Multiple environmental determinants of regional species richness and effects of geographic range size

J. Sebastián Tello and Richard D. Stevens

J. S. Tello (jtello1@lsu.edu), Dept of Biological Sciences, Louisiana State Univ., Baton Rouge, LA 70803, USA, and Museo de Zoología, Escuela de Ciencias Biológicas, Pontificia Univ. Católica del Ecuador, Av. 12 de Octubre 1076 y Roca, Apdo. 17-01-2184, Quito, Ecuador. – R. D. Stevens, Dept of Biological Sciences, Louisiana State Univ., Baton Rouge, LA 70803, USA.

Understanding patterns of species richness at broad geographic extents remains one of the most challenging yet necessary scientific goals of our time. Many hypotheses have been proposed to account for spatial variation in species richness; among them, environmental determinants have played a central role. In this study, we use data on regional bat species richness in the New World to study redundancy and complementarity of three environmental hypotheses: energy, heterogeneity and seasonality. We accomplish this by partitioning variation in species richness among components associated with unique and combined effects of variables from each hypotheses, and by partitioning the overall richness gradient into gradients of species with varying breadths of geographic distribution.

These three environmental hypotheses explain most variation in the species richness gradient of all bats, but do not account for all positive spatial autocorrelation at short distances. Although environmental predictors are highly redundant, energy and seasonality explain different and complementary fractions of variation in species richness of all bats. On the other hand, heterogeneity variables contribute little to explain this gradient. However, results change dramatically when richness is estimated for groups of species with different sizes of geographic distribution. First, the amount of variation explained by environment decreases with a decrease in range size; this suggests that richness gradients of small-ranged species can not be explained as easily as those of broadly distributed species, as has been implied by analyses that do not consider differences in range size among species. Second, the relative contribution of environmental predictors to explained variation also changes with change in range size. Seasonality and energy are good predictors of species with broad distributions, but they loose almost all explanatory power for richness of species with small ranges. In contrast, heterogeneity, which is a relatively poor predictor of richness of species with large ranges, becomes the main predictor of richness gradients of species with restricted distributions. This suggests that range size is a different dimension on which heterogeneity and other environmental characteristics are complementary to each other. Our results suggest that determinants of species richness gradients might be complex, or at least more complex than many studies have previously suggested.

Interest in how numbers of species change across large geographic extents began nearly two centuries ago with the work of Alexander Von Humboldt (Brown and Sax 2004). During these two hundred years of research, and starting with Von Humboldt's original idea that climate affected species richness, the number of explanations that have been hypothesized to account for spatial patterns of biodiversity has increased enormously. In 1966 the main mechanisms considered were only six (Pianka 1966), but by 2003 these included more than 30 (Willig et al. 2003). These hypotheses include a variety of ecological, biogeographic and evolutionary processes.

Environmental determinants have played a major role in our understanding of diversity patterns at many scales, from local communities (Borcard et al. 1992) to the entire globe (Currie 2007a). Environmental characteristics have been frequently correlated with variation in species richness at large geographic scales and the vast majority of results have found significant associations. Generality of species–environment relationships has been suggested to be evidence of the importance of environmental determinants in the geographic distribution of biodiversity (Field et al. 2009).

Environment, however, does not represent a simple mechanism. Most environmental variables that have been associated with species richness can be grouped into at least three distinct hypotheses: energy, heterogeneity and seasonality. These three hypotheses have been mechanistically linked to patterns of species richness in a multitude of ways (Supplementary material), which include effects on co-existence of species within communities, turnover of species composition across space, or rates of speciation and extinction (Pianka 1966, MacArthur 1972, Rohde 1992, Willig et al. 2003, Currie et al. 2004, Evans et al. 2005b, Allen et al. 2007, Mittelbach et al. 2007).

The energy or energy–water hypothesis has been frequently supported and is one of the most broadly accepted ideas to explain geographic patterns of species richness. A number of studies have associated measures of temperature, productivity or water availability with numbers of species (Currie 1991, Hurlbert and Haskell 2003, Storch et al. 2006). These studies frequently find that the relationship is not only significant but also strong. Environmental heterogeneity has also been commonly investigated. Coincidence of high species richness with geographically complex areas is usually readily apparent (Simpson 1964). In general, evidence in favor of this mechanism is less than for energetic determinants. Nevertheless, environmental heterogeneity has frequently been found to significantly account for variation in species richness (Badgley and Fox 2000, Rahbek and Graves 2001, Diniz-Filho et al. 2004). Seasonality has been much less empirically investigated than energy or heterogeneity. However, studies that have considered seasonality provide mixed evidence for seasonality as a strong determinant of large scale variation in species richness (Kay et al. 1997, Badgley and Fox 2000, Ruggiero and Kitzberger 2004, Qian 2008).

These multiple environmental mechanisms have been typically considered competing hypotheses (Currie 1991, Field et al. 2009). Nevertheless, it is reasonable to consider that a number of different forces can be simultaneously affecting species richness gradients. Thus, an important step forward to understand determinants of species richness gradients will be to develop a conceptual framework that considers relationships among numerous proposed mechanisms, in particular interactions and complementarity (multiple hypotheses might explain different portions of species richness gradients). Recent studies have suggested complementarity among mechanisms and have provided some evidence for its existence (Kerr and Packer 1997, Diniz-Filho et al. 2004, Davies et al. 2007, Kreft and Jetz 2007, Kreft et al. 2008). For example, Kerr and Packer (1997) demonstrated complementarity between energy and heterogeneity, where energy was a good predictor of richness only in places with low energy levels but heterogeneity became the main predictor in areas of high energy availability. Similarly, there is evidence that different environmental hypotheses might be more important determinants of richness in different taxonomic groups (Ruggiero and Kitzberger 2004), in different geographic locations (Davies et al. 2007), or for richness gradients of species with different attributes (Jetz and Rahbek 2002, Evans et al. 2006, Terribile et al. 2009).

In this study, we explicitly estimate redundancy and complementarity among three major environmental hypotheses: energy, heterogeneity and seasonality. We accomplish this by partitioning variation in richness gradients of bats in the New World into components of unique and shared effects among variable sets representing each hypothesis. Furthermore, we examine whether different environmental hypotheses can explain richness gradients of species with different breadths of geographic distribution; we achieve this by repeating our analyses for four groups of species defined by their geographic range size.

These analyses could lead to at least three distinct possible outcomes, each with a different interpretation (Fig. 1). First, multiple hypotheses might explain significant portions of variation even after accounting for other environmental determinants (significant unique components; Fig. 1A); this result is consistent with an independent effect of each hypothesized mechanism, and would suggest that mechanisms are complementary to each other by explaining different fractions of variation. Second, if variation in species richness that a hypothesis explains is included in variation that other more important hypotheses account for, the proposed mechanisms can be considered nested-redundant (Fig. 1B). In this scenario, the most parsimonious interpretation is that the likely determinant of species richness is the hypothesis that can account for most variation, and only this hypothesis should be interpreted as receiving support from the data. Finally, it is possible that all variables explain similar amounts of variation and that explained variation is completely shared among hypotheses (Fig. 1C); redundant variation cannot be clearly associated to any particular hypothesis, and none of the mechanisms achieve primacy.

Although important gradients in taxonomic, functional and morphological diversity of bats have been described at broad geographic extents (Stevens et al. 2003, 2006), few studies have tested mechanisms behind these gradients (but see Willig and Lyons 1998, Stevens 2006, Willig and Bloch 2006), particularly in terms of the environmental correlates of species richness (but see Patten 2004, Ulrich et al. 2007). Ours is the first detailed test of the effects and interactions of multiple environmental hypotheses as determinants of large scale patterns of variation in taxonomic diversity of bats for the entire New World.

