

Ecological and evolutionary components of body size: geographic variation of venomous snakes at the global scale

LEVI CARINA TERRIBILE^{1,3*}, MIGUEL ÁNGEL OLALLA-TÁRRAGA²,
JOSÉ ALEXANDRE FELIZOLA DINIZ-FILHO³ and MIGUEL ÁNGEL RODRÍGUEZ²

¹*Programa de Pós-Graduação em Biologia Animal, Universidade de Brasília, Campus Universitário Darcy Ribeiro, 70.910-900, Brasília, DF, Brazil*

²*Department of Ecology, University of Alcalá, 28871 Alcalá de Henares, Spain*

³*Departamento de Biologia Geral, ICB, Universidade Federal de Goiás, CP 131, 74.001-970, Goiânia, GO, Brazil*

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Biogeographical patterns of animal body size and the environmental and evolutionary mechanisms that may be driving them have been broadly investigated in macroecology, although just barely in ectotherms. We separately studied two snake clades, Viperidae and Elapidae, and used phylogenetic eigenvector regression and ordinary least squares multiple regression methods to perform a global grid-based analysis of the extent at which the patterns of body size (measured for each species as its log₁₀-transformed maximum body length) of these groups are phylogenetically structured or driven by current environment trends. Phylogenetic relatedness explained 20% of the across-species size variation in Viperidae, and 59% of that of Elapidae, which is a more recent clade. Conversely, when we analysed spatial trends in mean body size values (calculated for each grid-cell as the average size of its extant species), an environmental model including temperature, precipitation, primary productivity (as indicated by the global vegetation index) and topography (range in elevation) explained 37.6% of the variation of Viperidae, but only 4.5% of that of Elapidae. These contrasted responses of body size patterns to current environment gradients are discussed, taking into consideration the dissimilar evolutionary histories of these closely-related groups. Additionally, the results obtained emphasize the importance of the need to start adopting deconstructive approaches in macroecology. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 98, 94–109.

ADDITIONAL KEYWORDS: Bergmann's rule – ectotherms – interspecific variation – model selection – niche conservatism – phylogenetic eigenvector regression – snakes.

INTRODUCTION

The trend of body sizes to increase towards cold macroclimates has been termed Bergmann's rule in honor of its proposer Carl Bergmann, in 1847, and has been broadly reported in macroecology (Lindsey, 1966; Miller, 1991; Hawkins, 1995; Hawkins & Lawton, 1995; Arnett & Gotelli, 1999; Ashton, 2001; Ashton & Feldman, 2003; Jones *et al.*, 2005; Olalla-Tárraga, Rodríguez & Hawkins, 2006; Olalla-

Tárraga & Rodríguez, 2007; Ramirez, Diniz-Filho & Hawkins, 2008; Rodríguez, Olalla-Tárraga & Hawkins, 2008; for a review, see also Meiri & Dayan, 2003). The interest in this ecogeographic rule, along with other well-known rules in geographical ecology and biogeography (e.g. Allen's rule, Rensch's rule or Rapoport's rule), has grown in recent years (Lomolino *et al.*, 2006; Gaston, Chown & Evans, 2008). It is worth noting the intense debate that exists around several aspects of Bergmann's rule, including the taxonomic level at which the rule should be considered to act (Rensch, 1938; Mayr, 1956; Blackburn, Gaston & Loder, 1999), the mechanisms (or

*Corresponding author. E-mail: levicarina@unb.br

hypotheses) explaining body size gradients (James, 1970; Van Voorhies, 1996; Blackburn *et al.*, 1999; Olalla-Tárraga *et al.*, 2006; Yom-Tov & Geffen, 2006; Kubota *et al.*, 2007; Olalla-Tárraga & Rodríguez, 2007), and even the degree of generality of these gradients across taxa (Willemsen & Hailey, 1999; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007).

To some extent, these discussions have been fuelled by an increased recent trend to test the rule in its original, interspecific formulation (Blackburn *et al.*, 1999). In general, recent studies have found support for the rule and its original explanation for endotherms (mammals: Blackburn & Hawkins, 2004; Rodríguez, López-Sañudo & Hawkins, 2006; Rodríguez *et al.*, 2008; birds: Blackburn & Gaston, 1996; Ramirez *et al.*, 2008) based on the heat conservation mechanism. That is, larger endotherms take advantage of living in colder regions because their lower surface area-to-volume ratio facilitates heat retention (Meiri & Thomas, 2007; Meiri, Yom-Tov & Geffen, 2007).

For ectotherms, broad-scale patterns of body size have not yet been studied as intensely as they have in endotherms. Perhaps the most controversial point regarding body size gradients in this case is that, although some ectothermic groups exhibit Bergmann's trends (e.g. ants in Europe: Cushman, Lawton & Manly, 1993; lizards in Argentina: Cruz *et al.*, 2005; lizards in Europe: Olalla-Tárraga *et al.*, 2006; anurans in Europe and North America: Olalla-Tárraga & Rodríguez, 2007), others either display the converse trend, or do not show clear patterns of variation (e.g. bees in the USA: Hawkins, 1995; flies in Brazil: Kubota *et al.*, 2007; snakes in the New World: Reed, 2003; urodeles and snakes in Europe and North America: Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007; Adams & Church, 2008; see also Lindsey, 1966; and lizards in South America: Pincheira-Donoso, Hodgson & Tregenza, 2008). Hawkins & Lawton (1995) also found that gradients in butterfly body sizes were inconsistent across different geographical regions (North America, Europe, Australia, and Afrotropics) and families. These inconsistencies lead to two possible alternatives. First, generalizations about the patterns and associated mechanisms of body size variation cannot be made for these groups. Second, a general explanation for the observed patterns is difficult to be attained across all taxa because, even if the mechanisms driving body size trends were the same for all groups, these mechanisms may have given rise to different geographical gradients in each case (Ashton & Feldman, 2003; Angilletta *et al.*, 2004).

