







ORIGINAL ARTICLE

## Responses of phyllostomid bats to forest cover in upland landscapes in Chiapas, southeast Mexico

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### ABSTRACT

Forests are a key habitat for bats, but tend to be lost and fragmented in some agri-environment schemes. We studied the effects of forest cover change on phyllostomid bats in agricultural landscapes with increment of open areas in an upland region in Chiapas, southeast Mexico. We tested whether with forest cover increase there is a directly proportional response on assemblage species diversity measures, on the capture success and body condition of particular ensembles. Depending on the spatial analysis window, and presumably on vagility, we found positive and significant associations with the sanguivore ensemble's capture success, as well as with the nectarivore and shrub frugivore ensembles' body condition. We support the idea that appropriate amounts of forest over small geographic extents may propitiate favorable environments for some phyllostomids, which can also provide important ecological services. Furthermore, the arrangement of ecologically similar species proved to be valuable for exploring adaptive traits, and adequate for conservation strategies of species-rich taxa.

### ARTICLE HISTORY

Received 19 March 2016  
Accepted 13 February 2017

### KEYWORDS

Assemblage; chiropterans;  
deforestation; ensemble;  
vagility

## Introduction


The ongoing loss of biodiversity as a consequence of human activities is an issue of great concern, and the object of much of contemporary research. The loss and fragmentation of natural areas lead to adverse environments for sensitive species, and often a decrease in their survival probability (Groom Vynne 2006; Bennett & Saunders 2010; Ávila-Gómez et al. 2015). While facing habitat disruption, the resilience of many organisms depends on traits including abundance and mobility (e.g. García-García et al. 2014; Bader et al. 2015). Consequently, different species require different amounts of habitat to persist in a given landscape, and likely exhibit differential susceptibilities to local extinction (Fahrig 2003; Fischer & Lindenmayer 2007).

When studies of animal communities are based on the idea that these are collections of organisms living in the same place and time, delimited naturally or arbitrarily (e.g. all organisms in a plot), concepts such as phylogeny, geography and resource use may provide operational

definitions that can be a valuable field of ecological inquiry (Jaksić 1981; Fauth et al. 1996). For instance, phylogenetically related groups within a community (this is the intersection between phylogeny and geography) are termed “assemblages” (Fauth et al. 1996). Similarly, phylogenetically related groups that use a similar set of resources within a community (this is the intersection between phylogeny, geography and resource use) are termed “ensembles” (Fauth et al. 1996). Approaches such as these allow the identification of patterns of community structure, and understanding of factors that underlie its organization (Kalko et al. 1996; Schnitzler & Kalko 2001; Denzinger & Schnitzler 2013).

Bats are an ideal study system for investigating consequences of habitat loss and fragmentation because most are colonial, central-place foragers or depend on spatially scattered resources across landscapes (Rainho & Palmeirim 2011). They are also known to be useful indicators of disturbance because of their high abundance and ecological, taxonomical, and trophic

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representation (Fenton et al. 1992; Medellín et al. 2000). Moreover, their sensitivity to habitat disruption can be addressed by specific traits (e.g. Meyer et al. 2008; García-García et al. 2014; Farneda et al. 2015).

For instance, the bats foraging behavior during flight can be described by mobility traits (similarly in birds) in terms of wing loading (body mass per wing area) and wing shape (as a function of wing length to width) (Findley et al. 1972; Norberg & Rayner 1987; Bader et al. 2015). The foraging behavior and the associated traits affect the bats' ability to access particular habitats such as cluttered vegetation, and consequently their ability to access food (Fenton et al. 1992; Marciente et al. 2015). Less mobile species with slow flight but high maneuverability exhibit large-surfaced, broad wings, and are thereby adapted for the use of cluttered habitats and covering short distances (Norberg & Rayner 1987; Fenton et al. 1992; Bader et al. 2015). In contrast, more mobile species with fast flight but less maneuverability exhibit small-surfaced, narrow wings, adapted for open spaces, and are able to cover long distances at low energetic cost (Norberg & Rayner 1987; Bader et al. 2015; Rodríguez-San Pedro & Simonetti 2015).

Likewise, body condition can provide a proxy for eco-physiological responses to food shortage in the environment, and it can offer insights into consequent animal stress (Fleming 1988; Ramos et al. 2010). Body condition indices are generally calculated as the relationship between body mass and a linear aspect of the animal (e.g. forearm length in bats), and can be related to habitat quality (Speakman 2008). For instance, Ramos et al. (2010) found a decline in body condition of the phyllostomid *Artibeus planirostris* when fruits were scarcer, which might indirectly reflect a decrease of the amount of suitable vegetation cover in the given landscape.

Here, we investigated phyllostomid bats in a region exposed to human activity that has left few forested remnants, which are immersed in agricultural landscapes with increment of open areas. We used concentric spatial analysis windows (hereafter buffers) to analyze the effect of forest cover (FC) as a predictor variable on assemblage-level, and ensemble-level measures. We began with the hypothesis that the increase of FC is directly proportional to assemblage species diversity measures, on the capture success and body condition of particular ensembles.

