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BIRD SPECIES AND TRAITS ASSOCIATED WITH LOGGED AND UNLOGGED FOREST IN BORNEO

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Abstract. The ecological consequences of logging have been and remain a focus of considerable debate. In this study, we assessed bird species composition within a logging concession in Central Kalimantan, Indonesian Borneo. Within the study area (~196 km^2) a total of 9747 individuals of 177 bird species were recorded. Our goal was to identify associations between species traits and environmental variables. This can help us to understand the causes of disturbance and predict whether species with given traits will persist under changing environmental conditions. Logging, slope position, and a number of habitat structure variables including canopy cover and liana abundance were significantly related to variation in bird composition. In addition to environmental variables, spatial variables also explained a significant amount of variation. However, environmental variables, particularly in relation to logging, were of greater importance in structuring variation in composition. Environmental change following logging appeared to have a pronounced effect on the feeding guild and size class structure but there was little evidence of an effect on restricted range or threatened species although certain threatened species were adversely affected. For example, species such as the terrestrial insectivore *Argusianus argus* and the hornbill *Buceros rhinoceros*, both of which are threatened, were rare or absent in recently logged forest. In contrast, undergrowth insectivores such as *Orthotomus atrogularis* and *Trichastoma rostratum* were abundant in recently logged forest and rare in unlogged forest. Logging appeared to have the strongest negative effect on hornbills, terrestrial insectivores, and canopy bark-gleaning insectivores while moderately affecting canopy foliage-gleaning insectivores and frugivores, raptors, and large species in general. In contrast, undergrowth insectivores responded positively to logging while most understory guilds showed little pronounced effect. Despite the high species richness of logged forest, logging may still have a negative impact on extant diversity by adversely affecting key ecological guilds. The sensitivity of hornbills in particular to logging disturbance may be expected to alter rainforest dynamics by seriously reducing the effective seed dispersal of associated tree species. However, logged forest represents an increasingly important habitat for most bird species and needs to be protected from further degradation. Biodiversity management within logging concessions should focus on maintaining large areas of unlogged forest and mitigating the adverse effects of logging on sensitive groups of species.

Key words: bird species composition; environmental variation; Indonesia; Kalimantan; logging; ordination; redundancy analysis (RDA); RLQ analysis; spatial variation.

Introduction

The impact of human-induced habitat modification on tropical rainforests is an issue of major concern (Andersen 1999, Jepson et al. 2001, Summerville and Crist 2002), particularly in Southeast Asia, which harbors among the most diverse and most threatened rainforests in the world (Harrison 2000, Myers et al. 2000, Jepson et al. 2001). Borneo, the second largest tropical island in the world and home to some 358 bird species (MacKinnon and Phillipps 1993), is exemplary in this respect. As elsewhere in the tropics, the rainforests of Borneo have been logged to supply international demand for timber. The federal timber industry is a dominant factor in Borneo, which is unique due to the high stocking and commercial value of its dipterocarp forests. Over the last 20 years exports from Borneo alone have exceeded all wood exports from tropical Africa and Latin America combined (Hamer et al. 2003, Curran et al. 2004). At present, Borneo still harbors one of the

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last large stands of relatively intact forest within the Sundaland biodiversity hotspot. However, the rainforests of Borneo are severely threatened and lowland forests in particular are disappearing at an alarming rate (Jepson et al. 2001).

At present there is considerable debate over the impact of logging on forest diversity (Jepson et al. 2001, Putz et al. 2001, Dunn 2004), much of which is related to the fact that rainforest communities are in general characterized by losing few, if any, species as a result of logging, although there is often a marked impact on community composition (Johns 1996, Cannon et al. 1998, Willott et al. 2000, Lewis 2001, Cleary 2003, 2004, but see Thiollay 1992, 1997). Variation in composition may be a result of patterns of dispersal or due to the spatial arrangement of environmental conditions. Logging is known to severely affect the forest environment (Johns 1992, Cannon et al. 1998, Kinnaird and O'Brien 1998, Hamer et al. 2003). Similar communities in adjacent habitats may be a result of spatial or environmental processes or a function of both. Separating the contribution of space and the contribution of environment to patterns of community similarity is essential for understanding the mechanisms structuring communities across landscapes and for designing and placing conservation refugia (Plotkin and Muller-Landau 2002, Spencer et al. 2002, Tuomisto et al. 2003, Legendre et al. 2005). Patterns of recovery following logging will depend on the relative importance of spatial (patterns of dispersal) vs. environmental (the spatial arrangement of disturbed and undisturbed forest patches) processes in structuring communities.

Barring random dispersal events to unsuitable habitat, the occurrence of a given species in a habitat patch will depend on the fit between its traits and the environmental conditions of the habitat patch in question. Niche theory predicts that species will apportion resources among themselves and that their biological characteristics will determine their relative locations in the ecosystem with species exhibiting maximum abundances in sites with optimal environmental conditions (Legendre et al. 1997). From a conservation perspective, understanding relationships between environmental conditions and key species traits can help us to understand which traits are associated with increased sensitivity to disturbance (Ribera et al. 2001).

Despite the large number of studies addressing logging, few have focused on which ecological traits are associated with shifts in composition following logging (but see Jones et al. 2001). The physical effects of selective logging on tropical rainforests have, however, been well documented (Cannon et al. 1994, Johns 1996). These effects include an opening of the canopy, followed by mass germination of predominantly pioneer tree species and lianas, creating dense undergrowth (Heydon and Bulloh 1997). Because of structural habitat changes following logging, concomitant changes are expected in species with traits adapted to climax or disturbed conditions. Primary unlogged forests, for example, are generally characterized by having a well-developed canopy and sparse ground cover (Jones et al. 2001). It is intuitive then that species largely restricted to canopy or terrestrial strata should exhibit greater sensitivity to logging-induced disturbance. In addition, logging has been shown to affect fruit production (Chapman and Chapman 1997); frugivores will therefore probably be adversely affected. Numerous studies have noted the sensitivity of insectivores and restricted range species to disturbances such as logging (Kattan et al. 1994, Canaday 1996, Renjifo 1999, Castelleta et al. 2000, Lehtonen et al. 2001, Lewis 2001, Charrette et al. 2006, Cleary and Mooers 2006). Finally, globally threatened (red listed) species may be expected to respond negatively to logging-induced disturbance.

In this study bird assemblages were assessed within a rainforest in Central Kalimantan province, Indonesian Borneo, located within the Sundaland biodiversity hotspot (Myers et al. 2000). The aims of this study were to (1) assess to what degree variation in composition could be explained by spatial variables, environmental variables, or covariation of both in relation to logging and (2) test for significant associations between bird species traits and environmental variables, particularly in relation to logging activity. We related feeding guild (foraging diet and position), global distribution, conservation status, and size to logging and other environmental variables. All of these traits have been previously found to influence species response to disturbance and local extinction (Castelleta et al. 2000, Lips et al. 2003, Henle et al. 2004).

