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PAPER



Local-regional relationships and the geographical distribution of species

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ABSTRACT

Aim Local-regional (LR) species diversity plots were conceived to assess the contribution of regional and local processes in shaping the patterns of biological diversity, but have been used also to explore the scaling of diversity in terms of its alpha, beta, and gamma components. Here we explore the idea that patterns in the geographical ranges of species over a continent can determine the shape of small region to large region (SRLR) plots, which are equivalent to LR plots when comparing the diversity of sites at two regional scales.

Location To test that idea, we analysed the diversity patterns at two regional scales for the mammals of North America, defined as the mainland from Alaska and Canada to Panama.

Method We developed a theoretical model relating average range size of species over a large-scale region with its average regional point species diversity (RPD). Then, we generated a null model of expected SRLR plots based on theoretical predictions. Species diversities at two scales were modelled using linear and saturation functions for Type I and Type II SRLR relationships, respectively. We applied the models to the case of North American mammals by examining the regional diversity and the RPD for 21 large-scale quadrats (with area equal to 160,000 km²), arranged along a latitudinal gradient.

Results Our model showed that continental and large-scale regional patterns of distribution of species can generate both types of SRLR relationship, and that these patterns can be reflected in LR plots without invoking any kind of local processes. We found that North American nonvolant mammals follow a Type I SRLR relationship, whereas bats follow a Type II pattern. This difference was linked to patterns in which species of the two mammalian groups distribute in geographical space.

Conclusion Traditional LR plots and the new SRLR plots are useful tools in exploring the scaling of species diversity and in showing the relationship between distribution and diversity. Their usefulness in comparing the relative role of local and regional processes is, however, very limited.

Keywords

Geographical range, local-regional relationship, macroecology, mammals, North America, scales, species diversity, species saturation.

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INTRODUCTION

A current debate in ecology is on how local and regional processes generate patterns of biological diversity at different scales (Huston, 1999; Lawton, 1999; Gaston, 2000; Godfray & Lawton, 2001; Whittaker *et al.*, 2001; Kaspari *et al.*, 2003). One way of studying the interaction between processes acting at different

scales is through the analysis of the local-regional (LR) relationship of species diversity (Terborgh & Faaborg, 1980; Cornell, 1985; Ricklefs, 1987). Studies addressing the issue have used bivariate LR plots, in which species diversity of localities within a region is plotted against the corresponding regional species diversity (Cornell, 1985; Ricklefs, 1987, 2000). According to some authors, the patterns formed by several points on these

graphs, each representing a local-regional pair, can provide clues regarding the relative strength of local and regional processes in shaping the composition of ecological communities (Ricklefs, 1987; Cornell & Lawton, 1992).

Recently, other authors have argued that the shape of the LR graphs is determined mostly by patterns in the scaling of species diversity and provides little information about the interaction between local and regional processes (Rosenzweig & Ziv, 1999; Loreau, 2000). Rosenzweig & Ziv (1999) called the relationship between local and regional diversity the Echo pattern, meaning that a LR plot for a given set of regions within a larger area echoes the information contained in species-area relationships within and among the regions. In a similar vein, Loreau (2000) has shown that the shape of LR curves reflects the pattern in which beta diversity (measured in this case as the additive difference between regional and local species diversity) varies with regional diversity.

Two basic patterns have been described for LR plots. Type I (proportional sampling) relationships produce a straight line on a LR plot, whereas in Type II (saturating) relationships the local species diversity reaches an asymptote as the regional species diversity increases, so there is a limit to the number of species that can coexist in a given local community, regardless of the magnitude of the corresponding regional diversity. In the original postulation of LR plots, Type I relationships were interpreted as suggesting that local ecological interactions were too weak to constrain the species composition of local communities, whereas Type II patterns were interpreted as suggesting that local interactions limited the membership of species that potentially could co-occur in local assemblages (Ricklefs, 1987; Cornell & Lawton, 1992; Hugué & Cornell, 2000).

