Structure and diversity of phyllostomid bat assemblages on riparian corridors in a human-dominated tropical landscape

Erika de la Peña-Cuéllar¹, Julieta Benítez-Malvido¹, Luis Daniel Avila-Caballero², Miguel Martínez-Ramos¹ & Alejandro Estrada³

¹Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, Michoacán, México
²Escuela Nacional de Estudios Superiores, Universidad Nacional Autónoma de México, Morelia, Michoacán, México
³Estación de Biología Tropical “Los Tuxtlas”, Instituto de Biología, Universidad Nacional Autónoma de México, Morelia, Michoacán, México

Keywords
Agricultural matrix, corridors, diversity, frugivores, indicator taxa.

Abstract
Tropical forests around the world have been lost, mainly because of agricultural activities. Linear elements like riparian vegetation in fragmented tropical landscapes help maintain the native flora and fauna. Information about the role of riparian corridors as a reservoir of bat species, however, is scanty. We assessed the value of riparian corridors on the conservation of phyllostomid bat assemblage in an agricultural landscape of southern Mexico. For 2 years (2011–2013), mist-netting at ground level was carried out twice during the dry season (December to May) and twice during the wet season (June to November) in different habitats: (1) riparian corridors in mature forest, (2) riparian corridors in pasture, (3) continuous forest away from riparian vegetation, and (4) open pastures. Each habitat was replicated three times. To determine the influence of vegetation structure on bat assemblages, all trees (≥10 cm dbh) were sampled in all habitats. Overall, 1752 individuals belonging to 28 species of Phyllostomidae were captured with Sternotherus being the most rich and abundant subfamily. Riparian corridors in mature forest and pastures had the greatest species richness and shared 65% of all species. Open pastures had the lowest richness and abundance of bats with no Phyllostominae species recorded. Six of the 18 species recorded could be considered as habitat indicators. There was a positive relationship between bat species composition and tree basal area. Our findings suggest that contrary to our expectations, bats with generalist habits and naturally abundant could be useful detector taxa of habitat modification, rather than bats strongly associated with undisturbed forest. Also in human-dominated landscapes, the maintenance of habitat elements such as large trees in riparian corridors can serve as reservoirs for bat species, especially for those that are strongly associated with undisturbed forest.

Introduction
Habitat loss and fragmentation are considered the most serious threats to biodiversity and the main cause of the current extinction crisis (Laurance and Bierregaard 1997). In tropical regions, many biodiversity hot spots have been converted to agricultural lands (Myers et al. 2000; Achard et al. 2002). In many of these landscapes, the presence of vegetation along streams is a common feature and is relatively resistant to agricultural practices and small-scale land use changes (Lundy and Montgomery 2010). Riparian habitats provide some of the most diverse and complex terrestrial habitats (Naiman et al. 1993). Especially, in fragmented landscapes, riparian vegetation contrasts with adjacent grassland areas as it provides the following landscape elements for the native biota: habitat for many species, corridors for flying and terrestrial animals, connectivity between forest fragments and for fostering network dispersion (Naiman et al. 2000; Estrada and Coates-Estrada 2001). In particular, bird species composition and density differ considerably between riparian vegetation and the surrounding agricultural matrix (Warkentin et al. 1995; Seaman and Schulze 2010). Similarly, bats use riparian vegetation as flyways during foraging activities, reducing the distance that they need to travel from and to their refuges (Daniel et al. 2008).
Intensification of agricultural practices in the tropics is likely to threaten the persistence of some bat species; nonetheless, the presence of landscape elements like live fences, isolated trees, and riparian vegetation disrupts the homogeneity of pastures and has been shown to be important in the maintenance of bat diversity (Harvey et al. 2006; Griscom et al. 2007; Medina et al. 2007). Riparian habitats provide flyways and foraging areas for bats, serving as stepping stones to isolated patches of primary vegetation. In addition, riparian zones offer important sources of water and food for bats (Estrada and Coates-Estrada 2001; Galindo-González and Sosa 2003).

Bats are widely studied because they play a crucial role in the ecosystem functioning as pollinators, seed dispersal agents and controllers of invertebrate and small vertebrate populations (Muscarella and Fleming 2007; Kalka et al. 2008; Kunz et al. 2011). Particularly in the Neotropics, bats are considered an important component of mammal biodiversity accounting for over 50% of the species (Medellín 1994). The response of bats to habitat loss in the Neotropics is ambiguous, compared to the Stenodermatinae (frugivore bats), and the Phyllostominae bats are very sensitive to disturbance and tend to decrease in degraded and fragmented habitats because of their limited range sizes, specialized resource needs (food and roosting), and because of their avoidance of open pastures (Kalko et al. 1999; Medellín et al. 2000; Schulze et al. 2000; Castro-Luna et al. 2007a; de la Peña-Cuéllar et al. 2012; García-Morales et al. 2013). We selected the Phylllostomidae family because it is the most species rich and functionally diverse bat family in the Neotropics. Furthermore, because of the broad spectrum of biological interactions in which they are involved, phyllostomids have been recognized as useful indicators of habitat quality (Fenton et al. 1992; Medellín et al. 2000; Jones et al. 2009).