MATERIAL AND METHODS

Study area

The research area was located in the large (~300 000 ha) Kayu Mas concession in the Indonesian province of Central Kalimantan (0′18″ S, 112′23″ E), previously described by Asdak et al. (1998), Cleary (2003), and Cleary et al. (2005). The concession consisted of a mosaic of forest types that were unlogged or had been logged once. Logging in the area was selective, with a cutting cycle of 35 years, extracting mainly dipterocarp tree species. The research area is at the headwaters of the Mentaya river, ~175 km to the north-northwest of the town of Sampit in Central Kalimantan province, Indonesia. The topography is undulating, and the altitude generally lies between 100 and 400 m above sea level. The forest in the area is classified as lowland dipterocarp hill forest. Actual slopes in the area tend to be gentle but can exceed 35%. The whole area was selected as a research area of this and a number of other studies because it was deemed representative of the natural vegetation and regional topography of the inland, upstream hill area in Borneo that has hitherto received low priority for scientific study (Asdak et al. 1998). Mean upper tree layer height is in the range of 40–55 m. The undergrowth consists of small saplings and poles of 2–5 m. Dominant tree families in the area include Dipterocarpaceae, Caesalpinaceae, Euphorbiaceae, and Myrtaceae. Borneo is located in the intertropical convergence zone, and the climate experiences influences from both the east and west monsoons. Rainfall is somewhat seasonal, with the maximum occurring in November (305 mm) and the minimum in July (154 mm; Asdak et al. 1998).

Sampling

Thirty-seven sites (Appendix A) were sampled from June to October 1997 and July to October 1998 across the following three contiguous areas; unlogged primary forest (P, 14 sites), forest logged in 1993–1994 (L93, 13 sites), and forest logged in 1989–1990 (L89, 10 sites) over a total survey area of ~196 km^2. Minimum/maximum distances between pairs of sites were 178/2919 m in P, 588/5158 m in L89, and 165/6338 m in L93. Elevation of the study sites ranged from 100 to 400 m with a mean ± SD of 236 ± 73 m. The primary unlogged forest area (P) formed the central core of the study area; L93 was located to the north of the primary area and L89 to the south. Survey sites (3 ha, 300 × 100 m each) were designated a priori to lower, middle, and upper slope habitats on a digital elevation map of the area based on an environmental classification of slope position (B. Mackey, *unpublished data*); the sites were subsequently located in the field and geo-referenced using a global positioning system (Garmin 12 XL; Garmin International, Olathe, Kansas, USA). The altitude and elevation were recorded in each sample site in addition to a series of quantitative and categorical habitat structure variables.

Birds were surveyed using spot mapping based on bird calls and visual observations (Terborgh et al. 1990, Robinson et al. 2000, Clergeau et al. 2001). Locations of all individuals seen or heard were recorded. Sound recordings of individual species from each site were retained for reference. In order to provide even coverage, two parallel 300-m linear transects (50 m apart) were established in each site. Each site was sampled twice, between 06:00 and 13:00 hours, the principal period of activity for most species. If this period was interrupted by rain the survey was continued the next day at the time when the rain interrupted the previous days' recording. In this way it was possible to ensure that an equal amount of time was spent at each site during the same period of avian activity. The minimum number of birds sampled per site was 130 individuals. All individuals were identified to genus level and all except 11 to species level. The remaining 11 individuals belonged to the genera *Ducula* ($n = 1$) and *Pycnonotus* ($n = 10$). Species of special conservation concern were identified using the Red Data Book of globally endangered Asian bird species (Collar et al. 2001; Appendix B).

A number of traits for each species were noted. These included feeding guild, i.e., vertical foraging position and diet, global distribution, conservation status, and size (Appendix B). All species traits were categorical variables. The feeding guilds included raptors, canopy bark-gleaning insectivores, canopy foliage-gleaning frugivores, canopy foliage-gleaning insectivore/frugivores, canopy foliage-gleaning insectivores, canopy nectarivores, canopy sallying insectivores, frugivore/carnivores, terrestrial insectivores, understory bark-gleaning insectivores, understory foliage-gleaning insectivore/frugivores, understory foliage-gleaning insectivores, undergrowth insectivores, understory nectarivores, understory sallying insectivores, and understory sallying substrate insectivores. Note all nectarivores fed on other resources (insects and/or fruit) in addition to nectar. Global distribution was defined as Sundaic endemic or non-endemic. Conservation status was defined as threatened (including the red list categories "threatened" and "near threatened") or not threatened. Finally, species were classified with respect to wing size as very small (<10 cm), small (10 cm $< x <$ 20 cm), medium (20 cm $< x <$ 30 cm), large (30 cm $< x <$ 60 cm), and very large (>60 cm). Data on distribution and wing size were obtained from MacKinnon and Phillipps (1993).

Analyses

Community composition was assessed with constrained ordination, i.e., redundancy analysis (RDA), using CANOCO for Windows 6.1 (ter Braak 1986, ter Braak and Smilauer 1998). Input for the RDA consisted of $\log_{10}(x + 1)$ species abundance data that were first transformed with the program TRANSFORMATION (*available online*).[7] Through this transformation the species abundance data is adjusted so that subsequent analyses, such as principal components analysis (PCA) and RDA, preserve the chosen distance among objects (sample sites). The species abundance data were transformed because of the inherent problems of the Euclidean-based distance metric (in standard PCA) for community data (see Legendre and Gallagher 2001). In the present case, the Hellinger distance (Rao 1995) was used, which gave very good results in a comparison of various distance metrics (Legendre and Gallagher 2001). In particular, the Hellinger distance gave low weights to rare species, was monotonically related to the geographic distance along a model gradient, and reached an asymptote for sites with no species in common. It also produced little "horseshoe effect" or inward folding of sites at opposite ends of the gradient, in ordinations (Legendre and Gallagher 2001). Redundancy analysis arranges sites and species in a multidimensional space whereby the axes are constrained to be linear combinations of environmental variables (Ohmann and Spies 1998). In RDA, the amount of species variation explained by the explanatory variables, or the total variation explained (TVE), is the sum of all constrained

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[7] ⟨http://www.bio.umontreal.ca/casgrain/en/labo/transformations.html⟩

eigenvalues divided by the total variation (TV) in the species data.

The environmental data set used in the RDA consisted of the following variables: elevation, slope position (lower [1], middle [2], and upper [3]), logging (P [1], L89 [2], and L93 [3]) and the $\log_{10}(x + 1)$-transformed mean values of 33 habitat structure variables assessed in six subplots per plot (Appendices C and D). These included the volume of fresh dead wood, dead wood with sound wood but flaking bark, dead wood with sound wood but no bark, dead wood with rotting wood but firm, dead wood with wood rotten and soft, fallen dead wood, and standing dead wood; total volume of dead wood; abundance of nonwoody lianas, small woody lianas (stem diameter < 5 cm), large woody lianas (stem diameter > 5 cm), epiphytes, bryophytes, ground cover of seedlings, herbs, ferns, grasses, small woody debris (dead wood <10 cm diameter), mesophyll (from 4500 to 20 000 mm^2) leaf litter, notophyll (from 2000 to 4500 mm^2) leaf litter, and microphyll (up to 2000 mm^2) leaf litter; mean litter depth; dbh (diameter at breast height); tree height; bifurcation index; crown depth; crown radius; density of short (<5 m) saplings (<5 cm dbh), tall (>5 m) saplings (<5 cm dbh), short (<10 m) poles (5–10 cm dbh), tall (>10 m) poles (5–10 cm dbh), and trees (>10 cm dbh); and canopy cover. The importance of space in explaining variation in composition was assessed by supplementing the spatial Universal Transverse Mercator (UTM) coordinates (easting "x" and northing "y") with all the terms of a bi-cubic trend surface (i.e., x, y, x^2, xy, y^2, x^3, x^2y, xy^2, and y^3; see Borcard et al. 1992).

