

## **Annotated Bibliography: Continuous Trait Evolution**

### **Felsenstein (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39(4).**

Felsenstein argues for the use of bootstrapping to infer the variability in a sample by doing so across characters, assuming they all evolved independently. He addresses the fact that traits being completely independent is rarely the case, which results in many fewer characters in the matrix than if all characters were independent. Additionally, if character states are boiled down to binary factors, this can pose the same dependence problem. The paper continues on to discuss how confidence intervals can be obtained using bootstrapping and why it is important to know your hypotheses a priori, as to not influence your statistics. This paper introduces a method of standardized independent contrasts. "Bootstrapping provides us with a confidence interval within which is contained not the true phylogeny, but the phylogeny that would be estimated on repeated sampling of many characters from the underlying pool of characters."

### **Huey and Bennett (1987). Phylogenetic Studies of Coadaptation: Preferred Temperatures Versus Optimal Performance Temperatures of Lizards. *Evolution* 41(5).**

This study investigated coadaptation, correlated evolution, in thermal traits in several genera of Australian skinks. To achieve high fitness it is hypothesized that thermal behavior and thermal physiology should be highly correlated in ectotherms, such that high preference temperatures along a lineage should match high optimal performance temperatures. This study incorporated both phylogenetic and non-phylogenetic approaches to measure coadaptation. Overall, preference temperature correlates with optimal performance temperature but not at a 1:1 ratio, which they deemed partial coadaptation. However, two taxa evolved much lower preference temperatures and the basis for this could only be tested with a phylogenetic approach. For the phylogenetic approach, the authors used a minimum-evolution approach (derived partially from Felsenstein 1985) with parsimony methods to determine the ancestral preference temperature. The thermal preference seemingly evolved faster than the thermal optimum, reinforcing the idea of partial coadaptation. But in the cool-adapted species, one shows a shift of both traits toward cooler temperatures while the traits evolved in opposite directions for the other species. Only with both analyses, could the authors decide these states are derived rather than ancestral.

### **Martins & Garland (1991). Phylogenetic Analyses of the Correlated Evolution of Continuous Characters: A Simulation Study. *Evolution* 45(3).**

This paper compares three approaches to dealing with correlated evolution of continuous characters: the "TIPS" method (a Pearson product-moment correlation between the raw values of two traits for a series of species), computing statistics that describe the available data but are independent of each other (as in Felsenstein 1985), and by using a randomization test that takes phylogeny into account. These three approaches can be thought of as a model, where realized evolutionary correlation is a function of the input correlation, the sampling distribution of such (correlation across generations), and a random error term that is not directly

addressing the non-independence problem. The first method had the lowest power and the second method had the highest power in modeling slow, continuous character state shifts. No method showed significant bias, although the second method was the only one with an acceptable Type I error rate. For punctuational shifts, certain applications of each method were found to have acceptable Type I error rates but the power was lowest again for the first method. This paper stresses that there is no reason to assume that evolution of phenotypic traits evolve at constant or proportional rates. Branch lengths are critical for appropriate Type I Error Rate when using independent contrasts.

**Pagel (1997). Inferring evolutionary processes from phylogenies. *Zoologica Scripta* 26(4).**

This paper, among other things, reviews the approaches for inferring evolutionary processes (e.g. direction of change, rate of change, the nature of the evolutionary process) from phylogenies. Using maximum likelihood is helpful when seeking quantitative estimates of many parameters (such as rates of evolution, transitions between character states, correlations, variances, covariances) without directly inferring ancestral character states. Not only can phylogenies be useful in doing comparative tests, they can also tell us what is causing the underlying phenomenon. The generalized least squares approach is specifically for investigating continuously co-varying trait evolution. The GLS model treats each species' value of the trait as an observation to be predicted from the regression of the trait on total path length from the root to the species. This model does not explicitly calculate values at internal nodes, but estimates the correlation of a trait's value and total divergence. This GLS approach solves the non-independence problem without doing independent contrasts, as done in Felsenstein 1985. GLS can also estimate outside of the trait values observed and gets rid of less data than independent contrasts.

