

CONSEQUENCES OF DEFORESTATION ON BIRD DIVERSITY IN THE HAMUMA FOREST, SOUTHWESTERN ETHIOPIA

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ABSTRACT: The Afromontane forests of Ethiopia are global biodiversity hotspots, known for their high biological diversity and endemism. However, conservation of these areas is challenging due to increasing human-induced threats. In this study, the effects of forest disturbances on birds were examined in the Hamuma Forest, an Important Bird Area, in the south-western Ethiopia. Birds were sampled across two seasons in three habitat types: intact forest, cultivated land (forest converted to settlement and cultivation), and open land (open bush land, grasslands and open woodlands). Using bird assemblage and functional traits of birds related to habitat type, the differences among the habitat types were examined in terms of avian species richness, taxonomic diversity, abundance, and assemblage composition. Bird assemblage species richness and abundance were not significantly different between the forest and cultivated land habitats, but were significantly lower in the open land habitat than the former two habitat types. Mean taxonomic diversity of bird assemblages was also significantly greater in the forest than in the cultivated land and open land, but the difference between the latter two habitat types was statistically not significant. At guild level, however, species richness and abundance of forest specialists were significantly greater in the forest habitat than the other habitat types. Assemblage composition was distinct among the habitat types and the pattern of assemblage was attributed to variations in vegetation structure among sites, mainly by tree and shrub abundances. These findings suggest the need for continued protection of intact forest ecosystems to maximize functional heterogeneity associated with specialist tropical forest taxa.

Key words/phrases: Assemblage, Forest specialist guild, Habitat change, Important Bird Area, Species composition, Species richness, Taxonomic diversity

INTRODUCTION

Birds are important to human-beings in many ways. They provide critically important ecosystem services that contribute to the socio-economic development and well-being of humans (Bird Life International, 2018; Şekercioğlu *et al.*, 2016; Şekercioğlu and Buechley, 2016). For example, insectivorous birds control pests; seed-eaters and frugivores disperse seeds; nectarivores pollinate plants (Breitbach *et al.*, 2010; Wenny *et al.*, 2016; Bird Life International, 2018); vultures clean up the environment by feeding on carcasses (Buechley and Şekercioğlu, 2016); and many species are used as food sources and as cultural symbols in arts and folklore (Muiruri and Maundu, 2010; Bird Life International, 2019). Birds, through avitourism, are also a source of income and incentive for local communities around protected

areas (Şekercioğlu, 2002a; Addisu Asefa, 2015a, 2018). They are also best indicators of environmental change and thus serve as a model biodiversity group to be used in biodiversity and environmental monitoring programmes (Wormworth and Şekercioğlu, 2011; Addisu Asefa and Girma Mengesha, 2019). Despite the immense benefits of birds to human-beings, many species globally are currently facing extinction (Bird Life International, 2018). According to the 2017 Bird Life International's status assessment report, 276 bird species (11% of bird species of the total 2,477 species known to be occur in Africa) are globally threatened with extinction (Bird Life International, 2018). The major causes of bird extinction are direct (e.g., hunting for food and traditional uses) and indirect (habitat destruction and climate change) anthropogenic-induced threats (Arcilla *et al.*, 2015). Such species-

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specific local or global extinction entails not only loss of species, but also loss of the ecosystem services associated with the species (Harmon, 1996; Maffi, 2005). Therefore, effective conservation of birds and their ecosystem services in countries like Ethiopia where bird diversity and endemism are high, but change in their habitat is taking place at overwhelming rate (Addisu Asefa *et al.*, 2017), should be seen as an important priority management action. This in turn requires updated and reliable ornithological data and how birds respond to habitat changes. Information derived from sound ornithological studies could help decision makers understand the conservation importance and status of sites to prioritize for conservation and develop appropriate conservation measures needed (EWNHS, 2001; Addisu Asefa and Kinahan, 2014; Addisu Asefa, 2015b).

One major cause of global biodiversity decline is habitat degradation and destruction due to anthropogenic actions (Brooks *et al.*, 2006). Understanding the responses of biodiversity components, such as birds, to human disturbances is important to enable informed conservation decision making (Bruner *et al.*, 2001; Bleher *et al.*, 2006; Addisu Asefa *et al.*, 2017). In forest ecosystems, alteration of vegetation structure and habitat fragmentation through deforestation and forest degradation due to settlement and cultivation land expansion and livestock over grazing are among the main threats affecting biodiversity (Trzcinski *et al.*, 1999; Chace and Walsh, 2006; Chown, 2010; Mulwa *et al.*, 2012; Yosef Mamo *et al.*, 2016; Addisu Asefa *et al.*, 2017). Forest birds are particularly susceptible to alterations in vegetation structure and forest extent because of their dependence on vertical vegetation structure (Davies and Asner, 2014; Addisu Asefa *et al.*, 2017). However, many studies of forest birds have found variable responses of different species to disturbance, depending on certain species-specific ecological traits and the nature and severity of disturbance (New bold *et al.*, 2013). Nonetheless, many forest specialist species are known to be negatively affected by forest disturbance (Canaday, 1997; Gove *et al.*, 2008; Addisu Asefa *et al.*, 2017). In contrast, habitat generalist species that are better adapted to a wider range of habitats, such as woodland, open and/or shrub habitats can positively exploit habitat changes induced by disturbance (Chace and Walsh, 2006; Gove *et al.*, 2008; Sekercioglu, 2012b). To manage the drivers with the greatest ecological impact, it is therefore apparent that conservation management actions

need to be based on scientific knowledge of the impacts of anthropogenic activities on biotic communities (Blair, 1996; Entwisle and Stern, 2005). However, such information is lacking in biologically important areas across the globe, especially tropical forests of developing countries like Ethiopia.

Ethiopia hosts high diversity and endemism of flora and fauna in the African continent, attributed to the high altitudinal variation (116 m bsl to 4543 m asl) and the concurrent wide range of ecological diversity (EWNHS, 2001). As such, the country harbors about *c.* 837 bird species of which 18 of them are endemic to the country (Ash and Atkins, 2009). To promote the conservation and sustainable use of these birds and their habitats, 69 Important Bird Areas (IBAs) have been identified in the country so far (EWNHS, 2001). However, many of these IBAs exist outside formally protected areas and ornithological data for many of the IBAs are inadequate, with some area remain unexplored (EWNHS, 2001; Asefa 2014; Addisu Asefa and Kinahan, 2014; Addisu Asefa, 2015b). Given the unprecedented rate of natural habitat alteration and degradation recorded in the country in the last three decades (FAO, 2010), ornithological studies in poorly known IBAs is a priority research action to aid effective conservation management decisions (EWNHS, 2001).

Hamuma Forest, in the Ilu-Ababora Zone of the Oromia National Regional State, southwestern Ethiopia, is one of the IBAs of Ethiopia where human pressure has been growing, but ornithological data and impacts of such pressure have been lacking. This forest is part of the Metu-Gore-Teppi Forest National Priority Forest Area, which has also been designated as IBA (IBA code: ET046; IBA National code: 52; EWNHS, 2001). The Metu-Gore-Teppi Priority Forest Area, which currently is managed under the auspices of the Oromia Forest and Wildlife Enterprise (OFWE) (OFWE, 2016), represents the majority of the high elevation forest in southern-western Ethiopia (EWNHS, 2001). This forest has remained intact until recently, due to poor accessibility and relatively low human population compared to other areas in the country (EWNHS, 2001; OFWE, 2016). However, recent development activities, such as resettlement programs and expansion of commercial farming have dramatically changed the previous conditions, are putting pressure on the existing forest cover (OFWE, 2016). Generally, due to the increasing population pressure, land is being heavily altered and degraded mainly through subsistence agricultural and settlement expansion,

overgrazing and deforestation for cash-crop plantations and illegal logging (OFWE, 2016). All of these human-induced activities could have a profound effect on the biodiversity in general and avifaunal assemblages in the area in particular, but the magnitude of the impacts has not been examined yet.

This paper presents results of a study conducted to determine bird diversity and how this varies across land use types. Specifically, we examine the impacts of human disturbance (land use change) on (1) avian species richness and abundance on the entire assemblage, and on two habitat guilds (forest specialist vs generalist guilds), and (2) assemblage composition. We also examined the relationship of bird population abundance with vegetation variables. We predicted that (1) compared with open land and forest converted to cultivation land, the relatively intact forest (assuming lower levels of human-induced disturbance) would contain higher species richness and bird abundance of overall species and of forest specialist species; and (2) as a result of reduced forest cover and increased crop cultivation, open land and forest converted to cultivation land habitats would host higher richness and abundance of species associated with open land, open woodland, and shrub land habitats.

