EXPLORING PATTERNS OF INTERSPECIFIC VARIATION IN QUANTITATIVE TRAITS USING SEQUENTIAL PHYLOGENETIC EIGENVECTOR REGRESSIONS

José Alexandre Felizola Diniz Filho,[1,2] Thiago F. Rangel,[1] Thiago Santos,[3] and Luis Mauricio Bini[1]

[1]*Departamento de Ecologia, ICB, Universidade Federal de Goiás. CxP 131, 74001–970 Goiânia, GO, Brasil*

   [2]*E-mail: diniz@icb.ufg.br*

[3]*Programa de Pós-Graduação em Ecologia and Evolução, Universidade Federal de Goiás, Goiânia, GO, Brasil*

A number of metrics have been developed for estimating phylogenetic signal in data and to evaluate correlated evolution, inferring broad-scale evolutionary and ecological processes. Here, we proposed an approach called phylogenetic signal-representation (PSR) curve, built upon phylogenetic eigenvector regression (PVR). In PVR, selected eigenvectors extracted from a phylogenetic distance matrix are used to model interspecific variation. In the PSR curve, sequential PVR models are fitted after successively increasing the number of eigenvectors and plotting their R^2 against the accumulated eigenvalues. We used simulations to show that a linear PSR curve is expected under Brownian motion and that its shape changes under alternative evolutionary models. The PSR area, expressing deviations from Brownian motion, is strongly correlated ($r = 0.873$; $P < 0.01$) with Blomberg's K-statistics, so nonlinear PSR curves reveal if traits are evolving at a slower or higher rate than expected by Brownian motion. The PSR area is also correlated with phylogenetic half-life under an Ornstein-Uhlenbeck process, suggesting how both methods describe the shape of the relationship between interspecific variation and time since divergence among species. The PSR curve provides an elegant exploratory method to understand deviations from Brownian motion, in terms of acceleration or deceleration of evolutionary rates occurring at large or small phylogenetic distances.

KEY WORDS: Brownian motion, comparative methods, K-statistics, O-U process, phylogenetic eigenvector regression, phylogeny.

It is widely recognized that species cannot be considered independent units in statistical analysis. This has been clear ever since Charles Darwin's 1837 "I think" tree (see Felsenstein 1985; Harvey and Pagel 1991). Because species share ancestors, their traits tend to be phylogenetically autocorrelated, albeit to different extents and over different time scales. More closely related species tend to be more similar to each other than expected by chance alone, creating phylogenetic signal (see Blomberg and Garland 2002 for a review). The presence of phylogenetic autocorrelation or signal precludes the use of traditional statistical tests, so an initial motivation for estimating this signal was the need to determine how much (if any) correction must be made to take the phylogenetic relationships among species into account when modeling correlated evolution or using interspecific variation to understand ecological and evolutionary patterns (see Felsenstein 1985; Martins and Garland 1991; Martins et al. 2002; Stone et al. 2011). There is a growing interest in using phylogenetic signal to infer broad-scale evolutionary and ecological patterns and processes (Hansen and Martins 1996; Diniz-Filho 2001; Hansen et al. 2008; Cooper et al. 2010; Hof et al. 2010; but see Revell et al. 2008).

In fact, detailed examination of interspecific variation reveals that different autocorrelation patterns arise under alternative evolutionary processes (Hansen and Martins 1996; Diniz-Filho 2001). Over the last 30 years, a number of methods have been proposed to address these problems, including methods that analyze the relationships between traits while taking phylogenetic structure into account, as well as methods that measure the magnitude of phylogenetic signal in a dataset.

Freckleton et al. (2002) and Blomberg et al. (2003) developed interesting and widely used "model-based" metrics for estimating phylogenetic signal. These metrics are obtained using forms of phylogenetic generalized least squares (PGLS). The Blomberg et al. (2003) K-statistic estimates whether relatives resemble each other less ($K < 1$) or more ($K > 1$) than expected under Brownian motion evolutionary model, whereas Pagel's λ (Pagel 1999), championed by Freckleton et al. (2002), allows the detection of departures from Brownian motion if λ is significantly smaller than 1.0. In an ecological context, the K-statistic has been particularly useful in evaluating patterns of phylogenetic niche conservatism (see Cooper et al. 2010; Hof et al. 2010; Wiens et al. 2010), especially after Losos (2008) pointed out that "documentation of niche conservatism requires demonstrating that phenotypic similarity of closely related species is significantly greater than would be expected based on phylogenetic relatedness (i.e., phylogenetic signal would have to be even greater than expected to result from Brownian motion)."

Phylogenetic signal can also be estimated using a framework based on statistical models that separate the total variation of a trait (T) into phylogenetic (P) and specific (S) components, such that $T = P + S$. In this framework, the P-component expresses the part of the variation in the trait that is phylogenetically autocorrelated and shared among species, whereas the S-component is the unique variation in each species arising after the divergence from the most recent common ancestor. This framework was pioneered by Cheverud et al. (1985), who used an autoregressive model (ARM) to partition trait variation into P- and S-components (see also Gittleman and Kot 1990; Martins 1996). Later, Diniz-Filho et al. (1998) proposed a different approach, called phylogenetic eigenvector regression (PVR), to partition the variation in a similar way. In both PVR and ARM, the R^2 value of the model can be interpreted as a measure of the phylogenetic signal because it expresses the ratio between the phylogenetic component and the total variation of a trait.

