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Species richness and community composition of songbirds in a tropical forest-agricultural landscape

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Abstract

Management strategies that attempt to mitigate tropical biodiversity loss require detailed studies of biodiversity in different land-uses. In this study the community structure and species richness of songbirds was characterised along with the vegetation structure, in three land-use types in and around a tropical forest reserve in Uganda (intact, mature forest; regenerating secondary forest; smallholder agriculture). Each land-use type had 30–35 count stations that were sampled twice by means of a 15-min recording session. In total, 118 bird species were recorded from 192 station counts. Number of species/station was similar in intact and regenerating forest and lower in smallholder agriculture. Songbird communities in intact forest were highly distinct from those in smallholder agriculture and were composed of forest-dependent species. Communities in regenerating forest were intermediate between intact forest and agriculture, although much closer to intact forest. Generalised Linear Model (GLM) modelling revealed that tree density and distance to the nearest intact forest had strong positive and non-linear effects on the community composition and forest species richness of songbirds. Simulations using these models showed that agroforestry programmes would not raise tree densities to levels that would shift agricultural songbird communities towards forest communities. Current and best-case agricultural practices are therefore unlikely to contribute to the conservation of the songbird component of forest biodiversity in this area.

INTRODUCTION

Land-use change is a key driver of current and future biodiversity change (Sala *et al.*, 2000). In the tropics, conversion of native forests to pastures, croplands and other human-dominated habitats is the primary cause of biodiversity loss (Myers, 1992; Sala *et al.*, 2000). However, other land-use dynamics also occur in the tropics. In areas that have been logged or cleared and then abandoned, regenerating secondary forest is a significant land cover type (Kammesheidt, 2002). The amount of secondary forest in the tropics is likely to increase in the future as logging activity and shifting cultivation increase (Laurance, 1999). In addition, afforestation in smallholder agricultural areas (Place & Otsuka, 2000) is an important land-use dynamic that has received little attention in the conservation literature. Smallholder agriculture (i.e. agriculture, often for subsistence, practiced by farmers on small pieces of land) can provide habitat for a variety of organisms normally associated with forest (Thiollay, 1995; Perfecto & Vandermeer, 2002), and hence may be an important component of landscape- or regional-level conservation strategies.

The effects of land-use dynamics and land cover types on tropical biodiversity are the subjects of a burgeoning literature. There has been a large amount of research on the responses of various elements of biodiversity to tropical deforestation, which emphasises the negative effects of forest conversion to unsuitable human-dominated habitats (e.g. Myers, 1992; Brooks, Pimm & Collar, 1997; Castelletta, Sodhi & Subaraj, 2000). More recently, studies have assessed biodiversity in regenerating forest and/or agricultural areas compared to undisturbed forest (Daily, Ehrlich & Sanchez-Azofeifa, 2001; Ricketts *et al.*, 2001; Perfecto & Vandermeer, 2002). Much of this work focused on bird responses to such habitat modification. Studies that compared the avifauna between forested and agricultural areas have generally shown that forested areas contain more species than agricultural areas (Blankespoor, 1991; Ranjit Daniels, Joshi & Gadgil, 1992; Thiollay, 1995; Estrada, Coates-Estrada & Meritt, 1997; Pomeroy & Dranzoa, 1997–1998; Daily *et al.*, 2001). Most research has also shown that the species composition of avian communities differs significantly between land-use types, however,

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agricultural habitats vary in terms of their vegetational complexity and, therefore, in their ability to harbour forest biodiversity. Some authors have emphasised the dramatic shift from forest-interior species towards open or bushland species in regenerating, disturbed, or agricultural habitats (Johns, 1991; Raman, Rawat & Johnsingh, 1998), while others noted more optimistically that many forest species were found in habitats other than primary forest (Thiollay, 1995; Gascon *et al*., 1999; Daily *et al*., 2001; Hughes, Daily & Ehrlich, 2002; Luck & Daily, 2003).

Agroforestry, i.e. the increased use of trees within agroecosystems (Winterbottom & Hazlewood, 1987) has been touted as a means of both reducing pressure on contracting forests and raising the conservation potential of smallholder agricultural areas. By encouraging farmers to grow trees on their own land, degradation of adjacent woodlands and forests may be halted or even reversed (Murniati, Garrity & Gintings, 2001). More controversially, it has been suggested that agroforestry may enhance the suitability of agricultural areas for biodiversity conservation, to the extent that they may function as 'buffer zones' between protected forest reserves and large-scale, intensive production areas (Gajaseni, Matta-Machado & Jordan, 1996; Roberts, Cooper & Petit, 2000; Cullen *et al*., 2001). Few studies, however, have assessed the degree to which agroforestry systems may actually contribute to the conservation of forest biodiversity (Perfecto *et al*., 1996, 2003; Roberts *et al*., 2000; Reitsma, Parrish & McLarney, 2001).

The aims of this study were to characterise the species richness and community structure of songbirds in forested *versus* smallholder agricultural land-uses, to determine the capacity of current smallholder agricultural practices to support forest songbirds and to assess whether agroforestry programmes may be capable of enhancing aspects of forest biodiversity in agricultural areas. The study was conducted in sub-Saharan Africa (Uganda), where population growth, deforestation and rural poverty are acute problems that are likely to persist for the near future (World Bank, 2001). An assessment of biodiversity in forested and smallholder agricultural areas, and the potential role of agroforestry in mitigating against forest biodiversity loss, is thus particularly critical in this region.

METHODS

Study area

The study was conducted in and around the Mabira Forest Reserve (0°30′ N, 32°55′ E), a 300 km^2 remnant of tropical lowland rainforest in southern Uganda (Fig. 1). Study sites were selected in three land-use types in and around the Reserve: intact forest, regenerating forest and smallholder agriculture. Habitat types were identified from land-use maps and Geographic Information System (GIS) coverages compiled by the Forest Department and were verified by ground-truthing. Intact forest in the Nature Reserve zone of Mabira Forest Reserve was characterised by relatively undisturbed forest with no large-scale logging activity, although localised pitsawing and snaring of wild game does occur. Regenerating forest was located in the Ecotourism/Recreation zone of the Reserve and consisted of secondary regrowth 13 years in age. The smallholder agriculture area was outside the Reserve boundaries, in an area proposed as a 'buffer zone' between more intensive agricultural areas further away from the forest and the Reserve itself.

