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High semi-natural vegetation cover and heterogeneity of field sizes promote bird beta-diversity at larger scales in Ethiopian Highlands

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Abstract

1. The intensification of farming practices exerts detrimental effects on biodiversity. Most research has focused on declines in species richness at local scales (alpha-diversity) although species loss is exacerbated by biotic homogenization that operates at larger scales (i.e., affecting beta-diversity). The majority of studies have been conducted in temperate, industrialized countries while tropical areas remain poorly studied. Agricultural landscapes of sub-Saharan Africa are still largely dominated by small-scale subsistence farming, but strenuous efforts to intensify farming practices are currently spreading to meet a growing food demand. It is therefore crucial to understand how these intensified practices affect biodiversity to mitigate their negative impacts.
2. We investigated how farming system (small- vs large-scale farming) and landscape complexity (semi-natural vegetation cover) drive bird species composition, community turnover, and beta-diversity patterns in Ethiopian Highlands' agroecosystems. We evaluated the following hypotheses: (1) large-scale farming homogenizes bird communities, (2) community turnover is higher in small-scale farms, (3) interactive effects between landscape complexity and farming systems shape avian communities, (4) heterogeneity of field sizes increases community turnover at larger scales.
3. Bird communities underwent greater compositional changes along the landscape complexity than along the agricultural intensity gradient. Contrary to our expectations, beta-diversity was not significantly lower within large-scale farms (no biotic homogenization), and complex landscapes that still offer a high amount of semi-natural vegetation promoted community turnover in both farming systems.
4. Semi-natural vegetation cover mediated how avian communities responded to agricultural intensification: the compositional differences between small- and large-scale farms increased with vegetation cover, further promoting avian community heterogeneity at the landscape level.
5. The heterogeneity in field sizes also enhanced bird community turnover, suggesting that a combination of both small- and large-scale farming systems within a given landscape unit would promote beta-diversity at larger scales, provided large-scale farms do not become dominant.
6. *Synthesis and applications:* Landscape complexity shaped avian communities to a stronger degree than farming intensity, emphasizing the importance of semi-natural

vegetation and landscape heterogeneity for the maintenance of diverse bird communities and for achieving multifunctional landscapes promoting biodiversity and associated ecosystem services on the High Ethiopian plateaus.

Keywords: Ethiopia, agricultural intensification, large-scale farming, landscape complexity, bird diversity, beta-diversity partitioning, turnover, multifunctional landscapes

1 Introduction

Agricultural intensification represents one of the greatest threats to biodiversity globally (Green, Cornell, Scharlemann, & Balmford, 2005). Habitat loss, landscape simplification and the use of agro-chemicals (e.g., pesticides and fertilizers) triggered the collapse of many taxa, including birds, for which species declines are particularly well documented (Benton, Vickery, & Wilson, 2003; Donald, Green, & Heath, 2001; Glemnitz, Zander, & Stachow, 2015; Green et al., 2005). Yet, most studies have focused on local species loss (alpha-diversity), despite the fact that agricultural intensification homogenizes biotic communities at larger spatial scales (Gossner et al., 2016; Mckinney & Lockwood, 1999). Indeed, as biodiversity loss is exacerbated at larger scales, understanding beta-diversity (i.e., compositional variation between communities) patterns is essential for conserving regional (gamma) biodiversity (Socolar, Gilroy, Kunin, & Edwards, 2016). Moreover, a growing body of evidence suggests that beta-diversity is not only important for biodiversity conservation, but that it also plays a major role in ecosystem functioning as taxonomically or functionally distinct communities provide multiple functions across spatial and temporal scales (Mori, Isbell, & Seidl, 2018). It is therefore crucial to investigate how anthropogenic disturbances affect farmland birds' beta-diversity (e.g., homogenization *vs* heterogenization of species communities) in order to mitigate the negative effects of land use intensification (Ponisio, M'Gonigle, & Kremen, 2016; Marcacci et al. 2021).

However, the interpretation of beta-diversity can be challenging (Anderson et al., 2011; Mori et al., 2018). For example, total beta-diversity, the variation observed between communities, confounds two distinct ecological processes and can be partitioned into two additive components (Baselga, 2010, 2013). The first component, called turnover, corresponds to species replacement between communities, in practice between study sites. The second component, called nestedness,

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corresponds to differences in species richness between communities, implying that a community is a subset of another.

Agricultural intensification can thereby affect beta-diversity in multiple ways. For example, beta-diversity typically increases when a new disturbance (e.g., converting small-scale to large-scale agriculture) occurs within a region, leading to local biodiversity loss (i.e., nestedness) and an increase in compositional dissimilarity through environmental filtering or neutral sampling effect (Chase, Kraft, Smith, Vellend, & Inouye, 2011; Socolar et al., 2016). On the other hand, this conversion may also potentially increase landscape heterogeneity, allowing immigration by new species (i.e. turnover), which would further increase overall beta-diversity. Nevertheless, most studies have reported biotic homogenization in intensified land uses, which are either more homogeneous or act as ecological filters of biological communities (Karp *et al.* 2012; Gámez-Virués *et al.* 2015; Gossner *et al.* 2016). Moreover, agricultural intensification and landscape homogenization often occur simultaneously (Chiron, Chargé, Julliard, Jiguet, & Muratet, 2014). As a result, few studies have succeeded in disentangling the effects of intensified farming practices (e.g., large-scale farming) and the loss of semi-natural habitat (e.g., semi-natural vegetation) on beta-diversity. Nonetheless, Karp *et al.* (2018) showed that bird communities exhibited a higher turnover in forest, where vegetation structure was more heterogeneous, than in agricultural landscapes. In contrast, Dormann *et al.* (2007) found that avian communities were more homogenous (more similar) in landscapes with a higher amount of semi-natural habitats. In this study, we investigated the effect of agricultural intensification on birds in Ethiopian Highlands' agroecosystems. With more than 100 million inhabitants, Ethiopia is already Africa's second most populated country and its population is predicted to reach 190 million by 2050 (www.prb.org). An increase in crop production is thus of utmost importance to guarantee food security, resulting in strenuous efforts to intensify its agricultural management. Although

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smallholder farming still forms the backbone of food security in Ethiopia (Tschardtke *et al.* 2012; Taffesse *et al.* 2013), recent political reforms have led to the establishment of large-scale commercial farms (Logan, 2014), creating a dichotomous agricultural landscape comprising two drastically contrasting farming systems (Taffesse *et al.*, 2013). In addition, these large-scale farms can be surprisingly highly complex in terms of semi-natural vegetation cover and landscape configuration (Fig 1). As a result, Ethiopian Highlands are an exemplary model system to study the effect of small- vs large-scale farming on avian communities. Although most of Ethiopian Highlands are already turned into agriculture (Taffesse *et al.*, 2013), their avifauna is still remarkably rich and unique. Indeed, these agroecosystems harbour several endemic and near-endemic species (Redman *et al.* 2011), and serve as overwintering grounds for several endangered migratory landbirds (e.g., Ortolan Bunting, Jiguet *et al.* 2019). How these agricultural landscapes are managed is therefore critical for many species that rely on them.