Within CANOCO a forward selection procedure using a Monte Carlo permutation test (999 permutations) and the full model option (ter Braak and Smilauer 1998) was used to test environmental and spatial variables for significance (ter Braak and Verdonschot 1995). In the results the conditional effects of environmental and spatial variables on composition (λ_A) are presented in addition to P values from the Monte Carlo test. The conditional effects (λ_A) represent the additional fit or increase in eigenvalue with each consecutively selected environmental variable. Only variables with $P < 0.1$ were included in the final model. The significance of the association between the species and environmental data sets was also assessed using Monte Carlo simulations (999 permutations) of constrained ordination scores against environmental variables. Variance partitioning was subsequently used to partition the spatial variation in composition into variation only explained by spatial variables, variation only explained by environmental variables, and variation explained by covariation of environmental and spatial variables. A quantitative variance partitioning technique, described in detail by Borcard et al. (1992), Økland (2003), and Legendre et al. (2005), was used on results of separate partial RDAs. Monte Carlo tests were used to assess the significance of spatial variables only and environmental variables only in structuring bird assemblages.

Species traits were directly linked to environmental variables with a three-table ordination method known as RLQ analysis (Dolédec et al. 1996, Ribera et al. 2001, Dray et al. 2002). RLQ analysis is an extension of co-inertia analysis: "R" is a table of p environmental variables at m locations; "L" is a contingency table representing the abundance of k species at m locations; and "Q" is a table of k species with n biological traits (see Supplement). With RLQ analysis both traits and environmental conditions affected by disturbance, as well as their interrelationships, can be assessed (Dolédec et al. 1996, Ribera et al. 2001, Dray et al. 2002, Hausner et al. 2003). The method has been previously used to relate bird species traits to land use in northern European birch forests (Hausner et al. 2003) and to test whether morphology and life history traits of ground beetles could be related to the main underlying axes of environmental variability of their habitats in Scotland (Ribera et al. 2001).

Three separate ordinations of the R (environmental variables), L (species composition), and Q (species trait) tables were performed prior to the co-inertia analysis. First, the species abundance table containing the $\log_{10}(x + 1)$-transformed number of individuals in each species occurring at each site was analyzed by correspondence analysis (CA), an eigenanalysis approach that provides a joint scaling of sites and species scores. Only species with five observations or more were included in the analyses due to the sensitivity of correspondence analysis to "rare" species (Lesica and Cooper 1999). We also excluded *Ceyx rufidorsa* and *Chalcophaps indica* because they were the only species (≥ 5 observations) in the "miscellaneous insectivore" and "terrestrial frugivore" feeding guilds. The sites and species scores (or coordinates) were used to link the R and Q tables, as sites are shared by the R and L tables and species are shared by the Q and L tables (Ribera et al. 2001, Dray et al. 2002, Hausner et al. 2003, Choler 2005). Next, the relationship between sites and environmental attributes (i.e., R table) was analyzed. For the quantitative set of variables, PCA was applied, using weights obtained with the correspondence analysis of species, thereby linking the R to the L table. The final step in this initial procedure was the analysis of the Q table of categorical species traits with row weights obtained with the correspondence analysis of species using multiple correspondence analysis (MCA; Tenenhaus and Young 1985).

After these three steps a single inertia analysis was performed on the cross-matrix of R, L, and Q. The site scores in the R table constrain the site scores in the L table, and the species scores in the Q table constrain the species scores in the L table. Within these constraints, co-inertia analysis selects axes that maximize covariance between the R and Q tables. As a result, the environmental attributes are directly related to species traits

(Dolédec and Chessel 1994). RLQ analysis is a symmetric analysis, in the sense of finding scores that are optimally related to each table, without emphasizing environmental variables or species traits. Scores are a compromise between maximizing the correlation and explaining the variation in each table. The significance of the relationship between the environmental attributes (R) and species traits (Q) was investigated with a Monte Carlo permutation test (Dolédec et al. 1996). The results of 1000 random permutations between the R and Q tables were compared to observed values. The number of random permutation values that were more than or equal to this observed value can be considered to be the best estimation of its probability and a measure of the significance level of the analysis. All analyses were carried out using the ADE4 software package within R (*available online*).[8,9]

RESULTS

A total of 177 ($n = 9747$) bird species (64 ± 11 species per sample site; mean ± SD) were recorded across all three study areas belonging to 30 families and 103 genera. Total species richness pooling sites from all three study areas was estimated at 184 species using nonparametric richness estimators (incidence-based coverage estimator [ICE] and Chao2; Colwell 2000). Richness estimates of the sample sites varied from 154 species (ICE and Chao2) in P to 157 (Chao2) to 158 (ICE) species in L89 and 156 (ICE) to 157 species (Chao2) in L93 (Appendix E).

Relating species to environmental variables

In the RDA, the sum of all constrained (canonical) eigenvalues was 0.475. The environmental and spatial parameters thereby explained 47.5% of the variation in the data set of which 10.8% ($P = 0.075$) was due to spatial variables only, 10.3% due to covariance of spatial and environmental variables, and 26.4% ($P = 0.003$) due to environmental variables only. The eigenvalues of the first four axes of the ordination were 0.119, 0.050, 0.046, and 0.043 for the first, second, third, and fourth axes, respectively. The species–environment correlations of the first four axes were high (range 0.936–0.956), indicating a strong association between the species matrix and the environmental matrix. A Monte Carlo test showed the first axis, and trace, to explain highly significant amounts of variation in community structure ($P < 0.001$ for both tests).

Significant environmental variables selected with a Monte Carlo forward selection procedure included logging ($\lambda_A = 0.11$, $P < 0.001$), slope position ($\lambda_A = 0.04$, $P < 0.001$), nonwoody liana abundance ($\lambda_A = 0.03$, $P = 0.002$), canopy cover ($\lambda_A = 0.04$, $P = 0.009$), fern cover ($\lambda_A = 0.03$, $P = 0.026$), tree height ($\lambda_A = 0.03$, $P = 0.066$), large liana abundance ($\lambda_A = 0.03$, $P = 0.096$), notophyll-sized leaf litter cover ($\lambda_A = 0.03$, $P = 0.091$), and mean litter depth ($\lambda_A = 0.03$, $P = 0.096$). Significant spatial factors included x ($\lambda_A = 0.04$, $P < 0.001$), y ($\lambda_A = 0.07$, $P < 0.001$), y^3 ($\lambda_A = 0.07$, $P < 0.001$), and x^2 ($\lambda_A = 0.03$, $P < 0.001$). Ordinations of the constrained RDA using environmental variables only are presented in Figs. 1 and 2, whereby arrows represent significant environmental variables superimposed onto the ordination; the length of the arrow indicates the correlation between the environmental variable and the ordination axis.

