

Effects of ground fires on understorey bird assemblages in Amazonian forests

Jos Barlow*, Tor Haugaasen, Carlos A. Peres

Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK

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Abstract

Avifaunal responses to understorey fire disturbance and subsequent changes in habitat structure were examined within 20 burnt and unburnt forest plots of 0.25 ha (10×250 m), 10–15 months after an unprecedented understorey fire swept through the Tapajós-Arapiuns Extractive Reserve of central Brazilian Amazonia following the severe 1997–1998 El-Niño dry season. Although these surface fires in the previously undisturbed primary forest were relatively mild, they resulted in dramatic changes in forest structure consistent with those found elsewhere in Amazonia. Bird species negatively affected by these changes tended to be the least common, the most disturbance-sensitive, and habitat specialists. Considering different guilds, ant followers, dead-leaf gleaners, terrestrial gleaners, and arboreal sallying insectivores were the most negatively affected, whereas nectivores and arboreal granivores became more abundant in the burnt forest. The results highlight the severe consequences of even relatively mild surface fires in neotropical forests, and the importance of controlling haphazard frontier expansion for the conservation of susceptible species that are endemic to fire-prone regions. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The Amazon basin is frequently thought to safeguard the highest biological diversity on earth (Myers and Myers, 1992), and this is particularly the case for birds (e.g. Terborgh et al., 1984; Hilty and Brown, 1986). Even “species poor” central Amazonian forests can contain over 400 species within the terra firme forest matrix (Cohn-Haft et al., 1997) including the highest diversity of woodcreepers (Dendrocolaptidae) in the neotropics (Oren and Parker, 1997). Despite these exceptionally high levels of local and regional diversity, Amazonia has been excluded from the world’s top biodiversity hotspots owing to the large amount of forest cover still remaining and the few threatened endemic species (Myers et al., 2000). However, the Amazon forest is experiencing the highest rate of tropical deforestation (Whitmore, 1997; Alves et al., 1998) and extensive deforestation in the region south of the Rio Amazonas and east of the Rio Madeira is potentially

threatening to a number of endemic bird species (Stotz et al., 1996). Furthermore, conventional deforestation mapping exercises overlook human disturbance underneath the forest canopy, much of which is seriously reducing the biodiversity value (Peres, 2000) and hydrological sustainability of forest ecosystems (Cochrane et al., 1999, Nepstad et al., 1999a).

Historically, fire events within Amazonian forests were apparently rare and associated with long duration “El-Niño” events over the past 7000 years (Turcq et al., 1998). However, within recent years understorey wildfires in tropical forests have become increasingly common (Goldammer, 1999), and an estimated 1 million km² of Amazon forests were at risk of burning during 1997–1998 (Nepstad et al., 2001). Three factors explain this unprecedented increase of fires within Amazonia. Firstly, the increasing frequency of El-Niño events (Dunbar, 2000) means that many parts of the Amazon suffer abnormally long droughts in the dry season. During these events soil water can become depleted beyond a critical depth, and canopy trees are forced to shed their leaves in order to maintain water balance (Nepstad et al., 1999a). The resulting increase in sunlight dries the fine fuel layer and allows normally fire-

* Corresponding author. Tel.: +44-1603-593115; fax: +44-1603-250588.

E-mail address: j.barlow@uea.ac.uk (J. Barlow).

resistant forests to become flammable. Secondly, selective logging lowers the flammability threshold of forests further, by reducing canopy cover whilst increasing fuel loads on the forest floor (Holdsworth and Uhl, 1997). The final factor is related to the prevalence of fire in Amazonian agriculture (790 fires were registered by satellite from just 256 km² in 1997 alone, Nepstad et al., 1999a). Although fire in Amazonian agriculture is not new, frontier expansion is bringing these ignition sources closer to forest tracts at risk of becoming flammable.

Unlike the more dramatic and widely reported canopy fires, these surface (or ground) fires move slowly through the leaf litter, burning the fine and coarse fuel layer, and flame heights rarely exceed 10–30 cm under normal fuel loads and humidity conditions (Holdsworth and Uhl, 1997; Cochrane and Schulze, 1999). However, although restricted to the understorey, these surface fires result in severe changes in forest structure and can lead to significant biotic impoverishment of previously unburnt forests if subsequent burns occur (Cochrane et al., 1999; Nepstad et al., 1999b; Peres, 1999).

We examined these biotic consequences by focusing on understorey birds, which are one of the most vulnerable vertebrate taxa to forest disturbance (Wong, 1985; Lovejoy et al., 1986; Johns, 1991; Thiollay, 1992; 1999; Canaday, 1996; Mason, 1996; Aleixo, 1999) due to their often sedentary nature (Stotz et al., 1996) and intolerance of canopy gaps (Bierregaard and Lovejoy, 1989). This inability to disperse across forest edges, or use secondary growth, renders a number of species particularly vulnerable to habitat disturbance within increasingly degraded and fragmented forest landscapes.