In a previous study, we investigated how agricultural intensification affected Ethiopian Highlands' bird communities from the viewpoint of alpha-diversity (Marcacci *et al.* 2020).

However, alpha-diversity does not tell the full story and a second step is needed to understand the relative effects of the farming system (small- vs large-scale farming) and the amount of semi-natural vegetation cover on species composition, community turnover and beta-diversity patterns.

This step will significantly contribute to a better understanding of how we could mitigate the negative effects of agricultural intensification and restore biodiversity in this changing agroecosystem. To this end, we surveyed birds along 80 walk-transects carefully selected to embrace the contrasted landscape complexity (i.e., semi-natural vegetation cover and landscape heterogeneity) and farming intensity encountered in the Ethiopian Highlands. We evaluated the following four hypotheses. (1) Beta-diversity within large-scale farms is lower than within small-scale farms because intensive agriculture leads to biotic homogenization (Gossner *et al.*, 2016;

Karp et al., 2012). (2) Community turnover is stronger in small-scale than large-scale farms because small-scale farms harbour more complex vegetation structures (Karp et al., 2018). (3) Interactive effects between farming systems and landscape complexity shape avian communities, because bird response to increasing amount of semi-natural vegetation in the landscape depends on the farming system (Marcacci *et al.*, 2020). (4) Increasing heterogeneity in field size enhances bird community turnover, because a combination of both farming systems (i.e., small- vs large-scale) increases environmental heterogeneity (Stein, Gerstner, & Kreft, 2014) and promotes avian diversity at larger scales.

2 Material & Methods

2.1 Study area

This study was conducted in the southeastern Ethiopian Highlands between 2340 and 2670 m above sea level, north of the Bale Mountains National Park (Fig 1). Due to the prime condition for cultivation, the landscape is largely dominated by a mosaic of small-scale farms interspersed with semi-natural habitats such as field-margins, natural grasslands, bushes, forest fragments, woodlands, planted Eucalyptus trees, rivers and wetlands. The majority of grown crops are cereals (teff, wheat, barley) and pulses (horse bean, chickpea). However, the recent establishment of large commercial farms dramatically changed this traditional landscape. These commercial farms (> 25 ha, see also Taffesse *et al.* 2013) are composed of an assemblage of large monocultures (mostly wheat) harvested by combine machines and with access to new farming technologies (e.g., pesticides, chemical fertilizers, enhanced crop varieties; Marcacci et al., 2020; Tadele, 2017). They contrast drastically with the traditional small-scale farms where most labour is done manually and production is mostly dedicated to subsistence farming (Taffesse *et al.* 2013; Logan 2014; see Fig 1).

Research permits and authorizations were obtained from Ethiopian Wildlife Conservation Authority (EWCA), the governmental organization responsible for the conservation and utilization of Ethiopian wildlife. This study did not require ethical approval.

2.2 Study design

We selected 80 transects distributed among six study sites, located between Adamogne (7.038059, 39.000987) and Sinana (7.067561, 40.212925) (40 in small-scale farms and 40 in large-scale farms). All transects had a length of 400 m (399.3 ± 0.5 m) with a 50 m buffer around them (≈ 3.9 ha). The mean distance between sites was 19.99 km and the mean distance between transects within a site was 717.3 m. We selected the transects in order to disentangle the effects of the farming system (small- vs large-scale farming) from those of semi-natural vegetation cover on avian communities. While these two factors are often correlated, i.e. intensively managed farms generally lack natural structures, the proportion of semi-natural vegetation cover (mapped in the field and calculated in QGIS; Quantum GIS Development team, 2017) within the transect buffers ranged from 0-47% and was independent from the farming system (Kruskal-Wallis: $\chi^2 = 0.137$, p-value = 0.71) in our study area, thereby allowing to assess their relative contributions (see Fig 1). Moreover, to perfectly balance the design between farming systems and the landscape complexity gradient and to prevent any spatial bias, we selected the same number of transects (6-8) in small- and large-scale farms in both complex and simple landscapes in each site.

2.3 Bird surveys

We surveyed birds using the line-transect method following Guyot *et al.* (2017). This method consists in slowly walking a predefined path (the transect) and record all the birds heard or seen

within the transect buffer during 30 (± 5) min. Birds flying over the transect were excluded. The surveys were conducted under good weather conditions (no wind, no rain) and in early morning hours (up to four hours after dawn) when bird activity peaks. Three observers with similar ornithological expertise (GM, JG and JM) conducted all surveys. Each transect was surveyed on two consecutive days by the same observer. In addition, the surveys were carefully planned to equally balance the different transect categories (farming system and landscape complexity) between the three observers. All surveys took place between November 2017 and February 2018 when Palearctic migrants overwinter and/or migrate across Ethiopian Highlands.

2.4 Beta-diversity metrics

Throughout our analyses, we used pairwise Sørensen (incidence-based beta-diversity – unshared species between communities) and Bray-Curtis (abundance-based beta-diversity – unshared species abundances between communities) dissimilarities. Overall beta-diversity confounds two distinct ecological processes and can be partitioned in two additive components (Baselga, 2010, 2013). Using the *betapart* R-package (Baselga & Orme, 2012) we therefore decomposed Sørensen dissimilarity (β_{sor}) into species turnover (β_{sim}), which corresponds to species replacement between communities, and nestedness (β_{sne}), which corresponds to richness differences between communities. Similarly, Bray-Curtis dissimilarity (d_{BC}) can be partitioned into two components as well, accounting for balanced variations in abundance ($d_{\text{BC-ba}}$, i.e. individuals turnover), and an abundance gradient ($d_{\text{BC-gra}}$, i.e. nestedness).

Additionally, to ensure the robustness of our results, we implemented a null model approach to factor out effects of species richness on beta-diversity metrics (Chase et al., 2011; Socolar et al., 2016). Specifically, following several authors (Chase et al., 2011; Karp et al., 2018; Ponisio et al., 2016), we created 1000 randomly assembled communities, maintaining abundance and richness

(column and row sums), using a quasi-swap algorithm (*vegan* R-package; Oksanen *et al.* 2020). We then added individuals by drawing species with probabilities proportional to their relative abundance in the observed community until it reached the total number of individuals present at each site (transect). Next, we calculated the expected pairwise Sørensen and Bray-Curtis dissimilarities for each randomly assembled community. Lastly, we computed the proportion of randomized communities with dissimilarity values lower than (and half of those equal to) that of the observed community (Chase *et al.*, 2011). We used these proportions as “corrected beta-diversity” metrics (Ponisio *et al.*, 2016).

