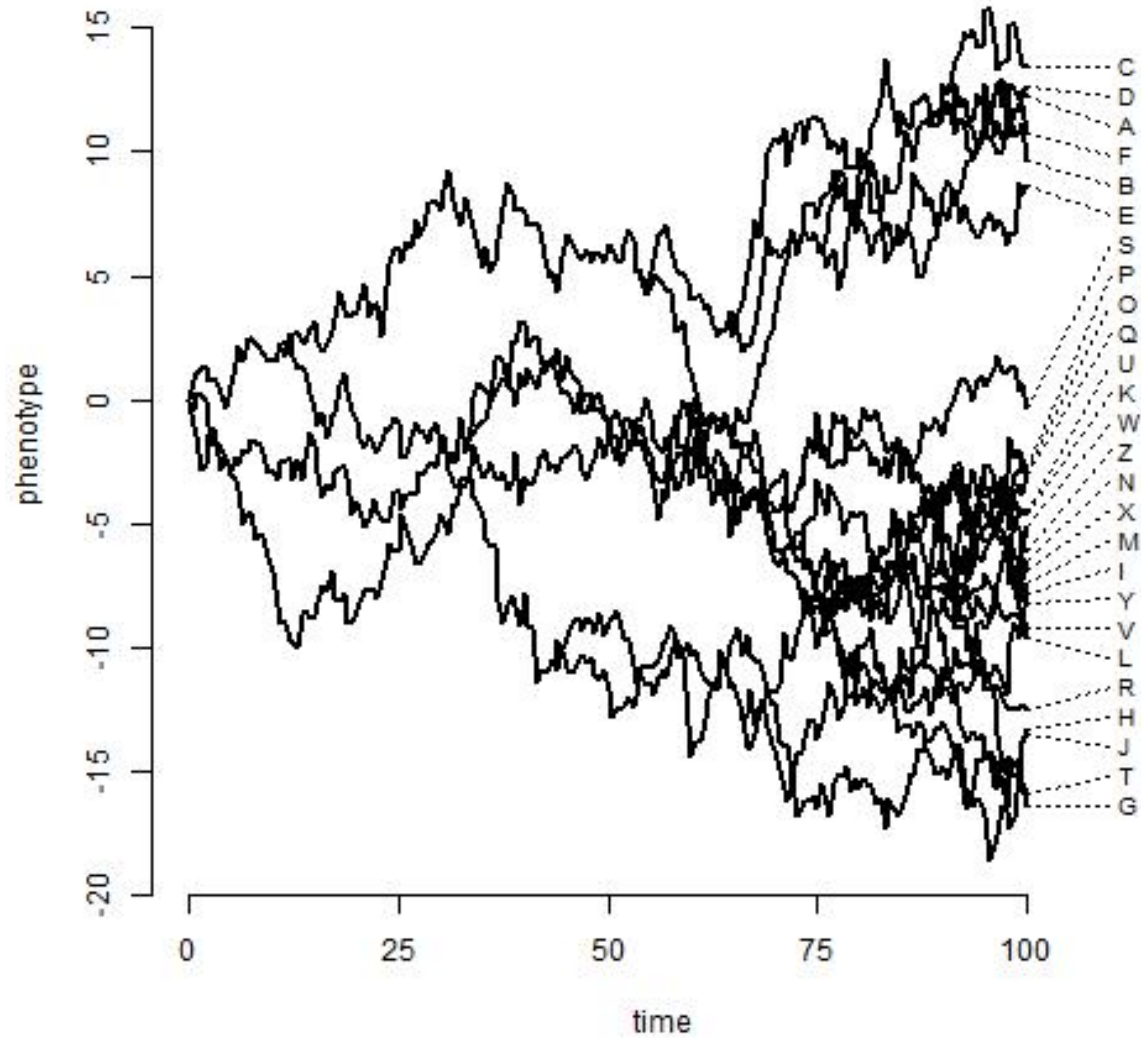# Modeling adaptive evolution

Give me your best estimate of the evolutionary rate (back of the napkin calculation)

Genetic Drift + Natural Selection
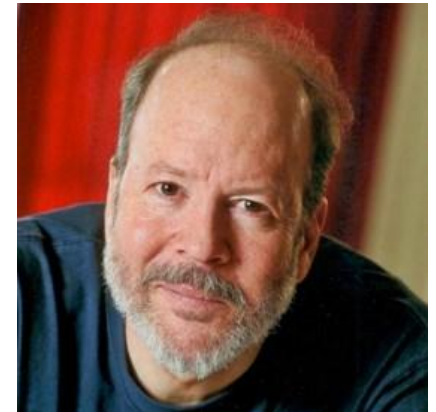

Russ Lande

Genetic drift only:

$\Delta z = G/Ne * dW$

Genetic drift + Natural selection to a Gaussian adaptive peak:
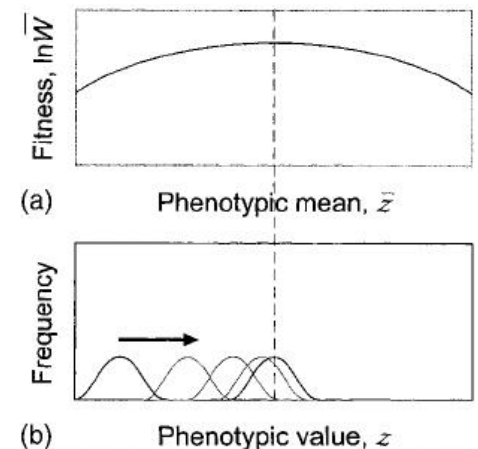
$\Delta z = G/(\omega + P)*(\theta - z) + G/Ne * dW$

