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RESEARCH PAPER

Ecological characterization of bat species distributions in Michoacán, México, using a geographic information system

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ABSTRACT

Aim To investigate the relationship between chiropteran species distributions and four fundamental environmental factors — temperature, precipitation, soil and vegetation — and to construct a species richness prediction map based on the environmental factors.

Location The state of Michoacán, México.

Methods Bat specimens collected during a 2-year project were combined with museum specimens to form a dataset of over 3200 entries pertaining to 71 species of bats. Coordinates of the collection localities were recorded with GPS receivers or determined from maps. ArcView GIS was used to characterize the distribution of the species relative to the four environmental factors by projecting coordinates of the collection sites onto digitized maps of those factors. Correspondence analysis (CA) was used to evaluate the relationship between species distributions and the environmental factors.

Results The CA results indicated that the order of importance of these factors is (from highest to lowest): temperature, vegetation, precipitation and soil. A predicted distribution map was constructed for each species of bat, based on the result of the CA analysis, using correspondences of each species to climate, vegetation and precipitation. Soil types were excluded from the prediction model because soil type does not appear to carry high predictive value for bat species in Michoacán. Distribution maps of the 71 bat species were then overlaid to generate a map of bat species richness for the state of Michoacán.

Main conclusions Neither family membership nor feeding guild affiliation appear to play important roles in chiropteran species distributions in Michoacán. The bat species richness prediction map will be a useful tool for conservation works in the region.

Key words bats, conservation, correspondence analysis, environmental factor, GIS, Michoacán, species distribution.

INTRODUCTION

Understanding the factors that contribute to biodiversity and zoogeographical patterns is crucial to the work of systematists, ecologists and conservation biologists. These studies provide information not only for basic scientific understanding, but also for land and wildlife management planning. Despite recent increased successes of reductive works from experimental ecological and molecular evolutionary studies, macroscopic studies are needed to extrapolate such results to explain patterns and processes on larger scales (Brown, 1995).

Tropical regions contain much richer and more diverse faunas than other ecosystems (Wilson, 1985, 1988). Moreover, these regions face some of the most critical problems of species extinction and natural resource depletion (Ceballos & Navarro, 1991). For the rich tropical faunas to be protected adequately, surveys and species inventories for geographical areas in the tropics are research priorities in conservation biology (Soulé & Kohm, 1989).

Being in the transition zone between the Nearctic and Neotropical regions, Middle America has one of the richest and most distinct faunas of the world (Arita & Ortega, 1998). Central México exhibits the sharpest transition between the

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Nearctic and Neotropical biogeographical realms (Brown & Gibson, 1983). A major geological and topographic component of the region is the Trans-Mexican Neovolcanic Belt (TNB). The TNB is a mountain range in central México between 17°30′ and 20°25′N latitude, and 96°20′ and 105°20′W longitude (Ferrusquía Villafranca, 1998). The range extends from southern Veracruz through Michoacán, Colima, and into southern Jalisco, reaching both the Pacific and Gulf coasts of México. The range forms a partial barrier between faunas of the subtropics to the north and those of the more tropical regions to the south, with many species distributions terminating within it (Fa & Morales, 1991).

Factors such as climate, spatial heterogeneity and environmental stability all affect the number and type of species found within a particular region. In fact, such abiotic factors are considered to be among the ultimate regulators of species distribution (Brown, 1995). The TNB has high spatial heterogeneity, resulting in high biodiversity, species interactions and endemism.

Animal species diversity is also affected strongly by habitats and vegetation (Fa & Morales, 1991). In the TNB, vegetation ranges from lowland tropical forests to high elevation grasslands. Cloud forests (with trees such as *Quercus*, *Clethra* and *Liquidambar*) at higher elevations contain the highest mammalian species diversity, and tropical associations such as semideciduous forests (with *Bursera*, *Ceiba*, *Neobuxbaumia*, *Brosimum*, etc.) also exhibit high diversities (Ramamoorthy *et al.*, 1998).

Notwithstanding the extremely rich mammalian fauna of México, knowledge of distributions, habitat preferences and reproduction is poor for most species. This is true especially in the western portion of the TNB in the state of Michoacán on the south-west coast of México (Fig. 1). Despite the recent attention that Michoacán has received from mammalogists, and despite its high mammalian diversity, it is one of the more poorly known states in México (Sánchez-Hernández *et al.*, 1999).

Michoacán extends from 17.93°N to 20.40°N latitude, and between 100.05°W and 103.75°W longitude. Bounded by the Pacific Ocean and the states of Colima, Jalisco, Guanajuato, Querétaro, México and Guerrero, Michoacán covers an area of 59 864 km^2. The state contains extreme topographic variation (sea level to over 3800 m) and a high diversity of

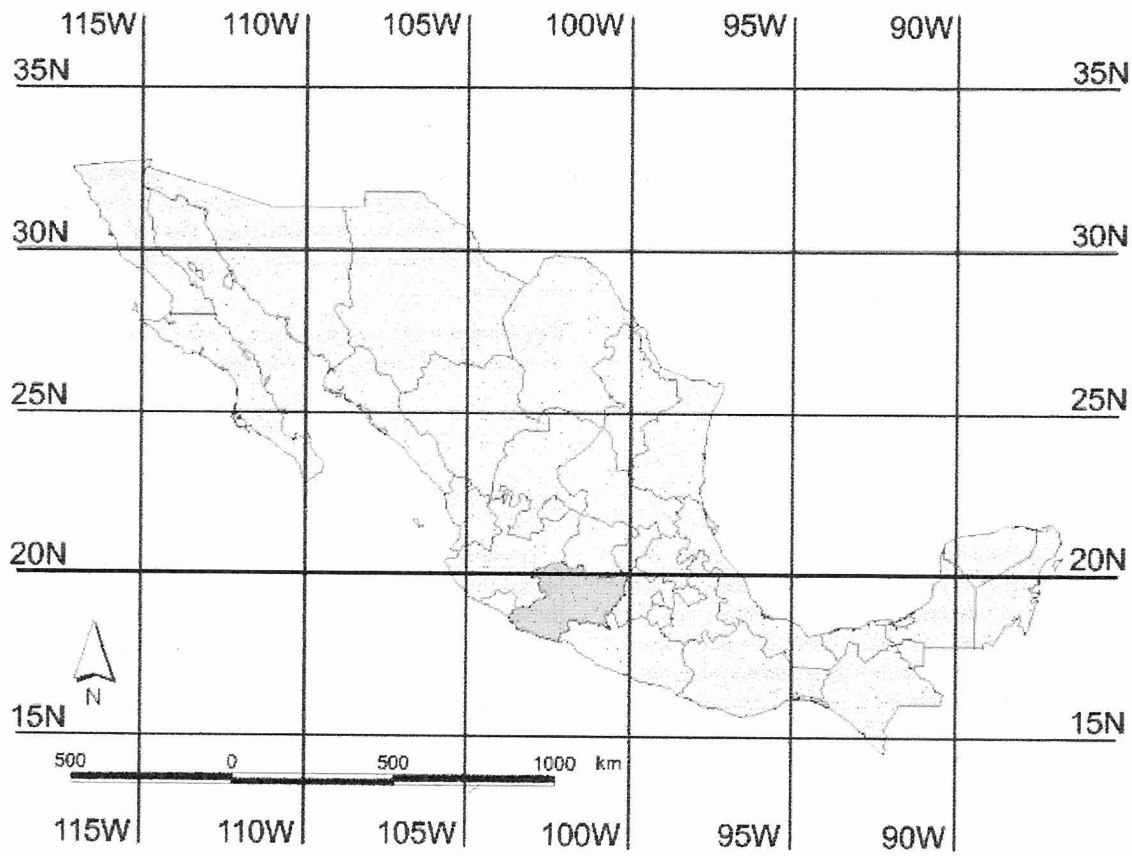

Fig. 1 Location of study area (shading) in México.

climatic regions and vegetation types (Sánchez-Hernández *et al.*, 1999).

Although 26 protected areas (parks and reserves) exist within the TNB (Vargas Marquez, 1984), protection of habitats is inadequate in western areas such as Michoacán (Fa & Morales, 1991). Fortunately, because of historical and physiographic reasons, the state of Michoacán has suffered less degradation than some of the eastern regions. Nevertheless, many species have become extinct or extirpated since the early twentieth century, largely due to over-exploitation and habitat perturbation by humans (Ceballos & Navarro, 1991).

A comprehensive study of Michoacán's biodiversity is essential to the understanding and better management of the state's mammalian fauna. Knowledge gained from such studies will also be invaluable towards land usage management decisions. Planning for activities such as forestry and farming can utilize this information for the choice of locations and management. Furthermore, states adjacent to Michoacán with similar ecological conditions may also extrapolate the results to implement management strategies.

The focus of this study is on investigating the relationship between chiropteran (bat) species distributions and four fundamental environmental factors (climate, precipitation, soil and vegetation) within Michoacán. Bats are an Order of mammals that is abundant, species-rich and biologically diverse. They are found in virtually all terrestrial biomes except tundra and polar regions (Nowak, 1999). Consequently, bats play various and important ecological roles in both tropical and temperate communities. They have, unfortunately, been largely neglected in conservation and environmental education programmes (Marinho-Filho & Sazima, 1998). Due to their high richness and diversity, bats are ideal subjects by which species distributions and their interrelationships with the environment can be examined.

The specific objectives of this study are to: (1) determine the relative importance of the four environmental factors, with respect to the distributions of bat species within Michoacán; (2) determine the component within each factor that correlates most strongly with each species' distribution within Michoacán; (3) construct a predictive map for each species' distribution within Michoacán; and (4) construct a predictive map of bat species richness for the state of Michoacán.

MATERIALS AND METHODS

The distribution patterns of 71 bat species were evaluated in this study, utilizing a geographical information system (GIS), with respect to the four selected environmental factors. GIS is useful for such analyses in that it is capable of organizing and analysing large sets and multiple layers of spatially related but distinct data (Witham & Kimball, 1996). GIS technology has wide applications in ecological modelling (e.g. Aspinall & Matthews, 1994; Liu *et al.*, 1995; Witham & Kimball, 1996; Kadmon & Heller, 1998), wildlife management and conservation (e.g. Bojórquez-Tapia *et al.*, 1995; Lewis, 1995; Ostro *et al.*, 1999) and pattern analysis (Sheeler-Gordon & Owen, 1999).

