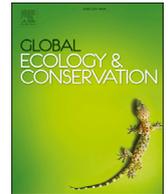




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Original Research Article

Sacred groves hold distinct bird assemblages within an Afrotropical savanna

Katharina Kühnert ^{a, *}, Ingo Grass ^b, Matthias Waltert ^a^a Workgroup on Endangered Species, J.F. Blumenbach Institute of Zoology and Anthropology, Georg-August-Universität Göttingen, Bürgerstr. 50, 37073, Göttingen, Germany^b Department of Crop Science- Agroecology, Georg-August-Universität Göttingen, Grisebachstr. 6, 37077, Göttingen, Germany

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ABSTRACT

Riparian forests, an integral part of savanna ecosystems, are threatened across West Africa by agricultural expansion. However, some patches of original riparian vegetation are protected by traditional beliefs as 'Sacred Groves'. We assessed the role of Sacred Groves in maintaining landscape-scale bird assemblages by conducting 144 1-h point counts, distributed over 24 plots in eastern Guinea-Bissau. The plots were situated in three riparian habitat types with different levels of human modification (Sacred Grove, Young Secondary Forest, Annual Cultures) and the adjacent Wooded Savanna. We accumulated 4572 records of 174 species and compared total species richness, composition, and functional traits among the four habitat types. At the plot level, species richness was higher in Wooded Savannas and Annual Cultures compared to Secondary Forests and Sacred Groves. Bird communities in Wooded Savannas were similar to those in Annual Cultures and differed the most from those of Sacred Groves. Bird community composition in Young Secondary Forests was similar to that in Annual Cultures but showed a shift towards the community composition found in Sacred Groves. Certain traits were strongly specific to habitat type. For example, Sacred Groves were characterized by a high number of forest specialists and insectivorous birds. Our results suggest that the rapid successional dynamics in riparian habitats enable disturbance tolerant forest species to recolonize fallow areas after a relatively short period of time. However, Sacred Groves hold a distinct avifauna and their conservation may therefore be crucial for forest specialist species and the re-establishment of bird assemblages in fallow riparian areas. Our findings also stress the importance of respecting and strengthening traditional forms of nature protection.

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1. Introduction

Many societies traditionally possess sites set aside for spiritual rituals and their deities that guard and provide for their communities (Bhagwat and Rutte, 2006). Examples of sacred sites include monastery gardens in Europe (Helms, 2002), sacred caves in Kazakhstan (Lymer, 2004), Indian Sacred Groves (Ormsby and Bhagwat, 2010) and Sacred Groves in the coastal savannas of Ghana (Campbell, 2005). Numerous case studies have demonstrated the value of Sacred Groves for biodiversity conservation (Decher, 1997; Ormsby and Bhagwat, 2010; Aerts et al., 2006).

* Corresponding author.

E-mail addresses: katharina_kuehnert@mailbox.org (K. Kühnert), ingo.grass@agr.uni-goettingen.de (I. Grass), mwalter@gwdg.de (M. Waltert).<https://doi.org/10.1016/j.gecco.2019.e00656>2351-9894/© 2019 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).Please cite this article as: Kühnert, K et al., Sacred groves hold distinct bird assemblages within an Afrotropical savanna, Global Ecology and Conservation, <https://doi.org/10.1016/j.gecco.2019.e00656>

The relevance of Sacred Groves as a conservation tool is augmented in places where governmental protection of natural resources is weak or non-existent. This is the case in most of West Africa, a highly biodiverse region with relatively fragile political stability and poor law enforcement (Maconachie et al., 2015). The existence of Sacred Groves in the region has been described in a number of studies (e.g. Lebbie and Freudenberger, 1996; Oteng-Yeboah, 1996; Campbell, 2005; Ceperley et al., 2010). The conservation of these traditionally protected sites becomes more important as forests vanish (Barre et al., 2009).

Deforestation took place across the whole of West Africa during the last decades, caused by the demand of a growing human population and associated land use changes (Brink and Eva, 2009; Goetze et al., 2006; Jalloh et al., 2012). Decreases in forest cover have been particularly rapid in the transition zone between the Guinean forest and the Sudanian savanna, where about 20% of forest cover has been lost between 1975 and 2000 (Brink and Eva, 2009). In this transition zone, the landscape consists of multiple habitat types: grasslands cover large areas, interspersed with woody vegetation ranging from isolated bushes to small islands of dry forest. Evergreen riparian forests constitute additional conspicuous features in this landscape. These riparian forests disappear faster than other forest types, mainly being converted for agriculture (Goetze et al., 2006). The effects of these changes on biodiversity remain largely undocumented, although general and severe declines across taxa have been described in the region (Mallon et al., 2015).

For example, strong population declines in both migratory and non-migratory birds have been reported (Sanderson et al., 2006; Thiollay 2006a; Vickery et al., 2014). These declines are caused by a combination of factors which include climate change (Møller et al., 2008), increased hunting pressure (e.g. Trail, 2007; Whytock and Morgan, 2010; Whytock et al., 2016), and deliberate poisoning (Ogada et al., 2012). Nevertheless, land use changes and forest disturbance can be considered the main causes for the decline of bird populations in the region (Arcilla et al., 2015; Waltert et al., 2005).

The effects of forest disturbance and modification on bird communities are well known. Previous research shows that feeding guild is a good predictor of disturbance sensitivity in tropical bird communities (Gray et al., 2007). For instance, insectivores are very sensitive to tropical forest disturbance, mainly due to limitations in their dispersal ability (Şekercioğlu et al., 2002). For large frugivorous species, body size can serve as an indicator for vulnerability to the indirect effects of forest disturbance, such as increased hunting pressure or selective logging (Mark et al., 2012). In contrast, granivorous species usually thrive in areas cleared for smallholder agriculture (Gray et al., 2007; Wiens and Johnston, 2012). Although these drivers are well understood for tropical forest landscapes, comparatively little is known from savanna landscapes in West Africa, where dry forests and riparian forests are patchily distributed.

In eastern Guinea-Bissau, the last remaining patches of primary vegetation in riparian areas are conserved as Sacred Groves. This mirrors the situation in other countries in the region, such as Côte d'Ivoire (Goetze et al., 2006) and Benin (Ceperley et al., 2010). Yet pressures on Sacred Groves are high due to an increased demand for arable land, driven by population growth and the spread of Cashew as a cash crop (Temudo and Abrantes, 2014). This pressure, in combination with a weakening of traditions and beliefs can lead to the abandonment and subsequent cutting of Sacred Groves for agriculture. Although small scale agriculture may benefit some bird species (Söderström et al., 2003;), effects of riparian forest loss on overall bird assemblage remain largely undocumented. Moreover, little is known on the role of Sacred Groves in reducing the impacts of riparian forest loss in West African savannas (but see Ceperley et al., 2010). To address these knowledge gaps, we here analysed the role played by Sacred Groves in maintaining landscape-scale bird assemblages in the Boé sector of eastern Guinea-Bissau.

We studied the bird communities of Sacred Groves (representing near-primary riparian forests) and the adjacent Wooded Savannas. To better understand the effects of riparian forest modification, we also studied the bird communities of modified habitats located in riparian areas, i.e. Annual Cultures and Young Secondary Forests. These modified habitats represent different successional stages of formerly forested riparian area.

Given that savannas cover a comparably larger area in the study region (Wit and Reintjes, 1989), and across Africa (White, 1983), we expected that Wooded Savannas support a higher number of bird species compared with the riparian habitat types (Sacred Grove, Young Secondary Forest, Annual Culture) (Rosenzweig, 1995).

We expect that bird community composition clearly differs between the structurally more open Wooded Savannas and closed Sacred Groves, as they represent very distinct habitat types. We predict that the bird assemblages of modified riparian habitat types (Annual Culture and Young Secondary Forest) are intermediate to Sacred Grove and Wooded Savanna.

Finally, we anticipated to find trait-related effects in the composition of the bird community, associated with different stages of succession. In particular, we expected a loss of forest specialist species and insectivores in the Annual Cultures and Young Secondary Forests (Waltert et al., 2005; Arcilla et al., 2015). In contrast, we expected granivorous species to be positively associated with Annual Cultures (Wiens and Johnston, 2012).

2. Methods

2.1. Study area and plots

The Boé region in eastern Guinea-Bissau (Fig. 1) is situated between 11°30' and 12°05' northern latitude and between 13°45' and 14°30' western longitude, having a tropical climate and an annual precipitation between 1600 and 2100 mm. The major part of the Boé region is covered by a hardpan of laterite rock, allowing only grasses to establish (Wit and Reintjes, 1989). In depressions, where soil accumulates, islands of dry forest are common. The numerous streams of the region were originally framed by evergreen riparian forests, which are now almost completely cut for shifting cultivation.

