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Bird community changes in response to single and repeated fires in a lowland tropical rainforest of eastern Borneo

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Abstract. Our current understanding of bird community responses to tropical forest fires is limited and strongly geographically biased towards South America. Here we used the circular plot method to carry out complete bird inventories in undisturbed, once burned (1998) and twice burned forests (1983 and 1998) in East Kalimantan (Indonesia). Additionally, environmental variables were measured within a 25 m radius of each plot. Three years after fire the number of birds and bird species were similar for undisturbed and burned forests, but species diversity and turnover were significantly lower in the burned forests. The bird species composition also differed significantly between undisturbed and burned forests, with a strong decline of closed forest preferring bird species accompanied by a strong increase in degraded forest preferring species in burned forests. These differences were strongly related to differences in environmental conditions such as shifts in vegetation cover and layering and differences in ground and understorey vegetation structure. We also found significant shifts in body mass distribution, foraging height and feeding guilds between the bird communities in unburned and burned forests. Surprisingly, repeated burning did not lead to increasing impoverishment of the avifauna, and both once and twice burned forests still contained most of the bird species that were also present in undisturbed forest, even though their densities were considerably lowered.

Introduction

Forest fires currently form a major threat to the last remaining patches of undisturbed lowland tropical rain forest in Southeast Asia (Siegert et al. 2001; Cochrane 2003; Hoffmann et al. 2003; Laurance 2004). However, only a few studies, which were mostly carried out in the Amazon region, have thoroughly investigated the impact of forest fires on tropical bird communities (Kinnaird and O'Brien 1998; Barlow et al. 2002; Haugaasen et al. 2003; Peres et al. 2003; Barlow and Peres 2004a, b). This means that our current understanding of bird community responses to tropical forest fires is very limited and strongly geographically biased. More information about the impact of forest fires on tropical bird communities, especially in Southeast Asia, is therefore urgently needed. Such information is essential for designing bird conservation strategies for the growing expanses of burned tropical lowland forest in Southeast Asia.

Studies available from the Amazon region show that fire can have a substantial impact on the understorey avifauna. One year after fire the understorey bird community was found to be significantly less abundant and diverse than that of undisturbed forest (Barlow et al. 2002). Although species richness and abundances increased considerably 3 years after fire, the avifaunal assemblage also became increasingly dissimilar to unburned forest and contained a higher abundance of species associated with second-growth habitats (Barlow 2003; Barlow and Peres 2004a). These changes in avifaunal assemblage were strongly associated with changes in habitat structure such as canopy cover and understorey regeneration (Barlow and Peres 2004b). Foraging guilds were also strongly affected by fire. In the Amazon region, most insectivorous guilds declined, while arboreal nectarivores, granivores and frugivores became more abundant after fire (Barlow and Peres 2004a, b). This contrasts considerably with findings from Sumatra in Southeast Asia Kinnaird and O'Brien 1998), where insectivorous species increased, while frugivorous and omnivorous species declined in numbers after fire.

With this study we try to bridge the geographical gap that exists in our current knowledge on bird community responses to forest fires in the tropics. Our main aims are (1) to study the effects of single and repeated fires on bird community structure, composition and diversity; (2) relate changes in bird species composition and abundances to habitat variables; (3) compare our results to those found for bird communities in burned forests in South America; and (4) use the outcomes of this study to formulate recommendations for bird conservation in burned tropical lowland forests.

Material and methods

Study site

The study was carried out three and a half years after the 1998 fires in the area north of the city of Balikpapan, in the province of East Kalimantan, Indonesia (Figure 1). There are three small unburned forest patches in this area: (1) Sungai Wain Protection Forest (ca. 4000 ha unburned), (2) Wartono Kadri Research Forest (ca. 30 ha unburned), and (3) Bukit Bangkirai (ca. 500 ha unburned). These unburned forest fragments, which were never affected by large scale human activities such as logging, once belonged to the same continuous forest block and are climatically, floristically and structurally very similar (Nieuwstadt 2002; Slik and Eichhorn 2003; Slik et al. 2003), meaning that differences in the avifaunal composition are unlikely to be caused by large differences in climatic or floristic composition between these forest fragments. All three unburned forest fragments are surrounded by a once burned (1998) and/or twice burned (1983 and 1998) forest matrix (Figure 1). These burned forests were also unaffected by any large scale human activities before they burned, except for Bukit Soeharto, which was logged previous to fire. No information on fire intensity is available for these forests, but their vegetation structure indicates that they were more or less equally and severely damaged by the 1998 fires (Slik and Eichhorn 2003).

Bird surveys

The Variable Circular Plot method (Reynolds et al. 1980) was used to assess bird numbers in the three studied forest disturbance types between October and

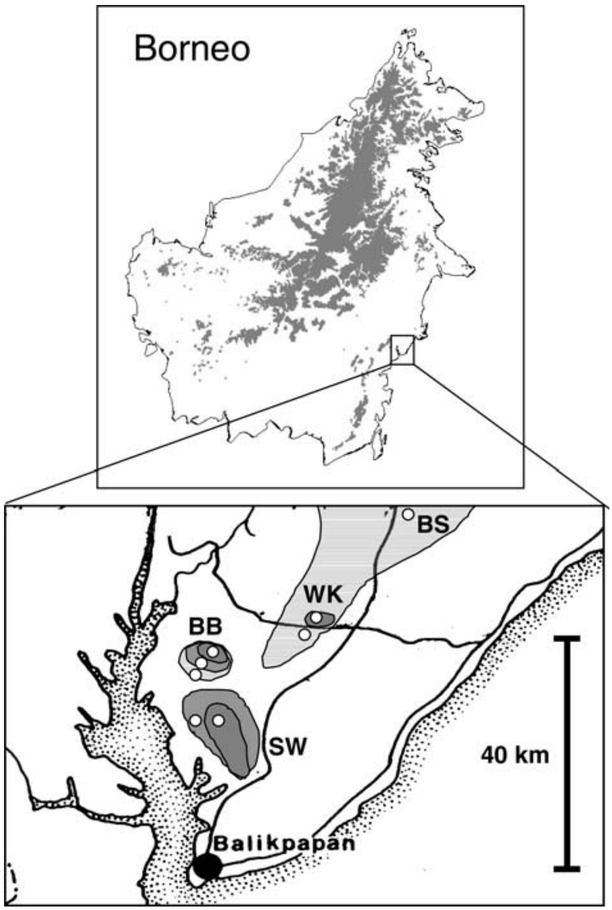

Figure 1. Map of the research area in Borneo. White is grassland, scrub or plantation forest, light grey is twice burned forest (1983 and 1998), intermediate grey is once burned forest (1998) and dark grey is unburned forest. BB = Bukit Bangkirai, BS = Bukit Soeharto, SW = Sungai Wain, and WK = Wartono Kadri. The white dots indicate the location of the bird count stations in the different forest disturbance types.

November 2001. In total we established 80 plots, 34 in undisturbed forest, 23 in once burned forest, and 23 in twice burned forest. These plots were spaced 200 m apart along 1 km long transects (Table 1). The transects within each forest disturbance type were also spaced ca. 200 m apart. Unfortunately, we were unable to replicate each burned forest disturbance type around each unburned forest fragment because some unburned forest fragments were surrounded by once or twice burned forest only.

In each plot two morning (dawn) and two afternoon (dusk) counts were carried out on separate, but subsequent days. Morning counts were carried out between ca. 30 min before sunrise and ca. 3 h thereafter; afternoon counts were carried out between ca. 3.5 h before sunset and sunset. The end points for the first morning and first afternoon counts at each transect were the start points for the second counting round. Separate counts lasted 20 min each, resulting in a total of 80 min of observation time per plot (40 min in the morning and 40 min in the afternoon). During these 20 min standing counts the identity, numbers, and distance to observer of all birds were registered. Most contacts were made aurally, whereby each contact (individual, pair or group) counted as one. It was assumed that group sizes between undisturbed and burned forests did not differ. Voice recordings were made of species needing confirmation, e.g., unknown calls, rare and/or confusing species. No counts were carried out during rain.