In short, PVR starts by extracting eigenvectors (using a principal coordinate analysis [(PCoA]) from pairwise distance matrices that describe the phylogenetic relationships among species and then use some of the eigenvectors (which can be selected using different criteria—see Diniz-Filho et al. 2012 for a recent review and evaluation) to model trait variation with a standard ordinary least-squares (OLS) regression. The coefficient of determination (R^2) of the multiple regression model is an estimate of phylogenetic signal (see also Borcard and Legendre 2002; Borcard et al. 2004; Griffith 2003; Diniz-Filho and Bini 2005; Griffith and Peres-Neto 2006; Peres-Neto 2006; Dray et al. 2006; Tiefelsdorf and Griffith 2007; Bini et al. 2009 and Peres-Neto and Legendre 2010 for the most recent developments and comparative tests of analogous eigenvector mapping approaches in spatial analyses). Many studies have used PVR to estimate the magnitude of phylogenetic signal, to partition interspecific variation into evolutionary and ecological components and to estimate the phylogenetically-corrected correlation between traits (e.g., Monteiro and Abe 1999; Morales 2000; Bisson et al. 2010; Sakamoto et al. 2010; Safi and Pettorelli 2010; Staggemeir et al. 2010; Beltran et al. 2010; Hill and Kotanen 2011). However, partitioning methods such as PVR and ARM have been criticized because the expected relationships among species defined in these models do not correspond to evolutionary models currently used in comparative analysis (Martins and Hansen 1996; Rohlf 2001; Freckleton et al. 2011; but see Lynch 1991; Housworth et al. 2004; Hadfield and Nakagawa 2009). Furthermore, Rohlf (2001) identified problems with the interpretation of the R^2 values derived from PRV (see below).

Here, we revisit the PVR approach to show that its coefficient of determination can serve as a valid measure of phylogenetic signal, and we show how it can be used to compare observed patterns against the expectations of phenomenological evolutionary models, such as Brownian motion or an Ornstein-Uhlenbeck (O-U) process. To do this, we must take into account the amount of phylogenetic information retained by the eigenvectors used to represent the matrix of phylogenetic distances among species. Moreover, when sequential PVR models are computed by successively adding eigenvectors to model trait variation, it is possible to plot R^2 against the accumulated eigenvalues associated with the eigenvectors extracted from the phylogenetic distance matrix. We called this plot a phylogenetic signal-representation (PSR) curve, and we use simulations to show that the shape of the PSR curve can be interpreted in terms of evolutionary models driving trait variation. For instance, a Brownian motion model generates a linear relationship between R^2 and the accumulative eigenvalues. Deviations from Brownian motion in a PSR curve are strongly correlated with the Blomberg's et al. (2003) K-statistic. In addition to graphical inspection of evolutionary patterns, which can be used to show which traits evolve at accelerating or decelerating rates with respect to Brownian motion, a PSR curve also allows one to determine when these deviations might have emerged during the evolutionary history of the group under study. Finally, we discuss the implications of PSR curves for investigating correlated evolution and patterns of interspecific variation while taking phylogenetic structure into account.

Methods

THEORETICAL BACKGROUND

PVR, as originally formulated by Diniz-Filho et al. (1998), begins with the extraction of eigenvalues (λ) and associated eigenvectors from a double-centered phylogenetic distance matrix. To accomplish this, a PCoA is used (see Legendre and Legendre 1998 for a detailed account of this multivariate method). As the eigenvectors are orthogonal, each one depicts a particular pattern of relationships among the species. For instance, the first eigenvectors (associated with the largest eigenvalues) represent the largest phylogenetic distances, usually the distances between the main clades closer to the root. Progressively, eigenvectors with smaller eigenvalues are associated with smaller phylogenetic distances (however, the first eigenvector of a strongly asymmetric phylogeny will tend to show a gradient among species, representing the overall "shape" of the relationships with the node of the phylogeny).

After the eigenvector selection procedure (see Diniz-Filho et al. 2012), some of the eigenvectors are used as explanatory variables ($\mathbf{X}$) in a standard OLS multiple regression model ($\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \boldsymbol{\varepsilon}$) in which the response variable ($\mathbf{Y}$) is the phenotypic character under study. The R^2 value of this multiple regression model is, as we will show later, an estimate of the phylogenetic signal (or, more precisely, of the part of the variation in trait $\mathbf{Y}$ that can be explained by the phylogenetic relationships among the species, which, in turn, are represented by the selected eigenvectors). The PVR residuals ($\boldsymbol{\varepsilon}$) express the specific component, the equivalent of the S-component under the partitioning approach proposed by Cheverud's et al. (1985) ARM (see also Desdevises et al. 2003 for a similar use of phylogenetic eigenvectors in a partial regression approach). In this study, we focus on describing phylogenetic patterns and interpreting them with respect to evolutionary models, such as a Brownian motion model or an O-U process, and not on measuring the evolutionary correlation among two or more traits (which can be done by correlating the S-components of independent PVR or ARM models—see Martins et al. 2002).

As Rohlf (2001) pointed out, when all eigenvectors are used as explanatory variables in the multiple regression model (a necessary condition to take the entire phylogeny into account), the resulting coefficient of determination is trivial: "Thus, the fit will always be perfect, $R^2 = 1$, and there will be no residual variation in which to investigate correlations with other variables." Conversely, Rohlf (2001) also acknowledged that, originally, ". . . Diniz-Filho et al. (1998) only retained the first few eigenvectors—those for which the corresponding λ_i exceed the values expected from the broken stick model. The fit is then no longer perfect and the R^2 values simply measure the proportion of the variance attributable to average differences among the nodes corresponding to the retained eigenvectors. Leaving out any eigenvector with $\lambda_i > 0$ corresponds to ignoring some part of the structure of the tree near the tips and thus not taking the entire phylogeny into account. By ignoring eigenvectors with small eigenvalues, this approach confounds variation due to divergence among species that diverge near the tips of the tree with variation within the branches connecting each species to its more recent common ancestor. Thus, this only estimates part of the variation in a variable that can be accounted for by phylogeny."

Rohlf's (2001) argument is valid. To overcome his criticism it is necessary to understand how ignoring some of the eigenvectors will lead to a decrease in the PVR R^2 value. Under Brownian motion, the relationship between interspecific divergence and time is linear, when divergence is measured as the proportion of shared-branch length among species, or standardized phylogenetic covariance $\boldsymbol{\Sigma}$ matrix (or the "correlation" among species—see Hansen and Martins 1996; Rohlf 2001). Thus, excluding part of the phylogeny from an analysis causes a proportional decrease in signal. If using 100% of the phylogeny leads to an R^2 of 1.0 and, obviously, using zero eigenvectors will lead to an R^2 of 0, then we can expect that leaving out one particular eigenvector will cause a decrease in the estimate of R^2 that is proportional to the relative importance of the eigenvalue associated with that eigenvector. Thus, under Brownian motion the expected proportion of variability in a trait explained by an eigenvector is equal to its relative importance in describing species divergence in the phylogeny, such that $\lambda_i \approx R^2_i$. In this formula, λ_i is the eigenvalue of the ith eigenvector extracted from a pairwise distance matrix along the branches of a phylogeny (which is inversely and linearly proportional to $\boldsymbol{\Sigma}$ defined above) and is expressed as a proportion of the trace of the double-centered phylogenetic distance matrix, whereas R^2_i is the coefficient of determination resulting from a PVR based on the ith eigenvector.

