



Metacommunity analysis of Mexican bats: environmentally mediated structure in an area of high geographic and environmental complexity

Celia López-González^{1*}, Steven J. Presley², Abraham Lozano¹, Richard D. Stevens³ and Christopher L. Higgins⁴

¹CIIDIR Unidad Durango, Instituto Politécnico Nacional, Sigma 119, Fraccionamiento 20 de Noviembre II, Durango, Durango 34220, México, ²Center for Environmental Sciences and Engineering and Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-4210, USA, ³Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA, ⁴Department of Biological Sciences, Tarleton State University, Stephenville, TX 76402, USA

ABSTRACT

Aim We tested the hypothesis that distributions of Mexican bats are defined by shared responses to environmental gradients for the entire Mexican bat metacommunity and for each of four metaensembles (frugivores, nectarivores, gleaning insectivores, and aerial insectivores). Further, we identified the main environmental factors to which bats respond for multiple spatial extents.

Location Mexico.

Methods Using bat presence–absence data, as well as vegetation composition for each of 31 sites, we analysed metacommunity structure via a comprehensive, hierarchical approach that uses reciprocal averaging (RA) to detect latent environmental gradients corresponding to each metacommunity structure (e.g. Clementsian, Gleasonian, nested, random). Canonical correspondence analysis (CCA) was used to relate such gradients to variation in vegetation composition.

Results For all bat species and for each ensemble, the primary gradient of ordination from RA, which is based on species data only, recovered an axis of humidity that matched that obtained for the first axis of the CCA ordination, which is based both on vegetation attributes and on species composition of sites. For the complete assemblage as well as for aerial and gleaning insectivores, analyses revealed Clementsian or quasi-Clementsian structures with discrete compartments (distinctive groups of species along portions of an environmental gradient) coincident with the humidity gradient and with the Nearctic–Neotropical divide. Within-compartment analysis further revealed Clementsian or quasi-Clementsian structures corresponding to a gradient of elevational complexity that matched the second ordination axis in CCA. Frugivores had quasi-nested structure, whereas nectarivores had Gleasonian structure.

Main conclusions Our hierarchical approach to metacommunity analysis detected complex metacommunity structures associated with multiple environmental gradients at different spatial extents. More importantly, the resulting structures and their extent along environmental gradients are determined by ensemble-specific characteristics and not by arbitrarily circumscribed study areas. This property renders compartment-level analyses particularly useful for large-scale ecological analyses in areas where more than one gradient may exist and species sorting may occur at multiple scales.

Keywords

Canonical correspondence analysis, Chiroptera, community ecology, elevational complexity, environmental gradients, inventory data, Mexico, reciprocal averaging.

*Correspondence: Celia López-González, CIIDIR Unidad Durango, Instituto Politécnico Nacional, Sigma 119, Fraccionamiento 20 de Noviembre II, Durango, Durango 34220, México.
E-mail: celialg@prodigy.net.mx

INTRODUCTION

Community ecology has witnessed the rapid development of a new paradigm that unites local and regional processes to understand more clearly the spatial structure of groups of communities within regions (Leibold & Mikkelsen, 2002; Leibold & Miller, 2004; Leibold *et al.*, 2004; Holyoak *et al.*, 2005). Currently, we are experiencing a change in focus from local community-oriented research to a regional large-scale perspective in which the foci of study are populations that are distributed over ecological and geographic gradients (Rodríguez & Arita, 2004; Cottenie, 2005; Lewinsohn *et al.*, 2006; Stevens *et al.*, 2007; Presley *et al.*, 2009, 2010; Keith *et al.*, 2011; Willig *et al.*, 2011). The local community concept is gradually being replaced by a 'regional community' concept in which the spatial distributions of populations and their relationship with ecological or geographic attributes at the regional level become the primary focus for understanding biodiversity patterns (Ricklefs, 2008).

The metacommunity concept has revolutionized large-scale community ecology by integrating within-community phenomena such as biotic interactions and environmental tolerances with larger-scale spatial phenomena such as dispersal, spatially structured biotic interactions, and habitat fragmentation (Leibold & Miller, 2004; Leibold *et al.*, 2004; Holyoak

et al., 2005). Moreover, the conceptual underpinnings of the metacommunity approach have broad applicability not only to communities, but to sets of coexisting species that are geographically, taxonomically, or functionally restricted, such as assemblages, guilds, local guilds, and ensembles (*sensu* Fauth *et al.*, 1996).

The metacommunity concept (Leibold *et al.*, 2004) provides a framework to evaluate the organization of species composition along environmental gradients. In general, two complementary approaches have been followed to evaluate patterns of spatial variation in the species composition of metacommunities. A mechanistic approach for understanding variation in species composition considers the roles of patch dynamics, species sorting, mass effects and neutrality (Leibold *et al.*, 2004; Cottenie, 2005; Holyoak *et al.*, 2005), whereas a pattern-based approach evaluates characteristics of species distributions along environmental gradients that emerge as a result of those mechanisms and manifest as particular metacommunity structures (Leibold & Mikkelsen, 2002; Presley *et al.*, 2010). The three-pronged approach of Leibold & Mikkelsen (2002) is conceptually unique in that three elements of metacommunity structure – coherence, range turnover and range boundary clumping – are combined to identify the idealized structure that best describes a metacommunity (Table 1). Each non-random structure assumes that species distributions are

Table 1 Six patterns of species distribution proposed by Leibold & Mikkelsen (2002). Patterns represent idealized characteristics hypothesized to result from at least one potentially important ecological or biogeographical process. Coherence, turnover, and boundary clumping refer to the three attributes evaluated to identify best fit patterns. Presley *et al.* (2010) defined four additional quasi-structures (marked as *) that are conceptually analogous to four of the idealized structures of Leibold & Mikkelsen (2002), but for which turnover is non-significant. The level of significance of turnover is proposed to be a measure of the strength of structuring mechanisms. Presley *et al.* (2010) further divided quasi-nested structures into three different structures, characterized by their pattern of species loss (clumped, stochastic, hyperdispersed).

Description of pattern	Pattern	Coherence	Turnover	Boundary clumping
Species pairs have mutually exclusive distributions (i.e. 'forbidden combinations') but such pairs occur independently of other pairs	Checkerboards	Negative	Not applicable	Not applicable
Species lists from species-poor sites are subsets of those from species-rich sites	Nested subsets Quasi-nested subsets*	Positive	Negative Non significant, but less than average expected by chance	May be positive, negative or stochastic
Gradients result in discrete communities that replace each other as a group	Clementsian Quasi-Clementsian*	Positive	Positive Non-significant	Positive
Gradients result in species turnover, but the arrangement of species along the gradient is random	Gleasonian Quasi-Gleasonian*	Positive	Positive Non-significant, but greater than average expected by chance	Non significant
Gradients result in no discrete communities but species ranges are arranged more evenly than expected by chance	Evenly spaced gradients Quasi-evenly spaced*	Positive	Positive Non-significant	Negative
There are no gradients or other patterns in species distributions among sites	Random	Not significantly different than expected by chance	Not applicable	Not applicable

moulded by a combination of biotic interactions (e.g. competition, habitat associations) and responses to abiotic factors (e.g. temperature, rainfall) that vary among sites along environmental gradients. Importantly, the theoretical underpinnings of each idealized structure are unique (Clements, 1916; Gleason, 1926; Diamond, 1975; Tilman, 1982; Patterson & Atmar, 1986), allowing analyses to test simultaneously multiple hypotheses associated with metacommunity structure.

