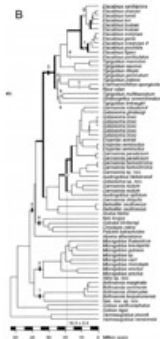


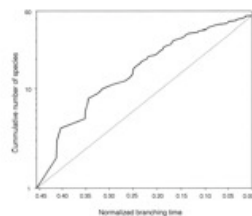
## Outline

- How do lineages accumulate under the birth-death model?
- Estimating speciation and extinction rates from trees
- Testing hypotheses about diversification



Ruber et al. 2003

## Slowdown in Speciation Rate



## Slowdown statistic

- Tests for longer branches near the tips of a phylogenetic tree
- Signature of an early, rapid radiation

$$\gamma = \frac{\left( \frac{1}{n-2} \sum_{i=1}^{n-2} \left( \sum_{j=i}^{n-1} l_{ij} \right) \right) - \left( \frac{T}{2} \right)}{T \sqrt{\frac{1}{12(n-2)}}}, T = \left( \sum_{i=1}^n l_i \right)$$

## Slowdown statistic

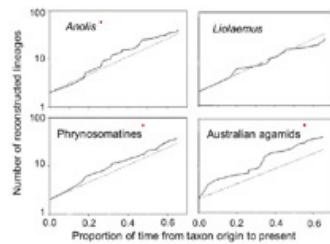
- Under pure-birth model,  $\gamma \sim N(0,1)$
- $\gamma < 0$  means diversification has slowed
- $\gamma > 0$  difficult to interpret

$$\gamma = \frac{\left( \frac{1}{n-2} \sum_{i=1}^{n-2} \left( \sum_{j=i}^{n-1} l_{ij} \right) \right) - \left( \frac{T}{2} \right)}{T \sqrt{\frac{1}{12(n-2)}}}, T = \left( \sum_{i=1}^n l_i \right)$$

## Slowdown statistic

- Many (most?) clades show this signature of slowing rates of diversification through time
- Signature of adaptive radiation?

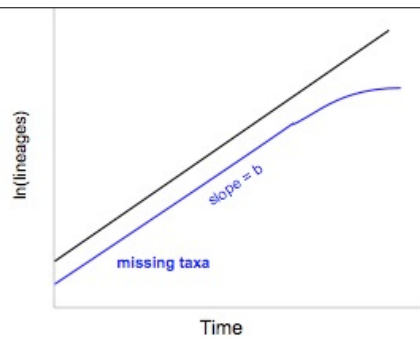
## Examples



(Harmon et al. 2005 Science)

## What about missing taxa?

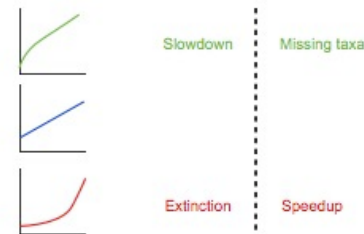
- Missing taxa are more likely to connect to the tree near the tips
- You are missing taxa in your tree
- Randomly missing taxa looks like a slowdown



## Missing Taxa

- Have to account for missing taxa when interpreting a slowdown
- Can use simulations
- What if missing taxa are non-random?

## The problem...



## Outline

- How do lineages accumulate under the birth-death model?
- Estimating speciation and extinction rates from trees
- Testing hypotheses about diversification

## Brownian Motion



Lecture 4

## Brownian Motion

- A model for the evolution of continuously-valued characters
- States change continuously through time
- After some time, expected character states follow a normal distribution

## Outline - BM

- What is Brownian motion?
- When might characters evolve in a Brownian-like way?
- Simulating Brownian motion on trees
- Independent contrasts

## Outline - BM

- What is Brownian motion?
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## Brownian Motion: The Model

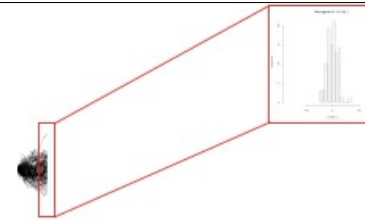
- Usually called the Wiener process
- A continuous-time stochastic process
- Describes a "random walk" of evolution for continuously-valued characters