In human-impacted landscapes, information about the importance of riparian vegetation in maintaining bat species diversity is crucial for understanding bat behavioral and ecological flexibility. In this framework, we recorded the richness and abundance of phyllostomid bats present in different habitat types within an agricultural matrix to determine the following: (1) bat assemblages attributes (i.e., species composition and species density) in riparian and nonriparian habitats; (2) the extent to which the structural complexity of the vegetation explains bat species composition; and (3) the distribution of species, genera and subfamilies in the different habitats in order to identify indicator taxa.

**Methods**

**Study area and sampling sites**

The study was conducted in the tropical rain forest region of Lacandona, Chiapas, Mexico. The original vegetation consists of semideciduous and lowland tropical rain forests. Mean annual temperature is 24°C, and average annual rainfall is 3000 mm with June to October as the wettest months (551 mm per month) and February to April as the driest months (<100 mm per month) (Breugel et al. 2006; CFE 2006). Deforestation of the region began in the 1970s, resulting in the reduction of closed forest from 95% in 1976 to 56% in 1996 (de Jong et al. 2000); only 36% of closed forest remains today (Carabias et al. 2008). The main practices of the region consist of grazing pastures, maize and other crops, and patches of secondary and old-growth forests (de Jong et al. 2000).

We sampled four different habitats: (1) riparian sites within mature continuous forest (RM); (2) riparian sites in open pastures (RP); (3) mature continuous forest away from riparian vegetation (MF); and (4) open pastures (P). Each habitat type was replicated three times, and sites were at least 1.5 km away from each other. Streams were all permanent (although with variable amounts of running water throughout the year); stream width varied from two to eight meters. Study sites in pastures were located in the fragmented landscape of the Marqués de Comillas municipality, on the south side of the Lacantún River. Mature continuous forest sites were located in the 330,000 ha Montes Azules Biosphere Reserve (MABR) on the north side of the river (16°04′N–90°45′ W; Fig. 1) (INE 2000).

**Bat and vegetation sampling**

Bat sampling was performed twice during the dry season (December to May) and two times during the wet season (June to November) for three consecutive years (2011, 2012, and 2013). Eighteen nights were sampled at RM, RP, and P habitats, and sixteen nights were sampled at the MF habitat. Bats were surveyed at all sites using the same standardized method. Five nets (12 m long × 2.6 m high) were set at ground level and were opened at dusk for four consecutive hours, which corresponds to the peak foraging time for most phyllostomid species (La Val 1970). The nets were arranged following three configurations located roughly 50 m apart: (1) one individual net and two pairs of nets were placed in the “L” position (two nets connected perpendicularly); (2) in the riparian habitats nets were located parallel and diagonally across the stream depending on site characteristics, in the MF habitat nets were placed in natural corridors that represented flyways for bats; and 3) in P, nets were located in open spaces devoid of vegetation. Bat sampling avoids nights with a full moon or heavy rain (Morrison 1978). Captured individuals were temporarily stored in cloth bags and identified to species following Medellín et al. (2011). We used Koopman’s classification (1993) for bat
families, subfamilies and genera. For species and feeding guilds, we followed Timm and La Val (1998) classification (i.e., aerial insectivores, carnivores, gleaning insectivores, frugivores, nectarivores, and sanguivores).

Tree sampling was carried out once at each habitat to determine the influence of vegetation structure on bat assemblages; we recorded all trees ≥10 cm dbh within a 0.1 ha (20 × 50 m) plot (Gentry 1982). Plots were located along streams in RM and RP habitats and randomly located in MF and P habitats. We considered the following vegetation attributes: number of individuals (NI), number of species (NS), total basal area (BA), and height (H).

Statistical analyses

Bat sampling completeness

We assessed the completeness of the bat survey by calculating the percentage of estimated species richness that was effectively covered by our samples. To ensure a good representation of bat richness, species richness was estimated by computing the average of the following indices: ICE, Chao2 and Bootstrap (Colwell et al. 2004). Ninety percent of completeness was considered to be a satisfactory level of sampling efficiency (Moreno and Halffter 2001).

We used a Mantel test with 999 permutations to determine whether bat assemblages closer together were more similar than those farther apart (Mantel 1967). We computed the correlation between the matrix representing the Euclidean distance among sites (represented in UTM units) and the matrix of Bray–Curtis indices representing ecological distances. These analyses were performed in R (R Development Core Team 2009) with the vegan package (Oksanen et al. 2011).

