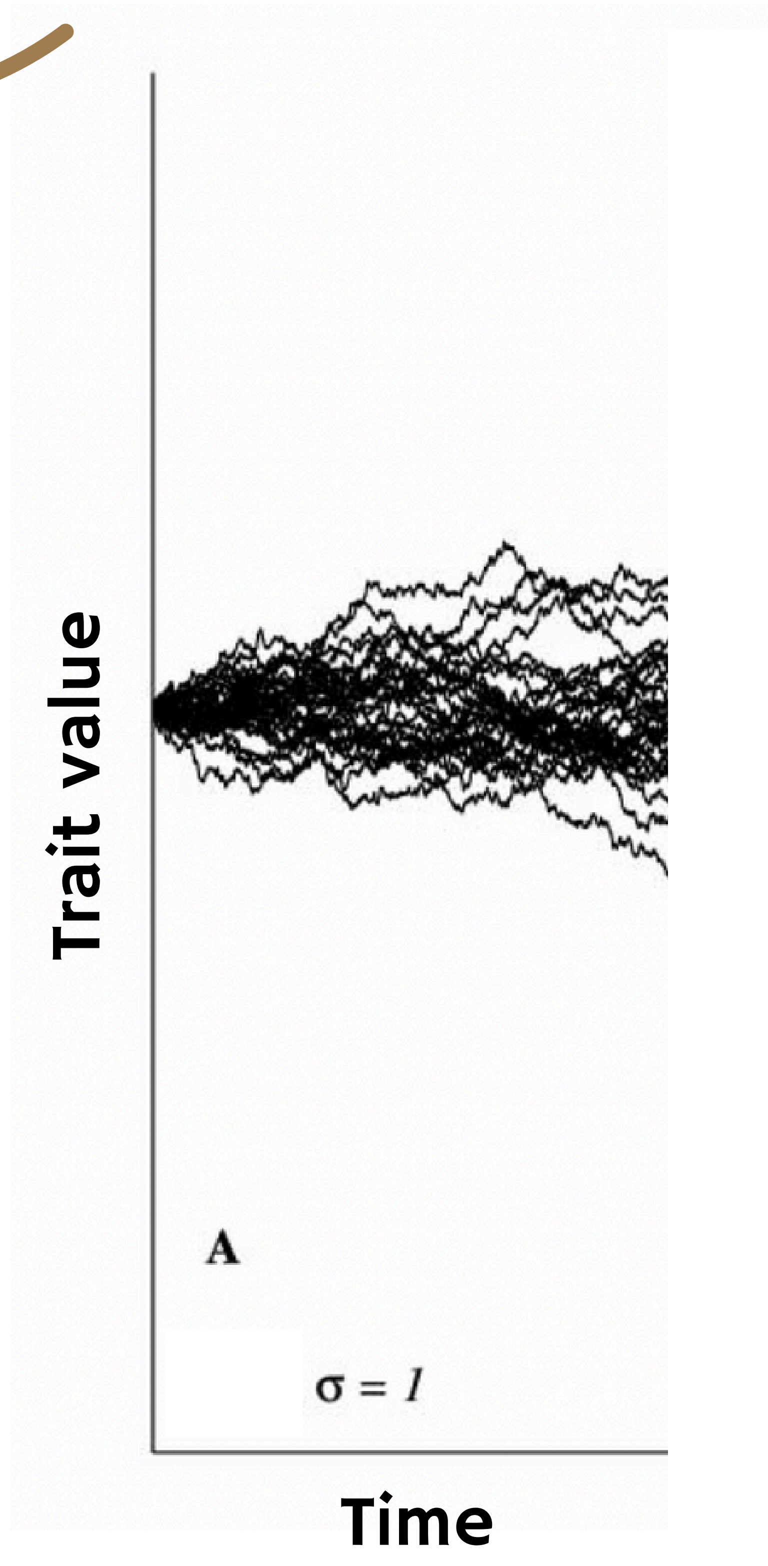
Adaptation, Constraint, and Convergence
(on Trees)

Brownian motion:

$$dX(t)=\underline{\sigma}dW(t)$$

Rate

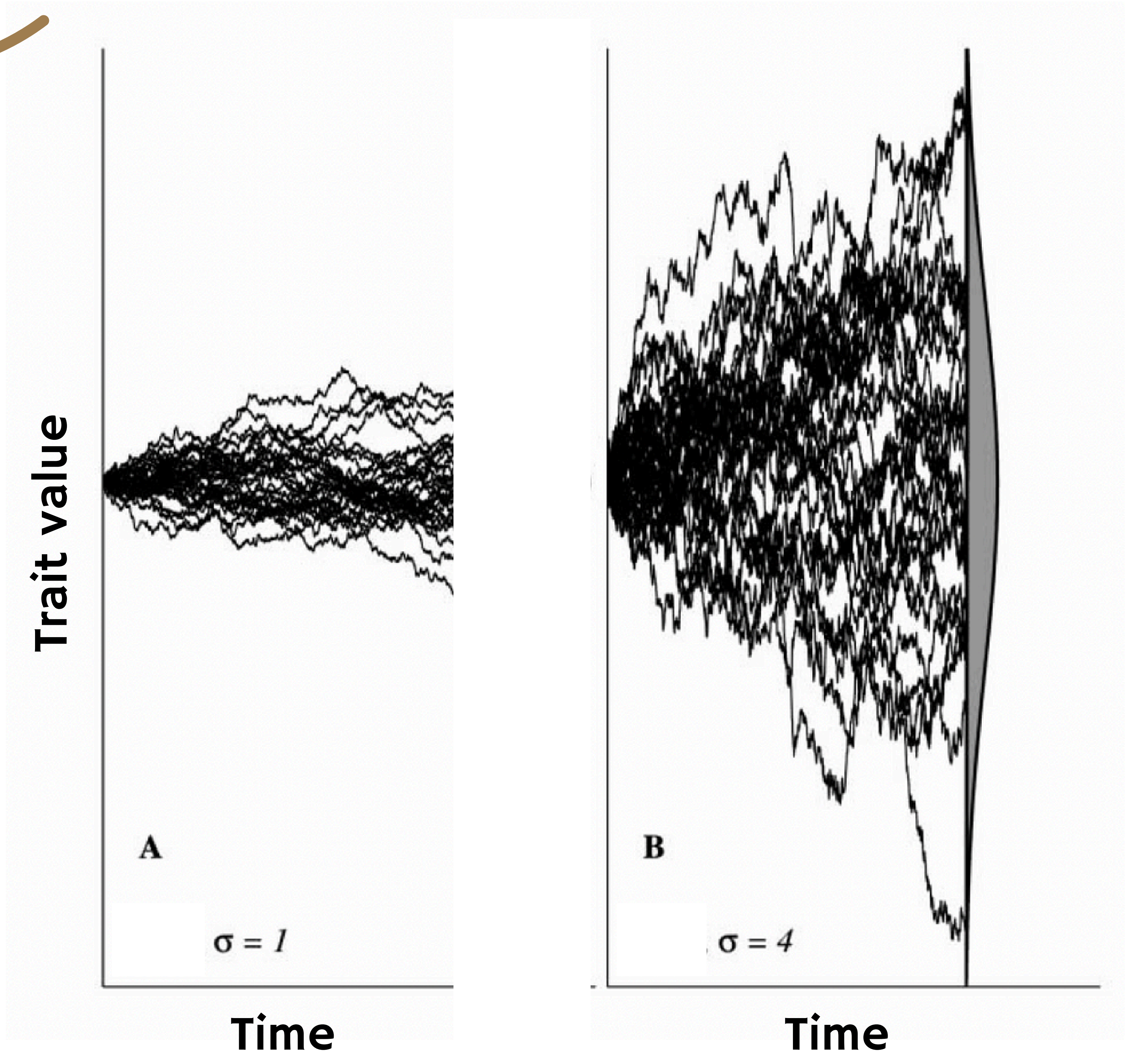


Butler and King 2004 Am Nat

Brownian motion:

$$dX(t) = \underline{\sigma} dW(t)$$

Rate



Butler and King 2004 Am Nat

Ornstein-Uhlenbeck (OU):

$$dX(t)=\alpha(\theta-X(t))dt+\boxed{\sigma dW(t)}$$

BM

Butler and King 2004 Am Nat

Ornstein-Uhlenbeck (OU):

$$dX(t)=\underline{\alpha}(\underline{\theta}-X(t))dt+\boxed{\sigma dW(t)}$$

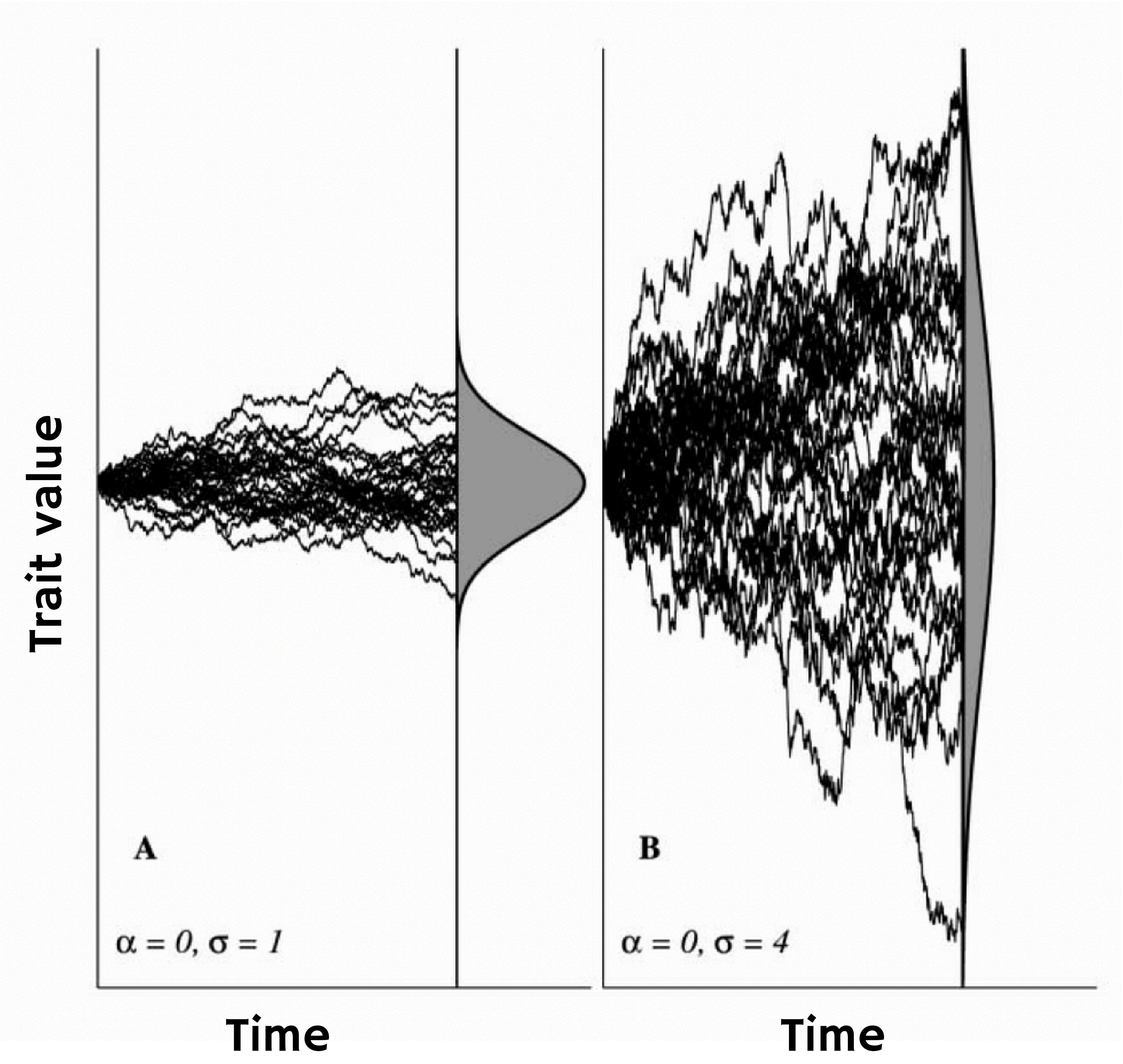
Trait optimum

Strength of selection

Butler and King 2004 Am Nat

Ornstein-Uhlenbeck (OU):

$$dX(t) = \alpha(\theta - X(t))dt + \sigma dW(t)$$

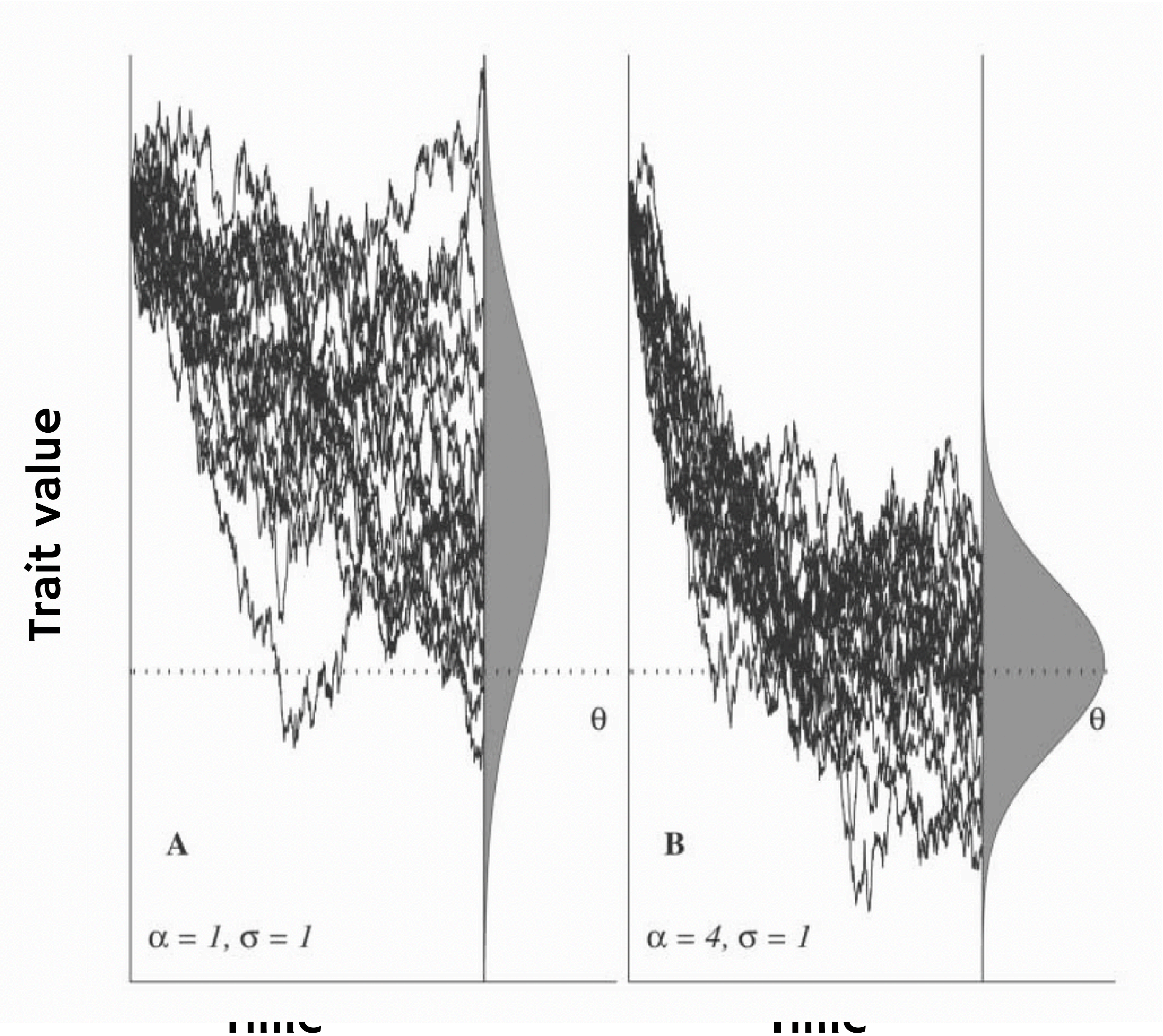


When **alpha = 0**, the model reduces to Brownian motion

Butler and King 2004 Am Nat

Ornstein-Uhlenbeck (OU):

