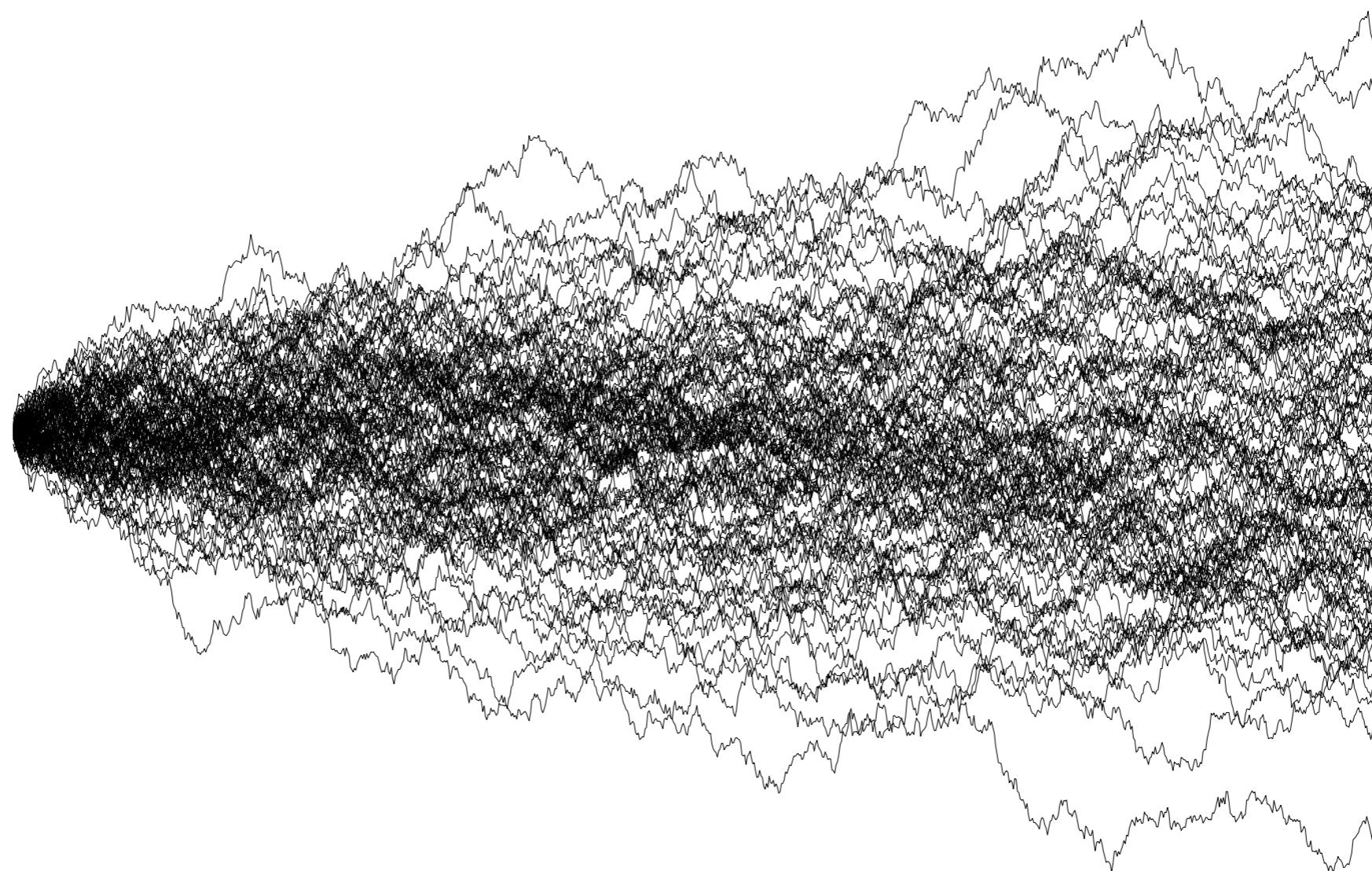


Brownian Motion



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

Outline - BM

- What is Brownian motion?
- When might characters evolve in a Brownian-like way?
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Brownian Motion: The Model

- Sometimes called the Wiener process
- A continuous-time stochastic process
- Describes a “random walk” of evolution for continuously-valued characters

Three Facts Describe Brownian Motion

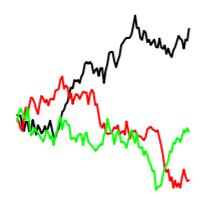
- Let $W(t)$ be the value of the character at time t . Then:
 - $E[W(t)] = W(0)$
 - Successive steps are independent
 - $W(t) \sim N(W(0), \sigma^2 t)$

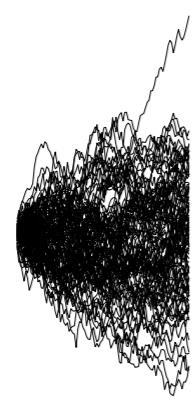
Parameters of BM

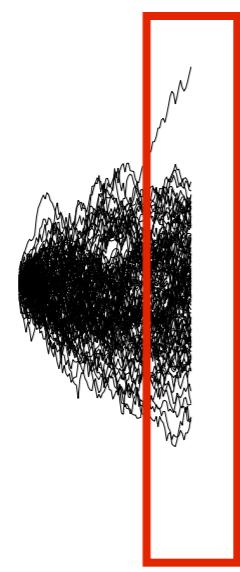
- Brownian motion models have two parameters:
 - Θ , the starting value; $W(0) = \Theta$
 - σ^2 , the rate parameter

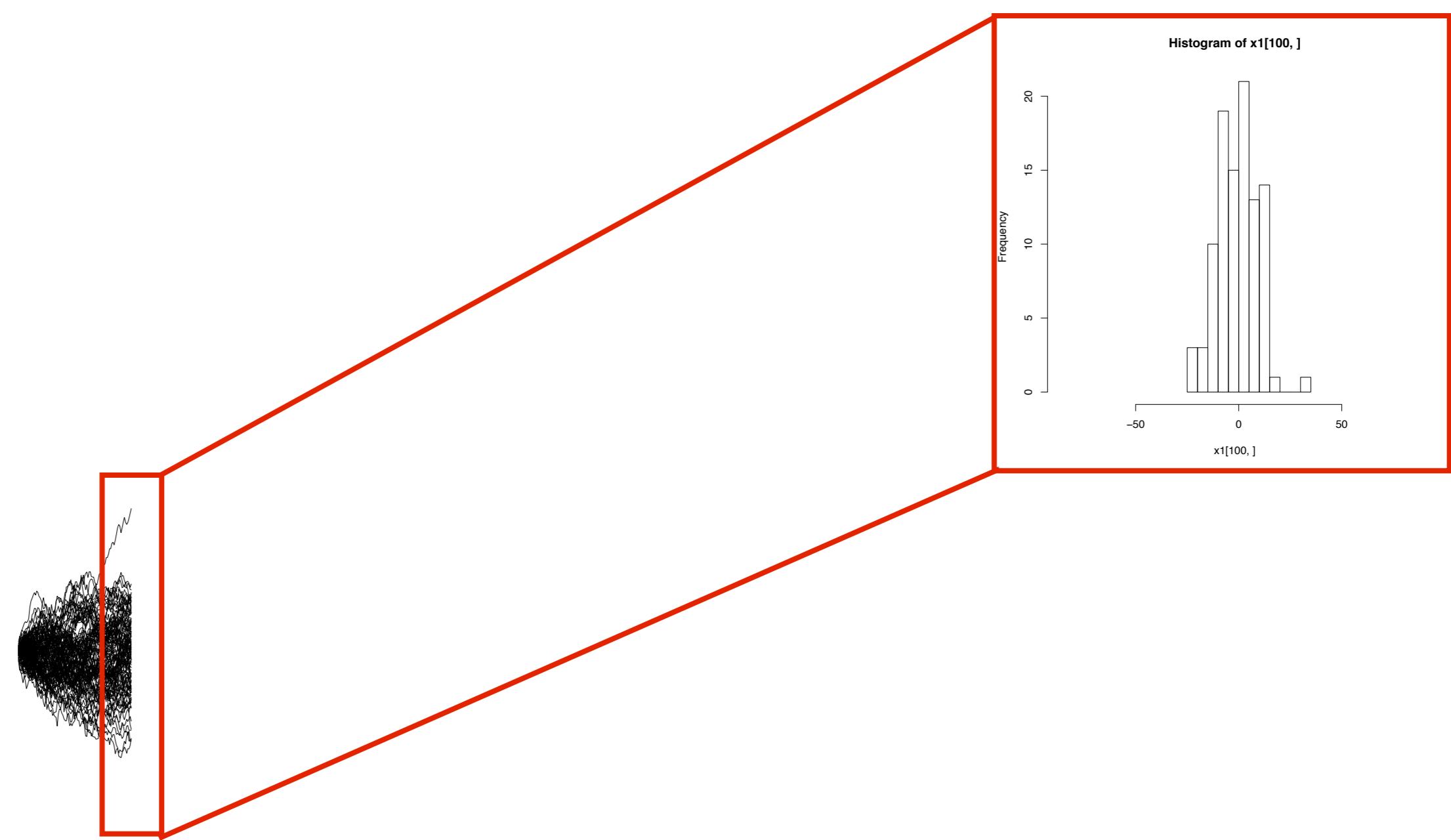




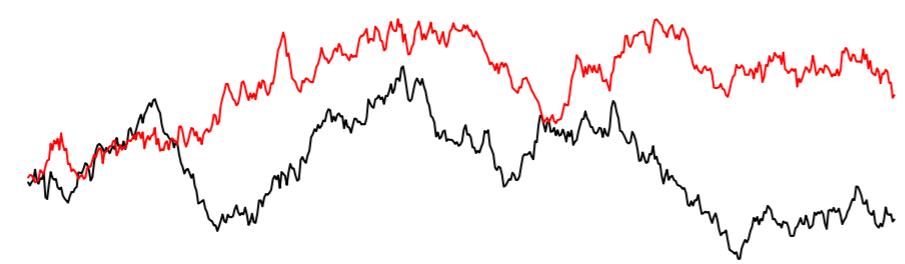


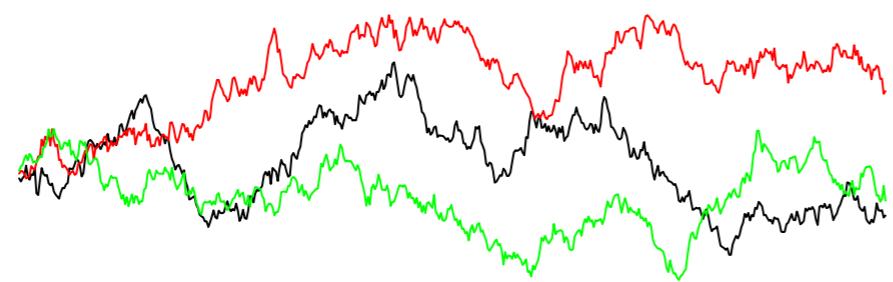


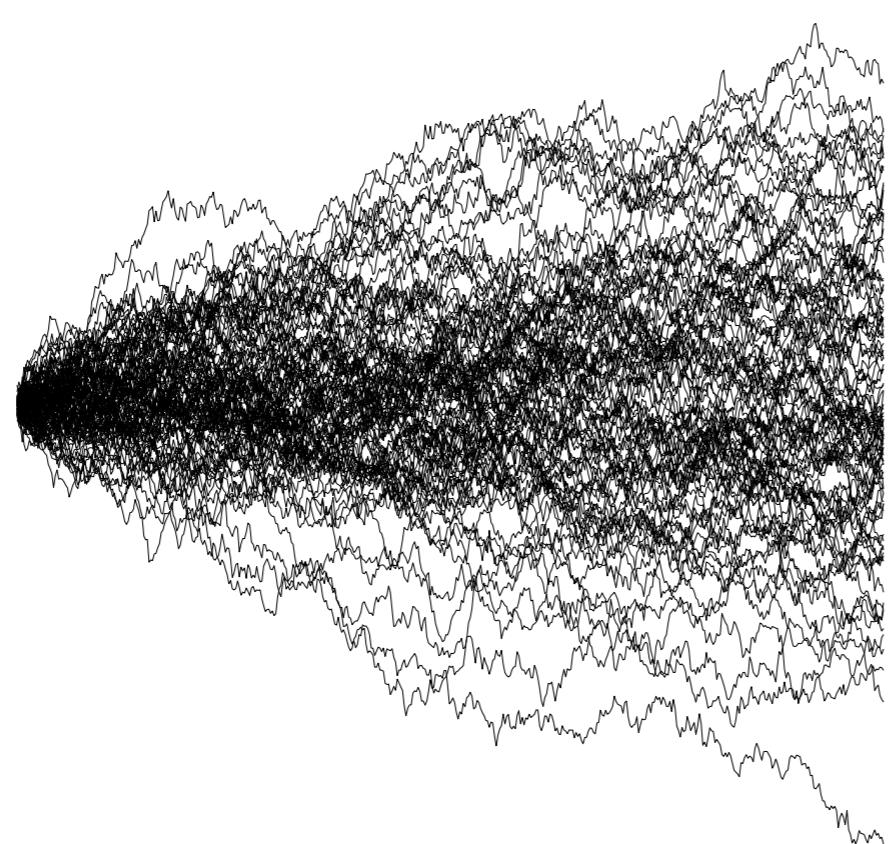


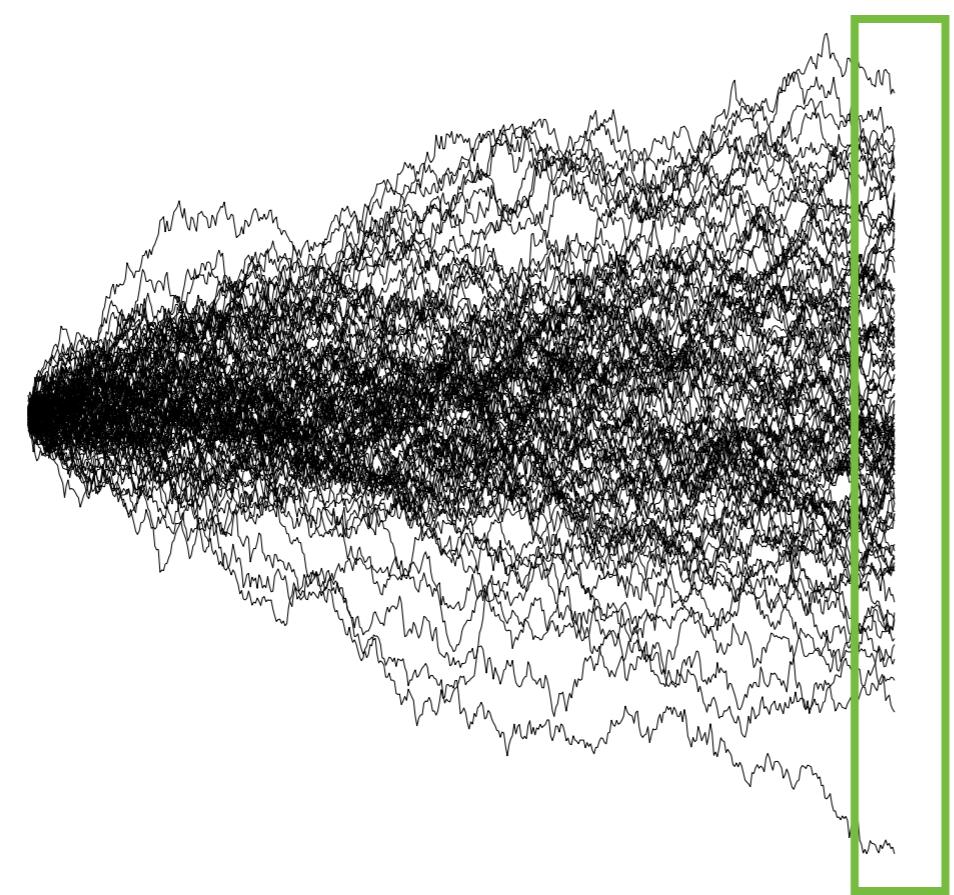




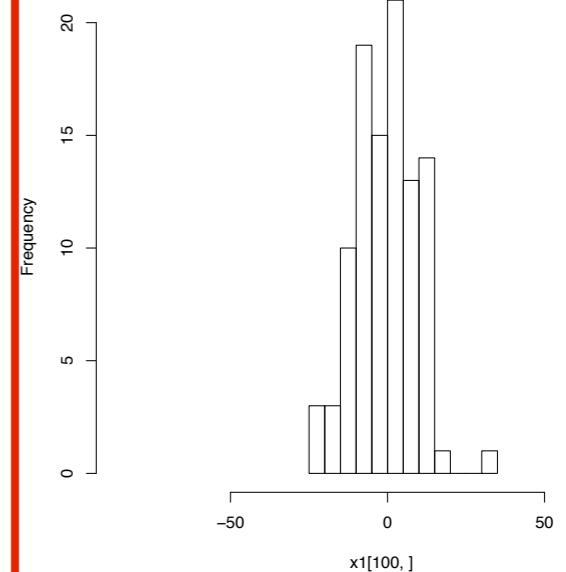




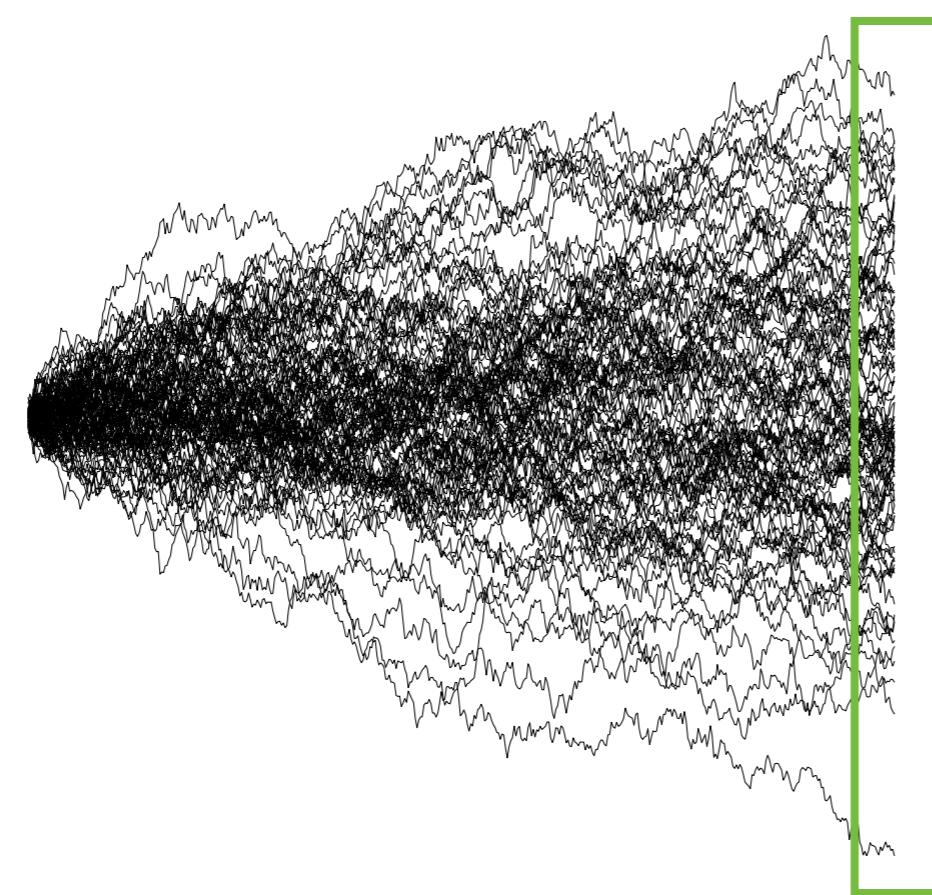
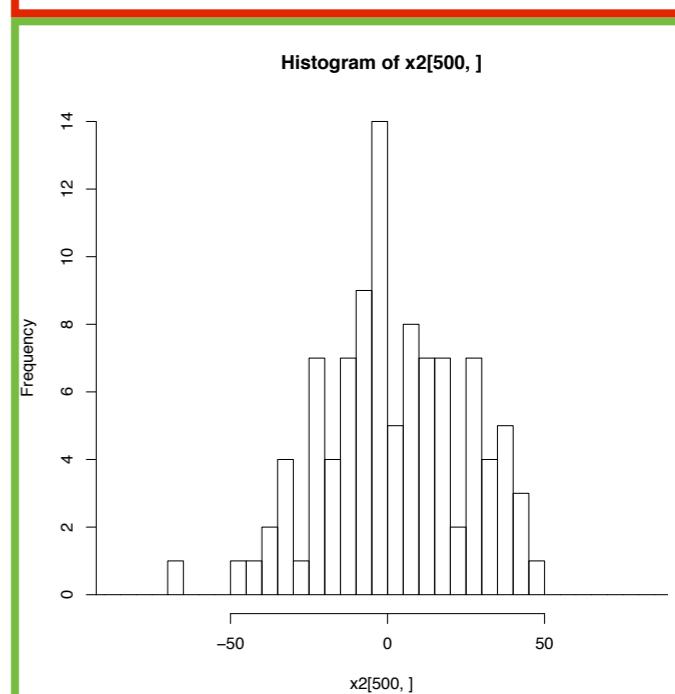


