

# Effects of an ENSO-related fire on birds of a lowland tropical forest in Sumatra

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## Keywords

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## Abstract

Comparisons of bird community composition in burned and unburned areas of a lowland tropical rainforest in Sumatra, Indonesia indicated the following during the first 5 years after burning: (1) original burn severity strongly affected bird community composition at both the genus and family levels; (2) bird community composition continued to change progressively away from immediate post-burn composition in medium and severely burned forest as well as adjacent unburned forest; and (3) the degree of impact was both taxon and guild specific, with understory insectivores most detrimentally affected. Although species richness may temporarily increase in burned areas, this study suggests that multiple wildfires will lead to a decline in diversity over a large scale as birds of open fields replace interior forest specialists.

## Introduction

The increase in the frequency and severity of fires in tropical forest ecosystems has become a major conservation concern in the last decade (FAO, 1999; Davies, 2001; Laurance & Williamson, 2001). During the El Niño Southern Oscillation (ENSO) event of 1997, fires burned throughout the tropics, including *c.* 20 million ha in Asia and Latin America (Cochrane, 2003). Although fires may recur over long time scales in some tropical forests (Sanford *et al.*, 1985), they are not considered typical in humid tropical forests (Cochrane, 2003). Recent large-scale fires in the tropics have been of anthropogenic origin, exacerbated by climatic effects. Clearing, logging, road building and settlement activities interact to increase the vulnerability of forests to fire (Goldammer, 1999; Cochrane, 2001; Nepstad *et al.*, 2001), creating a situation in which tropical forests burn more easily than ever before (Cochrane *et al.*, 1999).

In Indonesia, drought conditions stemming from regularly recurring ENSO events (Holmgren *et al.*, 2001) have increased the extent and severity of wildfires caused by human activity (Barber & Schweithelm, 2000). The 1997 fires affected an estimated 9.7 million ha, including up to 1.7 million ha in Sumatra (FAO, 1999; Davies, 2001).

Timber extraction during former Indonesian President Suharto's New Order administration (1968–1998) left large areas degraded and vulnerable to fire (Siegert *et al.*, 2001). In the 1990s, the use of fire to clear land for oil palm plantations contributed to many uncontrolled fires (Barber & Schweithelm, 2000; Harwell, 2000). A campfire left by hunters caused the fire that is the subject of this study (O'Brien *et al.*, 1998). ENSO events are expected to increase in frequency and severity in the coming years (Timmermann *et al.*, 1999), making serious fires in Indonesia and other areas of the tropics likely to remain a critical conservation issue.

Known impacts of fire in tropical forests include changes in species composition, abundance and diversity of plants (Woods, 1989; Slik, Verburg & Kessler, 2002) and animals (Kinnaird & O'Brien, 1998; Barlow, Haugaasen & Peres, 2002; Barlow & Peres, 2004a), loss of seed banks, increased tree mortality, reduced regeneration potential (Sunarto, 2000; Davies, 2001), and changes in microclimate and soil conditions (Cochrane, 2003). Tropical trees can suffer extremely high mortality just from being superficially exposed to fire (Cochrane, 2003). The interaction of fire with other disturbance factors can have dramatic impacts on the ability of natural systems to recover (Curran *et al.*, 1999; Hartshorn

& Bynum, 1999). Forests that burn repeatedly are likely to be permanently converted to savannah or grassland (Goldammer, 1999).

Although few studies examine the effects of fire on Indonesian bird communities, studies of various disturbances, including fire, in other tropical forests may be applicable. These indicate that avian community composition changes after disturbance. Species most negatively affected are rare and specialized forest species (Raman, 2001), and understory birds, particularly understory insectivores (Bierregaard & Stouffer, 1997; Barlow *et al.*, 2002). Secondary specialists, nectivores, arboreal frugivores and granivores sometimes increase in disturbed areas (Bin Husin & Francis, 2001).

We examine differences in avian community composition along a gradient of burn severity in a Sumatran protected area. We use point count data, collected over 5 years following the occurrence of ENSO-related wildfires, to address the general dynamics of bird communities over time. Mist net data, collected at the end of the fifth year, allow for a comparison of the composition of understory avian communities in burned and unburned areas. We find that bird

