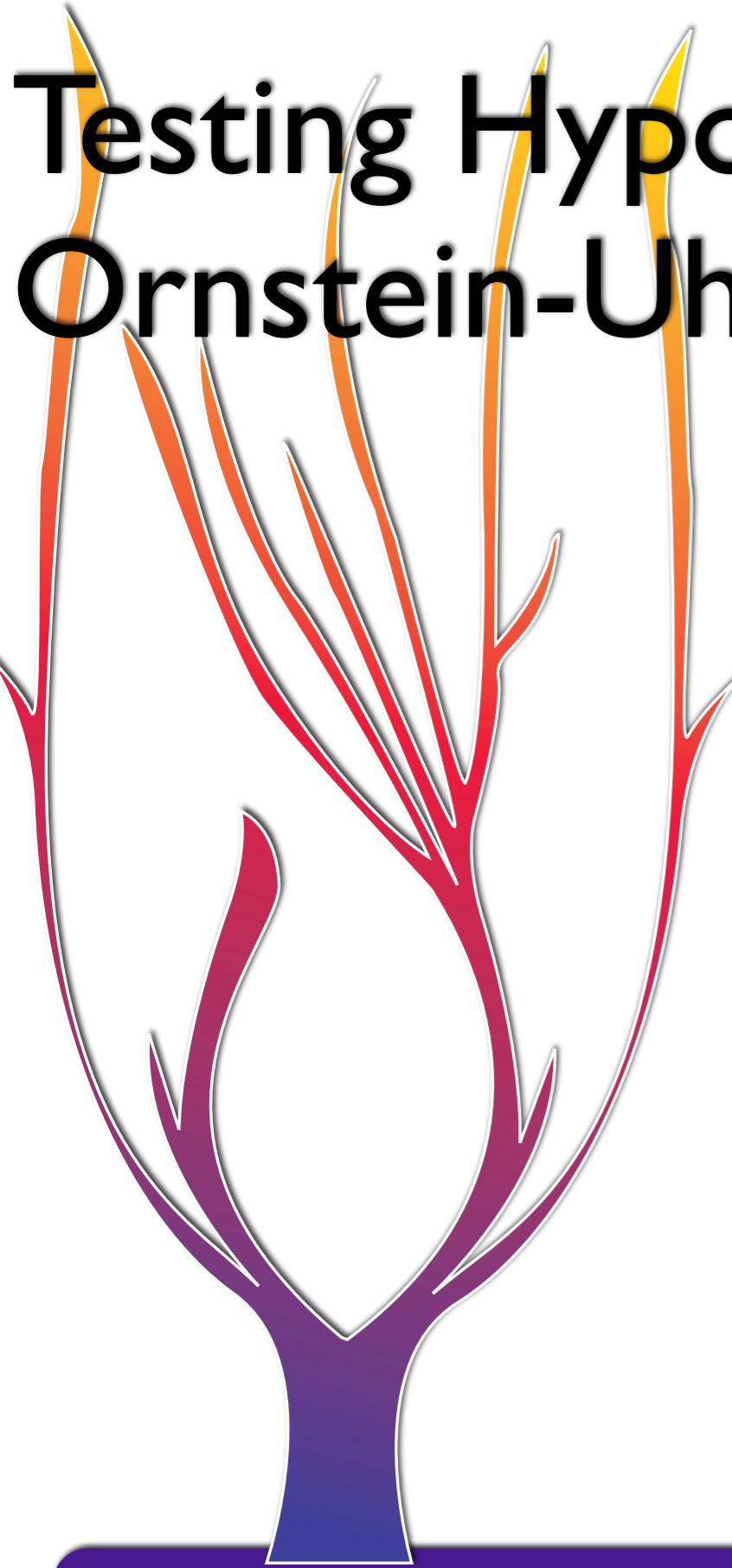


Testing Hypotheses of Adaptation using Ornstein-Uhlenbeck Models (OUCH)

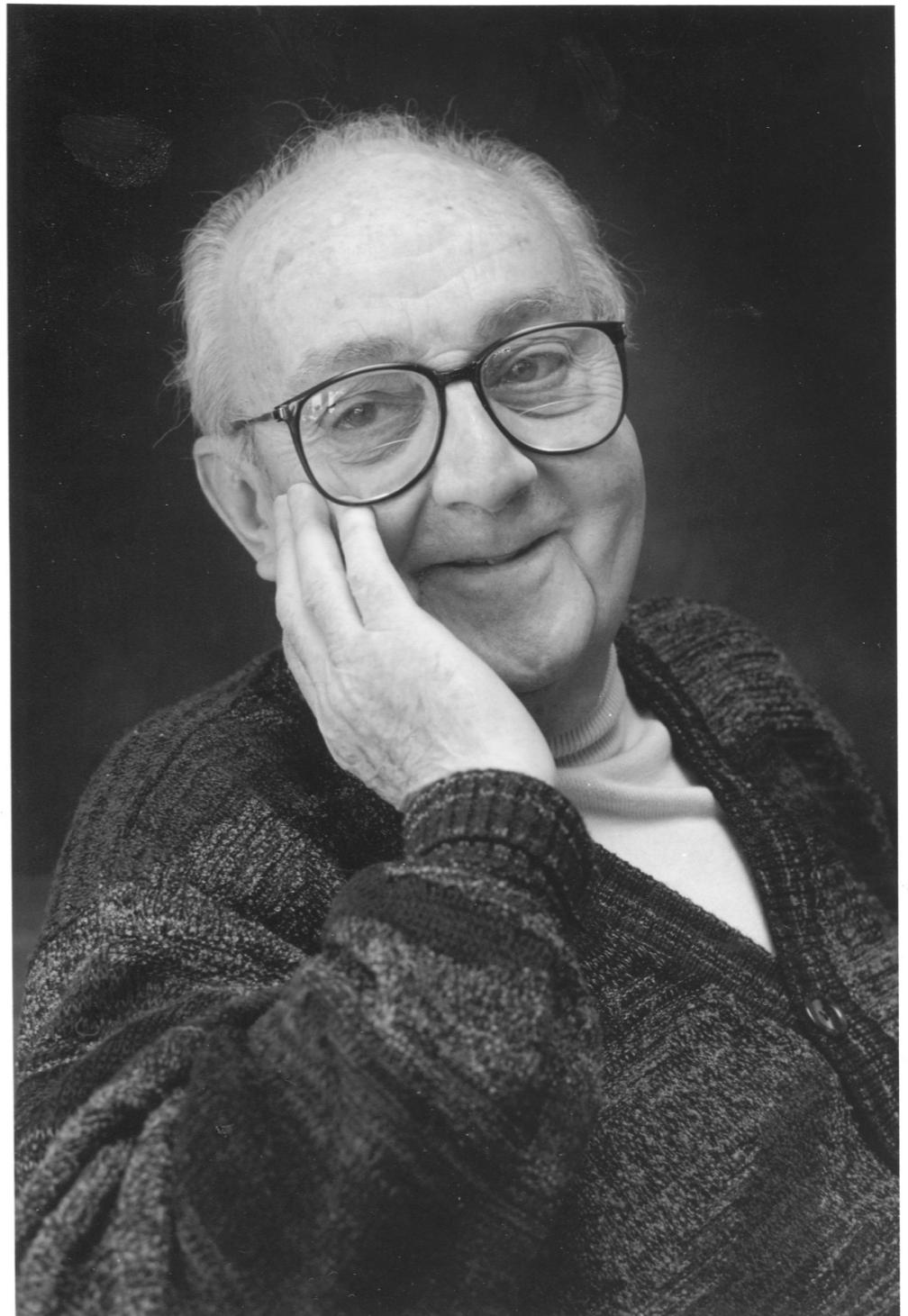
Marguerite Butler

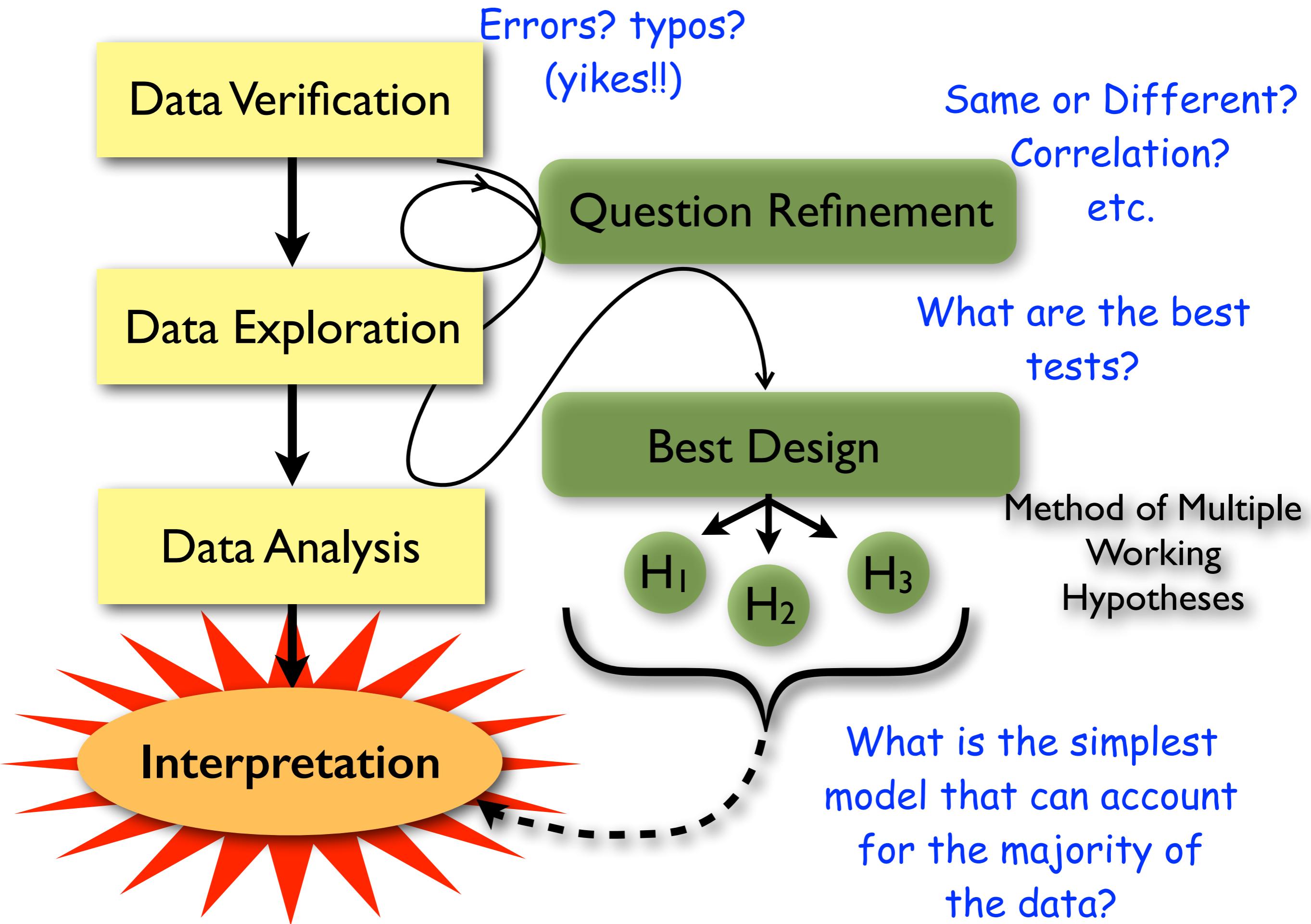
University of Hawaii, Department of Biology



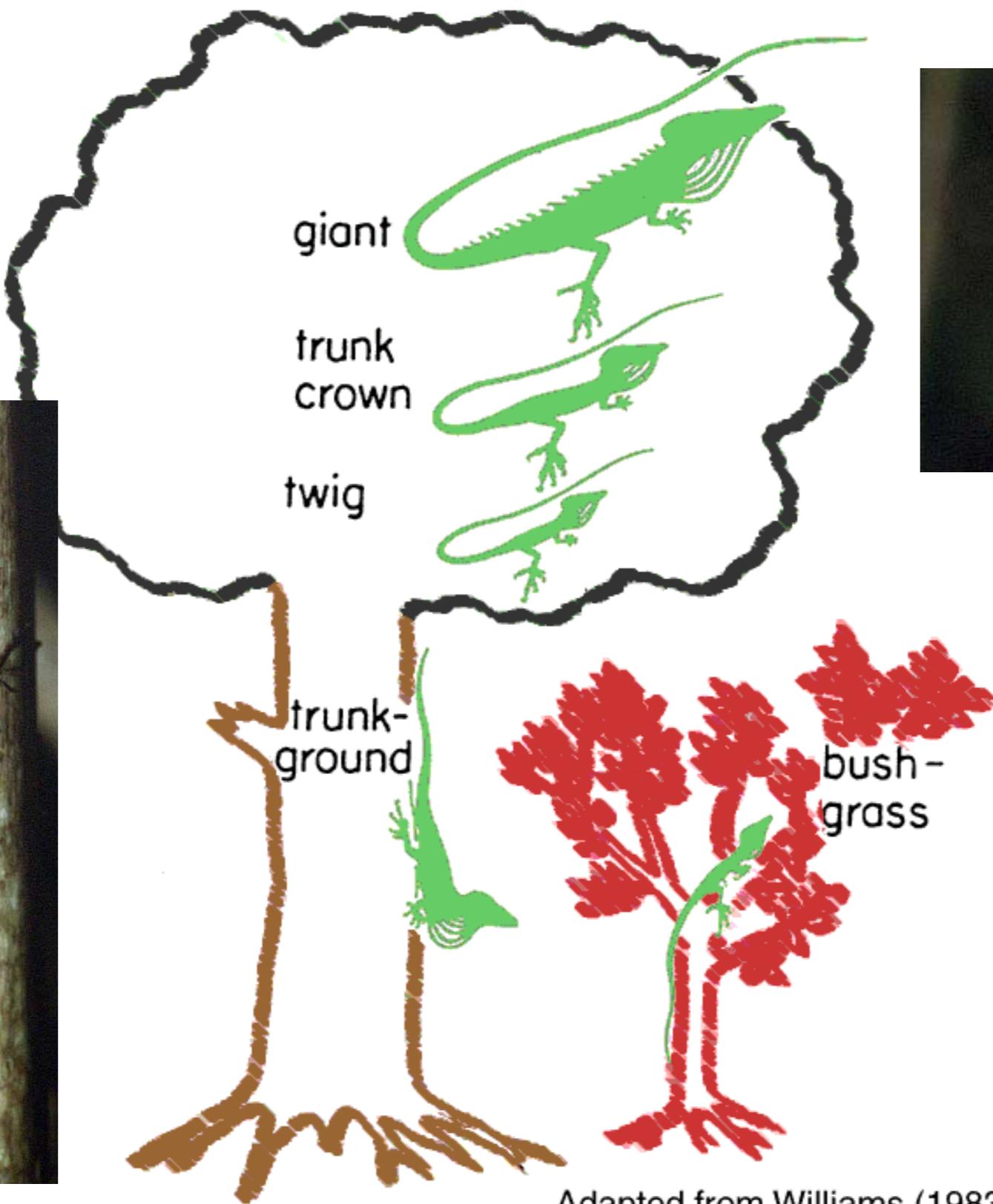
Essentially, all models
are wrong, but some
are useful