Songbird community censuses

In each land-use type, between 30 and 35 count stations were placed, at intervals of 150–250 m. Because of access limitations, stations were placed along 20 km of existing trails, footpaths and motorable tracks in each land-use type (intact: 5.9 km; secondary: 4.7 km; agricultural: 4.4 km). Visual detections at sampling stations in dense tropical forest generally approach nil (Karr, 1981), whereas in open agricultural habitats visual detectability is much greater. Therefore, it was decided that the most efficient and equitable way of sampling birds in all three habitats would be to record sounds at each station for 15 min and then identify the vocalisations from the tapes. This procedure has been advocated for tropical avifauna surveys (Parker, 1991) and can be a suitable (in some cases preferable) alternative to point counts in tropical rainforest habitat (Haselmayer & Quinn, 2000). This method is not appropriate for surveying silent and/or aerial species, including most raptors, woodpeckers, swifts, swallows, rollers and bee-eaters. The analyses and conclusions presented here are therefore restricted to the more vocal assemblage of bird species that will be referred to by the generic term 'songbirds'.

Breeding activity and hence detectability, may vary with seasonality in Uganda (Owiunji & Plumptre, 1998). Recording at each station was therefore conducted both during the 'wet' season (May 16–May 26, 2001) and the 'dry' season (August 1–August 7, 2001). For each sampling period, stations were visited within a 3 h period from sunrise (6:40–6:50 am) to 3 h post-sunrise, on days with little or no wind and rain. At each station, an observer (three in total, rotated among stations over sampling rounds) used a parabolic microphone and portable cassette recorder to record bird vocalisations for a 15 min timed count. Observers changed direction every minute so that 360° coverage of the station was obtained. Based on field estimates of distance to singing birds, it appeared that all but the loudest birds were not recorded beyond a range of 75 m. Species vocalisations were identified from tapes made at each station using personal knowledge and a reference CD set (Chappuis, 2000). Those vocalisations that could not be identified using this procedure were sent to an expert ornithologist for identification (David Moyer, Wildlife Conservation Society, Tanzania). Given the 75 m effective sampling radius around stations, about 170 hectares were surveyed over the three land-use types (intact: 62 hectares; secondary: 53 hectares; agricultural: 55 hectares).

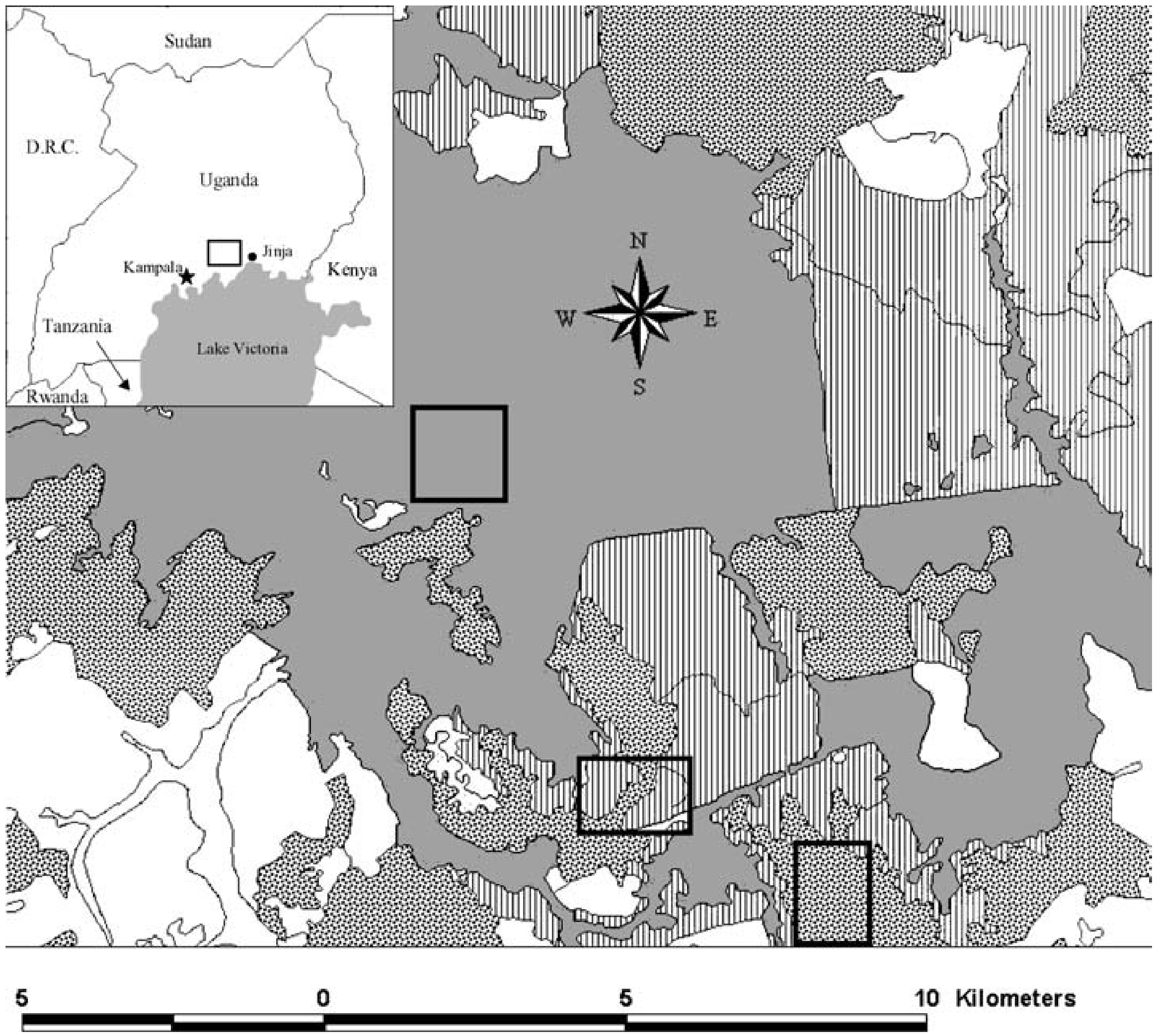

Fig. 1. Location of Mabira Forest and surrounding areas in southern Uganda. Solid grey indicates intact forest, vertical lines indicate regenerating forest and stippled areas indicate smallholder agriculture. Other land-uses (large-scale agriculture, bushland, etc) are represented by white. Boxes indicate sampling locations for the three land-use types.

Local vegetation

Local vegetation is one of the strongest determinants of avian community composition (Schmiegelow, Machtans & Hannon, 1997; Lichstein, Simons & Franzreb, 2002). Local vegetation characteristics were quantified using protocols adapted from several sources (Schemske & Brokaw, 1981; Drapeau *et al*., 2000; Hobson & Bayne, 2000). Four 10 m × 10 m quadrats were placed 25 m from each station, each at a 45° angle from the trail. Within each quadrat, every tree with a diameter at breast height (DBH) greater than 10 cm was measured for height and DBH. Within a 2 m × 2 m subplot in each quadrat, the number of woody stems between 1 and 10 cm DBH ('shrubs') was counted. Finally, a 10 m transect running across the quadrat was used to measure vertical foliage structure at various heights. At positions 1, 3, 5, 7 and 9 m along the transect, foliage touches along a real (0–3 m) or hypothetical (heights greater than 3 m) pole were scored at the following height classes: 0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–2 m, 2–3 m, 3–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, 25–30 m and >30 m. Vegetation sampling was conducted from May 28–June 16, 2001.

