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Statistical inference of correlated evolution between macroecological variables using phylogenetic eigenvector regression

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Abstract. *In this paper, a recently developed method for comparative data analysis, called phylogenetic eigenvector regression (PVR), was applied to macroecological data of five groups of mammals and birds from South America. In these data sets, the relationship between geographic range size and body length was functional or generated a constraint envelope in the bivariate space, in which minimum geographic range size increased with body length. Using the PVR, eigenvectors were extracted from the double-centered phylogenetic distance matrix, derived from phylogenies based on different sources. These eigenvectors were used as predictors in a multiple regression in which the response variables were body length and geographic range size. Body size usually displayed significant phylogenetic inertia, measured by the coefficient of determination (R^2) of the PVR regression model. The partial correlation between these two variables, after controlling for phylogenetic eigenvectors, varied in the different groups. Only for the primate data set, with 50 species, the correlation disappeared after controlling phylogenetic inertia in both variables. For the owl data set (29 species), the constraint envelope was transformed in a significant functional relationship after using the PVR. One thousand simulations assuming a Brownian motion pattern of phenotypic evolution, with a parametric correlation of input equal to zero, permitted to calculate the true Type I error of the method at 5% as being around 10% for most data sets. This was considered to be satisfactory in comparison with other methods, specially with the non phylogenetic standard correlation (TIPS). Power curves of PVR were also estimated for all data sets, using 5000 simulations with input correlations ranging from 0.20 to 0.95, and indicated a relatively low statistical power when samples sizes are smaller than 25 species. In general, the PVR method works fine with macroecological data and the results supported the importance of controlling for phylogenetic patterns before using ecological or evolutionary mechanisms to explain geographic range size - body size relationships.*

Introduction

In the last 10 years, there has been an increasing interest in the historical components of ecological and life history traits and their relationships. This interest stimulated the continuous application and development of new comparative methods in different areas of ecology and evolutionary biology (Harvey and Pagel 1992, Martins and Hansen 1996). As a consequence of these methodological and conceptual advances, some recent papers (Taylor and Gotelli 1994, Letcher and Harvey 1994, Gaston and Blackburn 1996a,b, Murray et al. 1998, Ruggiero and Lawton 1998, Pyron 1999) applied these methods in the new field of macroecology, which evaluates the relationships among complex ecological variables (usually body size, geographic range size and population density), measured for multiple species on a continental scale (Brown and Maurer 1987, 1989, Brown 1995, Maurer 1999).

Since these macroecological relationships are usually established using interspecific data, they are subjected to common statistical problems of comparative data. Most evolutionary processes generate phylogenetic structure in data that, in turn, cause a lack of independence among species (Hansen and Martins 1996). This structure increases the Type I error rate of standard correlation analyses (i.e., using Pearson correlation coefficient) and so comparative methods are necessary to avoid incorrect interpretations of these relationships. More importantly, the comparative methods are designed to estimate the intrinsic correlation between the two traits, that is the correlation between processes of change across the phylogeny and then could be better interpreted in an adaptive sense (Martins and Garland 1991, Martins 1996). Indeed, Blackburn and Gaston (1998) recently pointed out that the control of phylogenetic trends is, in fact, a first step before inferring which ecological mechanisms are responsible for the relationship between macroecological variables. In a more general context, Brown (1999) recently discusses that a major emphasis in macroecological analyses have been in the establishment of patterns, but not in discovering the underlying ecological and evolutionary process.

Gaston and Blackburn (1996a) recently proposed four different (but not mutually exclusive) mechanisms that could explain the positive correlation between geographic range size and body size:

1. *The minimum viable population size model,* also called Brown's model - minimum geographic range size is correlated with body size because large species require more energy and so must use a large area of the environment to keep viable population densities. Small geographic range of large species implies in higher interspecific competition, low local population density and, therefore, higher probability of extinction;
2. *Realized: potential geographic range sizes* - minimum geographic range size is correlated with body size because larger species disperse more rapidly and successfully than small species, or because these larger species are evolutionary older and had longer periods to disperse and colonize most of its potential geographic range;
3. *Homeostatic and environmental variabilities* - species with large body size are able to maintain homeostasis over a wider array of conditions than a small-bodied species. If larger geographic ranges enclose greater environmental variability, then only larger species will be able to maintain these ranges;
4. *Latitudinal gradients in body size and geographic range* - when these gradients exist (called Bergmann's and Rapoport's effects, respectively) the correlation between the two variables can be a simply indirect effect of a common spatial structure.