Genetic variance

Width of the adaptive landscape

Distance from the optimum

(a) Fitness, $\ln \overline{W}$ — Phenotypic mean, $\bar{z}$

(b) Frequency — Phenotypic value, z

Ornstein-Uhlenbeck Process

$$\Delta z = \alpha(\theta - z) + \sigma\, dW$$
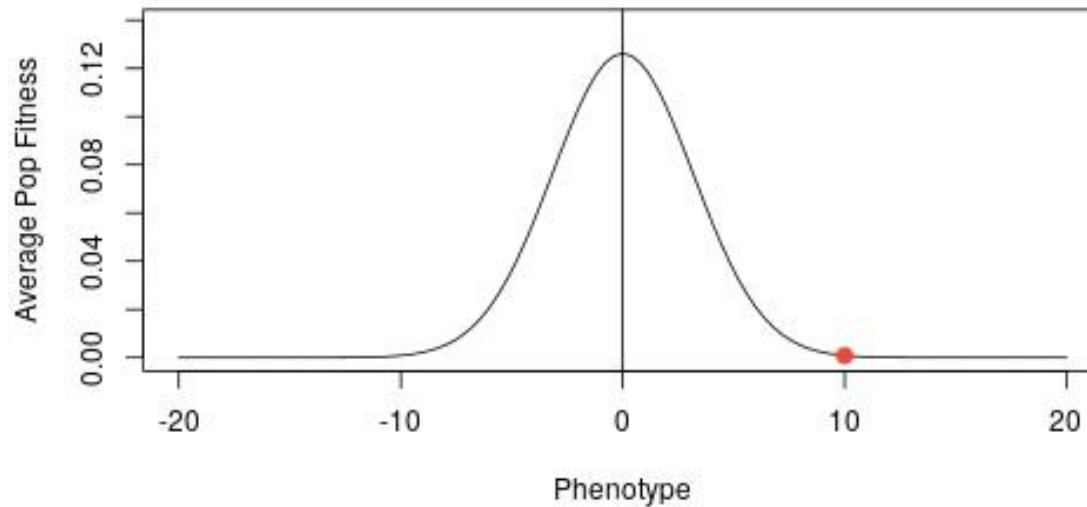
α - Rate of adaptation
   Units: (1/time)

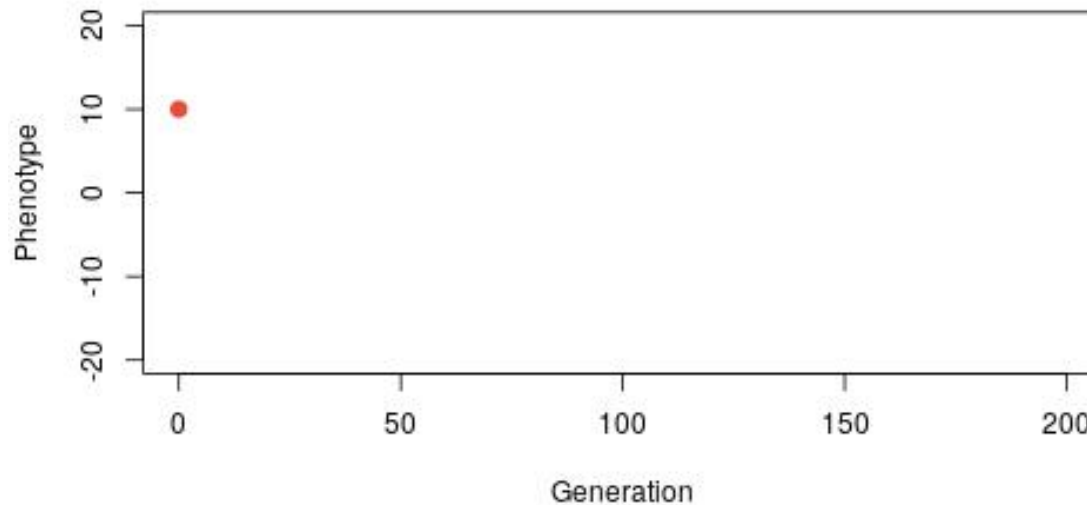σ - Rate of stochastic evolution
   Units: trait units/time

