

"PRINCIPLES OF PHYLOGENETICS: ECOLOGY AND EVOLUTION"

*Integrative Biology 200*  
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D.D. Ackerly

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**Readings**

Hansen, T. 1997. Stabilizing selection and the comparative analysis of adaptation. *Evolution* 51:1341-1351.

Ackerly, D. D. 2009. Conservatism and diversification of plant functional traits: Evolutionary rates versus phylogenetic signal. *Proceedings of the National Academy of Sciences USA* 106:19699-19706.

Blomberg, S. P., and T. Garland, Jr. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. *J. Evol. Biol.* 15:899-910.

**Other strongly recommended readings!**

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution* 57:717-745. (Focus on pp. 719-723 on methods for measuring phylogenetic signal)

Harmon, L. J., J. B. Losos, T. J. Davies, et al.. 2010. EARLY BURSTS OF BODY SIZE AND SHAPE EVOLUTION ARE RARE IN COMPARATIVE DATA *Evolution* 64:2385-2396.

**I. Phylogenetic signal**

*Pattern and Process*

Pattern is not process. No matter how many times we hear and repeat this phrase, the temptation to infer the action of specific processes from pattern alone is inevitable. In comparative biology, it has been all too common to equate stasis (pattern) with 'inertia' or 'constraint' (process?) and evolutionary change (pattern) with the action of selection (process). It is essential at the outset to see these dichotomies of pattern and process as orthogonal, setting up a 2x2 table:

<u>Evolutionary process</u>	<u>Pattern of trait evolution</u>	
	Stasis	Change
Adaptive	Stabilizing selection Fluctuating directional selection	Directional or disruptive selection
Non-adaptive	Lack of genetic variation (= constraint?) Antagonistic correlations among traits under selection Swamping by gene flow	Mutation Genetic drift Genetic correlations with traits under selection

In this case, I equate the term 'adaptive' with patterns resulting from the action of selection. It is not a statement about the functional significance of a particular trait, nor is it the same as stating that a particular trait represents an 'adaptation'. More on that in the next lecture.

It is critical to remember, as well, that these processes are neither exclusive nor independent of each other. For example, the action of drift and selection in small populations may simultaneously contribute to changes in gene frequency, and it may be difficult or impossible in an individual instance to separate their contributions. Replication in space (populations) or time (across generations) is critical, as selection is the only process we currently know of in evolutionary biology that can cause repeated, heritable change in the same direction in response to environmental conditions. Note also that selection leads to the loss of genetic variation. Thus, strong selection on a trait may lead to fixation of genes responsible for variation, such that future maintenance of the trait is due to the absence of sufficient variation (even if the selective context shifts).

As discussed in the Blomberg and Garland paper, there is a long history of usage of terms such as phylogenetic inertia or constraint, and other more recent terms such as phylogenetic effect and conservatism. To a greater or lesser degree, all of these terms imply the action of some underlying process. The term *phylogenetic signal* is useful as the implication is clear that we are only speaking about the pattern. I also like phylogenetic conservatism, though it is now taking on its own intellectual baggage and may suggest particular hypotheses about process (e.g., see Losos 2008 Ecology Letters).