A different interpretation of LR plots is through the dissection of the regional species diversity into its alpha and beta components (Cornell & Lawton, 1992; Srivastava, 1999; Loreau, 2000; Gering & Crist, 2002). The idea of separating the regional species diversity into different components goes back to Whittaker (1960), who proposed that the total number of species of a region (gamma diversity) could be understood as a combination of the average diversity of the localities forming the region (alpha diversity) and the differences in composition among them, that is, the species turnover component (beta diversity). As LR plots show the relationship between the diversities at two different scales, the shape of the curve is obviously related to beta diversity, although the exact relationship depends on the formulation used (Srivastava, 1999; Loreau, 2000).

Several problems haunt the use and interpretation of LR plots (Srivastava, 1999). One is the use in different studies of different scales to define what is local and what is regional (Srivastava, 1999). Others include the lack of null models defining the background against which patterns putatively produced by local and regional processes could be contrasted, the use of a between-habitat scale instead of a within-habitat scale for comparisons, the pseudoreplication of local communities, the overestimation of the regional pool by adding species across habitats, and statistical problems associated with the difficulty in distinguishing between a linear and a saturation pattern.

A related set of problems arise when interpreting LR relationships in terms of ecological interactions. Type I relationships can be generated even with models that include interactions among the species (Cornell & Lawton, 1992; Caswell & Cohen, 1993), so a linear LR relationships does not necessarily imply a neutral (noninteractive) community. On the other hand, Type II relationships are not predicted by noninteractive models, so they can be interpreted as indirect evidence of ecological interactions; however, pseudo-saturating patterns can be generated by errors in the sampling or analytical procedures, so interpretations have to be reached with extreme care (Srivastava, 1999).

In this paper, we show that both types of LR relationships can be generated when comparing species diversity at two large (i.e. coarse) scales. In doing so, we contribute an additional factor that has to be considered when interpreting LR plots, that is, whether the observed pattern is in fact generated by the effect (or lack of effect) of local interactions or is simply a reflection of processes occurring at a regional scale. We provide a theoretical framework with predictions that we test with data for North American mammals.

CONCEPTUAL FRAMEWORK

In this section we develop a theoretical model linking LR plots to the geographical range of species. Imagine the map of a continent over which the ranges of species are drawn (Fig. 1). Within the continent, define a number of large-scale quadrats of equal area, which we will call 'sampling regions' or simply 'regions'. Species diversity of a given region, S , is the total number of species of the continent whose ranges intersect the region. For a given region, define the proportional range of species i (p_i) as the percentage of the area of the sampling region that is covered by the geographical range of species i (Fig. 1(a)).

Define the 'regional point diversity' (RPD) for a hypothetical zero-area point within the region as the number of species whose ranges coincide with the location of that point (Fig. 1(b)). This regional point diversity has been called gamma diversity and has been used in some studies as the regional pool of species in local-regional comparisons (Stevens & Willig, 2002; cites therein). Note that we use 'point diversity' in the sense that we measure the value for zero-area points, and 'regional' in the sense that the diversity value is determined completely by regional patterns in the distribution of species. It can be shown (Arita & Rodríguez, 2002; see Appendix) that the average RPD for a region is $\bar{s} = \sum_{i=1}^S p_i$, and, because the average proportional range is, $\bar{p} = (\sum_{i=1}^S p_i) / S$, by definition, it follows that

$$\bar{s} = \bar{p}S \quad (1)$$

So far, we have defined species richness at three different grains: the species diversity of the whole continent, the species diversity within each of the sampling regions, and the average RPD within each region. Note that these three estimates of diversity are defined solely by the size, shape, and location of the geographical ranges of species occurring in the continent. A fourth kind of species count can be obtained if for several local sites with