Landscape context

The landscape context of avian sampling sites may be an important influence on local community structure (Lichstein *et al*., 2002; Pearman, 2002). To quantify landscape-level variables around count stations, station co-ordinates (recorded using a handheld Global Positioning System (GPS)) were entered into a GIS coverage of the study area. The GIS coverage was part of a nationwide land cover map derived from manual interpretation of SPOT XS satellite imagery (February 1989–December 1992), as well as LANDSAT^{TM} images and aerial photographs (early 1995) and verified through extensive field surveying from 1993–1995 (Forest Department, 2000). The straight-line distances to the nearest intact, regenerating and agricultural edge, as well

Table 1. Variables used in the analysis of the relationships between avian community composition, forest species richness and environmental conditions

Variable	Category	Mean	S.D.	Min.	Max.	Abbreviation
Response variables						
Number of forest species per station	Species-level	15.0	7.98	1	28	FF_F_SPP
1st axis of NMDS, all species	Community-level	2.50×10^{-7}	0.88	−1.65	1.03	NMDS1_MA
Explanatory variables						
Distance to nearest edge (m)	Landscape	623	691	75	2903	EDGE
Distance to nearest intact forest edge (m)	Landscape	273	332	0	1087	DIST_PRI
No. trees (stems >10 cm DBH) per hectare	Local	429	309	0	1050	TREES_HA
Tree diameter at breast height (cm)	Local	23.1	7.8	10.2	61.6	AVGDBH
% foliage cover at 0–0.5 m	Local	0.73	0.18	0.25	1	FOL1
% foliage cover at 2–3 m	Local	0.44	0.22	0	0.9	FOL5
Index of shrub density (stems/4 m^2)	Local	7.9	5.2	0	21.8	SHRUBS
Weighted average of number of forest birds within 400 m	Spatial	0.34	0.20	0.04	0.88	WT_400M

S.D., standard deviation; DBH, diameter of breast height; NMDS, non-metric multidimensional scaling.

as the geographical centre of the forest reserve, were determined for each count station using ArcGIS 8.1 (ESRI Systems, Redlands, CA).

Statistical analyses

Because it was not possible to accurately determine the number of conspecific individuals at a station from the recorded vocalisations, inferences regarding species richness and community composition were drawn from the presence–absence of species at stations. A species recorded during one or both of the two sampling periods was counted as being present at a station.

Community structure

Non-Metric Multidimensional Scaling (NMDS) was used to characterise songbird community structure. NMDS is an ordination technique that is quite different from the family of correspondence analysis methods that permeate the community ecology literature (McCune & Grace, 2002). NMDS functions in an iterative manner by minimising the difference ('stress') between distance in the original matrix and distance in the reduced ordination space. The optimal number of axes in a solution is determined through low stress and a Monte Carlo test of significance. NMDS has recently been used in tropical bird community analyses (Luck & Daily, 2003), and is the ordination method of choice for most community ecology applications (McCune & Grace, 2002). Because ordination results can be overly sensitive to rare species, only those species with at least five total detections were used in the community analyses.

Avifauna – environment relationships

Widespread collinearity among both local and landscape variables necessitated a reduction in the pool of variables used to analyse avifauna – environment relationships. For each group of variables (local and landscape), the number of variables was reduced by considering pairwise correlations and eliminating one variable from each pair that had a correlation coefficient >0.8. This procedure was then repeated between the two groups, resulting in a final set of only $n = 7$ variables. Local-scale variables were vertical foliage means at heights of 0–0.5 m and 2–3 m, tree density, average DBH and shrub density (Table 1). Because of the importance of tree density in potential policy applications, its square term was added to models to assess possible non-linear responses. Landscape variables were: distance to the nearest intact forest (0 for stations in this land-use) and distance to the nearest land-use edge of any type (i.e. for intact forest stations, the minimum of distance to nearest regenerating forest edge and distance to nearest agricultural edge). Squared terms of each of these two variables were added to assess possible non-linear responses.

Relationships between community composition (as represented by values on the NMDS axes), forest species richness and environmental variables were assessed using Generalised Linear Models (GLM). For community composition, NMDS scores were continuous, therefore a GLM with a normal probability distribution was used (ordinary least-squares (OLS) regression). For forest species richness, data were counts and examination of dispersion scores from models indicated that GLMs with a Poisson probability distribution were appropriate. For each GLM, an information–theoretical approach was used to assess performance from a set of candidate models (Burnham & Anderson, 1998). A set of six candidate models were formed from the available local and landscape variables: (1) local variables only; (2) landscape variables only; (3) local + landscape variables; (4) local variables allowing non-linear responses; (5) landscape variables allowing non-linear responses and (6) local + landscape variables allowing non-linear responses. The small sample size version of Akaike's Information Criterion (AIC_c) was used to rank models according to the likelihood of being the best model in the

Table 2. Broad measures of avian species richness and community composition between land-use types

	Intact forest	Regenerating forest	Agriculture
Number of species detected	58	76	66
% overlap with intact†	1	0.54	0.19
% overlap with regenerating†	–	1	0.23
All species	21.2[a] (2.98)	22.5[a] (4.20)	18.2[b] (3.67)
Forest specialists	11.5[a] (2.11)	9.80[b] (3.40)	0.35[c] (0.66)
Forest generalists	9.06[a] (1.86)	9.63[a] (2.06)	4.23[b] (1.98)
Forest visitors	0.60[c] (0.60)	2.93[b] (1.23)	9.65[a] (1.66)
Open habitat species	0.00[b] (0.00)	0.17[b] (0.46)	3.13[a] (1.41)

† Jaccard coefficient of similarity, multiplied by 100, where 0 = complete dissimilarity and 100 = identical. Superscripts denote significantly ($P < 0.05$) different means among land uses (Anova, Tukey's HSD); standard deviations are given in brackets.

group. Best models were selected according to differences in AIC_c: models with a difference of less than 2 units from the 1st-ranked model are considered to have substantial support, while those with a difference of 10 or greater have almost no support (Burnham & Anderson, 1998). Akaike weights (i.e. the probability of a model being the best for the given data) were also used to identify best models. Goodness-of-fit and statistical significance of best models were assessed using the relevant statistics (R^2 and F-test for OLS, deviance explained and χ^2 test for Poisson regression).

