Phylogenetics

Introduction to comparative methods

RL-V3 MPP

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Phylogenetic comparative methods

Comparative methods

The distribution of traits among species is the result of evolution

Traits can be **discrete** or **continuous**

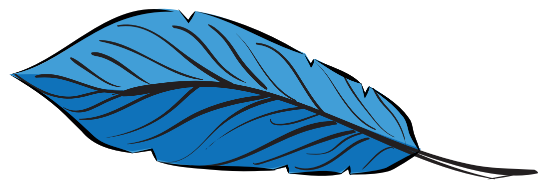
Comparative methods are approaches used to study trait evolution

Why do we need to take phylogeny into account when we study trait evolution?

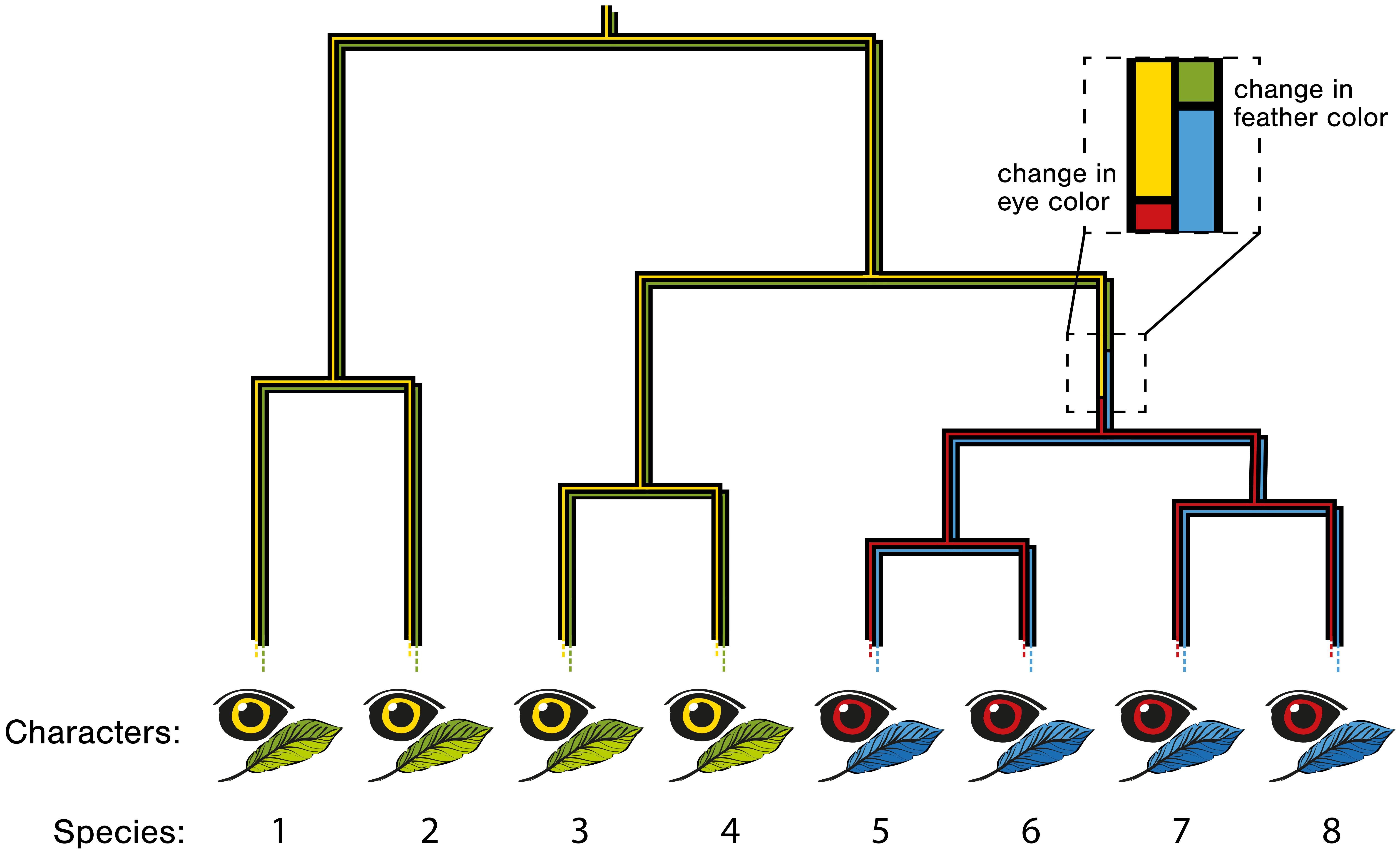
Characters:

Species: 1 2 3 4 5 6 7 8

Contingency table

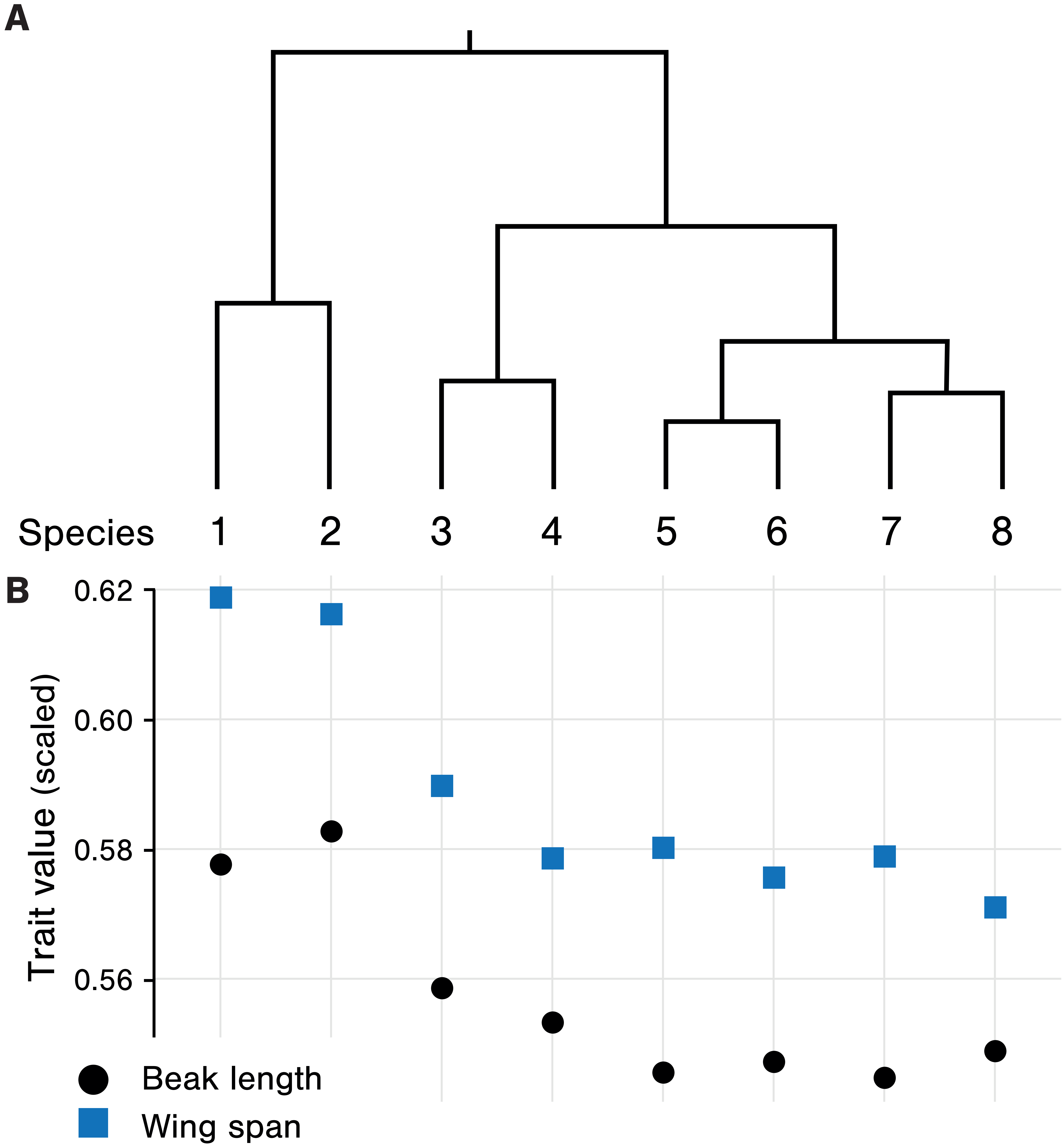
			Totals
	4	0	4
	0	4	4
Totals	4	4	8

Example: Decoding Genomes *Stadler et al.* (2024)



Contingency table (changes per branch)

	Change	No change	Totals
Change	1	0	1
No change	0	13	13
Totals	1	13	14



The tree shows bird species, along with continuous wing span and beak length traits for each one

Note the trait values highly depend on which of the two main clades of a given species belongs to!

