



The diversity field of New World leaf-nosed bats (Phyllostomidae)

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ABSTRACT

Aim To analyse how the patterns of species richness for the whole family Phyllostomidae determine the structure of diversity fields (sets of species-richness values) within the ranges of individual bat species.

Location The range of the family Phyllostomidae in North and South America.

Methods We generated a database of the occurrence of 143 phyllostomid bat species in 6794 quadrats, analysing the species-richness frequency distribution for all sites, and for subsets of sites defined by the geographic ranges of species. Range–diversity plots, depicting simultaneously the size and the mean species richness of ranges, were built to explore the patterns of co-occurrence in wide-spread and restricted species. We compared the empirical patterns against two null models: (1) with scattered (non-cohesive) ranges, and (2) with cohesive ranges modelled with the spreading-dye algorithm. Diversity fields were analysed with richness maps for individual species and with comparisons of species-richness frequency distributions.

Results Overall richness frequency distribution showed a multimodal pattern, whereas simulated distributions showed lower values of variance, and were unimodal (for model 1) and bimodal (for model 2). Range–diversity plots for the empirical data and for the cohesive-ranges simulation showed a strong tendency of species to co-occur in high-diversity sites. The scattered-ranges simulation showed no such tendency. Diversity fields varied according to idiosyncratic features of species generating particular geographic patterns and richness frequency distributions.

Main conclusions Phyllostomid bats show a higher level of co-occurrence than expected from null models. That tendency in turn implies a higher variance in species richness among sites, generating a wider species-richness frequency distribution. The diversity field of individual species results from the size, shape and location of ranges, but also depends on the general pattern of richness for the whole family.

Keywords

Bats, distribution, diversity, diversity field, geographic range, Neotropics, Phyllostomidae, species richness.

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INTRODUCTION

The geographic variation in species richness across continents remains one of the most enigmatic patterns in biogeography and evolutionary biology (Rosenzweig, 1995; Mittelbach *et al.*, 2007). Despite years of investigation, there is no consensus on the underlying causes of such an obvious pattern, although recent research shows that species richness correlates closely

with environmental variables, especially those related to productivity and energy availability (Hawkins *et al.*, 2003; Field *et al.*, 2009). As a complement to correlative studies, other lines of research have focused on the mechanisms that determine the distribution of individual species to understand the aggregate pattern of species richness (Gotelli *et al.*, 2009). Modelling the dynamics of geographic ranges has already yielded intriguing insights into the processes that shape geographic gradients

Table 1 Equivalence of terms and variables of the dispersion and diversity fields. Mathematical notation follows Arita *et al.* (2008). δ_{ij} is the element of the presence-absence matrix corresponding to site i and species j ($\delta_{ij} = 1$ if species i is present in site j , $\delta_{ij} = 0$ otherwise).

	Analysis by species	Analysis by sites
Type of analysis	By rows (R and Rq)	By columns (Q and Qr)
Total number of rows or columns	Number of species (S). Continental (gamma) diversity or number of species in group under study	Number of sites (N); Size of continent or of combined range of all species
Summation along a row or column	Range size of species i : $n_i = \sum_{j=1}^N \delta_{ij}$	Species richness of site j : $s_j = \sum_{i=1}^S \delta_{ij}$
Field	Diversity field	Dispersion field
Definition	Set of species assemblages of the sites forming the range of a given species	Set of the ranges of species occurring in a given site
Statistical definition	Set of species-richness values of sites within the range of a given species	Set of range-size values of species occurring in a given site
Frequency distribution	Species-richness frequency distribution	Range-size frequency distribution
Sample size	Range size of species i (n_i)	Species richness of site j (s_j)
Mean	Average richness of sites within the range of species i : $\bar{s}_i = \frac{1}{n_i} \sum_{j=1}^N s_j \delta_{ij}$	Average range size of species occurring in site j : $\bar{n}_j = \frac{1}{s_j} \sum_{i=1}^S n_i \delta_{ij}$
Volume	Summation of richness values of sites containing a given species: $D_i = \sum_{j=1}^N s_j \delta_{ij} = n_i \bar{s}_i$	Summation of range-size values of species occurring in a given site: $R_j = \sum_{i=1}^S n_i \delta_{ij} = s_j \bar{n}_j$

of species richness (Rangel *et al.*, 2007; Roy & Goldberg, 2007; Arita & Vázquez-Domínguez, 2008).

Species richness at the continental level is generally measured with the overlap of the geographic ranges of species (Simpson, 1964). Because the overlap is determined by the size, shape and location of individual ranges, studies of their geometric properties can lead to an understanding of large-scale patterns of diversity (Arita & Rodríguez, 2002). The study of geographic ranges is further enhanced when considering their internal structure, which has been described for example in terms of variation in abundance (Brown *et al.*, 1996; Sagarin *et al.*, 2006) or genetic composition (Eckert *et al.*, 2008; Barbour *et al.*, 2009). Here we examine the internal structure of ranges in terms of geographic variation in the number of overlaps with other species. In doing so, we measure the species richness in different parts of the range of a species. The pattern is ultimately determined by the overall variation in species richness across the continent, but also depends on the location and geometric properties of the range of individual species. The internal structure of the range as measured here is a reflection of the tendency of species to occur in species-rich or species-poor locations.

We take advantage of recent analytical developments in extracting information from presence-absence matrices to link diversity and distribution. In particular, we explore the properties of the 'diversity field', the set of species-richness values of sites that are within the range of a given species (Arita *et al.*, 2008). Graves & Rahbek (2005) analysed the distribution patterns of South American birds, and visualized the 'dispersion field' of the set of species occurring in a site by overlaying their continental ranges. They also computed the dispersion field volume as the product of the mean range size and the richness of the set of species; thus, the dispersion field volume equals the summation of all range-size

values of species occurring in a given site. As shown by Arita *et al.* (2008), the diversity field volume of a species is computationally equivalent to the dispersion field volume of a site, given the mathematical properties of presence-absence matrices, and equals the summation of all species-richness values of sites that are within the range of a given species (Table 1).

