

Global richness patterns of venomous snakes reveal contrasting influences of ecology and history in two different clades

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Abstract Recent studies addressing broad-scale species richness gradients have proposed two main primary drivers: contemporary climate and evolutionary processes (differential balance between speciation and extinction). Here, we analyze the global richness patterns of two venomous snake clades, Viperidae and Elapidae. We used ordinary least squares multiple regression (OLS) and partial regression analysis to investigate to what extent actual evapotranspiration (AET; summarizing current environmental conditions) and biogeographical regions (representing evolutionary effects) were associated with species richness. For viperids, AET explained 45.6% of the variance in richness whereas the effect of this variable for elapids was almost null (0.5%). On the other hand, biogeographic regions were the best predictors of elapid richness (56.5%), against its relatively small effect (25.9%) in viperid richness. Partial

regressions also revealed similar patterns for independent effects of climate and history in both clades. However, the independent historical effect in Elapidae decreased from 45.2 to 17.8% when we excluded Australia from the analyses, indicating that the strong historical effect that had emerged for the global richness pattern was reflecting the historical process of elapid radiation into Australia. Even after excluding Australia, the historical signal in elapid richness in the rest of the globe was still significant and much higher than that observed in viperid richness at a global scale (2.7% after controlling for AET effects). Differences in the evolutionary age of these two clades can be invoked to explain these contrasting results, in that viperids probably had more time for diversification, generating richness responses to environmental gradients, whereas the pattern of distribution of elapid richness can be more directly interpreted in an evolutionary context. Moreover, these results show the importance of starting to adopt deconstructive approaches to species richness, since the driving factors of these patterns may vary from group to group according to their evolutionary history.

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Introduction

As a result of the interest of ecologists in large-scale diversity gradients and their determinants over the last two centuries (von Humboldt 1808; Hutchinson 1959; Pianka 1966; Glazier 1987; Currie 1991; Hawkins et al. 2003a), there have been considerable advances in our knowledge about the most important drivers of global patterns in species richness (Hawkins et al. 2003a, b, 2007a; Ricklefs

2003; Willig et al. 2003; Wiens and Donoghue 2004; Wiens et al. 2006a). Research on this subject has evolved into two well-founded frameworks: contemporary climate influences diversity gradients through energy inputs and/or water availability (Currie 1991; Francis and Currie 1998; Hawkins et al. 2003a; Rodríguez et al. 2005; Kreft and Jetz 2007; Buckley and Jetz 2007); and evolutionary history determines broad-scale richness patterns through a number of potential mechanisms such as niche conservatism, older age and stability of tropical regions, geographically structured variation in speciation and extinction rates, and differential species' dispersal capabilities of colonizing new areas (Latham and Ricklefs 1993; Ricklefs 2003; Hawkins et al. 2003b; Jablonski et al. 2006; Buckley and Jetz 2007; Mittelbach et al. 2007; Montoya et al. 2007; Svenning et al. 2008).

Ecological hypotheses based on the contemporary climate have been intensively tested over the past 50 years (see Hawkins et al. 2003a for a revision), and there is a consensus in that energy, through direct or indirect effects (via plant productivity), drives higher diversity in the tropics. However, it is also important to consider the evolutionary mechanisms underlying patterns in richness. In general, historical hypotheses assume that the tropics support more species due to two reasons: the tropics are older and historically larger than temperate regions, so they accumulated more species over time and/or; tropical regions have higher diversification rates due to higher speciation and lower extinction rates (see Mittelbach et al. 2007 for a recent review of hypotheses). Even so, we still lack good explanations for how environmental (or ecological) factors interact with evolutionary mechanisms to generate current geographic gradients in species richness, although recent studies have proposed hypotheses based on niche conservatism as a way of integrating ecology, evolution and historical biogeography to explain these gradients (see Wiens and Donoghue 2004; Wiens et al. 2006a; Ricklefs 2006; Hawkins et al. 2005, 2007a; Rangel et al. 2007). Moreover, the paucity of global datasets for a wide array of organisms prevents us from proposing a general explanation for all taxa as well as limiting our abilities to test the suggested ecological and evolutionary hypotheses underlying the patterns. Hence, if we are to understand the large-scale richness patterns and the causes underlying them, we need to consider the particular responses of different taxonomic groups.