Example: Decoding Genomes *Stadler et al.* (2024)

Phylogenetic comparative methods (PCMs)

A large family of statistical approaches used to study trait evolution that take into account phylogenetic non-independence

The input is usually a tree, combined with trait data

Examples: tests for phylogenetic signal, phylogenetic PCA (morphometrics), ancestral state reconstruction, evolutionary model fitting analysis (tempo and mode), multi-type diversification models (see previous weeks), many more

Can you think of any questions you would ask about trait evolution?

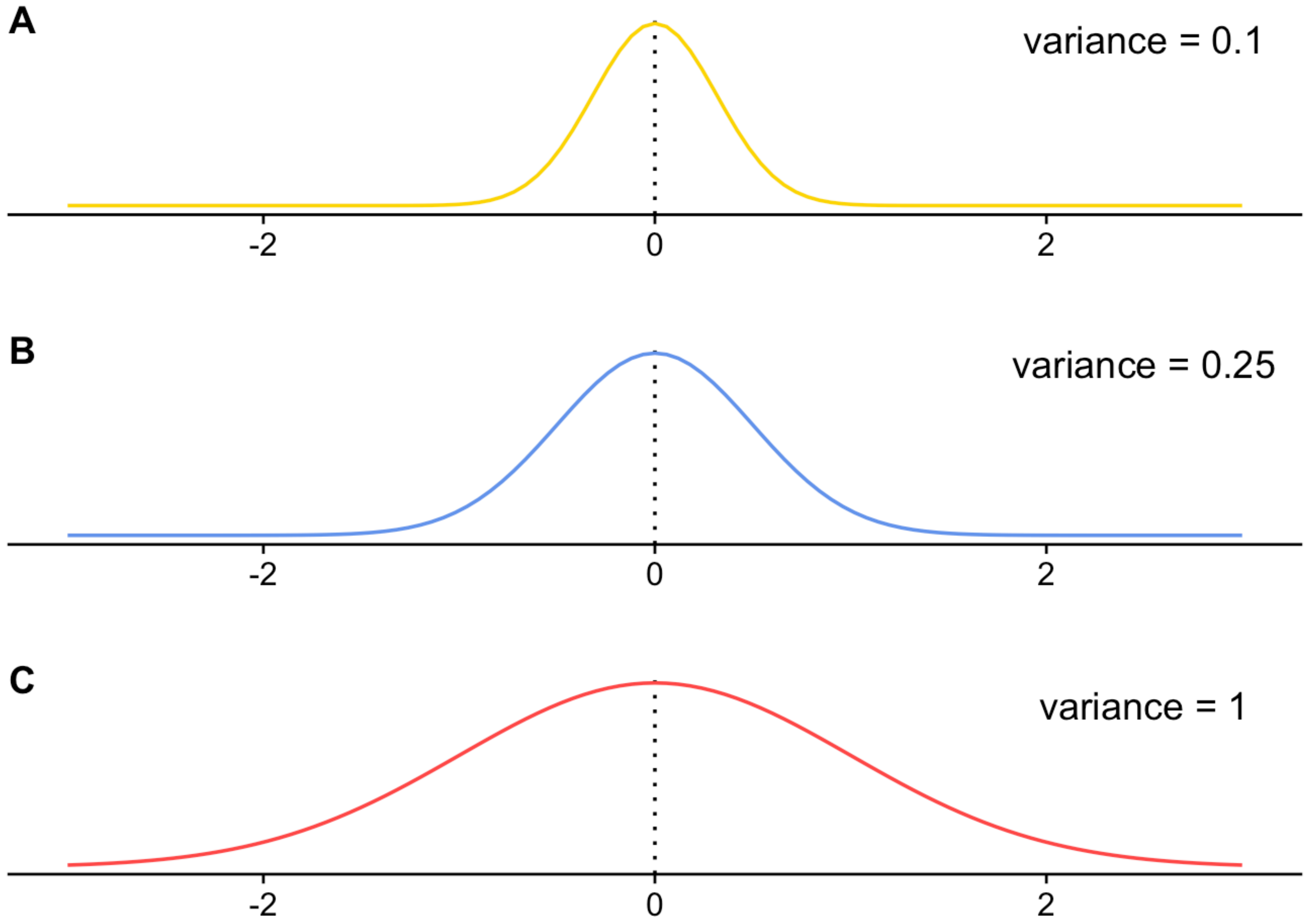
Models of continuous trait evolution

Brownian motion (BM)

The amount a trait changes over time is drawn from a normal distribution with a **mean of 0** and a **variance of σ^2**

Positive numbers cause the trait to increase

Negative numbers cause the trait to decrease



PCM Primer *Cooper and Freckleton* (2026)

