**Ecography 30: 598–608, 2007**
doi: 10.1111/j.2007.0906-7590.04988.x

Subject Editor: Douglas Kelt. Accepted 20 June 2007

# Seeing the forest for the trees: partitioning ecological and phylogenetic components of Bergmann's rule in European Carnivora

**José Alexandre F. Diniz-Filho, Luis Mauricio Bini, Miguel Á. Rodríguez, Thiago Fernando L. V. B. Rangel and Bradford A. Hawkins**

*J. A. F. Diniz-Filho (diniz@icb.ufg.br) and L. M. Bini, Dept de Biologia Geral, ICB, Univ. Federal de Goiás (UFG), CP 131, 74.001-970, Goiânia, Brazil. – M. A. Rodríguez, Dept de Ecología, Univ. de Alcalá, ES-28871 Alcalá de Henares, Madrid, Spain. – T. F. L. V. B. Rangel, Dept of Ecology and Evolutionary Biology, Univ. of Connecticut, Storrs, CT 06269-3043, USA. – B. A. Hawkins, Dept of Ecology and Evolutionary Biology, Univ. of California, Irvine, CA 92697, USA.*

Comparative methods have commonly been applied in macroecological research. However, few methods exist to map and analyze phylogenetic variation in geographical space. Here we develop a general analytical framework to partition the phylogenetic and ecological structures of macroecological patterns in geographic space. As an example, we apply the framework to evaluate interspecific patterns of body size geographic variation (Bergmann's rule) in European Carnivora. We model the components of variance attributable to ecological and phylogenetic effects, and to the shared influence of both factors. Spatial patterns in the ecological component are stronger than those in the original body size data. More importantly, the magnitude of intraspecific body size patterns (as measured by the correlation coefficient between body size and latitude) is significantly correlated with the ecological component across species, providing a unified interpretation for Bergmann's rule at multiple levels of biological hierarchy. This approach provides a better understanding of patterns in macroecological traits and allows improved understanding of their underlying ecological and evolutionary mechanisms.

Macroecology has been developed as a unifying conceptual framework for understanding broad-scale patterns of abundance and diversity, incorporating methods and concepts from a range of areas of biological research, including biogeography, physiology, ecology, and evolutionary biology (Brown 1995, Gaston and Blackburn 2000, Blackburn and Gaston 2003). Brown et al. (2003) recently argued that macroecology also can be understood as the analysis of a large number of ecological particles, so that the research program should focus on the "... statistical distribution of variables among large collections of equivalent, but not identical, units such as individual organisms within species or species within communities and biogeographical regions."

Beyond the evaluation of statistical patterns, it is also paramount to focus on the dynamical processes of speciation, extinction, and adaptation that move these particles through geographic space and evolutionary time, in an explicitly phylogenetic context. Indeed, phylogenetic comparative methods developed since the 1980s are now commonly applied in macroecological research and have been used to deal with two basic (and related) questions: 1) how much phylogenetic signal is in macroecological traits, and 2) how does this phylogenetic signal affect the evaluation of the correlation between species-level traits? It is well known that species (or other taxonomic units) may not represent independent observations for statistical analyses, such as ANOVA, regression, and correlation (Felsenstein 1985, Martins and Garland 1991, Martins et al. 2002). Thus, many methods have been developed to incorporate phylogenetic structure into data analyses (Harvey and Pagel 1991, Gittleman and Luh 1992, Martins and Hansen 1996, Garland et al. 2005), mainly to take into account the lack of independence among species due to phylogenetic relationships (i.e. phylogenetic autocorrelation) and then to estimate correctly the Type I errors of statistical analyses (Martins and Garland 1991, Martins et al. 2002). Further, some studies suggested that incorporating phylogenetic structure into data analyses allowed a better understanding of processes underlying ecological, behavioural, and physiological data (Diniz-Filho 2001). However, it is possible to go beyond these applications and use phylogenetic comparative methods to understand the dynamical nature of macroecological patterns and the evolutionary processes driving them (Freckleton et al. 2002, 2003a, Blomberg et al. 2003).

Thus far, however, comparative methods have been unable to incorporate geographic structure of both phylogenetic and non-phylogenetic components in analyses of macroecological patterns. Ruggiero and Hawkins (2006) recently argued that a major limitation in understanding macroecological patterns is the inability to quantify phylogenetic patterns in geographical space (Kidd and Ritchie 2006). Here we develop such a framework and use it to evaluate a widely studied problem in macroecology, namely, Bergmann's rule.