Methods

Species richness and range maps

We calculated taxonomic richness based on bat species distributions from Patterson et al. (2005). Only those bat species that had polygon layers were included in analyses.
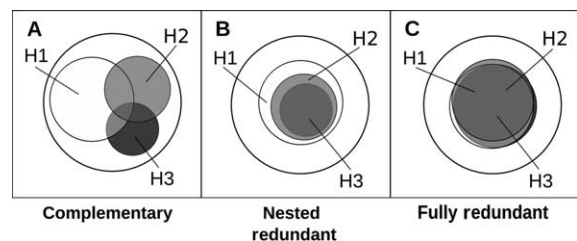

Figure 1. Venn diagrams representing probable outcomes from analyses. Three hypotheses are represented (H1, H2 and H3). Size of circles represents relative amount of variation accounted for by a particular hypothesis. Overlapping regions symbolize variation that is redundant and explained by multiple hypotheses. Non-overlapping regions represent independent effects. Three scenarios are presented: (A) despite some redundancy among hypotheses, each one has a significant unique component, and hence different hypotheses are complementary to each other; (B) hypotheses explain different amounts of variation, however hypotheses that explain less variation are all contained within variation associated with the most important hypothesis; in this case, explanatory powers of different hypotheses are redundantly nested; (C) different hypotheses all account for some variation in species richness, but they are fully redundant, there are no unique effects and effects of multiple mechanisms cannot be differentiated.

These maps were created by compiling distribution information from a number of different references. Distribution shape files for each species were transformed into Diva-GIS 5.4 grid files using a template map of the New World divided into equal area cells of 100 by 100 km (using a Mollweide projection). Then, the number of species expected to co-occur in each cell was calculated by counting range overlaps. The species richness map was further reduced by excluding: a) all cells that represented islands, b) cells that had >25% of their area over water (mainly coastal cells), and c) cells that did not have information for environmental predictors (see below). This resulted in deletion of ca 15% of the original cells. This process led to a map with 3523 cells representing variation in species richness values based on distributions of 286 species of bats. Similar species richness maps were produced for four groups of species defined by the quartiles of geographic range size: 1) $\leq 812\,500$ km^2, 2) $>812\,500$ and $\leq 3\,320\,000$ km^2, 3) $>3\,320\,000$ and $\leq 9\,247\,500$ km^2, and 4) $>9\,247\,500$ km^2. The first and fourth groups had 72 species each, while the second and third groups had 71 species each. These richness maps had 708, 2268, 3128 and 3518 cells respectively.

Much recent attention has been given to issues of how scale affects our understanding of ecological phenomena, and a number of studies have found effects of spatial scale in relation to determinants of species richness (Rahbek and Graves 2001, Lyons and Willig 2002, Hurlbert and White 2005). Thus, a precise awareness of scale of analysis is fundamental to make sense of results from different studies. Our analyses represent a study of variation in regional species richness that occurs at a supra-continental extent across the New World. A more detailed analysis of how grain size and extent affect observed species–environmental relationships will be presented elsewhere.

Environmental predictors

Most environmental variables were obtained from World-Clim (Hijmans et al. 2005). These data are generated by spatial interpolation of basic climatic variables collected by thousands of stations around the planet. Elevation data were also obtained from WorldClim, which is based on information from the Shuttle Radar Topography Mission. Resolution of these environmental maps was of 30 arc-seconds (ca 1 km^2). Net primary productivity (NPP) data were obtained from Imhoff et al. (2004). This estimation of productivity is based on modeling release and retention of carbon using satellite and climate data (Imhoff et al. 2004), and it provides an estimation of annual carbon production. Resolution of these data is of 0.25 degrees.

All environmental variables were obtained as rasters with resolutions smaller than the cell size used for analyses. Consequently, we calculated statistics that reflect central tendency (average) or spatial variability (standard deviation) of environmental variables within each cell. This was done using Hawth's Tools v.3.26 for ArcMap (Beyer 2004). For all environmental predictors except NPP, average number of raster pixels within a richness map cell was 11 326.5; for NPP, this number was 12.6.

The energy hypothesis was represented by cell averages of NPP, annual precipitation and mean annual temperature. These variables represent the main forms of energy that have been considered in the literature. Kinetic energy is represented by temperature and many studies have used it as an explanatory variable (Rahbek and Graves 2001, Hawkins et al. 2007b, Kalmar and Currie 2007). NPP represents the potential energy stored in biomolecules produced by autotrophs, which is available to support food webs (Allen et al. 2007). Finally, precipitation represents water availability, which is fundamental for the transformation of light energy into potential energy, and is also fundamental for metabolism (Allen et al. 2007). This variable has been used as a measure of energy, especially in studies of warm desert ecosystems where soil moisture is a strong determinant of biomass production (Brown and Liemberma 1973, Brown and Ernest 2002, Lima et al. 2008). The environmental heterogeneity hypothesis was estimated by spatial standard deviations of elevation, NPP, annual precipitation, and mean annual temperature. These variables have been selected to represent spatial variation in climatic and topographic characteristics that have been proposed to influence isolation of populations and consequent speciation (Simpson 1964), and co-existence of species based on breath of niche space (MacArthur 1964). Finally, the seasonality hypothesis was estimated by cell averages of monthly standard deviation of temperature and monthly coefficient of variation of precipitation. This represents temporal heterogeneity in climatic conditions that occur within a year. This temporal variability can either allow temporal niche partitioning (Tilman et al. 1993), or can be considered to be a form of environmental instability that drives species extinct or forces them to develop broader niches (Pianka 1966, MacArthur 1972). Each of these three environmental hypotheses is characterized by variables that have high levels of correlation with other variables within the same hypothesis (mean $r_P = 0.525$; Supplementary material Fig. S1 and S2), but lower levels of co-variation with variables representing a different hypothesis (mean $r_P = 0.273$; Supplementary material Fig. S1 and S2).

Variation partitioning analysis

A variation partitioning analysis is based on a series of multiple regressions (also RDA's or CCA's when multivariate) that allow decomposition of variation in a dependent variable of interest among components associated with two or more hypotheses and their interactions (Borcard et al. 1992, Legendre and Legendre 1998). In our study, we used variation partitioning analysis to decompose spatial variation in bat species richness among three environmental hypotheses: energy, heterogeneity and seasonality. This process produced eight components of variation (Fig. 2). Three components represent variation that can be explained independently by each hypothesis. Three other components represent variation that can be explained only by each pair of hypotheses simultaneously. One additional component corresponds to variation that can be explained simultaneously by all three hypotheses. Finally, one component represents unexplained variation. Additionally, to produce results comparable to most other

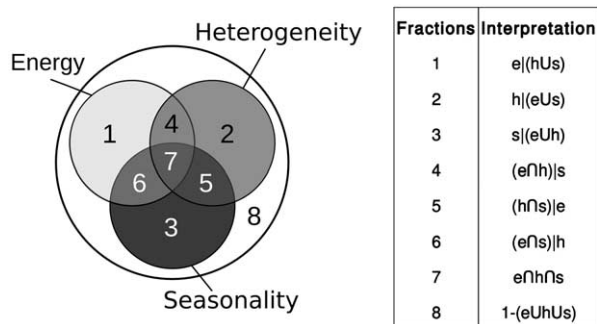| Fractions	Interpretation
1	e|(h∪s)
2	h|(e∪s)
3	s|(e∪h)
4	(e∩h)|s
5	(h∩s)|e
6	(e∩s)|h
7	e∩h∩s
8	1-(e∪h∪s)

Figure 2. Venn diagram representing variation partitioning analysis. Variation in species richness was partitioned among three sets of predictors: energy, heterogeneity and seasonality. Fractions 1, 2, and 3 represent unique effects of energy, heterogeneity and seasonality respectively. Fractions 4, 5 and 6 represent variation shared by each pair of predictor sets. Fraction 7 is variation associated with the intersection of all three environmental hypotheses. Finally, fraction 8 is variation in species richness that is not accounted for by any environmental predictor. e: energy; h: heterogeneity; s: seasonality; ∩: intersection; ∪: union; |: after accounting for.

studies that have investigated effects of environmental predictors, we also estimated the full amount of variation associated with each environmental hypothesis. These analyses were carried out for richness values based on all species, and also for richness of four species groups based on geographic range size (as defined above). To account for differences in numbers of variables among sets of predictors, we used adjusted R^2 to estimate explained variation (Peres-Neto et al. 2006). Variation partitioning analyses were conducted in R ver. 2.8.1, using the function "varpart" available in the package "vegan" ver. 1.15-3. No particular variable transformation was most appropriate for all groups of species; thus, in an effort to make results comparable, both species richness and environmental predictors were log transformed before all analyses.