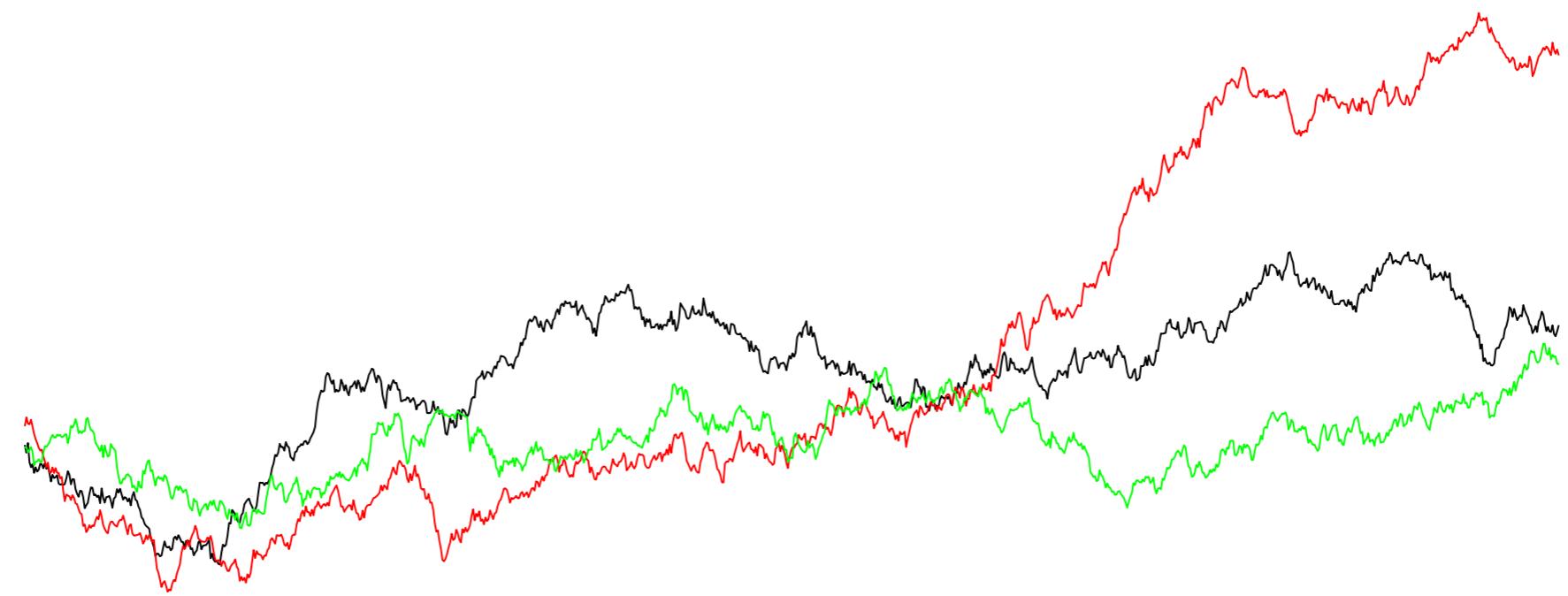


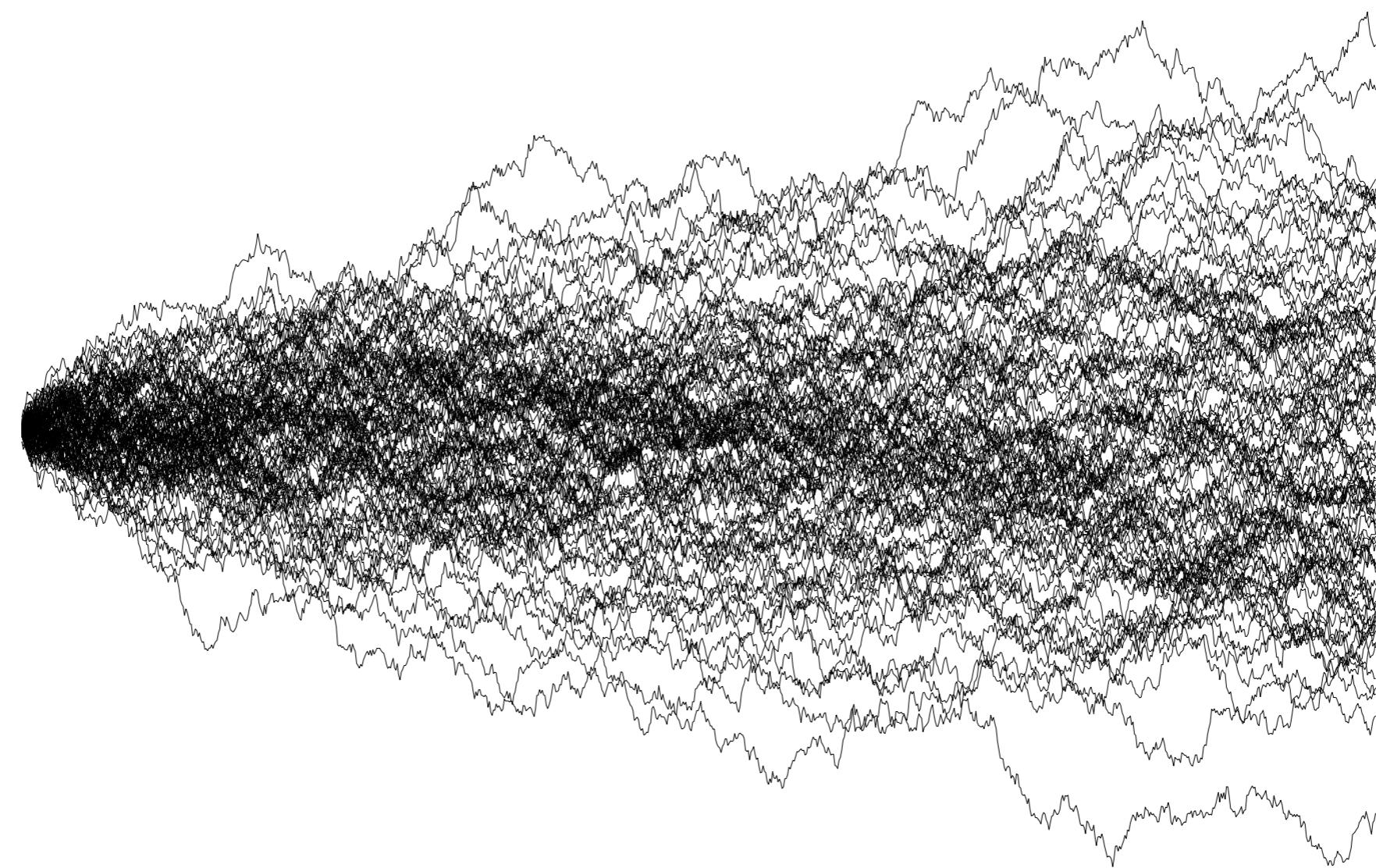
Histogram of $x1[100,]$

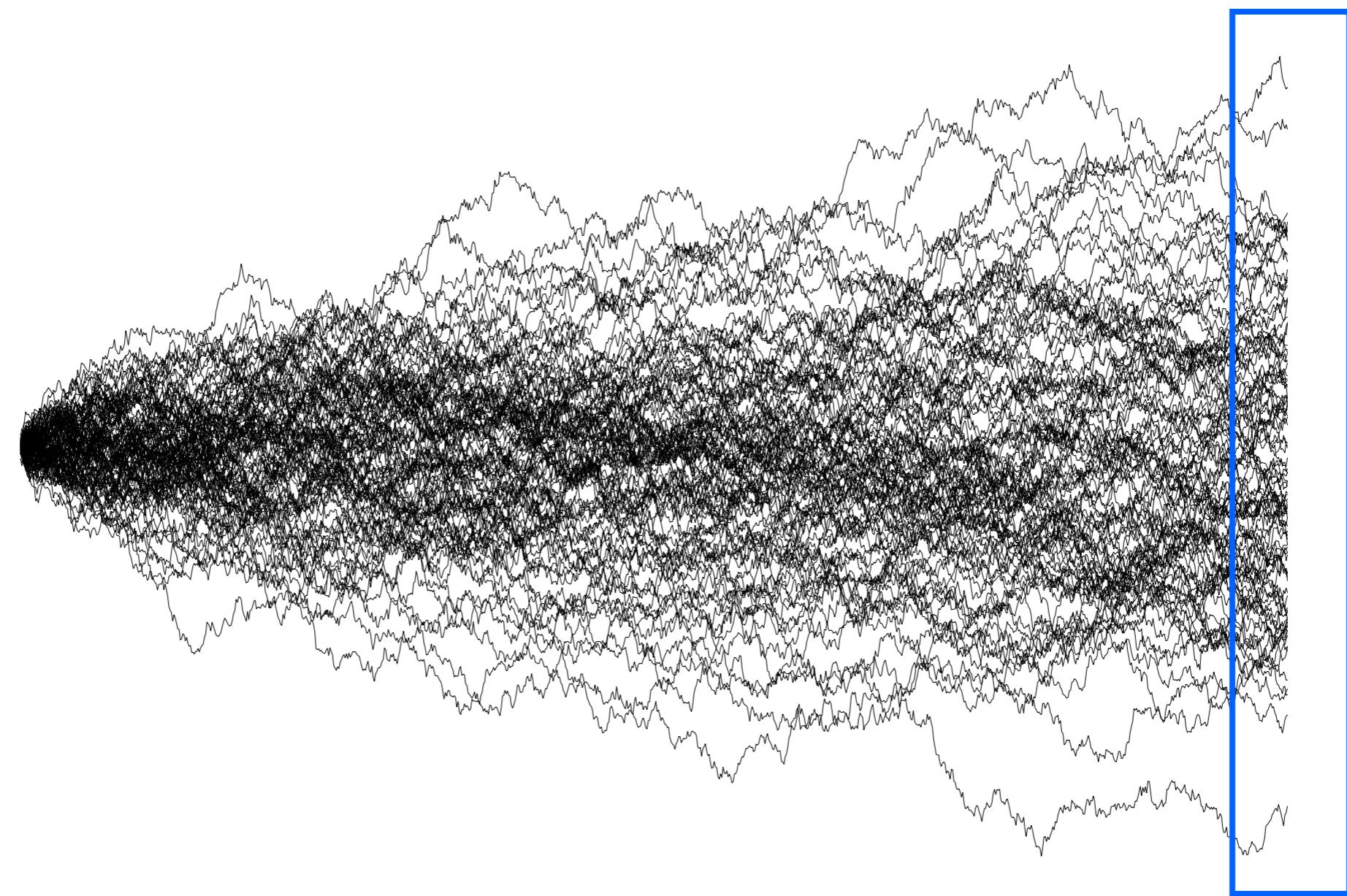


Histogram of $x2[500,]$

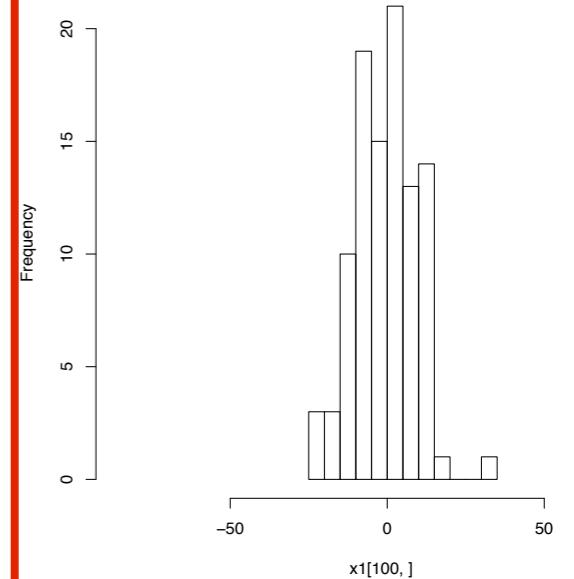




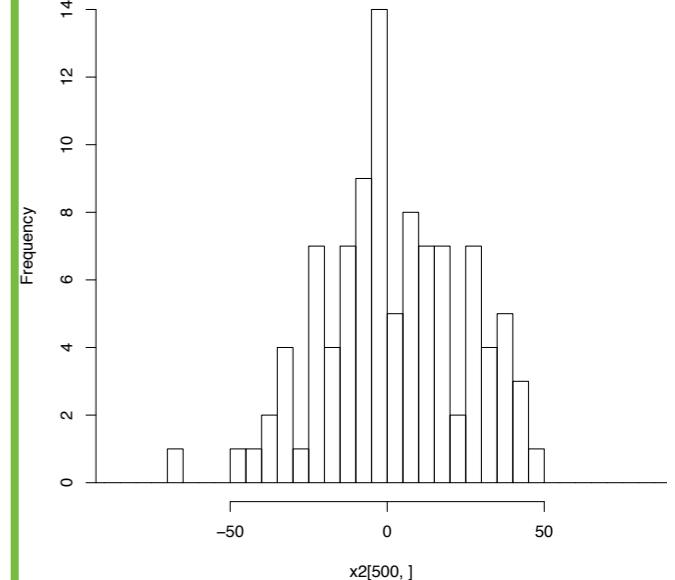




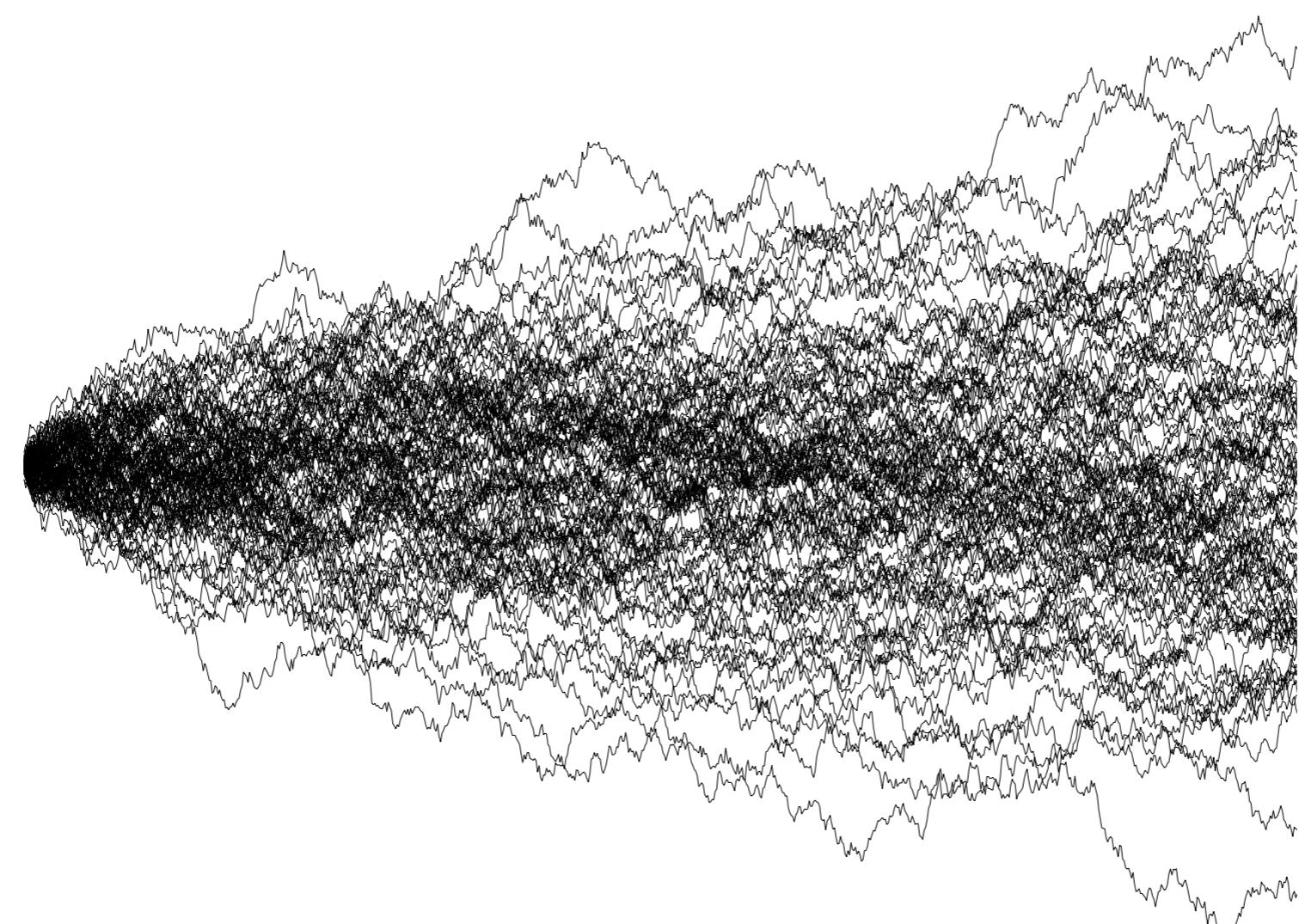
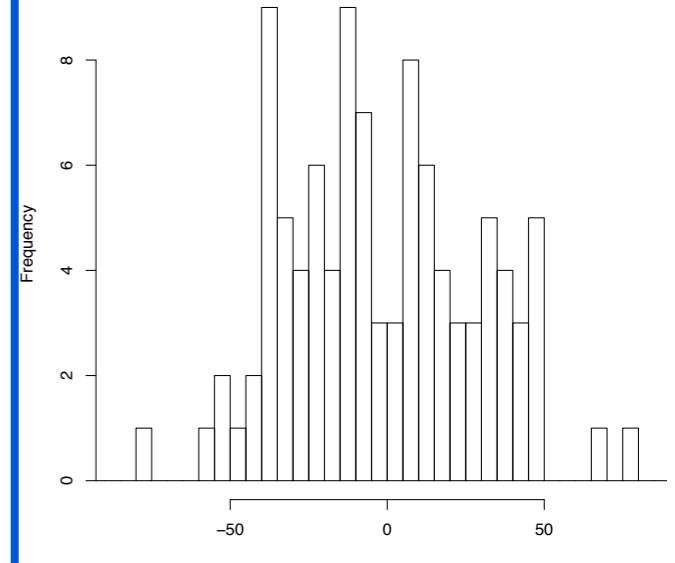
Histogram of $x1[100,]$



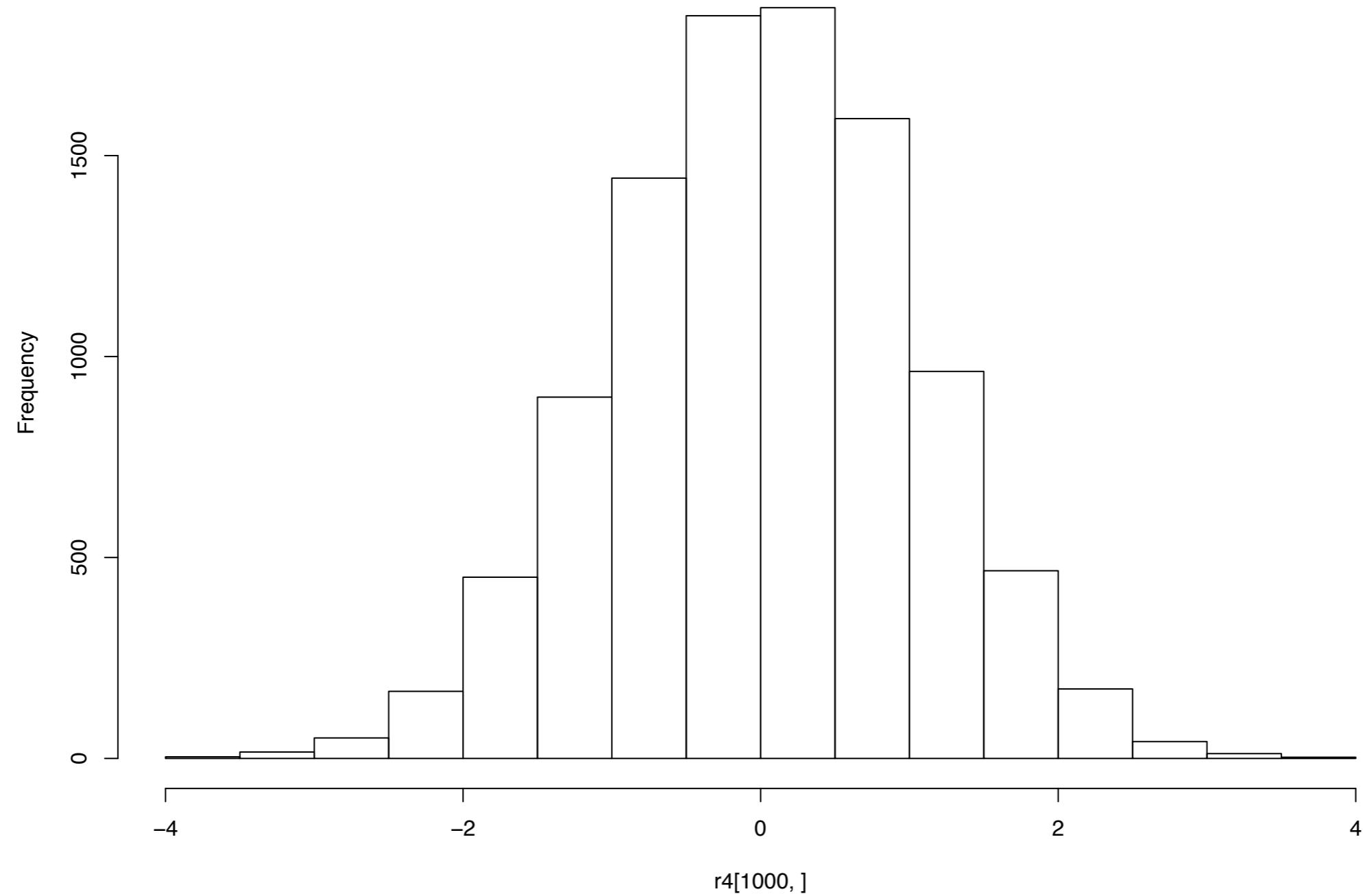
Histogram of $x2[500,]$

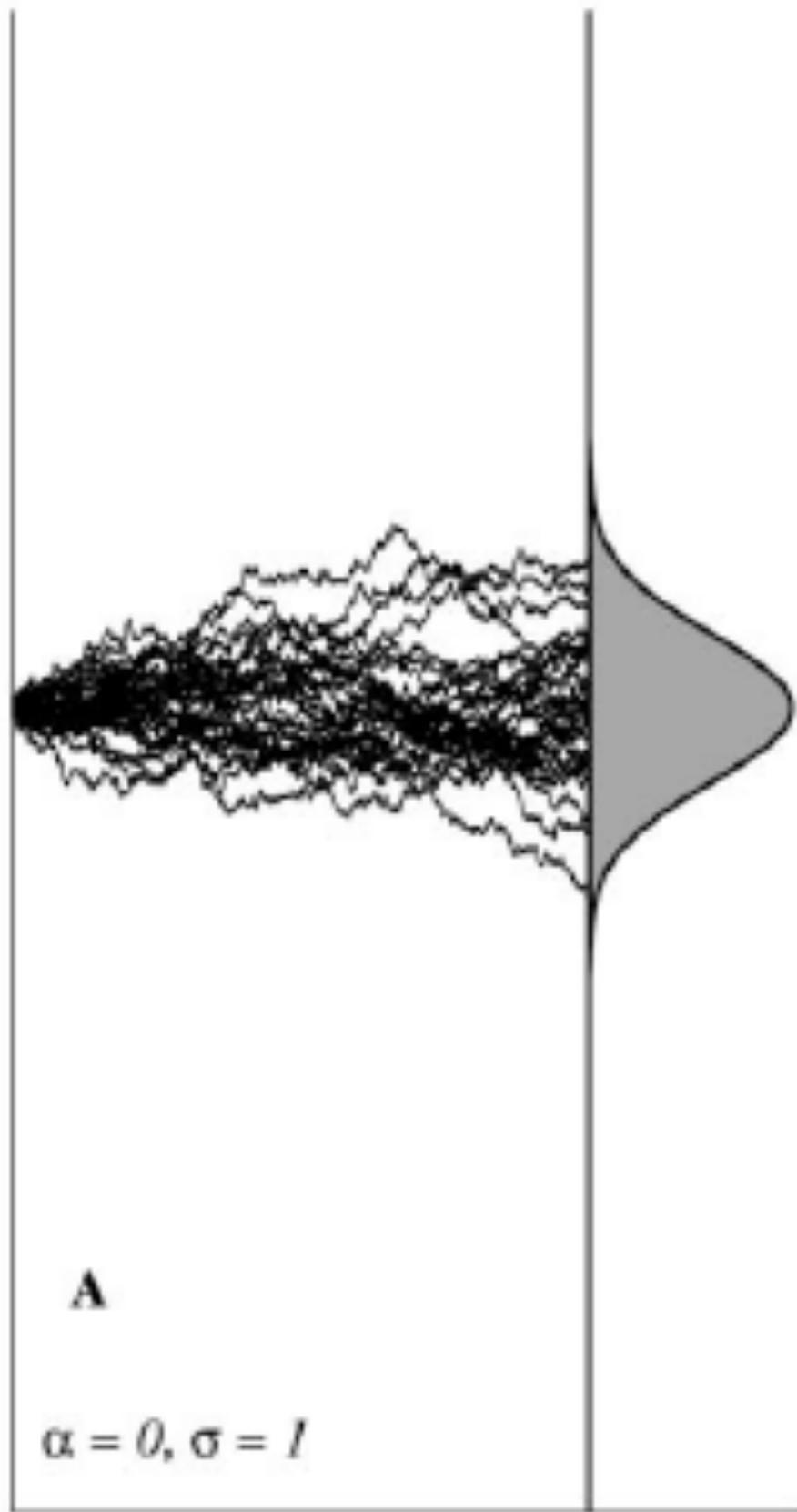


Histogram of $x3[1000,]$



Histogram of r4[1000,]





Outline - BM

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

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)

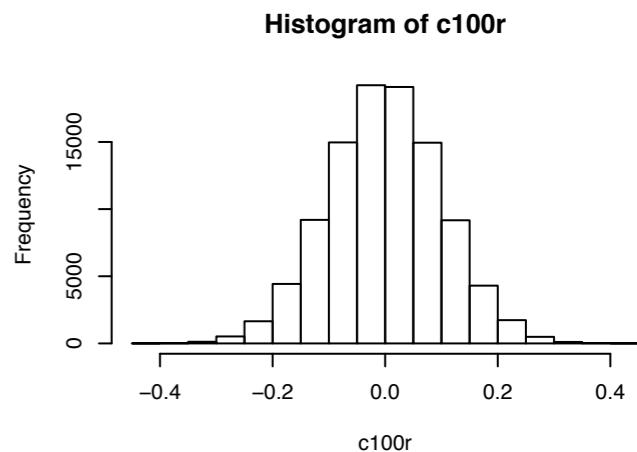
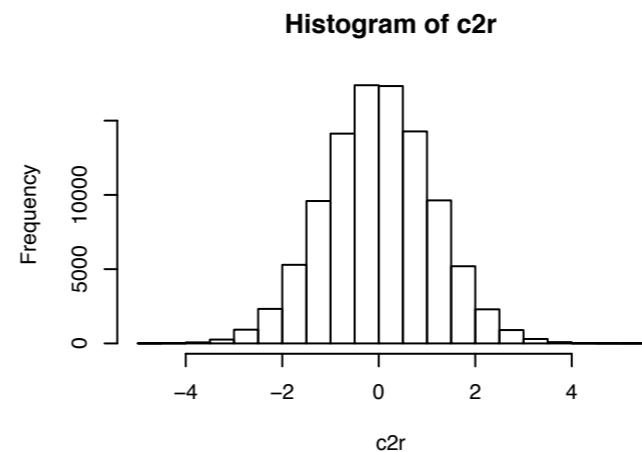
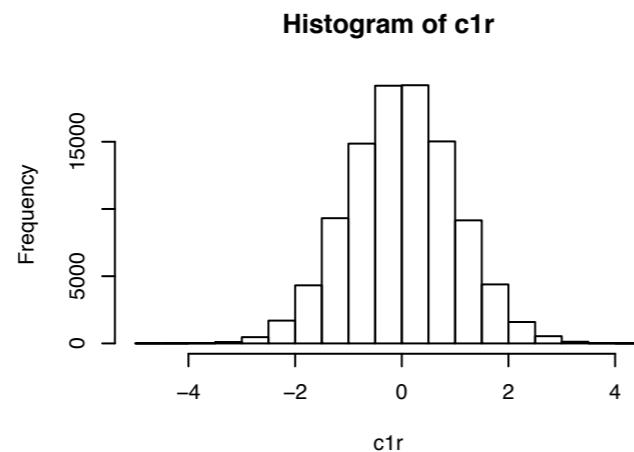
Mean of

$n=1$

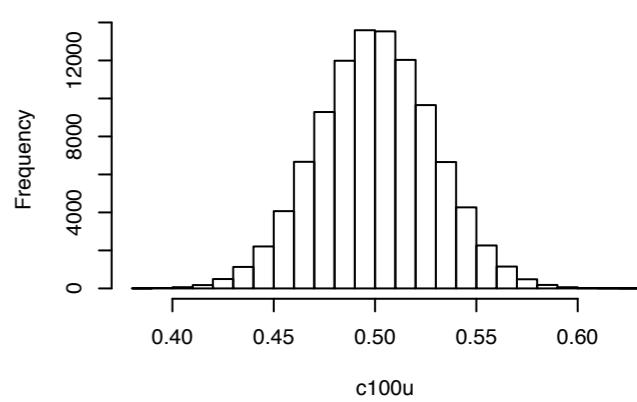
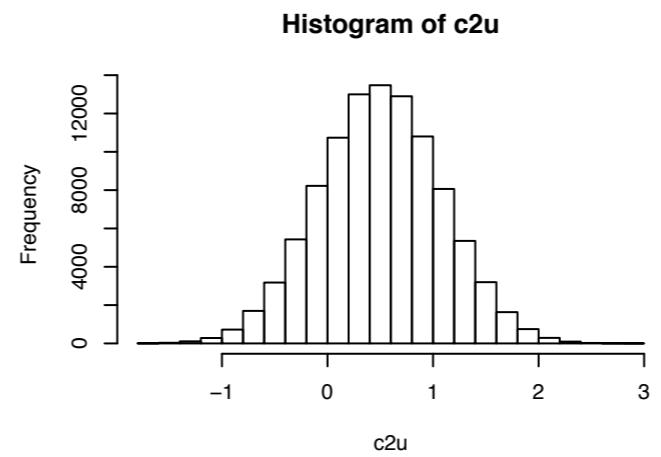
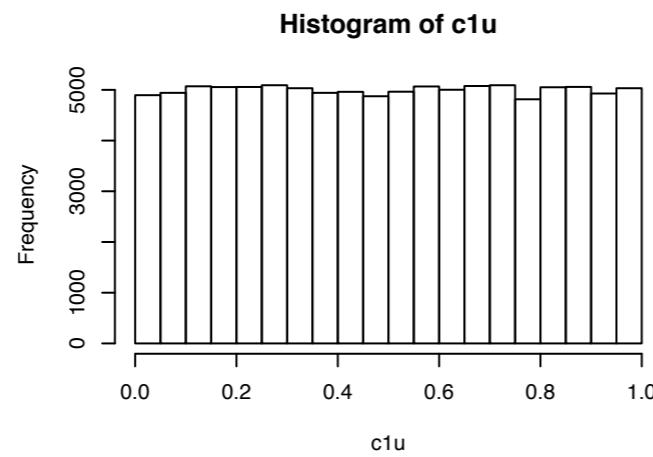
$n=2$

