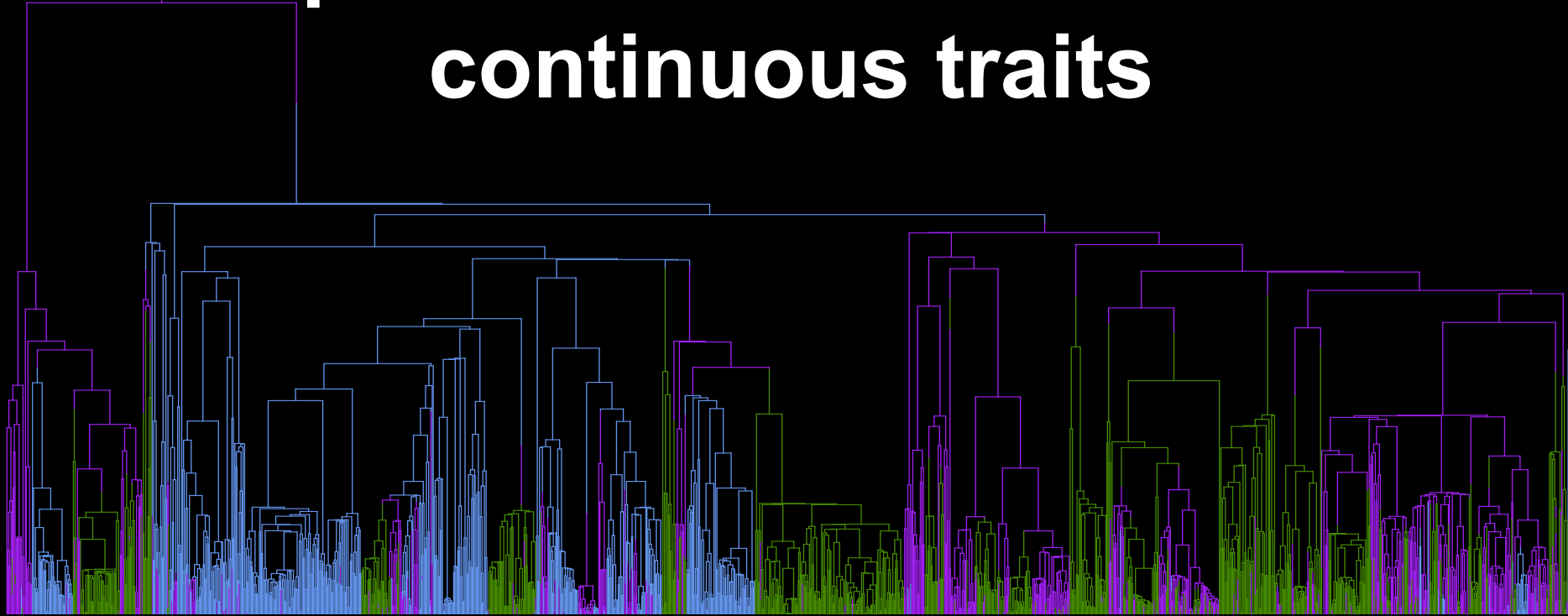
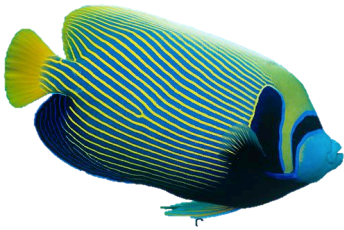


Testing hypotheses of state-dependent diversification in continuous traits



**March 2014 Bodega Bay
Phylogenetics Workshop
Samantha Price**

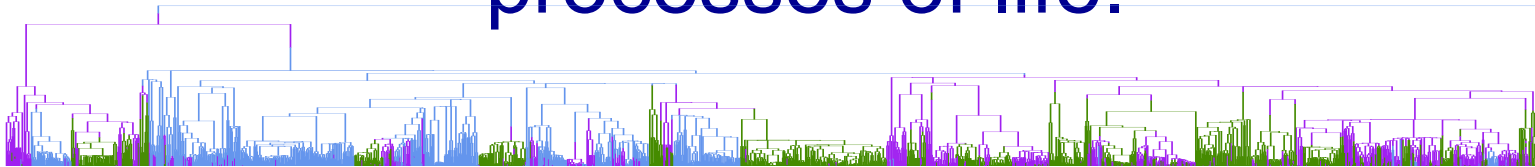




A bit about Me



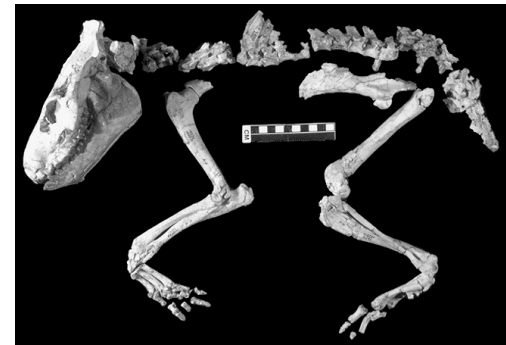
Understanding the grand patterns and great processes of life.



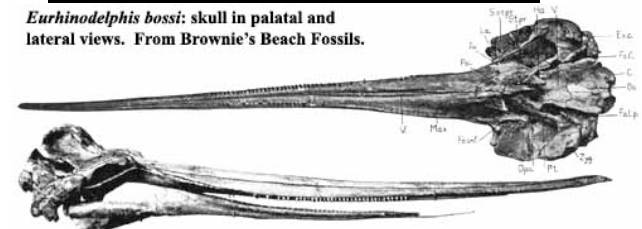
How species' biology influences the evolution of diversity

- Morphological & ecological diversity
- Lineage diversity

Integration of palaeobiological data



Eurhinodelphis bossi: skull in palatal and lateral views. From Brownie's Beach Fossils.