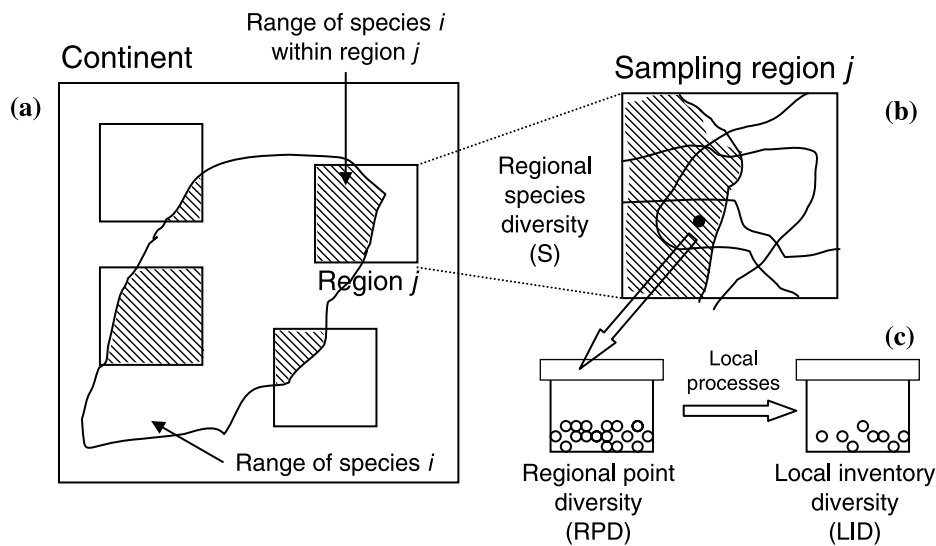


Figure 1 Species diversity at four spatial scales. (a) At a continental scale, species diversity is the number of species occurring within a bounded continent or province. Regional species diversity, S , is equal to the number of species whose range intersects the region. In the figure, the intersection of the range of one species with four quadrangular regions is shown with the dashed pattern. (b) Still at the regional level, but at a smaller scale, the regional point diversity (RPD) for a hypothetical zero-area point is determined by the number of ranges that coincide with the point. (c) This RPD constitutes the pool of species from which the actual local inventory community has to be formed.

homogeneous habitat within each region a species inventory is performed, measuring the actual number of species that co-occur in the localities, that is, the local inventory diversity (LID). These LID values would be equal to or less than the corresponding RPD, so in that sense, the sets of species quantified by the RPD constitute a pool of species from which actual local communities (LID) have to be built (Fig. 1(c)). Which species from that pool occur or do not occur in actual communities would depend on local conditions (suitable habitat, adequate nesting grounds, for example) or on local ecological interactions.

Most studies using LR plots have measured species diversity at the local scale considering the species occurring in actual communities, i.e. their local inventory diversity. Comparing these LID counts with corresponding regional measures, LR plots are drawn, and inferences about the comparative effect of local and regional processes are made. Here we show that plots comparing RPD values with their corresponding regional diversity measures can generate patterns similar to those of regular LR plots, without invoking any kind of local condition or interaction. In fact, our new SRLR (small region to large region) plots can take either of the Type I and Type II shapes described for LR plots. We argue that SRLR plots can be considered null models for LR plots, in the sense that the new model does not take into account local processes.

Equation 1 provides the necessary mathematical relationship for predicting the shape of SRLR plots. For example, if for several sampling regions with different values of species diversity the average range of species within them is the same, that is, \bar{p} remains constant, then the SRLR relationship should be linear with a slope equal to \bar{p} (Fig. 2). Alternatively, because $\bar{p} = 1/\beta$ (Arita & Rodríguez, 2002), the slope of the line would be equal to the inverse of Whittaker's beta, as pointed out by Srivastava

(1999). Therefore, for SRLR plots to follow a straight line, the average range size of species within the compared regions must remain constant, regardless of the number of species.

In a different scenario, if the average range decreases with increasing regional species richness, then the SRLR relationship is curvilinear and similar to a saturation curve (Fig. 2). For example, the simple function $\bar{p} = 1 - cS$, where c is a constant, generates an SRLR curve defined by the equation $\bar{s} = S - cS^2$, which for a given range of S -values looks like a saturation curve. A more complex function for \bar{p} , such as $\bar{p} = c_1/(c_2 + S)$, where c_1 and c_2 are constants, generates a true saturating curve for the SRLR relationship, defined by the equation $\bar{s} = c_1S/(c_2 + S)$.

