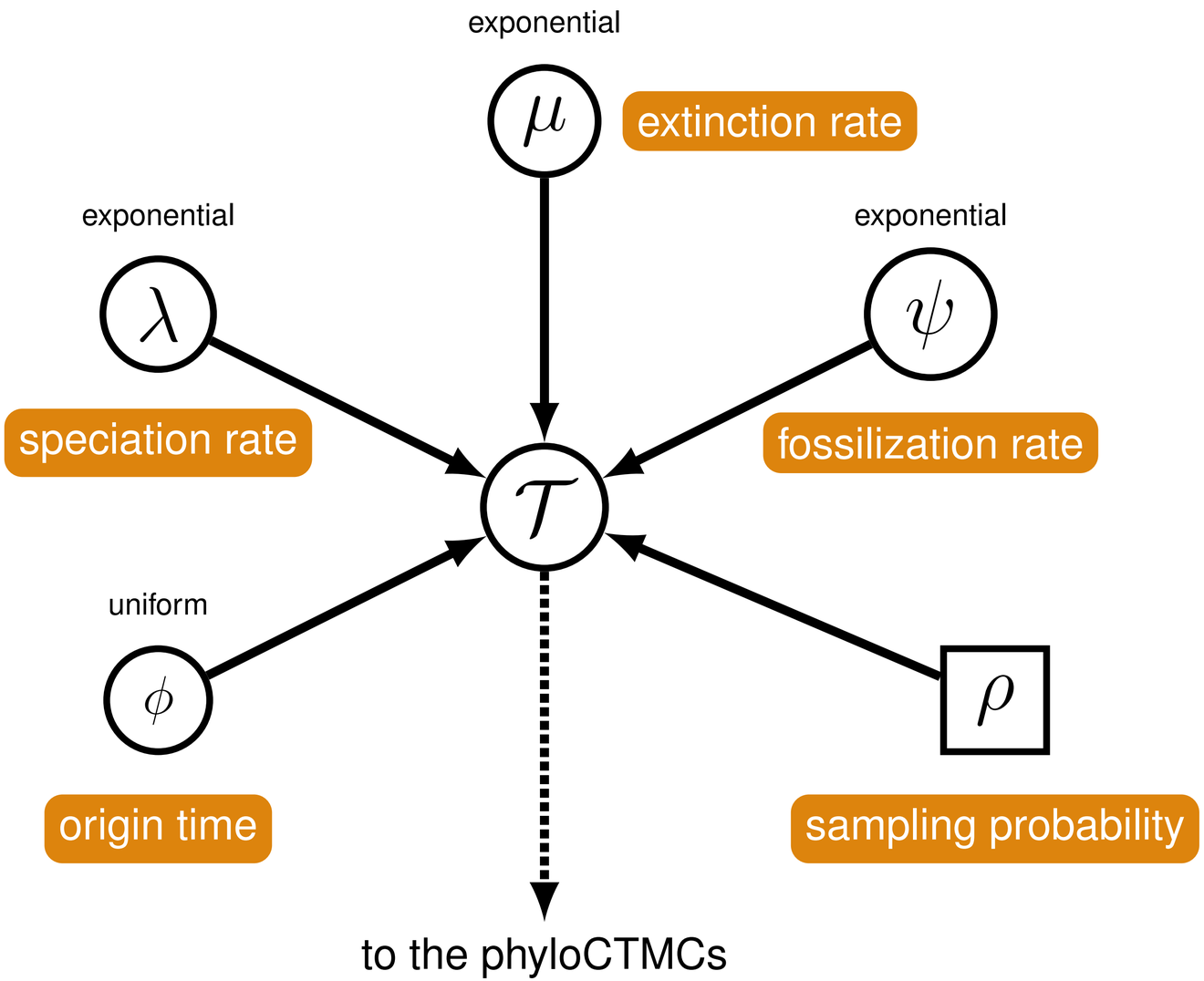


The **fossilised birth-death (FBD) process** allows us to calculate the probability of observing the reconstructed tree

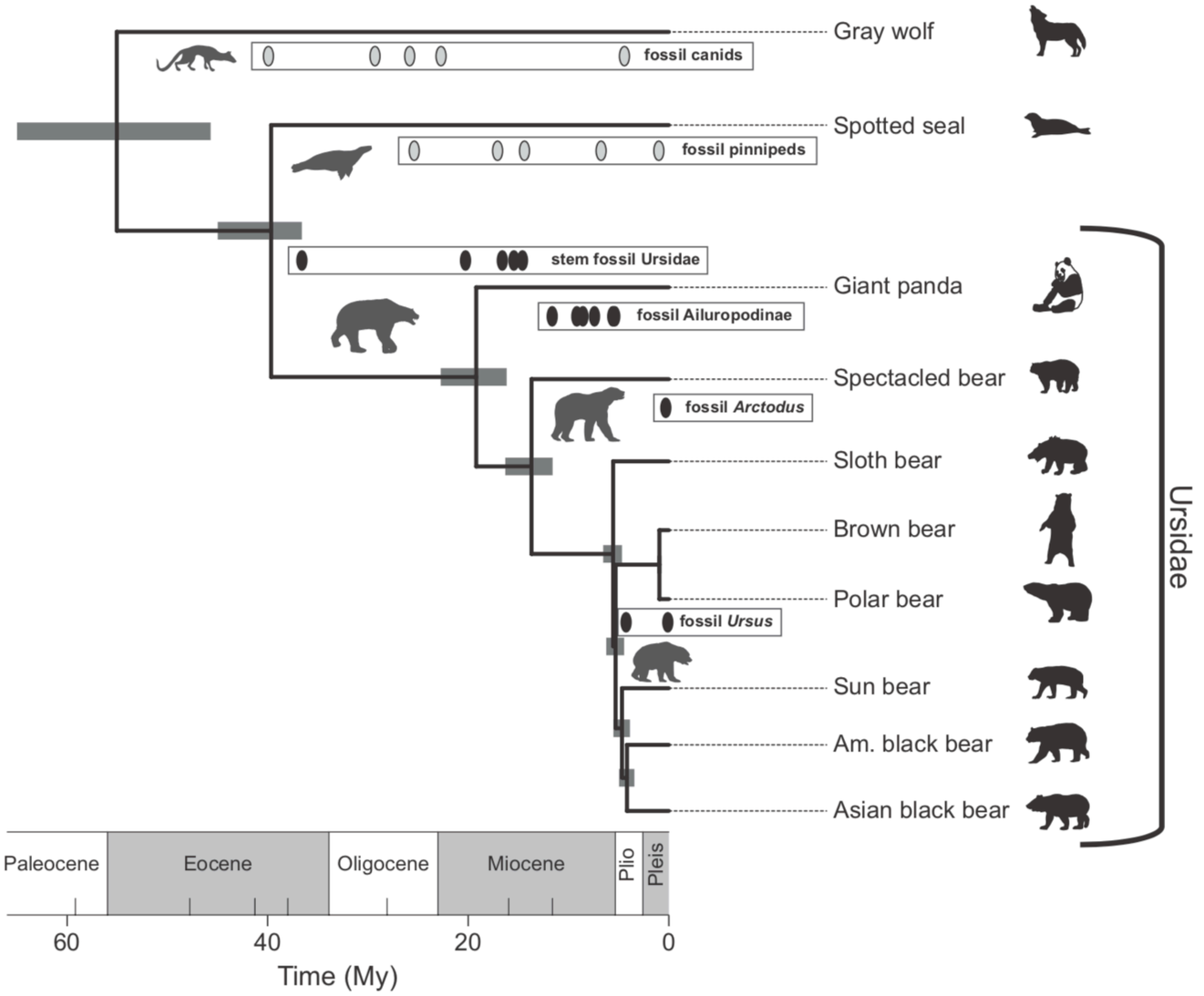


Sampling-through-time in birth-death trees. Stadler. (2010)
First implemented: Heath et al. (2014) and *Gavryushkina et al.* (2014)

Graphical model representation of the FBDP



Time calibrated tree of living and fossil bears

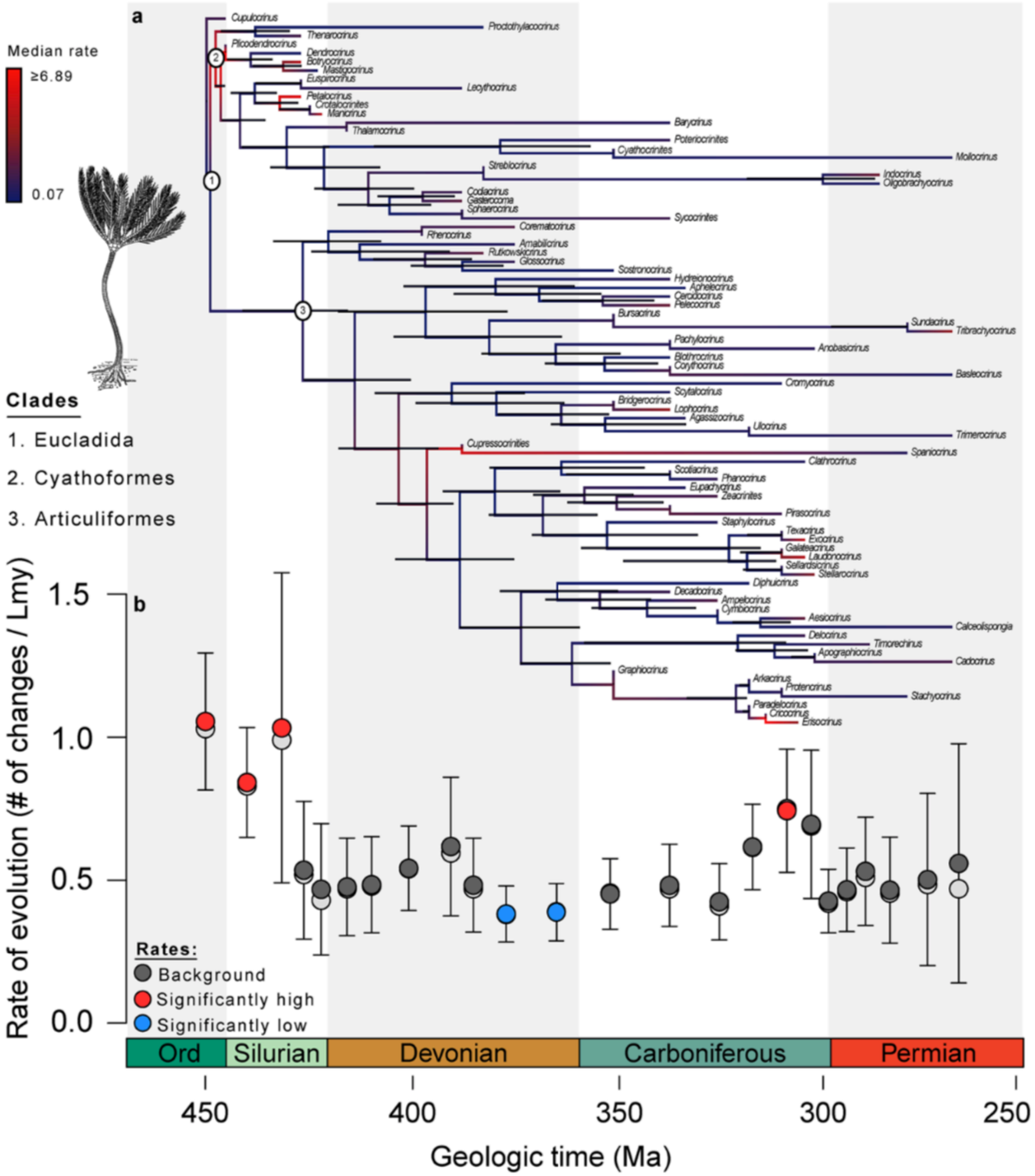


First application of the FBD model.

Fossils are incorporated via constraints, not character data. Their precise placement can not be inferred, but this uncertainty will be reflected in the posterior

Heath et al. 2014. PNAS

Analysis of fully extinct clades



Wright (2017) *Scientific Reports*

Analysis type	Phylogenetic data			No. of analyses
	Molecular	Morphology	Morphology†	
Total evidence	✓	✓	✓	53
Extant only	✓			78
Morphology		✓	✓	26
Extinct only			✓	35
No phylogenetic data				16

Fossils can be incorporated via **taxonomy** or **character data** (total-evidence)