**Ackerly (2000). Taxon sampling, correlated evolution, and independent contrasts. *Evolution* 54(5).**

This paper points out how sampling bias in choosing species to compare in an ecological context can influence results and cause high error rates. Often, incorporation of taxa beyond extant taxa is difficult because trait values are not easily observed in the fossil record for many organisms. Ackerly ran simulations on correlated evolution of continuous phenotypic traits using the independent contrasts method to investigate how taxon sampling influences resulting conclusions. Six taxon sampling algorithms were used to look at various levels of random and non-random sampling. Results showed that estimates of trait correlations based on random samples of different sizes are unbiased, but variance in the outcome of interspecific correlations is much greater than for independent contrast correlations. While paired comparisons have many advantages in the way of needing less starting information, they lack statistical power for continuous traits. For studies of associations between evolutionary changes in continuous traits, random samples of species within clades provide robust estimates of correlation coefficients. Biological or methodological factors that lead to non-random taxon samples with respect to univariate or bivariate trait distributions may introduce systematic discrepancies between interspecific and phylogenetically structured analyses and bias estimates of evolutionary correlations.

**Butler and King (2004). Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution. *The American Naturalist* 164(6).**

Many analyses of interspecific trait correlation suffer from the same problem. Brownian motion (BM), a neutral model of evolution, is the underlying method of many types of analyses but natural selection is not neutral. This paper discusses methods that can model selection directly. Ornstein-Uhlenbeck (OU) processes, developed by Hansen (1997), differ from BM in that they have a selection optimum but include the random factor of the BM. By varying the model parameters, one can achieve a model with both selection and drift. Further enhancements that they call the “Hansen model” can model evolution of a single lineage or multiple lineages with optima which can vary between branches on a phylogeny. These models use a maximum likelihood statistical approach. The only drawback is that the selection factor enters the maximum likelihood in a nonlinear fashion and thus nonlinear methods must be used to estimate that parameter. Model selection using Hansen models uses standard approaches such as likelihood ratio tests and AIC.

**O’Meara, Ané, Sanderson, & Wainwright (2006). Testing for Different Rates of Continuous Trait Evolution Using Likelihood. *Evolution* 60(5).**

This study highlights the importance of testing for the presence of rate shifts. The model used in phenotypic evolution is commonly Brownian motion (BM), which is defined by the fact that the character state can increase or decrease at any instant. The magnitude of these shifts is independent of state and have a net change of zero. This is not always the most accurate, as we know that phenotypic traits near the edge of their natural limits in the environment are constrained. This paper assumes that each branch of the tree has its own optimal trait value, Brownian rate parameter, and OU parameter that describes the “pull” towards the optimal. Thinking about the implications of this study in the context of correlated trait evolution, we can imagine that the model becomes highly parameterized. These phenotypic traits, especially ones acted upon by the environment, are often highly correlated and have co-evolved to maximize performance.

**Lartillot and Poujol (2011). A phylogenetic model for investigating correlated evolution of substitution rates and continuous phenotypic characters. *Molecular Biology and Evolution* 28(1)**

Instead of correlating two phenotypic traits, these authors endeavor to correlate phenotypic characteristics with molecular substitution rates. The model used in this paper model both molecular parameters as well as phenotypic characters in one multivariate process. The parameters are estimated jointly in a Bayesian framework with Monte Carlo estimation. This approach relies on previously aligned sequences, phenotypic characters, and a previous tree. The program described here (Coevol; available online) reconstructs the history of the phenotypic traits and substitution process so that the correlation between the two can be calculated. Drawbacks of this method include the high error rates estimations of substitutions

rates. Studies should include multiple genes and many closely related taxa to circumvent this problem.

