

modelling trait  
evolution on  
phylogenies:  
continuous traits

## Character Types:

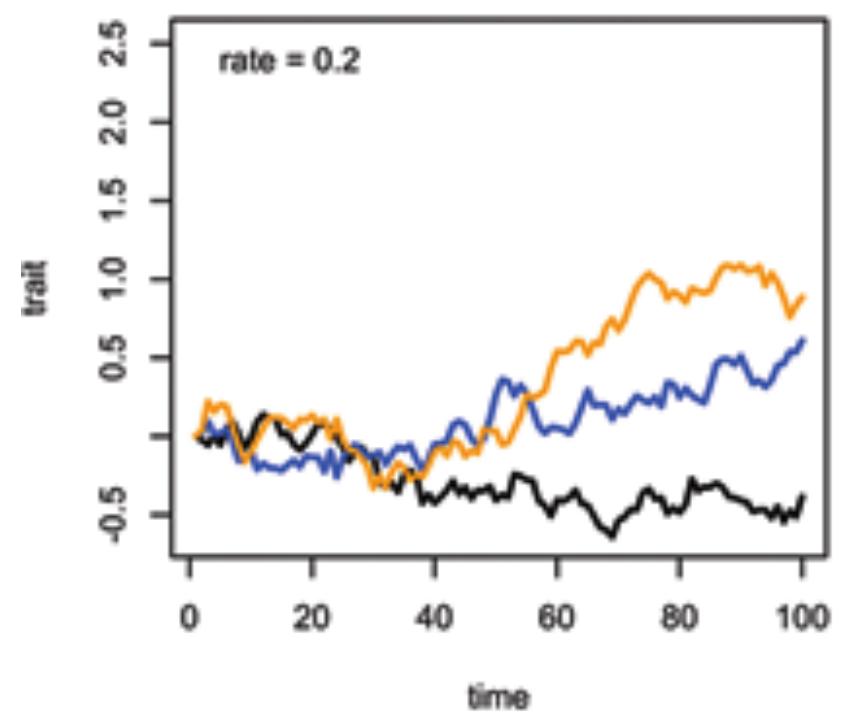
- **Discrete Characters:** traits with a finite number of distinct states.  
*Examples:* presence or absence of wings, flower color categories.
- **Continuous Characters:** traits that vary along a measurable scale.  
*Examples:* body length, enzyme activity levels, beak depth.

## Analytical Approaches:

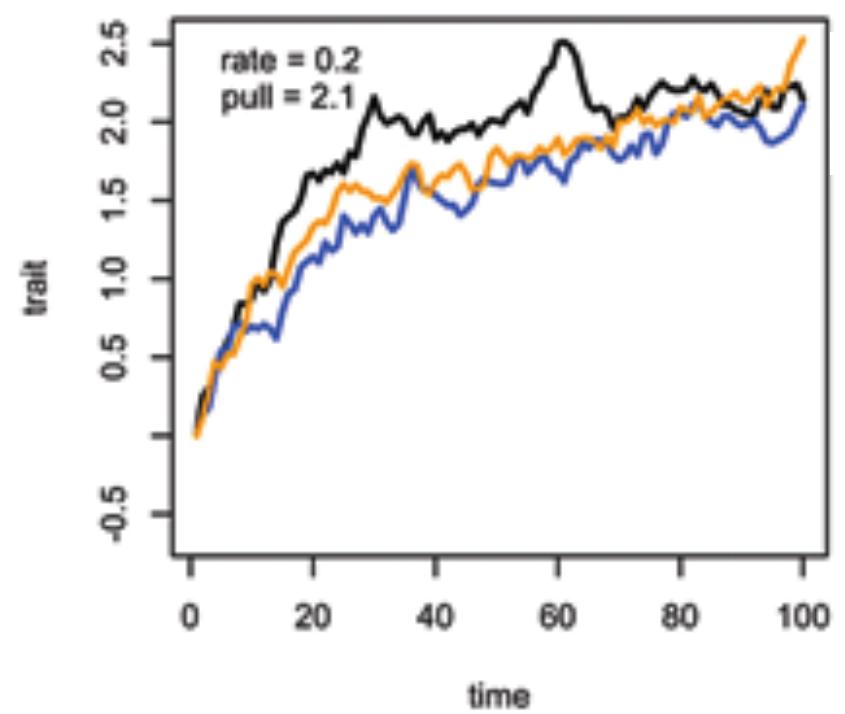
- **Discrete Characters:** Mk model
- **Continuous Characters:** ??!