For vertebrates, the available distributional databases and studies of gradients richness with a global coverage are those for fishes (Oberdorff et al. 1995), amphibians (IUCN 2006; Buckley and Jetz 2007), birds (Hawkins et al. 2003b, 2007a; Orme et al. 2005), and mammals (Ceballos and Ehrlich 2006). Overall, reptiles remain insufficiently documented in the macroecological and biogeographical

literature and only a few studies have examined the existence of broad-scale richness gradients for this group (Schall and Pianka 1978; Owen 1989; Rodríguez et al. 2005; Costa et al. 2007). Furthermore, most of these studies have been geographically restricted to temperate regions, which limits the generalizability of their findings (e.g., Rodríguez et al. 2005). For snakes, the only investigation focused on macroecological patterns is the one by Reed (2003) and, as far as we know, there are neither global datasets nor global richness analyses for any group of reptiles (but see Lamoreux et al. 2006, for an analysis using species list on WWF ecoregions).

In this paper we present a global analysis of the richness patterns of two monophyletic clades within Caenophidia (the “advanced snakes”): Viperidae and Elapidae (Knight and Mindell 1994; Vidal and Hedges 2002; Kelly et al. 2003; Vidal et al. 2007). Although the snakes in these two families are similar in that they have front-fanged venom systems, they arose independently from non-venomous snake ancestors (Knight and Mindell 1994). Based on fossil venom fangs from the Lower Miocene, Kuch et al. (2006) dated the evolution of both Viperidae and Elapidae from the Early Cenozoic, thus stating that both clades evolved at the same time and before colubroid radiations of Miocene. However, studies inferring divergence times within snakes suggested that viperids diverged from colubroids between 60.9 and 43.0 million years ago (Rage et al. 1992; Wiens et al. 2006b). Recently, estimates of age clade provided by Sanders and Lee (2008) suggest that viperids evolved between 48.9 and 31.0 million years ago (mean divergence at 39.9 million years ago; see also Szyndlar and Rage 1999; Lenk et al. 2001 for similar conclusions), whereas elapids diverged between 32.2 and 21.1 million years ago (mean divergence at 26.2 million years ago). The study of Sanders and Lee (2008) is consistent with previous assertions of Heise et al. (1995), Keogh (1998), and Kelly et al. (2003), which proposed that Elapidae is a more recent clade in comparison with Viperidae. Taken into account the recent discussion about niche evolution and niche conservatism (see Peterson et al. 1999; Wiens and Donoghue 2004; Pearman et al. 2007), this evolutionary aspect is important if one consider that a “younger” clade had less time to disperse, diversify and adapt to new climatic conditions.

Here, we investigate whether current global richness patterns of Viperidae and Elapidae are associated with contemporary environmental variation or still reflect a signal of historical effects (barrier for dispersal, speciation, and extinction) considering the difference in evolutionary age between both lineages (i.e., the more recent origin of Elapidae). For this, we tested the relative importance of the current environment (present climate and primary productivity conditions) and history (biogeographical zooregion) to account for the global richness patterns of each clade. We

also investigate the differences in historical and environmental effects across six zooregions, which allows us to identify a potential role for history in the current richness pattern of viperid and elapid snakes.

Materials and methods

Viperidae comprises around 256–260 species (Kelly et al. 2003; Castoe and Parkinson 2006) that are distributed across mainlands and islands of Asia, Africa, Europe and the New World, but are absent from Australia, possibly because the advanced caenophidians evolved during the Cenozoic (from 65.5 million years ago) when this region had already become a separated landmass (Keogh 1998). Elapidae comprises about 290–300 species (Keogh 1998; Castoe et al. 2007) of which around 60 are marine (sea snakes), and is distributed across Africa, Asia, Australia, the New World, and the Indian and Pacific Oceans. These two families represent around 20% of the caenophidians diversity (Kelly et al. 2003; Vidal et al. 2007), but are the only families within this large group for which distributional data is available at a global scale.