The predictions for the increase of FC are: (a) higher richness that incorporates rare species because of potential increment in environmental heterogeneity; (b) higher species equitability, with lower dominance of generalist species because of presumably decrease in

disturbance; and (c) higher capture success and body condition in some ensembles because of possibly more resource availability. Finally, we highlight that the arrangement of ecologically similar species can be a valuable approach in conservation strategies.

## Material and methods

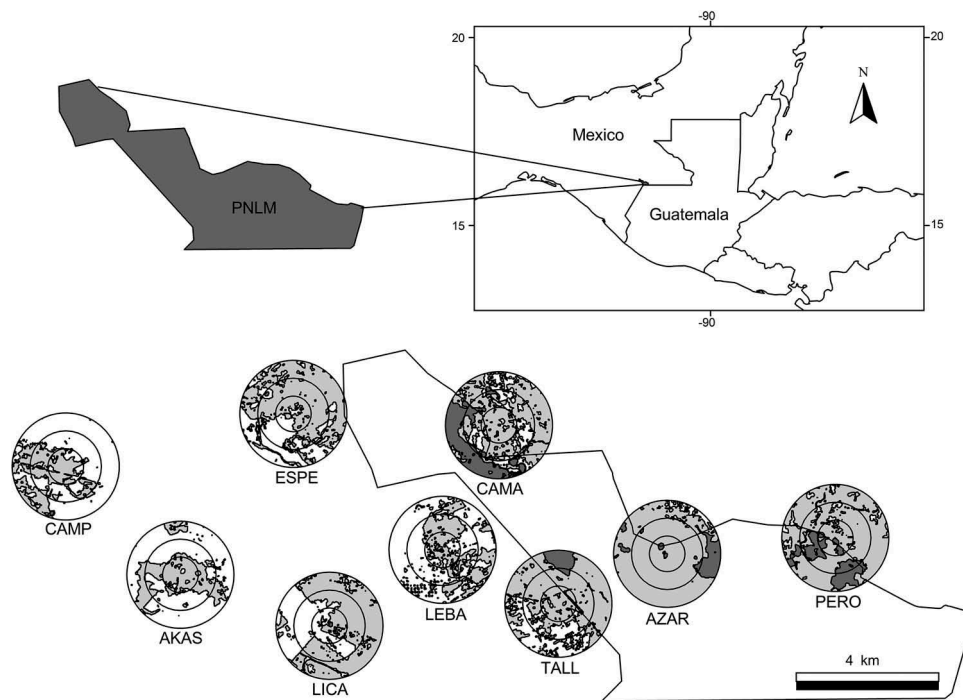
### Study area

The study area is located on a plateau in upland Chiapas, southeast Mexico, and it falls within and extends beyond the Lagos de Montebello National Park (hereafter PNLM) (Figure 1). Average elevation in the PNLM is 1500 m asl (above sea level), and its extension covers 6425 ha (CONANP 2007). There was no considerable variation in elevation in the study area (1460 m–1540 m asl), which prevented this variable from being a confounding factor (Carrara et al. 2015).

The predominant vegetation type in the PNLM is coniferous forest, and the most frequent species are pines (Pinaceae), with *Pinus oocarpa* in the driest areas and *P. maximinoi* in wetter areas. Nevertheless, oaks (Fagaceae: *Quercus* spp.), cypresses (Cupressaceae: *Cupressus* spp.), and sweetgum (Altingiaceae: *Liquidambar styraciflua*) are also common in mixed associations (CONANP 2007). The surroundings of the PNLM are mostly characterized by agricultural activities (extensive cornfields), livestock husbandry (grasslands), human settlements, and scattered forest remnants. The cornfields, grasslands, and human settlements lack tree cover (i.e. they are characterized by open space), and hence we consider these as unsuitable environments for forest specialists. In the area, the secondary vegetation is not distinguishable by satellite imagery and, when present, it is mixed into the forests as a result of land management practices.

### Bat sampling

Field work was carried out monthly between July 2014 and July 2015 during nights close to a new moon, in order to avoid effects of lunar phobia (Santos-Moreno et al. 2010; Saldaña-Vázquez & Munguía-Rosas 2013). We sampled nine points (Figure 1): CAMP (−91° 52'17.39"W, 16°8'3.15"N), TALL (−91°44'33.39"W, 16°5'55.39"N), AKAS (−91°49'42.76"W, 16° 5'27.96"N), ESPE (−91°48'42.37"W, 16°8'49.92"N), LICA (−91°48'9.46"W, 16°5'36.56"N), LEBA (−91° 46'22.37"W, 16°6'45.2"N), CAMA (−91°45'28.44"W, 16°8'38.5"N), PERO (−91°40'11.82"W, 16°6'53.85"N), AZAR (−91°42'50.51"W, 16°6'40.32"N). The latter sampling point (AZAR) was the only location within



**Figure 1.** Study area in upland Chiapas, southeast Mexico. The Lagos de Montebello National Park is highlighted next to the Guatemalan border. The sampling points are surrounded by concentric buffers of 0.5, 1, and 1.5 km radius. Light gray = forest cover; dark gray = water; white = open areas.

continuous forest, while the rest were located at the PNLM limits and beyond, specifically in forest remnants. Each sampling point was visited twice (once in both wet and dry seasons), for three consecutive nights each visit.

