

Research Article

Associations of bird species richness and community composition with local- and landscape-scale environmental factors in Borneo

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Received 13 April 2004; accepted 24 May 2005

Key words: Akaike's information criterion (AIC), Community similarity, Habitat heterogeneity, Habitat structure, Indonesia, Kalimantan, Logging, Topography

Abstract

A comprehensive understanding of variables associated with spatial differences in community composition is essential to explain and predict biodiversity over landscape scales. In this study, spatial patterns of bird diversity in Central Kalimantan, Indonesia, were examined and associated with local-scale (habitat structure and heterogeneity) and landscape-scale (logging, slope position and elevation) environmental variables. Within the study area (c. 196 km²) local habitat structure and heterogeneity varied considerably, largely due to logging. In total 9747 individuals of 177 bird species were recorded. Akaike's information criterion (AIC) revealed that the best explanatory models of bird community similarity and species richness included both local- and landscape-scale environmental variables. Important local-scale variables included liana abundance, fern cover, sapling density, tree density, dead wood abundance and tree architecture, while important landscape-scale variables were elevation, logging and slope position. Geographic distance between sampling sites was not significantly associated with spatial variation in either species richness or similarity. These results indicate that deterministic environmental processes, as opposed to dispersal-driven stochastic processes, primarily structure bird assemblages within the spatial scale of this study and confirm that highly variable local habitat measures can be effective means of predicting landscape-scale community patterns.

Introduction

Understanding and identifying factors that determine patterns of spatial diversity is of central importance for conservation within species-rich

environments. Rainforests contain a high proportion of Asia's critically endangered bird species (Collar et al. 2001). However, little is known about how these assemblages respond to local- and landscape-scale environmental variation. This

inhibits effective forest management with respect to bird conservation (Pearman 2002). Most biological assessment and forest management decisions take place at landscape scales and utilise the best available habitat data to make predictions of faunal biodiversity. To make informed management decisions concerning the fauna present, there is a need to test for patterns of association between landscape variables, local measures of habitat structure and heterogeneity, spatial processes and the fauna present.

Spatial patterns of species composition may be largely uniform, be spatially autocorrelated due to dispersal limitation, or be environmentally determined (Tuomisto et al. 2003). Landscape-scale topographical or climatological variables have been identified as the major environmental determinants of plant and invertebrate community structure in many forest environments (Svenning 1999; Condit et al. 2000; Harms et al. 2001). This category of variables can also significantly influence the structure of bird communities. For example, it has been shown that bird endemism in East Africa can be predicted to an accuracy of 89% using climate and remotely-sensed vegetation classification information (Johnson et al. 1998). Climatic variables also explained most of the spatial structure in European bird species richness at large spatial scales (Diniz-Filho et al. 2003), while landscape-scale effects of agriculture and logging were important in determining Canadian boreal forest bird community composition (Drapeau et al. 2000).

However, landscape-scale variables are not the only factors structuring spatial patterns of diversity; local environmental variables can be highly influential (Potts et al. 2002). Indeed, some studies on bird assemblages have indicated that local environmental variables may be of greater importance than landscape-scale variables. For example Schmiegelow et al. (1997) found impacts of landscape-scale fragmentation were small on Canadian boreal bird communities, while in Spain local habitat factors had a more significant impact on understory bird species than landscape factors (Herrando and Brotons 2002). Urban bird species richness has also been found to be independent of surrounding landscape and city size in North America and Europe, instead primarily depending upon local habitat structure (Clergeau et al. 2001). Taken together, it would appear that there is a

lack of consensus on the relative importance of local- and landscape-scale environmental factors on bird assemblages, but both appear to be influential.

In this study, spatial variation in the diversity of bird assemblages was examined within a rainforest landscape mosaic in Central Kalimantan on the island of Borneo. The region possesses high levels of natural landscape-scale topographical heterogeneity, but also substantial local-scale habitat heterogeneity due to natural and anthropogenic impacts, including logging. Primary aims were to: (i) identify major environmental gradients in the study area, (ii) test the extent to which spatial variation in species richness and community composition are associated with environmental variation, and (iii) determine whether local- or landscape-scale variables are of greater importance for determining spatial patterns of bird diversity.

Materials and methods

Sampling sites

Sampling was conducted between June and October 1997 and July and October 1998 within the 300,000 ha Kayu Mas logging concession, close to Sangai, Central Kalimantan (Figure 1). The area was selected as representative of natural vegetation and regional topography of the inland, upstream area in Borneo. The concession consisted of a mosaic of forest types that were either primary or had been logged once. Logging in the area has been selective, extracting mainly dipterocarp species with a cutting cycle of 35 years. The forest consisted of lowland hill dipterocarp rainforest with an average upper tree layer height of 40–55 m. Undergrowth consisted of small saplings and poles of 2–5 m in height. Dominant tree families in the area included Dipterocarpaceae, Euphorbiaceae, Fabaceae and Myrtaceae. Climate is related to the East and West monsoons and the intertropical convergence zone. Rainfall is somewhat seasonal with maximum in November (305 mm) and minimum in July (154 mm; Asdak et al., 1998).

Thirty-seven sites (Appendix I) were sampled across three habitat classes; unlogged primary forest (P: 14 sites), forest logged in 1993/94 (L93: 13 sites), and forest logged in 1989/90 (L89: 10

