

Response of phytophagous bats to patch quality and landscape attributes in fragmented tropical semi-deciduous forest

BEATRIZ BOLÍVAR-CIMÉ^{1,5,6}, JAVIER LABORDE¹, M. CRISTINA MACSWINEY G.², CARLOS MUÑOZ-ROBLES³,
and JUAN TUN-GARRIDO⁴

¹*Red de Ecología Funcional, Instituto de Ecología, A.C., Carretera antigua a Coatepec No. 351, El Haya, C.P. 91070, Xalapa, Veracruz, México*

²*Centro de Investigaciones Tropicales, Universidad Veracruzana, Casco de la ExHacienda Lucas Martín, Privada de Araucarias S/N, Col. Periodistas, C.P. 91019, Xalapa, Veracruz, México*

³*Instituto de Investigación de Zonas Desérticas y Coordinación de Ciencias Sociales y Humanidades, UASLP, Altair # 200 Col. Del Llano, C.P. 78377, SLP, México*

⁴*Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Carretera a Xmatkuil Km 15.5, C.P. 97315, Mérida, Yucatán, México*

⁶*Corresponding author: E-mail: bolivar_cime@yahoo.com*

Forest fragmentation reduces the amount of forest cover and negatively affects the habitat quality of forest remnants. Landscape attributes and habitat quality should therefore be evaluated together to improve our understanding of how fauna respond to fragmentation. We evaluated how patch quality (vegetation structure) and landscape characteristics influence the abundance of phytophagous bats in two contrasting types of landscape that differ in percent forest cover and matrix type: landscapes dominated by man-made pastures and landscapes with large tracts of continuous forest (tropical semi-deciduous forest). Bats were sampled in forest patches in both types of matrices, and for each matrix two sites with a cenote (water filled sink-holes, typical of the Yucatan) and two with no cenotes were sampled. Sites with cenotes offer better habitat quality than sites without cenotes: the richness and basal area of plants eaten (flower or fruit) by bats are higher in the forest vegetation surrounding them. At the landscape level, phytophagous bat abundance was negatively correlated with the amount of forest cover and proximity to other forest fragments, but positively correlated with forest edge density, patch density and landscape heterogeneity. At the patch level, bat abundance was positively correlated with plant richness and the basal area of edible tree species. In the Yucatan's agricultural landscapes the area and spatial distribution of forest remnants are not the only variables affecting bats. Habitat patch quality and high heterogeneity of land cover types are also important, and have a positive effect on phytophagous bat abundance and movement.

Key words: frugivorous bats, landscape complementation, landscape heterogeneity, nectarivorous bats, vegetation structure

INTRODUCTION

The factors that influence the ecology of populations and communities have been traditionally studied at the local level (Dunning *et al.*, 1992), however the development of analytical tools such as Geographic Information Systems (GIS) makes it possible to evaluate these factors across much broader scales. The concurrent analysis of habitat characteristics (i.e., the structure and composition of vegetation) and landscape characteristics (the composition and configuration of habitat patches) are important for evaluating the use of habitat remnants by native wildlife in fragmented landscapes (Gorresen and Willig, 2004; Pinto and Keitt, 2008; Klingbeil and Willig, 2009).

Phytophagous bats provide crucial environmental services by pollinating (nectarivorous species) and dispersing the seeds (frugivorous species) of native woody plants across anthropogenic landscapes, and they do this over larger areas than other fauna, including birds, owing to their greater vagility in these landscapes (Galindo-Gonzalez, 2004). The ability of some bat species to fly long distances and cross open areas has made these volant mammals a useful group for evaluating the response of native fauna to habitat fragmentation (Gorresen and Willig, 2004; Klingbeil and Willig, 2009). In environments that have been modified by humans, it has been shown that bat species respond differently to changes in the habitat; some bat species that depend directly on plants as their main source of food benefit from

the creation of a few, scattered sites with secondary vegetation, but suffer when their foraging or roosting areas are subjected to drastic changes by extensive deforestation (Castro-Luna *et al.*, 2007). Recent studies have found that bat abundance responds more to landscape composition (i.e., the proportion of different habitat types) than to landscape configuration (the spatial arrangement of different habitat types) (Gorresen and Willig, 2004; Klingbeil and Willig, 2009). In Mexico the abundance of frugivorous bats was robustly and positively associated with the proportion of area covered by primary and riparian forest, both high quality habitats for bats (Pinto and Keitt, 2008; Avila-Cabadilla *et al.*, 2012), while the abundance of three nectarivorous bat species tended to be negatively associated with the mean area of dry forest patches (Avila-Cabadilla *et al.*, 2012). Other studies have shown that phytophagous bat species richness and abundance are higher in moderately fragmented landscapes than in intact forest (Willig *et al.*, 2007; Klingbeil and Willig, 2009). A matrix of mature forest with few patches of secondary vegetation provides more niches for some bat species than intact forests do (Castro-Luna *et al.*, 2007). Most studies on bat responses to forest fragmentation describe quantitatively the amount of forest area and the spatial distribution of forest fragments but fail to take into account quality in terms of their suitability as habitat for bats and this may confound or at least slow our progress in understanding bat responses in fragmented habitats.

The state of Yucatan in Mexico is characterised by a remarkable homogeneity in its topography owing to the absence of mountains and rivers (Duch-Gary, 1988). Over the last five decades vegetation cover there has changed drastically, with only 18% of the native vegetation remaining. Deforestation has been highest in the north-east, where tropical dry forest and tropical semi-deciduous forest have been cleared to make way for pastures and crop fields (Durán-García and García-Contreras, 2010). Currently, in the north-eastern part of the state, there are different proportions of contrasting habitat types (i.e., forest versus non-forest) and different spatial arrangements of those habitat types. The topographic uniformity and the degree of forest fragmentation make for characteristics that are useful for assessing the response of bats to forest fragmentation.

In the Yucatan there are many cenotes, natural sinkholes that form after the dissolution and collapse of limestone bedrock, exposing the groundwater underneath (Duch-Gary, 1988). Cenotes often

constitute the only source of fresh water for fauna in the region. The presence of cenotes may also increase food availability for insectivorous fauna (MacSwiney *et al.*, 2009) and frugivorous fauna, since the woody vegetation surrounding them is characterised by relatively large trees of evergreen species such as *Ficus*, *Brosimum* and *Manilkara* (Flores-Guido, 2010), which are also key species for frugivorous bats in tropical regions (Schulze *et al.*, 2000). Differences in intra- and interspecific phenology for trees located around cenotes and those far from them have been recorded, with the greatest and longest-lasting fruit production occurring in those located at the edge of cenotes (Valdez-Hernández *et al.*, 2010). The differences in vegetation structure and composition between sites with cenotes and those without, together with the greater variety and availability of food for bats offered by the woody vegetation surrounding cenotes, provide an ideal means for evaluating the effects of differential patch quality on the abundance of phytophagous bats, and the response of these bats to forest fragmentation.

