Spatial and environmental variation in phyllostomid bat (Chiroptera, Phyllostomidae) distribution in Mexico

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Abstract

Spatial and environmental variation in phyllostomid bat (Chiroptera, Phyllostomidae) distribution in Mexico. Species' spatial distribution patterns allow us to understand the establishment of different biotic components in different environmental conditions. This study analyzes the spatial distribution of the Phyllostomidae family in Mexico to identify groups of species that occur in similar sites, the environmental conditions associated with species distribution, and the percent of overlap with human–modified areas. The results suggest six groups of sites with particular species composition. The spatial variation in richness pattern was associated with species tolerance to environmental conditions, such as minimum temperature and tree cover. The convergence between species distribution and modified areas varied per species feeding guild. Insectivorous and nectarivorous bats were sensitive species because they occurred in narrow environmental conditions and their distributions overlapped with areas modified by human activities. The approach implemented here analyzes regional species distributions and estimates their environmental requirements, contributing to the development of optimal conservation strategies for susceptible bat species.

Key words: Biodiversity conservation, MaxEnt, Multivariate analysis, Niche breadth, Species diversity

Resumen

Variación espacial y ambiental en la distribución de murciélagos filostómidos (Chiroptera, Phyllostomidae) en México. Los patrones de distribución espacial de las especies permiten comprender el establecimiento de distintos componentes bióticos en diferentes condiciones ambientales. En este estudio se analiza la distribución espacial de la familia Phyllostomidae en México para identificar grupos de especies que están presentes en sitios similares, las condiciones ambientales asociadas a su distribución y el porcentaje de solapamiento con zonas modificadas por el hombre. Los resultados sugieren que existen seis grupos de sitios con una composición de especies particular. La variación espacial en el patrón de riqueza se asoció con la tolerancia de las especies ante condiciones ambientales, como la temperatura mínima y la cobertura arbórea. La convergencia de la distribución de las especies y las zonas modificadas varió según el gremio trófico de las especies. Los murciélagos insectívoros y nectarívoros se consideraron especies sensibles, debido a que se encuentran en un reducido rango de condiciones ambientales y su distribución se solapa con zonas modificadas por actividades humanas. El planteamiento utilizado consistió en analizar la distribución regional de las especies y estimar sus requerimientos ambientales, lo que permite elaborar estrategias de conservación óptimas para las especies susceptibles de murciélagos.

Palabras clave: Conservación de la biodiversidad, MaxEnt, Análisis multivariante, Amplitud de nicho, Diversidad de especies

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Introduction

Species diversity distribution is heterogeneous in space, so understanding and predicting this variation in different environments and taxa is a fundamental goal in ecology and biogeography (Lomolino et al., 2005). Species richness and community assembly variation may occur either gradually or abruptly, depending on the spatial scale analyzed and associated factors (e.g. availability of energy and water; Hawkins et al., 2003; Field et al., 2009). Species' spatial distribution patterns are useful to understand the establishment of different biotic components in different environmental conditions (Morrone, 2009). However, the persistence of biological diversity and the functionality of ecosystems are at risk due to the increase in anthropogenic activities such as agriculture, livestock, and urban activities (Klein–Goldewijk and Ramankutty, 2004). Changes in native vegetation, for example, have modified 12 % of Earth's land surface, affecting wildlife habitats and the diversity of species distribution (Ries et al., 2004). Therefore, the patterns of species composition vary depending on the environment, and high biodiversity areas that are threatened by human land cover changes must be evaluated to optimize conservation strategies, a key topic in conservation biology (Margules and Sarkar, 2009).

Species potential distribution models are a useful tool to identify environmental conditions related to species presence, high biodiversity areas and zones with similar species composition (Mateo et al., 2013). Despite being locally biased by the number of collections records, the type of sampling, the choice of predictors or the algorithm used (Peterson et al., 2011), the fact that species distribution models provide reliable results at a regional scale (Raxwhorty et al., 2007; Lee et al., 2012) makes this technique appropriate to study bat communities at larger scales. The superposition of information from a distribution model and land–use cartography provides an estimate of the degree of overlap between human–modified areas and can be a useful strategy to identify areas at risk from human activities (Wu et al., 2014). An integrative approach to distribution models allows helps to evaluate ecological suitability in biodiversity areas to identify species that are susceptible to environmental changes and important as conservation targets (Peterson et al., 2015).

The Phyllostomidae family is a Neotropical taxa that can be used to identify high biodiversity areas and zones at risk of human activities because it occurs in several different environments (Stevens, 2006) and has different specific feeding preferences (Giannini and Kalko, 2004). The regional distribution of phyllostomids has been associated with oscillations in temperature and humidity (McCain, 2007) and is locally determined by sensitivity to disturbance (Wordley et al., 2015). However, little is known about areas with a similar species composition, species environmental tolerances, and the degree of overlap between the distribution of bats and modified areas (López–González et al., 2011; Razgour et al., 2016). Phyllostomid bats provide ecosystem services as agents of seed dispersal, pollination, and pest regulation (Kunz et al., 2011).High diversity areas that may include species susceptible to constant human degradation must therefore be identified.

Mexico has a wide range of environmental conditions, produced by altitudinal variations, the influence of two oceans, and the convergence of two biogeographical regions (i.e., the Neotropical and the Nearctic; Morrone, 2005) that offer multiple environments for 60 phyllostomid bat species (Ramirez–Pulido et al., 2014). However, these bat species are at risk from human activities, mainly the conversion of tropical forests (Challenger and Dirzo, 2009). This study analyzes the distribution of Phyllostomidae family species in Mexico, as well their different trophic guilds, since this information is useful to understand the response of the community structure to human disturbance (Klingbeil and Willig, 2009). The objectives of this study were to identify the spatial richness patterns, define groups of sites with a similar species composition, estimate the environmental tolerance of each species, and calculate the convergence between species distribution and human–modified areas.

Methods

Species potential geographic distribution

Potential geographic distribution models for phyllostomid bat species in Mexico were developed using the maximum entropy algorithm (MaxEnt ver 3.3; Phillips et al., 2006, 2016), which has proven to be robust (Elith et al., 2006). The algorithm searches a combination of variables with maximum entropy and estimates the importance of each in species distribution with respect to sites where the species was recorded (Elith et al., 2011). Presence records were obtained from the database provided by the *Instituto de Biología* of the *Universidad Nacional Autónoma de México*. The database was complemented with records from the Global Biodiversity Information Facility (www.gbif.org). A total of 64,773 records were compiled, from which doubtful records or those with spatial redundancy were removed, resulting in 11,701 records.

The variables for predicting the species distribution included those that limit their presence at regional scales, such as temperature, precipitation, and elevation, and those variables related to niche requirements such as type of vegetation and a regionalization variable, at a spatial resolution of 0.0083º (~0.85 km^2; see table 1s in supplementary material). Climatic factors (such as temperature and precipitation) were used as direct variables that have physiological importance for bat species, but are not consumed; vegetation cover variables (such as trees or herbaceous plants) were related to resources used directly (López–González et al., 2011). Elevation was an indirect ecological variable that has no direct physiological relevance for species' persistence in response to future changes in environmental conditions (Guisan and Zimmermann, 2000), while the categorical variable of regionalization represents unique fauna and flora of the world’s continents (Olson et al., 2001). The suite of predicted variables allows us to evaluate bat species' responses to the environmental gradient present in Mexico. The layers of climatic variables were modified to generate new layers (see table 2s in supplementary material) using the Image Calculator in IDRISI (edition Selva; Eastman, 2012). However, using a set of variables is biased to autocorrelation (Peterson et al., 2011) and so to reduce information redundancy, we deleted continuous variables with a high correlation ($r^2 > 0.8$) and performed a cluster analysis (1–Pearson *r* distance and Ward algorithm). The cluster analysis was performed with a sample of 500 random points, generated in ArcGIS (ver. 10.1; ESRI, 2010) using the Random Points Extension. The number of groups of correlated variables was defined from the amalgamation graph (threshold value = 1.1). From each group, we chose one variable and excluded the rest (see fig. 1s in supplementary material). Potential distribution models were performed with one categorical and 10 continuous low correlated variables to represent the environmental heterogeneity in the country (table 1).

