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Large-scale *versus* small-scale agriculture: Disentangling the relative effects of the farming system and semi-natural habitats on birds' habitat preferences in the Ethiopian highlands

Gabriel Marcacci[a,e,*], Jérémy Gremion[b], Julien Mazenauer[a], Tolera Sori[d], Fanuel Kebede[d], Mihret Ewnetu[d], Philippe Christe[b], Raphaël Arlettaz[a], Alain Jacot[a,c]

[a] University of Bern, Division of Conservation Biology, CH-3012 Bern, Switzerland
[b] University of Lausanne, Department of Ecology and Evolution, Le Biophore, CH-1015 Lausanne, Switzerland
[c] Swiss Ornithological Institute, Field Station Valais, CH-1950 Sion, Switzerland
[d] Ethiopian Wildlife Conservation Authority, Addis Ababa, Ethiopia
[e] University of Goettingen, Functional Agrobiodiversity, D-37077 Göttingen, Germany

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ABSTRACT

While the Western World is facing an inexorable decline of its farmland biodiversity following continuous intensification of production modes, agricultural landscapes in Africa are still largely dominated by small-scale subsistence farming operated by smallholders, mostly harbouring high biodiversity. However, as most African countries are confronted to an unprecedented population growth and a rapid economic development, efforts to intensify food production are widespread, with concomitant potentially negative effects on biodiversity. We conducted a study in a highly contrasted agricultural landscape of the Ethiopian highlands comprising two distinct farming systems: large-scale farming relying on modern, combine machinery and technology (e.g. enhanced crop varieties, application of herbicides, pesticides and synthetic fertilizers) *vs* small-scale traditional farming. Our objective was to disentangle the effects upon avian biodiversity of the operating farming system and the extent of semi-natural habitat features in the wider landscape. We performed a model selection approach to assess habitat selection by the overall bird community as well as the wintering, endemic and open habitat species, respectively. Our results show that habitat preferences of birds in the Ethiopian highlands were mainly driven by the amount of semi-natural habitats within the landscape, with varying effects depending on the farming system itself. While large-scale farming had overall more negative effects on birds, some typical open habitat species were mostly restricted to these wide-open landscapes. Our findings thereby suggest that both farming systems could coexist as long as semi-natural habitats are preserved and agricultural management maintained in its current practices. We emphasize the urgent need to conduct further studies integrating the socio-economic aspects in order to better predict future impacts of agricultural intensification processes on African farmland biodiversity.

1. Introduction

In the late 19th and early 20th century, European countries faced the challenge of feeding their rapidly growing human populations. As a consequence, drastic changes in agricultural practices occurreddriven by new technologies, mechanization, enhanced crop varieties and use of agrochemicals (Smill, 1999; Pingali, 2012). These processes triggered the slow and inexorable decline of farmland biodiversity, which has continued in Western countries (Batáry et al., 2017; McDonald et al., 2007). Farmland avifauna represents the taxon for which biodiversity loss is best documented (Donald et al., 2001; Green et al., 2005; Krebs et al., 1999), mainly triggered by habitat loss, fragmentation, homogenisation (Benton et al., 2003; Fahrig, 2003) and a marked decrease in food availability (Newton, 2004).

Agriculture in most parts of sub-saharan Africa is still often characterized by subsistence farming at small-scale, which forms the backbone of food security on the continent (Tscharntke et al., 2012). However, the need to increase food production has in turn become a pressing issue in Africa due to a rapid population growth combined with land scarcity (Headey et al., 2014; Tadele, 2017) while crop yield

* Corresponding author.
E-mail address: gabriel.marcacci@uni-goettingen.de (G. Marcacci).

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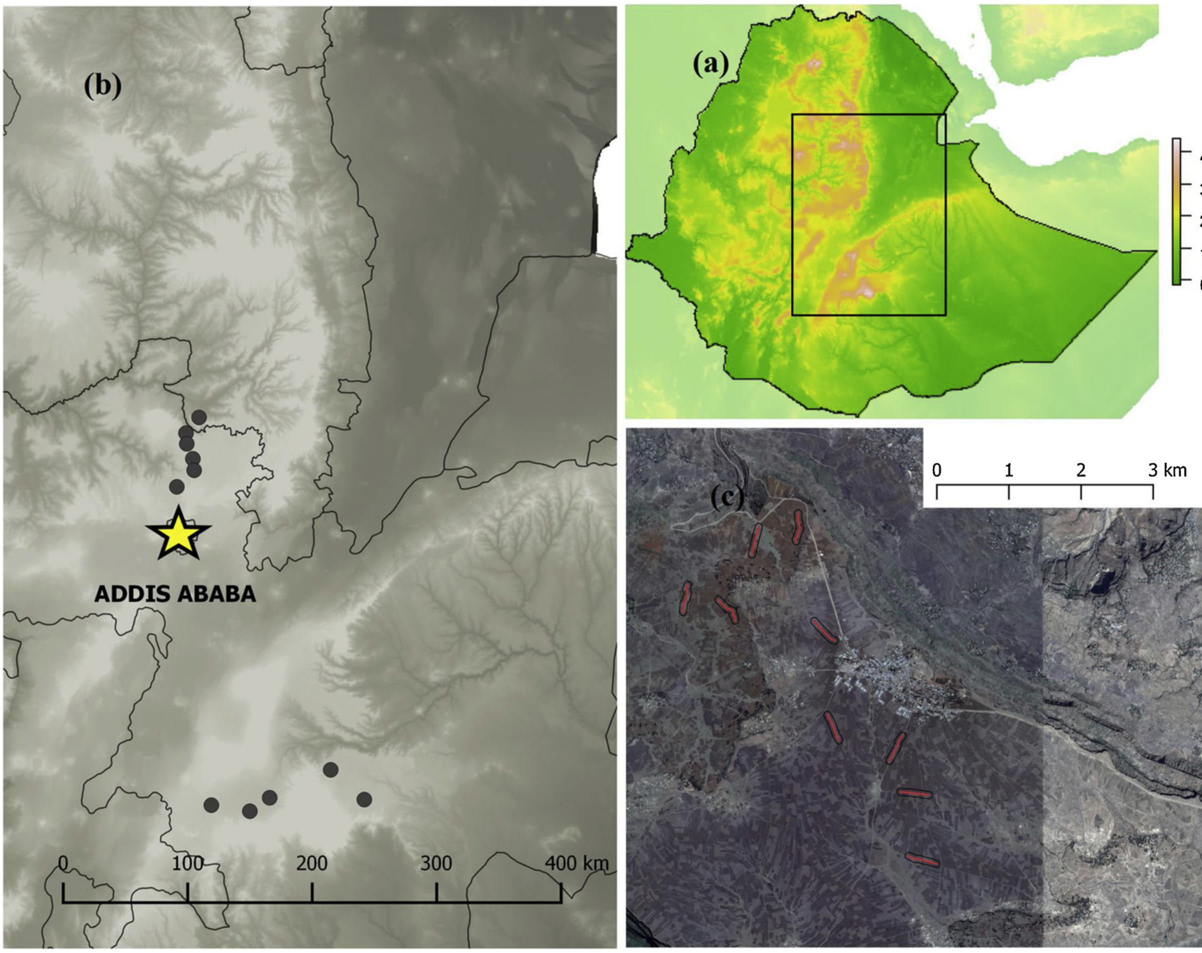