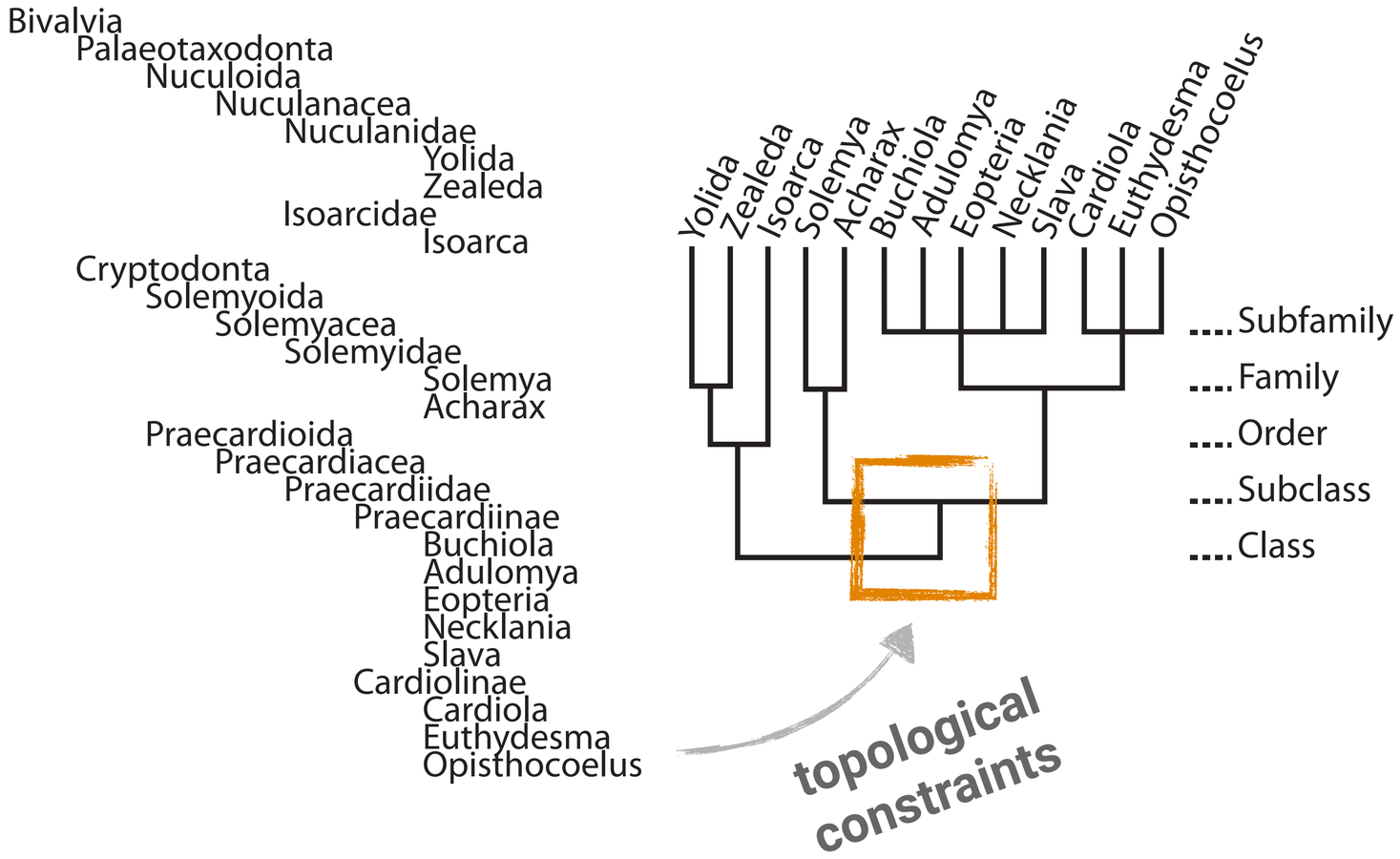
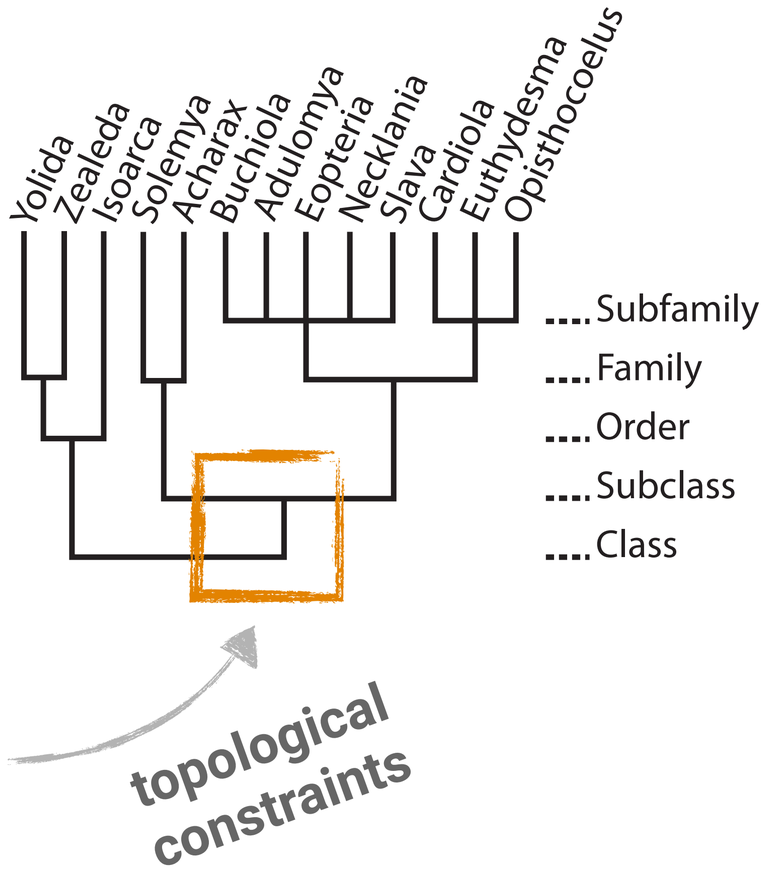


Image source Soul & Friedman (2015)

Fossils can be incorporated via **taxonomy** or **character data** (total-evidence)



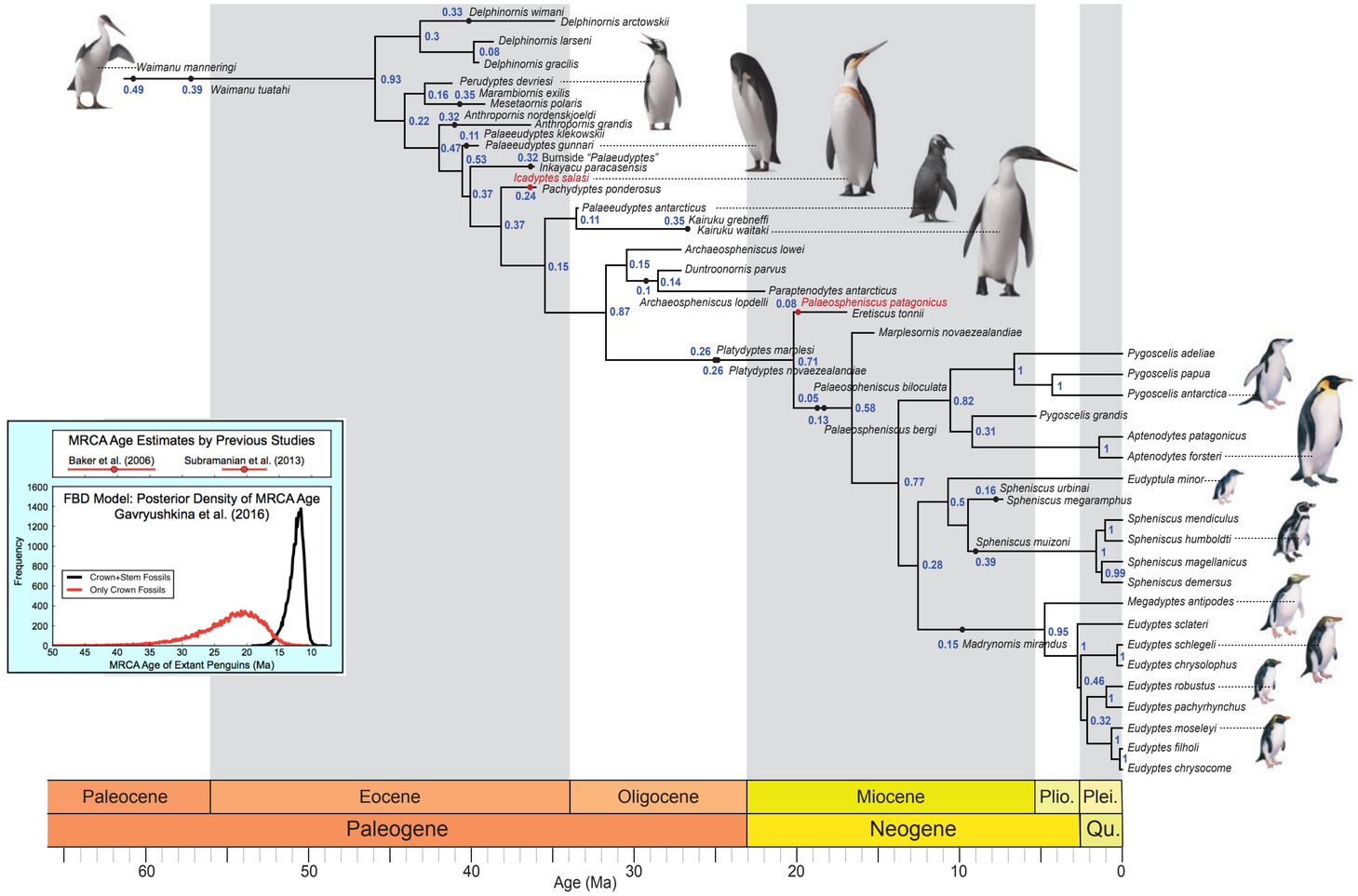
ATAT...
TCAC...
????...

OR

1001...
1101...
0100...

Image source Soul & Friedman (2015)

Time calibrated tree of living and fossil penguins

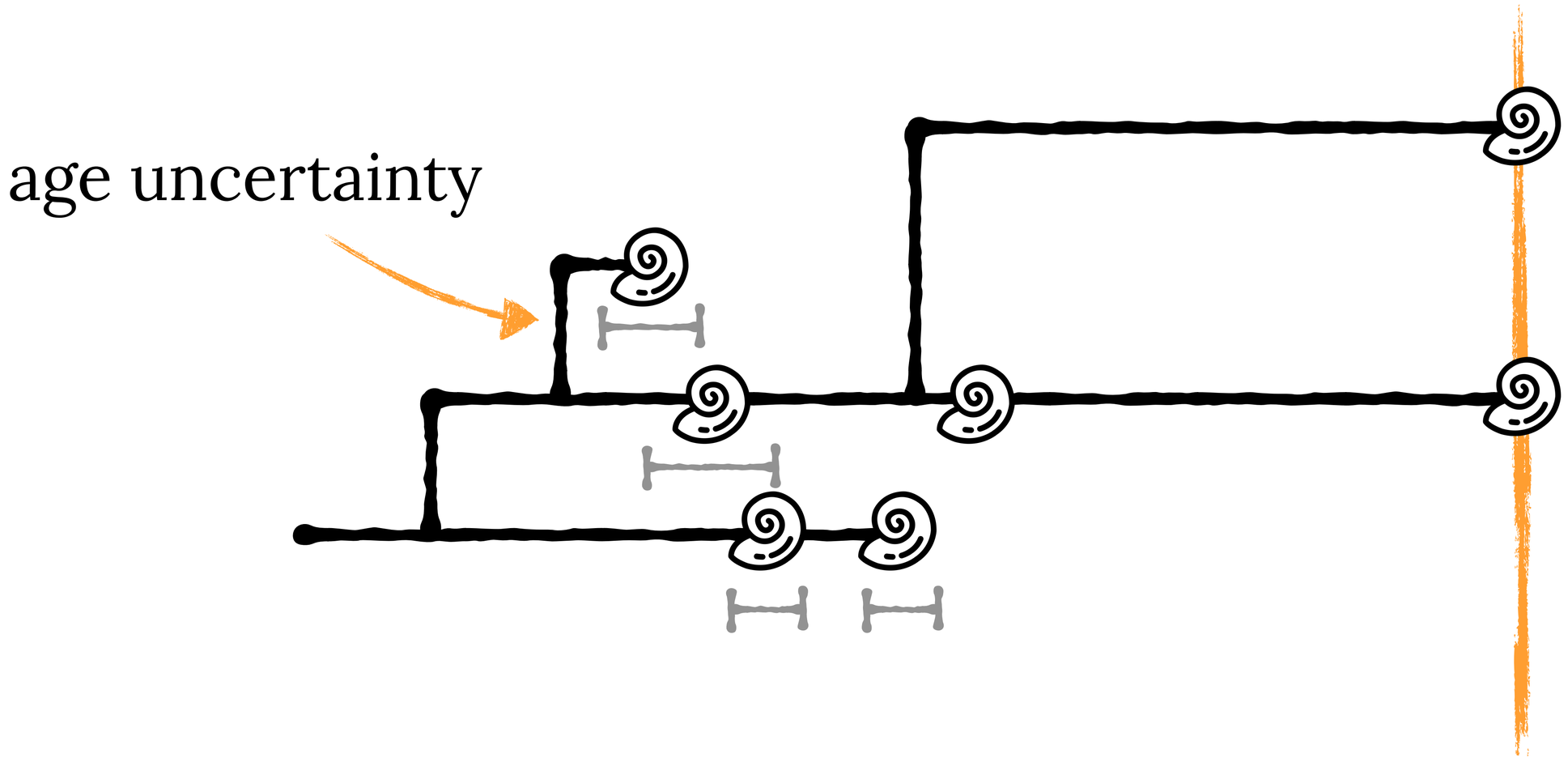


First application of total evidence dating using the FBD model

Fossils are incorporated using character data

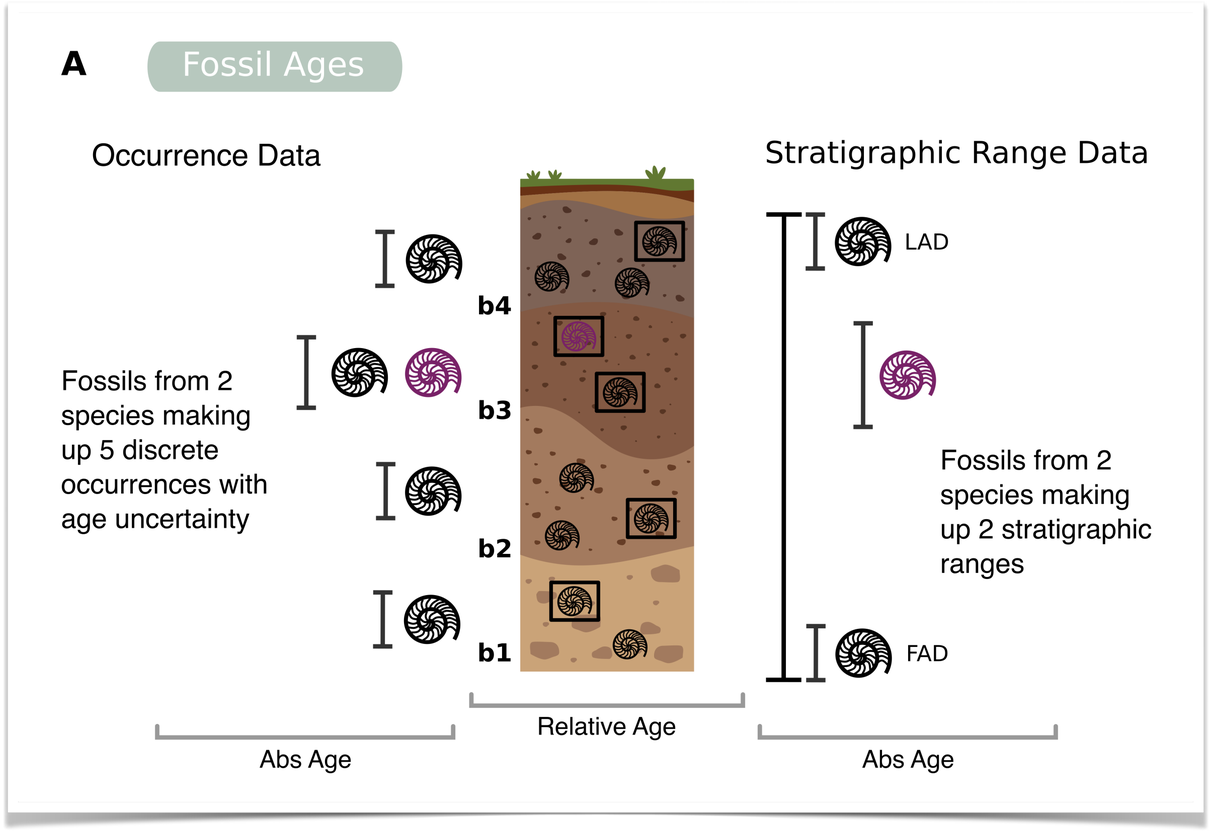
Gavryushkina et al. (2016)