Species data

A survey and inventory of small mammals was conducted in Michoacán. The project was designed to collect data to answer questions concerning the systematics, ecology and zoogeography of the mammalian and ectoparasite fauna of south-western México. In addition, preliminary collection of material had been conducted beginning in 1975, mainly by Cornelio Sánchez-Hernández and his students. Intensive fieldwork for the project was carried out between 1992 and 1996, with the most intensive periods in 1994 and 1995. Several thousand mammalian specimens (mainly rodents and bats) were collected during this period.

Over 50 localities were sampled throughout the state to ensure that the collections were as representative as possible. Collecting methods for bats included mist-nets, hand-nets and by hand. Specimens were processed as soon as possible (within the same day of capture). Each bat specimen was preserved in one of three ways: skin and partial skeleton, full skeleton, or in spirits (formalin, followed by ethanol). Information on each specimen including collecting locality, primary specimen identification, sex, reproductive status and associated information concerning ectoparasites was recorded into a database system. Some of the later collections (934 of 3564) from the project also included coordinates of the collection sites, recorded with hand-held global positioning system (GPS) receivers. This database has been updated periodically as final identifications were determined.

The portion of the database containing information for all chiropteran specimens from the field project was augmented with information from specimens in museum collections in the United States and México. Thus 3564 bat specimens were examined for this study, representing 277 localities. For localities not including coordinate data, latitude and longitude were determined from maps of the state of Michoacán (1 : 250 000; Instituto Nacional de Estadística Geografía e Informática 1980) using the collection site information of those specimens. Specimens that were only identified to the generic level, or bearing localities that could not be located, were excluded from the dataset and the analyses. The resulting dataset was based on a total of 3236 entries representing 71 species of bats (Appendix I) and 259 localities (Appendix II).

Although we recognize that this dataset may omit a few species that may be rarely encountered in Michoacán (e.g. Sánchez-Hernández *et al.*, unpublished data), and that taxonomic and geographical coverage can never be uniform based on cumulative survey data, we are not aware of any comparably complete database for any major taxonomic group, in an area of comparable size and biotic complexity, outside the United States and Europe. Recognizing that additional intensive collection efforts might add a few predicted habitat associations to our understanding of a few bat species, we undertook this study under the assumption that our understanding of most, if not all, of the species' distribution patterns could be discerned well from the available data, and moreover that the generally predicted species richness patterns would not be affected by the accumulation of additional collection-based information. Furthermore, this region of Mexico is currently undergoing substantial and rapid habitat degradation and the bat species' distributions are undoubtedly being altered, and in most cases diminished. Thus, we anticipate that future collections will tend to document changes in species distributions, rather than simply extending our understanding of presumably stable distributions.

A dataset was constructed indicating the presence or absence of each of the 71 species at each of the collecting localities. This dataset was used in the analysis to nullify the bias that a large collection of a particular species at a particular locality might have on the results of the correspondence analysis.

Analyses were conducted based on each species' distribution individually, as well as those of the species grouped by families and by trophic category (guild). The species were evaluated by guilds because feeding habits probably affect the occurrence of bat species in an area.

Trophic categorization

Each species was assigned to one of eight trophic categories (guilds): forest and clearing aerial insectivores; open-air insectivores; water bats (piscivores); gleaning insectivores/carnivores/omnivores; nectarivores, ground-storey frugivores; canopy frugivores; and sanguinivores (Findley, 1993).

Environmental data

Digitized maps of climate (Fig. 2), precipitation (Fig. 3), vegetation (Fig. 4) and soils (Fig. 5) of Michoacán were

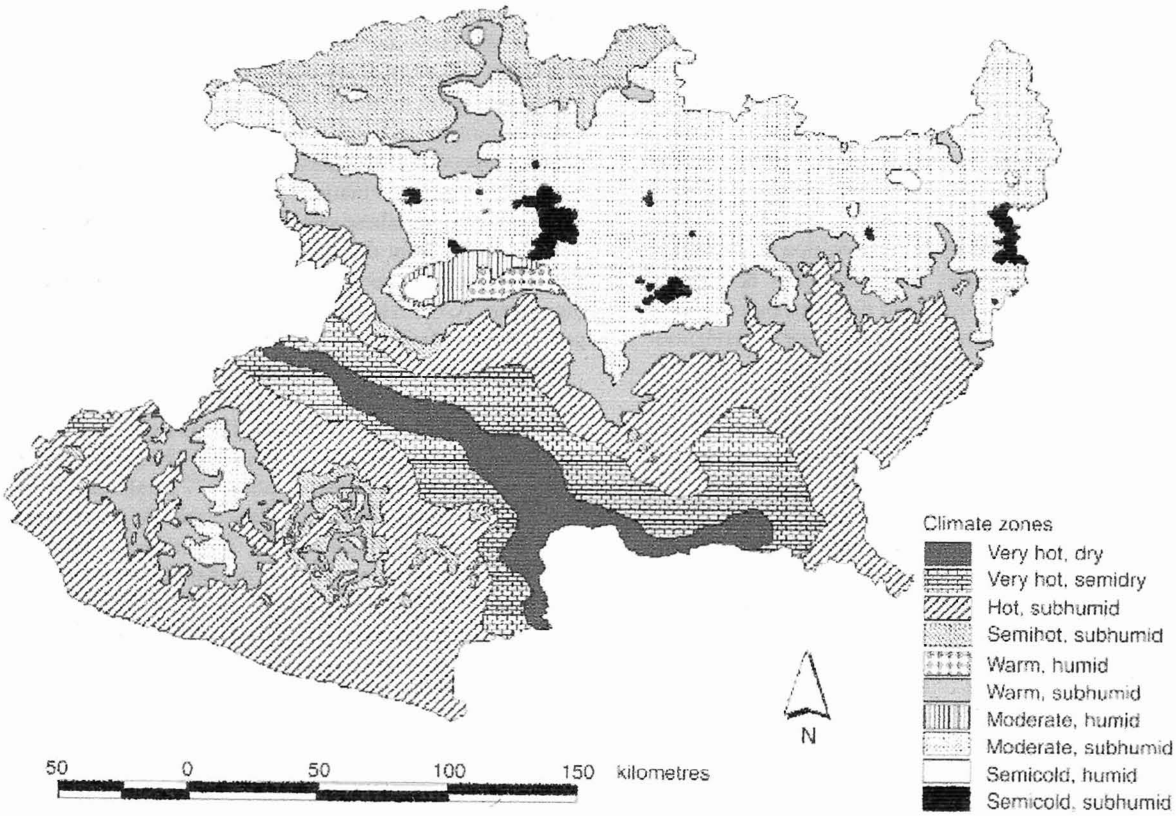

Fig. 2 Climatic zones of Michoacán. The climate in Michoacán ranges from very hot and dry to semicold and subhumid conditions. This map was digitized from a paper map (Instituto Nacional de Estadística, Geografíca & Informática 1985). For the analyses, the categories were pooled to depict only temperature, because humidity is reflected in the precipitation map.

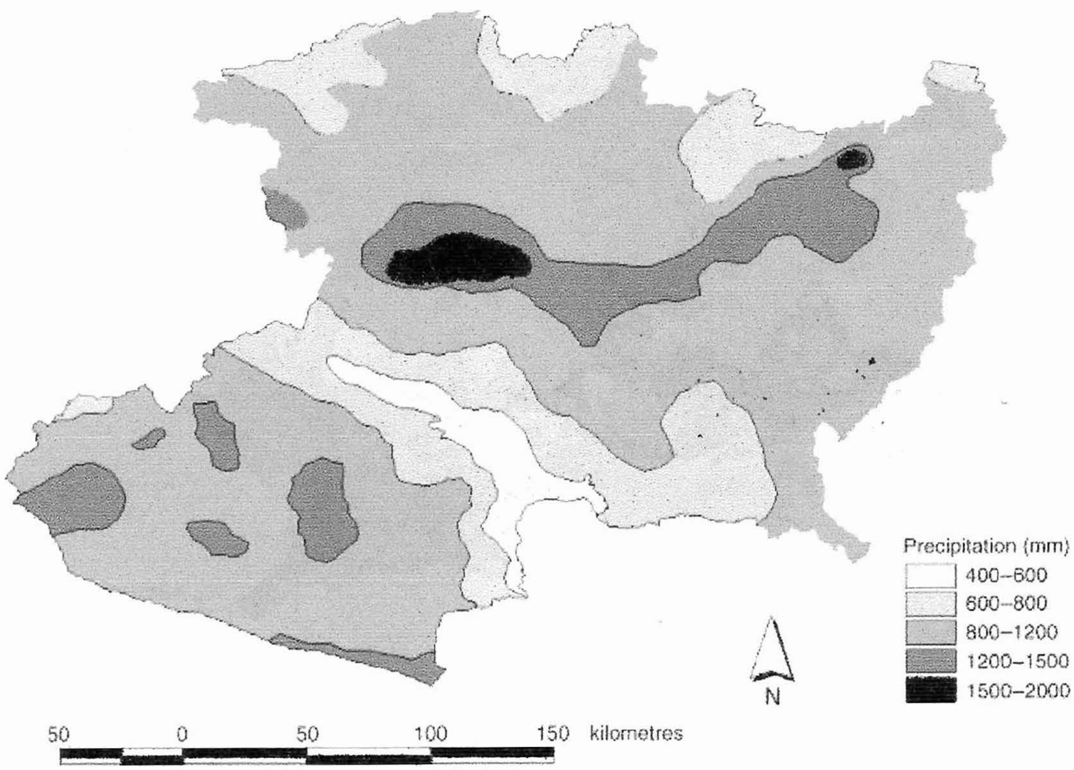

Fig. 3 Precipitation levels of Michoacán. This map was digitized from a paper map (Instituto Nacional de Estadística, Geografíca e Informática 1985). The precipitation gradient was subdivided into five categories.

provided by Lorinda Sheeler-Gordon, who constructed them by digitizing from paper maps (1 : 500 000; Instituto Nacional de Estadística, Geografíca e Informática 1985) using a 486 Dell PC, running ARC/INFO version 3.4.2b (ESRI, 1994), and a digitizing board (CalComp 9500, 36 × 48). Each environmental factor comprises different numbers of variables or components (Figs 2–5). These maps were converted from the Universal Transverse Mercator (UTM) coordinate system to the latitude-longitude coordinate system using PC ARC/INFO version 3.5.2 (ESRI, 1998).