Sampling events were conducted in the understory using three 12 m long and 2.5 m high mist nets (Ecotone®, Gdynia, Poland), during 4-h periods beginning at sunset. Mist netting effort was calculated with the area of the nets deployed (length by height in meters) divided by the number of hours sampled (see García-García et al. 2010), giving an effort of  $2,160 \text{ m}^2 \text{ h}^{-1}$  in each sampling point and a total sampling effort of  $19,440 \text{ m}^2 \text{ h}^{-1}$ .

The bats captured were identified using the field key of Medellín et al. (2008), weighed to the nearest 0.1 g with a 100 g scale (Pesola AG®, Baar, Switzerland), and their forearms were measured to the nearest 0.1 mm with a digital caliper (Mitutoyo®, Aurora, IL, USA). Bat taxonomy was based on Ramírez-Pulido et al. (2014). We also registered reproductive activity (non-pregnant, pregnant, lactating) and age (juvenile, sub-adult, adult); the latter was based on the degree of fusion of the metacarpal epiphysis (Anthony 1988). For each individual captured, we obtained a 4 mm diameter biopsy of the wing membrane using a dermatological punch (Biopunch®, Ted Pella, Inc., Redding, CA, USA) at a standardized position between the fourth and fifth

digits in order to allow recognition of re-captures and avoid re-measuring (Ripperberg et al. 2014). Samples were stored in 96% ethanol for future analyses.

### Spatial analyses

A non-supervised classification of the study area was available in the Laboratory of Geographic Information and Statistic Analysis of ECOSUR, which was based on multispectral SPOT satellite images of 2011, with a spatial resolution of 10 m. This classification was verified during 2014–2015 through 211 control points around the sampling points and within the buffers, which allowed for polygon rectification using the software ArcView® version 3.2 (ESRI, Inc., Redlands, CA, USA). We chose to base our analysis on FC, because it is a variable highly correlated to other measures of habitat loss and fragmentation (Fahrig 2003). The FC was corroborated in the field by the presence of woody plants and a distinguishable canopy.

The sampling points were established with the intention of avoiding spatial autocorrelation, because if they are too close to one another observations can be spatially correlated, and the assumption of independence is violated (Popescu & Gibbs 2010); in other words, as distance between sampling points decreases, similarity among samples increases. Information about the home ranges of Neotropical bats is scarce; however,

*Carollia perspicillata* is a phyllostomid with body size comparable to some of the species previously registered in the study area, and has average flight distances from day roosts to feeding areas of 1.6 km (Heithaus & Fleming 1978). Therefore, the minimum distance between sampling points was set starting from ~ 3.5 km.

Several authors have provided evidence that a single buffer may fail to recognize phyllostomids species-level, assemblage-level, and ensemble-level perceptions of their surroundings and resource distribution (e.g. Pinto & Keitt 2008; Klingbeil & Willig 2009; Avila-Cabadilla et al. 2012; Bolívar-Cimé et al. 2013; García-García & Santos-Moreno 2014). Therefore, we constructed concentric buffers around the sampling points with 0.5, 1, and 1.5 km radii (Figure 1). These were non-overlapping in order to avoid re-measuring of land units (Popescu & Gibbs 2010). The minimum radius was chosen to encompass the home range of the smallest species in the study area, perhaps as wide as 0.5 km for *Glossophaga soricina* (Lemke 1984; Gorresen & Willig 2004). These focal buffers also facilitate comparison with previous research on phyllostomid spatial-dependent associations (e.g. Pinto & Keitt 2008; Ávila-Gómez et al. 2015). We measured FC in square kilometers (km<sup>2</sup>) in each buffer using the software ArcView® version 3.2 (ESRI, Inc.), and include the calculations in Table 1.

### Delimitation of variables and statistical analyses

#### Assemblage level: species diversity measures

The number of species or species richness (S) in a sample is among the simplest descriptors of community structure (Maurer & McGill 2011). It is an essential, intuitive and natural index, for which many calculation methods have been proposed (Gotelli & Colwell 2011). Given that our samples differed in the number of captured individuals, we calculated the assemblage S with rarefaction, hereafter referred to as interpolation (Gotelli & Colwell 2011). This calculation

was performed using the software Ecosim® version 7.71 (Gotelli & Entsminger 2004).