Fig. 1. Location of the study area (a) in the central and south eastern Ethiopian highlands; (b) the 11 study sites (grey points); (c) example of one study site (small-scale farming) with the transects depicted in purple. Source: GADM (a), Google Maps (c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

is stagnating (Snapp et al., 2010). The challenge of increasing the production of food and cash crops while simultaneously conserving biodiversity is a major issue in conservation biology in order to implement appropriate land use strategies. It is often addressed from the perspective of the land sharing/sparing options (Grau et al., 2013; Tscharntke et al., 2012). Most current African farmland conforms to a land sharing approach, i.e. the cultivated landscape is largely dominated by traditional small-scale agriculture interspersed with natural elements, forming a biodiversity-rich mosaic (Headey and Jayne, 2014; Tscharntke et al., 2012). However, increasing food production could lead to landscape homogenisation, highlighting the need to understand both the effects of intensification processes on biodiversity and the biological value of the remaining natural habitats.

Yet, while numerous studies in western Europe have demonstrated the negative effects of agricultural intensification on birds and other taxa (Donald et al., 2001; Fuller et al., 1995; Robinson and Sutherland, 2002), few studies have succeeded in disentangling the relative effects of farming practices vs landscape structure in the wider surroundings, i.e. beyond the cultivated fields. This is mainly because agricultural intensification and loss of natural habitat (landscape simplification) often occur concomitantly (Chiron et al., 2014). Although the positive effect of natural landscape structures on overall bird densities has been demonstrated (Chiron et al., 2010; Devictor and Jiguet, 2007; Guerrero et al., 2012; Vickery and Arlettaz, 2012), these same studies found that ground breeders and specialist species are mainly affected by the farming practices at the field-scale, highlighting the importance to investigate different bird groups to better understand the impact of agricultural intensification processes on the avifauna (Chiron et al., 2014). The same trend was found when disentangling crop diversity and overall landscape heterogeneity (i.e. including natural elements): except for crop nesting birds, landscape heterogeneity always had a stronger effect on bird diversity (Redlich et al., 2018b). Other studies showed higher biodiversity within smaller fields (Fahrig et al., 2015), with notably more important positive effects of small-scale agriculture, irrespective of management mode (i.e. organic *vs* conventional), due to higher landscape complexity within small-scale agriculture matrices (Batáry et al., 2017; Gayer et al., 2019).

The framework offered by the Ethiopian highlands' agroecosystem, with its highly contrasted farming practices (large – *vs* small-scale farming), is an exemplary model system to address this topic. Ethiopia is currently experiencing a drastic socio-economical change driven by its rapidly increasing population and its steady economic growth (Headey et al., 2014), which impact both the agricultural practices and the environment (Logan, 2014): for the last two decades, Ethiopia has increased its area of production (Taffesse et al., 2013) until almost all available land in the highlands was converted into agriculture, offering limited opportunities for agricultural expansion (Taffesse et al., 2013). Therefore, the country needs to adapt its land use practices in order to ensure food security in a sustainable way. At the moment, even though natural habitats are increasingly degraded and fragmented, with large areas of native Afromontane forest having vanished (Aerts et al., 2008), Ethiopia still has a high level of endemism and a rich biodiversity: 18 bird species are endemic to Ethiopia and 54 are endemic or near-endemic to the Horn of Africa (Redman et al., 2011), with many of these endemic species occurring in the highland agroecosystems. Furthermore, many Palearctic migrants overwinter in Ethiopia or use the highlands as important staging sites on migration. Some threatened species, like the Ortolan Bunting (*Emberiza hortulana*), might be directly associated with agriculture for their wintering diet (Jiguet et al., 2016).

As the ongoing agricultural intensification is expected to negatively impact both resident and wintering avian biodiversity, the purpose of this study was to investigate the effect of agricultural intensification on different bird communities in two distinct farming systems (small-*versus* large-scale farming) in order to get insights for evidence-based management recommendations. We aimed to disentangle the relative effects of the farming system and the amount of semi-natural habitat surrounding the fields upon bird abundance and species richness at a landscape-scale. Here we try seeking long-lasting sustainable solutions to guarantee food security without jeopardizing ecological functions and services and by maintaining the high biodiversity in an agroecosystem.

2. Methods

2.1. Study Area

The study was carried out in the highlands of central and south eastern Ethiopia (Fig. 1), which offer optimal conditions for cultivation: highest rainfall and productive soils (Taffesse et al., 2013). The country is undergoing rapid population growth (2017: 107 million people vs 190.9 million (+ 78%) predicted in 2050 by www.prb.org), where an increase in yield is of prime importance to guarantee food security on the long run. Partly as a consequence of this demographic change, the government has created some state-owned farms since the Land Reform Proclamation of 1975 where all rural land was taken by the state (Headey et al., 2014; Kebede, 2008). These estates reflect an assemblage of large-scale monocultures harvested by combine machines and farmed using latest technologies (i.e., enhanced crop varieties, pesticides and synthetic fertilisers). These new agricultural practices contrast dramatically with the traditional small-scale farms where most labour is done manually (Logan, 2014) and whose production is mainly dedicated to subsistence farming (Taffesse et al., 2013). Nowadays, the landscape of these highland agroecosystems is divided into these two drastically different farming systems (Fig. 2): large-scale farming by state farms and small-scale farming by smallholders (Taffesse et al., 2013).

