Biodiversity and environmental change in the rainforests of Borneo

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Chapter 3

Beta diversity and species richness of bird guilds in a Bornean rainforest under logging-induced disturbance

Daniel F. R. Cleary, Timothy J. B. Boyle, Titiek Setyawati, Celina D. Angraeti and Steph B. J. Menken

The impact of logging on species richness and community similarity of five bird guilds (viz., canopy omnivores, canopy insectivores, frugivores, understory omnivores, and understory insectivores) in Indonesian Borneo was assessed. There was no overall difference in mean species richness among forest types (recently logged, older logged, or primary forest) in four of the five guilds. Only canopy insectivores had significantly higher local species richness in primary and older logged forest than recently logged forest. Total rarefied species richness, however, of canopy and omnivore guilds was significantly lower in logged forest than primary forest. Frugivore total rarefied species richness was significantly higher in recently logged forest than older logged and primary forest whereas understory insectivore total rarefied species richness was significantly higher in older logged forest than primary and recently logged forest.

Changes in community similarity (beta diversity) in all guilds was surprisingly not negatively related to spatial distance between plots, but was related to changes in the physical environment and habitat structure at local and landscape scales. All guilds except frugivores responded significantly to habitat structure. Both generalist omnivore guilds responded to landscape-scale habitat structure, but this was not the case with the canopy guilds or frugivores. Within the understory guilds landscape-scale changes in habitat structure explained considerably more variation in generalist omnivores (12% versus 2%) than specialist insectivores. Both omnivore guilds and frugivores responded significantly to variation in the physical environment reflecting large-scale changes in topography, edaphic conditions and light radiation. The implications of a differential response to large-scale and local processes for bird guilds under changing disturbance regimes are discussed.
Introduction

How logging affects biodiversity has profound implications for conservation and resource management since maintaining biodiversity is a key component of sustainable forest use (Andersen et al., 2000; Summerville and Crist, 2002). Assemblages, however, from diverse ecosystems such as coral reefs and tropical rainforests are interesting to study, but they are not, unfortunately, conducive to experimentation because of the difficulty of manipulating the often large-scale disturbance events and complex communities (Petraitis and Latham, 1999). In order to address issues, such as disturbance, that affect these complex ecosystems we therefore need to rely on comparative approaches. A problem, however, with comparative approaches is the potential impact of spatial (or temporal) autocorrelation of disturbance events and other site-specific factors. Unknown ecological processes may be highly correlated with a given disturbance so that any relation found might actually be due to these unknown variables and not directly related to the disturbance event.

Another problem in comparative studies is the scale of assessment (Hamer and Hill, 2000). Previous studies, for example, have shown that logging can have a threshold effect on species richness depending on the scale of sampling (Hamer and Hill, 2000; Summerville and Crist, 2002). Several tropical studies, for example, failed to reveal an effect of logging on biodiversity at small spatial scales (refs in Summerville and Crist, 2002). Logging has, however, been hypothesised to increase large-scale diversity by affecting species turnover between disturbed and undisturbed patches within logged areas. Williams et al. (2002) therefore recommend addressing ecological phenomena at both the local scale as well as larger scales so that processes acting at different scales may be revealed.

In addition to recognising the importance of scale it is important to recognise the collective ecological characteristics of guilds as these can reveal important insights into community structure (Pearman, 2002). A species’ life history can, for example, constrain how resources are exploited and the spatial scales at which this occurs (Hansen and Urban, 1992). Pearman (2002) found that some bird guilds responded to local habitat structure whereas others responded to large-scale landscape relationships. His results of bird community response to habitat variation indicated that mechanisms regulating local assemblages could fall into two main groups. First mechanisms which regulate communities at very small scales, such as competition or physiological adaptations. The second group of mechanisms includes factors that may not directly affect individuals and that occur over very large areas, such as fragmentation.

Like species richness, community similarity between animal populations can be influenced by both local and landscape-scale processes (Andrén, 1994; Findlay and Houlan, 1997; Drapeau, 2000). Drapeau (2000), for example, found that overall variation in Canadian bird community similarity was determined as much by large-scale (landscape) as by small-scale (local) processes. The scale at which communities are studied also affects relationships between habitat structure and species similarity (Pearman, 2002; Robinson et al., 2000). The mixed success of studies in relating habitat structure to faunal diversity has, in fact, often been related to an inappropriate scale of assessment (Williams et al., 2002).

In the present study, we address the impact of logging on species richness and community similarity of bird guilds at both local and large spatial scales. Guilds or functional groups are here considered to be groups of species likely to interact competitively because of their similar resource-use (Pearman, 2002; Root, 1967; Wilson, 1999). Habitat patches with species-rich guild assemblages provide suitable habitat for individual species and sufficient
complexity for niche separation (Pearman, 2002). Disturbance may, however, disrupt the habitat and lead to species loss.

Our goal is to assess patterns of species richness and community composition of bird functional groups. These patterns of species are assessed spatially across three forest types (chronosequences) whereby we infer that differences among forest types are due to logging and post-logging regeneration. Ideally, the impact assessment of logging would entail studying specific sites from an unlogged state until a given period after logging. However, for most purposes this is impractical and forest types are used as a substitute. We additionally measured the habitat structure using relatively easy-to-measure habitat structure variables that are a large subset of those proposed by Stork et al. (1997) and are assumed to be important in maintaining biodiversity.

