



Ecological biogeography of Mexican bats: the relative contributions of habitat heterogeneity, beta diversity, and environmental gradients to species richness and composition patterns

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Mexico has higher mammalian diversity than expected for its size and geographic position. High environmental heterogeneity throughout Mexico is hypothesized to promote high turnover rates (β -diversity), thus contributing more to observed species richness and composition than within-habitat (α) diversity. This is true if species are strongly associated with their environments, such that changes in environmental attributes will result in changes in species composition. Also, greater heterogeneity in an area will result in greater species richness. This hypothesis has been deemed false for bats, as their ability to fly would reduce opportunities for habitat specialization. If so, we would expect no significant relationships between 1) species composition and environmental variables, 2) species richness and environmental heterogeneity, 3) β -diversity and environmental heterogeneity. We tested these predictions using 31 bat assemblages distributed across Mexico. Using variance partitioning we evaluated the relative contribution of vegetation, climate, elevation, horizontal heterogeneity (a variate including vegetation, climate, and elevational heterogeneity), spatial variation (lat-long), and vertical heterogeneity (of vegetation strata) to variation in bat species composition and richness. Variation in vegetation explained 92% of the variation in species composition and was correlated with all other variables examined, indicating that bats respond directly to habitat composition and structure. Beta-diversity and vegetational heterogeneity were significantly correlated. Bat species richness was significantly correlated with vertical, but not horizontal, heterogeneity. Nonetheless, neither horizontal nor vertical heterogeneity were random; both were related to latitude and to elevation. Variation in bat community composition and richness in Mexico were primarily explained by local landscape heterogeneity and environmental factors. Significant relationships between β -diversity and environmental variation reveal differences in habitat specialization by bats, and explain their high diversity in Mexico. Understanding mechanisms acting along environmental or geographic gradients is as important for understanding spatial variation in community composition as studying mechanisms that operate at local scales.

One of the most universal features of natural systems is spatial variation in species richness. Several hypotheses have been proposed to explain these patterns, from latitudinal gradients (Rohde 1992, Gotelli et al. 2009, Qian et al. 2009) to local patterns of variation (Palmer 1994). Despite a large array of available hypotheses, the relative importance of mechanisms responsible for spatial variation in species richness remains poorly understood and is the focus of debate in ecology and biogeography (Pianka 1966, Rosenzweig 1995, Willig and Lyons 1998, Gaston 2000, Gotelli et al. 2009). Indeed, the question ‘What determines species diversity?’ is considered to be one of the 25 most important scientific questions to answer before 2030 (Pennisi 2005). One hypothesis frequently invoked to explain regional patterns of species richness focuses on habitat heterogeneity (Simpson

1964, Currie 1991, Tognelli and Kelt 2004, Rodríguez et al. 2005). This hypothesis is based on the premise that spatial variation in environmental conditions provides greater niche diversity and facilitates coexistence, all of which results in greater species richness. Habitat heterogeneity generally is estimated based on topographic variability, number of ecosystems present in a given area, or both (Currie 1991, Kerr and Packer 1997, Rahbek and Graves 2000, Kerr et al. 2001, Tognelli and Kelt 2004).

Mexico is one of the most species-rich countries in the world for both flora and fauna. For mammals, Mexico has the third greatest species richness of any country (525 species), surpassed only by that of Indonesia and Brazil (Ceballos et al. 2005). Patterns of mammalian species richness in Mexico have been attributed to its size and

geographic position, encompassing a mixture of Neotropical and Nearctic elements (Ortega and Arita 1998, Morrone 2005 and references therein). However, it has been noted that in apparent contradiction, individual localities in Mexico do not support exceptionally rich assemblages of mammals compared to other sites in the Neotropics (Arita 1997, Rodríguez et al. 2003), and that area and geographic position are insufficient to explain the high species richness of mammals in Mexico. Instead, it has been proposed that spatial variation in species composition (β -diversity) associated with regional environmental heterogeneity contributes more to the observed mammalian diversity (γ -diversity) of Mexico than does local, within-habitat or α -diversity (Arita 1997, Arita and Rodríguez 2002, Rodríguez et al. 2003, Rodríguez and Arita 2004, Halffter and Moreno 2005). Thus, great habitat diversity in a landscape and close associations of mammal species to particular sets of environmental conditions will result in high β -diversity (turnover), even though local α -diversity is not particularly high. This hypothesis predicts a significant positive relationship between environmental heterogeneity and β -diversity, as well as a significant relationship between β -diversity and γ -diversity, but no relationship between α -diversity and β -diversity (Arita 1997, Hubbell 2001, Rodríguez et al. 2003). These relationships did not hold true for bats, a species-rich group of mammals in Mexico (137 species – Ceballos et al. 2005).

Presumably, because of their ability to fly, geographic barriers and habitat variation that limit dispersal of non-volant mammals are less restrictive for bats (i.e. they would be able to overcome at least some topographic barriers). Such mobility potentially provides dispersal potential and reduces their dependence on particular habitats or environmental characteristics (Willig and Moulton 1989). Furthermore, it has been proposed that bat distributional ranges are determined primarily by continental-wide climatic patterns, and not by regional or local conditions (Arita 1997, Rodríguez et al. 2003, Rodríguez and Arita 2004, Koleff et al. 2008). Another fundamental difference between volant and non-volant mammals in Mexico is that the former have a significant relationship between species richness (α -diversity) and latitude. At large scales, latitude and its correlates (e.g. precipitation, temperature, solar insolation, productivity) have been proposed as important factors to explain the high species richness of Mexican bats, whereas regional habitat variation and associated β -diversity are invoked to explain the high richness of non-volant species (Arita 1997, Rodríguez et al. 2003).

