



Evaluating phyllostomid bat conservation potential of three forest types in the northern Neotropics of Eastern Mexico

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Abstract: Forest conversion to anthropogenic uses is a generalized phenomenon throughout tropical Latin America. We evaluated whether patches of secondary forest, which develop relatively rapidly after field abandonment, contribute to conservation of phyllostomid bat assemblages. Our objective was to compare patterns of phyllostomid bat abundance and the structure and composition of phyllostomid bat assemblages across three forest types in the northern neotropics of eastern Mexico. We studied phyllostomid bats within secondary evergreen, primary semi-deciduous, and primary evergreen forests. For each forest type, three representative sites were sampled with mist nets once during the dry season and once during the rainy season for a total of nine sites. Richness, diversity, and assemblage composition patterns were compared among forest types for all phyllostomid species, and for three groups of sensitivity to habitat fragmentation. Abundance of individual species was also compared among forest types. A total of 646 individual bats from 15 species, 11 of which were phyllostomids, were registered. Combining both seasons, more than 250 captures were accomplished at both the primary evergreen and secondary evergreen forests, and only 81 individuals were caught at primary semi-deciduous forests. Overall richness and diversity of species and sensitivity groups were greater in the rainy than the dry season. Richness was greater in secondary evergreen than in primary semi-deciduous forests, and diversity was greatest in the primary evergreen, intermediate in the secondary evergreen, and lowest in the primary semi-deciduous forest. Some overlap in composition was also evident, although there was separation between forest types and seasons. Mean abundances were higher for some species at primary evergreen and secondary evergreen forests, but were three-fold lower (though not significantly) in secondary evergreen forests in the dry season for some other species. We also found that primary evergreen forests have the greatest importance for phyllostomids during the dry season. These results suggest that maintenance of secondary evergreen forests, which cover a large proportion of the northeastern Mexican neotropics, would contribute to the conservation of diverse tropical bat communities. Therefore, large areas of this forest type should necessarily be incorporated in the landscape.

Abbreviation: dbh–Diameter at breast height; NMDS–Non-metric Multidimensional Scaling; PERMANOVA–Permutational Multivariate Analysis of Variance; SIMPER–Similarity Percentage Analyses.

Introduction

Tropical ecosystems of Latin America harbor some of the most diverse biotas of the world (Myers et al. 2000). Extensive areas that once were covered by tropical ecosystems are being replaced by agricultural lands, and fields used for grazing by domestic animals (Velásquez et al. 2002). Despite this pressure, some regions still contain extensive areas covered by relatively undisturbed primary tropical forests which provide habitat for native flora and fauna. There are also large areas covered by secondary forests which have established through natural processes after significant disturbance of the original forest, and differ in forest structure or composition from nearby primary forests (Baar et al. 2004, Mas et al. 2004). The conservation potential of these secondary forests has been recognized, though substantial gaps in our knowledge

of potential disadvantages and the processes that determine their conservation potential still exist (Chazdon et al. 2009).

The Huasteca region of northeastern Mexico, includes portions of the states of Veracruz, Hidalgo, Tamaulipas, Querétaro, Puebla, and San Luis Potosí at latitudes above 20° N. This region contains most of the northern neotropics of eastern Mexico and harbors an outstandingly high diversity of tropical forest types (Rzedowski 2006). However, due to land-use change, up to 50% of the native forests of the Huasteca region have been replaced by grasslands, farmlands, and patches of secondary vegetation that have developed through the natural process of succession following field abandonment (Puig 1991). This system is ideal for examining research questions related to the conservation potential of secondary forests in relation to primary forests.

Bats are among the most diverse vertebrate taxa in tropical ecosystems (Patterson et al. 2003) and provide various ecological services depending on their specific trophic guild. Insectivorous bats control insect pest populations (Kunz et al. 2011) whereas nectarivores and frugivores pollinate and disperse seeds of important flowering plants throughout entire landscapes (Galindo-González et al. 2000, Arizmendi et al. 2002, Bernard and Fenton 2003, García-Morales et al. 2012). The specificity of feeding habits and specialized habitat requirements make many tropical bat species sensitive to environmental degradation (Fenton et al. 1992, Medellín et al. 2000, Bernard and Fenton 2002, Galindo-González 2004, Castro-Luna et al. 2007). Bats from the family Phyllostomidae are abundant, diverse, easy to sample, and different species have dissimilar responses to habitat degradation. Therefore, phyllostomids have been used as indicators of habitat quality (Galindo-González 2004) and as a focal group for evaluations of habitat fragmentation and habitat change (Moreno et al. 2007). Bat species have been found to differ in terms of their degree of sensitivity to anthropogenic disturbance (e.g., Galindo-González 2004). Therefore, bats are ideal study organisms for investigations of the effects of habitat degradation at the community level. Mexico is one of the top countries in terms of bat diversity with 138 species including residents and migrants (Medellín et al. 2008). In tropical ecosystems, diversity and abundance patterns of phyllostomid bat assemblages differ between successional vegetation and primary tropical forests, and these parameters increase with consecutive stages of succession (Medellín et al. 2000, Castro-Luna et al. 2007, Willig et al. 2007, Avila-Cabadilla et al. 2009, Bobrowiec and Gribel 2010, de la Peña-Cuéllar et al. 2012) such that in some cases, late stages of secondary succession may not differ significantly in phyllostomid bat structure and composition from mature tropical forests (e.g., Castro-Luna et al. 2007). The magnitude of responses to late successional stages at the community level, however, may vary depending on habitat type (e.g., dry vs. moist forests), and geographic location (Stoner 2005). In addition, habitat-specific abundance patterns may vary among sensitivity groups, and some species may require mature forests to maintain their abundance throughout the year. Therefore, the simultaneous maintenance of both primary and secondary forests may be a feasible strategy for bat conservation. To assess the potential of Mexican secondary forests for phyllostomid bat conservation, it is important to evaluate if these habitats have phyllostomid bat structure and composition patterns comparable to those in different types of primary tropical forests.