The assessment of bird guild assemblages and habitat structure enable us to relate changes in bird guilds to logging-induced changes in their environment. For this purpose (multiple) matrix regression was used (Casgrain, 2001) based on permutations to assess the relationship between community similarity and a set of predictor matrices based on spatial (distance) and environmental variation (e.g. local habitat structure).

In addition to habitat structure, natural environmental variation such as radiation, edaphic and topographical factors on a landscape scale can significantly influence community composition (Baduni and Sharma, 1996; Clark et al., 1999; Furley and Newey, 1979; Hairston and Grigal, 1991). We therefore used an environmental classification based on topography, wetness, and radiation as an additional predictor variable of guild community similarity.

We also measured the impact of local and large-scale environmental variation on community similarity and therefore constructed an additional predictor matrix using only mean habitat structural values across the forest types. This is based on the observation that species can respond to gross differences between habitats within a landscape and not to relative differences of any adjacent pair of patches within a habitat (Morris, 1996). The absence of fine-scale differences indicates that assemblages are primarily responding to landscape-scale processes.

Finally, we assessed the impact of spatial (distance) variation on community similarity. Dispersal limitation is seen as a key structuring force in many communities (Hubbell, 2001). In general though little is known about rates of dispersal in rainforest animal communities.

With this study a number of hypotheses were tested. First we tested the hypothesis that levels of species richness are affected by logging by comparing species richness in primary versus logged forest types. Secondly, we tested the hypothesis that changes in community similarity are related to logging-induced shifts in habitat structure. Thirdly we predicted that specialist guilds would respond more to local habitat structural complexity whereas generalist guilds would respond more to landscape-scale difference in habitat structure, reflecting mean values across forest types, and landscape-scale processes acting at the topo-scale such as topographical and edaphic variation across the landscape. Fourthly, we predicted that community similarity would differ greatest between primary and recently logged forest reflecting predictions of how habitat structure should be affected by logging. Because of forest regeneration older logged forest is expected to maintain guild assemblages that are intermediate between primary and recently logged forest. Importantly this will allow us to assess how forest regeneration affects bird guild assemblages. Finally we assessed whether spatial patterns of community similarity (beta diversity) were primarily related to distance (and thus stochastic events) or primarily to environmental factors (and thus deterministic processes).
Chapter 3

Materials and Methods

A. Data collection

Study Site

All research was conducted in the large (ca. 300 000 ha) Kayu Mas concession in the Indonesian province of Central Kalimantan (Figure 1; 0 18 S, 112 23 E). The topography is undulating and the altitude generally lies between 50 and 350 metres above sea level with a few isolated peaks exceeding 500 metres. 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 area in Borneo that has hitherto received low priority for scientific study (Asdak et al., 1998). Dominant tree families in the area include Dipterocarpaceae, Caesalpinaceae, Euphorbiaceae, and Myrtaceae. The average annual rainfall in the area was 2802 mm (averaged over 13 years of measurement). Maximum rainfall occurred in November (305 mm) and minimum in July (154 mm).

Fig. 1. a) Map of Borneo; the research site location is indicated. b) Distribution of recently logged (L93: open triangles), older logged (L89: open diamonds), and primary forest (P: black circles) plots over a spatial scale of ca. 14 x 14 Km.

Within the Kayu Mas concession, which includes some smaller concessions, we established a series of plots across three forest types of differentially disturbed forest. The first area is the Wanariset Sangai Research Forest, a 600 ha area of primary rainforest (hereafter known as P). This area is administered by the ‘Balai’ forest research agency in Samarinda, East Kalimantan. The other two areas are logged over forest types. These include the Kayu Tribuana Rama forest concession monitored by Kayu Mas in which we sampled in forest that had been logged in 1989/90 (L89) and lies to the south of our primary forest. The other logged forest type lies just to the north of our primary forest (Figure 1) and was logged
Our primary forest is thus juxtaposed between these two logged forests. A substantial area of primary forest, however, surrounds our 600 ha core area.

The logging concession further maintains a selective logging cycle of 35 years rotation so both logged forest types have only been disturbed once. The minimum tree size felled is 60 cm (diameter at breast height) and skid trails are prohibited on slopes steeper than 40%. Commonly ca. ten trees were felled per ha during logging operations, but this was less under adverse conditions, e.g., low stocking or swamps. This level of extraction is moderate for Southeast Asian standards (Danielsen and Heegaard, 1995).

1. Plots- A total of 37 plots were sampled across the three areas. The forest types include an area of primary forest (P: 14 plots), an area of recently logged forest (logged in 1993/94; L93: 13 plots), and an area of older logged forest (logged in 1989/90; L89: 10 plots). Each sample plot covered three hectares.

Across the three forest types, we examined the primary environmental regimes at the top-scale by establishing sampling plots on the basis of a landscape classification using the following landscape characteristics: topography: slope position (elevation percentile), wetness: topographic wetness index, and radiation: average daily radiation for the month of June. These environmental variables were predicted using a digital elevation model generated from 1:10,000 topographic surveys. Topographic wetness index (wet versus dry) and average daily radiation (exposed versus shaded) were divided into two classes each and, while slope position was divided into three classes (lower-, middle-, and upper-slope). In total there were thus 12 discrete environmental classes.