$$dX(t)=\alpha(\theta-X(t))dt+\sigma dW(t)$$



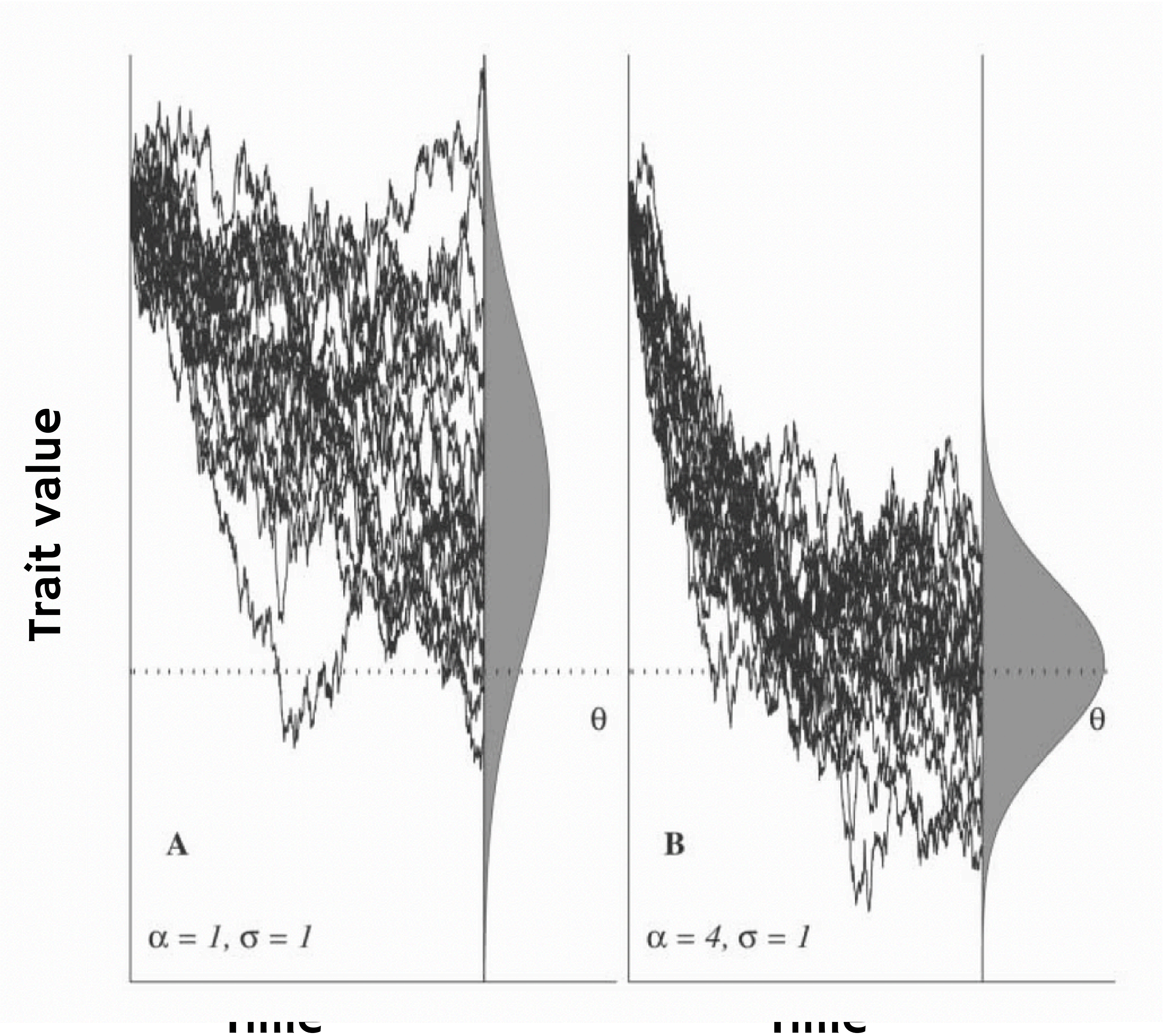
When **alpha > 0**, how fast the trait evolves toward the optimum

Strong/weak constraint
Strong/weak selective pressures
Fast/slow adaptation

Butler and King 2004 Am Nat

Ornstein-Uhlenbeck (OU):

$$dX(t) = \alpha(\theta - X(t))dt + \sigma dW(t)$$



A useful way to interpret **alpha** is through the phylogenetic half-life:

Phylogenetic half-life = ln(2) / α

This is the time it takes for a lineage to move halfway toward the trait optimum (theta) from its ancestral state.

Butler and King 2004 Am Nat

WHAT DOES THE OU MODEL TELL US ABOUT EVOLUTION?

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- OU adds the idea of selection and constraint

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Stabilizing selection: traits are “pulled” toward an “optimal” value

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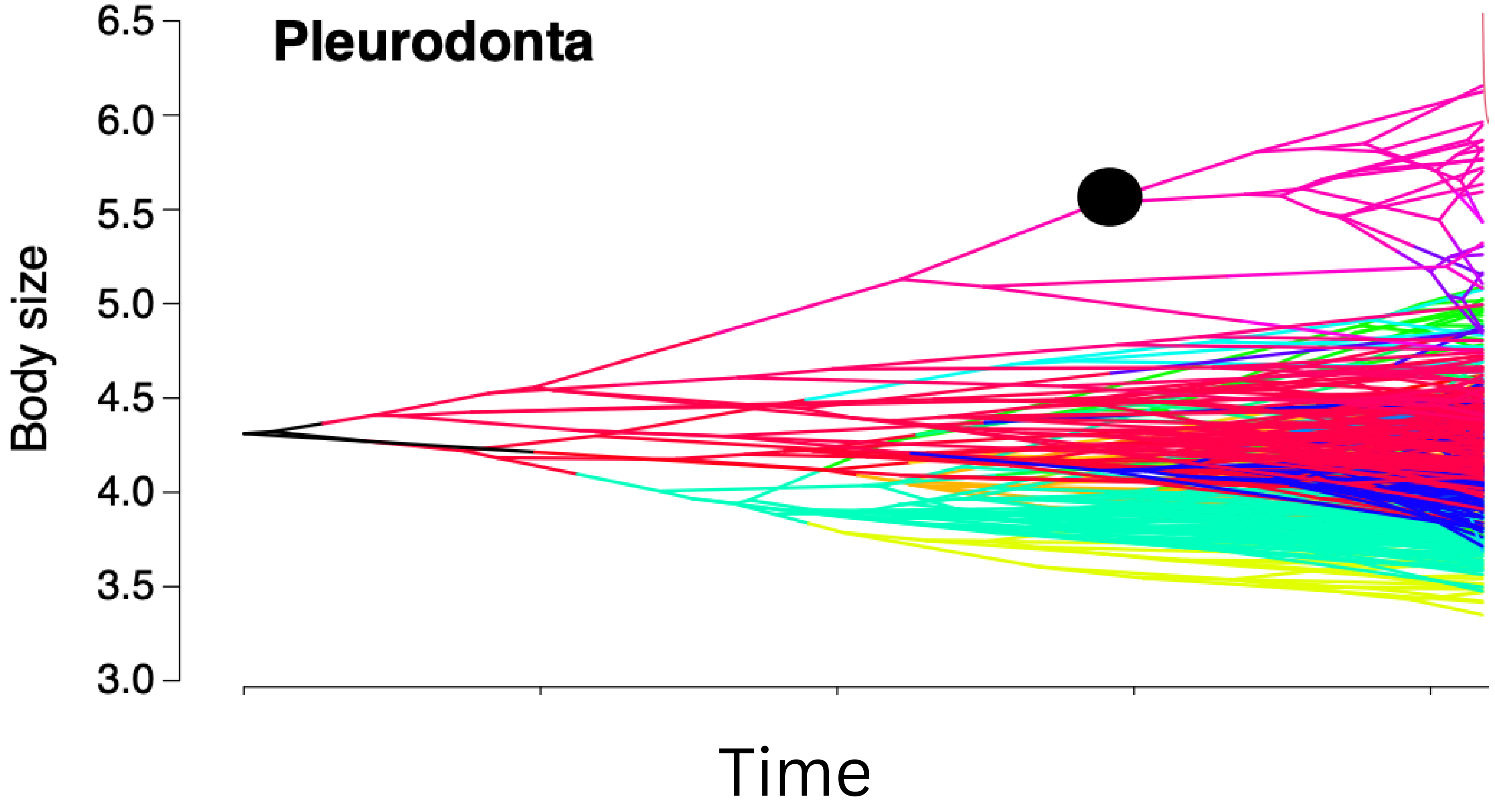
Shifts in the optima or adaptive peaks: different lineages might be evolving toward different optima

Convergence: distant related lineages evolving toward the same optima

WHAT DOES THE OU MODEL TELL US ABOUT EVOLUTION?



Stabilizing selection

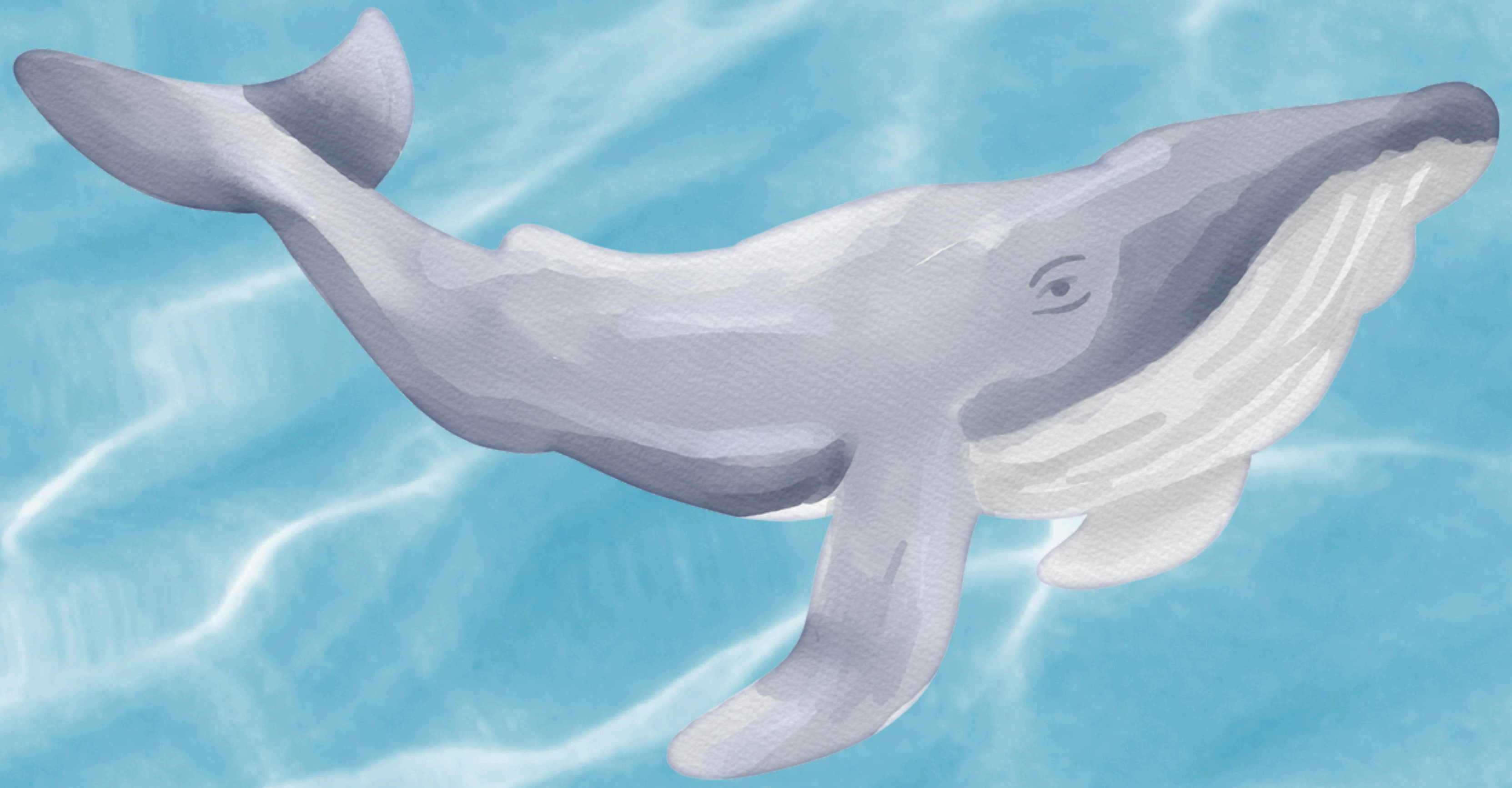
Phymaturus lizards

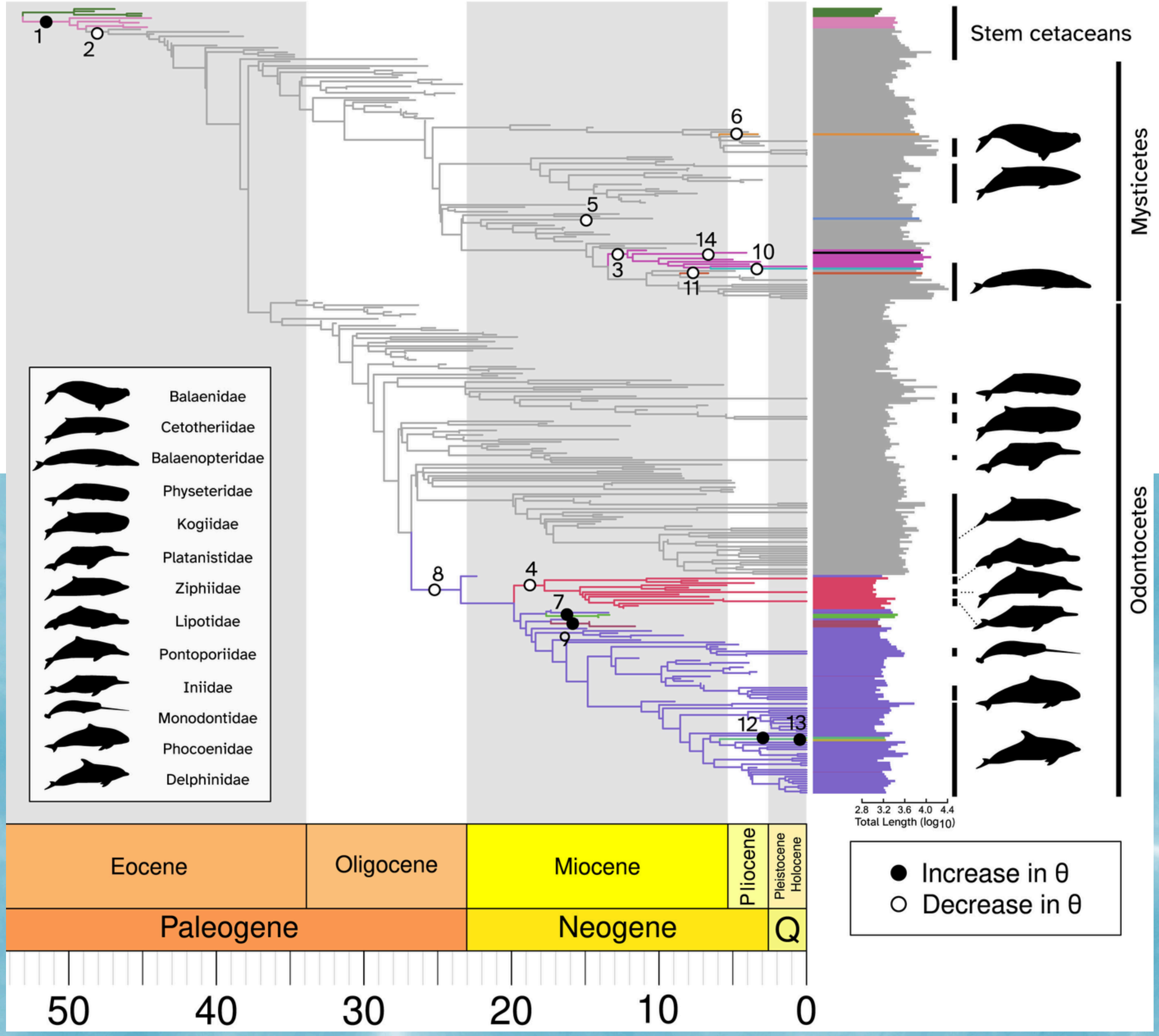
Dry environments?
Viviparity?