θ - Phenotypic optimum

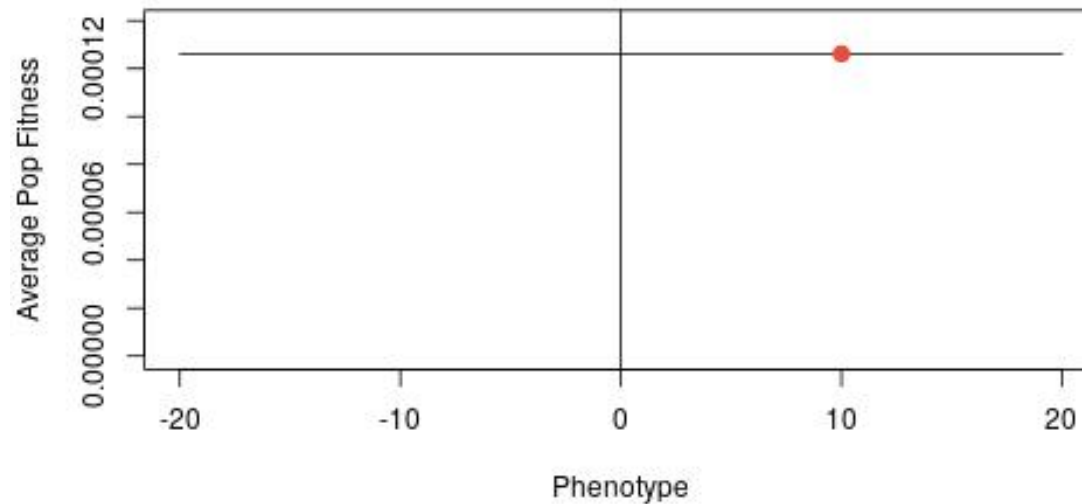# Ornstein-Uhlenbeck process

α = 0.1
σ²= 1

Ornstein-Uhlenbeck process

α = 0.000001
σ² = 1

Ornstein-Uhlenbeck process

α = 0.1
σ² = 1

Ornstein-Uhlenbeck process

α = 0.1
σ² = 1
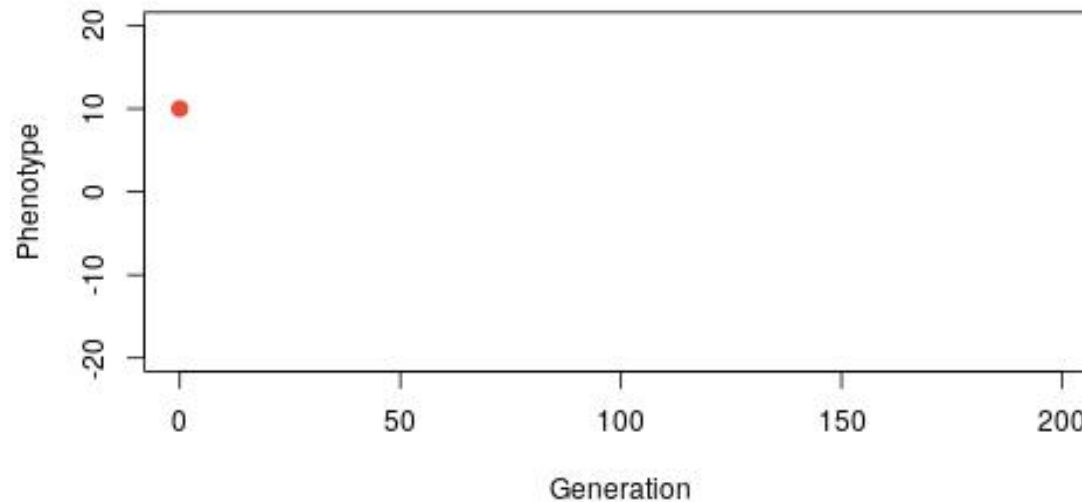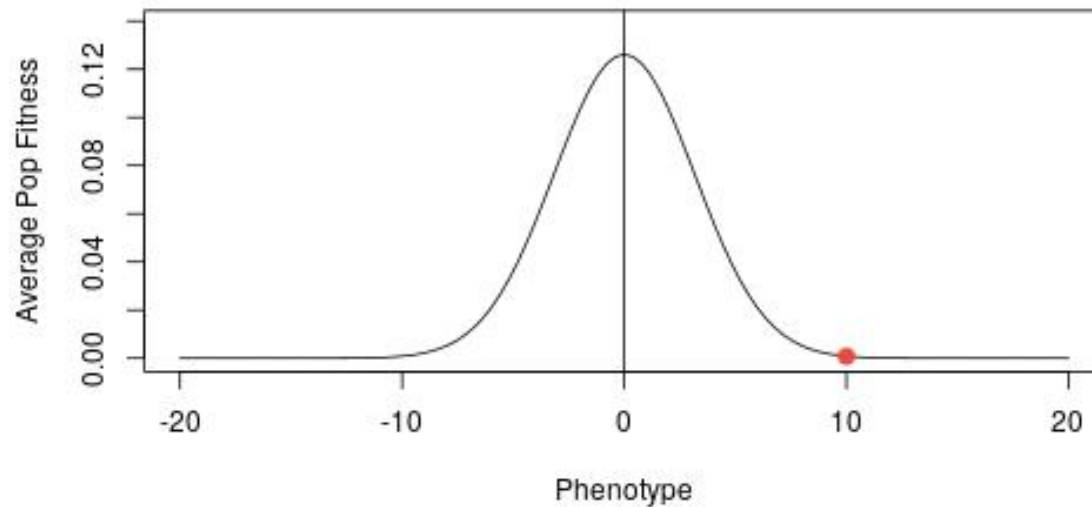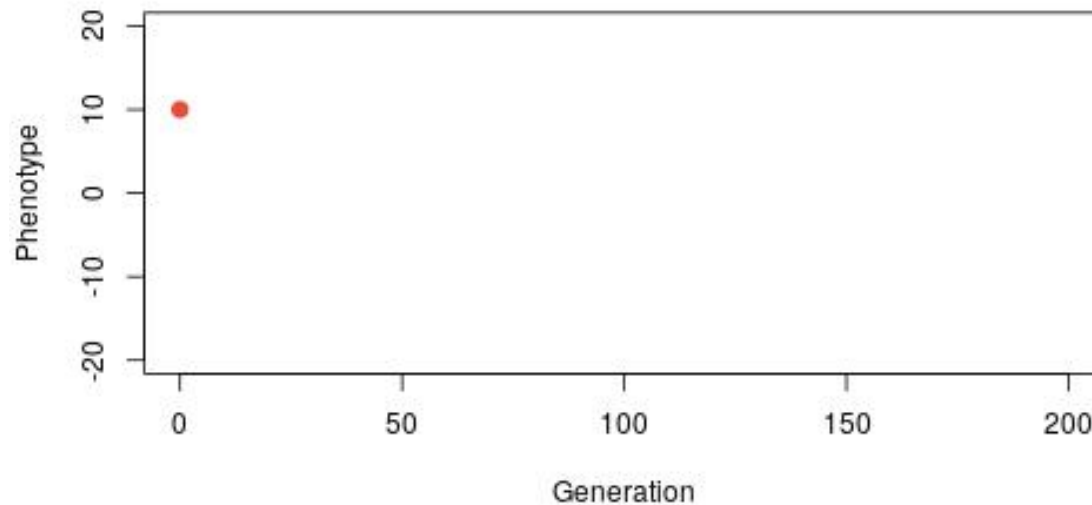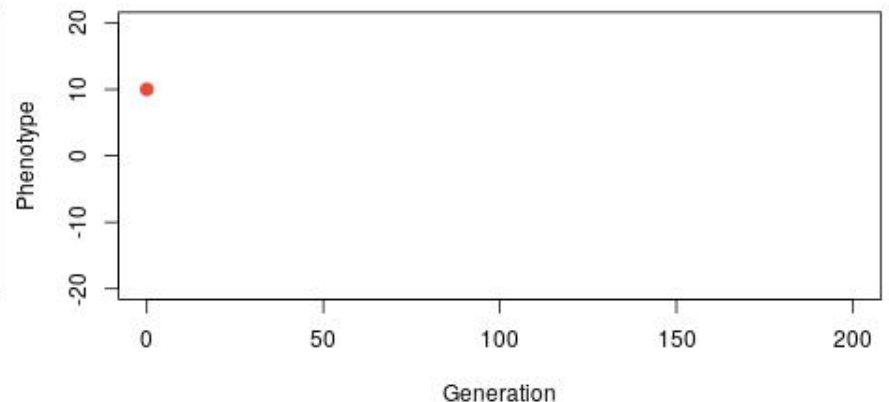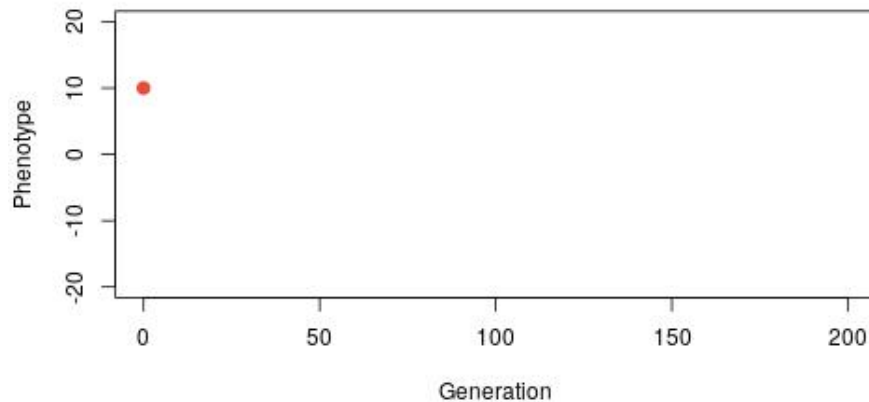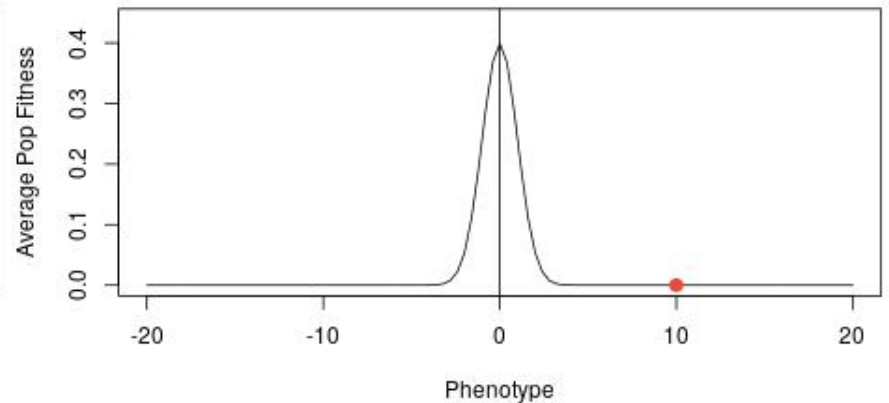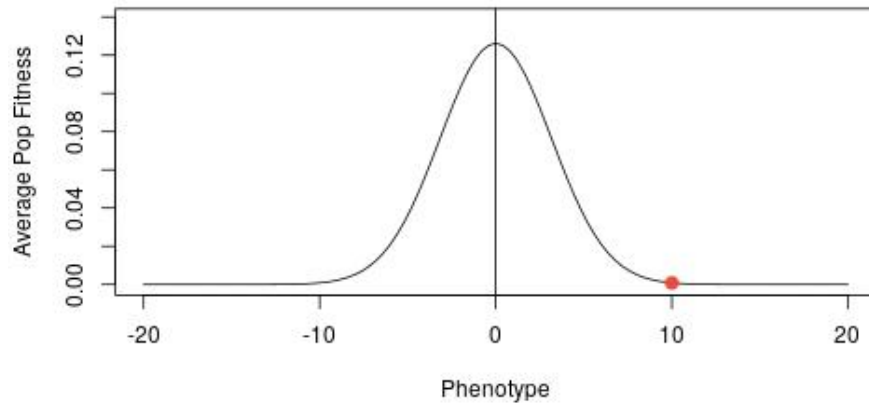
α = 1
σ² = 10