Bergmann's rule states that within, and among, warm-blooded vertebrate species, organisms living at higher latitudes or higher altitudes are generally larger than those living at lower latitudes or altitudes (Gaston and Blackburn 2000, Meiri et al. 2004). The contemporary interest in this pattern, which was first described in the mid 19th century, is evident by the numerous recent papers evaluating its generality (Ashton et al. 2000, Meiri and Dayan 2003, de Queiroz and Ashton 2004, Meiri et al. 2004). Although these papers dealt with Bergmann's rule within species, the original formulation of the rule was in the context of variation among closely related species, and a number of papers dealing with interspecific patterns of spatial variation in body size have appeared recently as well (Blackburn and Hawkins 2004, Olalla-Tárraga et al. 2006, Rodríguez et al. 2006, Olalla-Tárraga and Rodríguez 2007). The interspecific approach also opens the possibility of using alternative analytical techniques to evaluate the strength of different, but not mutually exclusive, evolutionary and biogeographical mechanisms that could be involved in the origin of the pattern, including selection at higher levels of biological hierarchy, energetic constraints to abundance, community-wide character displacement, and life-history mediated species turnover through evolutionary time (Alroy 1998, van Valkenburg et al. 2004, Webster et al. 2004, Dayan and Simberloff 2005).

In this paper, we partition the interspecific variation of body size of European Carnivora (Mammalia) into phylogenetic, niche conservatism, and ecological components. We then evaluate how phylogenetic and ecological components vary in geographical space and how they are correlated with environmental variation. This partitioning strategy allows an understanding for this group of which part of Bergmann's rule can be explained by the independent responses of species to the environment or through evolutionary patterns in deep time. Consistent with energy-based explanations, we also show that the magnitude of independent adaptive responses revealed by comparative methods is positively correlated with intraspecific geographical patterns in body size, providing a first step towards unification of intra- and inter-specific approaches for studying spatial variation in body size.

## Material and methods

### Data and phylogeny

Our analyses are based on a subset of the data recently analyzed by Rodríguez et al. (2006), and involve the 19 species of native terrestrial carnivores currently existing in continental western Europe and Great Britain (Fig. 1). This group was chosen because its phylogeny is relatively well-known and because of the large variation in body size within the order. Range maps for each species were redrawn on a standard grid with 386 cells of 110×110 km covering the study area, and the presence or absence of each species in each cell was recorded. Adult body masses (in kg) were obtained from field guides (see Rodríguez et al. [2006] for detailed description of data sources and processing procedures), and their phylogenetic relationships were taken from the supertree by Bininda-Emonds et al. (1999), updated with new information by Bardeleben et al. (2005) and Johnson et al. (2006) (Fig. 1). This phylogeny was used to generate a phylogenetic distance matrix **D** among species in which the distance between each species pair corresponds to the age of their most recent common ancestor.

We employed 6 environmental variables (potential evapotranspiration [PET], mean annual temperature [TEMP], actual evapotranspiration [AET], range in elevation [ELEV], average annual precipitation [PREC], and average monthly global vegetation index [GVI]; see Rodríguez et al. [2006] for further details on data definition) as predictors of body size. Because of the high level of correlation among these environmental predictors (i.e. $r > 0.8$ in most cases), we reduced the dimensionality of predictors by a Principal component analysis (PCA), and the number of principal components to be retained was established using a broken-stick criterion (Legendre and Legendre 1998). All regression analyses using environmental predictors were then based on the principal component scores, and the

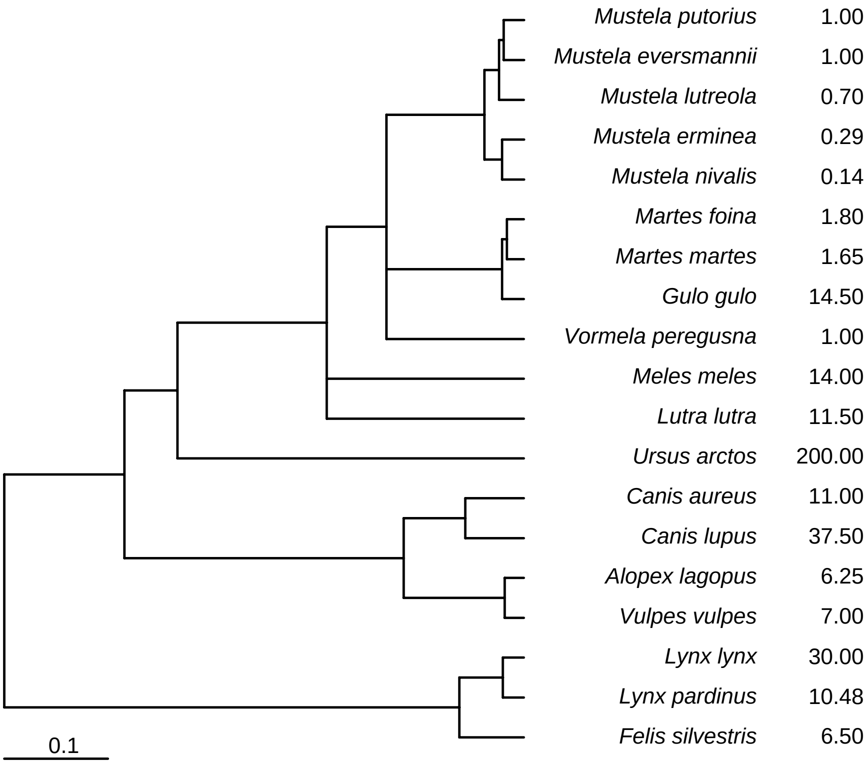

Fig. 1. Phylogeny of the 19 species of western Palearctic Carnivora analyzed in this study. Total length of the phylogeny was standardized to 1.0, and numbers after species names are average body size, in kg (see Rodríguez et al. 2006, for details).

contribution of each original predictor was established by combining the loadings of the retained components with regression coefficients of body size against principal component scores (see below) (Legendre and Legendre 1998).