Because a primary motive of this study was to evaluate habitat associations of the bat species in this biologically complex region as accurately as possible, we elected to utilize information from as many available specimens as we were able to determine with confidence, both the specific identity and the collection locality. Because many of these specimens were collected without elevational data, this critical information is unavailable for a substantial proportion of the available specimens. Although topographic maps are available for the state, the topographic complexity of many regions, and the imprecision of collection locality descriptions for many specimens, precludes our capability of determining accurately the elevation of the collecting locality for many of these specimens. Thus, elevational data were not included in our analyses.

The bat species dataset was imported into the GIS to generate a point coverage of all the collecting localities (Fig. 6). This coverage was overlaid on the environmental factor maps by means of ArcView GIS version 3.2 (ESRI, 1999), and each specimen was associated with the corresponding environmental component of each factor. Components of the climate factor initially included both temperature and humidity. These components were pooled to give categories that pertain only to temperature, given that humidity is already reflected in the precipitation factor. Temperature categories include 'semicold' (mean annual temperature, MAT 8–14 °C), 'moderate' (MAT 14–18 °C), 'warm' (MAT 18–20 °C), 'semihot' (MAT 20–22 °C), 'hot' (MAT 22–26 °C) and 'very hot' (MAT 26–32 °C). Gradients of precipitation were assigned to categories of 'very low' (mean annual precipitation, MAP 400–600 mm), 'low' (MAP 600–800 mm), 'medium' (MAP 800–1200 mm), 'high' (MAP 1200–1500 mm), and 'very high' (MAP 1500–2000 mm). Vegetation categories reflect vegetation and actual use of land in Michoacán (Instituto Nacional

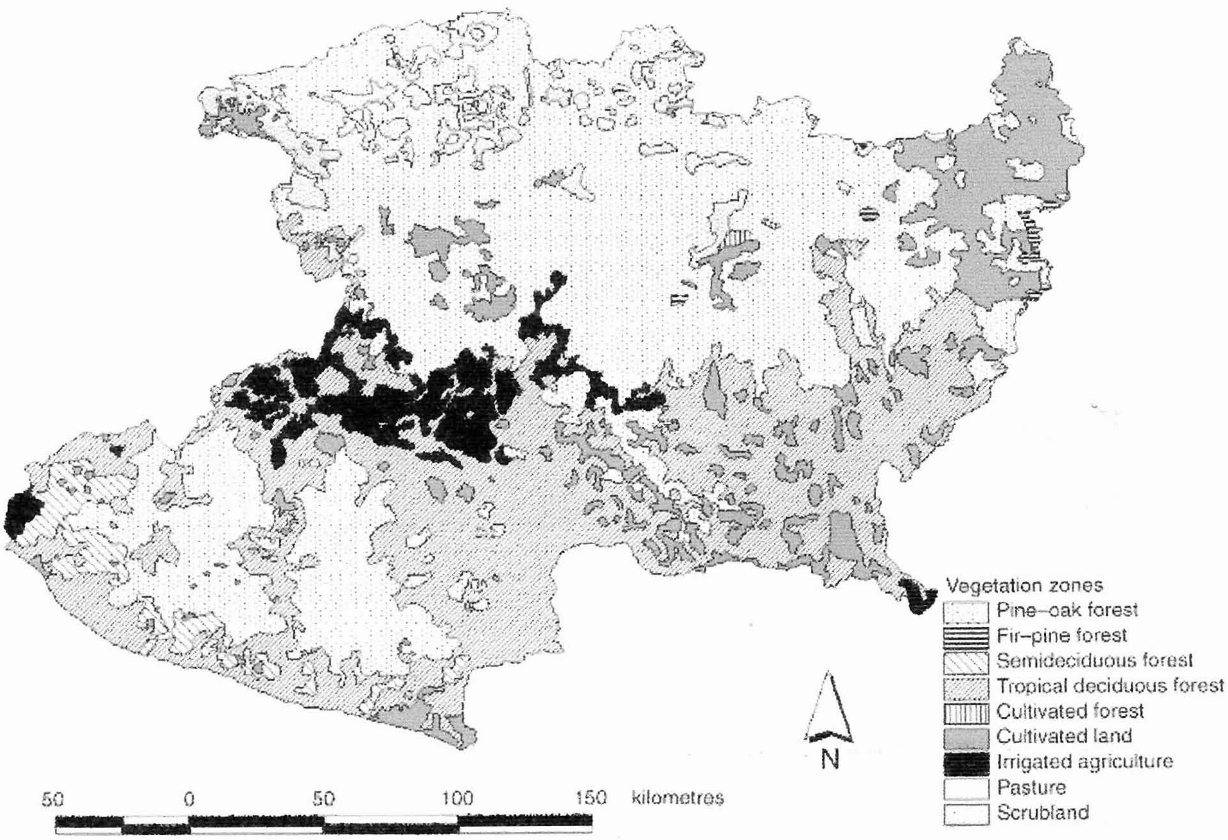

Fig. 4 Vegetation zones of Michoacán. This map depicts the vegetation and actual use of land in Michoacán, and was digitized from a paper map (Instituto Nacional de Estadística, Geografíca e Informática 1985).

de Estadística *et al.* 1985). A raw categorical data matrix of the specimens and environmental variables was constructed.

Statistical analyses

Correlations of the species distribution and the environmental variables were examined with correspondence analysis (CA) using SAS PROC CORRESP (SAS Institute, 1999). CA is a multi-dimensional graphical method of analysis that is suitable for categorical data (Greenacre, 1993). Although canonical correspondence analysis (CCA) has been a popular method for community ecology and macroecology studies (e.g. Martin & Lepart, 1989; Poulin *et al.*, 1993; Spitzer *et al.*, 1993), CA and its modified forms have been utilized extensively for analyses in various sectors of quantitative science (e.g. David *et al.*, 1974; Melguen, 1974; Greenacre & Vrba, 1984; Montaña & Greig-Smith, 1990; Bojórquez-Tapia *et al.*, 1995). Correspondence analysis uses graphical display to obtain a summary description of a large dataset comprising a large number of variables. Greenacre (1984: p. 54) describes correspondence analysis as: 'a technique for displaying the rows and columns of a data matrix ... as points in dual low dimensional vector spaces'. CA is similar in method to principal components analysis (PCA), but is particularly suitable for discrete data, whereas PCA is more suited to continuous data' (Greenacre & Vrba, 1984; Lebart *et al.*, 1984). The graphical representation of data generated by CA allows visual examination of the correlations among the data points. Correspondence analysis is considered to be an exploratory analysis (Greenacre & Vrba, 1984; Lebart *et al.*, 1984) in that it detects possible patterns of associations and differences in the data, rather than evaluating specific hypotheses (Greenacre & Vrba, 1984).

The concept behind correspondence analysis is to determine the correlation of the data (the rows and columns of the matrix) in a multi-dimensional space as two clouds of points, and simplify the projection into a low (usually two-) dimensional space, while conserving as much of the information as possible (Melguen, 1974). The configuration of the row and column points in the multi-dimensional space is based on the relative frequency (profile) of the data (in this case, species and environmental variables). The distance between two data

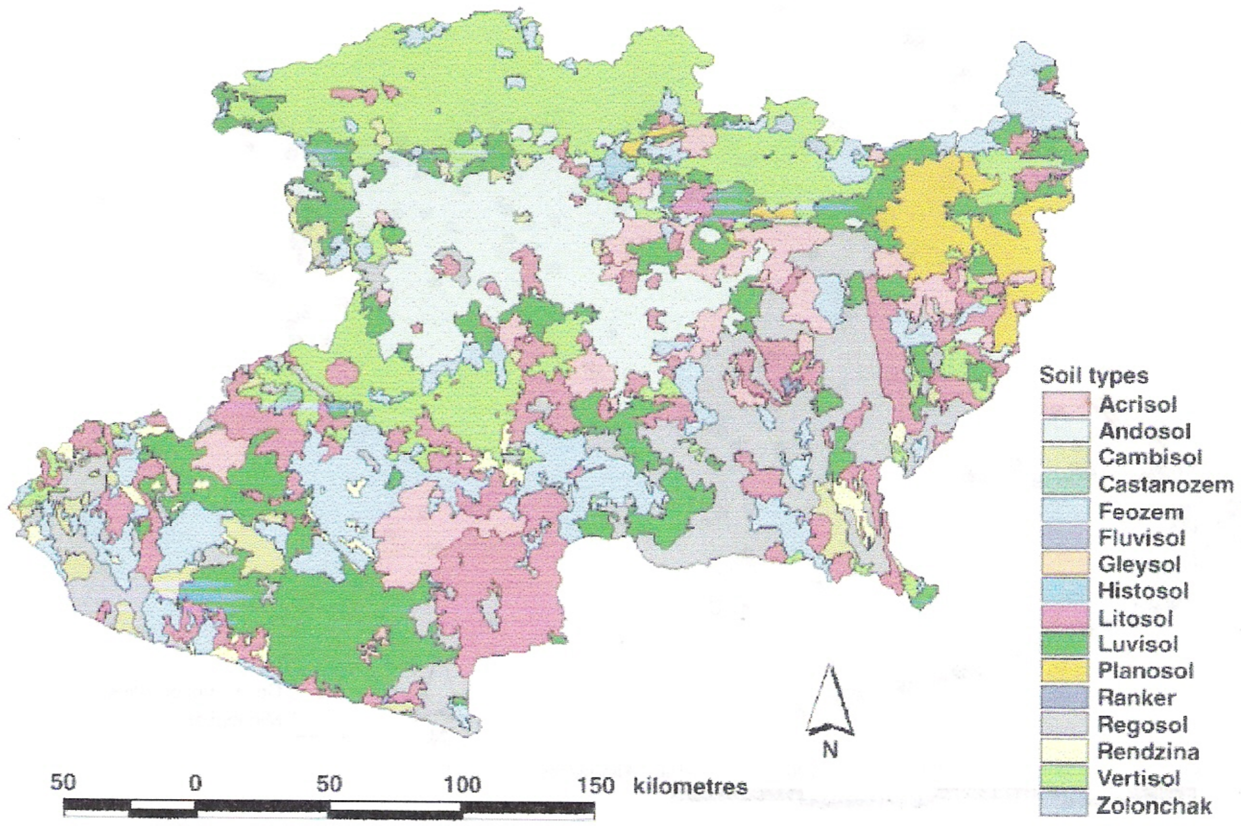

Fig. 5 Soil types of Michoacán. The categories follow those of the Food and Agriculture Organization (FAO). This map was digitized from a paper map (Instituto Nacional de Estadística, Geografíca e Informática 1985). Information from this map was not included in the prediction model.

points, known as the χ^2 distance, is calculated based on the relative frequency of the data point. On the other hand, the χ^2 statistic is a measure of the association between rows and columns of a table (SAS Institute, 1999). The inertia (referred to as 'eigenvalue' by Lebart *et al.*, 1984) is calculated by dividing the χ^2 statistic by the grand total of the table (and hence is proportional to the χ^2 statistic).