Nonetheless, bats may respond strongly to spatial environmental variation, and potential vagility of species does not necessarily reduce the importance of the environment on distribution and abundance of bats (López-González 2004, Stevens et al. 2007, Frick et al. 2008, López-González et al. 2012). Because environmental heterogeneity and associated potential β -diversity have been considered to be less important for bats (Rodríguez and Arita 2004), the relative contribution of these factors to regional bat species richness (γ -diversity) in Mexico has not been quantified.

We analyzed 31 bat assemblages distributed across Mexico (Fig. 1) to evaluate the relative contributions of two suites of environmental characteristics (vegetation and climate), one physiographic attribute (elevation), environmental

heterogeneity, geographic variation, and vertical complexity, to variation in bat species richness and composition across Mexico. If local environments are relatively unimportant determinants of spatial patterns of bat diversity in Mexico, then variation in species richness and composition can be explained by the dispersal capabilities of species (barring inter- and intraspecific relationships). In such a case one would expect to find: 1) no significant relationship between species composition and environmental variables. This hypothesis was recently tested and rejected (López-González et al. 2012) based on vegetation data. In the present study we include two factors, topography and climate, to capture additional environmental variation; 2) no significant relationship between species richness and environmental heterogeneity. Multiple aspects of environmental heterogeneity may affect bat community composition and richness, via spatial variation that occurs horizontally across the landscape and via variation in vertical complexity of the habitat (Kalko et al. 1996, Kalko and Handley 2001); thus, we used variables that account for each of these aspects of environmental variation to test this hypothesis; 3) no significant relationship between β -diversity (turnover) and environmental heterogeneity. Turnover in species composition can result from a variety of factors, but turnover associated with habitat heterogeneity occurs only when species are specialists with restrictive home ranges.

Material and methods

Species data

The bat species dataset consisted of a site-by-species (31 sites \times 128 species) incidence matrix that included 93.4% of the 137 species of bats known from Mexico. Data were collected from published and unpublished bat surveys across Mexico (Fig. 1, Table 1) that combined covered the country as homogeneously as possible. A detailed description of how sites were selected is given in López-González et al. (2012). For each site, we defined a central point that was estimated from maps presented in each published account. From this point, a circular buffer of 25 km radius was defined and all bat records within this circle were pooled to represent the local assemblage from a site. The actual inventories cover areas that can be much smaller than the 1963.5 km² that the circle covers, but because some bats can travel long distances (over 50 km) in one night in search for resources, change roosts throughout the year, or have local, seasonal migrations (Pierson 1998, Best and Geluso 2003), we delimited an area that covered most vegetative resources that a bat could use during its lifetime.

Environmental data

We generated a 31 \times 28 site-by-vegetation matrix by estimating for each site (i.e. each 25 km-radius buffer delimited to build the species matrix) the percent area covered by each of 28 vegetation types (for details see López-González et al. 2012). Percent coverage was calculated from the digital version of INEGI 1:250 000 and vegetation maps



Figure 1. An outline of the Mexican physical geography and study sites. Points represent the center of 25-km-radius circles where bat species and environmental variables were sampled. Numbers refer to sites in Table 1.

scaled to 1:1 000 000 from the geographic information system of BIOTICA 5.0 (CONABIO 1999, 2008). Similarly, a 31×39 site-by-climate matrix (percent area covered by each category) was created from INEGI 1:250 000 digital climate maps provided in BIOTICA (Supplementary material Appendix 1). A 31×35 site-by-elevation matrix was built from digital elevation models (scale 1:50 000 – INEGI 2003) by estimating within each 25 km-radius buffer the percent area covered by the area between 100 m-contours (0–100, 100–200 m and so forth), from 0 to 3500 m a.s.l. Elevations higher than 3500 m were only recorded at site 16, so these data were not included to avoid collinearity in the analyses. Processing of data was performed in ArcView GIS 3.2 (ESRI 1996) and Idrisi Kilimanjaro ver. 14.01 (Clark Labs 2003).

Data analysis

Structural attributes

Three physical attributes of the landscape were examined: geographic position of sites (latitude and longitude); spatial heterogeneity of vegetation and climate at each site (= horizontal heterogeneity, H_h); and vertical heterogeneity of vegetation (H_v) at each site. Geographic position was

represented by a 31×2 sites-by-coordinates matrix of latitude and longitude (in decimal degrees) taken at the center of each site. Horizontal heterogeneity was calculated from vegetation, climate, and elevation data. For each metric, the Shannon–Wiener index ($H = -\sum p_x \ln p_x$) was calculated as a measure of heterogeneity, where p_x is the proportion of the total area of each buffer (25 km radius = 1963.5 km²) covered by environmental feature x using 28 categories for vegetation, 39 for climate, and 35 for elevation. The Shannon–Wiener index summarizes the number of different objects in a system and the proportion in which they occur. It is a measure of the entropy or lack of regularity of a system (sensu Gell-Mann and Lloyd 1996). Unlike the Jost (2006) modification to the Shannon–Weiner index, this is not a measure of species diversity, but a measure of environmental heterogeneity (Jonsen and Fahrig 1997, Concepción et al. 2008, Sattler et al. 2010). Because heterogeneity values for vegetation, climate, and elevation variables (H_{veg} , H_{clim} , H_{elev}) were highly correlated, i.e. they have a high degree of overlap (Fig. 2) we summarized them via principal component analysis. The first principal component accounted for 67% of the total variation, and was used to represent horizontal heterogeneity (H_h); thus H_h summarizes the horizontal heterogeneity based on a single index (31×1 vector of principal component scores).