The purpose of our study was to assess the effect of patch quality (as a function of vegetation structure) and landscape characteristics (composition and configuration) on the abundance of phytophagous bats in two different landscape matrices: forest matrix and pasture matrix. We hypothesise that (i) given the greater availability of food resources for bats (flowers and fruit) provided by the woody vegetation around cenotes in comparison with that growing at sites without cenotes, we expected a higher abundance of phytophagous bats in sites with cenotes for both types of landscape matrices but especially in the pasture matrix where resources can be scarce, and (ii) since large tracts of continuous forest provide more perching and feeding sites for phytophagous bats, we expected a higher abundance of these bats in sites with continuous forest cover (i.e. forest matrix) than in sites where the forest has been fragmented (i.e. with a pasture matrix). Thus, we expected phytophagous bat abundance to be positively related to the landscape characteristics associated with continuous forest vegetation.

MATERIALS AND METHODS

Study Sites

The study was carried out in the municipalities of Buctzotz, Espita and Tunkas in north-eastern Yucatan between 20°50'–21°20'N latitude and 87°50'–89°00'W longitude (Fig. 1). The original vegetation of the area was tropical semi-deciduous forest with a 15- to 20-m-tall forest canopy (Durán-García

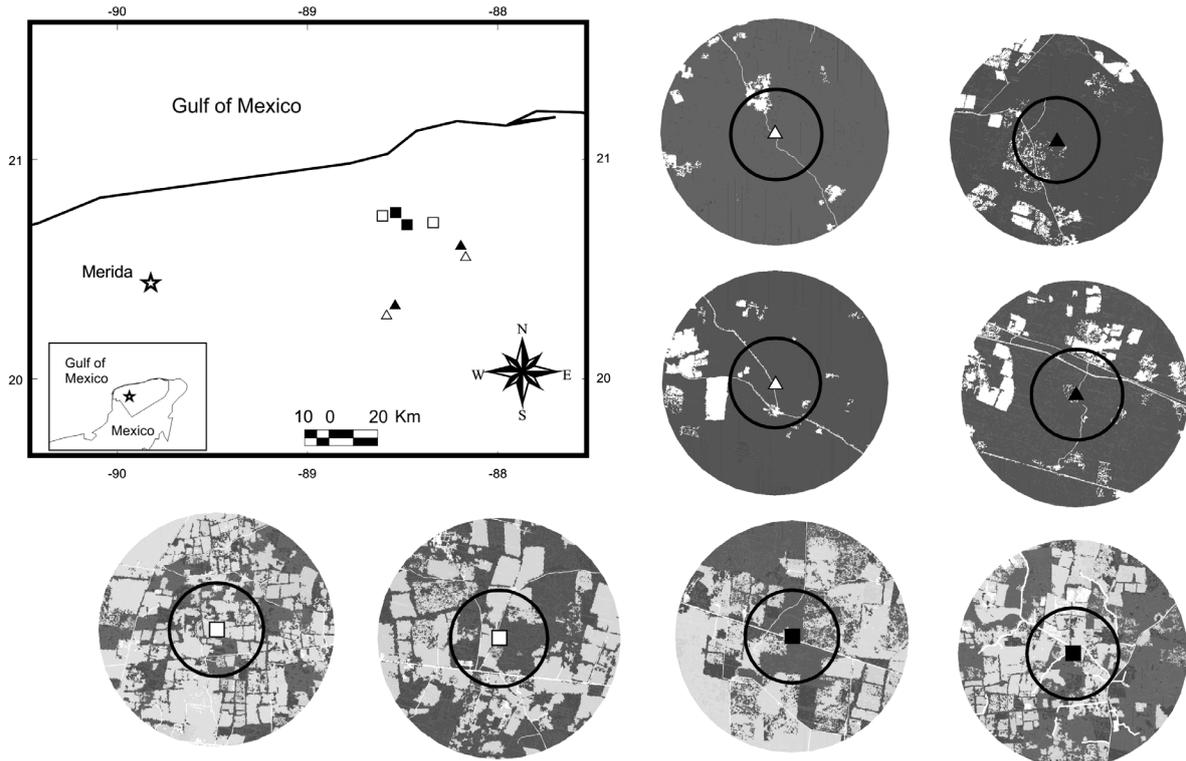


FIG. 1. Location of bat sampling sites in the Yucatan, Mexico, for two landscape matrices. Forest patches within pasture matrix (squares) and within continuous forest matrix (triangles), with a cenote present (black symbols) or with no cenote (empty symbols). There are two sites per matrix and cenote condition. Forest cover in the concentric circles of 1 and 2.5 km radius around each sampling site is in dark gray

and García-Contreras, 2010). Currently, this area is characterised by extensive pastures, a few small crop fields (traditional milpas; a multi-crop field with maize, beans and squash), numerous scattered patches of secondary forest in different stages of succession, and old forest patches of different sizes surrounded by pasture. The forest patches are almost always connected by what is known as the T'olche', a 10- to 20-m-wide stretch of forest, left intact as part of the traditional practice of the milpa, and which serve as boundary markers (Remmers and Koeijer, 1992). Annual rainfall is 900–1037 mm and average temperature ranges from 25.9°C to 26.4°C (Duch-Gary, 1988).

In total, we selected eight sampling sites (four per matrix type) in landscapes with two types of matrices: pasture and continuous forest (tropical semi-deciduous forest). The four sites of the pasture matrix were located in the municipality of Buctzotz, where 93.5% of the area is pasture and 6.5% secondary forest (INEGI, 2006). The four sites in continuous forest matrix were located in the Tunkas and Espita common lands (ejidos), each with more than 70% forest cover, corresponding to secondary forest in different successional stages (INEGI, 2006) and with only a few small areas of crop fields scattered within the forest. Two sites per cenote treatment were established in each matrix type: in the pasture matrix two forest patches with a cenote and two forest patches with no cenotes were sampled. In the continuous forest matrix, two large tracts of forest with a cenote and two with no cenotes were sampled. Cenotes were 50–65 m in diameter, and in the pasture matrix sites they were surrounded by woody vegetation at least 30–40 m wide. Sampling sites were all separated by at least 5 km.

