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Research Article

Deforestation thresholds for phyllostomid bat populations in tropical landscapes in the Huasteca region, Mexico

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Abstract

The loss and degradation of forests in tropical regions have modified tree cover, creating deforested landscapes. It has been suggested that there are thresholds in these landscapes beyond which the diversity, distribution, abundance, and fitness of different biological groups can be affected. In this study, the ecological habitat thresholds were detected for eight populations of phyllostomid bats along an environmental gradient of forest loss in the Huasteca region, Mexico. At a local scale, we analyzed canopy loss, and we also detected these thresholds at the landscape level, as a function of forest remnant area at three scales with radii of 1, 3 and 5 km. The data were analyzed using the Threshold Indicator Taxa Analysis (TITAN) method for detecting indicator species along gradients. The bats exhibited three different types of response to habitat loss: 1) *Leptonycteris yerbabuenae*, *Chiroderma salvini*, *Sturnira hondurensis*, and *Artibeus lituratus* were more abundant where canopy cover was present at the local site, even though the landscape had been deforested; 2) *Sturnira parvidens* and *Artibeus jamaicensis* required tree cover at all spatial scales; and 3) *Glossophaga soricina* and *Desmodus rotundus* are species that might be locally abundant in habitats with little canopy, but both species need landscapes that have not been deforested. In conclusion, these populations of phyllostomid bats were sensitive to deforestation in different ways, their response to the habitat loss gradient varying among species and with spatial scale.

Keywords: habitat loss, tropical forests, ecological thresholds, Chiroptera, Phyllostomidae

Resumen

La pérdida y degradación de selvas en las zonas tropicales han modificado la cobertura vegetal creando paisajes deforestados, en los que se ha sugerido que existen umbrales a partir de los cuales la diversidad, distribución, abundancia y adecuación de distintos grupos biológicos pueden verse afectadas. En este trabajo se detectaron los umbrales ecológicos del hábitat para ocho poblaciones de murciélagos filostómidos a lo largo de un gradiente ambiental de pérdida de selvas; a escala local en función de la cobertura del dosel y a escala de paisaje en función del área con vegetación forestal remanente, en tres escalas de 1, 3 y 5 km de radio. Para analizar los datos se utilizó el método *Threshold Indicator Taxa Analysis* (TITAN), que se basa en la detección de especies indicadoras en gradientes. Los murciélagos tuvieron tres tipos de respuesta a la pérdida de hábitat: 1) *Leptonycteris yerbabuenae*, *Chiroderma salvini*, *Sturnira hondurensis* y *Artibeus lituratus* son más abundantes en zonas con cobertura de dosel, aunque el paisaje se encuentre deforestado, 2) *Sturnira parvidens* y *Artibeus jamaicensis* requieren de cobertura vegetal en todas las escalas espaciales analizadas y, 3) *Glossophaga soricina* y *Desmodus rotundus* pueden ser abundantes en hábitats con poca vegetación a escala local, pero requieren de paisajes no deforestados. En conclusión, se observó que las poblaciones de murciélagos filostómidos son sensibles de diferentes maneras a la deforestación ya que muestran una respuesta al gradiente de pérdida de hábitat que varía en función de la especie y de la escala espacial de observación.

Palabras clave: pérdida de hábitat, selvas tropicales, umbrales ecológicos, Chiroptera, Phyllostomidae

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Introduction

The loss and degradation of forests due to deforestation, logging, and land use changes—all caused by human activities—have long been recognized as the main threats to biological diversity in tropical regions [1, 2-4]. These processes have modified natural landscapes, creating mosaics that are much more heterogeneous than the original forests, and are characterized by remnants of the original vegetation with different shapes and sizes immersed in a matrix of transformed habitats: pastures, areas of intense agriculture, secondary vegetation, roads, and urban development, among others [2, 5, 6].

These heterogeneous mosaics may be adverse environments for many organisms, and there may be critical thresholds at which the probability of survival for populations decreases, because there is a minimum number of patches or fragments required for populations to inhabit them [6, 7, 8]. Ecological thresholds can be defined as *the points at which there is an abrupt change in the quality, in a characteristic, or in a phenomenon of the ecosystem, or where small changes in an environmental variable can produce a large response in the ecosystem* [9, 10-13]. In particular, at the landscape level, a threshold occurs when the response of a species or a group of species changes suddenly in the presence of a certain area of habitat [9, 14-16]. For example, for the Howler Monkey (*Alouatta palliata*) there are thresholds of forest fragment occupation at areas of 8 and 5 ha, and at isolation distances of 200 and 66 m, in low and highly deforested landscapes, respectively [14]. Also, there is a threshold response in species richness of woodland-dependent birds in landscapes with less than 10% habitat cover [16].

