Outline

- How do lineages accumulate under the birth-death model?

- Estimating speciation and extinction rates from trees

- Testing hypotheses about diversification

B

Elecatinus xanthiprora
Elecatinus chanosi
Elacatinus horsti
Elacatinus lori
Elacatinus louisae
Elacatinus louisae
Elacatinus evelynae
Elacatinus genie
Elacatinus oceanops #
Elacatinus prochilos
Elacatinus figaro
Elacatinus puriculatus
Tigrigobius macrodon
Tigrigobius saurus
Tigrigobius dtepis
Tigrigobius gemmatum
Tigrigobius pallens
Evermannichthys spongicola
Risor ruber
Tigrigobius multifasciatum
Ginsburgellus novemlineatus
Tigrigobius limbaughi
Garmannia robustum #
Gobiosoma ginsburgi
Gobiosoma bosc
Gobiosoma bosc
Gobiosoma bosc
Gobiosoma bosc
Enypnias aceras
Enypnias seminudus
Enypnias seminudus
Garmannia paradoxum
Garmannia paradoxum
Garmannia homochroma
Garmannia homochroma
Garmannia sp. nov.
Austrogobius hildebrandi
Gobiosoma sp. nov.
Garmannia nudum
Garmannia nudum
Austrogobius spilotum
Garmannia chiquita
Barbulifer ceuthoecus
Barbulifer ceuthoecus
Aruma histrio
Nes longus
Gobulus birdsongi
Chriolepis zebra
Psilotris batrachodes
Aboma etheostoma
Microgobius thalassinus
Microgobius brevispinis
Microgobius gulosus
Microgobius sp.
Microgobius carri
Microgobius microlepis
Microgobius erectus
Microgobius erectus
Akko sp. nov.
Bollmannia marginalis
Bollmannia communis
Bollmannia chlamydes
Bollmannia boqueronensis
Gen. nov. sp. nov.
Gobius xanthocephalus
Gobius niger
Vanneaugobius pruvoti
Vanneaugobius canarensis

18.3 ± 0.4

50   40   30   20   10   0 Million years

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

$$\gamma = \frac{\left(\frac{1}{n-2}\sum_{i=2}^{n-1}\left(\sum_{k=2}^{i}kg_k\right)\right)-\left(\frac{T}{2}\right)}{T\sqrt{\frac{1}{12(n-2)}}}, \; T = \left(\sum_{j=2}^{n}jg_j\right).$$
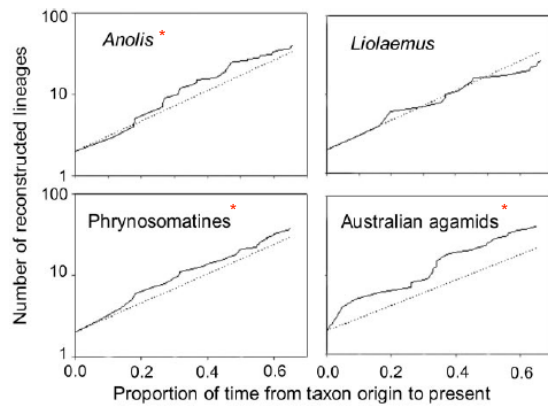
Slowdown statistic

- Under pure-birth model, γ~N(0,1)
- γ<0 means diversification has slowed
- γ>0 difficult to interpret

$$\gamma = \frac{\left(\frac{1}{n-2}\sum_{i=2}^{n-1}\left(\sum_{k=2}^{i}kg_k\right)\right)-\left(\frac{T}{2}\right)}{T\sqrt{\frac{1}{12(n-2)}}}, \; T = \left(\sum_{j=2}^{n}jg_j\right).$$

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
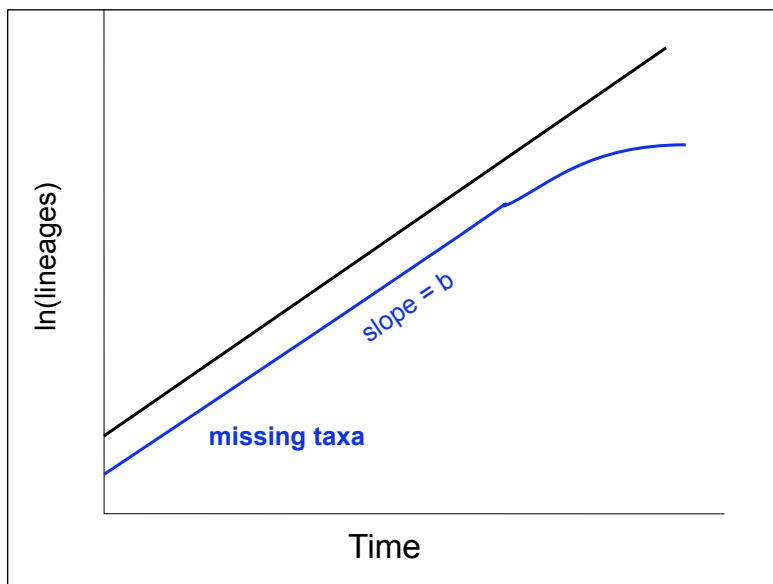
Missing Taxa