Because the diversity field of a species is a set of species-richness values, it can be described and analysed with the standard statistical descriptors of central tendency and variation. However, species-richness frequency distributions (FDs) are surprisingly absent from the literature, and their statistical properties remain largely unknown. This is in sharp contrast with the attention that the FD of other macroecological variables, such as abundance, range size and body mass, has received (Brown, 1995; Graves & Rahbek, 2005; McGill *et al.*, 2007; Nekola & Brown, 2007).

We use the family Phyllostomidae of New World leaf-nosed bats as a study case. The family is a diverse group of 160 species distributed in tropical and subtropical areas of the Americas (Simmons, 2005). The group originated approximately 38 Myr BP (Jones *et al.*, 2005; Teeling *et al.*, 2005) and radiated to include a wide gamut of feeding strategies, including insectivory, carnivory, frugivory, nectar feeding and even blood feeding. Because the group is monophyletic, widespread but endemic to a single land mass, and because species show a great deal of variation in range size, Phyllostomidae represents an ideal clade for large-scale studies of diversity and distribution (Stevens, 2006).

METHODS

We constructed a database of the continental (non-insular) distribution of phyllostomid bats, following the current taxonomic

arrangement (Simmons, 2005). Distributional maps were built using ArcGIS with data from the primary literature up to 2004 and from the Nature Serve database (Patterson *et al.*, 2007). The final set included a total of $S = 143$ species with distribution in continental America. A grid of $N = 6794$ equal-area quadrats (2500 km^2 , corresponding to approximately $0.5^\circ \times 0.5^\circ$ latitude and longitude near the Equator) was overlaid on the distributional maps to generate a $143 \text{ species} \times 6794 \text{ sites}$ presence-absence matrix. The sum of elements along rows of the matrix yielded the range size of species (n_i), measured as the number of quadrats that are overlapped by the distributional map of each species. The number of distributional maps that overlapped a given site was defined as the species richness of that site (s_j), which equals the sum of elements of the column of the presence-absence matrix corresponding to that site.

For analytical convenience, all richness and range size variables can be converted to proportional values by dividing them by the corresponding total of species or quadrats for the whole system (Arita *et al.*, 2008). Thus, any richness value divided by S and any range size value divided by N are proportional variables and are denoted by adding an asterisk to their symbols. For example, n_i^* is the proportional range size of species i , and is equal to n_i/N ; equivalently, $s_j^* = s_j/S$ is the proportional species richness of site j .

We computed the diversity field for each species with the set of species-richness values of quadrats in which the focal species occurs. This was done with an Rq analysis whereby information was extracted from the presence-absence matrix row by row, but incorporating data calculated by columns (Arita *et al.*, 2008; Table 1). Thus, diversity fields were samples, of size equal to the range size of species, taken from the pool of richness values of the whole assemblage. The composition and statistical parameters of such samples depend on the size, shape and location of the species' geographic range. We described and examined the statistical characteristics and the spatial variation of diversity fields with three complementary approaches: (1) the analysis of species-richness FDs, (2) the examination of maps showing the internal structure of the range in terms of species richness, and (3) the construction of range-diversity plots (Arita *et al.*, 2008).

Preliminary analyses showed a tendency of richness FDs to be much less skewed than range-size FDs, so we opted not to use the logarithmic transformations routinely employed to deal with continental range size FDs and other highly skewed FDs (Graves & Rahbek, 2005; Nekola & Brown, 2007). To describe and compare richness FDs, we used the standard statistical parameters of central tendency, deviation and shape, that is, the first (mean), second (variance) and third (skewness) moments. In particular, we defined $\bar{s}_i$ as the mean species richness of sites in which species i occurs, and $\bar{s}_i^* = \bar{s}_i/S$ as its proportional equivalent. Also, we computed the diversity field volume of a species as $D_i = n_i \bar{s}_i$, that is, the summation of species-richness values of sites within the range of species i . We associated the histogram of the richness FD for each species with a range map showing the variation in species richness among the sites forming that range. Maps allowed the visualization of the structure of ranges as spatial patterns of co-occurrence with other species.

Range-diversity plots are visual analytical tools that allow the simultaneous depiction of diversity and distributional data (Arita *et al.*, 2008). In such plots, ordinates are proportional range sizes (n_i^*) and abscissas are mean proportional richness values of sites within the range of species, that is, proportional averages of the diversity field ($\bar{s}_i^*$). Mathematical properties of presence-absence matrices impose constraints on the possible combinations of values in such a way that the interval of possible values of $\bar{s}_i^*$ for species with small ranges is always wider than for widespread species (Arita *et al.*, 2008). Range-diversity plots also allow the interpretation of richness patterns in terms of the association (covariance) among the species, whose statistical significance can be assessed using Schluter's variance ratio test (Schluter, 1984; Gotelli, 2000). For example, if a vertical line is drawn where $\bar{s}_i^* = \bar{s}$, then points to the right of this line (that is, those for which $\bar{s}_i^* > \bar{s}$) will correspond to species with positive average covariance with the rest of the species (Arita *et al.*, 2008). It can be shown that, if species arrange along the vertical line (that is, if for all species $\bar{s}_i^* \approx \bar{s}$), then

$$V = \text{var}(s) / \sum \text{var}(n_i),$$

which is the ratio of the variance in species richness and the summation of range-size variances, should be close to 1.0. A value of $V > 1.0$ would indicate a positive overall association among species (Schluter, 1984) and would imply that most points in a range range-diversity plot are to the right of the vertical line (that is, that for most species $\bar{s}_i^* > \bar{s}$).

We developed null models to envision scenarios under which the distribution patterns of species were independent of each other. As in all null models (Gotelli & Graves, 1996), we retained some part of the empirical information and allowed other parameters to vary. We maintained the range size of species and randomized their shape and location, so the row sums of the presence-absence matrix, that is, the empirical range size FD remained intact in all models. We examined models with and without cohesion of ranges, as this factor has been shown to exert an important influence on the outcomes of models of continental diversity and distribution (Jetz & Rahbek, 2001; Rahbek *et al.*, 2007; Arita & Rodríguez-Tapia, 2009).