It is important to detect these thresholds when examining deforested landscapes, because often only a few habitat fragments escape human disturbance. The wild populations that persist in these degraded landscapes could have response thresholds to deforestation as a function of biological necessities that can only be met in certain environments [7, 9, 10]. Therefore, ecological thresholds can identify where and how to protect native species and their biotic interactions, a necessity in

conservation planning, for example, in selecting places to protect within a given area and determining how much even a certain disturbance in the landscape matrix will be tolerated by the species of interest [10, 12, 13, 17].

Phyllostomid bats (Chiroptera: Phyllostomidae) are trophically diverse and exploit different dimensions of the feeding niche in tropical ecosystems. They have different roles in complex ecological processes, such as preying on insects, some of which might otherwise become pests [18], and as pollinators and seed dispersers of plant species that are of economic and ecological importance [19-21]. Owing to their adaptations to the environment, some species exhibit a high degree of habitat specificity and are sensitive to anthropogenic changes in tropical ecosystems, particularly deforestation [22-30].

Although they are ecologically important and studies of these bats are increasing, there are still many aspects of their ecology that are unknown, making their conservation difficult to plan. For example, at the community level some authors report that bat species richness decreases as forests are cut down [22, 31, 32], while others state that the number of species of certain groups of bats might not be affected or might even increase in disturbed environments [33].

These variable and sometimes contradictory responses by the bat community suggest that not all species have negative response thresholds to deforestation; i.e., not all bat populations decrease in persistence at a critical ecological threshold of habitat loss [27]. Rather, there may be populations that persist regardless of the deforestation degree at the landscape level, or even populations whose abundance increases in highly deforested landscapes. For some species of frugivorous and nectarivorous phyllostomids in our study area, we predict their persistence in deforested landscapes, because some studies have reported high abundances of species of *Artibeus*, *Sturnira* and *Glossophaga* even in deforested landscapes and isolated forests [27, 34-36], although the Jamaican Fruit-eating Bat (*Artibeus jamaicensis*) and the Great Fruit-eating Bat (*Artibeus lituratus*) are more abundant in primary than in secondary forests [37]. Therefore, our objective was to detect whether there are critical points of change (ecological thresholds) in the different populations of phyllostomid bats where tropical forest is being lost, in one of the northernmost points of their current distribution. We analyzed the frequency and abundance of the populations along a continuous gradient of forest cover loss, and evaluated these response variables at different spatial scales in order to determine how populations of these organisms respond to deforested tropical landscapes.

Methods

Study area

The study was done in La Huasteca region, located in the northeastern part of the state of Hidalgo, Mexico (Fig. 1). The region covers 56.07 km² and represents 0.27 % of the state's total area. It is characterized by hills and mountain ranges with elevations from 18 to 200 m a.s.l. The soil is sedimentary in origin, sharing the structural and lithological characteristics of the Sierra Madre Oriental and Llanura Costera del Golfo Norte provinces [38]. The climate is warm and semiwarm humid with a mean annual temperature of 24 °C. The rainy season occurs from June to October, annual precipitation is 1,200 to 3,000 mm, and the dry season occurs from November to April [38, 39].

Vegetation is mainly tropical rain forest. However, human activities have considerably decreased the area of original vegetation in the region. Extensive areas have been cut due to the favorable climate for permanent irrigation-free agriculture and for animal husbandry, mainly cattle raising [40].

Study site selection

Six sampling sites were located in four of the region's municipalities (Atlapexco, Calnali, Huejutla de Reyes, and San Felipe Orizatlán), with elevations 193, 65, 113, 250, 224, and 92 m a.s.l. at sites 1 to 6, respectively. The minimum distance between sites was 10 km (Fig. 1) to ensure spatial independence and include habitat configurations representative of the study region [34-35, 41].

We evaluated the degree of deforestation of the six sampling sites at four spatial scales: a local scale and three landscape scales, as has been done in other studies [34-35, 41]. At the local scale, the percent canopy cover above each of the bat sampling nets (see following section) was measured using a spherical densiometer (Model A, Robert Lemmon Forest Densiometers, Bartlesville, OK). Four readings were taken at one end of the net, four in the middle, and four at the other end of the net for a total of 12 measurements per net. These measurements were used to calculate mean canopy cover above each net.

