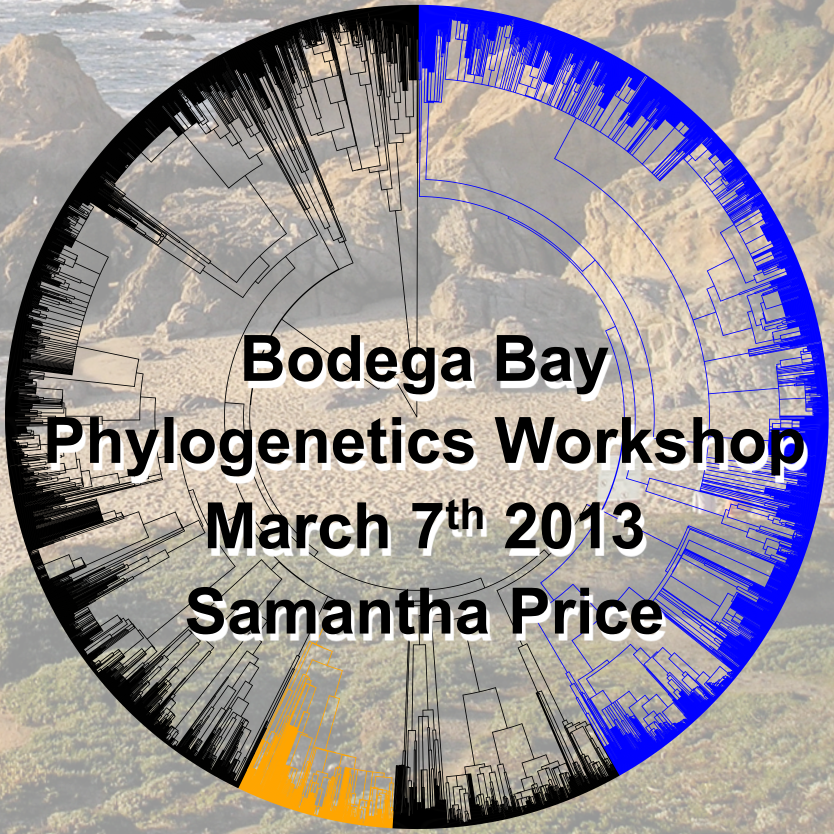
Rates of continuous trait evolution & phenotypic diversity



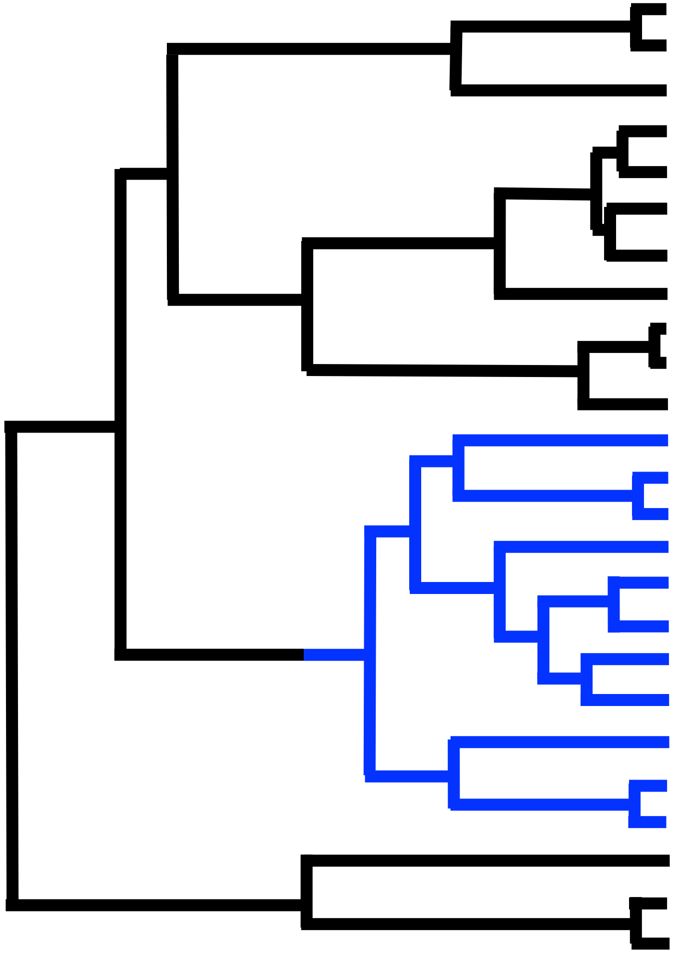
Bodega Bay
Phylogenetics Workshop
March 7th 2013
Samantha Price

Rates of Evolution

1. **Continuous trait measurements**
2. **Tree(s) with meaningful branch lengths**
   - **Time** or relative time
   - Molecular changes
3. **Model of evolution**
4. **Optional – discrete character**

