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AVIFAUNAL RESPONSES TO SINGLE AND RECURRENT WILDFIRES IN AMAZONIAN FORESTS

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Abstract. Although forest wildfires threaten to impoverish vast expanses of once fire-resistant humid tropical forest, their effects on the vertebrate fauna remain poorly understood. We report results from a study in central Brazilian Amazonia examining a large area of terra firma (unflooded) forest that had been affected by fires during the 1997–1998 El Niño-mediated dry season. By sampling 0.25-ha forest plots both one and three years after fire disturbance, we noted that over time the bird community became increasingly dissimilar from that in unburned control plots. The influences of burn severity and recurrent fires were then examined across 28 plots that were all sampled three years after the fires. Foraging guilds differed in their responses to the gradient of increasing burn severity; most guilds declined, although arboreal granivores, frugivores, and nectarivores showed unimodal responses and arboreal gleaning insectivores increased. These responses were strongly correlated with associated changes in the habitat structure and reflected differences in resource abundance where this was quantified. Rates of species turnover were high, and there was virtually no species overlap between unburned forest plots and those that had burned in more than one El Niño dry season. Our results indicate that, unless conservation strategies can prevent a recurrent fire regime from becoming established in seasonally dry tropical forests, only nonforest and second-growth bird species, which are of minimal conservation importance, will be able to persist in fire-prone landscapes of the future.

Key words: Amazonia; avifauna; Brazil; community change; disturbance; El Niño; fire ecology; fragmentation; guilds; selective logging; tree mortality; tropical forests.

INTRODUCTION

Tropical forest biodiversity is increasingly threatened by human disturbances such as deforestation (Skole and Tucker 1993, Laurance et al. 2001), selective logging (Johns 1997, Putz et al. 2001), fragmentation (Lovejoy et al. 1986, Bierregaard and Lovejoy 1989), and hunting (Peres 2000, Robinson and Bennett 2000). However, in recent years wildfires have emerged as a leading threat, both as a form of disturbance in their own right (Cochrane et al. 1999, Nepstad et al. 1999, Cochrane 2003) and because of their synergistic interactions with logging (Uhl and Buschbacher 1985, Holdsworth and Uhl 1997, Siegert et al. 2001) and fragmentation (Cochrane 2001*a, b*, Cochrane and Laurance 2002). Significant tracts of tropical forest have burned in recent years (Goldammer 1999) and future scenarios are alarming. Climate change may be inducing increasingly severe and frequent El Niño Southern Oscillation (ENSO) events (Sun 1997, Timmermann et al. 1999), thereby reducing dry-season precipitation in many forested tropical regions and allowing previously fire-resistant forests to burn (Uhl 1998). In the 1998 El Niño alone, $\sim 1.5 \times 10^6$ km^2 of forest in the Brazilian Amazon were estimated to have crossed the flammability threshold (Nepstad et al. 2001), while an estimated 200 000 km^2 of forested land was estimated to have burned in Latin America and Asia (Cochrane 2001*b*).

Although forest biodiversity may be protected from other forms of disturbance inside large reserves, fires represent a much less predictable threat, and can spread through the understory of even undisturbed primary forest during severe El Niño-mediated dry seasons (Nepstad et al. 1998, Peres 1999, Nelson 2001). In 1997, ground fires damaged forests in at least 17 of Indonesia's parks and protected areas (Kinnaird and O'Brien 1998), and a substantial part of the newly created Tapajós-Arapiuns Extractive Reserve and several other parks and reserves of Brazilian Amazonia (Prins et al. 1998). Furthermore, ignition sources are plentiful, because agricultural practices in tropical forests are heavily reliant on fire (19 404 possible fires were counted in the Brazilian Amazon state of Pará from June to December 1998 alone; see Hot Spots Brazil in 1998 [online]).[2] Although some monitoring and educational measures have had limited success in reducing the risk of fires spreading into forest from agricultural plots (Monitoramento e Avaliação do Risco de Incêndios Florestais em Áreas Críticas [online]),[3] the good intentions of many responsible farmers are often undone

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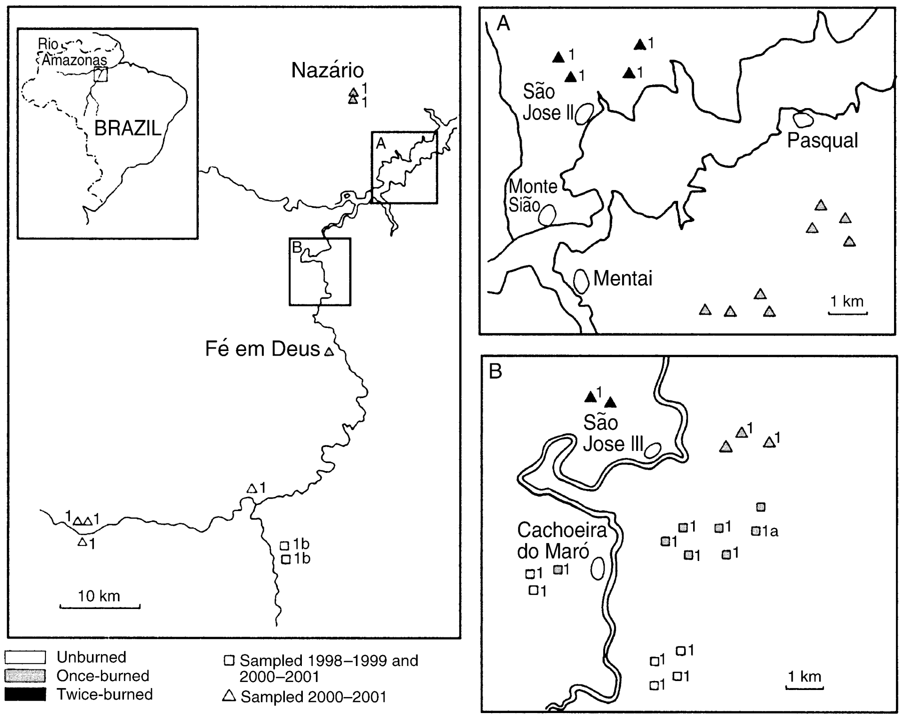

FIG. 1. Map of study region, showing sampling plots. Plots marked with a "1" indicate those where mist-netting was conducted. Although mist-netting was conducted in both sampling periods at the plot marked "1a," this was excluded from the temporal change analysis because the original plot could not be located precisely. Mist-netting was only conducted in 1998–1999 in plots marked "1b," although vegetation data were obtained in both periods.

by the mistakes or negligence of others (Barlow and Peres 2004), or even from natural ignition events such as lightning (Tutin et al. 1996). Additionally, initial low-severity burns encourage recurrent burns with far greater impacts on tree mortality (Cochrane et al. 1999, Cochrane 2003, Barlow and Peres 2004).

Despite the recent prevalence of fires in humid tropical forest, their effects on forest wildlife remain poorly understood and are outlined in only a few studies (Berenstain 1986, Kinnnaird and O'Brien 1998, Peres 1999, Barlow et al. 2002, Peres et al. 2003). Furthermore, studies on the understory birds (Kranz 1995, Barlow et al. 2002) have only examined short-term effects, within 15 months of the fires, when much of the postfire understory regeneration and tree mortality were yet to occur (Holdsworth and Uhl 1997, Cochrane et al. 1999, Barlow et al. 2003). Moreover, the effects of recurrent burns, which at present threaten to convert ~259 000 km² of forest in the southeastern Brazilian Amazon into scrub savannahs in the next decade (Cochrane 2001*b*), have not been quantified for forest wildlife.

Here we present data on the effects of fire disturbance on bird assemblage structure, both one and three years after a widespread surface fire burned ~1140 km² of forest in the central Brazilian Amazon (Nelson 2001). By sampling the same plots both one year (see Barlow et al. 2002) and three years after the fires, we examine how the avifauna responded to the early stages of forest regeneration. Our sampling protocol three years after the fires also examined how the avifaunal assemblage changed along a disturbance gradient that included once-burned and twice-burned forest, and results are discussed in light of existing hypotheses that explain shifts in abundance of tropical forest birds and the conservation implications of fire in the humid tropics.