Assemblage level studies addressing the interspecific variation in body size of ectothermic vertebrates

have tested, or at least suggested, a wide range of environmental hypotheses (e.g. heat conservation, heat balance, primary productivity, climatic variability, migration abilities, starvation resistance, size dependence, and water availability; Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006, 2009; Olalla-Tárraga & Rodríguez, 2007). The relative support for each of these potential explanations has varied in different groups of fishes (Garvey & Marschall, 2003), amphibians (Lindsey, 1966; Olalla-Tárraga & Rodríguez, 2007; Adams & Church, 2008), and non-avian reptiles (Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008). However, these studies often did not consider the effect of evolutionary history in constraining body size variation, independently of environmental variation. Omitting evolutionary aspects when analysing macroecological patterns, especially those of body size, can bring about some limitations in interpreting the mechanisms associated with these patterns (Ruggiero & Hawkins, 2006). To solve this problem, Diniz-Filho *et al.* (2007) and Ramirez *et al.* (2008) recently developed a deconstructive approach to incorporate phylogenetics into assemblage-based interspecific analyses of body size variation. This approach allows the partition of the interspecific variation of body size into phylogenetic, or niche conservatism, and ecological components. It has been applied to interpret how much body size variation in European Carnivora (Diniz-Filho *et al.*, 2007) or New World birds (Ramirez *et al.*, 2008) could be attributed to unique and independent adaptive responses of each species to contemporary environmental conditions (e.g. such as Bergmann's *per se* effects).

In relation to squamate reptiles, contrasting body size gradients have been documented in several intra- and interspecific studies (Lindsey, 1966; Ashton & Feldman, 2003; Reed, 2003; Cruz *et al.*, 2005; Olalla-Tárraga *et al.*, 2006; Pincheira-Donoso *et al.*, 2008). For example, in a recent interspecific assemblage-based analysis, Olalla-Tárraga *et al.* (2006) found that lizard and snake mean body sizes show opposing trends and associations with environmental energy predictors (potential evapotranspiration and temperature) in Europe, with the mean sizes of lizards increasing and those of snakes decreasing towards the cold, northern areas. Moreover, similar associations with environmental energy were also evident in North America, although the patterns of mean size variation were less clear in this region. These results reinforce that, at least in temperate regions, the body size patterns of each particular group might be determined by a unique and specific set of factors and processes (Olalla-Tárraga *et al.*, 2006).

Along these lines, it is important to note that the studies mentioned above virtually represent the only

ones that have documented mean body size patterns in these reptiles, most likely as a result of the greater scarcity of data regarding the distribution of squamate species at broad geographical scales. Also, few studies (Ashton & Feldman, 2003; Pincheira-Donoso *et al.*, 2008) have explored the extent to which macroecological patterns for squamates are structured phylogenetically (and therefore reflect historical legacies) or are driven by contemporary gradients of environmental variation. In the present study, we addressed these issues in two venomous snake families, Viperidae and Elapidae, in accordance with the analytical framework proposed by Diniz-Filho *et al.* (2007). Recently, Terribile *et al.* (2009) found that the global patterns of species richness in these two families were differently linked with current climate variation and history (i.e. as represented by the distribution of these clades across biogeographic regions): current climate was more associated with the gradients of viperid richness, and history was associated with the variation in elapid richness. Similarly, in the present study, we investigate to what extent patterns in body size variation of these groups support explanations based on current environment effects or reflect the presence of historic (i.e. phylogenetic) legacies. Furthermore, we evaluate whether trends observed at the global scale are reproduced within biogeographical regions.

Accordingly, we also tested four environmental hypotheses for body size variation of viperids and elapids:

1. *Heat balance*: this hypothesis has been developed for ectotherms as an expansion of the classical heat conservation mechanism for endotherms (Olalla-Tárraga & Rodríguez, 2007). For larger thermoregulating ectothermic groups such as snakes, this hypothesis predicts a converse Bergmann pattern because the low surface area-to-volume ratio of these organisms increases heating times in colder regions and limits the time available for other activities such as feeding (Huey & Slatkin, 1976; Shine & Lambeck, 1990; Ayers & Shine, 1997; Blouin-Demers & Weatherhead, 2002; Shine *et al.*, 2002) and reproduction (Gregory, Crampton & Skebo, 1999; Shine *et al.*, 2000). Thus, small-bodied snakes in cooler climates have benefit of more rapid heating (Bogert, 1949; Stevenson, 1985) and greater ability to control their body temperatures (Ashton & Feldman, 2003), thus allowing them to spend more time pursuing activities other than thermoregulation (Blouin-Demers & Weatherhead, 2002).
2. *Habitat availability*: this hypothesis was proposed by Rodríguez *et al.* (2008) to explain the effects of topography in driving converse patterns of Ber-

gamnn in mammals from south Neartic and Neotropic (i.e. the occurrence of small species in mountains and large species in lowlands; Rodríguez *et al.*, 2008). It was based on the proposition that strong climatic variation across tropical and subtropical mountains generates greater habitat zonation, which in turn reduces habitat areas (Janzen, 1967; Hawkins & Diniz-Filho, 2006) and consequently limits the occurrence of large species (Rodríguez *et al.*, 2008). Given that temperate regions have less habitat zonation and montane habitats tend to be more similar to lowland habitats, it is expected that habitat availability would not limit the occurrence of large species across mountains in these regions. Reed (2003) found a positive association between range size and body size in New World snakes species. He also found that species with a small geographic range and small body size did not occur randomly at higher elevations, which may suggest the possible effects of habitat availability acting to constrain the body size of these organisms. Thus, the importance of this hypothesis to explain broad-scale variation in snake body sizes deserves further investigation.

3. *Primary productivity*: this hypothesis states that, for some species, geographical trends in body size may be better explained in terms of food availability than of temperature (Rosenzweig, 1968; Blackburn *et al.*, 1999). According to this hypothesis, decreased food availability reduces growth rate and size at maturity, such that low productivity regions tend to harbour more small bodied-species. For snakes, intraspecific studies have found that the individual growth rate is more positively associated with food availability than with other environmental variables (e.g. temperature; Lindell, 1997; see also Bronikowski & Arnold, 1999; Madsen & Shine, 2000). Thus, the effect of food availability, if any, on interspecific body size variation at a broad scale in these ectotherms warrants examination.
4. *Seasonality* (or *starvation resistance*): this hypothesis suggests that larger organisms can take advantage in highly seasonal climates because they are more resistant to starvation when availability of resources fluctuates seasonally (Lindsey, 1966; Murphy, 1985; Blackburn *et al.*, 1999; Gaston & Blackburn, 2000). However, Mousseau (1997), Blanckenhorn *et al.* (2006) and Olalla-Tárraga *et al.* (2006) emphasized that the length of growing season is a more plausible mechanism for explaining body size variation in ectotherms than starvation resistance (Geist, 1987) as a result of the interaction between season length and the time available for physiological development. This

may explain the converse of Bergmann's rule that is frequently observed in these organisms (Mousseau, 1997; Blanckenhorn *et al.*, 2006).

