

# An Overview of Comparative Methods (only slightly biased ;) & a bit of ramble on adaptation

Marguerite Butler

University of Hawaii, Department of Biology

# Hawai'i's Megalagrion Damselflies



**Hawaiian Damselflies** have evolved to use different microhabitats: swift-moving **streams**, **pools**, **seeps**, **plants** and **leaf litter**.

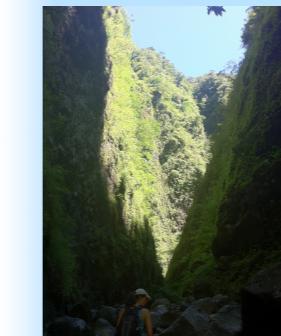
### terrestrial



### plant breeder



### streams



### pools



### seeps

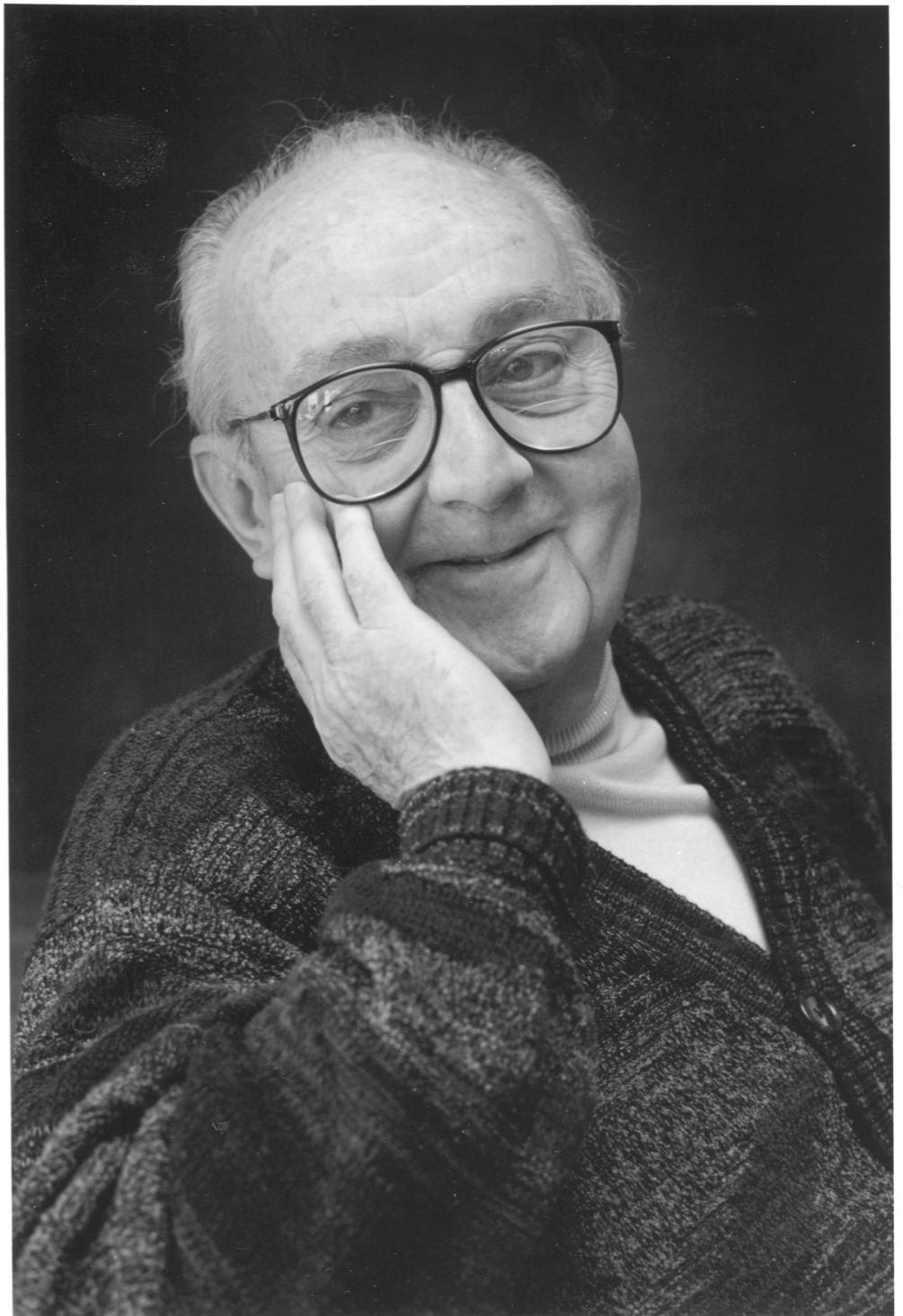


### pools



Essentially, all models  
are wrong, but some  
are useful

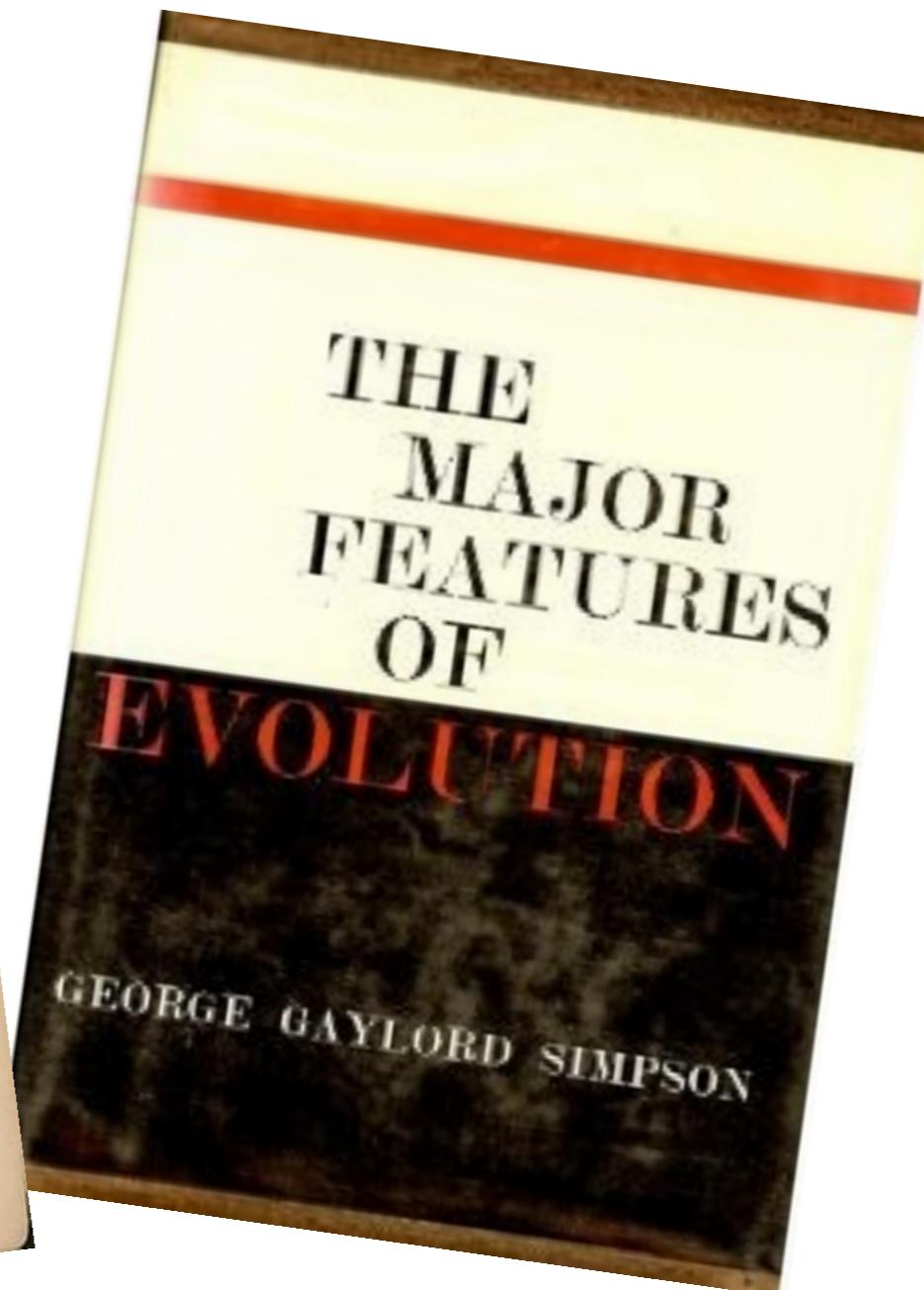
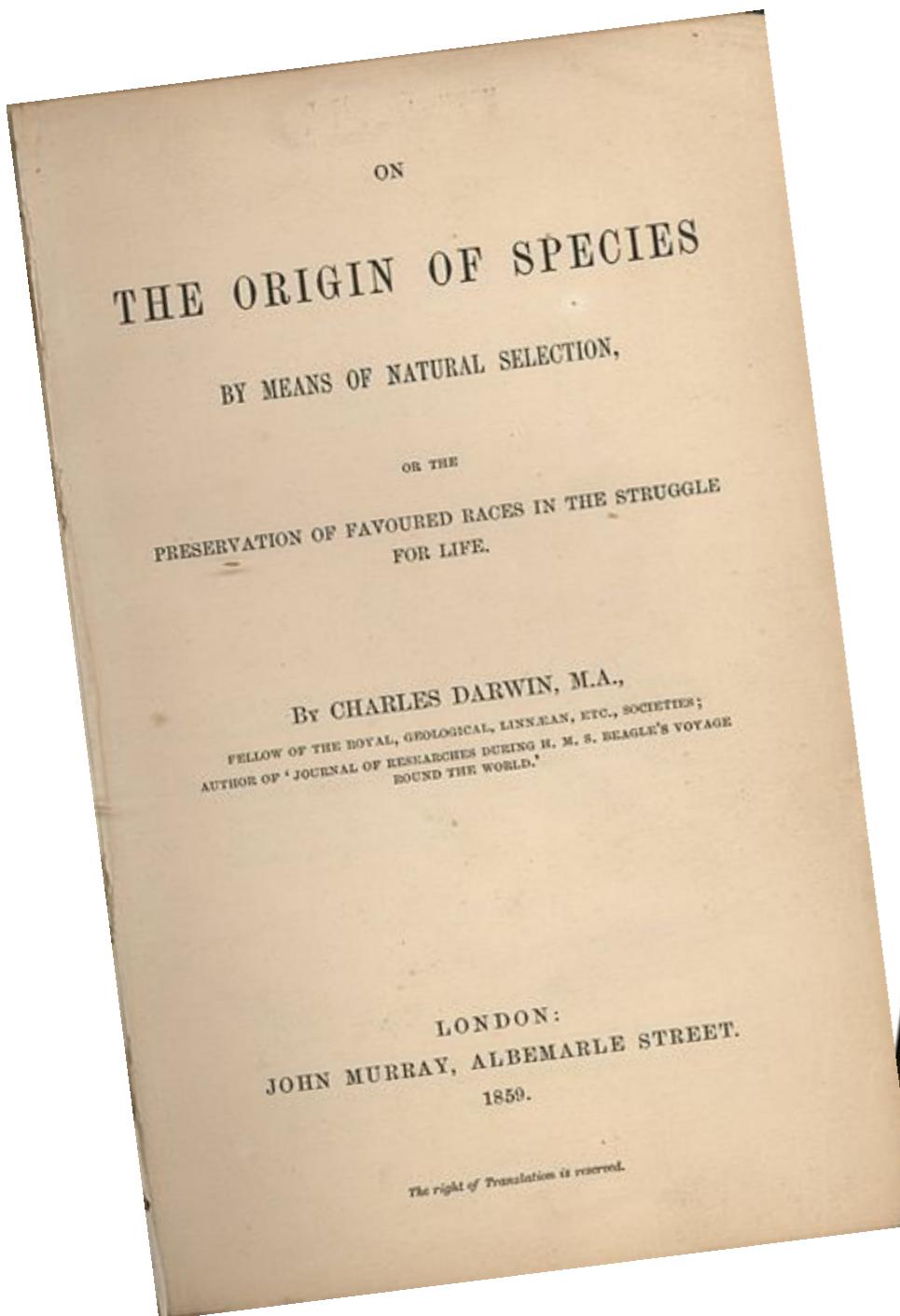
- George E. Box



# Adaptation is one of the oldest ideas in evolutionary biology

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Evolution. A heady discipline



Diversification,  
rapid evolution,  
character  
displacement,  
Cope's rule,  
ecological  
opportunity,  
vicariance, island  
biogeography, niche  
partitioning, and  
many more...

# Adaptation becomes adaptationist

Proc. R. Soc. Lond. B 205, 581–598 (1979)

581

Printed in Great Britain

## The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme

BY S. J. GOULD AND R. C. LEWONTIN

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Cambridge, Massachusetts 02138, U.S.A.

An adaptationist programme has dominated evolutionary thought in England and the United States during the past 40 years. It is based on faith in the power of natural selection as an optimizing agent. It proceeds by breaking an organism into unitary 'traits' and proposing an adaptive story for each considered separately. Trade-offs among competing selective demands exert the only brake upon perfection; non-optimality is thereby rendered as a result of adaptation as well. We criticize this approach and attempt to reassert a competing notion (long popular in continental Europe) that organisms must be analysed as integrated wholes, with *Baupläne* so constrained by phyletic heritage, pathways of development and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs. We fault the adaptationist programme for its failure to distinguish current utility from reasons for origin (male tyrannosaurs may have used their diminutive front legs to titillate female partners, but this will not explain *why* they got so small); for its unwillingness to consider alternatives to adaptive stories; for its reliance upon plausibility alone as a criterion for accepting speculative tales; and for its failure to consider adequately such competing themes as random fixation of alleles, production of non-adaptive structures by developmental correlation with selected features



FIGURE 1. One of the four spandrels of St Mark's; seated evangelist above, personification of river below.

# Adaptation becomes rigorous!

AMER. ZOOL., 23:347–361 (1983)

## Morphology, Performance and Fitness<sup>1</sup>

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**SYNOPSIS.** Selection can be measured in natural populations by the changes in the means, variances and covariances of phenotypic characters. Furthermore, selection can be measured in conventional statistical terms that also fit theoretical equations for evolutionary change. The problem of measuring the effects of 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 morphological variation 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 hypothetical 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**

