

Ecologists push back

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FORUM

On misinterpreting the ‘phylogenetic correction’

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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-

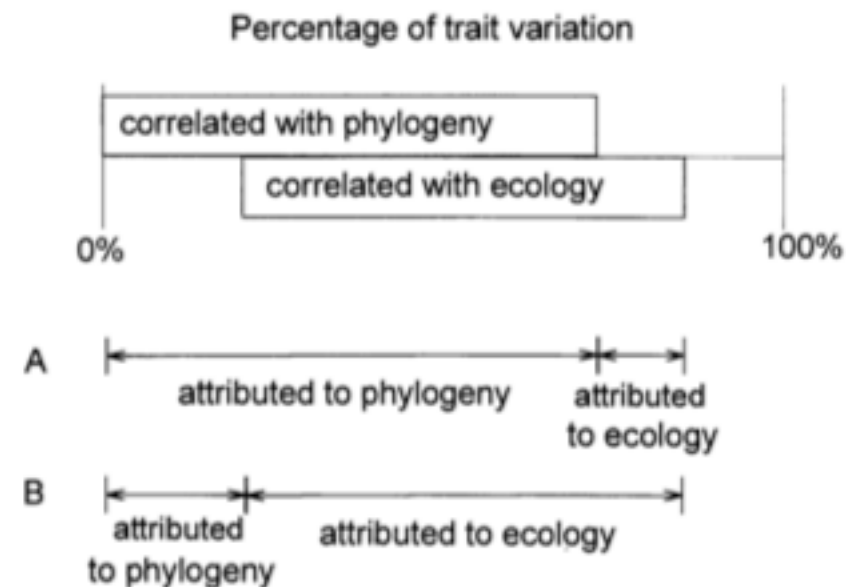


Fig. 1 Schematic illustrating percentages of variation between species in a trait such as seed mass correlated with phylogeny and ecology, and the two extremes (A and B) of the spectrum of possible attributions of variation. Extreme A is phylogenetic correction (PC).

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

All comparative analyses are constructed of 3 pieces

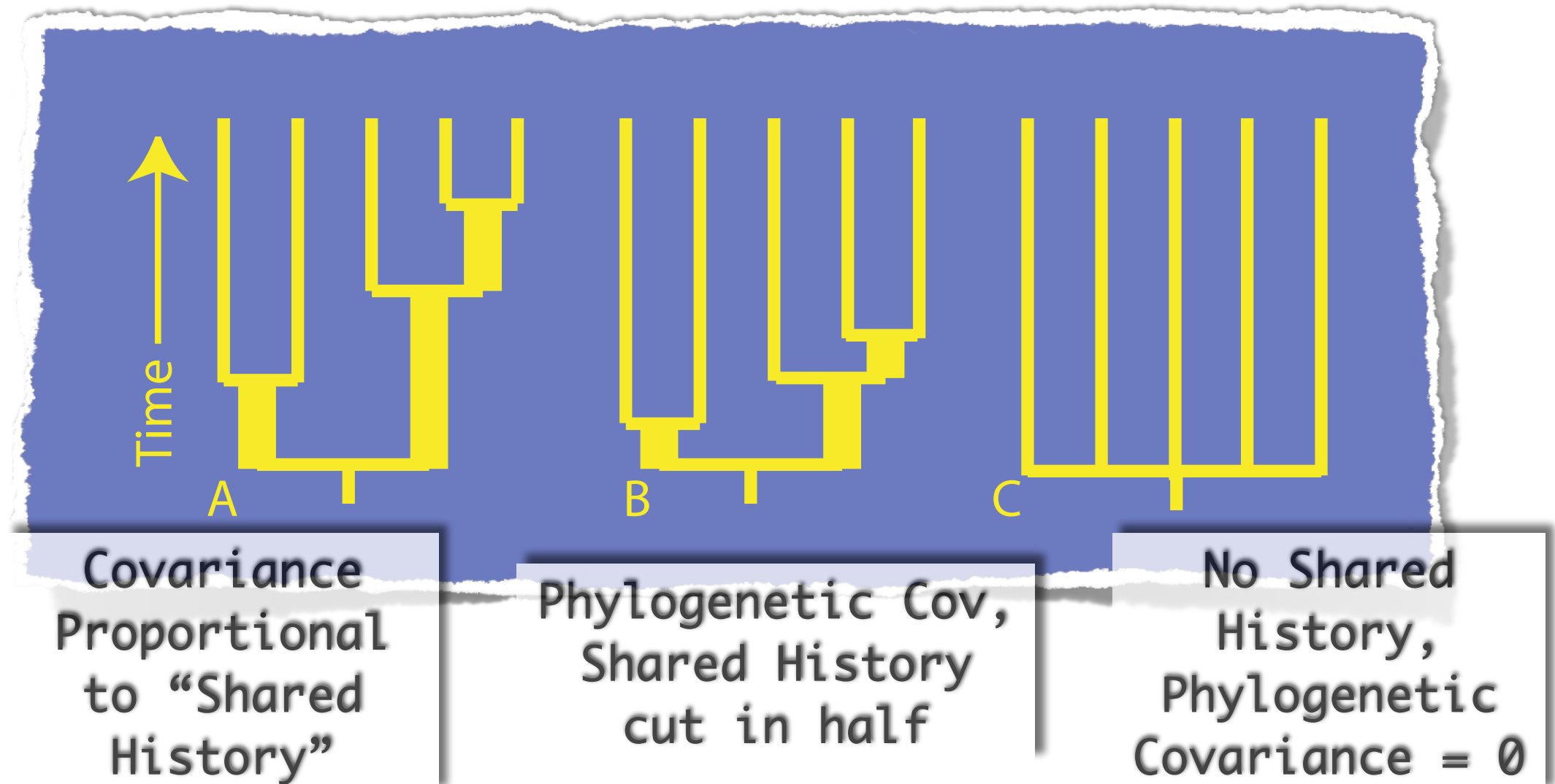
1. The comparative **dataset** (body size, plumage color, etc. for each species)
2. A particular pattern of shared ancestry (**phylogeny and branch lengths**)
3. A **model of evolutionary change** along each branch of the phylogeny

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

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

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

A popular approach improves fit by “scaling” branch lengths



Why change the phylogeny?

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

2. A particular pattern of shared ancestry (**phylogeny and branch lengths**)

3. A **model of evolutionary change** along each branch of the phylogeny

What about the Biology?

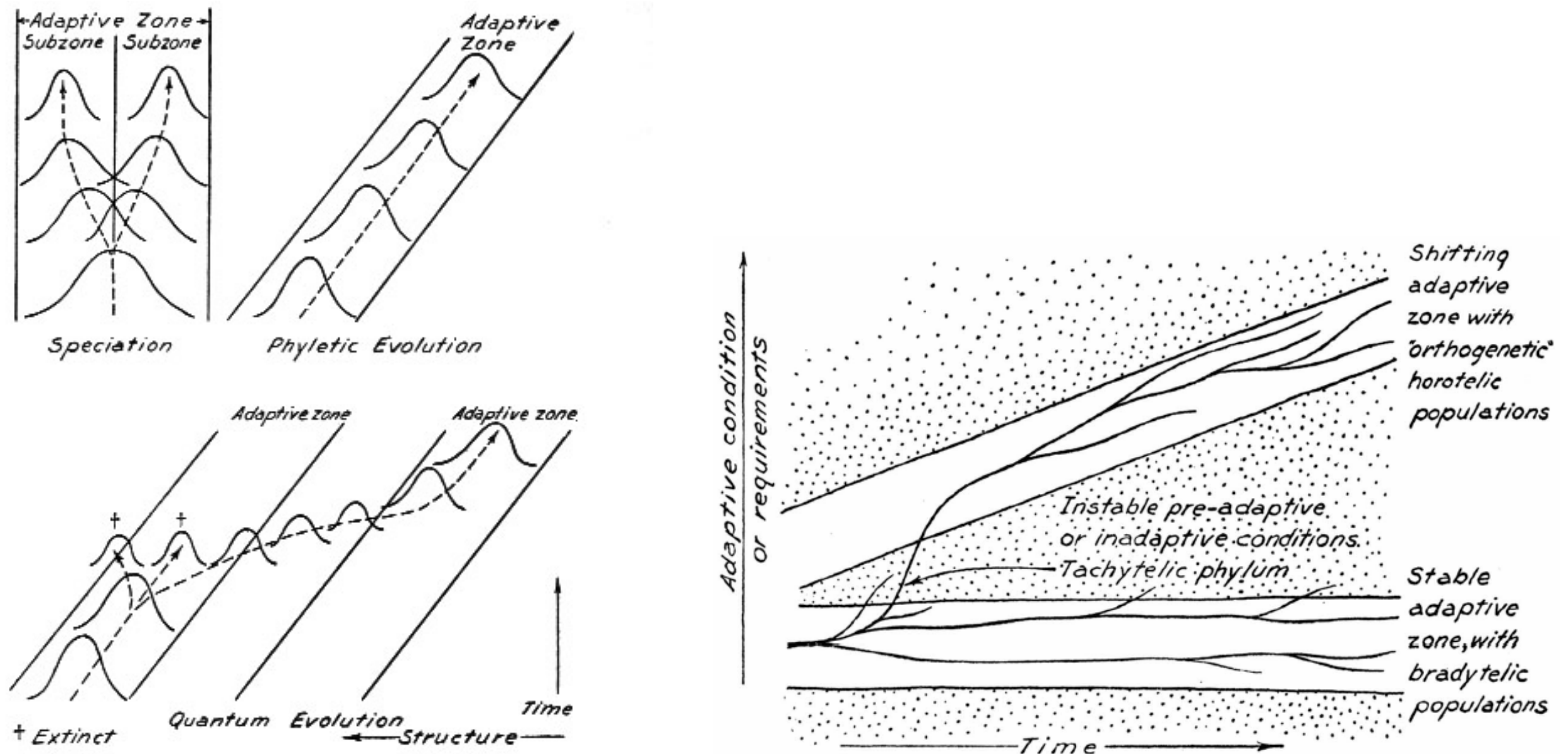


FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.

