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Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest

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With the aim of quantitatively evaluating the usefulness of phyllostomid bats as ecological indicators, we compared intra-family levels and feeding guilds between tropical old-growth forest and patches of secondary vegetation growing where the land had been used for shifting agriculture. There were significant differences between vegetation types in bat species composition, with the frugivore guild most abundant in secondary vegetation and the animalivore guild most abundant in the old-growth forest. These results are congruent with the findings for other Neotropical zones and appear to be associated with the type of soil management that allows secondary vegetation to grow. Using the Indicator Value method, two subfamilies, five genera and five species were found to have a significant indicator value. However, these numbers only represent a small proportion of the five subfamilies, 20 genera and 28 species recorded, indicating that under the disturbance conditions that characterize the study area, phyllostomid bats were poor ecological indicators. Even so, some species and subfamilies are useful as disturbance detectors.

Key words: assemblages, indicators, Phyllostomidae, shifting agriculture

INTRODUCTION

The use of indicator species and taxa to evaluate the degree of disturbance to a landscape has been widely discussed (Watt, 1998; Rolstad *et al*., 2002; Lindenmayer *et al*., 2006), and their usefulness in the context of conservation and management has been satisfactorily demonstrated (Chase *et al*., 2000). To be a good indicator, a taxon must be abundant and diverse, as well as responsive to changes to the environment in a predictable and quantitative way. It is also desirable for it to have a wide geographic distribution and that abundant captures result from sampling effort (Noss, 1990).

For bats it has been suggested that the family Phyllostomidae could be useful as an ecological indicator in the neotropics, owing to the great diversity and abundance of its species and the different responses they display in the face of disturbances. It has been indicated that the richness and abundance of subfamily Phyllostominae is greater in vegetation with a lesser degree of disturbance, while a greater abundance of species belonging to subfamilies Stenodermatinae, Carolliinae and Glossophaginae has been recorded in secondary vegetation. These patterns appear to be associated with changes in the composition and structure of the vegetation that result from disturbance

(Fenton *et al*., 1992; Medellín *et al*., 2000; Schulze *et al*., 2000), and in forest fragments are inversely proportional to the distance away or isolation from continuous forest (Estrada *et al*., 1993; Galindo-González and Sosa, 2003). These studies were done on a landscape where the secondary vegetation was adjacent to the rainforest or was the main vegetation matrix. However, in a landscape comprised of patches of secondary vegetation surrounded by a matrix of old-growth forest, such as in the present study, the reported patterns of habitat selection could be less rigorous, i.e. more frugivorous and nectarivorous species would be expected to visit old-growth forest and more Phyllostominae species would be expected to visit secondary forest patches because of their proximity to the old-growth forest.

An advantage to using bats as ecological indicators is the ease with which they can be sampled (Medellín *et al*., 2000). However, the species that are most sensitive to disturbance are also the most rare (i.e., the species of subfamily Phyllostominae) and are poorly represented in samples (Fenton *et al*., 1992; Arita, 1993). Hence, the changes in bat assemblages that are related to disturbances, though conspicuous on visual inspection of the data, have not yet been quantitatively evaluated. It has been suggested that frugivorous species, because of their greater abundance, could be individually used as indicators (Medellín *et al*., 2000). The use of taxonomic levels above that of species (i.e., subfamily), could also be useful to identify groups of species with similar ecological characteristics and potential as indicators. This would help us to obtain more reliable information without the need to invest additional time or money. This group could also offer a practical advantage if we consider the funds and effort in person-hours required to identify specimens and obtain representative data bases for other taxonomic groups (Noss, 1990; Lawton *et al*., 1998; Andersen *et al*., 2004).

