

Responses of Phyllostomid Bats to Traditional Agriculture in Neotropical Montane Forests of Southern Mexico

Miguel Briones-Salas^{1,*}, Mario C. Lavariega¹, Claudia E. Moreno², and Joaquín Viveros³

¹Laboratorio de Vertebrados Terrestres (Mastozoología), Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional, Unidad Oaxaca, Instituto Politécnico Nacional (CIIDIR-OAX, IPN). Hornos 1003, Santa Cruz Xoxocotlán, 71230, Oaxaca, Mexico.

*Correspondence: Tel: +52-951-5170610. E-mail: mbriones@ipn.mx (MB-S). E-mail: mlavariegan@ipn.mx (MCL)

²Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería Universidad Autónoma del Estado de Hidalgo, Carretera Pachuca-Tulancingo Km 4.5, Colonia Carboneras, 42184, Mineral de la Reforma, Hidalgo, México. E-mail: cmoreno@uaeh.edu.mx

³Universidad Autónoma Benito Juárez de Oaxaca, Avenida Universidad, Ex-Hacienda Cinco Señores, 68120, Oaxaca, Mexico. E-mail: jbv666999@hotmail.com

Received 5 October 2018 / Accepted 15 April 2019 / Published 12 June 2019
Communicated by Teng-Chiu Lin

Bat communities' responses to land use change in neotropical montane forests have scarcely been studied. We hypothesized that, like in lowland forests, a montane agricultural area will have a lower species richness, abundance, diversity and species composition of understory phyllostomid bats than a native forest (montane cloud forest and pine-oak forest). Monthly surveys over the course of a year gave an overall low species richness and abundance (167 captures corresponding to nine species). We found a slight loss of species richness in agricultural areas with respect to the montane cloud forest (one species) and pine-oak forest (two species). However, differences in abundance were noteworthy: 45% and 73% fewer captures in agricultural areas than in the montane cloud forest and pine-oak forest, respectively. Species diversity was higher in the montane cloud forest than the pine-oak forest, but the diversity of agricultural areas did not differ between the types. Species and guild compositions did not differ between crops and forests. At least for the understory phyllostomid bats, and at the spatial scale studied, traditional management of agricultural areas in the study area and the surrounding matrix could explain the similarity in species richness, composition, and diversity between the agricultural area and native montane forests; however, other indicator groups should be evaluated to understand the effects of habitat loss on montane forests.

Key words: Montane cloud forest, Pine-oak forest, Bat diversity, Adaptable species, Oaxaca.

BACKGROUND

The neotropical realm is one of the most biodiverse regions in the world, but it is facing a rapid process of land use change and fragmentation, mainly due to agricultural practices (Brooks et al. 2002; FAO 2009; Hansen et al. 2013). These processes affect biodiversity, changing species richness, abundance, composition, ecological functions and, therefore, the environmental services (Haddad et al. 2015). In the Neotropics, the

responses of animal communities to agriculture have been studied broadly in tropical lowland forests (e.g., Estrada and Coates-Estrada 2002; Daily et al. 2003; Gorresen and Willig 2004; Michalski and Peres 2005; Pardini et al. 2005; Martensen et al. 2012; Thornton et al. 2012). However, studies on the montane tropical forest are scarce (Pérez-Torres and Ahumada 2004; Tabarelli et al. 2010). Addressing and understanding change processes in montane ecosystems is necessary and urgent, since they harbor a high proportion of the

biotic diversity and endemism in relatively small areas, and their biologic communities are more vulnerable to changes in climate patterns than other biological communities (Brown and Kappelle 2001; González-Espinosa et al. 2012; Vegas-Vilarrúbia et al. 2012).

Due to their high diversity, abundance and variety of guilds, bats have been frequently used as a biological indicator group to study changes in ecosystems (Medellín et al. 2000; García-Morales et al. 2013). In America, Phyllostomidae is the most diverse family of bats (Simmons 2005); its species occupy a broad variety of niches and they stand out by their ecological functions as seed and pollen dispersers for many species of plants (Galindo-González et al. 2000; Soriano et al. 2000; Rost et al. 2015). In addition, phyllostomid bats are important consumers of arthropods and small vertebrates (Giannini and Kalko 2004; Kalka et al. 2008).

In lowland neotropical forests it has been observed that mosaics of natural vegetation and agriculture lands, and occasionally live fences, maintain a moderate proportion of bat species richness and abundance found in well-conserved forests (Estrada et al. 1993; Estrada and Coates-Estrada 2001; Gorresen and Willig 2004). However, within communities, the response to the configuration, connection between patches, and landscape matrix is usually species-specific (Gorresen and Willig 2004). For example, species that forage for animals in the canopy, particularly species of the Phyllostominae subfamily, diminish in abundance in fragmented landscapes; other species, however, can use both transformed and well-conserved forests in the same intensity; and adaptable species with the potential to move over large areas and that eat plants adapted to disturbances increase in abundance in fragmented landscapes (Schulze et al. 2000; Estrada and Coates-Estrada 2002; Gorresen and Willig 2004). However, when natural vegetation has been eliminated completely, effects on bat species' richness and abundance are more severe (Brosset et al. 1996; García-Morales et al. 2013).

In one of the few bat studies in montane tropical forests, Pérez-Torres and Ahumada (2004) in an Alto-Andino forest of Colombia reported a decrease of a quarter of the bat species and 43% fewer captures of frugivorous bats in fragmented forests compared to continuous ones. In another study, Mena (2010) found in an evergreen forest that there were more carnivorous species (Phyllostominae subfamily) in sites with higher vegetation cover, as predicted, but overall there was no relationship between landscape composition and configuration when it came to the abundance of frugivorous species. There is little knowledge on the effects of the change from a native neotropical montane environment to an agricultural one on a local scale, so

this study compared the relative abundance, species richness, diversity and compositional similarity of phyllostomid bats in two native forests (montane cloud forest and pine-oak forest) and agricultural areas (mixed small crops of maize, beans and sugar cane) in southern Mexico. As it has been observed in lowland forest, we expected species diversity to be lower in agricultural areas than in native tropical montane forests, and different species compositions among the cover types.

MATERIALS AND METHODS

Study site

The study site is located in the Municipality of San Andrés Solaga, district of Villa Alta, in the State of Oaxaca, Mexico, between the parallels 17°14' and 17°19' North and meridians 96°10' and 96°17' Western. The area has an elevational range from 500 to 2,400 m a.s.l. (Fig. 1). The predominant climates are temperate subhumid and semi-warm sub-humid. The annual temperature fluctuates between 12 and 18°C, and the annual precipitation is between 1,200 and 2,000 mm (Vidal-Zepeda 1990; García and CONABIO 1998).