Testing hypotheses of state-dependent diversification in continuous traits

Testing hypotheses of state-dependent diversification in continuous traits

- Does changing from terrestrial to arboreal foraging lead to changes in hind limb and tail morphology in pigeons and doves?



(Lapiedra et al. 2013, Proc. Roy. Soc. 280)

Testing hypotheses of state-dependent diversification in continuous traits

- Do changes in habitat use lead to changes in body size and shape in monitor lizards?



(Collar et al. 2011 Evolution 65(9), 2664-2680)

Testing hypotheses of state-dependent diversification in continuous traits

- Does the loss of heterostyly lead to changes in floral morphology in primroses ?



Testing hypotheses of state-dependent diversification in continuous traits

Two main ways a change in behaviour/region/morphology/ecology can promote an evolutionary change in continuous traits:

Testing hypotheses of state-dependent diversification in continuous traits

Two main ways a change in behaviour/region/morphology/ecology can promote an evolutionary change in continuous traits:

1. Create the opportunity for further diversification through removal of previous constraints or allowing new adaptation.

Testing hypotheses of state-dependent diversification in continuous traits

Two main ways a change in behaviour/region/morphology/ecology can promote an evolutionary change in continuous traits:

1. Create the opportunity for further diversification through removal of previous constraints or allowing new adaptation.
2. Pull the population towards a new optimal phenotype.

Ornstein-Uhlenbeck (OU model)

Strength of selection
is proportional to distance of
current trait value from optimum

$$dX_{(t)} = \overbrace{\alpha[\theta - X_{(t)}]}^{\text{Pull towards optima (Strength of selection)}} dt + \underbrace{\sigma dB_{(t)}}_{\text{Brownian motion (Brownian motion rate } \sigma^2 \text{)}}$$

Pull towards optima
(Strength of selection)

Brownian motion
(Brownian motion rate σ^2)

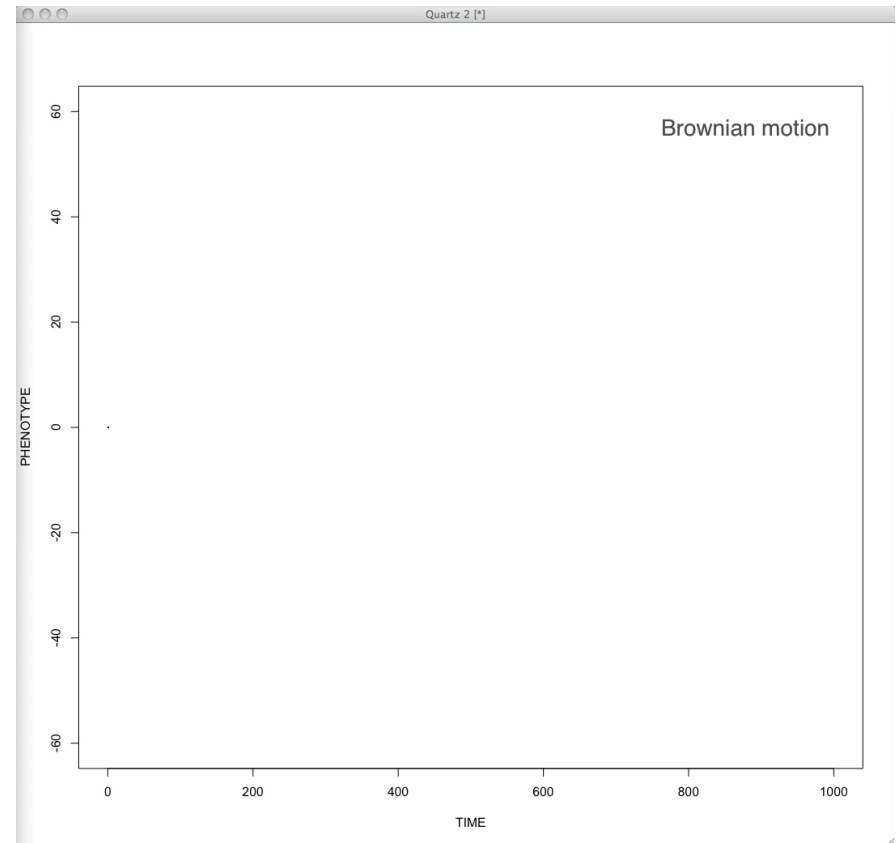
OU model collapses to Brownian motion when $\alpha = 0$

$$dX_{(t)} = \textcolor{red}{0}[\theta - X_{(t)}]dt + \underbrace{\sigma dB_{(t)}}_{\text{Brownian motion}}$$