The agricultural matrix consists typically of agricultural fields, mainly cereal cultures (wheat, tef and barley) and semi-natural habitats composed of isolated patches of native woodland, eucalyptus plantations, natural grasslands, communal lands (field-margin pastures used for grazing by the whole community), field-margins (demarcation lines between the fields) and bushy vegetation, hedges or natural fences (succulent spiny bushes) along the paths, rivers and around villages. Habitat configuration of these semi-natural structures was not assessed. Spatial heterogeneity seemed to be higher in small-scale farming and were likely to be more clumped in large-scale farming.

2.2. Study design

Bird surveys were carried out using a transect sampling method (Bibby et al, 2000; Assandri et al., 2016; Guyot et al., 2017). The transects had a length of 400 m (399.33 ± 0.48 m) with a 50 m buffer around them (≈ 3.9 ha) (Fig. 1). In order to disentangle the effects of the farming system and the amount of semi-natural habitat on bird abundance and species richness, we selected transects along a gradient from low to high occurrence of semi-natural habitat (0–68 %) in both farming systems (large-scale vs small-scale). Using mean field size as proxy for the farming system (continuous variable), the two groups of variables (field size versus total semi-natural habitats) were uncorrelated ($r_s = 0.035$) thereby allowing to quantify their relative contribution and interactions (Marini et al., 2010; Mortelliti et al., 2011).

The study design consisted of 120 transects (80 in small-scale farming and 40 in large-scale farming) distributed between 11 study sites (Fig. 1, Tab A.3). Six study sites (small-scale farming only) were located west of the Rift valley and five study sites (small-scale and large-scale farming) were located east of the Rift valley. The mean distance between sites was 19.99 km and the mean distance between transects within sites was 717.27 m. All transects were located between 2340 and 2670 m above sea level. The six sites where only small-scale farming occurred did not differ in species richness (13.19 ± 4.84) compared to small-scale farming where both farming systems occurred (12.20 ± 5.62). All analyses are therefore based on the whole dataset, while having ‘side’ (2 levels: east / west of the Rift valley) as covariate in our analyses.

2.3. Habitat mapping

All transects were mapped a few days before the bird surveys, directly in the field, on a paper map (satellite picture of 1:1300, Google Maps) before being numerized in QGIS (Quantum GIS Development Team, 2017). Semi-natural habitats were divided into six categories: grove (area covered by woody plants such as bushes, hedges, both indigenous and planted trees, but also corrals and natural fences, see Guyot et al., 2017), savannah (all savannah-like habitats, including the so called “common land”, a kind of natural pastureland used for grazing), river (including the riverbed), field-margin (grassy strips between the fields), track (vegetated tracks) and human settlements (all human settlements, mostly traditional houses). Additionally, we recorded the crop type (18 levels) for each agricultural field: wheat, tef (cereal endemic to Ethiopia and Eritrea), barley, pasture, maize, horse bean, chickpea, guaya (sort of pea), garlic, niger seed, oilseed, rapeseed, lentil, potato, linseed, fallow, burnt (slash-and-burn agriculture) and ploughed field. Additional variables such as crop richness, crop

Fig. 2. Illustration of the two contrasting farming systems. Satellite picture (7.098871, 39.425518) of large-scale farms embedded in a matrix of small-scale farms (a); picture of the same area (b). Source: Google Maps (a) and Gabriel Marcacci (b).

diversity and habitat diversity (proxy for landscape heterogeneity) were calculated afterwards. See Table A.1 for more details.

2.4. Bird surveys

The surveys were conducted between November 2018 and February 2019. This time window coincides with the presence of palearctic migrants overwintering and/or migrating in the Ethiopian highlands. It also corresponds to the harvesting time for most of the crops (Taffesse et al., 2013). All surveys took place during the first four hours after dawn under favourable weather conditions (no rain, no wind) and lasted for 30 (± 5) minutes per transect. All transects were surveyed twice by the same observer (JM, JG or GM) on two consecutive days. The surveys were carefully planned so that the different transect categories (farming system and amount of semi-natural habitat) were shared between the three observers who surveyed in every site.

2.5. Statistical analyses

All statistical analyses were conducted in R version 3.4.0 (R Core Team, 2018). We investigated four different bird groups using the same statistical approach: “all species” (all species recorded during the surveys), “wintering” (overwintering species), “endemic” (including endemic and near-endemic species of the Horn of Africa, Redman et al., 2011) and “open habitat species” (see Appendix 1). The three latter are all subsets of the group “all species”, hence one species may belong to several groups.

A model selection approach was used to model habitat preferences of bird communities. GLMMs from the *lme4* R-package (Bates et al., 2015) were built with the environmental predictors (farming system, total semi-natural amount, grove cover, savannah cover, river cover, field-margins cover, human settlements cover, track cover) as explanatory variables (fixed effect) and species richness and abundance as response variables using a Poisson distribution. “Site” was set as first random effect. As all transects were surveyed twice, “transect” was set as second nested random effect to avoid pseudoreplication. Overdispersion was checked with the function dispersion_glmer from the blmeco R-package (Korner-Nievergelt et al., 2015) and corrected using an observation level as third random effect in the model when needed (Korner-Nievergelt et al., 2015). All variables were standardized (mean = 0, standard deviation = 1) and the proportion variables were arcsin-square root transformed (Fernandez, 1992). The Spearman correlation test was used to check for collinearity between semi-natural habitat variables. If the coefficient was $|r_s| > 0.7$, the biologically less meaningful variable was discarded. We performed our model selection using the *dredge* function from the *MuMIn* R-package (Barton, 2018) including interaction between the environmental predictors and the farming system (categoric variable with two levels: large-scale and small-scale) as well as quadratic terms. “Time” (hour when the survey started) and “date” with their polynomials were added as covariates to correct for variability in bird activity and seasonal movements. Additionally, “side” (2 levels: east/west) and “observer” (3 levels: JM, JG, GM) were also used as covariates to account for potential Rift Valley side and/or observer effect. The models with the lowest Akaike’s Information Criterion corrected for small sample size (with $\Delta AICc < 2$, Burnham and Anderson, 2002) score sorted by the *dredge* function were selected as competitive models. Finally, the *model.avg* function (*MuMIn)* was performed over the set of candidate models to average the predictors’ coefficients (estimates, SE, z-value and P-values). We checked the residuals’ normality, normal distribution of the random factor(s) and the temporal autocorrelation before validating the fit of the averaged models. In order to draw inferences of the fitted values with their uncertainties (95% Bayesian Credible Interval) from our selected models, we used the *sim* function from the R-package *arm* (Gelman and Su, 2016) with 10,000 simulations of their posterior distribution according to Korner-Nievergelt et al. (2015).