Bat assemblages

We built rank-abundance (dominance-diversity) plots for each habitat; these graphs have been suggested as an alternative to diversity indexes when comparing communities in different habitats (Feinsinger 2001). Individual-based rarefaction curves were constructed to compare species richness among habitats (EstimateS software, version 7.5, Copyright R. K. Colwell: http://viceroy.eeb.uconn.edu/estimates). The 95% confidence intervals of the moment-based estimator for species richness (sobs Mao Tau) were used to determine significant differences among habitats (Colwell et al. 2004).

To evaluate dissimilarity patterns among phyllostomid assemblages we used nonmetric multidimensional scaling (NMDS) based on Bray–Curtis similarity. The NMDS is one of the most appropriate ordination methods in community ecology (McCune and Grace 2002) as it can properly handle nonlinear species responses (Oksanen 2010), high beta-diversity and data not adjusted to a particular underlying model (i.e., multivariate normality), which are common in community dataset (McCune and Grace 2002). We used the stress value to evaluate the ordination. Low stress values indicate that the distances between objects in space ordination are similar to the distances between objects in the original space, defined by

Figure 1. Study area and bat sampling sites at the Lacandona forest, Chiapas, Mexico.
n-dimensions (in this case, the species considered in the matrix). The lower the stress value, the more reliable the results achieved by the ordination.

**Phyllostomid bats as indicator taxa**

We evaluated if phyllostomid taxa (subfamily, genus and species) were associated with particular habitats, and therefore considered as indicators of such habitats. Indicator taxa are characteristic of a particular habitat whereas detector taxa exhibit different degrees of preferences for different habitat types and consequently are useful in indicating habitat change. For this purpose, we performed the “indicator value analysis” (Dufrene and Legendre 1997). This method assigns an indicator value (IV) to each taxon, in each habitat, based on the taxon’s relative frequency of occurrence (fidelity) and relative abundance (specificity). We then selected the maximum IV (IVmax) for each taxon and identified the corresponding habitat. The IVmax statistical significance was evaluated through a Monte Carlo test based on 1000 iterations. Following Castro-Luna et al. (2007b), and Avila-Caballila (2011), we considered as detectors all taxa with an IVmax ≥ 0.5 and considered as indicators those taxa in which IVmax was statistically significant. These analyses were carried out in the R package labdsv, version 1.4-1.

**Phyllostomids and site attributes**

We examined correlations between phyllostomid response (abundance, species composition) and all the explanatory variables (season, habitat and tree basal area) using a generalized linear mixed model (GLMM). The GLMM is an extension of generalized linear models (GLMs) that include both fixed and random effects. In our models, we considered as fixed effects the season, habitat and tree basal area and as a random effect the sampling nights. In this way, we are accounting for the correlation structure caused by repeated sampling night on the same sites. For each model, we calculated Akaike’s information criterion corrected for small sample size (AICc) following Burnham and Anderson (2002). This approach allowed us to select the most plausible models from a set of models. The set of models considered for every response variable, at each scale, included the null model (without explanatory power) and other models that considered each explanatory variable independently. We compared the model using Δw, which is the difference of AICc between a given model and the best (lowest AICc) model. We also calculated the AIC weights (wi) for each model. The wi represents the weight of the evidence that a certain model is the best model given the data and the set of candidate models. The 95% confidence set of the best models was defined by summing the wi, from the largest to the smallest, until the sum is = 0.95. Only models with an AICc lower than the null model were considered to define the 95% confidence set of plausible models. All previous analyses were performed with R program (R Development Core Team 2009).

**Results**

We completed 70 nights of capture effort, 34 during the dry season, and 36 during the rainy season, resulting in a total capture effort of 180 net hours in RM, RP, and P, and 140 net hours in MF habitats. Overall, 1752 individuals belonging to 28 species of Phyllostomidae were captured. The Stenodermatinae was the richest and most abundant subfamily with 16 species (57.1% of all species) and 1598 individuals (91.2% of all captures). The completeness values were above 85% for all habitats, which is considered appropriate to characterize the phyllostomid bat assemblages (Table 1).

The individual-based rarefaction curves (Fig. 2) showed that we sampled all species occurring in RM and RP habitats. Captures in all habitats were dominated by five species: *Sturnira lilium* (30.1%), *Artibeus lituratus* (22.9%), *A. jamaicensis* (11.4%), *Uroderma bilobatum* (9.6%), and *Glossophaga soricina* (6.1%), which together represented 80.4% of all captures (Fig. 2). Bat composition did not show a significant spatial correlation according to the Mantel test ($R = 0.057$, $P = 0.27$).

**Bat assemblages and guilds**

Species richness declined from 23 species in RM, to 21 in RP, to 20 in MF and 14 species in P, resulting in a total of 28 species (Fig. 3). Habitats shared 10 species. The RM habitat presented three exclusive species; in addition, the RP had two exclusive species and the MF one exclusive species, while open pastures had none. Species of the subfamily Phyllostominae were absent from open pastures (Table 1).

