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Bird communities in rainforest fragments: guild responses to habitat variables in Tabasco, Mexico

Stefan L. Arriaga-Weiss · Sophie Calmé · Christian Kampichler

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Abstract The effects of habitat loss and fragmentation in tropical forests are difficult to separate, as they usually occur concurrently. In the state park La Sierra, in Tabasco, Mexico, the rainforest is being cleared for pasture, and fragments are being used by local inhabitants. This study examined the response of bird feeding guilds to habitat characteristics, including human disturbance, in five fragments of different sizes (1 ∼ 4,500 ha, 2 ∼ 150 ha, and 2 ∼ 80 ha). Using point count observations, 125 species were recorded and were grouped into 11 feeding guilds. As expected, the largest fragment had higher species richness and abundances than the smaller fragments. However, five habitat features differed significantly among fragment sizes, including tree density, the number of tree stumps and the number of trails. Thus the larger fragment was also less disturbed. Fragment size alone was significant only for scavenger species richness, and for the abundance of bark gleaning insectivores and insectivore/nectarivores. Raptors were more diverse and abundant in the large fragment and less disturbed sites. Arboreal frugivores and bark or foliage gleaning insectivores, depended on higher trees and less disturbed sites. A better understanding of the mechanisms that affect persistence is essential for the planning of conservation actions.

Keywords Birds · Feeding guild · Fragment size · Habitat structure · Mexico · Tropical rainforest fragmentation

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S. L. Arriaga-Weiss (✉) · C. Kampichler
División Académica de Ciencias Biológicas,
Universidad Juárez Autónoma de Tabasco,
Km 0.5 Carretera Villahermosa-Cárdenas, Villahermosa, Tabasco 86100, Mexico
e-mail: slaw2000@prodigy.net.mx

S. L. Arriaga-Weiss · S. Calmé
Conservation of Biodiversity Area,
El Colegio de la Frontera Sur, AP 424,
Chetumal, QR, Mexico

Introduction

Tropical forests are deteriorating rapidly through deforestation and habitat fragmentation, which are major causes of biodiversity loss (Wilcox and Murphy 1985; Turner 1996; Laurance 1999; Debinski and Holt 2000). Thus, the relative effects of rainforest fragmentation and degradation have become important issues for conservation biology and protected area management.

At the landscape level, habitat fragmentation has three main effects: degradation of habitat quality and extent (e.g., rainforest); separation of habitat fragments by an anthropogenic matrix (e.g., pasturelands, settlements); and increased intensity of edge effects (Saunders et al. 1991; Forman 1995). Fragmentation also has a well-documented effect on biodiversity, which has been well studied in birds. Intensity and type of response substantially depend on the natural history and ecology of each species (Simberloff 1994). Habitat changes particularly affect less abundant and range-restricted birds, rainforest specialists and altitudinal migrants (Brooks et al. 1999; Raman 2001). Other factors that influence species vulnerability to habitat degradation (e.g. selective logging) include: habitat specialization (Estrada et al. 1997; Thiollay 1999; Beier et al. 2002; Watson et al. 2004); life history traits, such as large territories; sedentary lifestyles and preference for mature forest (Stratford and Stouffer 1999); body size (Turner 1996; Castelletta et al. 2000); dispersion capacity (Johns 1991; Şekercioĝlu et al. 2002); and diet (Kattan et al. 1994; Renjifo 1999; Castelletta et al. 2000; Dale et al. 2000). An ultimate effect of habitat fragmentation and degradation is the reduction of population size and an increased vulnerability to extinction (Simberloff 1994). This makes many resident species in tropical forests particularly at risk, as they are sparsely distributed and do not tolerate conditions outside the forest (Turner 1996).

Foraging guilds may be useful tools for examining changes in species-rich communities because their functional organization can be investigated even if they do not share any species (Terborgh and Robinson 1986). This is the case when analyzing fragmentation effects. For example, insectivores of understory or terrestrial microhabitats are rarely resilient to the more severe forms of disturbance (Johns 1991), and large canopy frugivores, understory insectivores, and forest interior raptors are particularly vulnerable to fragmentation (Johns 1991; Kattan et al. 1994; Renjifo 2001; Stratford and Stouffer 1999; Newmark 2006). Many rainforest understory insectivores are specialists in their foraging techniques, use specific habitats and microhabitats, are sedentary and have large territories (Terborgh et al. 1990; Stouffer and Bieregaard 1995b). Thus, it is not trivial to assess the role of habitat factors on rainforest feeding guilds.

The state of Tabasco (25,000 km^2), in southern Mexico, has not escaped the phenomena of deforestation and habitat fragmentation (Pérez et al. 2005). Alteration has occurred because of slash and burn agriculture and logging (Tudela 1989). Rainforest originally covered 60% of the state's area, but presently only covers 4–6%, mostly on the mountains to the south (Tudela 1989). In this area, approximately 25% of the tropical rainforest of the Sierra de Tapijulapa remains interspersed in a pasture-dominated matrix, with subsistence agriculture and secondary growth (Galindo-Alcántara et al. 2004). The Sierra has been identified as an Important Bird Area due to its high avian diversity with approximately 300 species recorded (Arriaga-Weiss et al. 2000).

In this paper we aimed to determine the influence of habitat characteristics, including degree of human disturbance, on resident bird feeding guilds in different sized rainforest fragments. We hypothesized that resident bird communities would differ in feeding guild composition with respect to habitat characteristics in addition to fragment size. We predicted that bird communities in less disturbed sites would differ from bird communities in more disturbed sites in relation to guild composition. Specifically, we predicted that insectivores, frugivores and raptors would be negatively influenced by perturbation and reduction of fragment size.