Positions of plots were selected for homogeneity according to the classes in the environmental classification. They were positioned on a map in advance, and subsequently located in the field with a compass and clinometer, and georeferenced with a handheld GPS device (Garmin 12XL). An even distribution of plots for each class was not possible due to the scarcity of some classes in the study area. The number of plots per class, however, represents its percent coverage in the area. Two plots, for example, were allocated to upper wet shaded areas, which covered 3.4% of the total area, whereas five plots were allocated to upper dry shaded areas, which covered 16.7% of the total area.

2. Species sampling: For surveying the bird community spot-mapping was used which is one of the most frequently used methods for assessing bird communities (Clergeau et al., 2001; see Terborgh et al., 1990 and Robinson et al. 2000 for a description of the advantages and disadvantages of spot-mapping). Spot-mapping, for example, is highly effective for estimating abundances of species that are highly territorial, but less effective with highly mobile species such as frugivores and raptors. Locations of all individuals seen or heard were spot-mapped. In order to provide even coverage of each plot we walked parallel 300 metre transects, ca. 50 metres apart. For each individual, the distance and direction was estimated from marked locations along the transect at 10-metre intervals. A record of sound recordings of individual species was kept as a reference from each plot.

Birds were sampled over two days from 6:00 to 13:00 (except during rain). This is the principal period of activity for most species. We always conducted sampling during the same time of day, and never extended sampling beyond previously agreed and delimited times due, for example, to rained out mornings. If this period was interrupted by rain then the research at the plot was continued the next day at the time when the rain interrupted the previous days recording. In this way, an equal amount of time was spent at each plot and during the same daily period of activity.
Chapter 3

The bird guilds used in this study were based on food type utilisation and habitat stratification (Castelletta et al., 2000). We assigned species to functional groups based on 1) the stratum at which they feed (i.e. canopy or understory), and 2) food type (i.e. omnivores that feed on a combination of fruit, nectar, insects, and/or small vertebrates, and specialist insectivores). For 1) we grouped ground species and species that use the undergrowth and understory into a single group. For 2) we additionally assess specialist frugivores. Although frugivores can be partitioned into understory and canopy feeders there were not always enough recorded individuals per plot so we had to group the understory and canopy feeders into a single guild.

We distinguished five guilds. These are

1) canopy omnivores: feed on a combination of fruit, nectar, insects, and/or other small animals in the canopy
2) canopy insectivores: feed on insects in the canopy
3) frugivores: feed on fruit
4) understory omnivores: feed on a combination of fruit, nectar, insects, and/or other small animals in the understory
5) understory insectivores: feed on insects in the understory

Four species of raptor and five species of insectivores that were not associated with a particular vertical stratum were not included in any functional group and are not considered in further analyses.

B. Analyses

i. Species richness

Species richness was assessed at two spatial scales, at the plot scale and over the whole forest type landscape for L93, L89, and P separately. At the plot scale, we rarefied species richness from each guild by assigning a standard minimum abundance and calculating the rarefied species richness at that value using the program PRIMER (Clarke and Gorley, 2001). The abundance used for each guild is shown in Table 1. At the landscape-scale we pooled all individuals from all plots within a given forest type in order to assess cumulative rarefied species richness. At the larger scale, rarefaction analysis was conducted with the Species Diversity option of the EcoSim program (Gotelli and Entsminger, 2001) using 100 iterations and independent sampling of randomly chosen individuals from the total species pool in each landscape. At the landscape-scale, interpretations of statistical significance are based on the simulated 95% confidence intervals generated by EcoSim, and sensu McCabe and Gotelli (2000). At the plot scale we tested for significant differences among forest types with one-way ANOVAs using Statistica for Windows (1996) on independent means using the forest type (P, L89, and L93) as the independent variable and (rarefied) species richness as the dependent variable. A Tukey HSD post hoc test was used to compare means across treatments (forest types).

ii Habitat structure and physical environment
Six 200-m² (10 x 20 m) subplots were established in each plot using a systematic sampling design (comprising 4.0% of the total plot area). Thirty-five habitat structure variables were assessed at each 200-m² subplot, and the slope was measured with a clinometer (Suunto). The variables are grouped into six main categories:

1) Dead wood: The length and diameter at each end of all dead wood (greater than 10 cm in diameter) was measured (in order to calculate total volume) in six 200-m² subplots per sample plot (3 ha). This was then divided into five decay states and it was further noted if the dead wood was standing or had fallen. The decay states are (1) fresh, (2) wood sound, bark flaking, (3) wood sound, no bark, (4) wood rottin but firm, and (5) wood rotten and soft. Dead wood provides a habitat substrate for numerous arthropods, small mammals and birds, and has been shown to be an important factor in maintaining biodiversity in many forest ecosystems (Ratcliffe, 1993; Franklin, 1988; McCarthy and Bailey, 1994).