Theoretically, if the species in an assemblage are equally common or equivalent in number, then the diversity (as a combination of S and equitability) has to be proportional to the specific richness (Moreno et al. 2011). Nevertheless this is improbable, and the estimation of changes in diversity are useful when comparing samples spatially and/or temporarily (Moreno et al. 2011). Therefore, we calculated the Shannon diversity index ( $H'$ ) with rarefaction in order to control for sample differences (Gotelli & Entsminger 2004), but transformed these calculations into effective number of species ( ${}^1D$ ), also known as “true diversity” (Jost 2006; Moreno et al. 2011). The  ${}^1D$  measure conserves intuitive properties of the diversity concept and allows for direct comparison of magnitudes among assemblages (Moreno et al. 2011). The calculation of  $H'$  was performed using the software Ecosim® version 7.71 (Gotelli & Entsminger 2004), and the calculation of  ${}^1D$  using Microsoft® Office Excel version 2003 (Microsoft Corporation, Redmond, WA, USA). Finally, we include an evenness measure which attempts to examine how abundance is apportioned among species: such measures rely on the basic concept that evenness is highest when an assemblage is not dominated by a few species of very high abundance, or equivalently that all species have an equal abundance (Maurer & McGill 2011). We calculated the Hurlbert's PIE index (probability of an interspecific encounter), which calculates the probability that two randomly sampled individuals from the assemblage represent two different species, and is unbiased by sample size (Gotelli & Entsminger 2004; Maurer & McGill 2011). This calculation was performed using the software Ecosim® version 7.71 (Gotelli & Entsminger 2004).

#### Ensemble classification allocation procedure

We classified species into “guilds” based on Kalko et al. (1996), Kalko and Handley (2001), Sampaio et al. (2003),

**Table 1.** Phyllostomid bat sampling points, acronyms, and forest cover (FC) calculated in square kilometers (km<sup>2</sup>) in concentric buffers (0.5, 1, and 1.5 km radius) in upland landscapes in Chiapas, southeast Mexico. For each buffer the FC is indicated along with its percentage in parenthesis, according to the total surface.

	0.5 km radius (total surface = 0.79 km <sup>2</sup> )	1 km radius (total surface = 3.14 km <sup>2</sup> )	1.5 km radius (total surface = 7.07 km <sup>2</sup> )
CAMP	0.53 km <sup>2</sup> (67.1%)	1.2 km <sup>2</sup> (38.2%)	2 km <sup>2</sup> (28.3%)
TALL	0.68 km <sup>2</sup> (86.1%)	2.3 km <sup>2</sup> (73.2%)	4.7 km <sup>2</sup> (66.5%)
AKAS	0.67 km <sup>2</sup> (84.8%)	1.4 km <sup>2</sup> (44.6%)	2.1 km <sup>2</sup> (29.7%)
ESPE	0.53 km <sup>2</sup> (67.1%)	2.1 km <sup>2</sup> (66.9%)	4.3 km <sup>2</sup> (60.8%)
LICA	0.35 km <sup>2</sup> (44.4%)	1.7 km <sup>2</sup> (54.1%)	4.4 km <sup>2</sup> (62.2%)
LEBA	0.47 km <sup>2</sup> (59.5%)	1.3 km <sup>2</sup> (41.4%)	2.3 km <sup>2</sup> (32.5%)
CAMA	0.69 km <sup>2</sup> (87.3%)	2 km <sup>2</sup> (63.7%)	4 km <sup>2</sup> (56.6%)
PERO	0.58 km <sup>2</sup> (73.4%)	2.4 km <sup>2</sup> (76.4%)	5.5 km <sup>2</sup> (77.8%)
AZAR	0.75 km <sup>2</sup> (94.9%)	3 km <sup>2</sup> (95.5%)	6.1 km <sup>2</sup> (86.3%)



and Morim et al. (2014): highly cluttered space gleaner, canopy frugivore (HCSGCF); highly cluttered space gleaner, shrub frugivore (HCSGSF); highly cluttered space gleaner, nectarivore (HCSGN); highly cluttered space gleaner, sanguivore (HCSGS); highly cluttered space gleaner, carnivore (HCSGC). Nevertheless, the guild definition by Root (1967), later described by Fauth et al. (1996), is interpreted as a resource-bounded but non-taxonomically circumscribed set of species (e.g. foliage gleaners). Because the study area species are phylogenetically related groups that use a similar set of resources, they therefore fulfill the characteristics of an ensemble (see Fauth et al. 1996), and we use the latter term instead of guild. For those species with unknown guild membership, the allocation was based on measures of wing load and wing aspect ratio as proxies for mobility (Norberg & Rayner 1987; Bader et al. 2015). For this purpose, the voucher specimens measured are indicated in the Appendix, the statistical procedure is described in the Supplementary Material, and the results are included in Figure S1 and Table S1.

#### **Ensemble level: capture success and body condition**

Once all the species registered in the study area were classified into ensembles, we calculated the capture success at each sampling point as a surrogate for abundance (Pinto & Keitt 2008). We considered the total number of individuals belonging to a particular ensemble divided by the mist netting effort ( $2160 \text{ m}^2 \text{ h}^{-1}$ ).

