
Bat Diversity and Abundance as Indicators of Disturbance in Neotropical Rainforests

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Abstract: *Evaluating the degree of disturbance of any region to determine its relative importance for conservation purposes requires procedures that are relatively inexpensive and that yield accurate results fast. Because bats are abundant, diverse, and easy to sample, especially in the Neotropical rainforest, they fulfill several of the requirements of indicator species as identified in the literature. For 10 months we sampled bat communities in the Selva Lacandona in Chiapas, Mexico, at 15 sites representing five habitats. We also measured 10 variables representing vegetation structure and diversity at each site. With fuzzy-set techniques we produced a gradient classification of disturbance for the 15 sites based on the vegetation data. We explored the relationship between vegetation conditions, described as the membership degrees in the construct "fuzzy forest set" (the complementary fuzzy set of "disturbance"), and four bat community variables. Bat species richness, number of rare bat species, and the bat diversity index were positively correlated with the vegetation scores, and relative abundance of the most abundant bat species was negatively correlated with vegetation scores. A high number of phyllostomine species in a community is a good indicator of low levels of disturbance. Although a single indicator group will probably not be sufficient for decision-making processes in conservation, evaluating bat populations may be a good first step in assessing an area's conservation value, especially in rainforest regions.*

Diversidad y Abundancia de Murciélagos como Indicadores de Perturbaciones en Selvas Húmedas Neotropicales

Resumen: *La evaluación del grado de perturbación de una región particular para determinar su importancia relativa para propósitos de conservación requiere que los procesos de toma de decisiones utilicen tecnologías relativamente baratas y que proporcionen resultados precisos pronto. Puesto que los murciélagos son abundantes, diversos y fáciles de muestrear, particularmente en las selvas húmedas del Neotrópico, llenan varios de los requerimientos de las especies indicadoras. Muestreamos por 10 meses comunidades de murciélagos en la Selva Lacandona de Chiapas, México, en 15 sitios representativos de cinco hábitats. También medimos 10 variables representativas de la estructura y diversidad de la vegetación en cada sitio. Mediante el uso de técnicas de conjuntos difusos produjimos una clasificación gradual de la perturbación de la vegetación para los 15 sitios. Exploramos las relaciones entre las condiciones de la vegetación, descritos como los grados de membresía en la construcción de los conjuntos difusos del bosque (el conjunto difuso complementario de la perturbación) y cuatro variables de la comunidad de murciélagos. La riqueza de especies de murciélagos, el número de especies de murciélagos raros, y el índice de diversidad de murciélagos estuvieron positivamente correlacionados con los valores de la vegetación y la abundancia relativa de la especie más abundante estuvo negativamente correlacionado con estos valores. Un alto número de especies de Phyllostominae en la comunidad es un buen indicador de bajos niveles de perturbación. Sin embargo, un solo grupo indicador probablemente no es suficiente en el proceso de toma de decisiones en conservación. La evaluación de poblaciones de murciélagos puede ser un buen primer paso en la evaluación del valor de un área para la conservación, especialmente en regiones de selva húmeda.*

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Introduction

Understanding the causes and consequences of variation in the distribution and abundance of life forms is paramount to the conservation of biological diversity. Many studies have sought to determine and measure the variables influencing biodiversity at local, regional, and global scales (e.g., May 1988, 1990; Arita 1993; Wilson 1993; Erwin 1997; Ceballos et al. 1998). Pristine ecosystems continue to dwindle at alarming rates, and the effects of human activities on biodiversity range from dramatic to subtle. These anthropogenic effects have resulted in a global pattern of seminatural matrix (which consists of patches of pristine habitat among habitats with different levels and types of human-induced disturbances [Franklin 1992]). Evaluation procedures need to be relatively inexpensive and yield accurate results fast. Evaluating disturbance effects on ecological patterns and processes in specific areas yields important information on which to base conservation and management decisions. For conservation purposes, the use of adequate biodiversity indicators is particularly helpful in this sense (Mooney et al. 1995). To be useful as indicators, taxa should be at least abundant, and ecologically, taxonomically, and trophically diverse. They should have a substantial functional role in the ecosystem and respond to environmental changes in a quantitative, predictable way (Noss 1990; Mooney et al. 1995). In addition, good indicators should have wide geographic distributions and sampling techniques should be cost-effective (Noss 1990). Indicator species should be surrogates for the state of health of ecosystems (Rapport et al. 1981; Rapport 1990; Keddy 1991). Using a single, traditional indicator criterion, such as high habitat specificity or large size, is not useful in monitoring population trends or habitat quality (Landres et al. 1988). Stating the level at which a given indicator is expected to work, from genetic to landscape scales, is critical for logical, reasonable use of the indicator (Noss 1990). Monitoring of populations or communities in the context of known environmental change, such as those due to human disturbances, can also provide a basis for improved management decision making (Kremen 1992). We argue that bats are good indicators of habitat disturbance at the community level in a rainforest within a river floodplain.

Bats are ubiquitous in the vegetated terrestrial ecosystems of the world and are particularly diverse and abundant in the tropics (Fenton 1992). They are relatively easy to find and represent the second largest order of mammals in terms of numbers of species (Wilson & Reeder 1993). Because of their dramatic ecological and evolutionary radiation, bats occupy virtually every trophic level, from primary to tertiary consumers. Bats feed on fruit, insects, nectar, pollen, fish, blood, vertebrates, and leaves, and in many cases they select specific habitats (Hill & Smith 1985; Fenton 1992). They are important in

ecological processes through interactions such as seed dispersal, pollination, and insect population regulation (Fleming 1988, 1993; Whittaker 1993; Medellín & Gona 1999). Their roosting habits are diverse, ranging from caves and crevices to hollow trees, to curled young leaves, to leaf roosts they construct (Timm 1987; Fenton 1992). Many bats have specialized needs in diet, roosting sites, and habitat selection (Fenton 1992). Diet and habitat specialization have been identified as correlates of rarity and are significant predictors of the probability of local extinction (Leck 1979; Laurance 1991). All these traits make bats good indicators of the status of several habitat features, such as particular structures (e.g., specialized roosts), food variety, and an assortment of microhabitats. These features are found in the pristine, intact conditions under which these species evolved. From this it follows that absence of these features will determine absence of these species. The relationship of an indicator species to environmental variables tells how this species or group of species, such as bats, may function as a measure of habitat integrity (Blair 1999).

