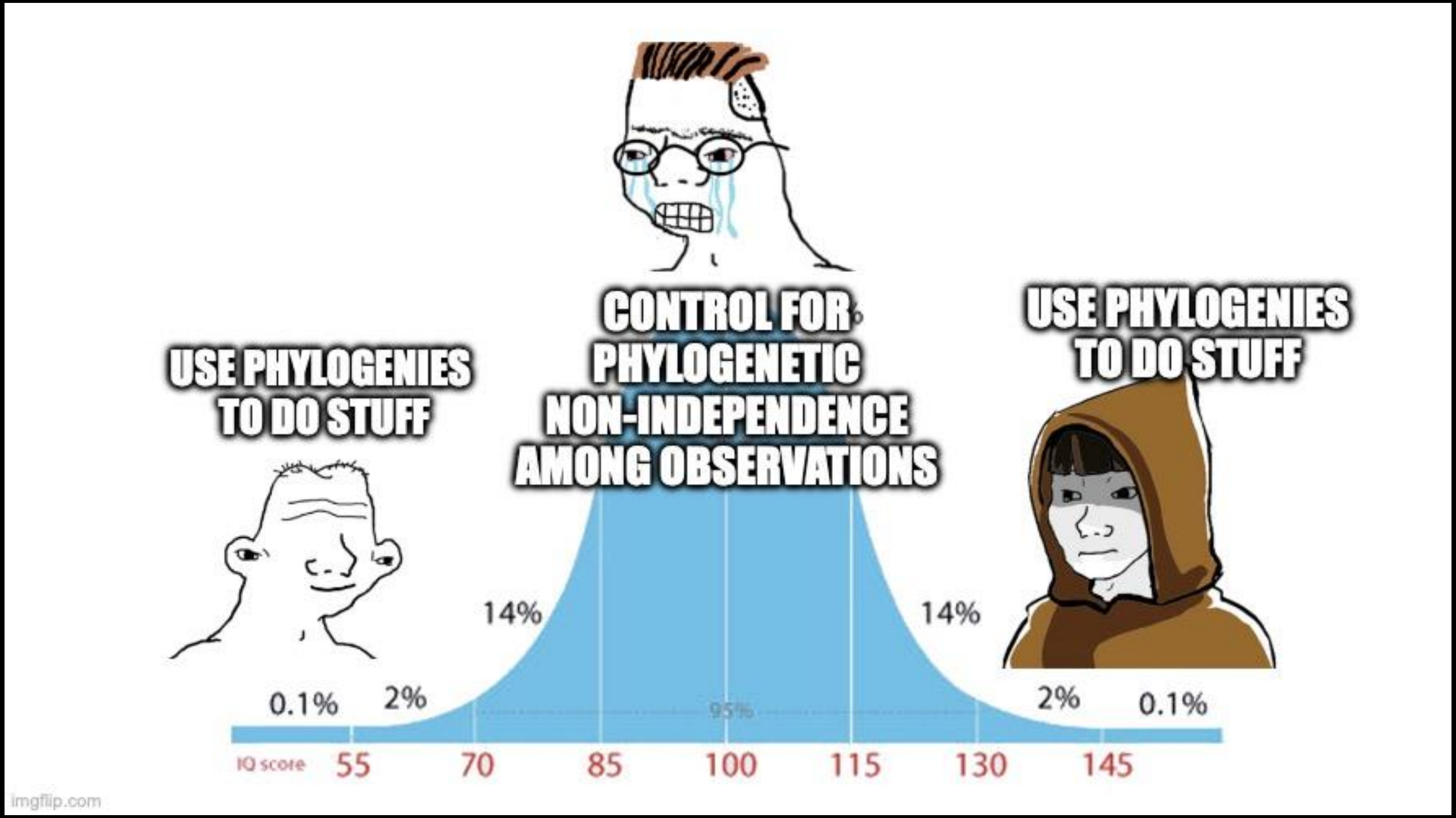
BEST PRACTICES IN PHYLOGENETIC COMPARATIVE ANALYSES

EQGW 2025

PHYLOGENETIC COMPARATIVE METHODS



interpretation

Models

“Estimated data”
(phylogenies)

Data

interpretation

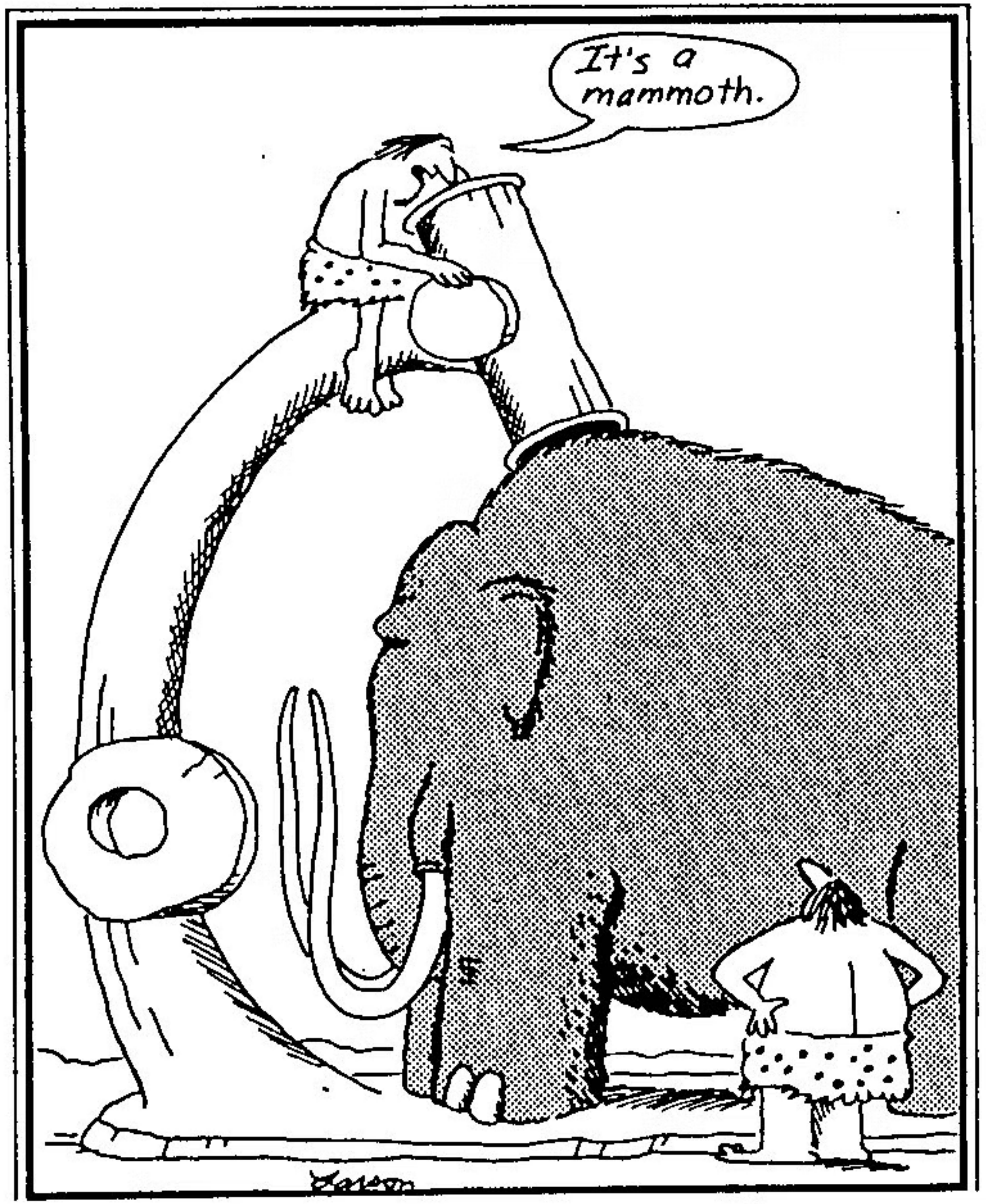
Models inadequacy

"Estimated data" (phylogenies) error/ inadequacy

Data error

MEASUREMENT ERROR

Measurement errors are not perfect (and sometimes we screw up)



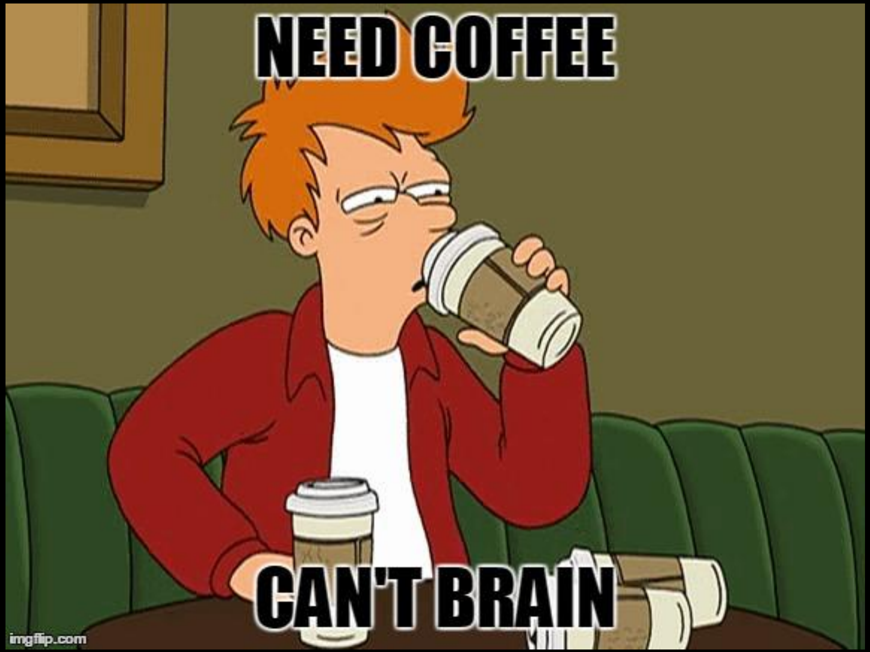
Early microscope

MEASUREMENT ERROR

Multiple sources:
    Equipment error/imprecision

MEASUREMENT ERROR

Multiple sources:
- Equipment error/imprecision
- Interobserver error



MEASUREMENT ERROR

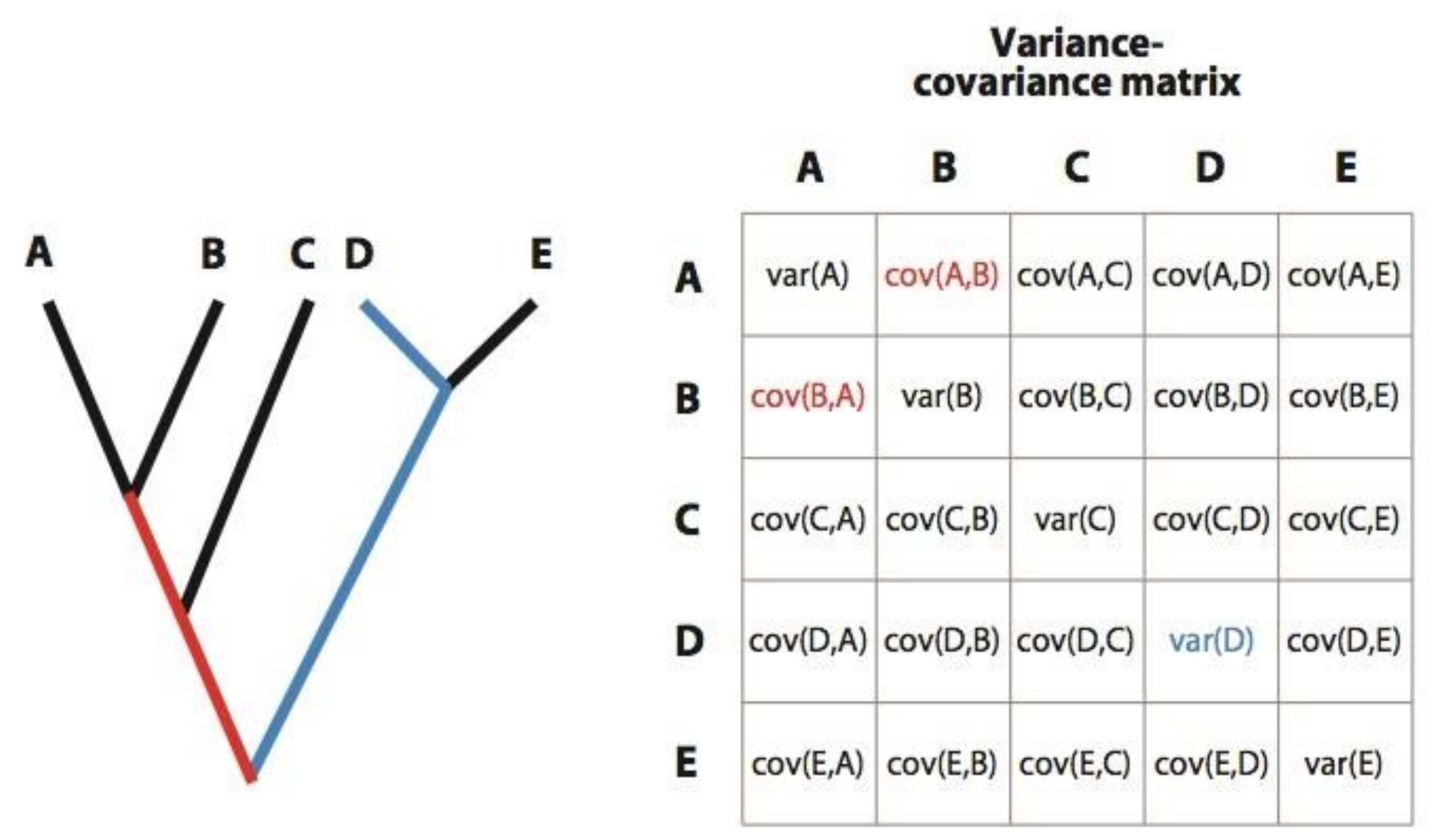
Multiple sources:
  - Equipment error/imprecision
  - Interobserver error
  - Interobserver error

MEASUREMENT ERROR

Multiple sources:

- Equipment error/imprecision
- Interobserver error
- Interobserver error
- Intraindividual- behavior/physiology
- Blocks – treatments
- …
- etc

Why would it matter in PCM?

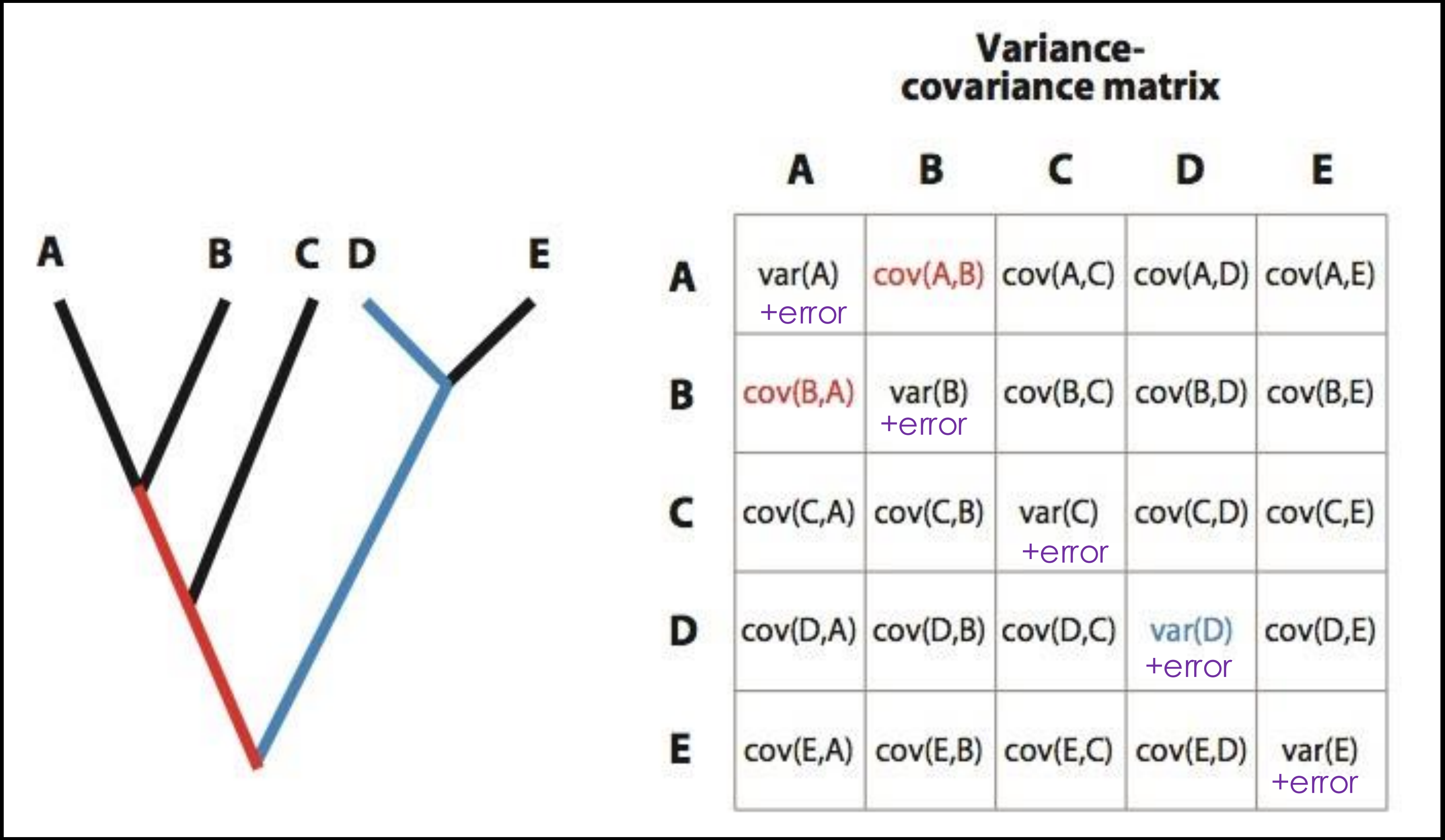


Variance-covariance matrix

	A	B	C	D	E
A	var(A)	cov(A,B)	cov(A,C)	cov(A,D)	cov(A,E)
B	cov(B,A)	var(B)	cov(B,C)	cov(B,D)	cov(B,E)
C	cov(C,A)	cov(C,B)	var(C)	cov(C,D)	cov(C,E)
D	cov(D,A)	cov(D,B)	cov(D,C)	var(D)	cov(D,E)
E	cov(E,A)	cov(E,B)	cov(E,C)	cov(E,D)	var(E)

If we have error, this is imprecise

O’Meara 2012

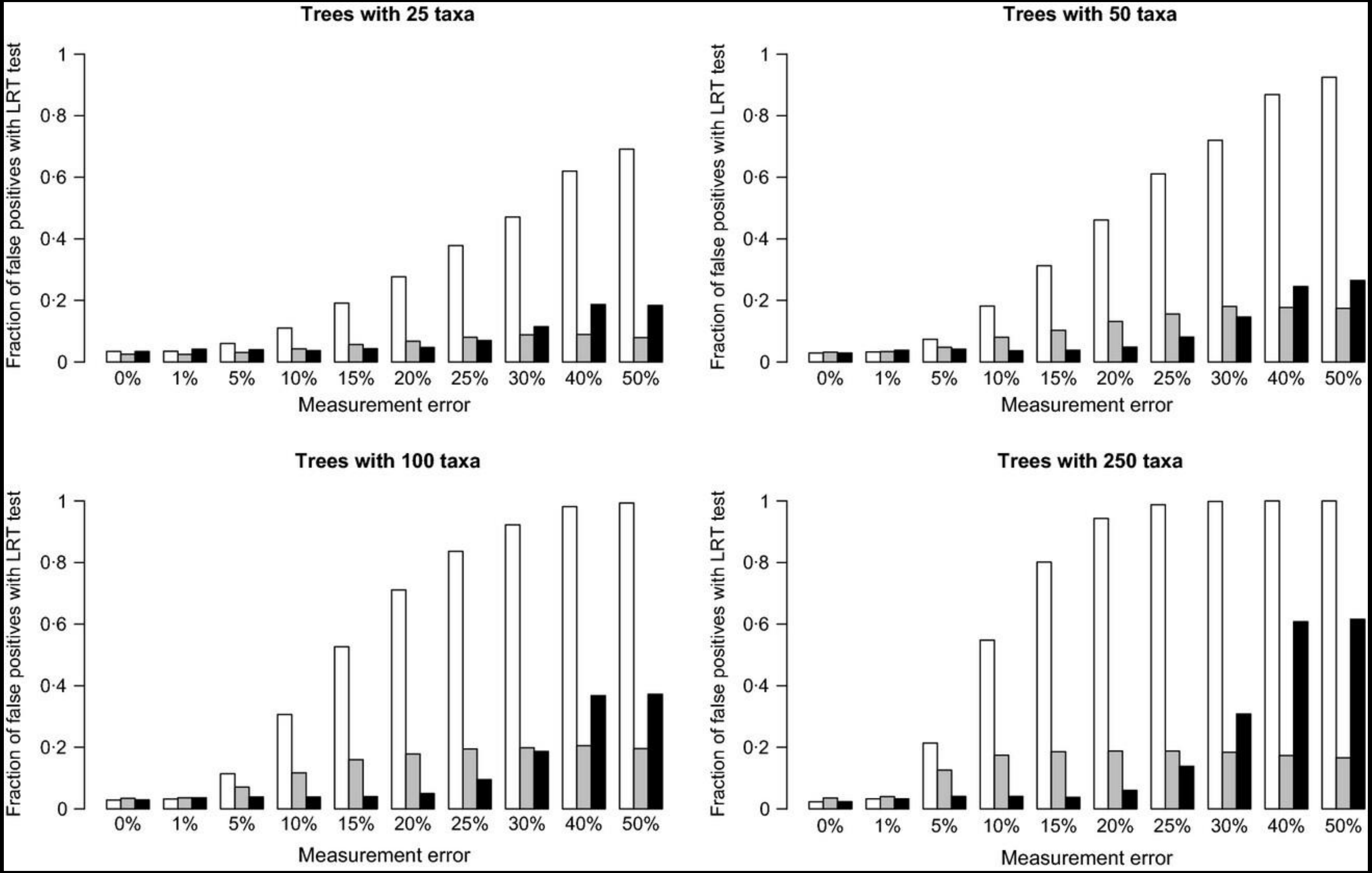


Variance-covariance matrix

	A	B	C	D	E
A	var(A) +error	cov(A,B)	cov(A,C)	cov(A,D)	cov(A,E)
B	cov(B,A)	var(B) +error	cov(B,C)	cov(B,D)	cov(B,E)
C	cov(C,A)	cov(C,B)	var(C) +error	cov(C,D)	cov(C,E)
D	cov(D,A)	cov(D,B)	cov(D,C)	var(D) +error	cov(D,E)
E	cov(E,A)	cov(E,B)	cov(E,C)	cov(E,D)	var(E) +error

Does in matter in reality?