Models were generated only for species with a minimum of 10 records (53 species; table 2), since MaxEnt is stable with this number of records (Wisz et al., 2008). Default MaxEnt settings were used, with 75 % of the records used to create the model and 25 % to test it. Due to this random component, 10 single models were generated for each species to compile a consensus map via the weighted average method (Marmion et al., 2009). This method provides a continuous map and to obtain the species presence/absence, we calculated the average occurrence threshold from the single models. The threshold was the fixed cumulative value for 10 % probability of occurrence. Species were considered present in values above the threshold and absent in values below the threshold. Thus, a binary consensus map was obtained, increasing accuracy and decreasing the uncertainty of single models.

Species richness variation

The spatial pattern of richness for phyllostomids in Mexico was obtained from the sum of the consensus presence/ absence (binary) models for each species in IDRISI (Eastman, 2012). Additionally, we generated a richness map for trophic guild classification (Giannini and Kalko, 2004; table 2). Richness maps show the variation in species richness and spatially to identify highly specific richness areas.

Sites with similar species composition

Binary maps were used to define sites with a similar species composition. We used 500 random points (sites) to extract the presence/absence from each model and to compile a binary matrix that contained all the possible species combinations. We defined groups of sites with similar species composition using a generalized *k*–means analysis, which finds the optimum 'partition' for dividing a number of objects into *k* clusters in function of categorical variables (presence–absence) in STATISTICA (StatSoft, 1984–2013). The used *k* groups were defined from the amalgamation graph of a cluster analysis (Sorensen–Dice distance and Ward algorithm). The analysis searches for a combination of sites that maximize significant differences in local species composition between groups based on individual χ^2–tests for each species. The null hypothesis was that the frequency of sites per group was similar at a probability of 0.05. The result was the assignment of each site in a group as a function of local species composition. We present a map that shows the spatial tendency in the geographical distribution of groups of sites that differ in bat species composition. In addition, we identified species that distinguish each group based on their proportional distribution affinity, obtained as the percentage of sites by group where each species occurs. The affinity values (from 0 to 100 %) indicate the species geographical distribution along the different groups of sites.

Species environmental segregation

Bat community–level response to environmental conditions was identified via the outlying mean index (OMI) to estimate the preference (marginality) and the amplitude (tolerance) of conditions used by each species (Dolédec et al., 2000). The analysis estimates the distance between the average conditions (centroid) in which each species was present with respect to the average conditions of the study area (center of gravity). The OMI generates canonical variables that account for the highest variability of sites, which were associated with sites where species were recorded by a canonical correspondence. As a result, the variability (inertia) associated with the species distribution is decomposed in three components (Dolédec et al., 2000): (1) marginality or OMI, which is the deviation of average conditions used for the species in the study area. High values for species were found in different conditions of the average evaluated and low values for species were found in the average; (2) tolerance, which is the number of sites with which species are associated and their location in an environmental gradient (i.e., niche breadth). Low values imply that a species occurs in a narrow range of conditions (i.e., specialist) and high values imply that a species occurs in a wide range (i.e., generalist); and (3) residual tolerance, which is the variation in species occurrence not explained by the variables.

The OMI analysis was performed in ADE–4 software (Thioulouse et al., 1997) using a faunal matrix with species presence/ absence and an environmental matrix with environmental characteristics; both were extracted from the 500 sites. The faunal matrix was used in the *k*–means analysis, while the environmental matrix included values of the 10 continuous variables used to generate the models (table 1). Additionally, we included a new column in the faunal matrix containing points where species absence was predicted. The column identifies environmental conditions that limit the species distribution. Statistical significance was estimated with a Monte Carlo permutation test

Table 1. Variables used to generate species distribution models: Cl, climatic; Tp, topographic; Lc, land cover; Ct. categorical; SD, standard deviation. (Measurement units for each variable type in parentheses).

Tabla 1. Variables usadas para generar los modelos de distribución de las especies: Cl, climática; Tp, topográfica; Lc, cubierta de tierra; Ct, categórica; SD, desviación estándar). (Unidades de medida para cada tipo de variable entre paréntesis).

Variables	Code	Type	Source	Mean	SD
Maximum of yearly maximum temperatures (ºC)	MXXT	Cl	www.worldclim.org	22.9	4.6
Mean yearly minimum temperatures (ºC)	MMNT	Cl	www.worldclim.org	12.1	4.9
Percentage of precipitation in March	PP03	Cl	www.worldclim.org	6.4	2.8
Percentage of precipitation in May	PP05	Cl	www.worldclim.org	7.7	4.2
Percentage of precipitation in July	PP07	Cl	www.worldclim.org	14.3	6.3
Mean yearly evapotranspiration (mm)	MMEV	Cl	www.worldclim.org	1,562.1	174.1
Elevation (m a.s.l.)	ELEV	Tp	https://lta.cr.usgs.gov/hydro1k	744.6	716.2
Percentage of bare cover	BARP	Lc	www.glcf.umd.edu	18.5	27.1
Percentage of tree cover	TREP	Lc	www.glcf.umd.edu	23.4	24.4
Percentage of herbaceous cover	HERP	Lc	www.glcf.umd.edu	57.1	22.6
Ecoregions	ECOR	Ct	Olson et al., 2001	–	–

(1,000 permutations; Metropolis and Ulam, 1949). We report eigenvalues, factor loadings, and a graph of species centroids.

To identify bat species that tend to co–occur in similar sites, we grouped the species according to the environmental conditions where their presence was predicted. The grouping was conducted with a *Q* agglomerative analysis for the faunal matrix via cluster analysis (Sorensen–Dice distance and Ward algorithm). The groups found are highlighted on the species marginality graph to determine whether a tendency exists for species to be homogeneously dispersed within the available environmental gradient. All cluster analyses were performed in STATISTICA (ver. 12; StatSoft, 1984–2013).

Species incidence with anthropic changes

The degree to which species occurrence overlapped with human activities was analyzed by estimating the percentage of area in which a species distribution converges with modified areas. Modified areas were obtained using a layer of land use/vegetation in Mexico (INEGI serie V, www.inegi.org.mx). The layer was reclassified into cropland, livestock, and urban zones. We obtained the percent of overlap between family and trophic guild richness using the classified land–use layer. A convergence percentage was calculated from the ratio of overlain pixels to the total pixels in the study area, multiplied by 100 (Venegas–Barrera and Manjarrez, 2011). Additionally, we present the convergence percentage by richness proportions for the family and guilds in groups of sites where species diversity was highest.

Results

Spatial patterns in phyllostomid bat richness

The Phyllostomidae family is potentially distributed in 79.6 % of Mexico's land surface, and we found that the highest richness areas were in the southern tropical environments (> 40 spp., fig. 1A). Nectarivorous bats were the guild with the widest geographic distribution (73.9 %), whereas hematophagous species were found in 46.2 % of Mexico and frugivorous and insectivorous bats occurred in 51.5 % and 59 % of Mexico, respectively. Nectarivorous bats showed a potential highest richness on the Pacific coast, while the other guilds had a higher richness on the Atlantic coast (fig. 1B–1E). Richness for all groups was lowest in the northern arid environments.

