



Richness patterns, species distributions and the principle of extreme deconstruction

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ABSTRACT

Aim To analyse the global patterns in species richness of Viperidae snakes through the deconstruction of richness into sets of species according to their distribution models, range size, body size and phylogenetic structure, and to test if environmental drivers explaining the geographical ranges of species are similar to those explaining richness patterns, something we called the extreme deconstruction principle.

Location Global.

Methods We generated a global dataset of 228 terrestrial viperid snakes, which included geographical ranges (mapped at 1° resolution, for a grid with 7331 cells world-wide), body sizes and phylogenetic relationships among species. We used logistic regression (generalized linear model; GLM) to model species geographical ranges with five environmental predictors. Sets of species richness were also generated for large and small-bodied species, for basal and derived species and for four classes of geographical range sizes. Richness patterns were also modelled against the five environmental variables through standard ordinary least squares (OLS) multiple regressions. These subsets are replications to test if environmental factors driving species geographical ranges can be directly associated with those explaining richness patterns.

Results Around 48% of the total variance in viperid richness was explained by the environmental model, but richness sets revealed different patterns across the world. The similarity between OLS coefficients and the primacy of variables across species geographical range GLMs was equal to 0.645 when analysing all viperid snakes. Thus, in general, when an environmental predictor it is important to model species geographical ranges, this predictor is also important when modelling richness, so that the extreme deconstruction principle holds. However, replicating this correlation using subsets of species within different categories in body size, range size and phylogenetic structure gave more variable results, with correlations between GLM and OLS coefficients varying from –0.46 up to 0.83. Despite this, there is a relatively high correspondence ($r = 0.73$) between the similarity of GLM-OLS coefficients and R^2 values of richness models, indicating that when richness is well explained by the environment, the relative importance of environmental drivers is similar in the richness OLS and its corresponding set of GLMs.

Main conclusions The deconstruction of species richness based on macroecological traits revealed that, at least for range size and phylogenetic level, the causes underlying patterns in viperid richness differ for the various sets of species. On the other hand, our analyses of extreme deconstruction using GLM for species geographical range support the idea that, if environmental drivers determine the geographical distribution of species by establishing niche boundaries, it is expected, at least in theory, that the overlap among ranges (i.e. richness) will reveal similar effects of these environmental drivers. Richness patterns may be indeed viewed as macroecological consequences of population-level processes acting on species geographical ranges.

Keywords

Distribution modelling, extreme deconstruction, range size, snakes, species richness, Viperidae.

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INTRODUCTION

There is a consensus among ecologists that diversity is not randomly distributed at broad scales in geographical space. For instance, it has been recognized since the 18th century that tropics possess more species than temperate regions for most kinds of organisms (Hawkins, 2001), although the detailed ecological and evolutionary mechanisms that may be underlying the so-called latitudinal diversity gradient are still debated (Hawkins *et al.*, 2003; Willig *et al.*, 2003; Hillebrand, 2004; Ricklefs, 2006; Mittelbach *et al.*, 2007). Currently, a multicausal approach seems to be the most appropriate form of analysis for complex biological and ecological systems, as multiple causes can generate simultaneously the same patterns at different scales and for different groups of organisms (Elliot & Brook, 2007). In this type of approach, the relevant question is not if a given mechanism accounts for a given pattern, but rather what the relative importance of each one is to the overall patterns.

Marquet *et al.* (2004) also pointed out that part of the difficulty in finding overall explanations for broad-scale patterns of species richness is due to the fact that species richness is actually an 'aggregate' variable, usually obtained by overlapping geographical ranges (i.e. extents of occurrence) in macroecological studies. This overlap, in turn, may encompass groups of species with traits evolving in distinct ecological functions and under multiple evolutionary pathways, so that species and their overlap can present different geographical patterns and may respond in complex and different ways to environmental variation. Under niche conservatism, for example (see Wiens & Graham, 2005; Losos 2008a,b; Wiens, 2008), phylogenetically related species can have similar ecological requirements and environmental tolerances, and thus they should respond in more similar ways to environmental factors, creating as a consequence more similar patterns of geographical distribution that should overlap more frequently (increasing richness). Indeed, McPherson & Jetz (2007) showed that geographical range models vary among species with similar life-history characteristics.

Marquet *et al.* (2004) highlighted the advantages of partitioning richness patterns into sets of species that are defined according to particular traits (e.g. to be geographically restricted or widespread, small-bodied or large-bodied, exhibiting slow/short-dispersal or fast/long-dispersal). Under the assumption that these groups show more similar responses to intrinsic and extrinsic ecological processes, such as responses of abundance and distributions to environmental drivers, or extinction in the face of human pressures, it would be easier to interpret the factors driving species richness. Beyond other advantages, this 'deconstructive' approach can be used to clarify the causes underlying species richness patterns by framing questions concerning richness patterns in a clearer comparative way (see also Bini *et al.*, 2004).

The approach of defining sets of similar species has actually been used for a long time (e.g. Badgley & Fox, 2000; Bhattarai & Vetaas, 2003), but the work by Marquet *et al.* (2004) tried to formalize the use of deconstructive analyses and a priori thinking in planned comparisons of richness patterns. Two examples from

recent macroecological literature reinforce the utility of deconstructing species richness to help understand the mechanisms underlying its geographical patterns. Hawkins *et al.* (2005, 2006, 2007) used a 'phylogenetic deconstruction' and calculated geographical patterns of richness separately for basal and derived groups. In all cases, overall richness was more related to richness calculated from basal species, which reinforces the idea that these patterns are related to a niche conservatism process, as proposed by Wiens & Donoghue (2004). Jetz & Rahbek (2002; see also Rahbek *et al.*, 2007) also showed that richness calculated using species with different geographical range sizes has different geographical patterns, so that richness from wide-ranging species clearly shows stronger correlations with environmental and climate variation than richness calculated for narrow-ranging species, which seem to be more randomly distributed in geographical space (see also Rahbek *et al.*, 2007; but see Hawkins & Diniz-Filho, 2006, and Ruggiero & Hawkins, 2008, for an alternative explanation related to mountain effects). Even though these studies did not explicitly use the term 'deconstruction', they clearly show that the causes underlying large-scale richness patterns can be better understood by decomposing richness into historical or ecologically distinguished groups of species.

In this context, we follow here the suggestion of Marquet *et al.* (2004) and use several criteria to deconstruct global patterns in species richness of Viperidae snakes (Serpentes). Our previous analyses (Terribile *et al.*, 2008) did not reveal strong evolutionary signals explaining richness patterns for this taxon and we found that present climate explains a reasonable amount of the variation in richness at global scales, as previously found for many other groups of organisms (see Hawkins *et al.*, 2003). Thus, we initially tested the hypothesis that sets of species with different ecological and evolutionary characteristics (range size, body size and phylogenetic structure) have different richness patterns that can be explained by different sets of environmental factors.