$n=100$

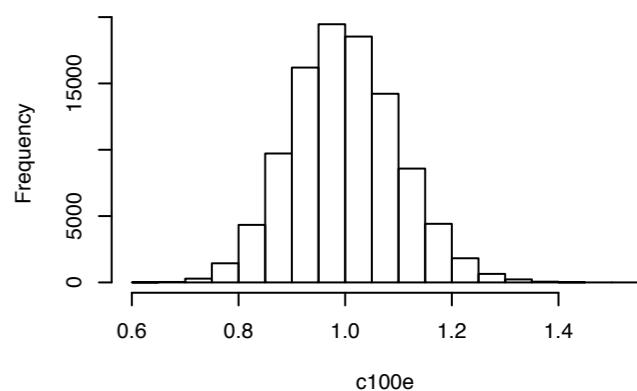
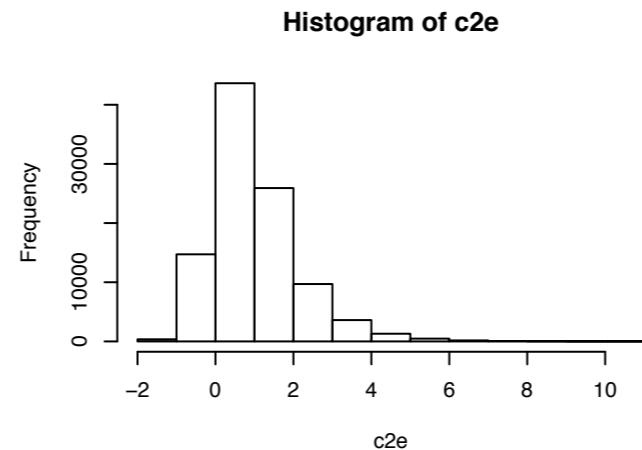
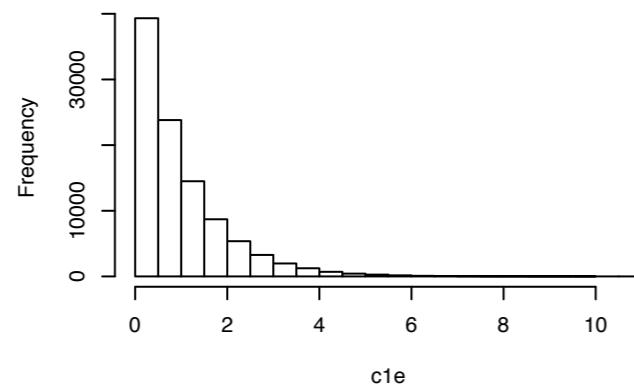
Normal



Uniform



Exponential

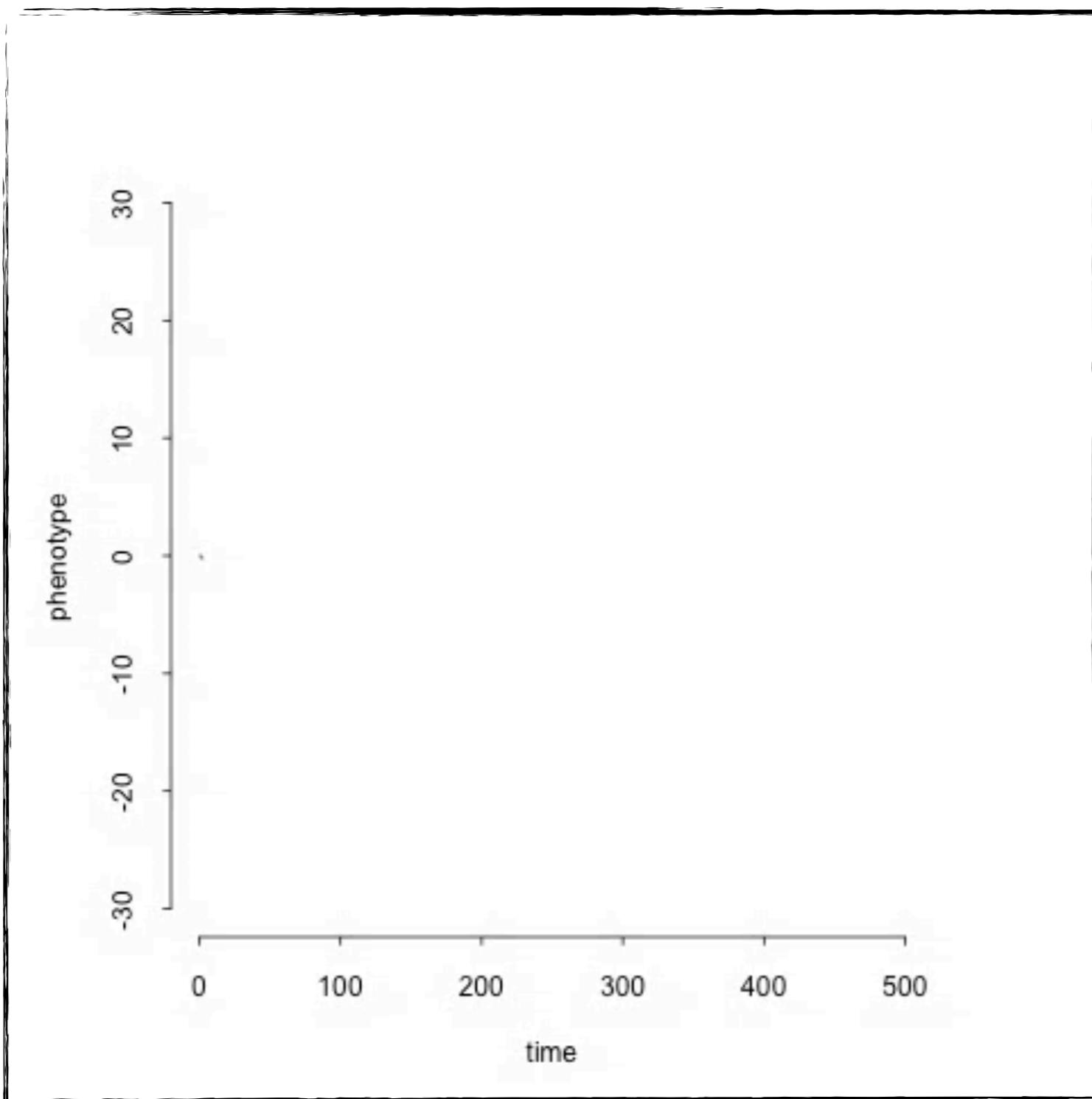


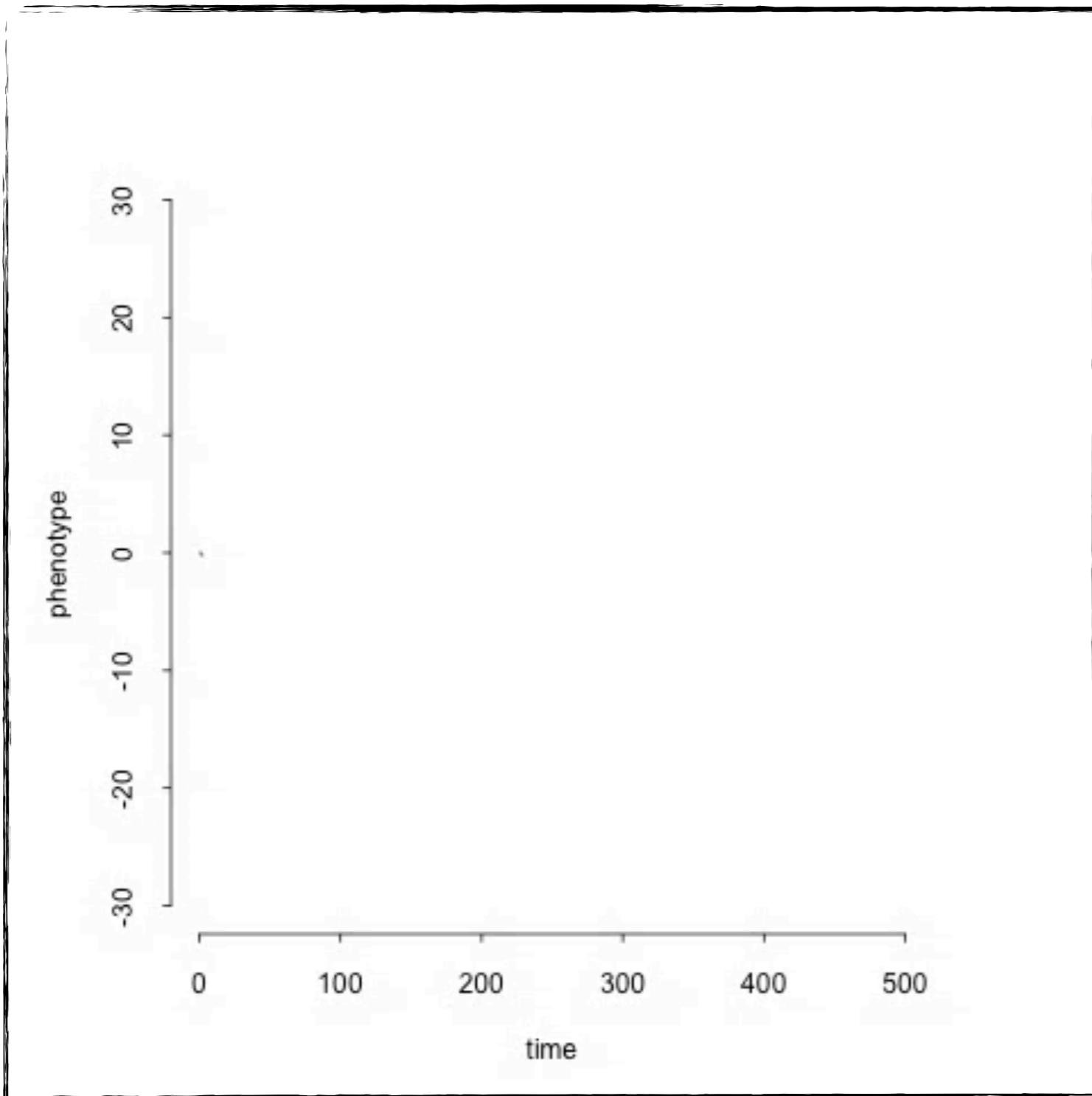
Evolution might approximate BM...

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

Outline - BM

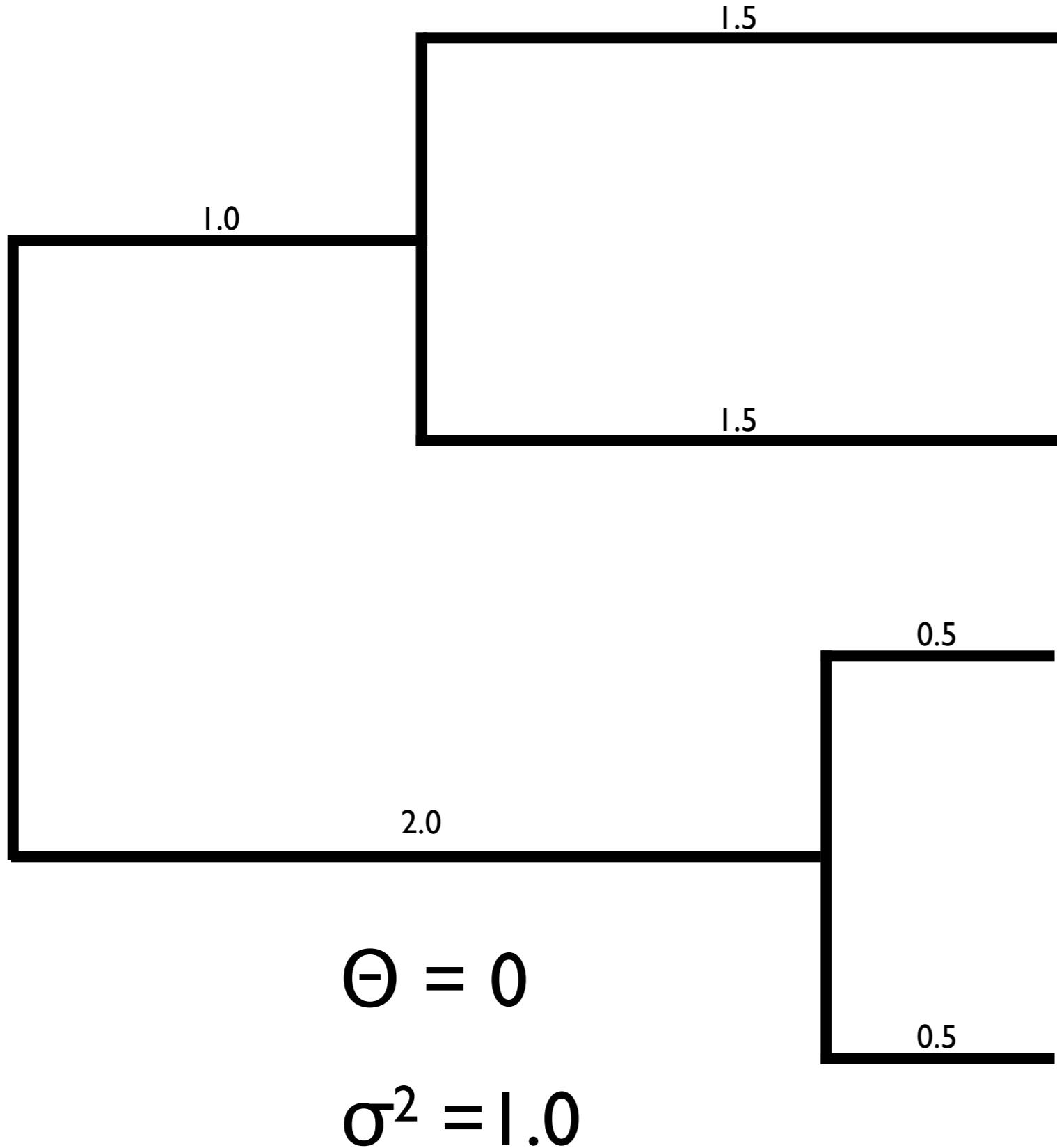
- What is Brownian motion?
- When might characters evolve in a Brownian-like way?
- Simulating Brownian motion on trees



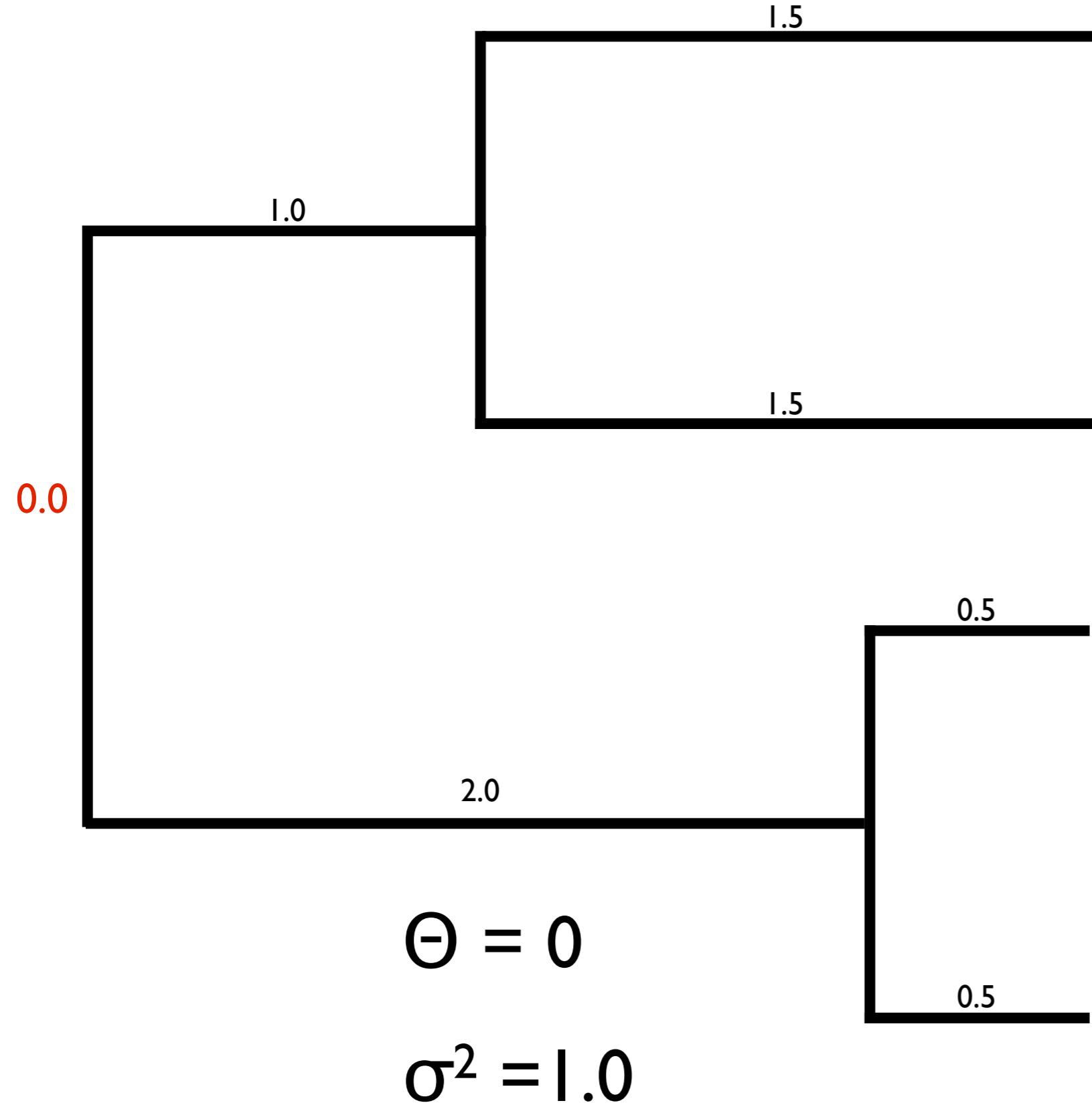


Simulating BM

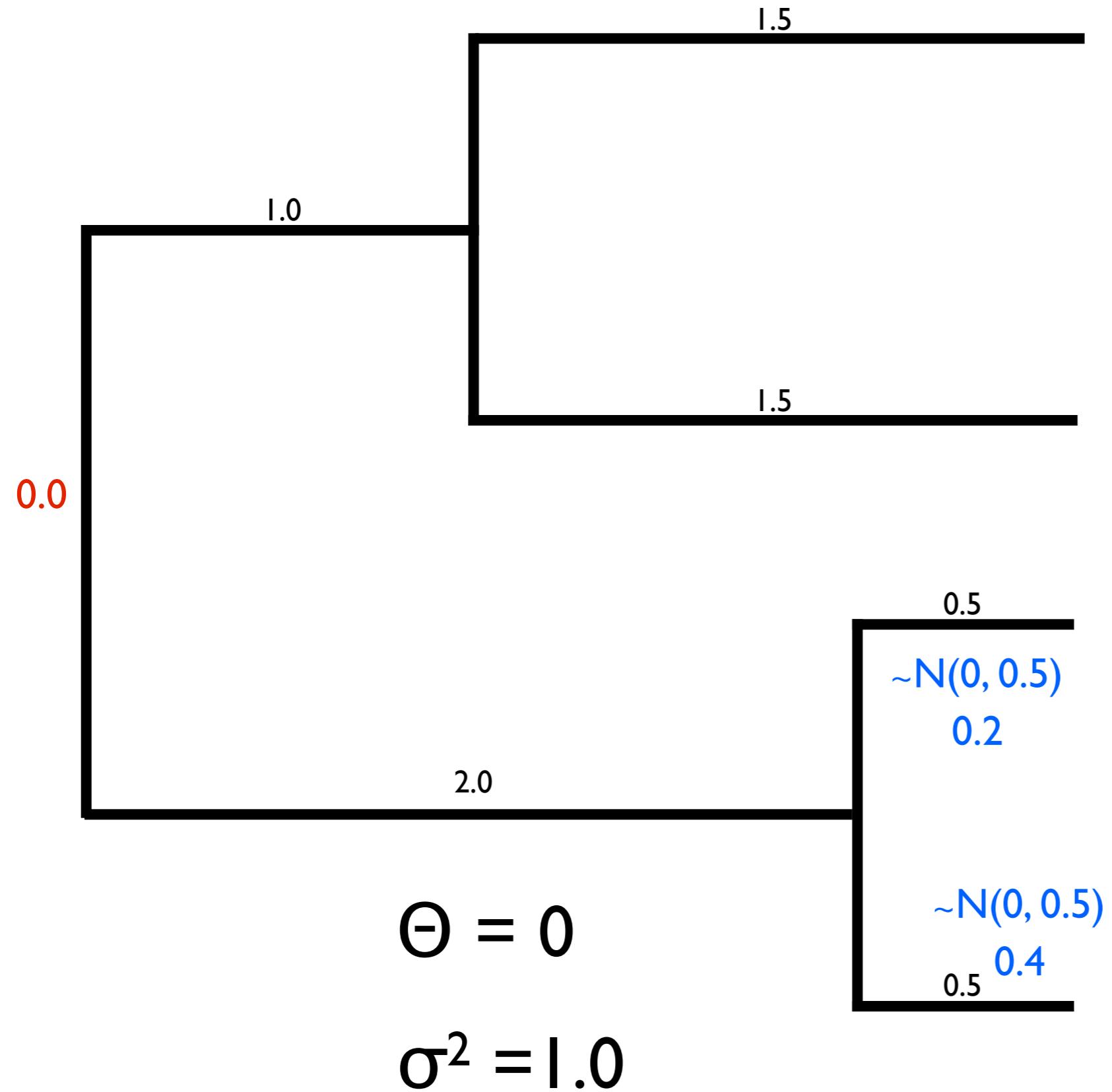
- Simulating Brownian motion involves drawing values from normal distributions
- Variance of the distribution depends on σ^2 and t
- Values along adjacent branches are added from the root to the tips of the tree



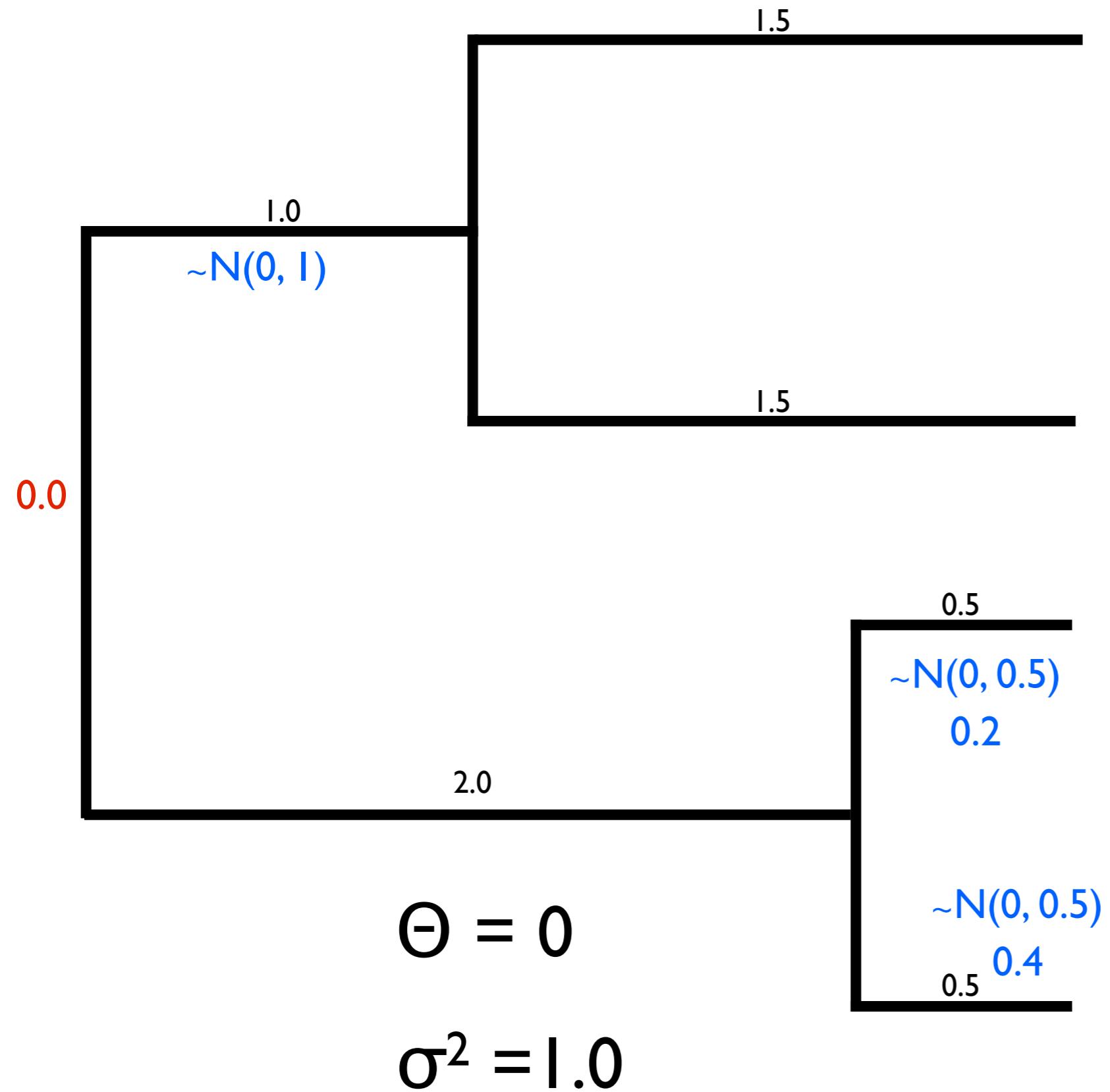
1. Set root state
2. Draw random normal deviate for each branch
3. Add along path from root to each tip to get tip values