Simpson (1953) The major features of evolution

There is another option...

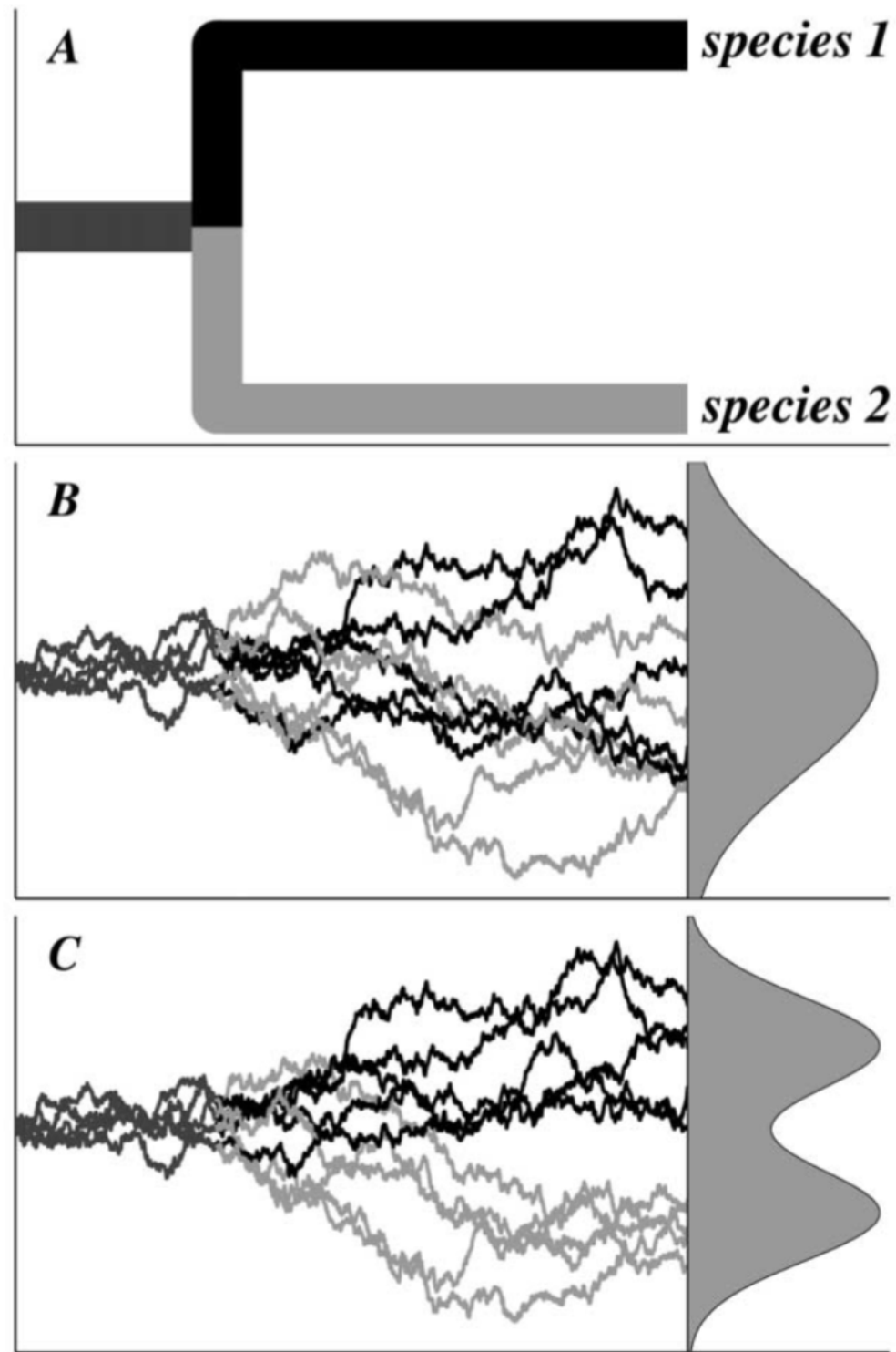
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Change the model of evolution !

How do we explain Patterns of Biodiversity?



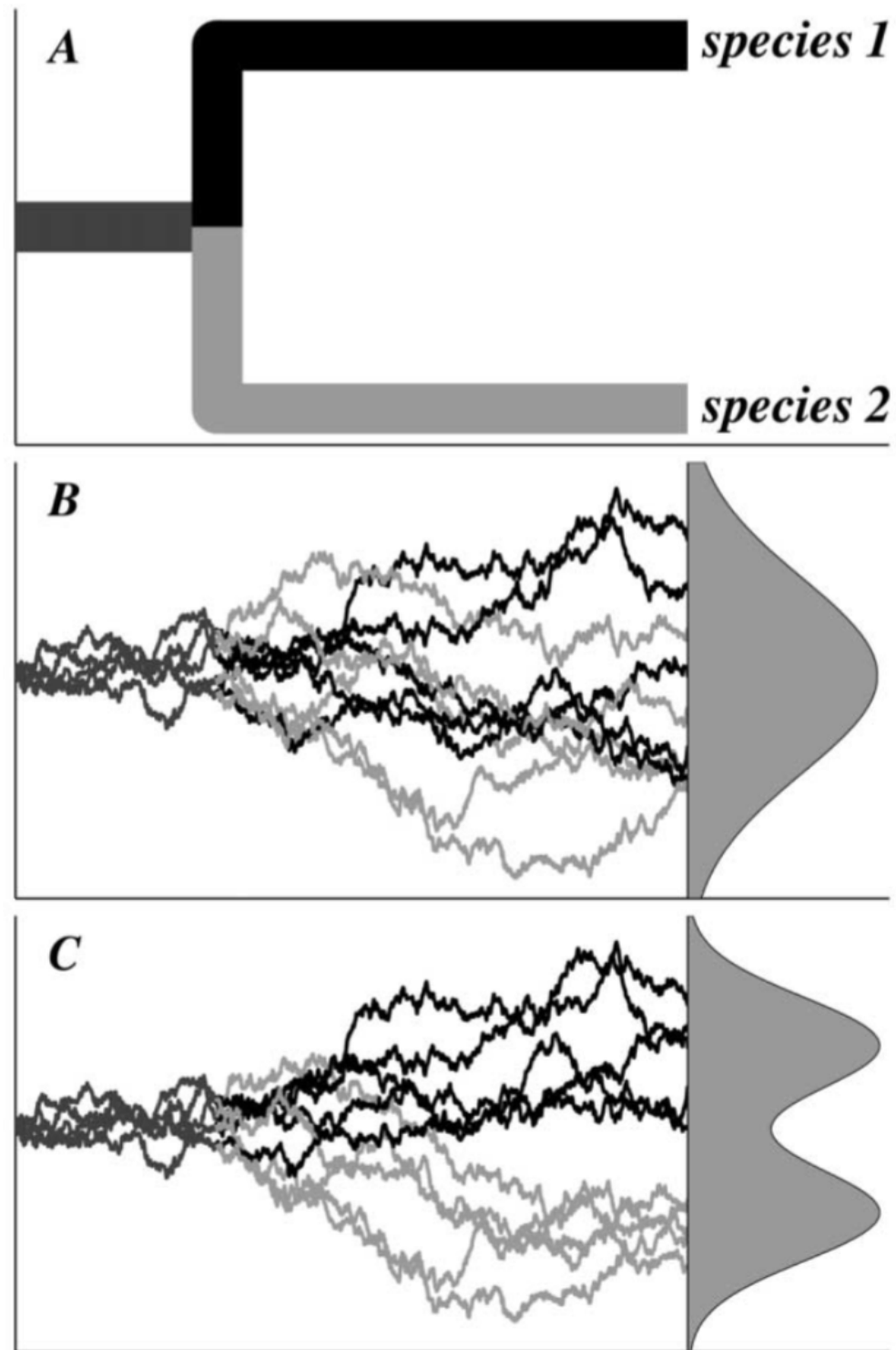
Pattern of relationship

Are species phenotypes just subject to random evolution “drift”?

Or are other forces shaping the phenotype?

- Shifts in Selection
- Shifts in Environment
- Changes in Constraints

How do we explain Patterns of Biodiversity?



How do we tease apart the factors?