How does Hansen 1997 interpret the "Primary Optimum"?

What is a Primary Optimum?

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

Adaptive Zone

Subzone | Subzone

Speciation

Adaptive Zone

Phyletic Evolution

Adaptive zone

Adaptive zone

† Extinct

Quantum Evolution

Structure

Time
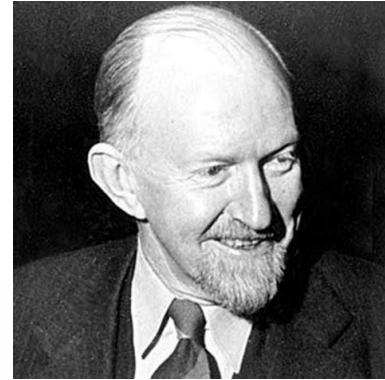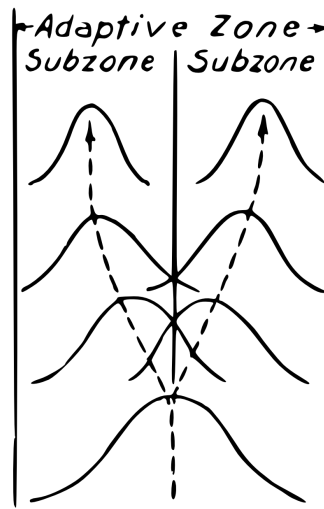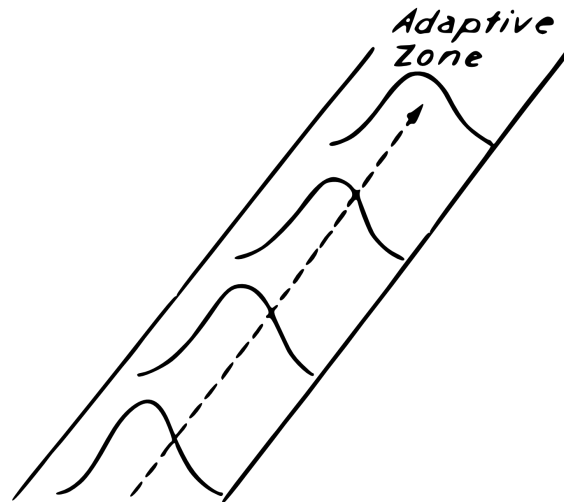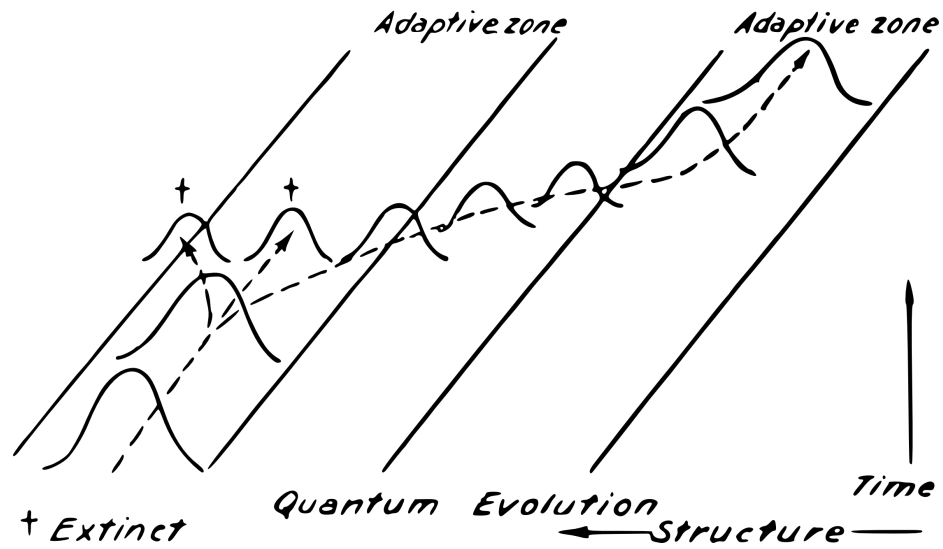
Hansen 1997
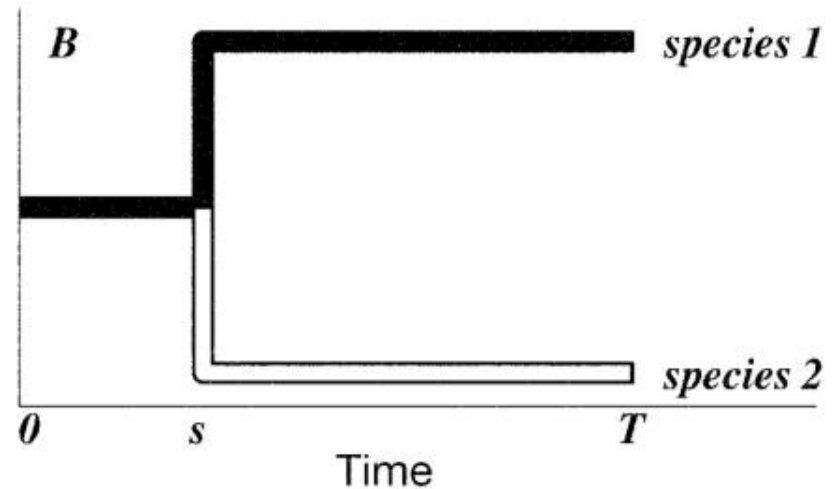
$$E[X_1(T)] = \theta_0 e^{-\alpha T} + \theta_1(1 - e^{-\alpha T})$$