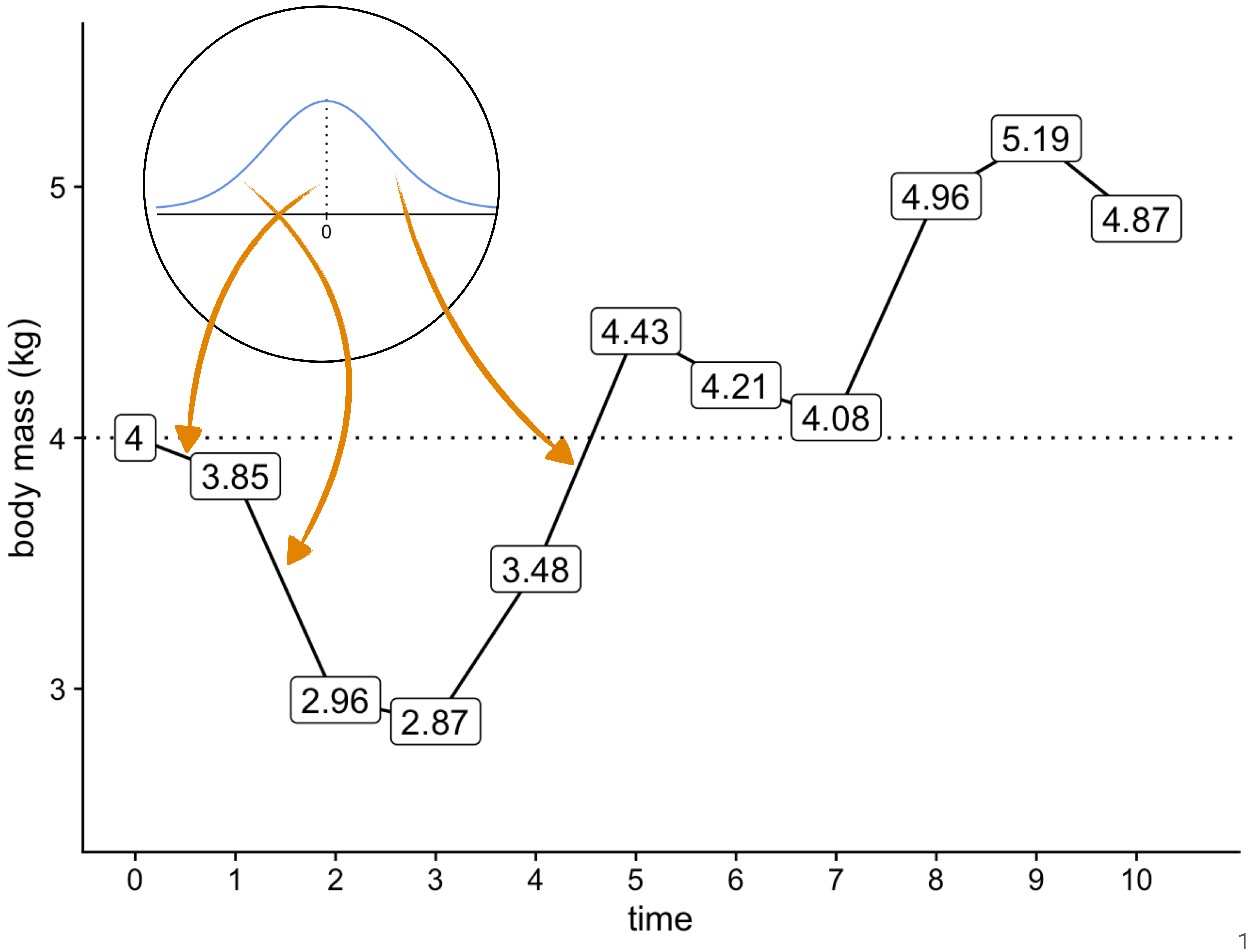
Brownian motion

Also known as a “random walk” model

Model parameters: σ^2 and the root value

Equivalent to the rate of evolution, larger σ^2 = faster evolution

Figure shows a simple example of body mass change through time, with starting value = 4 and σ^2 = 0.25

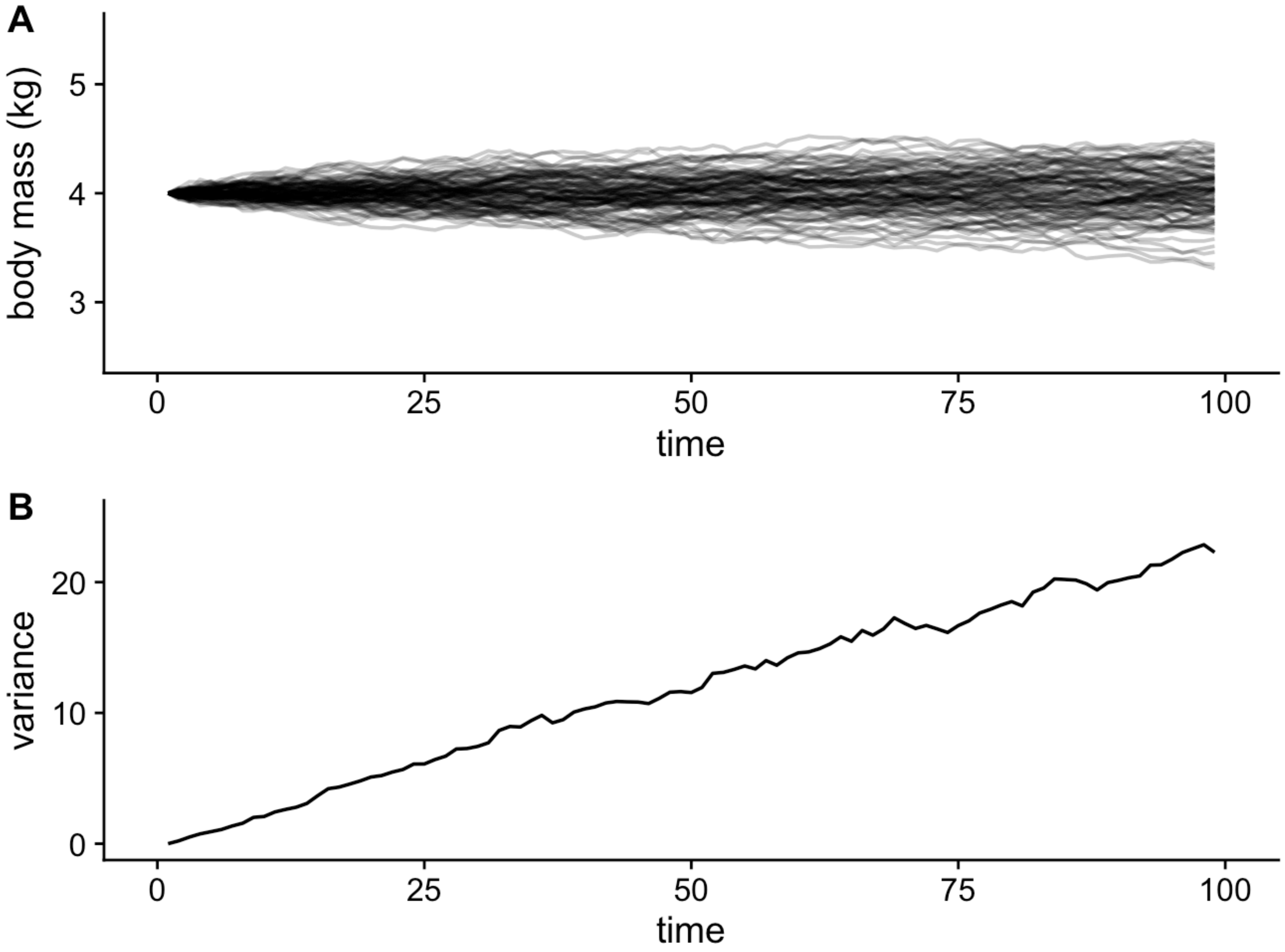


PCM Primer *Cooper and Freckleton* ([2026](2026))

Brownian motion

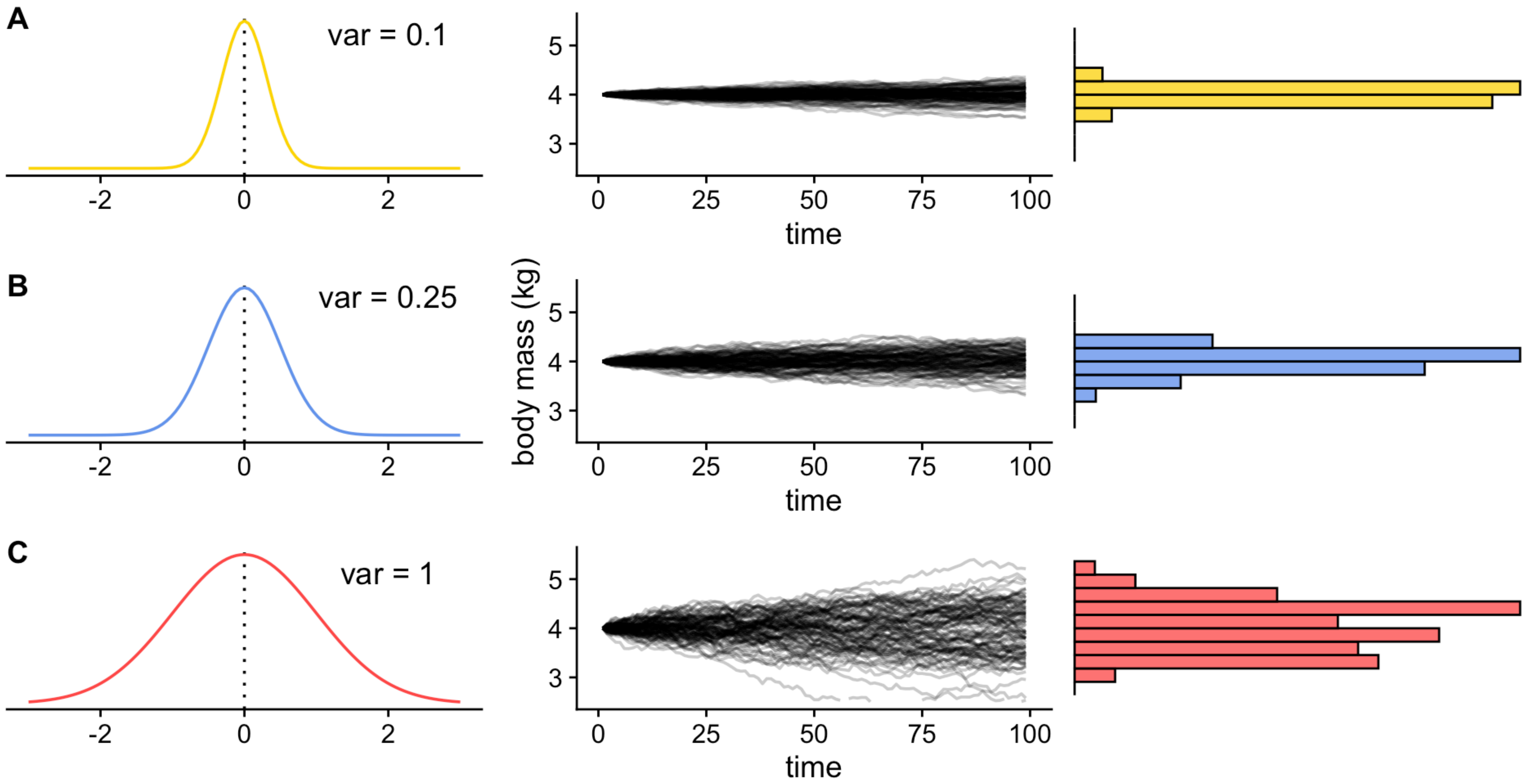
100 examples of body mass change through time under a BM model, with starting value = 4 and $\sigma^2 = 0.25$

