Testing Hypotheses of Adaptation using by Varying the Evolutionary Model

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Big ideas about Evolution

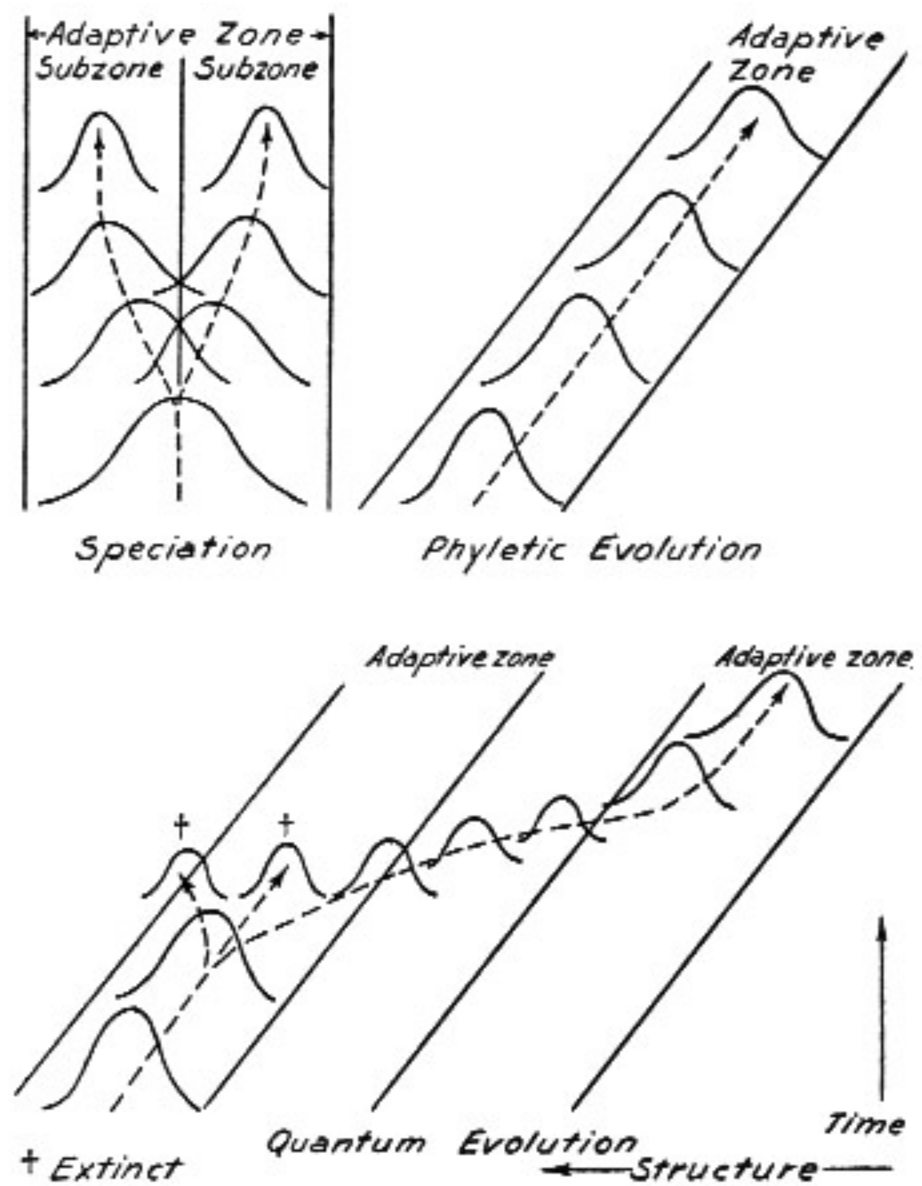
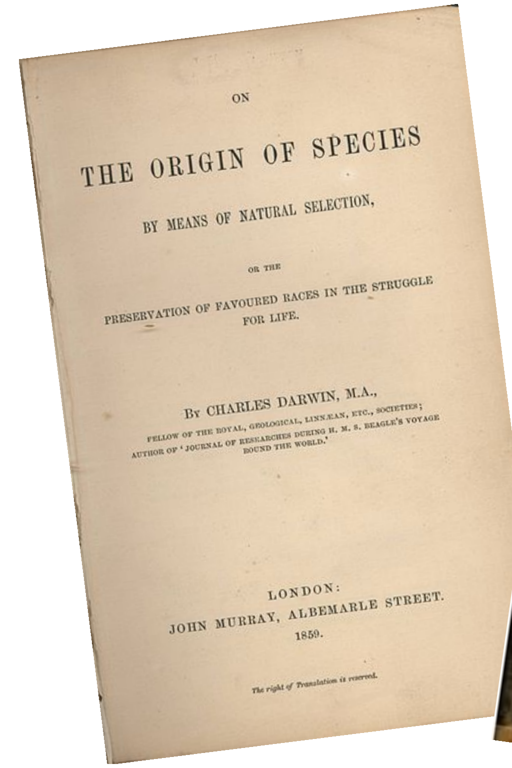
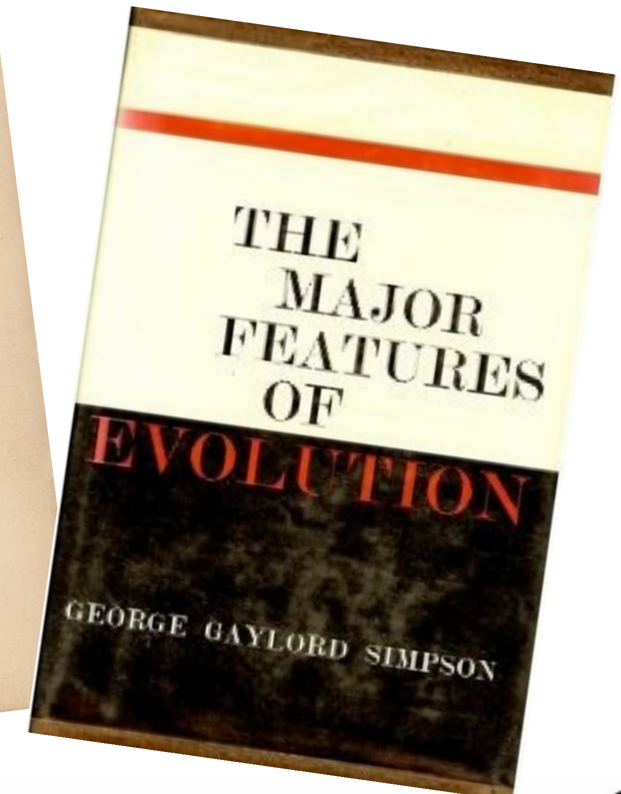
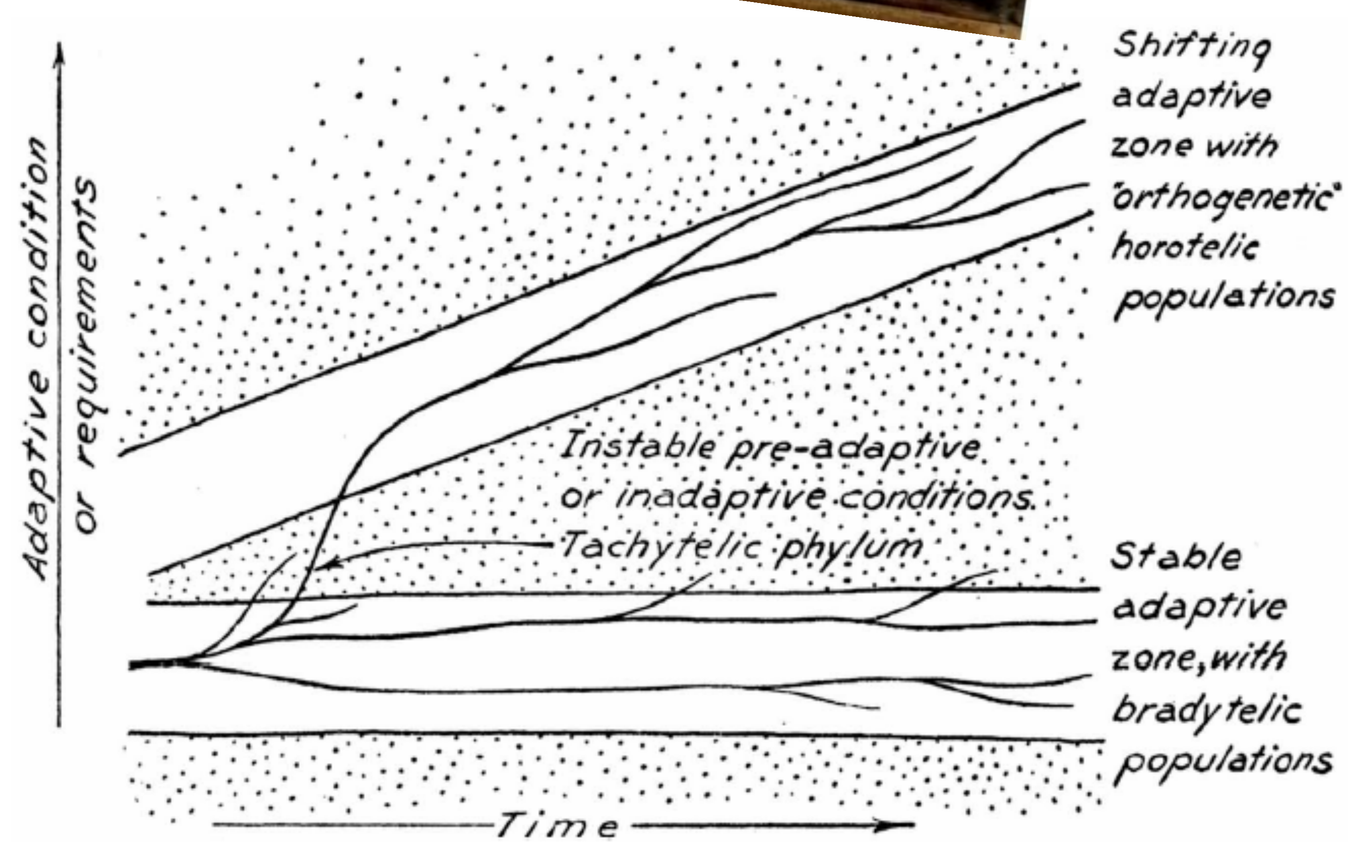