Spatial autocorrelation

Spatial autocorrelation may bias the interpretation of results in environmental studies if not accounted for (Legendre, 1993). Given the rather close spatial proximity of count stations in this study, autocorrelation concerns centred around unmeasured spatial gradients that may influence community structure (e.g. moisture regime, conspecific attraction) and the possibility of 'double-counting' of species at adjacent sites through individual movement or loud individual vocalisations heard at more than one station. Two separate approaches were used to reduce the possibility of autocorrelation bias in the analyses. For analyses involving NMDS, Mantel correlograms were constructed first, to determine the structure of spatial autocorrelation among songbird communities at stations. Mantel correlograms are multivariate analogs of correlograms of Moran's I and compare the autocorrelation across distances of community matrices (Legendre & Legendre, 1998). Mantel correlograms showed that the songbird species data matrix was autocorrelated among stations that were less than 250 m apart. Therefore, stations were randomly selected from the complete data set such that only those more than 250 m apart were included in the NMDS analysis and also in the analysis of the relationship between NMDS scores and environmental variables ($n = 40$). For the analysis of forest bird species richness and environmental variables, spatial correlograms of Moran's I were used to identify a spatial 'neighbourhood' in which numbers of forest species were autocorrelated; this proved to be within distances of less than 400 m. For each station, a neighbourhood variable was then constructed using a weighted average of the number of forest species found at stations within 400 m, where weights were the linear distance to each station within the neighbourhood (Lichstein *et al*., 2002).

Guilds

Life-history traits of individual bird species were gleaned from the literature (Bennun, Dranzoa & Pomeroy, 1996; Owiunji & Plumptre, 1998) to determine which life-history characteristics affected species distributions between land-uses and also whether different guilds of forest species varied in their probability of detection in agricultural habitats. All recorded birds were assigned to a habitat guild: forest specialists (FF), forest generalists (F), forest visitors (f) and open habitat specialists (O). Forest-dependent species were defined as those in either the FF or F category. Each of these forest-dependent species was additionally assigned to a foraging guild (frugivore *versus* non-frugivore) and a preferred vertical stratum habitat (canopy *versus* understory). Body mass data for forest-dependent species were also recorded (Dunning, 1993). Mean values for agricultural detection and position along NMDS axes were compared between foraging and vertical stratum groupings and correlations between body mass and agricultural detections were also measured.

RESULTS

General results

In total, 118 bird species from 35 families were recorded over two rounds of sampling at the 96 count stations (see Appendix). Overall species richness of songbirds was highest in regenerating forest (76 species), followed by smallholder agriculture (66 species) and intact forest (58 species). At the station level, however, stations in intact forest and regenerating forest had greater numbers of species than agricultural stations (Table 2). Songbird communities in intact and regenerating forests were also much more similar to one another than either of

Table 3. Comparison of vegetation structure between land-use types

	Intact forest	Regenerating forest	Agriculture
Tree density (stems/ha)	725.7^{a} (154.6)	472.5^{b} (147.9)	52.4^{c} (59.3)
Average DBH (cm)	24.6^{a} (3.89)	21.5^{b} (4.32)	23.1^{a} (13.5)
Average height (m)	18.2^{a} (2.31)	13.4^{b} (2.03)	7.45^{c} (2.73)
Shrub density (stems/ha)	24,691^{a} (9879)	28,146^{a} (9419)	6,270^{b} (7385)
% foliage cover†	0.55^{a} (0.26)	0.45^{b} (0.29)	0.17^{c} (0.22)

Figures are means with standard deviations in brackets.
† Mean of 12 vertical foliage cover classes from 0–30+ m.
Superscripts denote significantly ($P < 0.05$) different means among land uses (ANOVA, Tukey's HSD).
DBH; diameter at breast height.

these were to communities in smallholder agriculture (Table 2). A significant gradient from intact forest through regenerating forest to smallholder agriculture was observed through abundance of species in different habitat guilds (Table 2). This trend was broadly related to trends in vegetation structure (Table 3). Vegetation structure was significantly more complex in intact forest than in regenerating forest, which, in turn, was much more complex than in smallholder agriculture.

Community structure

NMDS resulted in a 2-axis optimal solution. Final stress was 15.3, within the 10–20 range typically found in ecological community data sets (McCune & Grace, 2002). This final stress was unlikely to have been obtained by chance (Monte Carlo test, $P = 0.019$) and the axes together explained 89.1% of the variance, with almost all of this (86.3%) being due to the first axis. The ordination plot revealed a strong grouping of stations by land-use type (Fig. 2). Intact forest and regenerating forest stations clustered separately, yet showed some overlap and were much closer to one another than to smallholder agriculture stations. The 1st NMDS axis can thus be thought of as a gradient of songbird community composition, with high positive scores indicative of true forest communities and negative scores indicative of open or bushland communities. An ordination plot of the species scores revealed that species clustered according to habitat guild, although this clustering was not as tight as with stations (Fig. 3). Forest specialists and generalists both clustered to the far right of the diagram and open country species clustered to the left. Forest visitors showed less grouping and were dispersed throughout these two extremes.

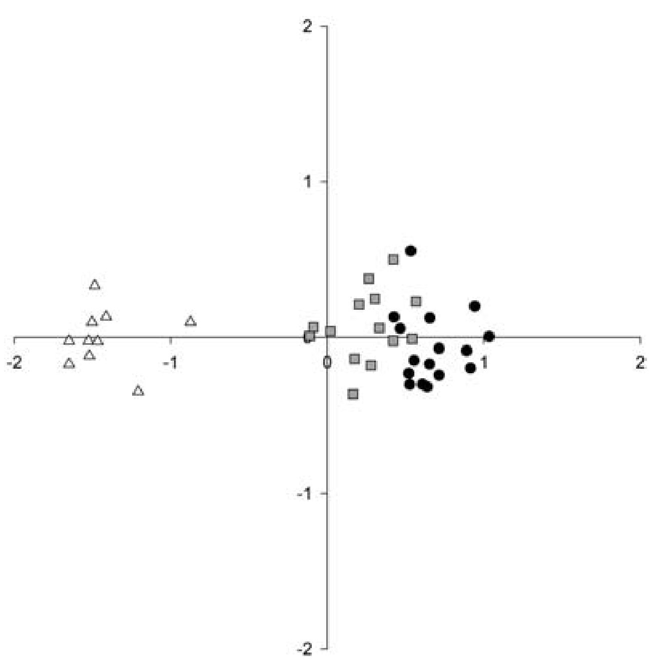

Fig. 2. Ordination plot of count stations along non-metric multi-dimensional scaling (NMDS) axes 1 (x-axis) and 2 (y-axis). The three land-use types are represented as follows: △, stations in agricultural habitat; ▧, stations in regenerating forest; ● stations in intact forest.