Based on the above reasoning, it is expected that progressively and consecutively adding eigenvectors to a series of sequential PVRs will generate a linear relationship between λ and R^2 (Fig. 1A). This curve, referred to here as a PSR curve, shows that the phylogenetic signal measured by PVR increases (y-axis in PSR curve) as more eigenvectors are used to represent the phylogeny (x-axis in the PSR curve) and model trait variation. The distribution of points along the PSR curve will not be uniform because of the nonlinear relationship between R^2 and the number of eigenvectors (the sum of the eigenvalues increases rapidly), and the distribution of λ_i depends on tree balance and stemminess (see Discussion section). The most important feature of the PSR curve is that the 45° line provides a reference for determining how fast a trait evolves relative to the rate expected under a Brownian motion model of evolution. Thus, if a trait evolves faster than expected under Brownian motion, the PVRs R^2 (the signal with respect to the amount of variation explained by the eigenvectors) would be larger than λ_i (the relative proportion of the phylogeny represented) because an eigenvector better explains
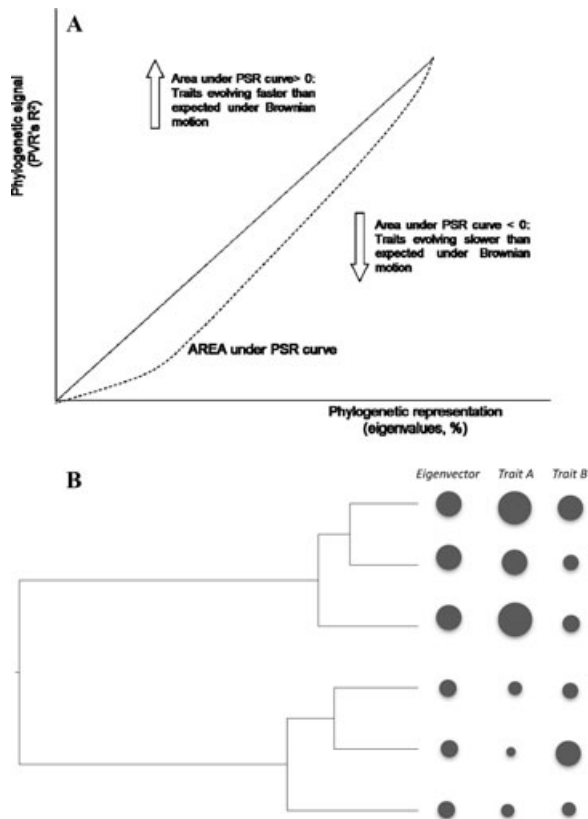
Figure 1. (A) Hypothetical phylogenetic signal-representation (PSR) curve derived from phylogenetic eigenvector regression with models progressively incorporating more eigenvalues. The shaded area under the 45° line is the PSR area, which measures deviation from Brownian motion. (B) Representation of the relative importance of trait variation among clades in respect to their divergence, expressed by an eigenvector. The size of the circles associated with each species represents the coordinates on an eigenvector and the trait values. It is possible to see that for trait A there is more variation among species than expected by the eigenvector (i.e., the divergence among the two clades), whereas in the trait B there is more random variation among species in the two clades and, therefore, less variation is accounted for by the eigenvector.

trait variability than expected at the corresponding phylogenetic distances (which define the time periods available for trait divergence under a Brownian model). Conversely, for a slowly evolving and more conserved trait, there would be only small differences among species or clades, and the variation described by an eigenvector would be smaller than its relative importance in describing phylogenetic distances (Fig. 1B).

Thus, the interpretation of deviations from the linear relationship between R^2 and λ is similar to the interpretation of the Blomberg's et al. (2003) K-statistic. Values of $K < 1.0$ indicate that related species resemble each other less than expected under a Brownian motion model of trait evolution, due to adaptive evolution independent of phylogeny or measurement error (and both

factors will cause R^2 to be smaller than λ in the PSR curve). Conversely, values of $K > 1.0$ indicate that species are more similar than predicted by the Brownian motion model, indicating a strong phylogenetic structure that appears as a higher R^2 in respect to λ in the PSR curve.

Deviations from Brownian motion can be measured in different ways using the PSR curve. The mean of R^2 and λ across the curve, the sum of their ratios, or the differences between them at each point of the curve can be used to describe it. These metrics, however, tend to generate nonlinear relationships with Blomberg's K, and we found that the area between the observed PSR curve and the 45° line (the shaded area in Fig. 1, henceforth referred as PSR area) is a better general metric for measuring deviation from Brownian motion. By convention, the PSR area below the 45° line is considered "negative" (i.e., signal smaller than expected under Brownian motion), whereas the PSR area above the 45° line is considered "positive" (i.e., signal stronger than expected under Brownian motion—see Fig. 1B).

It is useful to note that, beyond calculating a single metric that captures the deviations from a PSR curve (the PSR area), the curve allows one to determine where in the phylogeny (i.e., at which phylogenetic distances) these departures from Brownian motion occur for a given trait. This is possible because the profile provided by the PSR curve allows one to determine which eigenvectors increase disproportionately to the amount of explained trait variation.