Two other series of coefficients are useful for interpreting the axes: absolute contributions to principal inertia and squared correlations (squared cosines) (Lebart *et al.*, 1984). The absolute contribution of a variable is equal to the square of its coordinate multiplied by its frequency (Montaña & Greig-Smith, 1990), and indicates the proportion of variance explained by the variable in relation to each principal axis (Lebart *et al.*, 1984). The squared correlation is the squared cosine ($\cos^2$) of the angle between a variable's vector and a principal axis. This value indicates the part of the variance of the variable explained by the principle axis (Lebart *et al.*, 1984).

An overall correspondence analysis was performed with the components of all four environmental factors as column data and the bat species' presence and absence as row data. Inertia contributions from the environmental components (absolute contributions) were obtained. Mean contributions (i.e. total absolute contribution from all components of a factor divided by its number of components) instead of total absolute contributions were used as an indicator of importance of the factors, as suggested by Montaña & Greig-Smith (1990). This was due to the fact that total absolute contributions are associated positively with the number of categories in a factor (Montaña & Greig-Smith, 1990). All contributions used (both total and mean) refer to the total from all principal axes (i.e. sum of contributions from all axes).

A cluster analysis using Ward's minimum-variance method was performed on the species' coordinate output of the CA, using SAS PROC CLUSTER, and the resulting similarity pattern depicted as a dendrogram using SAS PROC TREE (SAS Institute, 1999). In Ward's method, the distance between two clusters is the ANOVA sum of squares between the two clusters added over all variables. This method tends to join clusters with a small number of observations, and is biased

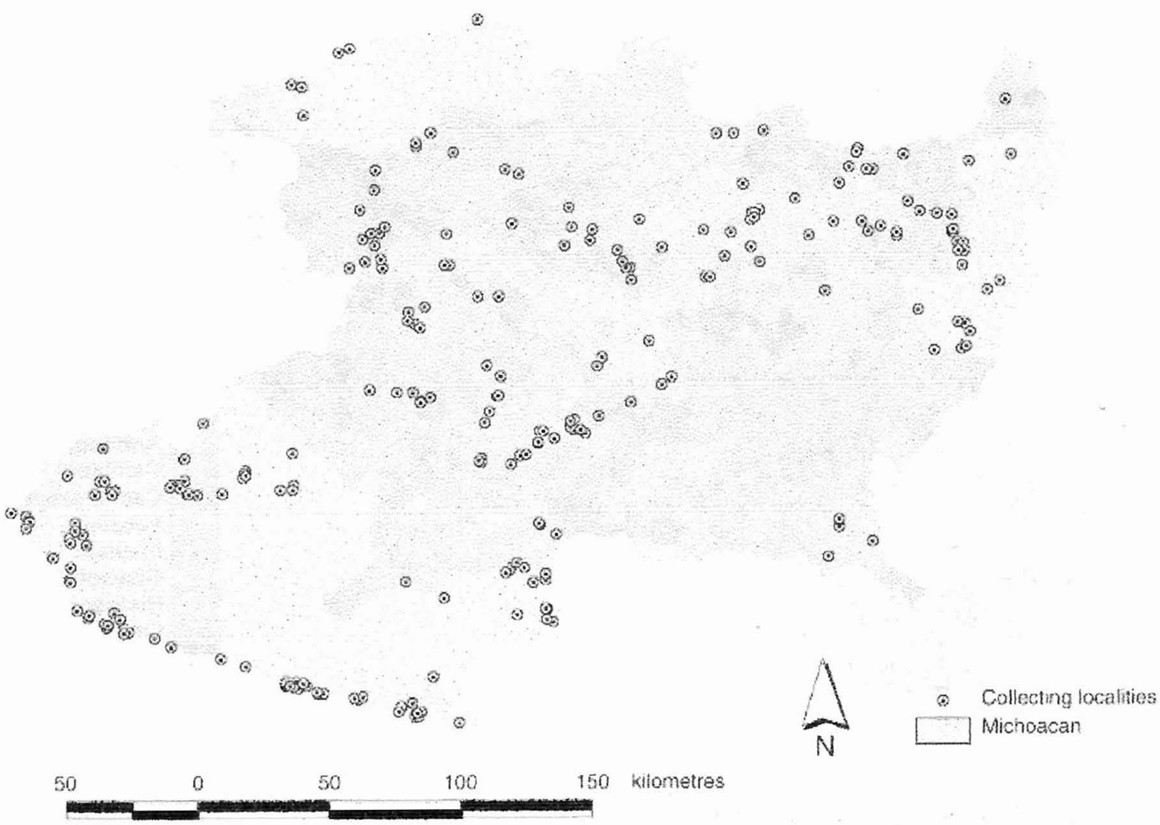

Fig. 6 Collecting localities for all specimens included in this study are represented by circles in this map.

toward producing clusters with roughly the same number of observations (SAS Institute, 1999). Doing so helped to identify groups of species with similar environmental requirements.

Associations between each species and the environmental factors were determined from the ordination of the CA. The CA scatterplot superimposes the gradients formed by the environmental variables onto the plot of the species data points. By examining each species' relative position on the environmental gradients in the plot, its associated variables were determined. A species towards either extreme of a gradient was associated with the corresponding environmental variable. In situations where the position of the species data point was less distinct (such as between two environmental variables), the presence and absence dataset was employed to facilitate interpretation of the graph. The 'more common' variable(s) of a factor in a species was (were) determined to be associated with the species. This methodology was used to characterize the species for each of three environmental factors (temperature, precipitation, and vegetation).

Species in each cluster established by Ward's cluster analysis were characterized by similar assignments (characterizations) of environmental variables. In essence, the position of each cluster on the environmental gradients was examined. The resulting matrix depicts the observed ecological and environmental associations of each species.

Predictive map

Grids of the state map were generated to construct the predictive map. A matrix of 1 km^2 grids was created using 'GENERATE — GRID' command of PC ARC/INFO. This layer of grids was overlaid on the state map in ArcView to trim off the grids outlying the state border, using the query function. The grids layer was also overlaid on the environmental factor maps to characterize each grid. The resulting grid cover forms the shape of the state, with each grid containing the appropriate combination of variables of the three environmental factors.

A map of the distribution, predicted by the CA result, was produced for each species. Grids that contain the exact combination of corresponding environmental variables for each species recorded in the environmental character matrix (Table 1) were queried in ArcView and saved as individual shape files. The predicted distribution range maps of the 71 bat species were then overlaid in ArcView

Table 1 Predicted ecological requirements of bats in Michoacán based on the graphical result of the correspondence analysis. The species are arranged by families, followed by the two-letter codes used in Figs 7, 8, 9, and 10. Variables represented by the vegetation abbreviations are cul-land, cultivated land; irrig-ag, irrigated agriculture; pine–oak, pine–oak forest; semidec, semideciduous forest; scrub, scrubland; trop-dec, tropical deciduous forest. A cell that reads 'all' indicates that the species may predictably be associated with any of the categories of that environmental factor which are encountered in Michoacán

Family/species	Two-letter code	Temperature	Precipitation	Vegetation
Emballonuridae				
Balantiopteryx plicata	BP	hot, very hot	all	trop-dec, irrig-ag
Diclidurus albus	DL	hot	high	trop-dec
Peropteryx macrotis	PM	warm	medium	pine–oak
Molossidae				
Eumops glaucinus	EG	hot	medium	trop-dec
Eumops underwoodii	EU	moderate	medium	pine–oak
Molossus aztecus	MZ	hot	medium	semidec
Molossus molossus	MM	hot	medium	trop-dec
Molossus rufus	MR	hot	medium, high	trop-dec
Molossus sinaloae	ML	all	medium, low	trop-dec, pine–oak
Nyctinomops aurispinosus	NA	hot	medium	trop-dec
Nyctinomops femorasaccus	NF	hot, very hot	all	trop-dec
Nyctinomops laticaudatus	NC	very hot	very low	trop-dec
Nyctinomops macrotis	NM	moderate, semihot	low	pine–oak, trop-dec
Promops centralis	PC	hot	medium	trop-dec
Tadarida brasiliensis	TB	moderate, semihot	medium, low	pine–oak
Mormoopidae				
Mormoops megalophylla	MP	hot medium,	high	trop-dec, cul-land
Pteronotus davyi	PD	hot	medium	trop-dec, cul-land
Pteronotus parnellii	PP	all	all	trop-dec, cul-land
Pteronotus personatus	PS	hot, very hot	all	trop-dec
Natalidae				
Natalus stramineus	NS	hot	medium, high	trop-dec, semidec
Noctilionidae				
Noctilio leporinus	NL	hot	medium, high	trop-dec
Phyllostomidae				
Anoura geoffroyi	AG	moderate, warm	medium	pine–oak, cul-land
Artibeus hirsutus	AH	all	medium, low	trop-dec, irrig-ag, cul-land
Artibeus intermedius	AI	all	all	all
Artibeus jamaicensis	AJ	all	all	all
Artibeus lituratus	AL	hot	medium, high	trop-dec, cul-land
Carollia subrufa	CS	hot	medium, high	trop-dec, semidec
Centurio senex	CN	hot	medium, high	trop-dec
Chiroderma salvini	CV	hot, warm	medium	cul-land
Choeronycteris mexicana	CM	moderate, semihot	medium	pine–oak, scrub
Dermanura azteca	DA	moderate, warm	medium	pine–oak, cul-land
Dermanura phaeotis	DP	hot	medium, high	trop-dec, semidec
Dermanura tolteca	DT	all	medium, high	trop-dec, cul-land
Desmodus rotundus	DR	all	all	all
Enchisthenes hartii	EH	hot	medium, high	trop-dec, semidec
Glossophaga commissarisi	GC	hot, very hot	all	trop-dec
Glossophaga leachii	GL	hot, very hot	all	trop-dec
Glossophaga morenoi	GM	hot, very hot	all	trop-dec
Glossophaga soricina	GS	all	all	all
Leptonycteris curasoae	LS	all	all	all
Leptonycteris nivalis	LN	moderate, warm	medium	cul-land, scrub, pine–oak

