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Authors: **Raf Aerts[1]*, Frederik Lerouge[1], Eva November[2], Luc Lens[3], Martin Hermy[1], and Bart Muys[1]**

[1] Division Forest, Nature and Landscape, K.U. Leuven, Belgium

[2] Royal Museum for Central Africa, Tervuren, Belgium

[3] Terrestrial Ecology Unit, Ghent University, Gent, Belgium

* Corresponding author: dr. ir. Raf Aerts, Celestijnenlaan 200E-2411, BE-3001 Leuven (Belgium).

Tel. +32-16-329721; Fax: +32-16-329760

E-mail: raf.aerts@biw.kuleuven.be

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a. Running head

Forest birds in a degraded Afromontane landscape

b. Title

Land rehabilitation and the conservation of birds in a degraded Afromontane landscape in northern Ethiopia

c. Authors

Raf AERTS[1]*, Frederik LEROUGE[1], Eva NOVEMBER[2], Luc LENS[3], Martin HERMY[1] and Bart MUYS[1]

d. Affiliations

[1]Division Forest, Nature and Landscape, Katholieke Universiteit Leuven, Celestijnenlaan 200E box 2411, BE-3001 Leuven, Belgium

[2]Royal Museum for Central Africa, Leuvensesteenweg 13, BE-3080 Tervuren, Belgium

[3]Terrestrial Ecology Unit, Ghent University, K. L. Ledeganckstraat 35, BE-9000 Gent, Belgium

e. *Full address for correspondence

dr. ir. Raf Aerts, at Division Forest, Nature and Landscape, Katholieke Universiteit Leuven, Celestijnenlaan 200E box 2411, BE-3001 Leuven, Belgium. Tel.: +32-16-329721, Fax: +32-16-329760, e-mail raf.aerts@biw.kuleuven.be

Abstract

The few remaining Afromontane forest fragments in northern Ethiopia and the surrounding degraded, semiarid matrix form a habitat mosaic of varying suitability for forest birds. To evaluate the effect of recent land rehabilitation efforts on bird community composition and diversity, we studied bird species distributions in ten small forest fragments (0.40–20.95 ha), five grazing exclosures (ten-year-old forest restoration areas without wood extraction and grazing livestock) and three grazed matrix sites during the rainy season (July-October 2004) using 277 one-hour species counts. Based on the distribution pattern of 146 bird species, sites were assigned to one of three bird communities (birds of moist forest, dry forest or degraded savanna), each occupying a well-defined position along an environmental gradient reflecting decreasing vegetation structure and density. All three communities were representative of the avifauna of Afrotropical Highland open forest and woodland with a high proportion of invasive and competitive generalist species (31%). Apart from these, exclosures shared more species with forest fragments (20%) than did the grazed matrix (5%), indicating local ecosystem recovery. By increasing habitat heterogeneity, exclosures have the potential to enhance landscape connectivity for forest birds and are, therefore, an effective instrument for conserving species in a fragmented landscape. However, 52 bird species (36%) occurred exclusively within forest patches and many forest birds that use exclosures are unlikely to maintain viable populations when forest fragments disappear, particularly as forest fragments may be a critical resource during the hot dry season. This highlights the high conservation value of small

isolated forest fragments for less tolerant, forest-limited and/or biome-restricted species.

Key words

avian species diversity; Ethiopia; exclosures; forest fragments; fragmentation; matrix habitat; protected area management; semiarid; small patches; restoration

Abbreviations

TSC	Timed species count
MRPP	Multiresponse permutation procedure
NMDS	Non-metric multidimensional scaling

Introduction

In the highlands of northern Ethiopia, widespread and long-standing land degradation has taken forest fragmentation to extremes. With the exception of a few formally protected areas (National Forest Priority Areas), fragments of the original Afromontane forest in the northern highlands are found almost exclusively in and around sacred sites such as holy springs, monasteries, and church yards (Aerts et al. 2006; Wassie and Teketay 2006; Aerts 2007) and are embedded in a matrix of cropland and semiarid, degraded savanna. A landscape approach that conserves the network of forest fragments is probably the only option to secure the survival of many wild species (Bhagwat and Rutte 2006).

Habitat fragments usually show reduced species richness with time after isolation (Hames et al. 2001), and small patches generally have fewer species than large fragments (Turner 1996). Species extinction is typically attributed to decreasing habitat area and quality and/or increasing isolation (e.g. Saunders et al. 1991; Lees and Peres 2006; Sekercioglu 2007). On the other hand, growing evidence shows that the ability of certain species to survive in fragments also depends on the quality of the surrounding matrix because of its potential role as a (suboptimal) habitat resource (Renjifo 2001; Sekercioglu et al. 2002; Wethered and Lawes 2003; Antongiovanni and Metzger 2005; Raman 2006). In this respect, efforts to restore degraded land by integrating recovery processes in the matrix and population processes in the remnants (Kupfer et al. 2006) may help alleviate the effects of forest fragmentation on bird populations. For instance, recovery of vegetation in the matrix may increase landscape connectivity through the emergence of stepping stone habitats and corridors that facilitate dispersal between fragments, thus amplifying the rescue effect for forest-dependent bird species (Lens et al. 2002; Castellón and Sieving 2006). Eventually, stepping stone habitats may develop into new source areas with reproducing species. Accordingly, the restoration of matrix habitats can be an effective instrument for the conservation of species in a fragmented landscape.

In northern Ethiopia, land rehabilitation depends largely on the region-wide establishment of grazing exclosures. Exclosures are often located on slopes and comprise several hectares in size. The harvesting of woody vegetation and the grazing by domestic livestock or other agricultural activities are no longer permitted in the exclosures. The aim is to restore the

Afromontane forest vegetation and its ecosystem services, such as watershed protection and erosion control (e.g. Aerts et al. 2004; Mengistu et al. 2005; Abebe et al. 2006; Mekuria et al. 2007). However, the value of exclosures to the conservation of fauna, in particular those bird species that are sensitive to forest fragmentation, is still poorly known. To provide baseline evidence for the conservation value of grazing exclosures, we studied bird communities in a landscape mosaic of semiarid degraded savanna, cropland, and Afromontane forest fragments, in the highlands of northern Ethiopia. The study was designed to:

(i) assess avian community compositions of forest fragments, grazing exclosures, and degraded grazing land;

(ii) test whether bird communities respond to land rehabilitation, and thus show differences along the grazed matrix-exclosure-forest fragment gradient; and

(iii) test whether exclosures provide a suitable habitat for forest-dependent birds.