EMPIRICAL TESTS

Methods

We applied the model of LR plots and geographical range to data on the distribution of the mammals of North America. From a complete list of North American mammals (Reid, 1998; Wilson & Ruff, 1999), we excluded introduced, marine, and insular species, rendering a database of 744 species. We drew range maps for all species, using distributional data published up to the end of 2000. Since the distribution patterns and species diversity gradients in North America are different for Chiroptera and the rest of the mammalian orders (McCoy & Connor, 1980; Arita *et al.*, 1997; Lyons & Willig, 1997), we analysed the data for bats and nonvolant mammals separately.

We constructed 21 large sampling regions, each of 160,000 km², arranged to encompass a latitudinal gradient extending from 12° to 64° North latitude. Because of the shape of the continent, there were more replicates on the northern section of the

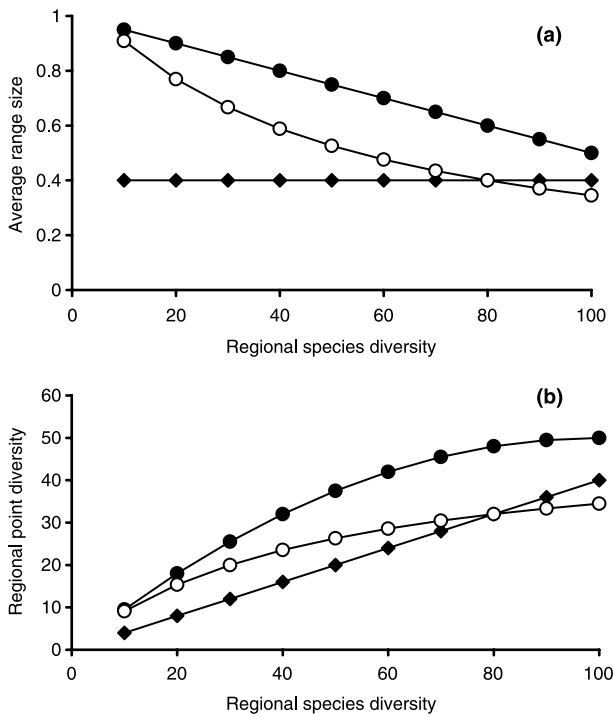


Figure 2 (a) Possible relationships between the average range size (measured as the proportion of the whole regional area, \bar{p} and species diversity (S) for several regions, showing a constant value for the average proportional range size ($\bar{p} = c$, where c is a constant), a linear negative function ($\bar{p} = 1 - cS$), and a curvilinear relationship ($\bar{p} = c_1/(c_2 + S)$). (b) SRLR plots, showing a Type I (linear) relationship corresponding to a constant range size ($\bar{s} = \bar{p}S$, where \bar{s} is the RPD) and two types of Type II (saturating) relationships ($\bar{s} = S - cS^2$, corresponding to the linear negative function of range size, and $\bar{s} = c_1S/(c_2 + S)$, corresponding to the curvilinear relationship of range size with species diversity).

continent (six squares at 64°N) than in Central America, where only one square could be fitted.

Regional diversity at the large scale was measured as the number of species whose range intersected a sampling region, and the RPD was measured within each region at 64 zero-area points arranged systematically in such a way that points were separated from each other by 50 km. RPD of a given sampling point was simply the number of species whose ranges included the point. To avoid pseudoreplication (Griffiths, 1999; Srivastava, 1999) and to minimize the effect of spatial autocorrelation (Diniz-Filho *et al.*, 2003), only one value for RPD was used for each sampling region (the average RPD value for the 64 sampling points within each large square). Thus, we had a total of 21 small region-large region pairs to assess the performance of our model.