METHODS

Habitat data and the understory bird community were sampled along the Arapiuns and Maró River catchments of western Pará, central Brazilian Amazonia (2°44′ S, 55°41′ W; Fig. 1). In total, 41 samples were obtained in 28 forest plots, with 13 of these plots being sampled twice, both one and three years postfire (Table 1). The 28 plots sampled three years postfire (from July 2000 to May 2001) were used to examine the influences of burn severity across the three burn treatments examined (Table 1). The 13 plots that had been previously sampled from October 1998 to March 1999 (one year postfire; Table 1) were used to compare changes over time in unburned and once-burned forest.

The history of recurrent fire disturbance in living memory was assessed using multiple independent interviews with local people of up to 70 years of age, and there was no evidence that previous wildfires had affected large parts of the study area within living memory. In total, the 1997–1998 fires were estimated

TABLE 1. Summary of the number of plots sampled in each treatment and sampling period.

	No. plots			Total	
No. years after fire	Unburned	Once-burned	Twice-burned	No. samples	Mist-net hours
1 and 3	6	7	0	13†	18 720
3	10	12	6	28	20 160
All plots	10	12	6	41	29 520

† The 13 plots sampled one year after fire are a temporal subset of the 28 plots sampled three years after fire.

to have burned around ~1140 km^2 of forested land in the Arapiuns area (Nelson 2001). Although fires spread many times into the forest from adjacent small slash-and-burn plots during the 1997–1998 dry season, local accounts suggest that the overall effect was of one large, continuous burn that swept up the Arapiuns River basin from east to west during the four driest months (October–January), before being extinguished by the onset of the rainy season. Fire severity varied greatly across the landscape, depending on the pre-burn forest structure and local ambient conditions at the time of the fire. We use the term once-burned forest to describe primary forest that burned for the first time in living memory during the 1997–1998 ENSO dry season, whereas twice-burned forest refers to forest that succumbed to recurrent fires during both the 1982–1983 and 1997–1998 ENSO years. However, the variability within each of these burn classes means that, where possible, fire severity is treated as a continuous rather than a categorical variable. A more detailed description of the fires, forest structure and species composition in the study area, and the causes of fire disturbance in this region are provided in Peres (1999), Barlow et al. (2002), and Barlow and Peres (2004).

Avifaunal sampling

A standardized mist-netting protocol was used to sample the understory avifauna 41 times in 28 forest plots (13 of these being sampled twice). For each avifaunal sample, 24 mist nets (12 × 2.5 m; mesh size 36 mm) were erected end-to-end in a straight line (with a gap of c. ~50 cm between nets, used to adjust tension and account for changes in humidity), creating a netline extending for ~320 m once large obstacles had been avoided. Nets were opened for two-and-a-half days (30 h), from dawn to dusk for the first two days, and from dawn to 1200 hours on the third day, accruing a total of 29 520 mist-net hours (mnh), calculated as number of samples (41) × number of nets (24) × number of hours open (30). The 2000–2001 sampling effort yielded a total of 3470 individuals belonging to 153 species, which included only a single capture of a North American migrant (*Catharus fuscescens*) that was excluded from the analysis.

All plots were located at least 500 m apart from one another, and were considered as spatially independent. This is consistent with the fact that fewer than 1% of all birds captured (and color-banded for each spatial and temporal replicate) were subsequently recaptured in a neighboring netline. Potential seasonal effects were minimized or eliminated by alternating sampling between burned and unburned forest. Nets were checked hourly and were closed during periods of heavy rain. Hours occasionally lost on the first two days of netting due to heavy rain were compensated for on the third day, and sampling was aborted on days of heavy (>3 h) rain. All birds captured were identified to species, weighed, and measured (standard measurements included wing, tail, bill, and total length) and, whenever possible, were aged, and sexed. All new captures were banded with a plastic ring that was color-coded for each site and sampling period, with the exception of hummingbirds (Trochilidae), which were marked by cutting small, individually identifiable notches in a single tail feather. All recaptures from the same sampling period and from the same netline were excluded from the analysis.

Mist-netting has many advantages over other census techniques in tropical forests, and is a useful technique for sampling nonvocal and secretive understory birds (Karr 1981), which are often the most susceptible to forest disturbance (Johns 1991, Aleixo 1999). However, we recognize that although the number of captures is used as an approximate measure of abundance, mist-netting can give a biased representation of the avifauna (Remsen and Good 1996) and capture rates may not always reflect true abundance (Thiollay 1994). In particular, the capture incidence of some species may be influenced if individuals alter their foraging height in response to disturbance-dependent changes in habitat structure (Bierregaard and Lovejoy 1989, Lambert 1992, Remsen and Good 1996). However, in this study only three of the 20 most abundant species showed a significant difference in capture height (i.e., mist net pocket height) between different disturbance treatments (J. Barlow, *unpublished data*), while the vocally (or visually) conspicuous and abundant birds were most frequently heard or seen in the plots where they were also most frequently captured. Furthermore, the validity of our results was confirmed by repeating analysis, but restricting it to those species classified by Stotz et al. (1996) as foraging either terrestrially or in the understory (hereafter referred to as understory species).

Vegetation sampling

A 0.25-ha (10 × 250 m) rectangle was measured and marked at each plot. All trees and lianas ≥10 cm diameter at breast height (dbh) lying within this area (but excluding those with more than half of their basal trunk outside the plot) were measured and carefully inspected in order to determine their survival status (i.e., alive or dead; for details, see Haugaasen et al. [2003]). Diameter measurements were taken at breast height (136 cm), or immediately above the tallest buttress whenever

TABLE 2. Summary of habitat variables measured at each 0.25-ha forest plot.

Description	Unit	Code
Live trees density	*n*	LT
Total tree density†	*n*	
Dead tree density	*n*	DT
Total standing basal area	m^3	BA
Basal area of live trees‡	m^3	
Dead standing basal area	m^3	DBA
Canopy cover	%	C
Bare ground	%	BG
Understory vegetation density	*n*	USD
Woody stems <10 cm dbh	*n*	WS
Nonwoody stems <10 cm dbh	log(*n*)	NWS
Habitat variable 1§		HV1
Habitat variable 2‖		HV2

† Excluded from analysis as highly collinear with variable LT.

‡ Excluded from analysis as highly collinear with variable BA.

§ Composite variable based on C, BG, and NWS.

‖ Composite variable based on LT, BA, C, USD, and BG.

this exceeded breast height. Canopy cover was quantified with the use of a spherical densiometer at 24 evenly spaced points within each plot, with four readings taken per point.

Forest floor regeneration was examined at 24 10-m^2 (2.5 × 4 m) quadrats spaced within each 0.25-ha plot. All saplings and stems <10 cm in diameter and >1 m in height were measured within each of these quadrats and, whenever possible, were identified to genus or species. In some quadrats, bamboo culms were too numerous to measure or count, so their abundance was subsampled within a smaller 1 × 1 m area representative of the larger 10-m^2 quadrat, and was multiplied 10-fold. Percentage of undergrowth cover was estimated within a smaller 2 × 2 m area from within each larger quadrat, following Barlow et al. (2002). Understory vegetation openness was measured using a 2.5-m graduated pole held vertically and examined at 12 m distance by an observer using ×10 binoculars. Readings were taken according to the number of conspicuously marked 10-cm pole sections (range: 0–25 cm) that were clearly visible, and the procedure was repeated every 12 m along both sides of each plot (n = 48), with the positions corresponding to the positioning of individual mistnets. Habitat variables used and their codes are summarized in Table 2.

Data analysis

Species were assigned to both foraging and dietary guilds (Appendix A) following Terborgh et al. (1990), with information on additional species extracted from Hilty and Brown (1986), Ridgley and Tudor (1989, 1994), Thiollay (1994), Sick (1997), and personal observations. Species were assigned to disturbance response guilds according to an independent assessment of their sensitivity to disturbance (Stotz et al. 1996). Guilds are a successful way of examining community changes in species-rich environments (Terborgh and Robinson 1986), and the classification groupings of both Terborgh et al. (1990) and Stotz et al. (1996) have been successful in classifying functional groups of species, facilitating easier comparisons among studies diverging in species composition. Unlike other avian guild classification schemes in Neotropical forests (e.g., Karr et al. 1990), foraging guilds are not split by their foraging strata. Instead, the classification of Stotz et al. (1996) is used to separate understory and terrestrial species from those that frequently forage above the height of mistnets.