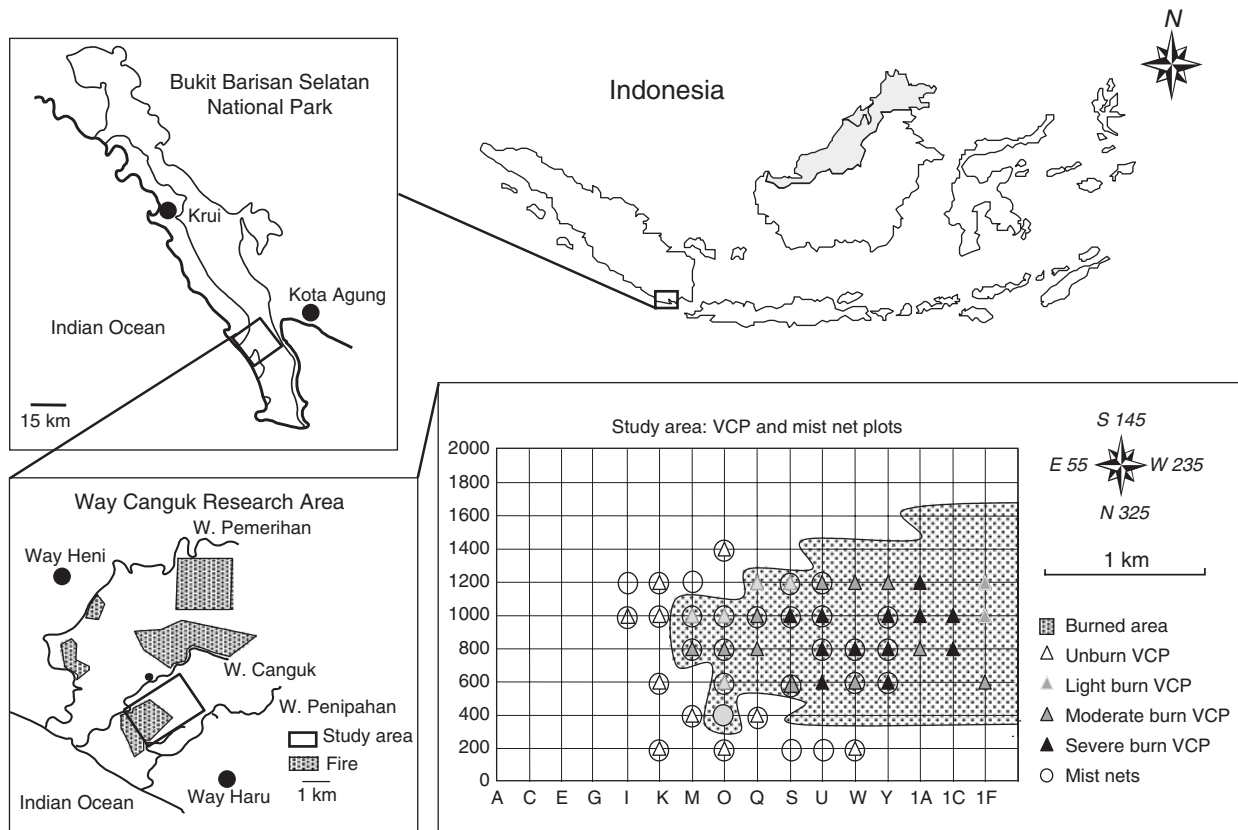
community composition was affected by the intensity of the fires and by the amount of time since burning. We also find that understory insectivores were more adversely affected than other guilds.

## Methods

### Study area

Bukit Barisan Selatan National Park (BBSNP) is the third largest protected area on Sumatra (Fig. 1). An important watershed for south-west Sumatra (104°E, 50°S), the park spans the provinces of Bengkulu and Lampung and is bordered by villages, agriculture and plantation forestry. Its 3568 km<sup>2</sup> area supports a full array of Sumatran fauna, including 355 species of birds, and contains important areas of intact lowland rainforest (O'Brien & Kinnaird, 1996).

The Way Canguk Research and Training Area, run by the Indonesian Department of Forest Conservation and Nature Preservation (Perlindungan Hutan dan Pelestarian Alam, PHPA) and the Wildlife Conservation Society



**Figure 1** Map of the study area located within Indonesia and Sumatra. The insets show (1) Bukit Barisan Selatan National Park and nearby towns, (2) the Perlindungan Hutan dan Pelestarian Alam (Department of Forest Conservation and Nature Preservation)/Wildlife Conservation Society Way Canguk Research and Training Area, with nearby villages, rivers, and burned areas (hash marks), and (3) the immediate study area showing burned (shaded area) and unburned forest, with variable circular point count and mist net sites color coded by burn severity. Gridlines are spaced 200 m apart.

(WCS), contains 900 ha of both intact primary forest and forest damaged by fire, drought, wind throws and earthquakes. It is bordered by large tracts of undisturbed lowland rainforest and by areas disturbed by illegal logging and agricultural activity. The study area is at 50 m elevation, has a grid of trails every 200 m, and is bisected by the Way Canguk River. One hundred 50 m × 10 m plots were established in 1997 for vegetation monitoring. Located at intersections along the 200 m grids, each plot is between 200 and 400 m from any adjacent plot in a pattern that ensures at least one plot every 16 ha.

During the ENSO-related drought of 1997–1998, less than 20 mm of rain fell in the park between June and October (Sunarto, 2000). This is extremely unusual for an area that normally receives up to 4000 mm year<sup>-1</sup>. Other records in West Sumatra indicate that the total rainfall for the year was around 1800 mm (Yoneda, Nishimura & Chairul, 2000). During this period, average daily temperatures hovered around 35 °C, also significantly higher than normal. The flora and fauna of the area were profoundly affected by the drought as well as by the fires (Kinnaird & O'Brien, 1998).

