

Modeling adaptive evolution

Genetic Drift + Natural Selection

Genetic drift only:

$$\Delta z = G/Ne * dW$$

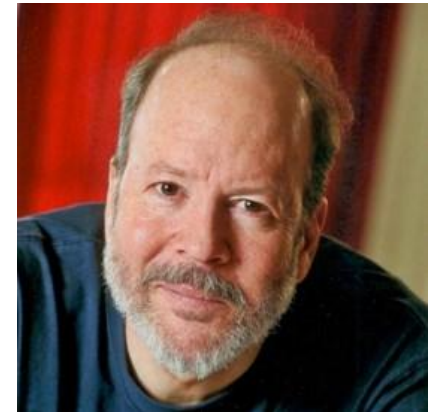
Genetic drift + Natural selection to a Gaussian adaptive peak:

$$\Delta z = G/(\omega + P) * (\theta - z) + G/Ne * dW$$

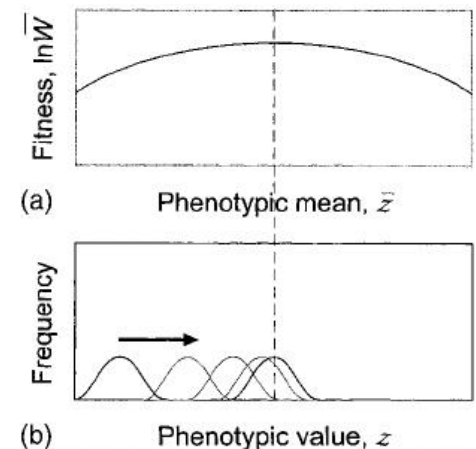
Genetic variance

Width of the adaptive landscape

Distance from the optimum



Russ Lande



Ornstein-Uhlenbeck Process

$$\Delta z = \alpha(\theta - z) + \sigma dW$$

α - Rate of adaptation

Units: (1/time)

