Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico

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Abstract

Under the hypothesis that bat diversity would be lower in the early stages of secondary succession and that species affected negatively by habitat modification would be more frequent in later successional stages, we evaluated how bats use 12 vegetation stands representing four stages of secondary succession, following disturbance caused by slash-and-burn agriculture and selective logging. We compared bat richness, abundance and diversity, and found that none of these variables was different among stages or rainy seasons. However, of the 10 most common bat species, two were significantly more abundant in stands at the early stages of secondary succession, while the opposite was true for three other species. Canopy cover mainly explains these patterns. Rainy season had no effect on the abundance of the common species. The results of this study indicate that although some frugivorous species were very abundant in the younger stands, the majority of the rare species were captured in older stands. The absence of rare and habitat-specialized species from young successional stages close to primary forest suggests that, for effective bat conservation in landscapes modified by human activity, areas with original vegetation should be maintained to ensure the survivorship of sensitive-to-deforestation species.

Introduction

Landscape modification and fragmentation are the main causes of the loss of biodiversity on the planet and their effects have been widely documented (Debinsky & Holt, 2000; Sala et al., 2000; Fahrig, 2003). In the tropics, the urgent and constant search for economic development has resulted in the transformation of vast expanses of forest to landscapes comprised of remnants of the original vegetation, and land modified by human activities (Saunders, Hobbs & Margules, 1991). These highly disturbed landscapes are becoming the only available refuge for fauna (Turner & Corlett, 1996; Russell, Swihart & Feng, 2003); hence, an understanding of the degree of sensitivity of each species and the plasticity of their response to different types of habitat modification would be of great value in conservation and management planning.

Bats have a high tolerance of landscape modification owing to their ability to fly and the ease with which they can cross open areas (Kalko et al., 1999; Medellín, Equihua & Amín, 2000). Consequently, most studies have focused on fragments of original vegetation immersed in highly disturbed matrices (Brosset et al., 1996; Schulze, Seavy & Whitacre, 2000), while fragments with relatively low disturbance surrounded by primary forest have received minor attention. Even so, studies demonstrate that owing to differences in the morphology and ecology of species, bats respond to habitat disturbances in different ways. For example, frugivorous species that depend directly on plants as their main source of food benefit from the creation of sites with secondary vegetation but suffer when their foraging or roosting areas are subjected to drastic changes (Jones et al., 2001; Soriano & Ochoa, 2001). Phyllostominae bats, whose refuges, foraging habits and morphology are strongly associated with primary forest, are among the first species to disappear when a disturbance occurs (Norberg & Rayner, 1987; Fenton et al., 1992). The scale, intensity and duration of the disturbance, as well as the characteristics of the surrounding landscape also influence these responses (Estrada, Coates-Estrada & Meritt, 1993; Gorresen, Willig & Strauss, 2005). Under the various combinations of these factors, a bat species may or may not be positively affected. Another outcome, unexplored for bats to date, is that under an intermediate level of disturbance, species richness will be higher than in an undisturbed habitat, as set forth in the intermediate disturbance hypothesis (Connell, 1978).

In this study, we examine how bats use the different elements of a landscape constituted by a matrix of primary tropical evergreen forest that surrounds patches of vegetation in different stages of secondary succession. Our first objective was to evaluate how the number of bat species (richness), abundance of all species (total abundance) and

evenness (diversity) vary between vegetation patches in different stages of succession. Because a greater degree of disturbance is associated with drastic changes in the floristic composition and structure of vegetation, we expected that the shorter the period of time that had elapsed since the disturbance, the greater the number of affected bat species would be, and consequently, the lower bat richness and diversity would be. Our second objective was to identify which bat species differ in their use of vegetation patches at different stages of secondary succession. We expected that (1) species negatively affected by habitat modification (i.e. Phyllostominae) would be found more frequently in later successional stages, while (2) those species that tend to feed in secondary vegetation and open areas (i.e. Carollinae) would be more frequent in sites of early succession than in primary forest. Finally, our third objective was to determine which habitat-specific variables (associated with the successional stage of the vegetation) and landscape variables explain the bats' response. Owing to the notable vagility of the bats, we expected vegetation variables to have greater explanatory power. Specifically, we expected higher bat richness, diversity and abundance to be associated with those stands that had higher plant diversity, higher canopies and greater canopy cover.

