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ORIGINAL ARTICLE

Continental and regional ranges of North American mammals: Rapoport's rule in real and null worlds

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ABSTRACT

Aim To assess the relationship between species richness and distribution within regions arranged along a latitudinal gradient we use the North American mammalian fauna as a study case for testing theoretical models.

Location North America.

Methods We propose a conceptual framework based on a fully stochastic mid-domain model to explore geographical patterns of range size and species richness that emerge when the size and position of species ranges along a one-dimensional latitudinal gradient are randomly generated. We also analyse patterns for the mammal fauna of North America by comparing empirical results from a biogeographical data base with predictions based on randomization null models.

Results We confirmed the validity of Rapoport's rule for the mammals of North America by documenting gradients in the size of the continental ranges of species. Additionally, we demonstrated gradients of mean regional range size that parallel those of continental range. Our data also demonstrated that mean range size, measured both as a continental or a regional variable, is significantly correlated with the geographical pattern in species richness. All these patterns deviated sharply from null models.

Main conclusions Rapoport's statement of an areographic relationship between species distribution and richness is highly relevant in modern discussions about ecological patterns at the geographical scale.

Keywords

Distribution, latitudinal gradient, macroecology, mammals, mid-domain models, North America, null models, species richness.

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INTRODUCTION

Thirty years ago, Rapoport (1975, 1982) posed the question: Are the geographical ranges of northern species of equal size, larger or smaller than those of southern species? As his analysis was based on the distribution of North American mammals, Rapoport was in fact positing the hypothesis of a latitudinal gradient of range size among animal species. This putative gradient, along with the older and more thoroughly studied latitudinal gradient in which the number of species decreases with increasing latitude (Hawkins, 2001; Willig *et al.*, 2003a; Hillebrand, 2004), are two of the pillars of our understanding of geographical patterns of biodiversity at the continental level. In attempting a fusion of the two concepts, Stevens (1989) postulated that an increase in average range size with increasing latitude, a pattern that he called Rapoport's rule, could explain the latitudinal gradient of species richness.

Stevens' (1989) rationale was that, in general, tropical species occupy smaller ranges than do temperate taxa, due to the tolerance of the latter to a broader gamut of environmental conditions. This fact, coupled with the 'rescue' (Brown & Kodric-Brown, 1977) or 'mass effect' (Shmida & Wilson, 1985), produces, according to Stevens, a higher diversity in tropical localities than in temperate sites. The rescue or mass effect consists of the presence at a given site of individuals belonging to species that cannot have viable populations there as a result of the movement of individuals from adjacent localities that do support reproducing

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populations of the species. Stevens (1989) argued that smaller ranges of tropical species favoured the mass effect, which would be precluded in temperate zones by larger distance between sources and sinks.

The hypothesis of Stevens (1989) in particular, and Rapoport's rule in general, have received much attention, and much criticism, in recent years. The validity of the rule has been championed by some empirical observations (e.g. for North American taxa, Stevens, 1989; Pagel *et al.*, 1991; Lyons & Willig, 1997), but exceptions are numerous, and the generality of the rule has been seriously questioned (Gaston *et al.*, 1998; Gaston, 2003). Key problems in the literature dealing with Rapoport's rule are: the proliferation of different definitions of what a species range is (Brown *et al.*, 1996; Gaston, 2003), the existence of several techniques for measuring the size of ranges (Stevens, 1989; Pagel *et al.*, 1991; Rohde *et al.*, 1993), and the variety of statistical methods used to assess the correlation between range size and latitude (Colwell & Hurtt, 1994; Lyons & Willig, 1997; Gaston *et al.*, 1998). Even if Rapoport's rule operates, the question of whether or not there is a functional connection, or even a correlation, between range size and species richness is still unresolved, as the evidence for a link is dubious (Gaston *et al.*, 1998; Kerr, 1999; Smith & Gaines, 2003).

Rapoport (1975, 1982) explored the relationship between richness and species ranges with a purely areographic approach. He quantified richness as the number of ranges intersecting a given point along a geographical gradient. He then reasoned that richness should be a function of the size, position and degree of overlap of individual ranges. Even if Rapoport's rule operates and ranges are smaller in the tropics, and even if more species are present at tropical latitudes for larger sampling units, the richness at finer scales might be, in principle, not different from that at temperate locations if the degree of overlap of ranges is similar at various latitudes.

Rapoport's (1975, 1982) reasoning becomes relevant in the context of recent discussion regarding several large-scale patterns of diversity. First, it has become clear that the gradient of species richness is scale sensitive and, in general, different patterns are observed depending on whether the analysis is performed at the local or at several regional scales (Rahbek & Graves, 2001; Lyons & Willig, 2002; Kaspari *et al.*, 2003; Hillebrand, 2004; Rodríguez & Arita, 2004). Secondly, a similar effect of scale is likely to be detected in testing Rapoport's rule, as the shape of the species-range frequency distribution curves varies with the scale of analysis and with the location on a continent, both in theoretical and empirical studies (Gaston & Blackburn, 2000; Arita, 2005). Thirdly, even if both species-range size and species richness show a latitudinal pattern, the search for a link between the two trends has failed to yield unequivocal results (Gaston *et al.*, 1998; Kerr, 1999; Rhode, 1999). Fourthly, there is a current and heated debate on the validity of mid-domain models, which analyse continental patterns of species richness as overlaps of randomly placed species ranges (Colwell & Lees, 2000; Hawkins & Diniz-Filho, 2002; Zapata *et al.*, 2003; Colwell *et al.*, 2004; Pimm & Brown, 2004).

In this paper, we assess the validity of Rapoport's rule and its relationship with species richness from a new perspective by introducing the concept of regional range. We also propose a conceptual framework to explore the implications of latitudinal gradients in answering Rapoport's old but still current questions: is there a latitudinal pattern in the size of species ranges?, if so, is there a link between this pattern and the latitudinal gradient of diversity?