#### *Quantifying phylogenetic signal for continuous traits*

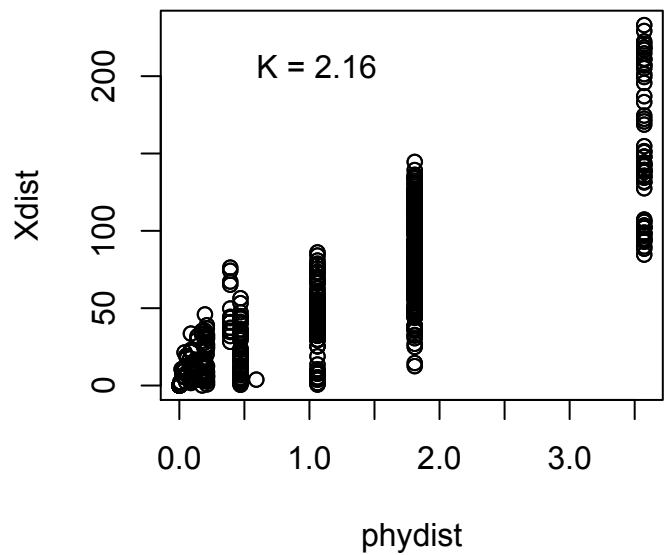
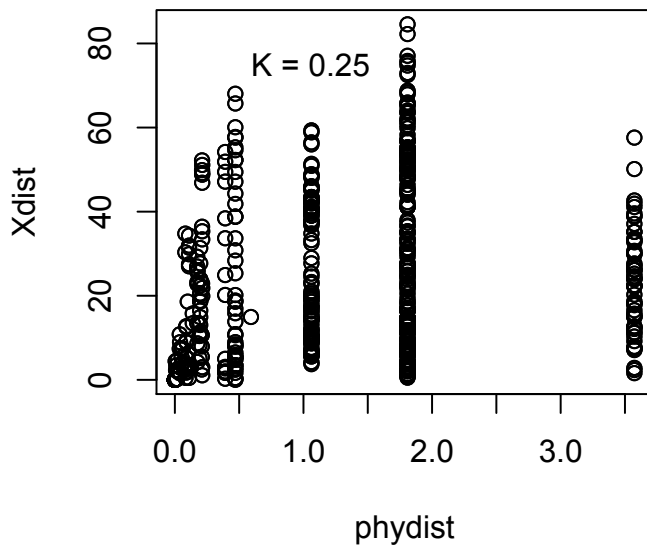
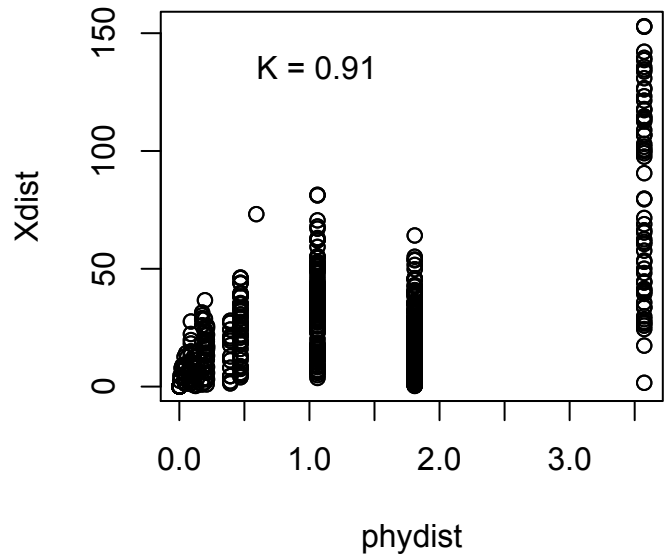
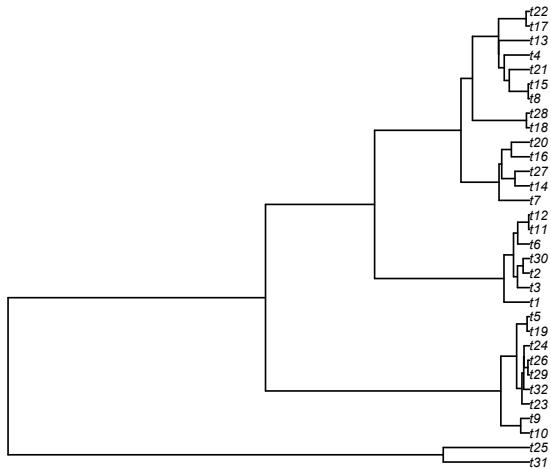
Several statistical have been developed to quantify phylogenetic signal, and test for significance relative to a null model of no signal. Freckleton et al. (200x) discuss the  $\lambda$  parameter, which is derived from Pagel's model fitting methods. I have worked more with Blomberg et al. (2003) K statistic.  $\lambda$  and K have the same general interpretation:

$\lambda, K < 1$	less signal than expected under Brownian motion
$\lambda, K = 1$	expectation under B.M.
$K > 1$	more signal than expected under B.M.