Table 1 *continued.*

Family/species	Two-letter code	Temperature	Precipitation	Vegetation
Macrotus waterhousii	MW	hot, very hot	all	trop-dec, irrig-ag
Micronycteris megalotis	MT	hot, very hot	all	trop-dec
Micronycteris silvestris	MS	hot	high	semidec
Musonycteris harrisoni	MH	hot, very hot	all	trop-dec
Sturnira lilium	SL	all	medium, high	trop-dec, cul-land
Sturnira ludovici	SV	moderate, warm	medium	pine–oak
Sturnira occidentalis	SO	hot	medium	trop-dec, semidec
Uroderma bilobatum	UB	hot	high	trop-dec
Vespertilionidae				
Corynorhinus mexicanus	CX	moderate	medium, high	pine–oak
Corynorhinus townsendii	CT	moderate, warm	medium	pine–oak
Eptesicus furinalis	ER	hot	high	semidec
Eptesicus fuscus	EF	moderate, warm	medium	pine–oak, cul-land
Idionycteris phyllotis	IP	all	medium	cul-land
Lasiurus borealis	LB	all	medium	pine–oak, trop-dec
Lasiurus cinereus	LC	moderate	all	pine–oak
Lasiurus ega	LE	hot	medium, high	trop-dec
Lasiurus intermedius	LI	semihot	low	pine–oak
Myotis auriculus	MA	moderate	low	pine–oak
Myotis californicus	MC	moderate, semihot	medium, low	pine–oak
Myotis carteri	ME	hot	medium	trop-dec
Myotis fortidens	MF	hot	medium, high	trop-dec
Myotis jaliciensis	MJ	moderate, warm	medium	pine–oak
Myotis leibii	MB	moderate	medium	pine–oak
Myotis lucifugus	MG	moderate, semihot	medium, low	pine–oak
Myotis nigricans	MN	moderate	low	pine–oak
Myotis velifer	MV	moderate, semihot	medium, low	pine–oak
Myotis yumanensis	MY	moderate, semihot	medium, low	pine–oak
Rhogeessa alleni	RA	very hot	very low	trop-dec
Rhogeessa mira	RM	very hot	very low	trop-dec
Rhogeessa parvula	RP	hot, very hot	all	trop-dec

to create a predicted chiropteran species richness map of Michoacán.

RESULTS

The first axis (Dimension 1) of the CA ordination accounted for 41.3% of the total variation in the data (Table 2). Temperature, vegetation and soil type formed gradients along Dimension 1 (Fig. 7). Species that scored low were associated with high temperature and tropical types of vegetation (e.g. tropical deciduous forest), and species with high scores were associated with moderate temperatures and temperate vegetation types (e.g. pine–oak forest and scrubland). Dimension 1 also ordered species according to their elevational ranges

The second axis (Dimension 2) explained 12.4% of the variation (Table 2). Precipitation formed a gradient along Dimension 2. Species correlated with high precipitation had low scores on Dimension 2 while those correlated with low precipitation scored high (Fig. 7).

The third (Dimension 3) and fourth (Dimension 4) axes accounted for 7.5% and 6.2% of the total variation, respectively (Table 2). The majority of the data clustered around the origin of Dimension 3 and Dimension 4. No discernible gradients among any of the environmental factors were present.

A data point on the ordination plot that is proximate to the origin of the axes represents an item with low contribution to the variation of the dataset (Lebart *et al.*, 1984). Consequently, a species that was near the origin had undifferentiated distribution throughout the whole state. Five species of the family Phyllostomidae (*Artibeus intermedius*, *A. jamaicensis*, *Desmodus rotundus*, *Glossophaga soricina* and *Leptonycteris curasoae*) have wide distributions in Michoacán, and were located near the origins of Dimensions 1 and 2. Several other species also had undifferentiated distributions for at

Table 2 Correspondence analysis result: inertia and chi-square decomposition. Total principal inertia, 0.813; χ^2, 2859.34; and degrees of freedom 1890

Dimension	Singular value	Principal inertia	χ^2	%	Cumulative %
1	0.579	0.336	1179.94	41.27	41.27
2	0.318	0.101	355.78	12.44	53.71
3	0.247	0.061	214.40	7.50	61.21
4	0.225	0.051	177.72	6.22	67.42
5	0.209	0.044	153.21	5.36	72.78
6	0.186	0.034	121.22	4.24	77.02
7	0.166	0.027	96.52	3.38	80.40
8	0.151	0.023	80.16	2.80	83.20
9	0.142	0.020	71.06	2.49	85.68
10	0.129	0.017	58.81	2.06	87.74
11	0.126	0.016	55.67	1.95	89.69
12	0.118	0.014	49.27	1.72	91.41
13	0.113	0.013	45.04	1.58	92.99
14	0.101	0.010	36.20	1.27	94.25
15	0.096	0.009	30.12	1.05	95.31
16	0.087	0.008	26.47	0.93	96.23
17	0.082	0.007	23.55	0.82	97.06
18	0.078	0.006	21.28	0.74	97.80
19	0.078	0.006	21.13	0.74	98.54
20	0.069	0.005	16.94	0.59	99.13
21	0.050	0.003	8.81	0.31	99.44
22	0.046	0.002	7.37	0.26	99.70
23	0.041	0.002	5.88	0.21	99.90
24	0.028	0.001	2.78	0.10	100.00

least one of the three environmental factors. Furthermore, certain species, although not undifferentiated, were correlated with two or more variables for at least one environmental factor (Table 1).

Similarly, an environmental variable with close proximity to the origin carried no influence on species distributions. Semicold temperature and medium precipitation level data points were located near the origin of Dimension 1 and Dimension 2 (Fig. 7). Very few species were encountered in semicold climate conditions, and none was found to associate primarily with regions of this temperature category (Table 1). Regions of medium precipitation, on the other hand, covered a majority of the state and were associated with most bat species. All but 11 species were depicted as having distributions in areas of medium precipitation levels (Table 1).

Relative importance of environmental factors

Mean contributions of inertia (MCI) indicated that the environmental factors, in descending order of importance in explaining species distributions, are: temperature (MCI = 0.0484), vegetation (MCI = 0.0396), precipitation (MCI = 0.0329) and soil type (MCI = 0.0283). In addition, using the presence and absence dataset as an aid in interpreting the CA result, soil type characters were demonstrated to have high heterogeneity of association with the species distributions. Soil type was therefore excluded from the prediction model.

Correlations between species distributions and environmental factors

The cluster analysis indicated two main clusters of species (Fig. 8). These clusters represented approximately the elevational distribution gradients of the species. Twenty-one species, 13 of which are from the family Vespertilionidae, belong to the high elevation cluster. The low elevation cluster included 50 species and represented all chiropteran families in the region.

On a more precise level, 12 groups of species with similar environmental requirements were identified. These groups were evaluated with respect to the ordination output of the CA (Fig. 7). Species–environment correlations were derived by examining the relative positioning of each species' data point with respect to all environmental factor data points. For example, in the characterization of precipitation associations of the species, the precipitation variables formed a gradient in which the 'very low' category scored positive in Dimension 2 and negative in Dimension 1 (i.e. top left corner of graph), the

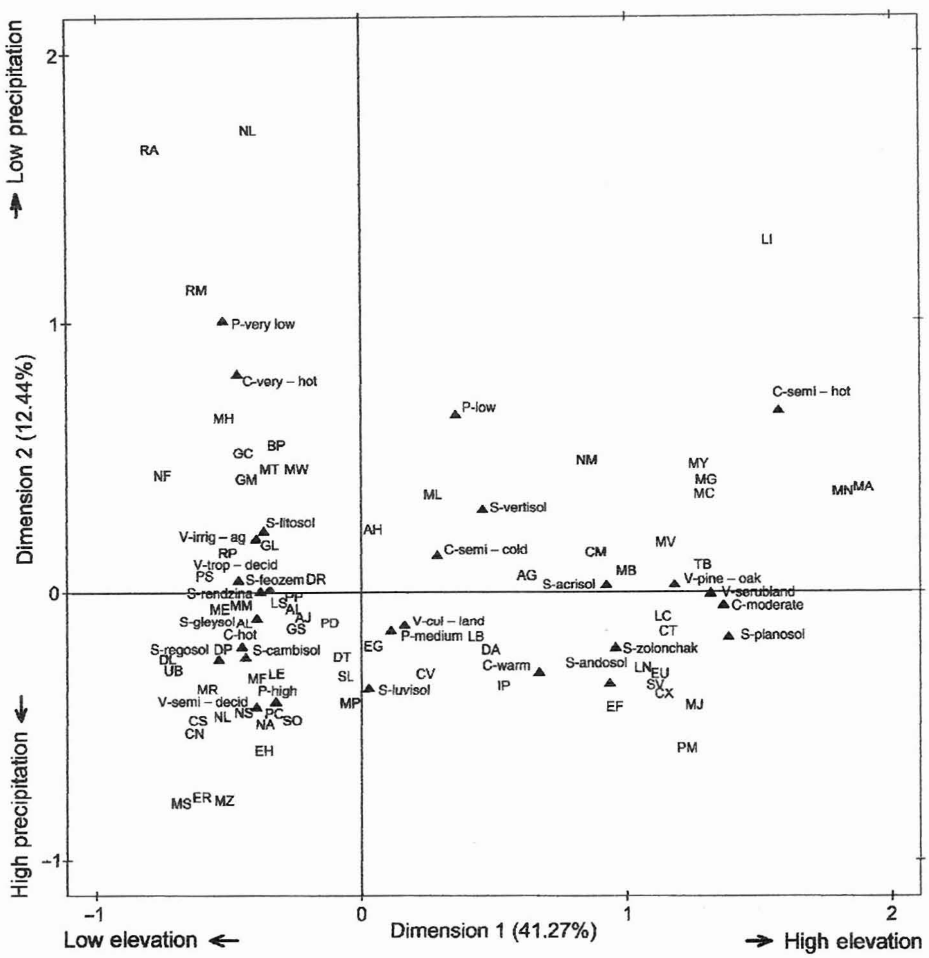

Fig. 7 Ordination plot of Dimension 1 and Dimension 2 of the CA. Environmental variables are represented by solid triangles (▲) and species are represented by their two-letter codes. Refer to Table 1 for full species names. The environmental variables are grouped as follows: C: climate; P: precipitation; V: vegetation; and S: soil type.