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

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

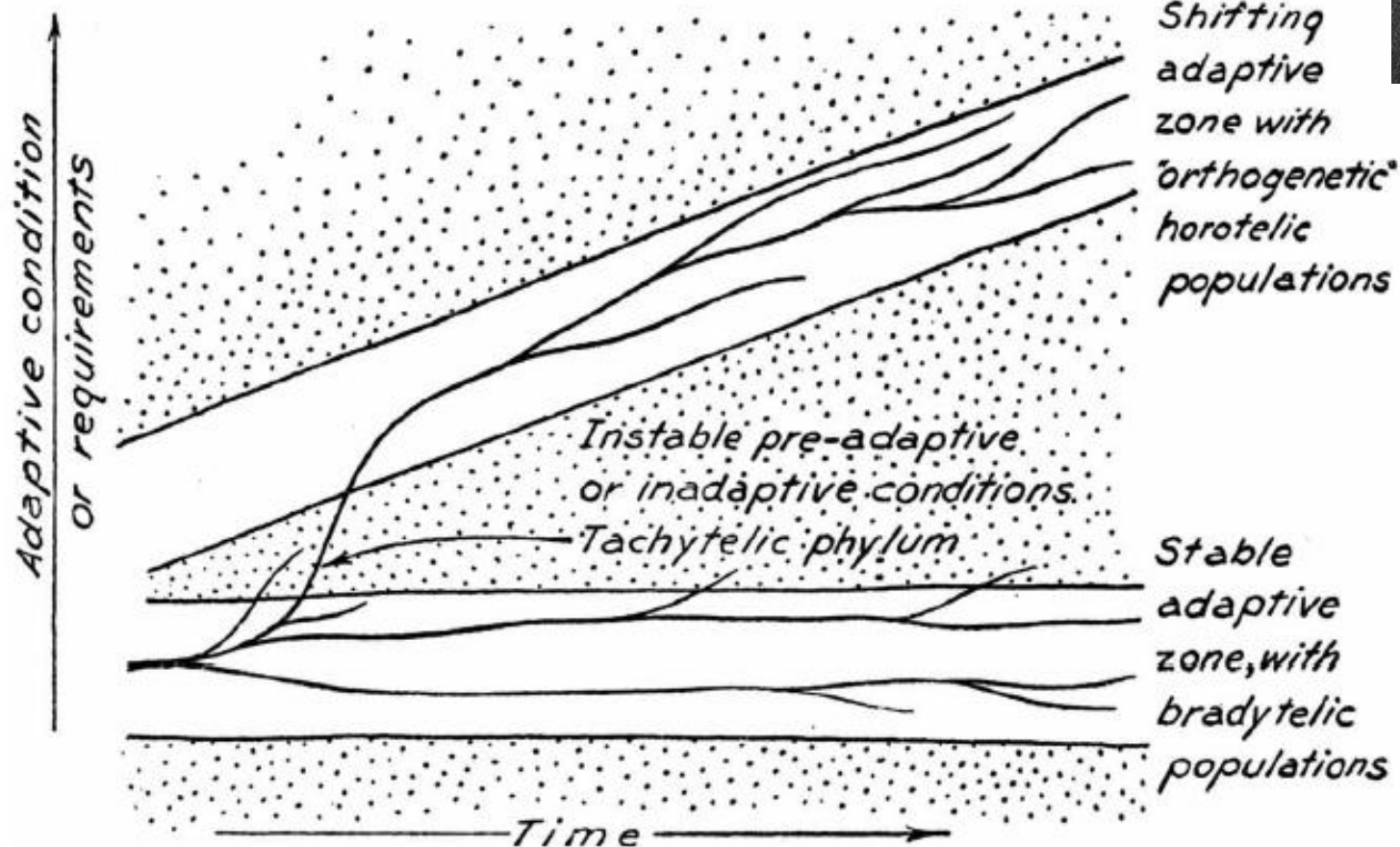$$+ \theta_2[1 - e^{-\alpha(T-s)}]$$

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

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 = σ²/(2α)

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

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

Phylogenetic half-life = ln2/(2α)