— Statistical considerations

— *Evolutionary* or *Tree Thinking*

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

Model the evolutionary process along each branch of the phylogeny

Brownian Motion

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

Orstein Uhlenbeck Process

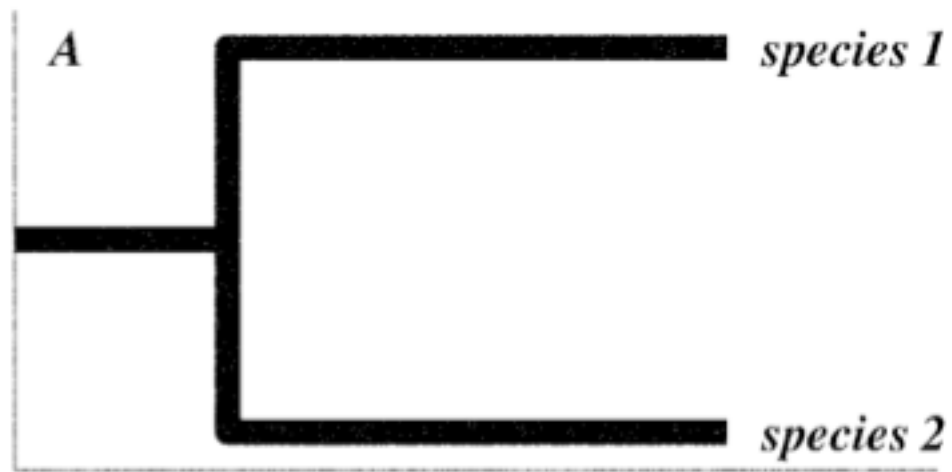
$$dX_i(t) = \alpha (\beta_i^j - X_i(t)) dt + \sigma dB_i(t)$$

Hansen (1997)

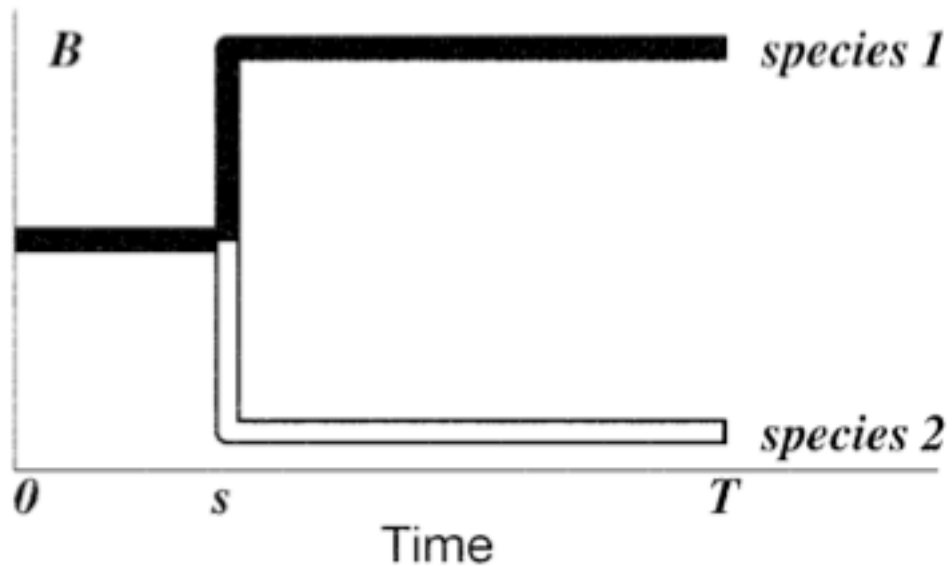
***Vary the models to reflect biology
Then compare to find the best model***

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

Nuts and Bolts: 2 species example



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

Expected Value
(mean at T)

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

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

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

Variance

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

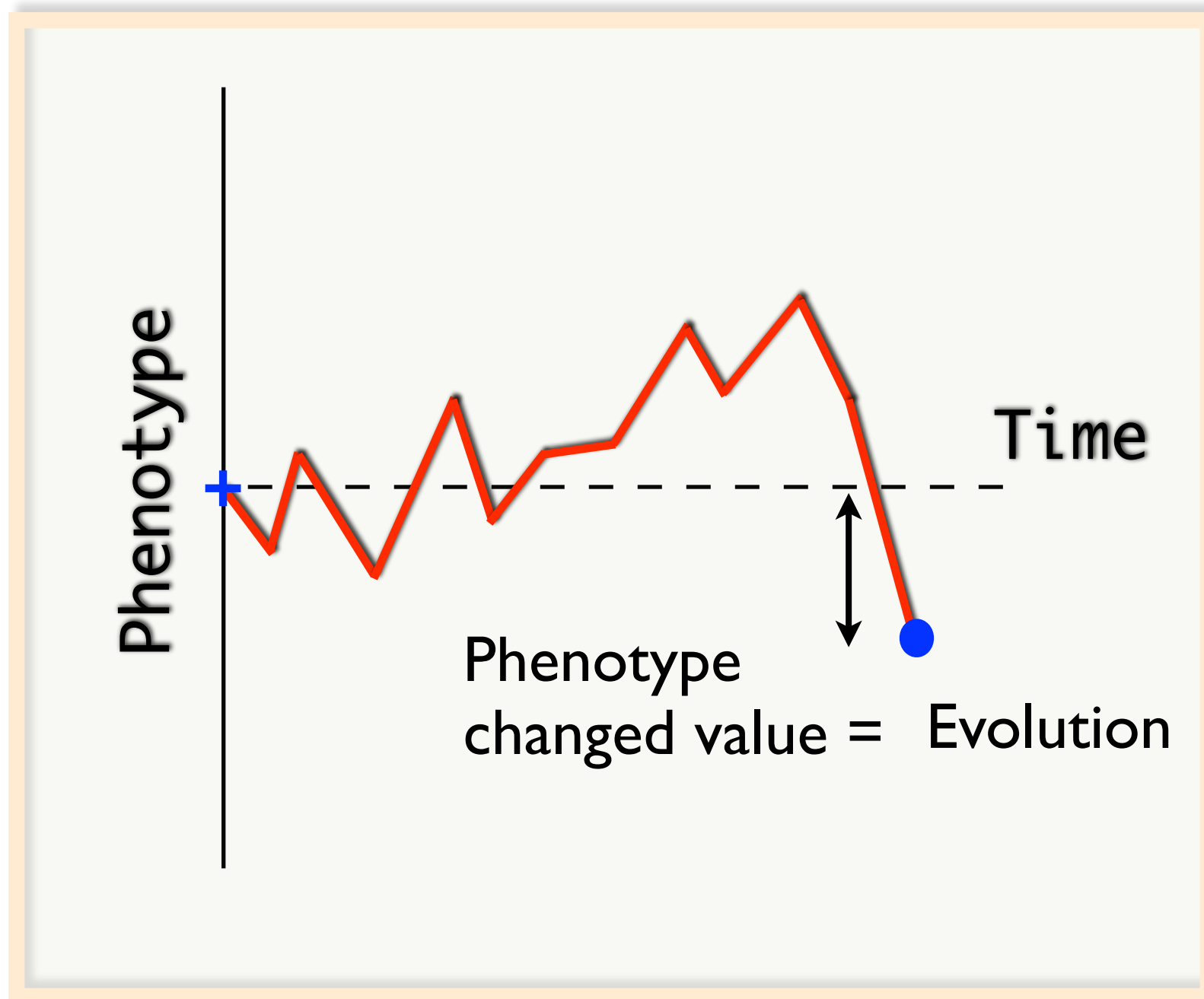
$$\mathbf{V} = \begin{bmatrix} 1 - e^{-2\alpha T} & e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) \\ e^{-2\alpha(T-s)}(1 - e^{-2\alpha s}) & 1 - e^{-2\alpha T} \end{bmatrix}$$

Hansen (1997), Butler & King (2004)