We aimed at assessing the potential of secondary forests of the region for phyllostomid bat conservation. Therefore, our objective was to determine if the patterns of structure and composition of phyllostomid bat assemblages and different sensitivity groups associated with secondary evergreen forests, the most widespread successional forests in the region, are similar to those within primary evergreen and primary semi-deciduous forests (see description below) across the Huasteca region of the State of San Luis Potosí. Food resources for phyllostomid bats may vary significantly between seasons (Olea-Wagner et al. 2007, García-Morales et

al. 2012). Differences between seasons may influence forest-type effects. Therefore, we established the additional goals of evaluating the effects of season and forest type by season interactions on structure and composition patterns of phyllostomid bat assemblages. This information could be important for conservation of bat communities across the northern neotropics of eastern Mexico because maintenance of secondary evergreen forests, which cover a large proportion of this region, could potentially contribute to conservation of bat populations and communities.

Materials and methods

Study area

We conducted our study within a portion of the Huasteca region corresponding to the state of San Luis Potosí (Fig. 1). This area covers a plateau of 1,118,400 ha and shares biogeographical features and patterns of land use change with the rest of the northern neotropics of eastern Mexico. It extends to the east from the Sierra Madre Oriental at up to 3,000 m a.s.l. towards the Gulf of Mexico nearly at sea level. The regional climate varies with elevation; the upper zones show a temperate-humid climate with average annual temperature of 18°C and annual total precipitation exceeding 1,000 mm. The lowlands have a warm sub-humid climate with an annual temperature average of 25°C and annual total precipitation below 700 mm (García 1988). More than 90% of rainfall in the region occurs in summer, generating a seasonally dry climate (García 1988). The location of the study area at the confluence of the neotropical and nearctic ecoregions, its rugged relief, and the variety of climatic conditions support the existence of several vegetation communities.

The two most dominant natural primary forest types covering 20–25% of the region are evergreen forests with canopies ranging from 25 to 35 m tall dominated by trees from the Moraceae family with a well-developed understory, and semi-deciduous forests with canopies between four and 15 m tall dominated by trees and shrubs from the family Burseraceae. Temperate forests dominated by pines and oaks are distributed above 1,500 m a.s.l. and cover < 10% of the region. These three vegetation communities are relatively well preserved due to a history of moderate human intervention. The remaining surface of the Huasteca region of San Luis Potosí, however, has been transformed to agricultural fields (Puig 1991). After abandonment of some of these fields, numerous patches of secondary vegetation developed through natural succession (Chapa-Vargas and Monzalvo Santos 2012, pers. obs.). Forest structure and composition of secondary forests change as succession advances. The type and pace of changes occurring in the ecosystem through succession depend on disturbance characteristics, seed and seedling availability, the biotic environment, and the abiotic conditions of each site (Guariaguata and Ostertag 2001). Secondary vegetation can be classified into three general successive stages (Castro-Luna et al. 2007; de la Peña-Cuéllar et al. 2012) depending on the time elapsed since abandonment: (1) early succession occurs during the first five years after abandonment, (2) intermedi-

ate succession follows the former stage with a highly variable duration that, on average, persists from five to 15 years, and (3) secondary forest which is dominated by fast-growing, softwood native trees, such as *Bursera* spp. *Guazuma* spp. and *Swietenia* spp. Secondary forests develop approximately 15 years after field abandonment (Castro-Luna et al. 2007, de la Peña-Cuéllar et al. 2012), and cover larger areas than any other plant community in the region (up to 40%).

Site selection and bat sampling

Understory bat assemblages were sampled at two “control” forest types; primary evergreen and primary semi-deciduous forests, and in secondary evergreen forests. We excluded temperate forests and patches of herbaceous and shrubby stages of secondary vegetation because they are relatively uncommon in the study area. We sampled secondary evergreen forest stands that have been abandoned for similar amounts of time (20–25 years). They contain large trees (>40 cm in dbh) which have reached reproductive maturity, but tree heights are smaller (~10 m) than the average tree height of primary evergreen forests (García-Morales et al. 2012), and contain well-developed, higher density herbaceous and shrubby vegetation layers in comparison with both primary evergreen and primary semi-deciduous forests of the region. For each forest type we randomly selected three representative sampling sites (replicates). To achieve independence among study sites, we imposed the restriction that each site should be located at a minimum distance of 10,000 m from any other sampling site. Ten mist nets (12 m long \times 2.5 m width \times 10 nets = 300 m² in total) were placed at ground level in random locations within each sampling site with the following restrictions: 1)

Nets were placed along trails which may function as flyways to obtain sample sizes as large as possible. These trails were located near dense vegetation because it has been reported elsewhere that trails near this type of vegetation may be used heavily by bats (e.g., Willig et al. 2007); 2) All mist nets were placed at > 300 m from all habitat edges and ecotones to control for the potential confounding effect of proximity to edges; and 3) Nets were not placed near specific microhabitats such as streams, and steep uphill and downhill sites (<45°) within study areas to avoid possible confounding effects. Nets were operated during three consecutive nights in the same location from 18:00 to 01:00 hrs. This is the period in which the peak of bat activity occurs (Esbérard and Bergallo 2005). To minimize risks to the organisms, nets were visited every 30 min., and checked for trapped bats. All captured bats were removed from the nets, identified to the species level using the field guide of Medellín et al. (2008), and the information pertaining to every individual was recorded before the organism was released. This sampling procedure was conducted at all sampling sites twice, first at the middle of the rainy season (July 2009), and then during the following dry season (February 2010). We avoided sampling bat communities in our study sites within three days of full moons (e.g., Willig et al. 2007), and during heavy rains or inclement weather. Each forest type was sampled a total of 9 nights each season. Therefore, the total sampling effort (E) was 54 nights, adding to a total of 113,400 m² h net (Straube and Bianconi 2002). Because mist nets were placed just above the ground, it is expected that this sampling procedure best represents the Phyllostomidae and Mormoopidae families. In our study area, only one species of the Mormoopidae family was recorded, and it occurred in low abundances (Table 1). Therefore, our species diversity and abundance analyses were restricted to phyllostomids.

