

FROM FOREST TO FARMLAND: HABITAT EFFECTS ON AFROTROPICAL FOREST BIRD DIVERSITY

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Abstract. Although the Guinea–Congolian rain forest region is an important focal point for conservation in Africa, very little information is available on the effects of forest modification and land use on the region’s biodiversity. We studied bird communities and vegetation characteristics in 24 sampling stations distributed over two near-natural forests (near-primary forest, secondary forest), and two land use types (agroforestry, annual cultures) in the lowlands of the Korup region, Cameroon. Repeated sampling was used to establish near-complete inventories of bird assemblages for each site. Despite a 90% average drop in tree basal area from forest to farmland, overall bird species richness did not decrease significantly with increasing habitat modification. However, different groups of birds responded in different ways. Frugivorous and omnivorous bird species richness did not differ between habitats, whereas richness in granivorous, flower-visiting, and nonbreeding species was higher in land use systems compared to forests. In contrast, insectivorous birds, especially terrestrial and large arboreal foliage gleaning insectivores, and ant followers showed a declining species richness from forest to farmland. Also, richness in species of those restricted to the Guinea–Congolian forest biome and of the family Pycnonotidae showed a pronounced decline with increasing habitat modification. Species richness of overall insectivores, terrestrial insectivores, large- and medium-sized arboreal foliage gleaners, ant followers, as well as pycnonotids and biome-restricted species, were strongly or even very strongly positively correlated with overstory tree density and, in most cases, also with basal area. In contrast, tree density and basal area were strongly negatively correlated with species richness of nonbreeding visitors and flower-visiting bird species. Species composition was most distinct between near-primary forest and annual culture sites, and the abundance of 23 out of 165 species was affected by habitat, suggesting considerable partitioning of habitat niches along the habitat gradient. Our results stress the importance of tree cover in tropical land use systems for the maintenance of resident forest bird populations and confirm that natural forest management is more beneficial for global bird conservation compared to other forms of forest exploitation, including agroforestry systems.

Key words: Africa; agriculture; agroforestry systems; ant followers; arboreal foliage gleaners; birds; deforestation; land use; terrestrial insectivores; tropical rain forest.

INTRODUCTION

Deforestation in the humid tropics is one of the major threats to global biodiversity (Dobson et al. 1997, Brooks et al. 2002). Ten years after the Rio declaration, the Agenda 21 of the Earth Summit in Rio 1992, rates of natural forest loss appear to have worsened in all tropical regions except Latin America. In absolute terms, more natural forest might have been lost in the 1990s than in the 1980s (Matthews 2001). Predictions of species loss from deforestation rates in the tropics have been made several times (e.g., Brooks and Balmford 1996, Brooks et al. 1999a, c, 2002), but have been criticized partly because of a failure to acknowledge

the ability of many tropical forest species to survive in agricultural production areas (Brown and Brown 1992, Pimentel et al. 1992, Budiansky 1994, Poudevigne and Baudry 2003).

Recently, several studies have addressed the conservation value of agricultural landscapes using community data from various taxonomic groups. In several cases, studies showed that a relatively high number of individuals and species can still be found in land use systems, and that a considerable proportion of these species are part of the natural forest fauna (Estrada et al. 1993, Petit et al. 1999, Daily et al. 2001, Hughes et al. 2002).

However, abundances may also be affected by interspecific interactions, as suggested in models of density compensation (MacArthur et al. 1972). Even if richness changes little with disturbance, trophic structure may be altered, and species characteristic of pri-

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mary and old-growth, secondary forest may be replaced by species associated with disturbed habitats (Estrada et al. 1994, Lawton et al. 1998, Lindell et al. 2004). Furthermore, a cautious interpretation of abundance and species richness data is necessary, since deforestation is a relatively recent phenomenon, intensification of the agricultural land is still ongoing and, so far, only little information on the long-term stability of faunal populations in land use systems is available (Donald 2004). In order to increase our understanding of how disturbed ecosystems and communities are structured, it is necessary to obtain information on species richness and distribution patterns in intact rain forest (Wilson 1988, Boulmier et al. 1998) and to examine responses of tropical species and ecosystems to landscape modification (Lugo 1988, Johns 1992, Estrada et al. 1993). This can help to design reserves more efficiently and lead to strategies for maintaining biological diversity and natural ecosystem integrity in human-dominated ecosystems (see also Fjelds  et al. 2004).

For birds, general findings have shown that traditional agroforests, with a mix of cultivated and natural shade trees, can support a high number of species, including many forest specialists, especially in close proximity to natural forest (e.g., Greenberg et al. 1997b). In contrast, agroforests with planted shade trees, even if composed of many tree species, only support a few forest specialist birds in the absence of nearby primary forest (Thiollay 1995, Greenberg et al. 1997a, 2000, Roberts et al. 2000). Annual cultures generally do not support high numbers of bird species in forest regions (Lawton et al. 1998, Waltert et al. 2004), but the picture can be different if groups of tall trees and forest fragments are left in the agricultural landscape (Daily et al. 2001, Hughes et al. 2002).

Most information on bird species richness in tropical land use systems is available from America (Estrada et al. 1997, Greenberg et al. 1997a, b, Calvo and Blake 1998, Daily et al. 2001, Hughes et al. 2002, Mas and Dietsch 2004). Only a few studies exist from Africa (Blankespoor 1991, Kofron and Chapman 1995, Plumtre 1997, Lawton et al. 1998), South/Southeast Asia (Beehler et al. 1987, Thiollay 1995), or Australasia (Poulsen and Lambert 2000). The objective of this paper is to document patterns of species richness and abundance of birds in two types of natural forest (near-primary forest, secondary forest) and two types of land use systems (agroforestry systems, annual cultures), which represent major components of the agricultural habitat mosaic in tropical landscapes worldwide, and to describe the potential role that vegetation characteristics (e.g., tree density) play for the species richness of different groups of birds of similar ecology, taxonomy, or geographic range.

Based on an earlier study from Cameroon (Lawton et al. 1998), and a similar one from Sulawesi, Indonesia (Waltert et al. 2004), we predicted that (1) overall bird species richness will decrease with increasing habitat

modification, (2) that species composition will change along the habitat gradient with species from disturbed habitats gradually replacing those of intact rain forest, and that (3) different bird groups (different taxa or guilds) will respond in different ways to habitat modification. We also predicted that habitat variables such as tree density and basal area are correlated positively with the species richness of bird groups characteristic of intact rain forest habitats.

STUDY AREA AND SITES

The study was carried out in the vicinity of Korup National Park in the Southwest Province of Cameroon. Korup National Park is part of the Guineo–Congolian forest, which encompasses ~2.8 million km² mostly below 600 m elevation, except for Precambrian highlands, such as the Jos Plateau of Nigeria and the Cameroon Highlands, with the highest point being Mount Cameroon at 4079 m (Lawson 1996). Annual rainfall in this vast region varies from 1500 mm to >10 000 mm, giving rise to a variety of vegetation floristic regions (White 1983). The region contains 84% of all known African primates, 68% of known African passerine birds, and 66% of known African butterflies (Groombridge and Jenkins 2000). For this reason, the Guineo–Congolian rain forest is an important focal point for conservation efforts in Africa.

The Southwest Province and adjacent portions of southeastern Nigeria are especially rich in biodiversity. Floristically, this area is part of the Hygrophyllous Coastal Evergreen Rainforest, which occurs along the Gulf of Biafra. This vegetation sub-unit is associated with high rainfall levels (White 1983) and is part of the Cross–Sanaga–Bioko Coastal Forest ecoregion, an area of 52 000 km² (Olsen et al. 2001, World Wildlife Fund 2001). The ecoregion is considered an important center of plant diversity because of its probable isolation during the Pleistocene (Davis et al. 1994) and holds an assemblage of endemic primates known as the Cameroon faunal group (see Oates 1996). The region is also exceptionally rich in butterflies (Larsen 1997) and birds (e.g., Rodewald et al. 1994, Bobo et al. 2004). Protected areas in the region include Cross River National Park (Nigeria) and Korup National Park, as well as an extensive network of forest reserves.