Alencar et al. 2024 Evol Lett

WHAT DOES THE OU MODEL TELL US ABOUT EVOLUTION?

Shifts in optima

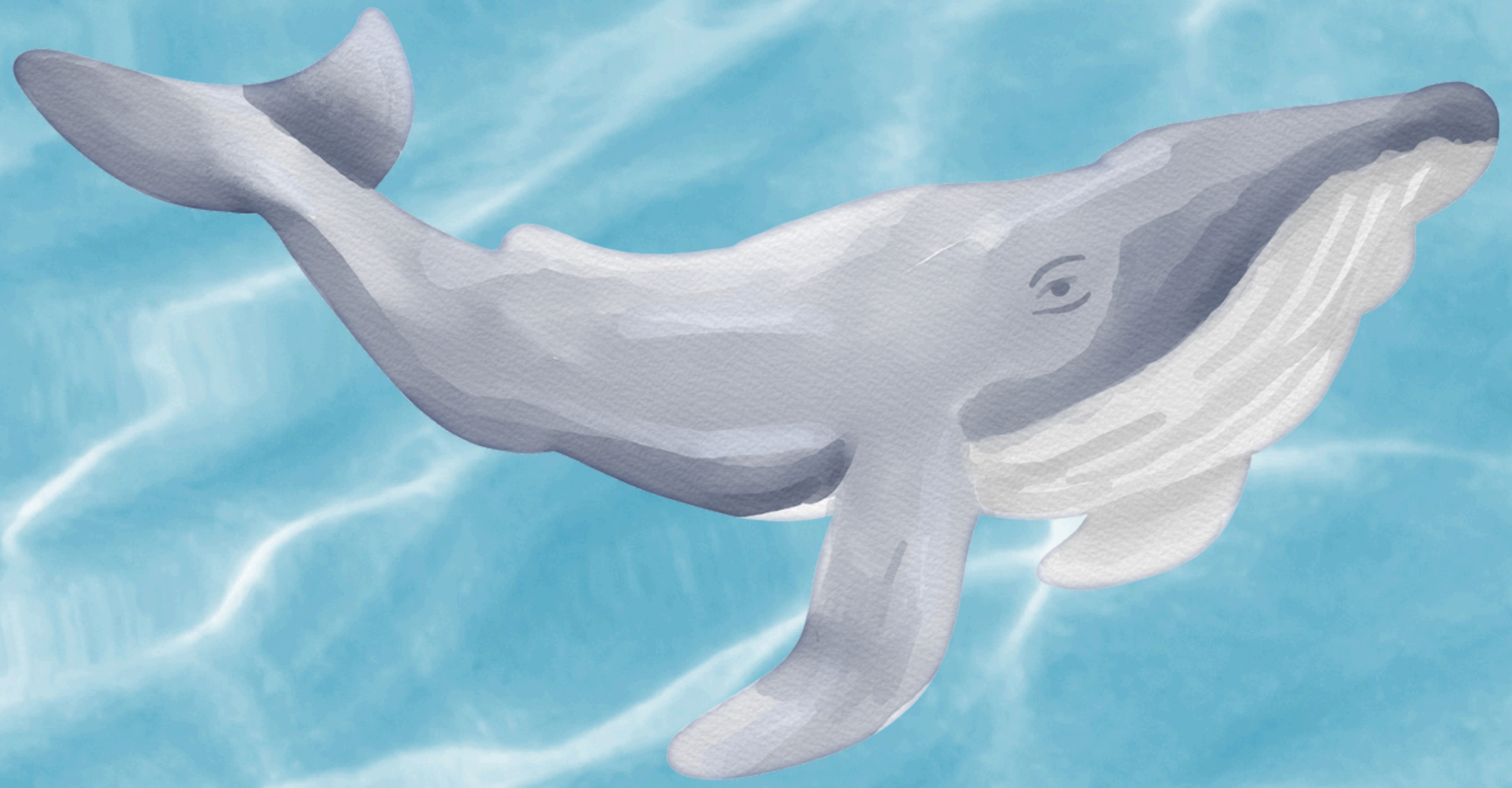




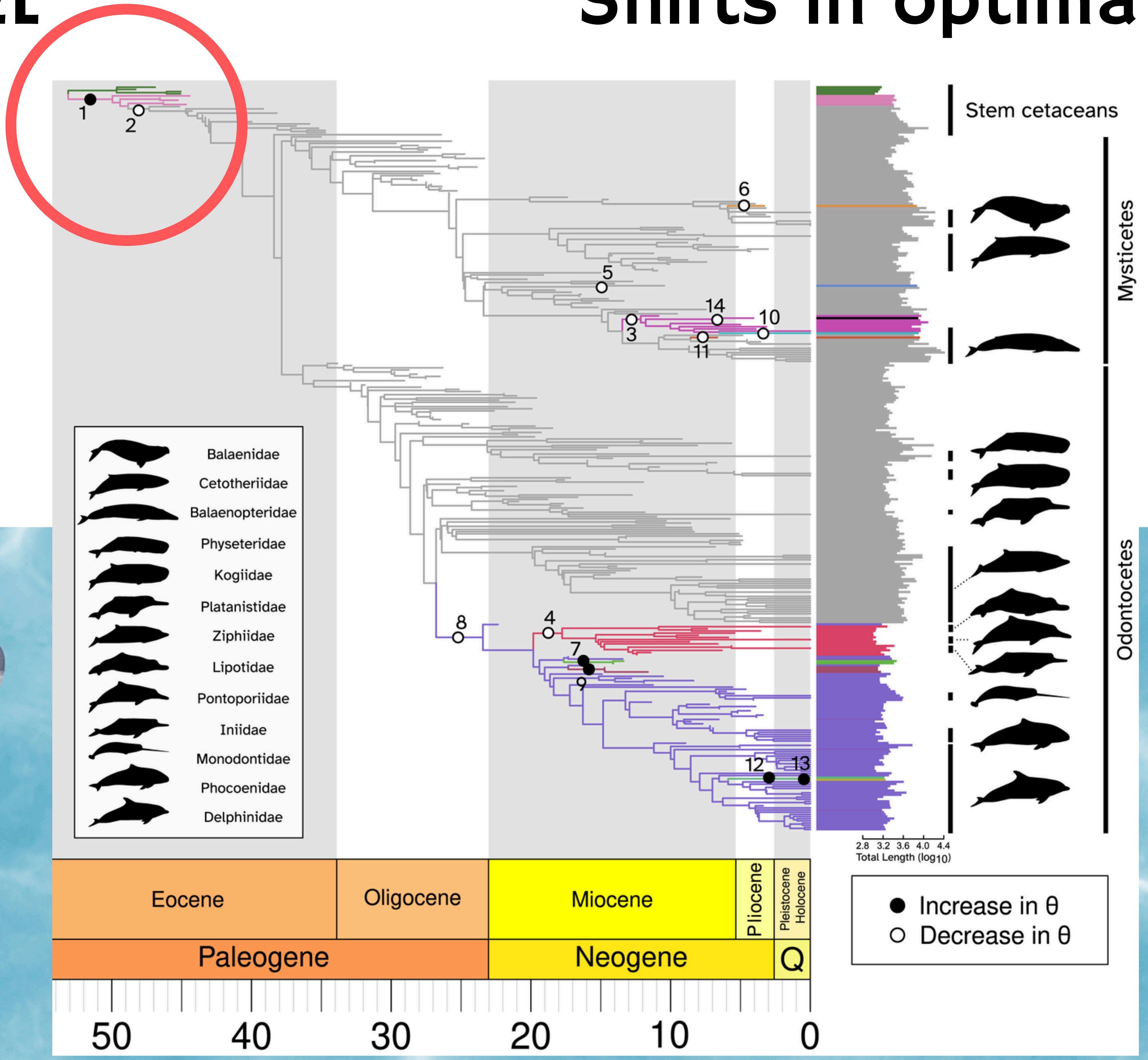
Burin et al. 2023 Curr Biol

WHAT DOES THE OU MODEL TELL US ABOUT EVOLUTION?

- Buoyancy reduces size constraints
- Thermoregulation might favor larger body size



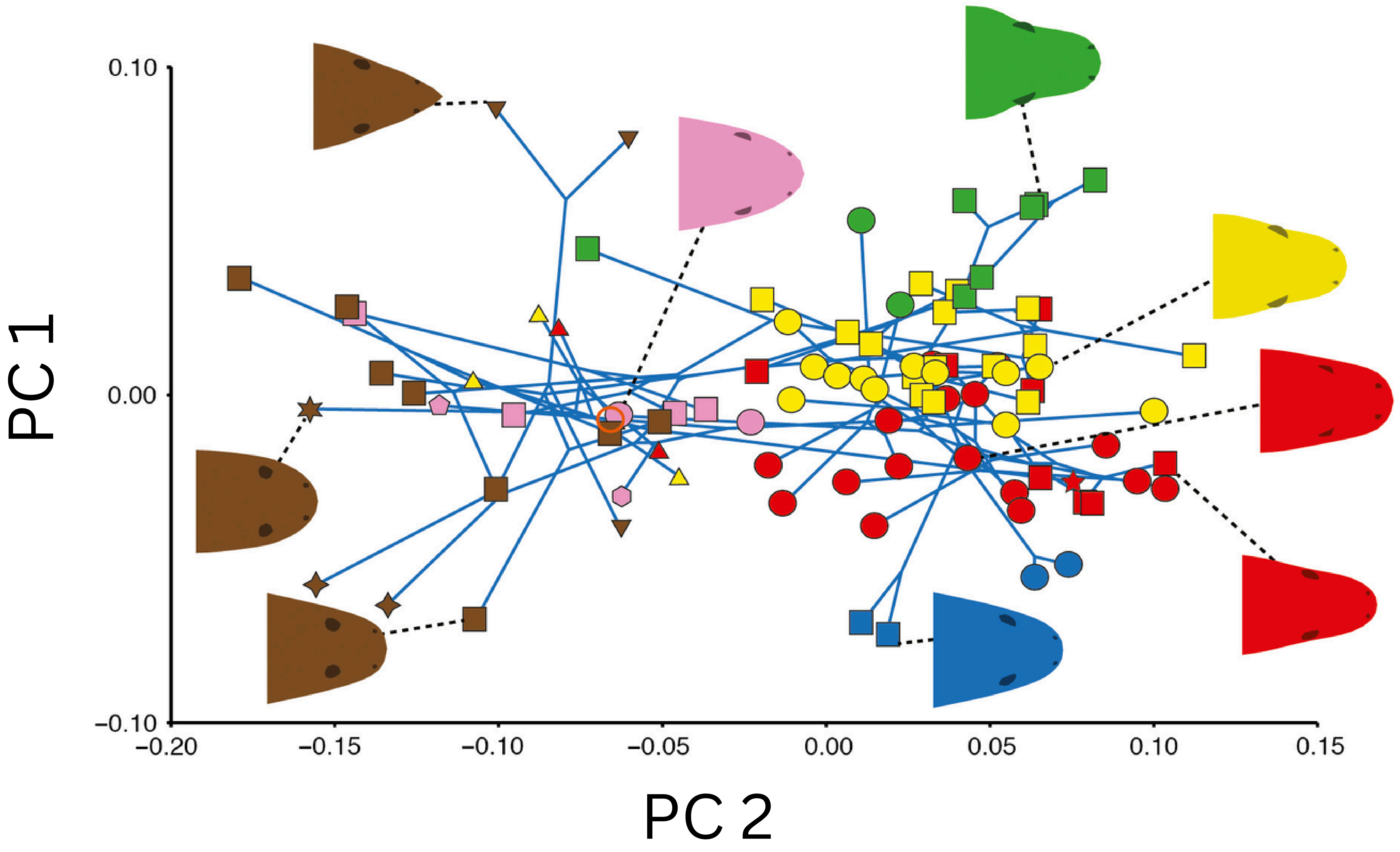
Shifts in optima



Burin et al. 2023 Curr Biol

WHAT DOES THE OU MODEL TELL US ABOUT EVOLUTION?

Convergence



Esquerré & Keogh 2016 Ecol Lett

EXTENSIONS OF OU MODELS

- We can relax the assumption of a single OU process and allow different regimes with distinct α, σ^2, or θ across the tree.

EXTENSIONS OF OU MODELS

	Single rate BM (BM)	Multi-rate BM (BMS)	Single-optimum OU (OU1)	Multi-optima OU (OUM)
sigma	Do not vary	Vary	Do not vary	Do not vary
alpha	0	0	Do not vary	Do not vary
Theta	NA	NA	Do not vary	Vary

EXTENSIONS OF OU MODELS

	Single rate BM (BM)	Multi-rate BM (BMS)	Single-optimum OU (OU1)	Multi-optima OU (OUM)	Multi-optima & rate OU (OUMV)	Multi-optima & alpha OU (OUMA)	Multi-optima & alpha & rate OU (OUMVA)
sigma	Do not vary	Vary	Do not vary	Do not vary	Vary	Do not vary	Vary
alpha	0	0	Do not vary	Do not vary	Do not vary	Vary	Vary
Theta	NA	NA	Do not vary	Vary	Vary	Vary	Vary

EXTENSIONS OF OU MODELS

	Single rate BM (BM)	Multi-rate BM (BMS)	Single-optimum OU (OU1)	Multi-optima OU (OUM)	Multi-optima & rate OU (OUMV)	Multi-optima & alpha OU (OUMA)	Multi-optima & alpha & rate OU (OUMVA)
sigma	**Do not vary**	**Vary**	**Do not vary**	**Do not vary**	**Vary**	**Do not vary**	**Vary**
alpha	**0**	**0**	**Do not vary**	**Do not vary**	**Do not vary**	**Vary**	**Vary**
Theta	**NA**	**NA**	**Do not vary**	**Vary**	**Vary**	**Vary**	**Vary**