Frugivores accounted for the greatest percentage of both captured species and individuals (59.2% of species and 90.3% of individuals), followed by gleaning insectivores (18.5% of species and 0.7% of individuals) and nectarivores (11.1% of species and 7.7% of individuals). Sanguivores were represented by *Desmodus rotundus* with 11 individuals and *Diphylla ecaudata* with two individuals; in addition, carnivores were represented only by *Trachos cirrhosus* (Table 1). The number of bat guilds per habitat type declined from five in the RM and the MF, to four in RP, and three guilds in P (Fig. 4).
Bats as indicator taxa

Six of the 18 species recorded could be considered as habitat indicators (Table 2). The subfamilies Glossophaginae and Stenodermatinae were tightly associated with RP; however, at the genus level Glossophaga was mostly associated with MF, and Sturnira was tightly associated with RP.

We identified twice as many detector taxa as indicator taxa (Table 2). The subfamily Desmodontinae was associated with RP. We found Lonchorhina and Vampyrodes were associated with RM, and Mimon, Platyrhinus and Uroderma were associated with RP. Finally, most of the detector species were associated with RP (Carollia perspicillata, Mimon crenulatum, Platyrhinus helleri, and U. bilobatum), and only two species were

Table 1. Number of bats captured by species in different habitat types at Lacandona, Chiapas, Mexico. Bat guilds are as follows: F, frugivores; GI, gleaning insectivores; N, nectarivores; C, carnivores; and S, sanguivores.

| FAMILY          | Subfamily | Species                  | Guild | Habitats        | Riparian mature (RM) | Riparian pasture (RP) | Mature forest (MF) | Pasture (P) | Total |
|-----------------|-----------|--------------------------|-------|-----------------|----------------------|----------------------|-------------------|-------------|-------|
| PHYLLOSTOMIDAE  | Carolliinae| Carollia perspicillata   | F{s}  | 20 (1.11)       | 34 (1.8)             | 5 (0.31)             | 1 (0.05)          | 60          |
|                 |           | Carollia sowelli         | F{s}  | 9 (0.5)         | 6 (0.33)             | 8 (0.5)              | 2 (0.11)          | 25          |
| Desmodontinae   |           | Desmodus rotundus        | S     | 1 (0.05)        | 8 (0.44)             | 1 (0.06)             | 4 (0.22)          | 14          |
|                 |           | Diphylla ecaudata        | S     | 0               | 1 (0.05)             | 1 (0.06)             | 0                | 2           |
| Glossophaginae  |           | Glossophaga soricina     | N     | 6 (0.33)        | 80 (4.44)            | 2 (0.12)             | 20 (1.11)         | 108         |
|                 |           | Hylonycteris puseo      | N     | 0               | 0                    | 1 (0.06)             | 0                | 1           |
|                 |           | Lichonycteris obscura    | N     | 1 (0.07)        | 0                    | 0                   | 0                | 1           |
| Phylostominae   |           | Lamproonycteris brachyotis| GI{n}| 1 (0.05)       | 0                    | 0                   | 0                | 1           |
|                 |           | Lonchorhina aurita      | GI{n} | 2 (0.11)       | 0                    | 0                   | 0                | 2           |
|                 |           | Mimon crenulatum        | GI{n} | 0               | 7 (0.38)             | 0                   | 0                | 7           |
|                 |           | Phyllostomus discolor   | GI{n} | 0               | 1 (0.05)             | 0                   | 0                | 1           |
|                 |           | Trachops cirrhosus      | C{n}  | 2 (0.11)        | 0                    | 1 (0.06)             | 0                | 3           |
|                 |           | Tonatia sauraphia      | GI{n} | 3 (0.16)        | 2 (0.11)             | 0                   | 0                | 8           |
| Stenodermatinae |           | Artibeus jamacicensis  | F{n}  | 72 (4)          | 59 (3.27)            | 41 (2.56)            | 29 (1.61)         | 201         |
|                 |           | Artibeus lituratus      | F{n}  | 113 (6.27)      | 190 (10.55)          | 25 (1.56)            | 74 (4.11)         | 402         |
|                 |           | Artibeus phaeotis       | F{n}  | 8 (0.44)        | 11 (0.61)            | 0                   | 6 (0.33)          | 25          |
|                 |           | Artibeus tolteos       | F{n}  | 1 (0.05)        | 0                    | 2 (0.12)             | 0                | 3           |
|                 |           | Artibeus watsoni       | F{n}  | 3 (0.16)        | 8 (0.44)             | 4 (0.25)             | 1 (0.05)          | 16          |
|                 |           | Centurio senex         | F{n}  | 1 (0.05)        | 1 (0.05)             | 2 (0.12)             | 1 (0.05)          | 5           |
|                 |           | Chiroderma salvini     | F{n}  | 2 (0.11)        | 3 (0.16)             | 2 (0.12)             | 1 (0.05)          | 8           |
|                 |           | Chiroderma villasum    | F{n}  | 0               | 3 (0.16)             | 1 (0.06)             | 0                | 4           |
|                 |           | Platyrhinus helleri    | F{n}  | 24 (1.33)       | 47 (2.61)            | 2 (0.12)             | 9 (0.5)           | 82          |
|                 |           | Stumira ilium          | F{s}  | 68 (3.77)       | 315 (17.5)           | 27 (1.68)            | 119 (6.61)        | 529         |
|                 |           | Stumira ludovici       | F{s}  | 1 (0.05)        | 1 (0.05)             | 0                   | 0                | 2           |
|                 |           | Uroderma bilobatum     | F{n}  | 48 (2.66)       | 92 (5.11)            | 0                   | 29 (1.61)         | 169         |
|                 |           | Vampyresa thyone       | F{n}  | 7 (0.38)        | 5 (0.27)             | 1 (0.06)             | 3 (0.16)          | 16          |
|                 |           | Vampyrodes caracalli   | F{n}  | 39 (2.16)       | 11 (0.61)            | 1 (0.06)             | 0                | 51          |
| Total abundance |           |                          |       | 434             | 885                  | 134                 | 299             | 1752        |
| Samples         |           |                          |       | 18              | 18                   | 16                  | 18              | 70          |
| Richness        |           |                          |       | 23              | 21                   | 20                  | 14              | 28          |
| Completeness(%) |           |                          |       | 87              | 92                   | 92                  | 89              | 94          |