Most previous studies attempting to contrast effects of different environmental hypotheses have taken one of two approaches. First, many studies have simply compared effects sizes (e.g. R^2, standardized slopes, or F values) among variables or groups of variables representing distinct hypotheses (Tognelli and Kelt 2004, Field et al. 2009). Comparing effect sizes can determine which hypotheses explain more variation; however, this approach cannot be used to reject the effects of mechanisms that explain less variation since these hypotheses could still be complementary and explain a different portion of the species richness gradient (Fig. 1A). Various other studies use some form of variable selection to construct minimally adequate models (MAMs) to explain species richness gradients (Currie 1991, Hawkins et al. 2003a). Although these analyses can suggest complementarity among mechanisms represented in a MAM, they do not typically consider how much variation is explained by different variables, nor give a clear idea about the magnitude of complementarity or redundancy of different hypotheses. Additionally, it is usually unclear why some variables are not selected for the model. These rejected variables can either explain no variation or can explain large proportions of variation, but this variation is already explained by other variables in the model. This lack of

distinction can have two problems. First, when numerous variables are co-linear, the production of MAMs can be unstable and hence conclusions from them can be unreliable. Second, the redundancy among hypotheses could be interpreted in terms of the interactions among mechanisms, but this information is lost in the construction of MAMs.

Contrary to these approaches, variation partitioning analysis permits more explicit determination of redundancy and complementarity among multiple hypotheses by estimating proportion of variation that is 1) explained uniquely by each predictor set and 2) accounted for simultaneously by two or more predictor sets. Few studies have used this approach to disentangle effects of various environmental mechanisms on richness gradients at large geographic extents (Lobo et al. 2004, Hortal et al. 2008), or of environmental variables and variables representing other processes like space or history (Hawkins et al. 2003b, Lobo et al. 2004, Currie and Kerr 2008).

Bootstrap confidence intervals and permutation test of difference from random

To make meaningful statistical comparisons among different components of variation, we built 95% confidence intervals (CI) for adjusted R^2 values by bootstrapping (Chernick 2008). A bootstrap sample was created by randomly sampling with replacement rows (map cells) of the original dataset (by definition, bootstrapped data has the same number of observations as empirical data; Chernick 2008). We then used this bootstrapped dataset to conduct a variation partitioning analysis as described above. This process was repeated one thousand times, yielding frequency distributions of variation associated with each component. The 2.5 and 97.5% quantiles of these distributions were used to create 95% CI's around the original estimates.

We also performed a permutation test to estimate whether a particular variation partitioning component was larger than would be expected by chance. Each iteration of the test consisted of permuting the species richness vector, and then using this randomly reordered richness to conduct a variation partitioning analysis. One thousand repetitions of this process yielded a frequency distribution of adjusted R^2 values for each variation component expected under the null hypothesis of random association between species richness and environmental characteristics. If the original estimate of variation associated with a component of interest was greater than the 95% quantile of this random distribution, then this component was considered statistically greater than expected by chance. R code to run these analyses can be found in the Supplementary material.

Spatial Moran's I correlograms

To understand spatial structure in species richness and discover whether different hypotheses explain different spatial patterns in species richness, we constructed Moran's I spatial autocorrelograms for species richness and for residuals left by different environmental hypotheses. Autocorrelograms were built by plotting Moran's I indices versus distance classes that were used to calculate them. For our data, Moran's I values were calculated for 40 distance classes

of equal breadth using the function "Moran.I" available in the R package "ape" ver. 2.3-1. Correlograms were built for the original species richness, and for back-transformed (antilogarithm) residuals of energy, heterogeneity, and seasonality regression models.

Recently, much focus has been given to the importance of accounting for spatial autocorrelation in ecology and biogeography research (Legendre 1993, Beale et al. 2007, Hawkins et al. 2007a). However, the proper interpretation and use of spatial analyses are still unclear (Legendre 1993, Hawkins et al. 2007a). The most important difficulty associated with spatial autocorrelation is that it can represent a lack of independence among sampling units; consequently, standard statistical tests can generate inappropriate confidence intervals around test statistics and can produce rates of rejection of the null hypotheses than are different from expected (Fortin and Dale 2005); positive spatial autocorrelation produce liberal tests, while negative spatial autocorrelation produce conservative tests (Fortin and Dale 2005). However, recently Hawkins et al. (2007a) have demonstrated through a Monte Carlo experiment that regression result are not necessarily affected by the presence of autocorrelation, particularly when dealing with regression coefficients. Hawkins et al.'s study also showed that analyses where positive autocorrelation was removed produced R^2 values usually greater than those produced by non-spatial regressions. Thus, we believe that our analyses are appropriate; R^2 values from regular regressions are good, if not conservative, estimates of the true variation accounted for by a set of predictors.

Results

For all bats, the highest species richness in the New World occured near the equator, along the north and central Andes and in the northern most part of South America (Fig. 3). From these areas of high diversity there was an accelerated decrease toward higher latitudes. A similar latitudinal gradient existed for all four groups of species based on geographic range size. However, differences were also apparent. In particular, the species group with the largest geographic distributions had its peak richness in lowland tropical South America, while other groups of species had their highest richness associated with the northern Andes and the Guiana shield, and Central America for the species group with the smallest distributions. Spatial structure in species richness was also reflected in the U-shaped pattern of Moran's I values (Fig. 4 and 5). Nearby cells had similar richness values, but this positive autocorrelation rapidly decreased and became negative at intermediate distances, reflecting mainly dissimilarity in species richness between the Tropics and north and south temperate regions. Finally, autocorrelation increased quickly and became strongly positive at large distances, representing mainly similarity in richness between temperate regions at both extremes of the New World. Although latitude was clearly an important axis of variation in species richness, there was also a significant proportion of variation that changed independently of latitude (Fig. 3).

All-species richness gradient

The full model that included all environmental predictors explained almost all the observed variation in the richness of all species (92%; Fig. 6, Supplementary material Table S1). For all species, energy and seasonality accounted for very similar amounts of variation (∼81%; Fig. 6; Supplementary material Table S1). Heterogeneity also explained a significant proportion of variation, but this was much smaller than that related to energy or seasonality (∼43%; Fig. 6; Supplementary material Table S1). Although the amount of variation explained by energy and seasonality was very similar, variation partitioning analyses indicated that both hypotheses explained considerable fractions of variation independently of variables associated with other hypotheses (unique components of ∼8% each; Fig. 7A; Supplementary material Table S1). On the other hand, the amount of variation that was associated only to heterogeneity was extremely small (<1%; Fig. 7A; Supplementary material Table S1). The most important fractions of variation in the analyses for all species were fractions 6 and 7, which correspond to variation accounted for simultaneously by 1) energy and seasonality and 2) all three environmental hypotheses.

