Similar bird communities in homegardens at different distances from Afromontane forests

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Summary

Human modified landscapes make up a growing proportion of the tropics, but are relatively little studied. The spatial distribution of remnant vegetation can structure and shape local biodiversity, affecting the provisioning of ecosystem services and regulation of pest problems. We compared species composition, abundance and functional diversity of birds between forest and homegardens close to (0–100 m) and further away from (1,500–2,000 m) moist evergreen Afromontane forests in south-western Ethiopia. We thoroughly inventoried birds with point counts and mist netting in two forest sites and three garden sites of each type. Gardens differed in general species composition from forests, with fewer forest specialist species (7% versus 29% of recorded species), but instead supported many other species that were rarely encountered in the forests. Overall gardens had higher numbers of species than forests. Homegardens close to the forest and further from the forest were similar to each other in terms of species richness and overall species composition. Both garden types had a similar composition in terms of the relative proportion of species with different habitat preferences as well as the composition of species from different feeding guilds. The lack of forest specialists in even the most structurally complex part of the agricultural landscape close to forest edges suggests that the last larger forest remnants are critical for conservation of forest specialists. Nonetheless, homegardens maintain rich bird diversity that also should be considered in a biodiversity conservation context. Further research is needed to establish to what extent the richness and composition of the agro-ecological bird fauna is regulated by the existence of forest patches in the region. Our results could not resolve this question since gardens two kilometers from the forest edge were similar in composition to gardens close to the forest edges.

Introduction

Degraded and modified habitats make up a growing proportion of the tropics and it is therefore important to assess their capacity to sustain biodiversity (Gray *et al.* 2007, Laube *et al.* 2008, Renwick *et al.* 2014). Alterations in species richness and composition can affect the functional diversity of an ecological community (Gray *et al.* 2007, Şekercioğlu 2012a), which in turn could have an effect on ecosystem function and services. Birds play an important role in providing regulatory ecosystem services such as pollination, pest control, seed dispersal and scavenging (Şekercioğlu *et al.* 2016) and specialist birds are more likely to be threatened with extinction (Şekercioğlu 2011). However, birds can also provide ecosystem "disservices", with granivores sometimes becoming pests by feeding on cereals (de Mey *et al.* 2012) and birds of prey on poultry (Dessie and Ogle 2001).

Previous studies in the tropics have shown that birds from different feeding guilds respond differently to forest disturbance and conversion (Gray *et al.* 2007, Tscharntke *et al.* 2008, Sodhi *et al.* 2011). In general, forest modification and fragmentation result in an increase of granivores

and a decline of large frugivores and insectivores (Sodhi *et al.* 2008, Şekercioğlu 2012a, Bregman *et al.* 2014). For insectivores, the impact differs among the various sub-guilds (Dale *et al.* 2000) and is most severe for species of the understorey. These are thought to be sensitive to disturbance because of their inability to disperse in a non-forest matrix (Newmark 1991, Şekercioğlu *et al.* 2002). The effects of habitat disturbance on numbers of omnivores, carnivores and nectarivores are less general and differ among regions (Gray *et al.* 2007, Şekercioğlu 2012a). As Africa is understudied in this aspect, similar generalisations cannot be made for this continent (Gray *et al.* 2007).

In this study, we examine the bird communities of forest and homegardens located in an agricultural landscape in south-western Ethiopia by investigating the compositional changes, focusing on species richness and abundances of birds with different diet and habitat preferences. We compare homegardens close to and 2 km away from forest, in particular, to see whether distance to forest has an effect on bird functional and species diversity. Although bird species composition is primarily determined by vegetation complexity and tree density (Naidoo 2004, Laube *et al.* 2008, Douglas *et al.* 2014), proximity to forest has been observed to be an important factor for especially forest-dependent birds (Laube *et al.* 2008; Sodhi *et al.* 2011). Thus, in order to highlight the effect of distance, we chose homegardens of similar structural complexity. We combined point counts and mist netting to maximize our sampling effort.

Based on previous studies of agroecosystems in Ethiopia (Wilson *et al.* 1997, Gove *et al.* 2008, 2013) and East Africa (Naidoo 2004, Mulwa *et al.* 2012), we expect to find two distinct bird communities in forests and homegardens. The abundance and species richness of forest specialists and forest generalists would decline with distance from forest as homegardens closer to forest are more easily colonised or visited by foraging individuals (especially in the dry season; Laube et al. 2008). With regard to bird functional diversity, we hypothesise that with increasing distance from forest, absolute numbers of insectivorous and possibly frugivorous species will decline while granivores will increase (Şekercioğlu 2012a).

Methods

Study area and sites

The fieldwork took place during February–May 2012 in the countryside between Agaro and Gera, Jimma Zone, south-west Ethiopia (07°45″–07°48″N, 36°17″–36°24″E; 1,850–2,100 m asl). This agricultural landscape is bordered to the north and south by two large forest remnants belonging to the so called Belete-Gera national forest priority area (Figure 1).

