

# Geographic range, turnover rate and the scaling of species diversity

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The study of the relative roles of local and regional processes in determining the scaling of species diversity is a very active field in current ecology. The importance of species turnover and the species-range-size frequency distributions in determining how local and regional species diversity are linked has been recognised by recent approaches. Here we present a model, based on a system of fully nested sampling quadrats, to analyse species diversity at several scales. Using a recursive procedure that incorporates increasingly smaller scales and a multiplicative formula for relating local and regional diversity, the model allows the simultaneous depiction of alpha, beta and gamma diversity in a single “species-scale plot”. Species diversity is defined as the number of ranges that are intersected by sampling quadrats of various sizes. The size, shape and location of individual species ranges determine diversity at any scale, but the average point diversity, measured at hypothetical zero-area localities, is determined solely by the size of individual ranges, regardless of their shape and location. The model predicts that if the species-area relationship is a power function, then beta diversity must be scale invariant if measured at constant scale increments. Applying the model to the mammal fauna of four Mexican regions with contrasting environmental conditions, we found that: 1) the species-range-size frequency distribution at the scale of the Mexican regions differs from the log-normal pattern reported for the national and continental scales. 2) Beta diversity is not scale-invariant within each region, implying that the species-area relationship (SAR) does not follow a power function. 3) There is geographic variation in beta diversity. 4) The scaling of diversity is directly linked to patterns of species turnover rate, and ultimately determined by patterns in the geographic distribution of species. The model shows that regional species diversity and the average distribution range of species are the two basic data necessary to predict patterns in the scaling of species diversity.

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The way in which local and regional processes interact to produce patterns of biological diversity is currently a debated topic (Huston 1999, Lawton 1999, Gaston 2000, Gaston and Blackburn 2000, Hugueny and Cornell 2000, Whittaker et al. 2001). Biodiversity is commonly measured as the number of species occurring in a site, a parameter known as species richness or species diversity (Ricklefs and Schluter 1993, Rosenzweig 1995). One of the most puzzling patterns of diversity is the relationship between the number of species of a region, generally known as gamma diversity, and the

average number of species occurring at localities within the larger region, commonly called alpha diversity. Two contrasting kinds of relationships between local and regional species diversity have been proposed (Cornell and Lawton 1992). In Type I relationships the local number of species is directly proportional to regional species diversity, so a straight line is obtained on a plot of local vs. regional species diversity. Type I relationships suggest that local ecological interactions are not strong enough to limit the membership of species to local communities (Hugueny and Cornell 2000). Con-

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trarily, in Type II relationships the number of local species reaches an asymptote as the regional species diversity increases, and local communities are said to be saturated as a consequence of ecological interactions.

Available empirical evidence suggests that Type I species assemblages are more common in nature than saturated communities (Griffiths 1997, Caley and Schluter 1997, Cornell 1999, Lawton 1999, Gaston 2000). Additionally, the fact that some geographic gradients of species diversity follow similar trends at different sampling scales (e.g., for New World mammals, Lyons and Willig 1999) suggests a proportional-sampling structure for local and regional sets of species that are consistent with Type I models (Gaston 2000).

Species turnover rate, a measure of changes in species composition in spatial or temporal gradients, has been called by different names, including differentiation, between-habitat, and beta diversity (Whittaker 1972, Magurran 1988, Whittaker et al. 2001). Although nomenclature varies (see for example discussion in Rosenzweig 1995), here we use the term beta diversity to refer to species turnover in its broadest sense, including patterns of species composition at regional and continental scales (Cornell and Lawton 1992, Harrison et al. 1992, Schluter and Ricklefs 1993).

Although there is agreement on the fact that patterns of species turnover determine the relationship between local and regional diversity, no consensus exists on the mathematical form of such relationship or, for that matter, on the definition of beta diversity itself. Lande (1996), for example, has proposed an additive formula in which gamma diversity results from the sum of alpha and beta diversities. Using this formula, Loreau (2000) has interpreted species saturation curves as pictures of the relationship between alpha and gamma diversity at multiple scales (see also Cornell and Lawton 1992 for an earlier suggestion of this idea). An alternative approach is the classical multiplicative formula advanced by Whittaker (1972) in which regional diversity results from the product of beta diversity and the average local species diversity (Schluter and Ricklefs 1993). A Type I relationship between local and regional species diversity implies a proportional-sampling structure. Thus, such relationships also imply that beta diversity, defined using the multiplicative formula, must be identical for all local-regional pairs (Srivastava 1999, Gaston 2000). As we show here, the multiplicative approach allows the interpretation of scaling factors of diversity, such as  $z$ , the slope of the log-log species-area relationship, in terms of the species turnover rate and the average range of species.