Materials and Methods

The study area

Hamuma Forest is part of Metu-Gore-Tepi priority forests, a general name used for the forests found along the western edge of the plateaus of the country. This forest is found in the Ilubabor Zone of Oromia region, south-eastern Ethiopia, located in the geographical coordinates of 07°10'–08°15'N/ 34°55'–35°35'E, 640km from the capital city of the country, Addis Ababa (EWNHS, 2001; Figure 1). The altitudinal range of the area is between 1,500–1,900m asl. The area experiences eight months of rainfall and receives maximum annual rainfall of 2400mm (OFWE, 2016). The driest month in the area is December–February and the mean annual temperature of the area is 18.3°C (EWNHS, 2001).

Floristically, the area shares both transitional and Afro-montane forests and is the richest forest-type in Ethiopia, with over 100 tree species and a diverse understory (Friis, 1992). Floristically, the

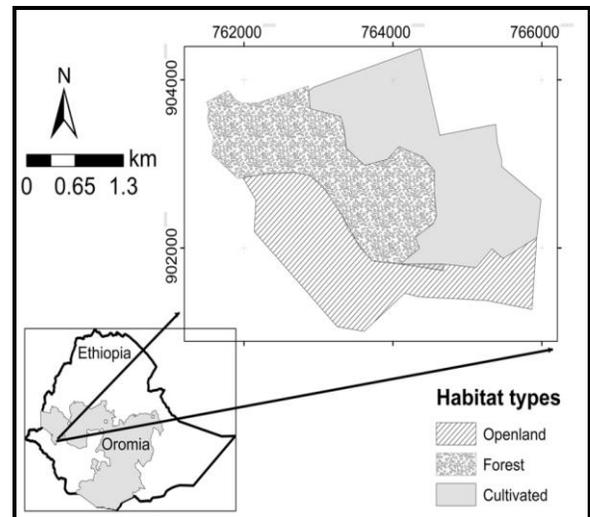


Figure 1. Map showing the location of the study area (base of the arrow lines) in Oromia National Regional State of Ethiopia and the three major habitat types.

area shares both transitional and Afro-montane forests and is the richest forest-type in Ethiopia, with over 100 tree species and a diverse understory (Friis, 1992). Among these tree species are *Aningeria adolfi-friederici*, *Podocarpus falcatus*, *Ocotea kenyensis*, *Sapium ellipticum*, *Macaranga capensis*, *Olea capensis*, *Albizia* spp., *Polyscia fulva*, *Schefflera abyssinica* and *Ficus* spp. The understory species include *Cyatea manniana*, *Dracaena steudneri*, *Coffee Arabica* and *Phoenix reclinata* (Friis, 1992). The forest is home to many wild mammal species, three monkey species [Blue Monkey (*Cercopithecus mitis*), DeBrazas Monkey (*Cercopithecus neglectus*) and Colobus Monkey (*Colobus guereza*)]; large-sized carnivores [e.g., Hyaena (*Crocuta crocuta*), Leopard (*Panthera pardus*) and Lion (*Panthera leo*)]; pigs such as Common Warthog (*Phacochoerus africanus*), Giant Forest Hog (*Hylochoerus meinertzhageni*) and Bush Pig (*Potamochoerus larvatus*) and ungulates like Common Bushbuck (*Tragelaphus sylvaticus*) (OFWE, 2016). Information on birds of Hamuma Forest has been lacking. Nonetheless, a rapid survey conducted in 1996 by EWNHS (2001) across all forests, including Hamuma forest, encompassed by the Metu-Gore-Tepi IBA indicates the presence of: (i) two threatened species: Rouget's Rail (*Rougetius rougetii*) and Abyssinian Long-claw (*Macronyx flavicollis*), (ii) two endemic species: Yellow-fronted Parrot (*Poicephalus flavifrons*) and Abyssinian Woodpecker (*Dendropicos abyssinicus*), (iii) 26 of the 49 species of Afro-tropical highland biome known from Ethiopia

Although part of the forest has been impacted by the surrounding people due to deforestation and agricultural expansion, there are still areas with intact forest. Most of the deforested part is currently transformed to settlement, agricultural land and grazing land. Local farmers usually cultivate maize and root crops, and collect and/or cultivate forest species, particularly coffee and the endemic spice *Aframomum corrorima* (OFWE, 2016). In addition to small-scale subsistence farmers, development of cash crop growing investments (Gumaro tea state) is also the major cause of deforestation in the study area (OFWE, 2016). Overall, the study forest has a total area of 1,140 ha and can be classified into three land use types: intact forest (with low human disturbance, covering an area of 400 ha), open land (grassland, bush lands and shrub lands, area 360 ha), and cultivated land (forest land converted to agriculture and settlement, area 380 ha) (Figure 1). The intact forest and open land habitat types were free of cultivation and/or settlement and thus were considered as undisturbed sites compared to the cultivated land.

Data Collection

A preliminary survey was conducted in July 2018 to assess the physical features and land use/land cover of the study area. Accordingly, three broad habitat types were recognized based on dominant vegetation cover and land use: intact forest (covered by dense forest and relatively low human disturbances where there settlement and cultivation were absent), open land (covered by open bush land, open woodland and grassland where settlement and/or cultivation were absent), and cultivated land (forest land converted to settlement and cultivation). Geographic coordinates of the boundaries of these habitats were marked using a Garmin GPS unit. Stratified systematic sampling technique was used to establish transects in each habitat type (Bibby *et al.*, 1998; Gregory *et al.*, 2004). Thirty-nine line transects of 1 km long each were systematically established: 15 in the intact forest, and 17 in cultivated land and 7 in the open land. In each habitat type, transects were established systematically, at a minimum distance of 200m apart, and were oriented parallel to each other along altitudinal gradients (1500–1800 m asl).

Along each transect, four sampling points were established at every 200m distance, to reduce double counting (to reduce pseudo-replication). Point transect counting was used because it has been considered more suitable for sampling cryptic, shy and skulking species in forest habitats where

detection probability is reduced by dense vegetation cover, and to relate bird occurrences with habitat features (Gibbons *et al.*, 1996; Bibby *et al.*, 1998; Gregory *et al.*, 2004).

Bird surveys were carried out in the August/September 2017 (wet season) and in January/February 2018 (dry season) by Sena Gashe. Only one transect was surveyed per a day. Each point along each transect in each season was surveyed twice on a given day (Gregory *et al.*, 2004; Asefa *et al.*, 2017). Bird surveys were conducted early in the morning, between 0630 and 1030 hours, and late in the afternoon, between 1530 and 1730 hours, when the majority of birds are assumed to be active (Gibbons *et al.*, 1996). Bird counting at each point, during each counting session, lasted eight minutes, allocating two additional minutes prior to commencement of counting to allow birds settle due to intrusion of the surveyor (Gibbons *et al.*, 1996; Bibby *et al.*, 1998). Within the eight minutes, birds seen and/or heard within a radius of 50 m were recorded along with their number. Birds flushed away from the census point while approaching the station and those that flew away while counting were recorded from the point they were first seen (van Rensburg *et al.*, 2000; Gregory *et al.*, 2004). Birds that were seen flying over the census area and not necessarily making use of the habitat were not recorded. A Garmin GPS unit was used to navigate between survey points, and Bushnell binoculars and Redman *et al.*'s. (2009) field guide book was used for bird identification.

Six habitat variables, known to affect birds (Addisu Asefa *et al.*, 2017), were recorded at each bird sampling point: tree abundance, tree cover, shrub cover, herb cover, grass cover and bare ground. For trees, this was undertaken within quadrats of 20 m × 20 m, where the number (abundance) of trees (DBH > 2.5cm or height > 5m) was counted and canopy cover was visually estimated (Newton, 2007). At the corners of each of the 20 m × 20 m quadrats, four 5 m × 5 m sub-quadrats were established to estimate shrub, herb, grass, and bareground percentage covers.

Data Analysis

Bird species richness

Bird species were classified into two guilds based on their broad habitat type preferences, following Gove *et al.* (2008), Redman *et al.* (2009), Kissling *et al.* (2012), and Addisu Asefa *et al.* (2017): forest specialist guild (those species that

predominantly depend on forest habitat), and generalist guild (non-forest species that depend on one or more habitats, including woodland, shrub land, and/or open land). For species-specific habitat guild memberships in our study, see Appendix 1. These habitat guilds were identified for two main reasons. First, from an avian perspective, the primary goal of conserving the study area's forest is to maintain the diversity of bird species typically associated with forest habitats (OFWE, 2016), and second, forest-specialist species have repeatedly been shown to be especially negatively impacted to forest change (e.g., Pollock *et al.*, 2015, Powell *et al.*, 2015; Addisu Asefa *et al.*, 2017).