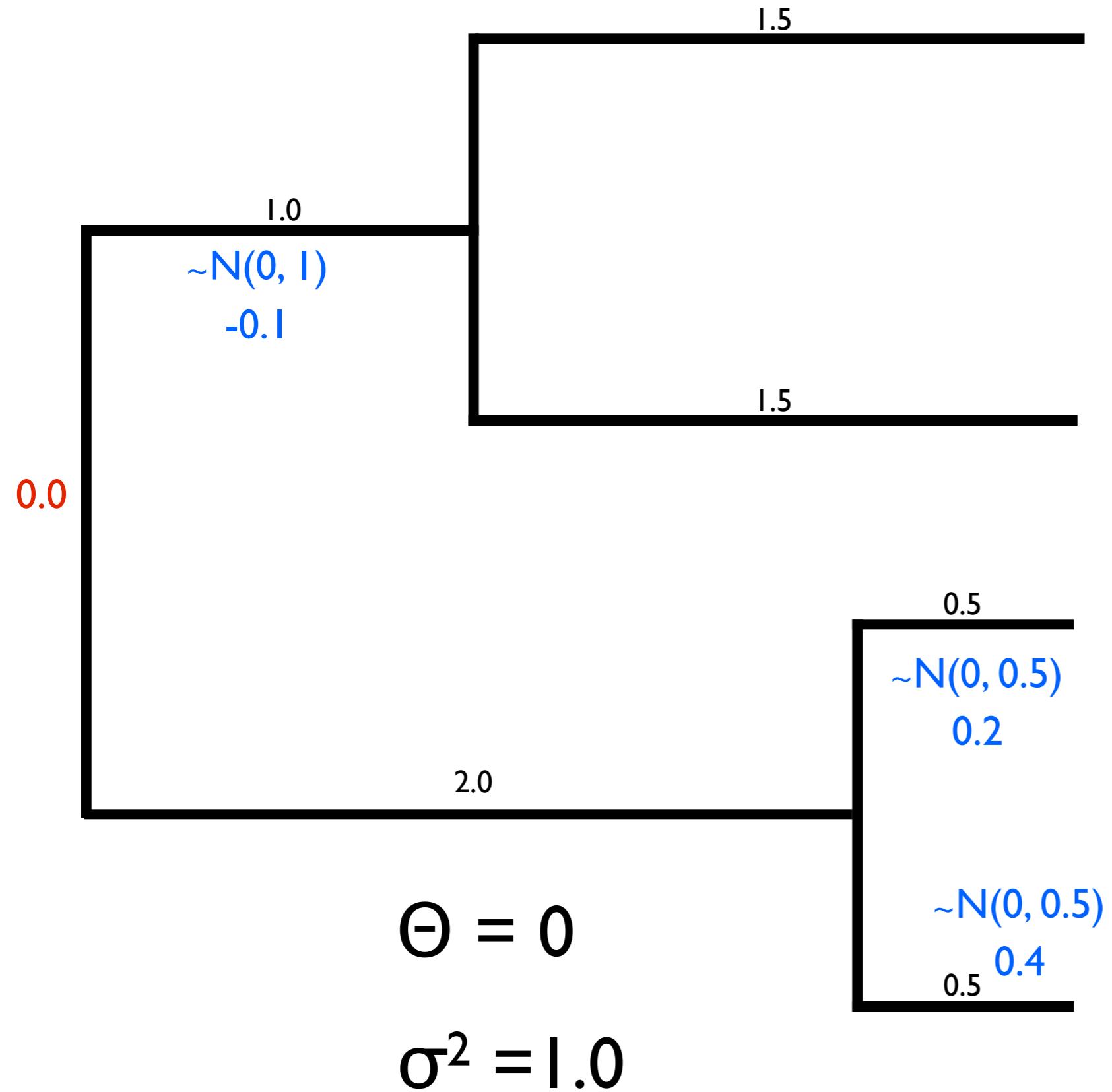
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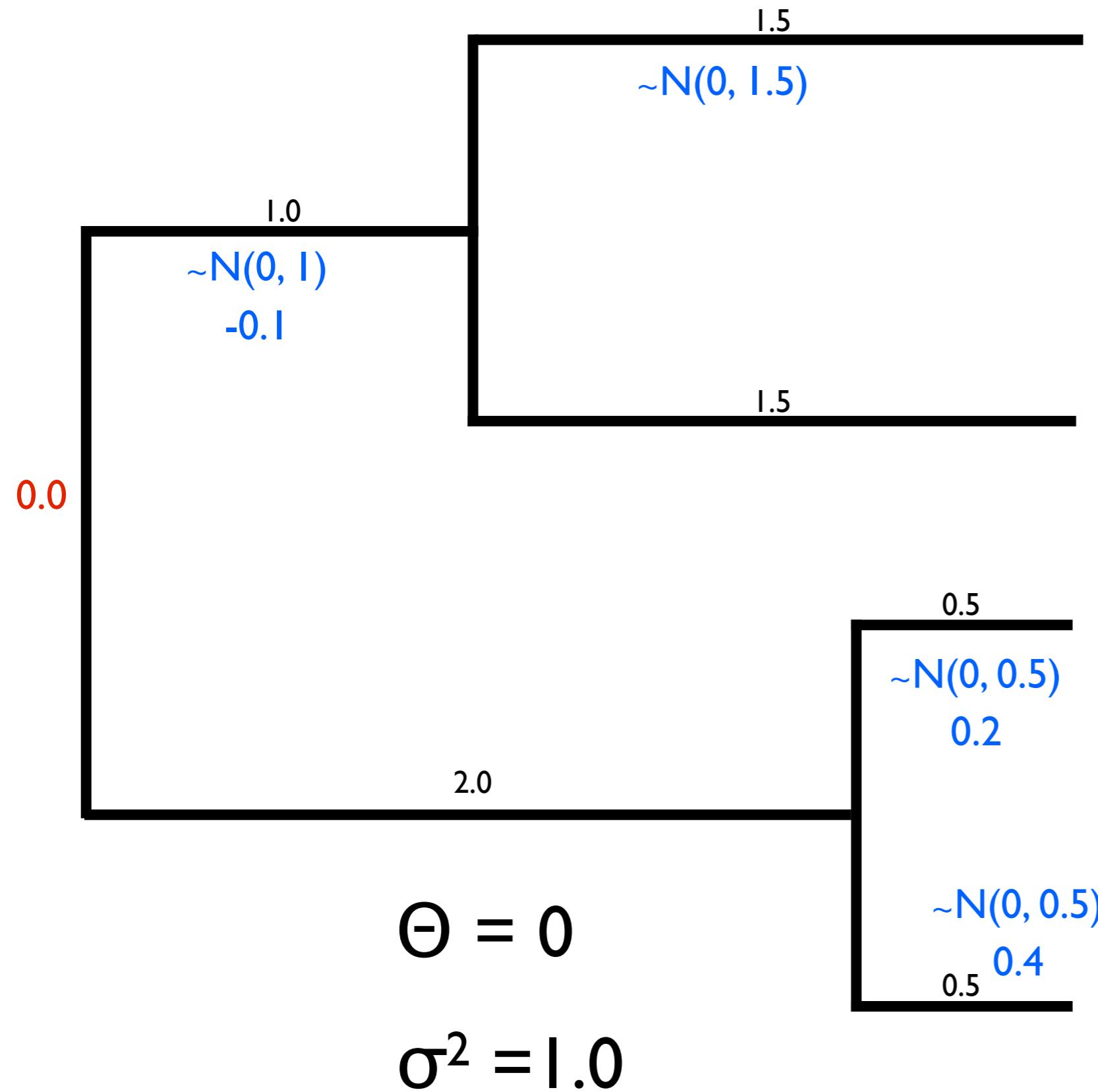
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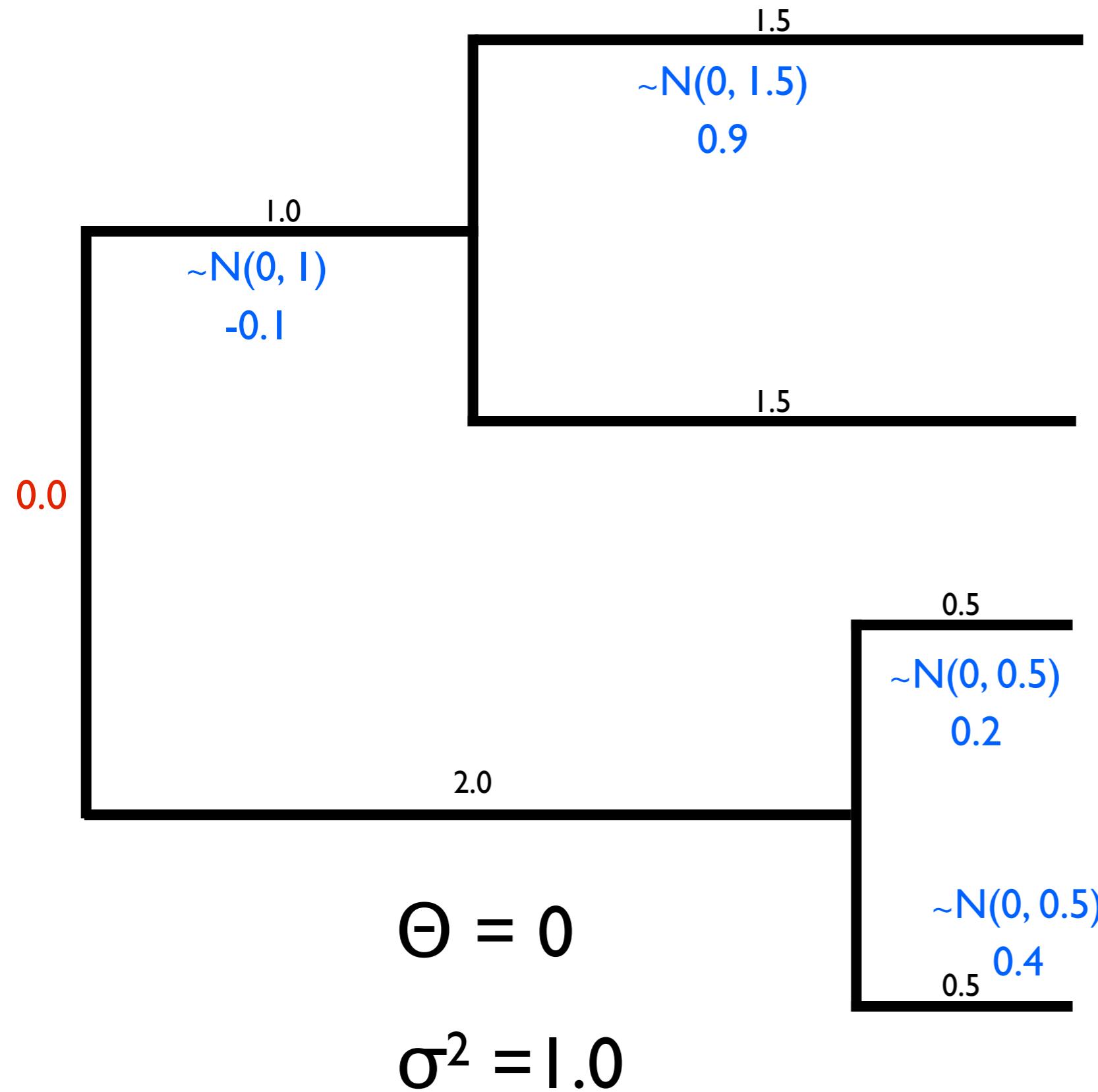
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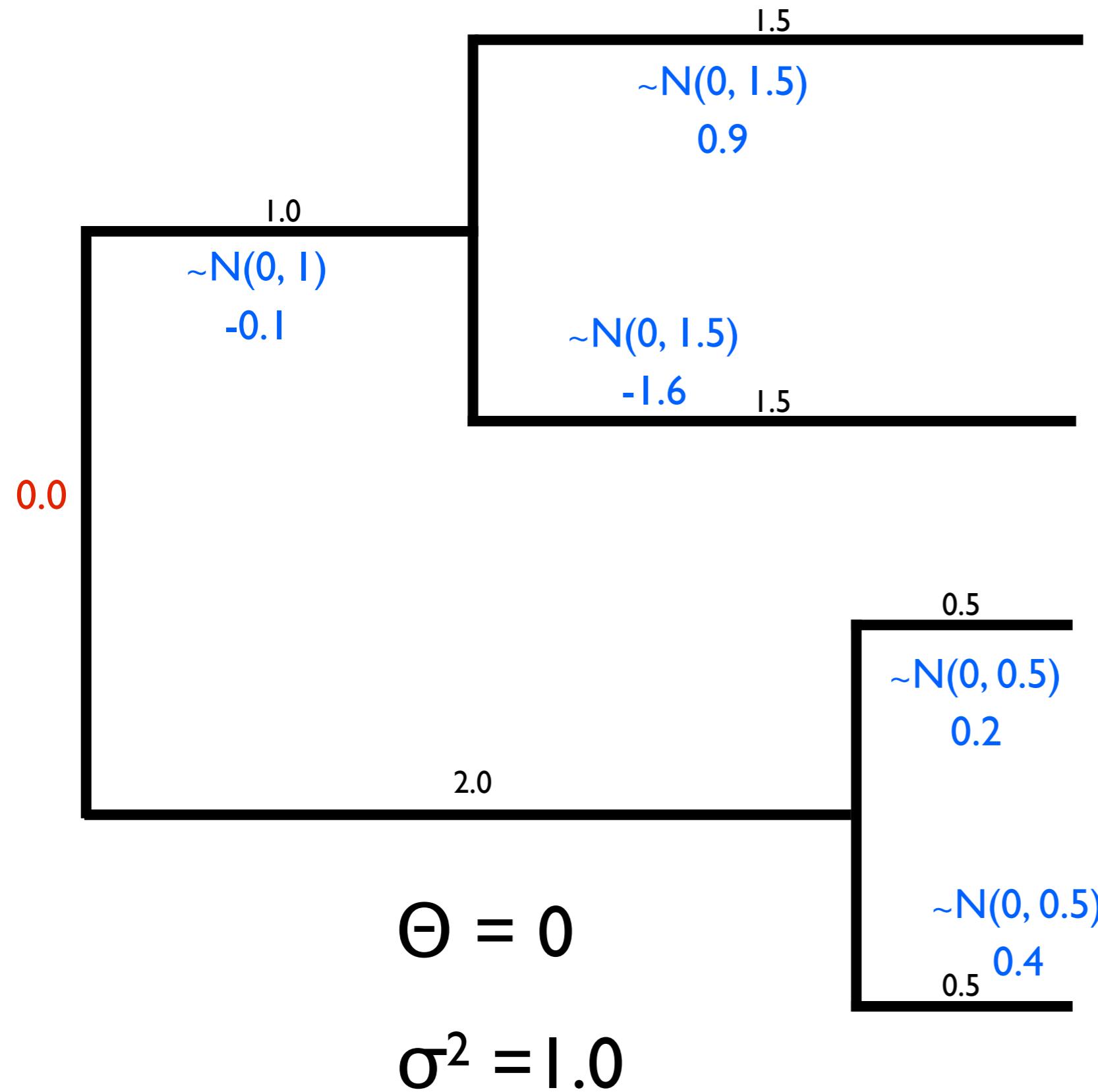
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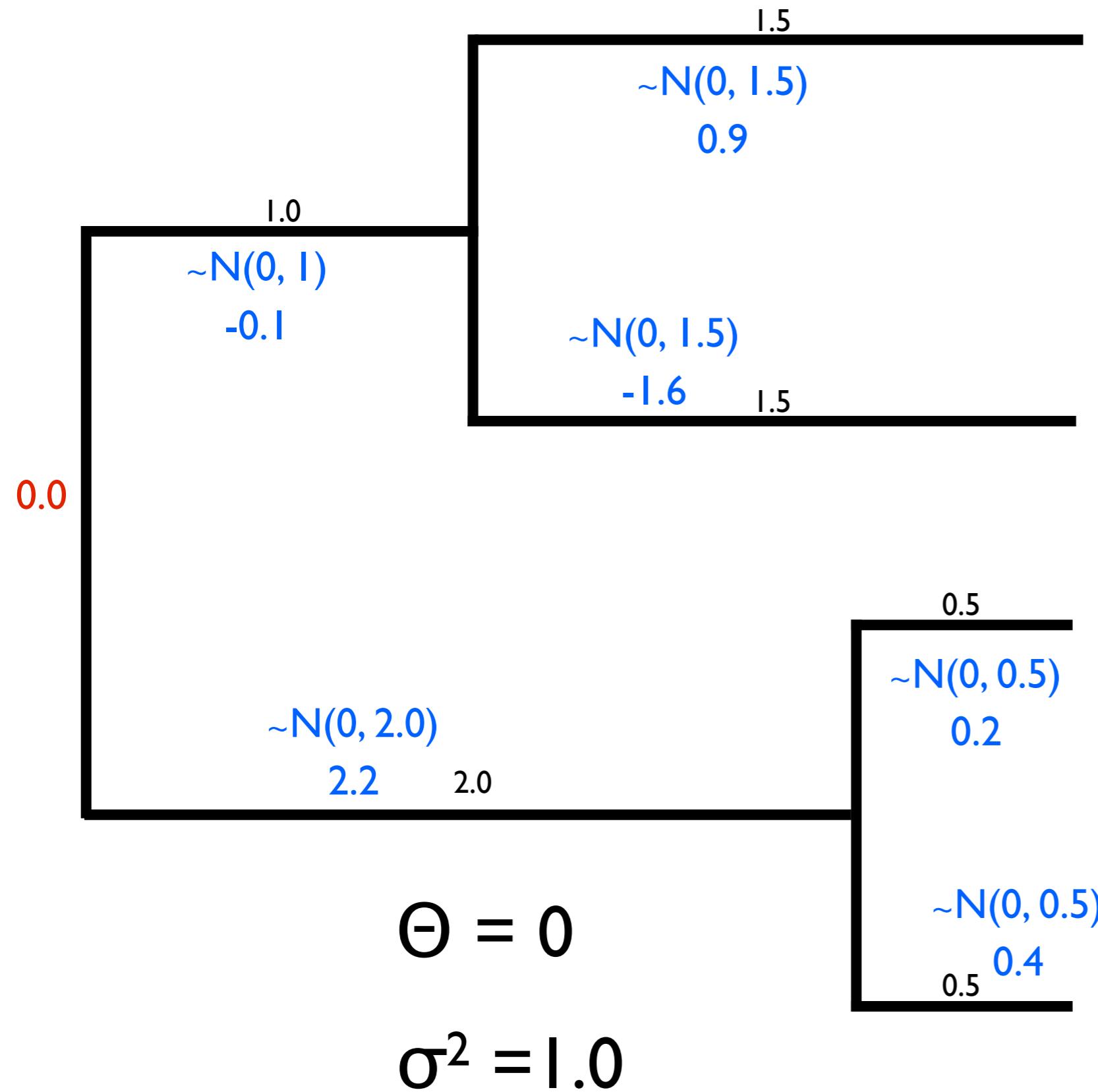
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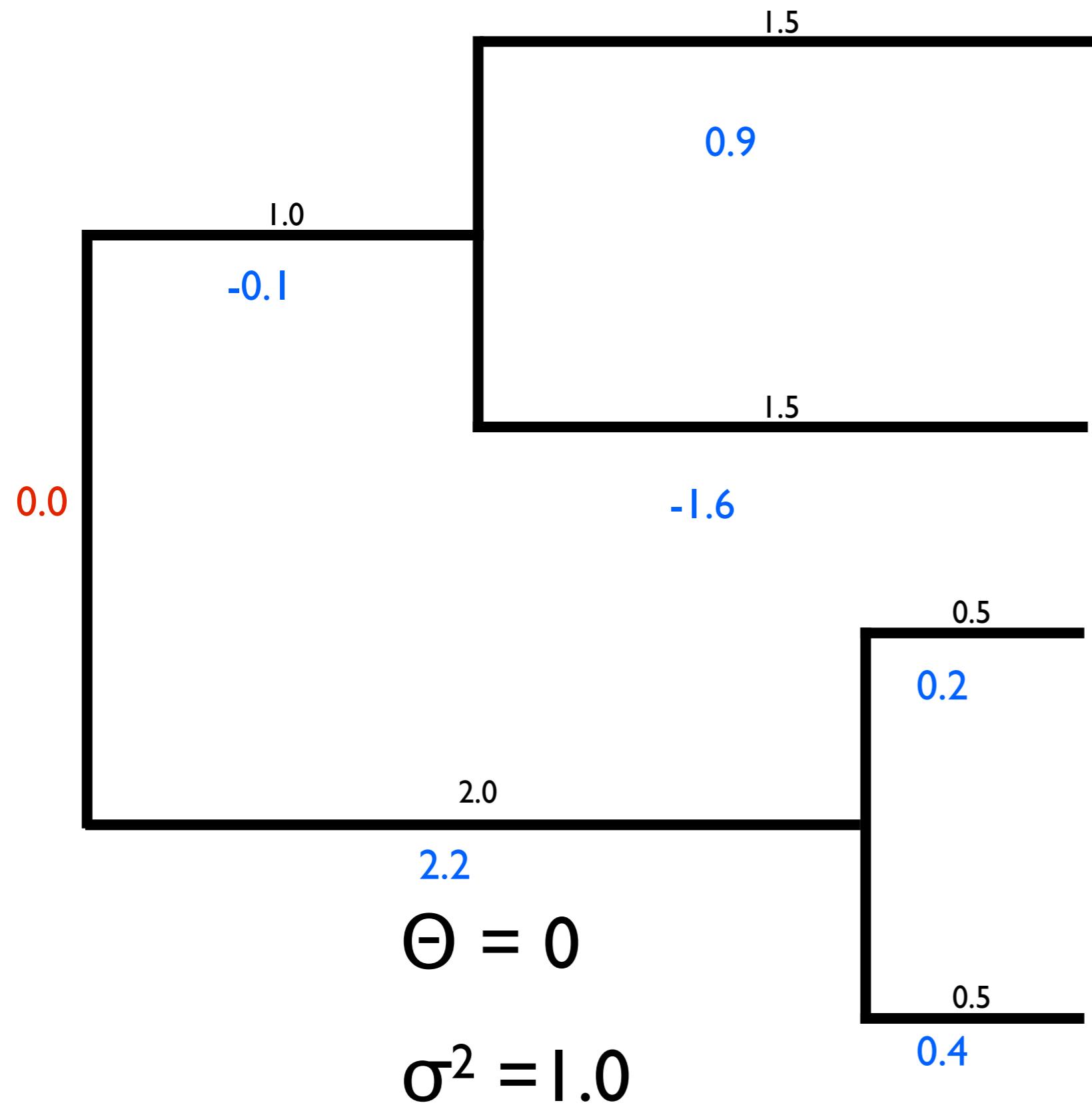
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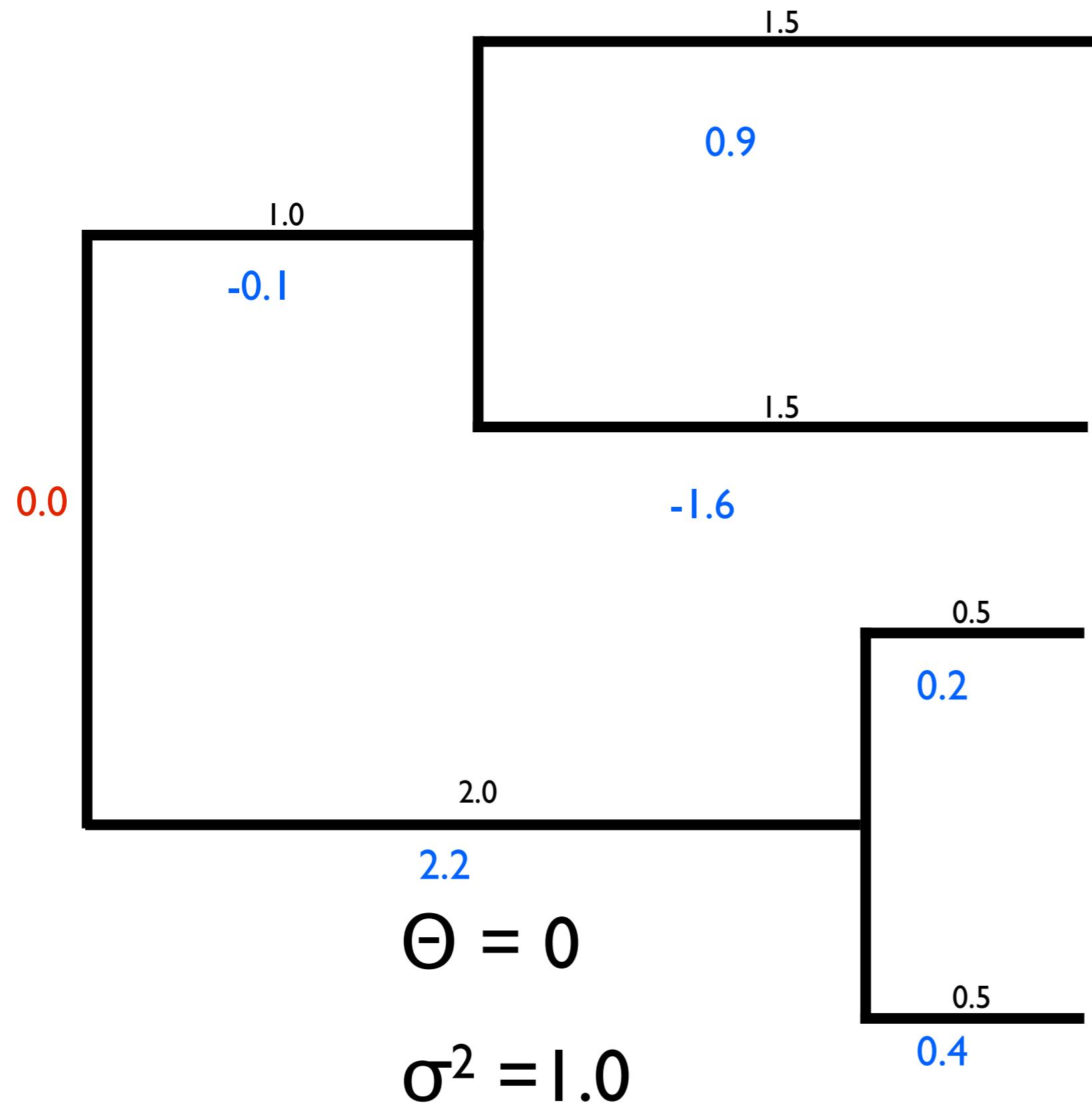
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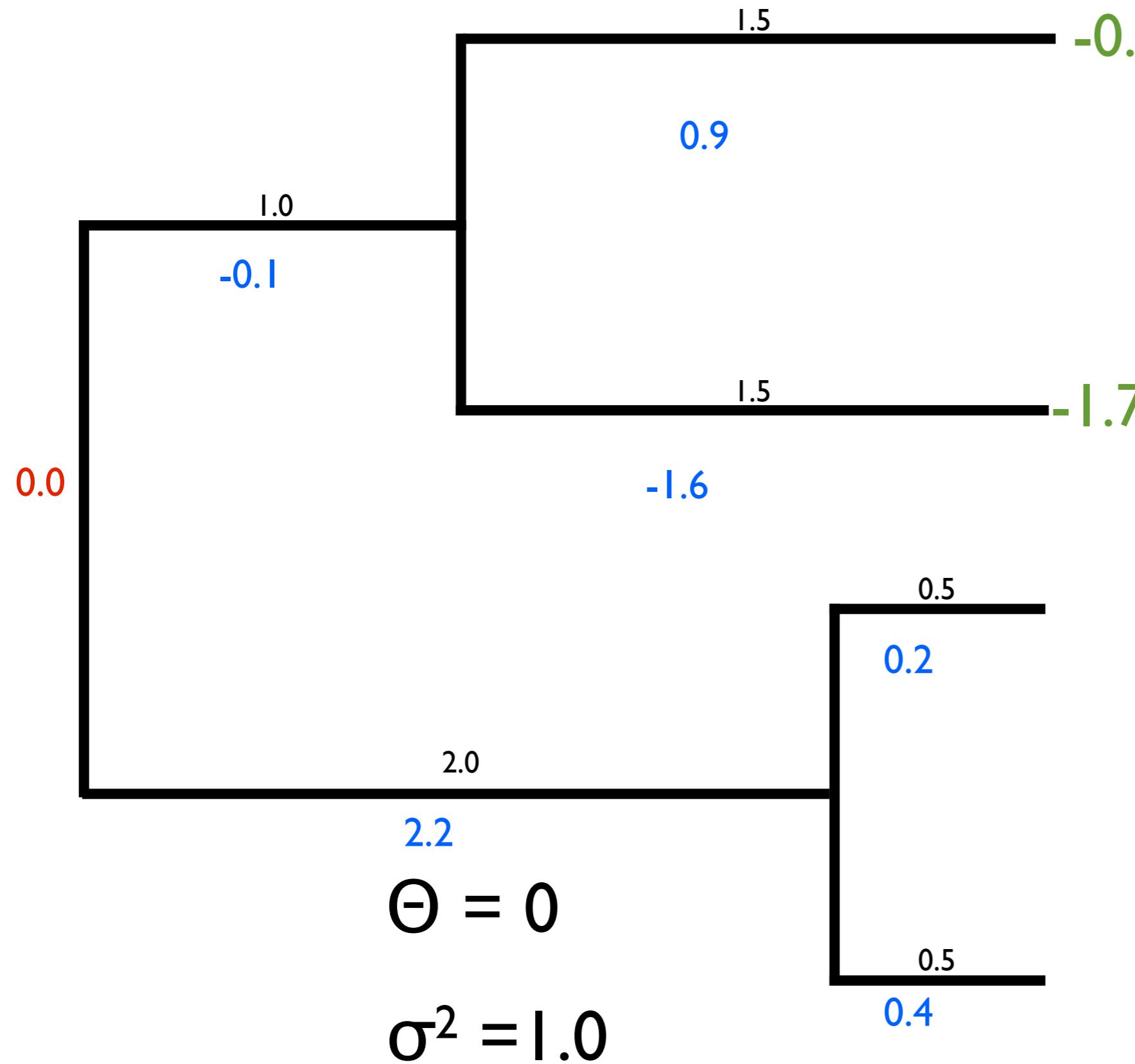