In the Neotropics, bats are numerically more abundant than all other mammalian groups and are equal to or greater than all frugivorous birds (Bonaccorso 1979; Terborgh 1983). They are also diverse, with about 220 species (Emmons & Feer 1997) representing over 50% of mammal species locally and 24% of the number of bat species worldwide. Literature on bat systematics, natural history, and ecology is extensive, but we found only a few studies in which bats have been evaluated as indicators of habitat disturbance (Johns et al. 1985; Fenton et al. 1992; Wilson et al. 1996). The results of these studies suggest that bats in the subfamily Phyllostominae are sensitive to habitat disturbance. High levels of abundance of certain species such as *Desmodus rotundus* and *Carollia perspicillata* may also indicate habitat disturbance.

The mammal fauna of the Selva Lacandona in Chiapas, Mexico, is the most diverse in the country, containing 116 species of mammals, including 64 bat species. This fauna is typical of many Neotropical rainforest sites and is as diverse as most (Medellín 1994). Proportions and patterns of disturbance in the region are complex (Cuarón, this issue) and constitute a mosaic of human-transformed habitats creating a disturbance gradient from pastures and cornfields to oldfields and cacao plantations.

We studied the bat community to evaluate changes in species richness, composition, and abundance as they relate to vegetation diversity, structure, and complexity along a human-produced disturbance gradient. Our objective was to show that the diversity and structure of the bat community indicates how closely a given site resembles a rainforest, as evidenced by a compound variable composed of various raw vegetation variables. We show that bats can be used to assess the level of disturbance of a site beyond what can be perceived visually or

by a single measure of vegetation diversity or structural variable. We distinguish between several degrees of forest disturbance and present some specific, quantitative ways in which bats respond to disturbance.

Study Area and Methods

Our base was the Chajul Tropical Biology Station (lat 16°7'N, long 90°56'W, 120 m above sea level) at the southern edge of the Montes Azules Biosphere Reserve. The forest in this reserve, embedded in the Selva Lacandona, is extensive, covering over 3000 km² (Medellín 1994). The Lacantún River is its southern boundary and to the south is a complex mosaic of human-disturbed habitats. We focused on a disturbance gradient including active cornfields, oldfields, cacao plantations, and rainforest.

Active cornfield was corn-dominated agricultural field mixed with beans, squash, and other crops. It was cultivated and harvested during our study. Vegetation never grew above 3.5 m in height and was not diverse or structurally complex.

Oldfields were inactive agricultural fields covered with secondary vegetation that had been abandoned for a period between 8 and 18 years. Dominant tree species were *Cecropia* spp., *Schizolobium parahybum*, *Ochroma pyramidale*, and *Tropis mexicana*. Oldfields were characterized by two vegetational strata: an abundant herbaceous-shrub layer up to 4 m tall and a discontinuous canopy between 10 and 25 m with little complexity because intermediate vegetation layers were poorly developed or absent and because there was almost a complete lack of lianas (Medellín & Equihua 1998) and low-tree species richness. We included a younger (8–12 years since abandonment) and an older (>12 years since abandonment) representative of oldfields.

Cacao plantations are common in tropical America. Cacao (Sterculiaceae: *Theobroma cacao*) is planted as an understory tree; the original, diverse canopy of trees of the forest—such as *Spondias radlkoferi*, *Licania platypus*, *Inga* spp., *Ceiba pentandra*, and others—is left as shade for the cacao trees. Cacao plantations were harvested during our study.

We compared each disturbance stage—corn-dominated agriculture, oldfield, cacao plantation—against rainforest habitat. The rainforest vegetation was structurally complex and diverse, with many large trees and lianas of many species.

We selected three study areas within each habitat, for a total of 15 sites. Each site shared the following conditions: forested on at least one side; 1–7 ha in area (only the rainforest was extensive); 500 m or more from the next study site; and in the Lacantun River flood plain. At each site, we captured bats one night per month from April 1993 to April 1994, except in January, February,

and March of 1994, when sociopolitical problems in the Selva Lacandona prevented us from visiting the site. We placed four, 9-m-long mist nets configured in two T layouts 5 m apart near the center of the site and worked them for 4 hours consecutively starting at sunset. In the case of heavy rain (≥ 3 times a month in June–September), we waited until the storm had passed, shook excess water from the nets, and resumed counting the 4-hour period.

Each captured bat was identified and individually marked with a numerical combination of colored beads on a plastic necklace. The bat was kept in captivity for up to 1 hour for another study and then released at the site of capture. As indicators of the bat diversity and abundance at each site, we used four variables: number of bat species recorded, diversity as measured by the Shannon-Wiener index (H' ; Magurran 1988), percentage of the total bats captured that were of the most abundant species, and number of rare species (those represented by <10 individuals in all habitats). These four variables are commonly used as indicators of community diversity and structure and are easily recordable. The number and representation of rare species is affected by sampling effort. Nevertheless, the log-normal characteristics of most species-abundance curves—a few species with many individuals and many species with a few individuals (Magurran 1988; Krebs 1989)—leads to the conclusion that the length of the distribution tail (how leptokurtic the distribution is) is another good and simple indicator of its diversity. The longer the tail of the distribution (i.e., more rare species in the community among comparable communities and equal sampling efforts), the more diverse the community.

Vegetation variables were measured in one rectangular plot of 30 × 10 m (300 m²) per site. Diversity and structure are good habitat descriptors because they represent three-dimensional complexity at the ground, subcanopy, and canopy layers and describe in quantitative terms the variation and patterns of abundance of individual species of plants, from trees to shrubs to herbaceous layers. In each plot we measured diversity by the number of species of vascular plants, the number of individuals per species, and the Shannon-Wiener diversity index. Vegetation structure was determined by herbaceous cover and was measured as the percentage of a measuring tape along the 30-m length that intercepted herbaceous cover, canopy cover (with a spherical densiometer; Lemmon 1956), tree basal area measured at breast height, and number of trees in each of four strata (2–5, 5–10, 10–25, and >25 m tall).