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

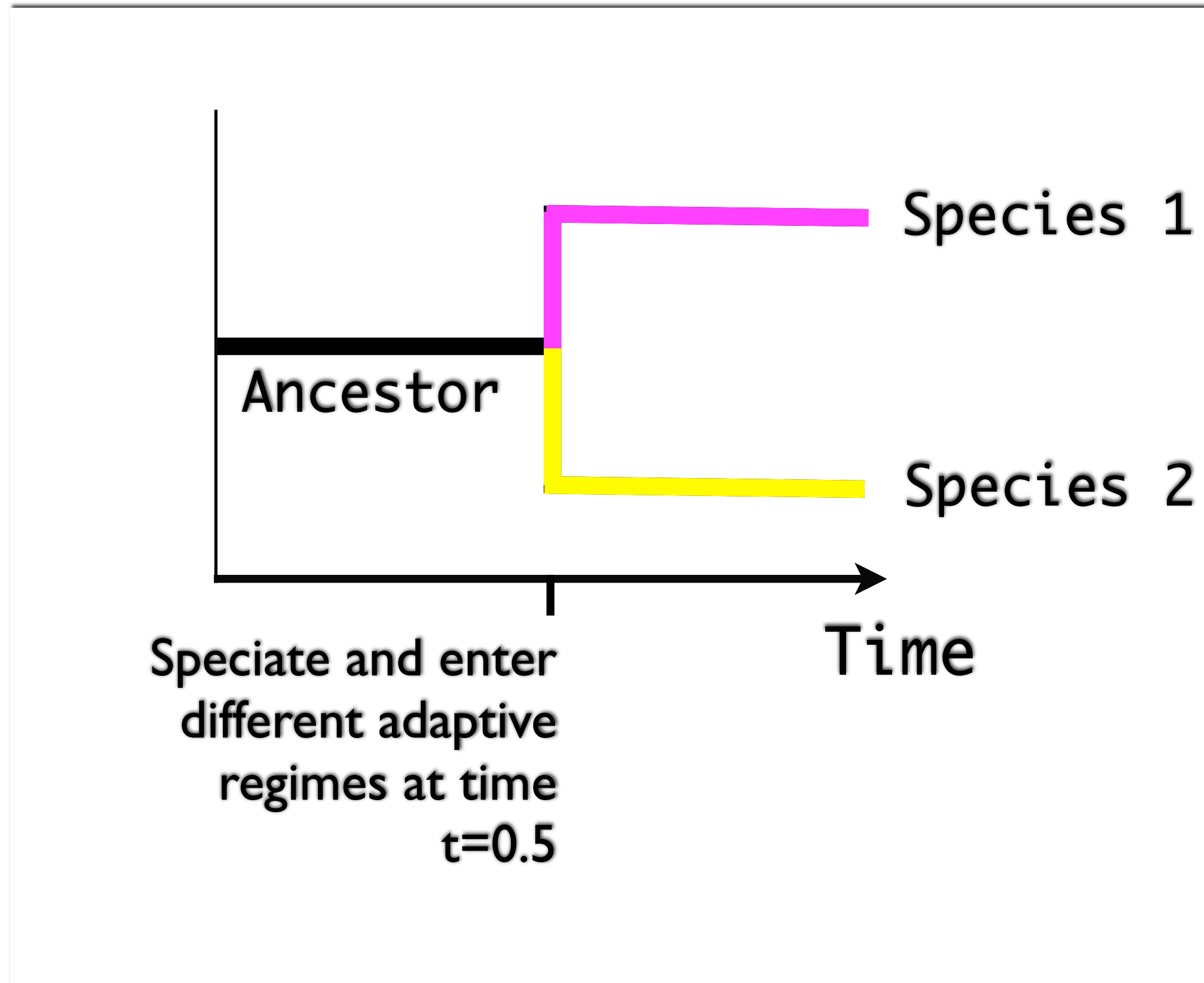
let's do some simulations!

Evolution in Cartoon

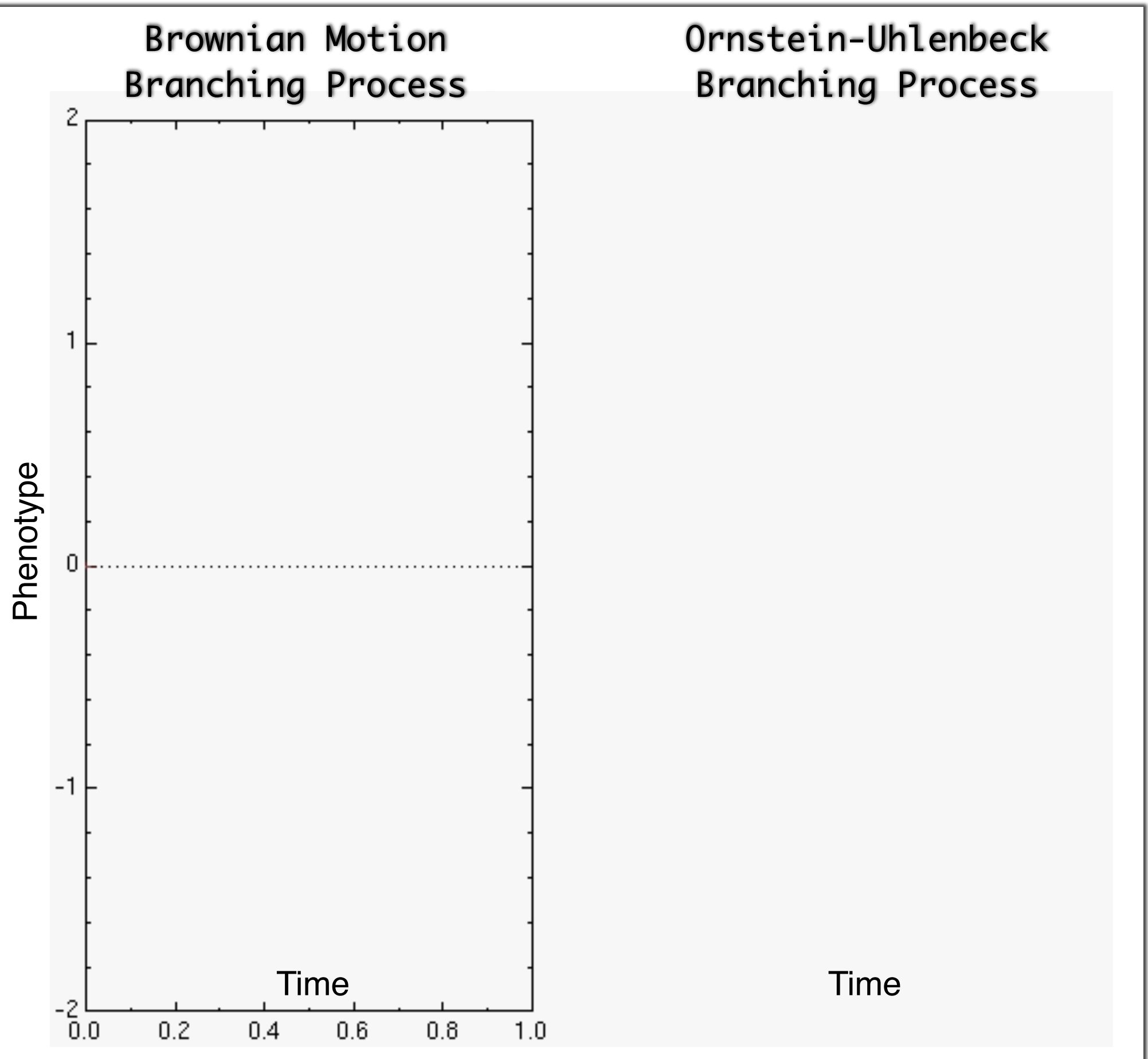


- At each infinitesimal increment of time, there is a probability of change in the phenotype.
- The probability is drawn from a normal distribution, thus the BM is “Gaussian.”
- The state at any given time is only dependent on the previous state.

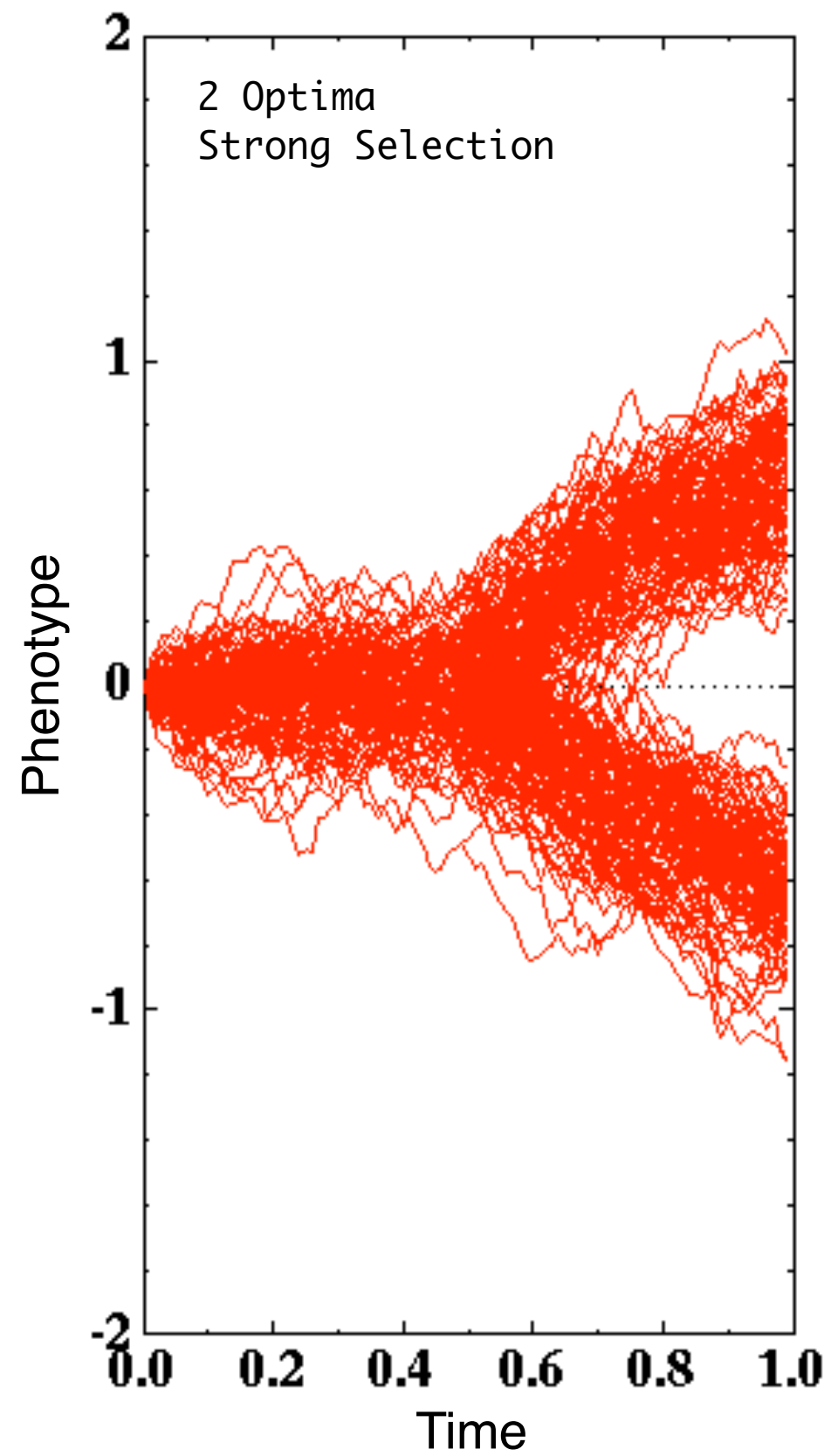
BM and OU models make different predictions