Two sets of analyses were conducted, as explained below, requiring different organization of the datasets. First, we performed a standard cross-species comparison in which the body size of each species was paired with the average values of these environmental variables across its geographic range (i.e. the centroid of each species in the 6-dimensional environmental space – Diniz-Filho et al. 2007). Due to the high correlation among these environmental predictors, using minimum or maximum values within species' ranges instead of averages did not qualitatively affect our results. Second, we used the standard approach for the interspecific analyses of geographical variation across the continent (Blackburn and Hawkins 2004, Rodríguez et al. 2006). That is, for the case of calculations involving body size values, the log body masses of the species present in each grid cell were averaged and then paired with the cell-values of the 6 environmental variables. Similarly, once the phylogenetic and specific components of body size for each species had been decoupled (see method in the next section), they were treated the same way as the species' log body masses; that is, for each component, the values corresponding to the species present in each cell were averaged and paired with the values of the environmental variables.

## Phylogenetic comparative methods

There are currently many methods to incorporate phylogenetic structure into data analyses (Harvey and Pagel 1991, Gittleman and Luh 1992, Martins and Hansen 1996, Garland et al. 2005). In this paper, we applied Phylogenetic eigenVector Regression (PVR; Diniz-Filho et al. 1998) and its expansion based on partial regression proposed by Desdevises et al. (2003). The comparative analysis allows us to determine in an explicit phylogenetic context the environmental factors associated with body size gradients at multiple hierarchical levels. We first performed a standard evaluation of evolutionary and ecological components of body size variation across species, using PVR and the partial regression expansion of Desdevises et al. (2003), and then moved to a novel application by performing a geographical analysis to evaluate which environmental variables drive each of these components. A brief description of these methods is given below.

In some comparative methods, it is assumed that the total variance ($\sigma^2_T$) of a trait **Y** (e.g. body size) measured in a group of species can be decomposed into phylogenetic ($\sigma^2_P$) and unique, or ecological ($\sigma^2_S$) variances, such that $\sigma^2_T = \sigma^2_P + \sigma^2_S$. This is a simple generalization of the classic partitioning of phenotypic variation into genetic and environmental components, and Cheverud et al. (1985) were the first to formally propose that an autoregressive model (ARM) could be used to obtain phylogenetic (**P**) (among lineages) and specific (**S**) (within species) components of trait variation (see also Gittleman and Kot 1990, for an improved ARM model).

Diniz-Filho et al. (1998) developed a new technique called Phylogenetic eigenVector Regression (PVR) to perform this same partitioning, using a more general approach based on multivariate analysis. The idea is that phylogeny can be expressed as a set of orthogonal vectors obtained by an eigenanalysis of a phylogenetic distance matrix. These vectors can then be used as predictors of **Y** in any form of linear or non-linear modeling (see also Borcard and Legendre 2002, Diniz-Filho and Bini 2005 and Griffith and Peres-Neto 2006, for analogous applications in a spatial context). Thus, PVR follows the standard framework of general linear models, such that

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

where **V** are the orthogonal eigenvectors extracted from the double-centered phylogenetic distance matrix **D**, and β are partial regression coefficients. The phylogenetic structure is incorporated into the model structure ($\mathbf{V}\beta$), whereas the residual term ε is an estimate of the within-species component **S**, expressing the part of variation in **Y** that contains unique and independent responses of each species (to underlying and unmeasured ecological factors – but see below). Thus,

$$\mathbf{Y} = \mathbf{P} + \mathbf{S}.$$

The $R^2$ of the multiple regression model of the trait **Y** against the eigenvectors in **V** provides an estimate of the phylogenetic signal in the data ($\sigma^2_P/\sigma^2_T$). More importantly, since **P** and **S** values can be directly attributed to each species, they can be used as "new" traits and further analysed. These components can also be correlated with other traits and their averages can be mapped to analyse spatial variation in different components of any macroecological trait (see below).

In our analysis of the 19 European Carnivora, the eigenanalysis of the double-centered **D** matrix allowed us to extract a maximum of 18 ($n-1$) eigenvectors describing the phylogenetic relationships among species, and 4 of these were retained in PVR based on different model selection procedures (i.e. the reduction in the residual phylogenetic autocorrelation in **Y**, the statistical significance of a correlation between **Y** and each eigenvector in **V**, and Akaike's information criterion – Diniz-Filho and Tôrres 2002, Desdevises et al. 2003). It is important to highlight that PVR is more robust when dealing with small sample sizes than other methods to perform the same partitioning, such as ARM (Martins et al. 2002).