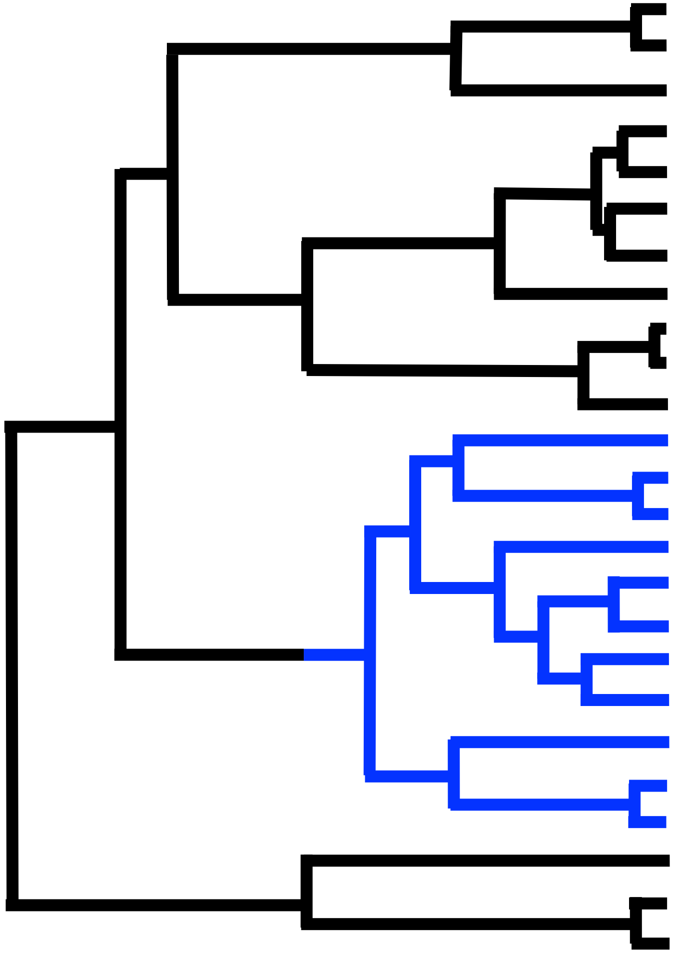
Rates & Diversity

Rates & Diversity



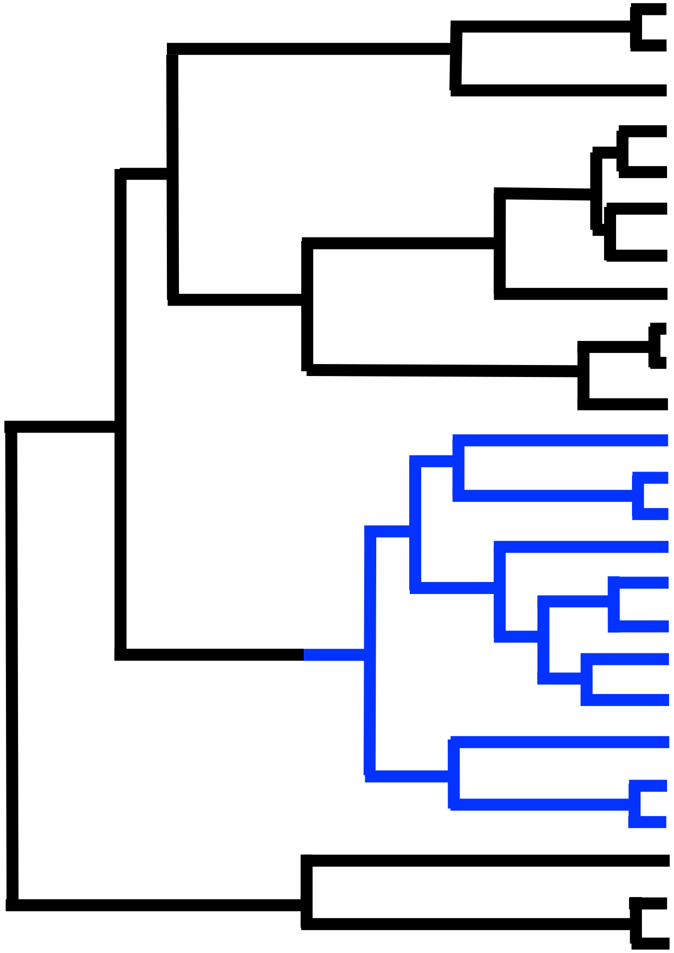
- **Blue** species have had far less time to accumulate trait changes

Rates & Diversity



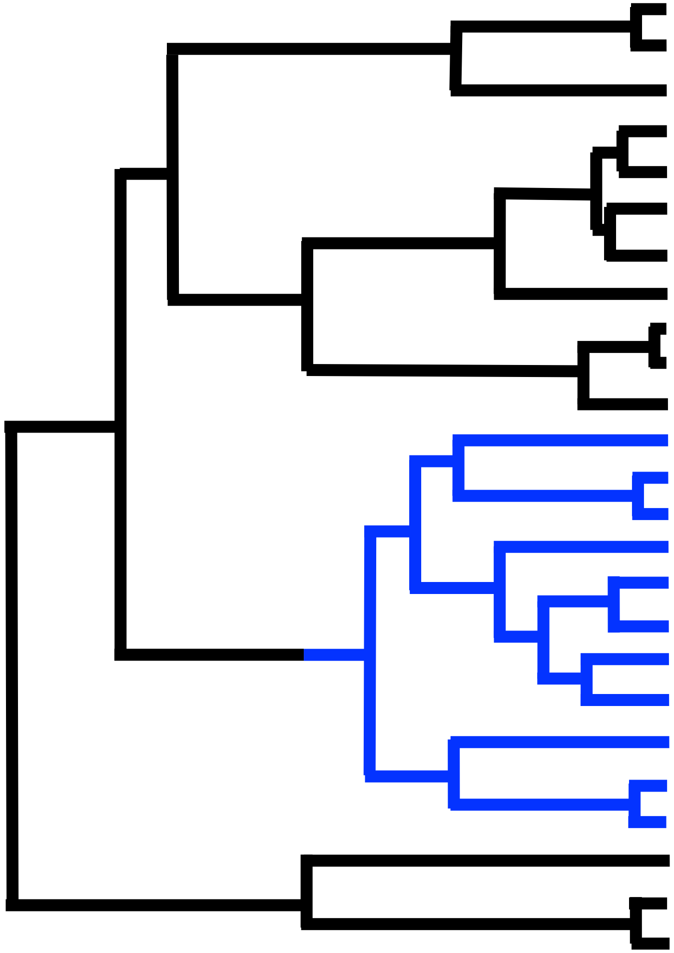
- Blue species have had far less time to accumulate trait changes
  - **Morphological variance within blue species < black species**

Rates & Diversity



- Blue species have had far less time to accumulate trait changes
- **Measure of diversity that takes into account time**