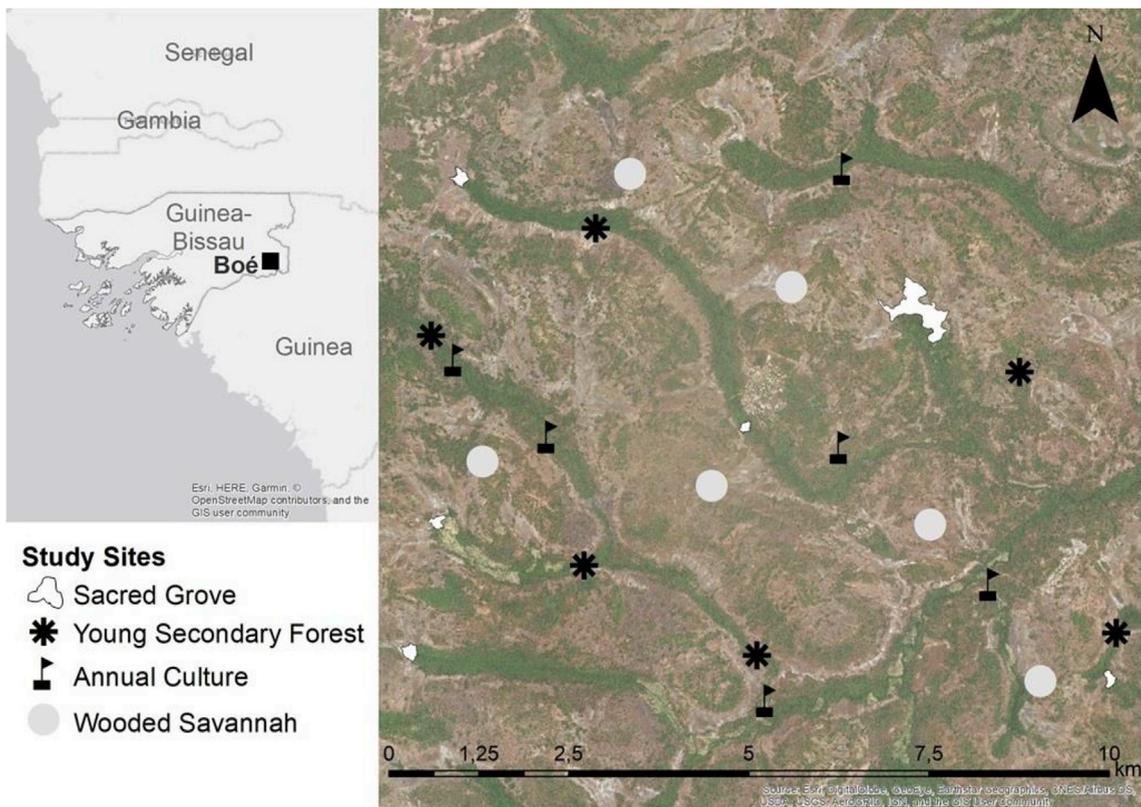


Fig. 1. Study area. To the left, a map indicating the location of the study area in eastern Guinea-Bissau. To the right, a map of the distribution of study plots across the study area, with the original shape and extent of Sacred Groves in white, Annual Cultures are marked with a flag, Young Secondary Forests represented by a star, and Wooded Savannas by a grey circle. 1.5 column fitting image, printed in color only for online version.

Study plots were chosen non-randomly due to the geographical characteristics of the study region, being distributed over an approximate area of 100 km² around the village of Béli. The average distance between any two plots was 5 km, with a minimum distance of 470 m.

Sacred Groves represent the last remaining patches of unlogged riparian forest, often situated at the origins of streams or rivers, comparable to the ones described for Benin by Ceperley et al. (2010). The average size of Sacred Groves visited was 2.8 ha, except from “Bundu Njuuri”, which was exceptionally large (29 ha). This larger forest patch is still used for rituals as they were commonly carried out in sacred sites in the past (pers. comm, Bucari Cassama, 2015). For this reason, “Bundu Njuuri” is possibly better protected by traditional beliefs than the other Sacred Groves in our study (pers. comm, Mussa Sané, 2015).

The subsistence agriculture in the Boé is similar to the slash-and burn practices found across West Africa. In the Boé, Annual Cultures are often situated in stream or river valleys and forested buffer zones (ranging from single trees to a few meters of forest stand) are usually kept on the valley borders to act as fire- and windbreaks (pers. comm., Mussa Sané, 2015). However, due to the low soil quality, the same field can only be cultivated for a maximum of two consecutive years, and is then left fallow for 4–7 years (pers. comm., Mussa Sané, 2015; Temudo and Santos, 2017). The plots classified as Annual Cultures corresponded to fields which had been cultivated for rice, millet, and sorghum in 2014 and had been left fallow for about 4 months before the start of our study. Only one plot had been cultivated again in 2015 (Annual Culture “Quinhique”, Table A1). All Annual Culture plots were situated in river valleys, except from one, which was situated on a valley border (Annual Culture “Béli”, Table A1). This location was chosen due to the limited number of suitable Annual Culture plots within an accessible distance, because most riverine areas close to the village are cultivated for with cashew.

Young Secondary Forest plots chosen for our study were found in areas that had been previously cultivated and had been left fallow for 4–6 years, allowing young trees to establish with an approximate height of 3–5 m (Fig. 2). Information on the age of Young Secondary Forest plots was retrieved from the local guides and, if necessary, confirmed by the owner of the plot (pers. comm., Mussa Sané and Balu Séra, 2015).

Finally, locations of Wooded Savanna plots were chosen based on their logistic suitability, as all plots had to be accessible by bicycle.



Fig. 2. Successional chrono-sequences among studied habitats. The arrows (1–4) indicate the successional habitat chrono-sequence as follows: 1: Riparian forest (i.e. Sacred Grove, $n = 6$, top left) is cut and cultivated in Annual Culture ($n = 6$, bottom left). 2: Annual Culture is left fallow for 4–6 years and develops into Young Secondary Forests ($n = 6$, top right). 3: In theory, Young Secondary Forests could develop into mature riparian forests again, a process that is unlikely given high population pressure. 4: Instead, Young Secondary Forests most often gets cut again after 4–6 years of fallow and become Annual Cultures. Adjacent Wooded Savanna is displayed at the bottom-right ($n = 6$). All pictures were taken in March 2015. 1.5 column fitting image, printed in color only for online version.

2.2. Bird counts

Fixed-radius point counts were carried out by KK during the morning between 06h30 and 12h00 from March to July 2015. During 1 h, observations of individual birds were recorded only if the possibility of double-counting could be excluded. To account for time and temperature effects on counting success, counts were carried out twice during early, mid and late morning, totaling six visits per plot. All counts were done under dry conditions, with 2–3 weeks between each visit. Only detections within an estimated distance of 50 m were considered for analysis (Sutherland, 2006). Birds were detected either visually or acoustically, after waiting for 3 min quietly in the center of the plot.

2.3. Vegetation and GIS survey

Vegetation structure estimates were done twice; once at the beginning of the study period and once at the end of it, to account for the level of structural changes during the five-month study period (Table A.2). Percentage of vegetation cover was visually estimated within a 50 m radius around the center of each plot on four different height bands. Height bands were placed at 1 m, 2 m, 4 m, 8 m, and 16 m, to account for variation in height structure among the investigated habitat types. The 50 m radius was quartered, resulting in four estimates per plot and height band. Canopy cover estimates were retrieved from the center of each quarter by using a sighting tube. All estimates were taken by the same observer and in accordance with Bibby et al. (2000). To retrieve an index of vegetation height heterogeneity, Shannon diversity was calculated by using estimates of vegetation cover for each height band and per plot. Estimates were averaged over the four plot quarters prior to calculation. For final analyses, estimates from the beginning and end of the study period were averaged and are referred to as “vegetation height heterogeneity” hereafter.

To retrieve a measure of landscape diversity for each plot, we mapped habitat composition within a 200 m radius around each plot in ArcGIS (Morelli et al., 2013). By using satellite imagery (Google Earth, 2015) we distinguished five habitat categories corresponding to the habitat types investigated: Old growth forest (corresponding to Sacred Groves), fallow (corresponding to Young Secondary Forests), savanna (corresponding to Wooded Savanna, but also including open savanna areas), cultivation (Annual Cultures), and village (no correspondence). The latter category was included, because the 200 m radius of few plots stretched into village area. Almost all plots included shares of all five habitat categories, so we were unable to use category richness as an indicator, but instead calculated category diversity (Morelli et al., 2013). We calculated the Shannon-Wiener index based on percentage shares of the prementioned classification types within a 200 m radius around each plot (Morelli et al., 2013).

2.4. Species traits

Species trait data were retrieved from [Borrow and Demey \(2008, 2011\)](#), [Fry and Fry \(2010\)](#), and the [IUCN \(2015\)](#). We focused on six traits: feeding guild, migratory behavior, body mass, habitat guild, biome association and global population trend ([Table A.3](#)). Birds were divided into feeding guilds based on their primary feeding behavior: carnivorous, insectivorous, frugivorous, nectivorous, granivorous, and omnivorous ([Borrow and Demey, 2008, 2011](#)). Moreover, species were classified into resident, breeding visitor, or nonbreeding visitor since migratory birds might respond differently to habitat modification than resident species (e.g. [Sanderson et al., 2006](#)). Our dataset contains four species of Palearctic migrants: European Bee-eater *Merops apiaster*, Eurasian Golden Oriole *Oriolus oriolus*, Sand Martin *Riparia riparia*, and Common Swift *Apus apus*, which were not treated separately, but classified as nonbreeding visitors.