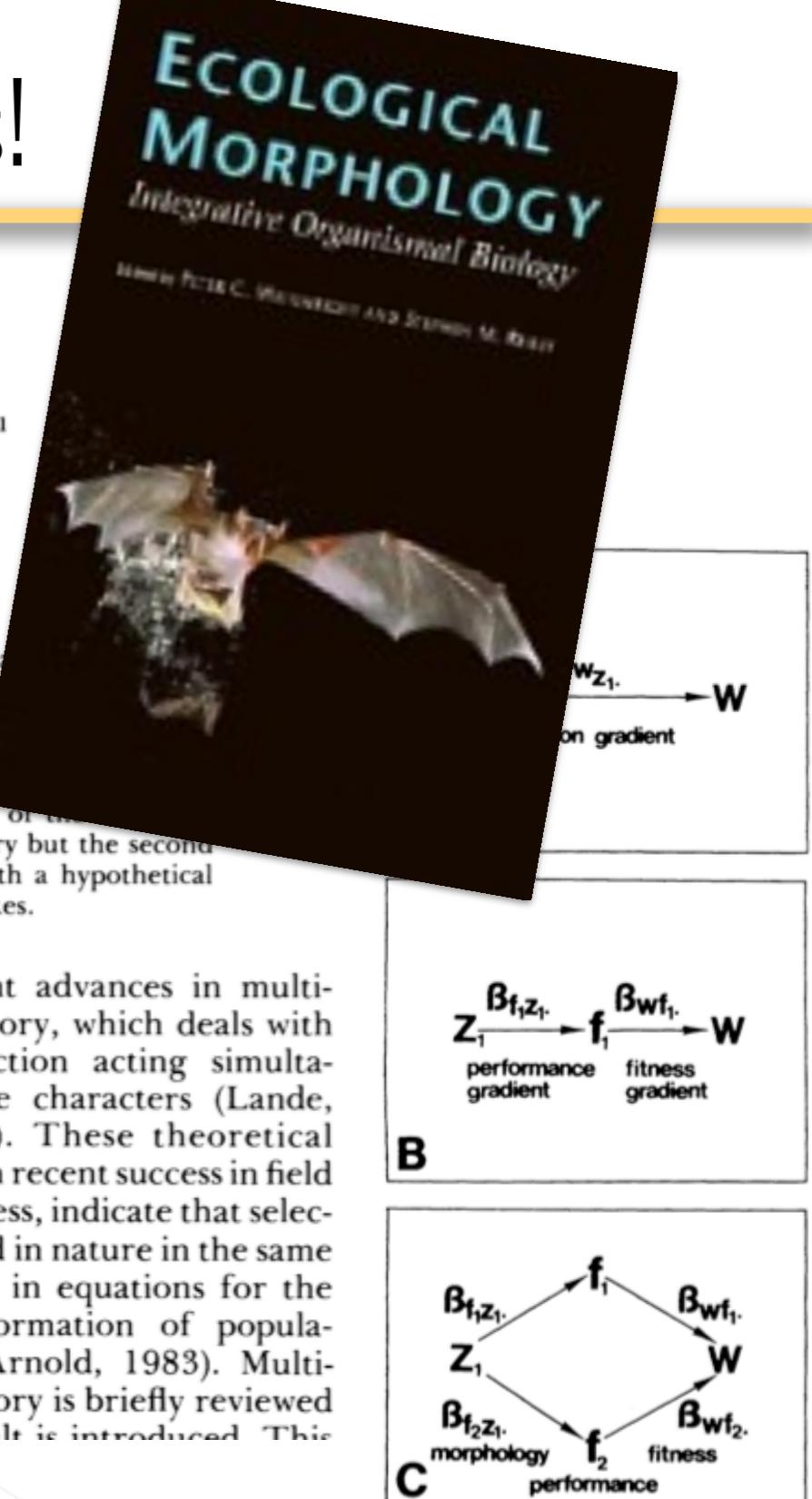


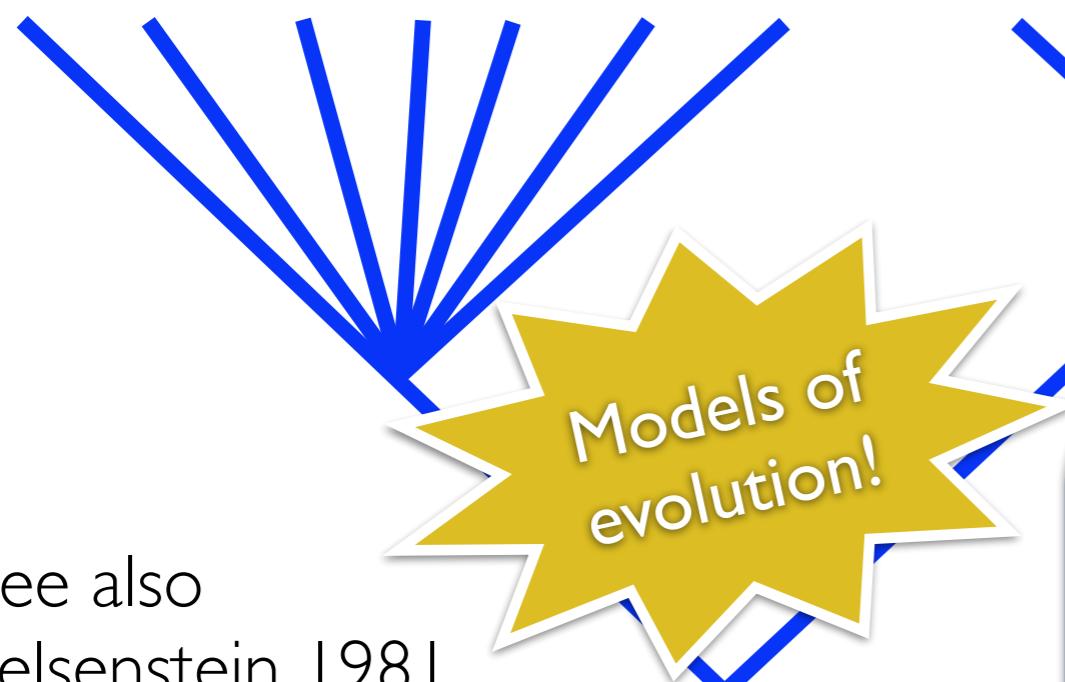
FIG. 4. A diagrammatic partitioning of the selection gradient. The selection gradient for a character (Fig. 4A) can be partitioned into two parts if the character affects a single performance variable,  $f_1$ : the performance gradient,  $\beta_{f_1, Z_1}$ , and the fitness gradient  $\beta_{wf_1}$  (Fig. 4B). If the character affects two performance variables,  $f_1$  and  $f_2$ , the selection gradient can be partitioned into the paths  $\beta_{f_1, Z_1}, \beta_{wf_1}$  and  $\beta_{f_2, Z_1}, \beta_{wf_2}$  (Fig. 4C).

# Species are historically related

## *Independent Contrasts*

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



Phylogenies are fundamental to comparative biology; there is no doing it without taking them into account



See also  
Felsenstein 1981  
Felsenstein 1988

A “degrees of freedom” problem? Another way to think about the issue is as *covariance among species*

# Species are historically related

## *Phylogenetic Autocorrelation*

Cheverud, Dow, and Luetenegger (1985)

*Evolution*, 39(6), 1985, pp. 1335–1351

THE QUANTITATIVE ASSESSMENT OF PHYLOGENETIC CONSTRAINTS  
IN COMPARATIVE ANALYSES: SEXUAL DIMORPHISM IN  
BODY WEIGHT AMONG PRIMATES

A formal model to separate “**phylogenetic inertia**” from  
independent evolution “**specific effects**”



A Partitioning of Variance Model (a la Quantitative Genetics)

$$\mathbf{V_t} = \mathbf{V_p} + \mathbf{V_s}$$

$$\mathbf{y} = p\mathbf{W}\mathbf{y} + \mathbf{e}$$

trait values

A regression model, therefore can expand to multiple variables (e.g., sexual dimorphism, diet, size, etc.) and examine correlations among them

specific values

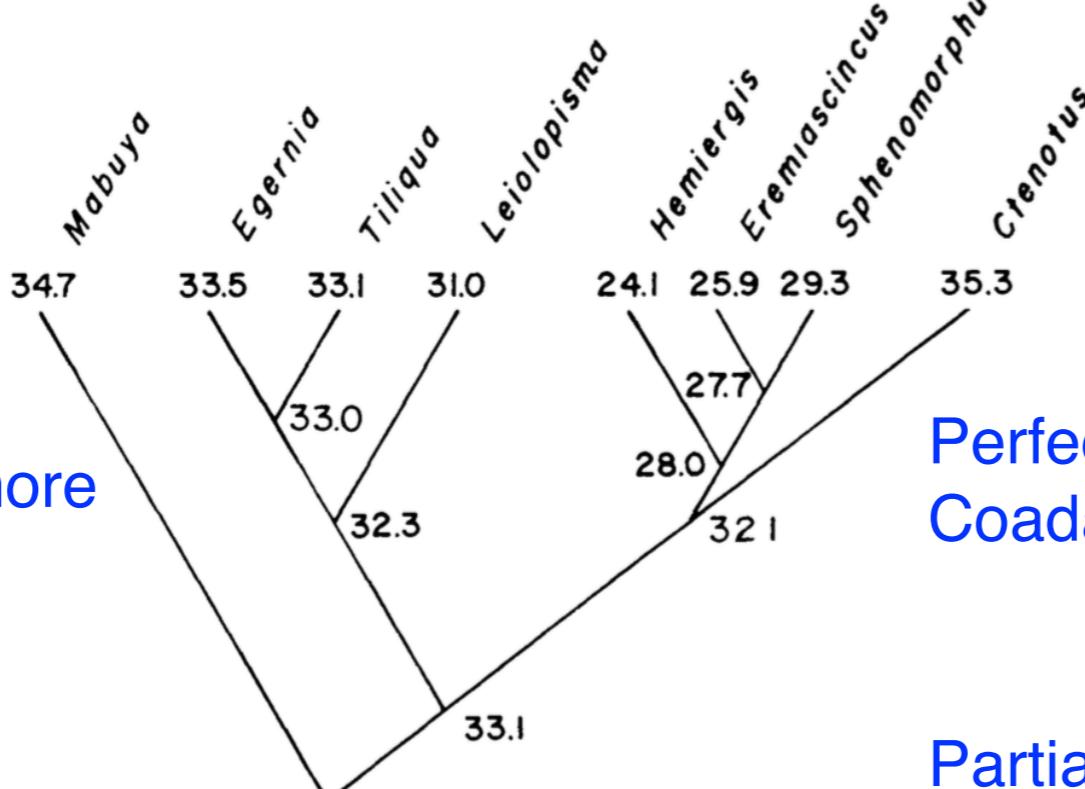
↑  
phylogenetic relatedness matrix

phylogenetic autocorrelation coefficient ( $\sim h^2$ )

\*note: phylogeny in mean structure

# Ancestral Character State Reconstruction

Preferred temperature varies widely



Optimal temperature more conserved (32-35C)

*Evolution*, 41(5), 1987, pp. 1098–1115

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

RAYMOND B. HUEY

Department of Zoology NJ-15, University of Washington, Seattle, WA 98195

AND

ALBERT F. BENNETT

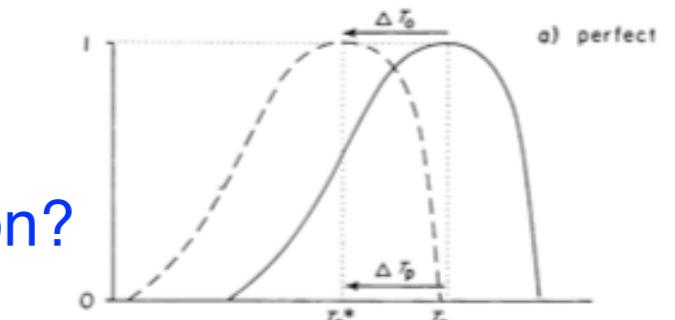
School of Biological Sciences, University of California, Irvine, CA 92717

**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

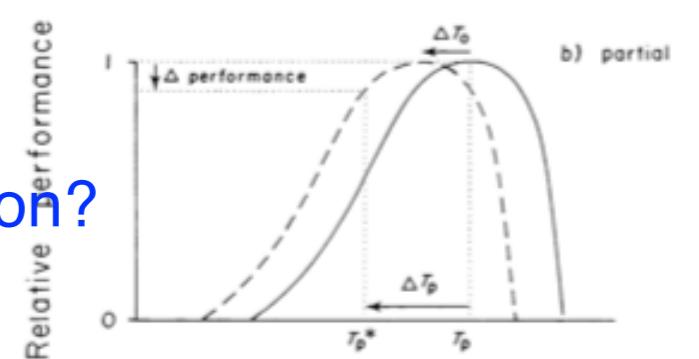
Ushered in era of “Tree Thinking”

- Timing
- Order of Evolution

Perfect Coadaptation?



Partial Coadaptation?



Antagonistic Coadaptation?

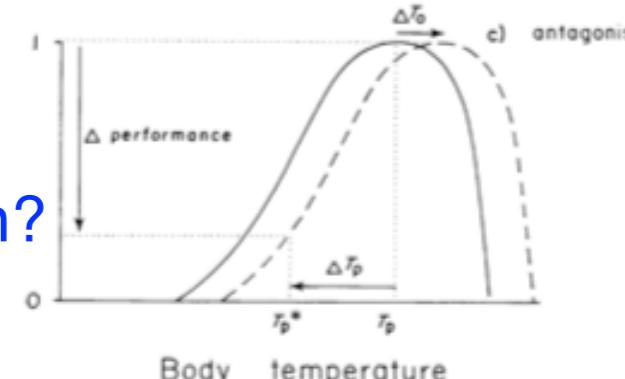
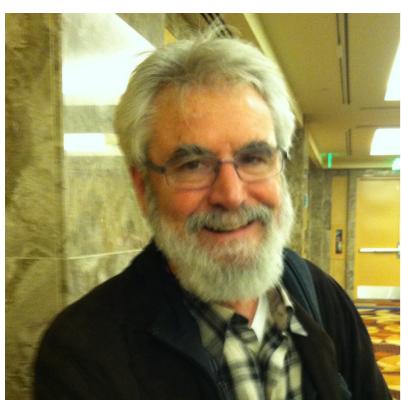


FIG. 1. a) A hypothetical case of perfect coadaptation, showing the thermal dependence of performance (solid line) and the thermal preference ( $T_p$ ) of an ancestral species, as well as the performance curve (dashed line) and  $T_p^*$  of a derived species. The change



# Ancestral Character State Reconstruction

# Ancestral Character State Reconstruction

First Pass Down:  
assign initial values to nodes

Second Pass Up:  
calculate Ancestral States

**Optimizing Criterion:**  
Minimum evolution (Linear Parsimony)  
Weighted Squared Change Parsimony  
(related to BM)

*Evolution*, 41(5), 1987, pp. 1098–1115

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

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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 Aus-

# Ancestral Character State Reconstruction

## Continuous Characters

### Optimizing Criteria:

Minimum evolution (Linear Parsimony)

ALL minimize evolution across the tree!

Ignores Branch Lengths (minimizes  $|change|$ )

Weighted Squared Change Parsimony

uses Branch Length Information ( $\min change^2$ )

Unweighted Squared Change Parsimony

Ignores Branch Lengths (all set = 1)

Maximum Likelihood

When Evolutionary Model is Brownian motion,  
should give identical results to WSCP

Bayesian

Most of these methods (except Bayesian) are implemented in R package “ape” via the “ace” function

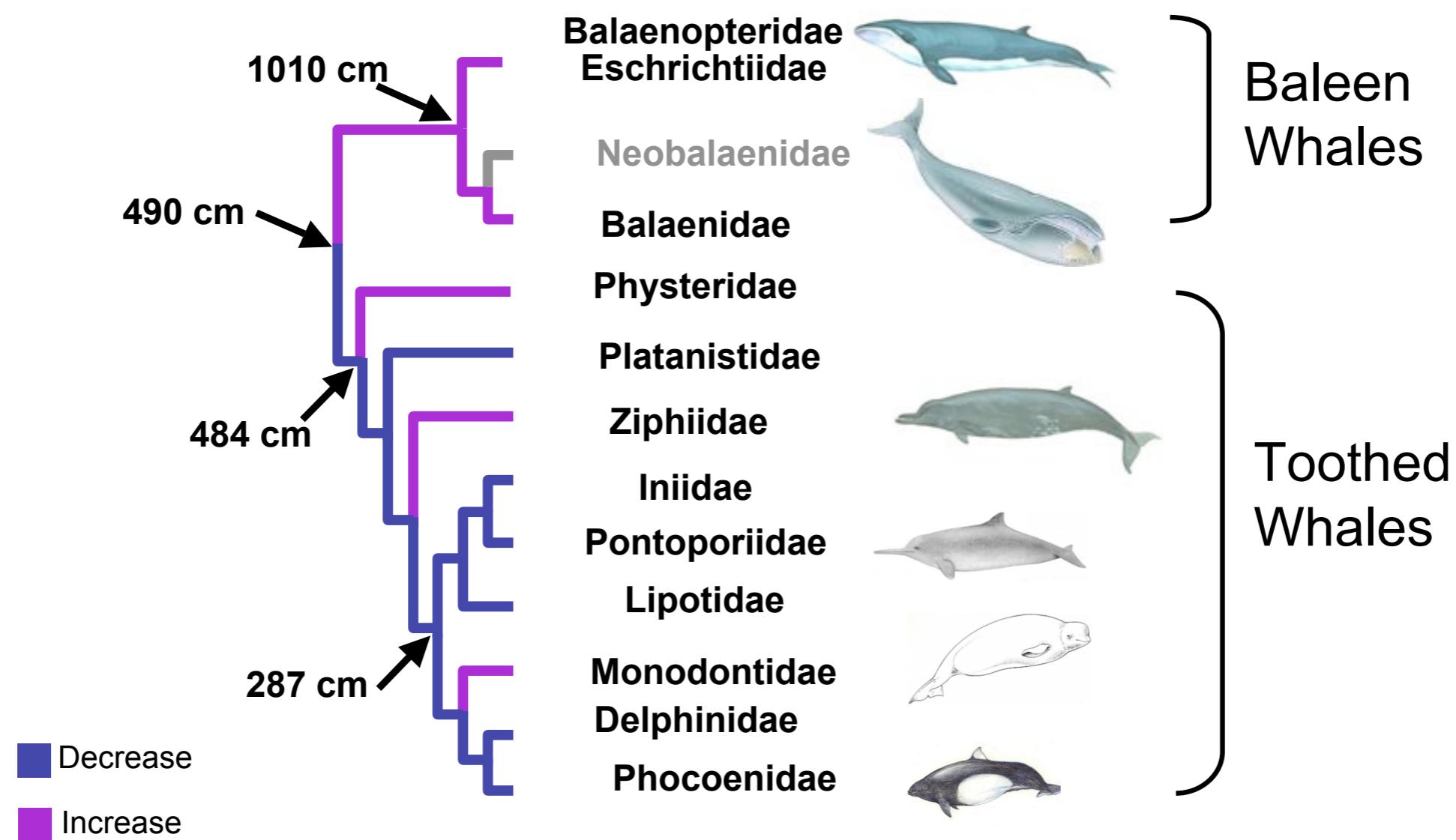
> `ace(method="ML")`



# Ancestral Character State Reconstruction

## Continuous Characters

### Evolution of Size in Whales



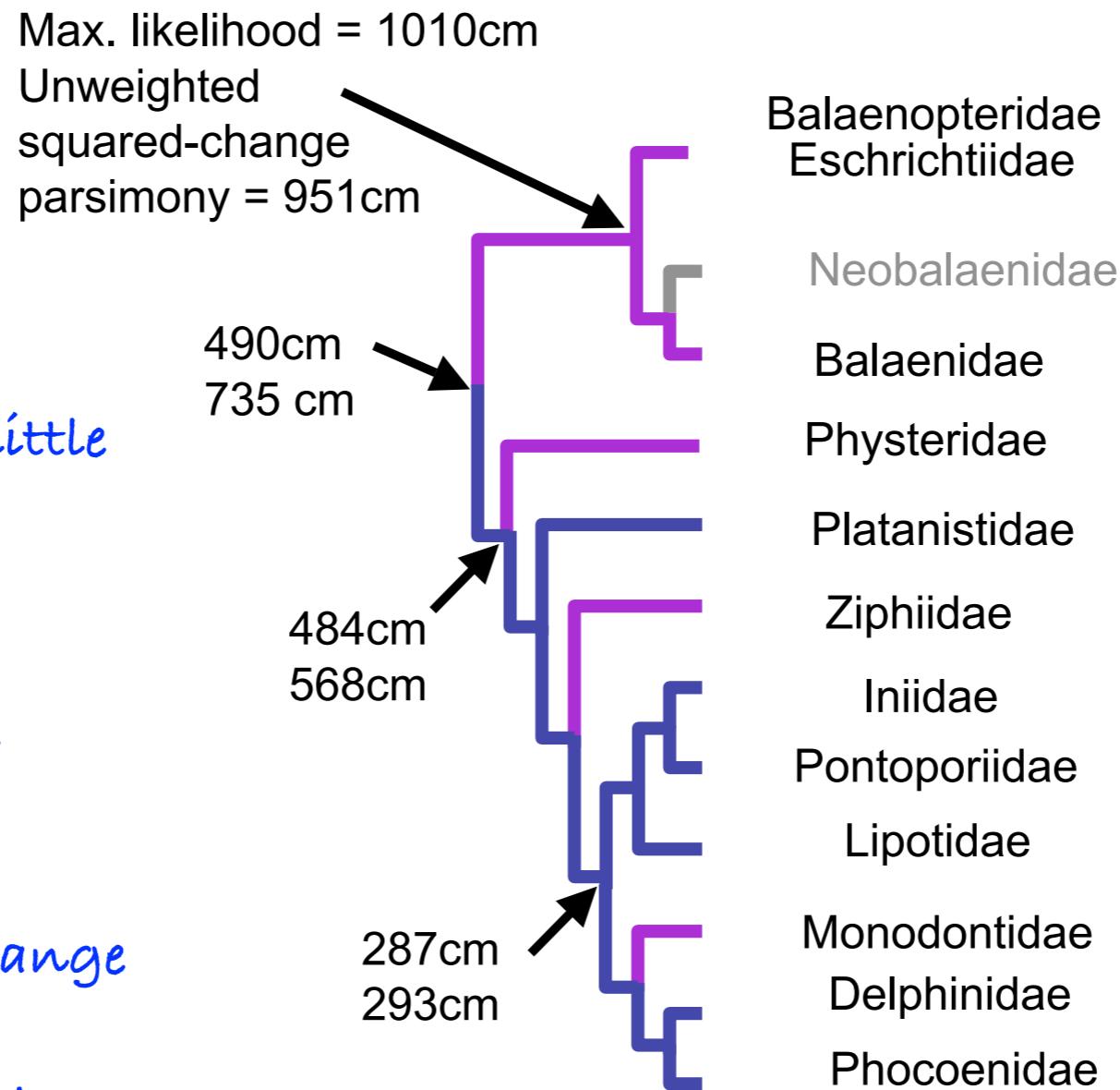
\*Thanks to Mike Alfaro for this figure!