In our first model, we built the simulated range of a given species by sequentially selecting quadrats, randomly without replacement, until the empirical range size of that species was reached. Thus, sites had equal probabilities of being included in a range (SIM2 case, Gotelli, 2000). Notice that under this model, the geographic location of the selected sites is ignored, so quadrats are scattered all over the continent, forming non-cohesive geographic ranges. In our second model, we used the spreading-dye algorithm (Jetz & Rahbek, 2001) to generate the simulated ranges. For each species, we started by selecting a single quadrat from the pool of sites of the combined distribution of the whole family. Then, in each step, a new quadrat was added in a random position at the periphery of the growing range, with the restriction that new quadrats could be added only within the original area occupied by the family. Consequently, limits to the distribution of phyllostomids, as well as sea borders, constituted hard boundaries to the spreading ranges. The process was iterated

until the simulated range reached the size of the empirical area of distribution. This second model generated random, cohesive ranges that were equal in size to the empirical ranges, but that were different in shape and location.

For both models, we built species-richness FDs for the whole assemblage and for the resulting diversity fields by species. Unless otherwise stated, all statistical inferences were made contrasting the empirical data against FDs of variables generated by 100 repetitions of the models. Simulations were performed using R software (R Development Core Team, 2008).

RESULTS

Empirical data

The family Phyllostomidae distributes over an area of approximately 17 million km² from the south-western United States to northern Argentina and Chile (Fig. 1a). Within that area, the number of ranges overlapping our 6794-quadrat grid varied from 1 to 73, peaking in the tropical part of the Andes in South America and declining towards the northern and southern extremes, following the strong latitudinal gradient of species richness that has been documented for New World bats (Willig & Bloch, 2006). The geographic pattern of richness generated a multimodal FD (Fig. 2a) with an over-representation of quadrats with very low richness (fewer than five species) but that was much less skewed than other macroecological FDs (Brown, 1995; Nekola & Brown, 2007). Mean species richness was $\bar{s} = 33.96$ species ($\bar{s}^* = 0.237$), but figures varied widely (SD = 21.86) and showed a significant negative skew ($g_1 = -0.133$, $P[g_1 = 0] < 0.001$), indicating that in most sites the number of species was higher than the average.

Geographic ranges of species varied in size from $n_i = 1$ quadrat (2500 km²; $n_i^* = 1.5 \times 10^{-4}$) to 6223 quadrats (15.6×10^6 km²; $n_i^* = 0.92$, see Appendix S1 in Supporting Information). The range size FD followed the highly skewed shape typical of continental assemblages (Brown *et al.*, 1996; Nekola & Brown, 2007) (Fig. 3, right-hand panels). As expected from theory (Arita *et al.*, 2008), average richness within the ranges varied widely among species with small ranges ($\bar{s}_i = 3.2 - 70.8$ species; $\bar{s}_i^* = 0.022 - 0.495$, bottom of the range-diversity plot in Fig. 3a), but was constrained to average values for the most widespread species, such as the common vampire bat (*Desmodus rotundus* $\bar{s}_i = 36.82$; $\bar{s}_i^* = 0.257$). One hundred and twenty species (84%) had an average species richness within their ranges higher than the overall mean ($\bar{s}_i^* > 0.237$), corresponding to points to the right of the vertical dashed line in Fig. 3(a). Only five species, all occurring in the northern extreme of the area of distribution of the family, coexisted on average with 20 or fewer species ($\bar{s}_i^* \leq 0.140$; Fig. 3a, lower left corner of the plot). These patterns generated a very high value of Schluter (1984) variance ratio ($V = 26.99$), indicating a high degree of association among species.

The FDs of diversity fields showed a great deal of variation (Fig. 4, see Appendix S1). Small ranges coincided with species-poor or species-rich areas, but they tended to show little varia-

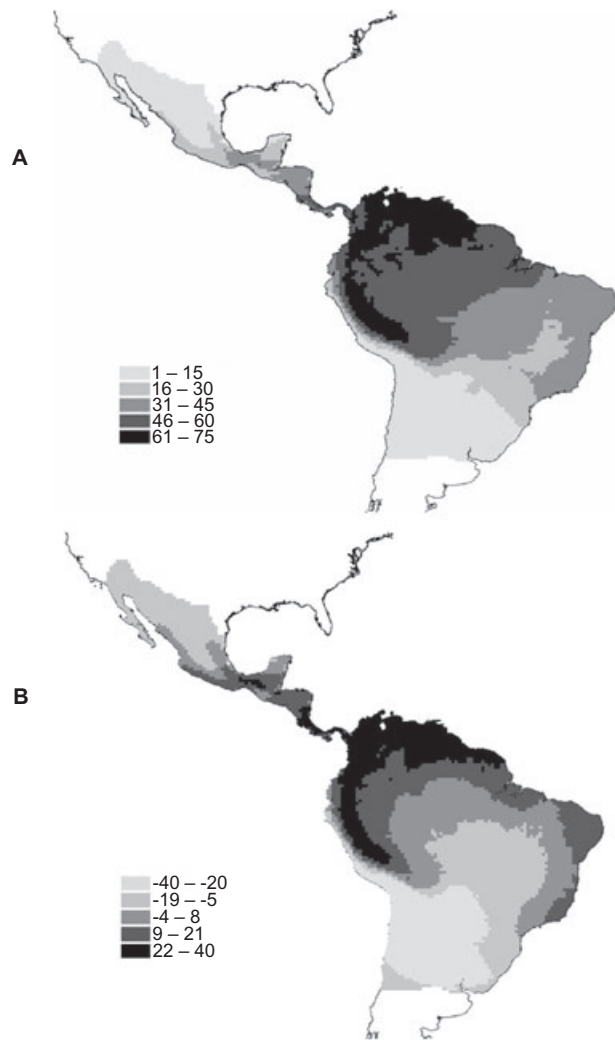


Figure 1 Geographic pattern of species richness of New World leaf-nosed bats (Phyllostomidae). (a) Empirical pattern. (b) Residual values calculated by subtracting, quadrat by quadrat, the average richness of 100 runs of the spreading-dye model from the observed species richness values.