Brownian motion $dX_{(t)} = \sigma dB_{(t)}$

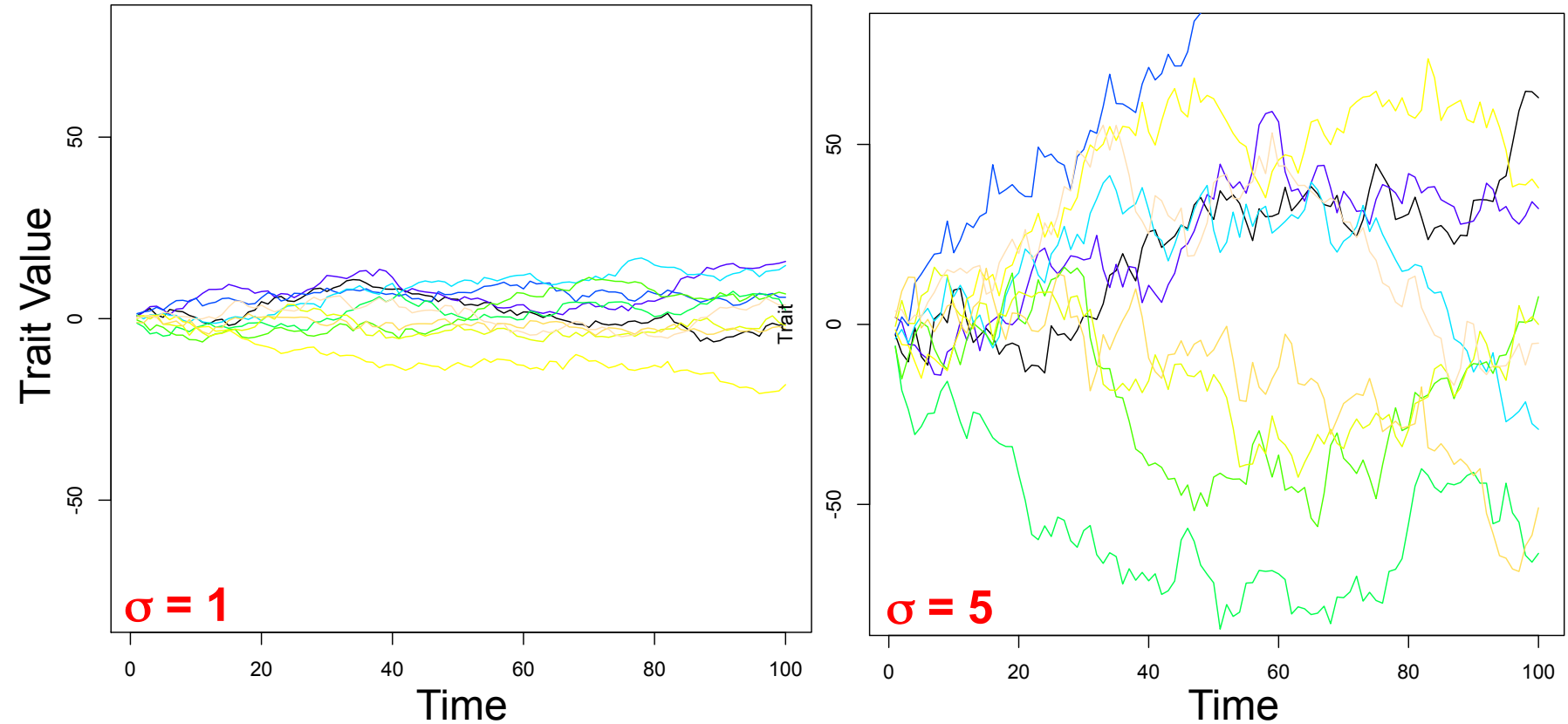
At a point in time :

- A character can increase, decrease or stay the same
- Direction and magnitude of change is independent of current or past character states
- Constant rate



Learn to simulate Brownian motion: [BM&OUsimulations.R](#)

Brownian motion $dX_{(t)} = \sigma dB_{(t)}$



Variance is proportional to time and rate

Ornstein-Uhlenbeck (OU model)

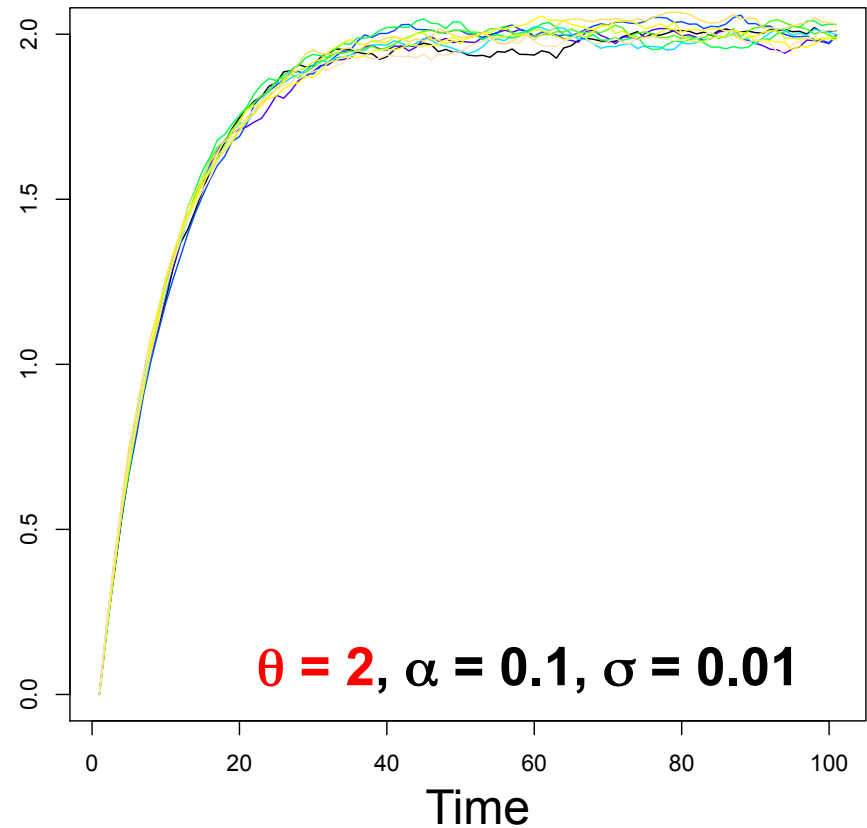
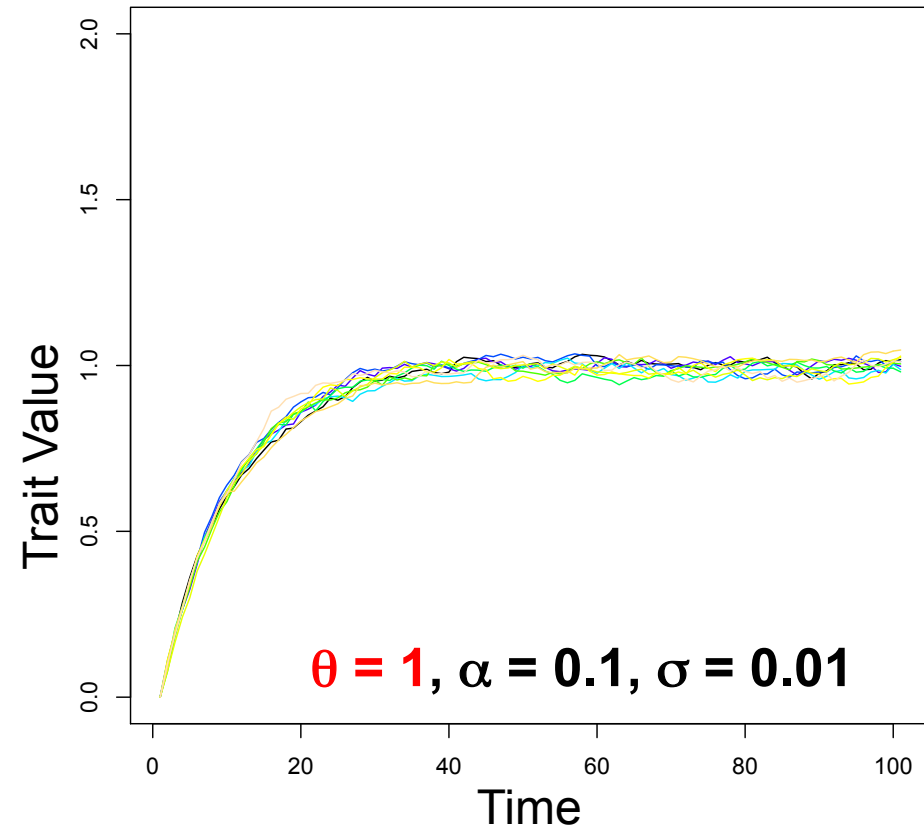
$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \underbrace{\sigma dB_{(t)}}_{\text{Brownian motion}}$$