2. Methods and study areas

Fieldwork was carried out on both banks of the Rio Maró, both inside and outside of the recently created Tapajós-Arapiuns Extractive Reserve of westernmost Pará, central Brazilian Amazonia (2°44' S, 55°41' W; Fig. 1). The reserve is characterised by relatively low and strongly demarcated annual rainfall with a dry

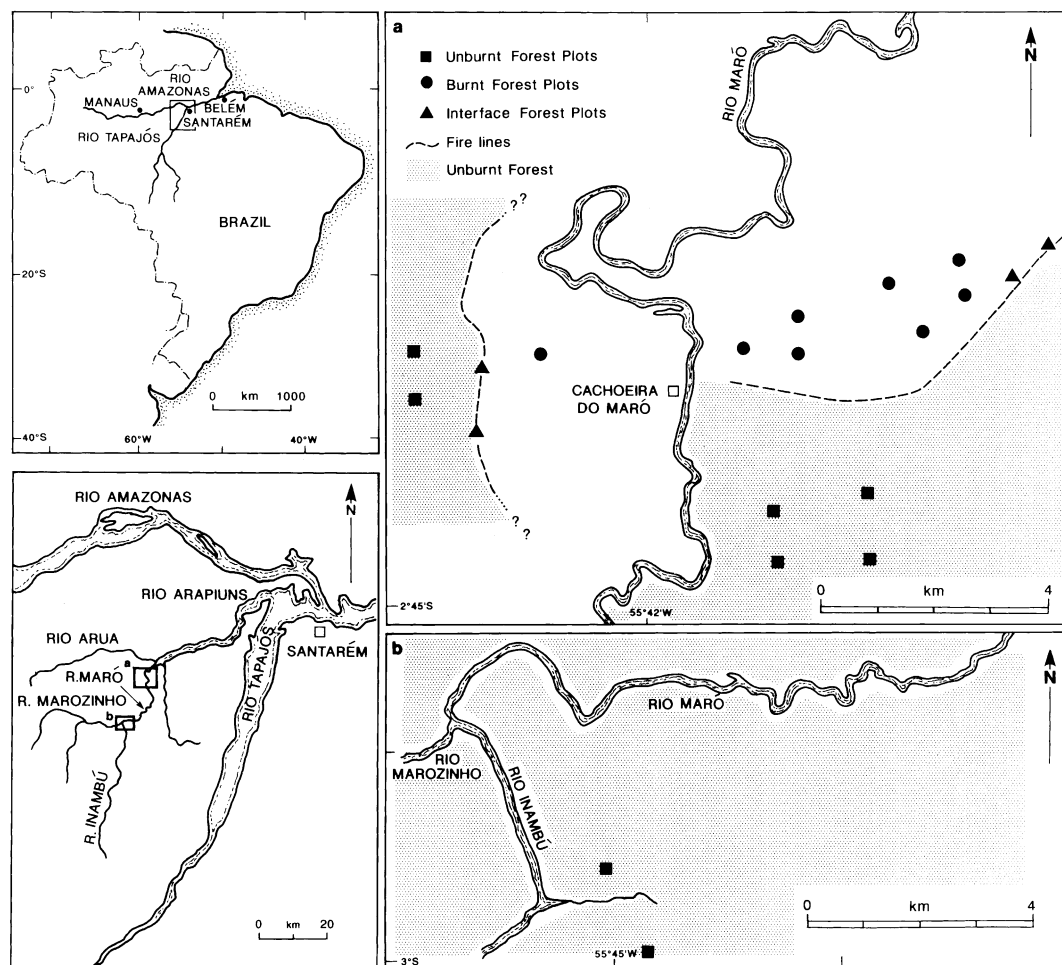


Fig. 1. Map of study area in central Brazilian Amazonia. Solid squares, circles and triangles represent the location of netlines and quarter-hectare forest plots (see label) in either unburnt (shaded) and burnt forest (unshaded).

season typically lasting 3–5 months. Average annual rainfall at the nearest meteorological station (Santarém) is 2041 mm/year (range = 1287–2538 mm/year, 1992–1997: INFRAERO, 1998). The combination of a marked dry season and the predominantly white-sand (podzolic) soils of the Arapiuns basin largely explain why the study area is within the highest level of forest flammability risk predicted for central Amazonia (Nepstad et al., 1999b). The study took place between 10 and 15 months after a widespread accidental wildfire had swept through large parts of the reserve, leaving an area of at least 400 km² of forests with a scorched understorey. Prior to this wildfire, all forest plots sampled had consisted of relatively undisturbed upland (terra firme) primary forest; selective logging was primarily restricted to one relatively rare timber species (*Mezilaurus itauba*, Lauraceae) although there has been a long history of game hunting and small-scale extraction of non-timber forest products. The recent Arapiuns wildfires occurred in November–December 1997 at the end of the longest dry season in living memory, following a rainless period of at least 110 days linked to the 1997/1998 El Niño/Southern Oscillation (ENSO) event.

2.1. Habitat data

Forest structure was quantified 1 month after the fires (Peres, 1999) and in more detail the following year. During the second study period, a total of 14 habitat variables were examined within 20 plots of 0.25-ha (10×250 m), including eight in the burnt forest, eight in the unburnt and four intersecting a clearly distinguishable fireline separating the burnt and unburnt forest (Fig. 1). Within each plot all trees ≥10 cm DBH (diameter at breast height) were measured and carefully inspected so that their survival status (i.e. alive, dead, dying) could be determined. Including the interfaces a total of 2643 trees ≥10 cm DBH were measured, with 1302 and 1341 being found in the burnt and unburnt forest, respectively. All saplings (defined as woody stems <10 cm DBH and taller than 1 m) were measured and inspected to determine survival status within a 2.5×100 m subplot.

Canopy openness was quantified with the use of a spherical densiometer at 24 evenly spaced points within each plot (with four readings taken per point; see Lemmon, 1957). Forest floor regeneration was assessed within a 2×2 m quadrat laid to the left hand side of the transect at each point where a canopy cover reading was taken (24 quadrats per plot). Within each quadrat the total % cover of undergrowth vegetation was estimated, and broken down into easily distinguishable groups consisting of *Cercropia* spp., *Palicourea guianensis* (Rubiaceae), palms (Palmae), vines and lianas, slender bamboo (*Guadua* sp.), terrestrial bromeliads, grasses (Gramineae, excluding *Guadua* sp.), sedges (Cyperaceae,

Carex spp.), and herbaceous plants consisting of all ferns (Pteridophyta), *Heliconia* spp. and species from the three genera of Marantaceae. Understorey density was measured using a 2.5-m graduated pole held vertically by one observer and examined from 15 m away by another. A total of 40 readings were recorded in each plot corresponding to the number of 10-cm pole sections (range: 0–25) that were clearly visible.