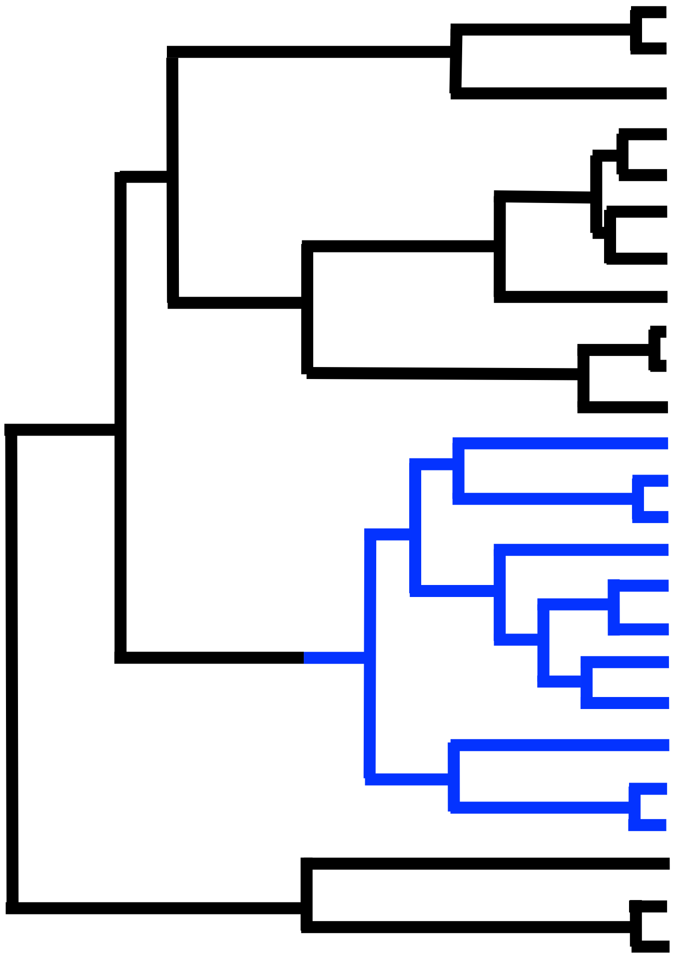
Rates & Diversity



- Blue species have had far less time to accumulate trait changes
- **Measure of diversity that takes into account time**
  - **Rate**

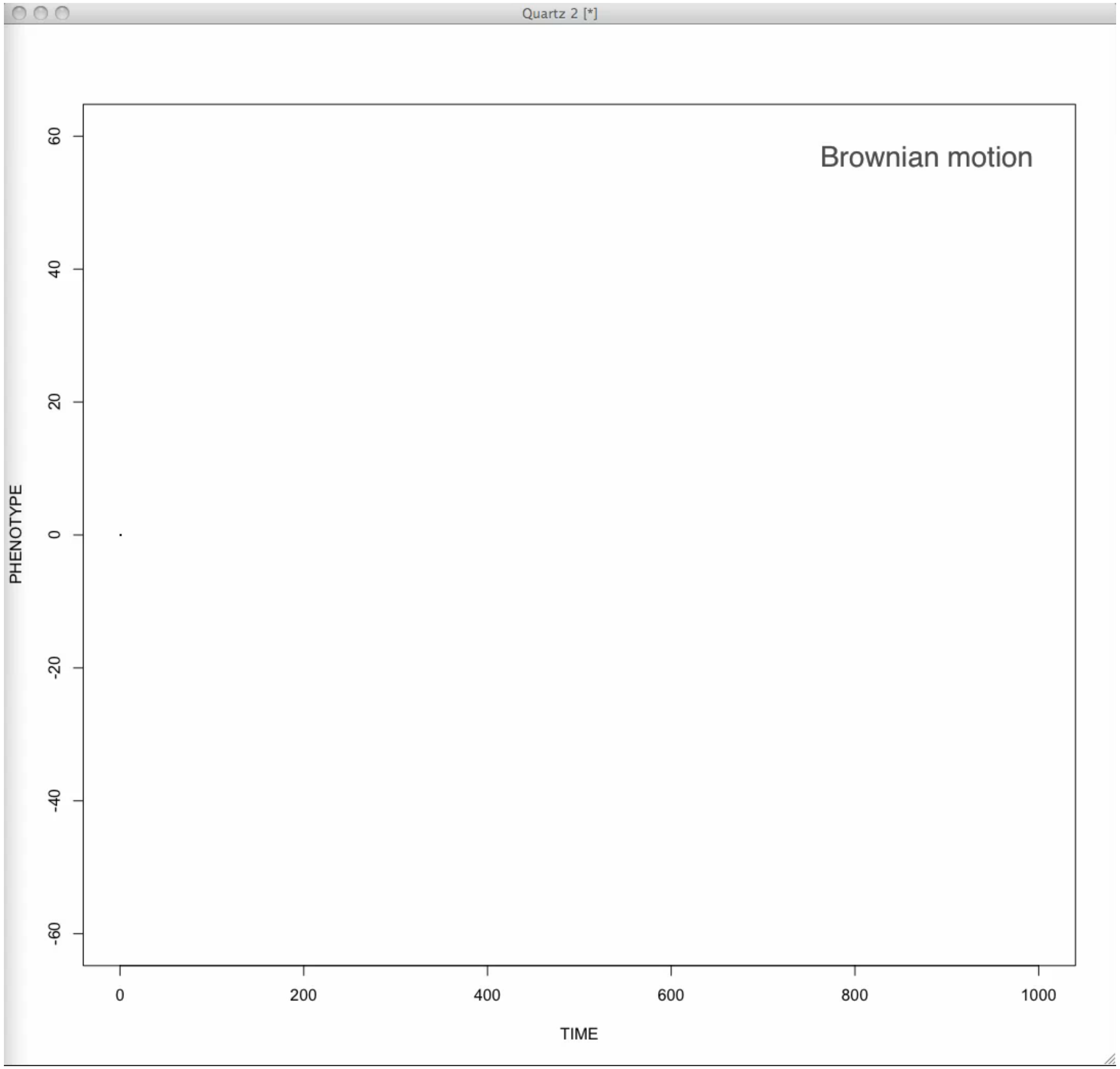
    Darwin - e-fold change in a trait over one million years (Haldane 1949)

Rates & Diversity



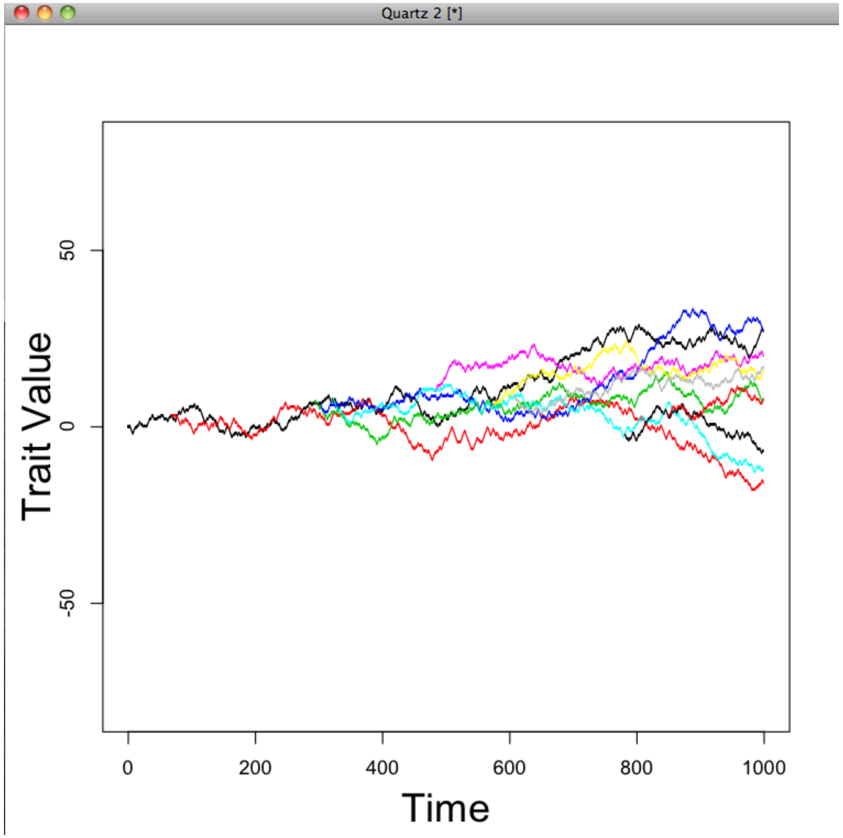
- Blue species have had far less time to accumulate trait changes
- **Measure of diversity that takes into account time**
  - **Brownian rate (σ^2) estimated on the phylogeny (branch lengths = time)**