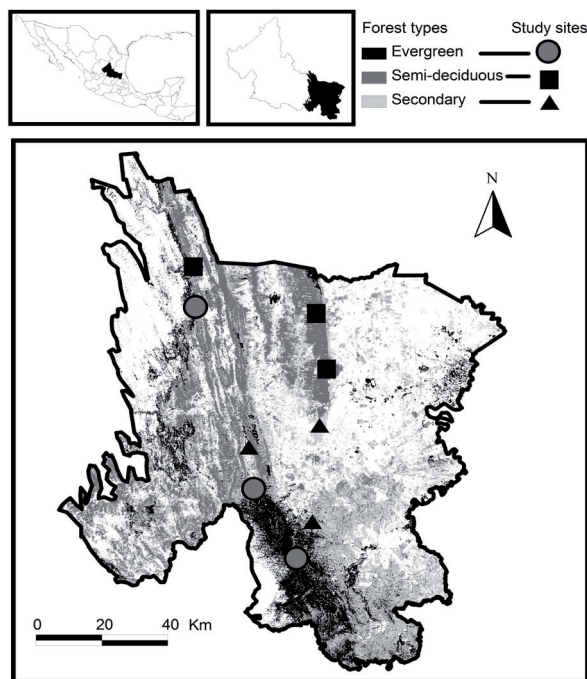


Figure 1. Study area and sites.

Species diversity analysis

Rarefaction analysis was conducted to compare rarefied observed phyllostomid species richness (S) with the Chao2 estimator to determine if our sample of the phyllostomid bat community was sufficient to capture the entire species richness. For each forest type, we calculated the Chao2 species richness estimator which adjusts for the number of species likely to be present in a given area, but that were absent from the sampling. The degree to which the Chao2 estimate exceeds the total observed species richness provides an indication of how thoroughly the species assemblage was sampled (Magurran 2004). Chao2 values for each forest type were computed using sample-based rarefaction (Colwell 2010). Then the mean and 95% confidence intervals (CI's) from the sample-based rarefaction were calculated. Whenever the 95% CI's of Chao2 did not include the value of species richness (S) estimated at the maximum sampling size, we concluded that a substantial number of species was omitted (Gotelli and Colwell 2001). We also calculated percent completeness as the percentage of the maximum estimated number of species represented by the observed species.

Rarefaction analyses were performed with the software EstimateS v8.2 (Colwell 2010) using individual nights, con-

sisting of 2,100 m² h net (Straube and Bianconi 2002) each night, as the sampling unit. In these analyses, community attributes were estimated as the sample size at each forest type (n = number of nights accumulated) decreased from a maximum value (N = 9 per season, and 18 for the entire period) which in our case was given by the total number of samples (Gotelli and Colwell 2001). We computed the values of Chao2, S , and the index of proportional diversity of Shannon-Wiener (H') for each forest type by randomly selecting 1,000 re-samples without replacement for each sampling size. The 1,000 values of Chao2, S , and H' for each level of n were then averaged and the average values of these community attributes were plotted against their corresponding values of n .

To determine whether diversity of phyllostomid bat assemblages varied between forest types, we estimated species richness (S) and the index of proportional diversity of Shannon-Wiener (H'). The effects of forest type and seasons on phyllostomid bat richness (S) and diversity (H') were evaluated using permutational multivariate analysis of variance (PERMANOVA) (Anderson et al. 2008) based on 9,999 permutations and type III sums of squares. PERMANOVA tests estimate multivariate variation in a design similar to that of a multiple-way analysis of variance through a *Pseudo-F* statistic using permutations (Anderson 2001, Anderson et al. 2008). This analysis is unrestricted by assumptions of normality of error terms and equality of variances. Therefore, it is appropriate for multiple comparisons of community attributes. All single-factor and interaction effects were assessed. Before running the analyses, species abundances were fourth-root transformed. PERMANOVA's were performed using the Bray-Curtis similarity matrices based on species abundance data. Significant terms were evaluated using *a posteriori* pairwise comparisons through *Pseudo t* statistics. All PERMANOVA analyses were performed using PRIMER V6 (Clarke and Gorley 2006), as suggested by Anderson et al. (2008). To evaluate effects of habitat type and season considering sensitivity of Phyllostomid bat species, the same PERMANOVA procedures as described above were applied on abundances of three groups of sensitivity to habitat fragmentation that have been previously identified by Galindo-González (2004). These sensitivity groups included adaptable, vulnerable, and habitat-dependent.

Species abundance analysis

We explored the composition of phyllostomid bat assemblages for each forest type and season; Nonmetric Multidimensional Scaling Analyses (NMDS; Clarke 1993) based on Bray-Curtis similarity of fourth-root transformed abundance data was utilized to generate groups of phyllostomid bat assemblages. We conducted two-way Similarity Percentage Analyses (SIMPER) based on Bray-Curtis similarity to determine the contribution of species to within-group average similarity and between pairs of groups dissimilarities (Clarke and Warwick 2001). We conducted NMDS considering Galindo-González (2004) species sensitivity classes (see above).

We also evaluated the effect of forest type and season on abundance of those species which yielded at least 30 captures for the entire study. For each of these species we fitted generalized linear models using the R v2.12 programming environment (R Development Core Team 2010). For these count data we used a Poisson distribution of error terms to account for the lack of normality of error terms, and the log link function to ensure that the fitted values were not bounded below zero (Crowley 2005). For these analyses, forest type and season were the independent variables, and bat abundance (number of captures for each of the three day sampling periods on each site) was the dependent variable. Whenever a significant response to forest type, season, or the interaction of these two effects was detected, *a posteriori* tests were conducted to evaluate all possible pairwise comparisons using the R programming environment and the *multcomp* library version 1.2-12 (Hothorn et al. 2008).