Quantitatively, one of the main differences is that  $\lambda$  has a maximum around 1.1 or 1.2, so it has little resolution to describe patterns with a high degree of signal (Freckleton et al. don't report values  $> 1$ ). K on the other hand has a theoretical maximum of infinity and can provide some insight into differing degrees of signal greater than expected under Brownian motion.

Fortunately, there is a simple graphical interpretation of these statistics, based on a plot of the difference in trait values between species pairs (all pairwise comparisons, not just sister taxa!) versus the phylogenetic distance between the taxa (Figure on next page). Remember from Brownian motion, the expectation of the squared difference between trait values (the variance) goes up linearly with the phylogenetic distance. It turns out that this translates approximately into a filled half triangle in a plot of the absolute difference vs. phylogenetic distance for all species pairs (assuming the tree is ultrametric). Concave curvature of the upper surface of this plot means that close relatives are less similar than expected, compared to distant relatives ( $K < 1$ ). Convex curvature, or an absence of points in the lower right, means that close relatives are more similar than expected ( $K > 1$ ). The details of the plot structure will depend on tree topology, but in general examining these plots is quite informative. Significance tests for the correlations in such plots must be tested using Mantel tests for matrix correlations (another topic!).

## THE TREE

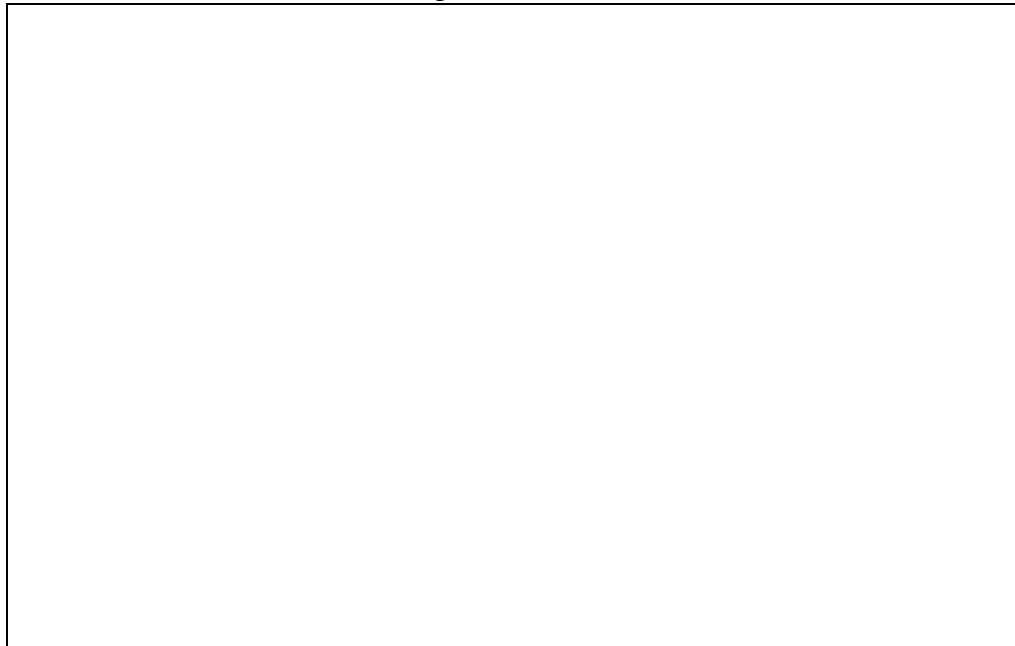


Another approach to asking about phylogenetic signal and patterns is to ask whether the trait data fit an alternative model of trait evolution, and whether the parameters of this model then shed light on the processes influencing the trait and its evolutionary history. One of the very important alternative models is to introduce stabilizing selection, i.e. a model in which there is a 'pull' towards some central optimal value (which may fluctuate along different lineages), and Brownian motion reflects the random processes and/or the excursions in the action of selection around this underlying optimum. The stabilizing selection model is known as an Ornstein-Uhlenbeck stochastic process, so you will see references to OU models (and there is an R library called 'ouch' for OU models).