SIMULATION ANALYSIS

We initially tested the above interpretation by using Brownian motion simulations (for a trait with zero mean and unity variance) and performing an analysis of the relationship between R^2 and λ. We successively increased the number of eigenvectors used to model trait variation in the analysis. In all 1000 simulations, the phylogenetic relationships among the 209 species were based on the terrestrial Carnivora supertree (Bininda-Emonds et al. 1999, 2007; see also Diniz-Filho et al. 2009), which was scaled so that phylogenetic distances from root to tips vary between 0 and 1. We also randomized values across species to produce a null model that shows the PVR results in the absence of phylogenetic signal. This phylogeny was used only as a reference for Brownian motion evolution and as a representation of a real topology. By using PCoA, eigenvectors were extracted from the double-centered phylogenetic distance matrix containing the pairwise distances between species. We did not square the distances to perform the PCoA (see Legendre and Legendre 1998), so we avoided distorting the representation of original phylogenetic distances among species by the eigenvectors, and we gave more weight to deeper branch lengths that were closer to the root of the phylogeny. Sequential PVRs were then performed for each simulated dataset (each dataset was a trait vector of length 209) using

1–150 eigenvectors (see Results). The first 150 eigenvectors explained 99% of the phylogenetic distance matrix. A PRS curve was produced by plotting the cumulative eigenvalues against the R^2 value for each simulation.

We also used more complex models of trait evolution to evaluate how a PSR curve captures different forms of departure from Brownian motion. O-U models with restraining forces α ranging from 2.0 to 10.0 in steps of 2.0 (for a phylogeny with branch lengths summing to 1.0—see Diniz-Filho 2001) were used to model trait variation under stabilizing selection (Felsenstein 1988; Hansen 1997; Martins and Hansen 1997; Martins et al. 2002; Hansen et al. 2008). To facilitate interpretation, we rescaled the α value from the O-U model to express the phylogenetic half-life ($t_{1/2}$), which is the time it takes for the trait value to move half the distance from the ancestral state to the primary optimum (Hansen 1997; see also Hansen et al. 2008). This is given by $t_{1/2} = \ln(2)/\alpha$, where α is the adaptation rate. A low value of $t_{1/2}$ is obtained if strong adaptation occurs, indicating that the trait changes very quickly to approach the adaptive peak. A high value of $t_{1/2}$ is obtained if adaptation is weak, indicating that the trait changes very slowly. We note that in Hansen et al.'s (2008) more recent model, the shifts in trait values track another trait evolving under Brownian motion, so signal and adaptive variation are correlated. However, because we are analyzing a single trait in our simulations, we used a primary adaptive optimum in the O-U process (Hansen 1997), and the statistical interpretation for the relationship between PSR area and half-life is that a low $t_{1/2}$ value is found when the species will not shift away from the peak, being thus strongly constrained throughout the phylogeny (the PVR R^2, or the PSR area, will be smaller when $t_{1/2}$ values are low). Although the α parameter of the O-U process and the associated phylogenetic half-life ($t_{1/2}$) do not actually measure phylogenetic signal, they do describe the shape of the relationship between interspecific variation in the phenotype and time since divergence between species. Thus, α is statistically related to departure from Brownian motion, which is detected with the PSR curve or Blomberg's K.

We also analyzed more complex patterns by using Brownian motion simulations after transforming branch lengths using different Grafen's (1989) ρ parameters (0.1, 0.5, 2.5, and 5.0). Values of ρ smaller than 1.0 tend to shrink deeper branches and lengthen those near the tips (thus simulating recent diversification of the trait), whereas values larger than 1 increase branch lengths near the root of the tree and simulate early diversification (Fig. 2).

We also calculate, for each simulation, Blomberg's K-statistic under Brownian motion using the package "ape" in the R programming environment (R Development Core Team 2010), and we correlate the K-values with PSR area. PSR curves and their areas were generated by using a sequential PVR algorithm implemented in the software PAM 0.9 (Phylogenetic Analysis in
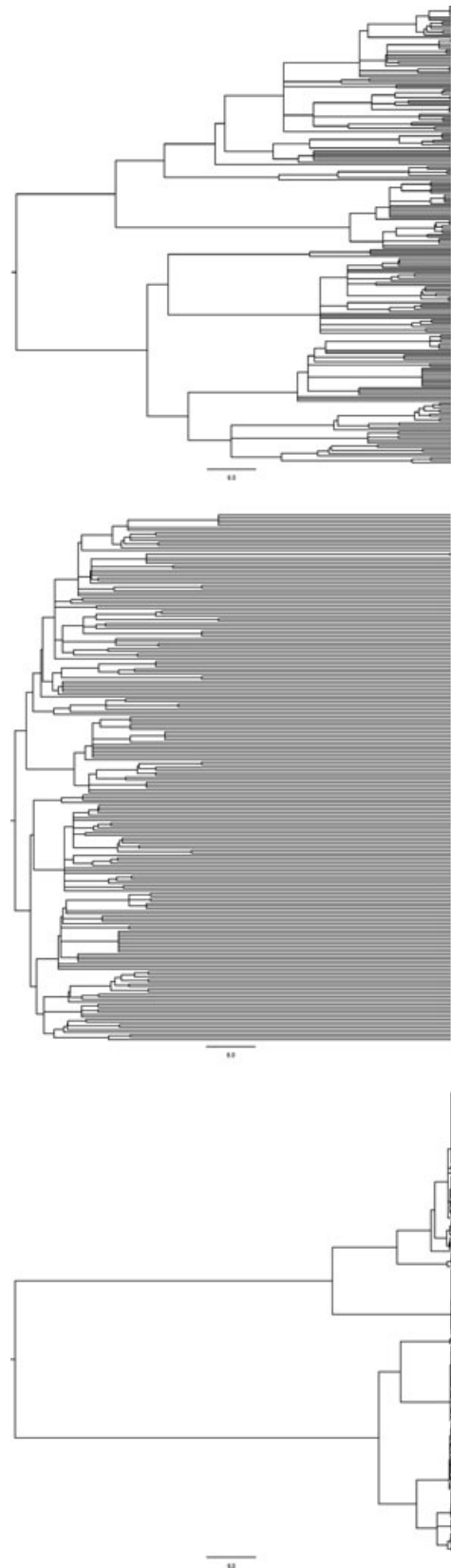