We calculated a body condition index (BCI) for the members in each ensemble at each sampling point (sub-adults, adults, and non-pregnant individuals), based on the relationship between body mass and forearm length, in  $\text{g mm}^{-1}$  (Speakman 2008). Our initial assumption was that species grouped in the same ensemble behave similarly, specifically forage in similar habitats in similar ways for similar foods (Kalko & Handley 2001), and that members reflect the sustenance capacity of the habitat (e.g. larger and better conditioned bats demand more food in the environment). We are aware that this approach may be biased because different species differ in physiology, and distinct resources might not be energetically equivalent. Nevertheless, we consider that it may offer insights about resources in the environment in general terms (e.g. availability of forest-associated floral nectar). We include the median BCI as a measure of central tendency, and to minimize the effect of the outliers.

#### **Variables' responses to forest cover change**

In order to measure the direction, magnitude, and significance of association between FC, the assemblage species diversity measures, ensembles' capture success and body condition, we calculated the Spearman non-

parametric correlation coefficient in each focal buffer. This coefficient is adequate for small samples, and makes no assumptions about the data distribution. We excluded the HCSGC ensemble because of insufficient samples (registered in a single sampling point). These calculations were performed in the software STATISTICA® version 8.0 (StatSoft, Inc. 2007), which also provides probability tests for statistical significance. All the tests were considered statistically significant with  $p \leq 0.05$ .

## **Results**

### **Assemblage level: species diversity measures**

We captured a total of 264 phyllostomids, registered four subfamilies, 10 genera and 14 species (Table 2). Among sampling points, overall abundance ranged between 12 and 77 individuals (Table 2), and averaged 29.3 individuals ( $\sigma = 19.7$ ). The values of S differed among sites (ranged between 5 and 9 species), and the lowest  ${}^1D$  and Hurlbert's PIE index values were detected for LICA and CAMP, which were sampling points characterized by a high capture rate of *A. jamaicensis* and *Sturnira parvidens* (constituting 91% of captures), and *A. jamaicensis* and *Anoura geoffroyi* (80% of captures), respectively (Table 3). The highest  ${}^1D$  was detected in CAMA (4.76), more than twice as large as LICA, which showed the lowest value (2.27).

### **Ensemble level: capture success and body condition**

The maximum value in overall capture success was from LICA (0.036), the minimum was from AZAR (0.005), and the average was 0.014 ( $\sigma = 0.009$ ). Capture successes in each sampling point are presented in Table 4. The median BCI in each sampling point is presented in Table 5. The average BCI was highest for the HCSGCF ensemble (0.77;  $\sigma = 0.11$ ), followed in rank order by HCSGS (0.59;  $\sigma = 0.07$ ), HCSGSF (0.48;  $\sigma = 0.06$ ), and HCSGN (0.32;  $\sigma = 0.06$ ).

### **Variables' responses to forest cover change**

In the smallest buffers, the sampling points with more than 80% of forest cover (TALL, AKAS, CAMA, AZAR) showed higher values of interpolated S (with the exception of ESPE), and the addition of rare species (e.g. *Chiroderma salvini*, *Diphylla ecaudata*, and *Chrotopterus auritus*). LICA, which was the sampling point with least forest cover (< 50%), exhibited the lowest values of interpolated S and  ${}^1D$ , and it was dominated by *A. jamaicensis* and *S. parvidens*. Besides

**Table 2.** Number of phyllostomid bats registered in the study area in upland Chiapas, southeast Mexico.

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR	Total	Guild
<b>Stenodermatinae</b>											
<i>Artibeus lituratus</i> <sup>1,2,3,4</sup>	–	–	3	1	1	–	–	–	–	5	HCSGCF
<i>Artibeus jamaicensis</i> <sup>1,2,3</sup>	16	9	19	8	22	3	–	–	–	77	HCSGCF
<i>Chiroderma salvini</i>	–	1	1	–	2	–	–	–	–	4	HCSGCF
<i>Dermanura azteca</i>	–	1	1	1	–	–	–	1	–	4	HCSGSF
<i>Dermanura tolteca</i>	–	–	–	–	–	2	1	2	1	6	HCSGSF
<i>Sturnira hondurensis</i>	1	1	–	–	–	–	3	10	7	22	HCSGSF
<i>Sturnira parvidens</i> <sup>2,3,4</sup>	2	–	1	5	48	6	2	–	–	64	HCSGSF
<i>Centurio senex</i>	1	–	–	1	–	–	–	–	–	2	HCSGSF
<b>Glossophaginae</b>											
<i>Anoura geoffroyi</i> <sup>4</sup>	4	1	3	2	1	3	4	2	2	22	HCSGN
<i>Glossophaga soricina</i> <sup>1,2,3,4</sup>	–	–	–	3	1	–	–	–	1	5	HCSGN
<i>Glossophaga commissarisi</i> <sup>1</sup>	–	–	1	–	–	–	1	–	–	2	HCSGN
<b>Desmodontinae</b>											
<i>Desmodus rotundus</i> <sup>1,2,3,4</sup>	1	5	3	16	2	3	5	13	–	48	HCSGS
<i>Diphylla ecaudata</i>	–	1	1	–	–	–	–	–	–	2	HCSGS
<b>Phyllostominae</b>											
<i>Chrotopterus auritus</i> <sup>1,2,3,4</sup>	–	–	–	–	–	–	–	–	1	1	HCSGC
Total individuals (n)	25	19	33	37	77	17	16	28	12	264	

Abbreviations: HCSGCF = highly cluttered space gleaning, canopy frugivore; HCSGSF = highly cluttered space gleaning, shrub frugivore; HCSGN = highly cluttered space gleaning, nectarivore; HCSGS = highly cluttered space gleaning, sanguivore; HCSGC = highly cluttered space gleaning, carnivore. The superscript numerals indicate species previously classified in guilds based on Kalko et al. (1996)<sup>1</sup>, Kalko and Handley (2001)<sup>2</sup>, Sampaio et al. (2003)<sup>3</sup>, and Morim et al. (2014)<sup>4</sup>.