Optimal trait value

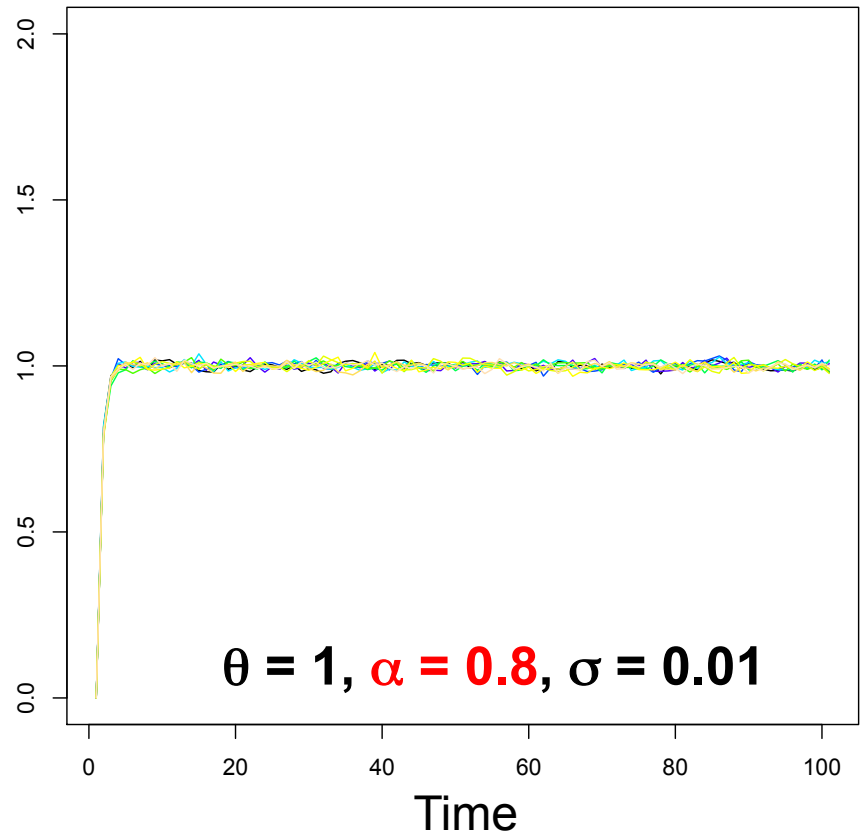
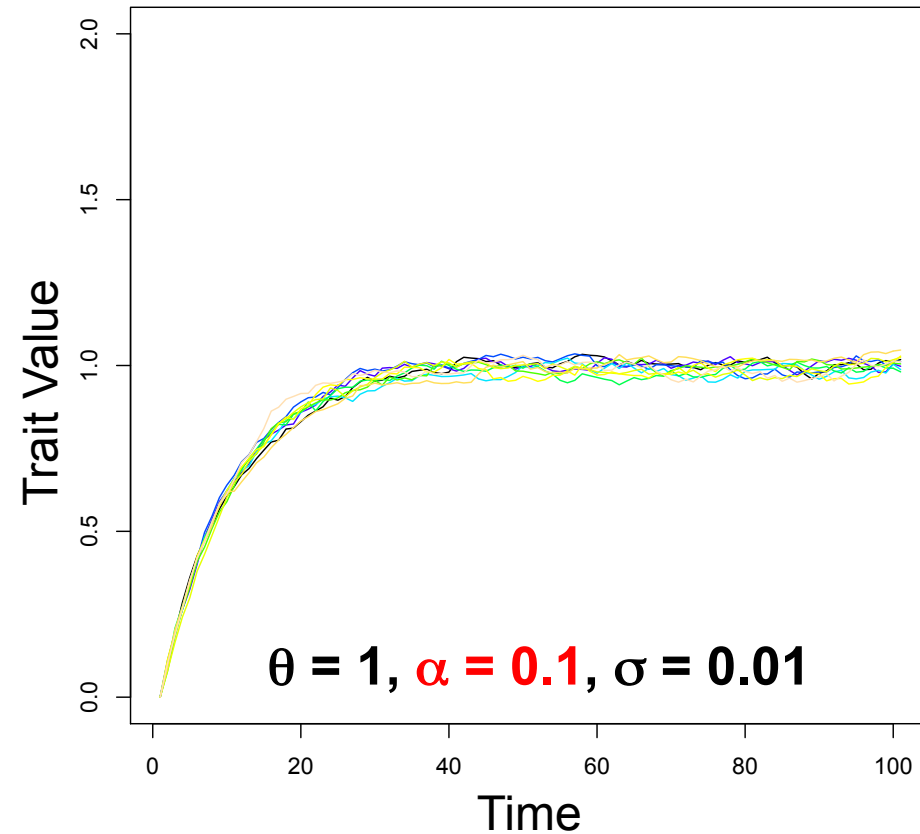
Pull towards optima
(Strength of selection)