Results

Bat diversity

We captured a total of 645 individual bats, including 635 phyllostomids. A total of 16 bat species from four families were represented in our sample (Table 1), eleven of which were phyllostomids. The total number of phyllostomid captures at both the primary evergreen and secondary evergreen forests exceeded 250 each, whereas only 77 phyllostomid captures were accomplished at the semi-deciduous forest (Table 1). This observation of lower bat abundances at semi-deciduous forest was consistent between seasons, and also held when we only analyzed phyllostomids. Our sampling was sufficient to closely approximate the total phyllostomid bat species richness; in all three forest types the 95% CI of the Chao2 estimates contained the phyllostomid bat species richness values estimated at the maximum number of nights (Fig. 2a) with 100% completeness obtained for all three habitats. Phyllostomid bat species richness was higher during the rainy than the dry season (*Pseudo-T*=1.09551, $P=0.004$) (Fig. 2 a, c, e) and in secondary evergreen forests in comparison with primary semi-deciduous forests (*Pseudo-T*=2.4244, $P<0.001$) (Fig. 2a). The Shannon-Wiener index was significantly higher during the rainy than the dry season (*Pseudo-T*=2.8299, $P=0.007$) (Fig. 2 b, d, f) and at primary evergreen forest in comparison with both secondary evergreen forest (*Pseudo-T*=3.0266, $P=0.005$) and primary semi-deciduous forest (*Pseudo-T*=1.9568, $P=0.05$) (Fig. 2b). All other pairwise comparisons were not significant ($P<0.05$).

Considering only phyllostomids, 504 individuals from 10 species were captured during the rainy season. During the dry season, 128 individuals from 9 species were recorded. Two species, *Carollia sowelli* and *Leptonycteris yerbabuenae* were not recorded in the dry season, whereas *Diphylla ecaudata* was recorded in the dry but not during the rainy season (Table 1). During both the rainy and dry seasons, observed phyllostomid species richness closely approximated the Chao2 estimate (Fig. 2). With the exception of primary semi-deciduous forest during the dry season, the maximum observed phyl-

Table 1. Total number of bats captured by species on three forest types at the Huasteca region during the rainy and the dry seasons.

Family	Species name	Sensibility ⁽¹⁾	Rainy season			Dry season		
			Semi-deciduous forest	Ever-green forest	Secondary forest	Semi-deciduous forest	Ever-green forest	Secondary forest
Mormoopidae	<i>Pteronotus parnelli</i> (Gray, 1843)(*)		1	2	0	1	0	0
Natalidae	<i>Natalus stramineus</i> (Gray, 1838) (*)		0	0	1	0	1	0
Phyllostomidae	<i>Artibeus jamaicensis</i> (Allen, 1908)	A	0	27	57	0	2	12
	<i>Artibeus lituratus</i> (Allen, 1904)	A	7	14	52	1	14	6
	<i>Artibeus toltecus</i> (Saussure, 1860)	A	6	12	5	2	2	2
	<i>Carollia sowelli</i> (Baker, Solari and Hoffmann, 2002)	V	0	12	2	0	0	0
	<i>Desmodus rotundus</i> (Geoffroy, 1810)	A	0	24	23	2	6	12
	<i>Diphylla ecaudata</i> (Spix, 1823)	A	0	0	0	1	0	0
	<i>Glossophaga soricina</i> (Pallas, 1766)	A	1	56	32	1	5	12
	<i>Leptonycteris yerbabuenae</i> (Martinez and Villa, 1940)	A	0	0	2	0	0	0
	<i>Micronycteris microtis</i> (Miller, 1898)	Hd	1	4	1	1	1	0
	<i>Sturnira lilium</i> (Geoffroy, 1810)	A	11	23	22	2	12	3
	<i>Sturnira ludovici</i> (Anthony, 1924)	Hd	35	26	52	6	17	6
	<i>Myotis keaysi</i> (Allen, 1914) (*)		0	1	0	1	0	0
	<i>Rhogeessa tumida</i> (Allen, 1866) (*)		1	0	0	0	0	1
Vespertilionidae	Total number of captures		63	201	249	18	60	54
	Total number of species		8	11	11	10	9	8
	Total number of species per season			14			13	
	Total number of captures per season			513			132	

(*) Species not included for the diversity and abundance analyses. (1) Sensibility categories include: Adaptable (A), vulnerable (V), and habitat dependent (Hd).

lostomid species richness values were contained within the 95% CI of their respective Chao2 estimates independently of forest type and season (Fig. 2c and 2e). Completeness for the semi-deciduous forest was 93% and 73% during the rainy and dry seasons respectively, and 100% for primary evergreen and secondary evergreen forests regardless of season.

Regarding our analysis based on species sensitivity groups, richness was higher during the rainy season in comparison with the dry season ($Pseudo-t=2.8299$, $P=0.007$) and lower in primary semi-deciduous in comparison with both primary evergreen ($Pseudo-t=1.9412$, $P=0.07$) and secondary evergreen forests ($Pseudo-t=2.6738$, $P=0.02$). Diversity was independent of season ($Pseudo-F=0.8793$, $P=0.4$), forest type ($Pseudo-F=0.5344$, $P=0.7$) and the interaction of these two terms ($Pseudo-F=0.5484$, $P=0.7$) (Fig. 3).