The species-area relationship (SAR) is one of the pillars of the study of the spatial patterns of species diversity (Connor and McCoy 1979, Rosenzweig 1995, Durrett and Levin 1996, Ney-Nifle and Mangel 1999, Lomolino 2000). Although alternative models have been proposed, the most commonly used form of the

SAR is the power-function relationship, which produces straight lines when plotting the log values of species number and area. The slope of such lines, called  $z$ , is related to species turnover (Westoby 1993, Caswell and Cohen 1993, Rosenzweig 1995). A larger value of  $z$  corresponds to a faster accumulation of species as area increases, indicating higher rates of species turnover among the sites that compose the larger region. Recently, different authors have shown a direct relationship between the slope of the SAR and the patterns of geographic ranges of species (Harte and Kinzig 1997, Leitner and Rosenzweig 1997, Ney-Nifle and Mangel 1999). Although the slope  $z$  of the SAR is generally constant for relatively narrow scale intervals, it seems that the pattern does not hold when considering wider intervals, in which the log-log species-area curves show different patterns at different scales (Rosenzweig 1995, Rosenzweig and Ziv 1999, Plotkin et al. 2000, Crawley and Harral 2001, Lomolino and Weiser 2001). This pattern, in which  $z$  is scale invariant within narrow intervals but is scale dependent for wider intervals, implies similar variations with scale in the patterns of the distribution of species and of species turnover.

In this paper we present a simple model for a nested, multiscale system of quadrats that demonstrates a direct relationship between average range, species turnover rate, and the slope of the SAR. We also introduce the species-scale graphs, simple figures that allow the simultaneous depiction of alpha, beta, and gamma diversities. With this tool we examine the patterns of scaling of diversity for the fauna of Mexican non-volant mammals.

## The model

Our model is similar to the recursive procedure developed by Harte et al. (1999, 2001) to examine the scaling of abundance and distribution of species in sampling windows of increasingly smaller size. However, our model is specifically designed to incorporate real data on distributional records based on quadrats and incorporates explicitly the relationship between species diversity, beta diversity and the average range of species. Consider a square-shaped region of side  $L_0$  and area  $A_0 = L_0^2$ , containing  $S_0$  species (Fig. 1). Divide this square into four smaller squares of side  $L_1 = L_0/2$  and area  $A_1 = A_0/4$ . The average species diversity in the four smaller squares is  $\bar{S}_1$ . By performing repeated divisions of the quadrats  $i$  times, a set of smaller and smaller nested squares of area  $A_i = A_0/2^{2i}$  is obtained, each containing, on average,  $\bar{S}_i$  species.

The range of species  $w$  within the region is defined as the proportion of  $A_0$  in which that species occurs ( $p_w$ ). This range is estimated at a given scale as  $p_{w,i} = n_{w,i}/N_i$ , where  $n_{w,i}$  is the number of quadrats of area  $A_i$  in

which species  $w$  is present, and  $N_i = 2^{2i}$  is the total number of quadrats of area  $A_i$  filling the region. The average number of squares of area  $A_i$  occupied by a species is  $\bar{n}_i = (\sum_{w=1}^{S_0} n_{w,i})/S_0$  and the average range is  $\bar{p}_i = (\sum_{w=1}^{S_0} p_{w,i})/S_0 = (\sum_{w=1}^{S_0} n_{w,i})/(S_0 N_i)$ . There is no standard definition for the geographic range of a species (Gaston 1996, Brown et al. 1996). The number of quadrats on a grid system from which a species has been recorded, called the occupancy (Ney-Nifle and Mangel 1999), is one possible measure. Our parameter  $p_w$  represents an estimate of the range relative to the

area of a region, a measure that has been used in patch-occupancy models (Hanski 1982, Caswell and Cohen 1993, Ney-Nifle and Mangel 1999) and in some biogeographic studies (Gaston 1996, Colwell and Lees 2000). Our definition of range, however, can be applied also when using a grid system to estimate the range of a species measured as an extent, that is, the area defined by a line that encompasses the limits to the recorded localities for that species (Gaston 1996).

The multiplicative relationship between regional and local diversity (Whittaker 1972) can be expressed in terms of the number of local sites that constitute a region and the mean number of localities occupied by species:

$$S_\gamma = \bar{S}_\alpha N \bar{n}^{-1}, \quad (1)$$

where  $S_\gamma$  is the regional or gamma species diversity,  $\bar{S}_\alpha$  is the average local or alpha diversity in the  $N$  sites that form the region, and  $\bar{n}$  is the average number of sites in which a given species occurs (Schluter and Ricklefs 1993). In Whittaker's (1972) definition, turnover rate, or beta diversity ( $\beta$ ) is a dimensionless factor relating alpha and gamma diversities, so beta diversity can be defined as  $N \bar{n}^{-1}$  and eq. (1) can be written  $S_\gamma = \bar{S}_\alpha \beta$  (Leitner and Rosenzweig 1997). Defined this way, beta diversity is determined by the related but different effects of the habitat breadths of species and the spatial variation of sites. To separate these two contributions to beta diversity, Schluter and Ricklefs (1993) suggested that turnover should be expressed exclusively in terms of the distribution of species, defining beta diversity as  $\bar{n}^{-1}$ , the inverse of the average number of sites in which a species occurs. Accordingly, eq. (1) would read  $S_\gamma = \bar{S}_\alpha N \beta$ . Although we recognise the two components of beta diversity discussed by Schluter and Ricklefs (1993), we chose to use Whittaker's (1972) more inclusive concept of beta diversity, so in the rest of this paper we use the equality  $\beta = N \bar{n}^{-1}$ . Note that this relationship implies that for our system of nested quadrats turnover rate is, at any scale,  $\beta_i = \bar{p}_i^{-1}$ .

Equation (1) has been demonstrated empirically (Schluter and Ricklefs 1993), and can be derived analytically by examining the scaling of species diversity in nested squares of varying sizes (Leitner and Rosenzweig 1997). It can be shown that eq. (1) is valid for any combination of number of subdivisions of the larger region, number of species, and frequency distribution of number of sites occupied by species (Soberón and Rodríguez unpubl.).