Methods

Study area

This study was carried out in the Agua Blanca State Park (ABSP) in the state of Tabasco, Mexico, a 2025 ha reserve run by the inhabitants of the Manatinero–Palomas *ejido* (communal property), located in the physiographical province of the Chiapas Mountain Range (17°35′52″N–92°27′3″W to 17°37′16″N–92°28′43″W; Cruz-Hernández, 1999; Fig. 1). Its climate is warm and humid with rainfall throughout the year.

The mean annual precipitation is 3500 mm, and the mean temperature is 26 °C. Rain is distributed in an abundant rainy season (June–November, mean month of 419.8 mm), and a light rainy season (December–May, mean month of 174.9 mm; INEGI, 1994). Importantly, for bat diversity, the ABSP has a system of caves measuring 5200 m in length (Pisarowicz, 1988). These caverns serve as a refuge for numerous colonies of bats belonging to the families Mormoopidae (five species) and Phyllostomidae (eight species; Castro-Luna, 1999).

Plant diversity is high (*c.* 1950 species) in the ABSP, which has one of the last remnants of natural vegetation in the region (Castillo & Zavala, 1996). The park is mainly tropical evergreen forest (80%), but selective logging and slash-and-burn agriculture is permitted in a section of the reserve. We limited our study area to the section comprised of a mosaic of vegetation patches that have been subjected to different degrees and causes of disturbance, and varying elapsed time of abandonment when secondary succession began (Fig. 1). Based on the type and degree of disturbance, we identified four types of vegetation: (1) tropical evergreen forest (TEF) is the original vegetation of the reserve, and presents the least degree of disturbance; in the study area, this type of forest is only found on the roughest terrain, (2) old secondary growth forest (OSF; 12.6% of the studied area) is the result of selective logging in the TEF during the 1970s, and is characterized by the loss of arboreal cover and the proliferation of secondary vegetation, (3) middle-aged secondary growth forest (MSF) and (4) young secondary growth forest (YSF) are characterized by a greater degree of disturbance and are located in areas that were used for agriculture. They can be distinguished by the amount of time that has elapsed since they were abandoned (8 and 3 years, respectively). We refer to these four vegetation types as successional stages. Both, MSF and YSF, are comprised of 2–3 ha plots (the area used by a local farmer over the
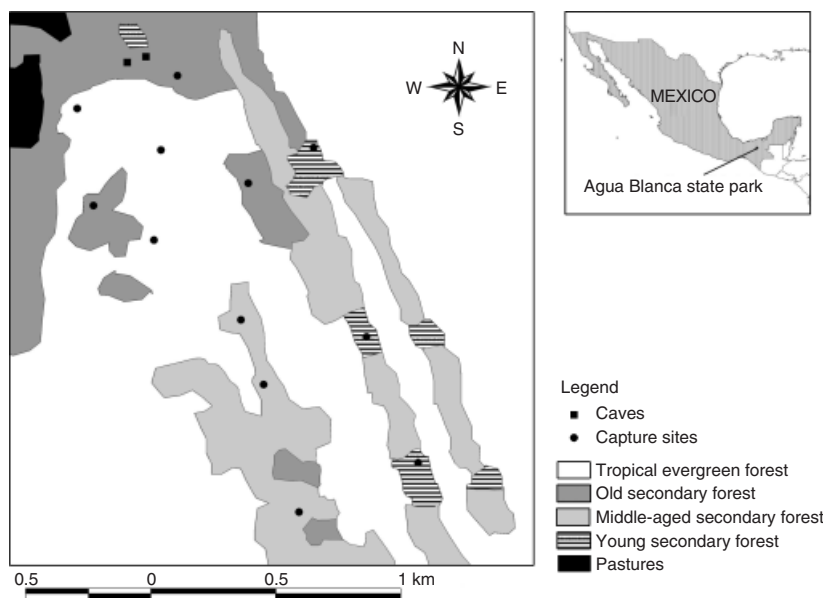
Figure 1 Location of the Agua Blanca State Park in south-eastern Mexico and the sites for bat sampling in each vegetation patch.

