Effects of forest fragmentation on bird communities in NW Ethiopia

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Abstract

Anthropogenic disturbance regimes in areas that were once large continuous habitats have been major drivers of habitat fragmentation and loss which in turn form the largest worldwide threat to avian biodiversity. Studies suggest that functional trait based approaches provide better understanding of fragmentation effects on ecological processes in human-modified landscapes. However, research on these thematic areas is limited in many tropical regions, such as Ethiopia. In this study, we evaluated sensitivity of bird communities and functional groups to fragmentation processes in Ethiopia. Standard point counts were used to survey birds in 16 remnant forest patches of variable sizes and degrees of isolation. The information theoretic model selection approach was used for precise understanding of avian functional group responses to habitat loss and fragmentation. Results showed strong impacts of forest loss and fragmentation on forest specialists, insectivores, frugivores, open nesters, understorey nesters and resident birds. Protection and restoration of the remnant forest patches may help mitigate the negative effects of fragmentation on such specialist bird functional groups.

Keywords: Avian Ecology; Conservation; Diversity; Functional group; Patch isolation; Patch size

1. Introduction

Tropical forest ecosystems cover large areas representing the richest ecosystems globally (Giam *et al.* 2012). They offer a range of services to humankind besides their role in supporting other organisms belonging to the system. Unfortunately, these resources are continuously declining at unexpectedly high rates because of human-induced and natural factors (Bradshaw *et al.* 2009; FAO. 2011). The most notable impacts are, however, anthropogenic disturbances and conversion to other land use types and related activities (Bradshaw *et al.* 2009). Such disturbances have repeatedly been reported as the major drivers of forest degradation, loss and fragmentation (Ewers *et al.* 2006; Fahrig 2003).

Forest fragmentation, originally conceived from the theory of Island Biogeography (MacArthur & Wilson 1967), has been characterized by reduced patch size and increased patch isolation, each of which has distinctive impacts on biodiversity (Fahrig 2003; Martensen *et al.* 2008; Sekercioglu 2007; Sekercioglu & Sodhi 2007). For instance, it is broadly understood that certain avian parameters like density, abundance, richness and diversity are usually positively correlated with remnant habitat amount in a fragmented landscape (Fahrig 2003). This means that as fragmentation keeps on reducing habitat amount, though the effects may vary from species to species or among functional groups, one can generally expect reduction in avian species richness, density, abundance, diversity or other parameters like mobility (e.g., of forest specialists). This can affect species persistence, population dynamics and ecological interactions within and among avian communities thus leading to local extermination of avian species and functional groups in small fragments (Lens *et al.* 2002; Sekercioglu *et al.* 2004).

The abovementioned and other measures of avian biodiversity are also negatively impacted by increasing patch isolation in fragmented landscapes (Van Houtan *et al.* 2007).

Patch isolation indicates the amount of habitat loss surrounding a patch in fragmented landscapes and is usually estimated or measured as the nearest neighbor distance or nearest neighbor patch area (McGarigal *et al.* 2005). Larger nearest neighbor distances indicate higher degrees of patch isolation or larger amounts of habitat loss in a landscape. The fundamental thought behind the idea of isolation is that it hinders gene flow among populations by limiting for instance mobility of avian species among habitat patches in human-modified landscapes (Herrera & Garcia 2010; Van Houtan *et al.* 2007). Numerous studies thus have shown negative consequences of habitat isolation on various attributes of avian species such as species richness and abundance (Bailey *et al.* 2010; Manu *et al.* 2007), community composition (Zurita & Bellocq 2010), landscape occupancy (Mortelliti *et al.* 2010), and dispersal ability or mobility and functional connectivity (Awade & Metzger 2008; Sekercioglu 2007; Stratford & Robinson 2005). However, some studies (Dorp & Opdam 1987; Ferraz *et al.* 2007) found variable responses by different avian species or communities to the extent of patch isolation.

Thus, forest loss and forest fragmentation (Fahrig 2003) have been widely recognized for their significant impacts on avian biodiversity. Their effects are especially manifested in sedentary and dietary and forest specialist bird species (Sekercioglu 2007; Sodhi *et al.* 2010). Also, forest loss and fragmentation have been shown to have adverse effects on large-bodied and functionally specialized bird species like mixed species flock participants and army ant followers (Clavel *et al.* 2011; Sigel *et al.* 2010; Sodhi *et al.* 2004).

Most past fragmentation studies have used species richness or abundance of entire bird communities without emphasis for functional traits (Castelletta *et al.* 2005; Telleria *et al.* 2003; Watson *et al.* 2005). Fragmentation effects are, however, easier to generalize or predict if species functional traits are used when evaluating bird sensitivity to fragmentation processes (Kennedy *et al.* 2011; Kennedy *et al.* 2010; Sigel *et al.* 2010; Vetter *et al.* 2011).

However, data are generally limited on the use of functional traits to assess the effects of forest loss and fragmentation. Although many studies exist on fragmentation effects on species richness and abundance, fragmentation researchers are calling for more work on functional trait based approaches (Tscharntke *et al.* 2008; Vetter *et al.* 2011; Wellstein *et al.* 2011). Functional traits are defined as ‘measureable characteristics of organisms with demonstrable links to the organism’s fitness’ (McGill *et al.* 2006; Vandewalle *et al.* 2010). Functional traits are easily comparable across species and hence are ideal for ecological generalization and prediction at the community level as well as for conservation prioritization (McGill *et al.* 2006).

Environmental changes due to forest loss and fragmentation are highly likely to affect bird dispersal ability (Kennedy & Marra 2010) and resource use (Lehouck *et al.* 2009) as well as the role of birds in ecosystem functioning such as pollination, seed dispersal and insect pest controls amongst others. These changes eventually impair proper ecosystem functioning, which in turn compromises ecosystem benefits enjoyed by humankind. The mechanisms behind these could be better understood by investigating the associated responses of bird functional traits or groups (Petchey & Gaston 2006) because functional traits of species and communities are important indicators of biodiversity (Vandewalle *et al.* 2010) that could provide better information for species conservation. In particular, traits such as habitat use, dietary guild, foraging strata, nest type, nesting strata and flocking guild may be better predictors of species responses to fragmentation processes in human dominated landscapes (Kennedy *et al.* 2010; Sigel *et al.* 2010; Vetter *et al.* 2011).

Some functional trait-based studies have been published recently (Luck *et al.* 2013; Newbold *et al.* 2013; Sekercioglu 2012a). However, most of these are based on reviews of global databases and are mostly addressing questions other than fragmentation *per se*. There are a few exceptions (Ding *et al.* 2013; Hernandez *et al.* 2013; Kennedy *et al.* 2011; Kennedy *et al.* 2010; Sigel *et al.* 2010; Vetter *et al.* 2011). For instance, Ding et al. (2013) analyzed the impacts of patch size and isolation on bird functional diversity and functional evenness in China. Kennedy et al. (2010) assessed the role of landscape matrix and species traits in mediating responses of Neotropical birds to fragmentation processes. Sigel et al. (2010) assessed the responses of bird functional groups in Central American reserves. Nevertheless, these studies focused in regions other than tropical Africa, an immense species diverse but relatively undiscovered region (Sekercioglu 2012b). Thus we believe that our study will have a valuable contribution especially from a little-studied Afrotropical region, Ethiopia, to existing knowledge in this developing theme.

In this study, we sought to understand how various bird functional groups respond to remnant forest-habitat amount or patch size and isolation in fragmented landscapes in North-western (NW) Ethiopia. This region contains remnant patches of Afromontane rainforest interspersed with agricultural or range lands. To date, there are no published studies of the effects of forest fragmentation on bird communities in the region. Here we evaluated the hypothesis that forest loss and fragmentation considerably affect bird functional groups. We investigated these effects on habitat use, dietary guilds, nest type, nesting strata, foraging strata, flocking guilds and residency status. Specifically, we evaluated whether a) habitat or food specialist bird species are more affected by fragmentation than generalist species; b) army ant-followers and mixed species flock participants are more sensitive to fragmentation than non-flocking birds; c) open and cavity nester bird species are more affected by fragmentation than closed nesters; d) understorey or ground nesters/foragers are more sensitive to fragmentation than canopy/sub-canopy nesters/foragers; e) large-sized birds are more sensitive to fragmentation than medium and small-sized birds; f) resident birds are more sensitive to fragmentation than non-resident birds.