Additionally, the effects of habitat diversity (habdiv) vs crop diversity (cropdiv) on species richness (response variable) of our four groups were investigated. Both habdiv and cropdiv variables were calculated as Shannon Index (R-package *vegan*) (Oksanen et al., 2017) of the six semi-natural habitat types and the 18 crop types respectively (see 2.3. habitat mapping). GLMMs, where habitat diversity (habdiv) and crop diversity (cropdiv) as well as their interaction (habdiv:-cropdiv) were set as fixed effects and “site” and “transect” as random effect, were built under the procedure as above.

Finally, we performed an indicator species analysis to investigate species that might be closely related to one of the farming systems (large *vs*. small-scale) using the function *multipatt* of the R-package *indicspecies* (De Cáceres and Legendre, 2009). An indicator value (IndVal) varying between 0 and 1 was calculated for each species with the maximum value 1 attributed to a species found in all sites of a group (i.e. small-scale farming). To be an indicator, a species needs to have an IndVal ≥ 0.5 with $P \leq 0.1$ (Rodrigues et al., 2018).

3. Results

14,496 individuals of 151 species were recorded, of which 22 species are endemic or near-endemic to the Horn of Africa (Redman et al., 2011), 39 are wintering species and 29 belong to the open habitat species group (Tab A.2). The 10 most abundant species were Swainson’s Sparrow *Passer swainsonii* (1718 individuals), Yellow Wagtail *Motacilla flava* (1457), Red-throated Pipit *Anthus cervinus* (1445), Erlanger’s Lark *Calandrella erlangeri* (1263), Ortolan Bunting (1070), Dusky Turtle-Dove *Streptopelia lugens* (688), Isabelline Wheatear *Oenanthe isabellina* (495), Pied Wheatear *Oenanthe pleschanka* (488), Cape Crow *Corvus capensis* (459) and Thekla Lark *Galerida theklae* (404). Together these 10 species represent 58% of the total of individuals recorded. Note that among these 10 species, five are wintering species (Yellow Wagtail, Red-throated Pipit, Ortolan Bunting, Isabelline Wheatear and Pied Wheatear). In small-scale agriculture we found 12.7 ± 5.25 species, while 9.6 ± 4.4 were detected in large-scale agriculture. A similar pattern was observed looking at the overall abundance (65.4 ± 43.87 vs 50.3 ± 30.33). See Table A.2 for more details.

The agricultural landscape was characterized by six categories of semi-natural habitats (Table 1) and 18 different crops (including pasture, ploughed fields, fallow land and burnt fields) (Tab A.4). Cereal cultures (wheat, tef and barley) represent 60.35% of the cultivated areas, partly because the large-scale state farms are predominantly cultivating wheat. We found a crop richness and a crop Shannon diversity of 3.87 ± 1.34 and 0.63 ± 0.5 in small-scale agriculture while these parameters were 1.53 ± 0.75 (crop richness) and 0.79 ± 0.51 (crop Shannon diversity) in large-scale agriculture (Table 1).

3.1. Overall bird species habitat preference

A significant positive effect of grove and a negative effect of large-scale farming were found in the best model for species richness: bird species richness is predicted to double in agricultural landscapes, varying between 0–30 % of grove cover, independently of the farming system. The effect of grove on bird abundance was seemingly stronger in small-scale farming. The amount of savannah-like habitat was found to have positive effects on species richness while the extent of river habitat positively affected both species richness and bird abundance. A positive effect of field-margin on species richness was measured in large-scale agriculture only. See Tables 2a and 3 a for more details.

3.2. Habitat preferences of wintering bird species

The amount of riverine habitat was the predictor which best explained both wintering birds’ species richness and abundance whereas grove cover negatively affected birds’ species richness. A (non-significant) interaction between grove and the farming system suggested

Table 1
Bird responses and explanatory variables in large- versus small-scale agriculture (mean ± standard deviation).

	Small-scale farming	Large-scale farming
Bird responses		
Overall species		
Species richness	12.70 ± 5.25	9.60 ± 4.40
Abundance	65.40 ± 43.87	50.3 ± 30.33
Wintering species		
Species richness	4.20 ± 1.53	3.8 ± 1.61
Abundance	24.40 ± 25.02	20.00 ± 21.23
Endemic species		
Species richness	1.96 ± 1.24	1.54 ± 0.91
Abundance	17.38 ± 22.80	12.26 ± 8.42
Open habitat species		
Species richness	6.76 ± 2.66	5.24 ± 2.05
Abundance	36.02 ± 29.96	28.46 ± 22.70
Field layout		
Number of transects	80	40
Crop richness	3.87 ± 1.34	1.53 ± 0.75
Crop diversity	0.79 ± 0.51	0.63 ± 0.50
Semi-natural habitats		
Semi-natural habitat [%]	17.7 ± 13.01	18.78 ± 13.76
Grove cover [%]	4.76 ± 7.34	8.05 ± 11.70
River cover [%]	0.73 ± 2.26	0.8 ± 3.07
Savannah cover [%]	6.13 ± 12.00	0.49 ± 2.17
Field-margin cover [%]	1.43 ± 2.06	1.47 ± 3.36
Human settlement cover [%]	0.1 ± 0.40	0
Track cover [%]	4.54 ± 4.61	7.97 ± 4.90
Habitat diversity	0.50 ± 0.39	0.34 ± 0.40

that the negative effect of grove on wintering birds' species richness was seemingly stronger in small-scale agriculture. See Tables 2b and 3 b for details.