Study area

This study was conducted in the Parque Estatal de la Sierra (17°25′ N–17°40′ N; 92°37′ W–92°52′ W), a legally protected area in the Teapa and Tacotalpa municipalities of Tabasco, Mexico. The 16,000-ha park lies in the foothills of the Sierra Madre de Chiapas mountain range (Fig. 1). The mean annual rainfall and temperature are 3,200 mm and 24.5°C, respectively. Rainfall is distributed from June to February, generally interrupted by a mild dry season from March to May (Cardoso 1979). A major physical feature of the park is its very rugged topography with inclinations up to 70%.

Despite its status as a protected area, human activities are continuously modifying the tropical rainforest in the park, mainly by conversion to pasture and agriculture, a process that started 60 years ago. As a result, the park's landscape consists of intermixed natural and anthropogenic habitats. Human activities, mainly cattle ranching and to a lesser extent corn production, influence 71.2% of the area (Fig. 1). The remaining tropical rainforest is highly fragmented and largely restricted to mountaintops and very steep slopes. Not only is the park's biodiversity affected by habitat alteration and fragmentation, but also by other human activities such as subsistence hunting and subsistence selective wood extraction.

Methods

Selection of sites

Five study sites were selected based on field surveys and land-cover maps. Sites were selected only if they were covered by mature forest. Nevertheless, no site in the area was undisturbed, and all presented signs of anthropogenic disturbance (e.g., trails, sparse tree stumps, animal traps). Selection of sites was constrained by the scarcity of fragments <80 ha without signs of significant human activity. We finally established one large rainforest fragment, the only remaining in the region (~4500 ha, LF), two medium fragments (~150 ha, MF), and two small fragments (~80 ha, SF). All sites were located between 60 and 400 m-elevation. Potential sites at higher elevation were not considered because the bird and vegetation communities would include submontane species.

Habitat description

We predicted that the bird community composition would vary with vegetation structure and degree of human disturbance, so we characterized each sampling point by measuring a set of variables. The variables were chosen to represent a range of vertical structure, tree density and habitat complexity measurements that are known to be affected by human activities (Bentley and Catteral 1997).

Coverage of the three most conspicuous vegetation layers, namely herb (HECOV), shrub (SHCOV) and canopy (TRCOV), was visually scored as the percentage of ground

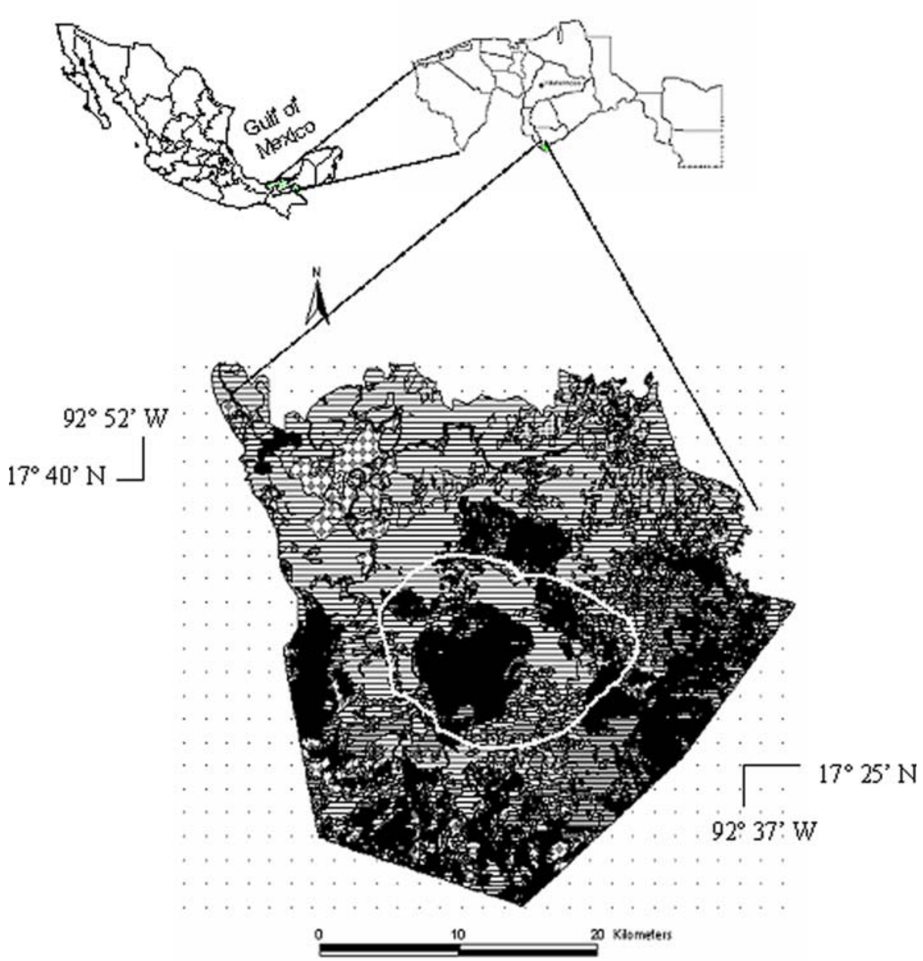

Fig. 1 Location of study area in southern Tabasco, Mexico. ▮ Rainforest,▤ Secondary growth, ≡ Pasture, ⁂ Agriculture