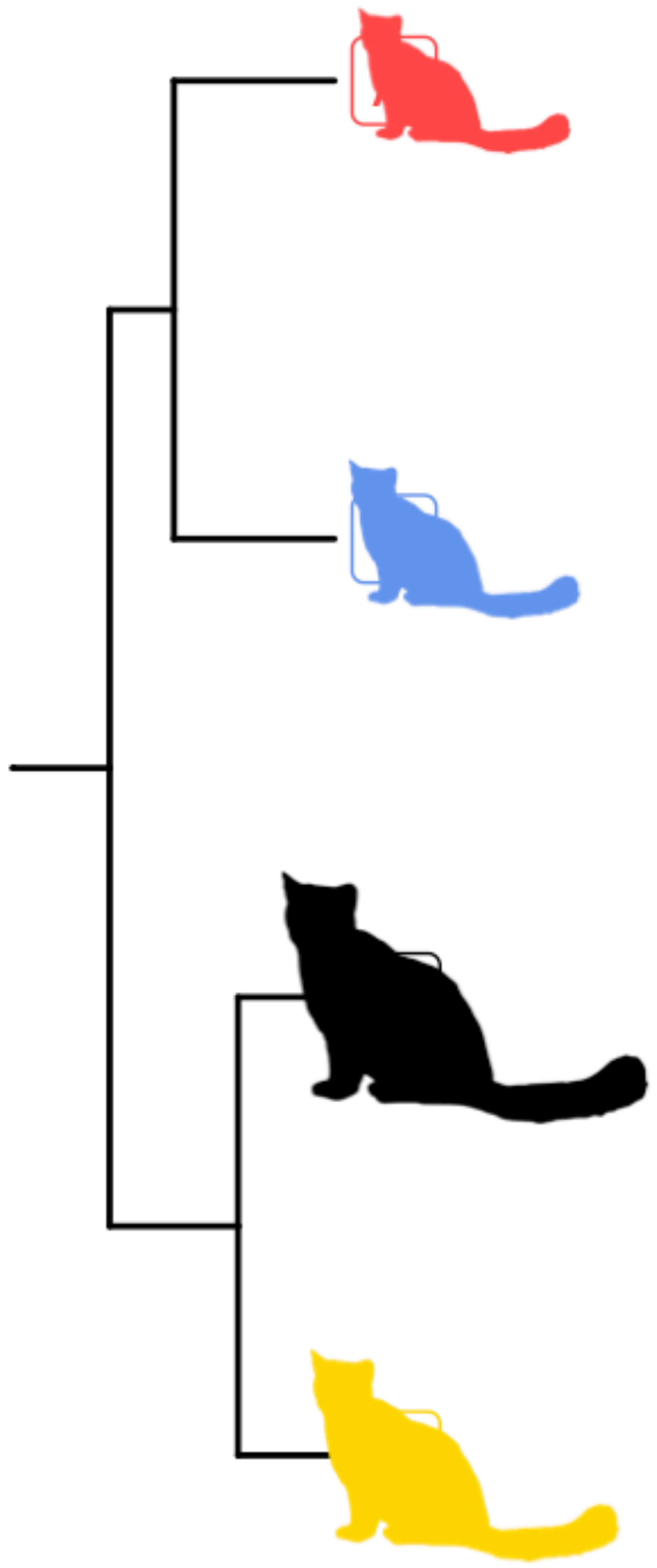
The plot below shows the increase in the variance in body mass through time

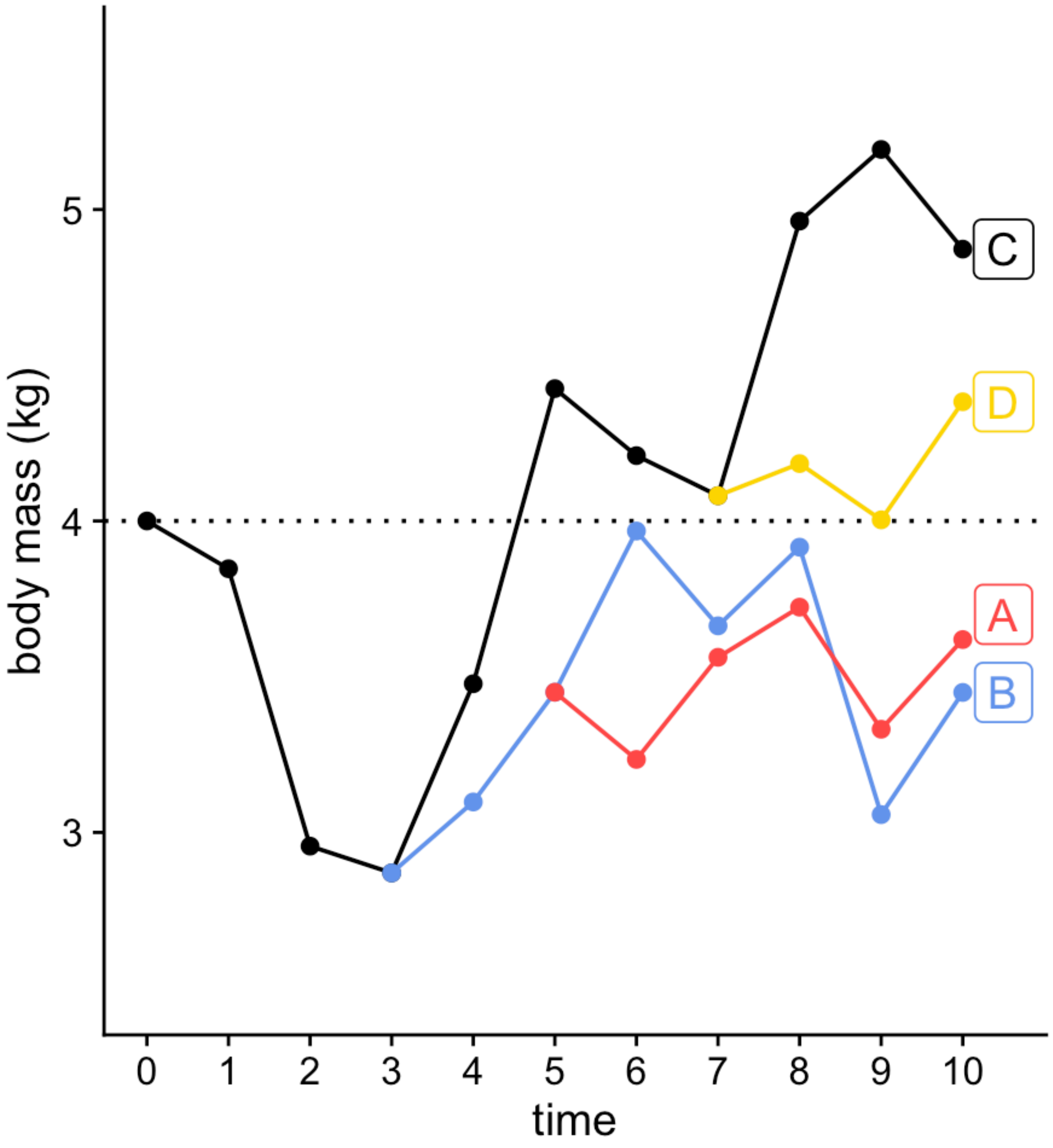


PCM Primer *Cooper and Freckleton* (2026)