3.3. Habitat preferences of endemic bird species

Grove cover had a positive effect on endemic species richness. The abundance of endemic birds was positively affected by grove in small-scale farming systems with a four times stronger effect size. Savannah and human settlements were found to be positive for species richness whereas river affected both species richness and abundance positively. See Tables 2c and 3 c for more details.

3.4. Habitat preferences of open habitat species

Open habitat species richness was negatively affected by grove cover, with a stronger negative effect in small-scale agriculture. Grove cover was found to be negative for endemic birds' abundance. Riverine habitat revealed a positive effect for birds' species richness and abundance whereas both were negatively affected by human settlements. See Tables 2d and for 3 d for more details.

3.5. Habitat diversity versus crop diversity

Habitat diversity had a positive effect on overall (0.18 ± 0.04, z = 4.24, $P < 0.001$) and endemic (0.26 ± 0.06, z = 4.11, $P < 0.001$) bird species richness. In contrast, only wintering species were positively affected by crop diversity (0.11 ± 0.4, z = 2.69, $P < 0.01$). Neither habitat diversity nor crop diversity were found to influence farmland birds. No significant interactions between crop and habitat diversity were recorded.

3.6. Indicator species analysis

We found three indicator species for small-scale agriculture: Ortolan Bunting (IndVal = 0.677; $P = 0.001$), Thekla Lark (IndVal = 0.812; $P = 0.001$) and Brown-rumped Seedeater *Serinus tristriastus* (IndVal = 0.497, $P = 0.25$). No species were identified as an indicator of large-scale farming.

4. Discussion

While most of the studies assessing the effect of agricultural intensification on bird communities focus on Western countries, we investigated the relative effects of two farming systems (small-scale versus large-scale farming) and the extent of semi-natural habitats within the wider landscape on avian community characteristics in Ethiopian highland agroecosystems. Disentangling these two independent factors allowed us to demonstrate that habitat preferences of birds were mainly driven by the amount of semi-natural habitats, with varying effect depending on the farming system. While large-scale farming had overall more negative effects, typical open-habitat species seemingly benefitted from these wide-open landscapes, highlighting the importance of investigating distinct avian guilds and communities. Furthermore, habitat diversity within small-scale farming matrices

Table 2
Competitive models from the model selection procedure for the four bird groups. Explanatory variables are written in bold when significant (P ≤ 0.05). G: grove cover (% trees, hedges, bushes, natural fences); S: savannah cover (% savannah-like habitat); R: river cover (% river and riverbed); F: field-margin cover (% grassy strips between fields); H: human settlements cover (% human constructions and buildings); FS: Farming System (large/small-scale farming); obs: observer (observer effect); "*": interaction between two variables.

Response variable	Nb Cand. models	Competitive models (ΔAICc ≤ 2)	Df	ΔAICc	Weight
a) all species					
Species richness	40	**G** + **S** + **R** + F + **FS** + **FS*F**	9	0	0.864
Abundance	20	**G** + **R** + **FS** + **time**	8	0	0.431
		G + **R** + **FS** + FS*G + **time**	9	0.01	0.429
b) wintering species					
Species richness	30	G + **R** + FS + **FS*G**	7	0	0.310
		G + **R** + FS + **FS*G** + date	8	1.20	0.170
		G + **R** + FS + **FS*G** + date + date^2	9	1.94	0.117
Abundance	8	**R** + **obs** + time	8	0	0.748
c) endemic species					
Species richness	16	**G** + **S** + **R** + **H**	7	0	0.738
Abundance	80	**G** + F + R + **FS** + **FS*FS** + **date** + **obs**	12	0	0.293
		G + F + **FS** + **FS*G** + **date** + **obs**	11	1.15	0.165
		G + R + **FS** + **FS*G** + **date** + **obs**	11	1.41	0.145
d) open habitat species					
Species richness	20	**G** + **R** + **H** + **FS** + **G*FS**	8	0	0.726
Abundance	32	**G** + **R** + **H** + **side** + **time**	9	0	0.762

Table 3
Model-averaged parameter estimates. Interaction terms are represented by the sign "*".

Explanatory variables	Species richness				Abundance			
	Estimate	SE	z	*P*	Estimate	SE	z	P-value
a) all species								
Intercept	2.50	0.04	60.32	< 0.001***	4.01	0.06	76.54	< 0.001***
Grove cover	0.26	0.02	11.19	< 0.001***	0.29	0.06	4.814	< 0.001***
Savannah cover	0.08	0.02	3.26	< 0.01**				
River cover	0.10	0.02	4.72	< 0.001***	0.13	0.04	3.05	< 0.01**
Field-margin cover	−0.05	0.04	−1.40	0.160				
Large-scale farming	−0.29	0.06	5.09	< 0.001***	−0.216	0.10	2.24	< 0.05*
Farming system * field-margin cover	0.14	0.05	2.85	< 0.01**				
Farming system * grove cover					−0.135	0.0.9	1.47	0.143
Time					−1.57	0.33	4.72	< 0.001***
b) wintering species								
Intercept	1.40	0.06	23.63	< 0.001***	3.12	0.22	14.03	< 0.001***
Grove cover	−0.03	0.05	0.65	0.518				
River cover	0.10	0.29	3.26	< 0.01**	0.06	0.06	2.60	< 0.01**
Large-scale farming	−0.09	0.08	1.06	0.291				
Farming system * grove cover	0.19	0.08	2.543	< 0.05*				
Time					−1.16	0.48	−2.40	< 0.05*
Date	−0.87	0.89	0.98	0.330				
Date^2	−1.04	0.86	1.21	0.227				
Observer JG					−0.61	0.17	−3.59	< 0.001***
Observer JM					−0.41	0.18	−2.31	< 0.05*
c) endemic species								
Intercept	0.55	0.05	10.54	< 0.001***	2.26	0.15	14.55	< 0.001***
Grove cover	0.21	0.05	4.37	< 0.001***	0.43	0.09	4.95	< 0.001***
Savannah cover	0.14	0.04	3.01	< 0.01**				
River cover	0.17	0.04	4.18	< 0.001***	0.11	0.06	1.79	0.074
Field-margin cover					0.13	0.07	1.86	0.06
Human settlements cover	0.09	0.04	2.25	< 0.05*				
Large-scale farming					−0.35	0.15	2.41	< 0.05*
Farming system * grove cover					−0.59	0.14	4.19	< 0.001***
Date					5.04	2.00	2.51	< 0.05*
Observer JG					0.28	0.16	1.74	0.081
Observer JM					0.51	0.17	3.01	< 0.01**
d) open habitat species								
Intercept	1.87	0.04	44.08	< 0.001***	3.08	0.09	35.07	< 0.001***
Grove cover	−0.23	0.04	−5.50	< 0.001***	−0.33	0.06	−5.65	< 0.001***
River cover	0.10	0.03	3.90	< 0.001***	0.15	0.05	2.83	< 0.01**
Human settlements cover	−0.06	0.03	−1.99	< 0.05*	−0.16	0.06	−2.76	< 0.01**
Large-scale farming	−0.23	0.07	−3.46	< 0.001***				
Farming system * grove cover	0.22	0.06	3.33	< 0.001***				
Side (west)					0.43	0.14	3.06	< 0.01**
Time					−1.16	0.41	−2.86	< 0.01**