Table 1 Explanatory vegetation (structure) and landscape variables (mean ± SE) used in the multiple regression analysis of bat richness, diversity and abundance

| | Successional stage | | | | Type of |
Variable	TEF	OSF	MSF	YSF	variable
Canopy height (m)	33 ± 1	27 ± 3	12 ± 9	7 ± 1	Vegetation
Canopy cover (%)	90 ± 2	78 ± 5	38 ± 1	29 ± 5	Vegetation
Herbaceous cover (%)	65 ± 8	56 ± 12	55 ± 8	74 ± 8	Vegetation
Woody cover (%)	87 ± 7	83 ± 4	81 ± 3	71 ± 6	Vegetation
Plant diversity (H')	3.14 ± 0.06	3.11 ± 0.07	3.28 ± 0.07	3.30 ± 0.06	Vegetation
Distance to the forest edge (m)	0	137 ± 16	62 ± 16	82 ± 38	Landscape
Distance to the caves (m)	563 ± 178	430 ± 250	1286 ± 137	1625 ± 381	Landscape

TEF, tropical evergreen forest; OSF, old secondary growth forest; MSF, middle-aged secondary growth forest; YSF, young secondary growth forest.

course of an agricultural cycle) that differ depending on what each farmer has used them for, the intensity of management and crop type. See Supplementary Materials Appendix S1 for the plant species composition of the different vegetation types.

Sampling design and bat capture

We selected three sampling sites for each successional stage, with a distance of at least 300 m between them. We chose sites according to the availability of each successional stage and their accessibility, that is the presence of paths and topography that allowed the nets to be erected. In the YSF and MSF, we chose sites on plots that were 2–3 ha in size and had been abandoned for a similar length of time. To ensure species representation, from November 2002 to November 2003, we made 10 sampling expeditions spending one night at each selected site, and randomly sampled the sites during periods close to the new moon. From the fourth expedition onwards, we eliminated one capture site per successional stage, leaving two sites per stage.

Bats were captured with 10 mist nets (9 m long × 2.6 m high) that were hung in the understory, opened at sunset and checked every 30 min for the 6 h they were in place. Sampling effort was 552 h over 92 sampling nights for 5520 net hours evenly divided among the four successional stages studied. Bats were identified to the species level using field keys (Medellín, Arita & Sánchez, 1997). Taxonomy follows Ramírez-Pulido, Arroyo-Cabrales & Castro-Campillo (2005). To identify recaptures between successional stages, we placed a numbered plastic collar on each bat (except Vespertilionidae).

Habitat-specific variables: successional stage of the vegetation

In each site that was sampled for bats over the course of a year ($n = 8$), we marked out four 10 × 10 m plots to record woody species. Within each of these, we placed three 2 × 2 m quadrats to record herbaceous species. For these plots, we estimated the plant diversity and cover per species using a one to nine logarithmic scale (Van der Maarel, 1979). With-

in the 100 m^2 plot, we visually estimated the canopy cover, its mean height and the per cent cover of woody and of herbaceous species (Van der Maarel, 1979), variables that we consider suitable descriptors of changes in the vegetation structure associated with the degree of secondary succession (Table 1).

Landscape variables

The landscape variables considered were the distance to the forest edge and the distance to the caves' entrances (see Table 1), assuming that the primary forest and the caves are the most likely sources of bat species in the park. To measure these variables, we plotted the coordinates, taken at the centroid of the 10 mistnets' locations, for our sites and the entrances to the caves (determined using a handheld global positioning system) on a geographical information system of the study area prepared by interpreting LANDSAT^{ETM+} (28-03-2000) satellite images and verified by extensive field excursions. Using ArcView 3.2 (ESRI Systems, Redlands, CA, USA) software, we calculated the linear distance from each sampling site to the caves and to the edge of the closest primary forest.

Statistical analyses

We estimated bat species richness, fitting accumulation curves for each successional stage, using the program EstimateS, version 7.0 (Colwell, 2004). To eliminate the influence of the order in which sampling was carried out, and to smooth out the species accumulation curves, sampling order was randomized 1000 times (Longino & Colwell, 1997). To ensure a good representation of bat richness for each successional stage, we used the following estimates: ICE, Chao2 and Bootstrap (Colwell, 2004). We set 90% estimated richness as a satisfactory level of sampling efficiency (Moreno & Halffter, 2001).