Table 1. Geographic position of each of 31 Mexican bat communities examined in this study. Coordinates are those of the center point.

Site	Site name	Center	Source
1	Janos-Casas Grandes, Chihuahua	30.888°N, -108.190°W	Pacheco et al. (2001)
2	Valle de los Cirios and Vizcaíno Reserve, Baja California	28.028°N, -113.399°W	Álvarez-Castañeda et al. (2008a)
3	Sierra Tarahumara, Chihuahua	27.025°N, -107.532°W	López-González and García-Mendoza (2006)
4	'La Laguna' region, Coahuila-Durango	25.544°N, -103.442°W	López-González and Rascón-Escajeda unpubl.
5	Huajuco Canyon, Nuevo León	25.465°N, -100.214°W	Moreno-Valdez (1998)
6	NW Durango	25.352°N, -106.045°W	Torres-Morales et al. (2010)
7	San Josecito, Nuevo León	24.020°N, -99.739°W	Zepeda González (2003)
8	El Cielo Reserve, Tamaulipas	23.318°N, -99.024°W	Monteagudo Sabaté and León Paniagua (2002)
9	Sierra Madre Oriental (Tamaulipas)	22.929°N, -99.026°W	León-Paniagua et al. (2004)
10	Aguascalientes State	21.879°N, -102.300°W	Álvarez-Castañeda et al. (2008b)
11	Sierra Gorda, Querétaro	21.182°N, -99.320°W	Monteagudo Sabaté and León Paniagua (2002)
12	Sierra de Pinal de Amoles, Querétaro	21.134°N, -99.625°W	Navarro and Leon-Paniagua (1995)
13	Tarascan Plateau, Michoacán	19.641°N, -102.047°W	Orduña Trejo et al. (2000)
14	Sierra de Manantlán, Jalisco	19.618°N, -104.203°W	Iñiguez Davalos (1993)
15	Chamela, Jalisco	19.527°N, -105.073°W	Ceballos and Miranda (1986)
16	Mexico City Basin	19.350°N, -99.162°W	Ceballos González and Galindo Leal (1984)
17	Jalcomulco, Veracruz	19.335°N, -96.758°W	Moreno Ortega (2000)
18	Morelos	18.761°N, -99.121°W	Alvarez-Castañeda (1996)
19	Los Tuxtlas Reserve, Veracruz	18.605°N, -95.139°W	Estrada et al. (1993)
20	Xbonil, Campeche	18.635°N, -90.166°W	Galindo-González (2004)
21	Sierra de Santa Marta, Veracruz	18.232°N, -94.873°W	Hernández-Huerta et al. (2000), Escalona-Segura et al. (2002), Vargas-Contreras (2004), Vargas-Contreras et al. (2005, 2008)
22	Michoacán coast	18.135°N, -102.885°W	González Christen (2008)
23	Sierra Mazateca, Oaxaca	18.130°N, -96.843°W	Polaco and Muñoz-Martínez (1987)
24	Tehuacán-Cuicatlán Reserve, Puebla and Oaxaca	17.956°N, -97.024°W	Briones-Salas et al. (2005)
25	Sierra de Juárez, Oaxaca	17.956°N, -97.024°W	N. González-Ruiz pers. comm.
26	Sierra de Atoyac, Guerrero	17.473°N, -100.369°W	Monteagudo Sabaté and León Paniagua (2002)
27	Los Chimalapas Reserve, Oaxaca	16.906°N, -94.683°W	Monteagudo Sabaté and León Paniagua (2002)
28	Yaxchilán, Chiapas	16.901°N, -90.969°W	Olguín Monroy et al. (2008), García-García and Santos-Moreno (2008)
29	La Sepultura Reserve, Chiapas	16.236°N, -93.702°W	Escobedo Morales et al. (2001)
30	El Triunfo Biosphere Reserve, Chiapas	16.202°N, -91.860°W	Monteagudo Sabaté and León Paniagua (2002)
31	Montes Azules Biosphere Reserve, Chiapas	16.118°N, -90.924°W	Espinoza Medinilla et al. (1998)
			Medellin (1993)



Figure 2. Variance partition of the total variation in bat species composition across 31 sites in Mexico accounted for by the environmental (vegetation, climate, elevation) and structural (horizontal heterogeneity H_h , vertical heterogeneity H_v , latitude and longitude) variables examined. The area of the figure represents the total variation in bat species composition as estimated from a CCA (total inertia = 2.69). Variation in bat species composition accounted for by elevation (1.757, 65% of the total variation), vegetation (2.476, 92.1%), climate (0.531, 19.8%), and structure (0.839, 31.2%) are represented by a different combination of color, fill color, and fill pattern. Proportions do not add to 2.69 or 100% because none of the variables examined was completely independent from the others (i.e. there were no 'pure effects'). Areas defined by multiple line colors or fill colors and patterns represent shared variance components.