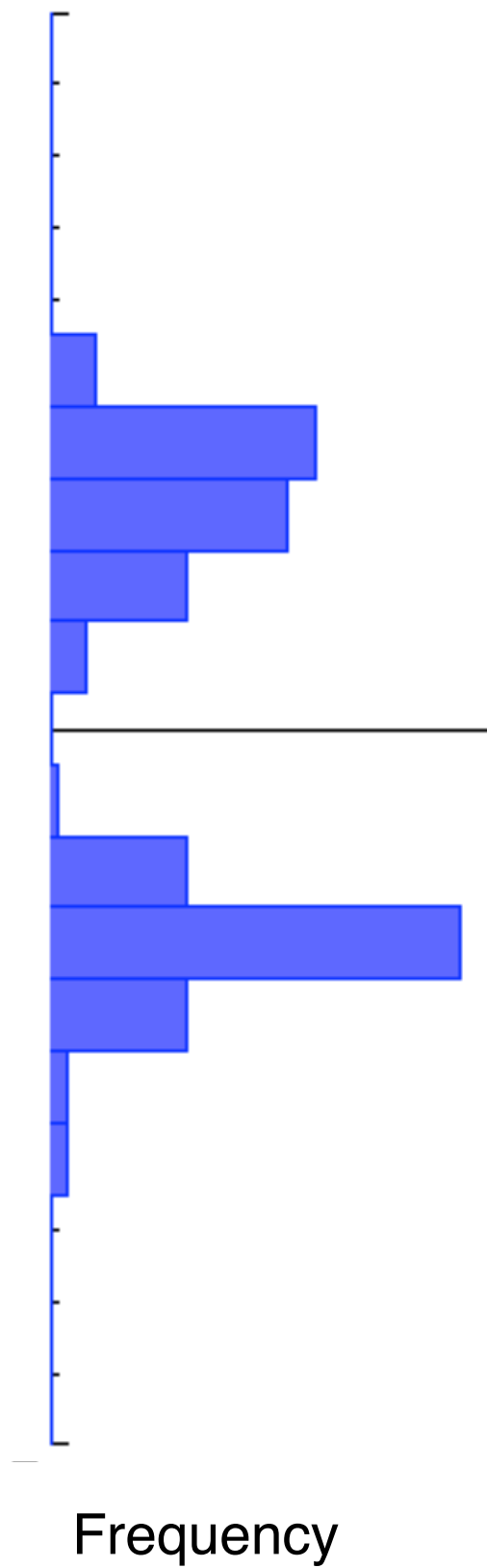
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OU Branching Process



Phenotypic Distribution



What about the Biology?

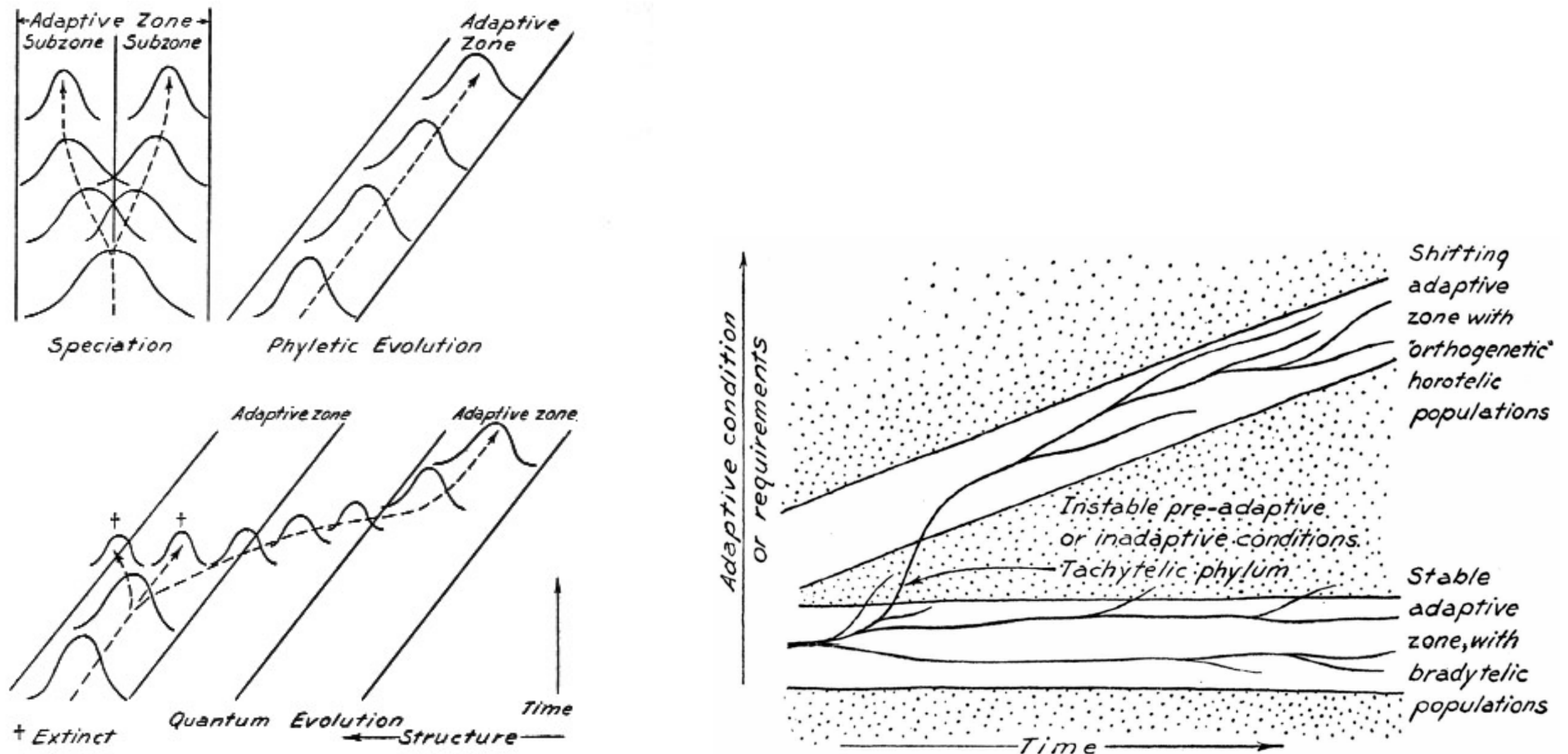


FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.

