Slightly more complex models of continuous trait evolution on trees

Liam J. Revell

16 December 2016

Mult-rate brownian motion

- This model permits multiple rates of Brownian evolution on the phylogeny.

- First developed by O'Meara et al. (2006).

TESTING FOR DIFFERENT RATES OF CONTINUOUS TRAIT EVOLUTION USING LIKELIHOOD

Brian C. O'Meara,[1] Cécile Ané,[2] Michael J. Sanderson,[3,4] and Peter C. Wainwright[3,5]

[1]*Center for Population Biology, University of California, Davis, One Shields Avenue, Davis, California 95616*
E-mail: bcomeara@ucdavis.edu
[2]*Department of Statistics, University of Wisconsin-Madison, Medical Science Center, 1300 University Avenue, Madison, Wisconsin 53706-1532*
E-mail: ane@stat.wisc.edu
[3]*Section of Evolution and Ecology, University of California, Davis, One Shields Avenue, Davis, California 95616*
[4]*E-mail: mjsanderson@ucdavis.edu*
[5]*E-mail: pcwainwright@ucdavis.edu*

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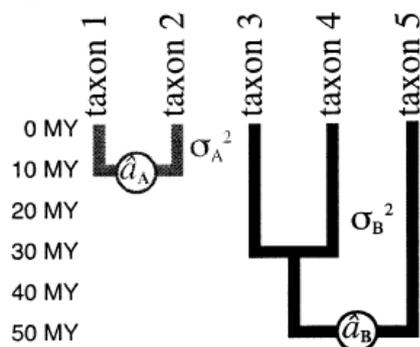
Key words.—Brownian motion, *Brownie*, comparative method, continuous characters, disparity, morphological evolution, rate.

Non-censored approach
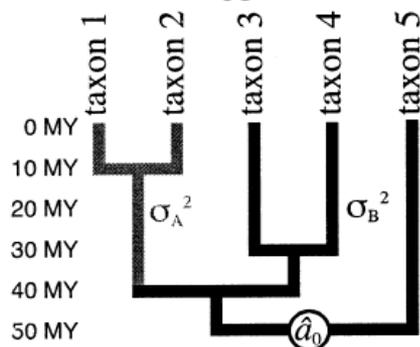
	taxon 1	taxon 2	taxon 3	taxon 4	taxon 5	$E(\mathbf{X})$
taxon 1	$40\sigma_A^2+10\sigma_B^2$	$30\sigma_A^2+10\sigma_B^2$	$10\sigma_B^2$	$10\sigma_B^2$	0	$\hat{a}_0$
taxon 2	$30\sigma_A^2+10\sigma_B^2$	$40\sigma_A^2+10\sigma_B^2$	$10\sigma_B^2$	$10\sigma_B^2$	0	$\hat{a}_0$
taxon 3	$10\sigma_B^2$	$10\sigma_B^2$	$50\sigma_B^2$	$20\sigma_B^2$	0	$\hat{a}_0$
taxon 4	$10\sigma_B^2$	$10\sigma_B^2$	$20\sigma_B^2$	$50\sigma_B^2$	0	$\hat{a}_0$
taxon 5	0	0	0	0	$50\sigma_B^2$	$\hat{a}_0$

Censored approach

	taxon 1	taxon 2	taxon 3	taxon 4	taxon 5	$E(\mathbf{X})$
taxon 1	$10\sigma_A^2$	0	0	0	0	$\hat{a}_A$
taxon 2	0	$10\sigma_A^2$	0	0	0	$\hat{a}_A$
taxon 3	0	0	$50\sigma_B^2$	$20\sigma_B^2$	0	$\hat{a}_B$
taxon 4	0	0	$20\sigma_B^2$	$50\sigma_B^2$	0	$\hat{a}_B$
taxon 5	0	0	0	0	$50\sigma_B^2$	$\hat{a}_B$

FIG. 3. Example showing the details of calculation for the noncensored and censored tests. The noncensored test uses the entire variance-covariance matrix shown with equation 3 to calculate the likelihood. One ancestral state is estimated for the entire tree. The optimal rate parameters under the unconstrained model must generally be estimated numerically (different rate parameter values are tried until the likelihood of the model is maximized). In contrast, the censored test analyses each subtree separately (indicated by the bold lines in the matrix and ancestral state vector). Each subtree has just one Brownian motion rate parameter, the value of which can be calculated analytically using equation 2 (the ancestral state for each subtree is also calculated analytically). In the simple example here, both the censored and noncensored tests would compare the likelihood of a model where σ_A^2 and σ_B^2 were set equal to each other with a model where the rates were free to vary.