2.2. Bird sampling

Understorey mist netting was used to examine the effects of these habitat changes upon the avifauna. A total of 20 linear netlines were operated along the centre of the 0.25-ha forest plots. Each netline consisted of 24 mist nets of 12×2.5 m (mesh size 36 mm), and had a total length of around 320 m as large treefalls were avoided. Nets were opened for two and a half days (30 h), from dawn to dusk for the first 2 days and from dawn to 1200 h on the third day, accruing a total of 14,400 net-hours. All netlines were at least 500 m apart from one another, and were thus considered to be spatially independent. This is supported by the fact that <0.5% of all birds captured were subsequently recaptured in a neighboring netline. Two unburnt netlines were situated 40 km upstream and served as control plots far from the nearest patch of burnt forest. Potential seasonal effects were reduced or eliminated by systematically alternating sampling between burnt and unburnt forest and by compressing the study into a 5-month period. Nets were checked hourly, and closed during periods of heavy rain. Hours lost due to heavy rain were compensated for on the third day of netting. All birds captured were identified to species, weighed and measured (standard measurements included wing, tail, bill and total length) and whenever possible aged and sexed. All new captures were given a plastic ring that was colour-coded for each site, with the exception of hummingbirds which were marked by cutting a small individually identifiable notch in a single tail feather. All captures and recaptures on different days were recorded, although recaptures are excluded from this analysis.

Although mist netting may be less effective in comparison with point counts (Thiollay, 1994) and can give a biased account of the avifauna (Remsen and Good, 1996), it does allow easy comparison with other avifaunal studies in the tropics and is a useful and highly standardised technique for censusing non-vocal and secretive understorey birds (Karr, 1981). This is particularly important since forest interior species restricted to the shaded understorey are those most susceptible to forest disturbance (Johns, 1991; Aleixo, 1999). In this paper, all reference to a species abundance refers to its capture frequency, although we recognise that this may not necessarily reflect the species' actual abundance.

2.3. Data analysis

Unless otherwise stated, data analysis comparing burnt and unburnt forest excludes the four interface plots and netlines across the fireline. Most species were assigned to different foraging guilds based on dietary and foraging modes following Terborgh et al. (1990) with information on additional species extracted from Thiollay (1994), Hilty and Brown (1986), Ridgley and Tudor (1989; 1994) and Sick (1985). Other species groupings including foraging height, number of habitats used, and classes of abundance and sensitivity to human disturbance, were taken from Stotz et al. (1996), except for some minor alterations in order to avoid functional groups including species that were rarely captured. Species nomenclature also follows Stotz et al. (1996). Assemblage similarity across samples were calculated using Spearman's rank correlation coefficients of species abundance between all pairwise comparisons of burnt and unburnt forest netlines ($n=120$). The resulting correlation coefficients were thus taken as a measure of assemblage similarity between any two netlines, and were then used in regression analysis to examine which habitat variables best explained the changes in assemblage similarity between forest plots. All measures variance around means shown here are standard errors (\pm S.E.), and P values shown are two-tailed.

3. Results

3.1. Qualitative effects after 1 month

Initial fieldwork, 1 month after the fires revealed that the flames had burnt standing trees at an average height of ca. 10–30 cm, and had consumed the leaf litter, root mat, and most of the coarse and fine woody material lying on the forest floor. Heat and smoke had scorched the understorey vegetation from the forest floor to an average height of ca. 2.5 m. Many trees were visibly heat-stressed given their leaf shedding and aborted fruit crops, and mortality was clearly apparent for the vast majority of understorey plants, and a large number of high-climbing woody lianas and subcanopy and canopy trees. There also appeared to be noticeable consequences for both the forest avifauna, with direct evidence of smoke-induced mortality for some cavity-nesters (e.g. toucans *Ramphastos* spp.; aracaris *Pteroglossus* spp.). A conspicuous absence of understorey avian activity, even during peak vocal periods, suggests that much of the avifauna in burnt forests had either succumbed to the fires or had emigrated to surrounding areas of unburnt forest. However, the subsequent lack of evidence of post-fire crowding in unburnt areas close to burnt forest 1 year after the fire (J. Barlow, unpublished data) suggests that even those birds that had

emigrated into unburnt forest had suffered density-dependent mortality in the following year.

3.2. Changes in forest structure after 10–15 months

Mean basal area in all 20 forest plots sampled was $28.33 \pm 1.55 \text{ m}^2 \text{ ha}^{-1}$, ($n=20$) and there was no significant difference between the burnt and unburnt forest (mean unburnt = $30.31 \pm 1.84 \text{ m}^2 \text{ ha}^{-1}$ ($n=8$), mean burnt = $26.35 \pm 2.40 \text{ m}^2 \text{ ha}^{-1}$ ($n=8$), $t=1.31$, d.f. = 14, $P=0.21$). Total tree mortality (% of dead trees in all plots) in the burnt forest was many times higher than the background level (36% compared with 4%). Tree mortality in burnt forest was clearly unequal across tree size classes: the proportion of dead trees declined significantly with increasing DBH ($r^2=0.77$, $F_{1,10}=33.69$, $P<0.001$, $n=12$). Saplings succumbed to the highest mortality, and only 25% of the 1076 saplings recorded in the burnt forest plots ($n=8$) were alive, as opposed to 96% of the 1451 saplings recorded in the unburnt forest plots ($n=8$).