MODELING STABILIZING SELECTION: EXPANDING THE ORNSTEIN–UHLENBECK MODEL OF ADAPTIVE EVOLUTION

Jeremy M. Beaulieu , Dwueng-Chwuan Jhwueng , Carl Boettiger , Brian C. O'Meara

Evolution, Volume 66, Issue 8, 1 August 2012, Pages 2369–2383,

R Package OUwie

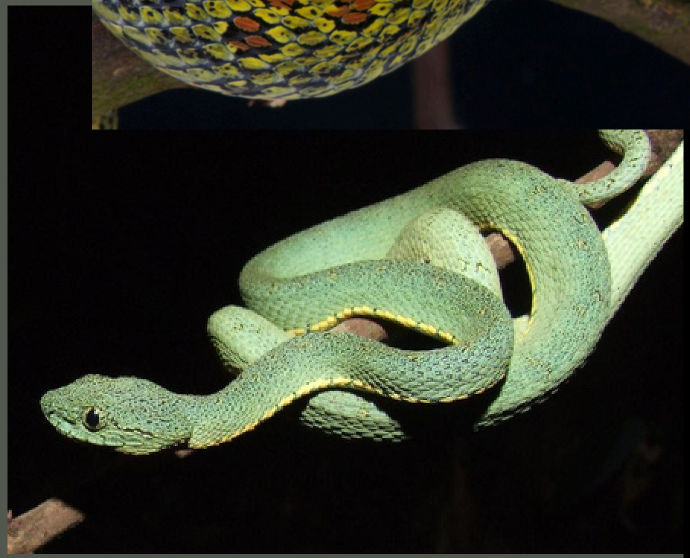
Study case

Arboreality as an adaptive zone in vipers

Alencar et al. 2017 Proc B

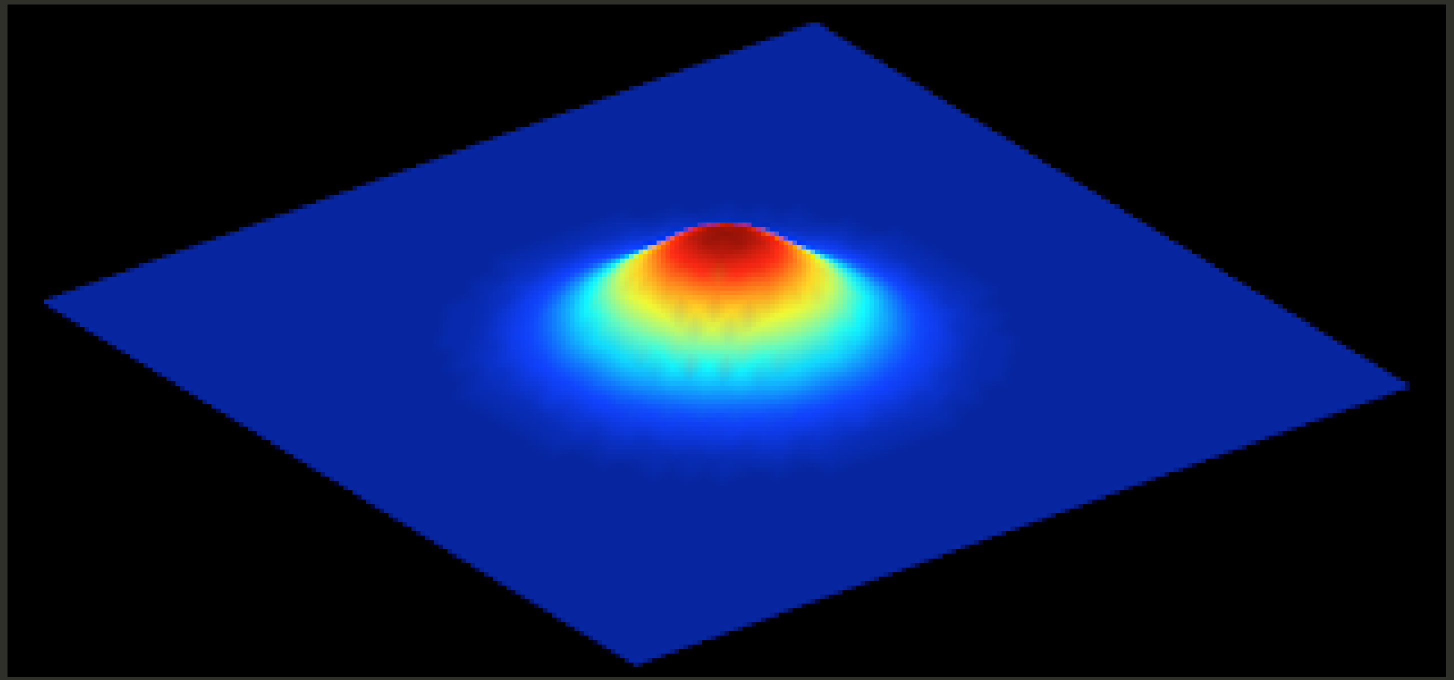
The arboreal environment

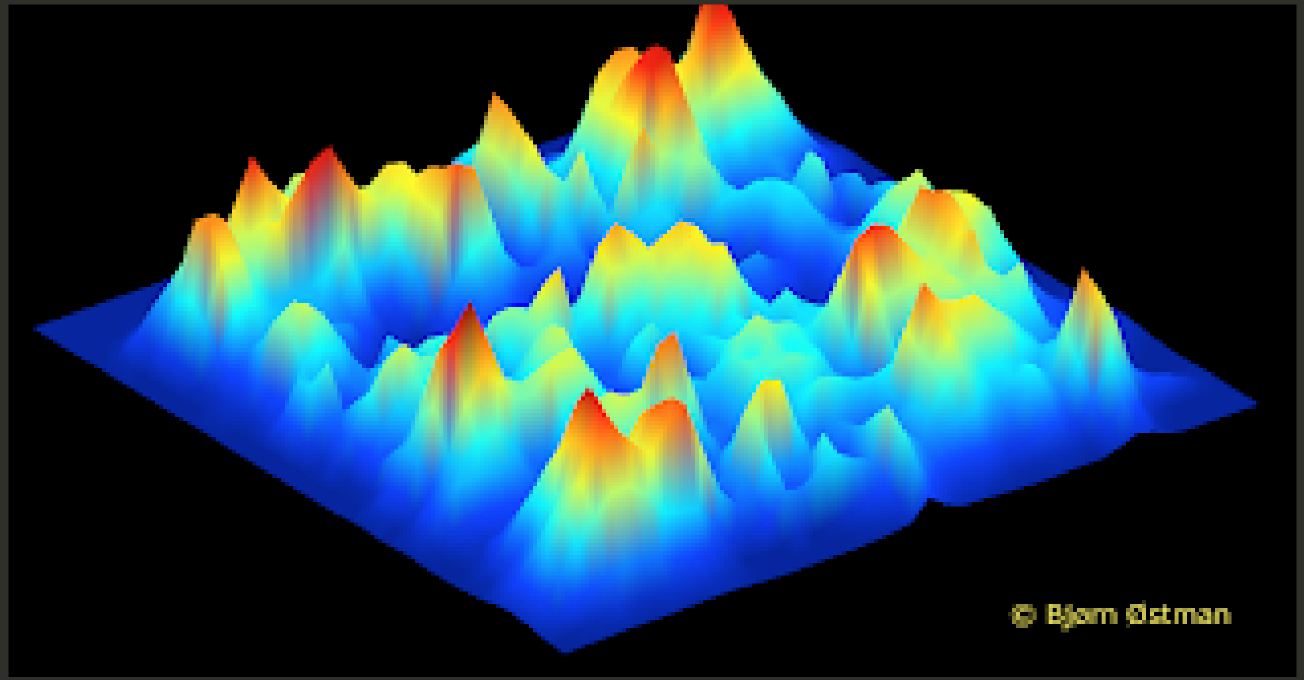
Arboreal



Terrestrial

Hypotheses





ARBOREAL

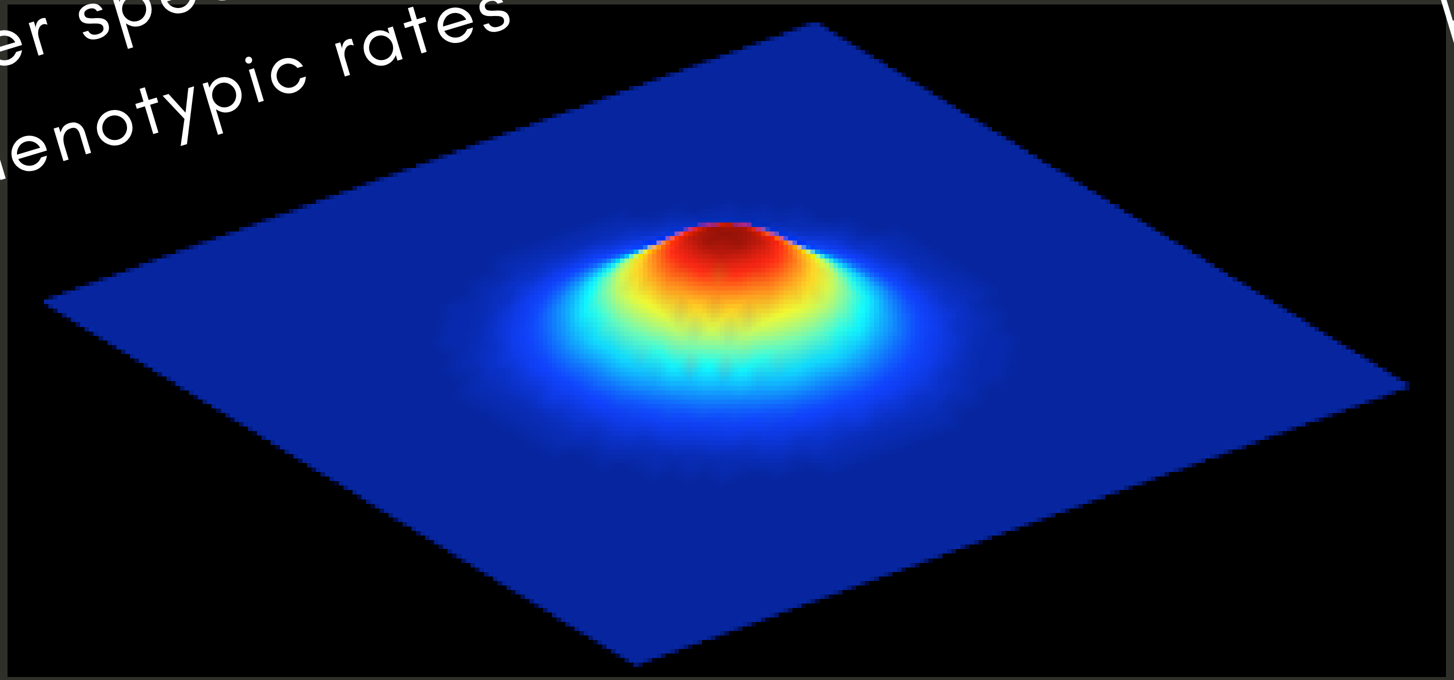
"restricted" adaptive zone

TERRESTRIAL

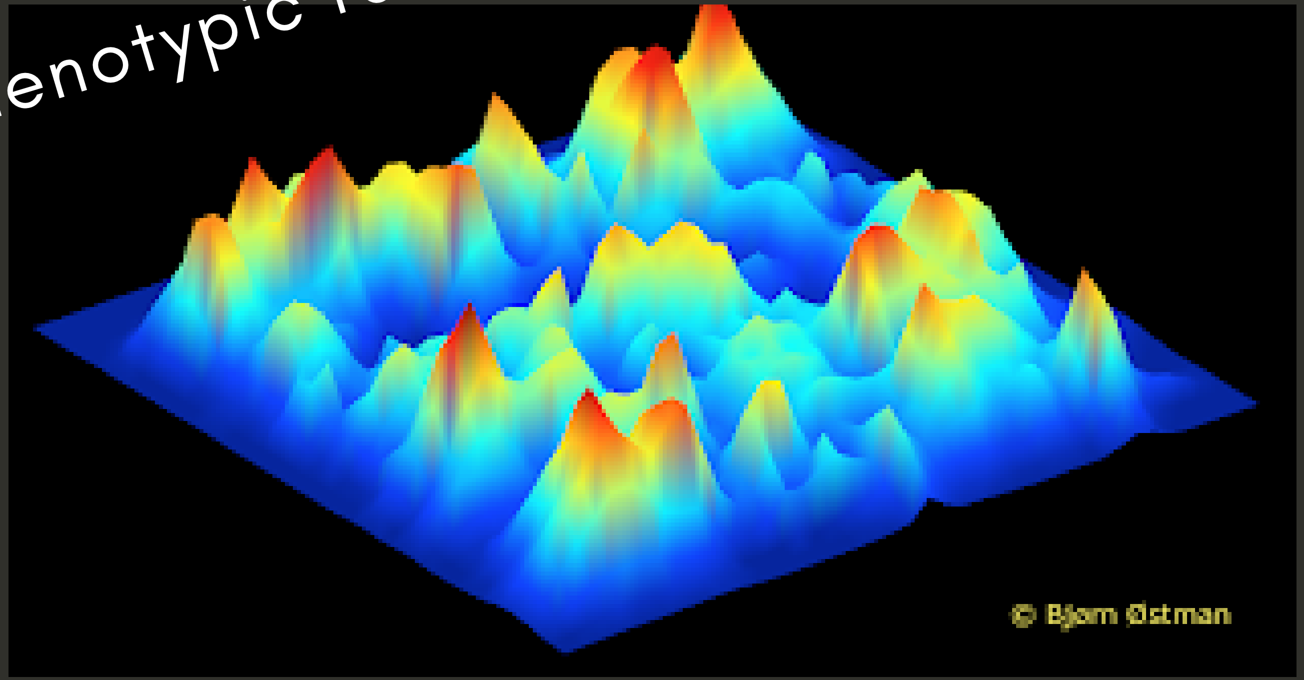
Full of ecological opportunities

Hypotheses

Lower speciation & phenotypic rates



Higher speciation & phenotypic rates



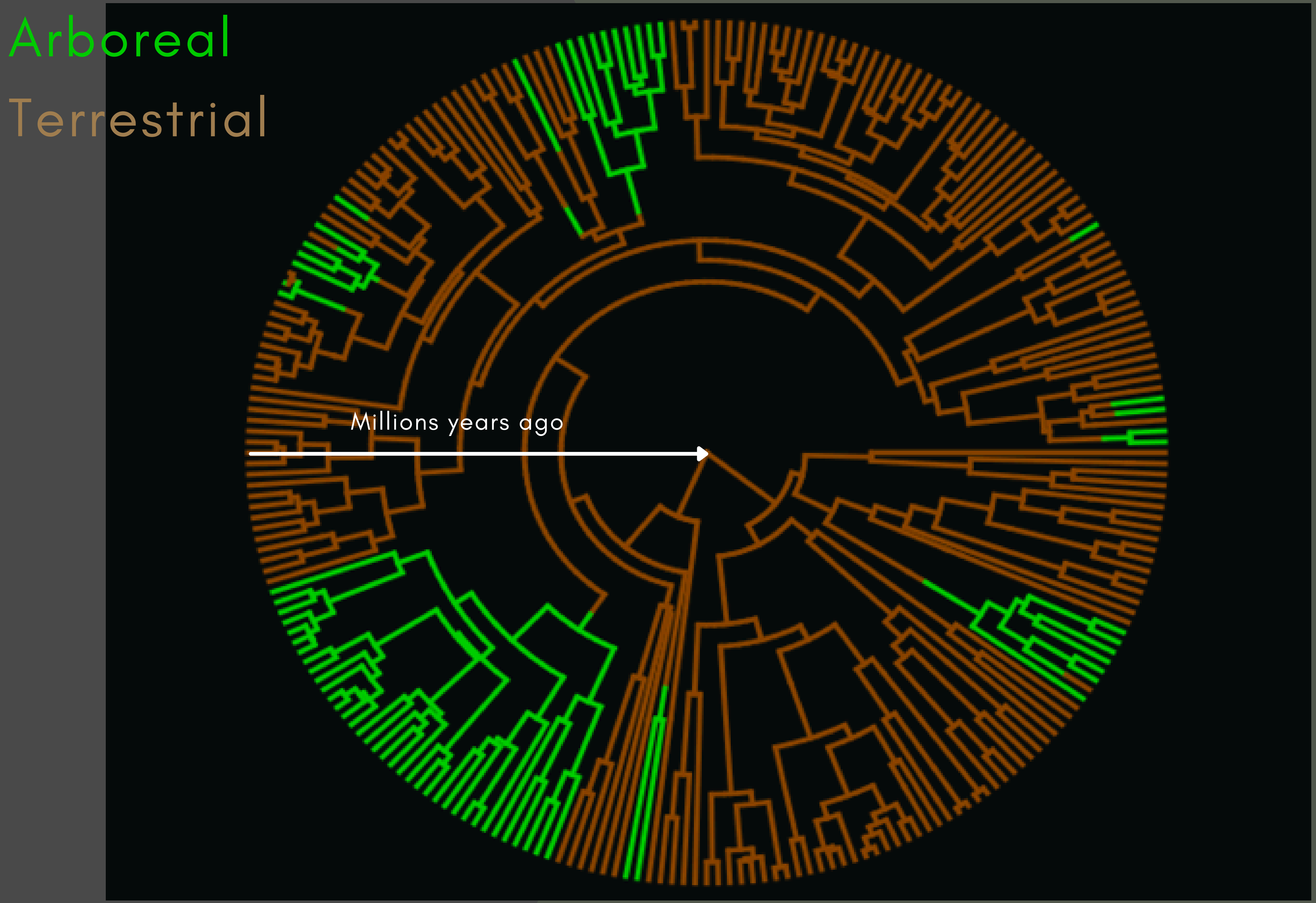
ARBOREAL

"restricted" adaptive zone

TERRESTRIAL

Full of ecological opportunities

Arboreality evolved several times in vipers



To test that...

MOLECULAR PHYLOGENY

Alencar et al. 2016 Mol. Phy. Evol.

COMPARATIVE METHODS

Trait evolution models and species diversification methods

SCIENTIFIC COLLECTIONS

Morphological data

To test that...

MOLECULAR PHYLOGENY

Alencar et al. 2016 Mol. Phy. Evol.