However, the richness deconstruction is in some sense subjective, since there is not a clear criterion (or actually there may be many alternatives) for establishing sets of species based on their ecological characteristics. In the limit, each species has its own and particular ecological niche that determines its response to environment, being thus a unique 'set'. Thus, here we have expanded and generalized the deconstructive approach to its theoretical limit by performing what can be called *extreme deconstruction*. The idea is to test if environmental predictors that are important to explain species geographical ranges are also important when modelling species richness. Thus, the 'extreme deconstruction' principle suggests that processes driving organism distributions in a lower hierarchical level (species geographical ranges) can be directly associated with environmental factors conditioning overlap of distributions at higher levels (species richness). There has been an increasing interest in techniques for modelling species geographical ranges (e.g. see Segurado & Araújo, 2004; Elith *et al.*, 2006; Philips *et al.*, 2006), but these techniques have been mainly used to estimate geographical ranges for conservation purposes or to predict shifts in geographical

ranges or species richness after climate changes (Peterson & Vieglais, 2001; Araújo & Pearson, 2005; Thuiller *et al.*, 2005; Araújo *et al.*, 2006). Only a few papers have tried to relate the outputs of such models to the life history or ecological characteristics of species (e.g. see McPherson & Jetz, 2007).

Moreover, the logic of extreme deconstruction discussed here underlies recent simulation studies on richness patterns, in which environmental constraints are coupled with stochastic processes (dispersal) to define and establish limits for species geographical ranges. Although processes are established at range level, the analyses are performed to evaluate geographical patterns in species richness (Rangel & Diniz-Filho, 2005a; Storch *et al.*, 2006; Rahbek *et al.*, 2007; Rangel *et al.*, 2007; see Dormann *et al.*, 2007, and Kissling & Carl, 2008, for a completely different strategy of simulating patterns in species richness). Changing parameters of these simulations for limiting geographical ranges (environmental drivers or species tolerances to these drivers) generates different richness patterns (e.g. Rangel & Diniz-Filho, 2005b; Rangel *et al.*, 2007).

Additionally, it is worthwhile mentioning that Araújo & Pearson (2005) showed that the current distribution of each species can be due, at least in part, to historical effects, thus increasing the list of elements that question the 'equilibrium' with current climate postulate (see Guisan & Thuiller, 2005), a basic assumption of species range bioclimatic modelling. So, it is expected that, for sets of species with high levels of non-equilibrium, a low environmental component for species richness is also observed. Therefore, we also tested here if lack of fit between current species geographical distribution and environment (which can in principle be interpreted as non-equilibrium) is related to a lower environmental component in species richness and, thus, indicates a larger number of historical effects explaining geographical patterns in species richness.

MATERIALS AND METHODS

Data

We generated a global checklist of 228 terrestrial viperid snakes based on the updated Reptile Database, supported by the Systematic Working Group of the German Herpetological Society (Uetz, 2007). Except for the Arabian Peninsula, we were able to compile distribution maps for all these species in large land masses, namely all mainland continental areas to which viperids are native (i.e. Australia was excluded) and the well-surveyed island of Great Britain, which is of sufficient size and proximity to mainland Europe to warrant that macroecological patterns are not affected by island effects. Range maps were obtained from Campbell & Lamar (2004), Branch (1988, 1998), Latifi (1991), Broadley & Doria (2003), Spawls *et al.* (2004), Ananjeva *et al.* (2006), Vogel (2006) and Dobiey & Vogel (2007), and were mapped at 1° resolution for a grid with 7331 cells each containing at least one species. Species richness was obtained by overlaying these geographical ranges for each cell.

We also obtained macroecological data at the species level that were used in the deconstruction processes. Log₁₀ of maximum

total length (a standard size measure commonly reported for snakes) was used as an estimate of a species' overall body size (see Ashton & Feldman, 2003, Boback, 2003, and Boback & Guyer, 2003, for examples of use of body length as a measure of body size for snakes). These body size data were obtained from the same literature used for the geographical range data (see above; L.C. Terribile, unpublished data). A crude estimate of geographical range size was obtained by counting the number of cells in which each species occurs.

Phylogenetic relationships among species were established at genus level using a phylogenetic tree that was built by combining the phylogenies by Lenk *et al.* (2001), Malhotra & Thorpe (2004) and Castoe & Parkinson (2006). Sets of basal and derived species were identified, respectively, using the lower and upper quartiles of the count of number of nodes between each species and the root of the tree (see Hawkins *et al.*, 2005, 2006, 2007). We also used this same phylogeny in a phylogenetic eigenvector regression (PVR) (Diniz-Filho *et al.*, 1998) to summarize the relationships among taxa (see Diniz-Filho *et al.*, 2007, and Ramirez *et al.*, 2008, for recent applications in macroecology). The first 20 eigenvectors of the matrix among genera were retained for further analyses and used to evaluate the relative magnitude of phylogenetic effects on macroecological traits across the 228 species (body size, range size and fit of individual species' distribution models; see below), as well as to take into account the phylogenetic non-independence among species when testing relationships among these traits. The association of macroecological traits with the phylogenetic eigenvectors was established through multiple regression techniques in which minimum models were reached through a simplification process based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008).

Environmental data

Five environmental variables were used to model species distributions and to analyse richness patterns: (1) total annual precipitation; (2) mean annual temperature, (3) range in elevation (i.e. the difference between maximum and minimum elevation within each cell, which we used as a proxy for mesoscale climatic gradients); (4) primary productivity – measured as the annual global vegetation index (GVI); and (5) seasonality in primary productivity – 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). Based on 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 in Olalla-Tárraga *et al.* (2006) and Rodríguez *et al.* (2008).

Primacy of variables across geographical range models

We estimated the effects of current environment on species geographical ranges using logistic regression to model the presence or absence of species in the cells with respect to the five environmental predictors. The parameters of each logistic regression were estimated by generating a saturated generalized linear model (GLM; i.e. a GLM including all five environmental variables) using a binomial distribution of error terms.

We evaluated the model fit in each range model using the McFadden's rho-squared (ρ^2), which is an attempt to approximate an ordinary least squares (OLS) standard coefficient of determination (R^2). It can be calculated by

$$\rho^2 = 1 - \left(\frac{\ln L_1}{\ln L_0} \right)$$

where ρ^2 is McFadden's rho-square, L_1 is the log-likelihood of the fitted model and L_0 is the log-likelihood of the null model (intercept-only model). ρ^2 has the desirable property of ranging between 0 and 1, which makes it analogous to R^2 . However, estimates of ρ^2 and R^2 are not entirely equivalent, and we used a rule of thumb that ρ^2 values higher than 0.2 indicate good fits. Low ρ^2 can be interpreted as expressing high levels of non-equilibrium or indicating failure to model the correct environmental or ecological drivers for species distribution.

Finally, the importance of each environmental driver in each geographical range model was established according to its odds ratio, and the variable with the highest importance identified. The odds ratio for an independent variable represents the proportion by which the odds of species presence change when there is a one-unit change in the independent variable. The odds ratio of a coefficient b can be calculated by $\exp(b)$. If $\exp(b)$ is larger than 1, b increases the logit and therefore also increases the odds of species presence. If $\exp(b)$ equals 1, the independent variable has no effect on the presence of the modelled species. If $\exp(b)$ is less than 1, the independent variable decreases the logit and the odds of species presence.