covered in a 25-m radius. For all coverage data, scores were as follows: 1, <25%; 2, 25–50%; 3, 50–75%; and 4, 75–100%. We scored tree height (TRHGT) using the following height classes: 1, 15–20 m; 2, 20–30 m; 3, 30–40 m; and 4, >40 m. Tree density (TRDEN) was obtained from the number of trees >20 cm DBH (diameter at breast height) within the 25-m radius circle (1,963.5 m^2). This variable was chosen because large trees are more dominant in a mature forest. Scores for this variable were as follows: 1, <15 trees; 2, 16–30 trees; 3, 31–45 trees; and 4, >45 trees. Another variable, degree of human disturbance (DHD), was assessed at each point based on signs of anthropogenic disturbance such as tree stumps and recent or abandoned trails. This variable was scored as follows: 1, very high (>5 tree stumps and/or recent trails within the 25 m radius circle); 2, high (3–5 tree stumps and/or abandoned trails); 3, medium (1–2 tree stumps and/or abandoned trails) and 4, low (no sign of anthropogenic disturbance).

Bird sampling

We sampled for the presence of birds using 40 point counts in each fragment size class. Each fragment class was sampled on three occasions from February 2004 to January 2005 resulting in a total of 360 counts. Point count sites were located toward the interior of the forest; each point was located at least 100 m from the forest edge and 150 m from the center of its closest neighbor. Point counts were conducted in the early morning from 0.5 to 3 h after sunrise, when visibility and bird activity were highest, avoiding mornings with strong winds or rain. At each point, all birds seen or heard within a 25-m radius during a 10 min interval were recorded; all counts were conducted by one observer (SLAW) to minimize observer effects (Ralph et al. 1995). Counts only recorded birds that were actually using the habitat (e.g., foraging, resting, etc.). Although mist-netting has been recommended for surveying tropical understory birds, especially cryptic species (Ralph et al. 1995), it was not considered practical for this study. Each bird species recorded was assigned to a feeding guild based on previously published information (Johns 1991; Howell and Webb 1995).

Analyses

To estimate the true species richness of each fragment class we used number of species-by-point data with the first-order jackknife non-parametric richness estimator from the software package EstimateS (Colwell 2005) with 100 randomizations without replacement. Bird communities were analyzed using only resident species which was determined from literature (Howell and Webb 1995) and field observations.

The similarity of species composition and species abundances between fragment classes was measured using the Chao-Jaccard similarity index (Chao et al. 2005), which is based on species incidence. This analysis was performed using the software package EstimateS (Colwell 2005).

We used non-metric multidimensional scaling (NMDS) to provide the best two-dimensional representation of the similarities between samples: samples with similar habitat features are placed close together, and dissimilar samples far apart. NMDS plots each site on a multi-dimensional space defined by several habitat axes, which represent combinations of the environmental variables used in the analysis. Similarities between the samples were calculated using the Jaccard metric. The analysis was carried out on the square-root-transformed (to normalize the distribution of the data) site × habitat description matrix with fragment size as a factor, using PC-ORD (version 4.34) software (McCune and Mefford 1999). We separated less disturbed (LD) samples from more disturbed (MD) samples on the habitat description gradient from the resultant Axis I and tested them for differences based on species richness and abundance using Kruskall-Wallis and Wilcoxon tests.

To estimate the predictive capability of the habitat variables (HECOV, SHCOV, TRCOV, TRHGT, TRDEN, and DHD), as well as the size of fragments for explaining the presence of feeding guilds, we performed backward logistic regressions (STATGRAPHICS Plus 4.0). We used stepwise selection of significant variables because it is an effective way to screen variables, especially when their associations with the dependent variable is unknown (Hosmer and Lemeshow 2000). Variables were slightly but not significantly correlated (Spearman = 0.05–0.48): all $p \geq 0.64$). A minimum tolerance of 0.05 was required to eliminate highly correlated variables. Explanatory variables were removed from the model when they explained less than 20% of the variance. The resulting models also had the lowest Akaike Information Criteria (AIC) values after testing them with R statistical software (R Development Core Team 2006).

Results

We recorded a total of 2,061 birds representing 125 resident species (Appendix 1); 123 species were visually detected and two species were only detected by their vocalizations. The samples' completeness (i.e., the percentage of true species richness estimates) in the fragment classes varied from 72.6 to 77% from the observed species richness in relation to the first-order jackknife. The whole sample's completeness was 81.7%.

Seventy eight percent ($n = 98$) of the species were detected at the Large Fragment (LF) sites, 62% ($n = 78$) at the Medium Fragment (MF) sites and 61% ($n = 77$) at the Small Fragment (SF) sites. Thirty eight percent of the birds were recorded at the LF sites, 28% at the MF sites and 34% at the SF sites. The most similar bird assemblages occurred between LF and MF which shared 60 species (88%) The other two pairwise comparisons showed very similar coefficients: LF-SF shared 63 species (86%) and MF-SF shared 53 species (85%). The only significantly different pairwise comparison was LF *versus* SF (Kruskal-Wallis = 6658.5, $p = 0.04$, all others $p > 0.15$).