For the quadrats of any scale  $i$  in Fig. 1, eq. (1) can be written  $S_0 = \bar{S}_i N_i \bar{n}_i^{-1} = \bar{S}_i / \bar{p}_i$ . Similarly, for the adjacent scale  $i - 1$ ,  $S_0 = \bar{S}_{i-1} / \bar{p}_{i-1}$ . Combining both equations yields

$$\frac{\bar{S}_{i-1}}{\bar{S}_i} = \frac{\bar{p}_{i-1}}{\bar{p}_i} \quad (2)$$

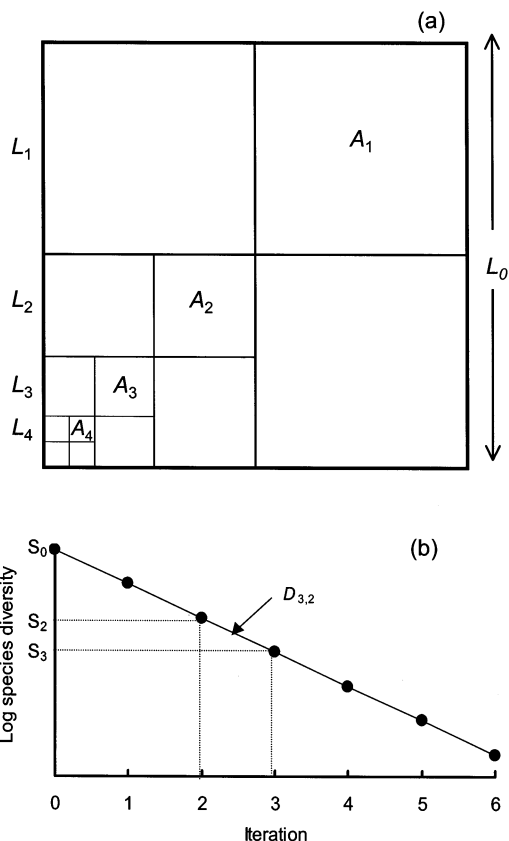


Fig. 1. System of fully nested squares designed to analyse the scaling of species diversity (a). A square-shaped region of side  $L_0$  and area  $A_0 = L_0^2$ , containing  $S_0$  species, is divided into four squares of side  $L_1 = L_0/2$  and area  $A_1 = L_1^2 = A_0/2^2$ . Each of the four smaller squares contains, on average,  $\bar{S}_1$  species. By iterating the division  $i$  times, a series of increasingly smaller squares of side  $L_i = L_0/2^i$  and area  $A_i = L_i^2 = A_0/2^{2i}$ , containing  $\bar{S}_i$  species, is obtained. Note that the number of small squares filling the original region is  $N_i = A_0/A_i = 2^{2i}$ , and that for areas of adjacent scales (separated by a single division),  $N_{i,i-1} = N_i/N_{i-1} = 4$ , so four small squares of size  $A_i$  fit into each square of area  $A_{i-1}$ . For clarity, the progressively finer squares are illustrated only in the lower left corners of squares. By plotting the log value of the number of species as a function of the iteration number, a species-scale plot is obtained (b). If the species-area relationship in the region follows a power function, a straight line is obtained. The figure shows the relationship between species diversity, scale and the slope  $D_i$  for  $i = 3$ ,  $i - 1 = 2$ .

On a log-log plot of species diversity versus area, the slope of a straight line connecting two points at adjacent scales  $i$  and  $i - 1$ , is

$$z_{i,i-1} = \frac{\log S_{i-1} - \log S_i}{\log A_{i-1} - \log A_i} = \frac{\log(S_{i-1}/S_i)}{\log(A_{i-1}/A_i)},$$

which, from eq. (2) and taking into account that for our system of nested squares  $A_{i-1}/A_i = 4$ , reduces to

$$z_{i,i-1} = \frac{\log(\bar{p}_{i-1}/\bar{p}_i)}{\log 4} = \frac{\log(\beta_i/\beta_{i-1})}{\log 4} \quad (3)$$

Assuming that the power-function SAR holds ( $z$  is constant at any scale), eq. (3) shows that if the area of sampling quadrats increases by a constant factor, the average species diversity increases also by a constant factor that can be predicted by the ratio of the average ranges of the species measured at the two scales. If the log-log SAR is not linear, however, then the value of  $z$  is not constant, and the ratio of the average ranges is not scale-invariant. This equation corroborates the idea that the slope of the SAR is directly related to the average range of species (Leitner and Rosenzweig 1997, Ney-Nifle and Mangel 1999), and incorporates the notion that a power-function SAR implies a self-similar pattern for the ratio of the average ranges measured at two scales (see also Harte et al. 1999).

The species turnover rate among quadrats of size  $A_i$  within quadrats of size  $A_{i-1}$  ( $\beta_{i,i-1}$ ) is equal to the ratio of the turnover rates measured among squares of size  $A_i$  and  $A_{i-1}$  within the whole region, that is,  $\beta_{i,i-1} = \beta_i/\beta_{i-1}$ . Consequently, from eq. (3), the slope of the SAR at a given scale is  $z_{i,i-1} = \log \beta_{i,i-1}/\log 4$ . This equation demonstrates a direct link between  $z$  and the species turnover rate, a relationship that had been proposed qualitatively by some authors (Westoby 1993, Rosenzweig 1995). The equation also shows that species turnover, measured between adjacent scales in our system of nested squares (Fig. 1), must be scale-invariant in the scale interval in which the power-function SAR holds.