# Ancestral Character State Reconstruction

## Continuous Characters

### Evolution of Size in Whales

- Generally, results are similar across methods if little evolution is happening
- Often there are bigger differences resulting from branch lengths/no branch lengths \*\*these are very different assumptions! Change promotional to “time” vs. numbers of speciation events



\*Thanks to Mike Alfaro for this figure!

# Ancestral Character State Reconstruction

## Discrete Characters - Markov Chain Monte Carlo

The model is now one of discrete change from one character state to another (instead from one continuous value to another according to a normal distribution).

The probability model is defined by rates of change between a set of discrete states (e.g., terrestrial <-> aquatic, terrestrial <-> aerial, etc. or A<->T, A<->G, C<->T, etc.)

When we consider evolution along a tree, the *Markov property says that the value at any given node is only dependent on the immediate ancestor (and not any earlier values)*. This property is the same as in the continuous case.

Maximum Likelihood used to fit Markovian models of discrete character evolution in R package “ape” via the “ace” function

```
> ace(type="discrete")
```



# Ancestral Character State Reconstruction

## Discrete Characters - Markov Chain Monte Carlo

**Equal**

Character  
states

	1	2	3
1	0	1	1
2	1	0	1
3	1	1	0

`ace(type=discrete,  
model="ER")`

**Symmetrical**

	1	2	3
1	0	1	2
2	1	0	3
3	2	3	0

`ace(type=discrete,  
model="SYM")`

**All-rates different**

	1	2	3
1	0	1	2
2	3	0	4
3	5	6	0

`ace(type=discrete,  
model="ARD")`

Maximum Likelihood used to fit Markovian models of discrete character evolution in R package “ape” via the “ace” function

> `ace(type="discrete")`



\*Thanks to Mike Alfaro for this slide!

# Ancestral Character State Reconstruction

## Uncertainty

Be mindful of the uncertainty!

Uncertainty grows (Confidence Intervals get huge) as you get farther from the tips.

Uncertainty grows as the rate of change increases! Only reliable when change is rare.

e.g., Fast evolving traits will tend to have changes inferred toward tips

Sometimes best to design tests that do not rely on inferring ancestral states or fossil data to anchor the deep nodes will help shrink Confidence Intervals

Know how much uncertainty there is in the estimates so that you are not misled.

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*Evolution*, 51(6), 1997, pp. 1699–1711

### LIKELIHOOD OF ANCESTOR STATES IN ADAPTIVE RADIATION

DOLPH SCHLUTER,<sup>1,2</sup> TREVOR PRICE,<sup>3</sup> ARNE Ø. MOOERS<sup>1,4</sup> AND DONALD LUDWIG<sup>1,5</sup>

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**Abstract.**—Theories of ecological diversification make predictions about the timing and ordering of character state changes through history. These theories are testable by “reconstructing” ancestor states using phylogenetic trees and measurements of contemporary species. Here we use maximum likelihood to estimate and evaluate the accuracy of ancestor reconstructions. We present likelihoods of discrete ancestor states and derive probability distributions for continuous ancestral traits. The methods are applied to several examples: diets of ancestral Darwin’s finches; origin of inquilinism in gall wasps; microhabitat partitioning and body size evolution in scrubwrens; digestive enzyme evolution in artiodactyl mammals; origin of a sexually selected male trait, the sword, in platies and swordtails; and evolution of specialization in *Anolis* lizards. When changes between discrete character states are rare, the maximum-likelihood results are similar to parsimony estimates. In this case the accuracy of estimates is often high, with the

# Ancestral Character State Reconstruction

## Discrete Character Models - Historical Biogeography

Exciting outgrowths of discrete character models!  
Reconstructing Historical Biogeography  
Characters are areas – geographical ranges  
Evolutionary rates for  
**DISPERSAL – EXTINCTION – CLADOGENESIS**

Syst. Biol. 57(1):4–14, 2008  
Copyright © Society of Systematic Biologists  
ISSN: 1063-5157 print / 1076-836X online  
DOI: 10.1080/10635150701883881

### Maximum Likelihood Inference of Geographic Range Evolution by Dispersal, Local Extinction, and Cladogenesis

RICHARD H. REE<sup>1</sup> AND STEPHEN A. SMITH<sup>2</sup>

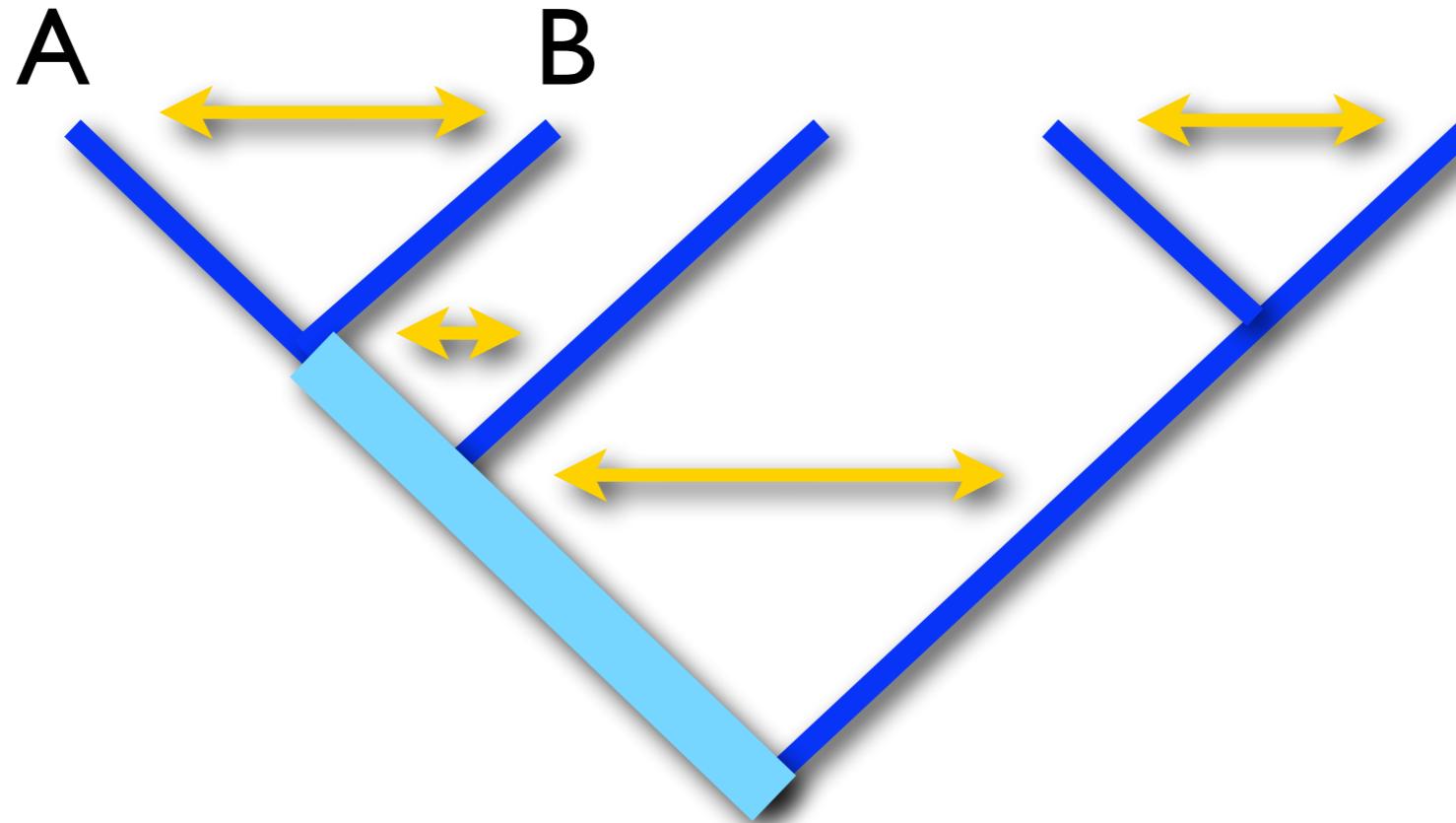
<sup>1</sup>Department of Botany, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, USA; E-mail: rree@fieldmuseum.org

<sup>2</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520, USA

**Abstract.**—In historical biogeography, model-based inference methods for reconstructing the evolution of geographic ranges on phylogenetic trees are poorly developed relative to the diversity of analogous methods available for inferring character evolution. We attempt to rectify this deficiency by constructing a dispersal-extinction-cladogenesis (DEC) model for geographic range evolution that specifies instantaneous transition rates between discrete states (ranges) along phylogenetic branches and apply it to estimating likelihoods of ancestral states (range inheritance scenarios) at cladogenesis events. Unlike an earlier version of this approach, the present model allows for an analytical solution to probabilities of range transitions as a function of time, enabling free parameters in the model, rates of dispersal, and local extinction to be estimated by maximum likelihood. Simulation results indicate that accurate parameter estimates may be difficult to obtain in practice but also show that ancestral range inheritance scenarios nevertheless can be correctly recovered with high success if rates of range evolution are low relative to the rate of cladogenesis. We apply the DEC model to a previously published, exemplary case study of island biogeography involving Hawaiian endemic angiosperms in *Psychotria* (Rubiaceae), showing how the DEC model can be iteratively refined from inspecting inferences of range evolution and also how geological constraints involving times of island origin may be imposed on the likelihood function. The DEC model is sufficiently similar to character models that it might serve as a gateway through which many existing comparative methods for characters could be imported into the realm of historical biogeography; moreover, it might also inspire the conceptual expansion of character models toward inclusion of evolutionary change as directly coincident, either as cause or consequence, with cladogenesis events. The DEC model is thus an incremental advance that highlights considerable potential in the nascent field of model-based historical biogeographic inference. [Ancestral state reconstruction; dispersal; extinction; Hawai'i; historical biogeography; *Psychotria*; speciation; vicariance.]

# Independent Contrasts

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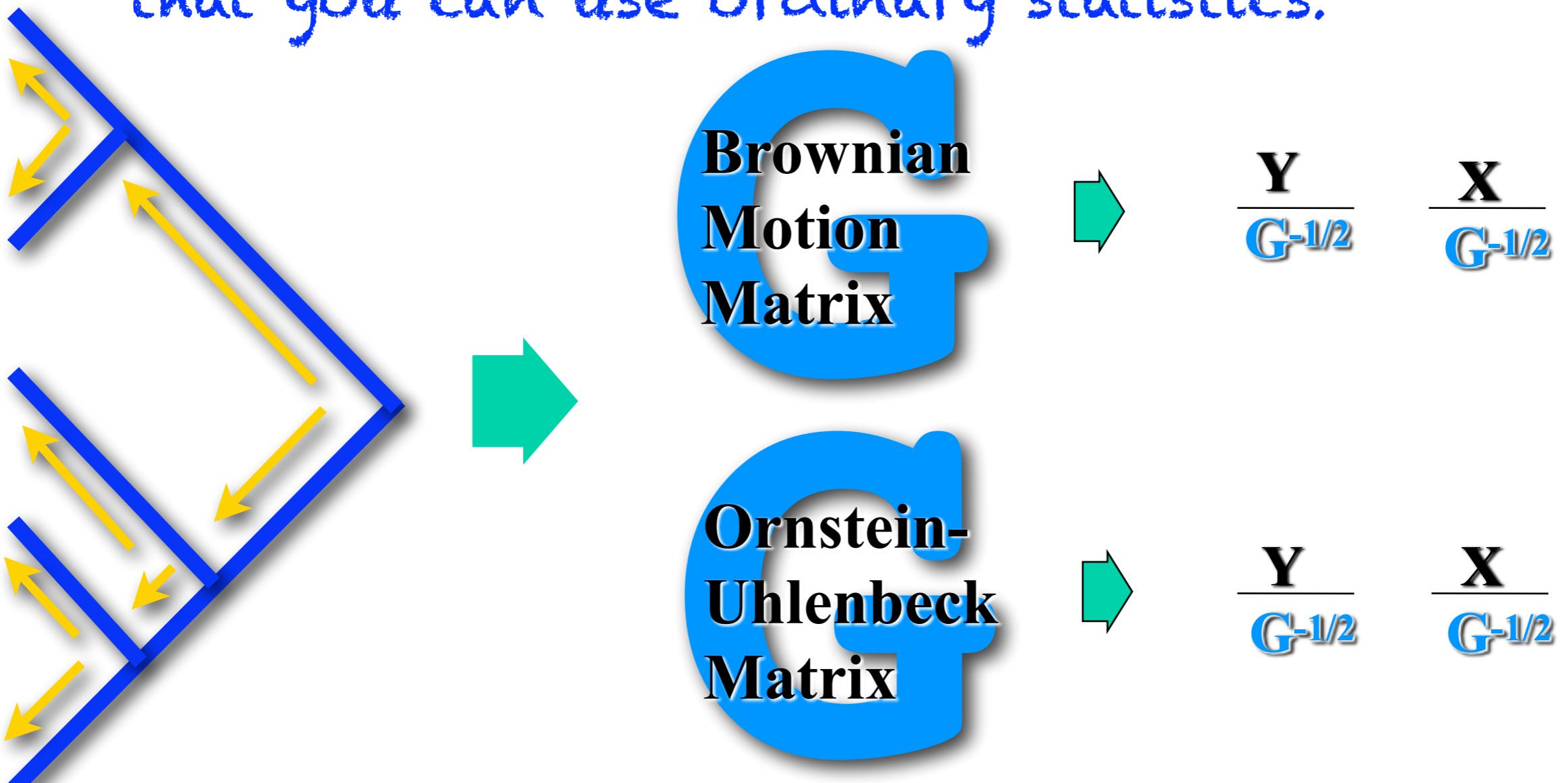


- Transform the interspecific data with covariances due to shared evolutionary history into a set of statistically independent “contrasts” with zero covariances among contrasts.
- Species A and B share more than 50% of their evolutionary history.
  - Thus, all else being equal, *if we assume a Brownian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

# Phylogenetic Regression Phylogenetic GLS (PGLS)

# Correcting phylogenetic variance (PGLS-like)

How to “correct” your interspecific data so that you can use ordinary statistics:

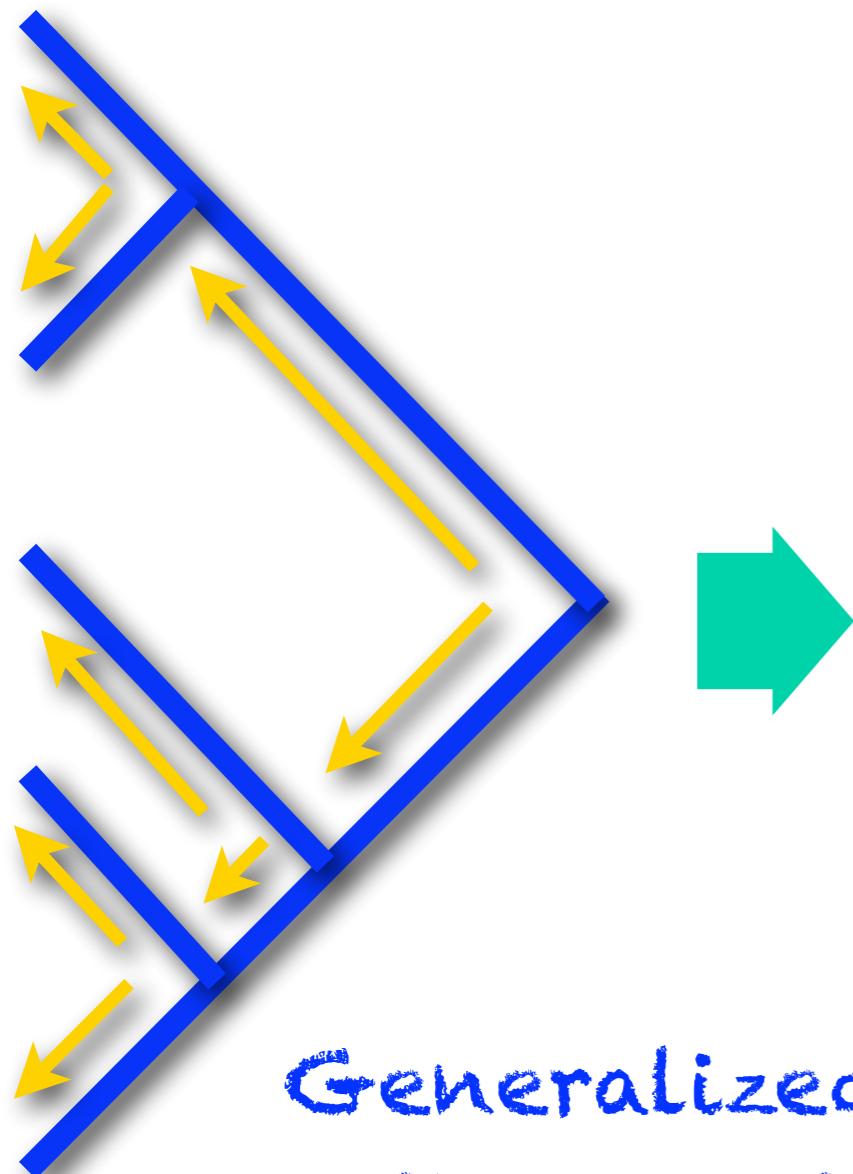


“Divide” (using matrix math) the interspecific dataset by the square root of the variance matrix to adjust for phylogenetic covariance.