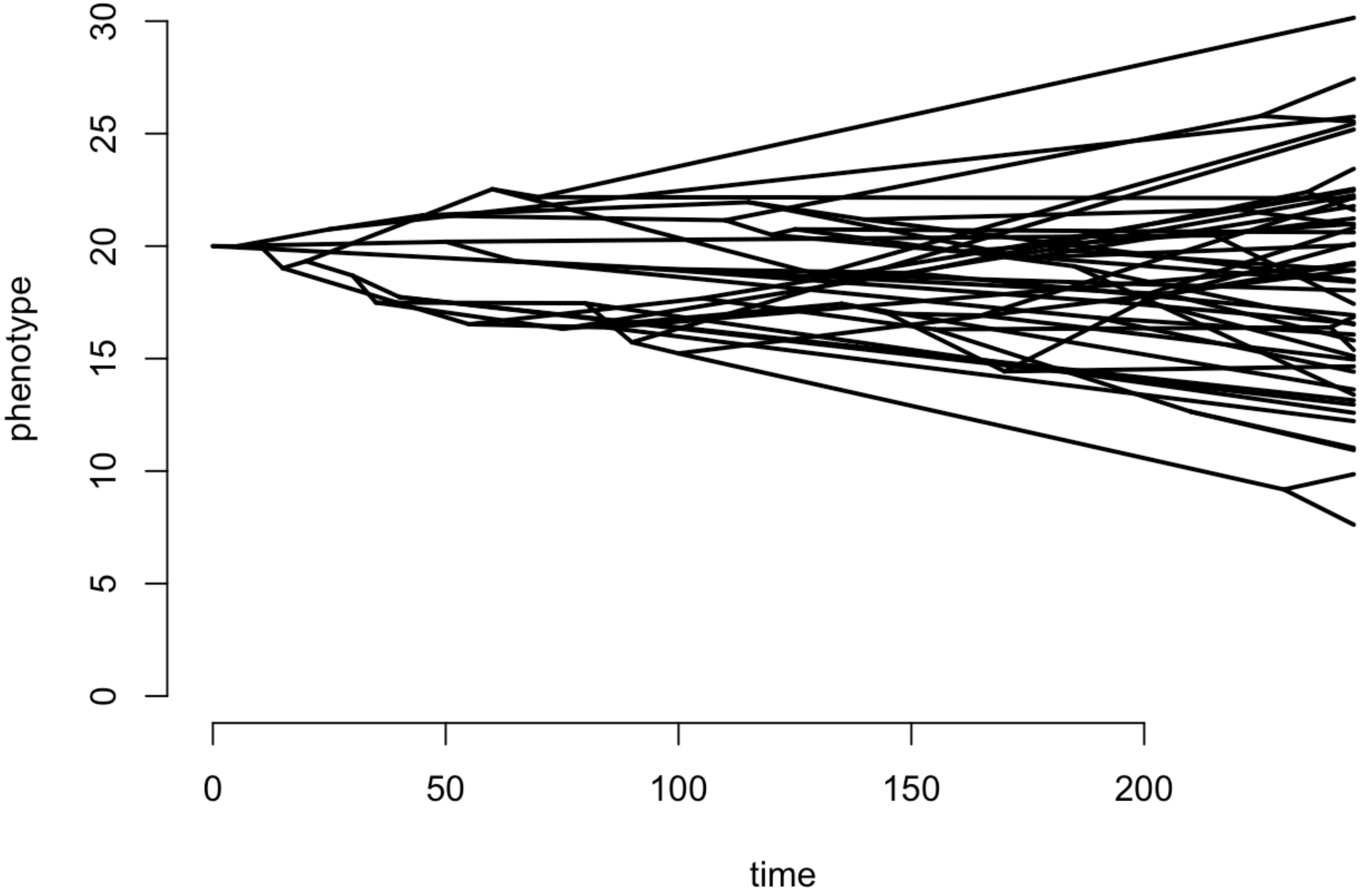
3 examples of body mass change under BM with the same starting value and 3 different values of σ^2