**Table 3.** Phyllostomid bat assemblage diversity measures in upland landscapes in Chiapas, southeast Mexico. S = species richness; <sup>1</sup>D = effective number of species; Hurlbert's PIE = Hurlbert's probability of interspecific encounter index.

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR
S (observed)	6	7	9	8	7	5	6	5	5
S (interpolation)	4.1	5.2	5.1	5.1	3	4.9	5.4	3.8	5
<sup>1</sup> D	2.80	3.82	3.39	3.94	2.27	4.39	4.76	2.97	3.42
Hurlbert's PIE	0.58	0.73	0.66	0.76	0.53	0.82	0.83	0.67	0.67

**Table 4.** Phyllostomid bat ensembles capture success (total number of individuals divided by the mist netting effort) in upland landscapes in Chiapas, southeast Mexico.

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR
HCSGCF	0.0074	0.0046	0.0106	0.0042	0.0116	0.0014	–	–	–
HCSGSF	0.0019	0.0009	0.0009	0.0032	0.0222	0.0037	0.0028	0.0060	0.0037
HCSGN	0.0019	0.0005	0.0019	0.0023	0.0009	0.0014	0.0023	0.0009	0.0014
HCSGS	0.0005	0.0028	0.0019	0.0074	0.0009	0.0014	0.0023	0.0060	–

Abbreviations: HCSGCF = highly cluttered space gleaning, canopy frugivore; HCSGSF = highly cluttered space gleaning, shrub frugivore; HCSGN = highly cluttered space gleaning, nectarivore; HCSGS = highly cluttered space gleaning, sanguivore.

**Table 5.** Median body condition of phyllostomid bat ensembles in upland landscapes in Chiapas, southeast Mexico. Condition was calculated through an index that considers body mass and forearm length (g mm<sup>-1</sup>).

	CAMP	TALL	AKAS	ESPE	LICA	LEBA	CAMA	PERO	AZAR
HCSGCF	0.77	0.72	0.77	0.86	0.78	0.79	–	–	–
HCSGSF	0.46	0.50	0.46	0.48	0.47	0.44	0.45	0.55	0.62
HCSGN	0.33	–	0.36	0.25	0.28	0.32	0.33	0.37	0.37
HCSGS	0.64	0.63	0.60	0.65	0.53	0.59	0.58	0.55	–

Abbreviations: HCSGCF = highly cluttered space gleaning, canopy frugivore; HCSGSF = highly cluttered space gleaning, shrub frugivore; HCSGN = highly cluttered space gleaning, nectarivore; HCSGS = highly cluttered space gleaning, sanguivore.

LICA, the sampling point with less forest cover in the intermediate and largest buffers (CAMP), below 40 and 30% respectively, exhibited the lowest <sup>1</sup>D and Hurlbert's PIE values, and it was dominated by *A. jamaicensis*.

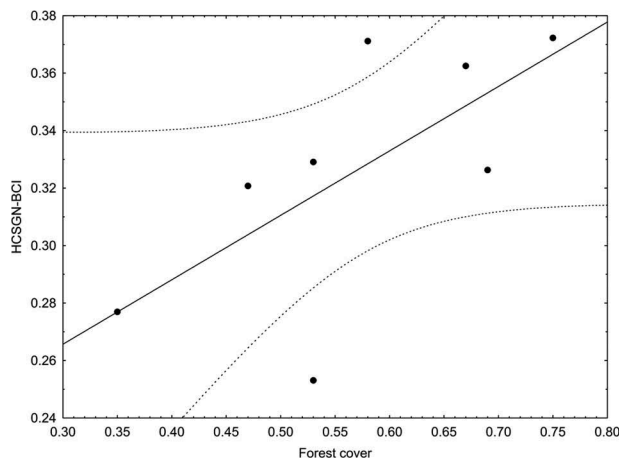
In Table 6, we present the correlations between FC, the assemblage species diversity measures, ensembles' capture success and body condition. We did not find assemblage-level statistically significant associations, except a weak, positive, and marginally non-significant correlation with the interpolated S ( $\rho = 0.66$ ;  $p = 0.053$ ).

