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Niche conservatism and evolutionary determinants of terrestrial vertebrate diversity patterns

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Abstract.

Large scale diversity patterns are the response of organisms to current environmental conditions and past environmental changes. Niche conservatism provides a conceptual framework allowing the integration of current and historical events to explain diversity. This thesis uses four case studies incorporating contemporary, evolutionary and historical determinants of diversity. To achieve a wide range of representation, the case studies analyze three eco-geographical rules explaining patterns in species richness, body size and range size, for three different taxonomic groups (i.e. reptiles, birds and mammals) and within three geographical regions (i.e. East and South of Africa, the New World, the Globe). Results illustrate how linking evolutionary and historical processes to niche conservatism is key to understanding diversity patterns. Accounting for evidence contained in the fossil record, in palaeoclimatic or palaeogeographic reconstructions, or expressed by phylogenetic relationships and past dispersal events will enable us to comprehend why Earth's biota is distributed as it does.

Keywords. Latitudinal diversity gradient, Bergmann's rule, Rapoport's rule, biotic exchange, phylogenetic signal, fossil record, palaeoclimatic reconstruction

Macroecology is a non-experimental research field concerned with the study of diversity, distribution, and abundance patterns of organisms at large spatial and temporal scales (Brown 1995). Macroecology has strong links to biogeography, but has a more specific purpose in describing emergent properties of the ecosystems and biota which often do not manifest in smaller-scale investigations. Initial approaches in macroecology were fundamentally inductive (Gaston and Blackburn 2000), that is, based on the description of patterns and their interpretation and explanation a posteriori. However, macroecologists are becoming increasingly interested in transcending correlative descriptive analyses and reaching mechanistic explanations of the observed patterns (Beck et al. 2012). Unfortunately, experimentation is rarely feasible at macroecological scales, but knowledge of natural history may inspire comparative analyses that allow us to gain insights into the mechanisms underlying the patterns (Kerr et al. 2007). At large scales, commonly used in macroecology and often utilized in biogeography, diversity patterns are the product of biota's responses to current environmental conditions and evolutionary responses to past environmental conditions (Ricklefs 2004). The latter is obvious given that evolution is the ultimate cause for species diversity and for variability in ecological, physiological, morphological, or behavioral traits of organisms. However, the integration of macroevolutionary and historical factors into macroecology is recent and the scientific community is yet to reach consensus on the appropriateness of the different methodologies.

Challenged with the necessity of coupling explanations based on current environmental factors and on historical and evolutionary factors, niche conservatism emerged as an integrative framework to study diversity gradients (Wiens and Donoghue 2004). Niche conservatism predicts the retention of traits related to the ecological niches

of species across evolutionary time (Wiens et al. 2010), and thus implies that ecological niches are not entirely labile and their adaptability to changing conditions is limited (Peterson 2011). It can be viewed both as a pattern of ecological similarity across evolutionary time and as a process able to generate phylogenetic patterns, when ecological similarity promotes local extinctions or migrations of organisms in the face of environmental changes (Wiens et al. 2010). For example, niche conservatism could explain why there are more species in the tropics (i.e., the Latitudinal Diversity Gradient, hereafter LDG) on the grounds of the retention of ancestral ecological niches originated under tropical conditions (Wiens and Donoghue 2004). Notably, niche conservatism coupled with the time-for-speciation effect would also explain exceptions to the LDG for clades whose ancestors had originated outside the tropics (Stephens and Wiens 2003, Hawkins 2008). In a phylogenetic context, niche conservatism would predict similarity of characteristics related to the ecological niches of closely related species (Harvey and Pagel 1991, Peterson et al. 1999). This is the case for fundamental biological traits such as body size, and perhaps also for other properties such as geographic range sizes, for which niche conservatism would predict more similar values among closely related species (Blomberg et al. 2003).

In this PhD thesis, I provided empirical evidence that the incorporation of contemporary, evolutionary and historical aspects is necessary if we want to deepen our understanding of the mechanisms that underlay diversity patterns of terrestrial vertebrates. I proposed four case studies focused on three amply known eco-geographical rules (see Gaston et al. 2008; LDG, Bergmann's rule and Rappoport's rule), comprising a wide range of vertebrates (i.e., reptiles, birds and mammals), and geographic regions (i.e., Eastern and Southern Africa, the New World, and the whole world). Although seemingly disparate, this set of case studies allowed extensive representation of systems for studying niche conservatism.