CONCEPTUAL FRAMEWORK

We use a one-dimensional approach to analyse geographical patterns of range-size variation. In principle, concepts and implications derived here could be applied to any geographical gradient (latitudinal or longitudinal) or even to altitudinal or bathymetric gradients. However, as our topic focuses on Rapoport's questions regarding latitudinal gradients, we shall focus our discussion on the effect of latitude. By using a one-dimensional approach, we concentrated on the more basic features of the latitudinal gradient, which is, by definition, a linear arrangement. We borrow concepts from mid-domain models, as they provide an adequate abstraction of the concept of species richness as a consequence of overlapping ranges of species.

In existing mid-domain models of diversity (Colwell & Hurtt, 1994; Colwell & Lees, 2000; Pimm & Brown, 2004), a gradient of latitude along a continent is modelled by a domain (0, 1) along which the range of each species is represented by a one-dimensional line. Each range can be defined by the position of its extreme points l_1, l_2, where $l_1 < l_2$, or by its size r ($r = l_2 - l_1$) and its midpoint m ($m = (l_1 + l_2)/2$). Species richness is defined as the number of ranges crossing a given point x along the domain. We will call this number the 'regional point richness' (RPR, dubbed 'regional point diversity' by Arita & Rodríguez, 2004), which represents the number of species that potentially occur at a hypothetical zero-area point on the continent, and which has been used in other contexts by other authors (Leitner & Rosenzweig, 1997; Ricklefs, 2004).

Here we extend the model to the case of a region, instead of a single point, within the domain (Fig. 1). Define such region B as a subset of the domain bounded by points x_1 and x_2 ($x_1 < x_2$). The midpoint of region B is $M = (x_1 + x_2)/2$, and its size is given by $D = x_2 - x_1$. Regions A and C are the sections of the domain to the left and to the right of region B, respectively. Species can take one of six possible configurations with respect to region B (Fig. 1): type 1 species, whose range is totally to the left of the region ($l_1, l_2 < x_1$); type 2 species, whose range enters the region from the left and have the right end within the region ($l_1 < x_1, x_1 < l_2 < x_2$); type 3 species, whose range includes the totality of the region but extends beyond it in both directions ($l_1 < x_1, l_2 > x_2$); type 4 species, which are endemic to the region ($x_1 < l_1, l_2 < x_2$); type 5 species, which enter the region from the right and have their

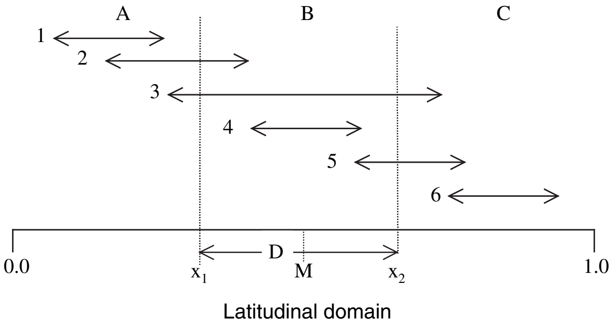

Figure 1 Six possible configurations of species ranges in relation to a region on a one-dimensional domain. A region *B* with midpoint *M* and extent *D* is defined by points x_1 and x_2 along a domain (0, 1). Types 2–5 occur in the region.

left end within the region ($x_1 < l_1 < x_2, l_2 > x_2$); and type 6 species, whose ranges are totally to the right of the region ($x_1,x_2 > l_2$).

Species of types 2, 3, 4 and 5 overlap their range with region *B*, and are considered to occur there. We define the 'regional richness' (RR) as the sum of the number of these species. In describing the range size of species occurring in region *B*, we will use two concepts: we will call the 'continental range' of a species the total latitudinal extent of its range in the continent, and we will use the term 'regional range' to describe the range size of a species within the limits of a given region.

Other studies on latitudinal gradients of species richness have used bands, extending west to east and having a given latitudinal width, to summarize the number of species at different latitudes (see review in Willig *et al.*, 2003a). Those bands differ from our regions in that they are two-dimensional areas of variable size depending on the continental shape, whereas our regions are one-dimensional latitudinal extents.

Previous studies of Rapoport's rule have used the continental range as the variable to measure in looking for latitudinal patterns. There are, however, good reasons to focus also on regional ranges when searching for the links with species richness. The average range of species within a region is equal to the inverse of beta diversity, if beta diversity is defined as the quotient of the RR and the average RPR (Whittaker's β: Leitner & Rosenzweig, 1997; Arita & Rodríguez, 2002, 2004). Thus, the average regional range size of species serves as a direct mathematical connection between values of diversity measured at two different scales. Furthermore, regional ranges are a more logical choice when looking for patterns of overlap that constitute the core of Rapoport's hypothesis linking species ranges and richness. Herein, we test both the 'classic' or original formulation of Rapoport's rule (using the continental range) and the new formulation, employing the average regional range.

In all analyses we will use the original method of Stevens (1989) of tallying all species intersecting a given region. Alternatively, Rohde *et al.* (1993) proposed a method that counts only the species for which the midpoint of their ranges is included in a given region. In studies employing mid-domain models the method of Stevens is more appropriate, as the variable of interest is the number of overlapping ranges at a given latitudinal position, regardless of the location of the midpoint of individual ranges (Colwell & Lees, 2000). In Fig. 1, it is clear that several species might overlap their distribution with a region even if the midpoint of their ranges is far from the region.