**Stinchcombe, Function-valued Traits Working Group, Kirkpatrick (2012). Genetics and evolution of function-valued traits: understanding environmentally responsive phenotypes. *Trends in Ecology and Evolution* 27(11).**

While traditional correlated trait studies use either univariate or multivariate traits, these authors suggest that for the most ecologically relevant data, we should use mathematical functions to describe the relationship between certain traits. These can then be correlated against other traits of interest. For example, size-at-age comparisons can be measured as a function because the strength of the correlation changes depending on the age range measured. This method has increased statistical power over multivariate analyses where the model loses power as the number of measurements per species/individual increases. While most of the studies described in this review do not use phylogenetic methods, that is one direction in which analyses of this type could continue. The following annotation was cited in this study and does use a phylogenetic approach.

**Functional Phylogenies Group (2012). Phylogenetic inference for function-valued traits: speech sound evolution. *Trends in Ecology and Evolution* 27(3):160-6**

This opinion paper uses phylogenetic methods to estimate when speech ability developed in humans using speech as a function rather than a univariate parameter. The approach they introduce leans heavily on approaches in historical linguistics. They apply Gaussian processes for phylogenetic inference. Both Brownian motion and OU models rely on Gaussian processes for comparative approaches so similar process might be able to help us infer how language changes over time. Observations regarding these function-valued traits can be thought of in two dimensions: evolutionary time and trait space. Covariances between observation of the path from the root of the tree to the tips can be used to calculate likelihoods for different tree topologies to later determine which phylogeny is most consistent with the data. Known covariance between different points on the tree can allow calculation of values at interior nodes.

**Ho and Ané (2014). Intrinsic inference difficulties for trait evolution with Ornstein-Uhlenbeck models. *Methods in Ecology and Evolution* 5.**

Ornstein-Uhlenbeck models are commonly used for measuring trait correlation but has some limitations. The authors discuss how three statistical properties, lack of identifiability of true parameter values, lack of power, and inaccurate model selection, can break down the tree. Additionally, ancestral trait value estimates do not improve in accuracy as the number of contemporary trait observations grow. Lack of identifiability can be diagnosed from maximum likelihood estimates that don't converge. This problem can be solved by reparameterizing the models, adding fossil data and assuming ancestral nodes are random from a prior distribution. AIC and BIC fail to properly model trees if the point at which the selection optima changes is unknown. The number of number of potential models quickly outnumbers actual data points. To best work around this the authors used a modified BIC which avoided overfitting their models.

The authors point out that while they have discussed several limitations to OU models, they are still useful with these recommendations.

**Khabbazian, Kriebel, Rohe, & Ané (2016). Fast and accurate detection of evolutionary shifts in Ornstein–Uhlenbeck models. *Methods in Ecology and Evolution* 7.**

This paper outlines the first time a lasso-type method has been proposed for phylogenetically structured data. It uses an OU model to seek out optima without predefined hypotheses. It uses a pBIC (defined here) to reduce the number of false shifts and avoid the tendency of AIC to overfit the model. As there are challenges with such a high dimensional model, the lasso regularization penalizes high numbers of predictors for the response. Using multiple traits should increase the robustness of the model and trait dimensionality should be reduced using a PCA. Uncertainty in the shifts was quantified using bootstrapping. One major strength of this method is the speed with which computations are completed.

**Clarke, Thomas, & Freckleton (2017). Trait Evolution in Adaptive Radiations: Modeling and Measuring Interspecific Competition on Phylogenies. *The American Naturalist* 189(2).**

This paper incorporates not only correlated traits but the pressure from competition from other species into modeling phylogenies. The idea behind this is that species rarely overlap in ecological niche space and thus competition forces trait evolution. This model predicts a breakdown of otherwise correlated traits with competition and elevated trait variance across species and a slowdown in evolutionary rate both across the clade and within each branch. This study argues that Brownian motion methods inaccurately represent trait correlations in this framework of interspecific competition. They use approximate Bayesian computation (ABC) to detect competition effects. This model is based on the BM method with an added term for interspecific competition.