Surveys were conducted in three cover types: montane cloud forest, pine-oak forest and agricultural areas. The agricultural areas surveyed are composed of mixed small plots (< 1 ha) of maize, beans and sugar cane, and 80% had irrigation systems (San Andrés Solaga 2012). There are also scattered trees, riparian vegetation surrounding small rivers, and backyard orchards near houses (Fig. 1). We sampled two sites within each land use, and monthly samples were carried out in the same sites. Sampling months were taken as subsamples to complete the bat inventories of each land use (Fig. 1). Therefore, we provided a cumulative description of the site's diversity and did not use traditional statistical inferences to compare land uses. Instead, we used resampling procedures to estimate confidence intervals of bat diversity, and a permutational procedure to assess bat composition (see below).

Data collection

Twelve monthly visits were done between April 2014 and March 2015; in each one, two nights of sampling were performed for every site. Surveyed sites were separated by ca. 3 km and chosen based on the following: condition of vegetation (for forests we only sampled primary forested, avoiding areas of secondary growth vegetation), the home range of phyllostomid species in montane habitats (0.4-1.4 km²; Cortés-Delgado and Sosa 2014), and for sampling the same

species pool in the area (Castro-Luna and Galindo-González 2012). Sampling two or more bat communities would probably have effects on the analyses and give biased conclusions.

Bats were captured with four mist nets (12 × 2.5 m) set between trees, and over animal trails (Kunz and Kurta 1988). Mist nets were opened for eight and a half hours (18:00 to 02:30 hrs). The taxonomic determination was made with the keys of Álvarez et al. (1994) and Medellín et al. (2008), and the nomenclatural arrangement according to Ramírez-Pulido et al. (2014). Guilds were assigned following Arita (1993) and Castro-Luna et al. (2007) as frugivorous, nectarivorous, insectivorous, and hematophagous. Research was conducted following the guidelines for animal care of Sikes and Gannon (2011) and under the permission number FAUT-043 for biological scientific samples proportionated by the Mexican environmental authorities.

Data analysis

We calculated sample coverage to quantify the survey completeness per type of cover, measured as the proportion of total individuals in the community that belong to the species present in our samples (Chao et al. 2014). This is a measure of sampling efficiency, as it means that the number of observed species constitutes a certain proportion of the total number of individuals in the communities.

As a proxy for abundance, the relative abundance index (RAI) was calculated with the quotient of individuals and survey effort (Medellín 1993), where survey effort was measured as the product of net length; the time the nets were open; and the number of nets, expressed as meters/net/hour (Medellín 1993). Number of captures were low, so to avoid very small numbers of relative abundance, relative abundance was multiplied by 1000.

We measured bat diversity with Hill numbers (*i.e.*, effective number of species). These measures are intuitive and mathematically rigorous (Jost 2006; Chao et al. 2014). The Hill numbers are parameterized by an order of diversity (q), which determines the importance of relative abundance of species. The most used Hill numbers are species richness ($q = 0$, *i.e.*, 0D), the exponential of the Shannon-Wiener entropy index ($q = 1$ or 1D), and the inverse of the Simpson diversity index ($q = 2$, 2D). When $q = 0$, 0D is the species richness, which counts the species without considering their relative abundances. When $q = 1$, it counts the species in proportion to their relative abundances. It can be interpreted as the effective number of common species in the community. When $q = 2$, it is very sensitive to dominant species and the rare species have little effect on the value; it can be interpreted as the effective number of dominant species in the community (Chao et al. 2014). Hill numbers and their 95% confidence intervals were obtained using the interpolation and extrapolation curves, and an asymptotic analysis, in

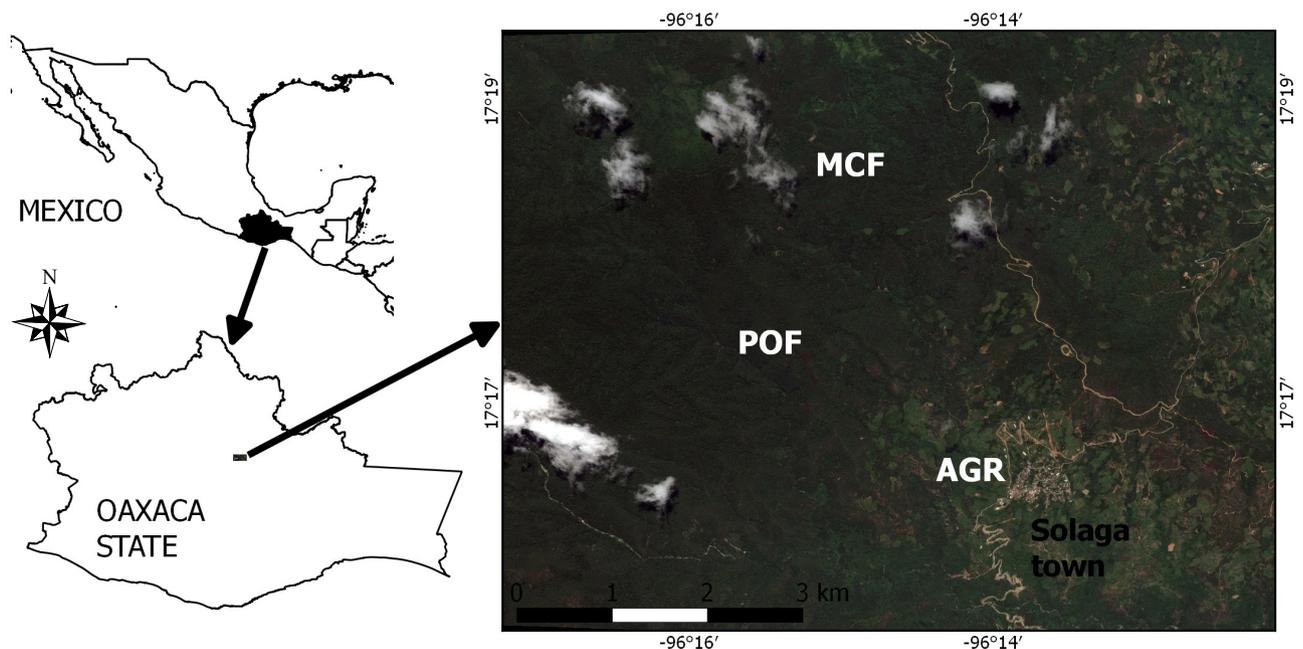


Fig. 1. Location of sampling localities (white dots; two sampling sites per locality) for phyllostomid bats in Oaxaca, Mexico. Cover types: agricultural areas (AGR), pine-oak forest (POF), and montane cloud forest (MCF). Source: Google Earth (February 2012), Digital Globe and NASA.

iNEXT (Chao et al. 2016).