## Models of continuous trait evolution

- **Brownian Motion (BM):**  
trait evolve randomly and variance increases with time



- **Ornstein-Uhlenbeck (OU):**  
add stabilizing selection and traits evolve toward an optimum



## Models of continuous trait evolution

### What is Brownian Motion (BM)?

- a random walk model of trait evolution.
- at each step, trait changes by a small, normally distributed random amount.
- no preferred direction or optimum - purely stochastic.

### Key Features

- trait variance increases linearly with time since divergence.
- closely related species tend to have more similar traits.
- trait evolution is neutral: no selection toward an optimum.

BM is a **null model** for trait evolution.

It is a good fit for traits evolving neutrally or with drift.

## Models of continuous trait evolution

### What is the OU Model?

- An extension of Brownian Motion that includes stabilizing selection.
- Traits evolve with a tendency toward an optimal value  $\theta$ .

### Key Features

- Variance increases with time but levels off as values are “pulled” toward the optimum.
- Includes three parameters:
  - $\theta$ : trait optimum
  - $a$ : strength of selection toward the optimum
  - $\sigma^2$ : evolutionary rate - as in BM!

### When to Use OU?

- When traits show selective constraints or adaptive peaks.
- For testing **adaptive hypotheses** or detecting **convergent evolution**.

## What Is Phylogenetic Signal?

- The tendency for related species to resemble each other more than expected under a model of random trait distribution.
- Reflects the non-independence of species due to shared ancestry.

## Why It Matters

- Strong signal: trait variation is structured by phylogeny.
- Weak signal: trait may evolve rapidly or independently of phylogeny.
- Helps choose the right model and correct for autocorrelation.

## Pagel's $\lambda$ (Lambda)

- A branch-length scaling parameter that quantifies how much the trait variation is explained by the phylogeny.
- Modifies the internal branches of the tree to best match the observed trait covariance.

### How It Works

The internal branches of a phylogenetic tree represent the shared evolutionary history between species.

Pagel's  $\lambda$  rescales these internal branches to reflect how much shared ancestry influences trait similarity.

$\lambda = 1$  - full phylogenetic covariance - trait evolves under Brownian motion.

$\lambda = 0$  - internal branches collapsed - trait evolve independently of phylo.

## Blomberg's K

- A variance-based metric that quantifies how much trait similarity among species is explained by their shared evolutionary history.
- Specifically, it compares observed trait variance across a phylogeny to the variance expected under Brownian motion (BM) evolution.

### How It Works

- The core concept: 
$$K = \frac{\text{Observed phylogenetic signal}}{\text{Expected signal under Brownian motion}}$$
- $K \approx 1$  Trait matches BM expectations (moderate signal)
- $K > 1$  Trait is more conserved than expected
- $K < 1$  Trait is less conserved (weak signal or convergence)

## a phylogenetic problem: non-independence in data

Species are not independent data points! 

They share evolutionary history! 

... and this creates statistical non-independence.

### What happens if we disregard phylogeny?

- Violates the assumption of independent distributed residuals.
- inflated Type I error rates - false positives!

**Use PIC and PGLS!**

## Phylogenetically Independent Contrasts (PIC)

- Developed by Joe Felsenstein (1985)
- Data transformation + regression
- Traits evolve under Brownian motion
- Simple, effective, fast

## Phylogenetic Generalized Least Squares (PGLS)

- Developed by Grafen (1989)
- Models covariance structure directly in regression
- Generalized least squares regression
- Flexible: can include  $\lambda$ , OU models

**FINISH**