MATERIAL AND METHODS

SPECIES DATA

Viperids are distributed across Asian, African, European, and New World mainlands and islands, and comprise some 256–260 species (Kelly, Barker & Villet, 2003; Castoe & Parkinson, 2006). This group is absent from Australia, possibly because it evolved during the Cenozoic when this region had already become a separated landmass (Keogh, 1998). Elapids are distributed across Africa, Asia, Australia, the New World, and the Indic and Pacific Oceans, and comprise some 290–300 species of which approximately 60 are marine (Keogh, 1998; Castoe *et al.*, 2007). However, we did not analyse sea snakes because their distribution is likely to be conditioned by different environmental factors than terrestrial species.

We generated a global checklist for both groups based on the updated Reptile Database, supported by the Systematics Working Group of the German Herpetological Society (Uetz, 2007). Except for the Arabian Peninsula, we were able to compile distribution maps for all terrestrial species inhabiting large land masses; namely all continents and the well-prospected island of Great Britain, which has enough extension and proximity to mainland Europe to warrant that body size patterns are not affected by insularity. Thus, our final database included 228 viperids and 224 elapids (i.e. approximately 90% and 75% of the overall diversity of these groups, respectively). For New World species, the species distribution maps were obtained from Campbell & Lamar (2004) supplemented with Renjifo & Lundberg (2003), Alvarado-Díaz & Campbell (2004) and Lavin-Murcio & Dixon (2004). For the Old World, we used Branch (1988, 1998), Latifi (1991), Arnold (2002), Arnold & Ovenden (2002), Broadley & Doria (2003), Spawls *et al.* (2004), Ananjeva *et al.* (2006), Vogel (2006), Dobiey & Vogel (2007), Whitaker & Captain (2004), supplemented with Cherlin (1981), Orlov & Tuniyev (1990), Tuniyev & Ostrovskikh (2001), Khan (2002), Mallow, Ludwig & Nilson (2003) and Geniez & Tynié (2005). For Australian elapids, we used Wilson & Swan (2003).

It is known that the interpretation of macroecological patterns and their underlying mechanisms are subjected to scale effects (Rahbek & Graves, 2001; Willis & Whittaker, 2002; Rahbek, 2005). Thus, choosing an appropriate scale of analysis is the first important step in examining such patterns. Some studies have suggested that the most appropriate scale to

evaluate continental-to-global patterns generated via range maps is at 1° or 2° of resolution (approximately 100 and 200 km, respectively; Rahbek & Graves, 2001; Hurlbert & Jetz, 2007). Therefore, in accordance with the previous studies of Olalla-Tárraga *et al.* (2006) and Olalla-Tárraga & Rodríguez (2007), we used grid systems of 110 × 110 km cells, which we consider as being not too coarse to result in an excessive loss of information or to cause spurious extrapolation, nor are they too fine to generate spatial discontinuities in the global body size patterns (Rahbek & Graves, 2001; Hurlbert & Jetz, 2007). We also used region-specific equal area projections, and those cells containing less than 50% of the land mass were excluded. Thus, area was held as constant as possible and was not included explicitly in the analyses. All range maps were digitized and rasterized using ArcGIS, version 9.2 (ESRI).

Some studies have suggested body mass as the best estimate of body size (Hedges, 1985; Gaston & Blackburn, 2000) mainly because body mass is a measure that allows comparison among several different taxa with different basic body shapes (Olalla-Tárraga *et al.*, 2006). However, body mass can be highly variable among individuals, and depends on such factors as season, breeding condition, health and individual history (Gaston & Blackburn, 2000). For snakes, individual variation in body mass may be strongly influenced by seasonal activities on feeding and reproduction, which is well known for most species (Shine, 1977; Marques, Almeida-Santos & Rodrigues, 2006), and by other seasonal changes in body conditions (McCue, 2007). On the other hand, for these elongate organisms, body length has been proposed to be less sensitive to seasonal variation (Boback, 2003; Boback & Guyer, 2003) and, therefore, more appropriate to compare closely-related species (Gaston & Blackburn, 2000). Furthermore, most previous studies have noted that the trends observed in broad-scale patterns of body length are very similar to those observed using body size (Kaufman & Gibbons, 1975; Brown, 1995; Ashton & Feldman, 2003). Therefore, for these organisms that grow indeterminately (Partridge & Coyne, 1997; Olalla-Tárraga *et al.*, 2006), we used maximum total length (i.e. a standard size measure commonly reported for snakes) of each species as a surrogate of its overall body size.

The data on maximum total length were obtained from Branch (1988), Orlov & Tuniyev (1990), Latifi (1991), Tuniyev & Ostrovskikh (2001), Arnold (2002), Arnold & Ovenden (2002), Khan (2002), Mallow *et al.* (2003), Campbell & Lamar (2004), Spawls *et al.* (2004), Whitaker & Captain (2004), Geniez & Tynié (2005), Vogel (2006), Dobiey & Vogel (2007) and Wilson & Swan (2003). To correct for allometric effects and heterocedasticity, as well to normalize statistical

distributions, all maximum total lengths were \log_{10} -transformed before calculating mean body size values (Peters, 1983; Brown, 1995), which consisted of arithmetic means being obtained separately for each family in each grid cell.

ENVIRONMENTAL HYPOTHESES

We first investigate the multiple environment-based hypotheses as potential mechanisms driving body size variation at broad scales based on different predictor variables: (1) *Heat conservation*: this hypothesis can be tested by two environmental energy variables, namely mean annual temperature and Priestley-Taylor's potential evapotranspiration (PET; Lu *et al.*, 2005). (2) *Habitat availability*: two indirect indicators of mesoscale climatic variation, namely range in elevation (i.e. the difference between maximum and minimum elevation within each cell) and 'interaction' (i.e. the standardized values of mean annual temperature multiplied by the standardized values of range in elevation in each cell), have been used to test this hypothesis (Hawkins & Diniz-Filho, 2006; Rodríguez *et al.*, 2008). (3) *Primary productivity*: the global vegetation index (GVI) and total annual precipitation (or annual actual evapotranspiration; AET) are normally used as proxies for plant productivity (Hawkins, Porter & Diniz-Filho, 2003). (4) *Seasonality* (or *starvation resistance*), which is measured as the number of months available for plant growth. For this measure (seasonality), we first calculated the xerothermic season length for each cell by counting the number of months in which the mean monthly temperature (in °C) was more than double the mean monthly precipitation (in mm) (Gaussen, 1954). On the basis of this calculation, we identified hot dry months (i.e. those summer months for which low precipitation limits plant productivity). We then established the length of the rainy season as 12 minus the number of hot dry months. We also calculated the number of months in which plant growth is limited by low temperatures by counting the number of months having mean monthly temperatures lower than 5 °C (cold months). The number of hot months then was calculated as 12 minus the number of cold months. Finally, we defined our 'seasonality' variable as the sum of months in the rainy season and hot months in each cell. All data sources and processing techniques to obtain these variables are provided and discussed in detail elsewhere (Rodríguez, Belmontes & Hawkins, 2005; Olalla-Tárraga *et al.*, 2006; Hawkins *et al.*, 2007; Rodríguez *et al.*, 2008).