Methods

Study area

The study was conducted in the Geba river catchment (13° 37’ N, 39° 21’ E, Fig. 1) in Central Tigray, northern Ethiopia, 20 km NW of the regional capital Mekelle and at an elevation of 1800–2000 m a.s.l. The climate is semiarid, with cold rainy seasons and hot dry seasons. The mean annual temperature is 18°C and the area receives between 470 and 780 mm of rainfall annually, mostly during June–September. The small forest fragments (0.40–20.95 ha in size) are classified as moist Afromontane forest with *Faidherbia albida* and *Celtis africana*, dry Afromontane forest with *Olea europaea* ssp. *cuspidata* and *Combretum collinum*, and shrub savanna dominated by thorny species, including *Acacia etbaica* and *Acacia abyssinica* (see Aerts et al. 2006 for details). The matrix is dominated by cropland and degraded grazing lands, the latter characterized by nearly bare soil and a discontinuous cover of pioneer shrubs whose height ranges 1–2 m (e.g. *Acacia etbaica*, *Aloe macrocarpa*, *Euclea racemosa* ssp. *schimperi*, *Leucas abyssinica*).

The exclosures surveyed in our study are recent (ca. 10 years), and were as degraded as the grazed matrix prior to land rehabilitation (Bureau of Agriculture and Natural Resources, pers. comm.). In the exclosures, shrub cover is more diverse than in grazed sites, and during the rainy season the space between shrubs is covered by herbaceous species, including the conspicuous Meskel flower (*Bidens prestinaria*) and many ruderal herbs such as *Rumex spp.* and *Solanum incanum*, together with grasses, principally *Hyparrhenia hirta*.

To quantify habitat structure, we recorded four ordinal variables: tree density (no trees, scattered trees, open forest, and closed-canopy forest), shrub density (no shrubs, scattered shrubs, and dense shrubs), grass cover (no grass, some grass, grass important, and grass dominant) and number of vegetation strata (barren, herbs + shrubs, herbs + shrubs + small trees, herbs + shrubs + small trees + tall trees). Two additional environmental variables were recorded: grazing intensity (no grazing, occasional grazing, frequent grazing, and overgrazed) and stone cover between the woody vegetation (no barren patches, some stony patches, many stony patches, and spaces between woody vegetation almost completely stony).

[Insert Fig. 1]

Field methods

The study was carried out during the cold rainy season (from 26 July to 15 October 2004), which is the best season for bird surveys because most bird species are breeding, migrant species are present and resources are more evenly spread throughout the landscape, which is not the case in the hot dry season when matrix conditions are rather harsh. In a study area of approximately 13,000 ha, we conducted 277 one-hour timed species counts (TSC, Freeman et al. 2003) in (the only remaining) ten forest fragments (188 counts), five exclosures (57 counts) and three grazing lands (32 counts). TSC is a flexible walking survey method that provides comprehensive species lists as well as data regarding relative abundance of individual species (Pomeroy and Dranzoa 1997; Freeman et al. 2003). It allows observers to move freely throughout the sites – a particular benefit in our study area where point counts were unreliable due to the flushing of birds by local shepherds attracted by static observers. Mean forest fragment size was 6.56 ± 2.04 ha. Grazing land (62 ± 24 ha) and exclosure sites (31 ± 24 ha) were larger but more easily covered due to their lower and more homogeneous vegetation. All surveys were conducted during the hours of bird activity, which was basically all day except at solar noon (between 07:30–12:30 and 13:30–16:00 local time). Surveys were not conducted during heavy rain showers and counts interrupted by rains were discarded. The order in which sites were surveyed were randomized and the walking trails chosen ad-lib to minimize any potential site or trail bias (e.g. due to site fidelity of individual birds). Sites were completely covered during each count. Birds observed by sighting or song were recorded; flyover birds were not counted. Species accumulation curves were used to determine the minimum sampling effort required per site to achieve species saturation. A larger sampling effort was required in forest sites than in matrix sites where accumulation curves leveled off soon. Accumulation curves only leveled off weakly for some individual forest sites. Following a stopping rule proposed by Bibby (2004), we assumed that these sites were sampled sufficiently when the number of bird species seen only once in that site was equal or less than the number of bird species observed only twice.

Data analysis

Habitat variables were coded as ordinal numerical values and compared using Kruskal-Wallis one-way ANOVA by ranks. Pairwise comparisons were computed manually using the multiple comparisons between groups procedure outlined in Siegel and Castellan (1988). Using the raw bird data, i.e. the 277 one-hour counts, and the EstimateS software (Colwell 2006), the estimated species richness (Chao2) was calculated for each site. Avian diversity values of forest fragments, exclosures and grazing land were summarized as mean alpha (within-site diversity = mean number of species observed per site), mean Chao2 (mean estimated species richness per site), gamma (total number of species observed) and beta (among-site diversity = gamma/alpha). One-way ANOVA was used to test for differences in species richness between forest fragments, exclosures and grazing land. The Fisher exact probability test was used to determine whether exclosures and grazing land had different proportions of species shared with forest fragments.

To reduce bias in the multivariate analysis, species observed in only one site on only one day were considered accidental visitors and removed from the dataset. Communities were examined using relative frequencies and an indirect gradient analysis approach. The 18 sites were repeatedly clustered into 2 to 5 groups using a Sørensen distance measurement (measured as percent dissimilarity between sites) and flexible beta linkage (β = –0.25) (McCune and Mefford 1999). For each run, indicator values and *p*-values for each species were determined using indicator species analysis (Dufrêne and Legendre 1997) and the overall average *p*-value was calculated. If groups are too finely divided or if groups are too large, then indicator values and significance will be low; indicator values peak at some intermediate level of clustering (McCune and Mefford 1999). Thus, the cluster step with the highest mean significance was selected as the most informative number of clusters. Statistical differences in species composition between communities were tested with multiresponse permutation procedures (MRPP).

Nonmetric multidimensional scaling (NMDS) was used to investigate indirect (environmental) gradients influencing distribution of bird species and communities. NMDS was run using the Sørensen distance measure, six starting dimensions, 40 iterations and an instability criterion of 10^{-5} (McCune and Mefford 1999). To test for concordance between environmental variables and the NMDS dimensions, Spearman rank correlation coefficients were calculated.

Meta-information on diet (intrinsic foraging or α_4-guild *sensu* Wilson 1999: insectivore, granivore, frugivore, omnivore, carnivore, nectarivore), feeding stratum (air, bark, low vegetation, middle vegetation, high vegetation, water, ground), feeding method (ground glean, foliage glean, bark drill, sally, aerial gape) and habitat specialization (habitat response or β_5-guild *sensu* Wilson 1999: forest, grass and savanna, aquatic or any habitat with some water) were compiled based on species accounts from Urban and Brown (1971); Van Perlo (1995) and Trager and Mistry (2003). After screening these variables for independence with χ^2 contingency tests, functional groups were defined using a categorical two-step cluster procedure.