Spatial variation in residuals left by environmental predictors provided insight into how environmental hypotheses might differ in the spatial variation they account for (Fig. 3, first column). For the richness gradient of all species, energy predictors produced a characteristic distribution of residuals, mainly representing inability of these variables to account for high numbers of species in mountainous regions of North and South America (Fig. 3). Additionally, areas like the southern tip of South America and east North America had fewer species than would be expected by levels of energy they receive. The spatial distribution of heterogeneity residuals indicated an interestingly contrasting pattern. In this case, most positive residuals were distributed from lowland tropical forests of South America to south-west North America (Fig. 3). In the case of seasonality, most positive residuals were in south North America, subtropical and north-temperate South America, and Atlantic forest. The southern tip, part of the west coast of South America, the Amazon, and other areas in the northern extreme of North America had fewer species than predicted by their levels of seasonality (Fig. 3).

Correlograms accompanying maps of distribution of residuals (Fig. 4) indicated that, in general, residuals had much reduced levels of spatial autocorrelation than richness of all species. Energy and seasonality removed all negative spatial autocorrelation at intermediate distances, but heterogeneity could not fully account for this spatial structure. No hypothesis was able to account for all positive spatial autocorrelation at short distances, but energy did a fairly good job of reducing the positive spatial autocorrelation at long distances, unlike heterogeneity or seasonality.

Richness gradients by geographic range size

Fractions of variation associated with each environmental hypothesis were different among range-size species groups (Fig. 6; Supplementary material Table S1). The amount of
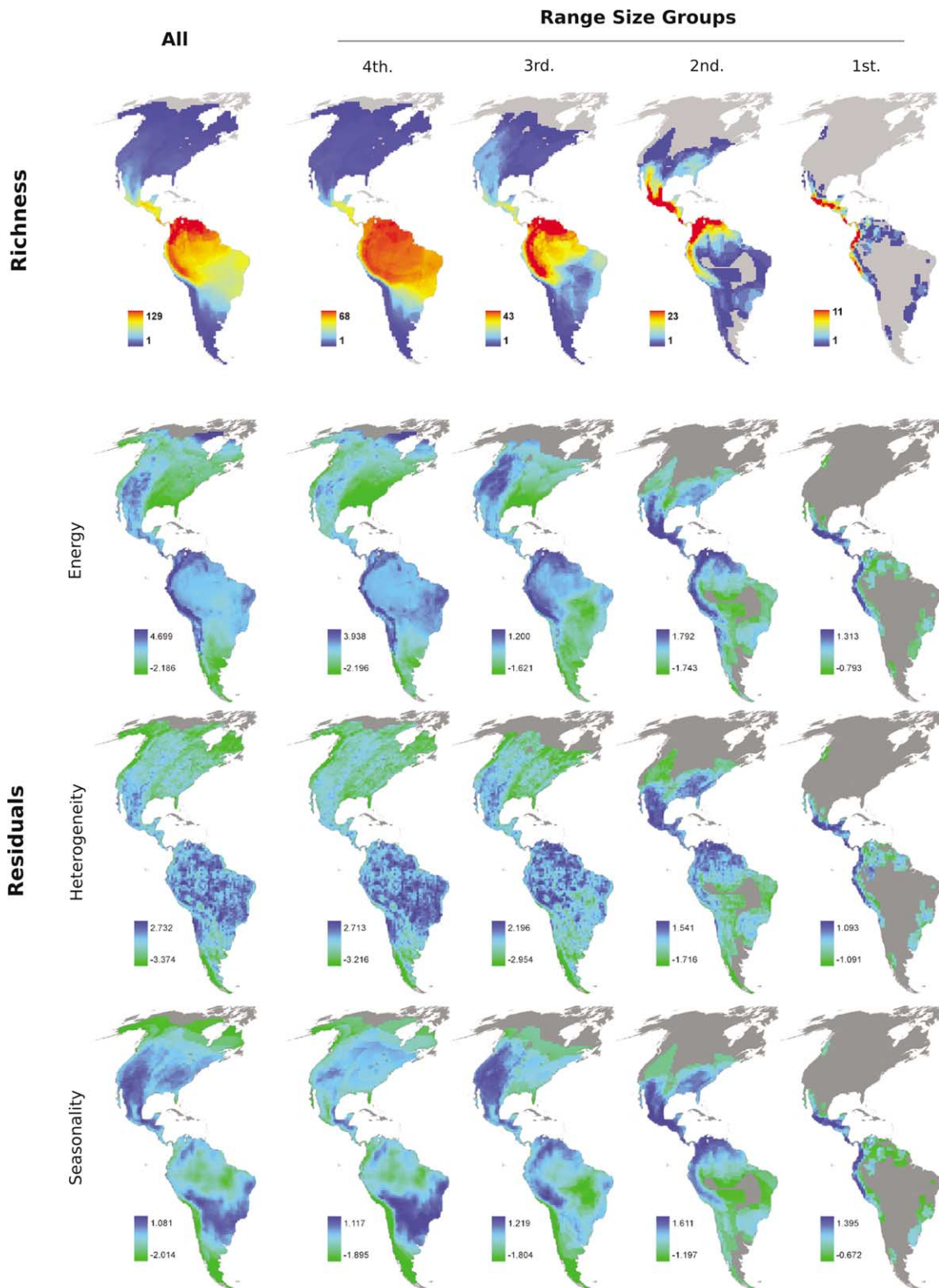
Figure 3. Maps of the distribution of species richness and residuals. Maps for all species and for each range size species group are defined by columns. Species richness and residuals left by three environmental hypotheses are given by rows. Areas excluded from analyses (see text) are shown in grey (online version) or as point patterns (print version).

variation explained by all predictors decreased significantly as the range size of species decreased (from ∼92 to ∼35%; Fig. 6; Supplementary material Table S1). Moreover, for both groups with large geographic range sizes, seasonality explained significantly more variation than any other hypothesis, while heterogeneity was the poorest predictor. In contrast, heterogeneity was the best predictor among the species with small ranges, while both energy and seasonality
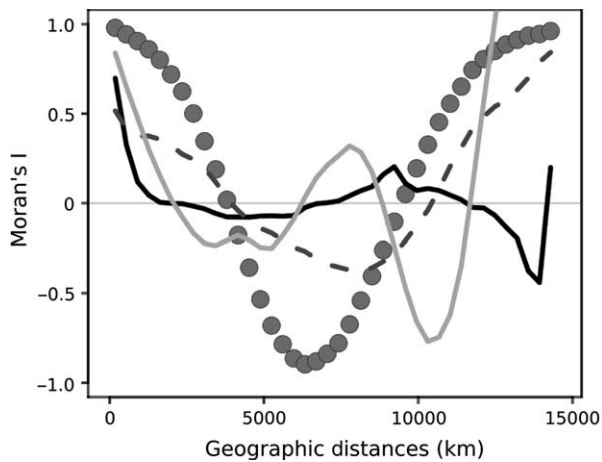
Figure 4. Moran's I correlograms of richness and its corresponding residuals for all species. Circles: species richness. Black solid line: residuals of energy. Dark-gray broken line: residuals of heterogeneity. Light-gray solid line: residuals of seasonality. Only Moran's I values in the range 1 to −1 are presented.

lost most of their explanatory power (Fig. 6; Supplementary material Table S1).

Similarly, components of unique variation associated with different hypotheses changed with range size (Fig. 7B; Supplementary material Table S1). For example, seasonality could explain a considerable proportion of unique variation in richness of species with large geographic ranges (component 3: ∼15%; Fig. 7B; Supplementary material

Table S1), but this component was minuscule for richness gradients of small-ranged species (<1%; Fig. 7B; Supplementary material Table S1). On the other hand, the amount of variation uniquely associated with heterogeneity had the opposite pattern: very little variation associated with this component for richness of large-ranged species (component 2: <1%; Fig. 7B; Supplementary material Table S1), and considerably higher variation accounted for in the richness gradient of small-ranged species (∼20%; Fig. 7B; Supplementary material Table S1). Furthermore, although components of variation that reflect redundancy among hypotheses were the most important for the gradient of all species and for those based on broadly distributed species, this was not the case for gradients based on small-ranged species, where the component representing unique effects of heterogeneity took over as the most relevant fraction of variation (Fig. 7; Supplementary material Table S1).