Fully stochastic model

In this section we explore the relationships between latitude, richness and range size under the assumptions of a fully stochastic mid-domain model. Colwell & Lees (2000) have presented a synthesis of these models for gradients of richness (see also reviews by Zapata *et al.*, 2003; Colwell *et al.*, 2004). Fully stochastic versions of mid-domain models are adequate to explore patterns that would emerge in the absence of patterned restrictions to species range sizes, but in general are considered inadequate for direct comparison with empirical data (Colwell *et al.*, 2004). For that purpose, randomization models based on empirical data, such as the one presented in the next section, are much more appropriate.

To build a fully stochastic model for the distribution of *S* species in a domain, endpoints (l_1,l_2) for each range are generated by randomly sampling from a uniform distribution $U(0, 1)$, or alternatively and equivalently, by sampling from the permissible range size–midpoint location pairs (Colwell & Lees, 2000). The expected number of species *s* at a given point *x* is a parabolic function of *x*, $s(x) = S(2x-2x^2)$, with a maximum at the middle of the domain ($x = 0.5$), where the expected richness is $s(0.5) = S/2$ (Willig & Lyons, 1998; Colwell & Lees, 2000). This equation represents the expected RPR for a given point along the domain. The average continental range size of species occurring in any point *x* is equal to 0.5 (half the latitudinal span of the continent, Colwell & Hurtt, 1994; Colwell & Lees, 2000; Arita, 2005), but the variance changes with *x* following the function $(1-2x+2x^2)/12$, so the lowest variance (1/24) is in the middle of the domain (Arita, 2005).

Using an extension of the binomial model of Willig & Lyons (1998), the exact probabilities of occurrence for the six types of ranges illustrated in Fig. 1 can be calculated as functions of the position (midpoint or endpoints) and size (extent) of the region. The probability that one endpoint of a given range falls within area *A* is $P(A) = x_1$. Similarly, $P(C) = 1-x_2$, and $P(B) = x_2-x_1$. Therefore, probability for type 1 species is equal to $[P(A)]^2$; probability for type 2 species is $P(A)P(B) + P(B)P(A) = 2[P(A)P(B)]$, and so on. Using this logic, the probabilities for the six types of ranges shown in Fig. 1 are: $P(1) = x_1^2, P(2) = 2x_1(x_2 - x_1), P(3) = 2x_1(1 - x_2), P(4) = (x_2 - x_1)^2, P(5) = 2(x_2 - x_2^2 - x_1 + x_1x_2)$, and $P(6) = (1-x_2)^2$. Note that the probability that a species occurs within region *B* is $P(\text{occurrence}) = P(2) + P(3) + P(4) + P(5) = 1 - P(1) - P(6) = 2x_2 - x_2^2 - x_1^2 = 2M(1 - M) + D(1 - D/2)$. This probability represents the expected RR, in proportion to

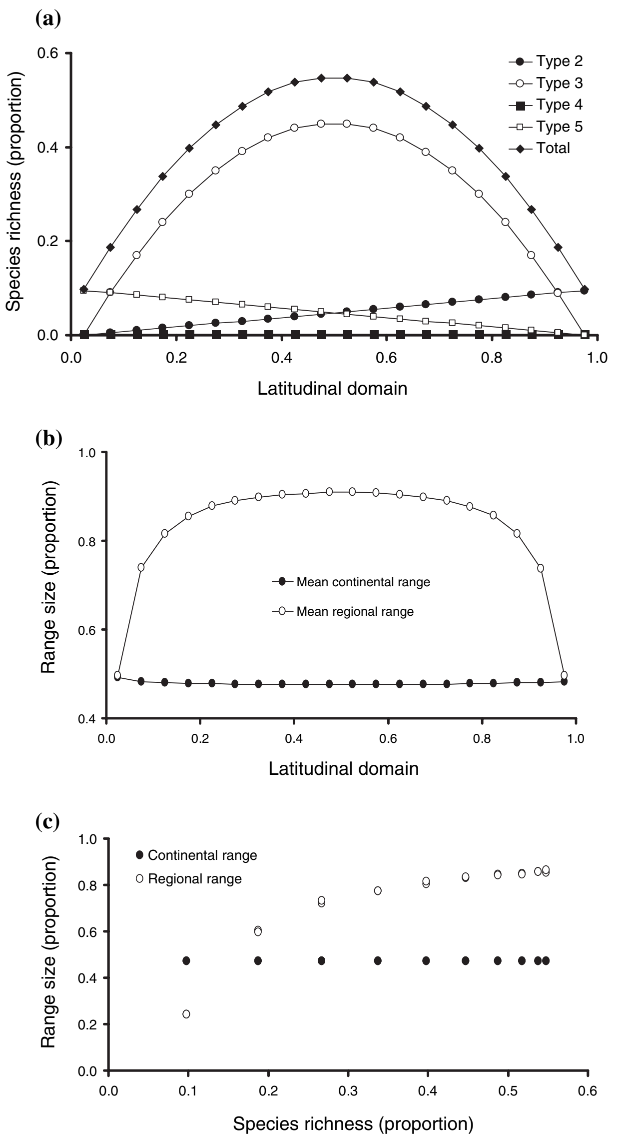

Figure 2 Species ranges and richness in 20 regions along a lineal domain as predicted by a fully stochastic mid-domain model. (a) Species richness of types 2–5 (Fig. 1) in regions along a latitudinal domain. Domain values correspond to midpoints of 20 0.05-unit regions; values for richness are in proportion to the total number of species in the continent. (b) Variation in mean continental range and mean regional range for species occurring in the 20 regions. Continental ranges are in proportion to the whole domain; regional ranges are in proportion to the size of the region. (c) Relationship between richness (as a proportion of the total richness of the continent) and mean continental and regional range size.

the continental diversity. This richness can be partitioned in the four categories of species occurring in the region. Figure 2 shows the expected number of species of each of these categories along the geographical domain, given $x_2–x_1 = 0.05$, that is, for 20 regions of 0.05 domain units in extent. The number of type 2 and type 5 species follows linear trends with opposite slopes (positive for type 2, negative for type 5), whereas the diversity of type 3 species follows a parabolic curve with maximum at 0.5. Interestingly, the number of type 4 species (endemic to the region) is constant, regardless of latitude.

