Effects of farmland consolidation in Southern China on wild bee species composition, nesting location and body size variations

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Abstract

1. Traditional smallholding-dominated agricultural landscapes in Southern China are increasingly homogenized and consolidated, resulting in large mono-cropped fields and impoverished pollinator communities. The exact impact of this farmland consolidation on composition and functional traits of wild bee communities remain poorly understood.
2. We studied these communities and functional traits in oilseed rape fields embedded in 18 agricultural landscapes located in Jiangxi Province, China, with 11 sites representing traditional (pre-consolidation) and the remaining 7 sites consolidated agricultural landscapes.
3. The composition of wild bee assemblages was not differentiated into consolidated and traditional farmland communities. The mean body size of wild bee species similarly did not show significant differences between consolidated and traditional farmland. The mean intraspecific body size for a dominant species, *Lasioglossum proximatum*, was larger in consolidated than traditional farmland, while individuals of co-dominant *Eucera floralia* showed no such differentiation. In consolidated farmland, the proportion of semi-natural habitat was positively linked to the abundance-based average interspecific body size of wild bee species. For abundance-based calculations, the proportion of aboveground nesting bee species was lower in consolidated landscapes than in traditional ones.
4. Our study suggests that farmland consolidation might affect intraspecific composition, particularly in abundant small-bodied species. Above-ground nesting bees may require specific management interventions in consolidated agricultural landscapes to promote their persistence, which could take the form of semi-natural habitat patches introduced to fields that can also benefit the pollinator community more widely.

Key words: insect pollinator, oilseed rape, beta diversity, semi-natural habitat, functional traits

Introduction

Pollinators provide essential pollination services for agricultural crops (Aizen et al. 2009; Dainese et al. 2019; Klein et al. 2007), with 35% of global food production from crops depending on pollinators (Klein et al. 2007). However, wild pollinators have been experiencing sharp declines due to a variety of factors, with landscape simplification due to agricultural intensification representing one of the most important drivers (Potts et al. 2010). In agricultural landscapes, semi-natural habitats, including forest, shrubland and grassland, can provide food resources such as pollen and nectar, as well as nesting sites for wild bee species (Hevia et al. 2021). Modern homogenized agricultural landscapes commonly contain large cropland areas and only few semi-natural habitat fragments, resulting in reduced nectar and pollen resources and bee nesting sites (Connelly et al. 2015). Accordingly, studies regularly report that the decrease of semi-natural habitat negatively impacts wild bee communities (Connelly et al. 2015; Cusser et al. 2019; Larkin and Stanley 2021; Papanikolaou et al. 2017), with further potential implications for crop pollination services (Holland et al. 2017; Klein et al. 2012).

Pollinator community composition plays an important role in determining interspecific and intraspecific interactions between individual pollinators and resulting pollination services (Willcox et al. 2017). Agricultural landscape simplification results in shifts in the pollinator community composition via trait-specific filtering (Rader et al. 2014; Wray et al. 2014). The effects of landscape simplification on bees can for example result in distinct body size variations. This relates to the observation that smaller bees show a greater vulnerability to landscape simplification than larger species (De Palma et al. 2015; Jauker et al. 2013), as smaller bee species are commonly foraging over shorted distances and have inferior dispersal abilities (Greenleaf et al. 2007). The long-distance flight capacity of large bees also leads to their ability to utilize potential resource hotspots further inside intensively managed agricultural areas, while small bees might be trapped near field edges with insufficient spatio-temporal availability of food resources. In some cases, landscape simplification has also been reported to negatively impact more strongly on large-bodied pollinator species (Bartomeus et al. 2013; Rader et al. 2014), while additionally constraining intraspecific body size in wild bee species (Renauld et al. 2016). Yet another set of studies appears to show only a limited differentiation of pollinators' body size related to the wider landscape structure (Forrest et al. 2015; Williams et al. 2010).

In addition to body size, nest location is an important trait potentially affected by agricultural intensification (Williams et al. 2010). Species that nest above ground-level have been reported to suffer particularly strongly when isolated from natural habitats in intensively managed agricultural landscapes when compared to species nesting below ground (Williams et al. 2010). Forrest et al. (2015) confirmed the particular importance of natural habitat in comparison to farmland habitats in supporting above-ground nesting bees. Most species that build nests above ground-level construct them within shrubby vegetation or in wooden cavities that are commonly removed or at least reduced in size by intensive agricultural practices (Williams et al. 2010). Nesting substrates for these species become limited as a result, while suitable substrate for ground-nesting species is often less severely altered by agricultural intensification (Kim et al. 2006).