Bat Sampling

The eight sites selected were sampled during four expeditions, each lasting approximately three months (two expeditions in 2010 and two in 2011). On each expedition, each site was sampled for three non-consecutive nights (8 sites \times 3 nights \times 4 field trips = 96 sampling nights). No fieldwork was performed from three days before to three days after the full moon, owing to its inhibitory effect on bat activity (Saldaña-Vázquez and Munguía-Rosas, 2013) and bat netting was suspended during intense rain (i.e. when the soil was saturated with water, and there were small puddles on the ground, the noise of the rain drowned out all other sounds and thus, bat sampling was impossible). For each sampling night, five mist nets (12 \times 2.6 m) were erected per site at ground level (0–3 m), left open for 5 hours starting at sunset and checked every 20–30 minutes. Mist nets were placed at least 10 m apart along paths between the woody vegetation; in sites with a cenote the nets were placed within 10 m of the edge of the water inside the surrounding woody vegetation also along paths. In total the capture effort for the eight sites was 480 hours over 96 nights for a total of 2400 total net hours. Bats were identified to species using field guides and taxonomic keys (Medellín *et al.*, 2008; Reid, 2009). To quantify recaptures, each bat was marked with a numbered plastic collar before being released where it had been caught.

A set of criteria were used to determine if captured bat species were phytophagous: observations of their diet in the study area (MacSwiney *et al.*, 2007; present study) and literature data

(Lobova *et al.*, 2009). *Lamproncycteris brachyotis* and *Mimon cozumelae* occasionally consume fruit (Lobova *et al.*, 2009), but were not included in our analysis because we did not record them consuming fruit. This approach to assigning guilds is appropriate for the objectives of the present paper considering that the specialised diet of some of these bat species does not preclude their ability to exploit a variety of food types (Rex *et al.*, 2010).

Vegetation Structure

Where the mist nets were set, vegetation was sampled using three 5 × 20 m plots (modified from Gentry, 1982), separated by at least 20 m. Only plants that were rooted within the plot and had a trunk diameter at breast height (DBH) greater than 1 cm were sampled. Each plant sampled was identified, its DBH and total height measured, as well as whether fruit, nectar or pollen from the plant species has been reported by Fleming *et al.* (2009) or Lobova *et al.* (2009) as eaten by bats (PEB). This information was used to estimate the following for each site: plant density, plant richness, PEB richness, mean height, PEB mean height, basal area of plant species not used as food by bats (Basal area) and basal area of PEB (PEB-Basal area).

Landscape Characteristics

Two cloud-free SPOT images provided by ERMEX/SEMAR (2010) for February and March 2010 were processed to obtain ortho-rectified images (30 control points per image; positional error: RMS <1 pixel). The panchromatic band (2.5 m/pixel) was fused with the four multi-spectral bands (10 m/pixel) to obtain multi-spectral images with a spatial resolution of 2.5 m. Six land cover types were distinguished: tall forest (i.e., forest canopy > 10 m tall, having several trees with DBH > 10 cm), young second-growth forest (i.e. forest canopy < 10 m tall, and trunks with DBH <10 cm, usually <5 cm), agricultural fields, bare soil, roads and water (i.e. cenotes). A supervised classification was performed on the whole mosaic image, using 83 sites spread throughout the mosaic that were verified by ground-truthing, as training regions to obtain a map with the six land cover categories described. All images were processed using PCI Geomatica software (PCI Geomatics, 2001). Classification accuracy was assessed by randomly distributing 60 points over the study area, and then visually checking these using the satellite imagery available in Google Earth. Overall classification accuracy was 93%. The classified image was then transferred to ArcView 3.2 (ESRI, 1996) and to Fragstats 3.3 (McGarigal *et al.*, 2002) for further analysis.

Two concentric circles of different sizes (1 km and 2.5 km in radius) centred on each bat sampling site were delimited using Arcview 3.2. The circles surrounding different sampling sites did not overlap and contained no cenotes other than the focal one. Within each circle, the extent and distribution of the different land cover categories were estimated. The choice of circle sizes (1 and 2.5 km) was based on similar studies done in Mexico (Pinto and Keitt, 2008; Avila-Cabadilla *et al.*, 2012), as well as on home range sizes and movement ranges of bat species reported for the area. In north-west Yucatan capture-recapture data indicates that *Dermanura phaeotis* (a small frugivore) has relatively restricted movements, since it moves 1.8 km on average within its home range, while *Artibeus lituratus* (a larger frugivore) covers up to 15 km (Montiel *et al.*, 2006).

The landscape structure within 1 and 2.5 km of each bat sampling site was analysed using Arcview and Fragstats, from which we obtained different quantitative estimators known to affect bats (Gorresen and Willig, 2004; Klingbeil and Willig, 2009). Since the results from the categories tall forest and young second-growth forest taken separately did not differ from results when these two categories were combined, we decided to combine them into one category called forest cover. The landscape metrics that we estimated were: percentage of total forest area (Total area), mean forest patch area (Patch area), mean forest patch density (Patch density) and landscape heterogeneity estimated with Simpson's Diversity Index (Heterogeneity). Forest edge density (Edge density), mean shape index (Shape Index), mean nearest-neighbour distance (Nearest-Neighbour), and mean proximity index (Proximity Index) were calculated as metrics of landscape configuration. More details on the indices and their formulas are found in McGarigal *et al.* (2002).

Statistical Analysis

Only phytophagous bats that consume fruit, nectar or pollen were included in the analysis. The relationships between phytophagous bat abundance and the explanatory variables—matrix type (pasture or continuous forest) and cenote presence or absence—were analysed using a Generalised Linear Model (GLM), assuming a negative binomial distribution. The models were compared using the Akaike Information Criterion (AIC).

A Principal Components Analysis (PCA) was used to compare structural characteristics among bat sampling sites, first for vegetation structure and then for landscape characteristics, in both the 1 and 2.5 km radius areas. The results of these multivariate analyses were used to identify the variables with no collinearity among them that best explained most of the variation in the characteristics of the sampling sites. Spatial variation in phytophagous bat abundance among sites was analysed with GLM, using the most important variables identified by the PCA and assuming a negative binomial distribution. AIC was used to select the best model.

To assess the relative importance of vegetation structure and landscape characteristics on the species composition of phytophagous bats, a Co-Inertia Analysis (CoIA) was performed. This analysis was used to determine the degree of correlation between two matrices: the bat species matrix (number of bats captured per bat species per site) and the explanatory variables matrix (vegetation and landscape characteristics per site). In CoIA the first step is to analyse each matrix separately, using a correspondence analysis or PCA to summarise each matrix identifying the orthogonal axes in which the projection of the sampled units have the maximum variance. The second step is to simultaneously analyse bat composition and the explanatory variables. CoIA searches for the axes (one per matrix) that maximise the covariance (co-inertia) between the two sets of projected data (Dray *et al.*, 2003). The relationship between bat species and explanatory variables was assessed with the RV coefficient, which ranges from 0% to 100% (100% when the correlation between the two matrices is perfect). A Monte-Carlo test (999 permutations) was conducted on the RV coefficient to determine the statistical significance of the relationship between bat species and explanatory variables (Aznar *et al.*, 2003). Statistical analyses were performed using R 2.15.1 software (R Development Core Team, 2008).