As sample size (number of transects surveyed, and number of individual birds recorded) varied among the three habitat types, bird species richness estimations were made without accounting for these differences (based on actually observed number of species during the survey), as well as by accounting for these differences (Addisu Asefa *et al.*, 2017). In the latter case, interpolation (standardizing all datasets to equal to the smallest data set available) and extrapolation (standardizing all datasets to equal the largest data set available) techniques were applied (Addisu Asefa *et al.*, 2017). An individual-based rarefaction method—an appropriate approach to estimate interpolated and/or extrapolated species richness (Colwell *et al.*, 2012; Colwell, 2013)—was used to calculate and compare interpolated and extrapolated species richness. The summed abundance for each habitat type of the number of individuals of each species recorded along each transect was used as the input for the individual-based richness computation. Chao 1 estimator (an appropriate estimator for individual-based data; Colwell *et al.*, 2012) was also used to estimate asymptotic species richness ($S(\text{est})$) (i.e., the total number of species expected in an area, including those species not observed during the survey period) for each habitat type to assess sampling completeness. All these analyses were conducted for each habitat type in each season and across season (season combined) and comparisons were made on overall species (assemblage) and the two habitat guilds.

Estimated species richness ($S(\text{est})$) was calculated using EstimateS 9.1.0 software (<http://vicero.eeb.uconn.edu/estimates>; Colwell, 2013). To compare estimated (based on interpolation and extrapolation) species richness among habitat types, rarefaction curves of estimated species richness $S(\text{est})$ were computed with 95% confidence

intervals (CI). Following the recommendations of various authors (e.g., Walther and Moore, 2005; Colwell *et al.*, 2012; Colwell, 2013; Addisu Asefa *et al.*, 2017), nonoverlapping 95% CIs of $S(\text{est})$ at the reference sample size (sample size of the habitat with the smallest sample size, for the interpolation technique; and sample size of the habitat with the largest sample size, for the extrapolation technique) was used as a conservative criterion of statistical difference (at $\alpha = 0.05$) in species richness between habitat types.

In addition to species richness, taxonomic diversity index was also computed and compared among habitat types. This diversity index, in addition to species identity and their abundances, also uses species relatedness information for the computation (for detail see, Clarke and Gorley, 2006). Thus, in addition to the species-sample data table used for richness computation, an aggregation data table containing the hierarchical taxonomic information of each species (i.e., species to order level; see Appendix 1) was created based on the taxonomic classification of birds of Africa provided by African Bird Club (2019) and used as an input in Primer software (Clarke and Gorley, 2006). As most species were represented in low abundances, data from the two seasons were pooled for each species and used for this analysis purpose. Finally, Kruskal-Wallis test was used to compare the difference in mean taxonomic diversity among the three habitats and Mann-Whitney test for pair-wise comparison in SPSS software (IBM, 2011).

Bird population abundance

The effects of habitat type and season on bird abundance were tested on the assemblage (all species taken together) and each of the two habitat guilds using a generalized linear model in SPSS 20 (IBM, 2011). These models were initially fitted with a poisson probability distribution and log-link function, which is suggested to be appropriate for count data that follow long-normal distribution (Quinn and Geough, 2002). However, goodness-of-fit test showed over dispersion of data, with the estimated scale parameters greater by far than the assumed value (around one) for all datasets (the scale parameters were 25.064, 10.457, and 18.361 for overall assemblage, the forest-specialist guild, and nonforest guild, respectively). Thus, models with a negative binomial probability distribution and log-link function were fitted, which fitted well with estimated scale parameters near one in all cases (parameter values = 0.641, 0.904 and 0.899 for overall

species, the forest-specialist guild and nonforest guild, respectively) (Quinn and Geough, 2002).

Bird assemblage composition

A Bray-Curtis Similarity Index was used to calculate similarities in bird species composition among assemblages using Primer v6 software (Clarke and Gorley, 2006). Data were square-root transformed before analysis to down weight common species relative to rare ones (Clarke and Gorley, 2006). Then, an analysis of similarity (ANOSIM) was performed to assess differences in bird species composition between habitat types (both within and across season) and between the two seasons based on habitat combined data (Clarke and Gorley, 2006). Global R values were used to determine the degrees of similarity among treatments. The closer this value is to 1, the more dissimilar are assemblages (Clarke and Gorley, 2006). Significances of differences were tested at $\alpha = 0.05$ level. Similarity percentage analysis (SIMPER) was also conducted in Primer v6 software to calculate the percentage contribution that each species made to the dissimilarity between bird assemblages of the forest types and to identify which species were contributing most to the differences (i.e. species that are characteristic of each habitat type) between assemblages (Clarke and Gorley, 2006). As seasonal difference in assemblage was not detected within each habitat type, this SIMPER analysis was conducted based on combined data from the two seasons.

Habitat variables and their association with bird diversity

Preliminary analysis showed a non-significant seasonal difference in mean values of each habitat variable considered within each habitat types, except herb cover that increased during wet season in the cultivated land. Thus, for each transect average values of the dry season and wet season data were computed for each variable and used for analysis. Prior to analysis, tree abundance was \log_{10} -transformed and other variables with percentage cover values were Arcsine-transformed (Quinn and Geough, 2002). Differences in mean values of each

habitat variable among the three habitat types were tested using one-way ANOVA. Tukey's multiple mean comparison was used to test whether differences in each variable between each pair of habitat type were significant.

Bird assemblage composition patterns were then matched to habitat variables across the three habitat types, with the bird species composition and habitat data matrices as the input according to PRIMER's RELATE permutation procedure (Clarke and Gorley, 2006). This was followed by the BEST procedure to find the 'best' match between the assemblage and that from the environmental variables; the extent to which these two patterns match reflects the degree to which the chosen habitat variables explain the assemblage pattern (Clarke and Gorley, 2006). Variable selection was made using a Bio-Env algorithm, which searches all possible combinations from the primary datasheet. In both cases (RELATE and BIO-ENV), Spearman rank correlation (P_s) was used to measure the strength of the relationship between the bird and habitat resemblance matrices (Clarke and Gorley, 2006). Finally, a simple Person's correlation test was used to examine the relationship of each habitat variable, as most of the habitat variables were correlated to each other, with bird abundance. This analysis was undertaken in SPSS ver 20 (IBM, 2011) separately for all birds and each bird guild.

RESULTS AND DISCUSSION

Bird species richness

A total of 4,727 individual birds from 117 species, grouped in 44 families and 13 orders, were recorded across the three habitat types throughout the study period (Appendix 1). Of these, 2,411 and 2,316 individuals, and 112 and 101 species, respectively, were recorded during the dry and wet seasons (Table 1). The total species pool of bird assemblage of the study area comprised: 2 endemic and 8 nearly-endemic (shared with Eritrea) species; 23 Afro-tropical highland biome-restricted species, representing 47% of total number of species of this biome known to occur in Ethiopia; and 5 globally

threatened species, including three critically endangered vulture species: White-headed Vulture (*Trigonoceps occipitalis*), Hooded Vulture (*Necrosyrtes monachus*) and White-backed Vulture (*Gyps africanus*) (Appendix 1). These results indicate that the area is one of ornithological IBA in the country.

Comparisons of observed and estimated (Chao 1 estimator) species richness for each dataset showed that sampling completeness in each habitat was > 95% (see Table 1). Consequently, estimated richness $S(\text{est})$ based on interpolation and extrapolation methods yielded similar results with the respective observed richness $S(\text{obs})$. Thus, all comparisons presented and discussed hereafter are based on the rarefied observed species richness $S(\text{obs})$ values.

Bird species richness [$S(\text{obs})$] was not significantly different between the forest and cultivated land habitats, but was significantly lower in the open land habitat compared to former two habitat types (Table 1). These results were consistent when each season was treated separately, except a slightly higher richness in the forest habitat during the dry season than in the cultivated land (Figure 2a and b). Furthermore, bird species richness of the entire study area (across habitats) was significantly greater during the dry season than the wet season (Table 1), but such significant seasonal difference was not detected within each habitat type (data not shown). At guild level, species richness of forest specialist guild was significantly greater in the forest habitat than the other habitat types, but that of the non-forest bird guild was significantly greater in the cultivated land both within each season and across season (Figure 3a-c).

Kruskal-Wallis Test indicated that mean taxonomic diversity of bird assemblages was significantly different among habitat types [Mean (\pm SD): open and = 77.44 (\pm 12.80), cultivated land = 77.17 (\pm 6.79), and forest = 81.83 (\pm 3.22); Kruskal-Wallis Test: Chi-square = 14.634; df = 2, $P < 0.01$]. Mann-Whitney test of each possible pair of habitats

revealed that bird taxonomic diversity was significantly greater in the forest compared to the cultivated land (Mann-Whitney Test Statistic (U) = 110.00, $df = 1$, $P < 0.01$) and with the open land ($U = 329.50$, $df = 1$, $P < 0.01$). However, the difference between cultivated land and open land was not statistically significant ($U = 214.00$, $df = 1$, $P = 0.358$).