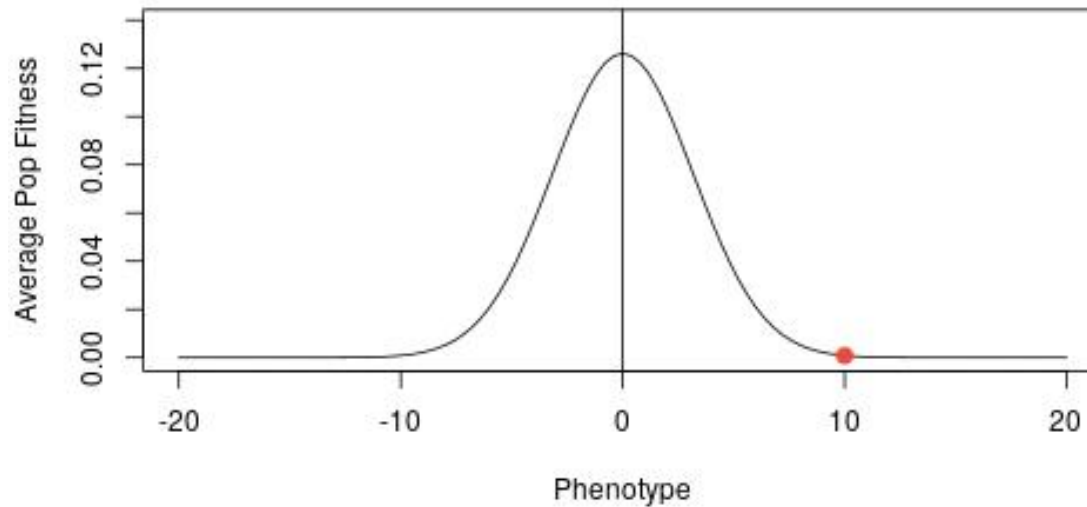
σ - Rate of stochastic evolution

Units: trait units/time

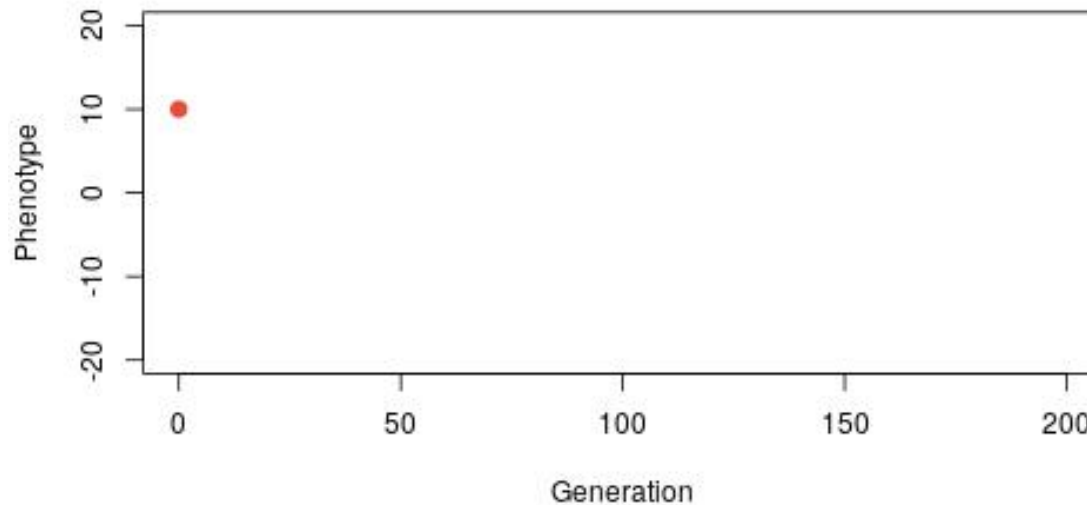
θ - Phenotypic optimum



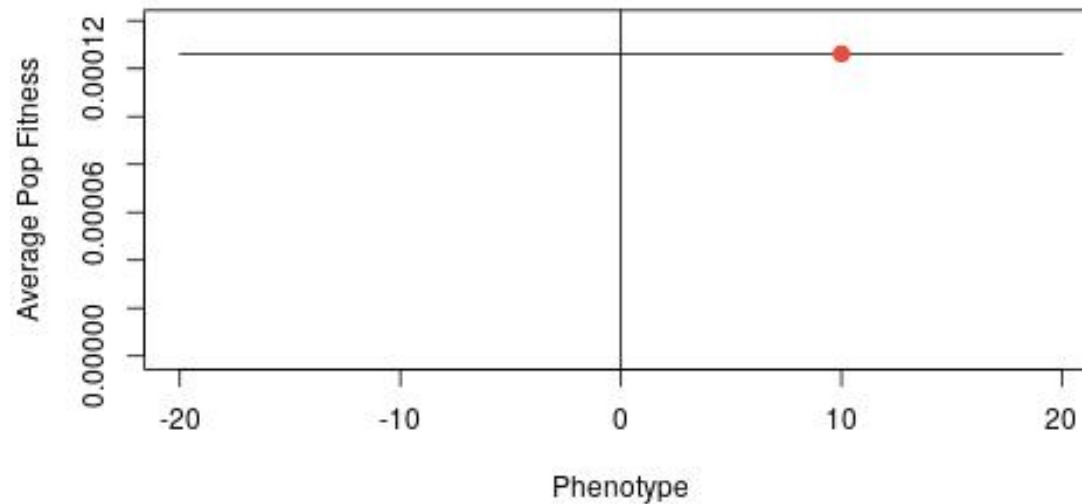
Ornstein-Uhlenbeck process



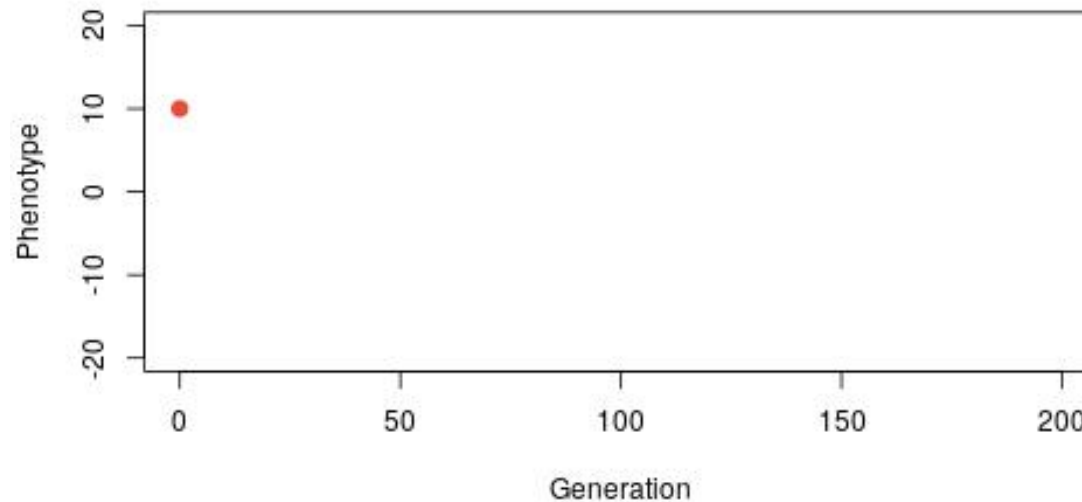
$\alpha = 0.1$
 $\sigma^2 = 1$