RESULTS

Bat Sampling

A total of 1398 phytophagous bats belonging to seven species were captured, six were mainly frugivorous and one, a nectarivore that is seasonally frugivore: *Glossophaga soricina*. *Artibeus jamaicensis* was the most abundant species by far in all sites; however, the second most abundant species was different in each matrix type: *Sturnira lilium* in the pasture matrix and *Dermanura phaeotis* in the continuous forest matrix (Table 1). The abundance of phytophagous bats was significantly higher ($Z = -5.03$, $d.f. = 7$, $P < 0.001$) in the pasture matrix than in the continuous forest matrix. There were no significant differences in bat abundance ($Z = 1.78$, $d.f. = 7$, $P = 0.08$) between sites with versus without cenotes. The interaction between matrix type and cenote condition was significant ($Z = -2.67$, $d.f. = 7$, $P = 0.008$); bat abundance was higher in sites with no cenote than in those with a cenote in the pasture matrix, while in the continuous forest matrix the opposite trend was found.

Vegetation Structure

A total of 142 plant species belonging to 38 families were recorded, Fabaceae was the richest family (25 species). Twelve species were identified only to family and 20 to genus. At least 30 of the plant species recorded have been reported as eaten by bats (Appendix). Sites with cenotes had the highest richness and basal area of plant species eaten by bats. Sites with no cenote in the continuous forest matrix were grouped by their similar and high values of plant density and the basal area of species

not eaten by bats (Fig. 2a). The first three components of the PCA explained 89.2% of the variation.

Landscape Characteristics

For both landscape scales (1 and 2.5 km), the PCA separated sites in continuous forest from those in pasture matrix along the first ordination axis (Fig. 2). At both scales, continuous forest sites had high values of total forest area, mean patch area and proximity index, while the sites in the pasture matrix had high values of patch density, forest edge density and heterogeneity in land cover types. The two first PCA components explained 93.4% of the variation of landscape characteristics within 1 km of the sampling sites. For the larger 2.5-km-radius circle the first two PCA components explained 85.9% of the variation.

Response of Phytophagous Bats to Vegetation and Landscape Characteristics

Of the vegetation variables we measured, tree density best explained variation in bat abundance ($Z = -3.95$, $d.f. = 7$, $P < 0.001$). Of the landscape characteristics within 1 km of the sampling sites, total forest area ($Z = 2.98$, $d.f. = 7$, $P < 0.01$) and heterogeneity ($Z = 5.55$, $d.f. = 7$, $P < 0.001$) were significantly related to phytophagous bat abundance. Over a larger distance from sampling sites (2.5 km), heterogeneity was the landscape attribute that best explained the variation in bat abundance among sites ($Z = 3.83$, $d.f. = 7$, $P < 0.001$).

Species-specific Responses

The abundance of four of the five phytophagous bat species for which we had sufficient abundance

TABLE 1. Phytophagous bat abundance (family Phyllostomidae) in two landscape matrices in the Yucatan, Mexico, each with (+cenote) and without a cenote (-cenote). Data in the columns are the sum of two bat sampling sites per matrix and cenote condition, over four sampling expeditions (see Materials and Methods)

Taxon	Pasture matrix		Forest matrix		Total
	+cenote	-cenote	+cenote	-cenote	
Glossophaginae					
<i>Glossophaga soricina</i>	22	27	7	8	64
Stenodermatinae					
<i>Artibeus jamaicensis</i>	375	584	106	55	1,120
<i>A. lituratus</i>	3	4	3	5	15
<i>Centurio senex</i>	1	3			4
<i>Chiroderma villosum</i>	2		1		3
<i>Dermanura phaeotis</i>	16	12	13	8	49
<i>Sturnira lilium</i>	51	82	6	4	143
Total	470	712	136	80	1,398

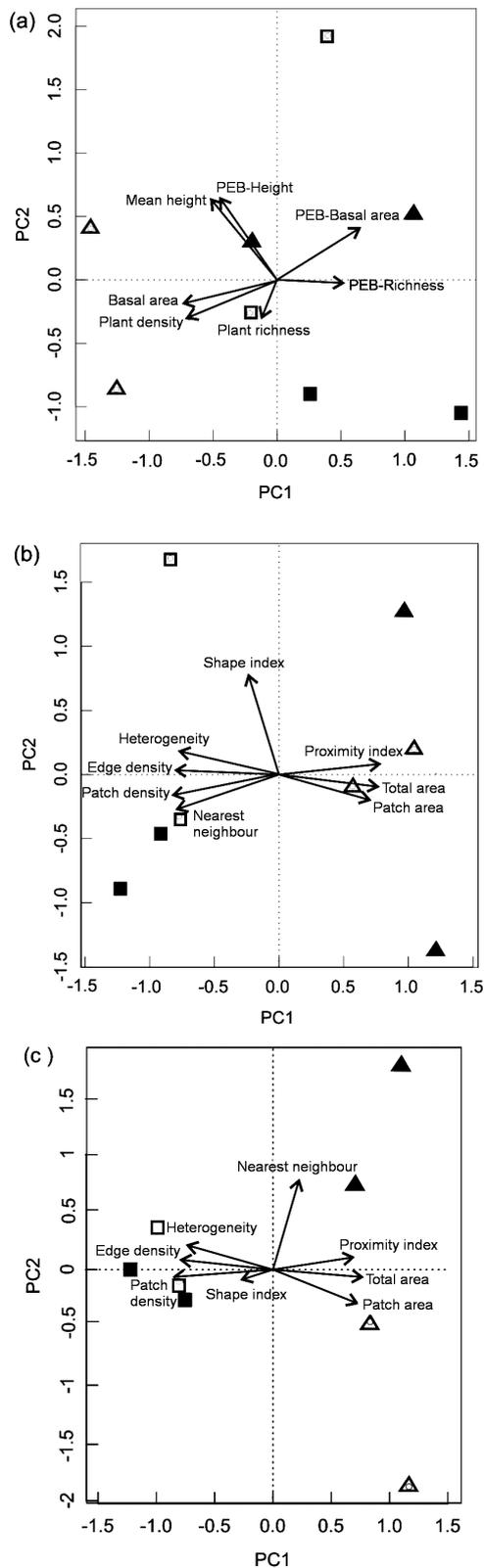


FIG. 2. Multivariate ordination (Principal Component Analysis; PCA) of bat sampling sites, based on different properties: a) vegetation structure and composition; b) landscape characteristics within a radius of 1 km around each site; c) landscape characteristics within a radius of 2.5 km. Bat sampling sites are indicated as in Fig. 1. PEB = Plant species eaten by bats

data per site (*A. jamaicensis*, *D. phaeotis*, *G. soricina*, *S. lilium*) was strongly and negatively correlated with tree density per site; *A. lituratus* was the only species with a positive correlation (Fig. 3). The abundance of *A. jamaicensis* was also negatively correlated with total plant richness per site, but was positively correlated with the basal area of plant species eaten by bats (PEB). For *D. phaeotis* abundance was positively correlated with the basal area and richness of PEB, as well as with total plant richness, while that of *A. lituratus* was negatively correlated with these variables. For *G. soricina*, abundance was positively and moderately correlated with the height and basal area of PEB. The abundance of *S. lilium* was strongly and positively correlated with the basal area of PEB and negatively correlated with total plant richness.