To visualize patterns in species composition among cover types, a non-metrical scaling analysis (NMDS) was done with the dissimilarity of Bray-Curtis. A PERMANOVA analysis was done to test for significant differences in species and guild compositions among cover types. The NMDS and PERMANOVA analyses was done with the Vegan package in R software (Team R Development Core 2012).

RESULTS

With a total of 26,496 meters of net used, 167 bats of nine species, nine genera and four subfamilies of the Phyllostomidae family were captured (Table 1). The subfamily best represented was Stenodermatinae (5 species), followed by Glossophaginae (2 species). The Carollinae and Desmodontinae subfamilies were represented by one species each. Also recorded were one species endemic to Mexico (*Glossophaga morenoi*) and one species (*Enchisthenes hartii*) subject to special protection according to Mexican laws (SEMARNAT 2010).

With respect to the type of cover, pine-oak forest had the highest number of captures (94 individuals; 56.3%) and the highest species richness (eight species). In montane cloud forest, 47 individuals (28.1%) of seven species were recorded, while in agricultural areas 26 individuals (15.6%) of six species were captured (Table 1). Sample coverage was 0.9789, 0.9787 and 0.9668 for pine-oak, cloud forest and agricultural areas, respectively. These high proportions indicate that our surveys sampled the communities accurately. With respect to guilds, six frugivorous, two nectarivorous, and one hematophagous species were recorded. Frugivorous represented 93.4% of the captures, whereas the hematophagous represented 3.6%, and nectarivorous 3.0% (Table 1).

Relative abundance

By combining the three cover types surveyed, *Sturnira hondurensis* represented 56.28% of the total of captures. *Centurio senex* and *Glossophaga morenoi*, however, were only recorded on one occasion (0.59% each). *Sturnira hondurensis*, *D. azteca*, and *C. sowellii* were the most abundant species in the three cover types (Fig. 2). *S. hondurensis* had the highest relative abundances for all three cover types; it was highest in the pine-oak forest (RAI = 2.38), followed by the montane cloud forest (RAI = 0.64) and agricultural areas (RAI = 0.53). *Dermanura azteca* had the second highest relative abundances in the three cover types: similar in both pine-oak and montane cloud forests (RAI = 0.377), but higher in the agricultural areas (RAI = 0.151). *Carollia sowellii* had the third highest relative abundance in the montane cloud forest (RAI = 0.264) and agricultural areas (RAI = 0.113). In the pine-oak forest, *C. sowellii* and *E. hartii* shared the third place in relative abundance (RAI = 0.226 each). Rank-abundance curves showed that the montane cloud forest had the most even community, whereas the pine-oak forest had a curve dominated by one species. Montane cloud forest and agricultural areas had two rare species, whereas the pine-oak, only one. No rare species were shared among cover types.

Species richness and diversity

Interpolation and extrapolation analyses showed no difference in species richness (⁰D) among vegetation covers, because their confidence intervals overlapped (Fig. 3). However, when including species abundance in Hill numbers ¹D and ²D, the mountain cloud forest was clearly more diverse than the pine-oak forest, while the diversity of agricultural areas was not statistically different from the diversity of both forest types (Fig. 3).

Table 1. Relative abundance index (RAI) and guilds of phyllostomid bats in neotropical temperate forest and agricultural areas in southern Mexico

Subfamily	Scientific name	Guild	Number of individuals	Montane cloud forest	Pine-oak forest	Agricultural areas
Glossophaginae	<i>Anoura geoffroyi</i>	Nec	4	0.113	0.038	-
	<i>Glossophaga morenoi</i>	Nec	1	0.038	-	-
Carollinae	<i>Carollia sowellii</i>	Fru	16	0.264	0.226	0.113
Stenodermatinae	<i>Centurio senex</i>	Fru	1	-	0.038	-
	<i>Sturnira hondurensis</i>	Fru	94	0.642	2.378	0.528
	<i>Enchisthenes hartii</i>	Fru	10	0.113	0.226	0.038
	<i>Dermanura azteca</i>	Fru	25	0.377	0.377	0.151
	<i>Artibeus jamaicensis</i>	Fru	10	0.226	0.075	0.075
Desmodontinae	<i>Desmodus rotundus</i>	Hem	6	-	0.189	0.075

Similarity in species and guild compositions

The NMDS and the PERMANOVA analyses showed no significant differences in species or guild compositions among cover types (species: Pseudo-F = 1.13, $R^2 = 0.09$, $P = 0.36$; guilds: Pseudo-F = 0.84, $R^2 = 0.07$, $P = 0.47$; Fig. 4).

DISCUSSION

In this study, we compared phyllostomid bat diversity between neotropical montane forests and agricultural areas. Although the sampling effort applied to the three cover types assessed was high, we found that abundance and species richness were low—167 bats and nine species, respectively. Compared to other studies in the neotropics, our sampling effort was higher (Monroy-

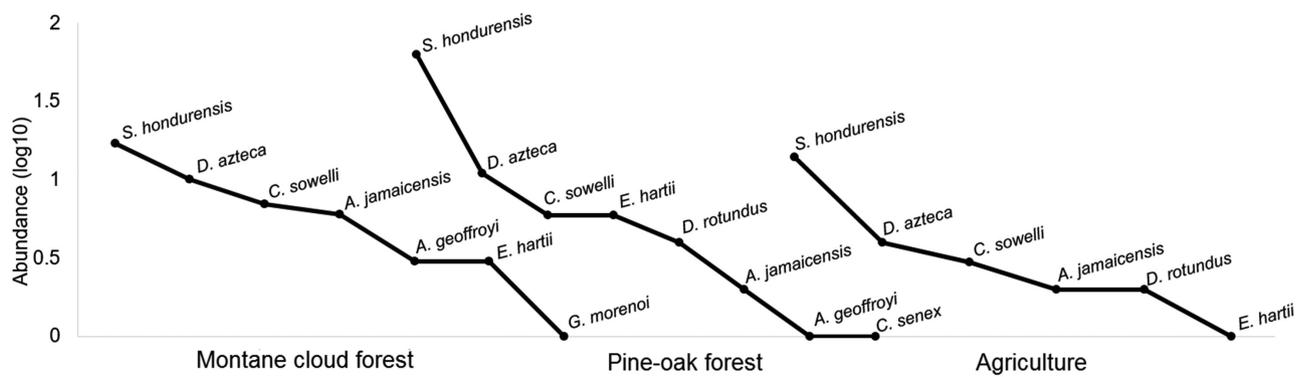


Fig. 2. Rank abundance curves of phyllostomids bats in neotropical temperate forest and agricultural areas in southern Mexico.