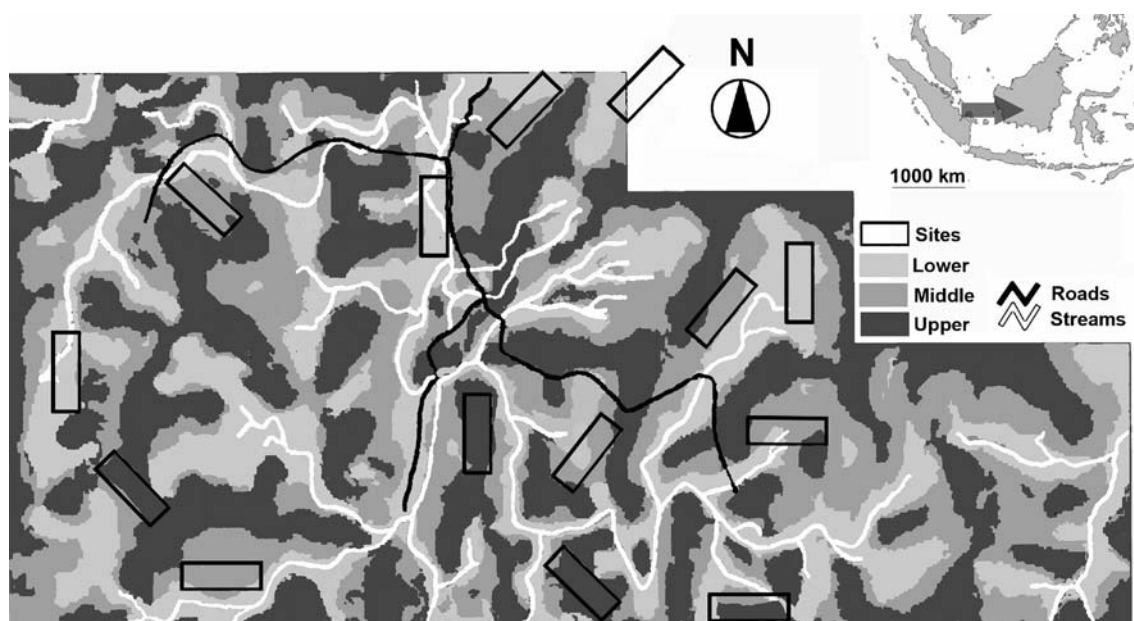


Figure 1. The primary forest area (P) included 14 sample sites. Sites were located over relatively homogeneous slope position. Sites: sample sites in area. Lower: Lower slope position, Middle: middle slope position, Upper: upper slope position. Each plot was 300×100 m. L93 (recently-logged forest) was to the northeast and L89 (older-logged forest) to the southwest. Inset shows Western Indonesia with Central Kalimantan indicated by an arrow on the island of Borneo. A similar sampling design was used for the logged areas L89 and L93.

sites) over a total contiguous survey area of 196 km^2 . Elevation of the study sites ranged from 100 to 400 m with a mean of 236 m (± 73 m S.D.). A few isolated peaks in the area exceeded 500 m. The primary forest area formed the central core of the study area; L93 was located north of the primary area and L89 south. Survey sites (3 ha, 300×100 m each) were designated *a-priori* to lower, middle and upper slope habitats on a GIS map (Figure 1) based on predictions generated by a digital elevation model (B. Mackey, unpublished data); plots were subsequently located in the field and geo-referenced using a handheld Global Positioning System (Garmin International Inc., Kansas, USA).

Habitat structure variables

Six 200 m^2 (10×20 m) subplots were established in each site using a systematic sampling design that comprised 4.0% of total site area. Thirty-three habitat structure variables were assessed at each 200 m^2 subplot. These were grouped into nine categories:

(a) *Dead wood*: Length and diameter at each end of all dead wood greater than 10 cm diameter was measured to calculate total volume. Each piece was allocated one of five decay states: (1) fresh; (2) wood sound, bark flaking; (3) wood sound, no bark; (4) wood rotting but firm; (5) wood rotten and soft. It was also noted if dead wood was standing or had fallen.

(b) *Lianas*: Abundance of non-woody lianas, small-woody lianas (stem diameter < 5 cm), and large-woody lianas (stem diameter > 5 cm) was estimated on a 4 point scale: 0 = absent; 1 = 1 or a few; 2 = moderately abundant; 3 = very abundant.

(c) *Ground cover*: Proportion of area covered by seedlings, herbs, ferns and grasses was estimated using the Domin scale, a non-linear scale from 0 to 10 (Mueller-Dombois and Ellenberg 1974).

(d) *Litter*: Leaf litter variables were recorded in four 1 m^2 plots located within each 200 m^2 subplot. Proportion of area covered by small woody debris (dead wood less than 10 cm diameter) and leaf litter was noted. Leaf litter was divided into three size classes: mesophyll ($< 20,000 \text{ mm}^2$), notophyll ($< 4500 \text{ mm}^2$), and microphyll ($< 2000 \text{ m}^2$) following Vanclay et al. (1997).

(e) *Tree architecture*: For all trees larger than 10 cm dbh (diameter at breast height), the dbh was measured in addition to total height, bifurcation index, crown depth and crown radius. The bifurcation index is the percentage of tree height below the first major branch, and crown depth is the distance from the lowest leaves to the total height measured with a spiegel relascope. Crown radius was measured four times, once at each point of the compass and averaged.

(f) *Density of tree size classes*: Densities of all saplings (< 5 cm dbh), poles (5 – 10 cm dbh), and trees (> 10 cm dbh) were estimated. These were divided into the following classes: (a) saplings < 5 m, (b) saplings > 5 m, (c) poles < 10 m, (d) poles > 10 m, and (e) trees.

(g) *Epiphytes*: Abundance estimated as lianas.

(h) *Bryophytes*: Abundance estimated as lianas.

(i) *Canopy cover*: Measured at the centre of each plot using a spherical densiometer, a tool that provides an estimate of canopy closure by counting the number of cells covered by vegetation in a concave mirror. Four readings were taken at each compass point and values were averaged.

Landscape-scale variables

The research area varied in elevation, slope position and logging prevalence. While logging influences local vegetation structure (Johns 1992; Cannon et al. 1998; Chappell et al. 2001), it also has larger-scale impacts including habitat fragmentation by skid trails and logging roads. These can remain in degraded states for long periods due to soil compaction and erosion (Malcolm and Ray 2000). In analyses logging was used as a variable to model bird species richness and community similarity. The sampling design was not adequately replicated to specifically test for differences in community structure between logged and primary forests.

Bird sampling

Birds were surveyed using spot-mapping, a method frequently used for assessing abundance based on calls and visual observations (Terborgh et al. 1990; Robinson et al. 2000). To provide even

coverage two parallel 300 m linear transects, 50 m apart, were established in each site. Sound recordings of species were retained for reference. Each site was sampled twice between 0600 and 1300 h, the principal period of activity for most species. If sampling was interrupted by rain the survey was continued the next day at the time when the previous recording was interrupted. The number of individuals sampled per site ranged between 130 and 460. In total, data comprised 9747 individuals belonging to 177 bird species with on average 64 (\pm 11 S.D.) species per sampling site. 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* ($n = 10$).

Analysis of habitat structure variables

To measure habitat structure within each site, the mean of each habitat variable from the six subplots was calculated. To measure habitat heterogeneity, standard deviation of each habitat variable over the six subplots was calculated (*sensu* Williams et al. 2002). Data were $\log_{10}(x + 1)$ transformed and summarised into fewer variables using Principal Components Analysis (PCA) in Statistica 6.1 (Statsoft, Tulsa, USA). Principal Component axes 1 to 4 were interpreted as representing the main habitat gradients. Variables with loadings greater than 0.5 were interpreted as having substantially contributed to the ordination.