Mexico harbours one of the highest bat diversities in the world (137 species), surpassed only by Brazil (146), Perú (152), Venezuela (154), and Colombia (178 – Ceballos & Simonetti, 2002). This reflects the size and geographic position of the country (bisected by the Tropic of Cancer and surrounded by warm marine currents), as well as its topographic complexity, which produce an intricate mosaic of landscapes, vegetation types, and climates. Unlike other megadiverse countries that comprise mostly tropical species, the Mexican bat fauna is a mixture of Neotropical and Nearctic elements. Furthermore, even though bats are vagile, the geographic position and complexity of the Mexican landscape has fostered a large number of endemics (15 species – Ceballos & Oliva, 2005).

A large body of literature documents large-scale biogeographical patterns of biodiversity in Mexico (see Morrone, 2005 for a review). For mammals and in particular for bats, historical events that resulted in the extant Mexican fauna are fairly well understood (Fa & Morales, 1993; Arita & Ortega, 1998; Ceballos *et al.*, 1998; Ortega & Arita, 1998). From an ecological standpoint, researchers have explored large-scale patterns of species diversity and richness, as well as latitudinal gradients of richness and turnover (Arita, 1997; Arita & Rodríguez, 2002, 2004; Stevens & Willig, 2002; Rodríguez *et al.*, 2003; Rodríguez & Arita, 2004), but to date no study has evaluated the structure of Mexican bat metacommunities, nor the ecological factors that could mould such structures at the regional level. Moreover, previous studies that cover large geographic areas were based on estimations of species occurrences from range maps that interpolated occurrence records where no actual data existed. Consequently, biases may exist in these large-scale ecological analyses as geographic ranges generally are drawn along proposed habitat boundaries, thereby making assumptions about habitat associations of species. More recently, data for many local bat assemblages have become available (e.g. Estrada *et al.*, 1993; Estrada & Coates-Estrada, 2001; Sánchez-Cordero, 2008; and references in Table 2), providing data with which to test specific hypotheses about the ecological factors that shape metacommunity structure at regional scales.

In this paper we evaluate the structure of the bat metacommunity in Mexico. Specifically, we (1) test the hypothesis that distributions of Mexican bats are defined by shared responses to environmental gradients, (2) determine the locations of compartments (i.e. unique species pools) within Mexico, and (3) identify the environmental factors to which bats respond at each spatial extent (i.e. factors that

define compartment boundaries and factors that define structures within compartments).

Because the relative importance of environmental characteristics can be contingent on trophic affiliation, we tested these hypotheses for the complete Mexican bat assemblage as well as for each of four species-rich metaensembles (frugivores, nectarivores, aerial insectivores, and gleaning insectivores). Using the methodology proposed by Leibold & Mikkelsen (2002) with the conceptual refinements introduced by Presley *et al.* (2010), we determined metacommunity structure of each group along latent (ordination) environmental gradients, and did so in a hierarchical fashion. In addition, we used canonical correspondence analysis and detailed environmental information from a geographic information system (GIS) to determine which environmental characteristics are most important in shaping metacommunity structures at each spatial extent.

MATERIALS AND METHODS

Species data

One of the main obstacles to the description of broad-scale patterns is the lack of comparable information on intensive sampling at numerous local sites across extensive geographic areas (Stevens & Willig, 2002). A reasonably large number of sites have been sampled in Mexico with various degrees of intensity within the last 30 years (Table 2). We selected 31 sites that met three criteria: each site covered a relatively small area, was intensively sampled (2 years minimum), and was sampled throughout the year to account for seasonal variation in species composition. Data for 29 sites were based on published accounts, with records based on different combinations of mist-netting, museum specimens and bibliographic data. The remaining two sites (4 and 24) were based on unpublished data. Records from La Laguna (site 4) were collected by C.L.G. and J.A. Rascón between 2004 and 2009 using mist nets and acoustic detectors for 65 nights during each (wet and dry) season. Data for Site 24 (Tehuacán-Cuicatlán) were compiled from examination of museum specimens and mist-netting by N. González Ruiz (Universidad Autónoma Metropolitana-Iztapalapa, Mexico) and collaborators intermittently for 10 years. We attempted to maximize a homogenous coverage throughout the country. Nonetheless, there is a sampling bias towards tropical, south-eastern areas of Mexico, resulting in a smaller number of comprehensive inventories for the northern two-thirds of the country, such that the density of inventories was greater in more heterogeneous portions of the country (Fig. 1). We defined a central point for each study site that was estimated from maps presented in each published account. A circle of 25 km radius was defined based on the central point and all sampled localities within this circle were included for each site. Estimates of abundances were not available for all datasets; therefore only bat presence-absence data were used. A site-by-species (31 × 128) incidence matrix was generated that includes 93.4% of the 137 species known from Mexico. Nomenclature across sites was standardized following

Table 2 Geographic position of each of 31 bat communities used to evaluate metacommunity patterns in Mexico. Coordinates are those of the centre point (see text for details).

Site	Site name	Centre	Source
1	Janos-Casas Grandes, Chihuahua	30.888° N, -108.190° W	Pacheco <i>et al.</i> (2001)
2	Valle de los Cirios and Vizcaíno Reserve, Baja California	28.028° N, -113.399° W	Álvarez-Castañeda <i>et al.</i> (2008b)
3	Sierra Tarahumara, Chihuahua	27.025° N, -107.532° W	López-González & García-Mendoza (2006)
4	'La Laguna' region, Coahuila-Durango	25.544° N, -103.442° W	C. López-González & J.A. Rascón-Escajeda (unpublished data)
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 <i>et al.</i> (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 & León-Paniagua (2002)
9	Sierra Madre Oriental (Tamaulipas)	22.929° N, -99.026° W	León-Paniagua <i>et al.</i> (2004)
10	Aguascalientes State	21.879° N, -102.300° W	Álvarez-Castañeda <i>et al.</i> (2008a)
11	Sierra Gorda, Querétaro	21.182° N, -99.320° W	Monteagudo-Sabaté & León-Paniagua (2002)
12	Sierra de Pinal de Amoles, Querétaro	21.134° N, -99.625° W	Navarro & León-Paniagua (1995)
13	Meseta Tarasca, Michoacán	19.641° N, -102.047° W	Orduña-Trejo <i>et al.</i> (2000)
14	Sierra de Manantlán, Jalisco	19.618° N, -104.203° W	Íñiguez-Davalos (1993)
15	Chamela, Jalisco	19.527° N, -105.073° W	Ceballos & Miranda (1986)
16	Mexico City Basin	19.350° N, -99.162° W	Ceballos González & Galindo Leal (1984)
17	Jalcomulco, Veracruz	19.335° N, -96.758° W	Moreno-Ortega (2000)
18	Morelos state	18.761° N, -99.121° W	Alvarez-Castañeda (1996)
19	Los Tuxtlas Reserve, Veracruz	18.605° N, -95.139° W	Estrada <i>et al.</i> (1993) Galindo-González (2004)
20	Xbonil, Campeche	18.635° N, -90.166° W	Escalona-Segura <i>et al.</i> (2002), Hernández-Huerta <i>et al.</i> (2000), Vargas-Contreras (2004), Vargas-Contreras <i>et al.</i> (2005, 2008)
21	Sierra de Santa Marta, Veracruz	18.232° N, -94.873° W	González-Christen (2008)
22	Michoacán state coast	18.135° N, -102.885° W	Polaco & Muñiz-Martínez (1987)
23	Sierra Mazateca, Oaxaca	18.130° N, -96.843° W	Sánchez-Cordero & Medellín (2005)
24	Tehuacán-Cuicatlán Reserve, Puebla and Oaxaca	17.956° N, -97.024° W	N. González-Ruiz (unpublished data)
25	Sierra de Juárez, Oaxaca	17.956° N, -97.024° W	Monteagudo-Sabaté & León-Paniagua (2002)
26	Sierra de Atoyac, Guerrero	17.473° N, -100.369° W	Monteagudo-Sabaté & León-Paniagua (2002)
27	Los Chimalapas Reserve, Oaxaca	16.906° N, -94.683° W	Olguín-Monroy <i>et al.</i> (2008), García-García & Santos-Moreno (2008)
28	Yaxchilán, Chiapas	16.901° N, -90.969° W	Escobedo-Morales <i>et al.</i> (2001)
29	La Sepultura Reserve, Chiapas	16.236° N, -93.702° W	Monteagudo-Sabaté & León-Paniagua (2002)
30	El Triunfo Biosphere Reserve, Chiapas	16.202° N, -91.860° W	Espinoza-Medinilla <i>et al.</i> (1998)
31	Montes Azules Biosphere Reserve, Chiapas	16.118° N, -90.924° W	Medellín (1993)