2) Dependents: The abundance of non-woody lianas, small-woody lianas and large-woody lianas, epiphytes, and bryophytes was estimated on a 4-point scale (0 = absent, 1 = 1 or a few, 10 = moderately abundant, 100 = very abundant) in each 200-m² subplot.

3) Ground cover: The percentage of each subplot covered by seedlings, herbs, ferns, grasses, and palms was estimated in four 1-m² plots within each 200-m² subplot.

4) Litter: Leaf litter variables were recorded in four 1-m² plots within each subplot. The percentage of small woody debris (dead wood less than 10 cm) and leaf litter was noted. Leaf litter was further divided into three size classes: mesophyll, notophyll, and microphyll (Vanclay et al., 1997).

5) Tree architecture: All trees larger than 10 cm dbh (at 130 cm) were measured in each 200-m² subplot. Measured variables included crown depth, crown radius, dbh, height, and the furcation index.

6) Density of tree size classes: Includes the densities of all saplings (<5 cm dbh), poles (5<x<10 cm dbh), and trees (>10 cm dbh) recorded in each 200-m² subplot. These were divided into the following five classes a) saplings smaller than 5 metres, b) saplings taller than 5 metres, c) poles smaller than 10 metres, d) poles taller than 10 metres, and e) trees. Canopy cover, which was measured four times (in each compass direction), at the centre of each plot using a spherical densiometer, is also included in this category.

We tested for significant differences in habitat structure among forest types using the 35 habitat structure variables in a multivariate analysis. A matrix of pairwise comparisons between plots was composed using normalised Euclidean distances with the program PRIMER (Clarke and Gorley 2001). Variation in the multivariate habitat structure among habitats was tested for significance using ANOSIM (non-parametric analysis of similarities) with the package PRIMER (Clarke and Gorley 2001). ANOSIM is roughly analogous to standard univariate ANOVAs, and tests the variance within and between a priori defined groups in ordinate space. The $R_{\text{ANOSIM}}$ statistic values are an absolute measure of how
Chapter 3

separated the a priori defined groups are. A zero (0) indicates that there is no difference among groups, while a one (1) indicates that all samples (here subplots) within groups are more similar to one another than any samples from different groups (Clarke and Gorley, 2001). In the results, the ANOSIM results are presented in addition to a multidimensional scaling (MDS) ordination based on the same distance matrix.

iii. Community composition

Two tests were performed to assess the degree of variation among forest types for bird community similarity, and to relate changes in the community similarity to variation in their environment. First, variation in the overall community composition among forest types was tested for significance with an ANOSIM using a matrix of pairwise comparisons between plots based on the Bray-Curtis similarity index. All pair-wise comparisons with zero values were replaced by group means. The Bray-Curtis similarity coefficient is frequently used in ecological work (Clarke and Gorley, 2001; Ellingsen, 2002).

Subsequently, in order to assess the degree to which variation in the response variables could be explained by the total set of predictor matrices and in order to quantify the relative contribution of spatial and environmental variation, we used multiple regressions. In the program PERMUTE! (Casgrain 2001) we used the matrix permutation option, 999 permutations, forward selection, and a Bonferroni-corrected p-to-enter level of 0.10 (the default). For a description of the methodology see:


An advantage of these tests is that no assumptions need be made about the distribution of data. The similarity response matrices of both taxa were regressed against predictor matrices of:

1) Difference in elevation between plots (Euclidean distance)
2) Local habitat structure
3) Local habitat heterogeneity
4) Distance (log$_{10}$ transformed)
5) Environmental classification (using a similarity matrix)
6) Large-scale habitat structure (averaged over forest type).

For 2) mean values of habitat structural distance (difference in habitat structure) in the six subplots per plot were used. For 3) standard deviations of habitat structure taken over the six subplots per plot were used. The multiple regression analysis resulted in partial regression coefficients and partial correlation coefficients, which measured the effect of the various predictor matrices on the response matrix after controlling for all other independent predictor matrices (Spencer et al., 2002). At each step of the forward selection procedure, the predictor matrix is entered that produces the equation whose $R^2$ coefficient has the lowest probability. This must also be smaller than or equal to the Bonferroni-corrected p-to-enter value. This continues until no more predictor matrices meet these criteria.
Chapter 3

Results

1. Species richness

During this study, 181 species of birds over 9747 individuals were encountered. There was no significant difference in mean species richness at the local scale among forest types in four of the five guilds (Table 1). Species richness of canopy insectivores was significantly lower in recently logged forest than in primary and older logged forest.

Table 1. Local mean (and standard deviation) species richness assessed in the three forest types.