The drought-related forest fires in BBSNP burned from mid-September to mid-November 1997, damaging 1500–2000 ha of forest in the southern portion of the park, including 165 ha of the study area and 20 vegetation plots (Kinnaird & O'Brien, 1998). Shortly after the fires were extinguished (12–15 November 1997) observers evaluated burn severity by assigning scores ranging from 0 (unburned) to 3 along both sides of the grid trail at 50 m intervals throughout the burned area. A score of '1' indicates a light ground fire that destroyed dead leaf litter and damaged saplings lightly, leaving most with green leaves; '2' a fire that severely damaged the sapling layer up to a height of 5 m and did some damage to canopy trees; and '3' a fire that destroyed the sapling layer, severely damaged the mid-canopy and damaged the canopy (O'Brien *et al.*, 1998). We assigned each plot an individual score representing the average of the two scores on the trail intersection site, and the eight scores from 50 m away on each of the four intersecting trails. We then grouped the burned plots into three categories of burn severity, which were used to group plots in the analyses: light (0.1–1.0), moderate (1.1–2.3) and severe (2.4–3.0).

### Sampling methods

Census techniques include mist netting and point counts (Rappole, Winker & Powell, 1998; Blake & Loiselle, 2001). Point count data provide a continuous picture of changes in the bird community for the first 5 years after the fire. Mist netting is useful for identifying species, such as understory specialists, that point counts may miss because they are difficult to see and seldom vocalize (Terborgh *et al.*, 1990). Mist netting alone, however, sometimes provides misleading estimates of relative species composition and abundance (Remsen & Good, 1996; Catry *et al.*, 1999). Our two data sets should complement each other (Dawson *et al.*, 1995) as

each highlights particular aspects of the avian community and its change over time.

We determined avian abundance and distribution using data from variable circular point counts (VCP) performed at 30 burned and 10 unburned plots, which included all of the burned vegetation plots. Fifteen WCS staff members skilled in the identification of Sumatran birds participated in point counts conducted every 2 months during 1998, 1999 and 2000, and twice yearly in 2001 and 2002. During 10 min of observation taken between 06:00 and 09:00 h, two observers recorded all visual and auditory identifications. Each individual record includes the location (plot), date, time, genus, species if available, detection method (seen, heard or both), estimated distance between the observers and the bird (up to 100 m), and the number of birds detected. The majority of identifications were at the genus level.

We analyzed the data using family or genus identifications and by feeding guilds. There is a trade-off between taxonomic resolution and the ability to detect patterns in community composition. Given the level of sampling in this study, some analyses revealed patterns at the family level that were less clear at the genus level. For this reason we will present results for both family- and genus-level analyses.

The guilds, derived from MacKinnon & Phillipps (1993), Castelletta, Sodhi & Subaraj (2000) and our own experience, included arboreal frugivore (AF), arboreal frugivore–insectivore (AFI), insectivore (I), nectivore (N), nectivore–insectivore (NI), raptor (R), understory insectivore (UI), understory insectivore–frugivore (UIF), arboreal insectivore (AI), omnivore (O), piscivore–insectivore (PI) and aerial insectivore (ArI). We removed raptors and aerial insectivores from all analyses because of the difficulty of seeing them in primary forest compared with more open burned areas. Because of the small number of records, we removed kingfishers (PI) from the point count data for the feeding guild analysis. We analyzed nectivores and nectivore–insectivores together because they are all members of one family (Nectarinidae). Birds classified as insectivores are species that were not obviously arboreal or understory birds, mostly cuckoos (Cuculidae), flycatchers (Muscicapidae) and warblers (Sylviidae).

We mist netted for 57 days between June and August 2002. The 18 burned and 15 unburned sites included all of the 10 unburned and 17 of the 30 burned VCP plots. At each site, we placed three 12 m × 2 m nylon nets (36 mm mesh) lengthwise along trails running next to each vegetation plot. We netted each plot 4–5 h daily for 3 days (typically 06:30 h until 12:00 h), alternating between sets of burned and unburned plots. For each capture we recorded the location, date, time, species, identifying mark, sex (if known) and age (if known). To identify recaptured birds we cut small notches in numbered primary or secondary feathers of each individual in a sequence that was repeated for each species.

### Statistical methods

We used Mantel's test (Mantel, 1967) to evaluate the degree to which differences in community composition among our

plots are related to their relative spatial location (Legendre & Fortin, 1989). Mantel's test quantifies correlation between variables by using regression to evaluate dissimilarity between pairs of samples in a dissimilarity matrix. The effect of a single variable, after others have been removed, can be examined in a partial Mantel's test. This requires three matrices: species dissimilarity, environmental dissimilarity and spatial location. Mantel's tests were conducted in S-Plus 6.2 (Venables & Ripley, 2003) using functions from the Ecodist library (Urban *et al.*, 2002).