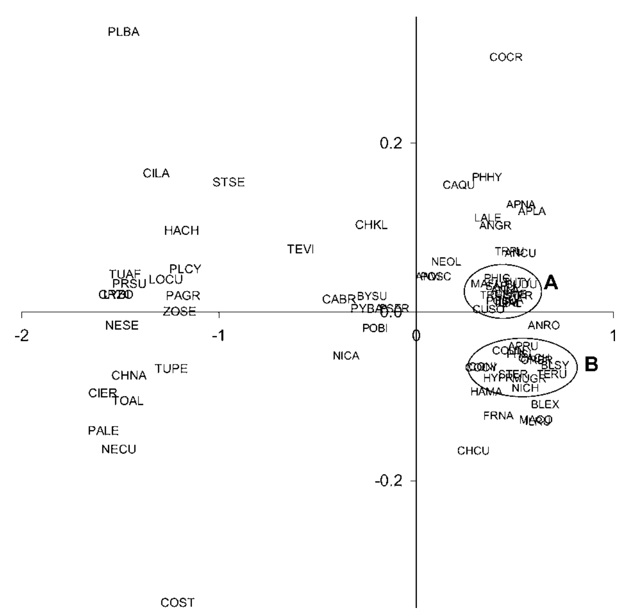

Fig. 3. Ordination plot of bird species along non-metric multi-dimensional scaling (NMDS) axes 1 (x-axis) and 2 (y-axis). See Appendix for species abbreviations. Species in cluster A: PHIC, MAFL, TUTY, BUDU, SAPU, ANLA, TRHI, CEME, STFR, POSU, PLCA, CUSO, ILFU, ILAL. Species in cluster B: APRU, COUN, PHSI, CACH, ORBR, BLSY, HYPR, STER, MUGR, TERU, NICH, COCY, CONI.

Table 4. Effect of life history characteristics on differences in agricultural detection and position along community structuring of NMDS axes

	Number of agricultural detections	% detections in agricultural	Score on NMDS axis 1	Score on NMDS axis 2
Foraging guild				
Frugivorous	5.50[b] (8.34)	0.12[a] (0.16)	−0.31[c] (0.33)	0.16 (0.28)
Non-frugivorous	1.03 (1.80)	0.049 (0.10)	−0.47 (0.15)	0.32[c] (0.19)
Activity stratum				
Canopy	3.13 (6.83)	0.100 (0.19)	−0.39 (0.28)	0.23 (0.25)
Understory	0.93 (2.69)	0.097 (0.24)	−0.46 (0.21)	0.27 (0.22)
Body size				
Log (body mass (g))	$r = 0.31^{b}$	$r = 0.26^{a}$	$r = 0.20$	$r = -0.09$

Values are means with standard deviations in brackets, or Pearson correlation coefficients (body size).
Superscripts indicate significant differences among guild groupings, or in the case of body mass, a significant correlation.
[a] $P < 0.10$; [b] $P < 0.05$; [c] $P < 0.001$.
NMDS, non-metric multidimensional scaling.

Agricultural detection and songbird guilds

Frugivorous forest songbirds were more likely to be found at agricultural stations than non-frugivores and this was also reflected in significant differences in their scores along NMDS axes 1 and 2 (Table 4). No significant differences in agricultural detections or NMDS scores were noted for species restricted to canopies as opposed to those generally foraging lower in the canopy. However, larger forest songbirds were more likely to be detected in agricultural stations. This effect was independent of a bird's foraging guild, since frugivores were not significantly different in mass from non-frugivores (mean log-transformed weight = 4.11 for frugivores *versus* 3.60 for non-frugivores, $n = 50$, $F = 2.27$, $P = 0.14$).

Songbird–habitat relationships

The presentation of results from GLM models of bird–environment relationships follows suggestions by Anderson *et al.* (2001), who strongly recommend against presenting tests of hypotheses for both overall models and individual variables. Model selection using an information–theoretical approach showed that both community composition and forest species richness of songbirds could be predicted equally well by two competing models: a model that included local-scale variables allowing non-linearity in tree density and a model that included both local and landscape variables allowing non-linearity in both groups (models 5 and 6; Table 5). In the case of community composition, degree of support was almost identical between these two competing models (Δ_i of less than 0.1 between the two models, w_i values of 0.498 *versus* 0.502), while in the case of forest species richness, somewhat more weight could be placed on the model that included both scales of variables (the probability of model 6 being the best model = 0.79). The goodness-of-fit tests suggested a slightly better fit for the non-linear model that combined local and landscape variables for both community composition and forest

Table 5. Summary of GLM model selection results for environmental explanation of community composition (as represented by axis 1 of a NMDS of species presence–absence matrix) and forest species richness

Model description	n	Parameters	Log-L	AIC_c	Δ_i	w_i
Community composition						
1. Landscape	40	3	−29.1	64.87	43.1	2E-10
2. Local	40	6	−15.1	44.74	23	5E-06
3. Local + landscape	40	8	−9.645	39.94	18.2	6E-05
4. Landscape: nonlinear effects	40	4	−28.12	65.38	43.6	2E-10
5. Local: nonlinear effects	40	7	−2.136	21.77	0	0.502
6. Local + landscape: nonlinear effects	40	10	2.899	21.79	0.02	0.498
Forest species richness						
1. Landscape	89	4	−264.2	536.8	35.5	2E-08
2. Local	89	7	−264.3	543.9	42.6	4E-10
3. Local + landscape	89	9	−251.3	522.9	21.6	2E-05
4. Landscape: nonlinear effects	89	5	−263.3	537.2	35.9	1E-08
5. Local: nonlinear effects	89	8	−243.1	504.0	2.7	0.207
6. Local + landscape: nonlinear effects	89	11	−238.0	501.3	0.0	0.793

Log-L, log-likelihood; AIC_c, Akaike's information criterion for small sample sizes; Δ_i, the difference between a given model and the best model, in units of AIC_c; w_i, Akaike weight, interpreted as the probability that the model is the best model for the data; GLM, generalisd linear model; NMDS, non-metric multidimensional scaling.

Table 6. Coefficients, standard errors, standardised coefficients and goodness-of-fit for GLM models predicting avian community composition (as represented by axis 1 of a NMDS on species presence–absence matrix) and forest species richness

Model term abbreviations	Community composition			Species richness		
	Coeff.	S.E.	Std coeff	Coeff.	S.E.	Std coeff
EDGE	1E-04	9E-05	0.1058	2E-05	5E-05	0.2673
DIST_PRI	−9E-04	0.0006	−0.5450	−1E-03	0.0004	−5.002
PRIM_SQ	4E-07	6E-07	0.3250	6E-07	5E-07	2.9275
TREES_HA	0.0044	0.0008	1.4456	0.0032	0.0006	14.794
TREES_SQ	−3E-06	6E-07	−0.9756	−3E-06	5E-07	−10.77
AVGDBH	1E-05	0.0002	0.0048	−0.008	0.0054	−0.962
SHRUBS	0.0021	0.0117	0.0818	0.0033	0.0075	0.2615
FOL1	−0.135	0.2923	−0.0314	0.1979	0.1686	0.5887
FOL5	0.5122	0.3531	0.1204	0.363	0.1855	1.2443
WT_400M	–	–	–	0.5424	0.2214	1.7193
Intercept	−1.115	0.2996	–	1.6762	0.2454	–
R^2	0.93			% dev	0.74	
$F(9,30)$	46.29			χ^2	84.2	
P	< 0.00001			P	< 0.00001	

For model term abbreviations, see Table 1; S.E., standard error; GLM, generalised linear model; NMDS, non-metric multidimensional scaling.

species richness (NMDS axis 1: R^2 values of 93.3% for model 6 *versus* 91.3% for model 5; forest species richness: deviances explained of 74.4 for model 6 *versus* 73.0 for model 5). This model was, therefore, chosen as the best predictor for both community composition and forest species richness.