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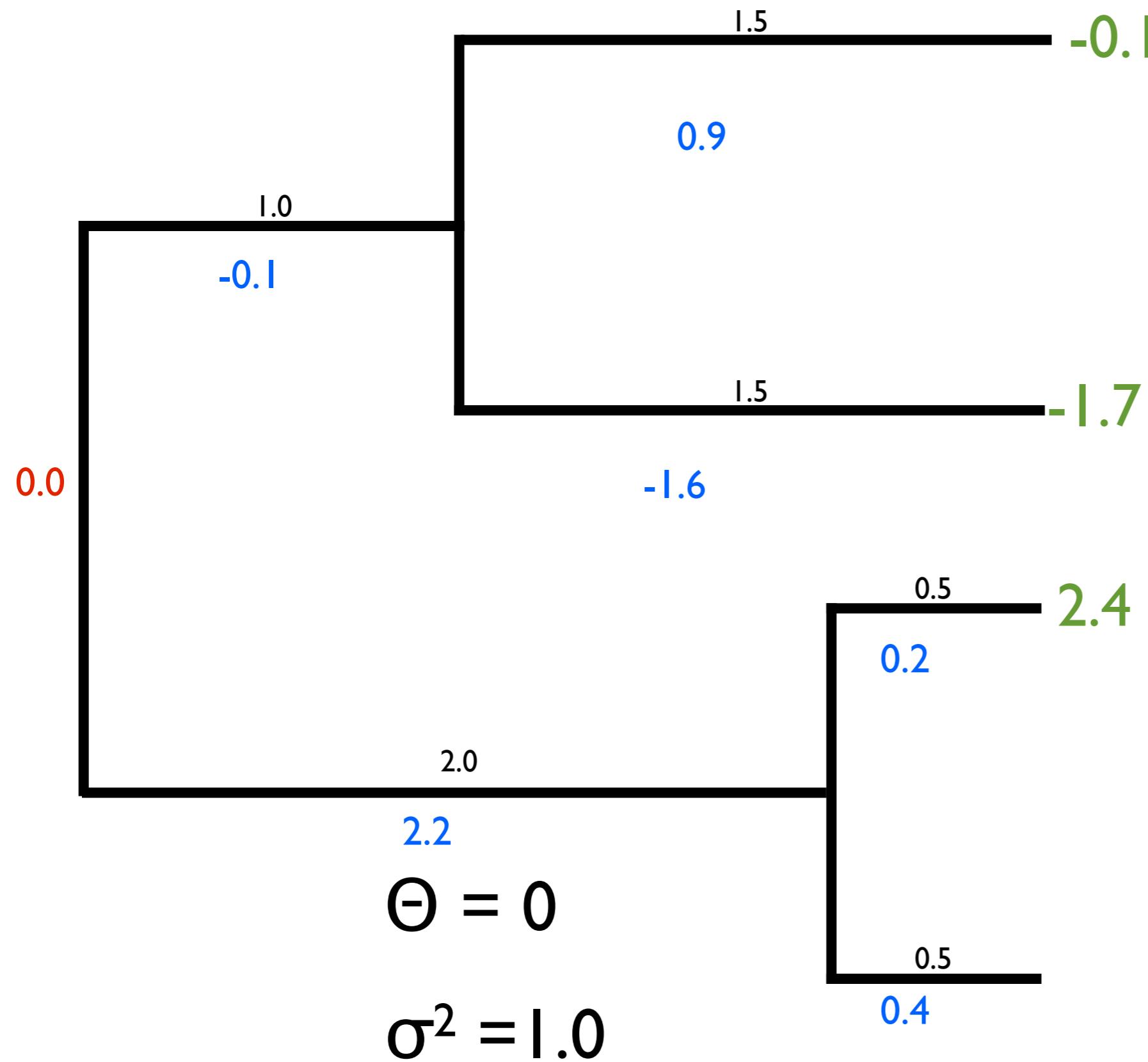
$$-0.1 + 0.9 = 0.8$$

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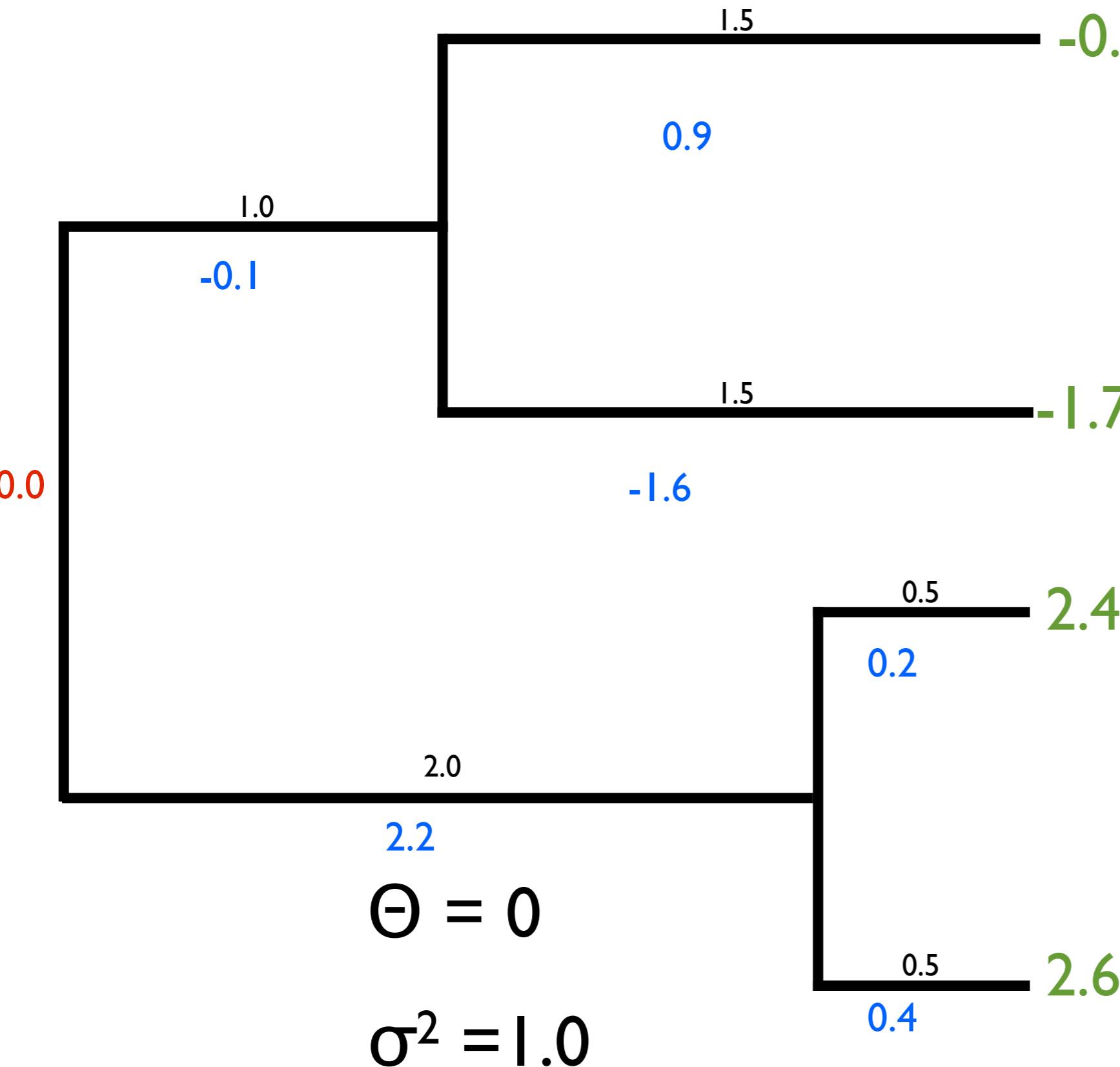
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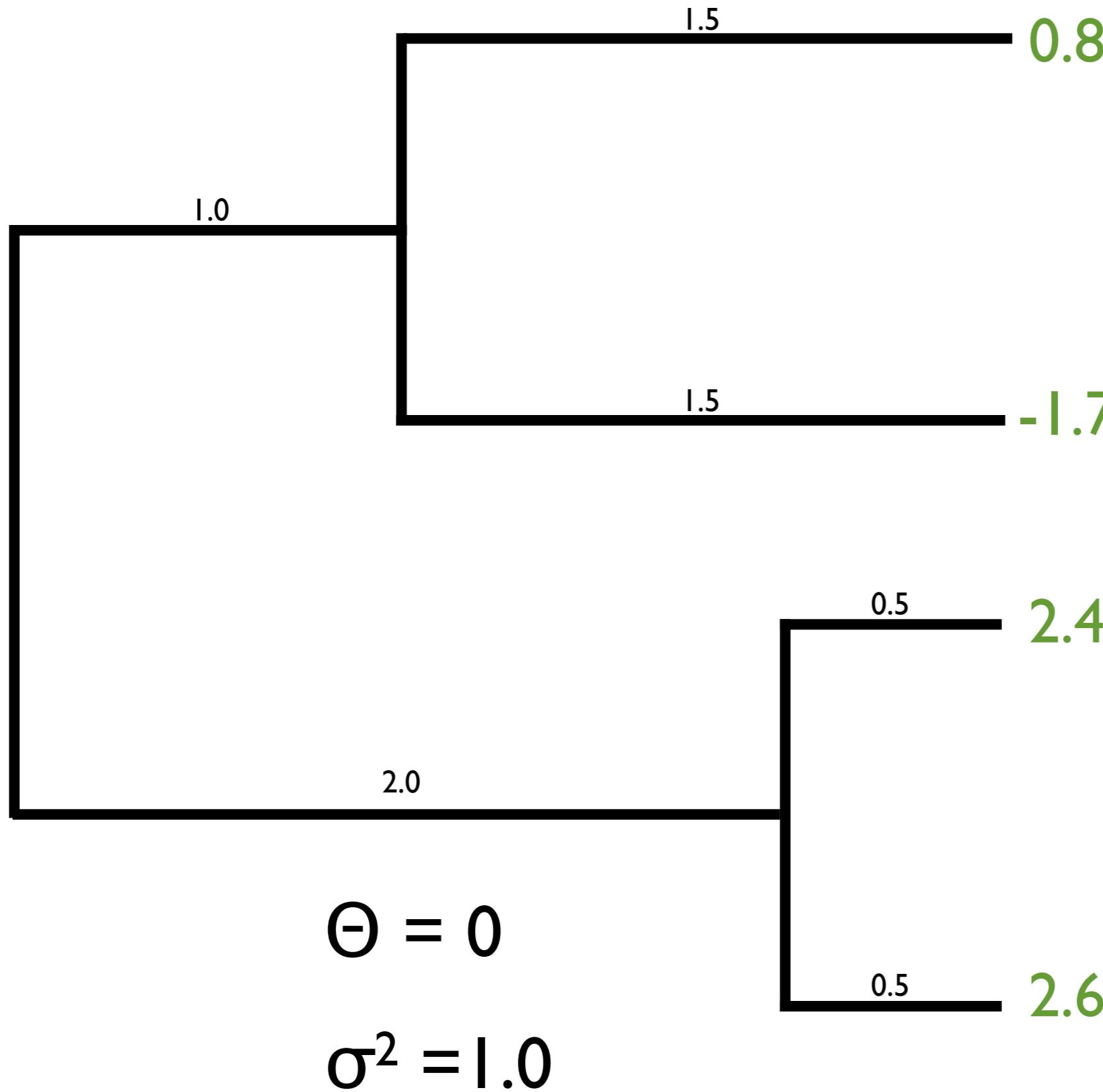


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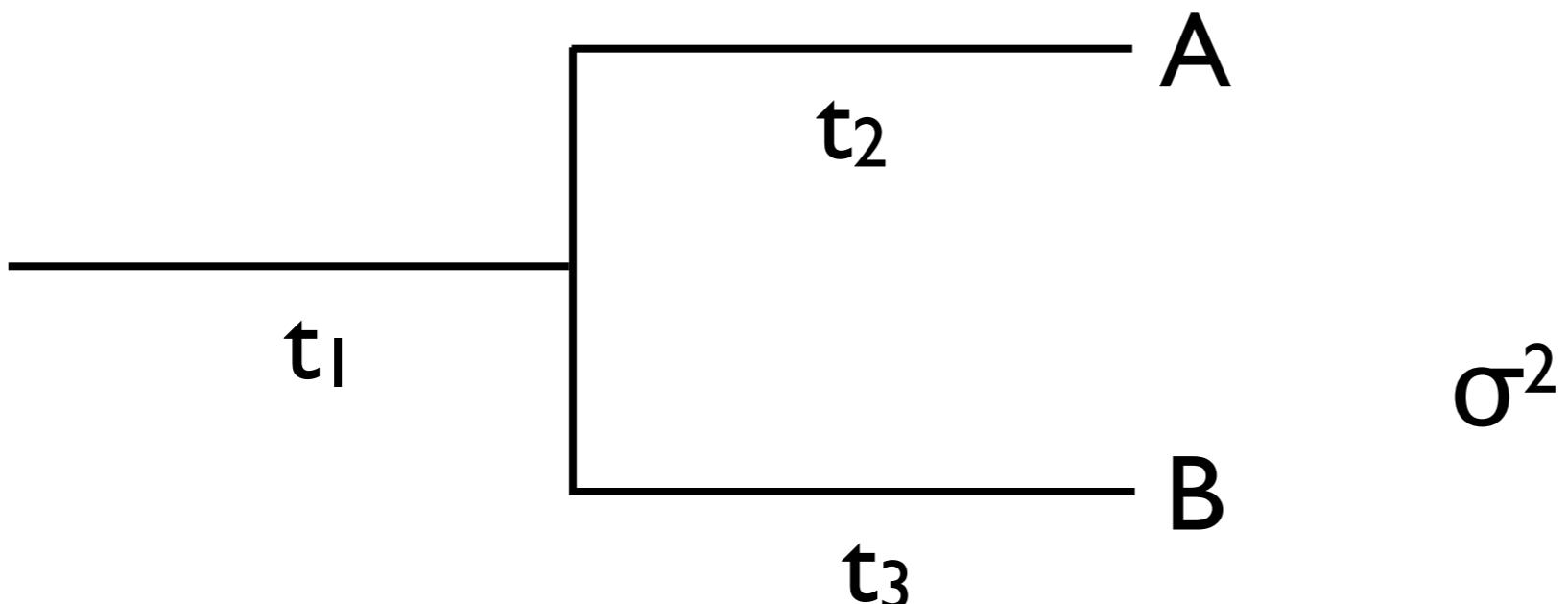


1. Set root state
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3. Add along path from root to each tip to get tip values

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?

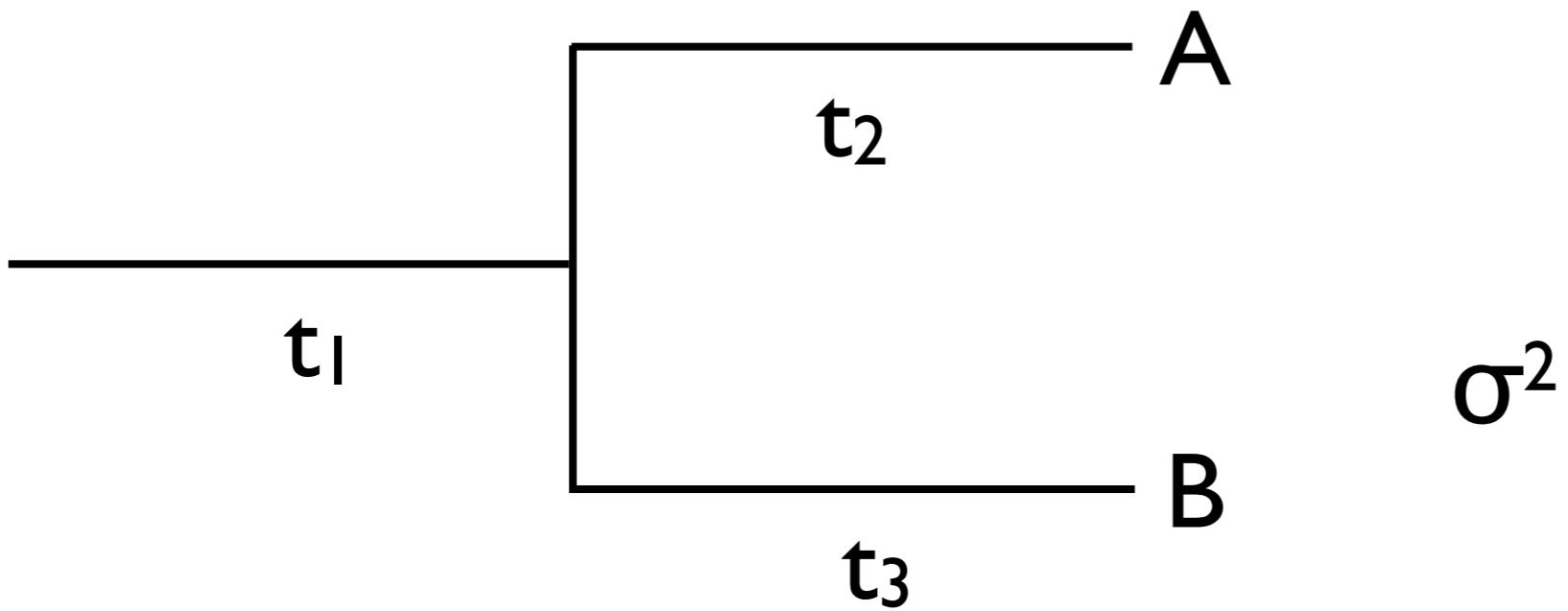


$\text{var}(A)$

$\text{cov}(A, B)$

$\text{var}(B)$

How do they covary?

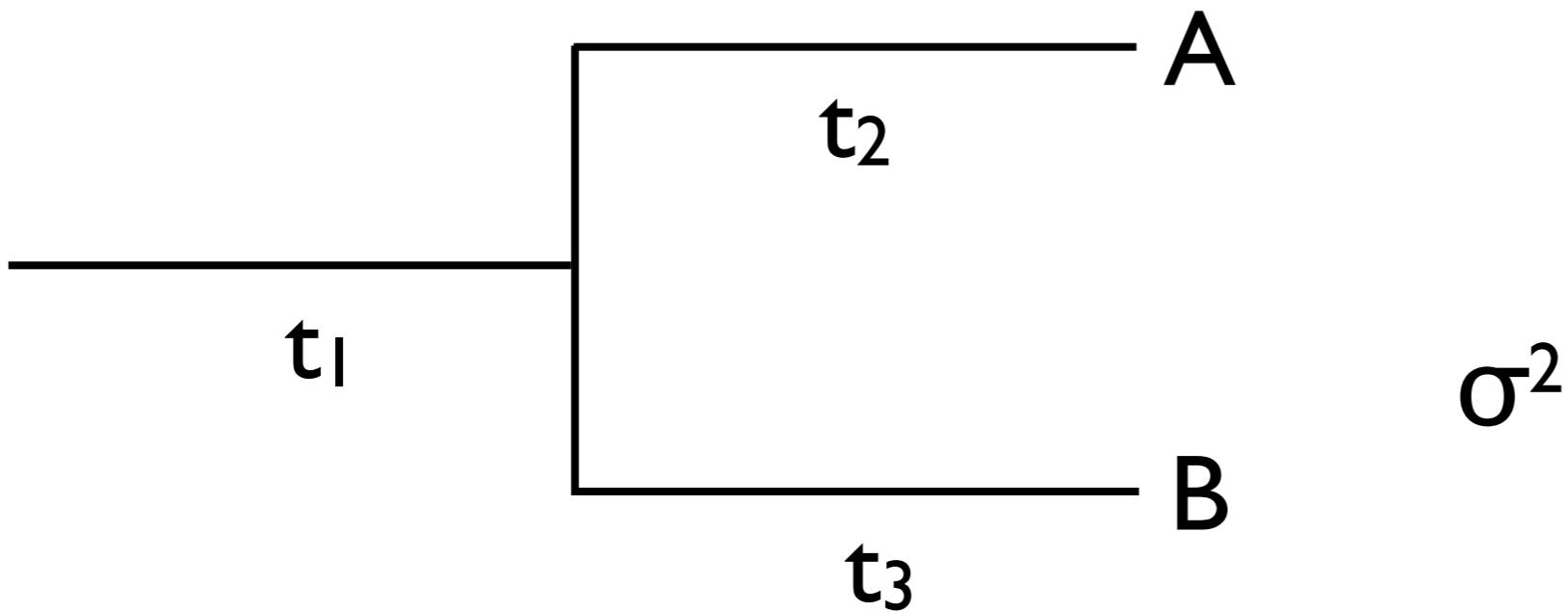


$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B)$$

$$\text{var}(B)$$

How do they covary?

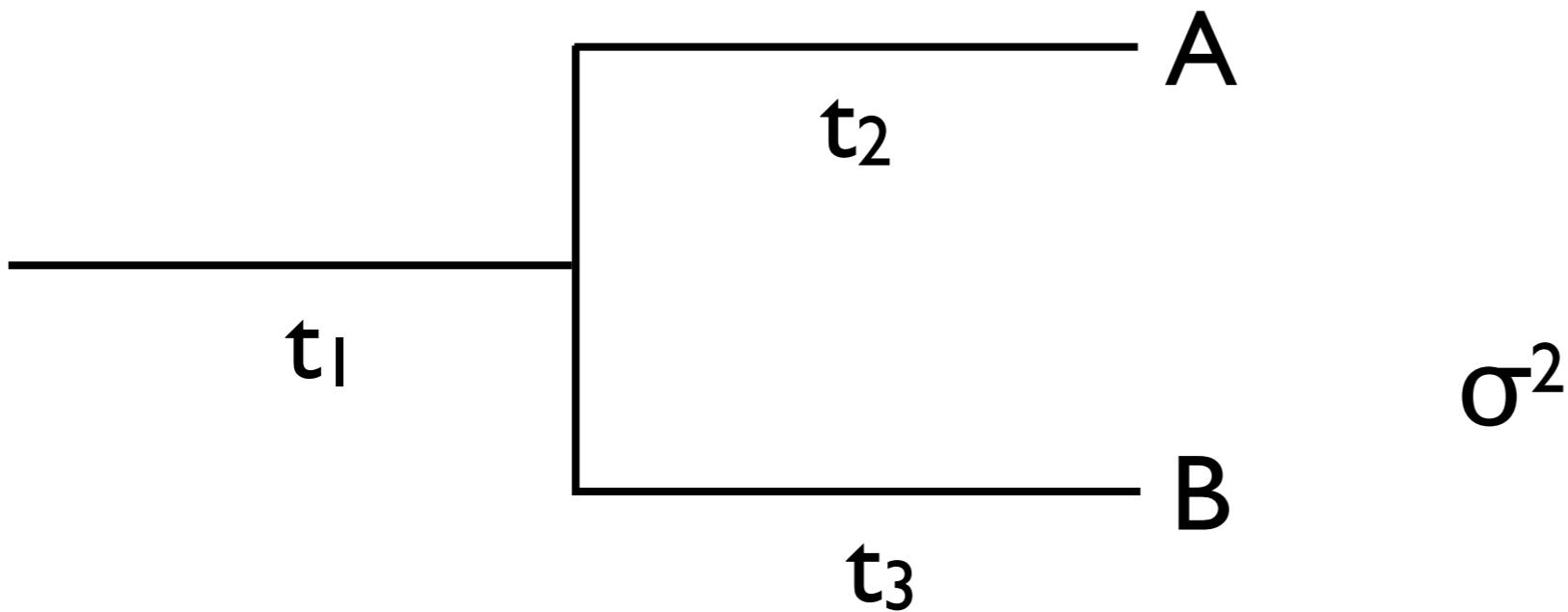


$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B)$$

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

How do they covary?

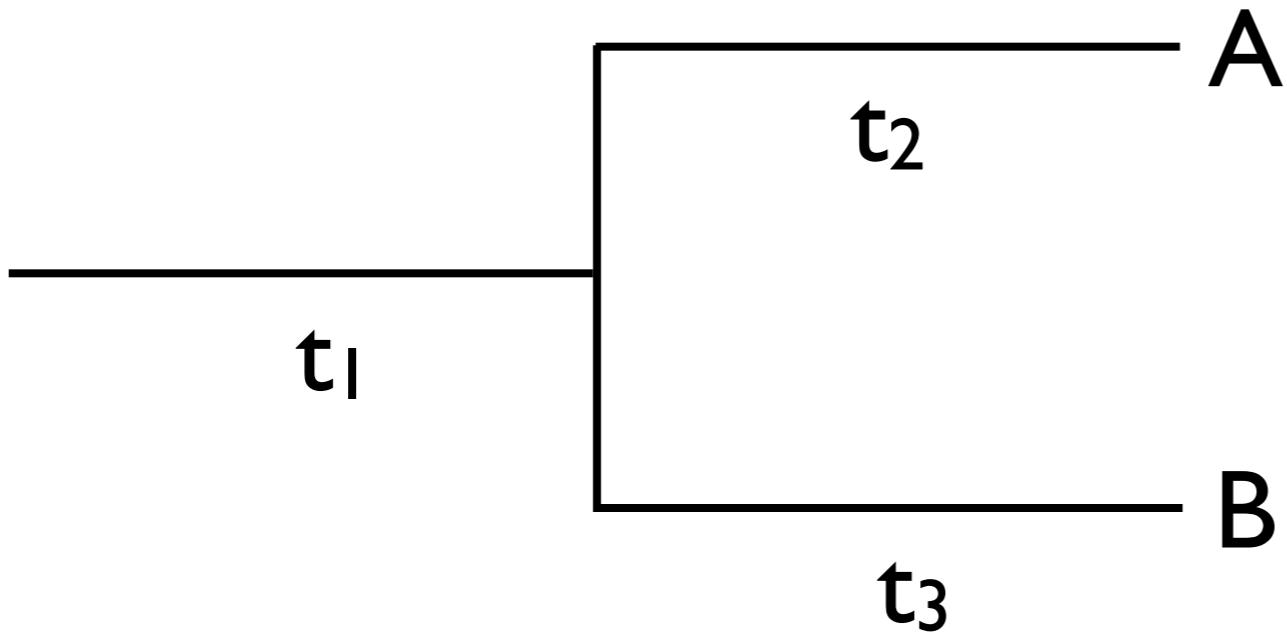


$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

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

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

How do they covary?