Korup National Park is part of the former Korup Project Area (KPA), which consists of the Park (1253 km²) and the surrounding Support Zone (5,357 km²). The Support Zone contains extensive forests and three forest reserves (Rumpi Hills, Nta Ali, Ejagham) situated south, east, and north of the Park. It also contains two logging concessions (1396 km²), which were active eight years before the study started. At present there are ~50 000 people in 182 villages living within KPA. Five of these villages are situated within the Park boundary.

The study sites were all situated in an area directly northeast to the Korup National Park, between the vil-

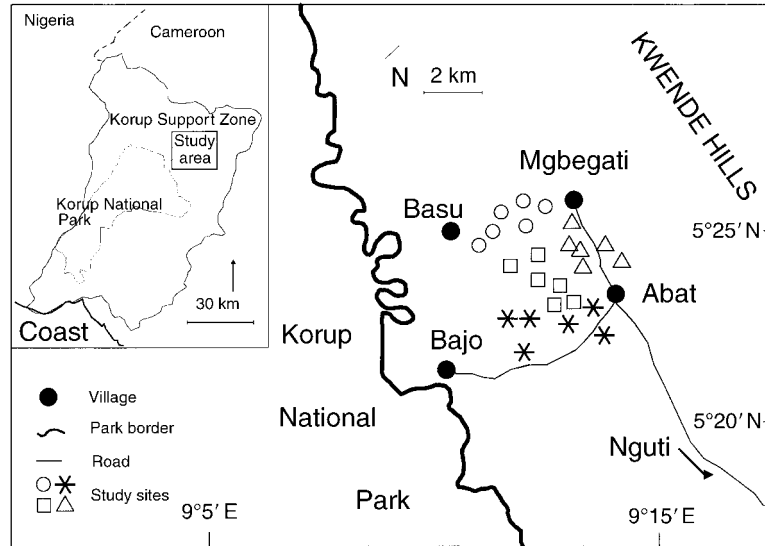


FIG. 1. Location of the study area in the Korup region, Southwest Cameroon (inset), and situation of study sites (sampling stations). Study sites are indicated by habitat type as circles (near-primary forest), triangles (secondary forests), squares (agroforestry systems), and asterisks (annual cultures).

lages Basu, Bajo, Abat, and Mgbegati, in the populated part of the Korup Support Zone (Fig. 1). In this area, farming is restricted to the immediate surroundings of the villages, leaving most of the area forested. Judged just from physical appearance, much of the forests in the area are in a good state; however, hunting and poaching has seriously reduced their larger mammals (Waltert et al. 2002), while larger birds (hornbills, turcoes, phasianids) were still common, probably because they were not (yet) the targets of hunters (M. Waltert, unpublished data).

At total of 24 study sites (or "sampling stations") were selected, representing the following four habitats: near-primary forest (NF), with very little or no anthropogenic activities; secondary forest (SF), overgrown agricultural areas along the main road, with a canopy cover of less than 60%; agroforestry sites (AF), where the land is used for cacao/coffee/plantain production; and annual cultures (AC), where the land is used for subsistence crop production (cassava, yams, maize, groundnuts). All sites were at least 500 m apart from each other. Topographically, all study sites were situated at an altitude of ~250 m above sea level.

METHODS

Bird surveys

Bird surveys were carried out between 23 December 2003 and 5 March 2004. Point counts located at the center of each sampling station were used to record all birds within a radius of 50 m from the observer. Most land use sites studied (AF, AC) were only small in size (<2 ha), so small-scale point counting was the only possible method, regardless of the fact that bird point diversity in tropical forest might reflect only a pro-

portion of the overall within-habitat diversity (see Terborgh et al. 1990 and discussions of tropical plot sizes therein). Points were visited between 6:00 and 9:00 a.m. for 20 min, and all visual and acoustical detections within a period of 15 min were recorded. A digital rangefinder was used to measure and estimate distances, and all observations beyond 50 m were discarded for analyses of site species richness. Sites were visited alternately, with a total of nine visits per site. Fieldwork was done exclusively by the same observer throughout the survey. Bird species were identified mainly by using Borrow and Demey (2001); also used were Brown et al. (1982), Urban et al. (1986, 1997), Fry et al. (1988, 2001), and Keith et al. (1992). Unfamiliar birds voices were taped in the field and identification was confirmed later using sound recordings (Chappuis 2000). Because of difficulties in acoustically identifying the two large resident hornbills, *Ceratogymna elata* and *C. atrata*, they were lumped during the survey.

Vegetation survey

At each study site, a sampling grid of nine 10 × 10 m plots was established to collect data on trees. On these nine plots, spaced at 10 m, and covering 900 m² in total at each study site, overstory tree density and overstory tree basal area were recorded. All trees >10 cm in diameter at 1.3 m height were recorded. In agroforestry sites, cocoa/coffee trees were not measured, but their numbers and size classes were estimated for each plot. In addition, in the center of each plot, a 1 × 1 m small subplot was used to collect data for understory plants. Understory plants are here defined as all vascular plants of <1.3 m in height. For the purpose

of this study, only the most common trees and understory plants were identified to species level.

Data analysis

For each study site, we counted the total number of species detected after the repeated surveys, here referred to as “observed” species richness. In most field studies, not all species that are actually present are also recorded (see Nichols and Conroy 1996). Therefore, we also quantified an “estimated” species richness, which takes into account that there are species that are not actually recorded, but whose presence can be inferred from the pattern of observed species occurrence. To calculate estimated species richness, we used the first-order jackknife method that was initially designed to estimate population size from capture-recapture data, allowing capture probabilities to vary by individuals (Burnham and Overton 1978, 1979). This model can equally be applied to estimations of species richness (see Heltshe and Forrester 1983, Colwell and Coddington 1994, Boulinier et al. 1998, Chazdon et al. 1998, Nichols et al. 1998, Hughes et al. 2002). The jackknife estimator performs well if the proportion of rare species (those that are represented in only one or two samples) is low (Nichols and Conroy 1996, Chao 1987). We also calculated beta-diversity between different sites using the classic Sorensen (qualitative) index (Magurran 1988). To calculate first-order jackknife estimates of bird species richness at each site and beta-diversity between different sites, we used the computer program of Colwell (2000) by randomizing samples 100 times. Parameters were used in a one-way ANOVA in order to analyze effects of habitat type on species numbers. Means are given with standard deviation if not mentioned otherwise. Tukey’s honest significance difference test (hsd test) was used for multiple comparisons of means. Analyses were done for all species combined, as well as separately, for different feeding guilds. These were: insectivores ($n = 92$ spp.), frugivores ($n = 23$ spp.), granivores ($n = 10$ spp.), flower-visiting/nectarivorous birds ($n = 15$ spp.), and omnivores ($n = 10$ spp.). In addition, we also separately analyzed the guild of ant-following species ($n = 18$ spp.), and the insectivorous subgroups of terrestrial insectivores ($n = 15$ spp.), as well as large-sized (>40 g), medium-sized (20–40 g), and small-sized (<20 g) arboreal foliage gleaners ($n = 13, 15, 18$ spp., respectively). We also grouped biome-restricted bird species ($n = 110$ spp. within our sample), all confined to the Guinea–Congolian forest biome, extending from Gambia in the west to Rwanda in the East and Zambia in the South (see Fishpool and Evans 2001). In addition, we grouped (nonbreeding) visitors, containing both Palaearctic and local migrants ($n = 12$ spp.). Furthermore, we specifically looked at habitat effects on the bulbuls (family Pycnonotidae, $n = 21$ spp.), a large taxon known to contain mainly forest-dwelling species. Information on ecology and taxonomic affinities were

compiled from the abovementioned literature sources (see *Methods: Bird surveys*).