O'Meara 2012



White- ME ignored; Gray- ME estimated; Black- ME known

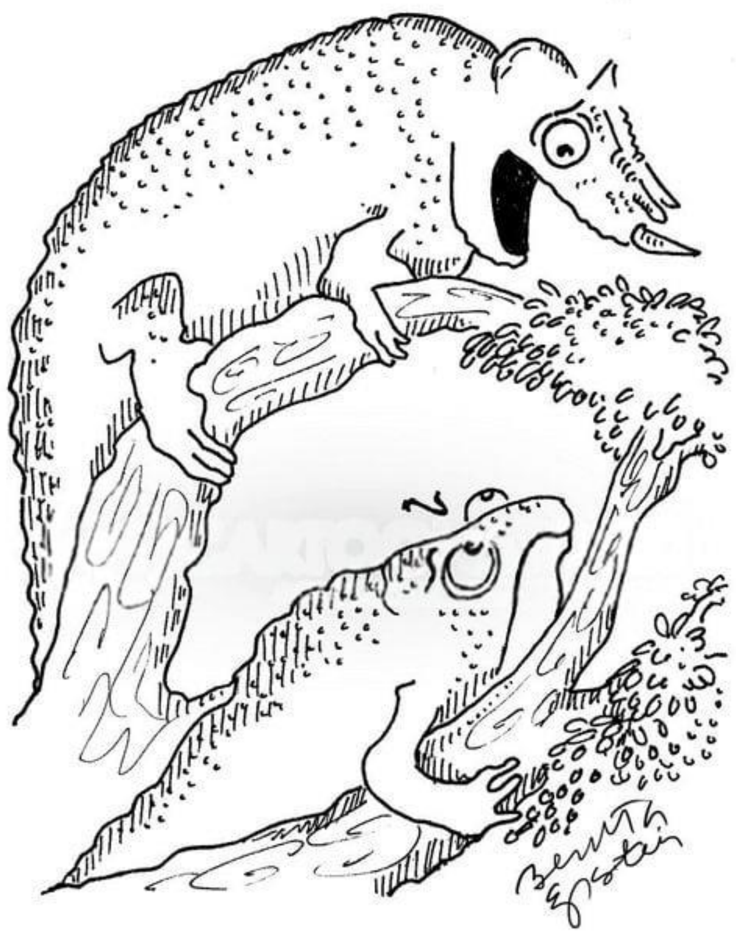
Silvestro et al 2015

LESSONS

Always account for measurement error

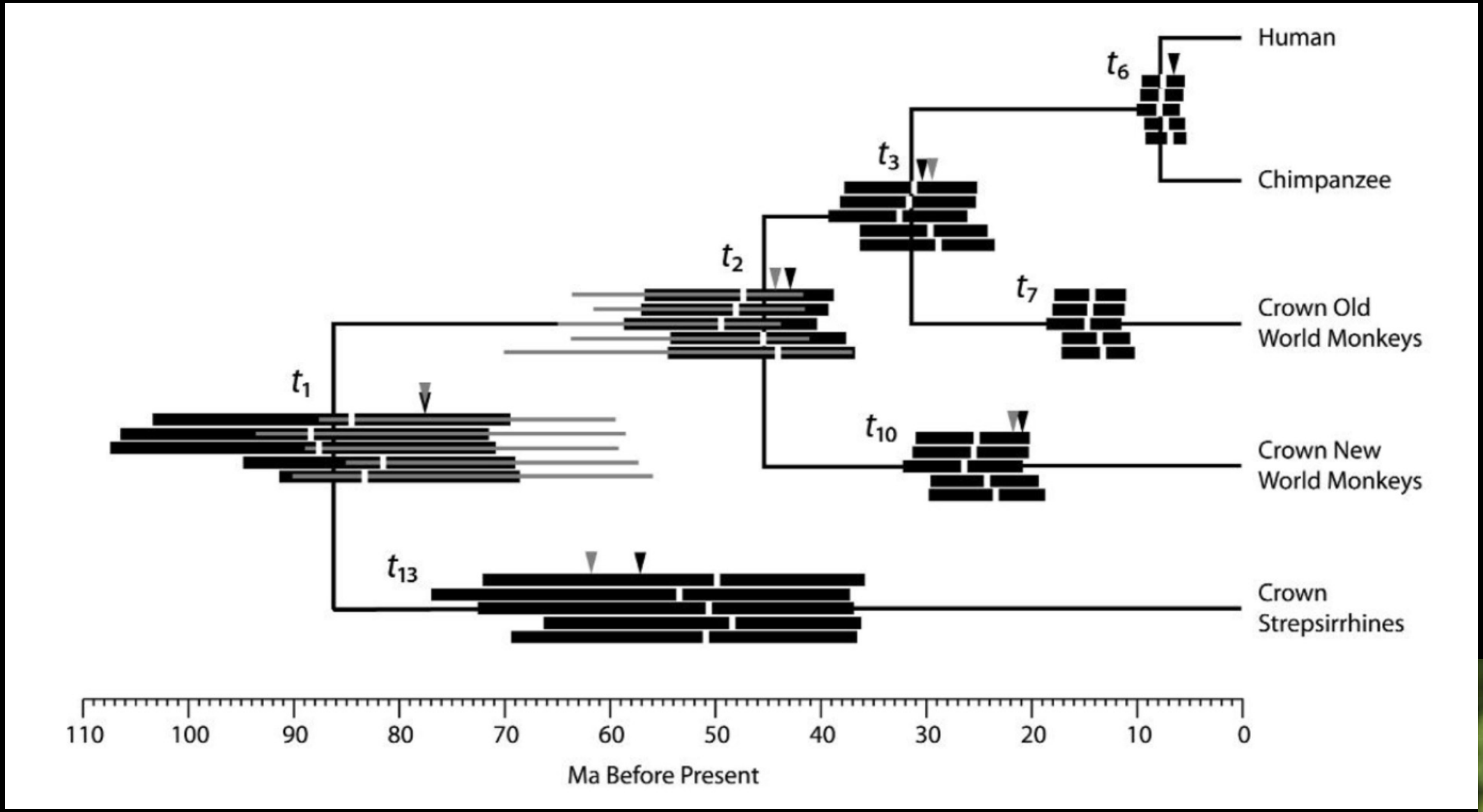
PHYLOGENETIC UNCERTAINTY

Phylogenies are estimated, and therefore have errors and uncertainties



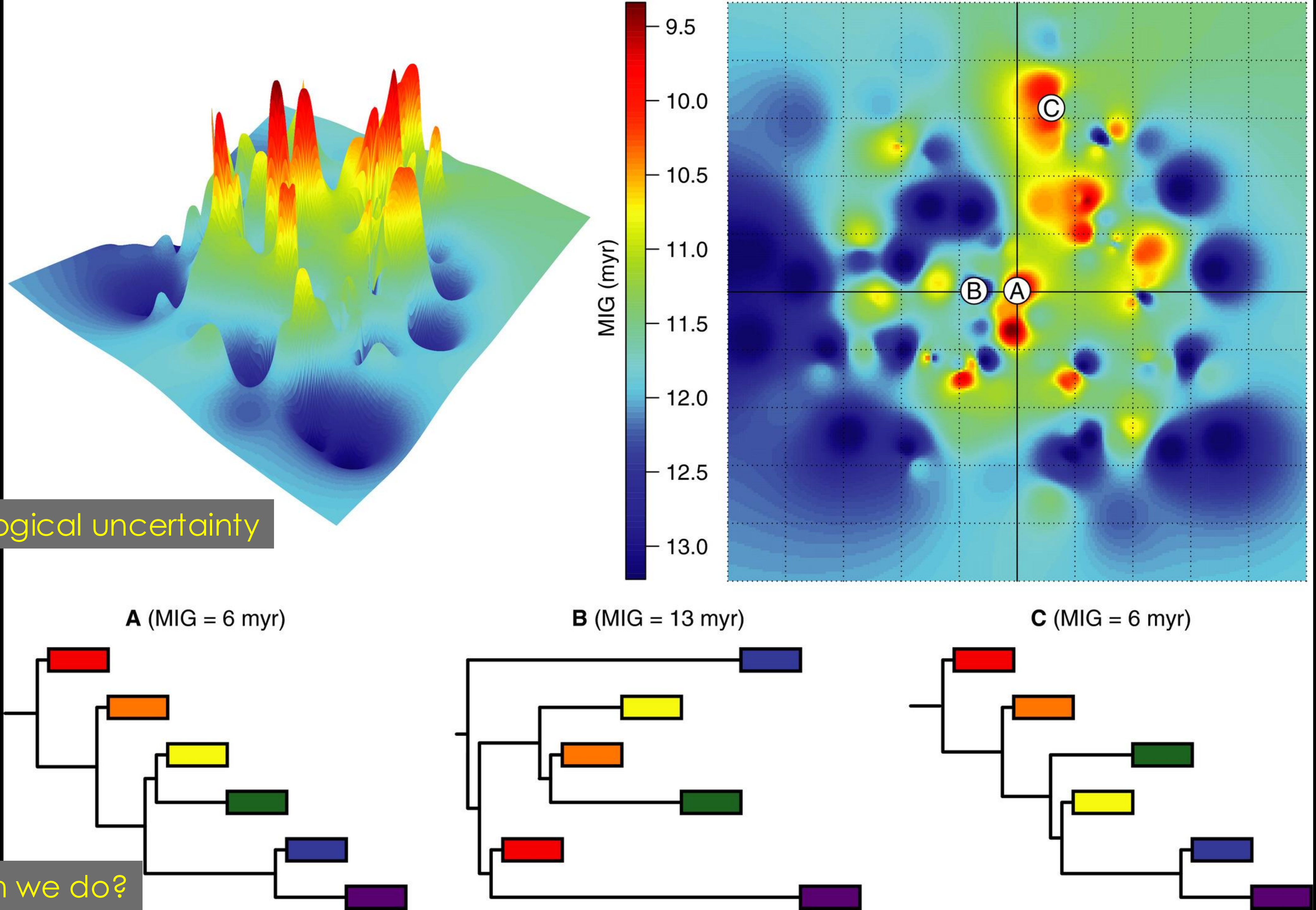
“What phylogenetic relationship? That was a million years ago.”

PHYLOGENETIC UNCERTAINTY



Age uncertainty

Wilkinson et al. 2011

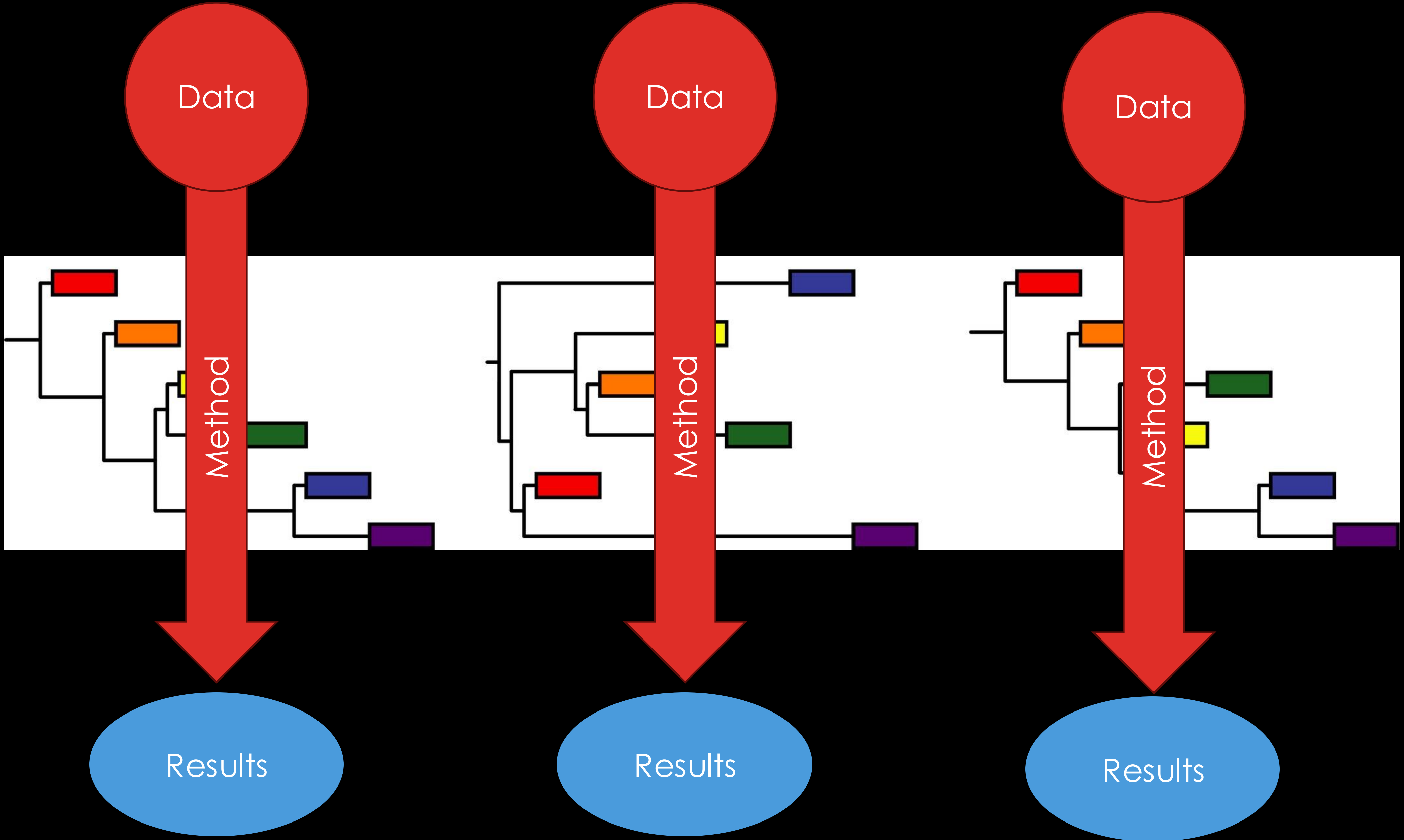


Topological uncertainty

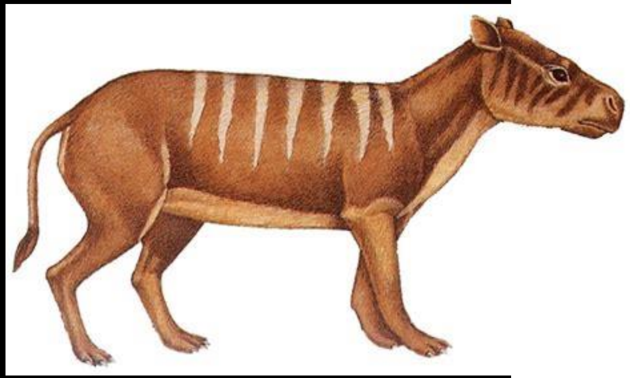
What can we do?

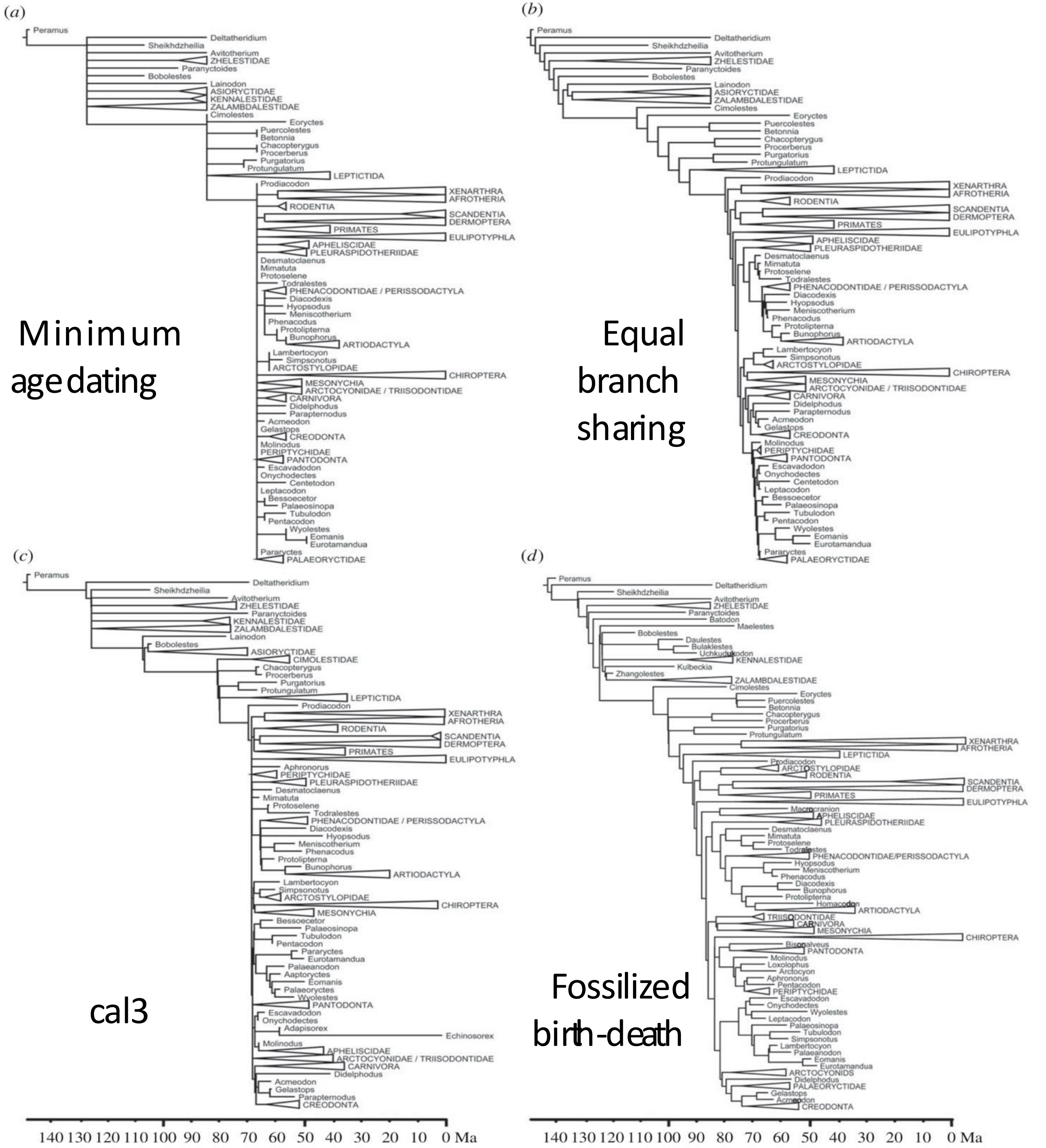
Wright & Loyd, 2020

Rerun analysis with a bunch of trees!