To characterize the diversity and structural variability in each habitat, we used a fuzzy-set description of the vegetation. This approach produces a flexible definition of vegetation conservation status that is useful for modeling purposes. Thus, what we sought was a mathematical map of the semantic notion of disturbance (Kosko

1993; Medellín & Equihua 1998). To this end, we summarized the sampled vegetation variables through an approach known as *k*-means fuzzy clustering (Bezdek 1981; Equihua 1990), which produced two fuzzy sets. One set represented a gradient toward forest resemblance (forest set) and the other a gradient toward a disturbed area (disturbed set). One set was the complement of the other, and both sets spanned the range of study sites from primary forest to active cornfield. For these analyses we used the forest set. In any fuzzy classification, the groups overlap each other, and every site has a degree of membership within the forest gradient measured on a scale from zero, complete lack of membership in the forest set, to one, full membership in the forest set, or primary forest. Thus, membership becomes a new variable that maps, in this case, the structural and diversity attributes and degree of disturbance of the vegetation, providing both a gradient of habitat characterization and a functional definition of groups. These fuzzy groups encompassed the habitats originally recognized as forest, cacao plantation, oldfield, and cornfield, which were then arranged in a gradient within the fuzzy sets.

To analyze the mapping of the bat community parameters on the fuzzy sets of the vegetation, we applied the same equation we used in the fuzzy clustering to calculate the fuzzy-set centroid:

$$v_{js} = \frac{\sum_{i=1}^n x_{is} u_{ij}^z}{\sum_{i=1}^n u_{ij}^z}$$

where v_{js} is the "centroid" value of the *s*th variable *x* within group *j*, u_{ij} is the membership value of site *i* within group *j*, and *z* is the "fuzziness parameter," which in this case was set to 3, the value used to produce the fuzzy clustering of the vegetation. The fuzziness parameter can be a value between one, a traditional "hard" classification, and plus infinity, a fuzzy classification with membership values $1/k$ everywhere, where *k* is the number of groups.

We analyzed the association between the fuzzy vegetation classification and the bat community by regression of the bat community variables on the fuzzy-forest membership variable. Where counts were involved, such as in richness and number of rare bat species, we used generalized linear models assuming a Poisson distribution. We used the package GENSTAT 5 release 3.2 (Lawes Agricultural Trust 1993) to fit them.

Results

We captured 2413 individual bats (160 were recaptures for a total of 2573 captures) representing 34 species (Ta-

ble 1). (The total bat fauna of the region includes at least 64 species [Medellín 1994]).

Raw vegetation data indicated that the disturbance gradient was detectable in variables such as herbaceous cover (greater percentage in disturbed conditions), Shannon-Wiener diversity index, number of plant species, number of trees (greater values in undisturbed conditions), and others (Table 2). There was, however, a notable difference between the lowest extreme of the gradient (cornfield) and the subsequent habitats; for example, canopy cover was much lower and grass cover was much higher in the cornfield than in any other habitat. This is partially reflected in the scores of the sites along the fuzzy classification (Fig. 1). Also, the age of oldfields did not seem to follow the gradient, because the older field scores were lower than those from the younger field; therefore, hereafter we do not discern between young or old fields and refer to them collectively as oldfields.

Table 1. Number of captures of bat species in four habitats in the Selva Lacandona of Chiapas, Mexico.

Species	Forest	Cacao	Oldfield	Cornfield
<i>Pteronotus parnellii</i>	20	4	4	
<i>Mormoops megalophylla</i> ^a			1	
<i>Micronycteris megalotis</i> ^a		2	1	
<i>Micronycteris brachyotis</i> ^a	1			
<i>Mimon cozumelae</i> ^a	2	1	4	
<i>Phyllostomus discolor</i> ^a	2		5	
<i>Phyllostomus stenops</i> ^a	3			
<i>Tonatia brasiliense</i> ^a	1	2		1
<i>Tonatia evotis</i> ^a		2		
<i>Trachops cirrhosus</i>	2			
<i>Chrotopterus auritus</i> ^a	5			
<i>Glossophaga soricina</i>	20	53	70	58
<i>Glossophaga commissarisi</i>	15	20	33	27
<i>Lichonycteris obscura</i> ^a				1
<i>Hylonycteris underwoodi</i>				2
<i>Carollia brevicauda</i>	72	159 ^b	250 ^b	45
<i>Carollia perspicillata</i>	49	100	92	60
<i>Sturnira lilium</i>	56	137	102	234 ^b
<i>Artibeus lituratus</i>	76 ^b	82	51	66
<i>Artibeus jamaicensis</i> ^a	73	96	35	30
<i>Enchisthenes bartii</i> ^a	1			
<i>Dermanura phaeotis</i>	6	4	5	3
<i>Dermanura watsoni</i>	17	13	12	15
<i>Platyrrhinus helleri</i>	6	10	17	18
<i>Vampyressa pusilla</i> ^a	1	3		
<i>Vampyrodes major</i>	1			
<i>Chiroderma villosum</i> ^a			1	5
<i>Uroderma bilobatum</i>	7	4	2	4
<i>Centurio senex</i> ^a	1	2		2
<i>Desmodus rotundus</i> ^a	4	3		1
<i>Diphylla ecaudata</i> ^a	1		1	
<i>Thyroptera tricolor</i> ^a	1	1		
<i>Bauerus dubiaquercus</i> ^a	1		2	
<i>Myotis keaysi</i> ^a		1	2	
Total	444	699	690	572

^aRare species, represented by <10 individuals.

^bMost abundant species in each habitat.

Table 2. Average of vegetation variables for each habitat in the Selva Lacandona, Chiapas, Mexico (range in parentheses).