First, I explored patterns of species richness, and implicitly the LDG, in African squamate reptiles and the extent to which niche conservatism explained their diversity-climate relationships. I compared clades that originated under different environmental conditions through geological history and tested whether their species richness patterns could be linked to the ancestral environmental conditions under which clades arose as predicted by niche conservatism.

Second, I focused on the widely studied Bergmann's rule, i.e., the tendency for increasing species' body sizes towards high latitudes due to large species possessing adaptive advantages in cold environments. The original rule was derived from reduced surface-volume ratios of endotherm vertebrates at high latitude (Bergmann 1847). I partitioned global bird body size patterns into their phylogenetically dependent and independent components to assess the relative contributions of evolutionary explanations versus ecological hypotheses such as the heat conservation hypothesis (Bergmann 1847), the resistance to starvation hypothesis (Lindsey 1966), the resource availability hypothesis (Rosenzweig 1968), or the effects of interspecific competition (Olson et al. 2009).

Third, I inspected the effects of historical large scale dispersal events (i.e., biotic exchanges that occurred during the Pleistocene) on geographic patterns of body size in New World mammals. I compared phylogenetic signal in body size and associations of body size with the current environmental conditions between the groups of mammals that participated in the biotic exchanges (i.e., allochthons) and the groups that did not participate (i.e., autochthons). As predicted by niche conservatism, I expected stronger evolutionary and environmental signals for the body size of allochthons given the shorter time that they would have had to diversify and adapt to newer ecological conditions.

Fourth, I investigated Rapoport's rule (Stevens 1989), which predicts increasing geographic ranges with increasing latitude given that cold and seasonal environments would select for species able to tolerate greater climatic variability and thus with wider geographic ranges (Stevens 1996). I used data on oscine passerine birds of the New World to evaluate the proportions of cross-

species variation in geographic range size that were associated with evolutionary relationships, with current environmental factors, or with both. Further, I compared ranges of sedentary and migratory species as well as breeding and non-breeding ranges of migrants, expecting a non-random phylogenetic signal in range sizes derived from conservatism of ecological characteristics. I also expected to see differences between migratory and sedentary species based on the evolution of the migratory character as a factor shaping geographical ranges (Levey and Stiles 1992).

Although methodologies varied among the study cases, certain aspects were common to all studies. For all of them, I used the assemblage approach (see Gaston et al. 2008), which uses uniformly distributed grid cells as analysis units. The grid cells contain summarized ecological information on the species found within the cell. This approach allows characterization of geographic two-dimensional variation in more detail than the alternative cross-species methods. The cross-species approach, applied for comparison in the study of Rapoport's rule, utilizes species as analysis units but constrains the description of species distributions and their environmental determinants to midpoints with the subsequent information loss (Ruggiero and Hawkins 2006, Olalla-Tárraga et al. 2010, but see Adams and Church 2010). Additionally, I introduced a novel approximation to the use of cross-species analyses (Morales-Castilla et al. 2013), where rather than reducing geographic and environmental space to midpoints, I applied a filtering procedure analogous to the spatial or phylogenetic filters (Borcard and Legendre 2002, Diniz-Filho et al. 1998). The advantage of this method is that it avoids the limitations imposed by either averaging spatial information into geographic midpoints (Freckleton and Jetz 2009) or averaging species trait data within each grid cell (Terribile et al. 2009). This novel method, coupled with partial regression, presents additional benefits of accounting for the overlapping contributions of variables, which is generally not achieved by the alternative GLS-based approximations (Freckleton and Jetz 2009).