Brownian motion
(Brownian motion rate σ^2)

$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$

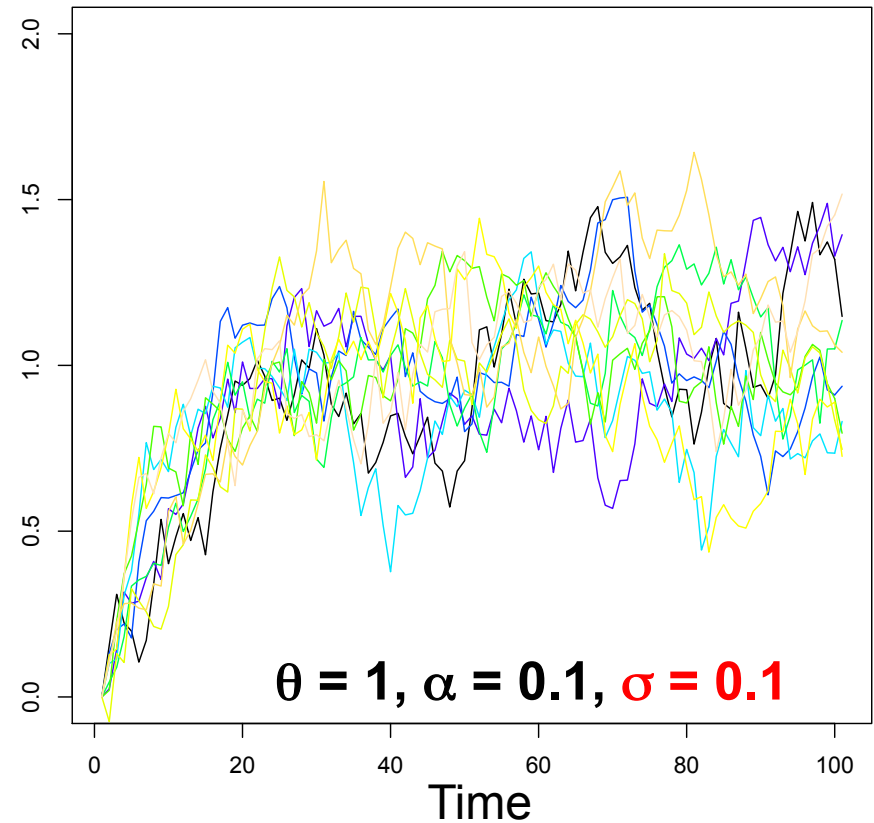
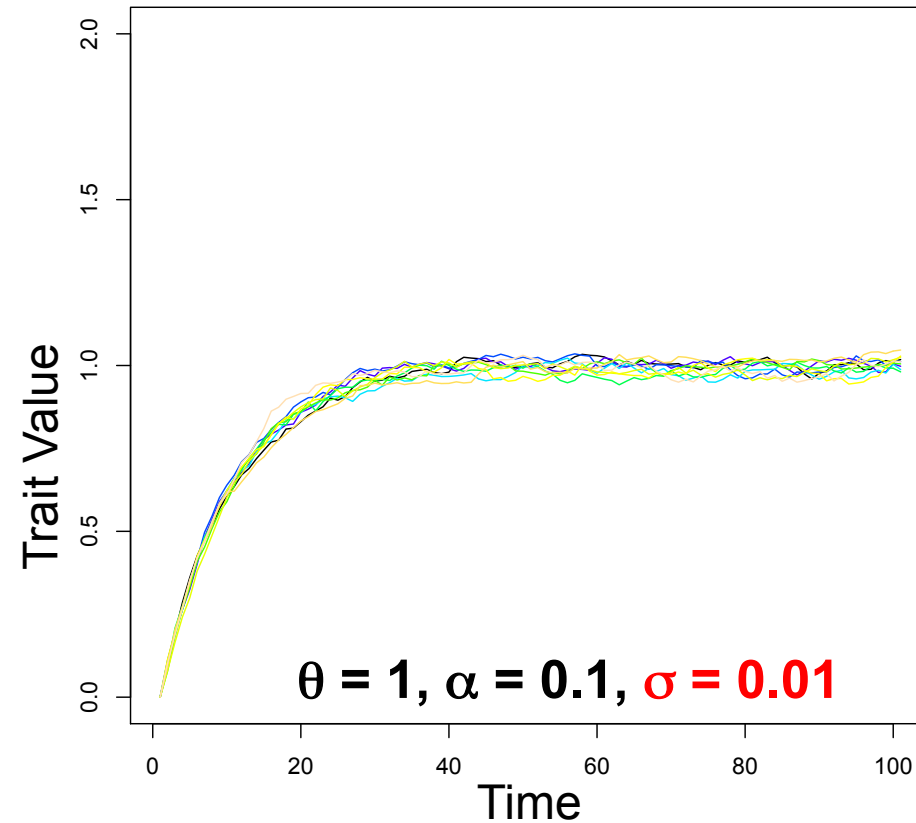