Body mass evolution in fossil mammals





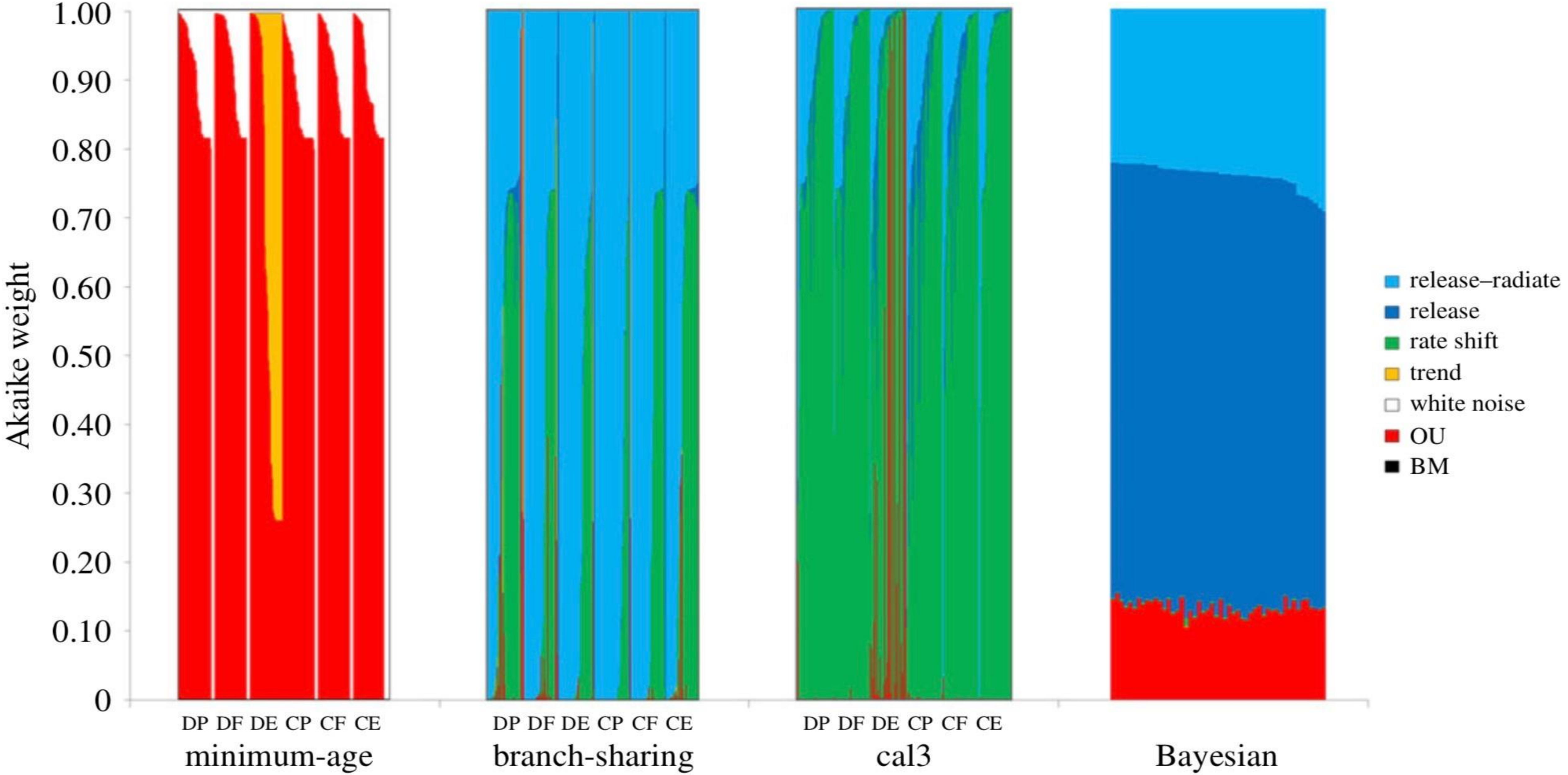
Minimum age dating

Equal branch sharing

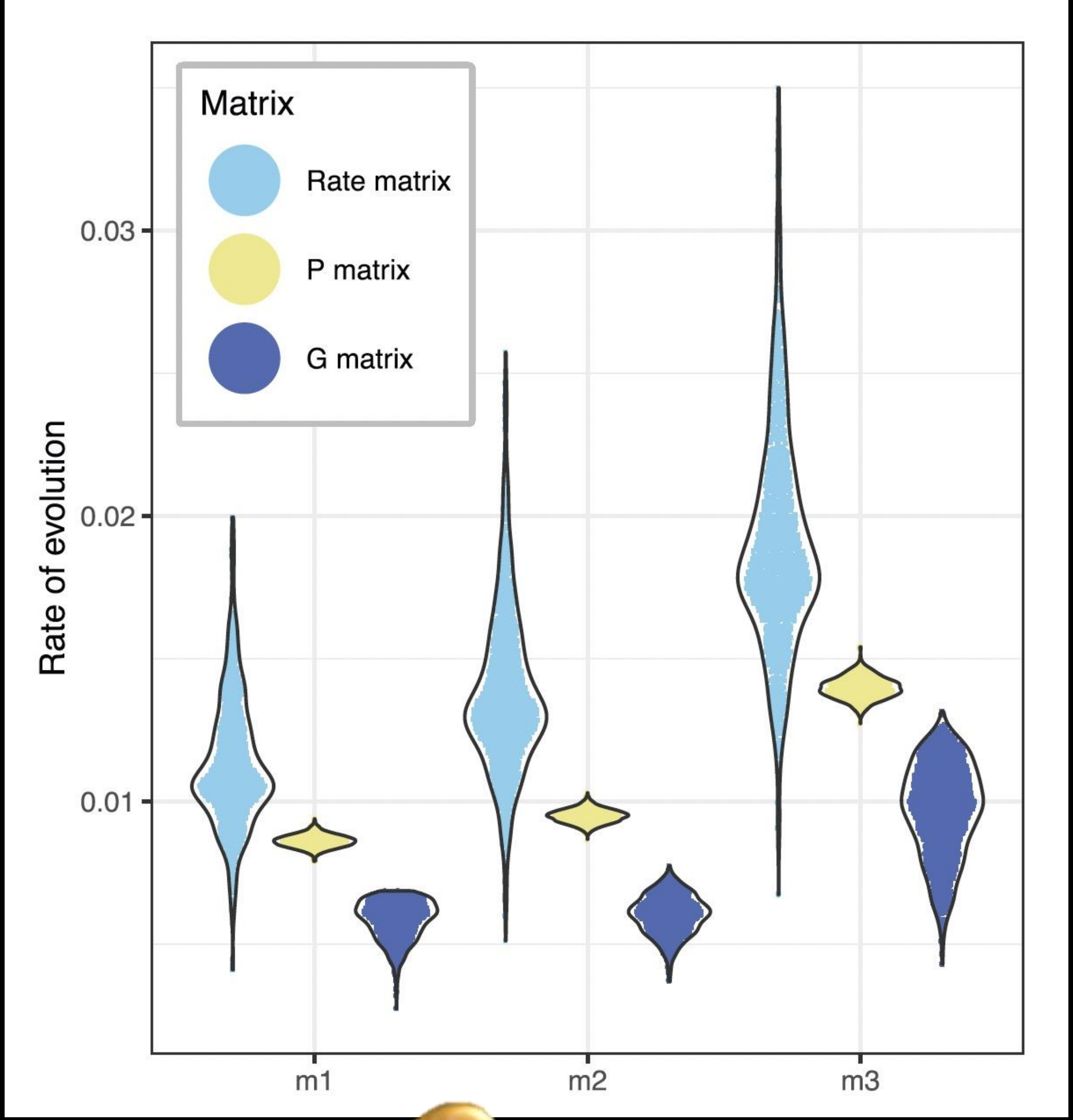
cal3

Fossilized birth-death

Halliday & Goswami 2016



Halliday & Goswami 2016



Mongle et al., 2022

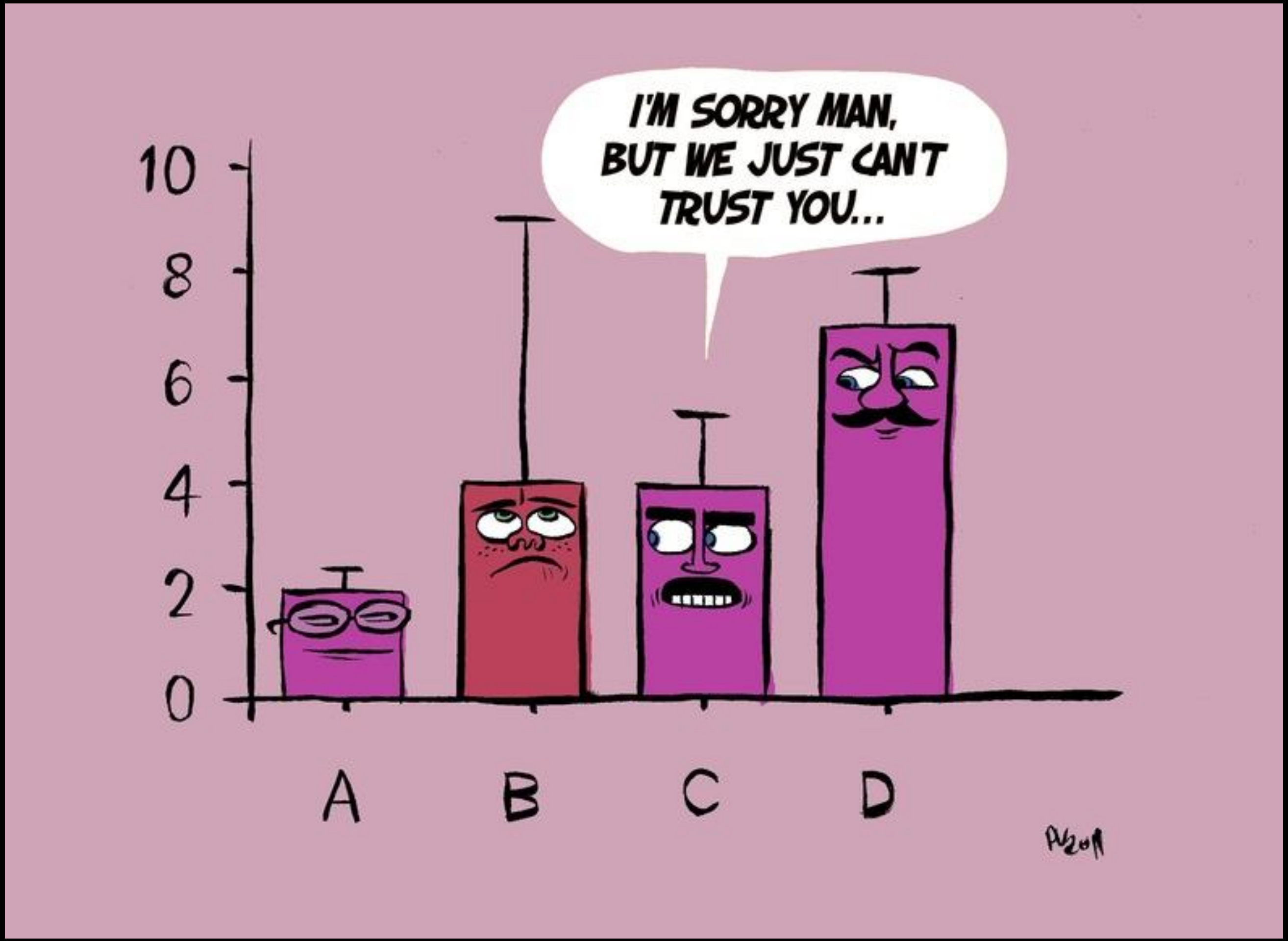
LESSONS

Always account for measurement error

Always account for phylogenetic uncertainty

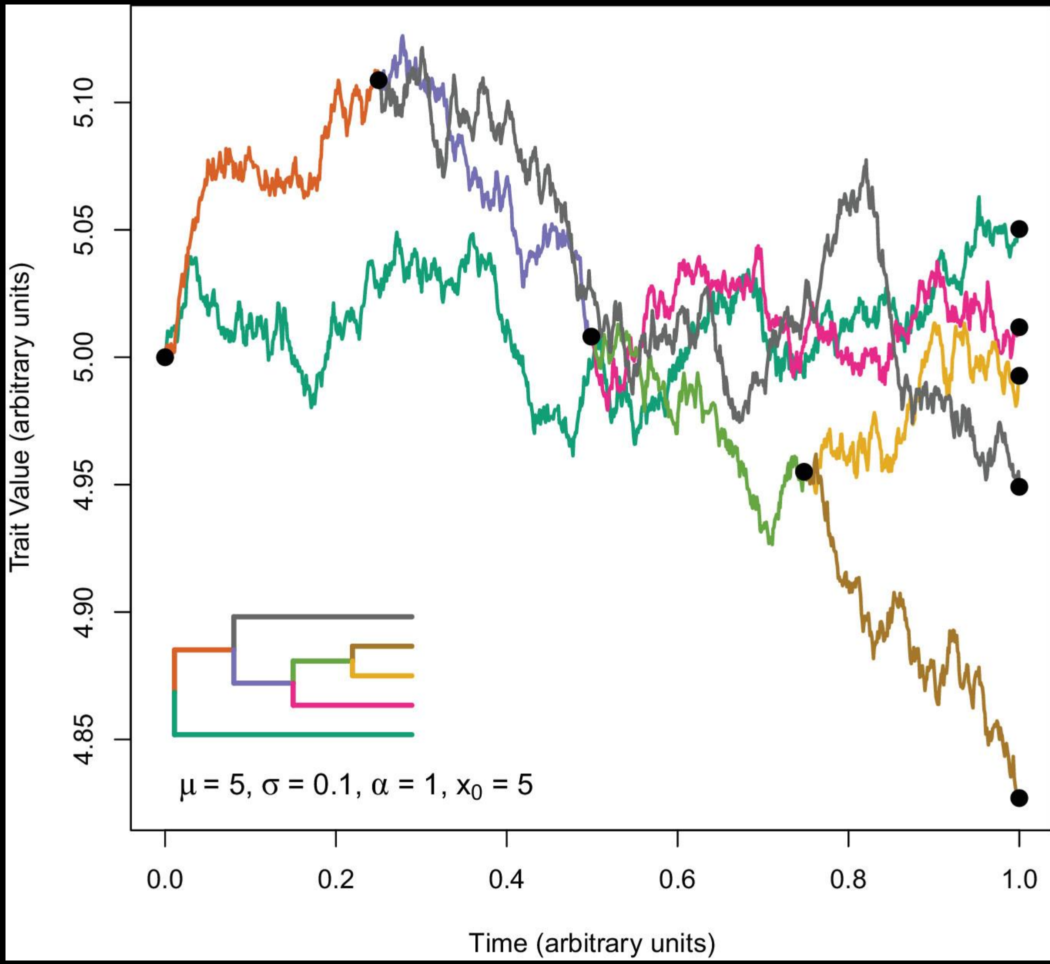
PARAMETER ESTIMATION ERROR

Model parameters are estimated with error



PARAMETER ESTIMATION