Canopy openness was four times higher in the burnt forest than in the unburnt, and was much more variable both within and between burnt forest plots than it was in the unburnt forest. There was also a significant increase in understorey regeneration which was largely explained by the % of canopy gap in different plots ($r^2=0.66$, $F_{1,14}=26.67$, $P<0.001$, $n=16$). This early process of understorey regeneration was also highly variable between burnt forest plots. While most plots contained pioneer tree species such as *Cecropia* Spp. and *Palicourea guianensis*, some plots were dominated by aggressive pioneers such as the sedges (*Carex* spp.) and slender bamboo (*Guadua* sp.). Coarse herbs such as *Heliconia* spp. and those in the family Marantaceae were somewhat more abundant in the burnt forest, although this difference was narrowly insignificant (unburnt forest = $1.84 \pm 0.34\%$ ($n=8$); burnt forest = $3.1 \pm 0.58\%$ ($n=8$), $t=-1.86$, d.f. = 14, $P=0.084$)

3.3. Changes in the understorey avifauna

A total of 2073 birds belonging to 131 species were captured in all 20 forest plots, a capture rate of 144 individuals per 1000 net hours. (see Appendix A for species details). There were far fewer captures per unit of mist-netting effort in the burnt forest netlines in comparison with those in unburnt forest, both for the 16 netlines placed away from the fireline (603 compared with 1091), and the four interface netlines across the fireline (95 compared with 284). Although unburnt and burnt forest plots away from the fireline had the same overall level of species richness (90 species in unburnt forest compared with 87 in burnt), individual burnt forest netlines were significantly less species-rich than those in unburnt forest (mean unburnt = 42.3 ± 0.86

species ($n=8$), mean burnt = 31.25 ± 2.33 species ($n=8$), $t=4.33$, d.f. = 14, $P=0.001$). Within the four interface netlines placed across the fireline, overall species richness sampled by nets strung within the burnt forest side was considerably lower than those in unburnt forest (36 compared with 62).

While the mean number of captures per netline of species insensitive to disturbance and those of medium tolerance did not change significantly between burnt and unburnt forest, those species independently classed as highly sensitive to disturbance were significantly less abundant in burnt forest plots (Table 1). There were also significant differences between the responses of species grouped by their relative abundance, with significantly fewer captures per netline of both 'fairly-uncommon' and 'uncommon' birds. The uncommon grouping showed the strongest negative response. There was no significant change in the number of captures of species classified as common (Table 1). Species that used only one or two habitat types (Fig. 2a) declined significantly in burnt forest while those classed as using three habitats showed the greatest relative increase

(>2000%) in burnt forests, although these differences were of marginal significance (Table 1).

3.4. Assemblage similarity and habitat structure

Pairwise comparisons of netline samples across all forest plots (excluding fireline interfaces) showed that assemblage similarities were highest within unburnt forest plots, lowest between unburnt and burnt forest plots and intermediate between different burnt forest plots (Table 2). When plotted against all habitat variables recorded, the differences in canopy cover between plots explained the greatest amount of variation in assemblage similarity between any two netlines closely followed by the differences in mean % undergrowth cover between any two netlines (Fig. 3). The difference in mean undergrowth cover per plot also explained differences in the avifaunal samples within the burnt forest as well as the highest amount of variation in the differences in the avifaunal samples within the burnt forest, as well as the highest amount of variation in the differences in bird assemblage between unburnt and burnt

Table 1

The mean number of captures per netline in burnt and unburnt forest, with captures grouped according to Stotz et al. (1996)

Stotz classification		Mean unburnt forest ^a	S.E.	Mean burnt forest ^a	S.E.	<i>t</i>	d.f.	<i>P</i>
Sensitivity to disturbance	Low	1.50	0.60	5.13	2.75	-1.30	7.66	0.21
	Medium	30.88	4.55	30.63	4.33	0.04	14	0.97
	High	104.00	6.28	39.63	5.46	7.74	14	<0.001
Relative abundance	Common	19.75	2.24	20.13	2.91	-0.10	14	0.92
	Fairly common	82.13	7.03	45.25	2.84	4.86	14	<0.001
	Uncommon	34.50	4.24	10.00	1.72	5.35	9.25	<0.001
Number of habitats used	1	99.25	6.27	42.50	4.92	7.12	14	<0.001
	2	28.88	4.89	12.63	1.91	3.10	14	0.008
	3	7.88	1.19	12.25	1.47	-2.31	14	0.04
	>3	0.38	0.18	8.00	3.35	-2.27	7.04	0.06

^a Excludes interface plots.

Table 2

The results of linear regressions between either (1) differences in mean % undergrowth cover between plots^a, or (2) the differences in mean % canopy between plots, and the bird assemblage similarity between netlines (r_s)

Regression between			r^2	d.f.	<i>F</i>	<i>P</i>
Differences in		Assemblage similarity (r_s)				
Mean % undergrowth cover	and	All netlines	0.54	1,118	137.49	<0.001
		Unburnt forest plots	0.01	1,26	0.17	0.69
		Burnt forest plots	0.32	1,26	12.45	0.02
		Unburnt and burnt forest plots	0.54	1,62	72.99	<0.001
Mean % canopy gap	and	All netlines	0.58	1,118	164.91	<0.001
		Unburnt forest plots	0.001	1,26	0.03	0.88
		Burnt forest plots	0.37	1,26	14.95	0.001
		Unburnt forest plots	0.41	1,62	43.05	<0.001

^a See Fig. 3.

forest. Neither of these variables explained the variation in assemblage similarity between unburnt forest netlines (Table 2).