2.5 Statistical analyses

Data from the two consecutive surveys were aggregated per transect, taking the list of species detected and their maximum abundances recorded within the two surveys (N = 80). Due to the sparse occurrence of lakes and other wetlands, strictly aquatic birds were excluded from the analyses. All statistical analyses were conducted in R version 4.0.2 (R Core Team 2020). As beta-diversity patterns can be challenging to analyze and interpret (Anderson *et al.*, 2011), we used different strategies largely inspired by Karp *et al.* (2018). We estimated the sampling completeness using Chao 1 species estimator (Chao, 1987).

To investigate the relative effects of the farming system (small- vs large-scale farming) and semi-natural vegetation cover on community composition, we first ran a Permutational Multiple Analysis of Variance (PERMANOVA) using the *adonis()* function from *vegan* (Oksanen *et al.* 2020). We set “site” as “strata” and calculated p-values with 999 permutations. Additionally, we used Non-Metric Multidimensional Scaling (NMDS) plots to visualize community changes across the two gradients.

Second, we were interested in the effects of the farming system (small- vs large-scale farming) on beta-diversity. Specifically, we tested whether our beta-diversity metrics (Sørensen and Bray-Curtis dissimilarities, their turnover and nestedness components and their corrected estimates) were higher or lower within one of the farming systems. To this end, we calculated the multivariate dispersion from each site to the centroid of all sites in the same farming system using the *betadisper()* function from *vegan* (Anderson, 2006; Anderson, Ellingsen, & McArdle, 2006). We extracted the estimates and fitted linear mixed models (LMMs) with “site” set as random intercept (*lme4* R-package, Bates *et al.* 2015). We added the observer as covariate in the models to account for differences in detection among observers. We tested whether the mean distance to the centroid between the two farming systems significantly differed through comparing nested models with likelihood ratio tests (i.e., evaluating the ratio of likelihoods against a chi-square distribution; Zuur *et al.*, 2009). To further assess whether agricultural intensification had different effects on species associated with forest or open lands, we classified species into guilds containing forest and woodland birds or semi-open to open farmland birds (based on Redman *et al.* 2011) and repeated the analyses. Because there were not enough forest species in too simple landscapes (low semi-natural vegetation cover), we could only model total beta-diversity.

Third, to investigate the interactive effects of landscape complexity and the farming system, we compared large- and small-scale farm communities along the semi-natural vegetation cover gradient. Following Karp *et al.* (2018), we calculated the distance from each small-scale farms to the centroid of all large-scale farms using Sørensen and Bray-Curtis dissimilarities. We then tested whether the average large-scale farms community (centroid) was more (or less) dissimilar to small-scale farms communities (distance to centroid) along the gradient of semi-natural vegetation using LMMs with site-ids set as random intercept. Significance was again estimated using likelihood ratio tests.

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Finally, we assessed the turnover rate of small- vs large-scale farms along spatial (geographic distance between transects) and environmental (semi-natural vegetation cover and mean field size) gradients using distance-decay relationships. Here, we used mean field size as a continuous variable (unlike the previous analyses where we compared the two contrasted farming systems) because we were interested in verifying whether an increase in field size heterogeneity promotes bird community turnover and because distance decay analyses require a continuous spatial or environmental gradient. Distance-decay relationships (i.e., increase of compositional dissimilarity with increasing spatial or environmental distance between pairs of sites) is one of the most commonly used method to analyze the rate of compositional changes in relation to spatial or environmental distances (Baselga, 2013; Nekola & White, 1999). We thus fitted negative exponential distance-decay models using the *decay.model()* function in *betapart* R-package with incidence- (β_{sim}) or abundance-based (d_{BC-bal}) turnover as a response variable. The explanatory variables were the geographical distance, the distance in semi-natural vegetation cover and the distance in mean field size between all possible transect pairs. Environmental distances were calculated as Euclidean distances with the *dist()* function from *vegan*. The use of negative exponential distance-decay models (compared to other linear models) meets the assumption of asymptotic increase of dissimilarity constraints between 0 and 1 (Baselga 2013). These models adjust a GLM (with a log link function and a Gaussian error distribution) to incorporate a dissimilarity matrix as response variable. P-values are computed by randomizing 1000 times predictions and calculating the number of times the model deviance is lower than the randomized deviance (Gómez-Rodríguez & Baselga, 2018). We finally assessed whether the slopes (turnover rates) of the two farming systems significantly differed by bootstrapping 1000 times the coefficients (*boot.coefs.decay()*). Two-tailed p-values were then calculated based on the

proportion of bootstrapped values larger or smaller than each other (Gómez-Rodríguez & Baselga, 2018). All models' assumptions were checked using diagnostic plots.

3 Results

Overall, we detected 8722 terrestrial birds from 112 species (see Table S3 in Supplementary Information). On average, per transect, there were 119 ± 69 individuals of 17 ± 7 species in small-scale farms and 99 ± 54 individuals of 13 ± 5 species in large-scale farms. 97 species were detected in total in the small-scale farms, of which 33 (30% of all species) were unique (were not recorded in large-scale farms). This is more than in large-scale farms, where we recorded 79 species, of which 15 were unique (13%). Chao 1 species estimator indicated that we sampled 94.12 % of the estimated regional bird richness.

3.1 Effect of farming system and semi-natural vegetation cover on community composition

Results from PERMANOVA indicate that bird community composition changed along both the agricultural intensity and the landscape complexity gradients. The farming system (small- vs large-scale farming) had a significant effect on both Sørensen ($F = 4.869$, p -value = 0.001) and Bray-Curtis ($F = 2.956$, p -value = 0.012) dissimilarities. Even stronger effects on bird community composition were detected in relation to semi-natural vegetation cover (Sørensen: $F = 18.767$, p -value < 0.001; Bray-Curtis: $F = 16.107$, p -value < 0.001), as illustrated by the NMDS plots (Fig 2).

3.2 Effect of farming system on beta-diversity metrics

We expected beta-diversity to be higher within small-scale farms than within large-scale farms. However, neither Sørensen and Bray-Curtis dissimilarities, nor their turnover and nestedness

components and corrected estimates significantly differed between the two farming systems (Table S1, Fig 3 and S1). Analyses on forest and open-habitat bird communities yielded the same results: no significant effects detected (Table S1, Fig S2 and S3). Overall, total beta-diversity was more driven by turnover than nestedness in both farming systems (p-value < 0.001).

3.3 Turnover rates along spatial and environmental gradients

The rate of community turnover increased with distance in semi-natural vegetation cover between sites for both Sørensen and Bray-Curtis index (Table S2, Fig 4). However, this increase was higher in small-scale farms than in large-scale farms (steeper slopes, bootstrapped p-values < 0.001). Bird communities thereby exhibited a higher turnover rate between small-scale farms that differed in semi-natural vegetation cover than between large-scale farms. In contrast, we only found a significant increase of turnover between large-scale farms that were spatially more distant for both Sørensen and Bray-Curtis index, whereas no effect was detected between small-scale farms. Bray-Curtis turnover increased with mean field size distance, whereas no relation was found for Sørensen turnover. This positive effect suggests that having both small- and large-scale farms in the landscape increases turnover.

