

Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda

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Abstract

I examined the lingering effects of past timber management practices on the vegetation structure and bird community of Kibale National Park, Uganda. I compared four forest treatments: unlogged native forest (UL), two that were selectively logged at low (LL) and high (HL) intensities in the 1960s, and a conifer plantation (PL). Forest-dependent birds were best represented at UL. LL was similar to UL in both vegetation structure and bird community composition, although some forest-dependent bird species were missing from the former. HL had significantly less canopy closure and lower tree density than other plots as a result of the combination of extensive secondary damage and natural disturbance patterns that prevented the reclosure of the forest canopy. Thirty-one percent of the forest-dependent bird species observed during the study were not detected at HL. At PL, bird species richness and bird abundance were about a third of those observed in other plots. There were significant correlations between heterogeneity of tree distribution (horizontal heterogeneity) and abundance and species richness of birds across plots. Abundance and species richness of all, forest-dependent, and forest generalist birds were highest in plots with intermediate measures of horizontal heterogeneity, which were mostly unlogged or lightly logged. If reduced-impact logging practices are not implemented during selective logging operations in tropical forests, consequent long-term changes in vegetation structure may result in significant declines in the populations of some forest-dependent species, as was observed in Kibale National Park. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Uganda; Tropical forestry; Selective logging; Vegetation structure; Bird communities

1. Introduction

Selective timber extraction is often proposed as a sustainable, low-impact alternative to clear-cut logging, and is the most frequent form of logging in the tropics (Repetto and Gillis, 1988; Abramovitz and Matoon, 1999; Anonymous, 2001). However, despite the long-term reductions in financial costs and environmental damage associated with reduced-impact logging (RIL), because of the initial costs and lack of governmental incentives, training and guidance, most tropical selective logging operations do not employ RIL, and cause high levels of secondary damage (Putz et al., 2000, 2001). Even though only 3–10% of the trees in a selectively logged area are removed for commercial use, 40–80% of the trees are destroyed as a result of the creation of logging tracks, falling trees bringing down neighboring trees, and heavy activity of forestry machinery.

Basal area, canopy cover, and canopy height are reduced while average gap size and distance between trees increase. The distribution of trees becomes less uniform, with gaps separating unlogged patches (Skorupa and Kasenene, 1984; Johns, 1985, 1988, 1992; Struhsaker, 1997; Thiollay, 1997).

Structural changes in vegetation modify the forest microclimate by altering temperature, humidity, light, and wind levels. Higher temperatures and lower humidity result in soil desiccation, higher seed mortality, and lower tree recruitment (Pinard and Putz, 1996). Stimulated by high light levels, rapidly growing shrubs frequently become dominant (Struhsaker, 1997). This dense shrub cover attracts seed predators such as rodents and insects (Isibirye-Basuta and Kasenene, 1987; Pinard and Putz, 1996), and herbivores such as African elephants (*Elephas maximus*) and red river hogs (*Potamochoerus porcus*; Nummelin, 1990; Struhsaker et al., 1996), which further retard tree regeneration. Increased wind breaks branches and fells trees, resulting in a more open forest canopy that promotes the growth

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of understory shrubs. These changes may persist for decades (Thiollay, 1997; Struhsaker, 1997).

After the wholesale clearance of large areas of tropical forest in southeast Asia and western Africa, the attention of the international logging community has now turned towards the remaining relatively pristine rainforests of Latin America and central Africa (Dranzoa, 1995). I investigated the long-term effects of forestry practices on the forest bird community and vegetation structure of a medium altitude Afrotropical forest. My objectives were to (1) assess the long-term changes in the vegetation structure of sites with different timber management histories, (2) compare the forest bird communities of these sites, and (3) investigate whether any measures of vegetation structure correlated with the abundance and species richness of forest bird species. Two of the sites had been selectively logged (14 and 21–80 m³/ha), one was almost unlogged and the fourth was a *Pinus* plantation.

2. Methods

2.1. Study area

This study was conducted at Kanyawara biological field station of Makerere University, situated in medium altitude (1530 m) moist evergreen forest of Kibale National Park (766 km²) in western Uganda (0°13'N–0°41'N and 30°19'E–30°32'E; see Struhsaker, 1997, for a detailed map). Mean annual rainfall at Kanyawara is approximately 1740 mm, with a dry season between May and August. Yearly mean temperature is 23.1 °C. The forest is a mixture of pure forest stands (60%) and successional grassland, swamp forests, and secondary forests (Chapman and Chapman, 1996).

2.2. Study sites

Between June and August 1996, I collected data from 10 plots distributed in approximately 80 ha in each of four compartments: unlogged forest (K-30, 282 ha), lightly logged forest (K-14, 405 ha), heavily logged forest (K-15, 347 ha), and an exotic *Pinus caribbaea*/*Pinus patula* plantation (K-34/ Nyakatojo, 400 ha; Struhsaker, 1997). Due to the limitations of the trail grid, I gathered data from only one compartment for each treatment. Because the study plots were widely separated, I make the assumptions that the data obtained is representative of the vegetation structure and bird community of Kanyawara and that the effects of pseudoreplication were minimal (Oksanen, 2001). The results should be interpreted in light of these assumptions.

The forest at Kanyawara was originally classified as *Parinari* forest and vegetative features such as cumulative basal area, canopy cover and stem density vary by

only about 5% across all *Parinari* forest subtypes (Kingston, 1967, in Chapman and Chapman, 1997). I will be using the abbreviations UL (unlogged), LL (lightly logged), HL (heavily logged), and PL (plantation) for the treatments throughout the paper.

UL is the least disturbed of the compartments. Although it was occasionally logged by pit-sawyers between 1950 and 1970, no commercial, mechanized, large-scale logging was done and fewer than three trees were removed per km² (Struhsaker, 1997). This is considered to be similar to natural treefall rates, with little, if any, impact on wildlife (Skorupa and Kasenene, 1984). Like past researchers (Dranzoa, 1995; Chapman and Chapman, 1996, 1997; Struhsaker, 1997), I used this “unlogged” site as the forest control treatment. *Parinari excelsa*, *Celtis durandii*, and *Markhamia platycalyx* are the dominant trees, and *Mimulopsis solmsii* and *Palisota schweinfurthii* commonly occur in the understory (Struhsaker, 1997). LL, vegetationally similar to UL, was selectively logged in 1969 at an average rate of 14 m³/ha (about 400 trees/km²) resulting in a tree basal area reduction of 25% (Skorupa and Kasenene, 1984; Struhsaker, 1997).