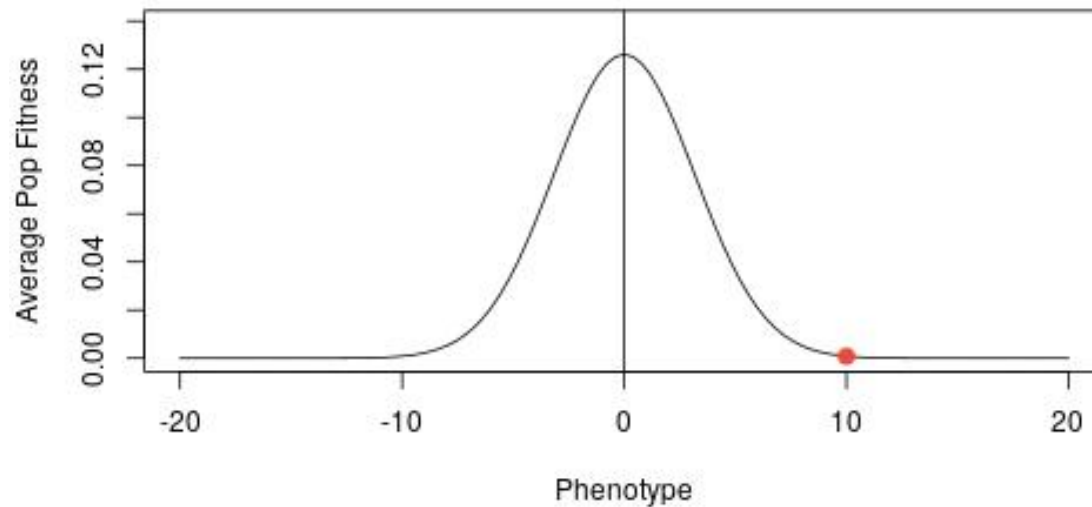
Ornstein-Uhlenbeck process



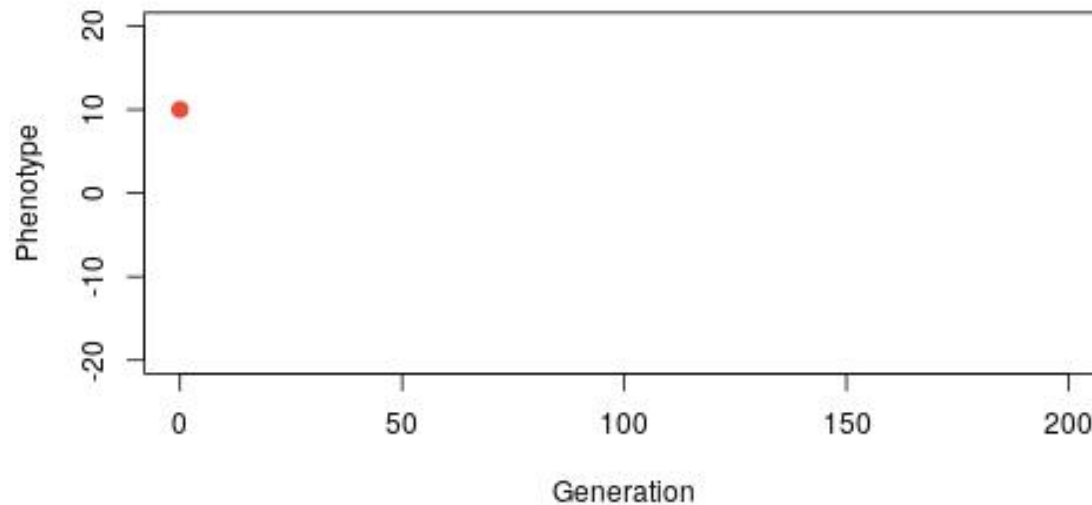
$\alpha = 0.000001$
 $\sigma^2 = 1$



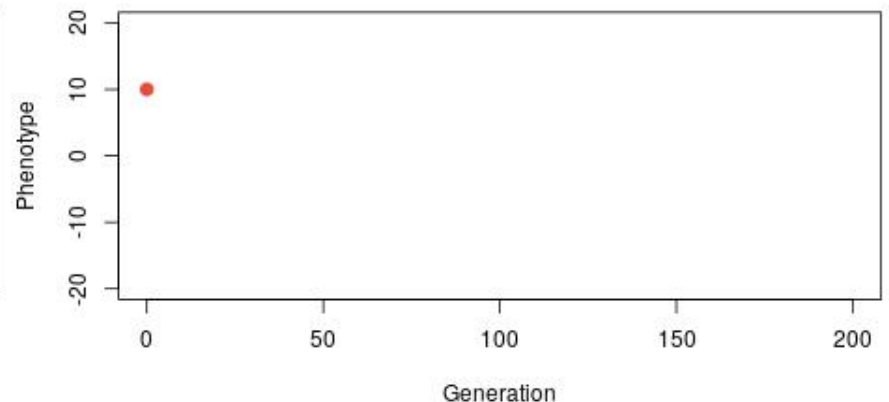
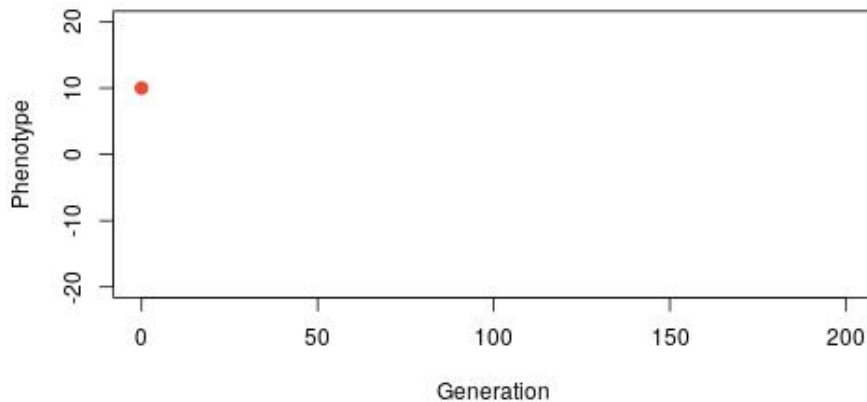
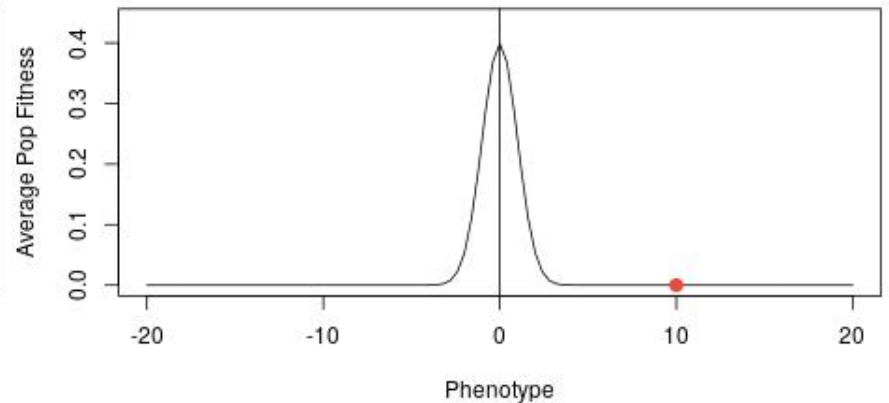
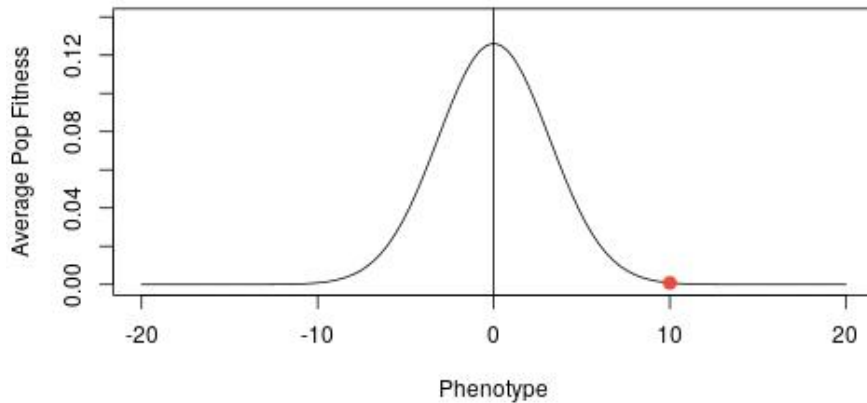
Ornstein-Uhlenbeck process