Groups of sites with similar phyllostomid bat composition

We found six groups of sites that contained a distinctive species (threshold value of 1.5 unities; fig. 2): (1) The Atlantic group, on the coast of the Gulf of Mexico and the Yucatan Peninsula, had the highest potential richness areas (10 to 49 species) with *Mimon crenulatum, Lophostoma brasiliense,* and *Vampyrum spectrum* as higher proportionality affinity species (table 2). (2) The Pacific group, located on the Pacific coast and in the Balsas Basin, had areas with potentially 15 to 45 species, such as *Uroderma magnirostrum, Musonycteris harrisoni,* and *Glossophaga morenoi*. (3) The Mountain group, in the mainly mountainous ranges of Mexico (Sierra Madre Oriental, Sierra Madre Occidental, Sie-

Table 2. Phyllostomid bat species included in the study. Trophic guilds (TG: Hem, hematophagous; Nec, nectarivorous; Ins, insectivorous; Fru, frugivorous). Proportional distribution affinity by group of sites (At, Atlantic; P, Pacific; M, mountain; Pl, plateau; Ar, arid; D, desert). Listed with conservation status in: [a] NOM–059–SEMARNAT (SEMANRNAT, 2010); [b] IUCN Red List (www.iucnredlist.org). Nicho parameters: OMI, outlying mean index; Tol, tolerance; TolR, residual tolerance.

Tabla 2. Especies de murciélagos filostómidos incluidas en el estudio. Gremios tróficos (TG: Hem, hematófago; Nec, nectarívoro; Ins, insectívoro; Fru, frugívoro). Afinidad de distribución proporcional por grupo de sitios (At, Atlántico; P, Pacífico; M, montaña; Pl, altiplano; Ar, árido; D, desierto). Incluida con categoría de conservación en: [a] NOM–059–SEMARNAT (SEMANART, 2010); [b] Lista Roja de la UICN (www.iucnredlist.org). Parámetros del nicho: OMI, índice de marginalidad media; Tol, tolerancia; TolR, tolerancia residual.

			Proportional distribution affinity						OMI Components			
Species	Code	TG	At	P	M	Pl	Ar	D	Inertia	OMI	Tol	TolR
Mimon crenulatum [a]	Micre	Ins	100	0	0	0	0	0	12.45	9.44	0.89	2.12
Lophostoma brasiliense [a]	Lobra	Ins	97.4	0	2.6	0	0	0	11.23	7.29	1.09	2.85
Vampyrum spectrum [a,b]	Vaspe	Ins	90.5	5.7	0	0	3.9	0	9.39	6.43	0.21	2.75
Mimon cozumelae [a]	Micoz	Ins	90.3	6.3	2	0	1.4	0	11.59	7.72	0.98	2.89
Artibeus watsoni [a]	Arwat	Fru	90.3	0	5.6	0	4.1	0	7.52	4.47	0.38	2.67
Phylloderma stenops [a]	Phste	Ins	85.5	1.8	11.5	0	1.2	0	11.52	7.20	1.38	2.94
Lonchorhina aurita [a]	Loaur	Ins	84.8	11.3	0	0	3.9	0	11.84	8.12	0.67	3.05
Macrophyllum macrophyllum [a]	Mamac	Ins	82.0	13.5	0	0	4.6	0	9.72	6.92	0.18	2.63
Micronycteris schmidtorum [a]	Misch	Ins	77.8	11.6	7.2	2.1	1.3	0	11.07	7.01	1.33	2.73
Vampyrodes major	Vamaj	Fru	77.6	13.8	8.6	0	0	0	6.96	3.57	0.29	3.11
Lampronycteris brachyotis [a]	Labra	Ins	77.1	16.8	3.5	0	2.5	0	11.48	7.42	0.92	3.13
Lophostoma evotis [a]	Loevo	Ins	76.7	21.7	0	0	1.6	0	13.00	7.97	0.50	4.54
Chrotopterus auritus [a]	Chaur	Ins	75.1	4.5	16.7	1.6	1.0	1.2	11.30	5.47	1.70	4.13
Carollia perspicillata	Caper	Fru	74.5	14.2	9.3	0	1.9	0	10.25	6.12	0.75	3.38
Tonatia saurophila [a]	Tosau	Ins	74.5	20.7	0	0	4.7	0	10.85	7.53	0.39	2.94
Uroderma bilobatum	Urbil	Fru	73.1	21.6	3.1	0	2.3	0	11.06	6.78	0.95	3.34
Diaemus youngi [a]	Diyou	Hem	67.5	18.4	9.4	0	3.4	1.3	10.09	5.98	0.50	3.62
Carollia sowelli	Casow	Fru	66.0	13.2	19.2	1.6	0	0	9.79	4.60	1.07	4.12
Trachops cirrhosus [a]	Trcir	Ins	65.2	23.8	8.6	0	2.5	0	10.60	5.92	1.05	3.64
Phyllostomus discolor	Phdis	Ins	59.4	32.6	5.4	0	2.6	0	9.48	5.33	0.74	3.41
Diphylla ecaudata	Dieca	Hem	57.1	0	37.0	5.1	0.8	0	9.22	3.44	1.98	3.81
Chiroderma villosum	Chvil	Fru	57.0	28.8	12.0	0	2.2	0	10.28	5.50	0.93	3.85
Vampyressa thyone	Vathy	Fru	50.6	48.0	0	0	1.4	0	10.40	5.69	0.60	4.11
Platyrrhinus helleri	Plhel	Fru	46.8	30.5	20.8	0	1.9	0	7.92	3.90	0.46	3.56
Artibeus phaeotis	Arpha	Fru	46.1	37.8	6.2	2.0	7.1	0.7	11.14	5.48	0.99	4.68
Micronycteris microtis	Mimic	Ins	42.5	31.5	22.3	1.6	2.1	0	9.52	3.98	1.17	4.37
Choeroniscus godmani	Chgod	Nec	41.5	34.0	13.5	3.3	7.7	0	9.75	4.28	0.98	4.49
Centurio senex	Cesen	Fru	36.2	31.0	18.9	8.1	5.1	0.7	9.83	3.03	1.54	5.26
Glossophaga leachii	Gllea	Nec	34.4	32.1	25.1	1.6	6.2	0.6	9.39	3.53	1.18	4.67
Artibeus jamaicensis	Arjam	Fru	32.6	31.6	24.9	4.7	5.6	0.5	9.08	3.28	1.16	4.64
Glossophaga soricina	Glsor	Nec	31.5	27.8	25.5	9.3	5.5	0.5	8.83	2.76	1.26	4.81
Artibeus lituratus	Arlit	Fru	31.3	29.9	26.9	6.3	5.6	0	8.68	2.61	1.24	4.83
Carollia subrufa	Casub	Fru	30.6	49.0	15.3	1.7	3.3	0	9.43	3.66	1.38	4.39
Sturnira lilium	Stlil	Fru	28.4	28.5	27.8	9.8	5.1	0.4	8.73	2.17	1.19	5.37

Table 2. (Cont)

			Proportional distribution affinity						OMI Components			
Species	Code	TG	At	P	M	Pl	Ar	D	Inertia	OMI	Tol	TolR
Hylonycteris underwoodi	Hyund	Nec	24.1	24.5	39.1	5.3	4.2	2.9	7.43	1.59	0.38	5.47
Desmodus rotundus	Derot	Hem	23.4	24.9	25.7	22.0	3.7	0.4	8.53	1.54	1.07	5.92
Glyphonycteris sylvestris	Glsyl	Ins	23.0	41.2	22.2	7.5	5.4	0.7	9.21	2.53	1.41	5.27
Glossophaga commissarisi	Glcom	Nec	19.9	50.7	16.6	6.3	5.6	0.9	9.74	3.23	1.77	4.74
Glossophaga morenoi	Glmor	Nec	17.5	76.8	0	0	5.7	0	10.01	6.30	0.89	2.82
Artibeus toltecus	Artol	Fru	14.2	32.5	36.5	10.8	5.4	0.6	7.72	1.72	0.45	5.55
Sturnira ludovici	Stlud	Fru	13.8	26.1	41.4	14.0	2.8	1.9	7.29	1.26	0.20	5.83
Anoura geoffroyi	Angeo	Nec	13.3	30.7	38.4	14.3	2.7	0.6	7.72	1.35	0.19	6.17
Chiroderma salvini	Chsal	Fru	13.3	30.7	29.3	15.8	6.8	4.1	8.57	1.61	0.44	6.52
Enchisthenes hartii [a]	Enhar	Fru	13.0	30.4	38.9	10.9	2.5	4.3	8.43	1.57	0.19	6.67
Leptonycteris yerbabuenae [a,b]	Leyer	Nec	7.8	23.4	24.1	25.6	14.7	4.3	7.50	0.90	1.33	5.28
Artibeus aztecus	Arazt	Fru	7.1	18.1	47.3	22.4	1.3	3.7	7.62	1.96	1.02	4.64
Leptonycteris nivalis [a,b]	Leniv	Nec	5.2	20	23.0	26.8	7.2	17.9	7.33	0.66	0.44	6.23
Choeronycteris mexicana [a,b]	Chmex	Nec	2.5	16.1	22.2	24.4	17.4	17.4	7.83	0.26	1.30	6.27
Artibeus hirsutus	Arhir	Fru	1.7	33.7	20.8	20.9	19.4	3.5	7.88	2.98	0.86	4.04
Uroderma magnirostrum	Urmag	Fru	0	94.2	0	0	5.8	0	12.46	9.91	0.33	2.22
Musonycteris harrisoni [a,b]	Muhar	Nec	0	85.4	0	0	14.6	0	12.17	9.70	0.59	1.88
Macrotus waterhousii	Mawat	Ins	0	40.5	24.7	22.2	10.3	2.2	7.71	2.26	1.28	4.18
Macrotus californicus	Macal	Ins	0	8.7	3.5	13.4	70.5	3.9	10.03	2.43	0.65	6.95