HL was selectively logged in 1968–1969. Even though the official estimate of logging for HL is 21 m³/ha, Dranzoa (1998) suggested that the actual logging density was much higher, possibly 80 m³/ha or more. The basal area reduction was 47% (Struhsaker, 1997). The most common tree species are *Diospyros abyssinica*, *Markhamia platycalyx*, and *Celtis durandii*, and there is dense undergrowth of *Acanthus* and *Mimulopsis* spp. UL, LL, and HL have originally been classified as *Parinari* forest, are well matched in their vegetative affinities, topography, and climate (Skorupa and Kasenene, 1984; Struhsaker, 1997).

PL is a *Pinus caribbaea*/*Pinus patula* plantation dating from 1963 when trees were planted over elephant grass (*Pennisetum purpureum*). Although this is not native forest, it is a useful site for the purpose of this study since exotic tree plantations often form a part of tropical forestry operations to facilitate the reformation of native forest cover, and PL hosts many colonizing forest plants utilized by forest birds and mammals (Chapman and Chapman, 1996). The shrubs *Achyranthes aspera*, *Polliia condensate*, and *Pteridium aquilinum* as well as many recolonizing indigenous tree species commonly occur in the understory. Since September 1993, logging operations involving portable sawmills and/or pit-sawing have taken place at this site (Chapman and Chapman, 1996).

2.3. Vegetational surveys

Vegetational structural measurements were conducted as point surveys and included diameter at breast-height (DBH), point-centered quarter measurements of tree

distance (PQD), percent canopy closure (PCC), and vertical vegetation distribution (VVD).

The locations of point surveys were evenly distributed across the trail grid in each compartment, with at least 50 m between each survey. The surveys were conducted at least 10 m away from the trails, which were approximately 1 m wide on average. Ten surveys were conducted in each plot, for a total of 100 surveys for each treatment. Percent canopy closure (Jennings et al., 1999) was measured using a convex mirror (type-A spherical) densiometer. Densiometer readings in four directions were averaged for each point. This method over-estimates canopy closure in areas with a high understory-to-canopy ratio, such as HL (Kasenene, 1987, in Dranzoa, 1995).

To measure vertical vegetation structure, I used a clinometer and a 3-m measuring stick to estimate vegetation presence-absence at 0.5, 1, 2, 3, 5, 10, 15, 20, 25, and 30+ m. Facing north, I placed the stick vertically on the ground, and checked for vegetation presence within a circle of 5 cm radius at each height level. For heights > 5 m, I looked along the stick up into the canopy, and estimated each height level. Based on estimates of tree heights that were later measured, height estimations were accurate to approximately $\pm 6\%$. When I had a doubt, I measured the height with a clinometer.

At each sampling point, I measured the distance from the point to the nearest tree with at least 10 cm DBH in each quarter of a hypothetical circle (the point-quarter distance, PQD; Roth, 1976). I also measured the DBH of each tree.

2.4. Bird surveys

I used the fixed-area survey method of Thiollay (1997), which makes cross-site comparisons possible and reduces the bias that results from unequal detectability. Even though all the sites surveyed were forested, there are bound to be differences in habitat openness, which affects bird detectability (Bibby et al., 2000). Like most bird survey methods, this method is biased against nocturnal species and against quiet and secretive species that do not flush easily (Bibby et al., 2000). The results must be interpreted with these caveats in mind.

I use the survey results only as indicators of relative frequency of occurrence rather than as estimates of absolute density. Each bird survey covered an area of 50×50 m (0.25 ha). Survey areas were distributed evenly, with at least 100 m between areas and at least 200 m between surveys conducted in the same day. For each survey, I covered 50 m in 20 min, noting the presence of any birds seen or heard within 25 m on each side of transect. I included the birds that I flushed from the survey area. Birds that were flying over or through the survey area were not counted. Each survey

covered one habitat, all surveys took place at least 50 m away from any habitat edges and swampy areas were avoided. All surveys were conducted between 06:30 and 12:00, the time of greatest bird activity. Six bird surveys were conducted in each plot, for a total of 60 surveys per treatment.

2.5. Data analysis

2.5.1. Vegetation structure

Since higher habitat structural heterogeneity often increases bird species richness due to the presence of more diverse nesting and foraging resources (MacArthur and MacArthur, 1961; Roth, 1976), I calculated indices of horizontal heterogeneity of vegetation (IHH) and vertical heterogeneity of vegetation (IVH). IVH is the Shannon–Wiener index for vertical vegetation distributions (H'_{VVD}), taking the number of vegetation touches at each height as individuals in that class. I compared the IVH (H'_{VVD}) values using the appropriate *t*-test (Magurran, 1988). IHH (Roth, 1976) is the coefficient of variation of point-centered quarter distance (PQD) measurements where:

$$IHH = (\text{Standard deviation (PQD)})/(\text{Average (PQD)})$$

IHH is lowest if trees are distributed uniformly, higher for a random distribution and highest for a clustered distribution.