FIG. 31.—Diagrams of characteristic examples of the three major modes of evolution. In this and Figs. 32-33 the broken lines represent phylogeny and the frequency curves represent the populations in successive stages.





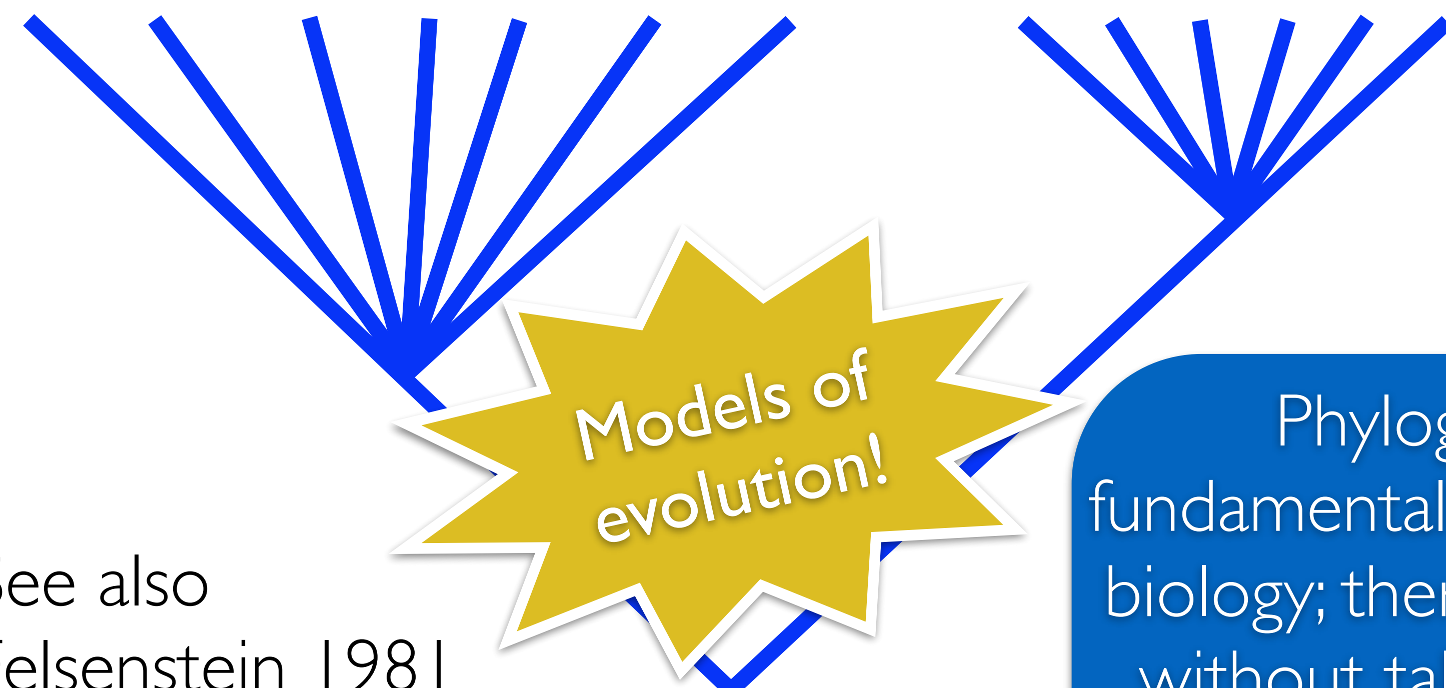


Simpson (1953) The major features of evolution

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

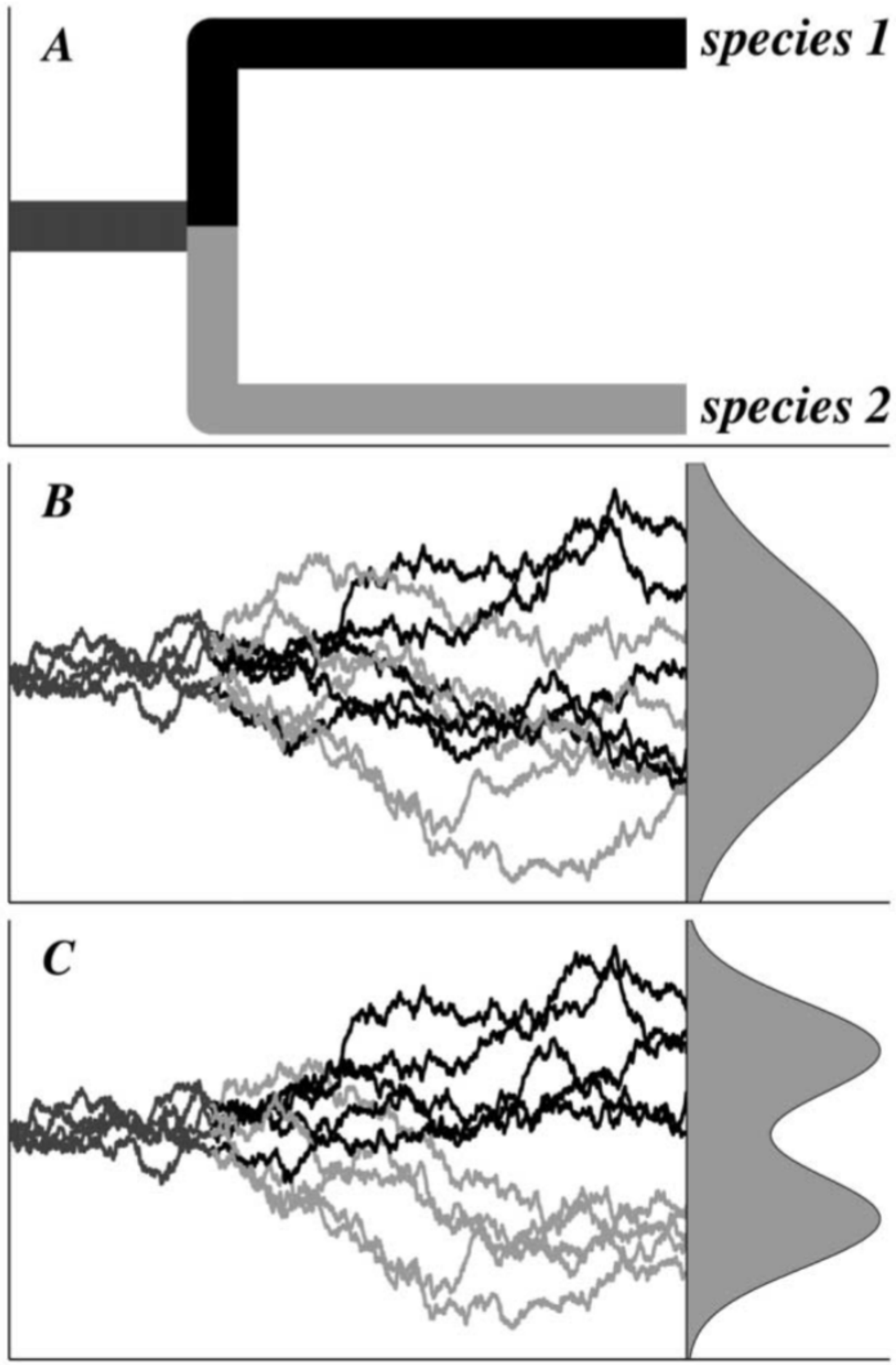


See also
Felsenstein 1981
Felsenstein 1988

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

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

How do we explain Patterns of Biodiversity?