Species associated with logged forest (negative axis 1 values) include *Orthotomus atrogularis*, *Cacomantis merulinus*, *Orthotomus sericeus*, *Macronous ptilosus*, *Anthreptes malacensis*, and *Phylloscopus borealis*, whereas species associated with unlogged forest (positive axis 1 values) include *Pitta guajana*, *Reinwardtipicus validus*, *Celeus brachyurus*, *Pityriasis gymnocephala*, *Anorrhinus galeritus*, *Pitta granatina*, *Argusianus argus*, *Gracula religiosa*, *Mulleripicus pulverulentus*, *Buceros rhinoceros*, and *Pycnonotus plumosus* (Fig. 1). Species associated with large lianas and a deep litter layer (negative axis 2 values) include *Cacomantis sonneratii*, *Anthreptes simplex*, *Phaenicophaeus diardi*, *Hypothymis azurea*, *Ficedula mugimaki*, and *Copsychus saularis*, whereas species associated with closed-canopy conditions (positive axis 2 values) include *Tephrodornis gularis*, *Aegithina tiphia*, *Cyornis superbus*, and *Philentoma pyrhopterum* (Fig. 1). Species associated with lower slope habitats (negative axis 3 values) include *Enicurus ruficapillus*, *Anorrhinus galeritus*, *Eurylaimus javanicus*, *Megalaima australis*, and *Phaenicophaeus chlorophaeus*, whereas species associated with upper slope habitats (positive axis 3 values) include *Stachyris erythroptera*, *Pityriasis gymnocephala*, and *Prionochilus percussus* (Fig. 2). Finally, species associated with decaying dead wood, fern abundance, and closed canopy conditions (negative axis 4 values) include *Arachnothera robusta*, *Anthreptes singalensis*, *Aceros undulatus*, *Pitta granatina*, *Megalaima chrysopogon*, *Buceros rhinoceros*, *Argusianus argus*, and *Anorrhinus galeritus*, whereas species associated with tree density, notophyll- and microphyll-sized leaf litter cover, and litter depth (positive axis 4 values) include *Irena puella*, *Hemiprocne comata*, *Picus puniceus*, *Cuculus micropterus*, and *Hemipus hirundinaceus* (Fig. 2).

Relating species traits to environmental variables

The RLQ analysis revealed a highly significant (permutation test; $P < 0.001$) association between environmental variables and species traits. We only consider the first two RLQ axes, which together explained 77% of variance in the analysis. Because the RLQ analysis represents the partial ordination of the environmental characteristics, the species abundances, and the species traits, the proportion of variance attributed to each matrix was compared to that resulting from their separate analyses; the coordinates of the projections of inertia axes onto the co-inertia axes obtained are presented graphically in Fig. 3. The first

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[8] ⟨http://pbil.univ-lyon1.fr/ADE-4/⟩

[9] ⟨http://www.r-project.org/⟩

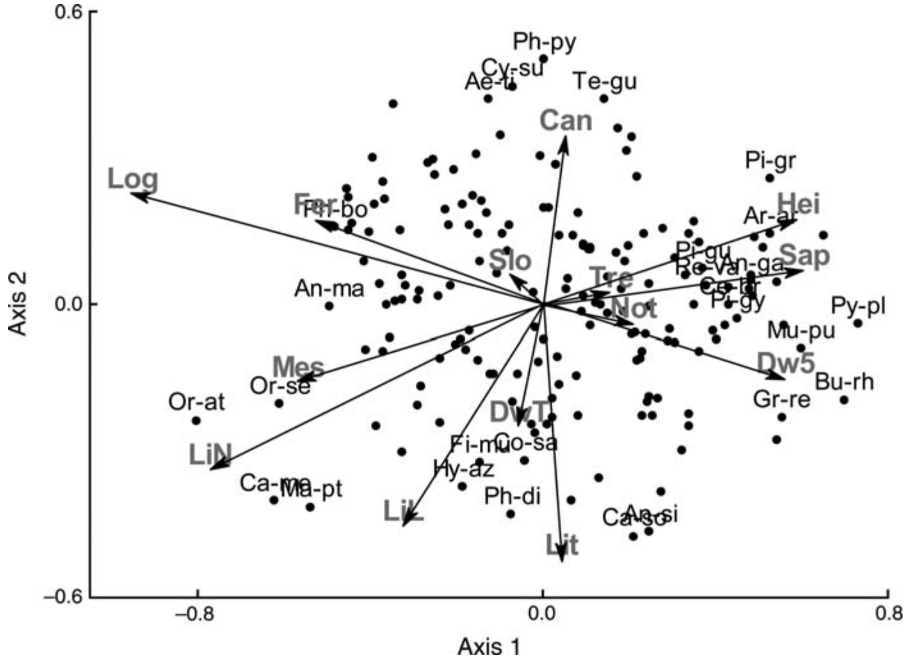

FIG. 1. Ordination based on redundancy analysis (RDA) showing the first and second axes. The biplot shows species and environmental variables. Selected species are indicated by four-letter codes. Arrows represent significant environmental factors: Log, logging; Slo, slope position; Fer, fern cover; LiN, nonwoody liana abundance; Lit, litter depth; Hei, tree height; LiL, large liana abundance; Can, canopy cover; Not, notophyll-sized leaf litter cover. Additional supplementary environmental parameters that did not influence the ordination are shown. These include: Sap, tall sapling abundance; Tre, tree density; Dw5, volume of rotten dead wood; DwT, total volume of dead wood; and Mes, cover of mesophyll leaf litter. The orthogonal projection of a species point onto an environmental arrow represents the approximate center of the species distribution along a particular environmental gradient. Species abbreviations are: Ae-ti, *Aegithina tiphia*; An-ga, *Anorrhinus galeritus*; An-ma, *Anthreptes malacensis*; An-si, *Anthreptes simplex*; Ar-ar, *Argusianus argus*; Bu-rh, *Buceros rhinoceros*; Ca-me, *Cacomantis merulinus*; Ca-so, *Cacomantis sonneratii*; Ce-br, *Celeus brachyurus*; Co-sa, *Copsychus saularis*; Cy-su, *Cyornis superbus*; Fi-mu, *Ficedula mugimaki*; Gr-re, *Gracula religiosa*; Hy-az, *Hypothymis azurea*; Ma-pt, *Macronous ptilosus*; Mu-pu, *Mulleripicus pulverulentus*; Or-at, *Orthotomus atrogularis*; Or-se, *Orthotomus sericeus*; Ph-bo, *Phylloscopus borealis*; Ph-di, *Phaenicophaeus diardi*; Ph-py, *Philentoma pyrhopterum*; Pi-gr, *Pitta granatina*; Pi-gu, *Pitta guajana*; Pi-gy, *Pityriasis gymnocephala*; Py-pl, *Pycnonotus plumosus*; Re-va, *Reinwardtipicus validus*; Te-gu, *Tephrodornis gularis*.

axis of the RLQ analysis (eigenvalue, 0.072; variance explained, 65.1%; covariance, 0.268; correlation, 0.172) accounted for 91.4% (6.64/7.26), 75.6% (0.365/0.483), and 42.8% (0.172/0.402) of the variance in the separate analyses of environmental variables (eigenvalue, 7.25; variance explained, 18.43%), traits (eigenvalue, 0.483; variance explained, 6.96%), and species composition (eigenvalue, 0.172; variance explained, 13.20%) respectively. The second axis of the RLQ analysis (eigenvalue, 0.013; variance explained, 11.9%; covariance, 0.114; correlation, 0.095) accounted for 90.2% (4.71/5.22), 68.6% (0.311/0.454), and 34.3% (0.095/0.276) of the variance in the separate analyses of environmental variables (eigenvalue, 5.22; variance explained, 13.09%), traits (eigenvalue, 0.454; variance explained, 5.93%), and species composition (eigenvalue, 0.276; variance explained, 7.25%), respectively. Due to the fact that the RLQ analysis rearranges species and site scores to maximize the covariance between the environmental variables and species traits, the L table will usually account for less variance than either the R or Q tables.