Smallholder agricultural landscapes in Southern China form highly heterogeneous and fragmented mosaics, with 98% of Chinese farms being <2 ha in size (Rapsomanikis, 2015). Particularly in mountainous regions, field shapes are highly irregular and varying in size, and they are often surrounded by vegetated field margins. Small-scale agricultural ecosystems can benefit wild pollinator communities and enhance their pollination services (Geppert et al. 2020; Hass et al. 2018; Marja et al. 2019; Zou et al. 2017). However, to improve agricultural productivity, small fields have been reorganized and transformed into uniform large, rectangular fields during farmland consolidation projects (Li et al. 2019; Tang et al. 2019). These projects therefore greatly simplify and homogenize the agricultural landscape. Our recent studies of smallholder farmland in Jiangxi province found that this farmland consolidation resulted in a reduced pollinator richness when compared to traditional agricultural areas (Shi et al., 2021), indicating a negative effect especially from the reduction of interspersed semi-natural habitat patches in consolidated farmland on wild pollinator diversity. However, it remains unclear how farmland consolidation specifically affects the pollinator community composition and functional trait spectra such as body size and dominant nesting location. Here, we investigate these influences, focusing specifically on the following three research questions:

i). What is the impact of farmland consolidation on the pollinator community composition? We hypothesize that the pollinator community in consolidated farmland differs significantly from traditional agricultural landscapes and is overall more homogenous in its composition when compared to communities in traditional landscapes.

ii). What are the effects of farmland consolidation and the landscape-scale proportion of semi-natural habitats on pollinators' body size? We hypothesize that pollinators' mean body size is larger in consolidated farmland than in traditional agricultural landscapes. In addition, we hypothesize that pollinators' body size is negatively correlated with the proportion of semi-natural habitat at landscape level.

iii) What is the effect of farmland consolidation on bees' nesting location? We hypothesize that there is a lower proportion of above-ground nesting bees in the wild bee assemblages in consolidated when compared to traditional agricultural landscapes.

Methods

Study site and land use investigation

The study was carried out in 2019 at Jiangxi Province, China (E115°53′, N28°41′), at the sites outlined in Zou et al. (2020). In the year where our sampling occurred, no oilseed rape was cultivated at two of the original 20 sampling sites, and we therefore only sampled the remaining 18 sites. Seven of these sites were located in consolidated agricultural landscapes, while the remaining 11 represent traditional farmland matrices (Figure 1, Appendix 1). It is worth to mention that farmland consolidation in Jiangxi is generally conducted at the village level, while management is still in the hands of the individual small-holder farmer. Therefore, local agricultural practices and management approaches do not change due to consolidation.

The minimum distance between two sampling sites was 4.5 km, exceeding the longest foraging distance for most bee species (Steffan-Dewenter et al., 2002; Chifflet et al., 2011). All sampling sites were at the similar elevation (39.9 ± 17.2 m).

The proportion of semi-natural habitat in consolidated farmland and traditional farmland were 0.33 ± 0.19 and 0.38 ± 0.22, respectively. The field size in consolidated farmland and traditional farmland were 857.6 ± 139.9 m^2 and 836.8 ± 115.0 m^2, respectively. We assessed land use in the respective landscape surrounding the oilseed rape fields based on land-use maps generated from 2014 remotely sensed imagery with a resolution of 2.5 m. These maps were obtained from the Chinese Academy of Sciences Data Centre. A total of 45 land-use types were initially distinguished (see Zou et al., 2020, for details). Land use investigations in 2014 were conducted at a radius of 2000 m. For our analysis, we focused specifically on the role of the proportion of semi-natural habitats (including forest, grassland and shrubs) within an radius of a 1000 m, which is a sufficient radius for the distance covered by most pollinator species (Steffan-Dewenter et al. 2002). The selected, relatively large scale can also guarantee that all land use types were representatively covered in sites that were not perfectly centered in the investigated landscape. Forest was included as a semi-natural habitat since it has been reported to benefit wild bee communities (Papanikolaou et al. 2017; Rivers-Moore et al. 2020, but see also Wu et al., 2019) and had been included in previous studies at our research sites (Shi et al. 2021; Zou et al. 2017). In 2020, we additionally assessed the current land use using drone-generated (DJI® Mavic Pro) imagery within a 1000m radius centered on our study fields. These investigations showed that the proportion of semi-natural habitat had remained unchanged since 2014 (Pearson $r = 0.92$, $p<0.001$). Therefore, we used the 2014 data to determine the proportion of semi-natural habitats around our study fields in this investigation.