**variance-covariance
matrix**

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

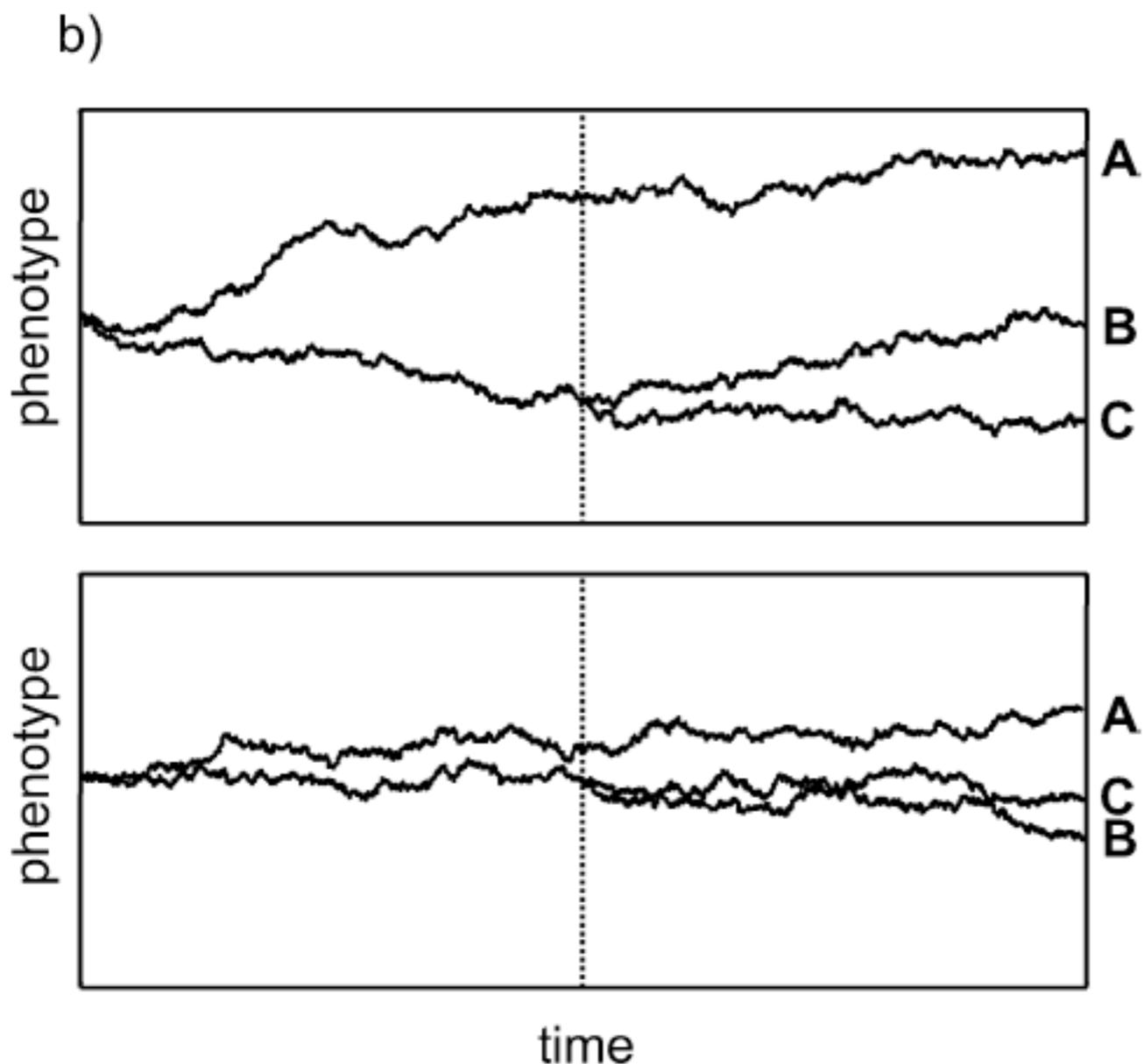
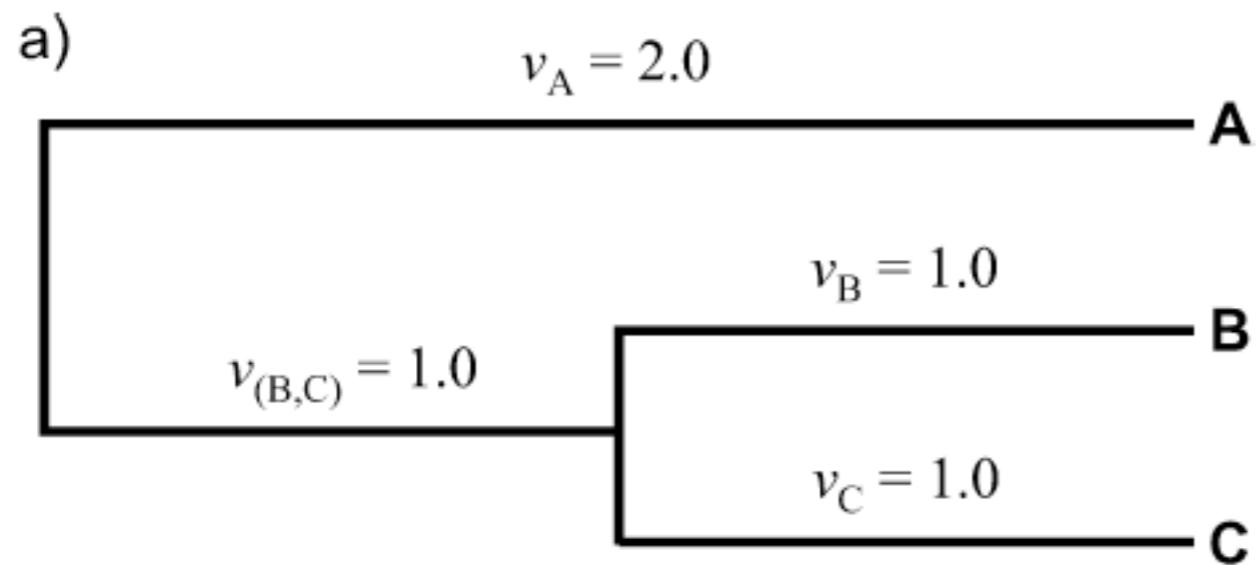
$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

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

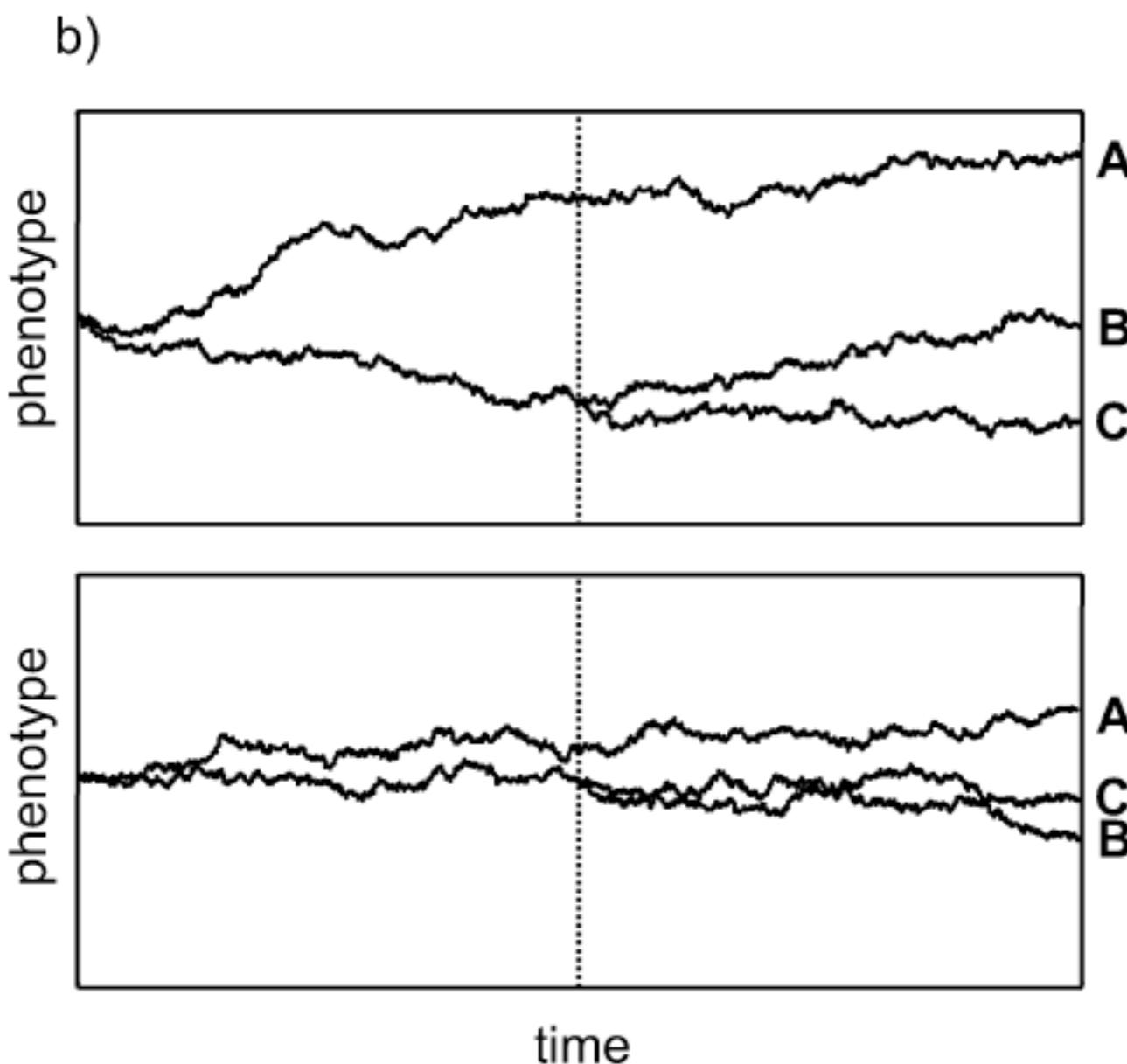
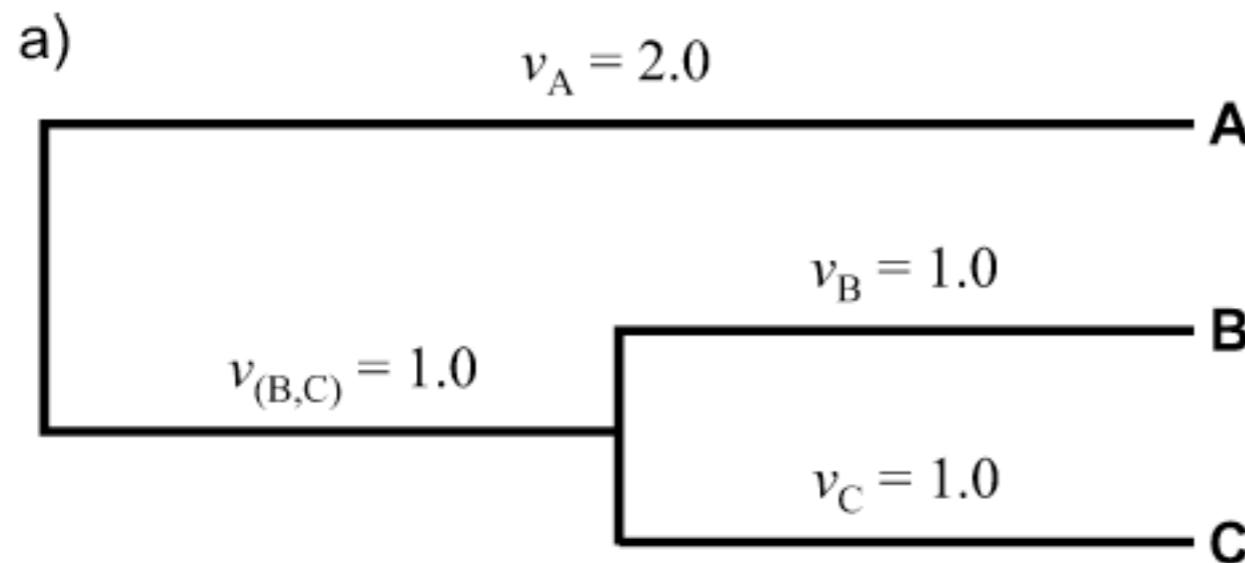
$$\text{var}(B) = \sigma^2(t_1 + t_3)$$

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



from Revell et al. 2008



c)

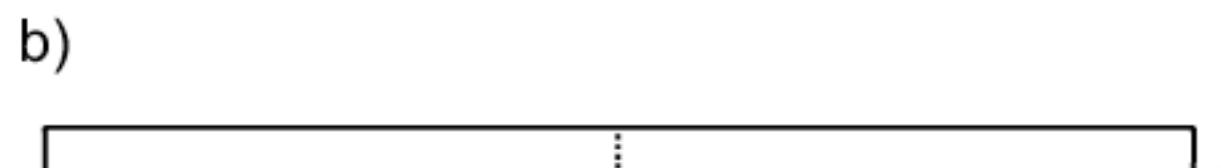
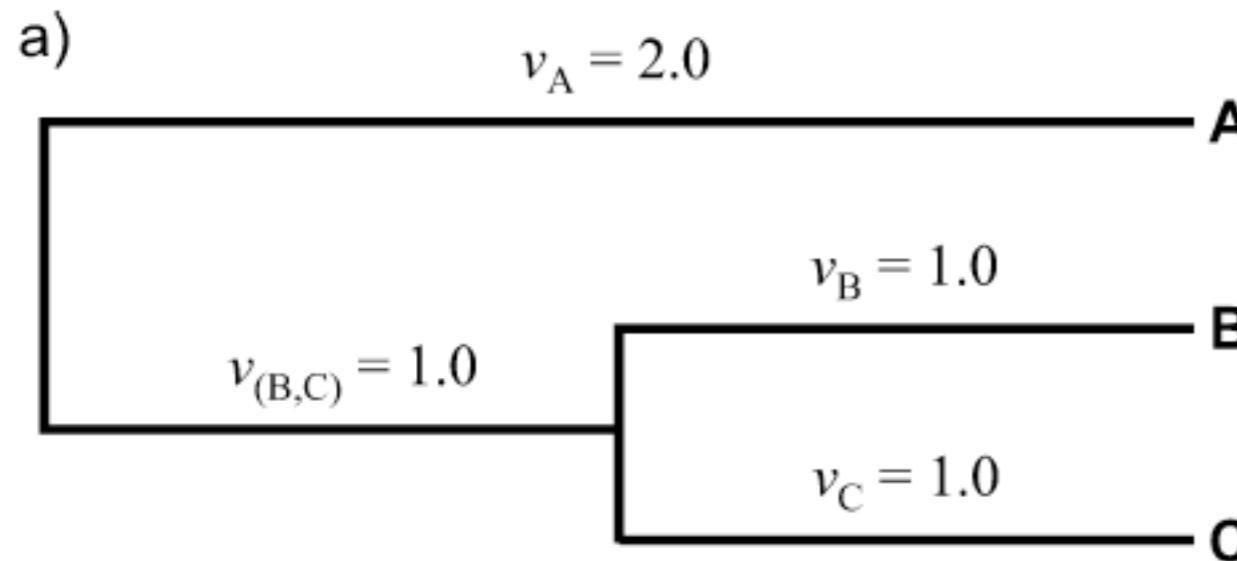
Expected covariance among species ($\sigma^2 = 1.0$):

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

Observed covariance among species
(N=100 simulations):

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

from Revell et al. 2008

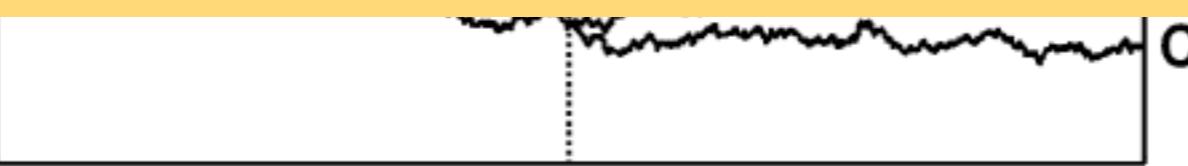


c)

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

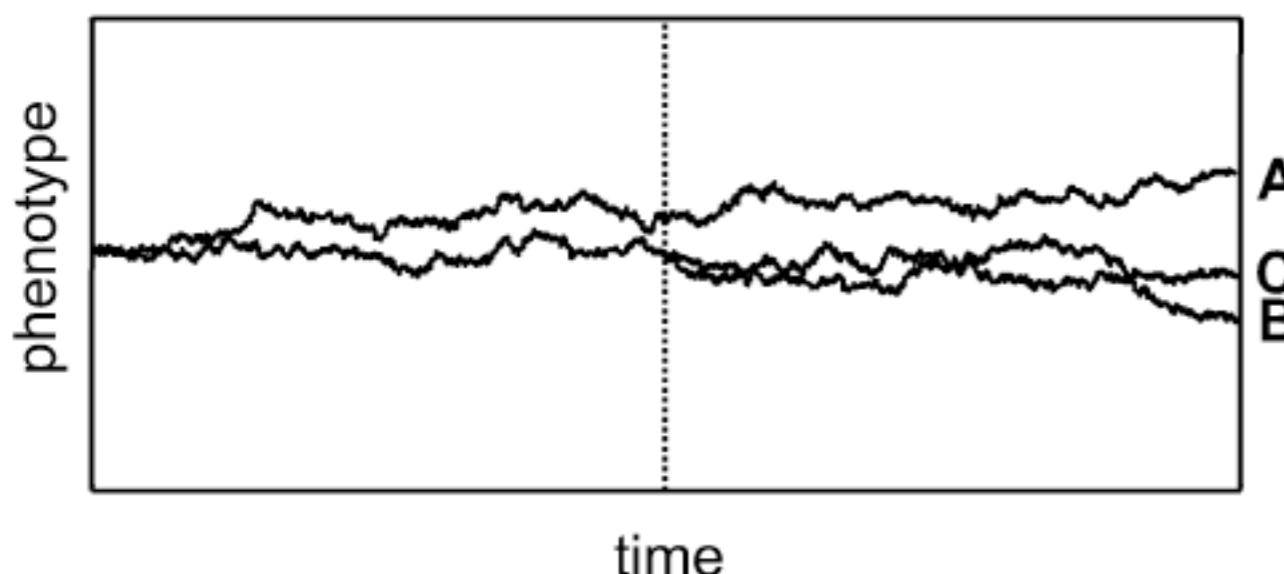
$$\mathbf{C} = \begin{bmatrix} v_A & 0.0 & 0.0 \\ 0.0 & v_B + v_{(B,C)} & v_{(B,C)} \\ 0.0 & v_{(B,C)} & v_C + v_{(B,C)} \end{bmatrix} = \begin{bmatrix} 2.0 & 0.0 & 0.0 \\ 0.0 & 2.0 & 1.0 \\ 0.0 & 1.0 & 2.0 \end{bmatrix}$$

phenotype



$$\bar{\mathbf{C}} = \begin{bmatrix} 1.00 & 0.11 & -0.24 \\ 0.11 & 2.08 & 0.84 \\ -0.24 & 0.84 & 1.94 \end{bmatrix}$$

phenotype

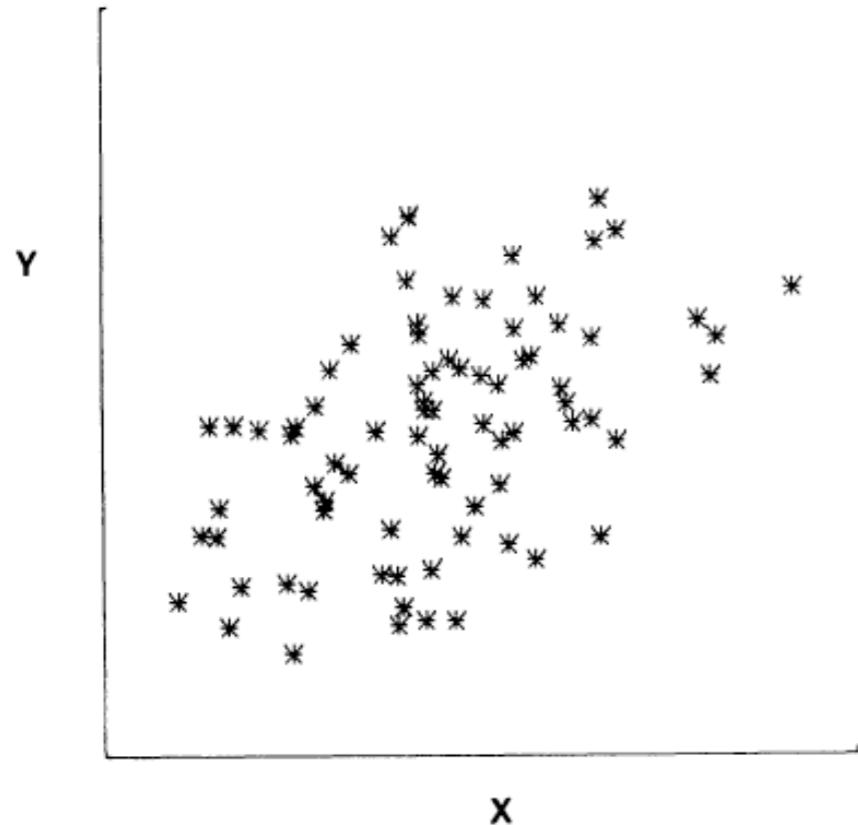


from Revell et al. 2008

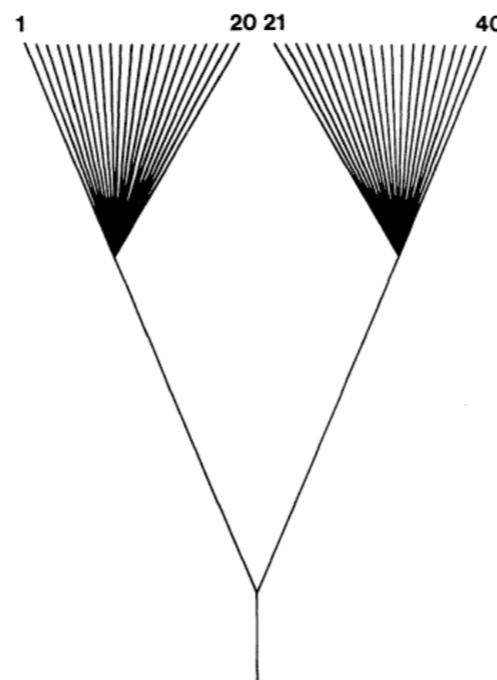
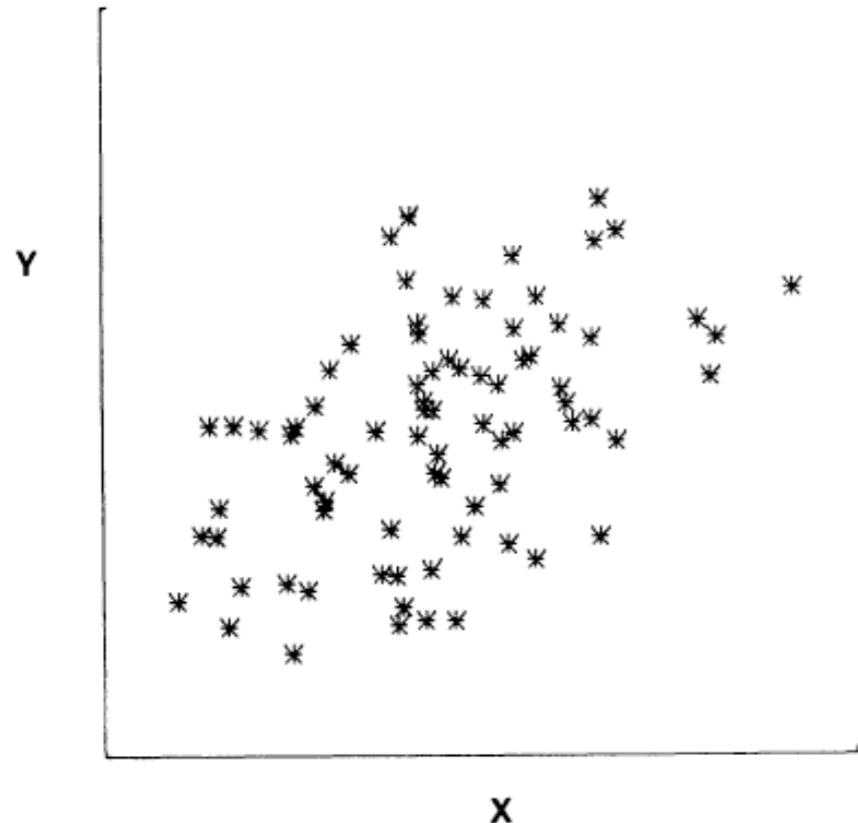
Phylogenetic Independent Contrasts

(PICs)