Another graphical approach is to draw a 'traitgram', a phylogeny where the tips are arranged left to right based on species trait values, and internal nodes show the maximum likelihood reconstructions. This can get a bit messy, as the branches cross over each other. Lots of crossovers shows that a trait has exhibited many reversals of trait evolution during its history. If those crossovers occur particularly among the most recent divergence events, then it's evidence of rapid evolution and a departure from Brownian motion, as the trait is not continuing to diverge at constant rates. Figure below is from Ackerly (2009).

As you can see from this example, the Brownian Motion model predicts a certain pattern of relative similarity – how similar are close relatives compared to the similarities among distant relatives. It is not a statement about the absolute rate of evolution, and how much the actual trait values have diverged over time. You can rescale the trait axes in the figure below so each clade spans much less or more actual trait space, and that doesn't change the fit of the data to Brownian Motion. This is because of the unbounded assumption of the model – evolving more quickly does not result in more convergence and loss of phylogenetic signal – and in this regard continuous and discrete characters are very different.

As we discussed earlier, the variance of the Brownian Motion process is a direct measure of evolutionary rate – how quickly are trait values diverging from each other over time. Ackerly (2009) proposed using this rate parameter with standardized measures of trait variation – using log-transformed data – and branch lengths scaled in millions of years as a measure of the rate of character evolution based on comparative data (without fossils).



There are many other possible models that one can simulate and use to fit empirical trait distributions for continuous characters, which have received more or less attention in the literature.

Mode	Model	Verbal explanation
Brownian	$x_{t+1} = x_t + N(0,s)$	random walk
Brownian + trend	$x_{t+1} = x_t + N(t,s), t \neq 0$	random walk with a trend
Bounded Brownian	$x_{t+1} = x_t + N(0,s)$ if $x_{t+1} < \min X$ or $> \max X$ , resample	random walk with lower and/or upper limits to trait values
Proportional	$x_{t+1} = x_t * LN(\log mean = 0, \log sd = s)$	multiplicative random walk (equivalent to a random walk on log of trait)
ACDC	$x_{t+1} = x_t + N(0,s)$ $s = s_0 \gamma^{-t}$ $\gamma < 1$ , accelerating $\gamma > 1$ , decelerating	random walk with an accelerating or decelerating rate parameter
OU-1 (Ornstein-Uhlenbeck)	$x_{t+1} = \mu + \theta(x_t - \mu) + N(0,s)$ $\mu$ = trait optimum $\theta = 1$ : brownian $\theta = 0$ : complete stabilizing selection	stabilizing selection; random walk with a 'pull' towards the optimum for the clade; theta is strength of the pull
OU-2+ (Ornstein-Uhlenbeck)	$x_{t+1} = \mu_i + \theta(x_t - \mu_i) + N(0,s)$ $\mu_i$ = trait optimum on branch i $\theta = 1$ : brownian $\theta = 0$ : complete stabilizing selection	stabilizing selection; random walk with a 'pull' towards different optima on different branches, to test a priori hypotheses of adaptive evolution
Speciational	Brownian, with change only at time of speciation	random walk, but only one change per speciation event (i.e. branch length = 1 between each speciation event)
Punctuational	Brownian, with change only at time of speciation and only in one daughter lineage	like speciational, but change only occurs in one daughter lineage and the other exhibits stasis

There are many evolutionists who believe that stabilizing selection is the overarching cause of evolutionary stasis and the maintenance of similarity among close relatives. The OU model has been termed a stabilizing selection model, because trait values are 'pulled' back towards an optimum value. Paradoxically, an OU process with a single optimum generates traits with  $K < 1$ , so stabilizing selection reduces phylogenetic signal, which is not intuitive at first! Estes and Arnold (2007, American Naturalist) offer an important discussion of stabilizing selection and apply it to a large data set compiled by Gingerich (1983, Science) on rates of morphological evolution (mostly from fossils, not comparative data).

OU models can be used in a very different way when we have an a priori hypothesis that evolution has favored different trait values in different clades, or on different branches of a tree.

These are two-rate (or more) OU models that can use a nested-likelihood ratio approach to test whether a model with two (or more) different optima are significantly better than one optimum. This is a powerful alternative to independent contrasts, because it doesn't focus on divergence between sister taxa; rather, the focus is on the degree of similarity among taxa hypothesized to be experiencing similar adaptive regimes. We will look at the first example (Hansen 1997).

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