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

The problem...

Slowdown   Missing taxa

Extinction   Speedup

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

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:
  - Θ, the starting value; $W(0) = \Theta$
  - σ^2, the rate parameter
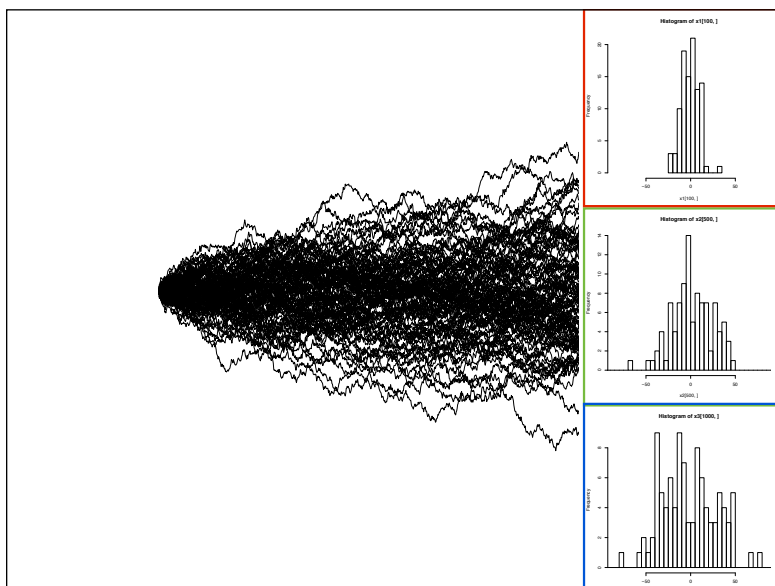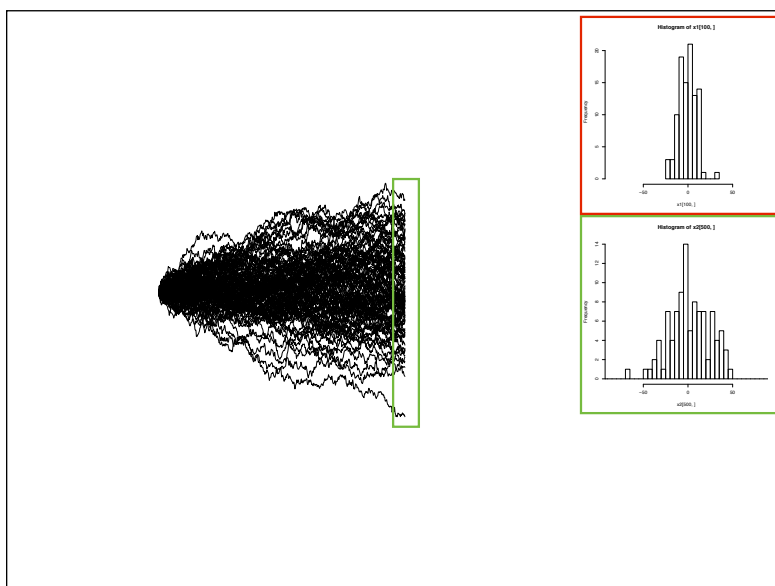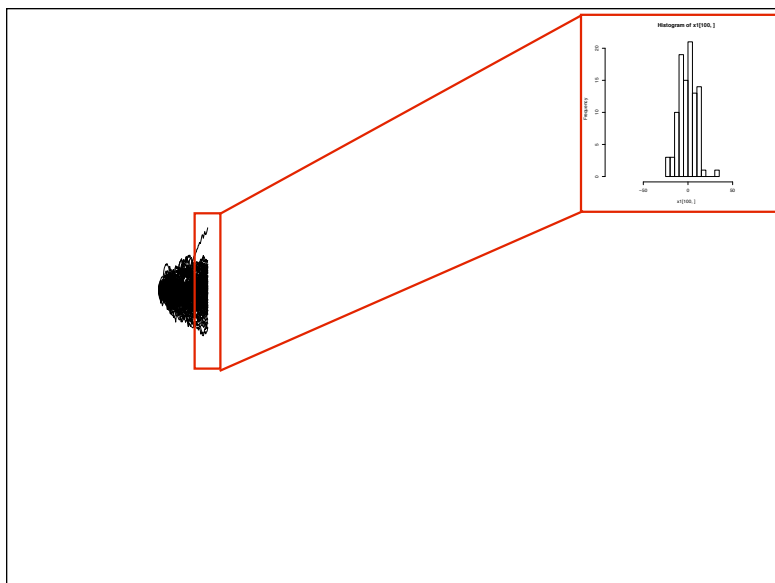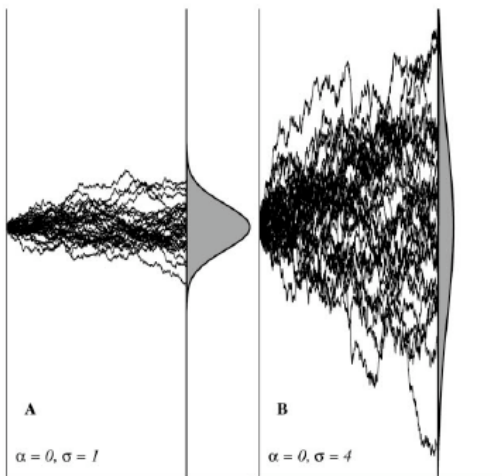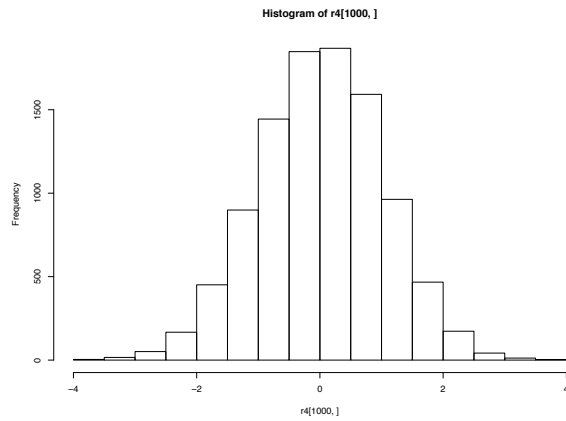
Histogram of r4[1000,]