For each study site and species, a measure of relative abundance was calculated as the maximum number of individuals detected at each study site during any visit, and one-way ANOVA was done to detect species-specific responses to habitat variation. We applied the sequential Bonferroni technique (Holm 1976 in Rice 1989) to reduce the probability of statistical Type I errors by calculating table-wide significances, α , for each bird species, and listed only those species with $\alpha \leq 0.05$. Using post hoc tests (Tukey’s honest significant difference test), single species were assigned to different response categories. The proportions of biome-restricted species and those of the different feeding guilds in different response categories were then tested to differ from their overall representation within the sample bird community using a chi-square goodness-of-fit test.

Many similarity indices have been proposed to analyze patterns in abundance data (see Legendre and Legendre 1998). However, we simply analyzed abundance data (see preceding paragraph) in a correspondence analysis (CA) and ordinated our study sites two-dimensionally to depict avifaunal similarity between habitat types. This procedure was preferred to an ordination based on similarity indices since it is more simple, incorporates species’ abundance, and (according to previous experience; Waltert et al. 2004) produces results similar to a matrix analysis of quantitative similarity measures.

Spearman rank correlation coefficients, r_s , were established to describe relationships between the three vegetation parameters ([overstory] tree density, basal area, understory plant density) and bird species richness and abundance, for the different guilds of birds separately. Again, table-wide significances were calculated using the sequential Bonferroni correction (see Rice 1989). Spearman correlations, one-way ANOVA, and all other statistical analyses were performed using STATISTICA 5.1 (StatSoft 1995).

RESULTS

Species richness of sampling stations (spot diversity)

During the point counts, a total of 4530 records (single detections of bird individuals or groups) belonging to 180 positively identified species were obtained (Appendix). The number of bird records per sampling station was significantly affected by habitat type (one-way ANOVA, $F_{3,20} = 7.44$, $P = 0.002$): Within the 50 m radius of each sampling station, the number of accumulated records after the nine repeat visits were highest in annual cultures (379.7 ± 77.8 ; mean \pm SD) and significantly lower in secondary forests (243.8 ± 48.9 ; Tukey’s hsd test, $P = 0.002$), near-primary forest (255.2 ± 24.2 ; Tukey’s hsd test, $P = 0.005$), or ag-

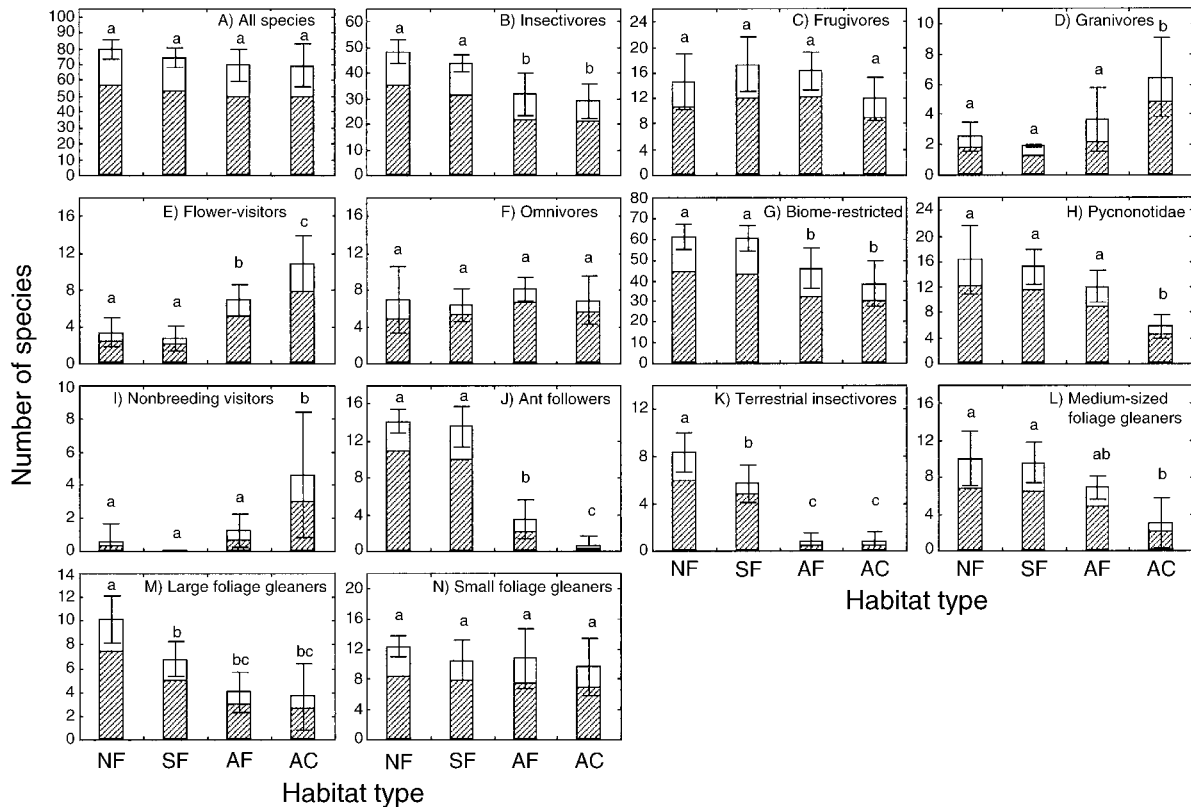


FIG. 2. Bird species diversity in the Korup region, Southwest Cameroon, given as estimated species richness (mean \pm SD; open bars) based on the first-order jackknife species richness estimator and mean observed species richness (hatched portion of bars) per study site, given for each habitat type, for (A) all bird species detected, (B–F) different feeding guilds, (G) biome-restricted species, (H) Pycnonotidae, (I) nonbreeding visitors, (J) ant followers, and (K–N) different subgroups of insectivores. Different letters indicate significant differences (Tukey's honest significant difference test) between mean estimated species richness. Habitats are: NF, near-primary forest; SF, secondary forest; AF, agroforestry systems; AC, annual cultures.

roforestry systems (288.3 ± 56.6 ; Tukey's hsd test, $P = 0.044$).

Jackknife species richness estimators revealed that assemblages per studied bird group were not yet completely recorded: Completeness of the surveys at single sites ranged from an average of 70.9% in the six agroforestry sites to 72.1% in the near-primary forest sites (for all species combined). Completeness in the different groups was variable, e.g., in terrestrial insectivores between 68.6% and 86.6%, or in visitors between 52.9% and 75.8%, but reached 100% only at a few single sites. In all bird groups studied, observed species richness was significantly correlated with estimated species richness (Spearman Rank correlation coefficients $r_s > 0.87$, $P < 0.001$, $n = 24$, in all cases; see also Fig. 2).

Despite of the significantly higher number of accumulated records in annual cultures, highest species richness was found in near-primary forest, but there was no significant difference in estimated species richness between habitat types (Table 1). Estimated and observed numbers of species were only slightly lower

in secondary forest, in agroforests, and annual cultures (see Fig. 2A).

Based on the jackknife estimates, species richness in omnivorous and frugivorous species did not differ significantly between habitat types (Table 1, Fig. 2C, F). However, steady declines in species richness with increasing habitat modification appeared in insectivores (Fig. 2B), ant followers (Fig. 2J), and in most insectivorous subgroups (Fig. 2K–N), such as terrestrial insectivores, large arboreal foliage gleaners, and medium-sized arboreal foliage gleaners. Based on Tukey's hsd tests, species richness of medium-sized arboreal foliage gleaners did not differ significantly between near-primary forest, secondary forest, and agroforestry sites, but was lower in annual cultures than in near-primary and secondary forest sites. Furthermore, species richness of terrestrial insectivores and large arboreal foliage gleaners was significantly lower in secondary forest compared to near-primary forest. Small foliage gleaners did not show significant differences in species richness between habitat types (Fig. 2N).

TABLE 1. Estimated bird species richness (mean \pm SD), per habitat type, as well as results of one-way ANOVA testing the hypothesis of no difference among habitats, based on first-order jackknife species richness estimator, for all bird species as well as various bird groups and guilds separately.