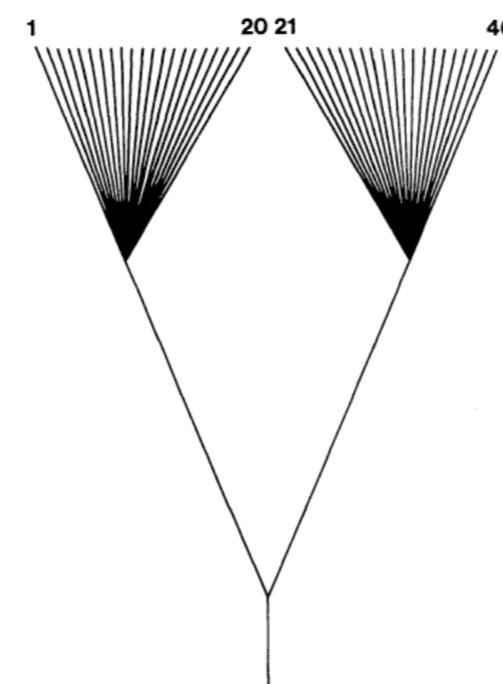
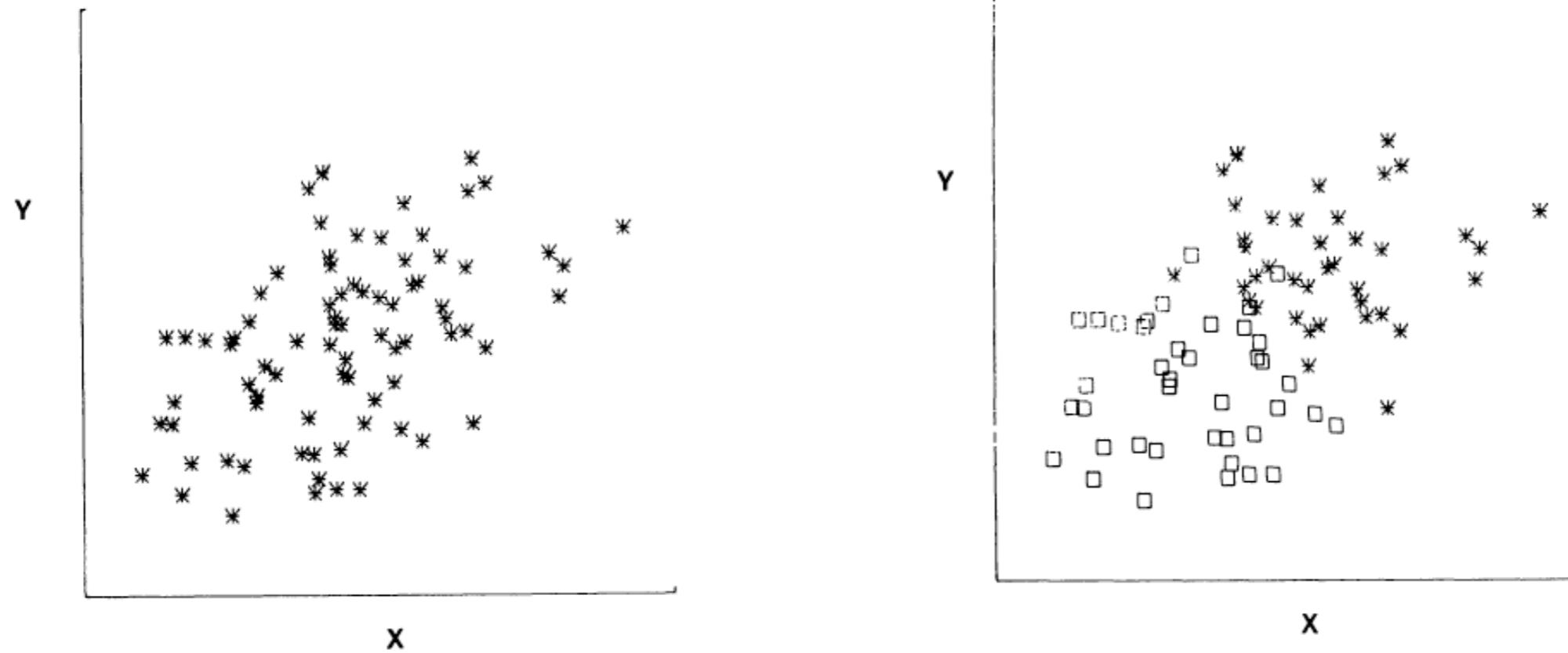
Felsenstein's “Worst Case”



Felsenstein's “Worst Case”



Felsenstein's “Worst Case”



Phylogenetic Independent Contrasts

- PICs are a way to analyze data that comes from phylogenetic trees
- Test for *evolutionary correlations* among characters
- We can think of PICs as a statistical transformation that creates independent data points

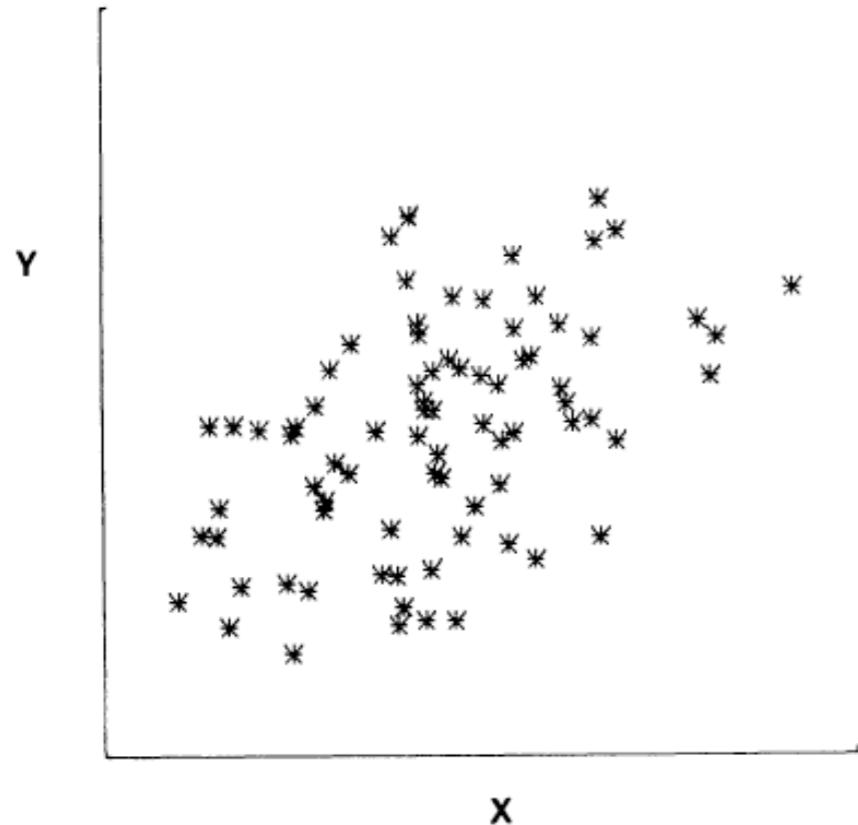
Standard correlation

- Can we predict Y from X?
- We might be able to do this for two reasons: species are related, or X and Y tend to evolve together

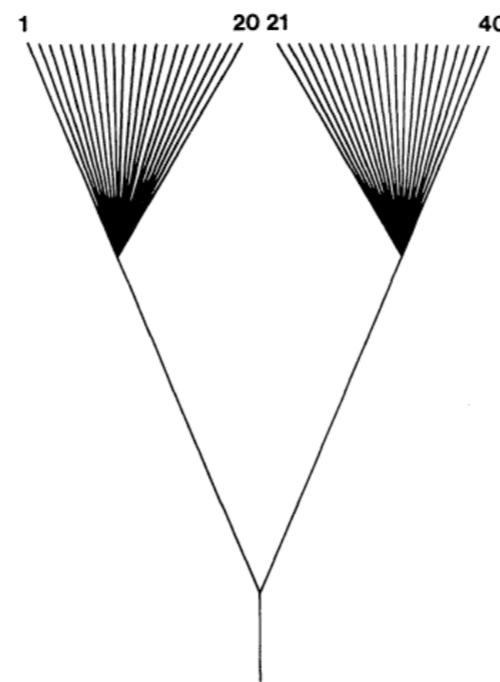
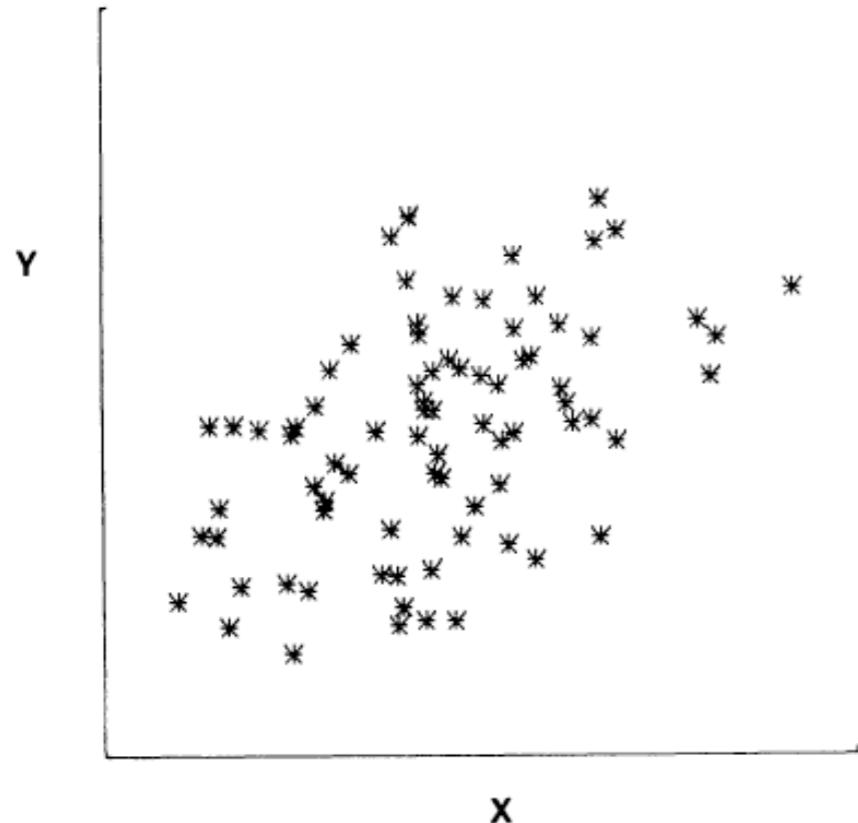
Evolutionary correlation

- X and Y evolve in a correlated fashion
- When X changes, Y tends to change in a predictable way

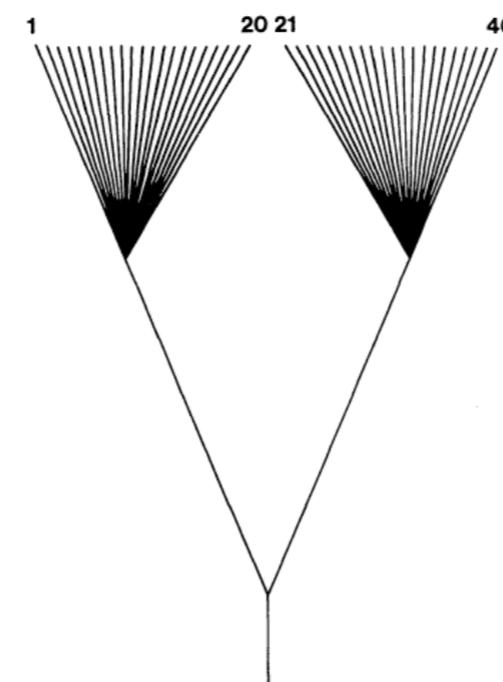
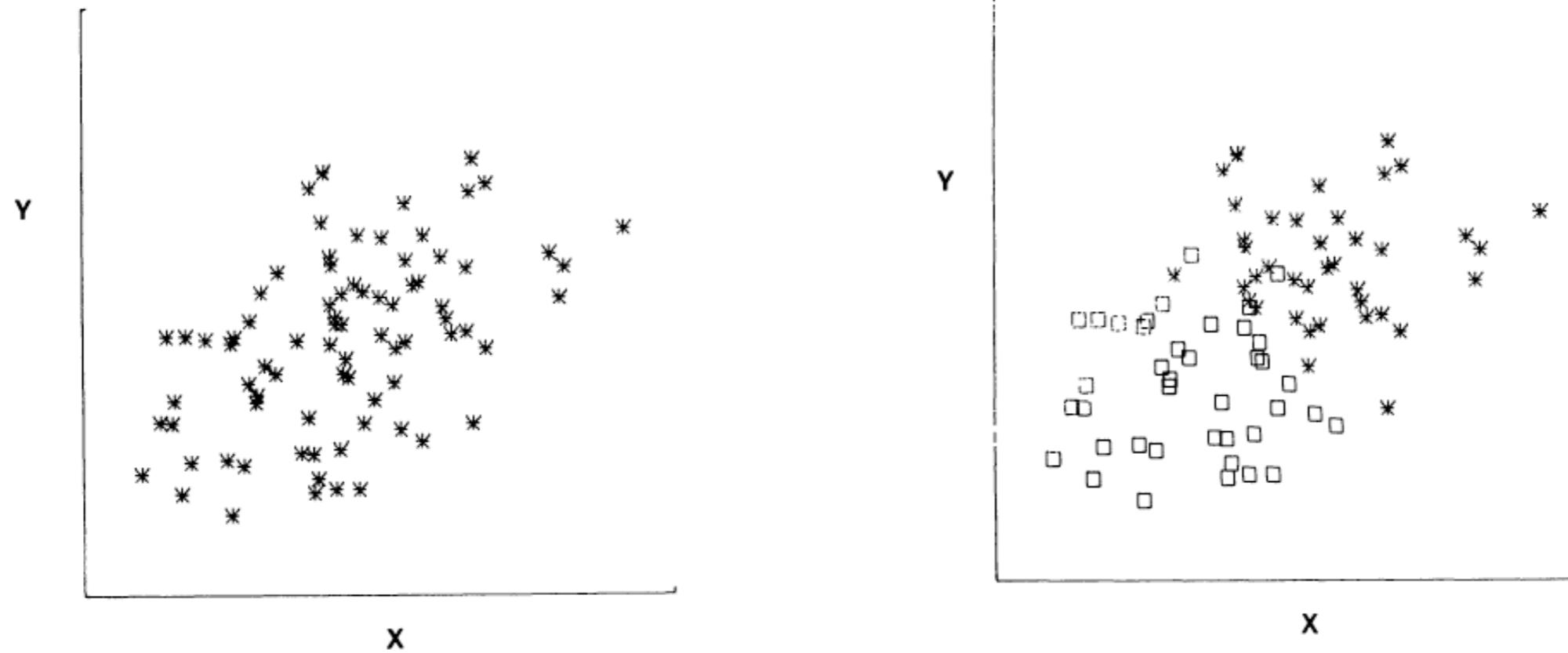
Felsenstein’s “Worst Case”



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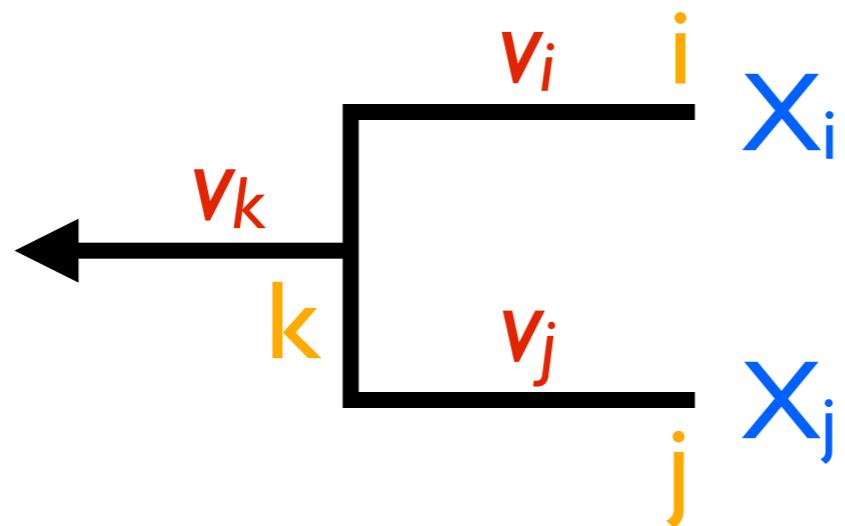


Felsenstein's “Worst Case”



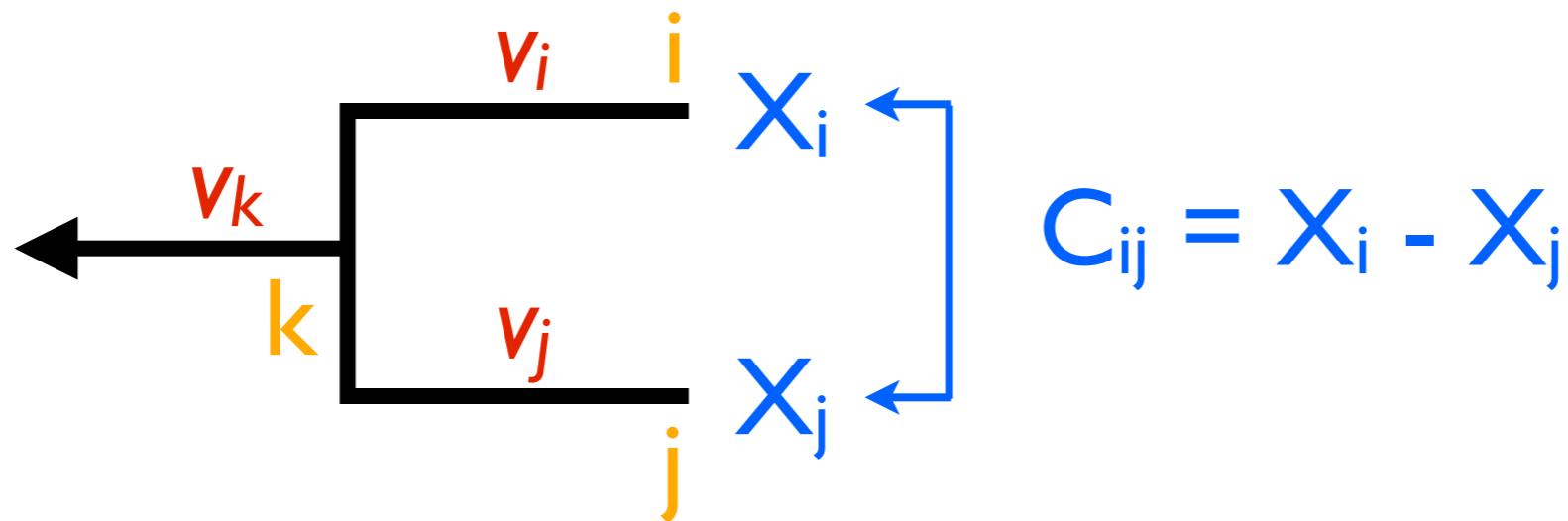
Calculating Contrasts*

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 $v_i + v_j$



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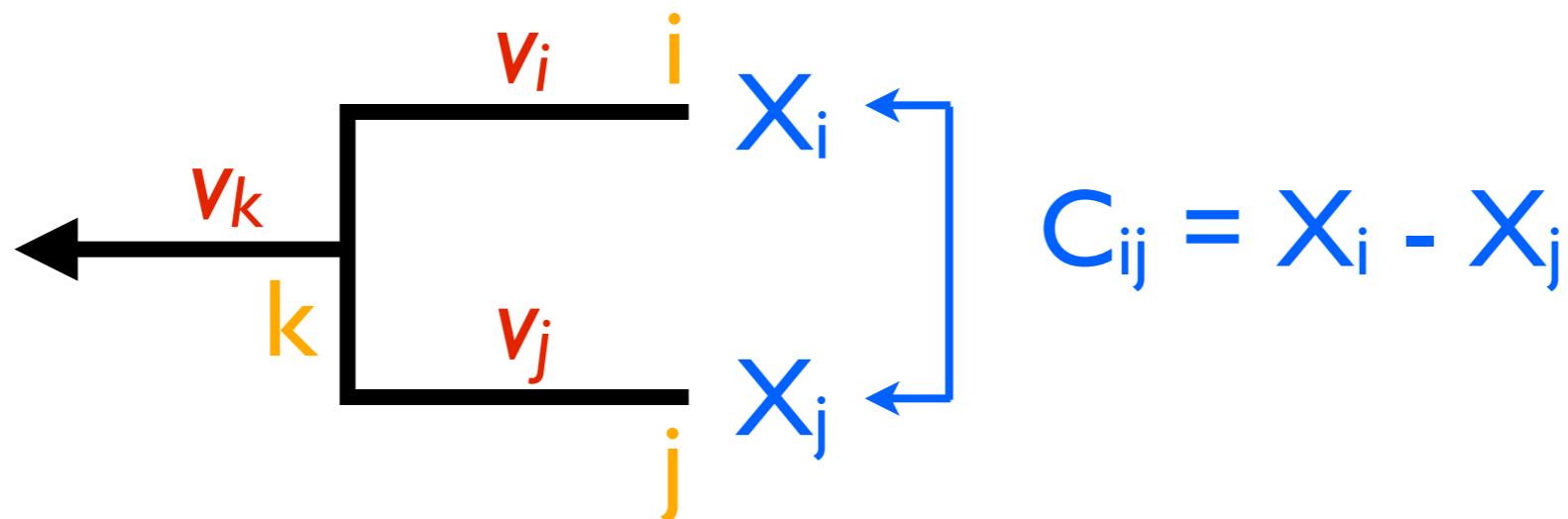


Calculating Contrasts*

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.

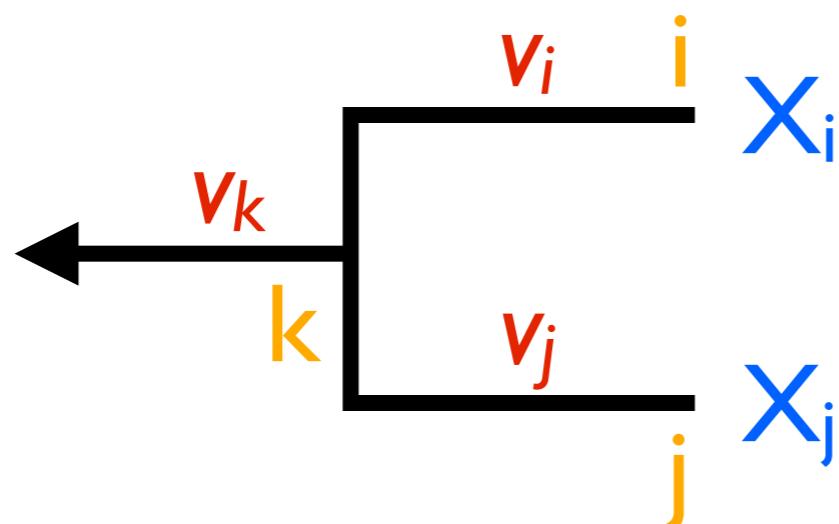


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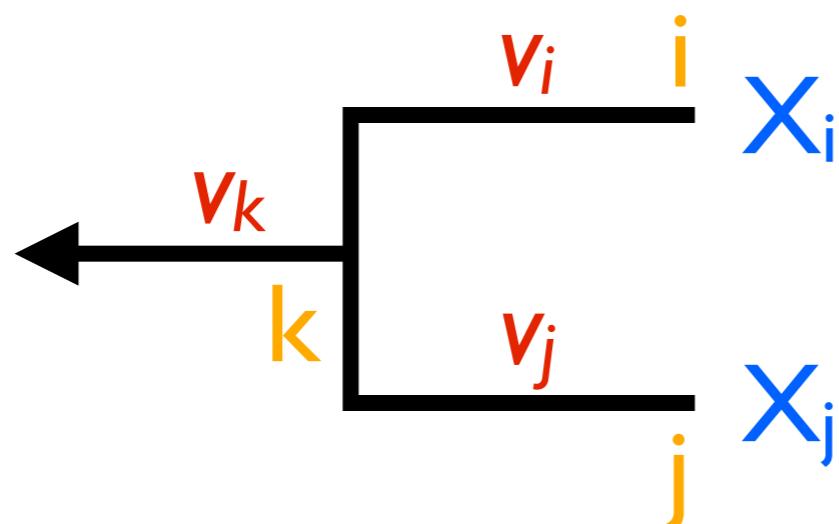
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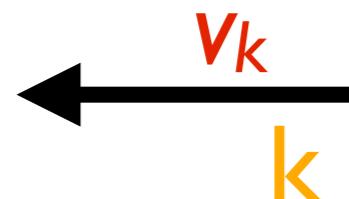
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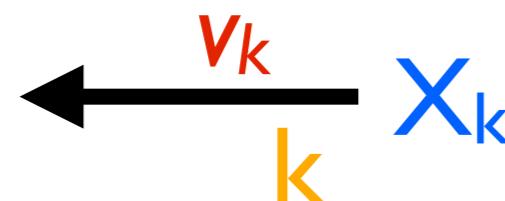
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Calculating Contrasts*

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*

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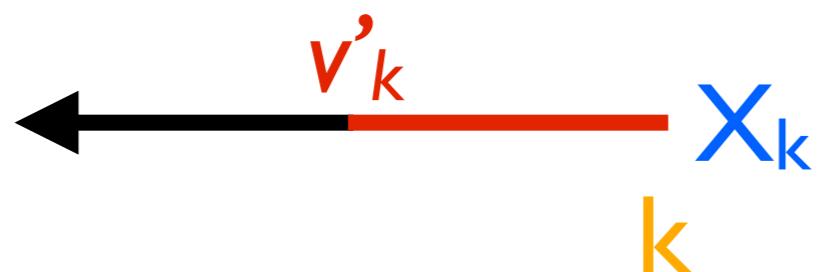
5. Calculate the standardized contrast by dividing the raw contrast by its variance

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Calculating Contrasts*

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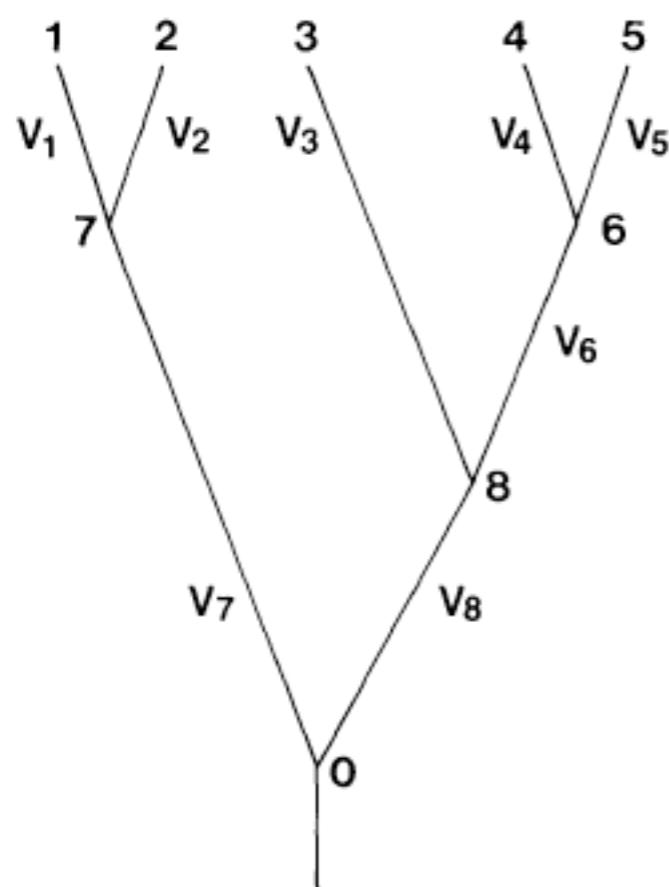


$$C_{ij} = X_i - X_j$$

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

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

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

$$v'_6 = v_6 + v_4 v_5 / (v_4 + v_5)$$

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

$$v'_7 = v_7 + v_1 v_2 / (v_1 + v_2)$$

$$X_8 = \frac{v'_6 X_3 + v_3 X_6}{v_3 + v_6}$$

$$v'_8 = v'_7 + v_3 v'_6 / (v_3 + v'_6)$$

What are contrasts?

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

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“amount of change”

What are contrasts?

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

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

“amount of change”
“time”

What are contrasts?