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

Interpreting half-life

ln2/α
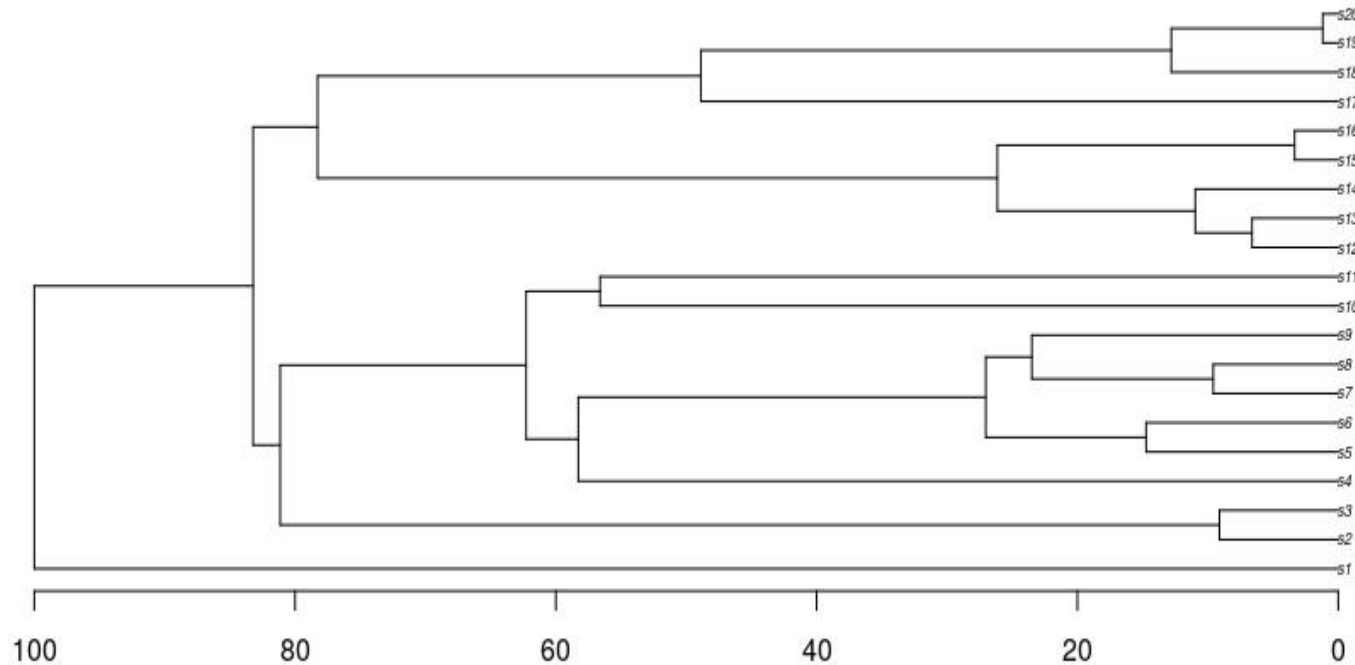
BM-like   White noise

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 ->
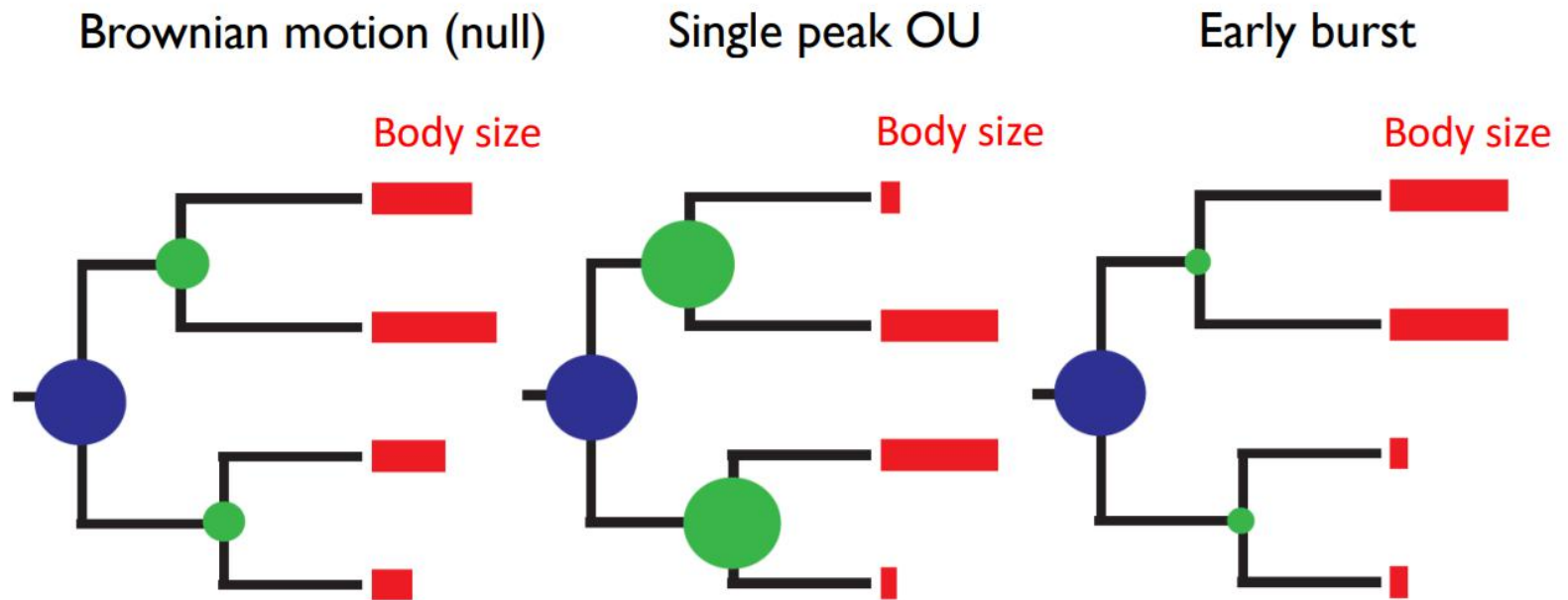### Ornstein-Uhlenbeck

Brownian motion (null)   Single peak OU   Early burst

Body size   Body size   Body size

Early Burst ->
Brownian Motion ->
Ornstein-Uhlenbeck

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

Luke J. Harmon,[1,2,3] Jonathan B. Losos,[4] T. Jonathan Davies,[5] Rosemary G. Gillespie,[6] John L. Gittleman,[7] W. Bryan Jennings,[8] Kenneth H. Kozak,[9] Mark A. McPeek,[10] Franck Moreno-Roark,[11] Thomas J. Near,[12] Andy Purvis,[13] Robert E. Ricklefs,[14] Dolph Schluter,[2] James A. Schulte II,[11] Ole Seehausen,[15,16] Brian L. Sidlauskas,[17,18] Omar Torres-Carvajal,[19] Jason T. Weir,[2] and Arne Ø. Mooers[20]

[1]Department of Biological Sciences, University of Idaho, Moscow, Idaho 83844

[2]Biodiversity Centre, University of British Columbia, Vancouver, BC V6T1Z4, Canada