We used ordination to examine differences in bird community composition among plots. First, we used correspondence analysis (CA) and nonmetric multidimensional scaling (NMDS) to test whether variation in the species abundance matrix independently matched the known environmental gradient (burn severity). CA (Legendre & Legendre, 1998) assumes that species are unimodally distributed along environmental gradients. Both species and sites are assigned scores that represent a location along the same environmental 'axis'. The scores result from sites and species being simultaneously sorted so as to maximize their weighted correlation along this axis, where the abundance of a given species at a site determines the weighting. CA makes no assumption about the environmental meaning of the axes. After they are defined by the correlation, the site scores can be overlaid with information about known environmental parameters (in this case the burn scores) to see whether there is a relationship. CA is useful as an exploratory tool to determine whether *any* sort of gradient in species composition exists, and what measurable variable or variables it may be composed of. NMDS (Kruskal, 1964) arranges plots according to their relationship in a dissimilarity matrix composed of species, such that similar community composition results in smaller distances in ordination space. NMDS makes no assumptions about the distribution of species along environmental gradients.

Canonical correspondence analysis (CCA; ter Braak, 1986) differs from CA and NMDS in that it evaluates the correlation of sites and species along predetermined environmental gradients. It is widely used in ecology to test hypotheses about causes of variation in communities. It performs well in the face of noisy data and skewed species distributions (Palmer, 1993) and has been used effectively to describe overall patterns in the relationship between avian species abundance and environmental variation (Pearman, 2002). CCA assumes that species are unimodally distributed along gradients that are linear functions of these known variables. The number of canonical axes equals the number of environmental variables evaluated. The significance of the measured environmental variables in determining species composition may be evaluated using randomization tests (Legendre & Legendre, 1998).

Canonical and noncanonical ordination techniques are complementary. CA with the *post hoc* overlaying of burn severity scores establishes whether the most obvious gradient is related to burn severity. CCA best orders the data according to burn severity and assesses the significance of the relationship.

We used the software package PC-Ord (McCune & Melford, 1999) to perform the ordinations. All ordination results presented here use matrices of  $\ln(\text{genera abundance} + 1)$  in order to reduce the impact of occasional highly abundant species on comparisons of community composition. We also performed the analyses using raw abundances, in which case the patterns obtained were largely the same.

We calculated rarefaction curves using EstimateS (Colwell, 2005) and used presence-absence and abundance-based measures of community similarity (Jaccard's index and community concordance, respectively) to assess the relative degree of year-to-year change in different burn categories.

## Results

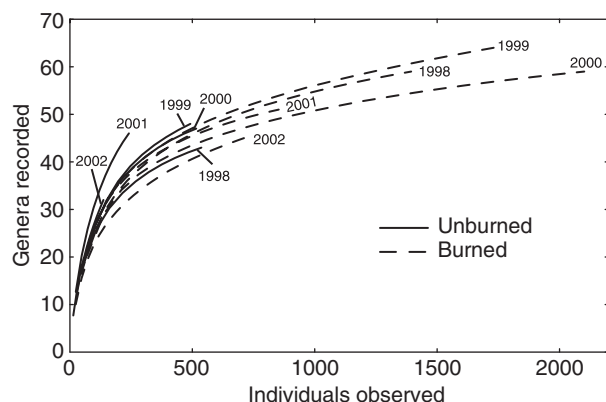
Five years of point counts yielded 9756 birds in 99 genera, and in 57 days of mist netting we caught 884 birds of 46 genera (64 species; Supplementary Material Appendix S1). Most results here refer to point count data; mist net data revealed similar patterns but were not included in analyses with point counts as mist nets sample a different subset of the bird community. Shannon-Weiner diversity was higher in the burned areas, but species evenness – a positive contributor to diversity measures – was consistently higher in unburned areas (Table 1). There was no difference in the accumulation rate of genera in our samples between burned and unburned areas or between years (Fig. 2). Strong Mantel correlations indicate that burn score is much more important than the effect of spatial location in determining genus composition (Table 2). This suggests that burn severity is the driving force behind bird composition in the various plots.

## Ordination

CA of genus-level point count data from separate years, with burn severity scores overlaid on site scores, reveals a relationship between burn severity and axis 1 in all years (Fig. 3). The relationship is strongest in 2000, 3 years after the burn. Similar analyses for family level data (not shown) give the same result. This result confirms that the most important environmental variable affecting the taxonomic composition of bird communities is burn severity. Other

**Table 1** Basic statistics for variable circular point count data. Diversity indices were calculated using the Shannon-Weiner index

Point count statistics	1998	1999	2000	2001	2002	Average
Burn genera	57	64	58	50	44	54.6
Unburn genera	42	49	47	45	31	42.8
All genera	59	70	65	58	50	60.4
Burn diversity	3.2371	3.2922	3.2358	3.2411	3.0070	3.2026
Unburn diversity	3.0974	3.2493	3.1854	3.3453	2.8638	3.1483
All diversity	3.2743	3.3534	3.3141	3.3475	3.0648	3.2709
Burn equitability	0.8006	0.7916	0.7969	0.8285	0.7946	0.8025
Unburn equitability	0.8287	0.8349	0.8274	0.8788	0.8340	0.8407
All equitability	0.8030	0.7893	0.7939	0.8244	0.7834	0.7988



**Figure 2** Sample rarefaction curves for point count data, scaled to the number of individuals to compensate for variation in sampling efforts between years, show no difference in the rate of accumulation of genera between years or between burned and unburned plots.