rra de Chiapas, and Eje Neovolcánico Transversal), showed a richness area with 10 to 35 species, such as *Artibeus aztecus, Sturnira ludovici* and *Hylonycteris underwoodi.* (4) The Plateau group, in the inner slopes of the Neovolcanic Belt in the southern part of the Mexican plateau, had areas with up to 20 species, such as *Leptonycteris nivalis, Leptonycteris yerbabuenae* and *Choeronycteris mexicana*. (5) The Arid group, in the Sonoran Desert, included areas with one to 10 species where *Macrotus californicus* was distinctive. (6) The Desert group, in a portion of the Chihuahuan Desert, had areas where one to six species occurred, such as *Choeronycteris mexicana* and *Leptonycteris nivalis*. In a seventh group, in a large part of the Chihuahuan Desert, no species were observed (i.e., the Absence group

Environmental segregation of phyllostomid bats

The multidimensional distances of environmental conditions in which all species were recorded are significantly different from the study area average ($p < 0.05$); that is, at least one species occurred in different environmental conditions that averaged all sites (table 2). The first two axes of the OMI analysis accounted for 92.2 % of the total variance. The first axis explained 81.4 % of the variation, mainly due to variations in the yearly mean minimum temperature and the tree–cover percentage. The second axis explained 10.8 % of the variation due to variations in the precipitation percentage in July and the herbaceous cover percentage (fig. 3A). The first OMI axis separates the environments where the family occurs from those where it is absent. Phyllostomid bats were present in environments that have a yearly minimum mean temperature above 13.5 ºC (from 12 to 20 ºC; fig. 3B) and a mean tree–cover percentage higher than 24 % (from 20 to 80 %; fig. 3C). The second axis revealed an environmental gradient associated with variations in precipitation in which the species are distributed. Most species (e.g., *Mimon crenulatum, Phylloderma stenops*) occurred in environments where six to 12 % of the annual rainfall occurs in July (fig. 3D) and the herbaceous cover percentage is from 20 to 40 % (fig. 3E). Conversely, several species (e.g., *Choeronycteris mexicana*, *Macrotus californicus*) occurred in environments where 12 to 18 % of the annual precipitation occurs in July and the herbaceous cover constitutes 40 to 60 %.

We found three groups of bat species that occurred in similar sites (threshold value of 2.5 units, fig. 3F). The groups were differentiated according to species distribution range: (1) Widespread distribution (across 17 to 51 % of Mexico's surface) was found throughout the entire study area, occurring in groups in all sites. This species group was composed of 24 species with mainly frugivorous or nectarivorous bats (e.g.,

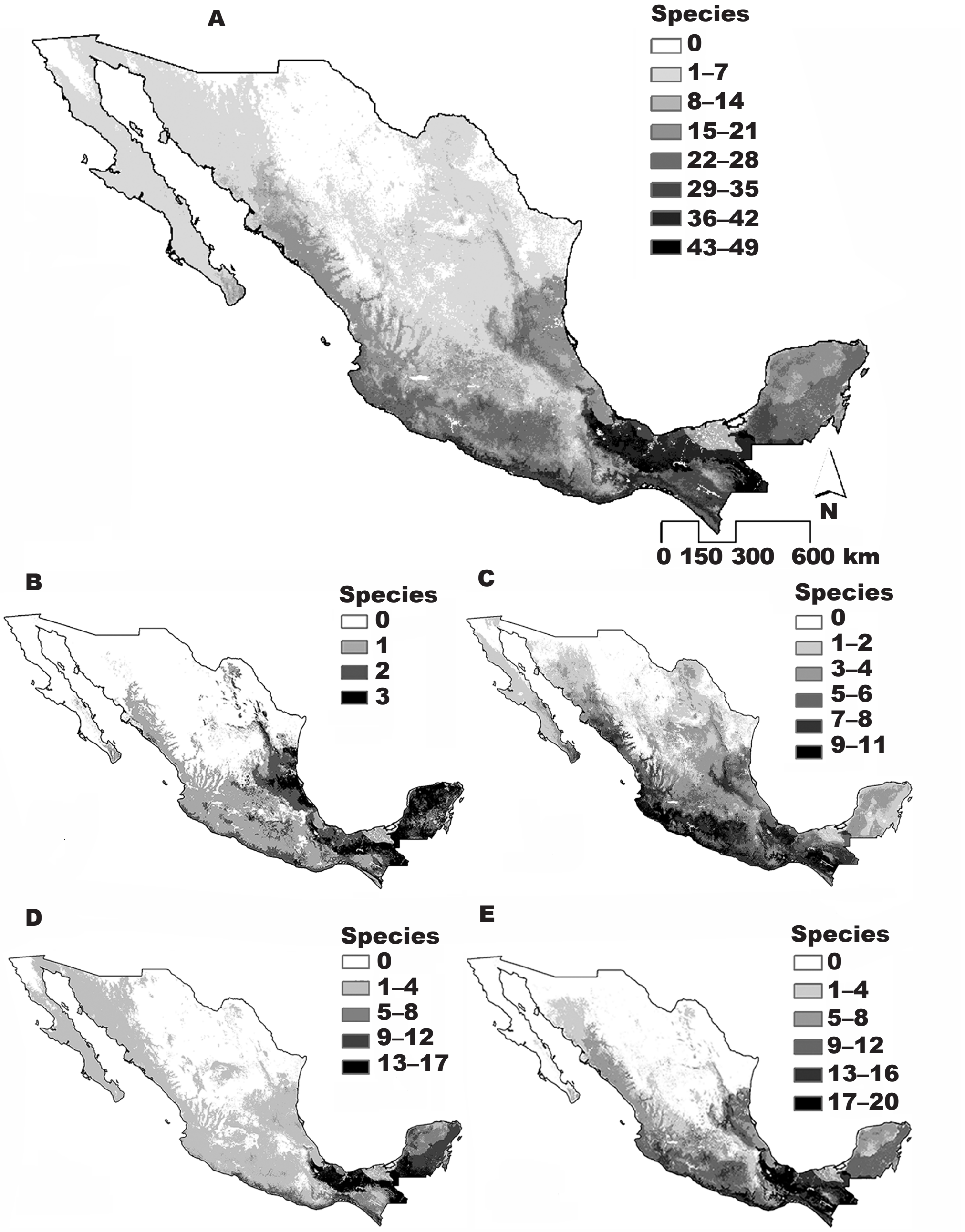


Fig. 1. Spatial richness pattern in Mexico: A, Phyllostomidae family; B, hematophagous bats; C, nectarivorous bats; D, insectivorous bats; E, frugivorous bats.