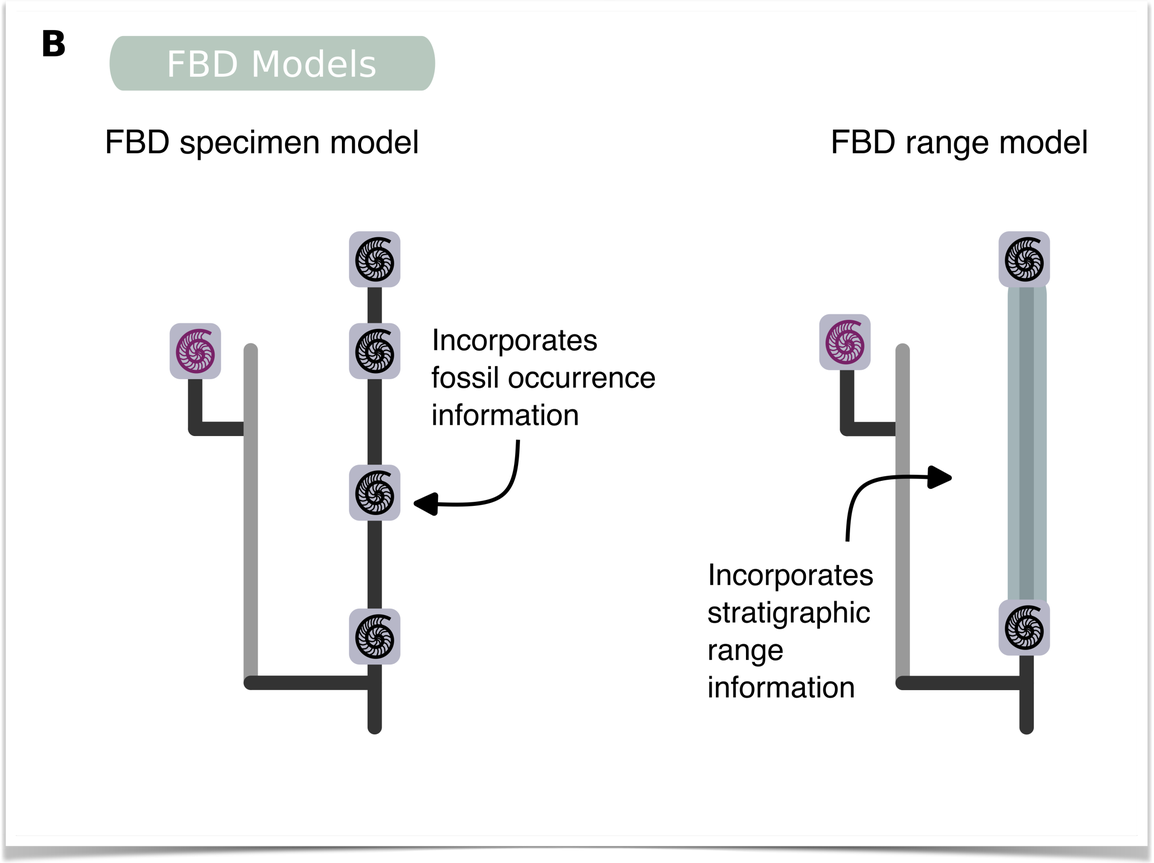
Sample age uncertainty



Barido-Sottani et al. 2018, 2020, Ignoring Fossil Age Uncertainty Leads to Inaccurate Topology in Time Calibrated Tree Inference

Barido-Sottani et al. 2023. *Putting the F in FBD analyses: tree constraints or morphological data? Palaeontology*





The fossilised birth-death model for the analysis of stratigraphic range data under different speciation modes. Stadler et al. (2018)

Joint phylogenetic estimation of geographic movements and biome shifts

Landis et al. (2023) Systematic Biology

Global diversity of *Viburnum*

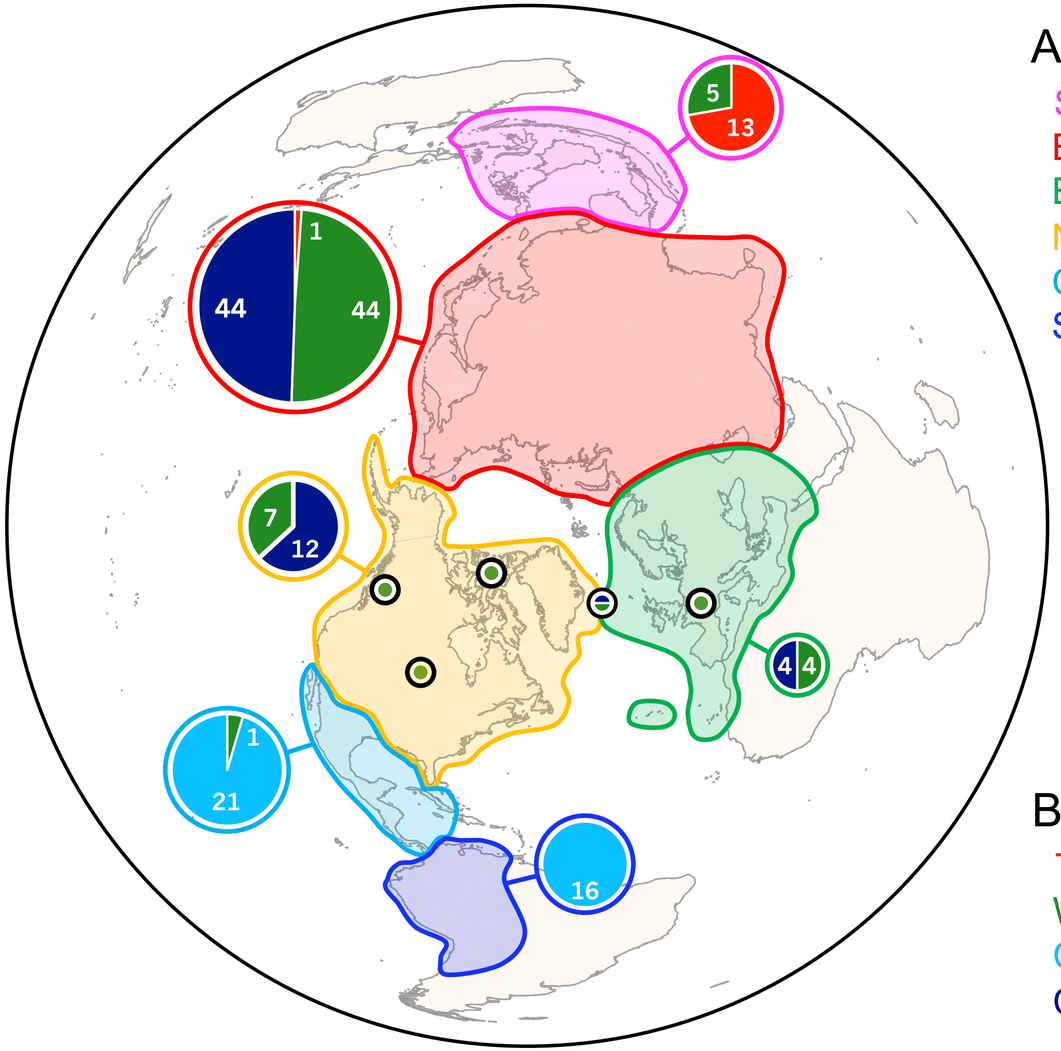
Data

163 extant species (127 with DNA)

5 fossils (with taxonomic constraints)

6 geographic areas

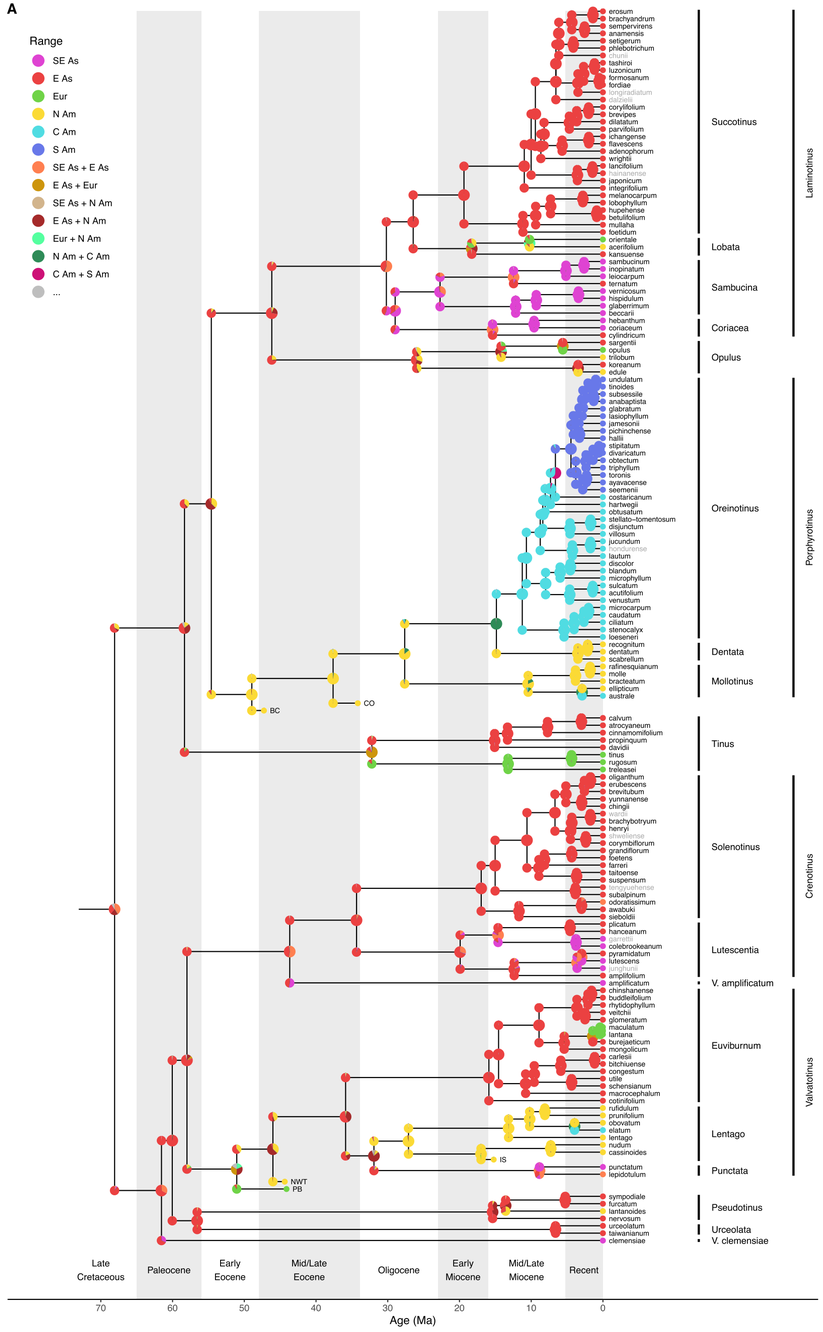
4 biomes

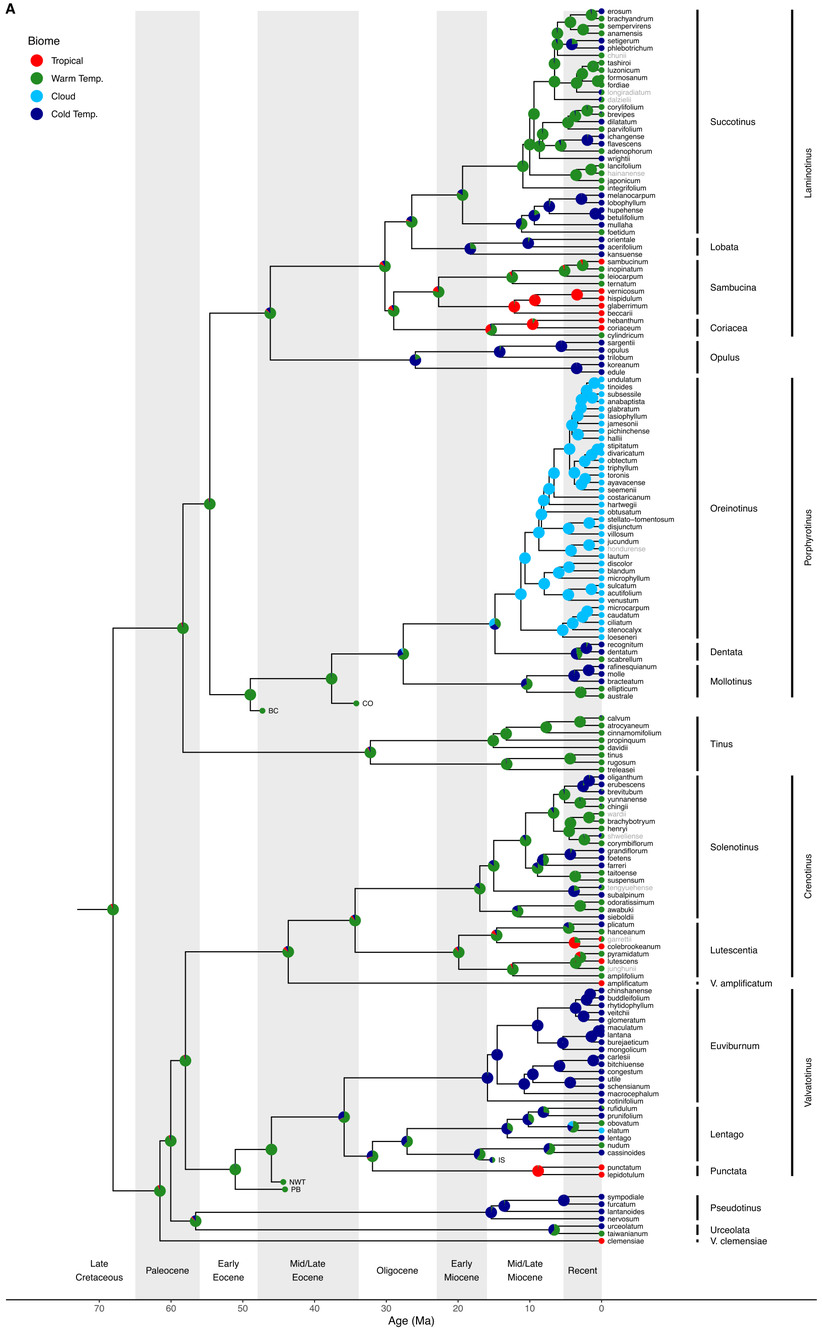


- Can we integrate **geographic range** and **biome data** into analysis using the FBD model?
- What can we learn about the **diversification history** of the *Viburnum*?