2. Methods

2.1 Study sites

This study was conducted in highly fragmented remnant forest patches of Guangua District in Awi Zone, Gojjam, Amhara National Regional State, North-western Ethiopia (Figure 1). Unlike forest remnants in some areas of southwestern Ethiopia, the remnant forest patches in this region are not cultivated for coffee production. The region has been recognized by BirdLife International as one of the important bird areas (BirdLife_International 2012). Over the last couple of centuries, NW Ethiopia has experienced extreme levels of forest destruction due to conversion to agricultural land uses, fuel wood production and timber extractions (Teketay 2004). This has resulted in loss of the majority of the natural forests in this region and today only remnant forest patches can be seen surrounded by a matrix of agricultural land or pasture. The study sites are located at about 10°45’-11°04’ N and 36°25’-36°48’ E. This region has a tropical climate with the major rainy season extending from June to October. Mean annual rainfall is about 1500 mm whereas mean annual temperature ranges between 19 °C and 30 °C. The humid Afromontane remnant forest patches of this area range in their altitudinal distribution between approximately 1750 and 2390 m. Remnant forest patches range in size from 2 ha to 1388 ha and their nearest neighbor distances range from 103 m to 540 m (Table 1). The canopy layer of these remnant forest patches is mostly dominated by *Albizia gumifera* and sometimes *Prunus africana*, *Celtis africana*, *Millettia ferruginea*, *Ficus toninge*, *Ficus vasta*, and *Croton macrostachyus*. Pasture, bush thickets and cultivation of crops such as millet, corn, tef (*Eragrostis tef*), wheat, barley and rarely beans form the major land use patterns in the matrix area surrounding forest patches. Also, remnant scattered individuals of tree species such as *Prunus africana*, *Millettia ferruginea*, *Ficus vasta*, *Croton macrostachyus* and *Albizia gumifera* are frequently seen in the matrix area.

2.2.Imagery, patch metrics computation and sampling

We used high resolution landsat/spot images accessed from Google Earth products (2006 satellite imagery) to digitize remnant forest patches in the study area. We converted digitized images into kml files and imported them into Arc-GIS (ArcMap10) software (ESRI Inc.) to process and convert them into raster images and then to ASCII file formats. We verified accuracy of these data by evaluating matches with ground recorded data i.e., GPS readings of latitude and longitude. We used the output from ArcMap10 (ASCII file) as an input file in Fragstats software version 3.3 (McGarigal *et al.* 2002) and computed relevant patch metrics in this software including patch area (ha), core area (ha), radius of gyration (m), nearest neighbor distance (m) and shape index. Core area represents forest interior area after eliminating a user-specified forest edge depth. We considered a fixed edge depth of 25 m for the core area computation. Radius of gyration (gyrate) indicates the extent of a forest patch and is ‘equal to the mean distance between each cell in the patch and the patch centroid’. Shape index is a ‘diversity index based on shape for quantifying habitat edge’ (*sensu* Patton 1975 cited in McGarigal et al. 2002). It ‘measures the overall complexity of patch shape compared to a standard shape (square or almost square) of the same size’ (McGarigal *et al.* 2002). We evaluated neighbor distances from the centre of each patch within a 25 km search radius. Table 1 shows further details of the sixteen forest patches sampled in this study.

2.3.Bird Survey

Standard point counts (n=125) were used to survey birds in the 16 forest patches in August and September 2010. This is the season with highest rainfall in the study region and resources are expected to be abundant, which may encourage breeding activities in resident birds in particular. Point count stations were established along transect lines, representing different microhabitats with respect to canopy cover, upper canopy composition and ground cover.

Each station was visited only once. Canopy cover was visually estimated for each station as the proportion (%) of sky obscured by vegetation at the canopy layer (Newton 2007). We marked each station using colored tapes and took readings of elevation and geographical position using a handheld Garmin GPS. To minimize duplication of sightings, stations were kept at least 150 m apart on the transect line.

Counts were performed for a 10 minute period in a radius of 30 meters at each point count station (area ~ 0.283 ha). The order of counts was randomized to minimize biases arising from sampling a site at a specific weather condition. Both visual and auditory cues were used to record bird species and count the number of individuals of each species. Maximum care was taken to minimize potential bird flushing during each count. Most counts were performed in good weather conditions and during times of high bird activities i.e., 6:00 AM to 10:30 AM. However, to include roosting birds, at least one point count for each patch was done in the late afternoon between 4:00 PM and 6:00 PM. To avoid bias arising from different observer inconsistencies, a single observer did all point counts during the survey. Counts were stopped when the number of bird species seen only once in a site was equal to or less than the number seen only twice (Bibby 2004). This approach has been used by some authors (Aerts *et al.* 2008) to check for saturation of species counts. It assumes that species counts in a site can fairly represent actual species richness when the number of bird species seen only once is equal to or less than the number seen only twice.

2.4.Functional group assignment

We recorded the number of individuals observed of each species during the counts but inferred their functional attributes after the counts. To assign species to functional groups, We used information from the literature, in particular, The Birds of Africa volumes I-VII (Brown *et al.* 1982; Fry *et al.* 1988, 2000, 2004; Keith *et al.* 1992; Urban *et al.* 1986, 1997) and previous work on the birds of semi-forest coffee systems in south-western Ethiopia (Yineger *et al.* unpublished data). For instance, We grouped bird species based on their habitat preferences as 1) forest specialists – species known to occur in forest habitats only; or 2) forest-associated – generalist species found in forest as well as some other types of habitats; or 3) Non-forest – species that prefer non-forest habitats. Based on the major diets of bird species, we assigned dietary guilds as 1) Frugivores, 2) Insectivores, 3) Granivores, 4) Nectarivores, and 5) Carnivores/scavengers. We assigned feeding strata according to Yineger *et al.* (unpublished) as 1) Canopy/sub-canopy, 2) Understorey, 3) Air, and 4) Multistrata. We defined nest types in three categories (Sigel *et al.* 2010): 1) closed nests are ball or oval nests with side entrances, or retort-shaped with long entrances; 2) cavity nests are burrow nests formed in tree stems or in ground and 3) open nests are nests that allow unobstructed free entrance and exit. We assigned nesting strata following Sigel *et al.* (2010): 1) Canopy/subcanopy, 2) Understorey, and 3) Ground. We grouped birds based on their flocking guilds (after Sigel *et al.* 2010): 1) ant-followers – birds following army ant crowds to feed on flushed arthropods   2) mixed – birds frequently flocking with other species 2) single – birds flocking with their own species only 3) none – birds which do not flock with their own or other species.

We assigned residency status as 1) intra-Afrotropical migrant, 2) palearctic migrant, 3) partial migrant - in which some part of the population migrates, 4) presumed resident - indicates apparent breeding, but not proven, and 5) resident - apparently always present and breeding in the area (Ash & Atkins 2009). We recorded body size (bill to tail length) data from bird guide books (Redman *et al.* 2009; Zimmerman *et al.* 1999) and categorized body size classes as Large ≥ 15 cm, Medium 6-15 cm, and Small < 6 cm.

2.5.Data Analysis

Species richness and diversity statistics were determined in EstimateS8.2.0 (Colwell 2006). The first order jackknife estimator of bird species richness and Shannon Diversity Index were used to compare the overall differences among remnant forest patches based on patch size and isolation. We used the student's t-test to evaluate differences in species richness and Shannon Diversity Index (H') among the small and large patches. Non-metric multidimensional scaling (MDS) was run in Primer software (version 6.0) (Primer-E Ltd) to assess the degree of similarity in species composition between patch size and isolation groups. Further, two-way nested analysis of similarity (ANOSIM) i.e., patches nested within size and isolation groups, was run in Primer 6 (Primer-E Ltd) to evaluate similarities in species assemblages between each of these groups. All other analyses were performed after excluding non-forest and flyover birds. Eighty-nine bird species were retained for final analyses. For each functional group, the mean number of individuals of a bird species per point survey per patch was used in generalized linear models (PROC GLM and PROC GLIMMIX in SAS 9.2) to minimize bias arising from unbalanced sample sizes between large and small forest patches when evaluating the magnitude and direction of bird community and functional group sensitivity to fragmentation processes.