RESULTS

The 21,160,000-km² sampling regions ranged in regional diversity from one species of bat and 20 nonvolant mammals to 110

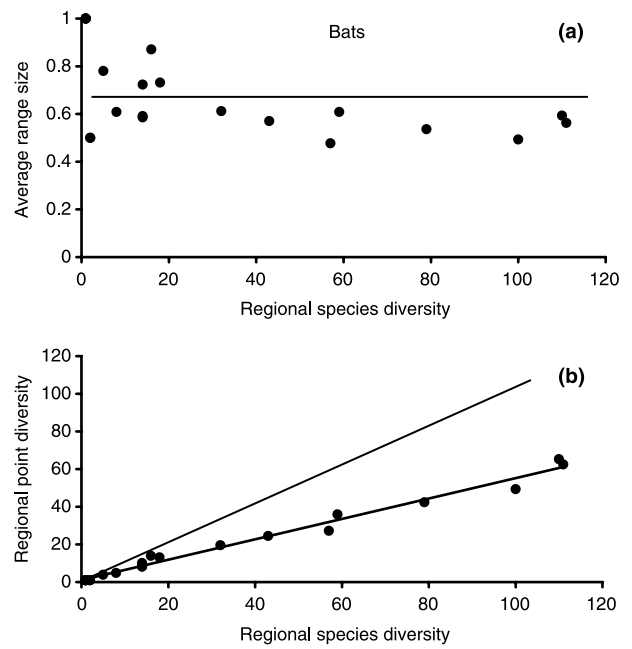


Figure 3 (a) Relationship between the average range size (measured as a proportion of the total area of a region) and regional species diversity for North American bats. (b) Corresponding small region to large region (SRLR) species diversity plot. Points are pairs of regional diversity and RPD for 21 regions arranged on a latitudinal gradient in North America. The best-fit equation for the SRLR is $\bar{s} = 0.56S$.

and 133 species of bats and nonvolant mammals, respectively. The average RPD among sampling points within the 21 regions varied from 1.0 to 65.28 species of bats, and from 13.54 to 71.0 species of nonvolant mammals.

Bats and nonvolant mammals showed contrasting patterns of SRLR relationships. The SRLR relationship for bats could be fitted to a straight line intersecting the origin of the graph (Fig. 3, $r^2 = 0.99, P < 0.01$), demonstrating a Type I relationship in which about 56% of the species occurring in a large region are also part of the RPD. In contrast, the SRLR relationship for nonvolant mammals was better described by a saturation equation (Fig. 4, $r^2 = 0.98$), showing a Type II relationship with an asymptotic value of 89.75 species. As predicted by the model, the average proportional range size within regions did not vary with species diversity in the case of bats (Fig. 3), but showed a decreasing relationship in the case of nonvolant mammals (Fig. 4).

DISCUSSION

Our model and empirical results show that both Type I and Type II diversity plots at the regional scales can be generated by variations in the geographical distribution of species, without considering any kind of local condition or interaction. This is true because both parameters of the SRLR relationship, the average RPD and the regional species diversity, are determined by the way in which species distribute in space, at the continental and regional levels.