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

# Correcting variance using Phylogenetic GLS

Leave in the Phylogenetic Covariance, but account for the "correlated errors" in the statistical methods



Non-Phylo

Brownian Motion Matrix

Ornstein-Uhlenbeck Matrix

$$Y = \beta X + e$$

$$e \sim N(0, V)$$

Standard covariance matrix

$$e \sim N(0, \sigma^2 t)$$

Proportional to time of shared history

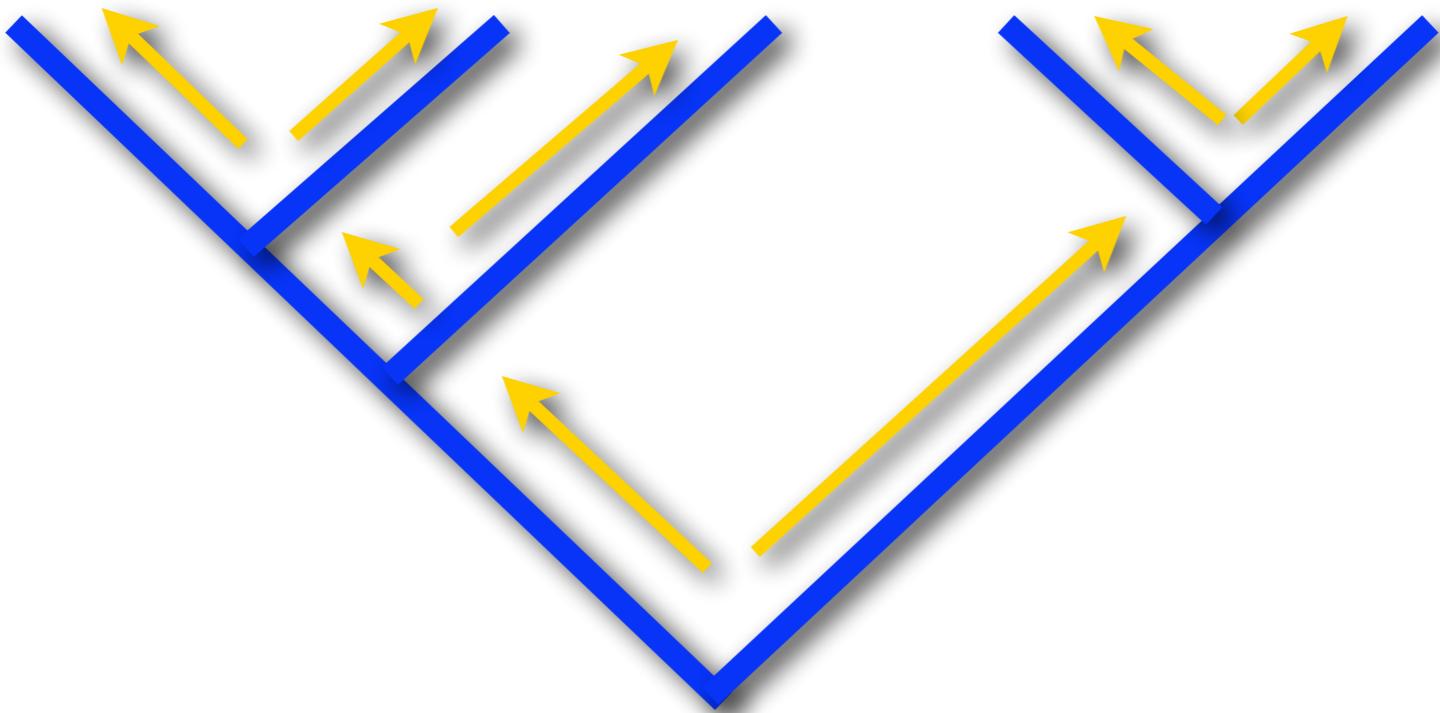
$$e \sim N(0, G_{ou})$$

\*\*Decays with time, affected by optima

Generalized Least Squares allows regression with non-standard error models

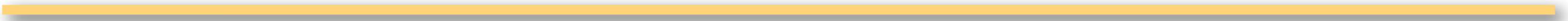
# Phylogenetic Simulation

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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’

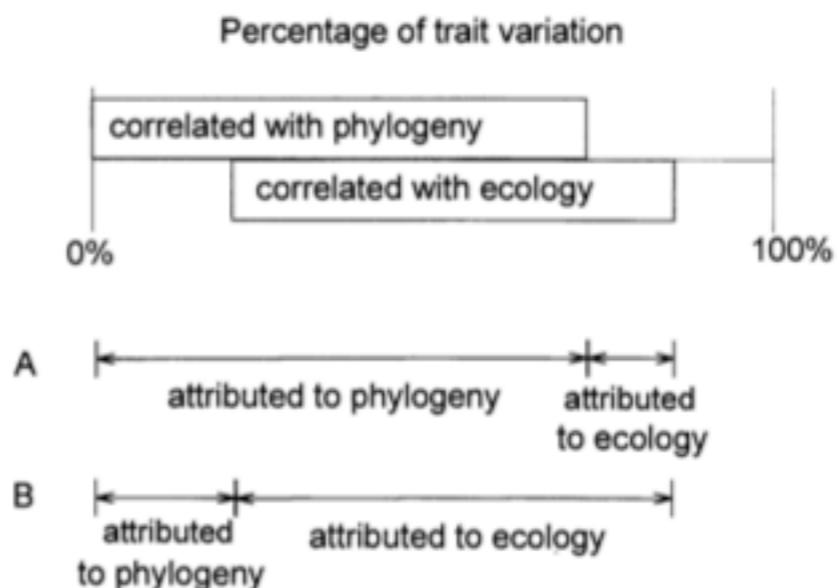
MARK WESTOBY, MICHELLE R. LEISHMAN and JANICE M. LORD

*School of Biological Sciences, Macquarie University, NSW 2109 Australia*

#### Introduction

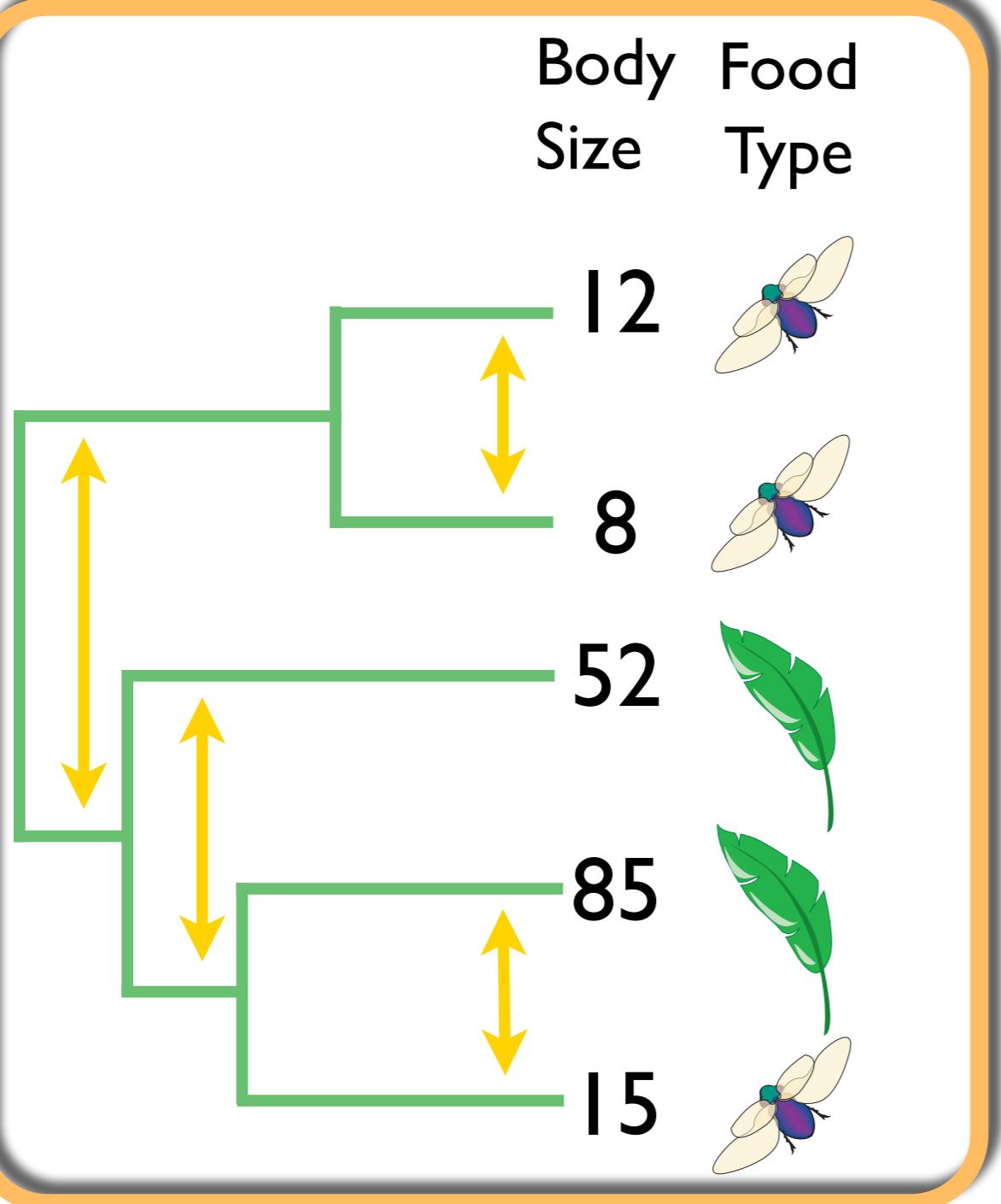
The last 10 years have seen important advances in methodology for taking phylogeny into account when analysing a comparative dataset. This commentary is about a class of interpretive procedures associated with these new statistical methods. We will call the interpretive logic ‘phylogenetic correction’ (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?)



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)*

# All comparative analyses are constructed of 3 pieces

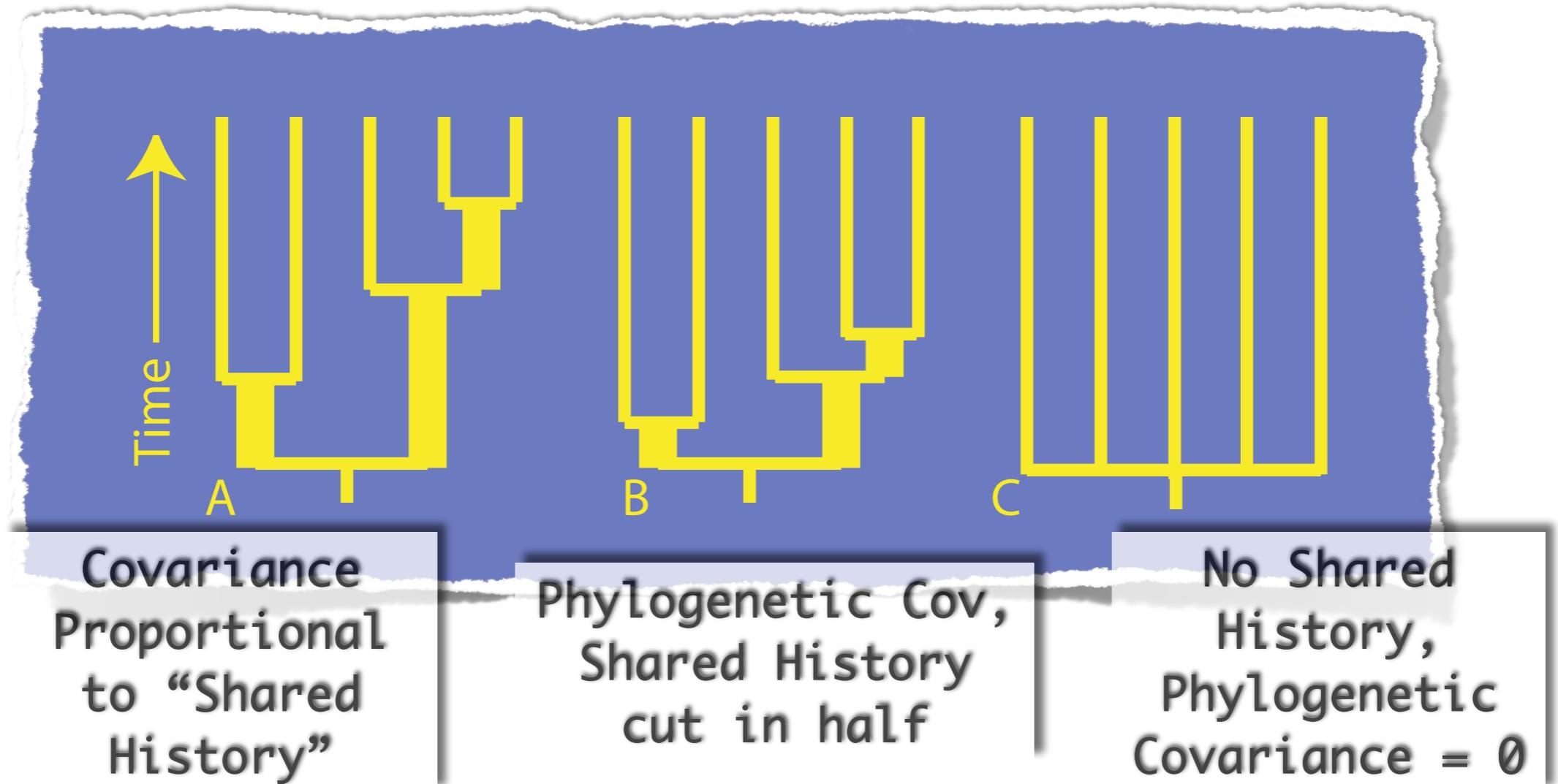
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- I. The comparative **dataset** (body size, plumage color, etc. for each species)
2. A particular pattern of shared ancestry (**phylogeny** and **branch lengths**)
3. A **model of evolutionary change** along each branch of the **phylogeny**

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?

---

- I. 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?