These moist evergreen forests belong to the Eastern Afromontane global biodiversity hotspot. The average annual temperature is 20°C and the annual precipitation ranges from 1,500 to more than 2,000 mm (Friis *et al.* 2011). Dominant canopy tree species include *Pouteria adolfi-friederici*, *Albizia gummifera*, *Croton macrostachyus*, *Syzygium guineense*, and *Millettia ferruginea* (Cheng *et al.* 1998, Friis *et al.* 2011). The shrubby understorey is diverse, as are the number of epiphytes and lianas. In 1998, the Belete-Gera forest covered an area of 150,000 ha, but its size is continuously reduced due to agricultural encroachment (Cheng *et al.* 1998, Hylander *et al.* 2013). Like most of the forest remnants in Ethiopia (Teketay *et al.* 2010) and Eastern Africa (Borghesio 2008), our study forests are also heavily disturbed by human activities such as selective logging, livestock grazing and coffee production (Cheng *et al.* 1998, Hundera *et al.* 2013, Hylander *et al.* 2013). Coffee *Coffea arabica* is a native species in the forests, but is also widely promoted in the study area and many trees and shrubs of the understory are therefore frequently cleared (Hundera *et al.* 2013). The more intensively used areas along forest margins and in forest patches are denoted semi-forest coffee or even in some cases semi-plantation coffee (Hundera *et al.* 2013).

The agricultural landscape is structurally complex and contains shrublands, (wet) grasslands, exotic tree plantations and cultivated areas. The smallholder farmers grow several crops such as
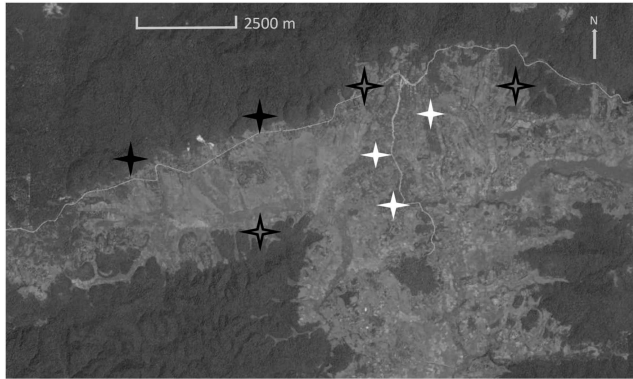
Figure 1. Overview map of the study area in south-west Ethiopia. Black – forest sites, dark grey – homegardens close to forest (0–100 m) and white – homegardens further away from forest (1,500–2,000 m). (Google Earth; Image © 2016 CNES/Astrium).

teff, maize, sorghum, khat, avocado, banana and ensete (Lemessa *et al.* 2013). Their live fences consist of natural vegetation and planted species of *Euphorbia* and *Erythrina*. Scattered across the landscape are remnant forest trees, which are used for shading coffee and hanging beehives, but there are also introduced trees such as several *Eucalyptus* spp., which mostly serve as firewood or construction material (Ango *et al.* 2014).

Study design and bird surveys

We selected nine sites: three forest sites inside the major forest block, three homegardens close to that forest (0–100 m) and three homegardens further away from that and any other larger forest block (1,500–2,000 m), but had to omit one forest site due to unforeseen circumstances (Figure 1). All eight sites were at least 1,500 m apart. Forest sites were selected to be as undisturbed as possible and at 300–400 m from the edge (see Dale *et al.* 2000). Although there had been some understorey clearing for promoting coffee, our selected sites had many other native trees and shrubs. Since the forest is located on hilly slopes, the selected sites were situated at c.100 m higher elevations than the garden sites. Homegarden sites were typical smallholder farms with several crops and live fences with an area of around 1 ha. Homegardens vary a lot in tree species richness, in the amount of trees and shrubs and in their vertical complexity. Therefore, we chose six sites that were at the complex end of these gradients and as similar to one another as possible. These sites were part of a larger study involving 40 homegardens (Lemessa *et al.* 2015), so more details on vegetation characteristics can be found there.

Each site was visited six times in total. These visits were equally divided between only mist netting, only point counts or conducting both methods simultaneously. Consequently, the data from each site are based on four mist netting days and four point-count days. Point counts at each site were separated by at least eight days and mist netting was done twice for two consecutive days, with at least a two-week gap.

For mist netting, we used 14 2.5 m-high, 4-shelf nets (12 x 12 m nets and 2 x 9 m nets), for a total of 162 m at each site. The nets were opened every day from 06h00 to 12h00, but had to be occasionally closed during periods of rain, passing cattle, etc. (for a total of 10 h in close gardens, 2.5 h in far gardens and 0 h in forest). Nets were checked every half hour by two people working in opposite directions in order to limit the time spent around the nets. After the birds were extracted, they were identified using Redman *et al.* (2011) and banded with numbered metal rings. Biometric and demographic data were collected on age, sex, wing length, tail length, weight, wing moult, body moult and fat score (for Palearctic migrants). Birds that were positively identified

but escaped before ringing were included in the data as "unringed". Recaptured individuals were used only once in the analyses.

Point counts were conducted at four locations in each site, all at least 50 m apart from one another. For homegardens, these places were selected in a way so that the entire garden could be overseen and surveyed. In forests, point count locations were positioned in a more or less square constellation and chosen in such a way that combining these locations enabled us to survey both the understorey and the canopy in every site. Point counts took place between 07h00 and 10h30 and all four locations within a site were visited twice during this period for 20 min each time. Species name, number of individuals and location (tree, bush, ground) were recorded. Birds observed from a point count location that were outside the site area were not counted, but over-flying species were included in the count. However, overflying birds were not used in all analyses (see below).

Due to unforeseen problems we had to close the mist nets for one entire day in one of the homegardens close to forest. Despite this, the correction of mist netting data by effort shows that capture rates were highest in close gardens (5.2 captures per 100 m of mist net per hour, compared to 4.4 for far gardens and 0.88 for forest sites).