Pattern of relationship

Are species phenotypes just subject to random evolution "drift"?

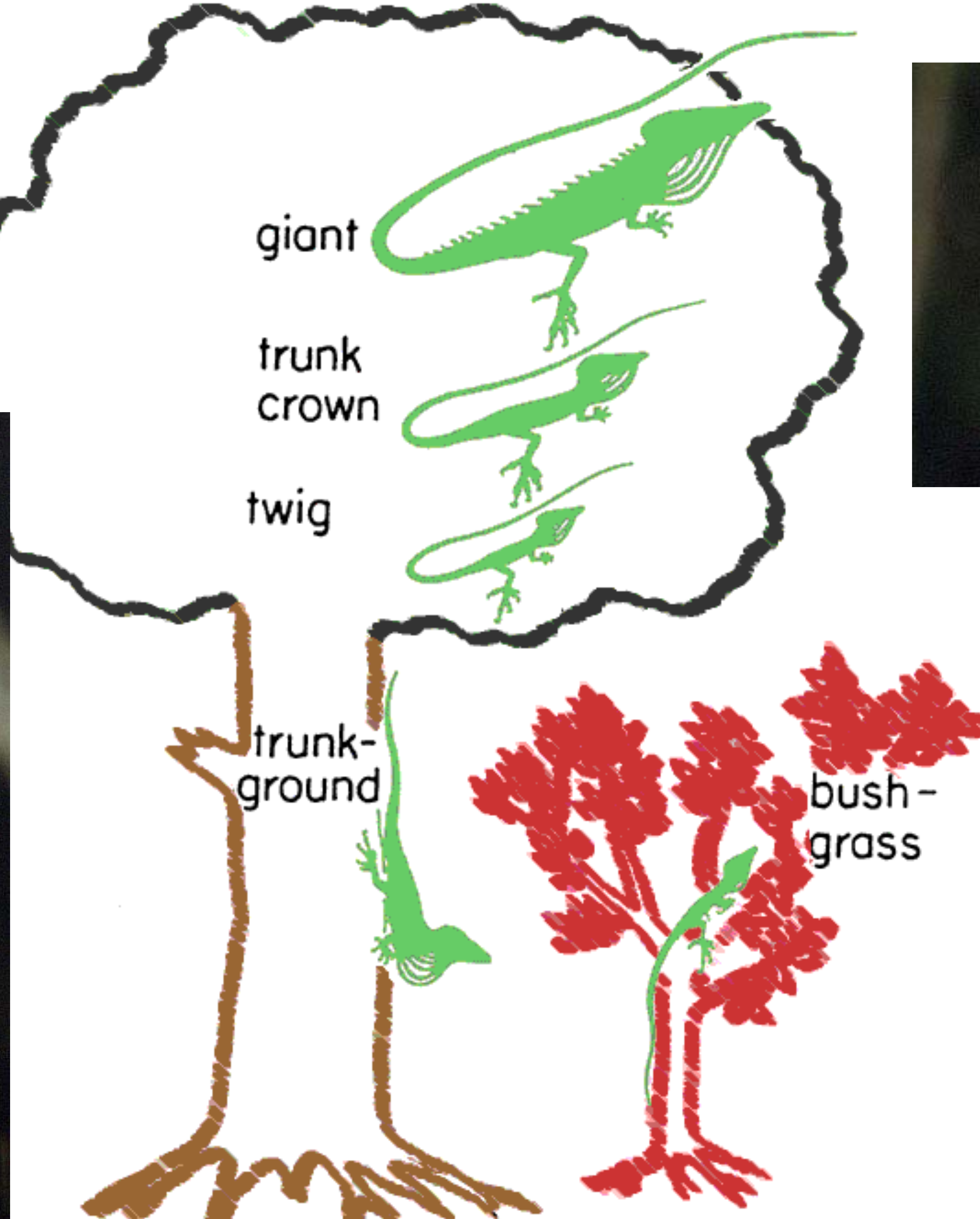
Or are other forces shaping the phenotype?

— Shifts in Selection
— Shifts in Environment
— Changes in Constraints

Figure from Butler & King 2004

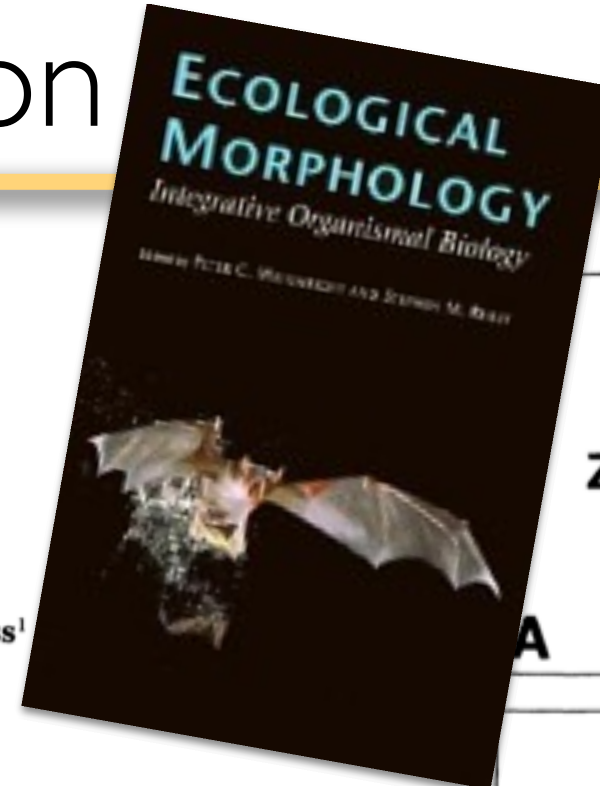
How do we tease apart the factors?

Anolis Lizards and Adaptive Diversification



Adapted from Williams (1983)

Morphology and Adaptation



AMER. ZOOL., 23:347–361 (1983)

Morphology, Performance and Fitness[1]

STEVAN J. ARNOLD

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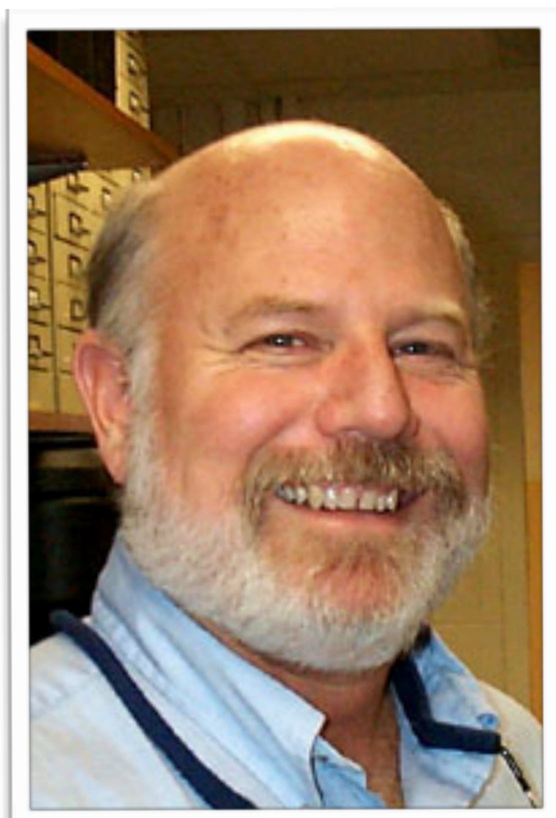
SYNOPSIS. Selection can be measured in natural populations by the changes it causes in the means, variances and covariances of phenotypic characters. Furthermore the force of selection can be measured in conventional statistical terms that also play a key role in theoretical equations for evolutionary 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 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