Classification, ordination, clustering and statistical tests were conducted using PCord 4.0 (McCune and Mefford, 1999) and SPSS 12.0 (SPSS Inc., Chicago, IL).

Results

Patterns in the overall bird community

A total of 170 species were recorded at 18 sites. Twenty-four species (14%) were biome-restricted (Tilahun et al. 1996): 18 species belonged to the Afrotropical Highland Biome; four to the Somali-Masai Biome; and two to the

Sudan-Guinea Savanna Biome (for a detailed account of species, see Appendix).

The mean number of bird species observed per site, the estimated site species richness and the among-site diversity were significantly higher in forest fragments than in exclosures and grazed matrix sites (Table 1). After removal of 24 visitors (see Appendix), forest (133 species) and non-forest sites (94 species) shared 81 species (55%) indicating a high similarity between the avifauna of both habitats.

[Insert Table 1]

Environmental correlates of community composition

Three distinct bird communities were identified: birds of moist Afromontane forest and associated riverine shrub savanna (6 sites, 119 species), birds of dry Afromontane forest (4 sites, 121 species), and birds of degraded semiarid savanna (8 sites, 84 species). The latter comprised exclosures and grazed matrix sites which could not be separated at the bird community level.

[Insert Table 2]

For the NMDS ordination, two axes explained 93% of the variance (NMDS axis 1: 80%; NMDS axis 2: 13%). Bird communities occupied a well-defined position along an environmental gradient reflecting decreasing vegetation structure and density (Table 3), highlighting the contrast between the two communities living in forest from the community inhabiting the exclosures and grazed matrix (Fig. 2a). The main gradient is one of increasing landscape openness, with high tree cover and multilayered vegetation in forests at one end, open shrubland with many stony patches in grazing lands at the other end, and exclosures at an intermediate position along the gradient (Table 1). The observed number of bird species gradually declined along this degradation gradient (r_s = –0.808, p < 0.001), with an abrupt decrease in species richness at the transition between forest and non-forest habitats. The estimated number of bird species followed the same pattern (r_s = –0.711, p = 0.001) (Fig. 2b).

The second NMDS dimension was negatively correlated to stone cover but this correlation was not significant when taking Bonferroni correction for multiple tests into account (Table 3).

[Insert Fig. 2]

[Insert Table 3]

Shared species among groups

Fifty-two bird species (36%) were restricted to the forest fragments, whereas 13 species (6%) occurred only outside forests (Fig. 3). Exclosures and grazing land did not differ significantly in the proportions of species shared with forest fragments (p = 0.246), mostly due to the presence of many generalist species (45 species, 31%). When these generalists were excluded, exclosures shared significantly more species exclusively with forest fragments (29 species, 20%) than grazed matrix sites shared with forests (7 species, 5%) (p = 0.016) (Fig. 3).

[Insert Fig. 3]

Habitat (habitat response guild) was independent from diet (intrinsic foraging guild) (χ^2 = 0.298, *p* = 0.182) while feeding stratum (χ^2 = 0.375, *p* = 0.021) and feeding method (χ^2 = 0.754, *p* < 0.001) were not. Diet and habitat defined six functional groups: frugivores and nectarivores; birds of moist (forest) habitats; insectivores and omnivores of forest habitat; insectivores of grassland and savanna; omnivores of grassland and savanna (open area generalists); and granivores and carnivores of grassland and savanna. All functional groups were represented by more species in the exclosures than in the grazed matrix sites. No particular guild benefited more than the others from recovering vegetation in exclosures (Fig. 3).

Discussion

Loss of core forest habitat

Among the biome-restricted species in the Afrotropical Highlands we recorded, Black-winged Lovebird (*Agapornis taranta*), Abyssinian Woodpecker (*Dendropicos abyssinicus*), Rüppell's Robin-chat (*Cossypha semirufa*), Tacazze Sunbird (*Nectarinia tacazze*) and Montane White-eye (*Zosterops poliogaster*) are typical forest species, and Banded Barbet (*Lybius undatus*), Brown-rumped Seed-eater (*Serinus tristriatus*), Streaky Seed-eater (*Serinus striolatus*) and Baglafecht Weaver (*Ploceus baglafecht*) are species of woodland, scrubland and forest edges. Species of this biome known from large Afromontane forests in Ethiopia (pers. obs.) – i.e. White-cheeked Turaco (*Tauraco leucotis*) and Black-headed Forest Oriole (*Oriolus monacha*) (e.g. in Hugumburda National Forest Priority Area, Tigray Region), Abyssinian Ground Thrush (*Zoothera piaggiae*) and African Hill Babbler (*Illadopsis abyssinica*) (e.g. in Wondo Genet, Southern Nations, Nationalities and Peoples Region) and Abyssinian Catbird (*Parophasma galinieri*) (e.g. in Adaba-Dodola, Bale Mountains, Oromiya Region) – were not recorded during this study, which suggests that the loss of core forest habitat and consequently the extinction of area-sensitive species already have occurred (Manu et al. 2007). The recorded bird community is representative of Afrotropical Highland open forest and woodland with a high proportion of invasive and competitive generalist species (31%).

Bird communities along a degradation gradient

The sharp gradient between forest and non-forest habitats is reflected in the composition of the bird communities. Species-rich communities of moist Afromontane and dry Afromontane forest with a high number of forest-restricted species and species-poor communities of exclosures and grazed matrix sites with few species restricted to non-forest habitats, arranged, as expected, along a gradient of increasing landscape openness and decreasing vegetation structural complexity (Table 1). In semiarid areas, comparable relationships between avifauna and vegetation structural complexity were found in various ecosystems, including steppe desert (van Heezik and Seddon 1999), grassland (Trager and Mistry 2003) and savanna woodland (Skowno and Bond 2003; Thiollay 2006). Church forests and other forest fragments offer stands of high indigenous trees that can be used for foraging (e.g. olives and figs for frugivores), nesting (e.g. *Euphorbia* trees for lovebirds) and roosting, or as an observation post for foraging in the surrounding more open landscape matrix (e.g. for bee-eaters) (Thiollay 2006). Thus, like kopjes in grassland or wadis in desert, forest fragments act as insular patches providing specific high-quality resources that cannot be found readily in the open matrix (Graham and Blake 2001; Trager and Mistry 2003).