Analysis

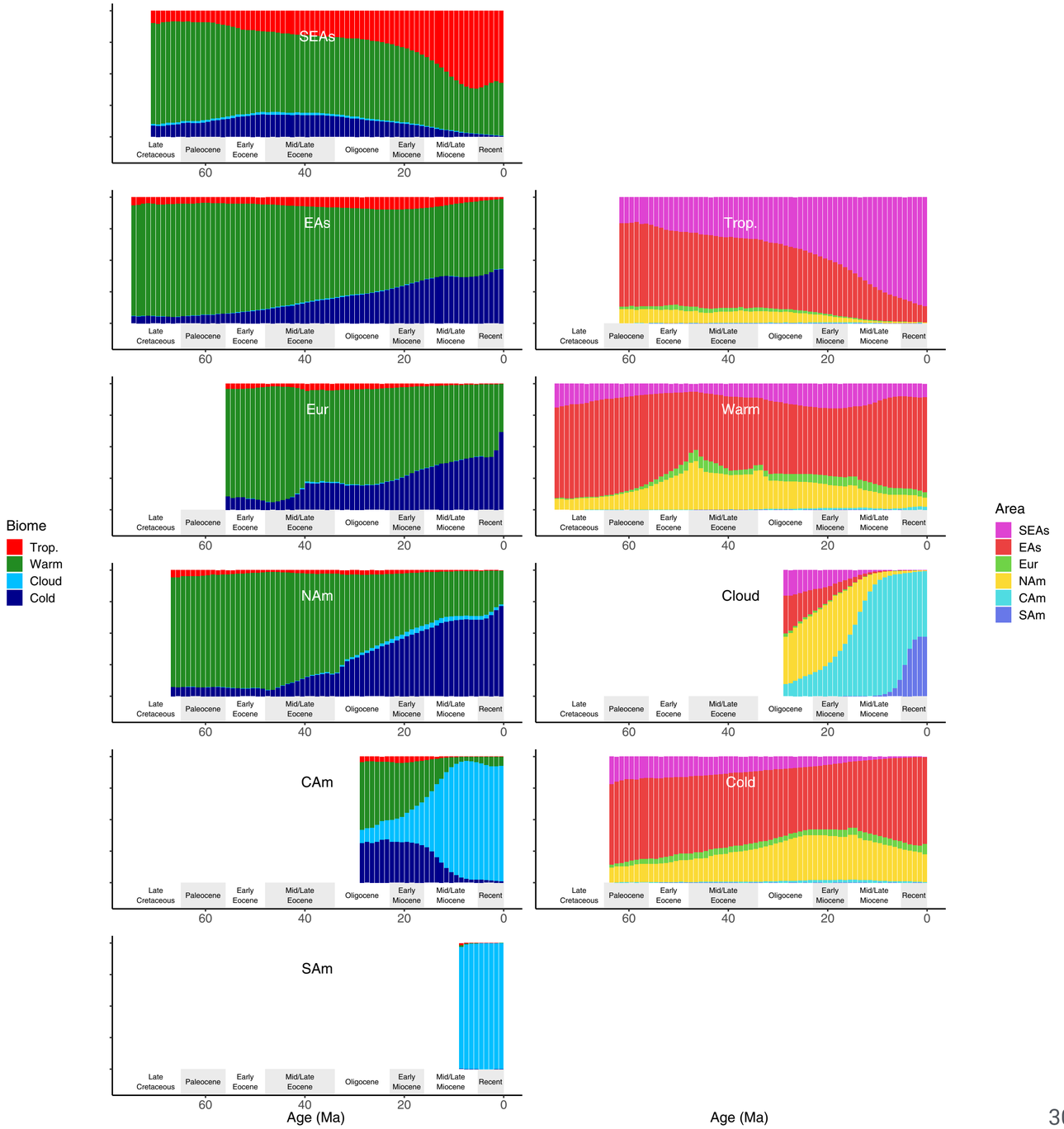
1. Estimate the extant topology using maximum likelihood
2. Joint inference divergence times, biogeographic and biome history (normally we *first* infer a dated tree, and *then* separately infer biogeographic history)
3. Ancestral state reconstruction
4. + various sensitivity analyses


A
Range
SE As
E As
Eur
N Am
C Am
S Am
SE As + E As
E As + Eur
SE As + N Am
E As + N Am
Eur + N Am
N Am + C Am
C Am + S Am
...
Laminotinus
Succotinus
Lobata
Sambucina
Coriacea
Opulus
Porphyrotinus
Oreinotinus
Dentata
Mollotinus
Crenotinus
Tinus
Solenotinus
Lutescentia
V. amplificatum
Valvatotinus
Euviburnum
Lentago
Punctata
Pseudotinus
Urceolata
V. clemensiae
BC
CO
IS
NWT
PB
Late Cretaceous
Paleocene
Early Eocene
Mid/Late Eocene
Oligocene
Early Miocene
Mid/Late Miocene
Recent
70
60
50
40
30
20
10
0
Age (Ma)


A
Biome
Tropical
Warm Temp.
Cloud
Cold Temp.
Laminotinus
Succotinus
Lobata
Sambucina
Coriacea
Opulus
Porphyrotinus
Oreinotinus
Dentata
Mollotinus
Crenotinus
Tinus
Solenotinus
Lutescentia
V. amplificatum
Valvatotinus
Euviburnum
Lentago
Punctata
Pseudotinus
Urceolata
V. clemensiae
BC
CO
IS
NWT
PB
Late Cretaceous
Paleocene
Early Eocene
Mid/Late Eocene
Oligocene
Early Miocene
Mid/Late Miocene
Recent
70
60
50
40
30
20
10
0
Age (Ma)

Results summary

- Joint inference using the FBD and biogeographic models allows us to estimate a rich diversification history
- Major lineages of *Viburnum* likely originated in warm / temperate regions and later adapted to the cold
- Fossils can change the results



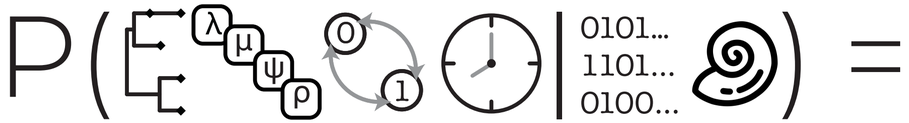
*“It is, it must be admitted, a **humbling** task to infer ancient events, and the results in many cases are tenuous at best. Given the obvious limitations of working with extant species and few, if any, fossils, **it is necessary to integrate all of the available sources of evidence** if we hope to produce assuring answers.”*