Aerial, raptorial and nocturnal species, which are often omitted from similar analyses of bird census data, have been included in our calculations as far as they showed clear affinity to some of the census plots. Moreover, while reaching the starting points and leaving the ending points of the transect counts, i.e. during pre-dawn and post-dusk conditions, night birds were tallied.

Habitat surveys

At each bird count plot we scored several habitat variables (within a 25 m radius): Slope (flat, gentle slope, moderately steep, very steep); topography (swamp, plain, valley, lower slope, middle slope, upper slope, ridge); soil

Table 1. Number of bird count plots per forest disturbance type per location (see also Figure 1).

Location	Disturbance	Transects	Plots
Bukit Bangkirai	Undisturbed	2	12
	Burned once	1	6
	Burned twice	1	5
Bukit Soeharto	Burned twice	2	12
Sungai Wain	Undisturbed	3	17
	Burned once	3	17
Wartono Kadri	Undisturbed	1	5
	Burned twice	1	6

moisture (wet, dry); number of logs and snags; vegetation cover (%) of ground (up to 1.5 m height), understorey (1.5–5 m height), midstorey (5–15 m), and upperstorey (above 15 m); number of bole climbers (none, 1 or 2, more than 2), lianas, small palms, large terrestrial ferns, gingers, and pioneer individuals of the Euphorb genera *Mallotus* Lour. and *Macaranga* Thou.; presence of epiphytic ferns, epiphytic mosses, grasses, rattan, bamboo, and wild bananas; number of vegetation layers (1,2,3,4); maximum tree height; upper moss line; presence of flowering and fruiting trees; presence of flowering and fruiting shrubs.

Bird community structure

Bird ecological and morphological attributes were used to detect changes in bird community structure. Based on literature (Dunning et al. 1992; Lambert 1992; MacKinnon and Phillipps 1993; Hoyo et al. 1994; Thiollay 1995; Davison and Fook 1996; Robson 2000; Lambert and Collar 2002) we determined the following characters for each bird species: weight class (< 10 g, 11–20 g, 21–40 g, 41–80 g, 81–160 g, 161–320 g, 321–640 g, 641–1280 g, 1281–2560 g); solitary or gregarious behaviour; maximum altitude class (0–500 m, 510–1000 m, 1001–1500 m, 1501–2000 m; 2001–2500 m, 2501–3000 m, 3001–3500 m); habitat preference (primary forest, gaps/degraded forest, open forest/cultivated land); forage layer (ground, understorey (0–10 m height), middlestorey (10–20 m height); upperstorey (> 20 m height), whereby some bird species can occur in more than one class; aerial (above canopy); food source (fruits, insects, nectar, vertebrates), whereby some species are included in more than one class; nest type (cup/platform nests, closed ball or hanging nests, (excavated) nests in river banks, (excavated) nests in tree cavities, nest parasites); nest height class (0–5 m; 5.1–10 m, 10.1–20 m; > 20 m), whereby some species can occur in more than one class; and the combination of foraging height and food source.

Statistical analyses

Differences in total number of individuals, species and diversity (Shannon and Simpson indices) per plot between the three forest disturbance types were tested with General Linear Models (GLM), to compensate for differences in sample size. A *post hoc* Fishers Least Significant Difference Test was used to determine which forest disturbance types differed significantly from which for the tested variables. When data were not normally distributed, or standard deviations between factors differed too much to apply GLM, we used the non-parametrical Kruskal–Wallis test. These tests were also applied to determine differences in habitat variables, and differences in bird attributes between the three forest disturbance types. For the difference between the combination of foraging height and food source between the forest types, we used a G-test, which gives a Chi-square test statistic.

We constructed species accumulation curves using the program EstimateS 6.0b1 (freely available at http://viceroy.eeb.uconn.edu/EstimateS), whereby increase in species number with increasing number of plots is calculated. This procedure was randomly repeated 50 times for each forest disturbance type so that the resulting figures were based on the average of these 50 repeats.

To determine species turnover within the three forest disturbance types, we also calculated the similarity in species composition between plots placed 200 m apart within each transect, using the Sørensen similarity index (based on presence–absence of species only). This gives an indication of beta-diversity within these forests.

To determine which species were significantly more common in each of the three forest disturbance types, we ran a Monte Carlo permutation test with the computer program 'INDVAL 2.0' (freely available at http://www.fas.umontreal.ca/BIOL/legendre/indexEnglish.html) with advanced options choice 2 and weight 1. This means that only the abundance of species was tested for significant differences between forest disturbance types. This test compares the observed abundances in each forest disturbance type to a number of randomly generated abundances (made by randomly reallocating observed plot abundances over the plots). We used 999 random permutations, which allowed for testing of statistical significance at the $p < 0.001$ level.

The relation between bird abundances and presence with habitat variables was explored using a Canonical Correspondence Analysis (CCA) in combination with log-transformed abundance data and, in a second analysis, with only presence–absence data. Regression analysis was used to determine which habitat variables were significantly associated with the first two axes of the CCA (i.e., plot scores on the first two axes were regressed against the habitat values of the plots for each environmental variable). For presence absence data we used logistic regression analysis, while for continuous data we used a simple regression analysis.

All standard statistical analyses (except the randomization tests) were performed with 'Statgraphics for Windows 2.1' (Statgraphical Graphics Corp., Rockville, USA), while all multivariate analyses were performed using 'Multi Variate Statistical Package 3.01' (Kovach Computing Services, Anglesey, UK).

Results

Changes in habitat variables between undisturbed and burned forests

The abiotic variables (slope, topography and soil water content) were significantly different between plots from undisturbed, once burned and twice burned forests (Table 2). Twice burned forest was located significantly more often on steep slopes than once burned and undisturbed forest, while once burned forest

Table 2. Habitat variables measured in the three forest disturbance types (see Material and methods section for exact explanation of the variables).