Exclosures provide additional habitat for forest birds

While exclosures clustered with grazed sites at the community level, they shared more species with forests than with grazing land (Fig. 3). Even though non-forest communities showed a sharp decline in species richness due to a loss of forest specialists (Fig. 2b), exclosures comprised suitable habitat of varying quality for at least 29 forest species (20%) which were not present in the grazed matrix. For many forest-related birds the landscape matrix thus acted as a habitat gradient rather than a discrete patchwork of habitat versus non-habitat (Wilson et al. 1997; Fisher and Lindenmayer 2002; Kupfer et al. 2006). This may be related to the high habitat heterogeneity created by intensive human land-use (i.e., small-holder field mosaics with grazing lands, exclosures, forest fragments and solitary trees in a landscape incised by more or less wooded gullies, rivers and ravines, all providing resources and to a certain extent, facilitating dispersal). The adaptation of several African forest birds to fragmentation over geological and recent times (Manu et al. 2007) and the ability of certain species to move large distances through habitat patches of lower quality may also contribute to the persistence of forest birds in the matrix (Skowno and Bond 2003; Sekercioglu et al. 2007; Van Houtan et al. 2007).

Despite their relative short period of recovery, exclosures were situated between forest fragments and grazed matrix sites in terms of bird species composition (Fig. 2a). These results suggest that the initial recovery of vegetation in exclosures has been sufficient for an important proportion of forest bird species to recolonize the exclosures. Exclosures are not quite "forest" (and their avifauna not quite a forest community), but this study confirms that the forest vegetation and its dependent avifauna are slowly recovering. In the future, as trees grow taller and the canopy closes, birds of shrubland that now inhabit the exclosures may be expected to be joined or replaced by species characteristic of true woodland or forest (Avery and Leslie 1990; Blankespoor 1991).

Implications for conservation

This study demonstrates that grazing exclosures have the potential to enhance landscape connectivity by increasing the structural complexity of the landscape matrix, and thus reducing the matrix resistance to movement by forest birds belonging to a variety of functional types (Castellón and Sieving 2006). Exclosures efficiently contribute to the conservation of biodiversity by mitigating the effects of fragmentation on Afromontane forest bird communities (Tubelis et al. 2004; Antongiovanni and Metzger 2005). One of the direct feedbacks is the alleviation of dispersal limitation of fleshy-fruited trees such as *Olea europaea*, a cause of slow succession in the exclosures. Establishment of exclosures should thus be encouraged. When exclosures are established near forest fragments, they increase forest patch size, decrease edge effects, and increase the likelihood of recolonization by fauna and flora (Wethered and Lawes 2003). Deeper in the matrix exclosures could serve as dispersal stepping stones.

However, 52 bird species (36%) occurred exclusively within forest patches and many forest birds that use exclosures are unlikely to maintain viable populations when forest fragments disappear, particularly as forest fragments may be a critical resource during the hot dry season. This highlights the high conservation value of small isolated forest fragments for less tolerant, forest-limited and/or biome-restricted species.

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1 Appendix

Relative frequencies of birds within habitat groups defined by the presence or absence of species in forest fragments (F), exclosures (EX) and grazed matrix sites (G) in northern Ethiopia.

Functional types were defined by diet and habitat specialization: FN-X, frugivores and nectarivores; X-AF, birds of moist (forest) habitats; IO-F, insectivores and omnivores of forest habitat; I-GS, insectivores of grassland and savanna; O-GS, omnivores of grassland and savanna (open area generalists); GC-GS, granivores and carnivores of grassland and savanna. *E* denotes endemic to the Abyssinian plateau (Ethiopia and Eritrea), *P* Palearctic migrant. Species sequence is according to decreasing frequencies. Indicator species (ISA $p < 0.05$) for forests are marked: * moist Afromontane forest and associated shrub savanna, ** dry Afromontane forest. Biome-restricted species: AHB, Afrotropical Highland Biome; SMB, Somali-Masai Biome; SGSB, Sudan-Guinea Savanna Biome.

Forest-limited species				F	EX	G
Vinaceous Dove	*Streptopelia vinacea*	O-GS		0.44		
Black-headed Weaver*	*Ploceus cucullatus*	I-GS		0.44		
Black-billed Barbet*	*Lybius guifsobalito*	FN-X		0.35		
Red-billed Oxpecker	*Buphagus erythrorhynchus*	I-GS		0.34		
Ring-necked Dove*	*Streptopelia capicola*	O-GS		0.27		
White-billed Starling* (AHB)	*Onychognathus albirostris*	O-GS	*E*	0.23		
Grey-headed Kingfisher*	*Halcyon leucocephala*	X-AF		0.18		
Rüppell's Robin-chat (AHB)	*Cossypha semirufa*	IO-F		0.18		
Crimson-rumped Waxbill*	*Estrilda rhodopyga*	GC-GS		0.15		
Olive Thrush*	*Turdus olivaceus*	IO-F		0.14		
African Paradise-flycatcher	*Terpsiphone viridis*	IO-F		0.13		
Bruce's Green Pigeon*	*Treron waalia*	FN-X		0.13		
African Mourning Dove*	*Streptopelia decipiens*	O-GS		0.13		
Golden-breasted Bunting**	*Emberiza flaviventris*	O-GS		0.13		
Indigo-Bird*	*Hypochera chalybeata*	GC-GS		0.12		
Green-backed Eremomela** (SGSB)	*Eremomela icteropygialis*	I-GS		0.11		
Abyssinian Roller	*Coracias abyssinica*	I-GS		0.11		
Nightingale*	*Luscinia megarhynchos*	I-GS	*P*	0.11		
Somali Chestnut-winged Starling* (SMB)	*Onychognathus blythii*	O-GS		0.11		
Red-fronted Tinkerbird	*Pogoniulus pusillus*	IO-F		0.10		
Violet-backed Starling*	*Cinnyricinclus leucogaster*	IO-F		0.10		
Steppe Eagle[1]	*Aquila rapax*	GC-GS	*P*	0.08		
Blackstart	*Cercomela melanura*	O-GS		0.08		
Abyssinian Woodpecker (AHB)	*Dendropicos abyssinicus*	IO-F	*E*	0.07		
White-winged Black Tit**	*Parus leucomelas*	IO-F		0.07		
Erckel's Francolin (AHB)	*Francolinus erckelii*	X-AF		0.06		
Common Redstart*	*Phoenicurus phoenicurus*	IO-F	*P*	0.06		
Banded Barbet (AHB)	*Lybius undatus*	FN-X	*E*	0.06		
Chestnut-crowned Sparrow-weaver (SGSB)	*Plocepasser superciliosus*	I-GS		0.05		
Drongo	*Dicrurus adsimilis*	I-GS		0.05		
African Pygmy Kingfisher*	*Ceyx picta*	X-AF		0.05		
Red-billed Hornbill	*Tockus erythrorhynchus*	O-GS		0.05		
Nubian Woodpecker	*Campethera nubica*	I-GS		0.04		
White-collared Pigeon (AHB)	*Columba albitorques*	IO-F	*E*	0.04		
Brown Woodland-warbler	*Phylloscopus umbrovirens*	IO-F		0.03		
Golden Oriole	*Oriolus oriolus*	O-GS		0.03		
Hamerkop*	*Scopus umbretta*	X-AF		0.03		
Black-eared Wheatear	*Oenanthe hispanica*	I-GS	*P*	0.03		
Northern Brubru	*Nilaus afer*	O-GS		0.03		