$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$



Stronger α the more quickly the optima is reached and the lower variance

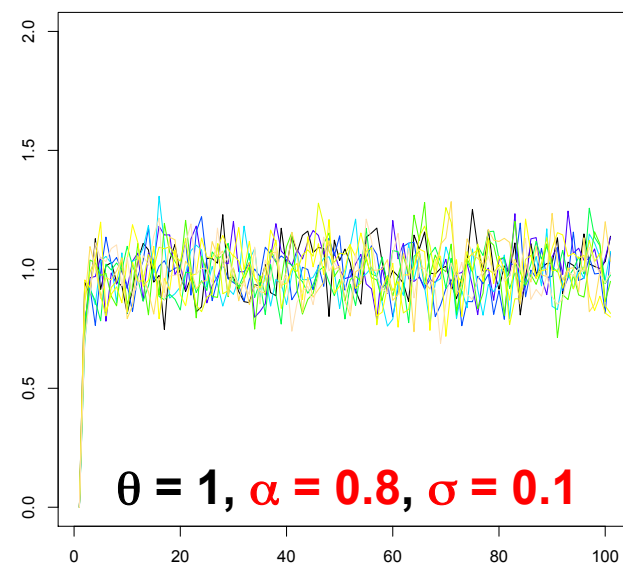
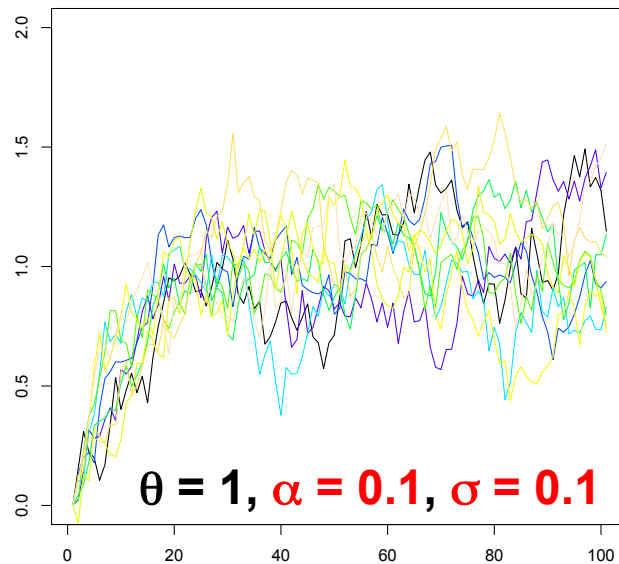
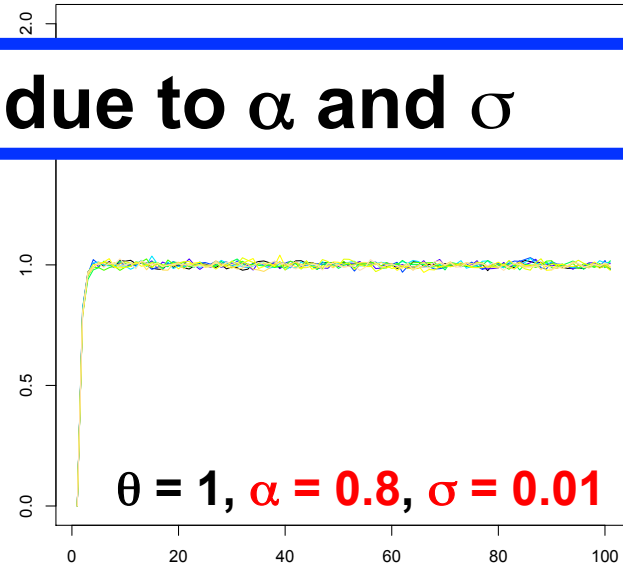
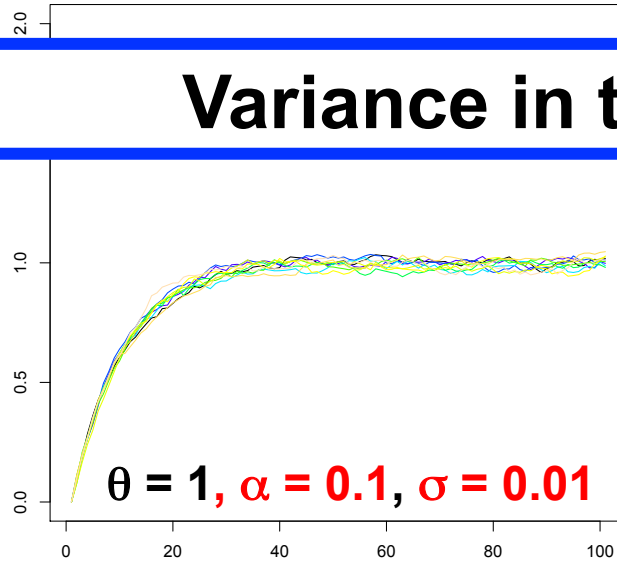
$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$



Higher σ the greater the variance

$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$

Variance in trait due to α and σ



$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$

Variance in trait due to α , σ and time

So are σ and α identifiable? As a decrease in rate (σ^2) and an increase in α both reduce variance of the trait at the tips of the tree.