Pollinator sampling

Insect pollinators were sampled using pan traps. These pan traps were composed of three plastic cups (diameter: 8.3cm and volume: 450ml) painted with white, yellow and blue paint with a strong additional reflectance in the ultraviolet spectrum inside the cups, respectively (Westphal et al. 2008). We added detergent and table salt into the water in the cup for killing trapped pollinators. The three cups were fixed on a wood stick (~1.5 m height above the ground), which was about oilseed rape plants height in the sampling field. We placed four pan traps at each site, one each in the corners of a 15 m x 15 m square in the center of each field. Traps were also placed at least 2m from any field margin.

Pan traps were operated between February and April (51 ± 2 days), which coincides with the mass flowering period of oilseed rape in the 18 study landscapes. No pesticides were applied to the focal oilseed rape fields during the sampling period. Pan traps were emptied and filled again for five times at an interval of ~10 days. Insects sampled were then stored in the refrigerator for further analysis. All insect pollinator specimens were pooled for each site and subsequently identified. Eighty-two percent of the wild pollinator individuals were identified to species-level, while the remaining individuals were identified either to genus or family-level.

Body size measurement and nesting locations of wild bees

We explored the effect of farmland consolidation on interspecific and intraspecific body size of two dominant wild bee species. Interspecific body size was measured as the average body size for each species, with the species value for each field/landscape setting measured as the average from at least 20 individual female bees (where all samples yielded > 20 specimens), or from all female specimens if collections contained a total of <20 individuals (Appendix 2). The body size of an individual was measured as the intertegular distance (ITD), which is the distance between the bases of the two wings on the bee's throax (Cane 1987). ITD can serve as an effective proxy to reflect wild bees' flight capability (Greenleaf et al. 2007). The ITDs were measured under the microscope (Nikon SMZ745T) using an Industrial Digital Camera (20MP Sony Exmor CMOS Sensor) and scaled in ImageView. Intraspecific body size considers the variation for a species at individual level. For this analysis, we focused on the two dominant wild bee species *Eucera floralia* and *Lasioglossum proximatum*, of which we measured all collected specimens except for those badly damaged (13 out of 94 specimens for *Eucera floralia*; 13 out of 81 for *Lasioglossum proximatum*).

Furthermore, we separated wild bee species into two categories according to their nesting location: above- and below-ground nesting (Appendix 2). We sorted them based on these two nesting location types because nesting location (below- and above-ground) is the major trait that can lead to differences in the functional diversity between natural habitat and agricultural area, which reflects different accessibility of nesting substrates, such as dead wood or hollow tree stems, in various habitat types (Forrest et al. 2015). Specimens of the European honeybee

(*Apis mellifera*) were excluded from all analysis, since they are generally managed by local beekeepers.

Data analysis

The Chord-Normalized Expected Species Shared (CNESS) dissimilarity (Trueblood et al. 1994) was used for comparing the differences in wild pollinator as well as wild bee assemblages between consolidated and traditional farmland. The CNESS dissimilarity is not sensitive to the sample size, since it can specifically allow for the standardization of all samples to a specific sample size randomly (value *m*), hence allowing for direct, standardized comparisons (Zou and Axmacher 2020). This index is particularly suitable to compare the species dissimilarity for mobile arthropods where sample size and completeness varies (Beck and Khen 2007; Bonifacio et al. 2020). We used the modified version of CNESS as proposed by Zou and Axmacher (2020), with value varying between 0 and 1. We measured the probability-based similarity in dominant species (sample size parameter m=1), as well as the similarity in the community for a larger sample size (m=20), reflecting the difference in the general composition of the species assemblage. The CNESS dissimilarity matrices were then visualized using Non-metric multidimensional scaling (NMDS).

In order to investigate the influence of field size on the species composition, we computed a Redundancy Analysis (RDA), including both field size and proportion of semi-natural habitat as explanatory environmental variables. Monte Carlo permutation tests (n=999) were used to test the significance of the constraint linked to each explanatory variable. As the result showed that field size has no significant association with species composition (Appendix 3), we did not include the RDA results in further discussions.

We used linear regressions to explore the effect of farmland consolidation and semi-natural habitat in the agricultural landscape on the average inter-species body size. Linear mixed models were used to explore the effect of farmland consolidation on the intraspecific body size of two dominant wild bee species (*Eucera floralia* and *Lasioglossum proximatum*), in which research site was the random factor. For the average inter-species body size, we calculated both abundance-based as well as species-based average body size. After we established that semi-natural habitat per se had no significant effect on intraspecific body size variations (full model included in Appendix 4), and there were no interactions between semi-natural habitat proportion and farmland consolidation (full model again included in Appendix 4), we subsequently only focused on the impact of farmland consolidation, and we excluded the proportion of semi-natural habitat at the 1000m radius.