Patterns of phyllostomid bat abundance and species composition

The NMDS based on species suggested that phyllostomid bat assemblages could be split into two groups based on season of the year. There is, however, some overlap among

these groups (Fig. 4a). Two species, *Sturnira ludovici* which is habitat dependent, and *Artibeus lituratus* which is adaptable, each contributed > 20% to within-group similarities. *Glossophaga soricina* also contributed to similarities within the rainy season (Appendix 1). In terms of dissimilarities, six species from the genera *Artibeus*, *Sturnira*, *Glossophaga*, and *Desmodus* had the highest contribution (Table 1, Appendix 1). In terms of forest type, three groups could be identified, but some overlap was also evident (Fig. 4b). For both primary semi-deciduous and primary evergreen forest, one habitat dependent and one adaptable species (*S. ludovici*, and *A. lituratus*) had the greatest combined contribution to within-group similarities (Appendix 1). Two *Artibeus* and one *Glossophaga* species contributed the most to similarities within the secondary evergreen forest (Appendix 1). In terms of dissimilarities among forest type groups, in all cases species from the genera *Artibeus*, *Sturnira*, *Glossophaga*, and *Desmodus* had the highest contribution (Table 1, Appendix 1).

The NMDS based on phyllostomid bat sensitivity to fragmentation suggested that three groups of phyllostomid bat assemblages with moderate overlap could be identified based on forest type (Fig. 4c), and two groups also having some overlap were identified based on season of the year (Fig. 4d).

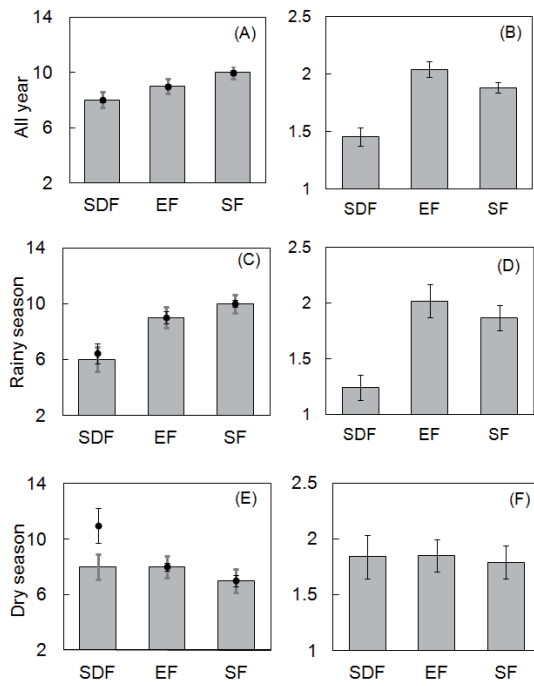


Figure 2. Estimated values of phyllostomid bat species richness (A, C, E) and Shannon-Wiener diversity index (B, D, F) for primary semi-deciduous (SDF), primary evergreen (EF), and secondary evergreen (SF) forests for the entire period of study (A, B), the rainy season (C, D), and the dry season (E, F). Values are means (\pm 95% CI's) estimated at the maximum sampling size (nights) through rarefaction techniques. Confidence intervals in black for the species richness graphs represent *Chao2* estimates (\pm 95% CI's) of total phyllostomid bat species richness.

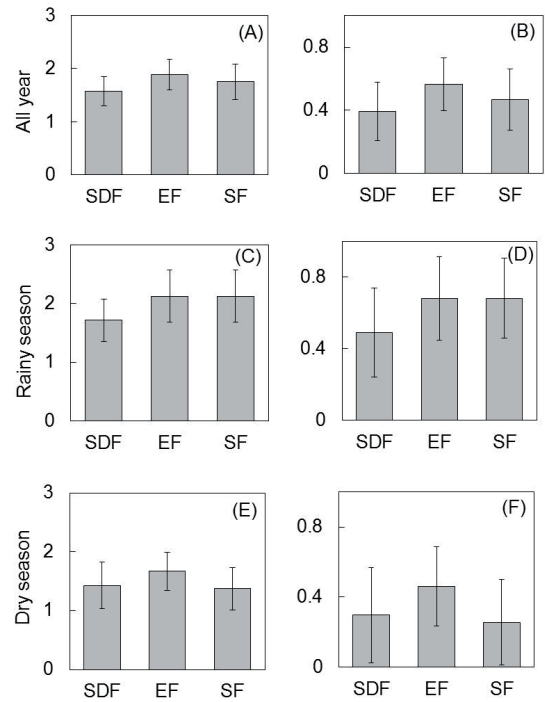


Figure 3. Estimates based on phyllostomid bat sensitivity groups of species richness (A, C, E) and Shannon-Wiener diversity index (B, D, F) for primary semi-deciduous (SDF), primary evergreen (EF), and secondary evergreen (SF) forests for the entire period of study (A, B), the rainy season (C, D), and the dry season (E, F). Values are means (\pm 95% CI's) estimated at the maximum sampling size (nights) through rarefaction techniques.