We employed the information theoretic (Burnham & Anderson 2002) model selection approach for a more precise understanding of avian functional group responses to habitat loss and fragmentation. We initially attempted to use the log-transformed patch metrics i.e., patch area, core area, radius of gyration, nearest neighbor distance and shape index as predictor variables in the candidate model sets. We did the log-transformation for these variables in order to approximate normality because the untransformed data showed high deviations from the normal distribution. We constructed a Q-Q plot for each variable before and after transformation to check for improvements. The transformation certainly helped to approximate normality. However, we detected significant correlation among all these parameters (Figure 2). We also computed the variance inflation factor (VIF) through multiple regression analysis in SAS 9.2 (SAS Institute Inc.) to check for the presence of multicollinearity among the predictor variables. All parameters except one i.e., 'nearest neighbor distance' had a very high degree of inflation (VIF >10). As a result, we employed principal components analysis to minimize multicollinearity and obtain more independent predictor variables. This approach is also used by other researchers (Mortelliti *et al.* 2010) (Mortelliti *et al.* 2011) to avoid multicollinearity problems. Predictor variables obtained after interpretation of outcomes of the principal components analysis include habitat amount and isolation or habitat loss.

2.5.1. Model selection

We used canopy cover and the principal components scores of the first and second axes as continuous predictors of bird abundance for selected bird functional groups in the generalized linear mixed model (PROC GLIMMIX in SAS 9.2). As canopy cover was the only data we have to represent habitat condition, we included this variable in the models without subjecting for principal component analysis. All possible combinations of the three variables i.e., forest-habitat amount, isolation and canopy cover were considered to construct the candidate model sets. The number of point counts (npc) per patch was always fitted in the models to account for potential biases in our sampling efforts. The most heavily parameterized model in each functional group was tested for spatial autocorrelation using the PROC VARIOGRAM procedure in SAS 9.2. Moran's we values in all these analyses were non-significant (p>0.05). In the PROC GLIMMIX procedure, we chose the maximum likelihood estimation technique based on the quadrature approximation method. We also chose a lognormal response distribution with an identity link function. As such, the variance function was set to default options with a diagonal variance matrix. Parameter estimates and Type III tests of fixed effects were obtained by adding the term 'solutions' in the model options of the syntax used for analysis. The model convergence criterion was satisfied for each analysis. The maximum number of estimable parameters (k) in the models was six. Model fit was checked by examining ΔAICc values for each candidate model set.

Model selection was performed using the 2nd order bias correction for Akaike's Information Criterion (AICc) that corrects biases due to small sample sizes when $n/k < 40$ (Burnham *et al.* 2011); where n represents sample size and k represents the number of estimable parameters. AICc values were directly taken from the PROC GLIMMIX analysis output for each model. These values were arranged in ascending order from the lowest to the highest and differences from the lowest AICc value were computed to facilitate ranking of models according to the Kullback-Leibler information loss (Burnham & Anderson 2002) when approximating full reality given the data. The best approximating model given the candidate model set is the one that minimizes this information loss i.e., the one with the lowest ΔAICc value (Burnham & Anderson 2002; Burnham *et al.* 2011; Symonds & Moussalli 2011). Given the data and the candidate model sets, the relative likelihood of each model *li*, the probability of each model *wi*, and evidence ratios ER, were computed according to Burnham et al. (2011) and Symonds and Moussalli (2011).

$$li = L(gi/x) = \exp(-1/2 * \Delta i)$$

$$ER = \exp(-1/2\Delta best) / \exp(-1/2\Delta i)$$

$$wi = \exp(-1/2\Delta i) / \Sigma \exp(-1/2\Delta r)$$

In all, we evaluated nine alternative hypotheses explaining bird abundance for each selected functional group. Detailed information about these alternative hypotheses and related computations is shown in Supplementary Tables 1 and 2.

Finally, we tested for correlation among selected functional groups to check for disadvantageous combinations of functional groups that may increase their vulnerability due to habitat fragmentation. Specifically, we tested for correlation among forest specialists, which are insectivores, feed in the understory, have open nests and are resident birds. We found that each of these functional groups is sensitive to fragmentation (see results section). When there is strong correlation among these groups, we conclude that bird species belonging to these groups have been more vulnerable to fragmentation because of such disadvantageous combinations.

3. Results

The test for correlation among initially considered predictor variables was significant (Figure 2). The principal components analysis used to minimize the multicollinearity problem identified five independent components each of which is a linear combination of the original variables (see eigenvalues and eigenvectors in Supplementary Tables 3 & 4, respectively). The first component explained over 95% of the total variance while the second component explained only about 3% of the total variance (Supplementary Table 3). The first axis had the highest loadings on core area, radius of gyration and patch area whereas the second axis had the highest loading on 'nearest neighbor distance' (Supplementary Table 4). Consequently, we interpreted the first axis (Prin1) as remnant forest-habitat amount whereas the second axis (Prin2) as forest-habitat isolation or loss. Other axes were difficult to interpret and were omitted from subsequent statistical analyses.

3.2.1. Species diversity and community composition

A total of 2356 individuals of 102 species (Supplementary Table 5) were recorded, of which 89 species were retained for analyses. The mean first order jackknife estimate of species richness for the overall bird data was higher in large than small forest patches and less-isolated than isolated patches (Figure 3) but the differences were not statistically significant (t-test: large vs Small: df=14, t=1.3, *p*=0.2151; Isolated vs less-isolated: df=14, t=-0.85, *p*=0.4095). Similarly, the mean Shannon Diversity Index (H') was higher in large than small patches and in less-isolated than isolated patches (Figure 3) with no statistically significant difference (t-test: large vs Small: df=14, t=1.35, *p*=0.1989; Isolated vs less-isolated: df=14, t=-1.4, *p*=0.1837). The mean bird abundance of a species per point survey per patch ranged from 1 to 4. The summary of mean raw species richness per patch and mean bird abundance per patch for each functional group is shown in Figures 4 and 5, respectively.

Non-metric multidimensional scaling (MDS) analysis of the overall data in Primer software (version 6.0) (Primer-E Ltd) reflected considerable overlap in species composition between large and small forest patch groups (Figure 6). Further, two way nested analysis of similarity (ANOSIM) i.e., patches nested within size groups (i.e., large vs small) showed significant difference between patches (Global R=0.215, *p*=0.001, permutations=999) but not between size groups (Global R=0.081, *p*=0.082, permutations=999) indicating similarities in species assemblages between size groups. Species composition showed significant variation between patches (ANOSIM Global test, R=0.212, *p*=0.001, permutations=999) or between isolation groups (i.e., isolated vs less-isolated) (R=0.185, *p*=0.002, permutations=999) on nested analysis of patches within isolation groups.

3.2.2. Fragmentation sensitivity of bird functional groups

2.3.2.1. Forest specialists

For forest specialists, the most heavily parameterized model i.e., model 3 (Intercept + Amount + Isolation + Canopy cover + npc) had the highest chance (*wi*=0.64) of being the best approximating model describing the abundance data from among the nine alternative models (Supplementary Table 1). In the PROC GLIMMIX output of this model, the estimate for the parameter ‘forest-habitat amount’ was positive (β=0.021, SE=0.008) whereas the estimate for ‘isolation’ was negative (β=-0.108, SE= 0.0316) indicating that the mean bird abundance per point survey per patch was directly related with forest-habitat amount but inversely related with isolation or forest loss (Supplementary Table 2). This model also incorporated canopy cover, which was directly related to bird abundance. The remaining eight models for forest specialists except model 4 were less likely and hence received less support from the data. For forest-associated species, the most heavily parameterized model had the highest probability (wi=0.90).

2.3.2.2. Dietary guilds

Only insectivores and frugivores had sufficient sample sizes for analysis. The top ranked model for insectivores was the model that contained all combinations of intercept, npc, canopy cover, forest-habitat amount and isolation. This model had an 83% probability of being the best model describing insectivore abundance in the remnant forest patches of NW Ethiopia (Supplementary Table 1). Similar to forest specialists, the parameter estimate was positive for forest-habitat amount (β=0.012, SE=0.005) and canopy cover (β=0.001, SE=0.000) but negative for isolation or forest loss (β=-0.066, SE=0.020) (Supplementary Table 2).

In frugivores, however, the top ranking model had a probability of only 59% and was closely followed by the 4th model, which had a ΔAICc value of 1.32 and probability of 31 % (Supplementary Table 1). Even so, the observed support for the top ranked model was about 2 times, 9 times, and 47 times than that of the 4th, 8th and 6th models, respectively (Supplementary Table 1). Parameter estimates based on the top ranking model again demonstrated a direct relationship of the mean bird abundance per point survey per patch with forest-habitat amount and canopy cover but an inverse relationship with forest loss (Supplementary Table 2).