tion in within-species richness values (Fig. 4a–c). The Mexican long-nosed bat (*Leptonycteris nivalis*), for example, occurs over areas of south-western United States and northern Mexico that represent about 6% of the range of the whole family ($n_i = 0.99 \times 10^6$ km², $n_i^* = 0.058$), sharing quadrats with few other phyllostomids ($\bar{s}_i = 7.98$ species), but also occurs also in tropical and subtropical sites of central Mexico, where diversity is intermediate (up to 28 species). Consequently, the FD of its diversity field showed a positive skew ($g_1 = +1.21$) determined by a conspicuous peak of sites with very low species richness and a shallow right-hand tail that ends below 30 species (Fig. 4a). Bokermann's nectar bat (*Lonchophylla bokermanni*) is endemic to a small area of south-eastern Brazil with intermediate species richness ($n_i = 152,000$ km², $n_i^* = 0.009$, $\bar{s}_i = 34.23$ species; $g_1 = 0.08$; Fig. 4b). Species that are endemic to areas of the Andes, such as the tailless bat (*Anoura luismanueli*) occur only in a few

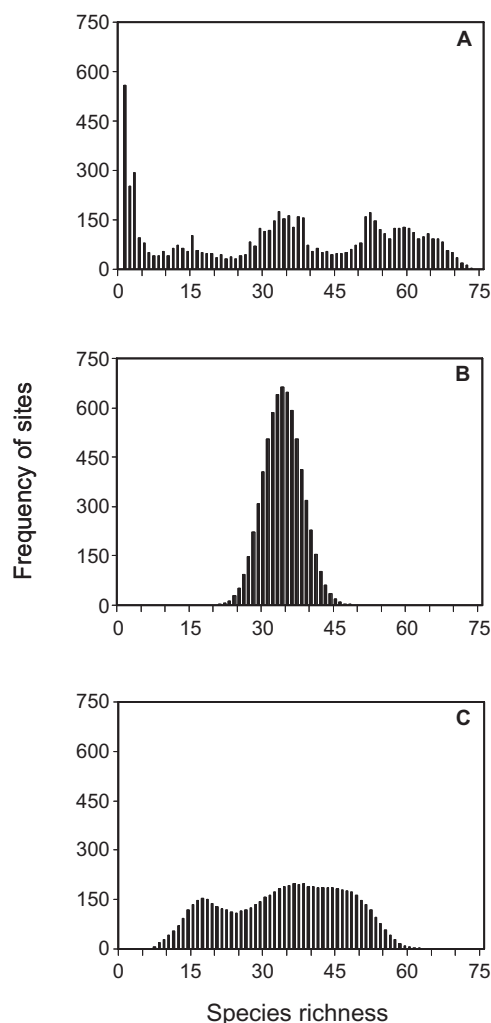


Figure 2 Species-richness frequency distributions of 143 phyllostomid bat species in 6794 quadrats. (a) Empirical data. (b) Result of simulations using scattered (non-cohesive) ranges, as described in the main text. (c) Result of simulations using cohesive ranges, applying the spreading-dye algorithm. To allow comparisons with (a), histograms in (b) and (c) show the cumulative frequency of 100 simulations, adjusting the ordinates scale to correspond to a single assemblage.

sites that are consistently very rich in species ($n_i = 40,000 \text{ km}^2$, $n_i^* = 0.002$, $\bar{s}_i = 70.81$ species, $g_1 = -0.39$; Fig. 4c).

The diversity fields of large ranges tended to resemble the pattern for the whole assemblage. In the limit, a species occurring in all quadrats would have, by definition, a diversity field identical to the richness FD of the whole family. Palla's long-tongued bat (*Glossophaga soricina*), for instance, has a wide distribution ($n_i = 13.9 \times 10^6 \text{ km}^2$, $n_i^* = 0.818$) encompassing moderate- to high-richness areas ($\bar{s}_i = 40.85$ species). The FD of its diversity field showed a multimodal pattern that is negatively skewed ($g_1 = -0.291$), indicating that most sites within the range have richness values above the average (Fig. 4d). There were several species with ranges encompassing between 30% and 60% of the extent of the whole family that tended to concentrate

on the most species-rich areas. The false vampire (*Vampyrum spectrum*) belongs to this group, distributing over a wide area ($n_i = 5.1 \times 10^6 \text{ km}^2$, $n_i^* = 0.300$) of high richness ($\bar{s}_i = 53.57$ species; $g_1 = -0.093$; Fig. 4e).

There was a strong positive correlation between the diversity field volume and the size of the range of a species ($r = 0.986$, Fig. 5). In a plot of volume versus range size, points aggregated close to the line of maximum volumes that is constructed by plotting the cumulative species richness of the sites ordered from the richest to the least rich (Fig. 5). For a given number of sites, the line shows the highest possible number of cumulative overlaps, that is, the maximum value that the diversity field volume can attain.

Null models

By design, our null models retained the empirical range size FD. As a consequence, the average richness of sites was exactly equal to the empirical value in all simulations ($\bar{s} = 33.96$ species, $\bar{s}^* = 0.237$). The richness FD generated by scattered ranges followed a normal distribution (Fig. 2b) with $SD = 4.18$ species (mean for the 100 simulations). The interval of actual values was $15 \leq s_i \leq 53$ species. The geographic distribution of species richness was homogeneous, with sites presenting random noise variation from the mean richness independently of their geographic location.