We performed numerical simulations showing that the expected value for continental range varies very little with latitude, but forms an almost unnoticeable u-shaped pattern because of slight variation at both extremes of the domain (Fig. 2). The expected mean regional range, in contrast, follows an inverted u-shaped curve along the domain, with a peak in the centre of the continent of *c.* 91% of the size of the region, that is, of 0.045 domain units for regions extending 0.05 units (Fig. 2). Note, however, that at intermediate latitudes the mean regional range shows comparatively little variation, attaining low values only near the boundaries of the continent. These patterns produce contrasting relationships with species richness: a positive correlation between mean regional range size and regional richness (Pearson's $r = 0.97$, d.f. $= 19$, $P < 0.001$, for range size and log richness, based on the simulation of 20 regions), and a non-significant correlation between mean continental range and regional richness (Fig. 2).

An additional analysis was performed to assess the variation in total richness and in composition of type 2 to type 5 species due to changes in the size of regions. We fixed the midpoint of a region to the centre of the domain (i.e. $M = 0.5$), and varied its size from $D = 0$ (a zero-area region, or sampling point) to $D = 1.0$ (a region encompassing the whole domain), tallying in each case the number of species in each of the categories shown in Fig. 1. It can be shown analytically that, when holding M constant at 0.5, the number of species of types 2 and 5 are always equal, both changing in a curvilinear fashion with different region sizes (Fig. 3). Obviously, type 3 species represent the totality of richness when $D = 0$, and their number decreases with increasing size of the region. Endemic (type 4) species represent, of course, the totality of species when the region encompasses the whole domain, and decrease their number in a complementary manner with type 3 species (Fig. 3).

In summary, predictions of the fully stochastic null model regarding species ranges and diversity along a latitudinal gradient are as follows: (1) a parabolic pattern for both regional point and regional species richness, with a peak at the middle of the domain; (2) no gradient of average continental range of species occurring at a single point (thus, no gradient obeying Rapoport's rule, classic formulation); (3) an almost flat, only very slightly u-shaped pattern for average continental range of species occurring within regions (thus, no gradient obeying Rapoport's rule, new formulation); (4) a pattern of average regional range showing a peak at the centre of the domain; (5) as a consequence of (4), a u-shaped pattern of beta diversity in which the lowest value is at the middle of the continent; (6) a positive correlation of RR with average regional range; and (7) a non-significant correlation between RR and average continental range.

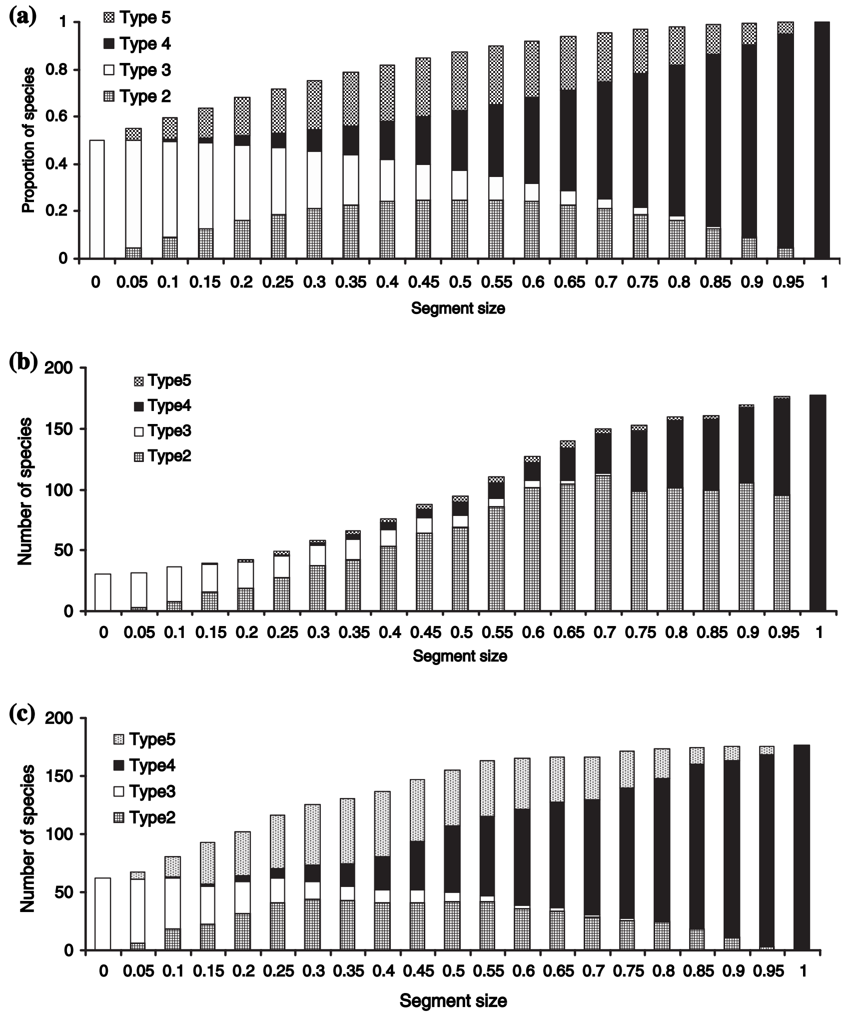

Figure 3 Species composition for segments of different sizes centred at the middle of a one-dimensional latitudinal domain. Bars show the proportion or the number of species in types 2–5 as defined in Fig. 1, (a) corresponding to the fully stochastic mid-domain model, (b) the empirical data for 177 North American bat species, and (c) one reshuffling of the empirical data for bats following the first null model described in the text.