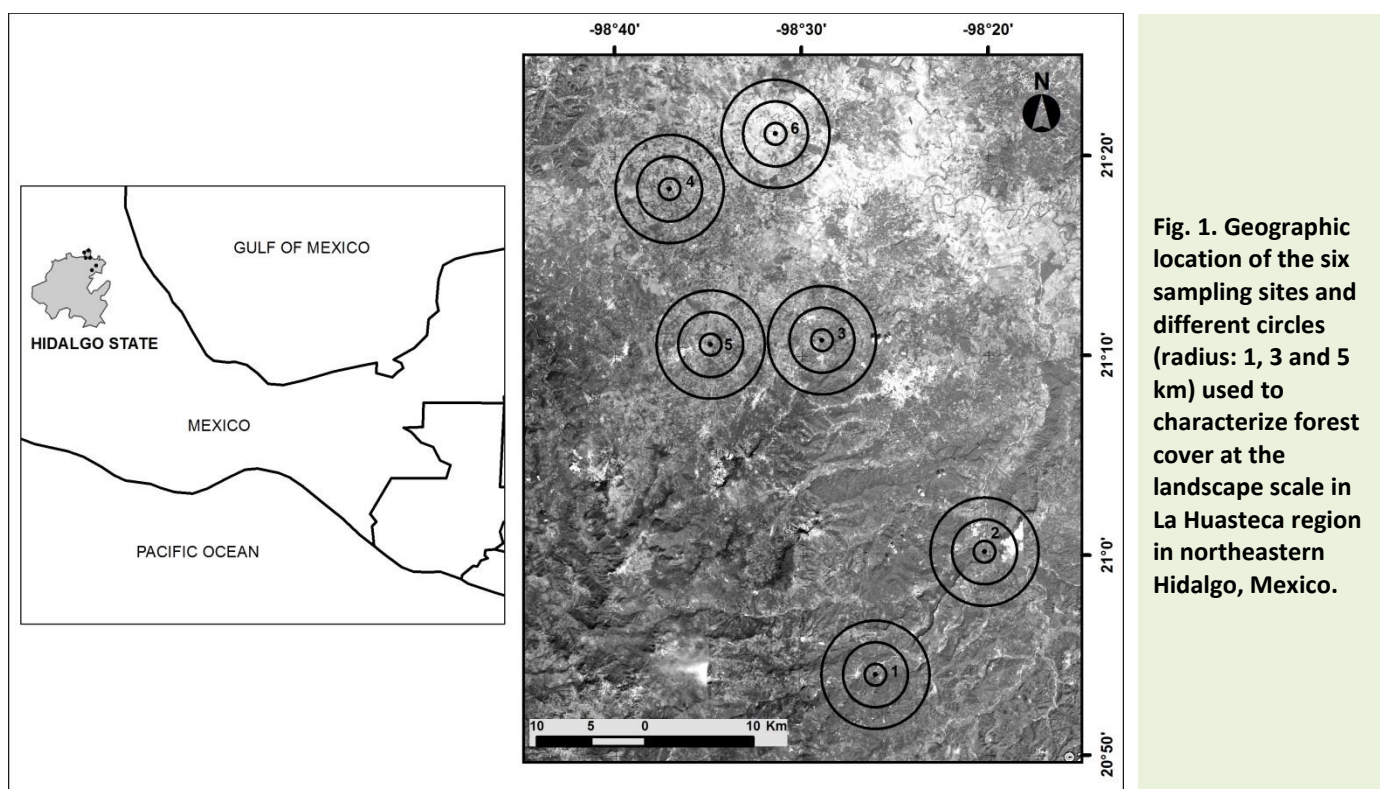


Fig. 1. Geographic location of the six sampling sites and different circles (radius: 1, 3 and 5 km) used to characterize forest cover at the landscape scale in La Huasteca region in northeastern Hidalgo, Mexico.

At the landscape level, the area covered by forest vegetation was measured at three scales using concentric circles that were 1, 3 and 5 km in radius, centered at the site where bats were sampled [41]. The size of the circles was based on previous studies done at the landscape scale and according to the likely response of bats to the habitat [34-35, 41]. Forest vegetation included continuous forest, forest remnants, secondary and riparian vegetation, clearly differentiated from

environments with no tree cover such as agricultural areas, water bodies, and urban areas. Different cover classes were digitized on satellite images with a resolution of 1 m² obtained from Google Earth for the years 2007 (site 5) and 2008 (sites 1, 2, 3, 4, and 6). Google Earth images were georeferenced using control points and digital orthophotographs from the study site (year: 1995, resolution: 2 m²). For these analyses, ArcView (version 3.2, ESRI) was used.

Forest cover varied among the six sampling sites at both the local scale and the three landscape scales, representing a gradient of deforestation (Table 1). This gradient is the result of expanding agricultural activities. Water bodies and urban areas cover only a small portion of the landscapes studied (<5% and <10%, respectively).

Bat sampling

For each of the six sites, three nights of sampling were conducted during the rainy season (from July-October 2011), and three nights during the dry season (from February-April 2012). On each sampling night, eight mist nets (12 m long x 2.5 m high) were hung at the understorey level and left open for six hours starting at dusk. Total effort for each sampling site was 240 m² of net over 36 effective sampling hours, which equals 8,640 m²·h [42]. Species were identified in the field using the key of Medellín et al. [43], and taxonomic nomenclature was based on that proposed by Ramírez-Pulido et al. [44]. Bats were captured under the authority of scientific collecting permit SGPA/DGVS/05036/11 obtained from the Ministry of the Environment (SEMARNAT), and all bats were freed where they had been caught on the same night they were captured.