SCIENTIFIC COLLECTIONS

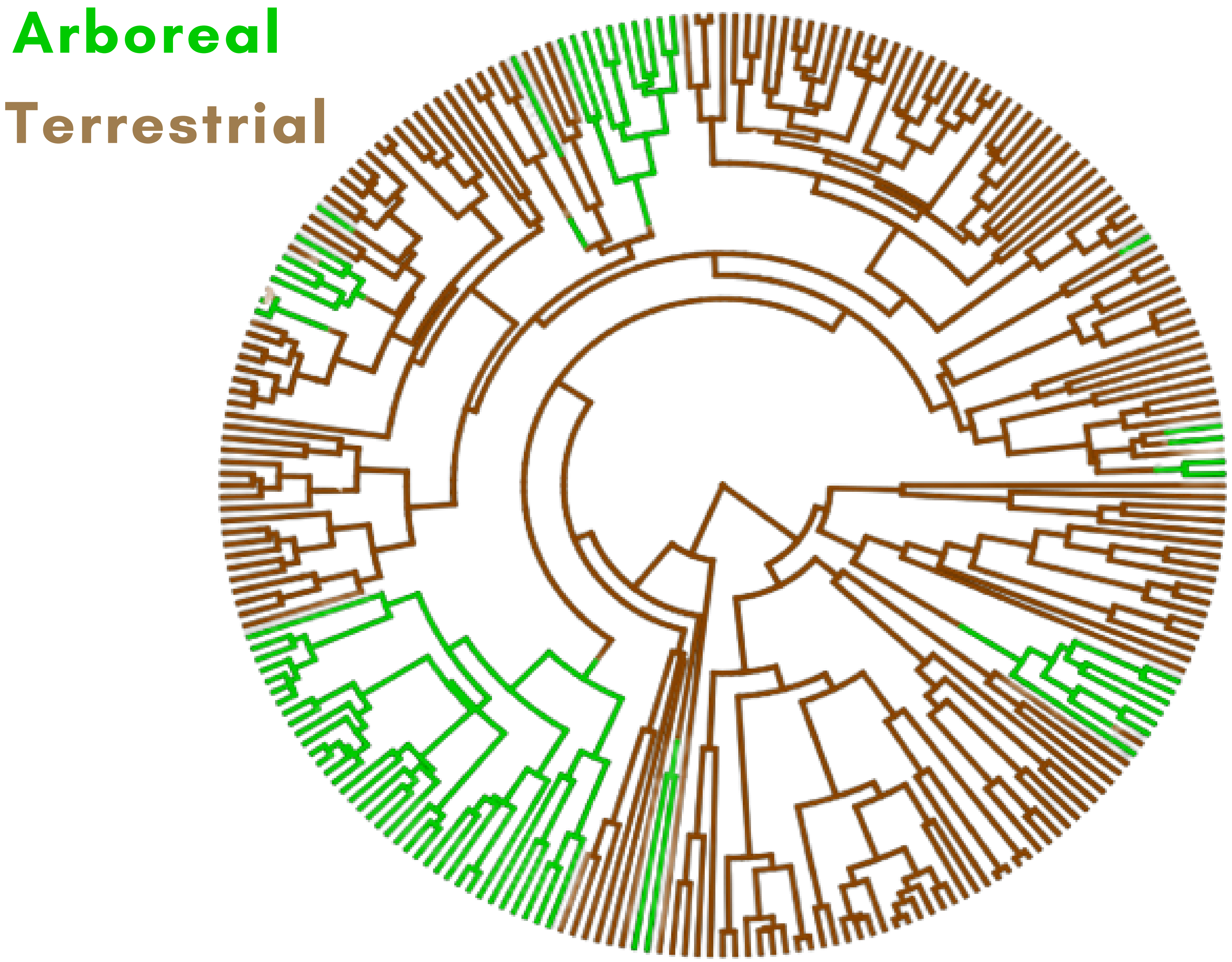
Morphological data

COMPARATIVE METHODS

Trait evolution models and species diversification methods

- Stochastic Character Mapping (habitat use)
- R package OUwie

Stochastic Character Mapping x 1000

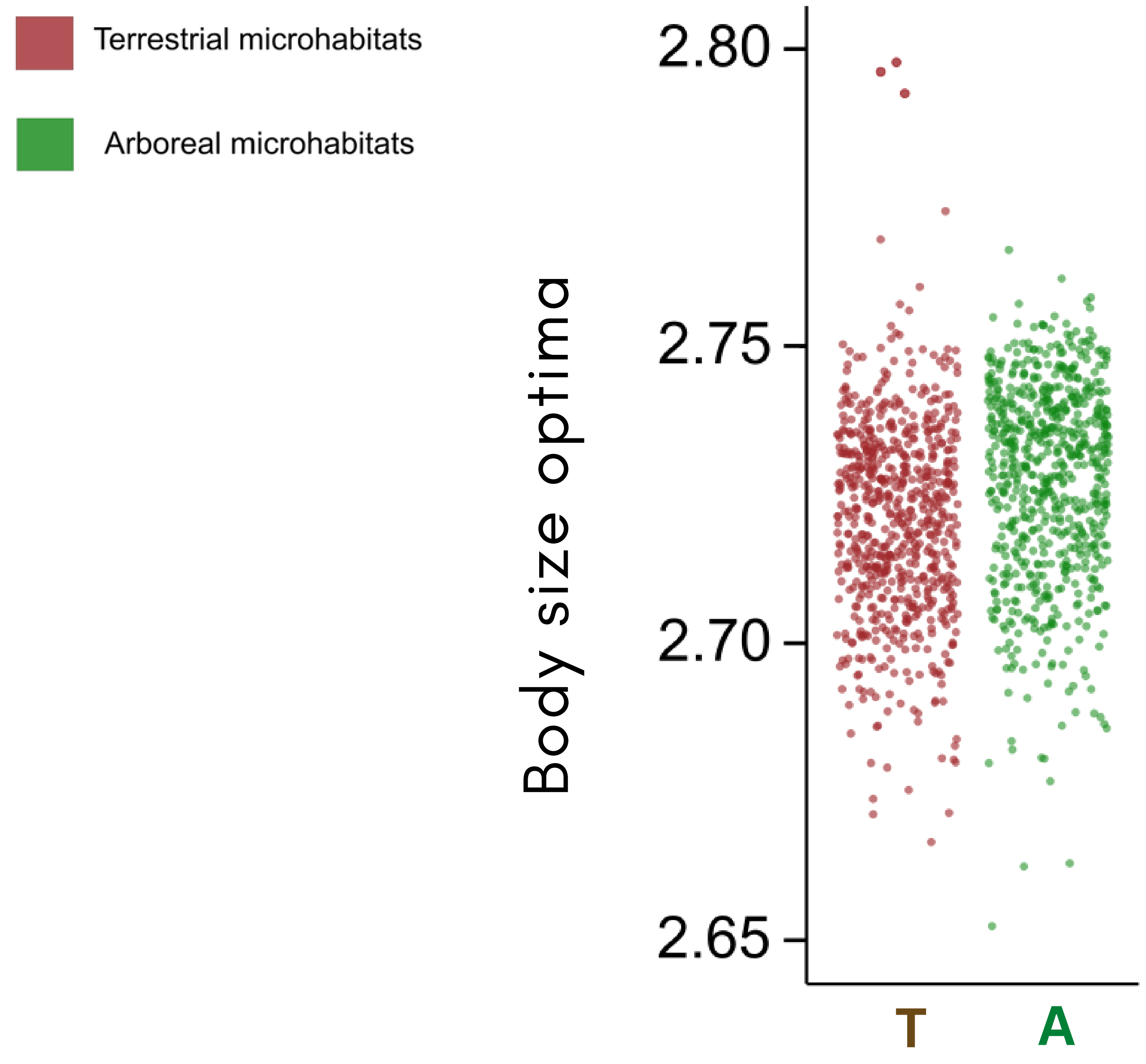


R Package OUwie

	Single rate BM (BM)	Multi-rate BM (BMS)	Single-optimum OU (OU1)	Multi-optima OU (OUM)	Multi-optima & rate OU (OUMV)	Multi-optima & alpha OU (OUMA)	Multi-optima & alpha & rate OU (OUMVA)
sigma	Do not vary	Vary	Do not vary	Do not vary	Vary	Do not vary	Vary
alpha	0	0	Do not vary	Do not vary	Do not vary	Vary	Vary
Theta	NA	NA	Do not vary	Vary	Vary	Vary	Vary

What we found

Arboreal and terrestrial vipers are evolving toward similar <u>body sizes</u>

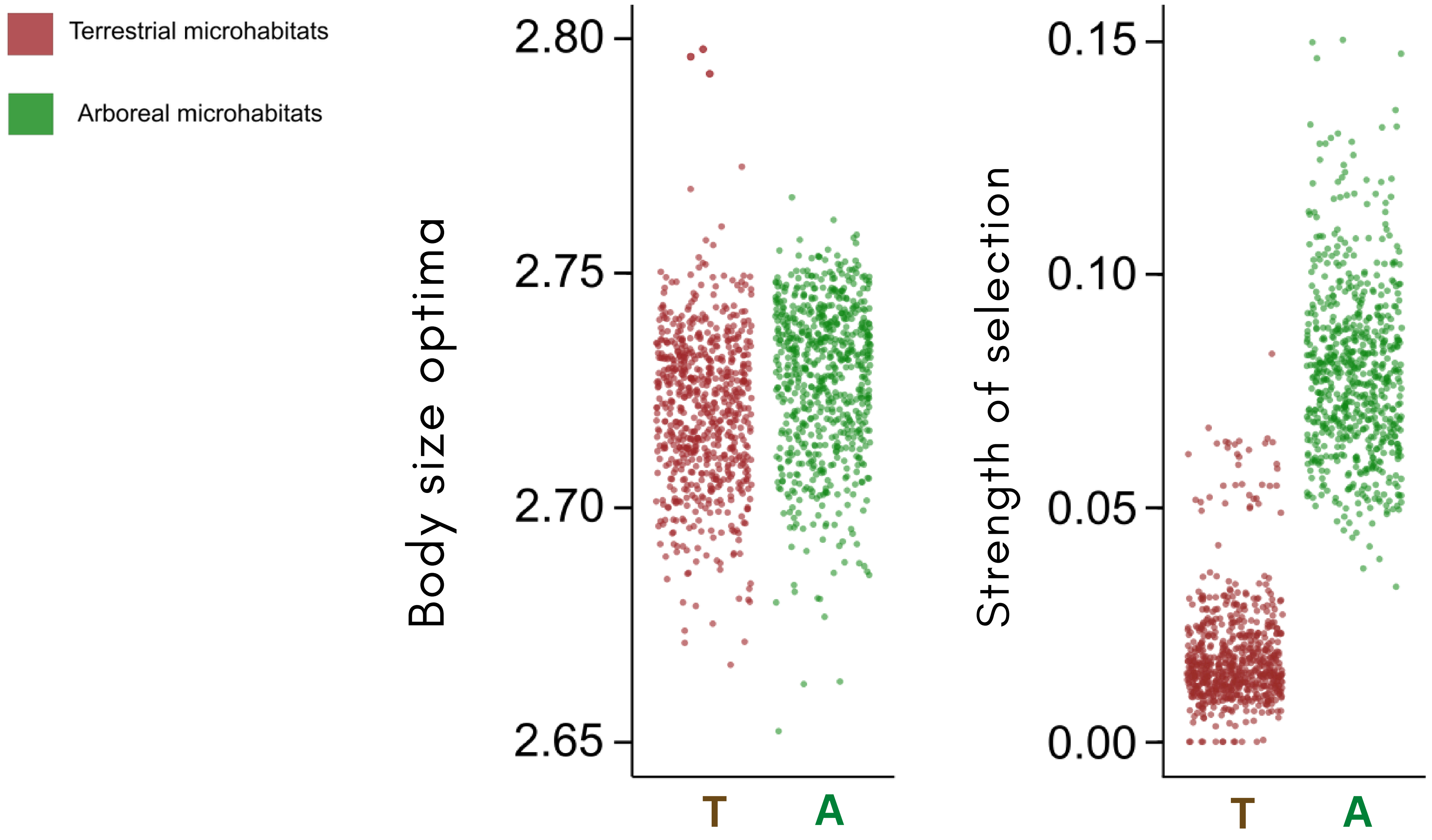


Multi-optima & alpha & rate (OUMVA)

$$dX(t)=\alpha(\theta-X(t))dt+\sigma dW(t)$$

What we found

Body size in arboreal vipers is evolving under stronger selective forces

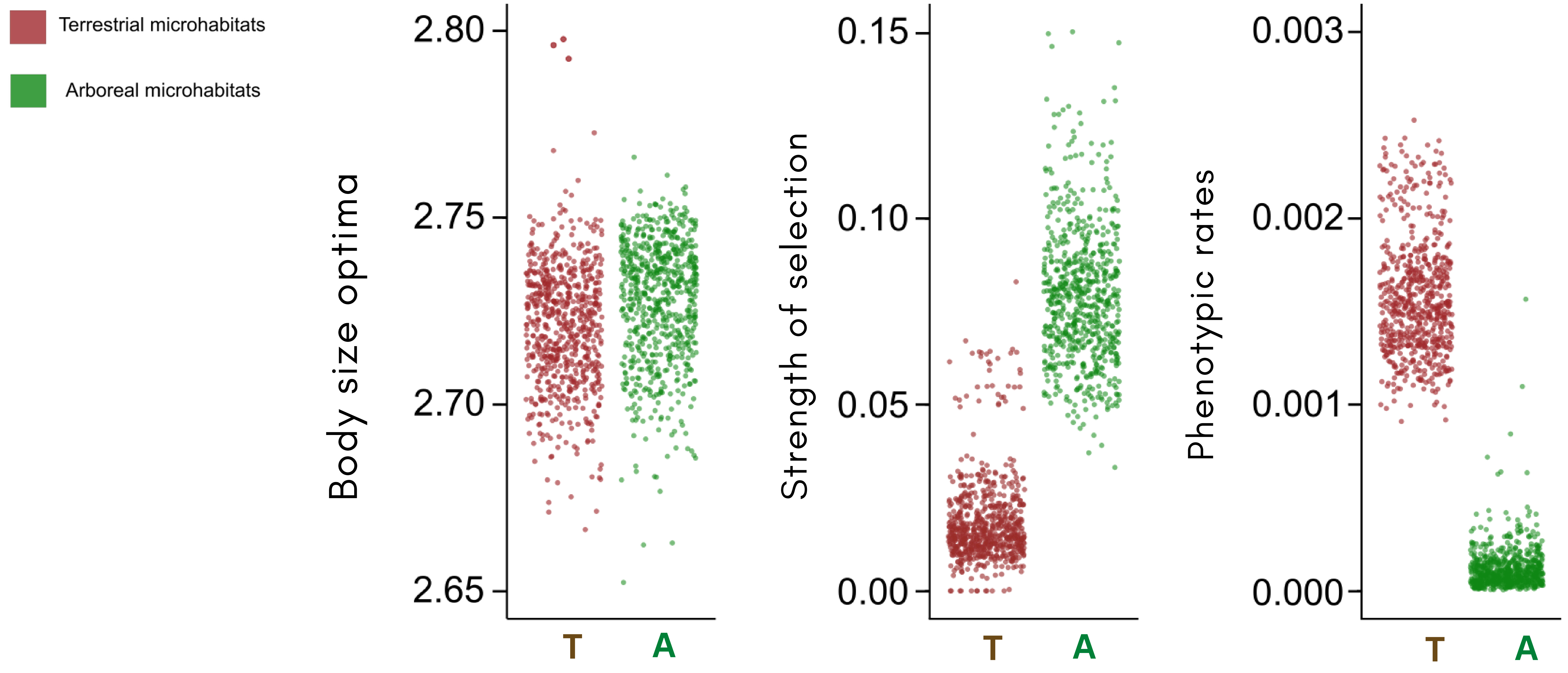


Multi-optima & alpha & rate (OUMVA)