STUDY CASE: THE MAMMALS OF NORTH AMERICA

Methods

We analysed the latitudinal patterns of range size and diversity for the fauna of North American mammals. We used a data base built using distributional maps drawn from data in Hall (1981), Reid (1998) and Wilson & Ruff (1999), updating the information to the end of 2000. We excluded marine, introduced, and insular species, and treated bats and non-volant mammals separately, producing a final data base with 176 species of Chiroptera and 537 non-volant species. We chose not to exclude non-endemic species, as has been done in several studies using mid-domain models (Colwell & Lees, 2000). As a considerable proportion of North American species occurs also in South America, exclusion of non-endemics would have diminished drastically the studied fauna, especially for bats. Any analysis of gradients of species ranges and diversity for North American mammals would be incomplete without the tropical component found in Southern Mexico and Central America. We feel that sensible null models should be constructed with complete faunas (see Colwell *et al.*, 2004 for further discussion).

We measured the range size of each species as the span between the minimum and maximum latitudes included in our data base. Thus, we considered ranges as one-dimensional, continuous, coherent units, an approach that is considered adequate at the scales used in this study (Colwell *et al.*, 2004). We defined separate domains for bats and for non-volant species, based on the southernmost and northernmost record for each group. Thus, the domain for bats extended from 7 to 66° N, and that for non-volant species spanned from 7 to 83° N. For comparative purposes, both domains were standardized to a scale from 0.0 to 1.0.

Twenty regions were defined by dividing the domains in intervals measuring 0.05 domain units each. Thus, regions for bats measured 2.8°, and for non-volant mammals extended 3.8°. Using a Visual Basic program, we measured the following variables for each region: (1) the RR: the number of ranges intersecting the region; (2) the RPR: the number of ranges intersecting the midpoint of the region; (3) the mean continental range: the average continental extent of all species occurring in the region; (4) the mean regional range: the average range of species *within the region*; (5) the number of species of types 2–5 (see Fig. 1), and (6) Whittaker's β diversity, calculated as the ratio between RR and RPR.

We explored the effect of a variation in the size of regions using the same procedure as with the fully stochastic model. Fixing the midpoint of a region at the centre of the domain ($M = 0.5$), we varied its size from $D = 0$ to $D = 1.0$ and computed the total richness and the number of species in each category depicted in Fig. 1.

Null models

We built null models by randomly moving the species ranges along the domain, without changing their size. Thus, while controlling one of the central traits of a range (its size), we manipulated another (its location) to explore the effect on species richness among regions located along the domain. Colwell *et al.* (2004, see also Pimm & Brown, 2004) have likened such procedure to shaking a box containing several pencils of different size. Pencils, like species ranges, will accommodate randomly along the box (domain), and more pencils will touch the centre of the box than the extremes, simply by geometric constraints. Extending the analogy, we were interested not only in tallying the pencils, but also on measuring their average lengths (species ranges) at several points along the box. Furthermore, we were also interested in quantifying the portion of each pencil that was included within marked sections of the box (our regions). To explore the effect of scale, in one case we manipulated also the size of the regions (Fig. 3). However, in all other simulations, we used the system of 20 regions of size $D = 0.05$ to allow comparisons with empirical data.

The null models fixed the range size of each species (r) and randomly assigned a position in the domain within the permissible values allowed by the 'hard' boundaries, that is, a range could not protrude beyond the limits of the domain. Thus, a range of size r could have its left extreme point (l_1) with equal probability at any point on the interval $(0,1-r)$ (Lees *et al.*, 1999). We performed three variants of this basic null model. In the first, we retained the species richness for each taxon (176 for Chiroptera, 537 for non-volant mammals), and simply moved the range of each species at random, with the restriction already described. Thus, this model produced a single null community for each taxa, maintaining the number of species and the extent of each range, and varying only the position of ranges.

In a second model, to know the expected distribution of variables, we used an algorithm that sampled 10,000 times, with replacement, from the pool of real range sizes. An algorithm with replacement constitutes a bootstrapping procedure, which is normally used to make inferences about a population by randomly resampling from a set of data. Thus, in this analysis, we built random communities of 10,000 species with a frequency distribution of range size determined by the empirical data.

Finally, in a third kind of analysis, to generate the frequency distribution of correlation coefficients between pairs of variables, we used an algorithm with no replacement to build 10,000 s-species assemblages, where s is the number of species in the real sets. Thus, in this third case, we used 'shuffling' procedures that rearrange a set of data in several ways, but maintaining the basic composition of the original community. In our simulations, in each of the 10,000 simulations every real species is included, maintaining its range size, but with its latitudinal position altered by the randomization procedure. This third model is mathematically equivalent to repeating 10,000 times the first model. As discussed by McCain (2004), both bootstrapping and shuffling procedures are appropriate for building mid-domain null models, depending on the question being asked.

RESULTS

The latitudinal gradient of bat species richness in North America, in which many more species occur in Southern Mexico and Central America than in northern latitudes, is very well documented (Willig *et al.*, 2003a). With our method, we observed a negative correlation ($r = -0.945$) between richness and latitude among our 20 regions, with a peak of 130 species in the region centred at latitude 0.18 (18° N, corresponding to Central Mexico, Table 1, Fig. 4). The latitudinal pattern for total richness is paralleled by the pattern of type 3 species, but the peak is enhanced by the presence of several type 2 and type 5 species (taxa that show their southern or northern limit within a given region). Thus, results confirm that the high bat diversity in Central Mexico is caused by the confluence of tropical and temperate species that intermix in this biogeographical transition zone (Ortega & Arita, 1998). The null model produced patterns similar to those predicted by the fully stochastic model and contrasting with the empirical observations (Fig. 5). In particular, the model produced no correlation of RR with latitude ($r = -0.008$), although a distinctive dome-shaped pattern with a mid-domain peak was generated (Fig. 5). In general, type 2 to type 5 species distributed latitudinally in patterns similar to those predicted by the fully stochastic model, but showing more random fluctuations.