enhanced overall and endemic bird species richness, whereas wintering species were more closely related to crop diversity.

Habitat preferences of birds were largely driven by the amount of semi-natural habitat in our study system. Not only are our findings in line with other studies demonstrating a positive effect of grove cover on birds (Assandri et al., 2016; Chiron et al., 2014; Guyot et al., 2017; Hinsley and Bellamy, 2000; Radford and Bennett, 2007; Vickery and Arlettaz, 2012; Zingg et al., 2018), but the effect was shown to depend on the farming system: grove cover had a stronger effect in small-scale farming where overall bird abundance is predicted to double and endemic species abundance to quadruple when compared to large-scale farming (Fig. 3b and g). These results could be explained by a higher spatial heterogeneity in grove configuration in small-scale farming where demarcation lines between fields could support more semi-natural structures (Vickery et al., 2009) or by impoverished grove structures (e.g. eucalyptus trees) in large-scale farming (MacDonald and Johnson, 1995). In our study we did not quantify the spatial configuration of semi-natural structures. This aspect could be important, especially so in landscapes with low grove cover where a high aggregation could have positive effects on species richness and abundance (Radford et al., 2005). However, grove cover was also found to have negative effects, especially so on typical open habitat species in small-scale farming. These typical open habitat species (e.g. Erlanger's Lark, Yellow Wagtail) seem to avoid too complex landscapes with high heterogeneity of vertical structures as they favour more open, flat habitats (Chiron et al., 2010; Gayer et al., 2019; Gilroy et al., 2010). This negative effect of groves is seemingly less pronounced in large-scale farming potentially due the clumped occurrence of grove structures. The coexistence of the two farming systems could thereby represent an adequate strategy for conservation planning on wide landscape units, favouring overall bird species richness and abundance as well as typical open habitat species. Yet, these large farms are harvested with combine machines, which increase yield (Hassena et al., 2000) but represent a considerable loss of seeds available for the seed-eating bird species. Three seed-eating bird species (Ortolan Bunting, Thekla's Lark and Brown-rumped Seedeater) turned out to be indicator species for small-scale farming in our study, indicating that small-scale farming provide good seed source for resident and wintering species. This result underlines the importance of left fallow after harvest (Moorcroft et al., 2002; Newton, 2004) and about future conservation strategies for such species.

Within small-scale agriculture matrices, habitat diversity (e.g. landscape heterogeneity) was found to be more important than crop diversity, except for both typical open habitat and wintering species (Fig. 4). These results are congruent with other studies (Chiron et al., 2014; Redlich et al., 2018b) demonstrating that semi-natural habitat plays a predominant role in explaining overall bird species richness irrespective of the farming system. In contrast, our study shows that