Along axis 1, recently logged forest (L93) with a high abundance of small saplings, nonwoody and small woody lianas, mesophyll leaf litter, fern cover, and dead wood state 3 contained species with a different set of traits than unlogged forest (P), which was associated with abundant tall saplings and poles, greater crown depth, higher canopy height, and a larger volume of rotten and soft dead wood (Figs. 4 and 5). Older logged forest had a habitat structure and bird composition that was intermediate between unlogged and older logged forest (Appendices F and G). Note that for axis 1, feeding guild and size class were the most powerful explanatory factors, whereas the axis did not separate species based on conservation status (threatened vs. unthreatened) or distribution (endemic vs. non-endemic). Undergrowth insectivores exhibited the most pronounced preference for logged forest while canopy foliage-gleaning insectivores and frugivores, raptors, large species, and particularly bark-gleaning insectivores, terrestrial insectivores, frugivore/carnivores, and very large species preferred unlogged forest (Fig. 6). Total abundances of bird guilds based on vertical

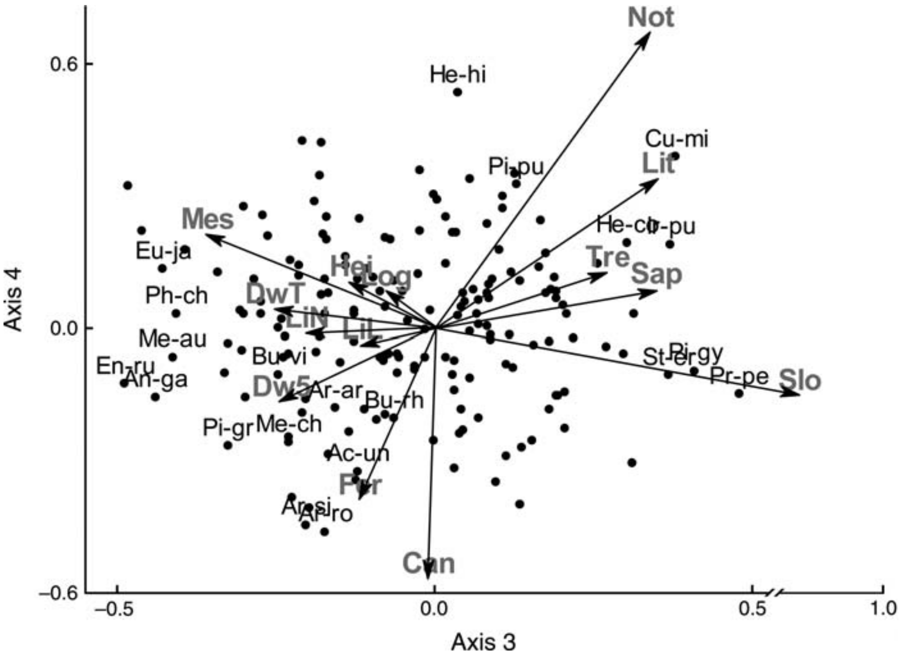

FIG. 2. Ordination based on redundancy analysis showing the third and fourth axes. Environmental factors are as in Fig. 1. Species abbreviations are: Ac-un, *Aceros undulatus*; An-ga, *Anorrhinus galeritus*; Ar-ar, *Argusianus argus*; Ar-ro, *Arachnothera robusta*; Ar-si, *Anthreptes singalensis*; Bu-rh, *Buceros rhinoceros*; Bu-vi, *Buceros vigil*; Cu-mi, *Cuculus micropterus*; En-ru, *Enicurus ruficapillus*; Eu-ja, *Eurylaimus javanicus*; He-co, *Hemiprocne comata*; He-hi, *Hemipus hirundinaceus*; Ir-pu, *Irena puella*; Me-au, *Megalaima australis*; Me-ch, *Megalaima chrysopogon*; Ph-ch, *Phaenicophaeus chlorophaeus*; Pi-gr, *Pitta granatina*; Pi-gy, *Pityriasis gymnocephala*; Pi-pu, *Picus puniceus*; Pr-pe, *Prionochilus percussus*; St-er, *Stachyris erythroptera*.

foraging position and diet also showed substantial differences among the study areas in line with results from the RLQ analysis (Appendix H). In particular the total abundances of bark-gleaning insectivores, terrestrial insectivores, and frugivore/carnivores were lower in both logged study areas than unlogged forest while canopy foliage-gleaning insectivores and frugivores only showed reduced abundance in the most recently logged area.

Along axis 2 there was a gradient from habitat with closed canopy, high fern cover, and a high volume of fallen dead wood to habitat with a high density of tall saplings, tall poles, trees, notophyll- and microphyll-sized leaf litter, and a deep litter layer. Understory bark-gleaning insectivores were associated with areas with abundant dead wood and mesophyll leaf litter (an indicator of pioneer trees), whereas canopy sallying insectivores and canopy bark-gleaning insectivores were associated with high tree density, litter depth, and notophyll leaf litter cover. In addition to their association with unlogged forest frugivore/carnivores, very large species and terrestrial insectivores were associated with

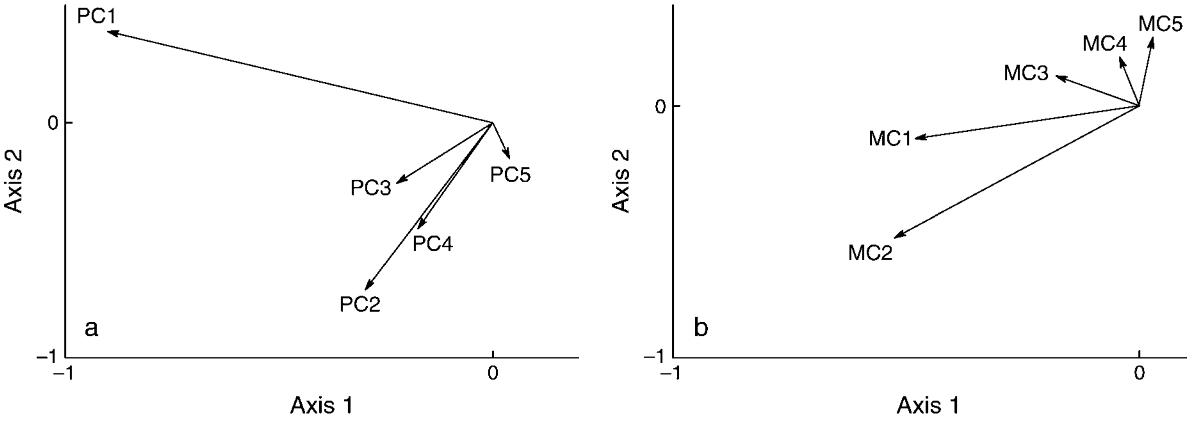

FIG. 3. Joint ordination of (a) principal components analysis (PCA) axes and (b) multiple correspondence analysis (MCA) axes with the first two RLQ axes.