3.4 Interactive effects of farming system and semi-natural vegetation cover on beta-diversity

The average large-scale farm communities (centroid) became more dissimilar to small-scale farms communities (distance to centroid) with increasing semi-natural vegetation cover, for both Sørensen ($\chi^2 = 16.13$; p-value < 0.001) and Bray-Curtis ($\chi^2 = 4.18$; p-value = 0.04) dissimilarities (Fig 5). This means that landscape complexity mediated the differences in community composition (beta-diversity) between the two farming systems.

4 Discussion

Both agricultural intensity and landscape complexity gradients influenced bird community assembly. However, changes in community composition were higher along the gradient of semi-natural vegetation (Fig 2). This result is in line with other studies, which found that vegetation cover (e.g., trees) was more important in determining bird community composition than field size within agroecosystems (Mellink, Riojas-López, & Cárdenas-García, 2017). Other studies also reported that the amount of semi-natural vegetation in the landscape had stronger effects on bird diversity than the agricultural management *per se* (Berg, 2002; Redlich, Martin, Wende, & Steffan-Dewenter, 2018). Semi-natural vegetation cover in the wider landscape not only favored forest species like African Paradise Flycatcher (*Terpsiphone viridis*) but also farmland species such as Ortolan Bunting (*Emberiza hortulana*) or Swainson's Sparrow (*Passer swainsonii*) that use these natural structures as shelter, perches (e.g., for hunting, displaying, resting) or nest sites. Overall, Ethiopian Highlands' bird communities tracked changes in vegetation structure in both farming systems (Fig 4a-b). However, species turnover (both Sørensen and Bray-Curtis turnover) was higher in small-scale farms that differed in semi-natural vegetation cover compared to large-scale farms. This is likely due to more heterogeneous vegetation structure and plant species composition in small-scale farms, leading to a greater avian community turnover (Karp et al., 2018). Although not measured here, tree species composition was more uniform in our large-scale farms, with a lower spatial heterogeneity (e.g., often clumped at the fields' edges), less understory vegetation and of impoverished ecological quality (e.g., Eucalyptus trees). Nonetheless, increasing semi-natural vegetation cover in the landscape yielded higher turnover in both small- and large-scale farming systems, suggesting it could be a promising strategy to mitigate the negative effects of the intensification of farming practices on avian communities.

Moreover, semi-natural vegetation cover mediated how avian communities responded to agricultural intensification: the compositional differences (beta-diversity) between small- and large-scale farms increased with increasing semi-natural vegetation cover (Fig 5). It is indeed well established that the landscape context (e.g., simple vs complex) influences the effects of farming management intensity on biodiversity (Batáry et al., 2011; Smith et al., 2020; Tschardtke, Klein, Krüss, Steffan-Dewenter, & Thies, 2005). Fostering structurally complex landscapes in both farming systems would thereby not only counter biotic homogenization, but further promote avian community heterogeneity at wider landscapes (interactive effects). The effects of the farming system (small- vs large-scale) on the taxonomic composition of our avian communities seemed much smaller than what was reported from other studies (e.g., Karp *et al.* 2012; see Fig 2). Although crop diversity and food availability were reduced in large-scale farms in our study areas (Marcacci *et al.* 2020), most open-habitat specialists such as Erlanger's Lark (*Calandrella erlangeri*), Yellow Wagtail (*Motacilla flava*) or Red-throated Pipit (*Anthus cervinus*) were commonly found in both farming systems. Other species typically associated with traditional small-scale farms (e.g., Ortolan Bunting, Thekla Lark (*Galerida teklae*) or Streaky Seedeater (*Serinus striolatus*)), which rely mostly on the leftovers after harvest (stubble) were much less numerous in the large commercial farms managed with mechanized harvesting methods (Marcacci *et al.* 2020; Gremion *et al.*, 2021). Besides, large-scale farms had considerably less people working permanently in their fields than small-scale farms (personal observation), which may affect birds' foraging efficiency and breeding success. While there is an omnipresence of people and livestock moving around in small-scale farms, local communities are not allowed to enter the large-scale farms on the Ethiopian plateaus. Birds such as bustards are known to be highly sensitive to human disturbance (Le Cuziat et al., 2005; Sastre, Ponce, Palacín, Martín, & Alonso, 2009). Not surprisingly, we observed Black-bellied Bustards (*Lissotis*

melanogaster), Kori Bustards (*Ardeotis Kori*) and even roosting Short-eared Owls (*Asio flammeus*) only in large-scale farms. These agroecosystems could thus act as important refuges for disturbance-sensitive species, and this would be worth confirming with deeper investigations. Moreover, contrary to our expectations, we did not find any significant differences between the two farming systems for any of the tested beta-diversity metrics (Fig 3, Fig S1). The same was true when looking only at forest or open-habitat species (Fig S2, S3). These results suggest that although large-scale farming reduced species richness (alpha-diversity, see Marcacci *et al.* 2020), it did not homogenize bird communities in our study regions, contrary to other studies conducted in Europe (Batáry *et al.*, 2017; Šálek, Kalinová, Daňková, Grill, & Žmihorski, 2021). We must however interpret this finding with care as we only conducted two survey rounds and we might have occasionally missed some bird species that are more difficult to detect. Indeed, our analyses did not account for differences in detection probabilities among species, which may have introduced more heterogeneity in the observed beta-diversity trends (Royle, 2004; Ruiz-Gutiérrez, Zipkin, & Dhondt, 2010). Furthermore, this result might not be true for other taxa as different taxa respond differently to agricultural intensification (Burel, Butet, Delettre, & De La Peña, 2004; Gossner *et al.*, 2016). We also have to bear in mind that the establishment of these large-scale farms in Ethiopia is quite recent and that there could be a delay in biodiversity loss (i.e. Extinction Debt to be paid), or that small-scale farms, which represent 96% of the agricultural landscape (Taffesse *et al.* 2013), act as sources for direct recolonization (Marcacci *et al.* 2020).

Surprisingly, the spatial turnover was higher in large-scale farms (Fig 4c-d). This result contrasts with other studies, which found a lower spatial turnover in intensified agriculture (Karp *et al.*, 2012). One possible explanation is that many open-habitat specialists we recorded in the large-scale farms belonged to migratory or overwintering species such as Yellow Wagtail or Red-

throated Pipit. As these species were not breeding and thus less territorial, they could be more mobile and disperse farther, tracking local food availability. Furthermore, these species are gregarious and moving in larger groups, hence potentially having a disproportional effect on community composition — at least for abundance-based / Bray-Curtis turnover.