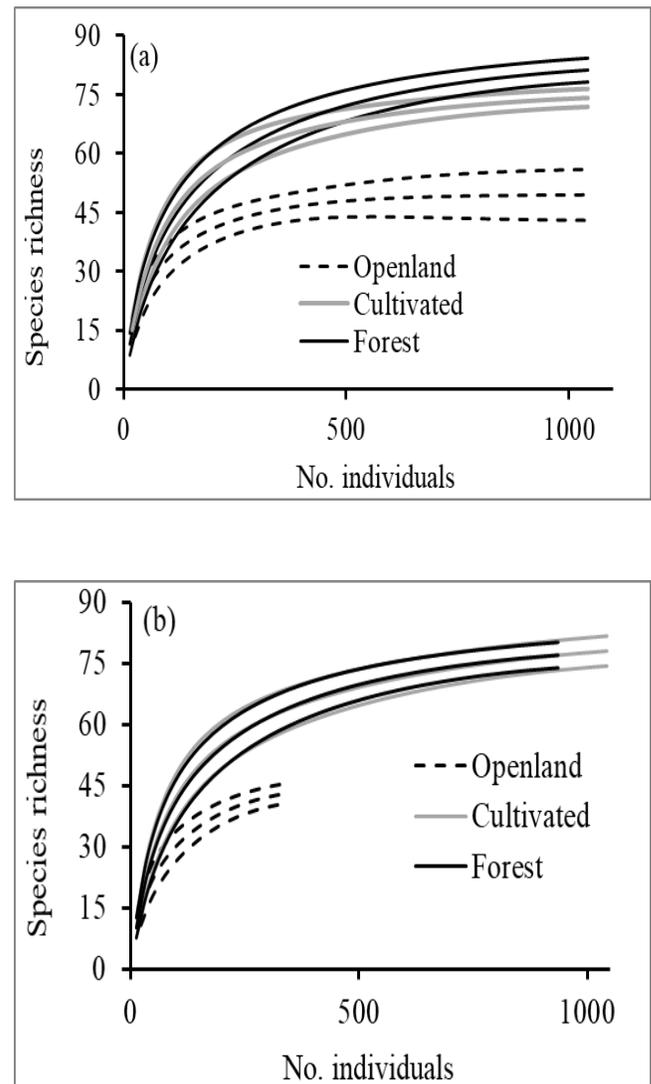


Figure 2. Assemblage richness during the dry season (a) and the wet season (b) of the three habitat types. Values given for each habitat type are mean and 95% lower and upper confidence bounds.

Table 1. Bird population abundance, observed S(obs) and estimated S(est, based on interpolation, extrapolation and Chao 1) species richness and sampling completeness (percent observed relative to estimated richness) in the three habitat types and in the dry and wet seasons at the study area.

Factor	Individuals	S(obs)	S(est) interp.	S(est) extrapol.	S(est) Chao 1	Sampling rate
<i>Habitat</i>						
Openland	699	54	54 (±3.03) ^a	54 (±3.03) ^a	55.66 (±2.22) ^a	96
Cultivated land	2070	83	74 (±3.85) ^b	83 (±2.46) ^b	84.00 (±1.77) ^b	99
Forest	1958	85	75 (±3.32) ^b	85 (±4.46) ^b	85.25 (±0.86) ^b	100
<i>Season</i>						
Dry	2411	112	111(±3.42) ^a	112 (±2.41) ^a	113.23 (±1.48) ^a	99
Wet	2316	101	101 (±2.01) ^b	100 (±1.01) ^b	100.17 (±0.69) ^b	100

Bird population abundance

Tests of model effects of habitat and season on bird abundance showed that only habitat had significant effect (season: Wald chi-square = 1.053, df = 1, P = 0.305; habitat: Wald chi-square = 6.524, df = 2, P = 0.038; habitat*season Wald chi-square = 1.328, df = 2, P = 0.515). Pair wise comparison among habitats showed significantly lower bird population abundance in the open land compared to both cultivated land and forest habitats (in both cases, df = 1; P < 0.05). However, no significant difference in mean bird abundance was found between cultivated land and forest habitats (df = 1, P = 0.327) (Figure 4a–b). Similar to the case of overall assemblage abundance, only habitat type had statistically significant effect on the abundances of forest-specialist guild (tests of model effects, habitat: Wald's chi-square = 18.183, df = 2, P < 0.05; season: Wald Chi-Square = 1.346, df = 1, P = 0.246; habitat*season: Wald's chi-square = 1.495, df = 2, P = 0.474), as well as non forest bird guild (tests of model effects, habitat: Wald's chi-square = 14.830, df = 2, P < 0.05; season: Wald's chi-square = 1.576, df = 1, P = 0.209; habitat*season: Wald chi-square = 1.712, df = 2, P = 0.425). Both within each season and across season, forest-specialist guild was significantly more abundant in the forest habitat than the other habitat types, which had similar abundances (Figure 4a). Conversely, the mean abundance of non forest bird guild was significantly greater in the cultivated land compared with the mean abundance in the forest and open land habitat types (Figure 4b).

Assemblage composition

The results of ANOSIM revealed that overall bird species composition was significantly dissimilar between each pair of the three habitat types both across season (combined seasonal data) and within each season (Table 2). However, statistically insignificant difference in bird species composition was found between the dry and wet seasons, both within each habitat type (Table 2) and across habitat types (i.e., when data from all habitat types were combined; R = -0.035; P = 0.984). Results of the SIMPER analysis showed that ~50% of the differences in assemblage composition between: (1) the cultivated land and the intact forest were driven by 16 species (7 forest specialist and 9 non-specialist species), (2) between the open land and the forest by 13 species (7 forest specialist and 6 non specialist species), and the open land and cultivated land by 14 species (3 forest specialists and 11 non-specialist species) (Appendix 2). Forest specialist species, such as Abyssinian Oriole (*Oriolus monacha*), Tropical Boubou (*Laniarius aethiopicus*), Red-chested Cuckoo (*Cuculus solitaries*), Kaffa White-eye (*Zosterops kaffensis*), Variable Sunbird (*Cinnyris venustus*), Bleating Camaroptera (*Camaroptera brachyuran*) and Silvery-checked Hornbill (*Bycanistes brevis*) were found to be the most characteristic species of the forest habitat. In contrast, habitat generalist species, such as the Lesser Masked Weaver (*Ploceus intermedius*), Black Saw-wing (*Psalidoprocne pristoptera*), Bronze Mannikin (*Spermestes cucullata*), Fantailed Widowbird (*Euplectes axillaris*), Hadada Ibis (*Bostrychia hagedash*) and Little Bee-eater (*Merops pusillus*) were most characteristic of the openland or the cultivated land (Appendix2).