ENVIRONMENTAL MODELLING OF MEAN BODY SIZE VARIATION

We analysed separately the patterns of mean body size for Viperidae and Elapidae. We first looked for

relationships between mean body size (i.e. calculated for each cell as the arithmetic mean of the \log_{10} -transformed maximum lengths of its extant species) and the eight environmental predictors above mentioned using Pearson's correlations. Because the variables used to generate these environmental models include some 'compounded' variables (e.g. AET, PET, interaction, and seasonality), the multi-collinearity among them and other 'primary' explanatory variables (i.e. mean temperature, precipitation, GVI, and range in elevation) could lead to a tangled interpretation of the importance of these predictors expressed on the regression coefficients (Graham, 2003). Indeed, the Pearson's correlation (r) matrix performed across all variables revealed values higher than 0.8 between the 'compounded' and 'primary' variables (see Supporting information, Table S1). To avoid this problem, we only used the four 'primary' predictors for modelling. Then, the environmental hypotheses were investigated by using ordinary least squares multiple regression (OLS), in which body size was regressed against multiple environmental predictors.

We used an Akaike's-based approach (Akaike information criteria; AIC) (Burnham & Anderson, 2004; Diniz-Filho, Rangel & Bini, 2008) for model selection. Specifically, for each snake family, besides calculating the AIC of each model, we also computed its ΔAIC_i value (i.e. $\Delta AIC_i = AIC_i - \min AIC$; where an $\Delta AIC > 10$ represents a poor fit, and an $\Delta AIC \leq 2$ corresponds to a model equivalent to the best model; Burnham & Anderson, 2004) and Akaike's weighting (w_i), an index representing the probability that model i is actually the best explanatory model among all possible models with four variables (i.e. 15 models). The use of these indexes has become common in geographical ecology analyses (Olalla-Tárraga & Rodríguez, 2007; Kissling & Carl, 2008; Ramirez *et al.*, 2008), mainly as an alternative to deal with multi-inferential uncertainty generated by spatial autocorrelation in ecological data (Diniz-Filho *et al.*, 2008). However, as stressed by Diniz-Filho *et al.* (2008), using an AIC approach in OLS does not avoid all potential autocorrelation problems because AIC-derived values are related to residual variance of the models, which can be affected in turn by the spatial structure of the data. Additionally, although the best AIC models selected using spatial methods (e.g. autoregressive models and spatial eigenvector mapping; for details, see Diniz-Filho *et al.*, 2008) have no spatial autocorrelation in the residuals, they are often unstable regarding the variables included in the models and have different uncertainty levels. To avoid these problems, Diniz-Filho *et al.* (2008) proposed that, instead of using the best nonspatial OLS (as a result of spatial autocorrelation) or the best spatial model (as a result of their uncertainty), a suitable

approach is to interpret the averaged model because it generates consistent and robust results across different methods and may comprise the best approach for understanding the macroecological patterns. In these averaged models, coefficient estimates from spatial and nonspatial models tend to converge (Diniz-Filho *et al.*, 2008). Accordingly, the relative importance for body size variation of the four predictors selected for modelling were established taking into account the standardized regression coefficients of best model (i.e. the one with lowest AIC value), as well as those resulting from calculating w_i -weighted averages of the coefficients of all 15 possible models.

This analytical framework was applied to the data at the global extent and also separately to each zoogeographical region (Cox, 2001) (African, Australian, Eurasian, North American, Oriental, and South American). However, it should be noted that elapids are mainly tropical and absent from Europe and most parts of North America and extratropical Asia. Furthermore, although viperids are more globally distributed (but absent from Australia), they are scarcely represented northward Russia (species richness maps for Viperidae and Elapidae are provided in the Supporting information, Fig. S1; see also Terribile *et al.*, 2009). Taking this into account, together with the idea that low cell occupancies may strongly affect analyses of mean body size variation (Olalla-Tárraga *et al.*, 2006), we did not analyse the body size pattern of the Eurasian and North American zoogeographic regions separately. Even so, the data corresponding to these two regions were used to provide a global picture of the patterns (moreover, excluding these data did not qualitatively change our global analyses).

After excluding grid cells containing zero species, global analyses were performed with a total of 7331 cells for Viperidae and 4698 cells for Elapidae.

ANALYSIS OF PHYLOGENETIC AND ECOLOGICAL COMPONENTS OF BODY SIZE

Sensu Diniz-Filho *et al.* (2007), we partitioned the variation in snake body size into phylogenetic and adaptive responses with phylogenetic eigenvector regression (PVR) (for the original proposition of PVR, see Diniz-Filho, Sant'ana & Bini, 1998). Phylogenies for the two groups were built based on different sources, which were combined to generate a single phylogenetic tree. For Viperidae, we combined phylogenies provided in Lenk *et al.* (2001), Malhotra & Thorpe (2004), and Castoe & Parkinson (2006), including 36 genera. For Elapidae, we used the phylogeny generated by Scanlon & Lee (2004) for the Australian monophyletic group, and combined it with those described by Slowinski & Keogh (2000) and

Castoe *et al.* (2007) to include all 41 genera. All these phylogenies were analysed at the generic level because detailed information for relationships at the species level are not available for all known species.