Agroforestry and songbird communities

Examination of the standardised coefficients of variables in the best-fitting models showed that the magnitude of variable effects were similar for both songbird community composition and forest species richness (Table 6). In each case, tree density and the square of tree density had the strongest effects on the response variable, with the signs of the coefficients (positive on tree density, negative on tree density squared) indicating that both community composition and forest species richness increased at low numbers of trees but eventually reached a maximum before declining at the highest densities. The next strongest effect was that of distance to intact forest, which exerted a negative effect on the numbers of forest species and on the community scores from the 1st NMDS axis. Effects of other variables on songbird community composition were weaker, but consistent with the hypothesis that habitat features characteristic of closed forest favoured forest songbird communities. In addition, the coefficient on the neighbourhood variable that represented localised spatial effects was positive and was the strongest predictor of forest species richness after tree density and distance to intact forest.

To assess how increases in tree density could affect songbird community composition at various distances from intact forest, the best fitting model (Table 6) was used to simulate changes in the value of NMDS axis 1 over a range of these two variables, while holding other variables at their agricultural means. In particular, an estimation was made of what levels of tree density would be needed to shift the community composition 1/3, 1/2 and 3/4 of the way towards the mean value of the NMDS axis 1 scores from intact forest stations. Increases in tree density necessary to reach each of these targets were always higher at distances further away from intact forest (Fig. 4). This was particularly noticeable for simulations at the highest degree of community similarity.

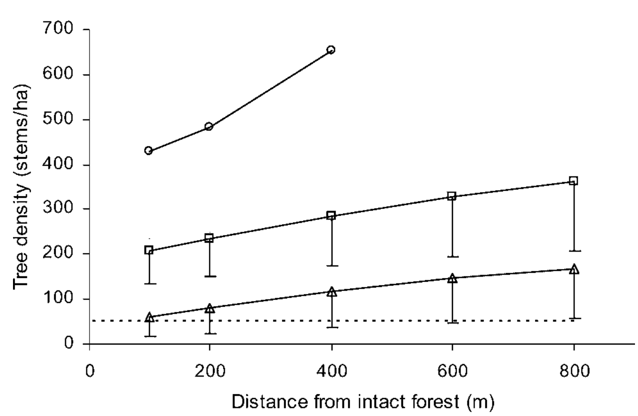

Fig. 4. Tree density required to achieve various targets for forest bird community structure at count stations of varying distance from intact forest. Three targets for community structure are shown: values of non-metric multidimensional scaling (NMDS) axis 1 that are one-third (△), one-half (□) and three-quarters (○) of the mean NMDS value for intact forest count stations. Confidence limits for estimates are also shown (lower only, for figure clarity). Broken horizontal line represents current agricultural tree density.

DISCUSSION

General results

Assessing biodiversity levels in tropical landscapes is vital if we are to conserve a substantial number of species in developing countries with rapidly changing land-uses.

Songbird species richness (per unit area) in a landscape in southern Uganda was similar in intact and regenerating forest and lower in agricultural areas. This is consistent with previous results showing tropical forests to be more biodiversity-rich than nearby agricultural areas (Andrade & Rubio-Torgler, 1994; Warkentin, Greenberg, & Ortiz, 1995; Plumptre, 1997; Owiunji & Plumptre, 1998; Fjeldsa, 1999; Thiollay, 1999). Note that this is true only for species in the aggregate; species richness of open habitat specialists and forest visitors was far greater in agricultural habitats than in either forest type. Within agricultural habitats, forest songbirds considered to be less dependent on closed forest interiors were more likely to be detected than those with a higher forest dependence. In addition, larger birds and birds that were mostly frugivorous were also more likely to be detected in agricultural areas than smaller species and non-frugivores. Other studies have shown that frugivores use individual trees in agricultural landscapes for feeding (Da Silva, Uhl & Murray, 1996; Hamann & Curio, 1999; Luck & Daily, 2003) and infrequent detections of smaller forest species in agricultural areas, particularly those far from intact forest, have also been noted (Luck & Daily, 2003). Unlike many previous studies, however, no significant differences were found in agricultural detection rates of insectivores *versus* non-insectivores.

Songbird community structure

Land-use strongly influenced songbird community structure, a non-surprising result given the plethora of studies that have demonstrated the dependence of bird communities on habitat type (Thiollay, 1990; Brawn, Robinson, & Robinson 2001; Pearman, 2002). Community structure was somewhat different between intact forest and regenerating forest, while agricultural communities clustered very far away from those of either forest type. Stations in intact forest were characterised by high proportions of forest specialists and forest generalists, whereas agricultural stations were dominated by open habitat specialists and forest visitors. Regenerating forest stations were somewhat intermediate between these two, although forest-dependent species were more prevalent than open specialists or forest visitors. These results demonstrate that current smallholder agricultural practices in this system contribute little to supporting the songbird communities that are characteristic of tropical forests in the region.

Regenerating forest stations, while intermediate in songbird community structure between smallholder agriculture stations and intact forest stations, were much closer in character to intact forest. After only 13 years, therefore, the songbird community has shifted from a community presumably characteristic of open/bushland species to one that is close to an intact forest community. Other studies have documented the convergence of tropical avian communities along a chronosequence of regenerating sites (Raman *et al*., 1998), and the convergence noted here is probably facilitated by the proximity of relatively large tracts of intact forest. Nevertheless, these results are a promising sign that songbird communities of regenerating secondary forest in southern Uganda may quickly return to communities characteristic of intact forest.