The species-area relationship can be expressed alternatively as a species-scale plot in which the log value of species diversity is plotted as a function of scale  $i$  (Fig. 1b). The slope of a straight line connecting two adjacent points (separated by a single iteration in our divisive procedure) is  $D_i = (\log \bar{S}_i - \log \bar{S}_{i-1})/(i - (i - 1)) = \log(\bar{S}_i/\bar{S}_{i-1})$ . Substituting for  $\bar{S}_i/\bar{S}_{i-1}$  (eq. (2)) yields

$$D_i = \log \bar{p}_{i-1}/\bar{p}_i = \log \beta_{i-1}/\beta_i = -\log \beta_{i,i-1} \quad (4)$$

Note, from eqs (3) and (4), that  $z_i = -D_i/\log 4$ . This implies that, if the power-function law holds and  $z$  is constant for different scales, then the slope  $D$  of the species-scale plot must be also constant. The absolute

value of the slope  $D_i$  is equal to the log value of the species turnover rate at scale  $i$  within quadrats of size  $A_{i-1}$ . Therefore, in Fig. 1b the abscissa represents changes in scale, the zero-ordinate value ( $S_0$ ) is the regional species diversity, and the absolute value of the slope  $D_i$  is equal to the log value of species turnover rate.

Equation (4) shows that the scaling of species diversity within a region is directly related to the average range of species. Logically, this average is determined by the size of the ranges of individual species. However, the probability of occurrence of species in a given area within a region is determined also by the shape and location of ranges (Colwell and Hurtt 1994, Leitner and Rosenzweig 1997, Colwell and Lees 2000) and by the size and shape of the sampling window (Kunin 1997). Our iterative method is analogous to the general grid method, based on the box-counting theorem, for estimating the fractal dimension of objects (Sugihara and May 1990). Increasingly smaller sampling windows estimate with finer detail the extent of individual ranges, and species count for a given square is equal to the number of individual ranges intersecting that square. Obviously, smaller squares have lower probabilities of intersecting ranges, thereby presenting lower species diversity than larger squares (Fig. 2).

Equation (1) can be written  $S_0 = \bar{S}_i N_i \bar{n}_i^{-1}$ , or  $\bar{S}_i = S_0 \bar{n}_i N_i^{-1} = S_0 \bar{p}_i$ . Because  $\bar{p}_i = (\sum_{w=1}^{S_0} p_{w,i})/S_0$ , it follows that  $\bar{S}_i = \sum_{w=1}^{S_0} p_{w,i}$ . Therefore, at any scale, the average species diversity is equal to the summation of the range sizes of species measured as proportions of the area of the whole region. To illustrate the implications of this relationship, we present a simple example in Fig. 2. Imagine a region of area  $A_0$  (Fig. 1) containing  $S_0 = 5$  species. The ranges of these species are drawn for convenience as regular shapes, and four of them are of the same size but different shape and location. Using our system of nested squares, the range size of species is measured, as a proportion of the area of the whole region, using sampling windows of increasingly smaller size (Fig. 2b). At any scale  $i$  we can calculate the average species diversity by adding the values of the estimated range sizes illustrated in Fig 2b. For example, for iteration  $i = 1$  the estimated range sizes of the five species, measured as proportions of  $A_0$ , are 1.0, 0.25, 0.75, 0.5 and 1.0, so the average species diversity in squares of size  $A_1$  is 3.5. This result can be corroborated by observing that the four squares  $A_1$  intersect the ranges of 3, 3, 4 and 4 species, yielding an average of 3.5 (Fig. 2a). Continuing the iterative process, so  $i$  and  $N_i$  are increasingly larger and  $A_i$  is progressively smaller, we obtain finer and finer estimates of the range size of species. As  $A_i$  tends to zero, the estimate of the range size of a species converges to the absolute area covered by that species (for example, 0.563 for the large square). The summation of these range sizes (measured as proportions of the area of the whole region) is equal