$$dX(t)=\alpha(\theta-X(t))dt+\sigma dW(t)$$

What we found

Body size in arboreal vipers is evolving under a more constrained trajectory

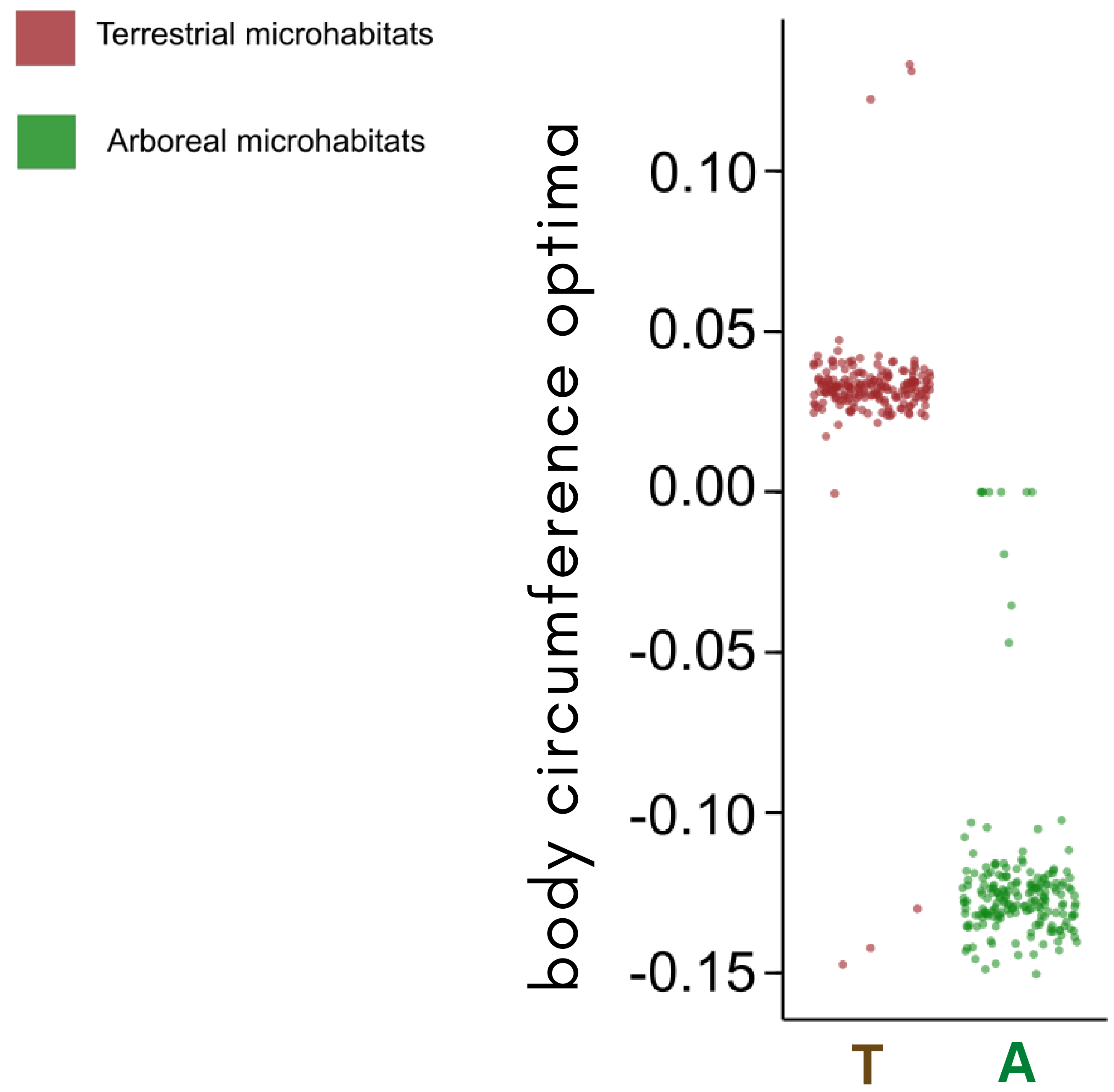


Multi-optima & alpha & rate (OUMVA)

$$dX(t)=\alpha(\theta-X(t))dt+\underline{\sigma}dW(t)$$

What we found

Arboreal vipers are evolving toward smaller <u>body circumference</u>

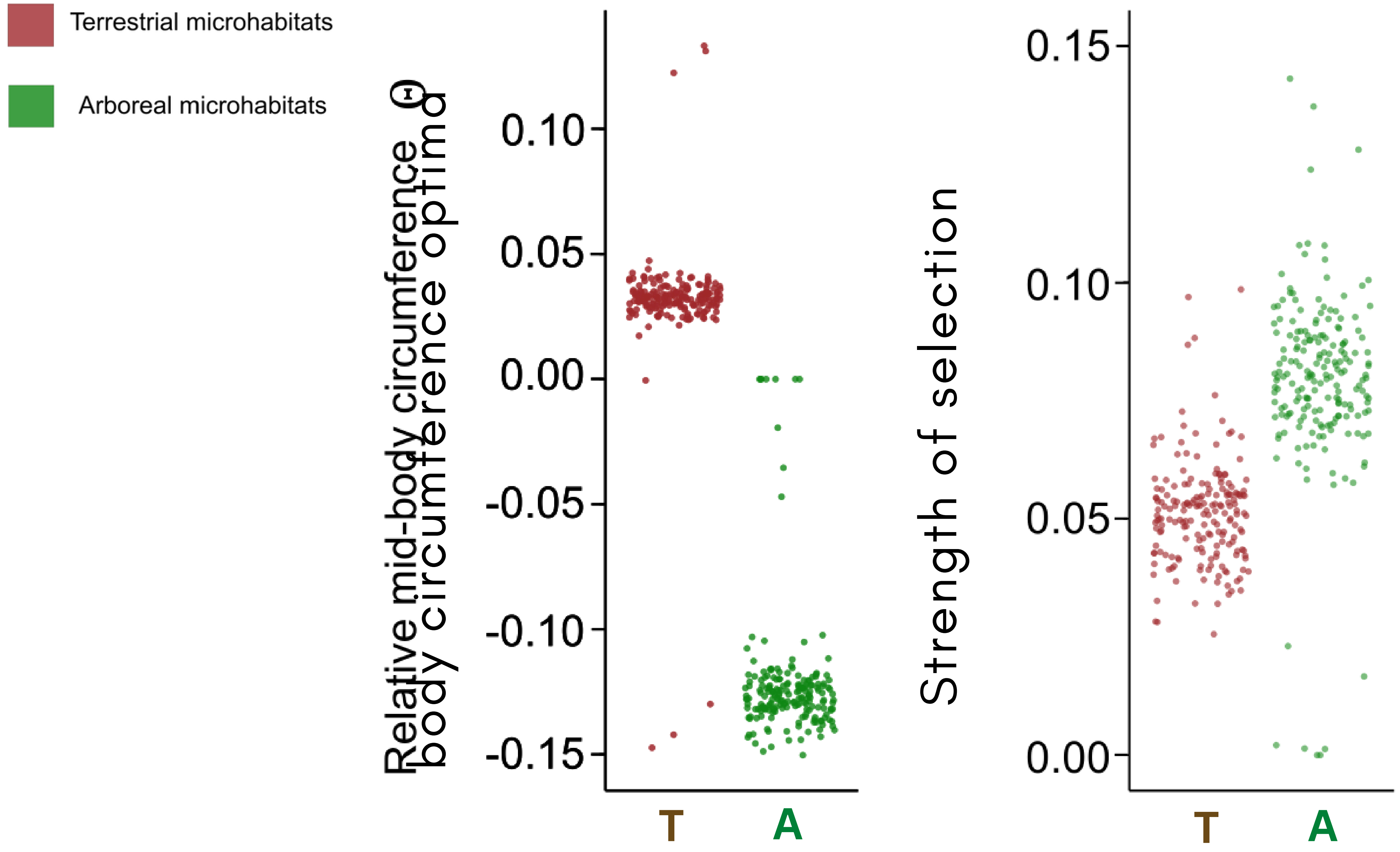


Multi-optima & alpha & rate (OUMVA)

$$dX(t)=\alpha(\theta-X(t))dt+\underline{\sigma}dW(t)$$

What we found

Body circumference in arboreal vipers is evolving under stronger selective forces



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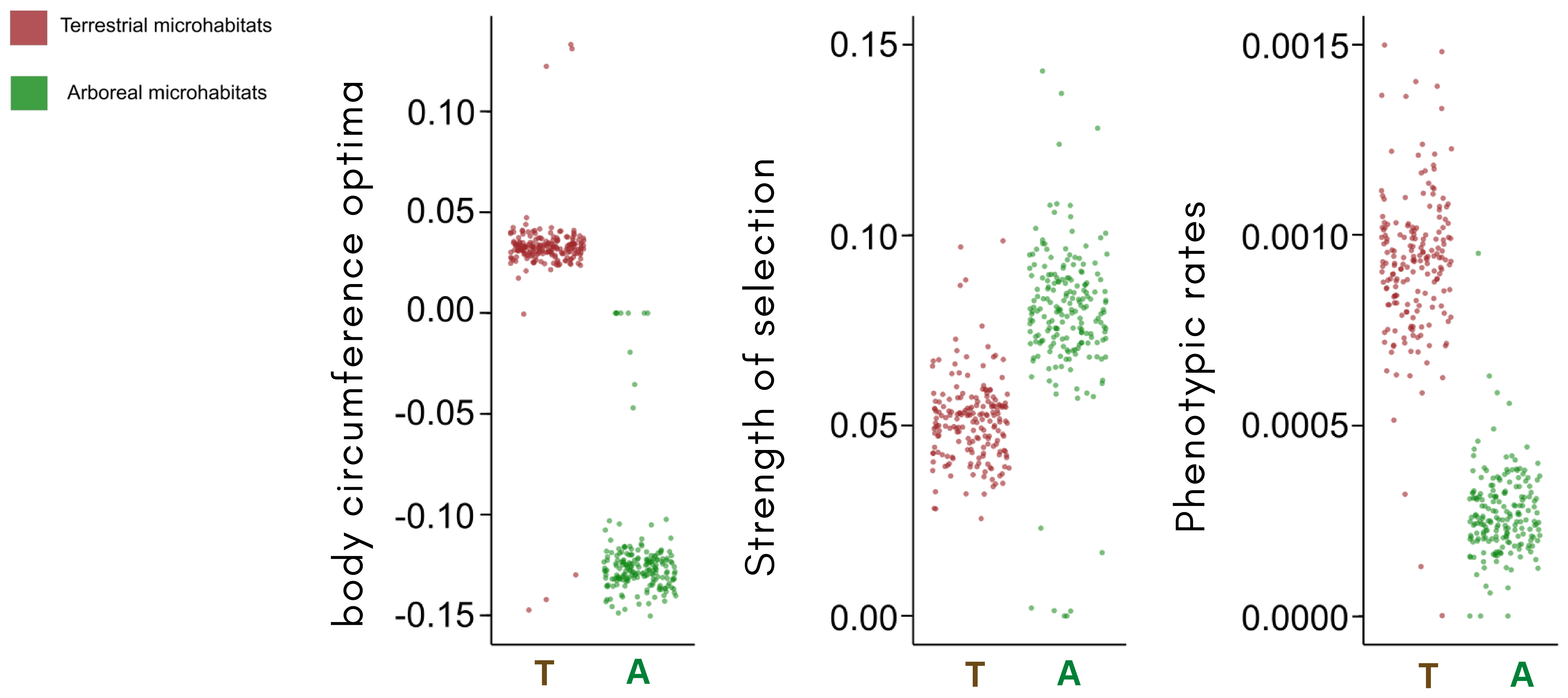
What we found

Body circumference in arboreal vipers is evolving under a more constrained trajectory



Multi-optima & alpha & rate (OUMVA)

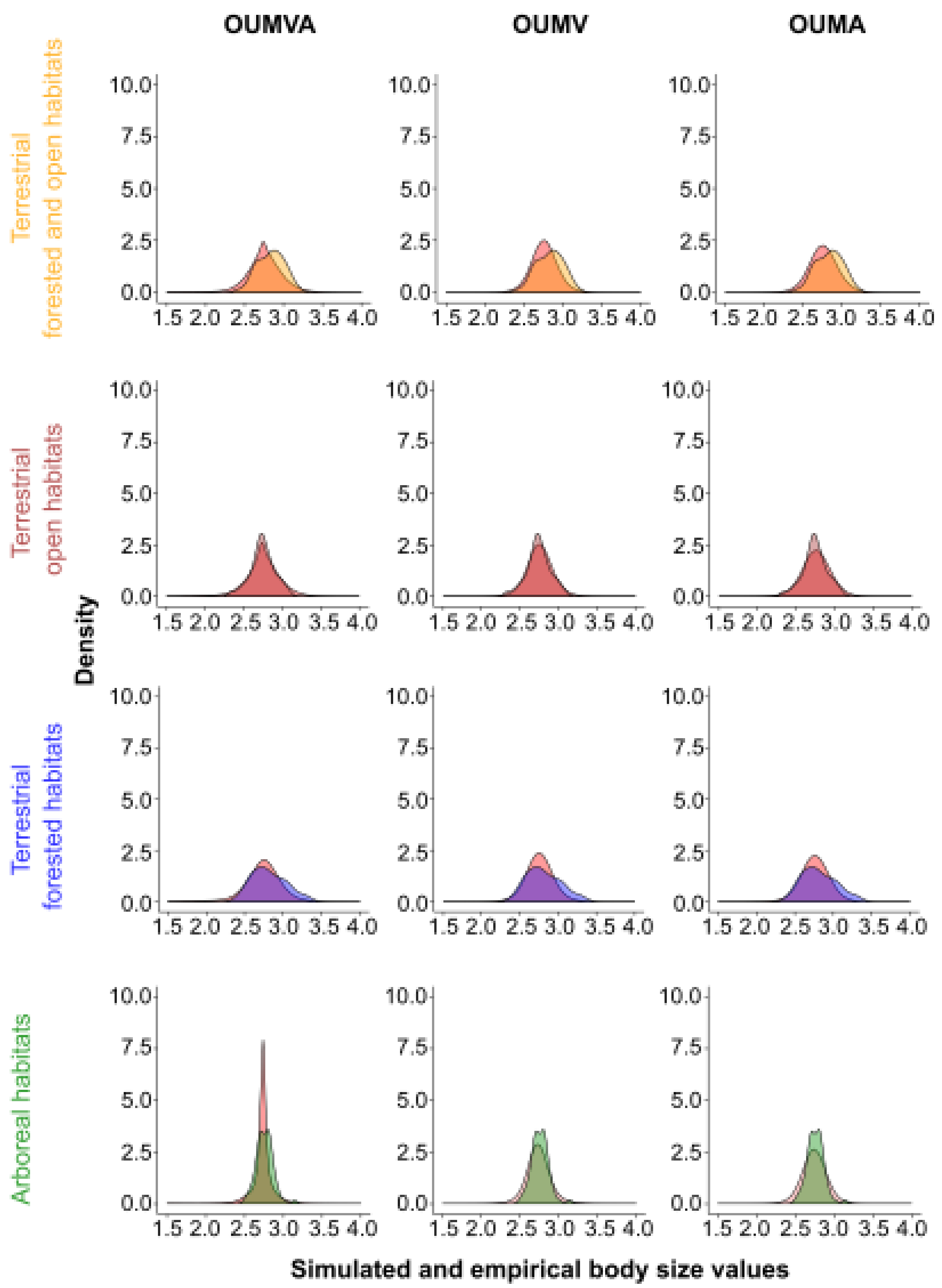
$$dX(t)=\alpha(\theta-X(t))dt+\sigma dW(t)$$

Simulations

The best model isn’t always a good model.

OUwie.sim function

OUwie uses the function OUwie.sim() to simulate trait data under a specified evolutionary model, using parameters provided, typically the ones estimated under your best-fitting model.



Simulated and empirical values show substantial overlap, suggesting that the best model is a good fit to the data.