We defined bat abundance as the number of captures. Because bat abundance may change with season in the tropics (Kalko, 1998), we took this variation into account by grouping captures in the two different rainy seasons at the study area (adding the captures from five sampling

expeditions in each season). We tested for differences in richness, diversity (estimated by the Shannon–Wienner index; Magurran, 1988), and total bat abundance, among successional stages, seasons and their interaction levels, using a repeated measures MANOVA to deal with the correlation of these three variables. We treated season as the between-subject factor and successional stage as the within-subject factor to maximize the power of the test for the factor we were most interested in: successional stage (Sahai & Ageel, 2000). To assess the effect of successional stage and season on the abundance (total captures per season) of the more common ($n > 30$) bat species, we fitted linear mixed-effect models (Pinheiro & Bates, 2000). Succession stage, season and their interaction were treated as fixed factors and the replicate as a random one. When significant effects were found, we used contrasts to investigate differences between factor levels. Recaptures were not included in the analyses. Count data were normalized using the logarithm function before carrying out the analyses.

To determine which vegetation and landscape variables explained the abundance of the most common species, we used a stepwise multiple regression with the Akaike information criterion to retain independent variables in the minimum adequate model (Crawley, 2002). The pool of variables with which we started the regressions is listed in Table 1. We also included a dummy variable to label the season (Cottingham, Lennon & Brown, 2005) and assumed that there were no important interactions among the independent variables in order to avoid running out of degrees of freedom. In these analyses, we only used the data of the eight sites where we had measured the vegetation structure variables (8 sites × 2 seasons – 1:15 total d.f.). Independent variables measured as percentages were transformed before analysis using the $\sin^{-1}\sqrt{p}$ function. All statistical analyses were run using the S-Plus 2000 program (MathSoft, 1999).

Results

Results at the community level: richness, diversity and sample representativeness

We captured 2264 bats, of which 180 (8%) were recaptures, for 2084 individuals belonging to 34 species and four families (Table 2). The fitted species accumulation curves for each successional stage showed similar tendencies, except for MSF, for which the asymptote indicates notably lower species richness (Fig. 2). Values superior to or near 90% of the estimated number of species were reached for all four successional stages, indicating data representative of the bat assemblages (mainly Phyllostomidae and Mormoopidae) in the study area (Table 2).

Bat richness, diversity and total abundance were statistically indistinguishable among the successional stages of vegetation and seasons. The interaction of these two factors was not significant (Table 3). However, nine species were captured in only the oldest stages, and five species were captured in only the youngest stages.

Results at the species level

Of the 10 species analyzed, abundance was significantly different for six among successional stages (Fig. 3): *Artibeus jamaicensis* was more abundant in OSF and TEF (Linear mixed models: $F_{3,8} = 21$, $P < 0.001$), whereas *Artibeus lituratus* was frequently captured in all stages but MSF ($F_{3,8} = 6.84$, $P < 0.013$). *Natalus stramineus* and *Pteronotus parnelli* were more frequent in TEF than in the early stages of secondary succession (YSF and MSF; $F_{3,8} = 6.28$, $P < 0.017$, and $F_{3,8} = 4.01$, $P < 0.052$), while the opposite was observed for *Carollia perspicillata* and *Sturnira lilium* ($F_{3,8} = 6.25$, $P < 0.017$, and $F_{3,8} = 5.37$, $P < 0.026$, respectively). Four species exhibited no pattern at all with respect to the degree of succession in the vegetation: *Carollia sowelli, Dermanura phaeotis, Desmodus rotundus* and *Glossophaga soricina* ($F_{3,8} < 3.33$, $P > 0.07$ in all cases). There were no differences in abundance for any of these 10 species in relation to season ($F_{1,2} < 13.29$, $P > 0.06$ in all cases); similarly, there was no significant interaction between season and successional stage ($F_{3,8} = 3.25$, $P < 0.07$).