Feeding guilds

We assigned the species recorded in all fragment classes to 11 feeding guilds (See Appendix 1 for guild description). Arboreal insectivore/frugivore (AIF) was the predominant guild with 24.8% of the recorded species (Table 1). Four more guilds, sallying insectivores (SAI), arboreal frugivores (AF), foliage gleaning insectivores (FGI), and bark gleaning insectivores (BGI) totaled 52.8% of the species. Insectivore–nectarivores and

Table 1 Feeding guild frequency distribution as percentage of observed species richness in large (LF), medium (MF) and small (SF) tropical rainforest fragments

Guild	LF ($n = 40$)	MF ($n = 40$)	SF ($n = 40$)	Total ($n = 120$)
Arboreal frugivores	16.3 (16; 180)	16.7 (13; 187)	16.9 (13; 176)	13.6 (17; 543)
Arboreal insectivore frugivores	22.4 (22; 265)	26.9 (21; 201)	26.0 (20; 263)	24.8 (31; 729)
Bark gleaning insectivores	11.2 (11; 52)	11.5 (9; 33)	9.1 (7; 27)	10.4 (13; 112)
Foliage gleaning insectivores	15.3 (15; 107)	14.1 (11; 100)	16.9 (13; 144)	13.6 (17; 351)
Insectivore–nectarivores	9.2 (9; 73)	9.0 (7; 37)	6.5 (5; 26)	8.8 (11; 136)
Raptors	8.2 (8; 13)	3.8 (3; 3)	3.9 (3; 4)	8.8 (11; 20)
Sallying insectivores	14.3 (14; 50)	15.4 (12; 29)	15.6 (12; 45)	15.2 (1; 124)
Scavengers	0 (0; 0)	0 (0; 0)	2.6 (2; 9)	1.6 (2; 9)
Sweeping insectivores	1.0 (1; 35)	0 (0; 0)	0 (0; 0)	0.8 (1; 35)
Terrestrial frugivores	1.0 (1; 1)	1.3 (1; 1)	1.3 (1; 1)	1.6 (2; 3)
Terrestrial insectivores	1.0 (1; 1)	1.3 (1; 1)	1.3 (1; 1)	0.8 (1; 3)
Total	(98; 777)	(78; 592)	(77; 696)	(125; 2065)

Species richness and abundance values are given within brackets raptors each accounted 8.8% of the species. The composition of guilds did not vary according to fragment size with the exception of scavengers which were present only in small fragments (scavengers: G = 5.71, df = 2, $p = 0.057$; all others $G < 2.30$, df = 2, $p \geq 0.317$). Guild abundance varied with fragment size only for bark gleaning insectivores (Kruskal-Wallis = 7.3; $p = 0.04$) and insectivore–nectarivores (Kruskal-Wallis = 11.99; $p = 0.002$) (Table 1). Scavengers and sweeping insectivores were excluded from further analysis because their recorded numbers were too small, and because they are not inhabitants of the forest interior.

Habitat characterization

In general, five of the six measured variables differed significantly among fragment classes: HECOV, TRCOV, TRHGT, TRDEN, and DHD (Kruskal-Wallis values 4.3–64.0, all $p < 0.05$; Table 2). The large fragment sites had the highest scores for all variables except for tree coverage. The medium fragment sites had the highest tree coverage, and the lowest herb coverage and tree density. The small fragment sites had the lowest shrub and tree coverage, tree height and were more disturbed than sites in the other fragment classes.

The NMDS extracted a 3-axis optimal solution that accounted for 88.8% of the variance in the data set. Final stress was 12.7, within the 10–20 range found in most data from ecological communities (McCune and Grace 2002), and was unlikely to have been obtained by chance (Monte Carlo test, $p = 0.019$). The ordination plot revealed a grouping of sites by fragment size (Fig. 2). Sites in large and medium fragments clustered separately from sites in small fragments, yet showed some overlap and were closer to one another. Axis I represented a gradient of habitat features with positive scores indicative of less disturbed and/or mature forest and negative scores indicative of sites with a high degree of human disturbance. Thus, this axis corresponds to a gradient of young/perturbed to mature/undisturbed forest. Most sites in LF were grouped toward the right end of the ordination plot because of high individual scores in tree density, tree coverage and low scores for degree of human disturbance. MF and SF had diffused arrangements mainly due to variation in degree of human disturbance among sites.

The sample distribution along the habitat description gradient on Axis I (Fig. 2) showed that 54 (45%) samples were in the more disturbed (MD) group and 66 (55%) are in the less disturbed (LD) group. Species richness and abundance of all guilds were higher in MC sites (Table 3). MC and LC shared 77 species (Chao-Jaccard index = 63%).

Table 2 Mean and standard deviation (within brackets) of habitat variable scores in large (LF), medium (MF), and small (SF), rainforest fragments

Variable	LF	MF	SF	Overall
Herb coverage	2.22 (0.58)	1.63 (0.59)	1.75 (0.71)	1.87 (0.067)
Shrub coverage	2.22 (0.70)	2.25 (0.44)	2.05 (0.32)	2.18 (0.51)
Canopy coverage	1.42 (0.50)	1.73 (0.75)	1.32 (0.53)	1.49 (0.62)
Tree height	2.53 (0.51)	1.70 (0.46)	1.27 (0.45)	1.83 (0.70)
Tree density	2.10 (0.67)	1.27 (0.51)	1.37 (0.63)	1.58 (0.71)
Degree of human disturbance	3.65 (0.48)	3.10 (0.90)	3.07 (1.00)	3.28 (0.86)

See methods section for further details

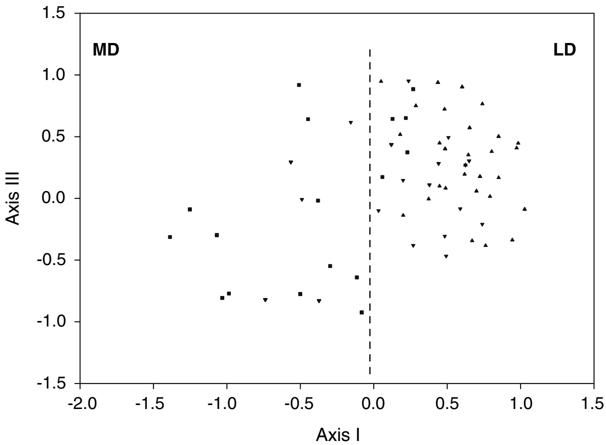

Fig. 2 Spatial representation of site similarities in habitat features, revealed by non-metric multidimensional scaling (NMDS). The number of points <120 is due to overlap of sites with identical habitat conditions. The line separating less disturbed (LD) from more disturbed (MD) samples was fitted by eye. ▲, Large fragment; ▼, Medium fragment; ■, Small fragment. See methods for descriptions of habitat variables