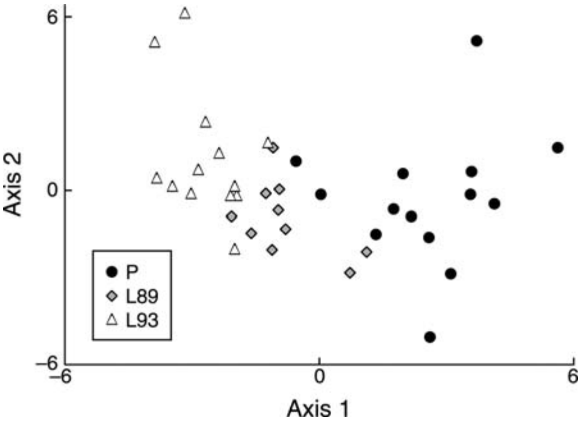

FIG. 4. Row scores of sites for the first and second RLQ axes. Symbols indicate sites from unlogged primary forest (P), older logged forest (L89), and recently logged forest (L93).

habitat containing a high volume of recently fallen and rotten dead wood and closed canopy conditions, whereas canopy bark-gleaning insectivores seemed to prefer areas with high densities of tall saplings, poles, and trees and a high cover of microphyll leaf litter (Fig. 5).

DISCUSSION

Spatial and particularly environmental variables separately explained substantial amounts of variation in community composition, but including both sets of variables gave best results. The importance of space contrasts with a previously published study in which distance had very little explanatory power for variation in bird community similarity (Cleary et al. 2005). This discrepancy is probably due to the fact that the present study used a more complex set of spatial predictor variables and the significant variables selected by the Monte Carlo forward-selection procedure clearly showed that variation in composition with space was nonlinear in nature. The importance of space indicates that dispersal limitation is playing a significant role in structuring the bird assemblage. However, Cleary et al. (2005) and the present study confirm that deterministic ecological processes are of greater importance in structuring spatial variation observed in the bird assemblage than purely spatial processes. Therefore spatial contrasts in vegetation, particularly in relation to disturbance such as logging, and variation in topography (slope position) are influencing distributions of essential resources for bird species including food, shelter, and territorial space. This relationship is further confirmed by the significant relationship between environment and species traits.

Trait variation was significantly related to logging-induced variation in habitat structure variables such as sapling density, dead wood abundance, liana abundance, fern ground cover, and canopy height. In other tropical rainforests, increases (for example, in liana and fern abundance) have been reported following logging

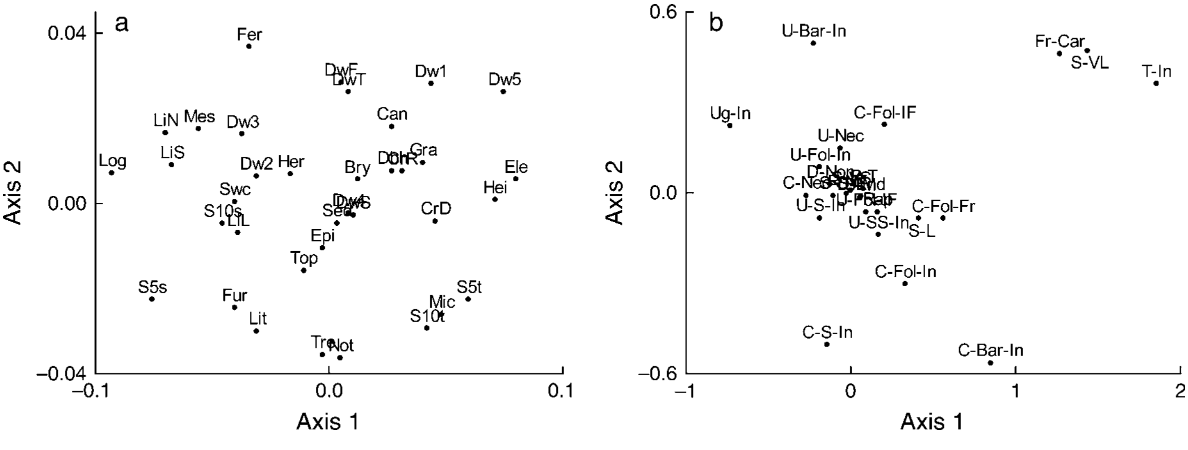

FIG. 5. The RLQ scores of (a) environmental variables and (b) species traits. The abbreviations for the environmental variables are: Bry, bryophytes; Can, canopy cover; CrD, crown depth; CrR, crown radius; Dbh, diameter at breast height; Dw1, dead wood, state 1; Dw2, dead wood, state 2; Dw3, dead wood, state 3; Dw4, dead wood, state 4; Dw5, dead wood, state 5; DwF, dead wood, fallen; DwS, dead wood, standing; DwT, dead wood, total; Ele, elevation; Epi, epiphytes; Fer, ferns; Fur, bifurcation index; Gra, grasses; Hei, tree height; Her, herbs; LiL, large woody lianas; LiN, nonwoody lianas; LiS, small woody lianas; Lit, litter depth; Log, logging; Mes, mesophyll leaves; Mic, microphyll leaves; Not, notophyll leaves; S10s, short poles; S10t, tall poles ; S5s, short saplings; S5t, tall saplings; Sed, seedlings; Swc, small woody chips; Slo, slope position; Tre, trees. The abbreviations for the species traits are: Rap, raptors; C-Bar-In, canopy bark-gleaning insectivores; C-Fol-Fr, canopy foliage-gleaning frugivores; C-Fol-IF, canopy foliage-gleaning insectivore/frugivores; C-Fol-In, canopy foliage-gleaning insectivores; C-Nec, canopy nectarivores; C-S-In, canopy sallying insectivores; Fr-Car, frugivore/carnivores; T-In, terrestrial insectivores; U-Bar-In, understory bark-gleaning insectivores; U-Fol-IF, understory foliage-gleaning insectivore/frugivores; U-Fol-In, understory foliage-gleaning insectivores; Ug-In, undergrowth specialist insectivores; U-Nec, understory nectarivores; U-S-In, understory sallying insectivores; U-SS-In, understory sallying substrate insectivores; D-End, endemics; D-Non, non-endemics; R-T, threatened; R-NT, not threatened; S-VS, very small; S-S, small; S-M, medium; S-L, large; S-VL, very large.