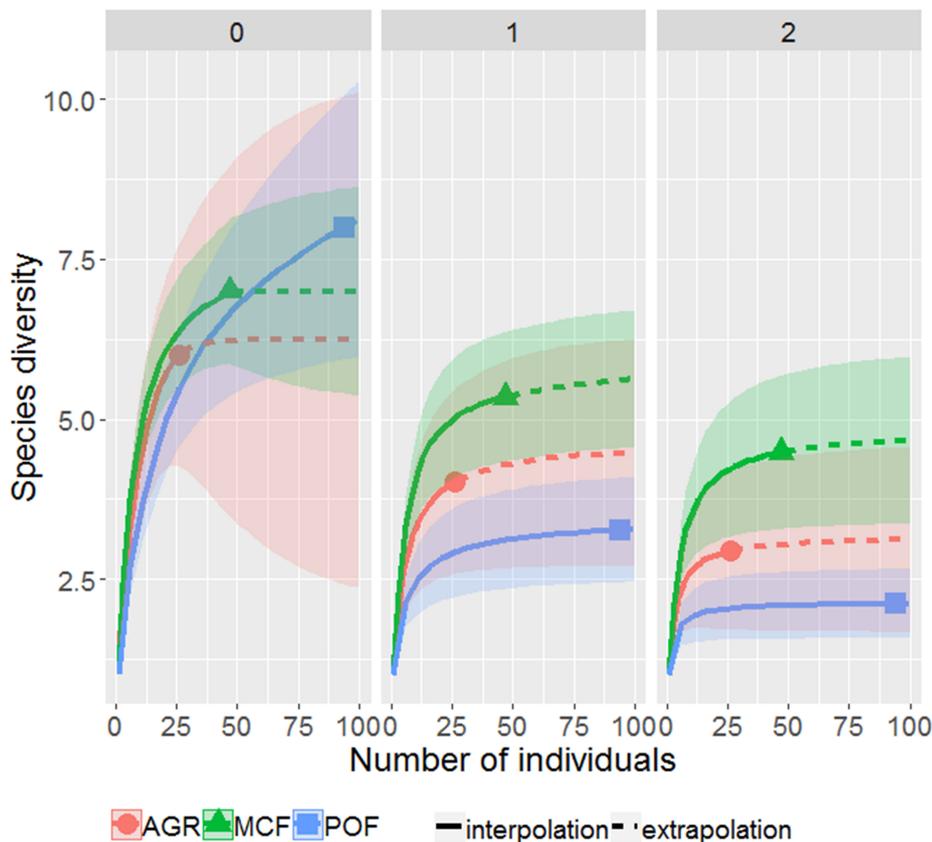


Fig. 3. Asymptotic analysis of the diversity (Hill numbers, $q = 0, 1$ and 2) of phyllostomid bats in neotropical temperate forests (MCF: montane cloud forest, POF: pine-oak forest) and agricultural areas (AGR) in southern Mexico. Shaded areas are confidence intervals at 0.95%.

Vilchis et al. 2011; Calderón-Patrón et al. 2013; Rodríguez-Macedo et al. 2014) or comparable (Castro-Luna and Galindo-González 2012; Montaña-Centellas et al. 2015; Arias et al. 2016); however, the capture rate was low (0.63 bats/sampling effort per 100). For the cited studies, the capture rate goes from 0.73 to 3.0 bats/sampling effort per 100, but in subtropical montane environments, the capture rate usually is below 1.0 (Monroy-Vilchis et al. 2011; Rodríguez-Macedo et al. 2014; Arias et al. 2016). The species richness was also comparable to other neotropical montane ecosystems. For example, in the Sierra Mazateca, southern Mexico, Briones-Salas et al. (2005) only reported four species, in both montane cloud forest and pine-oak forest; in the Atlantic montane forest of Brazil, Moras et al. (2013) recorded 10 species; and in the Serra Negra, Brazil, Nobre et al. (2013) found 14 species. Overall, these findings show that montane environments have lower abundance and species richness of phyllostomid bats than lowland forests. This is due to the fact that the bat richness is inversely related to elevation, with higher diversity in lowland forests and lower diversity in highland forests (Soriano 2000; McCain 2007; Martins et al. 2015).

We found noteworthy differences in abundance among covers (45% and 73% fewer captures in agricultural areas than montane cloud forest and pine-oak forest, respectively). Changes in bat abundances in fragmented and agroecosystems (e.g., coffee crops) with respect to primary vegetation has been observed in montane environments in the Neotropics with

contrasting findings. Whereas some studies found higher abundances in primary vegetation (Pérez-Torres and Ahumada 2004; Williams-Guillén and Perfecto 2010; this study), others reported higher abundances in fragmented or agroecosystems areas (García-Estrada et al. 2006). It seems that bat abundance is lower when intensification of agricultural systems is high, such as in monocultures or pastures for livestock (Williams-Guillén and Perfecto 2010; Castro-Luna and Galindo-González 2012). On the other hand, higher abundances occur in crops that maintain a similar cover structure of primary vegetation (García-Estrada et al. 2006; Mendoza-Sáenz and Horváth 2013). In such cases, bat abundances are affected by an increase in the numbers of frugivorous and nectivorous species, as they are able to exploit resources in altered environments (Williams-Guillén and Perfecto 2010; Castro-Luna and Galindo-González 2012; Mendoza-Sáenz and Horváth 2013; Montaña-Centellas et al. 2015).