$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$

Variance in trait due to α , σ and time

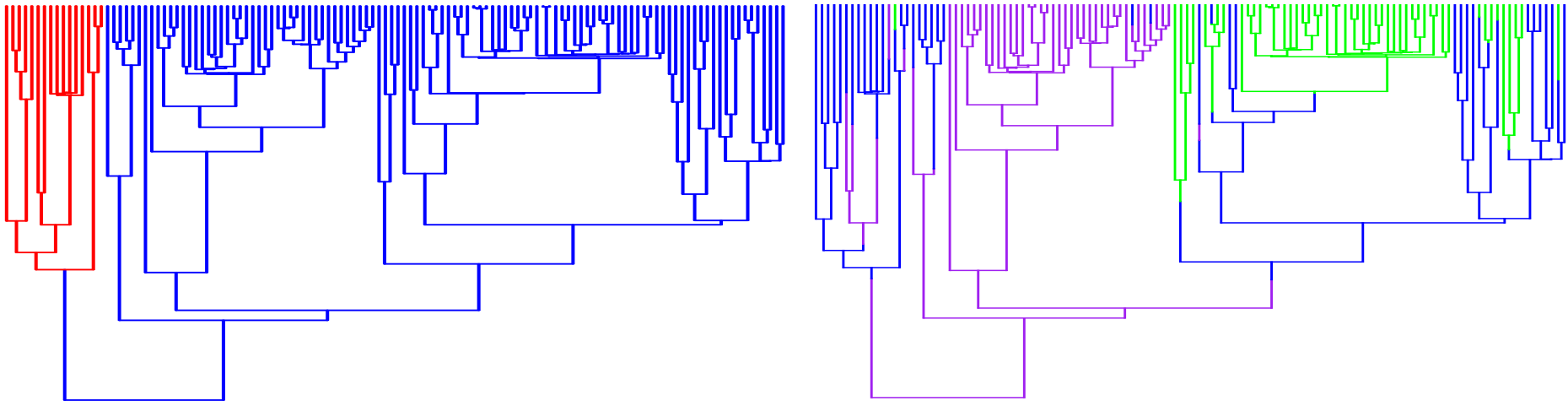
So are σ and α identifiable? As a decrease in rate (σ^2) and an increase in α both reduce variance of the trait at the tips of the tree.

- **Increase in α will erode the phylogenetic pattern of the trait but a decrease in σ^2 will not however there will be cases various estimates σ of and α are equally likely.**

Testing hypotheses of state-dependent diversification in continuous traits

$$dX_{(t)} = \alpha[\theta - X_{(t)}]dt + \sigma dB_{(t)}$$

Allow α , θ and σ to vary depending on state of discrete trait





Testing hypotheses of state-dependent diversification in continuous traits



Model-fitting or model-averaging framework

Model	θ	σ	α
BM1	-	Universal	-
OU1	Universal	Universal	Universal
BMS	-	State-dependent	-
OUM	State-dependent	Universal	Universal
OUMA	State-dependent	Universal	State-dependent
OUMV	State-dependent	State-dependent	Universal
OUMVA	State-dependent	State-dependent	State-dependent

OUwie package in R

doi:10.1111/j.1558-5646.2012.01619.x



MODELING STABILIZING SELECTION: EXPANDING THE ORNSTEIN–UHLENBECK MODEL OF ADAPTIVE EVOLUTION

Jeremy M. Beaulieu,^{1,2} Dwueng-Chwuan Jhwueng,^{3,4} Carl Boettiger,⁵ and Brian C. O'Meara⁶

¹*Department of Ecology and Evolutionary Biology, Yale University, P.O. Box 208106, New Haven, Connecticut 06520–8106*

²*E-mail: jeremy.beaulieu@yale.edu*

³*National Institute for Mathematical and Biological Synthesis, 1534 White Ave, University of Tennessee, Knoxville, Tennessee, 37996–1527*

⁴*Department of Statistics, Feng-Chia University, Taichung, Taiwan 40724, R.O.C.*

⁵*Center for Population Biology, University of California, Davis, 1 Shields Avenue, Davis, California, 95616*

⁶*Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee, 37996–1610*

Received September 2, 2011

Accepted February 6, 2012

Comparative methods used to study patterns of evolutionary change in a continuous trait on a phylogeny range from Brownian motion processes to models where the trait is assumed to evolve according to an Ornstein–Uhlenbeck (OU) process. Although these models have proved useful in a variety of contexts, they still do not cover all the scenarios biologists want to examine. For models based on the OU process, model complexity is restricted in current implementations by assuming that the rate of stochastic motion and the strength of selection do not vary among selective regimes. Here, we expand the OU model of adaptive evolution to include models that variously relax the assumption of a constant rate and strength of selection. In its most general form, the methods described here can assign each selective regime a separate trait optimum, a rate of stochastic motion parameter, and a parameter for the strength of selection. We use simulations to show that our models can detect meaningful differences in the evolutionary process, especially with larger sample sizes. We also illustrate our method using an empirical example of genome size evolution within a large flowering plant clade.

Testing hypotheses of state-dependent diversification in continuous traits

Two main ways a change in behaviour/region/morphology/ecology can promote an evolutionary change in continuous traits:

1. Create the opportunity for further diversification through removal of previous constraints or allowing new adaptation. BM model fits best with higher σ in new state or multi-optima OU with lower α in new state.
2. Pull the population towards a new optimal phenotype. Multi-optima OU model fits best with $\alpha > 0$.

Testing hypotheses of state-dependent diversification in continuous traits

- 1. Continuous trait measurements**
- 2. Tree(s) with meaningful branch lengths**
 - Time or relative time
- 3. Discrete character(s)**
- 4. Model of evolution – flexible OU**