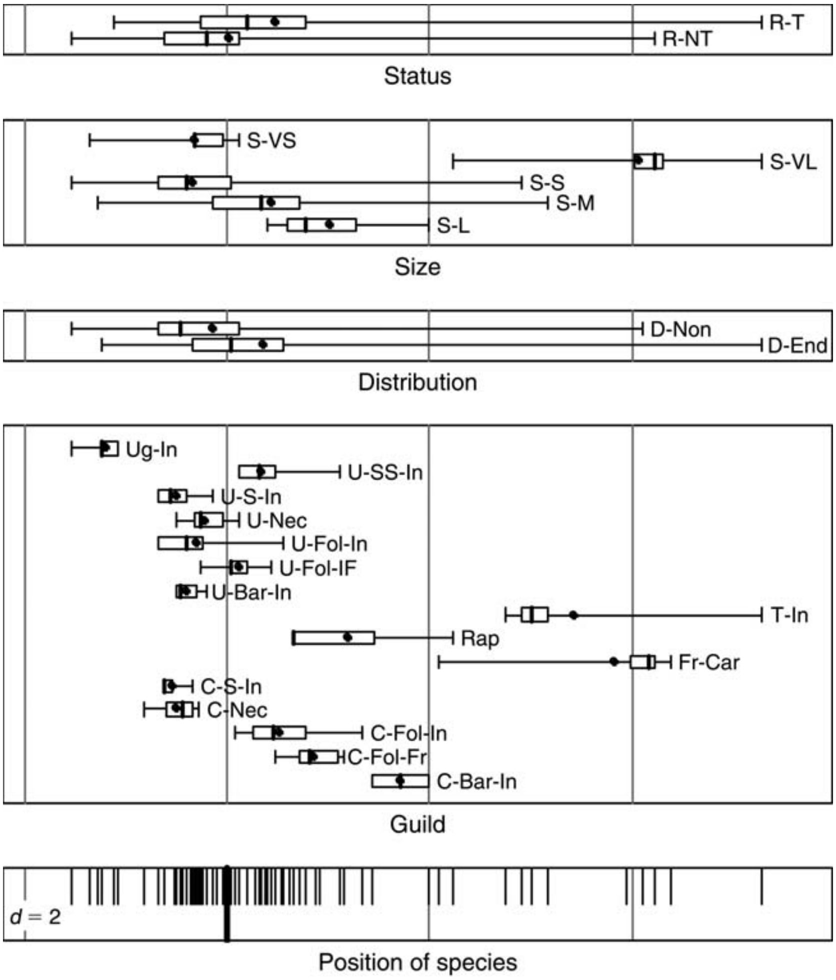

FIG. 6. Minimum and maximum (horizontal lines), quartiles (boxes), median (vertical lines), and mean (solid circles) values of species traits along the first RLQ axis. Small vertical lines at the bottom of the figure represent the position of species along the axis. The thick vertical line at the bottom of the figure corresponds with the value zero on the first axis. Values to the right of this line indicate a global preference for unlogged forest, and values to the left a preference for logged forest. See Fig. 5 for abbreviations of species traits. The abbreviation *d* represents the size of the grid lines with respect to the RLQ axis shown.

(Johns 1992, Cannon et al. 1998, Peres 1999, Schnitzer and Bongers 2002). Logging appeared to affect bird composition with respect to feeding guilds and size classes but had no pronounced effect on distribution classes or threatened status in contrast to expectations. In the same area, for example, restricted range butterflies were much more abundant in unlogged forest (Cleary and Mooers 2006).

In line with expectations we found that undergrowth insectivores preferred logged forest, whereas terrestrial insectivores and canopy guilds including canopy bark-gleaning insectivores, foliage-gleaning insectivores, foliage-gleaning frugivores, and foliage-gleaning insectivore/frugivores (but not canopy nectarivores or sallying insectivores) preferred unlogged forest. Understory guilds in general showed little pronounced preference for logged or unlogged forest. Undergrowth insectivores, however, revealed a particularly strong association with logged forest. Undoubtedly these species are responding to the marked increase in forest undergrowth (pioneer sapling density and the abundance of vine tangles) following logging (Slik 2004). In the present study, undergrowth insectivores consisted of thrushes, babblers, and warblers, of which the last (e.g., *Orthotomus atrogularis*, *Orthotomus ruficeps*, and *Orthotomus sericeus*) had the most pronounced preferences for recently logged forest (L93). In contrast canopy foliage-gleaning insectivores (e.g., the Bornean Bristlehead [*Pityriasis gymnocephala*] and the Green Iora [*Aegithina viridissima*]) and frugivores (e.g., the Hill Myna [*Gracula religiosa*] and Blue-eared Barbet [*Megalaima australis*]) were markedly more abundant in unlogged forest than logged forest. Various studies have noted the sensitivity of insectivores to disturbance (Kattan et al. 1994, Canaday 1996) but the present study indicates that insectivory alone is not a good indicator.

Clearly, the occurrence of a given species in a habitat patch will depend on the fit between its traits and the environmental conditions of the habitat patch in question. Importantly, previous studies over a diverse array of taxa have shown that vertical position, size, and specialization can influence how species respond to disturbances such as logging and are important predictors of extinction susceptibility (Ribera et al. 2001, Driscoll and Weir 2005). Some traits, however, can interact to produce disparate outcomes. In Colombia, for example, Renjifo (1999) found that terrestrial insectivores and large frugivores were highly extinction-prone due to forest fragmentation. Nectarivores, small frugivores, and aerial insectivores were, however, highly resilient, indicating that size and vertical foraging position interact with diet to determine responses to disturbance. Renjifo (1999) noted that terrestrial insectivores were particularly extinction-prone due to their difficulty in moving through matrix habitat and their vulnerability to feral predators. In Malaysia, many terrestrial bird species were entirely absent from logged forest, even after 12 years of regeneration, largely due to the effects of microclimatic changes on leaf litter microfauna; species absent included partridges (Phasianidae) and pittas (Pittidae) (Johns 1989). Additionally, many terrestrial species are physiologically unadapted to sun and often die within 15 min if left unattended in mist nets. This makes for very poor dispersers that are unable to cross large areas of open habitat (Lambert and Collar 2002). In the present study terrestrial insectivores such as *Argusianus argus* and *Pellorneum capistratum* were completely absent from recently logged forest while *Pitta granatina* was rare. Elsewhere in Borneo (Kayan Mentarang National Park) Nijman (1998) reported that *Argusianus argus* was most common in primary forest and progressively less common in old and young secondary forests. Pheasant densities were positively correlated with increasing tree diameter, height, furcation index, canopy cover, and increasing remoteness.

Most species that excavate tunnels in rotting tree stumps or termite mounds are sensitive to logging-induced disturbance. Although the availability of dead or dying trees may seem to increase with logging, they may not always provide a suitable substrate for many bird species (Lambert and Collar 2002). For example, although woody debris was relatively scarce in unlogged forest in comparison to logged forest, the woody debris in the logged forest was still relatively hard in comparison to unlogged forest in which the dead wood was generally soft and decayed and therefore more suitable to the needs of many bird species.

In addition to terrestrial insectivores, all four canopy bark-gleaning insectivores (the woodpeckers *Dryocopus javensis*, *Mulleripicus pulverulentus*, *Picus puniceus*, and *Reinwardtipicus validus*) were more abundant in unlogged forest than logged forest, whereas this was only the case for two (*Blythipicus rubiginosus* and *Celeus brachyurus*) of the eight woodpecker species that feed predominantly in the understory. Previously, Lambert and Collar (2002) noted that species that do not tolerate severe degradation include broadbills, barbets, woodpeckers, trogans, and hornbills, species that coincidentally have largely disappeared from forest isolates in Singapore, an indication that species that are sensitive to logging will be the first to disappear from isolated patches of forest.

In the present study we found a very strong association between unlogged forest and large and very large species, particularly frugivore/carnivores such as the hornbill *Buceros rhinoceros*. This species has been shown to avoid disturbed forest due to a paucity of fruiting trees (Anggraini et al. 2000). Importantly, a large body size has been related to an increased extinction risk (Bennett and Owens 1997, Castelletta et al. 2000, Purvis et al. 2000, but see Foufopoulos and Ives 1999 and Munoz-Duran 2002). In Singapore, for example, Castelletta et al. (2000) found that large-bodied forest bird species were particularly sensitive to extinction risk in the early stages of habitat loss. This is an indication that large-bodied species may be early indicators of habitat degradation (Castelletta et al. 2000). The link, however, between body size and extinction risk is often indirect and related to demographic variables such as abundance, population fluctuations, and population growth rates (Henle et al. 2004). It must be noted, however, that frugivore/carnivores and very large species were mainly species of hornbills (Bucerotidae) and that the association with unlogged forest and associated environmental parameters may be due to other communal traits of these species and therefore not directly due to diet and/or size. The terrestrial insectivores in contrast represent a diverse group of birds in the families Cuculidae, Pittidae, Timaliidae, and Phasianidae.