Analysis of bird community diversity

Total rarefied species richness was assessed using the Species Diversity option within EcoSim (Gotelli and Entsminger 2001). Options for 1000 iterations and independent sampling of randomly chosen individuals within the total species pool were selected. Interpretations of statistical significance were based on simulated 95% confidence intervals generated within EcoSim.

Similarity of bird communities between sampling sites was calculated using $\log_{10}(x + 1)$ transformed species abundance data and the Bray-Curtis similarity index (Bray and Curtis 1957) within PRIMER 5 (Clarke and Gorley 2001). This

index is calculated as:

$$S_{jk} = 100 \left(1 - \frac{\sum_{i=1}^p |y_{ij} - y_{ik}|}{\sum_{i=1}^p |y_{ij} + y_{ik}|} \right)$$

where S_{jk} is similarity between j_{th} and k_{th} samples, y_{ij} is abundance of species i in sample j , whereby $i = 1, 2, \dots, p$, and y_{ik} is abundance of species i in sample k . Multi-dimensional scaling (MDS) was used to ordinate the resultant matrix enabling visual assessment of the similarity of bird communities among sampling locations. MDS is a robust non-parametric ordination procedure without the stringent model assumptions of Correspondence Analysis that assumes unimodal population abundance responses to continuous environmental variables (Beck et al. 2002).

The Indicator Value (IV) method was used to test for associations between individual bird species and particular habitat types (Dufrêne and Legendre 1997; Dufrêne 1998). The IV measure represents the degree to which a given species is associated with a habitat; higher IV values indicate species are more representative for a given habitat. All species with a minimum total abundance of ten individuals were tested for associations with (i) primary forest (P only), (ii) logged forest (L89 & L93 combined), (iii) older-growth forest (P & L89 combined) and (iv) recently-logged forest (L93 only). Analyses of statistical significance of associations were performed in IndVal 2.0 (Dufrêne 1998).

Analysing associations of species richness and community similarity with environmental variables

To obtain the best set of explanatory variables for species richness and community similarity Akaike's information criterion (AIC) was used. In contrast to stepwise multiple regression that often yields different results depending on the order in which models are computed, AIC yields consistent results and is independent of order of computation (Burnham and Anderson 2002). The following environmental variables were included: (1) elevation; (2) slope position (lower: 1, middle: 2 and upper: 3); (3) lower versus middle/upper slope (lower: 1, middle: 9, upper: 10), (4) upper versus lower/middle slope (lower: 1, middle: 2, upper: 10);

(5) logging (P: 1, L89: 2 and L93: 3), (6) P versus L89/L93 (P: 1, L89: 9, L93: 10); (7) L93 versus P/L89 (P: 1, L89: 2, L93: 10); (8–11) habitat structure PC axes 1 to 4; (12–15) habitat heterogeneity PC axes 1–4 and (16) the distance between sample sites. Note that we used three dummy variables each for slope position and logging. The analysis was initially conducted on all 16 variables, and was then repeated only on landscape-scale explanatory variables (variables 1–7), and again only on local-scale explanatory variables (variables 8–15). This enabled us to test whether local or landscape-scale variables were the most strongly associated with bird diversity. The best model has the lowest AIC value, and differences in AIC values between the best overall model and alternative models can be used to assess likelihood of alternative models. Differences in AIC values < 2 indicate substantial evidence for alternative models, differences between 3 and 9 indicate alternative models have considerably less support, differences > 10 indicate alternative models are very unlikely (Burnham and Anderson 2002). Multiple regressions in Statistica 6.1 (Statsoft, Tulsa, USA) were used to quantify the amount of variation explained (R^2) by the best sets of explanatory variables. The variance partitioning technique described by Borcard et al. (1992) was then used to determine the variance explained exclusively by landscape-scale variables, the variance explained exclusively by local-scale variables and the variance jointly explained by local- and landscape-scale variables.

Results

Local habitat structure and heterogeneity

Together PC1–PC4 explained 52.0% of variation in habitat structure (Appendix II). PC1 represented a gradient from predominantly logged sites with abundant non-woody and small-woody lianas, mesophyll-sized leaf litter, ferns, dead wood state 3 and fallen dead wood to predominantly primary sites with abundant tall poles, tall saplings, trees, microphyll-sized leaf litter, and greater crown depth and height. Within primary forest, there was separation of lower slope sites from middle and upper slope sites, a pattern that was not present in logged areas. Lower-slope habitats

in primary forest had habitat structure with greater similarity to logged forest than middle- or upper-slope habitats. PC2 represented a gradient from sites with abundant dead wood (fallen, states 1, 4, 5 and total) to sites with abundant short saplings and epiphytes and larger bifurcation index. PC3 represented a gradient from sites with larger mean crown radius, dbh and height to sites with the opposite properties. PC4 represented a gradient from sites with greater litter depth and dead wood (state 4) to sites with a greater mean crown radius and canopy cover (Figure 2; Appendix II).

In total, PC1–PC4 explained 48.2% of variation in habitat heterogeneity. PC1 separated predominantly primary sites with a high heterogeneity of dead wood (decay states 4, 5 and total) from predominantly logged sites with a strong heterogeneity of lianas, short saplings, trees, epiphytes, crown radius, bifurcation index and canopy closure. PC2 separated sites with a heterogeneous volume of dead wood (state 3 and fallen), small woody chip and canopy cover, from sites with a heterogeneous density of tall poles Figure 2; Appendix II). PC3 separated sites with a heterogeneous herb cover from sites with a heteroge-