To gain further information on the conservation value of the studied habitat types, information on biome-association was added for each species, following [Fishpool and Evans \(2001\)](#). Bird species were either restricted to the Guinean-Congo Forest biome, the Sudan-Guinean Savanna biome or non-restricted. Finally, the global population trend of each species was added, aiming to test whether increasing, decreasing, stable or unknown global population trends are associated to any of the studied habitat types ([IUCN, 2015](#)).

2.5. Data analyses

The number of species detected after six repeated visits was counted for each plot and is referred to as “observed species richness” hereafter. In total, 224 bird species were detected, out of which only 174 species were used for analysis, because all observations beyond 50 m distance were omitted. Normally, some species are missed during a field study ([Nichols and Conroy, 1996](#)), so to gain a more accurate picture of the actual number of species, we calculated an ‘estimated’ species richness, using the R package *vegan* ([Oksanen et al., 2015](#)), with the incidence-based and bias-corrected Chao 1 estimator ([Chao, 1987](#)). This method infers the number of missed species from the frequency of species in a collection of plots ([Palmer, 1990](#); [Colwell and Coddington, 1994](#)).

All further analyses were undertaken at plot level, i.e. we used the accumulated number of birds after six repeat visits per plot ($n = 24$ plots). To test for differences in species richness among habitat types, a general linear model (GLM) with Poisson distribution for count data was used, with vegetation height heterogeneity, canopy cover, and landscape diversity as covariates. To assess differences in species composition among habitat types, a permutational multivariate analysis of variance (PERMANOVA) was carried out, using a dissimilarity matrix, based on Bray–Curtis distances. This distance metric is insensitive to changes in absolute abundances, which is of importance for our data, since absolute abundances strongly differed among habitat types ([Anderson, 2001](#)).

Based on the dissimilarity matrix used for PERMANOVA, species community composition was more closely examined, using non-metric multidimensional scaling (NMDS). NMDS uses rank orders of species for ordination, making data less sensitive to transformations which are needed to obtain a meaningful ordination. Our data were standardized by square root and Wisconsin transformation. NMDS predicts values for each species per plot in a multidimensional space (one dimension per species). Then, it calculates the best two-dimensional solution for ordination, indicated by the lowest stress value (here: 0.138). The stress value quantifies the discrepancy between predicted values and values assigned to each data point by fitting it to a two-dimensional solution for displaying purposes. Species composition analysis was carried out using the R package *vegan* ([Oksanen et al., 2015](#)).

To investigate the effects of habitat and environmental variables on specific species traits, we used fourth corner analysis, model-type 1 with unadjusted p-values ([Dray and Legendre, 2008](#)). We included the following environmental variables: habitat type, vegetation height heterogeneity, canopy cover, and landscape diversity. Species-associated trait categories were: habitat, feeding, and migratory guild, biome affiliations, and the IUCN Red List of Threatened Species' population trend ([IUCN, 2015](#)). Since the fourth corner analysis is an abundance-based method, it could potentially yield stronger effects for plots with higher abundances. To preclude such a bias, we divided species-specific abundance by total abundance per plot prior to analysis. Hence, the fourth corner analysis was carried out using dominances per plot, rather than absolute abundances. Fourth corner analysis was done using the R package “*ade4*” ([Dray and Dufour, 2007](#)). All statistical analyses were done in R 3.2.2 ([R Core Team, 2015](#)).

3. Results

3.1. Bird species richness and diversity

In total, 174 bird species, accounting for 4572 individuals were analysed ([Table A.3](#)). Based on this, we estimated a joint total of 209 (± 17 SE) species (Chao1 estimator) across all studied habitat types and drew habitat-specific species accumulation curves ([Fig. A1](#)). According to species richness estimates, roughly, 87% of species were detected in Sacred Groves, 75% in Young Secondary Forests, 85% in Annual Cultures, and 78% in Wooded Savannas. The highest number of species was observed in Annual Cultures, followed by Wooded Savannas, Young Secondary Forests, and Sacred Groves ([Fig. 3](#)).

All further results refer to the plot level ($n = 24$ plots) and have been obtained using the accumulated number of observed bird species after six visits for each plot. The GLM analysis revealed, that observed species richness was determined by habitat

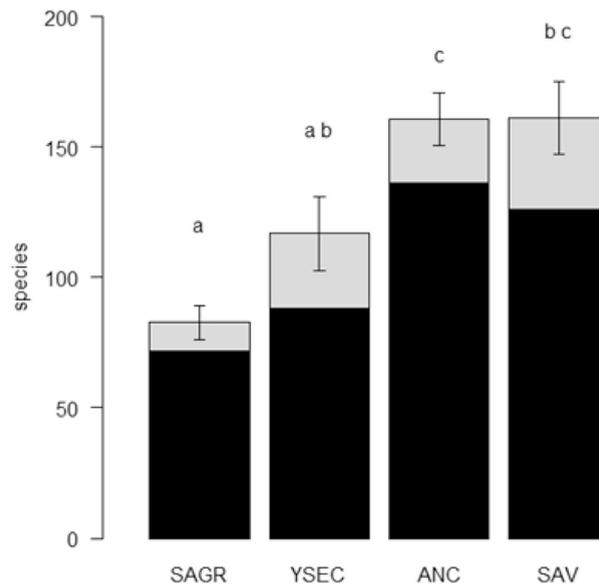


Fig. 3. Observed (black bars) and estimated (grey bars) bird species richness in each studied habitat type. Estimated species richness is based on Chao estimator (black lines indicating the standard error). Different letters (a, b, c, d) indicate whether habitats significantly differ in species richness, using a linear model with vegetation measures and landscape diversity as covariates (LM, $P < 0.05$). SAGR=Sacred Grove, YSEC=Young Secondary Forest, ANC=Annual Culture, SAV=Wooded Savanna 1 column fitting image.

type. Observed species richness was highest in Annual Cultures ($Z = 5.164$, $P < 0.001$), followed by Wooded Savannas ($Z = 3.287$, $P = 0.001$), and Young Secondary Forests, where habitat type had only a marginal influence on species richness ($Z = 1.686$, $P = 0.091$). Species richness in Sacred Groves however, was significantly determined by habitat type ($Z = 11.549$, $P < 0.001$) (Fig. 3).

Observed species richness in Annual Culture plots was significantly higher compared with Young Secondary Forest plots (Tukey's HSD, $P = 0.001$) and plots in Sacred Groves (Tukey's HSD, $P < 0.001$), but did not significantly differ from the species number observed in Wooded Savanna plots (Tukey's HSD, $P = 0.84$) (Fig. 4). Observed species richness in Wooded Savannas was, in turn, only different from Sacred Groves (Tukey's HSD, $P = 0.005$) (Fig. 4). The forested habitat types, i.e. Sacred Groves and Young Secondary Forests, did not show a difference in observed species richness on plot level (Tukey's HSD, $P = 0.32$) (Fig. 4).

Running a GLM with the same covariates as above, estimated bird species richness (Chao1 estimator) showed a very similar pattern. But for estimated species richness, Wooded Savanna plots held significantly more species than Young Secondary Forest plots (Tukey's HSD, $P < 0.001$). Shannon bird diversity did not differ between habitat types on the plot level (Fig. 4).

3.2. Effects of vegetation variables and landscape diversity

No difference in vegetation height heterogeneity (one-way ANOVA, $P = 0.7$) nor canopy cover (one-way ANOVA, $P = 0.3$) was detected at plot level. Nonetheless, vegetation height heterogeneity had a marginally negative effect on observed species richness ($P = 0.077$), but a significantly negative effect on estimated species richness ($P = 0.003$). Both, observed and estimated species richness decreased with increasing canopy cover (Poisson GLM, $P = 0.033$; and GLM, $P < 0.001$ respectively).

Landscape diversity differed among habitat types ($P < 0.001$), being particularly lower for Wooded Savanna plots compared to all other habitat types (Tukey HSD, $P < 0.05$ in all cases). However, landscape diversity had no effect on observed and estimated species richness.