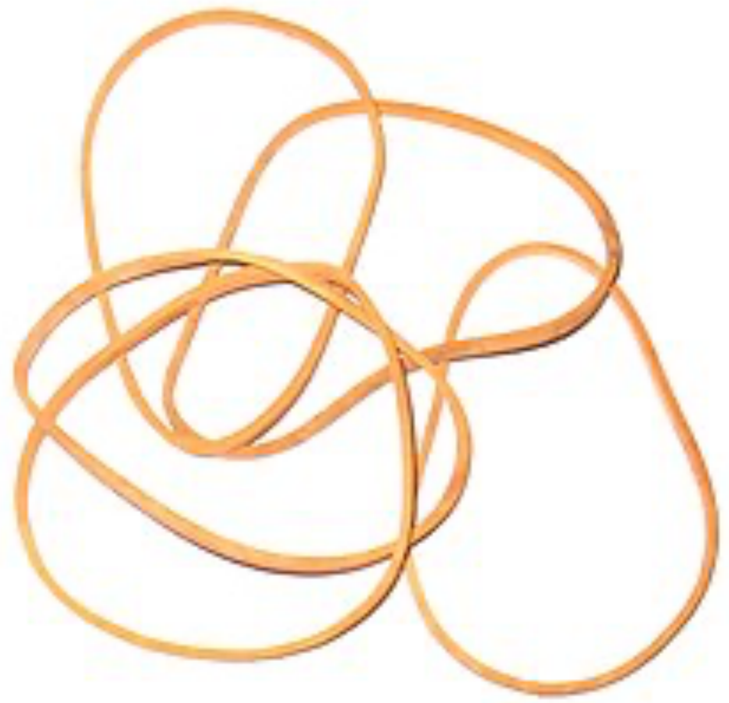




We can model BM along a tree


phenotype
0
5
10
15
20
25
30
time
0
50
100
150
200

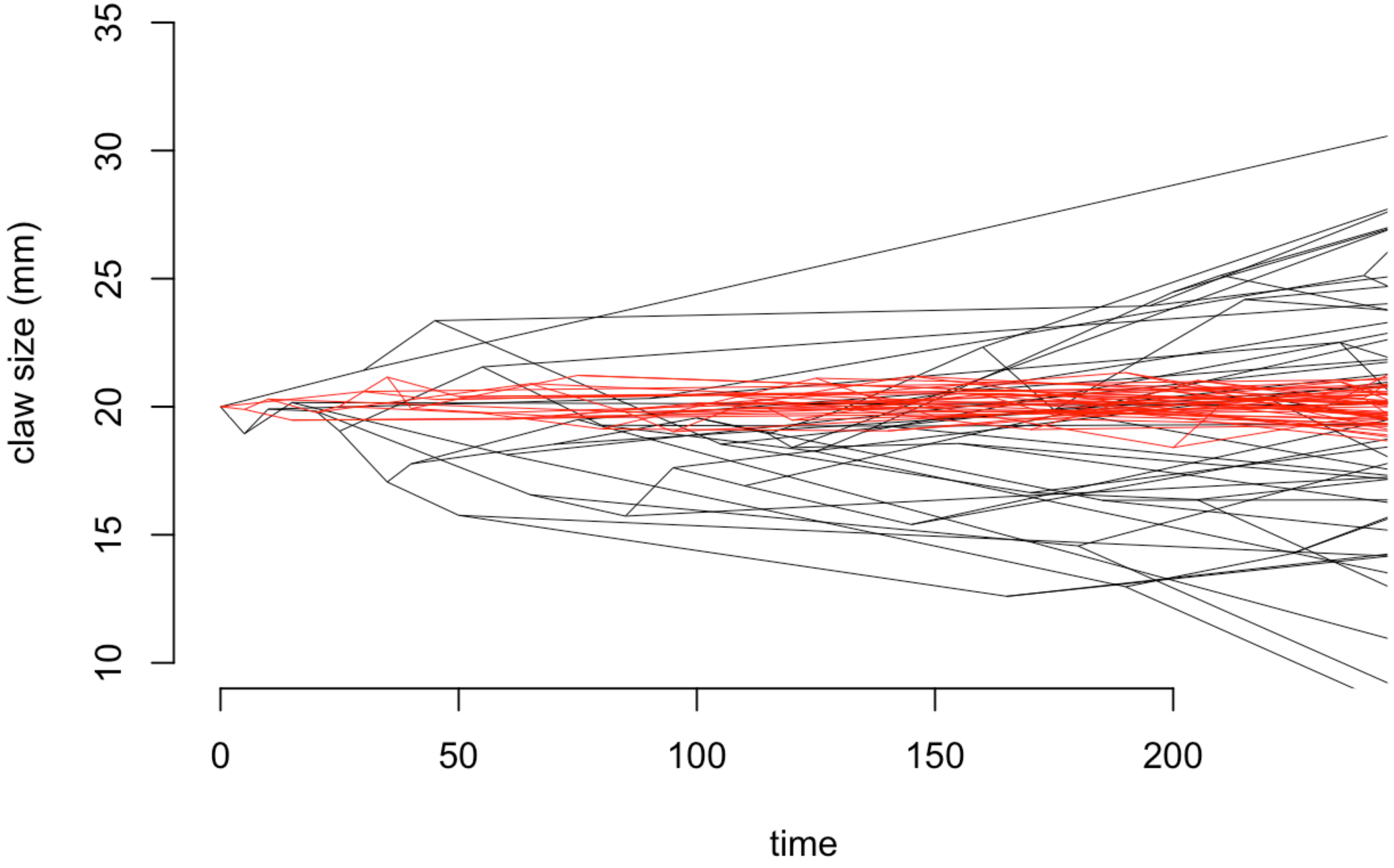
Ornstein-Uhlenbeck



Model parameters:

- the rate parameter σ^2
- the root value
- the rubber band parameter α
- the long term mean (optima)

Larger α means the trait evolves closer to the mean, α close to 0 is equivalent to a random walk, i.e., BM



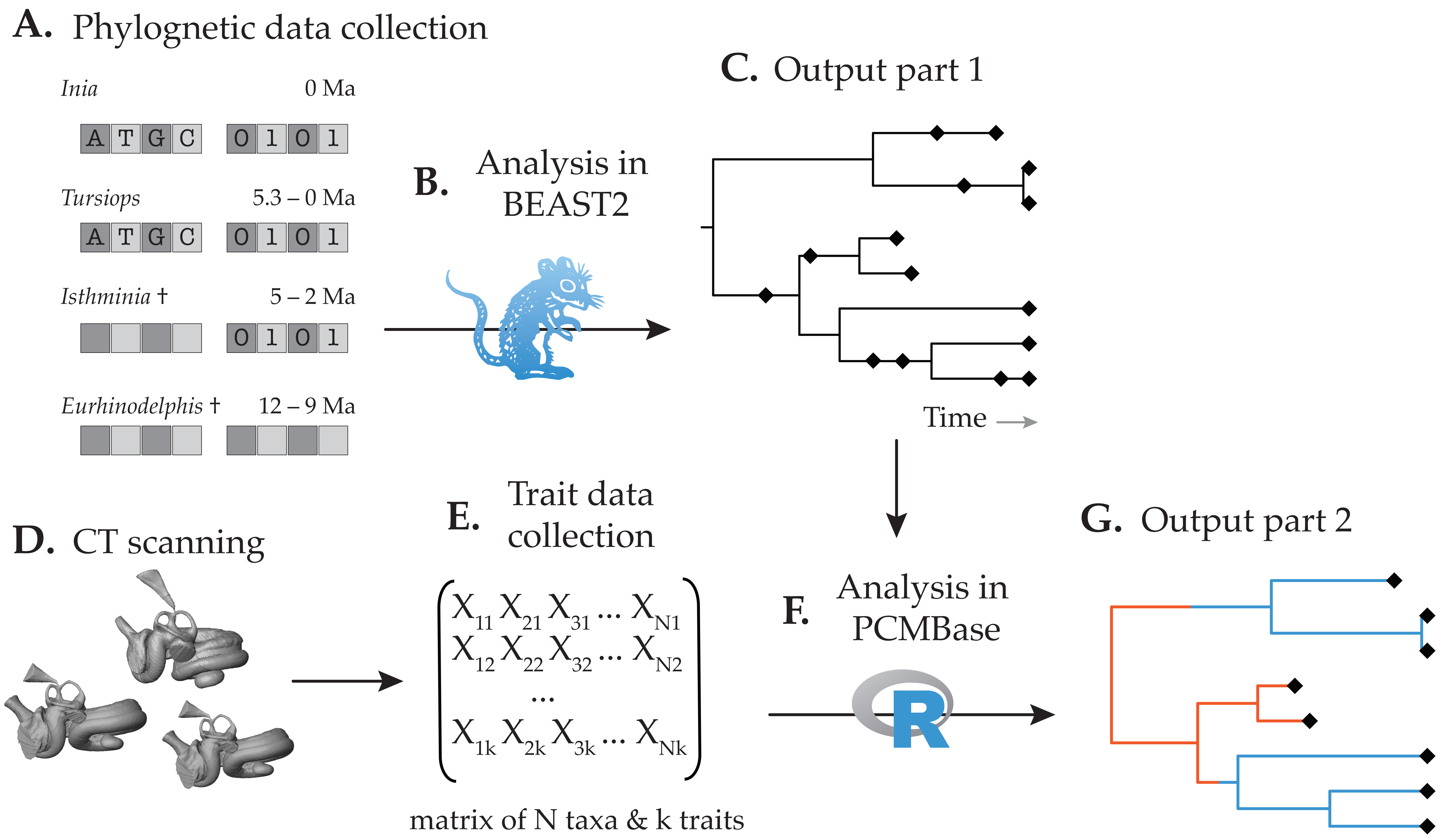
PCMs require time trees

In theory, we could infer the tree and PCM parameters at the same time (and sometimes we do), but this computationally tricky — usually we estimate the tree (topology and times) first

Make sure the method is appropriate for your data and don’t over interpret results
Cooper et al. [2016]

Fossils help! Simulation show including fossils improves our identify the correct model of trait evolution *Slater et al.* [2012], *Gearty et al.* [2026]