Common Chiffchaff**	*Phylloscopus collybita*	IO-F	*P*	0.03		
Egyptian Goose[1]	*Alopochen aegyptiaca*	X-AF		0.02		
Little Bee-eater	*Merops pusillus*	I-GS		0.02		
Peregrine	*Falco peregrinus*	GC-GS	*P*	0.02		
Yellow-throated Sandgrouse	*Pterocles gutturalis*	O-GS		0.02		
Striped Kingfisher	*Halcyon chelicuti*	GC-GS		0.02		
Wattled starling	*Creatophora cinerea*	O-GS		0.02		
Three-banded Plover	*Charadrius tricollaris*	X-AF		0.02		
Tacazze Sunbird (AHB)	*Nectarinia tacazze*	FN-X		0.02		
Pied Flycatcher	*Ficedula hypoleuca*	IO-F		0.02		
Yellow-shouldered Widow-bird	*Euplectes macrourus*	GC-GS		0.01		
Little Green Bee-eater	*Merops orientalis*	I-GS		0.01		
African Dusky Flycatcher	*Muscicapa adusta*	I-GS		0.01		
Forest species present in exclosures				F	EX	G
Tropical Boubou	*Laniarius aethiopicus*	IO-F		0.78	0.33	
Klaas' Cuckoo*	*Chrysococcyx klaas*	IO-F		0.46	0.02	
Green Wood-Hoopoe	*Phoeniculus purpureus*	I-GS		0.42	0.16	
Speckled Mousebird*	*Colius striatus*	FN-X		0.41	0.18	
Blue-breasted Bee-eater	*Merops variegatus*	IO-F		0.40	0.23	
Bonelli's Warbler	*Phylloscopus bonelli*	I-GS	*P*	0.31	0.12	
Yellow-breasted Barbet*	*Trachyphonus margaritatus*	O-GS		0.30	0.25	
Mocking Cliff-Chat**	*Myrmecocichla cinnamomeiventris*	I-GS		0.22	0.07	
Northern Crombec	*Sylvietta brachyura*	IO-F		0.18	0.11	
Scarlet-chested Sunbird	*Nectarinia senegalensis*	FN-X		0.17	0.04	
Spotted Eagle Owl**	*Bubo africanus*	GC-GS		0.16	0.09	
Blue-naped Mousebird	*Colius macrourus*	FN-X		0.15	0.04	
Mariqua Sunbird**	*Nectarinia mariquensis*	FN-X		0.14	0.07	
Eastern Grey Plantain-eater	*Crinifer zonurus*	FN-X		0.11	0.04	
Pin-tailed Whydah*	*Vidua macroucra*	GC-GS		0.10	0.02	
Blackcap	*Sylvia atricapilla*	IO-F	*P*	0.08	0.04	
Jackal Buzzard	*Buteo rufofuscus*	X-AF		0.07	0.05	
Eurasian Nightjar	*Caprimulgus europaeus*	I-GS	*P*	0.07	0.11	
Fan-tailed Raven**	*Corvus rhipidurus*	X-AF		0.06	0.02	
Tawny-flanked Prinia	*Prinia subflava*	O-GS		0.06	0.14	
White-rumped Babbler** (SMB)	*Turdoides leucopygius*	O-GS		0.05	0.11	
Garden Warbler	*Sylvia borin*	X-AF		0.05	0.02	
Pallid Flycatcher	*Bradornis pallidus*	I-GS		0.04	0.04	
Black Kite**	*Milvus migrans*	X-AF	*P*	0.03	0.04	
African Silverbill	*Lonchura malabarica*	GC-GS		0.02	0.05	
Black-and-white Cuckoo	*Clamator jacobinus*	I-GS		0.02	0.05	
Pallid Harrier	*Circus macrourus*	GC-GS	*P*	0.02	0.14	
Helmeted Guineafowl	*Numida meleagris*	O-GS		0.01	0.05	
White-browed Coucal	*Centropus superciliosus*	I-GS		0.01	0.02	
Generalists				F	EX	G
Laughing Dove*	*Streptopelia senegalensis*	O-GS		0.94	0.75	0.56
Swainson's Sparrow* (AHB)	*Passer swainsonii*	X-AF		0.93	0.46	0.44
Red-cheeked Gordon-bleu	*Uraeginthus bengalus*	GC-GS		0.88	0.84	0.59
Bleating Warbler	*Camaroptera brevicaudata*	I-GS		0.87	0.84	0.53
Blue-eared Glossy Starling	*Lamprotornis chalybaeus*	IO-F		0.87	0.37	0.41
Variable Sunbird	*Nectarinia venusta*	FN-X		0.84	0.96	0.66
Common Bulbul	*Pycnonotus barbatus*	X-AF		0.76	0.79	0.56
Speckled Pigeon	*Columba guinea*	O-GS		0.62	0.21	0.06
Baglafecht Weaver (AHB)	*Ploceus baglafecht*	IO-F		0.56	0.25	0.09
Dusky Turtle Dove* (AHB)	*Streptopelia lugens*	IO-F		0.48	0.04	0.03
Common Cuckoo	*Cuculus canorus*	I-GS	*P*	0.44	0.30	0.09
Red-billed Fire-finch*	*Lagonosticta senegala*	GC-GS		0.41	0.25	0.03
Yellow-rumped Seed-eater**	*Serinus atrogularis*	GC-GS		0.38	0.26	0.28

