

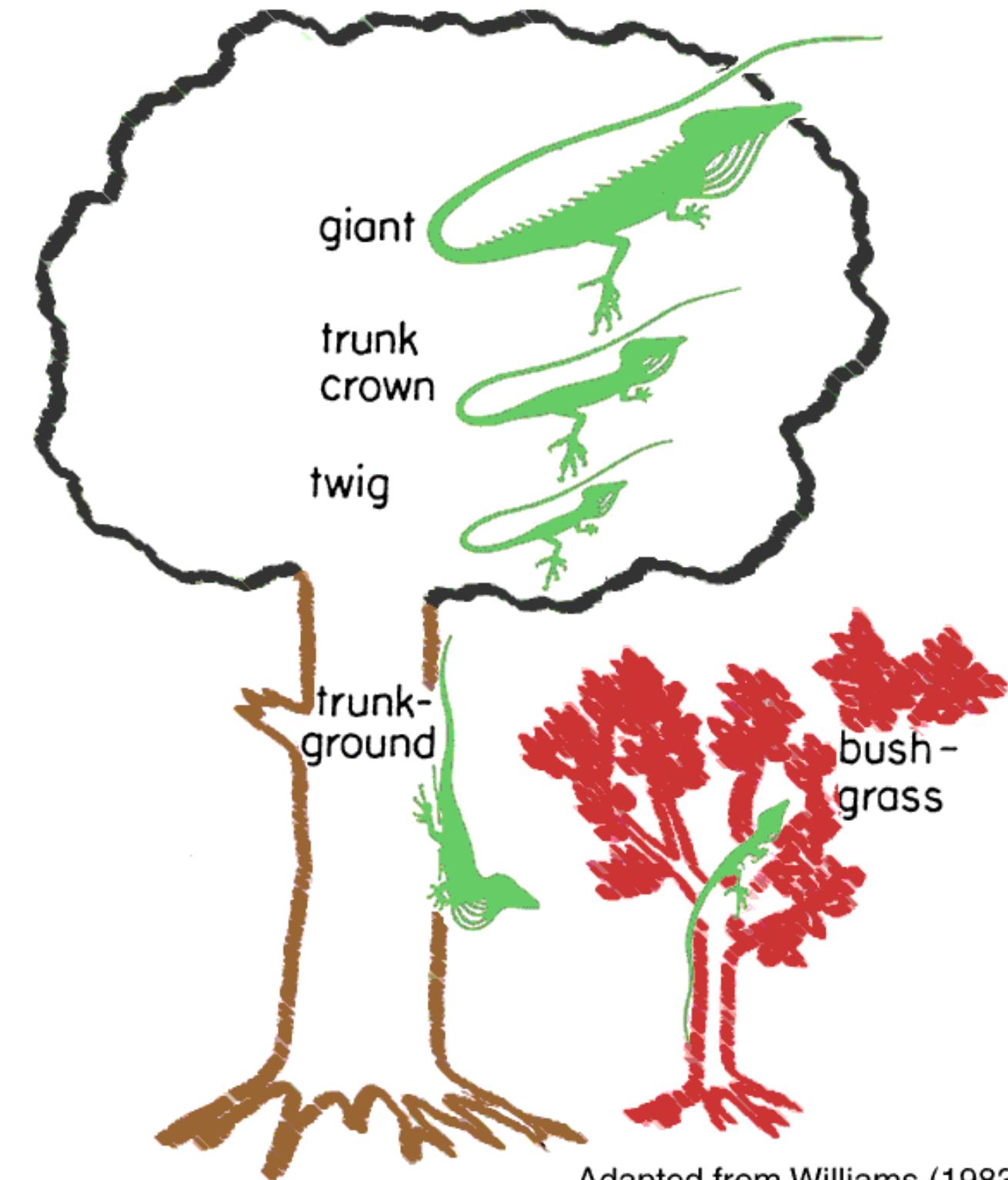
Intro to Ornstein-Uhlenbeck models on trees (& a bit of ramble on adaptation)

Marguerite Butler

University of Hawaii, Department of Zoology



Greater
Antillean
Anolis
repeatedly
evolve into
the same
“niches” or
ecomorph types



Adapted from Williams (1983)

Adaptation becomes rigorous!

AMER. ZOOL., 23:347–361 (1983)

Morphology, Performance and Fitness¹

STEVAN J. ARNOLD

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Chicago, Illinois 60637

SYNOPSIS. Selection can be measured in natural populations by the changes it causes in the means, variances and covariances of phenotypic characters. Furthermore the selection can be measured in conventional statistical terms that also play a key role in theoretical equations for evolutionary change. The problem of measuring selection on morphological traits is simplified by breaking the task into two parts: measurement of the effects of morphological variation on performance and measurement of the effects of performance on fitness. The first part can be pursued in the laboratory but the second part is best accomplished in the field. The approach is illustrated with a hypothesis concerning analysis of selection acting on the complex trophic morphology of snakes.

INTRODUCTION

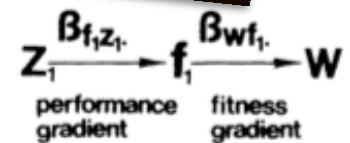
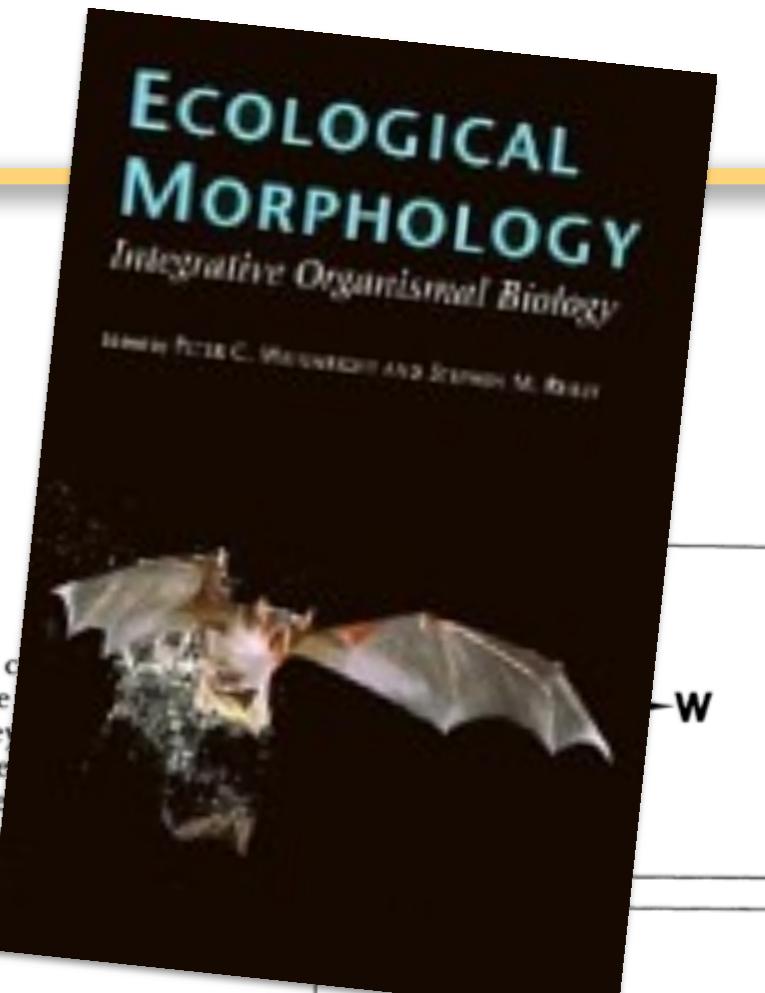
My thesis in this paper is that it is possible to measure adaptive significance directly. In particular it is possible to characterize statistically the relationship between fitness and morphology in natural populations. One can argue that this statistical approach constitutes the highest grade of evidence for selection and adaptation. I will stress this direct approach to selection because of the unique insights it can offer and because it has often been neglected.

here rests on recent advances in multivariate selection theory, which deals with the effects of selection acting simultaneously on multiple characters (Lande, 1979, 1980, 1982). These theoretical results, together with recent success in field measurement of fitness, indicate that selection can be measured in nature in the same terms that are used in equations for the evolutionary transformation of populations (Lande and Arnold, 1983). Multivariate selection theory is briefly reviewed and a new result is introduced. This



See also
Lande and Arnold 1983
Phillips and Arnold 1989

It is possible to
measure adaptive
significance directly



B

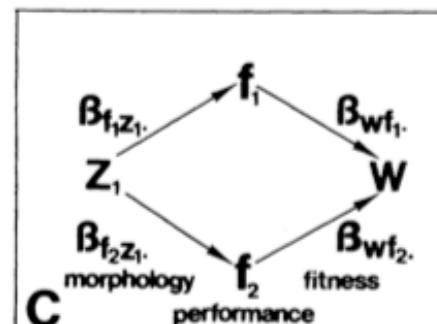
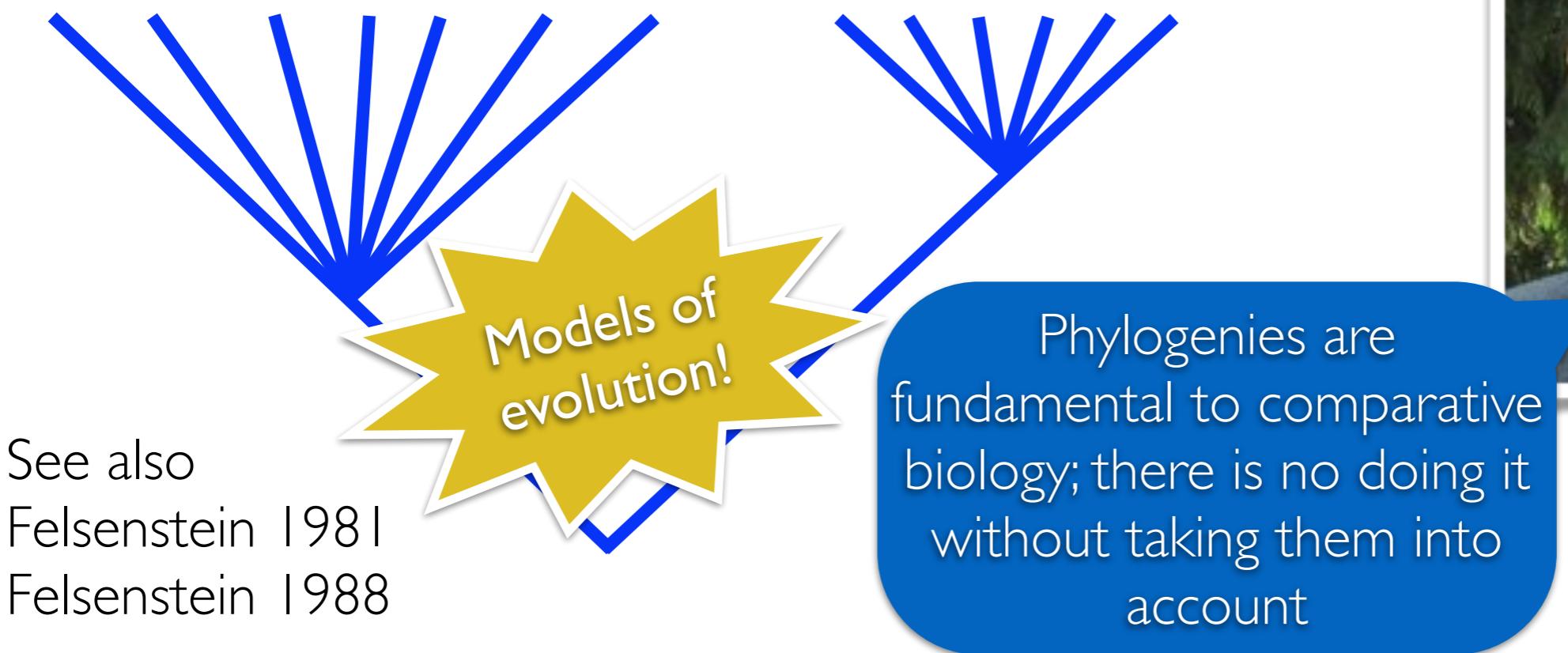


FIG. 4. A diagrammatic partitioning of the selection gradient. The selection gradient for a character (Fig. 4A) can be partitioned into two parts if the character affects a single performance variable, f_1 : the performance gradient, $\beta_{f_1 z_1}$, and the fitness gradient $\beta_{w f_1}$ (Fig. 4B). If the character affects two performance variables, f_1 and f_2 , the selection gradient can be partitioned into the paths $\beta_{f_1 z_1}, \beta_{w f_1}$ and $\beta_{f_2 z_1}, \beta_{w f_2}$ (Fig. 4C).

Species are historically related

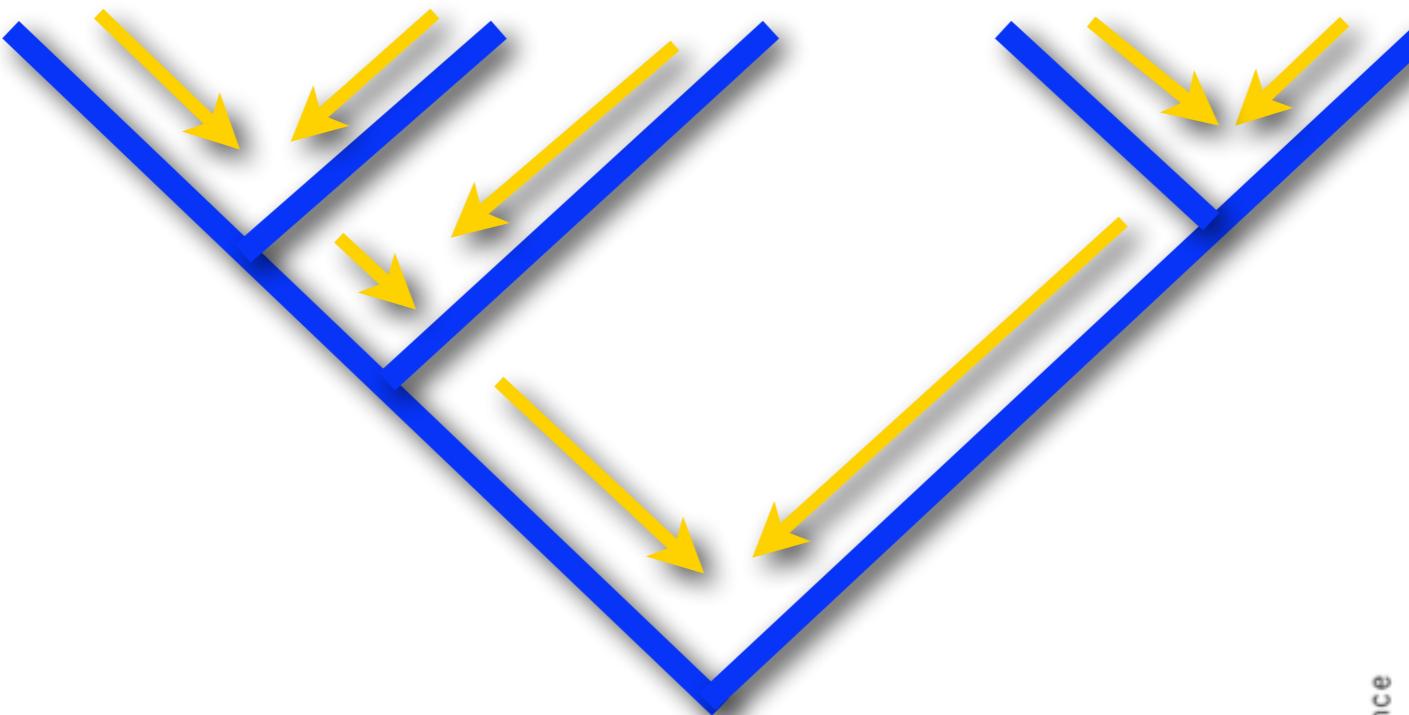
Thus, we might expect closely-related species to be more similar than distantly-related ones. (Felsenstein 1985)

A “potentially serious” problem shared by all comparative studies



A common misconception that it is a “degrees of freedom” problem, but it is really an issue of covariance among species

Ancestral Character State Reconstruction



Evolution, 41(5), 1987, pp. 1098–1115

PHYLOGENETIC STUDIES OF COADAPTATION: PREFERRED TEMPERATURES VERSUS OPTIMAL PERFORMANCE TEMPERATURES OF LIZARDS

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AND

ALBERT F. BENNETT

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Abstract.—The view that behavior and physiological performance are tightly coadapted is a central principle of physiological ecology. Here, we test this principle using a comparative study of evolutionary patterns in thermal preferences and the thermal dependence of sprinting in some Australian skinks (Lygosominae). Thermal preferences (T_p) differ strikingly among genera (range 24° to 35°C), but critical thermal maxima (CTMax) (range 38° to 45°C) and optimal temperatures for sprinting (T_o , 32° to 35°C) vary less. Diurnal genera have relatively high T_p , T_o , and CTMax. In contrast, nocturnal genera have low T_p but have moderate to high T_o and CTMax. Both nonphylogenetic and phylogenetic (minimum-evolution) approaches suggest that coadaptation is tight only for genera with high T_p . Phylogenetic analyses suggest that low T_p and, thus, partial coadaptation are evolutionarily derived, indicating that low thermal preferences can evolve, even if this results in reduced performance. In one instance, thermal preferences and the thermal dependence of

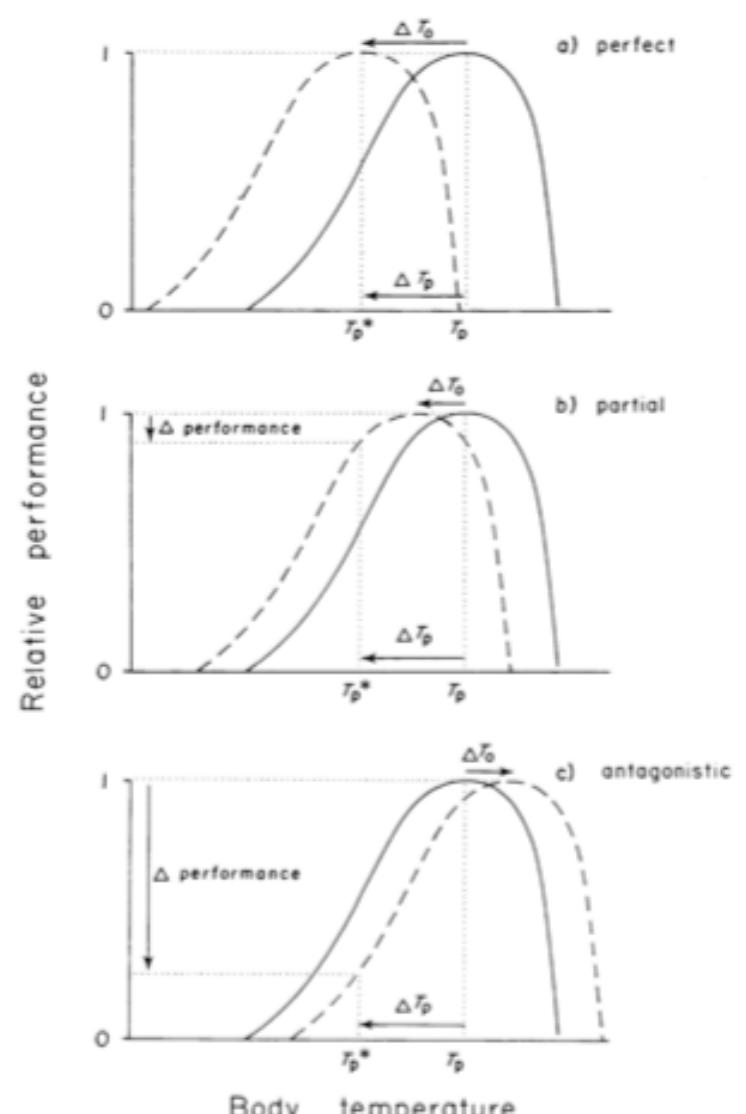
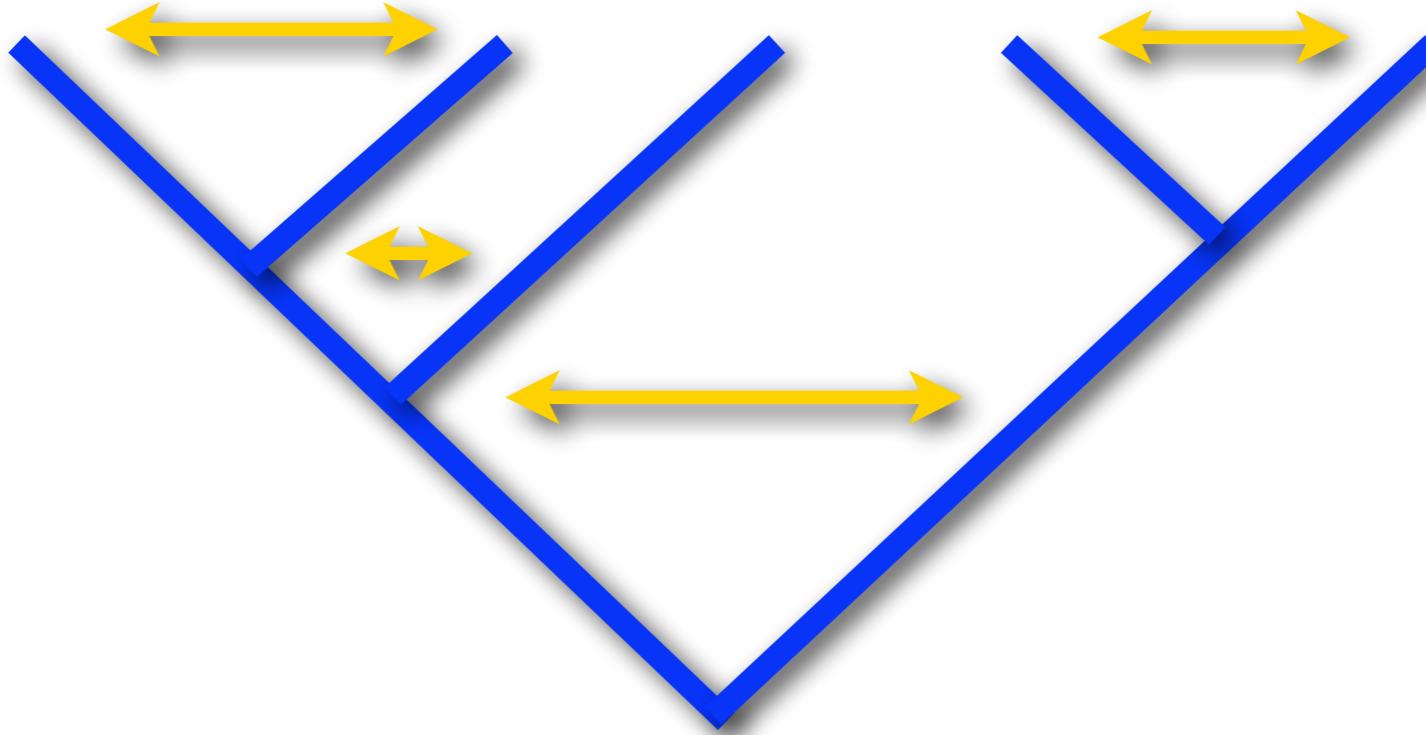


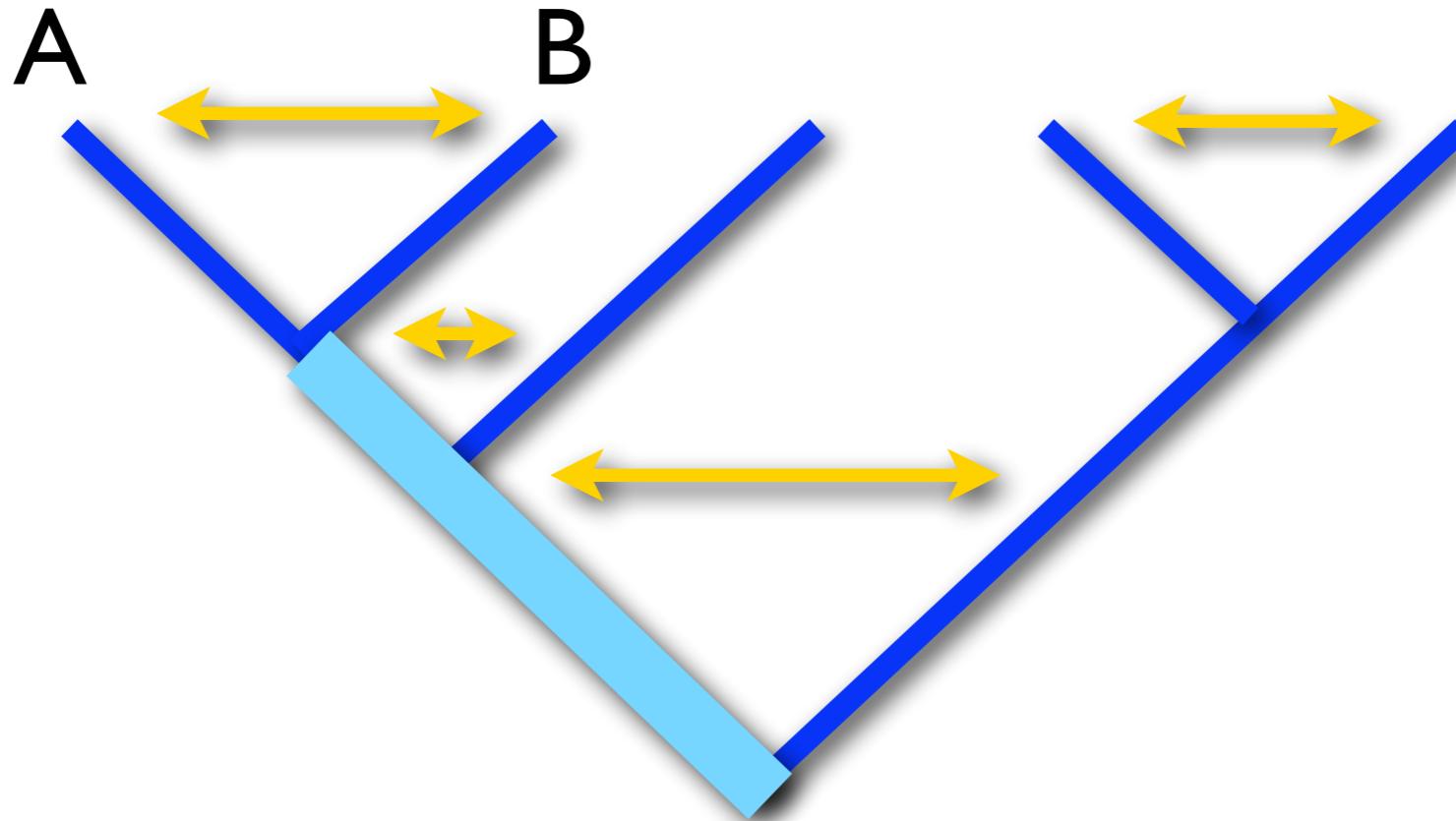
FIG. 1. a) A hypothetical case of perfect coadaptation, showing the thermal dependence of performance (solid line) and the thermal preference (T_p) of an ancestral species, as well as the performance curve (dashed line) and T_p^* of a derived species. The change