Also confirmed by our empirical data was the strong latitudinal pattern in average continental range size ($r = 0.992$), in accordance with Rapoport's rule and contrasting with the non-significant correlation generated by the null model ($r = 0.098$). Empirical average regional range, in contrast, showed no significant correlation with latitude ($r = 0.146$), but followed a dome-shaped pattern similar to the one predicted by the null model, which produced no correlation ($r = 0.016$, Figs 4 & 5). Observed trends for mean continental range deviated dramatically from values predicted by the null model (regression of observed vs. expected continental range, $r^2 = 0.003$). Empirical mean regional ranges also differed from expected, but less sharply ($r^2 = 0.66$). In this case, the regression produced a line with a slope that did not deviate significantly from the expected value of 1.0 (1.07)

Table 1 Pearson's correlation coefficients between latitude, species richness, and range size for the fully stochastic model, for empirical data for North American volant and non-volant mammals, and for assemblages built using the second null model described in the text. Correlations between mean regional range and richness were calculated with the latter log-transformed. Regression analysis comparing observed and expected values (based on the null models) for mean continental range size and mean regional range size. Shown are the coefficients of determination (r^2 values) and the least-square linear equations. In all cases, each pair of points corresponding to one of 20 segments in which a linear domain was divided. Thus, $n = 20$ points

	Correlation					Regression	
	Latitude			Species richness		Mean continental range	Mean regional range
	Regional richness	Mean continental range	Mean regional range	Mean continental range	Mean regional range		
Fully stochastic	0.000	−0.201	0.000	0.000	0.970***		
Chiroptera							
Empirical	−0.945***	0.992***	0.146	−0.937***	−0.203	0.003	0.660; $y = 1.07x + 0.09$
Null model	−0.008	0.098	0.016	0.972***	0.966***		
Non-volant							
Empirical	−0.769***	0.981***	0.622**	−0.794***	−0.352	0.009	0.639; $y = 1.01x + 0.126$
Null model	0.001	−0.049	−0.004	0.985***	0.970***		

**$P < 0.01$, ***$P < 0.001$

but that was above the expected line (zero-ordinate = 0.09). In other words, empirical regional ranges were almost always higher than expected.

These patterns produced a strong negative correlation between species richness and continental range for empirical data ($r = -0.937$), which contrasted sharply with the expectation based on our second null model ($r = 0.972$, Table 1). Empirical data also produced a non-significant correlation between log species richness and mean regional range ($r = -0.203$) that contrasted with the expected value ($r = 0.966$, Figs 4 & 5). In fact, none of 10,000 176-species random assemblages showed correlations between average range size and species richness as negative as those corresponding to the real data (thus, $P < 0.001$, Fig. 6).

Results for the analysis of regions of different sizes centred at $M = 0.5$ showed that the patterns of distribution of North American bats differ sharply both from the fully stochastic model and the null model (Fig. 3). The most striking difference is that the number of type 2 species is noticeably higher in empirical data than in the simulations, showing that the Chiropteran fauna of North America is dominated by tropical species that enter regions from the south, reaching the northern extreme only for very large regions. In contrast, the empirical number of endemic (type 4) species is lower than for the simulations, except of course for the very large regions (Fig. 3). These results confirm the fact that the distribution of North American bats differs from null models, thus showing a structured pattern that reflects the effect of environmental variables.

Results for non-volant mammals were qualitatively similar to those for Chiroptera, although the quantitative details differed because of different sample size and different empirical patterns. Patterns of species richness showed a less defined latitudinal trend, although a significant, negative correlation between RR and latitude was still detected (Table 1). Both mean continental and mean regional range sizes correlated with latitude (Table 1), thus following both the 'classic' and the new postulations of Rapoport's rule. As in the case of bats, the mean continental range correlated strongly and negatively with species richness. As in the case of bats, mean regional range size showed a negative correlation. Both correlations were more negative than 10,000 correlations calculated using our third (no-replacement algorithm) null model (thus, $P < 0.001$).

The null model for non-volant mammals yielded results that were basically identical to those for bats. In this case, as with bats and contrasting with the fully stochastic model, the mean continental range size showed a positive correlation with latitude. Also in concordance with the case for bats, the regression of observed vs. expected values for mean continental range size was not significant, and that for mean regional range size yielded a line with slope very close to the expected 1.0 and y-intercept close to 0.1 (Table 1).

DISCUSSION

Is there a latitudinal gradient in the continental size of species ranges?; if so, is this gradient related to the pattern of species richness? In the case of the North American fauna of mammals, the answer to Rapoport's two questions is certainly positive. Both bats and non-volant mammals show a clear gradient in which diversity increases with decreasing latitude, and mean continental range increases at higher latitudes (Table 1, see also Willig *et al.*, 2003b for a review of previous reports). Here we document also gradients of mean regional range size that parallel those of continental range, although with weaker correlations (Table 1). Our data also demonstrate that mean range size (both measured as a continental or a regional variable) is significantly correlated with the geographical pattern in the number of species (Table 1, Fig. 6).