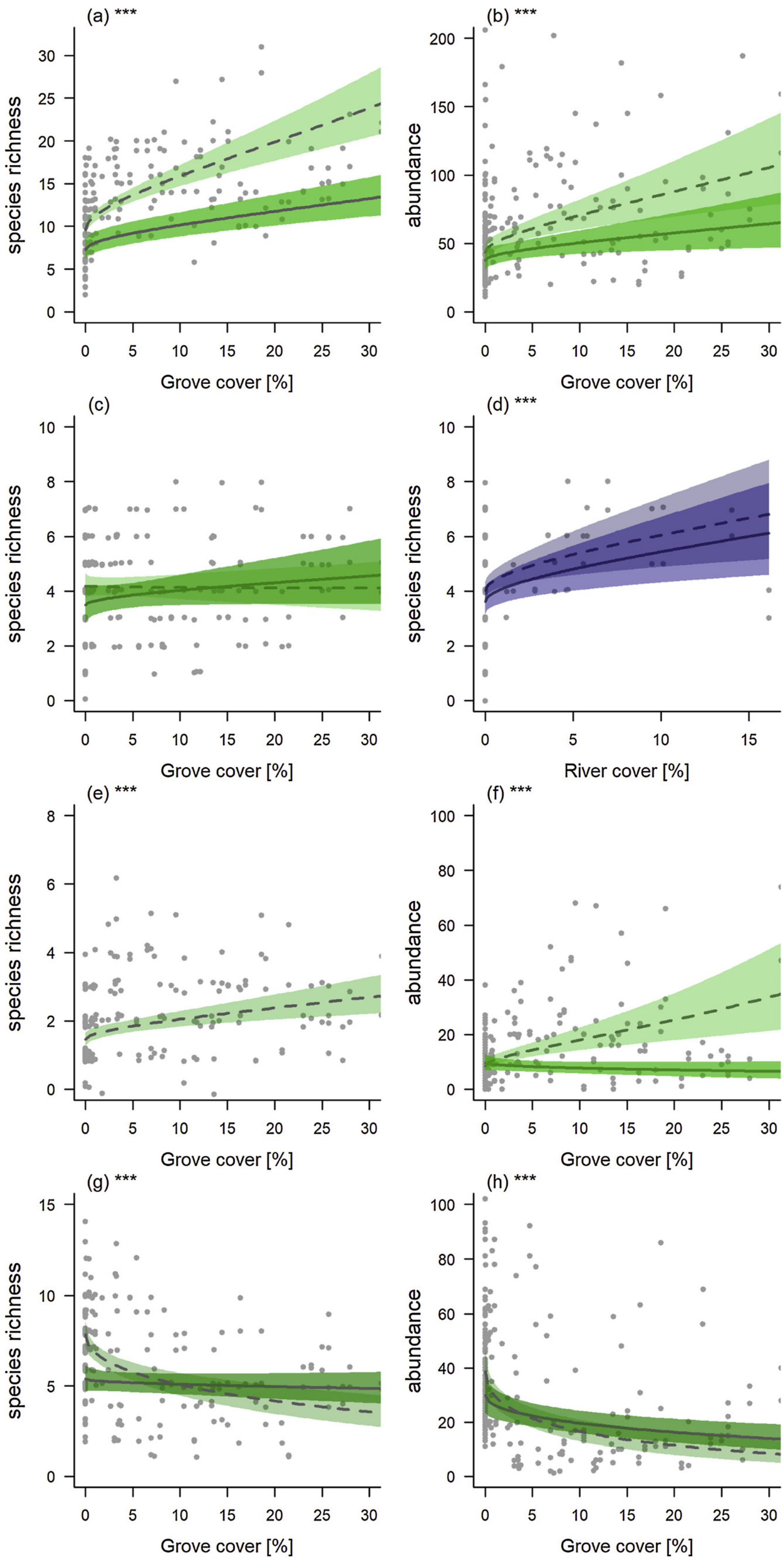

Fig. 3. Model-averaged predicted birds' species richness and abundance explained by the semi-natural habitats. (a) and (b) all species; (c) and (d) wintering species; (e) and (f) endemic species; (g) and (h) open habitat species. The effects of grove cover vary among the four different bird groups and depend on the farming systems (large- vs small-scale). Large-scale farming is represented with plain lines and darker colours whereas dash lines and lighter colours are used for small-scale agriculture. 95% Bayesian Credible Intervals are depicted by the different coloured belts and raw data are displayed with grey points. Note that there is only one line in plot (e) due to the lack of endemic species in large-scale agriculture. Significance levels: *** $P < 0.001$, * $P < 0.05$. (For interpretation of the references to colours in this figure legend, the reader is referred to the web version of this article).

wintering birds particularly depend on farming practice (crop diversity and farming system were correlated), making them more sensitive to agricultural intensification. Altogether, our findings suggest that non-farmland and endemic species are more vulnerable to landscape simplification that results from a decrease in semi-natural habitats (loss of habitat diversity) whereas wintering and farmland birds are more