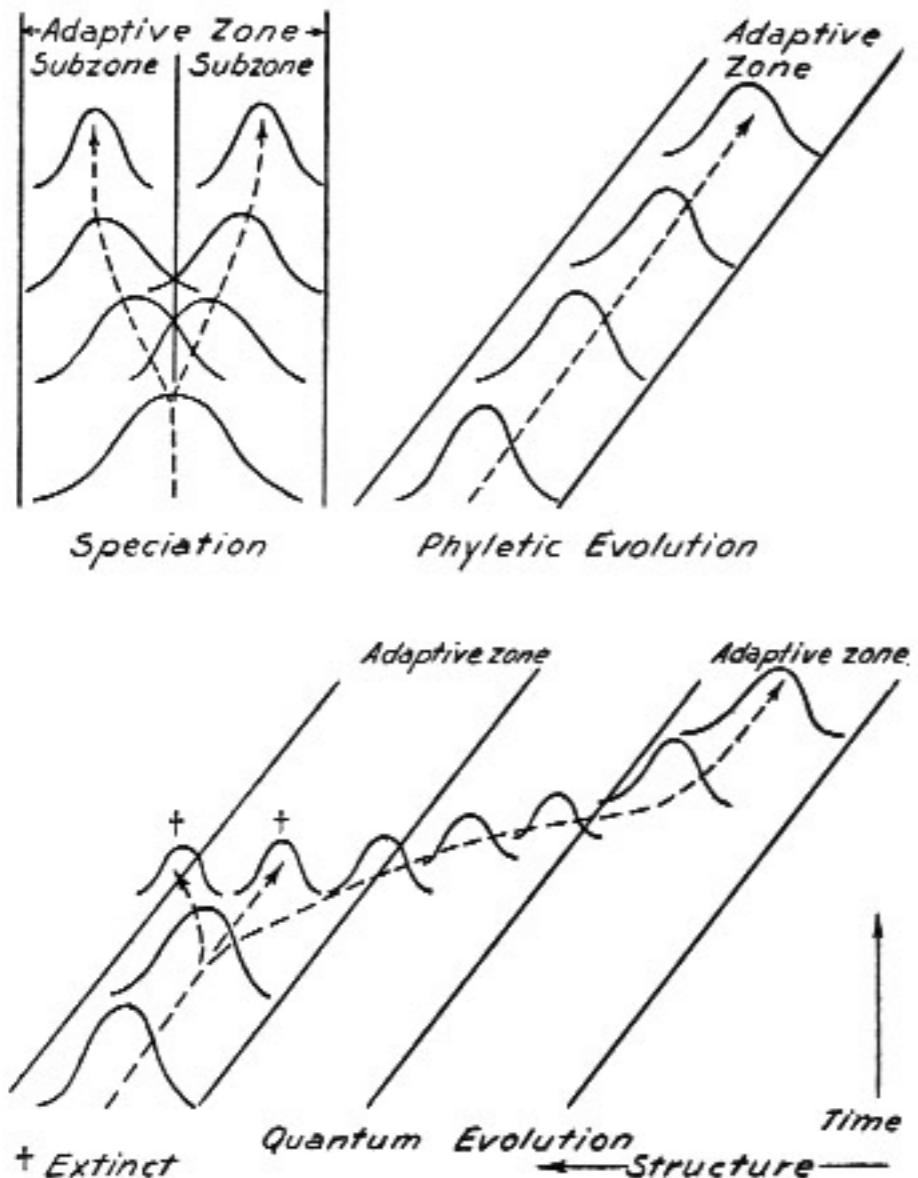
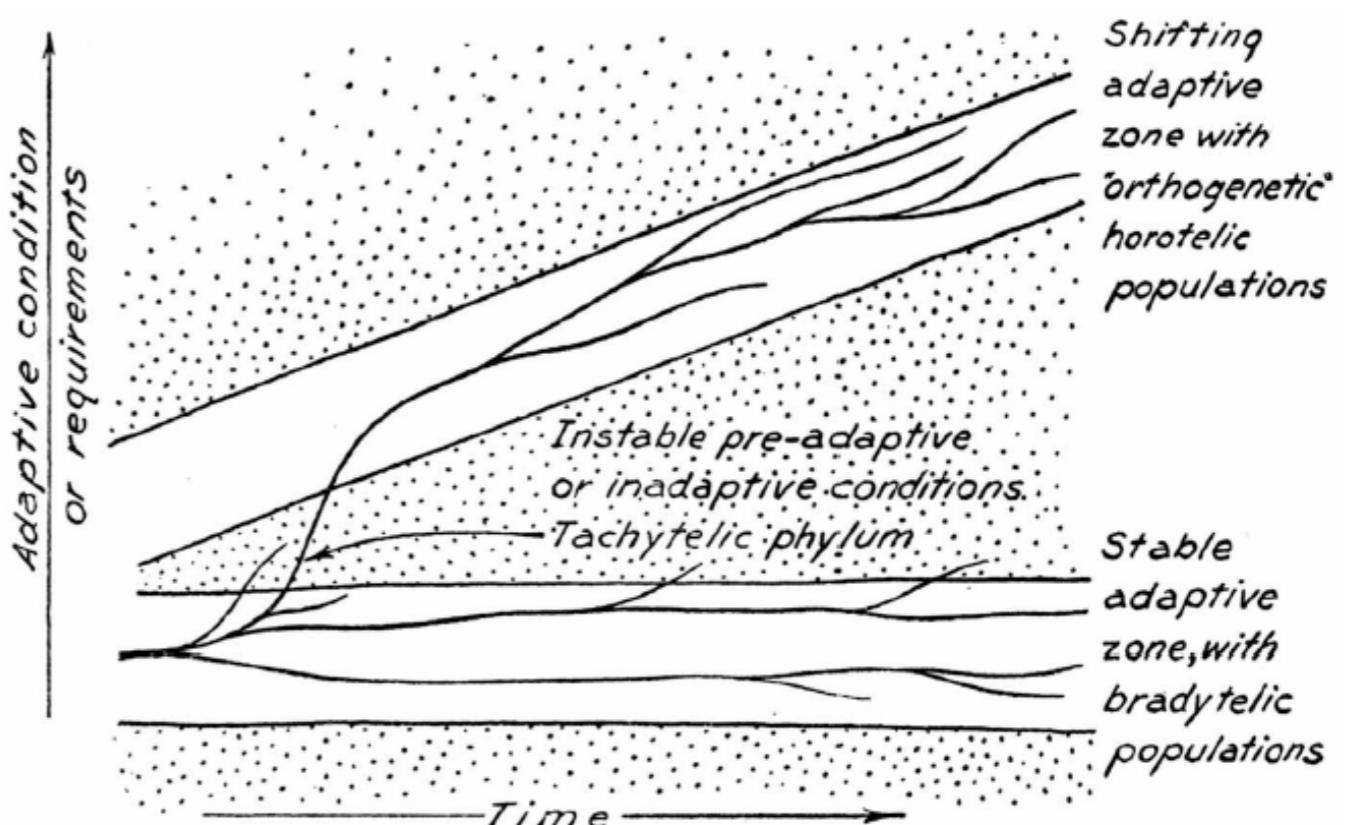


FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.



Simpson (1953) The major features of evolution

# There is another option...

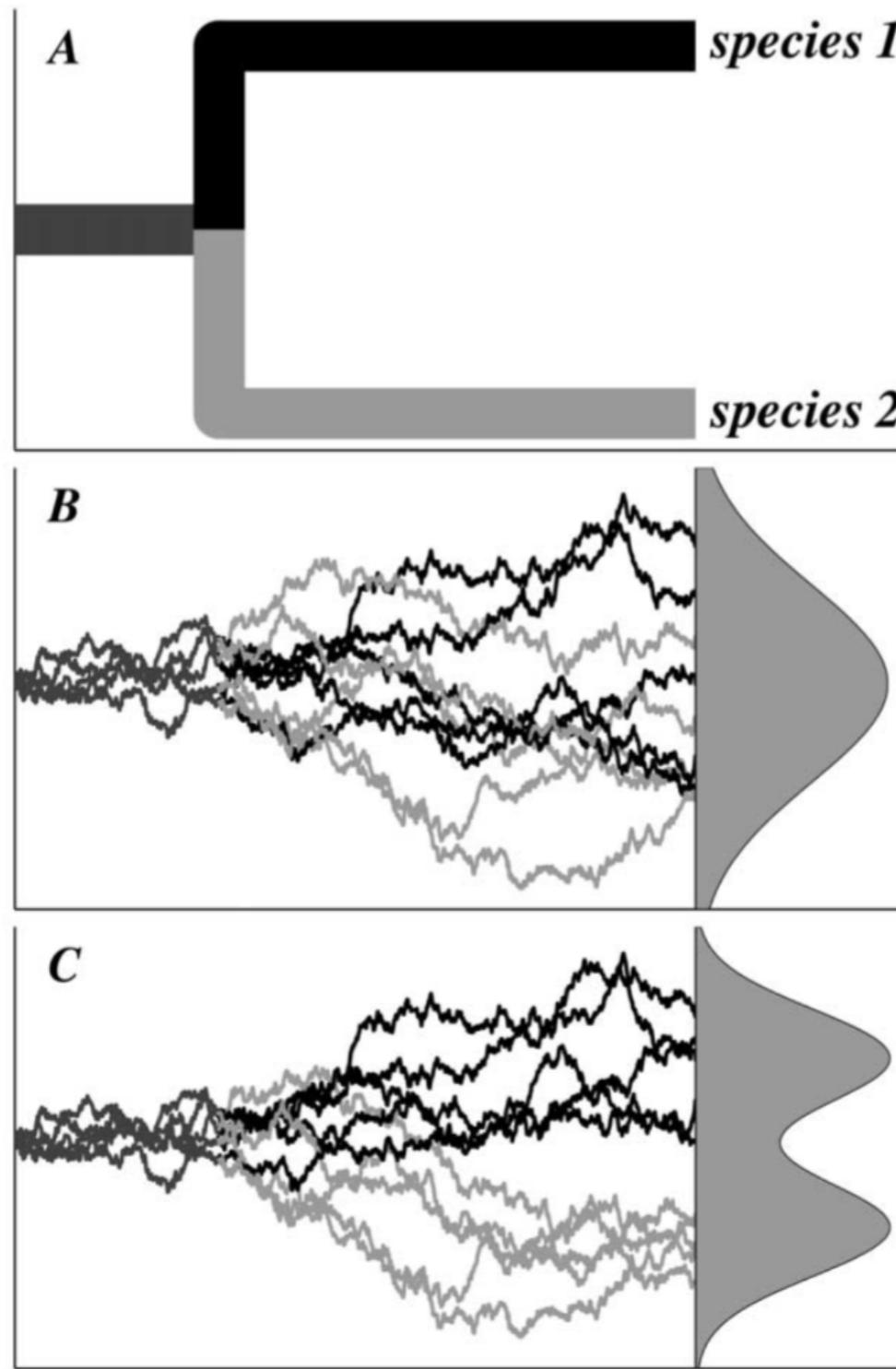
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1. The comparative **dataset** (body size, plumage color, etc. for each species)
2. A particular pattern of shared ancestry (**phylogeny** and **branch lengths**)
3. A **model of evolutionary change** along each branch of the phylogeny



Change the model of evolution !

# How do we explain Patterns of Biodiversity?



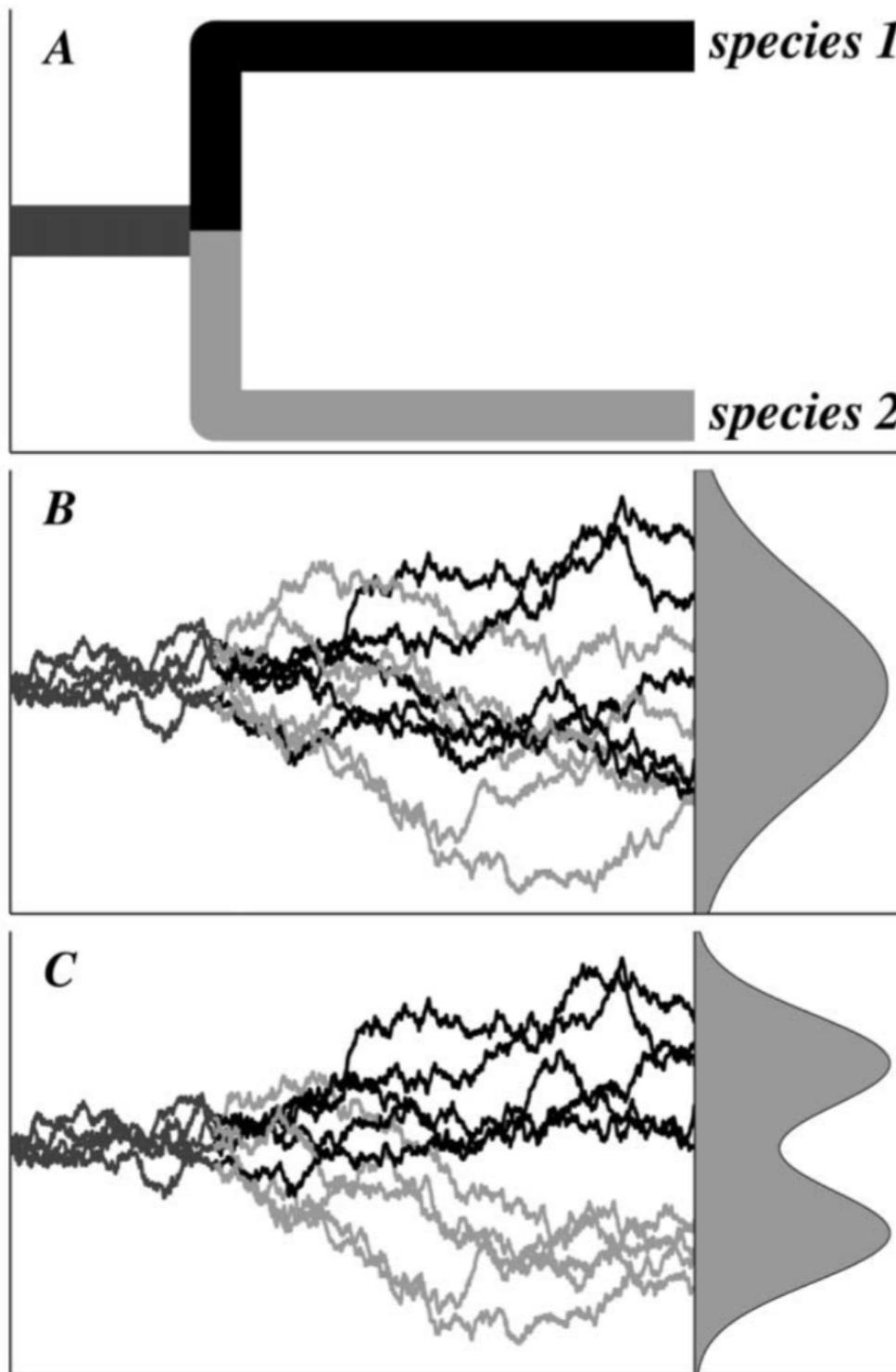
Pattern of relationship

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?**

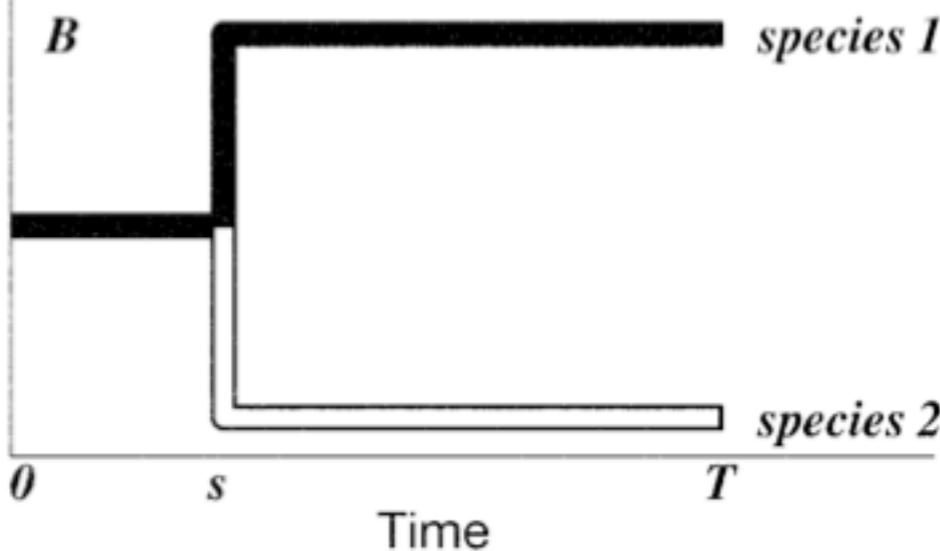
A

*species 1*

# Nuts and Bolts: 2 species example

*species 2*

B

*species 1*

**Expected Value**  
(mean at T)

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

**Variance**

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

**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**

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

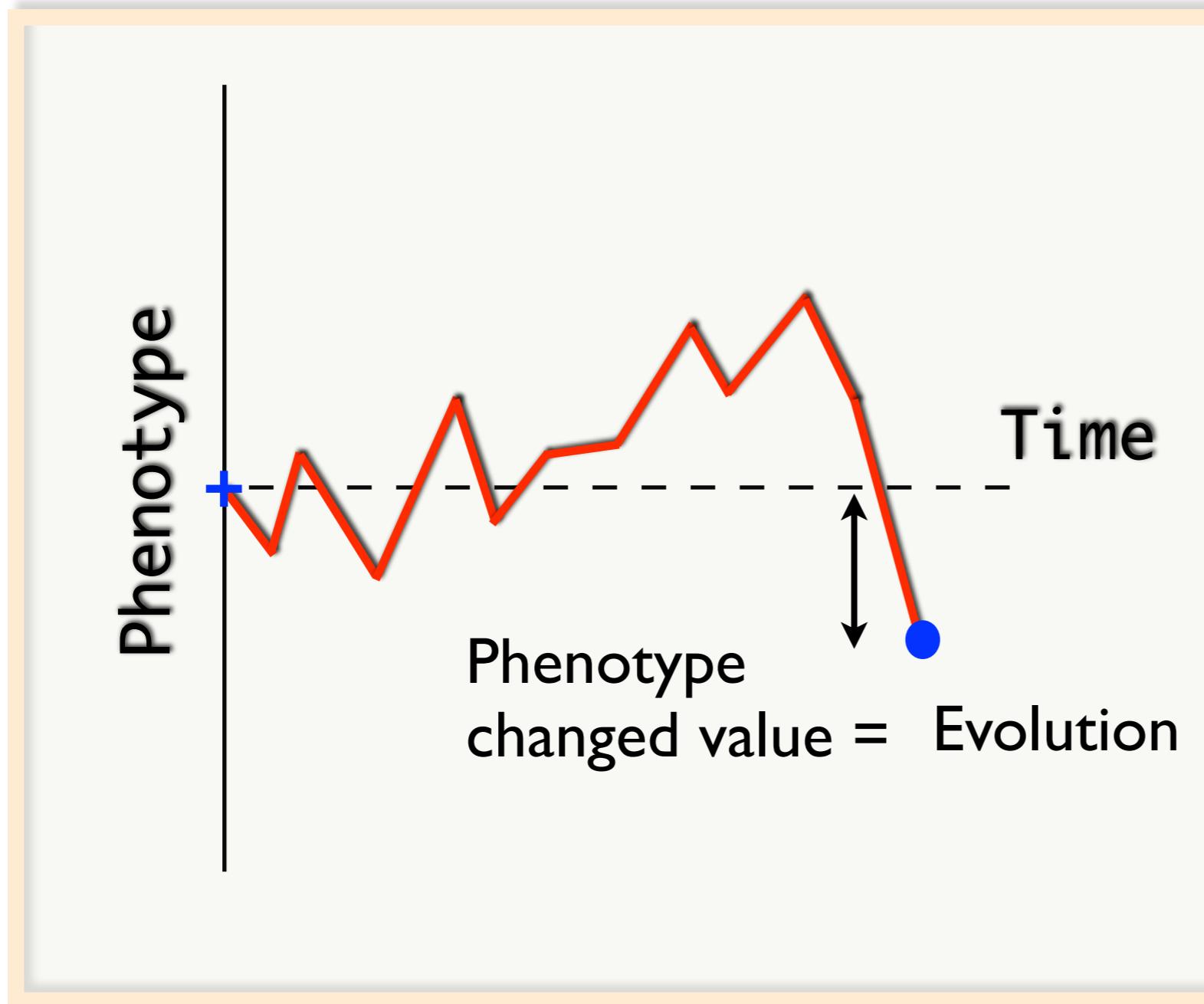
$$E[\mathbf{X}(T)] = \mathbf{W}\boldsymbol{\theta}$$