In the smallest buffers we found strong, positive, and significant correlations with the HCSGN-BCI ( $\rho = 0.72$ ;  $p = 0.044$ ), as illustrated in Figure 2. In the intermediate buffer we found strong, positive, and significant correlations with the HCSGS ensemble capture success ( $\rho = 0.86$ ;  $p = 0.006$ ), and with the HCSGSF-BCI ( $\rho = 0.87$ ;  $p = 0.002$ ). In the largest buffer we also found strong, positive, and significant correlations with the HCSGSF-BCI ( $\rho = 0.85$ ;  $p = 0.003$ ).

**Table 6.** Spearman correlation coefficients ( $\rho$ ) between forest cover (FC), phyllostomid bat assemblage diversity measures, ensembles capture success and body condition index (BCI) in upland landscapes in Chiapas, southeast Mexico.

	0.5 km radius	1 km radius	1.5 km radius
S (interpolation)	0.66	0.18	-0.09
${}^1D$	0.36	0.12	-0.05
Hurlbert's PIE	0.31	0.19	0.04
HCSGCF	-0.09	-0.03	-0.03
HCSGSF	-0.42	0.24	0.48
HCSGN	0.10	-0.32	-0.56
HCSGS	0.44	0.86*	0.62
HCSGCF-BCI	-0.70	-0.14	-0.09
HCSGSF-BCI	0.39	0.87*	0.85*
HCSGN-BCI	0.72*	0.33	0.24
HCSGS-BCI	0.13	-0.17	-0.40

Abbreviations: S = species richness;  ${}^1D$  = effective number of species; Hurlbert's PIE = Hurlbert's probability of interspecific encounter index; HCSGCF = highly cluttered space gleaning, canopy frugivore; HCSGSF = highly cluttered space gleaning, shrub frugivore; HCSGN = highly cluttered space gleaning, nectarivore; HCSGS = highly cluttered space gleaning, sanguivore. The asterisks indicate statistically significant correlations ( $\rho \leq 0.05$ ).



**Figure 2.** Plot with a linear model adjusted showing the strong positive association between forest cover (FC) in square kilometers ( $\text{km}^2$ ), and the highly cluttered space gleaning nectarivore body condition index (HCSGN-BCI), measured in 0.5 km radius buffers in upland landscapes in Chiapas, southeast Mexico. The discontinuous lines represent the 95% confidence intervals.

## Discussion

### Variables' responses to forest cover change

With regard to the predictions of the effect of increase of FC at the assemblage level, specifically a directly, proportional response on species richness and equitability, we did not find statistically significant associations, and hence we cannot support this hypothesis in the area. This lack of response might possibly be due to buffers failing to detect patterns which may be present over larger spatial extents. For instance, nested distribution of habitats is a possible cause of nested species

assemblages (e.g. Calmé & Desrochers 1999), and may be stronger over wider areas with increasing FC. Moreover, the degree of disturbance in the forest remnants might be high in the area, with a consequent dominance of generalist species (e.g. *A. jamaicensis*, *S. parvidens*).

At the ensemble level, we found that the HCSGCF members, who are presumed to be more vagile, did not respond to FC in the focal buffers in the study area. Nevertheless, dependent on buffers we found various statistically significant associations with the rest of the ensembles, composed of less mobile species, which are described below.

In the smallest buffers (0.5 km radius), we found a significant positive response in the HCSGN-BCI, which corroborates the prediction that with increase in FC, the body condition of some phyllostomids is higher. The lowest values for the HCSGN-BCI were associated with sampling points with less than 70% of FC. In accordance, Ávila-Gómez et al. (2015) found in their study area that *G. soricina*, which is a member of the HCSGN ensemble, was more frequent in areas with more than 70% arboreal cover. The glossophagines consume floral nectar using a hovering flight mode, and have to ingest large amounts of nectar each night in order to fulfill the high energetic requirements of this foraging behavior (Voigt & Winter 1999; Von Helversen & Winter 2003). Assuming that FC might be correlated with the quantity of floral resources, low availability of floral nectar in landscapes with low FC might affect both abundance and body condition of glossophagines. Lemke (1984) also indicates that individuals of *G. soricina* adopt an energetically costly territorial behavior in response to low plant diversity and food reliability, which could lead to stress and consequently poor body condition.

In the intermediate buffers (1 km radius), we found a significant positive response in the HCSGS ensemble capture success, which corroborates the prediction that with increase in FC the abundance of some species may be higher. The lowest values were associated to the sampling points with less than 60% of FC. For this ensemble, the most abundant member was *Desmodus rotundus*, while *D. ecaudata* was captured in low abundance, and at only two sampling points; the latter species is considered to be locally rare, and its population small in size (Greenhall et al. 1984; Elizalde-Arellano et al. 2007). Ávila-Gómez et al. (2015) suggest that *D. rotundus* requires landscapes in which a high percentage of forest has been preserved, but is more frequent where canopy cover is low. In other words, it benefits from areas with a high amount of forest and low tree density, which may improve flight

performance. Nevertheless, the latter finding may only be true as long as food sources (e.g. livestock) and roosts are available nearby. Even more, *D. rotundus* is known to be present in low abundance or absent from areas of continuous forest because of comparatively low prey availability, and it was not captured in the sampling point with 95.5% of FC (AZAR), which is located within the PNLM.