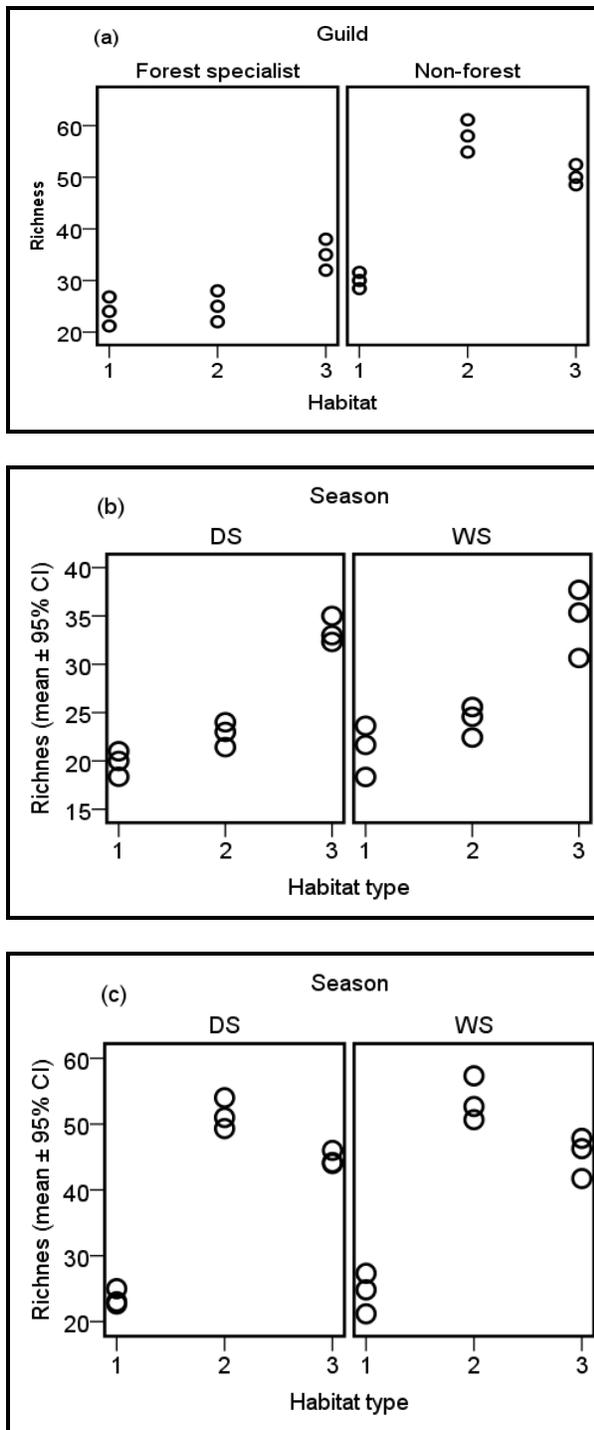


Figure 3. Dot plots showing the species richness of forest specialist and non-forest (generalist species) guilds in the three habitat types across season (a), and within each of the dry and wet seasons, for forest specialist guild (b) and generalist guild (c). (Dots indicate mean and 95% confidence intervals. Habitats: 1 = open land; 2 = cultivated land; 3 = forest. The three dots for each habitat are the mean and 95% lower and upper bounds. Non-overlapping of the 95% confidence bounds indicates statistically significant difference between habitats.)

Habitat variables and their relationships with birds

Both tree abundance and cover were significantly higher in the forest habitat and in the open land than in the cultivated land (tree abundance: $F_{2,36} = 133.941$; cover: $F_{2,36} = 111.211$, in both cases, $P < 0.05$; Table 3). Shrub cover was significantly greater in the forest habitat compared to both the open land and cultivated land ($F_{2,36} = 49.378$, $P < 0.05$). However, bare ground cover was significantly greater in the cultivated land ($F_{2,36} = 29.961$, $P < 0.05$) compared to the forest and open land habitats. Grass cover significantly lower in the forest habitat ($F_{2,36} = 82.780$, $P < 0.05$) than the other two habitat types. Herb cover was the only variable that varied among the three habitat types, highest in the cultivated land and higher in forest habitat ($F_{2,36} = 5.878$, $P < 0.05$) (Table 3). Most habitat variables showed strong correlations with each other (Table 4).

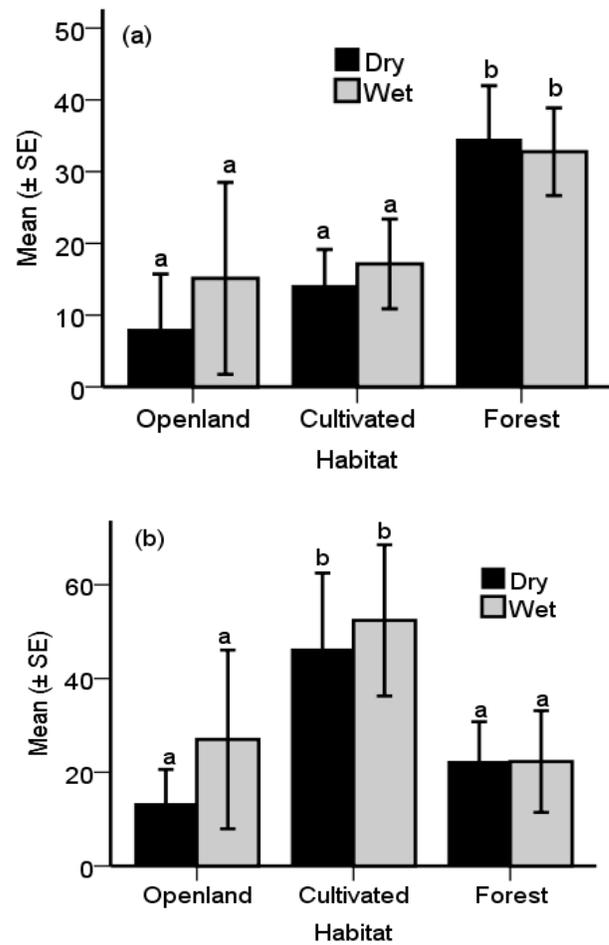


Figure 4. Abundance (mean ± SE) of forest specialist (a) and nonforest (b) birds in the three habitat types during the dry season (DS) and wet season (WS). Significant differences are indicated by different letters.

Table 2. Pair-wise tests of ANOSIM of bird assemblage composition between the three habitat types (based on combined seasonal data) and between dry (DS) and wet (WS) seasons within each habitat type. (Statistically significant differences are indicated by an asterisk.)

Factor groups	Global R-value	P-value
<i>Between habitat types</i>		
Cultivated vs. Forest	0.413	0.001*
Cultivated vs. Openland	0.316	0.001*
Forest vs. Openland	0.401	0.001*
<i>Within habitat type (DS vs WS)</i>		
Forest	-0.034	0.846
Openland	-0.162	0.987
Cultivated land	-0.060	0.968

The RELATE procedure indicated a positive bird-habitat relationship ($P_s = 0.304$, $P = 0.001$). Similarly, the BEST result selected a combination of two variables, tree abundance and shrub abundance, as the best variables explaining the bird assemblage pattern ($P_s = 0.407$, $P = 0.001$). Analysis of bird abundance-habitat relationships showed that tree abundance had strong, statistically significant positive relationships with both the population abundance of overall assemblage ($r_p = 0.776$, $df = 39$, $P < 0.05$) and with abundance of the forest-specialist

habitat guild ($r_p = 0.692$, $df = 39$, $P < 0.05$), but negative relationship with the abundance of non forest species guild (Table 4). Other habitat variables had non-significant relationships either with the assemblage abundance and non forest guild (Table 4). Nonetheless, tree cover was significantly positively related to population abundance of forest-specialist bird guild ($r_p = 0.492$, $df = 39$, $P < 0.05$). Grass cover and bare ground had significant negative relationships (in cases, $r_p = -0.554$, $df = 39$, $P < 0.05$; Table 4).

Table 3. Mean (\pm SD) of \log_{10} -tree abundance and proportion canopy cover (all arcsine-transformed), tree, shrub, herb, grass, and bare ground in each habitat type. For each variable, significant mean differences among habitats are indicated by different superscript letter.

Variable	Cultivated (n = 17)	Forest (n = 15)	Open land (n = 7)
Tree abundance	0.26 \pm 0.05 ^a	1.10 \pm 0.05 ^b	0.73 \pm 0.12 ^c
Tree cover	0.09 \pm 0.02 ^a	0.40 \pm 0.02 ^b	0.21 \pm 0.05 ^c
Shrub cover	0.04 \pm 0.12 ^a	0.19 \pm 0.02 ^b	0.17 \pm 0.13 ^b
Herb cover	0.20 \pm 0.02 ^a	0.13 \pm 0.02 ^b	0.10 \pm 0.05 ^c
Grass cover	0.26 \pm 0.02 ^a	0.05 \pm 0.02 ^b	0.23 \pm 0.05 ^a
Bareground	0.45 \pm 0.02 ^a	0.30 \pm 0.02 ^b	0.32 \pm 0.04 ^b

Table 4. Pearson correlation coefficients between each pair of habitat variables and between them and bird abundance in the study area (in all cases, n = 39).

Variables	Tree abundance	Tree cover	Herb cover	Shrub cover	Bare ground	Grass cover
Tree cover	0.836*					
Herb cover	0.06	-0.09				
Shrub cover	0.236	0.194	-0.366*			
Bare ground	-0.638*	-0.704*	-0.012	-0.614*		
Grass cover	-0.638*	-0.704*	-0.012	0.614*	1.000*	
Abundance of bird assemblage	0.776*	-0.07	0.27	-0.242	0.078	0.078
Abundance of Forest-specialist guild	0.692*	0.492*	-0.038	0.299	-0.554*	-0.554*
Abundance of non-forest guild	-0.367*	0.119	0.111	-0.289	0.038	0.038

Our results reveal that forest specialist species that require intact Afromontane forests with little human disturbance responded negatively to forest

conversion, both in species richness and population abundance. These species are primarily affected by disturbance-induced changes in vegetation structure

(and also possibly by plant species composition which was not considered in this study; see Newton 2007, and Buechley et al., 2015), especially by the abundance and cover of trees (Addisu Asefa et al., 2017). In contrast and as expected, generalist species that exploit various habitats exhibited positive responses to forest disturbance. Furthermore, bird species composition was distinct among the three habitat types studied, suggesting a significant change from specialists in the intact forest to generalists (non-forest birds) in the cultivated and open land habitats. These results support the findings of numerous studies from Ethiopia (e.g., Addisu Asefa et al., 2017) and around the globe that have shown forest specialist bird species to be among the most susceptible to forest disturbance (e.g., Stouffer and Bierregaard, 1995; Sekercioglu, 2012b; Newbold et al., 2013; Arcilla et al., 2015; Pavlacky et al., 2015). Thus, for the long-term conservation of forest specialists, particularly Ethiopian endemics or near endemics, such as the Abyssinian Woodpecker (*Dendropicos abyssinicus*), Yellow-fronted Parrot (*Poicephalus flavifrons*), Black-winged Lovebird (*Agapornis taranta*), and Afrotropical forest species more broadly, it is important to manage the drivers with the greatest ecological impact on the intact forest.