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

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

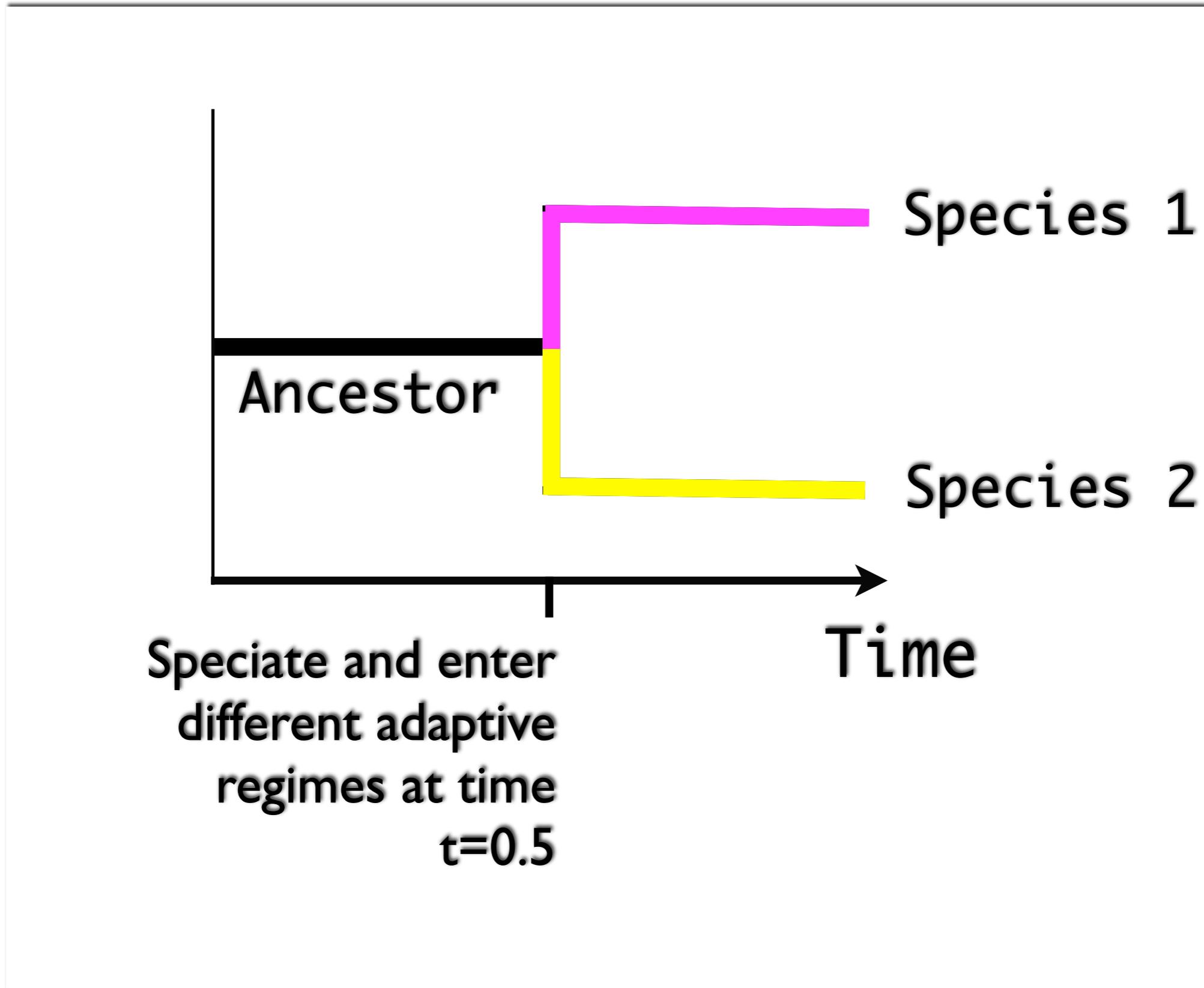
**let's do some simulations!**

# Evolution in Cartoon

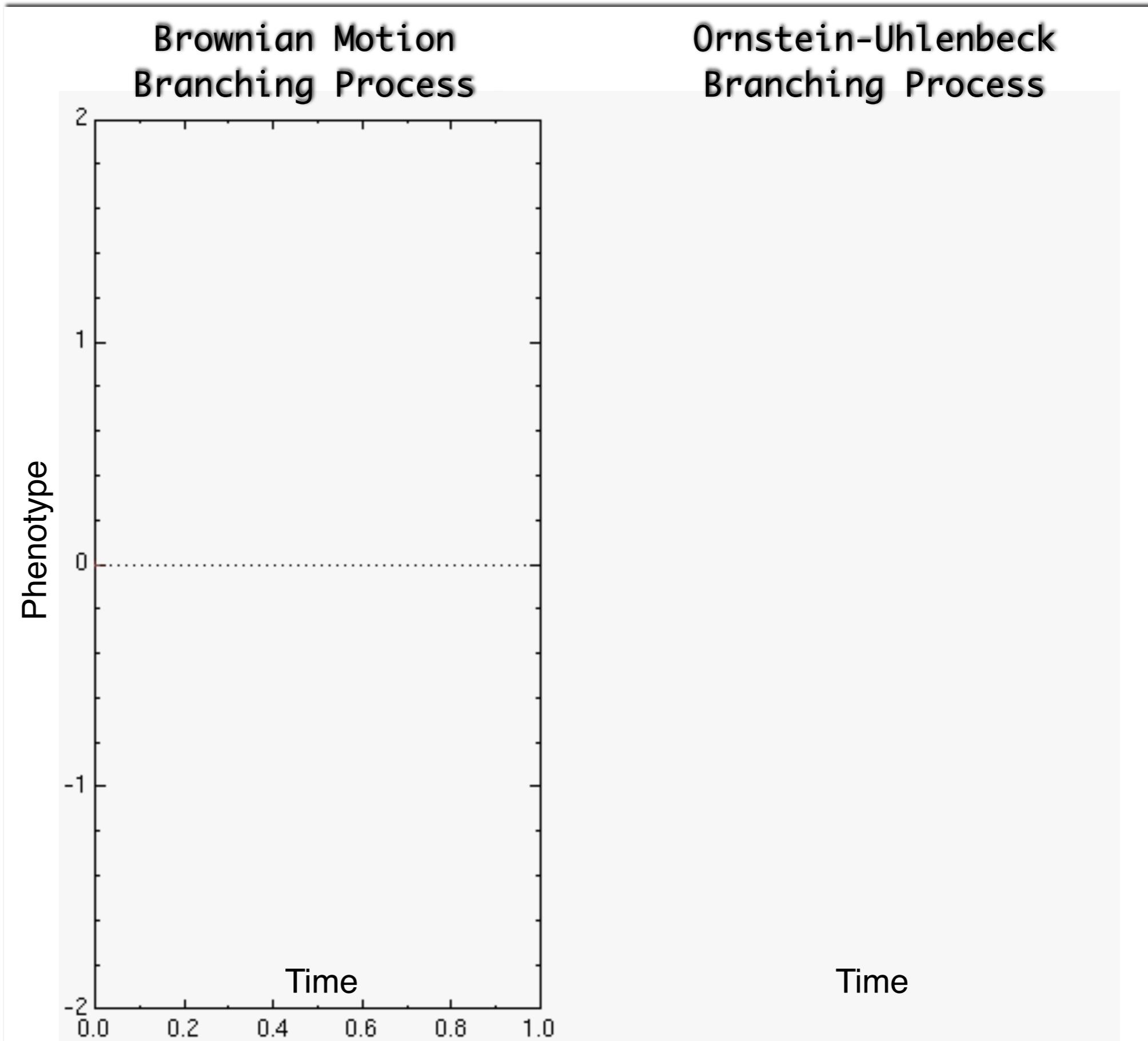


- At each infinitesimal increment of time, there is a probability of change in the phenotype.
- The probability is drawn from a normal distribution, thus the BM is “Gaussian.”
- The state at any given time is only dependent on the previous state.

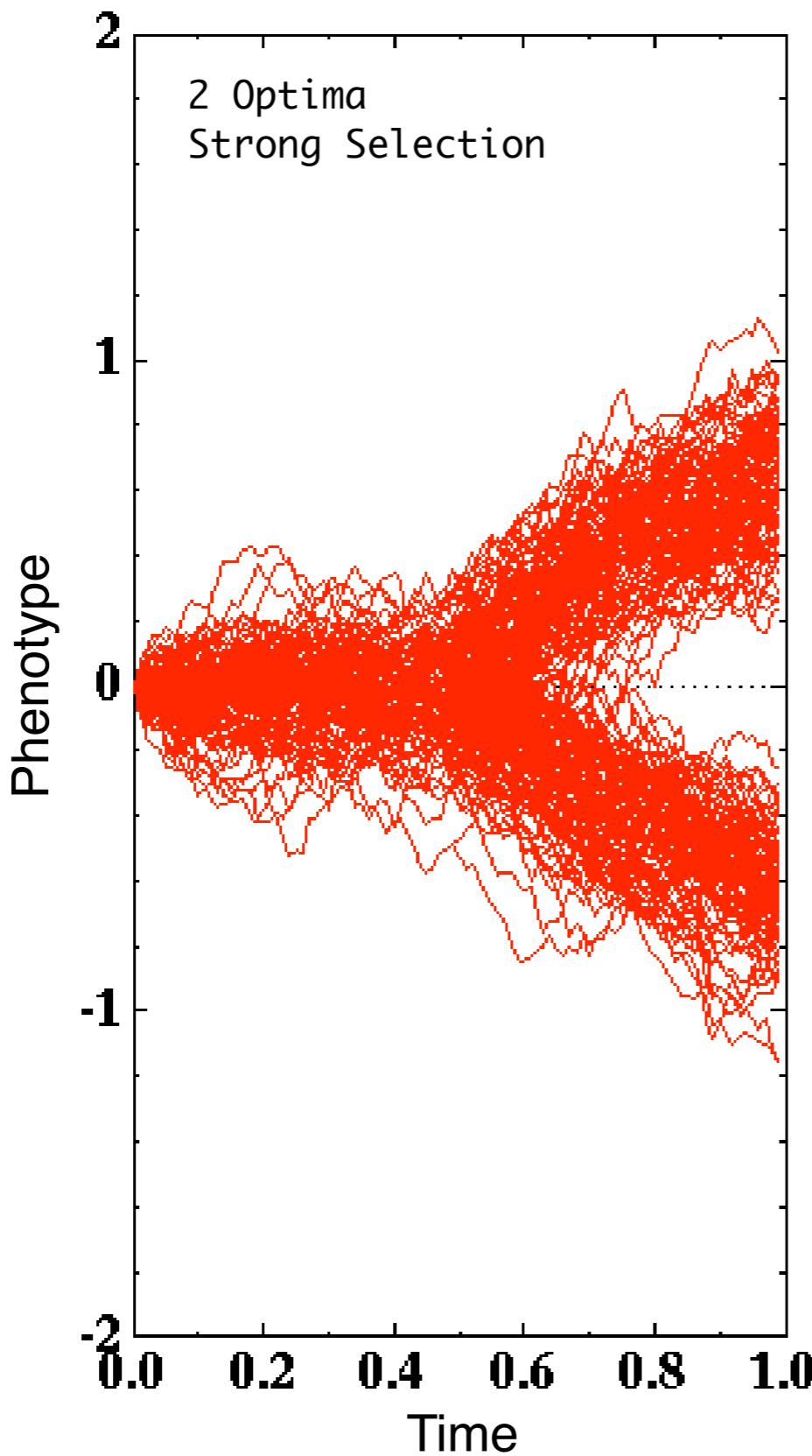
# BM and OU models make different predictions



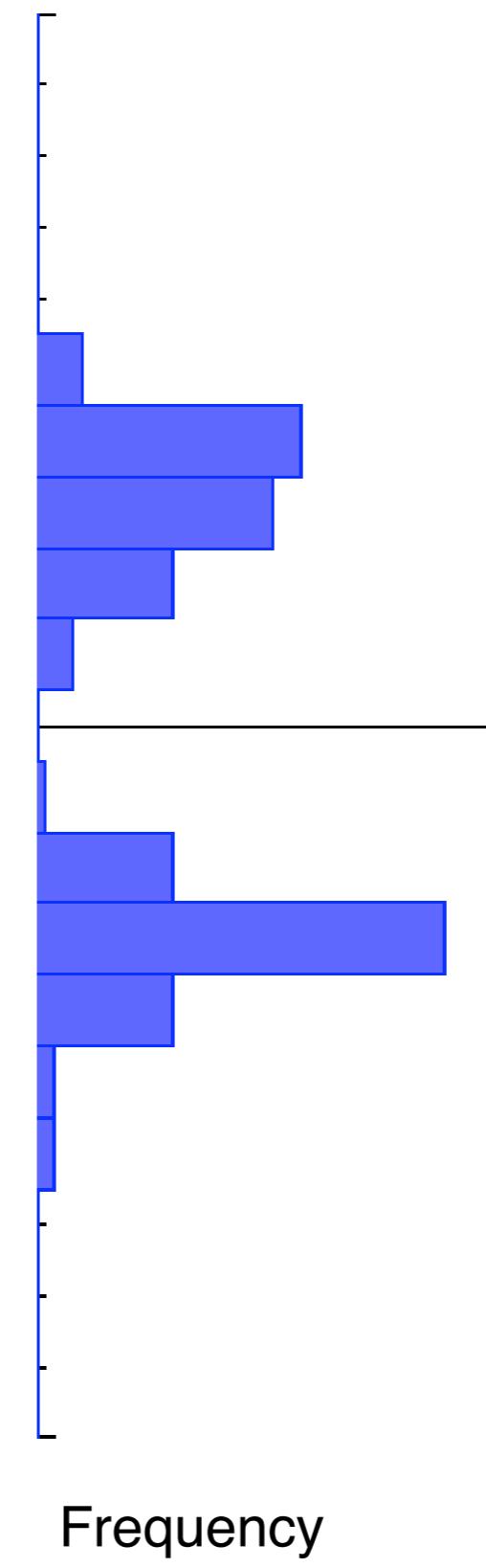
# BM and OU models make different predictions



## OU Branching Process



## Phenotypic Distribution



# What about the Biology?

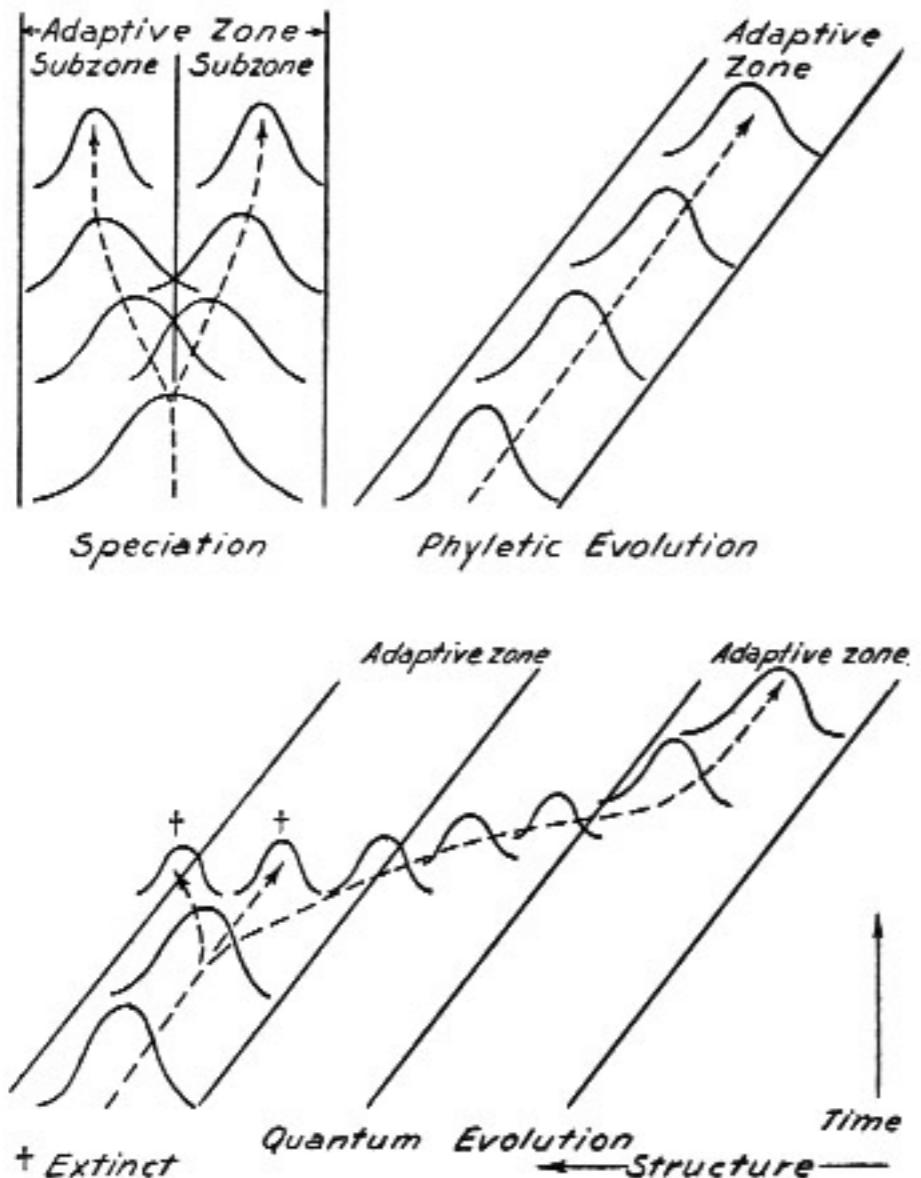
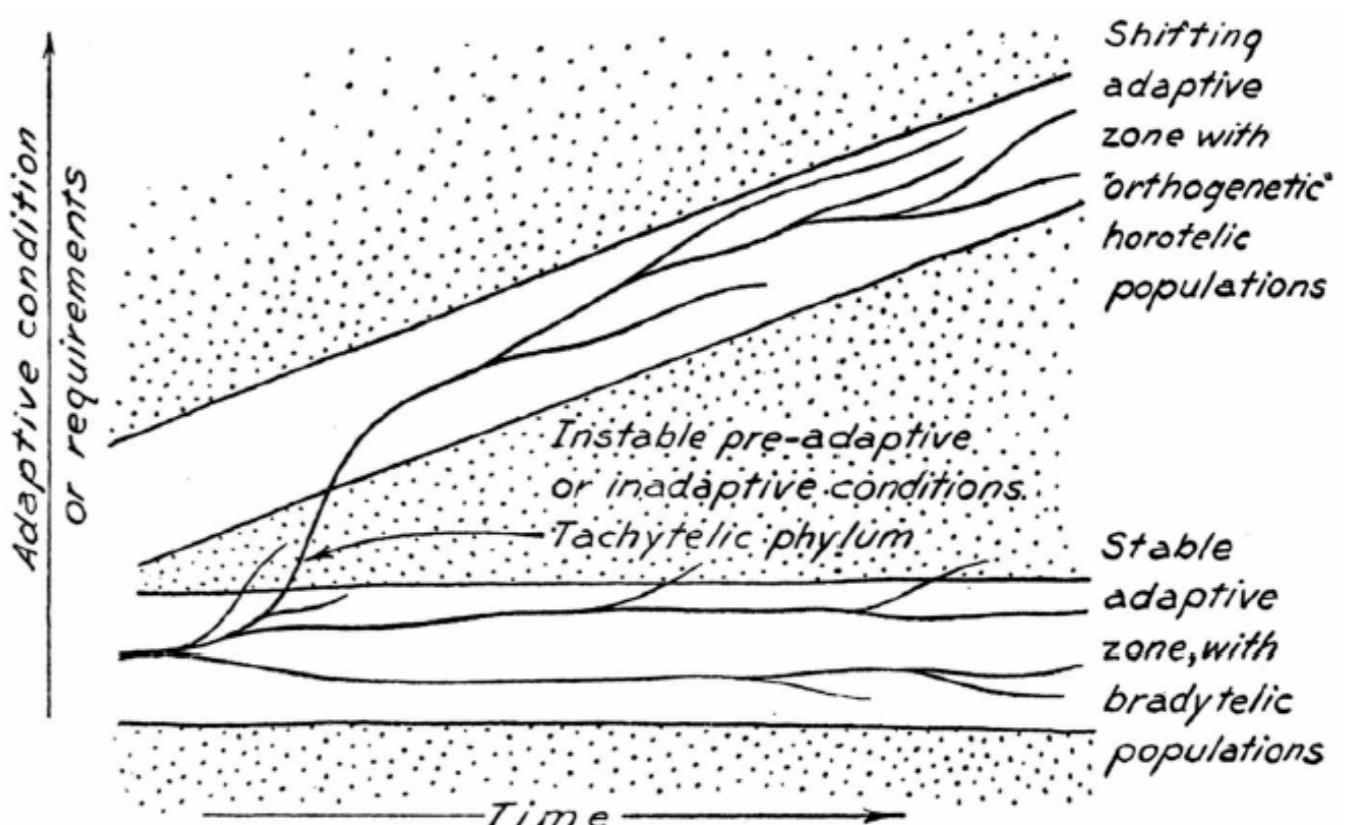