Table 1. Forest vegetation remaining in the six sites where bats were sampled in La Huasteca region in the state of Hidalgo, Mexico. Canopy cover at the local scale and forest cover at the landscape scale are given including forest remnants, secondary vegetation and riparian vegetation.

| Sampling Site | Canopy cover at the local scale (%) | Forest cover at the landscape scale (%) | | |
|---------------|-------------------------------------|---|-------|-------|
| | | 1 km | 3 km | 5 km |
| Site 1 | 93.77 | 66.29 | 72.41 | 85.96 |
| Site 2 | 87.01 | 58.68 | 71.28 | 71.25 |
| Site 3 | 75.76 | 36.10 | 35.72 | 50.14 |
| Site 4 | 67.33 | 32.53 | 30.43 | 38.97 |
| Site 5 | 34.54 | 27.27 | 30.19 | 28.01 |
| Site 6 | 28.38 | 13.16 | 27.62 | 23.42 |

Data analysis

First, in order to analyze the completeness of the species inventory at each sampling site we used the Abundance-based Coverage Estimator (ACE), a nonparametric species richness estimator based on the species' abundances (45).

To detect the ecological threshold of each bat population we used the Threshold Indicator Taxa Analysis (TITAN) method [13] programmed in R [46]. The TITAN method identifies ecological thresholds or change points along continuous environmental gradients. It is based on the index of the value that each species has as an indicator (IndVal), of the relative abundances and frequencies of species [47]. Originally the IndVal index was proposed to detect the indicator species of different types of habitat selected *a priori*, with habitat a categorical variable, and a set of samples for each

type of habitat [47]. However, with the TITAN method, the habitat is considered a continuous variable (in this case, a gradient of the percent forest cover remaining).

The method begins by randomly dividing the gradient into two groups, obtaining the IndVal values for the species of each group, and continues iteratively searching other possible divisions until it encounters a separation point in the gradient where the maximum IndVal value occurs on one of the two sides of the division. The IndVal values are standardized as Z values within TITAN by subtracting the mean value from the random permutations of observed IndVal values and dividing this by the permuted standard deviation. Species can have a negative response (Z-) if they obtain the maximum IndVal value in the group on the left of the gradient (in this study, when the maximum frequency and abundance occur on sites with low forest cover, i.e., greatly deforested), or a positive response (Z+) if their maximum IndVal value occurs on the right of the gradient (maximum frequency and abundance in sites with a high percent of remaining forest cover). The dividing point on the gradient where the maximum IndVal value occurs is considered the ecological threshold for the population on the gradient analyzed and is represented by a symbol whose size is proportional to the magnitude of the response (Z value) [13].

Using bootstrap resampling techniques, TITAN calculates the percentiles (5% and 95%) of the location of the threshold along the gradient for each population, along with the purity and reliability of the threshold. Indicator purity is “the proportion of change-point response directions (positive or negative) among bootstrap replicates that agree with the observed response” [13]. A high purity value means that the species is consistently assigned to the same direction of response, independently of the abundance and frequency distributions generated by resampling the original data. Indicator reliability is “the proportion of bootstrap change points whose IndVal scores consistently result in P-values below one or more user-determined probability levels (e.g., $P \leq 0.05$)” [13]. Species with a high reliability value are those for which a high proportion of the bootstrap repetitions reach a value of $P \leq 0.05$. Based on these measures, a species can be classified as a meaningful indicator if it has IndVal values with high purity and reliability [13, 17].

Results

A total of 902 bats belonging to the Phyllostomidae family were captured, representing four subfamilies, eight genera and 11 species. According to the ACE estimator, inventory completeness was 76.98% for site 1, and 100% for all the other sampling sites. These results indicate that almost all of the species present at the different sites were recorded, but more species still could be found at site 1, which is the landscape with the highest percentage of forest cover. The best represented subfamily was Stenodermatinae with 86% of all the bats caught, and the least represented was Carollinae. The most abundant species were the Highland Yellow-shouldered Bat (*Sturnira hondurensis*) and the Jamaican Fruit-eating Bat (*Artibeus jamaicensis*), with 224 and 218 bat captures respectively, and the least abundant species were the Toltec Fruit-eating Bat (*Dermanura toltecus*) and the Western Long-tongued Bat (*Glossophaga morenoi*), the first with two bats and the second with only one. Bat abundance, given as a function of the total number of bats captured per site, varied from 80 to 338 bats for sites 6 and 1, respectively, while richness varied from 6 to 11 species for sites 3 and 2, respectively. All the species captured and their abundances are given in Table 2, but only the populations of the eight most abundant bat species (with 10 or more bats) were included in the analyses.