In contrast to the guild analysis results, the species richness and abundance of bird assemblage (i.e., taking all species together) were similar in the cultivated land and forest, although significantly lower in the open land habitat. In this regard, previous studies report conflicting results. For example, many studies support a general trend of lower bird species richness and population abundance in forests that have been transformed into farmland and/or undergone some other form of extensive habitat transformation, both in the tropical regions (see, e.g., Daily et al., 2001; Waltert et al., 2004; Seavy, 2009), and in temperate regions (e.g., Heikkinen et al., 2004; Breitbach et al., 2010). In contrast, findings of some other studies, particularly in East Africa, report equal, even sometimes higher, species richness and abundance in forests converted to cultivation land compared with their counterpart intact forests (e.g., Mulwa et al., 2012; Gove et al., 2013; Buechley et al., 2015; Addisu Asefa et al., 2017). Such opposing findings could have arisen because most studies that have supported the general trend of decreased forest diversity with increased disturbance have typically investigated forests that are intensively utilized as agro ecosystems or have

been completely converted (e.g., Waltert et al., 2004; Seavy, 2009), as opposed to forests that have not been completely transformed, as with the cultivated land in our study site where considerable tree abundance was retained (see Table 3). Therefore, the equal species richness and abundance of bird assemblage were similar in the cultivated land and forest in the present study can likely be due to the persistence of some forest species (due to retention of canopy trees as a coffee shade) and invasion by non forest species (due to canopy openings as a results of tree cutting) in the cultivated land (Gove et al., 2013; Addisu Asefa et al., 2017). As shown in the guild analysis, non-forest bird guild that included species that are typically not associated with forests, such as open land, shrub land, and open woodland habitat guilds, had significantly higher species richness in the cultivated land and *vice-versa* for forest specialists (Figure 3a-c). Specifically, many non forest species were only recorded in the cultivated land. Conversely, several forest specialists, such as Ethiopian endemic or near endemic Abyssinian Woodpecker, Yellow-fronted Parrot, Black-winged Lovebird, were either restricted to or had higher abundances in the forest habitat (Appendix 2). Thus, this absence of significant difference in the species richness and abundance of bird assemblage in the forest and cultivated land (converted forest) is not surprising and attributed to disturbance-induced replacement of those forest specialist species lost in the cultivated land habitat by non forest species gained from the surrounding open land in the cultivated land habitat (Coetzee and Chown, 2016; Addisu Asefa et al., 2017).

However, the equal species richness and abundance of bird assemblage in the cultivated land and forest should be interpreted cautiously, because the impact of habitat disturbance on biota can be manifested in a number of forms. Specifically, habitat change does not only affect the species richness and abundance of bird assemblages and/or specific guilds, but also affects other diversity components, such as assemblage species composition and taxonomic diversity (taxonomic composition) (Yosef Mamo et al., 2016). Our findings support this hypothesis in that both bird assemblage composition and taxonomic diversity were different among the three habitat types, suggesting that the primary impact of forest degradation (due to conversion to cultivation land) on birds appears to reduce species richness and abundance of forest specialist species; conversely, increased richness and

abundance of generalist species, change in assemblage composition; and taxonomic and functional homogenization of bird assemblage (Aerts *et al.*, 2008; Coetsee and Chown, 2016; Yosef Mamo *et al.*, 2016). Our results also suggest that future similar works should consider applying various diversity measures to reliably quantify the true patterns of diversity and the impacts of land use changes on biodiversity (Yosef Mamo *et al.*, 2016).

CONCLUSION

Our study thus highlights the need for proper protection of intact forest ecosystems if our aim is to maximize functional heterogeneity associated with tropical forest taxa. This is particularly true for global biodiversity hotspots, such as the Ethiopian Afromontane forests, where species endemism is typically high, but degradation is occurring at unprecedented rate (FAO, 2010). Nonetheless, the considerably high avian species richness in the cultivated land might also indicate the potential importance of disturbed habitats for bird conservation (Addisu Asefa *et al.*, 2017). This is particularly pertinent in developing Afrotropical countries such as Ethiopia (FAO, 2010), where natural forest conversion is expected to rise, the remaining primary forests will not survive or be inadequate to conserve birds. Under such scenario, the best opportunities to conserve forest species may exist in degraded habitats (Sushinsky *et al.*, 2013; Thomas, 2013; Buechley *et al.*, 2015).

In conclusion, changes in vegetation structure caused by human disturbance in our study area have led to considerable changes in bird richness, taxonomic diversity, abundance, and assemblage composition. Habitat disturbance has also negatively affected the richness and abundance of forest specialist species, which could lead to functional homogenization. It is, therefore, important to note that our study highlights the need for proper protection of intact forest ecosystems if our aim is to maximize overall (assemblage) and functional heterogeneity associated with tropical forest taxa. This is particularly true for global biodiversity hotspots, such as the Ethiopian Afromontane forests, where species endemism is typically high. Furthermore, the persistence of some forest specialist species in the cultivated land is an important understanding of the value and the need for better management (e.g., restoration and agroforestry practices such as retaining trees) of disturbed

habitats to maximize conservation targets. Corroborating the findings of several authors (e.g., Buechley *et al.*, 2015; Addisu Asefa *et al.*, 2017), this study supports the value of disturbed habitats for bird conservation, although such values may depend on the disturbance history and level as heavy and recurrent disturbances usually result to reduced habitat and food available to birds and thus to reduced bird diversity.

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Appendix 1. List of species recorded (indicated as 'x') in the cultivated land (CL), openland (OL) and intact forest (less disturbed forest; FR) of Hamuma Forest of the southwest Ethiopia and their broad habitat guild (F = forest specialist; NF = non forest). Nomenclature follows the checklist of BirdLife International (2020). Superscript letters in front of each species English name denotes: a highland biome; e = endemic; ne = near endemic. IUCN threat category: LC = least concern; NT = near-threatened; VU = vulnerable; CR = critically endangered (for detail see BirdLife International, 2020).

Order	Family	English name	Scientific name	OL	CL	FR	Habitat	IUCN
Galliformes	Numididae	Helmeted Guineafowl	<i>Numida meleagris</i>		x		NF	LC
Galliformes	Phasianidae	Chestnut-naped Francolin ^{a,ne}	<i>Pternistis castaneicollis</i>	x			NF	LC
Columbiformes	Columbidae	Lemon Dove	<i>Aplopelia larvata</i>	x	x		F	LC
Columbiformes	Columbidae	Red-eyed Dove	<i>Streptopelia semitorquata</i>		x	x	F	LC
Columbiformes	Columbidae	Ring-necked Dove	<i>Streptopelia capicola</i>	x	x	x	NF	LC
Columbiformes	Columbidae	Laughing Dove	<i>Spilopelia senegalensis</i>	x			NF	LC
Columbiformes	Columbidae	Blue-spotted Wood-dove	<i>Turtur afer</i>		x		F	LC
Columbiformes	Columbidae	Tambourine Dove	<i>Turtur tympanistria</i>		x		F	LC
Columbiformes	Columbidae	Namaqua Dove	<i>Oena capensis</i>		x	x	NF	LC
Cuculiformes	Cuculidae	Blue-headed Coucal	<i>Centropus monachus</i>	x	x	x	F	LC
Cuculiformes	Cuculidae	Klaas's Cuckoo	<i>Chrysococcyx klaas</i>	x	x	x	NF	LC
Cuculiformes	Cuculidae	African Emerald Cuckoo	<i>Chrysococcyx cupreus</i>	x	x		NF	LC
Passeriformes	Cuculidae	Red-chested Cuckoo	<i>Cuculus solitarius</i>			x	F	LC
Cuculiformes	Cuculidae	Black Cuckoo	<i>Cuculus clamosus</i>	x	x	x	F	LC
Gruiformes	Rallidae	Rouget's Rail ^{a,ne}	<i>Rougetius rougetii</i>		x		NF	NT
Gruiformes	Gruidae	Black Crowned Crane	<i>Balearica pavonina</i>	x	x		NF	VU
Ciconiiformes	Ciconiidae	African Woollyneck	<i>Ciconia microscelis</i>		x		NF	LC
Ciconiiformes	Threskiornithidae	African Sacred Ibis	<i>Threskiornis aethiopicus</i>		x	x	NF	LC
Ciconiiformes	Threskiornithidae	Hadada Ibis	<i>Bostrychia hagedash</i>	x	x	x	NF	LC
Ciconiiformes	Ardeidae	Black-headed Heron	<i>Ardea melanocephala</i>	x		x	NF	LC
Falconiformes	Accipitridae	African Harrier-hawk	<i>Polyboroides typus</i>		x	x	F	LC
Falconiformes	Accipitridae	Bateleur	<i>Terathopius ecaudatus</i>			x	NF	NT
Falconiformes	Accipitridae	White-headed Vulture	<i>Trigonoceps occipitalis</i>		x		NF	CR
Falconiformes	Accipitridae	Hooded Vulture	<i>Necrosyrtes monachus</i>	x	x	x	NF	CR
Falconiformes	Accipitridae	White-backed Vulture	<i>Gyps africanus</i>			x	NF	CR
Falconiformes	Accipitridae	Augur Buzzard	<i>Buteo augur</i>	x	x	x	NF	LC