**Table 2** Simple and partial Mantel's tests of three dissimilarity matrices: VCP genera data from all years (Bray–Curtis dissimilarity), burn score and distance between plots (Euclidean distance). Starred (\*) entries are partial Mantel's tests for each pair, controlling for the unused variable (e.g. genera and space, controlling for burn scores). All tests are significant ( $P > 0.01$ ), but not all correlations are strong. The boxed in partial shows the effects of burn score on genus composition, controlling for the effects of spatial location. This high correlation indicates that burn scores, not spatial proximity, are driving the dissimilarity in genus composition between the plots

	Genera	Burn score	Space
Genera	N/A	0.5365857	0.2495127
Burn score	0.5071172*	N/A	0.2398253
Space	0.1474891*	0.1296452*	N/A

potentially influential environmental gradients either closely correspond to this gradient and thus to the effects of burn severity, or would correspond with another axis that has less effect on species composition. (Grouping point count data from all 5 years also reveals a strong gradient using NMDS, but these patterns are weaker or absent when analyzed on a year-by-year basis. This leads us to conclude that CA is a more informative technique for these particular data.) Beginning in 2000, the CA diagrams also reveal a separation of unburned plots along axis 2, which suggests that unburned sites are undergoing a variety of further post-fire changes in bird community composition.

Our results affirm the validity of using the burn scores as a predictor variable when applying CCA. CCA shows that burn severity is a significant predictor of genus and family composition in individual years and when years are combined ( $P < 0.001$  in all cases).

The next question we address is whether or not taxonomic composition is changing progressively with time. Within each burn category we perform CCA using year as the predetermined environmental variable. We find that at moderate and high levels of burn severity, there is significant

change over time at both the genus and family levels ( $P < 0.01$ ), whereas lightly burned plots do not change progressively over time. Interestingly, as suggested by the CA diagrams, unburned plots also show significant change at both the family and genus level ( $P < 0.005$ ). Both Jaccard's index and community concordance in adjacent years decrease with time post-fire in all burn categories, indicating that the rate of change in composition is accelerating (Fig. 4). There are no differences between burn categories in the degree of year-to-year similarity.

### Taxonomic and guild-specific differences

All of our results were repeated at both genus and family levels. Separation of plots along a gradient of burn severity was most distinct at the family level, but is also clear at the genus level. The same can be said for change over time within a given burn severity category. Thus the effects of burn severity on the bird community are manifested at both broad and more specific taxonomic levels.

At the species level, higher diversity in burned areas in our study resulted from a greater abundance and diversity of birds commonly found in fields and gardens, in addition to some forest species. Examples of common birds include hill mynas *Gracula religiosa*, magpie robins *Copsychus saularis* and bar-winged prinias *Prinia familiaris*. Forest birds that utilized burned areas included many bulbuls (Pycnonotidae) and woodpeckers (Picidae). Understorey forest specialists such as pittas (Pittidae) and babblers (Timalidae) were much less common.