In both the intermediate and largest buffers (1.5 km radius) we found a significant positive response of the HCSGSF-BCI, which indicates that with increase in FC the shrub frugivore's body condition is also higher. The lowest values for the HCSGSF-BCI were found in the sampling points with less than 75% of forest cover. The *Sturnira* species, which were the most abundant members of this ensemble, are known to respond to the amount of secondary and primary forest over small geographic extents (Pinto & Keitt 2008; Mena 2010). This genus is strongly associated with vegetation succession elements, specifically pioneer plants in the genera *Solanum* and *Piper*, which produce edible, fleshy fruits (Bolívar-Cimé et al. 2013; Kraker-Castañeda et al. 2016). Nevertheless, pioneer plants in the study area are mixed into forests, complicating the spatial characterization of secondary vegetation, and consequently the inference of its relative importance for this particular ensemble.

### Ecological generalization in conservation strategies

Here, we considered the arrangement of ecologically similar species in order to explore the effects of FC in high contrast agricultural landscapes. By pooling species into sets based on ecological traits, we explored an alternative to the species-specific approach, and offered an insight into the responses of phyllostomids. This way, “keystone ensembles” can be considered useful in conservation strategies of species-rich taxa by protecting sets of species that behave similarly. Nevertheless, it is important to recognize that a generalized approach may obscure specialized interactions which can be ecologically relevant (Ávila-Gómez et al. 2015), and which may also be at risk of being disrupted by habitat loss and fragmentation. Moreover, the presence of bats does not only depend on landscape context (e.g. FC), as other extrinsic factors (e.g. habitat variables) might be involved (Bader et al. 2015).

Understanding of phyllostomid responses to landscape features in the region is usually based on lowland species, and general conclusions are drawn from these environments (e.g. Bolívar-Cimé et al. 2013; García-García & Santos-Moreno 2014; Arroyo-Rodríguez

et al. 2016). Nevertheless, the importance of forests may be context-dependent, and as Rodríguez-San Pedro and Simonetti (2015) point out, the type of matrix can influence the direction, magnitude, and spatial extent operating on species. Therefore, we highlight that more research effort should be directed towards upland ecosystems, which also benefit from ecological services provided by this group of mammals. Finally, as Ávila-Gómez et al. (2015) discuss, we agree that estimating appropriate amounts of habitat for target species (or ensembles as an alternative approach) is a necessity in conservation planning, and for the selection of places to protect in transformed landscapes.

### Acknowledgments

We would like to thank the authorities of the Comisión Nacional de Áreas Naturales Protegidas (CONANP) for permission to work in the Lagos de Montebello National Park, particularly A. Mendoza, E. González, and the PNLM staff. We thank E. Leiva, J.A. González, A. García, F. Falconi, and J. Bolaños for their help during fieldwork, S. Calmé and M.A. Martínez for the revision of different versions of the manuscript, and M. Ruiz for the language revision. We are also grateful to land owners, and local authorities for work permissions. The Instituto Politécnico Nacional (IPN) of Mexico provided equipment, and the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) provided the Scientific Collection License no. FAUT-0143.

### Disclosure statement

No potential conflict of interest was reported by the authors.

### Funding

This work was supported by the Instituto Politécnico Nacional [grant SIP-20151481]. The first author received a scholarship awarded by the Consejo Nacional de Ciencia y Tecnología of Mexico [CONACYT-244510].

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## Appendix. Voucher specimens of the mammal collection of ECOSUR

*Artibeus lituratus* (ECO-SC-M 943, 953, 1018, 1019, 1508, 1513, 1517); *Artibeus jamaicensis* (ECO-SC-M 777, 778, 779, 795, 1487, 1488, 1489, 1298); *Chiroderma salvini* (ECO-SC-M 337, 765, 7591); *Dermanura azteca* (ECO-SC-M 242, 247, 699, 940, 941); *Dermanura tolteca* (ECO-SC-M 27, 241, 404, 1311, 1509); *Sturnira hondurensis* (ECO-SC-M 240, 245, 1278, 1869, 1900, 1937, 1977, 2451); *Sturnira parvidens* (ECO-SC-M 25, 26, 28, 290, 500, 1762, 6087, 6180, 6297, 6502, 6610); *Centurio senex* (ECO-SC-M 239, 525, 1330, 1352, 1363, 1713, 2992, 5571, 5593, 6296); *Anoura geoffroyi* (ECO-SC-M 71, 315, 497, 1934, 2478, 2479, 2480, 2481, 2484); *Glossophaga soricina* (ECO-SC-M 107, 513, 768, 1008, 1303, 1434, 5246, 5501, 6492, 6514); *Glossophaga commissarisi* (ECO-SC-M 2017, 2133); *Desmodus rotundus* (ECO-SC-M 564, 1353, 1459, 1975, 6286, 6598, 6605, 6655); *Diphylla ecaudata* (ECO-SC-M 1431, 6405, 6657, 7064); *Chrotopterus auritus* (ECO-SC-M 469, 793, 1872, 5503, 6578).