The individual response to landscape attributes both 1 and 2.5 km from the capture sites, showed that three of the five fruit-eating bat species (*A. jamaicensis*, *G. soricina* and *S. lilium*) responded similarly to landscape characteristics (Fig. 3). The abundance of these species was negatively correlated with the characteristics of continuous forest matrix (e.g. total forest area, mean distance to the nearest patch, proximity index), and positively correlated with the characteristics indicative of forest fragmentation (e.g., forest edge density, shape index, landscape heterogeneity). Although the response pattern of *D. phaeotis* was similar to the three species described above, its abundance was positively related to the nearest forest patch and negatively related to shape index. Finally, *A. lituratus* abundance was weakly correlated with landscape variables within one km of the sampling sites, while in the larger circle it was the only species whose abundance was positively correlated with proximity index (Fig. 3).

The Co-Inertia analysis explained 67.8% of the relationship between the specific abundance of phytophagous bats and the vegetation structure and landscape variables evaluated in this study. Since the Monte Carlo test result was significant ($P=0.017$), the relationships depicted cannot be explained by random variation. The variables with the greatest weight and that were most negatively correlated with phytophagous bat abundance were the density and richness of all woody plants, total forest area within one km, and total forest area and proximity index within 2.5 km. Bat abundance was positively correlated with the basal area and richness of plant species eaten by bats, with shape index and forest edge density within 1 km, as well as landscape heterogeneity within 2.5 km of the capture site.

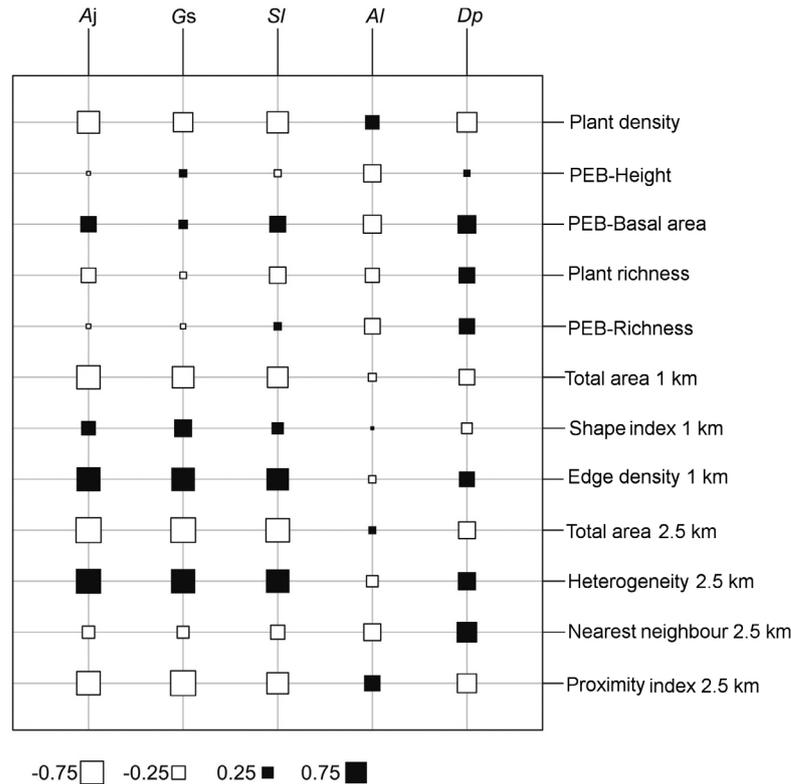


FIG. 3. Factorial Co-Inertia map, showing positive (■) and negative (□) correlations for each phytophagous bat species and selected characteristics of the sampling sites. The size of the square is proportional to the magnitude of the correlation between site characteristics and bat species (see inset legend). PEB = Plant species eaten by bats

DISCUSSION

The Response of Phytophagous Bats to Vegetation and Landscape Characteristics

Given that the richness and basal area of edible tree species in the woody vegetation surrounding cenotes is greater than that of wooded sites without them, we expected to find a higher abundance of phytophagous bats in sites with cenotes than in sites without them in both types of landscape matrices, but particularly in the pasture matrix. Our results, however, do not support our original hypothesis. In the neighbouring state of Quintana Roo, also on the Yucatan Peninsula, MacSwiney *et al.* (2007) report a higher number of bat captures at locations with cenotes in both forest and pasture habitats, than in sites without cenotes. This apparent contradiction with our data may be explained by the different habitats in which the mist nets were placed. In our study, mist nets were placed within forest remnants in both landscape matrices and cenote treatment, whereas MacSwiney *et al.* (2007) placed mist nets for pasture habitats out in the open where capture

rate of phytophagous bats is usually low (Estrada *et al.*, 1993; Avila-Cabadilla *et al.*, 2012). In pastures with a relatively high proportion of tree cover (16–25%) bat capture rates increase (Medina *et al.*, 2007). Even under the canopy of fig trees isolated in large pastures, capture rates can be quite high (Galindo-González and Sosa, 2003). The great habitat heterogeneity in our pasture matrix resulting from the different types of land use (forest, secondary vegetation, crop-fields and pastures), and other elements of the landscape such as living fences, isolated trees and the t'olche', where phytophagous bats can find food, could explain why though unexpected, sampling sites with cenote were not significantly different from sites without cenote, particularly in pasture matrix sites. The presence of only one or a few trees of the species that are highly attractive to bats, such as *Vitex gaumeri*, *Ficus* spp. and *Brosimum alicastrum* within the small forest patches sampled in pasture matrix, along with the fact that these trees had lots of ripe fruit on our sampling nights (BB, personal observations), increased bat activity in sites with and without cenotes.