Relationship between bats and the successional stage of the vegetation

The vegetation variables (surrogates for successional stage) explained ($P < 0.05$) the abundance of six bat species (Table 4). In contrast, *S. lilium* was the only species for which a landscape variable, distance to forest edge, had explanatory power. Canopy cover explained the greatest per cent of the variation in all the fitted models whether alone or in combination with woody and/or herbaceous cover. The abundances of *C. perspicillata* and *S. lilium* were inversely proportional to canopy cover, while the abundances of *A. jamaicensis, A. lituratus, P. parnelli* and *N. stramineus* were directly proportional to canopy cover.

Discussion

Results at the community level

Our first objective was to evaluate whether bat richness, diversity and total abundance vary across successional stages of a tropical evergreen forest. Contrary to our expectations, none of these variables was significantly different among stages. However, this similarity in richness and diversity is due to compensation caused by significant changes in the relative abundance and composition of species. These results support the intermediate disturbance hypothesis, which states that due to the different responses of species to disturbances, a mixture of different successional stages of vegetation can promote high species diversity (Connell, 1978; Sheil & Burslem, 2003). Apparently, a matrix of mature forest with patches of secondary vegetation provides more niches for bats than intact forests do. Nevertheless, it would be valuable to corroborate our findings with further studies, as we cannot rule out the possibility that our failure to find any differences among

Table 2 Total bat richness, diversity and abundance in four secondary successional stages of tropical evergreen forest in the Agua Blanca State Park, Tabasco, Mexico

Family	Subfamily	Species	Guild	Successional stage				Total
				TEF	OSF	MSF	YSF	
Mormoopidae		*Mormoops megallophylla*[a]	Aein	0	1	0	0	1
		Pteronotus davyi	Aein	0	15	0	0	15
		Pteronotus parnelli	Aein	78	72	20	10	180
Phyllostomidae	Micronycterinae	*Lampronycteris brachyotis*[a]	Glin	1	1	0	0	2
		Micronycteris microtis	Glin	4	8	8	4	24
		Micronycteris schmidtorum[a]	Glin	3	0	0	0	3
	Phyllostominae	*Lonchorhina aurita*[a]	Glin	1	0	0	3	4
		Lophostoma brasiliense[a]	Glin	0	0	0	2	2
		Lophostoma evotis[a]	Glin	3	2	0	0	5
		Mimon crenulatum[a]	Glin	0	1	0	0	1
		Mimon cozumelae	Glin	8	2	0	0	10
		Phyllostomus discolor[a]	Nec	0	0	0	2	2
		Trachops cirrhossus[a]	Glin	2	2	0	0	4
		Chrotopterus auritus[a]	Car	3	1	0	0	4
	Glossophaginae	*Glossophaga soricina*	Nec	49	131	63	162	405
		Hylonycteris underwoodii	Nec	1	6	2	4	13
	Carollinae	*Carollia sowelli*	Fru	84	140	286	147	657
		Carollia perspicillata	Fru	7	27	36	31	101
	Stenoderminae	*Sturnira lilium*	Fru	11	32	61	82	186
		Platyrhinus helleri	Fru	2	11	1	15	29
		Uroderma bilobatum	Fru	0	0	1	9	10
		Vampyressa pussilla	Fru	8	4	0	9	21
		Chiroderma salvini[a]	Fru	0	0	0	2	2
		Chiroderma villosum[a]	Fru	1	0	0	0	1
		Artibeus jamaicensis	Fru	78	46	6	4	134
		Artibeus lituratus	Fru	39	44	7	39	129
		Dermanura phaeotis	Fru	24	49	46	49	168
		Dermanura tolteca[a]	Fru	0	0	0	1	1
		Dermanura watsoni	Fru	3	8	5	1	17
		Centurio senex	Fru	3	4	1	9	17
	Desmodontinae	*Desmodus rotundus*	San	16	12	1	3	32
Natalidae		*Natalus stramineus*	Aein	34	39	4	3	80
Vespertilionidae		*Myotis californicus*[a]	Aein	2	0	0	1	3
		Myotis keaysi[a]	Aein	0	1	0	0	1
Total				366	659	548	691	2264
Diversity (*H'*)				2.42	2.44	1.65	2.15	2.35
Recorded species richness				25	25	16	23	34
Estimated species richness[b]				28	30	19.4	24.5	38.2
% Coverage of species richness				89.3	83.3	82.5	93.9	89

TEF, tropical evergreen forest; OSF, old secondary growth forest; MSF, middle-aged secondary growth forest; YSF, young secondary growth forest. Guild code: Fru, frugivore; Nec, nectarivore; Glin, gleaning insectivore; Aein, aerial insectivore; Car, carnivore; San, sanguivore.
[a]Rare species ($n < 10$) in the study area.
[b]Based on the average of three non-parametric estimators: ICE, CHAO2 and Bootstrap.

successional stages was not also related to low power in our MANOVA tests (due to few replicates and several dependent variables) (Von Ende, 1993).