$\alpha = 0.1$
 $\sigma^2 = 1$

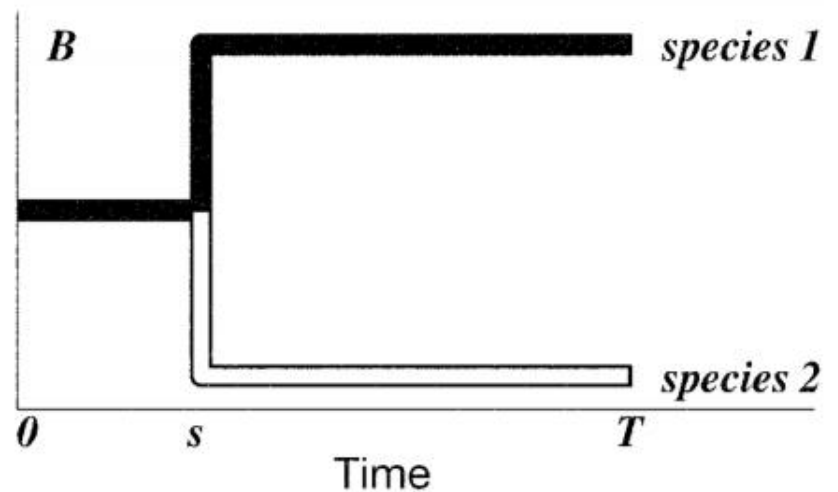


Ornstein-Uhlenbeck process



$$\alpha = 0.1$$
$$\sigma^2 = 1$$

$$\alpha = 1$$
$$\sigma^2 = 10$$



$$E[X_1(T)] = \theta_0 e^{-\alpha T} + \theta_1 (1 - e^{-\alpha T})$$

$$= W_{10}\theta_0 + W_{11}\theta_1,$$

$$E[X_2(T)] = \theta_0 e^{-\alpha T} + \theta_1 e^{-\alpha(T-s)}(1 - e^{-\alpha s})$$

$$+ \theta_2 [1 - e^{-\alpha(T-s)}]$$

$$= W_{20}\theta_0 + W_{21}\theta_1 + W_{22}\theta_2.$$

**Butler & King
2004**

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

Useful parameterization:

Stationary Variance = $\sigma^2/(2\alpha)$

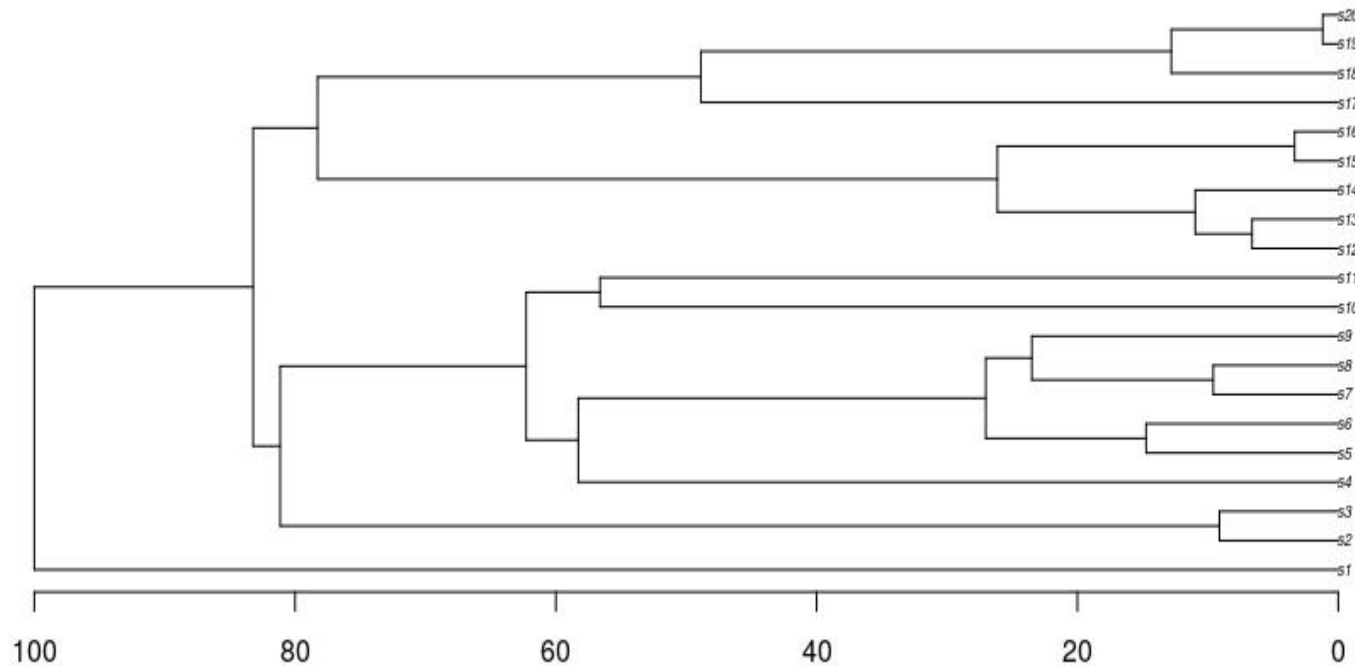
The amount of variance among a set of lineages with an infinite amount of time evolving at the optimum

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

Phylogenetic half-life = $\ln 2/(2\alpha)$

The expected amount of time for a lineage to get halfway to the optimum

Interpreting half-life



$$\ln 2 / \alpha$$

BM-like

White noise

OU

Phylogenetic signal - What does it mean?