We also found a positive relationship between Bray-Curtis turnover (but no relation with Sørensen) and increasing heterogeneity in field sizes (Fig 4e-f), suggesting shifts in species dominance between the two farming systems. This positive effect suggests that a combination of both small- and large-scale farms, independent of landscape complexity, increases community turnover and enhances avian beta-diversity. Indeed, although we recorded more unique species in small-scale farms (33 species, 30%), 15 species (13%) were only observed in large-scale farms. A coexistence of both farming systems might thereby promote farmland bird biodiversity at larger scales, but probably only as long as intensified farms do not dominate the cultivated landscape. While former studies have found limited potential of heterogeneous managements to mitigate the negative effects of land use intensification on beta-diversity (e.g., Gossner *et al.* 2016), our results are in line with the general principle that spatial environmental heterogeneity should allow more species to coexist through an increase in environmental gradients, resource complexity and available niche spaces (Stein *et al.* 2014; Vickery & Arlettaz 2012).

5 Conclusions

With growing human population and increasing food demand, it is urgent to design agroecosystems that benefit both people and nature. Our study demonstrates the utmost importance of landscape complexity in driving bird community turnover and composition in the high Eastern African plateaus. Increasing semi-natural vegetation cover through the preservation and/or plantation of hedges, stands with native trees, bushy cordons, etc., could promote farmland

bird communities on a wide scale. Such measures (e.g., Humbo assisted natural regeneration project in Ethiopia; Brown *et al.* 2011) will not only restore alpha-diversity (Marcacci *et al.* 2020) but also beta-diversity, thus preventing biotic homogenization in intensively-managed agriculture. Although we have to consider their limitations, our results further suggest the potential for the coexistence of traditional small-scale and industrialized large-scale farms, both farming systems providing habitat for distinct bird communities. Increasing landscape heterogeneity at larger scales, both in terms of farming system and landscape complexity, would result in multifunctional agroecosystems supporting both agricultural biodiversity and key associated ecosystem services upon which smallholders depend (Tscharntke *et al.* 2012; Fischer *et al.* 2014; Baudron *et al.* 2019). However, as incentives to intensify farming practices (Headey, Dereje, & Taffesse, 2014; Logan, 2014) and land grabbing are widespread in Ethiopia (Fischer *et al.*, 2017), we urge that efforts to maintain a sustainable balance between these two farming systems (large- vs small-scale) are bolstered. If large-scale intensive farms were to become dominant, Ethiopian Highlands' agroecosystems could undergo the same dramatic biodiversity erosion that is observed in Western industrialized countries (Donald *et al.* 2001).

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Authors' contributions

A.J. conceived and designed the study; G.M., J.G., J.M. and T.S. collected the data; G.M. and A.J. conceived the analyses; G.M. conducted the analyses; G.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

Data available via Zenodo <https://doi.org/10.5281/zenodo.5993251> (Marcacci et al., 2022).

Conflict of interest: none.

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Figures' legends

Fig 1. (a) Map of Ethiopia (©GADM). (b) Location of all the transects displayed in orange (large-scale farms) or green (small-scale farms). (c) Example of five transects with their buffer near Ali (7.303511, 39.869763). In the background, we can see how contrasted these two farming systems are. Pictures illustrating small-scale farming in simple (d) and complex landscapes (e), and large-scale farming in simple (f) and complex (g) landscapes.

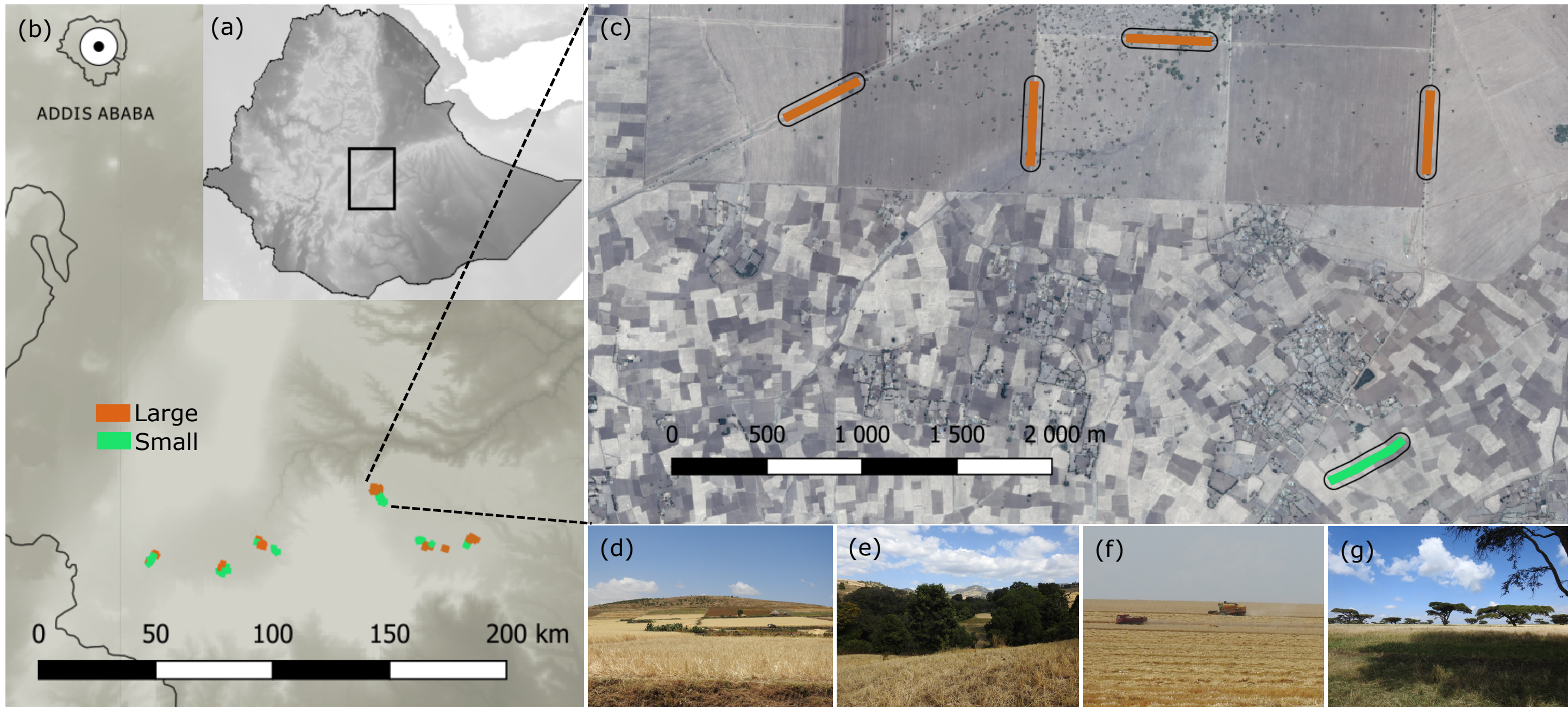
Fig 2. Non-metric Multidimensional Scaling (NMDS) plots showing the effect of farming system and semi-natural vegetation cover on communities' composition. Dots depict small-scale farms and triangles large-scale farms. The color gradient is proportional to semi-natural vegetation cover: the darker the symbol, the higher the semi-natural vegetation cover. Note that semi-natural vegetation cover has been log-transformed for plotting reasons. The Kori Bustard (*Ardeotis Kori*) represents species associated with large-scale farms (used as refuges against human disturbance), the African Paradise Flycatcher (*Terpsiphone viridis*) represents species associated with high landscape complexity (high amount of semi-natural vegetation), the Ortolan Bunting (*Emberiza hortulana*) species associated with highly structured small-scale farms and the Red-throated Pipit (*Anthus cervinus*) species associated with wide open landscapes (both small- and large-scale farms). ©Jérémy Gremion and Mathieu Bally for the bird pictures.