Because burn severity was highly variable within areas affected by fires (Barlow and Peres 2004), most responses to fire disturbance were analyzed along a continuous environmental gradient rather than within forest types. The number of live trees ≥10 cm dbh per 0.25-ha plot (hereafter, live tree density) was used as the single environmental variable that best described the fire disturbance gradient. The use of live tree density as an accurate predictor of local burn severity in any area was justified for the following reasons:

1) This variable was best explained by the mean char height on standing stems in 44 0.25-ha tree plots sampled three years after the fire ($F_{1,42}$ = 313, r^2 = 0.88, P < 0.001; Barlow and Peres 2004). Char height itself was not used in any analyses here, as it was not a continuous variable.

2) The variable is both simple to record and interpret, increasing comparability with other studies.

3) We were able to test the underlying assumption that tree densities in burned and unburned plots were similar before the fires by comparing the number of standing stems (alive and dead) one year after the burn, before many dead trees in the burned forest had fallen over. The stem densities and dbh distributions of unburned and one-year post–burn forests were statistically indistinguishable in all comparisons (Barlow et al. 2003).

Where displayed graphically, live tree density is reversed along the x-axis so that the degree of disturbance (burn severity) increases from left to right.

Regression lines were fitted to the relationship between guild abundance (or species richness) and live tree density, using linear, quadratic, and exponential functions in Sigmaplot Version 7 (SPSS 2001). Kruskal-Wallis tests were used to compare differences in species richness between disturbance treatments. The matching coefficient between the bird species similarity matrix and live tree density (calculated using the BIO-ENV procedure in PRIMER Version 5; Clarke and Ainsworth [1993]) was taken as an indicator of the strength of species turnover along the burn severity gradient.

Nonmetric multidimensional Scaling (MDS) was used to examine both community responses to changes in habitat structure in the 28 plots sampled in 2000–2001 and the change over time in community composition at all resampled plots. All MDS was under-

TABLE 3. Mean bird capture success (no. birds per netline) and avian species richness (no. species per netline) at resampled plots in unburned (UF) and once-burned (BF) forest.

	1998–1999		2000–2001				
Measure	Mean	1 SE	Mean	1 SE	df	t	P
Capture success							
UF	124.5	7.0	130.7	16.2	5	−0.6	0.59
BF	73.1	5.1	168.0	11.2	6	−7.3	<0.001
Species richness							
UF	42.2	2.6	43.3	4.7	5	−0.9	0.42
BF	31.6	2.7	49.4	2.4	6	−4.5	0.004

Note: Test statistics are for paired t tests.

taken in PRIMER Version 5 (Clarke 1993), and plots were rotated to display the highest amount of variance on axis 1. MDS was preferred over other ordination methods because fewer assumptions are made over the shape of species responses, and it enables the use of a similarity index that excludes joint absences. The validity of the technique was supported, because similar results were obtained from other ordination methods such as Canonical Correspondence Analysis using CANOCO Version 4.5 (ter Braak and Smilauer 1998).

Within PRIMER Version 5, ANOSIM (Analyses of Similarity; Clarke and Green 1988) was used to test for significant differences between disturbance treatments both within and between years, and SIMPER (Similarity Percentage; Clarke 1993) was used to examine the influence that each species had in distinguishing between disturbance treatments and locations. The sum of the average dissimilarity divided by the standard deviation (Av. diss/SD; as in Tables 4 and 8) was taken as the best measure of both the consistency and strength of the contribution that each species made toward the dissimilarity values generated, following Clarke and Warwick (1994). The BIO-ENV procedure (Clarke and Ainsworth 1993) was used to find the best fit (or matching coefficient) between the similarity matrices generated from habitat variables and that generated from the bird data. For a more detailed explanation of these procedures, see Clarke (1993) and Clarke and Warwick (1994).

The bird species similarity matrix was generated using the Bray-Curtis similarity index with untransformed data (although similar results were obtained with either log- or square-root transformed data). The normalized euclidean distance measure was used to create habitat similarity matrices based on the standardized habitat variables. Two habitat variables (basal area of live trees and the total tree density per plot) were excluded due to high collinearity ($r_S \geq 0.95$) with other variables (total basal area and the live tree density per plot, respectively) that were retained in the analysis. One variable (nonwoody stems) was log-transformed to improve normality, and thus the effectiveness of the euclidean distance measure. MDS plots were produced to examine the change in the bird community over time and to ordinate all samples from 2000–2001 according to the bird data and habitat variables. MDS attempts to ordinate the samples so that the distance between points is in the same order as the corresponding dissimilarity between samples. Stress values indicate how well this is achieved, with values <0.1 indicating an accurate ordination (Clarke 1993, Clarke and Warwick 1994).

RESULTS

Changes over time at resampled plots

Both the numbers of individuals and of species remained stable over time in unburned plots. However, many more individuals and species were caught in burned forest plots in 2000–2001 than in 1998–1999 (Table 3). The MDS ordination (Fig. 2) shows that there were consistent directional changes in bird abundance and composition within the burned plots over time, and that these shifts tended to make burned plots less similar to unburned plots. Species that consistently contributed to this trend include those typical of young second-growth forest, such as the Dot-winged and Blackish Antbirds, *Microrhopias quixensis* and *Cercomacra nigrescens* (Table 4), which increased in numbers over time in the burned forest. Although the red-headed manakin *Pipra rubrocapilla* contributed most of the species dissimilarity between years, this was not a consistent pattern because this species was only highly abundant in some burned plots. In total, 14 species declined in abundance in the burned forest between 1998 and 2000, including many primary forest specialists such as the Red-crowned Ant Tanager *Habia rubica*, Saturnine Antshrike *Thamnomanes saturninus*, and Long-tailed Woodcreeper *Deconychura longicauda*.

Recaptures.—There were few recaptures between years, and only 126 birds (8%) that had been captured and banded in 1998–1999 were recaptured in 2000–2001. Of these, 79 (63%) were caught at the same netline where they had been captured originally, and all other recaptures (with the exception of two individuals of *Deconychura longicauda*) took place in unburned forest netlines placed adjacently to that of the original capture. Considering recaptures from within the same netline, two-thirds (56 compared to 23) were

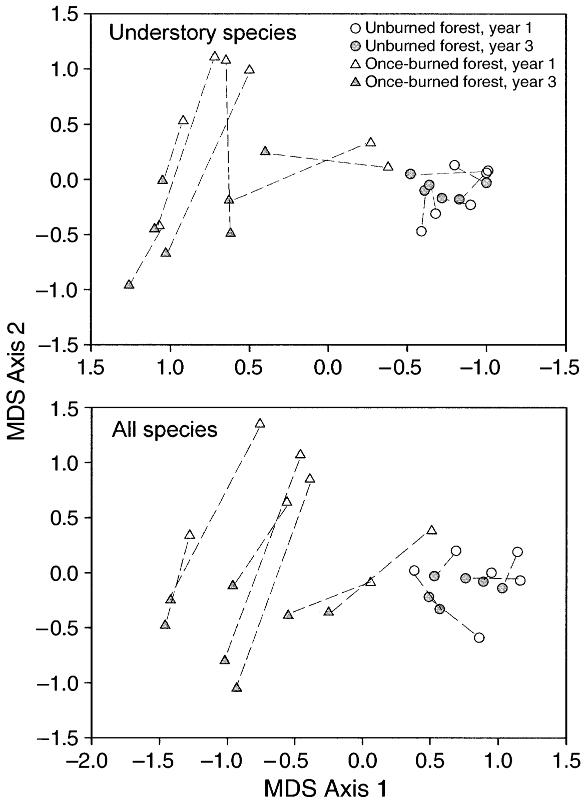

FIG. 2. Nonmetric multidimensional scaling (MDS) plots showing changes in bird assemblage over time in unburned and once-burned forest. Open and gray symbols indicate plots sampled in 1998–1999 and 2000–2001, respectively. Lines link the same plots. MDS stress values are 0.11 for understory only, and 0.14 for all species. There was a significant difference between years in the once-burned forest (ANOSIM for all species, global $R = 0.64$, $P = 0.004$; for understory species, global $R = 0.39$ $P = 0.005$), but not within the unburned plots (for all species, global $R = -0.05$, $P = 0.63$; for understory species, global $R = 0.06$, $P = 0.25$).

of birds captured originally in unburned forest. However, the observed difference in recapture rate was not significant between unburned and once-burned forest ($\chi^2 = 2.82$, df $= 1$, $P > 0.1$), on the basis of the original number of birds banded in each of these two classes of treatment.