Simmons (2005), with the exception of *Rhogeasa gracilis* (for which we followed Baird *et al.*, 2008), and *Artibeus jamaicensis* and *A. triomylus* (Guerrero *et al.*, 2004).

Metacommunity analyses

We follow Leibold & Mikkelsen (2002) in defining a metacommunity as a set of ecological communities at local sites that are potentially, but not necessarily, linked by dispersal, with a community defined as a group of species at a given site. Because metacommunity structures are proposed to be related to environmental gradients, and responses of bats to gradients can be contingent on trophic affiliation, we assigned species to one of seven trophic categories following Wilson (1973) and Findley (1993): carnivores, piscivores, sanguinivores, gleaning insectivores, aerial insectivores, frugi-

vores and nectarivores. We conducted metacommunity analyses for the complete dataset (128 species) and for each of the four trophic ensembles (phylogenetically bounded groups of species that use a similar set of resources – Fauth *et al.*, 1996) that were sufficiently species-rich and geographically pervasive to produce biologically meaningful and statistically powerful results (gleaning insectivores, aerial insectivores, frugivores and nectarivores). We use the term metaensemble to refer to these groups in a metacommunity setting.

We used the analytical methods of Leibold & Mikkelsen (2002) and Presley *et al.* (2010) to determine if the Mexican bat metacommunity has non-random structure, to identify which idealized metacommunity structure best describes empirical patterns, and to investigate the association of such structures to environmental factors. The merits of Clementsian versus Gleasonian views on community structure have been

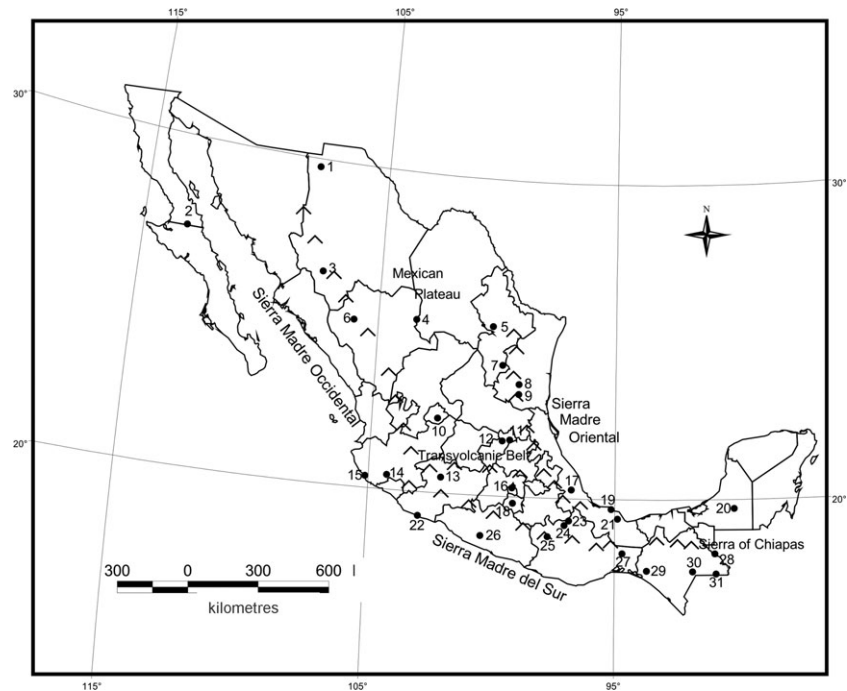


Figure 1 An outline of the Mexican physical geography and study sites. Points represent the centre of 25-km-radius circles where bat species and vegetation associations were sampled. The numbers refer to sites in Table 2.

long debated by ecologists (e.g. Whittaker, 1956, 1975; Whittaker & Niering, 1965; Shipley & Keddy, 1987; Hoagland & Collins, 1997). This has been recognized as a false dichotomy (Collins *et al.*, 1993; Nicholson & McIntosh, 2002), resulting in the proposal of more than two alternative models for community structure (Austin & Smith, 1989; Collins *et al.*, 1993), and in a greatly expanded framework of metacommunity structure (Leibold & Mikkelsen, 2002; Presley *et al.*, 2010 – Table 1). The expanded frameworks incorporated the terms Clementsian and Gleasonian to describe structures that are most consistent with how Clements (1916) or Gleason (1926) viewed structural changes in communities along environmental gradients. More specifically, Clements (1916) viewed communities as well-defined units with boundaries of many species distributions occurring in proximity to each other, whereas Gleason (1926) hypothesized that responses to the environment were species-specific, in which case the most common outcome would be boundaries of species distributions that occur randomly along the gradient. No mechanism is implied by use of these terms to define particular metacommunity structures.

Each matrix was ordered via reciprocal averaging (RA), which maximizes the proximity of sites with similar species compositions and the proximity of species with similar patterns of occurrence at sites. RA (= correspondence analysis) is appropriate for identifying patterns in response to latent environmental gradients because similarity in species patterns of occurrence determines the position of sites and species along an axis of correspondence (i.e. a latent environmental gradient) without a priori knowledge of or assumptions about the particular factors that govern the response of each species (Gauch *et al.*, 1977; Gauch, 1982; Leibold & Mikkelsen, 2002).

All analyses were conducted for the primary axis of correspondence. Ordered incidence matrices were tested against null models for coherence, turnover, and boundary clumping to find the best-fit pattern of idealized metacommunity structures (Table 1). An overview of these tests and their interpretation is presented below. Details on assumptions, construction of null models and hypothesis testing concerning analyses of metacommunity structures are available in Leibold & Mikkelsen (2002) and Presley *et al.* (2010).

Coherence

We assessed coherence by comparing the number of embedded absences (i.e. absences that have at least one presence toward each extreme in a row or column) in the ordinated data matrix to a distribution of embedded absences produced by a null model (Leibold & Mikkelsen, 2002). A metacommunity was considered significantly and positively coherent if the likelihood of having fewer embedded absences than observed was $\leq \alpha/2$ (a two-tailed test). A metacommunity was considered significantly and negatively coherent if the likelihood of having more embedded absences than observed was $\leq \alpha/2$. Negative coherence is characteristic of checkerboards, whereas positive coherence is characteristic of 12 other structures (Presley *et al.*, 2010; Table 1). Non-significant coherence indicates random structure. Species occurrences in random structures are scattered along the latent environmental gradient such that measures of species turnover and range boundary clumping do not effectively reflect the concepts that they are intended to measure. Consequently, range turnover and boundary clumping were only evaluated for metacommunities that exhibited positive coherence.