We estimated vertical heterogeneity of habitats (H_v) by estimating the number of vertical strata that occur in each vegetation type as described by Rzedowski (2006). We assigned a number of strata (combinations of 4 possible tree strata, 2 shrub strata, 2 herbaceous strata, 1 moss-lichen-liverwort stratum) to each of the 28 vegetation types. For each vegetation type we calculated the number of vegetation strata. At any given site, the mean of the number of strata per vegetation type present represented vertical habitat heterogeneity (H_v). A vector of one mean per each of 31 sites was constructed with these data.

Variance partitioning

To determine the total variation in bat species composition accounted for by environmental variables, we conducted a variance decomposition analysis in which bat species composition was the dependent matrix, and geographic and environmental matrices (vegetation, climate, elevation, geographic position, horizontal habitat heterogeneity, and vertical habitat heterogeneity) were treated as independent matrices and covariates. To determine pure effects each of these matrices was used as an independent matrix, and all remaining matrices, one by one, were used as covariates. For each of these combinations, variation due to each effect and their interactions were estimated. Because at large scales the relationship between presence or abundance of a species and gradients of environmental variation is not linear but Gaussian, i.e. there is a value of the environmental variable at which species abundance peaks or the likelihood of it being present is highest (Ter Braak and Prentice 1988, Ter Braak and Šmilauer 2002), variance partitioning was performed via canonical correspondence analysis (CCA) using CANOCO for Windows ver. 4.56.

Species richness and environmental heterogeneity

Horizontal (H_h) and vertical (H_v) heterogeneity provided independent measures of landscape variation (Spearman rank correlation $r = -0.0457$, $p = 0.8072$), and therefore were analyzed separately. Relationships between species richness and H_h and H_v were tested using Spearman's rank correlation as well.

Species turnover and environmental heterogeneity

As proposed above, if bats are strongly associated with particular habitats in heterogeneous landscapes, changes in habitat characteristics should result in changes in species composition. The result will be a significant, positive correlation between environmental heterogeneity and β -diversity (Arita 1997, Rodríguez et al. 2003, Rodríguez and Arita 2004, Koleff et al. 2008). In a homogeneous landscape, all sites would represent the same habitat, resulting in no environmental variation to which species may respond. As the landscape becomes more heterogeneous, sites would become more different from one another in their attributes. To capture these differences, we used a multivariate measure of horizontal heterogeneity for the complete region under study (Mexico) by creating a matrix of the degree of association (or differences) in environmental factors (e.g. vegetation composition) between all possible pairs of sites. In a homogeneous landscape, the result would be a symmetrical matrix of size 31×31 filled with ones. Pair-wise associations

would decrease as heterogeneity increases, i.e., sites with no elements in common would be represented by values of zero. A suitable test for the relationship between β -diversity and heterogeneity would be one that measured the degree of association between a 31×31 bat β -diversity matrix (generated using an index of similarity or distance) and a heterogeneity matrix of the same size. For this comparison we used a Mantel test to evaluate the hypothesis of no relationship between bat β -diversity (turnover) and horizontal vegetation heterogeneity (Manly 2005). This test was performed only for vegetation because this variable explained 92% of the total variation in bat species composition (see Results). We calculated β for all possible pairs of sites using the complement of the Jaccard index ($1 - J$, Tuomisto 2010a, Anderson et al. 2011). This index is useful when the goal is to examine how the β component varies and which external factors are correlated with such variation (Tuomisto 2010b). Although this number does not represent 'true beta diversity' sensu Tuomisto (2010b), it is a linear transformation of 'true beta diversity' (γ/α), and therefore it yields results that are consistent with it (Tuomisto 2010b).

Analogously, we calculated the Spearman's rank correlation in vegetational composition between all possible pairs of sites to create a 31×31 matrix of vegetation heterogeneity. Because β -diversity and similarity in vegetational composition may be spatially structured (i.e. have a significant spatial component), prior to evaluating the relationship between vegetational heterogeneity and species turnover we performed a linear regression between β -diversity values and pair-wise geographic distances, and between similarity in vegetational composition and pair-wise geographic distances, and calculated residuals for each of these two datasets. After accounting for spatial structure in vegetation data, residuals were used to perform the Mantel test. With the exception of variance partitioning, all analyses were performed in Matlab for windows ver. 7.10.0.499, R2010a (The Mathworks) using functions written by R. E. Strauss (available at <www.faculty.biol.ttu.edu/strauss/matlab/matlab.htm>) and C. L. Higgins (available at <<http://faculty.tarleton.edu/higgins/metacommunity-structure.html>>), as well as functions and scripts written by C. López-González.

Results

Variance partitioning

Vegetation explained most of the variation (92.1%) in bat species richness for the 31 sites examined (total inertia of bat presence-absence matrix = 2.690, variance explained by vegetation = 2.476, $F = 1.30$, $p = 0.04$, Fig. 2). Most of the variation in bat species composition that was accounted for by climate represented a shared variation component with vegetation ($0.226 + 0.094 = 0.320$ out of 0.531 or 60%). Similarly, 87.9% of the variation in bat species composition accounted for by elevation represented a shared variation component with vegetation ($1.320 + 0.226$ out of 1.757).