Brownian Motion

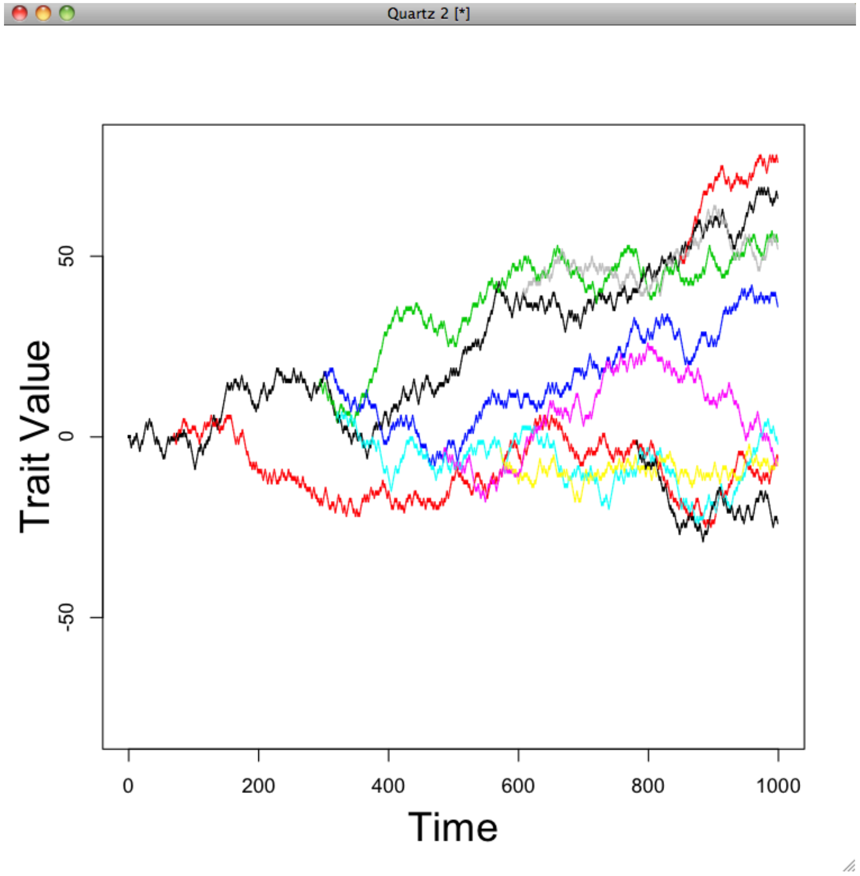


Brownian Motion

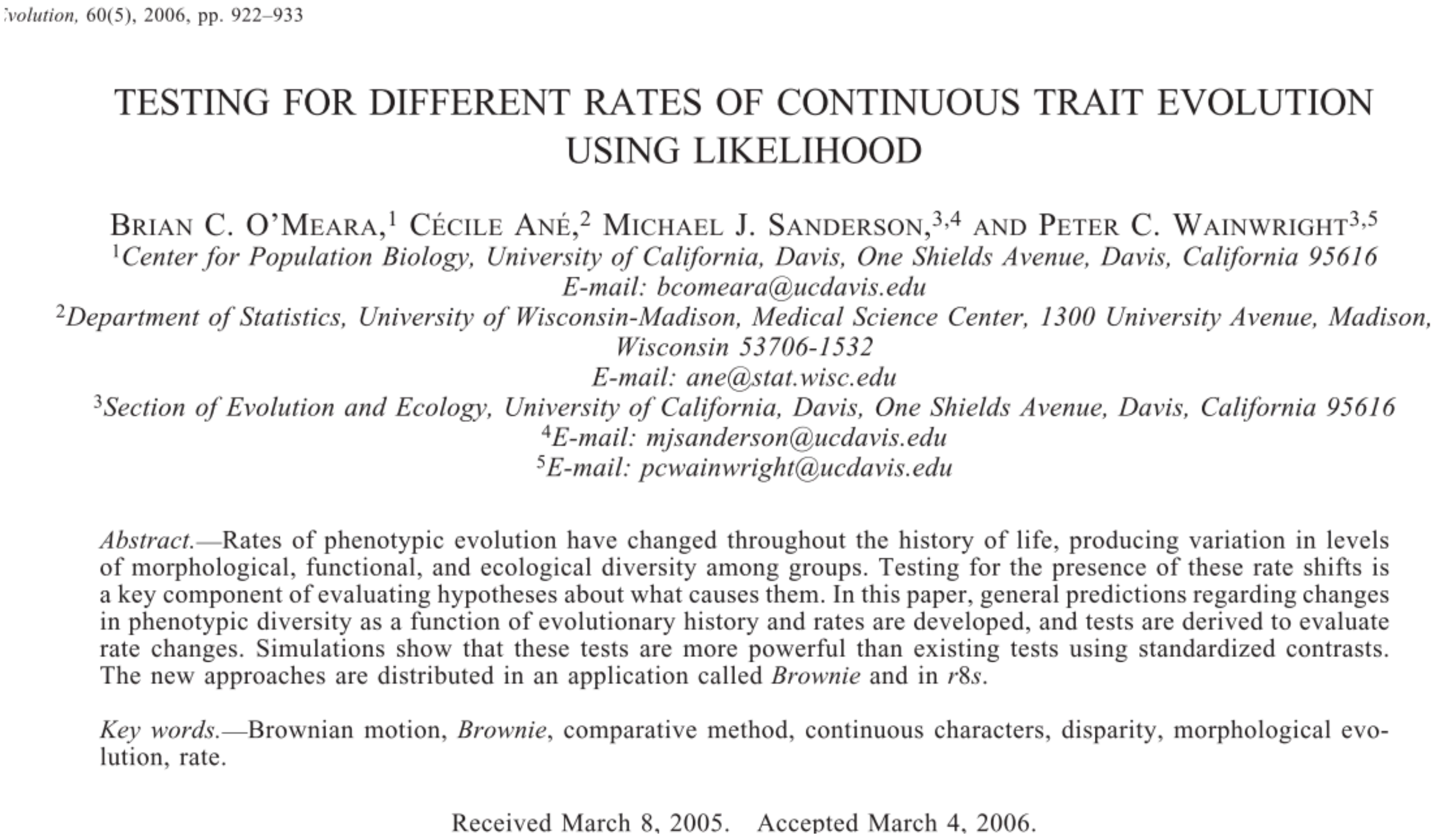
RATE = 1



RATE = 2



Estimating Brownian motion (BM) rate using ML



volution, 60(5), 2006, pp. 922–933

TESTING FOR DIFFERENT RATES OF CONTINUOUS TRAIT EVOLUTION USING LIKELIHOOD

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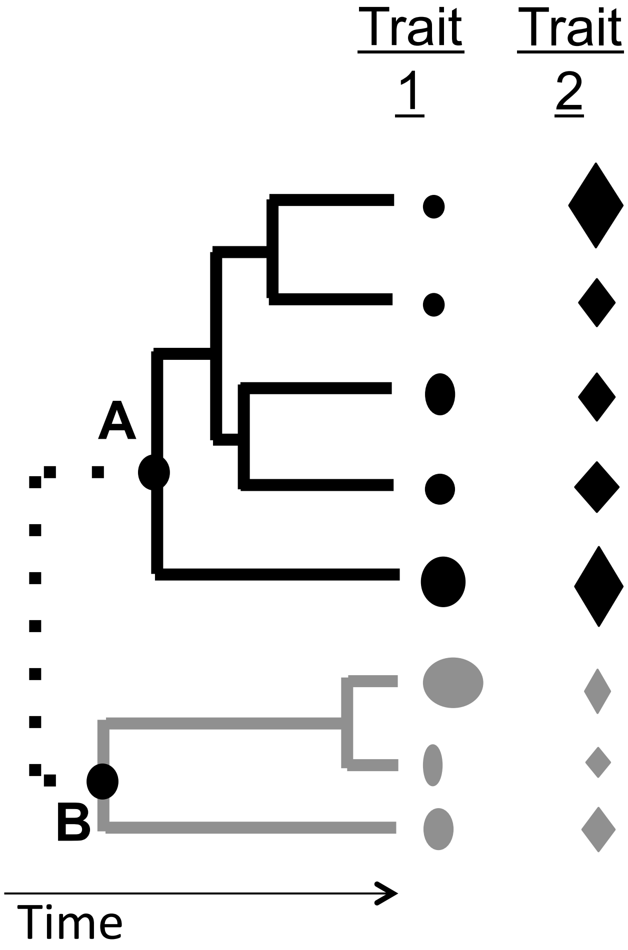
Abstract.—Rates of phenotypic evolution have changed throughout the history of life, producing variation in levels of morphological, functional, and ecological diversity among groups. Testing for the presence of these rate shifts is a key component