Threshold detection at the local scale

Most of the bat populations showed a positive response (Z+) to the percentage of canopy cover above the mist nets (the finest scale in spatial terms; Fig. 2A, Table 3). For example, *Artibeus jamaicensis* showed a positive response with a change point (threshold) at 53.64% canopy cover and its IndVal was 66.76% (purity=0.98, reliability=0.93, Table 3). This means that the highest indicator value for this species, based on its relative frequency and abundance, occurred when canopy cover above the nets was greater than 53.64%. Only two of the populations (the Pallas's Long-tongued Bat *Glossophaga soricina* and the Common Vampire Bat *Desmodus rotundus*) had a negative response (Z-); that is, their highest IndVal values occurred in sites with scarce canopy cover. *D. rotundus* had the lowest canopy cover threshold (31%). This means that the frequency of capture and abundance of this species were greater in nets placed where the canopy cover was less than 31%. However, for the *D. rotundus* population, purity and reliability for the threshold detected were low (Table 3), indicating this result should be taken with caution.

Table 2. List of phyllostomid bat species, total number of individuals per species and abundance and richness recorded at each sampling site in La Huasteca region in the state of Hidalgo, Mexico.

| Species | Site | | | | | | Total number of bats |
|--|------------|------------|------------|------------|------------|-----------|----------------------|
| | 1 | 2 | 3 | 4 | 5 | 6 | |
| <i>Sturnira hondurensis</i> (Highland Yellow-shouldered Bat) | 83 | 42 | 25 | 26 | 36 | 12 | 224 |
| <i>Artibeus jamaicensis</i> (Jamaican Fruit-eating Bat) | 106 | 24 | 26 | 35 | 14 | 13 | 218 |
| <i>Sturnira parvidens</i> (Little Yellow-shouldered Bat) | 55 | 22 | 40 | 24 | 25 | 8 | 174 |
| <i>Artibeus lituratus</i> (Great Fruit-eating Bat) | 67 | 21 | 7 | 21 | 13 | 20 | 149 |
| <i>Glossophaga soricina</i> (Pallas's Long-tongued Bat) | 9 | 7 | 3 | 5 | 9 | 21 | 54 |
| <i>Desmodus rotundus</i> (Common Vampire Bat) | 12 | 2 | 5 | 12 | 20 | 0 | 51 |
| <i>Leptonycteris yerbabuenae</i> (Lesser Long-nosed Bat) | 1 | 1 | 0 | 7 | 0 | 5 | 14 |
| <i>Chiroderma salvini</i> (Salvin's Big-eyed Bat) | 5 | 3 | 0 | 0 | 2 | 1 | 11 |
| <i>Carollia perspicillata</i> (Seba's Short-tailed Bat) | 0 | 4 | 0 | 0 | 0 | 0 | 4 |
| <i>Dermanura toltecus</i> (Toltec Fruit-eating Bat) | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| <i>Glossophaga morenoi</i> (Western Long-tongued Bat) | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| Total abundance | 338 | 129 | 106 | 130 | 119 | 80 | 902 |
| Total richness | 8 | 11 | 6 | 7 | 7 | 7 | |

Threshold detection at the landscape scale

When the landscape was analyzed at the 1 km radius scale, four species (*Artibeus jamaicensis*, the Little Yellow-shouldered Bat *Sturnira parvidens*, *Glossophaga soricina*, and *Desmodus rotundus*) showed a positive response (Z+) to the presence of forest cover, while four other species (the Lesser Long-nosed Bat *Leptonycteris yerbabuenae*, *Sturnira hondurensis*, the Great Fruit-eating Bat *Artibeus lituratus*, and the Salvin's Big-eyed Bat *Chiroderma salvini*) showed a negative response (Z-; Fig. 2B, Table 3). Populations with a positive response were observed to require at least 30% forest cover to maintain a high IndVal value, while populations with negative responses had a higher IndVal when there was 20 – 40 % forest cover (Fig. 2B, Table 3).

When analyzing the landscape at the 3 km radius scale, the same response as those for the 1 km radius analysis were observed for all eight species (Fig. 2C). However, the change points were notably different, given that on the 3-km-radius landscapes most of the positive indicator populations had high IndVal values when the threshold was around 70% forest cover, and only one had a threshold of 30%. Negative indicator populations maintained high IndVal values when there was 20-40% tree cover (Fig. 2C, Table 3).