Independent Contrasts



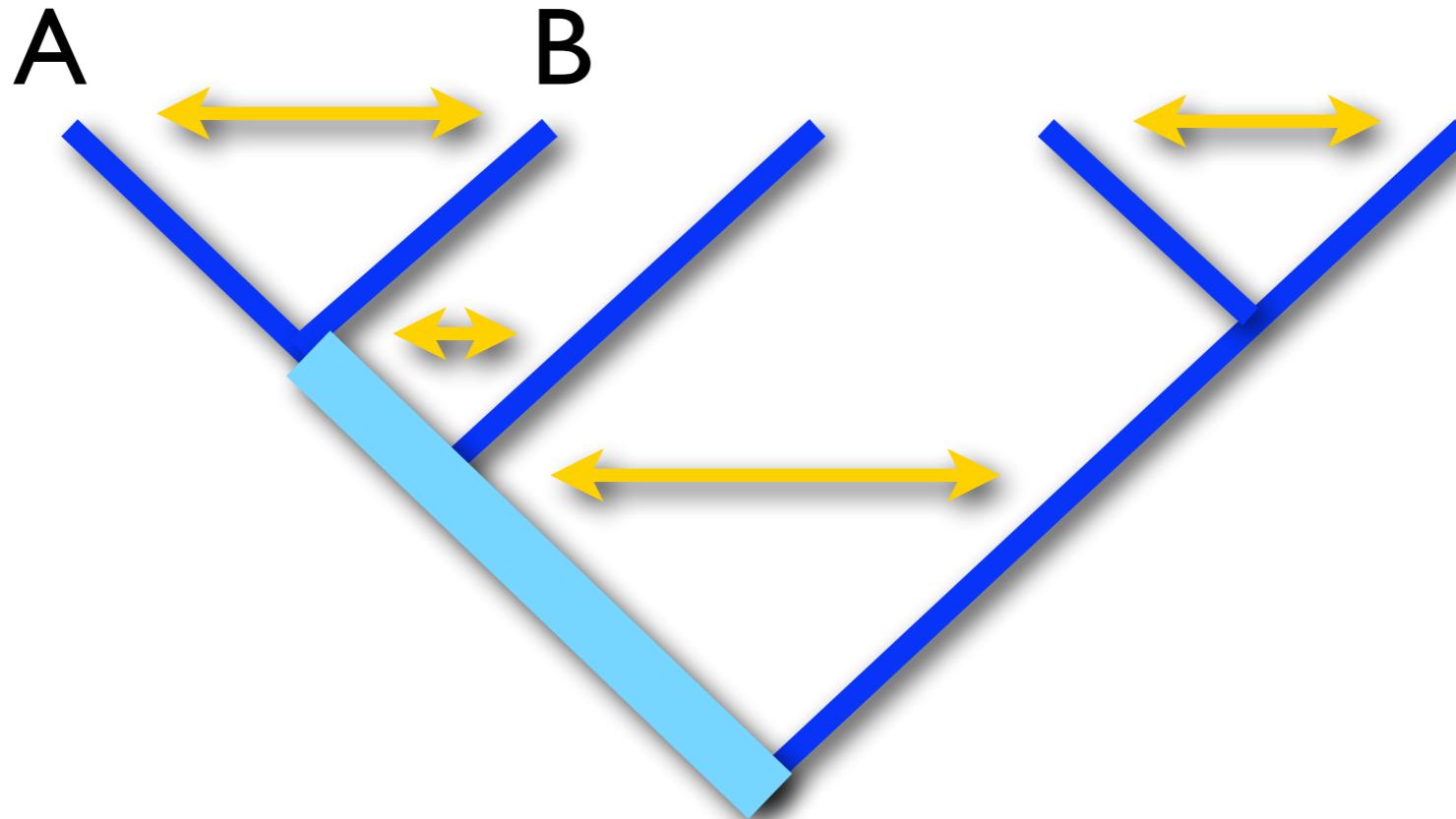
- Transform the interspecific data with covariances due to shared evolutionary history into a set of statistically independent “contrasts” with zero covariances among contrasts.

Independent Contrasts



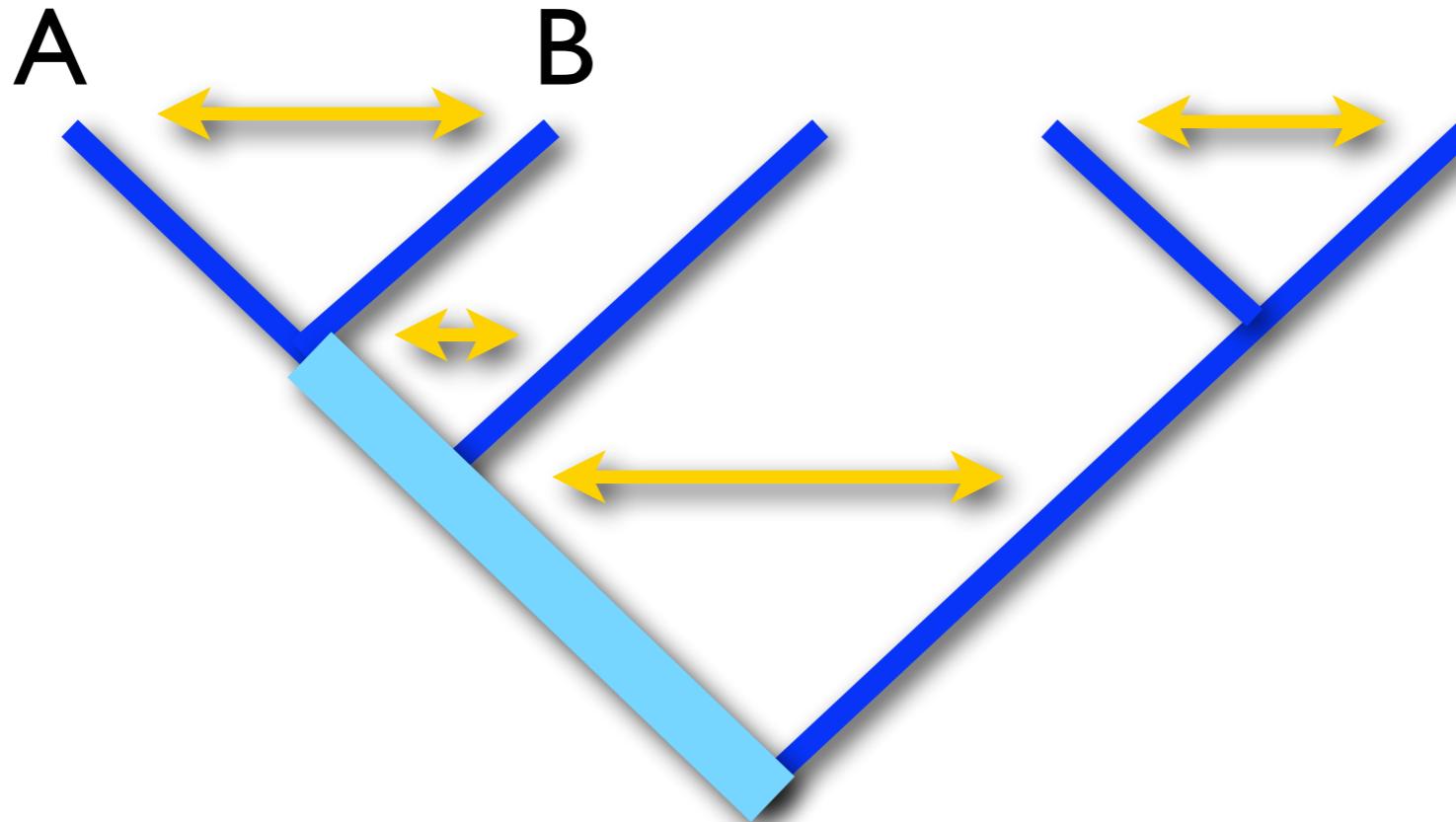
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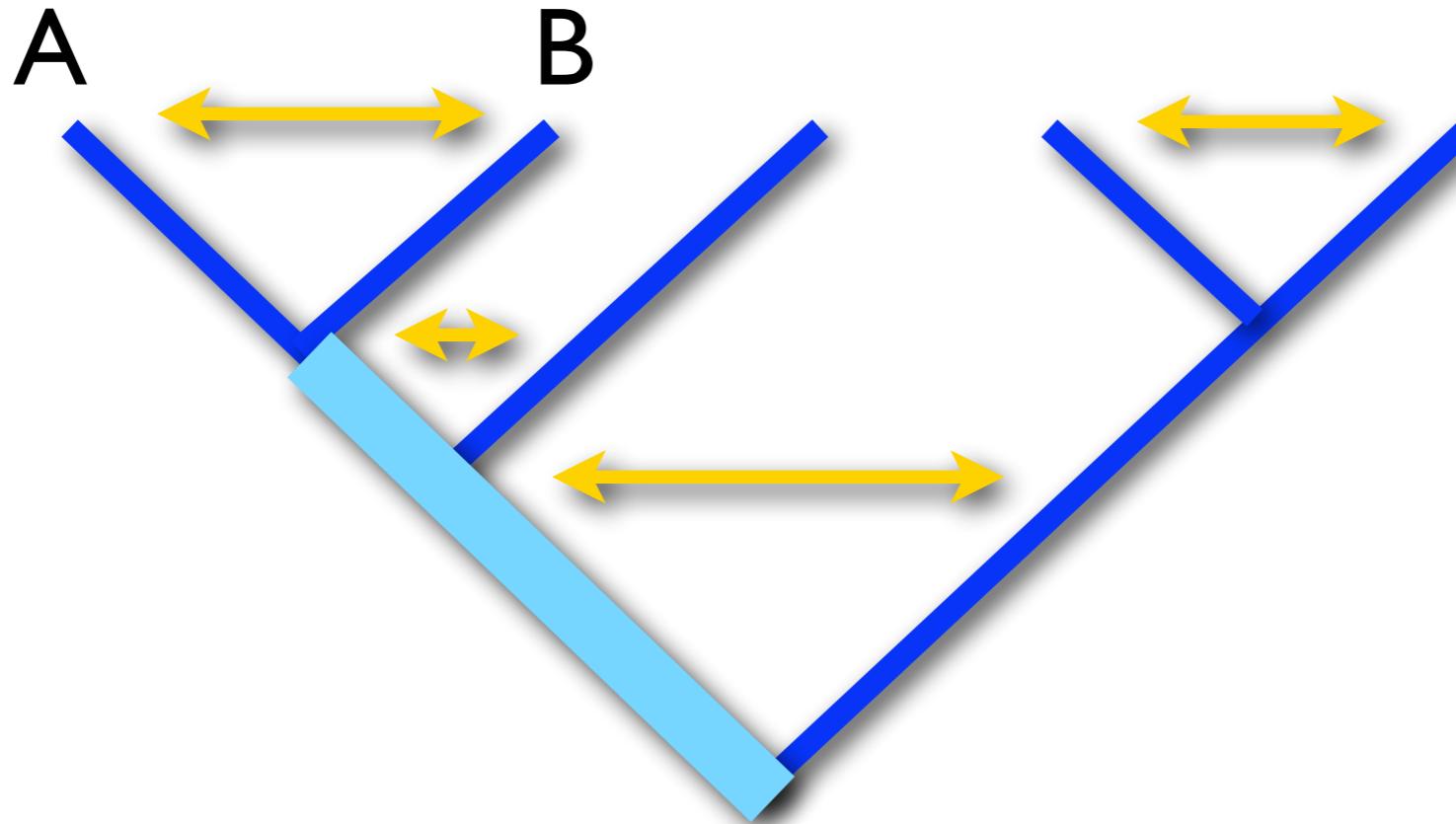
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- For example, species A and B share more than 50% of their evolutionary history.

Independent Contrasts



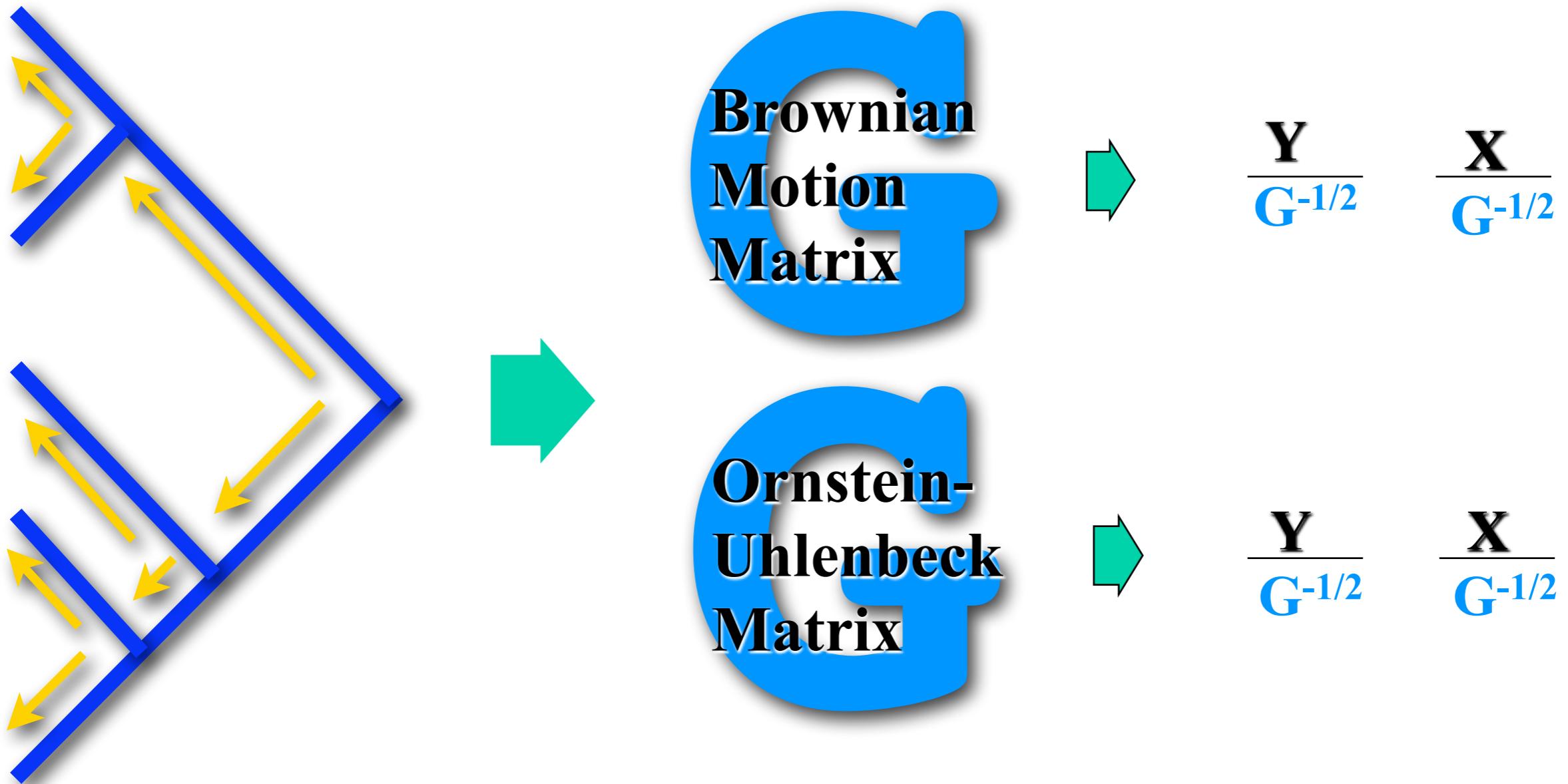
- Transform the interspecific data with covariances due to shared evolutionary history into a set of statistically independent “contrasts” with zero covariances among contrasts.
- For example, species A and B share more than 50% of their evolutionary history.
 - Thus, all else being equal, *if we assume a Brownian Motion model of evolution, we expect A and B to covary.*

Independent Contrasts



- Transform the interspecific data with covariances due to shared evolutionary history into a set of statistically independent “contrasts” with zero covariances among contrasts.
- For example, species A and B share more than 50% of their evolutionary history.
 - Thus, all else being equal, *if we assume a Brownian Motion model of evolution, we expect A and B to covary.*
- Use “independent contrasts” with phylogenetic covariance “removed” to test hypotheses using standard statistical tools

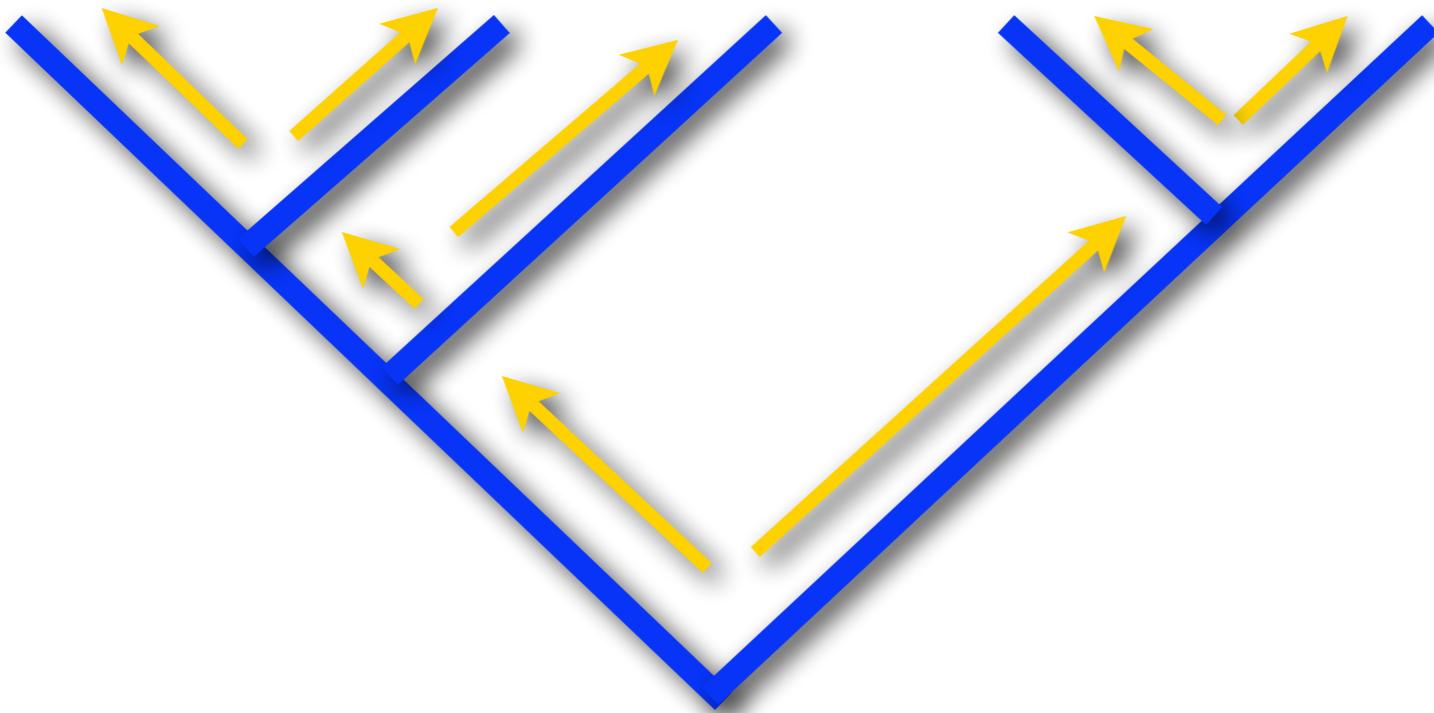
Correcting variance using Phylogenetic GLS



“Divide” (using matrix math) the interspecific dataset by the square root of the variance matrix to adjust for phylogenetic covariance.

This is analogous to the univariate case when you adjust each dataset to unit variance by dividing each by their standard deviation.

Phylogenetic Simulation



Instead of testing P-values against standard statistical distributions (bad!), simulate trait evolution along your phylogeny assuming a model of evolution.

Use this distribution with built-in phylogenetic covariance to draw statistical conclusions

Ecologists push back

*Journal of
Ecology* 1995,
83, 531–534

FORUM

On misinterpreting the ‘phylogenetic correction’

MARK WESTOBY, MICHELLE R. LEISHMAN and JANICE M. LORD

School of Biological Sciences, Macquarie University, NSW 2109 Australia

Introduction

The last 10 years have seen important advances in methodology for taking phylogeny into account when analysing a comparative dataset. This commentary is about a class of interpretive procedures associated with these new statistical methods. We will call the interpretive logic ‘phylogenetic correction’ (PC for short), because this phrase summarizes the approach. Our essential message, however, is that a PC procedure is not in fact a ‘correction’, an adjustment to remove errors. Rather, it is a conceptual decision to give priority to one interpretation over another. Accordingly, it is an error to believe that PC is a methodology that must routinely be applied in all comparative analyses.

The present Forum was proposed by the Editor during the review process for a paper about comparative ecology of seed mass (Leishman *et al.* 1995; see p. 517). Accord-

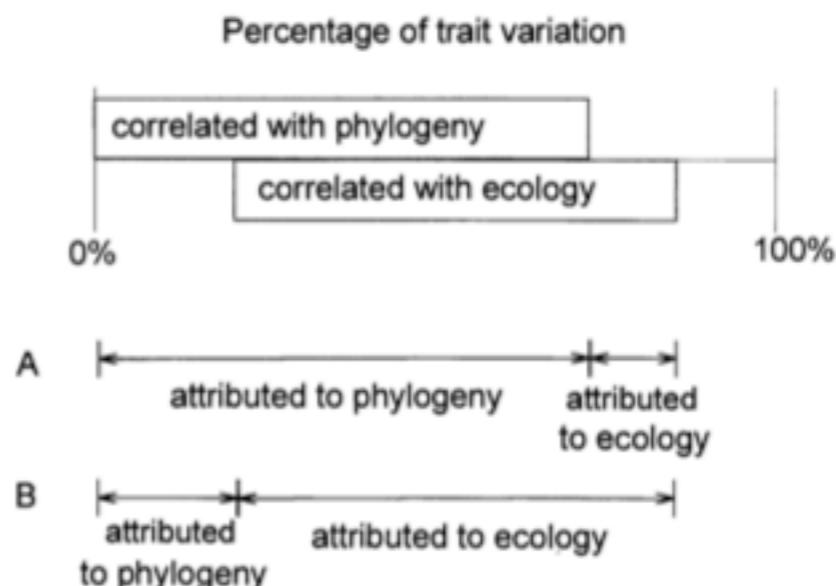
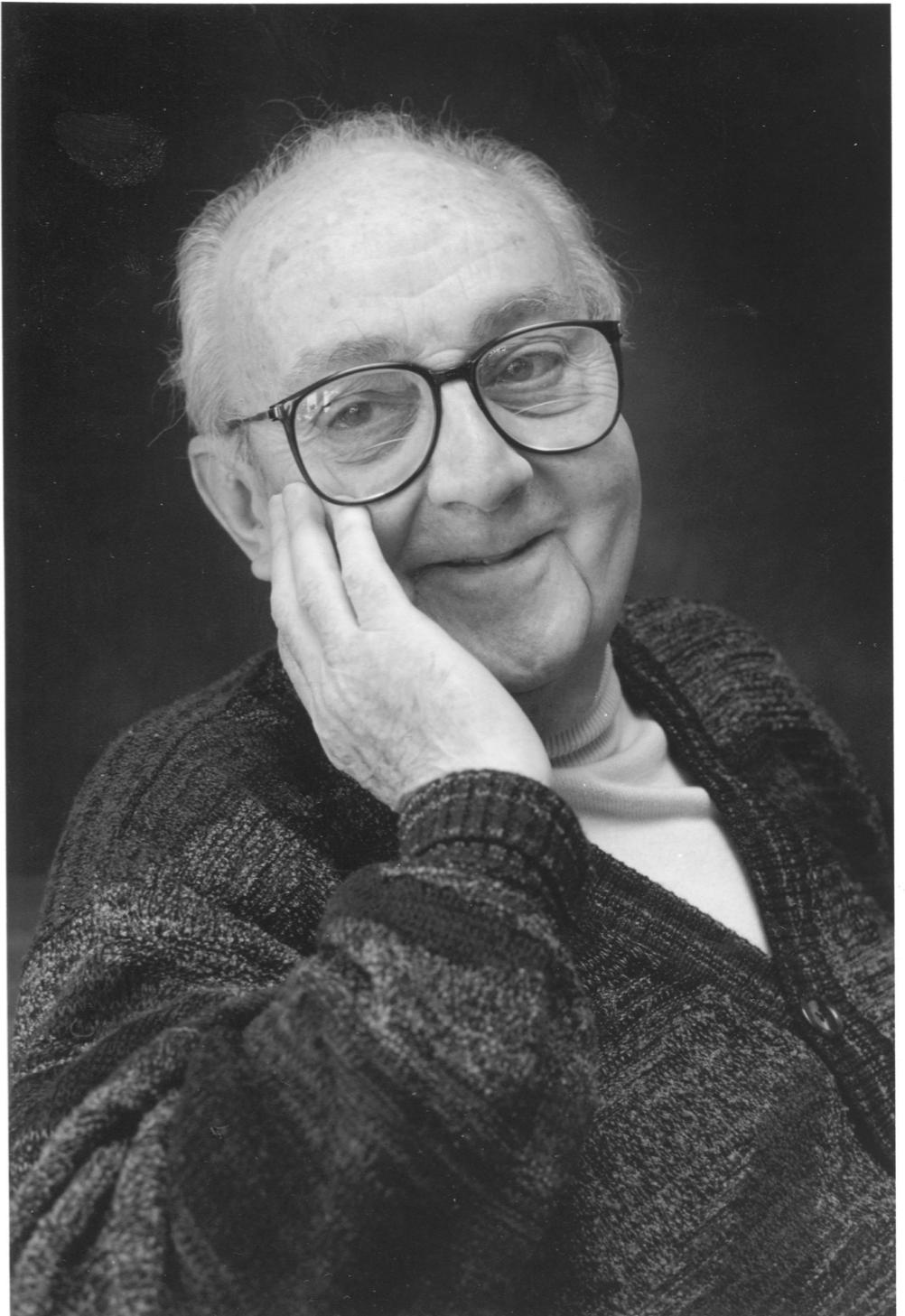


Fig. 1 Schematic illustrating percentages of variation between species in a trait such as seed mass correlated with phylogeny and ecology, and the two extremes (A and B) of the spectrum of possible attributions of variation. Extreme A is phylogenetic correction (PC).