It is important to note, however, that the mechanisms (2) and (4) do not imply necessarily in a "true" ecological relationship between geographic range size and body size, in an adaptive sense, because the relationship is only an artifact of common patterns of these two traits across the phylogeny and geographic space. In terms of the mechanism (2), it would be important to test if species analyzed arrived recently in the study area and so did not occupied its entire potential range yet (which is in fact difficult to estimate empirically), or if there is a phylogenetic structure in body size, in terms that larger species are evolutionary older. In terms of mechanism (4), it would be important to search for latitudinal clines in body size and geographic range size (Murray et al. 1998). So, to test the mechanisms (1) and (3), which imply a real adaptive ecological response in geographic range due to changes in body size throughout the evolution, it is important to control both phylogenetic and spatial patterns in data. These two mechanisms can then be considered as primary causes for the relationship

The analysis of comparative data in an explicit phylogenetic context has been widely done by means of Felsenstein's (1985) phylogenetic independent contrasts method (Garland et al. 1992, Martins and Hansen 1996). This method assumes that traits evolution follows a Brownian motion pattern, or at least that statistical transformations in the branch lengths of the phylogeny could be used to avoid violations in this assumption. In Brownian motion, the interspecific variance increases linearly with time since divergence and many evolutionary models, specially random changes by genetic drift and large-scale unidirectional trends, generate this linear pattern (Hansen and Martins 1996).

Although phylogenetic independent contrasts possesses very good statistical performance when all assumptions are met (Martins and Garland 1991, Martins 1996), it works poorly when traits show even moderate deviations of Brownian motion (Díaz-Uriarte and Garland 1996). This usually occurs with macroecological traits, specially geographic range size and population density, which are more "plastic" and do not show clear phylogenetic structure, when compared with body size (Brown *1995*, Gittleman et al. 1996). Although branch length transformations can be used to correct these problems (Garland et al. 1992), in this case the phylogenetic contrasts become simply a statistical approach, loosing its interesting characteristic of being an evolutionary model-based analysis (Martins and Hansen 1996, Butler et al. 2000). So, it would be important to consider and test the performance of other phylogenetic comparative methods, sometimes based on other conceptual and statistical assumptions.

In this paper we applied a new comparative method developed to estimate phylogenetic inertia and evolutionary correlations, called phylogenetic eigenvector regression (PVR) (Diniz-Filho et al. 1998, 1999), to evaluate the geographic range size - body size relationships in five groups of South American birds and mammals. In all these data sets, significant phylogenetic patterns were found for at least one trait, in such a way that standard correlation analyses may be biased. We also assessed the robustness of this new method in each situation by simulation procedures using Brownian motion that permitted to evaluate its true Type I error and statistical power in the specific conditions of each data set.

Materials and Methods

Data sets

We analyzed the geographic range size - body size relationship for five groups of mammals and birds from South America. In these data sets, a significant phylogenetic pattern was found at least for body size, that could then disturb the macroecological analyses using a non-phylogenetic approach. We used data compiled from the literature, with distinct phylogenetic structures (tree topologies) and with different sample sizes.

For mammals, data were extracted from Eisenberg (1989), Redford and Eisenberg (1992), Fonseca et al. (1996), Emmons (1997) and Wilson and Reeder (1993). For Plathyrrini primates (PRIM), Hystricognata rodents (HYSTR) and Carnivora (CARN), the phylogenetic relationships were obtained, respectively, from the composite estimate of Purvis (1995), from the immunological distances of Luckett and Hartenberg (1986) and from Wayne et al. (1989, 1997).