DBH distribution and vertical vegetation distribution were compared between sites using Morisita-Horn index of similarity (MHIS; Magurran, 1988) where:

$$MHIS = \left(2 \sum (n_{i,a} \cdot n_{i,b}) \right) / (N_a \cdot N_b \cdot (d_a + d_b))$$

for *i* classes (of DBH and vegetation height), $n_{i,a}$ is the number of measurements in the *i*th class at site A, $n_{i,b}$ is the number of measurements in the *i*th class at site B, N_a is the total number of measurements at site A, N_b is the total number of measurements at site B,

$$d_a = \left(\sum n_{i,a}^2 \right) / N_a^2$$

and

$$d_b = \left(\sum n_{i,b}^2 \right) / N_b^2.$$

2.5.2. Bird communities

Species were assigned to the category of forest-dependent species (FD), forest generalists (FG) and non-forest species (NF), based on Bennun et al. (1997) and Dranzoa (1995). Forest-dependent species such as

crowned hawk-eagle (*Steophanoaetus coronatus*) and gray parrot (*Psittacus erithracus*) do not occur outside primary forests and are mainly restricted to forest interior and understory. Forest generalists, such as crested guineafowl (*Guttera pucherani*) and African green-pigeon (*Treron calva*), mainly occur in the canopy, edge and treefall gaps of undisturbed forest. They are also frequently found in secondary forest and have higher tolerance of disturbance. Non-forest species such as common bulbul (*Pycnonotus barbatus*) African and yellow white-eye (*Zosterops senegalensis*) are not found in forest except in the herbaceous vegetation of large gaps, as transients and in the conifer plantation.

Birds were also categorized into 13 feeding guilds such as frugivores, bark-gleaning insectivores, granivores, etc. based on Dranzoa (1995). I used EstimateS (Colwell, 1997) to estimate richness of all species and species of different forest-dependence classes, using ACE (Abundance-based coverage estimator), ICE (Incidence-based coverage estimator; Chazdon et al., 1998), Chao1, Chao2, Jackknife1, Jackknife2, Michaelis-Menten, and Bootstrap methods (Colwell and Coddington, 1994).

I compared the avifaunas of different treatments using Morisita-Horn index of similarity, substituting the total number of individuals at site A for N_a and the number of individuals in the i th species at site A for $n_{i,a}$.

3. Results

3.1. Vegetation structure

HL had significantly less canopy closure (all $t > 5.23$, all $P < 0.0001$, $n = 100$ /treatment) than other treatments (Table 1), which were not significantly different from each other (all $t < 0.57$; all $P > 0.5$). Average DBH differed significantly among treatments (all $t > 2.60$, all $P < 0.001$, $n = 400$ /treatment), except between UL and LL ($t = 1.71$, $P = 0.087$). Average PQD values (Table 1) were also significantly different between treatments (all $t > 3.64$, all $P < 0.001$, $n = 400$ /treatment), except between UL and LL ($t = 1.75$, $P = 0.08$). DBH distribution was significantly different between PL and the other treatments (all $\chi^2 > 88.16$, all $P < 0.01$), but did not

significantly differ between other treatments (all $\chi^2 < 18.81$, all $P > 0.10$). At PL, the mode of DBH distribution was 35 cm whereas in other sites it was 10 cm.

Vertical vegetational distribution (Table 1) was significantly different between treatments (all $\chi^2 > 30.08$; all $P < 0.01$) as well, except between UL and LL ($\chi^2 = 5.29$, $P > 0.25$). HL had significantly less vertical heterogeneity (IVH) than the rest of the sites (all $t > 4.546$, all $P < 0.001$). The index of horizontal heterogeneity, based on PQD values (Table 1), revealed that PL was the least horizontally heterogeneous treatment, whereas HL had the highest horizontal heterogeneity and UL and LL had intermediate values.

MHIS was highest between UL and LL for all vegetational measures (Table 2). In terms of vertical distribution of vegetation, UL and LL were more similar to PL than to HL, whereas the opposite was true for DBH distribution.

3.2. Bird communities

3.2.1. Richness

One hundred and twenty-eight species were observed during the study (Fig. 1). HL had the highest numbers of individuals and species as a result of the high species richness of forest generalist and non-forest species at this site. However, it should be noted that HL also had the most open vegetation structure, hence best visibility. UL had the highest observed and predicted species richness of forest-dependent species.

3.2.2. Similarity

Non-plantation treatments shared 76–83% of their species and each shared 45–47% of its species with PL. When all species were considered, MHIS showed a similar pattern (Table 3). UL and LL shared 80% of their non-forest species, whereas UL and HL shared 36%, and LL and HL shared 45%. The MHIS values reflected these differences.

3.2.3. Abundance and rarity

A species was considered rare if it made up less than 1% of the total sample. When the proportion of rare species to the total number of species in all the surveys

Table 1
Vegetational structural parameters of sites with standard errors

Parameter	UL	LL	HL	PL
Average PCC (cm)	91.05 ± 0.85	91.56 ± 0.78	78.71 ± 2.20	91.04 ± 0.47
Average PQD (cm)	318.00 ± 8.98	296.29 ± 8.53	598.10 ± 25.17	259.88 ± 5.24
Average DBH (cm)	30.70 ± 1.15	28.09 ± 0.99	23.70 ± 0.69	34.04 ± 0.56
H' DBH	2.52	2.37	2.13	2.20
IHH (CV of PQD)	0.58	0.58	0.84	0.40
IVH (H' VVD)	2.28	2.29	2.13	2.26

CV, coefficient of variation; DBH, diameter at breast-height; H', Shannon's diversity index; IHH, index of horizontal heterogeneity; PQD, point-quarter distance; PCC, percent canopy closure; VVD, vertical vegetation distribution.

Table 2
Morisita-Horn similarity of diameter-at-breast height (below diagonal) and vertical vegetational distribution (above diagonal)

	UL	LL	HL	PL
UL	–	88	57	70
LL	80	–	60	72
HL	73	79	–	52
PL	44	39	36	–

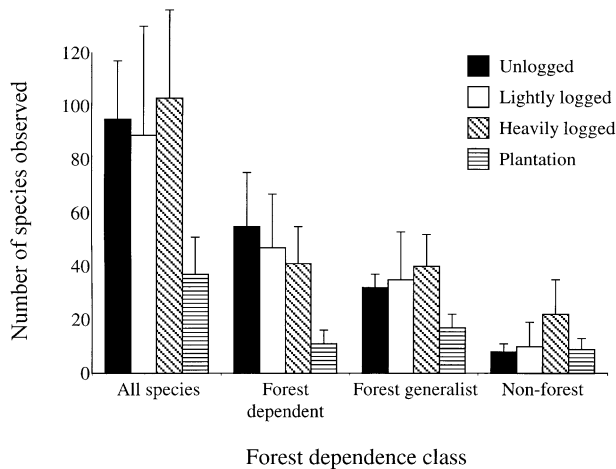


Fig. 1. Observed and estimated bird species richness values. Based on methods provided in EstimateS (Colwell, 1997). The solid bars are the observed numbers of species and the “error bars” indicate the range of species richness estimates provided by EstimateS.

was calculated, values for forest sites ranged from 65 to 71%, but this proportion for PL was 38% (Fig. 2). Yellow-whiskered greenbul (*Andropadus latirostris*) was the most abundant species in each treatment. The 10 species with the highest number of observations made up about 40% of the total counts in the forest treatments, while this figure was 75% for PL.