Comparison of the community structure analysis with more simplistic assessments of avifauna distribution reveals how the latter may overestimate the potential for agricultural areas to contribute to forest biodiversity conservation strategies. For example, simply noting the presence–absence of forest songbird species (forest specialists and forest generalists) in this data set results in the conclusion that 33.8% of the forest avifauna occurred in agricultural areas. Using a similar approach, Daily *et al.* (2001) recently cited a 29% occurrence of forest species in small-scale agricultural habitats as evidence of their high potential to contribute to forest bird conservation. Yet the community structure analysis presented here shows that the songbird communities in agricultural areas are entirely different from those found in forests. In addition, neither Daily *et al.* (2001) nor this study attempted to estimate the reproductive potential of different land-use types for forest bird species; it is not unreasonable to think that the reproductive potential of agricultural areas is likely to be much lower than that of forests. Applying simple presence–absence records of forest species in agricultural areas is thus a potentially misleading approach to assessing the suitability of agricultural habitats for forest biodiversity conservation strategies.

Agroforestry and forest bird conservation

The notion that agroforestry can result in 'win–win' scenarios of increased biodiversity preservation, reduced farmer dependence on natural forests and human welfare gains, has rarely been tested. While this study was not such an explicit test, the results did demonstrate a strong non-linear relationship between tree density and both forest bird species richness and overall songbird community structure. Quantitative predictions of the ecological outcome of various policy decisions and agroforestry strategies can therefore be made from the models used in this study. For example, at all distances within 800 m of intact forest, increases in tree density to 200 trees/ha would shift agricultural bird communities about one-third of the way towards intact forest communities. However, to shift songbird community structure three-quarters of the way towards intact forest communities would require much larger increases in tree density (400–650 trees/ha). In all cases, models of songbird community structure were sensitive to increases in distance from intact forest, with higher tree densities required to meet conservation targets at distances further from the forest.

To interpret the feasibility of such increases in tree density, information on the success of agroforestry programmes in other areas of East Africa (Scherr, 1995), was examined. Programmes in comparable ecozones in Kenya (two rainy seasons) raised tree density by an average factor of 2.5 (from 167 to 423 trees/ha). A similar factor raise in the agricultural lands surrounding Mabira Forest would result in a density of 126 trees/ha. This level of increase would have little general impact on songbird community structure; only areas within 400 m of intact forest would see as much as a one-third increase in community similarity towards forest communities. A heroic agroforestry programme, one that would result in a quadrupling of tree densities to 200 trees/ha, would still not manage to shift community structure by more than a third towards a songbird community showing a greater resemblance to that of intact forests. More realistic levels of tree planting in this area are, in fact, not likely to increase tree densities beyond 100 trees/ha (J.-M. Boffa, ICRAF Uganda, pers. comm.).

CONCLUSIONS

Both optimistic and pessimistic conclusions can be reached from the results of this study. On the positive side, songbird community composition and richness of forest bird species were similar between intact, mature forest and 13-year old regenerating forest. This rapid convergence following deforestation is a promising sign that abandoned agricultural lands in close proximity to forest remnants may hold considerable conservation value in this area of Uganda. However, current agricultural conditions support a songbird community that is entirely different from that of the forest and few forest interior species were detected in agricultural areas. Moreover, realistic agroforestry programmes are unlikely to increase the potential of agricultural habitat to support forest songbird biodiversity. To the extent that positive agroforestry contributions can be made, their value will be of most benefit in areas very close to existing forest and they are likely to favour frugivores and larger species. Despite recent suggestions that smallholder agricultural areas may have much to contribute to tropical forest biodiversity conservation (Daily *et al*., 2001; Hughes *et al*., 2002; Luck & Daily, 2003), this study found no evidence for this around the Mabira Forest Reserve in Uganda. Additional research in other regions regarding the role of agricultural areas in supporting forest biodiversity is therefore necessary before strong conclusions regarding the conservation value of tropical countryside habitats can be made.

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Appendix. List of species recoreded at count stations in Mabira Forest Reserve and surrounding agriculture areas

		No. stations detected at in:					
Species	Family	Intact forest	Regen forest	Agric	Total detections	Guild	Abbreviation
Alethe diademata	Turdidae	0	4	0	4	FF	ALDI
Andropadus curvirostris	Pycnonotidae	15	10	0	25	FF	ANCU
Andropadus gracilirostris	Pycnonotidae	7	0	0	7	FF	ANRO
Andropadus gracilis	Pycnonotidae	4	4	0	8	FF	ANGR
Andropadus latirostris	Pycnonotidae	31	26	0	58	F	ANLA
Andropadus virens	Pycnonotidae	3	30	11	44	F	ANVI
Anthreptes collaris	Nectariniidae	0	0	2	2	F	ANCO
Apalis cinerea	Sylviidae	3	0	0	3	FF	APCI
Apalis rufogularis	Sylviidae	19	8	0	27	FF	APRU
Apaloderma narina	Trogonidae	6	0	0	6	F	APNA
Aplopelia larvata	Columbidae	6	0	0	6	FF	APLA
Bleda eximia	Pycnonotidae	7	2	0	9	FF	BLEX
Bleda syndactyla	Pycnonotidae	5	3	0	8	FF	BLSY
Buccanodon duchaillui	Capitonidae	8	8	0	16	FF	BUDU
Bycanistes subcylindricus	Bucerotidae	22	17	29	69	F	BYSU
Camaroptera brachyura	Sylviidae	6	23	31	60	f	CABR
Camaroptera chloronota	Sylviidae	23	14	0	38	FF	CACH
Camaroptera superciliaris	Sylviidae	0	2	0	2	FF	CASU
Campephaga quiscalina	Campephagidae	3	4	0	7	FF	CAQU
Campethera caroli	Picidae	0	1	0	1	F	CACA
Centropus superciliosus	Cuculidae	0	2	1	3	O	CESU
Cercococcyx mechowi	Cuculidae	8	6	0	15	FF	CEME
Cercotrichas leucophrys	Turdidae	0	0	2	2	–	CELE
Ceuthmochares aereus	Cuculidae	1	0	0	1	F	CEAE
Chlorocichla flavicollis	Pycnonotidae	1	0	1	2	f	CHFL
Chloropeta natalensis	Sylviidae	0	0	11	11	O	CHNA
Chrysococcyx caprius	Cuculidae	0	0	6	6	O	CHCA
Chrysococcyx cupreus	Cuculidae	12	10	5	27	F	CHCU
Chrysococcyx klaas	Cuculidae	2	9	6	17	f	CHKL
Cisticola erythrops	Sylviidae	0	0	6	6	O	CIER
Cisticola lateralis	Sylviidae	0	0	7	7	O	CILA
Colius striatus	Coliidae	0	0	6	6	O	COST
Columba unicincta	Columbidae	4	3	0	7	FF	COUN
Corythaeola cristata	Musophagidae	3	8	3	14	F	COCR
Cossypha cyanocampter	Turdidae	3	7	1	12	F	COCY
Cossypha natalensis	Turdidae	0	1	2	3	F	CONA
Cossypha niveicapilla	Turdidae	2	3	4	9	F	CONI
Crinifer zonurus	Musophagidae	0	0	10	10	O	CRZO
Cuculus solitarius	Cuculidae	15	3	7	25	F	CUSO
Dicrurus modestus	Dicruridae	0	1	1	2	F	DIMO
Emberiza flaviventris	Monarchidae	0	0	4	4	–	EMFL
Eminia lepida	Emberizidae	0	0	1	1	f	EMLE
Erannornis longicauda	Sylviidae	0	0	4	4	f	ERLO
Francolinus nahani	Phasianidae	16	13	0	29	FF	FRNA
Guttera edouardi	Numididae	0	0	1	1	F	GUED
Gymnobucco bonapartei	Capitonidae	1	2	0	3	F	GYBO
Halycon chelicuti	Alcedinidae	0	0	5	5	O	HACH
Halycon malimbica	Alcedinidae	18	7	2	27	F	HAMA
Halycon senegalensis	Alcedinidae	0	1	0	1	O	HASE
Hylia prasina	Sylviidae	29	22	4	56	F	HYPR
Illadopsis albipectus	Timaliidae	32	27	2	62	FF	ILAL
Illadopsis fulvescens	Timaliidae	27	24	0	52	FF	ILFU
Illadopsis rufipennis	Timaliidae	10	2	0	12	FF	ILRU
Ispidina picta	Alcedinidae	0	0	1	1	f	ISPI
Lagonosticta rubricata	Estrildidae	0	0	1	1	O	LARU
Lagonosticta senegala	Estrildidae	0	0	3	3	–	LASE
Lamprotornis splendidus	Sturnidae	1	0	3	4	F	LASP
Laniarius ferrugineus	Malaconotidae	0	4	0	4	f	LAFE
Laniarius leucorhynchus	Malaconotidae	0	7	0	7	FF	LALE
Laniarius luehderi	Malaconotidae	1	0	0	1	F	LALU