Figure 2. Branch lengths generated under different values for the Grafen's (1989) rho parameter (ρ), for a phylogeny with 209 species used to demonstrate the properties of the PSR curve.
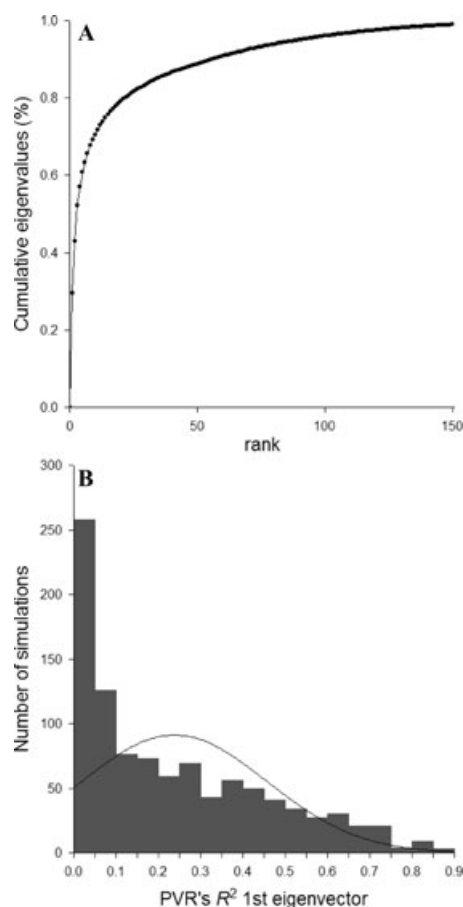
Figure 3. (A) Cumulative eigenvalues (%) and (B) frequency distribution of R^2 obtained under Brownian motion from 1000 PVRs using the first eigenvector only.

Macroecology; T. F. Rangel and J. A. F. Diniz-Filho, unpublished beta version available from the authors upon request). A script in *R* for calculating the PSR curve and area is also available from the authors upon request.

Results

The plot of cumulative eigenvalues (Fig. 3A) shows that the first eigenvector explains about 30% of the structure in the phylogenetic distances. The PVR R^2 based on the first eigenvector alone has a value of $23.7 \pm 21.8\%$, slightly smaller than the respective observed eigenvalue, although the distribution is right skewed (Fig. 3B). However, when performing sequential PVRs by successively adding eigenvectors to the model and generating the PSR curve, the mean relationship between R^2 and λ is strongly linear under Brownian motion, as expected, although there is also a large variation for the first eigenvalues, creating a polygonal shape for the relationship across the 1000 simulations (Fig. 4). Tests of this relationship are difficult because values corresponding to the increasing number of eigenvectors are not independent
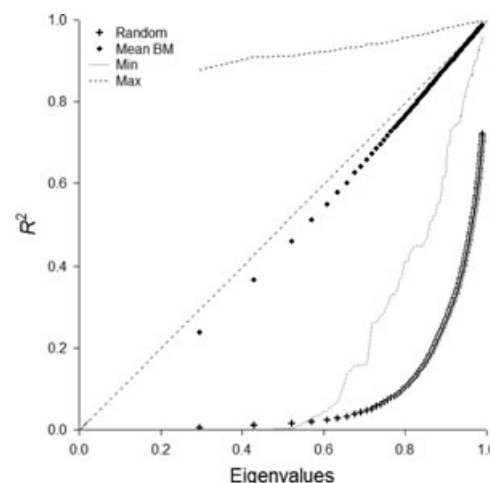

Figure 4. PSR curve under Brownian motion, including mean, maximum and minimum values obtained for 1000 simulations, and mean expected PSR curve in the absence of phylogenetic signal obtained by randomization of species values.

and distributions of R^2 for each λ are strongly skewed, but in general the slopes and intercepts do not differ greatly from 1 and 0, respectively. Notably, building the PSR curve in the absence of phylogenetic signal (randomizing values across species) produces a very different curve characterized by little or no increase in R^2 even when phylogenetic information accumulates along the abscissa of the curve (Fig. 4).

The mean value of Blomberg's K for the same data was 0.991 (about equal to 1.0, as expected under a Brownian motion model of trait evolution). However, the distribution was strongly right skewed (Fig. 5A), whereas the PSR area obtained from the curves was more symmetrically distributed (Fig. 5B). Because of the right-skewed distribution of K, we used a logarithmic transformation to normalize this metric so that the evolution under Brownian motion can be inferred when $\log(K)$ equals zero. There is a linear relationship between $\log(K)$ and PSR area (Fig. 6; $r = 0.873$; $P << 0.01$), and it is important to note that both metrics were centered on the expected value under Brownian motion (i.e., both $\log(K)$ and PSR area are equal to zero).

For the O-U processes, the R^2 values from sequential PVRs are smaller than expected based on the corresponding λ for the largest eigenvalues, which occur in the first steps of the PSR curve. An increase in the value of the O-U α parameter progressively moves the PSR curve away from the 45° line (and away from the predictions of the Brownian motion simulations; Fig. 7A) and increases the area into the "negative" direction. This means that higher levels of restraining force in the O-U model, corresponding to a low $t_{1/2}$ value in the Hansen et al. (2008) model, correspond approximately to a null pattern (in which phylogenetic signal is eliminated from the data—see Diniz-Filho 2001; Fig. 8).
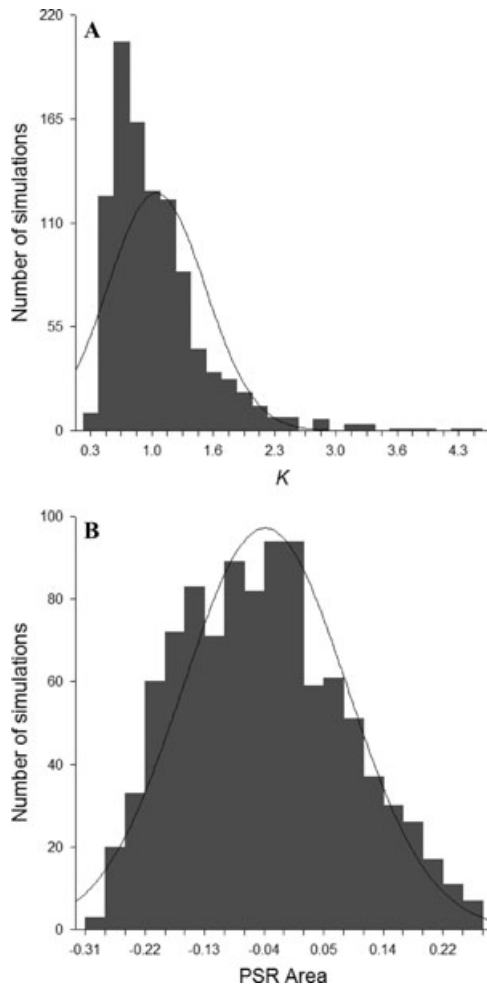
Figure 5. Frequency distribution of Blomberg's *K* and PSR area for Brownian motion models based on 1000 simulations.