Bird group or guild	Near-primary forest	Secondary forest	Agroforestry systems	Annual cultures	$F_{3,20}$	P
All species	79.7 \pm 5.8	74.5 \pm 6.2	69.9 \pm 10.0	69.4 \pm 13.6	1.54	0.234
Insectivores	48.5 \pm 4.4	44.1 \pm 3.1	31.7 \pm 8.5	29.0 \pm 6.7	14.50	<0.001
Frugivores	14.7 \pm 4.4	17.3 \pm 4.3	16.3 \pm 3.0	12.0 \pm 3.4	2.24	0.114
Granivores	2.5 \pm 1.0	1.9 \pm 0.1	3.7 \pm 2.1	6.5 \pm 2.6	7.97	0.001
Flower visitors	3.4 \pm 1.6	2.8 \pm 1.4	6.9 \pm 1.8	10.9 \pm 3.0	20.73	<0.001
Omnivores	7.0 \pm 3.7	6.4 \pm 1.8	8.1 \pm 1.3	6.9 \pm 2.7	0.54	0.663
Restricted-range species	61.1 \pm 5.9	60.6 \pm 6.1	45.9 \pm 9.9	38.4 \pm 11.0	10.35	<0.001
Pycnonotidae	16.3 \pm 5.4	15.2 \pm 2.8	12.1 \pm 2.5	5.8 \pm 1.9	11.48	<0.001
Visitors	0.6 \pm 1.0	0.0 \pm 0.0	1.3 \pm 1.0	4.6 \pm 3.8	6.25	0.004
Ant followers	14.1 \pm 1.3	13.6 \pm 2.2	3.5 \pm 2.1	0.6 \pm 1.0	97.84	0.001
Terrestrial insectivores	8.4 \pm 1.6	5.7 \pm 1.6	0.8 \pm 0.9	0.8 \pm 0.9	48.52	0.001
Medium-sized foliage gleaners	10.0 \pm 3.0	9.6 \pm 2.2	6.9 \pm 1.2	3.1 \pm 2.7	10.83	<0.001
Large foliage gleaners	10.2 \pm 2.0	6.8 \pm 1.5	4.0 \pm 1.6	3.7 \pm 2.8	12.77	<0.001
Small foliage gleaners	12.4 \pm 1.3	10.5 \pm 2.7	10.8 \pm 4.0	9.7 \pm 3.7	0.78	0.518

A clear decline in species richness from forest to farmland was equally found for biome-restricted species (Fig. 2G). It was highest in near-primary forest and secondary forest, and significantly lower in both land use systems.

Observed species richness of bulbuls (Pycnonotidae) also decreased with increasing habitat modification (Fig. 2H), but differences were not significant between near-primary forest, secondary forest, and agroforestry systems.

Three groups seemed to show a significant increase in species richness with increasing habitat modification. Species richness of flower visitors was highest in annual cultures, significantly lower in agroforestry systems, and still lower in secondary or near-primary forests (Fig. 2E). Granivorous birds also showed highest species numbers in annual cultures and were significantly less species rich in other habitat types (Fig. 2D). The same pattern was found for the group of nonbreeding visitors (Fig. 2I).

Species similarity between sampling stations (beta diversity)

Pairwise similarity of bird species composition (mean Sorensen incidence index \pm SD) was highest among the six near-primary forest sites (0.75 ± 0.04) and the six secondary forest sites (0.69 ± 0.04), and slightly lower among agroforestry (0.62 ± 0.07) and annual culture sites (0.60 ± 0.06). It was still high between near-primary and secondary forest sites (0.68 ± 0.03), intermediate between agroforestry systems and annual cultures (0.51 ± 0.09), agroforestry systems and secondary forest (0.51 ± 0.07), or near-primary forest and agroforestry systems (0.46 ± 0.08), but low between near-primary forest and annual cultures (0.27 ± 0.09), or secondary forest and annual cultures (0.32 ± 0.09). Two-dimensional ordination of study sites using abundance data in a correspondence analysis only showed overlap between near-primary and secondary forest sites (Fig. 3). A one-way MANOVA of the sample scores extracted from the two-dimensional ordination revealed a significant difference between the four groups of sites (Rao's $R_{6,38} = 43.08$, $P < 0.001$).

Vegetation characteristics

A total of 856 overstory trees were recorded on the 24 study sites, and a further estimated 600 planted cocoa/coffee trees >10 cm dbh. Both overstory tree density (the number of trees per 900 m²) and basal area were significantly different between habitats, showing a clear decrease from forest to farmland habitat (Table 2). Highest tree density (cocoa/coffee trees excluded) was recorded on near-primary forest sites, but differences were not significant between near-primary forest and secondary forest sites (Tukey's hsd test, $P = 0.870$ for numbers of trees, $P = 0.651$ for basal area).

Tree density (excluding cocoa/coffee) was significantly lower in agroforestry sites than in both natural forests (Tukey's hsd test, $P = 0.009$), but basal area was not (Tukey's hsd test, $P = 0.175$). This shows that

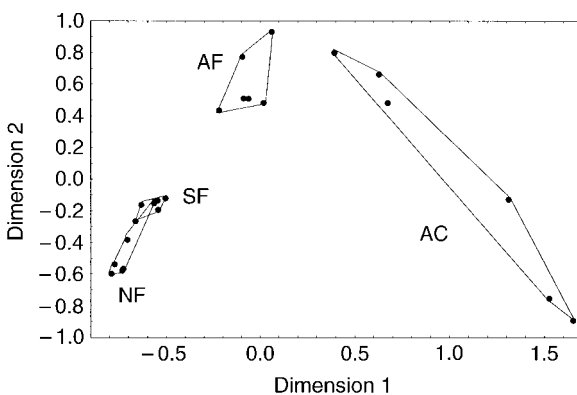


FIG. 3. Correspondence analysis plot of avifaunal similarity between different sampling stations based on abundance data, from the Korup region, Southwest Cameroon. Sampling stations belonging to the same habitat category are connected by lines. See Fig. 2 for abbreviations of habitats.

TABLE 2. Density of overstory trees, their basal area, and density of understory plants, per habitat type; values are means \pm SD.

Characteristic	Habitat				$F_{3,20}$	P
	Near-primary forest	Secondary forest	Agroforestry systems	Annual cultures		
Tree density (individuals/900 m ²)	51.3 \pm 12.0	47.7 \pm 8.1	34.0 \pm 7.9	9.7 \pm 2.0	30.92	<0.001
Tree basal area (m ² /ha)	48.7 \pm 14.6	40.0 \pm 19.7	32.7 \pm 7.1	4.9 \pm 3.9	12.85	<0.001
Understory plant density (individuals/9 m ²)	33.3 \pm 4.2	60.7 \pm 17.8	22.8 \pm 3.4	88.2 \pm 6.6	53.19	<0.001

Note: Planted cocoa/coffee trees are excluded from the agroforestry data.

the studied agroforestry sites still possessed a good stock of remnant forest trees, with \sim 70% of the tree density and basal area of the studied near-primary forest. When including the planted cocoa/coffee trees into the analysis, basal area in agroforestry reached 67.8 ± 7.1 m²/ha, being higher than in secondary forest (Tukey's hsd test, $P = 0.007$), but only marginally higher when compared to near-primary forest (Tukey's hsd test, $P = 0.081$).

Annual cultures had the lowest trees density and basal area, representing \sim 20% and 10%, respectively, of what was found in near-primary forest (Tukey's hsd test, $P < 0.001$). The difference between annual cultures and agroforestry sites was also significant (Tukey's hsd test, $P < 0.001$ for tree density, $P = 0.007$ for basal area).

In order to describe the diameter distributions of overstory trees, we pooled data from different study sites per habitat (Fig. 4): Secondary forest differed from near-primary forest in a lowered frequency of trees of the 21–30 cm dbh size class, as well as in some larger size classes (61–80 cm dbh and 91–100 cm dbh; Fig. 4A, B), but was otherwise similar to that of the near-primary forest. The main difference between agroforestry systems and annual cultures was the absence of large trees >80 cm dbh in annual cultivations (Fig. 4C, D).