<table>
<thead>
<tr>
<th>Guild</th>
<th>N</th>
<th>P</th>
<th>L89</th>
<th>L93</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy Omnivores</td>
<td>10</td>
<td>4.83±0.80</td>
<td>4.48±0.86</td>
<td>4.15±0.74</td>
<td>F_{2,31} = 2.381</td>
<td>0.109</td>
</tr>
<tr>
<td>Canopy Insectivores</td>
<td>10</td>
<td>5.73±0.33</td>
<td>5.85±0.62</td>
<td>4.91±1.11</td>
<td>F_{2,30} = 5.058</td>
<td>0.013</td>
</tr>
<tr>
<td>Frugivores</td>
<td>5</td>
<td>2.90±0.60</td>
<td>2.80±0.57</td>
<td>2.33±0.77</td>
<td>F_{2,35} = 1.905</td>
<td>0.170</td>
</tr>
<tr>
<td>Understory Omnivores</td>
<td>50</td>
<td>17.26±2.64</td>
<td>15.34±2.13</td>
<td>15.82±1.76</td>
<td>F_{2,33} = 2.311</td>
<td>0.116</td>
</tr>
<tr>
<td>Understory Insectivores</td>
<td>58</td>
<td>22.96±4.61</td>
<td>25.32±1.73</td>
<td>23.46±3.65</td>
<td>F_{2,32} = 1.252</td>
<td>0.299</td>
</tr>
</tbody>
</table>

At the landscape scale, total rarefied species richness was significantly higher in the canopy omnivore and understory omnivore guilds in primary forest than in logged forest (Table 2 and Fig. 2), but did not differ between the logged forests.

Table 2. Mean species richness and 95% confidence intervals based on simulations for bird guilds. N is the minimum sample size of a given guild in each forest type used for calculating cumulative rarefied species richness.

<table>
<thead>
<tr>
<th>Guild</th>
<th>Habitat</th>
<th>N</th>
<th>Mean</th>
<th>95% Low</th>
<th>95% High</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy Omnivores</td>
<td>P</td>
<td>220</td>
<td>12.88</td>
<td>12.24</td>
<td>13.52</td>
</tr>
<tr>
<td>L89</td>
<td></td>
<td></td>
<td>11.00</td>
<td>11.00</td>
<td>11.00</td>
</tr>
<tr>
<td>L93</td>
<td></td>
<td></td>
<td>10.42</td>
<td>9.20</td>
<td>11.64</td>
</tr>
<tr>
<td>Canopy Insectivores</td>
<td>P</td>
<td>260</td>
<td>16.88</td>
<td>16.24</td>
<td>17.52</td>
</tr>
<tr>
<td>L89</td>
<td></td>
<td></td>
<td>15.82</td>
<td>15.06</td>
<td>16.58</td>
</tr>
<tr>
<td>L93</td>
<td></td>
<td></td>
<td>14.95</td>
<td>14.52</td>
<td>15.38</td>
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<tr>
<td>Frugivores</td>
<td>P</td>
<td>70</td>
<td>7.25</td>
<td>5.71</td>
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<tr>
<td>L89</td>
<td></td>
<td></td>
<td>8.54</td>
<td>7.08</td>
<td>10.00</td>
</tr>
<tr>
<td>L93</td>
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<td></td>
<td>8.87</td>
<td>8.21</td>
<td>9.53</td>
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<tr>
<td>Understory Omnivores</td>
<td>P</td>
<td>750</td>
<td>35.32</td>
<td>34.11</td>
<td>36.53</td>
</tr>
<tr>
<td>L89</td>
<td></td>
<td></td>
<td>32.93</td>
<td>32.43</td>
<td>33.43</td>
</tr>
<tr>
<td>L93</td>
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<td></td>
<td>31.90</td>
<td>31.31</td>
<td>32.49</td>
</tr>
<tr>
<td>Understory Insectivores</td>
<td>P</td>
<td>1150</td>
<td>66.68</td>
<td>64.75</td>
<td>68.61</td>
</tr>
<tr>
<td>L89</td>
<td></td>
<td></td>
<td>71.92</td>
<td>71.39</td>
<td>72.45</td>
</tr>
<tr>
<td>L93</td>
<td></td>
<td></td>
<td>68.29</td>
<td>65.99</td>
<td>70.59</td>
</tr>
</tbody>
</table>
In the canopy insectivore guild, total rarefied species richness was higher in primary forest than logged forest, and higher in older logged than recently logged forest. In the richest guild, the understory insectivores, species richness was higher in older logged than in recently logged forest and higher in recently logged forest than primary forest. In the frugivore guild, total rarefied species richness was higher in recently logged forest than in the primary forest. Total rarefied frugivore species richness did not differ significantly between older logged and primary forest, or between older logged and recently logged forest (Table 2 and Fig. 2).

Fig. 2. Individual based cumulative rarefaction curves of number of bird species per guild, generated with Ecosim. Means and 95% confidence intervals are shown for each forest type. Figures shown are a) canopy omnivores, b) canopy insectivores, c) frugivores, d) understory omnivores, and e) understory insectivores. L93: recently logged forest (open triangles), L89: older logged forest (open diamonds), P: primary forest (filled circles).

**ii Habitat structure**
Chapter 3

Habitat structure differed significantly among forest types (Table 3). There was a significant difference between primary and recently logged forest, and recently and older logged forest, but no significant difference between primary and older logged forest. Because of the large number of possible comparisons a table-wide Bonferroni corrected alpha of 0.002 was used in Table 3.