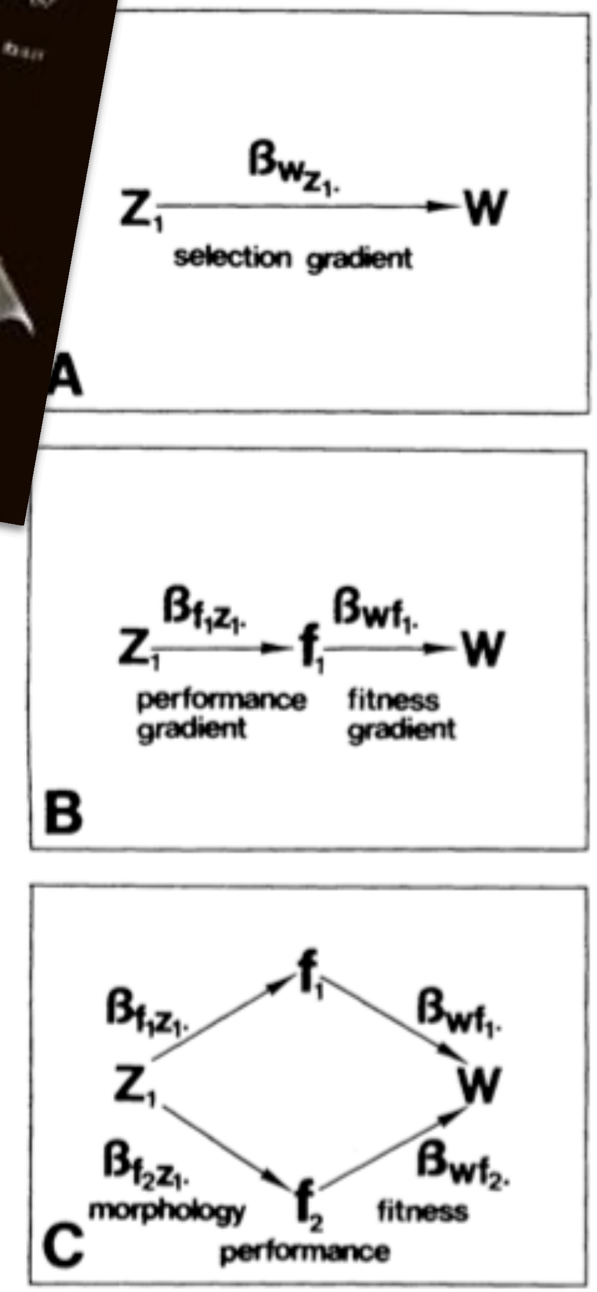


FIG. 4. A diagrammatic partitioning of the selection gradient. The selection gradient for a character (Fig. 4A) can be partitioned into two parts if the character affects a single performance variable, f_1: the performance gradient, $\beta_{f_1z_1\cdot}$ and the fitness gradient $\beta_{wf_1\cdot}$ (Fig. 4B). If the character affects two performance variables, f_1 and f_2, the selection gradient can be partitioned into the paths $\beta_{f_1z_1\cdot}\beta_{wf_1\cdot}$ and $\beta_{f_2z_1\cdot}\beta_{wf_2\cdot}$ (Fig. 4C).

See also
Lande and Arnold 1983
Phillips and Arnold 1989

Adaptative Evolution & Biodiversity

in Papuan Microhylid Frogs


91513

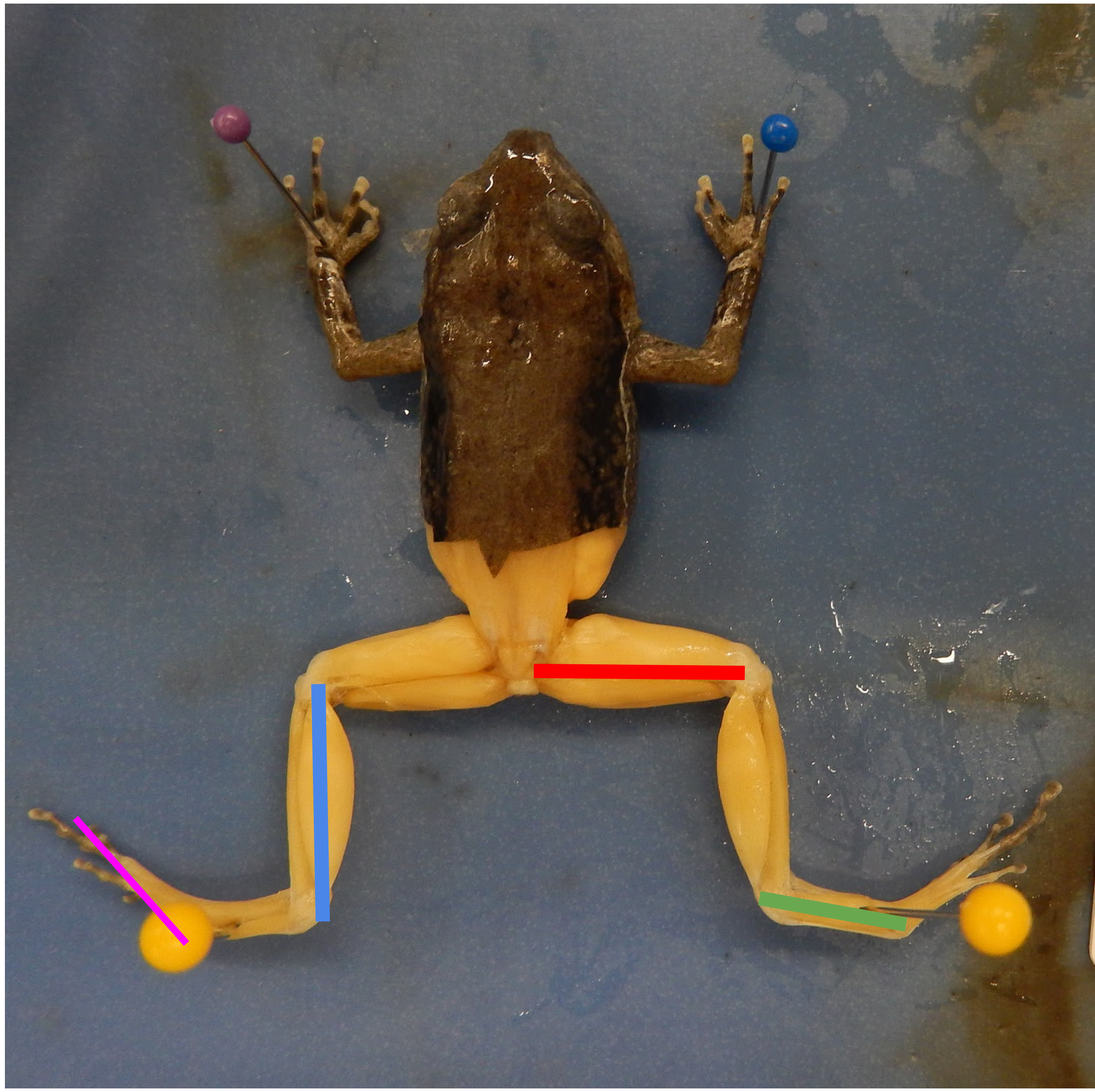
Morphology -> Performance

Morphology

- femur, tibiofibula, tarsus, and foot length
- Size

Muscles

	Adductor Magnus
	Cruralis
	Gluteus Magnus
	Gracilis Major
Thigh	Gracilis Minor
	Iliofibularis
	Sartorius
	Semimembranosus
	Semitendinosus
	Gastrocnemius
Shank	Peroneus
	Tibialis Anterior Longus