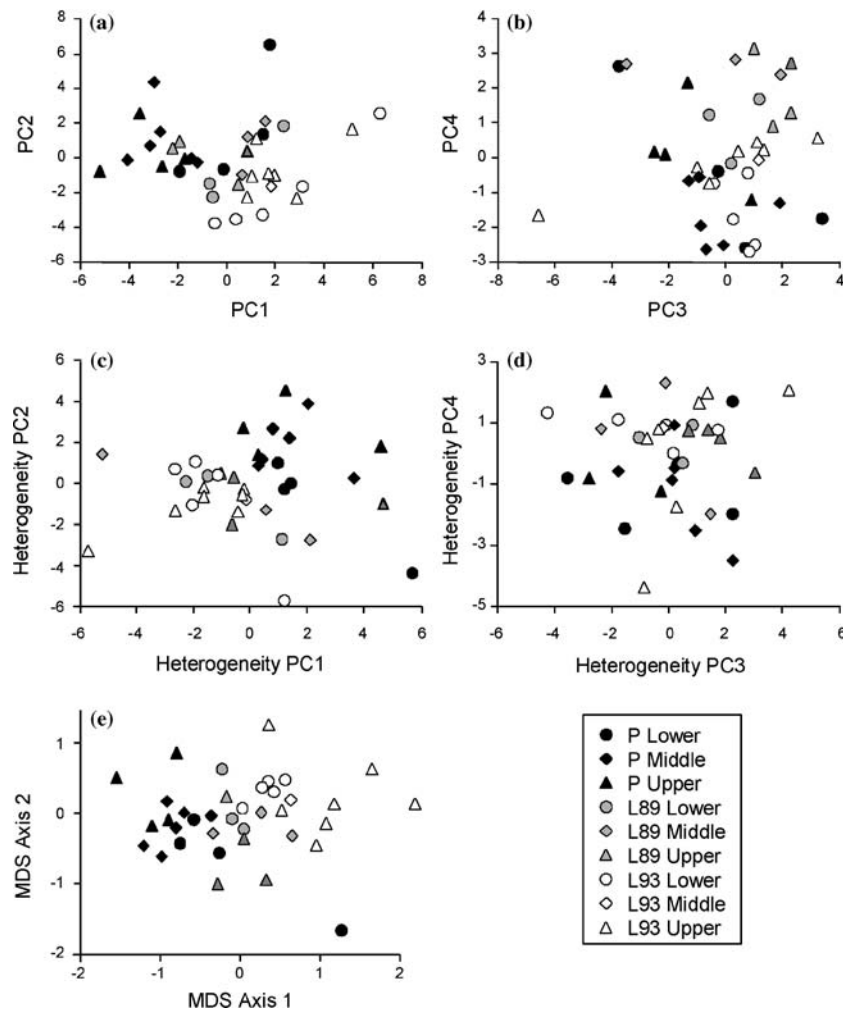


Figure 2. Principal Component ordination biplots of (a, b) mean habitat structure and (c, d) habitat heterogeneity. (e) Multi-dimensional scaling ordination biplot of bird community composition. Each symbol represents a sample site and closer symbols represent more similar sites: filled circles: P (primary forest); open diamonds: L89 (older logged forest); open triangles: L93 (recently logged forest).

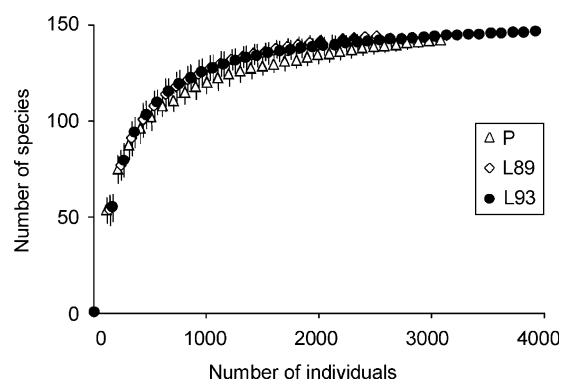


Figure 3. Total rarefied species richness of all individuals encountered in each habitat. Bars represent simulated 95% confidence intervals, filled circles: P (primary forest); open diamonds: L89 (older logged forest); open triangles: L93 (recently logged forest). Note similar trajectories of curves from each forest type indicating no significant differences in diversity.

neous volume of dead wood (state 2). PC4 separated sites with a heterogeneous cover of seedlings and mesophyll-sized leaf litter from sites with opposite properties.

Community diversity, geographic distance and environmental variables

Similar levels of total bird species richness were present in all three habitat classes (Figure 3). The primary forest had the most dissimilar bird community to the recently logged forest (Figure 2). Twenty two species had significant associations for designated habitat classes (Table 1). Of these, four were associated with recently logged forest, three with logged forest, eight with older-growth forest and seven with primary forest. The strongest associations were between *Orthotomus atrogularis* and logged forest (IV = 86.2), between *Buceros rhinoceros* and primary forest (IV = 81.0), and between *Pycnonotus plumosus* (IV = 80.2) and older-growth forest.

Local- and landscape-scale factors separately explained substantial amounts of variation in both bird rarefied species richness and community composition (Table 2), but models including both sets of factors gave best results. Environmental variables explained 43.6% of the variation in

Table 1. Taxa identified as possessing significant associations ($p < 0.05$) with one of four habitat categories using the Indicator Value (IV) method. Only species with an IV value ≥ 50.00 are shown.

Species	Family	Total number of observations				Category	IV
		Primary (P)	Older logged (L89)	Recently logged (L93)	All habitats		
<i>Orthotomus atrogularis</i>	Silviidae	10	37	66	113	Logged (L89 & L93)	86.24
<i>Malacocincla malaccense</i>	Timaliidae	30	44	77	151	Logged (L89 & L93)	61.79
<i>Orthotomus sericeus</i>	Silviidae	13	24	50	87	Logged (L89 & L93)	60.73
<i>Arachnothera longirostra</i>	Nectariniidae	32	9	72	113	Recently logged (L93)	76.43
<i>Nectarinia sperata</i>	Nectariniidae	6	0	19	25	Recently logged (L93)	59.12
<i>Picus miniaceus</i>	Picidae	5	2	16	23	Recently logged (L93)	55.97
<i>Cacomantis merulinus</i>	Cuculidae	2	6	15	23	Recently logged (L93)	53.71
<i>Rhipidura perlata</i>	Muscicapidae	195	111	46	352	Older growth (P & L89)	78.28
<i>Pycnonotus plumosus</i>	Pycnonotidae	100	61	8	169	Older growth (P & L89)	80.15
<i>Aegithina viridissima</i>	Chloropseidae	107	53	18	178	Older growth (P & L89)	75.90
<i>Pomatorhinus montanus</i>	Timaliidae	52	28	18	98	Older growth (P & L89)	61.82
<i>Harpactes diardii</i>	Trogonidae	13	12	3	28	Older growth (P & L89)	57.99
<i>Aethopyga temminckii</i>	Nectariniidae	31	15	6	52	Older growth (P & L89)	57.09
<i>Celeus brachyurus</i>	Picidae	20	15	4	39	Older growth (P & L89)	51.61
<i>Pellorneum pyrogenys</i>	Timaliidae	19	17	0	36	Older growth (P & L89)	50.00
<i>Buceros rhinoceros</i>	Bucerotidae	63	5	1	69	Primary (P)	81.02
<i>Dicaeum trigonostigma</i>	Dicaeidae	69	21	18	108	Primary (P)	74.40
<i>Malacopteron magnirostre</i>	Timaliidae	45	4	4	53	Primary (P)	70.90
<i>Criniger finschii</i>	Pycnonotidae	71	17	10	98	Primary (P)	63.80
<i>Pycnonotus brunneus</i>	Pycnonotidae	241	106	126	473	Primary (P)	63.05
<i>Mulleripicus pulverulentus</i>	Picidae	31	9	0	40	Primary (P)	54.63
<i>Malacocincla abbotti</i>	Timaliidae	41	11	4	56	Primary (P)	52.58

Table 2. Model selection analyses using Akaike's information criterion (AIC).