$$dy = -\alpha(y(t) - \theta(t))dt + \sigma dW$$



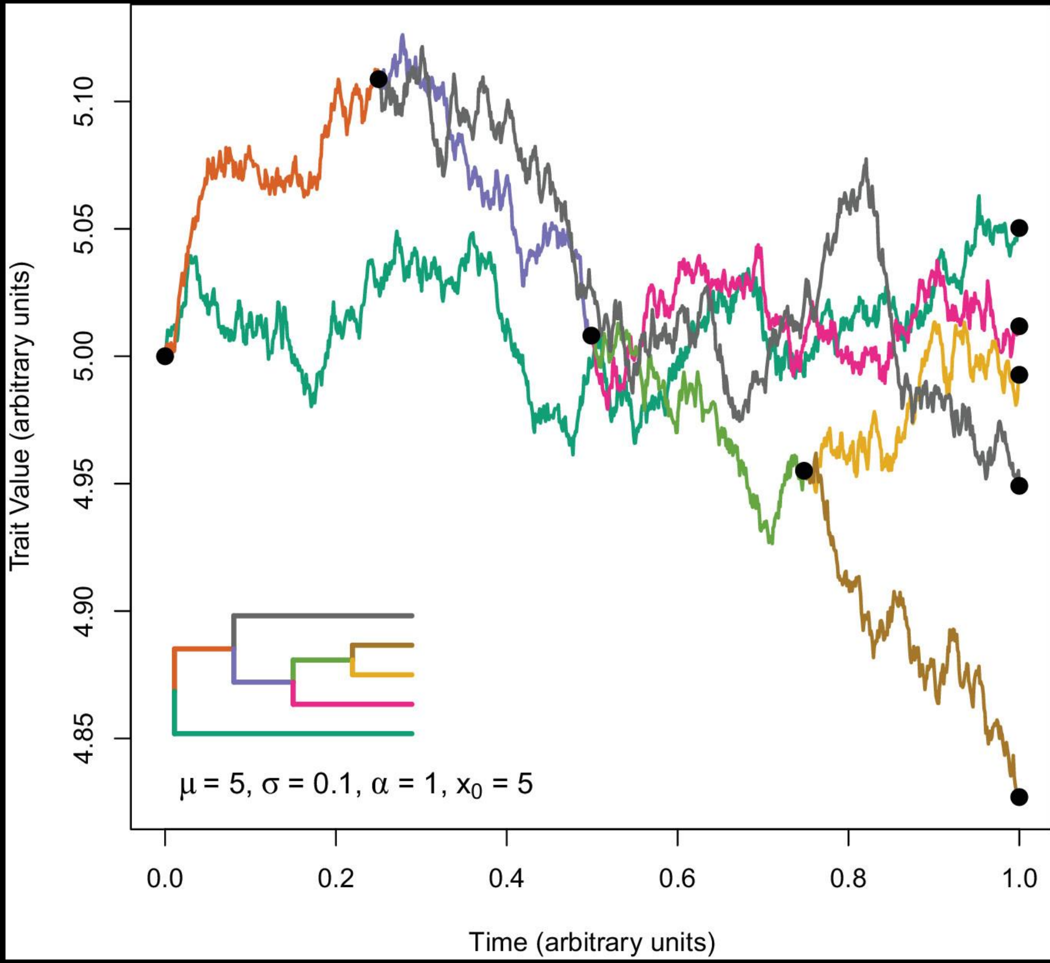
PARAMETER ESTIMATION

$$dy = -\alpha(y(t) - \theta(t))dt + \sigma dW$$

Rate of adaptation

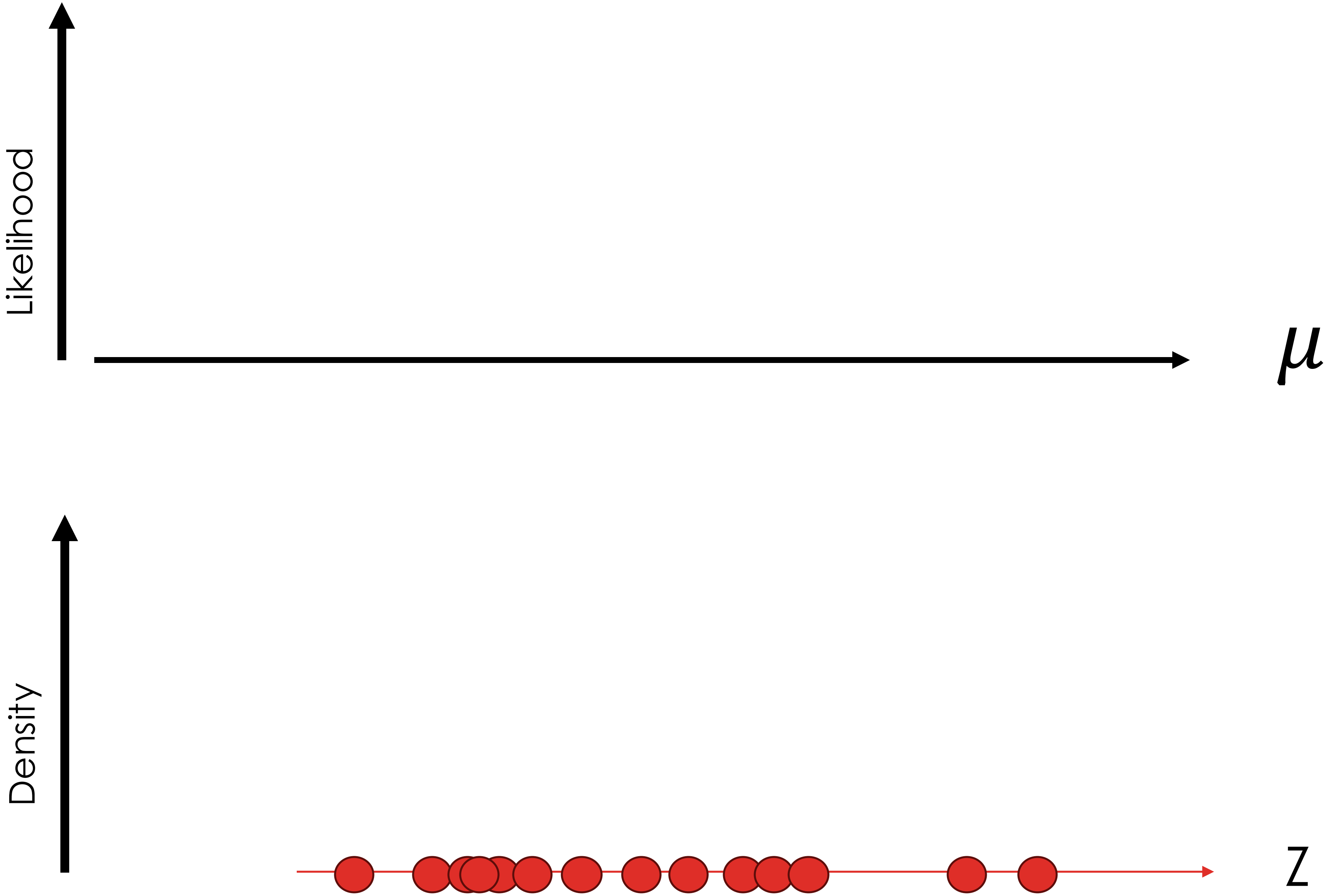
Primary optima

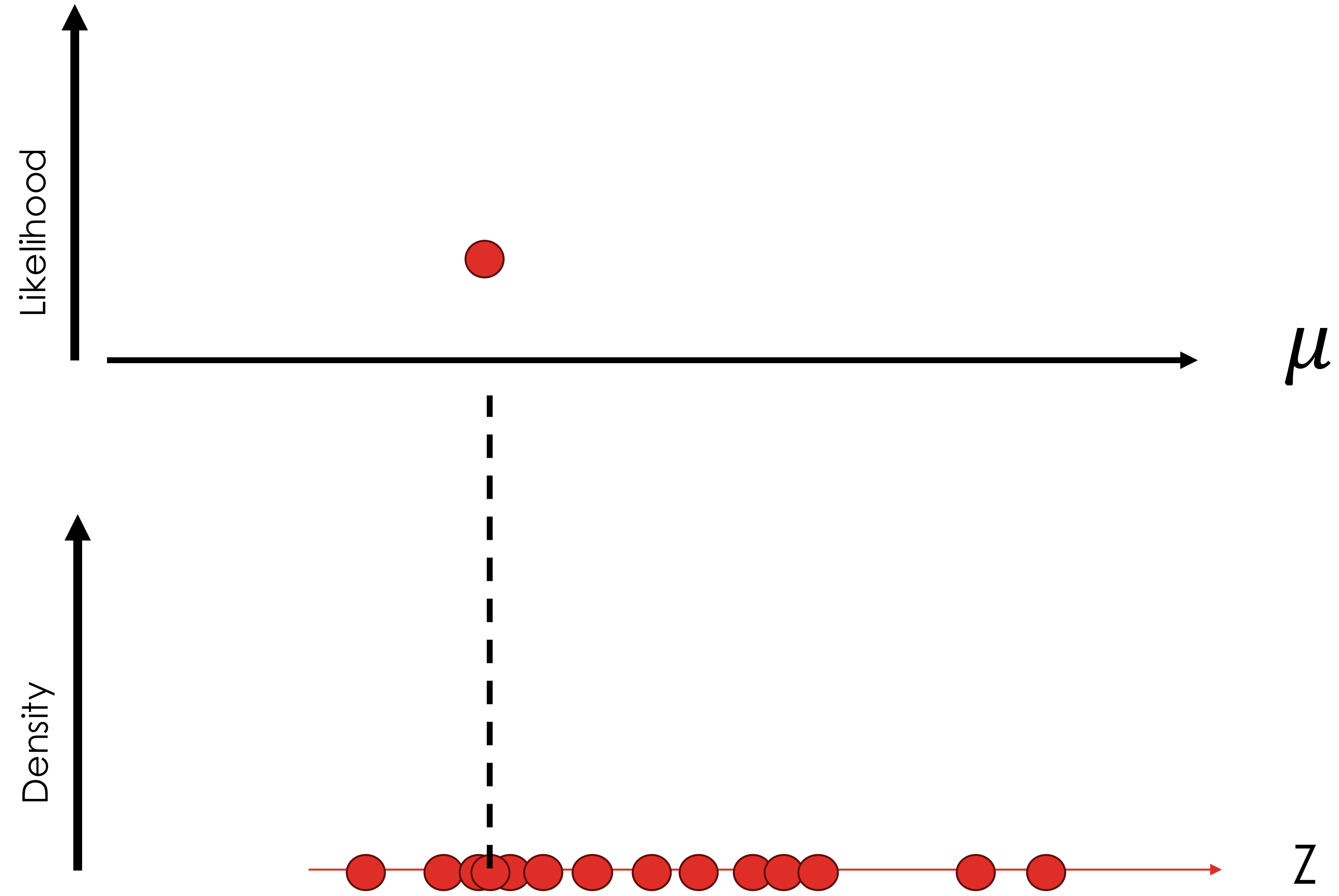
Rate of stochastic evolution

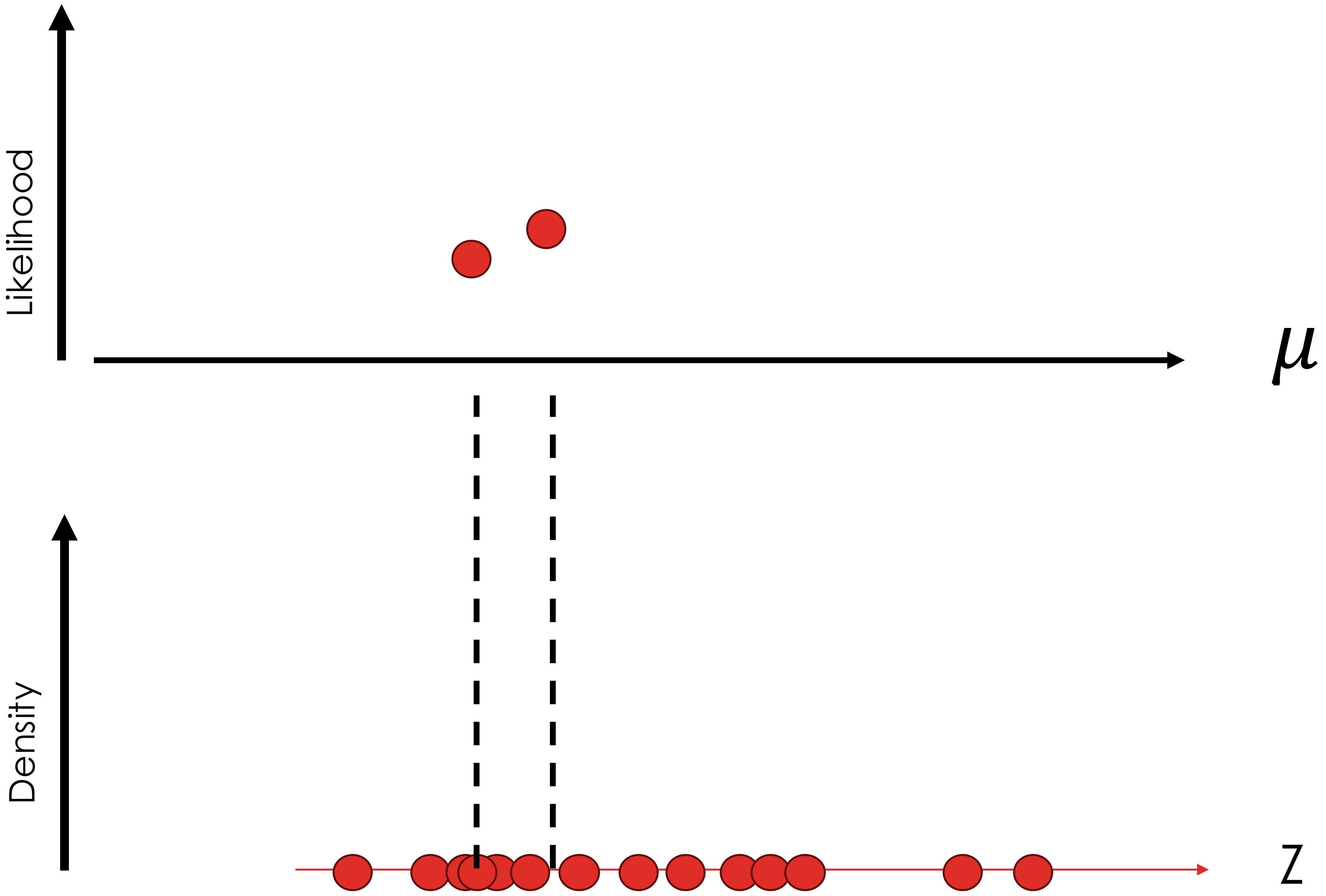


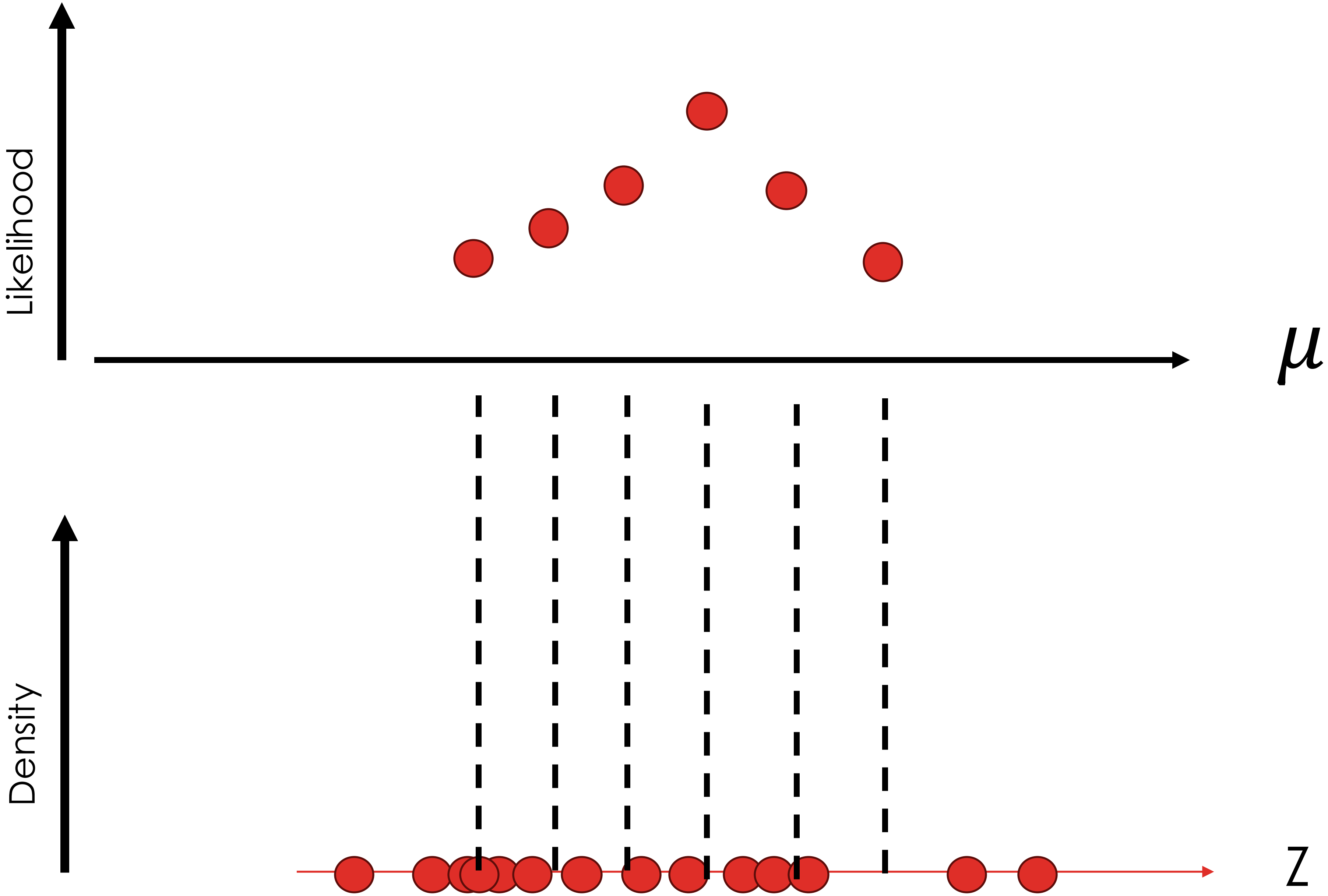
Evolutionary models have evolutionary parameters that must be estimated through data

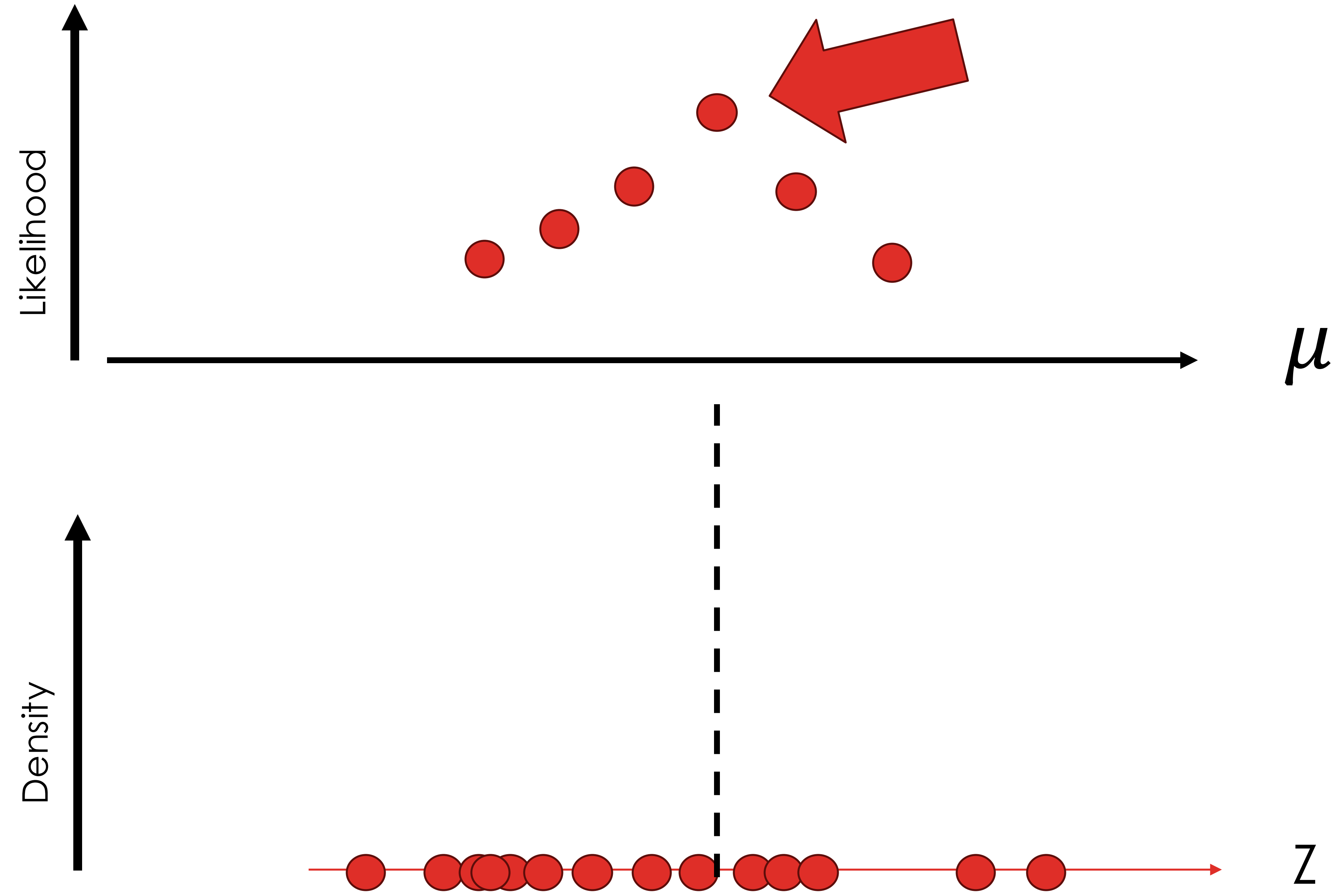
How is it done?