Habitat variable	Undisturbed	Once burned	Twice burned	df	F	p	Test
Slope	2.0 ± 0.9^{a}	1.7 ± 0.8^{a}	2.7 ± 0.9^{b}	79	5.9	0.004	GLM
Topography	3.8 ± 2.1^{b}	2.0 ± 0.6^{a}	4.7 ± 1.7^{b}	79	20.8	< 0.0001	K–W
Soil water	0.53 ± 0.51^{a}	0.96 ± 0.21^{b}	0.35 ± 0.49^{a}	79	18.7	< 0.0001	K–W
Logs (*n*)	4.4 ± 2.4	6.1 ± 5.8	4.2 ± 1.7	79	1.2	NS	K–W
Snags (*n*)	1.9 ± 1.6^{a}	4.7 ± 9.8^{a}	14.9 ± 3.5^{b}	79	33.9	< 0.0001	K–W
Ground cover (%)	57.8 ± 24.0^{b}	70.3 ± 26.8^{b}	43.7 ± 18.7^{a}	79	7.4	0.001	GLM
Low cover (%)	54.9 ± 18.9^{b}	44.3 ± 20.3^{a}	62.2 ± 18.5^{b}	79	5	0.009	GLM
Mid cover (%)	61.2 ± 11.7^{b}	25.4 ± 20.7^{a}	22.4 ± 15.7^{a}	79	43.6	< 0.0001	K–W
Upper cover (%)	59.3 ± 14.6^{b}	22.8 ± 15.0^{a}	16.7 ± 11.5^{a}	79	79.7	< 0.0001	GLM
Bole climbers	1.08 ± 0.57^{c}	0.74 ± 0.62^{b}	0.35 ± 0.49^{a}	79	11.9	< 0.0001	GLM
Lianas	1.15 ± 0.36^{c}	0.61 ± 0.66^{b}	0.26 ± 0.45^{a}	79	32.7	< 0.0001	K–W
Epiphytic ferns	0.21 ± 0.41	0.43 ± 0.51	0.22 ± 0.42	79	2.1	NS	GLM
Epiphytic mosses	0.79 ± 0.41^{b}	0.17 ± 0.39^{a}	0.13 ± 0.34^{a}	79	27.1	< 0.0001	GLM
Small palms	1.44 ± 0.50^{c}	0.96 ± 0.37^{a}	0.48 ± 0.51^{a}	79	29.0	< 0.0001	GLM
Terrestrial ferns	0.09 ± 0.38^{a}	1.57 ± 0.79^{c}	1.13 ± 0.69^{b}	79	48.1	< 0.0001	K–W
Grasses	0.15 ± 0.44	0.39 ± 0.58	0.30 ± 0.56	79	1.6	NS	GLM
Gingers	0.68 ± 0.59^{a}	1.26 ± 0.69^{b}	1.74 ± 0.69^{c}	79	18.9	< 0.0001	GLM
Mallotus spp.	0.26 ± 0.45	0.09 ± 0.29	0.35 ± 0.49	79	4.5	NS	K–W
Macaranga spp.	0.06 ± 0.24^{a}	0.61 ± 0.49^{b}	0.43 ± 0.51^{b}	79	20.4	< 0.0001	K–W
Rattan	0.09 ± 0.29	0.13 ± 0.34	0.09 ± 0.29	79	0.16	NS	GLM
Bamboo	0.03 ± 0.17^{a}	0.04 ± 0.21^{a}	0.39 ± 0.50^{b}	79	17.3	0.0002	K–W
Wild bananas	0^{a}	0^{a}	0.22 ± 0.42^{b}	79	13.1	0.0015	K–W
Vegetation layers	3.4 ± 0.6^{b}	2.1 ± 0.8^{a}	2.0 ± 0.6^{a}	79	38.8	< 0.0001	GLM
Max. tree height (m)	34.1 ± 6.5^{c}	29.1 ± 5.6^{b}	24.3 ± 8.0^{a}	79	14.7	< 0.0001	GLM
Upper moss line (cm)	103.8 ± 93.4^{b}	33.5 ± 68.1^{a}	5.7 ± 15.3^{a}	79	28.2	< 0.0001	K–W
Flowering trees	0.32 ± 0.47	0.43 ± 0.51	0.30 ± 0.47	79	0.5	NS	GLM
Fruiting trees	0.74 ± 0.45	0.61 ± 0.50	0.52 ± 0.51	79	1.4	NS	GLM
Flowering shrubs	0.12 ± 0.33	0.22 ± 0.42	0.13 ± 0.34	79	0.6	NS	GLM
Fruiting shrubs	0.26 ± 0.45	0.43 ± 0.51	0.26 ± 0.45	79	1.1	NS	GLM

Values followed by different characters indicate significant differences within each row. General Linear Models (GLM) were used to test for significant differences. If this was not possible (significant differences in standard deviations), we applied a Kruskal–Wallis test (K–W).

was significantly more often located on down slope areas with high soil water content compared to undisturbed forest.

Most biotic variables also differed significantly between undisturbed, once burned and twice burned forest (Table 2). Vegetation layering, especially in the mid- and upperstorey, was greatly reduced in both burned forest types in comparison to undisturbed forest. This was also visible in the decreased maximum tree height in burned forest plots. Ground cover was strongly dominated by terrestrial ferns and gingers after fire, while bamboo clumps and wild bananas were especially abundant in twice burned forest. Woody pioneer species of the Euphorb genus *Macaranga* also increased significantly after fire. Epiphytic mosses, bole climbers, lianas, and small palms all decreased in abundance or frequency after fire. No significant differences in flowering and fruiting trees and shrubs were detected between burned and undisturbed forest plots.

Changes in total bird abundance, species richness, diversity and composition

Three and a half years after the 1998 fire we found no significant differences in average number of birds and bird species between the undisturbed and burned forest plots (Table 3). However, species diversity (Shannon-index) was significantly higher and species dominance (Simpson-index) significantly lower in undisturbed forests, compared to burned forests. Species similarity between neighbouring plots (200 m distance) increased significantly from undisturbed (50.5%), to once burned (54.4%) to twice burned (58.0%), respectively (GLM for undisturbed vs. once burned vs. twice burned, $n = 66$, $F = 6.1$, $p = 0.004$). This result is also reflected in the species accumulation curves (Figure 2), where species numbers in the undisturbed forest increase much steeper with increasing number of plots than in the two burned forest types.

A total of 81 bird species (42%) were found to be significantly associated with one or several forest disturbance types, while another 27 bird species (14%) were equally common in all forest disturbance types (Appendix 1). The remaining 86 species (44%) were too rare to determine their habitat preference. Of the 81 bird species that were significantly associated with a forest disturbance type, 31 were most abundant in undisturbed forest, while 44 species were most abundant in the burned forest types.

Associations between habitat variables and bird species composition

The Canonical Correspondence Analysis (CCA) based on bird species abundance and presence–absence data gave almost identical results. Therefore, we decided to show only the results of the CCA based on abundance data. The three forest disturbance types were well separated by this CCA (Figure 3), although only 22.9% of data variance was explained by the first two axes. The

Table 3. Difference in average number of observed bird individuals, species, diversity (Shannon-index) and evenness (Simpson-index) per plot in undisturbed, once burned and twice burned forests after 80 min observation time (2×20 min morning and 2×20 min afternoon, spread over four subsequent days).

Disturbance	Individuals ($n \pm$ SD)	Species ($n \pm$ SD)	Shannon-index ($\pm$SD)	Simpson-index ($\pm$SD)
Undisturbed	64.1 ± 11.7	42.4 ± 6.9	3.61 ± 0.16[a]	0.015 ± 0.003[a]
Burned once	65.3 ± 12.2	39.0 ± 6.3	3.50 ± 0.17[b]	0.021 ± 0.007[c]
Burned twice	68.7 ± 8.5	40.0 ± 6.2	3.52 ± 0.19[b]	0.022 ± 0.009[b]
df	79	79	79	79
F	1.17	2.02	3.75	16.7
p	NS	NS	0.028	< 0.0002
Test	GLM	GLM	GLM	Kruskal–Wallis

Values with different characters within a column indicate that these values are significantly different.

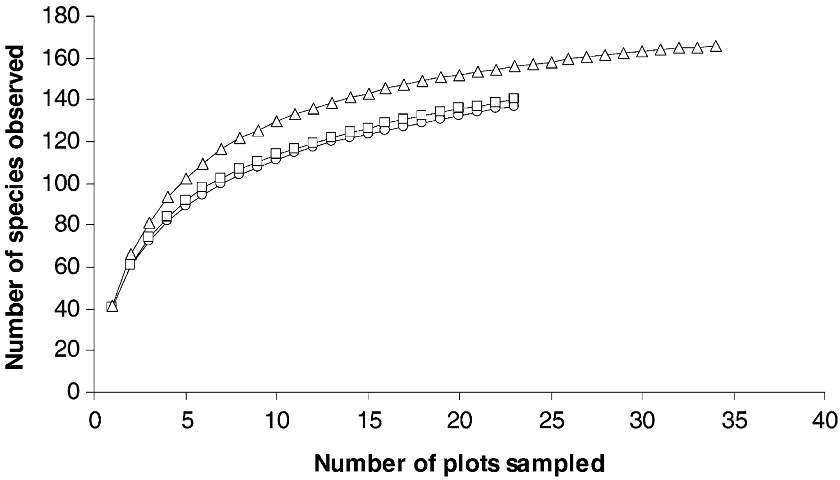

Figure 2. Bird species accumulation curves for undisturbed forest (open triangles), once burned (open circles) and twice burned (open squares) forest. Each curve reflects the average of 50 curves that randomly differed in plot input order.