Effects of recurrent fires and burn severity

Species richness.—Species accumulation curves show that once-burned forest had the highest species richness whether all species combined or only understory species were considered (see Appendix B). The twice-burned forest had the lowest species richness only when the curves were restricted to understory species, suggesting that species richness in twice-burned forest was greatly augmented by the capture of many midstory and canopy species. K-dominance plots (plots of cumulative percentage abundance vs. species ranked from most to least common) show that the three disturbance treatments had similar equitability when all species were considered, but that the most abundant understory species were markedly dominant in twice-burned forest (Appendix B). Overall species richness was highest at intermediate levels of burn severity, where the bird assemblage contained species typical of both extremes of the disturbance gradient (Fig. 3).

Differences between burn treatments.—The average similarity between plots was higher within than between burn treatments, and unburned forest was almost entirely dissimilar from forest sites that had burned twice (Table 5), indicating that very few species occurred in both unburned and twice-burned forest. The similarity between samples can be seen in the distinctively clustered groupings of fire disturbance in the MDS plots (Fig. 4). The three disturbance treatments were significantly different from each other, whether the distance matrix was derived from the bird assemblage or the habitat variables (ANOSIM; $P < 0.001$ for all comparisons between unburned, once-burned, and twice-burned forest plots), and stress values were low, indicating that these plots were an accurate representation of the similarity between samples. BIO-ENV analyses showed strong correlation coefficients between the distance matrices for the bird and habitat data (Table 6). Although canopy cover was the single variable with the highest matching coefficient for both the overall bird assemblage and understory species only, the inclusion of other variables increased the matching coefficient to 0.81 and 0.86, respectively (Table 6).

Spatial variation in assemblage structure in burned and unburned forest.—Within each disturbance treatment, plots were grouped according to their location in the study site (e.g., upper or lower Maró; Fig. 4), and ANOSIM was used to check for significant differences between groupings. In unburned forest, the upper and lower Maró groupings differed significantly from each other, either when all birds (global $R = 0.4$, $P = 0.01$), or only understory species (global $R = 0.39$, $P = 0.024$) were considered. In once-burned forest, the 10 lower Maró plots were significantly different from the two plots located at Nazário (for all birds, global $R = 0.93$, $P = 0.015$; for understory birds, global $R = 0.81$, $P = 0.015$), as seen in the MDS plots (Fig. 4a, b). Within twice-burned forest, there were no significant differences between the two Maró twice-burned forest plots and the four twice-burned plots located at São José II (for all birds, global $R = 0.43$, $P = 0.2$; for understory birds, global $R = 0.71$, $P = 0.07$).

Corresponding between-location ANOSIM tests were also carried out using distance measures generated from the composite habitat variables 1 and 2 (the variables that best explained changes in the bird assemblage; Table 7). There were no significant differences between different locations within each disturbance treatment (P values for unburned, once-burned, and twice-burned forest were 0.15, 0.38, and 0.40, re-

TABLE 4. Breakdown of the average dissimilarity (Av. diss.) of bird captures between seven burned forest plots, sampled both in 1998–1999 and 2000–2001.

Species	Guild†	Average abundance 1998	Average abundance 2000	Av. diss. measure‡	Diss./SD§	Cum.% diss.‖
Pipra rubrocapilla	FA	5.71	29.86	10.19	0.97	16.30
Passerina cyanoides	GA	2.57	8.14	2.52	1.54	20.34
Thalurania furcata	NA	3.14	6.86	1.90	1.12	23.37
Cercomacra nigrescens	IAG	0.57	4.57	1.77	1.43	26.21
Pipra nattereri	FA	6.29	8.71	1.75	1.38	29.02
Thryothorus genibarbis	IAG	0.57	4.43	1.68	1.11	31.71
Phaethornis malaris	NA	3.57	7.00	1.53	1.36	34.16
Myrmotherula axillaris	IAG	2.71	5.57	1.47	1.52	36.52
Microrhopias quixensis	IAG	0.71	3.57	1.28	1.59	38.56
Myrmoborus myotherinus	ITG	1.43	4.29	1.23	1.45	40.52
Machaeropterus pyrocephalus	FA	0.29	3.00	1.16	0.80	42.38
Oryzoborus angolensis	GA	0.14	2.86	1.12	1.16	44.17
Mionectes oleagineus	OA	0.29	2.71	1.08	1.22	45.89
Mionectes macconnelli	OA	0.71	2.57	1.03	0.94	47.54
Phlegopsis nigromaculata	IAF	0.43	2.71	1.01	1.46	49.15
Campylopterus largipennis	NA	0.14	2.43	0.99	1.18	50.74

Note: Contributions (reflecting 50% of the total dissimilarity between groups) of the top-ranking 16 species, in order of decreasing contribution, are shown.
† Guilds are identified in Table 7.
‡ The average dissimilarity between samples from within each forest treatment.
§ Average dissimilarity divided by standard deviation.
‖ Cumulative percentage of dissimilarity.

spectively, for habitat variables 1, and 0.20, 0.91, and 0.27 for habitat variables 2).

Guild responses.—Species captured in 2000–2001 were grouped into a total of 16 foraging and dietary guilds, although five guilds (aquatic birds, diurnal raptors, internal bark-searching insectivores, terrestrial insectivores and terrestrial granivores) were too rare to warrant further analyses. With the exception of arboreal omnivores and terrestrial gleaning insectivores, all guilds responded significantly to the gradient of burn severity (Table 7). The significant response types were unimodal, negative, or positive, and negative responses were either linear or nonlinear (Fig. 5). All guild responses were similar, whether analysis included all

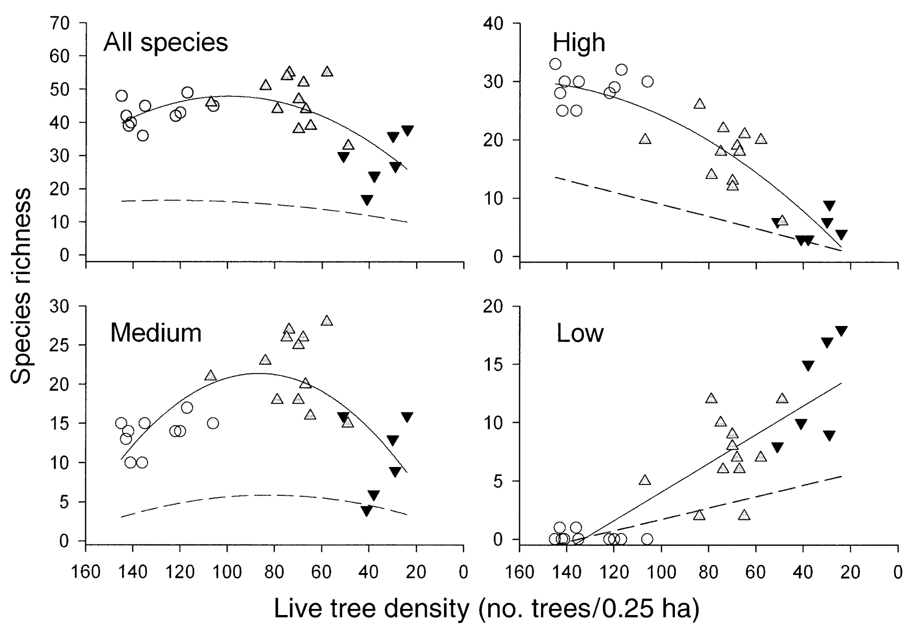

FIG. 3. Relationship between burn severity (measured as live tree density) and bird species richness, split by response guild sensitivity to disturbance (sensu Stotz et al. 1996). Solid lines and symbols represent values for all species, and dashed lines indicate relationships for understory and terrestrial species only. Open, gray, and solid symbols represent unburned, once-burned, and twice-burned forest plots, respectively. Statistics of curve fits are shown in Table 7.