Phytophagous bats appeared to respond to a greater degree to specific characteristics of the woody vegetation than to the presence of cenotes. The richness and basal area of edible plants in the sampling sites had a positive effect on bat captures, similar to the findings of other studies in Mexico (Saldaña-Vázquez *et al.*, 2010; Castro-Luna and Galindo-González, 2012). The abundance of *A. jamaicensis*, *D. phaeotis* and *S. lilium* was strongly and positively correlated with the basal area of plant species eaten by bats (PEB). *Artibeus* and *Dermanura* are known to eat the fruit or flowers of large trees such as *Ficus*, *Manilkara*, *Brosimum* and *Cecropia* (Schulze *et al.*, 2000; Lobova *et al.*, 2009); which were relatively common at our study sites. The positive relationship between *Sturnira* abundance and the basal area of PEB can be explained by the preference of this bat species for roosting in tall trees with wide trunks (Evelyn and Stiles, 2003).

Another vegetation characteristic that influenced phytophagous bat abundance was tree density. The sites with high tree densities had fewer captures. This can be explained by the difficulty of manoeuvring around obstacles (Swartz *et al.*, 2003), reported for many bats that preferentially forage above the forest canopy or in the less dense subcanopy (i.e., *A. jamaicensis*, *D. phaeotis* and *G. soricina*). For *S. lilium*, an agile understory specialist, the lower captures at sites with high tree density may result from the low availability of *Solanum* fruit — the main food of *Sturnira* (Marinho-Filho, 1991). Mature *Solanum* plants do not occur in heavily shaded areas, but are abundant in open sites (Estrada *et al.*, 1993; BB and CMG, personal observations).

Contrary to our second hypothesis that proposed a higher abundance of bats in landscapes with large tracts of continuous forest, we found that bat abundance was negatively correlated with the proportion of forest cover within radii of 1 and 2.5 km of the sampling sites, and positively correlated with landscape variables that reflect intense deforestation and forest fragmentation. Klingbeil and Willig (2009) report a similar trend in Peru, but the opposite has been found in Mexico (Pinto and Keitt, 2008; Avila-Cabadilla *et al.*, 2012) and Paraguay (Gorresen and Willig, 2004). In those studies in which a positive relationship between bat abundance and forest cover was found, the sampling sites had secondary forest cover (Pinto and Keitt, 2008) or riparian forest (Avila-Cabadilla *et al.*, 2012), and unlike our study they did not include sampling sites within large tracts of continuous forest. The high capture rates of phytophagous bats in fragmented landscapes such as

our pasture matrix sites could be related to the high availability of fruit from *Solanum* spp. and *Cecropia* spp. in the vicinity of sampling sites. These plants grow well in disturbed sites with a high density of forest edges, while they are uncommon in large expanses of undisturbed forest. Both genera are important sources of fruit for *A. jamaicensis*, *S. lilium*, *G. soricina* and *D. phaeotis* (Lobova *et al.*, 2009), explaining in part the higher abundance of bats in landscapes with a higher density of forest edges and a higher proportion of edge to forest interior.

Landscape heterogeneity (spatially complex configurations and different land cover types) also influenced the spatial variation in bat abundance at our sites, and was important within 1 and 2.5 km of the capture sites. The results of several studies and likewise our data, suggest that the high heterogeneity of some agricultural landscapes has a positive effect on the abundance and distribution of the bat species that eat pollen, nectar or fruit (Galindo-González and Sosa, 2003; Medina *et al.*, 2007; Castro-Luna and Galindo-González, 2012). We captured more bats in sites within landscapes dominated by a pasture matrix; i.e. landscapes that were more heterogeneous in their land cover types, than in those dominated by large tracts of continuous forest. Different land cover types such as old growth forest, secondary forest in old-fields, active pastures and crop fields appear to best meet the foraging and roosting needs of phytophagous bats (landscape complementation, *sensu* Dunning *et al.*, 1992).

Our higher rates of bat capture in the pasture matrix compared with that of the continuous forest matrix can also be explained by a concentration effect: forest patches in a matrix of open pastures limit the foraging and roosting activities of frugivorous bats to the small areas that retain arboreal vegetation, while in the large tracts of continuous forest, bat activities are not spatially restricted, and they can search for food and roosts over a much larger area, reducing the probability of capture in mist nets (Loayza and Loiselle, 2009). Furthermore, contrary to other fragmented sites in the Neotropics (e.g. Estrada *et al.*, 1993), the forest patches in our pasture matrix have retained much of the mature forest species component and thus provide a wider array of resources for phytophagous bats. We found that in 300 m² sampled in each site, the number of individuals of tree species eaten by bats was higher or similar in forest patches than in the continuous tropical semi-deciduous forest (Appendix). Therefore forest patches at the study site should concentrate foraging activities and attract not only species of bats that

feed mostly upon pioneer species (i.e. *Sturnira*), but also bats that feed in the canopy of mature forest tree species (i.e., *Chiroderma*, *Artibeus*). A similar trend was found in Bolivia by Loayza and Loiselle (2009) sampling with mist nets in continuous forests and forest islands in a savanna matrix.

Forest Fragmentation and Landscape Characteristics in the Yucatan

In our study site, indigenous farmers still use the traditional agro-forestry practice known by the Maya word T'olche' (Remmers and Koeijer, 1992), which in broad terms consists of leaving a 10- to 20-m-wide belt of forest between agricultural plots. Owing to the presence and current density of T'olche', the separation between forest fragments and other arboreal elements does not exceed 700 m, thus, T'olche' maintains a high degree of landscape connectivity. Furthermore, some of the tree species that form part of the T'olche' such as *Guazuma ulmifolia* and *Carica papaya* (Remmers and Koeijer, 1992) are sources of food for phytophagous bats.

The trees located in pastures and crop fields — especially those that produce fruit used by bats and humans (*Manilkara zapota*, *Psidium guajava*) — are used as forage for livestock (*Brosimum alicastrum*) or as shade trees (*Terminalia catappa*, *V. gaurmeri*, *Ficus* spp.), and likely favour the presence and movement of bats within agricultural landscapes in the Yucatan and other regions of Mexico (Estrada *et al.*, 1993; MacSwiney *et al.*, 2007; Castro-Luna and Galindo-González, 2012). The presence of isolated *Ceiba* and *Cecropia* trees and *Sabal* palms in pastures and crop fields also increases landscape connectivity for bats in pasture dominated landscapes.