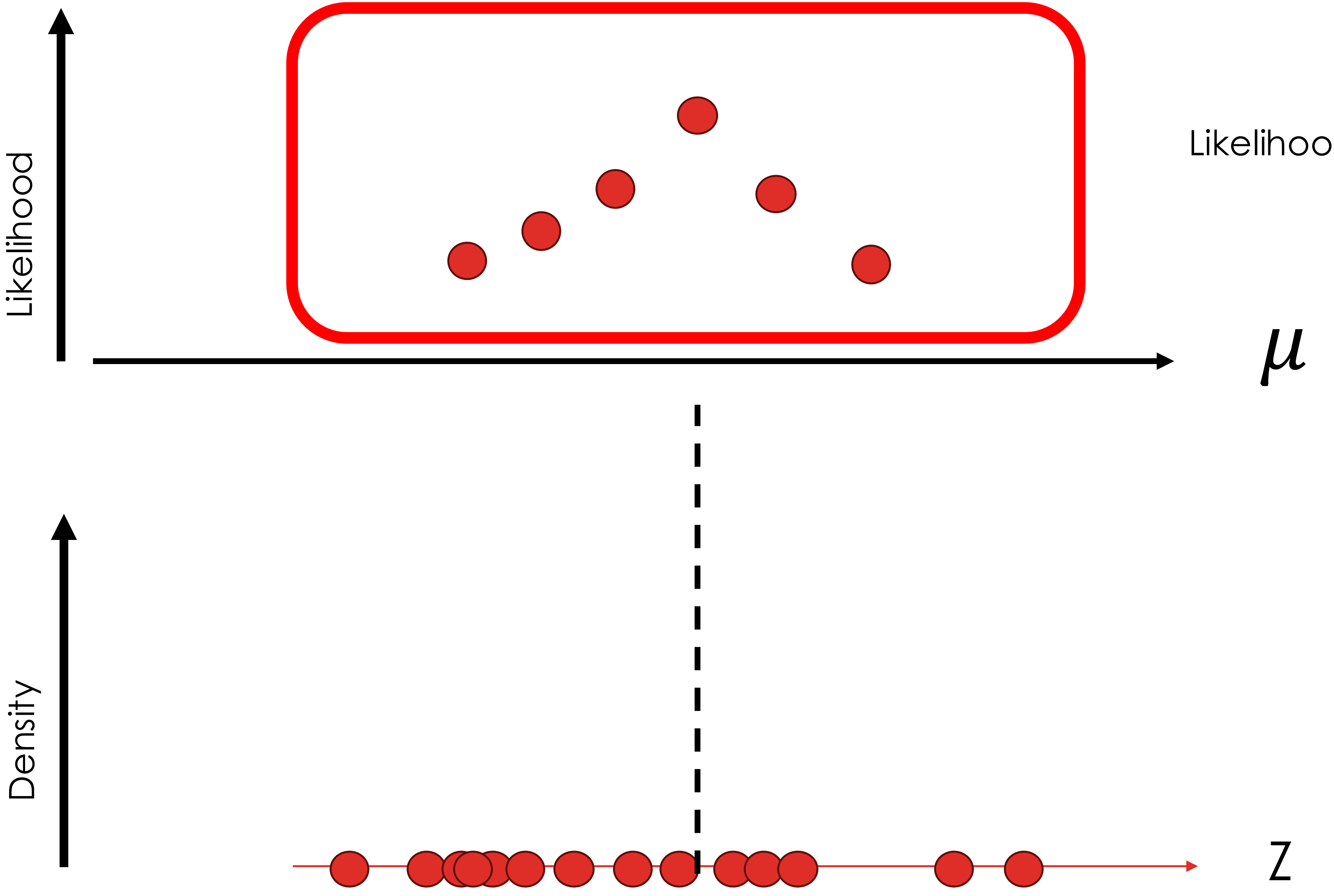

Likelihood
μ
Density
Z


Likelihood
μ
Density
Z

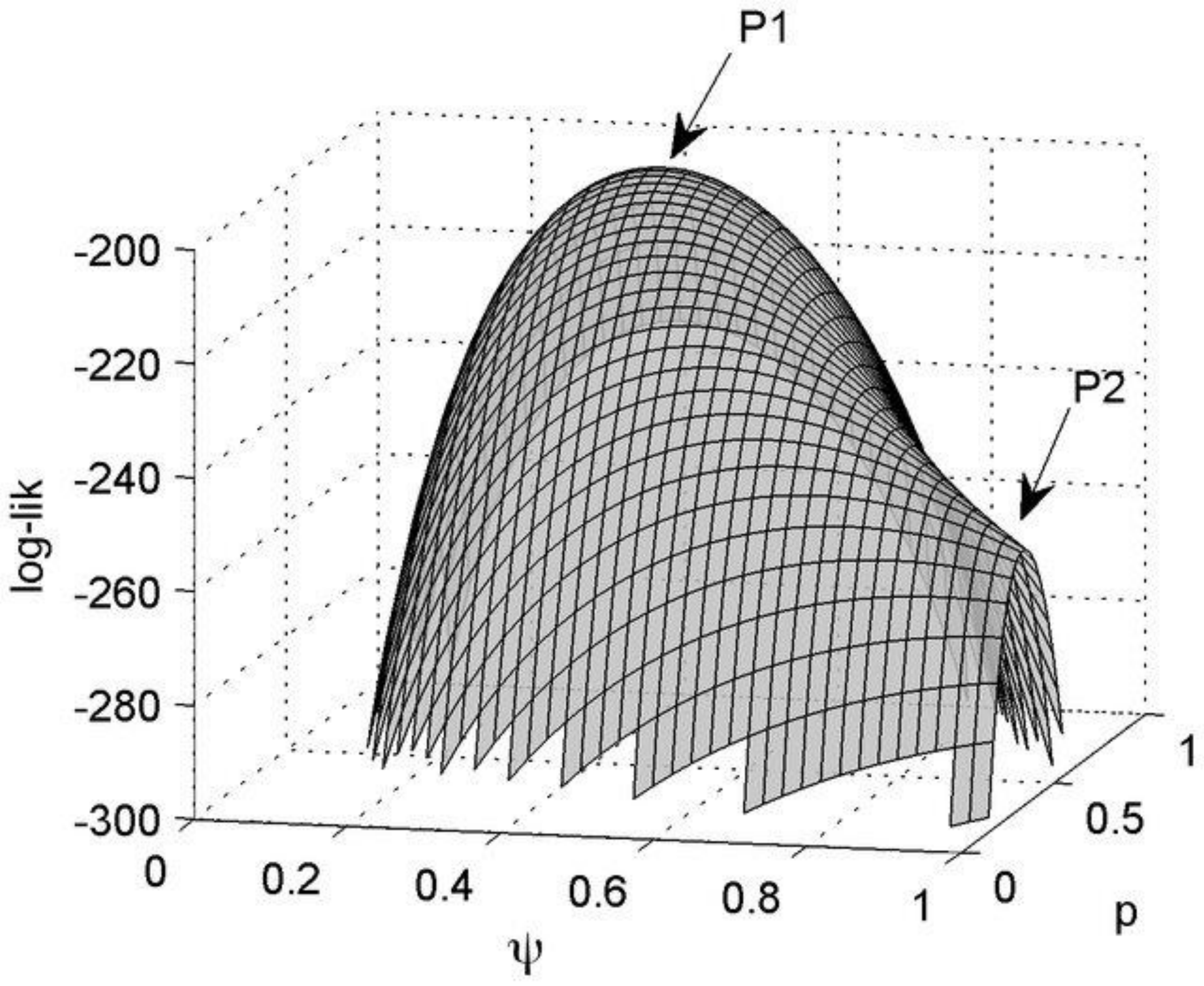

Likelihood
μ
Density
Z


Likelihood
μ
Density
Z

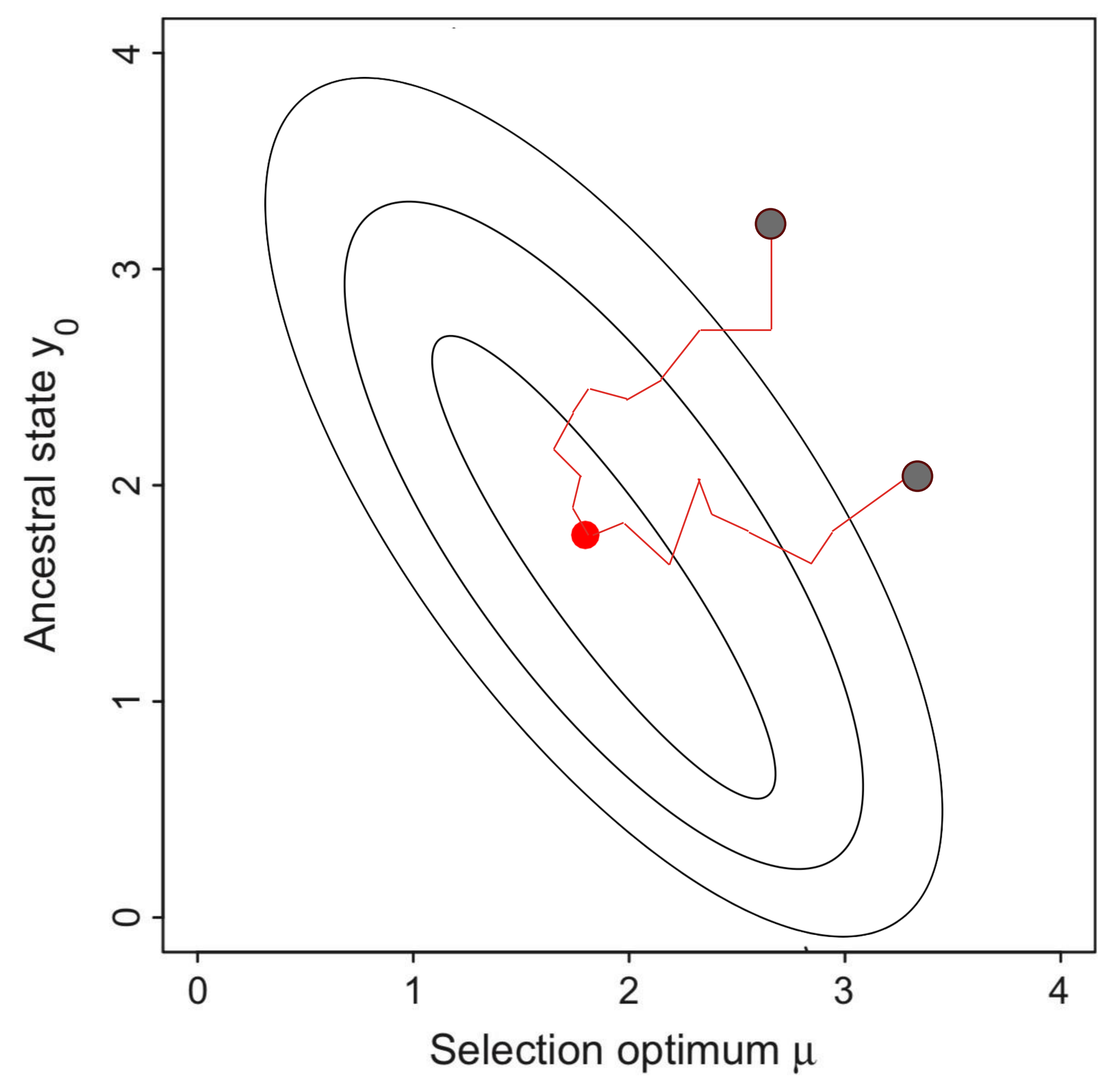

Likelihood
μ
Density
Z



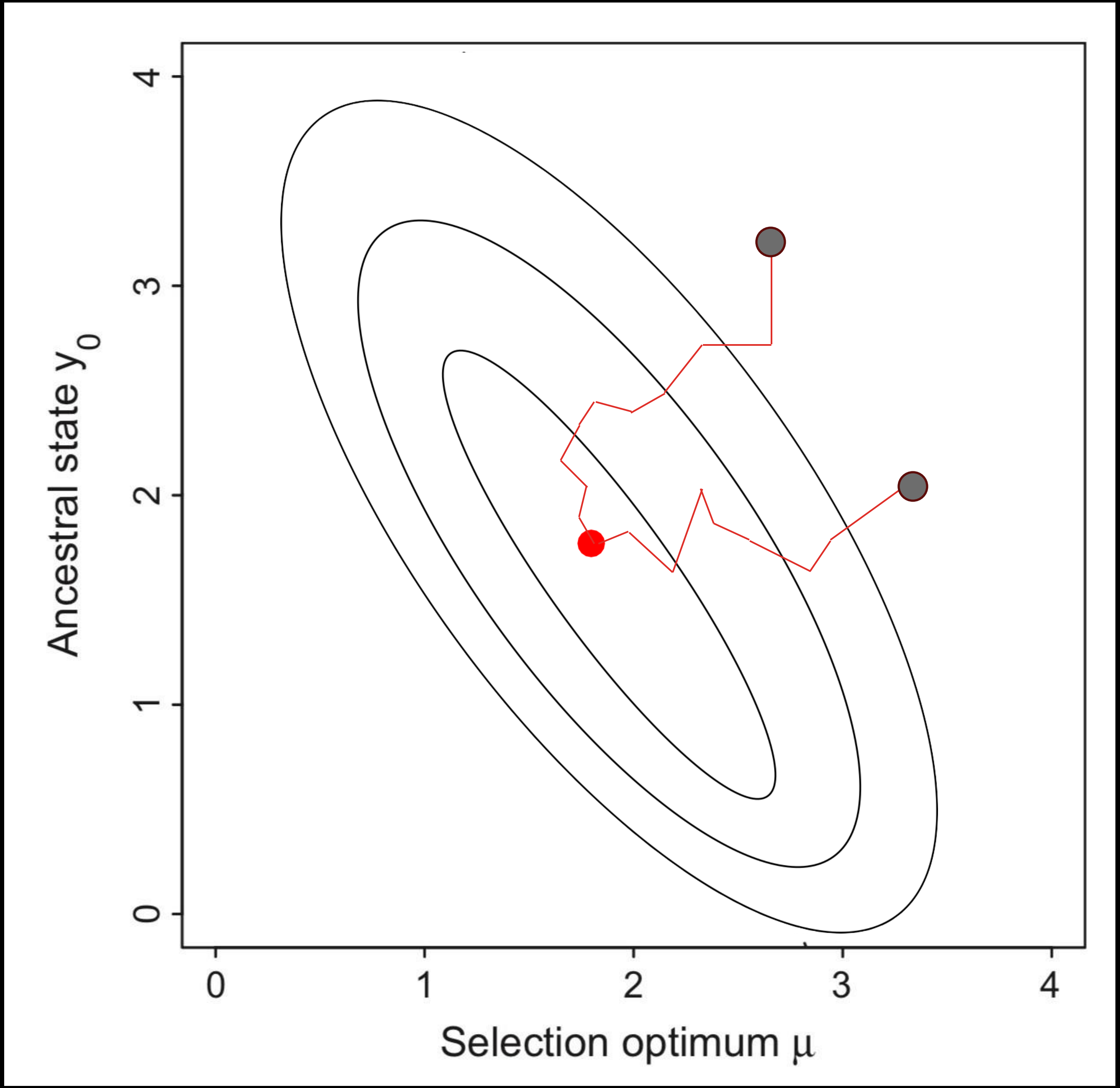
Likelihood surface



Parameter estimation is an optimization procedure on a likelihood surface

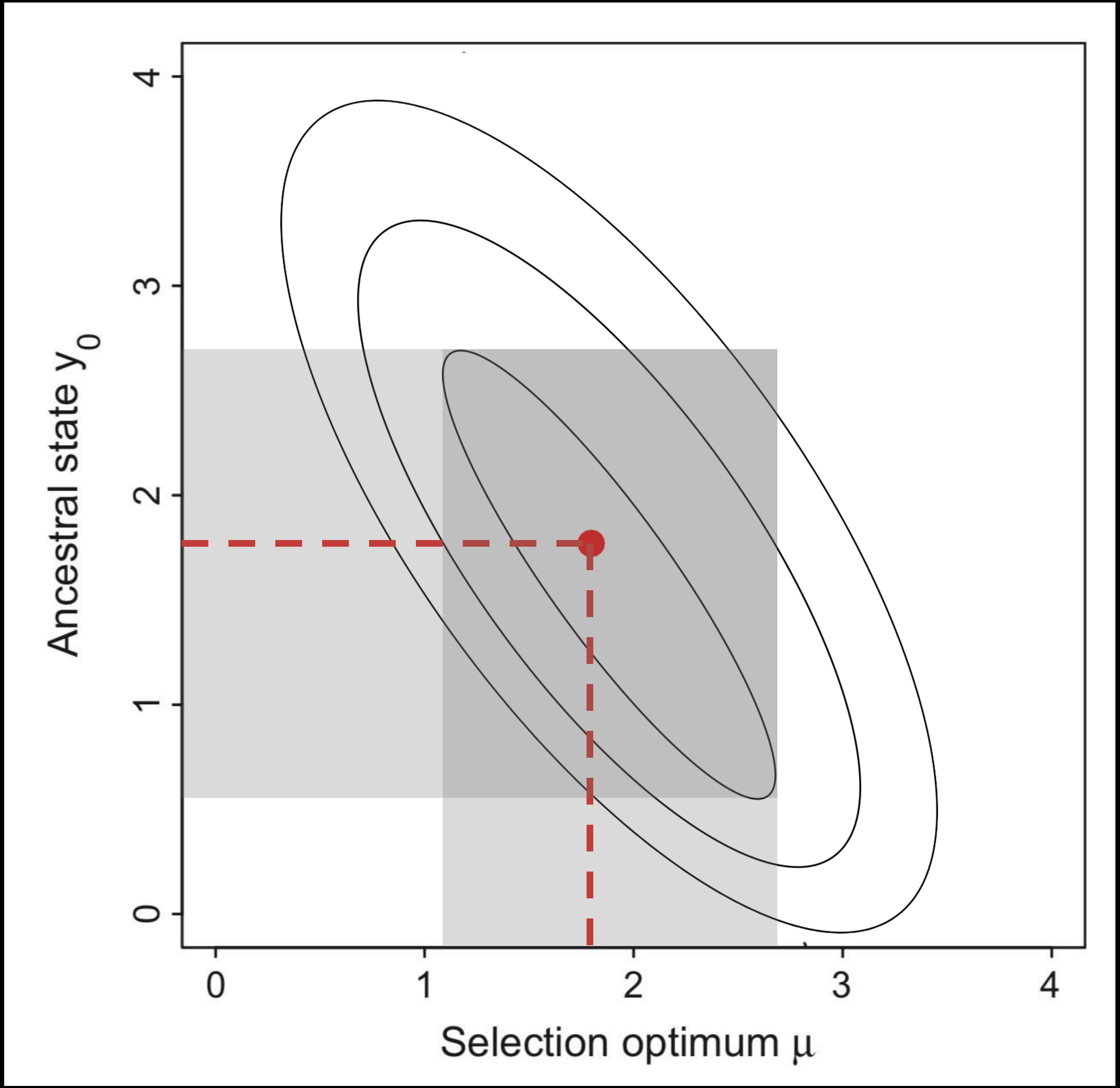


Parameter estimation is an optimization procedure on a likelihood surface



Sub-optimal likelihoods might also be considered "good enough", specifically 2 log-lik units away from the peak

Parameter estimation is an optimization procedure on a likelihood surface



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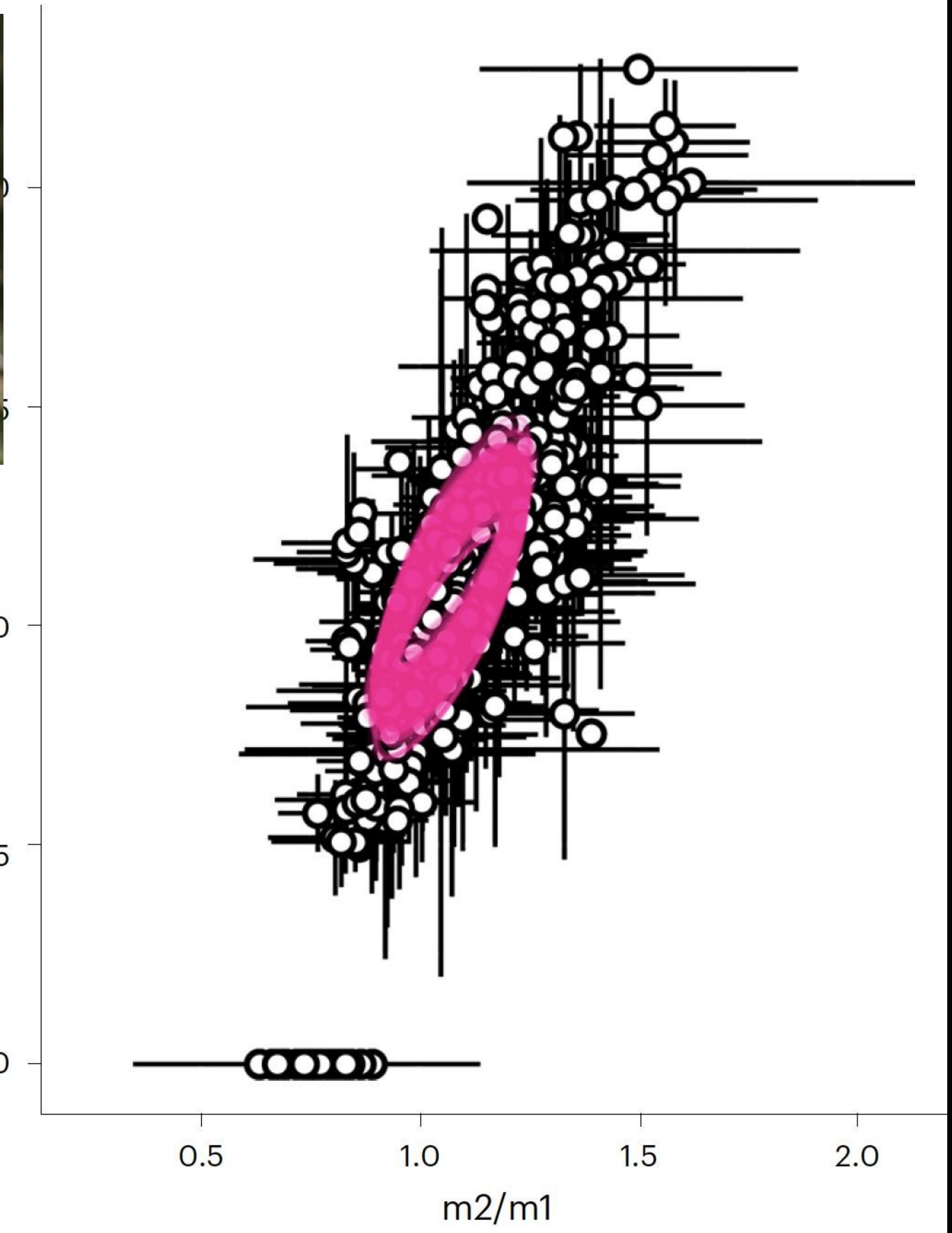
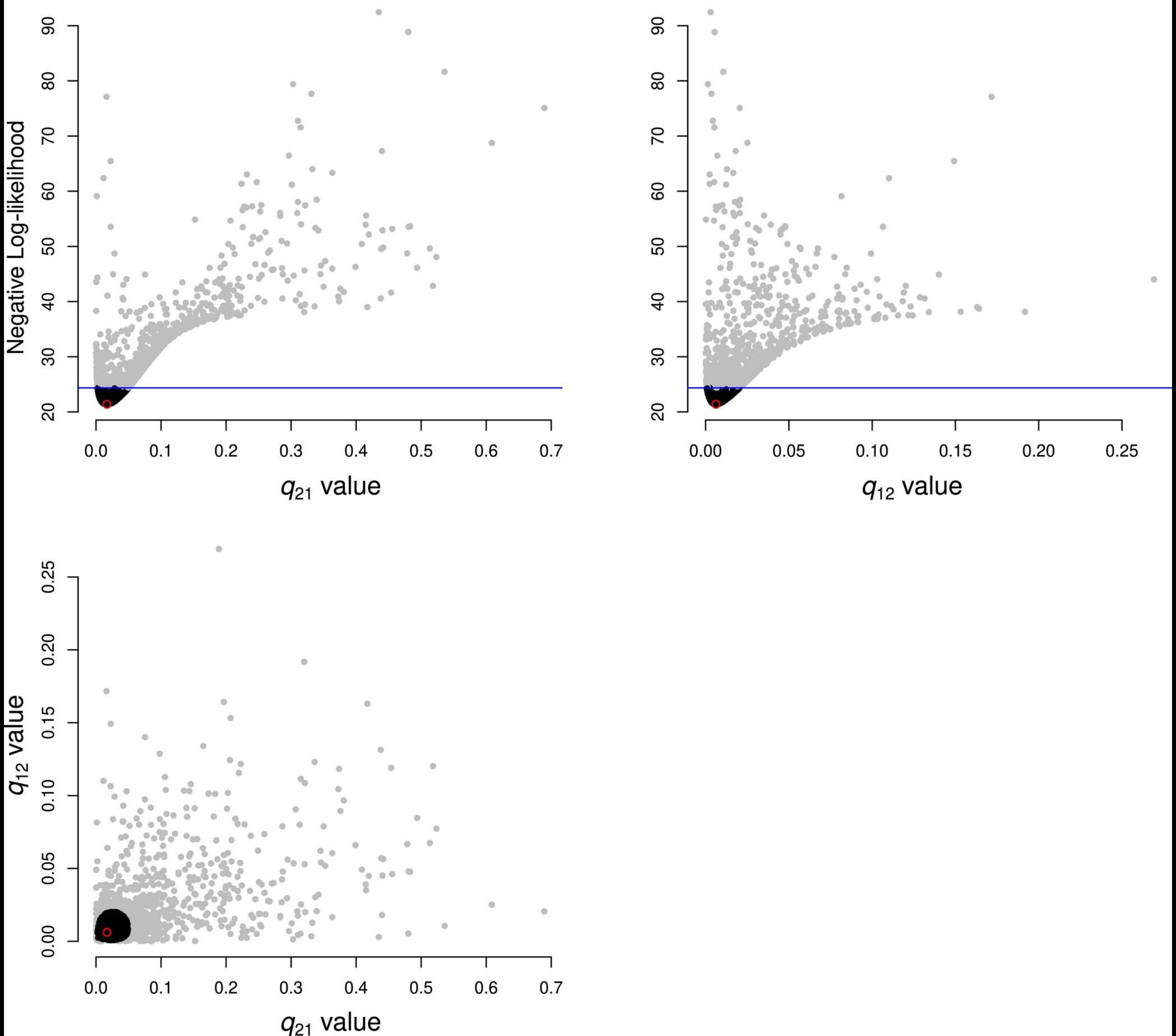
Parameter estimation is an optimization procedure on a likelihood surface



Rate matrix error

Can be done by exploring the likelihood surface

Machado et al. 2023



Dentist R package

“Dents” the likelihood surface for a fast exploration of parameter space

Boyko & O’Meara 2024

LESSONS

Always account for measurement error

Always account for phylogenetic uncertainty

Always account for parameter estimation error

MODEL ADEQUACY

Sometimes the best model is not the best model

The Far Side / BY GARY LARSON

Donning his new canine decoder, Professor Schwartzman becomes the first human being on Earth to hear what barking dogs are actually saying.

interpretation

Models inadequacy

“Estimated data”
(phylogenies)