'low' category scored positive for both dimensions (top right corner), the 'medium' category scored positive for Dimension 1 and negative for Dimension 2 (bottom right corner) but was very close to the origin of the plot, and the 'high' category scored negative for both dimensions (bottom left corner) (Fig. 7). Consequently, species near the top left corner of the graph were associated with very low precipitation levels, those near the bottom left corner were associated with high precipitation levels, and so on. Species near the bottom right corner and those near the origin of the dimensions (regardless of the quadrant they were in) were associated with medium precipitation. The presence and absence dataset was used as an aid for the interpretation of the CA graphical output. With the exception of soil type, all environmental factors had rather consistent variable associations with each species based on examination of the dataset.

Absolute distances between species' points and environmental points were not considered in the analyses and interpretation because proximity of two points corresponding to two different sets of points in a CA ordination plot is, in most cases, meaningless (Lebart *et al.*, 1984).

Distribution patterns by families and trophic guilds

Bats in Michoacán belong to one of seven families: Emballonuridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae and Vespertilionidae. Families Phyllostomidae and Vespertilionidae represent the majority (~65%) of the species. Neither the CA numerical output nor the cluster analysis revealed discernible groupings of species by families with respect to environmental variables. The CA graphical ordination, however, did indicate an elevational gradient

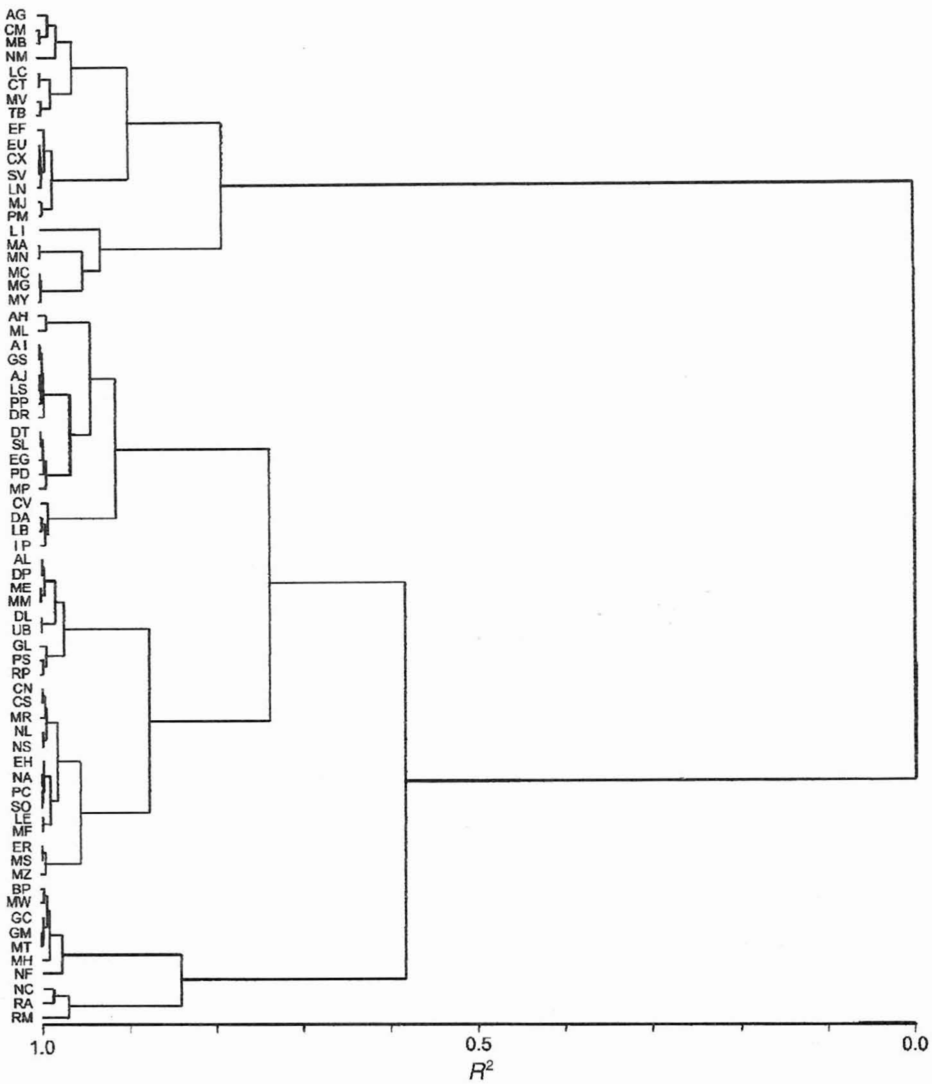

Fig. 8 Cluster analysis of Dimension 1 and Dimension 2 coordinates for each species, represented by their two-letter codes.

among the families. In particular, species of the family Phyllostomidae had distributional ranges concentrated in the low elevation region of the state, and species of the family Mormoopidae had exclusively low elevational distributions. Vespertilionid bats, on the other hand, were found more commonly in areas of high elevation. Elevational patterns of the other families were less distinct (Fig. 9).

Evaluation of distributions by trophic guilds revealed no particular associations between feeding guilds and environmental variables. The feeding guilds appeared to fall loosely along the elevational gradient in the CA ordination (Fig. 10). Most species with ranges in high elevation regions of Michoacán were aerial insectivores. Areas of low elevation were generally occupied by frugivores (both canopy and ground storey), open-air insectivores and gleaning insectivores/carnivores. Nectarivorous, piscivorous and sanguinivorous bats were composed of too few species to discern patterns (Fig. 10).

Predictive maps

Appendix III includes the predicted distribution ranges of the 71 chiropteran species derived from the species–environmental factor correlations. When overlaid, these maps resulted in the species richness prediction map (Fig. 11) for the state's chiropteran fauna.

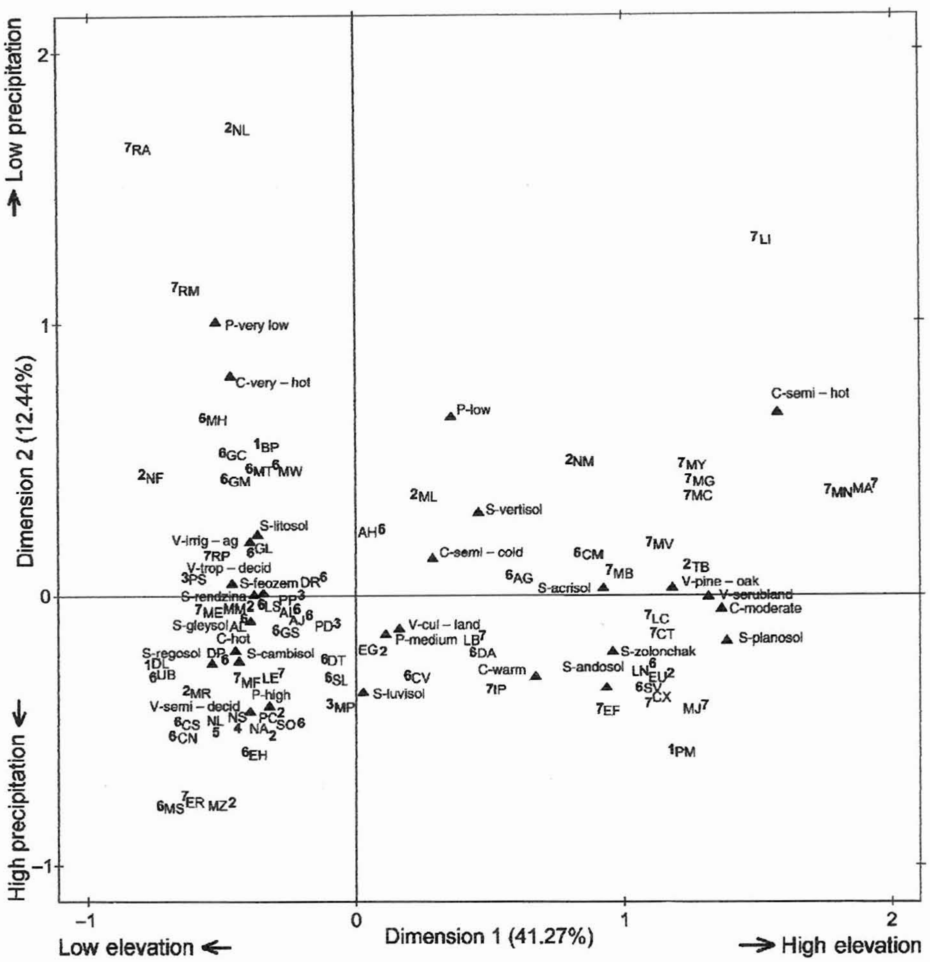

Fig. 9 Ordination plot of Dimension 1 and Dimension 2 of the correspondence analysis, with species grouped by families. The data point symbols are the same as in Fig. 7. The species data points' family numbering is as follows: 1: Emballonuridae; 2: Molossidae; 3: Mormoopidae; 4: Natalidae; 5: Noctilionidae; 6: Phyllostomidae; 7: Vespertilionidae.