Pagel's Lambda

Blomberg's K

Phylogenetic halflife

AC/DC model

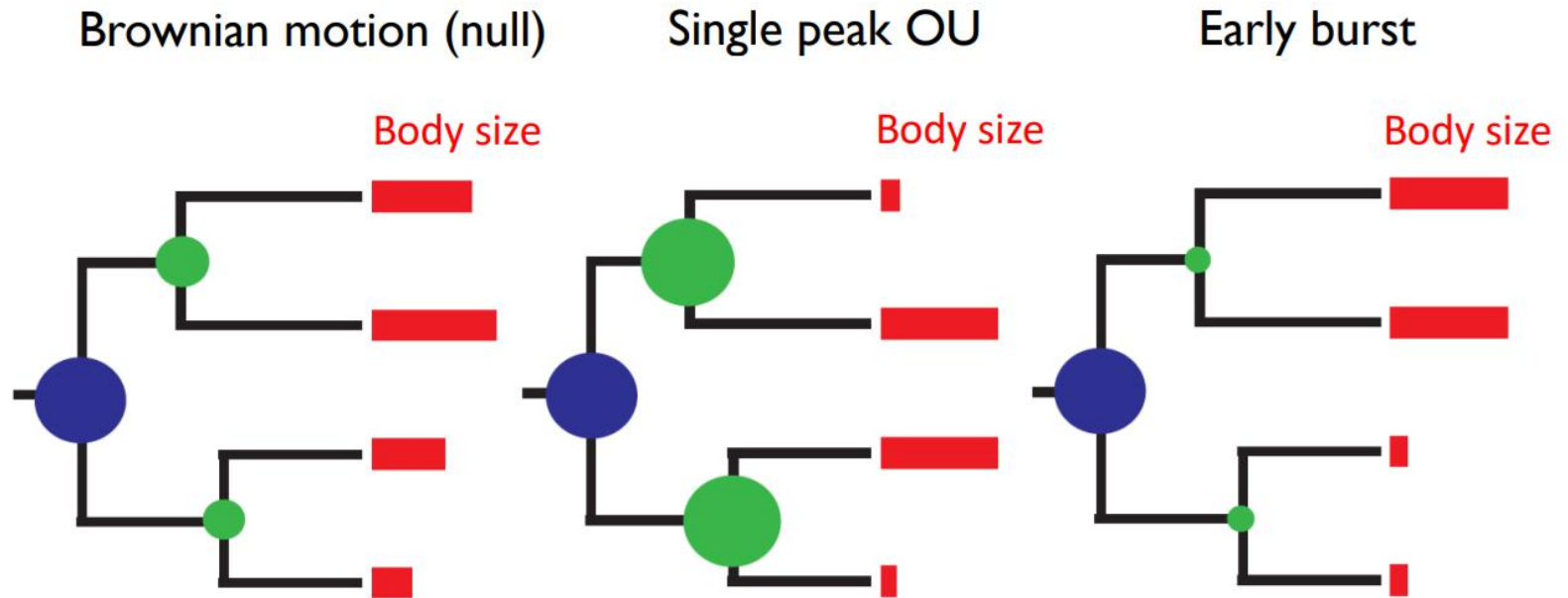
BM, but with a declining rate parameter:

$$\sigma^2(t) = \sigma_0^2 e^{bt}$$

If b is negative, declining rates (i.e. Early burst)

If b is positive, increasing rates (late bursts, not identifiable from OU in ultrametric trees)

Early Burst -> Brownian Motion -> Ornstein-Uhlenbeck



Early Burst -> Brownian Motion -> Ornstein-Uhlenbeck

EARLY BURSTS OF BODY SIZE AND SHAPE EVOLUTION ARE RARE IN COMPARATIVE DATA

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Early Burst -> Brownian Motion -> Ornstein-Uhlenbeck

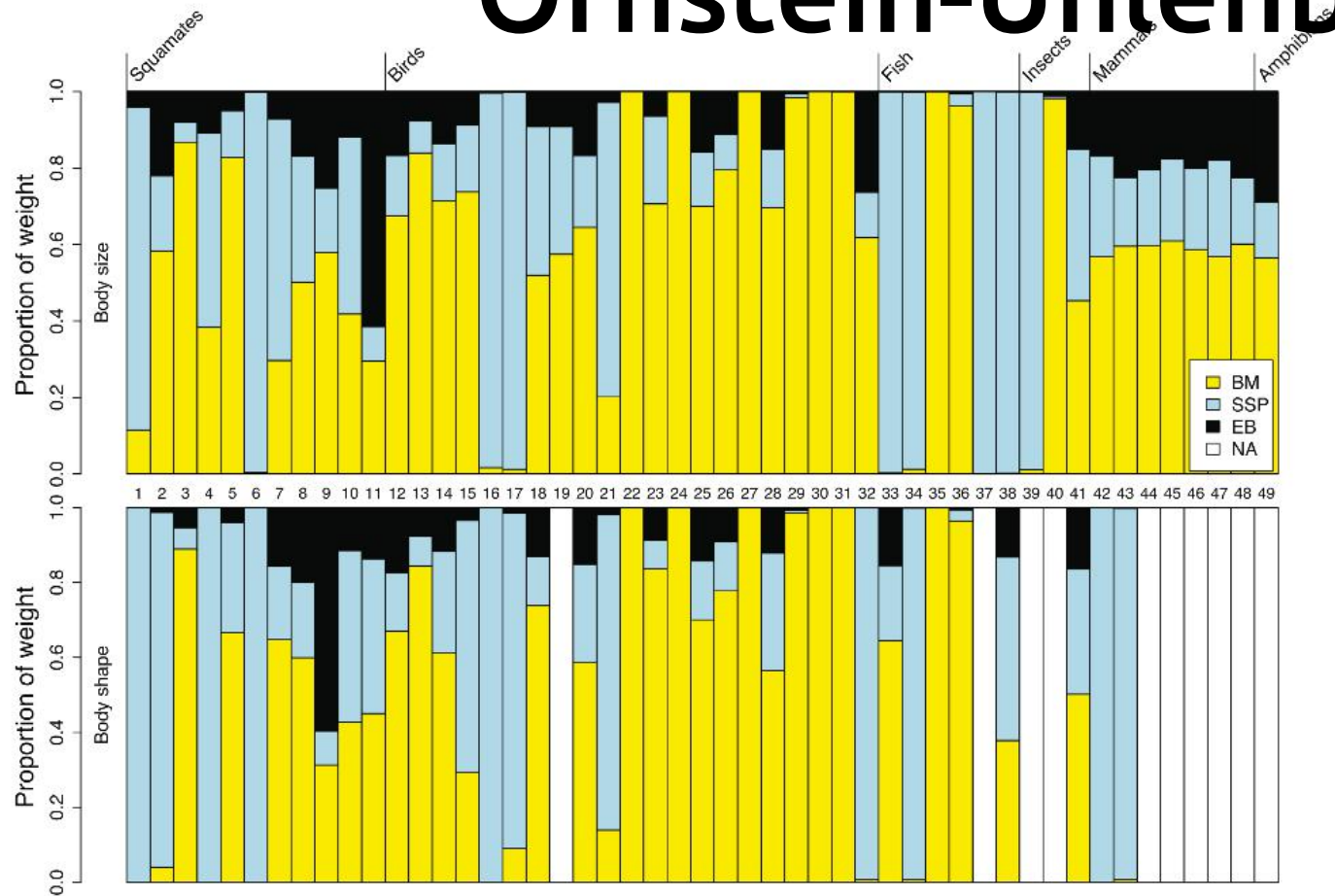


Figure 2. Akaike weights for three models of phenotypic evolution (BM, Brownian motion; SSP, single stationary peak; EB, early burst; NA, not applicable because shape data were unavailable) for all phylogenetic trees in the dataset. Numbers correspond to the datasets as listed in Table 1. Relative area of the bar filled with any color is proportional to the Akaike weight for that model given the data.