3.5. Guild responses

3.5.1. Insectivorous guilds

The four bird species classified as professional ant-followers declined dramatically in burnt forest (Fig. 2b), with declines particularly apparent for the harlequin antbird (*Rhegmatorina berlepschi*) and the black-spotted bare-eye (*Phlegopsis nigromaculata*). The two other species included within this guild, the scale-backed antbird (*Hylophylax poecilonota*) and the white-chinned woodcreeper (*Dendrocincla merula*), frequently foraged away from ant-swarms, and did not actually behave as

obligate ant-followers; in fact *Dendrocincla merula* was the most commonly captured bird in unburnt forest. Both of these bird species were, however, much less abundant in the burnt forest than in the unburnt forest (see Appendix for details).

Arboreal sallying, terrestrial gleaning (ITG) and dead-leaf gleaning (IDL) insectivores were all significantly less abundant in burnt forest than in the unburnt control plots (Fig. 2b). All eight species of dead leaf gleaners declined in abundance in the burnt forest, the most notable change being that of white-eyed antwren (*Myrmotherula leucoptalma*). Nine of the 11 species of terrestrial gleaning insectivores captured were less abundant in burnt than in unburnt forest. Declines of the leaf-tossers (*Sclerulus* spp) and the rufous-capped antthrush (*Formicarius colma*) are particularly noteworthy. However, the ruddy spinetail (*Synallaxis rutilans*) showed the reverse response and was only caught in burnt forest. Arboreal sallying insectivores also appeared to be negatively effected by the surface fires, with the exception of Sneath's tody-tyrant (*Hemitriccus minor*), which was twice as abundant in the burnt forest.

Although both arboreal gleaning (IAG) and bark-searching insectivores (IBS) were less abundant in burnt than in unburnt forest, these differences were not significant (Fig. 2b). In both cases the lower abundance of some primary forest specialists were compensated for by the invasion of species more often associated with gaps and second growth. For example, two arboreal gleaning insectivores, the long-winged antwren (*Myrmotherula longipennis*) and the plain-throated antwren (*Myrmotherula huxwelli*) were largely replaced by *Myrmotherula axillaris*, the warbling antbird (*Hypocnemis cantator*) and the dot-winged antwren (*Microrhopias quixensis*). For bark searching insectivores, the olivaceous woodcreeper (*Sittasomus griseicapillus*) replaced the wedge-billed woodcreeper (*Glyphorhynchus spirurus*) in the burnt forest.

3.5.2. Other guilds

Nectarivores (NA) were the only guild significantly more abundant in burnt forest than in unburnt forest (Fig. 2b), and only two species (which were rarely captured) were less abundant in burnt forest. Arboreal granivores (GA) were twice as abundant in burnt forest than in the control plots, showing the highest relative change of any guild, even though this difference was not significant (Fig. 2b). Of the three species caught, the blue-black grosbeak (*Passerina cyanoides*) was the most common and more than doubled in abundance. The other two species were only captured four times in total, although these were all in burnt forest. Arboreal frugivores (FA), a guild dominated by manakins (Pipridae), were moderately less abundant in the burnt forest, but this difference was not significant (Fig. 2b). While the

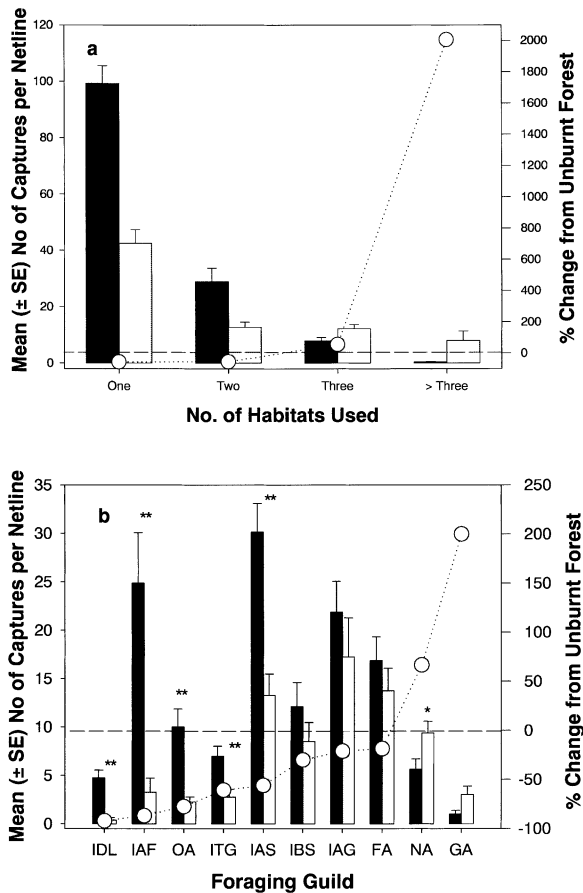


Fig. 2. Mean number of captures per netline in unburnt forest (black bars) and burnt forest (grey bars) and the % change in abundance (open circles) from unburnt to burnt forest. Captures are grouped by (a) the number of habitats used (from Stotz et al., 1996) and (b) their foraging and dietary guilds. Only guilds with more than 15 captures are included. Guild classification follows Terborgh et al. (1990) as follows; IDL, Dead leaf searching arboreal insectivore; IAF, ant-following insectivore; OA, arboreal omnivore; ITG, gleaning terrestrial insectivore; IAS, arboreal sallying insectivore; IBS, bark-searching insectivore feeding superficially; IAG, arboreal gleaning insectivore; FA, arboreal frugivore; NA, nectarivore; GA, arboreal granivore. *, $P < 0.05$; **, $P < 0.01$.

two most abundant manakin species in unburnt forest—the snow-crowned manakin *Pipra nattereri* and the red-headed manakin *Pipra rubrocapilla*—were less abundant in the burnt forest, they were compensated for by the fiery-capped manakin (*Machaeropterus pyrocephalus*) and the white-bearded manakin (*Manacus manacus*), which were only captured in burnt forest. Only two species of omnivores (the white-necked thrush *Turdus albicollis* and McConnell's flycatcher *Mionectes macconnelli*) were frequently captured, and both of them declined dramatically in burnt forest.