For birds, data for Strigiformes (STRIG) and Falconidae (FALL) were extracted from Dunning (1987), Sibley and Monroe (1990, 1993) and Sick (1997). In the two cases, the phylogenetic relationships were derived from Sibley and Ahlquist (1990) DNA-DNA hybridization analyses. Detailed data matrices and phylogenetic structures used in each analysis are available from the main author upon request.

In all cases, geographic range size was measured by the number of squares in a grid of 135 km of side, and assessed by redrawing distribution maps of each species in an standardized scale (1:35.000.000), using polyconic projection. Body size was measured as body weight or length, depending on the better available data for each group, in terms or number of species (usually body mass for mammals and body length for birds). Both variables were log transformed prior to the analysis to correct heterocedasticity and allometry, specially in body size data, and then analyzed using the PVR method. The standard Pearson correlation (called "TIPS" by Martins and Garland 1991*)* was also used to evaluate geographic range size - body relationships.

The PVR method

The general idea of partition methods in comparative data analysis (sensu Harvey and Pagel 1992*)*, in opposition to methods based on phylogenetic contrasts, is that the total variation in a quantitative trait (T) can be partitioned into two components, such that

$$T = P + S$$

where P is the phylogenetic component, which contains the part of variation that is shared with the other species, and S is the specific component, which contains the variation unique to each species. The correlation between S components or between S component and environmental variation must reflect Darwinian adaptations, i.e., true correlated responses across evolution independently of the phylogenetic constraints in the traits, that then can be better interpreted in an adaptive sense. In a more statistical sense, the correlation between specific components estimates the “input” or “intrinsic” correlation between the two processes of stochastic evolution (Martins and Garland 1991). The proportion of phylogenetic variation in data, called phylogenetic inertia, is given by the ratio P/T.

Different methods can be used to partition T into P and S components, for each variable. The original and most commonly used method is the autoregressive method (ARM) (Cheverud et al. 1985, Gittleman and Kot 1990, Martins 1996), that is given by

$$\mathbf{Y} = \rho\, \mathbf{WY} + \varepsilon$$

where **Y** is the vector of trait analyzed, p is the autoregressive coefficient, **W** is the weighting matrix, inversely related to phylogenetic distances between pairs of species (Gittleman et al. 1996), and E is the vector of the residuals of the model. The P component is given by the term ρ**WY**, and the S component is estimated by the residuals of the model. The autoregressive coefficientp usually varies between 1.0 and -1.0, and must be obtained by a maximum likelihood procedure.

The other method recently developed to obtain P and S components is the phylogenetic eigenvector regression (PVR) (Diniz-Filho et al. 1998). This method starts by the eigen-analysis (Sneath and Sokal, 1973) of the double-centered phylogenetic distances (**Q**) among species, which was in turn derived from phylogeny. Each element of the **Q** matrix is then given by

$$Qij = Bij + M - (Si. + S.j)$$

where $S_i.$ e $S_j.$ are rows and columns means, and M is the mean of all distances B_{ij}. The elements Bijare given by $-1/2D^2_{ij}$, where D_{ij}; are the original phylogenetic distances among species. The eigenvectors of **Q** are called principal coordinates and express the interspecific variation across multivariate phylogenetic space. These eigenvectors are used then as predictors in a standard multiple regression of the form

$$\mathbf{Y} = \mathbf{X}\beta + \varepsilon$$

where **X** is the matrix with the eigenvectors of **Q** and β is the vector with partial regression coefficients (Sokal and Rohlf 1995). The number of eigenvectors to be used in the analysis (k) can be estimated by analyzing the distribution of eigenvalues, by different methods. Previous work indicated that comparing eigenvalues with a broken-stick distribution furnishes the better results with less computational effort. In the PVR, the estimated values of Y by the regression model (**Y’**) express the P component, while the residual (ε=**Y**-**Y’**) estimate the S component. The coefficient of determination of the method (R’) indicates the part of the variance that can be attributed to the phylogenetic structure in data, that can be tested with standard F-statistics (Sokal and Rohlf 1995). The main advantages of the PVR in relation to the autoregressive method are the simplicity in the statistical test of phylogenetic structure (that can be performed using standard F distribution) and the enhanced estimation capability at low sample sizes (Diniz-Filho et al. 1998).