Turnover

Species ranges were made perfectly coherent by filling in all embedded absences prior to analyses of turnover (Leibold & Mikkelson, 2002). Species range turnover was evaluated based on the number of replacements of one species by another along the gradient. The observed number of replacements was compared to a null distribution of replacement values created from 1000 matrices that contained randomly shifted species ranges to determine significance (Leibold & Mikkelson, 2002). Significantly negative turnover is indicative of nested distributions. Significantly positive turnover is indicative of Gleasonian, Clementsian, or evenly spaced structures. Non-significant turnover is characteristic of quasi-structures (Presley *et al.*, 2010; Table 1).

Boundary clumping

Morisita's index (I) measures the clumping of species distributional boundaries by counting the number of terminal boundaries at each site. Significance was determined via a chi-square goodness-of-fit test that compared the observed distribution of range boundaries to an expected uniform distribution. Range boundaries that occurred at random have a Morisita's index of $c. 1.0$ and are consistent with Gleasonian, quasi-Gleasonian, or stochastic species loss in nested structures (Table 1). Morisita's index values > 1.0 with a significant chi-square test indicate clumped boundaries and are consistent with Clementsian, quasi-Clementsian, or clumped species loss in nested structures. Index values < 1.0 with a significant chi-square test indicate hyper-dispersed boundaries and are consistent with evenly spaced, quasi-evenly spaced, or hyper-dispersed species loss in nested structures (Table 1). For some Clementsian structures, large numbers of clumped species boundaries were identified along the ordination of sites; these boundaries defined compartments (i.e. distinctive groups of species along portions of an environmental gradient, Lewinsohn *et al.*, 2006). The structure of each of these compartments was analysed separately. All analyses were conducted using Matlab 7.5.0.342, Release 2007b (script files for Matlab are available for download at <http://www.tarleton.edu/~higgins/EMS.htm>). An α of 0.05 was used for all analyses. Species arrangement for each analysis is presented in Appendix S1 in Supporting Information.

Vegetation data

Vegetation in Mexico includes a vast array of plant associations, ranging from various forms of desert scrub in the north-central portion of the country and Baja California peninsula, to rain forests in the south-east and Yucatan peninsula. The Pacific plateau is dominated by an assortment of dry, deciduous and semi-deciduous tropical forests, whereas the Gulf of Mexico plateau was covered with rain forests of various heights, most of which have been replaced by tropical crops such as coffee, pineapple and oranges. Mangrove, palm

savannas and wetlands are common on the oceanic plateaus. The Sierra Madre Oriental, Sierra Madre Occidental and Transvolcanic Belt constitute elevational gradients that range from sea level to over 5500 m (Fig. 1). At higher elevations, mountain ranges are covered with combinations of species of pines (*Pinus* spp.), oaks (*Quercus* spp.) and firs (*Abies* spp., *Pseudotsuga* spp.). The humid (oceanic) slopes are or were covered by cloud, oak, or pine-oak forests, whereas the dry slopes (those facing the central plateaus) include oak forests, grasslands, chaparral, or desert scrub. The north-central plateau is a mosaic of chaparrals, desert scrub and agricultural land (Rzedowski, 1988).

For each of the 25-km-radius sites, percentage area covered by each of 27 vegetation types (Appendix S2) was calculated from the digital version of INEGI 1:250,000 vegetation maps scaled to 1:1,000,000, as included in the GIS of BIOTICA 5.0 (CONABIO, 1999, 2008), generating a 31×27 site-by-vegetation matrix. These maps provide information on the main vegetational associations (and hence climates) occurring at a given site. However, for sites with very complex topography, and therefore with a complex array of microclimates and vegetations, some variation necessarily will be lost at this scale. Processing of data was performed in ArcView GIS 3.2 (ESRI Inc., 1996, Redlands, CA, USA).

Analysis of the species-vegetation relationship

Mexico's complex mosaic of vegetation associations (Rzedowski, 1988) has been explained as a combination of climate, topography, geology and soils, and elevation (Flores Díaz, 1974; Rzedowski, 1988). Vegetation can be an effective surrogate for environmental variation because it reflects the combined effects of the entire suite of environmental factors. Moreover, the responses of bats to abiotic factors may be indirect, with vegetation responding to abiotic factors and bats responding to vegetation (López-González, 2004; Stevens *et al.*, 2007). We used vegetation data to evaluate the hypothesis that metacommunity structure is mediated, at least in part, by species associations with environmental gradients. We related the observed pattern of species distributions (matrix of all species and matrices for each trophic guild) among sites to the vegetational composition of sites (vegetation matrix) by means of canonical correspondence analysis (CCA – ter Braak & Prentice, 1988; ter Braak & Šmilauer, 2006). We used CANOCO for Windows v. 4.5 (ter Braak & Šmilauer, 2006) to extract eigenvalues, species scores, and site scores for the first two canonical axes. Species and site scores of these axes, as well as correlations between canonical axes and environmental variables, were plotted in ordination diagrams.

For each species group, significance of the relationship between species distributions and vegetational composition was tested as the correlation between site scores that are weighted averages of species scores (WA scores) and site scores that are linear combinations of environmental variables (LC scores – ter Braak & Prentice, 1988; ter Braak & Šmilauer, 2006). We tested the null hypothesis that there is no

relationship between species composition and vegetational composition of sites using the Monte Carlo test available in CANOCO. The test statistic (F) for this test is the ratio of the sum of all canonical eigenvalues (trace) and the residual sum of squares, thus evaluating the significance of the overall relationship between species occurrences and the set of environmental variables (ter Braak & Šmilauer, 2006).

RESULTS

Relationship between species composition and vegetation composition

The correlation between bat species composition and vegetational composition was marginally significant for the entire metacommunity (Table 3). Vector correlations between the first canonical axis and environmental variables, and order of

Table 3 Results of canonical correlation analysis (CCA) on 129 bat species and 27 vegetational attributes (Appendix S2) for 31 sites across Mexico. Loadings of each variable on the first two axes are shown as vector correlations. Canonical correlation between bat species data and vegetation data was marginally significant ($F = 1.3$, $P = 0.055$, Monte Carlo test, 1000 iterations).

	Axis 1	Axis 2
Eigenvalue	0.534	0.249
Species–vegetation correlation	0.995	0.998
% Cumulative variance explained	21.6	31.6
Vegetation attributes		
no veg	0.1741	-0.0180
con for	0.2874	0.0198
oak for	0.2586	-0.2266
pin for	-0.1182	0.2318
mes for	-0.0760	-0.2914
chap	0.1572	0.0611
towns	0.2126	0.0670
water	-0.3401	0.1302
agric	0.0751	-0.2307
mangrove	-0.2497	-0.0799
des shr	0.3993	0.4323
tho scr	0.3688	0.1188
des scr	0.3932	0.2999
des scr2	0.3282	0.3801
mes shr	0.0817	0.0539
palm	0.1735	0.1299
nat gras	0.3097	0.2192
pop tul	-0.4811	0.4843
savanna	-0.2338	-0.0392
evg fort	-0.6049	0.4498
dec forl	0.2319	-0.5203
tho for	-0.1397	0.1954
dec form	0.0369	-0.3591
evg form	-0.2774	0.1200
gal for	0.0056	-0.3031
sand veg	0.3076	0.3899
hal veg	0.3307	0.1817