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). Following this checklist, we used several sources of species distribution worldwide (see below) to obtain geographic 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 the mainland to warrant that richness patterns are not affected by island effects. Data scarcity for the Arabian Peninsula precluded the inclusion of this region in the analysis, and sea snakes were excluded because their distribution is likely to be conditioned by different environmental factors than terrestrial species. Thus, our final database comprised 228 viperids and 224 elapids (a full list of genera and number of species is provided in the Electronic supplementary material S1).

For the New World, species range maps were primarily obtained from Campbell and Lamar (2004), supplemented with the new species recently recognized by Renjifo and Lundberg (2003), Alvarado-Díaz and Campbell (2004) and Lavin-Murcio and Dixon (2004). For the Old World we used Branch (1988, 1998), Latifi (1991), Arnold (2002), Arnold and Oviden (2002), Broadley and Doria (2003), Spawls et al. (2004), Ananjeva et al. (2006), Vogel (2006), Dobiey and Vogel (2007), supplemented by Cherlin (1981), Orlov and Tuniyev (1990), Tuniyev and Ostrovskikh (2001), Khan (2002), Mallow et al. (2003) and Geniez and Tynié (2005). For Australian elapids we used Wilson and Swan (2003). All maps were digitized and rasterized in ArcGIS 9.2 in grid systems of

110 × 110 km using region-specific equal area projections. Species richness was calculated directly from the raster files. Although used for representation purposes, those cells containing less than 50% of the land mass were not included in the analyses to avoid potential area effects in the results.

To examine the influence of environment on richness patterns, we first considered seven variables that have been commonly used to analyze broad-scale diversity gradients. These included the total annual sums of Thornthwaite's actual evapotranspiration (AET), precipitation, Priestley–Taylor's potential evapotranspiration, and the global vegetation index, as well as mean annual temperature, the number of months available for plant growth, and range in elevation (i.e., the difference between maximum and minimum elevation within each grid cell) (data sources and processing techniques can be seen in Olalla-Tárraga et al. 2006 and Rodríguez et al. 2008). However, these variables typically have strong collinearity, which may cause misinterpretations of environmental models involving multiple predictors. In fact, in our dataset, AET, which represents the joint availability of energy and water in the environment (see Currie 1991 and Hawkins et al. 2003a), was a linear combination of the remaining environmental predictors, with $R^2 = 0.882$. Thus, we used AET as a surrogate of current environmental variation in our environmental models of richness.

To take into account evolutionary (or historical) effects in a broad sense (see Hawkins et al. 2003b; Buckley and Jetz 2007; Hortal et al. 2008), we classified the dataset according to six biogeographic regions: North American, South American, Eurasian, African, Oriental and Australian (Cox 2001). These biogeographic regions are based on the historic distribution patterns of plants and animals and were used here as a surrogate of the evolutionary history of Viperidae and Elapidae. Even though the use of biogeographic regions can be considered a relatively crude measure of historical contingencies on geographical patterns of species richness, this has proved to be a successful proxy variable to represent differential speciation and extinction rates and interregional barriers to dispersal (Hawkins et al. 2003b; Buckley and Jetz 2007; Hortal et al. 2008).

We investigated to what extent AET (a continuous variable summarizing current environmental conditions) and region (a categorical variable) were associated with species richness using ordinary least squares multiple regression (OLS), coupled with variance partitioning using partial regression analysis (Legendre and Legendre 1998; Hawkins et al. 2003a). For each multiple regression model, influence of spatial autocorrelation in model residuals was assessed by Moran's I coefficients (Diniz-Filho et al. 2003), and since some autocorrelation coefficients were high, we repeated the partial regression analyses based on R^2 derived from a simultaneous autoregressive error model (SAR; see

Dormann et al. 2007; Kissling and Carl 2008; Araújo et al. 2008). However, because the sample size is too large for spatial modeling, we created ten subsamples with 1,000 randomly chosen cells (see Hawkins et al. 2007a) and ran SAR for each subsample, obtaining the partial regression for each one. Before all statistical analyses, cells containing zero species were excluded. For the remaining cells, richness was transformed to its square root because of the relatively low number of species in some cells, which tend to produce a strongly non-normal distribution of model residuals in the original (count) scale. All statistical analyses were performed using SAM 3.0 (Spatial Analysis in Macroecology; Rangel et al. 2006).