Coliiformes	Coliidae	Speckled Mousebird	<i>Colius striatus</i>		x			NF	LC
Trogoniformes	Trogonidae	Narina Trogon	<i>Apaloderma narina</i>		x			F	LC
Bucerotiformis	Bucerotidae	Northern Ground-hornbill	<i>Bucorvus abyssinicus</i>	x	x	x		NF	VU
Bucerotiformis	Bucerotidae	Hemprich's Hornbill	<i>Lophoceros hemprichii</i>	x	x	x		NF	LC
Bucerotiformis	Bucerotidae	Silvery-cheeked Hornbill	<i>Bycanistes brevis</i>		x			F	LC
Coraciiformes	Meropidae	Blue-cheeked Bee-eater	<i>Merops persicus</i>		x	x		NF	LC
Coraciiformes	Meropidae	Little Bee-eater	<i>Merops pusillus</i>		x			NF	LC
Passeriformes	Alcedinidae	Malachite Kingfisher	<i>Corythornis cristatus</i>		x	x		NF	LC
Coraciiformes	Alcedinidae	Striped Kingfisher	<i>Halcyon chelicuti</i>	x		x		NF	LC
Coraciiformes	Alcedinidae	Woodland Kingfisher	<i>Halcyon senegalensis</i>		x	x		NF	LC
Piciformes	Lybiidae	Red-fronted Tinkerbird	<i>Pogoniulus pusillus</i>	x	x	x		F	LC
Piciformes	Lybiidae	Yellow-fronted Tinkerbird	<i>Pogoniulus chrysoconus</i>			x		F	LC
Piciformes	Lybiidae	Banded Barbet ^a	<i>Lybius undatus</i>	x	x	x		F	LC
Piciformes	Lybiidae	Double-toothed Barbet	<i>Pogonornis bidentatus</i>		x			F	LC
Passeriformes	Indicatoridae	Green-backed Honeybird	<i>Prodotiscus zambesiae</i>	x	x	x		F	LC
Piciformes	Indicatoridae	Greater Honeyguide	<i>Indicator indicator</i>			x		F	LC
Piciformes	Picidae	Nubian Woodpecker	<i>Campethera nubica</i>		x			F	LC
Piciformes	Picidae	Abyssinian Woodpecker ^{a,ne}	<i>Dendropicos abyssinicus</i>	x	x	x		F	LC
Piciformes	Picidae	Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	x		x		NF	LC
Psittaciformes	Psittacidae	Yellow-fronted Parrot ^{a,e}	<i>Poicephalus flavifrons</i>		x			F	LC
Psittaciformes	Psittacidae	Black-winged Lovebird ^{a,ne}	<i>Agapornis taranta</i>	x	x	x		F	LC
Passeriformes	Oriolidae	Ethiopian Black-headed Oriole ^{a,ne}	<i>Oriolus monacha</i>			x		F	LC
Passeriformes	Campephagidae	Red-shouldered Cuckooshrike	<i>Campephaga phoenicea</i>			x		F	LC
Passeriformes	Platysteiridae	Grey-headed Batis	<i>Batis orientalis</i>	x	x	x		F	LC
Passeriformes	Platysteiridae	Western Black-headed Batis	<i>Batis erlangeri</i>	x	x	x		F	LC
Passeriformes	Platysteiridae	Northern Puffback	<i>Dryoscopus gambensis</i>			x		F	LC
Passeriformes	Platysteiridae	Three-streaked Tchagra	<i>Tchagra jamesi</i>	x	x	x		NF	LC
Passeriformes	Platysteiridae	Black-crowned Tchagra	<i>Tchagra senegalus</i>	x				NF	LC
Piciformes	Platysteiridae	Tropical Boubou	<i>Laniarius aethiopicus</i>		x	x		F	LC
Passeriformes	Monarchidae	African Paradise-flycatcher	<i>Terpsiphone viridis</i>	x	x	x		F	LC
Piciformes	Laniidae	Red-backed Shrike	<i>Lanius collurio</i>		x			NF	LC
Piciformes	Laniidae	Grey-backed Fiscal	<i>Lanius excubitoroides</i>	x		x		NF	LC
Piciformes	Laniidae	Common Fiscal	<i>Lanius collaris</i>			x		NF	LC
Passeriformes	Corvidae	Pied Crow	<i>Corvus albus</i>	x				NF	LC
Passeriformes	Corvidae	Thick-billed Raven ^{a,ne}	<i>Corvus crassirostris</i>	x	x	x		NF	LC
Passeriformes	Corvidae	Fan-tailed Raven	<i>Corvus rhipidurus</i>	x	x	x		NF	LC
Passeriformes	Cisticolidae	Yellow-breasted Apalis	<i>Apalis flavida</i>	x				F	LC
Passeriformes	Cisticolidae	Bleating Camaroptera	<i>Camaroptera brachyura</i>	x	x	x		F	
Passeriformes	Cisticolidae	Stout Cisticola	<i>Cisticola robustus</i>		x			NF	LC