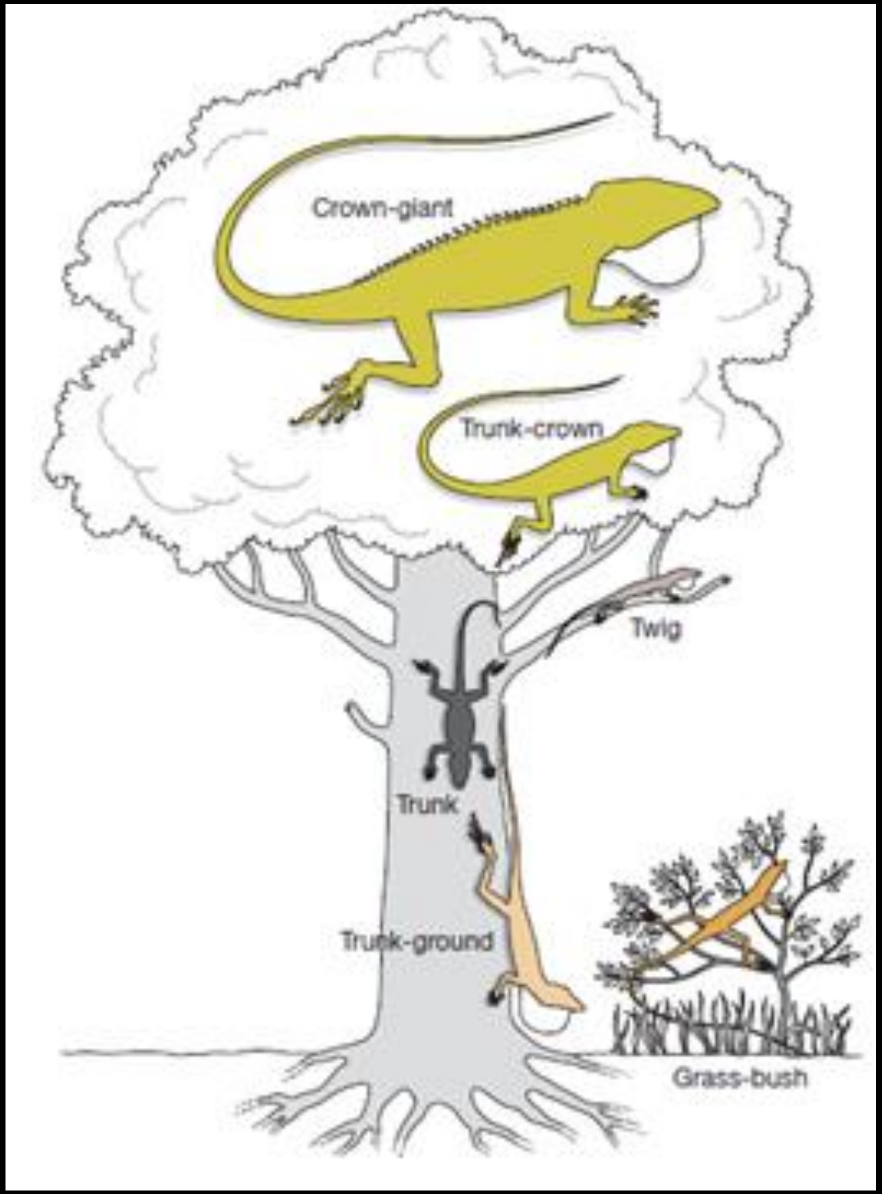
error/
inadequac

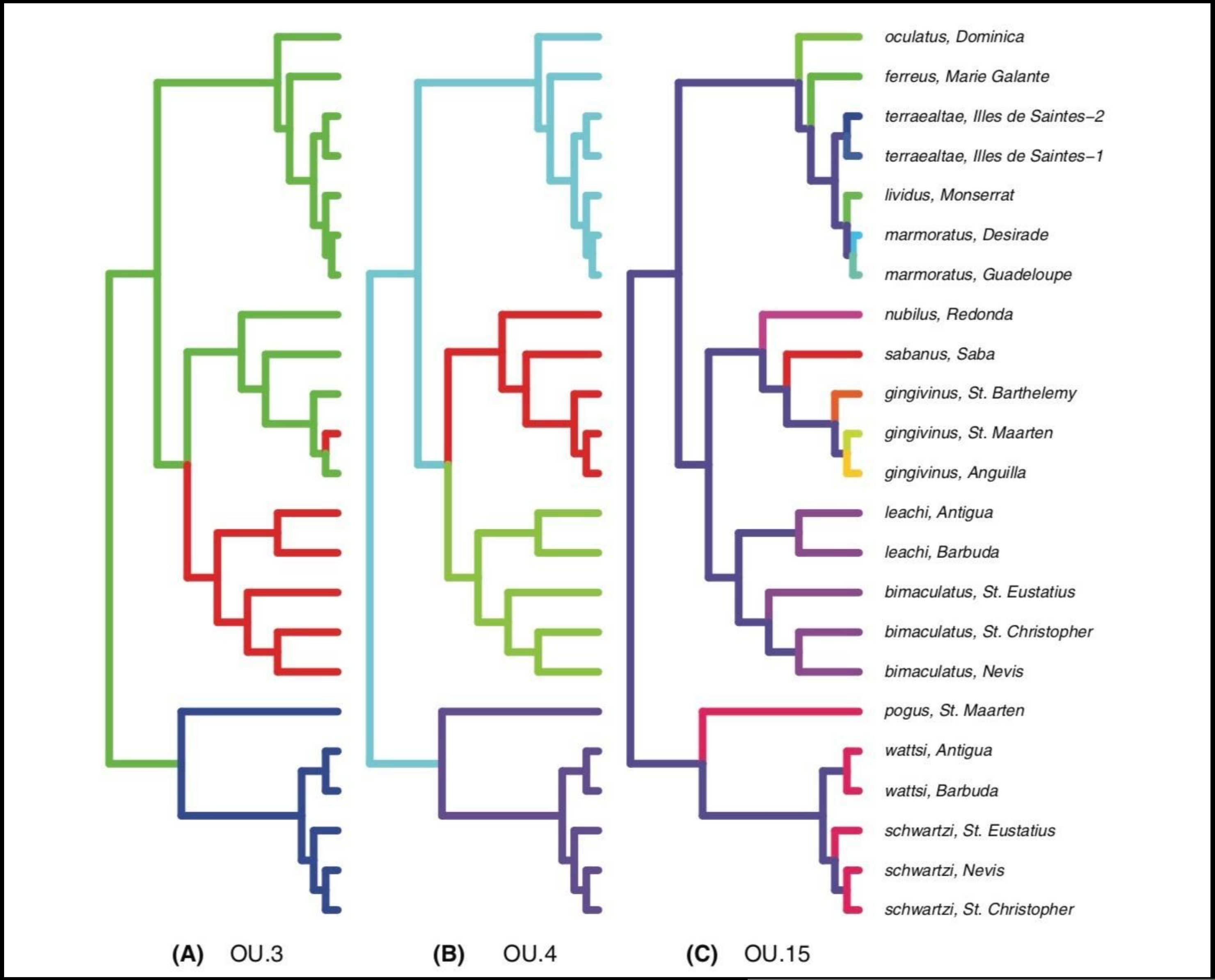
Data

error

It's possible for the best model is not the best

Adaptive radiation of Anoles

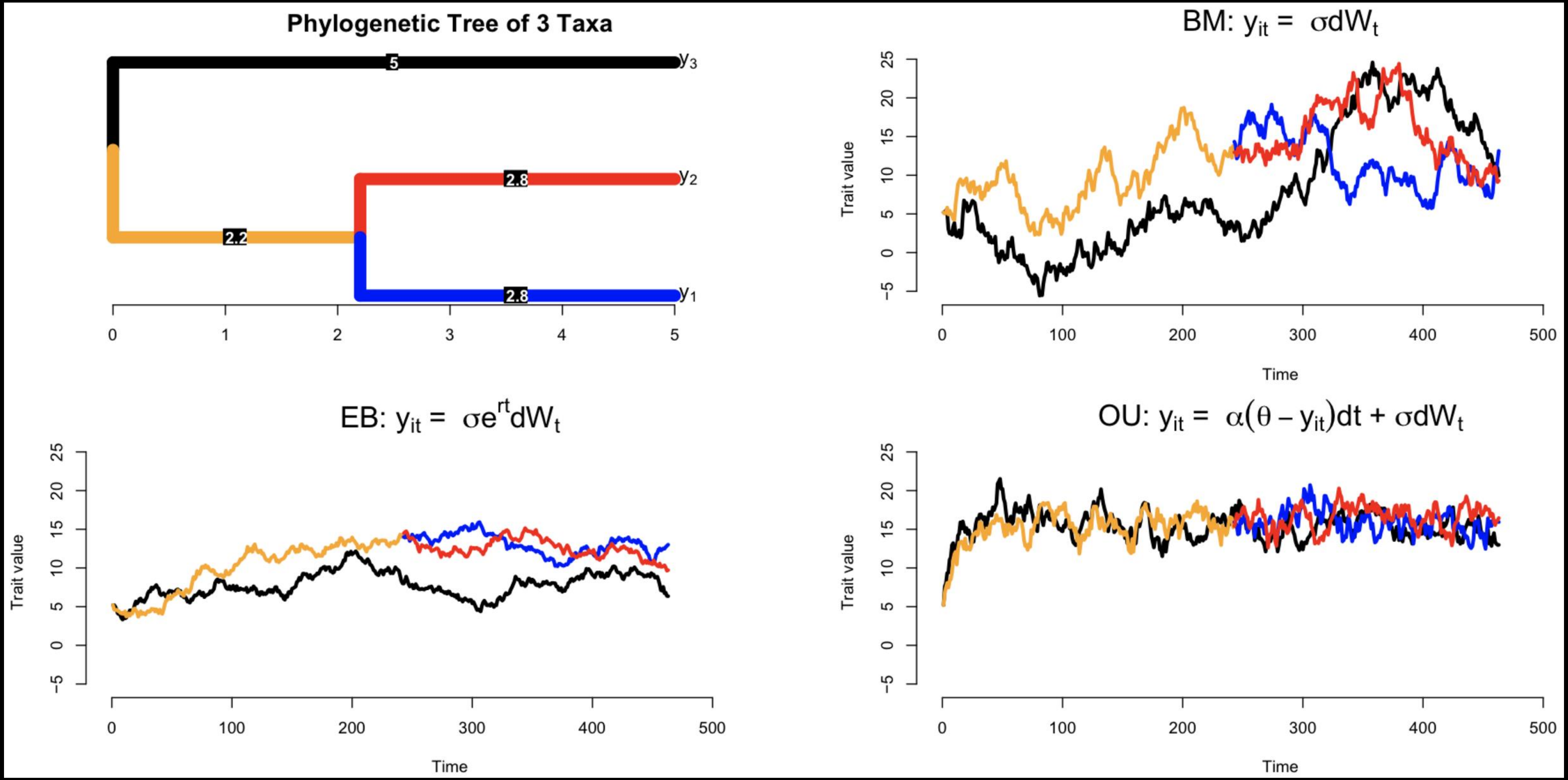




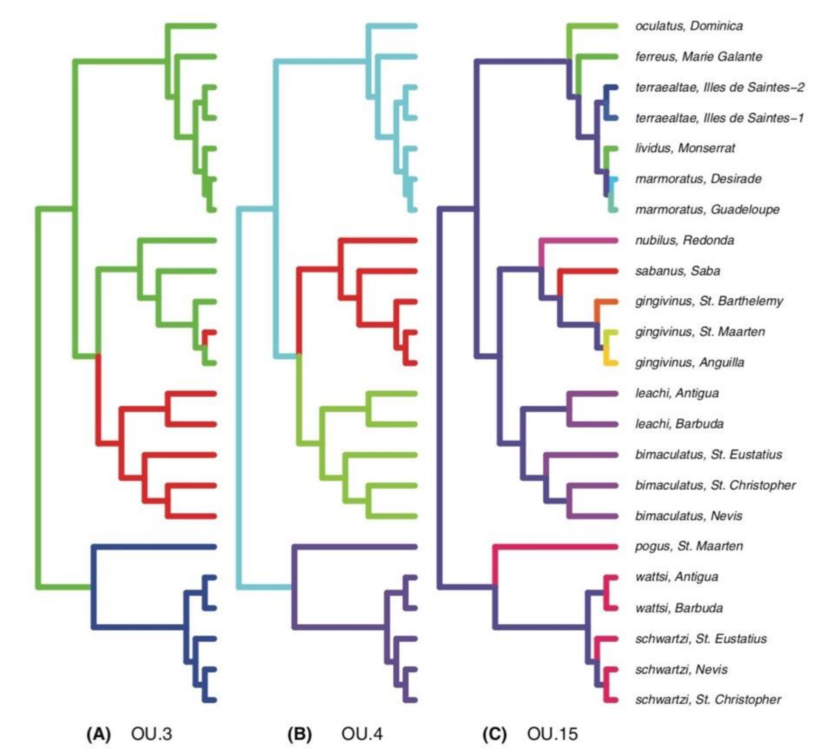
Boettiger, Coop, & Ralph 2012

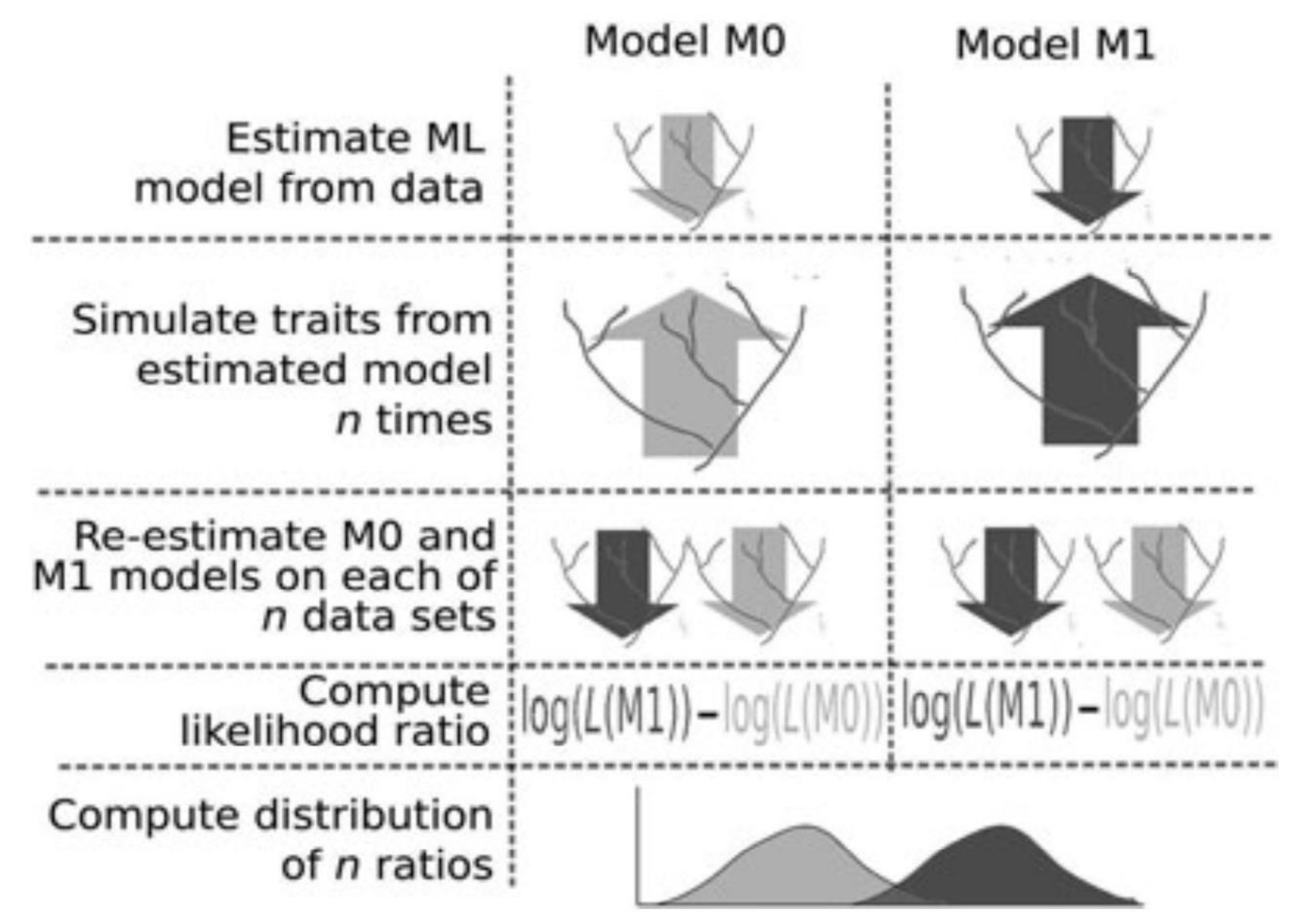
“Best models” (<2 loglik of best)

How different are they?

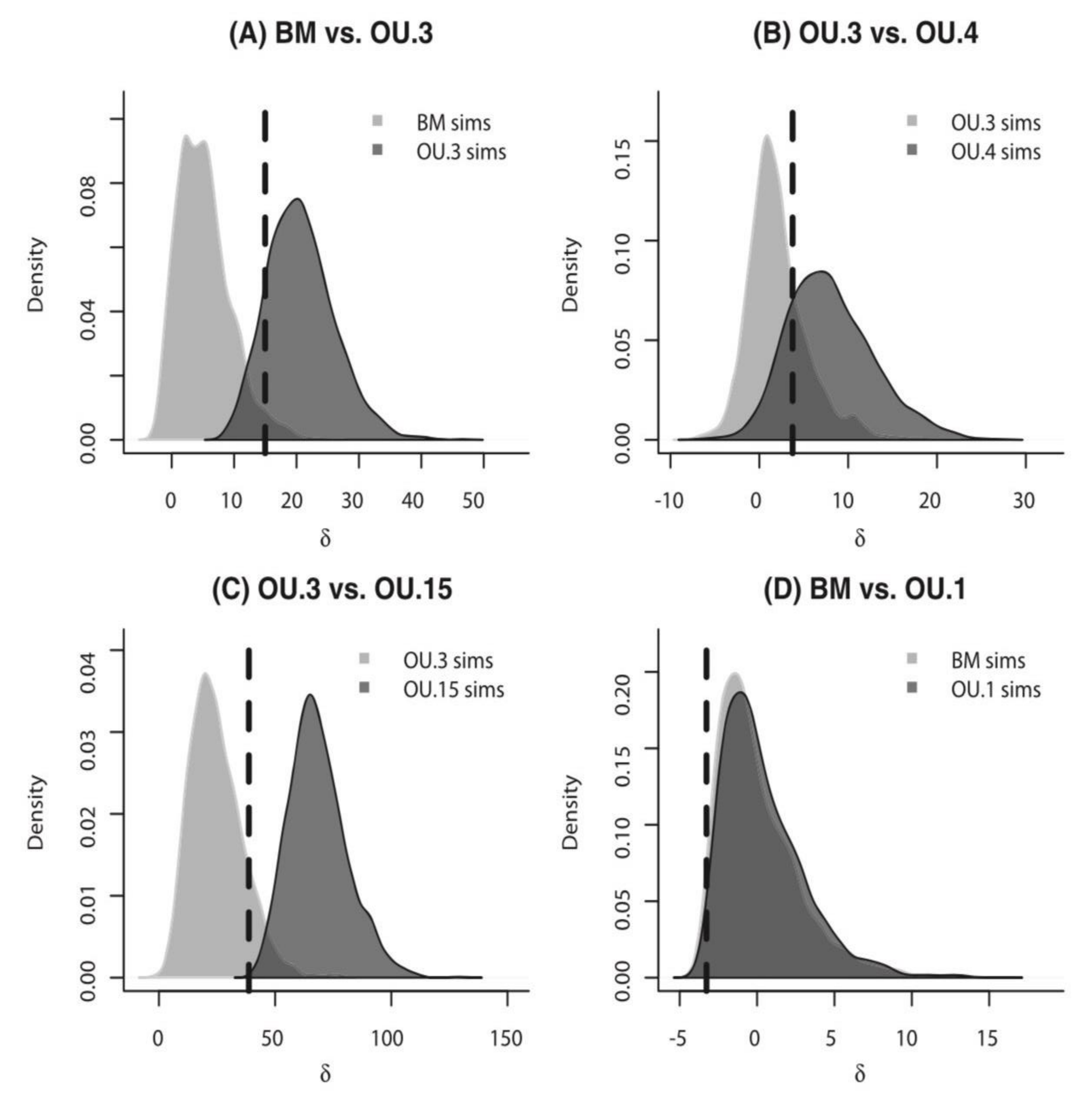


Simulations might help us understand our data



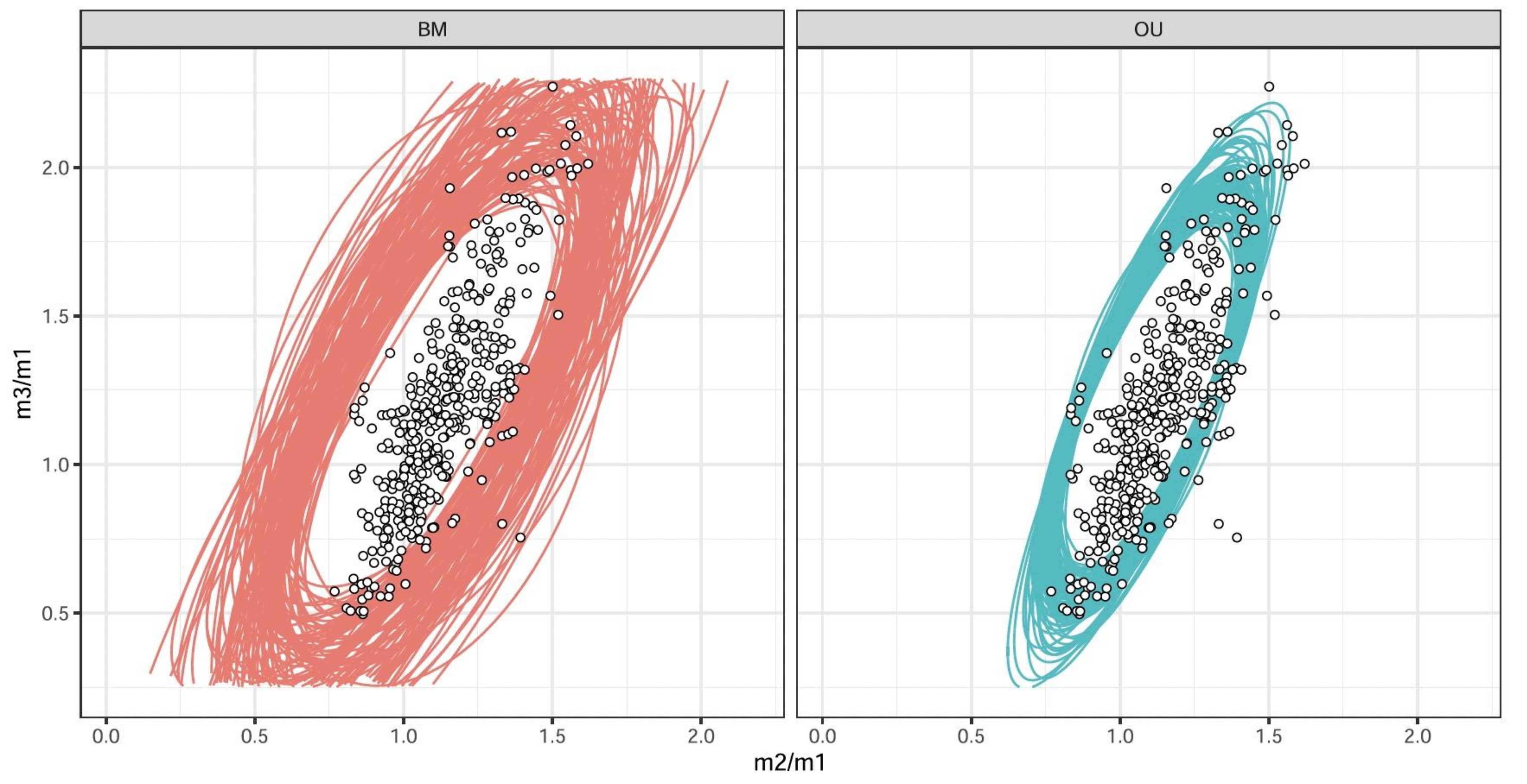


Boettiger, Coop, & Ralph 2012



Boettiger, Coop, & Ralph 2012

Visual inspection



Bad models will generate data that does not match empirical observations

Machado et al. 2023

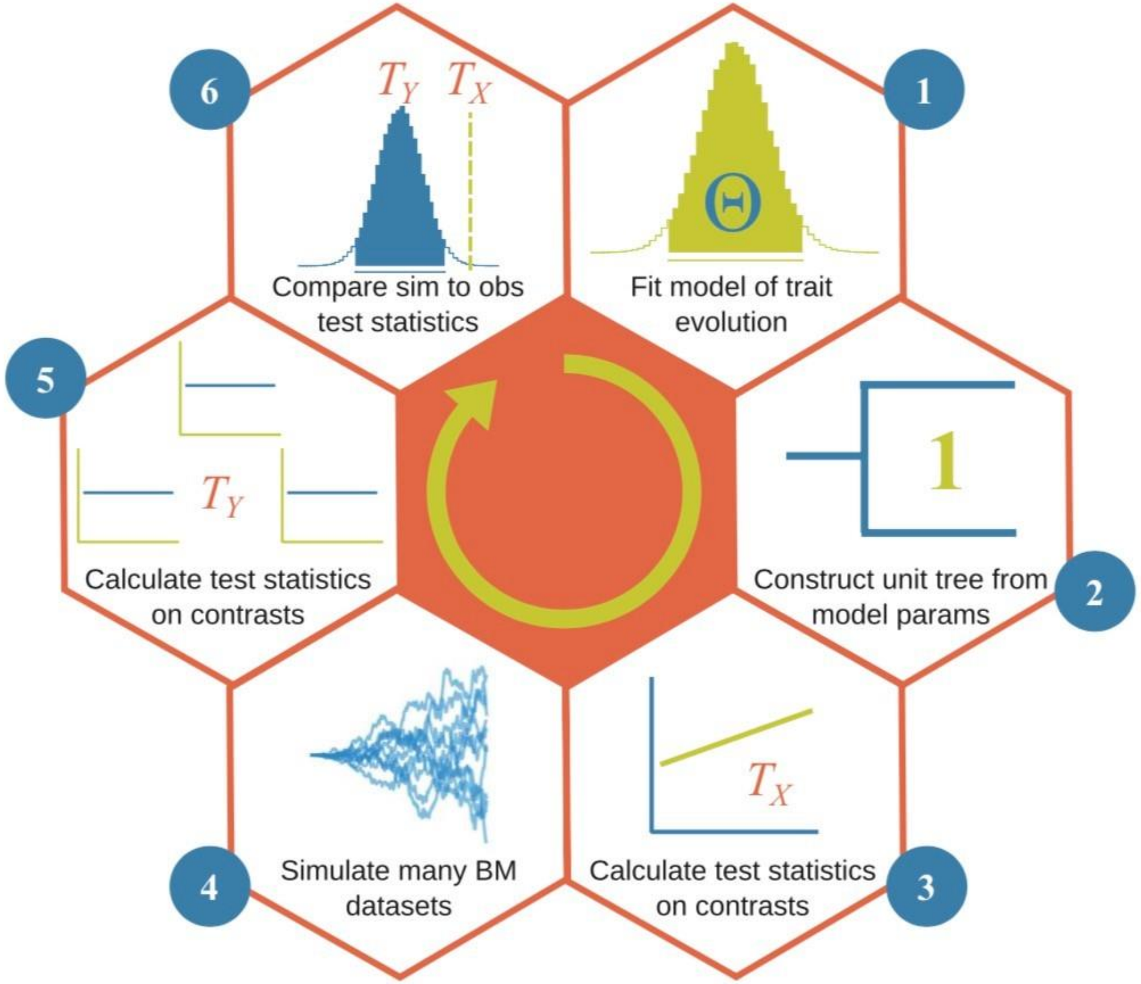


Figure 1: Schematic diagram representing our approach for assessing model adequacy. 1, Fit a model of trait evolution to the data. 2, Use the estimated model parameters to build a unit tree. 3, Compute the contrasts from the data on the unit tree and calculate a set of test statistics $\mathcal{T}_X$. 4, Simulate a large number of data sets on the unit tree, using a Brownian motion (BM) model with $\sigma^2 = 1$. 5, Calculate the test statistics on the contrasts of each simulated data set $\mathcal{T}_Y$. 6, Compare the observed and simulated test statistics. If the observed test statistic lies in the tails of the distribution of simulated test statistics, the model can be rejected as inadequate. The rotational circle in the center of the diagram indicates that assessing model adequacy is an iterative process. If a model is rejected as inadequate, the next step is to propose a new model and repeat the procedure.

Pennell, FitzJohn, Cornwell, Harmon 2015

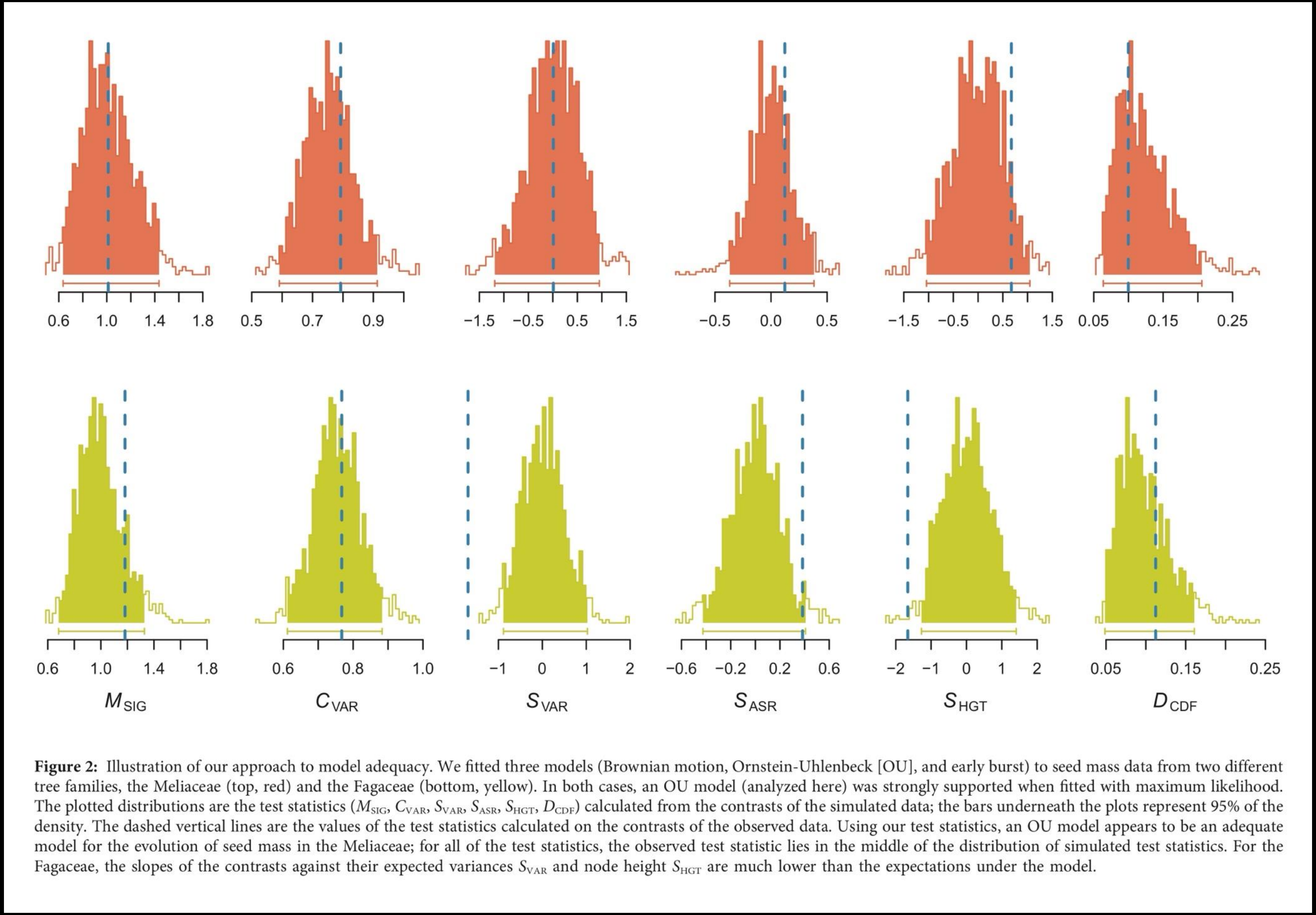


Figure 2: Illustration of our approach to model adequacy. We fitted three models (Brownian motion, Ornstein-Uhlenbeck [OU], and early burst) to seed mass data from two different tree families, the Meliaceae (top, red) and the Fagaceae (bottom, yellow). In both cases, an OU model (analyzed here) was strongly supported when fitted with maximum likelihood. The plotted distributions are the test statistics (M_{SIG}, C_{VAR}, S_{VAR}, S_{ASR}, S_{HGT}, D_{CDF}) calculated from the contrasts of the simulated data; the bars underneath the plots represent 95% of the density. The dashed vertical lines are the values of the test statistics calculated on the contrasts of the observed data. Using our test statistics, an OU model appears to be an adequate model for the evolution of seed mass in the Meliaceae; for all of the test statistics, the observed test statistic lies in the middle of the distribution of simulated test statistics. For the Fagaceae, the slopes of the contrasts against their expected variances S_{VAR} and node height S_{HGT} are much lower than the expectations under the model.