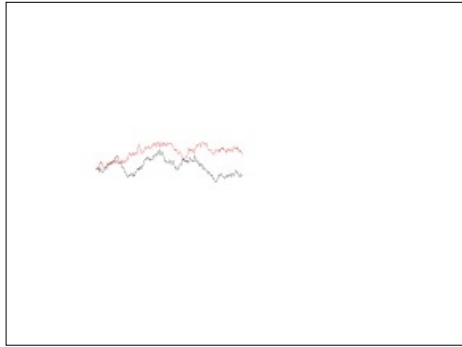
## Three Facts Describe Brownian Motion

- Let  $W(t)$  be the value of the character at time  $t$ . Then:
  - $E[W(t)] = W(0)$
  - Successive steps are independent
  - $W(t) \sim N(W(0), \sigma^2 t)$

## Parameters of BM

- Brownian motion models have two parameters:
  - $\Theta$ , the starting value;  $W(0) = \Theta$
  - $\sigma^2$ , the rate parameter





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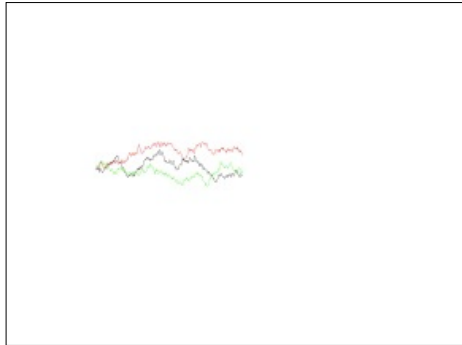
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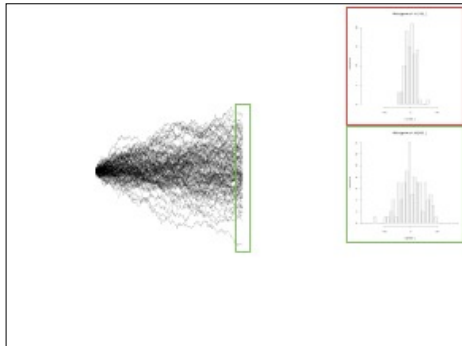
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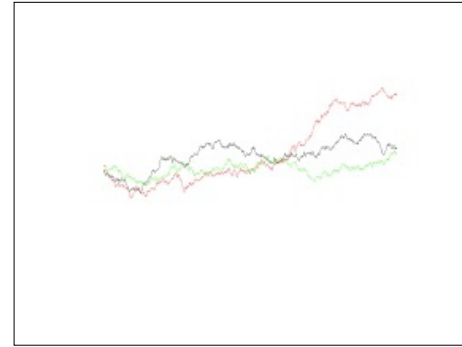
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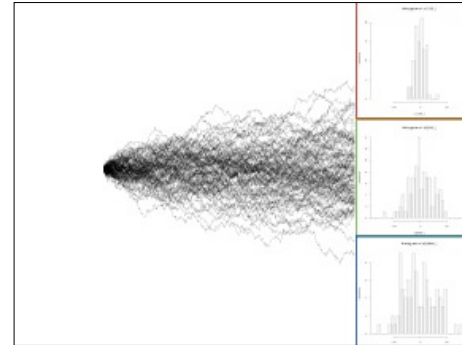
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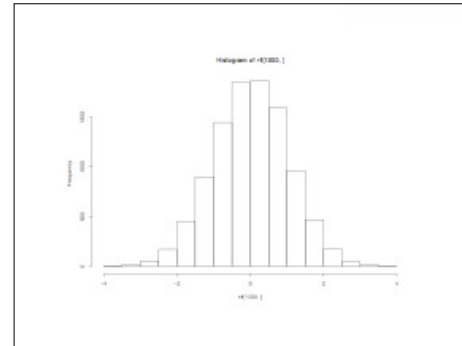
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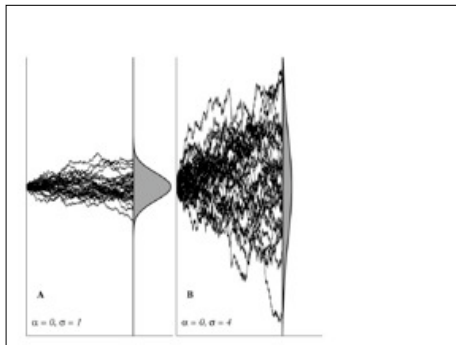
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## Outline - BM