In this paper we used the PVR method to evaluate phylogenetic inertia in each variable and to assess the true (intrinsic) evolutionary correlation between them, using the residuals (S components) of the model. The correlation between the residuals of the PVR method applied to each trait is in fact a partial correlation between body size and geographic range size, keeping the phylogenetic eigenvectors constant. The t test that furnishes the significance level of this partial correlation is given by

$$t = r\rho \,[\, (n - 2 - k) / (1 - r\rho^2) \,]^{½}$$

were r_p is the partial correlation between the two variables, keeping the k predictors (in this case, the phylogenetic vectors) constant (Sokal and Rohlf 1995). This t-value is tested with n-2-k degrees of freedom.

Simulations and statistical performance of PVR

It is important to note, however, that the comparative methods can be sensitive to violations in their assumptions, specially by deviations of linearity in data and to the own characteristics of the phylogeny used, in terms of balance, number of species, branch lengths distribution and politomies. Gittleman and Luh (1992) recommend so that the best approach to check eventual violations in the assumptions of the methods is to test each analysis using simulation procedures, defining the statistical properties of the method applied to a given specific data set. So, simulation procedures described by Martins and Garland (1991) and Martins (1996) were run for each data set, using the PDSIMUL program of the package PDAP (Jones et al. 1993).

The first step of this procedure was to simulate evolution by Brownian motion of two characters over the phylogeny of each group, with means and variances equal to those in real data set, varying the input correlation between them (Martins and Garland 1991). Simulated evolution begun at the base of each phylogeny, with the average values of each trait, and then random changes were added to the previous values at each step in time, following the topology of the phylogeny until trait values were obtained for each species. This stochastic process generates a linear relationship between interspecific variance (V_B) and time since divergence (t) in such a way that

$$V_B = \sigma^2 t + s$$

where σ^2 is the variance of changes at each time step (the rate of evolution) ands is the residuals of the linear model, caused by random fluctuations around the divergence pattern (Hansen and Martins 1996).

The input correlation in the simulations is the parameter of the “true” evolutionary correlation between the two traits across the simulations, i.e., the changes of one trait in response to changes in the other at each time step. These changes are sampled from a bivariate normal distribution with a known correlation parameter and are thus independent of the tree topology and of the ancestral states values at each step.

In this study, 1000 simulations were performed for each phylogeny, using six parameters for the input correlation: 0.0, 0.2, 0.4, 0.6, 0.8 and 0.95. The data generated by the simulations were then analyzed with the PVR and TIPS, using a program written in Basic language specially for these analyses by one of us (A.S.G.C.) and available from the main author upon request. When the input correlation in the simulation was equal to zero, a count of how many analyses using PVR or TIP method (out of 1000) furnished significant correlation at a given critical level (a false response, say, at the 5 % level) permitted to estimate the true Type I error at this significance level This is the frequency that ones reject the null hypothesis when, in fact, this hypothesis is true. On the other hand, using an input correlation larger than zero permitted to evaluate the value of 1-β (statistical power), where R is the Type II error, i.e., the frequency of non-significant correlations recovered by the method when in fact it exists. The R is given simple by counting the number of non-significant correlations found in the simulations when the parameric input correlation was different from zero. Because of the inflated Type I errors caused by the phylogenetic structure in the data generated by Brownian motion, the critical values in the null distribution of correlation coefficients (defined when using input correlation equal to zero) are usually larger than the tabulated ones. These critical values of the null distribution must then be used as a reference to the estimate of β (instead of the tabulated critical values), allowing a comparison among methods and avoiding an inflation in the statistical power simply because, for a given Type I error, the critical values are smaller than the real ones (Martins 1996).

Results and Discussion

Basic descriptive characteristics of the PVR analyses of the five data sets are shown in Table 1, including the number of eigenvectors used in the multiple regression, their relative explanation (cumulative associated eigenvalues) and the correlation between original phylogenetic distances and the distances in the reduced space of the eigenvectors. In all but one data set this correlation was larger than 0.90, indicating that eigenvectors represent well the phylogenetic structures. In all cases, cumulative eigenvalues explain more than 75% of variation in the phylogenetic distances.