We did not find differences in species richness, diversity, and composition among agricultural areas and forests. In contrast, previous studies found higher species richness in primary forests than forest converted to agriculture (Pérez-Torres and Ahumada 2004; García-Estrada et al. 2006; Williams-Guillén and Perfecto 2010; Montaña-Centellas et al. 2015). As has been broadly observed in lowland ecosystems, the impact of habitat loss and fragmentation on bat communities is influenced by different landscape conditions—such as size and shape of patches—surrounding matrix, distance between fragments, and/or the interactions among

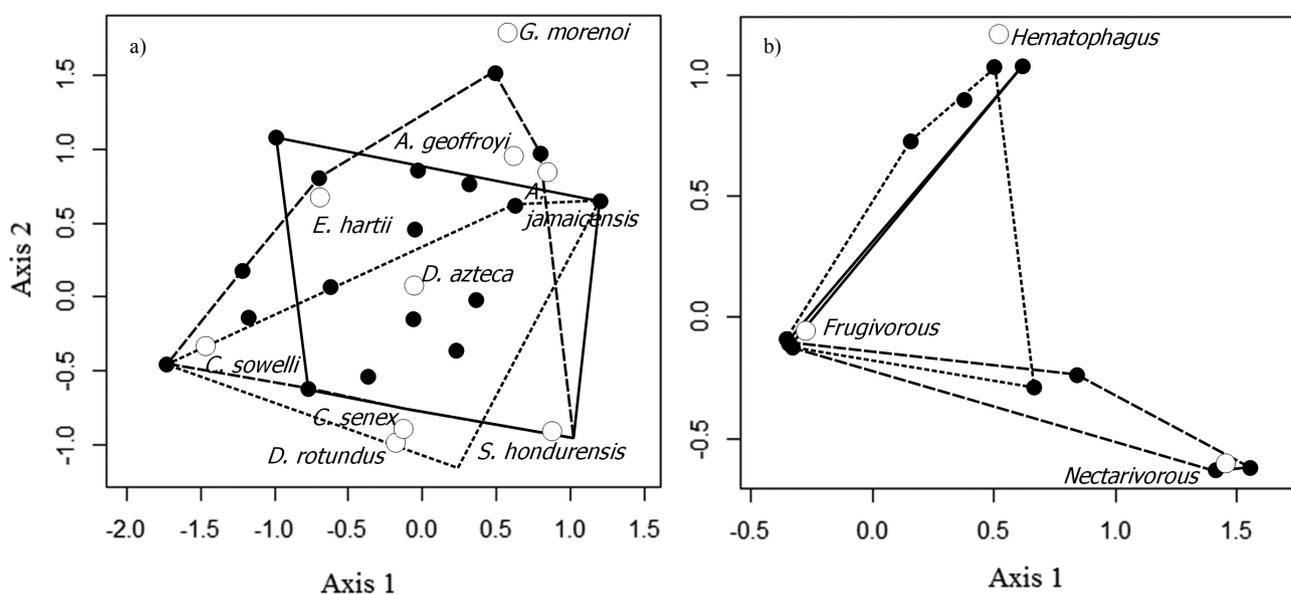


Fig. 4. Non-metric multidimensional scaling analysis (NMDS) ordination of phyllostomid bats in neotropical temperate forests and agricultural areas in southern Mexico. a) species composition, b) guilds. Cover types: agriculture (solid line), montane cloud forest (dashed line), and pine-oak forest (dotted line).

them (Estrada et al. 1993; Estrada and Coates-Estrada 2001; Gorresen and Willig 2004; Bernard and Fenton 2007). In this sense, our study areas have characteristics that can explain the lack of statistical differences in species richness, diversity, and composition between temperate forest and agricultural areas. For example: 1) agricultural areas are traditionally managed (*sensu* Toledo et al. 2003), *i.e.*, they have a high diversity of resources spaced in patches (Medina et al. 2007), possess backyard orchards near houses, which may offer refuge or food for bat species, particularly adaptable species such as those in *Artibeus*, *Sturnira* and *Desmodus* (Galindo-González 2004); 2) agricultural areas are immersed into a forest matrix, which includes riparian vegetation, so that species that perform long flights in search of food can cross the agricultural areas without making use of them, or only making marginal use of them (Estrada et al. 1993; Estrada and Coates-Estrada 2001; Bernard and Fenton 2007; García-Morales et al. 2014). However, we do not discard the possibility that the lack of differences in bat diversity and composition between the agricultural site and forest sites were due to the low capture rate, although the calculated sample coverage was high.

Among the three cover types, *S. hondurensis* was the dominant species, followed by *D. azteca*, and *C. sowellii*, all three of which have a similar body size (Reid 1997). These species feed on *Solanum* and/or *Piper* species, and forage at the understory level in both secondary and mature forests (Castro-Luna et al. 2007; Pinto and Keitt 2008). Meanwhile, food offer in the canopy of the sites studied may not be enough for species that forage in this stratum, like *Artibeus jamaicensis*, a large-sized *Ficus* specialist bat (Giannini and Kalko 2005; Lou and Yurrita 2005). Regarding the above, Saldaña-Vázquez et al. (2010) also found a higher abundance of *S. hondurensis* over *A. jamaicensis* in a montane cloud forest in Veracruz, Mexico. They explain that the species richness and diversity of chiropterochorous plants justify the higher abundance of *S. hondurensis*. *Artibeus jamaicensis* is a big-sized species, thus it must consume a high quantity of carbohydrates in the form of fruits to achieve enough thermoregulation to live in a temperate forest (Soriano 2000). However, this pattern is not found in montane forests, *e.g.*, in Quindío, Colombian Andes, *A. jamaicensis* was the most abundant species (Numa et al. 2005).

On the other hand, the Phyllostomidae family has not been a useful indicator group for demonstrating the effects of human perturbation on ecosystems (Coutinho and Bernard 2012; García-Morales et al. 2013), but analysis at the subfamily level or between guilds can show patterns of these effects. Stenodermatinae,

Carollinae, and Glossophaginae are subfamilies tolerant to disturbance in lowland forests, but Phyllostominae is usually more sensitive (Clarke et al. 2005; Giannini and Kalko 2005). In this study, agricultural areas had a lesser relative abundance of Carollinae and Stenodermatinae species than the temperate forests, while Glossophaginae was only observed in forests; in addition, Desmodontinae had higher relative abundance in the pine-oak forest than in agricultural areas, and it was not recorded in the montane cloud forest. These results, in association with the findings obtained in Alto-andinos forests of Colombia (Pérez-Torres and Ahumada 2004), could demonstrate that Stenodermatinae, Carollinae, and Glossophaginae species are capable of using agricultural areas, but they will remain in low numbers if the sites do not meet their requirements.