3.3. Effects of vegetation structure on bird species richness

Average canopy closure, tree diameter-at-breast-height and index of horizontal heterogeneity for plots all showed significant correlations ($P < 0.01$) with overall species richness and abundance of birds detected during surveys in plots. This was the case both when non-PL sites were examined separately and when PL was included. The correlations were negative for canopy closure and diameter-at-breast-height, and r^2 values were around 0.20. For these variables, the correlations were not significant when calculated for forest-dependent and non-forest birds separately ($r^2 < 0.09$, $P > 0.05$). The correlation was positive, however, for index of horizontal heterogeneity (for non-PL plots only, $r^2 > 0.42$ and $P < 0.0001$; for all plots, $r^2 > 0.56$ and

Table 3
Morisita-Horn similarity of bird community composition

	UL	LL	HL	PL
UL	–	76/69	69/49	40/57
LL	79/75	–	68/68	43/53
HL	70/68	71/63	–	48/52
PL	45/32	47/28	52/34	–

Values are given for all (below diagonal and left), forest-dependent (below diagonal and right), forest generalist (above diagonal and left), and non-forest (above diagonal and right) species.

$P < 0.0001$) for all groups except NF birds (Fig. 3). Bird species richness and abundance at plots reached an asymptote at intermediate values of horizontal heterogeneity around 0.7.

4. Discussion

The plantation and heavily logged treatments differed significantly from unlogged and lightly logged treatments in a number of parameters of vegetation structure and avian community composition. Despite a high rate of native plant colonization (Chapman and Chapman, 1996), the plantation’s avifauna was highly impoverished. Thirty-one percent of the forest-dependent bird species detected during the study were not observed at HL, in spite of its high overall bird species richness. In addition, the study took place during dry season, when most bird species were not breeding and would be expected to be less habitat-specific. UL and LL were almost identical in terms of vegetation structure and about 85% of the forest-dependent bird species present/predicted at UL were also present/predicted at LL, which indicates that at low intensities, selective extraction may have limited long-term impact on some forest bird communities.

4.1. Differences in vegetation structure

LL did not exhibit significant differences from UL in any aspects of vegetation structure measured in this study, which agrees with previous research (Struhsaker, 1997). The low intensity of initial logging seems to have prevented increased natural disturbance and made it possible for the vegetation structure to revert to that of unlogged forest.

On the other hand, three decades after logging, the vegetation structure of HL was still significantly different from the vegetation structure of other treatments. There was significantly less canopy closure, the average DBH was significantly lower and the trees were significantly further apart. There were more than three times fewer trees > 50 cm DBH in HL than at LL and at UL.

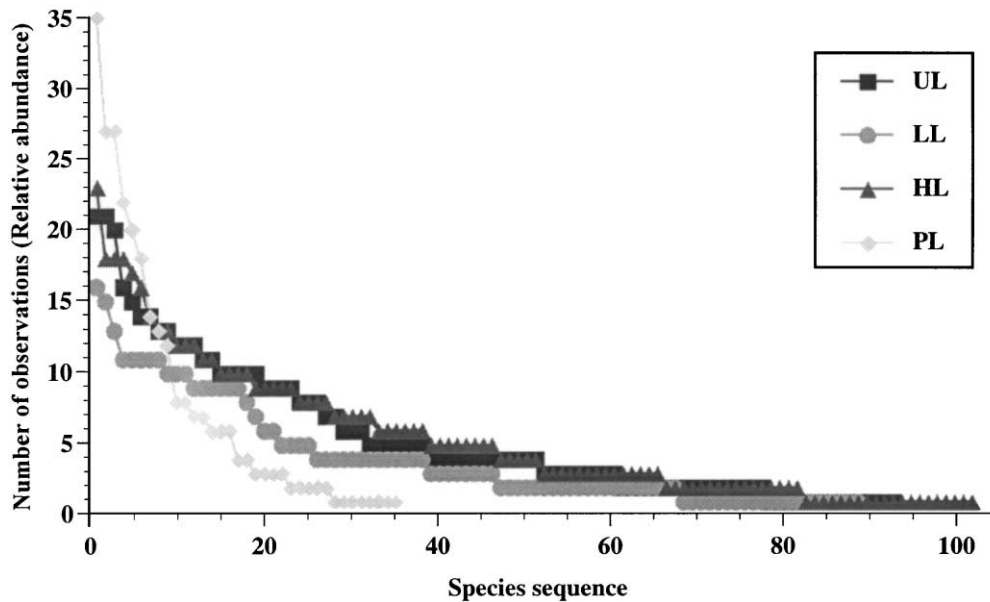


Fig. 2. Rank abundance plots of bird species observed. The most common species, yellow-whiskered greenbul (*Andropadus latirostris*), was not included because its high abundance at all sites (Appendix) obscures the differences between species distribution curves. The log–series distribution of PL reflects its low species richness.