For the landscape delimited by a 5 km radius, only three of the phyllostomid populations (*Artibeus jamaicensis*, *Artibeus lituratus* and *Desmodus rotundus*) showed a positive response (Z+) to forest cover, but their purity and reliability were very low, especially for *A. lituratus*. The other five populations (*Sturnira parvidens*, *Leptonycteris yerbabuenae*, *Glossophaga soricina*, *Sturnira hondurensis* and *Chiroderma salvini*) showed a negative response (Fig. 2D, Table 3).

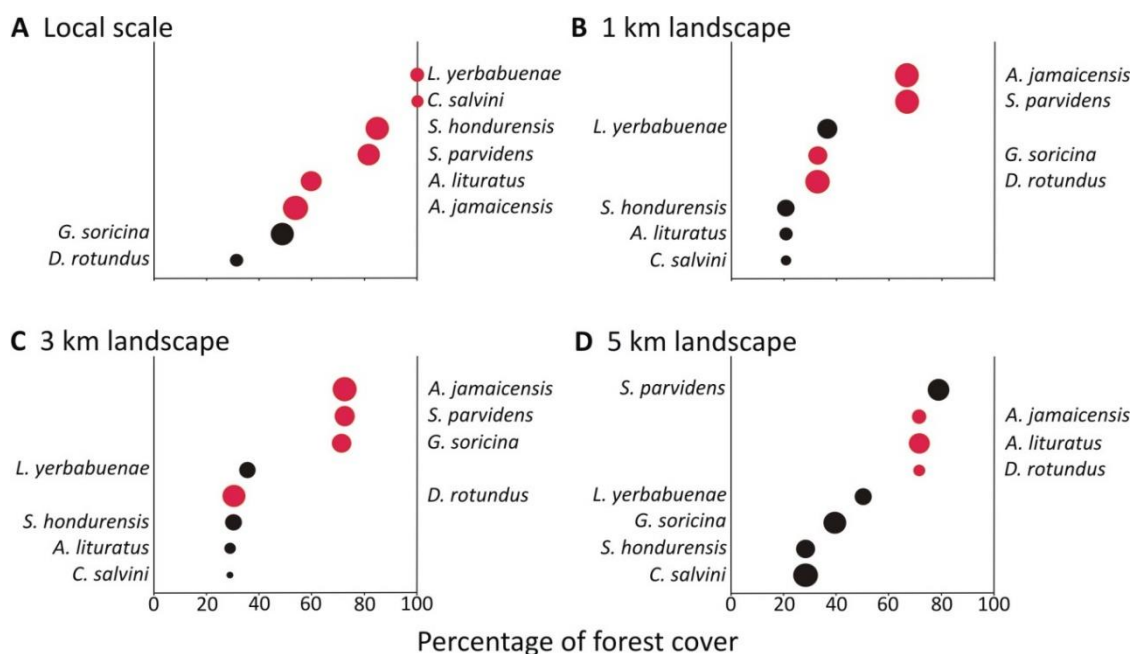


Fig. 2. TITAN analysis of the phyllostomid bat populations at the local scale (a) and at the landscape scale in areas with a radius of 1 km (b), 3 km (c), and 5 km (d), in which the abrupt points of change in the environmental gradient are shown. Black symbols represent negative indicator populations (Z-) and red symbols, the positive ones (Z+). Symbol size is proportional to the magnitude of the response (Z value).

Table 3. Type of response (positive or negative) to percent forest cover and Z values for phyllostomid bats at the local and landscape scales (radius: 1, 3 and 5 km) in La Huasteca region of the state of Hidalgo, México.

| Species | Local Scale | | Landscape scale | | | | | |
|---|-------------|------|-----------------|------|----------|------|----------|------|
| | | | 1 km | | 3 km | | 5 km | |
| | Response | Z | Response | Z | Response | Z | Response | Z |
| <i>Leptonycteris yerbabuenae</i> (Lesser Long-nosed Bat) | + | 1.03 | - | 1.15 | - | 0.89 | - | 1.08 |
| <i>Chiroderma salvini</i> (Salvin's Big-eyed Bat) | + | 0.82 | - | 0.27 | - | 0.11 | - | 2.25 |
| <i>Sturnira hondurensis</i> (Highland Yellow- shouldered Bat) | + | 3.17 | - | 0.9 | - | 0.93 | - | 1.25 |
| <i>Sturnira parvidens</i> (Little Yellow-shouldered Bat) | + | 2.78 | + | 1.81 | + | 1.5 | - | 1.66 |
| <i>Artibeus lituratus</i> (Great Fruit-eating Bat) | + | 2.37 | - | 0.51 | - | 0.41 | + | 1.61 |
| <i>Artibeus jamaicensis</i> (Jamaican Fruit-eating Bat) | + | 3.42 | + | 1.87 | + | 2.16 | + | 0.77 |
| <i>Glossophaga soricina</i> (Pallas's Long-tongued Bat) | - | 2.89 | + | 1.03 | + | 1.29 | - | 1.96 |
| <i>Desmodus rotundus</i> (Common Vampire Bat) | - | 0.91 | + | 1.85 | + | 1.88 | + | 0.45 |

(-) Negative response: species whose frequency and abundance (IndVal value) are greater in sites with less forest cover
 (+) Positive response: species whose frequency and abundance (IndVal value) are greater in sites with a high degree of forest cover.