- George E. Box





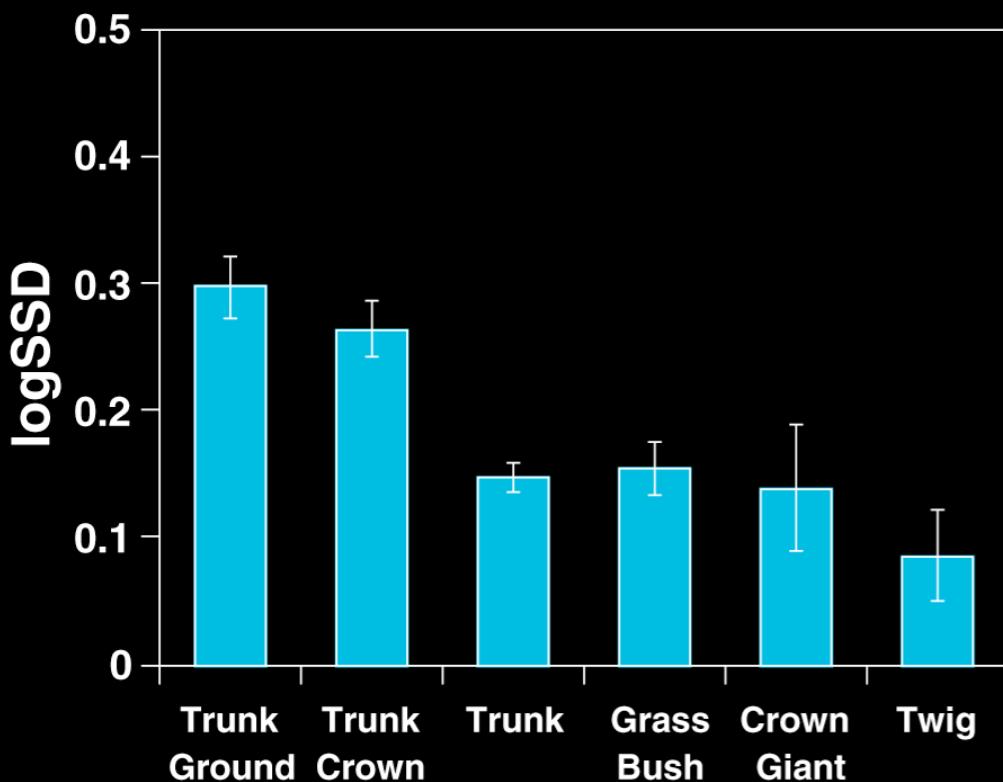
Anolis Lizards and Adaptive Diversification



Adapted from Williams (1983)

“Phylogenetic correction”

Ecomorphs differ in size dimorphism



Robust to phylogeny

Non-Phylogenetic

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

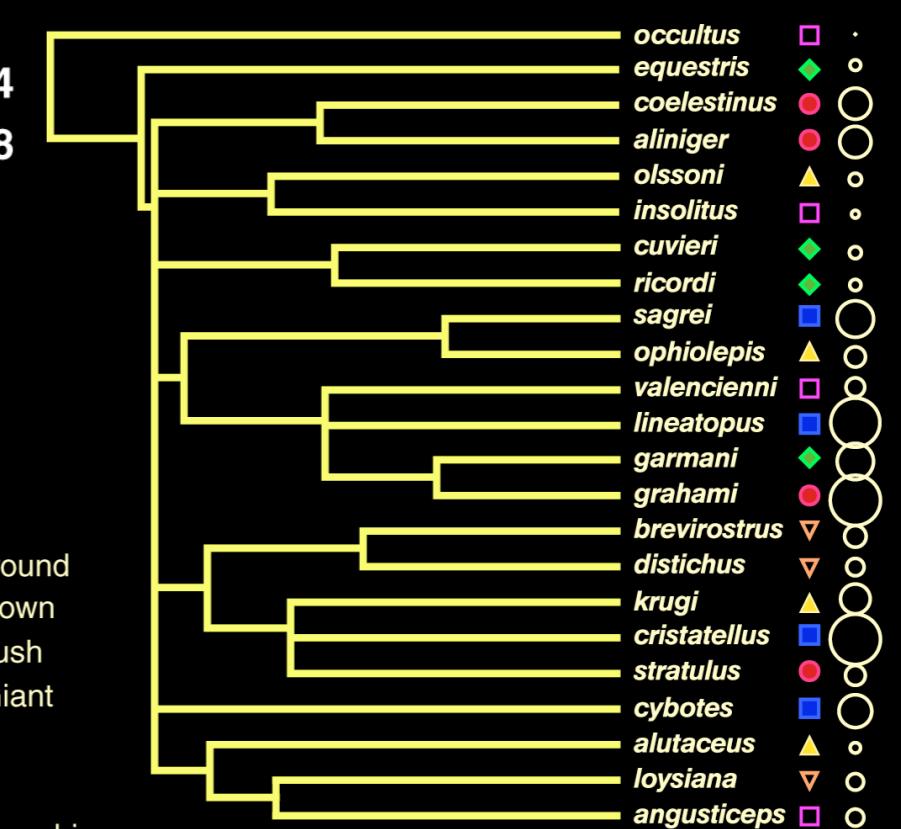
Phylogenetic Simulation (23spp)

Gradual Model

$P<0.004$

Speciation Model

$P<0.008$



But what have we learned
about evolutionary process?

Phylogeny modified from Jackman, et al.

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-

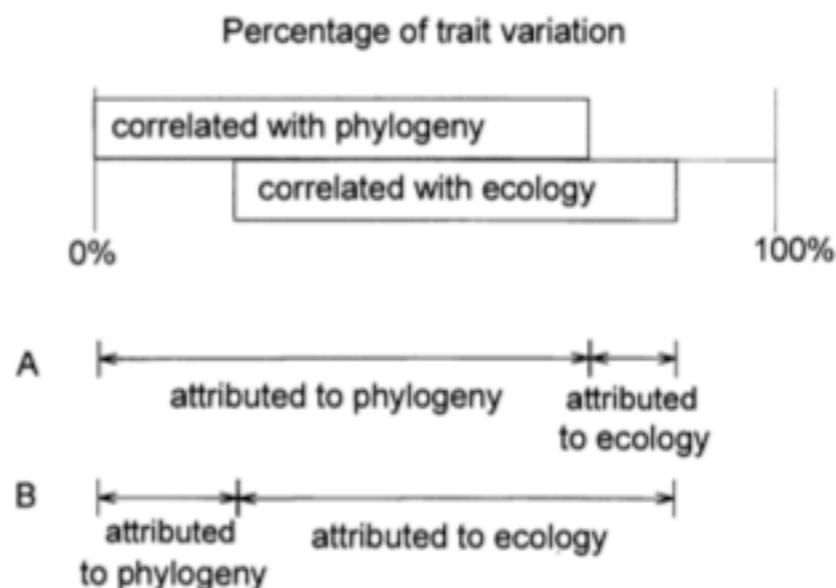


Fig. 1 Schematic illustrating percentages of variation between species in a trait such as seed mass correlated with phylogeny and ecology, and the two extremes (A and B) of the spectrum of possible attributions of variation. Extreme A is phylogenetic correction (PC).

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

Adaptative Evolution & Biodiversity



Hawai'i's Megalagrion

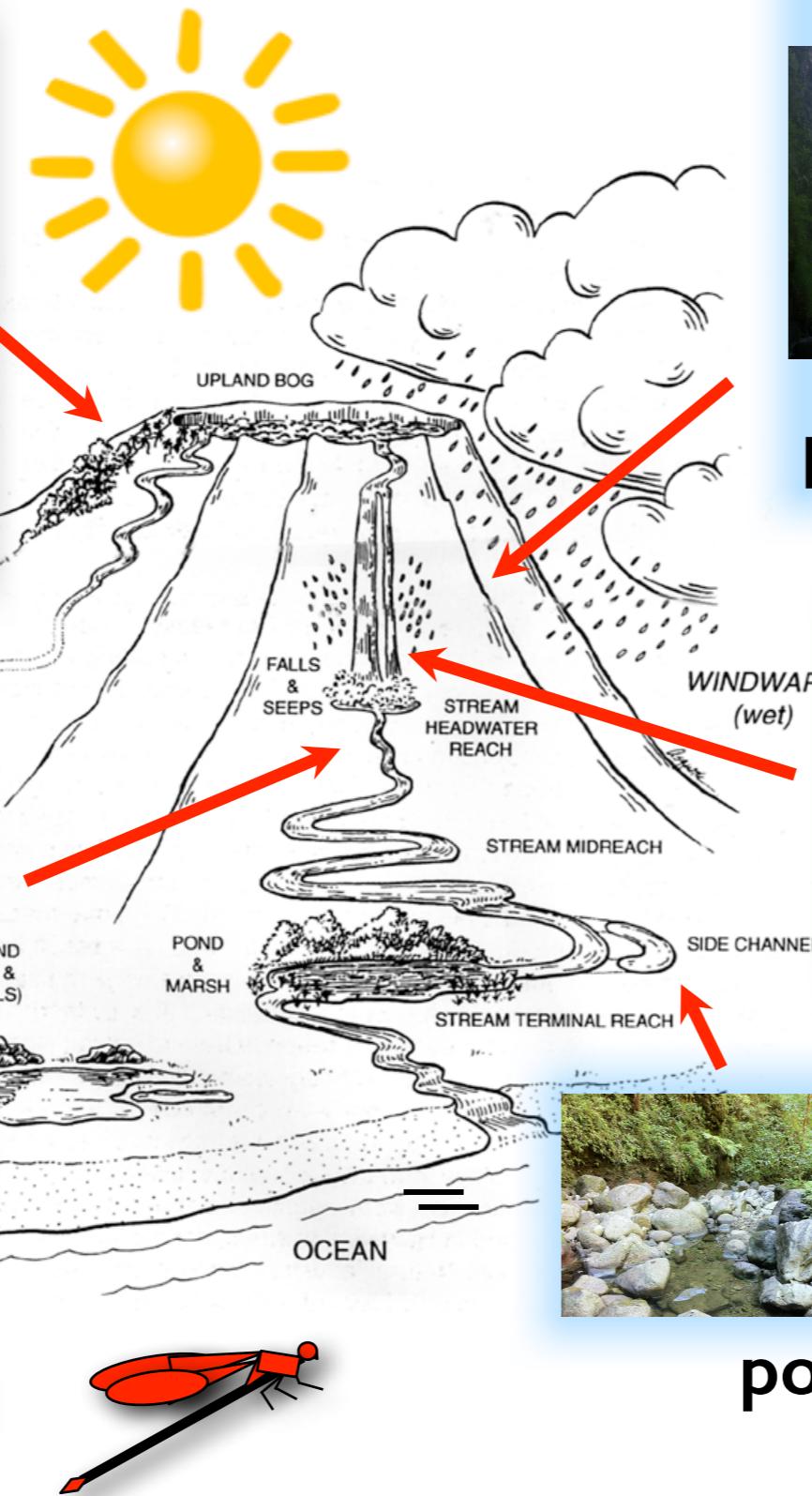
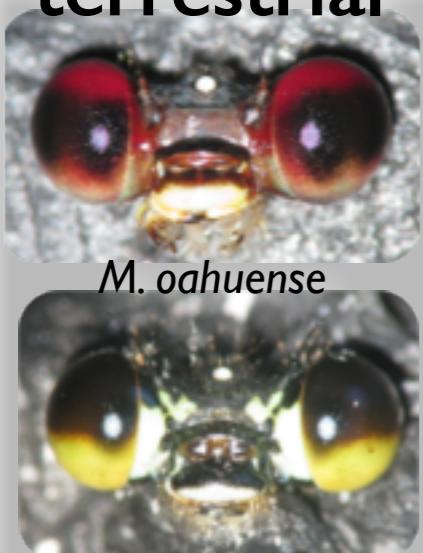