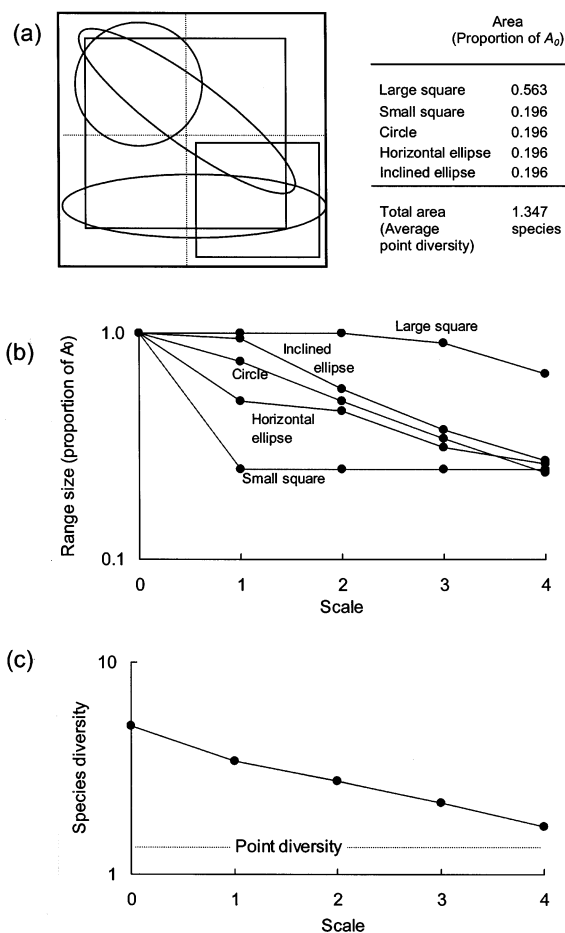


Fig. 2. The ranges of five species within a square-shaped region (of area  $A_0$ ), drawn as regular shapes (a). The four squares of size  $A_1$  created by the first division of the region are illustrated with the dashed lines. Using the system of nested squares (Fig. 1), range sizes are measured as proportions of the area of the whole region, using quadrats of increasingly smaller size (b). Each point in the plot is  $n_{i,w}/N_i$ , where  $n_{i,w}$  is the number of squares of size  $A_i$  that intersect the range of species  $w$  and  $N_i = 2^{2i}$  is the number of squares of area  $A_i$  filling the region. As shown in the main text, at any scale the average species diversity equals the summation of the distribution ranges. As  $A_i$  tends to zero, the estimate of the range size of a species converges to the real, absolute area covered by that species. The summation of these range sizes is equal to the average point species diversity of that region (c).

to the average number of species measured at an infinite number of points within the region. In other words, the average range size of species within a region is equal to the average expected point species diversity of that region.

The scaling of  $p_{w,i}$ , and consequently of average species diversity, depends on the size, shape and location of species ranges (Fig. 2). In contrast, the expected average point species diversity, that is, the species count at hypothetical zero-area localities within the region is determined solely by the species range sizes, indepen-

dently of their shape and location (see also proof in Leitner and Rosenzweig 1997). This generalisation applies only when considering geographic ranges as geometric figures with finite areas, as in Fig. 2. If species ranges are envisioned as true fractal structures, showing finer and finer detail as the size of the sampling window diminishes, then it would be impossible to define point diversity with our method. However, physical constraints set lower limits to the scale domain within which biological objects show true fractality (Sugihara and May 1990), so the fractal structure documented for the distribution patterns of some species (Gaston 1996) is apt to be limited to a few scales.

## Methods

The model of scaling of species diversity was applied to the non-volant mammal fauna of Mexico. Distributional information was extracted from an existing database that includes the whole fauna of Mexican mammals. Details of the method used to build the database are presented elsewhere (Arita et al. 1997), but briefly, distributional maps were drawn for all terrestrial non-insular mammal species in Mexico, updating the taxonomic and biogeographic information up to the end of 1997. A grid of 823 quadrats of  $0.5^\circ \times 0.5^\circ$  latitude and longitude was overlaid on each map and the quadrats intersecting the distributional extent of each species were recorded. Each of the quadrats, which are our minimum sampling unit, measures on average 53.25 km on each side, corresponding to an area of 2835.8 km<sup>2</sup>. The order Chiroptera was excluded from the analysis because North American bats show latitudinal patterns of species diversity that differ sharply from that of non-volant mammals (Wilson 1974, McCoy and Connor 1980, Lyons and Willig 1999), thus presenting different patterns of species turnover, and presumably of scaling of diversity. The database is available on the web page of the Mexican Commission on Biodiversity at <http://www.conabio.gob.mx>.

Four regions in Mexico with contrasting environmental conditions were chosen to illustrate the effect of physical heterogeneity and other landscape variables on the patterns of scaling of species diversity. In each of these regions a four-by-four-degree quadrat was laid in such a way that the area lying outside the mainland was minimised (Fig. 3, Table 1). Heterogeneity was measured within each of the quadrats with the standard deviation of three environmental variables (altitude above sea level, mean annual temperature and mean annual rainfall) calculated from data of several meteorological stations (García 1981). A quadrat located in northern Mexico, a fully Nearctic region (Ortega and Arita 1998), corresponded to a dry area of the states of

Chihuahua, Coahuila and Durango (Fig. 3). This region showed high variation in altitude (SD, 403.9 m a.s.l.,  $n = 23$  meteorological stations), but comparatively low levels of heterogeneity in mean annual temperature (SD, 1.3°C) and mean annual rainfall (SD, 128.3 mm). A second quadrat, located in central Mexico, incorporated parts of the Mexican volcanic belt and of the basin of the Balsas river, thus including Nearctic portions as well as areas lying in the Nearctic-Neotropical transition (Ortega and Arita 1998). This mostly mountainous area showed a high degree of heterogeneity (SD of altitude, 660.1 m; SD of temperature, 4.2°C; SD of rainfall, 331.9 mm;  $n = 60$  stations). A third quadrat, located in the Isthmus of Tehuantepec and including parts of the states of Veracruz, Oaxaca, Chiapas and Tabasco, included parts of the Nearctic-Neotropical transition, as well as some fully Neotropical areas (Ortega and Arita 1998). This region showed a high heterogeneity (SD of altitude, 530.6 m; SD of temperature, 2.5°C; SD of rainfall, 762.0 mm;  $n = 56$  stations). The scaling of body-mass diversity in this region has been analysed elsewhere (Arita and Figueroa 1999). The fourth quadrat, located in the mostly flat Yucatan Peninsula, is fully Neotropical and showed low levels of heterogeneity (SD of altitude, 47.7 m; SD of temperature, 0.8°C; SD of rainfall, 228.9 mm;  $n = 40$  stations).