Index	Model	df	AIC	L. ratio	<i>p</i>	Δ_i	R^2
Richness	Best overall model ^a	3	211	21	< 0.001		0.436
	Best local-scale ^b	3	219	14	0.003	8	0.315
	Best landscape-scale ^c	1	222	7	0.008	10	0.171
	Upper versus lower/middle	1	222	7	0.008	10	0.171
	PC3	1	222	6	0.011	11	0.170
	Slope	1	223	6	0.014	11	0.151
	Lower versus middle/upper	1	225	4	0.058	14	0.093
	PC1	1	226	3	0.079	14	0.083
	PC4	1	226	2	0.119	15	0.062
	P versus L89/L93	1	227	2	0.152	15	0.016
	HetPC4	1	227	2	0.152	15	0.056
	L93 versus L89/P	1	227	2	0.152	15	0.055
	HetPC1	1	227		0.198	16	0.045
	HetPC3	1	228	1	0.406	17	0.019
	Logging	1	228	1	0.440	17	0.055
	HetPC2	1	228	0	0.560	17	0.009
	Elevation	1	228	0	0.638	17	0.006
	PC2	1	229	0	0.969	17	0.000
Similarity	Best overall model ^d	5	4316	315	< 0.001		0.382
	Best landscape-scale ^e	3	4456	172	< 0.001	140	0.230
	Best local-scale ^f	3	4461	167	< 0.001	144	0.225
	Logging	1	4473	151	< 0.001	157	0.205
	PC3	1	4510	114	< 0.001	193	0.158
	P versus L89/L93	1	4519	105	< 0.001	203	0.146
	L93 versus L89/P	1	4521	103	< 0.001	204	0.144
	PC1	1	4556	68	< 0.001	240	0.097
	HetPC4	1	4575	49	< 0.001	259	0.071
	Elevation	1	4591	32	< 0.001	275	0.048
	HetPC1	1	4603	20	< 0.001	287	0.031
	Upper versus lower/middle	1	4609	15	< 0.001	293	0.022
	HetPC2	1	4618	6	0.013	301	0.009
	Distance	1	4618	6	0.017	302	0.008
	HetPC3	1	4618	5	0.019	302	0.008
	Slope	1	4621	3	0.106	305	0.004
	PC2	1	4622	2	0.201	306	0.002
	Lower versus middle/upper	1	4622	1	0.261	306	0.002
PC4	1	4623	1	0.438	307	0.001	

Values are given for best models using local-scale, landscape-scale, distance between sample sites and all explanatory variables. The best model for species richness and community similarity included both local- and landscape-scale environmental variables. Significance of the model was tested using the likelihood ratio (McCullagh and Nelder 1989). Δ_i = difference in AIC value between model *i* and the best overall model. Variables included in best models are below the table.

^aUpper vs lower/middle, PC1, PC3.

^bPC1, PC3, PC4.

^cUpper vs lower/middle.

^dElev, PC1, PC3, Upper vs lower/middle, logging.

^eElevation, Upper vs lower/middle, logging.

^fPC1, PC3, HetPC4.

species richness of which 26.4% was explained by local-scale variables only and 12.0% by landscape-scale variables. Shared effects of local- and landscape-scale variables explained 5.1% of the residual variation in species richness. Environmental variables explained 38.3% of the variation in community similarity of which 15.2% was ex-

plained by local-scale variables only, 15.7% by landscape-scale variables. Shared effect of local- and landscape-scale variables explained 7.3% of the residual variation in similarity. Distance had very little ($R^2 < 0.01$) explanatory power for explaining variation in bird community similarity. The best models explaining patterns of species

richness using either local- or landscape-scale factors independently received considerably less support than the best model using both sets of variables (Table 2). The best models explaining patterns of community composition using either local- or landscape-scale factors independently were both highly unlikely in comparison to the best model using both sets of variables (Table 2). Within best models local habitat structure variables were consistently more prominent in explaining bird community variability than local habitat heterogeneity variables (Table 2).

Discussion

This study was undertaken in a large area of continuous forest without obvious habitat discontinuities that could act as dispersal barriers to birds. The lack of significant association between community composition and geographic distance confirmed that no dispersal barriers were present. Instead, results revealed that bird community composition was most strongly associated with spatial variance in the environment, implying that deterministic ecological processes are of greater importance in structuring spatial variation observed in the bird assemblage. The variables measured also influence the community composition of other components of the rainforest ecosystem (butterflies) in the study area (D. Cleary unpublished results). Thus it is likely that spatial contrasts in vegetation, elevation and slope are influencing distributions of essential resources for bird species including food, shelter and territorial space, and thus also influencing the strength of ecological interactions.

The first principal component axes of both habitat structure and heterogeneity were primarily associated with logging-induced disturbance, characterised by greater liana and dead wood abundance, in addition to increased cover of ferns and mesophyll-sized leaf litter. In other tropical rainforests increases in lianas, ferns and accumulation of woody debris have been reported following logging (Johns 1992; Cannon et al. 1998; Peres 1999; Schnitzer and Bongers 2002). The multivariate ordinations of vegetation structure revealed a gradient from recently logged to primary forest, with older logged forest intermediate. This indicates that older logged forests were

returning to a habitat structure and species composition resembling primary forest. The bird community exhibited a similar gradient to habitat structure implying that logging was having an effect on structure of the bird assemblage, a result confirmed in the AIC model selection.

Bird communities are commonly influenced by logging-induced disturbances (Wardell-Johnson and Williams 2000; Thiollay 2002). One of the principal differences between logged and primary forest is the frequency of canopy openings (gaps). Primary forest areas contain these gaps due to tree-fall, and subsequent regeneration and succession may be inhibited for extended periods of time by liana growth (Schnitzer and Bongers 2002). However, such gaps are often more frequent in selectively logged forests, but their numbers can vary substantially depending upon topographical conditions and stocking densities of target species. For example, within the study area, a high frequency of steep slopes meant that even in the logged habitats, extensive areas of undisturbed habitat remained. This means that logged forest is not necessarily resource-poor, and indeed a greater frequency of gaps could mean that logged forests contain a higher abundance of resources essential for some of the species than primary forest. This may explain our results indicating contrasting bird community composition between logged and primary forests, but no apparent differences in overall species richness. The differences in composition are reflected in ecological traits of the selected indicator species. The hornbill *Buceros rhinoceros* was strongly associated with primary forest in this study, and has been shown to avoid disturbed forest due to a paucity of fruiting trees (Anggraini et al. 2000). In contrast the sunbird *Arachnothera longirostra* was strongly associated with recently logged forest and has been shown to be an important pollinator of pioneer tree species (Liu et al. 2001) which are associated with large gaps in logged forests.