Damselflies



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

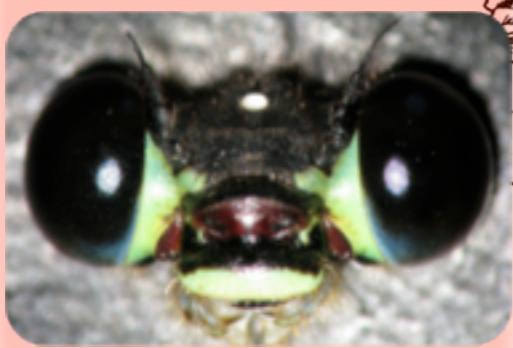
terrestrial



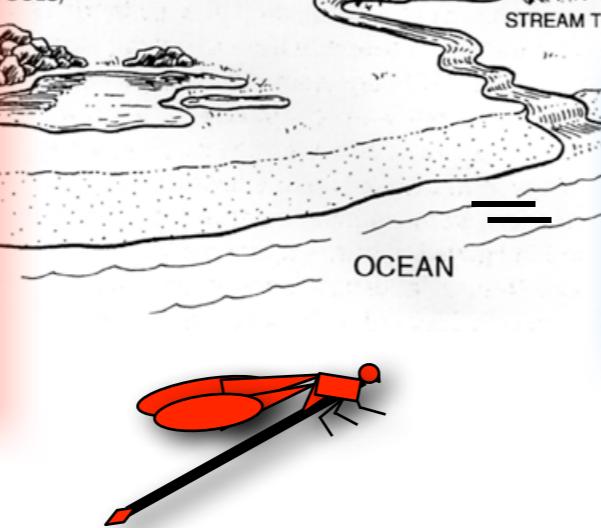
plant breeder



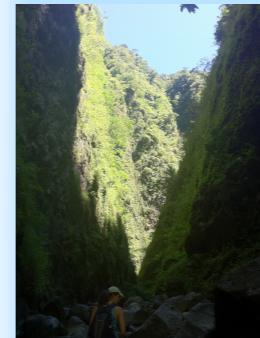
streams



Megalagrion blackburni



pools



M. n. nigrolineatum



M. n. nigrohamatum



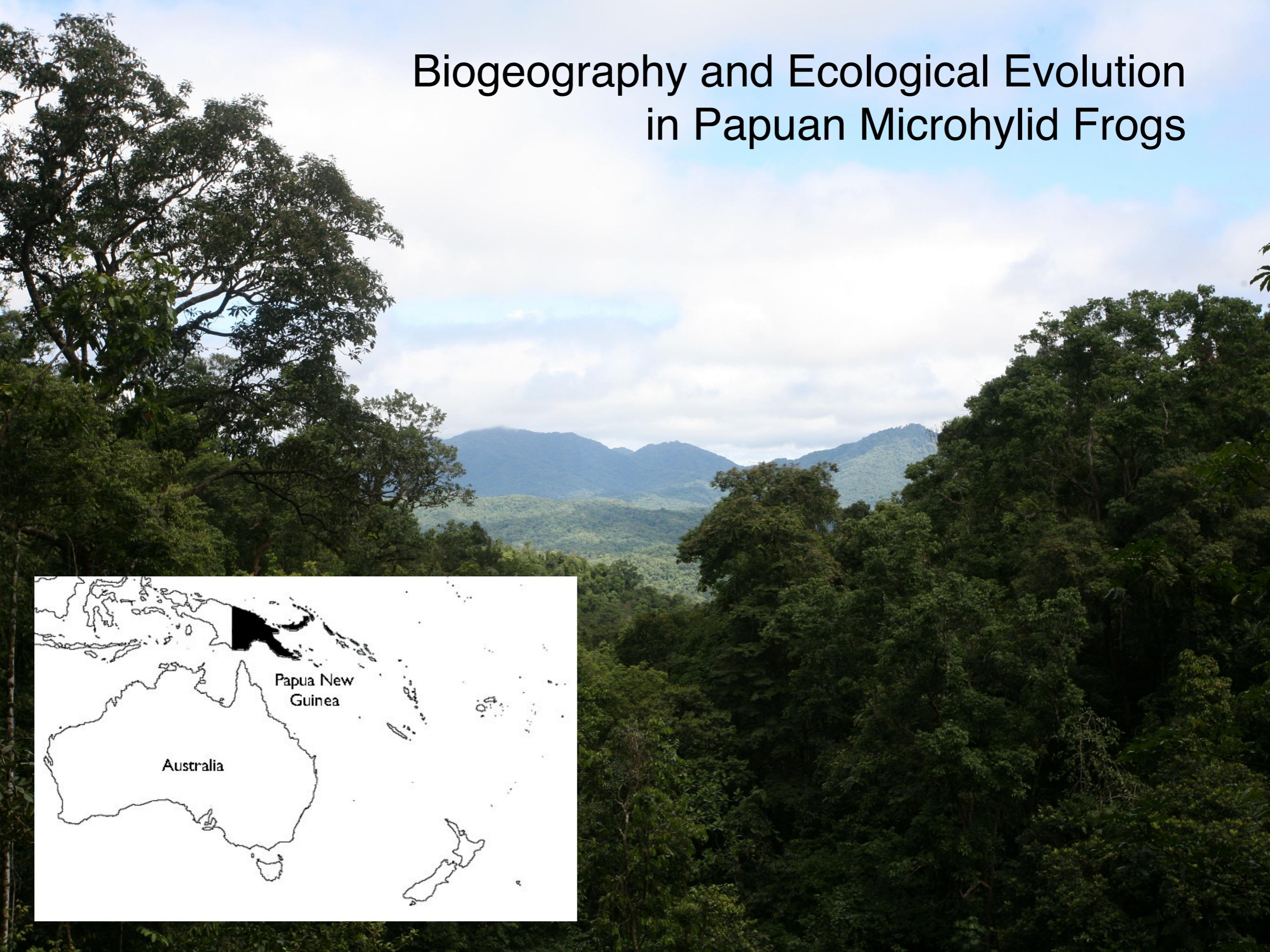
M. vagabundum

seeps



M. leptodemas

Biogeography and Ecological Evolution in Papuan Microhylid Frogs







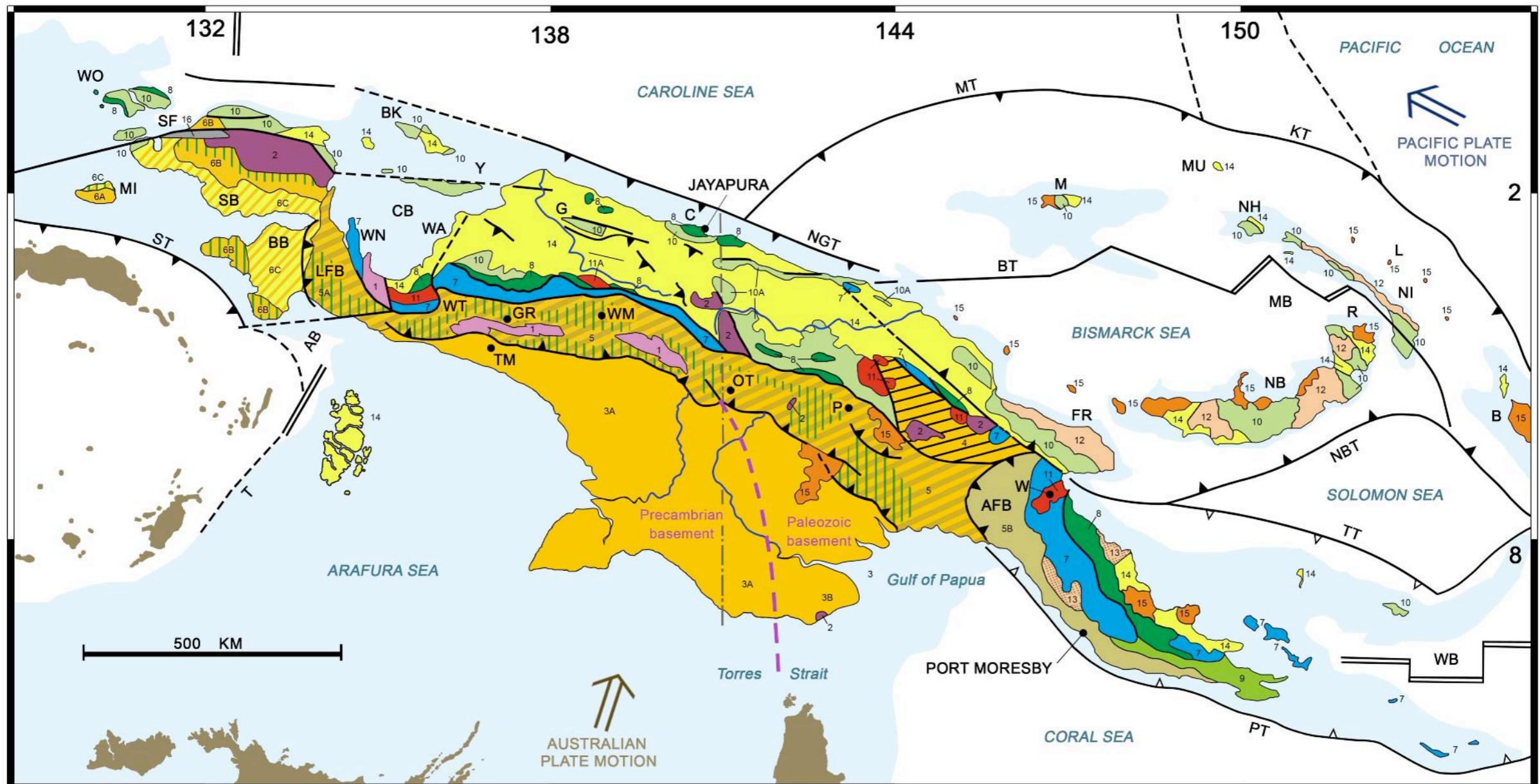
9013



915 13



Papua New Guinea



11A	Oligocene dioritic intrusion and volcanics	7	Mesozoic and Cenozoic metamorphic rocks	5	Papuan Fold Belt
11	Neogene dioritic intrusions	6C	Mesozoic to Quaternary sediments	4	Jimi-Kubor: Mesozoic sediments on Paleozoic basement
10A	Sepik Complex	6B	Mesozoic to middle Miocene sediments	3B	Papuan Basin Mesozoic to Cenozoic sediments
10	Paleogene to mid Miocene arc-type volcanics	6A	Paleozoic to middle Miocene sediments	3A	Papuan Basin Paleozoic to Cenozoic sediments
9	Cretaceous and Mid-Eocene ocean floor basalts	5B	Aure Fold Belt (accretionary prism in part)	2	Paleozoic basement
8	Ophiolite	5A	Lengguru Fold Belt	1	Late Proterozoic and Paleozoic sediments
16	Tectonite - Sorong fault zone				
15	Quaternary volcanics				
14	Neogene to Quaternary sediments				
13	Miocene volcanics and sediments (mainland)				
12	Miocene limestone and sediments (NI, NB, FR)				

Ancestral Character State Reconstruction

Uncertainty

Biogeography and Ecological Evolution in Papuan Microhylid Frogs

But you can still find interesting results!

You just have to check.

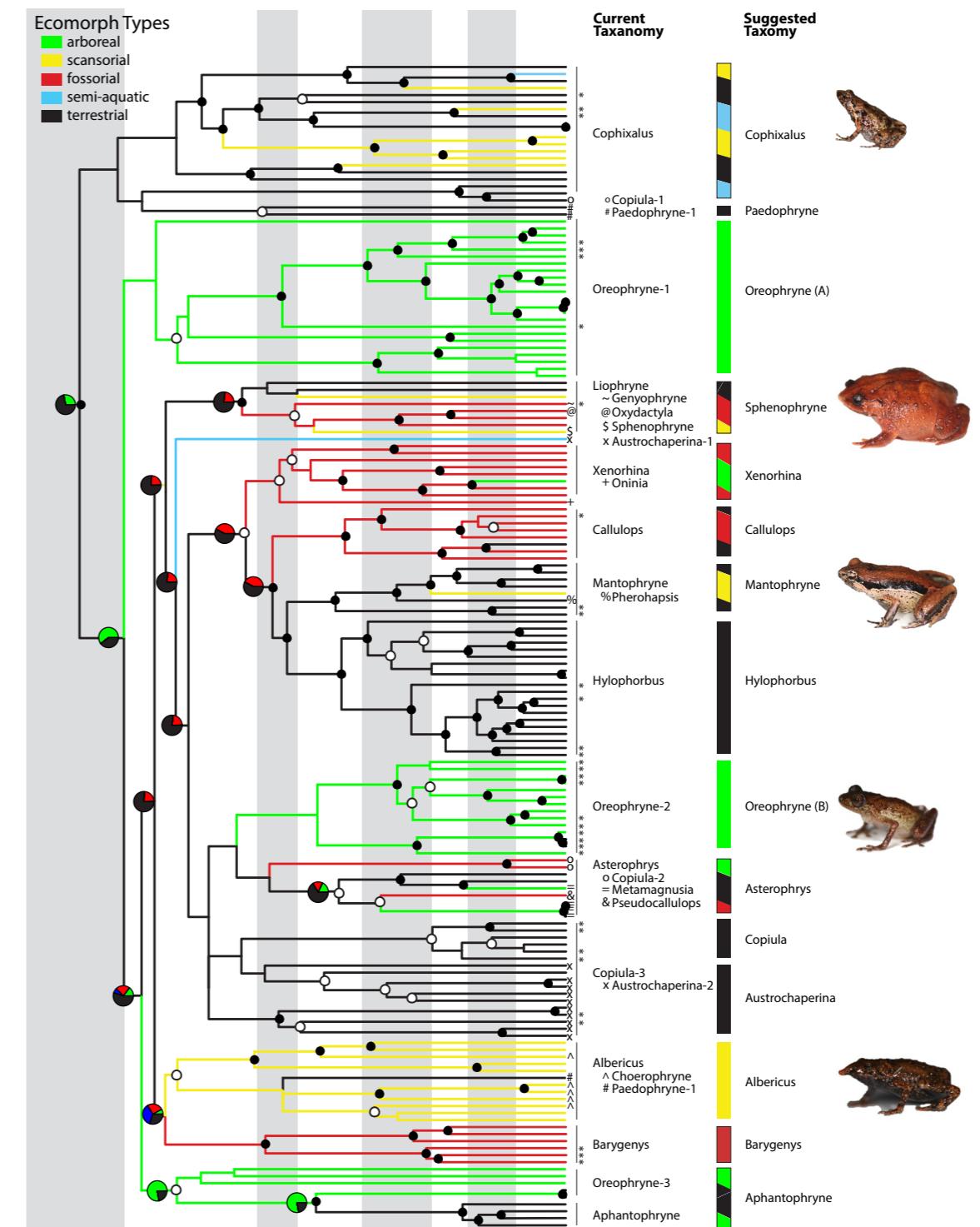
Ancestral microhylid was terrestrial

Ecomorph diversity evolved early ~20MYBP coincident with the formation of the central mountains

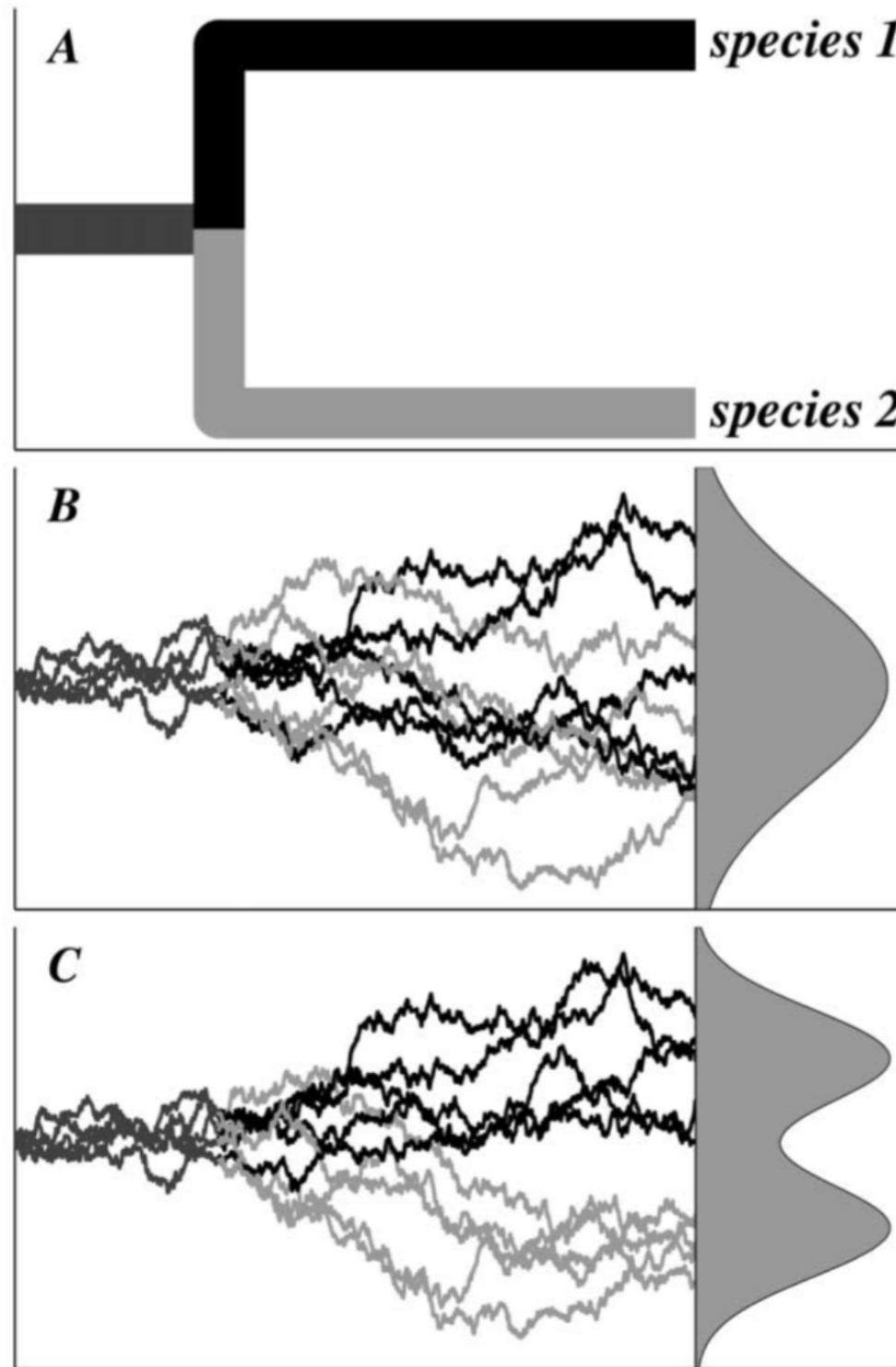
Rampant speciation and more ecomorph transitions followed



Julio Rivera



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

What about the Biology?