Despite a very similar diameter distribution in near-primary and secondary forest, these habitats differed considerably in the composition of the most common tree species recorded (Table 3): While the most often recorded trees in near-primary forests were regener-

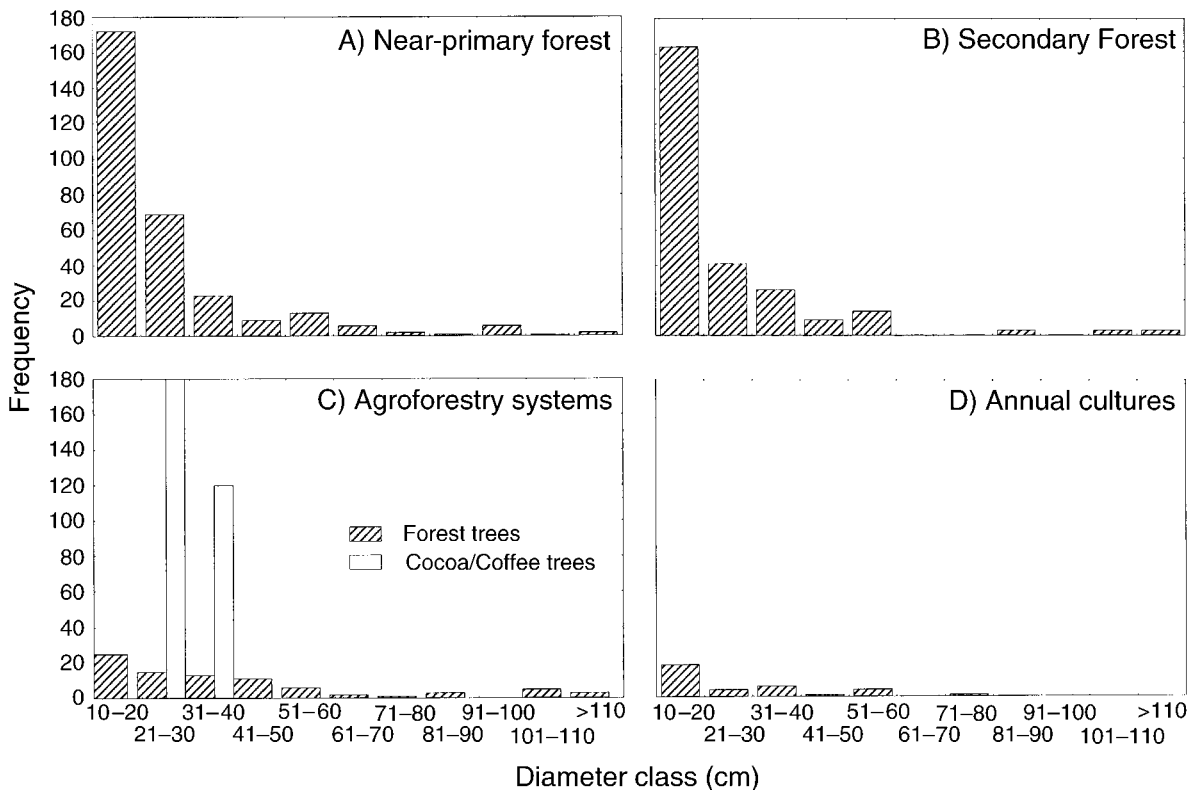


FIG. 4. Diameter distributions of overstory trees ≥ 10 cm dbh, per habitat type, from the Korup region, Southwest Cameroon. Data from six plots of 900 m² in each habitat were pooled, resulting in a total survey area of 5400 m² per habitat.

TABLE 3. The most common overstory tree and understory plant species recorded, and their frequency in different habitats.

Habitat type	Overstory trees		Understory plants	
	Species	Frequency	Species	Frequency
Near-primary forest (NF)	<i>Oubanguia alata</i>	23	<i>Scaphopetalum blackii</i>	39
	<i>Gilbertiodendron demonstrans</i>	14	<i>Cola</i> spp.	9
	<i>Dichostema glaucescens</i>	11	<i>Gilbertiodendron demonstrans</i>	7
	<i>Calpocalyx</i> sp. 1	11	<i>Crotonogyne stiginosa</i>	7
	<i>Pycnanthus angolensis</i>	8	<i>Rinorea subintegrifolia</i>	6
Secondary forest (SF)	<i>Elaeis guineensis</i>	23	<i>Auxopus kamerunensis</i>	5
	<i>Rauvolfia vomitoria</i>	13	<i>Anubias barteri/haustifolia</i>	29
	<i>Pycnanthus angolensis</i>	13	<i>Rinorea subintegrifolia</i>	15
	<i>Barteria fistulosa</i>	13	<i>Afromomum</i> spp.	15
	<i>Musanga/Macaranga</i>	10	<i>Raphidophora africana</i>	12
	<i>Hypodaphnis zenkeri</i>	8	<i>Scaphopetalum blaekii</i>	11
	<i>Coffea/Theobroma</i>	>600	<i>Araceae</i>	10
Agroforestry (AG)	<i>Elaeis guineensis</i>	10	<i>Albizia ferruginea</i>	17
	<i>Dacryodes edulis</i>	6	<i>Anchomanes difformis</i>	15
	<i>Rauvolfia vomitoria</i>	6	<i>Maranthochloa</i> sp.	11
	<i>Funtumia elastica</i>	6	<i>Brillantaisia</i> sp.	8
			<i>Costus afer</i>	7
			<i>Kigelia africana</i>	5
Annual culture (AC)	<i>Elaeis guineensis</i>	10	<i>Manihot</i> spp.	52
	<i>Ricinodendron heudelotii</i>	9	<i>Colocasia</i> spp.	41
	<i>Rauvolfia vomitoria</i>	4	<i>Chromolaena odorata</i>	39
	<i>Albizia zygia</i>	3	<i>Ipomea</i> spp.	22
	<i>Dacryodes edulis</i>	3	<i>Lusticia insularis</i>	16
		<i>Kaeyodendron</i> spp.	12	

ating trees and shrubs characteristic of mature rain forest (*Oubanguia alata*, *Gilbertiodendron demonstrans*), secondary forests were dominated by oil palms (*Elaeis guineensis*, which, at least partly, indicate agricultural activities) or by gap species and other fast growing pioneers such as *Pycnanthus*, *Rauvolfia*, or *Musanga* spp.

Apart from cocoa/coffee trees, the most common tree species on agroforestry and annual culture study sites were oil palms *E. guineensis*, and other cultivated trees such as plum *Dacryodes edulis* and *Ricinodendron heudelotii* trees. If *Coffea/Theobroma* trees are included in the analysis, there is a pronounced peak in medium-sized trees between 21 cm and 40 cm in agroforestry sites (Fig. 4C).

A total of 1230 individual understory plants were recorded. Understory plant density differed significantly between habitats (Table 2). Nearly twice as many understory plants were found in secondary forest and nearly three times as many in annual cultures than in near-primary forest (Tukey's hsd test, $P < 0.001$ in both cases). Understory plant density was slightly lower in agroforestry sites than near-primary forest, but differences were not significant (Tukey's hsd test, $P = 0.282$). In near-primary forest, mainly rain forest shrubs such as *Scaphopetalum*, *Cola* spp. (Sterculiaceae), or *Gilbertiodendron demonstrans* (Caesalpiniaceae) were found. Small shrubs such as *Rinorea subintegrifolia* (Violaceae) and monocotyledons such as *Anubias* spp., *Raphidophora africana* (and other Araceae), *Afromomum* spp. (Zingiberaceae) were common in secondary forest (Table 3). Herbs equally dominated the understory of agroforestry sites, with Araceae (*An-*

chomanes difformis), Maranthaceae (*Maranthochloa* sp.) or Acanthaceae (*Brillantaisia* sp.) as representatives. Understory plant species of annual cultures were mainly those subject to cultivations, such as cassava (*Manihot* spp.), and taro (*Colocasia* spp.), but the invasive pioneer *Chromolaena odorata* (Asteraceae) was also frequently recorded (Table 3).