Fig. 1. Patrón espacial de riqueza en México: A, familia Phyllostomidae; B, murciélagos hematófagos; C, murciélagos nectarívoros; D, murciélagos insectívoros; E, murciélagos frugívoros.

Sturnira lilium, *Leptonycteris yerbabuenae*) and one hematophagous species (i.e., *Desmodus rotundus*). (2) Regional distribution (in eight to 21%) was associated with the Neotropical region, with a limited presence in mountain systems, mainly present in the Atlantic group. This species group was composed of 18 species, mainly insectivorous bats (e.g., *Micronycteris microtis, Phylloderma stenops*) and the remaining two hematophagous species. (3) Narrow distribution (in three to 15%) had an endemic or restricted distribution in the Atlantic or Pacific groups. This species group had 11 species (e.g., *Uroderma magnirostrum, Musonycteris harrisoni*): six frugivorous, three insectivorous, and two nectarivorous species.

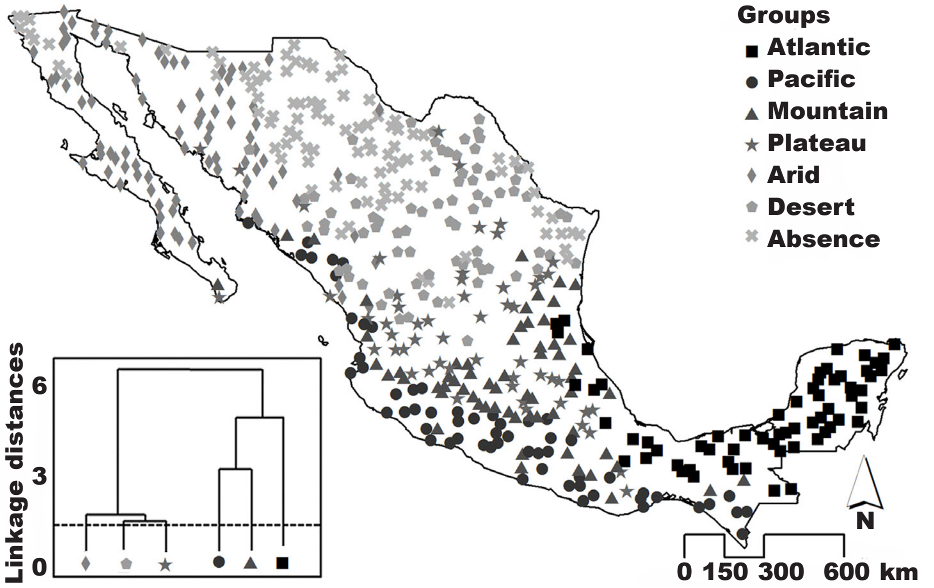


Fig. 2. Groups of sites with a distinctive phyllostomid bat species composition.

Fig. 2. Grupos de sitios con una composición distintiva de especies de murciélagos filostómidos.

Overlap between phyllostomid bat distribution and human modified areas

Native/secondary vegetation covers 72.2 % of Mexico, and the remaining 27.8 % has been human–modified for crops (17 %), livestock (9.9 %) and urban zones (0.9 %). We found 30.9 % of the entire Phyllostomidae family spatial distribution overlapped with human–modified areas (table 3). Cropland was the most broadly distributed cover type converging with the family and the four feeding guilds. In the Atlantic group, the high richness areas of the Phyllostomidae family and the guilds of hematophagous, insectivorous and frugivorous bats overlapped with livestock (fig. 4). In the Pacific group, the high richness areas for nectarivorous bats converged similarly with all types of human changes.

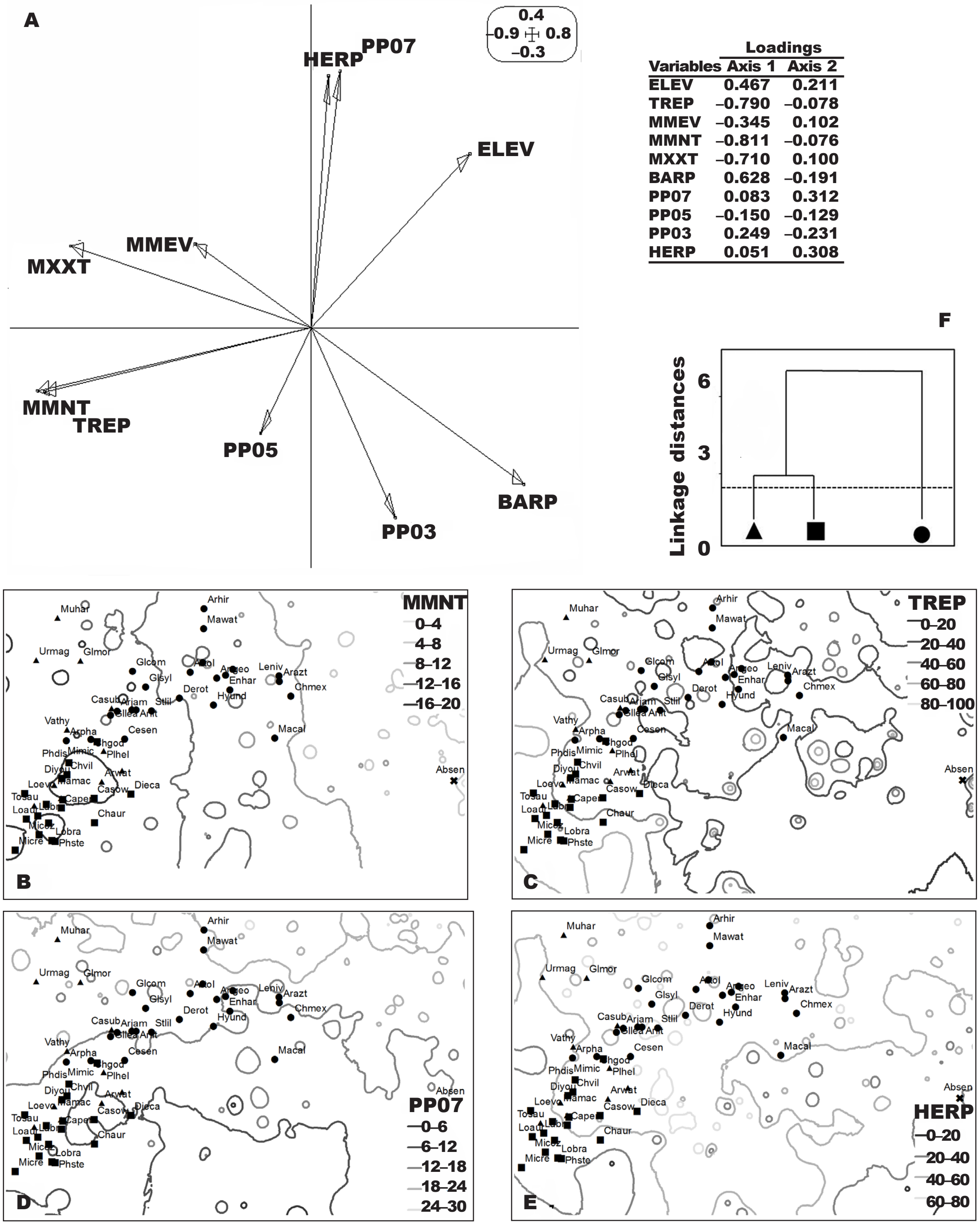
Discussion

In this study, we provide a perspective about phyllostomid bat distribution in Mexico. We identified six site groups with distinctive species assembly, three species groups that co–occurred in similar sites, environmental tolerances of each species, and the degree of overlap with human activities. The distribution of phyllostomid bats showed a spatial richness pattern that related negatively to latitude, decreasing the number of species from tropical environments in southern to arid environments in northern Mexico (fig. 1A; Stevens, 2006). The highest species richness areas were in the Tehuantepec Isthmus region, except for nectarivorous bats (figs. 1B–1E). The latitudinal pattern has been reported for groups such as reptiles (Ochoa–Ochoa and Flores–Villela, 2006), birds (García–Trejo and Navarro, 2004) and terrestrial mammals (Escalante et al., 2007). The

Table 3. Proportional convergence between phyllostomid bat distribution and human–modified areas in Mexico: Cr, cropland; Lv, livestock; Urb, urban; Phy, Phyllostomidae family; Hem, hematophagous bats; Nec, nectarivorous bats; Ins, insectivorous bats; Fru, frugivorous bats.