The total number of species of bats predicted to occur in any given grid ranged from six to forty. Regions of the state with the highest predicted richness included the south-western and south-eastern portions (Fig. 11). These areas generally contain tropical deciduous forest vegetation type and medium levels of precipitation.

DISCUSSION

Correlations between species distributions and environmental factors

The effect of temperature on species distributions has been documented for a wide variety of organisms, including birds (Rabinovich & Rapoport, 1975), parasites (Pozio *et al.*, 1998), macroinvertebrates (Lowe & Hauer, 1999) and microbes (Nishiguchi, 2000). Bojórquez-Tapia *et al.* (1995) reported mean annual temperature to have the highest contribution to variations in mammalian distributions in the Mexican states of Guerrero and Oaxaca.

Chiropteran species richness of Michoacán appears to be correlated positively with temperature. Although a quantitative measure of temperature was not used in the present study, results of the CA demonstrated a strong relationship between temperature and bat species distributions in Michoacán. More species were associated with hot temperatures than with warm or moderate conditions (Table 1). This correlation does not, however, apply to the very hot temperature category. Only 13 species were associated with this category (other than the species that were predicted to have homogeneous

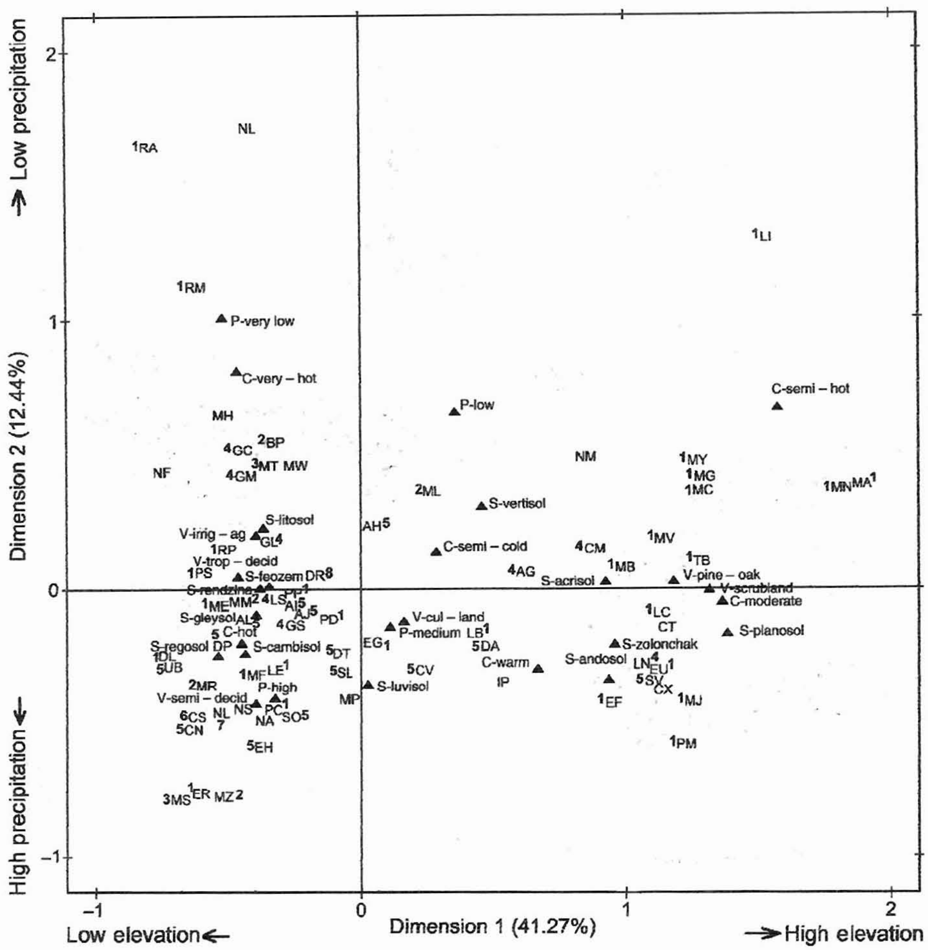

Fig. 10 Ordination plot of Dimension 1 and Dimension 2 of the correspondence analysis, with species grouped by feeding guilds. The data point symbols are the same as in Fig. 7. The species data points' feeding guild numbering is as follows: 1: aerial insectivore; 2: open-air insectivore; 3: gleaning insectivore/carnivore; 4: nectarivore; 5: canopy frugivore; 6: ground storey frugivore; 7: piscivore; 8: sanguinivore.

distributions). The relatively low number of species expected to occur in these regions may be a consequence of the association between this category and the very low precipitation category (see Fig. 7 and the discussion on precipitation).

Vegetation was the second most important factor in explaining chiropteran species distributions in Michoacán. Vegetation type within the state corresponds closely to the temperature gradient and, in turn, to elevation. Tropical deciduous forest and semideciduous forest occur mainly in low elevation regions of the state, where the temperatures generally range from hot to very hot. Pine–oak forest and scrubland are found more commonly in areas of high elevation in Michoacán, where temperature categories include moderate, warm and semihot.

Tropical deciduous forest and pine–oak forest are the two most common vegetation types in Michoacán (Fig. 4), and each supports substantial numbers of bat species. However, other than the five Phyllostomid species with homogeneous predicted distributions, only three (*Idionycteris phyllotis*, *Molossus sinaloae* and *Nyctinomops macrotis*) were associated with both of these vegetation categories (Table 1). Thus, it appears that vegetation type may be a good indicator of spatial segregation of bats.

Other important factors contributing to mammalian species distributions described by Bojórquez-Tapia *et al.* (1995) included soil type, mean annual precipitation and landform. In the present study, vegetation and precipitation level were considered better predictors of chiropteran species richness than was soil type. Soil types are heterogeneous within Michoacán (Fig. 5), and very little consistency of association was noted for the bat species. Consequently, although soil type formed a gradient along Dimension 1 of the CA output

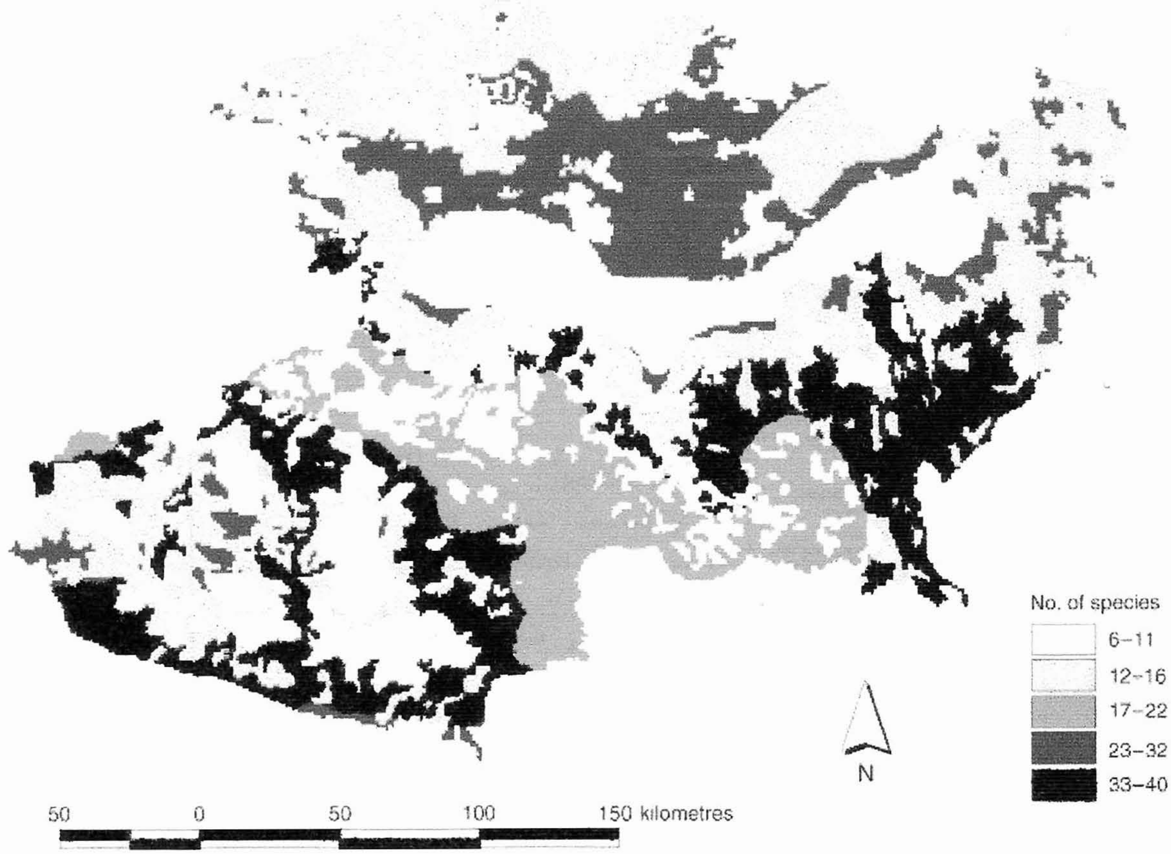

Fig. 11 Predicted chiropteran species richness in the state of Michoacán, México.

and seemed to correlate with vegetation type (Fig. 7), it was omitted as a factor in the bat species richness prediction model.

Elevation as an environmental factor

Elevation has been reported as an important factor affecting species distribution and richness (e.g. Graham, 1983; Zammuto & Millar, 1985; Loiselle & Blake, 1991; Bojórquez-Tapia *et al.*, 1995; Patterson *et al.*, 1998; Nathan & Werner, 1999; Lomolino, 2001). Given the extreme topographic variation within the state of Michoacán, elevation would potentially be a particularly useful predictor of species distribution patterns. Elevation was not included among the analyses of the present study because data regarding it were inconsistently available and, to an extent, were unreliable. Roughly only 70% of the collections included elevational data, and these were determined by a variety of methods.