Species richness of small-ranged species had reduced levels of autocorrelation compared to broadly distributed species, especially with respect to the negative autocorrelation seen at intermediate distances. The reduction in spatial autocorrelation in residuals was proportional, of course, to the amount of explained variation. Thus, residuals had much reduced levels of autocorrelation than the original gradient for large-ranged species richness; but, autocorrelation in residuals resembled more closely that of the original gradient for the richness of small-ranged species (Fig. 5). For the species with smallest ranges, heterogeneity variables were the only ones that reduce autocorrelation to
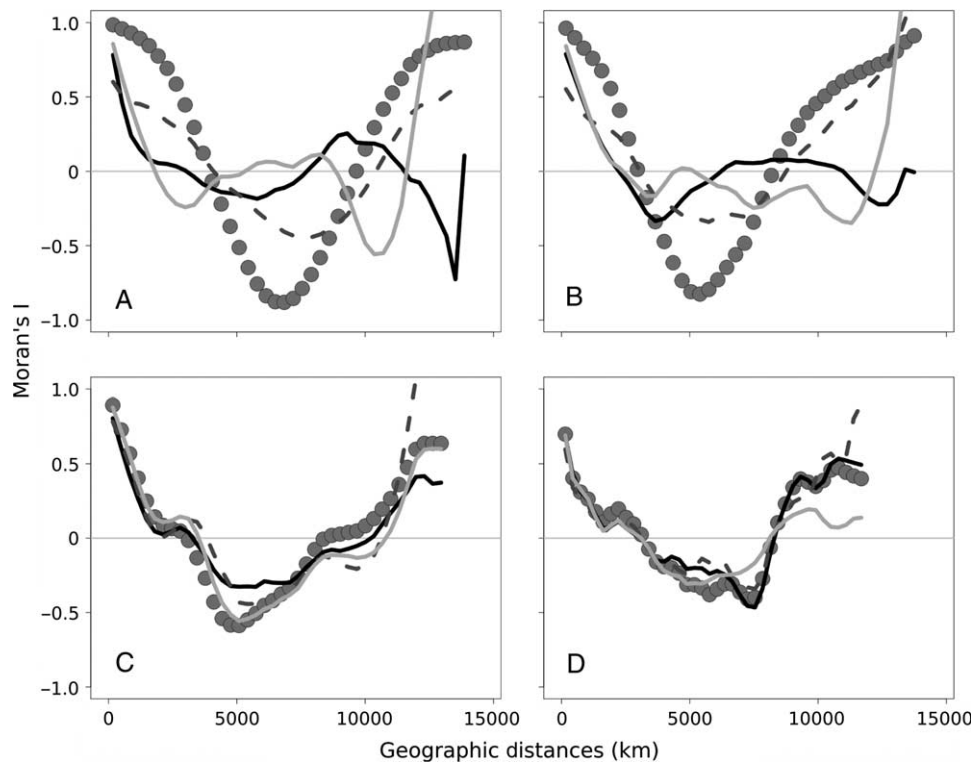

Figure 5. Moran's I correlograms of richness gradients and their corresponding residuals for each range size species group. (A) 4th group. (B) 3rd group. (C) 2nd group. (D) 1st group. Circles: species richness. Black solid line: residuals of energy. Dark-gray broken line: residuals of heterogeneity. Light-gray solid line: residuals of seasonality. Only Moran's I values in the range 1 to −1 are presented.
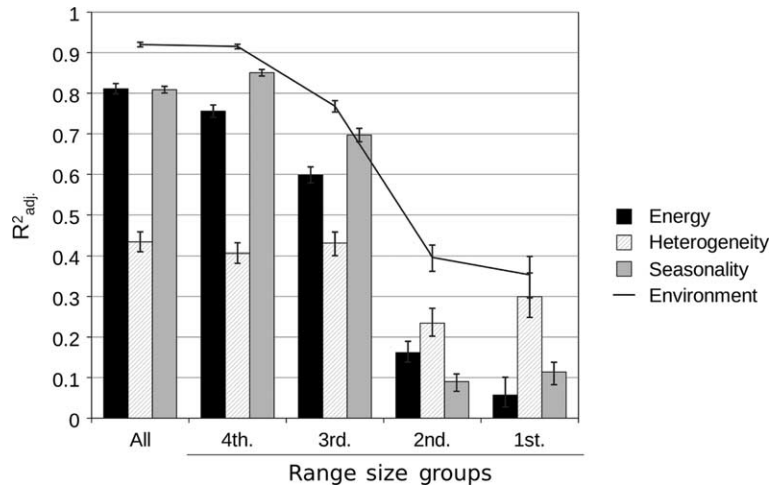
Figure 6. Adjusted R²'s associated to various regression models and species groups. Error bars around effects sizes for each model represent bootstrapped 95% confidence intervals. Environment model represents the regression of richness against all environmental predictors simultaneously.

some degree, and this reduction occured mainly at large geographic distances.

Discussion

Patterns of species richness at broad extents likely result from a number of environmental and non-environmental processes. However, most studies have treated different hypotheses simply as competing mechanisms, with little interest in explicitly considering the magnitude of their redundancy or complementarity. In this study we have tried to address just this issue by: 1) partitioning variation in bat species richness among independent and shared effects of energy, heterogeneity and seasonality, and 2) analyzing the correlation of environmental variables with richness gradients based on groups of species of varying geographic range size.

Environmental hypotheses and the all-species richness gradient: redundancy, complementarity and interactions

Environmental determinants were one of the first factors proposed to explain species richness patterns (Brown and Sax 2004) and are also the most broadly supported by evidence, to the point of recognition of an almost universal species-environmental relationship (Field et al. 2009). Not surprisingly, our results demonstrate a strong relationship between species richness of all bats and environmental predictors in the New World.

Energy and seasonality are the environmental hypotheses that are most closely related to the overall empirical pattern of bat species richness in the New World. Heterogeneity accounted for a much smaller fraction of variation in all-bat species richness (Fig. 6). These results match most recent studies considering relationships between large scale
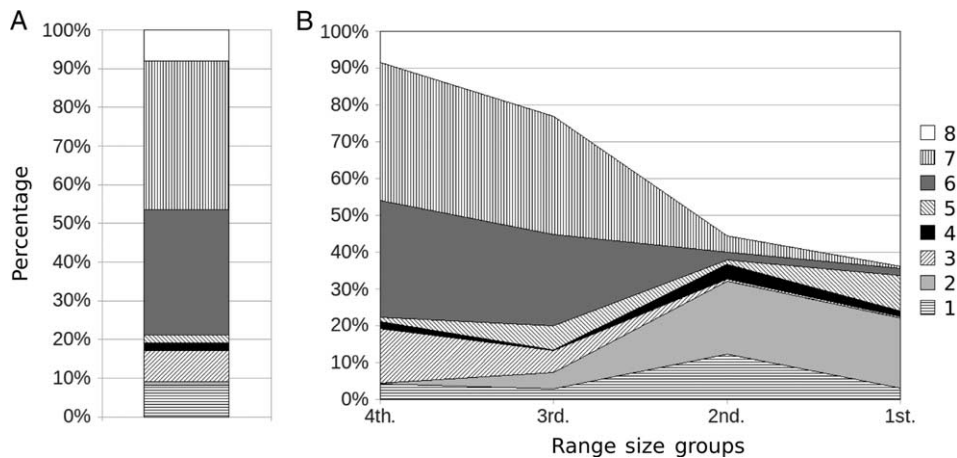

Figure 7. Percentage of explained variation (adjusted R² × 100) associated with components of variation partitioning analysis and species groups. (A) Stacked-bar showing partitioning of explained variation among components for all species. (B) Area graph showing change in amount of variation associated with each component with change in geographic range size group. Confidence intervals for each component can be found in Supplementary material Table S1.