Correlations with vegetation variables

Out of the 78 Spearman rank correlations between the three vegetation parameters ([overstory] tree density, tree basal area, understory plant density) and bird species richness and abundance, 38 were significant on the 5% level. However, table-wide significance after sequential Bonferroni correction revealed only 23 significant correlations, shown in Table 4. Tree density was very strongly correlated with species richness and abundance of ant followers, of medium-sized arboreal foliage gleaners, and of terrestrial insectivores. Tree density was strongly correlated with species richness of insectivores, of large arboreal foliage gleaners, and of pycnonotid birds and biome-restricted species.

There were also strong correlations between basal area and species richness/abundance of ant followers, and of medium-sized arboreal foliage gleaners, as well as between basal area and abundance of large arboreal foliage gleaners and species richness of terrestrial insectivores.

Tree density and basal area were strongly correlated ($r_s = 0.72$, $P < 0.001$), but species richness or abundance of most studied bird groups showed stronger correlations with tree density than with basal area.

TABLE 4. Spearman rank correlation coefficients, r_s , of correlations between species richness/abundance of the different feeding guilds, the Pycnonotidae family, biome-restricted species, nonbreeding visitors, and two different vegetation variables ($n = 24$ study sites in all cases).

Category	Density of overstory trees		Basal area of overstory trees	
	Species	Abundance	Species	Abundance
Positive correlations				
Ant followers	0.77***	0.87***	0.75**	0.71**
Insectivores	0.71**	NS	NS	NS
Large AFG†	0.66*	NS	NS	0.66*
Medium AFG	0.75**	0.88***	0.65*	0.71**
Pycnonotids	0.73**	NS	NS	NS
Biome-restricted species	0.68*	NS	NS	NS
Terrestrial insectivores	0.76**	0.76**	0.66*	NS
Negative correlations				
Flower visitors	-0.75**	-0.66*	-0.76**	-0.68*
Visitors‡	-0.69*	-0.81***	NS	-0.66*
No correlations				
Granivores	NS	NS	NS	NS
Omnivores	NS	NS	NS	NS
Frugivores	NS	NS	NS	NS
Small AFG	NS	NS	NS	NS

Note: Bonferroni-corrected table-wide significance level: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† Arboreal foliage gleaners.

‡ Including Palaearctic and (nonbreeding) local migrants.

Negative correlations were strongest between tree density/basal area and species richness of flower visitors and between tree density and abundance of nonbreeding visitors. Abundance of nonbreeding visitors was still strongly negatively correlated with basal area, as was their species richness with tree density. Species richness/abundance of omnivores, small arboreal foliage gleaners, or frugivores were not significantly correlated with any of the habitat variables. Understory plant density was not significantly correlated with species richness/abundance in any of the studied bird groups.

Species-level responses

Out of the 180 species recorded (Appendix), 165 species were found using the 24 sampling stations within the 50-m distance class (species occurring at larger distances, and those flying over or through excluded). Out of these, 68 species (including the two lumped bucerotids, *Ceratogymna* spp.), i.e., 41% of all species, showed significant responses to habitat type (ANOVAs, $P \leq 0.05$). When applying sequential Bonferroni correction to the P significance values of this list of species, responses to habitat type are still significant in 26 species (Table 5). Based on ANOVA and post hoc tests (Tukey's hsd test, $P < 0.05$), four main categories of responses were found. In response category 1, four species showed a clear preference for near-primary forest, with a significantly lower abundance in secondary forest and land use types. In response category 2, 10 species showed a preference for both natural forests (near-primary and/or secondary) and a significantly lower abundance in land use systems (agroforestry sys-

tems, annual cultures). Response category 3 only contained a single species, the Yellow-whiskered Greenbul, *Andropadus latirostris*, a widespread omnivorous pycnonotid, showing a high abundance in both natural forests and agroforestry systems, and a significantly lower abundance in annual cultures.

In contrast to the 15 species in the first three categories, another group of 11 species were grouped in response category 4, characterized by a significantly higher abundance in annual cultures and/or agroforestry systems compared to the other habitat types (Table 5).

Feeding guilds, restricted range, and responses to habitat type

Based on the distribution of species from different guilds among these response categories, a restricted geographic range seems to be linked to a preference for natural forests: Thirteen of the 14 species belonging to the first two response categories (preference for natural forest), were biome-restricted species. Among the 11 species in response category 4, there were only four biome-restricted species (chi-square test, $\chi^2 = 9.1$, Fisher's exact $P < 0.001$, $df = 1$). Many insectivorous species were also found in response categories with preference for natural forests: among the 14 species of the first two response categories (special preference for near-primary or near-primary/secondary forests), two-thirds (10 spp.) were insectivores (including five terrestrial/ant-following species), and only four were from other guilds (two frugivores, one granivorous columbid, and one species of rallid). Among the 11 species of response category 4 (preference for annual cultures

TABLE 5. Species with significant responses to habitat type, after sequential Bonferroni correction.

Family	Species	<i>n</i>	Habitat		
			Near-primary forest (NF)	Secondary forest (SF)	Agroforestry systems (AF)
Rallidae	White-spotted Flufftail	25	1.2 (0.4)	1.0 (0.6)	0.0 (0.0)
Columbidae	Blue-spotted Wood Dove	56	0.2 (0.4)	0.3 (0.8)	0.7 (0.5)
	Blue-headed Wood Dove	55	2.8 (0.8)	0.8 (0.8)	0.2 (0.4)
Cuculidae	Olive Long-tailed Cuckoo	7	1.0 (0.6)	0.0 (0.0)	0.0 (0.0)
Musophagidae	Yellow-billed Turaco	36	1.8 (0.8)	1.2 (0.8)	0.0 (0.0)
Alcedinidae	Grey-headed Kingfisher	12	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Bucerotidae	Wattled Hornbills (2 spp.)	133	5.0 (2.3)	3.5 (1.5)	0.0 (0.0)
Pycnonotidae	Yellow-whiskered Greenbul	144	1.0 (0.6)	3.5 (1.6)	3.5 (1.0)
	Simple Leaflove	96	0.0 (0.0)	0.0 (0.0)	0.7 (1.0)
	Xavier's Greenbul	69	3.3 (0.8)	2.5 (2.2)	0.0 (0.0)
	Lesser Bristlebill	118	4.7 (2.0)	3.7 (1.0)	0.5 (1.2)
	Red-tailed Greenbul	206	5.3 (1.8)	6.3 (2.3)	2.8 (2.2)
	Common Garden Bulbul	202	0.0 (0.0)	0.0 (0.0)	2.0 (1.7)
Turdidae	Forest Robin	49	1.0 (0.0)	1.0 (0.0)	0.2 (0.4)
	Fire-crested Alethe	45	1.2 (0.4)	1.3 (0.5)	0.0 (0.0)
	Rufous Flycatcher Thrush	16	0.8 (0.4)	0.7 (0.5)	0.0 (0.0)
Sylviidae	Grey-backed Camaroptera	38	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Yellow Longbill	26	1.5 (0.5)	0.0 (0.0)	0.2 (0.4)
	Green Crombec	39	0.0 (0.0)	0.0 (0.0)	0.5 (0.5)
Timaliidae	Blackcap Illadopsis	22	1.2 (0.8)	1.3 (0.5)	0.0 (0.0)
Nectariniidae	Fraser's Sunbird	47	5.5 (3.0)	1.7 (2.7)	0.0 (0.0)
	Olive-bellied Sunbird	81	0.0 (0.0)	0.0 (0.0)	1.2 (1.0)
	Tiny Sunbird	25	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	Superb Sunbird	34	0.0 (0.0)	0.0 (0.0)	0.7 (0.8)
Sturnidae	Splendid Glossy Starling	121	0.0 (0.0)	0.0 (0.0)	2.2 (2.2)
Ploceidae	Black-necked Weaver	16	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)

Notes: Bird abundance is expressed as total number of individuals recorded (*n*), and is given for each habitat type as mean \pm SD of the maximum number of individuals recorded at each study site during single visits (nine visit/samples in each of the 24 study sites). Results of one-way ANOVA, table-wide significance (*P*), as well as response category and preferred habitat type, are also given.