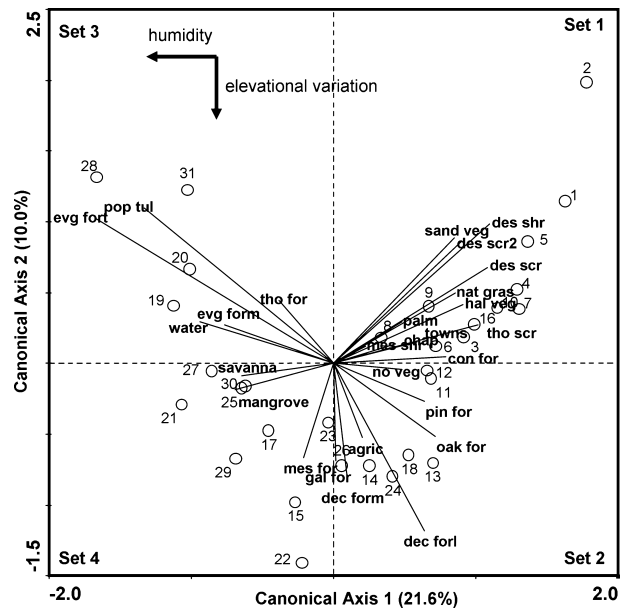


Figure 2 Ordination of 31 Mexican bat assemblages and 27 vegetation types along environmental gradients using canonical correlation analysis (CCA). Lines represent vector correlations of environmental variables (vegetation attributes) with ordination axes. Circles represent sites (as in Table 2). Vegetation categories are described in Appendix S2.

sites along this axis suggest that it represents a humidity gradient (mesic to arid – Fig. 2; Table 3). Axis 2 represented a gradient of elevational heterogeneity, from relatively flat sites to sites with a great deal of elevational relief. We tested the significance of the first gradient by conducting a canonical correlation analysis for the association between the species matrix and the average of the total annual rainfall at each site, taken from the weather station closest to the centre of each circle (García, 1988). Except for four sites (1, 22, 26, 31) all data came from stations within the 25-km²-radius circles. For the remaining four sites data were taken from the weather station closest to the circle. The canonical correlation was significant ($F = 2.58$, $P = 0.001$, CANOCO Monte Carlo test, 1000 iterations, 73.3% variance explained by relationship). We assessed significance of the second gradient by calculating the standard deviation of the upper limits of all elevational 100-m intervals occurring at each site (100 m, 200 m, and so forth) using 1:50,000 digitized contour maps (INEGI, 2003). We estimated the elevational variation at each site, and conducted a CCA using standard deviation of elevation as the independent variable and species presence–absence as the dependent matrix. Elevational variation accounted for a significant amount of variation ($F = 1.66$, $P = 0.030$, 55.1% variance explained by relationship) in species composition among sites.

Four sets of sites that corresponded to combinations of the two gradients were identifiable, as follows.

1. Temperate or semi-desertic areas characterized by desert scrub, mesquite grassland, chaparral, or sand dunes, and with little elevational variation (first quadrant in the CCA

ordination, Fig. 2). Species composition of communities includes primarily vespertilionids and molossids plus a few nectar-feeding phyllostomids and one mormoopid.

2. Areas of steep elevational gradients on the Transvolcanic Belt, Sierra Madre Oriental or Sierra Madre Occidental (mostly second quadrant). Vegetation ranges from deciduous and semi-deciduous tropical forests (on the Pacific and Gulf of Mexico slope), to desert scrub (on the continental side of the Sierras), to oak forests and conifer forests. Species composition includes bats of temperate origin, mostly vespertilionids, which constitute the main component of the desert and high-elevation areas. Also present are species of tropical origin with wide environmental tolerances that can occupy the seasonal forests of the Pacific plateau, and in some cases reach the lower edge of conifer forests.

3. Tropical, mesic areas with comparatively little elevational variation, covered with rain forests or cloud forests (fourth quadrant). Species composition is Neotropical (mostly a subset of the species that occur in the rain forests of Central America or Amazonian South America).

4. Areas of steep elevational gradients on or south of the Transvolcanic Belt (third quadrant). Vegetation also varies greatly along the elevational gradient, but includes mostly mesic associations of plants, ranging from rain forests or semi-deciduous forests to cloud, oak, pine–oak, and fir (*Abies*) forests. Lowland sites include species exclusive to rain forests as well as tropical species with wider environmental tolerances. As elevation increases there is a gradual loss of mostly Neotropical species, with a few widely distributed vespertilionids occurring on the highlands.

The relationship between bat and vegetation matrices was not significant for gleaning insectivores ($F = 0.623$, $P = 0.83$), frugivores ($F = 0.0$, $P = 1.0$) or aerial insectivores ($F = 1.212$,

$P = 0.13$); whereas for nectarivores the relationship was significant ($F = 1.96$, $P = 0.034$). Although only the ordination diagram for the complete bat dataset is illustrated (Fig. 2), this arrangement of sites and species is similar for each metaensemble even if the relationship between species and vegetation was not significant.

Metacommunity and metaensemble structures

The Mexican bat metacommunity as a whole exhibited highly significant coherence, species turnover, and boundary clumping (Fig. 3, Table 4), which is consistent with a Clementsian structure, in which major suites of species replace each other as a group along a gradient (Table 1). Boundary clumping is characteristic of this pattern and allows for the distinction of two discrete compartments (A, B) that coincide with the dry/seasonal/temperate (sets 1 and 2 in CCA) and mesic/warm/tropical (3 and 4) groups of sites described above. These compartments represent two distinct faunas that are characteristic of arid and mesic regions in Mexico. Compartment A was quasi-nested, and included mostly vespertilionids, molossids, and a few phyllostomids. Within this compartment, reciprocal averaging also distinguished CCA site set 1 from 2. Compartment B exhibited Clementsian structure, and included sites from more mesic regions, characterized primarily by species of tropical origin. Boundary clumping within this compartment (Fig. 3) further separated communities into two sets that coincide with CCA sets 3 and 4 (Fig. 2).

Aerial insectivores also exhibited a Clementsian structure with two compartments (Fig. 4) that coincided with the dry/temperate/seasonal (A) and mesic/warm/tropical (B) site sets. Compartment A had Clementsian structure and included lowland communities north of 18° N latitude as well as more