3.3. Community composition

We found a significant effect of habitat type on bird community composition, which was revealed by PERMANOVA test ($R^2 = 0.34$, $P < 0.050$). All other covariates (i.e. vegetation height heterogeneity, canopy cover and landscape diversity) did not significantly affect community composition. NMDS ordination visualized differences in bird community composition among habitat types at the plot level (NMDS, stress = 0.13, Fig. 5) and showed a clear divergence in bird assemblages of open habitat types (i.e. Wooded Savanna and Annual Culture) compared with closed habitat types (i.e. Sacred Grove and Young Secondary Forest). We observed an overlap in community composition between Annual Cultures and Wooded Savannas. However, this

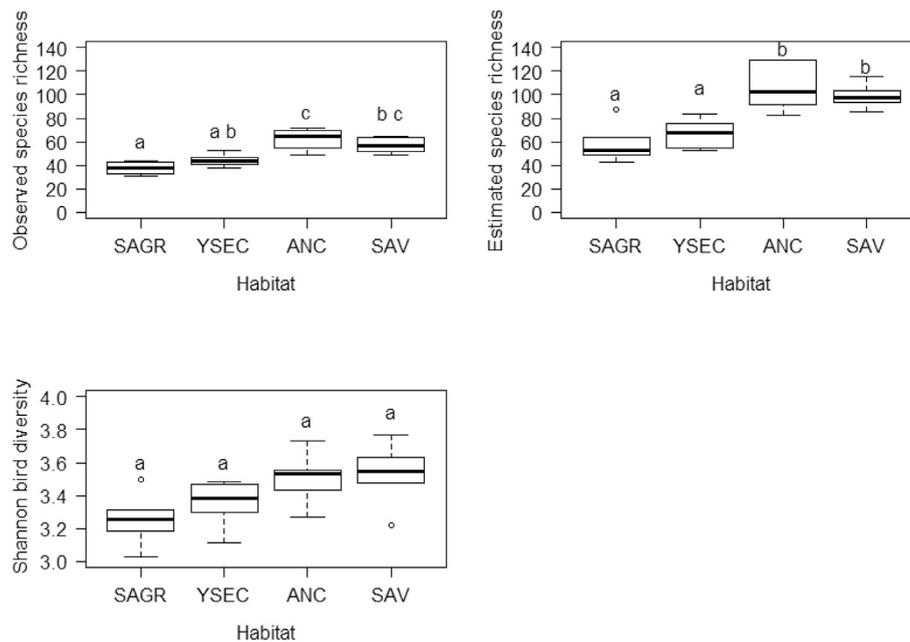


Fig. 4. Plot level biodiversity estimates. Observed and estimated species richness and Shannon diversity for Sacred Groves (SAGR, $n = 6$), Young Secondary Forests (YSEC, $n = 6$), Annual Cultures (ANC, $n = 6$), and Wooded Savannas (SAV, $n = 6$). Different letters (a, b, c) indicate, whether habitats significantly differ in the respective measure ($P < 0.05$). Open dots mark outliers. *1.5-column fitting image.*

overlap was caused by a single Annual Culture plot (Fig. 5). Plots of Young Secondary Forests and Sacred Groves were adjoining, but non-overlapping.

3.4. Trait-specific responses

We looked for trait-related effects which drive differences in community composition between habitat types. Fourth-corner analysis revealed significant relationships among certain species traits, environmental variables and habitat type (Table 1). For example, the bird community of Sacred Groves was positively associated with species belonging to habitat guilds characteristic to primary and secondary forest but negatively associated with species of rank herbage-/moist habitats, and (wooded) savannas (Table 1). Carnivorous, insectivorous, and nectivorous species were positively associated, while granivorous species were negatively correlated with Sacred Groves. Also, a positive association was found between Sacred Groves and Guinean-Congo forest biome-restricted species (Table 1). The bird community of Young Secondary Forests showed a comparatively higher number of frugivorous birds and was represented by species commonly described to favor secondary forests (Table 1). Birds described to live in savannas and wooded savannas were underrepresented in Young Secondary Forests but positively associated with Annual Culture - and Wooded savanna plots (Table 1). In contrast, Guinean-Congo forest biome restricted species were negatively associated with the open habitat types Annual Culture and Wooded Savanna. Birds typically found in secondary forests and forests were also still supported by the open habitat types of our study, i.e. Annual Culture and Wooded Savanna (Table 1). Annual Cultures were negatively associated with insectivorous bird species and positively with granivorous species (Table 1).

Migratory birds, categorized as breeding visitors or non-breeding visitors, were positively associated with Wooded Savanna plots. Resident species were positively associated with landscape diversity (Table 1). None of the investigated habitat types was associated with a particular IUCN population trend, nor any of the environmental indicators (Table 1).

4. Discussion

Sacred Groves help to maintain overall bird assemblages in the Sudan-Guinean savanna transition zone. The community composition of Sacred Groves was distinct from the bird assemblage of Wooded Savannas, but this distinction faded in modified riparian habitat types, with bird assemblages being intermediate to Sacred Groves and Wooded Savannas. We also demonstrated guild specific responses to habitat modification, with e.g. a loss of insectivorous species in Annual Cultures and Young Secondary Forests. In contrast, Sacred Groves of our study significantly support carnivorous, nectivorous and insectivorous species, despite a comparably low species richness.

The low species richness of Sacred Groves observed in our study contrasts other studies which find higher species richness in Sacred Groves compared with the surrounding landscape (e.g. Brandt et al., 2013). The higher species richness of Wooded

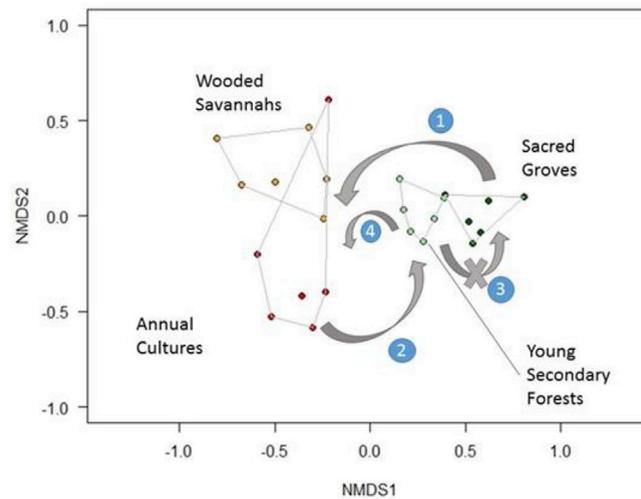


Fig. 5. Non-metric-multidimensional scaling ordination of the 24 plots sampled across four habitat types (Sacred Groves: dark green, Young Secondary Forest: light green, Annual Cultures: red, Wooded Savanna: yellow), based on Bray-Curtis distances of bird abundances. Plots belonging to the same habitat are connected by lines or fall within these lines. The chrono-sequence of habitat succession is additionally illustrated by arrows 1 to 4. 1: Riparian forest (i.e. Sacred Grove) is cut and cultivated (becoming Annual Culture). 2: Annual Culture is left fallow and develops into Young Secondary Forests. 3: Young Secondary Forests potentially develops into mature riparian forests 4: Instead, Young Secondary Forests get cut again after four to six years of fallow and become Annual Cultures again. *1.5 column fitting image, color printed only in online version.*

Table 1

Fourth corner analysis of the communities of each investigated habitat in relation to environmental variables and species traits. Positive (+) and negative (–) associations for a significance threshold of $P < 0.05$ are calculated based on Pearson correlation.

Traits		Habitat types				Environmental Measures		
Trait class	Trait Category	Sacred Groves	Young Secondary Forest	Annual Cultures	Wooded Savannas	Vegetation height heterogeneity	Canopy cover	Landscape diversity
Habitat guild	Forest	+		–	–			+
	Secondary Forest	+	+	–	–			+
	Wooded Savanna	–	–	+	+	+	+	
	Savanna	–	–	+	+			
Feeding guild	Rank Herbage/Moist Habitat	–		+				
	Carnivorous	+						
	Insectivorous	+		–				
	Omnivorous							
	Granivorous	–		+				
Body size	Frugivorous		+					
	Nectarivorous	+						
Migratory guild	Resident					+		+
	Breeding visitor		–					+
	Nonbreeding visitor				+			
Biome Association	Guinean-Congo	+		–	–			+
	Forest							
	Sudan-Guinean Savanna							
	None	–				+	+	

Savannas might be attributed to several factors acting at different spatial scales. Our study was set up in a context where savannas represent the dominating habitat type (Wit and Reintjes, 1989). Savannas also represent the dominating habitat type across Africa (White, 1983), so according to the species-area relationship, we could expect a higher species richness in savannas, compared to other habitat types (Rosenzweig, 1995). On a landscape level, the isolated patch character of Sacred Groves (Bender et al., 1998), combined with the limited width of river valleys might restrict avian species richness therein (e.g. Kinley and Newhouse, 1997; Shirley and Smith, 2005). At local level, Decher (1997) found a similar pattern for small mammals in Sacred Groves of Ghanaian savannas: although species richness of bats was lower in Sacred Groves, it comprised forest

specialist species uniquely observed there. Hence, despite being comparably species-poor, community composition of Sacred Groves was unique.

Also in our study, the bird communities between the near-natural habitat types Sacred Grove and Annual Culture were distinct. As expected, bird community composition of modified riparian habitat types (i.e. Annual Culture and Young Secondary Forest) was intermediate to the near-natural habitat types Sacred Grove and Wooded Savanna. Although Young Secondary Forests had been left fallow during only four to six years, the bird community had already shifted from one typical of Annual Cultures towards one that closely resembled Sacred Groves. Such a rapid convergence of the avian community exceeds that reported in other studies (Raman et al., 1998; Naidoo, 2004), and may have been facilitated by the exceptional conditions in riparian zones which accelerate vegetation growth (Gregory et al., 1991). More likely, though, this rapid convergence documents an already highly impoverished avifauna of Sacred Groves, being little different from Young Secondary Forests. The original riparian forests in the Boé region must have been gradually deforested since humans settled, with little more left today than small patchily distributed Sacred Groves. Likely, extinction events took already place and might still be ongoing (e.g. Brooks et al., 1999; Brooks et al., 2002). For example, there is anecdotal evidence on the earlier occurrence of the Great Blue Turaco *Corythaëola cristata* (pers. comm., Amadal Camara, 2015).