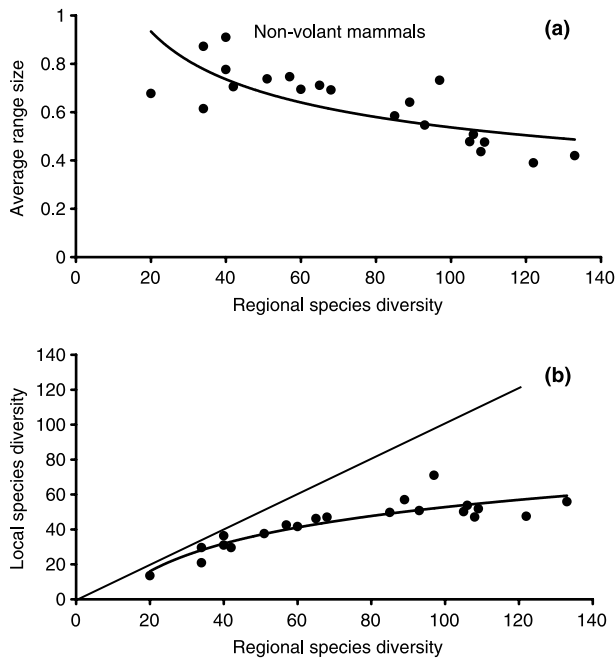


Figure 4 (a) Relationship between the average range size (measured as a proportion of the total area of a region) and regional species diversity for North American nonvolant mammals. (b) Corresponding small region to large region (SRLR) species diversity plot. Points are pairs of regional diversity and RPD for 21 regions arranged on a latitudinal gradient in North America. The best-fit equation for the SRLR is $\bar{s} = 89.7S/(70.8 + S)$.

The species diversity of a region is determined by the number of ranges that the region intersects (Fig. 1). Obviously, that value depends on the size of the region, so valid SRLR plots should be generated by comparing regions of the same size to avoid effects such as the pseudosaturation demonstrated by Srivastava (1999). Holding the size of the regions constant, the number of species whose ranges intersect a region will depend on the location of the region and on the size, shape, and location of the ranges of the different species. The ultimate explanations for the patterns of species diversity among regions are therefore related to the processes that determine the basic characteristics of the geographical range of species, which are of a biogeographical and historical nature (Ricklefs, 1987; Brown *et al.*, 1996; Gaston, 1996).

The average RPD of a given region is determined solely by the size of ranges within the region (Appendix). Note that the location or shape of ranges within the regions does not affect the pattern. Performing a thought experiment, one could imagine moving and distorting the ranges of species across the region, and these actions would not change the average point diversity, provided that ranges maintained their original area.

What would be the pattern if true LR plots were constructed using the actual local inventory diversity (LID) values instead of the RPDs? In principle, saturating LR patterns can appear as originally postulated, by the effect of some local process limiting the number of species to an asymptotic maximum (Terborgh & Faaborg, 1980; Ricklefs, 1987). However, similar patterns can be

produced even in the absence of any kind of local mechanism. Imagine an extreme case in which all species in the regional point assemblages co-occur in the corresponding local communities. Obviously, this is a case in which local interactions play no role in shaping communities, but still a saturating LR plot could appear if one compared the regional assemblage with the inventory diversity of local communities. Similar patterns could appear if the LID of communities were proportional subsamples of regional point assemblages. Imagine, for example, that local communities of North American nonvolant mammals were formed by proportionally sampling from the pool of species in the regional point set. When comparing those local communities with the corresponding regions, a saturating curve would be generated, even though no local interaction is considered. Clearly, saturating LR patterns are not necessarily a product of local interactions, and can be simple reflections of a larger-scale pattern.

On the other hand, saturating patterns could still contain the signal of ecological interactions, albeit of a different nature and of a grander scale. A saturating pattern in SRLR plots using our method implies that species in regions of higher diversity have ranges that are, on average, smaller. If the area of a region is envisioned as a resource that species must partition to be present in the region, then the saturating pattern would mean that as the diversity of a region increases, species would take smaller and smaller shares of available geographical space. Linear SRLR plots, in contrast, would indicate that as diversity increases, species take similar shares of available space. At the core of the interpretation of SRLR plots is the basic question posited by macroecology, that is, how species partition resources at regional and continental scales (Brown & Maurer, 1989). Whether the size of ranges at the regional scale is determined by environmental conditions, by the heterogeneity of the region, or by species interactions is still an open question in macroecology.

In the case of North American mammals, the pattern of geographical space sharing is different for bats and for nonvolant mammals, suggesting that the diversity of the two groups responds to different mechanisms. Our data show that more diverse regions of North America harbour nonvolant mammal species that, on average, occupy less geographical space within the regions. Regions with higher diversity of bats, in contrast, contain species that occur in regional ranges that are of similar size to those for poorer regions.