The structure of the database allowed the measurement of species diversity within each region at four

scales, using the nested structure depicted in Fig. 1:  $0.5 \times 0.5$ ,  $1 \times 1$ ,  $2 \times 2$  and  $4 \times 4$  degrees. These scales correspond to the areas  $A_3$ ,  $A_2$ ,  $A_1$  and  $A_0$  in Fig. 1, respectively. For the purpose of these analyses, the average species diversity in the smallest sample units (the 0.5-degree quadrats) was considered the alpha diversity within each region. Because of the physiography of the study areas, three of the quadrats included  $< 64$   $0.5^\circ$  quadrats. The central Mexico quadrat included 62 such quadrats, while the Isthmus and the Yucatan quadrats each consisted of 50 small quadrats. The four large quadrats included the full complement of 16 one-degree quadrats and four two-degree quadrats. Using data extracted from the database of Mexican mammals, species-scale plots were constructed for each of the four areas under study and analysed the effect of location and heterogeneity on the patterns of scaling of species diversity.

## Results and discussion

The mammalian faunas showed contrasting patterns of distribution within the four Mexican regions. For northern Mexico and the Isthmus of Tehuantepec, the frequency distribution of geographic range size showed a U-shaped pattern, with several restricted and widespread species and comparatively few species with ranges of intermediate size (Fig. 4). In both cases,

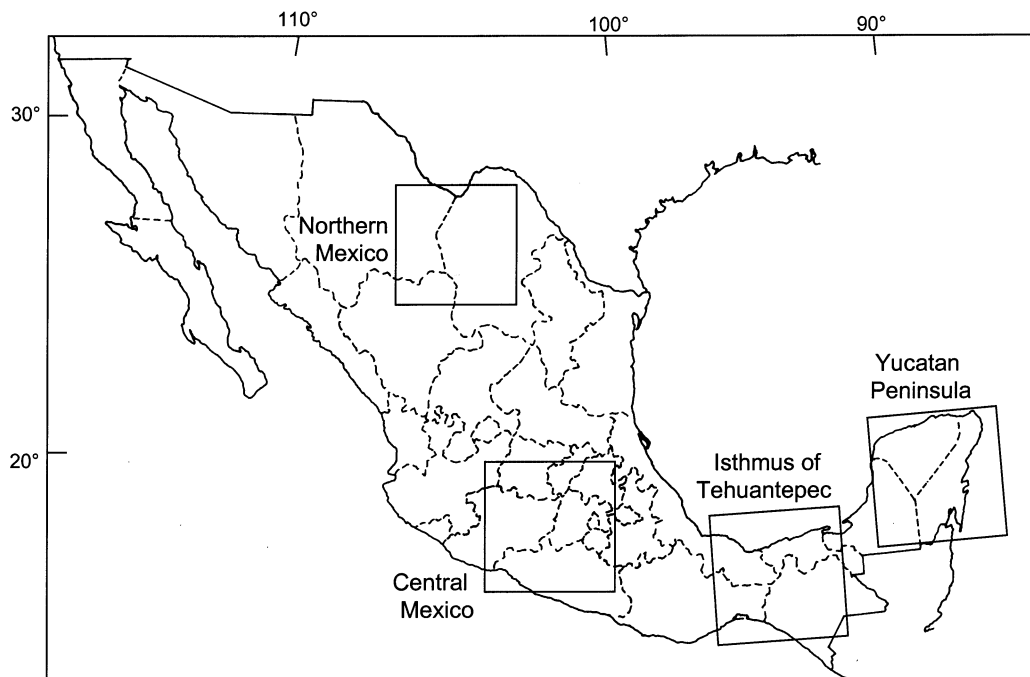


Fig. 3. Location of four Mexican regions with contrasting environmental conditions. Each region is a square measuring 4 degrees of latitude and longitude in each side and was subdivided as in Fig. 1 for the analysis of scaling of species diversity. Characteristics of these quadrats are detailed in Table 1.

Table 1. Environmental and biological characteristics of the four Mexican regions showed in Fig. 3. The allocation to biogeographic realms follows Ortega and Arita (1998). The criteria to measure heterogeneity are discussed in the main text. The regional (gamma) species diversity is the total number of species occurring within each of the quadrats. Average alpha diversity corresponds to the 0.5-degree quadrats that are the sampling units of the present work. Beta diversity was calculated as the ratio between the number of species in the whole 4×4-degree nested quadrat and the average diversity in the 0.5×0.5-degree quadrats.

	Northern Mexico	Central Mexico	Isthmus	Yucatan Peninsula
Realm	Nearctic	Nearctic – Transitional	Transitional – Neotropical	Neotropical
Heterogeneity	Intermediate	High	High	Low
Average range size (proportion of area)	0.583	0.396	0.575	0.842
Gamma species diversity	89	124	102	53
Average alpha species diversity	51.9	49.2	58.7	44.6
Beta diversity	1.71	2.52	1.74	1.19

about three-quarters of the species (74.1% for northern Mexico, 75.6% for the Isthmus) were present either in > 75% or in < 25% of the area of the region. The central Mexico quadrat showed a contrasting pattern in which only 15.3% of the species were present in > 75% of the area of the region, and a high percentage of species (39.5%) were restricted to < 25% of the area. Contrarily, in the Yucatan quadrat, the majority of species (81.1%) were present in > 75% of the area of the region, and very few species (5.7%) were restricted to < 25% of the area. Northern Mexico and the Isthmus had similar average range sizes (58.3% of the area for northern Mexico, 57.5% for the Isthmus; Table 1), whereas in central Mexico species were mostly restricted (average range, 39.6% of the area) and in the Yucatan were mostly widespread (average range, 84.2% of the area).