More recently, Desdevises et al. (2003) expanded this theoretical framework and proposed that part of the variation attributed to phylogeny estimated by PVR or ARM (the component **P**), previously interpreted as a purely non-adaptive component, could also include adaptive variation if ecological driving variables were structured in the phylogeny, in a phenomenon called "phylogenetic niche conservatism" by Harvey and Pagel (1991) (see also Westoby et al. 1995, Diniz-Filho and Bini 2007, and the recent review by Wiens and Graham 2005). At the same time, the specific component **S** could contain within-species variation explained by ecological variation and a pure "error" term, not explained by either phylogeny or ecology. In the method of Desdevises et al. (2003), a partial regression is used to partition trait variation into a fraction that contains a purely ecological component [a], containing the part of **Y** that is correlated with ecological variation but is not phylogenetically structured, a fraction [b] that is the phylogenetically structured environmental variation (the shared component, indicating the magnitude of niche conservatism), and a fraction [c] that may be attributed only to phylogeny (i.e. other unknown biological processes strongly structured in the phylogeny). The total amount of unexplained variation (residual) is given by [d]. These components are obtained by algebraic combination of adjusted $R^2$s derived from multiple regressions of trait (i.e. body size) against phylogenetic eigenvectors and ecological predictors, separately or in combination (Legendre and Legendre 1998).

Finally, it is important to know if the structures described above differ strongly from random processes of phylogenetic differentiation in body size and phylogenetically-structured environmental variation. To examine this, we built a null model by simulating the random independent evolution of body sizes and of an environmental predictor along the Carnivora phylogeny using an Ornstein-Uhlenbeck (O-U) process (Hansen and Martins 1996, Diniz-Filho 2001, 2004, Martins et al. 2002, Gotelli and McGill 2006).

Under a purely stochastic process of trait evolution, the divergence among species in a clade is modeled by a Brownian motion-like process with a linear relationship between divergence and time. Thus, under this model, a very strong phylogenetic signal will arise, which can be measured by the $R^2$ of the PVR (or ARM), or by other techniques such as phylogenetic correlograms (Diniz-Filho 2001, Diniz-Filho and Tôrres 2002). However, the evolution of complex quantitative traits subjected to multiple types of selection (especially stabilizing selection) usually is modeled by non-linear models such as the Ornstein-Uhlenbeck (O-U) process (Hansen and Martins 1996, Martins et al. 2002). In this case the relationship between divergence and time is described by an "exponential-like" relationship with an exponent $\alpha$ expressing the "restraining force" of the relationship. Biologically, the evolution of phenotypes under this model is due to constrained variation in which the mean phenotype is pushed toward an adaptive peak but, simultaneously, random drift causes fluctuation around it. Selection acts like an attractor, tending to return the population to the peak, so that the magnitude of the restraining force $\alpha$ can be interpreted as a measure of stabilizing selection (Hansen and Martins 1996, Diniz-Filho 2004). More importantly, phylogenetic signals measured by PVR, ARM or phylogenetic correlograms will have a negative relationship with the restraining force $\alpha$. Actually, Brownian motion is a particular form of the O-U process in which $\alpha$ is zero.

For the simulations performed here, we used an O-U model in which the restraining forces $\alpha$ were chosen independently for each trait to generate phylogenetic signals similar to those observed in the data (i.e. around 80 and 20% for body size and ecological variation, respectively – see results below), but that are evolving independently of each other across species. Thus, although we ensured independent evolution of the two traits, allowing us to test Type I error of the partial regression of Desdevises et al. (2003), the evolutionary patterns of each trait will be more similar to the real ones observed in body size and ecological variation among species. We performed 1000 replications of this process in PDSIMUL (Garland et al. 1993) and analyzed each one using partial regression. We then compared observed values of each component from the partial regression with their respective null distributions obtained by simulations.

### Geographic patterns in phylogenetic and ecological components

We used the PVR partitioning described above to evaluate the spatial structure of phylogenetic and specific components of body size. Thus, we calculated the average **P** and **S** components of our grid cells by averaging the phylogenetic and specific components of the species occurring in each cell. We mapped these average values and generated models describing their spatial patterns with respect to environmental variation. Notice that at this stage we cannot use the partitioning method of Desdevises et al. (2003) because we want to evaluate how phylogenetic and ecological components are geographically predicted by environmental variables, and thus adding these predictors "a priori" (to get the pure ecological component [a]) would generate a tautology.

Because of spatial autocorrelation in regression residuals, an explicit spatial regression approach using a simultaneous autoregressive method (SAR) was used to model environmental variation driving average **Y** (body size), **P**, and **S** values across geographic space (Cressie 1993, Haining 1990, 2002, Diniz-Filho et al. 2003, Fortin and Dale 2005; but see Hawkins et al. 2007). We fitted the SAR models in SAM 1.1 (<www.ecoevol.ufg.br/sam> – Rangel et al. 2006), establishing the spatial relationship to be used in the residual covariance matrix by connecting cells $<150$ km apart.