Bird classification

Observed birds were grouped into six different feeding guilds based on 'The Birds of Africa volumes I-VII' (Brown *et al.* 1982, Urban *et al.* 1986, 1997, Fry *et al.* 1988, Keith *et al.* 1992, Fry and Keith 2000, 2004). These guilds are carnivores, frugivores, granivores, insectivores, nectarivores and omnivores (Appendix S1 in the online supplementary material). A species that feeds equally on two or more food sources was considered to be an omnivore. Following Gove *et al.* (2013 [except the 'bees' category]) insectivores were further divided into seven different sub-guilds: aerial foragers, arboreal foliage gleaners, bark gleaners, pouncers, salliers, terrestrial species and understorey foliage gleaners. Definitions of the different insectivorous feeding strategies are described by Gokula and Vijayan (2000).

Birds were also classified according to habitat preference as forest specialist, forest general-ist, forest visitor or species of open country (Appendix S1). This was done primarily by fol-lowing Bennun *et al.* (1996), but also 'The Birds of Africa volumes I-VII' and BirdLife International (2015). Species not known to occur in forest were categorised as birds of open country.

Data analyses

We omitted all raptors (10 species), swifts (one species), and swallows/martins (four species) from the comparisons between forests and gardens, since these are mostly aerial species that are less detectable in the forest and not obviously associated with the specific site. However, all species were retained in the comparisons between close gardens and those fur-ther away.

In order to create one robust dataset that made use of both data from the point counts and mist-netting and at the same time included a ranking from frequent to rare, we defined a measure called "bird record" as follows. For each species observed during a point count, we used the frequency of observation days in one locality (1–4 occasions) as the number of records to be used in the analysis. Species only encountered during mist netting at a locality were counted as one record, since we assume that it was a rarer species than those encoun-tered also by the point count method. It was uncommon to encounter a species several times in mist nets at a site without ever recording it during a point count. This provides support for our scoring system, with the caveat that the occurrence of a few species of skulking understorey species might have been slightly underestimated. Thus, for each locality each species encountered got a value from one to four.

We used Permutational Multivariate Analysis of Variance with the ADONIS-function (with 999 permutations) in the *vegan* package to analyse the difference in species composition of the habitats (forest versus homegardens and close and far away gardens, respectively) using the data matrix of bird records. The same dataset was used in an Indicator Species Analysis to compare forest and gardens using the package *labsdv*. In order to compare compositions of habitat preference groups and feeding guilds, we ran a χ^2-test based on the combined data of the sites in each habitat. We created species accumulation curves from the pooled data from the two forest sites and the three garden sites of each type, respectively, using the software EstimateS (Colwell 2013). As input data we used the bird record matrix (see above).

The numbers of species belonging to different habitat preference groups were compared between close and far gardens with a generalised linear model with a Poisson distribution (or in case of over-dispersion, quasi-Poisson error structure). A significant interaction between garden type (close or far) and habitat preference group would indicate a difference in certain groups. A similar analysis was run for number of individuals caught in mist nets. The same approach was also followed for comparisons between garden types of species richness and abundances of mist netted birds categorized by feeding guilds. Model assumptions were evaluated by inspecting residual plots. All analyses were executed in R 3.1.1 (R Development Core Team 2014) unless otherwise stated.

Results

Species composition, mist netting and point counts

We recorded a total of 107 species belonging to 38 families at the eight different sites (Appendix S1). Among these were 12 Palearctic migrants, two inter-African migrants and seven species endemic to the Abyssinian Highlands. Four species (all vultures) are globally threatened with extinction (BirdLife International 2015). In total we observed 11 forest specialist species, 20 forest generalists, 57 forest visitors and 19 species of open country. In total we observed 98 bird species during 128 point counts and we caught 1092 birds of 68 species in the mist nets. Point counts were similarly efficient in all sites and recorded between 85% and 91% percent of all observed birds. Mist netting detections, however, were lower in forest sites (34–47 %) compared to both close (68–73 %) and far gardens (64–74 %). Without mist-netting, we would have missed Green Twinspot *Mandingoa nitidula* and Abyssinian Crimsonwing *Cryptospiza salvadorii* in the forest, while missing Black-and-white Mannikin *Lonchura bicolor*, Whinchat *Saxicola rubetra*, African Hill-babbler *Pseudoalcippe abyssinica*, Lemon Dove *Columba larvata*, Green Twinspot, Scaly-throated Honeyguide *Indicator variegatus*, Greater Honeyguide *Indicator indicator*, Pin-tailed Whydah *Vidua macroura*, Eurasian Reed Warbler *Acrocephalus scirpaceus*, Malachite Kingfisher *Alcedo cristata* and Common Fiscal *Lanius collaris* in gardens.