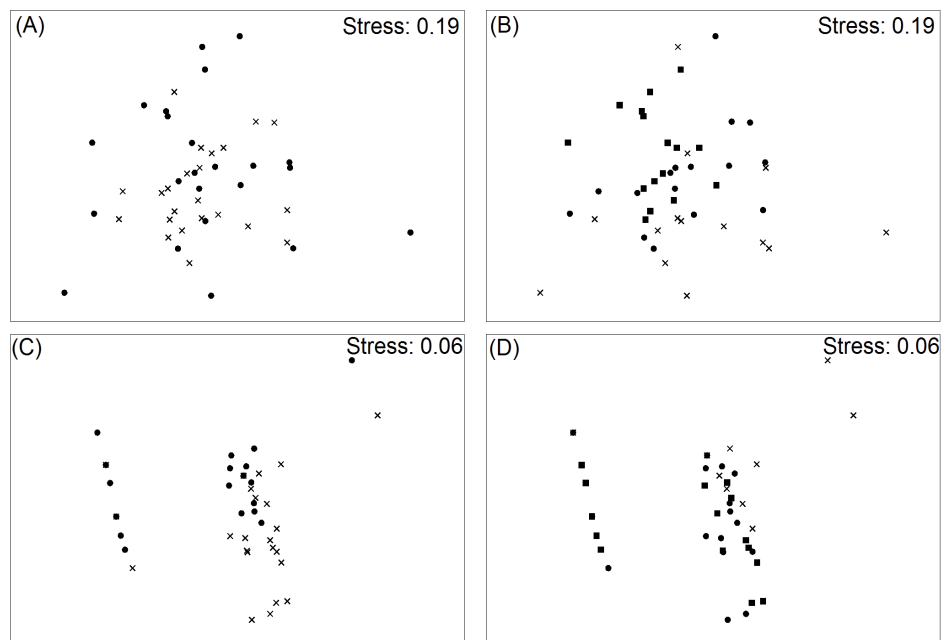
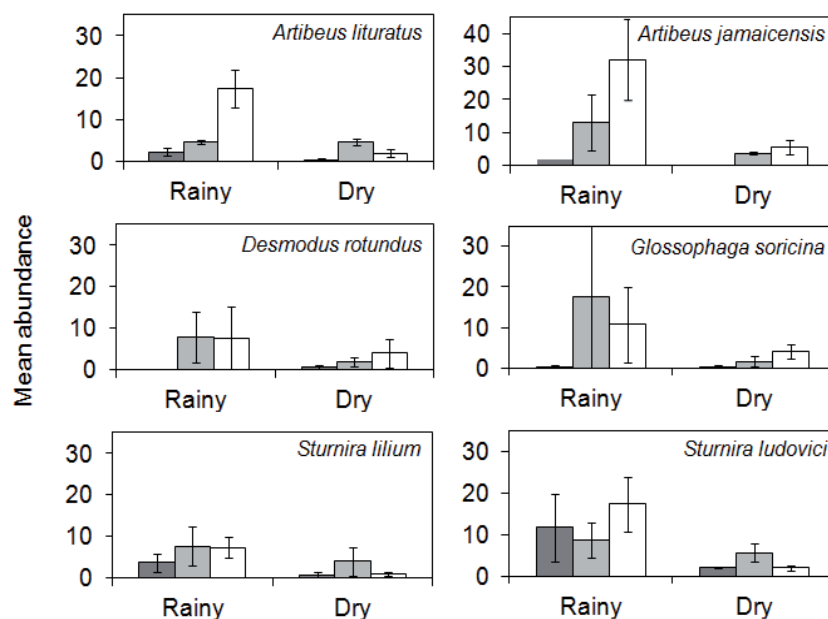


Figure 4. Non-metric Multidimensional Scaling (NMDS) ordination of study sites based on phyllostomid bat species and season (A), and forest type (B), and based on sensitivity groups and season (C), and forest type (D). Symbols for season are crosses (rainy season) and full circles (dry season). Symbols for forest types are full circles (primary evergreen), crosses (primary semi-deciduous), and squares (secondary evergreen).

Figure 5. Mean abundances of individual phyllostomid bat species in primary semi-deciduous (dark grey), primary evergreen (light gray), and secondary evergreen (white) forests during the rainy and dry seasons at the Huasteca region of San Luis Potosí, México. Error bars represent mean \pm one standard error. Abundance of *Artibeus lituratus* was smallest at primary semi-deciduous, intermediate at primary evergreen, and largest at secondary evergreen forests ($P < 0.05$). Abundances of *A. lituratus*, and *A. jamaicensis* were smaller during the dry season in comparison with the rainy season ($P > 0.05$).



The most abundant species at semi-deciduous evergreen forests was by far *Sturnira ludovici* representing 57.4% and 37.5% of all captures at the rainy and dry seasons, respectively. At evergreen forests, the most abundant species were *Glossophaga soricina* during the rainy season (27.2% of all captures) and *Sturnira ludovici* (28.8% of all captures) during the dry season. Finally, *Artibeus jamaicensis* (23% of all captures) during the rainy season, and *Artibeus jamaicensis*, *Desmodus rotundus* and *Glossophaga soricina* (each representing 22.6% of all captures) during the dry season were the most abundant in secondary evergreen forests (Table 1).

Abundances of *Artibeus lituratus* were lower at primary semi-deciduous forest in comparison with primary evergreen ($Z = 2.044$, $P = 0.041$) and secondary evergreen forests ($Z = 3.44$, $P = 0.002$), lower in primary evergreen than secondary evergreen forests ($Z = 2.07$, $P = 0.039$), and for this species and *A. jamaicensis* abundances were smaller during the dry compared with the rainy season (*A. lituratus*: $Z = 3.29$, $P = 0.002$, *A. jamaicensis*: $Z = 2.182$, $P = 0.029$). For all other species analyzed (*Desmodus rotundus*, *Glossophaga soricina*, *Sturnira lilium*, and *Sturnira ludovici*), abundances were independent of either forest type or season ($P > 0.05$, Fig. 5).

Discussion

Our study is the first systematic survey comparing bat communities among forest types in the northern neotropics of Eastern Mexico. Our sampling strategy allowed us to meet our goal of assessing the potential value of secondary evergreen forest patches for conservation of bat diversity. A previous bat inventory at the Huasteca Region of San Luis Potosí reported 21 bat species (Dalquest 1953), five of which (*Carollia perspicillata*, *Pteronotus davyi*, *Mormoops megalophylla*, *Eptesicus brasiliensis* and *Myotis nigricans*) were missed in our sampling. This difference could be partly related to the capture methods we used. Mist nets are biased

towards species that forage at the understory, such as those from the family Phyllostomidae, while canopy bat species such as *Eptesicus brasiliensis* and small insectivores capable of detecting the mist nets are not adequately sampled by our methods (Kalko et al. 1996). Mist-netting at ground level is known to be biased because high-flying, insectivorous bats and those with very low body mass such as *Myotis nigricans* are difficult to net (Pech-Canche et al. 2010). In our case, phyllostomid bats were the most abundant at all three forest types. This result was expected since our sampling was limited to mist netting at ground level and our results are consistent with the results of previous mist-netting studies at the neotropics (Medellín et al. 2000, Bernard and Fenton 2003, Giannini and Kalko 2004, Montiel et al. 2006, Zortéa and Alho 2008). Since we did not sample caves, we cannot assess if the species not detected in our study are still present or locally extinct from the region. It has been more than 55 years since the Dalquest (1953) inventory.