Multi-optimum OU

- Model permits multiple adaptive optima (θ) in different parts of the tree.

- First developed by Butler & King (2004).

Ⓔ

Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution

Marguerite A. Butler[*] and Aaron A. King[†]

Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610

ABSTRACT: Biologists employ phylogenetic comparative methods to study adaptive evolution. However, none of the popular methods model selection directly. We explain and develop a method based on the Ornstein-Uhlenbeck (OU) process, first proposed by Hansen. Ornstein-Uhlenbeck models incorporate both selection and drift and are thus qualitatively different from, and more general than, pure drift models based on Brownian motion. Most importantly, OU models possess selective optima that formalize the notion of adaptive zone. In this article, we develop the method for one quantitative character, discuss interpretations of its parameters, and provide code implementing the method. Our approach allows us to translate hypotheses regarding adaptation in different selective regimes into explicit models, to test the models against data using maximum-likelihood-based model selection techniques, and to infer details of the evolutionary process. We illustrate the method using two worked examples. Relative to existing approaches, the direct modeling approach we demonstrate allows one to explore more detailed hypotheses and to utilize more of the information content of comparative data sets than existing methods. Moreover, the use of a model selection framework to simultaneously compare a variety of hypotheses advances our ability to assess alternative evolutionary explanations.

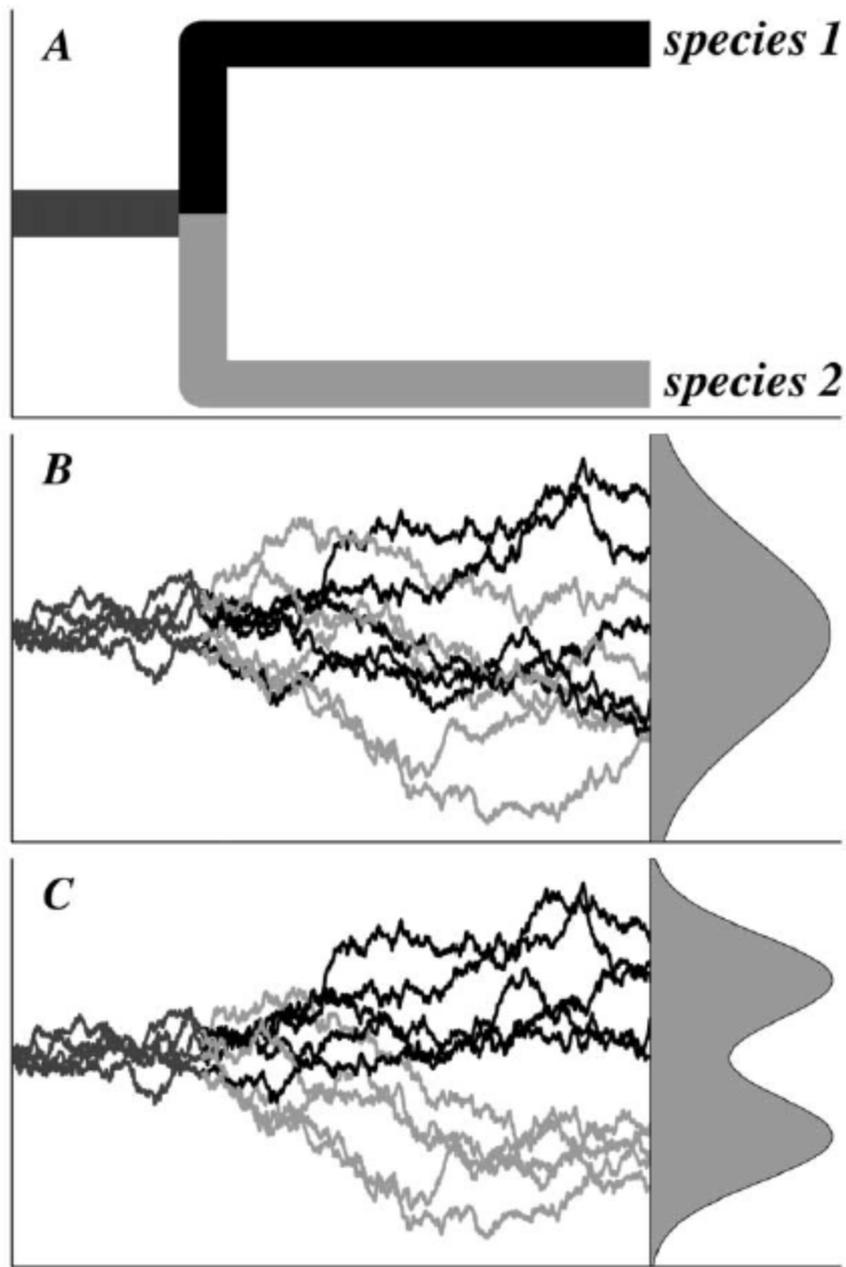Keywords: Ornstein-Uhlenbeck, Brownian motion, selective regime, adaptation, evolutionary model, Anolis lizards.