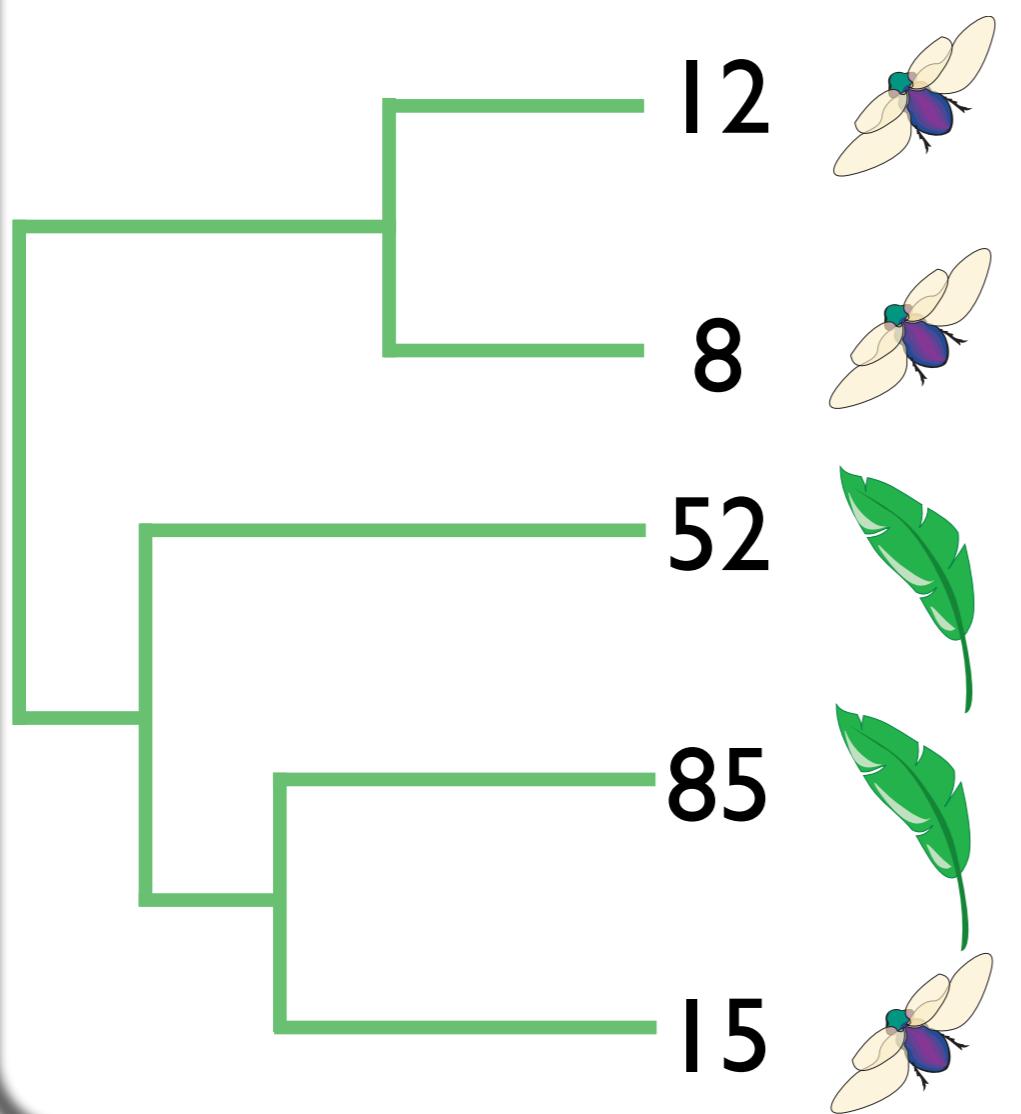
Are we attributing too much to evolution?
(and not enough to ecology?)

Essentially, all models
are wrong, but some
are useful

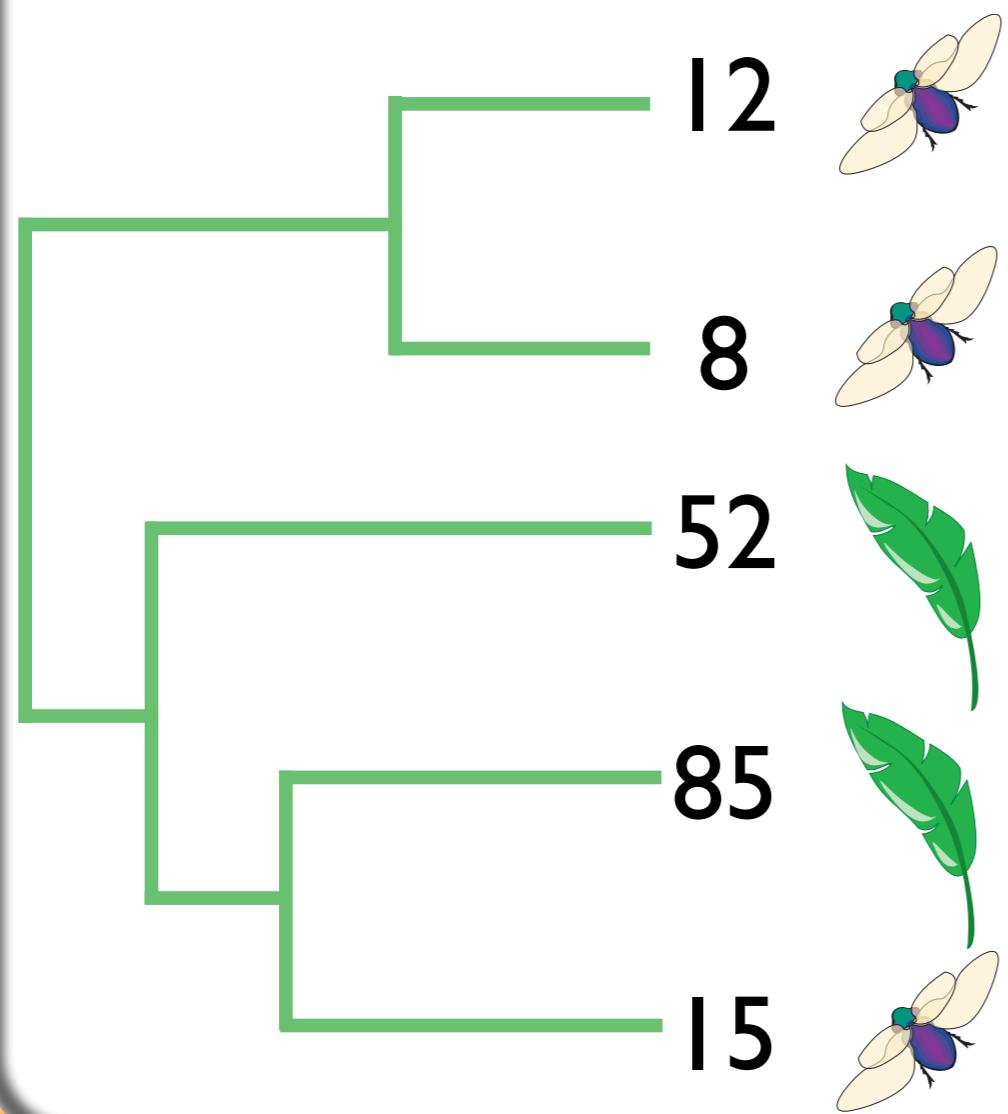
- George E. Box



Body Food
Size Type

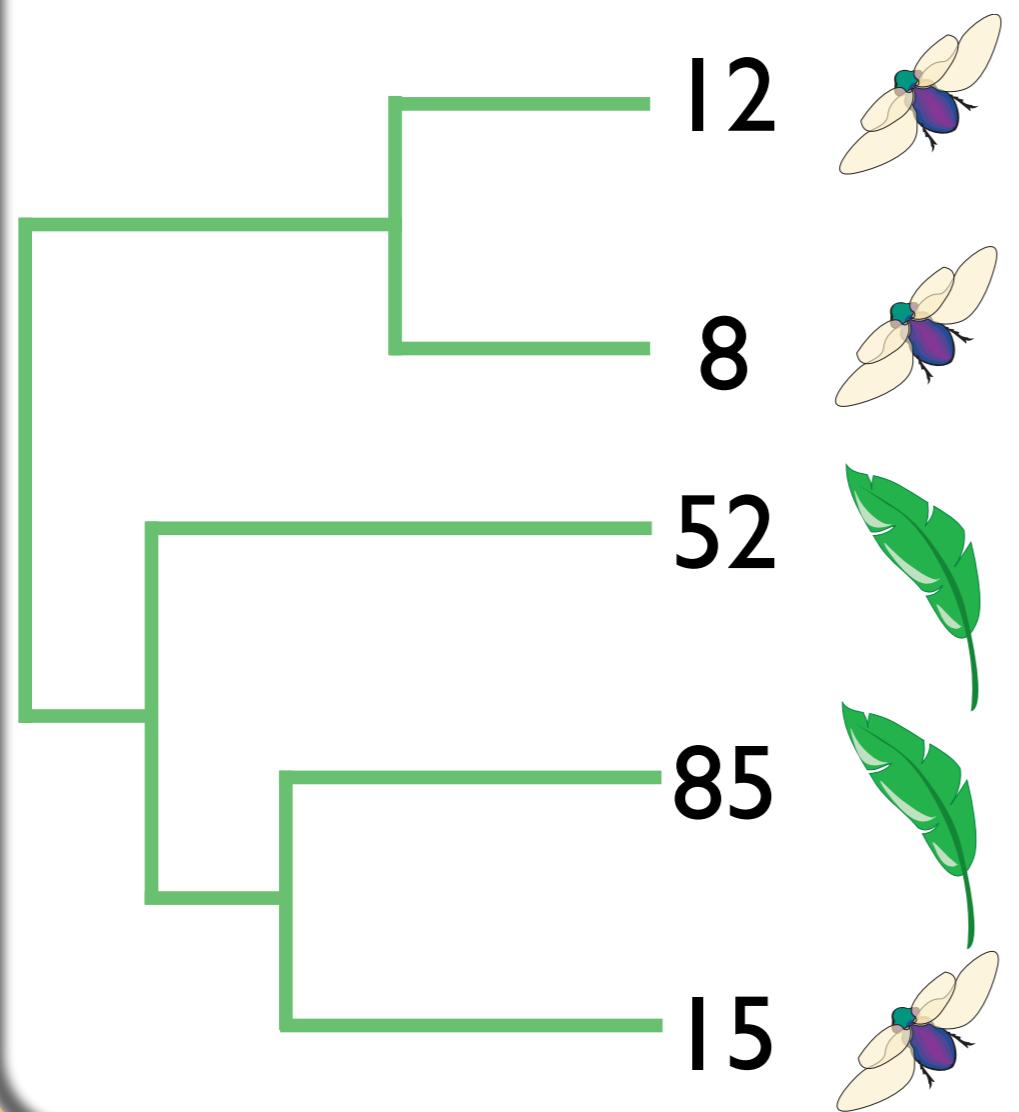


Body Size Food Type



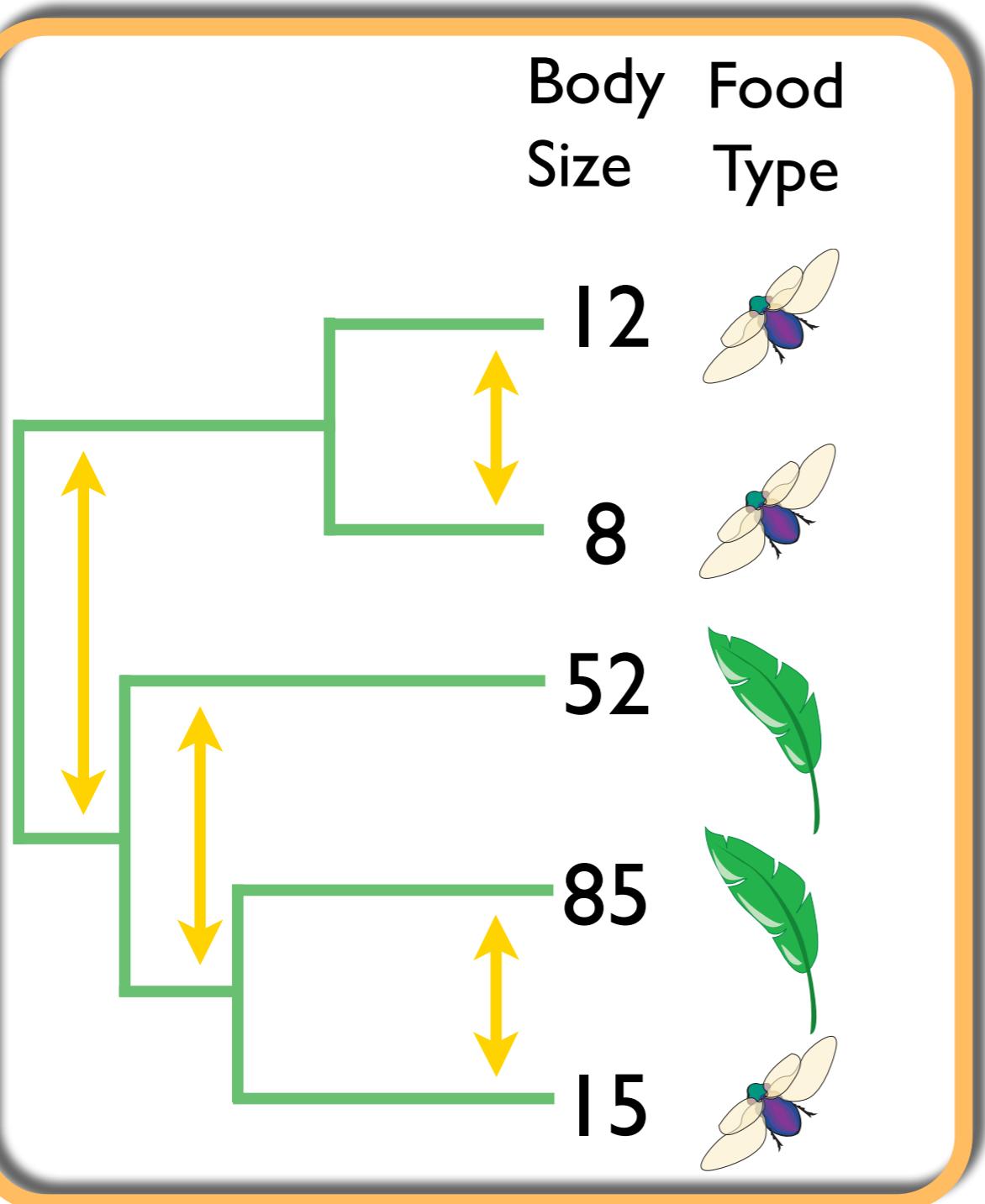
Quantitative character
associated with a particular
selective “regime”

Body Size Food Type



Quantitative character associated with a particular selective “regime”

We want to know the correlation between morphology and ecology



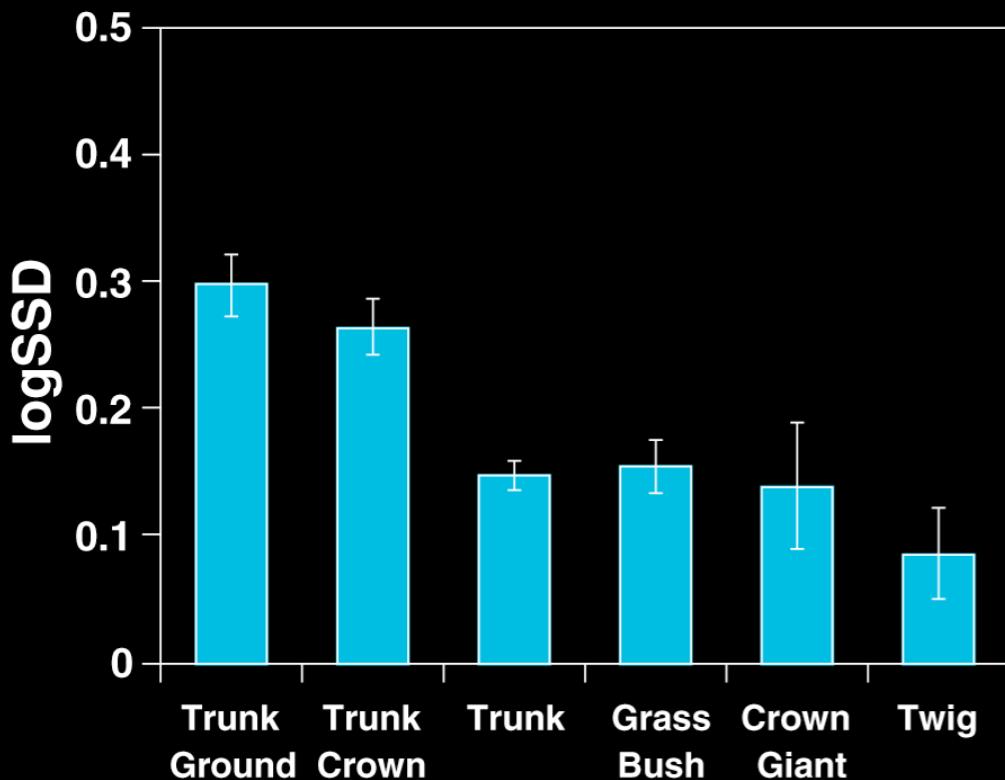
Quantitative character associated with a particular selective “regime”

We want to know the correlation between morphology and ecology

*Statistically remove the effects of phylogeny
(using Brownian Motion)*

I. “Phylogenetic correction”

Ecomorphs differ in size dimorphism



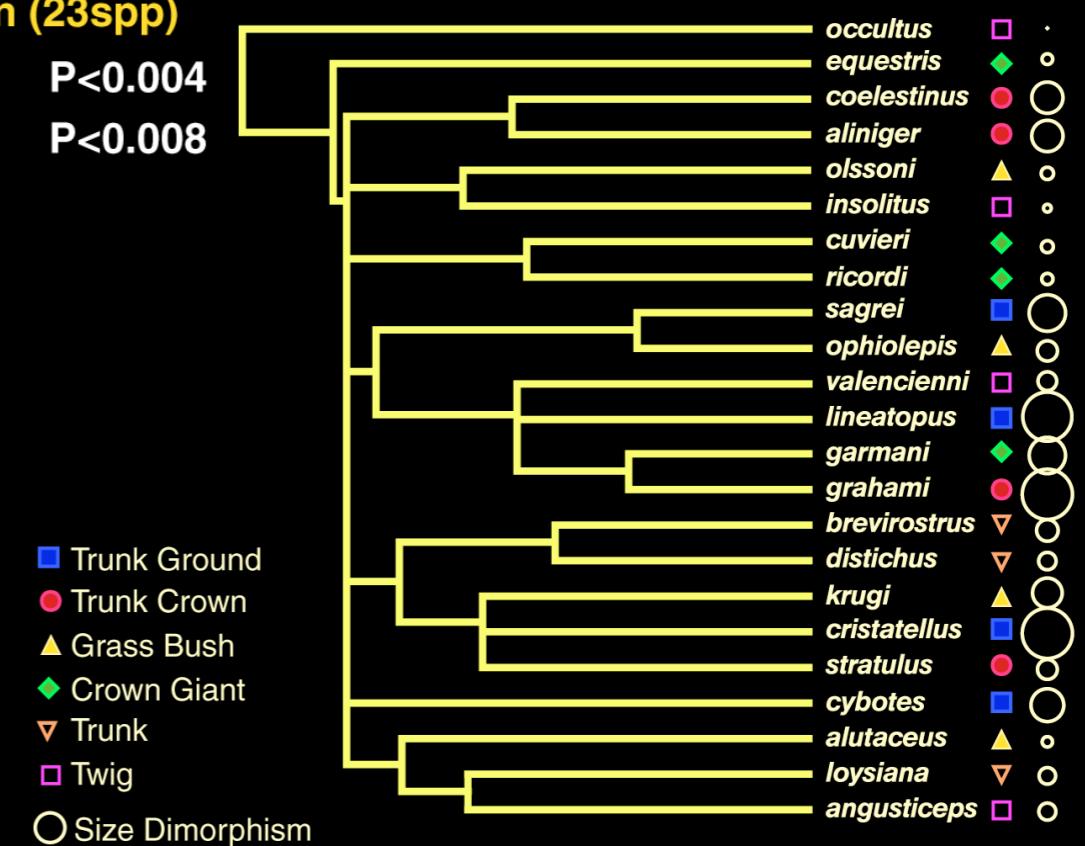
Robust to phylogeny

Non-Phylogenetic

Kruskal-Wallis (38spp) $P<0.001$
(23spp) $P<0.006$

Phylogenetic Simulation (23spp)

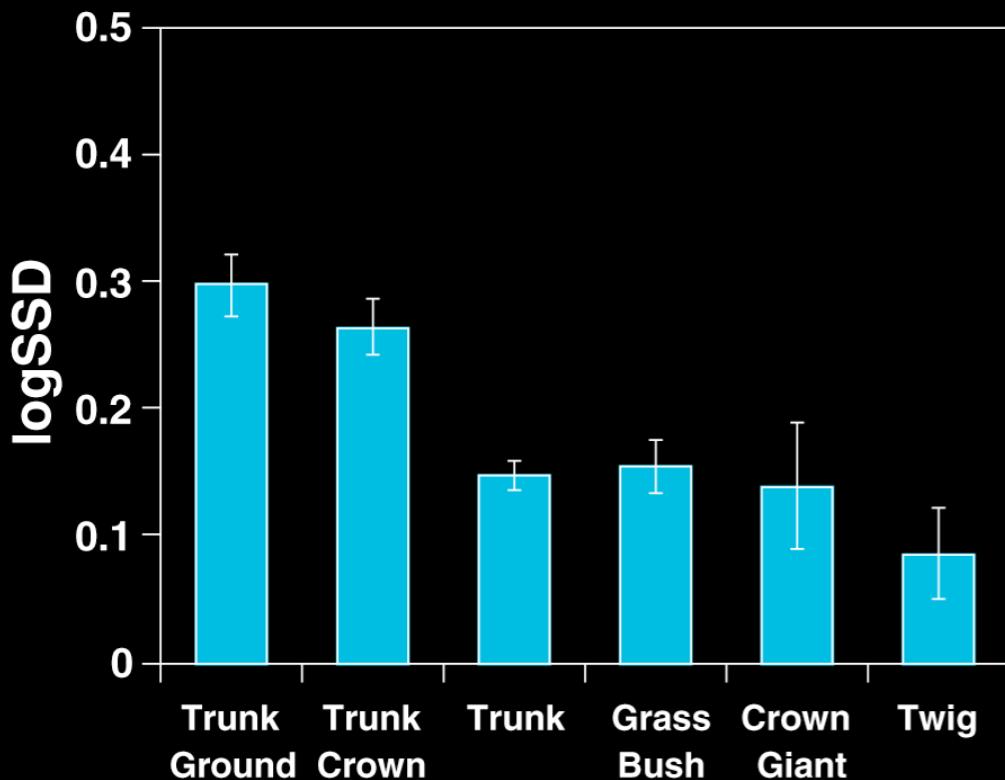
Gradual Model $P<0.004$
Speciation Model $P<0.008$



Phylogeny modified from Jackman, et al.

I. “Phylogenetic correction”

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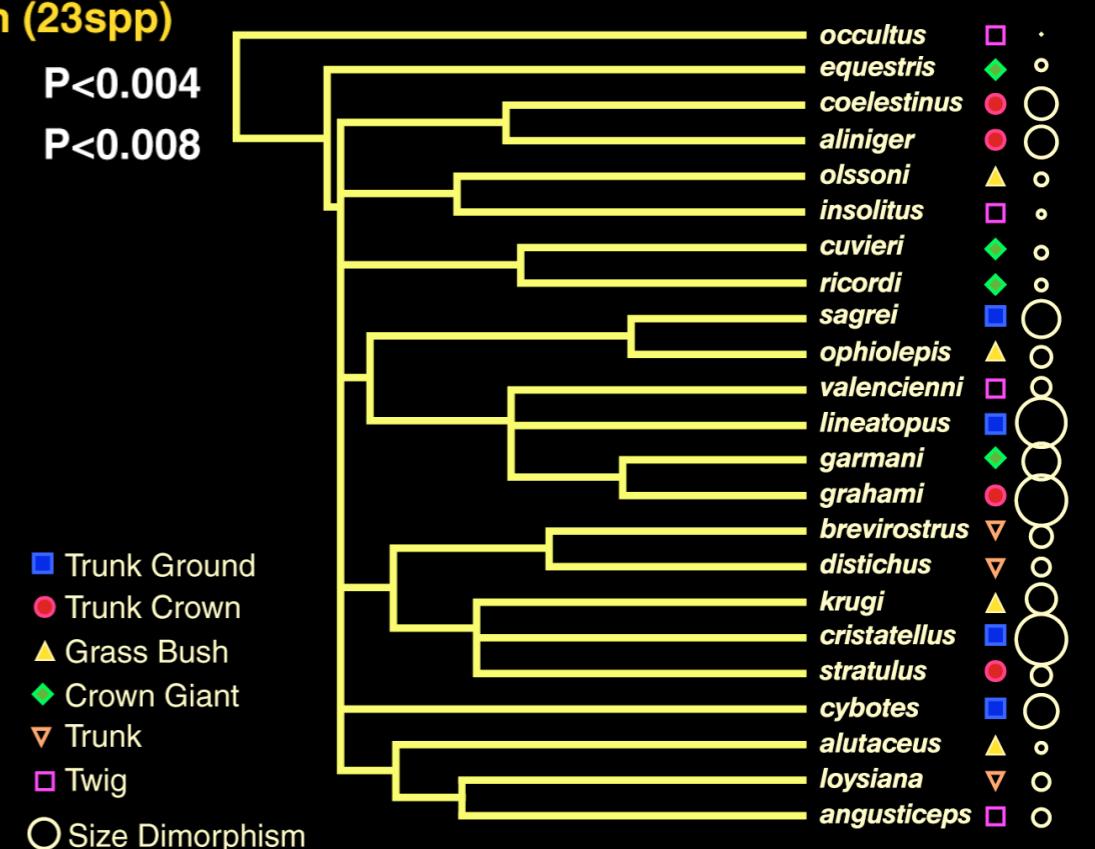
Phylogenetic Simulation (23spp)

Gradual Model

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Speciation Model

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**But what have we learned
about evolutionary process?**

Phylogeny modified from Jackman, et al.