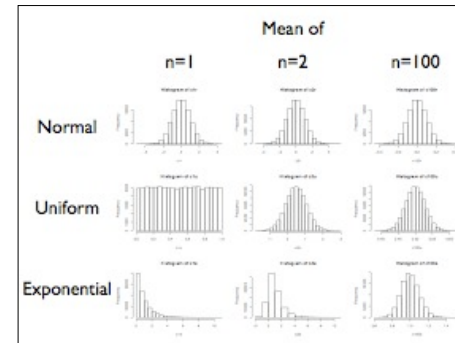
- What is Brownian motion?
- When might characters evolve in a Brownian-like way?
- Simulating Brownian motion on trees
- Independent contrasts

## A physical model for BM



## Why Normal?

- BM can be used to describe motion that results from the combination of a large number of independent weak forces
- Adding many small independent variables result in normal distributions, no matter the original distribution (Central limit theorem)



## Evolution might approximate BM...

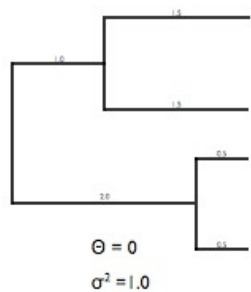
- Genetic drift
- Random punctuated change
- Selection that is weak relative to the time interval considered
- Selection that changes randomly through time

## Outline - BM

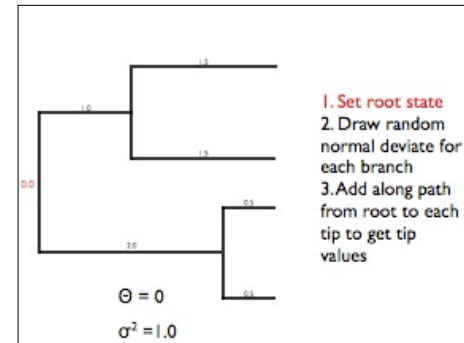
- What is Brownian motion?
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## Simulating BM

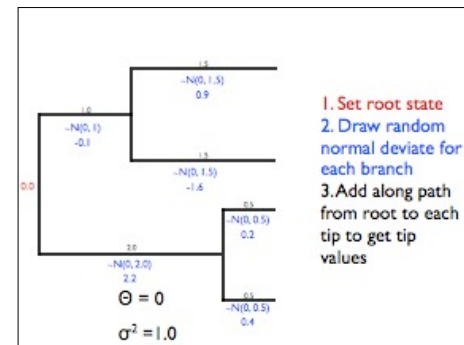
- Simulating Brownian motion involves drawing values from normal distributions
- Variance of the distribution depends on  $\sigma^2$  and  $t$
- Values along adjacent branches are added from the root to the tips of the tree



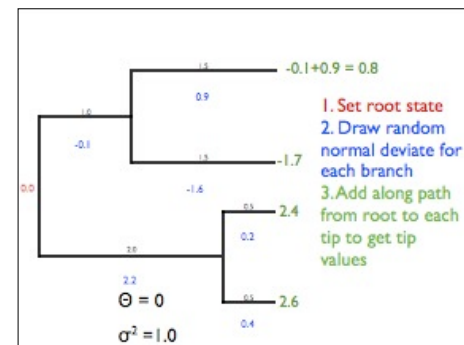
1. Set root state
2. Draw random normal deviate for each branch
3. Add along path from root to each tip to get tip values