With respect to guilds, in lowland forest fragments and secondary forests, frugivorous and nectarivorous species tend to show increases in abundance; instead, animalivorous species have either not been recorded or have been recorded in low abundances, showing dependence for continuous forests (Clarke et al. 2005; Giannini and Kalko 2005; Castro-Luna et al. 2007; García-Morales et al. 2013). In particular, the results of this study contrast with the ones mentioned above, because animalivorous species were not recorded (these are not common in highlands in the region; Briones-Salas et al. 2015) and nectarivorous species only were recorded in forests. Subsequent studies should explore the use of nectarivorous species as an indicator group in neotropical montane forests.

CONCLUSIONS

Overall, we found that the phyllostomid bat species richnesses in the highlands studied were low (nine species), fitting the altitudinal pattern that there are more bat species in lowlands than highlands.

In conclusion, at this study scale, there is a biotic homogeneity in the phyllostomid bats between forests and agricultural areas, *i.e.*, habitat loss does not affect bat communities, although the results may be different at other spatial scales. In addition, at least for the understory phyllostomid bats, the traditional management of agricultural areas and the surrounding matrix could explain the similarity in species richness, composition, and diversity between the agricultural area and native montane forests, so other indicator groups should be evaluated to understand the effects of habitat loss in montane forests.

Most literature about the response of phyllostomid bat communities to habitat loss and fragmentation

comes from lowland forests, so its study in montane ecosystems should be promoted. In addition, further research may focus on the physiologic adjustments developed by phyllostomid bats to live in cold climates, as well as on determining if bats move in an altitudinal gradient during feeding, which could explain the presence of small bats in temperate habitats.

Acknowledgments: The authors thank the Solaga authorities for helping to develop this study. E.T. Vigil provided invaluable assistance in the field. M. García-Luis and M.A. Peralta-Pérez provided comments that improved the manuscript. Instituto Politécnico Nacional (SIP: 20100263) by the support to field surveys. M. Briones-Salas thanks the support of the Comisión y Operación de Fomento Actividades Académicas (COFAA) and Programa de Estímulos al Desempeño a la Investigación (EDI), Instituto Politécnico Nacional and Sistema Nacional de Investigadores (SNI). M.S. García Velasco and N. Last reviewed the English version.

Authors' contributions: MB-S contributed to the study design; MCL collected the data, analyzed the information and wrote the paper; CM perform the data analyzes; JV collected the data. All authors helped write the manuscript.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: The data generated and/or analyzed during the current study are available from the corresponding author.

Consent for publications: All the authors consent to the publication of this manuscript.

Ethics approval consent to participate: This research followed the Guidelines of the American Society of Mammalogists for the use of wild mammals in research (Gannon et al. 2007).

REFERENCES

- Álvarez T, Álvarez ST, López J. 1994. Keys for Mexican bats. Centro de Investigaciones Biológicas del Noroeste, S. C. and Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico, Mexico City.
- Arias E, Pacheco V, Cervantes K, Aguilar A, Álvarez J. 2016. Diversidad y composición de murciélagos en los bosques montanos del Santuario Nacional Pampa Hermosa, Junín, Perú. *Rev Per Biol* **23**:103–116. doi:10.15381/rpb.v23i2.12381.
- Arita HT. 1993. Rarity in neotropical bats: correlations with phylogeny, diet and body mass. *Ecol Applic* **3**:506–517. doi:10.2307/1941919.
- Bernard E, Fenton MB. 2007. Bats in a fragmented landscape: species composition, diversity and habitat interactions in savannas of Santarém, Central Amazonia, Brazil. *Biol Conserv* **134**:332–343. doi:10.1016/j.biocon.2006.07.021.
- Briones-Salas M, Sánchez-Cordero V, Santos-Moreno A. 2005. Diversity of bats along a elevational gradient in the sierra Mazateca, Oaxaca, Mexico. *In*: Sánchez-Cordero V, Medellín RA (ed) *Mastozoological contributions in tribute to Bernardo Villa*. Instituto de Biología-Instituto de Ecología, UNAM, CONABIO, Mexico, Mexico City.
- Briones-Salas M, Cortés-Marcial M, Lavariega MC. 2015. Diversity and geographical distribution of the land mammals of the State of Oaxaca, Mexico. *Rev Mex Biodiver* **86**:685–710. doi:10.1016/j.rmb.2015.07.008.
- Brooks TM, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Rylands AB, Konstant WR, Flick P, Pilgrim J, Oldfield S, Magin G, Hilton-Taylor C. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conserv Biol* **16**:909–923. doi:10.1046/j.1523-1739.2002.00530.x.
- Brosset A, Charles-Dominique P, Cockle A, Cosson JF, Masson D. 1996. Bat communities and deforestation in French Guiana. *Canadian J Zool* **74**:1974–1982. doi:10.1139/z96-224.
- Brown AD, Kappelle M. 2001. Introduction to neotropical cloud forest: a regional synthesis. *In*: Kappelle M, Brown AD (eds) *Neotropical cloud forest*. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica.
- Calderón-Patrón JM, Briones-Salas M, Moreno CE. 2013. Diversidad de murciélagos en cuatro tipos de bosque de la Sierra Norte de Oaxaca, México. *Therya* **4**:121–137. doi:10.12933/therya-13-90.
- Castro-Luna AA, Sosa VJ, Castillo-Campos G. 2007. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. *Acta Chiropterol* **9**:219–228. doi:10.3161/1733-5329(2007)9[219:QPBADT]2.0.CO;2.
- Castro-Luna AA, Galindo-González J. 2012. Enriching agroecosystems with fruit-producing tree species favors the abundance and richness of frugivorous and nectarivorous bats in Veracruz, Mexico. *Mamm Biol* **77**:32–40. doi:10.1016/j.mambio.2011.06.009.
- Chao A, Chiu CH, Jost L. 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Ann Rev Ecol Evol Syst* **45**:297–324. doi:10.1146/annurev-ecolsys-120213-091540.
- Chao A, Ma KH, Hsieh TC. 2016. iNEXT (iNterpolation and EXTrapolation) Online. http://chao.stat.nthu.edu.tw/wordpress/software_download/. Accessed 1 September 2018.
- Clarke FM, Rostant LV, Racey PA. 2005. Life after logging: post-logging recovery of a neotropical bat community. *J Appl Ecol* **42**:409–420. doi:10.1111/j.1365-2664.2005.01024.x.
- Cortés-Delgado N, Sosa VJ. 2014. Do bats roost and forage in shade coffee plantations? A perspective from frugivorous bat *Sturmira hondurensis*. *Biotropica* **46**:624–632. doi:10.1111/btp.12142.
- Coutinho G, Bernard R. 2012. Neotropical bats as indicators of environmental disturbance: what is the emerging message. *Acta Chiropterol* **14**:143–151. doi:10.3161/150811012X654358.
- Daily GC, Ceballos G, Pacheco J, Suzán G, Sánchez-Azofeifa A. 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conserv Biol* **17**:1814–1826. doi:10.1111/j.1523-1739.2003.00298.x.
- Estrada A, Coates-Estrada R, Meritt D. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural

- habitats at Los Tuxtlas, Mexico. *Ecography* **16**:309–318.
- Estrada A, Coates-Estrada R. 2001. Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography* **24**:94–102. doi:10.1034/j.1600-0587.2001.240111.x.
- Estrada A, Coates-Estrada R. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. *Biol Conserv* **103**:237–245. doi:10.1016/S0006-3207(01)00135-5.
- FAO (Food and Agriculture Organization). 2009. State of the world's forest. Food and Agriculture Organization of the United Nations, Roma, Italia.
- Galindo-González J, Guevara S, Sosa VJ. 2000. Bat-and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conserv Biol* **14**:1693–1703. doi:10.1111/j.1523-1739.2000.99072.x.
- Galindo-González JG. 2004. Classification of the bats of the Los Tuxtlas region, respecting to their response to habitat fragmentation. *Acta Zool Mex (n. s.)* **20**:239–243.
- García E, CONABIO (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad). 1998. Climate. <http://www.conabio.gob.mx/informacion/gis/>. Accessed 12 April 2018.
- García-Estrada CG, Damon A, Hernández CS, Pinto LS, Núñez GI. 2006. Bat diversity in montane rainforest and shaded coffee under different management regimes in southeastern Chiapas, Mexico. *Biol Conserv* **132**:351–361. doi:10.1016/j.biocon.2006.04.027.
- García-Morales R, Badano EI, Moreno CE. 2013. Response of neotropical bat assemblages to land use. *Conserv Biol* **27**:1096–1106. doi:10.1111/cobi.12099.
- García-Morales R, Chapa-Vargas L, Badano E, Galindo-González J, Monzalvo-Santos K. 2014. Evaluating phyllostomid bat conservation potential of three forest types in the northern Neotropics of Eastern Mexico. *Community Ecol* **15**:158–168. doi:10.1556/ComEc.15.2014.2.4.
- Giannini NP, Kalko EKV. 2004. Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos* **105**:209–220. doi:10.1111/j.0030-1299.2004.12690.x.
- Giannini NP, Kalko EKV. 2005. The guild structure of animalivorous leaf-nosed bats of Barro Colorado Island, Panama, revisited. *Acta Chiropterol* **7**:131–146. doi:10.3161/1733-5329(2005)7[131:TG SOAL]2.0.CO;2.
- González-Espinosa M, Meave JA, Ramírez-Marcial N, Toledo-Aceves T, Lorea-Hernández FG, Ibarra-Manríquez G. 2012. Cloud forests of Mexico: conservation and restoration of their tree component. *Ecosistemas* **21**:36–54.
- Gorresen PM, Willig MR. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. *J Mammal* **85**:688–697. doi:10.1644/BWG-125.
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Song DX, Townshend JR. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* **1**:e1500052. doi:10.1126/sciadv.1500052.
- Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG. 2013. High-resolution global maps of 21st-century forest cover change. *Sci* **342**:850–853. doi:10.1126/science.1244693.
- Jost L. 2006. Entropy and diversity. *Oikos* **113**:363–375. doi:10.1111/j.2006.0030-1299.14714.x.
- Kalka MB, Smith AR, Kalko EKV. 2008. Bats limit arthropods and herbivory in a tropical forest. *Sci* **320**:71–71. doi:10.1126/science.1153352.
- Kunz TH, Kurta A. 1988. Capture methods and holding devices. In: Kunz TH (ed.) *Ecological and behavioral methods for the study of bats*. Smithsonian Institution Press, Washington, D.C.
- Lou S, Yurrita CL. 2005. Analysis of feeding niche in the frugivorous bat community of Yaxhá, Petén, Guatemala. *Acta Zool Mex (n. s.)* **21**:83–94.
- Martensen AC, Ribeiro MC, Banks-Leite C, Prado PI, Metzger JP. 2012. Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. *Conserv Biol* **26**:1100–1111. doi:10.1111/j.1523-1739.2012.01940.x.
- Martins MA, Carvalho WDD, Dias D, França DDS, Oliveira MBD, Peracchi AL. 2015. Bat species richness (Mammalia, Chiroptera) along an elevational gradient in the Atlantic Forest of Southeastern Brazil. *Acta Chiropterol* **17**:401–409. doi:10.3161/15081109ACC2015.17.2.016.
- McCain CM. 2007. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Glob Ecol Biogeogr* **16**:1–13. doi:10.1111/j.1466-8238.2006.00263.x.
- Medina A, Harvey CA, Sánchez D, Vilchez S, Hernández B. 2007. Bat diversity and movement in an agricultural landscape in Matiguás, Nicaragua. *Biotropica* **39**:120–128. doi:10.1111/j.1744-7429.2006.00240.x.
- Medellín RA, Equihua M, Amin MA. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conserv Biol* **14**:1666–1675. doi:10.1111/j.1523-1739.2000.99068.x.
- Medellín RA, Arita HT, Sánchez O. 2008. Identification of bats of Mexico: Field keys. Instituto de Ecología, UNAM, Mexico, Mexico City.
- Medellín RA. 1993. Structure and diversity of a bat community in the Mexican humid tropic. In: Medellín, RA, Ceballos G (eds) *Advances in the study of mammals of Mexico*. Special Publications, vol 1. Asociación Mexicana de Mastozoología, A. C., Mexico, Mexico City.
- Mena JL. 2010. Bat response to forest fragmentation in Pozuzo, Perú. *Rev Per Biol* **17**:277–284.
- Mendoza-Sáenz VH, Horváth A. 2013. Roedores y murciélagos en la zona cafetalera del Volcán Tacaná, Chiapas, México. *Therya* **4**:409–423. doi:10.12933/therya-13-116.
- Michalski F, Peres CA. 2005. Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biol Conserv* **124**:383–396. doi:10.1016/j.biocon.2005.01.045.
- Monroy-Vilchis O, Zarco-González MM, Ramirez-Pulido J, Aguilera-Reyes U. 2011. Diversidad de mamíferos de la Reserva Natural Sierra Nanchitla, México. *Rev Mex Biodiv* **82**:237–248.
- Montañón-Centellas F, Moya MI, Aguirre LF, Galeón R, Palabral O, Hurtado R, Galarza I, Tordoya J. 2015. Community and species-level responses of phyllostomid bats to a disturbance gradient in the tropical Andes. *Acta Oecol* **62**:10–17. doi:10.1016/j.actao.2014.11.002.
- Moras LM, Bernard E, Gregorin R. 2013. Bat assemblages at a high-altitude area in the Atlantic forest of southeastern Brazil. *Mastozool Neotrop* **20**:269–278.
- Nobre PH, Manhães MA, Bastos OJ, Rezende AC, Rodrigues AS. 2013. Bat assemblages from mountain forest areas in the Serra Negra region, southeastern Brazil. *Mastozool Neotrop* **20**:279–287.
- Numa C, Verdú JR, Sánchez-Palomino P. 2005. Phyllostomid bat diversity in a variegated coffee landscape. *Biol Conserv*