The idea of PVR is that the phylogenetic relationships among a set of species (or higher taxa) can be expressed as a set of orthogonal vectors obtained by an eigenanalysis (we used principal coordinates analysis; PCoA) of the phylogenetic distance matrix (Legendre & Legendre, 1998). These eigenvectors can then be used as predictors of the trait (i.e. body size) measured in the analysed species (Diniz-Filho *et al.*, 2007). We extracted eigenvectors at the generic level from the phylogenetic distance matrix of each group, so that our PVR analyses expressed the amount of deviation of each species' body size from the expected phylogenetic mean of its genus (for a similar approach at the family level, see Ramirez *et al.*, 2008). Specifically, for each clade, species' body sizes were regressed against the eigenvectors to obtain an estimate of the family's overall amount of phylogenetic signal (R^2 of the PVR) in body size. For this analysis, we took into account that, when eigenvectors are successively added to the model, and based on their associated eigenvalues, there is a curvilinear relationship between the magnitude of the phylogenetic signal and the number of eigenvectors added. Thus, for each snake family, we used the first 15 eigenvectors and an AIC-based model selection procedure to detect the best 'phylogenetic model' (i.e. formed by the selected eigenvectors) among the 32 767 possible models (2^{15} models minus the model with intercept only). On the other hand, the value estimated by PVR for each genus can be interpreted as the expected body size of its species in an explicitly phylogenetic context (i.e. for each species, this value measures the phylogenetic component, P, of its body size, *sensu* Diniz-Filho *et al.*, 1998, 2007), whereas the model residual corresponding to each species expresses the deviation of its body size from the expected phylogenetic value (its specific adaptive component, S, *sensu* Cheverud, Dow & Leutenegger, 1985; Diniz-Filho *et al.*, 1998).

The P and S components from PVR are components of total body size variation across species and, *sensu* Diniz-Filho *et al.* (2007), we took into account the P and S values corresponding to the species present in each cell to generate cell averages for each component. Then, these cell mean-P and mean-S values were subjected to the same multiple regression-based analyses that we used for mean body size (see above) to investigate their association with environmental variation.

All statistical analyses were performed using Spatial Analyses in Macroecology software, version 3.0 (Rangel, Diniz-Filho & Bini, 2006).

RESULTS

The global patterns of mean body size variation of Viperidae and Elapidae do not show simple latitudinal trends, as would otherwise be expected by Bergmann's rule or its converse, although they vary longitudinally, with their mean body sizes tending to be larger and smaller towards the New World, respectively (Fig. 1). The patterns also vary within different parts of the world. Viperids show the converse of Bergmann's rule across South America and in the Old World, whereas, in North America, there are no clear trends. For Elapidae, however, there are no clear clines, except in Australia, where a west-to-east longitudinal trend of increasing mean body sizes is detected.

The best environmental OLS models for the mean body sizes of both families (i.e. the model with lowest AIC value in each case) included all variables (mean annual temperature, precipitation, GVI, and range in elevation) and the evidence in favour of these models as being the best ones (as indicated by their respective Akaike's weightings: w_i) was of 100% for Viperidae and 75% for Elapidae (Table 1). The percentage of variance in mean body size explained by the best environmental models was 37.6% for Viperidae, but only 4.5% for Elapidae, which indicates that current environment is poorly associated with mean body size variation in the latter family. On the other hand, focusing on the standardized coefficients of the averaged model for viperid body size, mean