In this study the best explanatory models of bird diversity included both local and landscape-scale factors, and both categories explained similar amounts of variation in both species richness and community similarity. Studies on other bird assemblages have also found that models including both categories of data were superior predictors of bird abundance and distribution than either dataset on its own. However, they also showed

contrasting importance of local- and landscape-scale variables. For example, in North American birds MacFaden and Capen (2002) found communities were primarily associated with local microhabitat characteristics and secondarily to coarser scale characteristics. In contrast, Seoane et al. (2004) found that landscape-scale vegetation variables describing the surrounding habitat matrix were better predictors of bird abundance and distribution than the local vegetation cover on sampling sites. It is likely that these differing results are a consequence of the techniques used to measure environmental variables and analyse data, rather than any fundamental differences in the ecological characteristics of the bird species assemblages studied.

In conclusion, the lack of effects of geographic distance, but significant effects of habitat variables suggests that bird species were not dispersal limited at the moderate landscape scales of this study. Instead the results indicate that birds are probably able to locate optimal habitat within an altered landscape. This result has significance for conservation for it suggests that birds may be more resilient to environmental changes such as logging that alters a habitat matrix, but maintains substantial areas of primary-like vegetation. The results also suggest that bird community structure is more strongly associated with differences in local habitat structure rather than local habitat

heterogeneity. From a conservation management perspective our results indicate that attention should be given to maintaining (i) structurally complex forest with variation in gap-phase structure and tree size variables, (ii) forest in upper and lower/middle slope habitats and (iii) large areas of primary forest within forest concessions. Also, given that logged areas also contained a high diversity of species, they should not be given low conservation status or included as 'non-forest' (Curran et al. 2004) in landscape-scale forest assessments.

Acknowledgements

We acknowledge B. Mackey and colleagues from the Department of Geography, Australian National University for deriving and mapping environmental variables from a digital elevation model of the site. G. Hellier is gratefully thanked for field assessment of habitat structure variables. The staff of P.H.T. Kayu Mas and Wanariset Sangai, together with local Dayak field assistants provided valuable support during fieldwork. DFRC was supported by grant 895.100.005 of the Netherlands Foundation for the Advancement of Tropical Research (NWO-WOTRO) within Priority Programme 'Biodiversity in Disturbed Ecosystems'.

Appendix

Appendix I. Summary of site characteristics in the three classes of study sites.

Forest	Code	Top	Skid	Easting	Northing	Species	Rare $n = 130$	n	Remarks
Primary	S01	Low		651981	9856609	86	63.92	306	Flat; stream
	S03a	Mid	Close	652574	9855831	80	56.71	460	Tree fall; half steep; stream
	S03b	Upp		652417	9856066	55	52.31	162	Flat
	S04	Mid		652640	9857127	60	51.13	260	Large gap; steep
	S08	Low		653312	9856966	77	53.92	326	Large river; flat
	S09	Upp		653585	9856151	59	48.08	287	Flat
	S10	Upp		654030	9855773	64	51.78	286	Hilly
	S11	Mid		653923	9856067	68	52.76	277	Flat
	S12	Upp		654462	9855498	52	50.37	153	Flat; stream
	S13a	Low		654652	9856668	81	53.24	412	Hilly; stream
	S13b	Mid		654485	9856551	69	53.97	293	Half steep
	S14	Mid		654876	9856227	72	54.92	326	Half steep
	S16a	Mid		654187	9857398	65	52.40	298	Steep; stream
	S16b	Low		654053	9857516	38	38.00	130	Large gap; hilly

Appendix I. Continued.

Forest	Code	Top	Skid	Easting	Northing	Species	Rare $n = 130$	n	Remarks
Logged 1989	R01	Mid	Yes	649503	9851524	77	56.78	330	Swamp
	R02	Low	Yes	649537	9852227	72	60.01	243	Recent ulin extraction; stream
	R03	Upp	Yes	648006	9850906	58	51.10	206	
	R04	Upp		648307	9850341	65	53.15	259	Large gap; stream
	R05	Upp		649380	9853851	55	49.08	215	Large gap
	R06	Low		651470	9850488	68	53.29	258	Close to road; stream
	R07	Upp	Yes	649885	9850480	70	54.82	300	Stream
	R08	Mid		648812	9850972	58	51.48	199	Large gap; close to road
	R09	Low	Yes	650090	9851482	74	55.81	316	Stream
	R10	Mid	Close	652892	9850073	65	51.81	264	Stream
Logged 1993	Q01	Upp	Yes	653844	9858497	52	46.47	186	
	Q02	Upp	Close	653486	9859154	69	51.54	295	Tree fall; swamp
	Q03	Mid		656939	9860009	59	49.27	253	Ladang destroyed 40 m of plot; stream
	Q04	Low		658189	9858691	56	49.24	202	Very large gap; swamp, dead wood
	Q05	Upp	Yes	653952	9857783	53	46.82	190	
	Q06	Upp	Yes	657231	9858786	42	40.41	146	Very large gap in plot centre
	Q07	Upp	Yes	655055	9858927	56	48.35	243	
	Q08	Low		659754	9858334	65	52.13	270	Very large gap; gold mining; stream
	Q09	Low	Yes	659294	9858010	83	59.11	390	Stream
	Q10	Low		660097	9857461	67	54.48	266	Large gap; stream
	Q11	Low		659258	9858172	67	52.11	316	Large gap; logging close by; stream
	Q12	Upp		657658	9858713	62	54.38	213	Large gap; stream
	Q13	Upp	Close	653507	9859348	45	40.19	200	Very large gap and disturbed; stream

Top (topography): Low (lower slope), Mid (middle slope) or Upp (upper slope). Skid indicates sites where a logging 'skid' road was present (Yes) or nearby (Close). The Easting and Northing refer to UTM coordinates in zone 49 M. The total bird species (Species), rarefied species richness based on 130 individuals (Rare) and total individuals encountered (n) in each site are also indicated (not including 11 individuals identified to genus only). Remarks: site characteristics.

Appendix II. Mean observed values (+ 95% CI) and factor loadings on Principal Component (PC) axes 1 – 4 of local habitat variables.