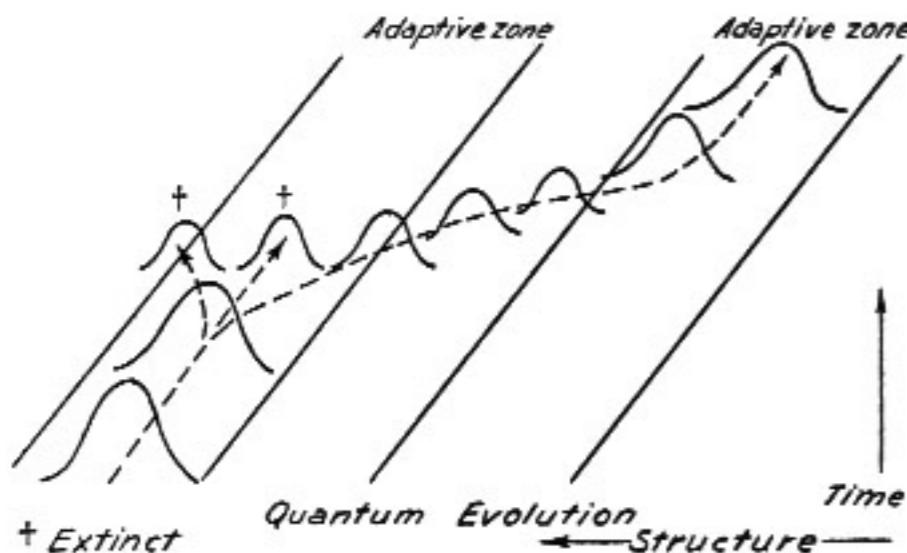
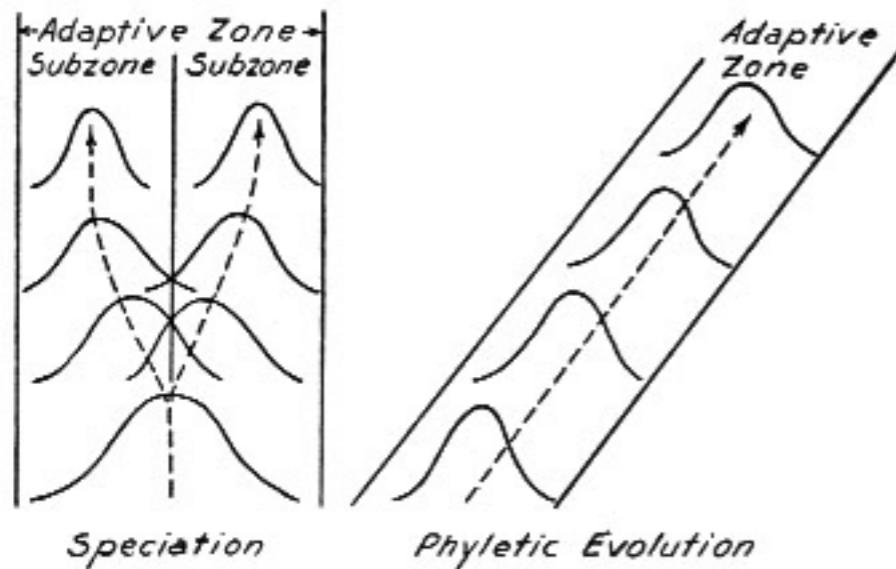
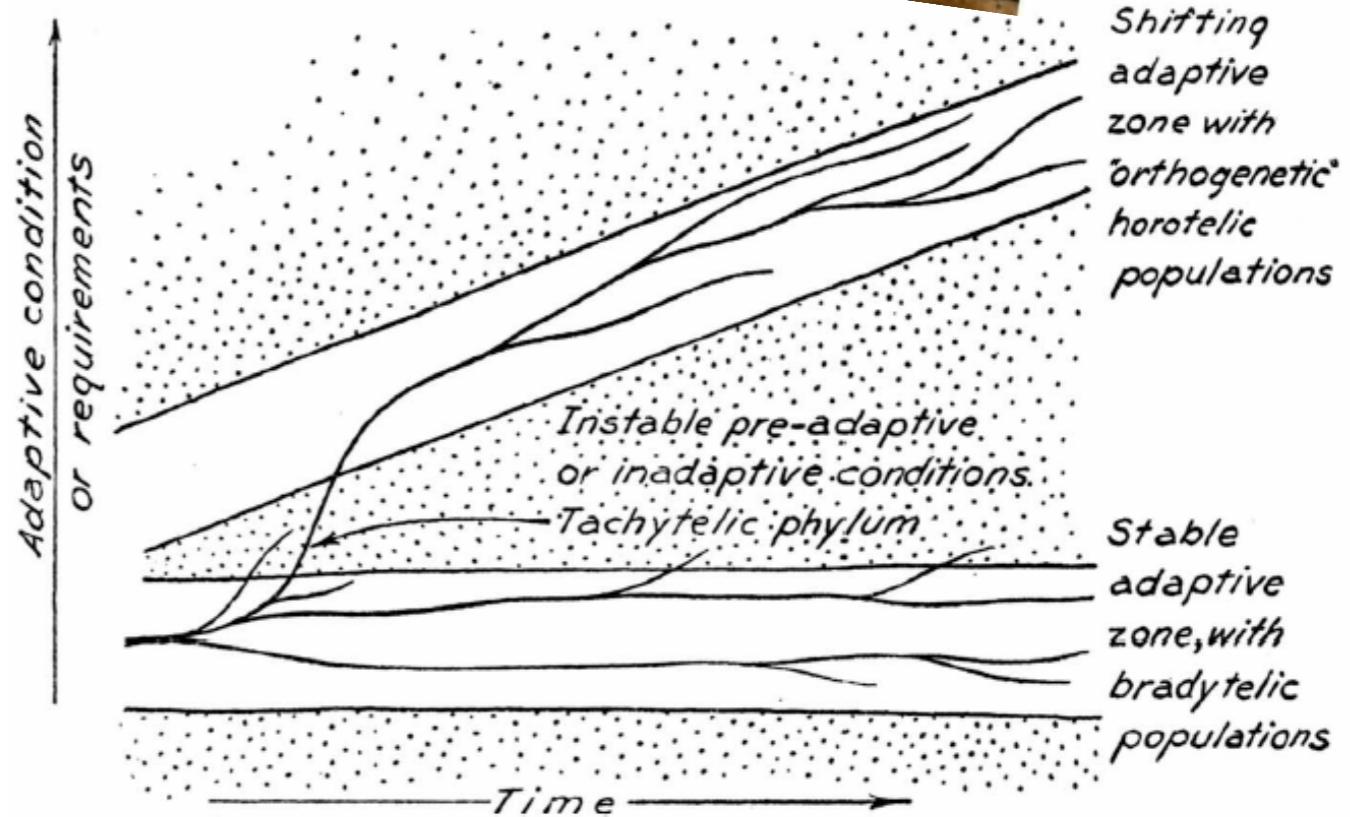
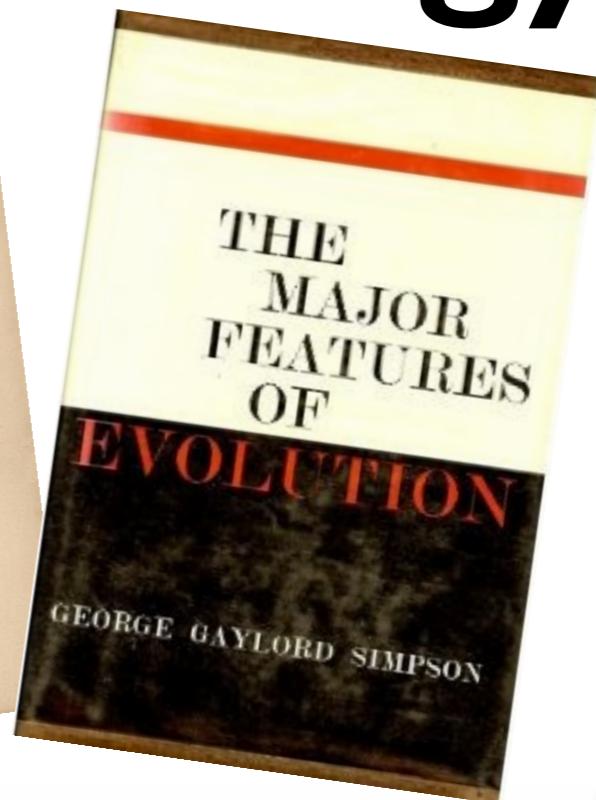
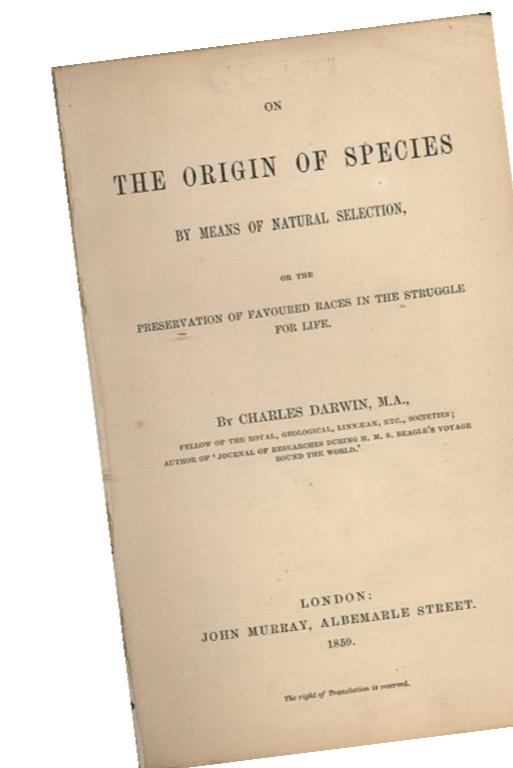
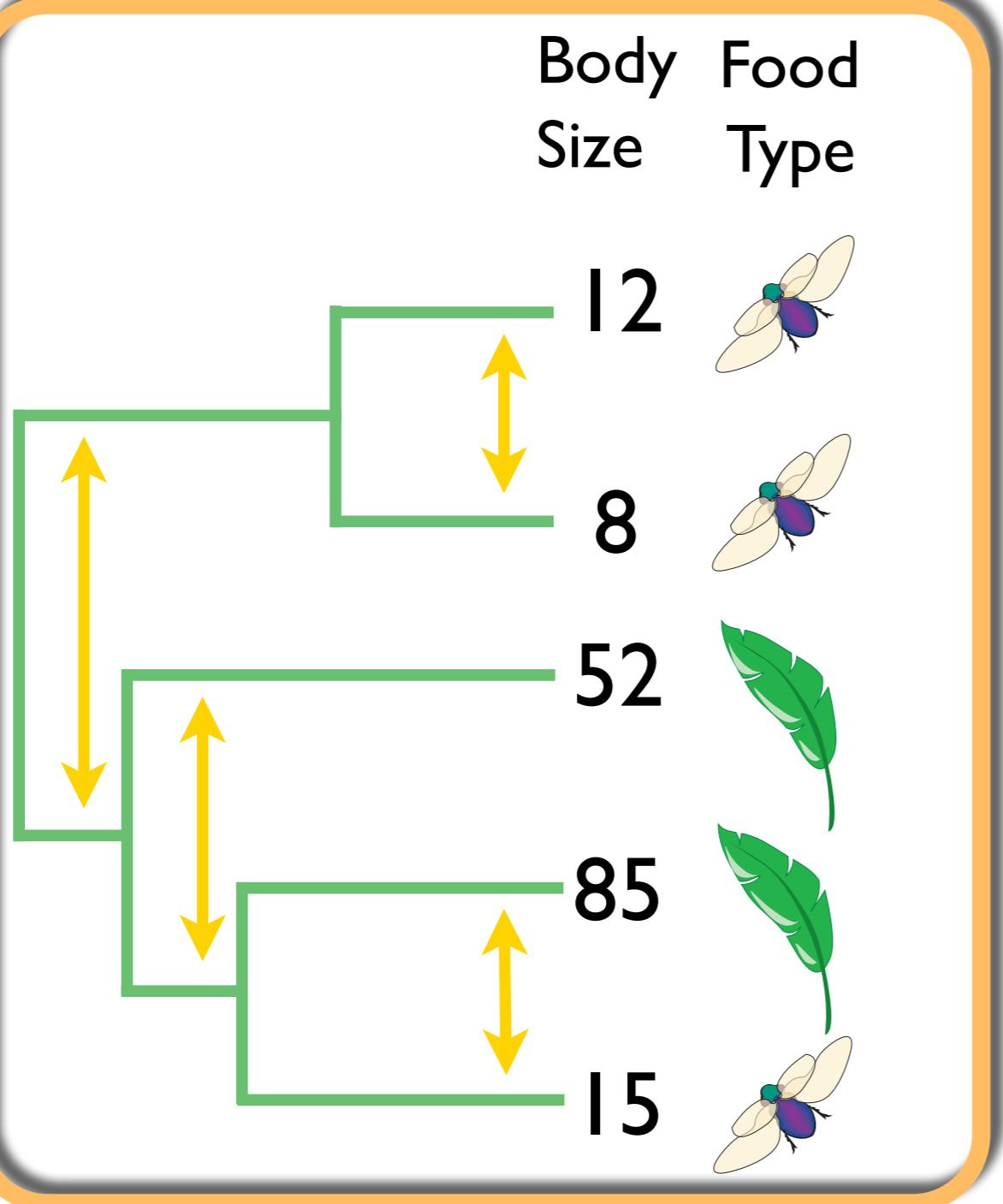


FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.