TABLE 5. Average similarity values from the Bray-Curtis similarity index on bird species data within and between habitat disturbance treatments.

Treatment†	All species	Understory species
Within habitats		
UF	53.86	50.48
BF	44.23	41.61
BF2	48.07	60.76
Between habitats		
UF and BF	30.93	29.11
BF and BF2	22.76	29.01
UF and BF2	6.24	7.21

† UF, unburned forest; BF, once-burned forest; BF2, twice-burned forest.

birds or understory species only, and the observed changes in abundance were reflected in very similar patterns of species richness (Fig. 5), all of which were significant (Table 7).

The change in the species richness of the three response guilds (Fig. 3) and the low similarity measures between unburned and twice-burned forest (Table 5) indicate that species turnover was high along the gradient of burn severity, although species turnover within guilds was variable. For example, the high matching coefficient between arboreal-gleaning insectivores and live tree density per plot (Table 6) shows that species turnover (or community dissimilarity) was strongly related to the gradient of burn severity for this guild. Shifts in abundance of the six most common species within this guild show the three typical species response types, with primary forest species (Plain-throated and Long-winged Antwrens *Myrmotherula hauxwelli* and *M. longipennis*) being replaced first by tree-fall gap-loving species (White-flanked Antwren *M. axillaris* and Warbling Antbird *Hypocnemis cantator*), and then by second-growth and edge species (Blackish Antbird *Cercomacra nigrescens* and Moustached Wren *Thryothorus genibarbis*; Fig. 6). Guilds apparently extirpated from twice-burned forest (such as dead-leaf gleaners and ant-followers) were either composed entirely of species unable to tolerate second-growth conditions, or were replaced in twice-burned forest by species that occasionally occupied that guild but were not captured (e.g., Greater Ani's, *Crotophaga major*, were observed following ant swarms in twice-burned forest).

For a limited number of guilds for which we have qualitative or quantitative information on resource (or foraging space) availability, changes in guild abundance were often strongly correlated with, and appeared to track, changes in the supply of that resource. Nectarivores were strongly correlated with the number of *Heliconia* stems per plot ($r_S = 0.77$, $n = 28$, $P < 0.001$), whereas arboreal frugivores were correlated

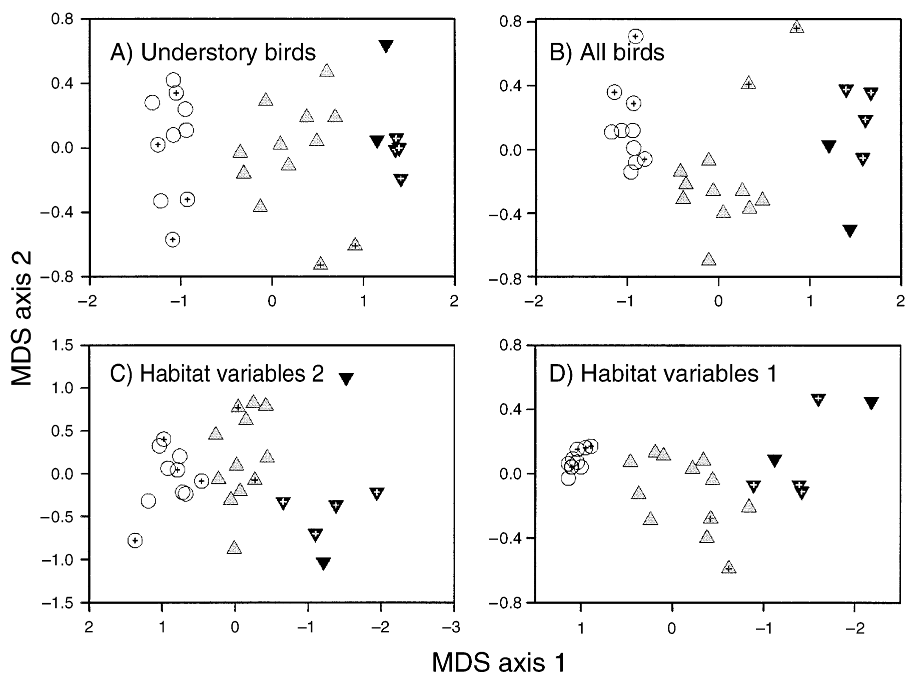

FIG. 4. MDS plots of (A) understory birds, (B) all birds, (C) five habitat variables with the highest matching coefficient with understory birds (habitat variables 2) and (D) three habitat variables with the highest matching coefficient with all birds (habitat variables 1; see Table 2). Stress values are 0.09, 0.08, 0.11, and 0.01, respectively. Open, gray, and solid symbols represent unburned, once-burned, and twice-burned forest plots, respectively. All groups were significantly different from other groups (ANOSIM, $P < 0.001$ for all differences between groups). Crosshairs within symbols refer to the location of the plots, and indicate Nazário plots in once-burned forest, the plots situated at São José II in the twice-burned forest, and upper Maró plots in unburned forest. All other plots were located in the lower Maró.

TABLE 6. Results of BIO-ENV similarity analysis for all bird species (All spp.), understory and terrestrial species (Und. spp.), and for the 10 most abundant foraging guilds.

Guild†	No. species	r_S for LT‡	Best variable‡	r_S	Second-best variable‡	r_S	Best combination of variables‡	r_S
All spp.	152	0.41	C	0.79	NWS	0.70	C, BG, NWS	0.81
Und. spp.	46	0.60	C	0.65	USD	0.61	LT, BA, C, USD, BG	0.86
IAS	40	0.51	C	0.60	LT	0.51	LT, BA, C, WS	0.66
IAG	27	0.76	BG	0.80	LT	0.76	LT, BG	0.82
NA	15	0.39	C	0.47	BA	0.47	BA, C	0.54
ITG	11	0.42	LT	0.42	BG	0.38	LT	0.42
OA	10	0.44	BG	0.53	BA	0.45	BA, BG	0.57
IBS	9	0.49	BA	0.61	C	0.56	BA, C, NWS	0.68
FA	9	0.41	C	0.63	BA	0.55	BA, C	0.68
IAF§	5	0.58	USD	0.69	BG	0.68	BA, USD, BG	0.72
GA§	5	0.23	C	0.32	WS	0.31	DT, BA, C, WS	0.50
IDL‖	4	0.13	WS	0.24	C	0.23	C, WS	0.29

Notes: Excluded guilds were captured too infrequently to be considered in this analysis. Canopy cover is the best overall variable, with the highest matching coefficients for the avifauna as a whole, and for four of the 10 guilds considered here. Matching coefficients (r_S) are the result of correlating similarity matrices based on habitat variables with those based on the avifauna.

† Guild codes are defined in Table 7.

‡ Variables entered were live trees per plot (LT), dead trees per plot (DT), total standing basal area (BA), dead standing basal area (DBA), canopy cover (C), percentage of bare ground (BG), understory vegetation density (USD), woody stems (WS), and log-transformed nonwoody stems (NWS).

§ Four samples were excluded due to absence of this guild.

‖ Ten samples were excluded due to absence of this guild.

with the number of small woody stems <10 cm dbh ($r_S = 0.72$, $n = 28$, $P < 0.001$), many of which produced fleshy berries and drupes. Both the species turnover (Table 6) and abundance ($r_S = 0.54$, $n = 28$, $P = 0.004$) of bark-searching insectivores were related to the standing-tree basal area, a proxy for the amount of foraging space available for these species. Likewise, terrestrial granivores appeared to show an exponential increase along the burn severity gradient, and were therefore correlated with the abundance of non woody stems such as bamboos and other seed-producing species ($r_S = 0.5$, $n = 28$, $P < 0.007$).