2.3.2.3. Nest types

The best approximating model to predict abundance of birds, which use an open nest type, is the one with all additive terms (*wi*=0.92). This model is 20 and 38 times more likely than the 8th and 4th models, respectively (Supplementary Table 1). Analysis of abundance data for open nesters based on this top ranked model using the PROC GLIMMIX procedure showed a direct relationship with the predictor variables forest-habitat amount (β=0.014, SE= 0.005) and canopy cover (β=0.001, SE= 0.000) whereas an inverse relationship with forest loss (β=-0.076, SE= 0.022) (Supplementary Table 2).

Similarly, for cavity nesters, the model with all additive terms was ranked first with a probability of 39%. This model was, however, more or less equally likely to the 4th model. The relationship between mean bird abundance per point survey per patch and predictor variables were similar to open nesters (Supplementary Table 2). Contrary to open nesters, however, the top ranked model for closed nesters received little support from the data (*wi*=0.30) (Supplementary Table 1).

2.3.2.4. Other functional groups

The most heavily parameterized model that incorporates intercept, npc, canopy cover, forest-habitat amount and isolation was also the top ranked model with a high probability of being the best model predicting bird abundance in other functional groups including understorey nesters (*wi*=0.68), canopy-subcanopy nesters (*wi*=0.64), understorey feeders (*wi*=0.62), canopy-subcanopy feeders (*wi*=0.70), medium-sized birds (*wi*=0.72) and resident birds (*wi*=0.98) (Supplementary Table 1). For these functional groups, the slopes in the respective models showed that the mean bird abundance per point survey per patch increased with increased remnant forest-habitat amount and canopy cover but decreased with increased forest-habitat isolation or loss (Supplementary Table 2).

The top ranking models for large-sized birds (*wi*=0.33), army ant-followers (*wi*=0.24) and mixed species flock participants (*wi*=0.46) had a relatively low weight indicating existence of uncertainties in the model selection procedures for these functional groups (Supplementary Table 1).

Results of correlation analyses among selected fragmentation-sensitive functional groups (i.e., forest-specialists, insectivores, understory-feeders, open cup-nesters, and resident birds) were significant (Figure 7). Thus, bird species, which are members of these functional groups, are expected to be more fragmentation-vulnerable than others.

4. Discussion

We employed a functional trait-based approach to assess fragmentation effects at the community level, an area that is not rigorously researched even in other regions but is critical for evaluating the status of ecosystem functioning and for making management decisions. We show strong impacts of remnant habitat amount and isolation on abundance of selected bird functional groups. Highly significant correlations were observed among forest-specialists, insectivores, understory-foragers, open-nesters and residents (Figure 7) suggesting that these groups have been especially vulnerable to fragmentation perhaps because of their disadvantageous functional combinations, i.e., when the same set of species become members of these sensitive functional groups. This result indicates that bird species belonging simultaneously to all these functional groups could serve as indicators for conservation priorities. We also found higher species richness and diversity for the large and less-isolated remnant forest patches than the small and isolated patches.

4.1.Fragmentation sensitivity of bird functional groups

4.1.1. Habitat use

Forest loss and fragmentation often differentially affect bird species in accordance with their forest-habitat use capabilities (Devictor *et al.* 2008; Pandit *et al.* 2009). For example, 'forest-specialist' birds are often reported as the most vulnerable groups of birds due to their high sensitivity to forest fragmentation, degradation and loss (Devictor *et al.* 2008). In contrast, some other bird species may use forest interiors for activities like breeding but are generally prepared to disperse to forest edges, disturbed sites and non-forest areas for foraging and other activities. Such generalist species, defined in this study as 'forest-associated birds', do not entirely depend on forest interiors and hence are expected to be relatively more resilient to forest fragmentation, degradation and loss (Devictor *et al.* 2008). In fact, many studies in other regions have documented that forest loss and fragmentation cause more significant reductions in abundance of forest-specialist birds than generalists (Kennedy *et al.* 2010). As predicted, we found very strong impacts of forest loss and fragmentation on forest-restricted species i.e. reduction in the mean bird abundance per point survey per patch with increasing patch isolation and with decreasing forest-habitat amount and canopy cover (Supplementary Tables 1 and 2). Unexpectedly, this pattern was similar in forest-associated species, implying that they were also sensitive to forest fragmentation (Supplementary Table 1). Vetter et al. (2011) found a similar result from a quantitative analysis of previously published studies. The adverse effect on forest-associated species let alone forest-restricted species implies that the study region has reached an extreme state of forest loss and fragmentation and as a result the surviving bird communities may soon vanish from this region unless urgent rehabilitation efforts are put in place.

4.1.2. Dietary guilds

Dietary guild is reported as one of the best predictors of avian responses to fragmentation processes (Kennedy *et al.* 2010; Vetter *et al.* 2011). This is because forest loss and fragmentation may change the abundance and quality of resources in fragmented landscapes and as a consequence may affect species ability to acquire and use those resources (Kennedy *et al.* 2010; Lehouck *et al.* 2009). As expected, especially for insectivores, the mean bird abundance per point survey per patch decreased with decreasing remnant forest-habitat amount and canopy cover but with increasing patch isolation or forest loss (Supplementary Tables 1 and 2). This result is in agreement with findings in other regions (Kennedy *et al.* 2010; Sigel *et al.* 2010; Stouffer *et al.* 2009; Tscharntke *et al.* 2008; Uezu & Metzger 2011) which have reported reduced insectivore abundance because of forest fragmentation processes. The vulnerability of insectivores to fragmentation has been increasingly recognized as a prevalent pattern throughout the tropics, which could partly be attributable to their ‘reluctance to cross unsuitable habitat’, reduced prey abundance or microhabitat loss (Kennedy *et al.* 2010; Sigel *et al.* 2010).

Likewise, we found adverse effects of forest loss and fragmentation on the mean abundance of frugivores per point survey per patch. This finding is also consistent with studies elsewhere (Giraudo *et al.* 2008; Kennedy *et al.* 2010; Martensen *et al.* 2008; Vetter *et al.* 2011), which reported high sensitivity of frugivores to forest loss and fragmentation. The increased sensitivity of frugivores may be credited to reduced fruit availability following forest loss and fragmentation (Vetter *et al.* 2011).

Unlike the cases of insectivores and frugivores, we did not find evidence for fragmentation impacts on granivores (Supplementary Table 1). Other studies also reported either neutral or even positive effects of fragmentation on granivores (Giraudo *et al.* 2008; Kennedy *et al.* 2010). The insensitivity of granivores may be explained by their preferences to forage mainly in forest edge habitats, disturbed sites and open areas including nearby croplands containing isolated trees (Giraudo *et al.* 2008; Hanspach *et al.* 2011). The relatively small sample sizes of nectarivores and carnivores-scavengers prohibited me from considering model selection procedures for these functional groups.

4.1.3. Nest types

Nest type is another good predictor of avian sensitivity to forest fragmentation processes (Matlock & Edwards 2006; Newmark & Stanley 2011; Poulin & Villard 2011). The relative risk of avian nest predation and associated bird sensitivity to forest fragmentation depend on the types of nests used by birds (Huhta *et al.* 1998; Newmark & Stanley 2011). Our results showed high impacts of forest loss and fragmentation on the mean abundance per point survey per patch of open-nesters but negligible impact on closed nesters (Supplementary Tables 1 and 2). In fact, open cup-nests have been frequently reported as the most predated nests as shown elsewhere from experiments based on artificial and real nests (Huhta *et al.* 1998; Matlock & Edwards 2006; Newmark & Stanley 2011) . In other words, open cup-nesters are more vulnerable and fragmentation sensitive than closed nesters because closed nesters somehow benefit from protection and can better hide themselves from potential predators (Matlock & Edwards 2006). Obviously, the vulnerability of open cup-nesters may be an outcome of structural simplification of forest canopies and shrub layers as a consequence of forest loss and fragmentation thus easily exposing open cup-nesters to nest predators (Huhta *et al.* 1998).