Category	Variable	P		L89		L93		Structure				Heterogeneity			
		μ	CI	μ	CI	μ	CI	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Dead wood volume (cm ³)	Fallen	2.9	1.7	3.6	1.8	3.1	1.8	0.47	0.75	0.36	0.07	0.46	-0.78	-0.05	0.09
	Standing	0.4	0.2	0.8	0.7	0.5	0.2	-0.06	0.14	0.38	0.38	0.37	-0.03	0.42	0.22
	State 1	0.3	0.5	0.0	0.1	0.1	0.1	0.11	0.61	0.36	-0.13	0.42	-0.44	0.35	-0.14
	State 2	0.2	0.2	0.3	0.3	0.8	0.6	0.37	-0.08	0.39	-0.01	0.12	-0.24	0.52	0.22
	State 3	0.7	0.3	1.6	0.8	2.4	2.1	0.55	0.30	0.10	0.06	0.10	-0.62	-0.40	0.43
	State 4	0.8	0.4	2.0	1.0	0.5	0.2	0.02	0.52	0.30	0.53	0.51	-0.30	0.31	0.01
	State 5	1.3	0.8	0.4	0.4	0.1	0.1	-0.12	0.74	0.22	-0.20	0.54	-0.29	0.23	-0.47
	Total	3.3	1.8	4.4	1.9	3.8	2.2	0.46	0.73	0.39	0.13	0.56	-0.77	0.04	0.11
Liana abundance	Large woody lianas	1.1	0.3	1.1	0.2	1.3	0.2	0.20	-0.23	0.39	0.28	-0.53	-0.02	-0.29	0.19
	Non-woody lianas	1.2	0.4	1.5	0.2	2.1	0.3	0.77	-0.38	-0.10	-0.03	-0.54	-0.19	-0.34	0.39
	Small woody lianas	1.9	0.3	2.3	0.3	2.4	0.2	0.73	-0.17	0.16	0.17	-0.43	-0.22	-0.28	-0.23
Ground cover (Domin-scale)	Ferns	1.5	0.5	1.8	0.4	2.9	0.6	0.59	0.06	-0.03	-0.13	-0.39	-0.39	0.41	0.06
	Grasses	1.2	0.4	0.8	0.7	0.5	0.7	-0.24	0.24	-0.36	0.07	-0.33	-0.26	0.09	-0.48
	Herbs	3.5	0.8	3.4	1.0	4.0	0.8	0.23	0.05	-0.07	-0.13	-0.02	-0.28	-0.63	0.14
	Seedlings	5.8	0.3	5.8	0.4	5.8	0.5	-0.13	-0.40	0.49	-0.19	-0.35	-0.06	-0.33	-0.61
Litter cover (Domin-scale)	Litter depth	5.3	1.0	7.0	0.9	4.7	0.8	-0.19	0.06	0.06	0.79	0.19	-0.03	-0.20	0.00

Appendix II. Continued.

Category	Variable	P		L89		L93		Structure			Heterogeneity				
		μ	CI	μ	CI	μ	CI	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Tree architecture	Mesophyll leaves	5.7	0.4	6.6	0.4	6.6	0.3	0.60	-0.21	0.38	0.22	0.47	0.06	0.19	-0.57
	Notophyll leaves	5.4	0.3	5.8	0.2	5.2	0.5	-0.41	-0.29	0.30	0.42	-0.48	-0.33	-0.11	-0.24
	Microphyll leaves	5.1	0.5	5.1	0.4	3.9	0.6	-0.64	0.14	0.08	0.22	-0.35	-0.23	0.06	-0.28
	Small woody chips	3.2	0.3	3.2	0.3	3.6	0.2	0.29	-0.47	-0.12	-0.14	0.15	-0.56	0.27	-0.06
	Crown depth (m)	8.8	1.4	7.6	1.1	7.5	0.7	-0.57	0.00	0.26	-0.43	-0.23	0.03	0.43	0.06
	Crown radius (m)	3.5	0.3	3.1	0.2	3.5	0.3	-0.20	-0.24	0.60	-0.53	-0.60	0.13	0.33	0.04
	Dbh (cm)	23.0	1.7	22.4	2.1	23.2	2.2	-0.23	-0.02	0.73	-0.26	-0.36	-0.10	0.31	0.36
	Bifurcation index	56.1	2.8	59.8	3.7	58.1	2.2	0.01	-0.51	0.26	0.43	-0.66	-0.28	0.11	-0.35
	Height (m)	20.6	1.9	19.1	1.4	18.1	1.3	-0.63	0.21	0.54	-0.28	-0.50	-0.01	0.46	0.00
Tree density (ind/200 m ²)	Short Poles	7.8	1.5	10.8	1.7	10.6	1.5	0.24	-0.35	0.41	0.08	-0.17	-0.18	0.44	0.05
	Short saplings	57.6	7.8	85.8	13.2	88.5	13.3	0.12	-0.67	0.25	0.33	-0.59	0.17	0.28	0.13
	Tall Poles	5.6	2.0	4.0	1.9	1.3	0.5	-0.73	-0.03	-0.11	0.33	0.15	0.54	-0.12	-0.28
	Tall saplings	22.2	7.0	17.2	6.6	10.5	3.1	-0.75	0.02	0.17	0.12	-0.05	0.40	0.49	0.23
	Trees	9.9	1.3	9.6	0.6	9.1	1.4	-0.51	-0.23	-0.03	0.25	-0.60	0.13	0.29	-0.07
Bryophyte abundance		1.8	0.3	1.9	0.4	1.8	0.3	0.08	-0.13	0.39	-0.08	-0.41	-0.38	0.05	-0.31
Epiphyte abundance		1.4	0.3	1.4	0.3	1.6	0.4	-0.02	-0.50	0.34	-0.25	-0.59	-0.43	-0.09	0.33
Canopy cover (%)		81.7	2.7	60.8	10.0	80.3	2.5	-0.01	-0.15	-0.08	-0.66	-0.59	-0.50	-0.01	-0.17
Eigenvalues								5.85	4.52	3.56	3.22	6.05	4.10	3.24	2.51
Percentage of variation explained								17.73	13.69	10.79	9.75	18.33	12.44	9.82	7.62