Typical workflow



A. Phylognetic data collection

Inia 0 Ma
A T G C 0 1 0 1

Tursiops 5.3 – 0 Ma
A T G C 0 1 0 1

Isthminia † 5 – 2 Ma
0 1 0 1

Eurhinodelphis † 12 – 9 Ma

B. Analysis in BEAST2

C. Output part 1

Time →

D. CT scanning

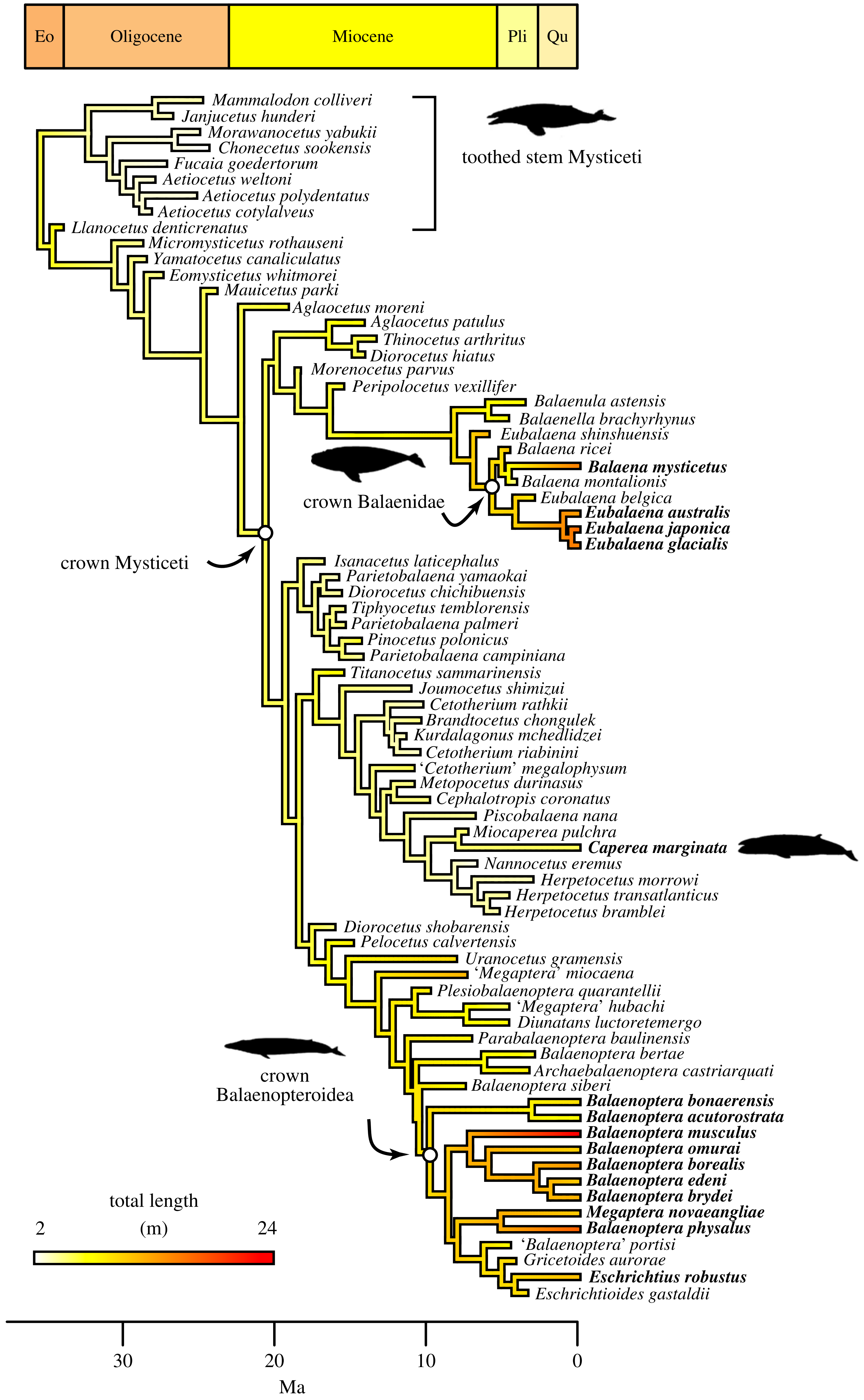
E. Trait data collection

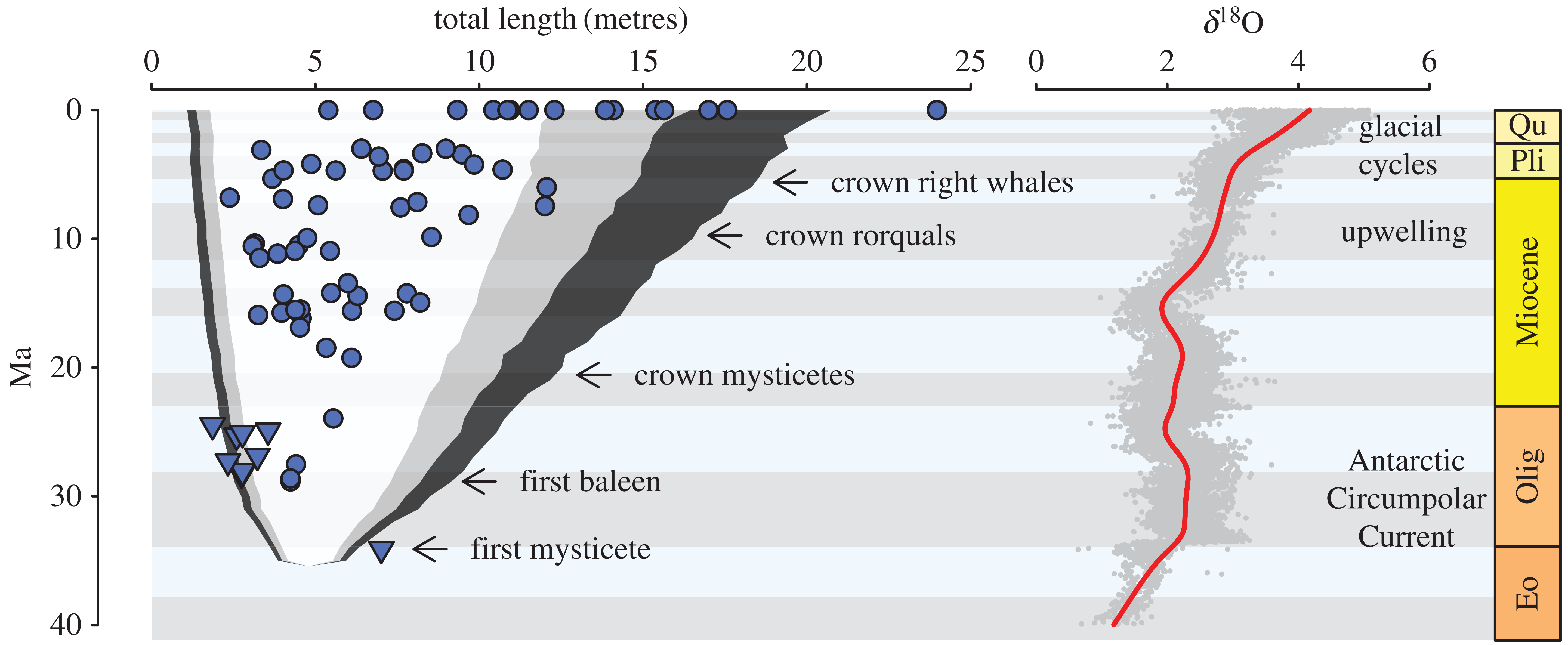
$$\begin{pmatrix} X_{11} & X_{21} & X_{31} & \dots & X_{N1} \\ X_{12} & X_{22} & X_{32} & \dots & X_{N2} \\ & & \dots & & \\ X_{1k} & X_{2k} & X_{3k} & \dots & X_{Nk} \end{pmatrix}$$