We then used linear regressions to explore the effect of farmland consolidation on the proportion of above-ground nesting bees in the wild bee community. The respective nesting traits of the wild bee species we encountered are summarized in Appendix 2. We found that semi-natural habitat again had no significant effect on the proportion of above-ground nesting bees in the wild bee community, and that there were no interactions between semi-natural habitat and farmland consolidation. Thus, we again only focus on the impact of farmland consolidation per se, and we excluded the proportion of semi-natural habitat at a 1000m radius.

All the statistical analyses were conducted in R Version 3.5.2 (R Core Team, 2016). We used the "vegan" package (Oksanen et al., 2019) to calculate stress for nonmetric multidimensional scaling (NMDS). The function "ESS()" developed by Zou & Axmacher (2020) was used for calculating CNESS values. We used the "nlme" package (Pinheiro et al., 2019) to build linear mixed models. We checked for spatial autocorrelation of model residuals using Moran's I coefficient (Gittleman and Kot 1990). There was no significant spatial autocorrelation in all models (at $p < 0.05$).

Results

The pan trap sampling in 2019 resulted in the collection of a total of 2211 wild insect pollinators representing 49 pollinator species. Wild bee individuals accounted for 97% (2135 individuals) of the wild insect pollinator specimens and for 76% (34 species) of the total species pool (Appendix 2). NMDS based on CNESS dissimilarity did not show distinct pollinator clusters differentiating between the fields located in consolidated and traditional farmland, neither for small (m=1) nor large sample size (m=20) (Figure 2), with similar results for wild bee communities (Figure 2) and the overall wild insect pollinator communities (Appendix 5). However, with regards especially to dominant species (Figure. 2 A), species composition showed a greater heterogeneity (i.e. higher mean dissimilarity values) in fields located within the consolidated landscape than in the traditional one.

With regards to the average body size of the sampled species based both on the actual size of individuals sampled (abundance-based) and on individual species, no significant differences were observed between communities sampled on traditional and consolidated farmland (Figure 3). Nonetheless, the average abundance-based body size of pollinators in the community decreased significantly ($p=0.018$) with a decreasing proportion of semi-natural habitat at consolidated farmland, while no significant relationship was found between the proportion of semi-natural habitat and average body size in the traditional farmland matrix ($p=0.14$) (Figure 3A). For the species pool, when weighing each species equally, no significant responses to the proportion of semi-natural habitat were observed for bee size in traditional ($p=0.11$) or consolidated landscapes ($p=0.38$) (Figure 3B).

In terms of the two dominant species, the body size for *Lasioglossum proximatum* was marginally higher in consolidated than traditional farmlands ($p=0.06$, Figure 4A), but there was no difference for *Eucera floralia* ($p=0.79$, Figure 4B). The proportional abundance of above-ground nesting bees based on species richness was significantly lower in consolidated farmland than in the traditional farmland ($p=0.04$) (Figure 5A), while there were no significant differences based on species richness ($p=0.47$) (Figure 5B).

Discussion

Land consolidation projects have been widely conducted in China (Li et al., 2019; Tang et al., 2019), but their impacts on agricultural pollinators and their different trait groups have remained poorly understood. In this context, our study offers important insights into both the general impact of this consolidation, and of the potentially interacting role with remnant semi-natural habitat patches, on the insect pollinator community.

Impacts of farmland consolidation on the species composition

Both wild pollinator assemblages and wild bee assemblages in consolidated and traditional farmland were surprisingly similar, which contradicts our hypothesis as well as previous studies (Wilson et al. 2020). Although the negative impact of farmland consolidation on wild pollinator diversity has been reported from the same area (Shi et al., 2021), the farmland consolidation has not resulted in a significant difference in the composition of the assemblages at rapeseed fields with regards to their dominant species, but also to the species pool containing less dominant species. A possible reason for this lack of differentiation relates to our study sites all being located in landscapes with relatively high semi-natural habitat coverage. Embedded in the farming landscape, these semi-natural habitats might strongly enhance the overall pollinator community structure, in turn compensating for any potential consolidation effect (Shi et al. 2021) that otherwise could lead to stronger differences in the general community composition between consolidated and traditional fields. Another possible reason relates to the studied mass-flowering crop, oilseed rape. This crop provides easily accessible food (pollen and nectar) for wild bees in the sampling period across the different landscapes (Beyer et al. 2021; Neumueller et al. 2021) that could be so attractive that it temporarily effectively draws in a great number of insect pollinators from across the various species present in different parts of the wider agricultural landscape (Shaw et al. 2020).