The capture of bats belonging to families that were barely represented (Vespertilionidae) or absent (i.e. Molossidae) could be considered incidental, given that the sampling technique used in this study underestimates their abundances (Kalko, Handley & Handley, 1996). However, as they do not respond significantly to habitat perturbation, we do not feel this has affected our results (Fenton *et al.*, 1998; Stevens, Willig & Gamarra de Foz, 2004). Differences in the foraging height of some species could also have biased the probability of capturing them (Bernard, 2001; Kalko & Handley, 2001). For these reasons, our conclusions apply mainly to the Phyllostomidae and Mormoopidae families, as they are usually well represented when mistnets are used (Moreno & Halffter, 2001). Long-term studies using other sampling techniques (i.e. ultrasound detectors) could provide a more complete picture of bat community changes after habitat disturbance.
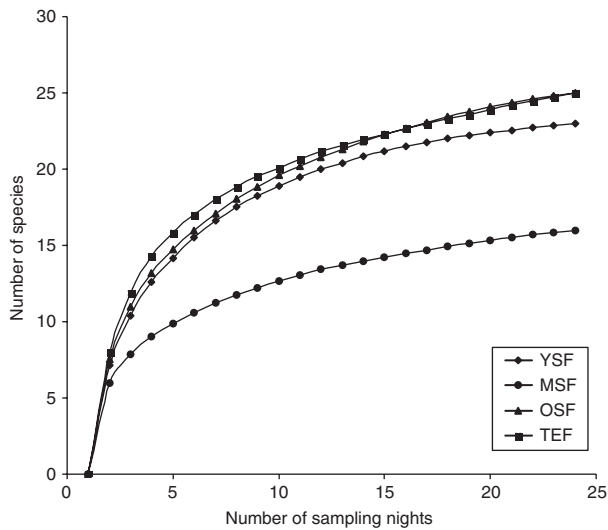
Figure 2 Fitted accumulation curves for the bat species inhabiting four vegetation successional stages (TEF, tropical evergreen forest; OSF, old growth secondary forest; MSF, middle-aged secondary growth forest; YSF, young secondary forest) in the Agua Blanca State Park, Tabasco, Mexico.

Results at the species level

The second objective of this study was to determine which, if any, bat species use successional stages differently. We found that six species exhibited a bias toward at least one successional stage in their capture frequency. We recognize that after an experiment-wise error rate correction of the significance level, the abundance of only one species (*A. jamaicensis*) varied among successional stages. However, the trends for the other species remain strong, and we have not applied a Bonferroni's correction in this study due to the recent critique of this approach (Moran, 2003).

For frugivorous species, our results can be explained by the diet of each species: the *Artibeus* species feeds mainly from canopy trees (Morrison, 1978; Bonaccorso, 1979) and its lower abundance in MSF and YSF could result from the fact that their original vegetation had been completely cleared and replaced by secondary vegetation. *Artibeus lituratus* was also captured frequently in YSF because some pioneer plants regularly constitute part of its diet (Charles-Dominique, 1986; Lobova *et al.*, 2003). Additional observations indicate that the fruit preferred by *A. jamaicensis* in the

Table 3 Summary of a repeated measure MANOVA to assess the effect of successional stage, season and their interaction on the correlated response variables richness, evenness (diversity) and total abundance

| Factor	Pillai's trace	Statistic	P
Successional stage	1.053	$F_{9,30}=1.80$	0.1091
Rainy season	0.192	$F_{3,8}=0.64$	0.6131
Successional stage × season interaction	0.372	$F_{9,30}=0.47$	0.8824

study area are *Poulsenia armata* and *Spondias radlkoferi* (A. A. Castro-Luna, unpubl. data), that is, those that are dominant in TEF, but scarce or absent from MSF and YSF (see Supplementary Material Appendix S1). In contrast, all the frugivorous bat species that were most frequent in MSF and/or YSF have a diet based on plant families like Piperaceae (*C. perspicillata*), which form part of secondary vegetation (Heithaus & Fleming, 1978; Fleming, 1988).