Table 3. Global and pairwise comparisons between forest types for community similarity. Significant differences are indicated by asterisks, 

\[ *** < 0.001, 0.001 < ** < 0.05. \]

<table>
<thead>
<tr>
<th>Guild/Habitat</th>
<th>Habitat</th>
<th>RAOSIM</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat Structure</td>
<td>Global</td>
<td>0.393</td>
<td>0.001***</td>
</tr>
<tr>
<td></td>
<td>P and L89</td>
<td>0.194</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td>P and L93</td>
<td>0.575</td>
<td>0.001***</td>
</tr>
<tr>
<td></td>
<td>L89 and L93</td>
<td>0.351</td>
<td>0.001***</td>
</tr>
<tr>
<td>Canopy Omnivores</td>
<td>Global</td>
<td>0.174</td>
<td>0.002**</td>
</tr>
<tr>
<td></td>
<td>P and L89</td>
<td>0.210</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td>P and L93</td>
<td>0.258</td>
<td>0.001***</td>
</tr>
<tr>
<td></td>
<td>L89 and L93</td>
<td>0.033</td>
<td>0.256</td>
</tr>
<tr>
<td>Canopy Insectivores</td>
<td>Global</td>
<td>0.112</td>
<td>0.006</td>
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<tr>
<td></td>
<td>P and L89</td>
<td>0.069</td>
<td>0.141</td>
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<td></td>
<td>P and L93</td>
<td>0.229</td>
<td>0.001***</td>
</tr>
<tr>
<td></td>
<td>L89 and L93</td>
<td>-0.005</td>
<td>0.477</td>
</tr>
<tr>
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<td>0.155</td>
<td>0.003</td>
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<td>P and L89</td>
<td>0.203</td>
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<td>P and L93</td>
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<td>L89 and L93</td>
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<td>0.162</td>
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<tr>
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<td>0.001***</td>
</tr>
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<td>P and L89</td>
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</tr>
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<td>P and L93</td>
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<td>L89 and L93</td>
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<td>0.001***</td>
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<td>0.001***</td>
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<tr>
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<td>P and L89</td>
<td>0.259</td>
<td>0.002**</td>
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<tr>
<td></td>
<td>P and L93</td>
<td>0.466</td>
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<tr>
<td></td>
<td>L89 and L93</td>
<td>0.160</td>
<td>0.018</td>
</tr>
</tbody>
</table>

iii Community Similarity

There was a significant global difference (using the RAOSIM values) in community similarity among forest types in all guilds except frugivores (Table 3). In all these guilds there was a significant difference between primary and recently logged forest. In only one guild (understory insectivores) was there a significant difference between primary and older logged forest, and in only one guild (understory omnivores) was there a significant difference between recently logged and older logged forest.
Chapter 3

The amount of variation explained by the environmental dataset and distance varied from less than 6% to 20% (Table 4). Local habitat structure proved significant for all functional groups except frugivores and canopy insectivores, and was the most important explanatory variable for canopy and understory insectivores (Fig. 3).

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**Fig. 3.** Response of community similarity ($\log_{10+1}$ transformed) to difference in local habitat structure. The normalised Euclidean distance metric was used for pairwise comparisons of habitat structure. Low distance values indicate a higher similarity in habitat structural composition. Regression lines are fitted using Statistica for Windows (1996). Filled circles (●) indicate pairwise comparisons between primary plots (PP), open circles (○) pairwise comparisons between logged plots (LL), and crosses (+) pairwise comparisons between a primary and a logged plot (PL). The graph is presented on a log-log scale.

The environmental classification variable explained a significant amount of variation in, frugivores and understory omnivores. Difference in elevation was only significant in canopy omnivores, but it was the most important explanatory variable in that guild. There was no
significantly negative relationship between distance and community similarity in any guild, but an unexpected significantly positive relationship in the understory insectivore guild (Fig. 4). Finally large-scale habitat structure explained a significant amount of variation in all guilds, and was the most important explanatory variable in the understory omnivores.

Fig. 4. As in Fig. 3 but now community similarity is compared with the Euclidean distance between plots.

Discussion

i. Species richness

We found very little difference in species richness among forest types in bird guilds at local scales. Only canopy insectivores showed a significantly higher number of species in primary than logged forest. At the larger spatial scale both canopy guilds and understory omnivores had their highest species richness in the primary forest, while the frugivores
Chapter 3

achieved their highest species richness in recently logged and understory insectivores in older logged forest. This lack of congruence in the impact of disturbance at different spatial scales (local versus larger spatial scale) reflects results from Drapeau (2000) who found that increases in bird diversity at the landscape-scale did not lead to a 'crowding effect' or higher diversity at the local scale.

Table 4. Results of multiple matrix regression analysis on relationship between community similarity and distance and environment. Significant predictor variables are shown with b (slope), p (probability) and r² (amount of variation explained by model). For each guild the total amount of variation explained by the model is shown.