Landis et al. (2023) *Systematic Biology*

Phylodynamics

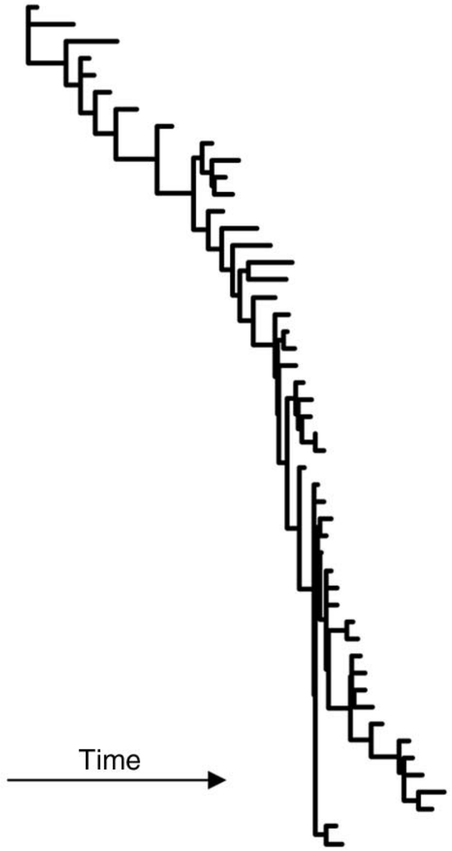
Diversification rate estimation

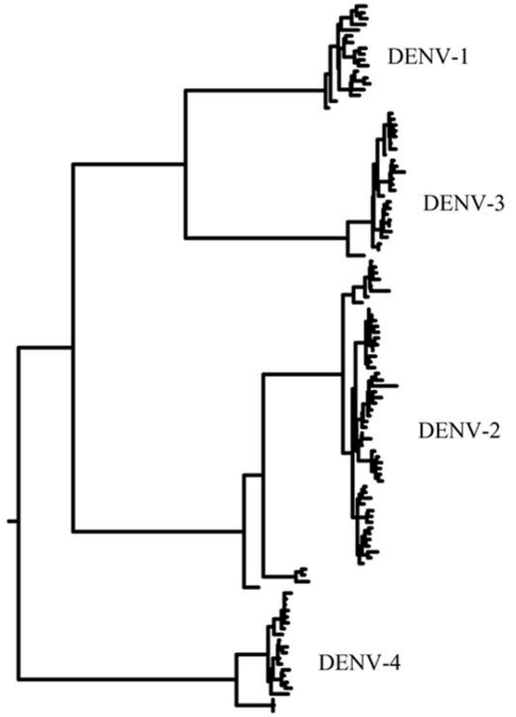
Bayesian divergence time estimation

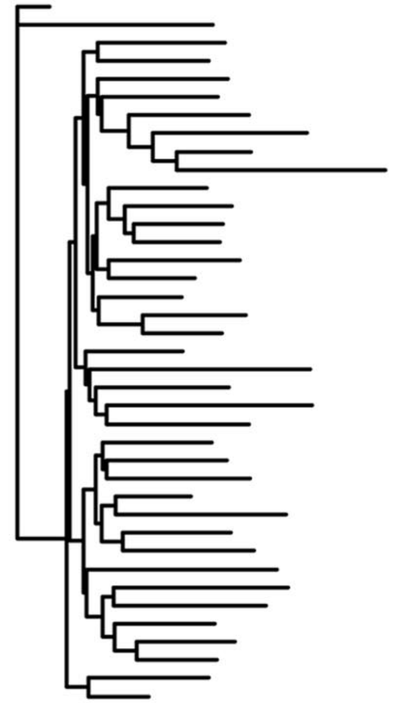


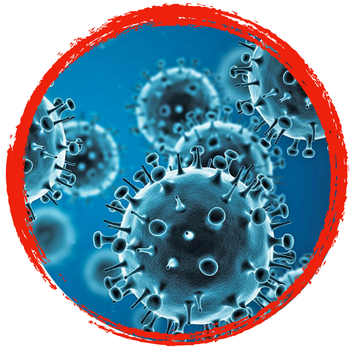
probability of the time tree

Tree shape is informative about underlying dynamics





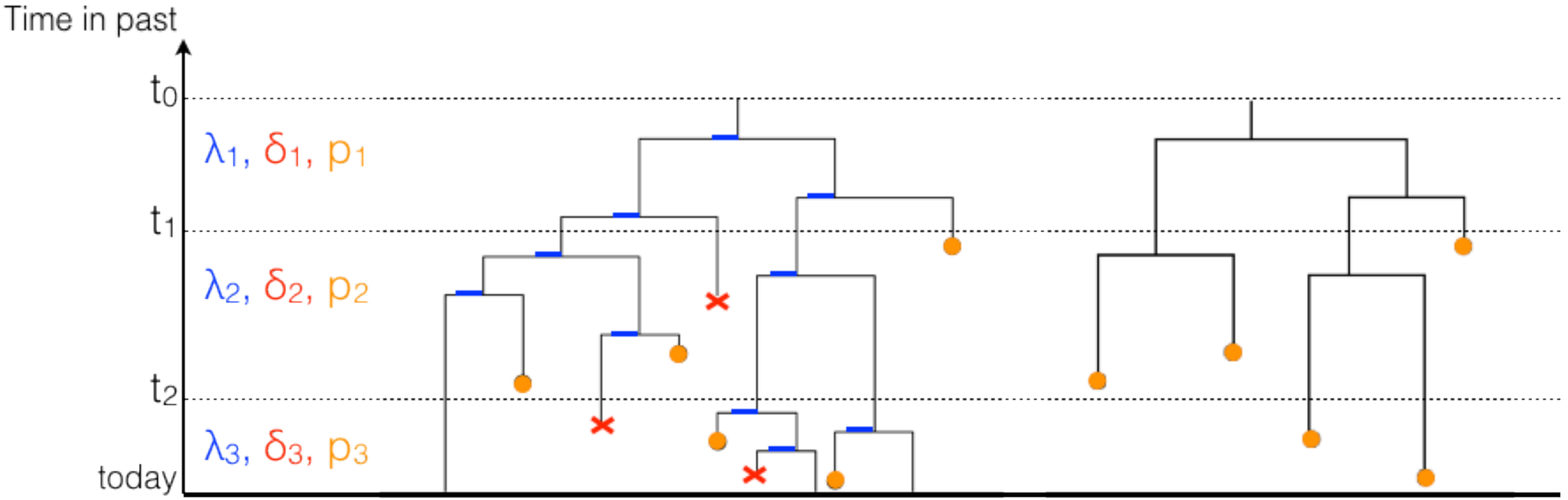




This paper coined the term phylodynamics
Grenfell et al. 2004. Science

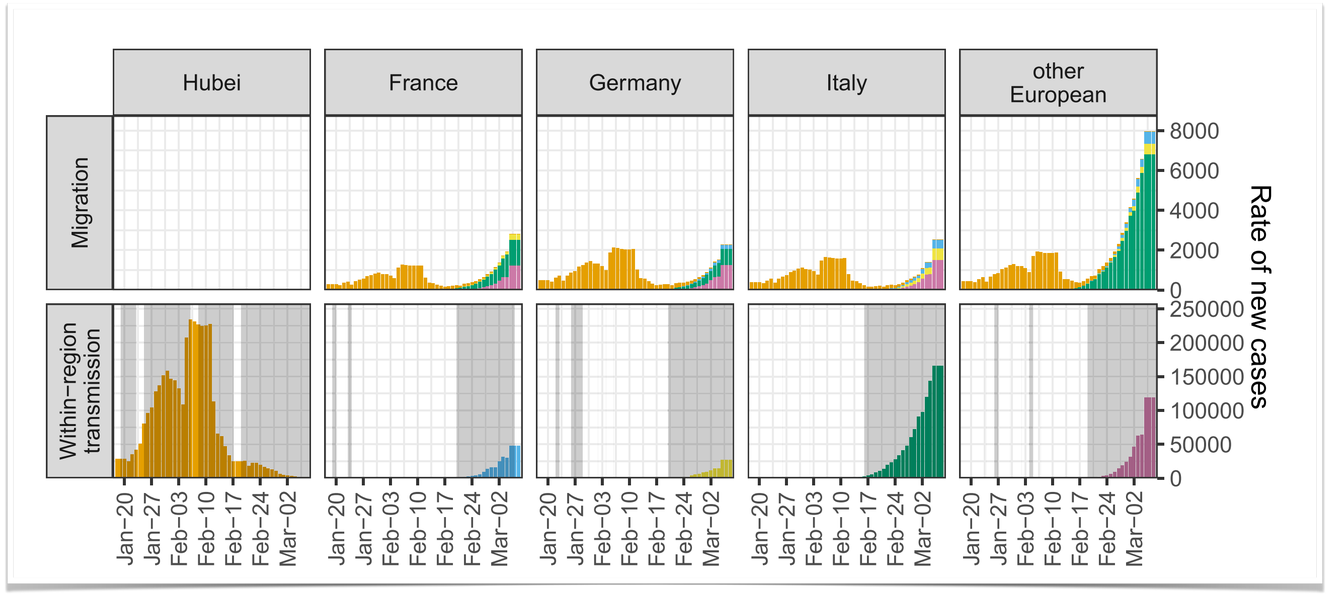
The skyline birth-death process

First used for tracking the spread of infectious diseases

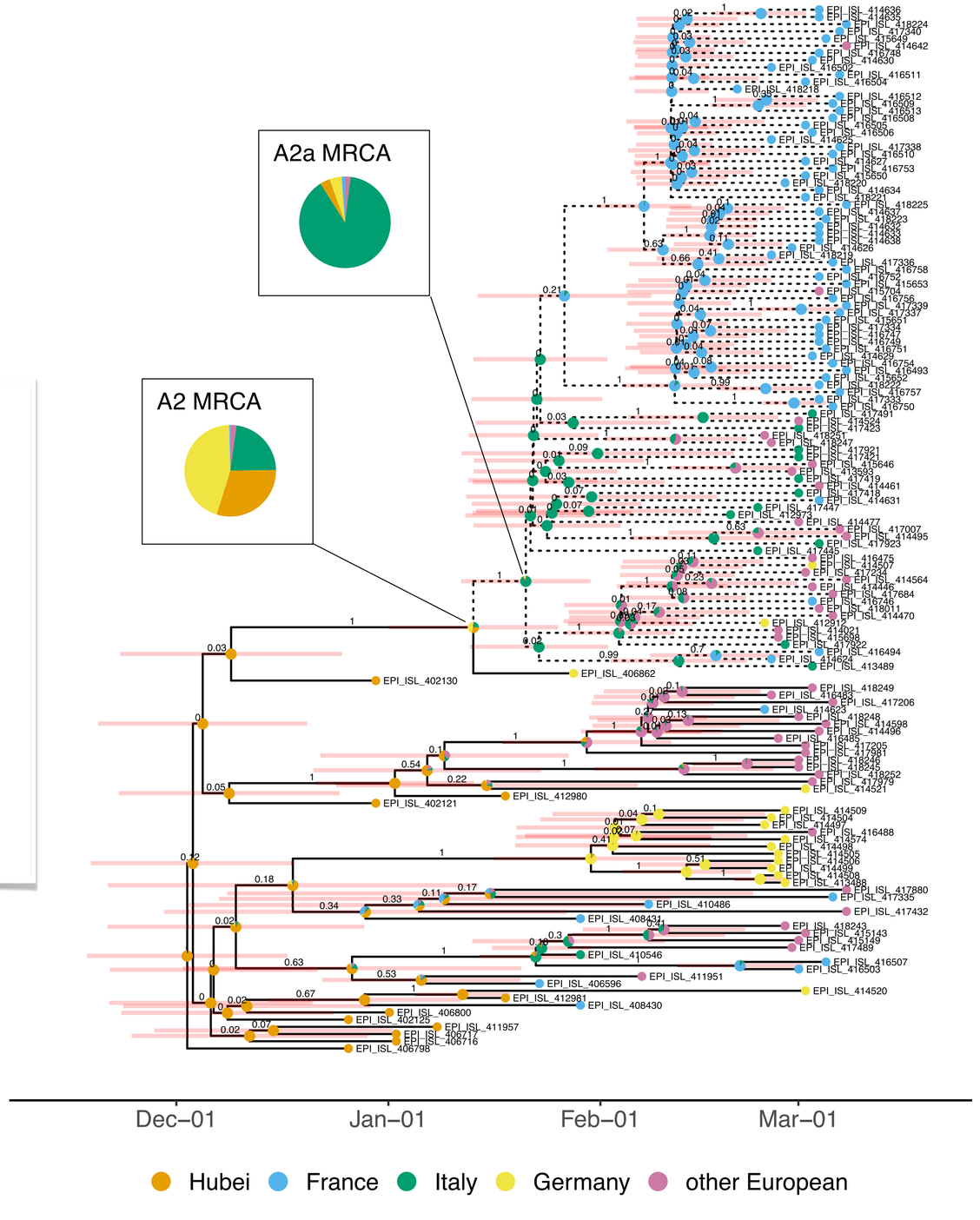


Stadler et al. 2012. PNAS
Gavryushkina et al. 2014. PLoS Comp Bio

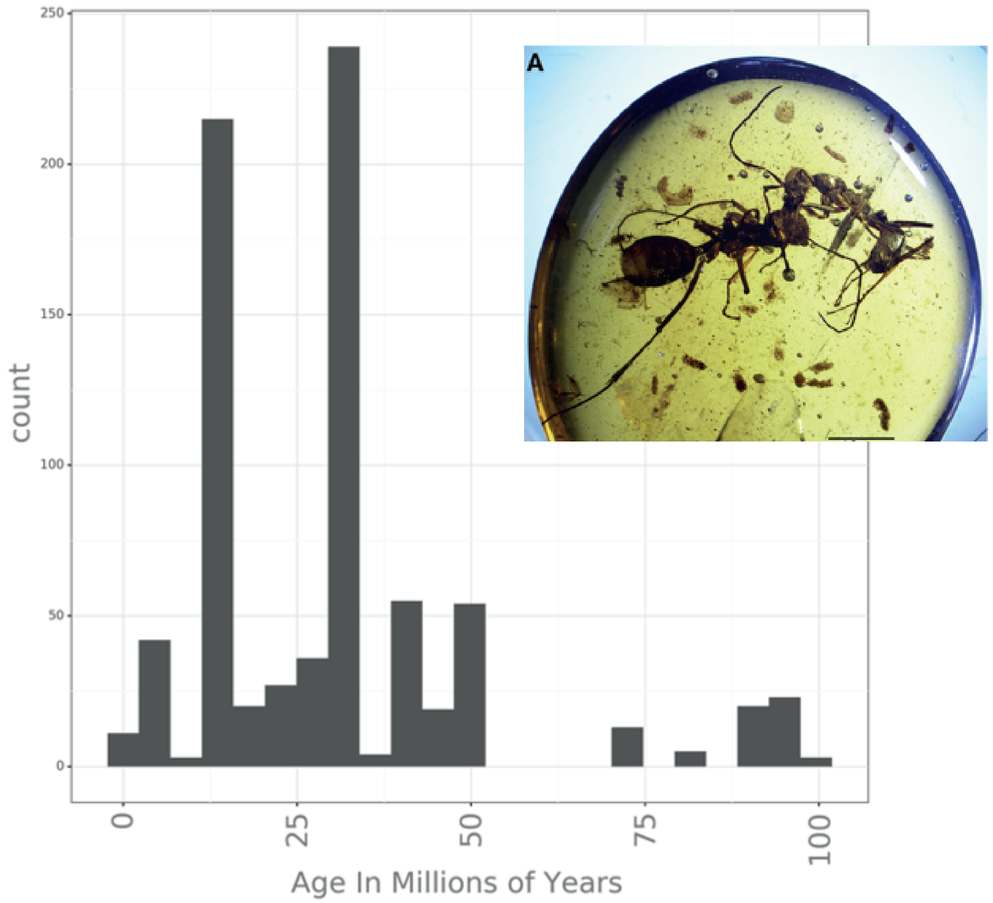
Models that include migration



The origin and early spread of SARS-CoV-2 in Europe
Nadeau et al. 2021. PNAS



Estimating parameters in macroevolution

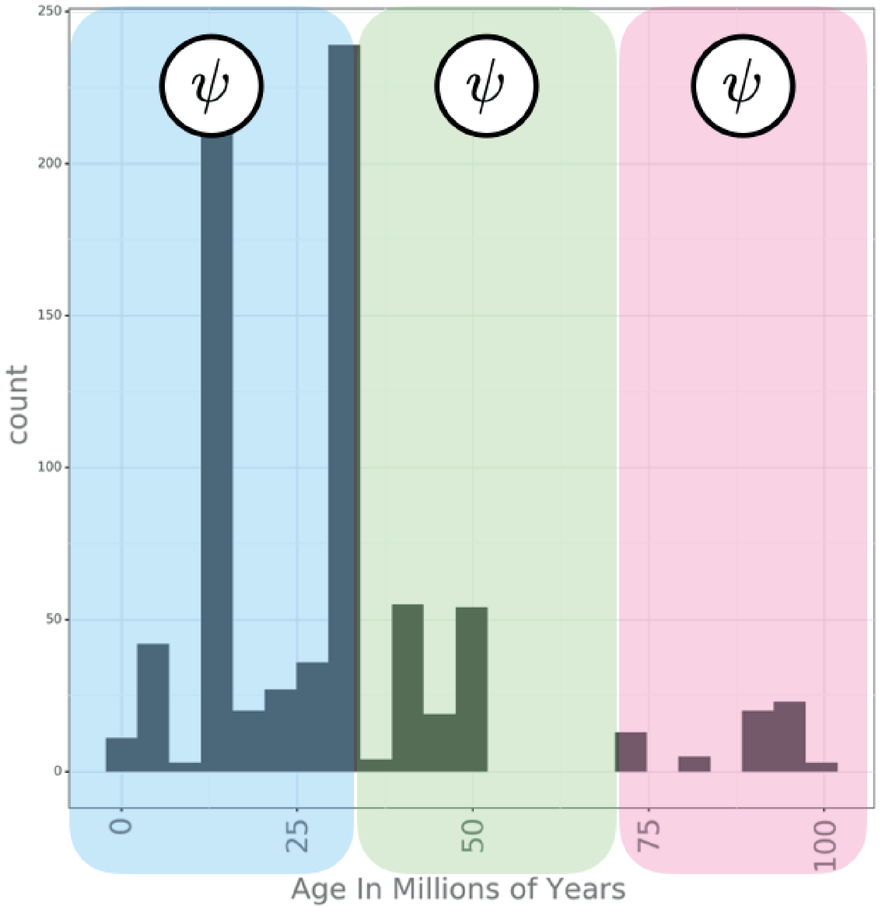


Ants have very variable fossil sampling over time

→We can take this into account using the FBD skyline model

Images adapted from April Wright

Estimating parameters in macroevolution



The oldest fossils are around 100 Ma

Different assumptions about the fossil sampling process produce different results

Skyline models recover an older age estimate for the origin of ants (= 140 Ma)

Case study: were dinosaurs in decline pre-KPg?

Dinosaurs in decline tens of millions of years before their final extinction

Manabu Sakamoto[a,1], Michael J. Benton[b], and Chris Venditti[a,1]

[a]School of Biological Sciences, University of Reading, Reading RG6 6BX, United Kingdom; and [b]School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, United Kingdom

Edited by Zhonghe Zhou, Chinese Academy of Sciences, Beijing, China, and approved March 1, 2016 (received for review October 30, 2015)

Whether dinosaurs were in a long-term decline or whether they were reigning strong right up to their final disappearance at the Cretaceous–Paleogene (K-Pg) mass extinction event 66 Mya has been debated for decades with no clear resolution. The dispute has continued unresolved because of a lack of statistical rigor and appropriate evolutionary framework. Here, for the first time to our knowledge, we apply a Bayesian phylogenetic approach to model the evolutionary dynamics of speciation and extinction through time in Mesozoic dinosaurs, properly taking account of previously ignored statistical violations. We find overwhelming support for a long-term decline across all dinosaurs and within all three dinosaurian subclades (Ornithischia, Sauropodomorpha, and Theropoda), where speciation rate slowed down through time and was ultimately exceeded by extinction rate tens of millions of years before the K-Pg boundary. The only exceptions to this general pattern are the morphologically specialized herbivores, the Hadrosauriformes and Ceratopsidae, which show rapid species proliferations throughout the Late Cretaceous instead. Our results highlight that, despite some heterogeneity in speciation dynamics, dinosaurs showed a marked reduction in their ability to replace extinct species with new ones, making them vulnerable to extinction and unable to respond quickly to and recover from the final catastrophic event.

dinosaurs | evolution | speciation | phylogeny | Bayesian methods

Nonavian dinosaurs met their demise suddenly, coincident with the Chicxulub impact in Mexico around 66 Mya; however, whether there was any long-term trend toward declining diversity leading to the Cretaceous–Paleogene (K-Pg) boundary has been controversial and debated for decades (1–14). This long-standing dispute has been prolonged partly because of differences in fossil datasets from different parts of the world and difficulties in rock dating but most importantly, methodological weaknesses—previous attempts have been nonphylogenetic, and analyses were conducted on simple time-binned tabulated data, resulting in a lack of statistical rigor (phylogenetic and temporal nonindependence have not been considered), and did not truly investigate evolutionary dynamics, such as speciation and extinction rates. In fact, patterns of speciation and extinction in dinosaurs have gone largely unstudied (8). Here, we study speciation dynamics (relationship between speciation and extinction rates) using an exclusively phylogenetic approach in a Bayesian framework.

If speciation and extinction rate were constant (but speciation was higher), we would expect to see a linear increase through time in the logarithm of the number of speciation events along each path of a phylogenetic tree (linear) (*Materials and Methods* and Fig. 1, model A). If speciation rate decreased through time but remained above extinction rate, then we would expect a curvilinear relationship (Fig. 1, models B and C). Such a relationship would reach an asymptote (speciation equals extinction) (Fig. 1, model B) and eventually, turn down as extinction rate surpasses speciation during the evolutionary history of the clade (Fig. 1, model C). The latter would correspond to a long-term pre–K-Pg demise in the case of dinosaurs. The distinction between such evolutionary dynamics can only be made using phylogenies with taxa sampled through time.

Results and Discussion

Using a phylogenetic generalized linear mixed model (GLMM) in a Bayesian framework (15) and three recent large comprehensive dinosaur phylogenies comprising 420 (8) and 614 taxa [two trees (16)], respectively, we found that the data are significantly better explained by a model, in which extinction rate exceeds speciation rate from ~24 My before the K-Pg boundary, than the simpler alternative model [difference in deviance information criterion (ΔDIC) between linear and quadratic models >11] (Fig. 2*A* and Table S1). Our findings are qualitatively identical across all three trees, and we report on results from one of the 614-taxon trees (16).