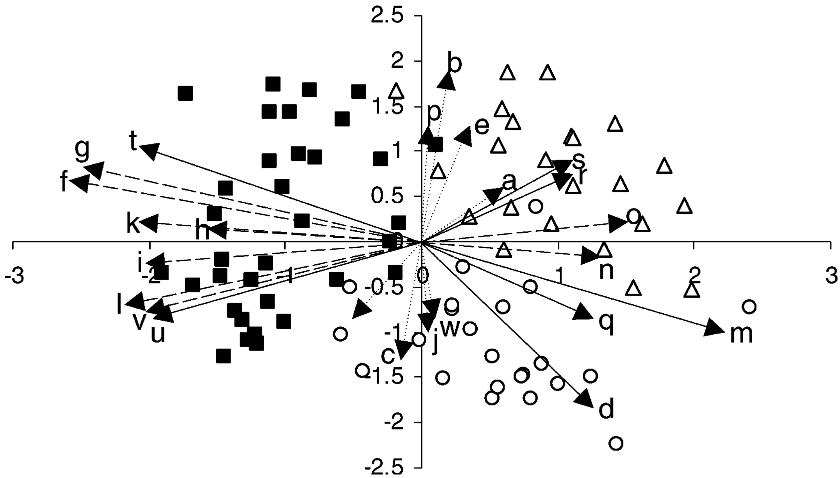

Figure 3. Results of the Canonical Correspondence Analysis (based on bird species plot abundances). Plots from undisturbed forest (black squares), once burned forest (open circles) and twice burned forest (open triangles) are clearly separated. The environmental variables are indicated with arrows (dotted arrows are significant with 2nd CCA-axis only, dashed arrows are significant with 1st CCA-axis only, solid arrows are significant with both CCA-axes). Environmental variables: (a) slope, (b) topography, (c) soil water, (d) snags, (e) understorey cover, (f) middlestorey cover, (g) upperstorey cover, (h) bole climbers, (i) lianas, (j) epiphytic ferns, (k) epiphytic mosses, (l) small palms, (m) terrestrial ferns, (n) grasses, (o) gingers, (p) *Mallotus* plants, (q) *Macaranga* plants, (r) bamboo, (s) wild bananas, (t) vegetation layers, (u) maximum tree height, (v) upper mossline, (w) flowering trees, (x) fruiting trees.

first axis represents the main disturbance gradient, separating undisturbed from the burned forest plots. Environmental variables significantly related with this axis are: (1) vegetation cover of the mid- and upperstorey, vegetation layering and maximum tree height; (2) presence or abundance of grasses, gingers, bamboos, wild bananas and terrestrial ferns in the forest understorey; (3) presence or abundance of bole climbers, lianas, and epiphytic mosses; (4) presence or abundance of small palms and *Macaranga* pioneer plants; (5) the amount of snags; and (6) the height of the upper mossline. The second axis represents a topographic, slope and soil water content gradient. Once and twice burned forest plots were clearly separated along this gradient, with twice burned forest plots associated with steep slopes, uphill areas with low soil water contents, and once burned forest plots associated with down slope areas, less steep slopes and high soil water contents. The second axis is significantly related to the following environmental variables: (1) slope, topography and soil water content; (2) understorey vegetation cover, vegetation layering and maximum tree height; (3) presence or abundance of terrestrial ferns, bamboos, and wild bananas; (4) abundance of epiphytic ferns; (5) presence or abundance of *Macaranga* and *Mallotus* pioneer plants; (6) the amount of snags; and (7) presence of flowering and fruiting trees.

Changes in bird community structure

Bird body mass distributions, although superficially similar, differed significantly between undisturbed and burned forest types (Figure 4a). Although all forest types showed highest bird numbers in the 21–40 g body mass class, this peak is higher and narrower in the two burned forest types. There occurred no shift towards either more solitary or gregarious bird species after fire (Figure 4b). However, undisturbed and burned forests did differ in the maximum potential altitude range of the observed bird species, with more altitude generalists found in the burned forests (Figure 4c).

Bird habitat preferences in relation to forest disturbance, as determined by another study (Thiollay 1995) also differed significantly between forest disturbance types (Figure 4d). Undisturbed forests had very few birds that prefer open, grassy forest types, and a lot of birds that are typical for closed forests. The number of birds that prefer open and degraded forests was much higher in the two burned forest types, while the number of birds that prefer closed forests was considerably lower in burned than in undisturbed forest. Foraging heights also differed between the undisturbed and burned forest types (Figure 4e). Burned forests showed a significantly higher number of birds that forage on the forest floor and above the canopy, and a significantly lower number of birds in the forest under- and midstoreys in comparison with undisturbed forest.

There were only small differences in nesting behaviour between the bird communities of burned and undisturbed forests. Twice burned forests showed

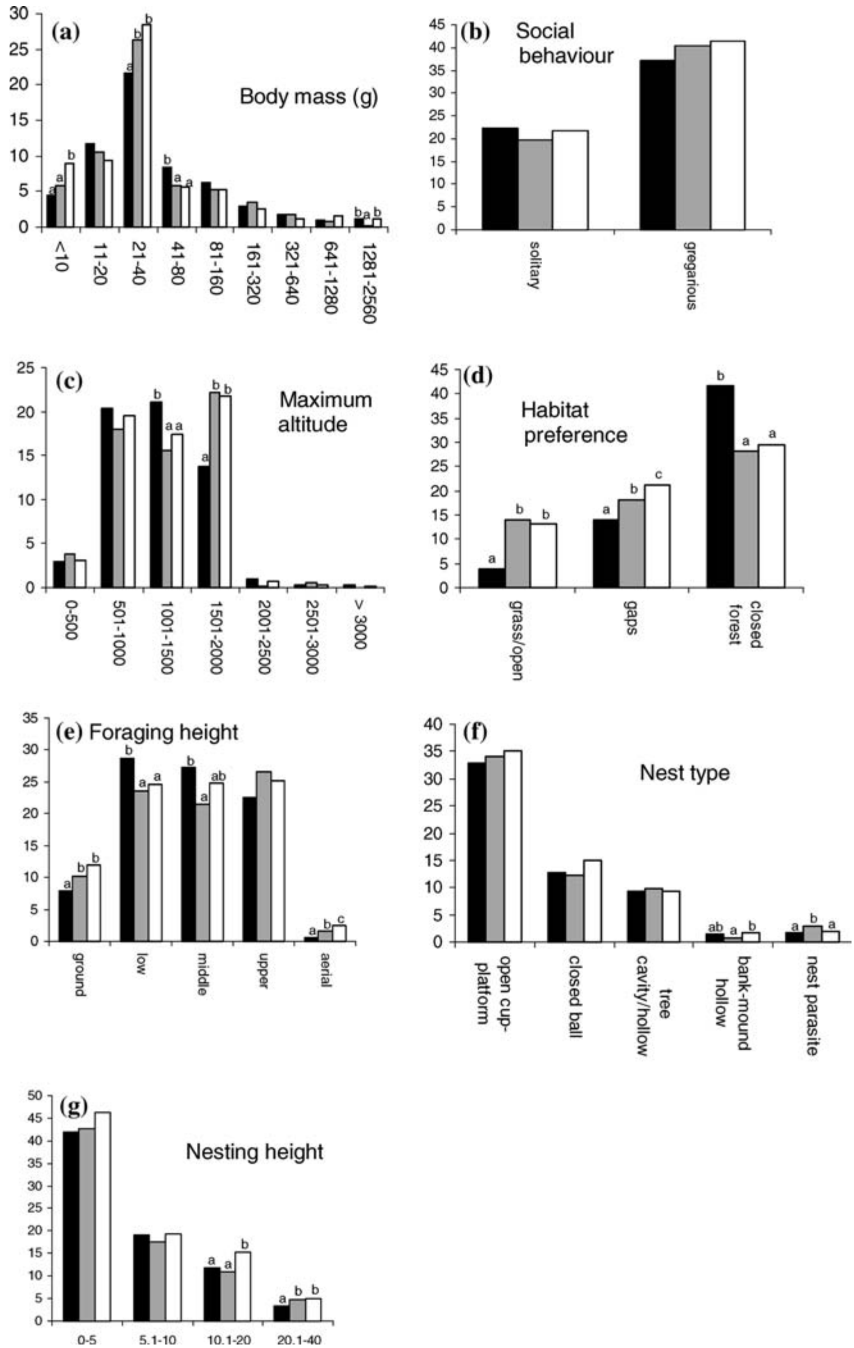

Figure 4. Bird community structure in undisturbed (black), once burned (grey) and twice burned (white) forest plots (y-axes indicate number of individuals per plot). Significant differences per class are indicated with different characters.