All comparative analyses are constructed of 3 pieces

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- I. The comparative **dataset** (body size, plumage color, etc. for each species)

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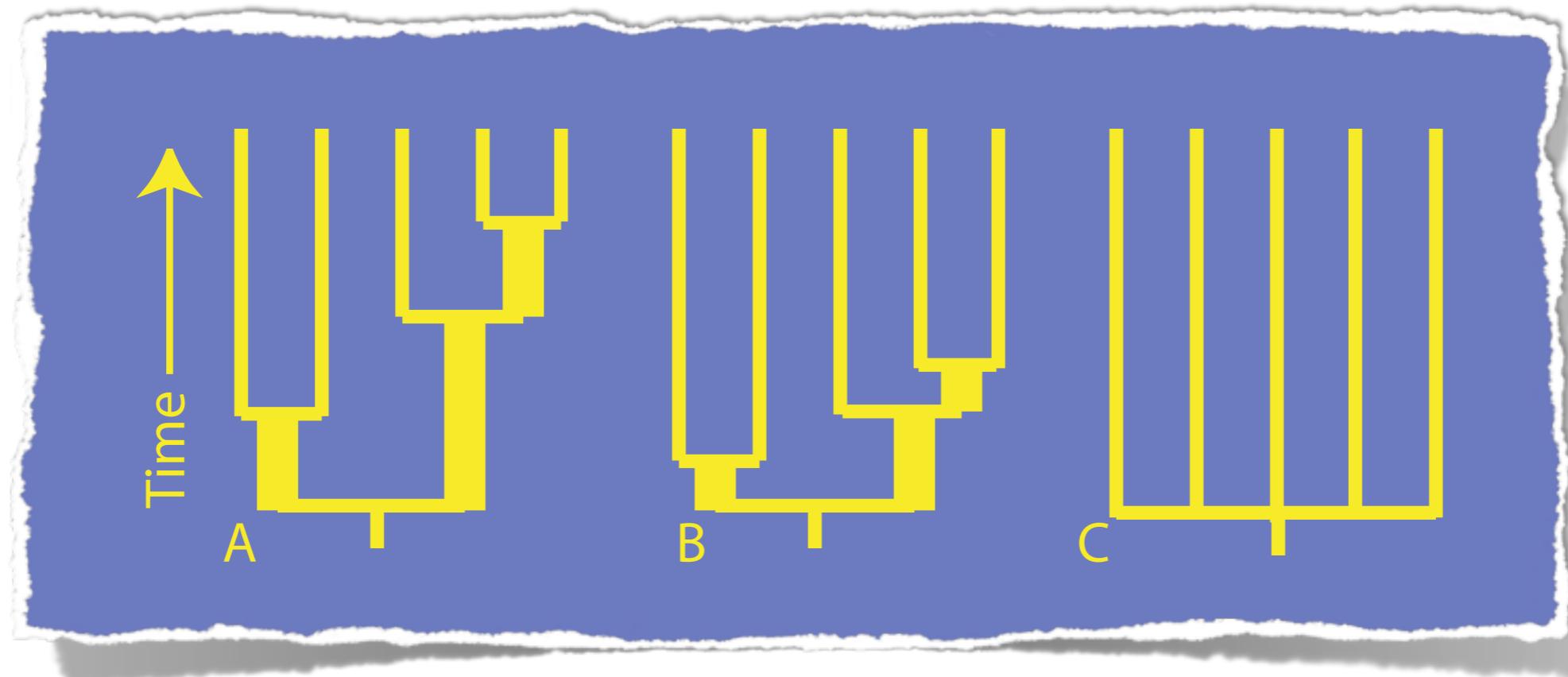
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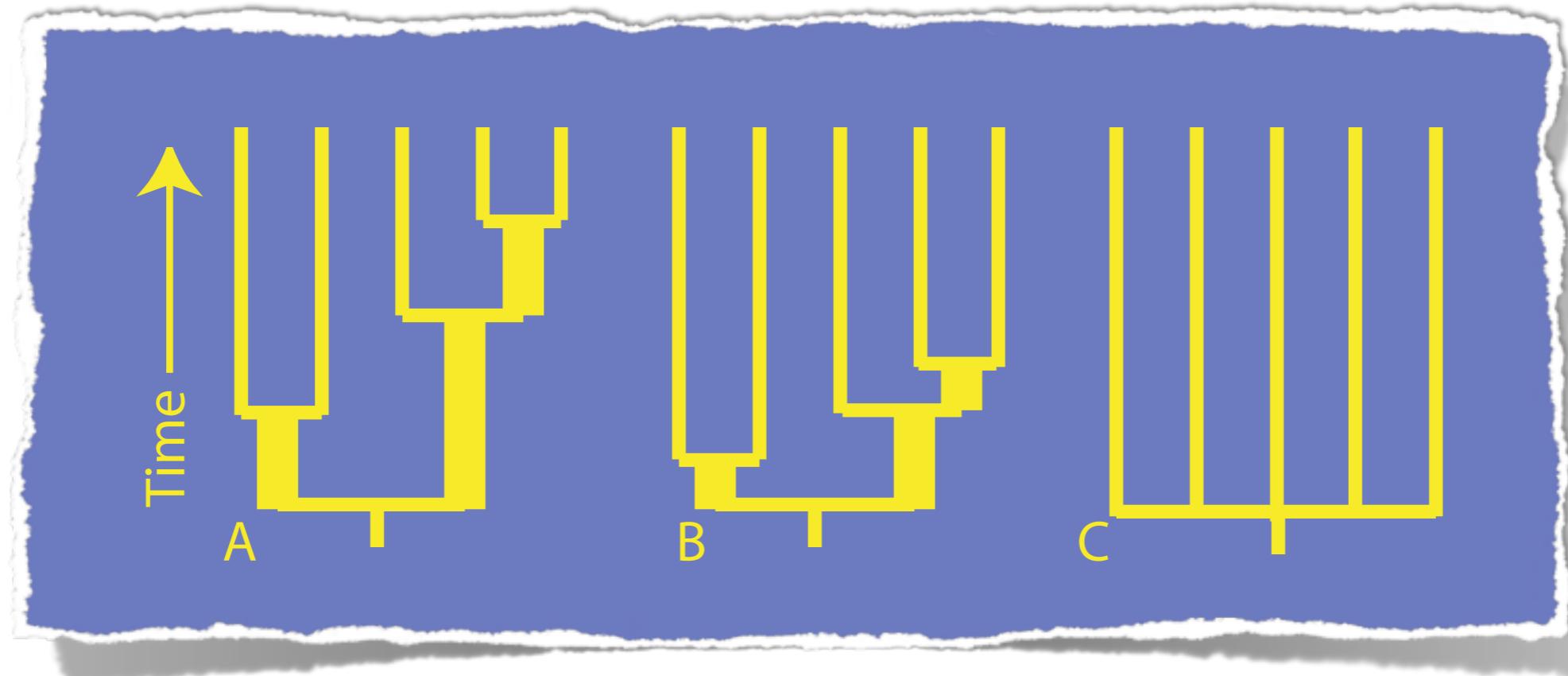
Together, these give you a **predicted distribution** for a **phenotypic character** among species

Most approaches use a BM (i.e., purely neutral) model



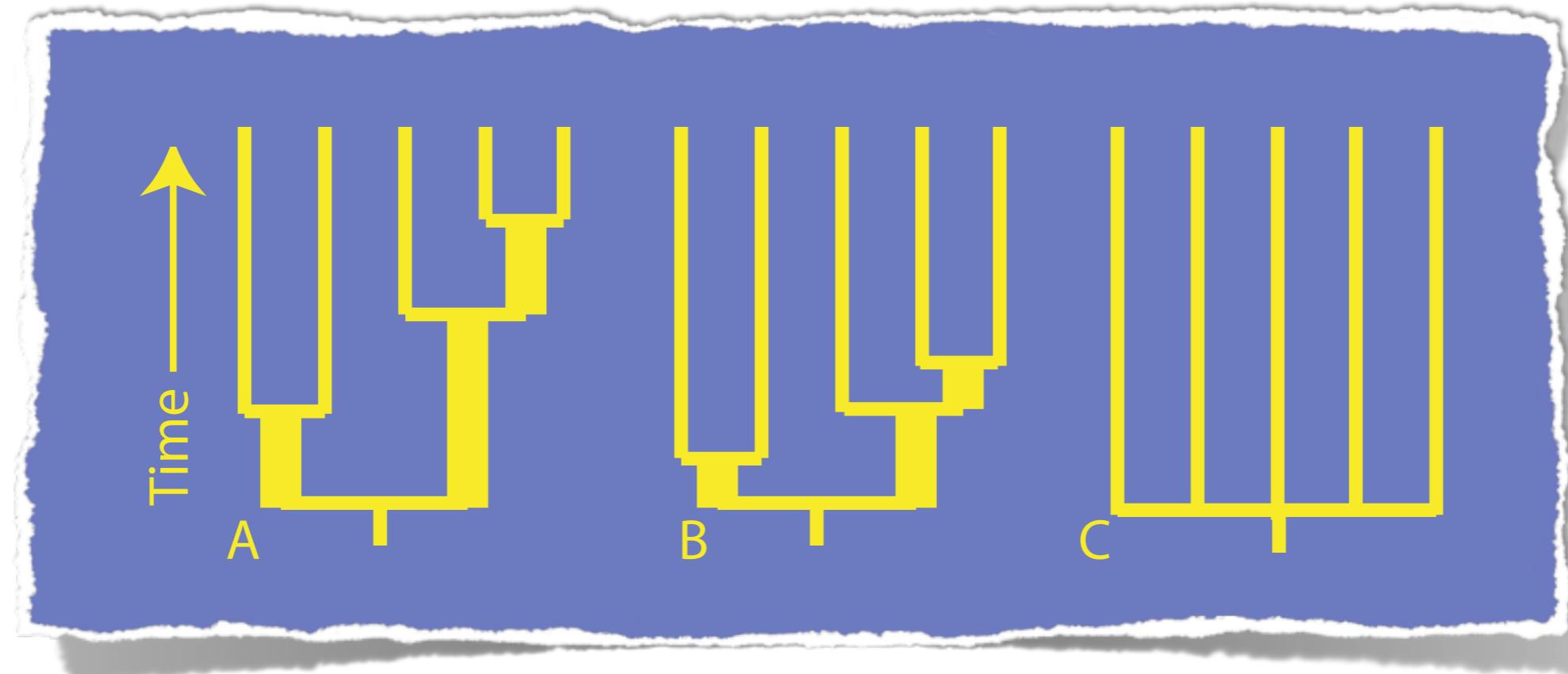
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But... many datasets do not fit BM well.



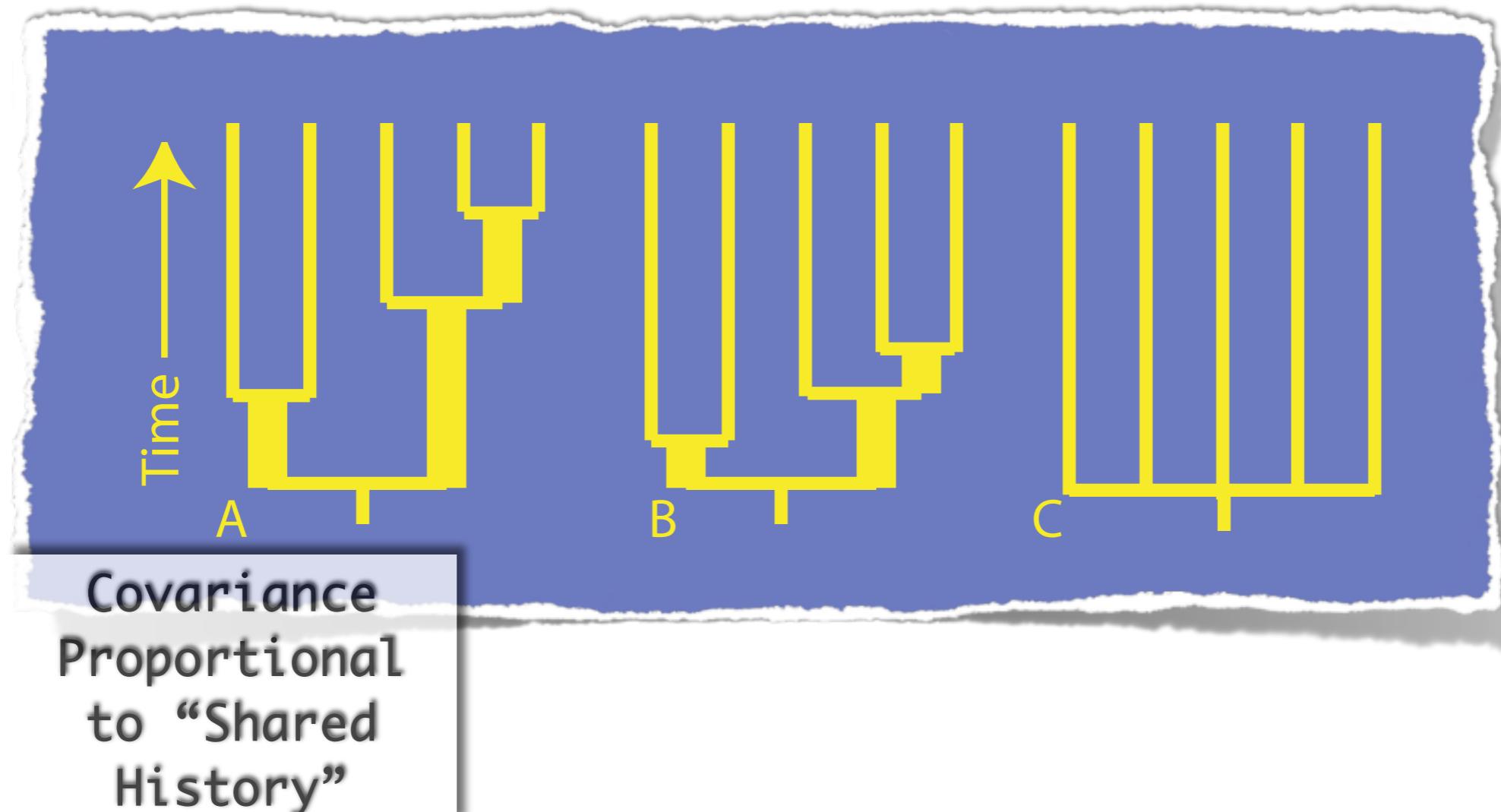
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But... many datasets do not fit BM well.
A popular approach improves fit by “scaling” branch lengths



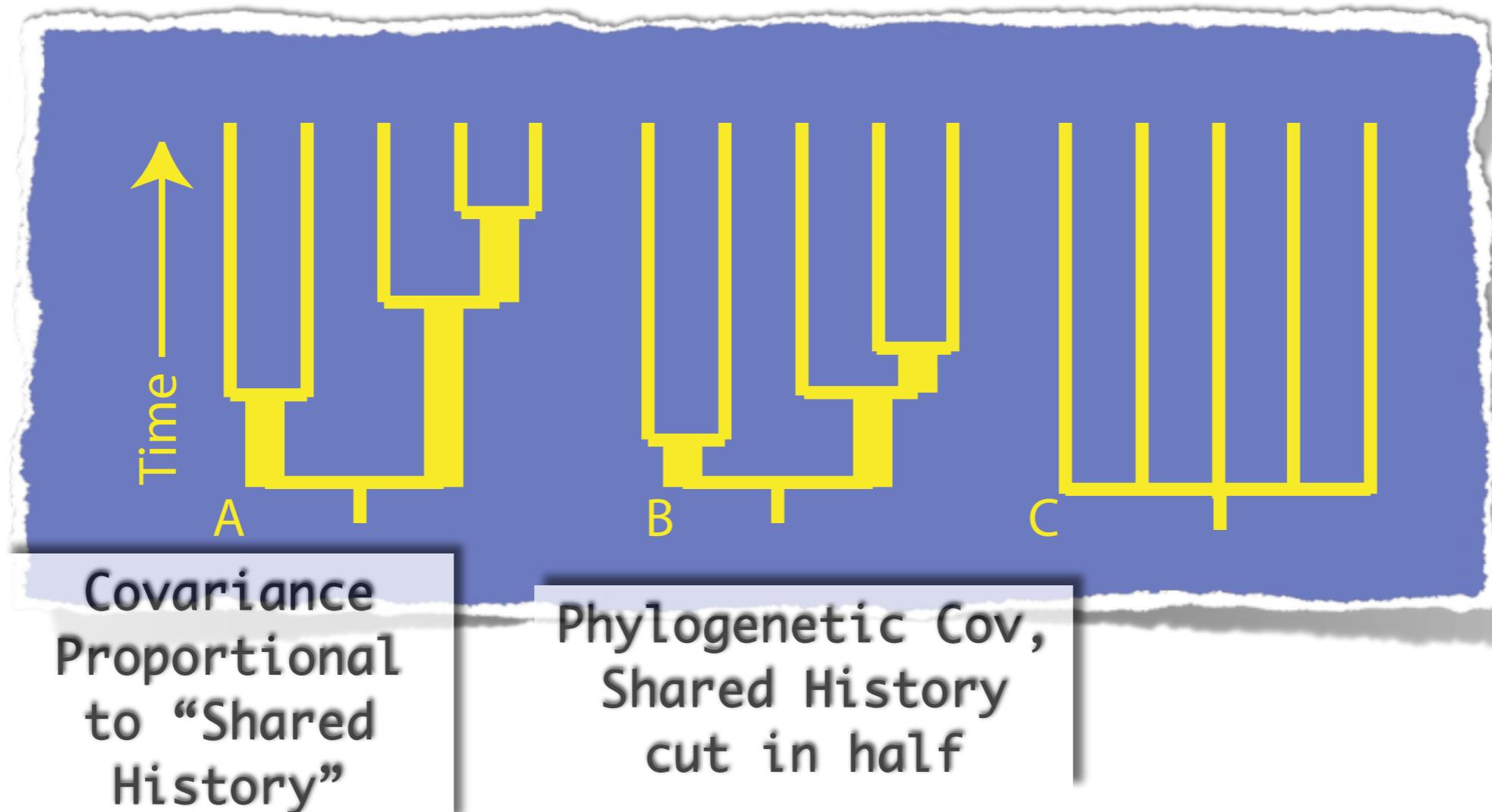
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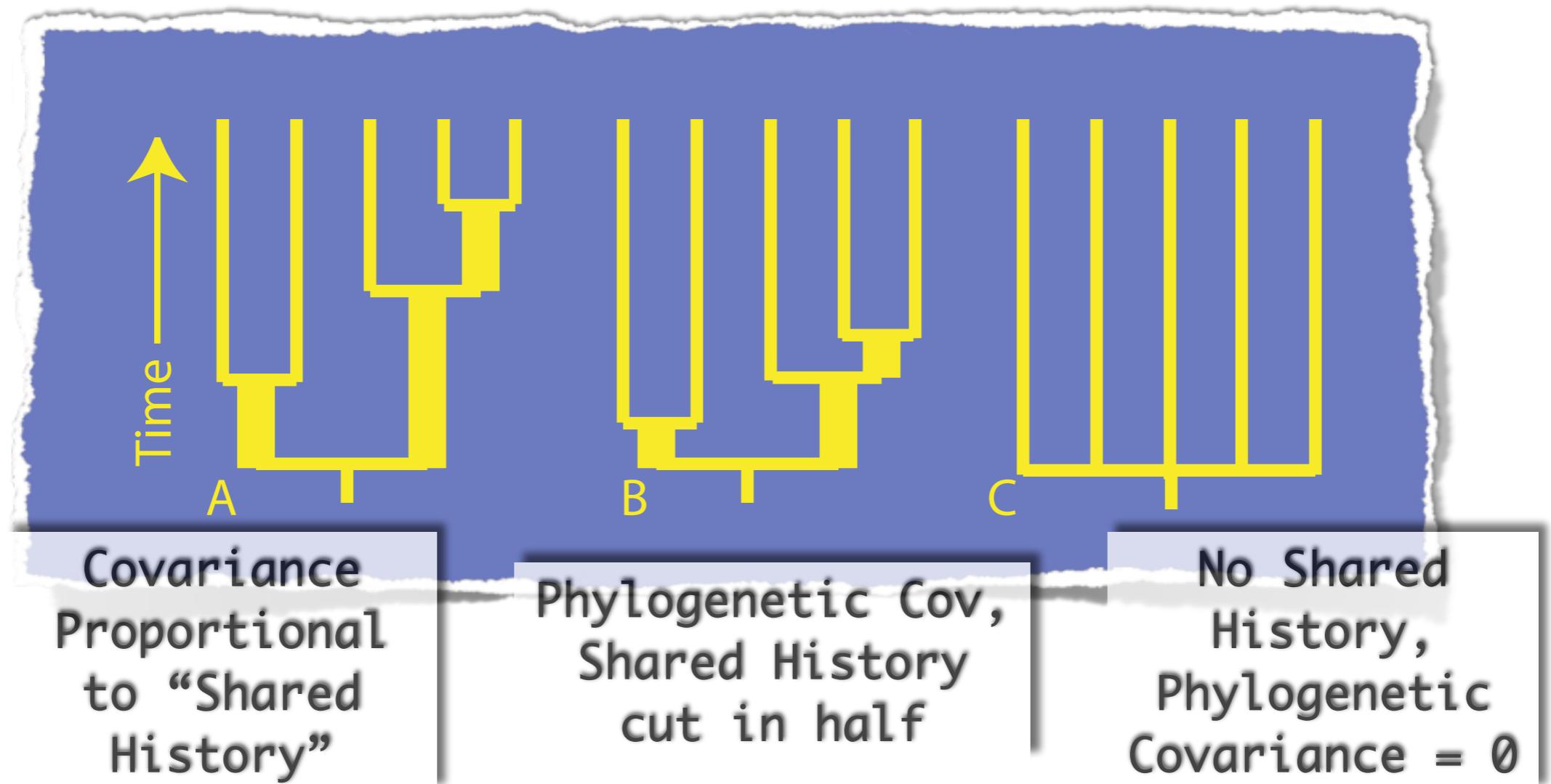
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Why change the phylogeny?

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There is another option...

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Change the model of evolution !

Modeling adaptive evolution using OUCH*!

Marguerite Butler

University of Hawaii, Department of Zoology



Aaron King

University of Michigan, Ecology & Evolutionary Biology

(*Ornstein-Uhlenbeck for Comparative Hypotheses)

2. “Model the Evolutionary Process”

The phylogeny (pattern and timing of evolutionary diversification) as well as the data contains important information

Brownian Motion

$$dX_i(t) = \sigma dB_i(t), \quad t_i^{j-1} \leq t \leq t_i^j.$$

Orstein Uhlenbeck Process

$$dX_i(t) = \alpha (\beta_i^j - X_i(t)) dt + \sigma dB_i(t)$$

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***Vary the models to reflect biology
Then compare to find the best model***

What about the Biology?