† Values of *P* are equal to or less than those shown.

‡ Response categories are: 1, preference for near-primary forest; 2, preference for both natural forests (near-primary, secondary); 3, preference for natural forests and agroforestry systems; 4, preference for agroforestry systems and annual cultures.

and/or agroforestry systems), there were four insectivores (three small-/medium-sized, and one larger alcedinid species), and seven from other guilds (three nectarivores, two omnivorous pycnonotids, and one granivorous columbid) (chi-square test, $\chi^2 = 3.1$, Fisher's exact *P* = 0.08, df = 1).

DISCUSSION

Differential responses of bird groups

Our study showed that species richness of several groups was adversely affected by forest modification and land use: insectivores (large arboreal foliage gleaners, terrestrial insectivores, and ant followers), pycnonotids (insectivores/insectivores-omnivores), and biome-restricted species (i.e., species that are confined to the Guineo-Congolian forest zone).

The observed changes in the species richness of several bird groups along the habitat gradient is remarkable because influences from adjacent forests must have been large, given that land use systems (farms and ag-

roforestry systems) were small in size, and their tree cover was relatively high compared to modernized production areas studied by other authors.

Large size (Thiollay 1995), understory dwelling rather than canopy- or edge-dwelling habit (Terborgh and Weske 1969, Andrade and Rubio-Torgler 1994, Thiollay 1995, Petit and Petit 2003), insectivorous feeding (Bowman et al. 1990, Johns 1991, Thiollay 1995, Canaday 1996, Plumtre 1997, Raman et al. 1998, Waltert et al. 2004), specialized foraging strategies (Terborgh and Weske 1969, Lindell and Smith 2003), and a restricted geographic range (Raman 2001, Waltert et al. 2004) have been previously identified as general characteristics of forest species sensitive to deforestation and land use. In addition, it has been suggested that resident birds (in contrast to nonbreeding visitors) particularly prefer forest habitats (Lindell et al. 2004). Resident forest species are often behaviorally inhibited to enter open agricultural land, functioning as a barrier for dispersal (Harris and Reed 2002).

TABLE 5. Extended.

Habitat				
Annual culture (AC)	$F_{3,20}$	P^\dagger	Category‡	Habitat with highest abundance
0.0 (0.0)	16.76	0.01	2	NF, SF
2.5 (1.4)	11.07	0.05	4	AC
0.5 (0.8)	17.22	0.01	1	NF
0.0 (0.0)	25	0.001	1	NF
0.0 (0.0)	17.45	0.01	2	NF, SF
1.3 (0.8)	16	0.01	4	AC
0.0 (0.0)	37.67	0.001	2	NF, SF
0.3 (0.8)	11.71	0.05	3	SF, AF
4.3 (2.9)	15.4	0.01	4	AC
0.0 (0.0)	16.35	0.01	2	NF, SF
0.0 (0.0)	20.44	0.001	2	NF, SF
0.0 (0.0)	12.21	0.05	2	NF, SF
6.5 (2.1)	31.76	0.001	4	AC
0.0 (0.0)	41	0.001	2	NF, SF
0.0 (0.0)	29.1	0.001	2	NF, SF
0.0 (0.0)	10.64	0.05	2	NF, SF
1.7 (0.8)	40	0.001	4	AC
0.0 (0.0)	22.67	0.001	1	NF
1.2 (0.4)	18.33	0.001	4	AF, AC
0.0 (0.0)	15.13	0.01	2	NF, SF
0.0 (0.0)	9.99	0.05	1	NF
3.0 (1.1)	18.88	0.001	4	AC
2.3 (0.5)	122.5	0.001	4	AC
2.0 (0.0)	32	0.001	4	AC
4.7 (2.9)	10.38	0.05	4	AF, AC
1.3 (1.0)	10	0.05	4	AC

Large foliage gleaners

Species richness of large (arboreal) foliage gleaners seemed significantly reduced in secondary forest compared to near-primary forest. This group contains five species of cuckoo, two species of orioles, and several shrike-type species (two malaconotids, two pycnonotids, and one campephagid). On species level, however, only the Olive Long-tailed Cuckoo, *Cercococcyx olivinus*, showed a clear preference for near-primary forest.

Secondary forests usually have a less complex vegetation structure and a lower species richness of larger trees compared to near-primary forest (Brown and Lugo 1990, Turner et al. 1997), which in turn could lead to reduced variability in foraging substrates. Indeed, the tree diameter distribution in our study sites showed that larger trees of certain size classes were reduced in the secondary forest sites compared to primary forest, and the architecture of secondary forests possibly was more homogeneous than near-primary forest. In addition, it is possible that the availability of larger insects is also reduced in modified habitats (e.g., Holloway et al. 1992), but an adequate assessment of arthropod food availability seems difficult, as far as many different bird species, especially arboreal ones,

are concerned (Hutto 1981, Wolda 1990, Poulin and Lefebvre 1997).

To our knowledge, no similar results have been documented before for this group of species, but previous studies on the feeding guild composition of secondary forest birds mostly did not consider different size classes of insectivores (but see Johns 1991, Lambert 1992, Thiollay 1999).

Terrestrial insectivores

There was also a significant pattern of decreasing species richness with increasing forest modification in terrestrial insectivores, and a significantly lower species richness in secondary, compared to near-primary, forest was found. The terrestrial insectivore group was composed of two centropid cuckoos, a phasianid, two timaliids, four turdids, and two pycnonotids. Among them, the phasianid *Francolinus lathami*, as well as the two larger thrushes *Neocossyphus poensis* and *Zoothera princei*, were exclusively recorded in near-primary forest, all species that search for food by manipulating the leaf litter. In contrast, the two large-billed pycnonotids of the genus *Bleda*, which pounce for large insects and small vertebrates from the ground, and two timaliids that glean foliage, were both found in near-primary as well as secondary forest.

Larger understory insectivores of the lowermost forest strata, especially true ground foragers, have frequently been considered especially vulnerable to forest modifications and seem to avoid the forest edge (Restrepo and Gomez 1998, Dale et al. 1999, Thiollay 1999). Particularly edge-avoidance behavior could be related to changes in soil invertebrate communities due to more variable temperature and moisture regimes in the secondary forest understory. But the fact that all the species that avoided secondary forest were active litter-moving birds could be due difficulties in manipulating the large leaves of umbrella trees, *Musanga cecropioides*, and of other pioneer trees in secondary forest (see also Stouffer and Bierregaard 1995).

Ant followers

In our study, for two species of kingfishers, one forest hornbill, five bulbuls (including the two terrestrial *Bleda* species), six thrushes (including all four terrestrial species), and three timaliids, special associations with ants (tribe Dorylini) are reported in standard ornithological works. All these species can be seen, more or less regularly, in the forest understory around swarming army ant columns, feeding mainly on flushing arthropods and small vertebrates (Willis and Oniki 1978, see also Poulin et al. 2001 for the relationship between ant-following habits and predation on herpetofauna). We found these ant followers in significantly lower species numbers in land use systems compared to natural forests.

Members of the Neotropical family Formicariidae (antbirds) are known to be particularly sensitive to deforestation (Terborgh and Weske 1968, Johns 1991, Stouffer and Bierregaard 1995, Lindell and Smith 2003, Lindell et al. 2004). But they also were found in heavily disturbed, small forest fragments, suggesting that changes in microclimatic conditions, light regime, and the consequential changes in food availability in secondary forests might not have a profound effect on them (Stouffer and Bierregaard 1995). However, it seems obvious that frequent disturbance in more open habitats, e.g., through cutting and mowing in agroforestry systems, prevents stable ecological conditions at ground level and produces an unstable supply of arthropod and other food resources such as small reptiles and frogs. From comparisons between low- and high-input agroecosystems, we know that ground-foraging ant diversity decreases with decreasing vegetational and structural complexity, and that this is accompanied by changing ground arthropod communities (Perfecto and Snelling 1995, see also Room 1971, 1975). Such changes could be also associated with habitat changes relevant to African ant-following birds.