Table 3 Guild distribution in samples from tropical rainforest fragments with different degree of human disturbance and size (LF = large fragment; MF = medium fragment; SF = small fragment, *n* = sample size, s = species richness, N = abundance)

Feeding guild		More disturbed (MD)				Less disturbed (LD)			
		LF (*n* = 1)	MF (*n* = 18)	SF (*n* = 35)	Total LC (*n* = 54)	LF (*n* = 39)	MF (*n* = 22)	SF (*n* = 5)	Total MC (*n* = 66)
AF	s	0	11	12	12	16	12	4	17
	N	0	82	151	233	180	105	25	310
AIF	s	2	19	19	26	23	13	14	26
	N	8	89	215	312	257	112	48	417
BGI	s	0	7	7	9	11	8	5	12
	N	0	8	18	36	52	15	9	76
FGI	s	2	10	12	14	15	8	12	17
	N	3	50	104	157	104	54	40	194
IN	s	1	6	5	8	9	5	3	10
	N	1	16	21	38	72	21	5	98
R	s	0	1	2	2	8	2	2	10
	N	0	1	2	3	13	2	2	17
SAI	s	1	10	8	14	14	5	6	17
	N	2	21	31	54	48	8	14	70
TF	s	0	0	0	0	1	1	1	2
	N	0	0	0	0	1	1	1	3

Guild responses

Four of the six habitat variables (TRHGT, DHD, TRDEN, and fragment size) explained the presence of all feeding guilds, except arboreal insectivores/frugivores that were not related to any of the habitat variables that we measured (Table 4).

Table 4 Relationships between bird feeding guild occurrences and rainforest fragments habitat variables, as determined by logistic regression

Guild	Model *P*	G.F.*	DR/DF**	Significant variables, all $p < 0.05$
AF (*n* = 17)	0.019	0.9	0.99	TRDEN, TRHGT, DHD
BGI (*n* = 13)	0.01	0.3	0.98	TRHGT
IN (*n* = 11)	0.002	0.6	1.2	Size
R (*n* = 11)	0.005	0.06	0.76	DHD
FGI (*n* = 17)	0.05	0.9	0.85	TRHGT, DHD
SAI (*n* = 19)	0.03	0.6	1.3	DHD
AIF (*n* = 31)	–	–	–	–
TF (n = 3)	0.02	–	0.26	TRDEN, TRHGT

Only significant variables are presented; *n* = species richness within guild

* G.F. = Chi-squared goodness of fit test; ** DR/DF = Deviance residual degrees of freedom ratio

Discussion

The fragments sampled in this study had a species richness accounting for 61.6% of the known resident bird species (*n* = 203) from the main landscape elements (i.e., rainforest, secondary growth, pasture) in the Parque Estatal de la Sierra (Arriaga-Weiss et al. 2004).

With a similar sampling effort in each fragment class, thus controlling for the passive sampling effect, we recorded higher species richness and abundance in the large fragment. Other studies in tropical forest fragments (Beier et al. 2002; Newmark 2006) have found a relationship between fragment size and bird species richness and abundance. In fact, 24 species (30% of total species richness) were exclusive to the large fragment (e g., *Leucopternis albicollis*, *Micrastur semitorquatus*, *Pionopsitta haematotis*, *Campephilus guatemalensis*, *Pipra mentalis*, *Euphonia gouldi*). Most of these species are considered rainforest specialists because they are dependant on less disturbed forest (Howell and Webb 1995). Although other species were recorded in all fragment classes, abundance was higher in the large fragment. For example, *Phaethornis longirostris*, a rainforest hummingbird, was three times more abundant in the large fragment than in the smaller ones. *Henichorina leucosticta*, a foliage gleaning insectivore and rainforest specialist, was recorded four times more often in the large fragment than in the smaller ones.

More than 80% of the species recorded in this study had frequencies of less than 10%, suggesting low population densities, although this could be an artifact of the sampling technique. Despite the possibility that point count censuses may exclude or underestimate species such as large terrestrial frugivores and small, secretive understory insectivores, our data agree with a general predominance of rare species in tropical avian assemblages (Orians 1969), due in part to their patchy distribution (Karr 1977; Terborgh et al. 1990). Thus, distributions in disturbed tropical landscapes are likely to be even more restricted as each species concentrates in those parts of the habitat mosaic to which it is most suited.

Responses of guilds to habitat variables

In general the 11 feeding guilds we identified were equally represented in all fragment sizes, except scavengers, that were only present in small fragments.

Data from this study suggests that the presence of wide ranging arboreal frugivore species (e.g., *Amazona autumnalis*, *A. albifrons*, *Aratinga nana* and *Ramphastos sulfuratus*) was dependant on high trees and less disturbed sites and was related to tree density. The latter variable, which may decrease with microclimatic changes associated with edge effects and human disturbance, is related to fruit availability and can influence changes in frugivore abundance (Restrepo and Gómez 1998). Furthermore, large frugivores, such as those examples given above, depend on tree cavities for nesting (Forshaw and Cooper 1977), and thus directly on the availability of large trees. Alternatively, our data does not support the premise that these species are not affected by habitat conditions within a small part of their ranges as suggested by Johns (1991).