Simulations

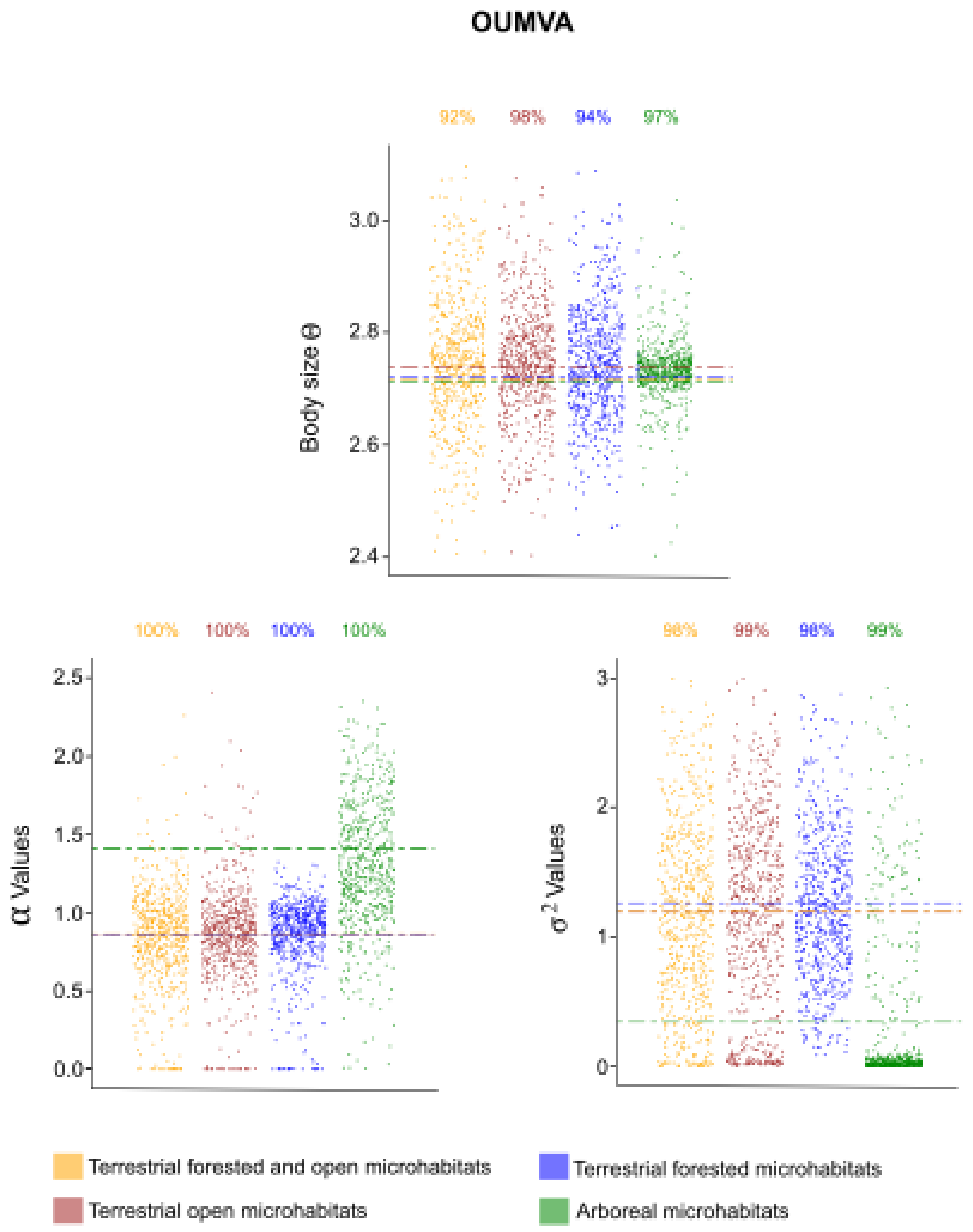
OUwie.boot function

Simulates trait data under your fitted model (using OUwie.sim) and <u>refits</u> the same model to each simulated dataset.

Allows to assess:

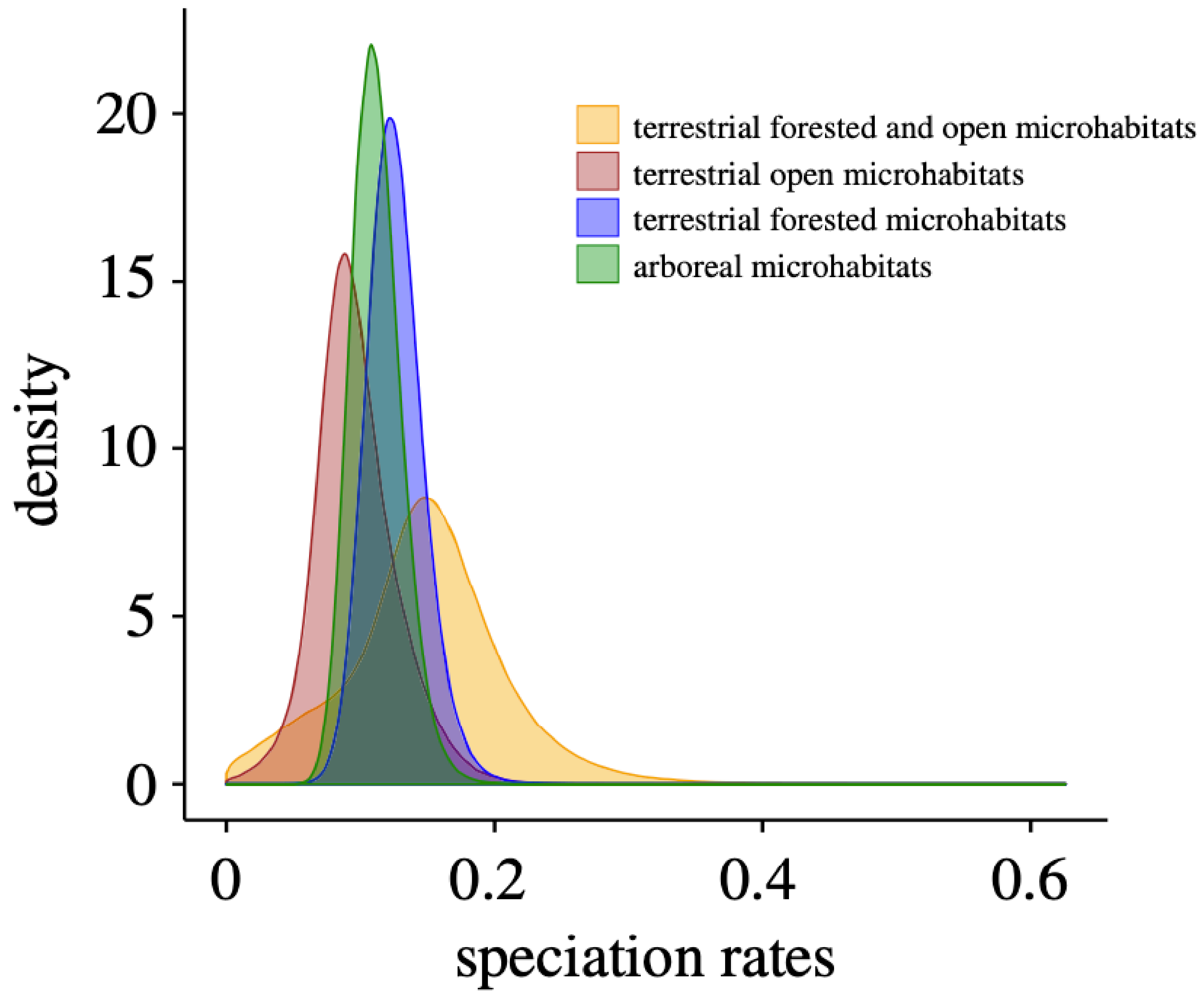
- How stable the parameter estimates are
- Whether the model can recover parameters similar to the original estimates

In general, parameter estimates based on the simulated traits showed the same pattern as the empirical analyses suggested.



What we found

Speciation rates do not differ between arboreal and terrestrial vipers



Conclusions

- Smaller morphological variability does not affect the pace of species formation in vipers
- Morphological evolution and species diversification are decoupled
- Adaptive zones can constrain instead of promote diversifcation

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

bayou

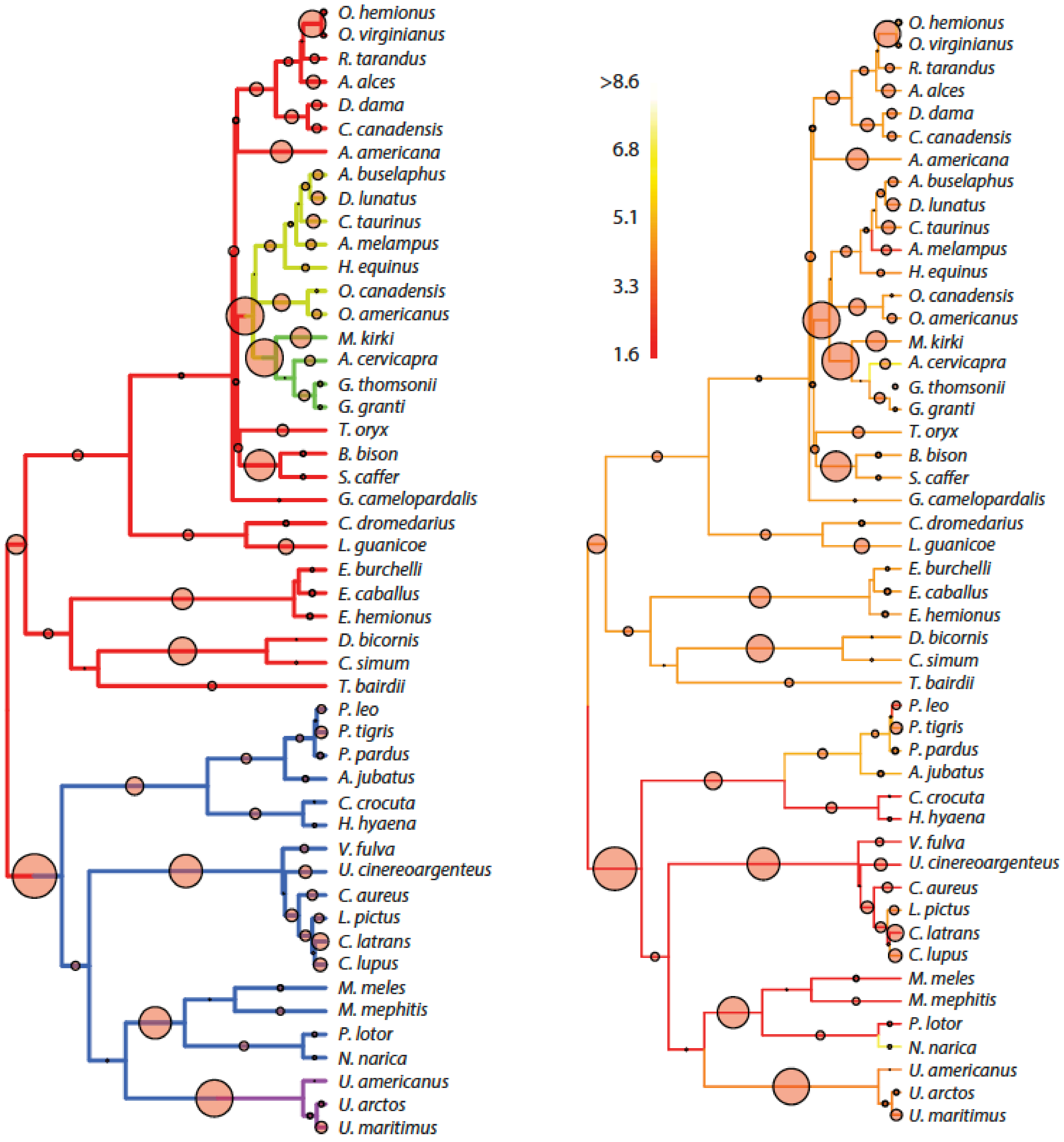
A Novel Bayesian Method for Inferring and Interpreting the Dynamics of Adaptive Landscapes from Phylogenetic Comparative Data

Josef C. Uyeda ✉ , Luke J. Harmon   Author Notes

Systematic Biology, Volume 63, Issue 6, November 2014, Pages 902–918,

- **Usually vary theta (optimum) but assumes single alpha/sigma**
- **Flexible**
- **Bayesian**
- **Model Relationships between traits**
- **Computational intensive**

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION



Revell and Harmon 2022. Phylogenetic comparative methods in R.

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

l1OU

Methods in Ecology and Evolution
British Ecological Society
Methods in Ecology and Evolution 2016, 7, 811–824 doi: 10.1111/2041-210X.12534

Fast and accurate detection of evolutionary shifts in Ornstein–Uhlenbeck models

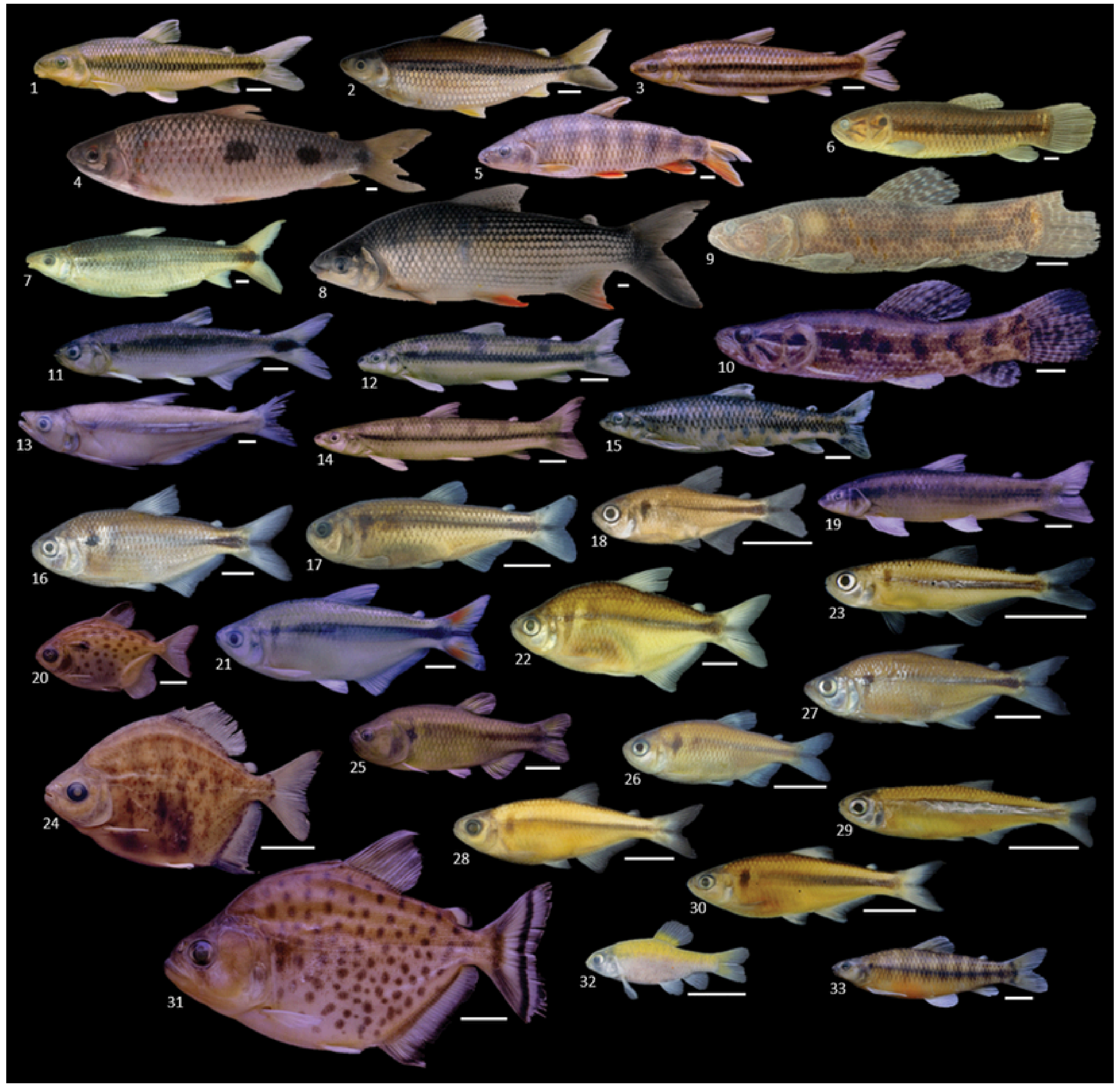
Mohammad Khabbazian[1], Ricardo Kriebel[2], Karl Rohe[3] and Cécile Ané[2,3]*