Based on the odds ratio defined above, the 'primacy' (*sensu* Field *et al.*, 2008) for each predictor was then calculated as the frequency across GLM models at which this predictor is the most important factor in modelling geographical ranges. All models were generated with the new logistic regression module included in the latest version of the Spatial Analysis in Macroecology program (SAM 3.0; see Rangel *et al.*, 2006).

Richness models

Four criteria of similarity among species, based on GLM modelling, body size, geographical range size and phylogenetic structure,

were used to obtain different sets of species and to calculate species richness: (1) species with geographical ranges having high and low fit in the GLM distribution models (above and below the median of McFadden's ρ^2 , which also approximates the heuristic value of 0.2 suggested above); (2) basal and derived species; (3) large- and small-bodied species (above and below the median of maximum total length); and (4) four classes of geographical range size (defined by the quartiles of the range size frequency distribution, RSFD). Thus, by overlaying geographical ranges for species within these categories we generated 11 different variables of species richness. This allowed us to test whether separating species into sets according to different criteria reveals different species richness patterns.

We used a principal components analysis (PCA) (Legendre & Legendre, 1998) to represent similarity among the 11 richness patterns based on deconstruction. Eigenvectors were extracted from the correlation matrix among pairs of richness and the broken-stick criterion was used to define the number of axes necessary to represent the similarity patterns. Richness patterns were also modelled against the five environmental variables through standard OLS multiple regressions, processed within a multimodel framework (Burnham & Anderson, 2002; Diniz-Filho *et al.*, 2008). First, we generated all possible different models that could be obtained by combining five predictors (i.e. 31), and calculated the Akaike weight (w_i) of each model, an AIC-derived index that reflects the probability that model i is actually the best explanatory model among all possible models. Then we combined these regression models into a summary model in which the standardized regression coefficient of each variable (reflecting its relative importance as predictor of richness patterns) corresponded to the w_i -weighted average of its coefficients in all models. These average regression coefficients are estimates of the relative importance of the variables as drivers of richness variation, and were retained for further analyses involving comparisons with the GLM range distribution results previously generated (see below). Finally, levels of spatial autocorrelation in model residuals were determined using Moran's I calculated globally at 20 geographical distance classes (Legendre & Legendre, 1998; Diniz-Filho *et al.*, 2003). All these analyses were also performed in SAM 3.0 (Rangel *et al.*, 2006).

Correspondence between drivers of species ranges and drivers of richness patterns

Extreme deconstruction can be tested by evaluating the degree of correspondence between factors driving species geographical ranges and patterns of species richness. This was done by calculating a Pearson correlation between the average regression coefficients of environmental variables on richness with the primacy values across range model GLMs. However, in principle, a single correlation can be obtained when analysing richness and geographical ranges for a given group of organisms. Thus, to replicate this correlation and provide a more general test of extreme deconstruction, we used the different subsets of species previously defined and obtained 11 sets of regression slopes for richness and primacy for geographical ranges.

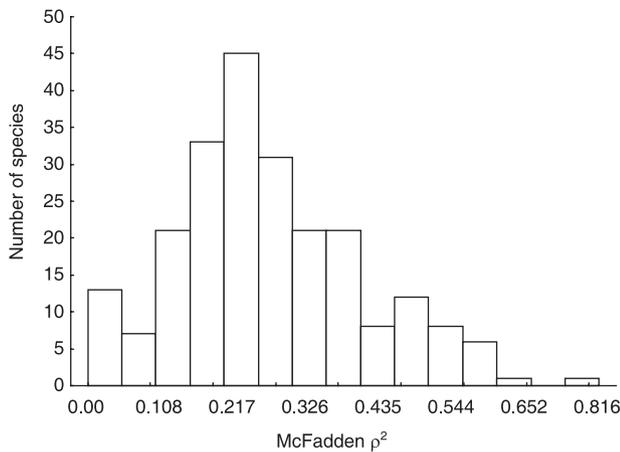


Figure 1 Frequency distribution of McFadden ρ^2 values (ranging from 0 to 0.816) from the 228 generalized linear modelling species distributions.

RESULTS

Modelling species geographical ranges

Values of McFadden's ρ^2 from the 228 GLMs modelling species distributions ranged from 0 to 0.816 (Fig. 1), with a median of 0.269. This indicates that about half of the viperid species have reasonable fit of their ranges to environmental variation. Notice that in our study McFadden's ρ^2 is not highly correlated with species geographical range ($r = 0.177$; $P = 0.05$ after taking into account the phylogenetic eigenvectors; see also Fig. 2a), so our conclusions will not be artefacts of prevalence (see Allouche *et al.*, 2006).

McFadden's ρ^2 is also not strongly phylogenetically structured ($R^2 = 0.125$ with 7 out of 20 eigenvectors selected by the AIC) nor can they be well predicted by log-transformed species body size ($r = 0.048$; $P = 0.02$ after taking phylogeny into account, see Fig. 2b). In general, McFadden's ρ^2 is not well predicted by simultaneous regression against phylogeny and any macroecological traits (body size and geographical range size) ($R^2 = 0.147$) across species.

Richness patterns

Overall, the richness of viperid snakes follows the well-known global diversity gradient, with high-richness cells concentrated in tropical regions (Fig. 3). The environmental model with five variables explained around 48% of the total variance in richness. Excepting a slightly higher effect of temperature and low effect of GVI, all environmental variables showed relatively homogeneous effects (Table 1).

Richness maps obtained by establishing sets of species according to different macroecological traits (i.e. geographical range size, body size, evolutionary level and environmental model fit of distributions) revealed different patterns across the world. The first component of the PCA used to represent similarity among the 11 sets of richness analysed explains only 38.8% of the variation