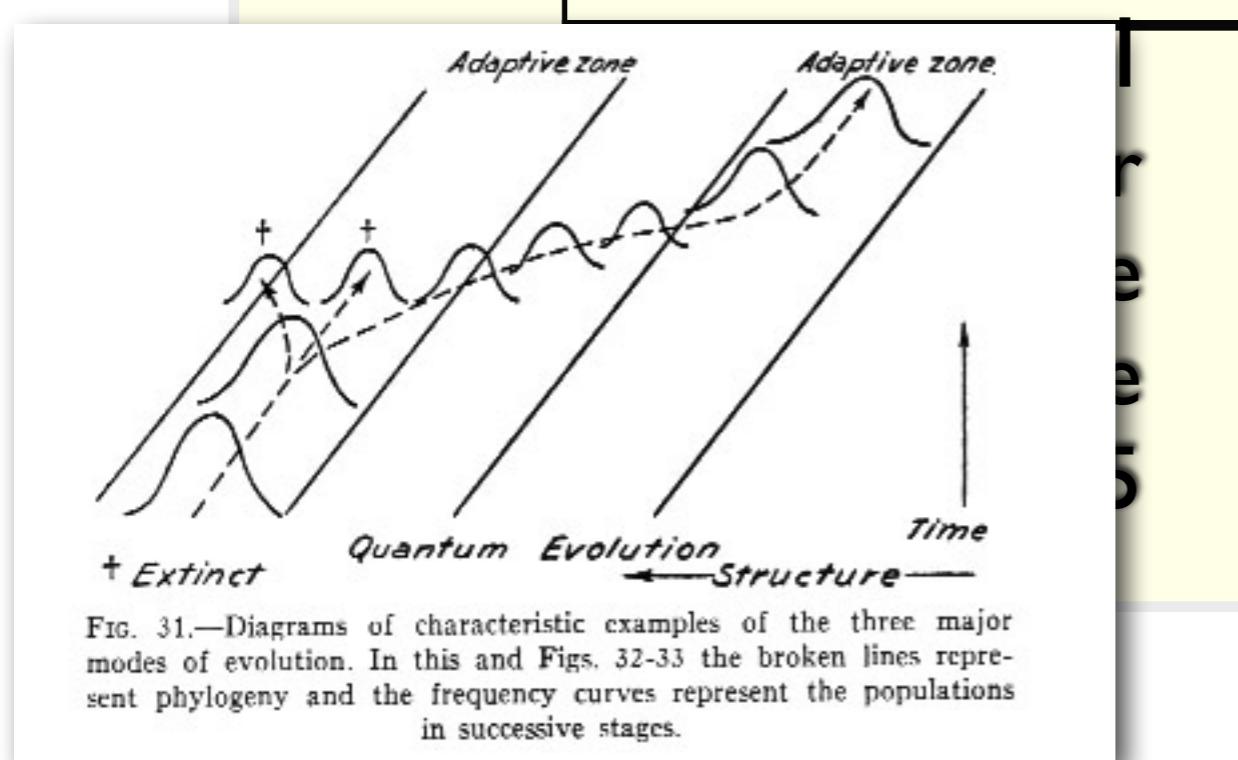
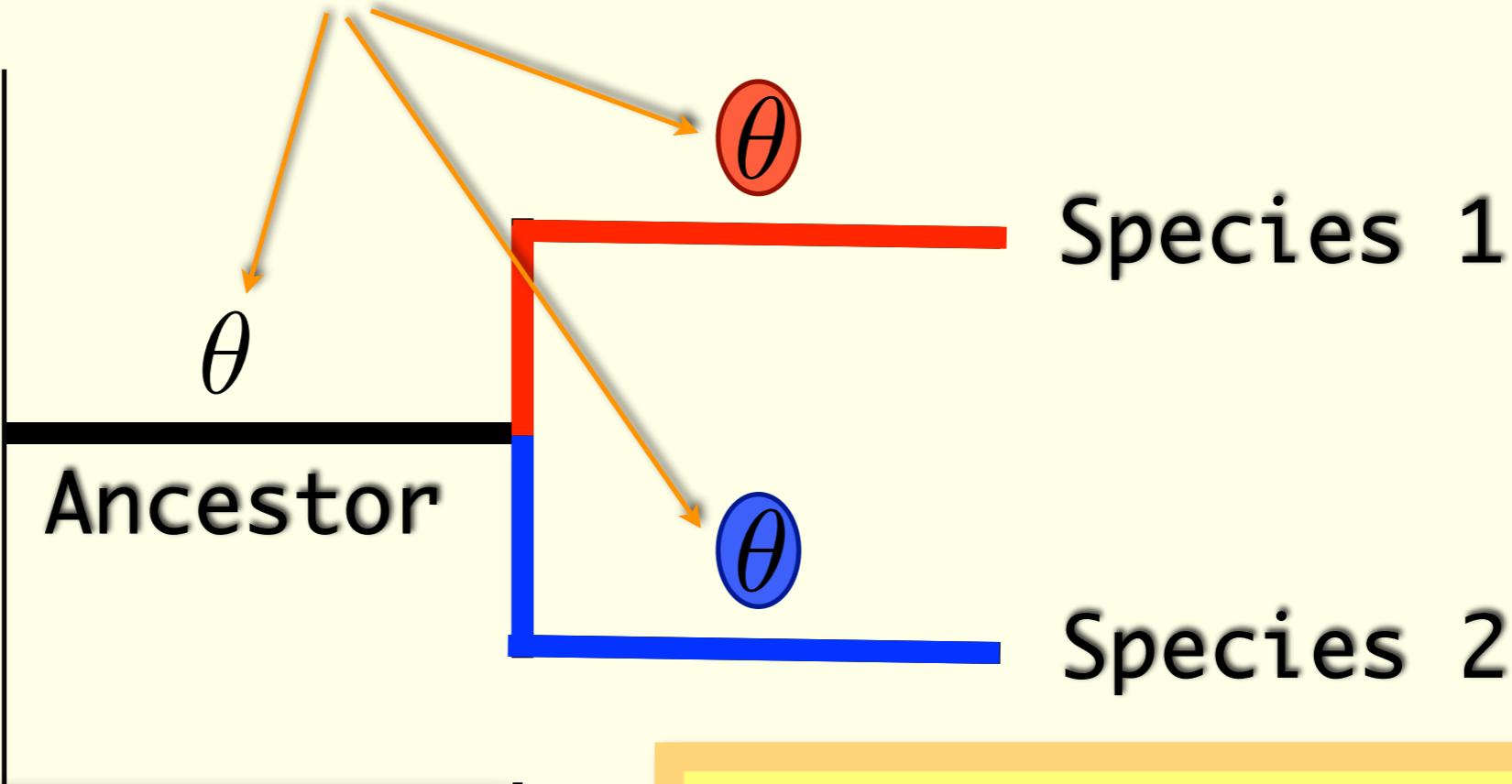
FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.



Simpson (1953) The major features of evolution

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

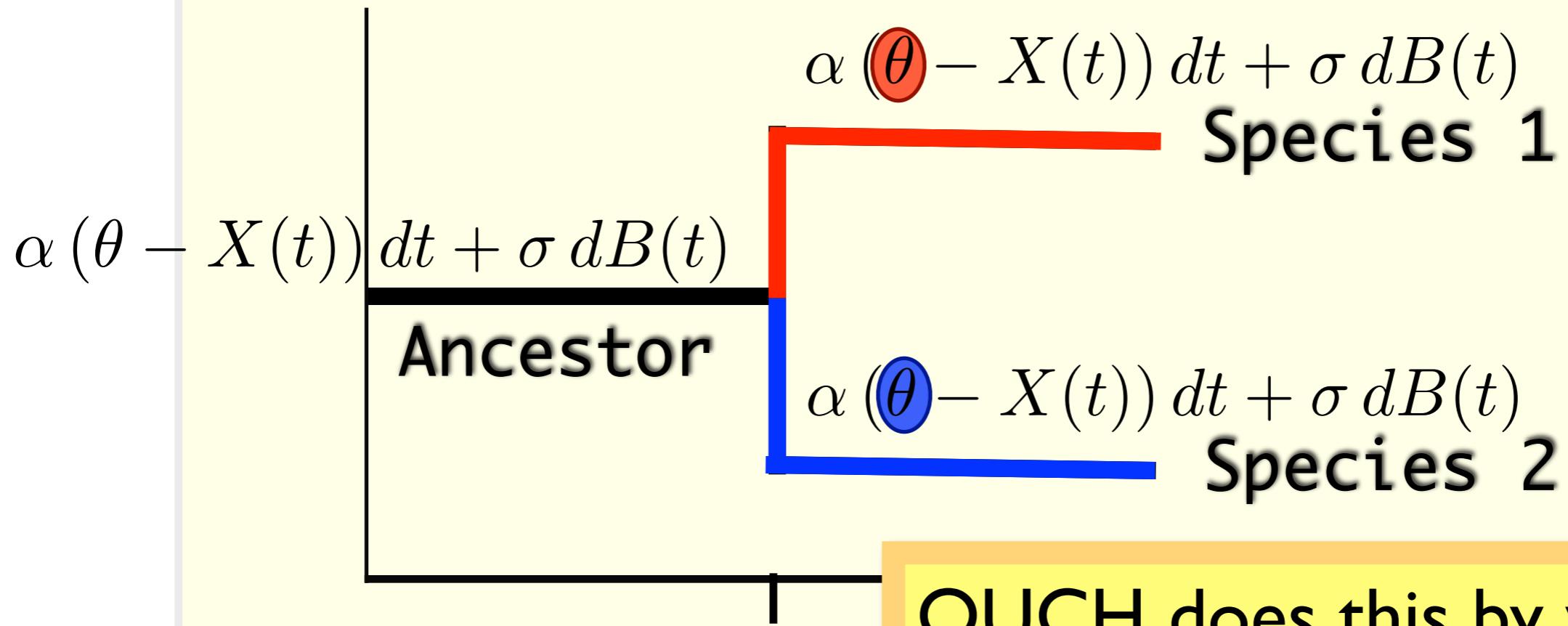
$$dX(t) = \alpha (\theta - X(t)) dt + \sigma dB(t)$$



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 painting new optimum!

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



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

**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.**

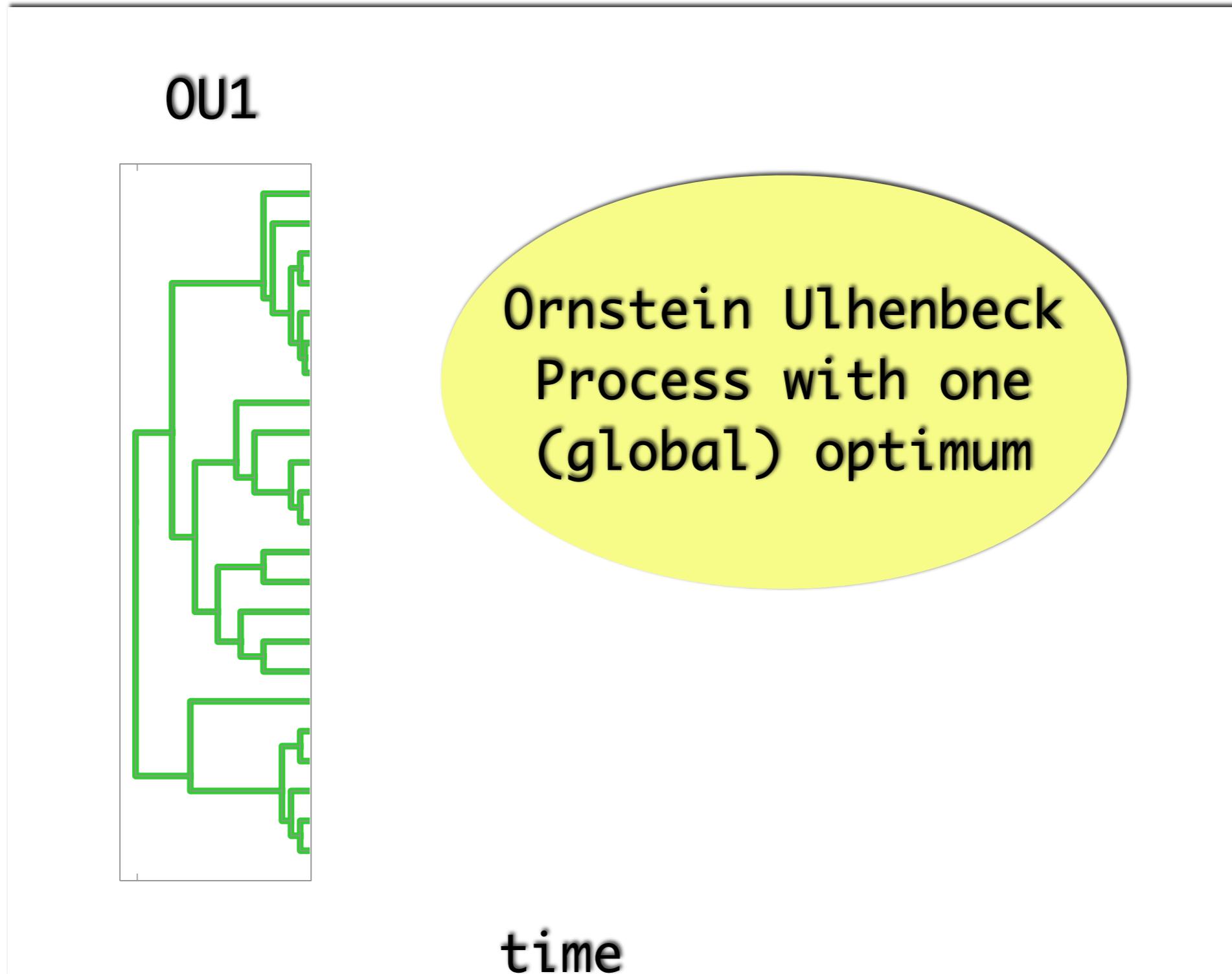
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**On the 2 species islands, anoles differ substantially in size.**