With cohesive ranges, the richness FD was bimodal, with peaks near the mean and at approximately 18 species (Fig. 2c). Variation in richness was higher than in the first model, but still much lower than with the empirical data ($SD = 12.52$ species, average of the 100 simulations). Ninety-five per cent of observed richness values were within the interval $10 \leq s_i \leq 60$ species. Drawn on a map, results of the spreading-dye simulations showed the typical mid-domain effect pattern whereby species richness peaks near the centre of the continent (Colwell & Lees, 2000; Jetz & Rahbek, 2001; Colwell *et al.*, 2009). A map of residual species richness (empirical minus simulated number of species) still shows the signature of the mid-domain effect as a series of concentric semicircles, but also highlights areas where biological processes determine deviations from expected richness (Fig. 1b).

Simulations using scattered ranges generated range–diversity plots with points arranged along the vertical dashed line and, consequently, with a very narrow FD of mean range richness (Fig. 3b). The mean value of V for our 100 simulations was $V = 0.946$ (interval, $0.85 \leq V \leq 1.12$). Simulations using cohesive ranges generated range–diversity plots with a pattern similar to that of the empirical data, in which most species tended to arrange to the right of the central dashed line, but the deviations from the mean were not as pronounced as with the empirical data ($0.08 \leq \bar{s}_i^* \leq 0.4$, Fig. 3c). The histogram of range richness values showed a distinctive peak located to the right of $\bar{s}^*$ (Fig. 3c top). The value of V in this case was significantly higher than that of the scattered-range simulations, but significantly lower than that of the empirical data (100 simulations, mean $V = 8.60$, interval $5.07 \leq V \leq 12.54$).

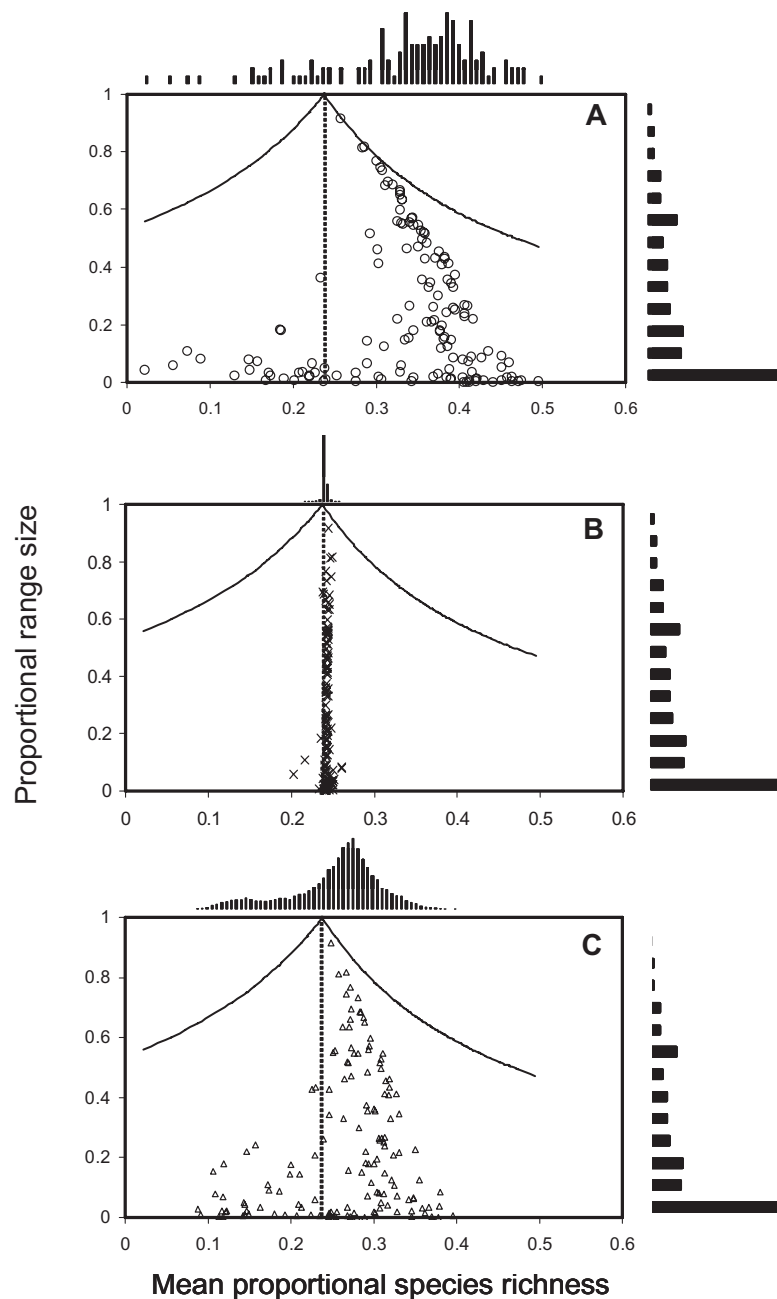


Figure 3 Range-diversity plots for 143 bat species of the family Phyllostomidae. (a) Empirical values. Range size and mean species richness within the ranges are proportional to the total number of quadrats (6794) and species (143), respectively. The vertical dashed line marks the average proportional species richness for all quadrats, and the curved lines are the absolute upper limits determined by mathematical constraints. The histogram in the right panel shows the range-size frequency distribution of the 143 species, and the histogram in the top panel depicts the frequency distribution of mean values of richness within the 143 ranges. (b) Results of the simulation using scattered (non-cohesive) ranges. (c) Results of the simulation with cohesive ranges, using the spreading-dye algorithm. In (b) and (c) points show the results of one simulation in each case; histograms on top of the plots depict the frequency distribution of mean species within the 143 ranges, summarizing the cumulative frequency of 100 simulations in each case. In both simulations the empirical range-size frequency distribution (right panel) was retained.

In the simulation using scattered ranges, the linear fit between diversity field volume and range size was perfect when the intercept was forced to be equal to zero ($r^2 = 1.0$, slope $m = 34.38$, average for the 100 repetitions; Fig. 5). Points for the simulation using the spreading-dye algorithm also showed a very strong positive correlation, but were more scattered than in the first model ($r^2 = 0.984$, $m = 38.82$, average for 100 runs).