Forests vs. gardens

Forest sites had a significantly different species composition than gardens (ADONIS, *P* = 0.035), exemplified by a higher relative proportion of forest specialists (29% of the recorded species in the forests versus 7% in gardens) and forest generalists (32% vs. 20%) (Fig 2, [$\chi^2_{(3)}$ = 18.8, *P* < 0.001]). An indicator species analysis showed that several forest specialists (e.g. Grey Cuckooshrike *Coracina caesia*, Abyssinian Oriole *Oriolus monacha*, White-cheeked Turaco *Tauraco leucotis*) were especially overrepresented in the forest sites, while several species classified as open habitat species, forest visitors and even some forest generalists (e.g. Abyssinian Slaty Flycatcher *Melaenornis chocolatinus* and Mountain Thrush *Turdus abyssinicus*) had a significant preference for garden sites (Appendix S1). The forest sites tended to have lower species richness than both garden types, as seen when comparing the species accumulation curves of observations in the three habitats (Fig. 3).
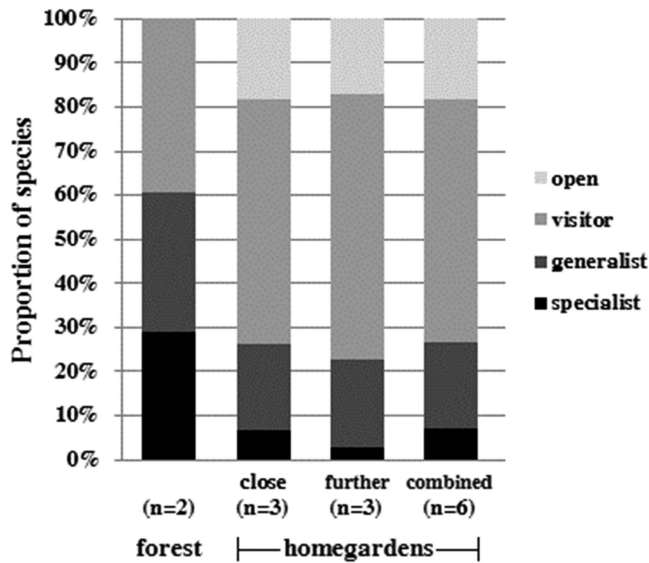
Figure 2. Compositions of bird communities divided into habitat preference groups for homegardens (pooled), forest, close and far gardens (based on combined data for every habitat).

Close and far gardens

The species compositions of close and far gardens were similar (ADONIS, P = 0.18), which was also seen when comparing the relative proportion of habitat preference groups (χ^2-test P = 0.75, Fig. 4a). Close and far gardens did not significantly differ in the number of species for any of the habitat preference groups (Figure 4a). Neither was there any significant effect on abundances of mist-netted birds in general or the interaction with habitat preference group (P = 0.18 for the interaction in a *glm* with quasi-Poisson error structure). However, there was a tendency for more individuals of forest generalists in close gardens (Figure 4c). There were no significant differences in either number of species (Figure 4b) or bird individuals caught in the mist-nets (Figure 4d) between close and far gardens when separated by feeding guilds (no significant effect of garden type or the interaction between garden type and feeding guild in *glms* with Poisson error terms, P > 0.4). All different sub-guilds of insectivorous species occurred both in close and far gardens and none of the groups seemed to be restricted to forest (Table 1).

Discussion

Our results show three important patterns of the bird communities across the landscape: (1) species richness of forest sites was lower than that of gardens; (2) forest and gardens were characterised by two distinct bird communities; (3) distance to forest (up to 2 km) had no significant effect on the species composition (close and far gardens were surprisingly similar). The first two results agree with those of other studies conducted in agro-ecosystems of East Africa (Naidoo 2004, Gove *et al.* 2008, 2013, Laube *et al.* 2008, Mulwa *et al.* 2012), but the absence of the effect of distance is interesting, as changes in community composition and a decline of forest specialist species have been attributed to distance from forest (Naidoo 2004, Gove *et al.* 2008, Laube *et al.* 2008). Forest specialists disappeared immediately at the forest border, while forest generalists were found across the entire 2-km gradient. With a longer gradient than 2 km, we might have seen a decline also for the forest generalists.
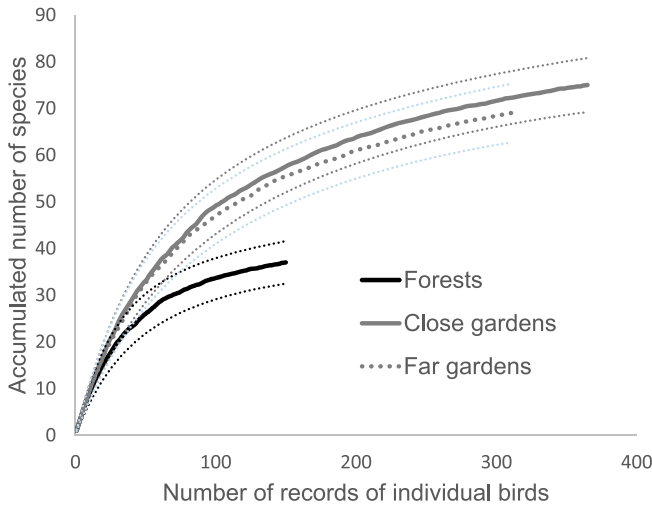
Figure 3. Number of accumulated species as a function of number of species records in the pooled data from forests, homegardens close to forests and homegardens 2 km further away from forests. A record is defined as a presence/absence record of the species during one day of point counting (possible values 0–4 per species). If a species was only observed by ringing, it was given a record number of 1. Pooled data are from the two forest sites and the three sites of each of the homegarden types (See also Methods). Accumulation curves with 95% confidence intervals shown.