of evaluating hypotheses about what causes them. In this paper, general predictions regarding changes in phenotypic diversity as a function of evolutionary history and rates are developed, and tests are derived to evaluate rate changes. Simulations show that these tests are more powerful than existing tests using standardized contrasts. The new approaches are distributed in an application called *Brownie* and in *r8s*.

Key words.—Brownian motion, *Brownie*, comparative method, continuous characters, disparity, morphological evolution, rate.

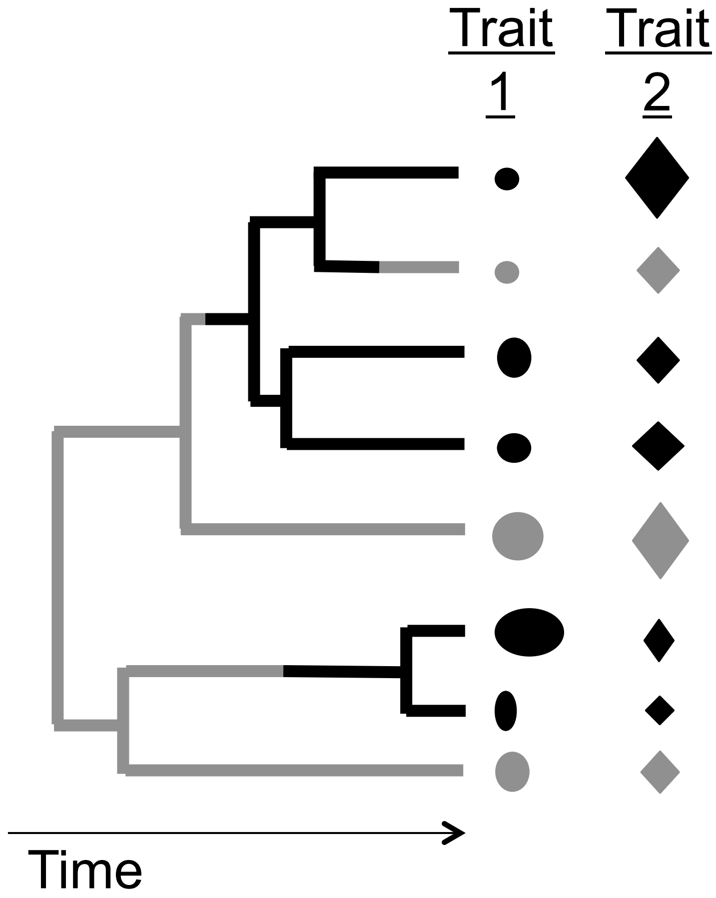
Received March 8, 2005. Accepted March 4, 2006.