We found that the arboreal insectivore–frugivore guild was not related to any of the habitat variables that we measured, which is consistent with previous studies which found that species of this guild are usually associated with secondary vegetation and tolerate a wide range of microclimate conditions. For example, tanagers of the genus *Ramphocelus* combine fruit and insects in several ways, while using different foraging heights and seasonal consumption patterns (Keast 1985).

In this study the insectivore–nectarivore guild showed no significant relationship between species richness and the habitat variables, with the exception of fragment size. We recorded the highest species richness and abundance of hummingbirds in the large fragment, as found in Amazonia by other studies (Stouffer and Bierregaard 1995a; Pearman 2002). The forest cover was relatively sparse at most sites where we found insectivore–nectarivore birds, and most hummingbirds were found at sites with flowering large herbs (e.g., *Heliconia* spp.), which are usually found at forest edges, in large natural gaps in the forest or in secondary vegetation. The only hummingbird that was abundant in this study was *Phaethornis longirostris* which is a known *Heliconia* specialist (Snow and Texeira 2005). None of the other species were detected in large numbers and several are known to be edge specialists (Johns 1991). This evidence suggests that most hummingbirds are not severely affected by forest fragmentation, though they must be affected by habitat loss, which will ultimately begin to reduce even edge habitat (Kattan et al. 1994; Renjifo 1999; Pearman 2002; Ribon et al. 2003).

In general, bark and foliage gleaning insectivores adapt to microclimatic changes associated with disturbance of the forest structure because they forage in the understory shrubs and trees, as well as in the upper canopy levels (Johns 1991). However, our results suggest that these birds were dependant on the size of trees (height and diameter) and on the degree of human disturbance in their habitat. For instance, bark gleaning insectivores will be favored by higher trees (i.e., higher trunks) because of the increased surface area for feeding. Other studies have suggested that bark surface feeders (mostly woodpeckers and woodcreepers) are likely to be negatively affected by low tree density (Thiollay 1994; Raman et al. 1998), which also indicates a reduction in the surface area of available feeding sites.

We found that the occurrence of foliage gleaning insectivores was significantly related to a low level of human disturbance and a lower tree height. Insectivores are particularly prone to fragmentation despite their relatively small sizes and lower hunting pressure from people (Kattan et al. 1994; Stouffer and Bierregaard 1995b; Renjifo 1999, 2001) since even selective timber logging can reduce their foraging habitat (Raman and Sukumar 2002). Their abundance also generally reflects the amount of understory vegetation and its associated insects as well as the microclimatic conditions (Johns 1991). Microclimatic conditions have a particularly strong influence on understory birds (Karr and Freemark 1983). In this study, the understory vegetation was sparse, especially in the medium and small fragments as indicated by the low scores in herb and shrub coverage. This condition can be attributed to the steep slopes, an almost absent soil layer, and human perturbation. These microclimatic/habitat conditions in the understory influenced the distribution of foliage gleaners: while abundances were similar in the canopy across all fragment sizes ($G = 0.64$, $df = 2$, $p = 0.72$), more individuals used the understory of LF, which was better developed, than the understory of MF and SF ($LF = 50$ vs. $MF = 33$ vs. $SF = 28$: $G = 6.95$, $df = 2$, $p = 0.03$).

We recorded the highest raptor species richness and abundance in the largest fragment and in the less disturbed sites. This guild is influenced by the degree of human disturbance in the forest, as indicated by the results of the logistic regression. It is well known that some forest dwelling raptors are especially sensitive to rainforest fragmentation and perturbation (Thiollay 1989; Renjifo 1999). Furthermore, their sensitivity to habitat fragmentation is related to their need for large territories, so their densities tend to be relatively low (Ribon et al. 2003).

The presence of terrestrial frugivore species (i.e., *Crax rubra*, *Penelope purpurascens*) was influenced by tree density and height. Thus, considering that this guild is mainly composed of forest interior species, we expected higher abundances, if not higher richness, in those less disturbed sites where tree density was high. Nonetheless, both abundance and richness were poor. *Tinamidae* species were noteworthy by their absence, since their presence has been recorded in less disturbed rainforest fragments by other authors (Johns 1991; Estrada et al. 1997; Thiollay 1999; Lindell et al. 2004). The terrestrial frugivore guild may have been impacted by hunting, indeed a hunter with a freshly killed *Crax rubra* was encountered in the large fragment during surveys.

Conservation implications

We have identified four main conservation implications from the results of our study. First, the large fragment hosted more bird species, and the less disturbed sites (high scores in TRDEN and TRCOV, low scores for DHD) were richer than smaller fragments and/or more disturbed sites. Second, species with restricted ecological traits (e.g., forest interior species and understory specialists) were more sensitive to disturbance (e.g., *Amazona autumnalis*, *Trogon melanocephalus*, *Celeus castaneus*, *Henichorina leucosticta*, *Thryothorus maculipectus*, and *Cercomacra tyrannina*) and should therefore be given a higher conservation priority than more generalist species. This implies that large fragments should be given a higher priority in conservation decision making. Third, habitat characteristics, such as tree coverage and density, must be maintained as they are significant for the preservation of resident species. Fourth, the sensitivity of bark gleaning insectivores and understory foliage gleaning insectivores to local disturbance make them useful as ecological indicators of forest degradation.