Tabla 3. Convergencia proporcional entre la distribución de murciélagos filostómidos y las zonas modificadas por el hombre en México: Cr, cultivo; Lv, ganado; Urb, urbano; Phy, familia Phyllostomidae; Hem, murciélagos hematófagos; Nec, murciélagos nectarívoros; Ins, murciélagos insectívoros; Fru, murciélagos frugívoros.

	Anthropic activities			
	Cr	Lv	Urb	Total
Phy	18.97	11.04	0.98	30.99
Hem	23.39	15.13	1.21	39.73
Nec	19.81	11.56	1.07	32.44
Ins	18.91	13.15	0.97	33.03
Fru	21.93	14.52	1.03	37.48



Variables	Loadings Axis 1	Loadings Axis 2
ELEV	0.467	0.211
TREP	–0.790	–0.078
MMEV	–0.345	0.102
MMNT	–0.811	–0.076
MXXT	–0.710	0.100
BARP	0.628	–0.191
PP07	0.083	0.312
PP05	–0.150	–0.129
PP03	0.249	–0.231
HERP	0.051	0.308

Fig. 3. Factor loadings for environmental variables along the two axes of the OMI analysis (3A), showing the most important occurrences of phyllostomid bats in Mexico (3B–3E). The cluster identified species that have similar distribution ranges (3F): widespread (●), regional (■), and narrow (▲). (For abbreviations see tables 1 and 2).

Fig. 3. Carga de factores para las variables ambientales en los dos ejes del análisis OMI (3A), donde se muestran las presencias más importantes de filostómidos en México (3B–3E). El clúster identifica las especies que presentan un rango de distribución similar (3F): amplio (●), regional (■) y estrecho (▲). (Para consultar las abreviaturas, véanse las tablas 1 y 2).

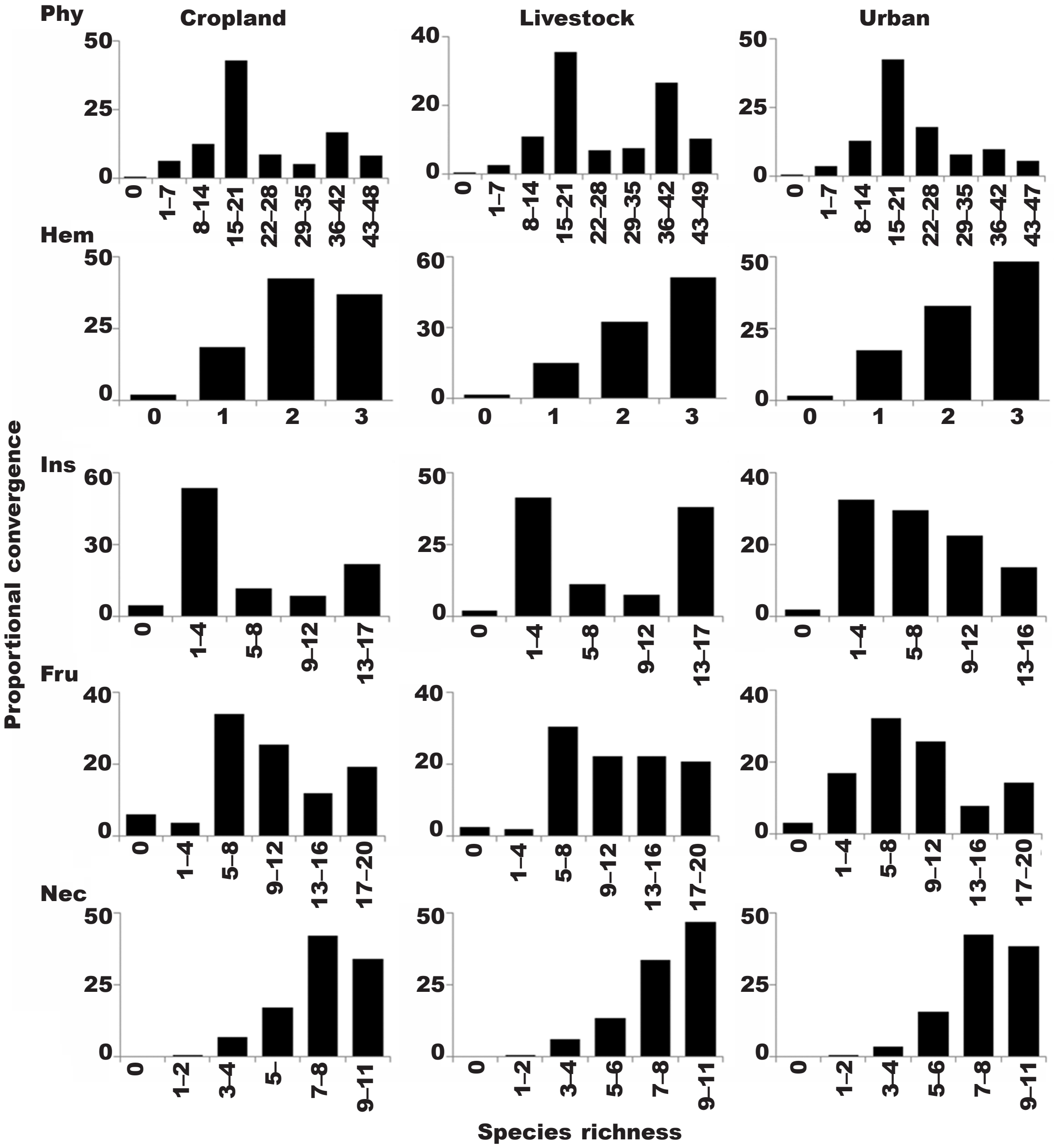


Fig. 4. Proportional convergence between phyllostomid bat richness and human–modified areas in groups of sites with the highest richness: the Atlantic group for the Phyllostomidae family (Phy) and hematophagous (Hem), insectivorous (Ins), and frugivorous (Fru) bats; and the Pacific group for nectarivorous bats (Nec).

Fig. 4. Convergencia proporcional entre la riqueza de especies de filostómidos y las zonas modificadas por el hombre en los grupos de sitios con la mayor riqueza: grupo del Atlántico para murciélagos de la familia Phyllostomidae (Phy) y para murciélagos hematófagos (Hem), insectívoros (Ins) y frugívoros (Fru); y el grupo del Pacífico para murciélagos nectarívoros (Nec).

identified groups of sites with distinctive bat species composition (fig. 2) showed a specific occurrence along with temperature and vegetation cover gradient (mainly tree cover; fig. 3; López–González et al., 2011) in relation to specific environmental tolerance.

The species occurrences with common origin and differential environmental preferences in the same area are related to their evolutionary histories leading to their diversification and current distributions (Dumont et al., 2012).

The groups of sites identified as the Neotropic region, the Atlantic and Pacific groups, present distinctive environments (i.e., tropical and subtropical) and are composed of ancestral bat species, such as *Micronycteris* or *Diphylla* genus. The Atlantic group containe mostly insectivorous species from the subfamily Phyllostominae (e.g., *Mimon crenulatum* and *Lophostoma brasiliense*), with a high marginality (mean OMI = 6; table 2) that occur in specific environmental conditions, such as perennial forests. Insectivorous bats are narrowly distributed (fig. 3) and have been associated with large forest fragments, where a high availability of resources is found (e.g., food and roost; Medellín et al., 2000). On the other hand, the Pacific group is composed principally of frugivorous and nectarivorous species with a narrow or widespread distribution (e.g., *Musonycteris harrisoni* and *Chiroderma salvini*), in deciduous forests. However, the species has a higher tolerance (mean Tol ~1) than species in the Atlantic group, allowing their persistence when resources are scarce through the variation in seasons found in deciduous environments (Chávez and Ceballos, 2001).