Brown & Maurer (1989) speculated that the continental distribution of species with small ranges is limited by the availability of adequate habitat, which ultimately is associated with topographic features. The distribution of species with large ranges is limited, continuing with Brown & Maurer's (1989) reasoning, mostly by major climatic zones and biomes. That difference could account for the patterns that we found for volant and nonvolant mammals. Bats have, on average, larger ranges than nonvolant mammals (Arita *et al.*, 1997) and, at least for the Mexican fauna, diversity of nonvolant mammals is highly correlated with regional heterogeneity, whereas bat diversity correlates better with variables that are related to potential productivity, such as mean temperature and mean precipitation (Arita, 1997). A possible explanation for the pattern is related to dispersal ability.

Because bats are more mobile animals, they are less sensitive to regional physiographic barriers to dispersal and have higher probabilities of colonizing new areas within the region; their ranges being probably limited by continental-wide patterns of climatic conditions. Less mobile nonvolant mammals, especially the smaller ones, are more prone to be restricted by regional barriers to dispersal, thus their diversity is more prone to be determined by regional heterogeneity. If this hypothesis is correct, then we could predict that groups of species with low dispersal capabilities will show patterns similar to those of nonvolant mammals, whereas vagile species will show patterns similar to those of bats. For vertebrates, birds would follow a linear SRLR pattern, whereas amphibians and reptiles would show a saturating SRLR plot.

In conclusion, traditional LR plots can show patterns that contain the signal of local interactions, but local and regional effects can be confounded. With our method using the RPD instead of the local component of species diversity, we have shown that purely regional and continental processes can generate both types of SRLR relationships. SRLR plots can be interpreted also in terms of patterns in the scaling of diversity, but not necessarily in a neutral, noninteractive sense, as macroecological processes of sharing of geographical space might be behind the observed patterns.

ACKNOWLEDGEMENTS

Funding for this project was provided by DGAPA-UNAM and by the Mexican Commission of Biodiversity (CONABIO). We thank G. Rodríguez for efficient technical support and G. Guerrero, J. Uribe and L. B. Vázquez for help in building the database. A. Christen, B. Hawkins, P. Koleff, and J. Soberón provided insightful discussions. P. Rodríguez participated with the support of a scholarship from DGEP-UNAM for graduate studies in the Biomedical Sciences Doctoral Program of UNAM.

REFERENCES

- Arita, H.T. (1997) The non-volant mammal fauna of Mexico: species richness in a megadiverse country. *Biodiversity and Conservation*, **6**, 787–795.
- Arita, H.T., Figueroa, F., Frisch, A., Rodríguez, P. & Santos del Prado, K. (1997) Geographical range size and the conservation of Mexican mammals. *Conservation Biology*, **11**, 92–100.
- Arita, H.T. & Rodríguez, P. (2002) Geographic range, turnover rate and the scaling of species diversity. *Ecography*, **25**, 541–553.
- Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.
- Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.
- Caswell, H. & Cohen, J.E. (1993) Local and regional regulation of species-area relations: a patch occupancy model. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 99–107. University of Chicago Press, Chicago.
- Cornell, H.V. (1985) Local and regional richness of cynipine gall wasps on California oaks. *Ecology*, **66**, 1247–1260.
- Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1–12.
- Diniz-Filho, J.A.F., Bini, L.M. & Hawkins, B.A. (2003) Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography*, **12**, 53–64.
- Gaston, K.J. (1996) Species range size distributions: patterns, mechanisms and implications. *Trends in Ecology and Evolution*, **11**, 197–201.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- Gering, J.C. & Crist, T.O. (2002) The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecology Letters*, **5**, 433–444.
- Godfray, H.C.J. & Lawton, J.H. (2001) Scale and species number. *Trends in Ecology and Evolution*, **16**, 400–404.
- Griffiths, D. (1999) On investigating local-regional species richness relationships. *Journal of Animal Ecology*, **68**, 1051–1055.
- Hugueny, B. & Cornell, H.V. (2000) Predicting the relationship between local and regional species richness from a patch occupancy dynamics model. *Journal of Animal Ecology*, **69**, 194–200.
- Huston, M.A. (1999) Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, **86**, 393–401.
- Kaspari, M., Yuan, M. & Alonso, L. (2003) Spatial grain and the causes of regional diversity gradients in ants. *American Naturalist*, **161**, 459–477.
- Lawton, J.H. (1999) Are there general laws in ecology? *Oikos*, **84**, 177–192.
- Loreau, M. (2000) Are communities saturated? On the relationship between α , β and γ diversity. *Ecology Letters*, **3**, 73–76.
- Lyons, S.K. & Willig, M.R. (1997) Latitudinal patterns of range size: methodological concerns and empirical evaluations for New World bats and marsupials. *Oikos*, **79**, 568–580.
- McCoy, E.D. & Connor, E.F. (1980) Latitudinal gradients in species diversity of North American mammals. *Evolution*, **24**, 193–203.
- Reid, F.A. (1998) *A field guide to the mammals of Central America and southeast Mexico*. Oxford University Press, New York.
- Ricklefs, E.R. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.
- Ricklefs, E.R. (2000) The relationship between local and regional species richness in birds of the Caribbean Basin. *Journal of Animal Ecology*, **69**, 111–116.
- Rosenzweig, M.L. & Ziv, Y. (1999) The echo pattern of species diversity: pattern and processes. *Ecography*, **22**, 614–628.
- Srivastava, D.S. (1999) Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1–16.