Inferences based on diet also explain why capture frequencies for *C. perspicillata* and *A. jamaicensis*, which are capable of flying great distances in a single night (13.2 and 10 km, respectively; Heithaus & Fleming, 1978; Morrison, 1980; Charles-Dominique, 1991), differed between adjacent successional stages with different floristic compositions. This argument is supported by the recaptures, the majority of which occurred in the same vegetation stand where the bats were originally caught (see Supplementary Material Appendix S2). Both the relatively high total per cent recapture (9%) and per cent recapture at the same stand of first capture (80%) suggest that a high proportion of bat species are either residents or recurrent visitors of specific successional stages of vegetation. In the cases of *N. stramineus* and *P. parnelli* (aerial insectivores), their highest abundance in TEF and OSF could be related to their foraging habits, which are associated with spatially complex environments, such as the forest interior (Kalko *et al.*, 1996; Jennings *et al.*, 2004).

Regarding the species for which abundance did not differ between successional stages, it is known that these species can modify their diets and behavior and therefore take advantage of the opportunities that are available in landscapes that have been modified for agricultural activities (Wilkinson, 1985; Racey & Entwistle, 2003). The results we present corroborate the high ecological plasticity of these species.

Relationship between bats and the successional stage

Our results demonstrate that bat abundance in the study area varied more as a function of vegetation variables than of the landscape variables we studied, and were consistent with findings for vespertilionid bats at the microhabitat level (Walsh & Harris, 1996; Zimmerman & Glanz, 2000; Gehrt & Chelsvig, 2003). At the vegetation (habitat) level, the variable with the greatest explanatory power was canopy cover, the importance of which has already been indicated with respect to bat movement and foraging behavior (Crome & Richards, 1988; Gorresen & Willig, 2004; Ford *et al.*, 2005). The importance of this variable to bat species could result from (1) its effect on the risk of predation by owls and hawks (Fenton *et al.*, 1992; Estrada *et al.*, 1993) and (2) its association with the plant species bats use as a resource (food, refuge, perching sites). Regarding the first point, it has been proposed that greater canopy cover could be associated with a decreased risk of predation. However, the main limitation of this argument has been the lack of direct corroborating evidence. A more plausible explanation
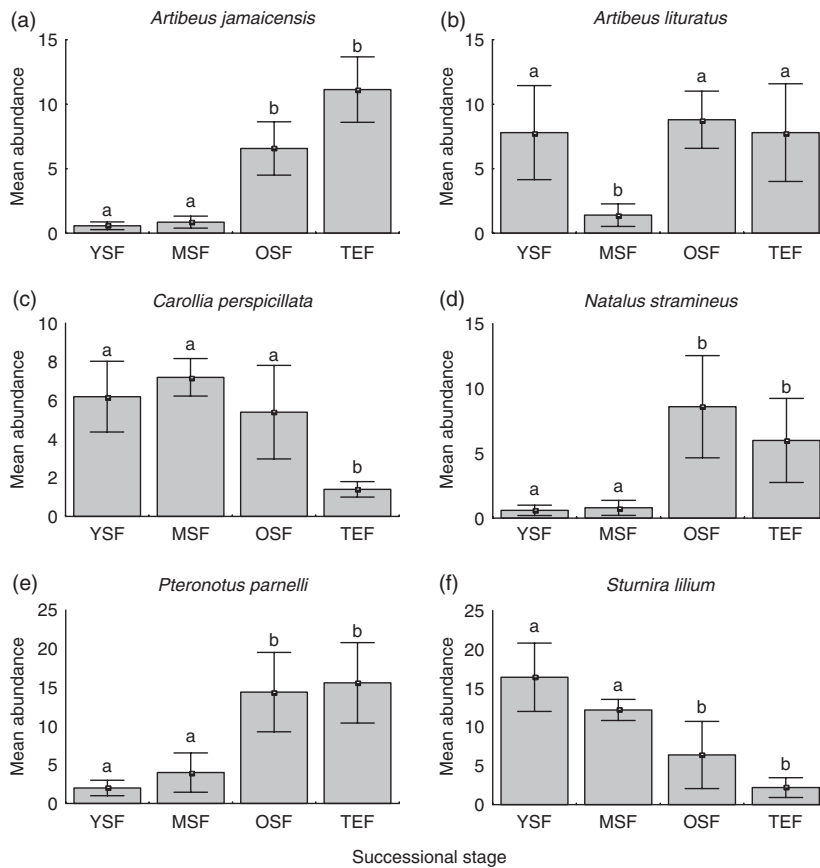
Figure 3 Vegetation had a significant effect on the mean abundance across rainy seasons (±SE) for the six most abundant bat species of the Agua Blanca landscape. YSF, young secondary growth forest; MSF, middle-aged secondary growth forest; OSF, old secondary growth forest; TEF, tropical evergreen forest. Columns marked with different letters were significantly different.