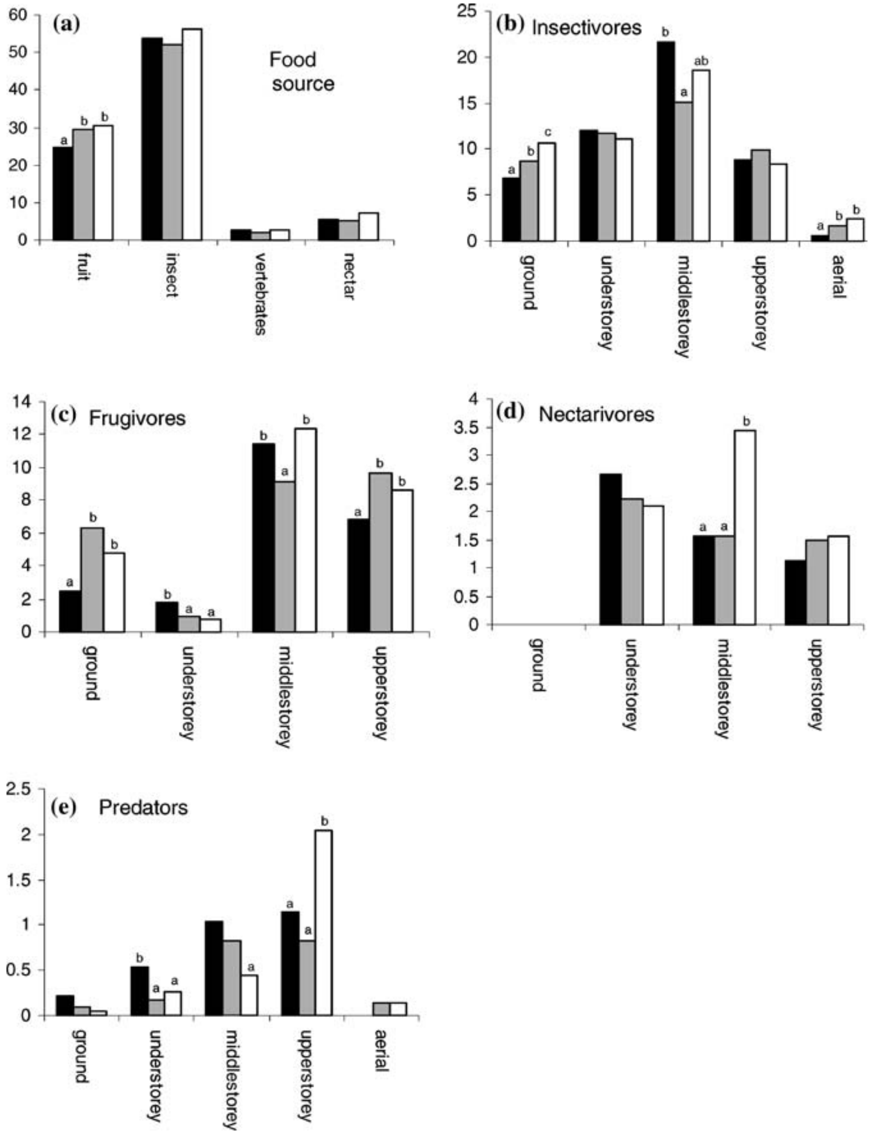

Figure 5. Foraging strategies in undisturbed (black), once burned (grey) and twice burned (white) forest, indicated in number of birds per class (y-axis). Significant differences within classes are indicated with different characters.

significantly higher numbers of birds that prefer to nest in river banks or termite mounts, while nest parasites were significantly more common in once burned forest (Figure 4f). Furthermore, in burned forest, the abundance of birds that prefer to build their nest high in the trees was significantly higher Figure 4g).

Changes in foraging strategies

Overall, we only detected a significant increase in frugivorous birds in burned forests (Figure 5a). However, when food choice was combined with foraging height, we found more significant changes in foraging strategies between the forest disturbance types. The abundance of insectivores foraging on the forest floor and above the forest canopy increased significantly in burned forests (Figure 5b), while those foraging in the forest midstorey decreased. Abundances of frugivores foraging on the forest floor also increased significantly in burned forests, as did those foraging in the tree canopies (Figure 5c). However, frugivore abundances in the forest understorey were lower in burned forest, while the abundance of frugivores in the midstorey decreased in once burned forest. Nectarivores showed little changes in abundance after fire, except for a strong increase in the middlestorey of twice burned forests (Figure 5d). Predators (raptors, nocturnal predators and piscivores combined) showed significant decreases in abundance in the lower forest storeys after fire, and a strong increase in the upperstorey in twice burned forest (Figure 5e).

Discussion

Effect of fire on bird species composition and diversity

Our study shows, similarly to the findings of Kinnaird and O'Brien (1998) in Sumatra and Barlow and Peres (2004a, b) in Brazil, that even though the total number of birds and bird species per sample point (species richness) in burned forests does not differ from those in undisturbed forests a few years after fire, the bird species composition, diversity (distribution of individuals over species) and turnover (difference in species composition between different sample points) do change considerably. Burned forests show less difference in bird species composition between plots, i.e., have lower species turnover than undisturbed forests, and also show a less even distribution of individuals over species, i.e., they are more strongly dominated by a few abundant taxa than undisturbed forests. These differences are probably related to the fact that undisturbed forests provide more spatial variation in vegetation structure (niche space) than burned forests. Especially the strong reduction of foliage in the middle and upper stories of burned forests seriously reduce vertical resource availability for birds. Reductions in plant diversity and the strong dominance of the forest understorey by only a few species of pioneer herbs, shrubs and trees (Slik and Eichhorn 2003) also strongly reduce habitat heterogeneity in burned forests.

Associations between habitat variables and bird species composition

The shift in bird species composition between undisturbed and burned forests was significantly related to changes in the forest understorey (appearance of pioneer herbs and woody plants after fire) and the middle- and upperstorey (strong decrease in foliage cover after fire). Based on vegetation studies in burned forests, we know that the increase in pioneer herbs and woody plants in the forest understorey is associated with a near complete destruction of the original understorey vegetation by the fire (Woods 1989; Nykvist 1996; Nieuwstadt 2002; Cochrane 2003; Slik and Eichhorn 2003). Overall, it is clear that habitat heterogeneity, both in terms of vegetation structure and plant species diversity and composition, is strongly reduced in burned forests. Bird species that profit from these circumstances have previously (Thiollay 1995) been classified as 'open forest' and 'gap and forest edge' species, while species that suffer from these circumstances were previously classified as 'closed forest' species (Figure 6). Our observation that habitat heterogeneity decreases, while 'open forest' and 'gap/edge' bird species increase and 'closed forest' bird species decrease in abundance after fire corresponds to the reported increase in abundance of habitat generalists and decrease in abundance of habitat specialists after fire in Brazilian rain forests (Barlow and Peres 2004a, b).

Differences in bird species composition between once and twice burned forests were also significantly related to environmental variables. In this case these variables were mainly related to differences in (1) the forest understorey, such as understorey vegetation density of woody and herbaceous plants, (2) the presence of flowering and fruiting trees, and (3) differences in topography and slope. One important difference between once and twice burned forests is the fact that once burned forests are characterised by a relatively low density of understorey woody plants in combination with a high density of understorey herbs (mainly ferns) in comparison to twice burned forests (Slik and Eichhorn 2003). This difference in understorey vegetation composition and structure might partly explain the difference in bird species composition between once and twice burned forests. For instance, the dense fern stands in once burned forest, with few perches for nesting and foraging, are likely less attractive and penetrable for birds than the dense but more diversified woody pioneer stands in twice burned forests.

How topography is related to the difference in bird composition between once and twice burned forests is unclear. However, it might be an indirect correlation that is related to fire chance and intensity. Slik and Eichhorn (2003) and Nieuwstadt (2002) have shown that topography is strongly related to the chance of fire occurrence and possibly also fire intensity. That twice burned forest is positively associated with upslope areas might thus be a result of the fact that upslope areas run a higher risk of burning, i.e., are more likely to burn repeatedly, than down slope areas.