<table>
<thead>
<tr>
<th>Guild</th>
<th>Variable</th>
<th>partial b</th>
<th>p</th>
<th>partial r²</th>
</tr>
</thead>
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<tr>
<td>Canopy Omnivores</td>
<td>Difference in elevation</td>
<td>-0.187</td>
<td>0.001</td>
<td>0.035</td>
</tr>
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<td></td>
<td>Local habitat structure</td>
<td>-0.146</td>
<td>0.001</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td>Large-scale habitat structure</td>
<td>-0.095</td>
<td>0.014</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>Local habitat heterogeneity</td>
<td>0.124</td>
<td>0.024</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>Total explained</td>
<td></td>
<td></td>
<td>0.070</td>
</tr>
<tr>
<td>Canopy Insectivores</td>
<td>Local habitat structure</td>
<td>-0.208</td>
<td>0.001</td>
<td>0.043</td>
</tr>
<tr>
<td></td>
<td>Large-scale habitat structure</td>
<td>-0.085</td>
<td>0.021</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>Distance</td>
<td>0.136</td>
<td>0.002</td>
<td>0.011</td>
</tr>
<tr>
<td></td>
<td>Total explained</td>
<td></td>
<td></td>
<td>0.061</td>
</tr>
<tr>
<td>Frugivores</td>
<td>Large-scale habitat structure</td>
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<td>0.001</td>
<td>0.031</td>
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<tr>
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<td>0.008</td>
<td>0.008</td>
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<tr>
<td></td>
<td>Total explained</td>
<td></td>
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<td>0.039</td>
</tr>
<tr>
<td>Understory Omnivores</td>
<td>Large-scale habitat structure</td>
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<td>0.001</td>
<td>0.124</td>
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<tr>
<td></td>
<td>Local habitat structure</td>
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<td>0.006</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Total explained</td>
<td></td>
<td></td>
<td>0.133</td>
</tr>
<tr>
<td>Understory Insectivores</td>
<td>Local habitat structure</td>
<td>-0.356</td>
<td>0.001</td>
<td>0.127</td>
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<tr>
<td></td>
<td>Large-scale habitat structure</td>
<td>-0.168</td>
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<td>Distance</td>
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<td>0.022</td>
<td>0.005</td>
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<tr>
<td></td>
<td>Total explained</td>
<td></td>
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<td>0.201</td>
</tr>
</tbody>
</table>

In another study, Johns (1996) found that species richness of birds in northern Borneo was highest in logged areas due to the presence of edge species. As in our study Johns (1996) found that differences between primary and logged forest were more pronounced in recently logged (6 years) than older logged (12 years) forest. He likewise found a decline in the species richness of canopy insectivores and understory omnivores and an increase in that of frugivores in logged forest. Contrary to our study, however, he also found a negative relationship between logging and understory insectivore species richness.

Renjifo (1999) found that in Colombia forest raptors, terrestrial insectivores, and large frugivores were highly extinction prone due to forest fragmentation. Nectarivores, small frugivores, and aerial insectivores were, however, highly resilient. Castellata et al. (2000) noted that insectivorous and specialist birds and birds using single vertical zones (e.g., the canopy) are especially sensitive to habitat disturbance, and exhibit a preponderance of local extinctions. Under the logging-induced disturbance in our research site, we did find lowered
richness in the canopy guilds suggesting that canopy birds are indeed more susceptible to disturbance, but although there were less canopy insectivore species in logged forest there were more understory insectivore species.

Our results thus seem to contradict previous studies assertions that understory insectivores were especially susceptible to anthropogenic disturbance. We found that understory insectivore species richness was actually higher in logged forests at larger spatial scales. Results from other studies may be partially explained by their selectively sampling in locally disturbed environments in which understory insectivores indeed show the greatest response to disturbance (see below). Because we sampled across forest types at large spatial scales, our plots were located both in locally disturbed and undisturbed forest.

Differential responses between studies may also be linked to temporal dynamics. Because the habitat quality is most often affected (positively or negatively), rather than being lost (or gained) completely, species tend not to respond to changed environmental conditions instantly (Janzen, 1986). Some are able to tolerate conditions below a threshold level for a limited time. Therefore, a species’ ability to persist in a logged landscape is linked to the temporal dynamics - and nature - of its habitat requirements. For example, if suitable reproductive sites are eliminated due to logging, but are re-established after a few years, many long-lived species may persist, whereas species with shorter life cycles have already gone extinct.

Despite such complexity, consideration of spatial scale can provide insights into the observed results (Pearson, 2002). For example, understory omnivores seemed to experience their environment at a much larger spatial scale than understory insectivores, and are probably not able to survive in small, disturbed (or primary) patches. The scale of assessment and how a species perceives its environment may also interact with other important life history traits, such as generation time, to lead to complex outcomes in community responses to disturbance phenomena such as logging (Morris, 1996). This may explain the increased species richness at the landscape-scale for understory insectivores. The logged forest may be a mosaic of remnant-disturbed patches (with disturbance-adapted species) interspersed with primary and regenerated patches that are acceptable to primary forest species. The mixing of faunas from this process could increase landscape-diversity (Rozenzweig, 1995).

\textit{ii Habitat structure}

We found a significant difference in habitat structure between primary and recently logged forest, and between recently logged and older logged forest, but not between primary and older logged forest. The greatest difference was, however, between primary and recently logged forest. This indicates that eight years post-logging is sufficient time for the habitat structure of a logged forest to roughly resemble that of a primary forest. Likewise, Holdsworth and Uhl (1997) found that the structure of a logged forest could revert to that of a primary forest as logging gaps became packed with saplings. Importantly, this can help to reduce the likelihood of future fires.

\textit{iii Community composition}

Overall community similarity of bird guilds was related to variation in the habitat structure. Community similarity differed most between primary and recently logged forest in all guilds except frugivores, despite the proximity of the primary and recently logged forest.
There were, however, pronounced differences in the relative contribution of different environmental variables to explaining community similarity within guilds.