Simpson (1953) The major features of evolution



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)*

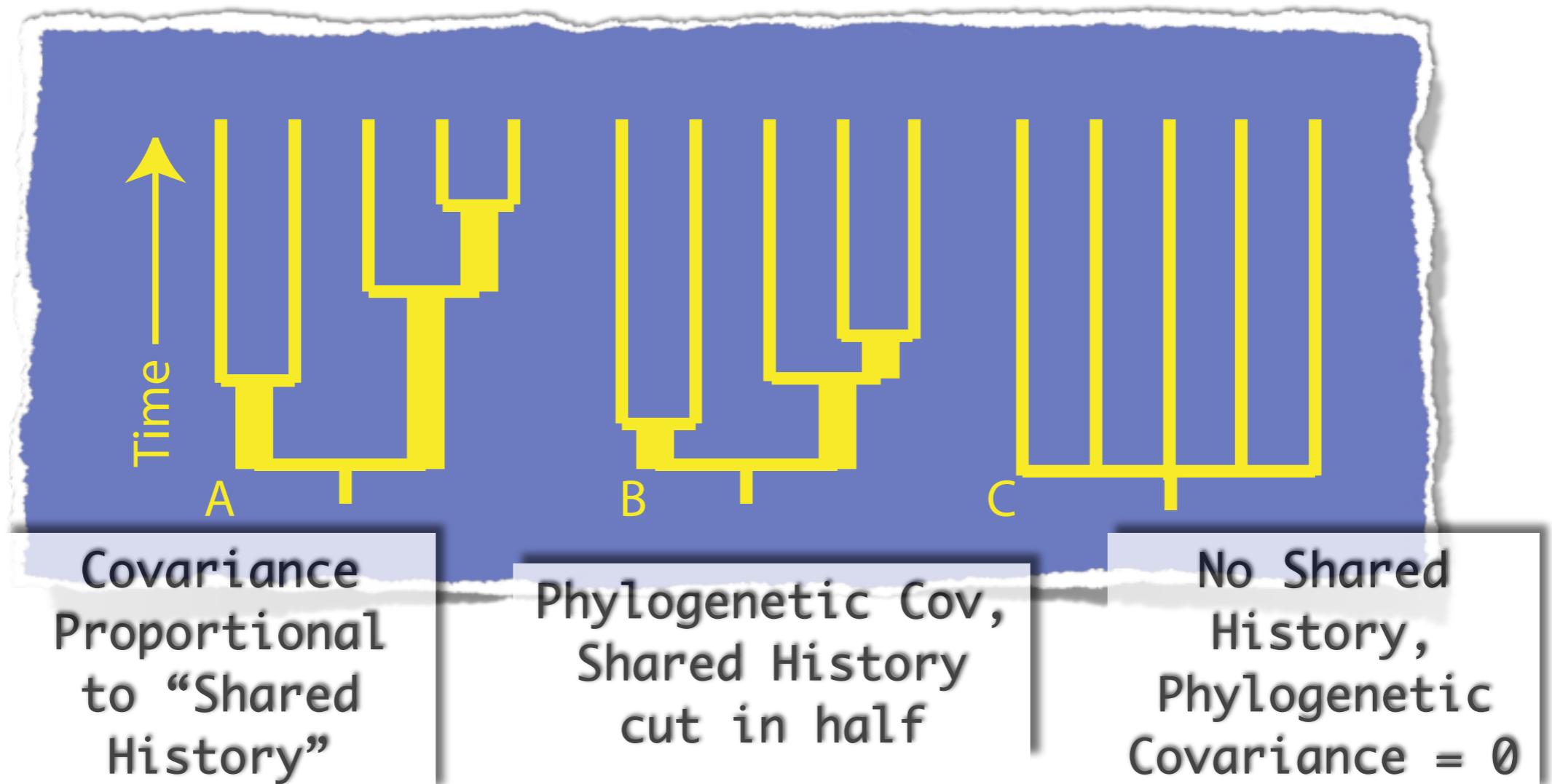
All comparative analyses are constructed of 3 pieces

- 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

There is another option...

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 !

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**

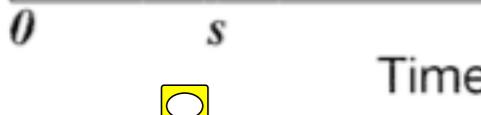
**How different are BM
and OU models?**

A

species 1

Nuts and Bolts: 2 species example

B

*species 1**species 2*

Time



Expected Value
(mean at T)

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

Variance

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

Hansen (1997), Butler & King (2004)

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

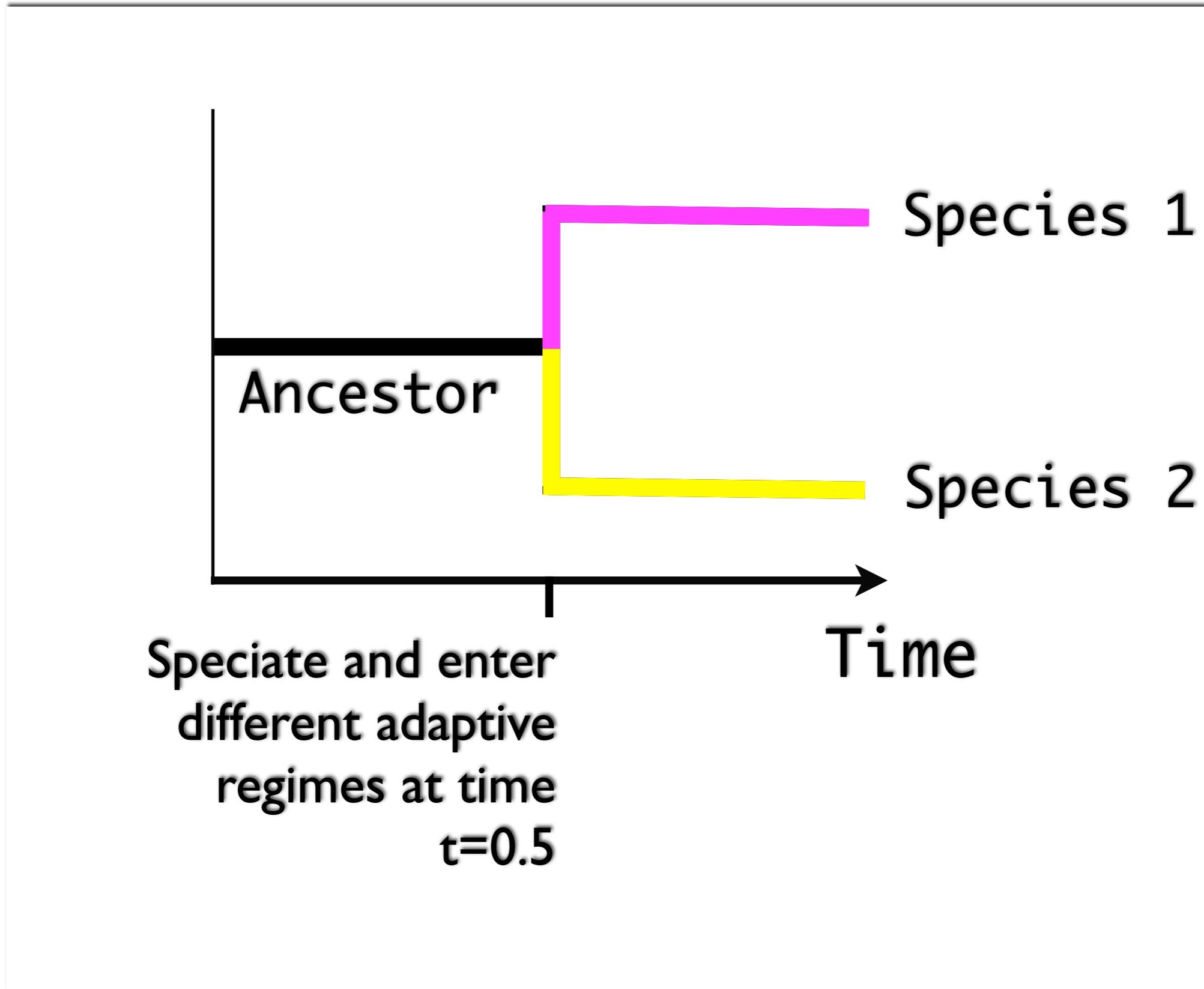
OU

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

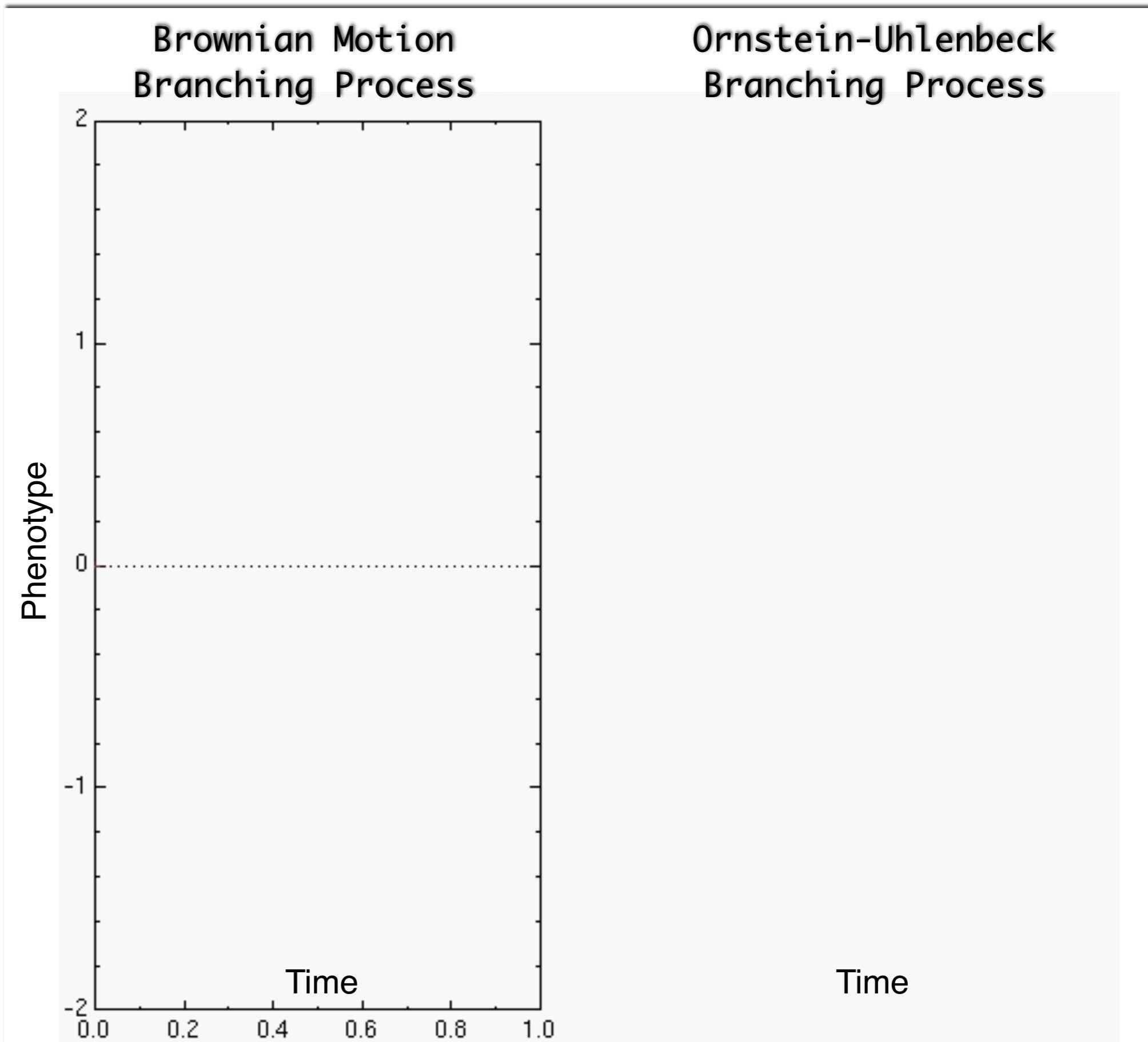
$$E[\mathbf{X}(T)] = \mathbf{W}\boldsymbol{\theta}$$

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

BM and OU models make different predictions

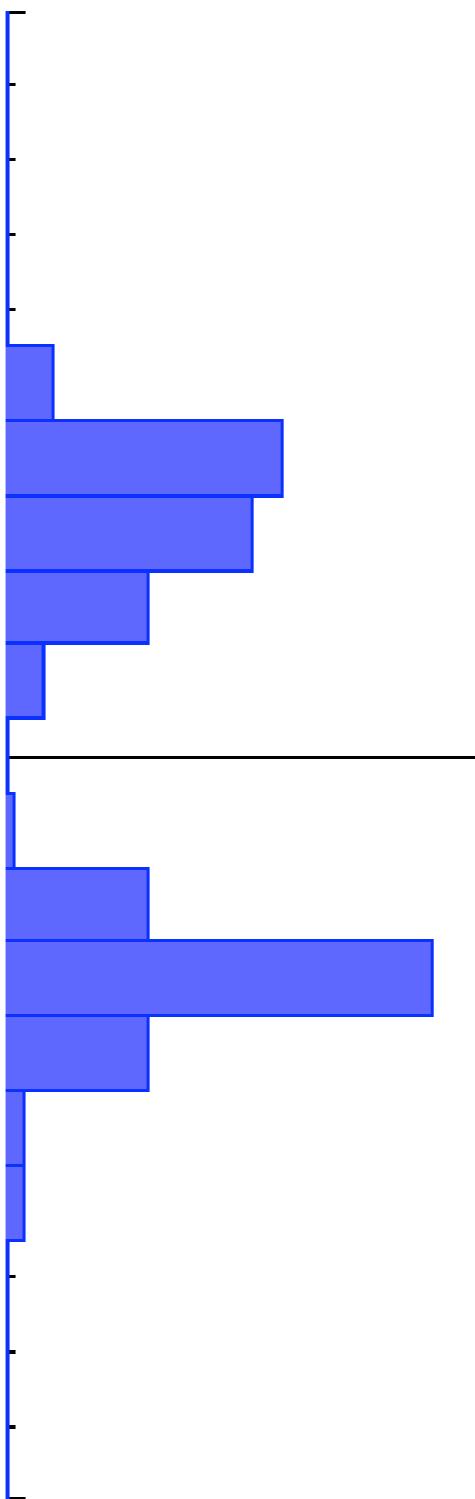
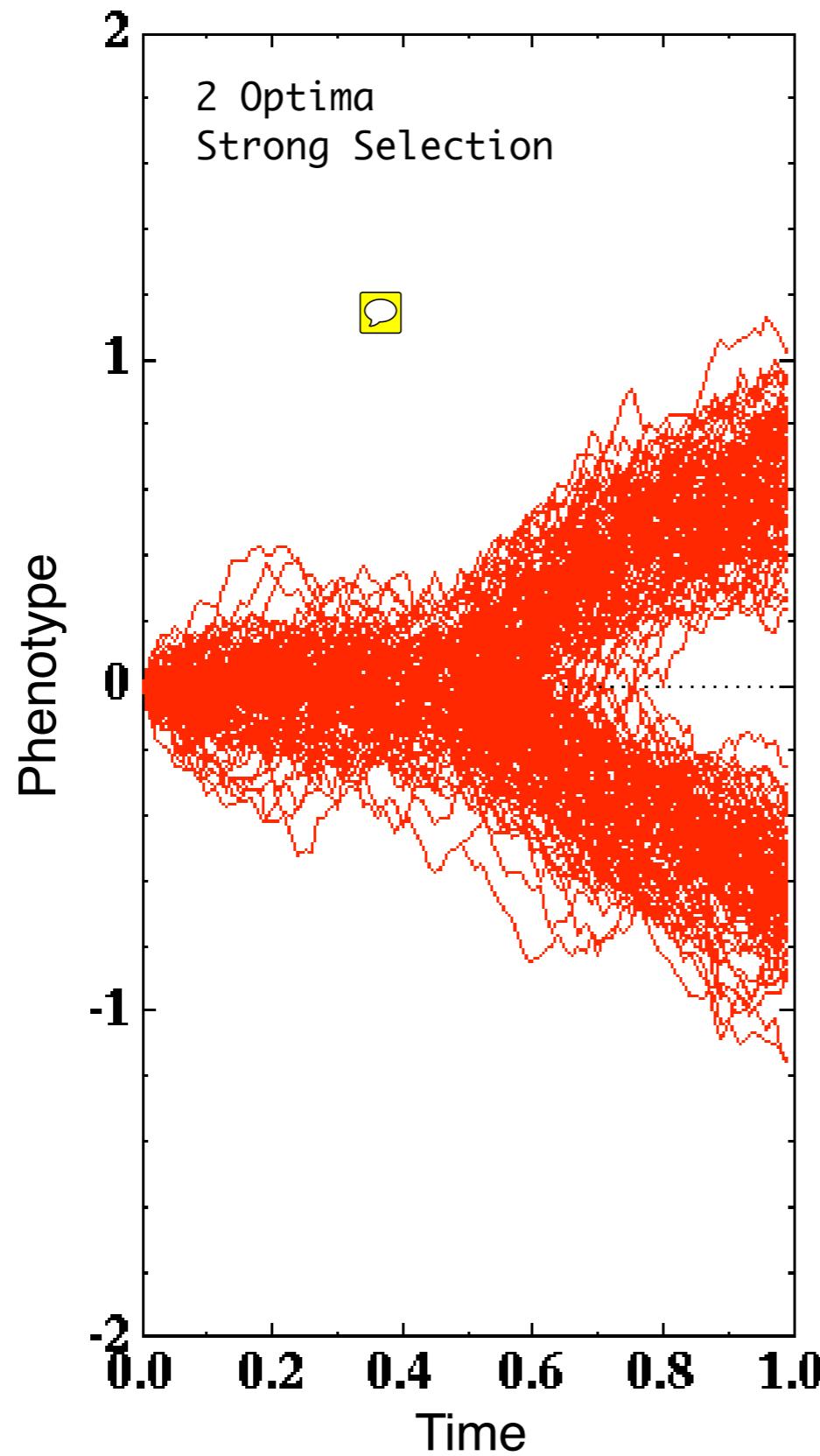