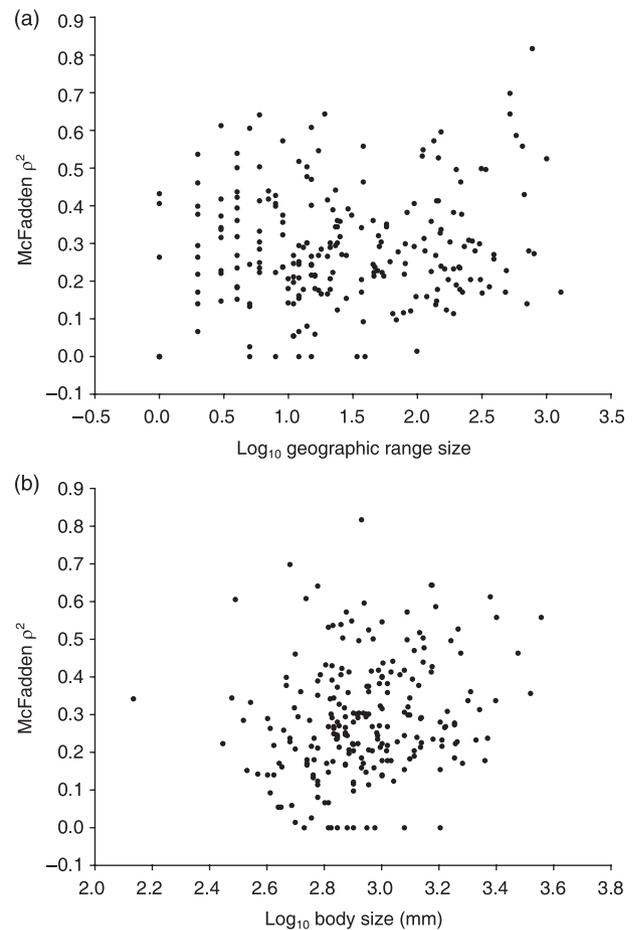


Figure 2 The relationships between McFadden ρ^2 values and Log_{10} -transformed geographical range size (a), and McFadden ρ^2 and Log_{10} -transformed body size (b) for the 228 viperid species. Geographical range size represents the number of occupied 1° cells by each species. Body size represents the maximum total length obtained for each species.

and, according to the broken-stick criterion, it is the only important direction of correlation among these sets. Higher loadings for this first axis are found for total richness, richness for large-ranged species, richness for small-bodied species and for derived species.

For geographical range size, maps showed that Central America and southern North America concentrate richness of small- and intermediate-ranged species (Fig. 4a,c), whereas South America and Central Africa hold high richness of large-ranged species (Fig. 4d). These differences were apparent in their environmental models as well. The R^2 s of richness models increase when dealing with large-ranged species, as previously found by Jetz & Rahbek (2001) and Rahbek *et al.* (2007) (Table 1). The average environmental model for large-ranged species richness explained up to 40% of the variation, and temperature was the most important environmental driver, followed by seasonality. For species with very small ranges, richness was also explained by temperature, but not seasonality, although the R^2 of richness was quite low anyway (see Table 1).

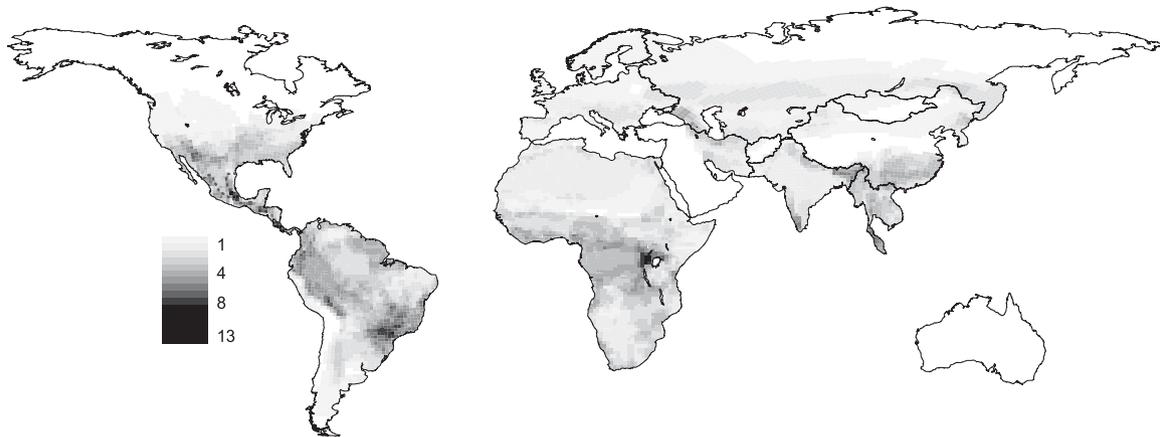


Figure 3 Global biogeographical patterns of Viperidae species richness.

For subsets of species distinguished according to body size (Fig. 5), high richness of small species occurs mainly in South America and Central Africa (Fig. 5a), whereas large species prevail in Central America and Southeast Asia (Fig. 5b). Environmental models, meanwhile, found no strong patterns of association between richness and environmental predictors for both species sets, as indicated by their relatively low explanatory power (around 20% in both cases), even though the importance of the variables in each model changed between them (Table 1).

Differences between the richness pattern for basal (Fig. 6a) and derived species (Fig. 6b) were quite strong (with all basal species occurring in the Old World and derived species in the New World), possibly reflecting the Afrotropical origin of Viperidae and their later expansion into New World. The five environmental variables explained around 50% and 35% of richness variation for basal and derived species, respectively, and temperature emerged as the most important predictor in both cases.

Modelling richness patterns for species with low ($\rho^2 < 0.269$) and high ($\rho^2 > 0.269$) fit in GLM range models (see Fig. 7a,b) as described above, revealed a similar overall explanatory power of the environmental variables (i.e. around 45%, although using high-fit models gives slightly higher R^2) (Table 1). However, the coefficients of these models are slightly different, with a marked effect of temperature and precipitation in both richness models, but a high effect of GVI when modelling richness for species with high-fit range models and a high effect of seasonality when modelling richness for low-fit range models. It is also interesting to note that the predictor's odd ratios in low-fitted GLMs exhibited little variance, matching the 'concentration' of explanatory power in a single predictor for species richness (mainly in precipitation). On the other hand, OLS models of richness based on species with high-fit GLM exhibited less concentrated effects of precipitation, GVI and temperature, which is consistent with a larger variance in the standardized coefficients of GLM for each species.

Testing extreme deconstruction principle

The similarity between the environmental drivers of the richness models (i.e. the standardized OLS coefficients for each richness

subset) and those on the GLM distribution models (i.e. the primacy of variables across species geographical range models) was equal to 0.645 when analysing all viperid snakes. Thus, in general, when an environmental predictor is important in modelling species geographical ranges, this predictor is also important when modelling richness.

However, replicating this correlation using subsets of species within different categories in body size, range size and phylogenetic structure gives more variable results, and correlations between GLM and OLS coefficients vary from -0.46 up to 0.83 (Table 1), depending on the dataset used. This variation in correlations would suggest problems with the extreme deconstruction and would eventually reveal that emergent properties are explaining richness patterns, independently of the processes acting at species geographical ranges. However, there is a relatively high correspondence ($r' = 0.73$; Table 1; see also Fig. 8) between the similarity of GLM-OLS coefficients (r values in Table 1) and R^2 values of richness models, which indicates that when richness is well-explained by the environment (high R^2), the relative importance of environmental drivers is similar in the richness OLS and its corresponding set of GLMs.

DISCUSSION

Richness deconstruction

The strong correspondence between environmental data and current patterns in species richness is well known (see Hawkins *et al.*, 2003). However, it is becoming clear that, independent of the ecological processes driving species richness, this high correspondence may appear because of common non-environmental components related to the geography and climate history of the Earth (Wiens & Donoghue, 2004; Rangel *et al.*, 2007). These non-environmental components create problems for interpreting richness patterns; thus it becomes important to find better approaches to evaluate mechanisms underlying the correlations between richness and environment, and one of the possibilities is to use species ecological characteristics to explain why these correlations arise.