The decline of forest dwelling species at a regional scale has been linked to the extent of reduction of the original habitat and isolation (Renjifo 2001). Disruption of the habitat by human activities may reduce the space occupied by large arrays of similar species and has an effect on food availability (Wong 1986; Turner 1996; Sodhi 2002). As a result, fewer species can occupy the habitat and only extensive tracts of forest can contain a full assemblage of resident species. Guarantees of protection from human alteration for such tracts should be a first priority for their conservation. With looming development pressure on the rainforest remnants in Tabasco, as well as in other tropical regions, urgent conservation actions are vital for the preservation of their biotas. This makes it imperative to prevent further fragmentation if possible. In any case, we expect that the future scenario for resident rainforest species will be towards extinction, especially in smaller fragments.

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Appendix 1 Bird species recorded in different sized forest fragments

Family and species	Feeding guild	Abundance			
		LF	MF	SF	Total
Cathartidae					
Coragyps atratus Bechstein	SC	0	0	4	4
Cathartes aura Linneus	SC	0	0	5	5
Accipitridae					
Chondrohierax uncinatus Temminck	R	1	0	0	1
Leucopternis albicollis Salvin	R	0	1	0	1
Buteogallus anthracinus Deppe	R	1	0	0	1
Buteo magnirostris Gmelin	R	0	0	1	1
Spizaetus tyrannus Wied	R	1	0	0	1
Falconidae					
Micrastur semitorquatus Vieillot	R	2	0	0	2
Herpetotheres cachinnans Linnaeus	R	2	0	2	4
Falco rufigularis Daudin	R	0	0	1	1
Cracidae					
Ortalis vetula Wagler	AF	16	25	38	79
Crax rubra Linnaeus	TF	1	0	1	2
Penelope purpurascens Wagler	TF	0	1	0	1
Columbidae					
Patagioenas cayennensis Bonnaterre	AF	2	5	1	8
Patagioenas flavirostris Wagler	AF	2	0	0	2
Patagioenas nigrirostris Sclater	AF	5	0	0	5
Leptotila verreauxi Bonaparte	AF	4	3	8	15
Leptotila plumbeiceps Richard & Bernard	AF	3	2	4	9
Psittacidae					
Aratinga nana Vigors	AF	17	20	19	56
Pionopsitta haematotis Sclater & Salvin	AF	2	0	0	2
Pionus senilis Spix	AF	24	30	14	68
Amazona albifrons Sparrman	AF	20	23	3	46
Amazona autumnalis Linnaeus	AF	49	47	56	152
Amazona oratrix Ridgway	AF	0	3	0	3
Cuculidae					
Piaya cayana Linnaeus	FGI	1	1	15	17

Appendix 1 continued

Family and species	Feeding guild	Abundance			
		LF	MF	SF	Total
Strigidae					
Pulsatrix perspicillata Latham	R	1	1	0	2
Glaucidium brasilianum Gmelin	R	3	0	0	3
Ciccaba nigrolineata Sclater	R	2	1	0	3
Caprimulgidae					
Nyctidromus albicollis Gmelin	SAI	0	2	0	2
Trochilidae					
Phaethornis longirostris Linnaeus	IN	47	23	14	84
Campylopterus curvipennis Lichtenstein	IN	1	0	0	1
Campylopterus hemileucurus Lichtenstein	IN	5	1	0	6
Florisuga mellivora Linnaeus	IN	5	0	1	6
Anthracothorax prevostii Lesson	IN	2	3	0	5
Hylocharis eliciae Bourcier & Mulsant	IN	1	4	0	5
Amazilia candida Bourcier & Mulsant	IN	3	2	5	10
Amazilia beryllina Lichtenstein	IN	0	3	0	3
Amazilia tzacatl Dela Llave	IN	0	1	1	2
Amazilia yucatanensis Cabot	IN	2	0	0	2
Heliomaster longirostris Audebert & Vieillot	IN	7	0	5	12
Trogonidae					
Trogon melanocephalus Gould	AIF	22	26	10	58
Trogon massena Gould	AIF	0	1	0	1
Momotidae					
Momotus momota Swainson	AIF	20	20	15	55
Electron carinatum Du Bos	AIF	0	0	2	2
Bucconidae					
Notharchus macrorhynchos	SAI	0	1	0	1
Malacoptila panamensis Lafresnaye	SAI	1	0	0	1
Galbulidae					
Galbula ruficauda Cuvier	SAI	0	1	1	2
Ramphastidae					
Pteroglossus torquatus Gmelin	AF	2	3	1	6
Ramphastos sulfuratus Lesson	AF	18	16	13	47
Picidae					
Melanerpes pucherani Malherbe	BGI	2	0	0	2
Melanerpes aurifrons Wagler	BGI	2	1	5	8
Veniliornis fumigatus D'Orbigny	BGI	0	0	1	1
Piculus rubiginosus Swainson	BGI	2	0	0	2
Celeus castaneus Wagler	BGI	20	6	2	28
Dryocopus lineatus Linnaeus	BGI	1	2	5	8
Campephilus guatemalensis Hartlaub	BGI	2	0	0	2