Pennell, FitzJohn, Cornwell, Harmon 2015

LESSONS

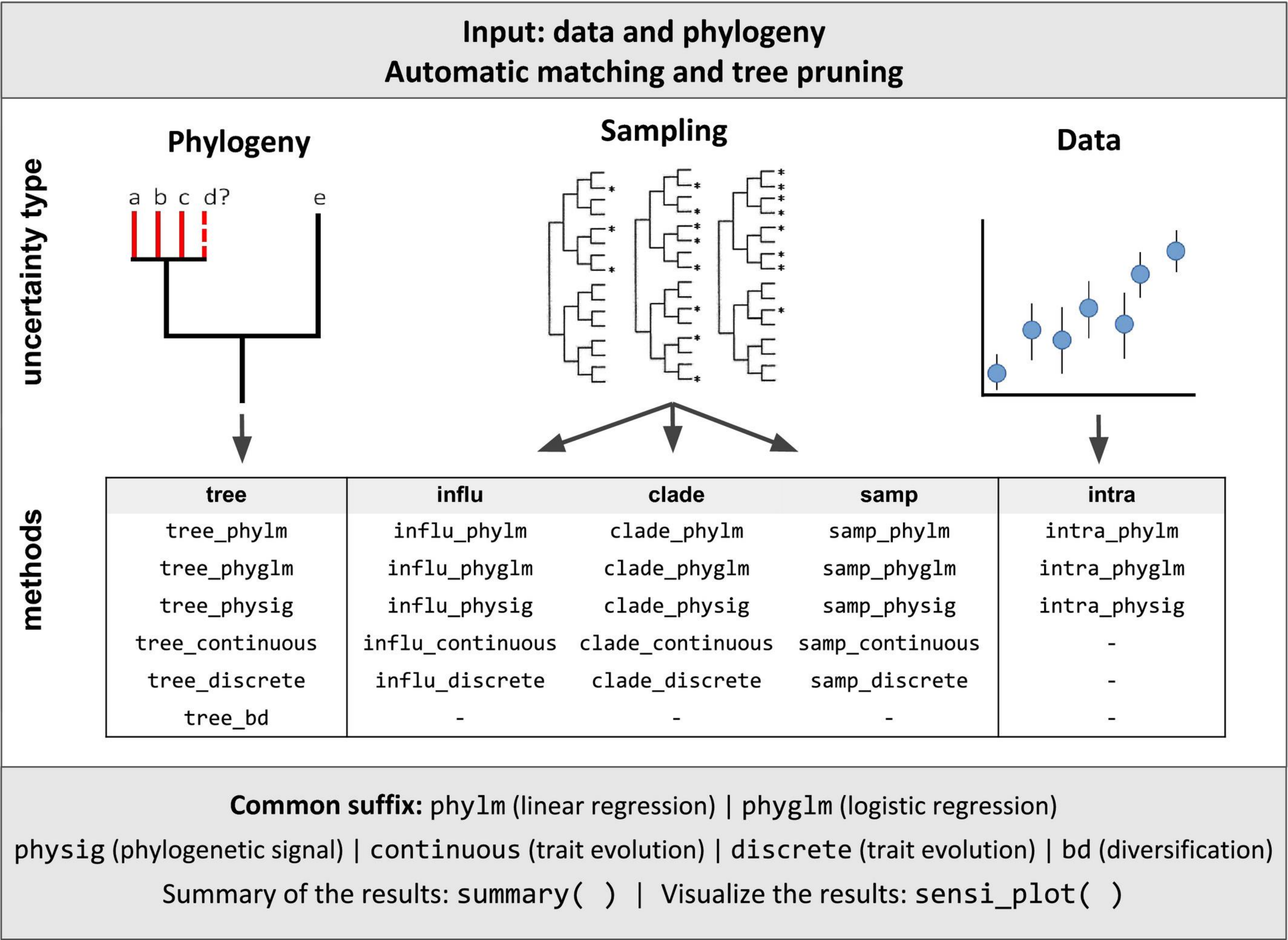
Always account for measurement error

Always account for phylogenetic uncertainty

Always account for parameter estimation error

Always account for model inadequacy

SENSITIVITY ANALYSIS



Input: data and phylogeny
Automatic matching and tree pruning

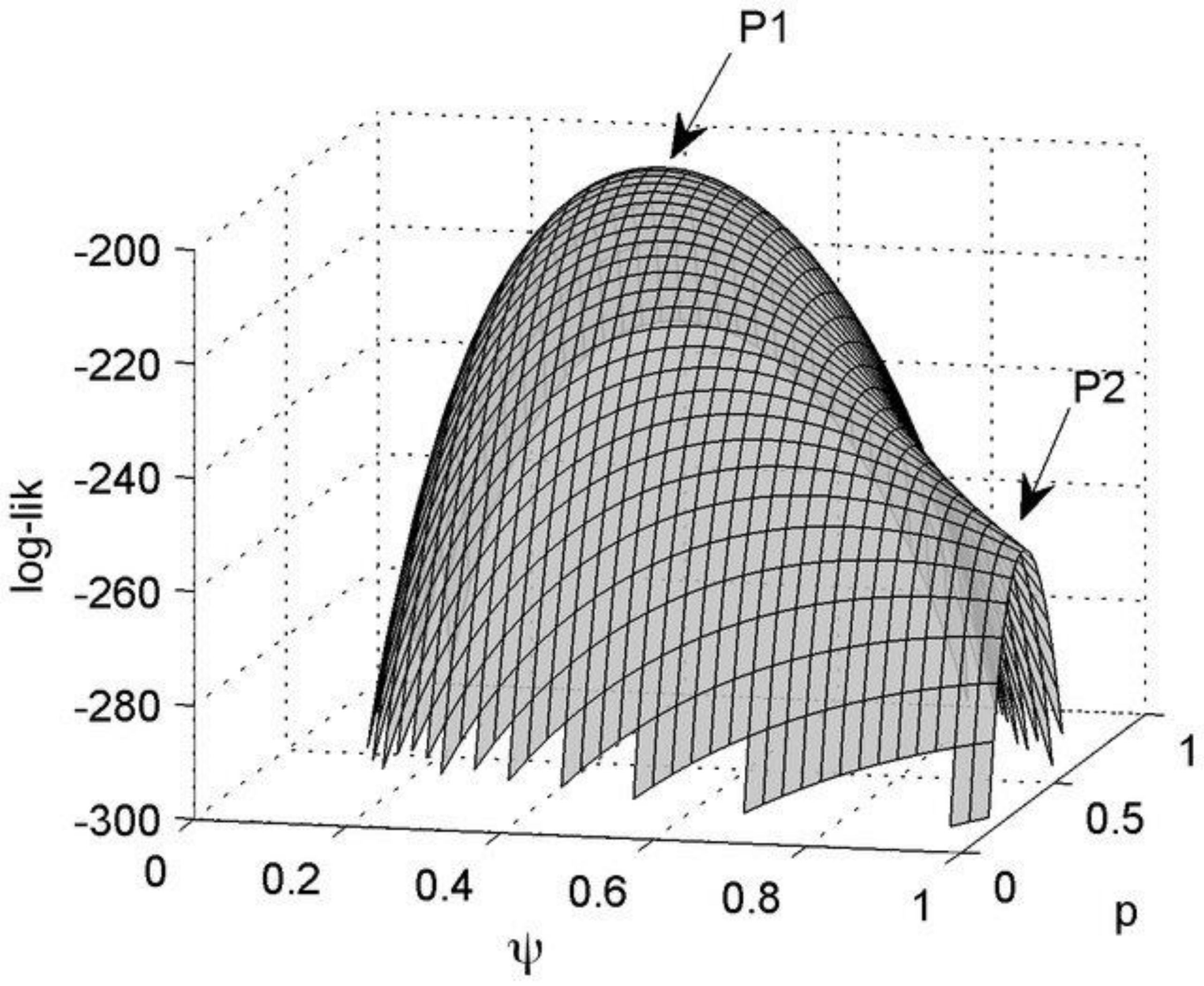
tree	influ	clade	samp	intra
tree_phylm	influ_phylm	clade_phylm	samp_phylm	intra_phylm
tree_phyglm	influ_phyglm	clade_phyglm	samp_phyglm	intra_phyglm
tree_physig	influ_physig	clade_physig	samp_physig	intra_physig
tree_continuous	influ_continuous	clade_continuous	samp_continuous	-
tree_discrete	influ_discrete	clade_discrete	samp_discrete	-
tree_bd	-	-	-	-

Common suffix: `phylm` (linear regression) | `phyglm` (logistic regression)
`physig` (phylogenetic signal) | `continuous` (trait evolution) | `discrete` (trait evolution) | bd (diversification)
Summary of the results: `summary( )` | Visualize the results: `sensi_plot( )`

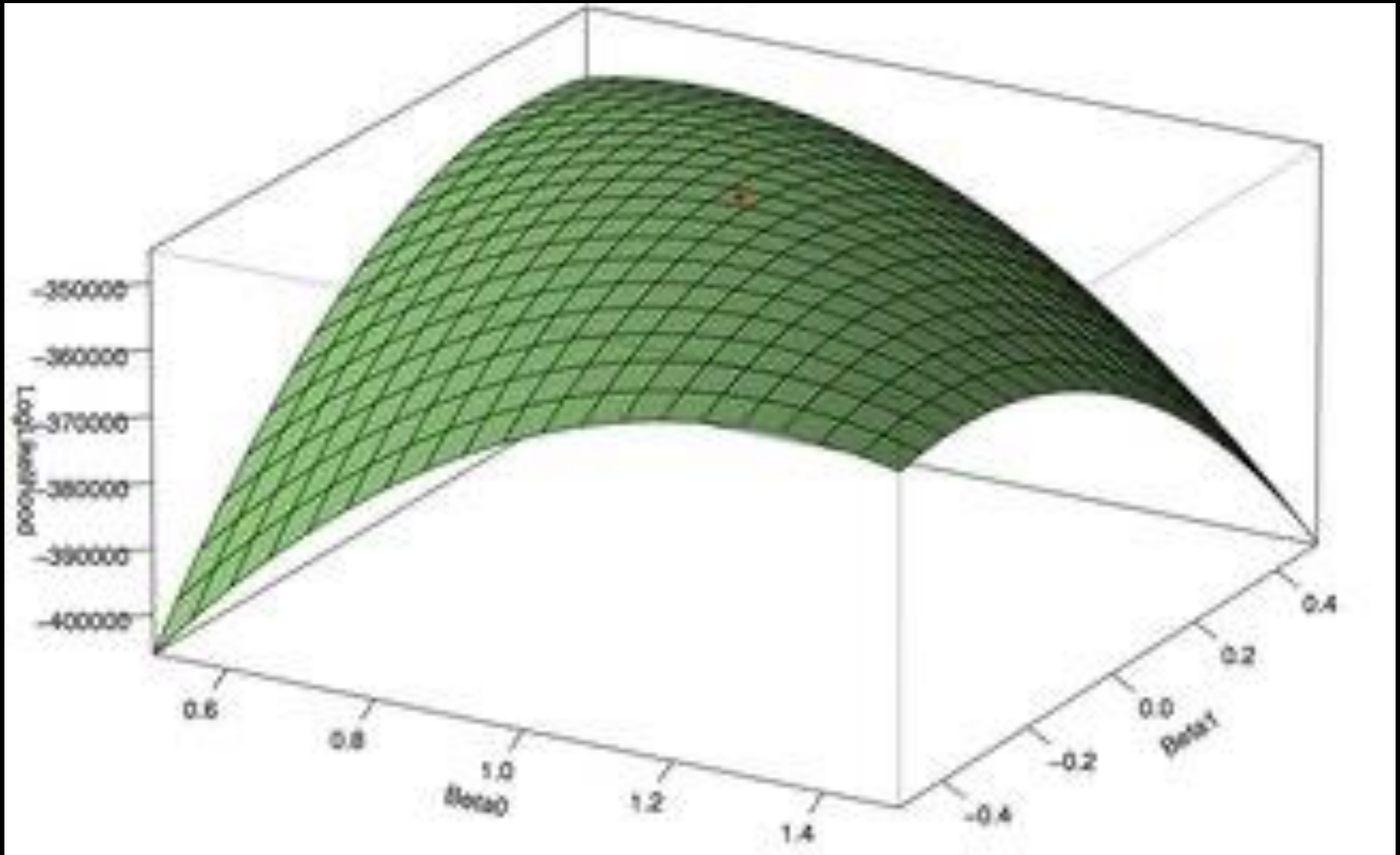
Patermo, Penone, Wener, 2018

IDENTIFIABILITY ISSUES

Sometimes model parameters interact with each other

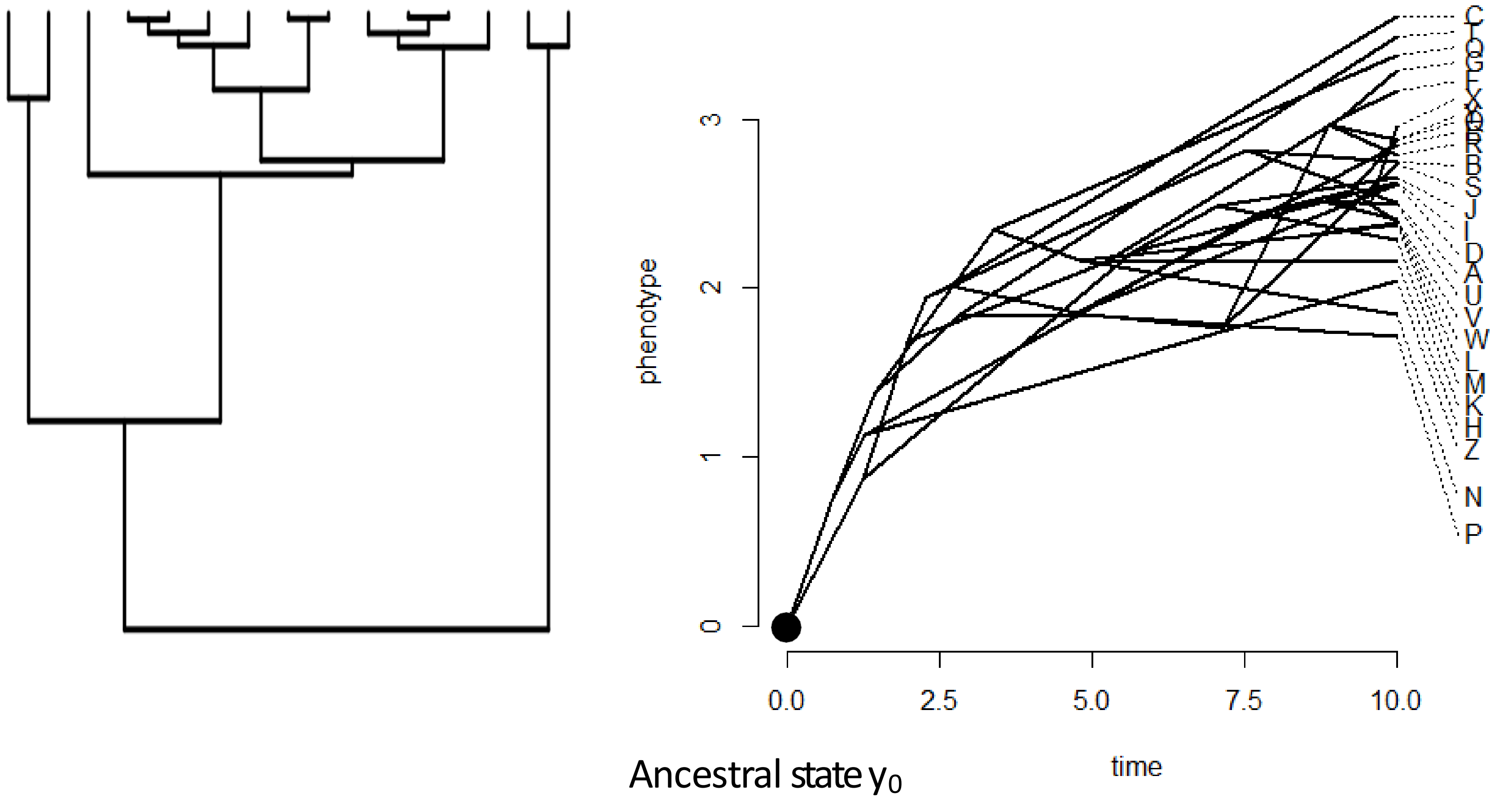


Parameter estimation is an optimization procedure on a likelihood surface



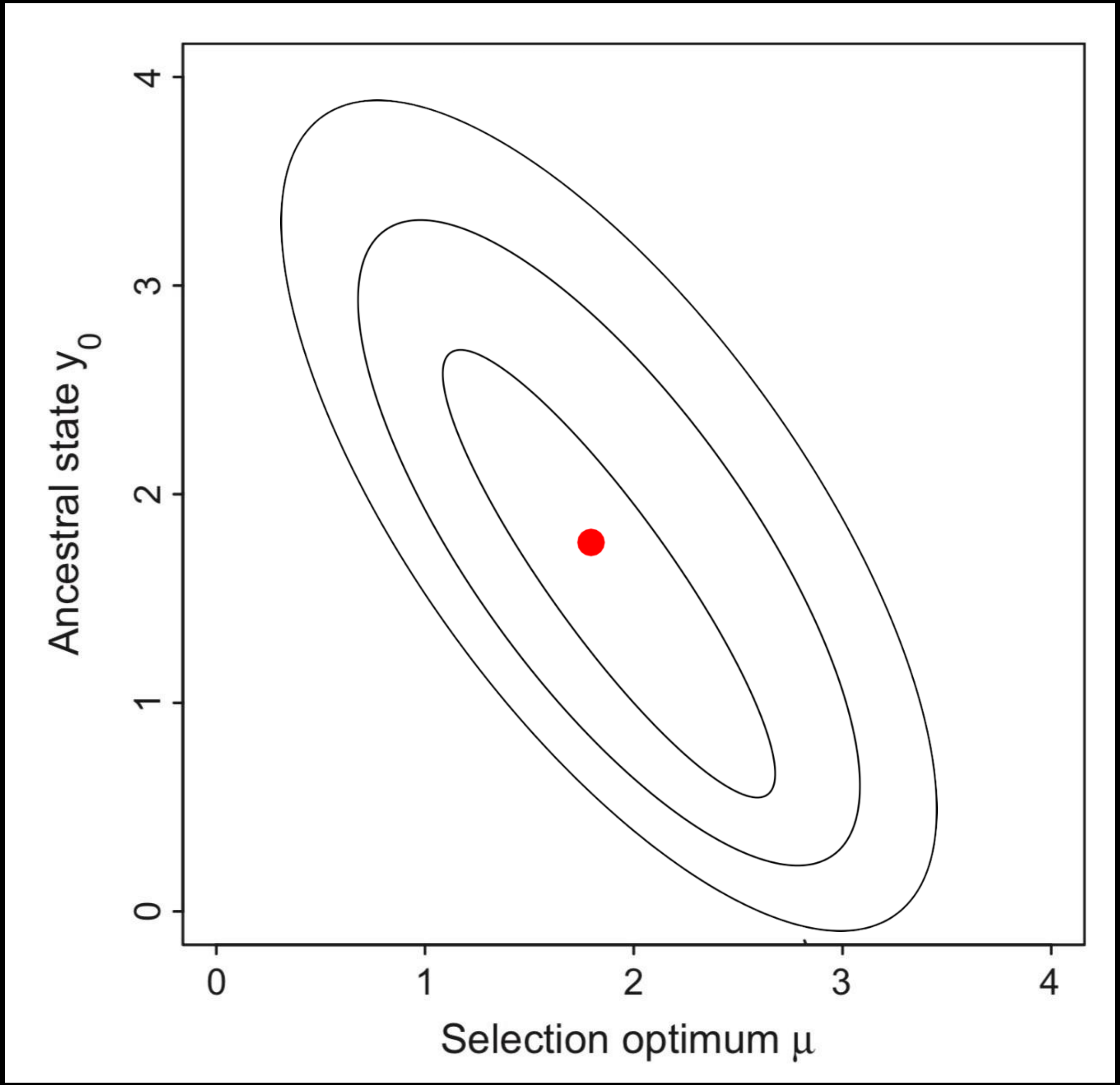
Sometimes likelihood surfaces can be flatter