The objectives of this study were to: 1) determine whether there are differences (richness and species composition) in the assemblages and feeding guilds of phyllostomid bats between old-growth forest and secondary vegetation and, 2) using the Indicator Value method (IndVal), to quantitatively evaluate the usefulness of phyllostomid bats as indicators of habitat disturbance at three taxonomic levels: subfamily, genus and species. These objectives were addressed in the Agua Blanca State Park, a natural reserve in southeastern Mexico. Our working hypotheses were: (i) For the distribution of Phyllostomidae assemblages across vegetation types, we expected a greater richness of frugivore and nectarivore species (subfamilies Stenodermatinae, Carolliinae and Glossophaginae) in secondary vegetation than in old-growth forest, and the opposite trend for insectivore and carnivore species (subfamily Phyllostominae), (ii) With regard to bats as ecological indicators, we expected that at the species level frugivore species would reach indicator values, owing to their greater abundance in the Neotropics; and at taxonomic levels above the species level, we expected that the subfamily Phyllostominae would work as indicators, owing to the sensitivity of this subfamily to deforestation.

MATERIALS AND METHODS

Study Area

This study was carried out in the Agua Blanca State Park (ABSP), Tabasco, Mexico, a 2025 ha reserve managed by the inhabitants of the Manatinero-Palomas ejido (communal land — Cruz-Hernández, 1999). The study area belongs to the Sierra de Chiapas physiographical province (17°35’52”N–92°27’30”W to 17°37’16”N–92°28’43”W — Fig. 1), and the climate is warm and humid with rain all year round (García, 1987). The elevation is 200 m a.s.l. and mean annual temperature is 26°C with little variation throughout the year. Mean annual precipitation is 3,500 mm, and mainly falls during the rainy season (June–November; monthly mean 419.8 mm) although there is some rain during the rest of the year (December–May; monthly mean 174.9 mm — INEGI, 1994).

The dominant vegetation in the ABSP is old-growth forest (Clark, 1996), located on steep, rocky terrain. The most accessible zones were subjected to selective logging during the 1970s and this gave rise to the proliferation of secondary vegetation (Cruz-Hernández, 1999). Since the disturbance ended, the local inhabitants have been using the land for subsistence hunting and gathering. This has allowed the vegetation to recover to the point where, visually, it is very difficult to distinguish between the two plant associations.

Slash and burn agriculture is also carried out in the ABSP. Areas of 1–3 ha are cut in order to sow annual crops (mainly corn, beans and squash). These plots are used for one or two years and then abandoned, allowing the secondary vegetation to establish. Given that the soil conditions in the ABSP are characterized by a calcareous substrate and very shallow soils, arable land is limited. This has allowed the cut areas to continue to be surrounded by old-growth forest, although it has also precipitated a much faster rotation of plots than normal. Consequently, it is difficult to find secondary vegetation that is older than 15 years and results from shifting agriculture.

Sampling Design and Capture

We selected four sites for bat capture in each of the following categories: 1) old-growth forest and 2) secondary vegetation (Fig. 1). The old-growth forest is a vegetation community comprised of tropical evergreen forest (Leopold, 1950), that is in very good condition from a conservation perspective, and sectors that have been disturbed by selective logging. There are trees that are up to 35 m tall and the species that are most characteristic of the canopy are *Quararibea funebris* and *Dialium guianense*. In the understory *Astrocaryum mexicanum* and *Rinorea guatemalensis* dominate. The secondary vegetation is derived from shifting agriculture and has a low (4–8 m) discontinuous canopy. The most characteristic tree species are *Heliocarpus mexicanus*, *Cecropia obtusifolia* and *Trema micrantha* and in the understory, *Hamelia patens*, *Acalypha diversifolia* and *Piper hispidum*. There was a minimum of 300 m between capture sites.