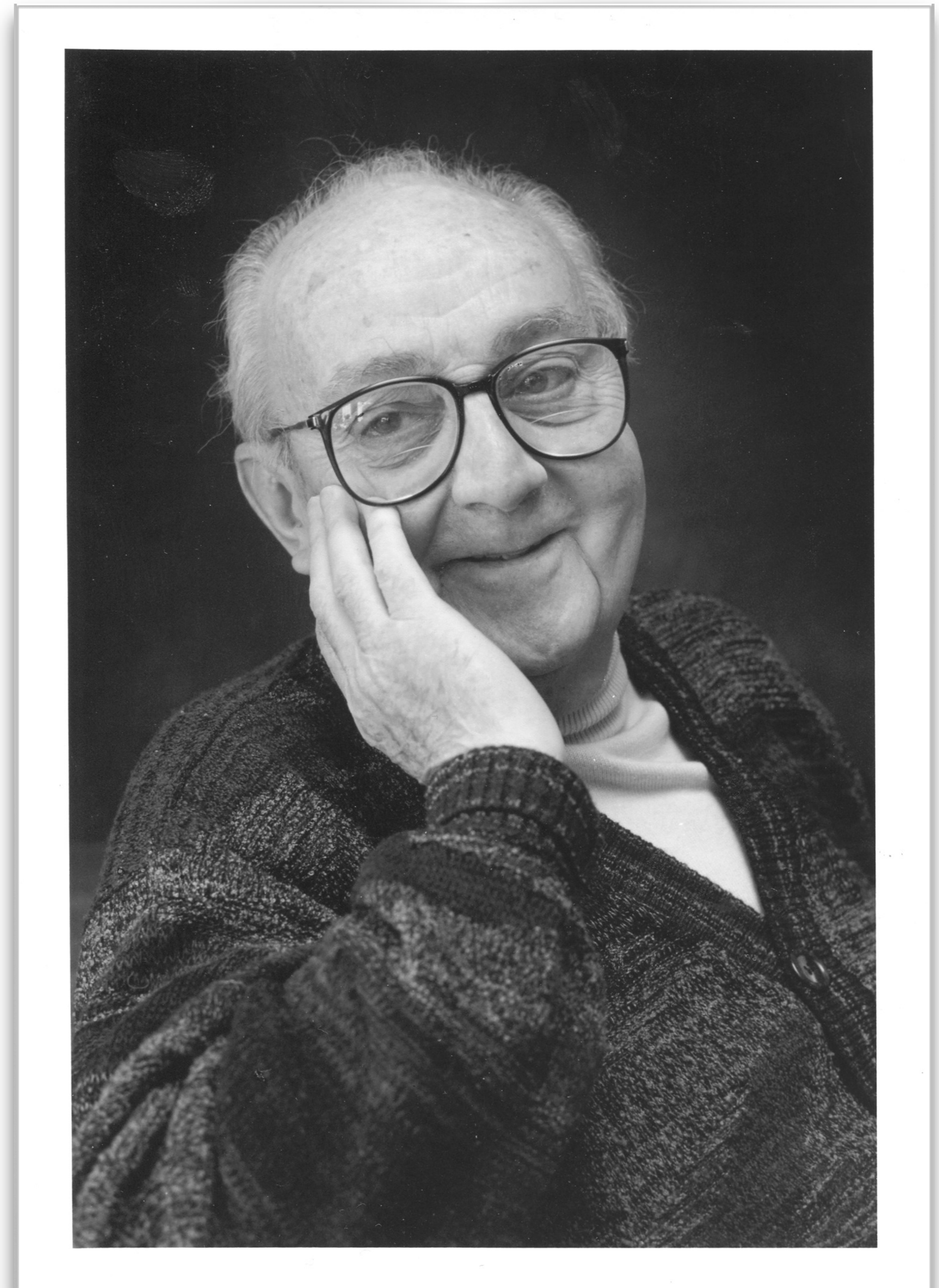


Joints

Timing - Kinematics and Biomechanics of Force Production

Essentially, all models are wrong, but some are useful

- George E. Box



What does Adaptive Diversification Look Like?

Uncertainty

Biogeography and Ecological Evolution in Papuan Microhylid Frogs

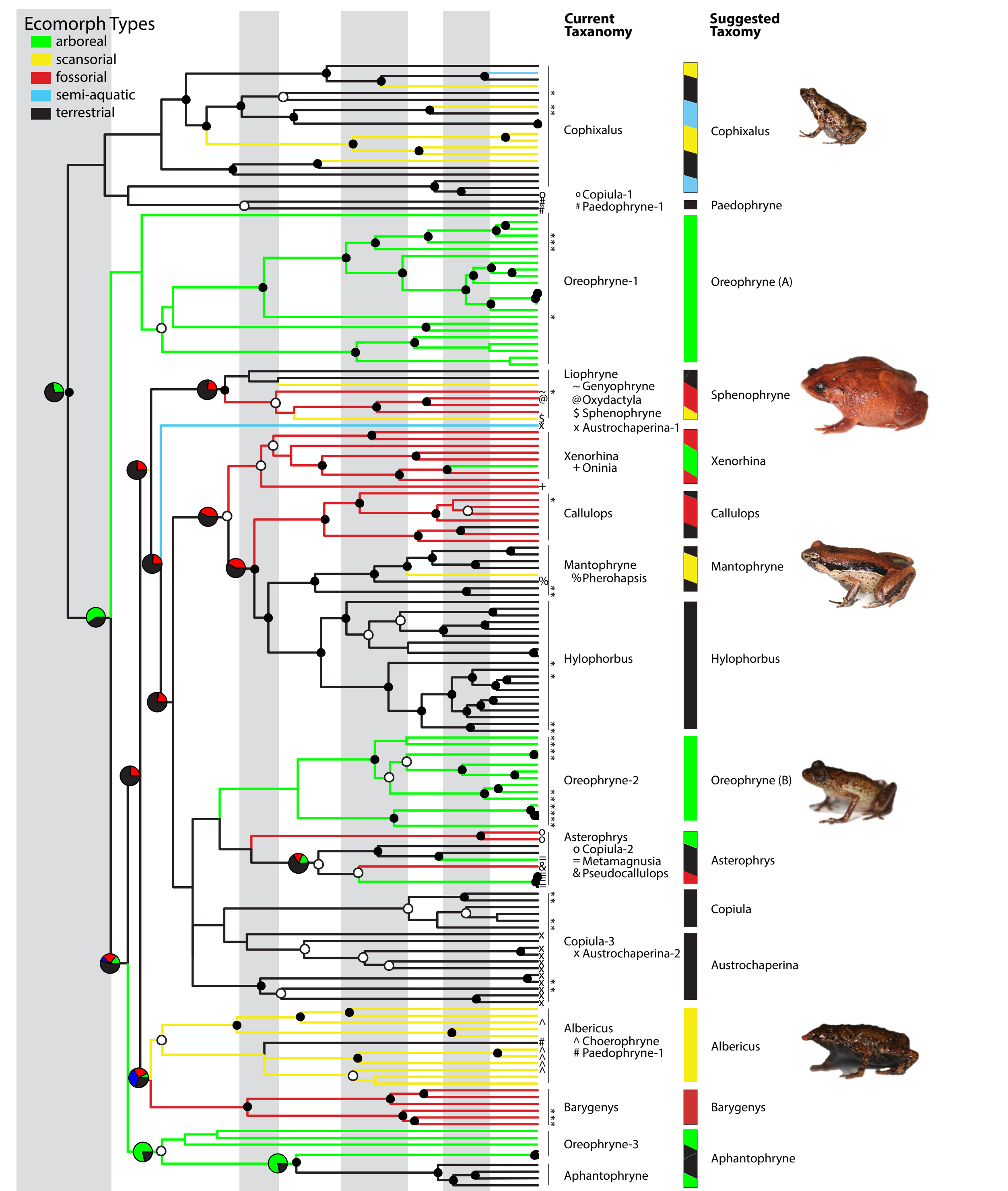
But you can still find interesting results!

You just have to check.