803

patterns of species richness and different environmental hypotheses, which have found that in general variables representing energy and energy-water interactions explain more variation than variables that represent topographic and habitat heterogeneity (van Rensburg et al. 2002, Diniz-Filho et al. 2004, Kreft and Jetz 2007, Hortal et al. 2008, Field et al. 2009). These results have lead to the conclusion by many that energy is the most likely determinant of patterns of species richness (Currie 1991, Hawkins et al. 2003b, Kreft and Jetz 2007). On the other hand, in contrast to various previous studies (Currie 1991, Ruggiero and Kitzberger 2004, Qian 2008), our results show that seasonality is a very important predictor and can explain as much variation in bat species richness as energy does.

By far the largest components of variation in the all-species richness gradient are those that reflect redundancy between energy and seasonality, and among all three hypotheses (Fig. 7A; Supplementary material Table S1). Interpretation of these components is complicated. This redundancy is caused by correlations among predictors representing different hypotheses. Multicollinearity has long been recognized as a problem in the study of species richness gradients at large geographic extents (Francis and Currie 1998), and it frequently prevents a clear discrimination among hypotheses. Among our redundancy components, the fraction of variation associated with all three hypotheses is the most problematic, since it provides no information to distinguish among mechanisms. Thus, at least 38% of the variation could be associated to any of the three hypotheses. However, it is clear that there is a large component of variation (32%) that can not be explained by heterogeneity, but that could be associated to energy or seasonality.

The large overlap between seasonality and energy could be interpreted as 1) simply the undifferentiated contribution of environmental characteristics that can not be associated to either hypothesis, or 2) a hierarchical interaction between energy and seasonality. The confounded effects interpretation is the most parsimonious and conservative one; nothing else can be said about what this component of variation really represents without further evidence. However, it is logical to expect a large overlap in the explanatory power of these two hypotheses since energy and seasonality are mechanistically linked; seasonality itself is an important constraining factor on the total amount of energy that a place receives in a given year. Consequently, this component of variation could represent, at least in part, an indirect effect of seasonality on species richness by affecting energy availability. More research needs to be done to differentiate whether variation associated simultaneously with energy and seasonality represents an inability to distinguish effects of these correlated characteristics, or whether effects of seasonality are mediated by energy.

Moreover, although energy and seasonality virtually explain the same amount of variation and are highly redundant, our results suggest that these two hypotheses might be complementary to each other to some degree. This is so because each can explain about 8% of unique variation in the richness of all-bat species (fractions 1 and 3, Fig. 7A; Supplementary material Table S1). This can be considered evidence that multiple hypotheses, and particularly energy

and seasonality, explain different portions of variation in species richness of all bats.

In contrast, heterogeneity has an extremely small unique component, accounting for <1% of variation (fraction 2, Fig. 7A; Supplementary material Table S1). The lower explanatory power of heterogeneity variables has been confirmed by many previous studies of richness gradients at large geographic extents (Patten 2004, Hortal et al. 2008, Field et al. 2009). However, other studies have also shown that variables representing heterogeneity are frequently included in MAM's with energy variables (Davies et al. 2007, Kreft et al. 2008), suggesting that these hypotheses are complementary. But, most of these studies did not include variables representing seasonality, which further reduces the importance of a unique component associated with heterogeneity in our analyses.

Maps of residuals left by the three environmental hypotheses illustrate strikingly different patterns of distribution of unexplained variation. Energy is clearly unable to account for high species richness in topographically complex areas; heterogeneity can not explain the high species richness in the tropical and subtropical lowlands of South America; and finally, according to seasonality, there is an excess of species in subtropical South America and in most of western North America. However, this visually striking contrast can be misleading since it corresponds to relatively small fractions of variation associated uniquely to each hypothesis, as seen in results of variation partitioning analyses.

Different environmental hypotheses produce different patterns of spatial autocorrelation in residuals, which can also provide information on how environmental determinants affect species richness patterns. Moran's I correlograms of model residuals reveal that negative autocorrelation at intermediate distances can be entirely accounted for by energy and seasonality, but to a much lesser degree by heterogeneity (Fig. 3). This large negative autocorrelation at intermediate distances is caused primarily by the latitudinal gradient in species richness, as the difference between the tropics and temperate zones. This suggests that energy and seasonality adequately explain the latitudinal gradient in species richness. Heterogeneity on the other hand produces residuals that still have negative autocorrelation at intermediate distances and a latitudinal gradient (Fig. 3).

Overall, we find that our results for the richness gradient based on all species are a mixture of our a priori expectations regarding relationships among variation explained by different environmental hypotheses (Fig. 1). First, energy and seasonality explain and include almost all of the variation accounted for by heterogeneity; hence, heterogeneity is nested-redundant with energy and seasonality. On the other hand, energy and seasonality have small, yet meaningful, portions of unique variation; this suggest that these two hypotheses are partially complementary to each other.

Size of species distributions and the effects of environmental characteristics

Various previous studies have decomposed richness gradients based on size of species distributions (Lennon et al.

2004, Vazquez and Gaston 2004, Arita and Rodriguez-Tapia 2009, Sizling et al. 2009). These studies have shown that the overall gradient is typically disproportionately dominated by the contribution of only the most broadly distributed species, and hence patterns of small ranged species have been underrepresented in most studies. This difference between richness gradients of broad and narrowly distributed species can also have an important influence on interpretation of hypotheses proposed to account for richness gradients. This was evident from our results.

First, the very strong species–environment relationship seen for the all-species gradient was maintained in analyses on large-ranged species, but became only moderate for small-ranged species. A similar decrease in strength of species–environment relationships has been reported from the few other case studies that have been considered: Sub-Sahara African birds (Jetz and Rahbek 2002), mammals of South America (Ruggiero and Kitzberger 2004), Aphodiid beatles in the Iberian Peninsula (Cabrero-Sanudo and Lobo 2006), and Viperidae snakes of the World (Terribile et al. 2009); but see Fu et al. (2006) for an exception. The widely recognized strong species–environment relationship of richness at large geographic scales could be driven primarily by the effects of only the most widely distributed species. Richness gradients of small- and even medium-ranged species might be much more difficult to explain using environmental characteristics. This suggests that gradients of small- and medium-ranged species might require a different explanation that might involve, perhaps, historical or spatial processes (Jetz et al. 2004, Jablonski et al. 2006, Wiens et al. 2007).

Second, the amount of variation associated with different hypotheses changed dramatically as range size of species decreased. For broadly distributed species, the best predictors were those corresponding to seasonality, followed closely by energy; heterogeneity explained far less variation. In contrast, heterogeneity is by far the best predictor of richness of small-ranged species. In terms of components of variation, the most important for the all-species gradient are also the most important for the gradient of the broadly distributed species, namely the redundancy of energy and seasonality and the redundancy of all three hypotheses. But, this redundancy disappears among gradients of small-ranged species. In its place, the most important component is the variation that can be uniquely attributed to heterogeneity. Few previous studies have evaluated the relative contribution of various environmental hypotheses to richness gradients of species with different breadths of distribution. Most of these studies suggest that variables representing energy are more strongly correlated with gradients of large-ranged species (Jetz and Rahbek 2002, Evans et al. 2005a, Kreft et al. 2006, Rahbek et al. 2007), while heterogeneity is a better predictor of richness of small-ranged species (Jetz and Rahbek 2002, Kreft et al. 2006, Rahbek et al. 2007). Seasonality has been evaluated in this context only in two studies, but their results are more difficult to interpret and do not show a clear pattern (Ruggiero and Kitzberger 2004, Terribile et al. 2009). Our results, and most of the few previous studies on this issue, suggest that geographic range size could be a different dimension on which environmental hypotheses complement each other, with seasonality and energy explaining gradients of broadly distributed species, while heterogeneity is the most important predictor of gradients of species with small distributions.