Figure 3: Simulations of Brownian motion (BM) and multiple-optimum Ornstein-Uhlenbeck (OU) processes with branching. Phenotypic value along *Y*-axis, time along *X*-axis. *A*, A single lineage evolves until a speciation event occurs from which two lineages (*light gray*, *black*) emerge. *B*, Lineages evolve according to BM, with light gray and black lineages evolving independently after the speciation event. *C*, Lineages evolve under an OU model. A single selective regime exists before the speciation event; two distinct selective regimes afterward. Distributions of the evolving quantitative character are shown at right. Brownian motion produces a unimodal trait distribution centered at the initial (ancestral) value, whereas the OU process results in a multimodal trait distribution with peaks near each optimum. An animation of this process is provided in the online edition of the *American Naturalist*.
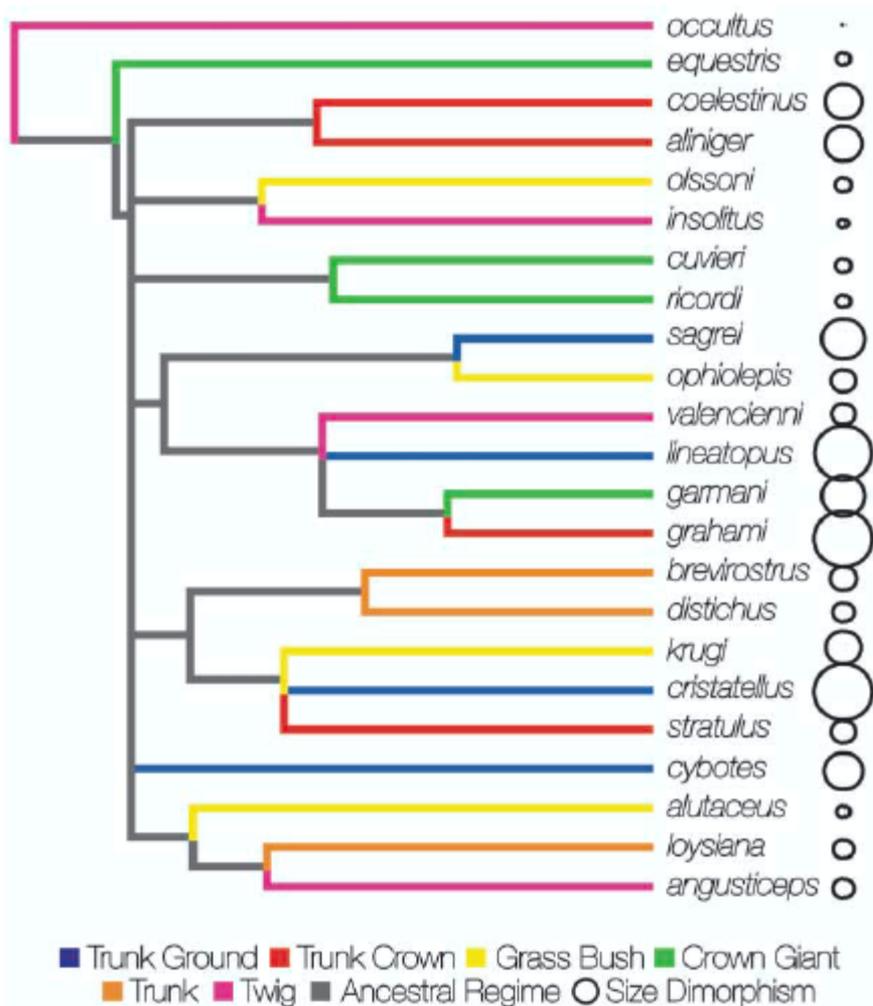
Figure 6: Full adaptive regime model for size dimorphism associated with habitat type. Color codes indicate separate adaptive regimes for the different habitat types (ecomorphs). Diameter of circles are proportional to the degree of sexual size dimorphism (log [male body length/female body length]). Data from Butler et al. (2000). Phylogeny (based on mtDNA) compiled from Jackman et al. (1997); Jackman et al. (1999; see Butler et al. 2000 for details). All species are within the genus *Anolis*. Timescale of the phylogeny is standardized to 1.0 from most basal node to terminal species.