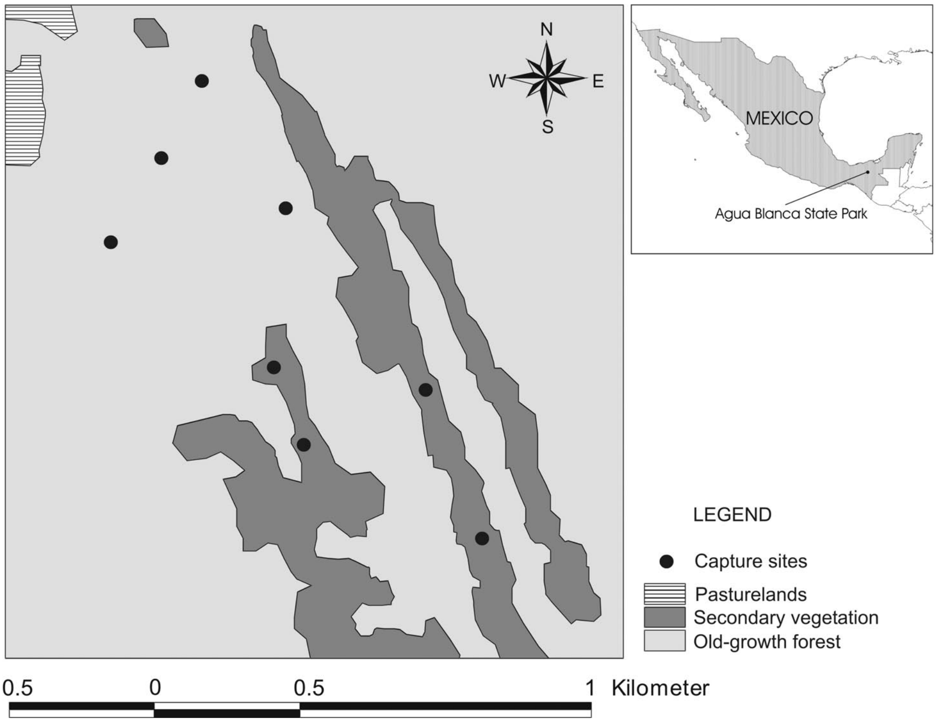

FIG. 1. Location of the Agua Blanca State Park in southeastern Mexico and the sites for bat sampling in each vegetation type

From November 2002 to November 2003 we made 10 sampling expeditions on dates close to the new moon. We spent one night at each site on each trip, using 10 mist nets (9 m long × 2.6 m high) hung at the understory level; an effective method for capturing phyllostomid bats (Kalko *et al.*, 1996). The nets were opened at nightfall for six hours and checked every 30 minutes. Sampling effort was 480 hrs over 80 sampling nights for a total of 4,800 net-hours, evenly distributed between the vegetation types studied. The bats caught were identified to the species level using field keys (Medellín *et al.*, 1997), and taxonomic classification followed Ramírez-Pulido *et al.* (2005). To detect recaptures, each bat was fitted with a numbered, plastic collar.

Statistical Analysis

To compare the composition and feeding guilds of the phyllostomid bats between vegetation types we used Analysis of Similarities (ANOSIM — Clarke, 1993). The R_{ANOSIM} statistic is a relative measure of the separation between groups, defined a priori, where zero indicates that there is no difference between groups and a value of 1 indicates that all the sites within the same type of vegetation are more similar to each other than they are to sites located in another type of vegetation (Clarke and Gorley, 2001). The probability associated with R_{ANOSIM} indicates the degree of certainty of the result obtained, relative to the result expected when random forces are operating. For this analysis, we set up similarity matrices with the Bray-Curtis coefficient, using incidence data (presence/absence) and abundance per species (Balmer, 2002). To eliminate the bias introduced to the results by the most abundant species, we fourth root transformed species abundances (Clarke and Warwick, 2001). Recaptures were not included. We categorized bats into broad feeding guilds: frugivore, nectarivore, animalivore (insectivores and carnivores) and sanguivore based on the relevant literature (Arita, 1993; Kalko *et al.* 1996; Giannini and Kalko, 2005). The sanguivore guild only had one species and so was not included in the analyses. It was not possible to use a more detailed level of classification (i.e., functional groups; Kalko *et al.*, 1996), since the low number of captures for some categories would have made statistical comparisons impossible. These analyses were done using PRIMER software v.5 (Clarke and Gorley, 2001).

The usefulness of the three taxonomic levels as indicators was quantified using the Indicator Value analysis (IndVal — Dufrêne and Legendre, 1997). This method has been widely applied to quantitatively evaluate the usefulness of different taxa as indicators because it combines the frequency of occurrence (fidelity) with the relative frequency of a taxon in a given habitat (specificity), as well as providing the associated probability. Following Van Rensburg *et al.* (1999), we only present those taxa with significant indicator values that were greater than 70 (indicator taxon) and those in the range of 50–70 (detector taxon). Indicator taxa are characteristic of a particular habitat (i.e., with a high degree of specificity and fidelity), while detector taxa exhibit different degrees of preference for different ecological states and could be more useful for detecting the direction of the change resulting from a disturbance (Van Rensburg *et al.*, 1999; McGeoch *et al.*, 2002). These analyses were carried out using PCORD software ver. 4 (McCune and Mefford, 1999).