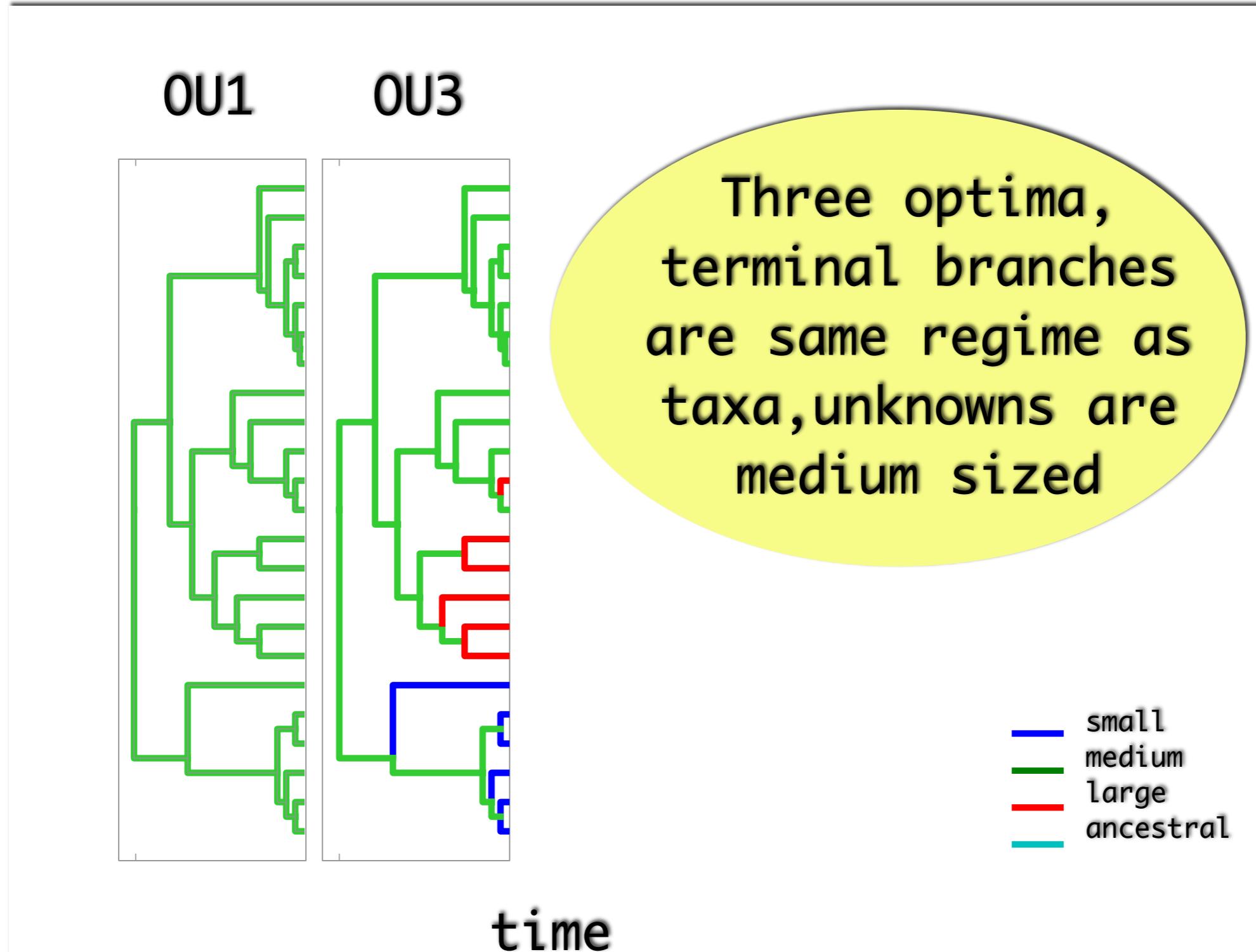
**On the single species islands, anoles are “intermediate” in size.**



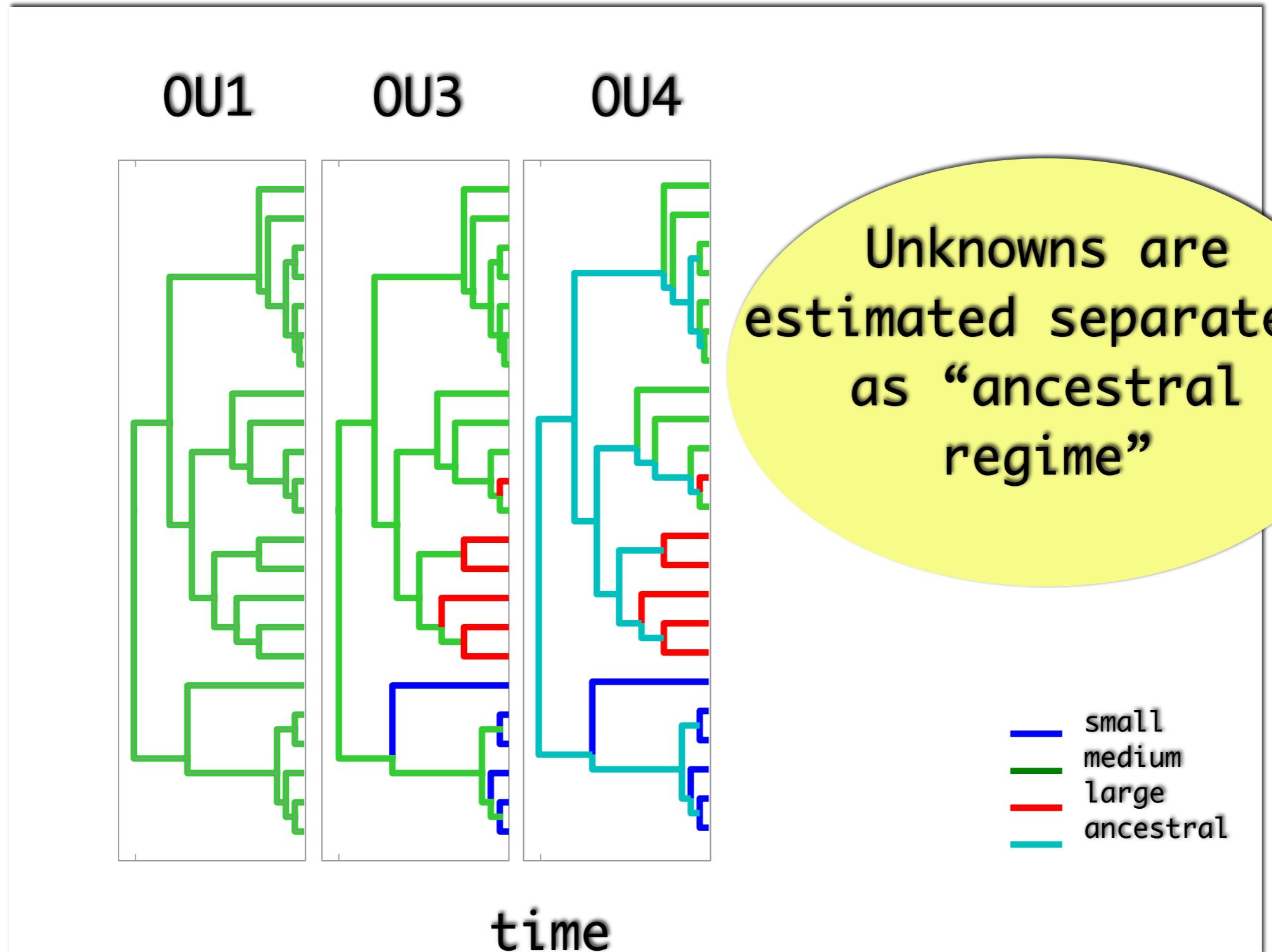
# Alternative Adaptive Regime Models



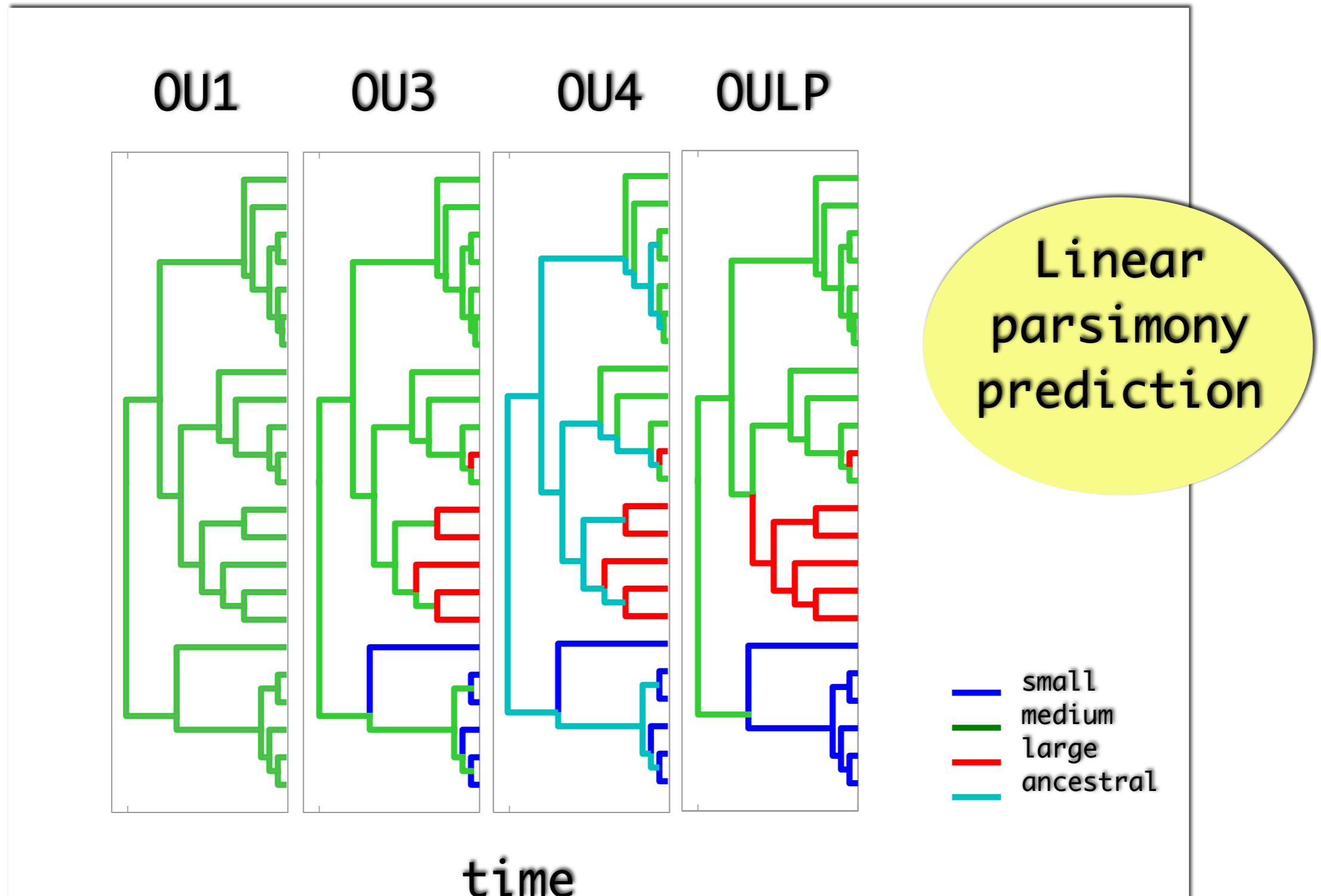
# Alternative Adaptive Regime Models



# 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

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

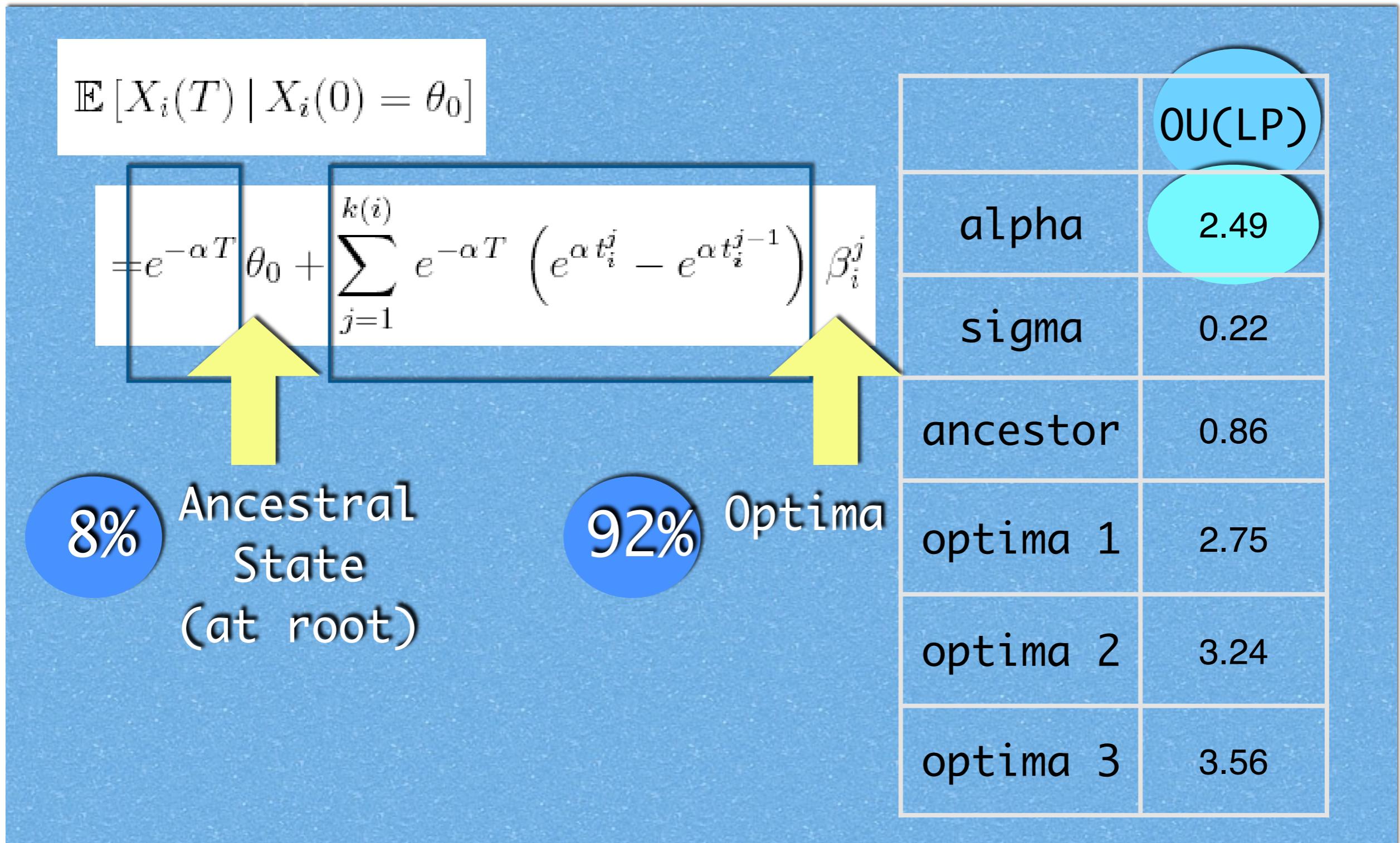
$$= e^{-\alpha T} \theta_0 + \sum_{j=1}^{k(i)} e^{-\alpha T} \left( e^{\alpha t_i^j} - e^{\alpha t_i^{j-1}} \right) \beta_i^j$$

Ancestral  
State  
(at root)

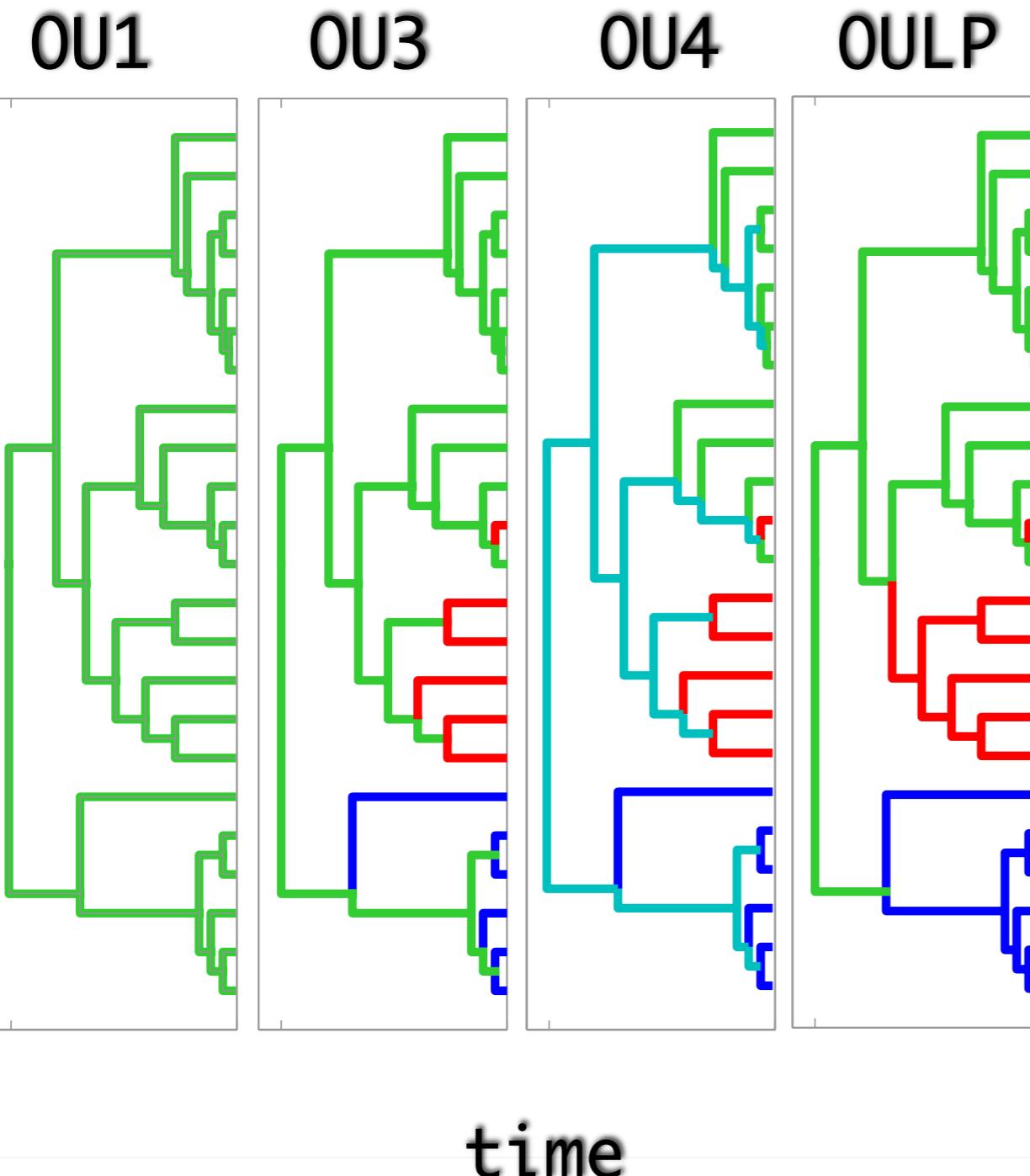
Optima

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

# 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)

# 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.