Rates of Continuous Trait Evolution



Compare rates in Traits 1 and 2 between clades A and B

Rates of Continuous Trait Evolution



Compare rates in Traits 1 and 2 between lineages in different states (black & grey)

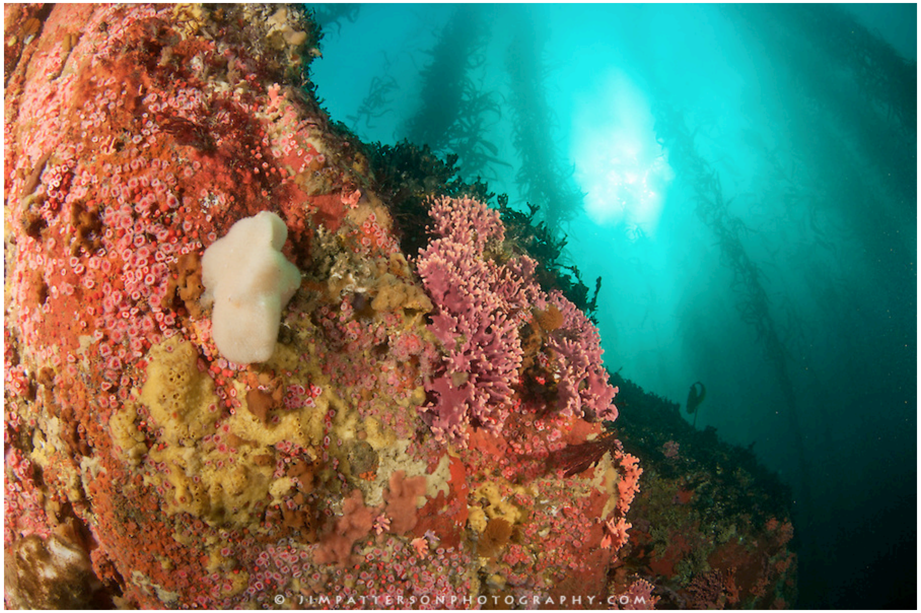
Incorporating Uncertainty

1. **Phylogenetic**
   - Random sample from the posterior distribution generated by MrBayes/BEAST etc.
2. **Character history**
   - Multiple samples using stochastic character mapping
3. **Model choice**
   - Model-averaging

TUTORIAL

Do reef habitats promote the evolution of morphological diversity?

Tropical



Temperate

Complex Reef Habitats

⬇

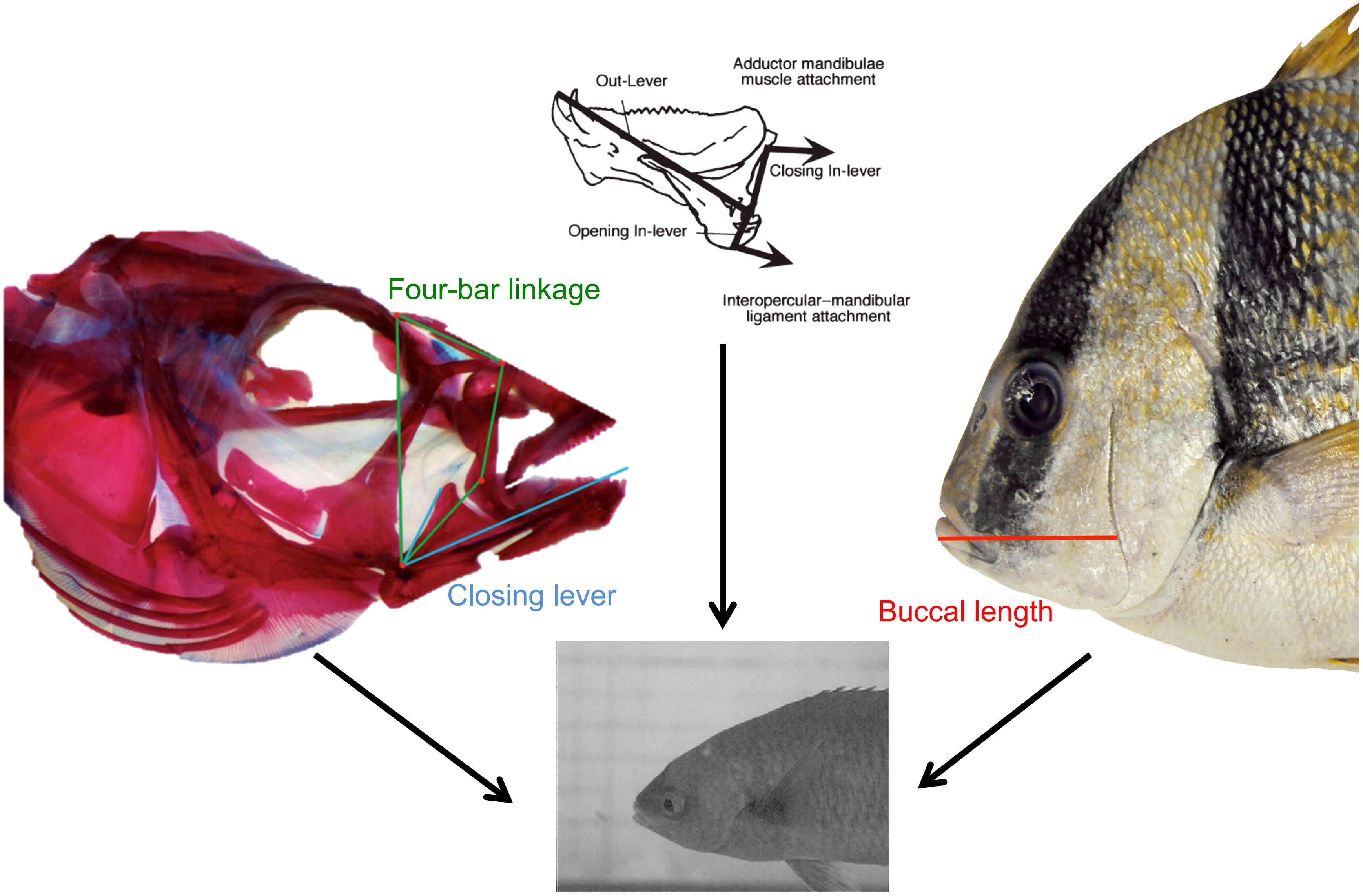
Promote ecological differentiation & speciation

Complex reef habitats promote ecological – morphological diversification

PREDICTION

Fishes living on reefs exhibit greater morphological diversity within traits underlying niche differentiation.