Appendix 1 continued

Family and species	Feeding guild	Abundance			
		LF	MF	SF	Total
Furnariidae					
Synallaxis erythrothorax Sclater	FGI	5	10	6	21
Automolus ochrolaemus Tschudi	FGI	6	0	2	8
Dendrocolaptidae					
Dendrocincla anabatina Sclater	BGI	1	3	0	4
Dendrocincla homochroa Sclater	BGI	4	7	6	17
Sittasomus griseicapillus Vieillot	BGI	0	2	0	2
Dendrocolaptes certhia Lichtenstein	BGI	3	3	4	10
Xiphorhynchus flavigaster Swainson	BGI	10	7	4	21
Lepidocolaptes souleyetii Des Murs	BGI	5	2	0	7
Thamnophilidae					
Thamnophilus doliatus Linnaeus	FGI	4	1	0	5
Microrhopias quixensis Cornalia	FGI	2	5	1	8
Cercomacra tyrannina Sclater	FGI	4	0	9	13
Tyrannidae					
Ornithion semiflavum Sclater & Salvin	SAI	3	1	1	5
Myiopagis viridicata Vieillot	SAI	4	0	0	4
Mionectes oleaginous Lichtenstein	SAI	0	3	0	3
Tolmomyias sulphurescens Spix	SAI	3	1	2	6
Onychorhynchus coronatus	SAI	2	1	3	6
Myiobius sulphureipygius Sclater	SAI	1	0	2	3
Contopus cinereus Spix	SAI	0	0	2	2
Attila spadiceus Gmelin	SAI	14	4	14	32
Myiarchus tuberculifer D'Orbigny & Lafresnaye	SAI	1	2	2	5
Megarynchus pitangua Linnaeus	SAI	3	3	1	7
Lipaugus unirufus Sclater	SAI	1	0	1	2
Pachyramphus cinnamomeus Lawrence	SAI	2	0	5	7
Pachyramphus aglaiae Lafresnaye	SAI	1	5	0	6
Tityra semifasciata Spix	SAI	13	5	11	29
Tityra inquisitor Lichtenstein	SAI	1	0	0	1
Pipridae					
Manacus candei Parduzaky	AIF	2	0	2	4
Pipra mentalis Sclater	AIF	8	0	0	8
Vireonidae					
Hylophilus ochraceiceps Sclater	AIF	1	3	0	4
Hylophilus decurtatus Bonaparte	AIF	6	7	8	21
Corvidae					
Cyanocorax yncas Boddaert	AIF	0	0	10	10
Cyanocorax morio Wagler	AIF	14	17	52	83
Hirundinidae					
Stelgidopteryx serripennis Audubon	SwI	35	0	0	35

Appendix 1 continued

Family and species	Feeding guild	Abundance			
		LF	MF	SF	Total
Troglodytidae					
Campylorhynchus zonatus Lesson	FGI	1	0	53	54
Thryothorus maculipectus Lafresnaye	FGI	33	24	23	80
Uropsila leucogastra Gould	FGI	0	1	0	1
Henicorhina leucosticta Cabanis	FGI	27	20	6	53
Microcerculus philomela Sclater	TI	1	1	1	3
Sylviidae					
Ramphocaenus melanurus Vieillot	FGI	1	0	0	1
Polioptila caerulea Linnaeus	FGI	2	10	11	23
Polioptila plumbea Gmelin	FGI	2	0	0	2
Mimidae					
Mimus gilvus Vieillot	FGI	2	0	5	7
Parulidae					
Basileuterus culicivorus Deppe	FGI	12	19	8	39
Cardellina rubrifrons Giraud	FGI	0	4	1	5
Coerebidae					
Coereba flaveola Linaeus	FGI	4	5	4	13
Thraupidae					
Eucometis penicillata Spix	AIF	0	1	0	1
Lanio aurantius Lafresnaye	AIF	2	3	0	5
Habia rubica Vieillot	AIF	17	26	46	89
Ramphocelus sanguinolentus Lesson	AIF	2	0	6	8
Ramphocelus passerinii Bonaparte	AIF	5	5	6	16
Thraupis episcopus Linnaeus	AIF	3	0	0	3
Thraupis abbas Deppe	AIF	3	2	2	7
Euphonia affinis Lesson	AF	8	3	8	19
Euphonia hirundinacea Bonaparte	AF	4	7	8	19
Euphonia gouldi Sclater	AF	4	0	3	7
Cyanerpes cyaneus Linnaeus	AIF	0	3	8	11
Chlorophanes spiza Linnaeus	AIF	3	0	2	5
Emberizidae					
Arremon aurantiirostris Lafresnaye	AIF	2	1	3	6
Arremonops rufivirgatus Lawrence	AIF	10	0	0	10
Arremonops chloronotus Salvin	AIF	0	0	6	6
Cardinalidae					
Saltator coerulescens Vieillot	AIF	1	7	19	27
Saltator atriceps Lesson	AIF	2	0	0	2
Caryothraustes poliogaster Du Bus De Gisignies	AIF	2	3	2	7
Cardinalis cardinalis Linnaeus	AIF	0	2	0	2

Appendix 1 continued

Family and species	Feeding guild	Abundance			
		LF	MF	SF	Total
Icteridae					
Icterus mesomelas Wagler	AIF	0	1	0	1
Icterus gularis Wagler	AIF	0	1	8	9
Amblycercus holosericeus Deppe	AIF	5	7	9	21
Psarocolius wagleri Gray	AIF	29	12	0	41
Psarocolius montezuma Lesson	AIF	105	51	45	201

Species names and systematic order follow AOU (2003). Habitat: RF = rainforest; FE = forest edge; SG = secondary growth; M = pasture matrix. Feeding guilds: AF = arboreal frugivore; AIF = arboreal insectivore/frugivore; BGI = bark gleaning insectivore; FGI = foliage gleaning insectivore; IN = insectivore–nectarivore; R = raptor; SAI = sallying insectivore; SWI = sweeping insectivore; SC = scavenger; TF = terrestrial frugivore; TI = terrestrial insectivore. LF = Large fragment; MF = Medium fragment; SF = Small fragment

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