DISCUSSION

Patterns for the whole family

Traditionally, continental patterns of species richness have been examined with maps (Simpson, 1964; Terribile *et al.*,

2009), through correlations with environmental variables (Hawkins *et al.*, 2003; Field *et al.*, 2009), or by exploring the properties of the species–area relationship (Rosenzweig, 1995; Nekola & Brown, 2007). Species-richness FDs, on the other hand, have been largely ignored, despite their potential importance in understanding the relationship between species richness and distribution (Arita *et al.*, 2008; Šizling *et al.*, 2009). The richness FD is an aggregate pattern that results from tallying the number of overlapping ranges in several sites. Thus, richness patterns can be interpreted as a measure of association (co-occurrence) among individual species and are ultimately determined by the size, shape and location of the geographic ranges of species (Arita & Rodríguez, 2002; Gotelli *et al.*, 2009).

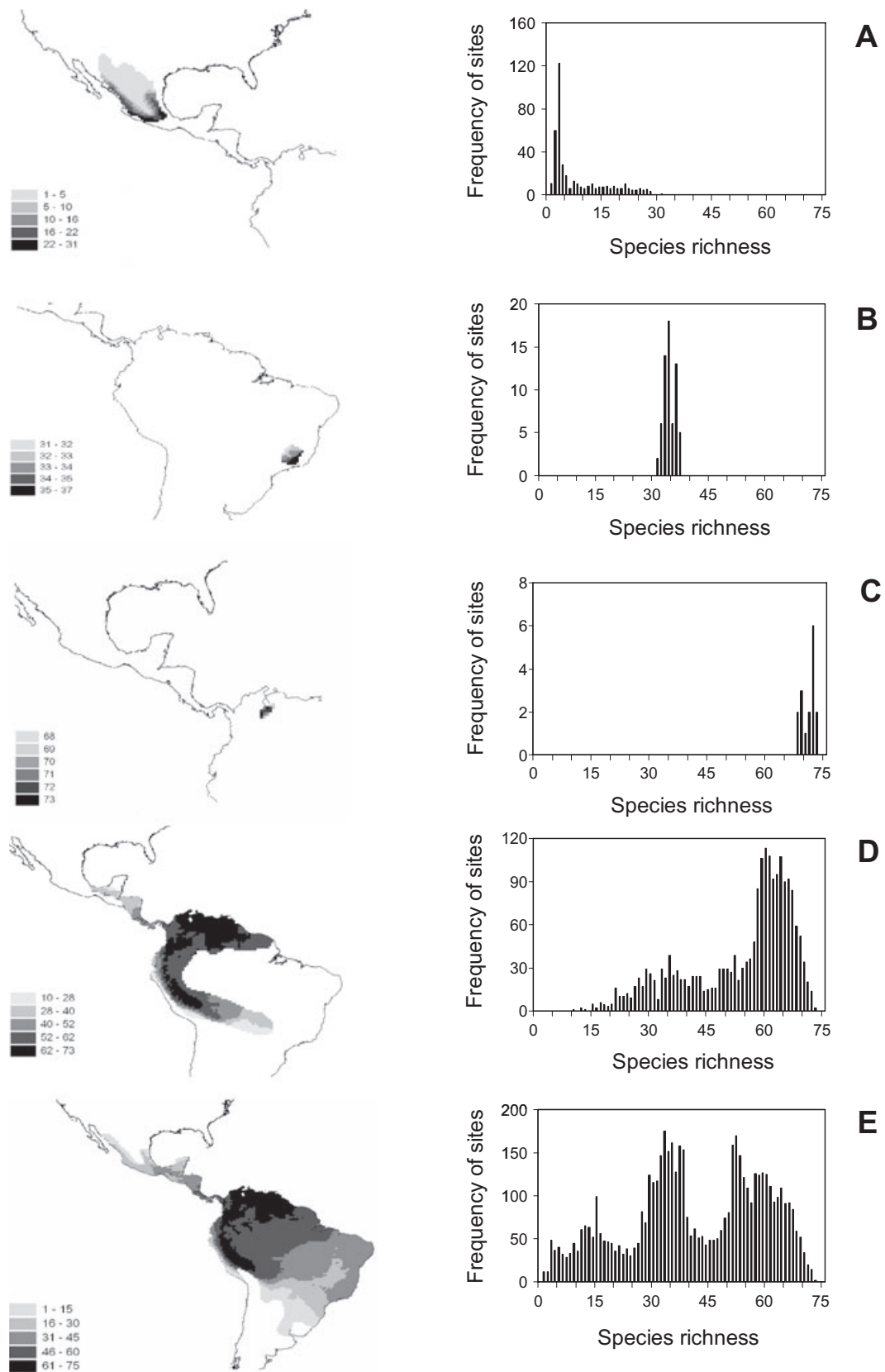


Figure 4 Diversity fields of five species of phyllostomid bats: (a) *Leptoncyteris nivalis*, (b) *Lonchophylla bokermanni*, (c) *Anoura luismanueli*, (d) *Vampyrum spectrum*, (e) *Glossophaga soricina*. Maps show the species-richness values of sites within the range of each species, and histograms show the frequency distribution of such richness values.

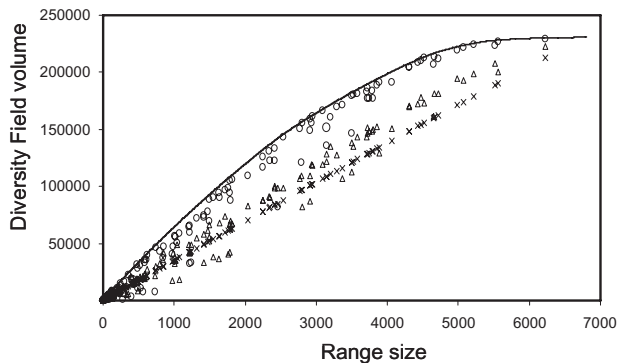


Figure 5 Volume of the diversity field of phyllostomid bats as a function of range size: circles, empirical data; crosses, result of one run of the simulation with scattered (non-cohesive) ranges; triangles, result of one run of the simulation with cohesive ranges, using the spreading-dye algorithm. The line representing the maximum values of the diversity field is built by plotting the cumulative species-richness values of sites ordered from the richest to the least rich.