Nonetheless, the greater overall heterogeneity particularly in dominant species on fields in the consolidated landscapes still indicates that farmland consolidation may affect the abundance patterns in dominant species, which also aligns with our observations on the proportions of above-ground nesting wild bees (see below). To establish the full impact of farmland consolidation on wild pollinator communities, we therefore recommend further long-term and large-scale monitoring, including the non-flowering season and landscapes that show a greater scarcity of semi-natural habitat areas.

The impact of farmland consolidation and semi-natural habitat on wild bee body size

We found that the mean interspecific body size of wild bees was not significant different between consolidated and traditional farmlands, while for mean intraspecific body size, *Lasioglossum proximatum* individuals were larger in consolidated than traditional farmland, whereas no significant difference was again observed for *Eucera floralia*. Relatively few studies have to date explored intraspecific body size variations, but Warzecha et al (2016) reported an increase in mean body size of wild bees with landscape simplification. Our results indicate that, while farmland consolidation does not filter out the entire small-bodied species in general, small individuals in small-bodied species (such as in *Lasioglossum proximatum*) are more sensitive to agriculture simplification, and likely to be filtered out. This could relate to smaller individuals likely having shorter foraging distances (Greenleaf et al. 2007), resulting in difficulties for them to access sufficient resources in simplified farmland. Specimens of the larger dominant species, *Eucera floralia,* are likely to have sufficiently long foraging distances for size-related differences not exerting their activity radii to a degree that they become influenced by farmland consolidation effects.

The above results can also explain the positive relationship between the proportion of semi-natural habitats and average body size in consolidated farmland (based on pollinator abundance, but not mean species size). In consolidated farmland where the proportion of semi-natural habitat is high, individuals of large-bodied species are more abundant. In this case, bees with larger body size, able to forage over longer distances (Greenleaf et al. 2007) while managing to forage in both oilseed rape fields as well as the surrounding semi-natural habitats, might rely more strongly on larger patches of semi-natural habitat to support their larger size when compared to small bee species.

Our results indicate that, while the consolidation did not alter the mean body size of the wild bee community overall, the proportion of semi-natural habitat determines the balance between bees of differing body size following landscape consolidation. It needs to be noted that larger pollinators are generally more effective in providing pollination services than smaller counterparts (Cruden 2000; Jauker et al. 2016). A reduction of larger pollinator species in the pollinator community, therefore, may lead to a pollination service degradation for smallholder farmers. Our study further emphasizes that semi-natural habitat can positively influence the mean community body (e.g. functionality), which may restore local wild bees' pollination services (Cruden 2000; Jauker et al. 2016).

The impact of farmland consolidation on wild bee nesting locations

Consistent with our respective hypothesis and previous studies (Forrest et al. 2015; Williams et al. 2010), we found a lower proportion of above ground-nesting bee species, based on abundance but not richness, in the consolidated when compared to the traditional farmland. In the smallholder agricultural landscape, shrubs, perennial grasses, forbs or dead woods can serve as nesting sites and materials for aboveground nesting bees (Lajos et al. 2021; Williams et al. 2010). However, during farmland consolidation, small fields are generally reorganized into larger areas, which inevitably remove both nesting substrate and materials from the landscape. As a result, potential nesting sites for these species become severely limited, while suitable nesting sites for ground-nesting species, such as open ground particularly along field margins, remain (Kim et al. 2006). Lack of these essential nesting sites may be the reason for the reduction in abundance of above-ground nesting bee species (Williams et al. 2010). Some above-ground nesting bees, such as mason bees (*Osmia* spp.), have been found to be highly effective agricultural pollinators that provide essential pollination services in China (Wei et al. 2002). The loss of these above-ground nesting species may lead to an overall decline in pollination services. We therefore suggest that specific conservation approaches should be considered during farmland consolidation projects, such as keeping fine-scale semi-natural habitats and providing targeted nesting substrates for solitary bees (Geslin et al. 2020), for example in the form of old trees or small islands of shrubs.

Conclusion

In conclusion, we did not find significant differences in wild bee community composition and interspecific body size between consolidated and traditional farmland. Instead, our study suggests that farmland consolidation might affect intraspecific composition and body size, particularly in small-bodied species. Farmland consolidation furthermore reduced the proportion of above-ground nesting wild bees. More traits of wild bees, such as dietary specialization and sociality, ought to be included in the future studies for better understanding how the farmland consolidation may affect the wild bees with specific traits. Semi-natural habitats in small-holder farmland provide general benefits for the pollinator community, and specific management interventions promoting such habitats might be required in consolidated agricultural landscapes to allow the persistence of diverse wild bee communities.