Table 4 Local and landscape variables of vegetation stands that accounted for bat species abundance in the Agua Blanca State Park, Tabasco, Mexico in multiple linear regression models

Species	MODEL Explanatory variables	Coefficients	R^2	Statistic
Artibeus jamaicensis	Intercept**	−0.93	0.84	$F_{2,13}=34.15$***
	Canopy cover***	1.77		
	Herbaceous cover*	0.86		
Artibeus lituratus	Intercept**	2.32	0.56	$F_{3,12}=5.03$***
	Canopy cover*	1.15		
	Woody cover*	−2.75		
	Season*	−0.18		
Carollia perspicillata	Intercept***	2.69	0.42	$F_{1,14}=10.28$**
	Canopy cover*	−1.71		
Natalus stramineus	Intercept**	−0.24	0.52	$F_{1,14}=14.89$**
	Canopy cover***	1.27		
Pteronotus parnelli	Intercept*	−0.29	0.75	$F_{1,14}=42.21$***
	Canopy cover***	1.58		
Sturnira lilium	Intercept**	−3.49	0.81	$F_{3,12}=17.04$***
	Canopy cover***	−1.99		
	Plant diversity**	1.88		
	Distance to the forest edge*	−0.27		

*$P<0.05$; **$P<0.01$; ***$P<0.001$.

is that canopy cover is associated with plant resources. This is a reasonable interpretation, given that all the species for which there was a negative relationship with canopy cover

are mutualists with plant species that make up secondary vegetation (i.e. the genera *Piper*, *Cecropia*, *Solanum*) (Charles-Dominique, 1986; Fleming, 1988; Brosset *et al.*,

1996). The species for which there was a positive relationship with this variable were canopy frugivores and aerial insectivores, all of which forage in forested sites.

We do not conclude from this study that landscape variables are not influencing bat diversity, as bats may respond to both the local and regional characteristics of a landscape over a range of scales (Kotliar & Wiens, 1990; Gorresen *et al.*, 2005). In our study area, the relatively small size of patches and the distance among them may have masked the effect of landscape variables that work on larger spatial scales.

To conclude, contrary to expectations, the richness, diversity and total abundance of bats were not correlated with the succession of vegetation. However, for the landscape's present configuration, changes in the relative abundance and composition of individual bat species were detected across successional stages. In spite of the proximity of vegetation patches, the distances among them and to the primary forest, some bat species select specific succession stages, and this selection is correlated positively or negatively with the canopy cover and floristic composition of the vegetation stand. As a result of this, and in accordance with the intermediate disturbance hypothesis, overall bat richness is greater over the patchy landscape than in the forest. Nevertheless, our results strongly indicate that we need to preserve the remaining areas of primary vegetation in landscapes that have been modified by human activities, to guarantee the persistence of the rare and habitat-specialist species that would otherwise be negatively affected.

Acknowledgements

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Supplementary material

The following material is available for this article online:

Appendix S1. Description of the four successional stages sampled.

Appendix S2. Bat recaptures in the same or different successional stage at the first capture.

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-1795.2006.00097.x primary_article

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