Red-backed Shrike	*Lanius collurio*	I-GS	*P*	0.36	0.23	0.22
Clapperton's Francolin	*Francolinus clappertoni*	GC-GS		0.32	0.30	0.34
White-throated Robin	*Irania gutturalis*	O-GS	*P*	0.30	0.63	0.88
Grey-headed Batis**	*Batis orientalis*	I-GS		0.30	0.11	0.03
Hoopoe	*Upupa epops*	I-GS	*P*	0.28	0.09	0.03
Cinnamon-breasted Bunting	*Emberiza tahapisi*	GC-GS		0.28	0.68	0.72
Olivaceous Warbler	*Hippolais pallida*	I-GS	*P*	0.27	0.11	0.19
Little Rock-thrush** (AHB)	*Monticola rufocinerea*	O-GS		0.26	0.35	0.03
Hemprich's Hornbill (SMB)	*Tockus hemprichii*	O-GS		0.26	0.14	0.03
Northern Red Bishop*	*Euplectes franciscanus*	X-AF		0.25	0.09	0.03
Black-winged Lovebird (AHB)	*Agapornis taranta*	FN-X	*E*	0.22	0.02	0.06
Green (Montane) White-eye** (AHB)	*Zosterops poliogaster*	IO-F		0.21	0.16	0.03
Lesser Striped Swallow	*Hirundo abyssinica*	X-AF		0.20	0.14	0.22
Lesser Whitethroat	*Sylvia curruca*	I-GS	*P*	0.16	0.49	0.34
Ortolan	*Emberiza hortulana*	GC-GS	*P*	0.15	0.07	0.03
Black-headed Bush-shrike	*Tchagra senegala*	O-GS		0.14	0.53	0.44
Thekla Lark	*Galerida malabarica*	I-GS		0.14	0.25	0.62
Common House Martin	*Delichon urbica*	I-GS	*P*	0.10	0.04	0.09
Namaqua Dove	*Oena capensis*	O-GS		0.09	0.35	0.13
Fiscal Shrike*	*Lanius collaris*	I-GS		0.07	0.04	0.34
Singing Cisticola	*Cisticola cantans*	IO-F		0.07	0.44	0.19
Streaky Seed-eater (AHB)	*Serinus striolatus*	GC-GS		0.06	0.02	0.03
Greater Short-toed Lark	*Calandrella brachydactila*	I-GS	*P*	0.05	0.02	0.25
Mourning Wheatear	*Oenanthe lugens*	I-GS		0.03	0.26	0.37
Abyssinian Ground-Hornbill	*Bucorvus abyssinicus*	O-GS		0.03	0.04	0.03
Tawny Pipit	*Anthus campestris*	I-GS	*P*	0.03	0.02	0.16
Plain-backed Pipit	*Anthus leucophrys*	I-GS		0.02	0.04	0.19
Great Grey Shrike	*Lanius excubitor*	GC-GS	*P*	0.02	0.04	0.31
Flappet Lark	*Mirafra rufocinnamomea*	I-GS		0.02	0.02	0.16
Common Whitethroat	*Sylvia communis*	I-GS	*P*	0.02	0.11	0.19
European Bee-eater	*Merops apiaster*	I-GS	*P*	0.02	0.04	0.22
Northern Wheatear	*Oenanthe oenanthe*	I-GS	*P*	0.02	0.02	0.34
Species of forest and grazing land				F	EX	G
Dark Chanting Goshawk	*Melierax metabates*	GC-GS		0.14		0.03
Didric Cuckoo	*Chrysococcyx caprius*	I-GS		0.07		0.03
Brown-rumped Seed-eater (AHB)	*Serinus tristriatus*	GC-GS		0.04		0.06
African Citril (AHB)	*Serinus citrinelloides*	X-AF		0.04		0.03
Cape Rook	*Corvus capensis*	O-GS		0.03		0.03
Cut-throat	*Amadina fasciata*	O-GS		0.02		0.03
Tree Pipit	*Anthus trivialis*	IO-F	*P*	0.01		0.03
Species of exclosures and grazing land				F	EX	G
Barn Swallow	*Hirundo rustica*	X-AF	*P*		0.12	0.06
Rüppell's Weaver (SMB)	*Ploceus galbula*	I-GS			0.11	0.06
Red-tailed Shrike	*Lanius isabellinus*	I-GS	*P*		0.09	0.13
Buff-bellied Warbler	*Phyllolais pulchella*	I-GS			0.04	0.03
Mountain Rock-thrush	*Monticola saxatilis*	O-GS	*P*		0.04	0.06
Common Kestrel	*Falco tinnunculus*	GC-GS	*P*		0.02	0.09
Species limited to exclosures				F	EX	G
Rufous-crowned Roller	*Coracias naevia*	I-GS			0.14	
Common Quail	*Coturnix coturnix*	GC-GS	*P*		0.09	
Pectoral-patch Cisticola	*Cisticola brunnescens*	I-GS			0.04	
Species limited to grazed sites				F	EX	G
Isabelline Wheatear	*Oenanthe isabellina*	I-GS	*P*			0.31
Horus Swift	*Apus horus*	I-GS				0.16

Black-bellied Bustard	*Eupodotis melanogaster*	O-GS				0.09
Woodchat Shrike	*Lanius senator*	I-GS	*P*			0.09
Species considered as accidental visitors (one site, one day)						
Sedge Warbler	*Acrocephalus schoenobaenus*		*P*	×		
Wattled Ibis (AHB)	*Bostrychia carunculata*		*E*	×		
African Short-toed Lark	*Calandrella somalica*					×
Plain Nightjar	*Caprimulgus inornatus*				×	
Montagu's Harrier	*Circus pygargus*		*P*			×
Winding Cisticola	*Cisticola galactotes*			×		
Eurasian Roller	*Coracias garrulous*		*P*			×
Yellow-bellied Eremomela	*Eremomela icteropygialis*				×	
Pearl-spotted Owlet	*Glaucidium perlatum*			×		
African Hawk-eagle	*Hieraaetus spilogaster*			×		
Icterine Warbler	*Hippolais icterina*		*P*	×		
Northern Wryneck	*Jynx torquilla*			×		
Bimaculated Lark	*Melanocorypha bimaculata*					×
Abyssinian Slaty Flycatcher (AHB)	*Melaenornis chocolatina*		*E*	×		
White-throated Bee-eater	*Merops albicollis*			×		
Spotted Flycatcher	*Muscicapa striata*		*P*			×
Black Saw-wing	*Psalidoprocne pristoptera*			×		
Brown-throated Sand-martin	*Riparia paludicola*			×		
Yellow-crowned Canary	*Serinus canicollis*					×
Speckle-fronted Weaver	*Sporopipes frontalis*			×		
Red-eyed Dove	*Streptopelia semitorquata*			×		
Green Sandpiper	*Tringa ochropus*		*P*	×		
Groundscraper Thrush	*Turdus litsipsirupa*			×		
African Wattled Lapwing	*Vanellus senegallus*			×		

[1]Remark: Some birds listed here in one of the seven groups, such as Steppe Eagle and Egyptian Goose in the group of forest-limited birds, are more common in other, unsurveyed habitats such as rocky areas, wetlands, pastures or villages. Their group membership, especially for birds limited to one habitat, must be evaluated in a context of forest, exclosures and grazing land only.

1

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Figure captions

Figure 1. Map of northeast Africa showing the distribution of the Eastern-African highlands and the location of the study sites in the Geba river catchment in Central Tigray, Ethiopia.