Habitat	No. individual plants	Herbaceous cover (%)	Canopy cover (%)	No. trees 5-10 m tall	No. trees 10-25 m tall	No. trees >25 m tall	Total basal area (cm ²)	No. of species of vascular plants	Shannon-Wiener index
Cornfield	9,183 (3,714-13,137)	79 (72-86.2)	13.1 (0-22.6)	0	0	0	2.3 (0-6.8)	52 (36-61)	1.19 (0.85-1.7)
Young field	754 (745-759)	50.8 (34.9-66.4)	94.8 (89-99)	13.6 (3-21)	17 (0-34)	0	396.8 (12.5-618.1)	82.3 (83-87)	3.24 (3.0-3.5)
Oldfield	740 (732-865)	33.9 (26.4-46.6)	93.2 (90.8-94.6)	2 (1-3)	10.3 (8-15)	2.6 (0-8)	264.6 (210.3-310.3)	70 (52-81)	2.9 (2.4-3.5)
Cacao	3,006 (1,250-4,970)	48 (19.5-70.7)	98.2 (96.5-99.4)	3.3 (1-9)	18 (13-23)	0	429.6 (312.1-534.3)	77.7 (55-109)	2.2 (1.1-3.4)
Forest	910 (730-1029)	27.2 (22.9-30.1)	97.6 (94.1-99.8)	10.6 (3-16)	16.3 (14-18)	1 (1-1)	384 (361.6-428.3)	95 (79-111)	3.4 (2.8-3.8)

Most of the rare species recorded from each habitat (Table 1) were phyllostomid bats (18 out of 22 rare species). Within that family, the subfamily Phyllostominae was the most species-rich (nine species). The forest had the largest number of rare species (15), half of which were phyllostomines, and it had 6 species exclusively recorded in that habitat (four phyllostomines). The cornfield had the lowest number of rare species (6), only 2 of which were exclusive to the habitat (both nectarivorous Glossophaginae). The vampire bat (*Desmodus rotundus*) was recorded in almost all habitats, but in numbers low enough to qualify it as a rare species.

The single most abundant species in each habitat was also indicative of disturbance. In the cacao plantation and oldfield sites (intermediate disturbance levels), the most abundant species were either *Carollia brevicauda* (eight sites) or *C. perspicillata* (one site). In all three cornfields, the most abundant species was *Sturnira lilium*. The most abundant species were different in each of the forest sites: *Artibeus jamaicensis*, *Sturnira lil-*

ium, and *Carollia brevicauda*. These three species were abundant in all habitats, but the fact that the single most abundant species varied among habitats suggests that this is a useful indication of disturbance. In each of the forest sites, the most abundant species represented between 18% and 24% of all bats captured, whereas *S. lilium* represented between 34% and 52% of those captured in the cornfields. The relative difference between the proportion represented by the single and next most abundant species showed a progressively skewed tendency. In the forest and cacao plantation, this difference was slight, but it was large in oldfield and cornfield (Fig. 2). Rarefaction curves showing accumulation of species over time also show the trend in which the forest curve grew faster and higher than the other three habitats, and the cornfield habitat had the lowest accumulated number of species (Fig. 3).

The results of the log-linear regression between bat species richness and the forest-set scores of the vegeta-

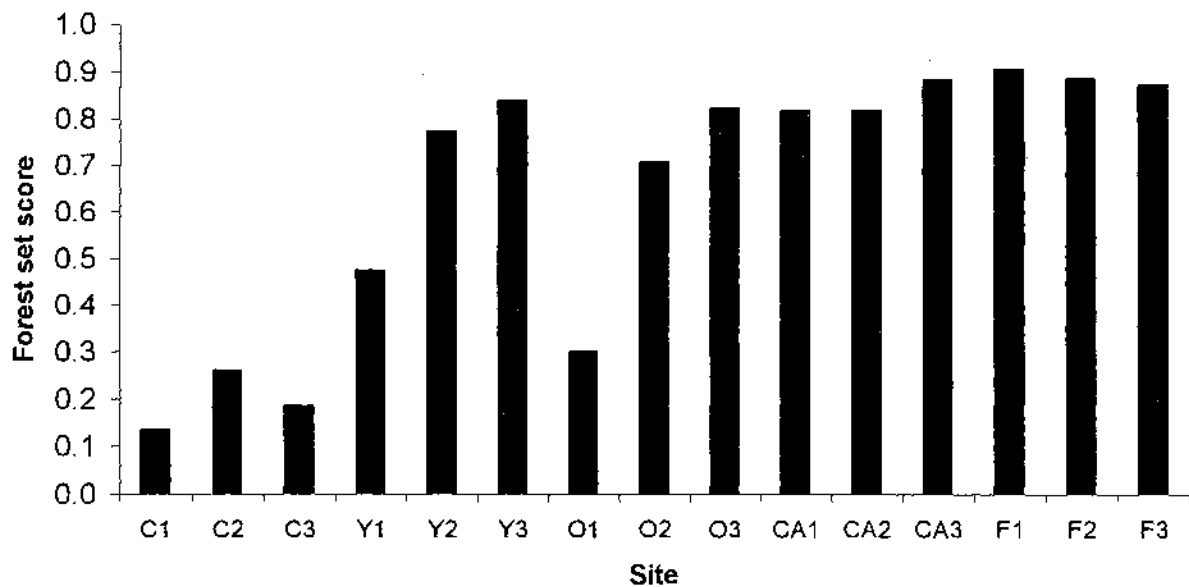


Figure 1. Scores in the fuzzy forest set classification of vegetation in 15 sites (three replicates per habitat) in Chiapas, Mexico, indicating a disturbance gradient (C, cornfield; Y, young abandoned field [8-12 years since abandonment]; O, old abandoned field [>12 years]; CA, cacao plantation; F, undisturbed forest).