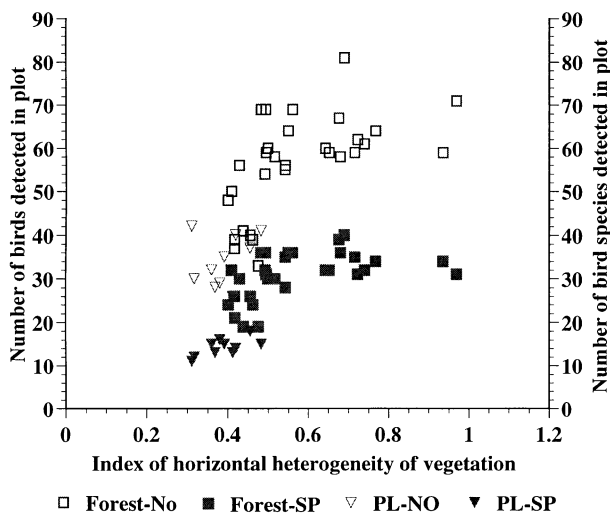


Fig. 3. Intermediate values of horizontal heterogeneity of vegetation result in highest overall abundance and species diversity in plots. ForestNO and ForestSP refer to cumulative abundance and species diversity values at HL, LL and UL plots. PlantationNO and PlantationSP refer to corresponding values in PL plots.

These results parallel the past findings of significantly lower canopy closure, foliage diversity index, basal area of trees, and number of stems, and significantly higher rates of treefall, undergrowth, and densities of elephants, deer, rodents, and other seed predators at HL when compared to UL and LL (Skorupa and Kasenene, 1984; Isibirye-Basuta and Kasenene, 1987; Struhsaker et al., 1996; Chapman and Chapman, 1997). Skorupa and Kasenene (1984) also noted that in Kibale, beyond a threshold of logging disturbance of about 25%, the high

rate of natural treefall hinders the reestablishment of forest cover.

PL was characterized by significantly lower diversity of tree DBH distribution (likely indicating limited recruitment) and a more uniform spacing of trees, which make PL significantly less heterogeneous in terms of vegetation structure than the non-plantation treatments.

4.2. Differences in bird communities

Even though the field work for this study was limited to 3 months, the bird community compositions of UL and HL were similar to those reported in Dranzoa's (1998) multi-year study and are unlikely to be artifacts of the relatively short but intensive sampling period.

High similarity values between the bird communities of LL and UL indicate that these treatments were more similar to each other than either was to HL. The lower number of primary forest species detected at LL may be partially explained by its location to a frequently used 3-m wide dirt road (Karambi road), but the presence of a highly secretive and shy understory specialist like green-breasted pitta (*Pitta reichenowi*) at LL indicates good potential habitat for sensitive primary forest understory specialists. Only a few timber trees were extracted from parts of LL (C. Chapman, personal communication), which may have contributed to the persistence of most forest-dependent bird species.

HL exhibited higher overall bird species richness than UL, LL and PL. As was also recorded by Dranzoa (1995, 1998), however, the high species richness of HL was mainly a result of the presence of many non-forest species (Fig. 1). The infusion of non-forest

species, such as white-chinned prinia (*Prinia leucopogon*) and blue-headed coucal (*Centropus monachus*), is thought to be caused by “vertical compression”, reduced canopy cover and increased open habitat making it possible for an abundance of non-forest and forest edge species to be present in addition to forest interior species (Thiollay, 1997; Dranzoa, 1995). Also, significantly fewer birds were recaptured with mist nets at HL than were recaptured at UL ($\chi^2 = 4.92$, $P < 0.05$) or LL ($\chi^2 = 6.61$, $P < 0.05$; C. Sekercioglu, unpublished data), indicating that many forest birds may be transients going through HL while moving between the unlogged areas around HL (Dranzoa, 1995).

Out of the 59 forest-dependent species detected during the course of the study in all treatments, six were not observed at UL, whereas 18 were not found at HL, five of which were terrestrial understory specialist insectivores, (such as red-tailed ant-thrush, *Neocossyphus rufus*), a group that was also shown to be sensitive to forest disturbance in other studies (Thiollay, 1997; Dranzoa, 1998; Aleixo, 1999; Sekercioglu et al., 2002). The species that were not observed at HL had low abundances at UL and LL, so it is possible that some were present at HL at densities below the detectability threshold. However, HL had the biggest sample size, had more open vegetation structure and hence better visibility, and all the richness estimators (Colwell, 1997) predicted about 20 fewer forest-dependent species at HL than at UL and about eight fewer than at LL. These figures indicate that even after three decades, the high-level of initial disturbance at HL, exacerbated by increased wind, shrub, rodent and elephant densities, has prevented the reformation of complete forest cover, resulting in the long-term loss of a large number of forest-dependent bird species, even though mostly intact forest surrounds HL (Struhsaker, 1997).

Forty-eight forest-dependent species detected at other sites were not found at PL. Overall bird species richness was less than a third of that observed in other treatments. Compared to the native forest treatments, fewer species dominated the samples and there were fewer rare species. Although PL is also surrounded by mostly intact primary forest and has had high recruitment of indigenous tree species (Chapman and Chapman, 1996), the low richness and abundance of forest-dependent species indicate that most native bird species were unable to establish resident populations. A few bird species dominated the plantation at the expense of many forest-dependent species that most likely disappeared as a result of the combination of low structural and botanical diversity.

4.3. *Vegetation structure and bird species richness*

Horizontal heterogeneity showed a highly significant relationship with all measures of bird species richness or

abundance, except those of non-forest birds, which would not be expected to be dependent on forest structural diversity. The abundance and species richness of all birds, as well as those of forest-dependent and forest generalist species graphed separately, reached an asymptote at intermediate values of horizontal heterogeneity of vegetation structure. Lowest overall abundance of forest birds was observed at PL, where trees were most homogeneously distributed. Compared to UL and LL, the forest bird abundance values were also lower at HL, where the variation in tree distribution was highest.

It is likely that forest birds were negatively affected by the highly homogeneous tree distribution at PL as a result of the number of niches being limited since patchy habitats are considered to provide more diverse nesting and foraging resources than locally uniform areas (Roth, 1976). In addition, forest-dependent birds declined at highly heterogeneous HL where there were many large, open patches avoided by forest-dependent birds (Dranzoa, 1995). It is possible that the number of niches and/or the area of suitable habitat available for forest birds is maximized at intermediate values of horizontal heterogeneity where there is sufficient variation in forest structure but not many large, open patches.