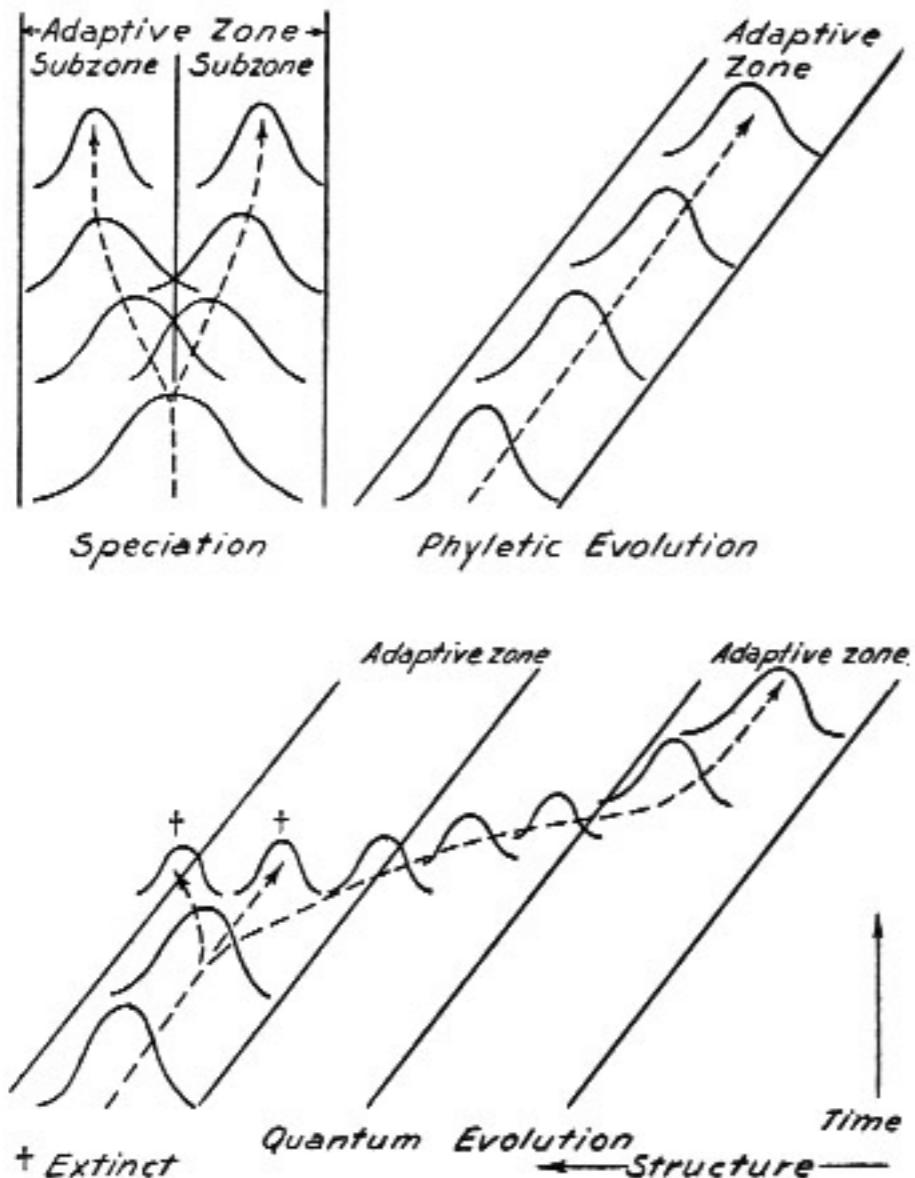
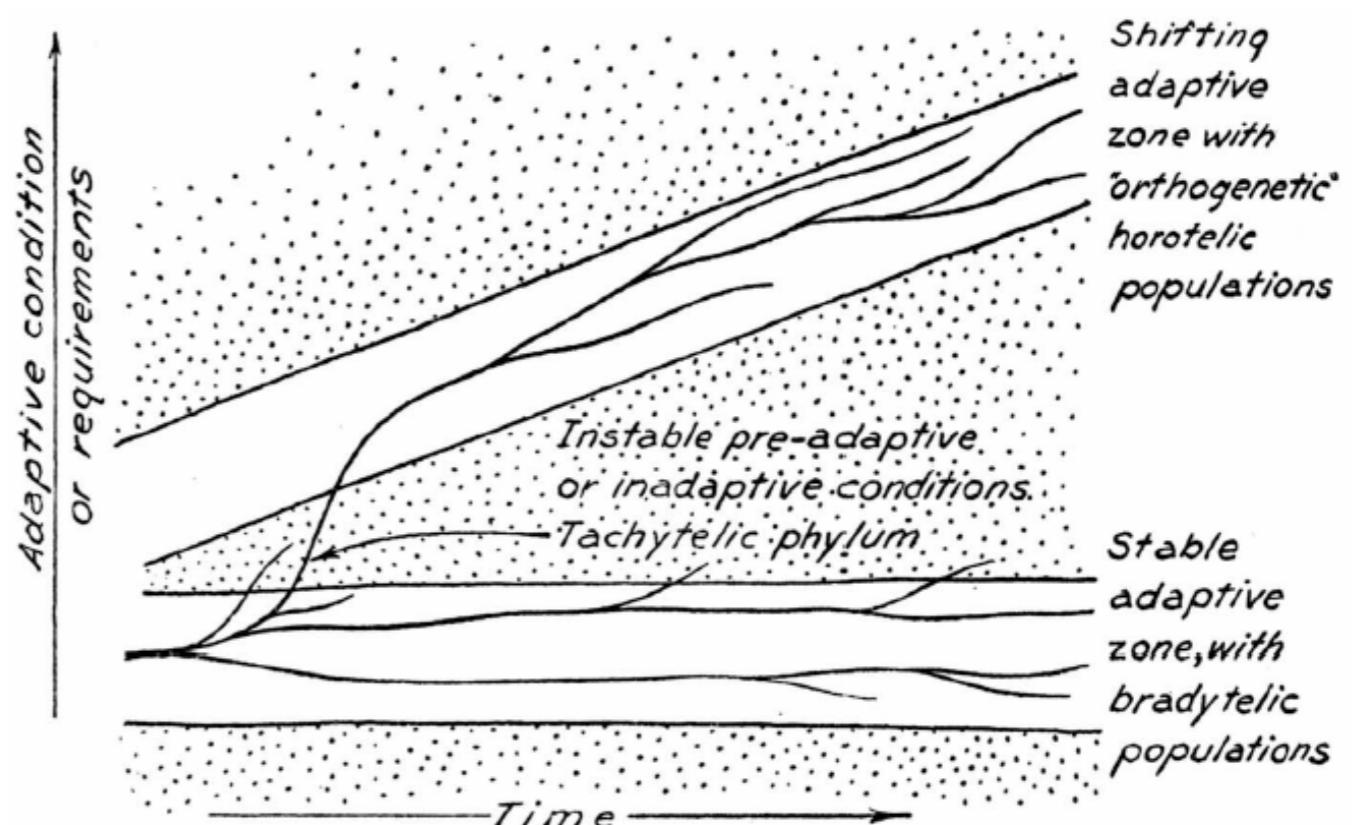


FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.



Simpson (1953) The major features of evolution

**How different are BM
and OU models?**

A*species 1*

Nuts and Bolts: 2 species example

*species 2***B***species 1*

Phenotype

$$\mathbf{X}(t) = \begin{bmatrix} X_1(t) \\ X_2(t) \end{bmatrix}$$

BM

Expected Value
(mean at T)

$$E[\mathbf{X}(T)] = \begin{bmatrix} \theta_0 \\ \theta_0 \end{bmatrix}$$

Variance

$$\mathbf{V} = \sigma^2 \begin{bmatrix} T & s \\ s & T \end{bmatrix}$$

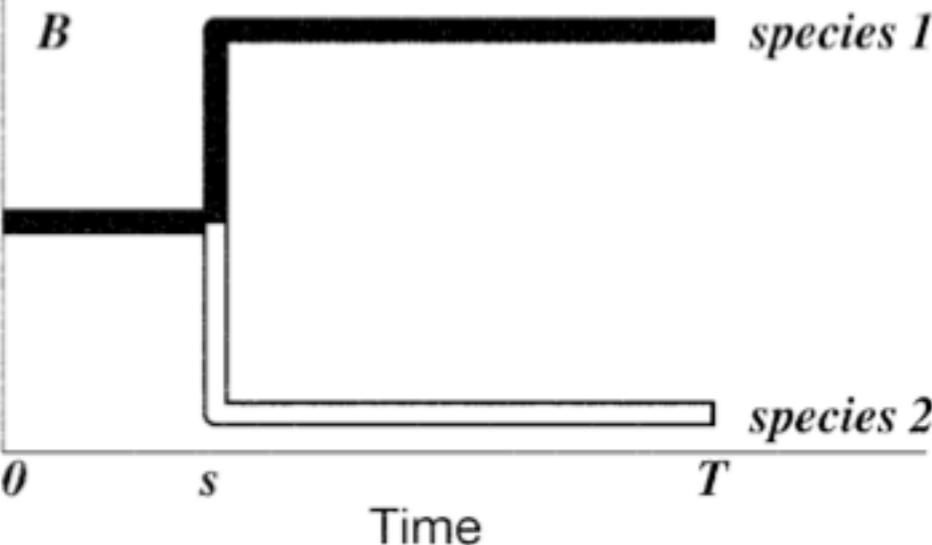
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OU

$$\begin{aligned} E[X_1(T)] &= \theta_0 e^{-\alpha T} + \theta_1 (1 - e^{-\alpha T}) \\ &= \theta_0 W_{10} + \theta_1 W_{11} \end{aligned}$$

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$$E[\mathbf{X}(T)] = \mathbf{W}\boldsymbol{\theta}$$

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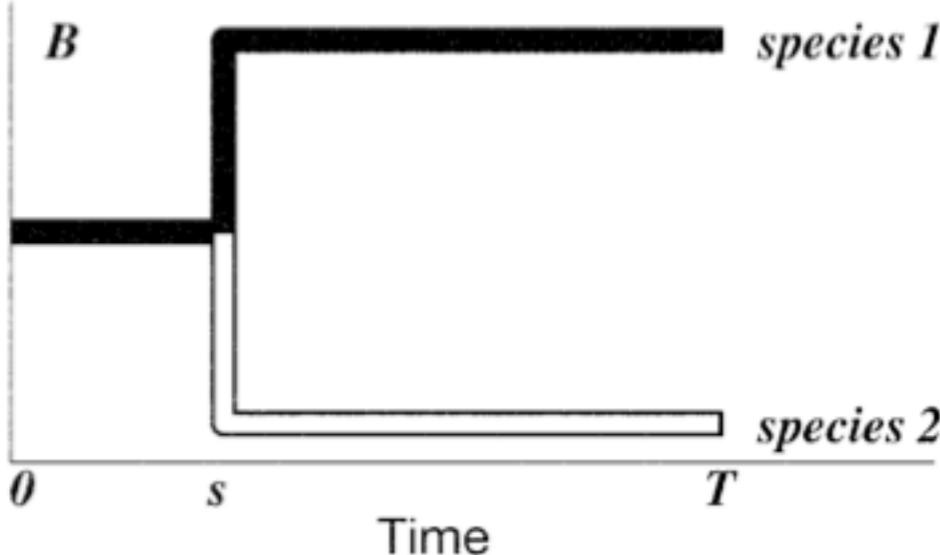
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Variance

$$\mathbf{V} = \sigma^2 \begin{bmatrix} T & s \\ s & T \end{bmatrix}$$

$$\mathbf{V} = \begin{bmatrix} 1 - e^{-2\alpha T} & e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) \\ e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) & 1 - e^{-2\alpha T} \end{bmatrix}$$

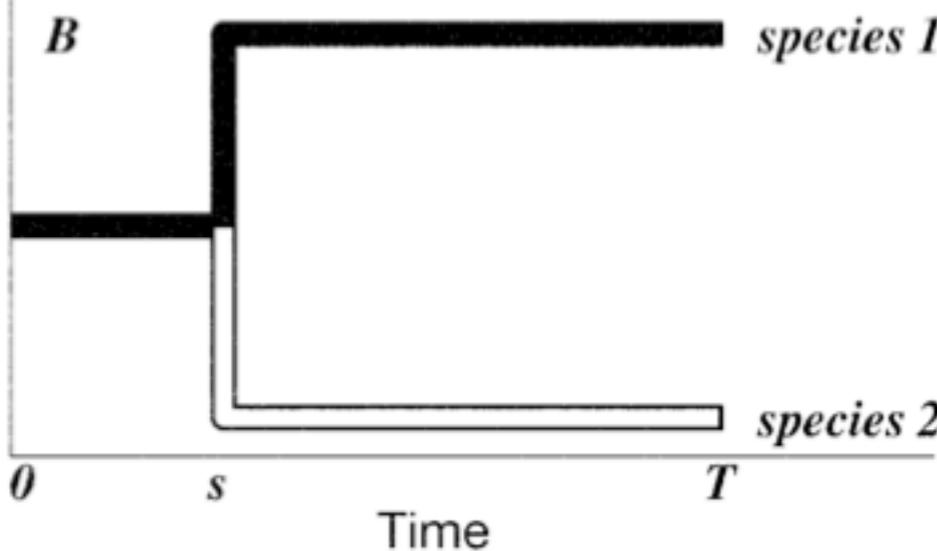
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Nuts and Bolts: 2 species example

species 2

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Expected Value
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Variance

$$\mathbf{V} = \sigma^2 \begin{bmatrix} T & s \\ s & T \end{bmatrix}$$

Phenotype $\mathbf{X}(t) = \begin{bmatrix} X_1(t) \\ X_2(t) \end{bmatrix}$

Log-likelihood equation

$$-2 \log \mathcal{L} = \{\mathbf{X}(T) - E[\mathbf{X}(T)]\}' \mathbf{V}^{-1} \times \{\mathbf{X}(T) - E[\mathbf{X}(T)]\} + N \log (2\pi \det \mathbf{V})$$

BM

OU

$$\begin{aligned} E[X_1(T)] &= \theta_0 e^{-\alpha T} + \theta_1 (1 - e^{-\alpha T}) \\ &= \theta_0 W_{10} + \theta_1 W_{11} \end{aligned}$$

$$E[\mathbf{X}(T)] = \mathbf{W}\boldsymbol{\theta}$$

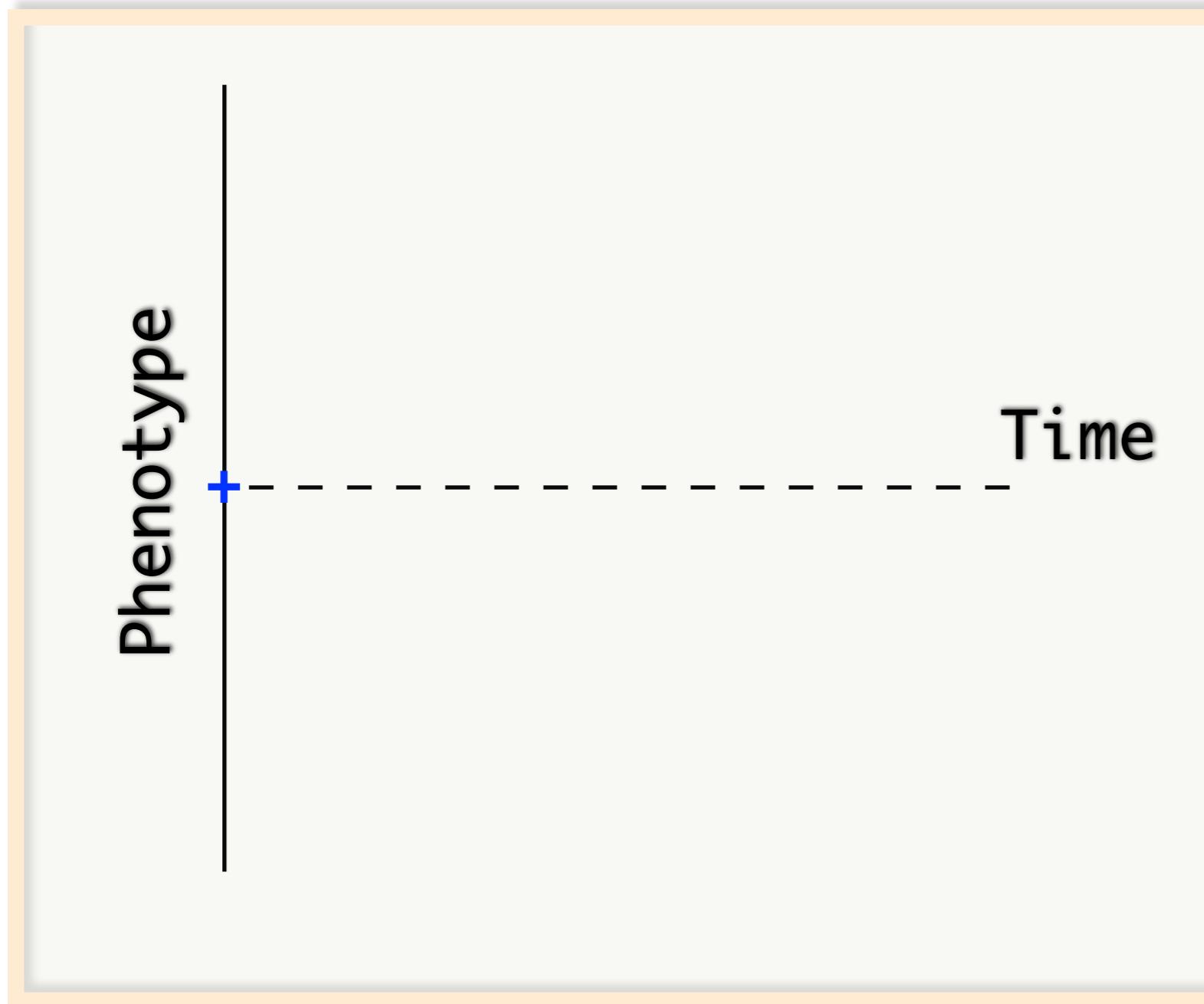
$$\mathbf{V} = \begin{bmatrix} 1 - e^{-2\alpha T} & e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) \\ e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) & 1 - e^{-2\alpha T} \end{bmatrix}$$

**That's great... but what
does it look like?**

**That's great... but what
does it look like?**

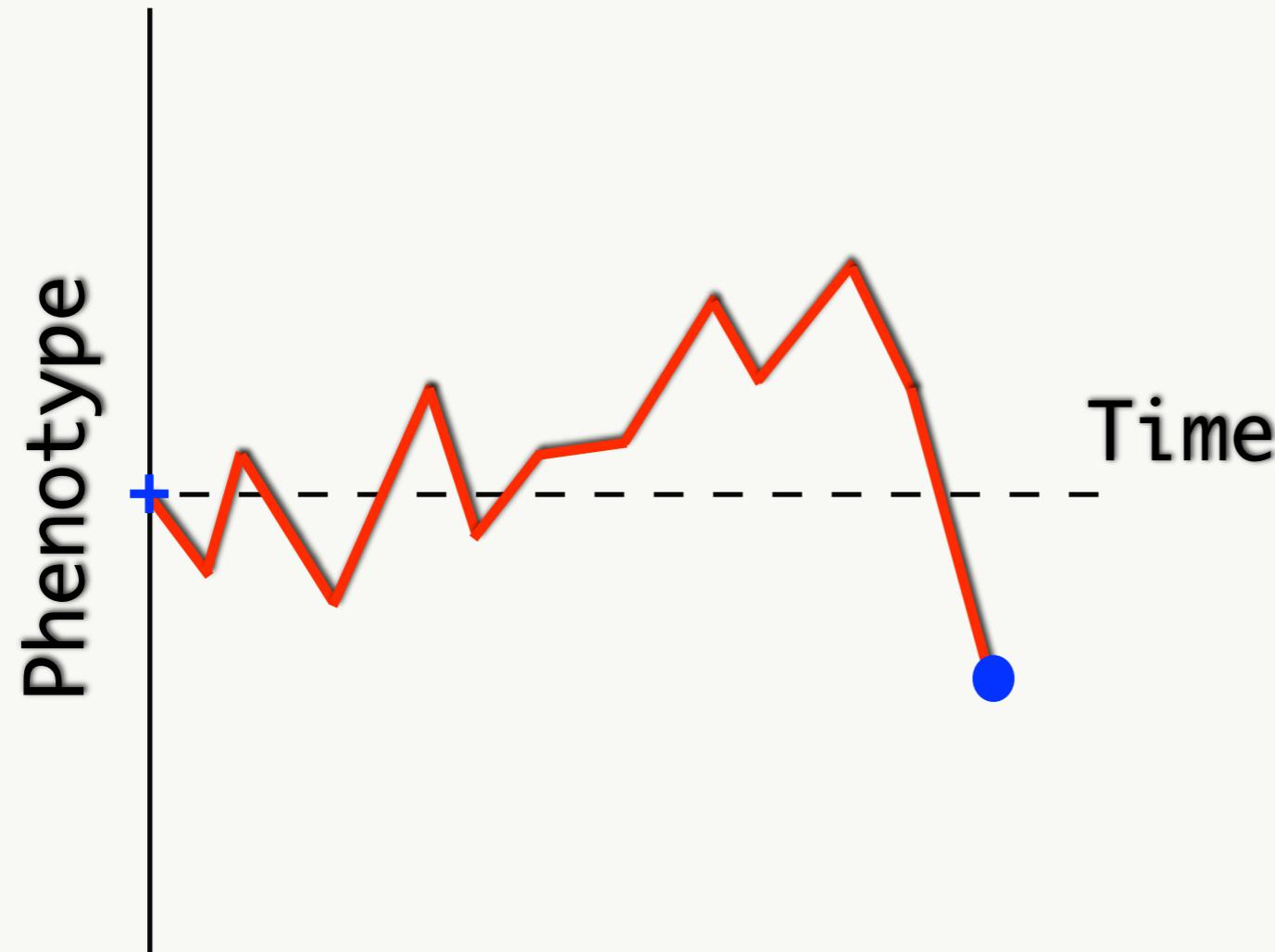
let's do some simulations!

Evolution in Cartoon



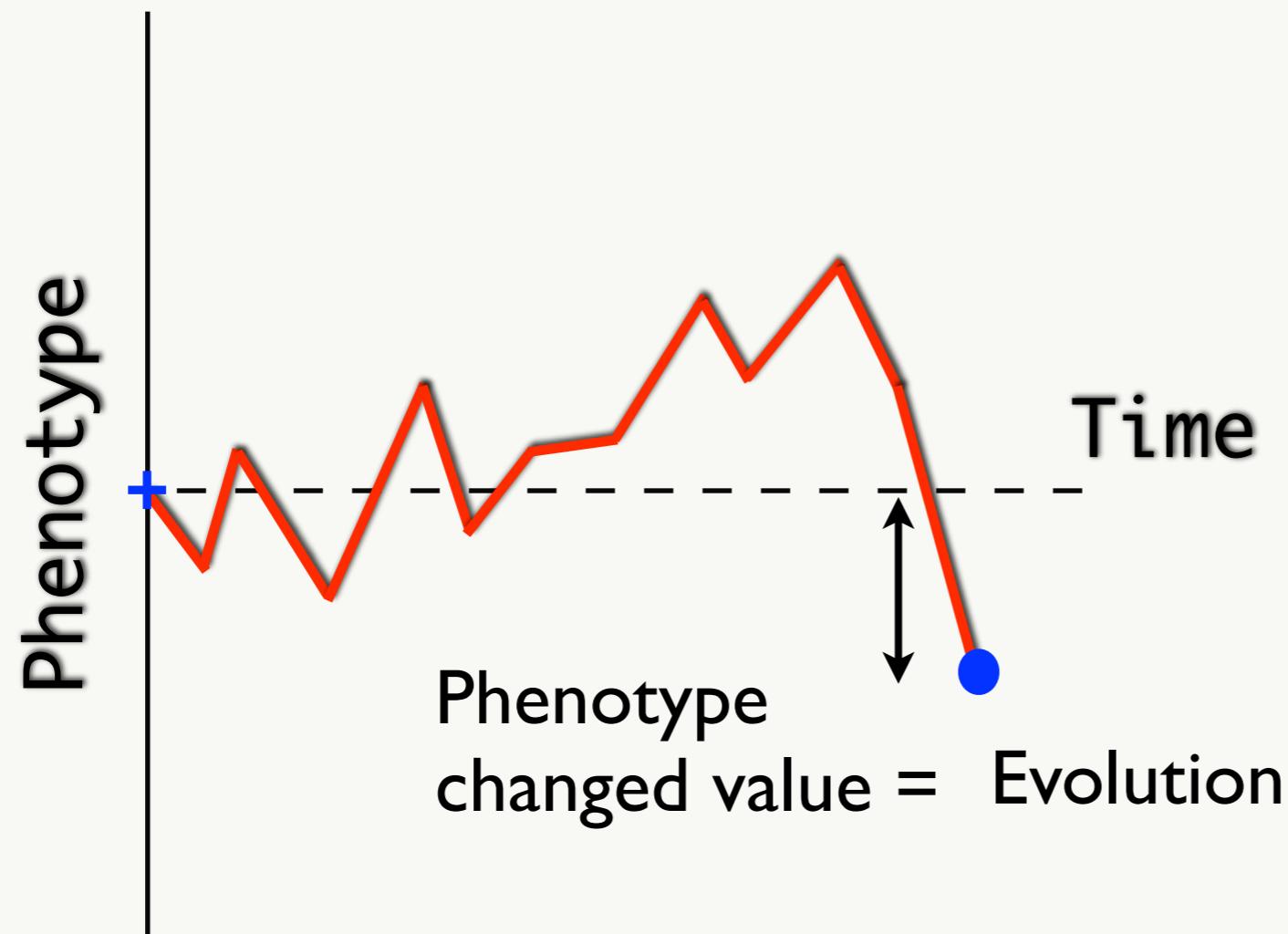
- At each infinitesimal increment of time, there is a probability of change in the phenotype.
- The probability is drawn from a normal distribution, thus the BM is “Gaussian.”
- The state at any given time is only dependent on the previous state.