Areas of 5 km or more that are completely devoid of trees greatly limit the movement of bats, and represent barriers for phytophagous bat species (Willig *et al.*, 2007). Remnant forest fragments, old-fields with secondary forest, living fences, isolated trees, and particularly the T'olche' forest belts that grid the landscape all greatly reduce the expanse of large open areas. Under these circumstances, bats are able to make use of the agricultural landscape prevalent in the Yucatan. Traditional agroforestry practices developed by the Maya have been performed over centuries in Yucatan and the resultant heterogeneous mosaic has been important not only for life sustenance of its inhabitants but also for the conservation of a great proportion of the native

biodiversity of the area (Toledo *et al.*, 2008), including phytophagous bats.

Our results show that the amount and spatial arrangement of forest cover are not the only important variables for bat fauna. Equally important are the quality of the remaining forest patches as habitat for bats and the variety of land cover types in agricultural landscapes. Our results also suggest that habitat quality for phytophagous bats is not only a function of the availability and quality of edible resources, but also of other habitat characteristics such as the presence of potentially attractive refuge and roost sites, that must be included in future studies.

ACKNOWLEDGEMENTS

We are grateful to the land owners of the Yucatan who gave us permission to sample bats and plants on their property. Many thanks to Alan Cuxim, Marisol Meza, Richard Chi, Juan M. Pech and José Guemez for help with the field work. Thanks to Rene Murrieta Galindo for advice on statistical analysis. This study was partially supported by the Consejo Nacional de Ciencia y Tecnología (CONACYT doctoral studies scholarship #212500 to BB) and by the Instituto de Ecología, A.C. (902-11-281). Bianca Delfosse helped with style revision and made useful comments. Collecting permit number 04316 was issued to CMG by the Mexican federal authority (SEMARNAT).

LITERATURE CITED

- AVILA-CABADILLA, L. D., G. A. SANCHEZ-AZOFEIFA, K. E. STONER, M. Y. ALVAREZ-AÑORVE, M. QUESADA, and C. A. PORTILLO-QUINTERO. 2012. Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forest. *PLoS ONE*, 7: e35228.
- AZNAR, J. C., A. DERVIEUX, and P. GRILLAS. 2003. Association between aquatic vegetation and landscape indicators of human pressure. *Wetlands*, 23: 149–160.
- CASTRO-LUNA, A. A., and J. GALINDO-GONZÁLEZ. 2012. Enriching agroecosystems with fruit-producing tree species favors the abundance and richness of frugivorous and nectarivorous bats in Veracruz, Mexico. *Mammalian Biology*, 77: 32–40.
- CASTRO-LUNA, A. A., V. J. SOSA, and G. CASTILLO-CAMPOS. 2007. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, 10: 219–228.
- DRAY, S., D. CHESSEL, and J. THIOULOUSE. 2003. Co-inertia analysis and the linking of ecological data tables. *Ecology*, 84: 3078–3089.
- DUCH-GARY, J. 1988. La conformación territorial del Estado de Yucatán. Los componentes del medio físico. Universidad Autónoma Chapingo, México, 427 pp.
- DUNNING, J. B., B. J. DANIELSON, and H. R. PULLIAM. 1992. Ecological processes that affect populations in complex landscapes. *Oikos*, 65: 169–175.
- DURÁN-GARCÍA, R., and G. GARCÍA-CONTRERAS. 2010. Distribución espacial de la vegetación. Pp. 131–135, in *Biodiversidad y desarrollo humano en Yucatán* (R. DURÁN-GARCÍA and M. MÉNDEZ-GONZÁLEZ, eds.). CICY, PPD-FMAM, CONABIO, Seduma, Mérida, México, 496 pp.