Fig 3. Effect of farming system on beta-diversity metrics (measured as the mean distance to the group centroids, see statistical analyses). Beta-diversity within large-scale farms was not significantly lower than within small-scale farms. No significant differences were detected for turnover and nestedness either. Significance was tested with likelihood ratio tests.

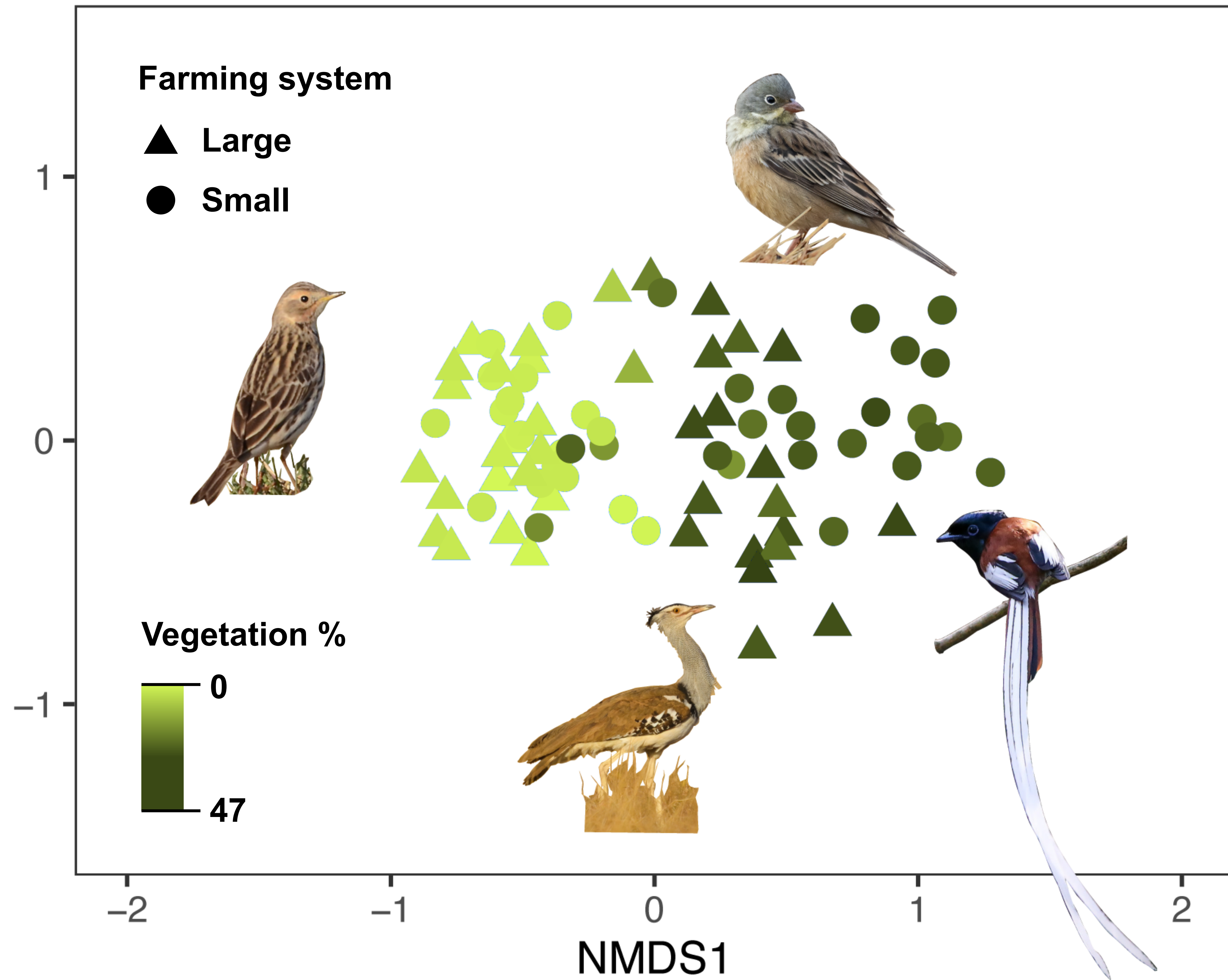
Fig 4. Distance-decay plots showing the rate of incidence- (Sørensen) and abundance-based (Bray-Curtis) turnover with (a and b) increasing distance in semi-natural vegetation cover, (c and d) geographic

distance, and (e and f) distance in mean field size between pair of sites. The lines (small-scale: dashed; large-scale: plain) represent decay models' (adjusted GLMs) predictions and the dots (small-scale: circles; large-scale: triangles) depict all pairwise comparisons. Level of significance: ns p-value > 0.05, ***p-value < 0.001.