Evolution in Cartoon



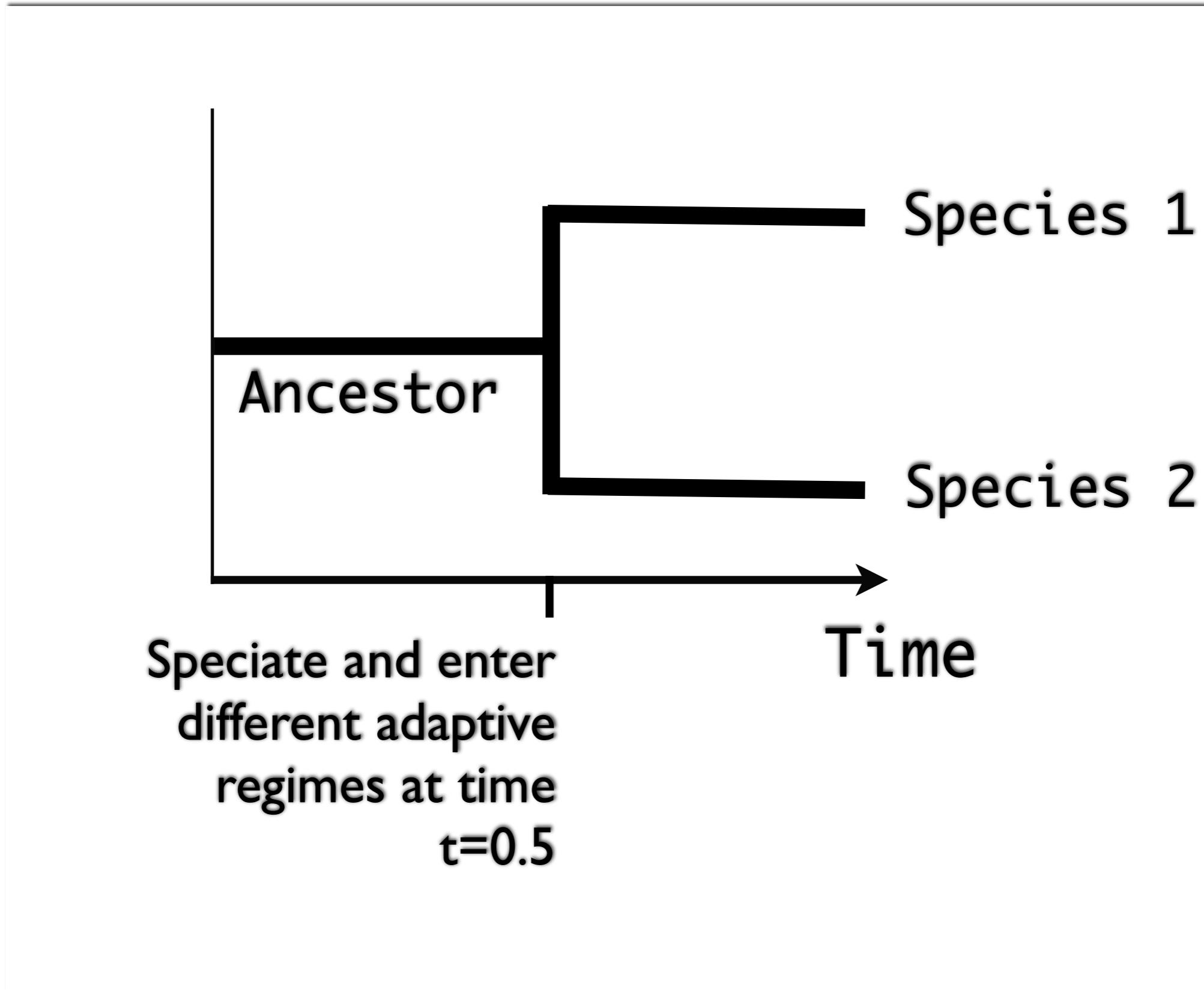
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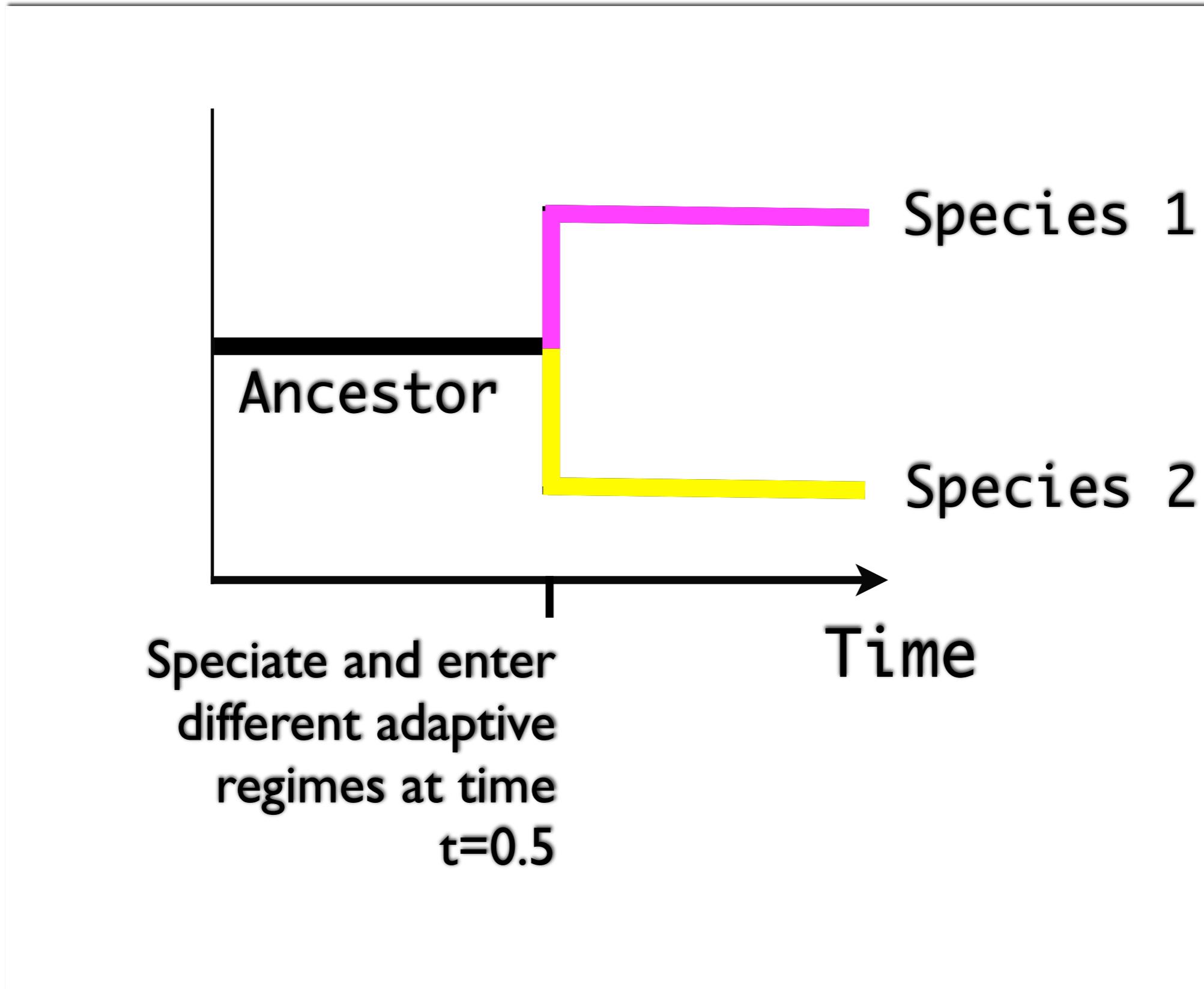


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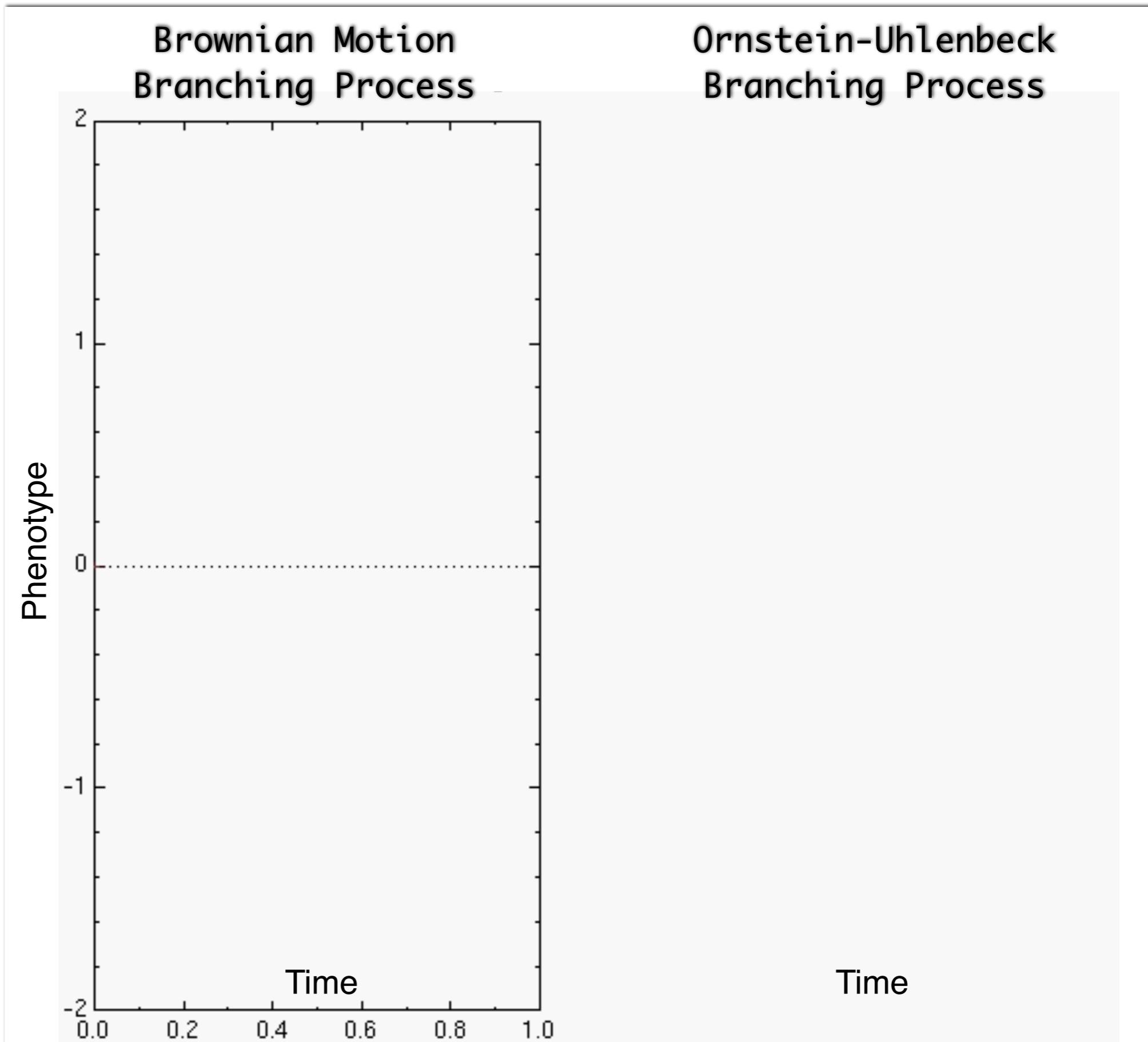
BM and OU models make different predictions



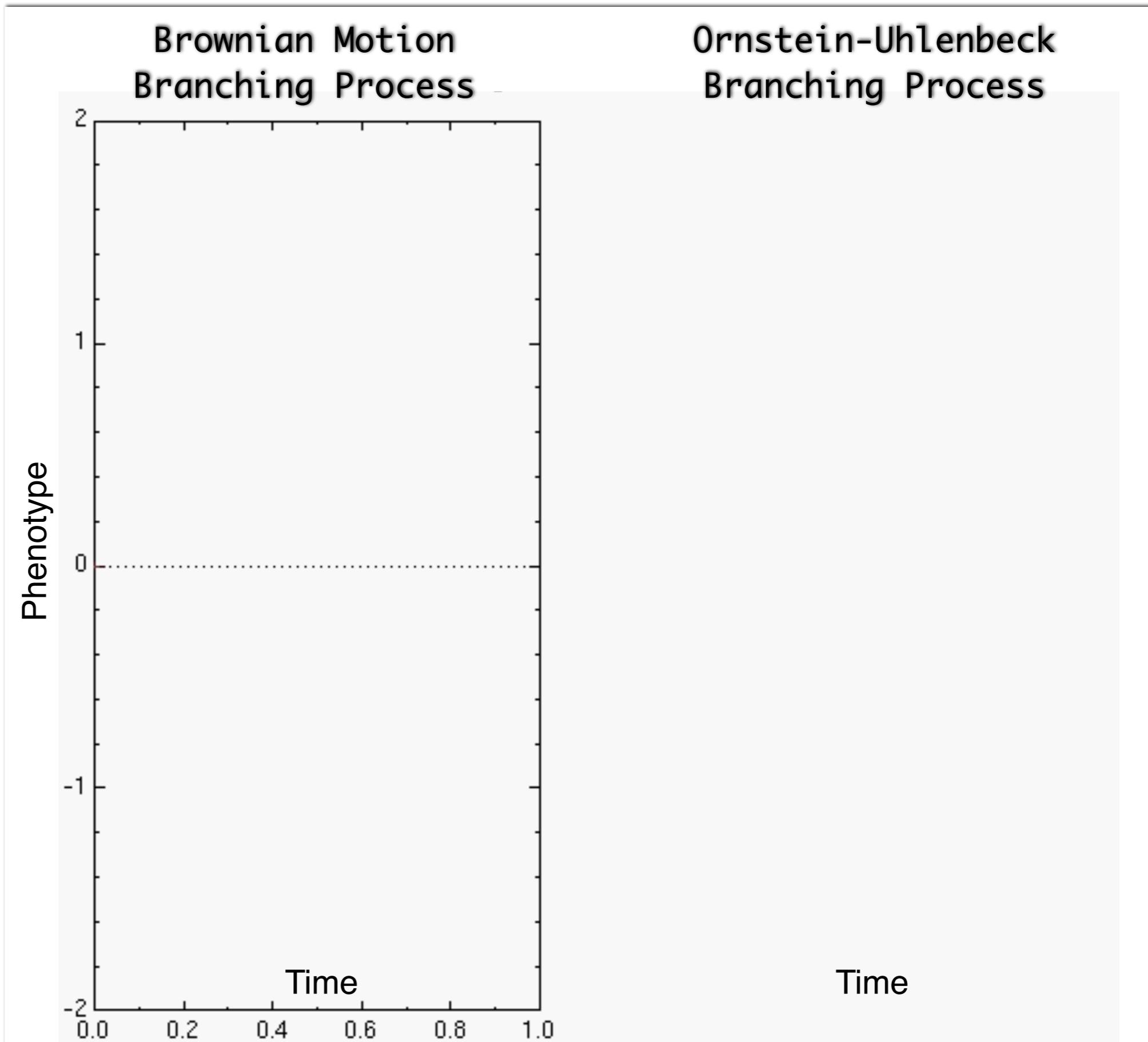
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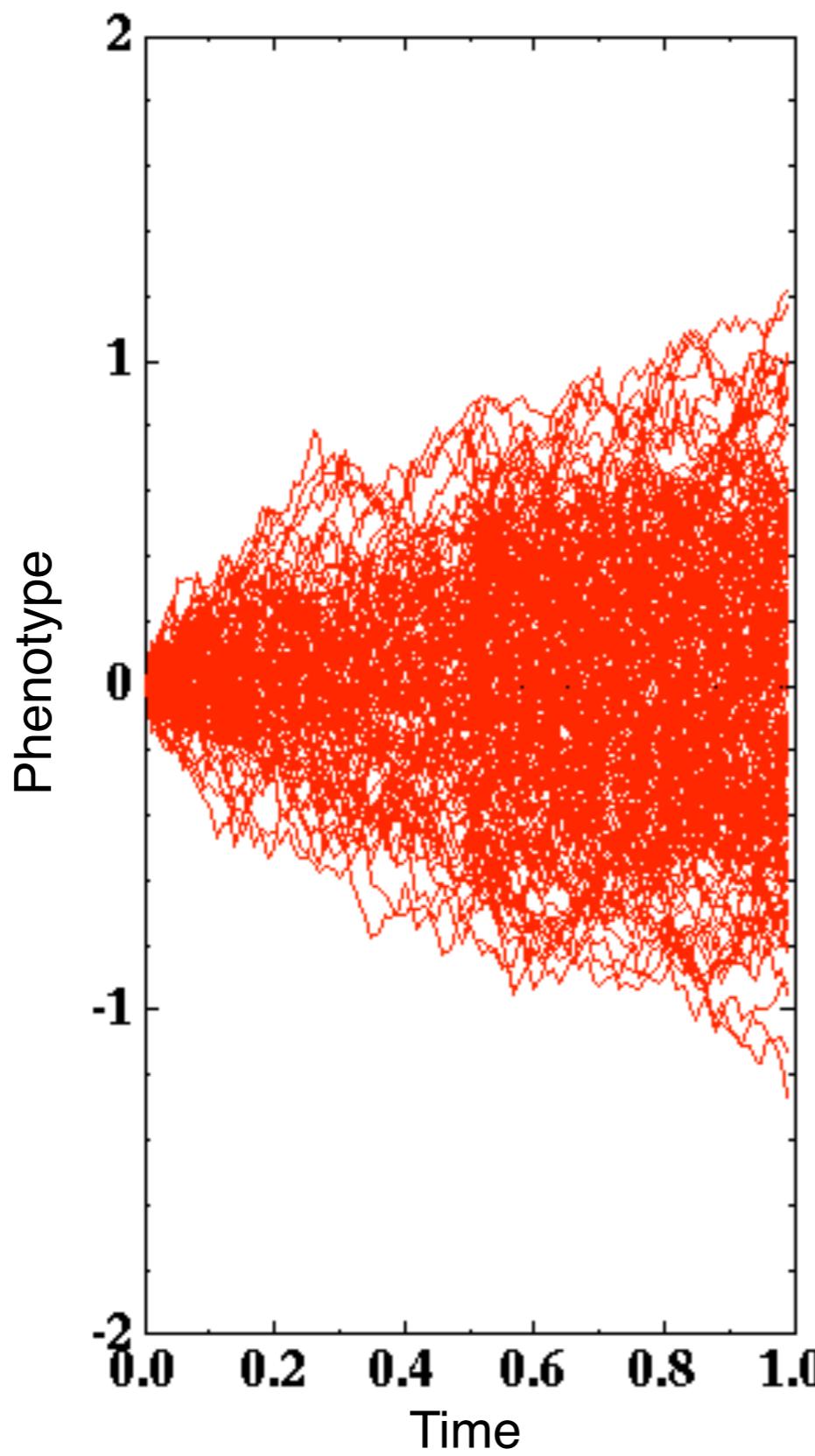
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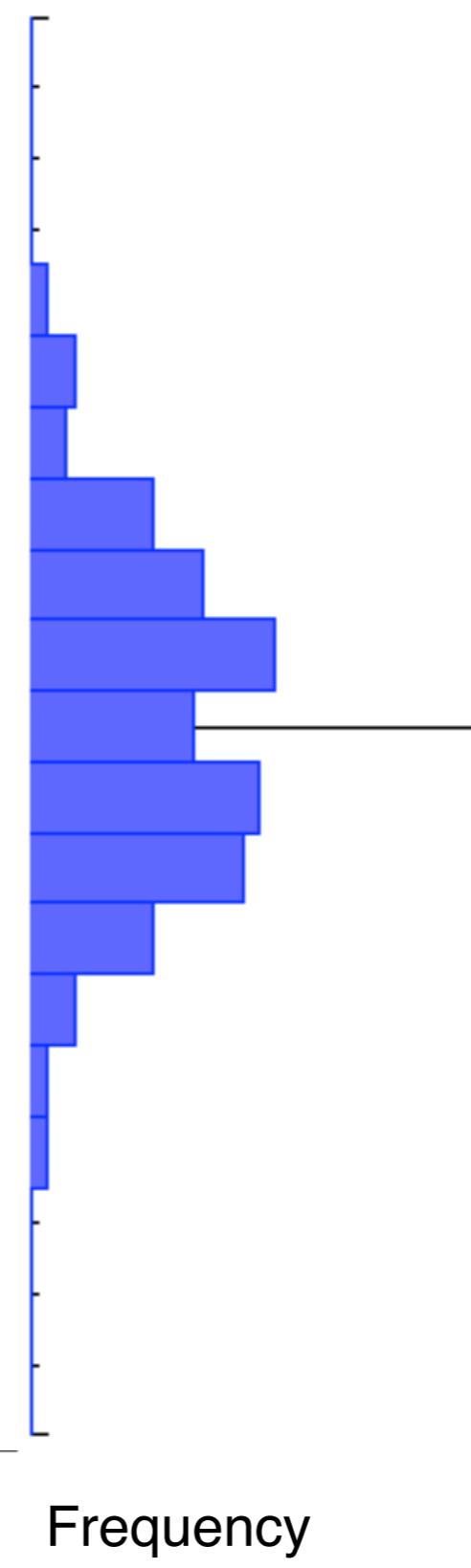
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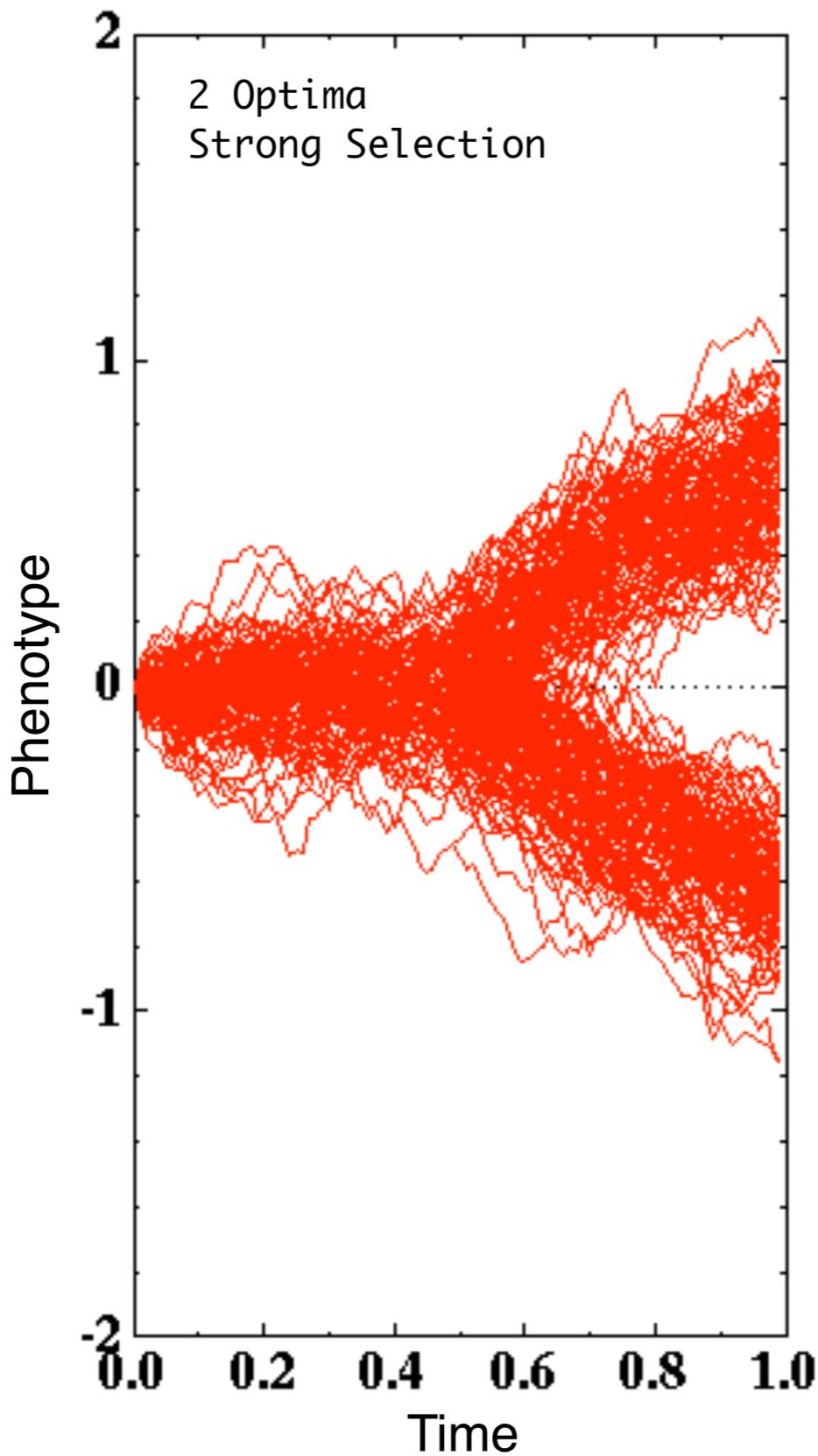
Brownian Motion
Branching Process



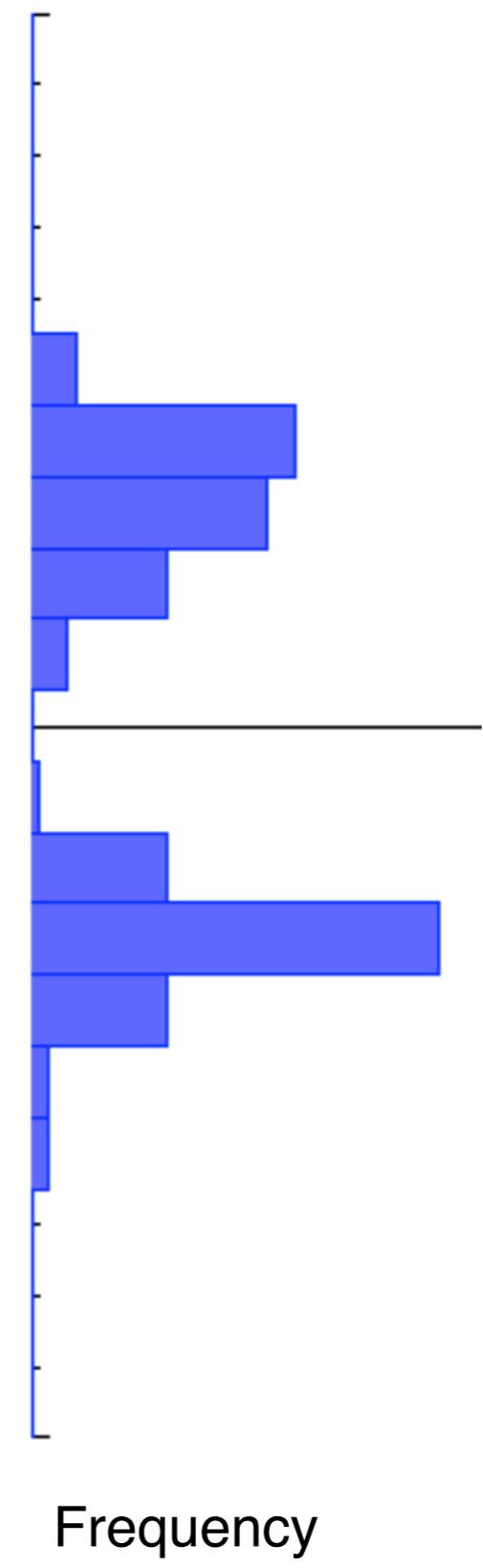
Phenotypic
Distribution



OU Branching Process



Phenotypic Distribution



What about the Biology?