- ESRI (Environmental Systems Research Institute, Inc.). 1996. ArcView[®] 3.2. ESRI, Redlands, CA.
- ESTRADA, A., R. COATES-ESTRADA, and D. MERITT, JR. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography*, 16: 309–318.
- EVELYN, M. J., and D. A. STILES. 2003. Roosting requirements of two frugivorous bats (*Sturnira lilium* and *Artibeus lituratus*) in fragmented Neotropical forest. *Biotropica*, 35: 405–418.
- FLEMING, T. H., C. GEISELMAN, and W. J. KRESS. 2009. The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany*, 104: 1017–1043.
- FLORES-GUIDO, J. S. 2010. Vegetación de cenotes, rejolladas, haltunes y cavernas. Pp. 496, in *Biodiversidad y desarrollo humano en Yucatán* (R. DURÁN-GARCÍA and M. MÉNDEZ-GONZÁLEZ, eds.). CICY, PPD-FMAM, CONABIO, Seduma, Mérida, México, 496 pp.
- GALINDO-GONZÁLEZ, J. G. 2004. Clasificación de los murciélagos de la región de Los Tuxtlas, Veracruz, respecto a su respuesta a la fragmentación del hábitat. *Acta Zoológica Mexicana*, 20: 239–243.
- GALINDO-GONZÁLEZ, J., and V. J. SOSA. 2003. Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. *Southwestern Naturalist*, 48: 579–589.
- GENTRY, A. H. 1982. Patterns of Neotropical plant species diversity. *Evolutionary Biology*, 15: 1–85.
- GEOMATICS, P. C. I. 2001. X-Pace reference manual, version 8.2. PCI Geomatics, Ontario, Canada, 316 pp.
- GORRESEN, P. M., and M. R. WILLIG. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *Journal of Mammalogy*, 85: 688–697.
- INEGI (Instituto Nacional de Estadística, Geografía e Informática). 2006. Anuario estadístico. Yucatán. Gobierno del Estado de Yucatán, INEGI, México. Available at <http://www.inegi.org.mx/est/contenidos/espanol/sistemas/aee06/estatal/yuc/index.htm>.
- KLINGBEIL, B. T., and M. R. WILLIG. 2009. Guild-specific responses of bats to landscape composition and configuration in fragmented Amazonian rainforest. *Journal of Applied Ecology*, 46: 203–213.
- LOAYZA, A. P., and B. A. LOISELLE. 2009. Composition and distribution of a bat assemblage during the dry season in a naturally fragmented landscape in Bolivia. *Journal of Mammalogy*, 90: 732–742.
- LOBOVA, T. A., C. K. GEISELMAN, and S. A. MORI. 2009. Seed dispersal by bats in the Neotropics. *Memoirs of the New York Botanical Garden*, 101: 1–465.
- MACSWINEY G., M. C., P. VILCHIS, F. CLARKE, and P. A. RACEY. 2007. The importance of cenotes in conserving bat assemblages in the Yucatan, Mexico. *Biological Conservation*, 136: 499–509.
- MACSWINEY G., M. C., B. BOLÍVAR-CIMÉ, F. M. CLARKE, and P. A. RACEY. 2009. Insectivorous bat activity at cenotes in the Yucatan Peninsula, Mexico. *Acta Chiropterologica*, 11: 139–147.
- MARIHNO-FILHO, J. S. 1991. The coexistence of two frugivorous bats species and the phenology of their food plants in Brazil. *Journal of Tropical Ecology*, 7: 59–67.
- MCGARIGAL, K., S. A. CUSHMAN, M. C. NEEL, and E. ENE. 2002. FRAGSTATS: spatial pattern analysis program for categorical maps. Available at <http://www.umass.edu/landeco/research/fragstats/fragstats.html>.
- MEDELLÍN, R. A., H. T. ARITA, and O. SÁNCHEZ. 2008. Identificación de los murciélagos de México, clave de campo, 2nd edition. Asociación Mexicana de Mastozoología, México, D.F., 83 pp.
- MEDINA, A., C. A. HARVEY, D. S. MERLO, S. VÍLCHEZ, and B. HERNÁNDEZ. 2007. Bat diversity and movement in an agricultural landscape in Matiguás, Nicaragua. *Biotropica*, 39: 120–128.
- MONTIEL, S., A. ESTRADA, and P. LEÓN. 2006. Bat assemblages in a naturally fragmented ecosystem in the Yucatan Peninsula, Mexico: species richness, diversity and spatio-temporal dynamics. *Journal of Tropical Ecology*, 22: 267–276.
- PINTO, N., and T. H. KEITT. 2008. Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos*, 117: 1725–1731.
- R DEVELOPMENT CORE TEAM. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.R-project.org>.
- REID, F. 2009. A field guide to the mammals of Central America and southeast Mexico, 2nd edition. Oxford University Press, New York, NY, 384 pp.
- REMMERS, G. G. A., and H. DE KOEIJER. 1992. The T'olche', a Maya system of communally managed forest belts: the causes and consequences of its disappearance. *Agroforestry Systems*, 18: 149–177.
- REX, K., B. I. CZACZKES, R. MICHENER, T. H. KUNZ, and C. C. VOIGT. 2010. Specialization and omnivory in diverse mammalian assemblages. *Ecoscience*, 17: 37–46.
- SALDAÑA-VÁZQUEZ, R. A., and M. A. MUNGUÍA-ROSAS. 2013. Lunar phobia in bats and its ecological correlates: a meta-analysis. *Mammalian Biology*, 78:216–219.
- SALDAÑA-VÁZQUEZ, R. A., V. J. SOSA, J. R. HERNÁNDEZ-MONTERO, and F. LÓPEZ-BARRERA. 2010. Abundance responses of frugivorous bats (Stenodermatinae) to coffee cultivation and selective logging practices in mountainous central Veracruz, Mexico. *Biodiversity and Conservation*, 19: 2111–2124.
- SCHULZE, M., N. SEAVY, and D. WHITACRE. 2000. A comparison of the Phyllostomid bat assemblages in undisturbed Neotropical forest and forest fragments of a slash-and-burn farming mosaic in Peten, Guatemala. *Biotropica*, 32: 174–184.
- SWARTZ, S., P. W. FREEMAN, and E. F. STOCKWELL. 2003. Ecomorphology of bats: comparative and experimental approaches relating structural design to ecology. Pp. 257–300, in *Bat ecology* (T. H. KUNZ, and M. B. FENTON, eds.). University of Chicago Press, Chicago, 798 pp.
- TOLEDO, V. M., N. B. BASSOLS, E. G. FRAPOLLI, and P. A. CHAIRES. 2008. Uso múltiple y biodiversidad entre los mayas yucatecos (México). *Interciencia*, 33: 345–352.
- VALDEZ-HERNANDEZ, M., J. L. ANDRADE, P. C. JACKSON, and M. REBOLLEDO-VIEYRA. 2010. Phenology of five tree species of a tropical dry forest in Yucatan, Mexico: effects of environmental and physiological factors. *Plant Soil*, 329: 155–171.
- WILLIG, M. R., S. J. PRESLEY, C. P. BLOCH, C. L. HICE, S. P. YANOVIK, M. M. DÍAZ, L. ARIAS CHAUCA, V. PACHECO, and S. C. WEAVER. 2007. Phyllostomid bats of lowland Amazonia: Effects of habitat alteration on abundance. *Biotropica*, 39: 737–746.

APPENDIX

Plant species eaten by bats recorded at sampling sites in the Yucatan, Mexico. Number of individuals with DBH > 1 cm and rooted inside three 5 × 20 m plots per site (300 m²/site). Two sites per landscape matrix and cenote treatment were sampled: +CEN (with a cenote), -CEN (no cenote) see Methods for sampling details

Taxon	Pasture matrix				Forest matrix				Total
	+CEN1	+CEN2	-CEN1	-CEN2	+CEN1	+CEN2	-CEN1	-CEN2	
ANACARDIACEAE									
<i>Spondias mombin</i>					1		1		2
<i>S. radlkoferi</i>		2			1			4	7
APOCYNACEAE									
<i>Thevetia gaumeri</i>	1						1		2
ARECACEAE									
<i>Sabal mexicana</i>					2				2
BIGNONIACEAE									
<i>Crescentia cujete</i>		1							1
<i>Parmentiera aculeate</i>								5	5
BORAGINACEAE									
<i>Ehretia tinifolia</i>				1	1				2
CACTACEAE									
<i>Acanthocereus pentagonus</i>						2			2
<i>Acanthocereus sp.</i>	1								1
FABACEAE									
<i>Acacia gaumeri</i>	15	18	8		1	3	1		46
<i>Erythrina standleyana</i>	1	2			2		1	1	7
<i>Lysiloma latisiliquum</i>			2		3	3	11	3	22
LAMIACEAE									
<i>Vitex gaumeri</i>				2		5	2	3	12
MALVACEAE									
<i>Ceiba aesculifolia</i>		3							3
<i>C. pentandra</i>				2					2
<i>Helicteres baruensis</i>								1	1
<i>Luehea speciosa</i>							2		2
MORACEAE									
<i>Brosimum alicastrum</i>	1	2		12					15
<i>Ficus cotinifolia</i>	2	4							6
<i>F. padifolia</i>		1			1				2
<i>Ficus sp.</i>	3	2		1					6
<i>Maclura tinctoria</i>		1	1	2					4
PIPERACEAE									
<i>Piper amalago</i>					15				15
SAPINDACEAE									
<i>Sapindus saponaria</i>								8	8
<i>Sapindus sp.</i>						1			1
<i>Talisia olevaiiformis</i>	8	2		1	4	2	1		18
SAPOTACEAE									
<i>Manilkara sapota</i>		1			2				3
<i>Sideroxylon foetidissimum</i>					9				9
<i>Sideroxylon sp.</i>				3			2		5
STERCULIACEAE									
<i>Guazuma ulmifolia</i>			2						2
Total	32	39	13	24	42	16	22	25	213