RESULTS

Species Composition and Feeding Guild Patterns

We caught 1,589 phyllostomid bats (180 were recaptures, for a total of 1,769 captures), representing six subfamilies, 20 genera and 28 species (Table 1).

There were significant differences in the incidence ($R_{\mathrm{ANOSIM}} = 0.45$, $P < 0.05$) and abundance ($R_{\mathrm{ANOSIM}} = 0.56$, $P < 0.05$) of phyllostomid bats between vegetation types. The most abundant species in secondary vegetation were: *Carollia sowelli*, *Glossophaga soricina*, *Sturnira lilium* and *Dermanura phaeotis*; while in old-growth forest the most abundant were *C. sowelli*, *G. soricina*, *Artibeus jamaicensis* and *A. lituratus* (Table 1).

At the feeding guild level we found marked differences in the animalivores between vegetation type, with respect to both incidence ($R_{\mathrm{ANOSIM}} = 0.61$, $P < 0.05$), and species abundance ($R_{\mathrm{ANOSIM}} = 0.59$, $P < 0.05$). There were no differences in species incidence for the frugivore guild ($R_{\mathrm{ANOSIM}} = 0.17$, $P > 0.05$), but there were differences in abundance ($R_{\mathrm{ANOSIM}} = 0.54$, $P < 0.05$). For the nectarivore guild there were no significant differences in species incidence ($R_{\mathrm{ANOSIM}} = 0.17$, $P > 0.05$), or in abundance ($R_{\mathrm{ANOSIM}} = 0.09$, $P > 0.05$).

Bats as Indicators

Of the six subfamilies we analyzed, two had significant indicator values as detector taxa, Phyllostominae for the old-growth forest and Carolliinae for secondary vegetation. Of the 20 genera recorded, only *Artibeus* and *Mimon* had significant indicator values for the old-growth forest and *Sturnira* for secondary vegetation. In addition, the values for *Uroderma* and *Carollia* classify them as detector taxa for secondary vegetation. At the species level, *A. jamaicensis* had a significant indicator value for old-growth forest as did *S. lilium* for secondary vegetation. The indicator values for three other species classify them as detectors: *C. sowelli* and *U. bilobatum* for secondary vegetation and *M. cozumelae* for the old-growth forest (Table 2). Indicator values for the remaining 23 species were not significant.

DISCUSSION

Our data show that some guilds and the complete assemblage of phyllostomid bats in tropical forest changed in response to the disturbances caused by shifting agriculture. However the analysis of the three taxonomic levels demonstrates that under the disturbance conditions of the study area, phyllostomid bats are poor ecological indicators even though several taxa at different levels had significant indicator values.

Assemblages and Guilds

We have shown that phyllostomid bat species richness and composition in patches of secondary vegetation derived from slash and burn agriculture differed significantly from the values for old-growth forest, and that these differences were most notable for the animalivore guild. The greatest abundance and incidence of animalivore species in the old-growth forest could result from the fact that these species belong to subfamily Phyllostominae. They have a sedentary foraging habit and are morphologically

TABLE 1. Total captures and feeding guilds of phyllostomid bats in old-growth forest and secondary vegetation in the Agua Blanca State Park, Tabasco, Mexico. OGF — old-growth forest and SV — secondary vegetation; guild: A — animalivore, F — frugivore, N — nectarivore, S — sanguivore