Proportions of forest specialists and generalists were higher in forest, while forest visitors and open country species were proportionally more abundant in farmland. Birds assigned to the latter group were completely absent from forest sites. The sensitivity of forest specialist species to forest disturbance and conversion has been documented extensively (Fjeldså 1999, Şekercioğlu 2002, Naidoo 2004, Borghesio 2008, Gove *et al.* 2008, Laube *et al.* 2008, Mulwa *et al.* 2012, Buechley *et al.* 2015). In this study only one forest specialist (out of 11), Olive Sunbird, was seen several times in both close and far gardens, which makes the classification of this species as a forest specialist by Bennun *et al.* (1996) questionable. The fact that proximity to forest did not seem to affect the presence of forest specialists in gardens could suggest that the vegetation complexity has already decreased to such an extent that distance is not important anymore. For birds in the agricultural landscape, distance might play a bigger role when it involves moving to secondary forests or coffee agroforest sites where tree density and vertical heterogeneity are much higher than in complex gardens (Naidoo 2004, Buechley *et al.* 2015). Forest remnants are important as a species pool for neighbouring regenerating forests (Newmark 1991, Naidoo 2004, Aerts *et al.* 2008, Mulwa *et al.* 2012). In contrast, heterogeneous farmland, despite hosting a large number of species, seems unable to support forest specialists (even as visitors) and will thus not offset forest loss (see also Naidoo 2004, Laube *et al.* 2008, Hulme *et al.* 2013, Buechley *et al.* 2015).

On the contrary, forest generalists were seen regularly in the agricultural landscape. However, observations of forest-dependent species in farmland may not indicate the actual suitability of agricultural habitats to sustain these species in the absence of surrounding forest (Naidoo 2004). Some species observed in the farmland may be travelling between forest remnants or could consist of declining sink populations that can only be identified through long-term demographic studies. Also, if the study had taken place during the breeding season, fewer forest generalists might have been observed in the homegardens (Bennun *et al.* 1996). Gove *et al.* (2008) observed birds during the wet season in a similar landscape in Ethiopia and did indeed find more forest generalists in the forest than in the agricultural landscape.
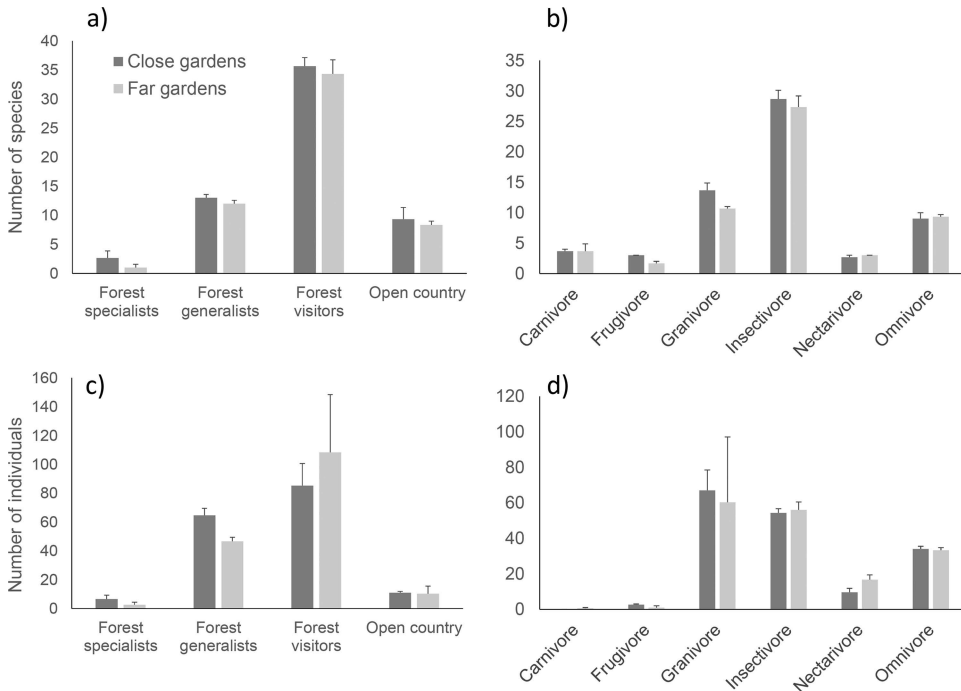
Figure 4. Mean number of species (a, b) and individuals caught in the mist nets (c, d) according to their habitat preference group (a, c) and feeding guilds (b, d) for close and far garden sites. Black lines indicate standard error.

What is clear from our results is that the feeding guild composition did not change with distance from forest over these rather short distances (2 km). Both garden types hold very similar number of species and abundances of each of the individual feeding guilds (Figures. 4b, 4d) and it could be argued that distance to forest does not affect the provisioning of ecosystem (dis)services by birds in this landscape. Even when insectivores were divided into sub-guilds, it seems like their occurrence pattern is uniform between the close gardens and those further away. Interestingly however, each of the sub-guilds was represented by a higher number of species in farmland than in forest (Table 1). This is surprising since many previous studies from other areas highlight the

Table 1. Number of encountered insectivore species per subguild for forest, close gardens and gardens 2 km from the forest (far gardens), and farmland based on the combined data for each habitat. n = number of sites.