[3]E-mail: lukeh@uidaho.edu

Early Burst ->
Brownian Motion ->
Ornstein-Uhlenbeck
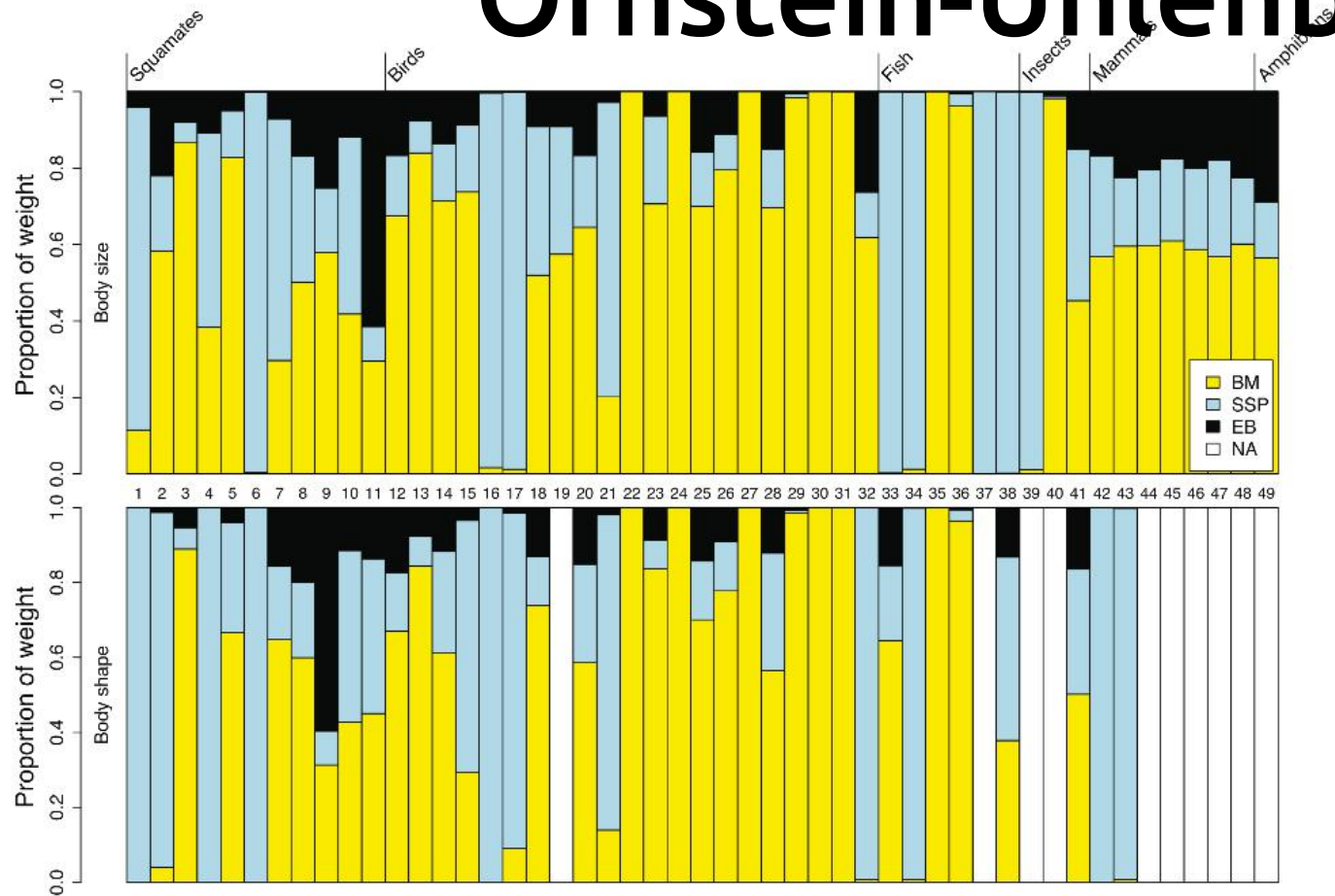
Figure 2. Akaike weights for three models of phenotypic evolution (BM, Brownian motion; SSP, single stationary peak; EB, early burst; NA, not applicable because shape data were unavailable) for all phylogenetic trees in the dataset. Numbers correspond to the datasets as listed in Table 1. Relative area 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

Matthew W. Pennell,[1,*] Richard G. FitzJohn,[2] William K. Cornwell,[3] and Luke J. Harmon[1]