- Stevens, R.D. & Willig, M.R. (2002) Geographical ecology at the community level: perspectives on the diversity of New World bats. *Ecology*, **83**, 545–560.
- Terborgh, J. & Faaborg, J. (1980) Saturation of bird communities in the West Indies. *American Naturalist*, **116**, 178–195.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- Wilson, D.E. & Ruff, S. (1999) *The Smithsonian book of North American mammals*. Smithsonian Institution Press, Washington.

BIOSKETCHES

Héctor Arita is interested in the statistical analysis of the composition and structure of species assemblages at several scales. Current projects involve the analysis of the scaling of biological diversity using different metrics, the study of patterns of body-mass diversity, and the development of mathematical models linking species diversity with the structure and dynamics of range sizes.

Pilar Rodríguez focuses her work on the analysis of beta diversity as a way to understand the scaling of biological diversity. Her current project involves the description and interpretation of geographical patterns of beta diversity among North American mammals.

Appendix Imagine a region divided into N sampling quadrats for which the distribution of the S species occurring in it is summarized in a presence-absence matrix whose elements are $d(i, j) = 1$ if species i is present in quadrat j and $d(i, j) = 0$ otherwise. The range of species i within the region is n_i , the sum of the elements of row i , and the species diversity of quadrat j is s_j , the sum of the elements of column j .

The average range size of the species within the region is:

$$\bar{n} = \frac{\sum_{i=1}^S n_i}{S}, \quad \text{and} \quad S = \frac{\sum_{i=1}^S n_i}{\bar{n}} \quad (1)$$

and the average diversity of quadrats is

$$\bar{s} = \frac{\sum_{j=1}^N s_j}{N}, \quad \text{and} \quad N = \frac{\sum_{j=1}^N s_j}{\bar{s}} \quad (2)$$

It is easy to see that $\sum_{i=1}^S n_i = \sum_{j=1}^N s_j$, since the first term is the sum of row totals and the second term is the sum of column totals. Both are equal to the fill of the matrix, that is, the total number of 1 s. Therefore, from (1) and (2):

$$\bar{s}N = \bar{n}S, \quad \text{and} \quad \bar{s} = \bar{n}S/N \quad (3)$$

Moreover, combining (1) and (3), and rearranging:

$$\bar{s} = \frac{\sum_{i=1}^S n_i}{N} = \sum_{i=1}^S p_i \quad (4)$$

where p_i is the range of species i measured as the number of quadrats in which it occurs proportional to the total number of quadrats within the region. If the quadrats become very small until $N \rightarrow \infty$, p_i is the range size of species i proportional to the total area of the region, and \bar{s} becomes the average regional point species diversity (RPD) of the region.