Diet & Trophic Morphology



HAEMULIDAE - GRUNTS

TUTORIAL

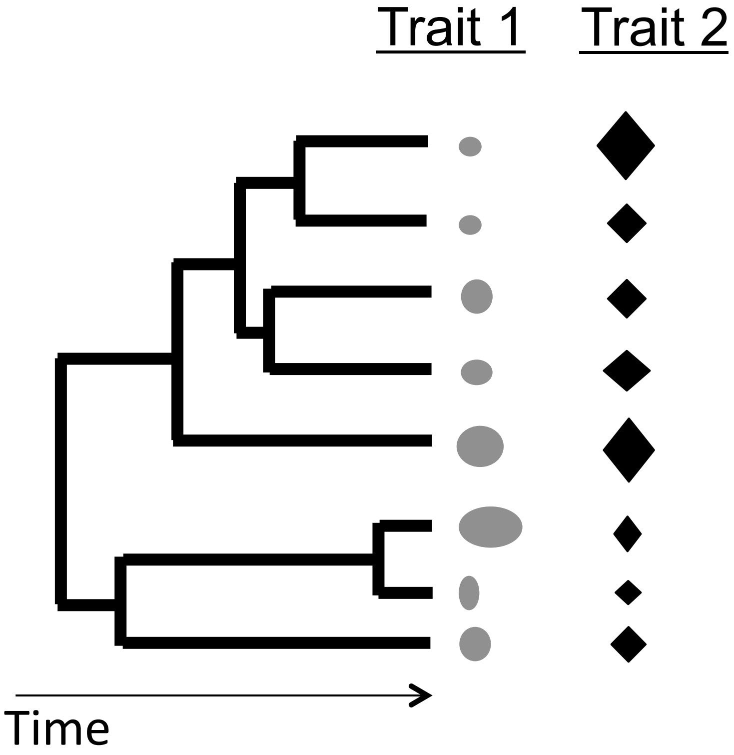
Are rates of evolution faster in reef lineages?

1. Model-testing using the Akaike Information Criterion: Does a 1-rate (fit a single rate across all species regardless of habitat) or 2-rate model (which allows the rate to vary depending on habitat) fit the data best?
2. Model-averaging: combine the parameter estimates of both 1 and 2-rate models weighted by the support for the model using Akaike weights.

ADDITIONAL METHODS:
Rates of Continuous Trait Evolution

ADDITIONAL METHODS

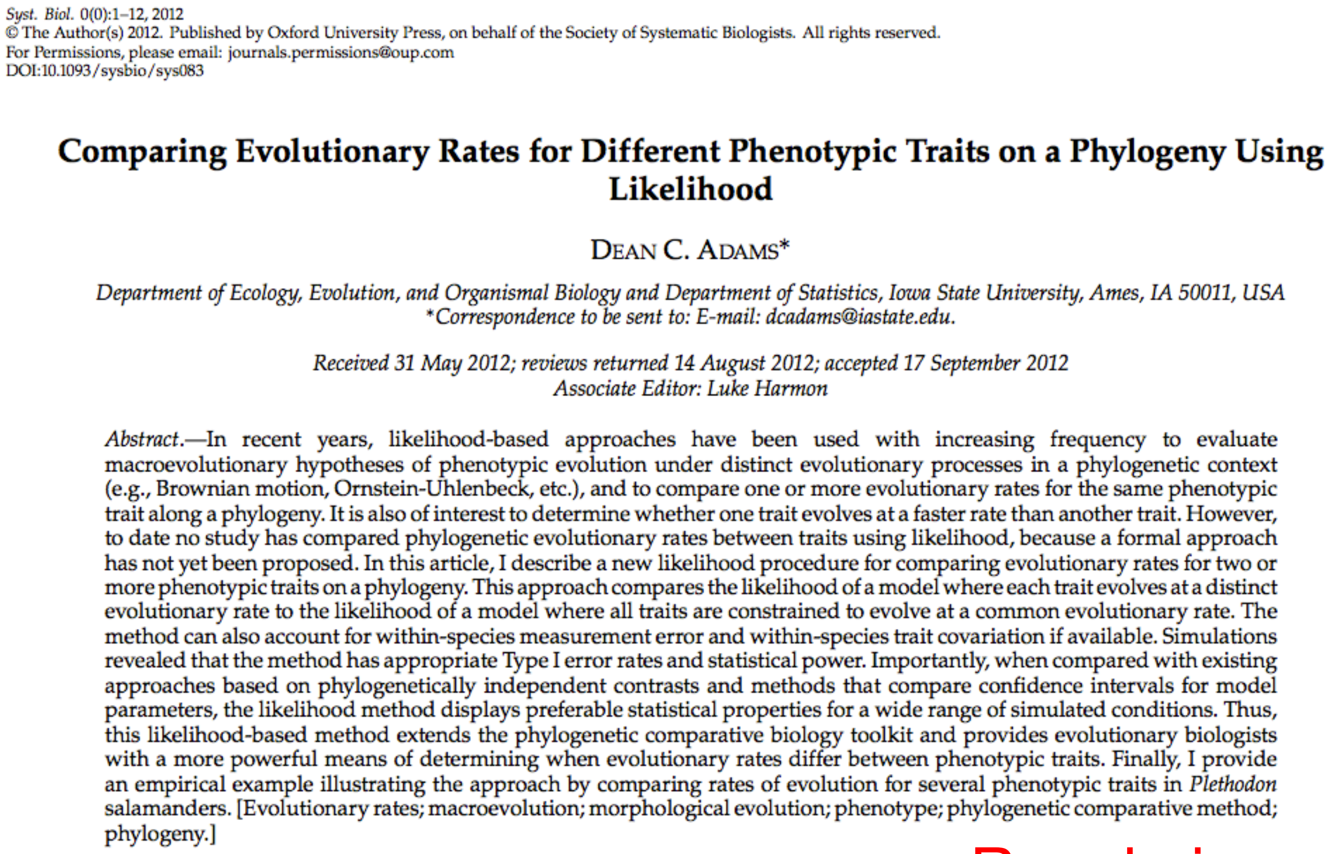
1. Comparing rates among traits



Compare rates between Trait 1 and 2 across the phylogeny

ADDITIONAL METHODS

1. Comparing rates among traits



Syst. Biol. 0(0):1–12, 2012

DOI:10.1093/sysbio/sys083

Comparing Evolutionary Rates for Different Phenotypic Traits on a Phylogeny Using Likelihood

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Received 31 May 2012; reviews returned 14 August 2012; accepted 17 September 2012
Associate Editor: Luke Harmon