Figure 6. Relationships between PSR area and Blomberg's *K*-statistics. Notice that a log *K* = 0, expected under Brownian motion, corresponds to PSR area equals to zero.

are affecting the data at any phylogenetic distance. As correctly pointed out by Rohlf (2001), a single PVR provides an $R^2 < 1$ only because some part of the phylogeny is missing. However, when this single R^2 is standardized by taking into account the amount of phylogenetic structure represented by the eigenvectors used to model trait variation, the ratio between R^2 and sum of the eigenvalues associated with these eigenvectors will approach 1.0, indicating that all trait variation is accounted for by phylogenetic relationships.

A ratio of 1.0 between R^2 and the associated eigenvalue (and a deviation area equal to zero if all successive PVR models are used to build the PSR curve) under Brownian motion is consistent with the results of other metrics for phylogenetic signal, such as Blomberg's *K* (Blomberg et al. 2003), Pagel's (1999) λ (not to be confused with the eigenvalues of phylogenetic distance, as used throughout this text) and Lynch's (1991) phylogenetic heritability h^2 derived from a mixed model (see Housworth et al. 2004). Indeed, Housworth et al. (2004) pointed out that Lynch's (1991) h^2 and the R^2 of partitioning methods (i.e., ARM) can be analytically derived from one another, although the relationship between h^2 and the original PVRs R^2 can be more difficult to establish exactly because of the eigenvector selection.

An advantage of the PSR curve over Pagel's λ or Lynch's h^2 is that the former can estimate phylogenetic patterns that are stronger than Brownian motion expectations (a necessary outcome to infer phylogenetic niche conservatism; see Losos 2008), which can also be detected using the *K*-statistic. Indeed, the PSR area is positively correlated with Blomberg's *K*, and they are both centered on their respective expectations under Brownian motion (i.e., zero for both PSR area and log(*K*)). A positive area, on the other hand, indicates that the R^2 values from multiple PVR analyses will tend to be above the proportionality line of the relationship between R^2 and λ, such that the phylogenetic eigenvectors explain more

On the other hand, Grafen's (1989) ρ parameters produced PSR curves below and above the expectation, corresponding to a process of early diversification (acceleration, such that the early clades tend to diverge more than expected early in the phylogeny) and more recent divergence alone, in which species tend to diverge from each other faster and eliminate the phylogenetic signal, as in the O-U process (Fig. 7B).

Discussion

PSR CURVE, PHYLOGENETIC SIGNAL, AND EVOLUTIONARY MODELS

We provide a new method to describe phylogenetic patterns in data and to infer how fast a trait has evolved in comparison with alternative evolutionary models, such as a Brownian motion or an O-U process. Our metric is related to the *K*-statistic described by Blomberg et al. (2003). Under a Brownian motion model of trait evolution, the mean expected metric derived from a PSR curve (the area) is equal to zero, indicating that no other processes
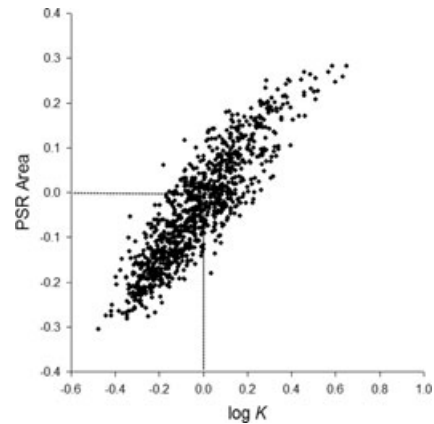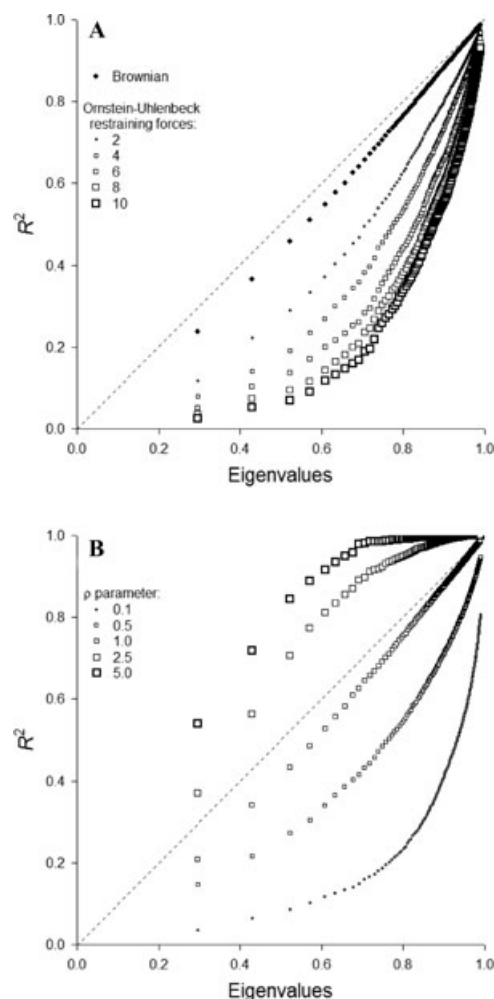
Figure 7. Mean R^2 from PVR under alternative evolutionary models, including O-U processes with increasing levels of restraining forces (from two to 10), and Brownian motion under transformed phylogenies according to Grafen's (1989) parameter (see Fig. 2), ranging from 0.1 to 5.