However, the high species richness in Annual Cultures proves that cultivated riparian areas can support a high number of bird species. A similar pattern is known from Burkina Faso, where avian species richness was highest in cultivated areas and decreased as the fallow became more “forest-like” (Söderström et al., 2003). Conversely, Thiollay (2006b) discusses a species decline in cultivated areas compared to surrounding Savannas in Burkina Faso. These different results may be because Thiollay (2006b) focused on large-bodied birds, but we also included small, granivorous species. Our results showed that granivorous species were particularly common in Annual Cultures. Wiens and Johnston (2012) described that granivorous species are particularly successful in agricultural areas, where seeds are seasonally highly abundant, and we observed several species feeding on grains left from cultivation. Moreover, the open structure of Annual Cultures facilitates the colonization by species of savanna habitats which are to a large proportion small, seed-eating species. We conclude, that traditional cultivation practices, as they are still carried out in the Boé, can provide a viable habitat for a great number of bird species (e.g. Selmi et al., 2002; Mandal and Shankar Raman, 2016), although under the exclusion of forest specialists and insectivores. Alarmingly, these traditional cultivation practices are under threat from the expansion of Cashew as a cash crop (Temudo and Abrantes, 2014). Annual Cultures are commonly transformed into Cashew plantations which interrupts the fallow cycle (Temudo and Santos, 2017) and has a landscape level impact on biodiversity (Monteiro et al., 2017).

The role of Sacred Groves as an important component for the protection of biodiversity at landscape level has received little attention so far (see Bhagwat et al., 2005; Sreevidya et al., 2016). In contrast, the role of landscape structure as a driver of bird diversity is well studied (Tschardt et al., 2008). However, we were unable to detect such an effect in our study. This might be attributed to the small landscape radius investigated (200 m), and an inadequate data resolution. Furthermore, data on landscape diversity were skewed due to the comparable small-scale mosaic of modified riparian areas contrasting with vast savannas, far from rivers, cultivations, and settlements. As a result, all riparian habitat types showed a consistently high landscape diversity in contrast to Wooded Savannas. Finally, landscape effects might simply be negligible in the semi-natural mosaic landscape of our study area. Here, and the effects acting at the plot level might be more important. At the plot level, we observed a negative relationship between vegetation structure, canopy cover, and bird species richness, i.e. we found fewer species in structurally heterogeneous plots with higher canopy cover, compared to more simply structured open plots. These results are contrasting those from the majority of studies (MacArthur and MacArthur, 1961; Willson, 1974; Tews et al., 2004), yet are in accordance with the overall picture of a generally species rich Wooded Savanna and a poorer avifauna in the small, isolated Sacred Groves therein. This pattern is also confirmed by the study of Söderström et al. (2003) from Burkina Faso.

We finally want to point out, that highly forest dependent species, such as ant followers, are missing in the bird assemblages of our study. By nature, fewer forest specialist species will persist in the forest-savanna transition zone than in the zonal Guinean-Congo forest biome and they will be rarer. Biome transition zones, however, have been attributed a crucial role for processes of speciation and adaptation (Smith et al., 1997), indicating an important role of forest habitats in savanna regions. For example, Little Greenbuls *Andropadus virens* in the Sudan-Guinean forest-savanna transition zone, show song- and morphological divergence compared to the zonal populations (Slabbekoorn and Smith, 2002). This phenotypic divergence has already decreased due to high deforestation across West Africa, reducing the species' adaptive diversity (Freedman et al., 2010).

We conclude that the persistence of Sacred Groves in eastern Guinea Bissau, despite their comparably low bird species richness, is vital for long-term conservation efforts. Apart from forest specialist bird species, primates of the region highly dependent on riparian forests (Binczik et al., 2017) and thereby on Sacred Groves. Moreover, findings from other regions suggest that Sacred Groves might serve as source habitat for species to recolonize or survive in modified habitat types (Gao et al., 2013; Ray et al., 2015). Finally, Sreevidya et al. (2016) pointed out that the benefits provided by Sacred Groves go far beyond species protection. For example, Sacred Groves might be of high importance for watershed protection and water availability (Ray et al., 2015; Vinay et al., 2017), which is a burning issue for the human population in our study region.

Our study offers the first comparative results on bird communities of modified riparian habitats and surrounding savannas in West Africa. Moreover, we add an insight into the conservation value of Sacred Groves, which are under threat in eastern Guinea-Bissau. Formal “conservation” however, holds some risks if initiated by outside institutions. A well-documented example of how outside interventions can weaken traditional forms of protection is the degradation of Sacred Groves in Cantanhez National Park (Guinea-Bissau), caused by shifts in power and a concurrent loss of perceived land security among

local communities (Temudo, 2012). Official policies may hence weaken traditional forms of protection of Sacred Groves (Brandt et al., 2015), if put in place without consideration of local power relations, beliefs and traditions. An effort to put the Sacred Groves of the Boé region under formal protection is currently underway (Chimbo Foundation, 2019). We support this initiative, with a strong focus on local communities. The understanding of local beliefs and power relations is crucial for this kind of endeavor, and the implementing organization has more than a decade of experience in actively engaging locals into conservation efforts in the Boé (Chimbo Foundation, pers. comm). Therefore, we trust that any efforts will respect and consider local power relations and lead to a long-term protection of the Sacred Groves in the Boé region.

Declaration of interests

None.

Acknowledgments

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APPENDIX

Table A.1

Information on studied plots. Name, habitat type, location (WGS 1984; UTM Zone 28N), and elevation of each point count location visited during the study in the Boé region (Guinea-Bissau).

Plot name	Habitat type	X coordinate (UTM)	Y coordinate (UTM)	Elevation (m)
Cael	Annual Culture	619299.5087	1306654.713	67.646
Quebube2	Annual Culture	613159.9913	1308700.045	73.5331
Béli	Annual Culture	617220.2954	1308556.27	61.2146
Quebube1	Annual Culture	611866.73	1309769.25	87.0459
Queco	Annual Culture	617265.2814	1312425.474	66.3698
Qunhique	Annual Culture	616195.1097	1305039.075	68.5074
Bantandjan	Sacred Grove	611938.9051	1312351.901	87.1116
Bandugada	Sacred Grove	615911.8625	1308848.019	40.911
Bundujuri	Sacred Grove	618618.6664	1310353.354	81.1985
Horegudum	Sacred Grove	611648.131	1307490.194	73.3746
Horejalede	Sacred Grove	611300.3894	1305756.273	71.5514
Bundugada	Sacred Grove	615441.7503	1308021.708	92.4495
Horeferanora	Wooded Savanna	620958.8311	1305376.473	87.3181
Belisinho	Wooded Savanna	618473.7045	1307482.806	75.6972
Cael	Wooded Savanna	620005.72	1305311.887	97.7949
Pataque	Wooded Savanna	614308.1185	1312351.522	94.0851
Quebube	Wooded Savanna	612253.2063	1308360.586	98.326
Queco	Wooded Savanna	616543.5767	1310782.185	89.9869
Quebube1	Young Secondary Forest	611540.741	1310107.795	70.9674
Bundjuri	Young Secondary Forest	619716.415	1309600.074	104.036
Quebube2	Young Secondary Forest	616063.8019	1305665.285	84.7418
Unduferanora	Young Secondary Forest	621056.3206	1305979.616	66.8507
Bantandjan	Young Secondary Forest	613829.1561	1311597.487	82.1682
Gudum	Young Secondary Forest	613668.6675	1306912.066	73.8264

Table A.2

Vegetation measures used for analysis. Vertical height heterogeneity (Shannon index), Canopy cover (%), Landscape diversity (Shannon index). Measures not considered for analysis are marked with an asterisk (*): Tree density (No of Trees), Diameter at breast height (DBH) and Tree Diversity (Shannon index), based in indigenous names.