A histogram showing Frequency on the y-axis (0 to 1500) versus r4[1000,] on the x-axis (-4 to 4).

Two panels labeled A and B showing Brownian motion simulations.

A: $\alpha = 0, \sigma = 1$

B: $\alpha = 0, \sigma = 4$

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)
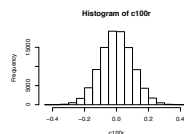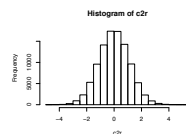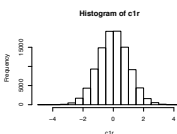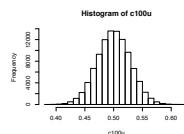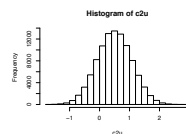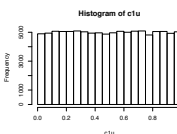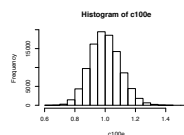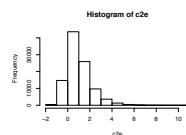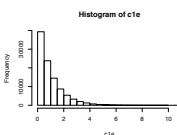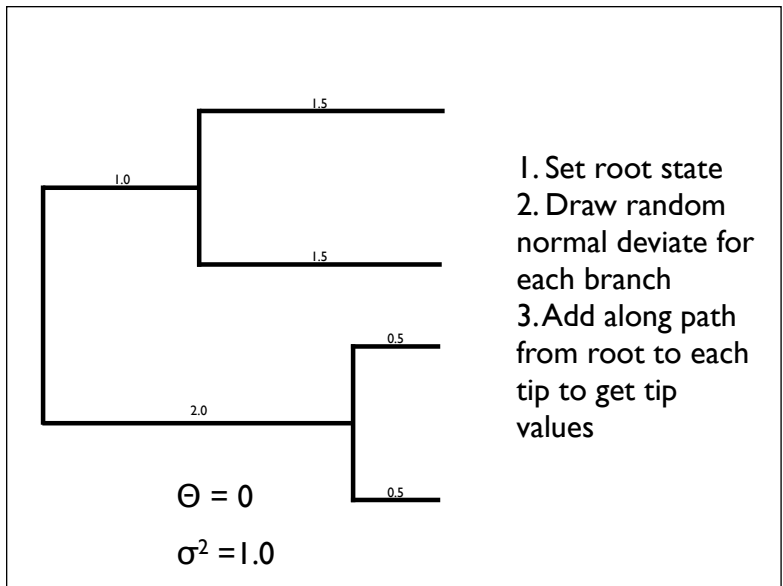
Evolution might approximate BM...