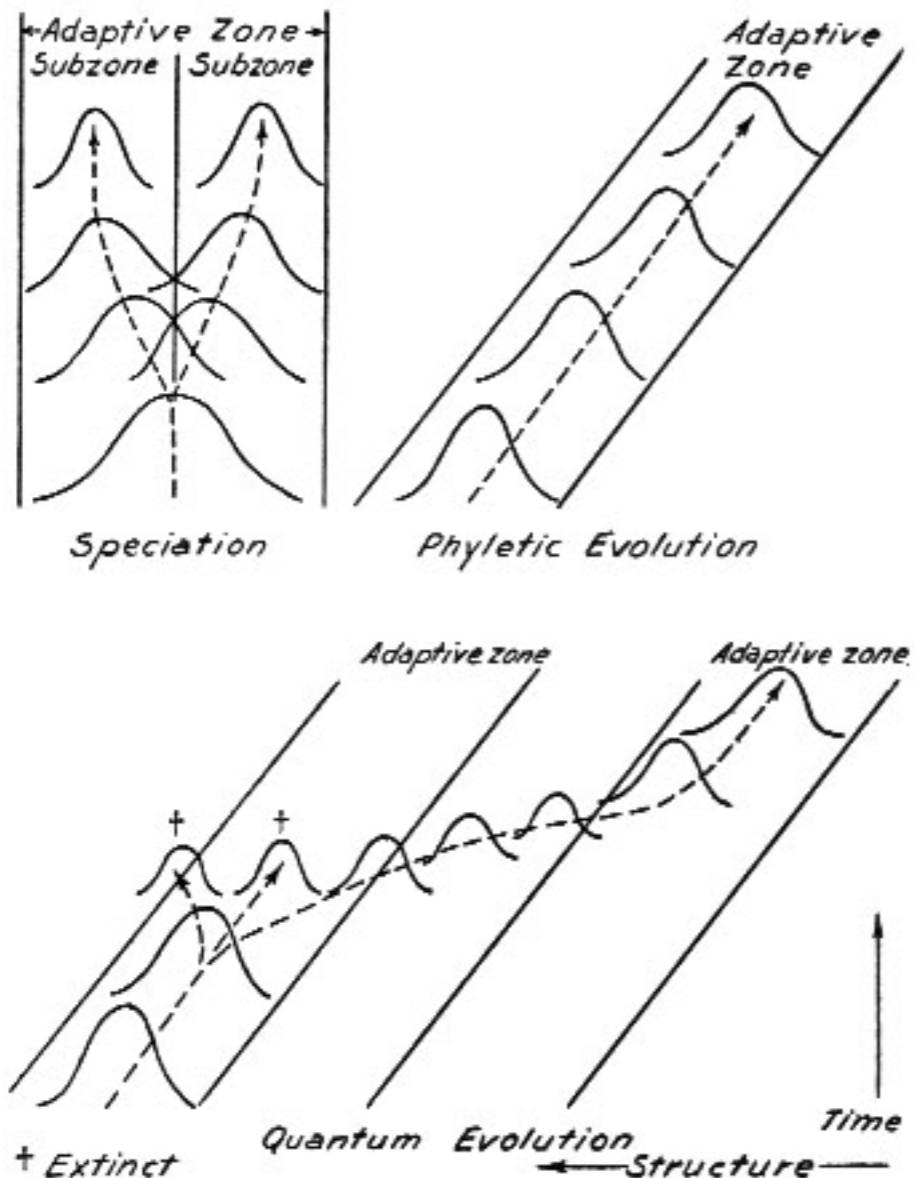
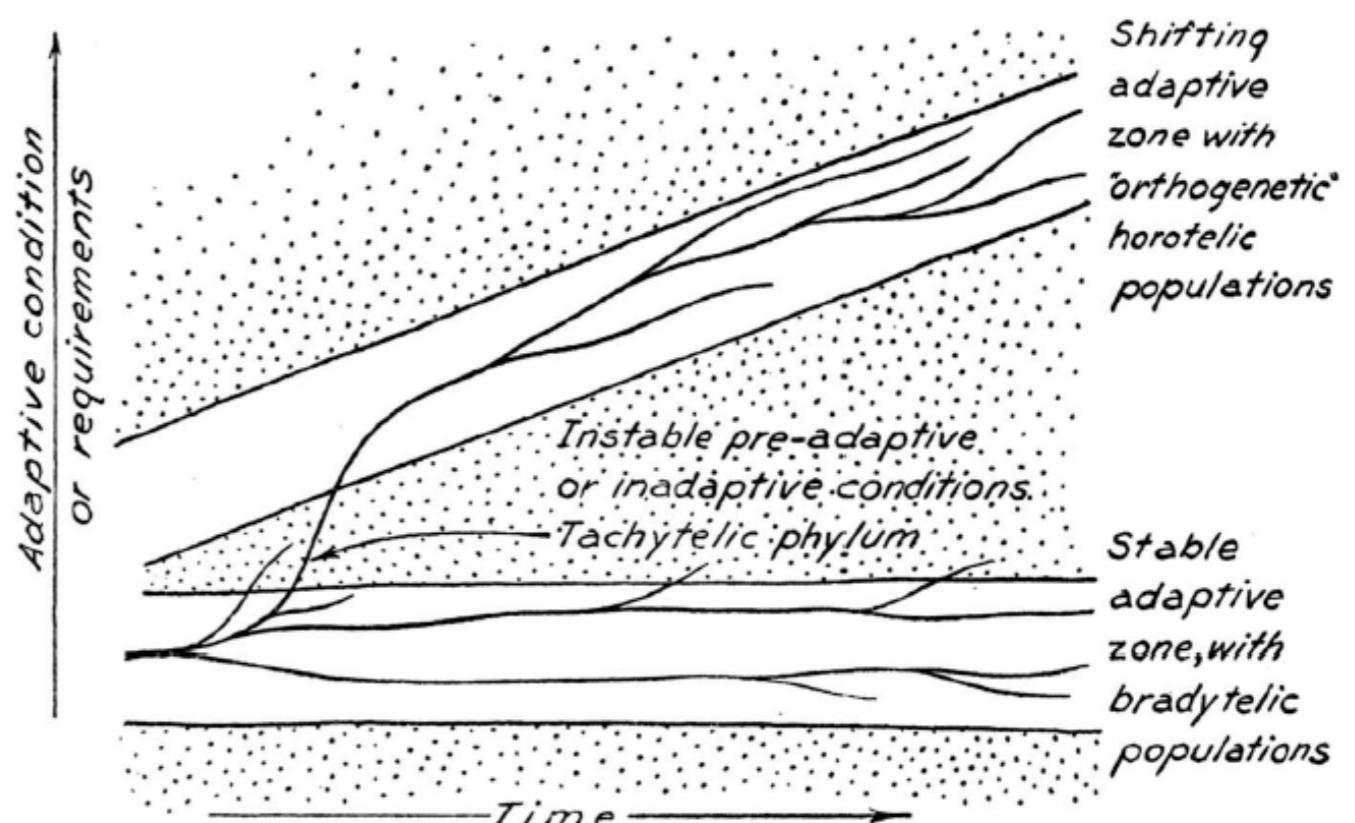


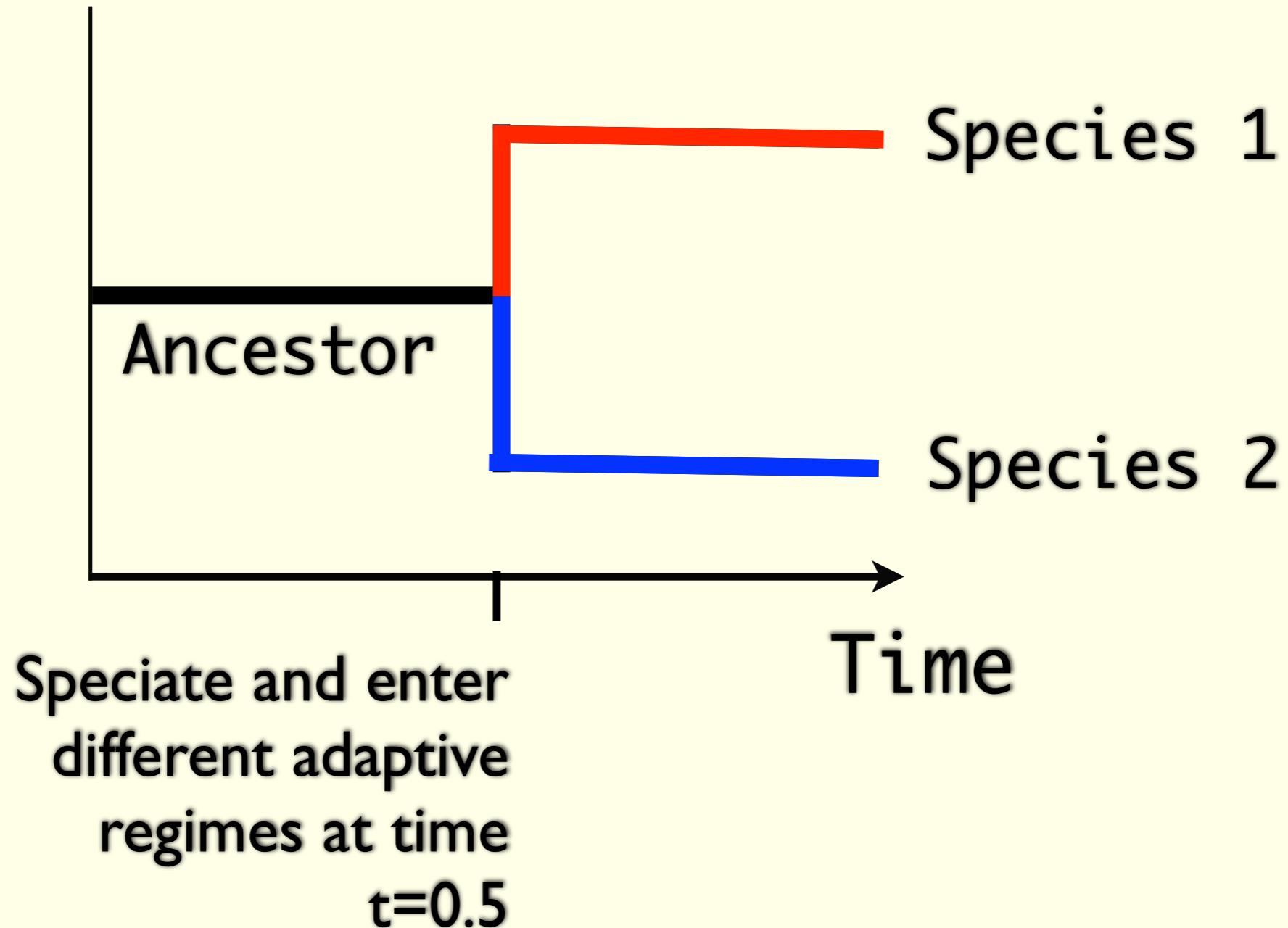
FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.



Simpson (1953) The major features of evolution

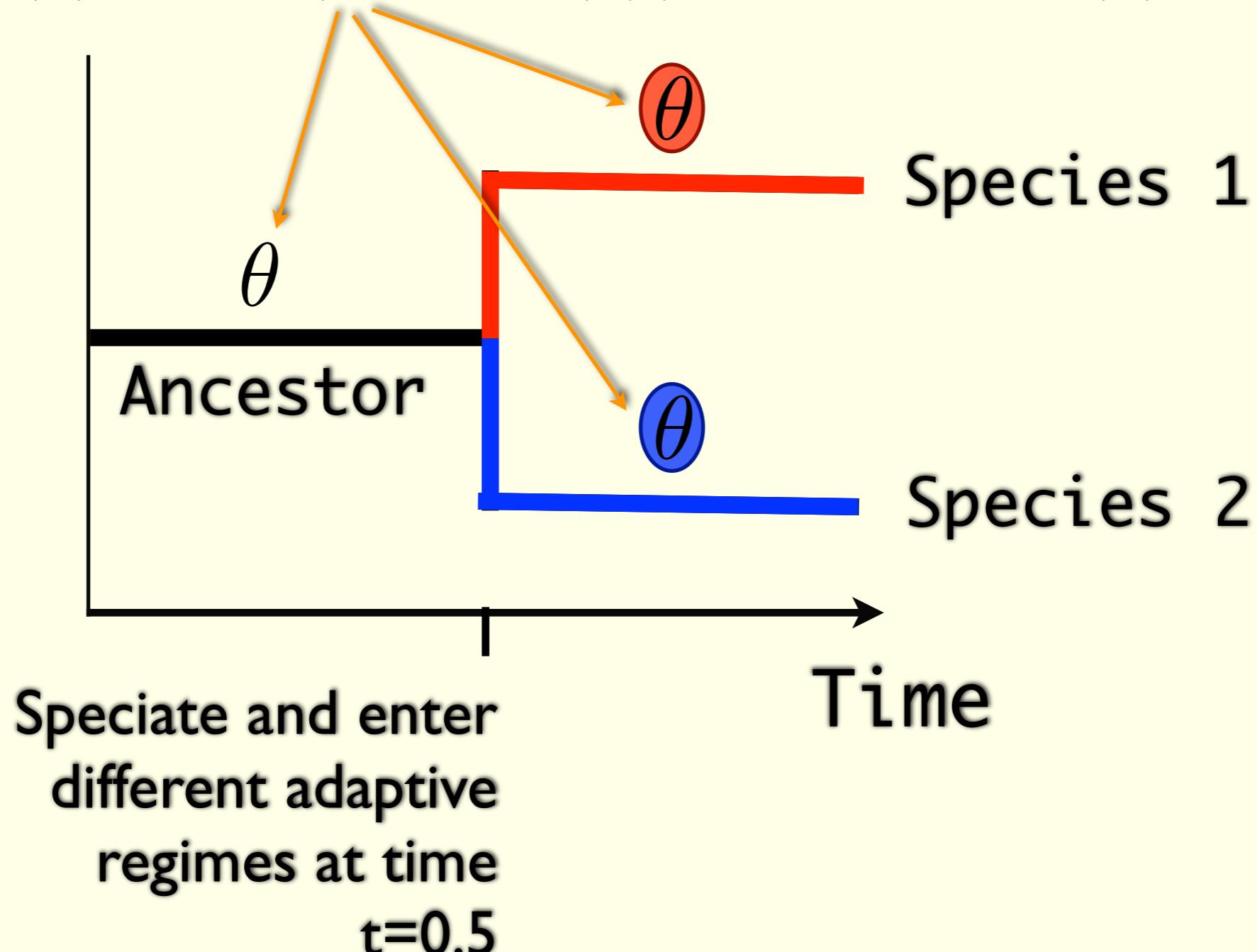
Shift in adaptive regimes: as easy as painting new optimum!

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



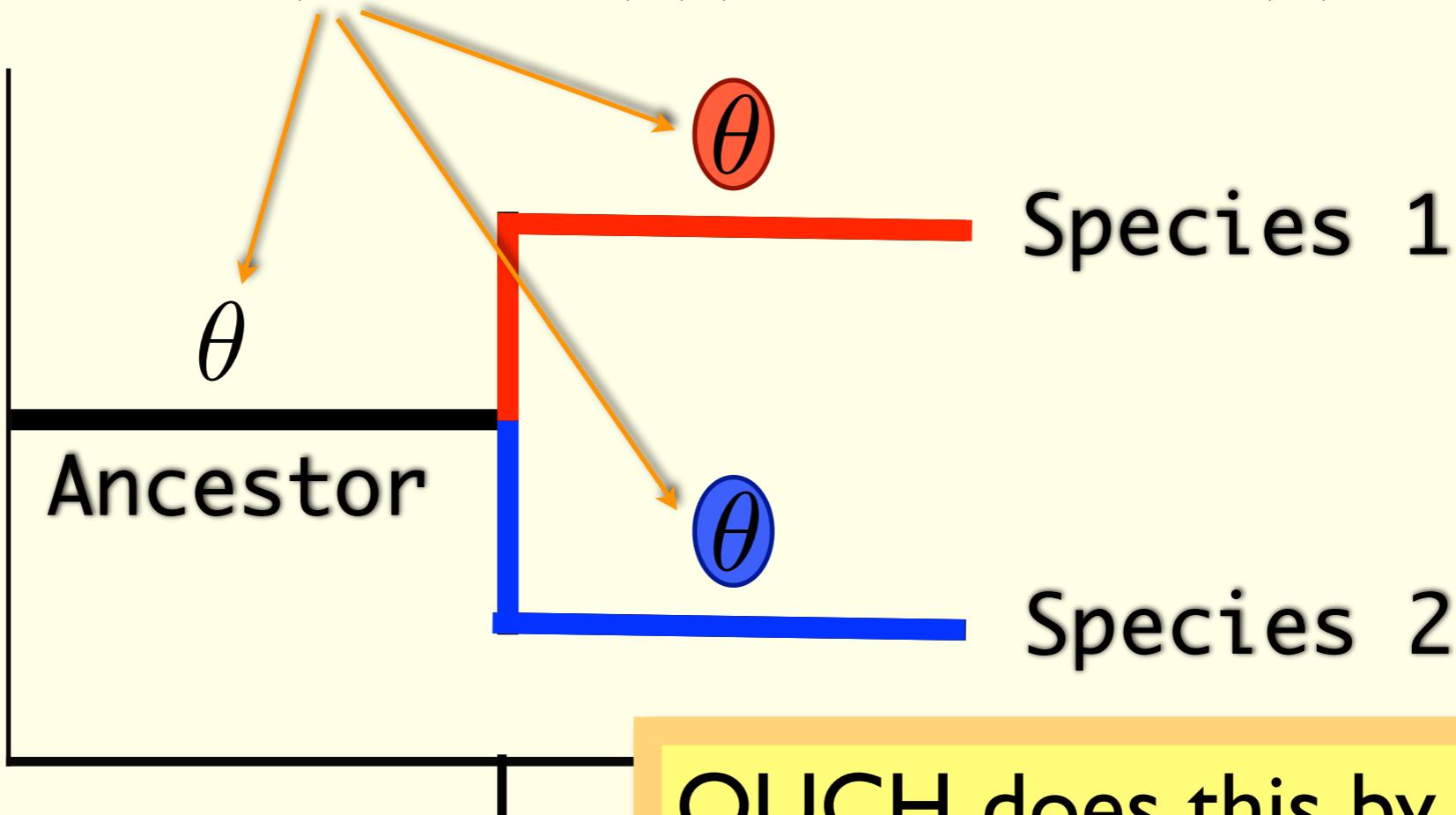
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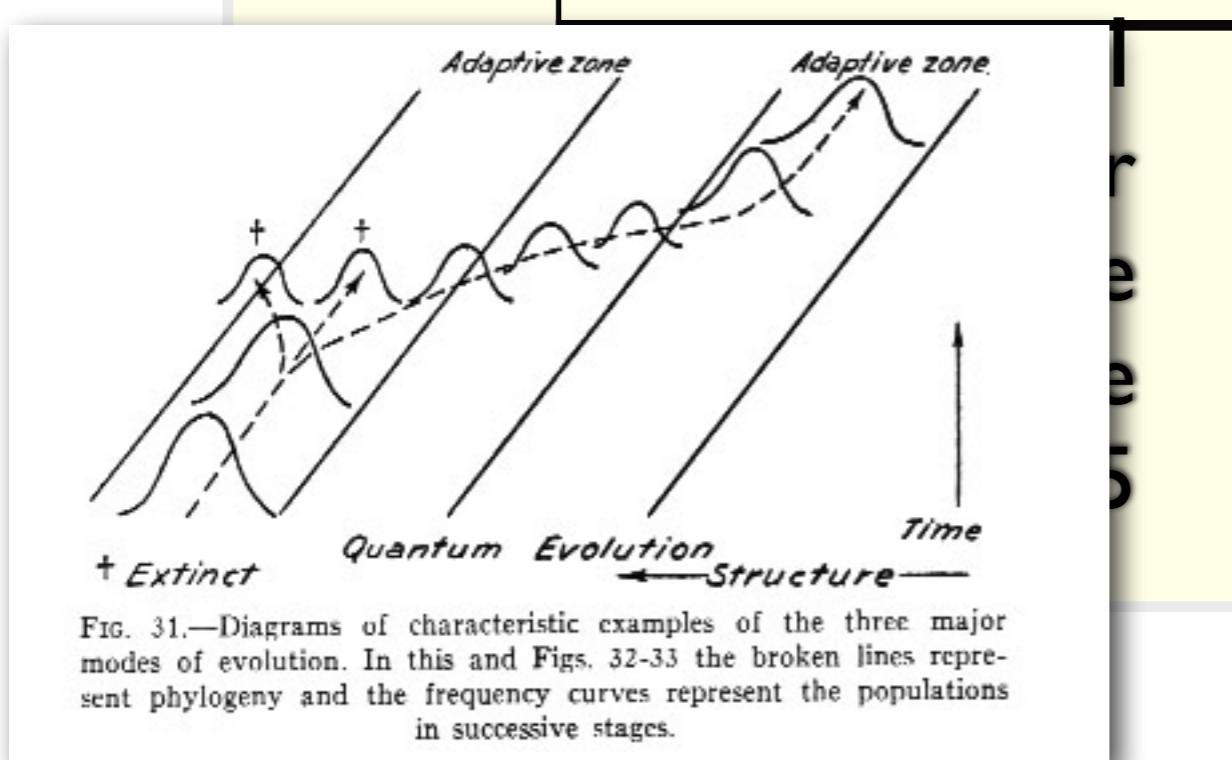
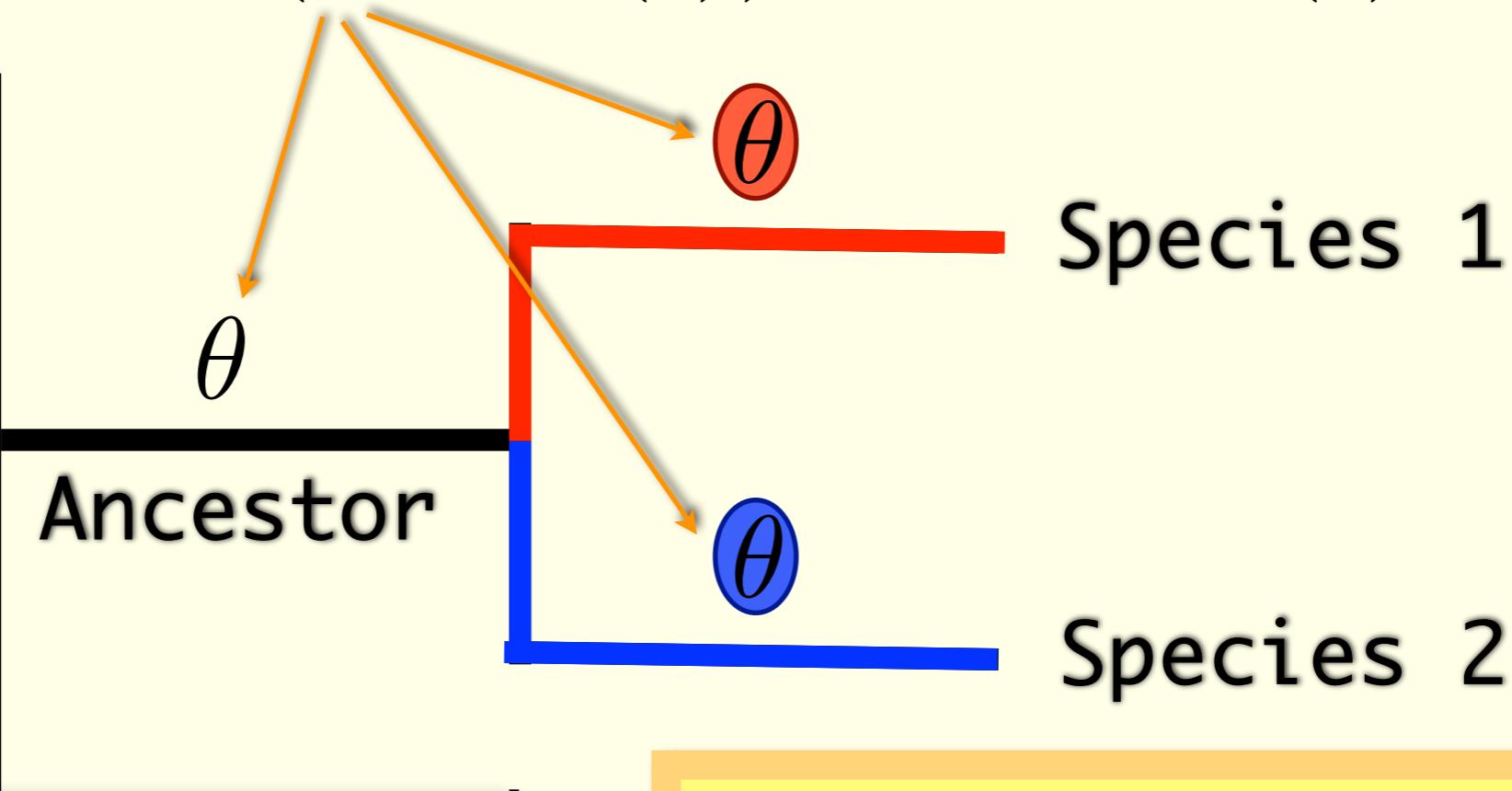


Speciate and enter
different adaptive
regimes at time
 $t=0.5$

OUCH does this by writing
a model for each branch of
the phylogeny, according to
the selective regimes we
hypothesize

Shift in adaptive regimes: as easy as a painting new optimum!

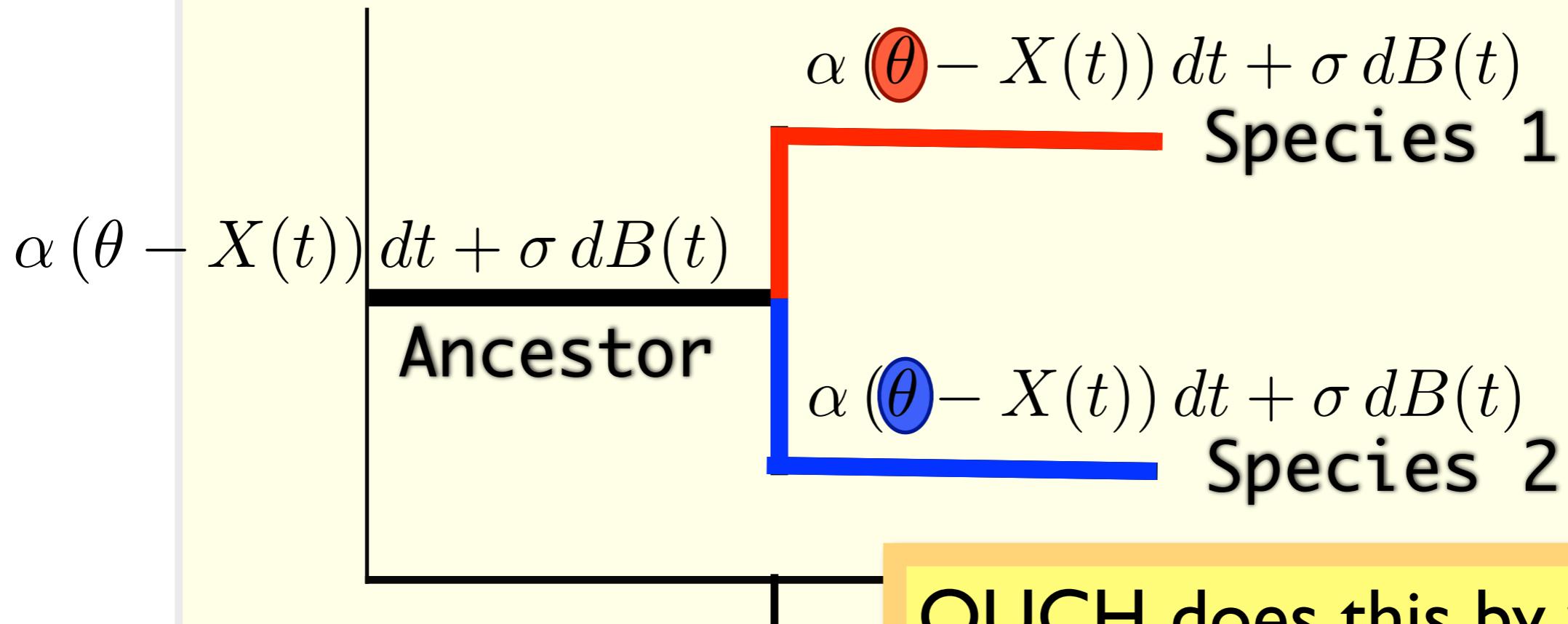
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and potentially make a statement about how characters evolved!