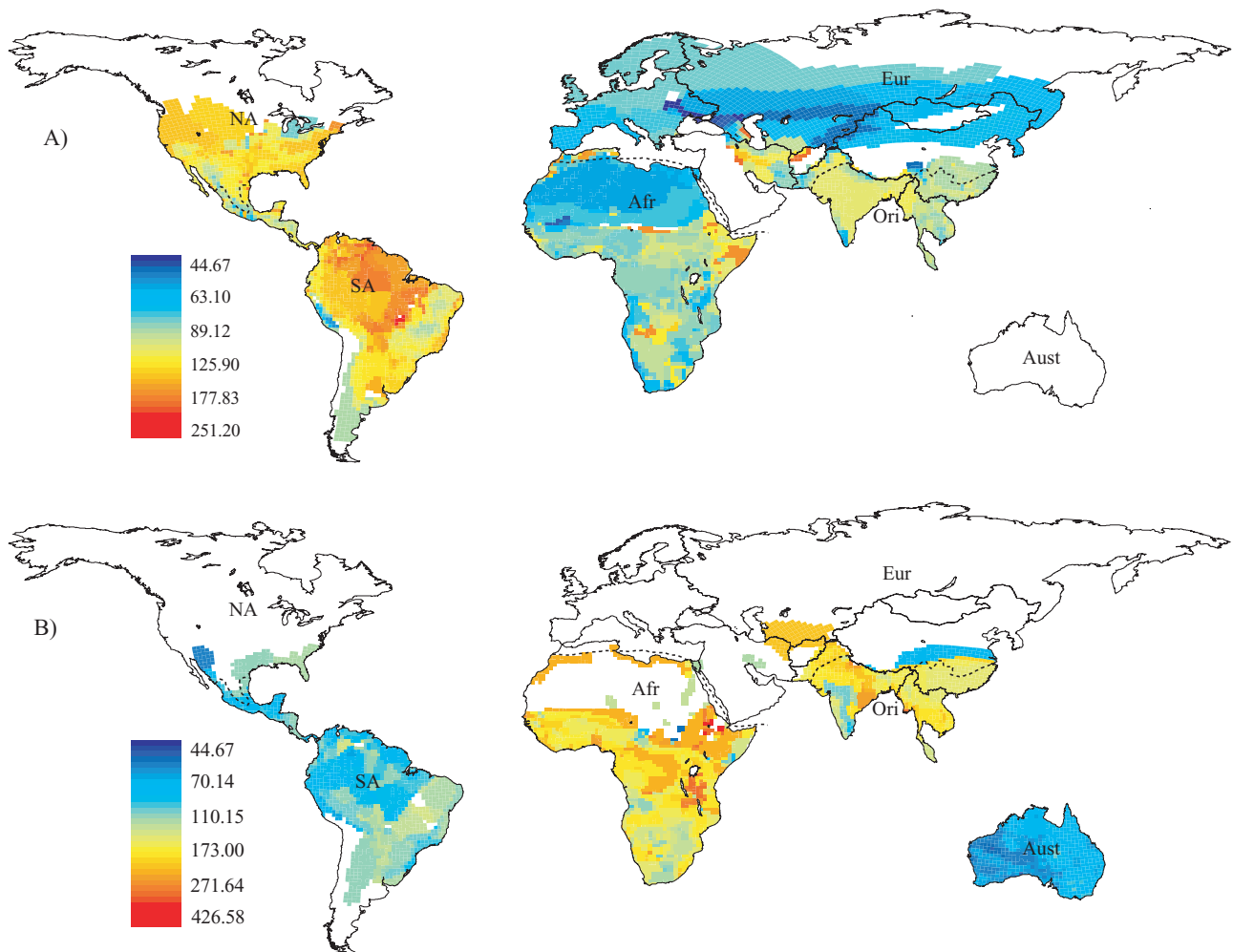


Figure 1. Geographical patterns of Viperidae (A) and Elapidae (B) mean body size. The maps were built using cell averages of \log_{10} -transformed maximum length values, whereas the numbers included in the legends have been recalculated by antilog transformation of the original values to reflect geometric means of maximum length in millimetres. Dashed lines separate ecogeographical regions, as described by Cox (2001). NA, North American; SA, South American; Afr, African; Eur, Eurasian; Ori, Oriental; Aust, Australian.

Table 1. Multiple regression models for the global analysis of viperid and elapid mean body sizes

w_i -weighted averaged models			AIC best model				
Variables	Viperids	Elapids	Model	AIC	Δ AIC	w_i	R^2
Mean temperature	0.415	0.224	Viperidae				
Precipitation	0.116	0.040	Mean temperature, GVI, precipitation, range	-11081.473	0.000	1.000	0.376
GVI	0.250	-0.127	Elapidae				
Range	0.104	0.195	Mean temperature, range, GVI, precipitation	-2780.738	0.000	0.750	0.045

The w_i -weighted averaged standardized regression coefficients are shown resulting from averaging the coefficients of all possible ($N = 15$) models with four predictors: mean annual temperature, annual precipitation, annual global vegetation index (GVI), and range in elevation. Also shown are the variables included in the 'best' model (i.e. with lowest AIC values and Δ AIC ≤ 2), ranked from the most to the least important variable according to their respective regression coefficients. Akaike information criteria (AIC) weighting or the probability of each model actually comprising the best model (w_i) and the models' coefficients of determination (R^2) are also included.

annual temperature showed the highest value, whereas GVI rated second, with both having positive signs. These results lend support to the mechanisms described in the heat balance and productivity hypotheses as being the main and secondary potential driving forces, respectively, of mean body size variation in this group. In the case of Elapidae, mean temperature followed by range in elevation comprised the most important variables in the averaged model (Table 1), but the low fit of the best environmental models makes it difficult to interpret the influence of these variables on mean body size variation.

PVR analyses showed that, for Viperidae, less than 20% of the among species variation in body size was explained by phylogenetic relatedness. By contrast, for Elapidae, this figure increased to 59%, which is a value similar to those observed for other vertebrate taxa (Diniz-Filho *et al.*, 2007; Ramirez *et al.*, 2008), indicating that the body sizes of elapid species are strongly determined by the phylogeny.

Taking into account the P and S components generated by PVR for each species, as well as the species presences in the grid cells, we calculated mean-P and mean-S cell values for each family, which we related with the environmental predictors in the same way that we did for mean cell body sizes. For Viperidae, the percentages of variance described by the best environmental models were 18.3% for mean-P, but 32.1% for mean-S (Table 2; for AIC selected models, see also Supporting information, Table S2), suggesting a moderate phylogenetically structured environmental variation of body size (see Diniz-Filho *et al.*, 2007), and a stronger adaptive response of this trait to environmental predictors, respectively. As for the environmen-

Table 2. Multiple regression w_i -weighted averaged models for the global analysis of the phylogenetic (mean-P) and specific (mean-S) components of viperid and elapid mean body sizes

Variables and 'best' model- R^2	Mean-P	Mean-S	Mean-BS
Viperidae			
Temperature	-0.171	0.410	0.415
Precipitation	0.184	-0.001	0.116
GVI	0.238	0.306	0.250
Range in elevation	0.171	-0.008	0.104
R^2	0.183*	0.321*	0.376*
Elapidae			
Temperature	0.225	0.031	0.224
Precipitation	0.084	-0.095	0.040
GVI	-0.288	0.346	-0.127
Range in elevation	0.208	-0.008	0.195
R^2	0.081*	0.090*	0.045*

Phylogenetic (mean-P) and specific (mean-S) component values were generated for each species through phylogenetic eigenvector regression and their mean values were obtained for each cell by taking into account its extant species. To facilitate comparison with the w_i -weighted averaged models for mean body sizes presented in Table 1, these models (mean-BS) are also included. The numbers reflect w_i -weighted averages of the standardized regression coefficients of all possible ($N = 15$) models with four predictors. * R^2 corresponding to those of the best models (see Supporting information, Table S2) and is provided to reflect the strength of the relationships of the variables of body size with current environment variation.

GVI, global vegetation index.

tal drivers of mean-S variation, the data suggest a leading role of environmental energy and a secondary one of primary productivity, as indicated by the regression coefficients of mean annual temperature and GVI, which rated first and second in the averaged model of S component (Table 2). GVI was also the best predictor for the P component in this group.

Compared with Viperidae, the best models for Elapidae mean-P and mean-S accounted for much less variance: 8.1% and 9.0%, respectively (Table 2; for AIC selected models, see also Supporting information, Table S2). These low figures are consistent with the findings described above regarding both the low dependence shown by elapid mean body size on environmental drivers (Table 1), and the strong influence of phylogenetic relationships on the across-species variation of this trait. Nevertheless, the slightly higher percentage of described variance corresponding to the mean-S component (which is also higher than the that described by the models for mean body size; i.e. 4.5%) suggests an adaptive response of size to environment, which would be mostly related to gradients of primary productivity, as indicated by the higher regression coefficient of GVI in the averaged model (Table 2).

Regional scale results were consistent in general with those observed at the global extent. For Viperidae, the regional environmental models explained from 14.2% (Oriental region) to 42.5% (South America) of body size trends, and temperature (in Oriental and South American regions) and GVI (in African and South American regions) again emerged as the most important predictors (Table 3; for AIC selected models, see also Supporting information, Table S3). Similarly, the regional environmental models for the mean values of the phylogenetic and specific components of body size had low explanatory power in all instances (described variance < 20%) except for mean-S in South America (41.2%). In this regard, it is interesting that mean-S variation was again primarily and positively associated with temperature and GVI in this and the Oriental region, and with GVI in the African region (Table 3). These results support the adaptive nature of the relationships of viperid body size with temperature and primary productivity that we found at the global extent.

