

# **Phylogenetic comparative methods**

## **Phylogenetics**

**Use traits to estimate tree**

## **Phylogenetic Comparative Methods**

**Assume tree is known, analyze evolutionary patterns**

# **Discrete trait evolution**

**Mk models (CTMC models!  
Not much new to learn)**

# **Continuous trait evolution**

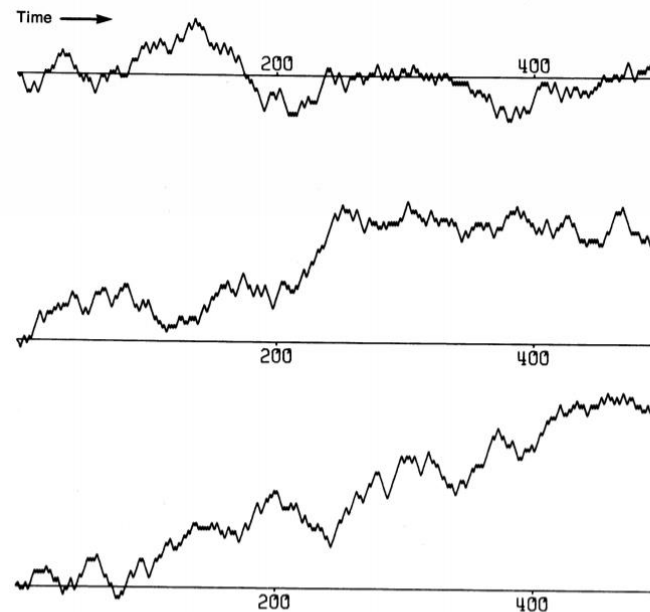
**Gaussian models (Stochastic  
differential equations)**

# Random walks

Are patterns of trait change in the fossil record significantly different from random?



David Raup

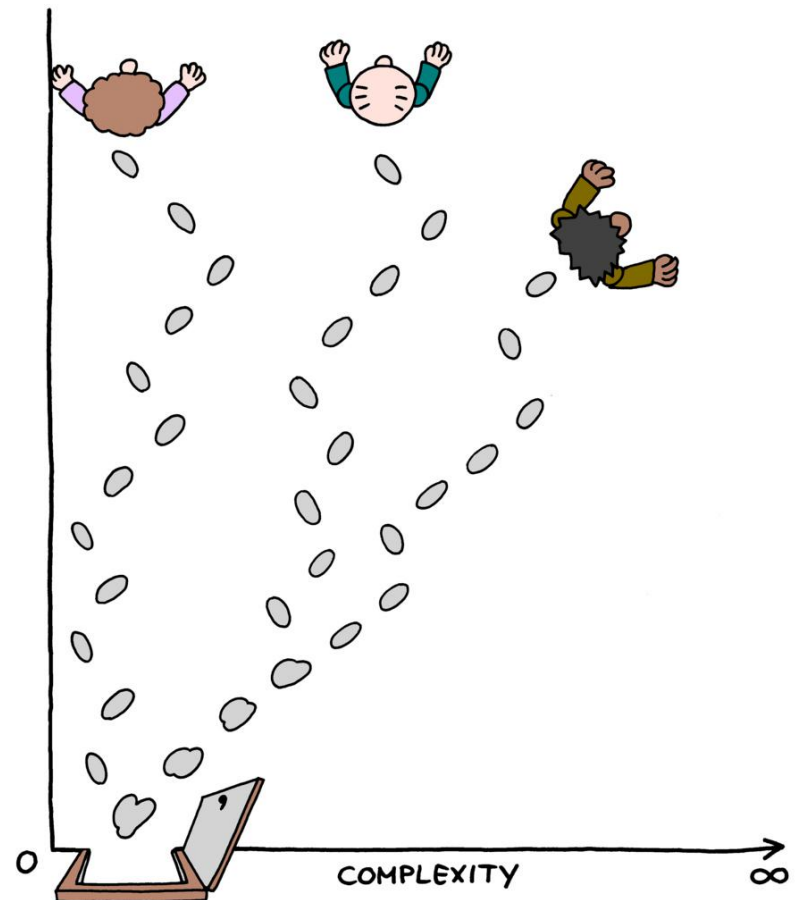
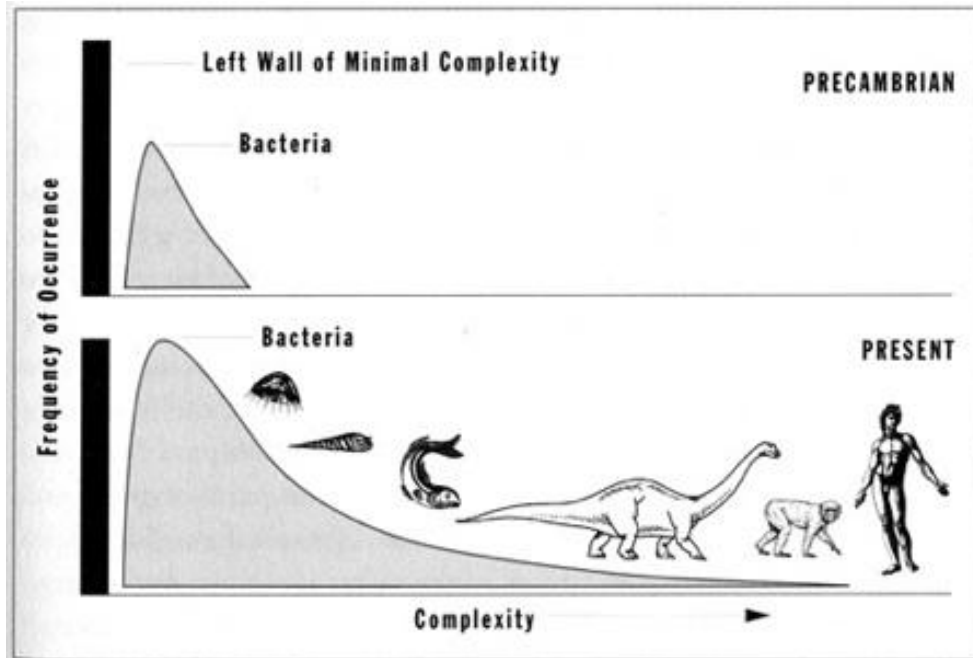