Figure 8. Relationship between PSR area (and 95% confidence interval) under O-U process and Hansen's et al. (2008) phylogenetic half-life, $t_{1/2}$, fitted using a logarithmic functions. Under Brownian motion, $t_{1/2}$ goes to infinity (because $\alpha = 0$), but for graphical purposes we set it to 1.0, which is the maximum distance allowed in our phylogeny.

of the trait than expected by Brownian motion. This is analogous to Blomberg's K when it is larger than 1.0 (or $\log(K) > 0$); when this condition is met, "... close relatives are more similar than expected under Brownian motion evolution" (Blomberg et al. 2003, p. 723).

It is important to note that the ability of eigenvectors to represent phylogenetic structure at distinct hierarchical levels depends on topology and stemminess (see Rohlf et al. 1990; Diniz-Filho et al. 2012). This effect is clearly visible in the distribution of the relative eigenvalues along the abscissa of the PSR curve. If, for example, the group of species under study is divided into two clades that diverged long ago, the first eigenvalue would be large because most of the variation in pairwise phylogenetic distances would be well represented by a single eigenvector whose scores would clearly differentiate the species into these two clades. On the other hand, when a strongly imbalanced phylogeny is
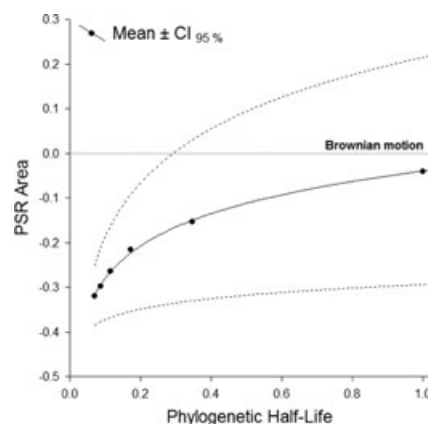
analyzed, the first eigenvector will ordinate the species along a gradient that measures the departure from the root. The eigenvalue associated with this eigenvector, however, would explain only a small portion of the phylogenetic structure due to its higher complexity. Blomberg's K-statistic is similarly affected by the topological structure of the phylogeny, as the denominator of the K-statistic represents the expected fit of a model (e.g., Brownian motion) for a given phylogenetic topology and stemminess.

Our general interpretation of the PSR curve is also supported when processes other than Brownian motion are considered. These other processes were simulated with a transformation of branch lengths to accelerate or decelerate evolutionary rates in different parts of the phylogeny. When using an explicit O-U process, the PSR curve falls below the expectation line of proportionality between λ and R^2, especially for the first few eigenvalues. Indeed, under an O-U model of trait evolution, there is an exponential relationship between divergence and time (Hansen and Martins 1996; Hansen et al. 2008). Although closely related species tend to be similar (i.e., positive autocorrelation), as temporal distances increase, species are gradually "pulled" toward an adaptive optimum, and trait variation at these deeper time scales thus becomes independent of the elapsed time since species divergence. Using Grafen's (1989) transformation to decelerate evolution is analogous to the O-U process and, as expected, the PSR curve produced consistent results. Increasing the Grafen's parameter accelerates evolution and, accordingly, the PSR curve lies above the expectation line of the Brownian motion model (i.e., positive PSR area; see Fig. 7B). We note, however, that all of the relationships discussed here give heuristic support to the PSR curve, and they do not ensure that the true evolutionary models can be unambiguously identified in real datasets. For instance, all

models tested have constant rates through time, and phylogenetic nonstationarity or multiple adaptive peaks could yield more complex signatures (e.g., Kozak and Wiens 2010; Diniz-Filho et al. 2010). Of course, this problem will arise not only in the description of patterns by a PSR curve but also when any metric is used to measure and describe phylogenetic signal (e.g., Blomberg's K-statistic and Pagel's λ).

Considering the strong theoretical foundation for generalized estimators (e.g., Grafen 1989; Rohlf 2001), we do not claim that PSR curves are better, more accurate, or more powerful than Blomberg's K-statistic (e.g., Hansen's et al. 2008; Kozak and Wiens 2010). Rather, we argue that the PSR curve can be interpreted in a similar way when describing phylogenetic signal or patterns in data. The correspondence between the shape of PSR curves and the K-statistic, as well as the behavior of the curve as a result of restraining forces of an O-U model, validate the new eigenvector approach proposed here. Also, the flexibility of PSR in describing patterns allows a better use of PVR as a variance partition technique (see below), improving the analytical options for selecting eigenvectors in more complex designs for comparative analyses (e.g., Desdevises et al. 2003; Diniz-Filho et al. 2007, 2009; Kuhn et al. 2009; see below).

Moreover, it may be advantageous to describe patterns in trait variation at distinct levels of the phylogeny, as opposed to describing them with a single number (see Diniz-Filho 2001; Ollier et al. 2006). This may be especially important when more complex patterns are found in empirical data (i.e., different levels of trait lability, nonstationary patterns, or O-U with multiple adaptive peaks—see Diniz-Filho et al. 2010; Kozak and Wiens 2010). In this case, although the PSR curve is not built based on any a priori evolutionary model, it is a useful way to visually assess where the deviations from the Brownian motion model happen across the phylogeny. More importantly, one can estimate the phylogenetic distance at which these deviations occur and determine if they are concentrated in particular regions of the phylogeny.

IMPLICATIONS FOR EVALUATING CORRELATED EVOLUTION AND PATTERNS IN THE S-COMPONENT

We believe that the PSR curve, as a new analytical strategy, can also shed light on some of the previous analyses based on PVR S-components, which have been used to study correlated evolution and to reveal geographical patterns in adaptive variation (e.g., Diniz-Filho and Torres 2002; Diniz-Filho et al., 2007, 2009).