Insectivore sub-guilds	Forest	Homegardens		
		Close	Far	Combined
	($n = 2$)	($n = 3$)	($n = 3$)	($n = 6$)
Aerial*	3	6	6	6
Arboreal foliage gleaner	7	12	10	14
Bark gleaner	0	3	3	4
Pouncer	0	3	6	6
Sallier	4	9	8	9
Terrestrial	4	5	3	5
Understorey foliage gleaner	4	5	5	6

*not included in the general comparison between forests and farmland

negative impact on insectivorous birds - terrestrial and understorey gleaners in particular - caused by forest disturbance (Fjeldså 1999, Dale *et al.* 2000, Şekercioğlu 2002, Borghesio 2008), fragmentation (Bregman *et al.* 2014) and conversion to farmland (Waltert *et al.* 2005, Mulwa *et al.* 2012). However, our results with many insectivores in the tree-rich agricultural landscape are in line with previous findings in Ethiopia (Gove *et al.* 2013, Buechley *et al.* 2015) and could possibly be explained by the impoverished forest avifauna of Ethiopia compared to other Afromontane regions (lacking understorey genera such as *Illadopsis*, *Sheppardia* and *Neocossyphus*, and other typical forest insectivores, like members of the greenbul family and the genus *Apalis*) as a result of extinctions linked to climatic changes in the past (Moreau 1966). With global climate once again threating tropical bird communities worldwide (Wormworth and Şekercioğlu 2011), in this traditional landscape where native coffee plants are often grown under the shade of native forest trees, it is essential to maintain and promote this biodiversity-friendly agriculture in order to connect native forest remnants surrounded by a growing agricultural matrix.

Previous studies have also shown that forest specialist frugivores especially decline with distance from forest (Laube *et al.* 2008) and forest disturbance (Borghesio 2008, Kirika *et al.* 2008). Of the nine frugivorous species observed in this study, the majority were forest-dependent (four forest specialist and three generalist species) and had a tendency to occur more frequently in forests than in gardens (Appendix S1). However, there was no significant difference in guild composition between gardens close to and 2 km away from forests. Although some other fruit-eating birds (e.g. barbets, tinkerbirds, thrushes) were classified as omnivores in this study, their services in terms of fruit removal are unlikely to replace those of forest specialists (Kirika *et al.* 2008). Frugivorous birds play an important role in seed dispersal and subsequent habitat regeneration (Şekercioğlu 2006, Şekercioğlu *et al.* 2016). A decline in their overall numbers, and in forest specialist frugivores in particular, could have serious negative impacts on future forest recovery. Even though there are other frugivorous animals besides birds and the distribution of frugivorous birds across the landscape can be affected by several other factors, such as season (Mulwa *et al.* 2013) and fruiting tree distribution (Laube *et al.* 2008), our observations of seed-dispersing frugivorous birds have important implications for a country with little natural forest left (Teketay *et al.* 2010).

Our results supported point counts as the preferred method because its success was equal among habitats and it detected over 84% of all observed species at every site. Especially in forest, this method was significantly more productive, as also noted by other studies in the tropics (Whitman *et al.* 1997, Blake and Loiselle 2001). However, mist netting did add unique species to each site and it can thus be argued that a combination of both methods is the best approach when there is enough time and available labour (Whitman *et al.* 1997) to detect the widest range of species (Dunn and Ralph 2004, Şekercioğlu 2012b). For example, without mist-netting we would have missed two of the most abundant forest specialists (*sensu* Buechley *et al.* 2015), Green Twinspot and Abyssinian Crimsonwing. Mist-netting is also essential for marking individual birds with numbered bands and for conducting capture-mark-recapture analyses of population dynamics (Şekercioğlu 2012b).

Conclusion

Our study confirms that complex agricultural landscapes can have higher species diversity than forests. This seems to be the rule rather than the exception for montane regions of Eastern Africa (Naidoo 2004, Laube *et al.* 2008, Gove *et al.* 2008, Buechley *et al.* 2015). Yet, in Ethiopia this difference is perhaps more striking because of a hypothesised impoverished state of the forest bird community (Moreau 1966, Gove *et al.* 2013). The majority of threatened and range-restricted tropical bird species are tropical forest specialists that do not occur in agricultural landscapes (Şekercioğlu 2012a). Consequently, when assessing the value of tropical agricultural landscapes for biodiversity, it is essential to go beyond the superficial measure of overall species richness and separately compare different species groups based on forest dependence, conservation status,

global distribution, diet, and other ecological characteristics. However, the high avian diversity of Ethiopian farmland underlines the importance of incorporating complex agroecosystems into conservation policies (Gove *et al.* 2013). As close and far gardens did not differ much in bird functional diversity, it seems that farmers living in complex gardens as far as 2,000 m from forest do not experience a different subset of ecosystem services and disservices. However, to what extent reduction in structural heterogeneity at garden level or landscape level influences bird richness and functional diversity deserves more attention since we do not know to what extent the bird fauna in these sites are dependent on the presence (or proximity) of forests in the landscape (cf. Gove *et al.* 2013). Finally, this study shows that point counts are the preferred method when comparing species diversity in habitats that are so different, but abundance, demographic and other hands-on data derived from mist netting can reveal additional patterns, which ultimately helps to better assess the bird community and conservation value of an area (e.g. Buechley *et al.* 2015).

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270916000162

Acknowledgements

References

Aerts, R., Lerouge, F., November, E., Lens, L., Hermy, M. and Muys, B. (2008) Land rehabilitation and the conservation of birds in a degraded Afromontane landscape in northern Ethiopia. *Biodivers. Conserv.* 17: 53–69.

Ango, T. G., Börjesen, L., Senbeta, F. and Hyander, K. (2014) Balancing ecosystem services and disservices: smallholder farmers' use and management of forest and trees in an agricultural landscape in southwestern Ethiopia. *Ecol. Soc.* 19: 30

Bennun, L., Dranzoa, C. and Pomeroy, D. (1996) The forest birds of Kenya and Uganda. *J. East. Afr. Nat. Hist.* 85: 23–48.