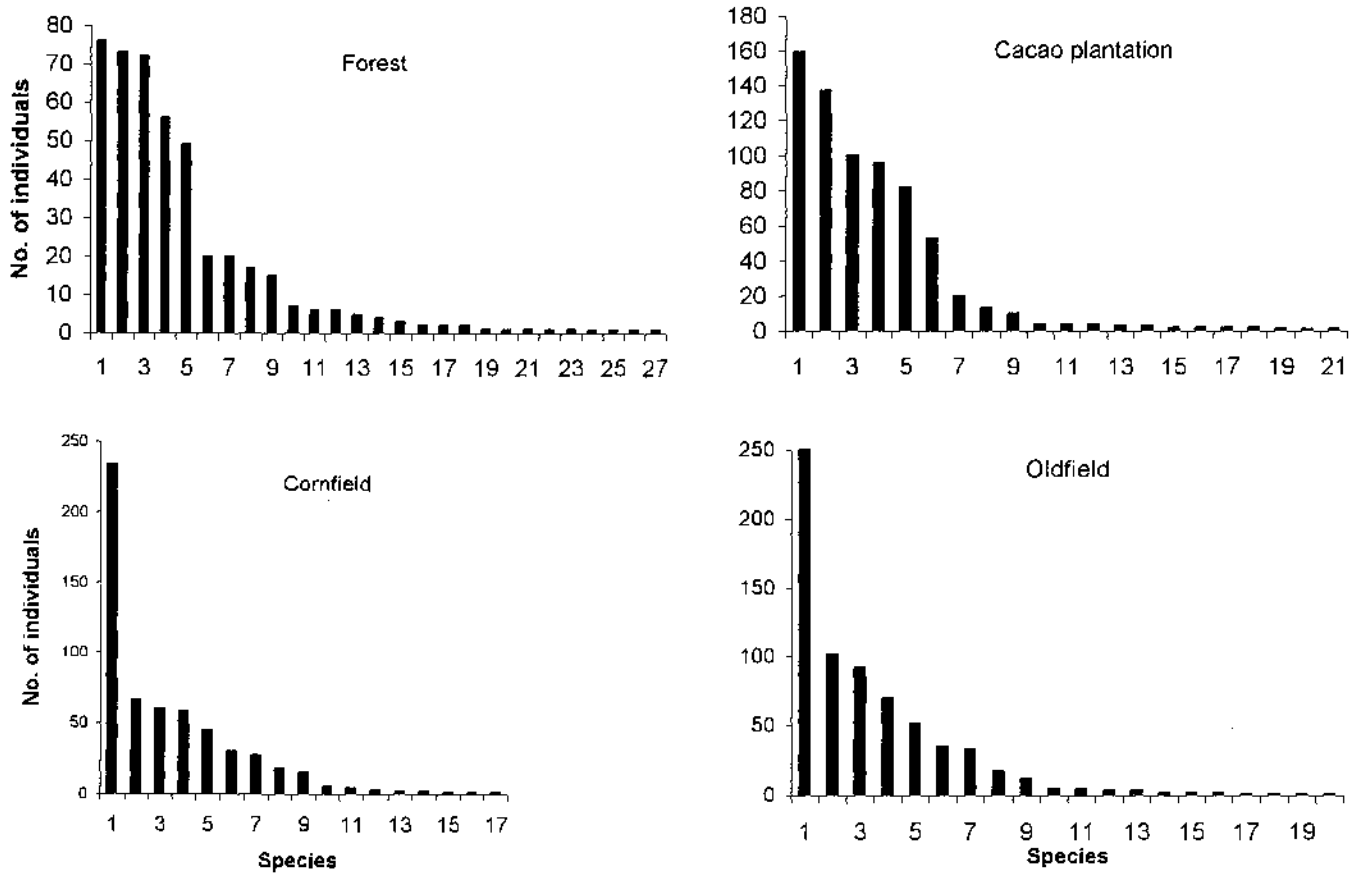


Figure 2. Relative abundance of bat species in three disturbed habitats compared with the original rainforest in Chiapas, Mexico.

tion was positive and significant ($G = 4.31$; $p = 0.03$; proportion of explained deviance, 0.375), as was the correlation between the number of rare species and the degree of membership in the forest set of the vegetation

($G = 6.2$; $p = 0.01$; proportion of explained deviance, 0.24; Fig. 4). Similarly, the regression between the Shannon-Wiener values for the bat community and the degree of membership in the forest set of the vegetation

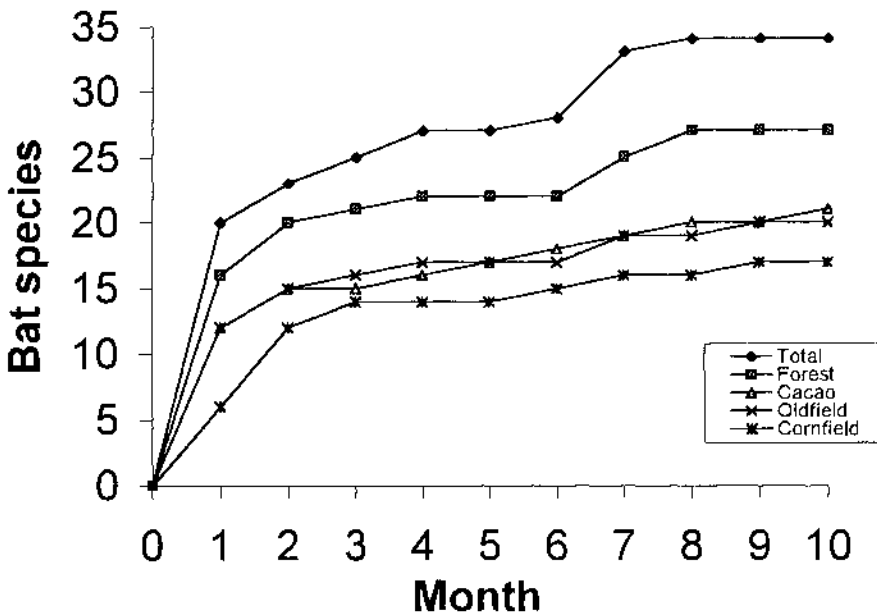


Figure 3. Rarefaction curves showing accumulation of species by month in four different habitats in Chiapas, Mexico.

showed a positive, significant association ($p = 0.01$, $r^2 = 0.35$). The percentage of individuals represented by the single most abundant bat species and the degree of membership in the forest set of the vegetation showed a negative, significant association ($p = 0.01$, $r^2 = 0.35$; Fig. 4).

These four relationships (Fig. 4) showed a consistent pattern of association between the vegetation structure and the basic attributes of the bat community structure. There is a wide spread of points, however, from the low to the high values. Low forest set scores (high disturbance) co-occur with low values in the bat diversity parameters, except, obviously, in the case of relative abundance of the most abundant bat species, where high values co-occurred with high abundance. In contrast, high forest set scores co-occurred with a wider range, including low and high values of the bat community parameters. Bat diversity dropped strongly below forest set

scores of 0.7, which further supports the idea of bats being highly sensitive to forest disturbance.