Because nonthomogeneity in evolutionary rates is widespread and common in nature (17–19) and dinosaurs are diverse—from the bipedal, carnivorous theropods to the quadrupedal, megaherbivorous sauropods—we might expect to find different speciation dynamics in the different dinosaurian subclades. When model parameters were estimated separately for each of the three main subclades (Ornithischia, Sauropodomorpha, and Theropoda), the same general pattern as in the total Dinosauria model was recovered but with extinction rates exceeding speciation rates earlier at 48–53 My before the K-Pg boundary (ΔDIC > 12) (Fig. 2*B* and Table S1). Ornithischia here refers to nonhadrosauriform, nonceratopsid ornithischians, because the two Cretaceous subclades, Hadrosauriformes and Ceratopsidae, show speciation patterns distinct from other ornithischians; Lloyd et al. (8) also identified significant diversification shifts at the base of comparable clades [i.e., Euhadrosauria (here Hadrosauriformes) and Ceratopsidae]. In line with this finding, these two subclades show no signs of speciation slowdowns or downturns (*SI Text*) and Ceratopsidae]. In line with this finding, these two

Significance

Whether dinosaurs were in decline before their final extinction 66 Mya has been debated for decades with no clear resolution. This dispute has not been resolved because of inappropriate data and methods. Here, for the first time to our knowledge, we apply a statistical approach that models changes in speciation and extinction through time. We find overwhelming support for a long-term decline across all dinosaurs and within all three major dinosaur groups. Our results highlight that dinosaurs showed a marked reduction in their ability to replace extinct species with new ones, making them vulnerable to extinction and unable to respond quickly to and recover from the final catastrophic event 66 Mya.

Author contributions: M.S., M.J.B., and C.V. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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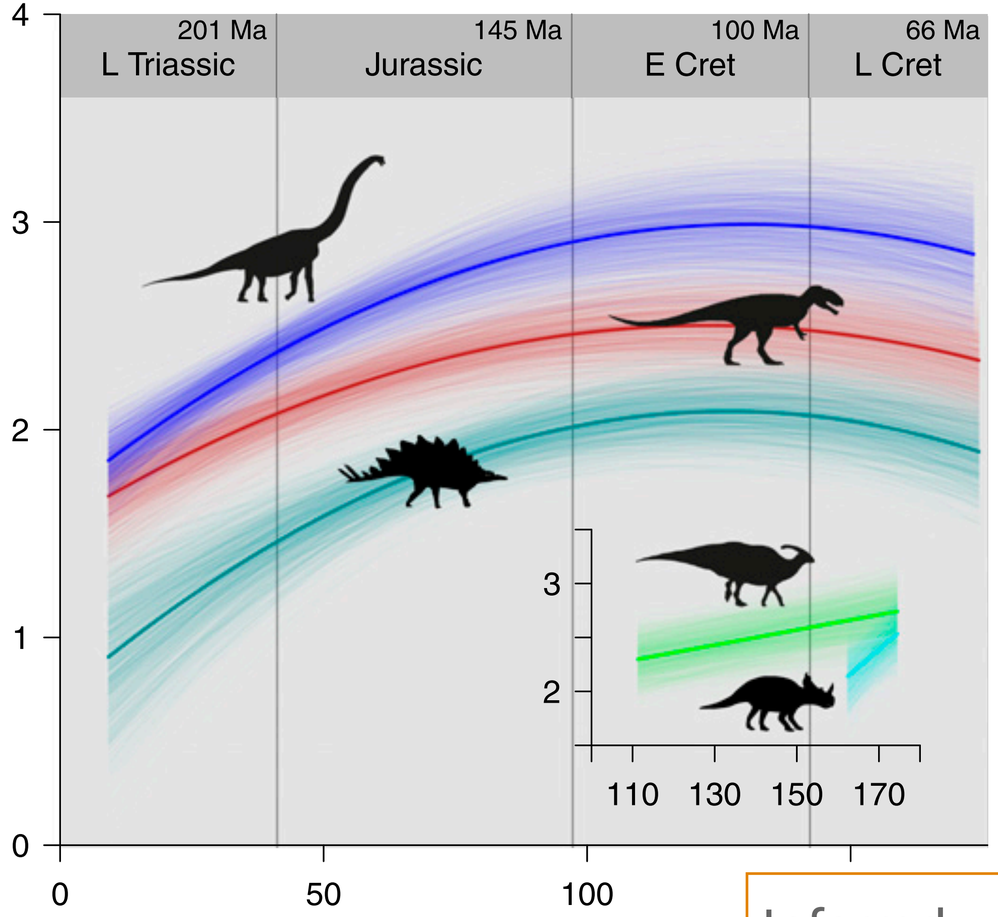
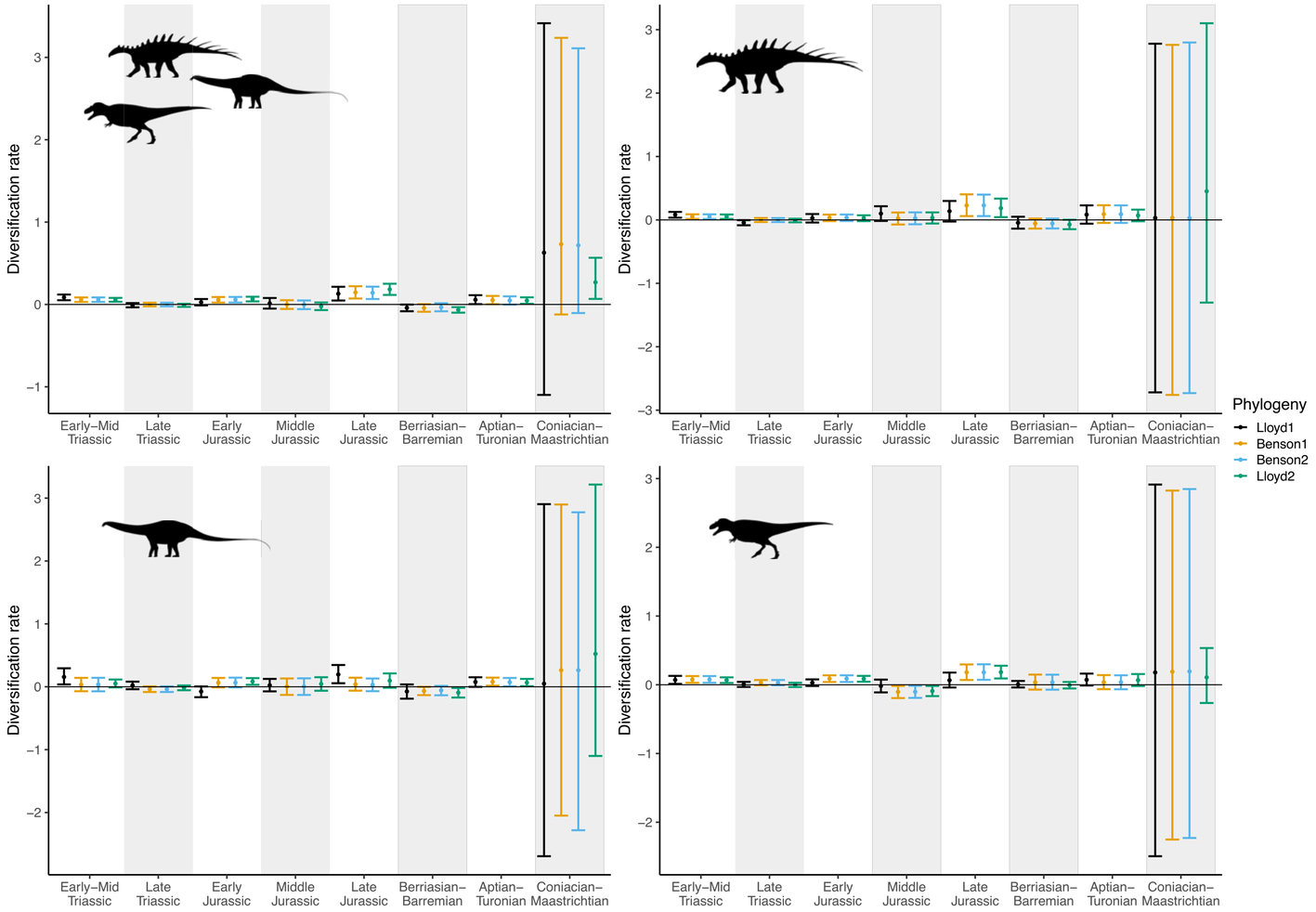
This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1521478113/-/DCSupplemental.



Inferred using phylogenetic GLMMs

Case study: were dinosaurs in decline pre-KPg?



We we reanalysed the data using the FBD process (and other models)

Our analyses show results are sensitive to the sampling model and suggest that we can not currently answer this question using available phylogenies

Allen et al. 2024. Extinction

Phylodynamic analysis of paleolithic stone tools

Matzig et al. 2024. Royal Society Open Science

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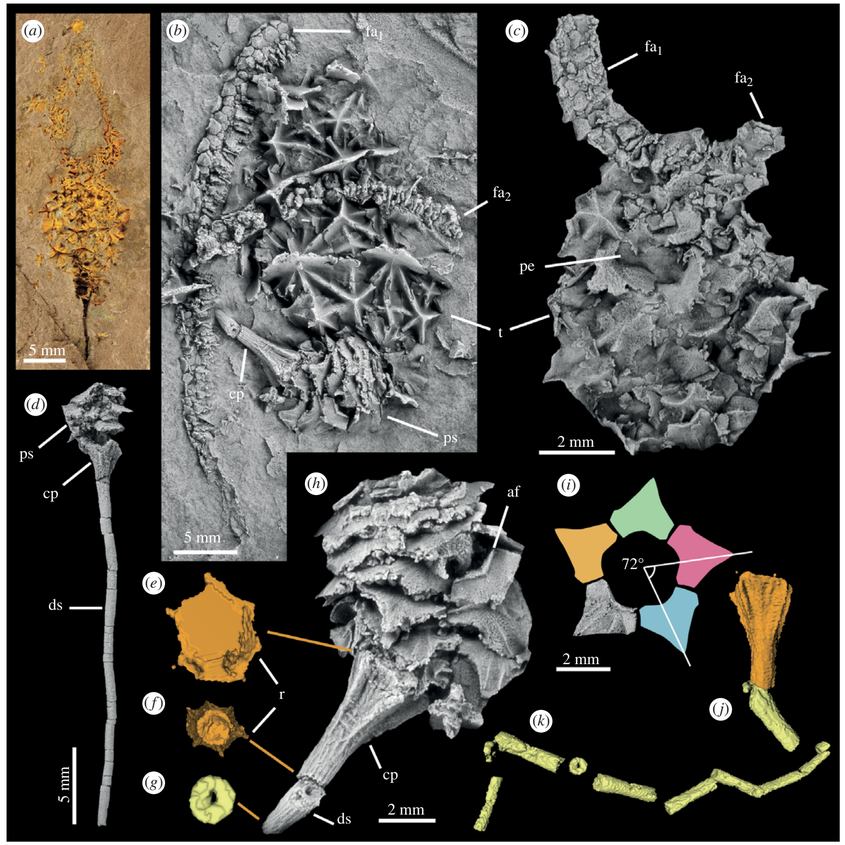


Dibrachicystis purujoensis

Cambrian stalked echinoderms show unexpected plasticity of arm construction
Zamora & Smith. (2012)

Continuous trait measurement data

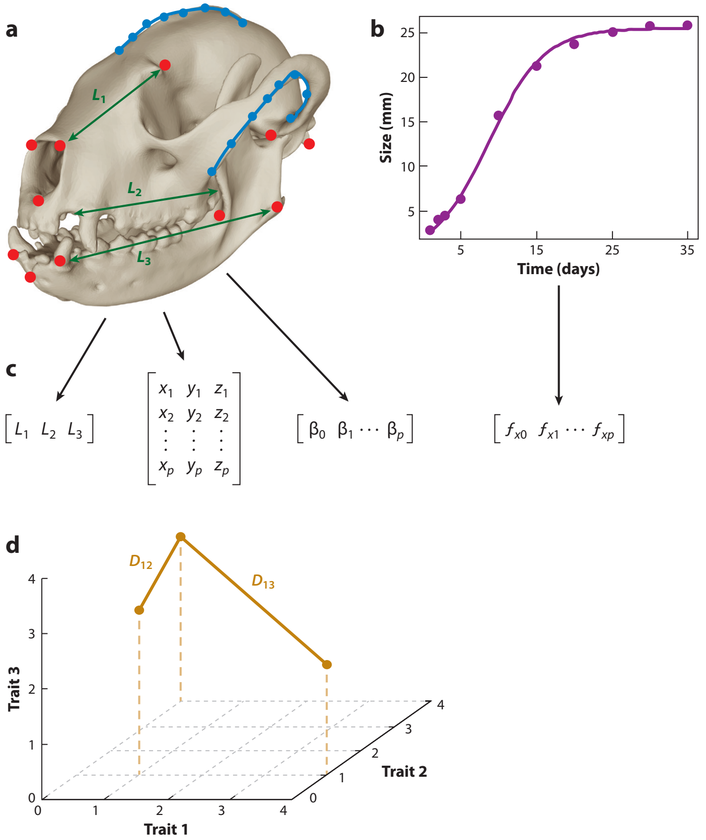
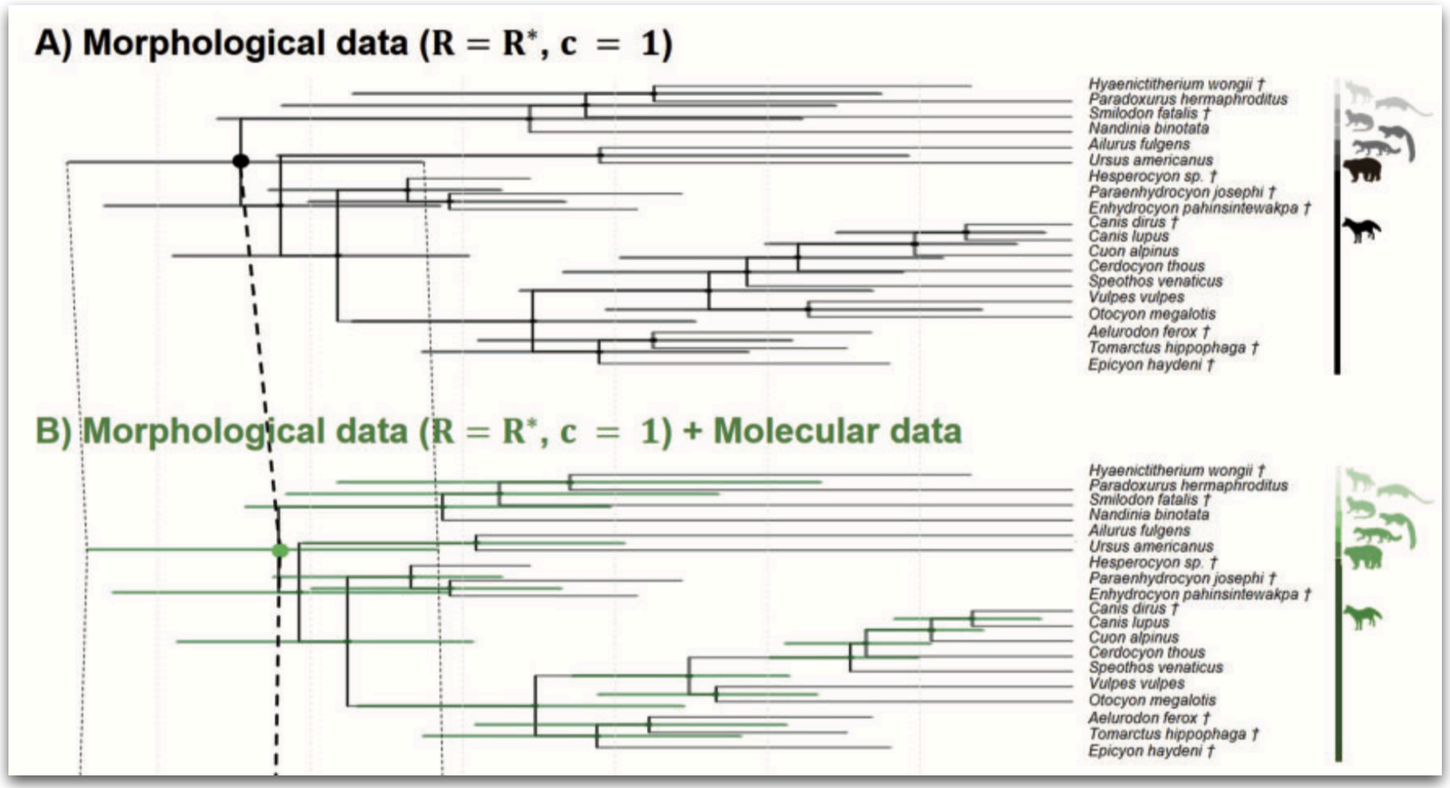
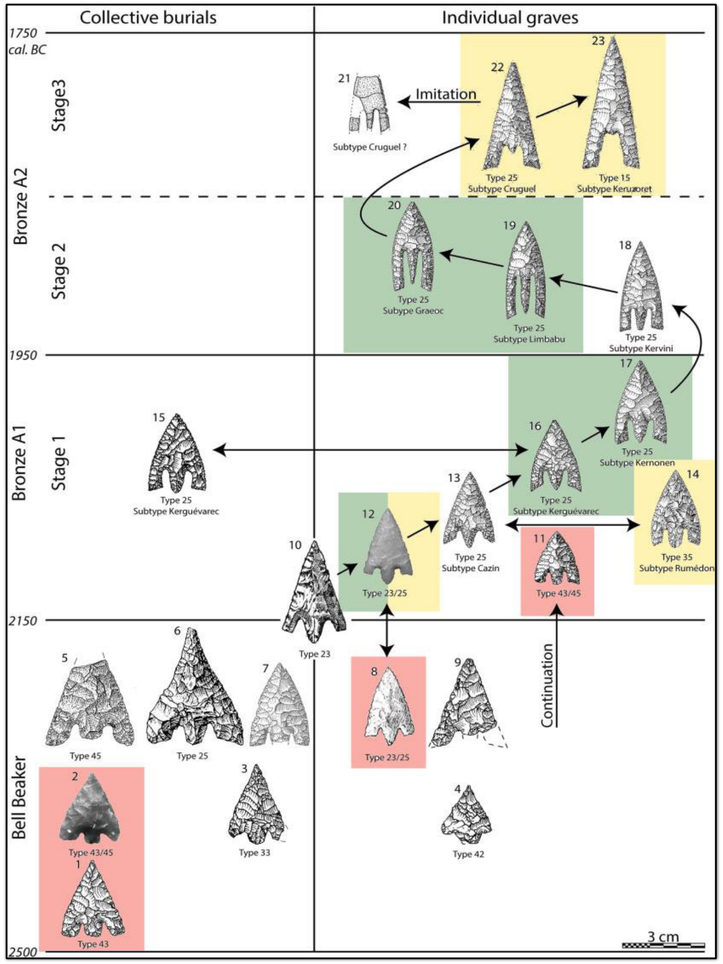