BM and OU models make different predictions



OU Branching Process

Phenotypic Distribution



What about the Biology?

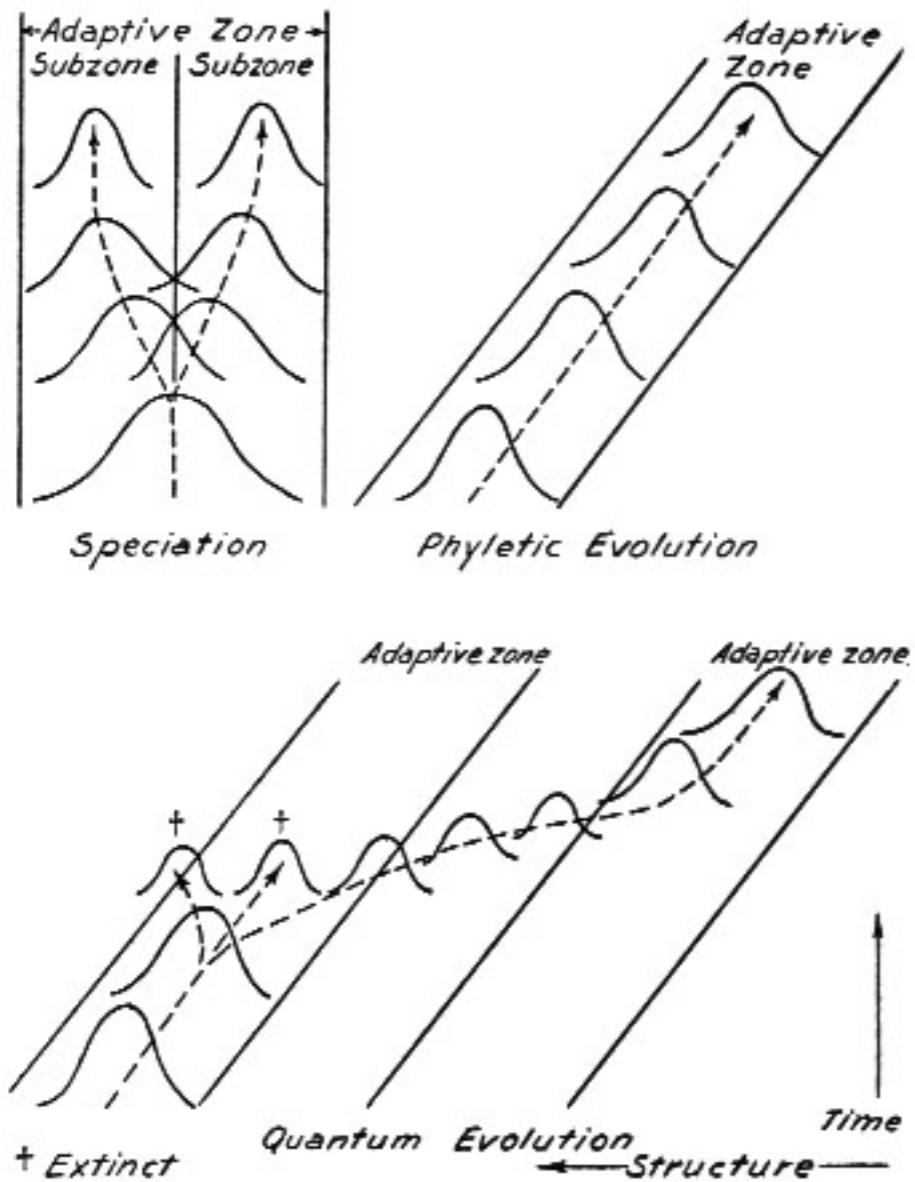
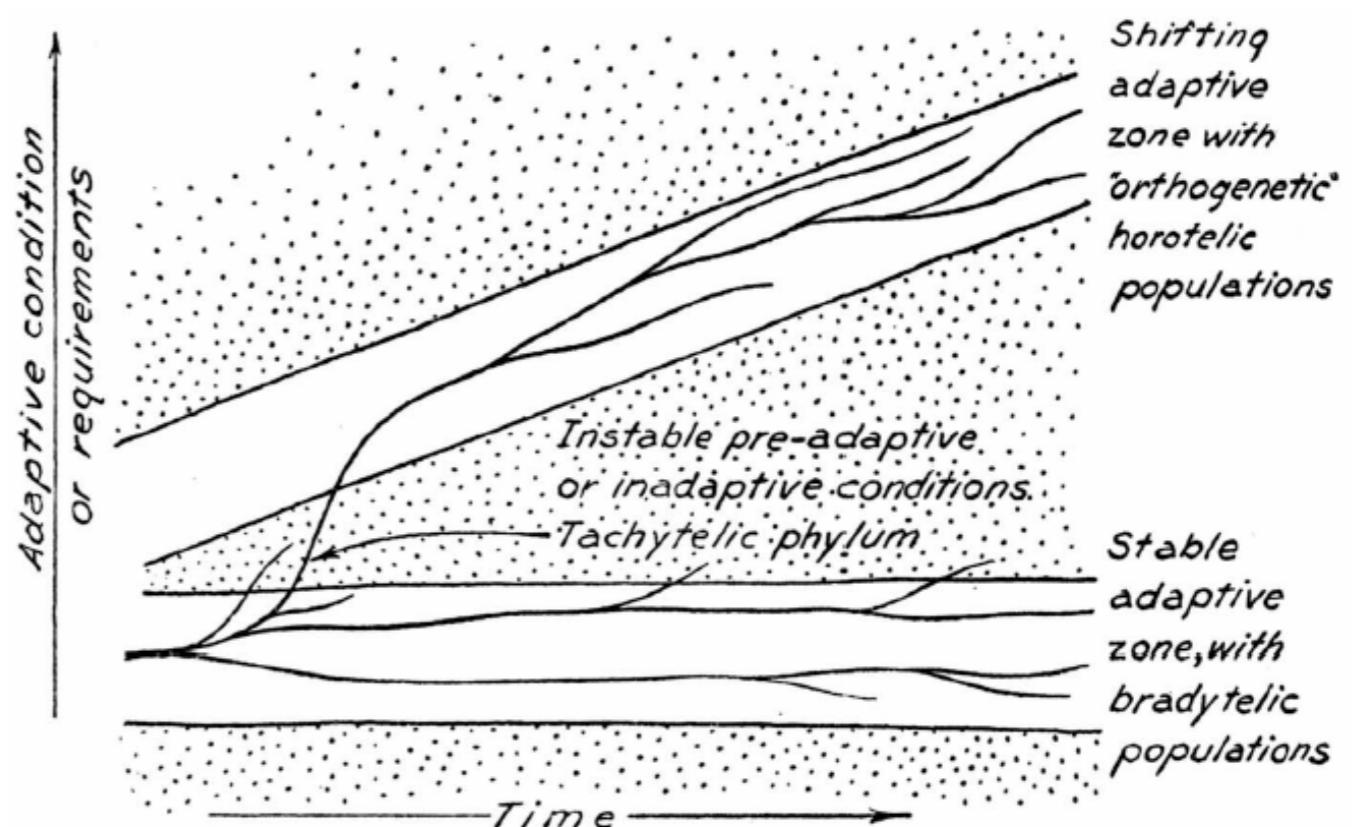


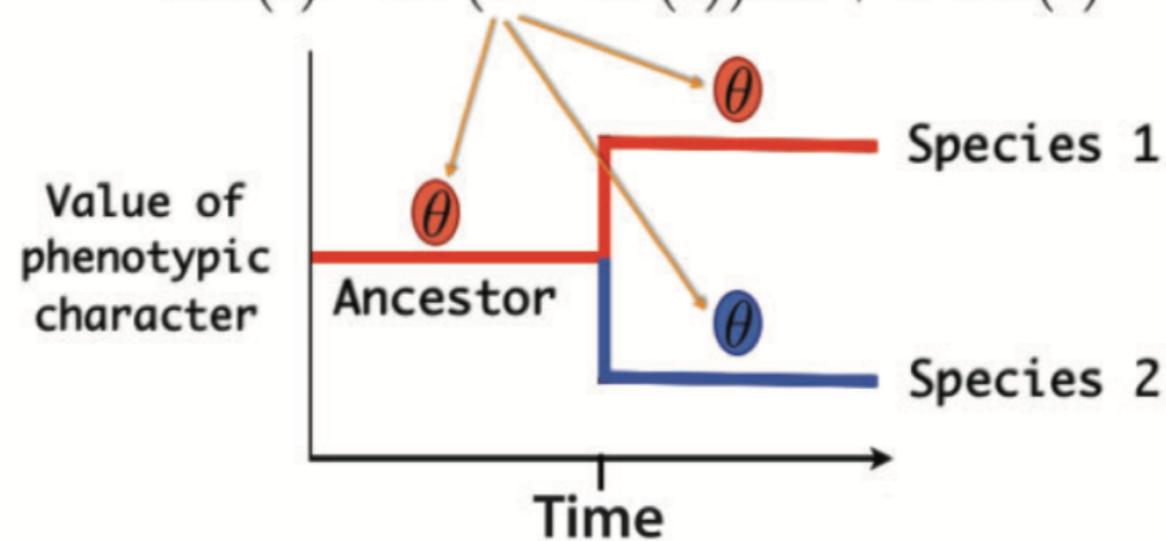
FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.



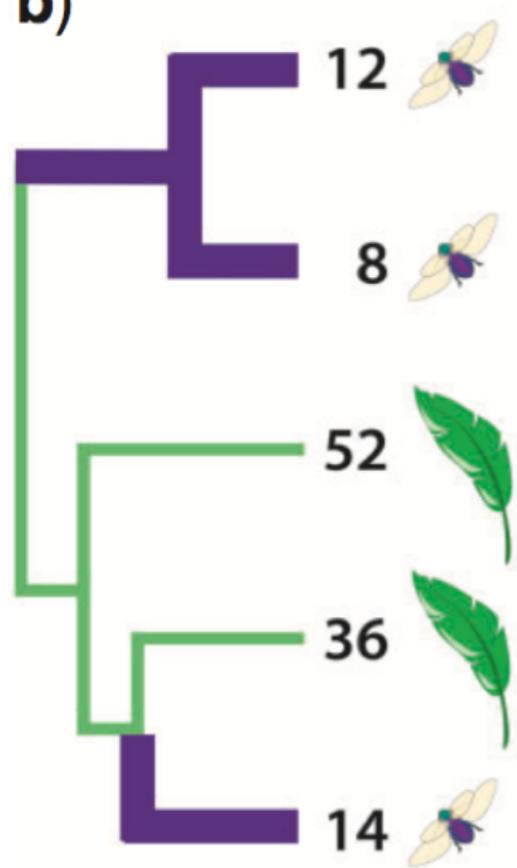
Simpson (1953) The major features of evolution



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



b)



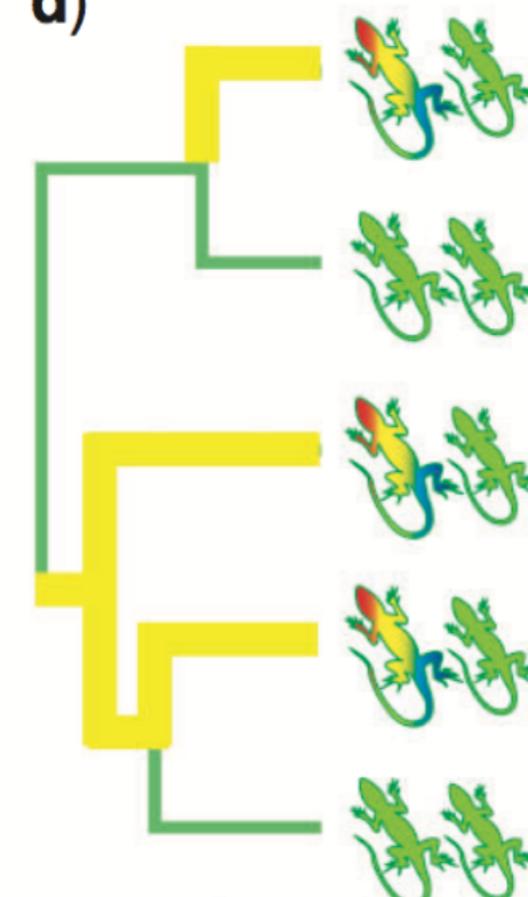
Niche
Partitioning

c)