Nonetheless, the effect of elevation on chiropteran species distributions in Michoacán appears to be reflected indirectly through its associations with the selected environmental factors. The temperature gradient in Michoacán corresponds to elevation, with very hot and hot temperature categories in regions of low elevation. Northern regions of Michoacán, which include part of the Trans-Mexican Neovolcanic Belt, are characterized by semihot, warm and moderate temperature categories. Similarly, the Sierra Coalcomán mountain range in south-western Michoacán is characterized by moderate to warm temperature. Areas of the state bearing high species richness as depicted by the predictive map correspond generally to those of low elevation, whereas areas of high elevation sustain fewer chiropteran species.

Precipitation levels within the state also appear to correspond with elevation. It has been shown that in arid regions, primary productivity is correlated positively with precipitation (Pearson, 1965). Bat species of Michoacán, however, attained peak richness at medium precipitation levels, and all but 11 species were predicted to have distributions in regions of medium precipitation. Very few species were associated with regions with the lowest precipitation ('very low' category). On the other hand, the low abundance of species in areas of high precipitation may be the result of the positive association between precipitation and elevation. High elevation areas often support fewer species than lowland counterparts (Graham, 1983; Patterson *et al.*, 1998; Nathan & Werner, 1999; Lomolino, 2001).

Distribution patterns by families and trophic guilds

Three families (Vespertilionidae, Phyllostomidae and Mormoopidae) exhibited a spatial pattern of distribution, corresponding to elevational pattern within the state. However, other than the family Mormoopidae, no bats of any family occurred exclusively in high or low elevations. In addition, no distinct taxonomic patterns were detected in any of the groups identified by the cluster analysis, indicating further that family membership is probably not an important facet of chiropteran species distributions in Michoacán.

Also, distribution patterns of trophic guilds are generally reflective only of elevational patterns. The abundance of frugivorous bats in low elevation areas of Michoacán reflects vegetation type, which in the tropical deciduous and semi-deciduous forests includes a wider variety and greater abundance of fruiting trees, than do the pine–oak forests of high elevation. Nevertheless, the feeding guilds did not appear to correlate directly with vegetation types or temperature of the state.

This lack of patterns for trophic and higher systematic levels could be attributable to the scale of the study. Spatial scale is an important factor in terms of ecological studies, and many ecological patterns and processes are not universal throughout all scales (e.g. Eagle *et al.* 2001; Lennon *et al.* 2001; Stevens & Willig, 2002). Gradient of familial level richness occurs at a latitudinal scale (Kaufman, 1995). Similarly, trophic guilds also display a gradient along latitudes (Stevens & Willig, 2000, 2002). It is therefore conceivable that, at a lesser scale such as that of Michoacán, patterns will be less obvious regarding higher levels such as family and trophic guilds.

Predicted chiropteran species richness

The species richness map (Fig. 11) predicts that areas of low elevation in the state generally support a higher number of chiropteran species. One possible explanation for this prediction is the spatial heterogeneity hypothesis of species diversity gradients (Pianka, 1966). On the regional (macro-) scale, this hypothesis states that the tropics (corresponding to low elevation regions in Michoacán) contain more habitats, thereby supporting a more diverse fauna. On the local (micro-) scale, this hypothesis predicts that the tropics contain higher number of microhabitats. Such abundance of microhabitats facilitates a finer partitioning of each habitat among species and thus enables more species to coexist (Davidowitz & Rosenzweig, 1998). In Michoacán, the southern half of the state contains both tropical habitats in low elevations and temperate habitats in regions of higher elevation. In its northern part, the state sustains only temperate habitats. This conforms to the macro-scale spatial heterogeneity hypothesis. Southern Michoacán may support more chiropteran species in part because it contains more habitat types of vegetation and temperature than the north.

Another hypothesis that may pertain is the climatic stability hypothesis (Pianka, 1966), which attributes high species richness of a region to its stable climates. This hypothesis states that the relative constancy of resources allows species to evolve more specializations and adaptations, and therefore more species can occupy the unit habitat space. Tropical regions have more consistent temperature and precipitation levels than the temperate (Pianka, 1966), hence sustaining more species. This can be discerned in the present study in that the hot temperature zones in southern Michoacán support higher numbers of bat species than do the temperate areas of comparable latitude (Fig. 11).

In addition, a form of species–area relationship is also a feasible explanation for the predicted richness pattern. Species richness should vary with the total area of each zone, and more species are expected to occur in larger areas (Godfray & Lawton, 2001; Lomolino, 2001). Because area is, in general, inversely proportional to elevation, the number of species is expected to be the highest at low elevation with the largest area. This agrees with the result of the present study, and cannot be excluded as a factor in the observed and predicted distribution patterns.

Conservation implications

Bats are biologically diverse and ecologically important organisms. Because of their high richness and diversity, bats are good ecological indicators. Areas of the highest chiropteran species richness should perhaps receive high conservation priority, in part because species-rich areas also tend to support more uncommon species (Patterson, 1987). In order to minimize conflicts between conservation and resource extraction, the species richness prediction map can be used to locate these species-rich areas and prioritize conservation efforts.

Analytical tools

CA is a useful multivariate descriptive analytical method. It is especially favourable for categorical data such as vegetation and soil type, making it suitable for analysing environmental factors in ecological studies. The descriptive nature of CA allows visual examination of two sets of data (in this case, species and environmental variables) in a joint display, and is a concise graphical summary of the nature of their correspondence (Greenacre & Vrba, 1984). The graphical plot of the analysis provides information on correlations not only between species and the environmental factors, but also within these two sets of data (i.e. among species and among the environmental components).

Correspondence analysis is apparently robust to differences in sample sizes among species. The species presence and absence dataset was used in this study to avoid the statistical effects of rare or abundant species. However, preliminary analyses (not reported here) were conducted using the original raw data prior to the construction of the presence and absence dataset. The two-dimensional graphical output of CA was not substantially altered by the use of the presence and absence data compared to that of the raw data. Greenacre & Vrba (1984) reported a similar outcome with reweighted data of antelope frequencies on African wildlife areas.

The use of GIS has proved to be an important element in analysing species richness and distribution patterns. Coupled with the multivariate statistical method, the GIS was critically important to the pattern analysis of species distributions. The system was used to select and characterize each specimen ecologically, which was the core of this study. The GIS also provided insights in examining correlations among the environmental factors. Furthermore, the GIS was an integral process in the construction of the species richness prediction map.

Given the scale limitations of the environmental factor maps, and the inevitable incompleteness of the bat distributional data, we recognize that these predictions of species distributions must include errors. We can, to a degree, evaluate the extent both of 'errors of commission' (which would result in the prediction of a bat–environment association which does not occur in nature), and 'errors of omission' (which would result in not predicting a bat–environment association, which does in fact occur in nature), by visual examination of the species prediction maps (Appendix III). Clearly, our results include some errors of both types, e.g. in the case of *Noctilio leporinus* (A21) and *Nyctinomops macrotis* (A13), respectively. It should be noted that these 'erroneous' predictions may also result from the analytical procedure, which tends to extract predicted associations based on frequency of observed association. Thus, if a species has also been recorded infrequently in several associations, in addition to its more commonly observed association, the infrequently recorded association(s) will not be among the predicted associations.

CONCLUSIONS

Chiropteran species distributions of Michoacán are seemingly influenced mainly by the temperature gradients within the state. Among the temperature categories, hot temperature (MAT 22–26 °C) supports the highest number of species. Vegetation type is the second most important factor in explaining species distributions of bats. Tropical deciduous forest sustains the greatest number of species, followed by pine–oak forest. Species of bats appear to segregate between the two vegetation types. The third most important environmental factor affecting bat species distributions is precipitation level. The medium precipitation (MAP 800–1200 mm) category sustains by far the most species. Soil types of Michoacán are very heterogeneous and do not seem to correlate with bat species distributions in the region.

There were no strong correlations between families or trophic guilds of bats and any of the environmental factors. Some families and feeding guilds, however, did appear to conform generally to the elevational gradient within the state.

Elevation is often an important element in explaining species distributions, especially in a topographically diverse region such as south-western México. Although it was not included in this study because of insufficient data, most associations with environmental factors appeared also to reflect elevational patterns within the state. Elevation should be considered in future studies of species distribution and richness in Michoacán and other similar regions.

Predicted distribution ranges for the bat species were mapped using the temperature, vegetation and precipitation factors associated with each species. A chiropteran species-richness prediction map was constructed by overlaying all 71 species distribution maps. This map indicates that the southern regions of the state generally support more species of bats. These regions generally have hot temperatures and tropical vegetation types, and are generally of lower elevation.

The species-richness map, as well as the individual species-distribution maps, will provide valuable tools for conservation efforts in the state of Michoacán. Species-rich areas tend to support more uncommon species (Patterson, 1987), and are prone to generate conflicts between conservation and resource extraction (Bojórquez-Tapia *et al.*, 1995). Such areas should be accorded priority for protection (Blockstein, 1990; Davis *et al.*, 1990). Our predictive maps can help to identify these priority areas for conservation.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwell-publishing.com/products/journals/suppmat/GEB/GEB318/GEB318sm.htm

Appendix I

Species included in analyses

Table S1 A list of the species included in the analyses is given. Families, genera, and species follow those in Koopman (1993), except *Dermanura azteca*, *D. phaeotis* and *D. tolteca*, following Owen (1987), and *Corynorhinus mexicana* and *C. townsendii*, following Bogdanowicz *et al.* (1998). Each species is followed by the locality number (Appendix II) where it was present.

Appendix II

Gazetteer of collecting localities

Table S2 A gazetteer of collecting localities of all the specimens in the presence and absence dataset used in this study is given. The localities are listed in alphabetical order. Grouped by latitude/longitude coordinates, some localities have slightly different descriptions, and only one is listed as the representative of the named locality. Descriptions of the localities include: location, reference, municipality (if available, in parenthesis), latitude/longitude coordinates. Each of these is separated by a semicolon.

Appendix III

A PDF file showing distibutional ranges of bat species in Michocán is also available to download from the above website.

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BIOSKETCHES

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Research in **Robert Owen's** programme includes a variety of systematic questions, as well as related questions of historical zoogeography. Current research includes long-term multi-disciplinary investigations of Paraguayan and Mexican mammals and associated ectoparasite communities.

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