Species	Guild	OGF	SV
Carolliinae			
Carollia sowelli	F	212	393
C. perspicillata	F	31	59
Desmodontinae			
Desmodus rotundus	S	24	4
Glossophaginae			
Glossophaga soricina	N	146	211
Hylonycteris underwoodi	N	6	6
Micronycterinae			
Lampronycteris brachyotis	A	2	0
Micronycteris microtis	A	9	10
M. schmidtorum	A	3	0
Phyllostominae			
Lonchorhina aurita	A	1	3
Chrotopterus auritus	A	3	0
Mimon cozumelae	A	10	0
M. crenulatum	A	1	0
Phyllostomus discolor	N	0	1
Lophostoma brasiliense	A	0	2
L. evotis	A	3	0
Trachops cirrhosus	A	3	0
Stenodermatinae			
Artibeus jamaicensis	F	98	9
A. lituratus	F	81	45
Centurio senex	F	7	8
Chiroderma salvini	F	0	2
C. villosum	F	1	0
Dermanura phaeotis	F	67	76
D. tolteca	F	0	1
D. watsoni	F	11	6
Platyrrhinus helleri	F	12	11
Sturnira lilium	F	43	120
Uroderma bilobatum	F	0	8
Vampyressa thyone	F	12	8
Total number of bats		786	983
Species richness		23	20

TABLE 2. Subfamilies, genera and species of bats with a significant Indicator Value (IndVal — Dufrêne and Legendre, 1997) in the Agua Blanca State Park, Mexico. OGF — old-growth forest, SV — secondary vegetation. D — Detector species (IndVal: 50–70), I — Indicator species (IndVal > 70)

Taxonomic level	Taxon	Vegetation type	IndVal	Category[a]
Subfamily	Phyllostominae	OGF	66.5^{*}	D
	Carolliinae	SV	63.4^{*}	D
Genus	*Artibeus*	OGF	76.8^{**}	I
	Mimon	OGF	75.0^{**}	I
	Carollia	SV	63.4^{*}	D
	Sturnira	SV	73.1^{*}	I
	Uroderma	SV	62.5^{*}	D
Species	*A. jamaicensis*	OGF	91.4^{***}	I
	M. cozumelae	OGF	62.5^{*}	D
	C. sowelli	SV	63.2^{*}	D
	S. lilium	SV	73.1^{*}	I
	U. bilobatum	SV	62.5^{*}	D

* — Probability level: $P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

[a] — Indicator categories based on the degree of specificity and fidelity of taxa for a particular type of habitat

adapted for flight in the complex interior of the forest, though with a limited capacity for long distance flights (Norberg and Rayner, 1987; Soriano, 2000; Jones *et al.*, 2003). These species also tend to use refuges such as termite mounds and the hollow trunks of old trees which are more likely to be found in mature forest (Fenton *et al.*, 2001; Soriano and Ochoa, 2001; Evelyn and Stiles, 2003). On the other hand, some animalivore species commute and forage at different heights within forest (Simmons and Voss, 1998; Simmons *et al.*, 2000; Weinbeer and Kalko, 2004). Therefore, we do not discard the possibility that some of the animalivore species might be flying at different heights in the two vegetation types as a result of the different structure. Some might fly low in old-growth forest (and hence be within range of our mist nets), and be flying higher (and hence out of reach) in secondary vegetation.

Frugivores, owing to their habits, can be affected by disturbances to the vegetation (Jones *et al.*, 2001). However, in our study, only those species that feed from fruit in the canopy were affected (i.e., *Artibeus* — Kalko and Handley, 2001). The majority of the other species belonging to this guild were very abundant in secondary vegetation and this coincides with the results reported for other areas of natural vegetation that has been disturbed by shifting agriculture (Medellín *et al.*, 2000; Schulze *et al.*, 2000). This apparently results from the fact that slash and burn agriculture allows secondary vegetation to grow and thus favors the creation of potential foraging sites for some frugivorous species (Estrada *et al.*, 1993; Brosset *et al.*, 1996; Evelyn and Stiles, 2003). In contrast, in cattle pastures that are far away from the forest — a drastic change in land use that usually occurs on a large scale — few or no bat species are reported (Estrada *et al.*, 1993; Galindo-González and Sosa, 2003).

From a conservation perspective, we can be encouraged by the high abundance of frugivores in secondary vegetation and a diversity of animalivores comparable to that recorded for relatively undisturbed Mesoamerican forests (see Medellín *et al.*, 2000 and Schulze *et al.*, 2000). However, it is important to keep in mind the following two points: 1) our results were influenced by the small magnitude of the disturbance in the studied area, and 2) although frugivores forage mainly in secondary vegetation, they are still highly dependent on primary vegetation where their refuges and perching sites are located (Bernard and Fenton, 2003; Evelyn and Stiles, 2003). So, as fragmentation and isolation between the patches of vegetation increase, foraging patterns, habitat use and the availability of some species are negatively affected, resulting in local extinction (Estrada *et al*., 1993; Estrada and Coates-Estrada, 2002).