Parentheses indicate the relative abundance (bats captured per night sampling) from 18 nights of sampling for RM, RP, and P, and 16 nights of sampling for MF.

Feeding strategy based on Soriano (2000); {n}=Nomadic and {s}=Sedentary.

Based on the average of the following indices: ICE, Chao2 and Bootstrap.
associated with RM (Lonchorhina aurita and Vampyrodes caraccioli).

**Response to habitat attributes**

Three axes were considered in the NMDS ordination (Fig. 4, stress = 2.3). We only used scores from axes 1 and 2 for the construction of the biplot. Axis 1 of the plot separated riparian and nonriparian habitats. Riparian pasture and RM habitat are closer together, showing more similarity in species composition than MF and P, which are strongly separated (Fig. 4).

The assemblage dissimilarities represented by NMDS (Fig. 4) were significantly associated with the type of habitat and total basal area of the vegetation. Phyllostominae species such as M. crenulatum, P. discolor, Lampronycteris brachyotis, and T. saurophila were associated with the sites with the greater basal area (Table 3). Sites with high basal area were the riparian habitats: RM with 25639.51 m²/0.1 ha and RP with 20,285.77 m²/0.1 ha. On the other hand, whereas in nonriparian habitats basal area was 8561.03 m²/0.1 ha in P and 6241.88 m²/0.1 ha in RM. Also, the variation in bat abundance was positively associated with the rainy season (Table 3).
Our results suggest differences in species richness and abundance of phyllostomid bats between riparian and nonriparian habitats. This suggests that riparian corridors in agricultural landscapes allow the persistence of sensitive phyllostomines, which demonstrates the importance of maintaining different vegetation cover types to conserve bat biodiversity in areas under agricultural land use (Medina et al. 2007; Williams-Guillén and Perfecto 2010).

**Bat assemblages**

There was a clear association of riparian habitats with greater richness and abundance of bat species (Seaman and Schulze 2010). The high species richness and number of individuals recorded in a riparian habitat corroborates their significance as flyways corridors within fragmented landscapes (Limpens and Kapteyn 1991). Riparian corridors offer a great diversity of chiropterophilic and chiropterocchoric resources (Sánchez-Merlo et al. 2005) and provide roosting sites, commuting habitats, water, and refuge from adverse climatic conditions and predators (Estrada and Coates-Estrada 2002; Galindo-González and Sosa 2003).

We found more nomadic bats (Stenodermatinae) in anthropogenic habitats as they frequently move among forest remnants probably searching for food, which increases their capture probability (Table 1 Soriano (2000)). This suggests that Stenodermatinae but especially
Artibeus and Sturnira may facilitate forest regeneration in open pastures through seed dispersal (García-Morales et al. 2012). Nonetheless, V. caraccioli (Stenodermatinae) was caught exclusively in undisturbed forest, and C. perspicillata (Carollia) was caught mainly in riparian pasture habitat, supporting the idea that sedentary bats seldom leave mature forests (Soriano 2000). In this context, open pastures generate impermeability, because they seem to limit the movement of frugivorous bats restraining seed-flux between fragments and their matrix process (Castro-Luna et al. 2007b). Contrary to other findings (Fenton et al.1992; Medellín et al. 2000) that suggest the Phyllostominae subfamily is an ecological indicator of habitat modification because of strong association with preserved forest, our results suggest that generalist abundant species like the subfamilies Glossopaginae and Stenodermatinae may be better as ecological indicators.