Finally, for the case of elapids, body size gradients across regions were poorly supported by the respective environmental models, as indicated by the generally lower proportions of variance that they described (Table 3; for AIC selected models, see also Supporting information, Table S3). However, there was a notable exception in the case of the mean-S variation in Australia, where the environmental model accounted for 55.8% of the variance, and two predictors of primary productivity (i.e. GVI and precipitation) emerged as the most important ones. This

suggests that regional adaptive responses have emerged in Australia; that is, in the region where Elapidae exhibits a greater diversification (see Elapidae species in Supporting information, Table S1; Terribile *et al.*, 2009).

DISCUSSION

The spatial variation in body size of Viperidae and Elapidae was idiosyncratic in general in our global analysis, both across the two clades and biogeographical regions. Elapidae showed no clear patterns, whereas Viperidae displayed a clinal variation tending to a Bergmann's converse at least in the Old World and South America. Many other studies have also found no trend or converse Bergmann's patterns in ectotherms (Masaki, 1967; Mousseau, 1997; Garvey & Marschall, 2003; Olalla-Tárraga & Rodríguez, 2007; Adams & Church, 2008; Pincheira-Donoso *et al.*, 2008) and, more specifically, in snakes (Ashton, 2001; Ashton & Feldman, 2003; Reed, 2003; Olalla-Tárraga *et al.*, 2006). Furthermore, in a recent review of ecogeographical patterns, Millien *et al.* (2006) found that, among all vertebrate groups with a significant positive relationship between latitude and across-populations body size variation, snakes presented the lowest percentage of agreement with Bergmann's rule. Moreover, incongruent patterns among cold-blooded vertebrate groups, such as those reported in the present study, are not surprising, and have been commonly found in studies of ectotherm body size gradients (Lindsey, 1966; Ashton & Feldman, 2003; Reed, 2003; Olalla-Tárraga *et al.*, 2006; Olalla-Tárraga & Rodríguez, 2007). Given these results, it is reasonably to think that the same mechanisms may not be influencing body size variation across different ectothermic groups.

On the other hand, our global scale analysis of mean body size trends and of those of its phylogenetic and specific components still revealed interesting gradients and relationships with environmental factors. In the case of viperids, the data lend support to the heat balance and primary productivity hypotheses because the environmental models revealed positive associations of mean body size with temperature (firstly) and GVI (secondarily), respectively. Additionally, our analyses of phylogenetic and specific (adaptive or ecological) components of body size indicated both that phylogeny has a low influence in the across-species variation of viperid body size (< 20%), and that the adaptive responses of species within this clade may be behind the observed relationships of mean body size with temperature and primary productivity. Indeed, this was indicated by the fact that, similar to that observed for mean body size, positive

Table 3. Multiple regression w_i -weighted averaged models for the regional analyses of the viperid and elapid mean body sizes (mean-BS), and of their phylogenetic (mean-P) and specific (mean-S) components

Variables and 'best' model- R^2	African			Australian			Oriental			South American		
	Mean-BS	Mean-P	Mean-S	Mean-BS	Mean-P	Mean-S	Mean-BS	Mean-P	Mean-S	Mean-BS	Mean-P	Mean-S
Viperidae												
Temperature	0.091	-0.109	0.1	-	-	-	0.313	< 0.001	0.32	0.318	0.554	0.257
Precipitation	0.060	-0.204	0.083	-	-	-	-0.142	-0.151	0.03	0.126	-0.249	0.157
GVI	0.404	0.286	0.357	-	-	-	-0.056	-0.302	0.283	0.227	0.051	0.227
Range in elevation	0.127	0.041	0.12	-	-	-	-0.032	-0.124	0.111	-0.126	0.259	-0.162
R^2	0.207*	0.051*	0.191*	-	-	-	0.143*	0.200*	0.150*	0.426*	0.186*	0.413*
Elapidae												
Temperature	0.144	0.147	0.055	0.050	0.259	-0.198	0.037	-0.177	0.183	-0.076	-0.033	-0.073
Precipitation	0.141	0.15	0.093	0.300	-0.014	0.385	0.085	0.055	0.109	-0.341	0.029	-0.344
GVI	-0.056	-0.176	0.149	0.245	-0.123	0.507	0.11	0.146	0.064	-0.116	0.009	-0.117
Range in elevation	0.141	0.176	-0.002	-0.267	-0.159	-0.206	-0.015	-0.104	0.080	-0.401	-0.052	-0.397
R^2	0.044*	0.049*	0.051*	0.171*	0.172*	0.561*	0.020*	0.047*	0.034*	0.217*	0.002*	0.217*

Values reflect w_i -weighted averages of the standardized regression coefficients of all possible ($N = 15$) models with four predictors. As in Table 2.

R^2 (italics) corresponding to those of the best models (see Supporting information, Table S3).

Although used for mapping mean body size patterns (Fig. 1), the North American and Eurasian regions were not included in our analyses as a result of the low richness values of both families in these areas (see Material and methods).

GVI, global vegetation index.

associations with temperature and primary productivity were also evident in the environmental models obtained for the mean specific component of viperid body size (i.e. mean-S), both at the global scale and for each biogeographic region (Tables 2, 3).

Selection for maintenance of preferred body temperatures in ectotherms constitutes the basis of the heat balance hypothesis, and provides a straightforward explanation for the trend of mean viperid body size to increase with warmth. In cooler regions, larger temperature and energy inputs fluctuations restrict snakes to reduced daily sunlight hours and low annual energy budgets that are necessary for their daily or seasonal activities, such as heating, growth, maintenance, and reproduction (Reed, 2003). Under these circumstances, the increased surface area-to-volume ratios of small-bodied snakes may be advantageous because it allows for faster basking and cooling rates and, hence, for a more effective thermoregulation (Ashton & Feldman, 2003). Moreover, by spending less time heating, small snakes may spend more time foraging for food and partners (Shine *et al.*, 2000; Blouin-Demers & Weatherhead, 2002), resulting in more frequent breeding and a potentially higher lifetime fitness (Lourdais *et al.*, 2002; Shine, 2003). By contrast, for larger snakes, the energy inputs necessary to attain minimum energetic thresholds for successful reproduction may result in lower breeding frequencies in cooler areas (Brown, 1991), thus disfavours them. In warmer regions, however, thermoregulation is less of a limiting factor for larger snakes (Shine & Madsen, 1996; Ashton & Feldman, 2003), which may explain why viperid body sizes increased with temperature. Even though these explanations were thought for variation in body sizes at the intraspecific (i.e. across-populations) level, it is reasonable to think that analogous adaptive pressures contribute to the interspecific trends observed in the present study. This was also supported by our data, particularly by the observation that temperature was as an important factor in our global and regional environmental models for the mean specific (mean-S) component of viperid body size. Moreover, a similar positive association between mean body size and energy was demonstrated by Olalla-Tárraga & Rodríguez (2007) for the amphibian faunas of Europe and North America, and the study also suggested that the trade-off between increased surface area-to-volume ratio and rapid heating (i.e. the heat balance hypothesis) was a likely explanation for these interspecific patterns.