Model Adequacy and the Macroevolution of Angiosperm Functional Traits

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Online enhancement: supplemental PDF.

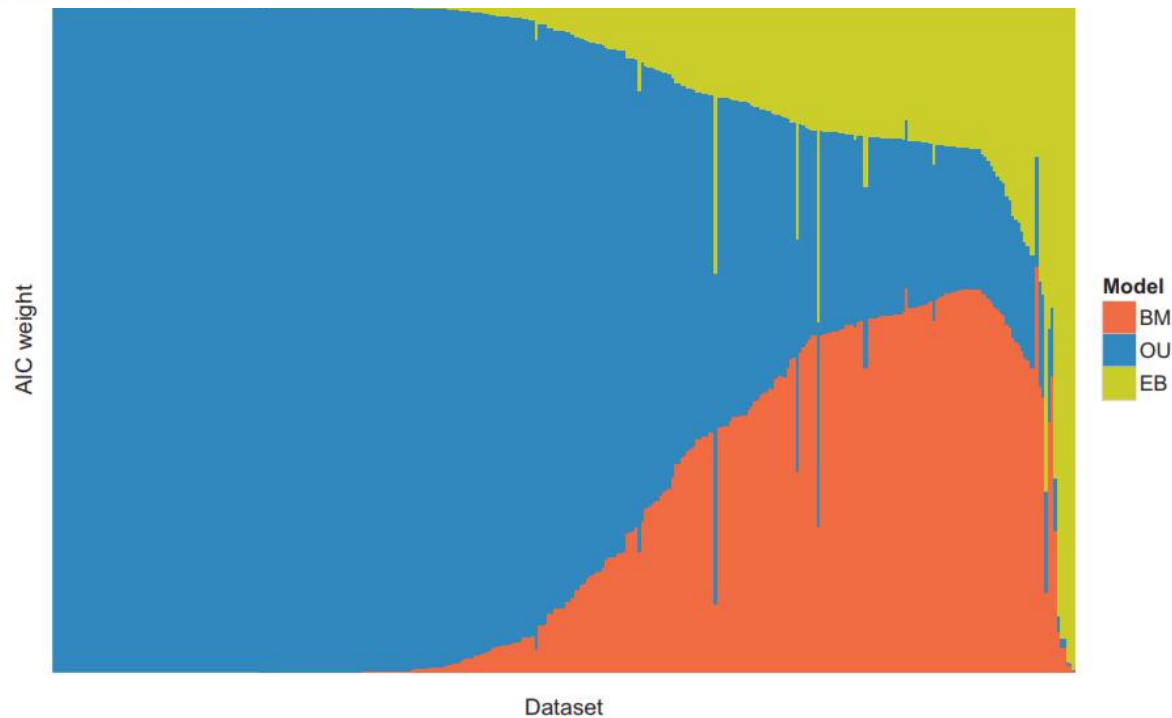


Figure 3: The relative support, as measured by Akaike information criterion (AIC) weight, for the three models used in our study (Brownian motion [BM], Ornstein-Uhlenbeck [OU], and early burst [EB]) across all 337 data sets. An OU model is highly supported for a majority of the data sets.

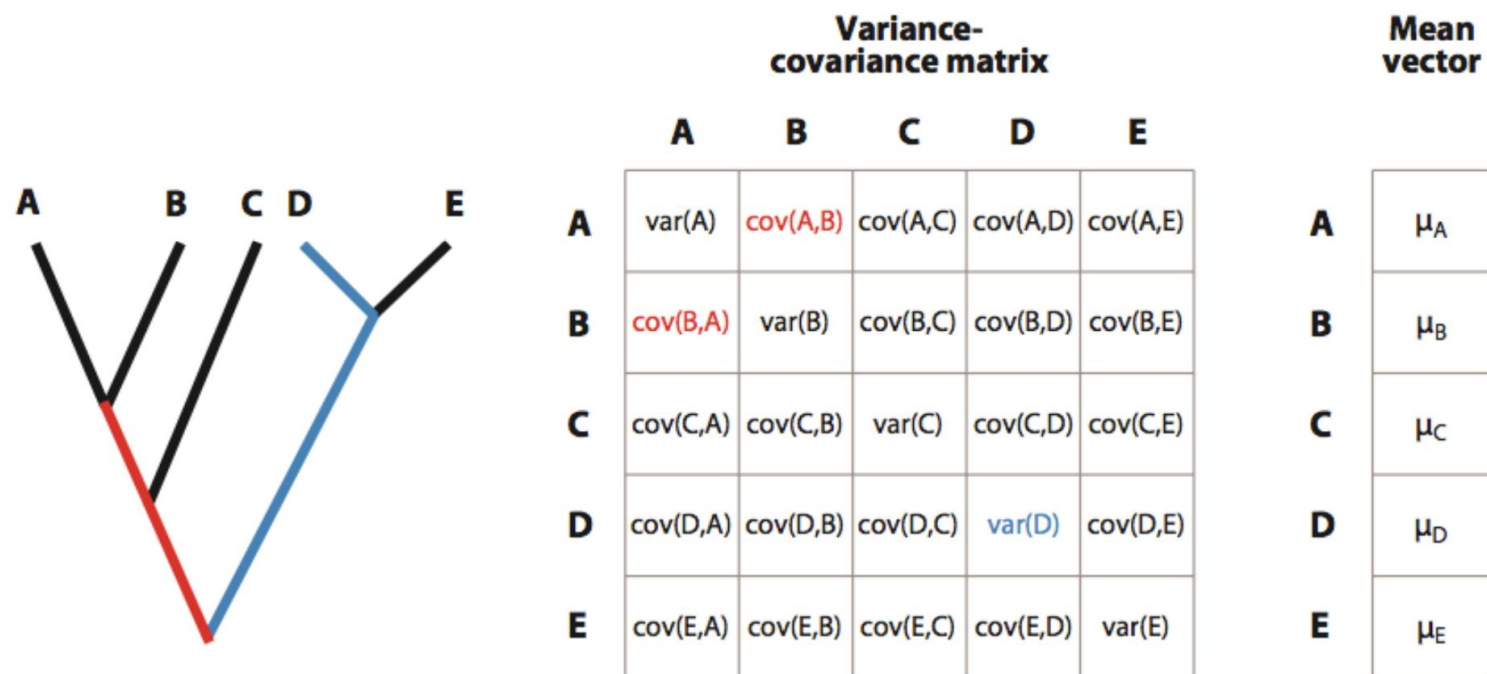


Figure 4

Multivariate normal distribution. The figure shows a tree, the tree's variance-covariance matrix, and the vector of means (which, under Brownian motion, would equal the root state). Highlighted are the branches leading to covariance between taxa A and B (*red*) and the branches leading to variance in D (*blue*).