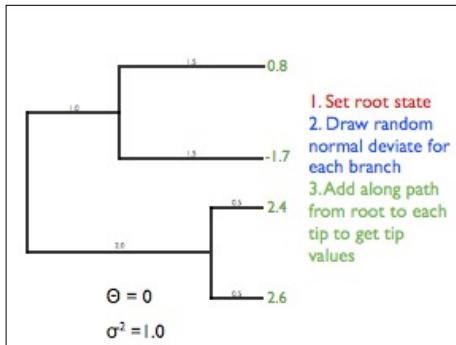
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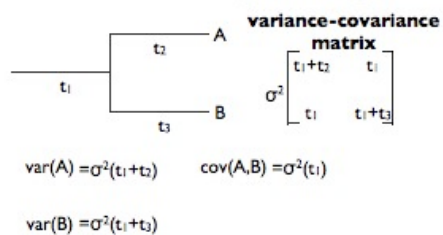
1. Set root state
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## Properties of BM on trees

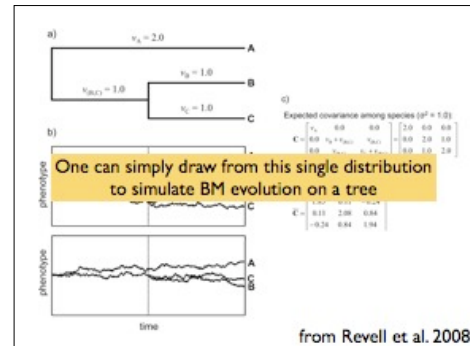
- Variance increases with both  $\sigma^2$  and  $t$
- Expected (mean) value of any tip is always  $\Theta$
- Closely related species tend to be similar (they covary)

## How do they covary?



## General form

- Tip data follow a multivariate normal distribution with mean vector  $\Theta$  and variance-covariance matrix where
- $\text{var}(i) = \sigma^2(d_i)$ ;  $d_i$  = distance from root to tip  $i$
- $\text{cov}(i, j) = \sigma^2(c_{ij})$ ;  $c_{ij}$  = shared path of tip  $i$  and  $j$

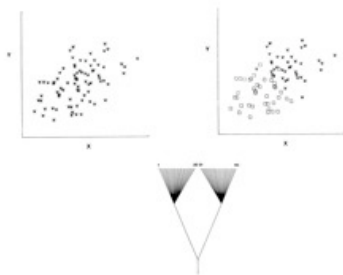


## Outline - BM

- What is Brownian motion?
- When might characters evolve in a Brownian-like way?
- Simulating Brownian motion on trees
- Independent contrasts



### Felsenstein's "Worst Case"



### Calculating Contrasts\*

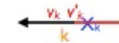
1. Find two tips on the phylogeny that are adjacent (say nodes  $i$  and  $j$ ) and have a common ancestor, say node  $k$ .
2. Compute the contrast  $X_i - X_j$ . This has expectation zero and variance proportional to  $v_i + v_j$ .



### Calculating Contrasts\*

4. Lengthen the branch below node  $k$  by increasing its length from  $v_k$  to  $v_k + v_i v_j / (v_i + v_j)$ . This accounts for the error in assigning a value to  $X_k$ .

$$C_{ij} = X_i - X_j$$



### Calculating Contrasts\*

5. Calculate the standardized contrast by dividing the raw contrast by its variance

$$C_{ij} = X_i - X_j$$

$$S_{ij} = \frac{X_i - X_j}{\sqrt{v_i + v_j}}$$



### Calculating Contrasts\*

3. Remove the two tips from the tree, leaving behind only the ancestor  $k$ , which now becomes a tip. Assign it the character value:

$$X_k = \frac{(1/v_i) X_i + (1/v_j) X_j}{(1/v_i) + (1/v_j)}$$

This is a weighted average of  $X_i$  and  $X_j$ , but not an ancestral state reconstruction.