Discussion

Our results show a significant relationship between bat community parameters and the fuzzy-set vegetation diversity and structure. This demonstrates the utility of this approach in indicating the degree of disturbance of specific areas in the Neotropics. Some key points arise from the literature (e.g., Johns et al. 1985; Fenton et al. 1992; Wilson et al. 1996) which confer robustness on the concept of using bats as indicators of disturbance in the Neotropical rainforest region, especially if the sampling effort is standardized among sites within regions and if vegetation variables are quantified. In all the studies we located, the subfamily Phyllostominae is a sensi-

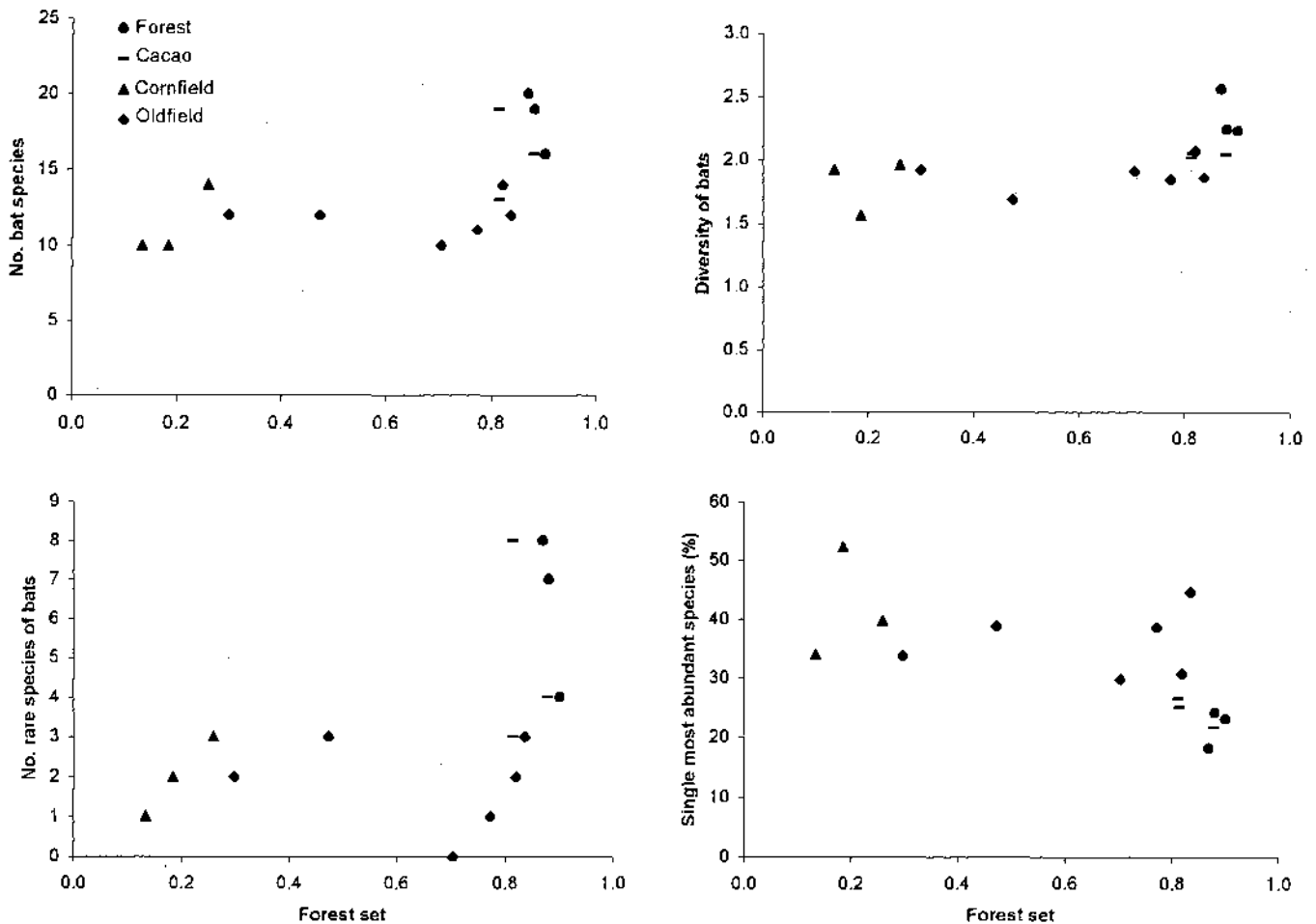


Figure 4. Relationships between four bat community parameters and vegetation fuzzy forest set scores indicating degree of disturbance. On the x-axis, values close to zero indicate habitat disturbance. Bat diversity is measured by the Shannon-Wiener index; rare species are those represented by a total of <10 individuals; and the single most abundant species indicates the percentage of the total number of bats caught at that site represented by the most abundant species.

tive group of species that tends to be represented poorly in disturbed areas. In this sense, they behave as "type I" species, those that indicate ecosystem integrity (Rapport 1992). There is no single species exclusive to the undisturbed forest in the four areas from which data are available (Quintana Roo and Chiapas, Mexico, the Peruvian Amazon, and Panama). *Chrotopterus auritus* was caught only in undisturbed forest in Quintana Roo and Chiapas (Fenton et al. 1992; this study) but was present in both disturbed and undisturbed conditions in Peru (Wilson et al. 1996). *Micronycteris brachyotis*, *Vampyroides major*, and *V. caraccioli* (a sister species in South America) were caught exclusively in undisturbed forest in Peru and Chiapas; the first species was caught in disturbed and undisturbed conditions in Quintana Roo. The most indicative parameter in this sense is the number of species of Phyllostominae caught in any site; these were always greatest in the undisturbed forest. In Peru (Wilson et al. 1996), 14 out of 18 phyllostomine species were caught in undisturbed forest; 7 out of 9 in Chiapas (this study) and all 6 species in Quintana Roo (Fenton et al. 1992) were found in undisturbed forest. In Panama (Johns et al. 1985), gleaning insectivores, a guild that includes phyllostomine species, decreased from 15.3% of all bats netted in an undisturbed area to 1.7% in a disturbed area.