The small fraction of the variation accounted for by climate or elevation that does not represent a shared variation component with vegetation (0.211 or 7.9%) represents a shared component for elevation and climate, indicating

that there are no 'pure' climatic or elevational effects on variation in bat species composition. Similarly, all variation in bat species composition due to structural effects (31.2% of the total variation in bat species composition) is accounted for by vegetational variation (Fig. 2). This variation includes the effects related to spatial structure of the landscape: geographic position (lat-long), vertical heterogeneity (H_v), and horizontal heterogeneity (H_h). When we dissected this into its component elements, the greatest contribution to the spatial and vertical variation component was geographic location (lat-long), which explained 22.44% (0.603/2.690, Fig. 3) of the total variance in species composition. Geographic location was not independent of vertical heterogeneity, as 31% (0.140 + 0.046 = 0.186/0.603) of the variation in lat-long was accounted for by H_v (Fig. 3). In contrast, geographic location accounted for only 7.6% (0.046/0.603) of the variation in horizontal heterogeneity (Fig. 3). Heterogeneity in vegetation (horizontal and vertical) not including lat-long, accounted for 8.8% (0.085 + 0.151 = 0.236/2.690) of the total variation in bat species composition (Fig. 3).

Species richness and environmental heterogeneity

The relationship between bat species richness and aspects of horizontal heterogeneity represented by variation in vegetation, climate, and topography combined (H_h) was complex. The linear relationship between richness and H_h was non-significant ($r = -0.029$, $p = 0.880$). However, the arrangement of sites with respect to environmental heterogeneity was not random (Fig. 4). On the x-axis sites followed a latitudinal gradient, with species richness increasing with decreasing latitude. Sites with negative values on the y-axis were environmentally homogeneous, exhibiting little elevational, climatic or vegetational variation, whereas sites with positive scores had greater topographic variation (montane sites). Thus, there is a clear pattern of variation in bat species richness with respect to heterogeneity across Mexico that followed elevational and latitudinal gradients. In contrast, the relationship between species richness and habitat vertical heterogeneity was significant ($r = 0.48$, $p = 0.0064$) and linear (Fig. 5).

Species turnover and landscape heterogeneity

The Mantel test of the relationship between bat species turnover (Jaccard's index) and environmental turnover (vegetation rank correlations) was positive and significant ($r = 0.313$, $Z = 8.44$, $p = 0.001$).

Discussion

In general, effects of spatial environmental variation and associated β -diversity on mammalian species richness and composition throughout Mexico have been considered important for non-volant mammals but unimportant for bats (Arita and Rodríguez 2002, Rodríguez et al. 2003, Rodríguez and Arita 2004). This hypothesis leads to testable predictions about the relationships between bat species richness, turnover among bat communities, and spatial environmental variation. We tested three of these predictions; results strongly support the idea that bat species richness and composition is strongly contingent on environmental composition and variation.

Prediction 1: spatial variation in topography, vegetation, and climate should explain little variation in bat species composition

Contrary to expectation, variation in vegetation explained most of the spatial variation in bat species composition, indicating that bats respond directly to composition and structure of their habitat. In addition, most of the variation in bat species composition explained by variation in climate, elevation and environmental heterogeneity represented variation components shared with vegetation (Fig. 2, 3), because spatial variation in local plant assemblages is primarily a function of variation in local climate and topography. Bat species composition in Mexico is strongly contingent on vegetational attributes, and the Mexican bat metacommunity is strongly structured by spatial variation in environmental factors (López-González et al. 2012).

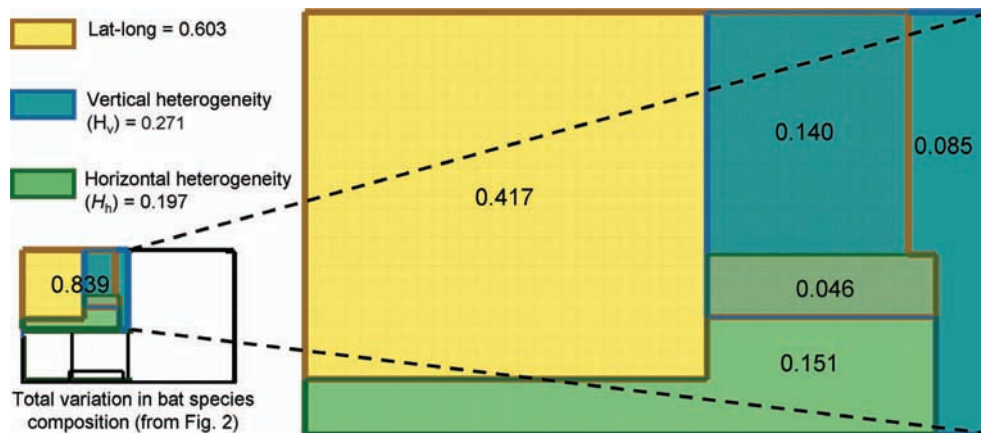


Figure 3. Variance partition of the total variation in bat species composition across 31 sites in Mexico accounted for by structure (horizontal heterogeneity H_h , vertical heterogeneity H_v , latitude and longitude). As with Fig. 2, areas defined by more than one line or fill color or pattern represent shared variance components. This figure represents the variance partition of the purple area on Fig. 2.