Appendix. Continued

Species	Family	No. stations detected at in: Intact forest	Regen forest	Agric	Total detections	Guild	Abbreviation
Lonchura cucullata	Estrildidae	0	0	8	8	O	LOCU
Lybius bidentatus	Capitonidae	0	0	16	16	f	LYBI
Macrosphenus concolor	Capitonidae	24	7	0	32	FF	MACO
Macrosphenus flavicans	Sylviidae	12	13	2	28	FF	MAFL
Malimbus rubricollis	Sylviidae	0	1	0	1	FF	MARU
Melierax metabates	Ploceidae	0	0	2	2	–	MEME
Muscicapa griseigularis	Accipitridae	22	11	0	33	FF	MUGR
Myioparus plumbeus	Muscicapidae	0	1	0	1	f	MYPL
Nectarinia cuprea	Muscicapidae	0	0	7	7	f	NECU
Nectarinia erythrocerca	Nectariniidae	0	0	2	2	O	NEER
Nectarinia olivacea	Nectariniidae	7	7	1	15	FF	NEOL
Nectarinia senegalensis	Nectariniidae	0	0	23	23	f	NESE
Nectarinia superba	Nectariniidae	0	3	0	3	F	NESU
Nectarinia venusta	Nectariniidae	0	0	3	3	f	NEVE
Nectarinia verticalis	Nectariniidae	0	0	2	2	F	NEVE
Nicator chloris	Nectariniidae	20	13	0	34	F	NICH
Nigrita canicapilla	Pycnonotidae	7	11	23	41	F	NICA
Oriolus branchyrhynchus	Estrildidae	34	9	0	44	F	ORBR
Parus leucomelas	Oriolidae	0	1	12	13	f	PALE
Passer griseus	Paridae	0	2	30	32	O	PAGR
Phoeniculus castaneiceps	Passeridae	0	1	0	1	FF	PHCA
Phyllastrephus cabanisi	Phoeniculidae	0	1	0	1	FF	PHCA
Phyllastrephus hypochloris	Pycnonotidae	8	20	0	29	FF	PHHY
Phyllastrephus icterinus	Pycnonotidae	14	15	0	30	FF	PHIC
Phylloscopus sibilatrix	Pycnonotidae	16	15	1	33	F	PHSI
Platysteira castanea	Sylviidae	8	9	0	17	FF	PLCA
Platysteira cyanea	Platysteiridae	0	2	27	29	f	PLCY
Ploceus baglafecht	Platysteiridae	0	0	6	6	f	PLBA
Ploceus nigricollis	Ploceidae	0	0	1	1	f	PLNI
Ploceus ocularis	Ploceidae	0	0	3	3	f	PLOC
Ploceus tricolor	Ploceidae	0	1	0	1	FF	PLTR
Pogoniulus bilineatus	Ploceidae	5	12	14	31	F	POBI
Pogoniulus scolopaceus	Capitonidae	29	22	15	66	F	POSC
Pogoniulus subsulphureus	Capitonidae	27	29	6	63	FF	POSU
Prinia subflava	Capitonidae	0	0	29	29	f	PRSU
Psittacus erithacus	Sylviidae	7	18	10	35	FF	PSER
Pycnonotus barbatus	Psittacidae	11	29	31	71	f	PYBA
Sarothrura pulchra	Pycnonotidae	14	26	0	41	F	SAPU
Serinus citrellinoides	Rallidae	0	0	3	3	f	SECI
Serinus mozambicus	Fringillidae	0	0	16	16	–	SEMO
Serinus sulphuratus	Fringillidae	0	0	1	1	O	SESU
Spermophaga ruficapilla	Fringillidae	0	1	0	1	F	SPRU
Stiphrornis erythrothorax	Estrildidae	22	13	0	35	FF	STER
Stizorhina fraseri	Turdidae	34	23	0	58	FF	STFR
Streptopelia semitorquata	Turdidae	1	3	12	16	f	STSE
Sylvietta virens	Columbidae	0	3	0	3	F	SYVI
Tchagra australis	Sylviidae	0	0	3	3	O	TCAU
Terpsiphone rufiventer	Malaconotidae	19	1	0	20	FF	TERU
Terpsiphone viridis	Monarchidae	0	6	8	14	f	TEVI
Tockus alboterminatus	Monarchidae	0	2	12	14	f	TOAL
Trachylaemus purpuratus	Bucerotidae	20	18	0	39	F	TRPU
Treron australis	Capitonidae	0	1	0	1	F	TRAU
Tricholaema hirsuta	Columbidae	9	11	0	20	F	TRHI
Turdus pelios	Turdidae	0	3	15	18	f	TUPE
Turtur afer	Columbidae	0	1	16	17	f	TUAF
Turtur tympanistra	Columbidae	6	7	1	14	F	TUTY
Uraeginthus bengalus	Estrildidae	0	0	2	2	–	URBE
Zosterops senegalensis	Zosteropidae	0	4	31	35	f	ZOSE

Habitat guilds: FF, forest specialist; F, forest generalist; f, forest visitor; O, open habitat specialist. Regen, regenerated; Agric, agriculture.