The groups of sites identified in the limits of the Neotropic region or in the Nearctic region present distinctive environments (i.e., temperate, arid) and are composed of the phylogenetically derived bat species, such as *Artibeus* and *Leptonycteris* genus (fig. 2). In the Mountain and Plateau groups, an elevational gradient derived from the mountains promotes variable climatic conditions (i.e., temperature and humidity) that results in different vegetation types (e.g., temperate forests and grasslands; Ramanoorthy et al., 1998). The groups are composed of frugivorous and nectarivorous species (e.g., *Artibeus aztecus* and *Leptonycteris nivalis*) that have low marginality (mean OMI < 1.3, table 2). However, the species are distributed widely (fig. 3) due to adaptations such as dietary changes and migratory movements that allow them to colonize temperate environments (Fleming et al., 2009). In Northern Mexico, the species most commonly present in the Arid and Desert groups are *Macrotus californicus* and *Leptonycteris nivalis*, species that have a widespread distribution and that are tolerant to average conditions in Mexico (mean Tol = 0.5). The species that occur in semi–arid environments, such as *Macrotus californicus*, tolerate desert conditions through behavioral and physiological adaptations (Bell et al., 1986), while *Leptonycteris nivalis* uses migration and mutualism with scrubland xeric plants (Fleming et al., 2009). The persistence of these species in arid zones is high. These zones are the best conserved ecosystems in Mexico because the low availability of water limits the establishment and growth of human populations (Challenger and Dirzo, 2009).

The potential distribution of the Phyllostomidae family in Mexico showed a 30 % overlap with areas modified by human activities (table 3). The percent of overlap with the modified areas varied among feeding guild species; for example, convergence of higher richness of hematophagous and nectivorous species with modified areas differed with insectivorous guild, so they may be affected differentially (fig. 4). Frugivorous bats will be less vulnerable to human activities because they have a higher niche tolerance and a lower marginality (e.g., genus *Sturnira* and *Artibeus*, table 2). These species are generalist, and they exploit a broad amplitude of resources in both preserved and disturbed environments (Klingbeil and Willig, 2009). Common vampire bats (*Desmodus rotundus*) have a negative interaction with humans because they cause economic loss to the beef industry and play a role in the epidemiology of bovine paralytic rabies in rural areas (Dantas–Torres, 2008). However, future climate projections predict an increase in the distribution of *D. rotudus* (Lee et al., 2012). In contrast, other endangered hematophagous species (i.e., *Diphylla ecaudata* and *Diaemus youngi*) that do not interfere with human activities are under risk through population control of the common vampire bat (Vercauteren et al., 2012). Insectivorous bats (e.g., *Micronycteris microtis* and *Mimon cozumelae*) are vulnerable to agricultural practices because they show a low tolerance and a high marginality (Medellín et al., 2000) and because they converge with croplands where humans regulate pests with chemicals that are toxic to bats (table 3; Lawer and Darkoh, 2016). The nectarivorous bats, due to their widespread distribution and high richness areas, overlap with human–modified areas (fig. 4) and their distribution can indirectly affect their vital biological processes, such as the loss of reproduction areas, mutualistic associations and modified migratory movements (Fleming et al., 2009).

The spatial–environmental distribution of the Phyllostomidae family in Mexico reveals a species response to niche requirements and human changes. For example, species in homogeneous environments (e.g., tropical forests) have smaller niche breadth and narrow distributions, being more sensitive to environmental changes (Brown, 2014). On the other hand, species in heterogeneous environments (e.g., deserts) have broad niche breadth and widespread distributions with tolerance to disturbance (Krebs, 2001). In the country, the highest native cover loss occurs in tropical forests of the Atlantic and Pacific coastal plains, because low slopes and precipitation provide optimal conditions for the development of agricultural activities (Challenger and Dirzo, 2009), while the human population is concentrated mostly in Meseta Central (Klein–Goldewijk and Ramankutty, 2004), areas where phyllostomid bat richness is also high (fig. 1). Medium (2023) and long–trend (2033) scenarios predict that if conservation actions are not implemented, an unstable to very critical scenario will occur in these areas (Sánchez–Salazar et al., 2013); in this sense, Protected Areas play a fundamental role in conserving biodiversity (Myers et al., 2000).

Mexico has decreed 181 Protected Areas (www.conanp.gob.mx) to maintain the integrity of ecosystems and environmental services. The decrees are supported by laws that regulate anthropogenic activities. However, most of these areas are surrounded by modified zones, are in mountainous regions, do not include high diversity areas, or show some degree of deterioration (Fuller et al., 2006). In the case of phyllostomid bats, nectarivorous and insectivorous bats are susceptible to constant environmental degradation caused by humans. Thus, conservation strategies may complement the surface of protected areas through the delimitation of areas with suitable environmental conditions to promote the persistence and flow of biodiversity (Nori et al., 2016). The approach used in this work can be extrapolated to other regions and taxa, which in turn will provide a better understanding of regional patterns of richness and species composition (Peterson et al., 2015). Our results showing the areas with the highest bat richness may be useful to propose biological corridors and conservation priority areas using approaches such as systematic conservation planning (Margules and Sarkar, 2009).

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Supplementary material

Table 1s. List of original environmental variables.

Tabla 1s. *Lista de las variables ambientales originales.*

Variable	Code	Type	Source
Maximum temperature in January	XT01	Climatic	www.worldclim.org
Maximum temperature in February	XT02	Climatic	www.worldclim.org
Maximum temperature in March	XT03	Climatic	www.worldclim.org
Maximum temperature in April	XT04	Climatic	www.worldclim.org
Maximum temperature in May	XT05	Climatic	www.worldclim.org
Maximum temperature in June	XT06	Climatic	www.worldclim.org
Maximum temperature in July	XT07	Climatic	www.worldclim.org
Maximum temperature in August	XT08	Climatic	www.worldclim.org
Maximum temperature in September	XT09	Climatic	www.worldclim.org
Maximum temperature in October	XT10	Climatic	www.worldclim.org
Maximum temperature in November	XT11	Climatic	www.worldclim.org
Maximum yemperature in December	XT12	Climatic	www.worldclim.org
Minimum yemperature in January	NT01	Climatic	www.worldclim.org
Minimum temperature in February	NT02	Climatic	www.worldclim.org
Minimum temperature in March	NT03	Climatic	www.worldclim.org
Minimum temperature in April	NT04	Climatic	www.worldclim.org
Minimum temperature in May	NT05	Climatic	www.worldclim.org
Minimum temperature in June	NT06	Climatic	www.worldclim.org
Minimum temperature in July	NT07	Climatic	www.worldclim.org
Minimum temperature in August	NT08	Climatic	www.worldclim.org
Minimum temperature in September	NT09	Climatic	www.worldclim.org
Minimum temperature in October	NT10	Climatic	www.worldclim.org
Minimum temperature in November	NT11	Climatic	www.worldclim.org
Minimum temperature in December	NT12	Climatic	www.worldclim.org
Precipitation in January	PI01	Climatic	www.worldclim.org
Precipitation in February	PI02	Climatic	www.worldclim.org
Precipitation in March	PI03	Climatic	www.worldclim.org
Precipitation in April	PI04	Climatic	www.worldclim.org
Precipitation in May	PI05	Climatic	www.worldclim.org
Precipitation in June	PI06	Climatic	www.worldclim.org
Precipitation in July	PI07	Climatic	www.worldclim.org
Precipitation in August	PI08	Climatic	www.worldclim.org
Precipitation in September	PI09	Climatic	www.worldclim.org
Precipitation in October	PI10	Climatic	www.worldclim.org
Precipitation in November	PI11	Climatic	www.worldclim.org

Table 1s. (Cont.)