Image source *Adams & Collyer* (2019)



Álvarez-Carretero et al. (2019) *Bayesian Estimation of Species Divergence Times Using Correlated Quantitative Characters*

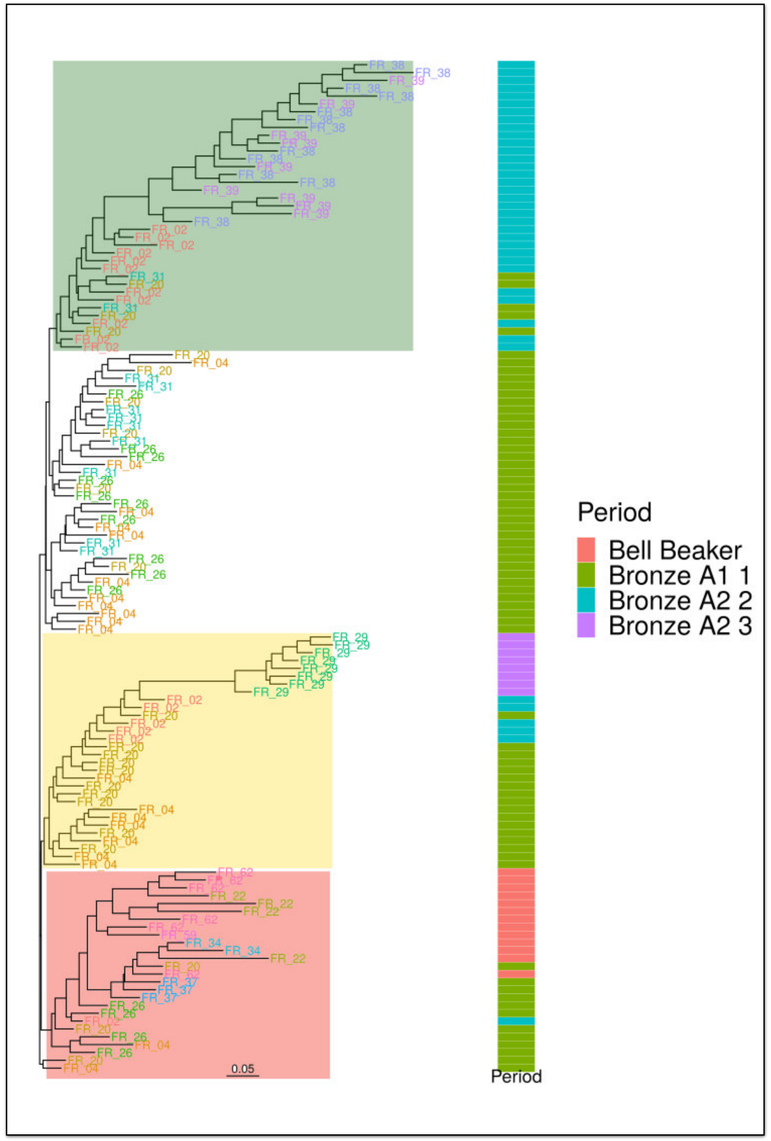
Cultural evolution



After Nicolas (2017)

←Typo-Chronology of Palaeolithic stone tools

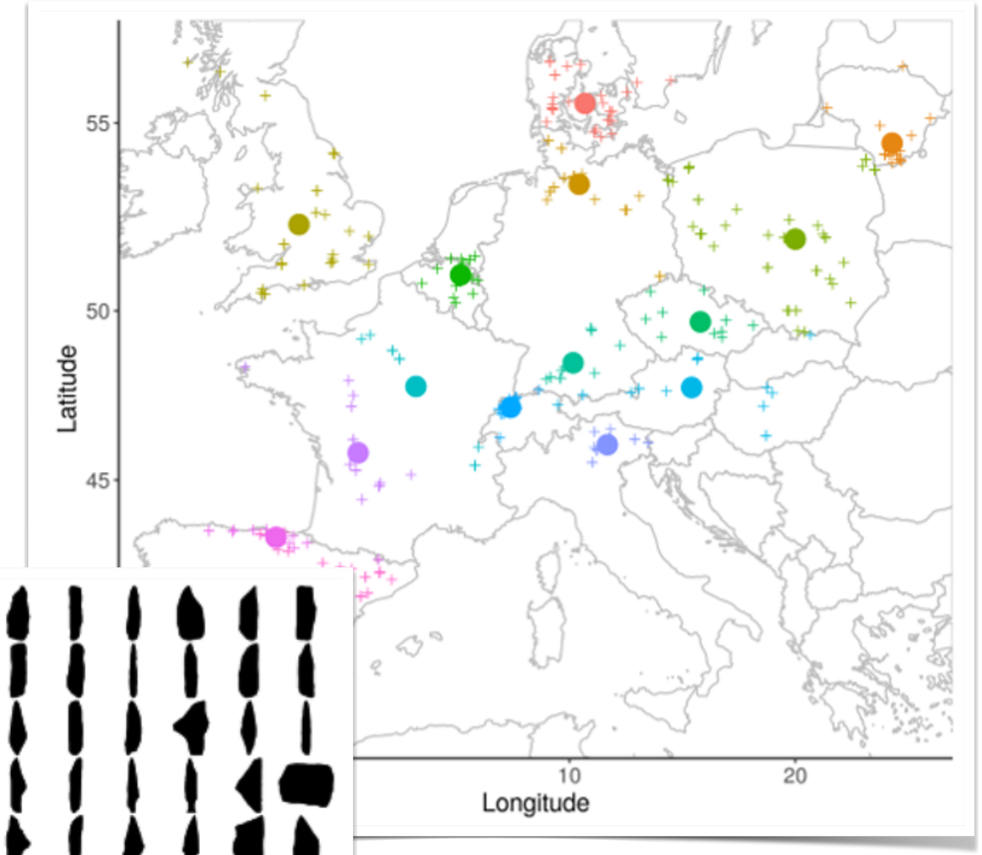
Outline based NJ tree →

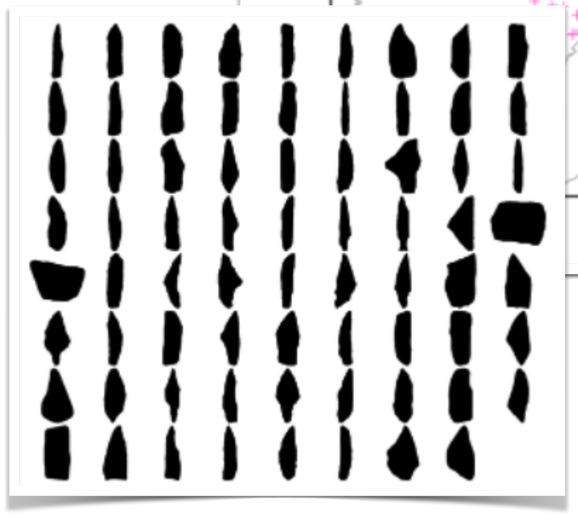


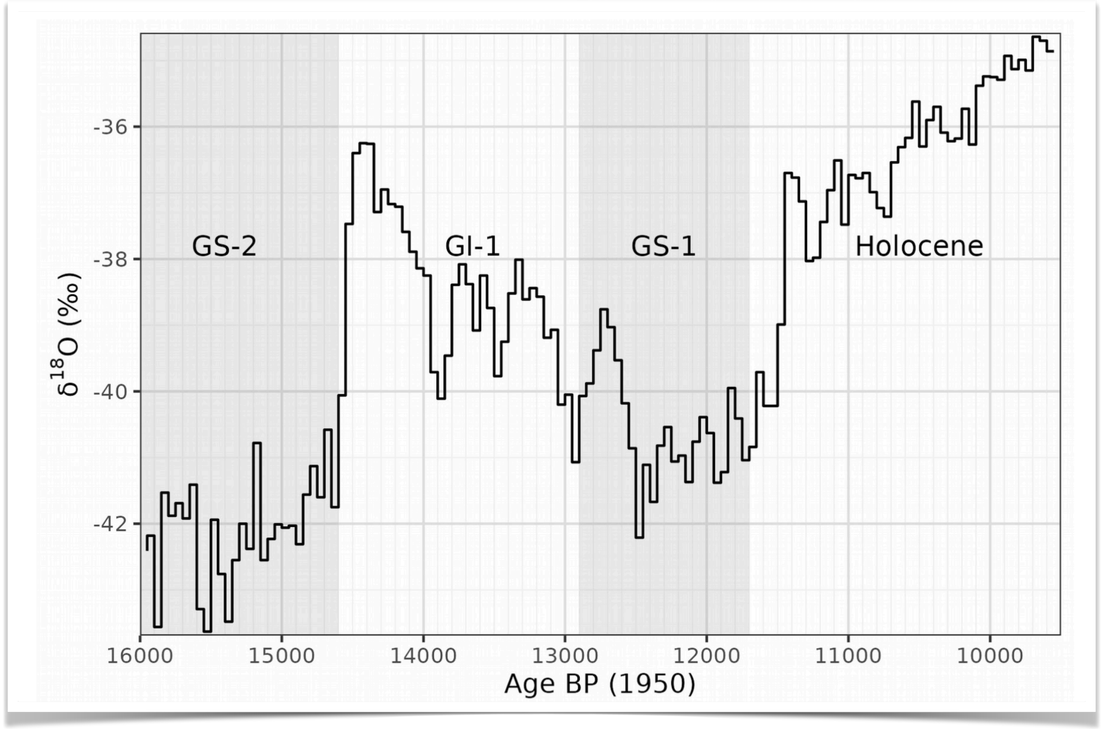
Matzig et al. 2021.

- Can we infer a topology of stone tools using the FBD process?
- Can we estimate phylodynamic parameters?