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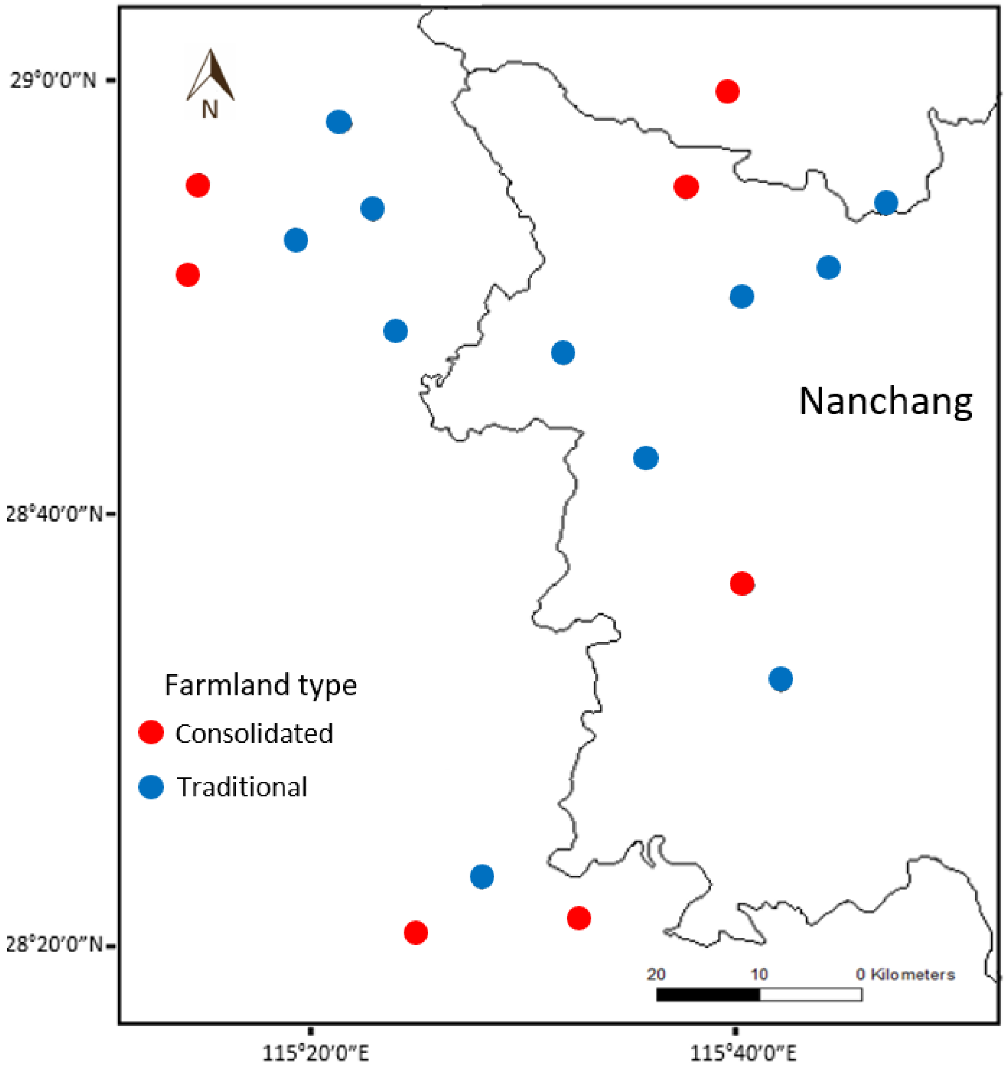

Figure 1. Locations of 18 study sites in Jiangxi province, China.