The incorporation of historical and evolu-tionary explanations of the patterns was achieved by incorporating phylogenetic analyses performed from an explicit geographic perspective, as well as historical and palaeontological evidence (i.e., the fossil record, palaeoclimatic reconstructions). Phylogenetic analyses were originally formulated to account for the non-independence of species in cross-species analyses (Felsenstein 1987, Harvey and Pagel 1991). However, further development of phylogenetic methods allowed investigation of evolutionary patterns as well as the tempo and mode of evolution (Purvis et al. 1995, Diniz-Filho et al. 1998). I utilized both pattern- and model-based phylogenetic metrics to disentangle the contribution of evolutionary determinants from other ecological factors to current diversity patterns. Whereas model-based metrics take a reference model of evolution (usually Brownian motion) and test how well the observed trait fits that model, pattern-based analyses (e.g., Diniz-Filho et al. 1998) transform phylogenetic relationships into a set of variables that, after selection, can be introduced as explanatory variables in multiple regression analysis. Pattern-based analyses, and particularly the phylogenetic eigenvector regression (i.e. PVR), have been criticized because inaccurate variable selection could lead to biased results (see Rohlf 2001, Freckleton et al. 2011). However, effective variable selection can be achieved (Diniz-Filho et al. 2012a) and results can be compared against different models of evolution (Diniz-Filho et al. 2012b). By combining both types of metrics, I showed that the information they provide is complementary, able to address different questions, and usually consistent among methods (Morales-Castilla et al. 2012a, 2013).

In Morales-Castilla et al. (2011), I detected diverging species richness patterns for five mono-phyletic clades of African squamate reptiles. Older clades (i.e., gekkonids, lacertids, cordylids) tend to show higher species richness in arid, dry, and savannah-like environments; modern clades (i.e., snakes and chameleons) are more species-rich in equatorial humid climates. Both the fossil record and palaeoclimatic reconstructions supported the coincidence between climatic conditions preferred nowadays and ancestral climatic conditions

for squamate clades. Hence, niche conservatism and time for speciation can explain African reptile richness patterns either when coincident with the LDG or with exceptions to it.

Regarding the avian body size gradient, I showed a strong effect of evolutionary relationships, and identified primary productivity either in combination with temperature in the New World or with seasonality in the Old World, as the primary environmental descriptor (Morales-Castilla et al. 2012a). Results supported the hypotheses of resistance to starvation and heat conservation to explain the portion of body size independent of evolutionary relationships.

The mammalian body size gradient across the New World contained a strong, geographically localized, influence of Cenozoic biotic exchanges (Figure 1) and marked differences were found among the distribution of autochthons and allochthons (Morales-Castilla et al. 2012b). The body size of the clades that participated in biotic exchanges had stronger phylogenetic signal and stronger associations with climate, irrespective of the megafaunal extinctions. The more recent arrival of allochthons to North and South America in

concert with niche conservatism could explain differences among clades (Morales-Castilla et al. 2012b).

Finally, for oscine range sizes, I found that a non-random phylogenetic signal that fully overlapped with environmental and geographical associations, probably as a result of phylogenetic conservatism of associated traits (Morales-Castilla et al. 2013). The geographic patterns similarly supported Rapoport's rule in the Nearctic and its converse in the Neotropics for both migratory and sedentary groups. However, the environmental and phylogenetic signals were stronger for the breeding ranges of migratory species reflecting that migration evolved according to niche conservatism for the subset of species able to breed in previously glaciated regions (Morales-Castilla et al. 2013).