4.1.4. Nesting and feeding strata

Birds that prefer understorey and canopy strata for nesting and foraging activities are usually considered sensitive to forest fragmentation (Barlow *et al.* 2006; Kennedy *et al.* 2010; Ribon *et al.* 2003; Sigel *et al.* 2010; Uezu & Metzger 2011). Our findings support this prediction in that forest loss and fragmentation had strong detrimental effects on the abundance of understorey nesters and feeders. The likely explanations are 1) in fragmented landscapes, the risk of nest predation by mammals and reptiles is usually greater in birds nesting at lower heights than those nesting at higher heights (Knutson *et al.* 2004; Lloyd *et al.* 2005); 2) loss of canopy trees and structural simplification of vegetation as a consequence of fragmentation affects resource availability and results in reduced canopy cover, which together could cause the decline in abundance of understorey and canopy nesters/foragers (Kennedy *et al.* 2010). However, our study did not necessarily identify the differential effects of understorey conditions on tropical bird response. That is, a given patch might have very different habitat attributes for different bird species depending on their use of understorey conditions. Thus, understorey condition is a variable potentially affecting bird functional groups and species in different ways (Newmark 1991; Pearman 2002; Restrepo & Gomez 1998; Schleuning *et al.* 2011; Uriarte *et al.* 2011; Van Bael & Brawn 2005).

4.1.5. Other functional groups

Other predictors of avian sensitivity to fragmentation include flocking guilds, residence and body size (Sigel *et al.* 2010). From among the flocking guilds, army ant-followers and mixed species flock participants are thought to be more susceptible to fragmentation than non-flockers because of their 1) unique and risky diet search strategies that easily expose them to predators such as raptors when forest cover is lost or fragmented; and 2) larger home range requirements (Sekercioglu 2007; Sigel *et al.* 2010; Stouffer & Bierregaard 1995). In this study, however, we found little evidence for effects of forest loss and fragmentation on bird flocking guilds. Limitations in view of our patch-scale analysis and lack of detailed data on vegetation composition and structure of the remnant forest patches might have contributed to the inability to detect fragmentation effects among the various flocking guilds.

Resident birds are claimed to be more susceptible to fragmentation than non-residents (Bender *et al.* 1998; Schmiegelow & Monkkonen 2002). This is because most resident birds are specialists of good quality and exceptional forest habitats (Smith *et al.* 2001) thus requiring large areas, old-growth forests, decaying wood, and intact or less-disturbed habitats for foraging and nesting activities (Schmiegelow & Monkkonen 2002) but such habitat features could easily be lost or fragmented as a result of anthropogenic factors. Further, most resident birds are less mobile and this may increase their risk of extinction as a result of habitat loss and fragmentation (Sekercioglu 2007; Sodhi *et al.* 2010). Our results are consistent with the above predictions because we found strong impacts of forest loss and fragmentation on the abundance of resident birds and negligible impacts on non-resident birds.

Lastly, body size is often cited as one of the good indicators of fragmentation sensitivity i.e., large-sized birds are claimed more fragmentation sensitive than small-sized birds due to their large area requirements (Schmiegelow & Monkkonen 2002) although some empirical studies have shown limited sensitivity to fragmentation processes (Sigel *et al.*

2010). Here we found negligible impact of fragmentation on abundance of large and small-sized birds but strong impacts on medium-sized birds. A high level of fragmentation effects for intermediate body size birds has been reported elsewhere (Barbaro & Van Halder 2009). Contrary to Our findings, however, a study (Olson *et al.* 2009) showed that ‘median body size within assemblages is systematically large on islands and small in species-rich areas’. Further landscape-scale research on fragmentation sensitivity of bird body size may unravel the underlying mechanisms behind these mixed results.

4.2.Species diversity and community composition

Our results showed that the large remnant patches of NW Ethiopia had higher species richness and diversity than the small ones (Figure 3). Further, less-isolated remnant forest patches had higher species richness and diversity than isolated remnant forest patches (Figure 3). However, both of these diversity comparisons were not statistically significant. This might be attributed to the lack of sufficient replicates. In addition, results concerning community composition revealed considerable overlap in species assemblages between large and small forest patches but slightly distinct assemblage between less-isolated and isolated patches (Figure 6). Given the study region was a once contiguous forest (probably 200 – 300 years ago), these findings have clear implications for conservation planning and underline the importance of management strategies that aim to protect the large and less-isolated remnant forest patches for the best representation of associated biota, in particular bird species of conservation concern. However, we suggest some caution in this conclusion in that although most patches especially the large ones considered in this study belong to different landscapes, we did not run a true landscape-scale study nor did we relate our data to matrix conditions or land use type. This means that prioritizing only large and well connected forest patches and ignoring small and isolated patches and matrix trees that could serve as stepping stones for bird mobility between patches, may result in loss of unique bird assemblages and diversity (Guldemond & van Aarde 2010; Kennedy *et al.* 2010).

4.3.Caveats

No control site i.e. continuous or unfragmented forest was available for this study because such extensive forests have already been lost from the study region. Hence, the results presented may not be used to determine what subset of the avifauna otherwise found in unfragmented and far more extensive forest was observed in the largest patches. Also, we acknowledge the potential role of the intervening matrix surrounding patches in mediating species responses to fragmentation processes (Kennedy *et al.* 2011; Kennedy *et al.* 2010) but we did not gather detailed matrix data. We did not account for differential detectability among bird species in our analyses and as a result, the Shannon Diversity Index was not an unbiased estimator of true bird species diversity. This work was based on analysis of data at a patch-scale and a short sampling season. Future intensive and landscape-scale studies are clearly warranted for better understanding of fragmentation effects on sensitive bird functional groups. Furthermore, results of our analyses based on patch size and isolation categories should be interpreted with some caution because these variables were slightly confounded with each other at some patches.

4.4.Conservation implications

We identified key indicator functional groups (e.g., forest-specialists, insectivores, understory-foragers, open-nesters and residents), which are more fragmentation-vulnerable than other groups. These indicator functional groups can be used to devise efficient conservation plans, which can be applied at a minimum cost while ensuring their adequate and long-term representation. This can be performed by using systematic conservation planning methods (Margules & Pressey 2000) while considering past, current and future conditions of the landscape features and distribution patterns of member species, amongst others. This, however, rests on the assumption that conservation of these sensitive indicator functional groups may also simultaneously achieve conservation of other bird functional groups and biodiversity elements in the region. Where resources are available, management strategies that aim to expand the area of remnant forest patches and prevent further loss of forest habitats may help in the conservation of restricted-range; specialist and disadvantaged bird groups. From personal observation, increasing demand for agricultural land, firewood, and timber as well as inappropriate investment permission by the government and lack of commitment from mandated authorities are key drivers of forest destruction, loss and fragmentation in the current study areas. We therefore suggest that conservation practitioners and local authorities strictly protect and restore the large and less-isolated remnant forest patches as well as maintain the small and isolated patches and matrix trees that could serve as stepping stones for bird mobility between patches. In addition, to save this important bird area (BirdLife_International 2012) other relevant governmental and non-governmental organizations should participate in providing awareness creation workshops for the local inhabitants and relevant stakeholders including authorities on the values, services and implications of protecting these threatened and fragile forest remnants for agro-biodiversity conservation and productivity linked to the functional roles of bird communities.

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Table 1. Study patch characteristics (Note: ENN = Euclidean Nearest Neighbor Distance).

Patch	**Area (ha)**	**Size**	**ENN (m)**	**Isolation**
Zalini Abo	364.75	Large	109.3951	Less-isolated
Bradi	1179.5	Large	102.8478	Less-isolated
Daraba/Sigsi	1061.5	Large	105.2176	Less-isolated
Chembleka'ka/Berbergemta	272.75	Large	126.3182	Less-isolated
Bizra Kimtsi	62.5	Small	117.575	Less-isolated
Shakani Kura	2	Small	539.8292	Isolated
Washa Mariam	133.5	Small	167.2869	Isolated
Kambo	647.5	Large	103.0009	Less-isolated
Deka Dali	310.75	Large	125.288	Less-isolated
Dishi	20	Small	245.119	Isolated
Dibeli Giorgis	8.5	Small	285.6434	Isolated
Wonse	1387.5	Large	113.2243	Less-isolated
Demba	8	Small	325.8554	Isolated
Wira	100.25	Small	131.2384	Isolated
Keseng	41.25	Small	125.9951	Less-isolated
Awewuha	236.75	Large	166.3763	Isolated

Figure captions

Figure 1. Remnant forest patches in NW Ethiopia.