Abstract.—In recent years, likelihood-based approaches have been used with increasing frequency to evaluate macroevolutionary hypotheses of phenotypic evolution under distinct evolutionary processes in a phylogenetic context (e.g., Brownian motion, Ornstein-Uhlenbeck, etc.), and to compare one or more evolutionary rates for the same phenotypic trait along a phylogeny. It is also of interest to determine whether one trait evolves at a faster rate than another trait. However, to date no study has compared phylogenetic evolutionary rates between traits using likelihood, because a formal approach has not yet been proposed. In this article, I describe a new likelihood procedure for comparing evolutionary rates for two or more phenotypic traits on a phylogeny. This approach compares the likelihood of a model where each trait evolves at a distinct evolutionary rate to the likelihood of a model where all traits are constrained to evolve at a common evolutionary rate. The method can also account for within-species measurement error and within-species trait covariation if available. Simulations revealed that the method has appropriate Type I error rates and statistical power. Importantly, when compared with existing approaches based on phylogenetically independent contrasts and methods that compare confidence intervals for model parameters, the likelihood method displays preferable statistical properties for a wide range of simulated conditions. Thus, this likelihood-based method extends the phylogenetic comparative biology toolkit and provides evolutionary biologists with a more powerful means of determining when evolutionary rates differ between phenotypic traits. Finally, I provide an empirical example illustrating the approach by comparing rates of evolution for several phenotypic traits in *Plethodon* salamanders. [Evolutionary rates; macroevolution; morphological evolution; phenotype; phylogenetic comparative method; phylogeny.]

R code in appendix 2

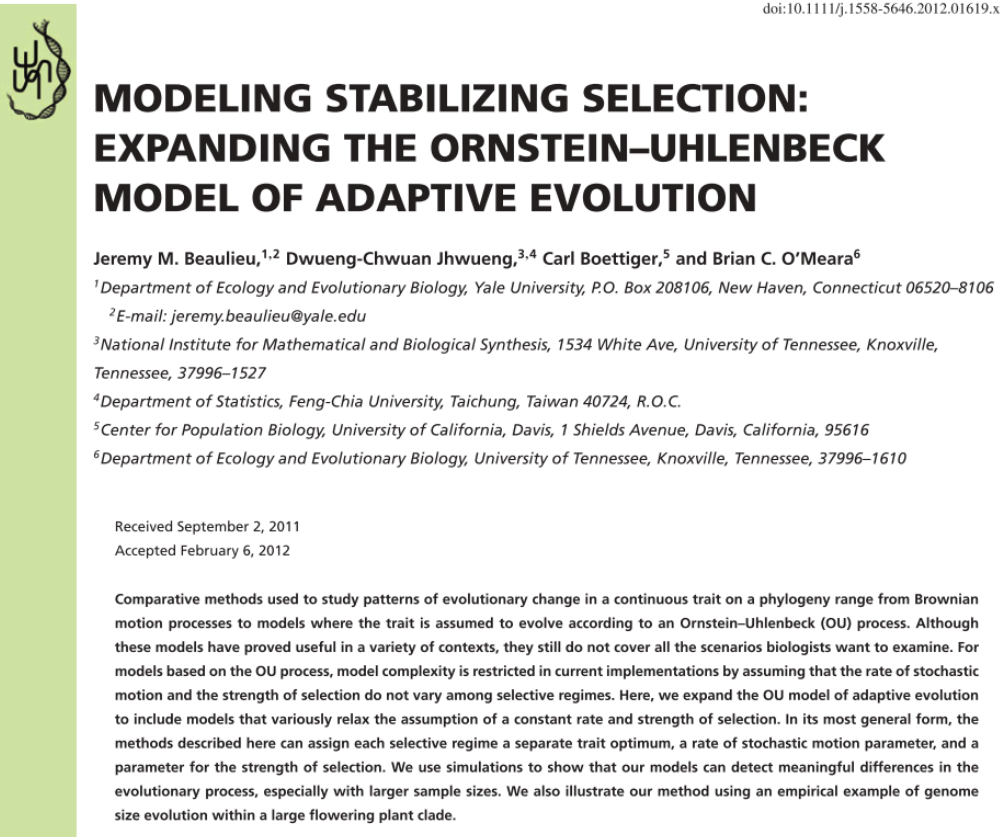
ADDITIONAL METHODS

2. Identifying rate shifts without *a priori* hypotheses

- Eastman et al. 2011: RJMCMC approach for fitting multiple shifts in rate class across the tree. auteur package in R
- Revell et al. 2012: MCMC approach for fitting a single rate shift to a tree. phytools package in R.
- Thomas & Freckleton 2011: maximum likelihood method 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

3. Methods that don't require Brownian motion?



doi:10.1111/j.1558-5646.2012.01619.x

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

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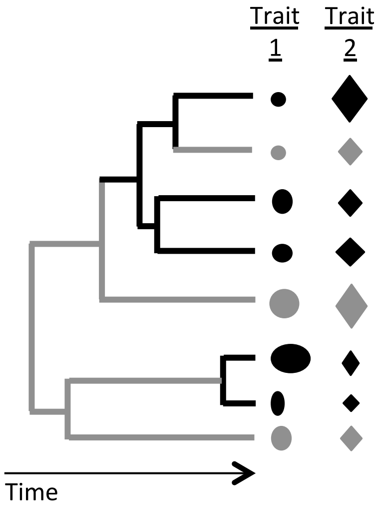
Received September 2, 2011
Accepted February 6, 2012

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.

R package OUwie

ADDITIONAL METHODS

3. **Methods that don’t require Brownian motion?**
   - Generalized Ornstein-Uhlenbeck-based models of continuous characters evolving under discrete selective regimes.



$$dX(t) \quad = \quad \overbrace{\sigma dB(t)}^{\text{Brownian motion}} + \alpha[\theta - X(t)]dt$$

Rate

Strength of selection

Optimal trait value

Change in time

GENERAL CAVEATS

GENERAL CAVEATS for phylogenetic comparative methods

Need to be able to answer YES:

1. Do your data fit the assumptions of the evolutionary model?
2. Do your tree and data have the power to estimate the parameters in the model?

GENERAL CAVEATS for phylogenetic comparative methods

Need to be able to answer YES:

1. **Do your data fit the assumptions of the evolutionary model?**
   - e.g Brownian: Pagel's λ, κ & δ parameters (can be implemented in Geiger using fitContinuous function)
2. **Do your tree and data have the necessary power?**
   - Simulations (parametric bootstrapping/ phylogenetic Monte Carlo (pmc)) to determine uncertainty in parameter estimates and power.

Photograph by David Doubilet