Why do phyllostomines disappear from disturbed areas? This probably has to do with the degree of specialization these bats have reached in niche dimensions such as diet (some are exclusively carnivorous and others glean calling insects from leaves or other surfaces; Belwood 1988) or roost (some species require unfurled *Heliconia* leaves, others termite nests, hollow trees, large and shaded leaves for tent making, or widely varying caves; Timm 1987; Fenton 1992).

Another point of convergence between the Peru study (Wilson et al. 1996) and ours is with respect to the single most abundant species. In the intermediate disturbance sites of both studies, the dominant species was consistently a Carollinae bat (an understory frugivore), whereas in the undisturbed sites no consistency was evident and the dominant species varied, including an *Artibeus*, a *Carollia*, and in Chiapas a *Sturnira* (23%). The latter was consistently dominant in our three cornfields (34%, 39.6%, and 52.3%).

The responses of these bat species to disturbance—and therefore their usefulness as indicators—can be explained by their diet. *Artibeus* is a canopy tree specialist feeding heavily on figs and other forest fruits (Bonaccorso 1979; Handley & Leigh 1991; Gaona 1997). *Carollia* is an understory species feeding heavily on successional trees and tall shrubs such as *Cecropia* and *Piper* (Bonaccorso 1979; Fleming 1988; Gaona 1997). *Sturnira* is a generalist that eats a variety of fruits (Bonaccorso 1979), and in our study site half of its diet was composed of solanaceous small shrubs abundant only in the heavily disturbed sites (Gaona 1997). The use of the single most

abundant species as an indicator has some important implications because they represent the most common species and those that are easiest to detect and most likely to be represented from the start in any sample. Consequently, this approach does not focus on accurate detection of rare species, whose representation on samples is strongly stochastic and therefore hard to standardize through sampling effort. In every case the most common species was a frugivore, whereas nearly all phyllostomines (all rare species) were insectivorous foliage gleaners. In our study sites vampire bats were not as abundant as in other areas (those with heavy cattle presence), which may indicate their original relative abundance levels.

Providing protocols for determining indicator species and how they respond to anthropogenic factors has been identified as a research priority for conservation biology (Soulé & Kohm 1989). Bats, as a community of consumers that occupies various trophic levels, are species-rich, abundant, widespread, ecologically diverse, easy to sample, and responsive to disturbance in a predictable way. They represent an important tool with which to assess the functional integrity of a community. They are a better tool than a group that represents a single trophic level, such as vegetation or top predators (the latter are rare and therefore hard to sample). It is clear then, that bats are useful as indicators of a wide variety of disturbance conditions in Neotropical rainforests because (1) the value of an indicator is applicable only to factors related to the indicator itself (i.e., a marsh bird can only indicate the state of a marsh or a meadow; Beintema 1983); (2) bats consume such a variety of resources, in most cases specializing on a few species (see above; Fenton 1992), (3) bats depend on availability of a wide range of resources and microhabitats; and (4) any type of disturbance in the Neotropical rainforests, from selective logging to clearcutting for agriculture, from cacao plantations that conserve the canopy to cattle ranching, will by necessity affect at least one of the attributes described above. Furthermore, bats are more numerous than all other mammal groups, and their abundance equals or exceeds that of all frugivorous birds (Bonaccorso 1979; Terborgh 1983). Bats have a significant effect on ecosystem processes through ecological interactions (Fleming 1988, 1993; Whittaker 1993). For example, bats disperse more seeds than birds in every step of the disturbance gradient (Medellín & Gaona 1999). These attributes make bats a valuable tool as indicators of habitat disturbance. Our study also shows that bats display the attributes established by Noss and Cooperrider (1994) for community-ecosystem indicators.

We present the first quantitative analysis of the parameters of the bat community as they relate to vegetation structure and diversity in an anthropogenic disturbance gradient through fuzzy logic. The number of rare species, the total number of species in the community, the

Shannon-Wiener value, and the relative abundance of the most common species are associated with the vegetation disturbance gradient in forest set values of >0.7 . These findings show that these traits of Neotropical bat communities can serve as indicators of habitat disturbance and therefore can be useful in assessment of the conservation status of specific sites.

Our results support the idea that high diversity values, indicated by the number of total and rare species as well as Shannon-Wiener values, and low relative abundance of the most common species are indicators of undisturbed habitats. The reverse combination of values, however, may be recorded in both disturbed and undisturbed sites. Also, a high number of phyllostomine species is another indicator of low levels of disturbance.

Our technique of using bats as disturbance indicators has been adopted by at least three biosphere reserves in tropical Mexico to evaluate the conservation state of different areas in each reserve (J. Bezaury, personal communication), and the data are being analyzed to evaluate their usefulness in conservation and reserve management decision making. A single indicator group does not provide a basis for decision making and management for conservation. Because bats are relatively easy to sample, and because the available evidence from three studies in the Neotropics (Quintana Roo and Chiapas, Mexico, and six sites in lowland Peru) agree on several important points, this ubiquitous, diverse, and abundant group of mammals may be used as one important indicator of habitat disturbance in Neotropical rainforests.