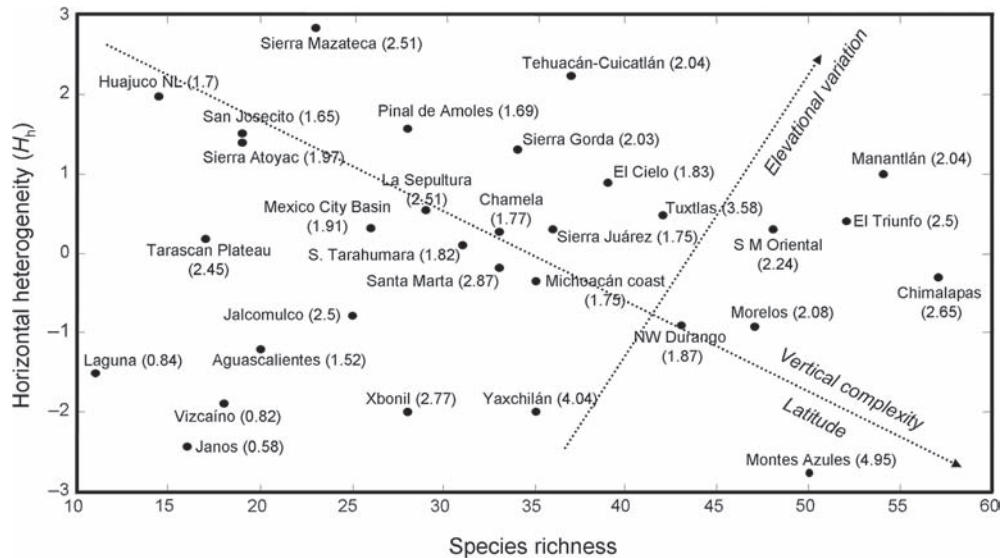


Figure 4. Relationship between species richness and horizontal heterogeneity (H_h) for 31 Mexican bat assemblages. Numbers in parentheses correspond to values of vertical heterogeneity (H_v) for each site. Site names correspond to those in Table 1. Dotted lines represent gradients of environmental variation.

All variation in bat species composition was accounted for in the variance partitioning analysis by the comprehensive set of environmental factors (Fig. 2 and 3). Previous work (López-González et al. 2012) suggested that variation in local habitat is strongly related to trophic requirements of bats. It is unlikely, however, that environmental variation is the only factor influencing bat species composition at a given site; regional processes (e.g. dispersal, source-sink dynamics) and local interspecific or intraspecific interactions likely affect local species composition. Nonetheless, the local environment sets the context that often affects outcomes of biological processes or mechanisms such as interspecific interactions or dispersal attempts. Consequently, at the scale considered, this comprehensive suite of environmental factors may represent environmental surrogates associated with outcomes of regional and local biotic mechanisms and interactions. Spatial variation alone accounted for 18.4% of the total variation in species composition across Paraguay (Stevens

et al. 2007), similar to that found for Mexican bats (15.5%, Fig. 3). However, for Paraguay this variation was independent of habitat variation (vegetation), whereas in Mexico it is associated with vegetation composition. Paraguay is smaller, but more importantly, it is topographically less complex, and the environmental gradient is longer, changing gradually from dry to humid from NW to SE. In addition, the Paraguayan bat fauna is essentially Neotropical, representing one species pool with no endemic species (Willig et al. 2000, Stevens et al. 2007). In contrast, Mexico has great variation in elevation associated with multiple mountain ranges that run in multiple directions and that can reach over 4000 m a.s.l. These mountains are effective geographic barriers to dispersal of bats, produce abrupt environmental changes, and help explain the existence of 15 endemic species of Mexican bats (Ceballos et al. 2005).

Prediction 2: no significant relationship would be found between species richness and environmental heterogeneity, but if found, the relationship would not be linear or monotonic because patterns of environmental heterogeneity in Mexico are complex

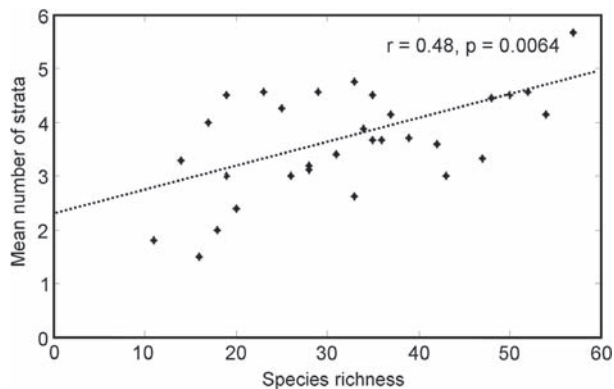


Figure 5. Relationship between species richness and vertical heterogeneity (H_v). H_v was measured as the mean number of vegetation strata for each site (see text for details). The dotted line is the best-fit linear regression.