Variable	Code	Type	Source
Precipitation in December	PI12	Climatic	www.worldclim.org
Evapotranspiration in January	EV01	Climatic	www.worldclim.org
Evapotranspiration in February	EV02	Climatic	www.worldclim.org
Evapotranspiration in March	EV03	Climatic	www.worldclim.org
Evapotranspiration in April	EV04	Climatic	www.worldclim.org
Evapotranspiration in May	EV05	Climatic	www.worldclim.org
Evapotranspiration in June	EV06	Climatic	www.worldclim.org
Evapotranspiration in July	EV07	Climatic	www.worldclim.org
Evapotranspiration in August	EV08	Climatic	www.worldclim.org
Evapotranspiration in September	EV09	Climatic	www.worldclim.org
Evapotranspiration in October	EV10	Climatic	www.worldclim.org
Precipitation in November	EV11	Climatic	www.worldclim.org
Precipitation in December	EV12	Climatic	www.worldclim.org
Elevation	ELEV	Topographic	https://lta.cr.usgs.gov/hydro1k
Aridity Index	ARIX	Land Cover	www.glcf.umd.edu
Bare cover percentage	BARP	Land Cover	www.glcf.umd.edu
Tree cover percentage	TREP	Land Cover	www.glcf.umd.edu
Herbaceous cover percentage	HERP	Land Cover	www.glcf.umd.edu
Evergreen vegetation cover percentage	PERP	Land Cover	www.glcf.umd.edu
Deciduous vegetation cover percentage	DECP	Land Cover	www.glcf.umd.edu
Broad–leaf vegetation cover percentage	BROP	Land Cover	www.glcf.umd.edu
Needle–leaf vegetation cover percentage	NEDP	Land Cover	www.glcf.umd.edu
Ecoregions	ECOR	Categorical	Olson et al. (2001)

Table 2s. List of new variables obtained by climatic variables modification.

Tabla 2s. Lista de nuevas variables obtenidas al modificar las variables climáticas.

New variables	Code
Mean yearly maximum temperatures	MXMT
Standard deviation of yearly maximum temperatures	MXSD
Maximum of yearly maximum temperatures	MXXT
Maximum of maximum temperatures in first quarter	MX1Q
Maximum of maximum temperatures in second quarter	MX2Q
Maximum of maximum temperatures in third quarter	MX3Q
Maximum of maximum temperatures in fourth quarter	MX4Q
Maximum of yearly minimum temperatures	MXNT
Maximum of minimum temperatures in first quarter	MN1Q
Maximum of minimum temperatures in second quarter	MN2Q
Maximum of minimum temperatures in third quarter	MN3Q
Maximum of minimum temperatures in fourth quarter	MN4Q
Mean of yearly minimum temperatures	MMNT
Minimum of yearly maximum temperatures	MNXT
Minimum of maximum temperatures in first quarter	NX1Q
Minimum of maximum temperatures in second quarter	NX2Q
Minimum of maximum temperatures in third quarter	NX3Q
Minimum of maximum temperatures in fourth quarter	NX4Q
Minimum of yearly minimum temperatures	YNNT
Standard deviation of yearly minimum temperatures	MTSD
Minimum of minimum temperatures in first quarter	NN1Q
Minimum of minimum temperatures in second quarter	NN2Q
Minimum of minimum temperatures in third quarter	NN3Q
Minimum of minimum temperatures in fourth quarter	NN4Q
Total of yearly precipitation	YTPP
Mean of yearly precipitation	YEPP
Percentage of precipitation in January	PP01
Precipitation percentage in February	PP02
Percentage of precipitation March	PP03
Percentage of precipitation April	PP04
Percentage of precipitation May	PP05
Percentage of precipitation June	PP06
Percentage of precipitation July	PP07
Percentage of precipitation August	PP08
Percentage of precipitation September	PP09
Percentage of precipitation October	PP10
Percentage of precipitation November	PP11
Percentage of precipitation December	PP12
Mean of yearly evapotranspiration	MMEV
Standard deviation of yearly evapotranspiration	EVSD
Maximum of yearly evapotranspiration	MXEV
Minimum of yearly evapotranspiration	MNEV

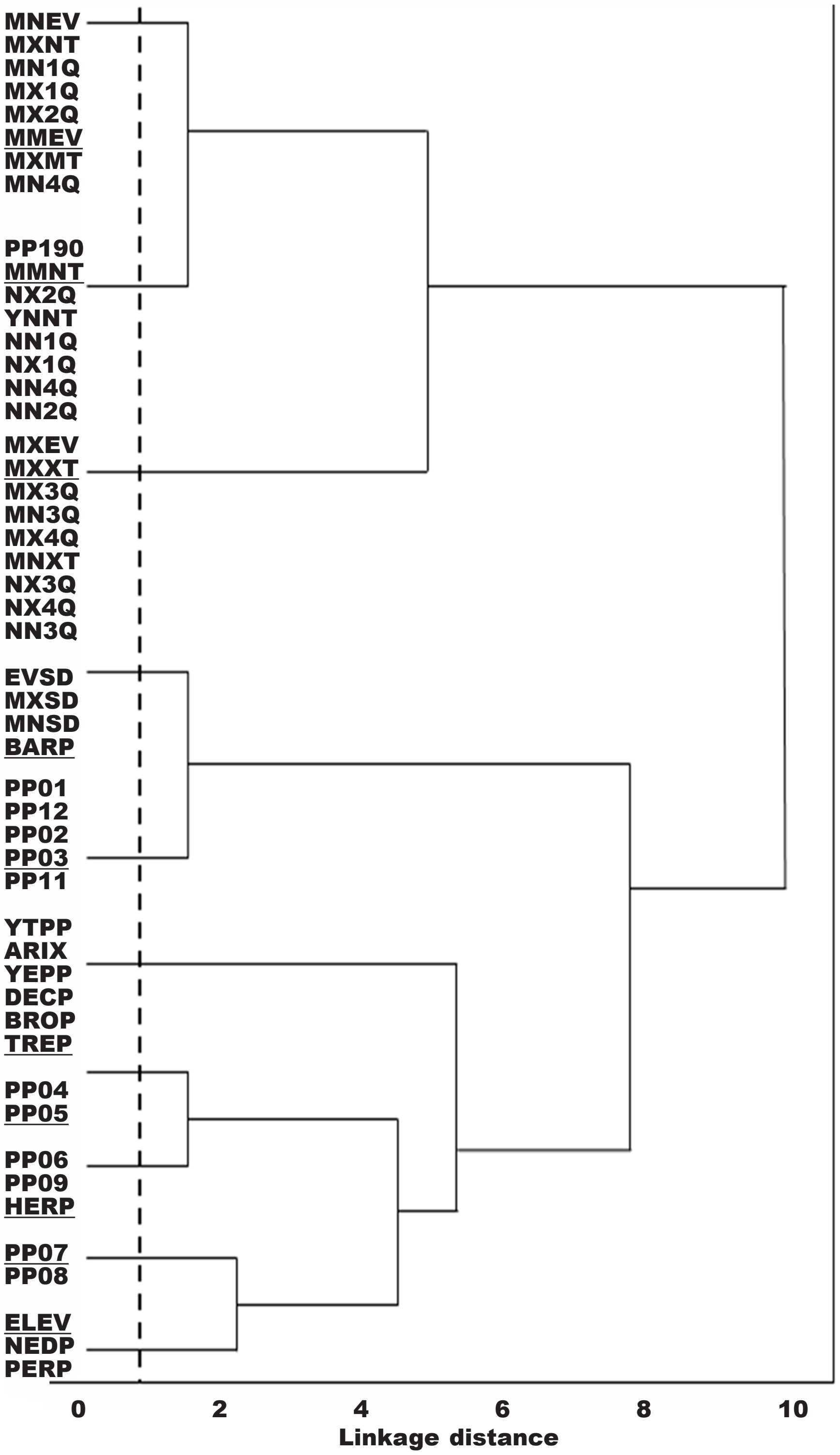

Fig. 1s. Cluster analysis to select the uncorrelated environmental variables (underlined).

Fig. 1s. Análisis de conglomerados para seleccionar las variables ambientales no correlacionadas (subrayadas).