Results

Global viperid diversity increases towards the equator (Fig. 1a) and the map of richness is analogous to those published earlier for other vertebrates at a global scale (Hawkins et al. 2003b; Ceballos and Ehrlich 2006; Grenyer et al. 2006; Buckley and Jetz 2007). Regions with the highest

richness include Central Africa, eastern and extreme southern parts of India and extreme southern Asia.

Elapidae has an almost exclusively tropical distribution (Fig. 1b). The group is most diverse on the east coast of Australia, where one cell (12,100 km²) might reach 25 species. However, compared to Australia, elapid richness is very low in other regions, where the highest richness values do not reach more than ten species per cell.

Viperid species richness was more strongly associated with AET (which accounted for 45.6% of the variance, though this amount varied across regions, see Fig. 2a) than with biogeographic regions (25.9%) in simple regression models including only one of these variables, suggesting that history is less important than environment in determining the richness patterns of this clade. Consistent with this interpretation, a full model that included AET and regions, explained little more variance than AET alone (48.3%), with AET accounting for 22.4% variance after controlling for regional effects, and region for only 2.7% after controlling for AET effects (Fig. 3a). Still, the amount of variance that was explained by the overlap of AET and region was relatively high (23.2%; see Fig. 3a). So, although our data

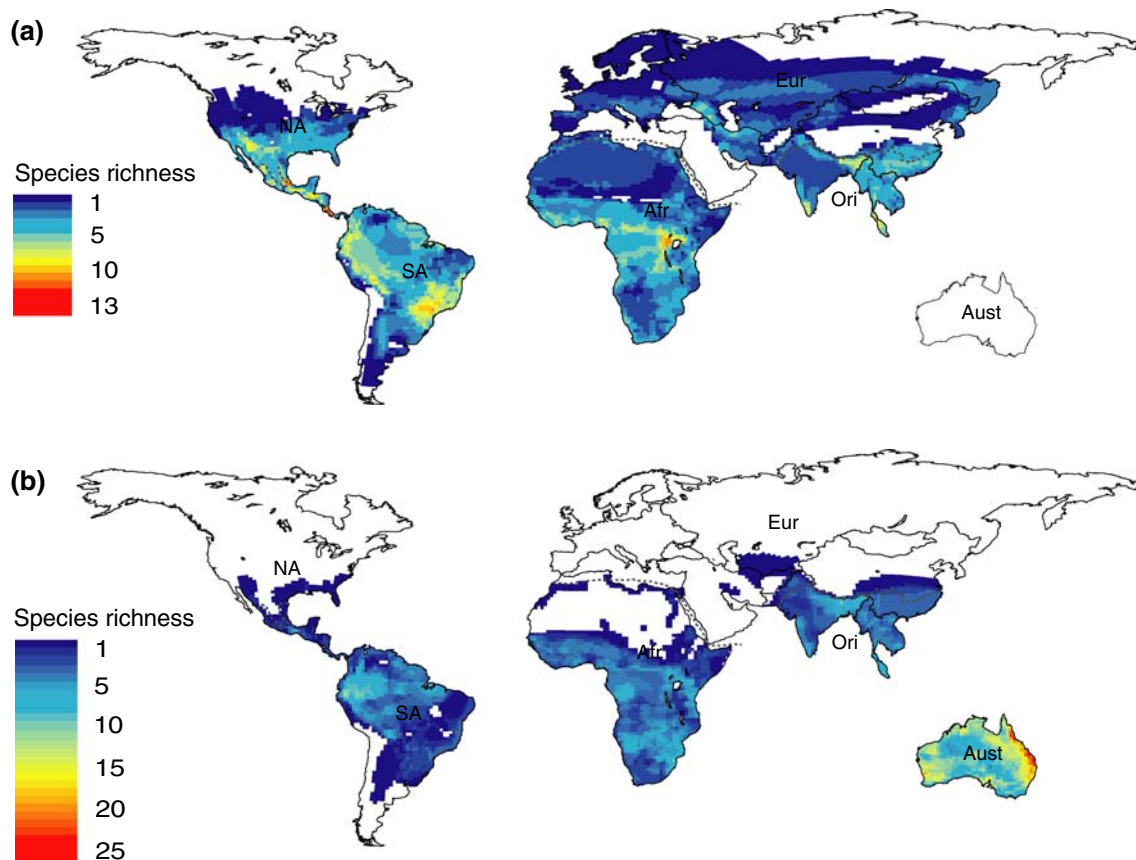
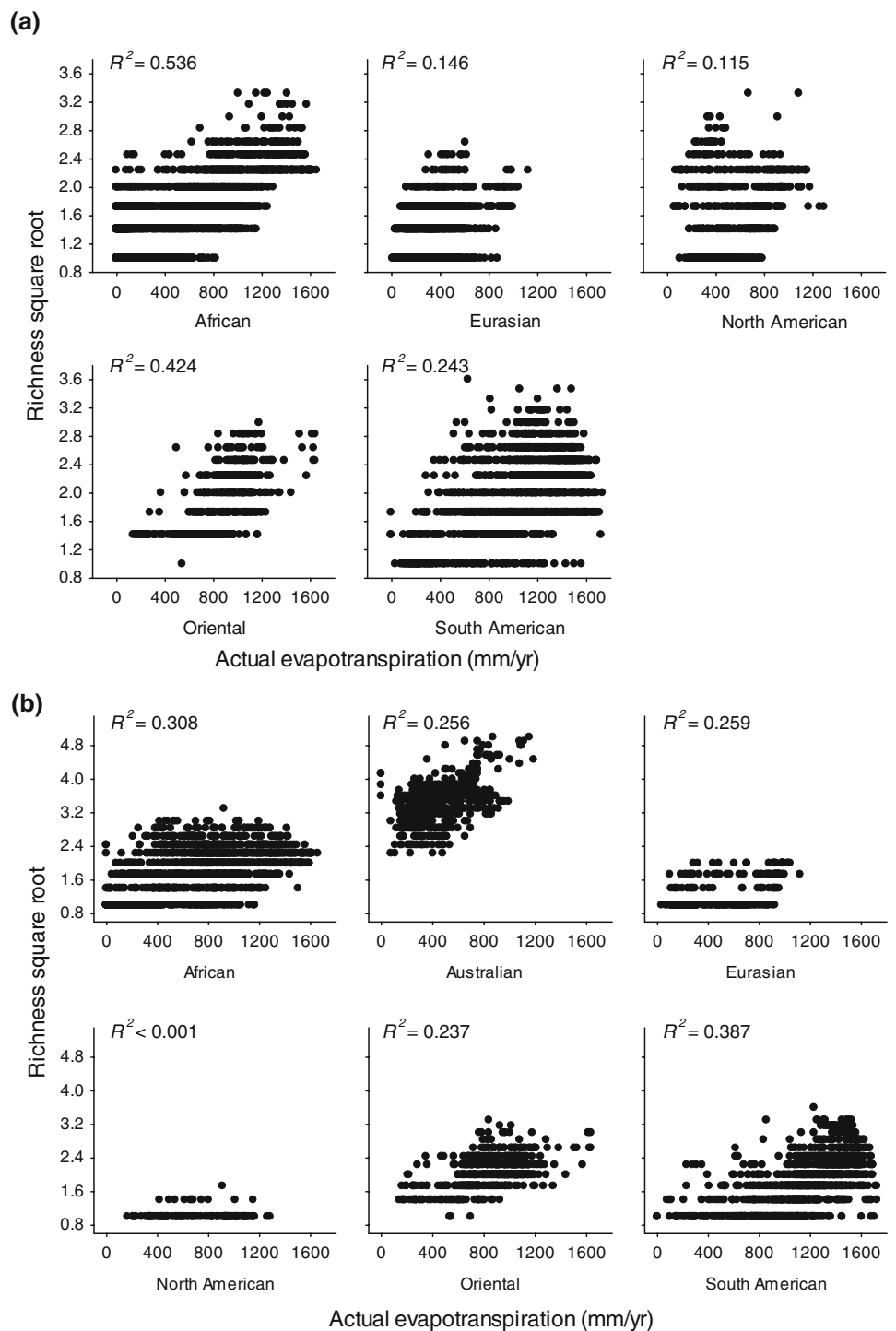