Figure 2. Degree of correlation among predictor patch metric variables initially attempted in the candidate model set (Note: ENN = Euclidean Nearest Neighbor Distance).

Figure 3. Species richness and species diversity comparisons between large vs small and less-isolated vs isolated patches of NW Ethiopia.

Figure 4. Mean raw species richness per patch of each functional group.

Figure 5. Mean bird abundance per patch of each functional group.

Figure 6. Non-metric multidimensional scaling (MDS) showing degree of similarity in community composition between A) large vs small, and B) less-isolated vs isolated patches of NW Ethiopia. Note (SK = Shakani Kura, DE = Demba, Bk = Bizra Kimitsi, B = Bradi, Wi = Wira, DIS = Dishi, DG = Dibeli Giorgis, KE = Keseng, AW = Awewuha, K = Kambo, DD = Deka Dali, DS = Daraba-Sigsi, Z = Zalini Abo, Wo = Wonse, WM = Washa Mariam, C = Chembleka'ka-Berbergemta).

Figure 7. Correlation among selected functional group categories (Note: understory = understory foragers, open = open-nesters).

Supplementary files

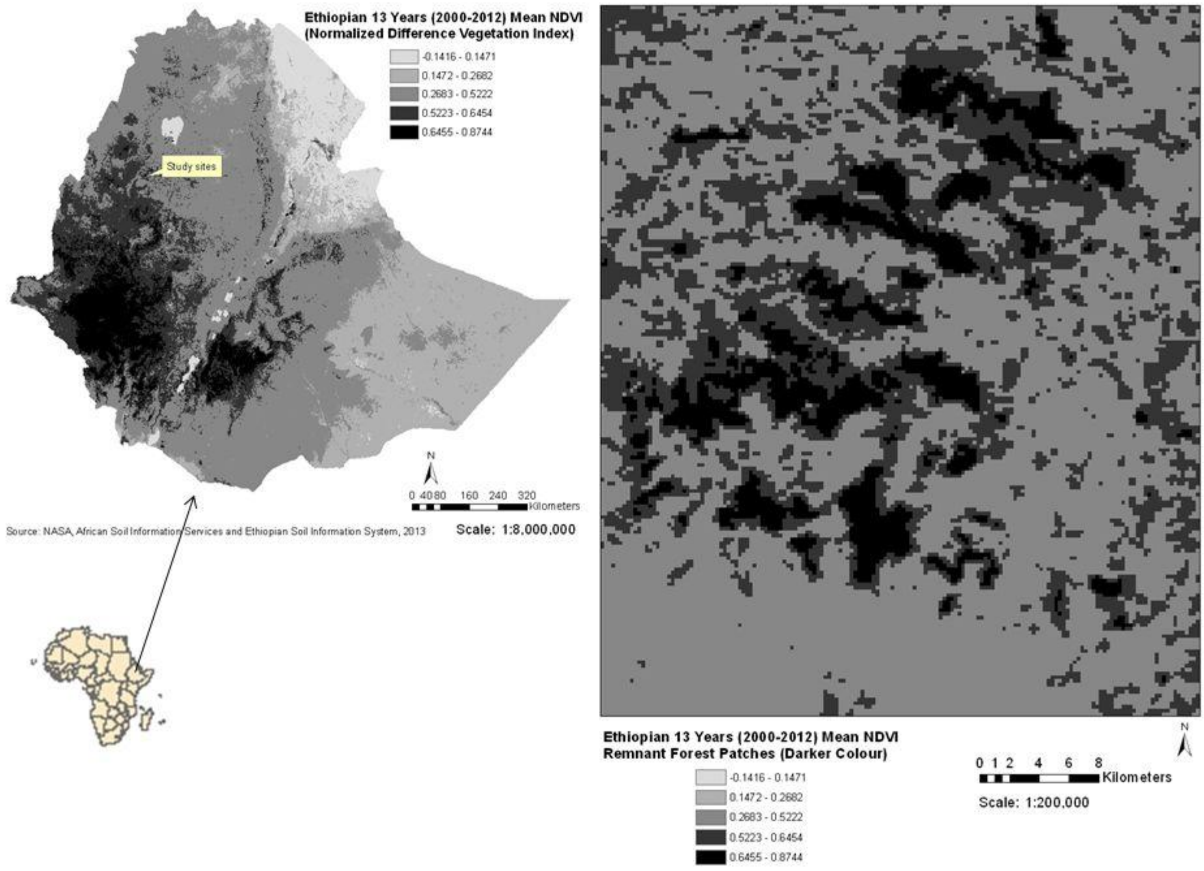
Supplementary Table 1. Generalized linear mixed models predicting bird abundance for selected bird functional group categories (Note: AICc = 2nd order bias correction for Akaike’s Information Criterion, ΔAICc = differences in AICc value of each model from the lowest AICc; *li* = relative likelihood of each model, *wi* = the probability of each model, and ER = evidence ratios = exp (-1/2Δbest)/exp (-1/2Δi)).

Supplementary Table 2. Parameter estimates and standard errors of top-ranked models.

Supplementary Table 3. Eigenvalues of the correlation matrix obtained from the principal component analysis of the predictor variables.

Supplementary Table 4. Eigenvectors obtained from the principal component analysis of the predictor variables.

Supplementary Table 5. Functional groups of bird species recorded from Guangua Wereda of Awi Zone, Gojjam, Amhara National Regional State, NW Ethiopia.



Source: NASA, African Soil Information Services and Ethiopian Soil Information System, 2013

Figure 1. Remnant forest patches in NW Ethiopia.