Vegetation measure	Vertical height heterogeneity (Shannon Index)	Canopy cover (%)	Landscape diversity (Shannon index)	Number of trees (trees/100 m ²)*	DBH (DBH/100 m ²)*	Tree Diversity/100 m ² (Shannon Index)*
Sacred Grove	1.4 ± 0.2	52.6 ± 25.7	1.0 ± 0.1	7.3 ± 2.5	30.2 ± 7.2	1.1 ± 0.4
Young Secondary Forest	1.2 ± 0.1	48.0 ± 25.7	1.1 ± 0.1	1 ± 1.2	15.8 ± 22.7	0.2 ± 0.3
Annual Culture Wooded Savanna	1.3 ± 1.7	30.2 ± 20.2	1.1 ± 0.1	0.8 ± 0.9	22.5 ± 26.4	0.1 ± 0.2
	1.3 ± 0.1	40.1 ± 12.5	0.5 ± 0.2	3.5 ± 3.0	17.2 ± 9.9	0.8 ± 0.9

Table A.3

Information on the studied species. The table includes the species analyzed in this study, identified by Family, English, and Scientific name. Trait categories are given for Biome association (N = non-restricted, GCF = Guinean-Congo forest restricted, SGS = Sudan-Guinean Savanna restricted), Body size (geometric mean, following Borrow & Demey, 2008), Feeding guild (c = carnivorous, i = insectivorous, o = omnivorous, g = granivorous, f = frugivorous, n = nectarivorous), Migratory behavior (r = resident, bv = breeding visitor, nb = nonbreeding visitor), Habitat guild (f = forest, sf = bush/secondary forest, ws = wooded savanna, sv = savanna, mh = rank herbage/moist habitats, a = aerial) and IUCN population trends (unknown, stable, decreasing, increasing).

Family	Common name	Scientific name	Biome-association	Body size (g)	Feeding guild	Migratory behavior	Habitat guild	IUCN population trend	Habitats of this study
Ardeidae	Grey Heron	<i>Ardea cinerea</i>	N	95	o	r	mh	unknown	ANC, YSEC
	Purple heron	<i>Ardea purpurea</i>	N	84	o	r	mh	decreasing	ANC
	Cattle Egret	<i>Bubulcus ibis</i>	N	52	o	r	mh	increasing	ANC
Scopidae	Hamerkop	<i>Scopus umbretta</i>	N	53	c	r	mh	stable	ANC, SAV, YSEC
Accipitridae	Shikra	<i>Accipiter badius</i>	N	29	c	r	ws	stable	ANC
	Red-thighed Sparrowhawk	<i>Accipiter erythropus</i>	GCF	25.5	c	r	f	decreasing	ANC
	African Goshawk	<i>Accipiter tachiro</i>	N	42	c	r	f	decreasing	SAGR
	Grasshopper Buzzard	<i>Butastur rufipennis</i>	N	42.5	c	bv	ws	decreasing	SAV
	Red-necked Buzzard	<i>Buteo auguralis</i>	N	45	c	r	ws	increasing	SAV
	Palm-nut Vulture	<i>Gypohierax angolensis</i>	N	60	o	r	f	stable	ANC
	Dark Chanting Goshawk	<i>Melierax metabates</i>	N	43	c	r	ws	stable	SAV
	Gabar Goshawk	<i>Micronisus gabar</i>	N	32	c	r	ws	stable	ANC, SAGR, SAV
	Black Kite	<i>Milvus migrans</i>	N	55	c	bv	sv	unknown	ANC, SAV
	Hooded Vulture	<i>Necrosyrtes monachus</i>	N	70	c	r	ws	decreasing	ANC, SAV
Falconidae	African Harrier Hawk	<i>Polyboroides typus</i>	N	64	c	r	ws	stable	ANC, SAV
	Grey Kestrel	<i>Falco ardosiaceus</i>	N	34.5	c	r	ws	stable	ANC, SAV
Fringillidae	African Hobby	<i>Falco cuvierii</i>	N	29.5	c	r	ws	decreasing	SAV
	Yellow-fronted Canary	<i>Serinus mozambicus</i>	N	12	g	r	ws	decreasing	ANC, SAV
Phasianidae	Ahanta Francolin	<i>Francolinus achantensis</i>	SGS	33	g	r	sf	decreasing	ANC, YSEC
	Double-spurred Francolin	<i>Francolinus bicalcaratus</i>	N	32.5	g	r	sv	decreasing	ANC, SAGR, SAV, YSEC
Odontophoridae	Stone Partridge	<i>Ptilopachus petrosus</i>	N	25	o	r	sv	stable	ANC
Rallidae	Black Crake	<i>Amauornis flavirostra</i>	N	21	o	r	mh	unknown	ANC, YSEC
Columbidae	Red-eyed Dove	<i>Streptopelia semitorquata</i>	N	32	g	r	ws	increasing	ANC, SAGR, SAV, YSEC
	Laughing Dove	<i>Streptopelia senegalensis</i>	N	24	g	r	ws	stable	ANC, SAGR, SAV, YSEC
	Vinaceous Dove	<i>Streptopelia vinacea</i>	N	25	g	r	sv	stable	ANC, SAGR, SAV, YSEC

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Table A.3 (continued)

Family	Common name	Scientific name	Biome-association	Body size (g)	Feeding guild	Migratory behavior	Habitat guild	IUCN population trend	Habitats of this study
	African Green Pigeon	<i>Treron calvus</i>	N	26.5	f	r	ws	decreasing	ANC, SAGR, SAV, YSEC
	Black-billde Wood Dove	<i>Turtur abyssinicus</i>	N	20	f	r	sf	stable	ANC, SAGR, SAV, YSEC
	Blue-spotted Wood Dove	<i>Turtur afer</i>	N	20	g	r	ws	stable	ANC, SAGR, SAV, YSEC
Psittacidae	Senegal Parrot	<i>Poicephalus senegalus</i>	SGS	23	f	r	ws	stable	ANC
	Rose-ringed Parakeet	<i>Psittacula krameri</i>	N	40	f	r	sv	increasing	SAV
Musophagidae	Western Grey Plantain-eater	<i>Crinifer piscator</i>	N	50	f	r	ws	stable	ANC, SAGR, YSEC
	Violet Turaco	<i>Musophaga violacea</i>	SGS	47.5	f	r	f	stable	ANC, SAGR, SAV, YSEC
	Green Turaco	<i>Tauraco persa</i>	GCF	41.5	f	r	f	stable	ANC, SAGR, SAV, YSEC
Cuculidae	Black Coucal	<i>Centropus grillii</i>	N	32.5	i	r	mh	stable	SAV
	Senegal Coucal	<i>Centropus senegalensis</i>	N	38	i	r	ws	stable	ANC, SAGR, SAV, YSEC
	Yellowbill	<i>Ceuthmochares aereus</i>	N	33	i	r	f	stable	ANC, SAGR
	Didric cuckoo	<i>Chrysococcyx caprius</i>	N	19	i	bv	ws	stable	ANC
	African Emerald Cuckoo	<i>Chrysococcyx cupreus</i>	N	23	i	bv	f	stable	ANC, SAGR, YSEC
	Klaas's cuckoo	<i>Chrysococcyx klaas</i>	N	18	i	r	ws	stable	ANC, SAGR, SAV, YSEC
	African Cuckoo	<i>Cuculus gularis</i>	N	32	i	nb	ws	stable	ANC, SAGR, SAV, YSEC
	Red-chested Cuckoo	<i>Cuculus solitarius</i>	N	29.5	i	bv	f	stable	SAGR, SAV, YSEC
	Levaillant's Cuckoo	<i>Oxylophus levaillantii</i>	N	39	i	bv	ws	stable	ANC, SAV
Strigidae	Greyish Eagle Owl	<i>Bubo africanus cinerascens</i>	N	45.5	c	r	ws	stable	SAV
Apodidae	Little Swift	<i>Apus affinis</i>	N	12.75	i	r	a	increasing	ANC, SAV
	Common Swift	<i>Apus apus</i>	N	17.75	i	nb	a	stable	ANC, SAV
	African Palm Swift	<i>Cypsiurus parvus</i>	N	16	i	r	ws	increasing	ANC, SAV
	Mottled Spinetail	<i>Telacanthura ussheri</i>	N	13.5	i	r	ws	stable	ANC
Alcedinidae	African Pygmy Kingfisher	<i>Ceyx pictus</i>	N	12	i	r	sf	stable	ANC, SAGR, SAV, YSEC
	Striped Kingfisher	<i>Halcyon chelicuti</i>	N	17	c	r	ws	stable	SAV
	Grey-headed Kingfisher	<i>Halcyon leucocephala</i>	N	22	c	bv	ws	stable	ANC, SAV
	Blue-breasted Kingfisher	<i>Halcyon malimbica</i>	N	25	c	r	f	decreasing	ANC, SAGR, SAV, YSEC
	Woodland kingfisher	<i>Halcyon senegalensis</i>	N	22	c	r	ws	stable	ANC, YSEC
Meropidae	European Bee-eater	<i>Merops apiaster</i>	N	24	i	nb	ws	stable	SAV
Coraciidae	Abyssinian Roller	<i>Coracias abyssinicus</i>	N	29	i	r	ws	stable	SAV
	Blue-bellied Roller	<i>Coracias cyanogaster</i>	SGS	29	i	r	ws	decreasing	ANC, SAV, YSEC
	Broad-billed Roller	<i>Eurystomus glaucurus</i>	N	29.5	i	r	ws	stable	ANC, SAV
Phoeniculidae	Green Wood Hoopoe	<i>Phoeniculus purpureus</i>	N	37.5	i	r	ws	decreasing	ANC, SAV, YSEC
	Black Scimitarbill	<i>Rhinopomastus aterrimus</i>	N	23	i	r	ws	decreasing	ANC, SAV
Bucerotidae	African Grey Hornbill	<i>Lophoceros nasutus</i>	N	48	o	r	ws	stable	ANC, SAGR, SAV, YSEC
	African Pied Hornbill	<i>Lophoceros semifasciatus</i>	N	51.5	o	r	f	unknown	ANC, SAGR, SAV, YSEC
Picidae	Golden-tailed Woodpecker	<i>Campethera abingoni</i>	N	20	i	r	f	stable	SAGR, SAV, YSEC
	Buff-spotted Woodpecker	<i>Campethera nivosa</i>	GCF	15	i	r	f	stable	SAGR