- 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

Using and Interpreting Contrasts

- Independent contrasts should be thought of as vectors
- They summarize information about the amount and direction of evolution at each node in the tree
- Standardized contrasts provide information about the rate of evolution

Using and Interpreting Contrasts

$$\hat{\sigma}^2 = \frac{\sum s_i}{n - 1}$$

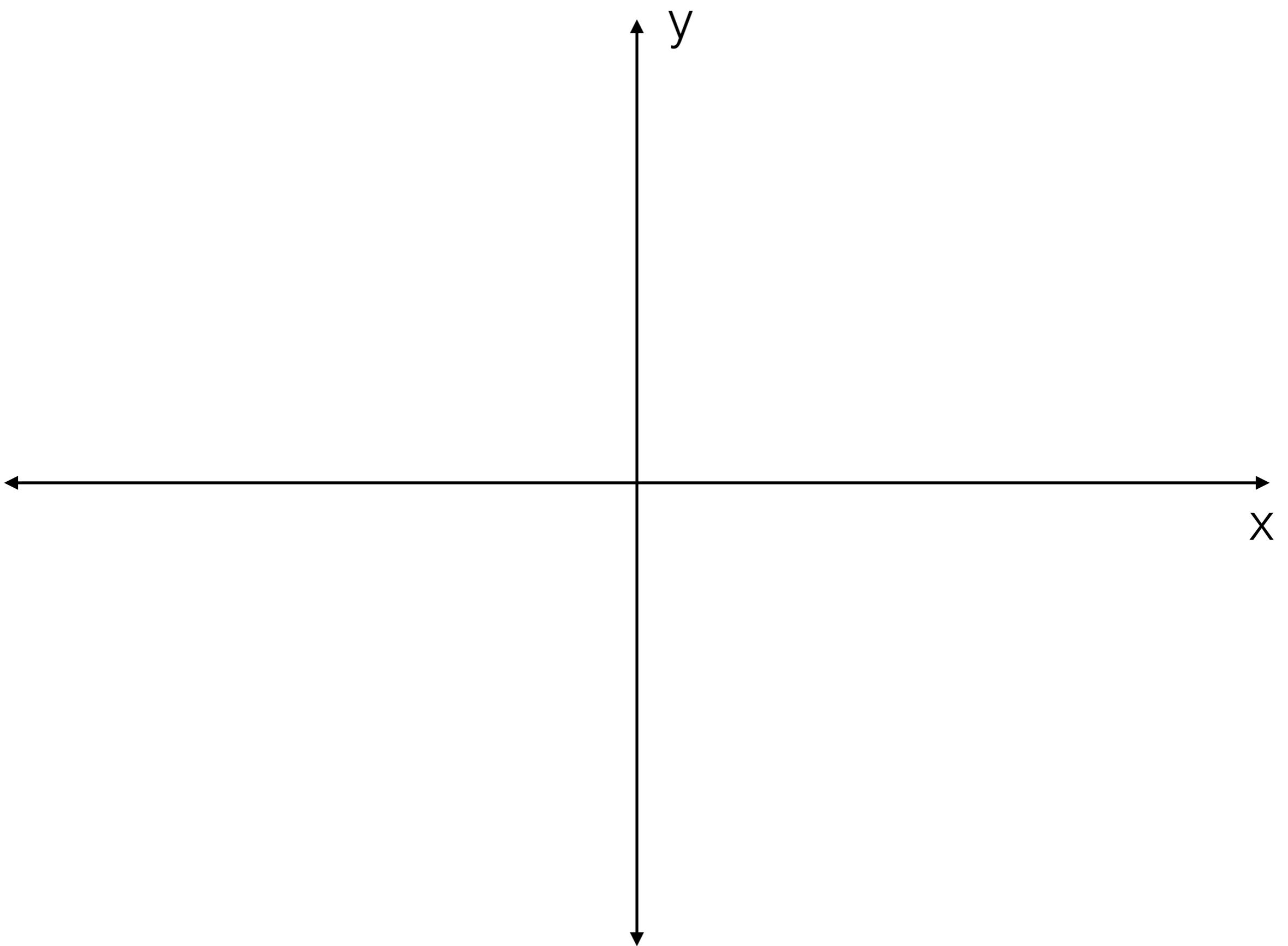
- This provides an unbiased estimate of evolutionary rate
- The expected value of this estimate is equal to the actual rate parameter
- The maximum likelihood estimate of the rate parameter is biased

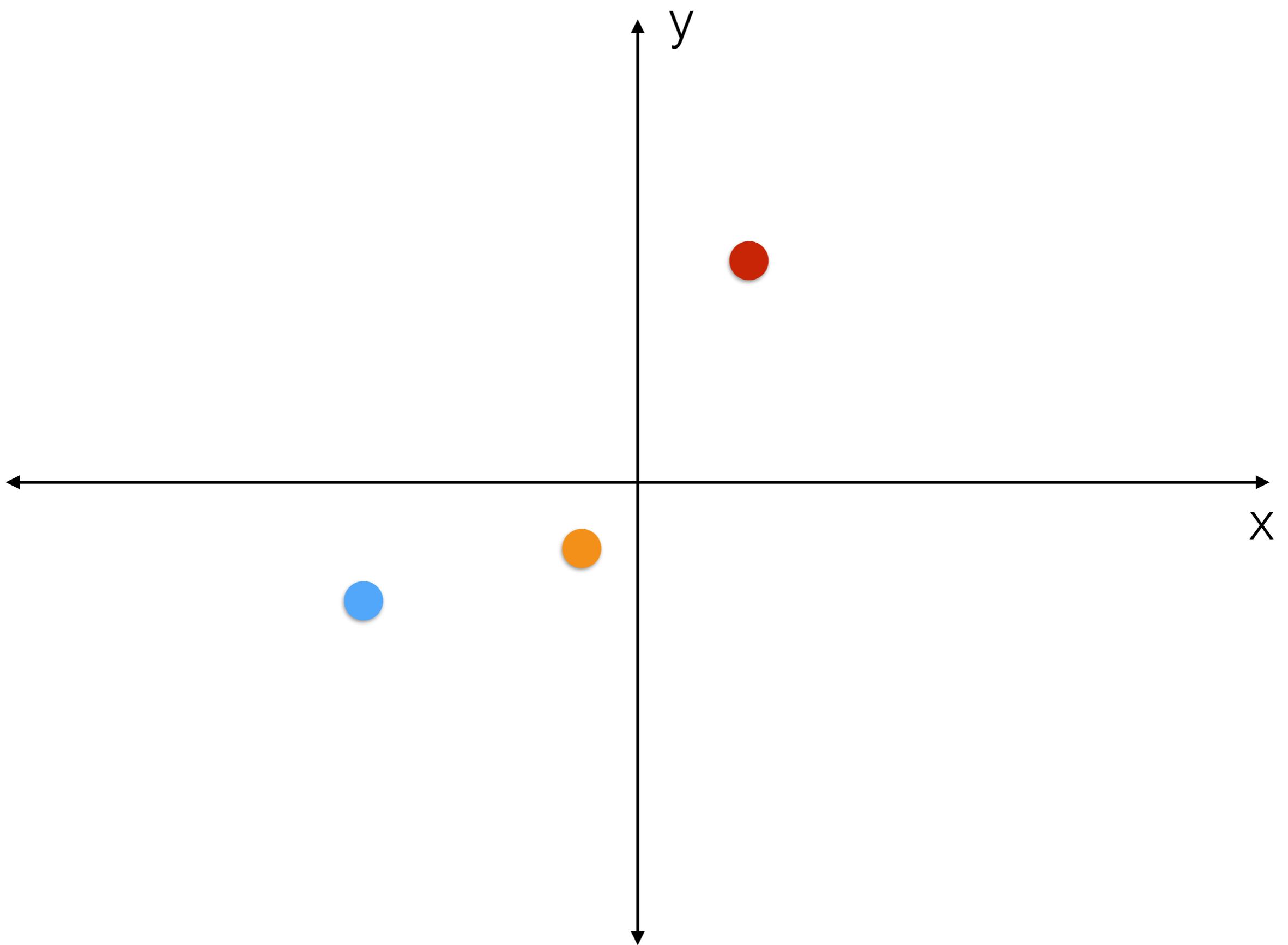
Character correlations

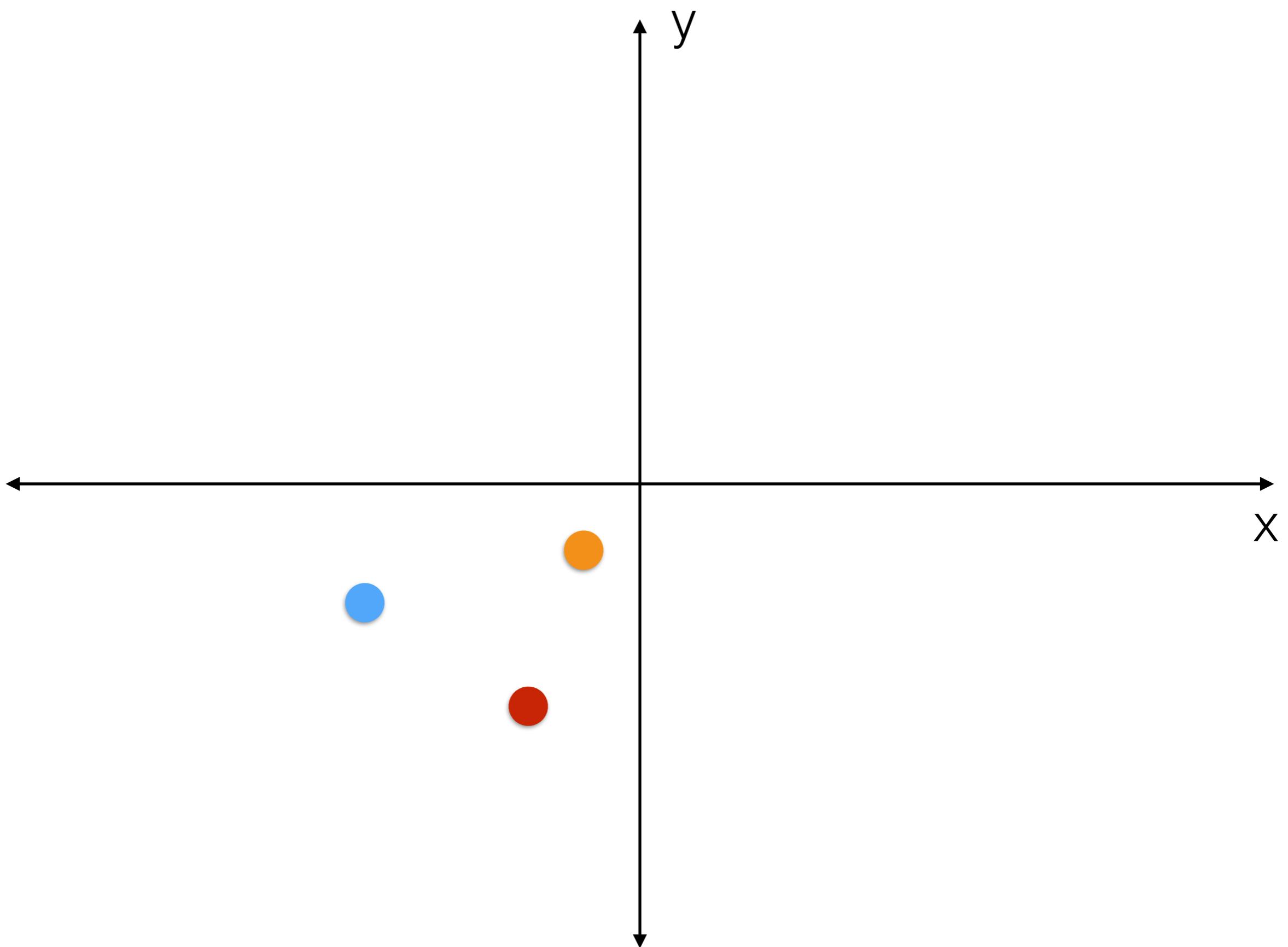
- Most common use for ICs: testing for character correlations
- Are two characters evolving in a correlated fashion?

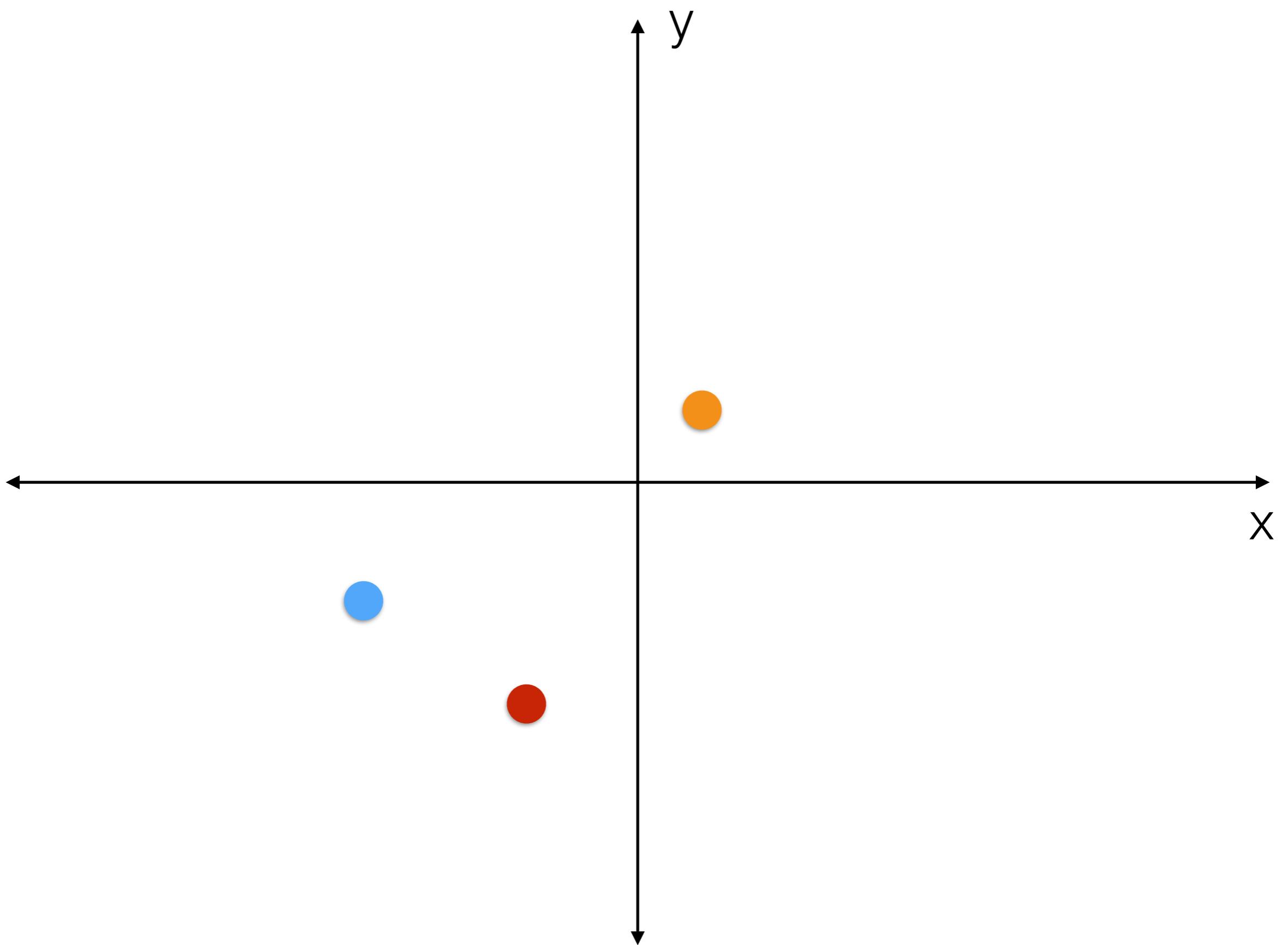
Character correlations

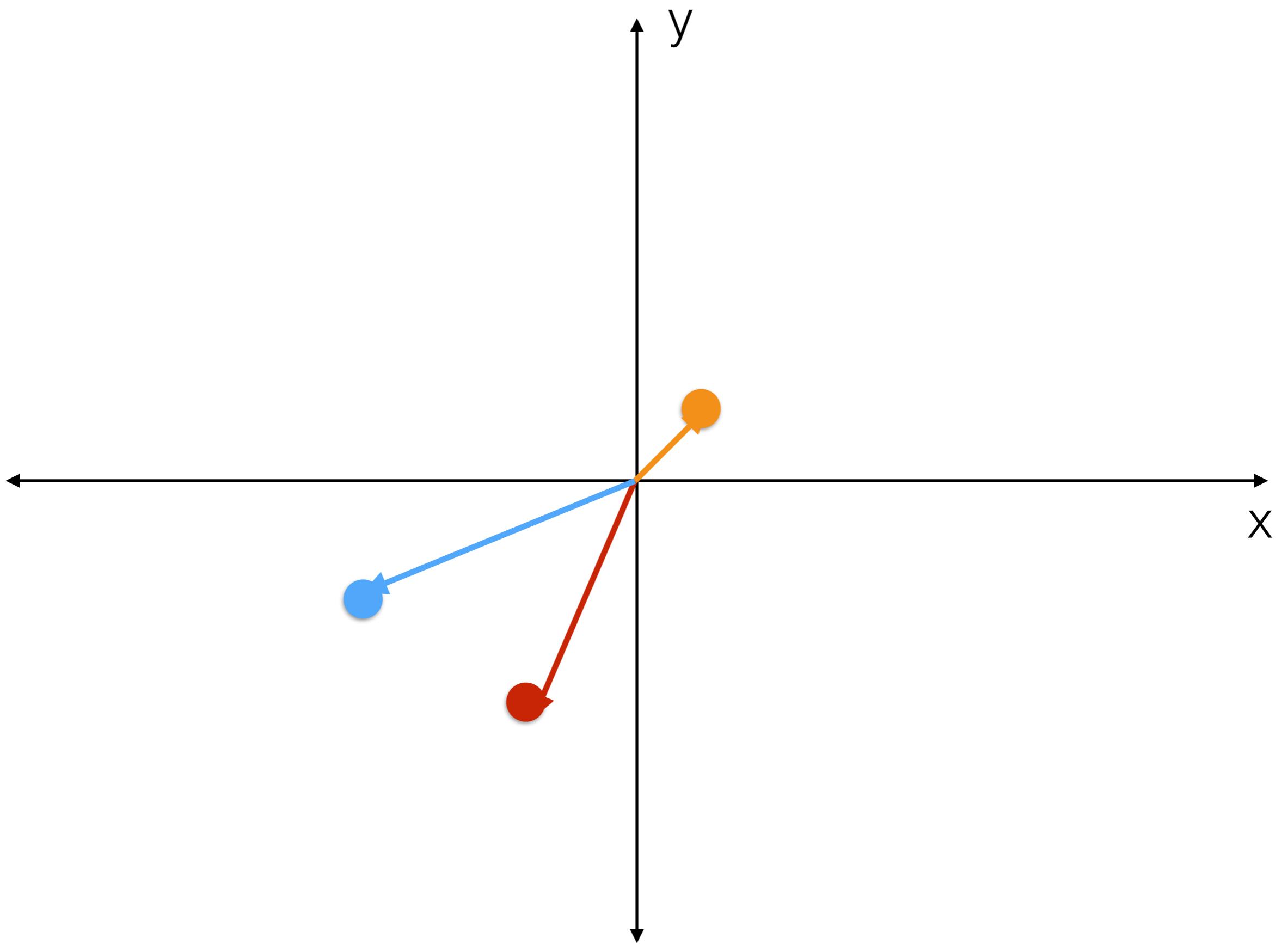
- Calculate independent contrasts for two characters, x and y
- Carry out a regression analysis of y on x with **no intercept** (force regression line through the origin)
- $P < 0.05$, then reject the null hypothesis of no evolutionary correlation

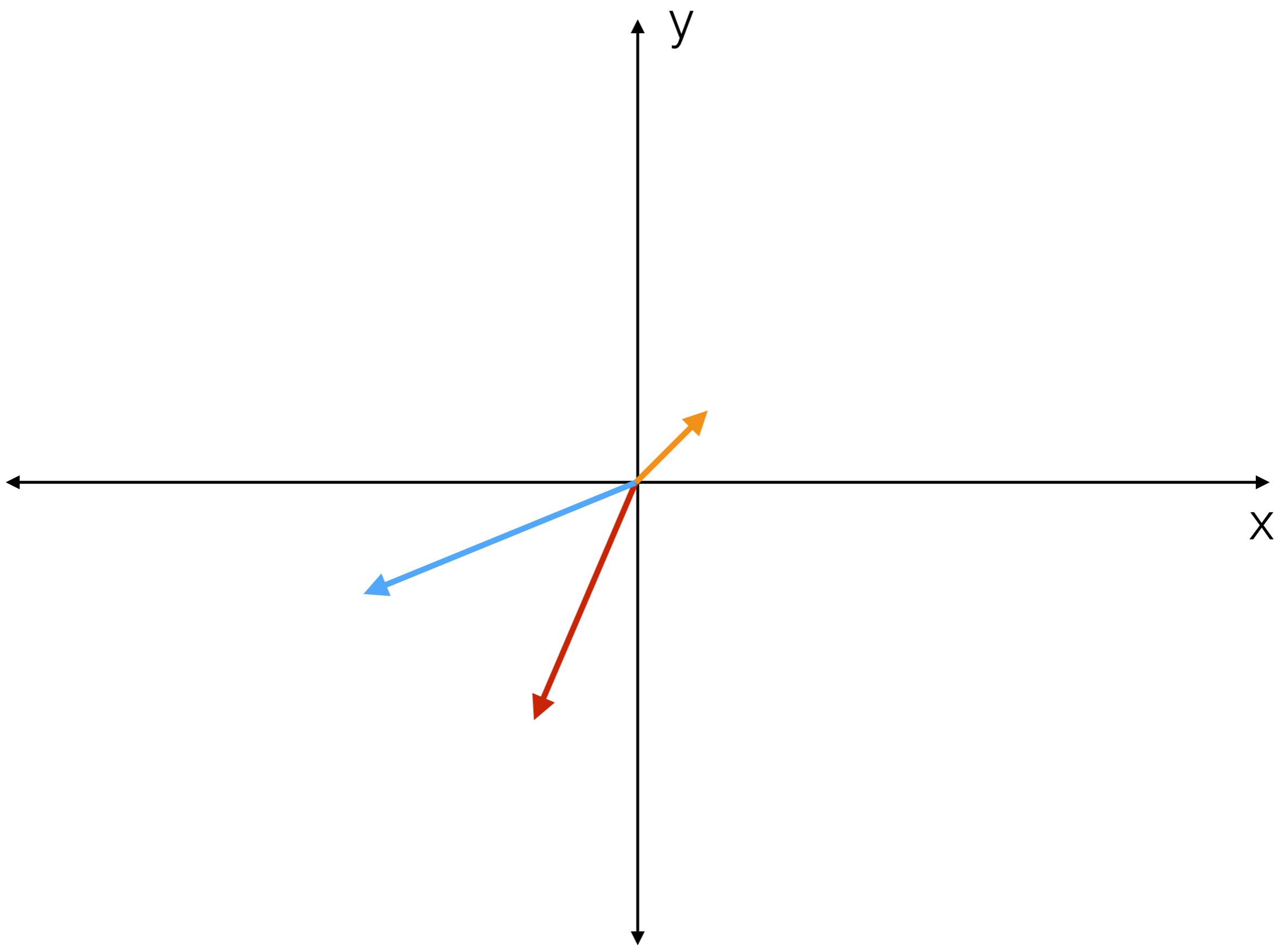


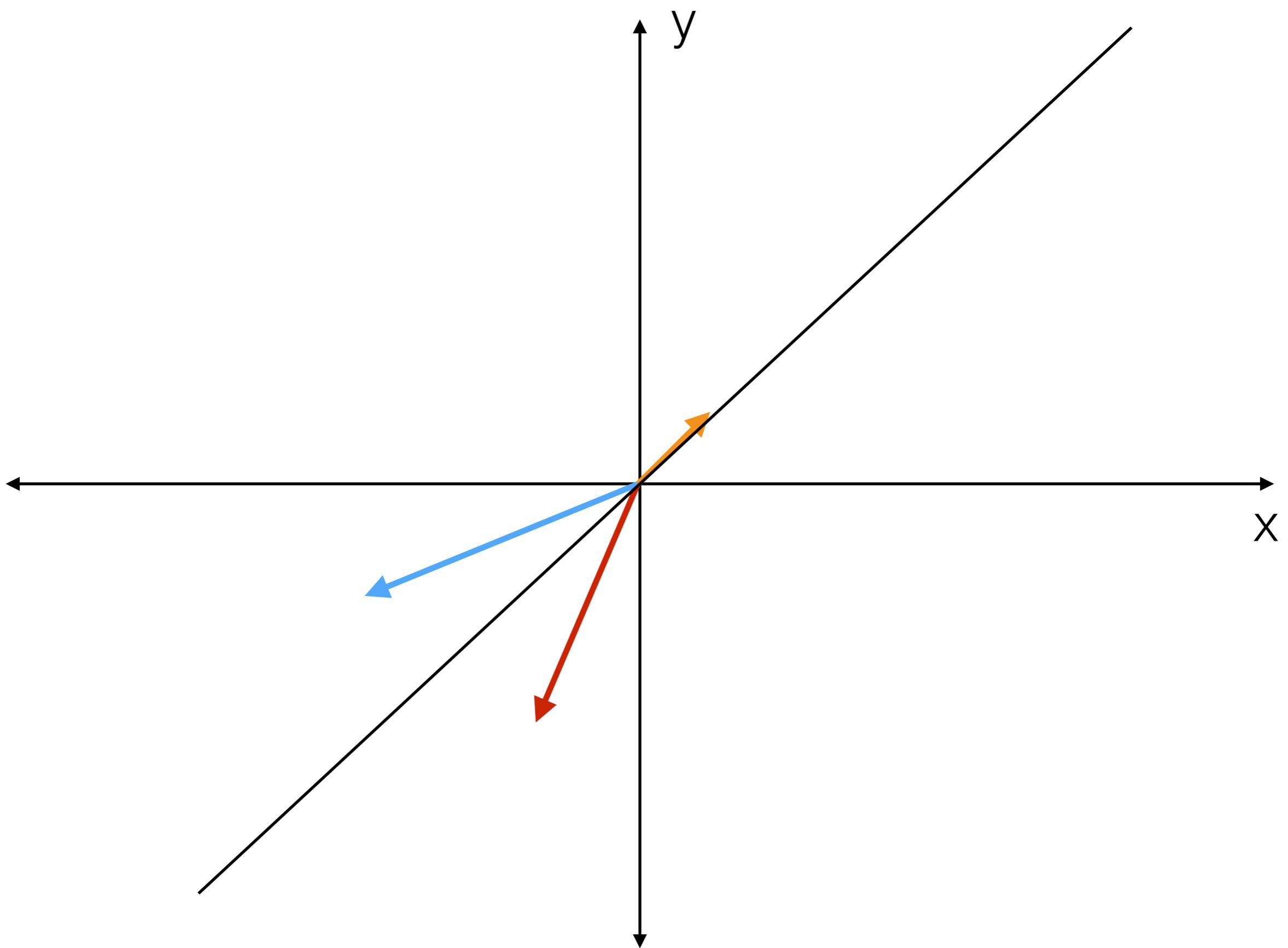












Character correlations

- Why force contrasts through the origin?
- Because, for each contrast, the direction of subtraction is arbitrary; the signs of all the contrasts could be reversed
- Regression through the origin treats the contrasts as vectors

Liam will tell you how to calculate contrasts in R and what you can use them for!