Multi-optimum OU

- Model permits multiple adaptive optima (θ) in different parts of the tree.

- First developed by Butler & King (2004).

- Subsequently Beaulieu et al. (2012) proposed a model in which all three parameters of an OU process (θ, α, and σ^2) could vary among clades or edges.

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'Meara[6]

[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

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.

Multivariate, multi-regime Brownian motion

- Multivariate evolution also involves non-diagonal elements (covariances) of the evolutionary process.

- Revell & Collar (2009) developed an approach to permit different evolutionary correlations in different parts of the tree.

PHYLOGENETIC ANALYSIS OF THE EVOLUTIONARY CORRELATION USING LIKELIHOOD

Liam J. Revell[1,2,3] and David C. Collar[1,3,4]

[1]Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138
[2]E-mail: lrevell@fas.harvard.edu
[4]E-mail: dcollar@oeb.harvard.edu

Many evolutionary processes can lead to a change in the correlation between continuous characters over time or on different branches of a phylogenetic tree. Shifts in genetic or functional constraint, in the selective regime, or in some combination thereof can influence both the evolution of continuous traits and their relation to each other. These changes can often be mapped on a phylogenetic tree to examine their influence on multivariate phenotypic diversification. We propose a new likelihood method to fit multiple evolutionary rate matrices (also called evolutionary variance–covariance matrices) to