- 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?

- When might characters evolve in a Brownian-like way?

- Simulating Brownian motion on trees

- Independent contrasts

Simulating BM

- Simulating Brownian motion involves drawing values from normal distributions

- Variance of the distribution depends on σ^2 and t

- Values along adjacent branches are added from the root to the tips of the tree

Panel 1:

1.5

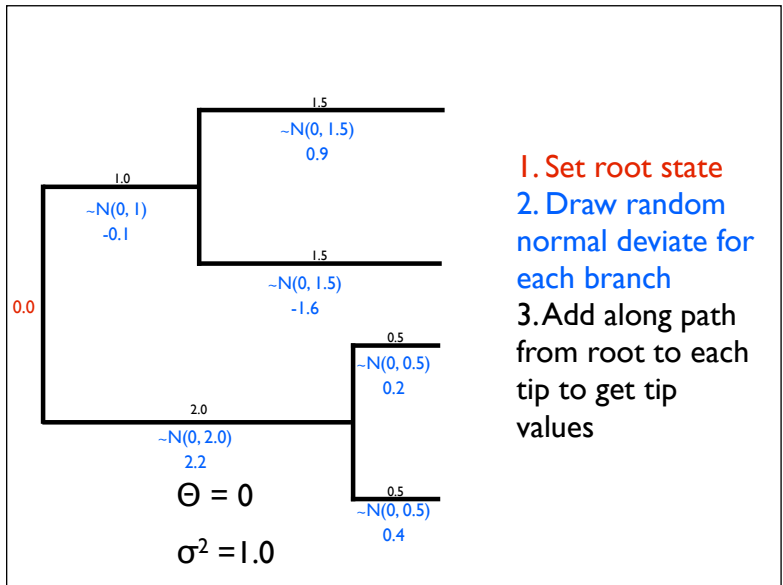1.0

1.5

0.5

2.0

Θ = 0

0.5

σ² =1.0

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

Panel 2:

1.5
~N(0, 1.5)
0.9

1.0
~N(0, 1)
-0.1

1.5
~N(0, 1.5)
-1.6

0.5
~N(0, 0.5)
0.2

0.0

2.0
~N(0, 2.0)
2.2

Θ = 0

0.5
~N(0, 0.5)
0.4

σ² =1.0

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

Panel 3:

1.5   -0.1+0.9 = 0.8

0.9

1.0

-0.1

1.5   -1.7

-1.6

0.5   2.4

0.2

0.0

2.0

2.2

Θ = 0

0.5   2.6

0.4

σ² =1.0

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
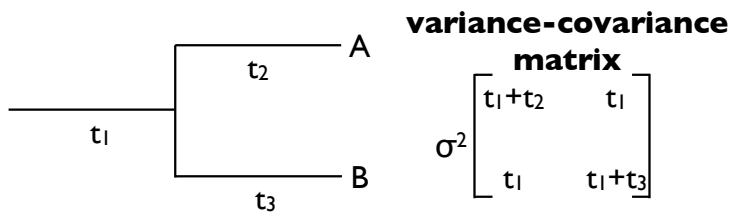
Properties of BM on trees

- Variance increases with both σ^2 and t

- Expected (mean) value of any tip is always Θ

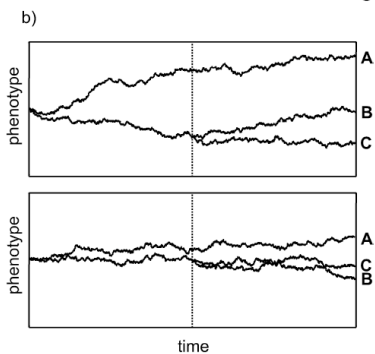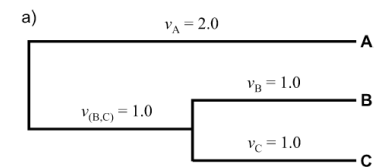- Closely related species tend to be similar (they covary)