5. **Conclusion and recommendations**

Even three decades after selective logging took place in Kibale, its effect on forest structure and on the bird community was still discernible, especially where the intensity of logging was highest. Of the vegetation structural variables examined, horizontal heterogeneity of vegetation had by far the most significant, positive relationship with abundance and richness of tropical forest birds. In some temperate areas, increased horizontal heterogeneity has been shown to correlate significantly with increased bird species richness (Roth, 1976; Berry and Bock, 1998) and increased nesting success (Nolte and Fulbright, 1996). The results of this study suggest that more attention should be given to horizontal heterogeneity in tropical habitats.

Selective logging in the tropics is compatible with the preservation of forest only when it is truly selective, not only of the trees that are taken, but also, in terms of the total number of trees that are destroyed through logging and related activities. This study provides support for the fact that selective timber extraction can be compatible with the preservation of the structural and biological integrity of a tropical forest when logging intensity is kept below a certain threshold and parts of the logging compartment are left unlogged to provide source populations of forest organisms. Above that threshold, natural disturbance patterns are likely to delay the formation of the original forest cover significantly and

result in the disappearance of some forest-dependent species, as was the case in Kibale National Park. Adherence to low-impact guidelines and ecologically sound harvest cycles in tropical logging operations can provide good habitat for many tropical forest species, as well as being more economically profitable in the long-run (Putz et al., 2000). In addition to providing valuable ecosystem services (Daily, 1997) such as water purification and carbon sequestration, selectively logged forests can be significant additions to the limited network of strictly protected areas.

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Appendix. Numbers of bird species observed during surveys at each compartment

ForDep is the degree of forest dependence based on Bennun et al. (1997). FD indicates forest-dependent, FG indicates forest generalist and NF indicates non-forest species. AFGIN, Aerial foraging insectivore; FRGR, Frugivore-Granivore; FRIN, Frugivore-Insectivore; FRUG, Frugivore; GRIN, Granivore-Insectivore; NECIN, Nectarivore-Insectivore; PRIN, Predator-Insectivore; SALIN, Sallying Insectivore; TUSIN, Terrestrial-understory insectivore; UFGIN, Understory foliage-gleaning insectivore; BGIN, Bark-gleaning insectivore. Nomenclature based on Clements (2000).

Guild	ForDep	Family and common name	Scientific name	UL	LL	HL	PL	Total
		Accipitridae						
RAPT	FD	Crowned Hawk-Eagle	<i>Sthephanoaetus coronatus</i>	2	0	1	0	3
		Phasianidae						
GRIN	FG	Scaly Francolin	<i>Francolinus squamatus</i>	1	1	2	0	4
		Numididae						
GRIN	FG	Crested Guineafowl	<i>Guttera pucherani</i>	10	4	5	0	19
		Columbidae						
FRGR	FG	African Green-pigeon	<i>Treron calva</i>	7	6	6	0	19
FRGR	FG	Tambourine Dove	<i>Turtur tympanistria</i>	9	9	2	0	20
FRGR	NF	Blue-spotted Wood Dove	<i>Turtur afer</i>	0	0	1	3	4
FRUG	FD	Rameron Pigeon	<i>Columbia arquatrix</i>	2	0	0	0	2
FRGR	FD	Afep Pigeon	<i>Columbia uncinata</i>	4	3	4	0	11
FRGR	FD	Lemon Dove	<i>Columba larvata</i>	1	2	0	0	3
FRGR	NF	Red-eyed Dove	<i>Streptopelia semitorquata</i>	3	3	9	13	28
		Psittacidae						
FRUG	FD	Gray Parrot	<i>Psittacus erithacus</i>	2	1	0	0	3
		Musophagidae						
FRUG	FG	Great Blue Turaco	<i>Corythaeola cristata</i>	12	11	12	0	35
FRUG	FD	Black-billed Turaco	<i>Tauraco schuettii</i>	6	3	10	0	19
		Cuculidae						
AFGIN	FG	Red-chested Cuckoo	<i>Cuculus solitarius</i>	11	15	7	8	41
AFGIN	FD	Dusky Long-tailed Cuckoo	<i>Cercococcyx mechowi</i>	13	11	7	0	31
AFGIN	FD	Olive Long-tailed Cuckoo	<i>Cercococcyx olivinus</i>	0	0	2	0	2
AFGIN	FG	African Emerald Cuckoo	<i>Chrysococcyx cupreus</i>	14	8	8	0	30
AFGIN	FG	Yellowbill	<i>Ceuthmochares aereus</i>	4	2	3	0	9

Appendix (continued)