Fig. 1 Global biogeographical patterns of Viperidae (a) and Elapidae (b) species richness. The dashed lines identify the biogeographical limits of Cox (2001) used in our analyses. NA North American, SA South American, Afr African, Eur Eurasian, Ori Oriental, Aust Australian

Fig. 2 Relationships between actual evapotranspiration (AET) and species richness of Viperidae (a) and Elapidae (b) in each biogeographic region. *yr* Year



support current water–energy dynamics as the primary determinant of viperid richness at the global scale, they also suggest some secondary role for history, the complete extent of which is uncertain given the amount of variance that is explained jointly by region and AET.

For elapids, the current environment model (i.e., including only AET) accounted for just 0.5% of the variance, and species richness values were almost evenly distributed

across all AET values in all regions (Fig. 2b). In contrast, the historical model (i.e., including only regions) had a much higher coefficient of determination ($R^2 = 0.565$), suggesting that history is a considerable determinant of species richness of this group at the global scale. The full model, with AET and regions, explained 68.3% of the variance in richness, and partial regressions revealed that AET tend to a negative value (which indicates that AET had actually no

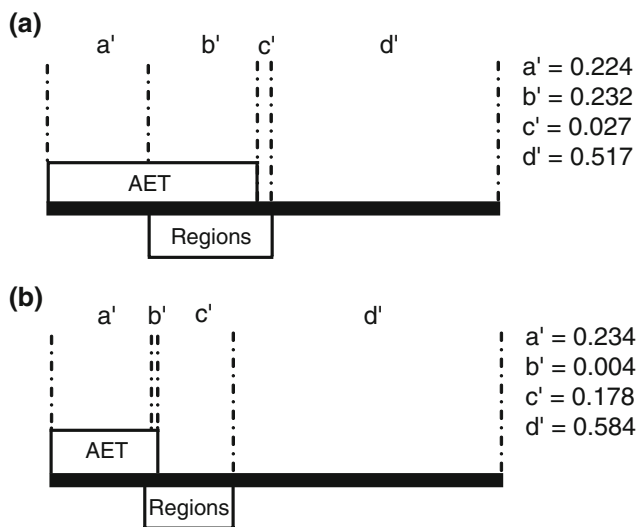


Fig. 3 Results of partial regression analyses using AET and biogeographic regions as predictors of global patterns in snake richness; **a** Viperidae and **b** Elapidae (in this case, Australia was excluded from the analyses of partial regression due to the strong interactive effect between this region and AET, see explanations in the text). The unexplained variance (d') is $1 - R^2$ of the ordinary least squares multiple regression including both AET and region, which corresponds to the portion ($a' + b' + c'$); the overlap between region and AET (b') is equal to $(a' + b') + (b' + c') - (a' + b' + c')$, where $(a' + b')$ is the R^2 of the regression using AET, and $(b' + c')$ is the R^2 of the regression using biogeographic region. a' Variance explained by AET only, c' variance explained by biogeographic regions only

independent effect), while region independently explained 45.2% of the variance. Overlapped effects of climate and history explained nearly 11%. So, in contrast to Viperidae, elapid species richness gradients appear primarily and strongly associated with history while the independent effects of current environment seem negligible.

It is important noting that the full model accounted for much more variance (68.3%) than the sum of regions independent effect (45.2%) and the overlapped variance (11%), and thus the effect of AET alone would provide a negative R^2 -value in partial regression analysis. This is actually due to an interactive effect between AET and regions, and indeed the effect of an interaction term between AET and Australia increases the R^2 from 0.005 (AET alone) to 0.481 (AET \times Australian region), although adding this term does not improve the overall model (i.e., the interaction between AET and all other regions do not increase the explanation power of AET alone). Thus, the higher sum of AET and region explaining global patterns is explained by a unique regional effect in Australia.