amples of orthoselection—that is, long-term response to single selective factors. Although the top one *does* depart significantly from expectations, and thus is a candidate for biological interpretation, tests using the Markov chain model on the bottom example demonstrate that the change could easily have occurred by chance—and the orthoselection explanation model is not justified (Raup, in press). The obvious trend here could have resulted either from

Figure 4. Three computer-generated random walks show the evolution of a morphological character or a genetic frequency. The three random walks, each 500 steps long, were selected from 20 that were constructed. The upper one comes closest to the normal idea of a random walk yet is a relatively uncommon type; the two lower ones are actually more typical because of the Markov property of random walks. In random walks that are reasonably long, the line of steps will cross the starting point (horizontal axis) in the second half of the walk in only 50% of the cases; in 20% of random walks, the line will stay on one side 97.6% of the time; in 10% of random walks, there will be no crossing after the first 3% of the walk. (Raup in press.)

# The Drunkard's Walk

Are patterns of trait change in the fossil record significantly different from random?

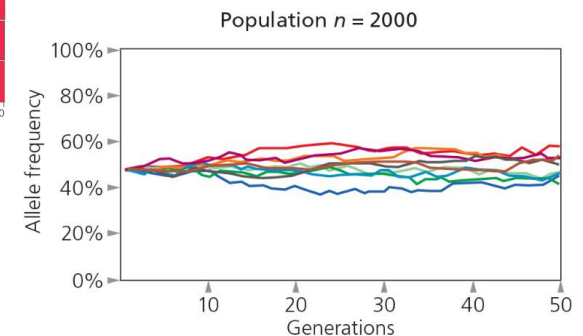
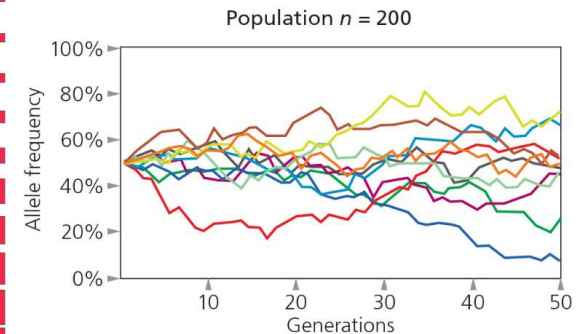
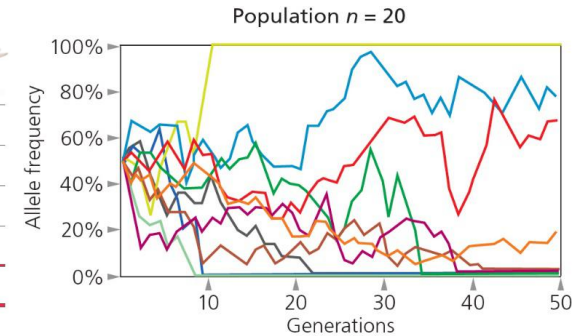
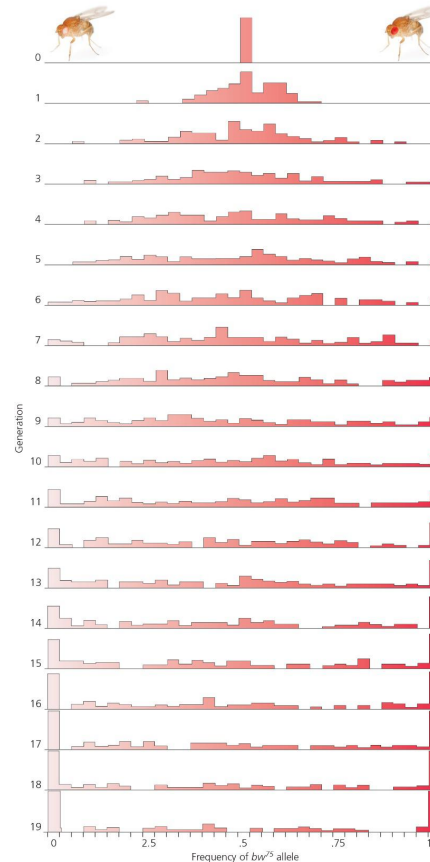