Hornbills in Africa have made recorded large-scale movements of up to 290 km, longer than any previously recorded movements of large avian frugivores. The ability of hornbills to track fruiting trees and their long-distance movements suggest that they may be crucial contributors to forest regeneration and diversity (Holbrook et al. 2002). In addition to this, the wide gape of hornbills enables them to consume fruit too large for most frugivores (Kitamura et al. 2004). Their diets also differ from those of other large frugivores. In Africa, for example, hornbills and primates feed on a number of tree species in common, but actual dietary overlap is limited, with primates feeding on more species and more non-fruit items such as seeds and leaves. Hornbills, furthermore, tended to feed higher in the canopy and eat fruit of different colors than primates. In Thailand, fruit consumed by hornbills tended to be large, easily accessible in the canopy, red, purple, or black, dehiscent or indehiscent, and thin-husked. It is therefore unlikely than the loss of one group will compensate for the loss of the other (Poulsen et al. 2002, Kitamura et al. 2004).

In addition to the hornbill frugivore/carnivores, species of canopy foliage-gleaning frugivores such as the Hill Myna (*Gracula religiosa*) and Yellow-crowned Barbet (*Megalaima henricii*) preferred unlogged forest. Frugivores often depend on keystone fruit species, such as figs, which are frequently reduced in logged forest (Lambert and Collar 2002). Chapman and Chapman (1997) noted that less fruit was produced in logged areas and months with low fruit abundance were much more frequent than in primary forest. If trees fruit aseasonally and unpredictably, as is the case for many rainforest species in Borneo, then the energetic cost of finding food will increase steeply as the total number of trees is diminished, leading to starvation. This is particularly a problem for species dependent on canopy epiphytes and has been identified as the cause of extinction for the Passenger Pigeon *Ectopistes migratorius* (Lambert and Collar 2002).

In Sabah, northern Borneo, although most primary forest species were present in forest logged eight years previously, certain taxa, such as flycatchers, woodpeckers, and trogons, had become comparatively rare while nectarivorous and opportunistic frugivorous species were substantially more abundant. In fact, the most pronounced change was an increase in the abundance of species that include nectar in their diet. This included specialized nectarivores (spider-hunters and sunbirds) and generalist species such as some flowerpeckers and leafbirds. These species tended to exploit the flowers of pioneer colonizers of disturbed forest such as *Mezoneuron* and various gingers. The increase in frugivores was in particular due to increases of *Pycnonotus* species, which are arboreal foliage-gleaning insectivore/frugivores that exploit the abundant small-fruited pioneer plants that colonize logged forest (Lambert 1992). In the present study, however, the genus *Pycnonotus* exhibited a varied response to logging with species, such as the near-threatened *Pycnonotus squamatus*, restricted to unlogged forest, whereas its congener *Pycnonotus eutilotus* was decidedly more abundant in logged forest. Interestingly, in the present study nectarivores were abundant in recently logged (L93) and unlogged forest but present in much reduced numbers in older logged forest (L89). The sunbird *Arachnothera longirostra* was, for example, strongly associated with recently logged forest but relatively rare in older logged forest. The species is an important pollinator of pioneer tree species (Liu et al. 2001), which are associated with large gaps in logged forests. In general, nectarivores depend on turnover in vegetation structure as a result of gap phase dynamics and therefore may be expected to vary in abundance as the forest regenerates (Lambert and Collar 2002). Nevertheless, reduced abundance of species of frugivores and nectarivores is cause for some concern because frugivores are important seed dispersers and nectarivores are important pollinators of numerous rainforest plant species. Their loss will probably have an important impact on rainforest stability (Şekercioğlu et al. 2004).

Although 1.3% of bird species have gone extinct since 1500, global bird abundance has dropped by 20–25% with many species critically endangered. According to the International Union for the Conservation of Nature and Natural Resources (IUCN), critically endangered species have a 50% chance of becoming extinct in the next 10 years, while endangered species have a 20% chance of becoming extinct in the next 10 years. In our study we found that although some threatened species were decidedly more abundant in unlogged forest (e.g., *Setornis criniger*, *Pityriasis gymnocephala*, *Rhinomyias umbratilis*, and *Pitta granatina*) they were also present in logged forest and some threatened species even seemed to prefer logged forest (e.g., *Macronous ptilosus* and *Malacopteron albogulare*). Importantly, logged forests provide a suitable matrix for a large number of, but not all, primary rainforest species and a crucial buffer for remnant primary forest. In a review of the impact of logging and fragmentation on bird assemblages, Lambert and Collar (2002) found that logged forests generally retain most primary forest species while forest fragments, even if primary, lose a substantial number of species. Of the 274 Sundaic bird species confined to lowland forest, 83 were adversely affected by fragmentation while 26 were negatively affected by logging; sallying insectivores, terrestrial insectivores, and woodpeckers were particularly susceptible to both forms of disturbance. Importantly, it is crucial to preserve the largest possible contiguous areas of forest. Isolated reserves of 10 000–20 000 ha that currently harbor a rich bird fauna will probably lose many of these species during the present century (Lambert and Collar 2002). Despite the need to protect logged forests from further degradation, areas of pristine forest (especially when imbedded in a large forest matrix) remain crucial to the survival of many species, including very large species (e.g., *Buceros rhinoceros*), terrestrial insectivores (e.g., *Pitta granatina*), and species inhabiting the canopy including canopy foliage-gleaning frugivores (e.g., *Gracula religiosa*) and canopy bark-gleaning insectivores (e.g., *Reinwardtipicus validus*). These species may require additional protective measures to ensure their survival in an increasingly disturbed forest environment.

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APPENDIX A

A summary of site characteristics in the three forest types/landscapes (*Ecological Archives* A017-043-A1).

APPENDIX B

A table of the abundance of all bird species recorded per sample site (*Ecological Archives* A017-043-A2).

APPENDIX C

A detailed description of the habitat/vegetation variables measured during the study (*Ecological Archives* A017-043-A3).

APPENDIX D

A table of values for each habitat/vegetation structure variable per subplot (*Ecological Archives* A017-043-A4).

APPENDIX E

Estimates of bird species richness per area, using sample-based rarefaction, and species richness estimators (the incidence-based coverage estimator [ICE] and the Chao2 estimator) in addition to the numbers of uniques and duplicates (*Ecological Archives* A017-043-A5).

APPENDIX F

Results of one-way ANOVAs testing for differences in (a) short sapling density, (b) tall sapling density, (c) volume of dead wood state 3, (d) volume of dead wood state 5, (e) canopy cover, and (f) canopy height among unlogged forest, older logged forest, and recently logged forest (*Ecological Archives* A017-043-A6).

APPENDIX G

Results of a principal component analysis on bird compositional data using the Hellinger distance (*Ecological Archives* A017-043-A7).

APPENDIX H

Results of one-way ANOVAs testing for differences in the abundance of bird guilds among unlogged forest, older logged forest, and recently logged forest (*Ecological Archives* A017-043-A8).

SUPPLEMENT

Three input files and an r script (*Ecological Archives* A017-043-S1).