The frequency distributions of geographic range sizes shown in Fig. 4 differ from the pattern generally reported for continental faunas, in which an approximate log-normal distribution is observed (Gaston 1994, 1996, Gaston and Blackburn 2000). For the terrestrial mammals of North America, for example, the species-range-size distribution is closely log-normal at the continental level (Pagel et al. 1991) and for the subset of Mexican mammals (Arita et al. 1997, Ceballos et al. 1998). Our data for northern Mexico and the Isthmus of Tehuantepec conform to the observation of Gaston and Blackburn (2000) that the frequency distribution of geographic range size of British vertebrates tends to be U-shaped at intermediate and small scales, with many restricted and widespread species and few with ranges of intermediate size. Our data for central Mexico and Yucatan, however, show that the pattern is not universal and suggest that such factors as environmental heterogeneity and biogeographic history might play a substantial role in shaping the frequency distribution of range sizes for mammalian faunas.

Central Mexico had the highest regional (gamma) species diversity (124 species), but only the second highest average alpha diversity (49.15 species; Fig. 5a). This pattern implies a high beta diversity for this region

( $\beta = 2.52$ ), a fact that can be inferred from the steep slope in Fig. 5a and can be seen in Fig. 5b. Northern Mexico and the Isthmus showed similar patterns of scaling of species diversity (Fig. 5a). Both regions had higher average alpha species diversity than central Mexico, but because of lower beta diversity (Fig. 5b) both regions presented lower diversity at the regional scale than that of central Mexico. The Yucatan Peninsula showed the lowest alpha and gamma species diversity and a very low species turnover rate (Fig. 5a, b).

The model predicts that, if the power-function SAR holds and  $z$  is constant, the species-scale plots should yield straight lines with a constant slope  $D$ . Because  $D$  at any given scale equals the absolute value of  $\log \beta$ , the power-function SAR implies that beta diversity (measured between any pair of adjacent scales in our model) should be constant, that is, scale invariant. Results for the Mexican regions do not adjust to this prediction. Species-scale plots of the four regions follow curved lines with increasingly less steep slopes (Fig. 5a), which implies that species turnover is lower at smaller scales (Fig. 5b). These results imply that at the scale of the Mexican regions the SAR does not follow a power function and beta diversity is not scale invariant. The power-function SAR describes adequately the scaling of species diversity at continental scales, but it is well

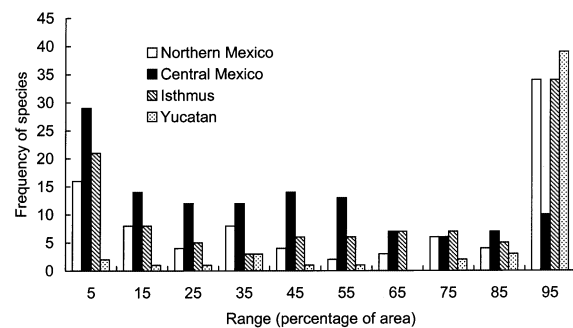


Fig. 4. Frequency distribution of geographic range size for the non-volant mammal fauna within each of the four regions shown in Fig. 3.

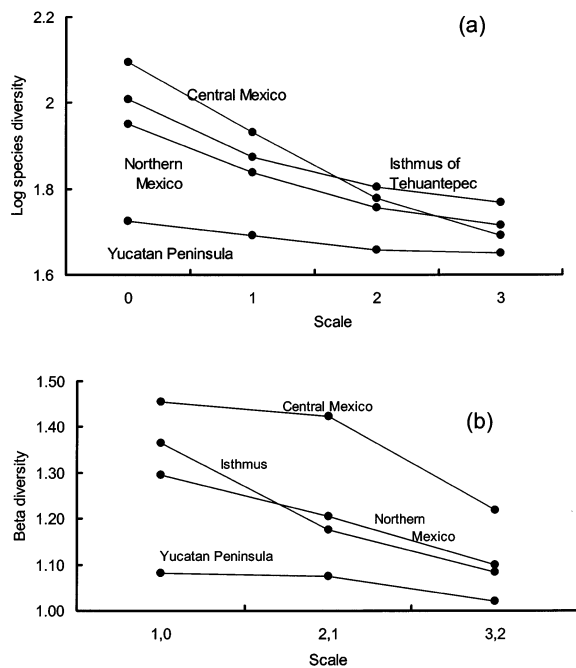


Fig. 5. Species-scale plots (Fig. 1b) corresponding to the four Mexican regions under study (a). The scaling of beta diversity in the four Mexican regions under study (b). Beta diversity is defined as the ratio of species diversity measured at adjacent scales, resulting from the iterative procedure detailed in Fig. 1. For example,  $\beta_{3,2}$  is equal to  $S_2/S_3$ .

known that the particular value of  $z$  varies with scale and with environmental conditions (Rosenzweig 1995, Rosenzweig and Ziv 1999). Our data suggest that different mechanisms act at the scale of our Mexican regions, producing different patterns of beta diversity and, consequently, of scaling of species diversity.