Habitat
Specialization

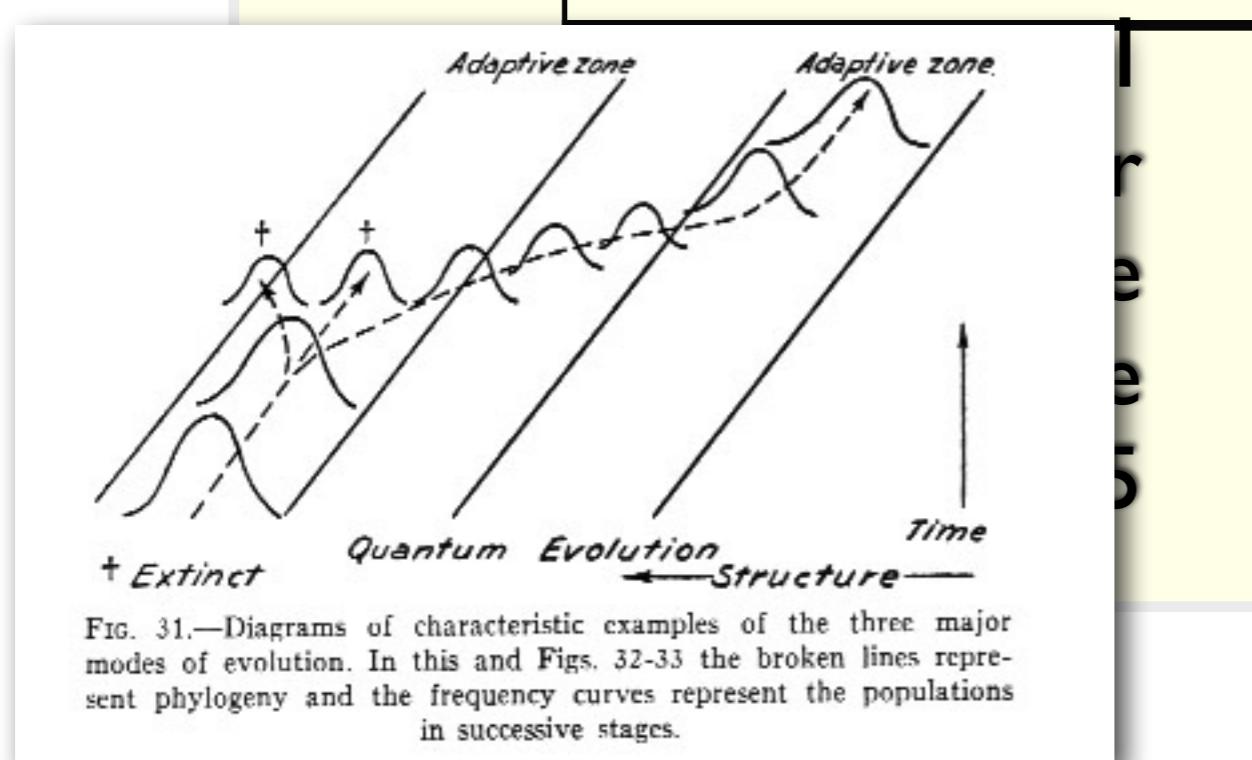
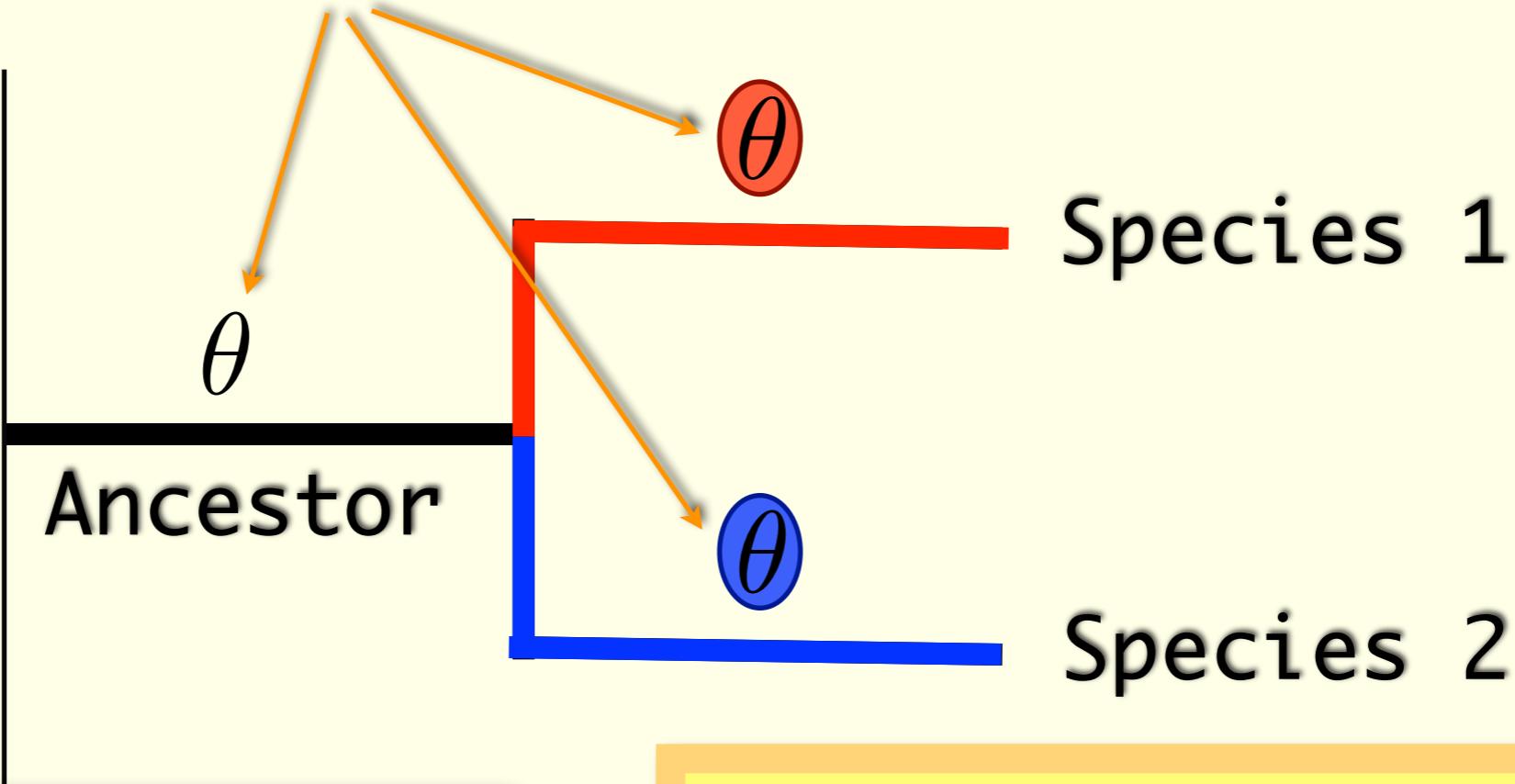
d)



Sexual
Selection

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

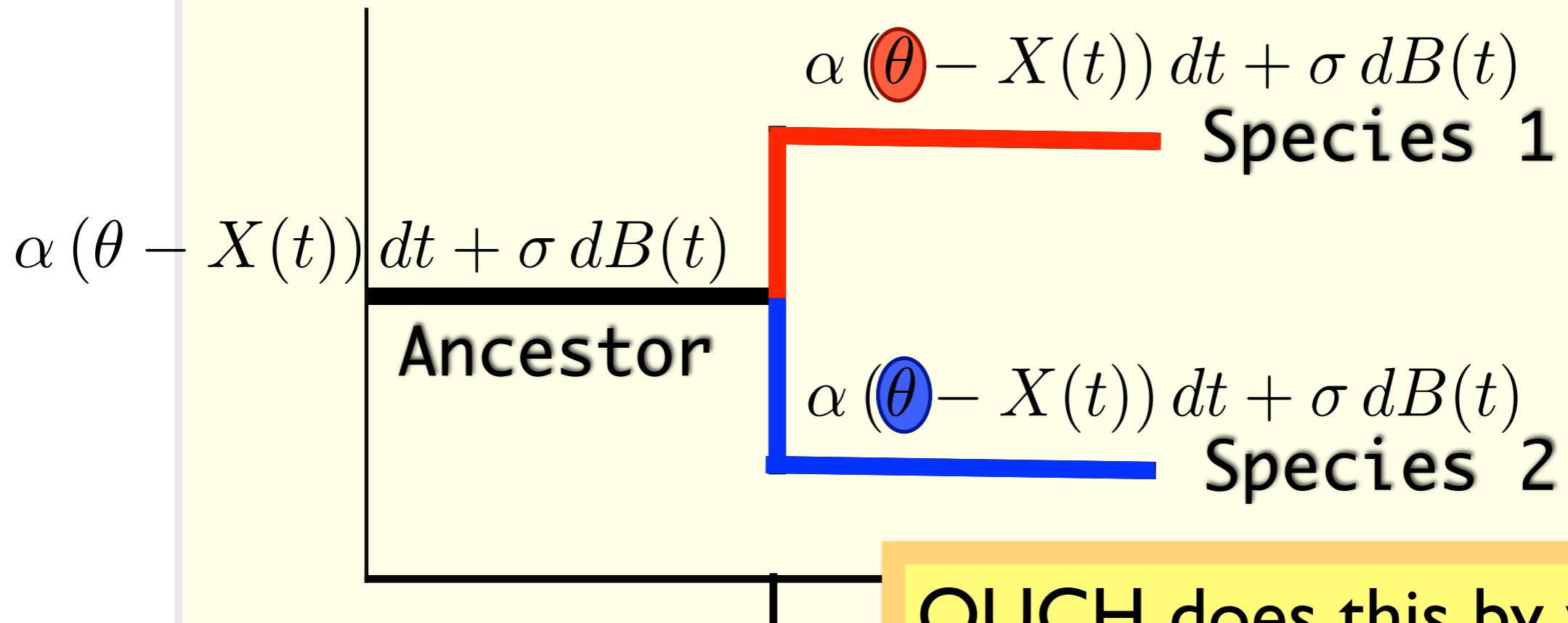
$$dX(t) = \alpha (\theta - X(t)) dt + \sigma dB(t)$$



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!

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



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

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!

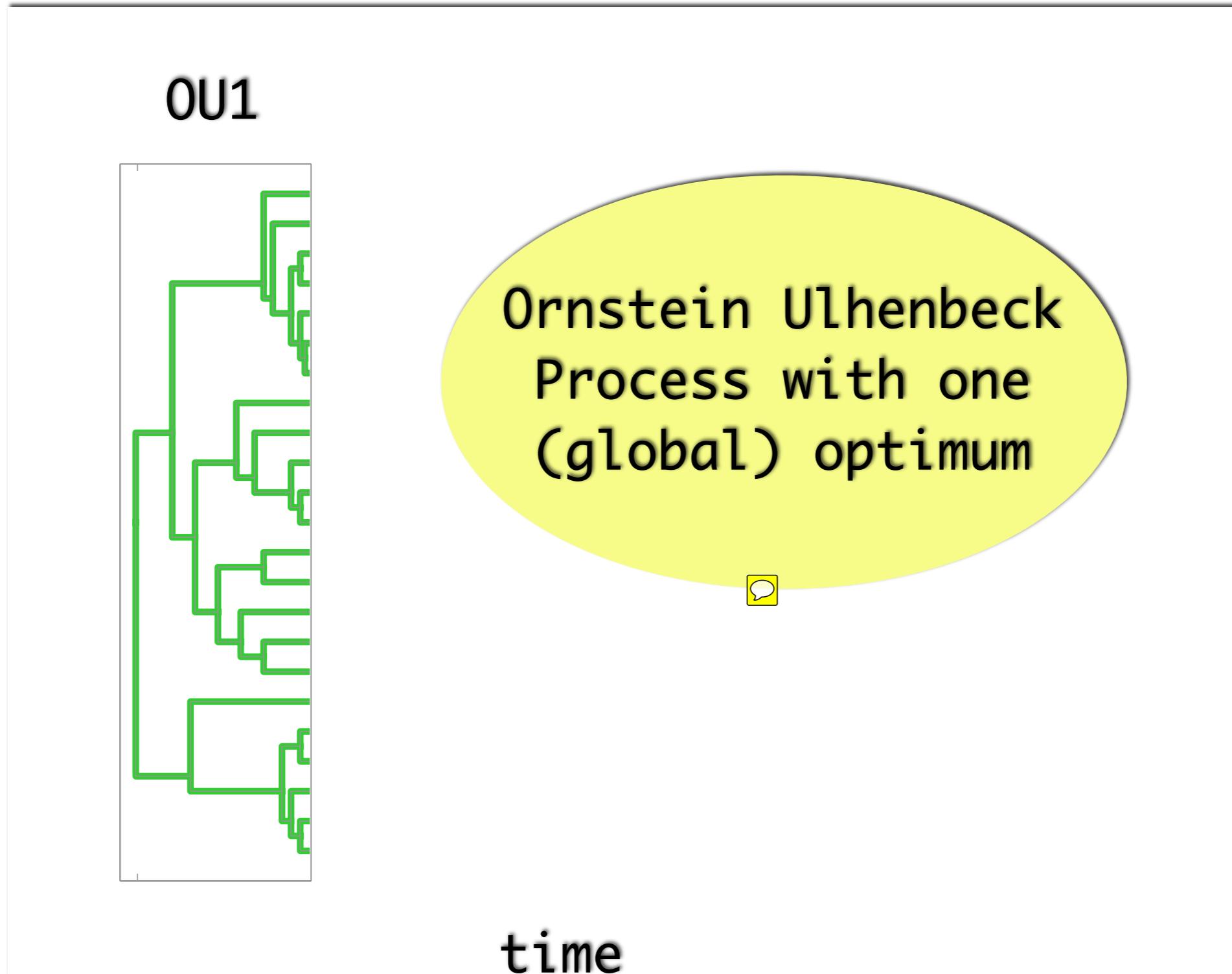
Islands in the Lesser Antilles have only 1 or 2 species of anoles.