Character Displacement in Lesser Antillean Anoles



**Islands in the Lesser Antilles have
only 1 or 2 species of anoles.**



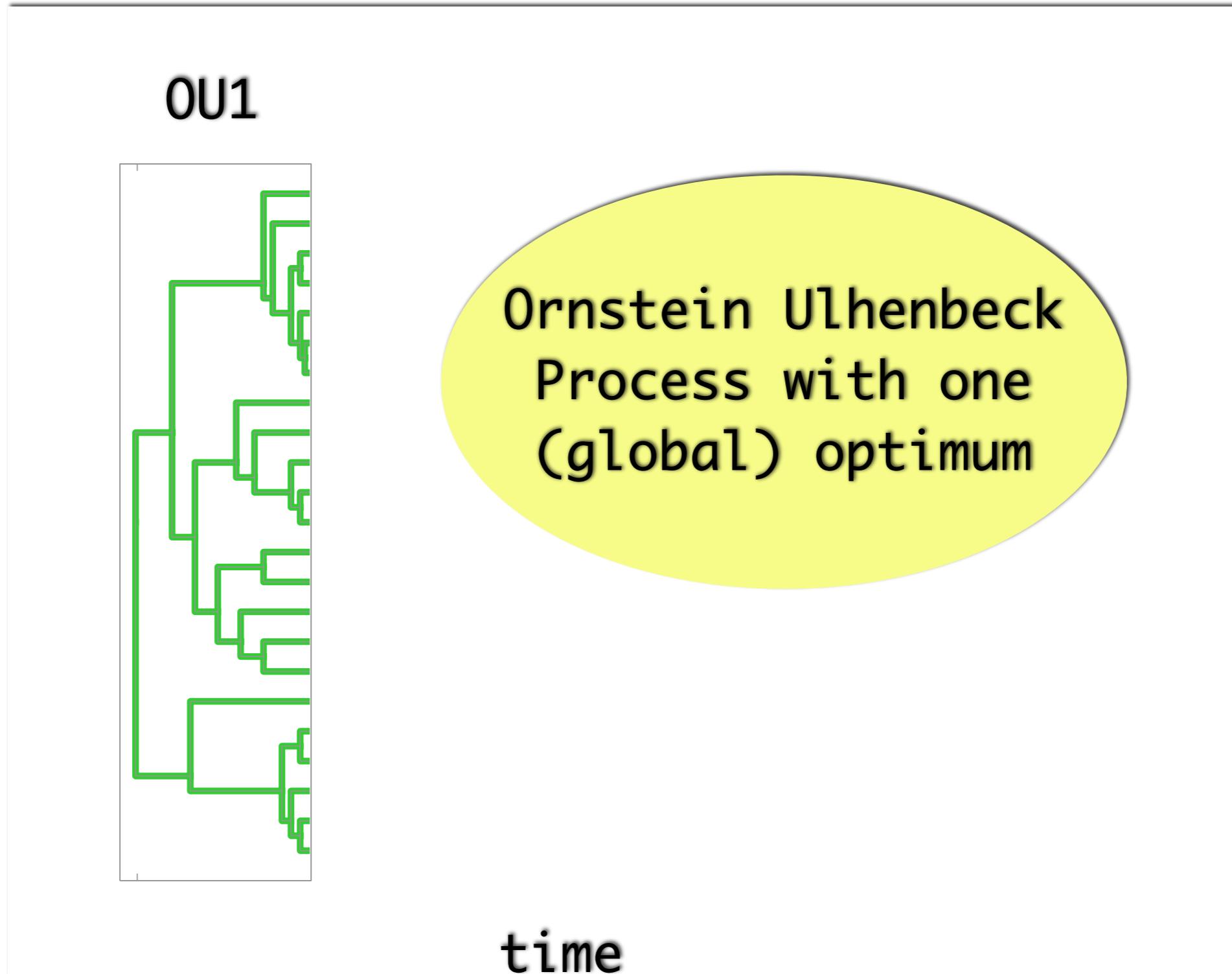
Islands in the Lesser Antilles have only 1 or 2 species of anoles.

On the 2 species islands, anoles differ substantially in size.

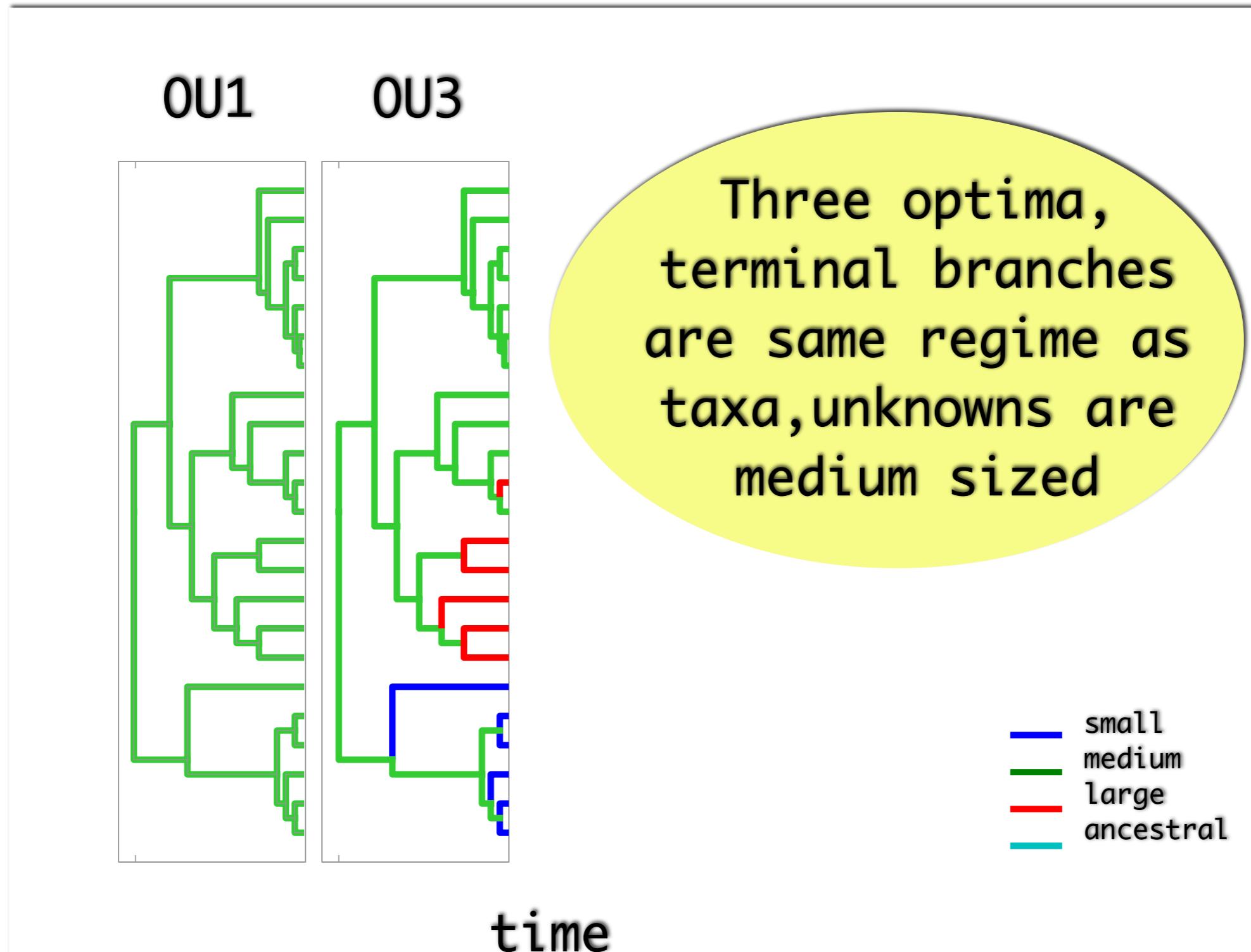
On the single species islands, anoles are “intermediate” in size.



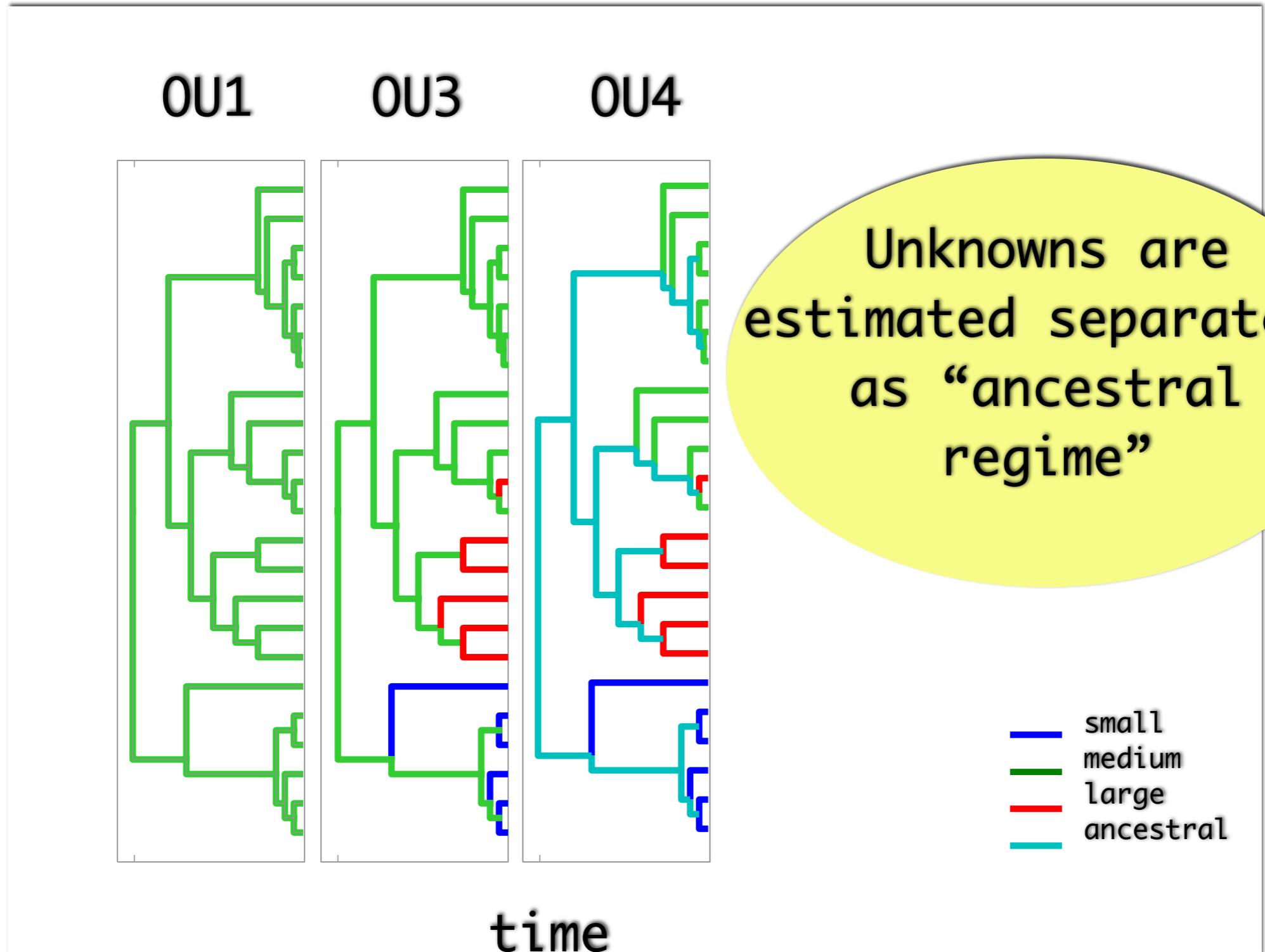
Alternative Adaptive Regime Models



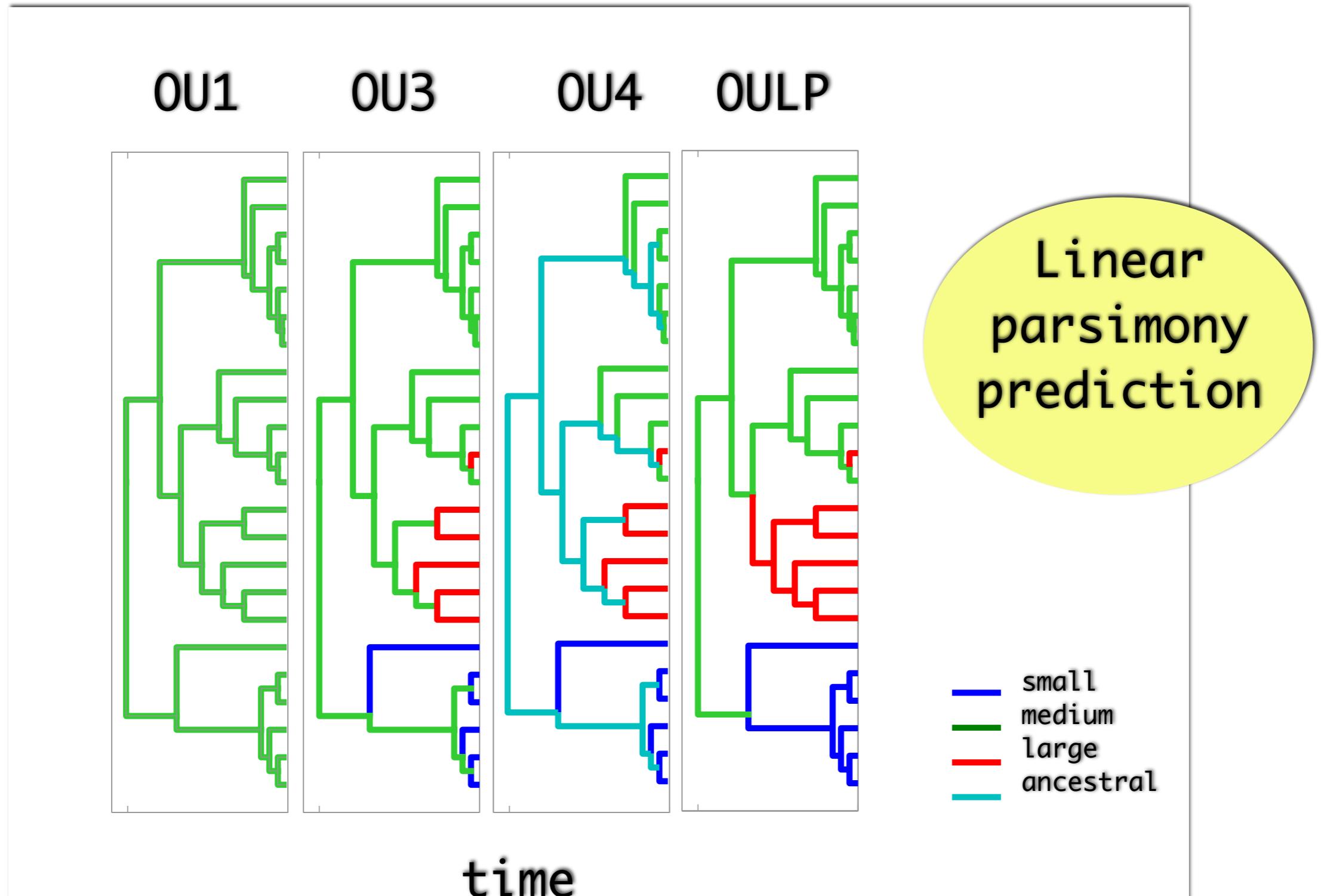
Alternative Adaptive Regime Models



Alternative Adaptive Regime Models



Alternative Adaptive Regime Models



Model Comparison

	BM	OU(1)	OU(3)	OU(4)	OU(LP)
-2x Log Likelihood	-36.31	-34.66	-40.06	-47.22	-49.69
AIC	-32.31	-26.66	-28.06	-33.22	-37.69
LR		0	0.56	0.95	0.99
Pvalue		1	0.44	0.05318	0.00955

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Bad Models

Strange Parameter Estimates

	BM	OU(1)	OU(3)	OU(4)	OU(LP)
alpha		0	0.32	14.67	2.49
sigma	0.2	0.21	0.2	0.47	0.22
ancestor	2.83	2.95	3.99	--	0.86
optima 1		--	-1.4	2.58	2.75
optima 2			0.18	3.11	3.24
optima 3			2.71	3.3	3.56
optima 4				2.83	

Best Model

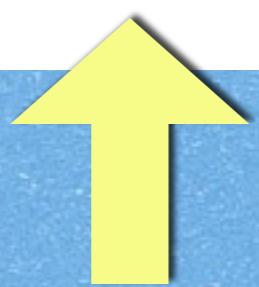
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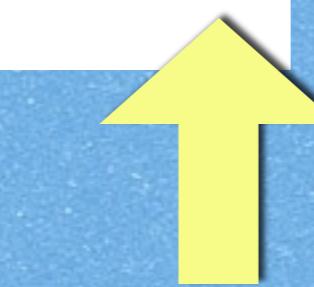
$$\mathbb{E} [X_i(T) \mid X_i(0) = \theta_0]$$

$$= e^{-\alpha T} \theta_0 + \sum_{j=1}^{k(i)} e^{-\alpha T} \left(e^{\alpha t_i^j} - e^{\alpha t_i^{j-1}} \right) \beta_i^j$$

Ancestral
State
(at root)

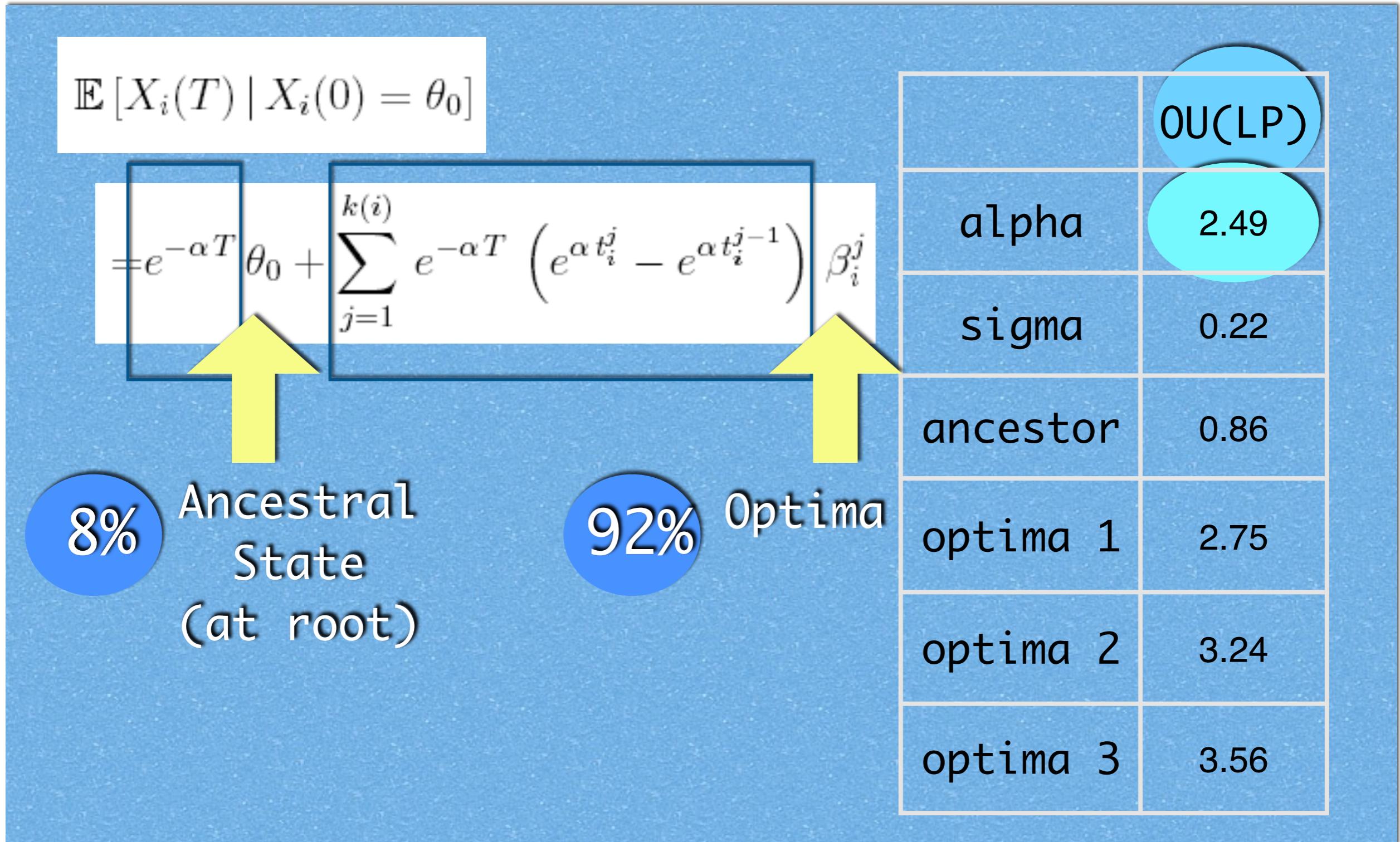


Optima

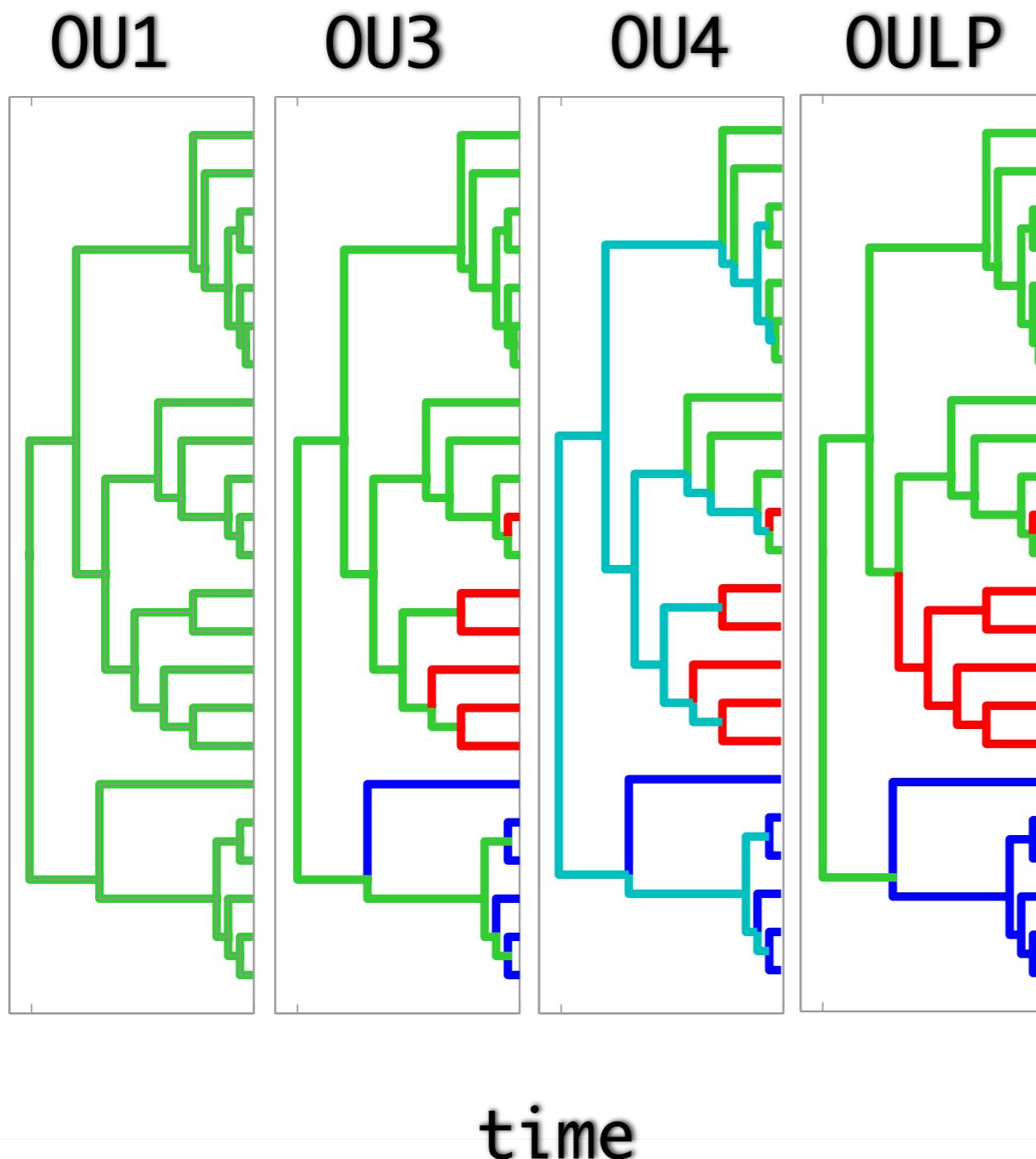


	OU(LP)
alpha	2.49
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optima 1	2.75
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Best Model



Univariate Conclusions



An Adaptive Model was best
BM was better than the wrong adaptive model
What happens on internal branches is important

Parametric Bootstrap indicates “high” and “low” SSD optima

associated with habitat type

	OU(7)	95% CI
alpha	1.44	(0.24, 4.5)
sigma	0.09	(0.04, 0.11)
ancestor	0.23	(0.03, 0.27)
optima tg	0.327	(0.26, 0.97)
optima tc	0.134	(0.00, 0.27)
optima gb	-0.013	(-0.28, 0.13)
optima cg	-0.06	(-0.39, 0.09)
optima tw	-0.074	(-0.42, 0.06)
optima tr	-0.051	(-0.39, 0.12)
optima uk	0.468	(0.34, 1.25)

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BE EXPLICIT about your models!!
It's important.

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