Table A.3 (continued)

Family	Common name	Scientific name	Biome-association	Body size (g)	Feeding guild	Migratory behavior	Habitat guild	IUCN population trend	Habitats of this study
	Fine-spotted Woodpecker	<i>Campethera punctuligera</i>	N	21	i	r	ws	stable	ANC, SAV
	Cardinal Woodpecker	<i>Dendropicos fuscescens</i>	N	14.5	i	r	ws	stable	ANC, SAV
	Grey Woodpecker	<i>Dendropicos goertae</i>	N	20	i	r	ws	stable	ANC, SAV, YSEC
	Brown-backed Woodpecker	<i>Picoides obsoletus</i>	N	13.5	i	r	ws	stable	ANC, SAV
Eurylaimidae	African Broadbill	<i>Smithornis capensis</i>	N	13	o	r	sf	decreasing	SAGR, YSEC
Alaudidae	Sun Lark	<i>Galerida modesta</i>	SGS	14	g	r	sv	stable	SAV
	Flappet Lark	<i>Mirafra rufocinnamomea</i>	N	13.5	g	r	sv	decreasing	SAV
Hirundinidae	Lesser-striped Swallow	<i>Hirundo abyssinica</i>	N	17	i	bv	ws	increasing	ANC, SAV
	Pied-winged Swallow	<i>Hirundo leucosoma</i>	SGS	12	i	r	ws	increasing	ANC, SAV
	Red-chested Swallow	<i>Hirundo lucida</i>	N	15	i	r	ws	increasing	ANC
	Fanti Saw-Wing	<i>Psalidoprocne obscura</i>	GCF	17	i	r	sf	stable	ANC, SAV
Campephagidae	Sand Martin	<i>Riparia riparia</i>	N	12.5	i	nb	a	decreasing	ANC
	Red-shouldered Cuckoo-Shrike	<i>Campephaga phoenicea</i>	N	20	i	r	f	decreasing	ANC, SAV, YSEC
Pycnonotidae	Ansorge's Greenbul	<i>Andropadus ansorgei</i>	GCF	16	f	r	f	stable	SAV
	Little Greenbul	<i>Andropadus virens</i>	N	16.5	o	r	sf	stable	SAGR
	Grey-headed Bristlebill	<i>Bleda canicapillus</i>	GCF	21.25	i	r	f	stable	ANC, SAGR, YSEC
	Yellow-throated Leaflove	<i>Chlorocichla flavicollis</i>	N	22.5	f	r	sf	stable	ANC, SAGR, SAV, YSEC
	Simple Leaflove	<i>Chlorocichla simplex</i>	GCF	21	o	r	sf	stable	SAGR, YSEC
	Western Nicator	<i>Nicator chloris</i>	GCF	22.5	i	r	f	stable	SAGR, YSEC
	Common Bulbul	<i>Pycnonotus barbatus</i>	N	19	o	r	ws	increasing	ANC, SAGR, SAV, YSEC
	Leaflove	<i>Pyrrhurus scandens</i>	GCF	22	i	r	f	stable	ANC, SAGR, YSEC
Turdidae	African Thrush	<i>Turdus pelios</i>	N	23	o	r	f	unknown	ANC, SAGR, SAV, YSEC
Sylviidae	Senegal Eremomela	<i>Eremomela pusilla</i>	SGS	10	i	r	ws	stable	SAV
	Yellow-bellied Hyliota	<i>Hyliota flavigaster</i>	N	12.5	i	r	ws	decreasing	ANC, SAV
	African Moustached Warbler	<i>Melocichla mentalis</i>	N	19.5	i	r	sv	stable	ANC
Cisticolidae	Yellow-breasted Apalis	<i>Apalis flavida</i>	N	11.5	i	r	sf	increasing	ANC, SAGR, YSEC
	Grey-backed Camaroptera	<i>Camaroptera brachyura</i>	N	11.5	i	r	ws	stable	ANC, SAGR, SAV, YSEC
	Singing Cisticola	<i>Cisticola cantans</i>	N	12.75	i	r	sf	stable	ANC, SAV
	Red-faced Cisticola	<i>Cisticola erythrops</i>	N	13	i	r	ws	stable	ANC
	Winding Cisticola	<i>Cisticola galactotes</i>	N	13.5	i	r	mh	stable	SAV
	Rufous Cisticola	<i>Cisticola rufus</i>	SGS	10	i	r	ws	stable	ANC, YSEC
	Whistling Cisticola	<i>Citicola lateralis</i>	N	13.25	i	r	ws	stable	ANC
	Red-winged Warbler	<i>Heliolais erythropterus</i>	N	12	i	r	ws	stable	ANC, SAV, YSEC
	Oriole Warbler	<i>Hypergerus atriceps</i>	SGS	20	i	r	sf	stable	ANC, SAGR, SAV, YSEC
	Tawny-flanked Prinia	<i>Prinia subflava</i>	N	11.5	i	r	ws	stable	ANC, SAGR, SAV, YSEC
Muscicapidae	Pale Flycatcher	<i>Bradornis pallidus</i>	N	16	i	r	ws	stable	SAV
	White-crowned Robin Chat	<i>Cossypha albicapilla</i>	SGS	26	i	r	sf	stable	ANC, SAGR, SAV, YSEC
	Snowy-Crowned Robin Chat	<i>Cossypha niveicapilla</i>	N	21.25	i	r	sf	stable	ANC, SAGR, SAV, YSEC
			N	20	i	r	ws	stable	

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Table A.3 (continued)

Family	Common name	Scientific name	Biome-association	Body size (g)	Feeding guild	Migratory behavior	Habitat guild	IUCN population trend	Habitats of this study
Platysteiridae	Northern Black Flycatcher	<i>Melaenornis edoloides</i>							ANC, SAV, YSEC
	Red-bellied Paradise Flycatcher	<i>Terpsiphone rufiventer</i>	GCF	18	i	r	sf	decreasing	ANC, SAGR, SAV, YSEC
	African Paradise-Flycatcher	<i>Terpsiphone viridis</i>	N	18	i	r	sf	stable	SAGR, SAV, YSEC
	Senegal Batis	<i>Batis senegalensis</i>	N	10.5	i	r	ws	decreasing	ANC, SAV
	Common Wattle-eye	<i>Platysteira cyanea</i>	N	13	i	r	sf	stable	ANC, SAGR, SAV, YSEC
Timaliidae	Brown Illadopsis	<i>Illadopsis fulvescens</i>	GCF	16	i	r	f	stable	SAGR, SAV, YSEC
	Capuchin Babbler	<i>Phyllanthus atripennis</i>	GCF	24	o	r	sf	unknown	ANC, SAGR, YSEC
	Brown Babbler	<i>Turdoides plebejus</i>	N	24	o	r	sf	stable	ANC, SAGR, SAV, YSEC
	Blackcap Babbler	<i>Turdoides reinwardtii</i>	SGS	25	o	r	mh	decreasing	ANC, SAGR, SAV, YSEC
Paridae	White-shouldered Black Tit	<i>Parus guineensis</i>	N	14	o	r	sv	decreasing	ANC, SAV
Zosteropidae	Yellow White-eye	<i>Zosterops senegalensis</i>	N	10.5	i	r	ws	stable	ANC, SAGR, SAV, YSEC
Nectariniidae	Scarlet-chested Sunbird	<i>Chalcomitra senegalensis</i>	N	14.5	fv	r	f	stable	ANC, SAGR, SAV, YSEC
	Western violet-backed Sunbird	<i>Anthreptes longuemarei</i>	N	13.5	fv	r	ws	stable	ANC, SAV
	Splendid Sunbird	<i>Cinnyris coccinigastrus</i>	SGS	14	fv	r	ws	stable	ANC, SAGR, SAV, YSEC
	Copper Sunbird	<i>Cinnyris cupreus</i>	N	12.5	fv	r	ws	stable	ANC, SAV, YSEC
	Beautiful Sunbird	<i>Cinnyris pulchellus</i>	N	10	fv	r	ws	stable	ANC, SAV, YSEC
	Variable Sunbird	<i>Cinnyris venustus</i>	N	10	fv	r	ws	stable	ANC, SAV
	Olive Sunbird	<i>Cyanomitra olivacea</i>	N	14	fv	r	f	stable	SAGR, YSEC
	Green-headed Sunbird	<i>Cyanomitra verticalis</i>	N	13.5	fv	r	ws	stable	ANC, SAGR, SAV, YSEC
	Collared Sunbird	<i>Hedydipna collaris</i>	N	10	fv	r	sf	stable	ANC, SAGR, SAV, YSEC
	Pygmy Sunbird	<i>Hedydipna platura</i>	N	9.5	fv	bv	ws	stable	ANC, SAGR, SAV
Laniidae	Yellow-billed Shrike	<i>Corvinella corvina</i>	SGS	31.5	i	r	ws	unknown	ANC, SAV
	Vieillot's Barbet	<i>Lybius vieilloti</i>	N	15	f	r	ws	unknown	ANC, SAGR, SAV
Indicatoridae	Yellow-rumped Tinkerbird	<i>Pogoniulus bilineatus</i>	N	10	f	r	f	stable	ANC, SAGR, SAV, YSEC
	Yellow-fronted Tinkerbird	<i>Pogoniulus chrysoconus</i>	N	11.5	f	r	ws	stable	ANC, SAGR, SAV, YSEC
	Greater Honeyguide	<i>Indicator indicator</i>	N	18.75	i	r	ws	increasing	SAV, YSEC
	Spotted Honeyguide	<i>Indicator maculatus</i>	GCF	17	o	r	f	decreasing	ANC, SAGR, YSEC
	Lesser Honeyguide	<i>Indicator minor</i>	N	14.5	o	r	ws	stable	ANC, SAV, YSEC
Malaconotidae	Wahlbergs's Honeybird	<i>Prodotiscus regulus</i>	N	12.5	i	r	sf	increasing	ANC
	Northern Puffback	<i>Dryoscopus gambensis</i>	N	18.5	i	r	ws	stable	ANC, SAGR, SAV, YSEC
	Yellow-crowned Gonolek	<i>Laniarius barbarus</i>	N	23	i	r	sf	stable	ANC, SAGR, SAV, YSEC
	Turatis Boubou	<i>Laniarius turatii</i>	GCF	23	i	r	sf	stable	ANC, SAGR, SAV, YSEC
	Grey-headed Bushshrike	<i>Malaconotus blanchoti</i>	N	25	i	r	ws	increasing	ANC, SAGR, SAV, YSEC
	Brubru	<i>Nilaus afer</i>	N	14	i	r	ws	stable	SAV
	White helmet-Shrike	<i>Prionops plumatus</i>	N	21	i	r	ws	stable	ANC, SAV, YSEC
	Black-crowned Tchagra	<i>Tchagra senegalus</i>	N	21	i	r	ws	stable	