Within the understory guilds, for example, large-scale habitat structure explained more variation in omnivores (12%) than insectivores (3%). This indicates that generalist omnivores probably experience their environment at different, and probably larger spatial scales, than specialist insectivores and may not be able to survive in disturbed areas. Differences in omnivore community similarity were only related to differences in microhabitat to a limited extent and most of the variation in community similarity was due to gross differences in habitat structure at the landscape-scale among forest types. Variation in local habitat structure, on the contrary, explained 12% of variation in community similarity of understory insectivores.

Species of understory insectivores thus seem to respond to more to variation in the microhabitat and preferentially select suitable microenvironments. This should prove advantageous when faced with an adverse habitat-matrix surrounding suitable isolated habitat patches. Understory insectivores (and canopy insectivores) also the responded significantly to distance, but contrary to all expectations, community similarity actually increased with distance. Firstly, this indicates that none of the bird guilds are dispersal limited within the spatial scales assessed during this study. Secondly, it indicates that insectivores may be preferentially dispersing from primary to the more distant older logged forest, but avoiding the proximate but structurally more different recently logged forest as shown in Fig. 4.

Previously, Pearman (2002) found that nectarivores and frugivores were found in areas of relatively low primary forest cover. Understory insectivores and omnivores, however, were found in areas of relatively high primary forest cover. Overall the community similarity of omnivores and insect gleaners was significantly related to the percentage of primary forest in a radius of hundreds of metres surrounding study sites.

Although it is very difficult and often impossible to experimentally test for large-scale mechanisms (Pearman, 2002) our results on the relationship between community similarity and environmental variation can suggest which guilds are affected by landscape-scale processes, and which seem to be more affected by local conditions. Overall, our results seem to indicate that understory guilds may be more responsive to large-scale phenomena than canopy guilds. Canopy guilds thus seem to select their preferred habitat based on local habitat structural or environmental cues reflecting variation in habitat complexity or heterogeneity. Both groups maintained significantly different assemblages in primary and recently logged forest, but there was no significant difference between the assemblages of older logged and primary forest or older logged and recently logged forest. This suggests that older logged forest is indeed a transition habitat between primary and recently logged forest as hypothesised. Overall, however, we found a reduced landscape-scale species richness of canopy guilds in logged forest. This may indicate that disturbance, especially within the canopy is spatially more pervasive than in other substrata. Laurance (1997; and references therein) define a number of reasons why the distribution of tree gaps in disturbed forest become contagious in space and time. This is related to, among other things, liana infestation around gaps, the tendency of trees bounded by a gap to fall inwards, and a proliferation of short-lived pioneer trees with rapid mortality. This may have the effect of reducing the total area of acceptable habitat to canopy guilds, thereby lowering species richness when compared to an equal area of primary forest.

Although the predictor matrices explained a substantial amount of variation (up to 20%) in guild community similarity, there was a large amount of unexplained variation in each guild. Part of this is inherent to studies of tropical assemblages; among other things this is due to the
abundance of singletons. There are, however, other processes acting on bird assemblages that we did not address. Previous studies (MacArthur et al., 1962; Pearman, 2002) have shown that habitat structure influences the selection of habitats by birds, although this relationship can be obscured by factors such as temporal variation, scale of observation, and regional and historical processes (references in Pearman, 2002). Guild composition can also change from forest interior to edge. In Uganda, frugivore-insectivore and nectarivores favoured edge habitats whereas terrestrial insectivores, bark-gleaning and leaf-gleaning insectivores favoured interior habitats (Dale et al., 2000). Bird species may also respond to phenomena at smaller spatial scales than that assessed during this study. In Panama, bird species that preferred treefall gaps were, for example, very patchily distributed, reflecting the distribution of gaps (Robinson et al., 2000). Future research should focus on assessing patterns of biodiversity at varying scales and ascertaining the scales at which different communities perceive their environment.

In the present study we showed that none of the guilds appeared to be dispersal limited, but instead selected habitat from among the available mosaic of disturbed and undisturbed patches. This may mean that bird guilds have some resilience to large-scale habitat disruption. According to Hubbell (cited in Whitfield, 2002) "if species are closely adapted to fit an ecological niche, communities will be stable, and hard to invade. Reserves can therefore be small." If, on the contrary, species are not adapted to local habitat conditions, but are rather disperse randomly over the landscape then large areas of forest would be necessary to buffer rare species from chance events (Hubbell, 2001). With this in mind we note that at the landscape-scale this study suggests that understory generalist omnivores may, in fact, be more susceptible to disturbance. Especially large-scale processes such as habitat loss and fragmentation associated with ENSO-induced burning (Nepstad et al., 1999) and land conversion as a result of illegal logging (Jepson et al., 2001) may be detrimental to generalist omnivores. As of present, we do not know of any landscape-scale studies of birds in recently fragmented landscapes in Borneo, but we expect guilds that respond to landscape-scale processes to be especially susceptible to species loss. This may have important consequences for Borneo's faunal diversity since generalist feeding habits and dispersal ability are strongly associated with high species diversity (Owens et al., 1999).

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References


Chapter 3