Diversity patterns

For our within-season analysis, the Chao2 estimates efficiently recorded the species richness of phyllostomid bat assemblages at the primary evergreen and secondary evergreen forests. For primary semi-deciduous forest during the dry season, Chao2 values surpassed observed bat richness. Because most species from the primary semi-deciduous forest occurred just once or twice in the samples at this season, the Chao2 values could have overestimated species richness for this forest type. Since we used the same sampling protocol at all forest types, our statistical comparisons are valid.

While phyllostomid species richness at the annual scale was highest at secondary evergreen and primary evergreen forests, the Shannon-Wiener index was highest for primary evergreen forests, indicating that this forest type has the highest evenness. In general, this result was similar with the

analysis based on sensitivity groups and consistent with the general notion that neotropical evergreen forests contain the highest diversity for different animal groups, including phyllostomids (Lim and Engstrom 2001, Vargas-Contreras et al. 2008, Barragán et al. 2010, García-Morales and Gordillo-Chávez 2011). The higher year-round phyllostomid bat diversity in secondary evergreen forests compared to the primary semi-deciduous forests supports the hypothesis that secondary forests contribute to conservation of bat diversity. In the Huasteca region, this successional stage derives from evergreen forest which originally covered the greatest proportion of land. Therefore, late successional stages contain plant species characteristic of the evergreen forest which likely promoted bat diversity. Previous results found that once secondary forests have reached advanced successional stages, their associated mammal diversity may not largely differ from undisturbed forests (e.g., Chávez and Ceballos 2001, Vargas-Contreras et al. 2008, García-Morales et al. 2011). The most advanced stages of succession facilitate the presence of bat species because the structure and composition of their vegetation is similar to the primary evergreen forest (Castro-Luna et al. 2007). The secondary evergreen forest patches considered in our study have been abandoned more than 20 years and their associated late-successional plant communities which derived from evergreen forest show advanced stages of succession with trees as tall as 10 m (García-Morales et al. 2012).

Our findings of a lack of differences in both phyllostomid bat species richness and diversity based on species sensitivity groups between primary evergreen forests and secondary evergreen forests is partially consistent with our hypothesis that phyllostomid bat assemblages in secondary evergreen forests would be similar to those in primary forests and confirm results from previous studies (Castro-Luna et al. 2007, Bobrowiec and Gribel 2010). On the other hand, during the rainy season, primary semi-deciduous forest yielded the lowest values for these indices. Medellín et al. (2000) suggested that small bat species richness and diversity, high richness corresponding to rare bat species, and high dominance are indicators of disturbed habitats. Although primary semi-deciduous forests at our study region fit these criteria during the rainy season, the trend did not hold for the dry season. In addition, primary semi-deciduous forests of this region contain the highest regional densities for some priority species including ocelots (*Leopardus pardalis*, Martínez-Calderas et al. 2011) and jaguars (*Panthera onca*, Villordo-Galván et al. 2010, Ávila-Nájera et al. 2011) and are occupied by bird species of conservation concern. Therefore, these forests should not be regarded as being disturbed or having less conservation value in comparison with primary evergreen and secondary evergreen forests. These patterns may be driven at least in part by differences in food resources. More than 88% of our captures were frugivorous or nectarivorous phyllostomids and most plant species from the Huasteca region produce their fruits during the rainy season (Rzedowski 2006). In addition, plants from the primary evergreen and secondary evergreen forests produce larger quantities of flowers and sugar-rich, juicy fruits (*Ficus* spp., *Piper* spp., *Solanum* spp.) than

those from the primary semi-deciduous forest (Puig 1991, Puig and Lacaze 2004).

The lower phyllostomid bat assemblage species richness and diversity during the dry season could be related to temporal changes in food availability. The lowest diversity and abundance of seeds from bat fecal samples were recorded during the dry season (García-Morales et al. 2012) indicating that this is the most critical time period for phyllostomids in this region. Similarly, previous research from the neotropics has reported the highest bat food availability during the rainy season (Olea-Wagner et al. 2007). Across the Huasteca region during the dry season, both fruits and flowers are scarce as most plant species at primary semi-deciduous and secondary evergreen forests cease the production of reproductive organs in response to drought (Rzedowski 2006). During the dry season, several plant species at primary evergreen forests still produce flowers and fruits (Puig and Lacaze 2004). Thus, many individual bats presumably move to the primary evergreen forest or elsewhere at this season, causing the patterns of diversity and abundance that we observed. This type of pattern has also been observed elsewhere (Bernard and Fenton 2003). Therefore, primary evergreen forests in the region are critical for bat conservation. Since many bats from different species were still caught at the primary semi-deciduous and secondary evergreen forests during the dry season, these forest types appear to foster suitable habitat for phyllostomid bat assemblages even in times when resources are scarce. Notwithstanding the potential value of alternative forest types for phyllostomid bats, the critical importance of primary evergreen forests during the dry season cannot be overemphasized.

Abundance patterns

The overlap among seasons and among forest types (Fig. 4) suggests the existence of some level of similarity in structure and composition of the Phyllostomid bat assemblages in our study region. The analysis based on sensitivity groups showed greater separation among groups, but overlap was still evident. Likewise, the SIMPER analyses showed that in many cases, the same species contributed to similarities and dissimilarities within and among groups. For highly-mobile phyllostomid bats in our study area, this pattern may have resulted from bat movements between habitats. As a result, phyllostomid bat assemblages in the forest types that we studied are characterized by having fairly high evenness, both within and between forest types. These results indicate that all three forest types provide resources for phyllostomids.