## Results

### Patterns of interspecific variation in body size across species

The first 4 eigenvalues of the phylogenetic distance matrix **D** explained 95.7% of the variation in phylogenetic structure, and thus were retained for further analyses. They accounted for 81% of the interspecific variation in body size, indicating a high value for the **P**-component of PVR. On the other hand, 22% of the variation in body size can also be explained by the first principal component derived from the correlation matrix among the centroids of the 6 environmental variables, within species' ranges. About 19% of the variation in this first principal component from environmental data is explained by the 4 phylogenetic eigenvectors. The two sets of predictors (combination of species' centroids and phylogenetic eigenvectors) together explain 86% of the variation in species' body size. Thus, there is a strong phylogenetic signal in the data and at the same time part of the variation is explained by the common influence of phylogeny and the environment, expressed by the overlap term (b, see below) of partial regression.

The partial regression reveals that 16.6% of the variation in body size across species is explained by the phylogenetically-structured environmental variation, or phylogenetic niche conservatism [b]. Phylogeny alone accounts for 64% of the variation, whereas purely (i.e. non-phylogenetically-structured) environmental variation alone explains only 5.3% of the variation. The simulations of evolutionary dynamics using O-U processes revealed that the probability of observing an overlap component $>17\%$ was 0.093 (Fig. 2). Further, purely ecological components as great as 5.3% appeared in no more than 0.16 of the simulations. Combining these two "adaptive" components (pure ecology plus niche conservatism), the probability of getting a value higher than the observed value of 22% is $<0.04$.

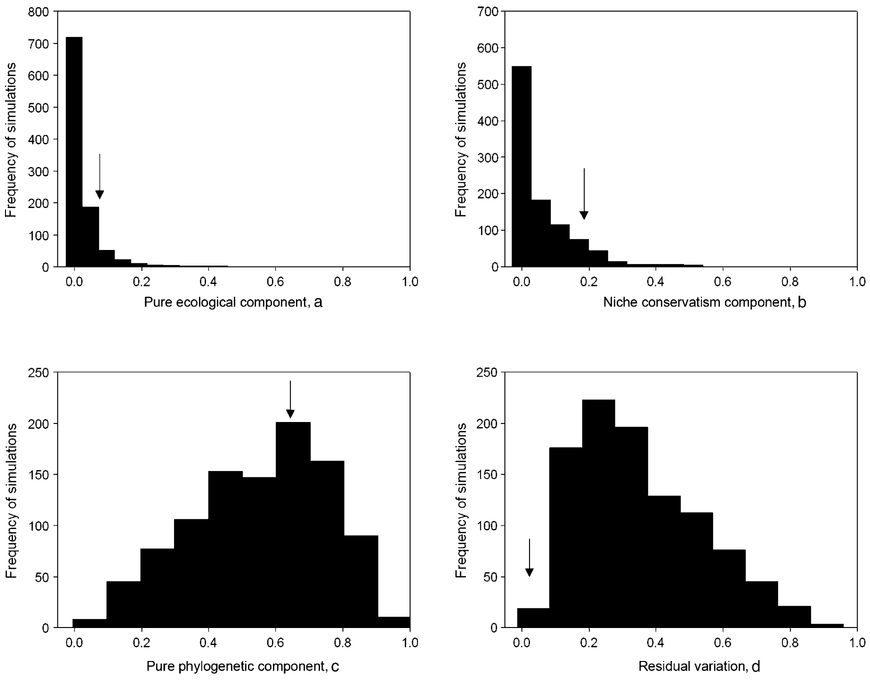

Fig. 2. Results of a null model using Ornstein-Uhlenbeck (O-U) simulations of the independent evolution of body size and ecological traits, with arrows indicating the observed values for the 19 species of European Carnivora. A total of 1000 simulations were performed, using restraining forces of O-U processes equal to 2.0 and 10.0 for body size and the ecological trait, respectively, to match the phylogenetic signal in each trait (see component [c]). Under this null model with an input correlation equal to zero, histograms of the components of partial regression showed that the probability of finding a pure ecological component [a] equal to 5% was equal to 0.16, whereas the probability of finding a niche conservatism component [b] equal to 17% was 0.09. Combining these two "adaptive" components, the probability of getting a value higher than the observed value of 22% is $<0.04$. The distribution of component [c] from the simulation indicates that the restraining parameter of the O-U process matches the observed phylogenetic component in the data (ca 65%). Finally, [d] is the null distribution of residual variation.

Despite the relatively low statistical power (i.e. small number of species), these simulations indicate a relatively low probability that the observed correlation between body size and ecological traits is due to phylogenetic structure alone and, consequently, that adaptive mechanisms are driving body size evolution. Regressing the component [a] across species against the original environmental predictors (Table 1) demonstrated that annual temperature (TEMP) was the best predictor of this component. To better understand Bergmann's patterns, however, it is necessary to evaluate how phylogenetic and ecological components are explicitly distributed in geographic space and which environmental variable is the best predictor of each component.