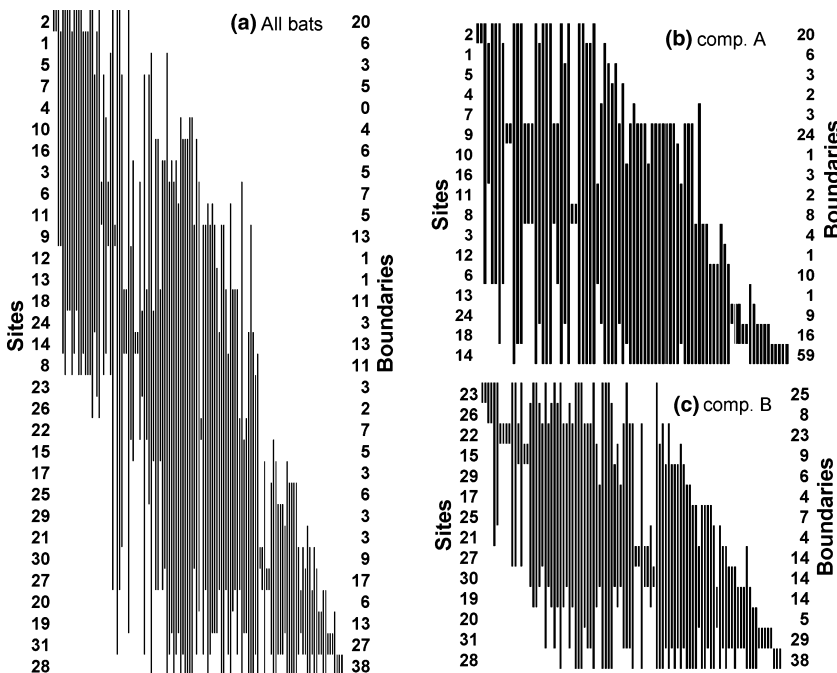
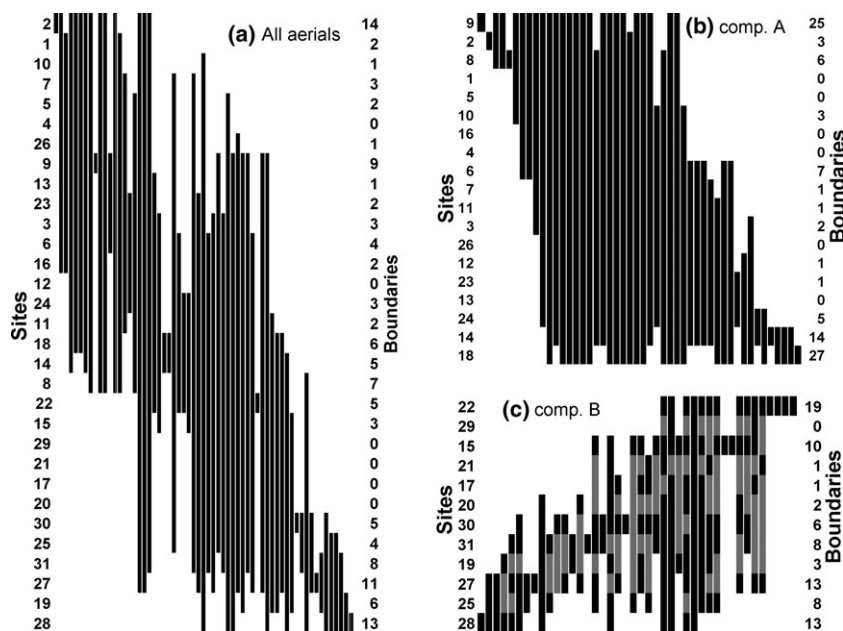


Figure 3 Bat distributions along an environmental gradient composed of 31 sites in Mexico. (a) All bats, ordination for the full extent of the metacommunity. Numbers on the left refer to sites (as in Table 2) arranged along a latent environmental gradient as derived via reciprocal averaging (RA). Each black bar represents the distributional range of one species along the gradient (species names are given in Appendix S1). The number of range boundaries at each site is shown along the right side of each structure. This metacommunity had Clementsian structure, with two distinct compartments. Each compartment was also ordinated via reciprocal averaging: (b) compartment A, associated with dry/seasonal/temperate regions, and (c) compartment B, associated with mesic/warm/tropical regions (see text for details).

Table 4 Results of analyses of coherence, species turnover, and boundary clumping for Mexican bats. Analyses were performed for all bats and separately for each of four metaensembles. For each Clementsian or quasi-Clementsian structure, analyses were performed separately for each compartment (portion of the environmental gradient characterized by a distinctive group of species). Significant results ($P \leq 0.05$) are bold. Abs, number of absences; % Abs, percentage of embedded absences; Rep, number of replacements; M, Morisita's index; SD, standard deviation.

	Coherence					Species turnover				Boundary clumping		Structure		
	Species	Sites	Abs	% Abs	<i>P</i>	Mean	SD	Rep	<i>P</i>	Mean	SD		M	<i>P</i>
All species	128	31	1234	15.5	< 0.001	2527	52.0	246184	< 0.001	169490	13701.0	1.537	< 0.001	Clementsian
Compartment A	86	17	469	16.0	< 0.001	741	29.3	13732	0.673	14481	1776.3	1.883	< 0.001	Quasi-nested, clumped species loss
Compartment B	100	14	437	15.6	< 0.001	699	26.9	21087	0.028	17338	1708.3	1.358	< 0.001	Clementsian
Gleaning insectivores	22	30	47	3.6	< 0.001	240	27.7	4771	0.057	3735	565.3	2.189	< 0.001	Quasi-Clementsian
Compartment A	10	17	38	11.2	0.067	48	5.7							Random
Compartment B	13	13	25	7.4	0.337	35	10.2							Random
Aerial insectivores	61	31	666	17.6	< 0.001	1075	38.3	53236	< 0.001	35769	4720.6	1.480	< 0.001	Clementsian
Compartment A	48	19	285	15.6	< 0.001	435	20.1	6188	< 0.001	3755	608.6	2.588	< 0.001	Clementsian
Compartment B	42	12	168	16.7	0.068	195	15.3							Random
Frugivores	24	27	111	8.6	< 0.001	263	15.7	4071	0.894	4193	919.8	1.471	< 0.001	Quasi-nested, clumped species loss
Nectarivores	11	29	67	10.5	< 0.001	107	9.1	2346	0.035	1294	499.0	1.029	0.882	Gleasonian

Figure 4 Distributions of aerial insectivorous bats along an environmental gradient composed of 31 sites in Mexico. (a) All aeri-als, ordination of all aerial species. Numbers on the left refer to sites (as in Table 2) arranged along a latent environmental gradient as derived via reciprocal averaging (RA). Each black bar represents the distributional range of one species along the gradient (species names are given in Appendix S1). The number of range boundaries at each site is shown along the right side of each structure. This metaensemble had Clementsian structure (Table 1) with two distinct compartments: (b) compartment A, associated with dry/ markedly seasonal/temperate, and (c) compartment B, associated with mesic/warm/tropical regions (see text for details). Grey areas represent embedded absences in metacommunities with random structure.



southerly sites that are located at higher elevations. Compartment B included mesic sites and had random structure (Fig. 4). Gleaning insectivore structure was quasi-Clementsian with compartments A and B having similar site composition to those of the complete bat metacommunity and the aerial insectivore metaensemble (Figs 3–5). Nevertheless, for gleaners structure was random within each compartment (Table 4). The frugivore metaensemble (subfamilies Stenodermatinae

and Carollinae) had a quasi-nested structure with clumped boundaries (Fig. 6). The nectarivore metaensemble had Gleasonian structure (Fig. 7). This ensemble included only glosso-phagine bats, which are widely distributed in arid lands, mesic forests, and dry tropical environments. For analyses based on all species as well as for those restricted to particular trophic guilds, the orders of sites along the primary axis of correspondence were very highly correlated (Appendix S3),