Phylogenetic inertia was detected for body size variation in the five groups analyzed, but only in the PRIM data set a significant phylogenetic inertia was found for the geographic range size. Under Brownian motion, high R^2 values are found in PVR based on these phylogenies, but only for PRIM and STRIG data sets the observed phylogenetic inertia in body size is larger than the median of the distribution of R^2 obtained under Brownian motion. All R^2 values for geographic range sizes, except in PRIM data set, are smaller than the median value under Brownian motion.

These relatively low R^2 values are an initial indication that more complex microevolutionary processes are acting in these traits, reducing phylogenetic inertia in relation to the expectation under a simple null model of phylogenetic divergence. Indeed, previous work suggests that body size is a more constrained variable, being better modeled by an Ornstein-Uhlenbeck stochastic process, that produces exponential relationships between interspecific variance and time since divergence (Gittleman et al. 1996, Hansen 1997, Diniz-Filho and Vieira 1998). On the other hand, geographic range size, as many other ecological and life-history traits, is a much more “plastic” trait, being usually strongly influentiated by short time scale environmental variation, and will not follow a null model of evolution, as modeled by Brownian motion (Gittleman et al. 1996). These results are important because they clearly show that, if macroecological relationships are to be analyzed using Felsenstein’s (1985) phylogenetic independent contrasts, as in many recent papers, there will be a violation of the basic assumption of Brownian motion. In this case, complex branch length transformations, such as those suggested by Garland et al. (1992), must be used in order to reduce bias in estimating the true evolutionary correlation between traits. However, for the PVR or autoregressive method, this relatively low inertia implies that residuals (used to estimate the correlations) are similar to the original trait values, in such a way that they tend to approach the standard correlation analyses, with a small bias. Also, since these two methods do not explicitly assume any evolutionary models, they are less sensitive to these different processes in the macroecological traits.

The standard Pearson product-moment correlations between original variables for the five data sets (TIPS) (Table 2) indicate that there is a significant relationship between geographic range size and body size for the 3 mammal data sets. In one of the groups of birds (STRIG), there seems to exist a triangular constraint envelope, as predicted by the minimum viable population model of Brown and Maurer (1987, 1989). For the FALC data set, no clear pattern (functional relationship or constraint envelope) was observed. So, in four of the data sets analyze, an ecological or evolutionary mechanism to explain this relationship could be invoked, but before accepting them it is necessary to take into account the phylogenetic effects previously discussed, specially in body size.

The simulation analyses confirmed that the true Type I error for the TIPS method is usually much higher than the assumed 5% (Table 2), reaching up to 44% in the CARN data set. When a data set is analyzed with TIPS there is a hidden assumption that all species are statistically independent, indicating, in a biological context, that all species evolved simultaneously from a single ancestor, at the same time (the so-called “star phylogeny” - Martins and Garland 1991). Obviously, this assumption is wrong for most traits and groups of organisms and this is the reason why the comparative methods are usually necessary in these cases.

For three of the five data sets analyzed, there was no qualitative changes in the correlation between body size and geographic range after using the PVR to correct for phylogenetic effects (but this includes the FALC data set, in which no relationship between original traits was previously found) (Table 2). For the STRIG data set, the correlation between the residuals of the PVR becomes

Table 1. General parameters of the Phylogenetic Eigenvector Regression (PVR) and results regarding phylogenetic inertia for the macroecological analysis of the five data sets of South American mammals and birds. For each data set, *n* refers to number of species, *k* the number of eigenvectors in the PVR, λ the cumulative eigenvalues associated with the eigenvectors and *Rc* is the correlation between original phylogenetic distances and distances in eigenvector space. *Phyl. Inertia* refers to the R^2 of PVR for body size (BS) and geographic range size (*GRS*), while R^2_{MED} is the median R^2 obtained with 1000 simulations of evolution under Brownian motion. *NF* is the proportion of significant PVR regressions (according to F-statistics) out of all simulations.