species data for two or more continuous characters and a phylogeny. The evolutionary rate matrix is a matrix containing the evolutionary rates for individual characters on its diagonal, and the covariances between characters (of which the evolutionary correlations are a function) elsewhere. To illustrate our approach, we apply the method to an empirical dataset consisting of two features of feeding morphology sampled from 28 centrarchid fish species, as well as to data generated via phylogenetic numerical simulations. We find that the method has appropriate type I error, power, and parameter estimation. The approach presented herein is the first to allow for the explicit testing of how and when the evolutionary covariances between characters have changed in the history of a group.
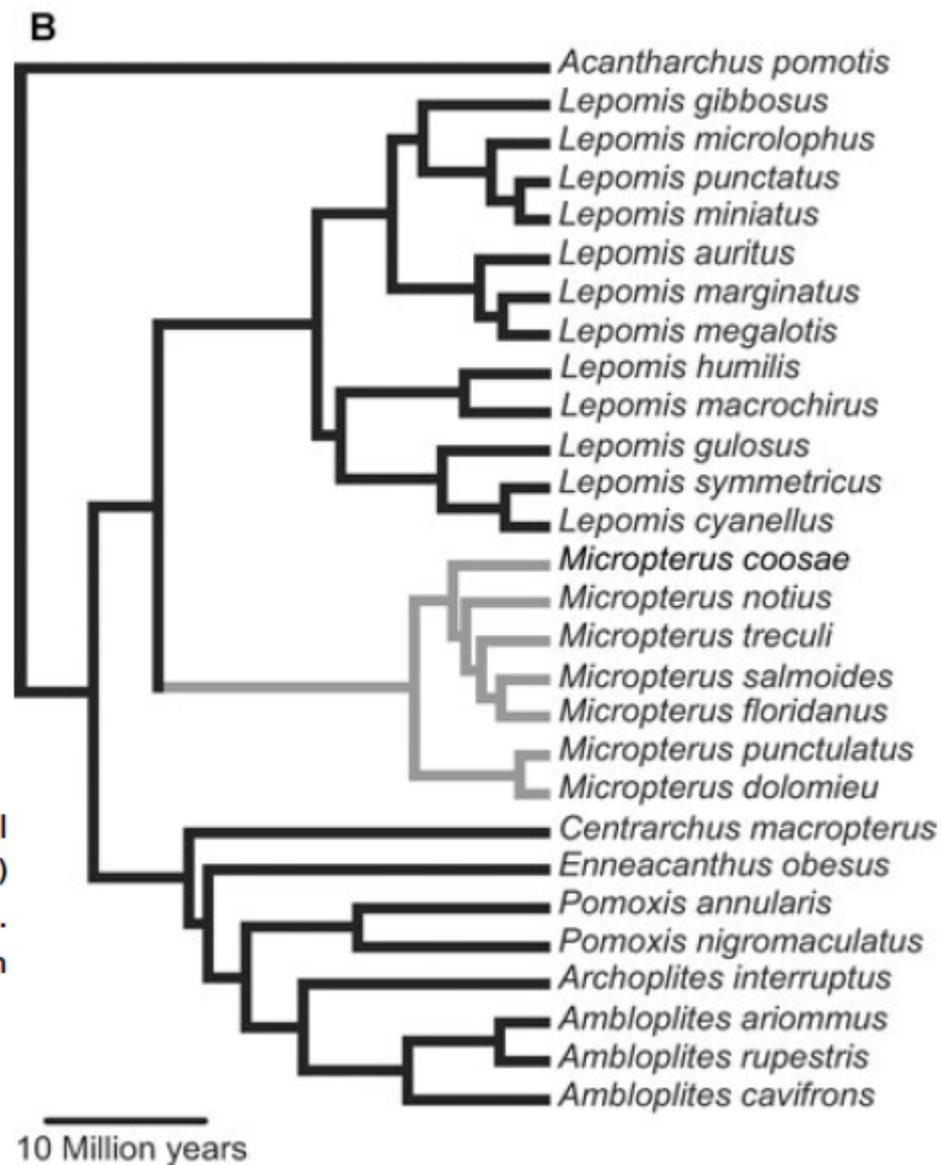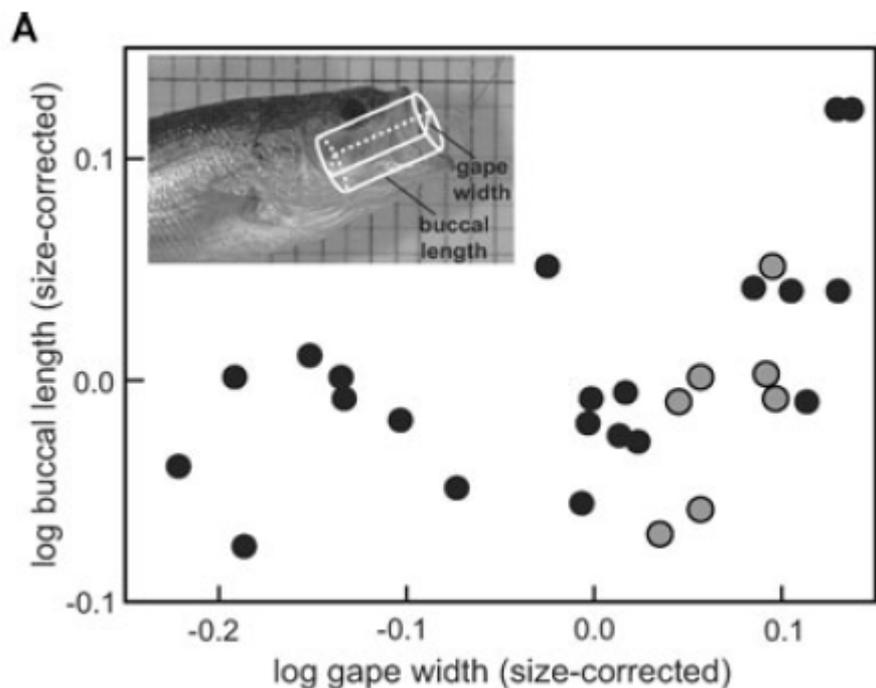
Figure 1. (A) Species mean trait values for gape width and buccal length (panel inset) for 28 species in the family Centrarchidae. (B) The phylogeny with branch lengths for the same 28 fish species. Species in the genus *Micropterus*, which consists of specialists on large, evasive prey, are highlighted in grey in both panels.

Multivariate, multi-regime Brownian motion

- Multivariate evolution also involves non-diagonal elements (covariances) of the evolutionary process.

- Revell & Collar (2009) developed an approach to permit different evolutionary correlations in different parts of the tree.

- This approach could theoretically be extended to OU models; however this would involve a rapid growth in the number of parameters.