Indicators

Owing to their notable vagility, some groups of birds and bats are not considered good indicators at a local scale (Temple and Wiens, 1989; Grand *et al*., 2004; Pineda *et al*., 2005). However in patches of secondary vegetation surrounded by old-growth forest we detected species, genera and subfamilies of phyllostomid bats with significant indicator values. In coffee agroecosystems and cloud forest, bats were apparently not good ecological indicators (Pineda *et al*., 2005). That study was based on changes in total bat richness between vegetation types, a variable for which we also found no differences. When we compared the abundance of specific groups (i.e., feeding guilds), we detected significant differences.

Indicator species are very specific to a single habitat type (Van Rensburg *et al*., 1999; McGeoch *et al*., 2002). Bats, however, are not, since the majority of them can fly over large distances and visit many different types of vegetation in a single night (Morrison, 1980; Estrada *et al*., 1993). This is particularly true of frugivores such as *A. jamaicensis*, which was very specific to the old-growth forest, even though it is one of the most resilient species in landscapes that have been disturbed by human activities (Fenton *et al*., 1992; Estrada *et al*., 1993). Consequently, frugivorous bats could be considered detector taxa, rather than true indicators since their degree of habitat specificity is moderate. This characteristic could be useful in studies aimed at evaluating different degrees of disturbance, given that highly specific taxa are only useful for one ecological condition and their populations decline rapidly when environmental conditions change (McGeoch *et al*., 2002). In addition, the majority of the species with significant indicator values were frugivorous, because they were abundant and the probability of capturing them can be predicted with greater certainty (Dufrêne and Legendre, 1997; McGeoch and Chown, 1998).

Carrying out the analysis for three taxonomic levels also allowed us to identify the genera and subfamilies with indicator characteristics. Subfamily Phyllostominae stood out with a significant indicator value even though the majority of its species, owing to their rarity, did not. This result confirms a pattern, reported in other studies, that the high species richness of Phyllostominae is indicative of relatively undisturbed rainforests, while the high abundance of subfamily Carolliinae indicates zones dominated by secondary vegetation (Fenton *et al*., 1992; Medellín *et al*., 2000). At the genus level, *Uroderma* and *Sturnira* were monospecific and showed no real indicator value for their respective genera, although the patterns recorded for *Mimon*, *Artibeus* and *Carollia* were consistent with those observed at the level of species. A point in favor of higher taxonomic levels is that they are based on phylogenetic analyses and these are compatible with specific dietary groups (Baker *et al*., 2000; Wetterer *et al*., 2000; Giannini and Kalko, 2004). This would increase their usefulness in ecological interpretations once the debate surrounding the degree of resolution for some taxonomic groups has been resolved (Ramírez-Pulido *et al*., 2005).

The main attributes that are associated with good indicators have to do with the capacity of a taxon to reflect ecological change, and its abundance or diversity as a function of its sensitivity to disturbances (Landres *et al.*, 1988; Andersen *et al.*, 2002). In this sense, some intra-family levels of family Phyllostomidae had indicator characteristics, although very few with respect to all the taxa we recorded. This result does not allow us to accept the hypothesis that as a group phyllostomid bats are effective disturbance indicators, at least not under the particular conditions of our study. However, information about the taxa that did qualify as indicators is valuable, particularly as a complement to information provided by other taxonomic groups such as birds. This approach, i.e., one which includes species from different taxonomic groups, has been found more useful in the area of conservation because it provides a more integral image of the quality and configuration of the area being studied (Hilty and Merenlender, 2000; Root *et al.*, 2003; Roberge and Angelstam, 2004). Evidently, the response of the bats to ecological change varies across a wide range of spatial and temporal scales, and also depends on the species (Lim and Engstrom, 2001; Gorresen and Willig, 2004; Gorresen *et al.*, 2005). As such it is necessary to carry out these studies under different environmental conditions in order to establish robust criteria for identifying some bat species as reliable indicators.

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