1. Department of Biological Sciences and Institute for Bioinformatics and Evolutionary Studies, University of Idaho, Moscow, Idaho 83844;
2. Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia;   3. School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, New South Wales 2052, Australia
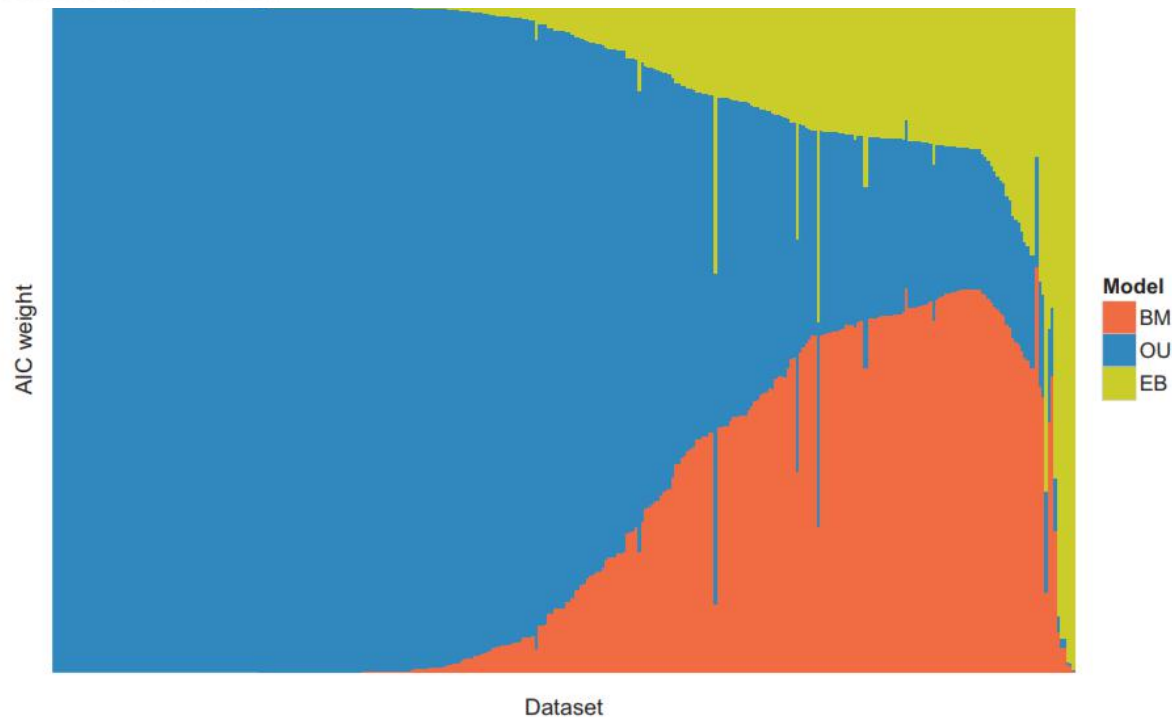
Figure 3: The relative support, as measured by Akaike information criterion (AIC) weight, for the three models used in our study (Brownian motion [BM], Ornstein-Uhlenbeck [OU], and early burst [EB]) across all 337 data sets. An OU model is highly supported for a majority of the data sets.
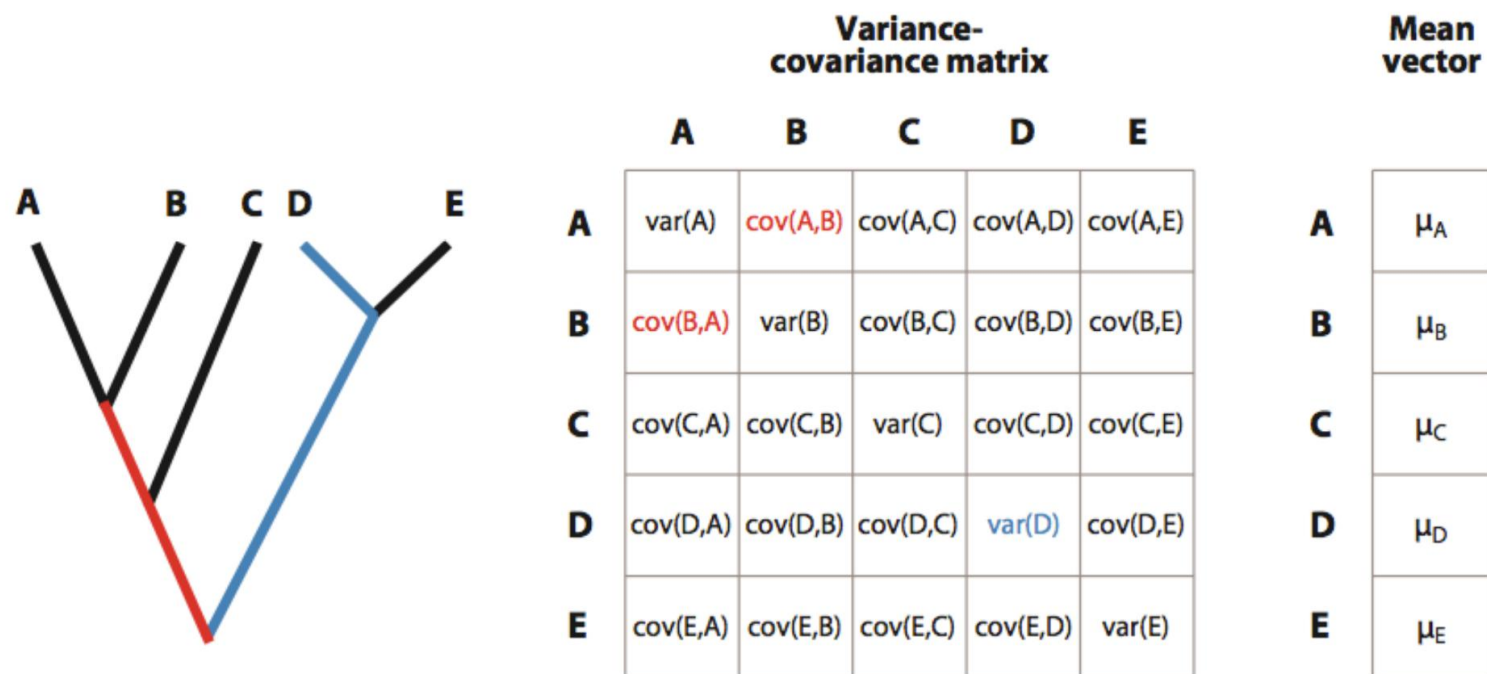
Figure 4

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*).
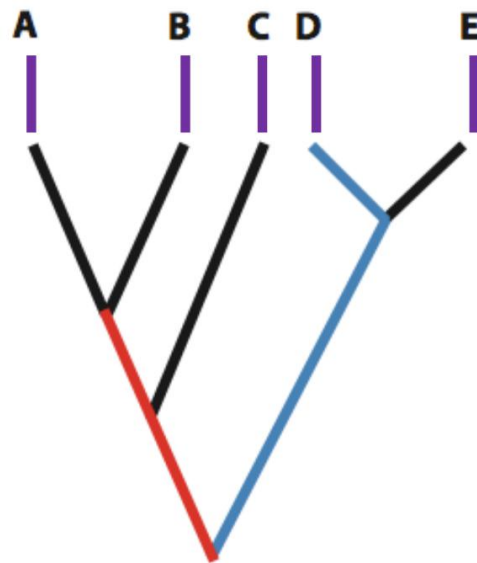
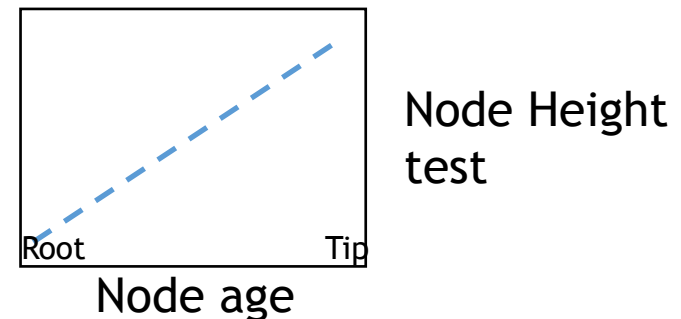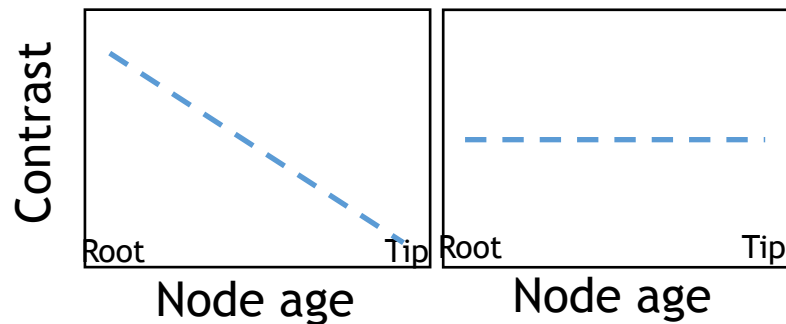# Why we must account for "measurement" error

Figure 4

EB   BM   OU   WN

α = 0   α   α =∞
halflife=∞   halflife=0   OU models

High phylogenetic signal   No phylogenetic signal

ACDC model
(EB/OU)

−   0   +

Contrast

Root   Tip | Root   Tip   Root   Tip

Node age   Node age   Node age

Node Height
test

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

Next time: Shifting adaptive zones