Results of our first null model (Fig. 2b) show the expected richness FD if the ranges of species were sets of sites randomly scattered all over the continent. Thus, this model excluded all kinds of geographic, geometric and biological determinants of richness, except for the empirical range size FD. Under these circumstances, the map of species richness is homogeneous, with variation limited to random statistical error around the mean and the FD is simply a normal curve with mean equal to the empirical $\bar{s}$ (33.96 species, Fig. 2b). Because in this first model the distribution of each species was independent of the rest, the diversity field volume (that is, the total number of co-occurrences within a given range) increased linearly with range size (Fig. 5).

The variance of any richness FD is determined by two components: one defined by the sum of the binary variances generated by individual ranges and one equalling the sum of pairwise covariances between species (Schluter, 1984). Randomly placed scattered ranges are independent of each other, so the covariance is null, as shown by the points arranged vertically in the range–diversity plot (Fig. 3b) and by Schluter's $V \approx 1.0$. Because the sum of covariances is close to zero, the variance of the richness FD has to be equal to the summation of the variances of individual ranges, which for phyllostomids is

$$\sum \text{var}(n_i) = \sum n_i^*(1 - n_i^*) = 17.7.$$

This is the 'background' variance generated by range size variation that will appear even in the most unrealistic null models, except the trivial cases in which all species occur in all sites or all species occur nowhere.

Simulations using the spreading-dye algorithm added the effects of geometric constraints and range cohesion (Colwell & Lees, 2000; Arita & Rodríguez-Tapia, 2009; Colwell *et al.*, 2009). In dynamic models, cohesive ranges imply a spatial limitation to

the distance to which a species can expand its range from already occupied sites (Rangel *et al.*, 2007; Gotelli *et al.*, 2009). In non-dynamic null models, cohesive ranges capture the spatial constraints determined by the size and shape of the continent, ignoring the effect of physical heterogeneity and biological processes. Drawn on a map, the typical result of spreading-dye models is a series of concentric circles of increasing richness peaking near the centre of the continent (Colwell & Lees, 2000; Jetz & Rahbek, 2001). For phyllostomid bats that general pattern was modified by the Central American land constriction, and resulted in a latitudinal pattern in which North American sites contained the fewest species (Fig. 1b). This land-constraint effect also explains the left-side peak in species richness of the richness FD, which corresponds to North American sites (Fig. 2c).

Our simulations confirmed the fact that range cohesiveness generates a positive association between species (Arita & Rodríguez-Tapia, 2009), and a concomitant increase in variance of the richness FD. The general positive association between species is shown in the range–diversity plot by the concentration of points to the right of the vertical line (Fig. 3c) and is confirmed by the value of Schluter's ratio ($V = 8.60$) being significantly different from 1.0. Due to the generalized positive association among species, the relationship between diversity field volume and range size showed a steeper slope than in the first model (Fig. 5).

The empirical richness FD of phyllostomids (Fig. 2a) shows the effects on the distribution of species of the shape, topographic elements and environmental features of the continent, but also of some idiosyncratic traits of the clade. The first peak, formed by low-richness quadrats, corresponded to sites in the south-western United States, northern Mexico and northern Argentina and Chile, where a small number of species distribute over large areas that encompass the subtropical and temperate limits of the distribution of phyllostomids. In comparison, the peak of quadrats with approximately 34 species corresponds to sites in south-eastern Brazil, where extensive areas support an intermediate number of species. Similarly, the peak of quadrats with approximately 50–60 species corresponds to areas within the Amazon basin that support a very high, but not the highest, number of phyllostomids. Finally, sites supporting the highest phyllostomid richness (> 65 species) are spread over a comparatively small area of the tropical Andes (Fig. 1a), accounting for the gentle negative slope at the right-hand end of the richness FD (Fig. 2a). The empirical richness FD (Fig. 2a) shows a high variance that cannot be explained solely by the effects of variation in range sizes (shown by the first model, Fig. 2b) and of range cohesion and geometric constraints (shown by the second model, Fig. 2c). This high variance can be also seen in the range–diversity plot, in which most points are to the right of the vertical line for which $\bar{s}_i^* = \bar{s}^*$ (Fig. 3a) and is confirmed by Schluter's variance ratio being significantly higher than in any of the two null models ($V = 26.99$, $P < 0.01$). The relationship between diversity field volume and range size for empirical data was less linear than with the null models, with points tending to aggregate to the line of maximum volume (Fig. 5). This pattern

also demonstrates the high degree of positive association in the distribution of species.

The empirical richness FD differs from the predictions of the two models mostly in the extremes of the distribution, that is, for sites with $s_i < 10$ species or $s_i > 60$ species. These differences are due to the combined effect of physical heterogeneity and the evolutionary history of the clade. Sites of extremely high bat diversity in the Andes contain a combination of widespread and endemic species that determine patterns of diversity similar to those documented for birds (Graves & Rahbek, 2005; Rahbek *et al.*, 2007). A combination of historical factors and diversity of environments is possibly responsible for such repetitive patterns. Sites with extreme low diversity differ in composition between North and South America. Phyllostomids that occur beyond the tropic of Capricorn are bats with very large ranges (e.g. the woolly false vampire *Chrotopterus auritus*, *G. soricina*, and *D. rotundus*). Species that occur beyond the tropic of Cancer, in contrast, are typically North American endemics with comparatively small ranges (the Californian leaf-nosed bat *Macrotus californicus*, *L. nivalis* and the Mexican long-tongued bat *Choeronycteris mexicana*) that tend to be taxa of recent origin (Stevens, 2006). This pattern suggests that different mechanisms have shaped the composition of bat faunas in the extremes of the range of phyllostomids.