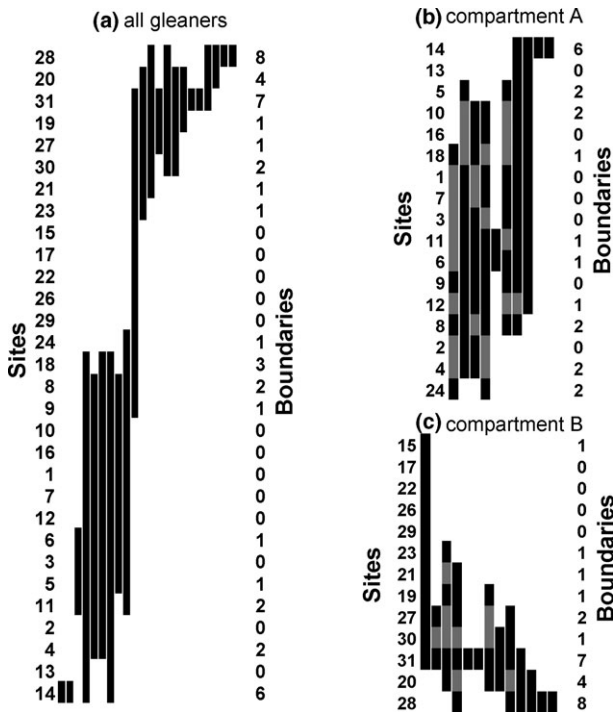


Figure 5 Distributions of gleaning insectivorous bats along an environmental gradient comprised of 30 sites in Mexico. (a) All gleaners, ordination for the full extent of the metaensemble. Numbers on the left refer to sites (as in Table 2) arranged along a latent environmental gradient as derived via reciprocal averaging (RA). Each black bar represents the distributional range of one species along the gradient (species names are given in Appendix S1). The number of range boundaries at each site is shown along the right side of each structure. This metaensemble had quasi-Clementsian structure (Table 1) with two distinct compartments. Each compartment was also ordinated via reciprocal averaging: (b) compartment A, associated with dry/markedly seasonal/temperate regions, and (c) compartment B, associated with mesic/warm/tropical regions (see text for details). Grey areas represent embedded absences in metacommunities with random structure.

indicating that the primary latent environmental gradients that moulded bat species distributions were similar regardless of trophic affiliation.

DISCUSSION

Metacommunity and metaensemble structures

Clementsian structures

The Mexican bat metacommunity, as well as the gleaning insectivores and aerial insectivores metaensembles, exhibited Clementsian or quasi-Clementsian structures with compartments that largely were coincident (i.e. compartments A and B included nearly the same groups of sites in each case; Figs 3–5). The fact that the entire metacommunity and two of four

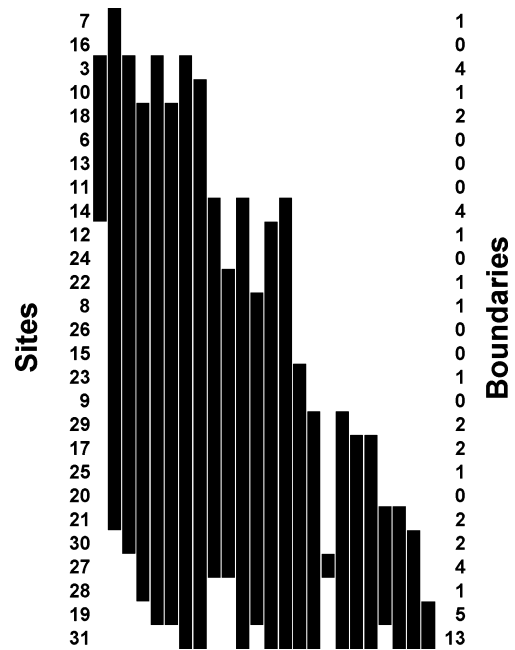


Figure 6 Distributions of frugivorous bats along an environmental gradient composed of 27 sites in Mexico. Numbers on the left refer to sites (as in Table 2) arranged along a latent environmental gradient as derived via reciprocal averaging (RA). Each black bar represents the distributional range of one species along the gradient (species names are given in Appendix S1). The number of range boundaries at each site is shown along the right side of each structure. This metaensemble had quasi-nested structure (Table 1) with all but three sites and two species conforming to the general nested structure.

species-rich ensembles exhibited Clementsian structures with distinct compartment boundaries coincident with the tropical–temperate transition, indicates sharp faunal discontinuities along that interface and not a gradual gradation from tropical to temperate bat faunas.

Compartment A of the bat metacommunity followed a gradient of elevational variation, with an increase in species richness with elevational heterogeneity. Species loss was significantly clumped (Table 4) due to the presence of widely tolerant species that are able to exist in tropical, desert areas or high elevations (e.g. *Myotis yumanensis*, *M. volans*, *M. lucifugus*, *M. velifer*, *Antrozous pallidus*, *Corynorhinus* spp., *Nyctinomops macrotis*, *Lasiurus cinereus*) combined with species restricted to tropical lowland environments (e.g. *Pteronotus parnellii*, *P. davyi*, *Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Glossophaga soricina*, *Balantiopteryx plicata*, *Noctilio leporinus*, *Molossus* spp., *Nyctinomops* spp.). Within compartment B of the bat metacommunity there was a lowland, mesic compartment (coincident with set 3) that included many species that are restricted to lowland rain forest (*Vampyrum spectrum*, *Tonatia* spp., *Macrophyllum macrophyllum*, *Peropteryx kappleri*, *Thyroptera tricolor* and *Mimon crenulatum*), and a more heterogeneous compartment that included montane and lowland habitats (coincident with set 4 in CCA) populated

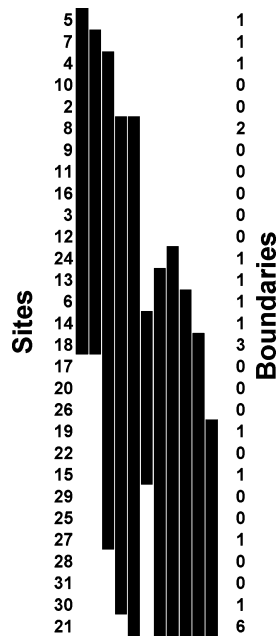


Figure 7 Distributions of nectarivorous bats along an environmental gradient composed of 29 sites in Mexico. Numbers on the left refer to sites (as in Table 2) arranged along a latent environmental gradient as derived via reciprocal averaging (RA). Each black bar represents the distribution range of one species along the gradient (species names are given in Appendix S1). The number of range boundaries at each site is shown along the right side of each structure. This metaensemble had Gleasonian structure (Table 1).

mostly by tropical species that occupy a wider range of habitats, including rain forests, dry semi-deciduous forests, wetlands, tropical scrub, and cultivated areas (*Pteronotus parnellii*, *P. davyi*, *Artibeus jamaicensis*, *A. lituratus*, *Sturnira lilium*, *Glossophaga soricina*, *Balantiopteryx plicata*, *Noctilio leporinus*, *Molossus* spp., *Nyctinomops* spp.), as well as a few widely tolerant species of temperate origin that inhabit the highlands of tropical areas.

Boundary clumping in compartment A for insectivores resulted from species that inhabit arid and semi-arid scrub and pine or pine–oak forests (e.g. *Myotis volans*, *M. yumanensis*, *Lasiurus cinereus*, *Eptesicus fuscus*) versus species that occur only along the coastal plains (*Rhogeessa*, spp., *Molossus* spp., *Natalus stramineus*, *Promops centralis*). In contrast, aerial insectivore compartment B had a random structure, with no common gradient that determined the distributions of insectivores. The lack of a common gradient may be related to species-specific habitat specializations by lowland aerial insectivores.

Compartments A and B of the gleaning insectivore metaensemble exhibited random structure, indicating that within each compartment species respond to different environmental gradients or that species occurrences were random (i.e. species did not respond to any gradient). With the exception of *Micronycteris microtis*, all other gleaning insectivores were restricted to one compartment or the other, creating highly

distinct units (Fig. 5). Thus, gleaning insectivores responded to gross variation along the xeric versus mesic gradient, but did not respond to environmental variation within each of these portions of the gradient.