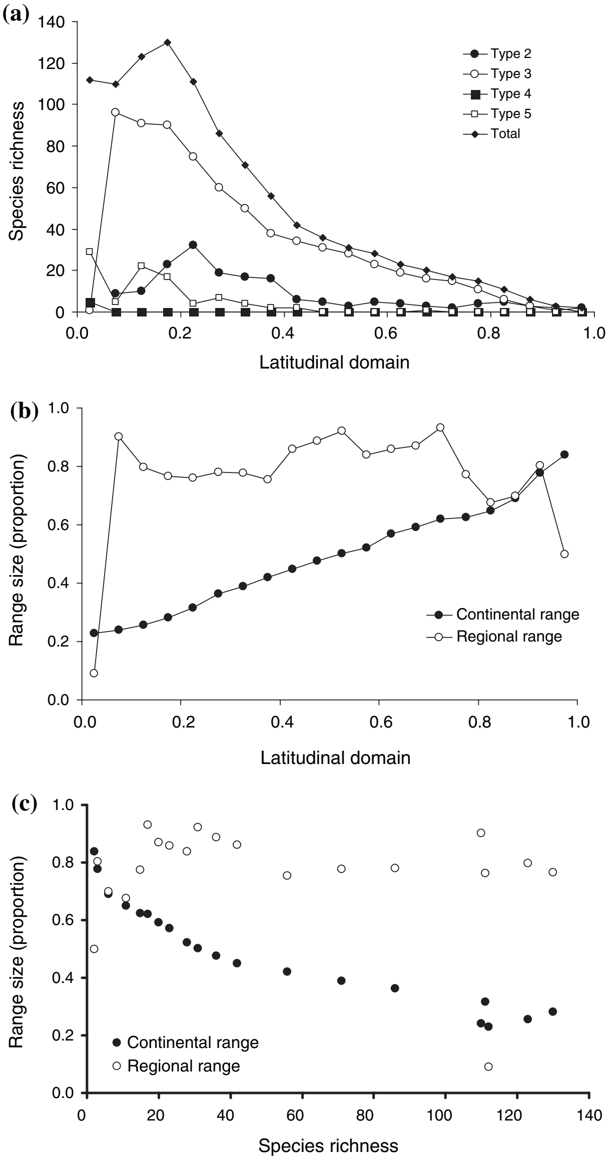

Figure 4 Species ranges and richness in 20 regions along a one-dimensional domain: empirical data for the North American bat fauna. Details as in Fig. 2. (a) Species richness of types 2–5 (Fig. 1) in regions along a latitudinal domain. (b) Variation in mean continental range and mean regional range for species occurring in the 20 regions. (c) Relationship between richness and mean continental and regional range size.

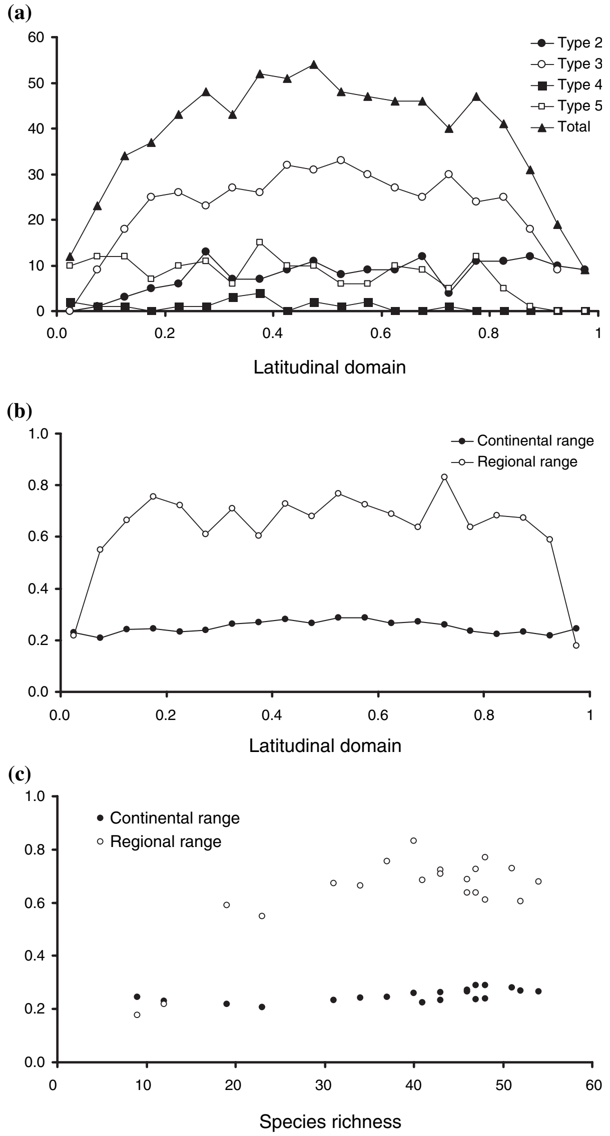

Figure 5 Species ranges and richness in 20 regions along a lineal domain: first null model for the North American bat fauna. Details as in Fig. 2. (a) Species richness of types 2–5 (Fig. 1) in regions along a latitudinal domain. (b) Variation in mean continental range and mean regional range for species occurring in the 20 regions. (c) Relationship between richness and mean continental and regional range size.

The geographical patterns of species range size and richness for North American mammals differ notably from expectations based on the null model. The strong latitudinal gradients shown by empirical data contrast sharply with the predictions of the null model and the fully stochastic model. Similar deviations have been documented for groups of New World birds (Koleff & Gaston, 2001; Hawkins & Diniz-Filho, 2002) and mammals (Lyons & Willig, 1997). Those deviations are so marked that critics of mid-domain models have argued that predictions based on those models are trivial and unrealistic (Hawkins & Diniz-Filho, 2002; Laurie & Silander, 2002; Zapata *et al.*, 2003). We argue that the 'failure' of mid-domain models to reproduce the natural geographical patterns of species richness in North America is simply a proof that faunas are highly structured.