## Geographic patterns in phylogenetic and ecological components

We followed our evaluation of body size patterns in European Carnivora with an explicit geographic analysis of the phylogenetic and specific components derived from PVR. On average, large-bodied species are found in northern Europe, with a north-south gradient of decreasing average body sizes (i.e. average **Y** values), as previously observed for all mammals (Fig. 3A) (Rodríguez et al. 2006). Because of the strong phylogenetic component in body size (i.e. $R^2 = 81\%$), the map of average **P** from PVR is very similar to the one

Table 1. Coefficients (loadings) of 6 environmental variables in the first two principal components (I and II), and the contribution of each predictor for the adaptive component **S** calculated across species and across geographical space, based on SAR spatial regressions.

| Predictor | PCA |  | **S** |  |
|---|---|---|---|---|
|  | I | II | Cross-species | Geographic |
| TEMP | 0.733 | −0.567 | 0.531 | −0.163 |
| PET | 0.860 | −0.235 | −0.174 | −0.141 |
| ELEV | 0.336 | 0.735 | 0.092 | 0.043 |
| PREC | 0.523 | 0.657 | −0.135 | 0.010 |
| AET | 0.872 | 0.129 | 0.041 | −0.099 |
| GVI | 0.856 | −0.099 | 0.101 | −0.124 |

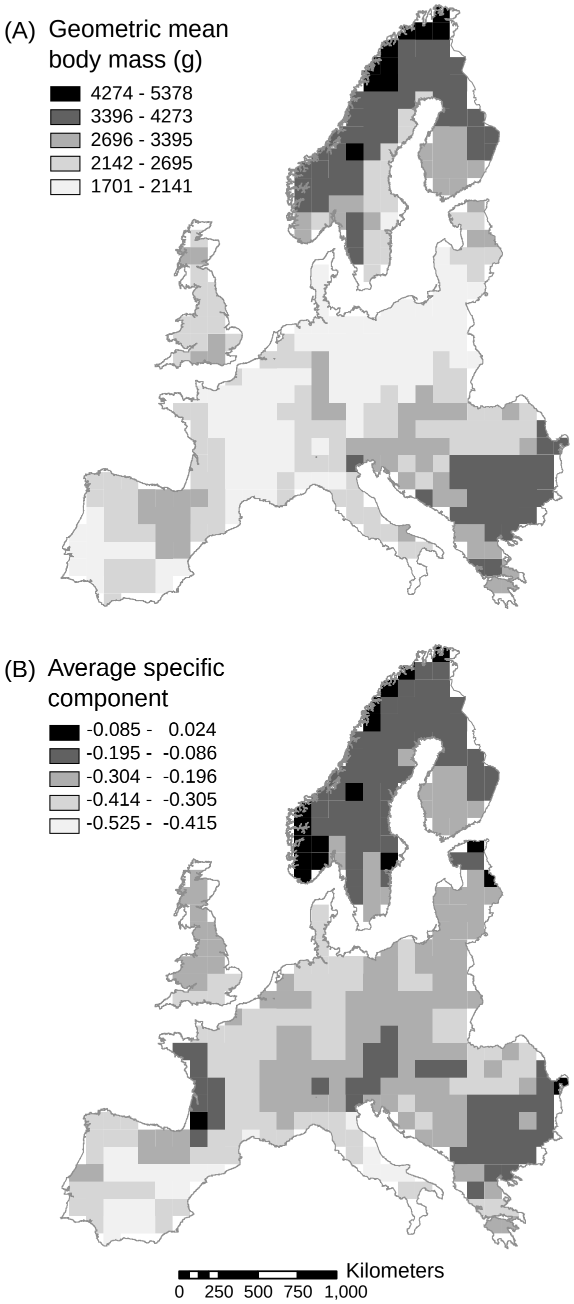

Fig. 3. Geographic patterns of body mass (geometric mean) for 19 species of European Carnivora, given by (A) the observed value (**Y**), and (B) the value of the specific component **S**.

for total body size. However, the geographical gradients are clearer when using averages of the ecological component **S** (Fig. 3B).

The first two principal components of the correlation matrix among the 6 environmental variables, explaining 77% of the variation in the original variables in geographical space, were then used as predictors of **Y**, **P**, and **S** (Table 1). High loadings on the first principal components appear for all variables except ELEV and PREC, which have higher loadings in the second principal component.

The SAR model explained 76% of the variation in total body size in geographic space (Table 2). However, only 16% can be attributed to the environmental variables (integrated by PCA) independently of their spatial structure. The two principal components are significant predictors ($p < 0.05$) for **Y**. However, this analysis may be misleading and biased because of the mixture of phylogenetic and ecological signals in data. Indeed, when analyzing the average phylogenetic component, the $R^2$ of the model is much smaller (ca 1%), and neither of the two principal components significantly explained patterns in **P**.