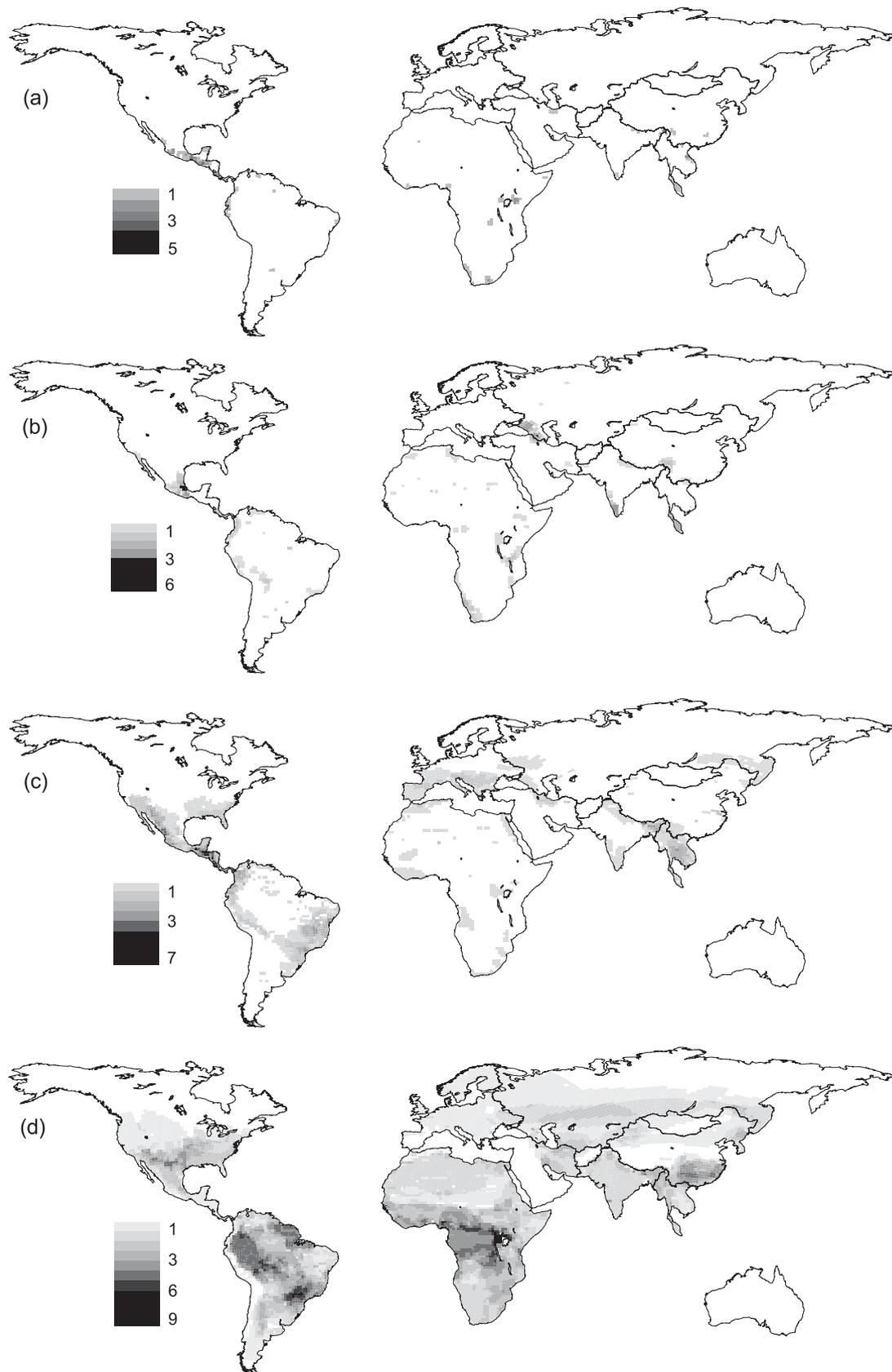


Figure 4 Global richness pattern of viperid species with: (a) small, (b) small to intermediate, (c) intermediate to large and (d) large range sizes. Range size was obtained by counting the number of cells in which each species occurs, and four classes of richness based on geographical range sizes were defined by the quartiles of the range size frequency distribution (RSFD).

Table 1 Summary of environmental models for total and deconstructed sets of richness. Upper rows in each model represent the results from the multimodel selection Akaike information criterion: R^2 's and the w_i -weighted averaged standardized regression coefficients resulted from averaging the coefficients of all 31 possible models with five predictors. Lower rows (in bold and italics) represent the primacy of each predictor, i.e. the importance frequency of each predictor across individual species' generalized linear model distribution models. In the right-most column (r) are the Pearson correlation values between the standardized coefficients (upper line) and primacy (lower line) of each model. r' is the correlation between R^2 and r values.

Richness	R^2	Temp.	Precip.	GVI	Elev.	Season	r
Total	0.476	0.318 0.360	0.204 0.219	0.149 0.167	0.211 0.048	0.223 0.140	0.675
Geographical ranges							
Small	0.073	0.287 0.35	0.005 0.17	0.03 0.15	0.27 0.04	0.039 0.17	0.201
Small–intermediate	0.003	−0.029 0.389	0.013 0.241	−0.025 0.148	< 0.001 0.074	0.045 0.167	−0.462
Intermediate–large	0.100	0.171 0.296	0.129 0.259	0.081 0.185	0.191 0.074	0.010 0.111	0.239
Large	0.403	0.295 0.481	0.190 0.241	0.119 0.222	0.027 0.019	0.214 0.130	0.832
Body size							
Small	0.233	0.252 0.333	−0.050 0.237	0.205 0.202	0.217 0.053	0.251 0.079	−0.227
Large	0.224	−0.005 0.389	0.209 0.204	0.001 0.133	0.170 0.044	0.256 0.195	−0.385
Phylogeny							
Basal	0.491	0.427 0.386	0.141 0.210	0.224 0.210	0.142 0.017	0.188 0.070	0.830
Derived	0.342	0.474 0.350	0.015 0.140	0.039 0.105	0.251 0.087	0.238 0.210	0.784
Distribution model							
Low ρ^2	0.448	0.197 0.327	0.379 0.274	0.032 0.159	0.08 0.035	0.216 0.080	0.524
High ρ^2	0.463	0.231 0.391	0.351 0.165	0.323 0.174	−0.077 0.061	−0.07 0.200	0.352
				$r' =$			0.734

Temp., mean annual temperature; Precip., annual precipitation; GVI, annual global vegetation index; Elev., range in elevation; season, seasonality.