Why we must account for “measurement” error

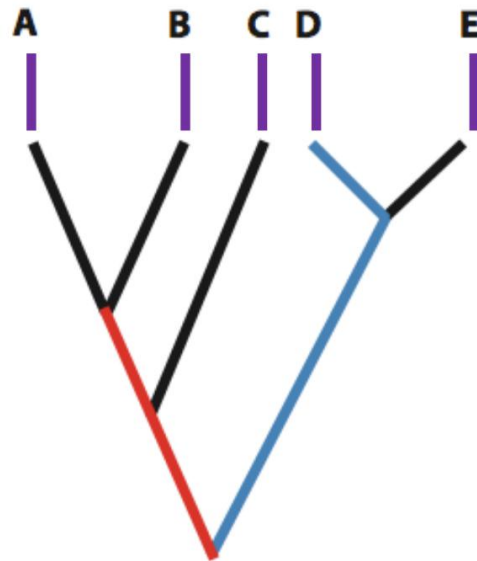


Figure 4

Variance-covariance matrix						Mean vector	
	A	B	C	D	E		
A	var(A) + error	cov(A,B)	cov(A,C)	cov(A,D)	cov(A,E)	A	μ_A
B	cov(B,A)	var(B) + error	cov(B,C)	cov(B,D)	cov(B,E)	B	μ_B
C	cov(C,A)	cov(C,B)	var(C) + error	cov(C,D)	cov(C,E)	C	μ_C
D	cov(D,A)	cov(D,B)	cov(D,C)	var(D) + error	cov(D,E)	D	μ_D
E	cov(E,A)	cov(E,B)	cov(E,C)	cov(E,D)	var(E) + error	E	μ_E

EB

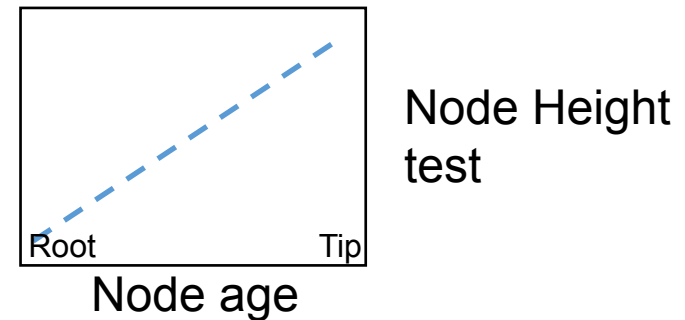
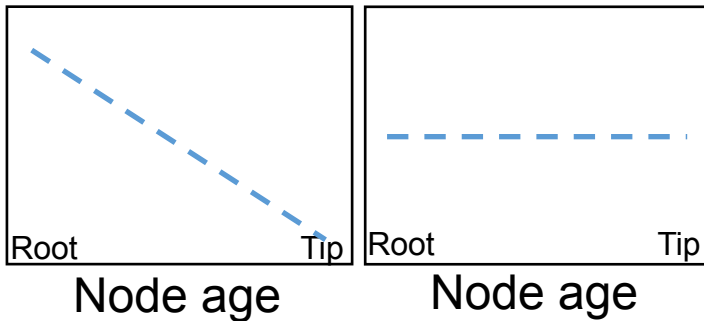
BM

OU

WN



Contrast



Measurement error +
“Biological error”



PGLS + OU : Not a full OU model

Statistically, much like PGLS + Lambda

**Appropriate only for “Allometric-type” relationships
between predictor and response**

**OU model in variance, but not in mean
(instantaneous adaptation)**

**Phylogenetic half-life with no predictors =
measure of phylogenetic signal**

**..... with predictors =
measure of REMAINING
phylogenetic signal in residuals**

What are macroevolutionary landscapes?