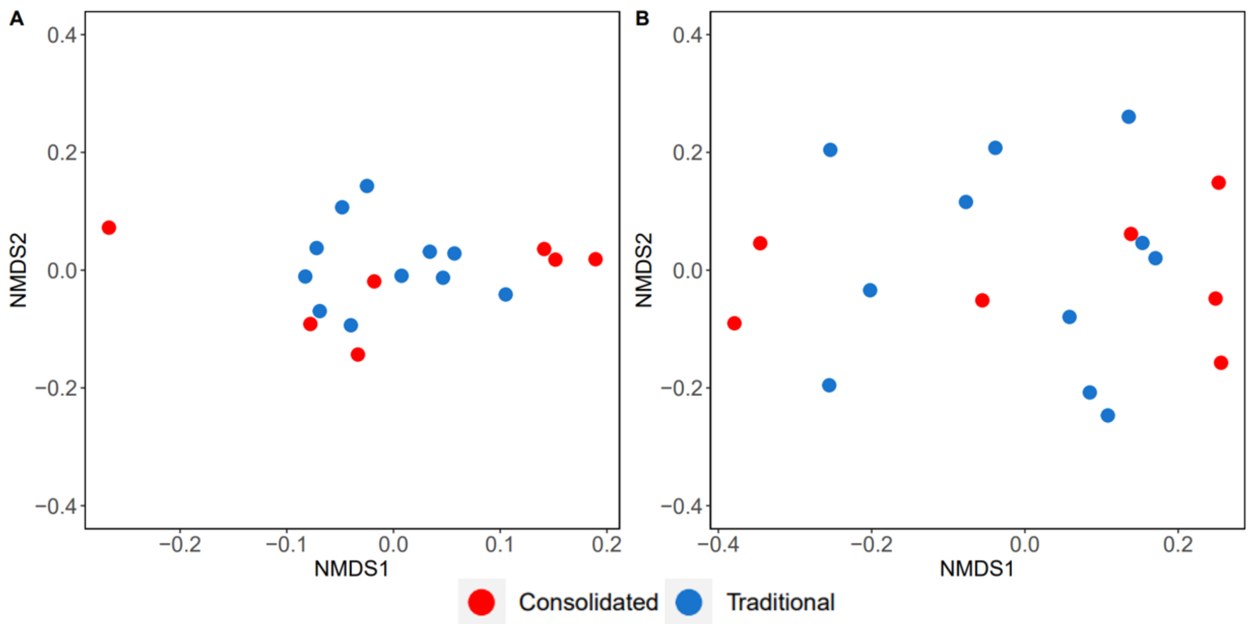

Figure 2. Non-metric multidimensional scaling (NMDS) plots based on Chord-Normalized Expected Species Shared (CNESS) dissimilarity for *m*=1 (A, stress=0.10) and *m*=20 (B, stress=0.18) for wild bee communities in different study sites.

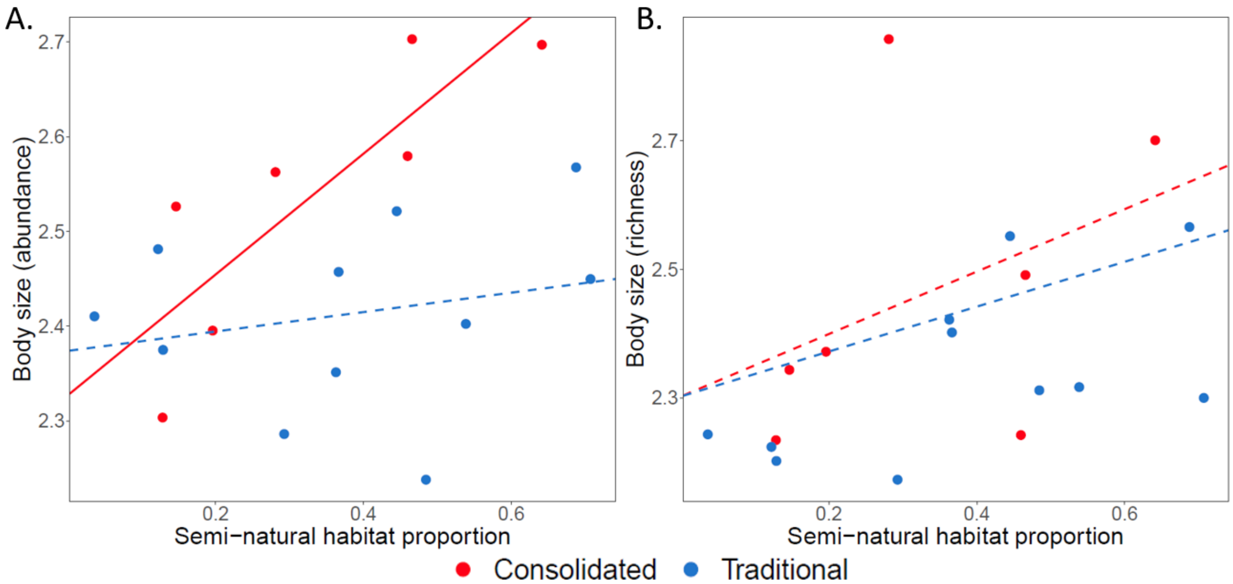

Figure 3. Relationship between the proportion of semi-natural habitat and community average body size based on abundance (A) and richness (B) respectively. Line color indicates regressions for consolidated fields (red) and traditional fields (blue). Solid and dashed regression lines indicate significant ($p<0.05$) and insignificant ($p>0.05$) relationships.