Marquet *et al.* (2004) suggested that a promising strategy for associating ecological characteristics of species and their richness patterns would be the decomposition of richness into subsets of ecologically homogeneous groups prior to analysis. In our study, deconstruction of species richness based on macroecological traits revealed that, at least for range size and phylogenetic level, the causes underlying patterns in richness may be different across different subsets of richness. For range size, our results for viperid snakes in principle match those of Jetz & Rahbek (2002) and Rahbek's *et al.* (2007) for birds, as we also found that environmental models successfully explained large-scale richness patterns of wide-ranging species but not those of small-ranging ones (as measured by regression R^2). Viperid species with small (and small to intermediate) ranges are mainly concentrated in Central America and along the continental edges of South America, Africa and India, which could reinforce the idea that the area and geometric constraints effects in geographical or niche space (Jetz & Rahbek, 2001, 2002; Rangel & Diniz-Filho, 2005b) or even assembly-level processes (predation, competition)

(see also Rahbek *et al.*, 2007) are also substantially important in determining species richness patterns.

On the other hand, Hawkins & Diniz-Filho (2006) showed, based on New World bird data, that differences in factors explaining richness for species with different range sizes may be related to mountain effects and, thus, may not reflect differences in factors *per se*, but only scale issues related to how effects are measured. Although this may be difficult to test directly, our results, at least in part, reinforce this alternative interpretation because the primacy for temperature is higher than all others and similar for all range size classes except for small to intermediate ones (although coefficients for richness vary in a more idiosyncratic way). Thus, differences in the explanatory power of environmental variables may be more related to scale issues and problems related to high measurement errors in small ranges than to historical or stochastic processes driving ranges with different sizes.

Patterns of richness deconstructed according to body size were weakly explained by the environmental models, for both small

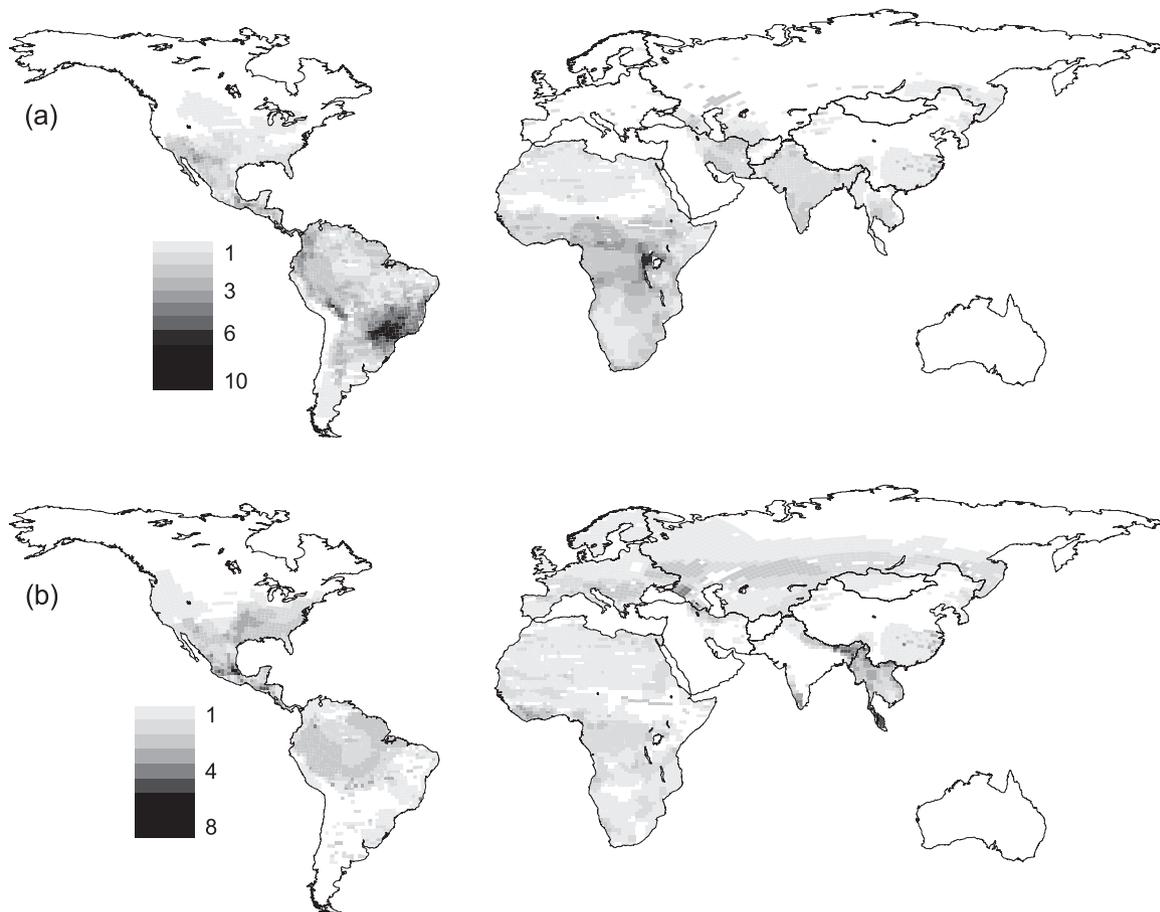


Figure 5 Global richness pattern of (a) small-bodied and (b) large-bodied viperid species. Maximum total length was used as a measure of body size, and two classes of richness (large- and small-bodied species) were obtained based on body sizes above and below the median of maximum total length.

and large-bodied viperids (R^2 s around 20%). Although the coefficients of determination of the models for both size classes were relatively small, it is worth noting that the importance of the predictors (indicated by the regression coefficients) changed considerably between the two models (except for seasonality, which had similar importance in both cases). Large- and small-bodied species occur in different regions, so it is possible that other factors (e.g. historical effects, differences in extinction and dispersal rates) are unequally influencing richness in these two sets of species. Another possibility is that environmental drivers do not affect the richness of large-bodied and small-bodied species *per se* but instead affect the relative balance of species with different body sizes within assemblages. Therefore, it is difficult to decouple the environmental drivers based on richness and the historical events generating diversification of body sizes.

For phylogeny, the clear longitudinal difference in the richness patterns of basal species (with higher richness values concentrated in Africa and, to a lesser extent, in Eurasia) and derived species (higher richness across the New World) is consistent with the evolutionary hypothesis of an Old World origin of the viperid ancestor, and subsequent expansion into the New World (see Parkinson, 1999; Lenk *et al.*, 2001). Additionally, the different importance of the current environment for basal and derived

clades (R^2 of average models is 0.491 and 0.342, respectively; difference in $R^2 = 0.149$) suggests some component of niche conservatism (*sensu* Wiens & Donoghue, 2004) in geographical richness patterns of viperids, with the most recent species being less determined by current environment than basal species. A possible explanation for these differences is that the group originated in environments more similar to current tropical habitats (see Lenk *et al.*, 2001), and that subsequent global changes that created temperate regions also caused rearrangements in the geographical distribution of the basal taxa, thus generating a trend for species to accumulate towards areas showing more similar conditions (i.e. tropical regions) to those prevailing in their ancestral niches (see Hawkins *et al.*, 2005, for similar trends and niche conservatism explanations in Australian birds). In contrast, most newly derived species may have appeared in, and adapted to, different and varied environments, which may explain why they show weaker relationships with current environmental gradients. Interestingly, differences of nearly identical magnitude between basal and derived clades in terms of predictive power of current environment models were found by Hawkins *et al.* (2007) for global patterns in terrestrial bird richness (basal bird richness $R^2 = 0.717$; derived bird richness $R^2 = 0.545$; difference in $R^2 = 0.172$), thus supporting