Because of this interaction, and due to the strong regional differences observed for Elapidae (i.e., Australia exhibits much higher diversity than the rest of the areas, see Fig. 1b), we reanalyzed the data excluding this region. We found that the independent effect of region decreased from

45.2 to 17.8% (see Fig. 3b), whereas the previously absent independent effect of AET was now 23.4%. This suggests that the strong historical effect that had emerged from the analysis involving all regions was reflecting historical processes of elapid radiation throughout Australia. Nonetheless, although the models are now similar with regard to their respective explanatory powers (i.e., 48.3% for Viperidae and 41.6% for Elapidae without Australia), there is still an independent effect of history on the richness patterns of Elapidae (17.8%) that is 6 times higher than the historical signal observed in Viperidae at the global scale (2.7%).

Finally, although some autocorrelation remains in model residuals (Moran's I in the first distance class = 0.21 in the full model for Viperidae, and 0.32 in the full model for Elapidae), this is unlikely to affect interpretation of the relative contribution of the main effects (contemporary climate and biogeographic region), based on coefficients of determination and partial regressions (see Hawkins et al. 2007b). Indeed, when repeating the analyses using the R^2 from a SAR model, no qualitative differences appear (see Araújo et al. 2008). The average R^2 in the ten subsamples of AET alone was 0.224 for Viperidae and tends to 0.00 (actually a slightly negative value, as discussed above) for Elapidae. For history, the average R^2 was 0.024 for viperids and 0.438 for elapids.

Discussion

The most striking result from our analyses was the contrasting association of viperid and elapid species richness gradients with our indicators of current environmental conditions (AET, a measure of the water–energy balance in the environment) and history (biogeographical region). As indicated by partial regressions, the relative importance of AET in explaining Elapidae richness was lower in general, whereas history alone accounted for a considerable amount of variance. Conversely, global richness patterns of Viperidae were reasonably explained by AET, and supported that the gradients are more strongly determined by current conditions than by historical effects. Still, in this latter clade, there was a relatively large amount of explained variation that could not be independently attributed to either factor, for which we cannot discard some secondary role of history in determining its gradients.

The findings regarding viperid richness variation concur with previous studies that have identified water–energy inputs as the most emergent determinants of animal diversity, at different geographical scales (Hawkins et al. 2003a, 2007a; Hawkins and Porter 2003; Rodríguez et al. 2005). Also, previous large-scale (but not necessarily global) studies focused on reptile diversity have found similar results; where environmental energy alone or in combination with

water availability was the best predictor (see Schall and Pianka 1978; Owen 1989; Currie 1991; Hawkins et al. 2003a; Rodríguez et al. 2005). Associated with these results, it is typically thought that the relationship between reptile richness and energy is due to the direct dependence of these organisms on solar energy to regulate and maintain their body temperatures (Owen 1989; Currie 1991; Hawkins et al. 2003a; Rodríguez et al. 2005; Whittaker et al. 2007).

However, in spite of the dependence on environmental energy to thermoregulate (which would suggest that energy inputs may restrict the distribution of Viperidae to some extent), Shine and Madsen (1996) showed that thermal constraints may influence snakes just in minor ways (e.g., some microhabitats may be too hot for long-term residence during daylight hours). This is because tropical species can maintain high and relatively stable body temperatures throughout the year (see Shine and Madsen 1996) and, in contrast with what happens with some lizards (Avery et al. 1982), snakes exhibit relatively little overt thermoregulatory behavior. In our analyses, viperid richness patterns were only weakly associated with pure environmental energy variables (i.e., potential evapotranspiration and temperature) after taking AET into account in multiple regression models (results not shown). This result suggests that the general explanation for reptiles' richness–energy association based on extreme energy dependence of these organisms might not be a rule and that viperid richness variation is mainly determined by combined influences of water and energy operating through effects of these variables on productivity and food supply (see Hawkins et al. 2003a, b; O'Brien 2006; see also Hawkins et al. 2007c for a recent global evaluation of energy hypothesis explaining richness patterns in the specific context of the metabolic theory of ecology).