Passeriformes	Cisticolidae	Croaking Cisticola	<i>Cisticola natalensis</i>		x		NF	LC
Passeriformes	Cisticolidae	Pectoral-patch Cisticola	<i>Cisticola brunnescens</i>	x	x	x	NF	LC
Passeriformes	Cisticolidae	Tawny-flanked Prinia	<i>Prinia subflava</i>		x		NF	LC
Passeriformes	Locustellidae	Cinnamon Bracken-warbler	<i>Bradypterus cinnamomeus</i>			x	NF	LC
Passeriformes	Hirundinidae	Black Saw-wing ^a	<i>Psalidoprocne pristoptera</i>			x	NF	LC
Passeriformes	Hirundinidae	Lesser Striped Swallow	<i>Cecropis abyssinica</i>		x	x	NF	LC
Passeriformes	Hirundinidae	Mosque Swallow	<i>Cecropis senegalensis</i>			x	NF	LC
Passeriformes	Hirundinidae	Barn Swallow	<i>Hirundo rustica</i>		x	x	NF	LC
Passeriformes	Pycnonotidae	Common Bulbul	<i>Pycnonotus barbatus</i>		x	x	F	LC
Passeriformes	Phylloscopidae	Willow Warbler	<i>Phylloscopus trochilus</i>		x	x	F	LC
Passeriformes	Phylloscopidae	Brown Woodland-warbler ^a	<i>Phylloscopus umbrovirens</i>		x	x	F	LC
Passeriformes	Sylviidae	African Hill-babbler ^a	<i>Sylvia abyssinica</i>			x	F	LC
Passeriformes	Zosteropidae	Kaffa White-eye ^a	<i>Zosterops kaffensis</i>			x	F	LC
Piciformes	Leiotrichidae	White-rumped Babbler ^{ne}	<i>Turdoides leucopygia</i>	x	x	x	NF	LC
Passeriformes	Buphagidae	Red-billed Oxpecker	<i>Buphagus erythrorhynchus</i>	x		x	NF	LC
Passeriformes	Sturnidae	Red-winged Starling	<i>Onychognathus morio</i>			x	NF	LC
Passeriformes	Sturnidae	Greater Blue-eared Starling	<i>Lamprolornis chalybaeus</i>	x	x	x	NF	LC
Passeriformes	Turdidae	Abyssinian Ground-thrush ^a	<i>Geokichla piaggiae</i>			x	F	LC
Passeriformes	Turdidae	Abyssinian Thrush	<i>Turdus abyssinicus</i>	x		x	F	LC
Passeriformes	Muscicapidae	African Dusky Flycatcher	<i>Muscicapa adusta</i>			x	NF	LC
Passeriformes	Muscicapidae	Abyssinian Slaty-flycatcher ^{a,ne}	<i>Melaenornis chocolatinus</i>		x	x	NF	LC
Passeriformes	Muscicapidae	Northern Black-flycatcher	<i>Melaenornis edolioides</i>		x	x	NF	LC
Passeriformes	Muscicapidae	Rüppell's Robin-Chat ^a	<i>Cossypha semirufa</i>	x	x		F	LC
Passeriformes	Muscicapidae	Northern Wheatear	<i>Oenanthe oenanthe</i>			x	NF	LC
Passeriformes	Muscicapidae	Isabelline Wheatear	<i>Oenanthe isabellina</i>	x		x	NF	LC
Passeriformes	Nectariniidae	Olive Sunbird	<i>Cyanomitra olivacea</i>	x	x	x	F	LC
Passeriformes	Nectariniidae	Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>	x	x		NF	LC
Passeriformes	Nectariniidae	Tacazze Sunbird ^a	<i>Nectarinia tacazze</i>	x	x	x	NF	LC
Passeriformes	Nectariniidae	Variable Sunbird	<i>Cinnyris venustus</i>			x	F	LC
Passeriformes	Ploceidae	Red-cowled Widowbird	<i>Euplectes laticauda</i>	x	x	x	NF	LC
Passeriformes	Ploceidae	Fan-tailed Widowbird	<i>Euplectes axillaris</i>	x		x	NF	LC
Passeriformes	Ploceidae	Baglafaecht Weaver ^a	<i>Ploceus baglafaecht</i>			x	NF	LC
Passeriformes	Ploceidae	Spectacled Weaver	<i>Ploceus ocularis</i>			x	F	LC
Passeriformes	Ploceidae	Lesser Masked Weaver	<i>Ploceus intermedius</i>		x	x	NF	LC
Passeriformes	Ploceidae	Vitelline Masked Weaver	<i>Ploceus vitellinus</i>		x	x	NF	LC
Passeriformes	Ploceidae	Village Weaver	<i>Ploceus cucullatus</i>	x	x		NF	LC
Passeriformes	Estrildidae	Red-billed Firefinch	<i>Lagonosticta senegala</i>	x		x	NF	LC
Passeriformes	Estrildidae	Ethiopian Firefinch	<i>Lagonosticta larvata</i>			x	NF	LC
Passeriformes	Estrildidae	Red-cheeked Cordon-bleu	<i>Uraeginthus bengalus</i>			x	NF	LC

Passeriformes	Estrildidae	Common Waxbill	<i>Estrilda astrild</i>			x	NF	LC
Passeriformes	Estrildidae	Abyssinian Crimsonwing ^a	<i>Cryptospiza salvadorii</i>	x	x	x	NF	LC
Passeriformes	Estrildidae	Yellow-bellied Waxbill	<i>Coccyzygia quartinia</i>		x	x	NF	LC
Passeriformes	Estrildidae	Bronze Mannikin	<i>Spermestes cucullata</i>	x	x	x	NF	LC
Passeriformes	Estrildidae	Black-and-white Mannikin	<i>Spermestes bicolor</i>	x	x	x	NF	LC
Passeriformes	Viduidae	Pin-tailed Whydah	<i>Vidua macroura</i>		x	x	NF	LC
Passeriformes	Passeridae	Swainson's Sparrow ^a	<i>Passer swainsonii</i>	x	x	x	NF	LC
Passeriformes	Motacillidae	Abyssinian Longclaw ^{a,e}	<i>Macronyx flavicollis</i>	x	x	x	NF	NT
Passeriformes	Motacillidae	Western Yellow Wagtail	<i>Motacilla flava</i>		x		NF	LC
Passeriformes	Fringillidae	Abyssinian Citril ^a	<i>Crithagra citrinelloides</i>	x	x	x	NF	LC
Passeriformes	Fringillidae	Brown-rumped Seedeater ^a	<i>Crithagra tristriata</i>		x		NF	LC
Passeriformes	Fringillidae	Streaky Seedeater ^a	<i>Crithagra striolata</i>	x	x	x	NF	LC
Passeriformes	Fringillidae	Yellow-crowned Canary	<i>Serinus flavivertex</i>		x		NF	LC

Appendix 2. Results of similarity percentage analysis (SIMPER) of bird assemblages between each pair of the three habitat types in the Hamuma forest, southwestern Ethiopia. Values given are the percentage contribution of each species that made most (50% cumulative dissimilarity) to the differences between assemblages.

(a) open (OL) vs cultivated (CL)						
Species	OL Av.Abund	CL Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lesser Masked Weaver	2.69	5.69	6.9	0.58	7.64	7.64
Fan-tailed Widowbird	0.96	4.31	4.49	1.26	4.97	12.62
Black Saw-wing	2.38	1.81	4.24	0.6	4.7	17.32
Bronze Manikin	0	4.22	3.46	0.54	3.83	21.14
Speckled Mouse bird	0.73	2.09	3.24	0.59	3.59	24.73
Little Bee-eater	1.85	1.16	3.05	0.54	3.38	28.11
Black-and-White Manikin	2.23	0.81	2.86	0.47	3.17	31.28
Common Bulbul	1	1.44	2.81	0.58	3.11	34.4
Hadada Ibis	0.31	2.38	2.76	0.67	3.06	37.46
Tropical Boubou	1.42	2.31	2.75	0.95	3.05	40.51
Baglafaecht Weaver	0.5	1.81	2.66	0.73	2.95	43.46
Variable Sunbird	0.77	1.75	2.54	0.96	2.81	46.27
Gray-backed Camaroptera	0.65	1.91	2.26	0.96	2.5	48.78
Red-billed Ox Picker	0	1.63	2.11	0.49	2.34	51.12
(b) open (OL) vs Forest (FR)						
Species	OL Av.Abund	FR Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Abyssinian Oriole	0.19	5.47	7.16	1.19	8	8
Tropical Boubou	1.42	4.88	5.23	1.27	5.84	13.84
Red-chested Cuckoo	0.46	3.15	4.1	1.28	4.58	18.42

Black Saw-wing	2.38	1.74	3.7	0.86	4.13	22.55
Lesser Masked Weaver	2.69	1.12	3.31	0.47	3.7	26.25
Common Bulbul	1	2.35	3.23	1.06	3.61	29.86
Montane White-eye	0.15	2.03	2.79	0.68	3.11	32.98
Variable Sunbird	0.77	1.91	2.74	0.76	3.07	36.04
Gray-backed Camaroptera	0.65	2.26	2.74	0.99	3.06	39.11
Hadada Ibis	0.31	2.09	2.63	0.91	2.94	42.05
Silvery-checked Hornbill	0.73	1.85	2.57	1.01	2.88	44.92
Black-and-White Manikin	2.23	0.82	2.54	0.59	2.84	47.76
African Dusky Flycatcher	1.85	0.97	2.44	0.64	2.73	50.5

(c) Cultivated vs Forest

Species	Av.Abund (Cultivated)	Av.Abund (Forest)	Av.Diss	Diss/SD	Contrib%	Cum.%
Abyssinian Oriole	0.09	5.47	4.89	1.21	5.93	5.93
Lesser Masked weaver	5.69	1.12	3.89	0.46	4.72	10.65
Tropical Boubou	2.31	4.88	3.43	1.16	4.16	14.81
Bronze Manikin	4.22	1.47	3.42	0.68	4.15	18.96
Fan-tailed Widowbird	4.31	1	3.01	1.32	3.66	22.61
Red-chested Cuckoo	0.16	3.15	2.72	1.33	3.3	25.92
Black Saw-wing	1.81	1.74	2.47	0.72	2.99	28.91
Hadada Ibis	2.38	2.09	2.31	0.9	2.81	31.72
Common Bulbul	1.44	2.35	2.28	0.98	2.76	34.48
Speckled Mousebird	2.09	1.09	2.09	0.81	2.53	37.01
Variable Sunbird	1.75	1.91	1.95	0.87	2.37	39.38
Gray-backed Camaroptera	1.91	2.26	1.94	1.11	2.36	41.73
Montane White-eye	0.28	2.03	1.89	0.75	2.29	44.03
Little Bee-eater	1.16	1.12	1.69	0.57	2.06	46.08
Silvery-checked Hornbill	0.56	1.85	1.66	0.95	2.02	48.1
Baglafaecht Weaver	1.81	0.41	1.63	0.82	1.98	50.08