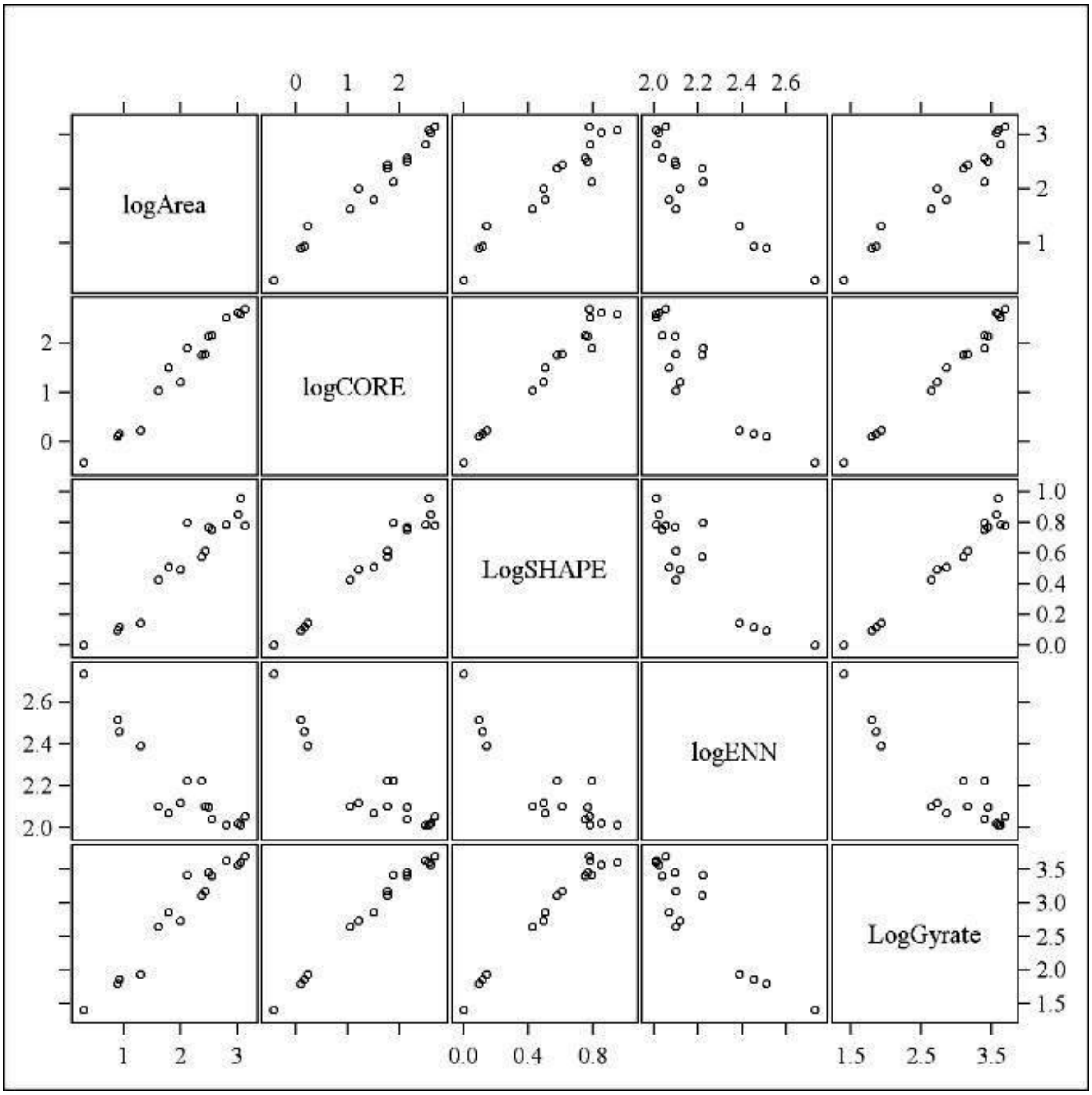


Figure 2. Degree of correlation among predictor patch metric variables initially attempted in the candidate model set (Note: ENN = Euclidean Nearest Neighbor Distance).

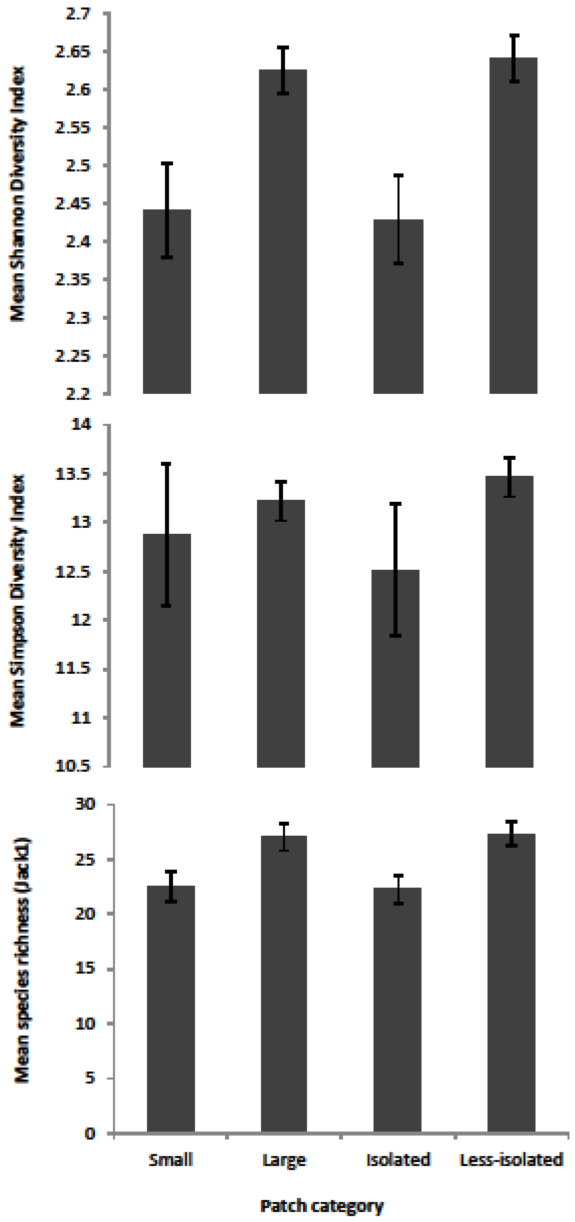


Figure 3. Species richness and species diversity comparisons between large vs small and less-isolated vs isolated patches of NW Ethiopia.

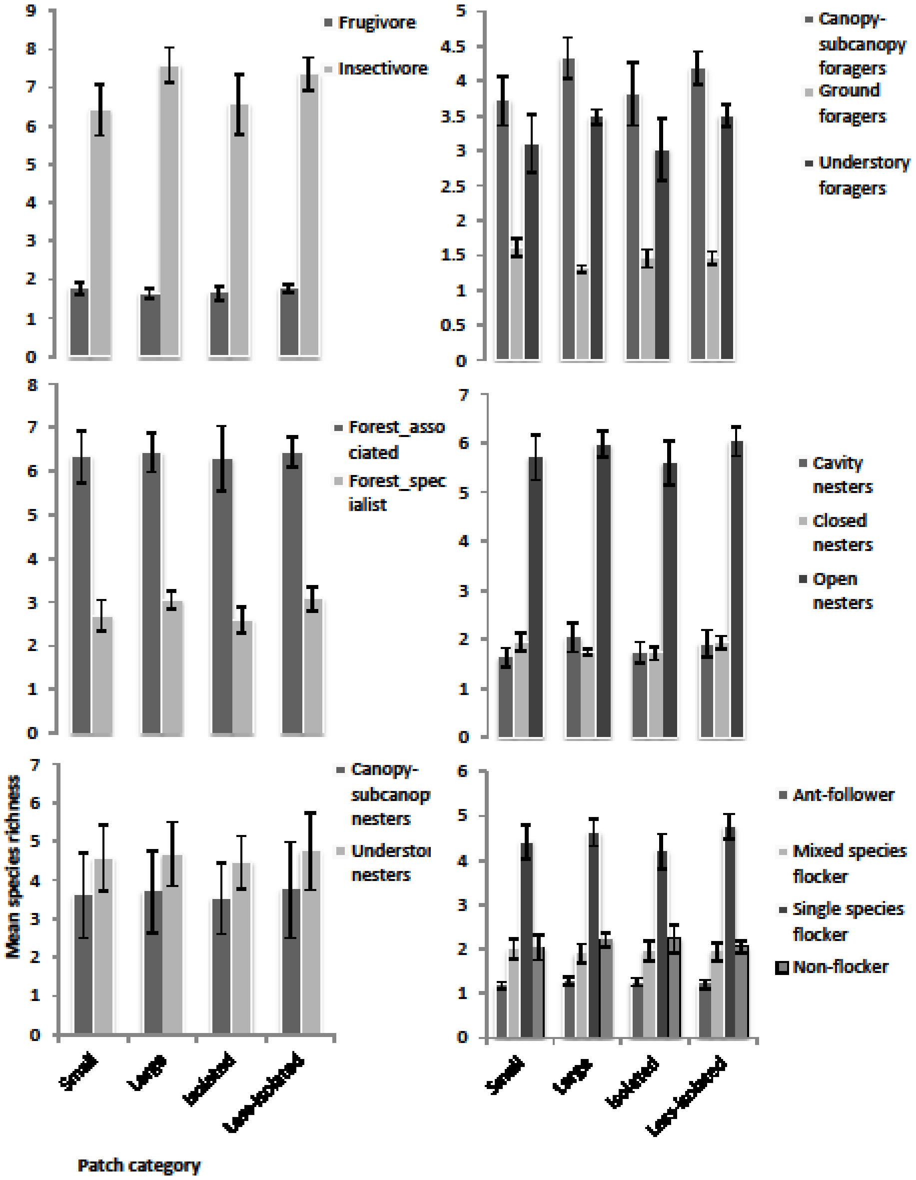


Figure 4. Mean raw species richness per patch of each functional group.