Figure 2. (a) NMDS ordination of bird communities in forest fragments, exclosures and grazed matrix sites in northern Ethiopia, showing significant differences between the avian community composition of forests (● moist Afromontane forest and associated shrub savanna; ▲ dry Afromontane forest) and non-forest habitat (○), as defined by cluster and indicator species analysis. (b) shows a decline in the observed number of bird species (data points) and the Chao2 species richness estimation (top of bars) along the first NMDS axis which represents a gradient of decreasing structural complexity of the vegetation.

Labels of forest fragments are woody species communities: mAF, moist Afromontane forest; dAF, dry Afromontane forest and savanna woodland; SS, (riverine) shrub savanna. Labels of non-forest habitats are EX, exclosure; and GR, grazed matrix.

Figure 3. Functional diversity and bird species richness within groups defined by the presence or absence of species in forest fragments (F), exclosures (EX) and grazed matrix sites (G) in northern Ethiopia. Functional types were defined by diet and habitat specialisation: FN-X, frugivores and nectarivores; X-AF, birds of moist (forest) habitats; IO-F, insectivores and omnivores of forest

habitat; I-GS, insectivores of grassland and savanna; O-GS, omnivores of grassland and savanna (open area generalists); GC-GS, granivores and carnivores of grassland and savanna.

Tables

Table 1 Comparison of habitat structure and diversity indices for birds in forest fragments, grazing exclosures and grazed matrix sites sampled in a study area of 13,000 ha in northern Ethiopia.

	Forest fragments	Exclosures	Grazing land		
s	N = 10	N = 5	N = 3		
Structure (Medians) [1]				χ^2	*p*
Tree density	Open – Closed-canopy forest [a]	Scattered trees [b]	No trees [b]	13.93	0.001
Shrub density	Scattered [a]	Dense [b]	Scattered [ab]	9.02	0.011
Grass cover	Some	Important	Important	4.70	0.095
Vegetation layers	4 [a]	3 [ab]	2 [b]	11.27	0.004
Grazing	Occasional	Occasional	Overgrazed	6.42	0.04
Stony patches	Some – Many	Some	Dominant	5.79	0.055
Bird diversity (Means) [2]				F	*p*
Within-site diversity (α = mean observed number of species)	70.3 (7.3)[a]	45.2 (6.1)[b]	42.7 (5.0)[b]	33.32	< 0.001
Estimated site richness (Chao2 = mean expected number of species)	74.8 (7.6)[a]	58.9 (11.5)[b]	57.7 (8.4)[b]	7.47	0.006
Among-site diversity ($\beta = \gamma/\alpha$)	2.13	1.90	1.59	–	–
Observed total richness (γ)	150	86	68	–	–

Superscript letters indicate significant differences between groups.

[1] Comparisons of ordinal variables using Kruskal-Wallis non-parametric ANOVA by ranks

[2] For α and Chao2, standard deviation of mean is given between brackets. Comparison of groups using ANOVA and Tukey's HSD.

Table 2. Summary statistics for MRPP analysis showing differences in species composition between bird communities of moist forest, dry forest and degraded savanna in northern Ethiopia.

Alternative hypothesis	*T*	*p*	*A*
Bird communities, determined by cluster and indicator species analysis, differ in species composition	–6.96	<0.001	0.18

The test statistic *T* and significance *p* describe separation between groups. The chance-corrected within-group agreement *A* describes within-group homogeneity compared to random expectation. If there is more homogeneity within groups than expected by chance, then $1 > A > 0$. $A = 1$ when all items are identical within groups; $A = 0$ when heterogeneity equals expectation by chance.

Table 3. Environmental correlates of bird community composition for 10 forest fragments, 5 exclosures and 3 grazed matrix habitats in northern Ethiopia.

	NMDS 1		NMDS 2	
	r_s	p	r_s	p
Tree density	–0.902	< 0.001	–0.001	0.997
Shrub density	0.253	0.310	0.265	0.288
Number of vegetation layers	–0.898	< 0.001	0.113	0.655
Grass cover density	0.470	0.049	–0.138	0.584
Grazing intensity	0.635	0.005	–0.466	0.052
Stony patches	0.580	0.012	–0.554	0.017

Spearman rank correlations between site environmental variables and NMS axes need to be evaluated against a corrected $\alpha_{corr} = 0.008$ to assure an overall significance of $\alpha = 0.05$ (Bonferroni correction for 6 tests).