References

- Anggraini K., Kinnaird M. and O'Brien T. 2000. The effects of fruit availability and habitat disturbance on an assemblage of Sumatran hornbills. *Bird Conservation International* 10: 189–202.
- Asdak C., Jarvis P.G., Van Gardingen P. and Fraser A. 1998. Rainfall interception loss in unlogged and logged forest areas of Central Kalimantan, Indonesia. *Journal of Hydrology* 206: 237–244.
- Beck J., Schulze C.H., Linsenmair K.E. and Fiedler K. 2002. From forest to farmland: diversity of geometrid moths along two habitat gradients on Borneo. *Journal of Tropical Ecology* 18: 33–51.
- Borcard D., Legendre P. and Drapeau P. 1992. Partialing out the spatial component of ecological variation. *Ecology* 73: 1045–1055.
- Bray J.R. and Curtis J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27: 325–349.
- Burnham K.P. and Anderson D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd ed. Springer-Verlag, NY, NY.
- Cannon C.H., Peart D.R. and Leighton M. 1998. Tree species diversity in commercially logged Bornean rainforest. *Science* 281: 1366–1368.
- Chappell N.A., Bidin K. and Tych W. 2001. Modelling rainfall and canopy controls on net-precipitation beneath selectively-logged forest. *Plant Ecology* 153: 215–229.
- Clarke K.R. and Gorley R.N. 2001. *Primer v5: User Manual/Tutorial*. Primer-E Ltd, Plymouth.
- Clergeau P., Jokimäki J. and Savard J-P.L. 2001. Are urban bird communities influenced by the bird diversity of adjacent landscapes? *Journal of Applied Ecology* 38: 1122–1134.
- Collar N.J., Andreev A.V., Chan S., Crosby M.J., Subramanya S. and Tobias J.A. (eds) 2001. *Threatened Birds of Asia: The BirdLife International Red Data Book*. BirdLife International, Cambridge, UK.
- Condit R., Ashton P.S., Baker P., Bunyavechewin S., Gunatilleke S., Gunatilleke N., Hubbell S., Foster R.B., Itoh A., LaFrankie J.V., Lee H.S., Losos E., Manokaran N., Sukumar R. and Yamakura T. 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288: 1414–1418.
- Curran L.M., Trigg S.N., McDonald A.K., Astiani D., Hardiono Y.M., Siregar P., Caniago I. and Kasischke E. 2004. Lowland forest loss in protected areas of Indonesian Borneo. *Science* 303: 1000–1003.
- Diniz-Filho J.A.F., Bini L.M. and Hawkins B.A. 2003. Spatial autocorrelation and red herrings in geographical ecology. *Global Ecology and Biogeography* 12: 53–64.
- Drapeau P., Leduc A., Giroux J.F., Savard J-P. L., Bergeron Y. and Vickery W.L. 2000. Landscape-scale disturbances and changes in bird communities of boreal mixed-wood forests. *Ecological Monographs* 70: 423–444.
- Dufrêne M. 1998. IndVal 2.0. programme freely available at: <http://mrw.allonnie.be/dgrne/sibw/outils/indval/home.html>.
- Dufrêne M. and Legendre P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

- Gotelli N.J. and Entsminger G.L. 2001. EcoSim: Null Models Software for Ecology. V. 6.0. Acquired Intelligence Inchtttp://homepages.together.net/~gentsmin/ecosim.htm..
- Harms K.E., Condit R., Hubbell S.P. and Foster R.B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.
- Herrando S. and Brotons L. 2002. Forest bird diversity in Mediterranean areas affected by wildfires: a multi-scale approach. *Ecography* 25: 161–172.
- Johns A.D. 1992. Vertebrate responses to selective logging: implications for the design of logging systems. *Philosophical Transactions of the Royal Society London B* 335: 437–442.
- Johnson D.D.P., Hay S.I. and Rogers D.J. 1998. Contemporary environmental correlates of endemic bird areas derived from meteorological satellite sensors. *Proceedings of the Royal Society London Series B* 265: 951–959.
- Liu A.Z., Li D.Z. and Wang H. 2001. Pollination ecology of a pioneer species: *Musa itinerans* (Musaceae) in Xishuangbanna, South Yunnan, China. *Acta Botanica Sinica* 43: 319–322.
- MacFaden S.W. and Capen D.E. 2002. Avian habitat relationships at multiple scales in a New England forest. *Forest Science* 48: 243–253.
- Malcolm J.R. and Ray J.C. 2000. Influence of timber extraction routes on Central African small-mammal communities, forest structure, and tree diversity. *Conservation Biology* 14: 1623–1638.
- McCullagh P. and Nelder J.A. 1989. *Generalized Linear Models*, 2nd ed. Chapman & Hall, New York.
- Mueller-Dombois D. and Ellenberg H. 1974. *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York. USA.
- Pearman P.B. 2002. The scale of community structure: habitat variation and avian guilds in tropical forest understory. *Ecological Monographs* 72: 19–39.
- Peres C.A. 1999. Tropical forest disturbance and dynamics in Southeast Asia. *Trends in Ecology and Evolution* 14: 217–218.
- Potts M.D., Ashton P.S., Kaufman L.S. and Plotkin J.B. 2002. Habitat patterns in tropical forests: a comparison of 105 plots in northwest Borneo. *Ecology* 83: 2782–2797.
- Robinson W.D., Brawn J.D. and Robinson S.K. 2000. Forest bird community structure in central Panama: influence of spatial scale and biogeography. *Ecological Monographs* 70: 209–235.
- Schmiegelow F.K.A., Machtans C.S. and Hannon S.J. 1997. Are boreal birds resilient to forest fragmentation? An experimental study of short-term community responses *Ecology* 78: 1914–1932.
- Schnitzer S.A. and Bongers F. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* 17: 223–230.
- Seoane J., Bustamente J. and Diaz-Delgado R. 2004. Competing roles for landscape, vegetation, topography and climate in predictive models of bird distribution. *Ecological Modelling* 171: 209–222.
- Svenning J-C. 1999. Microhabitat specialisation in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* 87: 55–65.
- Terborgh J., Robinson S.K., Parker T.A., Munn C.A. and Pierpont N. 1990. Structure and organisation of an Amazonian bird community. *Ecological Monographs* 60: 213–238.
- Thiollay J.M. 2002. Avian diversity and distribution in French Guiana: patterns across a large forest landscape. *Journal of Tropical Ecology* 18: 471–498.
- Tuomisto H., Ruokolainen K. and Yli-Halla M. 2003. Dispersal, Environment, and floristic variation of western amazonian forests. *Science* 299: 241–244.
- Vanclay J.K., Gillison A.N. and Keenan R.J. 1997. Using plant functional attributes to quantify site productivity and growth patterns in mixed forests. *Forest Ecology and Management* 94: 149–163.
- Wardell-Johnson G. and Williams M. 2000. Edges and gaps in mature karri forest, south-western Australia: logging effects on bird species abundance and diversity. *Forest Ecology and Management* 131: 1–21.
- Williams S.E., Marsh H. and Winter J. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. *Ecology* 83: 1317–1329.