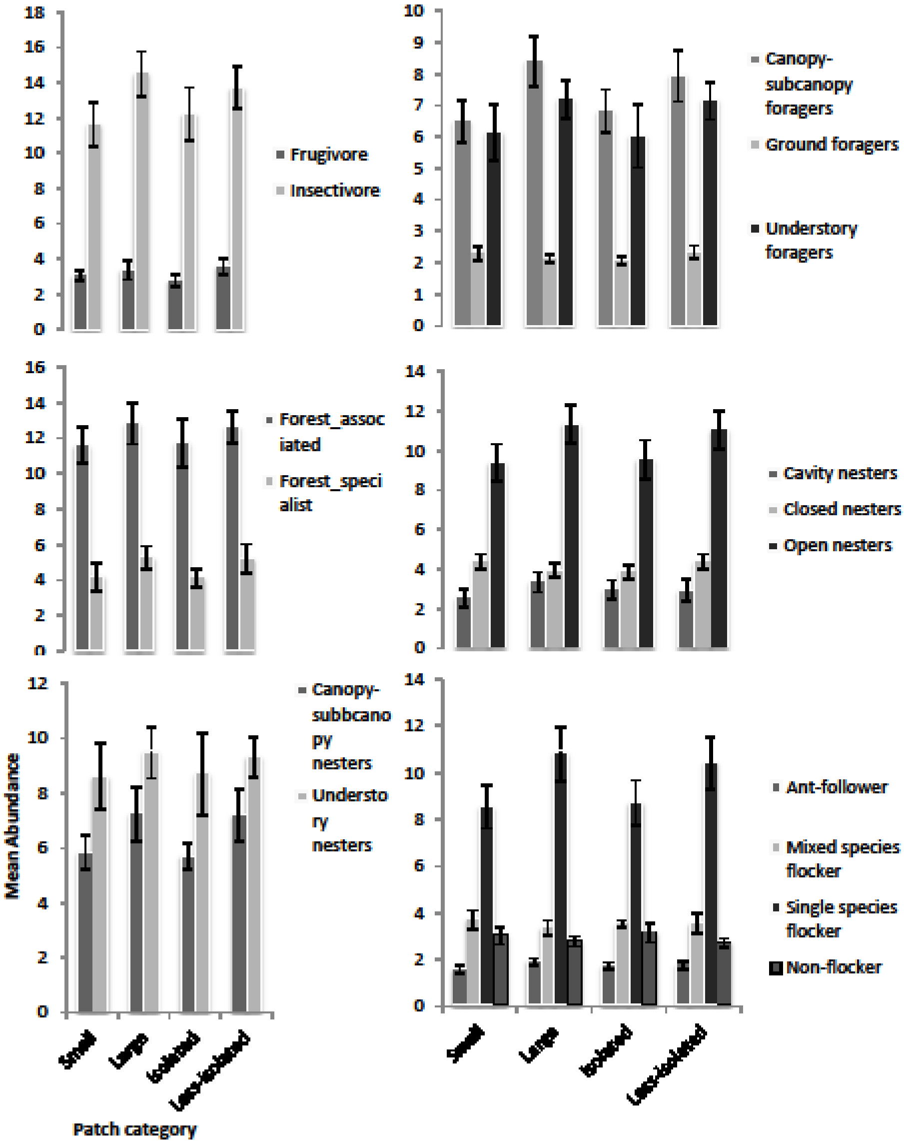


Figure 5. Mean bird abundance per patch of each functional group.

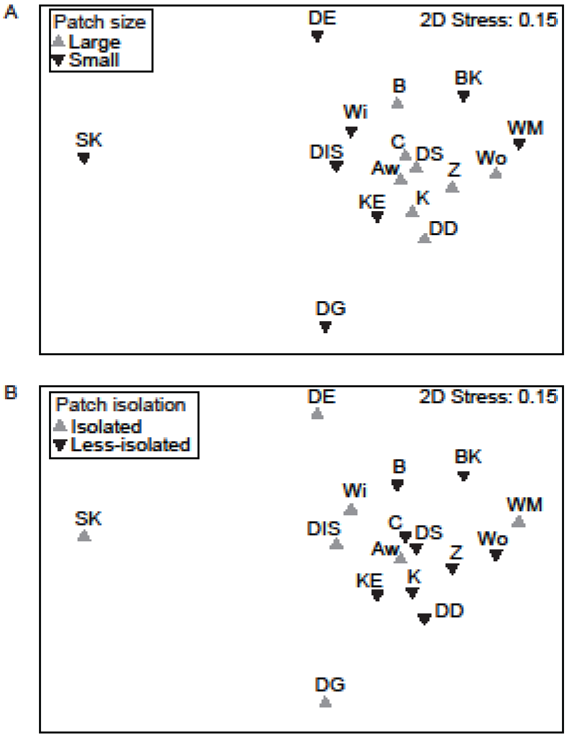


Figure 6. Non-metric multidimensional scaling (MDS) showing degree of similarity in community composition between A) large vs small, and B) less-isolated vs isolated patches of NW Ethiopia. Note (SK = Shakani Kura, DE = Demba, Bk = Bizra Kimitsi, B = Bradi, Wi = Wira, DIS = Dishi, DG = Dibeli Giorgis, KE = Keseng, AW = Awewuha, K = Kambo, DD = Deka Dali, DS = Daraba-Sigsi, Z = Zalini Abo, Wo = Wonse, WM = Washa Mariam, C = Chembleka'ka-Berbergemta).

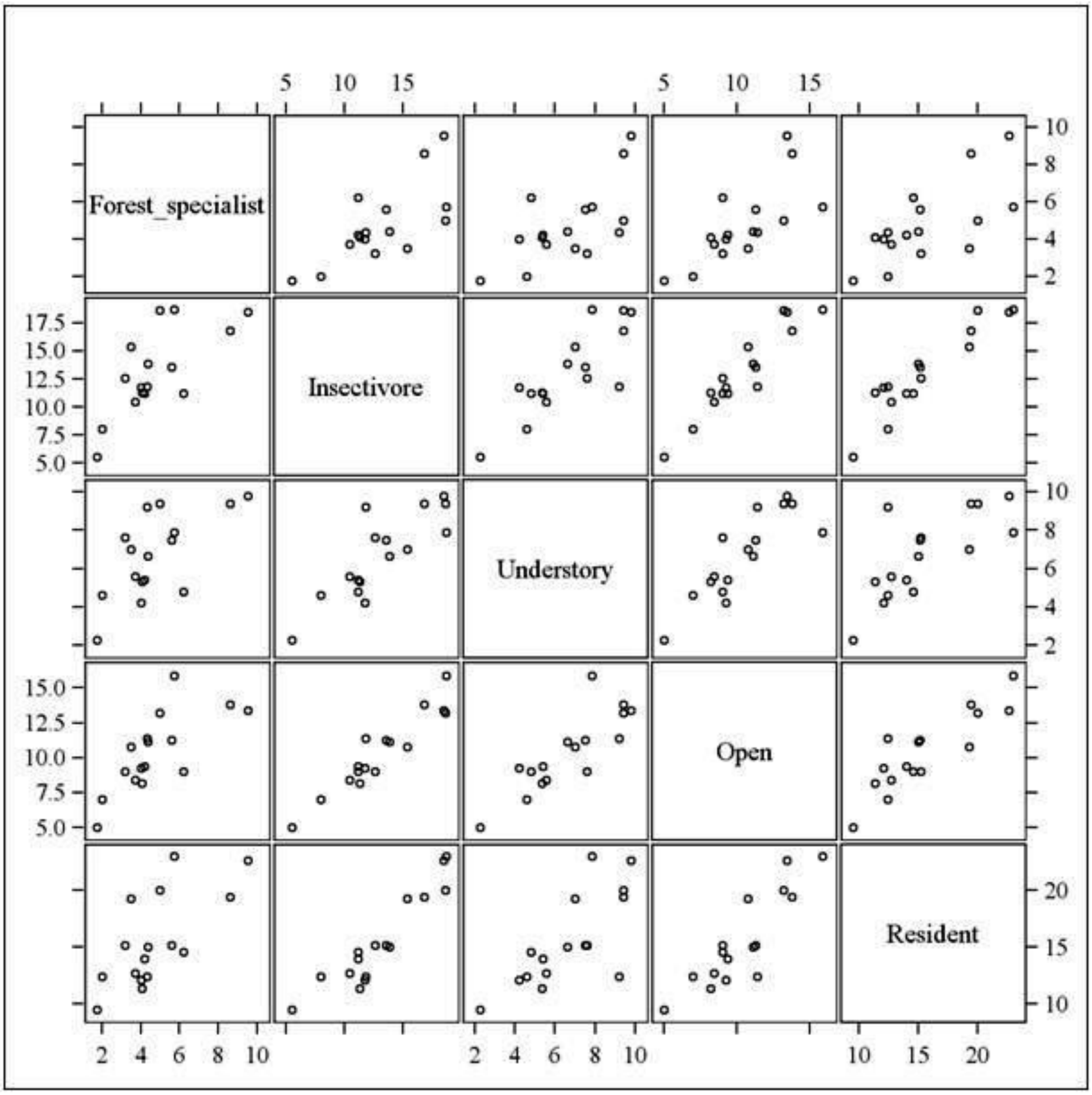


Figure 7. Correlation among selected functional group categories (Note: understory = understory foragers, open = open-nesters).