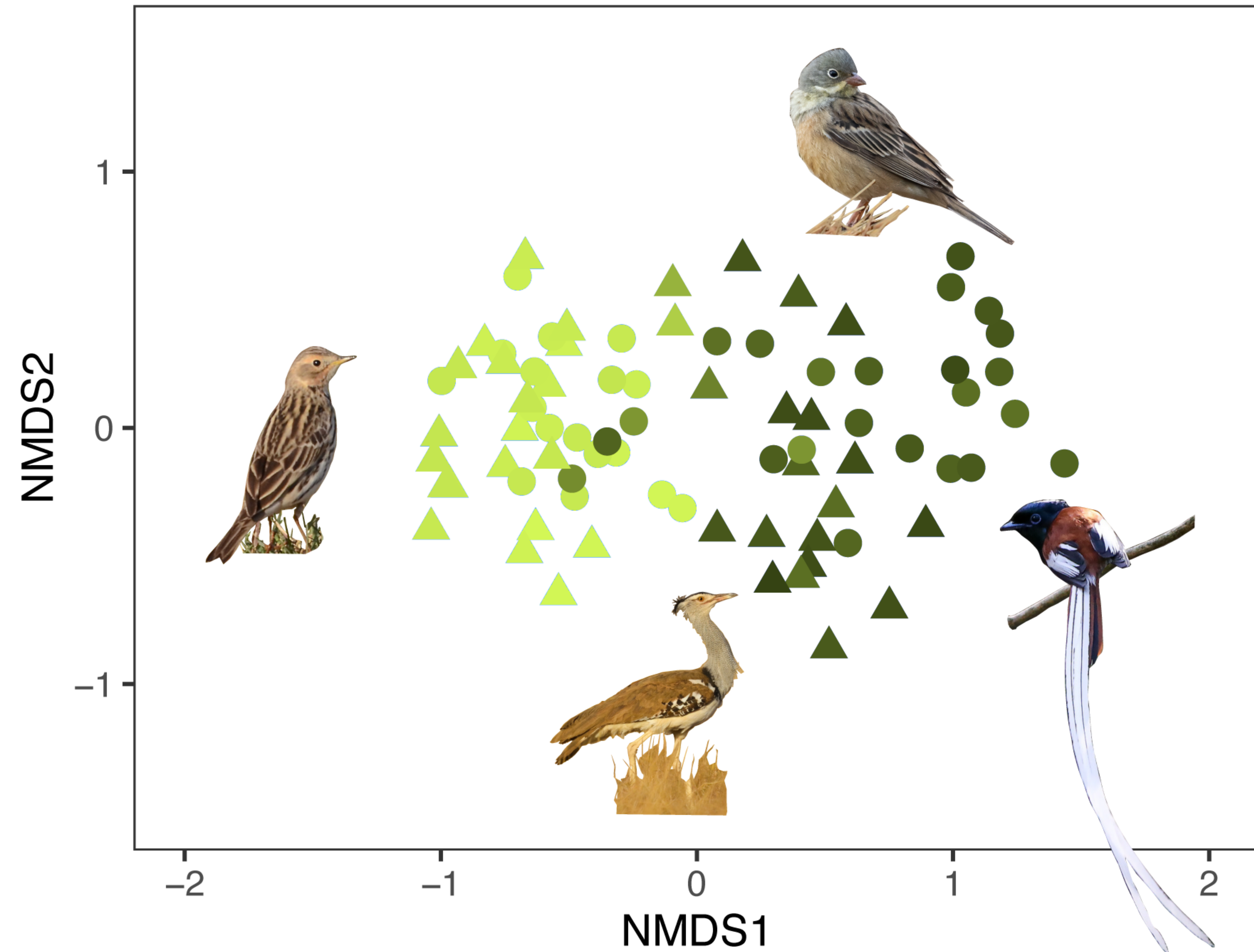
Fig 5. Bird communities inhabiting small-scale farms are more dissimilar to those of large-scale farms when semi-natural vegetation cover is greater in the landscape. The lines represent mean predictions from LMMs, the grey belt depicts the 95% confidence intervals and the dots the raw data. P-values were calculated with likelihood ratio tests. Level of significance: *p-value < 0.05, ***p-value < 0.001.

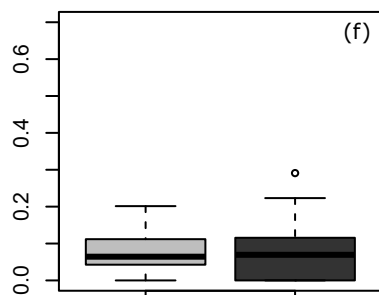
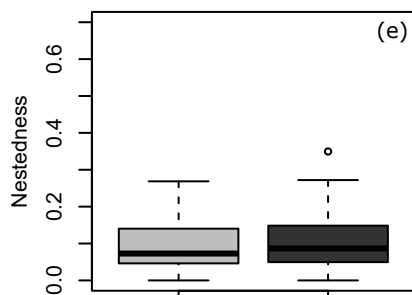
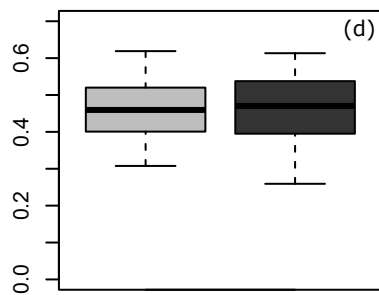
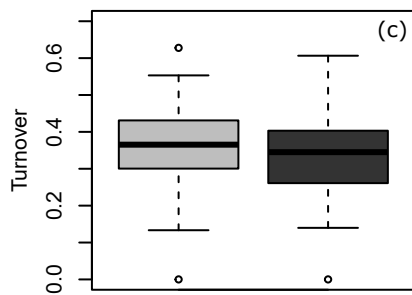
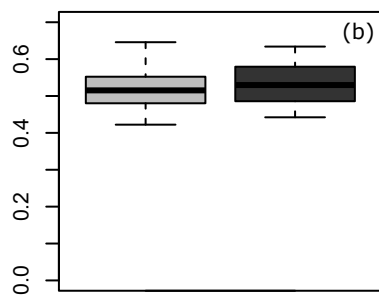
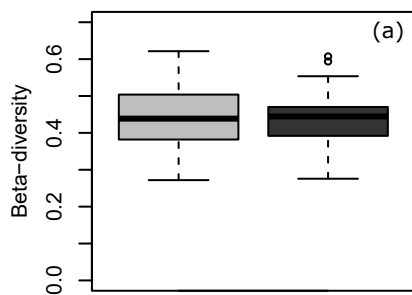