- 122:151–158. doi:10.1016/j.biocon.2004.07.013.
- Pardini R, de Souza SM, Braga-Neto R, Metzger JP. 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biol Conserv* **124**:253–266. doi:10.1016/j.biocon.2005.01.033.
- Pérez-Torres J, Ahumada JA. 2004. Bats in high-andean forest, fragmented and continuous in the western of the savanna of Bogotá (Colombia). *Univer Sci* **9**:33–46.
- Pinto N, Keitt TH. 2008. Scale-dependent responses to forest cover displayed by frugivore bats. *Oikos* **117**:1725–1731. doi:10.1111/j.1600-0706.2008.16495.x.
- Ramírez-Pulido J, González-Ruiz N, Gardner AL, Arroyo-Cabrales J. 2014. List of recent land mammals of Mexico, 2014. Special Publications Museum of Texas Tech University, Texas, U.S.A.
- Reid F. 1997. A Field Guide to the Mammals of Central America and Southeast Mexico. Oxford University Press, New York. U.S.A.
- Rodríguez-Macedo M, González-Christen A, León-Paniagua LS. 2014. Diversidad de los mamíferos silvestres de Misantla, Veracruz, México. *Rev Mex Biodiv* **85**:262–275. doi:10.7550/rmb.36143.
- Rost J, Jardel-Peláez EJ, Bas JM, Pons P, Loera J, Vargas-Jaramillo S, Santana E. 2015. The role of frugivorous birds and bats in the colonization of cloud forest plant species in burned areas in western Mexico. *Anim Biodiver Conserv* **38.2**:175–182.
- Saldaña-Vázquez RA, Sosa VJ, Hernández-Montero JR, López-Barrera F. 2010. Abundance responses of frugivores bats (*Stenodermatinae*) to coffee cultivation and selective logging practices in mountainous central Veracruz, Mexico. *Biodiver Conserv* **19**:2111–2124. doi:10.1007/s10531-010-9829-6.
- San Andrés Solaga. 2012. Plan Municipal de Desarrollo Sustentable 2012-2020. Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación. Oaxaca, Mexico.
- Schulze MD, Seavy NE, Whitacre DF. 2000. A comparison of the phyllostomid bat assemblages in undisturbed neotropical forest and in forest fragments of a slash-and-burn farming mosaic in Petén, Guatemala. *Biotropica* **32**:174–184. doi:10.1111/j.1744-7429.2000.tb00459.x.
- Sikes RS, Gannon WL. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mammal* **92**:235–253. doi:10.1093/jmammal/gyw078.
- Simmons NB. 2005. Order Chiroptera. In: Wilson D. E. and D. M. Reeder (eds) *Mammal Species of the World: A Taxonomic and geographic Reference*. Baltimore Johns Hopkins University Press.
- SEMARNAT (Secretaría de Medio Ambiente y Recursos Naturales). 2010. NOM-059-SEMARNAT-2010, Protección ambiental - Especies nativas de México de flora y fauna silvestres - Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio - Lista de especies en riesgo. Diario Oficial de la Federación, Mexico, Mexico City.
- Soriano PJ. 2000. Functional structure of bat communities in tropical rainforests and Andean cloud forest. *Ecotropicos* **13**:1–20.
- Tabarelli M, Aguiar AV, Ribeiro MC, Metzger JP, Peres CA. 2010. Prospects for biodiversity conservation in the Atlantic Forest: lessons from aging human-modified landscapes. *Biol Conserv* **143**:2328–2340. doi:10.1016/j.biocon.2010.02.005.
- Team R Development Core. 2012. R: A Language and Environment for Statistical Computing. 2.15.0 ed. Vienna, Austria: R Foundation for Statistical Computing. Available at <https://www.r-project.org/>. Accessed 14 October 2017.
- Thornton DH, Branch LC, Sunquist ME. 2012. Response of large galliforms and tinamous (*Cracidae*, *Phasianidae*, *Tinamidae*) to habitat loss and fragmentation in northern Guatemala. *Oryx* **46**:567–576. doi:10.1017/S0030605311001451.
- Toledo VM, Ortiz-Espejel B, Cortés L, Moguel P, Ordoñez MDJ. 2003. The multiple use of tropical forests by indigenous peoples in Mexico: a case of adaptive management. *Conserv Ecol* **7**:1–9.
- Vegas-Vilarrúbia T, Nogué S, Rull V. 2012. Global warming, habitat shifts and potential refugia for biodiversity conservation in the neotropical Guayana Highlands. *Biol Conserv* **152**:159–168. doi:10.1016/j.biocon.2012.03.036.
- Vidal-Zepeda R. 1990. Annual mean precipitation. <http://www.conabio.gob.mx/informacion/gis/>. Accessed 12 April 2018.
- Williams-Guillén K, Perfecto I. 2010. Effects of agricultural intensification on the assemblage of leaf-nosed bats (*Phyllostomidae*) in a coffee landscape in Chiapas, Mexico. *Biotropica* **42**:605–613. doi:10.1111/j.1744-7429.2010.00626.x.