Alternatively, positive size-temperature associations observed in ectotherms have been explained by invoking season length effects on growth and development of organisms (Ray, 1960; Mousseau, 1997; Blanckenhorn & Demont, 2004; Olalla-Tárraga *et al.*,

2006). However, when we added a variable expressing 'seasonality' to our environmental model (i.e. the model included temperature, precipitation, GVI, range in elevation, and seasonality), virtually no increment in the proportion of variance described was noted ($\Delta R^2 = 0.011$). Thus, it is unlikely that seasonality was behind the observed relationship with temperature.

Primary productivity (GVI) was a secondary, positive predictor of viperid mean body size, and was also detected as an important determinant of the mean specific component of viperid body size at both global and regional scales, thus supporting the adaptive nature of this relationship (Tables 2, 3). A potential explanation (i.e. the primary productivity hypothesis) is that the more productive tropics offer a greater stock of prey (Campbell & Lamar, 2004), thus enabling tropical viperids to attain larger sizes than those living in cooler regions, where seasonal and more limited food availability could constrain body sizes (Forsman, 1991; Blackburn *et al.*, 1999; Madsen & Shine, 2000; Jones *et al.*, 2005; Yom-Tov & Geffen, 2006; Meiri *et al.*, 2007). Also, bearing in mind that morphological traits associated with arboreality typically result in more elongated bodies (Martins *et al.*, 2001), this positive association with primary productivity could reflect the abundance of semi-arboreal and arboreal species in tropical forests (e.g. the Neotropical *Bothrops* and the Asiatic *Trimeresurus*) (Parkinson, 1999; Martins *et al.*, 2001; Campbell & Lamar, 2004). Similar indirect (i.e. habitat-mediated) influences of primary productivity on biogeographical gradients have been proposed to explain amphibian species richness patterns in Europe (Rodríguez *et al.*, 2005).

Regarding elapids, the environmental model for global mean body size variation had virtually no explanatory power (Table 1), suggesting either that environmental variables not included in the present study may be driving the patterns or, more likely, that they are weakly climatically determined at the global extent. Indeed, it should be noted that many terrestrial elapids are fossorial or semi-fossorial (How & Shine, 1999; Campbell & Lamar, 2004) and therefore spend most of the time in favourable and relatively constant microclimatic conditions (How & Shine, 1999; Campbell & Lamar, 2004). This may explain why mean body size was not affected by environmental gradients in this group (for similar trends and explanations in other vertebrate groups, see Rodríguez *et al.*, 2006). Complementarily, this lack of association with environmental factors may also reflect that elapids have had not enough time to diversify and generate adaptive responses of body size to environmental gradients in most areas (see below). Bearing in mind that, in an evolutionary context,

Elapidae is a more recent clade than Viperidae (Vidal *et al.*, 2007), this appears to be a plausible possibility, which in turn may explain why we found that the across-species body size variation of elapids was strongly phylogenetically determined. Moreover, our regional models for the mean specific (mean-S) component of elapid body size also support this explanation because they had low explanatory power in all areas except for Australia (Table 3) (i.e. for the region where this family has experienced a greater diversification). Notably, in this region, the mean specific component of elapid body size was mostly associated with primary productivity predictors (GVI and precipitation), which can be interpreted the same way as it was for relationships of primary productivity and viperid body size.

On the other hand, some studies have noted that some elapids are morphologically conservative (Silva & Sites, 2001; Campbell & Lamar, 2004; Castoe *et al.*, 2007), which suggests that the patterns of body size variation in this group may be reflecting niche conservatism (Wiens & Graham, 2005), such that elapid species would possess a stronger tendency to retain ancestral ecological characteristics. This interpretation is supported by the global environmental models generated for the mean specific component of both groups because the model corresponding to Viperidae had an explanatory power that was almost three-fold higher than the model for Elapidae (Table 2). However, the results mentioned above for this specific component in Australia weaken the plausibility of such an interpretation because the model obtained for this region had an explanatory power (55.8%) with no parallel either at global or regional scales, or when considering the models obtained for viperids. In other words, if niche conservatism was behind the stronger phylogenetic inertia of elapid body size, then Australian elapids should be considered an exception to this general trend.

There are two general conclusions based on our extensive analyses. First, it is unlikely that a general interspecific pattern of body size variation exists across different snake groups at very broad scales, even in closely-related taxa such as those of the present study. Second, the mechanisms constraining body size spatial distributions can vary across groups as well as according to differences in the evolutionary history of each clade. Viperidae and Elapidae constitute a good example because they showed distinct body size trends that were differently associated with environmental gradients and evolutionary history. This reinforces the importance of the need to start adopting deconstructive approaches (Diniz-Filho *et al.*, 2007) if we are to gain a better understanding of macroecological patterns.

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SUPPORTING INFORMATION

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

Figure S1. Global biogeographical patterns of Viperidae (a) and Elapidae (b) species richness. The dashed lines identify the biogeographical limits of Cox (2001). NA, North American; SA, South American; Afr, African; Eur, Eurasian; Ori, Oriental; Aust, Australian.

Table S1. Pearson's correlation matrix among environmental variables.

Table S2. 'Best' environmental models (i.e. with $\Delta\text{AIC} \leq 2$) for the cell mean values of the phylogenetic (mean-P) and specific (mean-S) components from phylogenetic eigenvector regression, for Viperidae and Elapidae at the global scale.

Table S3. Regional 'best' environmental models (i.e. with $\Delta\text{AIC} \leq 2$) for the cell mean values of Viperidae and Elapidae mean body sizes (mean-BS) and for their phylogenetic (mean-P) and specific (mean-S) components.

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