OU: OPTIMUM μ
ANCESTRAL STATE Y0

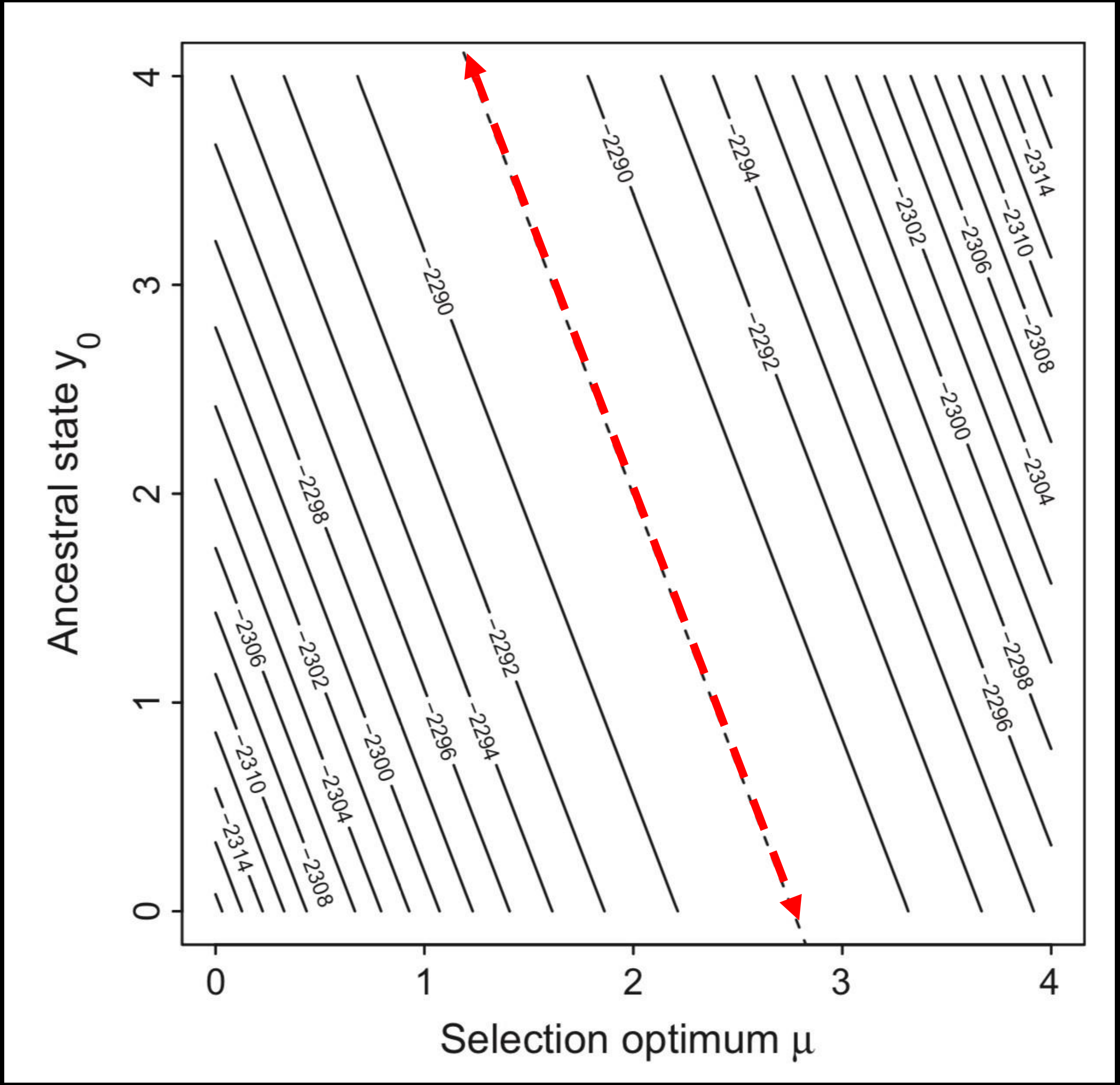


Ancestral state y_0

THIS IS WHAT WE WANT

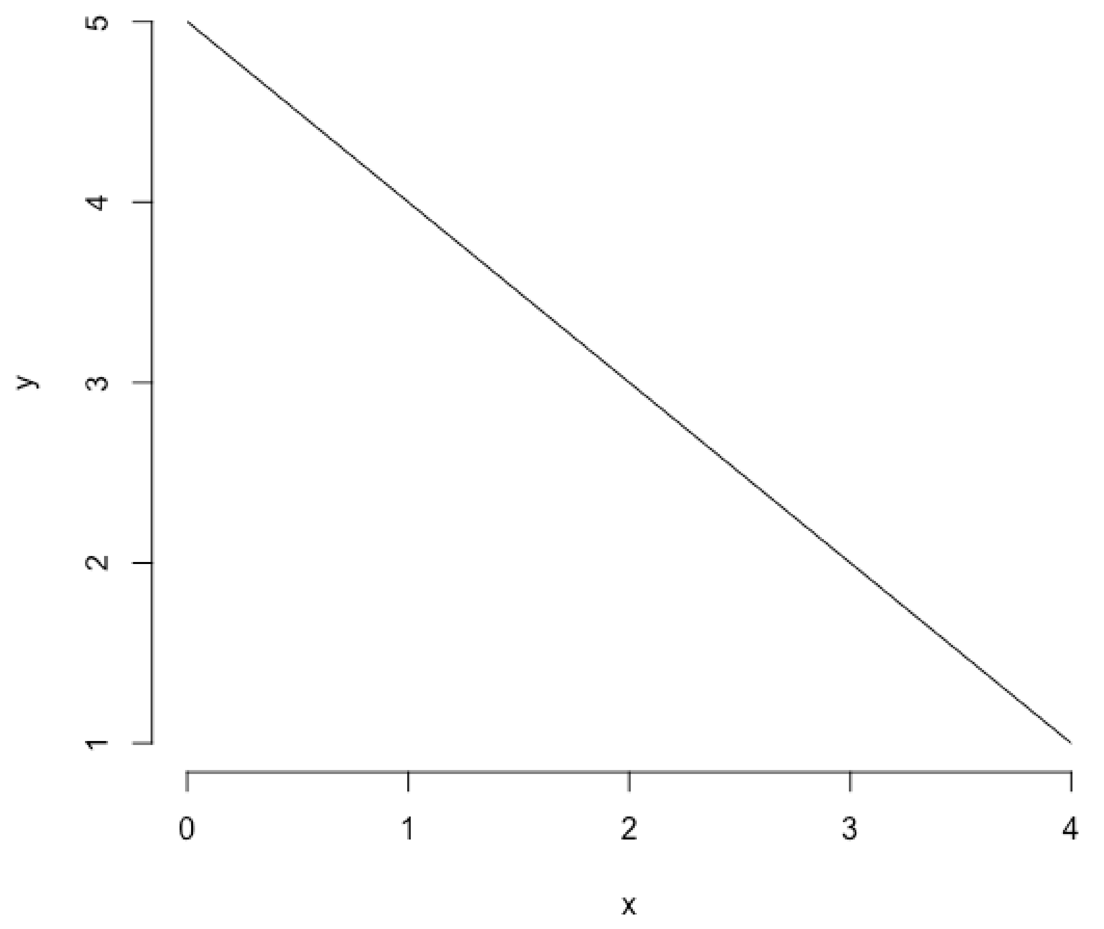


THIS IS WHAT WE GET

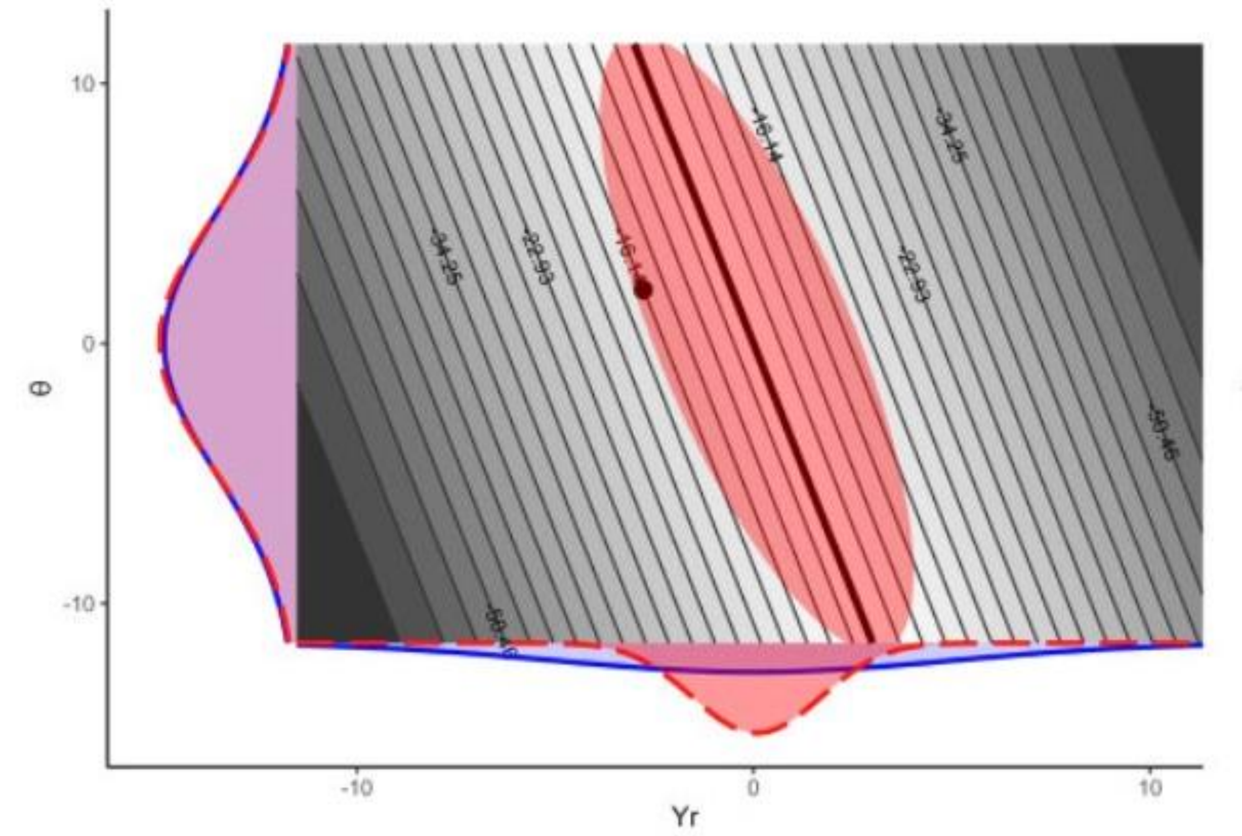


Ho and Ané,2014

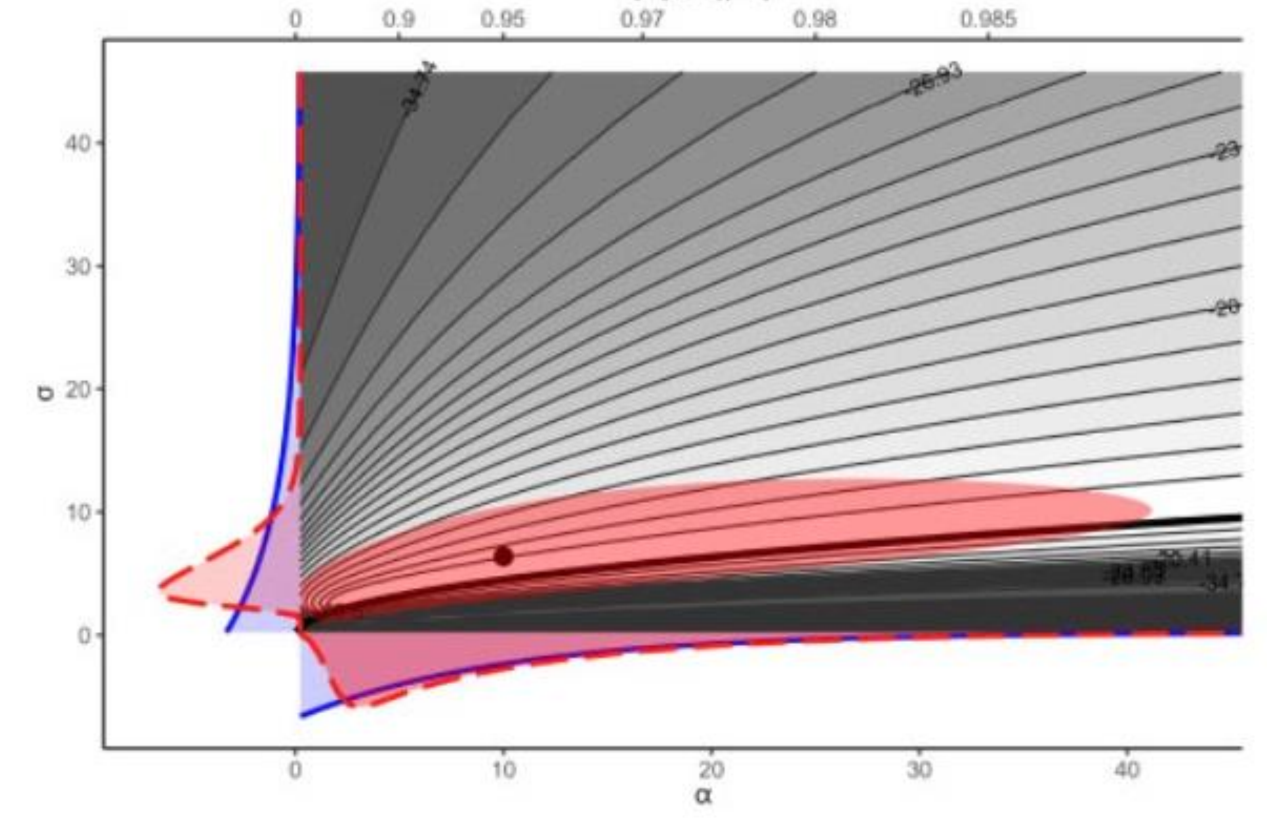
What is x in x+y=5



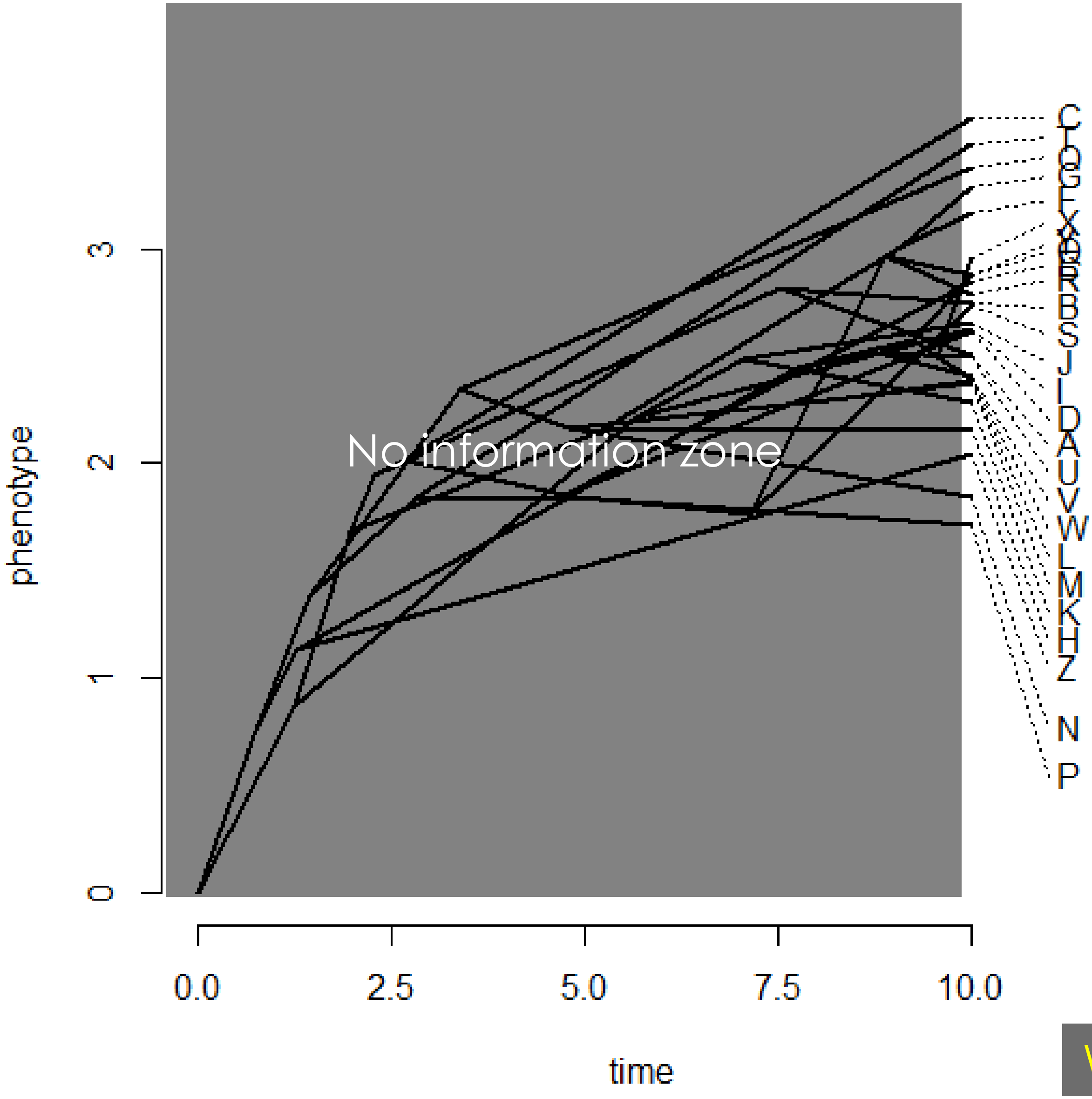
Theta and ancestral state



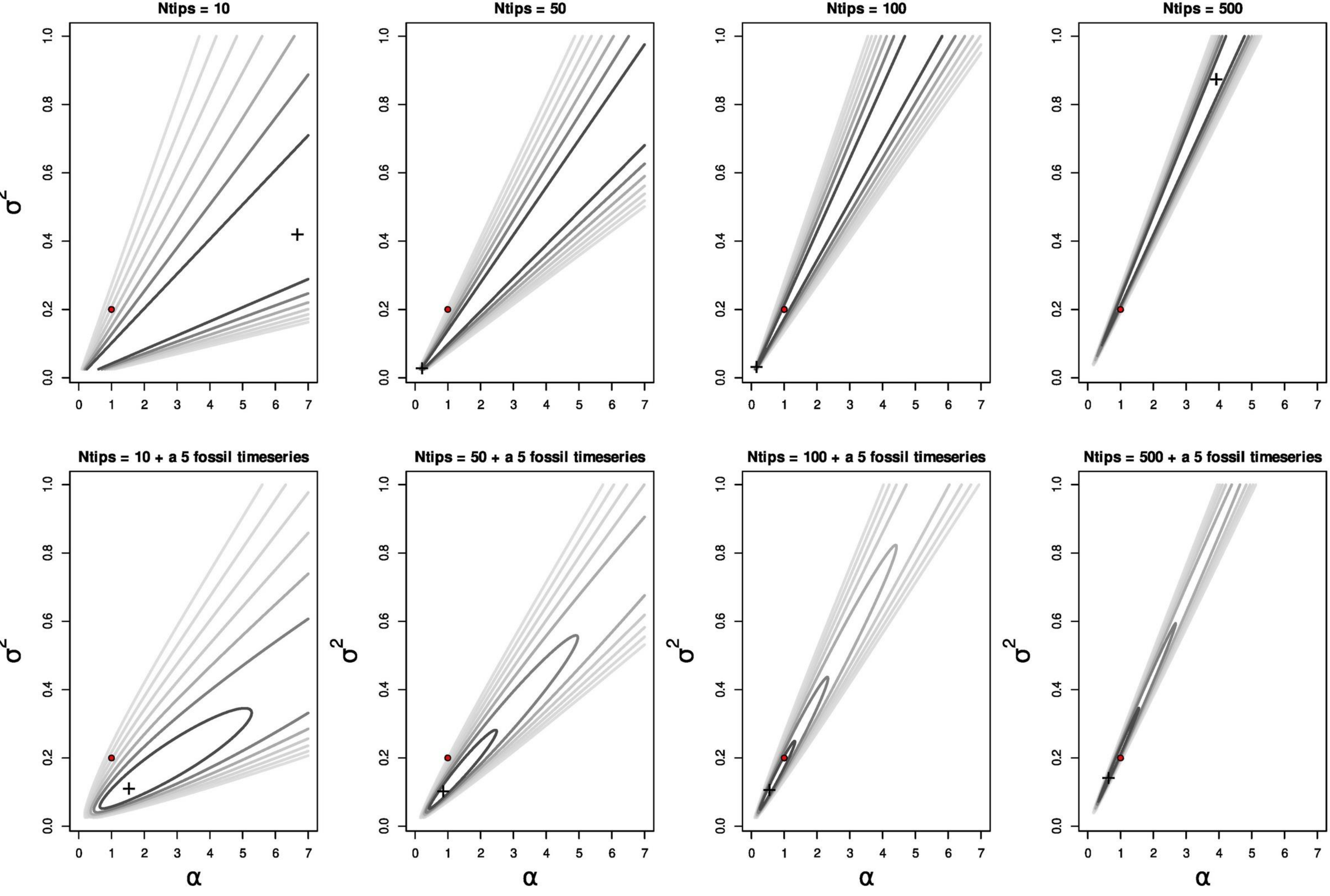
Alpha and rho



Cornuaut 2014



What can we do?



Trends in Ecology & Evolution

Add tips and fossils

Liow, Uyeda & Hunt, 2023

LESSONS

Always account for measurement error

Always account for phylogenetic uncertainty

Always account for parameter estimation error

Always account for model inadequacy

Always account for identifiability issues

CAN REV BAYES SAVE US ALL?

measurement error

phylogenetic uncertainty

parameter estimation error

model inadequacy

identifiability issues

CAN REV BAYES SAVE US ALL?

measurement error → not exclusively but yes

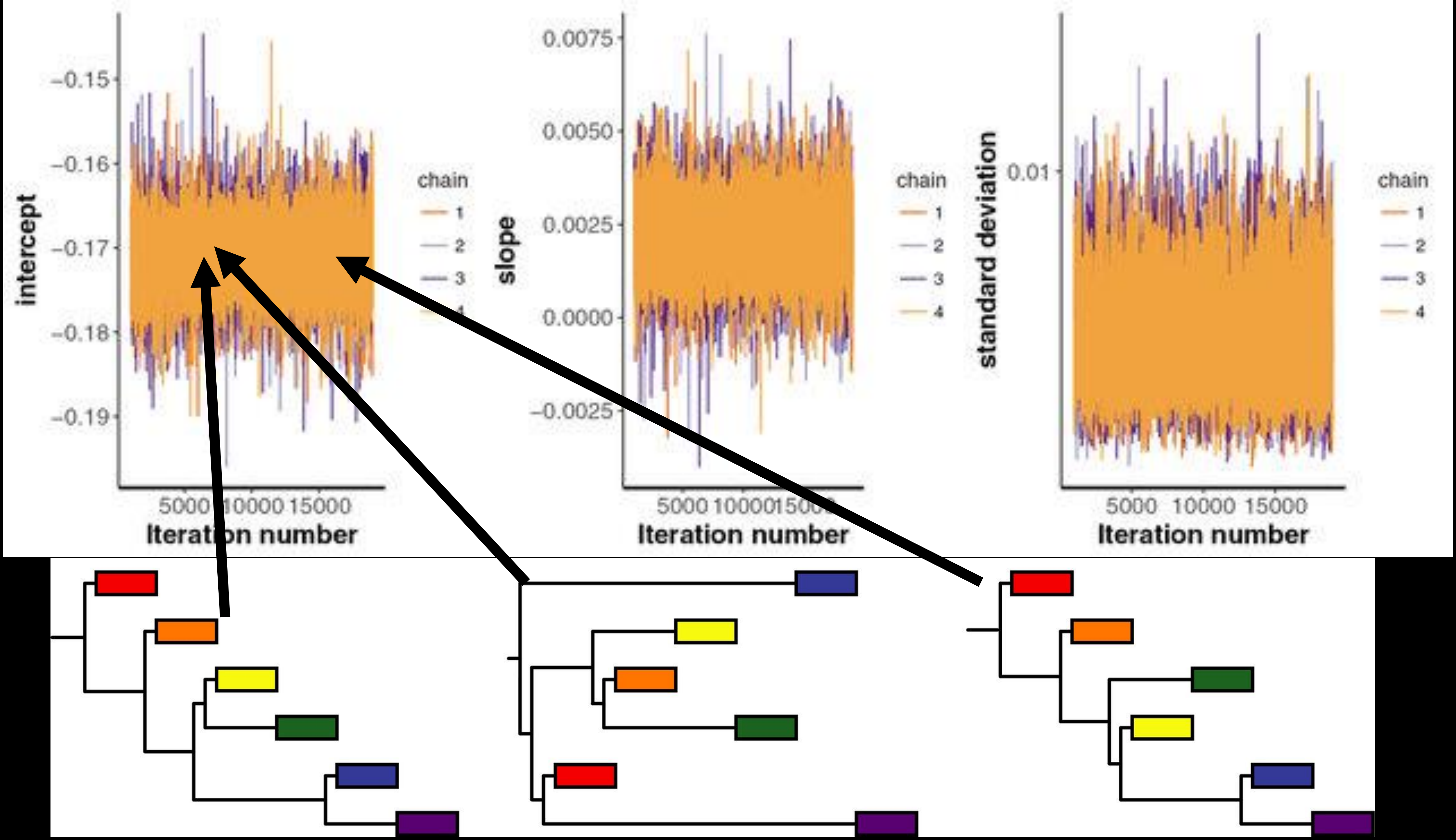
phylogenetic uncertainty→

parameter estimation error → yes

model inadequacy → no

identifiability issues → no

The MCMC machinery can incorporate phylogenetic uncertainty



CAN REV BAYES SAVE US ALL?

measurement error → not exclusively but yes

phylogenetic uncertainty→ yes

parameter estimation error → yes

model inadequacy → no

identifiability issues → no