Spatial structure and determinants of species richness patterns

Moran's I correlograms indicated that variation in species richness is strongly spatially structured (Fig. 4). The importance of spatial autocorrelation in ecology has been increasingly recognized and discussed in recent years (Beale et al. 2007, Dormann et al. 2007). However, most of this work has focused on addressing statistical consequences of spatial structure in regression residuals, and has provided relatively little insight into what ecological and evolutionary forces give rise to this autocorrelation and shape the overall spatial pattern in species richness. Spatial autocorrelation in species richness can arise either by intrinsic or extrinsic forces (Legendre and Legendre 1998, Currie 2007b). Intrinsic force is the spatially contagious processes of species movement (dispersal or migration). External forces causing spatial autocorrelation are variables 1) that are themselves spatially autocorrelated, and 2) that can influence species richness. External forces can be biological (e.g. competition or predation gradients), or abiotic (e.g. salinity or pH gradients). Our analyses indicate that external environmental characteristics can account for a large proportion of spatially structured variation in richness, but this effect is mostly restricted to the richness gradient of broadly distributed species.

A significant amount of autocorrelation remains in the unexplained variation (Fig. 3, 4 and 5). The spatially structured variation that cannot be accounted for by environmental predictors is variable among species groups, but in all cases the positive autocorrelation at short distances can result from estimating species richness by range map overlaps. This occurs because range maps commonly do not account for patterns of species occupancy within species distributions, and consequently generate stronger spatial autocorrelation in estimates of richness than other methods (McPherson and Jetz 2007). Another possible explanation for this unexplained similarity among nearby cells might be mass-effects, which are produced by species dispersal that is not controlled by environmental factors. Mass-effects can cause sites that are close together to share more species than would be expected by their environmental characteristics (Shmida and Wilson 1985). This process has been suggested to be a likely mechanism contributing to patterns of spatial distribution of bats at intermediate geographic scales (Stevens et al. 2007), and has also been shown to be potentially important for a number of other systems (Cottenie 2005). For small-ranged species, correlograms of residuals show little or no reduction in levels of autocorrelation at any geographic distances. This suggests that autocorrelation in richness gradients of these species cannot be simply accounted for by environmental variables; other processes, not included in our analyses, must be responsible for the spatial structure in richness of these species.

Conclusions

Our analyses have shown that environmental hypotheses can account for the vast majority of variation in species richness of all bats in the New World. There is very little spatially structured variation in this richness gradient that is not accounted for by environmental variables. Some positive spatial autocorrelation remains at short distances which may be associated with spatial processes, like mass-effects. Energy and seasonality are the environmental hypotheses that account for the most variation in species richness of all species; although highly redundant, these two hypotheses also have significant portions of unique variation which suggests they have complementary independent effects. For the all-species gradient and the gradients of large-ranged species, the effect of heterogeneity can not be disentangled from those of the other hypotheses, and the variation it explains is redundant with variation explained by energy and seasonality.

Range size has an important effect on interpretation of environmental correlates of richness gradients. As size of species distributions decreases, so does the explanatory power of environmental characteristics. Moreover, heterogeneity is the only environmental hypothesis that remains as a moderately good explanation to richness gradients of species with the most restricted distributions. This suggests that heterogeneity is complementary to energy and seasonality along this geographic range size dimension. The idea that measures of energy, climate and productivity are the strongest correlates of richness (Field et al. 2009) might be produced by studies that have used all-species gradients and consequently have relied disproportionately on the contribution of species with broad distributions (Sizling et al. 2009). Other processes, like habitat heterogeneity, might be required to explain richness patterns of species with restricted distributions (Jetz and Rahbek 2002). This and other studies have shown that determinants of species richness might be complex, and place into question the idea that there are only a few primary mechanisms (if not a single mechanism) responsible for species richness gradients.

References

Allen, A. P. et al. 2007. Recasting the species–energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. – In: Storch, D. et al. (eds), Scaling biodiversity. Cambridge Univ. Press, pp. 283–299.

Arita, H. T. and Rodriguez-Tapia, G. 2009. Contribution of restricted and widespread species to diversity: the effect of range cohesion. – Ecography 32: 210–214.

Badgley, C. and Fox, D. L. 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. – J. Biogeogr. 27: 1437–1467.

Beale, C. M. et al. 2007. Red herrings remain in geographical ecology: a reply to Hawkins et al. (2007). – Ecography 30: 845–847.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGis. – <www.spatialecology.com/htools>.

Borcard, D. et al. 1992. Partialling out the spatial component of ecological variation. – Ecology 73: 1045–1055.

Brown, J. and Liemberma, G. 1973. Resource utilization and coexistence of seed eating desert rodents in sand dune habitats. – Ecology 54: 788–797.

Brown, J. and Ernest, S. 2002. Rain and rodents: complex dynamics of desert consumers. – Bioscience 52: 979–987.

Brown, J. H. and Sax, D. F. 2004. Gradients in species diversity: why are there so many species in the Tropics? – In: Lomolino, M. V. et al. (eds), Foundations of biogeography. Univ. of Chicago Press, pp. 1145–1154.

Cabrero-Sanudo, F. J. and Lobo, J. M. 2006. Determinant variables of Iberian peninsula Aphodiinae diversity (Coleoptera, Scarabaeoidea, Aphodiidae). – J. Biogeogr. 33: 1021–1043.

Chernick, M. R. 2008. Bootstrap methods. A guide for practitioners and researchers. – Wiley-Interscience.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics. – Ecol. Lett. 8: 1175–1182.

Currie, D. J. 1991. Energy and large-scale patterns of animal-species and plant-species richness. – Am. Nat. 137: 27–49.

Currie, D. J. 2007a. Regional-to-global patterns of biodiversity, and what they have to say about mechanisms. – In: Storch, D. et al. (eds), Scaling biodiversity. Cambridge Univ. Press, pp. 258–282.

Currie, D. J. 2007b. Disentangling the roles of environment and space in ecology. – J. Biogeogr. 34: 2009–2011.

Currie, D. J. and Kerr, J. T. 2008. Tests of the mid-domain hypothesis: a review of the evidence. – Ecol. Monogr. 78: 3–18.

Currie, D. J. et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. – Ecol. Lett. 7: 1121–1134.

Davies, R. G. et al. 2007. Topography, energy and the global distribution of bird species richness. – Proc. R. Soc. B 274: 1189–1197.

Diniz-Filho, J. A. et al. 2004. A test of multiple hypotheses for the species richness gradient of South American owls. – Oecologia 140: 633–638.

Dormann, C. F. et al. 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. – Ecography 30: 609–628.

Evans, K. L. et al. 2005a. Relative contribution of abundant and rare species to species–energy relationships. – Biol. Lett. 1: 87–90.

Evans, K. L. et al. 2005b. Species–energy relationships at the macroecological scale: a review of the mechanisms. – Biol. Rev. 80: 1–25.

Evans, K. L. et al. 2006. Species traits and the form of individual species–energy relationships. – Proc. R. Soc. B 273: 1779–1787.

Field, R. et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. – J. Biogeogr. 36: 132–147.

Fortin, M. J. and Dale, M. R. T. 2005. Spatial analysis: a guide for ecologists. – Cambridge Univ. Press.