Bats as indicator taxa

Taxonomic level analysis demonstrates that in the study area phyllostomid bats are poor ecological indicators (Castro-Luna et al. 2007b). Contrary to other findings (Fenton et al.1992; Medellín et al. 2000) that suggest the Phyllostomatidae subfamily is an ecological indicator of habitat modification because of strong association with preserved forest, our results suggest that generalist abundant species like the subfamilies Glossopaginae and Stenodermatinae may be better as ecological indicators. Frugivorous bats like Stenodermatinae, which can fly over large distances and visit different vegetation types (Estrada and Coates-Estrada 2002), could be useful detector taxa for studies aimed at evaluating different degrees of disturbance, rather than highly specialized taxa in which populations decline rapidly under environmental changes (Mcgeoch et al. 2002; Castro-Luna et al. 2007b).

Nectarivorous G. soricina and frugivorous S. lilium can be both considered as indicator taxa of habitat change in RP. These species can forage in areas with a simple vegetation structure but with high abundance of chiropterophilic and chiropterocoric species, in particular, S. lilium that usually feeds on understory shrubs and pioneer tree species (Marinho-Filho 1991).
**Habitat attributes**

Despite the relatively stable climatic conditions throughout the year in tropical rain forests, the availability of resources varies seasonally, and our results suggest that bats could be forced to make adjustments in their foraging strategy to cope with seasonal variations of resources availability such as food and roosts (Ramos-Pereira et al. 2010). Frugivores diet varies over the year and throughout their geographic ranges as the abundance and availability of fruit species change (Bonaccorso 1979). Seasonal variation could be a cause of variation in resource abundance and diversity, reproductive constraints and forest fragmentation, intensifying the severity of seasonal changes in source availability, furthermore, this variation could be a cause of shifts in foraging strategy that may not be needed in unfragmented landscapes (Klingbeil and Willig 2010).

The positive relationship between species composition and basal area of trees can be explained by the preference of some bat species for roosting in large trees. Large trees provide more potential roost sites because there is a close relationship between tree size and the number of natural cavities (Evelyn and Stiles 2003; Ortiz-Ramírez et al. 2006).

**Conservation implications**

Our results suggest that more efforts are needed to preserve riparian corridors in order to conserve Neotropical bats in human-dominated landscapes. Specifically, increasing matrix heterogeneity at larger spatial scales through the retention and protection of riparian forests is important (Akasaka et al. 2012). In human-dominated landscapes, riparian vegetation is highly threatened by agricultural practices, cattle concentration, extraction of firewood and timber. This suggests that conservation strategies should provide incentives for landowners to conserve and restore riparian vegetation in their properties (Harvey et al. 2006). Maintaining diverse populations of bats in human-dominated landscapes can benefit agricultural practices via seed dispersal and pollination services and by limiting arthropod populations (Perfecto and Vandermeer 2008; Williams-Guillén et al. 2008). Additionally, management programs in human-dominated landscapes should also focus on the quality of the remaining riparian vegetation as a suitable breeding habitat for bats and other animals (Bolívar-Cimé et al. 2013).

**Acknowledgments**

We thank the Comisión Nacional de Areas Naturales Protegidas and to the National Autonomous University of Mexico (UNAM). This article constitutes a partial fulfillment of the Graduate Program in Biological Sciences of the National Autonomous University of México (UNAM). E. de la Peña-Cuéllar acknowledges the scholarship and financial support provided by the National Council of Science and Technology (CONACYT), as well as additional support from Bat Conservation International (BCI Student Research Scholarship Program). We thank K. Stoner for suggestions for improvement on earlier stages of this project. We are grateful to R. Lombera-Estrada, G. and I. Lombera, E. Ayala, G. Rodriguez-Barrera and J. L. Peña-Mondragón for their assistance in the field. We are also grateful for technical support provided by J. M. Lobato-García and H. Ferreria.

**Conflict of Interest**

None declared.

**References**

Achard, F., H. D. Eva, H. J. Stibig, P. Mayaux, J. Gallego, T. Richards, et al. 2002. Determination of deforestation rates of the world’s humid tropical forests. Science 297:999–1002.

Akasaka, T., M. Akasaka, and F. Nakamura. 2012. Scale-independent significance of river and riparian zones on three sympatric Myotis species in an agricultural landscape. Biol. Conserv. 145:15–23.

Avila-Cabadilla, L. D. 2011. Diversidad de murciélagos filostomídidos en estadios sucesionales de bosques neotropicales secos. PhD thesis, Universidad Nacional Autónoma de México, México.