DISCUSSION

Burn severity had a pronounced effect on the avifauna, with the species richness and abundance of foraging, dietary, and response guilds being related to the live-tree density at each plot. These changes are discussed in light of previous studies, focusing on whether the data presented here support existing hypotheses attempting to explain relative species abundance in tropical forest bird assemblages. We then examine the potential causes and consequences of the temporal changes detected at resampled plots, and explore the potential role that spatial location may have played in determining assemblage composition. Finally, we use these results to assess the conservation implications of fires in fragmented and logged tropical forest landscapes. Although the extensive coverage of the fires means that there is a lack of true replication within treatments, the generality of the inference and conclusions made here are supported by the spacing of plots across a large area of burned and unburned forest and by randomly sampling a wide range of the inherent variation in burn severity and pre-burn forest types.

Guild responses to burn severity

The guild responses to fire disturbance shown here are similar to those following other forms of structural disturbance in tropical forests, including selective logging (Wong 1986, Lambert 1992, Danielsen and Heegaard 1994, Mason, 1996, Thiollay 1997, Putz et al. 2001), habitat fragmentation (Stouffer and Bierregaard 1995*a*, *b*), gradients of increasing human impacts (Canaday 1996, Thiollay 1999, Pearman 2002), natural treefall gaps (Schemske and Brokaw 1981), regeneration following clear-felling (Raman Shankar et al. 1998, Borges and Stouffer 1999), and the short-term effects of surface wildfires (Kranz 1995, Barlow et al. 2002). Despite the potential for variation in other life history components, foraging and dietary guilds appear to form predictable and meaningful ecological groupings and valid indicators of change in tropical forests.

Several potential explanations have been proposed to account for patterns of habitat selection in tropical forest birds, including the light environment and other physiological factors (Pearson 1971, Fitzpatrick 1980, Karr and Freemark 1983, Karr and Brawn 1990, Pearman 2002), resource abundance (Karr and Brawn 1990, Stouffer and Bierregaard 1995*a*, Raman Shankar et al. 1998), the regional and local history of disturbance (Pearman 2002), interspecific competition (Robinson and Terborgh 1995), habitat structure (Terborgh 1985, Mason 1996, Raman Shankar et al. 1998), and exposure to predation threat (Canaday 1996, Thiollay 1997). Although we are unable to confirm or reject any of these

TABLE 7. Statistics for graphs shown in Figs. 3 and 5.

Guild	Guild code	No. individuals	No. species	Species richness†	Abundance of all species			Abundance of understory and terrestrial species		
				χ^2	r^2	F	P	r^2	F	P
Foraging guild										
Arboreal gleaning insectivore	IAG	705	27	7.9*	0.24	8.4	0.007	0.52	28.0	<0.001
Arboreal frugivore	FA	590	9	13.8**	0.32	5.8	0.009			
Arboreal sallying insectivore	IAS	485	40	17.3***	0.58	35.9	<0.001	0.69	57.8	<0.001
Arboreal nectarivore	NA	421	15	11.2**	0.25	4.1	0.03	0.27	4.5	0.02
Bark-searching insectivore‡	IBS	306	9	13.1**	0.29	5.1	0.014			
Ant-following insectivore	IAF	290	5	18.5***				71.2	66.8	<0.001
Arboreal omnivore	OA	196	10	6.4*	0.02	0.4	0.53			
Terrestrial gleaning insectivore	ITG	153	11	12.4**				0.11	3.4	0.08
Arboreal granivore	GA	135	5	13.8**	0.36	7.1	0.004	0.31	5.7	0.009
Dead-leaf searching insectivore	IDL	69	4	13.5**	0.39	16.5	<0.001	0.41	18.4	<0.001
Terrestrial frugivore	FRT	44	1							
Terrestrial granivore	GRT	29	4							
Internal bark-searching insectivore	IBI	27	5							
Terrestrial sallying insectivore	ITS	11	2							
Diurnal raptor	RDN	5	4							
Aquatic	AQ	3	1							
Response guild§										
All species		3469	152		0.41	8.8	0.001	0.37	7.5	0.003
High-sensitivity species		1736	66		0.82	57.9	<0.001	0.78	91.7	<0.001
Medium-sensitivity species		1276	54		0.44	9.9	<0.001	0.28	4.9	0.016
Low-sensitivity species		457	32		0.75	76.5	<0.001	0.72	67.8	<0.001

Notes: For guilds where tests were carried out, blank cells indicate either the absence of any species in this category, or that all species were in the other category. For F tests, df = 1, 26 for all regressions (except the quadratic relationships, with df = 2, 25).

† Kruskal-Wallis χ^2 results and significance. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

‡ Foraging externally on tree trunks.

§ For response guilds, r^2, F, and P values are given for species richness rather than abundance.

hypotheses with our correlative evidence, our results do lend support to some. In particular, strong correlations between the abundance of (relatively sedentary) guilds that are directly dependent on plant resources (i.e., frugivores, nectarivores, and granivores) and the abundance of those resources are consistent with findings by Wong (1986) and Terborgh (1985) for nectarivores, Terborgh (1985) and Blake and Loiselle (1991) for frugivores, and Raman Shankar et al. (1998) for granivores.

In other cases, guild abundance can be related to foraging substrate abundance or indirect estimates of arthropod abundance. The positive correlation between forest basal area and the abundance of external bark-searching insectivores is supported by the findings of Raman Shankar et al. (1998), whereas the resilience of this guild to light-intensity burns contrasts with their negative response to logging, where the removal of much of the forest basal area is correlated with decreases in their abundance (Johns 1989, Thiollay 1992). The increase of arboreal gleaning insectivores may also be associated with insect abundance, because the rapid regeneration and increase in leaf production following an increase in canopy openness can augment overall arthropod abundance (Basset et al. 2001).

Although the difficulty in quantifying the abundance and availability of arthropods means that resource-based explanations are poorly explored for insectivorous guilds (but see Karr and Brawn 1990, Sekercioglu et al. 2002), there is evidence that other factors are also important. For example, of the professional ant-followers, only the black-spotted bare-eye *Phlegopsis nigromaculata* appeared to be able to utilize the army-ant swarms that had recolonized the burned forest (J. Barlow, *personal observation*), and other species within this guild may be constrained by physiological conditions (Pearman 2002). Many other insectivorous birds appear to be similarly affected, because many primary-forest species are known to avoid open areas (Stouffer and Bierregaard 1995*b*, Canaday 1996, Develey and Stouffer 2001, Sekercioglu et al. 2002). It is possible that the greatly enhanced light environment in