BirdLife International (2015) Country profile: Ethiopia. Available from: http://www.birdlife.org/datazone/country/ethiopia. Checked: 2015-11-19.

Blake, J. G. and Loiselle, B. A. (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *Auk* 118: 304–326.

Borghesio, L. (2008) Effects of human subsistence activities on forest birds in northern Kenya. *Conserv. Biol.* 22: 384–394.

Bregman, T. P., Şekercioğlu, Ç. H. and Tobias, J. (2014) Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biol. Conserv.* 169: 372–383.

Brown, L. H., Urban, E. K. and Newman, K. (1982) *The birds of Africa – Volume I.* London, UK: Academic Press.

Buechley, E. R., Şekercioğlu, Ç. H., Duguma, G., Ndungu, J. K., Lens, L., Abdu, B., Beyene, T. (2015) Bird community structure and conservation on Ethiopian shade-coffee farms. *Biol. Conserv.* 188: 50–60.

Cheng, S., Hiwatashi, Y., Imai, H., Naito, M. and Numbata, T. (1998) Deforestation and degradation of natural resources in Ethiopia:

forest management implications from a case study in the Belete-Gera forest. *J. For. Res.* 3: 199–204.

Colwell, R. H. (2013) *EstimateS: Statistical estimation of species richness and shared species from samples. Version 9.1.0.* http://viceroy.eeb.uconn.edu/estimates/

Dale, S., Mork, K., Solvang, R. and Plumptre, A. J. (2000) Edge effects on the understory bird community in a logged forest in Uganda. *Conserv. Biol.* 14: 265–276.

De Mey, Y., Demont, M. and Diagne, M. (2012) Estimating damage to rice in Africa: evidence from the Senegal river valley. *J. Agr. Econ.* 63: 175–200.

Dessie, T. and Ogle, B. (2001) Village poultry production systems in the central highlands of Ethiopia. *Trop. Anim. Health Pro.* 33: 521–537.

Douglas, D. J. T., Nalwanga, D., Katebaka, R., Atkinson, P. W., Pomeroy, D. E., Nkuutu, D. and Vickery, J. A. (2014) The importance of native trees for forest bird conservation in tropical farmland. *Anim. Conserv.* 17: 256–264.

Dunn, E. H. and Ralph, C. J. (2004) Use of mist nets as a tool for bird population monitoring. *Stud. Avian Biol.* 29: 1–6.

Fjeldså, J. (1999) The impact of human forest disturbance on the endemic avifauna of the Udzungwa Mountains, Tanzania. *Bird. Conserv. Internatn.* 9: 47–62.

Friis, B., Demissew, S. and Breugel, P. (2011) *Atlas of the potential vegetation of Ethiopia.* Addis Ababa, Ethiopia: Addis Ababa University Press & Shama Books.

Fry, C. H., Keith, S. and Urban, E. K. (1988) *The birds of Africa – Volume III.* London, UK: Academic Press.

Fry, C. H. and Keith, S. (2000) *The birds of Africa – Volume VI.* London, UK: Academic Press.

Fry, C. H. and Keith, S. (2004) *The birds of Africa – Volume VII.* London, UK: Christopher Helm.

Gokula, V. and Vijayan, L. (2000) Foraging pattern of birds during the breeding season in the thorn forest of Mudumalai wildlife sanctuary, Tamil Nadu, southern India. *Trop. Ecol.* 41: 195–208.

Gove, A. D., Hylander, K., Nemomisa, S. and Shimelis, A. (2008) Ethiopian coffee cultivation – implications for bird conservation and environmental certification. *Conserv. Lett.* 1: 208–216.

Gove, A. D., Hylander, K., Nemomissa, S., Shimelis, A. and Enkossa, W. (2013) Structurally complex farms support high avian functional diversity in tropical montane Ethiopia. *J Trop. Ecol.* 29: 87–97.

Gray, M. A., Baldauf, S. L., Mayhew, P. J. and Hill, J. K. (2007) The response of avian feeding guilds to tropical forest disturbance. *Conserv. Biol.* 21: 133–141.

Hulme, M. F., Vickery, J. A., Green, R. E., Phalan, B., Chamberlain, D. E., Pomeroy, D. E., Nalwanga, D., Mushabe, D., Katebaka, R., Bolwig, S. and Atkinson, P. W. (2013) Conserving the birds of Uganda's banana-coffee arc: land sparing and land sharing compared. *PLoS ONE* 8: e54597.

Hundera, K., Aerts, R., Fontaine, A., van Mechelen, M., Gijbels, P., Honnay, O. and Muys, B. (2013) Effects of coffee management intensity on composition, structure, and regeneration status of Ethiopian moist evergreen Afromontane forests. *Environ. Manage.* 51: 801–809.

Hylander, K., Nemomissa, S., Delrue, J. and Enkosa, W. (2013) Effects of coffee management on deforestation rates and forest integrity. *Conserv. Biol.* 5: 1031–1040.

Keith, S., Urban, E. K. and Fry, C. H. (1992) *The Birds of Africa – Volume IV.* London, UK: Academic Press.

Kirika, J. M., Farwig, N. and Böhning-Gaese, K. (2008) Effects of local disturbance of tropical forests on frugivores and seed removal of a small-seeded Afrotropical tree. *Conserv. Biol.* 22: 318–328.