Ancestral microhylid was terrestrial

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

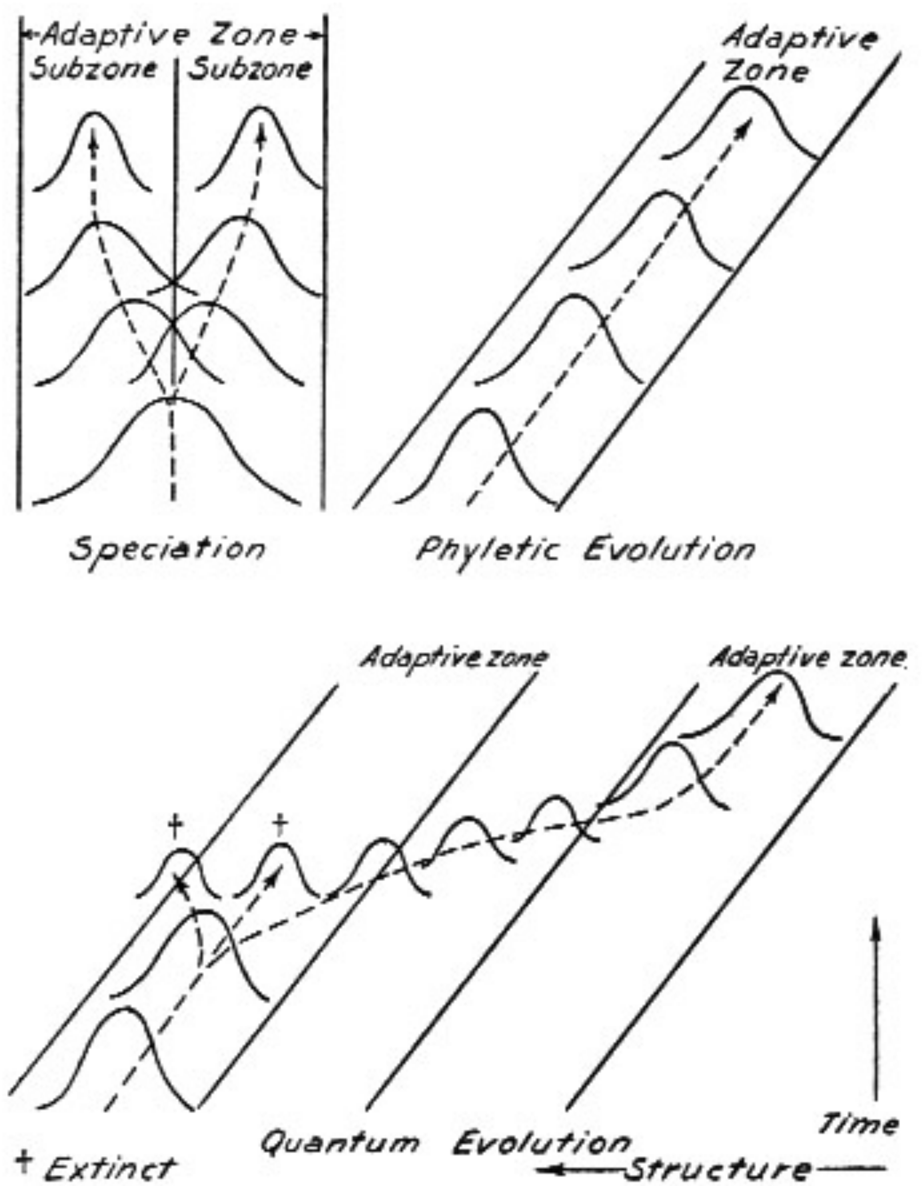
Rampant speciation and more ecomorph transitions followed



Julio Rivera

Rivera, Kraus, Allen, and Butler (2017) Molecular Phylogenetics and Evolution

Different Models of Evolution



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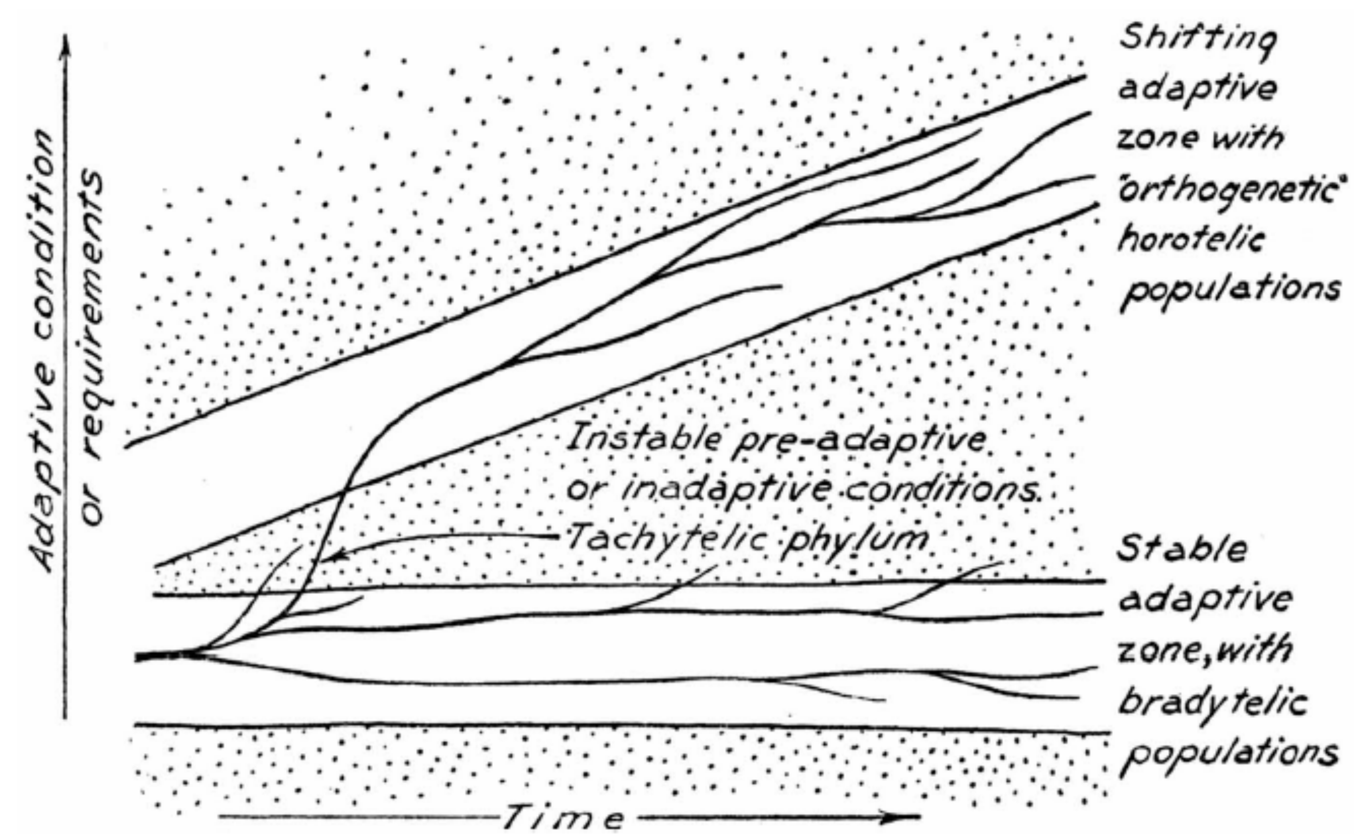
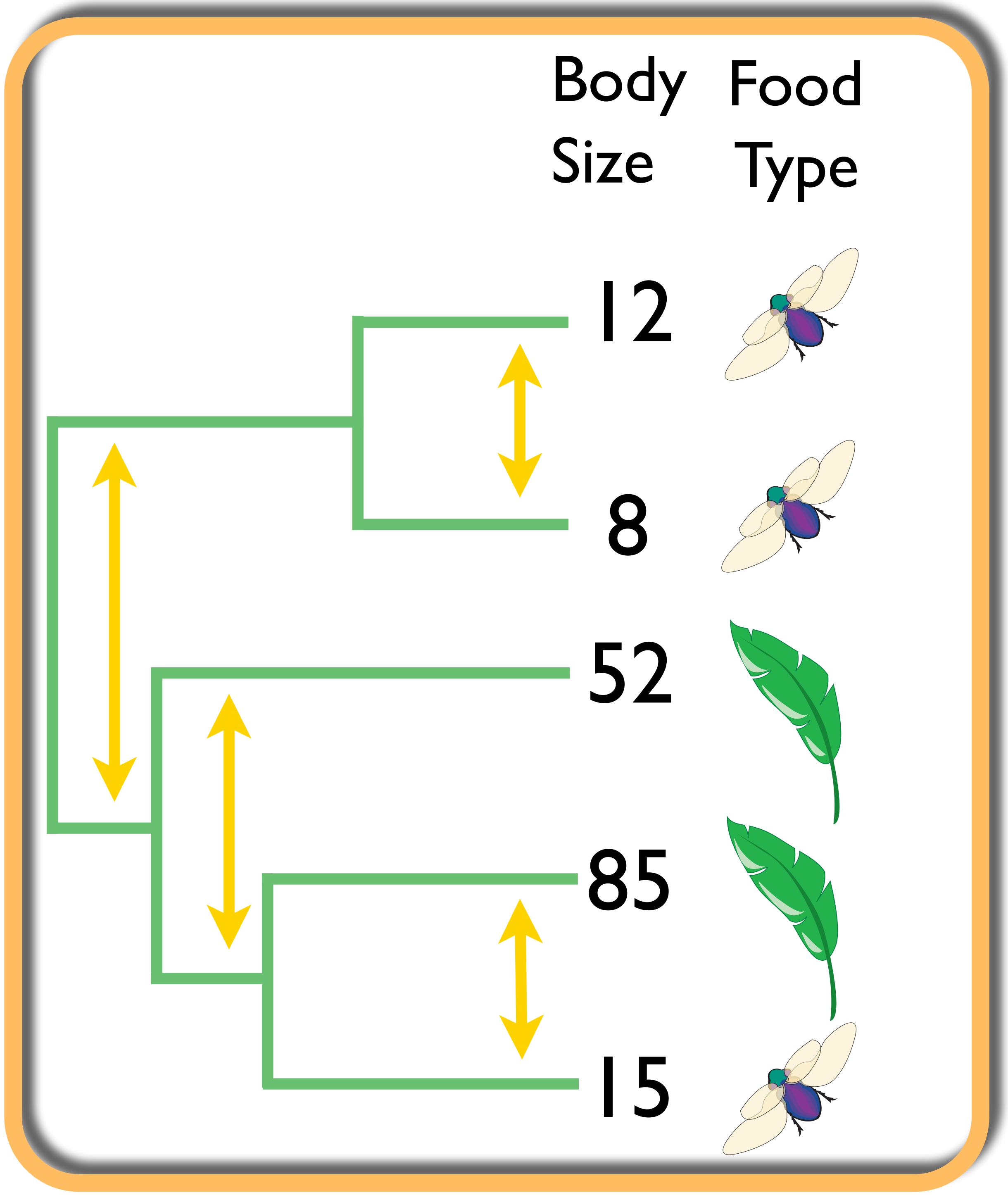