On the other hand, when analyzing the geographical structure of average ecological component **S**, the explanatory power of the SAR increases to 36% independent of the spatial structure of the predictors (the $R^2$ of the full SAR model was 72%), and again both principal components are highly significant predictors ($p < 0.01$) (Table 2). The contribution of each environmental predictor derived from the association between the PCA loading and SAR coefficients (Table 1) revealed that the energy variables TEMP and PET were the best spatial predictors for **S**. Thus, although most of the variation in body size can be attributed to the phylogenetic component **P**, the environmental predictors of its geographic variation are more highly associated with the component **S**.

## Discussion

Beginning in the early 1980s, there have been many attempts to link phylogeny and ecology, mainly focusing on methods to incorporate the effects of common inheritance in order to minimize bias in Type I errors in bivariate correlations (Gittleman and Luh 1992, Martins and Hansen 1996). Irrespective of the success of these applications, a more general framework may be useful, especially if a broad understanding of the geographical structure of ecological and macroecological traits, such as body size, is to be achieved.

We propose here that phylogenetic eigenvector regression (PVR), coupled with expansions proposed by Desdevises et al. (2003), allows the simultaneous evaluation of the magnitude of phylogenetic signal in data and the partitioning of the correlation components among traits. More importantly, the partitioning of trait variation into phylogenetic and ecological components allows us to evaluate geographic variation in these components. We applied this framework to evaluate one of the oldest recognized patterns in geographical

Table 2. Standardized partial regression coefficients (b) and associated t-values, from a simultaneous autoregressive (SAR) model for the two principal components (PC I and PC II), derived from the 6 environmental variables predicting spatial patterns in average body size (**Y**) of 19 species of Carnivora mammals in 386 cells covering western Palearctic, decoupled into phylogenetic (**P**) and ecological (**S**) components. The $R^2_{full}$ refers to the total coefficient of determination of the model (predictors+spatially structured error term), whereas $R^2_{pred}$ refers to the effect of predictors independently of spatial structure. ρ refers to the autoregressive coefficient of the SAR model, whereas Moran's I refers to the residual spatial autocorrelation.

| Predictor | **Y** | | **P** | | **S** | |
|---|---|---|---|---|---|---|
| | b | t | b | t | b | t |
| PC I | −0.167 | 2.545* | −0.047 | 0.683ns | −0.349 | 4.740** |
| PC II | 0.121 | 2.521* | 0.018 | 0.345ns | −0.348 | 6.404** |
| $R^2_{full}$ | 0.758 | | 0.656 | | 0.722 | |
| $R^2_{pred}$ | 0.161 | | 0.015 | | 0.358 | |
| ρ | 0.872 | | 0.837 | | 0.841 | |
| Moran's I | −0.119 | | −0.059 | | −0.131 | |

ns – $p > 0.05$; *$p < 0.05$; **$p < 0.01$.

ecology, Bergmann's rule. Thus, instead of analyzing the average body size of species in geographic space (the "community approach" of Blackburn and Hawkins 2004), we decoupled total variation into phylogenetic and ecological components and evaluated them independently (Ramirez et al. 2007).

The analyses of European Carnivora across species revealed that, although phylogenetic "inertial" effects can explain most of the variation in body size, there are still significant correlations between body size and the environment that have arisen independent of phylogeny. These correlations support the idea that Darwinian adaptation can explain body size evolution expressed both as an effect of niche conservatism (phylogenetically structured environmental variation) and as unique and independent adaptive responses of each species to environmental conditions.

These patterns are also confirmed when moving from a species' level perspective to an explicit geographical perspective. However, it is important to note that the spatial patterns differ when using total body size and the partitioned components provided by PVR analysis. The phylogenetic component is not explained by climatic variation, whereas the geographic patterns of the ecological component are better explained by potential evapotranspiration and annual temperature, supporting the original explanation for Bergmann's rule based on heat conservation (Millien et al. 2006, Rodríguez et al. 2006) and consistent with cross-species analysis (Table 1). Although it may be difficult to understand the role of each proposed mechanism in determining body size variation, the main message from these analyses is that using total body size provides at best a partial evaluation of Bergmann's rule.

Independent of the framework used (i.e. the community approach dealing with multiple species, or evaluating body size variation within species), geographic patterns in body size are expected to appear as an adaptive response to climate or other environmental factors. If so, this unique response must be measured by the ecological component, although other complex mechanisms at the phylogenetic level would reinforce patterns at broad scales. Following this reasoning, the phylogenetic component is not expected to be structured in geographic space or predicted by climatic variation, which matches observations reported here. Further studies are necessary to evaluate macroevolutionary variables that could predict the phylogenetic component of body size variation in geographic space.

On the other hand, interpretation of Bergmann's rule as an independent adaptive response of species clarifies the biological meaning of using the PVR partitioning to evaluate further the origin of the geographic pattern in body size. Earlier interpretations of the "ecological", or specific, component (Cheverud et al. 1985, Gittleman and Kot 1990) suggested that it represented the variation that could be attributed to unique responses of each species to current environmental conditions, independently of ancestry. Under this interpretation, species with larger values for the ecological component shifted farther from their ancestral body size than expected by the patterns observed for the entire clade, presumably as an adaptation to environmental variation (see Webster et al. 2004, for a related approach in respect to life-history variation).