Guild	ForDep	Family and common name	Scientific name	UL	LL	HL	PL	Total
PRIN	NF	White-browed Coucal	<i>Centropus superciliosus</i>	0	4	5	0	9
PRIN	NF	Blue-headed Coucal	<i>Centropus monachus</i>	0	1	11	0	12
		Strigidae						
RAPT	FG	African Wood-owl	<i>Strix woodfordii</i>	0	1	0	0	1
		Trogonidae						
SALIN	FG	Narina Trogon	<i>Apaloderma narina</i>	10	9	9	4	32
		Alcedinidae						
SALIN	FG	Blue-breasted Kingfisher	<i>Halcyon malimbica</i>	3	4	0	0	7
SALIN	NF	African Pygmy-kingfisher	<i>Ispidina picta</i>	2	0	0	1	3
		Coraciidae						
SALIN	FD	Blue-throated Roller	<i>Eurystomus gularis</i>	2	2	0	0	4
		Phoeniculidae						
BGIN	FD	White-headed Woodhoopoe	<i>Phoeniculus bollei</i>	6	11	10	0	27
		Bucerotidae						
FRUG	NF	Crowned Hornbill	<i>Tockus alboterminatus</i>	5	1	1	0	7
FRUG	FG	Black-and-white-casqued Hornbill	<i>Ceratogymna subcylindricus</i>	21	7	5	1	34
		Capitonidae						
FRUG	FG	Gray-throated Barbet	<i>Gymnobucco bonapartei</i>	1	1	0	0	2
FRIN	FG	Speckled Tinkerbird	<i>Pogoniulus scolopaceus</i>	5	3	5	0	13
FRIN	FG	Yellow-rumped Tinkerbird	<i>Pogoniulus bilineatus</i>	10	9	12	7	38
FRUG	FD	Yellow-spotted Barbet	<i>Buccanodon duchaillui</i>	4	6	6	0	16
FRUG	FG	Hairy-breasted Barbet	<i>Tricholaema hirsuta</i>	5	4	4	0	13
FRIN	FG	Yellow-billed Barbet	<i>Trachyphonus purpuratus</i>	10	2	8	0	20
		Indicatoridae						
AFGIN	NF	Lesser Honeyguide	<i>Indicator minor</i>	0	0	1	0	1
AFGIN	FD	Willcock's Honeyguide	<i>Indicator willcocksi</i>	1	1	0	0	2
		Picidae						
BGIN	FD	Tullberg's Woodpecker	> <i>Campethera tullbergi</i>	0	1	0	0	1
BGIN	FG	Brown-eared Woodpecker	<i>Campethera caroli</i>	4	1	5	6	16
BGIN	NF	Cardinal Woodpecker	<i>Dendropicops fuscescens</i>	0	0	1	0	1
BGIN	FG	Golden-crowned Woodpecker	<i>Dendropicops xantholophus</i>	3	0	2	0	5
		Eurylaimidae						
SALIN	FD	African Broadbill	<i>Smithornis capensis</i>	5	2	7	2	16
		Pittidae						
TUSIN	FD	African Pitta	<i>Pitta angolensis</i>	1	0	0	0	1
TUSIN	FD	Green-breasted Pitta	<i>Pitta reichenowi</i>	0	1	0	0	1
		Pycnonotidae						
FRIN	FD	Plain Greenbul	<i>Andropadus curvirostris</i>	5	2	6	0	13
FRIN	FG	Little Greenbul	<i>Andropadus virens</i>	12	10	18	8	48
FRIN	FG	Yellow-whiskered Greenbul	<i>Andropadus latirostris</i>	79	82	107	66	334
FRIN	FD	Slender-billed Greenbul	<i>Andropadus gracilirostris</i>	9	4	7	0	20
FRIN	FD	Eastern Mountain-greenbul	<i>Andropadus nigriceps</i>	2	1	3	0	6
FRIN	FD	Toro Olive-greenbul	<i>Phyllastrephus hypochloris</i>	0	0	3	0	3
UFGIN	FD	White-throated Greenbul	<i>Phyllastrephus albigularis</i>	9	16	3	0	28
FRIN	FD	Honeyguide Greenbul	<i>Baeopogon indicator</i>	4	4	0	0	8
FRUG	FD	Joyful Greenbul	<i>Chlorocichla laetissima</i>	10	5	16	2	33
FRIN	NF	Common Bulbul	<i>Pycnonotus barbatus</i>	0	2	6	35	43
UFGIN	FD	Common Bristlebill	<i>Bleda syndactyla</i>	20	10	13	6	49
UFGIN	FG	Yellow-spotted Nicator	<i>Nicator chloris</i>	16	4	9	4	33

(Appendix continued on next page)

Appendix (continued)

Guild	ForDep	Family and common name	Scientific name	UL	LL	HL	PL	Total
Timaliidae								
TUSIN	FD	African Hill Babbler	<i>Illadopsis abyssinica</i>	2	0	0	0	2
TUSIN	FD	Brown Illadopsis	<i>Illadopsis fulvescens</i>	21	9	11	1	42
TUSIN	FD	Pale-breasted Illadopsis	<i>Illadopsis rufipennis</i>	1	0	0	0	1
TUSIN	FD	Scaly-breasted Illadopsis	<i>Illadopsis albipectus</i>	9	5	6	0	20
Turdidae								
TUSIN	FD	Brown-chested Alethe	<i>Alethe poliocephala</i>	4	3	1	1	9
TUSIN	FD	Red-tailed Ant-thrush	<i>Neocossyphus rufus</i>	5	3	0	0	8
TUSIN	FD	White-tailed Ant Thrush	<i>Neocossyphus poensis</i>	4	2	1	0	7
TUSIN	FD	Rufous Flycatcher-thrush	<i>Neocossyphus fraseri</i>	2	1	2	0	5
TERIN	FG	Olive Thrush	<i>Turdus olivaceus</i>	0	2	0	0	2
TERIN	NF	African Thrush	<i>Turdus pelios</i>	3	4	1	3	11
Muscicapidae								
SALIN	FG	Ashy Flycatcher	<i>Muscicapa caerulescens</i>	0	0	2	6	8
SALIN	FG	Dusky-blue Flycatcher	<i>Muscicapa comitata</i>	2	2	1	0	5
SALIN	FD	Gray-throated Tit-flycatcher	<i>Myioparus griseigularis</i>	0	1	0	0	1
TUSIN	FD	Equatorial Akalat	<i>Sheppardia aequatorialis</i>	8	13	3	0	24
TUSIN	FG	Blue-shouldered Robin-chat	<i>Cossypha cyanocampter</i>	6	5	14	0	25
TUSIN	FG	Red-capped Robin-chat	<i>Cossypha natalensis</i>	7	2	1	0	10
Sylviidae								
UFGIN	FG	Green Hylia	<i>Hylia prasina</i>	4	4	10	0	18
UFGIN	FD	Black-faced Rufous-warbler	<i>Bathmocercus rufus</i>	2	2	10	0	14
UFGIN	NF	Tawny-flanked Prinia	<i>Prinia subflava</i>	0	0	3	0	3
UFGIN	FG	Banded Prinia	<i>Prinia bairdii</i>	0	2	7	0	9
UFGIN	FG	White-chinned Prinia	<i>Prinia leucopogon</i>	0	2	13	3	18
UFGIN	NF	Gray-backed Camaroptera	<i>Camaroptera brachyura</i>	11	11	23	27	72
AFGIN	FD	Olive-green Camaroptera	<i>Camaroptera chloronata</i>	8	4	8	2	22
AFGIN	FD	Masked Apalis	<i>Apalis binotata</i>	5	3	4	7	19
AFGIN	FD	Buff-throated Apalis	<i>Apalis rufogularis</i>	3	2	3	0	8
AFGIN	FD	Black-throated Apalis	<i>Apalis jacksoni</i>	2	1	1	0	4
AFGIN	FD	White-browed Crombec	<i>Sylvietta leucophrys</i>	1	0	3	0	4
AFGIN	FG	Green Crombec	<i>Sylvietta virens</i>	0	0	1	0	1
Zosteropidae								
AFGIN	NF	African Yellow White-eye	<i>Zosterops senegalensis</i>	8	5	12	18	43
Paridae								
AFGIN	FD	Dusky Tit	<i>Melaniparus funereus</i>	12	10	5	0	27
Monarchidae								
SALIN	NF	African Blue-Flycatcher	<i>Elminia longicauda</i>	0	1	0	0	1
SALIN	NF	African Paradise-Flycatcher	<i>Tersiphone viridis</i>	0	0	0	1	1
SALIN	FD	Black-headed Paradise-Flycatcher	<i>Tersiphone rufiventer</i>	4	4	8	14	30
Platysteiridae								
SALIN	FD	African Shrike-Flycatcher	<i>Megabyas flammulatus</i>	1	1	1	0	3
SALIN	NF	Black-and-white Shrike-Flycatcher	<i>Bias musicus</i>	4	2	2	1	9
SALIN	NF	Brown-throated Wattle-eye	<i>Platysteira cyanea</i>	3	3	3	0	9
SALIN	FD	Chesnut Wattle-eye	<i>Platysteira castanea</i>	1	2	3	0	6
SALIN	FD	Jameson's Wattle-eye	<i>Platysteira jamesoni</i>	2	0	3	0	5
Malaconotidae								
UFGIN	FG	Gray-green Bushshrike	<i>Telophorus bocagei</i>	0	0	5	0	5
UFGIN	FG	Luehder's Bushshrike	<i>Laniarius luehderi</i>	2	1	9	0	12
UFGIN	NF	Tropical Boubou	<i>Laniarius aethiopicus</i>	0	0	4	0	4
AFGIN	FD	Pink-footed Puffback	<i>Dryoscopus angolensis</i>	1	1	2	0	4
UFGIN	FG	Brown-crowned Tchagra	<i>Tchagra australis</i>	2	0	2	12	16