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Literature Cited

- Arita, H. T. 1993. Riqueza de especies de la mastofauna de México. Pages 109-128 in R. A. Medellín and G. Ceballos, editors. *Avances en el estudio de los mamíferos de México. Publicaciones especiales. Volumen 1. Asociación Mexicana de Mastozoología, A.C., México, D.F.*
- Beintema, A. J. 1983. Meadow birds as indicators. *Environmental Monitoring and Assessment* 3:391-398.
- Belwood, J. J. 1988. Foraging behavior, prey selection, and echolocation in phyllostomine bats (Phyllostomidae). Pages 601-605 in P. E. Nachtigall and P. W. B. Moore, editors. *Animal sonar*. Plenum Press, New York.
- Bezdek, J. C. 1981. *Pattern recognition with fuzzy objective function algorithms*. Plenum Press, New York.
- Blair, R. B. 1999. Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecological Applications* 9:164-170.
- Bonaccorso, F. J. 1979. Foraging and reproductive ecology in a Panamanian bat community. Pages 359-408 in *The Florida State Museum, Biological sciences bulletin* 24. The Florida State Museum, Gainesville.
- Ceballos, G., P. Rodríguez, and R. A. Medellín. 1998. Assessing conservation priorities in a megadiversity country: patterns of mammalian diversity, endemism, and endangerment. *Ecological Applications* 8:8-17.
- Emmons, L. H., and F. Feer. 1997. *Neotropical rainforest mammals: a field guide*. 2nd edition. The University of Chicago Press, Chicago.
- Equihua, M. 1990. Fuzzy clustering of ecological data. *Journal of Ecology* 78:519-534.
- Erwin, T. L. 1997. Biodiversity at its utmost: tropical forest beetles. Pages 27-40 in M. L. Reaka-Dudla, D. E. Wilson, and E. O. Wilson, editors. *Biodiversity II*. Joseph Henry Press, Washington, D.C.
- Fenton, M. B. 1992. *Bats. Facts on File*, New York.
- Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. Merriman, M. K. Obrist, D. M. Syme, and B. Adkins. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* 24:440-446.
- Fleming, T. H. 1988. *The short-tailed fruit bat*. University of Chicago Press, Chicago.
- Fleming, T. H. 1993. Plant-visiting bats. *American Scientist* 81:461-467.
- Franklin, J. F. 1992. *An ecologist's view of sustainability. Defining sustainable forestry*. Island Press, Washington, D.C.
- Gaona, O. 1997. *Dispersión de semillas y hábitos alimenticios de murciélagos frugívoros en la Selva Lacandona, Chiapas*. Undergraduate thesis. Universidad Nacional Autónoma de México, México, D.F.
- Handley, C. O., Jr., and E. G. Leigh Jr. 1991. Diet and food supply. Pages 147-149 in C. O. Handley Jr., D. E. Wilson, and A. L. Gardner, editors. *Demography and natural history of the common fruit bat, Artibeus jamaicensis, on Barro Colorado Island, Panamá*. Contributions to zoology 511. Smithsonian Institution, Washington, D.C.
- Hill, J. E., and J. D. Smith. 1985. *Bats, a natural history*. Texas University Press, Austin.
- Johns, A. D., D. E. Wilson, and R. H. Pine. 1985. Rain forest bats: an uncertain future. *Bat News* 5:4-5.
- Keddy, P. A. 1991. Biological monitoring and ecological prediction: from nature reserve management to national state of the environment indicators. Pages 249-267 in F. B. Goldsmith, editor. *Monitoring for conservation and ecology*. Chapman and Hall, London.
- Kosko, B. 1993. *Fuzzy thinking: the new science of fuzzy logic*. Hyperion, New York.
- Krebs, C. J. 1989. *Ecological methodology*. Harper & Row, New York.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2:203-217.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. *Conservation Biology* 2:316-329.
- Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conservation Biology* 5:79-89.
- Lawes Agricultural Trust. 1993. *GENSTAT five. Release 3. Reference manual*. Oxford University Press, Oxford, United Kingdom.
- Leck, C. F. 1979. Avian extinctions in an isolated tropical wet forest preserve, Ecuador. *The Auk* 96:343-352.
- Lemmon, P. 1956. A spherical densiometer for estimating forest overstory density. *Forest Science* 2:314-320.
- Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey.

- May, R. M. 1988. How many species are there on earth? *Science* 241: 1441-1449.
- May, R. M. 1990. How many species? *Philosophical Transactions of the Royal Society of London B* 330:293-304.
- Medellín, R. A. 1994. Mammal diversity and conservation in the Selva Lacandona, Chiapas, México. *Conservation Biology* 8:788-799.
- Medellín, R. A., and M. Equihua. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. *Journal of Applied Ecology* 35:13-23.
- Medellín, R. A., and O. Gaona. 1999. Seed dispersal by bats and birds in forest and disturbed habitats in Chiapas, México. *Biotropica* 31: 432-441.
- Mooney, H. A., J. Lubchenco, R. Dirzo, and O. E. Sala. 1995. Biodiversity and ecosystem functioning: basic principles. Pages 275-325 in V. H. Heywood, editor. *Global biodiversity assessment*. United Nations Environment Programme, Cambridge University Press, Cambridge, United Kingdom.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4:355-364.
- Noss, R. F., and A. Y. Cooperrider. 1994. *Saving nature's legacy*. Island Press, Washington, D.C.
- Rapport, D. J. 1990. What constitutes ecosystem health? *Perspectives in Biology and Medicine* 33:120-132.
- Rapport, D. J. 1992. What is clinical ecology? Pages 144-156 in R. Costanza, B. G. Norton, and B. D. Haskell, editors. *Ecosystem health: new goals for environmental management*. Island Press, Washington, D.C.
- Rapport, D. J., J. A. Regier, and C. Thorpe. 1981. Diagnosis, prognosis, and treatment of ecosystems under stress. Pages 121-137 in G. W. Barrett and R. Rosenberg, editors. *Stress effects on natural ecosystems*. Wiley, Chichester, United Kingdom.
- Soulé, M. E., and K. A. Kohm. 1989. *Research priorities for conservation biology*. Island Press, Washington, D.C.
- Terborgh, J. 1983. *Five New World primates. A study in comparative ecology*. Princeton University Press, Princeton, New Jersey.
- Timm, R. M. 1987. Tent construction by bats of the genera *Artibeus* and *Uroderma*. *Fieldiana Zoology (new series)* 39:187-212.
- Whittaker, J. O., Jr. 1993. Bats, beetles, and bugs: more big brown bats mean less agricultural pests. *Bats* 11(1):23.
- Wilson, D. E., and D. M. Reeder, editors. 1993. *Mammal species of the world, a taxonomic and geographic reference*. 2nd edition. Smithsonian Institution Press, Washington, D.C.
- Wilson, D. E., C. F. Ascorra, and S. Solari T. 1996. Bats as indicators of habitat disturbance. Pages 613-625 in D. E. Wilson and A. Sandoval, editors. *Manu, the biodiversity of southeastern Peru*. U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C., and Editorial Horizonte, Lima.
- Wilson, E. O. 1993. *The diversity of life*. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