Simpson (1953) The major features of evolution

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

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

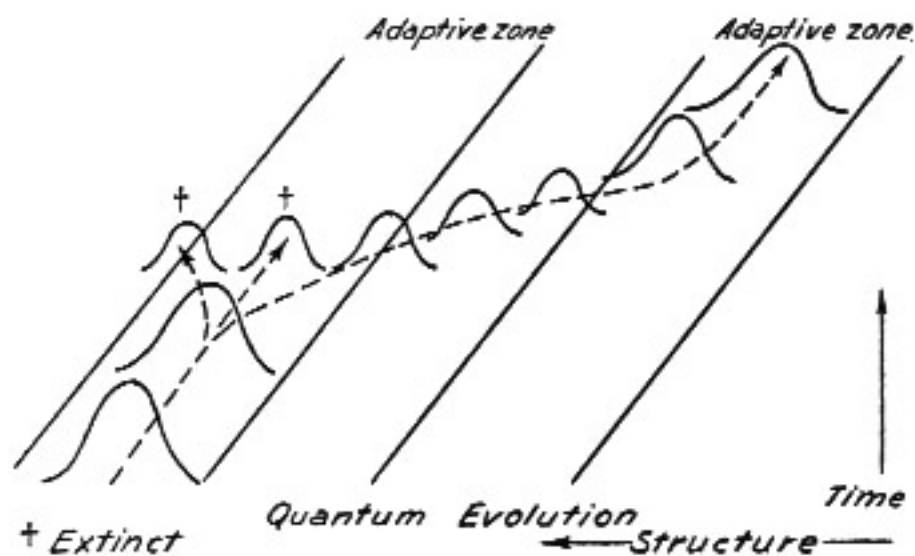
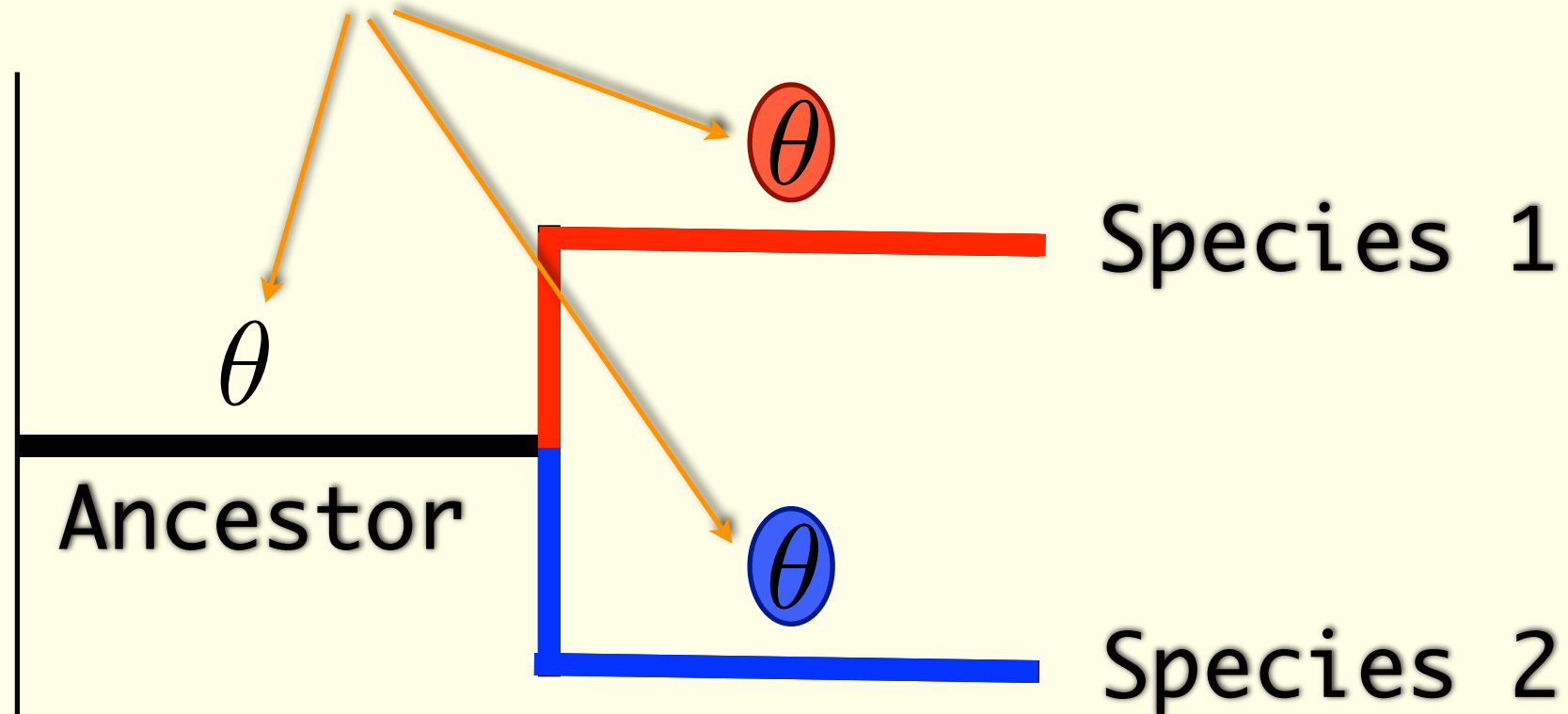
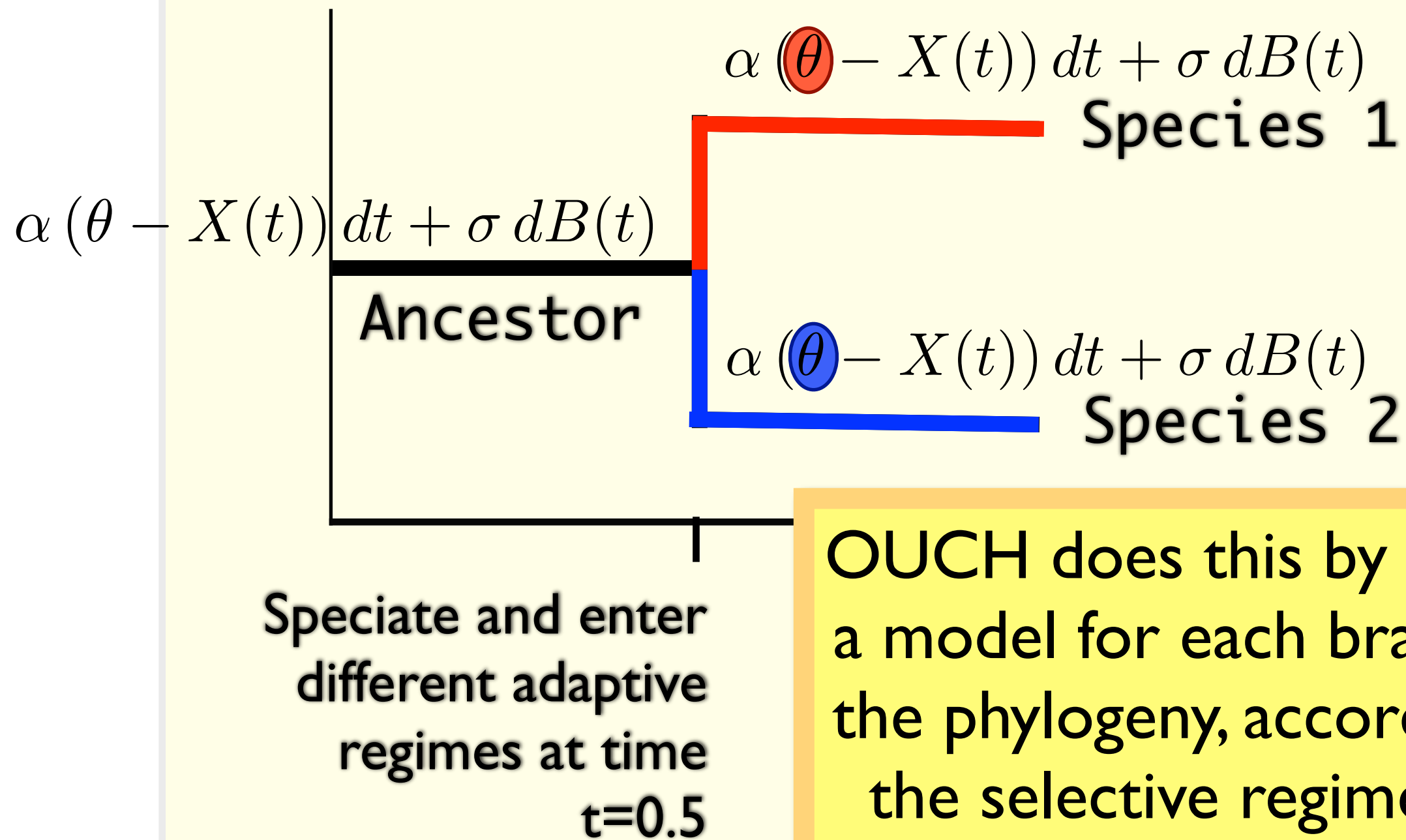


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OUCH does this by writing a model for each branch of the phylogeny, according to the selective regimes we hypothesize

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Thus, with:

a set of interspecific data,
a phylogeny, and
a little biological insight,

**we can explore alternative
evolutionary scenarios**

**and potentially make a statement
about how characters evolved!**

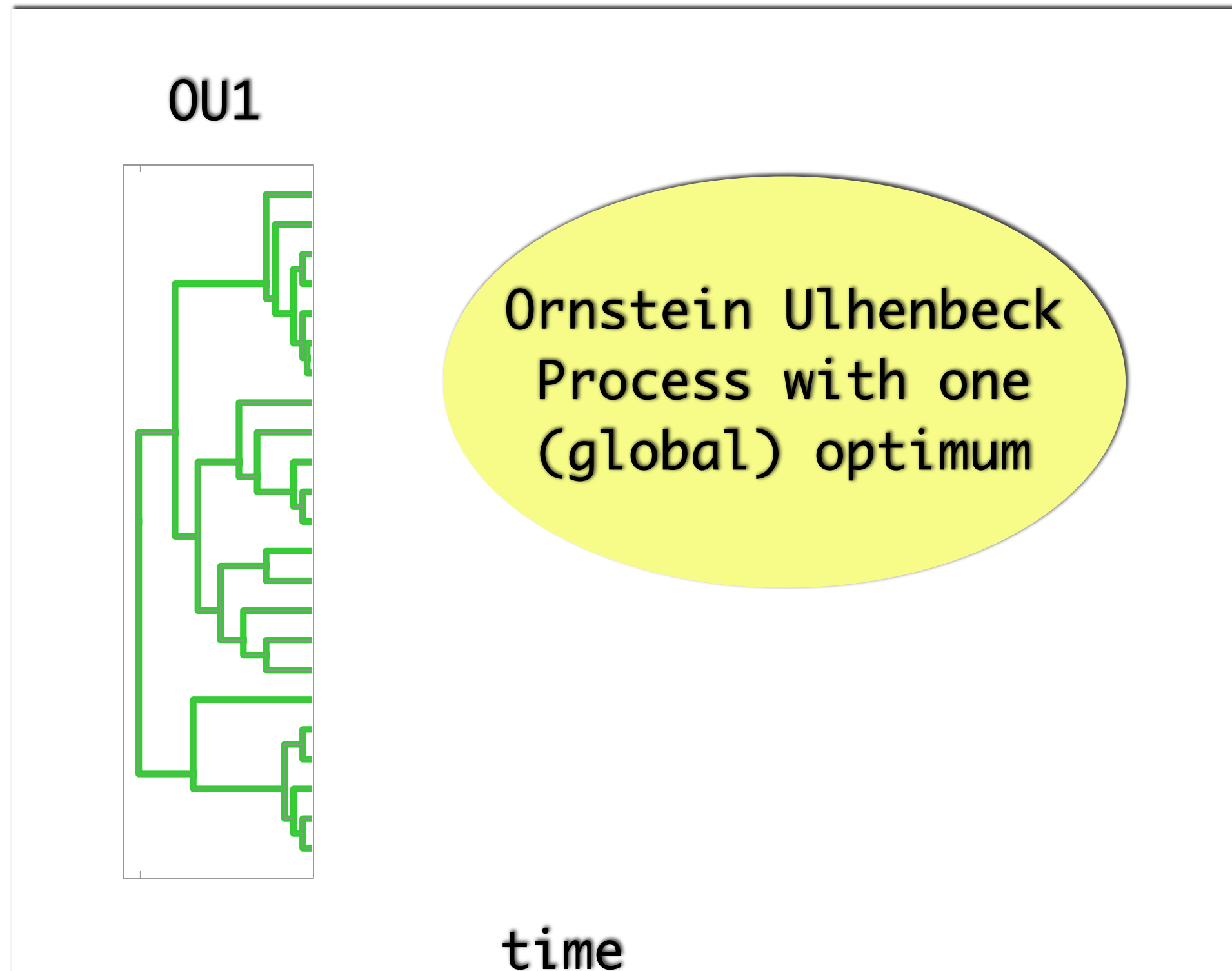
Islands in the Lesser Antilles have only 1 or 2 species of anoles.

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

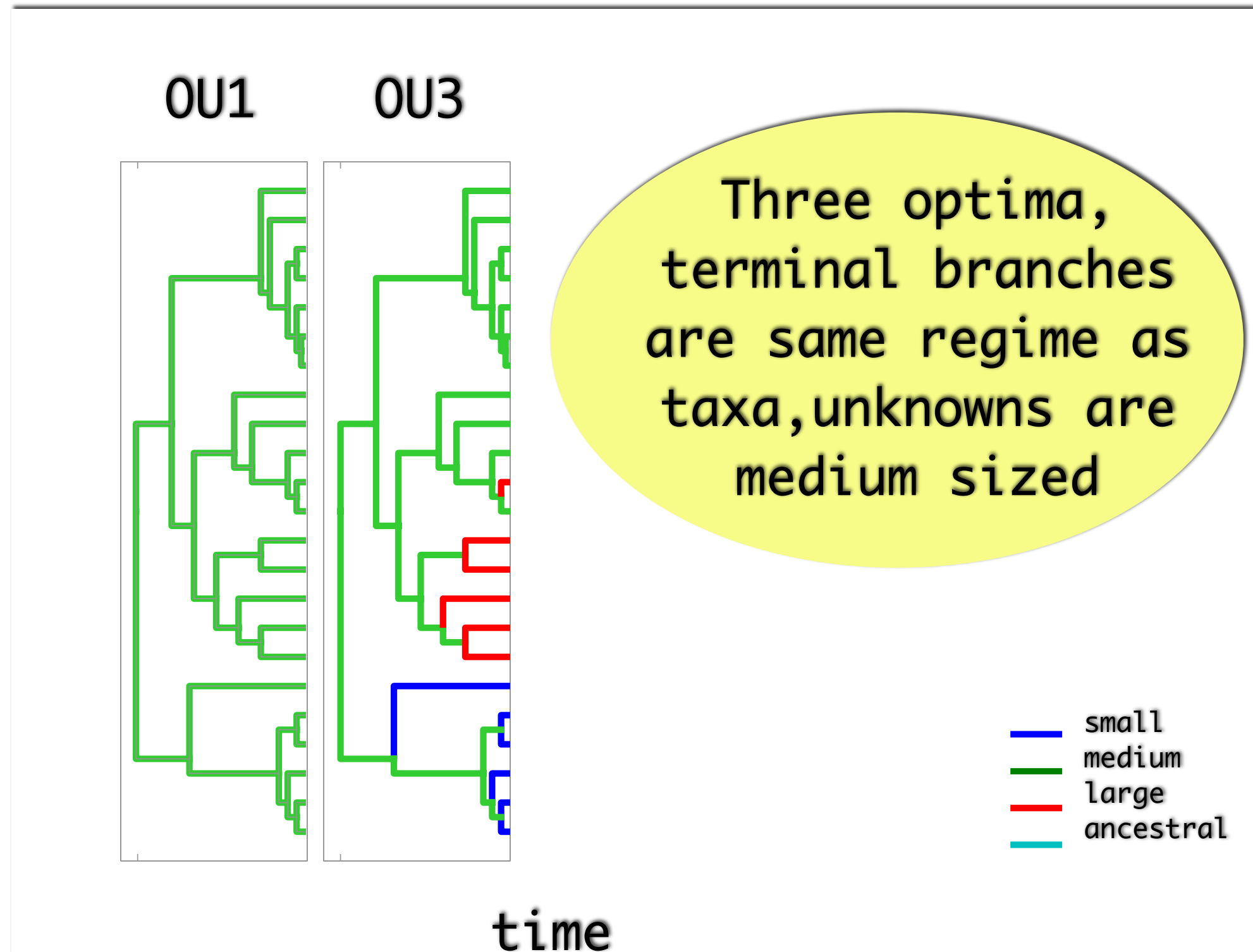
On the single species islands, anoles are “intermediate” in size.