Simpson (1953) The major features of evolution



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)

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

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

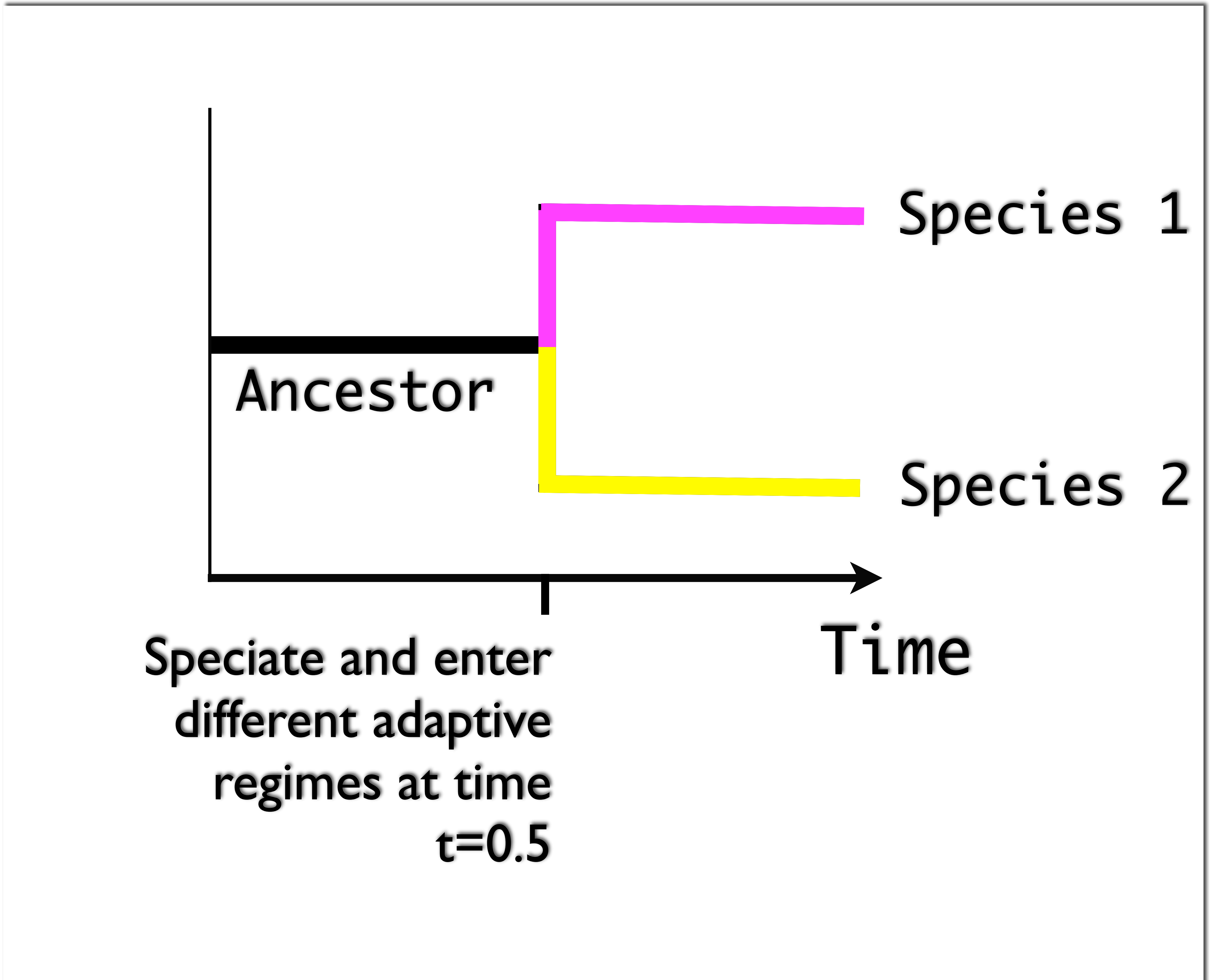
Orstein Uhlenbeck Process

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

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

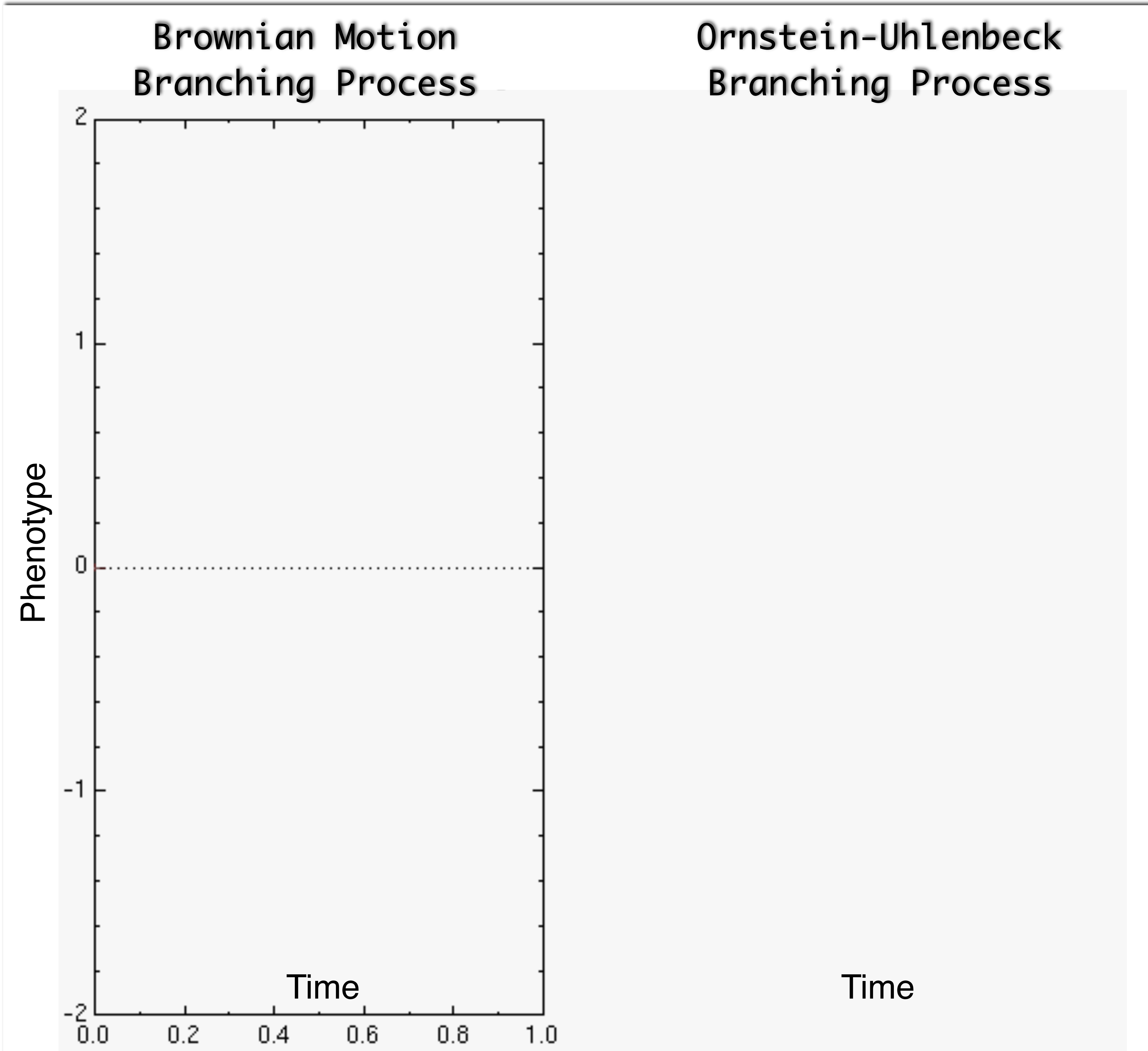
Hansen (1997)

BM and OU models make different predictions



How different are BM and OU models?