The PSR curve shows that, if a trait evolves under Brownian motion, PVR may ignore important phylogenetic information (Rohlf 2001). In this case, the problem is that the S-component estimated by PVR may contain a significant proportion of phylogenetic signal, as the PVR does not incorporate all the information contained in the phylogeny. Thus, when testing correlations between S-components obtained from two traits evolving independently, the Type I error rate may be inflated (although strongly reduced compared to nonphylogenetic correlations). This explains why previous simulation studies have failed to find correct Type I error rates, regardless of the approach used for eigenvector selection (Diniz-Filho and Torres 2002; Martins et al. 2002; Freckleton et al. 2011).

However, when more complex and nonlinear models of evolution are applied to the data, the idea of using only part of the eigenvectors to describe phylogeny and model trait variation makes much more sense because not all of the eigenvectors are equally useful for modeling trait variation. This effect is captured by the PSR curve, and it can be assessed by comparing the intervals along the abscissa of the PSR plot. As discussed above, under an O-U process, the PSR curve falls below the line that represents the expectation of a Brownian motion model (see Fig. 7B). Additionally, the shape of the PSR curve shows that the first eigenvectors are less important for explaining trait variation than those describing relationships at smaller phylogenetic distances. When analyzing empirical data, more complex patterns frequently emerge, and, in these cases, the PSR curve is useful for guiding the selection of eigenvectors for use in PVR to model trait variation. Alternatively, an iterative search that minimizes autocorrelation structure in the S-component (see Griffith and Peres-Neto 2006; Diniz-Filho et al. 2012), potentially picking eigenvectors that create peaks in the PSR curve, can also be used to implement an automated eigenvector selection and obtain valid estimates of the S-component.

The most important diagnostic measure for PVR is not the amount of variation explained (i.e., the R^2), but rather the independence of residuals (S-component), as originally pointed out by Diniz-Filho et al. (1998) and recently stressed by Diniz-Filho et al. (2012). This idea was originally proposed by Gittleman and Kot (1990) for evaluating the effectiveness of Cheverud et al's. (1985) ARM, and it was based on the use of Moran's I autocorrelation coefficient to test the independence among species for the S-component (see also Pavoine et al. 2007). If the S-component does not contain phylogenetic signal, then the partition was effective and the S-components can be reliably used for statistical inference (see Desdevises et al. 2003). Of course, the PSR curve developed here shows that, if the traits evolve under Brownian motion models, a very large portion of the eigenvectors (in theory, all of them) should be used to model trait variation using PVR. Even so, if the Moran's I values indicate that the S-component is not autocorrelated, containing only random noise and measurement error, it is unlikely that the S-component displays any geographical pattern or interspecific correlation with other traits (see Diniz-Filho et al. 2007, 2009).

Beyond the PSR curve proposed here, and mainly in the context of correlated evolution among traits, previous simulation analyses showed that PGLS tends to outperform any other

comparative method, including PVR, in terms of Type I error rates and parameter estimation (see Martins et al. 2002; Laurin 2010; Freckleton et al. 2011). Although the effectiveness of PVR depends on both the geometry of relationships and the evolutionary models used, as pointed out above (see also Diniz-Filho et al. 2012), there are some situations in which using methods that incorporate phylogeny into model structure (sensu Martins and Hansen 1997) can be advantageous over model-based methods (e.g., Desdevises et al. 2003; see also Griffith 2003; Griffith and Peres-Neto 2006 for a discussion in the spatial context). As pointed out by Griffith & Peres-Neto (2006), for Moran's eigenvector mapping used in spatial analyses, "the class of methods presented is flexible enough that it can be applied to any type of distribution under general as well as generalized linear model (e.g., logistic/binomial and Poisson regressions) procedures." Indeed, using eigenvectors to express the phylogeny makes it possible to apply other analytical strategies that are not as straightforward when PGLS is used, including (1) the partitioning of the variation of a trait into components that can be uniquely attributed to phylogeny, ecology, and to the common influence of these two factors (an explicit measure of phylogenetic niche conservatism; see Desdevises et al. 2003); (2) to map the S- and P-components of traits to study the phylogenetic components of ecogeographical rules (Diniz-Filho et al. 2007, 2009; Ramirez et al. 2008; Terrible et al. 2009; Ollala-Tárraga et al. 2010; but see Diniz-Filho et al. 2012); (3) to relate these components with environmental variation at the assemblage level (Kuhn et al. 2009; Pillar and Duarte 2010); (4) to estimate phylogenetic species diversity at multiple phylogenetic levels (e.g., Diniz-Filho et al. 2011); and (5) to deal empirically with more complex phylogenetic patterns that cannot be easily described by processes such as Brownian motion and some forms of O-U (i.e., phylogenetic nonstationarity—see Diniz-Filho et al. 2010).

Concluding Remarks

We propose here that, rather than using a single R^2 from PVR to measure phylogenetic signal, a more reliable way to understand phylogenetic patterns in comparative data analyses is to use a PSR curve. When high-quality phylogenetic information is available, the PSR curve can be interpreted in the same way as Blomberg's K-statistic. Our results indicate that, despite Rohlf's (2001) criticism, the R^2 derived from a single PVR can be compared with other "model-based" metrics for phylogenetic signal when it is rescaled by the corresponding eigenvalues of the eigenvectors used to model trait variation. Also, as in any autocorrelation-like approach, the measure of signal is strongly dependent on the way distances are defined or represented in the models. As pointed out by Freckleton (2009), it is important to consider plurality when

dealing with comparative methods, and this study shows that the eigenvector approach, used with the PSR curve, is a useful and flexible tool for describing phylogenetic patterns in data.

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Associate Editor: G. Marroig

Supporting Information

The following supporting information is available for this article:

Table S1. Comparative patterns of phylogenetic signal in 1000 simulations by Brownian motion, using Blomberg's K-statistics, the mean ratio between PVRs R^2 and eigenvalue, the PVRs using eigenvectors that explain 95% of the phylogenetic structure and the PSR area.

Table S2. Mean coefficients of determination (R^2) of sequential PVR models built with eigenvectors with increasingly eigenvalues, forming the PSR curve, for Brownian motion and Ornstein-Uhlenbeck (O-U) models, based on phylogenies transformed with Grafen's parameter (G) and on a pure randomization of tip values.

Supporting Information may be found in the online version of this article.

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