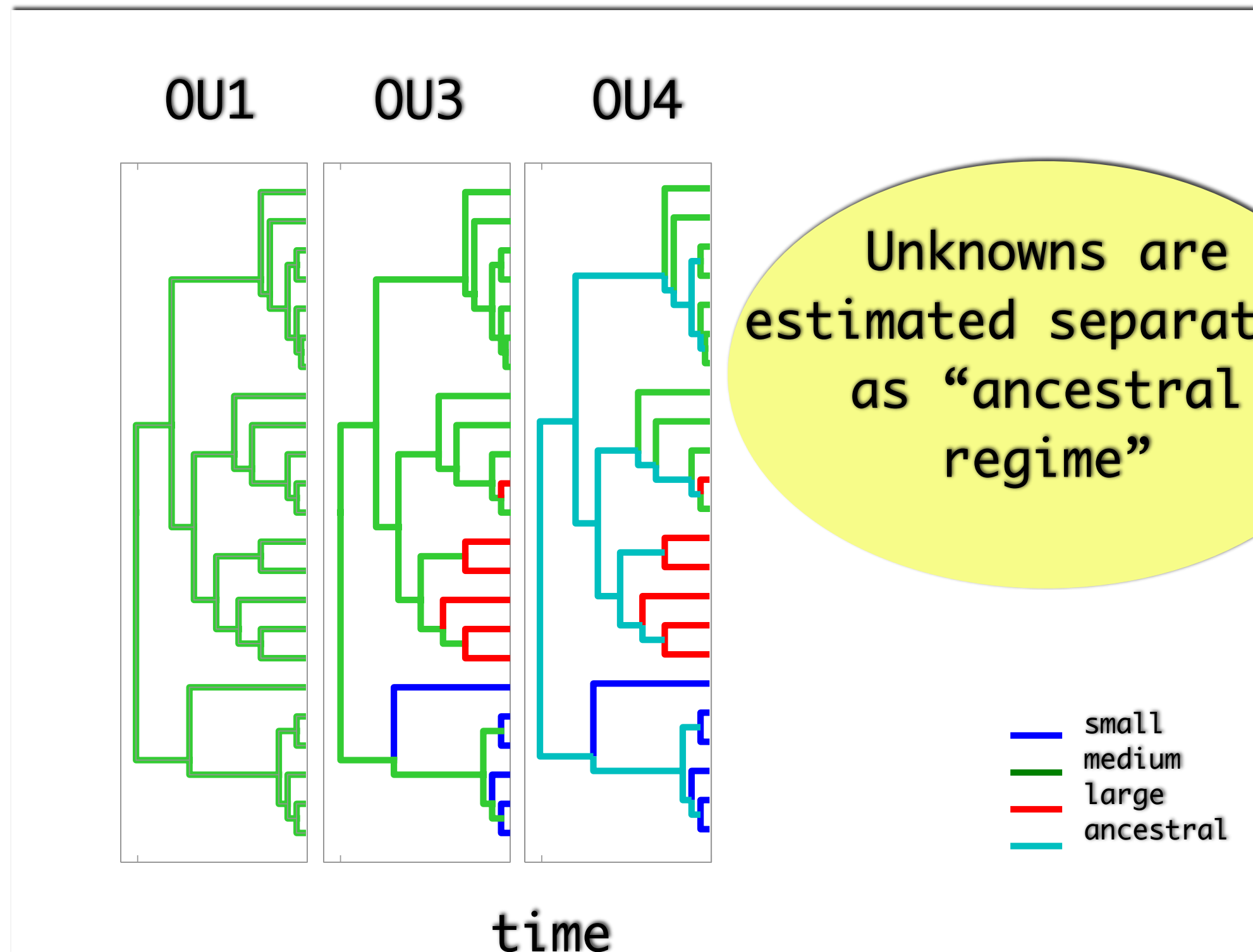
Alternative Adaptive Regime Models



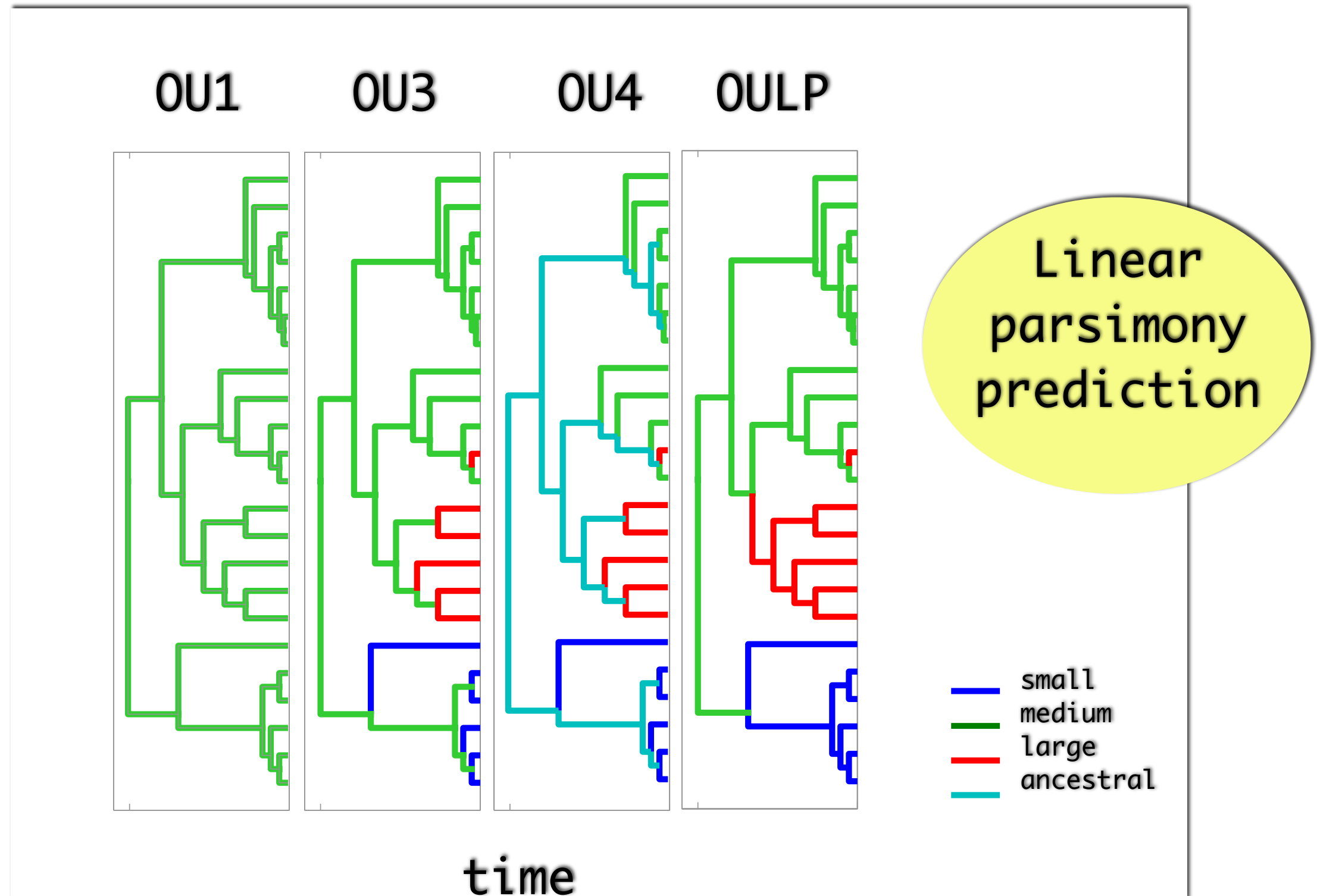
Alternative Adaptive Regime Models



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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Best Model

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

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

Ancestral
State
(at root)

Optima

	OU(LP)
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8%

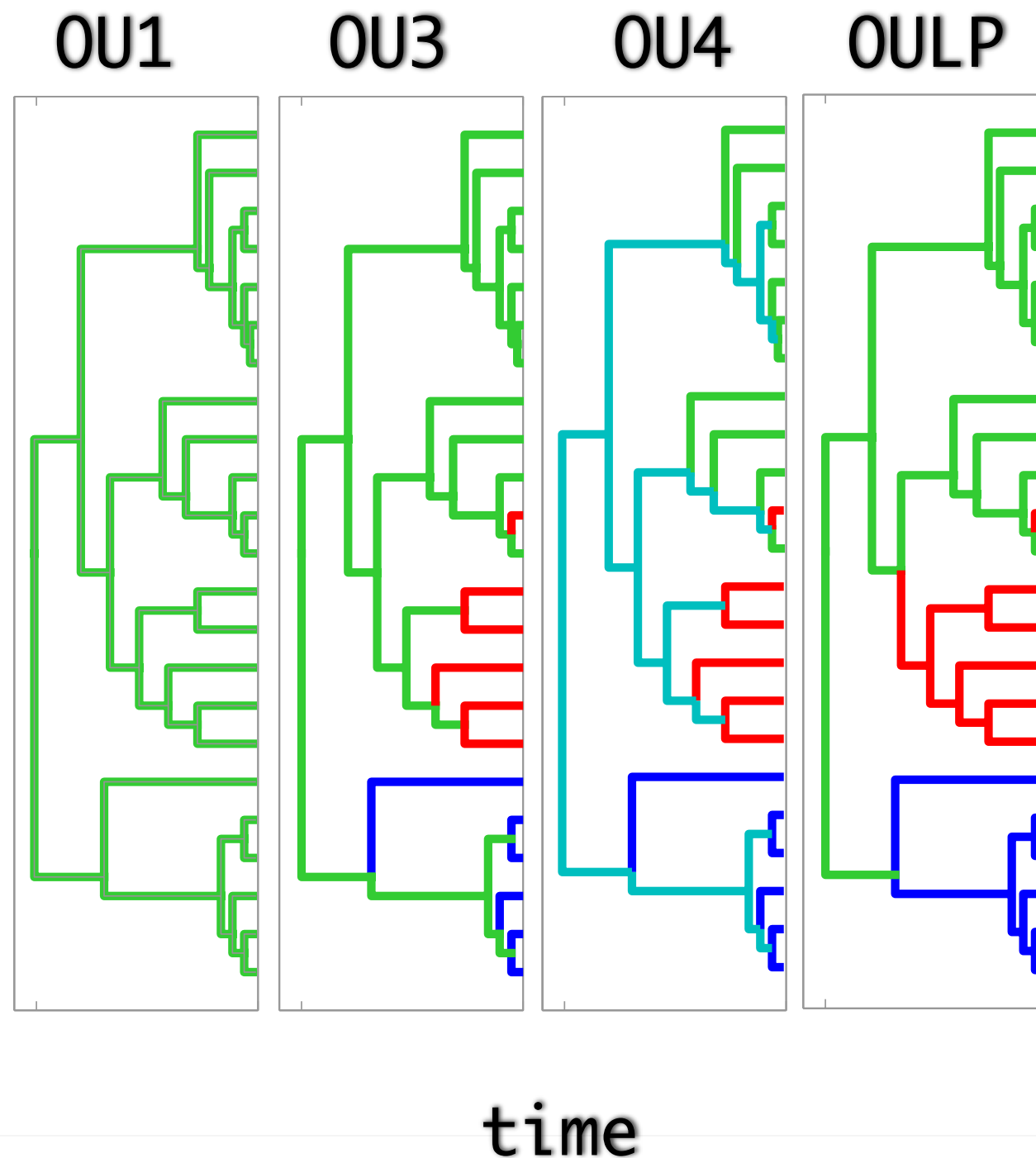
Ancestral
State
(at root)

92%

Optima

	OU(LP)
alpha	2.49
sigma	0.22
ancestor	0.86
optima 1	2.75
optima 2	3.24
optima 3	3.56

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)

Final Thoughts (Rantings):

Biologists think about adaptive evolution

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

tion, so WHY use a
tral?

This should be a conclusion, not an assumption.

We gain nothing by using a null model that is **really uninformative** and then rejecting it!

We gain much more insight by using models that approximate our best ideas and comparing them.

“Correcting for phylogeny” is not a useful way to think about comparative analysis.