matrix of N taxa & k traits

F. Analysis in PCMBase

G. Output part 2





Example: gigantism in baleen whales

Linked to ocean dynamics in the Plio-Pleistocene

→ upwelling resulted in high prey densities

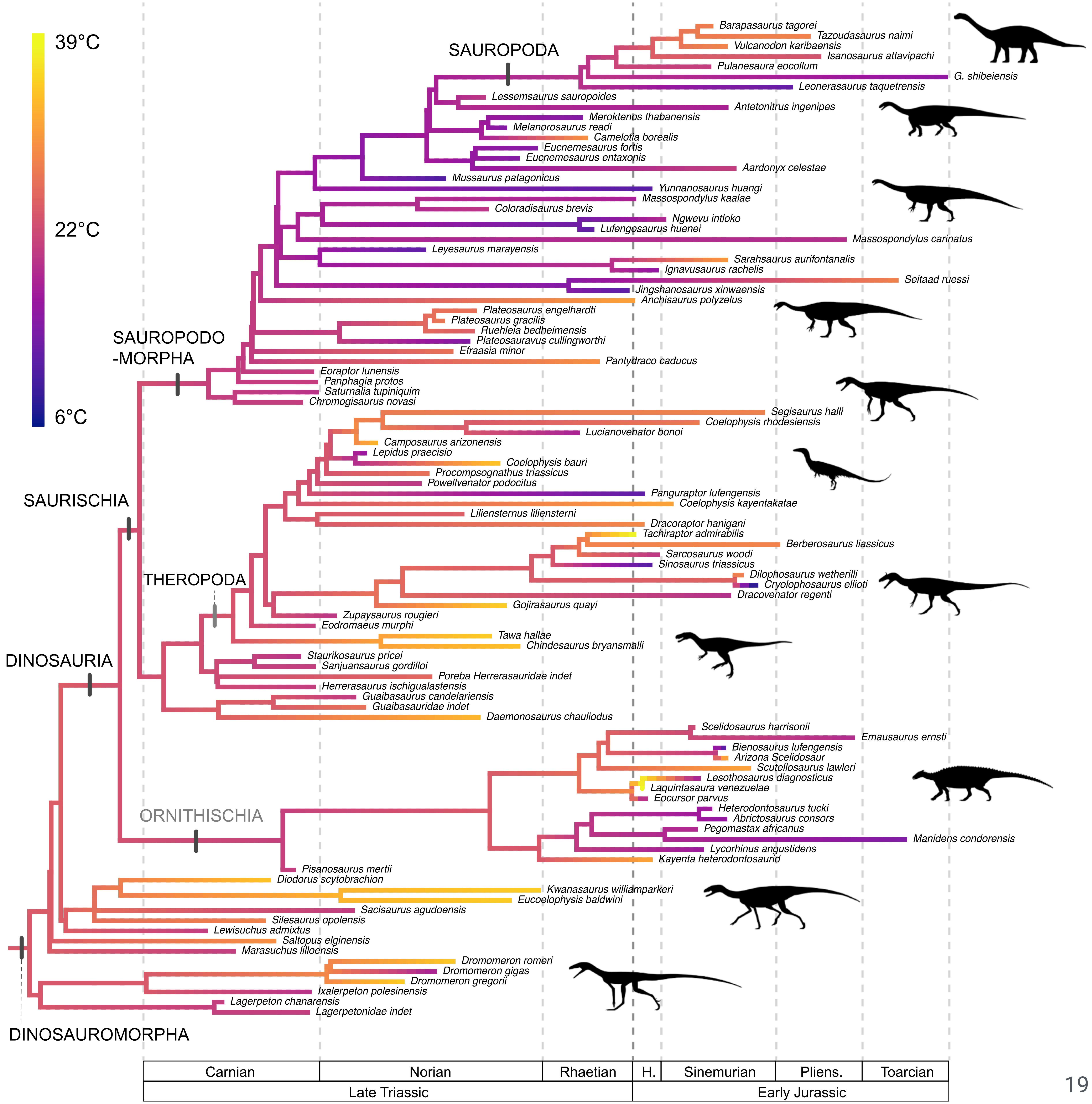
Slater et al. (2017)

Example: niche evolution in sauropodomorphs

Traits are climate variables

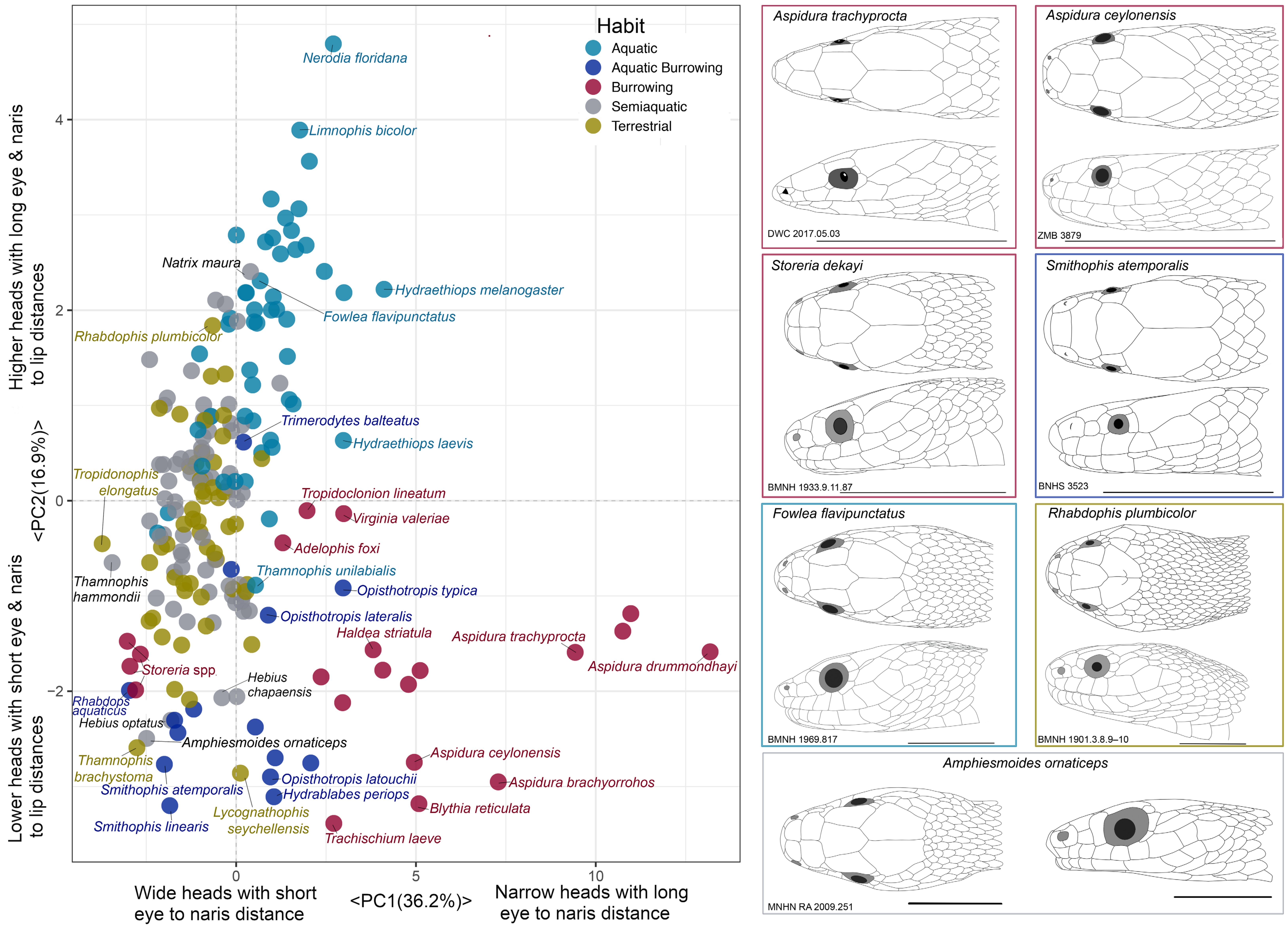
Shifts to warmer niches early on

Provides evidence that climate influence evolution of the group



Dunne et al. (2023)

Exercise



Natricine snakes
Exercise by Nathalie Cooper
Data from *Deepak et al.* (2022)

Further resources

Natalie Cooper has a comprehensive online book + accompanying exercises

Luke Harmon also has an excellent online book

Emma Dunne has a nice tutorial about frog eyes (phylogenetic signal, PGLS, continuous trait models, model selection)

Laura Soul has a nice tutorial about feeding ecology in crinoids (PGLS, continuous trait models, discrete models, model selection, model adequacy)

Graham Slater's phyloseminar (paleo-inspired models) ▶