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Bray-Curtis

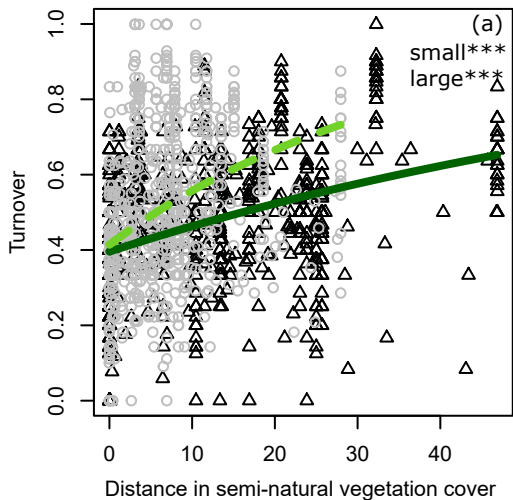


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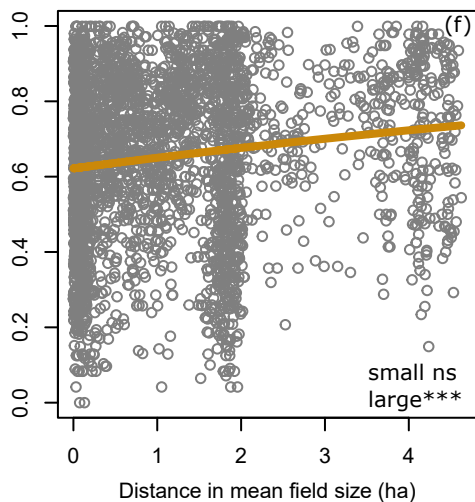
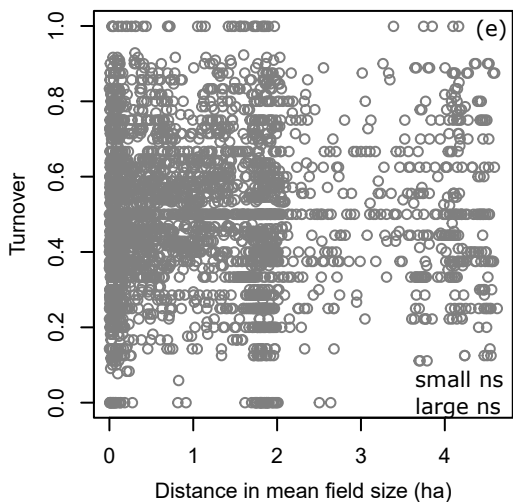
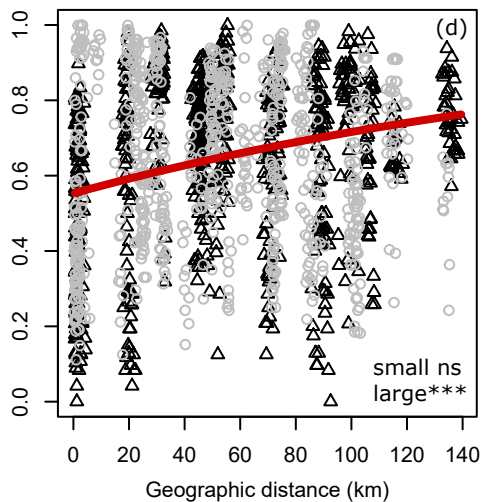
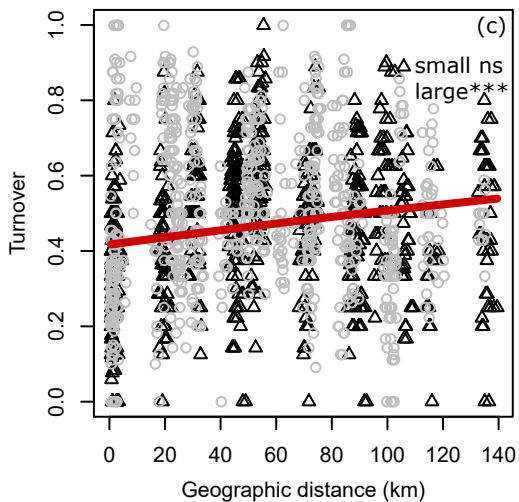
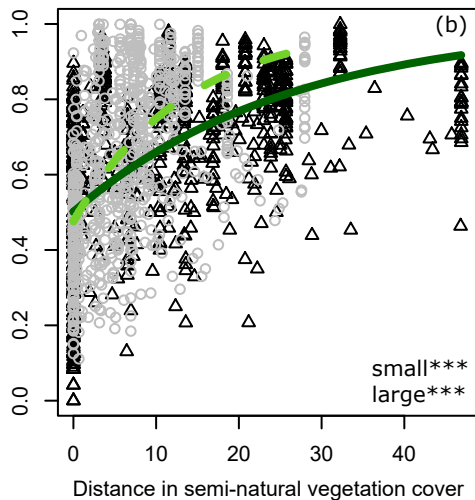
Farming system

Farming system

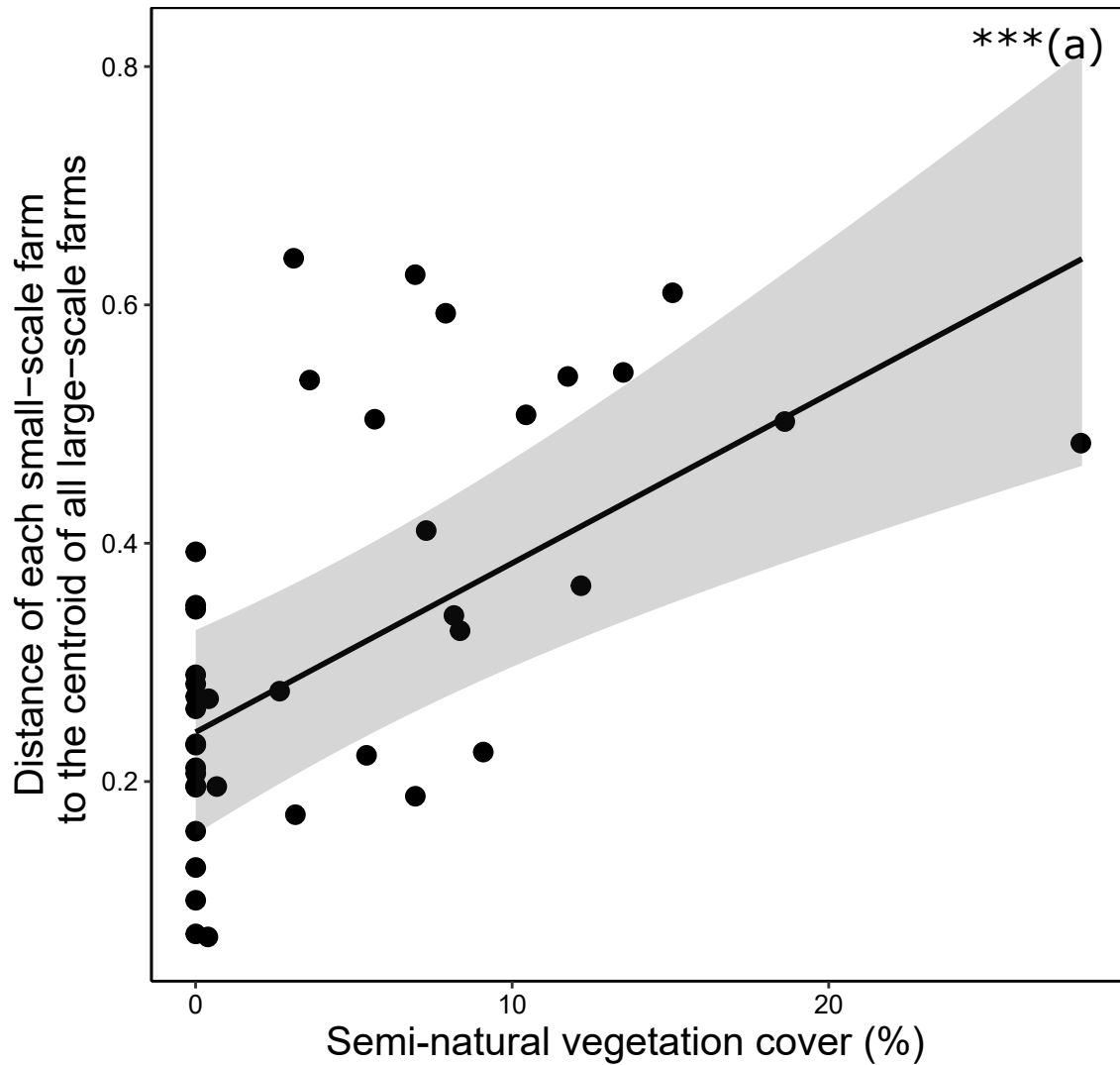
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