How do they covary?

variance-covariance matrix

$$\sigma^2 \begin{bmatrix} t_1+t_2 & t_1 \\ t_1 & t_1+t_3 \end{bmatrix}$$

$\text{var}(A) = \sigma^2(t_1+t_2)$ $\text{cov}(A,B) = \sigma^2(t_1)$

$\text{var}(B) = \sigma^2(t_1+t_3)$

General form

- Tip data follow a multivariate normal distribution with mean vector Θ and variance-covariance matrix where

- $\text{var}(i) = \sigma^2(d_i)$; d_i =distance from root to tip i

- $\text{cov}(i,j) = \sigma^2(c_{i,j})$; $c_{i,j}$ =shared path of tip i and j

a)

$v_A = 2.0$ — A

$v_B = 1.0$ — B

$v_{(B,C)} = 1.0$

$v_C = 1.0$ — C

b)

phenotype

A
B
C

phenotype

A
C
B

time

c)

Expected covariance among species ($\sigma^2 = 1.0$):

$$\mathbf{C} = \begin{bmatrix} v_A & 0.0 & 0.0 \\ 0.0 & v_B + v_{(B,C)} & v_{(B,C)} \\ 0.0 & v_{(B,C)} & v_C + v_{(B,C)} \end{bmatrix} = \begin{bmatrix} 2.0 & 0.0 & 0.0 \\ 0.0 & 2.0 & 1.0 \\ 0.0 & 1.0 & 2.0 \end{bmatrix}$$

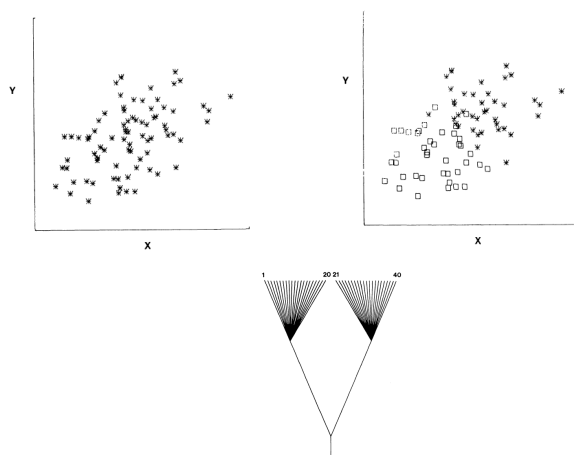Observed covariance among species (N=100 simulations):

$$\overline{\mathbf{C}} = \begin{bmatrix} 1.85 & 0.11 & -0.24 \\ 0.11 & 2.08 & 0.84 \\ -0.24 & 0.84 & 1.94 \end{bmatrix}$$

from Revell et al. 2008

Outline - BM

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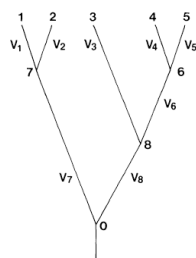

Felsenstein's "Worst Case"

Slide 1

TABLE 1

The Four Contrasts Extracted from the Phylogeny Shown in Figure 9, Each with Its Variance, All Computed Using Steps 1–4 in the Text

Contrast	Variance
$X_1 - X_2$	$v_1 + v_2$
$X_4 - X_5$	$v_4 + v_5$
$X_3 - X_6$	$v_3 + v_6'$
$X_7 - X_8$	$v_7' + v_8'$

where

$$X_6 = \frac{v_4 X_5 + v_5 X_4}{v_4 + v_5}$$

$$v_6' = v_6 + v_4 v_5/(v_4 + v_5)$$

$$X_7 = \frac{v_2 X_1 + v_1 X_2}{v_1 + v_2}$$

$$v_7' = v_7 + v_1 v_2/(v_1 + v_2)$$

$$X_8 = \frac{v_6' X_3 + v_3 X_6}{v_3 + v_6}$$

$$v_8' = v_7' + v_3 v_6'/(v_3 + v_6')$$

(Felsenstein 1981)

Slide 2

What are contrasts?

- Each standardized contrast is telling us something about the RATE of evolution

- The contrasts have a close relationship with σ^2, the rate parameter from BM

- The sum of the squared contrasts divided by n gives the ML estimate of σ^2