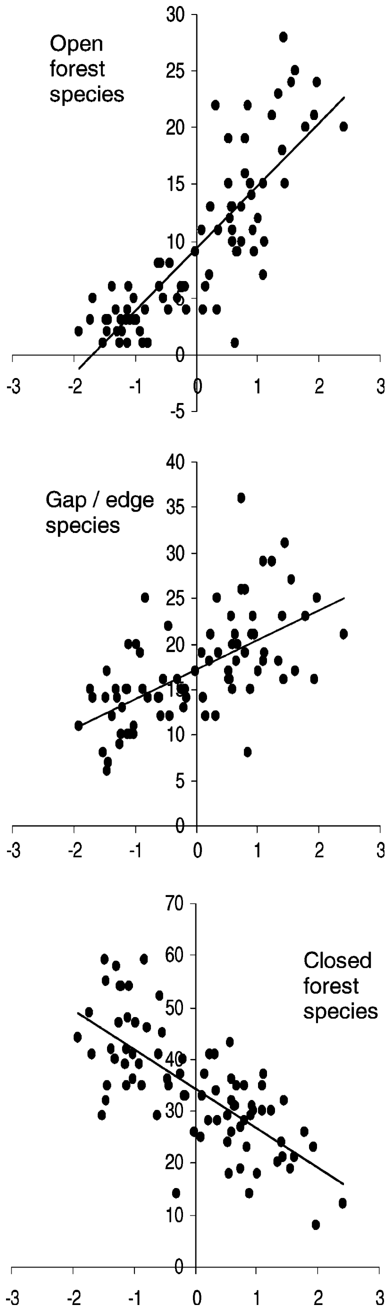

Figure 6. Relation between plot score on the first CCA-axis (x-axis) and the number of open forest, gap-edge, and closed forest preferring bird species in the plots (y-axis). Habitat preferences of birds were based on data from Thiollay (1995).

Changes in bird community structure after fire

The pronounced differences in environmental conditions between undisturbed and burned forests, and to a lesser extent between once and twice burned forests, resulted in some significant differences in bird community structure between these forests as well. These differences were mainly related to shifts in body mass distribution, abundance of generalist vs. specialist bird species, and foraging behaviour. The changes in foraging behaviour that we found are often conflicting with earlier studies from Sumatra and Brazil (Kinnaird and O'Brien 1998; Barlow and Peres 2004a, b). For example, in Brazil most insectivorous guilds declined in abundance after fire (Barlow and Peres, 2004a, b), in Sumatra they were found to increase (Kinnaird and O'Brien 1998), while we found in this study that they were equally abundant in undisturbed and burned forests. Barlow and Peres (2004a, b) report strong declines in understorey insectivores, while we find a significant increase in understorey insectivores. In Sumatra, the number of frugivorous birds declined after fire, while in our study this group shows a significant increase in numbers. Both from Sumatra and Brazil a decrease in numbers of canopy frugivores is reported, while we found an increase in this group.

The differences in sampling strategy between the three study areas make it rather difficult to interpret these conflicting results. The study by Kinnaird and O'Brien (1998) in Sumatra was carried out 1 year after fire (so during the earliest stages of forest recovery), while that of Barlow and Peres (2004a, b) in Brazil covered the first 3 years of bird species dynamics, but was based on mist net trapping rather than point counts. Also, our burned forest plots were located close to unburned forest, allowing for the possibility that many birds may have been recorded as passing through, while plots in the study of Barlow and Peres (2004a, b) were placed much further from undisturbed forest and probably do not have this problem. So even though fire severity, distribution of lightly and heavily burned forest patches, distance to unburned forest, connectivity of the burned and undisturbed forest areas, differential shifts in flowering and fruiting patterns of plant species between locations might all play an important role in explaining the differences in outcomes between the different studies, it is not possible to differentiate them from the differences caused by their different sampling strategies.

Implications of fire in tropical rain forests for bird conservation

Our results provide several important conclusions that are relevant for bird conservation in the tropics. Firstly, local bird species richness (i.e. the number of species at any specific point) and bird abundance are as high in burned as in undisturbed forests. The main differences in diversity and composition between burned and undisturbed forests are all related to shifts in abundances and turnover of bird species. Although beta diversity (at small spatial scales) was higher in undisturbed forest than in burned forest, we found almost no bird species that were exclusively restricted to undisturbed or burned forest. This might be related to the fact that our burned forest plots were all located near undisturbed forest (indicating the importance of these undisturbed forests for colonization of burned forests), or it might indicate that most bird species can survive in both types of forest, even though their densities can differ considerably between burned and undisturbed forest. Although it is not yet clear how these changes in abundance might affect future survival of some of these species, this observation still means that the basic condition for full regeneration, namely that most species are still there, is met in the burned forests that we studied, and thus that they are still worth conserving.

Secondly, the bird species composition in tropical forests is strongly related to (vertical) vegetation structure and plant species composition. This means that full recovery of the bird community in burned forests depends strongly on successful regeneration of the vegetation in those forests. Recent vegetation studies in burned tropical rain forests indicate that vegetation structure, in terms of numbers of trees and layered structure, recovers relatively quickly (ca. 15 years) in burned forests because of the fast growth of pioneer trees in these forests (Slik et al. 2002; Slik and Eichhorn 2003). Recovery of the original plant species composition might take considerable longer, even up to several hundreds of years (Cochrane 2003). However, as long as fire is not too frequent (i.e. preferably less than every few hundred years), or does not cover the whole extent of forest (i.e. when enough unburned remnant forest patches remain), recovery of both the vegetation and the avifauna could still be possible.

Thirdly, repeated forest burning does not automatically result in a more impoverished avifauna in comparison to single forest burning. However, when fires become too frequent for the vegetation to recover, both the flora and avifauna are likely to become seriously negatively affected to the point that recovery becomes impossible. Since burned forests have an increased susceptibility for fire due to increased fuel loads and the more open forest structure (Uhl and Buschbacher 1985; Uhl et al. 1988; Cochrane and Schulze 1999; Cochrane 2003), fire prevention (perhaps through construction of fire break networks) should be a main aim of any burned forest conservation strategy.

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Appendix 1

Average number of observations per species per plot in undisturbed, once burned and twice burned forest, and total number of observed individuals (nomenclature based on Andrew [1992]).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Undisturbed forest preferring bird species					
Alcippe brunneicauda (Brown fulvetta)	**0.76**	0.13	0.17	33	0.002
Anthracoceros malayanus (Black hornbill)	**0.88**	0.70	0.22	51	0.019
Argusianus argus (Great argus)	**1.09**	0.13	0.35	48	< 0.001
Calorhamphus fulliginosus (Brown barbet)	**0.74**	0.13	0.26	34	< 0.001
Calyptomena viridis (Green broadbill)	**0.38**	0.09	0.09	17	< 0.001
Ceyx erithacus (Oriental dwarf kingfisher)	**0.53**	0.17	0.26	28	0.024
Copsychus pyrropygus (Orange-tailed shama)	**1.00**	0.70	0.43	60	0.022
Criniger bres (Grey-cheeked bulbul)	**0.68**	0.13	0.35	34	0.028
Criniger phaeocephalus (Ochraceous bulbul)	**1.03**	0.30	0.57	55	0.006
Culicicapa ceylonensis (Grey-headed flycatcher)	**0.24**	0	0.04	9	0.015
Eurylaimus javanicus (Banded broadbill)	**1.06**	0.39	0.83	64	0.023
Harpactes diardii (Diard's trogon)	**0.41**	0	0	14	< 0.001
Hypogramma hypogrammicum (Purple-naped sunbird)	**1.21**	0.61	0.35	63	< 0.001
Hypsipetes criniger (Hairy-backed bulbul)	**0.88**	0.70	0.22	51	0.019
Kenopia striata (Striped wren-babbler)	**0.15**	0	0	5	0.039
Lacedo pulchella (Banded kingfisher)	**0.35**	0.04	0.09	15	0.006
Malacopteron affine (Sooty-capped babbler)	**0.26**	0	0	9	0.002