Appendix (continued)

Guild	ForDep	Family and common name	Scientific name	UL	LL	HL	PL	Total
		Campephagidae						
FRIN	FD	Petit's Cuckoo-shrike	<i>Campephaga petiti</i>	3	4	1	2	10
		Dicruridae						
SALIN	FG	Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	4	2	1	0	7
		Oriolidae						
FRIN	FD	Black-tailed Oriole	<i>Oriolus percivali</i>	3	1	0	0	4
FRIN	FG	Western Black-headed Oriole	<i>Oriolus brachyrhyncus</i>	14	11	18	22	65
		Sturnidae						
FRUG	FD	Narrow-tailed Starling	<i>Poeoptera lugubris</i>	2	2	0	0	4
FRUG	FD	Chesnut-winged Starling	<i>Onychognathus fulgidus</i>	1	1	1	0	3
FRUG	FG	Purple-headed Glossy-Starling	<i>Lamprotornis purpureiceps</i>	4	1	3	1	9
		Nectariniidae						
NECIN	FG	Collared Sunbird	<i>Hedydipna collaris</i>	1	1	6	0	8
NECIN	FD	Western Olive-Sunbird	<i>Cyanomitra obscura</i>	13	9	17	20	59
NECIN	FD	Blue-headed Sunbird	<i>Cyanomitra alinae</i>	4	2	2	0	8
NECIN	FG	Green-headed Sunbird	<i>Cyanomitra verticalis</i>	0	2	0	0	2
NECIN	FG	Green-throated Sunbird	<i>Chalcomitra rubescens</i>	0	0	2	0	2
NECIN	NF	Variable Sunbird	<i>Cinnyris venustus</i>	0	4	9	0	13
NECIN	FG	Olive-bellied Sunbird	<i>Cinnyris chloropygius</i>	0	0	1	0	1
NECIN	FG	Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>	0	0	3	0	3
		Ploceidae						
GRIN	NF	Grossbeak Weaver	<i>Amblyospiza albifrons</i>	0	0	1	0	1
GRIN	NF	Black-necked Weaver	<i>Ploceus nigricollis</i>	0	0	2	0	2
GRIN	NF	Spectacled Weaver	<i>Ploceus ocularis</i>	0	0	2	0	2
GRIN	FD	Black-billed Weaver	<i>Ploceus melanogaster</i>	1	0	1	0	2
GRIN	NF	Vieillot's Weaver	<i>Ploceus nigerrimus</i>	0	0	2	0	2
GRIN	FD	Yellow-mantled Weaver	<i>Ploceus tricolor</i>	1	0	0	0	1
GRIN	FG	Forest Weaver	<i>Ploceus bicolor</i>	15	9	18	27	69
BGIN	FD	Red-headed Malimbe	<i>Malimbus rubricollis</i>	3	0	5	0	8
		Estrildidae						
UFGIN	FD	Woodhouse's Antpecker	<i>Parmoptila woodhousei</i>	1	0	2	0	3
AFGIN	FG	Gray-headed Negrofinch	<i>Nigrita canicapilla</i>	2	0	1	0	3
AFGIN	FG	White-breasted Negrofinch	<i>Nigrita fusconata</i>	0	0	2	1	3
FRIN	NF	White-collared Oliveback	<i>Nesocharis ansorgei</i>	0	0	1	0	1
GRIN	FG	Red-faced Crimson-wing	<i>Cryptospiza reichenovii</i>	0	0	0	2	2
GRAN	FG	Red-headed Bluebill	<i>Spermophaga ruficapilla</i>	2	0	4	3	9
GRAN	FD	Green-backed Twinspot	<i>Mandingoa nitidula</i>	0	0	2	0	2
Total				589	452	657	340	2038

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