In this regard, a study of Owen (1989), based on the patterns of herpetofaunal species richness in Texas, proposed that most snakes are habitat generalists and that greatest snake richness does not occur in areas of highest productivity. However, this is not a compelling proposition, since opposite reasoning for the primary productivity hypothesis has been proposed to explain species richness (Hawkins et al. 2003a; Rodríguez et al. 2005). In other words, areas with high productivity and, consequently, wide resource availability, could benefit both specialist and generalist species, either through the food supply or habitat availability.

Further, the weak support of the historical hypothesis tested here to explain the global pattern of viperid richness does not concur with the proposition of Reed (2003) for New World diversity of Viperidae. According to this author, the viperid richness peak in Central America and southern Mexico may be associated with the historical biogeography of these regions (i.e., the occurrence of several

orogenic episodes), which could generate many opportunities for allopatric speciation. Apparently, and as shown above, this is not the main cause of the viperid richness pattern, even though the importance of climate or history to account for diversity can vary across different parts of world (Hawkins et al. 2003b), and historical biogeography could be important to some extent in explaining Viperidae richness. On the other hand, these biogeographic events appear to make sense when explaining the richness pattern of Elapidae.

In contrast to Viperidae, the global-scale variation of Elapidae richness seems to be primarily determined by the evolutionary history of the clade, as indicated by the strong explanatory power of the models including biogeographic regions. However, excluding Australia from the analysis led to the detection of a moderate effect of contemporary climate (indicated by AET) in the rest of the world, which lead us to suggest that the strong historical signal for this group is closely related to the particular evolutionary history in the Australian region. From a general perspective, the much stronger historical response of elapid richness suggests that a robust and unified explanation to global richness patterns of animals is a hard aim and points towards the need to adopt “deconstructive” approaches (sensu Marquet et al. 2004), in which richness is analyzed for groups that possess clear ecological or evolutionary unifying characteristics. In an evolutionary context, this is relevant if we consider that Viperidae is one of the most basal lineages of Caenophidia, which diverged prior to the separation of elapids from other colubroids (Heise et al. 1995; Kelly et al. 2003; Vidal et al. 2007). Thus, viperids probably had more time to diversify, generating richness responses to environmental gradients. In contrast, although the pattern of distribution of elapid richness responds to AET variation in some regions (Fig. 2b), it still reflects a recent history of colonization and diversification within tropical and subtropical regions (e.g., the Australian radiation), so that the frequently observed gradient of animal species richness may have not yet uniformly emerged in all regions.

Thus, the importance of the Australian region to an interpretation of the strong historical component in the richness pattern of Elapidae can be explained by the hypothesis of recent radiation of this clade into Australia (Keogh 1998; Scanlon and Lee 2004). This hypothesis was recently reaffirmed by Sanders and Lee (2008), whose divergence time estimation revealed that the terrestrial Australo-Papuan elapids (i.e., the Australian and Melanesian insular species) along with the sea snakes (both insular and marine species not included here) are a quite recent group, dating from the Late Miocene (~10 million years ago). This recent evolution implies that Australasian elapid radiation has undergone much more rapid species accumulation than

previously assumed (Sanders and Lee 2008). This high and rapid diversification could have been favored by an early colonization of new environmental conditions available in the Australasian continental and marine ecosystems, since they were relatively free of both competition (in the absence of similar predatory competitors, such as viperids) and predation (due to the defensive capabilities including potent venom and fangs).

In sum, we conclude that both contemporary climate and evolutionary history must be taken into account to elucidate global richness patterns, thus giving support to the most recent attempts to integrate ecological and evolutionary phenomena as drivers of biodiversity. Moreover, these results showed the importance of analyzing each clade independently and starting to adopting richness deconstructive approaches (*sensu* Marquet et al. 2004) to investigate macroecology patterns, as the factors acting on richness may vary from group to group, according to their evolutionary history.

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