The between-habitat differences that we encountered for *A. lituratus* are similar with trends of greater abundances of this species in intermediate and late successional stages reported by others (Ávila-Cabadilla et al. 2009, de la Peña-Cuellar et al. 2012). Although Fenton et al. (1992) caught more individuals of this species in disturbed habitats, none of the studies had large enough sample sizes of *A. lituratus* to make statistical comparisons among habitats. *A. lituratus* is a frugivorous species and thus its lower abundance in primary semi-deciduous forests is expected. The lack of significant

differences in abundances of all other species among forest types confirms our original hypothesis that phyllostomid bats would occur in secondary evergreen forests in numbers comparable to those in undisturbed forest. *A. jamaicensis* is a frugivore which feeds from canopy trees, mainly *Ficus* sp. and *Piper* sp. in our study area (García-Morales et al. 2012), and its highest abundances are consistently reported for old growth forests or advanced successional stages (Fenton et al. 1992, Medellín et al. 2000, Castro-Luna et al. 2007, de la Peña-Cuellar et al. 2012). Consistent with our results, differences in abundance of this species have also been reported between seasons (Stoner 2001). This highly mobile species may be moving in and out of the area as a result of seasonal changes in resource availability. *S. lilium* typically occurs in higher numbers in agriculture, early successional second growth, and highly degraded habitats (Medellín et al. 2000, Castro-Luna et al. 2007, Willig et al. 2007, Bobrowiec and Gribel 2010, de la Peña-Cuellar et al. 2012). The high abundance of this species and that of *S. ludovici* in mature forests has been linked to their association with large-diameter trees where *S. lilium* roosts (Evelyn and Stiles 2003, Ortiz-Ramírez et al. 2006, Bobrowiec and Gribel 2010), the existence of a mosaic of various successional stages at the landscape scale which offer a variety of feeding resources for these two species (Gorresen and Willig 2004), and the fact that these species occur naturally at high abundances, and thus may not be susceptible to habitat disturbance (de la Peña-Cuellar et al. 2012). In our study region during the dry season, however, these two species tended to have smaller abundances in both secondary evergreen and primary semi-deciduous than in primary evergreen forests. Though this trend was not statistically significant due to large confidence intervals, it could be regarded as biologically significant considering that the average abundance in evergreen forest was nearly two-to-three-fold larger (Fig. 5). Thus, primary evergreen forests could be critical for these species, and a management strategy only favoring secondary forests would potentially be detrimental for at least these two species. *G. soricina* is another species with highest abundances observed in agricultural areas and in early successional stages, but is also frequently documented in secondary and mature forests (Fenton et al. 1992, Medellín et al. 2000, Castro-Luna et al. 2007, Willig et al. 2007, Avila-Cabadilla et al. 2009, Bobrowiec and Gribel 2010, de la Peña-Cuellar et al. 2012). The high abundance of this nectarivorous bat in the secondary and primary forests that we studied may be linked to the presence in the surrounding landscape of disturbed habitats which provide flowers of early successional plants (Willig et al. 2007, Avila-Cabadilla et al. 2009). In our study area, most sites were located within moderate distances (5–10 km) of early successional vegetation, cattle grazing pastures, and/or agricultural lands. Natural treefall gaps within the forest patches that we sampled also provide additional feeding resources for this species. Finally, high abundances of the sanguivore *D. rotundus* in all of our study sites corresponds to the presence of anthropogenic grasslands that are maintained throughout the entire Huasteca region for cattle, providing food resources for this species throughout the landscape. In summary, all these results suggest that secondary

evergreen forests at the Huasteca have abundant populations of some phyllostomid species which are comparable to those found in primary forests. As long as some landscape heterogeneity is maintained along with large areas of primary evergreen forests that provide resources during the dry season, the inclusion of secondary evergreen forests in the landscape is likely to contribute habitat for these species.

Conservation implications

The lower numbers of captures at primary semi-deciduous forests during the rainy season suggest that this vegetation type is less used by phyllostomids than primary evergreen and secondary evergreen forests. High bat capture rates in a given habitat, however, may not necessarily translate into high habitat quality (Van Horne 1993). Because phyllostomids are highly mobile, the capture of a species in a particular habitat may not necessarily reflect preference for that habitat or that the habitat contains all the resources that the species needs (Willig et al. 2007). Bats also differ in their degree of dietary specialization (Hernández-Conrique et al. 1997). Therefore, it is likely that the best management strategy should focus at both the landscape and local scales. Such a strategy should likely promote some interspersed (i.e., high adjacency among patches) of primary forests with different successional stages. The fine details of landscape structure and composition (e.g., amount and spatial arrangement of different habitat types) that would maximize available resources for bats at the landscape level are still unknown and should be investigated. Taken together, our results indicate that the conservation of secondary evergreen forests, which cover approximately 40% of the Huasteca region, may contribute to increasing the amount of available habitat and overall resources for phyllostomid bat assemblages. Promoting the natural recovery of the vegetation at disturbed sites from the region would also likely enhance bat diversity. Finally, the importance of primary evergreen forests as providers of resources during the dry season should be emphasized. The recommendation of maintaining secondary evergreen forests should be implemented in combination of large areas covered by primary evergreen forest, since a management plan only favoring secondary evergreen forests would likely negatively influence populations of some species such as *S. ludovici* and *S. lilium*, and perhaps the entire phyllostomid bat community.

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Appendix 1. Phyllostomid bat species causing intra- group similarities and inter-group dissimilarities based on Bray-Curtis similarity. Groups are season (rainy vs. dry), and forest types (primary semi-deciduous, primary evergreen, and secondary evergreen).

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