Data set	n	k	λ(%)	Rc	Phyl. Inertia		R^2_{MED}	NF(%)
					BS	GRS		
PRIM	50	5	77.23	0.786	0.756*	0.412*	0.389	82.9
CARN	22	4	90.05	0.972	0.573*	0.180	0.848	95.5
HYSTR	20	4	80.66	0.901	0.457*	0.390	0.692	82.2
STRIG	29	4	78.50	0.973	0.824*	0.213	0.535	83.2
FALC	18	2	77.95	0.947	0.351*	0.071	0.550	75.9

* $P<0.05$

Table 2. Results of the analysis of correlated evolution between geographic range size and body size for each data, using TIPS and PVR with original data and simulations. α (5%) is the true Type I error of each method at 5%. For the PVR, $r\rho$ and *t* refers to correlation and t-test, respectively, of relationship between regression residuals (partial correlation between the two traits keeping the eigenvectors constant). The *t critical* value was derived from the null distribution obtained by the simulations (using input correlation equal to zero) and was used to assess statistical power of PVR.

Data set	TIPS		DF[1]	r_P	t	PVR	
	R	α (5%)				α (5%)	$t_{critical}$
PRIM	0.462*	27.0	43	-0.063	-0.414	9.2	2.393
CARN	0.513*	43.9	16	0.486	2.224*	11.8	3.054
HYSTR	0.841*	23.1	14	0.803	5.041*	17.3	3.003
STRIG	0.299	21.7	23	0.399	2.087*	10.5	2.629
FALC	-0.269	31.0	14	-0.097	-0.365	10.0	2.583

1. *DF* is the degree of freedom of the *t*-test for the partial correlation and is given by n–2–k, for each data set.

* $P<0.05$

significant, indicating that the constraint envelope found in the original data was transformed into a functional relationship after controlling for the phylogenetic effects. For the PRIM data set, the relationship disappears after controlling for the phylogenetic inertia, which was significant in the two traits.

Although some papers reported significant geographic range size - body correlations even after controlling for phylogenetic effects, in some cases the relationship tends to disappear after this control (see Gaston and Blackburn 1996a). According to Gaston and Blackburn (1996a) and Murray et al. (1998), it is difficult to achieve a consensus about the mechanisms involved and about the expected relationship in different organisms and spatial scales. However, there is an agreement that ecological models, such as Brown's minimum viable population model or Gaston's environmental heterogeneity model, should be invoked to explain the relationship only if spatial and phylogenetic trends in data are ruled out (Blackburn and Gaston 1998). In the FALL data set, for example, only a small sample of the species in South America were analyzed due to the low number of genera available in the phylogeny of Sibley and Ahlquist (1990). Adding more species can produce a qualitative change in the results obtained here for this group.

The simulations used in this paper also permitted to test if the estimates obtained using the PVR are accurate. Repeating the analyses of simulations with the input correlation equal to zero using the PVR, it was possible to assess the true Type I error of the method, in each case (Table 2). The Type I errors at 5 % were in fact reduced when compared with those obtained with TIPS, being usually around 10%. For the CARN data set, the true Type I error of the PVR was high and around

17 %, but it is important to consider that error of TIPS, in this case, was almost *44* %. Although the values of true error of the PVR are not very close to 5 %, they are similar to those obtained with other comparative methods, such as autoregressive method (Martins 1996). This value is also close to the one obtained with the phylogenetic independent contrasts when Brownian motion is violated (Diaz-Uriarte and Garland 1996). As previously discussed, these violations are indeed expected when analyzing macroecological traits such as those analyzed here. This relatively large Type I errors obtained with the comparative methods indicate that they were not able to remove all biases caused by the phylogenetic structure in the data, but the reduction of these values in relation to TIPS support the general idea that analyzing data with comparative methods always furnishes better results than ignoring phylogenetic structure (Losos 1999, Martins 2000).