Diversity fields of species

The variation in species richness within the range of a given species can be visualized with a range map showing the geographic pattern of overall species richness, or with an FD plot built by tallying the number of overlapping ranges in each quadrat in which the focal species occurs (Fig. 4). Incidence functions, depicting the presence or absence of species from islands of different levels of species richness (Diamond, 1975), are analogous to our diversity field FD plots. However, analyses for continental and insular faunas require different conceptual frameworks and analytical tools. Most analyses of insular faunas do not include the whole range of all species, and it is normally assumed that any species can potentially colonize any island. Observed patterns of co-occurrence were originally interpreted in terms of competitive exclusion (Diamond, 1975; Gotelli & McCabe, 2002), but can also be understood in terms of similarity in habitat preferences (Wiens, 1989). In most analyses of continental assemblages, ranges are assumed to show spatial cohesiveness, so dispersal to different sites has different probabilities depending on the location of those sites. Under this perspective, the presence of a species in a site is probably determined by the combined effects of evolutionary processes (speciation and extinction) and present-day environmental conditions and species interactions (Wiens & Donoghue, 2004; Ricklefs, 2007; Field *et al.*, 2009).

The distribution of species such as *L. nivalis* (Fig. 4a) is analogous to the Diamond (1975) 'super-tramp' category of species occurring only in the most species-poor sites. Diamond interpreted this pattern by likening it to an *r*-strategy, so super-tramps are species that are excluded through competition from

sites of high species richness. For phyllostomids, the pattern is explained by the group of North American endemics already discussed in the previous section, a set of a few species that have recently invaded the extratropical part of northern Mexico and the south-western United States. The diversity field pattern for Andean endemics, such as *A. luismanneli* is analogous to the Diamond (1975) 'high-S strategy', corresponding to species that occur only in the most species-rich islands (Fig. 4c). Diamond considered high-S species as highly competitive forms capable of co-occurring with many other species, that is, as *K*-strategists. For continental assemblages, the pattern is better explained by observing that these species are restricted to small areas of very high richness where the net diversification rate (speciation minus extinction) is high.

A pattern that does not fit any of Diamond (1975) categories is shown by species such as *L. bokermanni*, which are endemic to areas in south-eastern Brazil and whose diversity field includes only sites of moderate richness, generating a pattern that is intermediate between that of super-tramp and high-S species (Fig. 4b). In fact, as expected by theory (Arita *et al.*, 2008), mean species richness for the diversity fields of small-ranged phyllostomids varies widely along the continuum from super-tramp to high-S species (from the lower left to the lower right sectors of the range–diversity plot, Fig. 3a). The diversity field FD for widespread species resembles Diamond (1975) 'tramp' categories. For example, *V. spectrum* (Fig. 4d) corresponds roughly to a B- or C-tramp strategist and *G. soricina* (Fig. 4e) to a D-tramp. All tramp species aggregate in the right side of the range–diversity plot (Fig. 3a), forming a gradient from A-tramps in the lower sector to D-tramps in the upper part of the graph.

The diversity field of a species can be envisioned as a map of possible interactions with other species. Assuming that the number of populations of a species is proportional to its range size (Hughes *et al.*, 1997), the diversity field volume of any given species should be proportional to the total number of populations of all species potentially interacting with it. Parameters of the diversity field allow an analysis of the geographic distribution of these populations, thus contributing to a better understanding of the internal structure of ranges. From this perspective, the diversity field of a species is a geographic template of possible interactions and is closely related to the concept of the geographic mosaic of coevolution (Thompson, 2005). Given that the theory of the geographic mosaic of coevolution provides specific predictions of the possible outcomes of ecological interactions based on large-scale evolutionary processes (Gomulkiewicz *et al.*, 2007; Thompson, 2009), the concept of the diversity field can provide important elements to test such predictions through the analysis of continental patterns of co-occurrence.

From a different perspective, overlaps of species ranges can be interpreted as the result of species having similar large-scale environmental requirements, with no need to invoke any kind of ecological interaction. The existence of many species with similar Grinnellian environmental niches (Soberón, 2007), for example, would inevitably lead to a large number of overlaps in many sites of high species richness. At the other extreme, the

existence of taxa specialized to particular environments would tend to lower the species richness of sites. These factors can explain the peaks of phyllostomid diversity in the Amazon Basin and in south-eastern Brazil, where there are very large extents that support large assemblages of bat species with similar environmental requirements.

A third approach to explaining diversity fields is to envision present-day patterns of continental co-occurrence of species as the result of evolutionary processes over geological time. As discussed by Stevens (2006), latitudinal patterns of phyllostomid species richness are probably the result of historical processes that reflect the origin of the family in the tropics of the New World and its posterior diversification and dispersal to subtropical and temperate regions. In particular, the geographic pattern of species richness of phyllostomid bats is consistent with the niche conservatism hypothesis (Wiens & Donoghue, 2004; Losos, 2008) that has been posed to explain the origin and diversification patterns of some clades (Wiens *et al.*, 2006; Hawkins *et al.*, 2007). As pointed out by Stevens (2006), the average age of phyllostomid species is negatively correlated with latitude. This means that species that occur in the species-poor areas of northern Mexico and south-western United States are relatively young, just as predicted by the niche conservatism hypothesis.

CONCLUSIONS

We have shown that the diversity field is a versatile and powerful concept that allows the interpretation of diversity and distribution data from different ecological and evolutionary perspectives. It can help in identifying patterns for individual species as well as trends for whole assemblages. For phyllostomid bats, the strong latitudinal gradient of species richness that had been documented in previous papers can be better understood by analysing the patterns of overlap of species as part of the internal structure of geographic ranges. In particular, we have shown that present-day patterns of leaf-nosed bat species richness result from the interaction of different factors, including geometric ones (effect of range cohesion, including mid-domain effects); geographic, including the size and shape of the continent, in particular the Central American land constriction; climatic; and even some idiosyncratic traits of species, including their potential ecological interactions.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Parameters of the diversity field of 143 species of phyllostomid bats

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