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

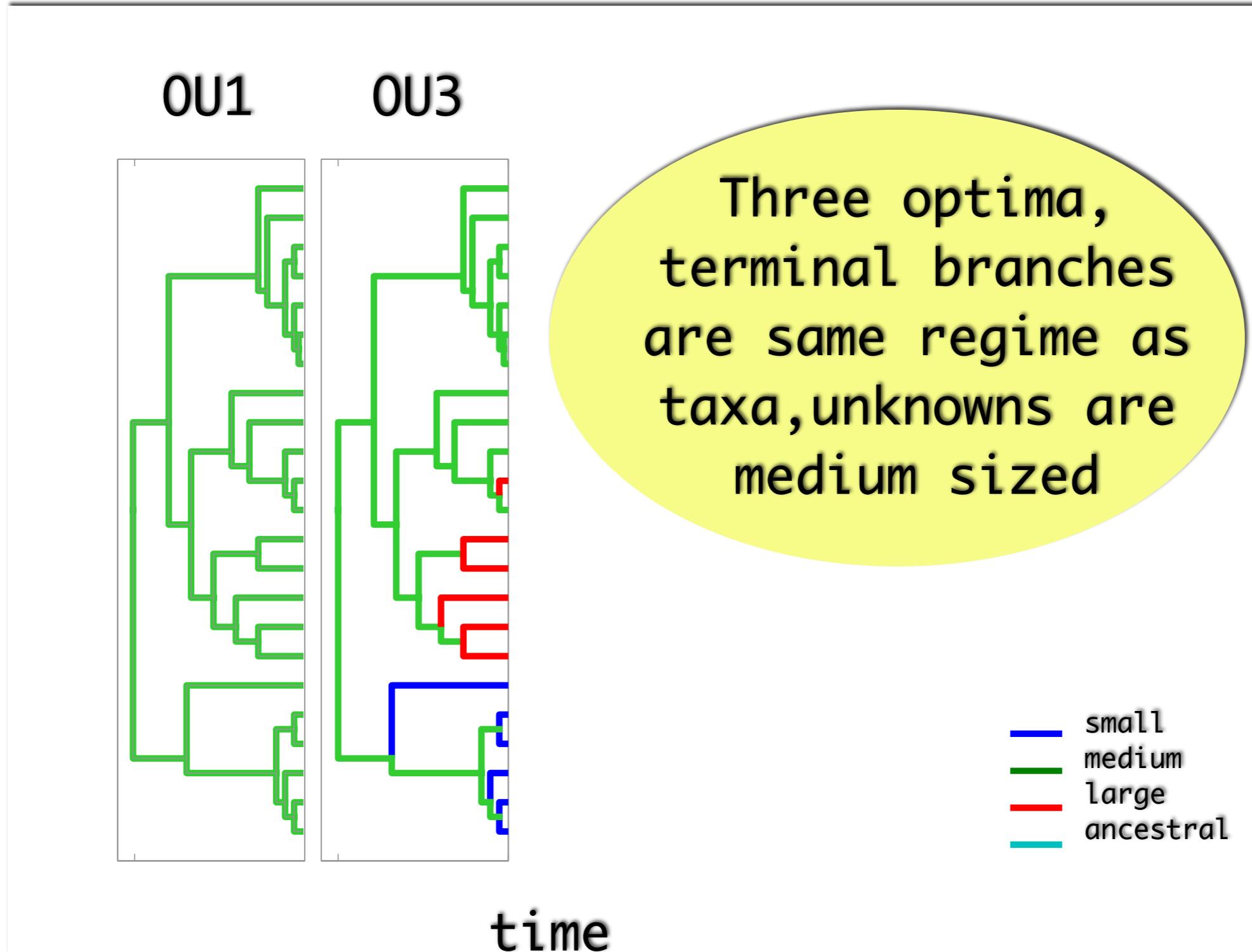
On the single species islands, anoles are “intermediate” in size.



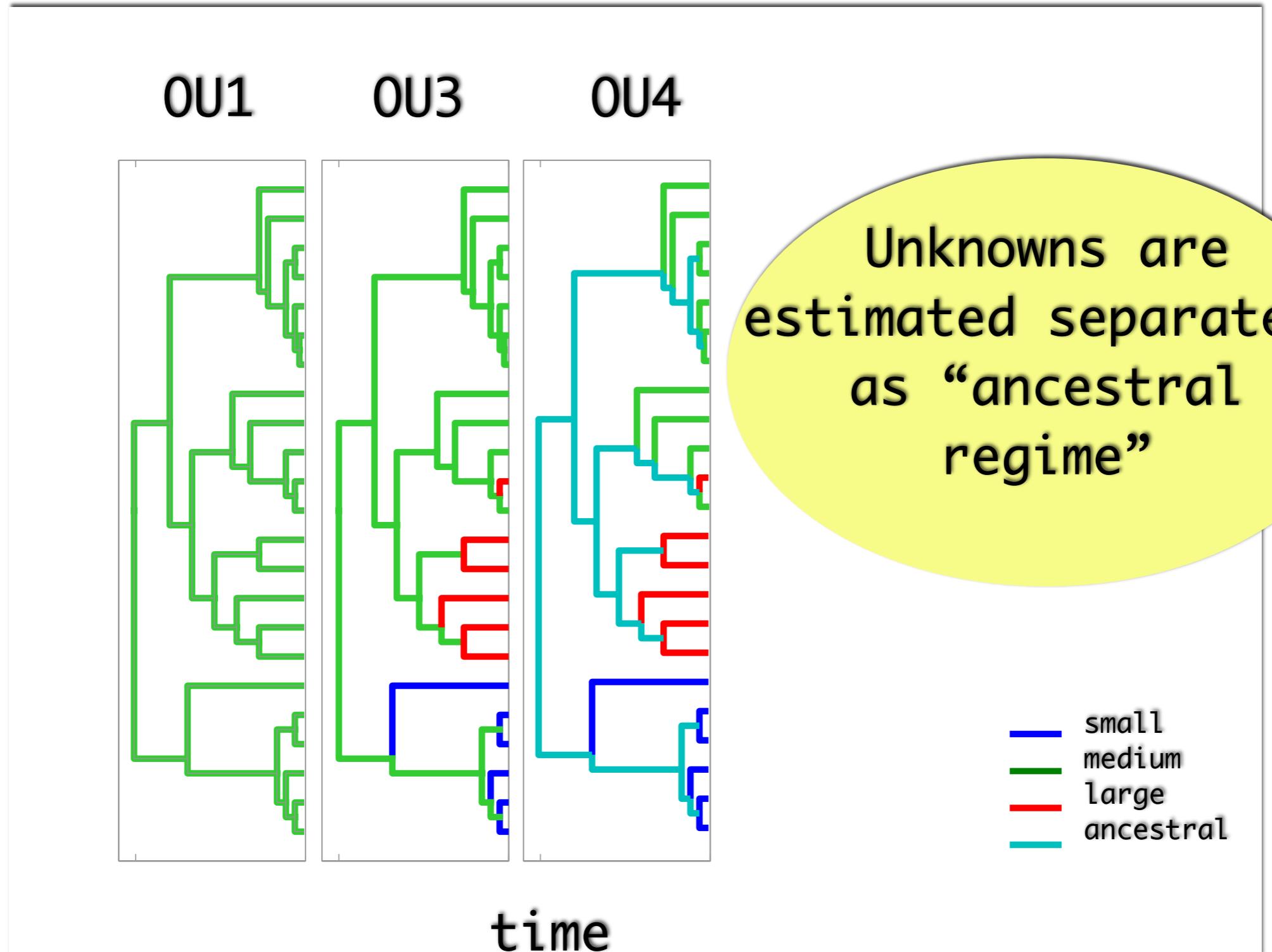
Alternative Adaptive Regime Models



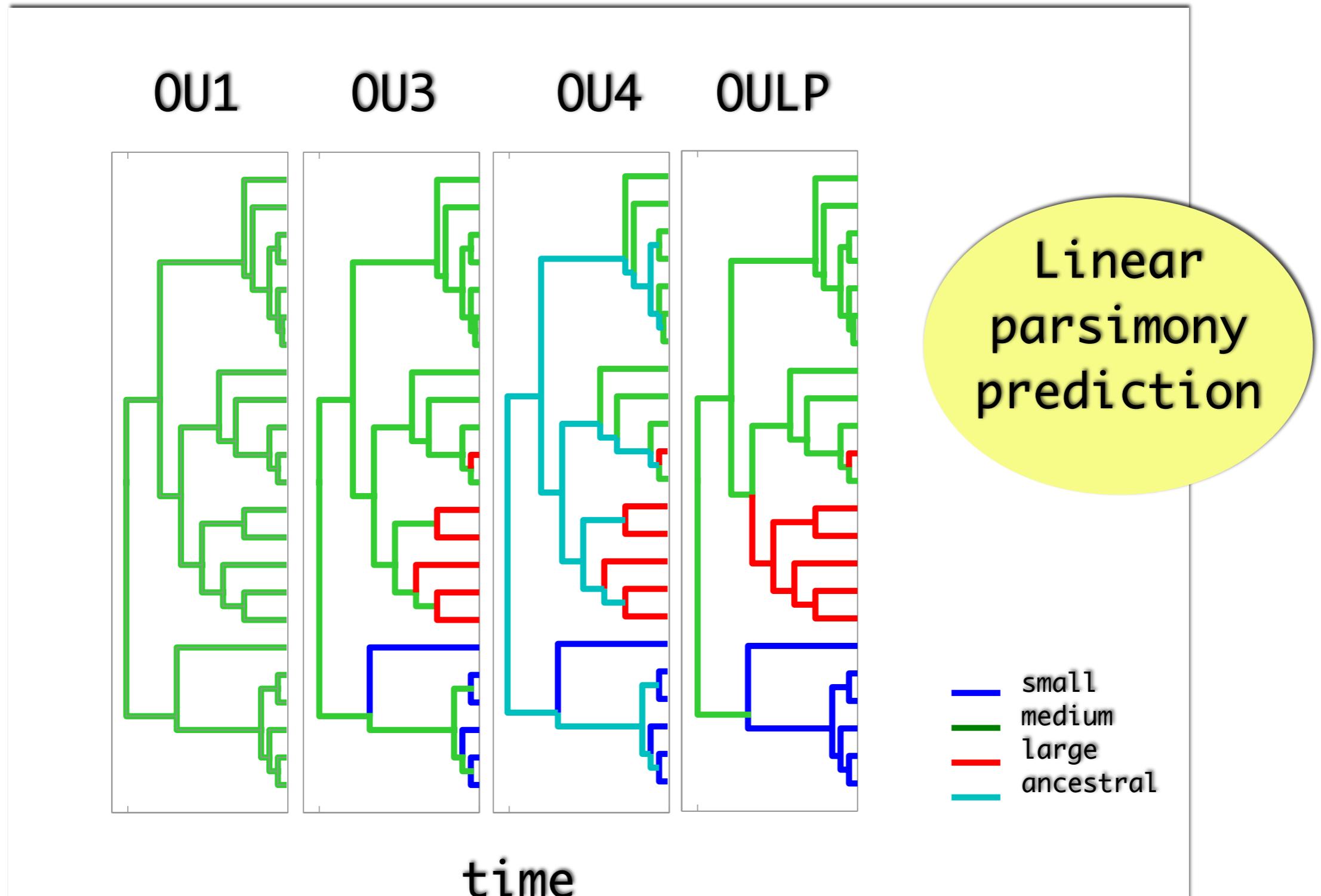
Alternative Adaptive Regime Models



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

Model Comparison

	BM	OU(1)	OU(3)	OU(4)	OU(LP)
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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	

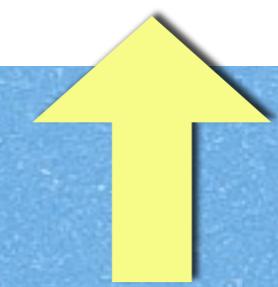
Best Model

	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

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

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



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

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

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

8%

Ancestral
State
(at root)

92%

Optima



OU(LP)

alpha

2.49

sigma

0.22

ancestor

0.86

optima 1

2.75

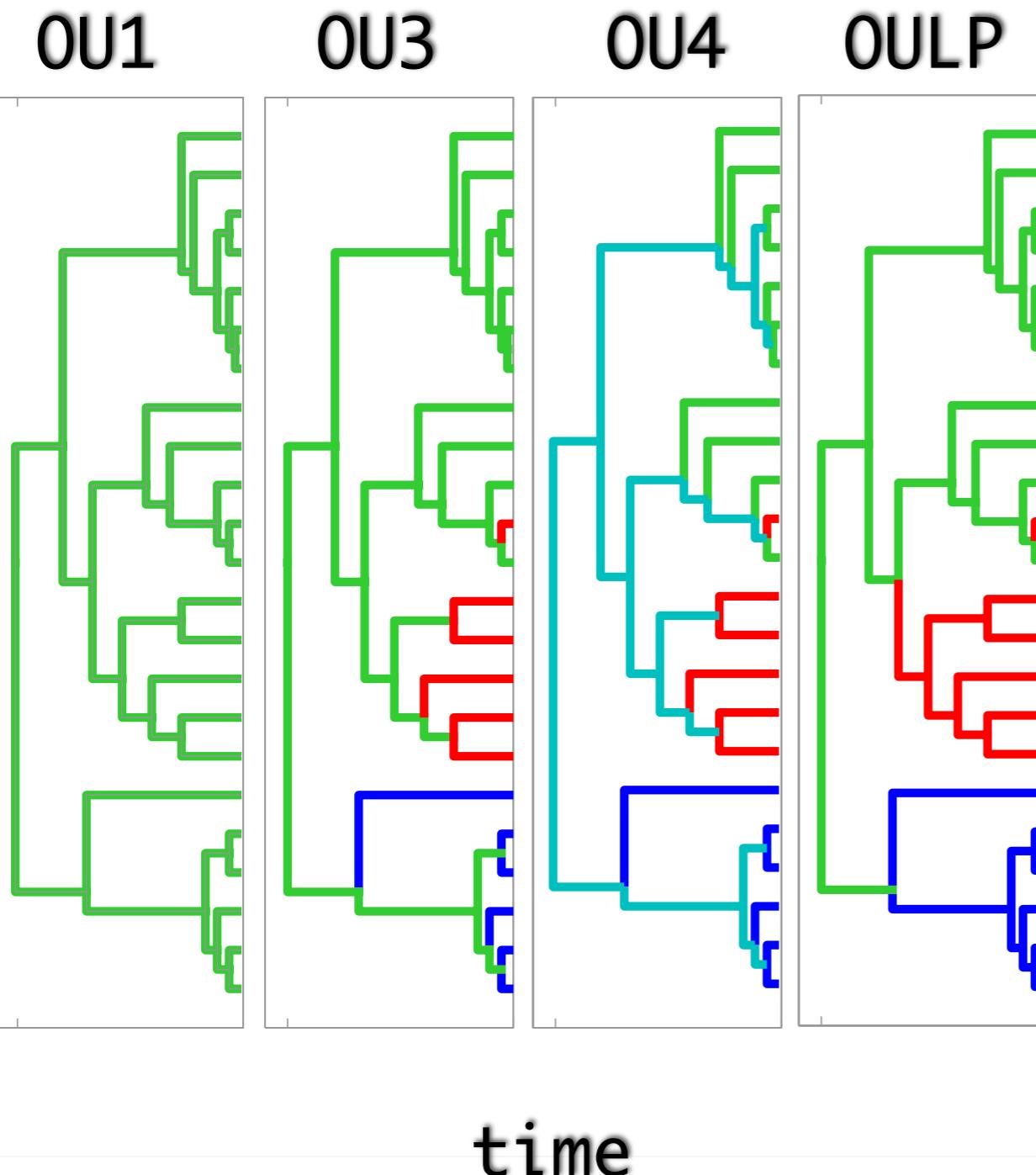
optima 2

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.