Table A.3 (continued)

Family	Common name	Scientific name	Biome-association	Body size (g)	Feeding guild	Migratory behavior	Habitat guild	IUCN population trend	Habitats of this study
									ANC, SAV, YSEC
	Sulphur-breasted Bush-Shrike	<i>Telophorus sulfureopectus</i>	N	18	i	r	ws	stable	ANC, SAGR, SAV, YSEC
Oriolidae	African Golden Oriole	<i>Oriolus auratus</i>	N	24	o	r	ws	stable	ANC, SAGR, SAV, YSEC
	Black-winged Oriole	<i>Oriolus nigripennis</i>	GCF	20	o	r	f	decreasing	ANC, SAGR, SAV, YSEC
	Eurasian Golden Oriole	<i>Oriolus oriolus</i>	N	24	o	nb	f	stable	SAV
Dicruridae	Fork-tailed Drongo	<i>Dicrurus adsimilis</i>	N	23.75	i	r	ws	stable	ANC, SAGR, SAV, YSEC
	Square-tailed Drongo	<i>Dicrurus ludwigii</i>	N	19	i	r	sf	stable	SAGR
Corvidae	Piapiac	<i>Ptilostomus afer</i>	SGS	35	o	r	ws	stable	SAV
Sturnidae	Yellow-billed Oxpecker	<i>Buphagus africanus</i>	N	22	o	r	ws	decreasing	ANC
	Violet-backed Starling	<i>Cinnyricinclus leucogaster</i>	N	17	o	bv	ws	decreasing	ANC, SAGR, SAV, YSEC
	Bronze-tailed Glossy Starling	<i>Lamprotornis chalcurus</i>	N	21.5	o	r	ws	stable	ANC, SAV
	Lesser Blue-eared Starling	<i>Lamprotornis chloropterus</i>	N	19.5	o	r	ws	stable	SAV
	Purple Glossy Starling	<i>Lamprotornis purpureus</i>	SGS	24	o	r	sv	stable	ANC
Passeridae	Northern Grey-headed Sparrow	<i>Passer griseus</i>	N	14	g	r	ws	stable	ANC, SAV
	Bush Petronia	<i>Petronia dentata</i>	N	13	g	r	ws	stable	SAV
	Chestnut-crowned Sparrow Weaver	<i>Plocepasser superciliosus</i>	SGS	17	g	r	ws	stable	SAV
Ploceidae	Northern Red Bishop	<i>Euplectes franciscanus</i>	N	11.5	g	r	mh	stable	SAV
	Back-winged Bishop	<i>Euplectes hordeaceus</i>	N	13.5	i	r	mh	stable	ANC
	Yellow-mantled Widowbird	<i>Euplectes macroura</i>	N	16.75	g	r	mh	stable	ANC, SAV
	Village Weaver	<i>Ploceus cucullatus</i>	N	16.25	g	r	ws	stable	ANC, SAGR, SAV, YSEC
	Little Weaver	<i>Ploceus luteolus</i>	N	11.5	g	r	ws	stable	ANC, SAV, YSEC
	Black-headed Weaver	<i>Ploceus melanocephalus</i>	N	14.5	o	r	mh	stable	ANC, SAV, YSEC
	Back-necked Weaver	<i>Ploceus nigricollis</i>	N	17	o	r	ws	stable	ANC, SAGR, YSEC
	Vitelline-masked Weaver	<i>Ploceus vitellinus</i>	N	14	g	r	sv	stable	ANC, SAGR, SAV, YSEC
	Red-billed Quelea	<i>Quelea quelea</i>	N	12	g	r	ws	stable	ANC, SAV
Estrildidae	Lavender Waxbill	<i>Estrilda caerulescens</i>	SGS	10	g	r	ws	stable	ANC, SAGR, YSEC
	Orange-cheeked Waxbill	<i>Estrilda melpoda</i>	N	10	g	r	sv	stable	ANC, SAV
	Dybowski's Twinspot	<i>Euschistospiza dybowskii</i>	SGS	12	g	r	ws	stable	ANC, YSEC
	Black-faced Firefinch	<i>Lagonosticta larvata</i>	SGS	11.5	g	r	ws	stable	ANC
	Black-bellied Firefinch	<i>Lagonosticta rara</i>	SGS	10	g	r	sv	stable	ANC, SAV
	Blue-billed Firefinch	<i>Lagonosticta rubricata</i>	N	10	g	r	ws	stable	ANC, YSEC
	Bar-breasted Firefinch	<i>Lagonosticta rufopicta</i>	SGS	11	g	r	sv	stable	ANC
	Red-billed Firefinch	<i>Lagonosticta senegala</i>	N	10	g	r	ws	stable	ANC, YSEC
	Bronze Mannikin	<i>Lonchura cucullata</i>	N	9	g	r	sf	stable	ANC, YSEC
	Crimson Seedcracker	<i>Pyrenestes sanguineus</i>	GCF	13.5	g	r	f	stable	SAGR
	Red-winged Pytilia	<i>Pytilia phoenicoptera</i>	SGS	12.75	g	r	ws	stable	ANC, SAV

(continued on next page)

Table A.3 (continued)

Family	Common name	Scientific name	Biome-association	Body size (g)	Feeding guild	Migratory behavior	Habitat guild	IUCN population trend	Habitats of this study
Viduidae	Red-cheeked Cordon-Bleu	<i>Uraeginthus bengalus</i>	N	13	g	r	sv	stable	ANC, SAV
	Exclamatory Paradise-Whydah	<i>Vidua interjecta</i>	N	12.5	g	r	ws	stable	SAV, YSEC
	Pin-tailed Whydah	<i>Vidua macroura</i>	N	12.5	g	r	ws	stable	ANC, SAV

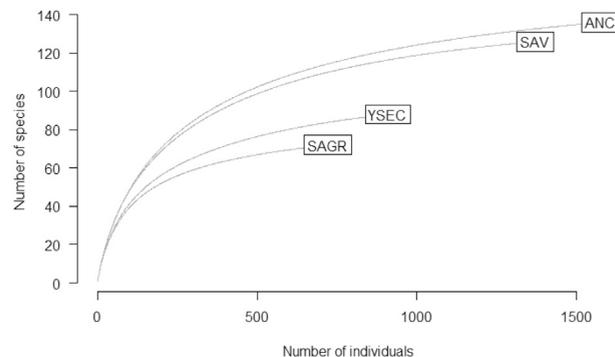


Fig. A1. Species accumulation curves per habitat type (SAGR= Sacred Groves, YSEC= Young Secondary Forests, SAV=Wooded Savannas, and ANC= Annual Cultures).

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