- Vary theta (optimum) and assumes single alpha/sigma
- ML
- Fast

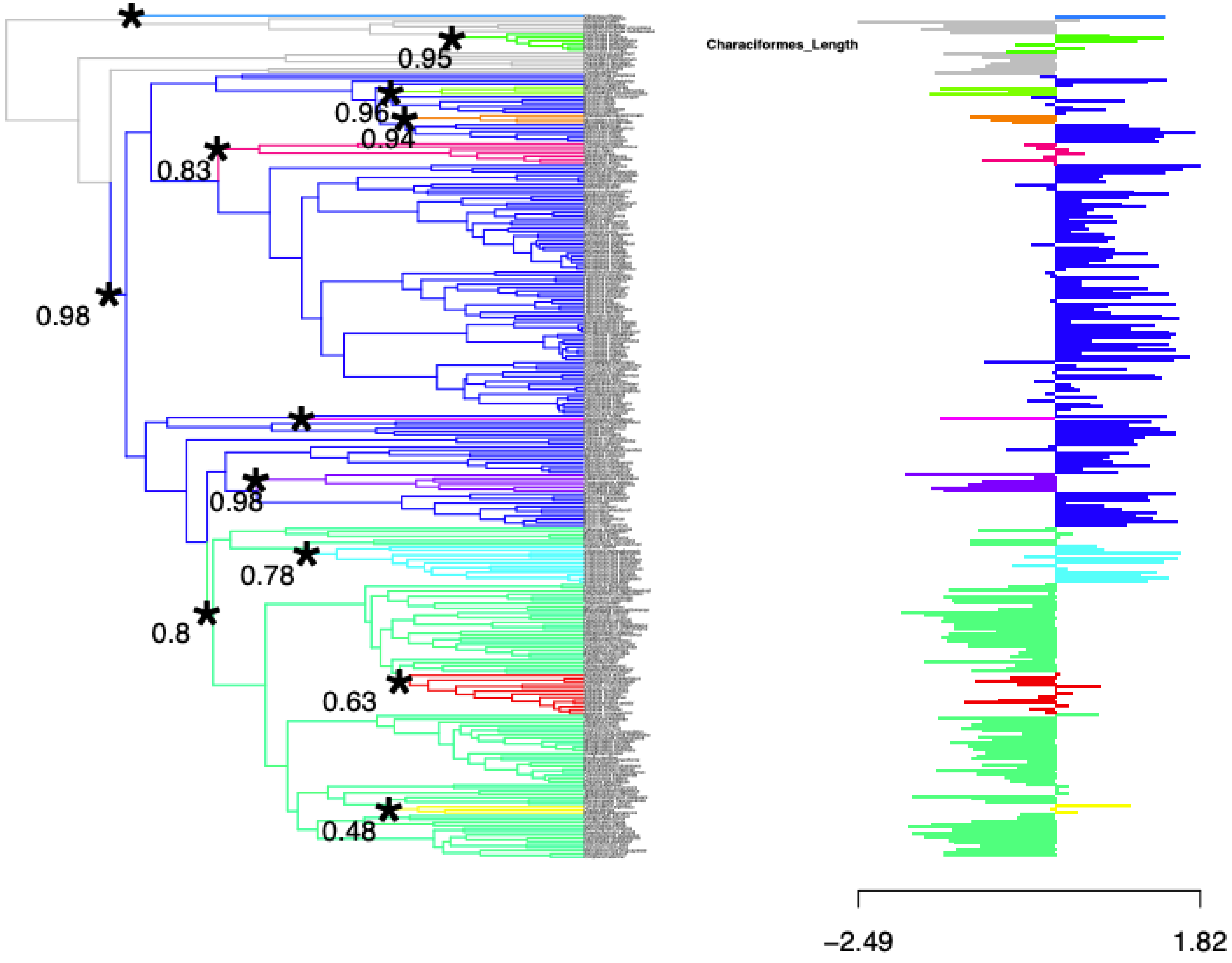
OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

l1OU



Order: Characiformes



Alencar et al. 2022 Evol Evol

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

Methods in Ecology and Evolution

British Ecological Society

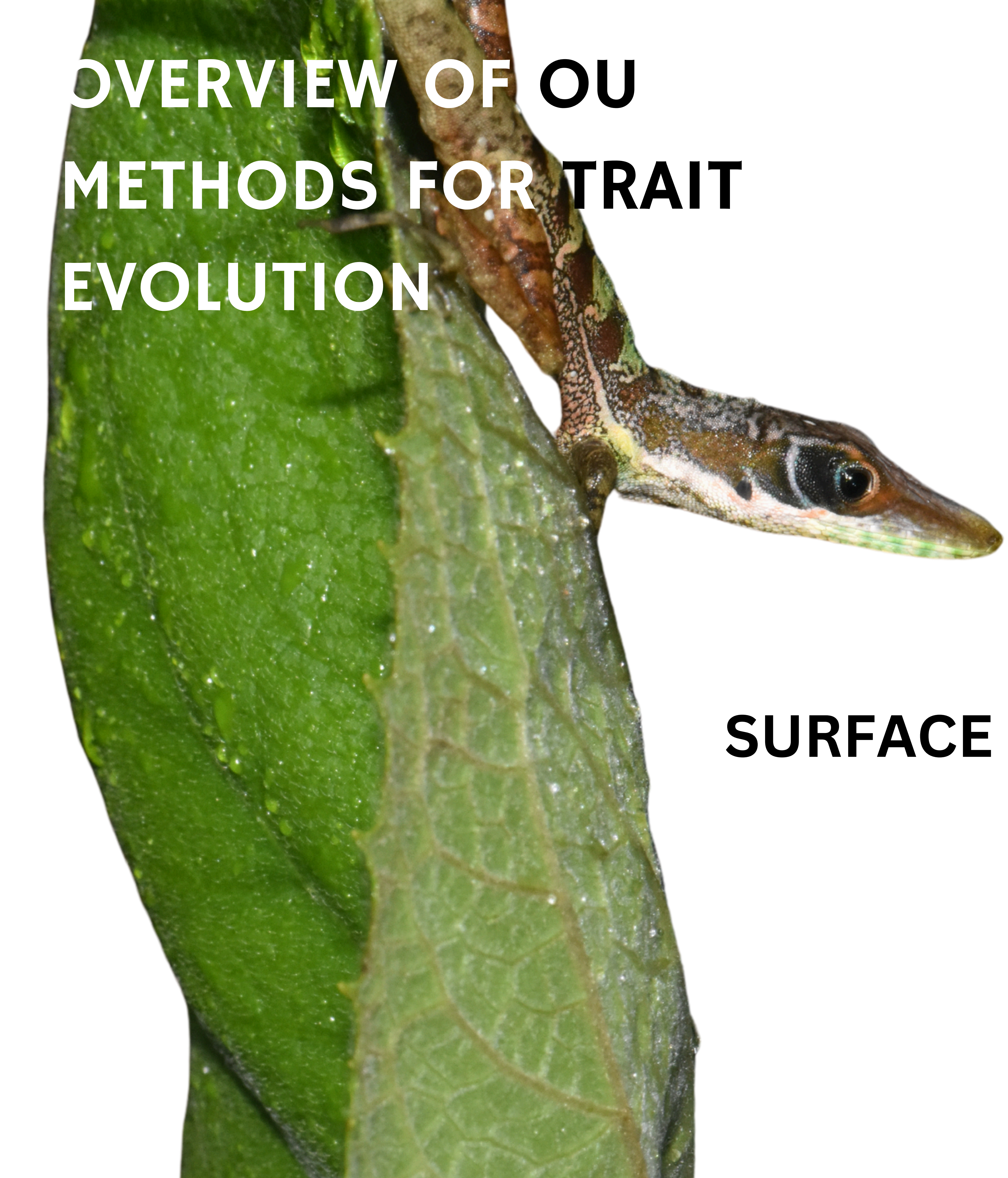
Methods in Ecology and Evolution 2013, **4**, 416–425 doi: 10.1111/2041-210X.12034

SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion

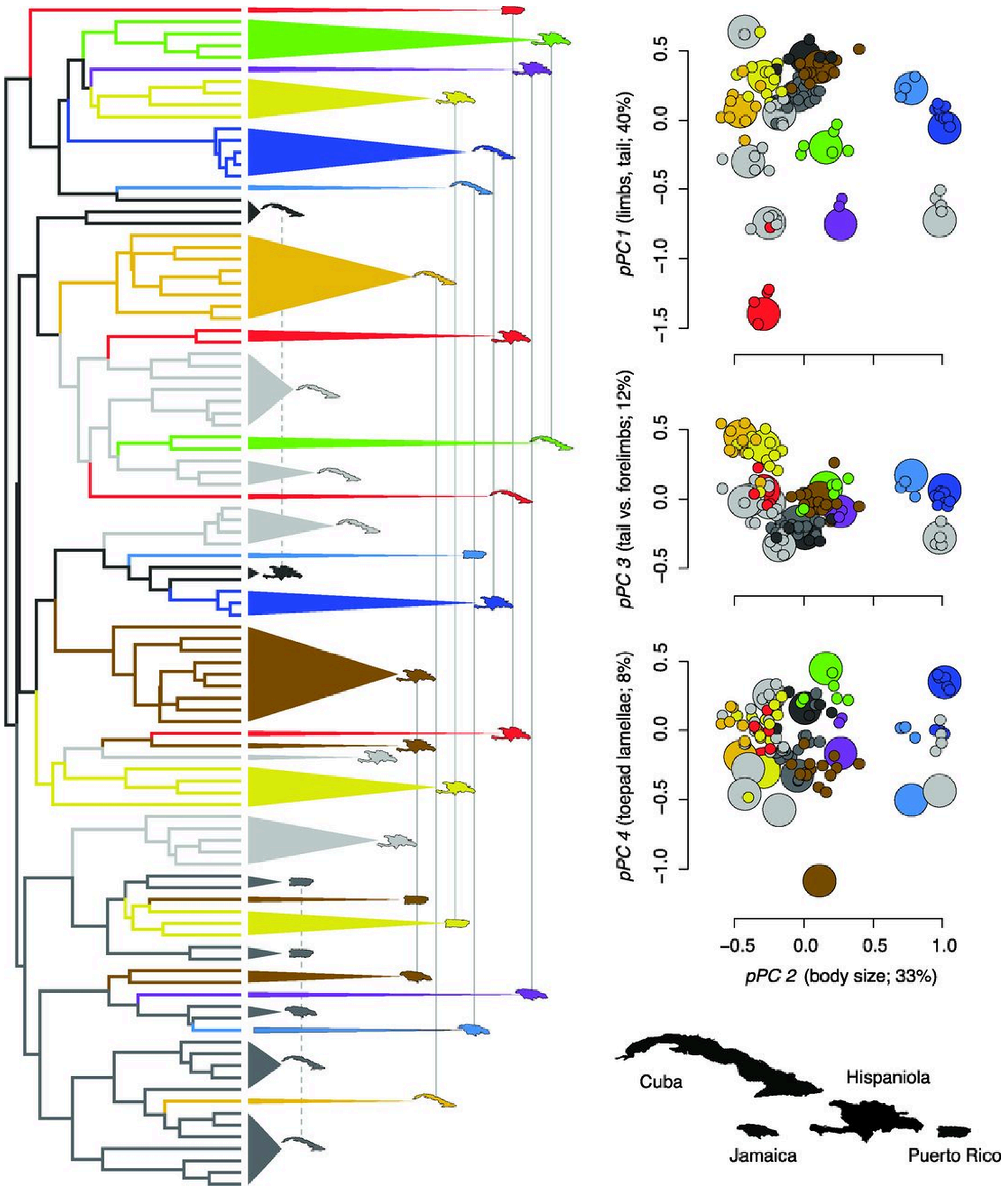
Travis Ingram[1]* and D. Luke Mahler[2]

- Vary theta (optimum) and assumes single alpha/sigma
- ML, Stepwise AIC
- Convergence
- Fast?

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION



SURFACE



Mahler et al. 2013 Science

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

Automatic generation of evolutionary hypotheses using mixed Gaussian phylogenetic models

Venelin Mitov, Krzysztof Bartoszek, and Tanja Stadler Authors Info & Affiliations

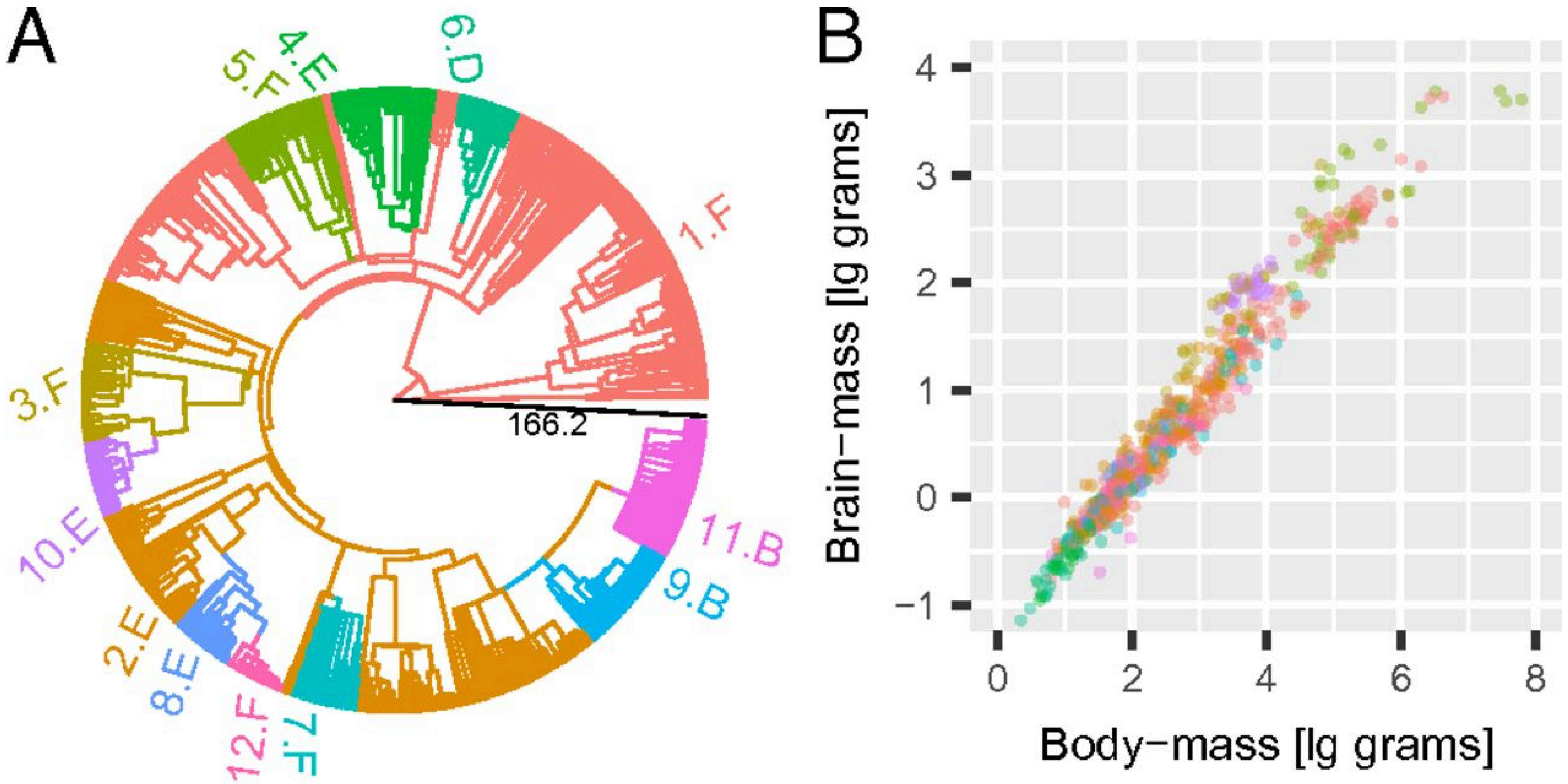
PCMFit

- Vary everything
- Different lineages can evolve under BM or OU
- Model Relationships between traits
- ML

OVERVIEW OF OU METHODS FOR TRAIT EVOLUTION

Modelling OU process without a priori expectations

PCMFit



Mitov et al. 2019 PNAS

CHOOSING THE RIGHT METHOD:

- Type of question (exploratory vs. hypothesis-driven)
- Available data (number of taxa, traits)
- Computational resources

SAMPLING:

- OU methods/models can be sensitive to taxon sampling :

Small sample sizes can affect the ability of the method to distinguish between, for example, BM and OU models.

- OU methods/models can be sensitive to sampling across clades or regimes:

Parameter estimates can be biased if you don’t have enough species across the distinct regimes

TUTORIAL 2