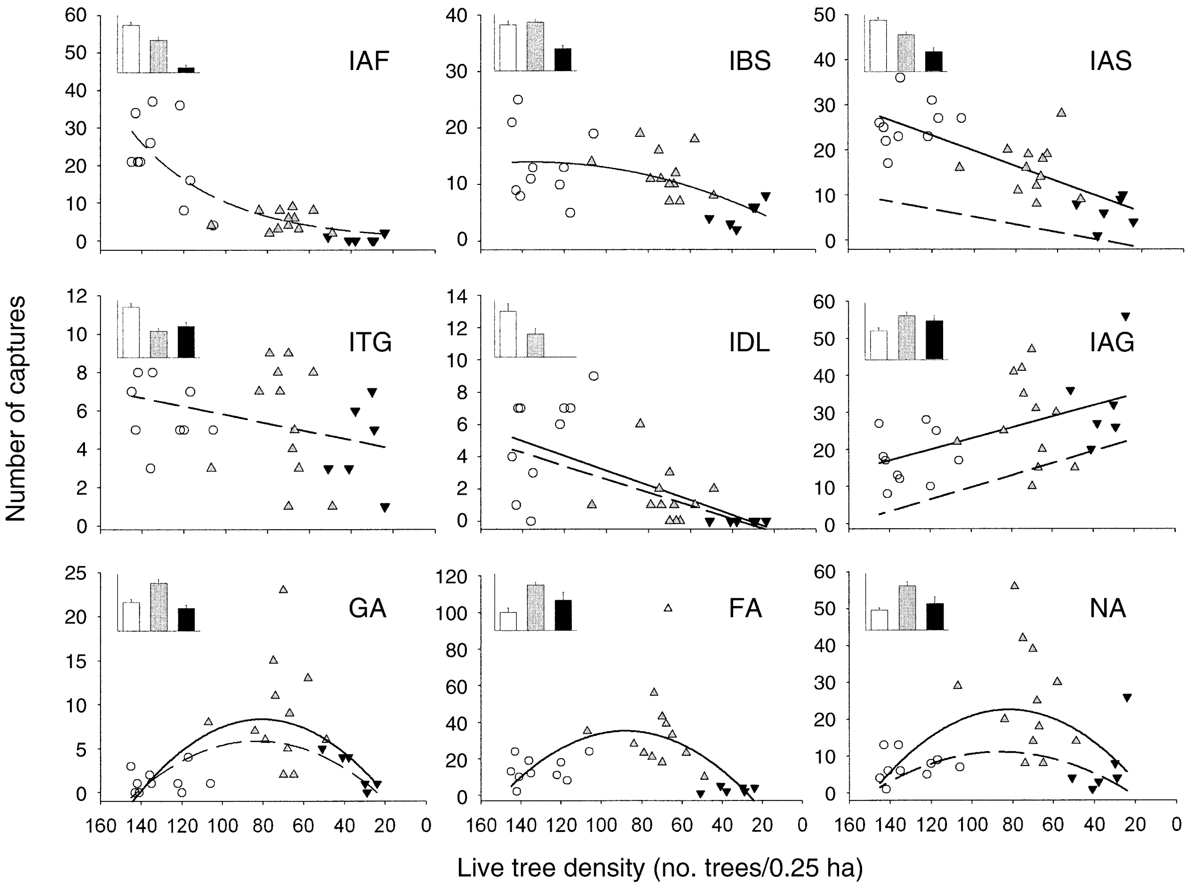

FIG. 5. Relationship between bird abundance and burn severity (main graphs) and mean (± SE) species richness (inset bar graphs) of nine foraging and dietary guilds (described in Table 7). Solid lines and symbols represent values for all species, and dashed lines indicate relationships for understory and terrestrial species. Open, gray, and solid symbols represent unburned, once-burned, and twice-burned forest plots, respectively. Shading (open, gray, and solid) on bars represents the same scheme and applies to species from all forest levels.

the burned forest may restrict their presence through changes in microclimatic conditions (Pearson 1971, Fitzpatrick 1980, Karr and Freemark 1983, Karr and Brawn 1990, Pearman 2002). Habitat structure in the understory also appears to be important; the similarity matrices of all but one of the insectivorous guilds were best correlated with variables describing habitat structure in the understory (Table 6), and understory regeneration also explains a large proportion of the changes in avifaunal structure in other tropical forest studies (Mason 1996, Barlow et al. 2002). Although this correlative evidence does provide insights into potential mechanisms, without experimental manipulation it is clearly difficult to divorce the closely correlated variables.

Temporal changes

Rather than showing signs of recovery and reverting toward a typical primary-forest avifauna, the bird assemblage within burned forest contained many more species typical of gaps and second growth, while many primary-forest specialists continued to decline in abundance (Table 4). No discernible trends were detected in unburned forest plots, indicating that background differences in community structure were relatively unimportant. Two factors may be associated with observed changes in burned forest plots.

Firstly, it is particularly significant that the directional shift of the avifauna structure away from a primary-forest state matches the shifts in tree mortality and forest structure. Mortality of trees (≥10 cm dbh) increased markedly between one and three years after fire, from 34% to 48%, in the same plots where the avifauna was sampled (Barlow et al. 2003). This continued mortality, combined with an elevated rate of treefalls continually puncturing the canopy, led to an increasingly open forest analogous to second growth. These changes were not reflected by a decrease in the overall canopy cover over the same time period, because the fractured canopy resulting from canopy tree mortality was compensated for by a subcanopy resulting from the strong pulse of understory regeneration.

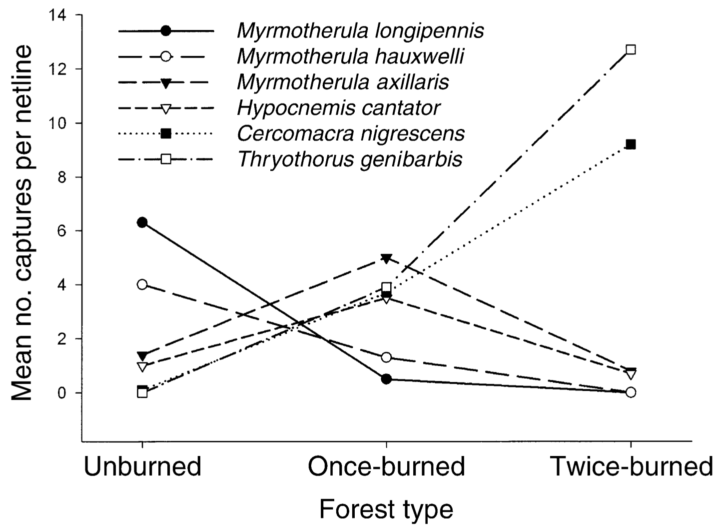

FIG. 6. The three response types exhibited by the six most abundant arboreal-gleaning insectivorous species (IAG), demonstrating how species responses within guilds can differ, and how disturbance-tolerant species replace intolerant species in once- and twice-burned forest.

However, this dense regeneration is, in itself, an important determinant of changes in understory bird community structure (Mason 1996, Barlow et al. 2002; Table 6), and explains the invasion of second-growth species such as *Thryothorus genibarbis* that are normally associated with dense scrub. Furthermore, this regeneration led to a marked pulse in some resources, which may account for the significant increases in the abundance of frugivorous and nectarivorous species. Secondly, the observed change in bird assemblages may also reflect a time lag in population expansion. Fires in this area burned ~1140 km^2 of primary and secondary forests (Nelson 2001), generating a hyper-abundance of habitat suitable for second-growth and gap specialists. As such, some of the difference between years may be due simply to a delay in colonization events and inertia in population growth.

It is difficult to predict the long-term potential for avifaunal recovery following recurrent fires in fire-intolerant ecosystems such as moist tropical forests. Although long-term data are available on forest and avifaunal recovery following selective logging, there is little agreement between studies conducted in different continents, using different methods, and at differing logging intensities (Johns 1997, Putz et al. 2001). However, in studies in which tree mortality rates were similar to those in once-burned forest at our study area, there was little sign of avifaunal recovery even up to 10 years after logging (Lambert 1992, Thiollay 1997). Furthermore, other things being equal, it is likely that fires represent a more severe agent of disturbance than selective logging. Logged forest is highly heterogeneous (Hill 1999), and most primary-forest species appear to be able to persist in unlogged refugia (Lambert 1992, Mason 1996, Johns 1997, Thiollay 1997, Lambert and Collar 2002). In contrast, the structure of the mostly small unburned patches in once-burned forest (<200 m^2) appeared to be influenced by the increased canopy openness in the surrounding forest, and were therefore either too small or too disturbed to effectively function as refugia for primary-forest species (J. Barlow, *personal observation*).

Spatial effects

Although we focused on the local importance of burn severity rather than on spatial effects of plot location, the marked dissimilarity (68.5%) between the two once-burned forest sites farthest from the fire line (Nazário) and the other 10 Maró plots indicate that spatial effects may be important. Two potential explanations, that there were pre-existing differences in the bird community or that there were differences in habitat structure, can be discounted as they are not supported by the data. Firstly, although neotropical forests sharing the same species pool can differ in species composition (Thiollay 2002), we consider it unlikely that pre-existing differences in the abundance of species typical of undisturbed forest could explain postfire differences in the abundance of species typical of disturbed forest. Secondly, we reject the importance of local habitat structure, because there were no significant differences between the Nazário and Lower Maró plots according to the combinations of habitat variables that best correlated with the bird assemblage (habitat variables 1 and 2). Moreover, although there may have been subtle differences that remained undetected by our measurements, the very high matching coefficients between the habitat variables quantified and the bird assemblage suggest that any additional variables would have only small effects.