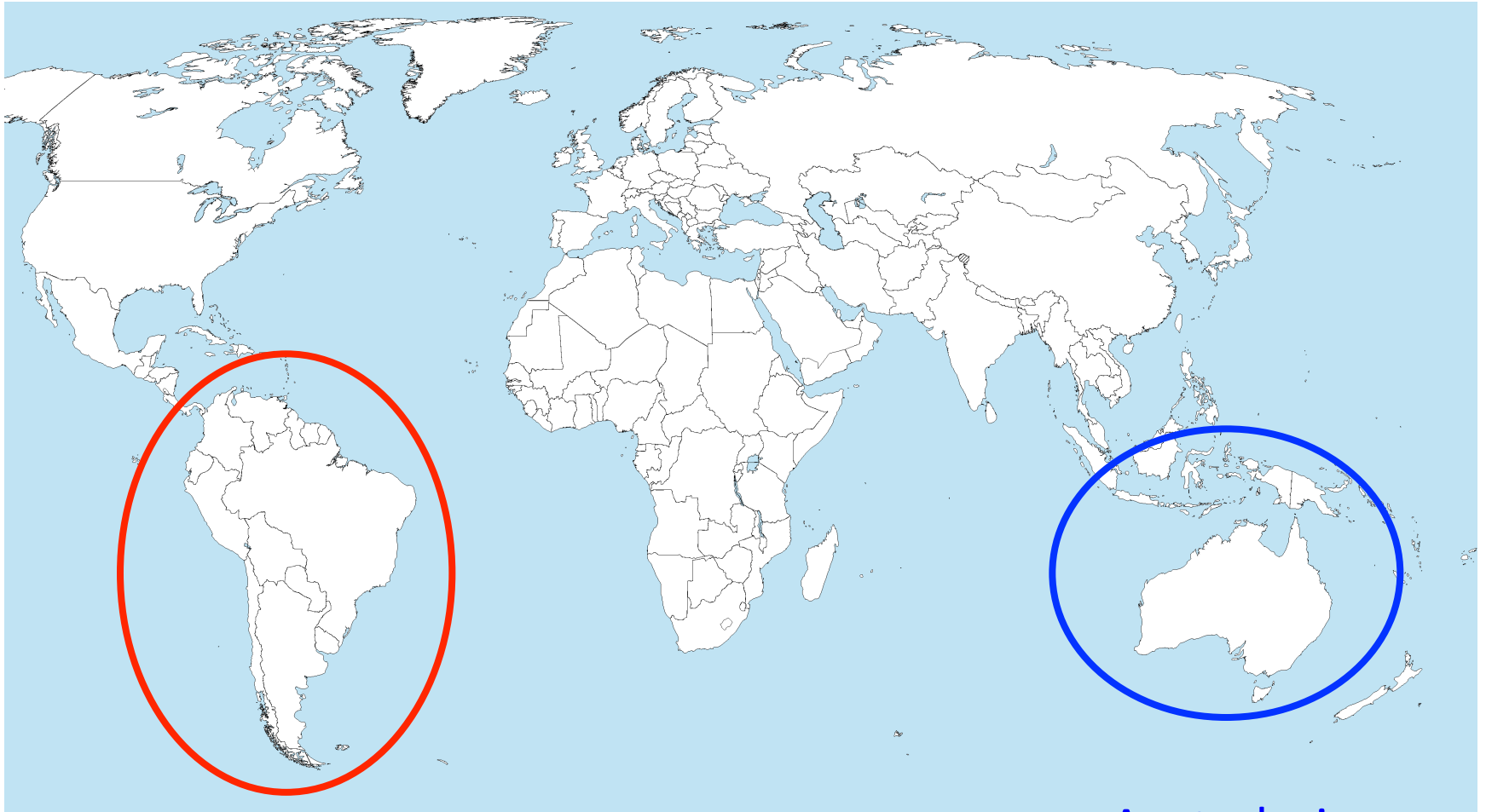
Tutorial



OuwieTutorial.R

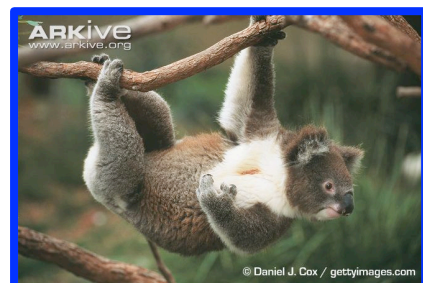


Two centers of marsupial Diversity



South America
~ 70 extant species

Australasia
~ 200 extant species



Hypotheses to test in OUwie

1. American marsupials exhibit less variable body sizes than Australian marsupials.

Predict: under a BM model lower rates (σ^2) or under OU stronger pulls towards an optimum (α) in South America)

2. Diet (Herbivory, Carnivory, Omnivory) influences body size evolution – highest optimal mass in herbivores. **Predict:** best-fitting model are multi-optima OU models.

Learn how to test these hypotheses using: [OuwieTutorial.R](#)

Caveats

Really important to make sure the information within your dataset is sufficient to distinguish between the models and estimate parameters. Do you have enough species in your tree and within each state?

- Check the likelihood surface and standard error estimates.
- Run forward simulations/parametric bootstrapping (e.g. see Boettiger et al. 2012, *Evolution* 66(7), 2240). OUwie has a simulation function that allows you do this relatively simply. These can also help generate an idea of model plausibility (see Jeremy Brown's lecture).

Caveats

MACROEVOLUTIONARY EXPERIMENTAL DESIGN

**Either pick your questions appropriate to
your clade (i.e. that you have the power to answer)
or pick your clade to answer your
question of interest.**

Other things to consider

Computational time

To run an analysis on a reasonably sized dataset with multiple stochastic maps per tree topology can take many days. Consider:

- Access to high performance computing
 - Many universities have a cluster
 - Free online access to clusters for particular analyses/taxa e.g. iplant discovery environment
 - Writing grants to get access to NSF xsede (not available to grad students ☹)
 - Pay to use cloud computing e.g. Amazon EC2
- Batch processing your analyses – running each tree/model on a different CPU.

Additional methods

NO *a priori* hypotheses needed

1. Identifying BM rate shifts

- Eastman et al. 2011: RJMCMC approach for fitting multiple shifts in rate class across the tree. **geiger package in R (formally auteur)**
- Revell et al. 2012: MCMC approach for fitting a single rate shift to a tree. **phytools package in R.**
- Thomas & Freckleton 2011: Stepwise AIC approach using Maximum Likelihood for identifying branches with (similar to Medusa for lineage diversification). **MotMot package in R.**
- Vendetti et al. 2011: RJMCMC with GLS approach for fitting multiple shifts in rate across the tree allows OU and time-dependent models ?

Additional methods

NO *a priori* hypotheses needed

1. Identifying BM rate shifts

- geiger package in R (formally auteur)
- phytools package in R.
- MotMot package in R.

2. Identifying optima shifts

- Ingram & Mahler 2013: Stepwise AIC approach using Maximum Likelihood for identifying branches with optima shifts. **surface package in R**