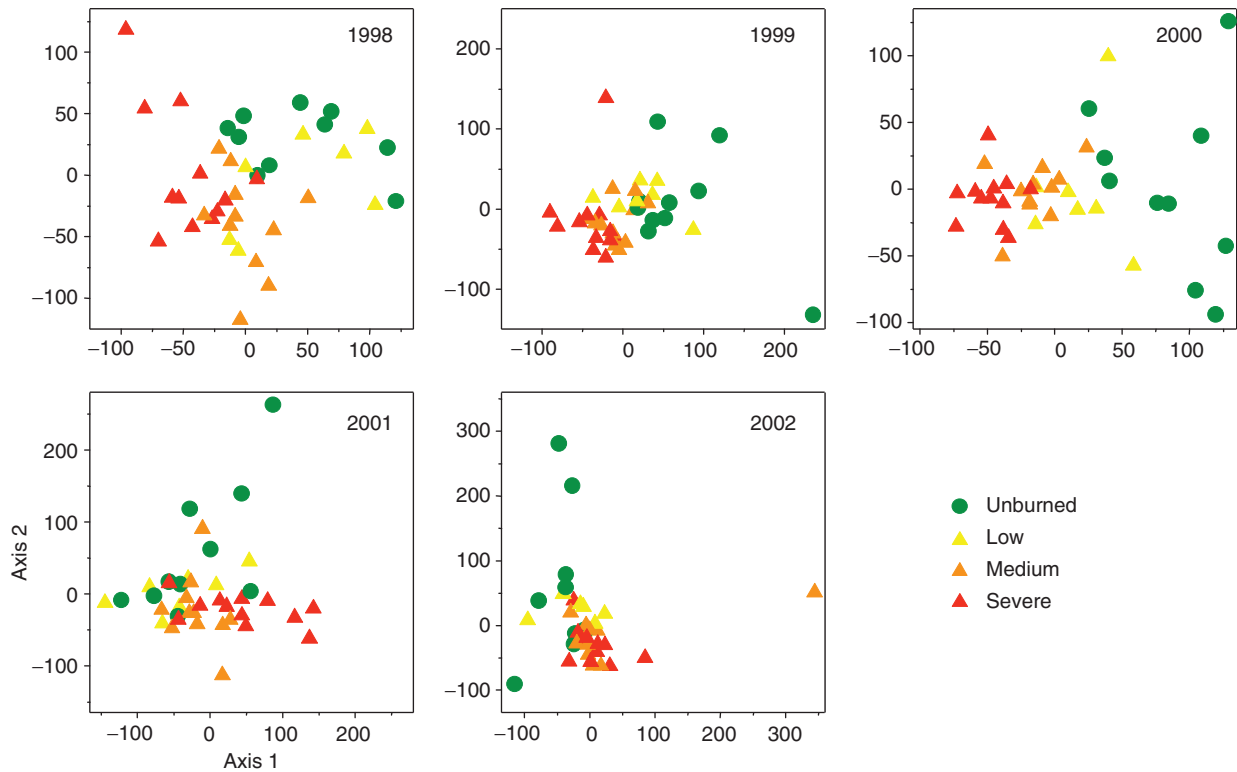
Examining the data by feeding guild both immediately after the burn (1998) and at the end of the study period (2002; Fig. 5) also reveals striking differences in the abundances of birds recorded in each burn category. Frugivore–insectivores and arboreal insectivores make up a large proportion of the birds found in severely and moderately burned plots. Arboreal frugivores are very abundant in unburned plots in 1998, but by 2002 have declined in unburned plots and become the most abundant guild in severely burned plots. Understorey insectivores are the only guild to show a dramatic decline with burn severity. In both 1998 and 2002, they comprise a significant proportion of the community in unburned plots but their numbers drop sharply as burn severity increases. This suggests that their ability to utilize burned areas decreases with increasing burn severity.

### Discussion and conclusions

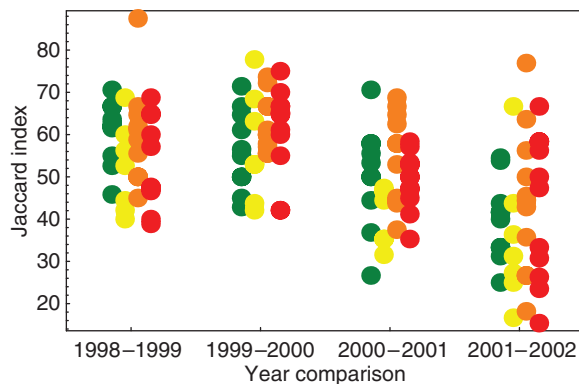
The bird community in the severely burned area within our study site is markedly different from that of the unburned forest several hundred meters away. CA shows burn severity to be the most important environmental gradient affecting avian community composition, but this effect is obviously mediated through changes in the plant community.

### Role of vegetation

In our study area, burn severity scores reflect differences in vegetation type and structure that are directly linked to the



**Figure 3** Correspondence analysis of yearly point count data analyzed by genus shows a clear pattern of separation of sites along axis 1 according to burn severity, which is color coded along a scale from yellow (less burned) to red (more burned). Dark green circles are completely unburned. In each year, the unburned plots and lightly burned plots are on the opposite end of axis 1 from the most severely burned plots, with the moderately burned plots distributed in between. As the time series progresses, unburned plots begin to diverge from each other along axis 2.



**Figure 4** Jaccard similarity indices for variable circular point count plots in adjacent years. Green points are unburned plots; yellow, orange and red points are lightly, moderately and severely burned plots, respectively. All types of plot show a greater degree of year-to-year dissimilarity over time, indicating an accelerating rate of community change.

intensity of the 1997 fires. O'Brien *et al.* (2003) quantified forest structure in the vegetation plots before and after the fire. Although areas that burned contained significantly fewer trees before the fire, the average diameter at breast height (DBH) was not significantly different, and distribu-

tion of DBH size classes was similar. After the fire, patterns of tree mortality differed in burned and unburned plots, with burned plots suffering significantly higher mortality in the first year post-fire (25% as compared with the unburned 11%). This pattern of higher mortality in the burned plots continued through 2001, with burned plots showing mortality rates triple that of the unburned plots (3.6–6.7% in burned as compared with 1.2–1.8% in unburned; O'Brien *et al.*, 2003). The patterns evident across the 5 years of this study, particularly the clear separation of burned and unburned plots in the first 3 years, are presumably a result of the immediate and drastic vegetation changes caused by the fire (Barlow *et al.*, 2002; Barlow & Peres, 2004b).