Figures

Fig. 1

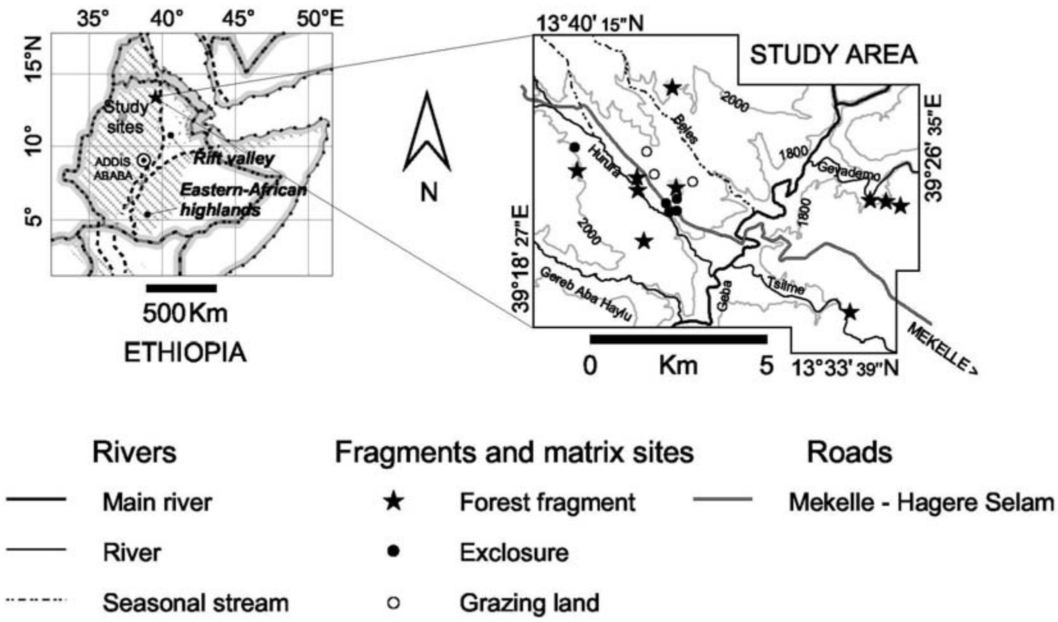


Fig. 2

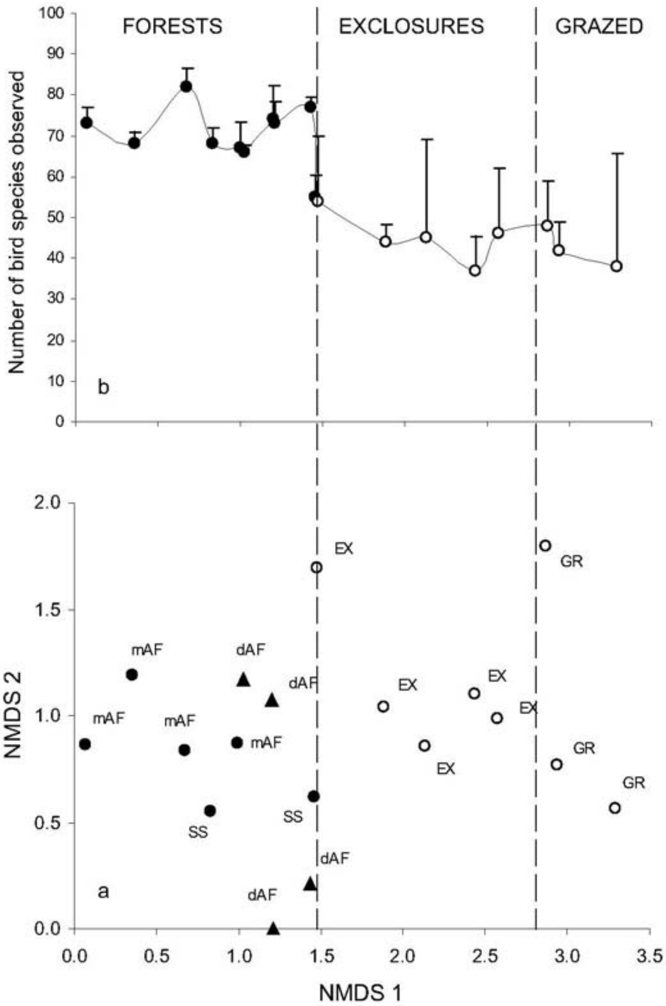
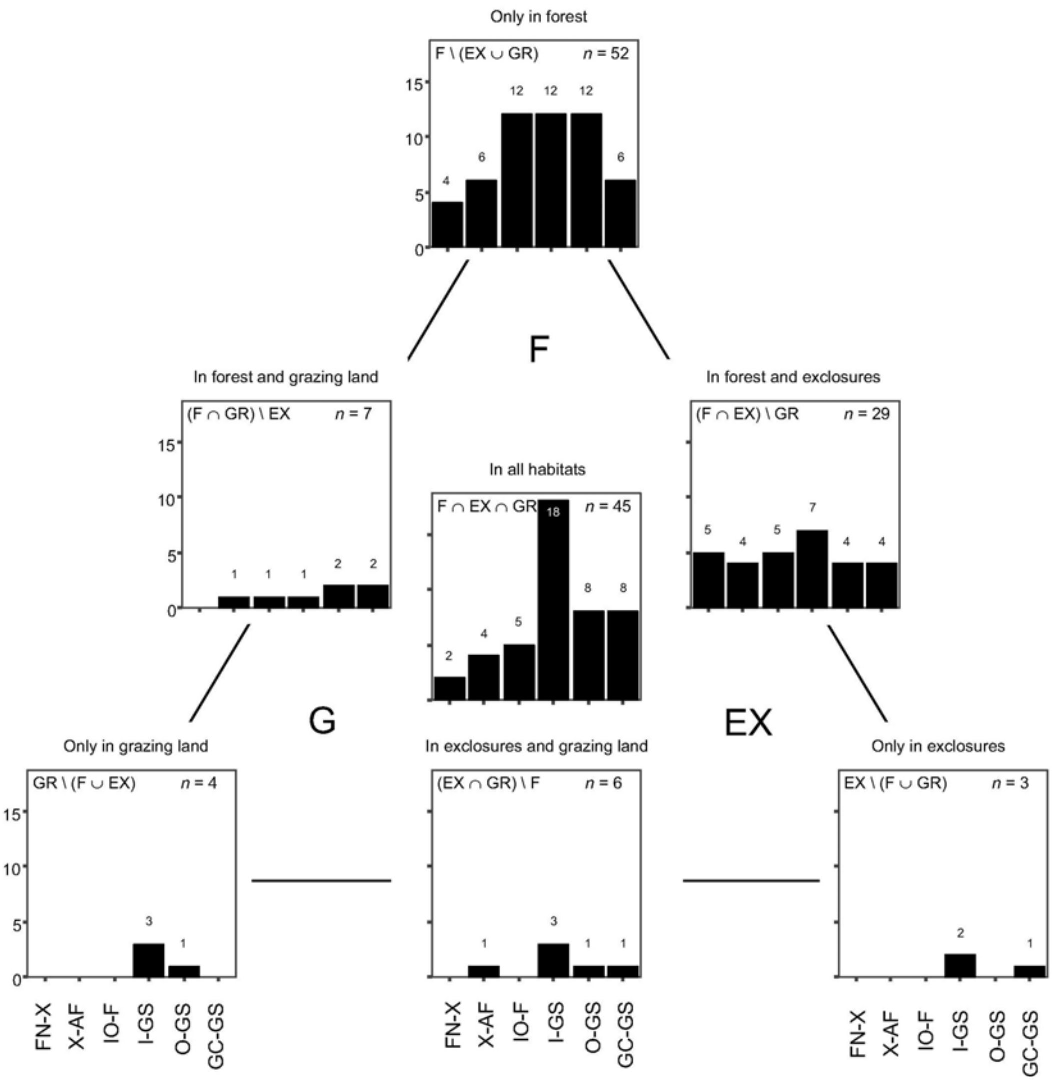

FORESTS
EXCLOSURES
GRAZED
Number of bird species observed
100
90
80
70
60
50
40
30
20
10
0
b
2.0
1.5
1.0
0.5
0.0
NMDS 2
mAF
dAF
SS
EX
GR
a
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
NMDS 1

Fig. 3



Only in forest
F \ (EX ∪ GR)
n = 52
F
In forest and grazing land
(F ∩ GR) \ EX
n = 7
In forest and exclosures
(F ∩ EX) \ GR
n = 29
In all habitats
F ∩ EX ∩ GR
n = 45
G
EX
Only in grazing land
GR \ (F ∪ EX)
n = 4
In exclosures and grazing land
(EX ∩ GR) \ F
n = 6
Only in exclosures
EX \ (F ∪ GR)
n = 3
FN-X
X-AF
IO-F
I-GS
O-GS
GC-GS