4. Discussion

4.1. Changes in habitat structure

Since there were no differences in mean stand basal area between burnt and unburnt forest plots, we have no reason to believe that burnt and unburnt forest was intrinsically different before the fires. Interviews with local people also helped us to conclude that the forests were structurally similar before the fires (J. Barlow, unpublished data). The slightly lower basal area in the burnt forest can be accounted for by the high treefall rates and increased volume of freshly fallen dead wood in burnt forest (Haugaasen et al., in prep.). Rates of tree mortality recorded in the burnt forest closely match those of other studies in the neotropics. Holdsworth and Uhl (1997) reported mortality of 44% for trees ≥ 10 cm DBH following a ground fire in the eastern Amazonian primary forest of Paragominas, and a post-burn mortality of 36–69% has been recorded in a primary forest in Panama (Kauffman, 1991). The figures recorded 1 year after the fires are also likely to underestimate the true tree mortality, as mortality from fire tends to increase even several years after fires (Kinnaird and O'Brien, 1998; Sunarto, 2000). The consistent pattern of size-dependent tree mortality recorded in the burnt plots of the Rio Maró was similar to that in the lower Rio Arapiuns (Peres, 1999) and a eastern Amazonian forest site, where tree size and bark thickness are key determinants of tolerance to heat stress (Uhl and Kauffman, 1990).

4.2. Avifaunal responses

4.2.1. Species richness

An increased species richness is often the result of structurally intermediate and highly heterogeneous habitats (Connell, 1978), and a lightly disturbed forest often contains a greater bird species richness than that of a pristine forest (Mason, 1996; Thiollay, 1999). Although the number of captures per unit of netting effort declined by almost half from unburnt to burnt forest, understorey fires appeared to have had little effect on overall species richness. This was partly

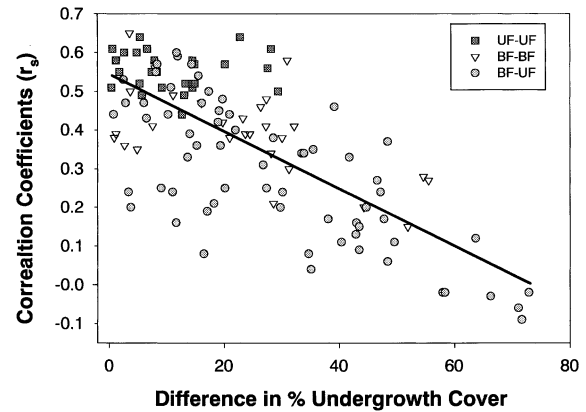


Fig. 3. Relationship between the difference in % undergrowth cover between all burnt and unburnt netlines and the bird assemblage similarity (see Section 2). Correlations between unburnt forest netlines ■, between burnt forest netlines ▽, and between burnt and unburnt forest netlines ○, respectively.

explained by the fire-generated disturbance mosaic in the burnt forest, which could accommodate primary forest, second growth and gap species. However, since single netlines in burnt forest contained significantly fewer species than unburnt forest netlines, it would appear that the highly variable regeneration between burnt forest plots (Haugaasen, 2000) resulted in a relatively high species dissimilarity between netlines (Fig. 3). The relatively high overall bird species richness in the burnt forest is therefore best explained by the greater variation between rather than within netlines, and higher levels of beta-, rather than alpha-diversity.

4.2.2. Responses of functional groups

From a conservation perspective, it has been suggested that it is more important to consider the responses of the sensitive or vulnerable species rather than the entire species assemblage, as these are the species most likely to be at risk in the future (Canaday, 1996). Analyses of Amazonian bird species grouped by Stotz et al. (1996) consistently show that species that are being lost in burnt forest are those that are most likely to be at risk from other patterns of forest disturbance. They tend to be the least common, the most disturbance-sensitive, and habitat specialists using only one habitat type (Table 1). Functional groups that either increased or showed no change in abundance exhibited the opposite traits, and tended to be the most common, the least sensitive to disturbance, and habitat generalists using three or more habitat types. The overall picture is clear: a history of ground fires is highly detrimental to precisely those species that are of greatest conservation concern.

4.2.3. Guild responses

Four of the five guilds significantly less abundant in the burnt forest were insectivorous (Fig. 2b), reflecting

their vulnerability to other anthropogenic forms of tropical forest disturbance such as logging (Wong, 1985; Johns, 1989; Thiollay, 1992; Canaday, 1996; Mason, 1996), forest fragmentation (Bierregaard and Lovejoy, 1989; Stouffer and Bierregaard, 1995) and both burnt and unburnt slashed forest (Borges and Stouffer, 1999). While Pearson (1997) suggests that the vulnerability of insectivores may be associated with increased direct sunlight confusing their search patterns, their reduced abundance in burnt forest may also be linked with changes in resource availability. For example, the marked decline in dead-leaf gleaners may have been caused by the loss of suspended dead leaves in the mid- to lower-storey (Rosenberg, 1990), and the decline in the ant-followers can be explained by the conspicuous absence of army ant swarms within the burnt forest (J. Barlow, unpublished data). Whatever the causes of decline, for conservation purposes it is important to note that fires are affecting the same foraging and dietary guilds as other types of forest disturbance, and that in each case it is the understorey insectivores which are most at risk. It is significant that three of the locally endemic species, *Rhegmatorina berlepschi*, the pale-faced ant bird (*Skutchia borbae*) and *Dendrocolaptes hoffmannsi* are within these guilds.