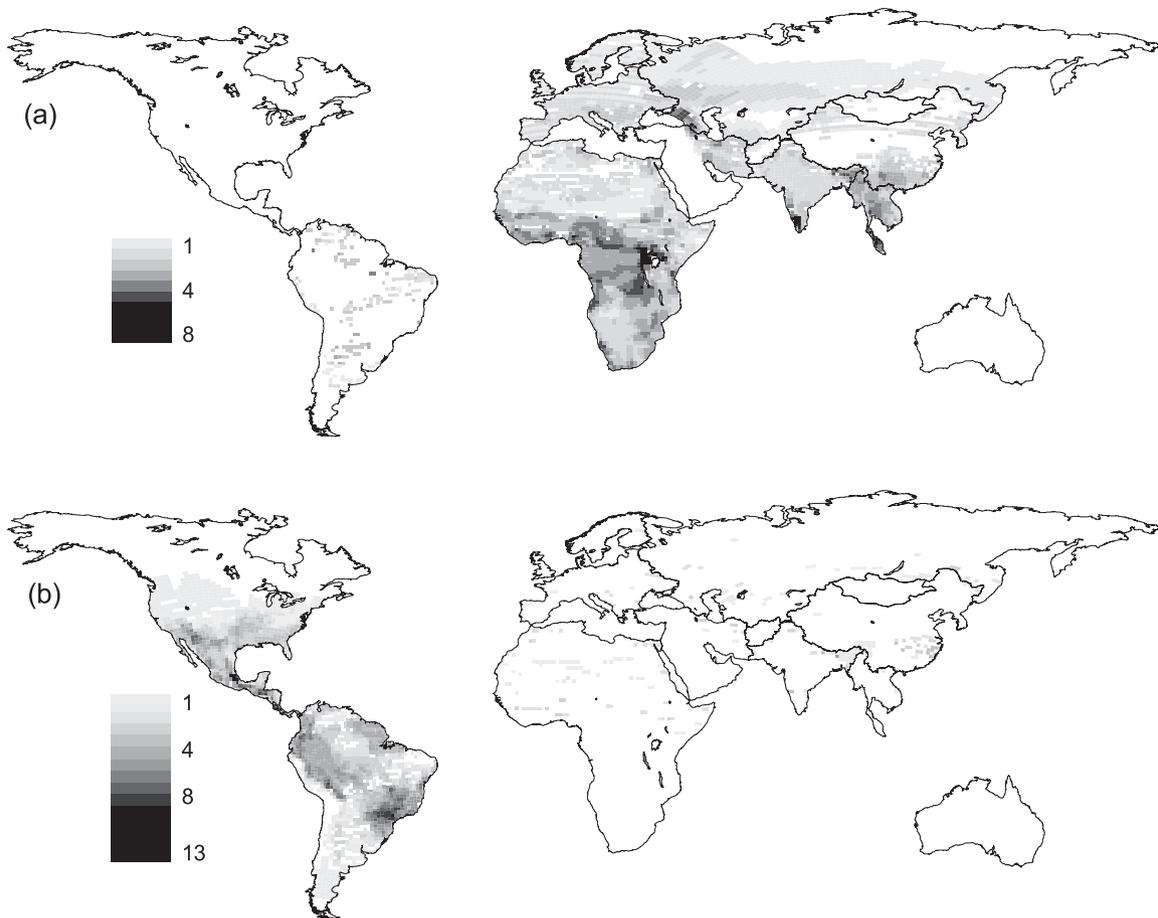


Figure 6 Global richness pattern of (a) basal and (b) derived viperid species. Sets of basal and derived species were identified, respectively, using the lower and upper quartiles of the count of number of nodes between each species and the root of the phylogenetic tree. Phylogenetic relationships among species were established at genus level using a phylogenetic tree that was built by combining the phylogenies by Lenk *et al.* (2001), Malhotra & Thorpe (2004) and Castoe & Parkinson (2006).

the prediction of these authors that niche conservatism would be shown to influence many groups.

Thus, the results of the 'standard' deconstruction approach described above furnish some insights about richness patterns and are in agreement with previous findings in the literature. The next step is then to think whether this idea can be pushed more so that ecological drivers of each species' geographical range can also be associated with the drivers explaining species richness.

Extreme deconstruction

Our analysis shows that, across all viperid species, environmental predictors that are important to explain species geographical ranges are also important when modelling species richness, so that the extreme deconstruction principle applies. Moreover, the 'standard' deconstruction approach described above provides 'replications' for supporting our extreme deconstruction principle, and shows that, because richness results from the overlap of geographical ranges, drivers of species distributions must also create patterns in species richness. Thus, our analyses support the idea that richness patterns may indeed be viewed as

macroecological consequences of population-level processes acting on species geographical ranges (see Gaston, 2003, for an overview, and Colwell *et al.*, 2004, and Rangel & Diniz-Filho, 2005b, for related discussions on mechanisms underlying mid-domain patterns). In other words, if environmental drivers determine the geographical distribution of species through the establishment of niche boundaries, it is expected, at least in theory, that the overlap among ranges will reveal similar effects of these environmental drivers.

However, it is clear that the causes driving species ranges will not always be responsible for their overlap pattern (*i.e.* richness), mainly because amounts of range overlap and the shape, location and size of these ranges might also arise due to non-environmental effects of different sorts. Non-environmental effects can affect species ranges just as much as they affect range overlap. For example, apparent differences in drivers will appear if richness is partially determined by additional components to those that determine species distributions, such as assemblage rules for communities. These effects will not cause differences in drivers for individual species and richness *per se*, but they weaken the correlation between GLM and OLS coefficients, and perhaps