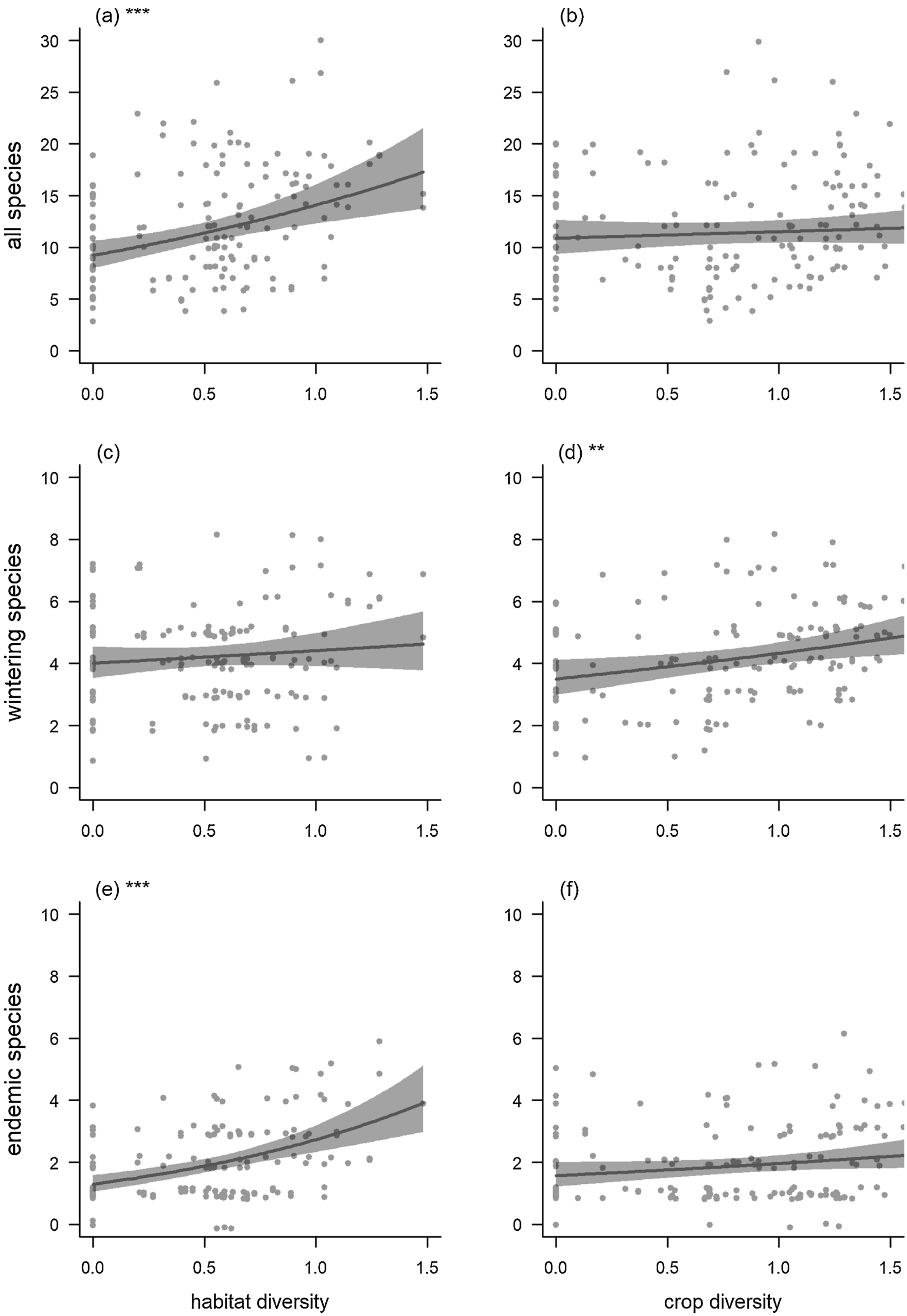

Fig. 4. Habitat and crop diversity (Shannon index) effects on bird species richness within small-scale farming matrix. Habitat diversity (proxy for landscape heterogeneity) has a positive effect on overall (a) and endemic birds (e) whereas crop diversity enhances only wintering species richness (d). Open habitat species are not displayed as neither habitat diversity nor crop diversity had any effect. 95% Bayesian Credible Intervals are depicted by grey coloured belts and raw data are displayed with grey points. Significance levels: *** $P < 0.001$; ** $P < 0.01$.

affected by the intensification of the farming practices resulting in large monocultures (loss of crop diversity).

While overall species richness (-24.4%) and abundance (-23%) was consistently lower in large- vs. small-scale farming, our results still indicate some potential of appropriate large-scale farming for avian biodiversity. Indeed, our findings show that a higher amount of semi-natural habitat (e.g. riverine, field-margins, groves) can markedly increase biodiversity in a large-scale farming context. Although the effect of grove cover was stronger in small-scale farming, we found higher species richness in large-scale farms with 30% of grove cover compared to small-scale farms devoid of vertical natural structures. Several non-mutually exclusive hypotheses could explain this pattern. First, the development of large-scale farming in Ethiopia is quite recent and there could be a delay in biodiversity decline in these agroecosystems. The processes of intensification are expected to be cumulative with long term negative effects of fertilizers on plant biodiversity and terrestrial ecosystems stability as seen in Western countries (de Schrijver et al., 2011; Melts et al., 2018). Secondly, large-scale state farms are still embedded in a matrix of small-scale traditional farms – 96% of the agriculture landscape is dominated by small-scale farming (Taffesse et al., 2013) – (Fig. 2), which could act as sources for direct recolonization. This hypothesis predicts that the negative effect of large-scale farming is proportional to the amount of extensive small-scale farms in the surroundings. Alternatively, there are indications that small-scale farming is more intensive in terms of fertilizer use due to high rural population density (Josephson et al., 2014; Mellor, 2014). More studies are clearly needed to quantify the input of fertilizers and pesticide in large – *vs* small-scale farming. Altogether, these results demonstrate that in large-scale farms where semi-natural habitats are fostered, diverse bird communities can persist. This suggests that an increase of semi-natural habitats within the landscape matrix could mitigate the negative effect of agricultural intensification, at least insofar farming practices allow vegetation recruitment. However, we must bear in mind that large areas of native Afromontane forest have vanished (Aerts et al., 2008) and the scattered occurrence of forest birds in human-dominated countrysides does not imply that these species can develop healthy populations in these habitats (Daily et al., 2001).

The complexity in assessing the full extent of the agricultural intensification's impact on the avifauna and variation of its effects might be related to a species life-history or to species-specific ecological requirements. This study illustrates the primordial importance of understanding the complexity of such anthropogenic systems, as well as the interactions underlying these systems and the natural habitats surrounding them, for providing evidence-based management recommendations that would benefit both local and wintering bird communities without neglecting the typical local economy of smallholders.

4.1. Management recommendations and conclusion

Although it is difficult to provide congruent management measures across the bird groups examined, all being of fundamental importance in terms of conservation (migratory, farmland and endemic species), our results enable us to frame first recommendations. In both large- and small-scale agriculture, the preservation and promotion of vertical natural structures such as hedges, native trees and bushes, ideally along existing riverbeds, are crucial for most of the bird communities in Ethiopian highland agroecosystems. Fostering these semi-natural habitats should be prioritized in the extensive, small-scale farming system due to their stronger effect sizes on avian biodiversity. In large-scale farms, particular management should ideally be adopted in order to allow tree regeneration. The resulting increased landscape complexity may deliver more efficient ecosystem services, notably those provided by insectivorous birds feeding on insect pests, which is in line with former studies that have evidenced higher biological control functions within more complex landscapes (Gergel et al., 2019; Pywell et al., 2015; Redlich et al., 2018a). Furthermore, promoting such structures could also directly benefit the smallholders themselves as it prevents soil erosion (Pender et al., 2001) and also favours water conservation (Adgo et al., 2013). Yet, despite the fact that irrigation and the prevention of soil erosion are two of the main challenges for Ethiopian smallholders, these naturally stabilizing structures are too rarely adopted (Fentie et al., 2013; Logan, 2014; Taddese, 2001). If such measures are implemented, the reliance on enhanced crop varieties that increase yield in small-scale farms would not dramatically impact bird communities, leading to a sort of sustainable, wildlife-friendly farming intensification system (Tadele, 2017; Tadele and Assefa, 2012). Although agricultural intensification is inevitable in Ethiopia, our findings suggest that a coexistence of the two farming systems (large- *versus* small-scale), as it exists now, might represent a possible option set for maintaining both Ethiopian resident and wintering avifauna inhabiting richly-structured and wide-open landscapes, at least insofar large-scale farms do not become hostile for biodiversity due to farming over-intensification and removal of natural landscape elements. In the end, the Ethiopian highlands context shows that land-sharing and land-sparing strategies can coexist side by side in multi-functional landscapes (Fischer et al., 2014, 2008), benefitting agricultural yield and biodiversity and ecosystem services (Gergel et al., 2019; Tscharntke et al., 2012). To which extent would such a dual approach to farmed landscapes be sustainable from a socio-economic point of view remains to be further investigated (Fischer et al., 2017; Grau et al., 2013).

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Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106737.

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