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Malacopteron cinereum (Scaly-crowned babbler)	**0.53**	0.04	0	19	< 0.001
Megalaima rafflesii (Red-crowned barbet)	**0.71**	0.61	0	38	0.021
Ninox scutulata (Brown boobook)	**0.35**	0	0.09	14	0.015
Philentoma pyrrhopterum (Chestnut-winged philentoma)	**0.53**	0	0	18	< 0.001
Pitta granatina (Garnet pitta)	**0.76**	0.13	0.35	37	0.037
Pycnonotus cyaniventris (Grey-bellied bulbul)	**0.18**	0.04	0	7	0.041
Reinwardtipicus validus (Orange-backed woodpecker)	**0.26**	0	0.09	11	0.011
Rhinomyias umbratilis (Grey-chested flycatcher)	**1.56**	0.35	0.26	67	< 0.001
Rhipidura perlata (Spotted fantail)	**0.65**	0	0.09	24	< 0.001
Rollulus rouloul (Crested partridge)	**0.18**	0	0	6	0.047
Stachyris maculate (Chestnut-rumped babbler)	**2.68**	0.65	0.04	107	< 0.001
Stachyris rufifrons (Rufous-fronted babbler)	**0.56**	0	0.04	20	< 0.001
Terpsiphone paradise (Asian paradise-flycatcher)	**0.74**	0.17	0	29	< 0.001
Trichastoma malaccense (Short-tailed babbler)	**1.59**	0.74	1.22	99	0.012
Undisturbed and once burned forest preferring bird species					
Aegithina viridissima (Green lora)	**0.88**	**0.96**	0.09	54	< 0.001
Ducula aenea (Green imperial pigeon)	**0.79**	**0.83**	0.09	48	< 0.001
Malacopteron magnum (Rufous-crowned babbler)	**0.35**	**0.35**	0	20	< 0.001
Picus puniceus (Crimson-winged woodpecker)	**0.68**	**0.70**	0.30	46	0.03
Platysmurus leucopterus (Black Magpie)	**0.29**	**0.26**	0.04	17	0.02
Surniculus lugubris (Drongo cuckoo)	**0.32**	**0.30**	0.04	19	0.018
Once burned forest preferring bird species					
Cacomantis merulinus (Plaintive cuckoo)	0.15	**0.78**	0.43	33	0.02

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Gracula religiosa (Hill myna)	0.56	**1.22**	0.61	61	0.022
Lanius tigrinus (Tiger shrike)	0	**0.17**	0	4	0.044
Macronous ptilosus (Fluffy-backed tit-babbler)	0.15	**0.35**	0	13	0.022
Psittacula longicauda (Long-tailed parakeet)	0.21	**0.61**	0.04	22	0.007
Pycnonotus atriceps (Black-headed bulbul)	0.91	**2.52**	1.13	115	< 0.001
Pycnonotus goiavier (Yellow-vented bulbul)	0.15	**4.70**	2.87	179	< 0.001
Stachyris erythroptera (Chestnut-winged babbler)	0.29	**0.57**	0	23	0.022
Burned forest preferring bird species					
Centropus sinensis (Greater coucal)	0.47	**1.00**	**0.74**	56	0.028
Coracina fimbriata (Lesser cuckoo-shrike)	0.21	**0.70**	**0.48**	34	0.017
Cuculus micropterus (Indian cuckoo)	0.85	**1.57**	**1.22**	93	0.024
Hemiprocne longipennis (Grey-rumped tree swift)	0.29	**0.78**	**0.83**	47	0.01
Hemipus hirundinaceus (Bar-winged flycatcher-shrike)	0.47	**1.22**	**1.00**	67	0.006
Lonchura fuscans (Dusky munia)	0	**0.26**	**0.13**	9	0.041
Loriculus galgulus (Blue-crowned hanging-parrot)	0.85	**1.22**	**1.48**	91	0.033
Orthotomus sericeus (Rufous-tailed tailorbird)	0.24	**1.26**	**1.30**	67	< 0.001
Psittinus cyanurus (Blue-rumped parrot)	0.21	**1.04**	**1.26**	60	< 0.001
Pycnonotus plumosus (Olive-winged bulbul)	0.62	**2.48**	**2.74**	141	< 0.001
Rhaphidura leucopygialis (Silver-rumped swift)	0.06	**0.35**	**0.22**	15	0.037
Trichastoma rostratum (White-chested babbler)	0.21	**0.39**	**0.65**	31	0.025
Twice burned forest preferring bird species					
Blythipicus rubiginosus (Maroon woodpecker)	0.18	0	**0.30**	13	0.035
Buceros rhinoceros (Rhinoceros hornbill)	0.06	0.04	**0.48**	14	0.003

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Copsychus malabaricus (White-rumped shama)	0.88	0.52	**2.13**	91	< 0.001
Copsychus saularis (Magpie robin)	0	0.04	**0.52**	13	0.01
Corvus enca (Slender-billed crow)	0.09	0	**0.26**	9	0.037
Dicaeum trigonostigma (Orange-bellied flowerpecker)	0.71	0.35	**2.74**	95	< 0.001
Eurylaimus ochromalus (Black-and-yellow broadbill)	1.12	0.74	**1.65**	93	0.007
Gerygone sulphurea (Flyeater)	0.21	0.04	**0.48**	19	0.032
Lonchura Malacca (Black-headed munia)	0	0	**0.43**	10	0.01
Lophura ignite (Crested fireback)	0.03	0	**0.17**	5	0.031
Macronous gularis (Striped tit-babbler)	0.12	1.91	**2.43**	104	0.003
Megalaima australis (Blue-eared barbet)	0.06	0	**0.43**	12	0.003
Merops viridis (Blue-throated bee-eater)	0.06	0.17	**0.87**	26	< 0.001
Nyctyornis amictus (Red-bearded bee-eater)	0.26	0.13	**0.61**	26	0.005
Orthotomus ruficeps (Ashy tailorbird)	1.03	1.61	**2.48**	129	0.003
Pomatorhinus montanus (Chestnut-backed scimitar-babbler)	0.35	0.17	**0.87**	36	0.004
Pycnonotus brunneus (Red-eyed bulbul)	0.79	1.22	**1.70**	94	0.042
Pycnonotus erythrophthalamus (Spectacled bulbul)	1.76	1.57	**2.43**	152	0.027
Rhyticeros undulates (Wreathed hornbill)	0.32	0.39	**0.83**	39	0.02
Treron capellei (Large green pigeon)	0	0.13	**0.35**	11	0.032
Treron olax (Little green pigeon)	0.03	0	**0.26**	7	0.017
Bird species unaffected by forest fire					
Anorrhinus galeritus (Bushy-crested hornbill)	**0.12**	**0.13**	**0.17**	11	
Anthreptes singalensis (Ruby-cheeked sunbird)	**0.23**	**0.48**	**0.35**	27	

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Arachnothera longirostra (Little spiderhunter)	**0.56**	**0.61**	**0.96**	55	
Centropus bengalensis (Lesser coucal)	**0.18**	**0.04**	**0.30**	14	
Chalcophaps indica (Emerald dove)	**1.03**	**1.26**	**0.65**	79	
Chloropsis cyanopogon (Lesser green leafbird)	**0.32**	**0.48**	**0.48**	33	
Chloropsis sonnerati (Greater green leafbird)	**0.44**	**0.70**	**0.13**	34	
Chrysococcyx xanthorhyncus (Violet cuckoo)	**0.18**	**0.17**	**0.17**	14	
Dendrocopus canicapillus (Grey-capped woodpecker)	**0.24**	**0.48**	**0.43**	29	
Dicrurus paradiseus (Greater racquet-tailed drongo)	**1.62**	**1.61**	**1.17**	119	
Dryocopus javensis (White-bellied woodpecker)	**0.53**	**0.43**	**0.43**	38	
Hypothymis azurea (Black-naped monarch)	**1.03**	**0.96**	**1.00**	80	
Hypsipetes charlottae (Buff-vented bulbul)	**1.59**	**0.90**	**1.26**	103	
Irena puella (Asian fairy bluebird)	**1.38**	**1.52**	**1.30**	112	
Mulleripicus pulverulentus (Great slaty woodpecker)	**0.06**	**0.09**	**0.30**	11	
Oriolus xanthonotus (Dark-throated oriole)	**0.21**	**0.30**	**0.39**	23	
Orthotomus atrogularis (Dark-necked tailorbird)	**0.88**	**1.22**	**0.87**	78	
Pellorneum capistratum (Black-capped babbler)	**0.85**	**0.65**	**0.87**	64	
Pericrocotus flammeus (Scarlet minivet)	**0.38**	**0.04**	**0.52**	26	
Pericrocotus igneus (Fiery minivet)	**0.06**	**0.22**	**0.26**	13	
Prionochilus xanthopygius (Yellow-rumped flowerpecker)	**0.59**	**0.35**	**0.39**	37	
Pycnonotus eutilotus (Puff-backed bulbul)	**0.47**	**0.48**	**0.35**	35	
Pycnonotus simplex (Cream-vented bulbul)	**0.12**	**0.22**	**0.39**	18	
Rhyticeros corrugatus (Wrinkled hornbill)	**0.29**	**0.26**	**0.39**	25	