General patterns as a function of bat's threshold responses at different spatial scales

In general, there were three types of threshold responses by the bat populations to deforestation in the study area:

(1) The populations of *Leptonycteris yerbabuenae*, *Chiroderma salvini*, *Sturnira hondurensis*, and *Artibeus lituratus* were frequent and abundant in sites that locally have a high percentage of canopy cover, even though the landscape has been deforested. That is to say, these species showed a positive response at the local scale (the finest scale in spatial terms), and a negative response at the landscape scale (though the response of *A. lituratus* at the 5 km scale was positive, purity and reliability were very low).

(2) The populations of *Sturnira parvidens* and *Artibeus jamaicensis* showed a positive response to tree cover at all scales (except *S. parvidens* at 5 km, though perhaps this scale is rather large for such a small species). At the local scale, the smallest species (*S. parvidens*) was more sensitive to deforestation, with its change point (threshold) at 81.63% tree cover. The threshold for the largest species (*A. jamaicensis*) was 53.64% cover, but at the 1 and 3 km landscape scales its responses were identical (threshold: 66.29 and 72.42%, respectively). That is, in the study region the relative frequencies and abundances of these species decrease significantly when tree cover falls below these values.

(3) *Glossophaga soricina* and *Desmodus rotundus* are species that are frequent and abundant in sites with little canopy cover at the local scale, but their response is positive at the landscape scales (except for *G. soricina*, which had a negative response at the 5 km scale, although like *S. parvidens* one would not expect its area of activity to be very large because of its small size). This suggests that these species require landscapes on which a high percentage of the original forest cover has been preserved.

Discussion

Our results suggest that the response of phyllostomid bats to the loss of tropical forest cover in Hidalgo's La Huasteca region varies with species and the scale of observation. Some studies that focused on the community level of tropical bats suggested that the effects of habitat loss depend on the specific traits of each species [27]. On one hand some studies report that habitat fragmentation has a negative effect on the abundance of some phyllostomid species [21, 27, 33, 37], and on the other hand, some studies report that different species appear to be less sensitive, or simply are not affected by habitat loss [27, 34-36, 48]. Our results confirm that the responses of populations can be negative or positive along a deforestation gradient.

Of the eight species studied, only *Sturnira parvidens* and *Artibeus jamaicensis* had the same response at all four scales. This contradicts the findings of Galindo-González [24] who classified *A. jamaicensis* as an adaptable species that tolerates the transformation of the environment and perhaps even benefits from fragmentation, since it uses both forests and transformed environments. At least in La Huasteca region, we found that the frequency of occurrence and the abundance of this species were significantly higher in sites with greater forest cover. These results coincide with those of studies showing that *A. jamaicensis* is more abundant in old-growth forest than in secondary vegetation [26], and also more abundant in rain forests than in managed and non-managed secondary forests [37]. However, as the basic diet of *A. jamaicensis* is *Ficus* fruit [49], which has a big-bang reproductive strategy [50], their response to landscape deforestation may be biased by the presence of fruiting *Ficus* trees. For further studies we therefore suggest an assessment of resource availability at the landscape level.

For the other six species, the response of abundance and frequency to deforestation varied depending on the spatial scale used to evaluate the landscape, similar to reports of bat communities in South America [34-35, 41]. Other studies have also reported that the same species can show different thresholds in different landscapes [10, 14]. This could be the result of factors such as the life history traits of the species, and the quality, spatial layout or degree of habitat isolation [15]. Two recent studies at the landscape scale using radio-telemetry have shown that frugivorous phyllostomids use restored areas, exotic forest plantations, early successional forest remnants, and anthropogenic land uses as feeding habitats and for commuting, but they strongly rely on forest fragments for day roosting, because they roost in the foliage of trees [30, 51].

Desmodus rotundus was more abundant and frequent in open areas due largely to its feeding habits, since it is a hematophage. Greater numbers of vampire bats have been recorded in sites with riparian vegetation, which offers more food such as chickens and small mammals that are very active in this type of habitat [32]. Additionally, it is important to note that although *Desmodus rotundus*

has a very specialized feeding habit, it is considerably adaptable to anthropogenic transformation [23], given that its main source of food is cattle.