In Amazonia, Barlow & Peres (2004b) found that temporal change of bird community composition in burned areas away from that in unburned areas was correlated with tree mortality in burned plots. In our plots, it was evident that intensely burned areas had suffered greater tree mortality. By the time of our mist net study (2002), lightly burned areas contained many more large trees and a more complex understory than the monoculture of herbaceous plants or grasses in moderately and severely burned areas. Specifically, severely burned plots were either dominated by a dense thicket of herbaceous ginger (Zingiberaceae) or were open with a cover of the invasive 'alang-alang' grass *Cylin-drica imperata* that now covers much of Sumatra. Neither of

these two cover types appears to allow for the possibility of a return to the original forest structure. When tropical forests burn repeatedly, there can occur a state change from forest to grassland (Goldammer, 1999). This appears to be occurring in the severely burned plots in our study area, some of which had been subjected to fire before 1997. On the other hand, as more forest species colonize lightly damaged plots, these may progress toward a condition that more closely resembles unburned forest. Changes in the bird community that reflect this progression reinforce the notion that the underlying factor driving avian community composition is

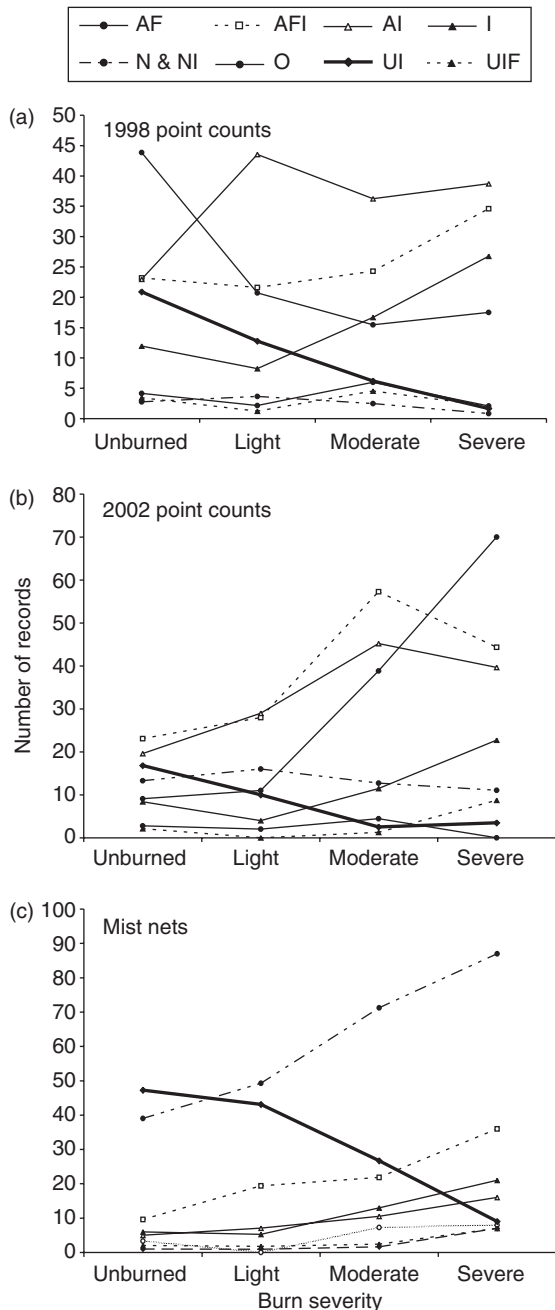
not disturbance *per se*, but the vegetation changes that this disturbance engenders (Petit *et al.*, 1999).

### Progressive change in unburned plots

Long-term studies suggest that it may take up to 100 years for forest bird communities to simply stabilize after *adjacent* disturbance (Brooks, Pimm & Oyugi, 1999; Castelletta *et al.*, 2000; Ferraz *et al.*, 2003). Well-understood causes include reduction in overall habitat, and edge effects (Murcia, 1995). All of our unburned plots were within 600 m of burned areas, and many were much closer, so these plots are likely to receive influxes of individuals from the burned area because of proximity alone (although Mantel's correlation indicated that the effect of spatial location on community composition is weak compared with the effect of the fire itself). Our observation of progressive change in adjacent unburned plots reinforces the idea that disturbances extend beyond the boundaries of their 'direct' effects.

We also note, however, that during the fires, surrounding areas were subjected to smoke and extremely high temperatures (up to 45°C at the Way Canguk WCS Research Station 2 km away; M. Kinnaird, pers. obs.). In the ensuing 5 years, tree mortality in unburned forest remained abnormally high and the structure and composition of the vegetation changed, possibly because of drought as well as fire (Sunarto, 2000). It follows that progressive changes in bird community composition in unburned plots are likely a response to more than just the indirect effects of being adjacent to severely burned areas, and environmental factors correlated with fire (such as drought). They are also a response to the extended direct effects of that burning.