Francis, A. P. and Currie, D. J. 1998. Global patterns of tree species richness in moist forests: another look. – Oikos 81: 598–602.

Fu, C. Z. et al. 2006. Elevational patterns of frog species richness and endemic richness in the Hengduan mountains, China: geometric constraints, area and climate effects. – Ecography 29: 919–927.

Hawkins, B. A. et al. 2003a. Energy, water, and broad-scale geographic patterns of species richness. – Ecology 84: 3105–3117.

Hawkins, B. A. et al. 2003b. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. – Ecology 84: 1608–1623.

Hawkins, B. A. et al. 2007a. Red herrings revisited: spatial autocorrelation and parameter estimation in geographical ecology. – Ecography 30: 375–384.

Hawkins, B. A. et al. 2007b. Climate, niche conservatism, and the global bird diversity gradient. – Am. Nat. 170: S16–S27.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – Int. J. Climatol. 25: 1965–1978.

Hortal, J. et al. 2008. Regional and environmental effects on the species richness of mammal assemblages. – J. Biogeogr. 35: 1202–1214.

Hurlbert, A. H. and Haskell, J. P. 2003. The effect of energy and seasonality on avian species richness and community composition. – Am. Nat. 161: 83–97.

Hurlbert, A. H. and White, E. P. 2005. Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. – Ecol. Lett. 8: 319–327.

Imhoff, M. L. et al. 2004. Global patterns in human consumption of net primary production. – Nature 429: 870–873.

Jablonski, D. et al. 2006. Out of the Tropics: evolutionary dynamics of the latitudinal diversity gradient. – Science 314: 102–106.

Jetz, W. and Rahbek, C. 2002. Geographic range size and determinants of avian species richness. – Science 297: 1548–1551.

Jetz, W. et al. 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. – Ecol. Lett. 7: 1180–1191.

Kalmar, A. and Currie, D. J. 2007. A unified model of avian species richness on islands and continents. – Ecology 88: 1309–1321.

Kay, R. F. et al. 1997. Primate species richness is determined by plant productivity: implications for conservation. – Proc. Nat. Acad. Sci. USA 94: 13023–13027.

Kerr, J. T. and Packer, L. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. – Nature 385: 252–254.

Kreft, H. and Jetz, W. 2007. Global patterns and determinants of vascular plant diversity. – Proc. Nat. Acad. Sci. USA 104: 5925–5930.

Kreft, H. et al. 2006. The significance of geographic range size for spatial diversity patterns in Neotropical palms. – Ecography 29: 21–30.

Kreft, H. et al. 2008. Global diversity of island floras from a macroecological perspective. – Ecol. Lett. 11: 116–127.

Legendre, P. 1993. Spatial autocorrelation – trouble or new paradigm. – Ecology 74: 1659–1673.

Legendre, P. and Legendre, L. 1998. Numerical ecology. – Elsevier.

Lennon, J. J. et al. 2004. Contribution of rarity and commonness to patterns of species richness. – Ecol. Lett. 7: 81–87.

Lima, M. et al. 2008. Chihuahuan desert kangaroo rats: nonlinear effects of population dynamics, competition, and rainfall. – Ecology 89: 2594–2603.

Lobo, J. et al. 2004. Modelling the species richness distribution for French Aphodiidae (Coleoptera, Scarabaeoidea). – Ecography 27: 145–156.

Lyons, S. K. and Willig, M. R. 2002. Species richness, latitude, and scale-sensitivity. – Ecology 83: 47–58.

MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. – Am. Nat. 98: 387–397.

MacArthur, R. H. 1972. Geographical ecology: patterns in the distribution of species. – Princeton Univ. Press.

McPherson, J. M. and Jetz, W. 2007. Type and spatial structure of distribution data and the perceived determinants of geographical gradients in ecology: the species richness of African birds. – Global Ecol. Biogeogr. 16: 657–667.

Mittelbach, G. G. et al. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. – Ecol. Lett. 10: 315–331.

Patten, M. A. 2004. Correlates of species richness in North American bat families. – J. Biogeogr. 31: 975–985.

Patterson, B. D. et al. 2005. Digital distribution maps of the mammals of the western hemisphere, ver. 2.0. – <www.natureserve.org/getData/animalData.jsp>.

Peres-Neto, P. R. et al. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. – Ecology 87: 2614–2625.

Pianka, E. R. 1966. Latitudinal gradients in species diversity – a review of concepts. – Am. Nat. 100: 33–46.

Qian, H. 2008. Effects of historical and contemporary factors on global patterns in avian species richness. – J. Biogeogr. 35: 1362–1373.

Rahbek, C. and Graves, G. R. 2001. Multiscale assessment of patterns of avian species richness. – Proc. Nat. Acad. Sci. USA 98: 4534–4539.

Rahbek, C. et al. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. – Proc. R. Soc. B 274: 165–174.

Rohde, K. 1992. Latitudinal gradients in species-diversity – the search for the primary cause. – Oikos 65: 514–527.

Ruggiero, A. and Kitzberger, T. 2004. Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. – Ecography 27: 401–416.

Shmida, A. and Wilson, M. V. 1985. Biological determinants of species-diversity. – J. Biogeogr. 12: 1–20.

Simpson, G. G. 1964. Species density of North American recent mammals. – Syst. Zool. 13: 57–73.

Sizling, A. et al. 2009. Rarity, commonness, and the contribution of individual species to species richness patterns. – Am. Nat. 174: 82–93.

Stevens, R. D. 2006. Historical processes enhance patterns of diversity along latitudinal gradients. – Proc. R. Soc. B 273: 2283–2289.

Stevens, R. D. et al. 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. – Ecol. Lett. 6: 1099–1108.

Stevens, R. D. et al. 2006. Latitudinal gradients in the phenetic diversity of New World bat communities. – Oikos 112: 41–50.

Stevens, R. D. et al. 2007. Geographical ecology of Paraguayan bats: spatial integration and metacommunity structure of interacting assemblages. – J. Anim. Ecol. 76: 1086–1093.

Storch, D. et al. 2006. Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity. – Ecol. Lett. 9: 1308–1320.

Terribile, L. C. et al. 2009. Richness patterns, species distributions and the principle of extreme deconstruction. – Global Ecol. Biogeogr. 18: 123–136.

Tilman, D. et al. 1993. The maintenance of species richness in plant communities. – In: Ricklefs, R. E. and Schluter, D. (eds), Species diversity in ecological communities. Univ. Chicago Press, pp. 13–25.

Tognelli, M. F. and Kelt, D. A. 2004. Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. – Ecography 27: 427–436.

Ulrich, W. et al. 2007. Environmental correlates of species richness of European bats (Mammalia: Chiroptera). – Acta Chiropterol. 9: 347–360.

van Rensburg, B. J. et al. 2002. Species richness, environmental correlates, and spatial scale: a test using South African birds. – Am. Nat. 159: 566–577.

Vazquez, L. B. and Gaston, K. J. 2004. Rarity, commonness, and patterns of species richness: the mammals of Mexico. – Global Ecol. Biogeogr. 13: 535–542.

Wiens, J. J. et al. 2007. Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. – Proc. R. Soc. B 274: 919–928.

Willig, M. R. and Bloch, C. P. 2006. Latitudinal gradients of species richness: a test of the geographic area hypothesis at two ecological scales. – Oikos 112: 163–173.

Willig, M. R. and Lyons, S. K. 1998. An analytical model of latitudinal gradients of species richness with an empirical test for marsupials and bats in the New World. – Oikos 81: 93–98.

Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. – Annu. Rev. Ecol. Evol. Syst. 34: 273–309.

Download the Supplementary material as file E5991 from <www.oikos.ekol.lu.se/appendix>.