Strong latitudinal gradients in the number of species and of mean range size probably produce such structure. Mid-domain null models predict positive correlations between species richness and mean range size. Large ranges, because of geometric constraints, are highly likely to intersect regions located near the centre of the domain. Thus, richer regions (which are those closer to the centre of the domain) will also

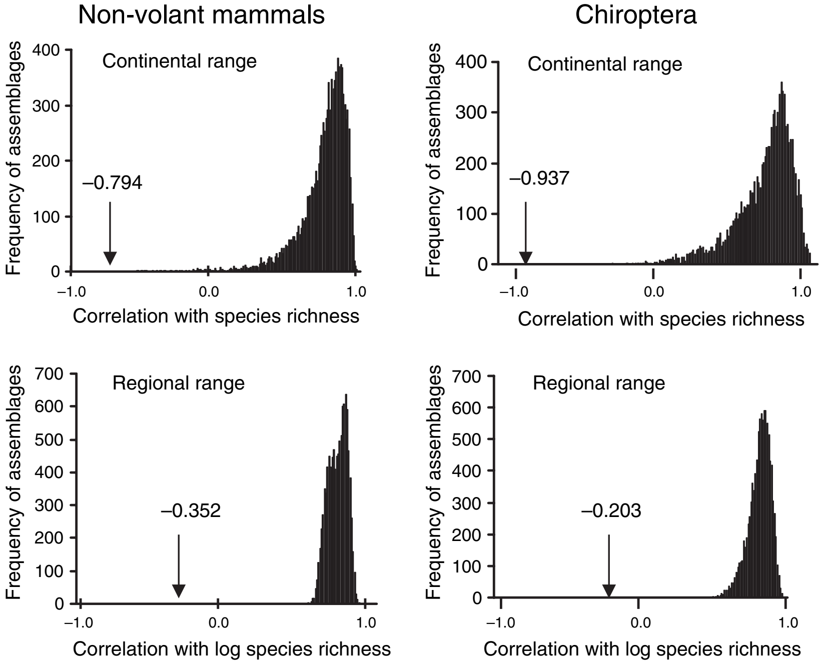

Figure 6 Correlations between species richness and continental and regional range. Histograms show the frequency distribution of values for Pearson's correlation coefficients for 10,000 null communities built by re-sampling the empirical data for North American volant and non-volant mammals, using the third null model described in the main text. Arrows show actual figures for the real assemblages.

tend to include species with larger ranges. Small ranges scatter randomly along the domain, contributing little to the gradient in species richness. Thus, a positive correlation between mean range size and species richness is expected. In real communities, different patterns are possible. In North American bats, for example, a large number of species with small ranges are concentrated in the south, producing a pattern in which the correlation between mean range and species richness is negative. Our simulations show that placing those ranges randomly along the domain can produce positive correlations. Therefore, our results show that the North American mammal fauna is highly structured in terms of the location of species ranges, forming patterns consistent with Rapoport's (1975, 1982) predictions.

Mid-domain models, as other null models, are not intended to reproduce natural patterns, so in that sense, they cannot be 'realistic'. Rather, null models are tools to test the effect of a given ecological force by analysing the structure of species assemblages in the absence of such force, that is, by randomly reshuffling a chosen empirical variable (Gotelli & Graves, 1996). Fully stochastic models should be used with caution when comparing their predictions with real communities, and they should be considered exploratory tools to envision particular patterns that can emerge simply by random arrangements (Colwell *et al.*, 2004). For comparisons with real data, null models based on reshuffling the empirical data are much more useful. For example, our fully stochastic model predicts particular geographical patterns for different types of species that can emerge even if the size and location of ranges are defined by a totally random procedure (Fig. 2). If observed in nature, these patterns could not be attributed to the effect of real-world processes.

Predictions based on mid-domain models do not differ so sharply from real patterns in other systems, such as Madagascan butterflies, sub-Saharan African birds and North American desert rodents (Lees *et al.*, 1999; Jetz & Rahbek, 2001; McCain, 2003). These results show the possibility of an effect of geometric constraints on the patterns of overlap of ranges. They show that any attempt to demonstrate the effect of an ecological or historical factor should consider the fact that random rules can generate complex structure that, in the mentioned cases, mimic the natural patterns.

Rapoport's areographic approach of quantifying species richness as the number of overlapping ranges is naturally amenable to analyses based on mid-domain models. The one-dimensional models discussed here can be extended to two- or even three-dimensional approaches that can yield interesting information to help attempts to relate local and regional patterns of diversity (Leitner & Rosenzweig, 1997; Arita & Rodríguez, 2002, 2004; Ricklefs, 2004). Rapoport's (1975, 1982) basic questions regarding geographical patterns of distribution and diversity and their interrelationship remain valid and current in the context of modern macroecology and biogeography.

A direct relationship between patterns of species richness and distribution can be analysed in two ways in looking for explanatory processes. One is to consider that the distributional patterns of species are determined by a simple combination of environmental variables, and that species richness results at any point simply by the sum of all species whose range intersects that particular location (see discussion in Ricklefs, 2004). Attempts to model the distribution of species using genetic algorithms based on geographical environmental variables (e.g. Peterson *et al.*, 2002) belong to this line of thinking in which distribution determines diversity. The other line of thinking goes the other way around: simple environmental variables (notably the level of available energy) correlate very well with diversity in general and species richness in particular (Hawkins *et al.*, 2003). Then, more species can co-occur in sites with higher levels of available resources, and the distributional patterns of individual species are determined by the patterns of diversity. Thus, from this perspective, diversity determines distribution. Our vision is that both perspectives can be correct at the same time, and that a synthesis is needed to analyse simultaneously geographical patterns and processes of species distribution and diversity. The study of Rapoport's rule and his areographic approach will surely be a powerful tool in this endeavour.

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