Nectarivorous birds

Although generally less specialized than Neotropical hummingbirds (Trochilidae), most African sunbirds (Nectariniidae) regularly use nectar as food resources

and supplement their diet with insects on flowering trees to a varying extent. Fifteen of the sunbird species were assigned to this group of birds. This nectarivorous group showed a significant increase in species richness with increasing forest modification. Most species were observed in annual cultures, with a gradual decrease from agroforest to near-primary forest.

This pattern could be explained by an increased availability of flowering resources in land use systems, as was found in previous studies (e.g., Thiollay 1995). However, the observed trend could also be caused by some sort of sampling bias. Many sunbird species recorded on the studied land use sites are also known to occur in mature forest treetops, where they are extremely difficult to detect because of their small size and comparatively thin vocalizations. For example, the Tiny Sunbird, *Cinnyris minullus*, and the Superb Sunbird, *Cinnyris superbus*, both significantly more abundant in land use systems than in natural forests, are easily overlooked in the canopy of mature forest. We recommend treating data on the presence/absence of small nectarivores/frugivores in mature tropical forests with caution, since changes in vertical foraging heights, in particular, could especially lead to false conclusions (see also Driscoll and Kikkawa 1989).

Granivores

Our data also revealed a significant increase in granivorous species numbers from forest to farmland. The observed granivorous species are mainly ground foraging and usually easily detected by their vocalizations. One phasianid, three species of resident columbids, two estrildids, two ploceids, and one mainly seed-eating parrot represented this group. The parrot, and two of the columbids, were mainly observed in forests, whereas the other species were frequently observed in farmland (see also Blankespoor 1991). Since grasses are more dominant in land use systems compared to natural forests, this result is not surprising. A high number of granivores in forests could even be seen as an indication of severe disturbance (Andrade and Rubio-Torgler 1994, Thiollay 1995).

Nonbreeding visitors

Only 12 nonbreeding visitors were recorded on our study sites. Nevertheless, a significantly higher number of visitor species was found in annual cultures compared to all other habitat types. For one species, we could even detect a significant response in abundance to habitat type. This species, the Grey-headed Kingfisher, *Halcyon leucocephala*, was exclusively recorded in annual cultures, while the three other resident *Halcyon* species were also found in the natural forests, either in the forest interior (the two different-sized species *Halcyon badia*, *H. malimbica*) or the forest canopy (*H. senegalensis*), probably an indication for interspecific competition. However, the other visitors simply seem to choose habitats with a vegetation structure similar to their breeding habitat. In Central America,

nonbreeding visitors coming from North America can occupy a range of habitats including agricultural areas (Conway et al. 1995), and they are often the principal bird guild in planted-shade cacao distant from closed forest (Greenberg et al. 2000).

Changes in overall bird species richness

In the Neotropics, agroforestry systems and annual cultivations have been found to support a considerable bird diversity if (1) tree cover is relatively high (Daily et al. 2001, Hughes et al. 2001, Lindell and Smith 2003) and/or (2) distances to forest habitats are small (e.g., Greenberg et al. 1997b). The land use systems studied here were all close to near-primary forest, and, although tree density and basal area dropped by 90% to 80% from forest to annual cultures, tree cover was still relatively high compared to mechanized agroforestry systems and intensive cultivations sampled in other studies. The continuous species turnover along our land use gradient in Cameroon was an effect of the gradual replacement of lost forest-dependent species by species typical for open habitats, resulting in overall unchanged species richness between habitats.

Another study dealing with habitat effects on local bird species richness from Cameroon indicated a much clearer effect of land use on overall bird species diversity (Lawton et al. 1998). In that study, a marked decrease in richness from forest to farmland was observed, with only very few species present in fallows and young tree plantations. Different from our study, however, the land use systems studied by Lawton (1998) lacked even small trees, which can possibly explain the observed difference, indicating once more the importance of tree cover for the maintenance of bird populations in tropical agricultural landscapes.

One study on Sulawesi (Indonesia), which compared natural forests with modernized cacao production systems with planted exotic shade trees and annual cultures with only very few trees (Waltert et al. 2004; see also Schulze et al. 2004) also revealed a marked decrease in overall bird species richness along the studied land use gradient. On Sulawesi, important natural shade trees were almost completely lacking, which could partly explain the observed differences. But also biogeographical factors could be responsible for this difference: Sulawesi, an island with a long history of isolation, has much smaller regional species pools than the African mainland, and, possibly, there are also general differences in habitat associations between Afro-tropical and Southeast Asian faunas: On Sumatra, as on Sulawesi, with its rich Sunda shelf avifauna, overall species numbers seemed markedly lower in agroforestry systems compared to primary forest. Thiollay (1995) found, on average, 41–62% less species in small samples (i.e., 50 observed birds) from agroforests compared to primary forest, and rarefied species richness after 25 samples in agroforests was also only roughly half that of primary forest (Thiollay 1995).

Forest birds in agricultural areas

As seen in the preceding paragraph, bird species richness in tropical agricultural areas can be remarkably high; however, more detailed analyses show that the composition of these communities is often far from original. The following considerations refer to larger (regional) scales than those of our study: A study on the Costa Rican avifauna indicated that 149 (55%) of 272 regionally extant bird species occurred in forest habitats only, while 123 species occurred in agricultural areas. Of these, only 60 species (22% of the total) were found in both forest and agricultural areas and 63 species (or 23% of the total) occurred in open habitats only. This means that of the 209 original species found in the forest (i.e., those confined to forest plus those found both in forest and agricultural land), 149 were not recorded in agricultural land, suggesting that a minimum regional species loss of 71% could be expected if the forest was converted (Daily et al. 2001). Thus, two-thirds of the original avifaunal community, and possibly even more, would be lost if remaining habitat edges and tree groups within the deforested landscape cannot support the remaining forest-dependent species for the long term.

Although conclusions have to be drawn with caution, comparable studies from West Africa suggest that the degree of species loss after deforestation might be comparable between tropical continental forest regions. In both Liberia and eastern Ivory Coast, a remarkably similar percentage of 70% of the species of a regional forest zone avifauna were not found in former forest areas after conversion to farmland (Kofron and Chapman 1995, Waltert 2000). In the Upper Guinean region, these results are not surprising, since its small-sized, and sometimes heavily disturbed, forest remnants might not support viable populations of many species, and therefore might not stabilize bird populations in the agricultural areas (e.g., Waltert 2000, Beier et al. 2002).

A study from the Lower Guinea region suggests similar rates of species loss. In Nigeria, only 25 (33%) of 75 species regularly occurring in forests could still be found in adjacent farms or derived savannah, implying that 66% of the species found inside the forest could be lost if all forest was cleared (Elgood and Sibley 1964).

Forest fragmentation and species extinction

There is a lot of empirical information showing that tropical forest bird species loss is considerable even in seemingly suitable habitats: Examples of forest fragmentation effects reach from lessons learned in Singapore and Java (see van Balen 1999, Castelletta et al. 2000) to examples from Africa (Newmark 1991, Brooks et al. 1999b, Beier et al. 2002), and Latin America (Kattan et al. 1994, Robinson 1999), and the experimental studies of South America and Australia (Laurance and Bierregaard 1997, Laurance et al. 2002).

Since extinctions of forest birds often only appear after considerable time lags (Brooks et al. 1999b), interpretation of presence/absence data in tropical land use systems should be done with caution (Hughes et al. 2002) and monitoring studies that address the long-term viability of forest species in tropical land use systems are urgently needed.

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APPENDIX

A table showing bird species observed during the survey, with numbers of records (detections), total number of observed individuals, and feeding guild information is available in ESA's Electronic Data Archive: *Ecological Archives* A015-036-A1.