Finally, it may not be safe to assume that vegetation (and therefore avian) communities in burned areas before the fires were exactly the same as those of unburned forest plots. BBSNP is located in a populous area where illegal logging and encroachment for agriculture have long been problematic (O'Brien & Kinnaird, 1996; Kinnaird *et al.*, 2003). The park is subject to natural disturbances such as storms, tree falls and elephants, as well as anthropogenic fire (O'Brien *et al.*, 1998). Within the area that burned in 1997, a



**Figure 5** Absolute abundance of individuals in each habitat type by feeding guild for point count and mist net data. Data are normalized for sampling effort. Because burn categories contain different numbers of plots and samples per year, we divided the number of individuals by the percentage of point counts or net hours undertaken, where the burn category with the least amount of effort is set equal to 100%, thus down-weighting numbers in plots with greater sampling effort. Point counts for 1998 and 2002 are shown in (a) and (b) respectively and mist net data in (c). Note the decline in understory insectivores (heavy black line) as burn severity increases. The only other guild to change significantly is arboreal frugivores, which are much more abundant in severely burned areas in 2002 than in 1998. [Guilds: arboreal frugivore (AF), understory insectivore-frugivore (UIF), understory insectivore (UI), omnivore (O), piscivore-insectivore (PI), nectivore and nectivore-insectivore (N & NI), insectivore (I), arboreal insectivore (AI), arboreal frugivore-insectivore (AFI).]

disproportionate amount was previously disturbed forest (O'Brien *et al.*, 1998; Sunarto, 2000). Samples taken before the forest burned would indicate whether bird species composition in unburned plots is recovering to a more 'original' state or if, like the burned areas, it continues to progress away from that of primary forest.

### Species and guilds most severely affected

Disturbance can enhance diversity by creating new microhabitats (Connell, 1978; Brawn, Robinson & Thompson, 2001; Molino & Sabatier, 2001). Avian species diversity in disturbed tropical forests has been both lower (Stouffer & Bierregaard, 1995; Sodhi, 2001; Barlow *et al.*, 2002) and higher (Dranzoa, 1998) compared with undisturbed areas. In Amazonia, Barlow & Peres (2004b) found little or no overlap in bird community composition between unburned and twice-burned forest. After the fire in BBSNP, some insectivores increased in burned areas, possibly due to an increase in insects infesting injured trees (Kinnaird & O'Brien, 1998). With the influx of generalist species discussed earlier, overall diversity became higher than in unburned areas even as forest specialists diminished.

An increase in local species richness is not necessarily beneficial if endemic or rare species decline. Studies of avian response to disturbance throughout the tropics have consistently found that certain groups, particularly large-bodied species, understory species and terrestrial insectivores, are especially vulnerable (Bierregaard & Lovejoy, 1989; Thiollay, 1992, 1997, 1999; Canaday, 1995; Stouffer & Bierregaard, 1995; Dranzoa, 1998; Marsden, 1998; Dale *et al.*, 2000; Bin Hussin & Francis, 2001; Barlow *et al.*, 2002; Pearman, 2002; Raman & Sukumar, 2002; Sekercioglu *et al.*, 2002; Barlow & Peres, 2004a). In South-east Asia, this general pattern holds for long-term effects of fragmentation in Singapore (Castelletta *et al.*, 2000) as well as shorter-term studies of disturbance in peninsular Malaysia and Sumatra (Johns, 1989; Thiollay, 1995).

The results of this study add to this body of literature. In the context of an increase in richness and abundance of birds in burned areas, we found a significant trend of declining understory insectivores along a gradient of fire severity. No other guild manifested a similar trend. Understory birds often have very specific habitat and foraging requirements (Canaday, 1995) and may not be able to adapt to changes in forest structure (Mason, 1996; Thiollay, 1997) which affect resource availability, dispersal, territoriality and predation (O'Brien *et al.*, 1998; Sekercioglu *et al.*, 2002). From a conservation perspective, the underlying reasons for the decline are less important than the fact that throughout the tropics, and in response to a wide variety of disturbance types, understory insectivores are among the first birds to decline.

Currently tropical forests are under pressure from multiple sources. The forest at BBSNP is no exception. If current rates of deforestation continue, the park area will be 70% agricultural lands by 2010 (Kinnaird *et al.*, 2003). Although in some areas disturbance may actually boost species rich-

ness, habitat specialists and disturbance-sensitive birds, which are typically of conservation concern, will be adversely affected. Fire, in particular, is known to be especially harmful to forest interior species (Barlow *et al.*, 2006). For endemic species, species with small ranges, and birds important to the commercial pet trade such as the white-rumped shama *Copsychus malabaricus*, loss of forest habitat and improved human access to disturbed areas where the birds persist may be devastating. With the amount of disturbed area growing all the time relative to primary forest, secondary specialists and edge-tolerant species are likely to replace interior forest specialists and endemics on a broad scale, leading to an overall decline in species diversity.

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## Supplementary material

The following material is available for this article online:

**Appendix S1** Family, genera, species and guild of birds identified during mist netting and variable circular point count surveys in the WCS/PHKA Way Canguk Research Area, BBSNP 1997–2002.

This material is available as part of the online article from <http://www.blackwell-synergy.com>