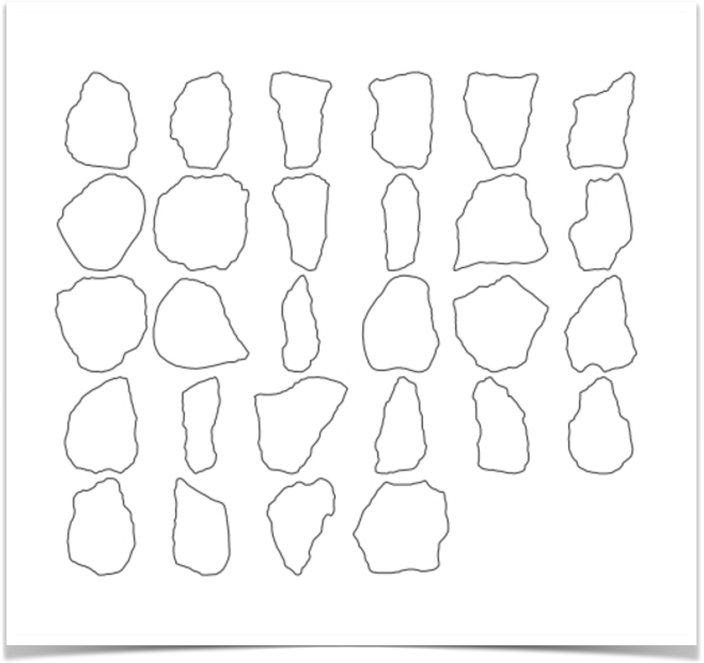
Data and context

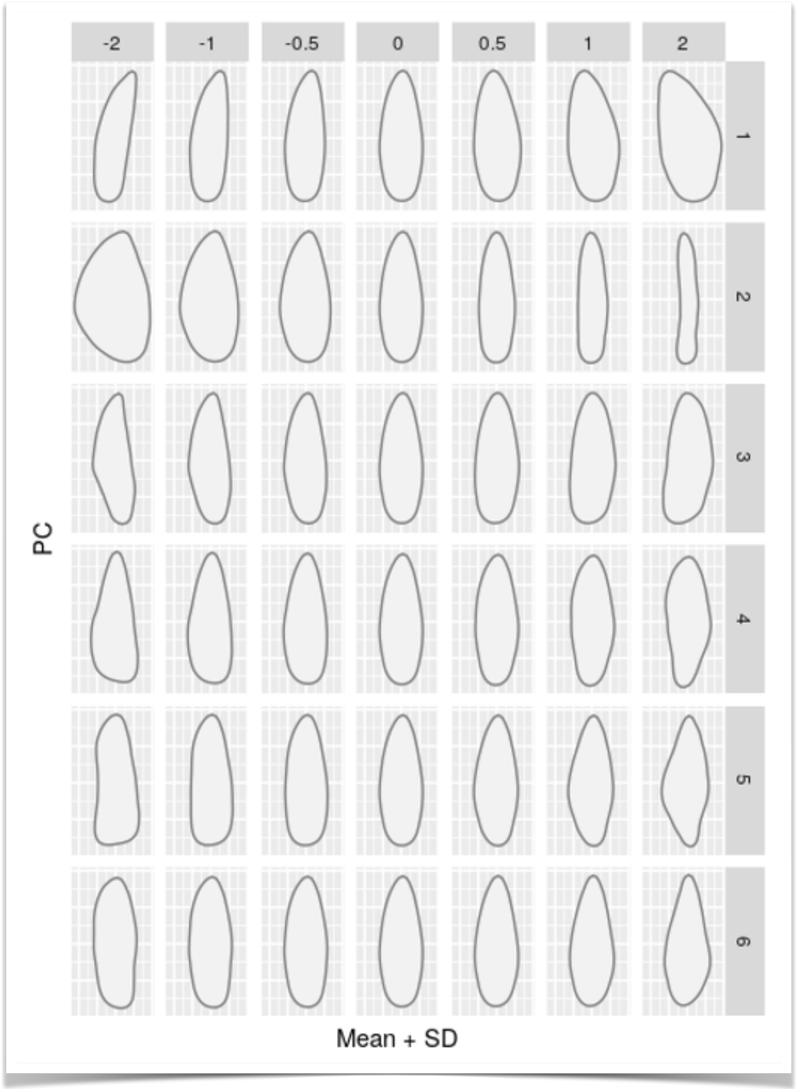




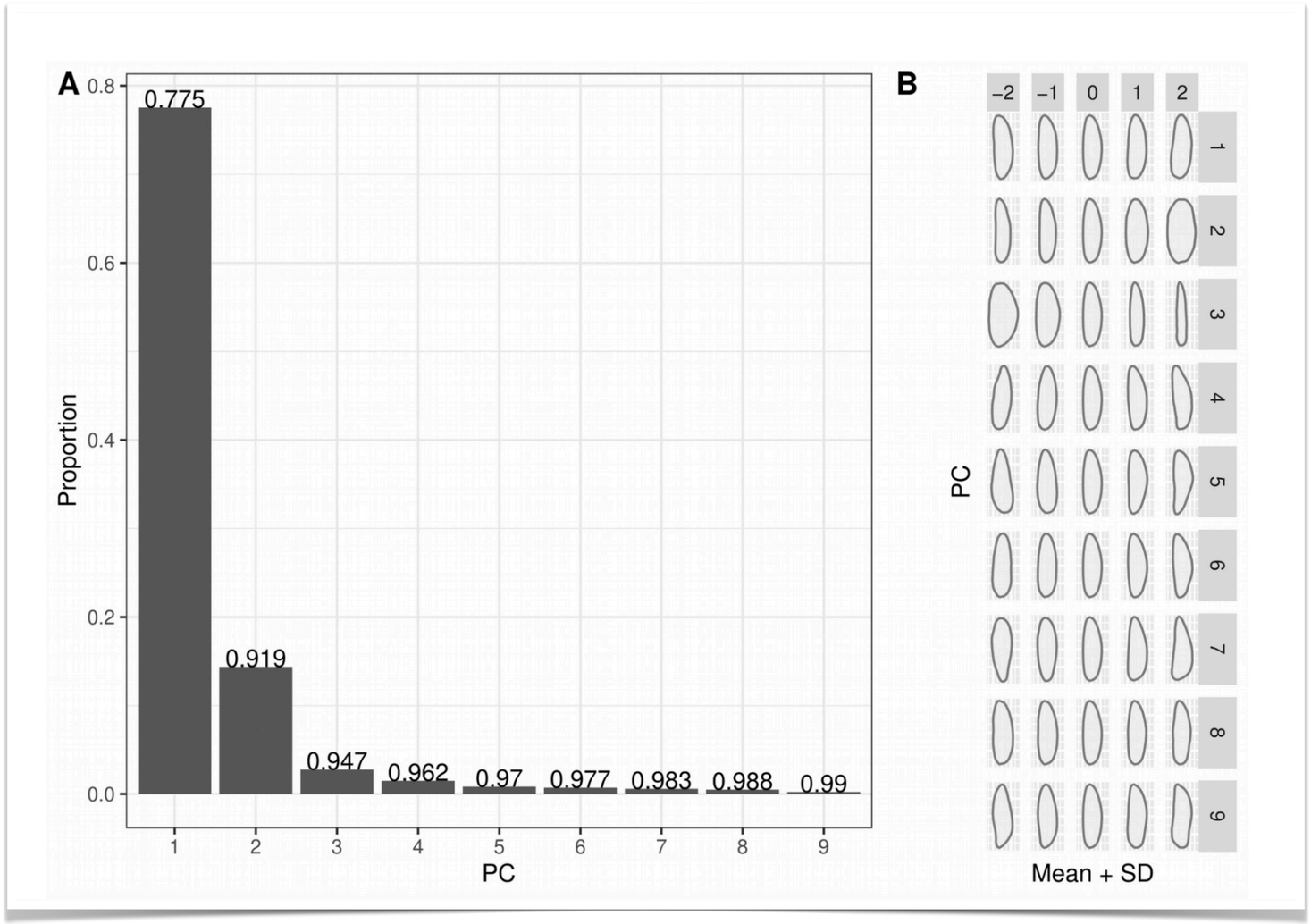


Geomorphic morphometrics





Analysis

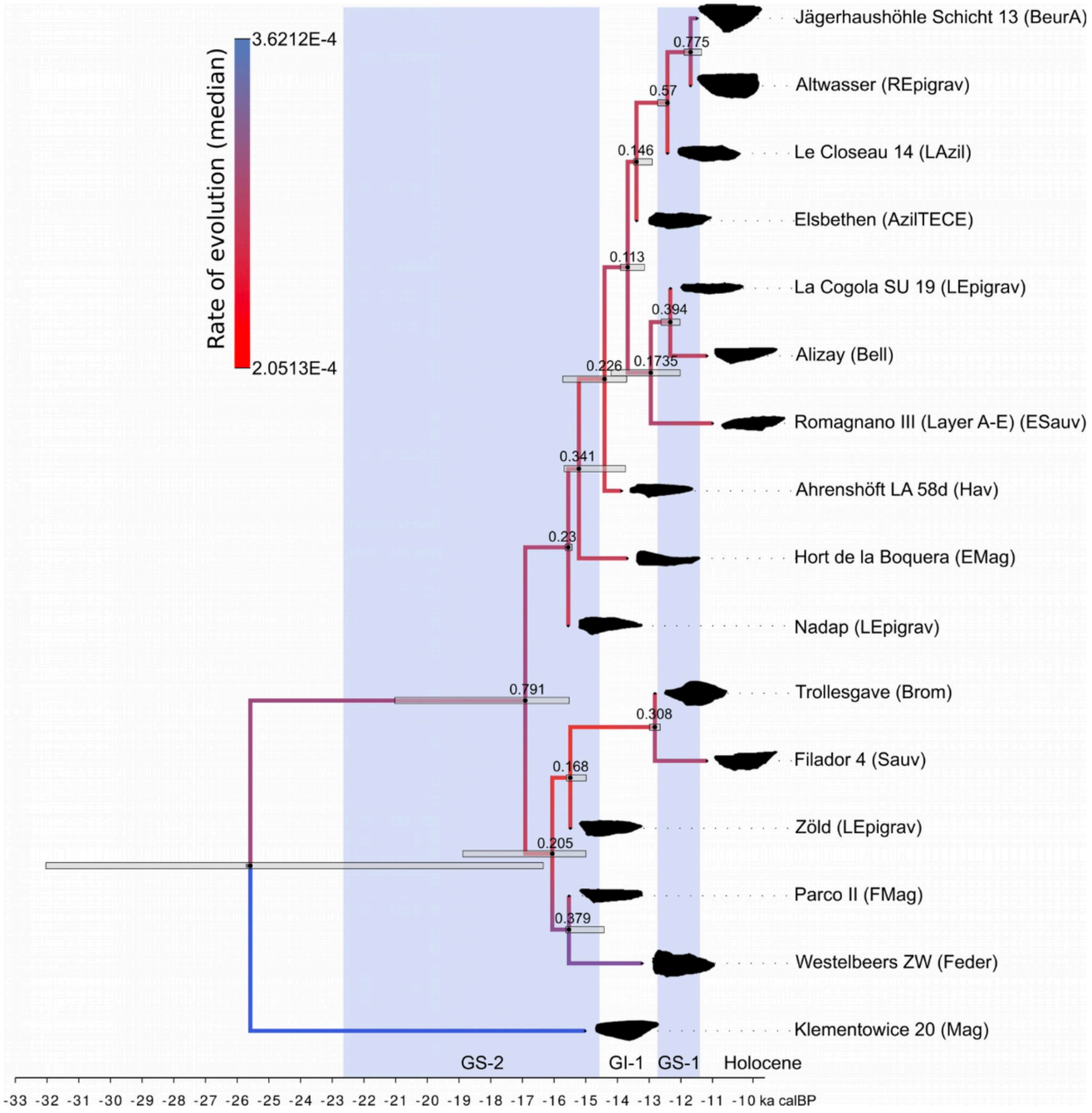


Tree inference

FBD skyline model (SA package)

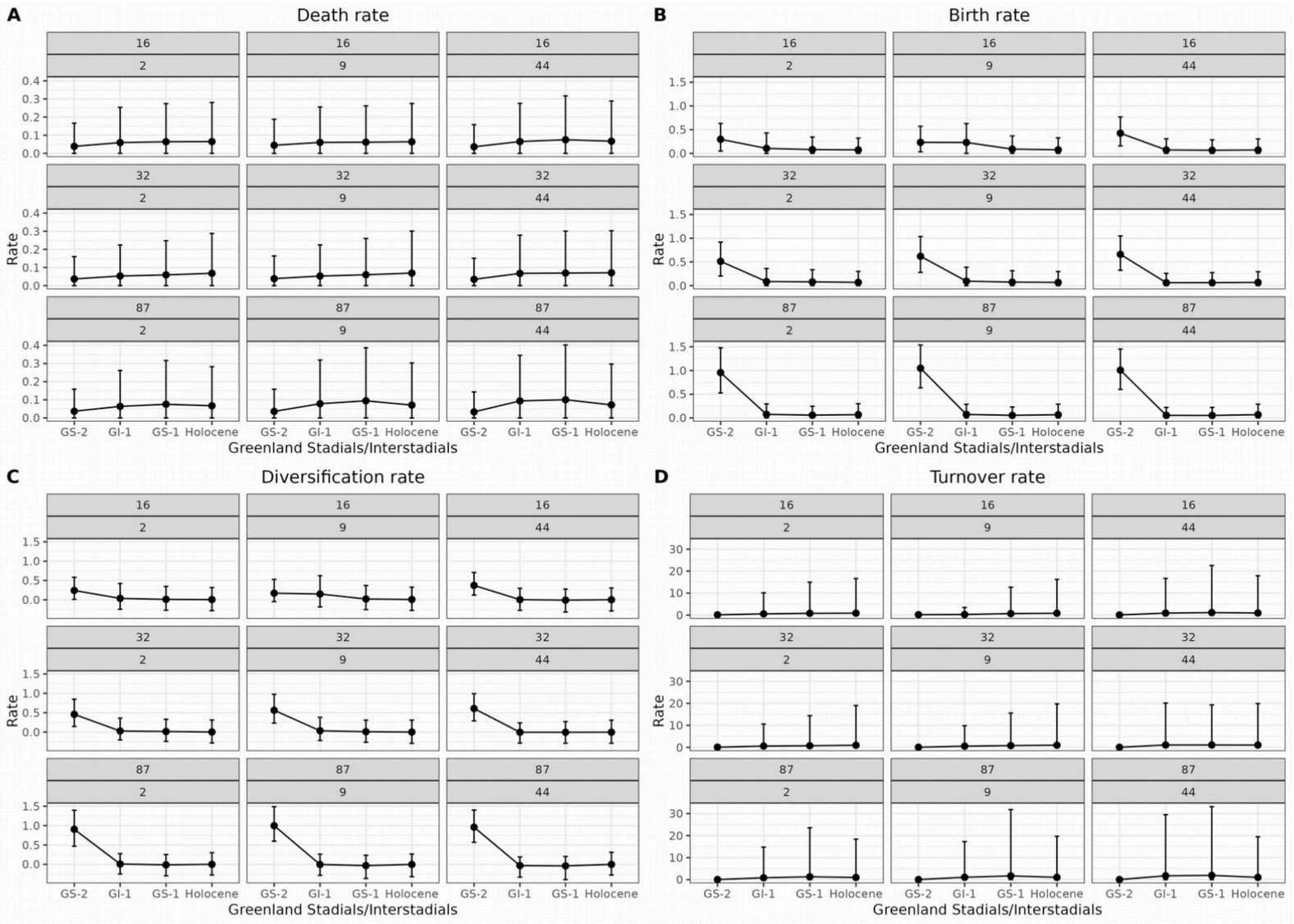
Brownian motion of trait evolution (contraband package)

The tree topology of stone tools exhibits a lot of uncertainty



Sensitivity analyses

Birth, death, and sampling rates are impacted by trait and taxon sampling



Results summary

- The FBD process combined with PCMs offers a promising framework for studying cultural evolution
- However, the results are sensitive to sampling and the use of continuous traits models for inference requires more scrutiny