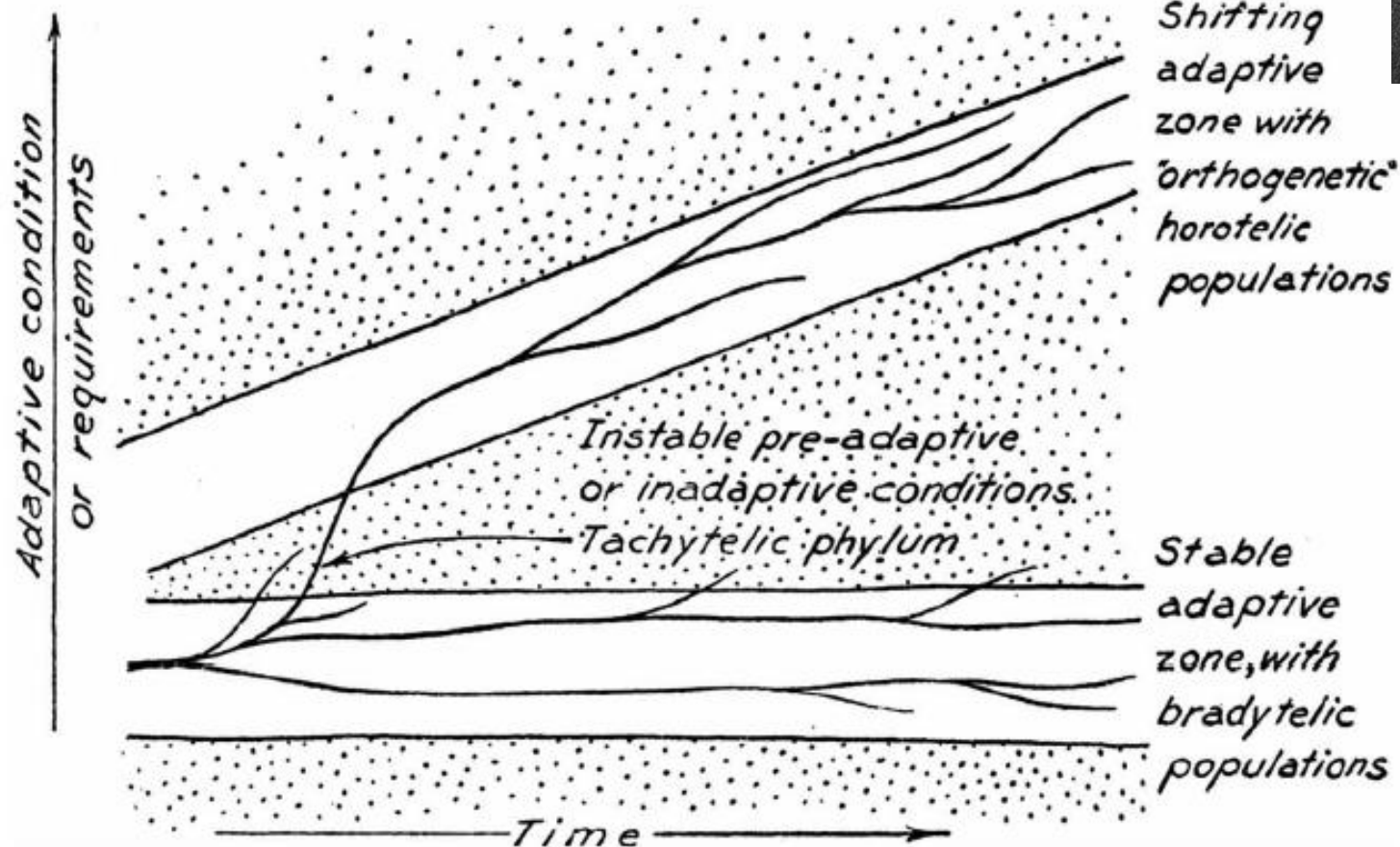
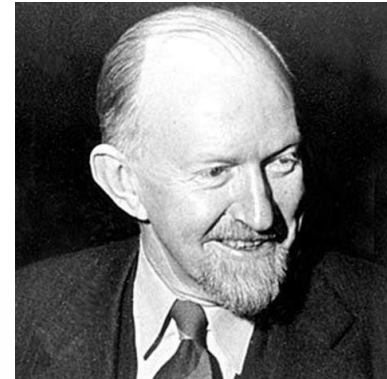
What does alpha measure?

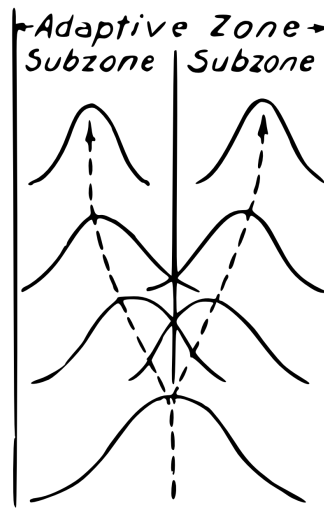
A: Strength of Natural Selection(?)

Problem: What if we measure selection pulling a species *AWAY* from the macroevolutionary optimum in a natural population?

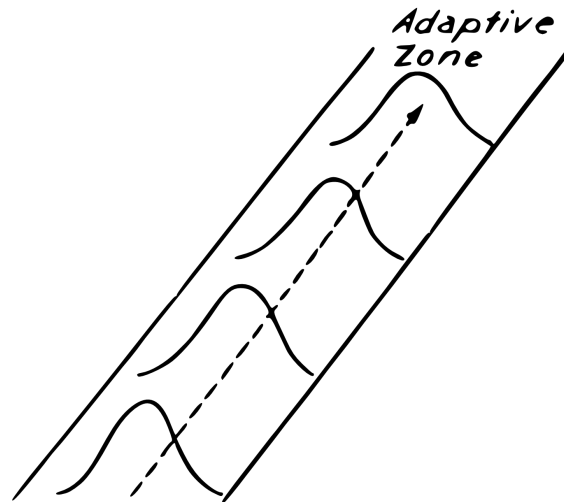
(This is VERY COMMON!)

Simpson's Adaptive Zones

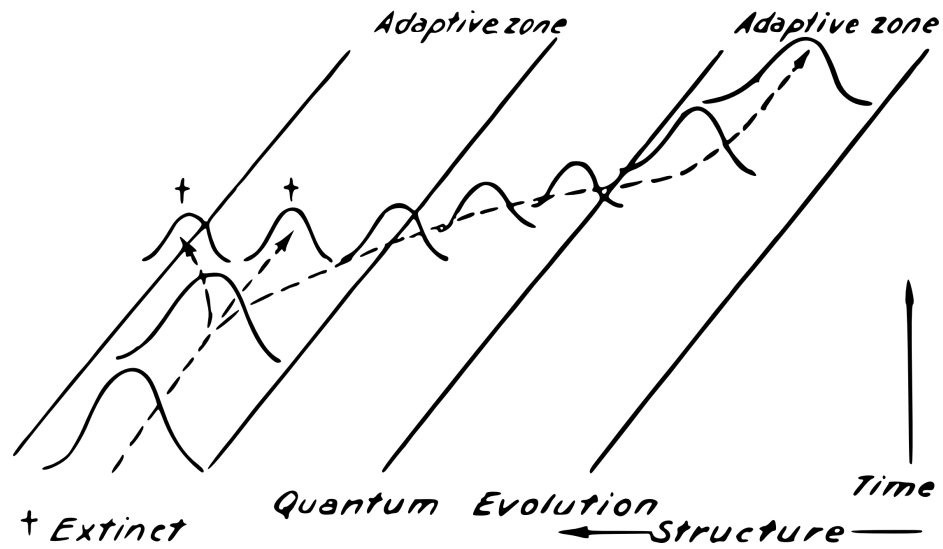




Speciation



Phyletic Evolution



**Next time: Shifting adaptive
zones**