Our model has the potential of rendering a method to determine the scales at which the SAR might be scale invariant. Our database allowed us to analyse only four scales and three slope values. By increasing the number of scales, it might be possible to determine statistically the scale intervals at which the slope of the species-scale plots is constant, thus detecting scales at which there is a constant  $z$  value for the SAR. Another potential refinement of the model would be to analyse the patterns of variance on the expected values of species diversity at different scales. This analysis would allow the study of differences among sites at different scales in terms of their deviation from the expected value of species diversity.

Our data document a geographic variation in beta diversity that is incompatible with Type I, unsaturated relationships between local and regional species diversity. Unsaturated relationships, by definition, imply a proportional sampling relationship between local and regional assemblages, implying a constant value for beta diversity across all local-regional pairs (Srivastava

1999, Gaston 2000). Differences among the four regions in terms of biogeographic affinity and physiographic features probably account for the different values of beta diversity. The method that we use here, based on geographic ranges and not taking into account local interactions among species, cannot be used directly to make inferences about the processes that ultimately determine the observed patterns. As pointed out by Loreau (2000), local-regional species diversity plots provide more information on patterns of scaling of diversity than on any kind of local ecological interaction. Thus, the debate about the ecological processes that ultimately determine Type I (unsaturated) and Type II (saturated) communities remains open.

The scaling of diversity seems to be determined both by the heterogeneity of the regions and by their geographic location. The quadrat with the highest beta diversity (central Mexico) corresponds with the most heterogeneous region and is located in the transition between two zoogeographical realms. Two regions with comparatively high heterogeneity but located in very different physiographic areas (northern Mexico and the Isthmus of Tehuantepec) showed similar patterns of scaling. Finally, the flat, homogeneous Yucatan Peninsula presented very low species turnover rate and low alpha species diversity, despite the completely Neotropical composition of the mammal fauna of the area.

The empirical results presented here corroborate the notion that the scaling of species diversity is determined by species turnover rate, and ultimately by the size of the geographic ranges of the species. In fact, as demonstrated by our model, some of the rows in Table 1, reported in the table from empirical data, could have been derived from two basic data: the regional species diversity and the average geographic range within the region. For the northern Mexico quadrat, for example, the observed average species diversity among the 64 0.5-degree quadrats was 51.9 species, a figure that could have been obtained simply by multiplying the average range size (measured as a proportion of the regional area, in this case 0.583) times the regional species diversity (89). Similarly, the observed beta diversity for this region ( $\beta = 1.71$ ) could have been derived also by obtaining the inverse of the average distribution range ( $1/0.583 = 1.71$ ).

The model shows that the average point species diversity can be predicted as the summation of the ranges of species measured as proportions of the area of a given region. Point species diversity is defined here as the number of ranges that overlap a given point on the region. Of course, the predicted value for the average point species diversity is based solely on the geographic patterns of distribution of species, regardless of any kind of local ecological interaction that could curtail the presence of certain species. In that sense, these expected point-diversity values could be used in ecological null models as neutral comparison figures for



real communities to test for the effect of local species interactions.

The direct link between the scaling of species diversity and the range of species has important implications for theoretical and applied ecology. It could combine in a single model the trend for higher species diversity and for smaller geographic ranges towards lower latitudes, the so-called Rapoport effect that has been reported for some animal groups in some parts of the world (Rapoport 1982, Stevens 1989, Gaston et al. 1998, Kolasa et al. 1998). Our model and our empirical results show that the measurement of species diversity varies with the size of the sampling quadrats in a way that depends on the distribution ranges of species (see also Anderson and Marcus 1993, Kunin 1997). Thus, the Rapoport effect and the higher species diversity in the tropics than in temperate regions might be manifestations of the same biogeographic phenomenon, ultimately defined by the way in which species distribute at the geographic scale.

Conservation projects at the continental scale (Soulé and Terborgh 1999) can benefit from a possible unification of criteria currently based either on species diversity or on the presence of species with small ranges, particularly endemics (Myers et al. 2000). Moreover, the dynamics of species ranges (Channell and Lomolino 2000) could be applied not only to the study of the extinction of particular species, but also to the prediction of changes in the geographic distribution of species diversity. Scott et al. (1999) speculated on the implications for continental conservation of the relationship between the scaling of species diversity and the patterns in the distribution of species. They concluded that regions in which most species present restricted distributions have high beta diversity and should require larger number of reserves to protect all species than regions in which most species are widespread.

Our results show a close mathematical relationship between regional parameters (regional species diversity, average species-distribution range) and the species composition of local communities. As our model shows, this composition can be accurately predicted by knowing the value of the regional parameters, suggesting that regional processes might have a strong influence on the assemblage of local communities (Ricklefs and Schluter 1993, Gaston 2000). However, as in all studies based on the analysis of pattern, inferences on processes should be made with great precaution. In any event, our results support the idea that the analysis of the processes by which species use resources to organise themselves in geographic space provides useful information to understand the distribution and scaling of biological diversity. This approach would partly shift the focus of research from classical community ecology to macroecology, the study of the way in which species divide resources at geographic scales (Brown and Maurer 1989, Brown 1995, Lawton 1999, Gaston and Blackburn 2000).

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