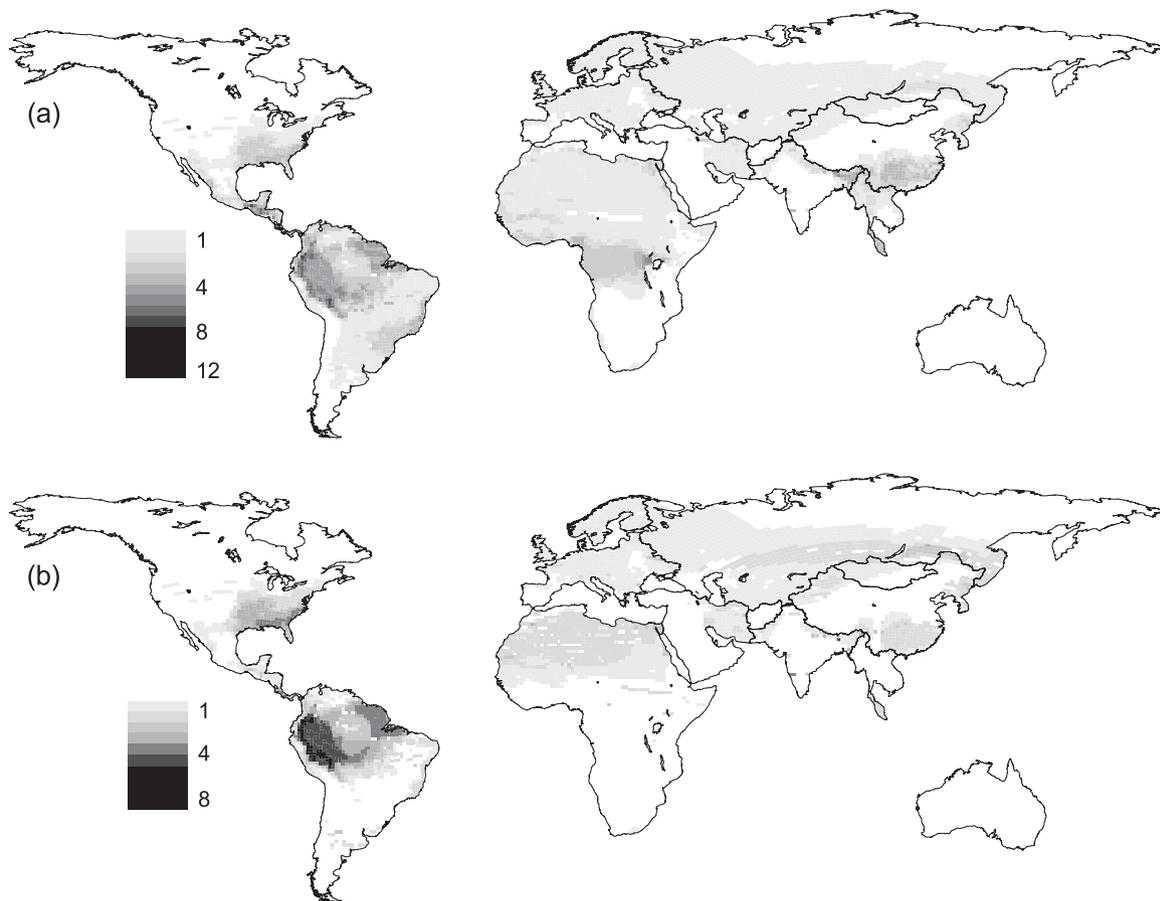


Figure 7 Global richness pattern of viperid species that have (a) low and (b) high fit of their ranges to environmental variation (i.e. species with lowest and higher McFadden ρ^2 in the generalized linear models ranges, respectively).

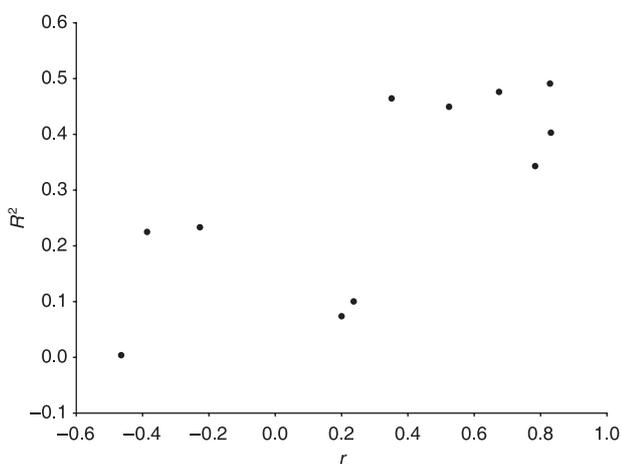


Figure 8 The relationship between R^2 values from each richness model and the similarity r values (r values are the correlation between the w_i -weighted averaged standardized regression coefficients of the five environmental predictors and the primacy of each predictor, i.e. their importance frequency across individual species' generalized linear model distribution models).

explain residual variation in the relationship between similarity GLM-OLS and the magnitude of environmental effects on richness (see Fig. 8).

In a general sense, historical processes are usually used to explain these deviations, but it is difficult to establish exactly how to define (and measure) 'history' in different time-scales. De Marco *et al.* (2008) recently showed that, for example, even when ranges are fully determined by environmental variation, a colonization lag will appear as non-equilibrium when modelling geographical distribution using niche models (i.e. Maxent), and this is actually a form of historical process causing a lack of high environmental effects. Indeed, our analysis also shows that although correlations between GLM-OLS results vary, they are at the same time correlated to the amount of environmental signal in richness (Fig. 8). Although it is not possible, as previously discussed, to establish if lack of fit is due to historical effects or a lack of relevant environmental predictors, this reinforces that, when models are well defined for both species richness and geographical ranges, the important predictors tend to be the same.

But it is important to realize that richness patterns in sets of species with low and high GLM fit are explained to more or less

the same extent by environmental factors, reinforcing that a lack of fit in GLM can be better explained by historical non-equilibrium and not due to missing crucial environmental predictors. The idea is that overlap of range can be due to historical factors (such as niche conservatism, also supported by our analyses based on derived and basal sets of species), so that correlations of richness appear at least in part purely as an indirect consequence of historical processes related to the geography and climate history, and not due to responses of each species to current environment (see Rangel *et al.*, 2007).

In a more methodological sense, some studies of species richness–environment relationships (e.g. Wisz *et al.*, 2007; Costa *et al.*, 2007; Terribile & Diniz-Filho, 2008) have started by using niche models (based on environmental variables) to generate predicted geographical ranges of species and, by overlapping them, the species richness values that were later related with the same (or similar) drivers to look for explanations of the patterns found. This sounds tautological in principle, and may actually inflate the effects of some drivers, but the logic underlying this discussion relies on the idea that both range patterns and their overlap (richness) may reflect the same processes appearing at different scales. Actually, any definition of a geographical range, independently of using a niche-based model (or other form of species distribution modelling), will generate bounds and patterns in environmental space because of spatial autocorrelation in the environment.

In summary, our study showed that using deconstructive analyses of richness may be useful to unveil different processes acting at different scales on present-day patterns of species richness. More importantly, taking this idea to an extreme, it is clear that if environmental factors strongly determined the distribution of individual species, it is likely that species overlap (richness) is associated with the same factors. Of course, deeper studies are necessary to improve the methods to be used in extreme deconstruction, especially methodological developments which are needed to better link richness models and species distribution (or niche) models in terms of parameter estimates of environmental factors. Also, it is important to better establish the conceptual relationships between deep-time historical processes explaining richness and term processes creating non-equilibrium species distribution. In this way, our analysis is a first step, showing that more dialogue is needed between ecologists interested in modelling species richness and those interested in modelling species distributions, a separation that is actually more due to alternative traditions in geographical ecology than to real differences in methods and theoretical issues.

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