# Population genetics

Luca Cavalli-Sforza  
& Anthony Edwards  
(remember them?)

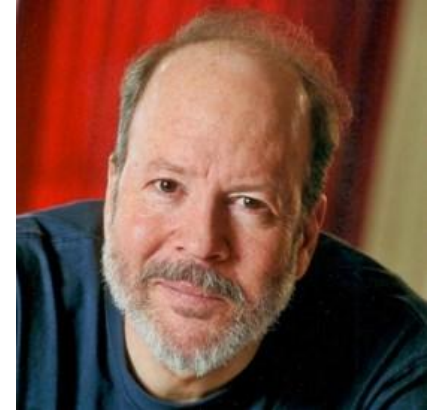
Allele frequency  
evolution by  
genetic drift can be  
approximated by  
*Brownian Motion*

$$E \left[ (\Delta p)^2 \right] = \frac{p(1-p)}{2N_e}$$



# Quantitative genetics

Lande demonstrated that genetic drift in a quantitative character can also be approximated by Brownian Motion



Russ Lande

Expected change per generation:

$$\Delta z = 0$$

$$\text{Variance} = G/N_e$$

# Generalized Random Walk

$$\mathbf{z}_{t+1} = \mathbf{z}_t + N(\mu, \sigma^2)$$

**Cool stats rule: Variances are additive**

**If:**

$$A \sim N(0, \sigma_A^2)$$

$$B \sim N(0, \sigma_B^2)$$

**Then:**

$$A + B \sim N(0, \sigma_A^2 + \sigma_B^2)$$



**So if you take many lineages  
evolving by a Random Walk for  $t$   
generations, what is the  
variance among them?**

# Continuous time Random Walk = Brownian Motion

$$dz = \mu t + \sigma^* dW$$



Wiener Process

# So what about phylogeny?

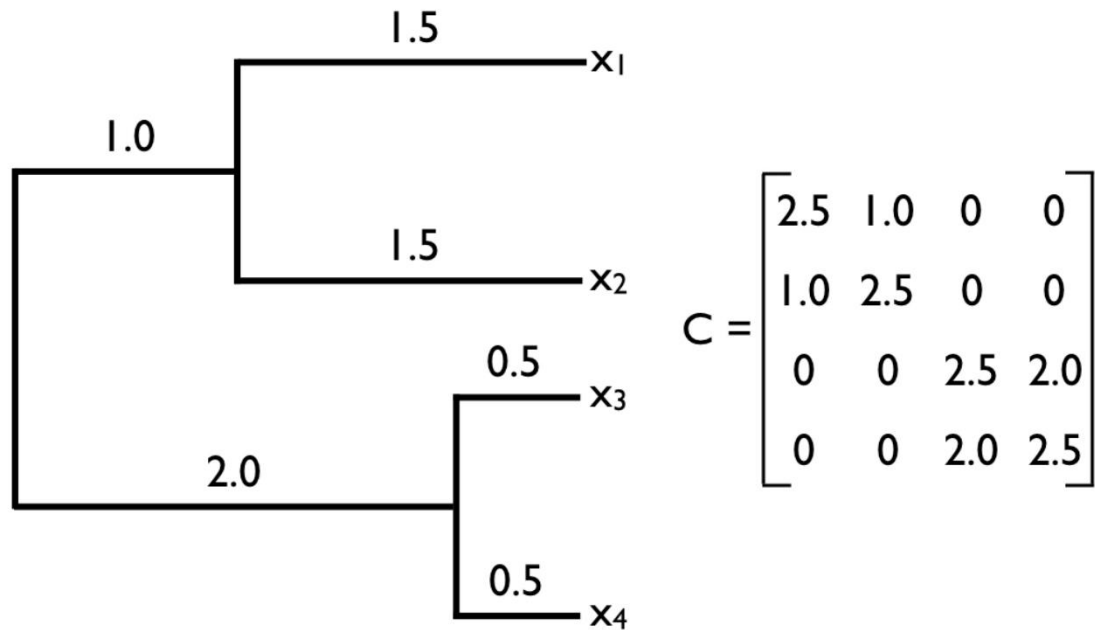
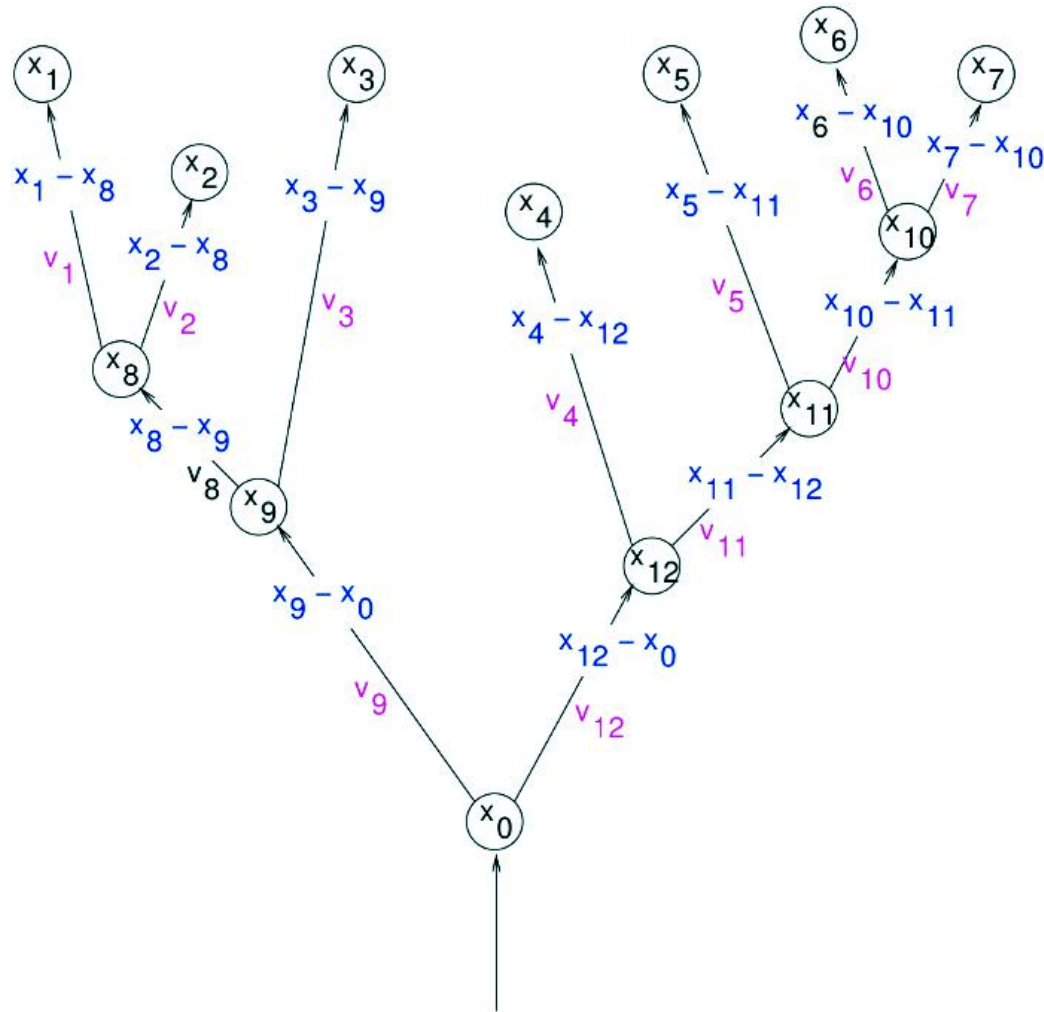
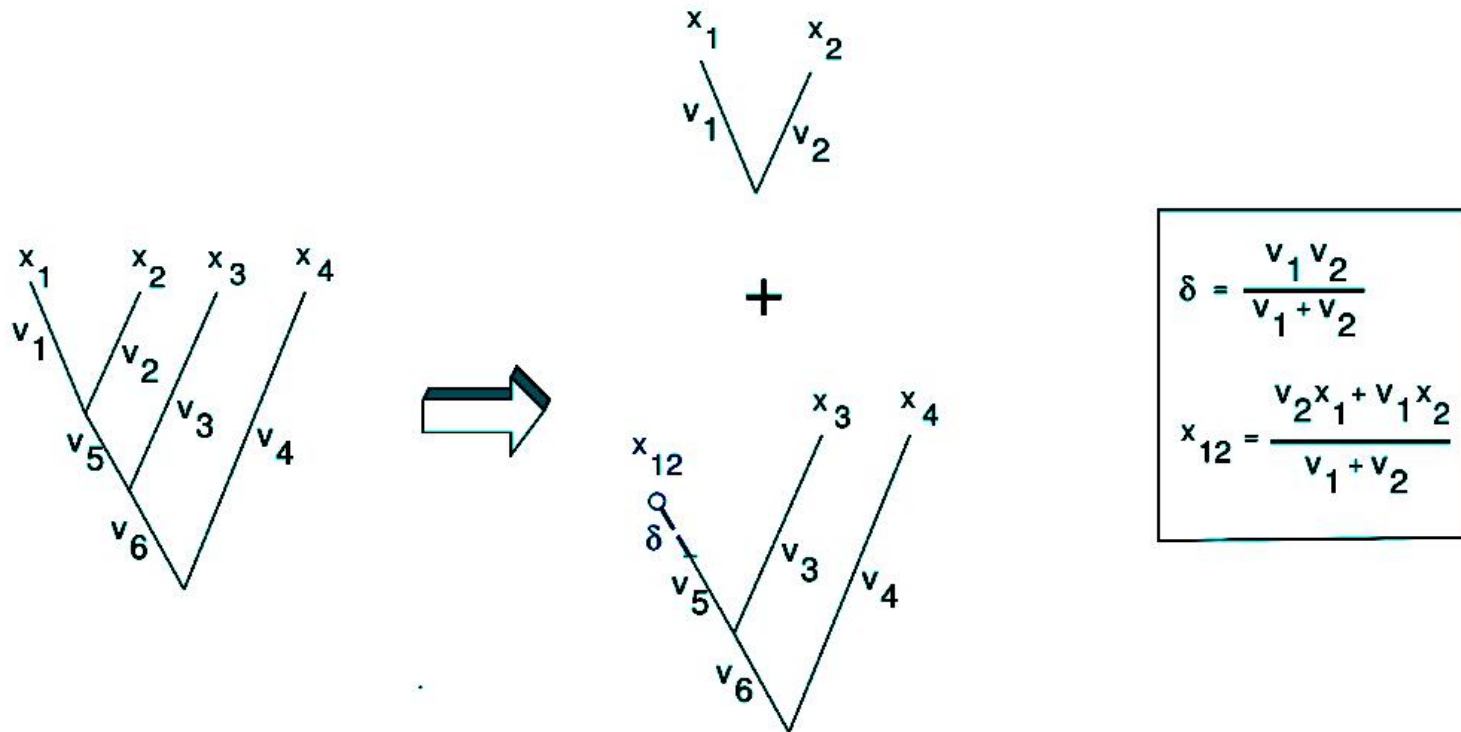


Figure 3.5. Example of a phylogenetic tree (left) and its associated phylogenetic variance-covariance matrix  $C$  (right).

# Phylogenetically “Independent” Contrasts



# Phylogenetically “Independent” Contrasts



**A tree of  $N$  tips leads to  $N-1$   
contrasts**

# Multivariate Brownian Motion

Univariate:

$$\text{root} = \mu$$

$$\text{step variance} = \sigma^2$$

Multivariate (N traits):

$$\text{root} = c(\mu_1, \dots, \mu_N)$$

$$\text{step variance} = \mathbf{R} = \begin{bmatrix} \sigma_x^2 & \sigma_{xy} \\ \sigma_{xy} & \sigma_y^2 \end{bmatrix}$$