Contrary to expectation, a significant, positive linear relationship occurred between H_v and species richness, whereas no significant relationship was detected between H_h and species richness. Nonetheless, the distribution of species richness with respect to H_h followed latitudinal, elevational, and vertical complexity gradients (Fig. 4). In general, relationships between species richness and environmental characteristics are likely to interact in complex ways (Gotelli et al. 2009, Fig. 2–4). As relationships between heterogeneity and richness often depend on the environmental factors chosen (Tews et al. 2004), the scale of analysis, and the scale at which study organisms perceive and respond to the landscape (Guisan et al. 2007),

the choice of environmental factors may explain the failure to confirm initially hypothesized relationships in some studies (Tews et al. 2004).

For Mexico, sites distributed throughout the horizontal heterogeneity gradient do not represent a single environmental gradient, but rather a composite of climatic and vegetational variation associated with variation in latitude, elevation, and position relative to mountain ranges. However, horizontal heterogeneity alone does not explain why rainforest sites with low topographic heterogeneity, such as Montes Azules or Yaxchilán, have high species richness. The pattern is better explained by a combination of both factors: sites that are northern, relatively dry, and in the mountains (left upper section of Fig. 4) had low species richness and low H_v . Richness increases as sites become flatter and more mesic, supporting taller and more vertically complex habitats. On the other hand, vertical complexity of habitats is lower on the lower left portion of the graph (grasslands, desert scrub in flatlands), and increases as topography becomes complex (upwards and to the right) because more vegetation types with different degrees of vertical complexity occur in small areas across the elevational gradient. Thus, species richness is greatest on the right side of the graph, corresponding to sites in rainforests of southeastern Mexico (lower portion), which have less horizontal heterogeneity but are vertically complex, or to sites along elevational gradients (upper portion), which are not as complex vertically, but are horizontally heterogeneous (Fig. 4).

Previous research on bats in tropical rainforests has demonstrated a relationship between vertical complexity and species richness (Kalko et al. 1996, Kalko and Handley 2001). Our study provides evidence that vertical complexity is a significant factor in explaining bat species richness (Fig. 5), and that this relationship may be independent of geographic position. Our results complement those of a metacommunity analysis of Mexican bats (López-González et al. 2012), which used reciprocal averaging to identify two main gradients of bat compositional variation: one related to geographic position of sites and the resulting relative contributions of species of Nearctic and Neotropical origin, and a second that ordered sites along an elevational heterogeneity gradient (i.e. from those occurring in relatively flat regions to those occurring in elevationally heterogeneous regions). Interestingly, the arrangement of sites found here (Fig. 4) does not reflect the Nearctic-Neotropical dichotomy. The Nearctic-Neotropical differentiation of Mexican faunas is historical (related to the dispersal and phylogenetic history of these bats), and associated more strongly with species composition, rather than with species richness. The gradient in this study is ecological, based on spatial variation of environmental conditions and complexity of sites, and it is associated with variation in species richness, not species composition.

Prediction 3: β -diversity (turnover) and landscape heterogeneity should have no relationship, and landscape heterogeneity accounts for little of the total variation in bat species composition

The proportion of variation in bat species composition explained by environmental heterogeneity (H_v , H_h) was

relatively small (Fig. 2, 3) compared to vegetation or elevation, but was still appreciable (31.2%). These results indicate that bats are more dependent on their habitat than their potential vagility would suggest, and that the primary importance of vagility is that it allows bats to inhabit suitable regional habitats. The large number of endemics (Ceballos et al. 2005) present in Mexico is consistent with this contention.

A significant relationship exists between turnover and latitude for New World bats, with lower species turnover in tropical regions (Willig and Sandlin 1991, Stevens and Willig 2002). Consequently, β -diversity for North and Central American bats would be expected to increase with decreasing latitude, but no significant relationship was detected (Rodríguez and Arita 2004). This result may be due to a 'possible break in the scaling rules as the sampling grain becomes very small' (i.e. local interactions might be important in shaping communities), and thus a pattern may not be discernible at the scale of their analysis (Rodríguez and Arita 2004). Our results indicate that there may be a scaling effect, but that it does not depend on local interactions, as environmental factors and geographic distance were each associated with β -diversity. Results also suggest that Mexican bats respond to complex geographic variation that is not related to latitude, and that this variation accounts for a considerable proportion of the spatial variation in bat species composition (Fig. 2). Species turnover occurs from north to south, but because of the orographic complexity of Mexico (Fig. 1) there is also strong turnover from east to west, and from lowlands to highlands across relatively short geographic distances (Navarro and León-Paniagua 1995, Torres-Morales et al. 2010). At a continental scale, the importance of these effects probably is secondary, and the latitudinal effect on β -diversity manifests (Willig and Sandlin 1991, Stevens and Willig 2002). The effect of latitude on species richness remains detectable at the finer scale of our work (Fig. 4), but it is obscured by environmental factors that mold local spatial patterns of species richness. The latitudinal effect is further obscured when species richness is measured across latitudinal bands that incorporate longitudinal variation in richness (Rodríguez et al. 2003) that can be caused by elevational heterogeneity and associated heterogeneity in climate and vegetation.