This interpretation leads to a potential link between the different levels of analysis that have been used to understand Bergmann's rule (i.e. using intra- and interspecific variation in geographic space). If species with a high ecological component **S** have responded more strongly to recent environments, then we expect these species to also have clearer patterns of Bergmann's rule at the intraspecific level. To test this, we evaluated the relationship between the **S** component from PVR obtained here with published, independent measures of intraspecific Bergmann's rule. We used as a measure of intraspecific Bergmann's rule the correlation coefficient between body size and latitude for each species for 14 of our 19 species, as calculated by Meiri et al. (2004). Even with a small sample size, there is indeed a significant relationship (weighted by the sample sizes for the intraspecific analysis within each species) between body size and the correlations between body size and latitude within species, such that larger-bodied species tend to reveal more clearly intraspecific Bergmann's rule ($r = 0.77$; $p = 0.001$) (Meiri and Dayan 2003, Freckleton et al. 2003b) (Fig. 4a). However, there is also a significant correlation between species values for the **S** component and the intraspecific correlations ($r = 0.55$; $p = 0.041$; Fig. 4b), even though the **S** component represents only ca 19% of the variation in total body size across species. Although it is not possible to rule out that this correlation between **S** and intraspecific correlation is being driven by total body size, it shows that species with high levels of body size evolution independent of phylogeny tend to show clearer intraspecific body size patterns in geographic space, reflecting recent adaptation to environmental conditions. Of course, further investigation of the generality of the relationship between intra- and interspecific approaches for Bergmann's rule are required, since there are scenarios in which no correspondence would be expected (e.g. if strong local adaptations occur without affecting the mean body size of the species).

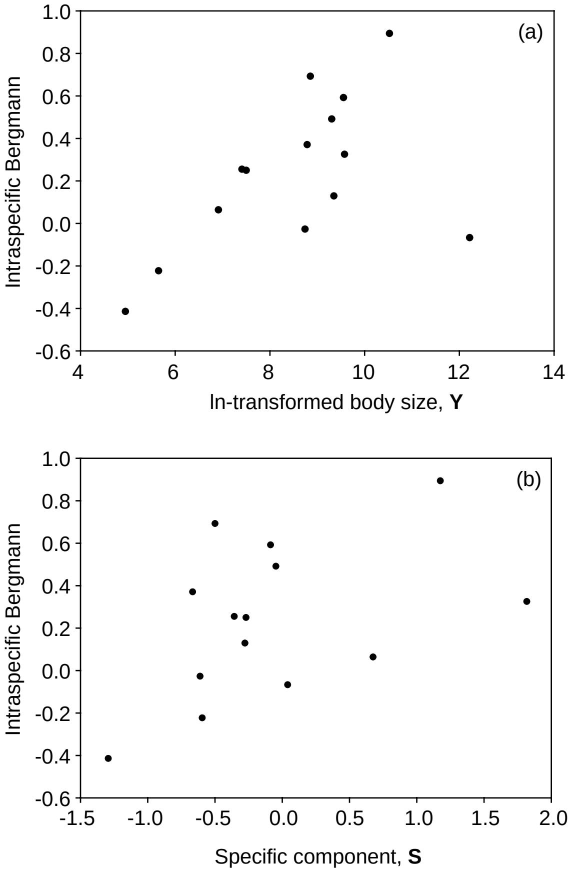

Fig. 4. The relationships between body size and specific component with the intraspecific Bergmann's pattern from Meiri et al. (2004), expressed by the correlation between body size and latitude. For ln-transformed body size **Y** (a), the correlation weighted by sample sizes was equal to 0.77 ($p = 0.0011$), whereas for specific component **S** (b) the correlation was equal to 0.55 ($p = 0.041$).

The two approaches that have been used to investigate body size variation in space (i.e. geographic gradients in average interspecific body size in assemblages or geographic variation within species) converge to the same results in our framework and, thus, support the same ecological interpretation for body size patterns. The approach adopted here, then, provides a unified interpretation for Bergmann's patterns at multiple levels of biological hierarchy and may be the basis for an integrated framework to understand macroecological variation and its underlying mechanisms in an explicitly geographical and phylogenetic context. Hopefully, this framework will be applicable to a wide range of questions in macroecology and geographical ecology.

*Acknowledgements* – We thank Douglas Kelt, Alan de Queiroz, and Shai Meiri for suggestions than improved previous versions of the manuscript. Work by J. A. F. Diniz-Filho and L. M. Bini have been continuously supported by many CNPq fellowships and grants, whereas work by T. F. L. V. B. Rangel is supported by a Fulbright/CAPES doctoral fellowship. M.A.R. was supported by the Spanish Ministry of Education and Science (grant REN2003-03989/GLO and CGL2006-03000/BOS).

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