4.3. Behavioural responses to wildfires

Pearson (1977) hypothesised that species may respond to different conditions by adjusting their foraging height. This could potentially bias mist net data as changes in foraging height alter the incidence of captures in understorey mist nets, making it difficult to divorce behavioural changes from actual changes in abundance (Remsen and Good, 1996). In this study, 82% of all captures (excluding interfaces) were of species classified by Stotz et al. (1996) as foraging either terrestrially, in the understorey, or between the understorey and mid-storey. Moreover, the sharpest declines in abundance came from within these groups (a 51% decline compared with an 8% decline of species foraging in or above the mid-storey). As these species are highly specialised to foraging in the lower strata of the forest it is unlikely that these declines are explained by any shifts in vertical stratification of foraging activity. In addition, this interpretation is supported by our direct observations along netline plots, and understorey species are also affected by forest disturbance in studies using point counts rather than mist netting (Thiollay, 1992; Aleixo, 1999).

4.4. Long term prospects of forest and avifauna recovery

Long-term studies of avifaunal recovery following selective logging may help predict the long term consequences of forest wildfires. Johns (1989) found that

the re-establishment of a closed canopy in logged forest can take 7–12 years to recreate micro-climatic conditions similar to those of unlogged forest, while Mason (1996) found that canopy cover recovered over a 5–6-year period. However, in the latter study, avifaunal assemblage similarity between logged and unlogged forest decreased as canopy cover recovered, a response attributed to the increasing understorey stem density. This demonstrates that changes in understorey structure can still affect the avifauna even after canopy continuity has been re-established. Since relative undergrowth cover was the best predictor of assemblage differences between the burnt and unburnt forest (Fig. 3 and Table 2), we predict a similar trend over time in our study area, with species assemblages in burnt forest becoming increasingly dissimilar from unburnt forest assemblages as the vegetation structure in the understorey continues to change.

However, the critical issue in the long term may be the significant risk of recurrent fires (Cochrane and Schulze, 1998, 1999; Cochrane et al., 1999; Nepstad et al., 1999b). As tree mortality in the burnt forest is expected to increase further (Kinnaird and O'Brien, 1998), and as the treefall rate in burnt forest was five-fold higher than that in unburnt forest (J. Barlow, unpublished data), we can expect forest recovery to be slow, making it unlikely that the canopy will close sufficiently in time to prevent future El Niño dry seasons from breaching the forest flammability threshold again (Cochrane et al., 1999). Furthermore, a subsequent fire is likely to produce a hotter and more severe burn due to the exceptionally high density of treefall gaps, standing and fallen dead trees, and flammable plants in the herbaceous layer. Such a fire is likely to be disastrous for these forests, and may cause the mortality of perhaps an additional 40% of all living trees remaining after the first burn (cf. Cochrane and Schulze, 1999). Clearly this would impact heavily on the avifauna, and could be expected to have an effect many times greater than that of these unprecedented low density surface wildfires examined here.

4.5. Wildfire prevention and control

Only a decade ago, unintentional wildfires were hardly a conservation issue in Amazonia and other regions of tropical evergreen forest. However, the synergistic effects of human disturbance and climate change have already shown that catastrophic fires can become one of the greatest agents of biodiversity erosion of our times. Nepstad et al. (2001) suggest that the risk of wildfires in Amazonian forests will be reduced as fire-sensitive investment in the land (such as fences and perennial crops) increases. This approach has a two-fold effect. Firstly, the use of perennial crops will reduce the need for fire outright. Secondly, fire-sensitive investment increases the cost of accidental fires for farmers, and

therefore their motivation to reduce fire risks through the use of fire-breaks and the timing of controlled burns. However, while these measures may be beneficial for retaining forest cover for carbon storage, the nature of frontier expansion within Amazonia is such that by the time an area has accumulated sufficient fire-sensitive investment to reduce the risk of fire, it is likely that much of its importance for wildlife conservation will have already been lost through selective logging and forest fragmentation, if not from an initial forest fire. As fires are inextricably linked to the slash-and-burn clearing involved in frontier expansion, the only viable method of reducing their impact on forest vertebrates is to restrict or prevent primary forest disturbance in the first place. Within this context, an environmentally sensitive realignment of the *Avança Brasil* blueprint, the multi-billion dollar infrastructure investment program earmarked for a new wave of development in the Brazilian Amazon, would be critical (Peres, 2001). By building new highways and paving many of the existing unpaved roads that dissect the Amazon, this program is expected to encourage frontier expansion into many

otherwise remote fire-prone areas (Laurance et al., 2001; Nepstad et al., 2001), where it will be only a matter of time before a recurrent fire regime is likely to become established.

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Appendix A. The 75 most abundant species in all forest plots^a