Avila-Cabadilla, L. D., K. E. Stoner, M. Henry, and M. Y. Álvarez-Añorve. 2009. Composition, structure and diversity of phyllostomid bat assemblages in different successional stages of a tropical dry forest. For. Ecol. Manage. 258:986–996.

Avila-Cabadilla, L. D., G. A. Sanchez-Azofeifa, K. E. Stoner, M. Y. Alvarez-Añorve, M. Quesada, and C. A. Portillo-Quintero. 2012. Local and landscape factors determining occurrence of phyllostomid bats in tropical secondary forest. PLoS ONE 7:e35228.

Bolivar-Cime, B., J. Laborde, C. MacSwiney, C. Muñoz-Robles, and J. Tun-Garrido. 2013. Response of phytophagous bats to patch quality and landscape attributes in fragmented tropical semi-deciduous forest. Acta Chiropt. 15:399–409.

Bonaccorso, F. J. 1979. Foraging and reproductive ecology in a panamanian bat community. Bull. Florida State Mus. Biol. Sci. 24:357–409.

Breugel, M. V., M. Martínez-Ramos, and F. Bongers. 2006. Community dynamics during early secondary succession in Mexican tropical rain forests. J. Trop. Ecol. 22:663–674.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York.
Bat Assemblages in a Human-Dominated Landscape

Carabias, J., G. Hernández, and P. Meli. 2008. Análisis comparativo de la deforestación de los ejidos de Marqués de Comillas, y determinación de corredores biológicos que conecten los fragmentos de selva de los ejidos con la Reserva de la Biosfera Montes Azules. Informe Final de Proyecto, INE, México.

Castro-Luna, A., V. J. Sosa, and G. Castillo-Campos. 2007a. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in southeastern Mexico. Anim. Conserv. 10:219–228.

Castro-Luna, A., V. J. Sosa, and G. Castillo-Campos. 2007b. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. Acta Chiropt. 9:219–228.

Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating and comparing incidence-based species accumulation curves. Ecology 85:2717–2727.

Comisión Federal de Electricidad. 2006. División Hidrométrica Sureste. Estación Lacantún, Marqués de Comillas, Chiapas, México.

Cortés-Delgado, N., and J. P. Pérez-Torres. 2011. Habitat edge context and the distribution of phyllostomid bats in the Andean forest and anthropogenic matrix in the Central Andes of Colombia. Biodivers. Conserv. 20:987–999.

Conson, J. F., J. M. Pons, and D. Masson. 1999. Effects of forest fragmentation on frugivorous and nectarivorous bats (Chiroptera:Phyllostomidae) as indicators of habitat disruption in the neotropics. Biotropica 24:440–446.

Danilo, S., C. Korine, and B. Pinshow. 2008. Central-place foraging in nursing, arthropo-gleaning bats. Can. J. Zool. 86:623–626.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species, the need for a flexible asymmetrical approach. Ecol. Monogr. 67:345–366.

Estrada, A., and R. Coates-Estrada. 2001. Bat species richness in live fences and in corridors of residual forest vegetation at Los Tuxtlas, Mexico. Ecography 24:94–102.

Estrada, A., and R. Coates-Estrada. 2002. Bats in continuous forest, forest fragments and in an agricultural mosaic habitat-island at Los Tuxtlas, Mexico. Biol. Conserv. 103:237–245.

Evelyn, M. J., and D. A. Stiles. 2003. Roosting requirements of two frugivorous bats (Sturmiura lilium and Artibeus intermedius) in fragmented neotropical forest. Biotropica 35:405–418.

Feinsinger, P. 2001. Designing field studies for biodiversity conservation. Island Press, Washington, DC.

Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. Merriman, M. K. Orbist, et al. 1992. Phylllostomid bats (Chiroptera:Phyllostomidae) as indicators of habitat disruption in the neotropics. Biotropica 24:440–446.

Garling-González, J., and V. J. Sosa. 2003. Frugivorous bats in isolated trees and riparian vegetation associated with human-made pastures in a fragmented tropical landscape. Southwest. Nat. 48:579–589.

García-Morales, R., L. Chapa-Vargas, J. Galindo-González, and E. I. Badano. 2012. Seed dispersal among three different vegetation communities in the Huasteca region, Mexico, analyzed from bat feces. Acta Chiropt. 14:357–367.

García-Morales, R., E. I. Badano, and C. Moreno. 2013. Response of neotropical bat assemblages to human land use. Conserv. Biol. 27:1096–1106.

Gentry, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Mo. Bot. Gard. 69:557–593.

Gorresen, P. M., and M. R. Willig. 2004. Landscape responses of bats to habitat fragmentation in Atlantic forest of Paraguay. J. Mammal. 85:688–697.