Glossophaga soricina is a nectarivorous bat that was more abundant and frequent in open areas at the local and 5 km scales, contrary to reports from earlier studies [35, 41]. The thresholds of *G. soricina* lie between 30-70% tree cover, indicating its adaptability. Some bats have been seen visiting primary and secondary vegetation during their foraging flights, flying between the different elements of the landscape, including cattle pastures and the edges of riparian vegetation where there are plant species that offer refuge, shade, and food resources [52, 53]. Other studies have documented their presence in large fragments of artificial forests and heterogeneous landscapes modified by humans (forest fragments and several types of agroecosystems) in other Neotropical sites [54-56].

Our results reject the possibility that the responses obtained could be homogeneous by trophic guild, because the responses of both nectarivorous (*Leptonycteris yerbabuenae* and *Glossophaga soricina*) and frugivorous species were species specific. Even within a trophic guild, each species responds in a very different way to habitat characteristics, depending on its capacity to use the different resources available [57]. For example, some species may rely exclusively on forest plants, but others feed on plants that may also be found in disturbed areas. There are therefore several intrinsic and extrinsic factors determining the dietary specialization of nectarivorous [58] and frugivorous bats species [49].

Estimating the species threshold for each population using TITAN is useful for determining how organisms respond to an environmental gradient. The response to any environmental change probably differs for various gradients, or depending on the specific life history of each population. Discerning between positive and negative response patterns makes sense from a broad conservation perspective; there are few reasons to expect that all of the populations in a community will respond to environmental disturbance in the same way or at the same level [13]. The TITAN method would, however, perform better with a greater number of sampling points along the gradient. Although we had six points that covered a good part of the values along the gradient (from around 20% to 80% tree cover), in our study region there were no sites with values below 20% or as high as 95% tree cover. Increasing the number of landscape units throughout the landscape along the gradient, perhaps with replicates of the different percent covers, would confirm our results in greater detail.

Another important point that deserves further analysis, is the inclusion of different spatial scales to study bat responses. We followed previous studies using three concentric circles of 1, 3 and 5 km in radius [34-35, 41], which may facilitate comparisons on scale-dependent associations of bats with landscape structure. These scales were selected according to the likely response of bats to the habitat. For example, the smallest scale was selected to encompass the expected home range of smaller bat species such as *Glossophaga soricina* [34]. However, different landscape scales may not be equally relevant to different species. A recent study [51] describes an average range of 124.4 ha and an average commuting distance of 1,158.8 m for *Artibeus lituratus*, which is the biggest bat in our study site. Our biggest scale may therefore be irrelevant for some of the species because they would never go that far.

In terms of conservation, observations over recent years have revealed that protected natural areas are generally not enough to conserve the majority of the biodiversity present. Outside of these areas, native species continue living in habitats that, while subject to production activities by humans, maintain the basic structure and functions of their original ecosystems [56]. For example, owing to their role in seed dispersal, frugivorous bat species are of great importance in maintaining different levels of biodiversity in ecosystems, and any negative impact on their populations could affect the regeneration of tree cover in deforested landscapes [19, 60, 61].

One thing that stands out from the results of this study is the importance of tree cover at different scales. At the local scale, sites with more than 50% tree canopy are required to maintain the abundance and frequency of the two species of *Artibeus* that eat large fruits such as the nightshade *Solanum hirtum*, the Trumpet Tree *Cecropia peltata*, the Walking Lady *Vitex gaumeri*, the candletree or cuachilote *Parmentiera edulis*, and two amate species *Ficus máxima* and *Ficus obtusifolia* [20, 61-63]. A closed tree canopy with more than 80% cover is required to maintain the abundance and frequency of *Sturnira* species, which eat small fruit such as those of the genera *Solanum*, *Piper* and *Clidemia* [20, 64, 65], and also maintain the species *Chiroderma salvini* and *Leptonicteris yerbabuena*. At the landscape scale, populations of *Artibeus jamaicensis* and *Sturnira parvidens* continue to be abundant and frequent in landscapes where treed habitats cover more than 65% of the landscape, while *Glossophaga soricina* will be abundant and frequent in landscapes where there is more than 70% arboreal cover (scale: 3 km).

Implications for conservation

Acknowledging the existence of threshold responses in bat populations along a disturbance gradient can be extremely useful for establishing the point to which a system can be modified (as measured in a quantitative manner, with tree cover) without setting off a response which once started, might be very difficult to reverse, and may have a negative effect on the processes that maintain the biodiversity of systems.

Our suggestions for the conservation of this group of bats, and to improve the methods used to study them include: 1) aim for the prevalence of tree cover between 50 and 80% in heterogeneous landscapes, 2) promote the conservation of treed and riparian corridors, 3) increase connectivity among pastures with living fences and isolated standing trees, and 4) include more landscapes with a broader range of forest cover percentages, measured at different scales, designing field studies to test for the effects of landscape composition and configuration.

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