BM and OU models make different predictions



Modeling adaptive evolution using OUCH*!

Marguerite Butler

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Aaron King

University of Michigan, Ecology & Evolutionary Biology

(*Ornstein-Uhlenbeck for Comparative Hypotheses)

All comparative analyses are constructed of 3 pieces

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

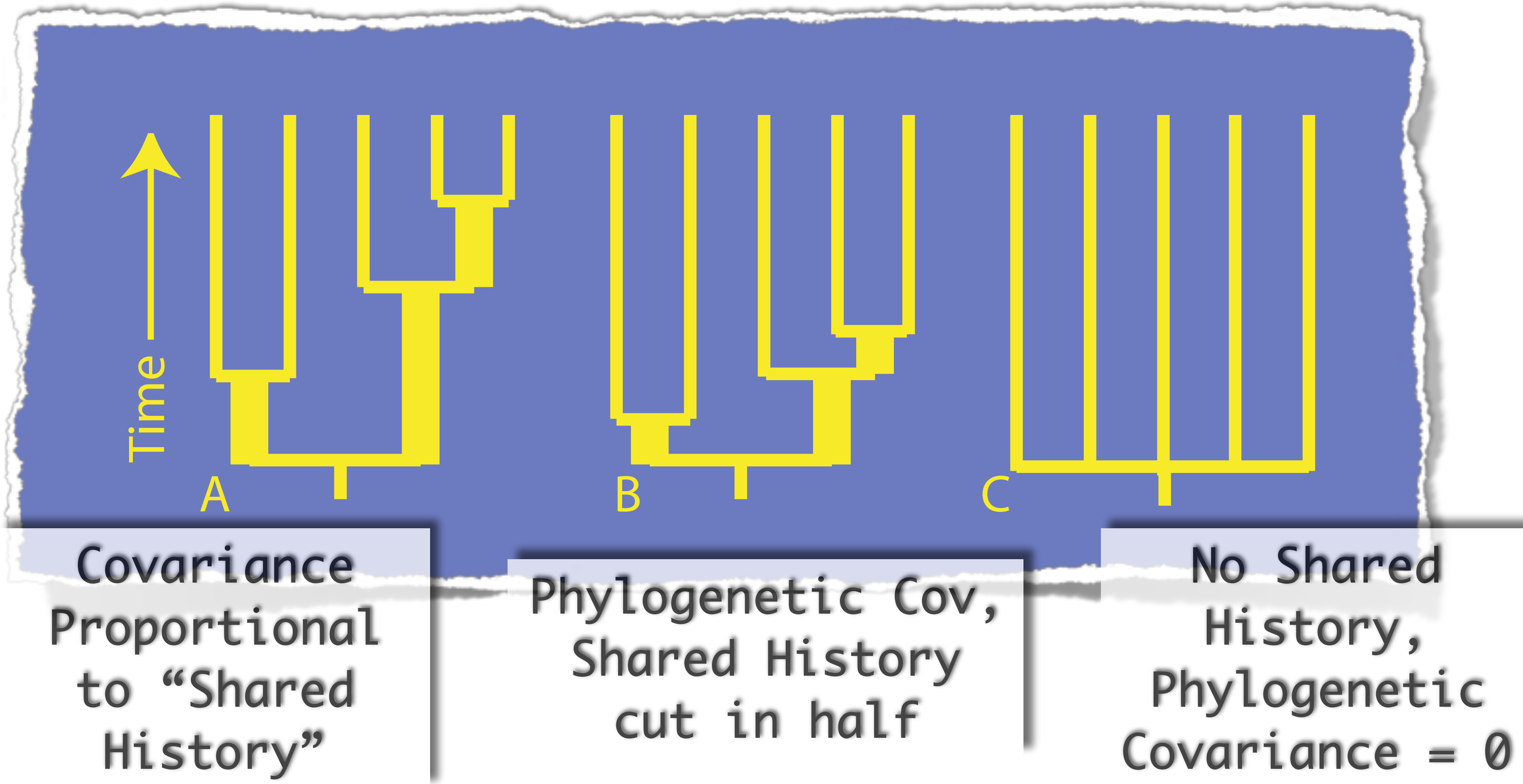
2. A particular pattern of shared ancestry (phylogeny and branch lengths)

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

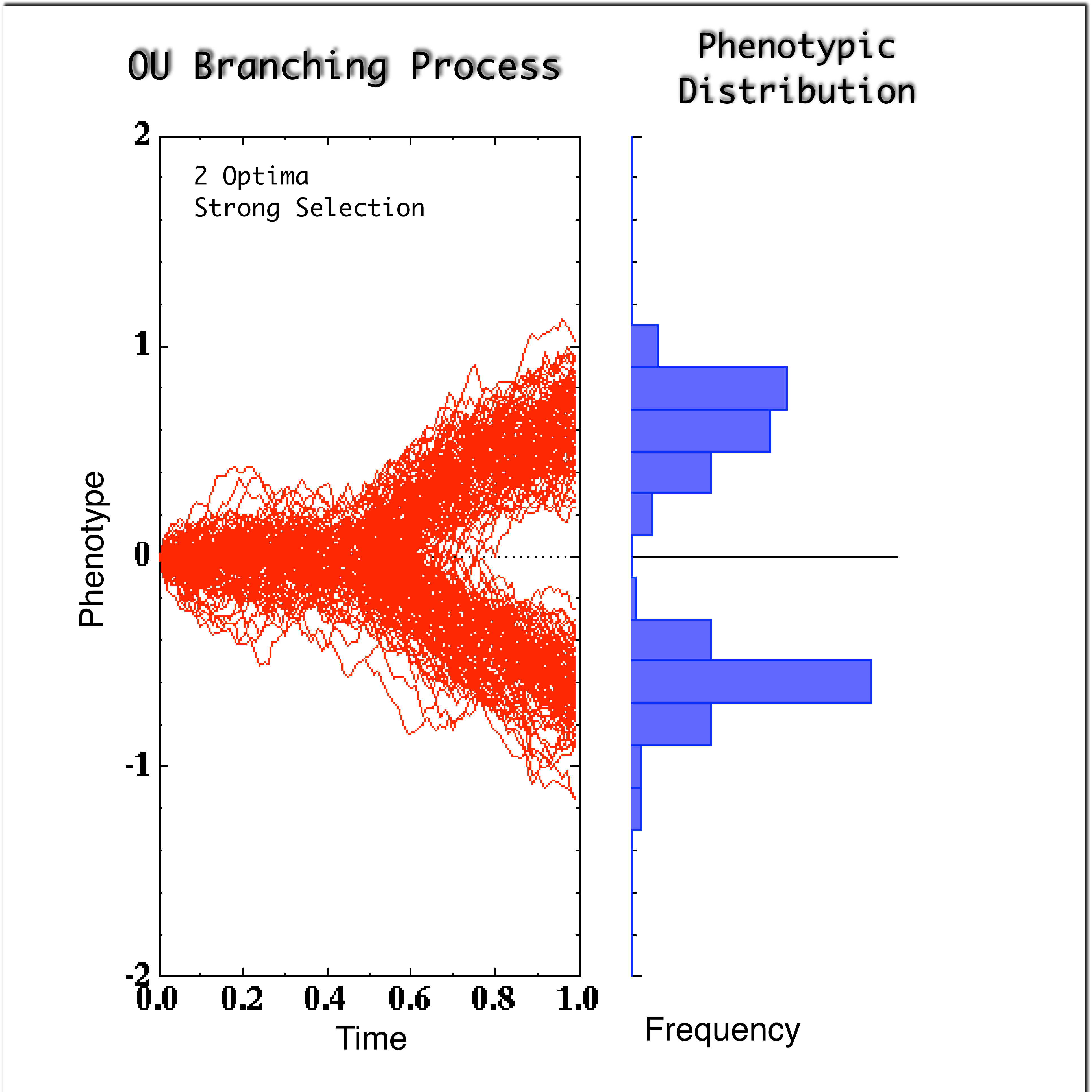
There is another option...

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 !


OU Branching Process
Phenotypic Distribution
2 Optima
Strong Selection
Phenotype
Time
Frequency
2
1
0
-1
-2
0.0
0.2
0.4
0.6
0.8
1.0