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Sitta frontalis (Velvet-fronted nuthatch)	**0.53**	**0.65**	**0.30**	40	
Tephrodornis gularis (Large wood-shrike)	**0.38**	**0.26**	**0.43**	29	
Trichastoma bicolor (Ferruginous babbler)	**0.32**	**0.35**	**0.30**	26	
Bird species that were too rare to detect habitat preference					
Actenoides concretus (Rufous-collared kingfisher)	0.12	0	0.04	5	
Aerodramus fuciphagus (Edible-nest swiftlet)	0	0.09	0	2	
Aerodramus maximus (Black-nest swiftlet)	0	0.04	0	1	
Aethopyga temmincki (Temmink's sunbird)	0.03	0.09	0	3	
Alcedo euryzona (Blue-banded kingfisher)	0.03	0	0	1	
Alcedo meninting (Blue-eared kingfisher)	0	0.09	0	2	
Apus pacificus (Fork-tailed swift)	0	0.04	0	1	
Arachnothera affinis (Grey-breasted spiderhunter)	0.06	0.17	0.04	7	
Arachnothera crassirostris (Thick-billed spiderhunter)	0.03	0.04	0	2	
Arachnothera flavigaster (Spectacled spiderhunter)	0.09	0.04	0.09	6	
Arachnothera robusta (Long-billed spiderhunter)	0.03	0.13	0	4	
Bubo sumatranus (Barred eagle-owl)	0.06	0	0	2	
Cacomantis sonneratii (Banded bay cuckoo)	0	0.04	0	1	
Carpococcyx radiceus (Sunda ground-cuckoo)	0.06	0	0.09	4	
Celeus brachyurus (Rufous woodpecker)	0.09	0.17	0.04	8	
Chloropsis conchinchinensis (Blue-winged leafbird)	0.18	0.13	0	9	
Chrysococcyx minutillus (Little bronze cuckoo)	0	0	0.04	1	
Coracina striata (Bar-bellied cuckoo-shrike)	0.03	0	0	1	
Criniger finschii (Finsch's bulbul)	0.06	0	0	2	
Cyornis caerulatus (Large-billed blue flycatcher)	0.06	0	0	2	

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Cyornis superbus (Bornean blue flycatcher)	0.03	0	0	1	
Cyornis unicolor (Pale blue flycatcher)	0	0.04	0	1	
Cypsiurus balasiensis (Asian palm-swift)	0	0.22	0.04	6	
Dicaeum concolor (Plain flowerpecker)	0.06	0	0.09	4	
Dicrurus aeneus (Bronzed drongo)	0.06	0	0	2	
Dinopium rafflesii (Olive backed woodpecker)	0.03	0	0	1	
Enicurus leschenaultia (White-crowned forktail)	0.06	0.04	0.09	5	
Enicurus ruficapillus (Chestnut-naped forktail)	0	0	0.04	1	
Eupetes macrocerus (Malaysian rail-babbler)	0.03	0	0	1	
Eurostopodus temminckii (Malaysian eared nightjar)	0.06	0	0.04	3	
Eurystomus orientalis (Common dollarbird)	0.06	0.04	0.09	5	
Ficedula dumetoria (Rufous-chested flycatcher)	0.12	0	0.17	8	
Harpactes kasumba (Red-naped trogon)	0.09	0	0	3	
Harpactes orrhophaeus (Cinnamom-rumped trogon)	0.03	0	0	1	
Hemicircus concretus (Grey-and-buff woodpecker)	0.06	0.09	0	4	
Hemiprocne comata (Whiskered tree-swift)	0.03	0.04	0.22	7	
Hirundapus giganteus (Brown-backed needletail)	0	0	0.04	1	
Hypsipetes malaccensis (Streaked bulbul)	0.15	0	0.04	6	
Ictinaetus malayensis (Black eagle)	0	0.04	0.04	2	
Indicator archipelagicus (Malaysian honeyguide)	0.12	0	0	4	
Malacopteron albogulare (Grey-breasted babbler)	0.03	0	0	1	
Malacopteron magnirostre (Moustached babbler)	0.15	0.09	0	7	
Megalaima mystacophanos (Red-throated barbet)	0.12	0	0.09	6	
Meiglyptes tristis (Buff-rumped woodpecker)	0.06	0.04	0.09	5	

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Meiglyptes tukki (Buff-necked woodpecker)	0.06	0	0	2	
Micohierax fringillarius (Black-tighed falconet)	0	0.13	0.13	6	
Muscicapa dauurica (Asian brown flycatcher)	0.12	0	0	4	
Otus lempiji (Collared scopsowl)	0.03	0	0.04	2	
Philentoma velatum (Maroon-brested philentoma)	0.12	0	0	4	
Phylloscopus borealis (Arctic warbler)	0.06	0.04	0	3	
Picus mentalis (Checkuer-throated woodpecker)	0.06	0.04	0.04	4	
Picus miniaceus (Banded woodpecker)	0.03	0.04	0	2	
Pitta baudii (Blue-headed pitta)	0	0	0.04	1	
Pitta sordida (Hooded Pitta)	0	0.04	0.13	4	
Platylophus galericulatus (Crested Jay)	0.09	0.04	0	4	
Polyplectron schleiermacheri (Bornean peacock-pheasant)	0	0	0.13	3	
Prinia flaviventris (Yellow-bellied prinia)	0	0.22	0.09	7	
Prionochilus maculates (Yellow-breasted flowerpecker)	0.24	0.04	0.04	10	
Ptilocichla leucogrammica (Bornean wren-babbler)	0.03	0	0	1	
Rhamphococcyx curvirostris (Chestnut-brested malkoha)	0.06	0.04	0.04	4	
Rhinoplax vigil (Helmeted hornbill)	0.03	0	0.04	2	
Rhinorta chlorophaea (Raffles' malkoha)	0.03	0.04	0	2	
Rhididura javanica (Pied fantail)	0	0.17	0.09	6	
Sasia abnormis (Rufous piculet)	0.03	0.13	0.09	6	
Spilornis cheela (Crested serpent-eagle)	0.09	0.04	0.13	7	
Spizaetus cirrhatus (Changeable hawk-eagle)	0	0	0.04	1	
Spizaetus nanus (Wallace's hawk-eagle)	0	0.04	0	1	

Appendix 1. (Continued).

Species	Undisturbed (n/plot)	Burned once (n/plot)	Burned twice (n/plot)	n	p
Stachyris nigricollis (Black-throated babbler)	0.09	0	0	3	
Treron curvirostrata (Thick-billed green pigeon)	0.18	0.13	0	9	
Treron vernans (Pink-necked green pigeon)	0	0	0.17	4	
Yuhina zantholeuca (White-bellied yuhina)	0.06	0	0	2	
Zanclostomus javanicus (Red-bellied makoha)	0.03	0	0	1	
Zosterops palpebrosus (Oriental white-eye)	0.09	0	0	3	

Habitat preference indicated in bold, followed by significance level. Species with no significant habitat preference, but more than 10 observations are considered habitat generalists.

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