The most parsimonious explanation for the observed differences relates to neighborhood effects resulting from the avifaunal composition of the surrounding landscape. Habitat heterogeneity is an important determinant of avian species richness at different spatial scales (Urban and Smith 1989), and the abundance of

TABLE 8. Breakdown of average dissimilarity of bird captures between the Lower and Upper Maró unburned forest plots (upper section) and the lower Maró and Nazário once-burned forest plots (lower section).

Species	Guild†	Average abundance‡ Area 1§	Area 2§	Av. diss.	Diss./SD	Cum. % diss.
Unburned forest						
Dendrocincla merula	IAF	15.17	11.5	4.26	1.64	8.78
Pipra rubrocapilla	FA	7.5	6.5	2.66	1.23	14.26
Glyphorhynchus spirurus	IBS	2.83	8.25	2.48	1.06	19.37
Mionectes macconelli	OA	6.17	1	2.11	1.26	23.71
Myrmotherula longipennis	IAG	7.83	4	1.76	1.17	27.33
Automolus ochrolaemus	IDL	0.33	4	1.54	1.86	30.5
Pipra nattereri	FA	7.67	4.25	1.47	1.46	33.51
Myrmotherula hauxwelli	IAG	5.17	2.25	1.39	1.63	36.39
Geotrygon montana	FRT	3	0.75	1.17	1.08	38.8
Rhegmatorhina berlepschi	IAF	3.33	2.25	1.08	1.52	41.02
Once-burned forest						
Pipra rubrocapilla	FA	24.4	10.5	6.92	0.78	10.13
Pipra nattereri	FA	9.3	0.5	3.79	1.77	15.68
Thalurania furcata	NA	9.3	1.5	3.27	1.12	20.47
Coereba flaveola	NA	0.2	7.5	3.11	1.86	25.03
Phaethornis malaris	NA	7.3	0	3	1.69	29.42
Myrmotherula axillaris	IAG	6	0	2.46	2.24	33.03
Passerina cyanoides	GA	7.3	2	2.17	1.47	36.21
Hypocnemis cantator	IAG	4.2	0	1.83	1.82	38.9
Thryothorus genibarbis	IAG	4	3.5	1.35	1.28	40.87
Ramphocelus carbo	OA	1.3	3.5	1.28	1.25	42.75

Note: Dissimilarity values in the last three columns are as defined in Table 4.
† Guild codes are defined in Table 7.
‡ Mean number of individuals captured, per netline.
§ For unburned forest, Area 1 is Lower Maró ($n = 6$), and Area 2 is upper Maró ($n = 4$); for once-burned forest, Area 1 is Lower Maró ($n = 10$), and Area 2 is Nazário ($n = 2$).

some guilds in tropical forests may relate more to landscape-scale processes than to local habitat structure (Gascon et al. 1999, Pearman 2002). Although all plots were in continuous forest, there was a much greater proportion of twice-burned forest in the landscape surrounding the Nazário plots (J. Barlow, *personal observation*). Significantly, the declines of species typical of once-burned forest (such as White-Flanked Antwren *Myrmotherula axillaris* and Snow-capped Manakin *Pipra nattereri*) and the increases of species abundant in twice-burned forest (such as the Silver-beaked Tanager *Ramphocelus carbo* and Bananaquit *Coereba flaveola*) account for much of the difference between the two locations (Table 8). The declines of wide-ranging species dependent on food resources in the surrounding forest matrix (Stouffer and Bierregaard 1995*a*), such as hummingbirds and frugivorous manakins, (*Pipra* spp.) (Table 8), provides further evidence for this hypothesis: the high proportion of twice-burned forest in the region probably would have led to food scarcity at the landscape level, because recurrent burns dramatically reduce the number of flowering and fruiting stems (Barlow 2003).

If landscape-scale processes are important determinants of community composition, then our results should be considered as conservative estimates of the effects of fire on biodiversity, because all plots were in continuous forest with very light histories of logging, and most were close to unburned forest. Equivalent surface fires in forest landscapes that are logged, fragmented, with a small proportion of remaining primary forest, or far from potential sources of recolonization, can all be expected to have greater synergistic impacts.

Conservation implications of interactions of fire with other disturbance events

Forest fragmentation.—Fires co-occur and operate synergistically with fragmentation, because forest edges are more likely to burn than are forest interiors (Cochrane 2001*a*, Cochrane and Laurance 2002). Although fragmentation alone can lead to the loss of many forest species (Stouffer and Bierregaard 1995b, Lambert and Collar 2002), this will be vastly exacerbated by fires if forest isolates burn. Species intolerant of the dense understory and open upper canopy (associated with the early stages of postfire forest recovery) are also those that avoid open areas and treefall gaps (Stouffer and Bierregaard 1995*b*, Develey and Stouffer 2001) and are highly unlikely to recolonize should suitable conditions return. Many species tolerant of fragmentation itself could therefore become permanently extirpated from the fragmented landscapes of the seasonally dry southeastern arch of Amazonia, where most forest fragments are adjacent to agricultural land and show signs of recent fire scars (C. Peres, *personal observation*).

Selective logging.—Although the changes in community structure following selective logging are proportional to the magnitude of forest disturbance (Mason 1996), it may be the association between logging history and increased burn severity (Siegert et al. 2001) that represents the greatest threat of poor logging practices to biodiversity. Species sensitive to other disturbance events are particularly threatened by more severe fires (Fig. 3), including many endemic species with restricted ranges and high conservation concern (such as the Pale-faced and Harlequin Antbirds, *Skutchia borbae* and *Rhegmatorhina berlepshi*). In this context, the role of logging in highly seasonal tropical forests must be considered carefully, and measures such as Reduced Impact Logging (see Putz et al. 2000), the use of wide, unlogged forest strips as firebreaks (Holdsworth and Uhl 1997), and the prevention of human incursions along new logging roads (Laurance 2001), need to be implemented and enforced in order to break the strong association between logging and fires (Siegert et al. 2001). Without these measures, the role of selective logging as the least environmentally damaging of the financially viable land uses in tropical rain forests today (Pearce et al. 1999) should be reconsidered in the light of increasingly greater forest flammability in fire-prone forests.

Conclusion

Our results show that fires pose a serious threat to avian diversity in tropical forests, even in continuous tracts of forests subjected to little or no logging, such as those studied here. Because the loss of forest birds was directly related to the local severity of fire events, these results present a strong case for limiting or carefully governing activities such as selective logging and the creation of forest edges, which increase both the likelihood and the severity of forest fires (Nepstad et al. 1999, Siegert et al. 2001, Cochrane and Laurance 2002). Furthermore, instead of showing any signs of recovery between one and three years post fire, the avifaunal composition became increasingly dissimilar from that occurring in primary forest, reflecting the concurrent continuation of canopy tree mortality and the rapid regeneration of pioneer species. The inability of many forest interior species to persist in this regeneration phase has important implications for the avifauna in fragmented habitats, where extirpated forest species will be unable to recolonize. Overall, the long-term fate of forest avifauna that is primarily or entirely restricted to closed-canopy forest in fire-prone Amazonian forests will be determined largely by the success of local and regional governments in enforcing environmental legislation during the current wave of Amazonian development (*Avança Brasil*; see Peres 2001, Laurance and Fearnside 2002, Nepstad et al. 2002*a*, *b*). The future predicament of the forest biota will also depend on the extent to which the combined effects of climate change and deforestation reduce precipitation, raise ambient temperatures, and increase seasonality across the Amazon basin (Costa and Foley 2000).

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APPENDIX A

A table of all bird species captured during the study, and their presence or absence within each habitat is available in ESA's Electronic Data Archive: *Ecological Archives* A014-026-A1.

APPENDIX B

Species accumulation curves and Lorenz's k-dominance curves for all bird species and for all understory and terrestrial species in the three disturbance treatments are available in ESA's Electronic Data Archive: *Ecological Archives* A014-026-A2.