The findings of this thesis are novel in a number of ways. I presented the first large scale study of richness patterns for African squamate reptiles that connects current species richness patterns with plausible ancestral patterns going back in time till the Jurassic period. By doing so, I confirmed the retention of broadly described cli-
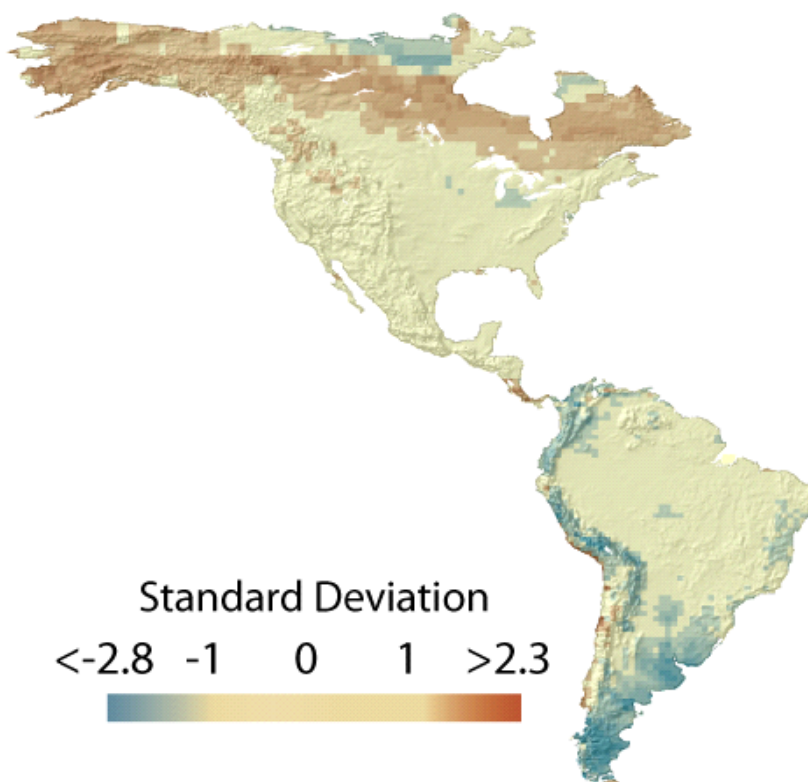
Figure 1. Influence of Pleistocene biotic exchanges on body size patterns of New World mammals. Effects are measured as the standard deviation of the difference between the body size patterns of all species and those of autochthon (i.e. non-migrating species). Red colors indicate a positive contribution in body size attributable to allochthon clades. Blue colors indicate a negative contribution in body size attributable to allochthons. Although the presence of allochthons in the Nearctic influences the body size pattern with an increase in the average size of species in the northernmost regions, it contributes with a decrease in the average size of species in the southernmost regions of the Neotropics. A likely explanation for this reversed pattern must be related to differences among the migrants to both subcontinents and particularly in the radiation of small-sized rodents belonging to the family Muridae, which are allochthons in the Neotropics. Extracted from Morales-Castilla et al. (2012b).

matic niches through long periods of time supporting niche conservatism as an explanation for the LDG and its exceptions (Morales-Castilla et al. 2011). Naturally, a work of this nature was limited by the lack of well-resolved palaeoclimatic, palaeontological and phylogenetic data and thus analyses were constrained to be rough and descriptive. The global analysis of avian body size expanded on the results of previous works in the same topic, which had not explicitly accounted for phylogenetic relationships and attributed a prominent role to interspecific competition (Olson et al. 2009). In contrast, I found that interspecific competition explained little variation in body size independently of both phylogeny and environmental factors (Morales-Castilla et al. 2012a). Also, the strong association of phylogenetic relationships with body size suggests that this factor should be explicitly included in further investigations. The strong evidence for an impact of historical dispersal events on current patterns of mammal body size takes us a step closer towards process-based explanations of macroecological patterns. In this case, a known historical event (i.e., Cenozoic biotic exchanges) provided a mechanism (past dispersal) on the basis of which grouping the New World mammals into those that participated in the exchanges and those that did not participate. This division allowed testing predictions such as an expected difference between the body sizes of the two groups of mammals (Morales-Castilla et al. 2012b). Similarly, migratory ability was used to separate New World oscines into migrating and non-migrating species, for which differences in their range sizes were expected based on theory explaining the development of migrations (the southern-home theory, see Morales-Castilla et al. 2013). Despite the constraints imposed by the gaps in historical and evolutionary data, the approaches used here provide examples of the suitability of fitting the past into the macroecological agenda.

None of the eco-geographical rules studied here (LDG, Bergmann's and Rapoport's rules) seems to be universal. Certain reptile clades did not show higher species richness in tropical areas, bird assemblages presented large body sizes in arid, low-latitude environments, mammals only followed Bergman's rule in the Nearctic, and oscines range size only conformed to Rapoport's rule in the Nearctic. Exceptions to the rules have been intensely debated (see Gaston et al. 2008), but rather than a problem, they may help elucidate mechanistic explanations. Exceptions undeniably point towards several mechanisms operating together to shape current diversity patterns or, in other words, one-size-fits-all explanations are unlikely to be encountered. Our results support the idea that among the array of mechanisms operating, historical and evolutionary factors played a key role either in concert with or independent of selective pressures derived from current environmental conditions. Even though it might not always be possible, disentangling past and present determinants of diversity will bring us closer to understanding why organisms and their characteristics distribute as they do and how they will in a future. This thesis takes a step in that direction.

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