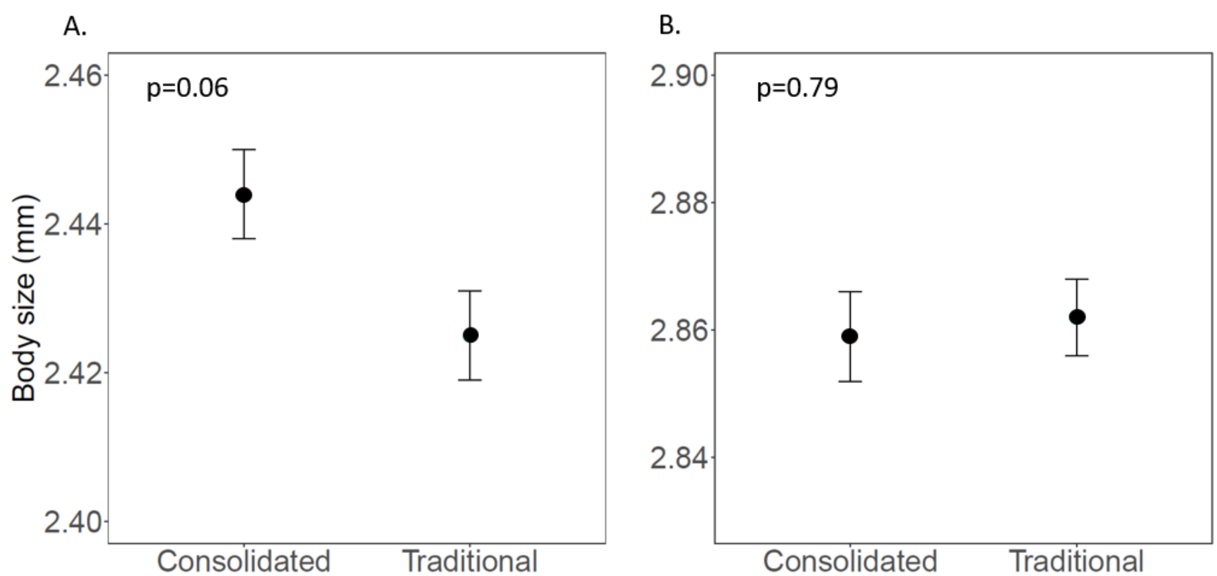

Figure 4. Mean body size of two dominant bee species (A. *Lasioglossum proximatum* and B. *Eucera floralia*) in consolidated and traditional farmland.

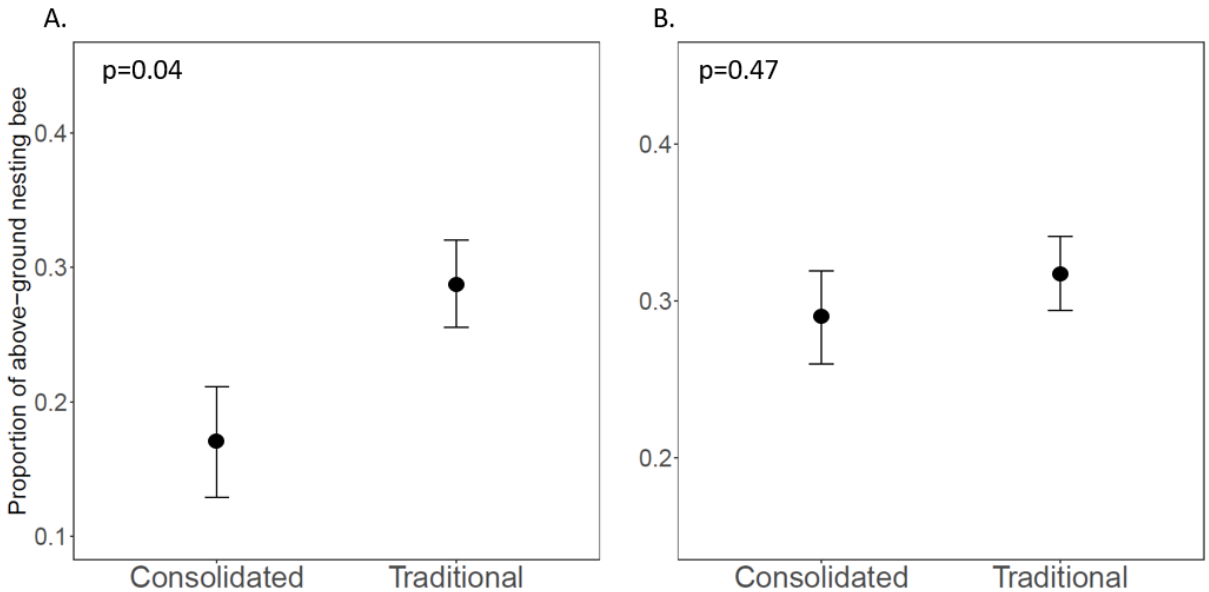

Figure 5. The proportion of above-ground nesting wild bees based on abundance (A) and richness (B) in consolidated and traditional farmland.