Using data derived from distribution maps Arita and Rodríguez (2002) and Rodríguez et al. (2003) concluded that the most important component to explain terrestrial mammal biodiversity in Mexico is β -diversity, rather than α - or γ -diversity. In other words, regions of high mammalian species richness in Mexico are species rich because of high turnover within those areas and not because of local assemblages being particularly species rich, with variation in β -diversity being correlated with environmental variation (Arita and Rodríguez 2002, Rodríguez et al. 2003). However, these results were applied only to terrestrial mammals and not to bats, with the high vagility of bats provided as an explanation for this difference (Rodríguez et al. 2003). Our results indicate that the same mechanisms invoked to explain patterns of terrestrial mammal biodiversity throughout Mexico also apply to bats. A possible explanation for the discrepancy between studies is that previous studies did not include most of the areas of highest turnover for bats (e.g. along the sierras Madre).

Mexican bat metacommunity structure based on the same dataset (López-González et al. 2012) identified Clementsian and quasi-Clementsian metacommunity patterns (i.e. discrete communities that replace each other as a group sensu Leibold and Mikkelsen 2002, Presley et al. 2010) with distinct boundaries coincident with the tropical–temperate transition along the sierras Madre and Transvolcanic Belt at the Nearctic-Neotropical boundary (Ortega and Arita 1998, López-González et al. 2012). At this boundary bat families of temperate origin (Vespertilionidae) enter in contact with families of tropical origin (Molossidae, Phyllostomidae). Also, a pattern of quasi-nested, clumped species loss was found that coincided with the sharp elevational gradients that characterize a large proportion of Mexico, both on the Nearctic and on the Neotropical realms. Likely as a result of this complexity, it is at these areas, in particular Sierra Madre Occidental and Sierra Madre del Sur, where most bats endemic to Mexico occur.

The observed metacommunity structures are consistent with the high turnover rates we detected at these areas. In contrast, part of the work of Arita and collaborators is restricted to four large geographic quadrats, one located at the Nearctic-Neotropical high-turnover area, one at a sharp elevational gradient, and two located at low turnover areas (Rodríguez et al. 2003), but missing most of the Nearctic-Neotropical transition, which would explain why they found little correlation between turnover and environmental variables, and low turnover rates in general. In addition, differences in scale (0.5×0.5 degree quadrats of Rodríguez and Arita 2004 versus sites with a 25 km radius) at which data were measured and the source of the data (distribution maps versus observational data at sites) differed greatly, which could affect the ability to detect environmental effects on local bat communities and geographical patterns of diversity. Data included in quadrats generated from distribution maps contain false positives that inflate estimates of α for any given area. This is particularly true for Mexico because algorithms to generate distribution maps do not include any information on habitat or elevation, but are interpolations based on scattered records. To determine β diversity as γ/α coupled with the way in which distribution maps are drawn greatly inflates alpha compared to gamma, artificially reducing β and reducing the power of the analyses to detect patterns of β -diversity.

Conclusions

Mexico comprises a high diversity of vegetative associations resulting from a complex topography and associated climatic variation, with both the diversity of climates and their geographic distribution affecting patterns of bat species richness and composition. For example, many arid and semiarid areas are isolated from one another by numerous sierras and smaller, isolated mountain ranges, which have promoted the evolution of endemic species of plants (Rzedowski 2006). Importantly, of 15 endemic Mexican bats, 12 occur at low elevations in montane areas of the western slopes of the Sierra Madre Occidental or Sierra Madre del Sur, mostly associated with deciduous or semi deciduous tropical forest, and three (*Myotis vivesi*, *M. peninsularis*, and *M. planiceps*) have

restricted distributions in arid regions of Baja California and the Mexican Plateau (*M. planiceps*). The latitudinal gradient in bat species richness is a generalization that holds for large spatial scales; however, at smaller scales the latitudinal pattern of species richness is overwhelmed by responses to local variation in landscape features and environmental factors. Variation in β -diversity with respect to variation in environmental factors provides evidence for habitat specialization affecting distributions of bats as well as variation in the composition of local communities.

The relative contribution of shared history (phylogeny) to large-scale ecological patterns deserves attention. Indeed, contemporary environmental characteristics account for much (92.1%) variation in bat β diversity in Mexico. One limitation of the present study is that we addressed only contemporary environmental conditions. At larger scales, latitudinal gradients are related to some degree to the relative ages of bat taxa, a relationship that reflects effects of historical processes on diversity gradients (Stevens 2011). At smaller scales significant relationships have been documented between functional diversity (FD), species richness, and phylogenetic diversity (PD). Moreover, almost 80% of variation in species richness, and 82% of the variation in PD, can be explained by a combination of environmental (climate and elevation) and spatial (geographic) factors (Cardillo 2011). Once environmental variation is accounted for, the remaining variation in FD will be due to phylogenetic structuring factors (Emerson and Gillespie 2008, Pausas and Verdú 2010, Cardillo 2011). Examination of effects of historical processes on beta diversity gradients would provide a productive avenue of future research and a richer understanding of determinants of the relationships among α , β , and γ diversity (Stevens 2011).

It is becoming increasingly evident to community ecologists that understanding the distribution of species along environmental or geographic gradients within a region may be biologically more meaningful than examining the coexistence of many species at one point (Ricklefs 2008). Additionally, an increased focus on the relationships between species distributions and environmental variation that define the limits of those distributions will complement the traditional focus on local community composition, will provide an important piece of information to separate ecological and spatial effects from historical factors, and will lead to greater understanding of the relative importance of mechanisms that structure communities.

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Supplementary material (Appendix ECOG-00813 at <www.ecogeography.org/readers/appendix>). Appendix 1.