Nested structures

Stenodermatinae and Carollinae frugivorous bats have their peak diversity and probably their evolutionary origins in north-central South America (Koopman, 1978). In Mexico they occur in the south-eastern forests and the Pacific and Gulf of Mexico coastal plains, with distributions of some species extending inland along major river basins (Ceballos & Oliva, 2005). A nested pattern arose because the majority of species occur in south-eastern rain forests, and gradually are lost as climates and vegetation become more seasonal and dry (on the Pacific versant) or drier and agriculturally dominated (on the eastern coast). However, three sites in the south-eastern lowlands (19, 28 and 31) and one species (*Artibeus hirsutus*) did not conform to the overall pattern, creating a quasi-nested structure (Fig. 6). These sites harboured many frugivores, but one or more widespread species (e.g. *Artibeus aztecus*, *A. intermedius*, *A. toltecus*, *Chiroderma salvini*, or *Sturnira lilium*) was absent from each site, substantially detracting from an otherwise nested structure. *Artibeus hirsutus* is endemic to Mexico with a unique distribution for a frugivore, restricted to the Pacific plateau from Guerrero to Sonora states (Ceballos & Oliva, 2005).

Frugivore species loss along most of the gradient was stochastic, indicating that idiosyncratic species-specific characteristics (e.g. environmental tolerance, availability of critical resources) determine the northern boundaries of species distributions. At the northernmost localities only *Sturnira lilium*, *Artibeus jamaicensis*, *A. intermedius*, *Chiroderma salvini*, *Centurio senex*, and a number of endemics persist. Frugivores rely on fruit-bearing plants that are found primarily in subtropical and tropical forests; the attenuation in diversity of these bats with latitude may reflect the latitudinal attenuation of the abundance and diversity of plants that provide fleshy fruit and nectar on which they rely (Findley, 1993; Stevens, 2004).

Gleasonian structures

The nectarivores were the only metaensemble to exhibit a Gleasonian structure (Table 1). Even so, occurrences of all nectarivore species were strongly associated with the humidity gradient. Mexican nectarivorous bats belong to a sister taxon (subfamily Glossophaginae) of frugivores, but did not conform to the same general trend of decreasing species richness with increasing latitude. This may be because the resources on which nectarivores rely are not as restricted to tropical forests as they are for frugivores. Many extra-tropical plants that are widely distributed in more xeric habitats have co-evolved with nectarivorous bats, developed pollination syndromes specifically for bats, and rely exclusively on bats for pollination

(von Helversen & Winter, 2003). Thus, this ensemble includes species that are widely distributed in arid lands, mesic forests, and tropical environments (*Leptonycteris yerbabuena*, *L. nivalis*, *Choeronycteris mexicana*), species that have restricted ranges along the Pacific plateau of Mexico (*Musonycteris harrisoni*, *Glossophaga morenoi*), and species that are widely distributed across the Neotropics (*Anoura geoffroyi*, *Choeronyctus godmani*, *Glossophaga soricina* and *G. commissarisi* (Ceballos & Oliva, 2005).

General patterns

Our results support the hypothesis that the Mexican bat metacommunity is strongly structured by spatial variation in environmental factors (e.g. vegetation, climate). In all instances, the order of sites along the primary canonical axis (Fig. 2) extracted via CCA was nearly identical to that based on reciprocal averaging, even though the latter analysis did not include information on environmental variables. In concert, these analyses also support the hypothesis that metacommunity structure of Mexican bats is strongly contingent on habitat characteristics. More specifically, results indicate that the primary latent environmental gradient along which metacommunity and metaensemble structures were evaluated corresponded to variation in vegetational composition along a humidity gradient, with seasonal, temperate or xeric sites at one end of the gradient and tropical, mesic sites at the other end. Ensemble-level analysis further demonstrated that the effect of habitat attributes is strongly related to ecological, specifically trophic, requirements of bats. In geographic space, the first axis of ordination in all analyses recovered the Nearctic–Neotropical dichotomy that characterizes the Mexican biota, including bats (Ortega & Arita, 1998), with dry/seasonal/temperate communities in the Nearctic realm and mesic/tropical/warm ones in the Neotropical realm.

Our approach further identified a second gradient of environmental variation. As explained above, compartments defined by Clementsian or quasi-Clementsian structures were associated with seasonal, temperate or xeric sites (compartment A) or tropical, mesic sites (compartment B). Within each compartment, reciprocal averaging revealed a second latent environmental gradient, as sites in each compartment-level analysis were ordered from those occurring in relatively flat regions to those occurring in elevationally heterogeneous regions (i.e. an elevational heterogeneity gradient). These gradients reflect site order along the second canonical axis of CCA (Fig. 2), in which elevationally heterogeneous sites (sets 2 and 4) had negative scores and elevationally homogeneous sites (sets 1 and 3) had positive scores. Thus, although no analysis of metacommunity structure for multiple latent environmental gradients (Presley *et al.*, 2009) was conducted, two distinct environmental gradients to which bats respond were revealed using this hierarchical approach.

In addition to the evaluation of ensemble-specific structures within a biota, future studies that investigate effects of phylogeny on metacommunity structure may lead to addi-

tional insights into large-scale patterns of species distributions (Leibold *et al.*, 2010). Phylogenetic structuring factors may include competition-mediated limiting similarity or highly conserved, shared key traits (Pausas & Verdú, 2010). Whereas examination of these constraints is beyond the scope of this paper, the relative contribution of shared history to large-scale ecological patterns deserves further study.

CONCLUDING REMARKS

It is becoming increasingly evident for 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). At the very least, a focus on species distributions, which place local communities in a regional context, will complement the traditional focus on local community composition and lead to greater understanding of the relative importance of mechanisms that structure communities.

This regional approach requires suitable tools to detect and describe patterns of variation at the regional level, and that allow for the formulation of meaningful hypotheses on the processes that shape species distributions. Our approach to metacommunity analysis represents a significant advancement in gradient analysis, being able to distinguish among several non-random structures (Leibold & Mikkelsen, 2002; Presley *et al.*, 2010). The evaluation of structures along latent environmental gradients that are produced via reciprocal averaging places structures in an environmental context that is more conducive to ecological interpretation than the use of existing packing algorithms that produce gradients of richness (Presley *et al.*, 2010). Importantly, the resulting structures and their extent along environmental gradients are determined by ensemble-specific characteristics and not by arbitrarily circumscribed study areas. Moreover, the hierarchical approach to evaluate patterns at multiple spatial extents will help to determine the scale at which different environmental gradients and associated mechanisms operate to structure communities and metacommunities. This is particularly true for evaluation of structures across complex landscapes, in which strong biotic changes can occur at multiple spatial scales and in response to independent axes of environmental variation.

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Instituto Politécnico Nacional, Escuela Nacional de Ciencias Biológicas, Mexico City.

SUPPORTING INFORMATION

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

Appendix S1 Species ordination via reciprocal averaging.

Appendix S2 Vegetation categories and abbreviations used in canonical correlation analysis.

Appendix S3 Rank correlations between scores for all possible pairs of species groups.

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BIOSKETCH

Celia López-González works on small mammal biology, with an emphasis on bats. Currently she works for Instituto Politécnico Nacional in north-western Mexico, her current research programme focuses on the systematics, evolution and zoogeography of small mammals of the Sierra Madre Occidental.

Author contributions: C.L.G. led the writing; C.L.G. and S.J.P. conceived the ideas, analysed the data and interpreted results; A.L. generated the maps and data matrices. C.L.H. wrote Matlab functions; and C.L.H. and R.D.S. helped interpreting the results and contributed to the writing.

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