The power curves of the PVR for the five data sets (the [1-β] values against input correlation) (Figure 1) indicated that sample size is the most important factor affecting statistical power, as previously found for other methods (Martins 1996). For a parametric input correlation of 0.40, the chance of rejecting the null hypothesis when it is not true was only around 65% for the PRIM data set, with 50 species, but is smaller than 20% for all other data sets, all with less than 30 species. This indicates that with a relatively weak correlation, such as those observed here between body size and geographic range size, there is a great chance that the correlation goes undetected. So, as previously found for all other comparative methods (Martins 1996, Diaz-Uriarte and Garland 1996), relatively large sample sizes must be used in order to avoid high Type II errors when analyzing macroecological relationships. In biological terms, large number of species must be analyzed to permit a clear evaluation of the ecological and evolutionary mechanisms underlying these relationships. Slight interactions between the power curves, involving specially the STRIG data set, however, could be explained by differences in topology and branch length distribution, affecting the statistical performance of the PVR, as previously shown (Diniz-Filho et al. 1998).

It is also important to note that the results of the simulations to check for statistical performance of PVR in analyzing correlated evolution are in fact conservative, because, as previously discussed, macroecological data hardly fit Brownian motion as a evolutionary model. Since more complex evolutionary models, such as O-U process (Hansen and Martins 1996), reduces phylogenetic pattern in data, the Type I errors found here for PVR are expected to be lower in real data sets than those obtained here. Further investigations and simulation analyses are needed to

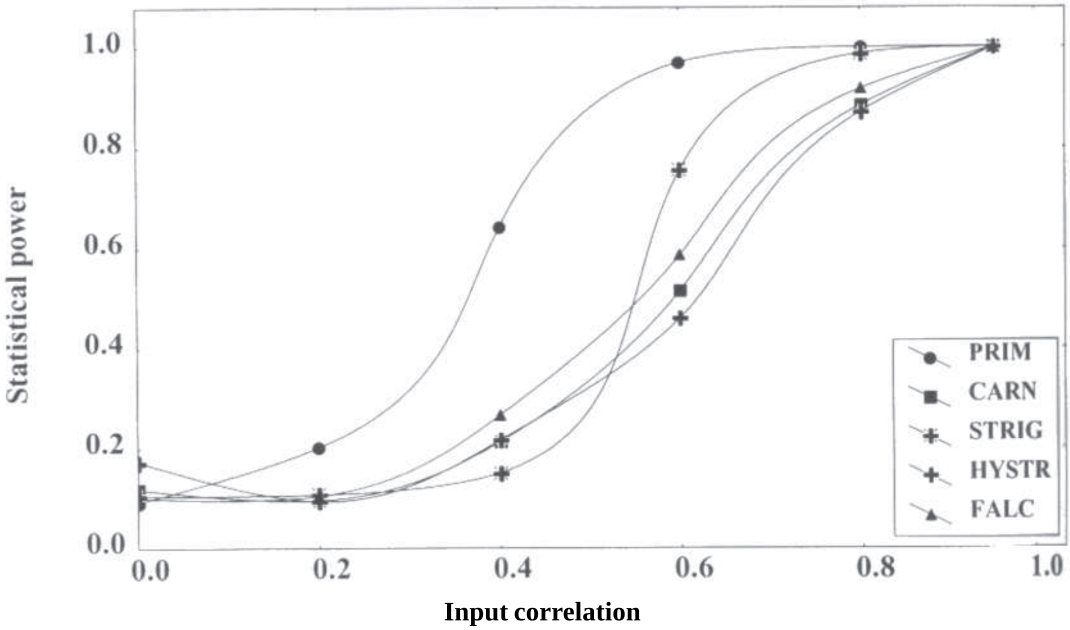

Figure 1. Power curves of PVR for analyzing the correlation of two traits under Brownian motion, for five different data sets. Each point was obtained using 1000 simulations of evolution under Brownian motion.

evaluate the impact of using distinct evolutionary models and phylogenetic structures in all comparative methods.

So, considering the results presented here and the conservative assumption that both traits evolved under Brownian motion, it *is* possible to conclude that PVR performs well for analyzing correlated evolution between the macroecological traits, specially at large sample sizes, permitting

to reject the hypothesis that correlation between them can be a simply consequence of the common phylogenetic inertia in the data sets analyzed. This must be the first step before invoking ecological or evolutionary mechanisms to explain this relationship.

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