Laube, I., Breitbach, N. and Böhning-Gaese, K. (2008) Avian diversity in a Kenyan agroecosystem: effects of habitat structure and proximity to forest. *J. Ornithol.* 149: 181–191.

Lemessa, D., Hylander, K. and Hambäck, P. (2013) Composition of crops and land-use types in relation to crop raiding pattern at different distances from forests. *Agr. Ecosyst. Environ.* 167: 71–78.

Lemessa, D., Hylander, K. and Hambäck, P. (2015) The effect of local and landscape land-use composition on predatory arthropods in a tropical agricultural landscape. *Landscape Ecol.* 30: 167–180.

Moreau, R. E. (1966) *The bird faunas of Africa and its islands*. London, UK: Academic Press.

Mulwa, R. K., Böhning-Gaese, K. and Schleuning, M. (2012) High bird species diversity in structurally heterogeneous farmland in western Kenya. *Biotropica* 44: 801–809.

Mulwa, R. K., Neuschulz, L., Böhning-Gaese, K. and Schleuning, M. (2013) Seasonal fluctuations of resource abundance and avian feeding guilds across forest- farmland boundaries in tropical Africa. *Oikos* 122: 524–532.

Naidoo, R. (2004) Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Anim. Conserv.* 7: 93–105.

Newmark, W. D. (1991) Tropical forest fragmentation and the local extinction of understory birds in the Eastern Usambara Mountains, Tanzania. *Conserv. Biol.* 5: 67–78.

R Development Core Team (2014) R 3.1.1. www.r-project.org

Redman, N., Stevenson, T. and Fanshawe, J. (2011) *The birds of the Horn of Africa*. Second edition. London, UK: Christopher Helm.

Renwick, A. R., Vickery, J. A., Potts, S. G., Bolwig, S., Nalwanga, D., Pomeroy, D. E., Mushabe, D. and Atkinson, P. W. (2014) Achieving production and conservation simultaneously in tropical agricultural landscapes. *Agr. Ecosyst. Environ.* 192: 130–134.

Şekercioğlu, Ç. H. (2002) Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biol. Conserv.* 107: 229–240.

Şekercioğlu, Ç. H. (2006) Ecological significance of bird populations. Pp. 15–51in J. del Hoyo, A. Elliot, and D. A. Christie, eds. *Handbook of the birds of the world. Volume 11*. Barcelona, Spain and Cambridge, UK: Lynx Edicions and BirdLife International.

Şekercioğlu, Ç. H. (2011) Functional extinctions of bird pollinators cause plant declines. *Science* 331: 1019–1020.

Şekercioğlu, Ç. H. (2012a) Bird functional diversity in tropical forests, agroforests and open agricultural areas. *J. Ornithol.* 153: 153–161.

Şekercioğlu, Ç. H. (2012b). Promoting community-based bird monitoring in the tropics: conservation, research, environmental education, capacity-building, and local incomes. *Biol. Conserv.* 151: 69–73.

Şekercioğlu, Ç. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. and Sandi, R. F. (2002) Disappearance of insectivorous birds from tropical forest fragments. *Proc. Natl. Acad. Sci. USA* 99: 263–267.

Şekercioğlu, Ç. H., Wenny, D. and Whelan, C. J. 2016. *Why birds matter: Avian ecological function and ecosystem services*. Chicago, USA: University of Chicago Press.

Sodhi, N. S., Posa, M. R. C., Lee, T. M. and Warkentin, A. G. (2008) Effect of disturbance or loss of tropical rainforest on birds. *Auk* 125: 511–519.

Sodhi, N. S., Şekercioğlu, Ç. H., Robinson, S. and Barlow, J. (2011) *Conservation of tropical birds*. Oxford, UK: Wiley-Blackwell.

Teketay, D., Lemenih, M., Bekele, T., Yemshaw, Y., Feleke, S., Tadesse, W., Moges, Y., Hundle, T. and Nigussie, D. (2010) Forest resources and challenges of sustainable forest management and conservation in Ethiopia. Pp. 19–64 in F. Bongers and T. Tennigkeit, eds. *Degraded forests in Eastern Africa: management and restoration*. London, UK: Earthscan.

Tscharntke, T., Şekercioğlu, Ç. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P. and Tylianakis, J. M. (2008) Landscape constraints on functional diversity of birds and insects in tropical agro-ecosystems. *Ecology* 89: 944–951.

Urban, E. K., Fry, C. H. and Keith, S. (1986) *The birds of Africa – Volume II*. London, UK: Academic Press.

Urban, E. K., Fry, C. H. and Keith, S. (1997) *The birds of Africa – Volume V*. London, UK: Academic Press.

Waltert, M., Bobo, S., Sainge, M., Fermon, H. and Mühlenberg, M. (2005) From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecol. Appl.* 15: 1351–1366.

Whitman, A. A., Hagan, J. M. and Brokaw, N. V. L. (1997) A comparison of two bird survey techniques used in a subtropical forest. *Condor* 99: 955–965.

Wilson, C. J., Reid, R. S., Stanton, N. L. and Perry, B. D. (1997) Effects of land-use and tsetse fly control on bird species richness in southwestern Ethiopia. *Conserv. Biol.* 11: 435–447.

Wormworth, J. and Şekercioğlu, Ç. H. (2011) *Winged sentinels: Birds and climate change*. New York, USA: Cambridge University Press.

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