Griscom, H. P., E. K. V. Kalko, and M. S. Ashton. 2007. Frugivory by small vertebrates within a deforested, dry tropical region of central America. Biotropica 39:278–282.

Harvey, C. A., A. Medina, D. Merlo-Sánchez, S. Vílchez, B. Hernández, J. C. Saenz, et al. 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. Ecol. Appl. 16:1986–1999.

INE. 2000. Programa de Manejo Reserva de la Biosfera Montes Azules, México. Dirección de Publicaciones de la Dirección Ejecutiva de Participación Social, Enlace y Comunicación, Instituto Nacional de Ecología, México. 256 pp.

Jones, G., D. S. Jacobs, T. H. Kunz, M. R. Willig, and P. A. Racey. 2009. Carpe noctem: the importance of bats as bioindicators. Endanger. Species Res. 8:1–23.

de Jong, B. H. J., S. Ochoa-Gaona, M. A. Castillo-Santiago, N. Ramírez-Marcial, and M. A. Cairns. 2000. Carbon flux and patterns of land-use/land cover change in the selva Lacandona, Mexico. Ambio 29:504–511.

Kalka, M., A. R. Smith, and K. V. E. Kalko. 2008. Bats limit arthropods and herbivory in a tropical forest. Science 320:71.

Kalko, E. K. V., D. Friemel, C. O. Handley Jr, and H. U. Schnitzler. 1999. Roosting and foraging behavior of two neotropical gleaning bats, Tonatia silvicola and Trachops cirrhosus (Phyllostomidae). Biotropica 31:344–353.

Klingbeil, B. T., and M. R. Willig. 2010. Seasonal differences in population ensemble and community-level responses of bats to landscape structure in Amazonia. Oikos 119:1654–1664.

Koopman, K. F. 1993. Order Chiroptera. Pp. 137–232 in D. E. Wilson and D. M. Reeder, eds. Mammal species of the world. Smithsonian Institution Press, Washington, DC.

Kunz, T. H., E. B. de Torres, D. Bauer, T. Lobova, and T. H. Fleming. 2011. Ecosystem services provided by bats. Year in Ecology and Conservation Biology. Ostfeld, R. S Schlesinger W. H., NewYork.

La Val, R. K. 1970. Banding returns and activity periods of some Costa Rican bats. Southwest. Nat. 15:1–10.

Laurance, W., and R. O. Jr Bierregaard. 1997. Tropical forest remnants: ecology, management, and conservation of
fragmented communities. The University of Chicago Press, Chicago, IL.

Limpricht, H., and K. Kapteyn. 1991. Bats, their behavior and linear landscape elements. Myotis 29:39–48.

Lundy, M., and J. Montgomery. 2010. Summer habitat associations of bats between riparian landscapes and within riparian areas. Eur. J. Wildl. Res. 56:385–394.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27:209–220.

Marinho-Filho, J. S. 1991. The coexistence of two frugivorous bat species and the phenology of their food plants in Brazil. J. Trop. Ecol. 7:59–67.

Mcgeoch, M. A., B. J. VanRensburg, and B. Antoinette. 2002. The verification and application of bioindicators: a case study of dung beetles in a savanna ecosystem. J. Appl. Ecol. 39:661–672.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MJM Software, Gleneden Beach, OR. 300 pp.

Medellín, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in neotropical rainforests. Conserv. Biol. 14:1666–1675.

Medellín, R. A., H. T. Arita, and O. Sánchez. 2011. Identificación de los murciélagos de México: clave de campo. Asociación Mexicana de Mastozoología, México, DF.

Medellín, R. A. 1994. Mammal diversity and conservation in the selva Lacandona, Chiapas, Mexico. Conserv. Biol. 8:780–799.

Medina, A., C. A. Harvey, D. S. Merlo, S. Vilchez, and B. Hernández. 2007. Bat diversity and movement in an agricultural landscape in Matiguas, Nicaragua. Biotropica 39:120–128.

Moreno, C. E., and G. Halffter. 2001. Assessing the completeness of bat biodiversity inventories using species accumulation curves. J. Appl. Ecol. 37:149–158.

Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, Artibeus jamaicensis (Chiroptera:Phyllostomidae). Anim. Behav. 26:852–855.

Muscarella, R., and T. H. Fleming. 2007. The role of frugivorous bats in tropical forest succession. Biol. Rev. 82:573–590.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecol. Appl. 3:209–212.

Naiman, R. J., R. E. Bilby, and P. Bisson. 2000. Riparian ecology and management in the Pacific coastal rain forest. Bioscience 50:996–1011.

Oksanen, J., F. Guillaume, R. Kindt, P. Legendre, R. B. O’Hara, G. L. Simpson, et al. 2011. Vegan: Community ecology package version 1.17-6 http://CRAN.R-project.org/package=vegan.