Species	Guild ^b	Sensitivity to disturbance ^c	Numbers of individuals captured in		
			Unburnt forest plots ^a	Burnt forest plots ^a	All forest plots ^a
COLUMBIDAE					
<i>Geotrygon montana</i>	FRT	Medium	8	6	14
TROCHILIDAE					
<i>Campylopterus largipennis</i>	NA	Medium	4	1	5
<i>Glaucis hirsuta</i>	NA	Low	1	2	3
<i>Hylocharis sapphirina</i>	NA	Medium	0	6	6
<i>Phaethornis malaris</i>	NA	High	25	28	53
<i>Phaethornis ruber</i>	NA	Medium	1	7	8
<i>Phaethornis squalidus</i>	NA	Medium	0	5	5
<i>Thalurania furcata</i>	NA	Medium	12	24	36
MOMOTIDAE					
<i>Baryphthengus ruficapillus</i>	IAS	Medium	3	0	3
GALBULIDAE					
<i>Galbula albirostris</i>	IAS	High	3	1	4
BUCCONIDAE					
<i>Monasa morphoeus</i>	IAS	High	9	6	15
<i>Malacoptila rufa</i>	IAS	High	7	1	8
DENDROCOLAPTIDAE					
<i>Dendrocincla merula</i>	IAF	High	127	18	145
<i>Deconychura longicauda</i>	IAS	High	6	5	11
<i>Deconychura stictolaema</i>	IAS	High	14	0	14
<i>Dendrocincla fuliginosa</i>	IAS	High	15	10	25
<i>Dendrocolaptes certhia</i>	IAS	High	1	7	8
<i>Glyphorhynchus spirurus</i>	IBS	Medium	37	10	47
<i>Hylexetastes perrotii</i>	IBS	High	11	7	18
<i>Sittasomus griseicapillus</i>	IBS	Medium	3	17	20
<i>Xiphorhynchus guttatus</i>	IBS	Medium	9	3	12
<i>Xiphorhynchus ocellatus</i>	IBS	High	22	25	47
FURNARIIDAE					
<i>Xenops minutus</i>	IBS	Medium	12	6	18
<i>Automolus ochrolaemus</i>	IDL	Medium	8	2	10
<i>Philydor erythrocerus</i>	IDL	High	5	0	5
<i>Sclerurus caudacutus</i>	ITG	High	13	0	13
<i>Sclerurus mexicanus</i>	ITG	High	8	0	8
<i>Synallaxis rutilans</i>	ITG	High	0	10	10
FORMICARIIDAE					
<i>Hylophylax poecilinota</i>	IAF	Medium	47	5	52
<i>Phlegopsis nigromaculata</i>	IAF	Medium	14	3	17
<i>Rhegmatorhina berlepschi</i>	IAF	High	11	0	11
<i>Cercomacra nigrescens</i>	IAG	Medium	0	9	9
<i>Cymbilaimus lineatus</i>	IAG	Medium	0	6	6
<i>Hylophylax naevia</i>	IAG	High	4	0	4
<i>Hypocnemis cantator</i>	IAG	Medium	8	21	29
<i>Microrhophias quixensis</i>	IAG	Medium	0	13	13
<i>Myrmotherula axillaris</i>	IAG	Medium	7	26	33
<i>Myrmotherula hauxwelli</i>	IAG	High	34	5	39

(continued on next page)

Appendix A (continued)

Species	Guild ^b	Sensitivity to disturbance ^c	Numbers of individuals captured in		
			Unburnt forest plots ^a	Burnt forest plots ^a	All forest plots ^a
<i>Myrmotherula longipennis</i>	IAG	High	65	6	71
<i>Thamnophilus aethiops</i>	IAG	High	11	4	15
<i>Thamnophilus punctatus</i>	IAG	Low	0	8	8
<i>Thamnomanes caesius</i>	IAS	High	14	3	17
<i>Thamnomanes saturninus</i>	IAS	High	59	8	67
<i>Myrmotherula leucophthalma</i>	IDL	High	20	1	21
<i>Conopophaga melanogaster</i>	ITG	High	3	0	3
<i>Dichrozona cincta</i>	ITG	High	4	1	5
<i>Formicarius analis</i>	ITG	Medium	3	0	3
<i>Formicarius colma</i>	ITG	High	18	1	19
<i>Myrmoborus myotherinus</i>	ITG	High	4	10	14
<i>Myrmeciza ferruginea</i>	ITS	High	0	3	3
COTINGIDAE					
<i>Lipaugus vociferans</i>	FA	High	3	4	7
PIPRIDAE					
<i>Machaeropterus pyrocephalus</i>	FA	Medium	0	11	11
<i>Manacus manacus</i>	FA	Low	0	3	3
<i>Pipra nattereri</i>	FA	High	69	45	114
<i>Pipra rubrocapilla</i>	FA	High	58	42	100
<i>Schiffornis turdinus</i>	IAS	High	48	9	57
TYRANNIDAE					
<i>Hemitriccus minor</i>	IAS	High	9	17	26
<i>Onychorhynchus coronatus</i>	IAS	High	14	12	26
<i>Platyrinchus plalyrhynchos</i>	IAS	High	15	3	18
<i>Platyrinchus saturatus</i>	IAS	High	3	0	3
<i>Rhynchocyclus olivaceus</i>	IAS	High	3	3	6
<i>Terenotriccus erythrurus</i>	IAS	Medium	12	12	24
<i>Corythopsis torquata</i>	ITS	High	5	0	5
<i>Laniocera hypopyrra</i>	OA	High	5	2	7
<i>Mionectes macconnelli</i>	OA	High	35	5	40
<i>Mionectes oleagineus</i>	OA	Medium	12	2	14
TROGLODYTIDAE					
<i>Thryothorus genibarbis</i>	IAG	Low	0	12	12
TURDINAE					
<i>Turdus albicollis</i>	OA	Medium	25	3	28
VIREONIDAE					
<i>Hylophilus ochraceiceps</i>	IAG	Medium	6	1	7
EMBERIZINAE					
<i>Oryzoborus angolensis</i>	GA	Low	0	3	3
THRAUPINAE					
<i>Habia rubica</i>	IAG	High	25	8	33
<i>Tachyphonus surinamus</i>	IAG	Medium	9	16	25
<i>Lanio versicolor</i>	OA	High	3	0	3
<i>Ramphocelus carbo</i>	OA	Low	0	3	3
CARDINALINAE					
<i>Passerina cyanoides</i>	GA	Medium	8	20	28

^a Excludes four interface plots.^b See Fig. 3 for guild codes; except FRT, terrestrial frugivore; ITS, terrestrial sallying insectivore (from Terborgh et al., 1990).^c From Stotz et al. (1996).

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