Manuscript Details

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Title	Contrasting effects of natural shrubland and plantation forests on bee assemblages at neighboring apple orchards in Beijing, China
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Abstract

Wild bees provide important pollination services for crops and wild plants. While land use intensification has resulted in steep declines of wild bee diversity across agricultural landscapes, the creation of semi-natural habitats has been proposed as a counter-measure. However, the relative value of semi-natural and natural habitats in promoting wild bees has rarely been studied, especially for China that harbors the world's largest plantation forest area, characterized by intensively managed, mono-dominant stands of wind-pollinated tree species. We sampled wild bees in apple orchards to assess how their assemblages were influenced by semi-natural habitats in the surrounding landscape and the local flowering ground-cover. Bee abundance declined with increasing isolation from natural shrubland. In contrast, wild bee diversity and abundance were negatively linked to plantation forests. For the abundance of large bees, this effect was partly ameliorated by local flowering ground-cover. Maintaining or restoring wild bee assemblages in agricultural landscapes therefore requires careful evaluations of restoration measures such as forest planting. Availability of local flower resources and nearby natural shrubland appeared particularly important to enhance wild bees and their potential services in apple orchards.

Keywords	dispersal ability, flowering ground-cover, habitat restoration, landscape composition, pollinator
Taxonomy	Landscape Ecology, Conservation of Biodiversity

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Research Data Related to this Submission

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Dear Editor,

We would like to submit our revised manuscript entitled "Contrasting effects of natural shrubland and plantation forests on bee assemblages at~~diversity in~~ neighboring apple orchards in Beijing, China" to Biological Conservation. The work is all original research carried out by the authors. All authors have no competing interests and have approved to submit it to your journal. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. Restored semi-natural habitats may counterbalance the decline of wild bee diversity in agricultural landscapes, but the value of plantation forest as an important restoration measure in promoting pollinator diversity has not been analyzed before, especially for China with the largest plantation forest area (69.33 million ha) in the world. The main aim of this work is to contrast the effects of natural shrubland with plantation forests on wild bee diversity in apple orchards, considering body size and different spatial scales of the surrounding landscape.
The results showed that the proximity of natural shrubland greatly benefited the diversity of wild bees in surrounding habitats. In contrast, amount of plantation forests exhibited negative effects on wild bees, possibly due to its intensive habitat management, and this trend was partly counterbalanced by a high percentage of flowering groundcover in the orchards. Hence, landscape management needs to carefully consider the habitat- and management-specific effects of different natural and restored habitats, as well as their interaction with local management, on bee diversity and potential crop pollination.

Sincerely yours,
Yunhui Liu (on behalf of all coauthors)

Comments from the editors and reviewers:

Editor

The reviewers have some additional, fairly minor, comments and suggestions that need to be addressed.

- Thanks for your kind help with the review process. We have now revised the manuscript according to the reviewers' suggestions and comments. Please find our detailed response to each comment below:

Reviewer 1

The grammar in the current revision remains rough in the Introduction. Beyond that I found the manuscript improved considerably following the edits. It will require a bit more editing throughout to catch the number and range of changes needed. Otherwise I see the authors have done a solid job of addressing comments from the previous submitted version and the manuscript is more cohesive throughout. My comments are minor overall and are listed below

- Thanks for your positive comments and appreciation of our revisions. We have now thoroughly revised the entire introduction and carefully checked the English grammar - please see lines 25-95.

Line 30 change TO to OF. Also the sentence doesn't quite make sense. "highlights the importance [of identifying (or you could alternatively write "the need to identify")] key factors causing the dramatic recent declines in wild bee diversity (NEED CITATION HERE).

- Thanks. In the process of editing the entire introduction, this sentence has now been deleted.

Line 25 the references included don't fully match sentence as it is written. These are not papers about the delivery of pollination to wild plants in agricultural landscapes. I fear that the attempt to edit has negatively affect things.

- This sentence has been changed to "Bees provide essential pollination services for both wild plants (Ollerton et al., 2011) and crops (Klein et al., 2007)." Please see lines 25-26.

Line 32 add the word bee before biodiversity.

- Changed to "wild bee diversity".

Line 45 Kennedy is not the right citation here. Potts et al or possibly Forrest et al 2015, for nesting

- Thank for your suggestions. This citation has been changed by Potts et al., 2003, Potts et al., 2005, Forrest et al., 2015: "thereby disregarding differences between habitats in their vegetation, nesting and food resources they offer as well as the specific habitat management – all factors known to affect wild bee assemblages (Potts et al., 2003; Potts et al., 2005; Forrest et al., 2015)." Please see lines 41-44.

Line 50 also consider Winfree and Kremen response diversity paper as a good reference for response diversity of bees to landscape change.

- Changed accordingly. This sentence has been changed to “Responses of pollinator species to such habitats in the surrounding landscape vary due to differences in their dispersal ability (Winfree et al., 2007; Jauker et al., 2009) related to body size (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007), the crop system (Joshi et al., 2016), the investigated pollinator group or taxon (Jauker et al., 2009; Carvalheiro et al., 2010) and the biogeographical context (Garibaldi et al., 2011).” Please see lines 48-53.

Line 86 add stands after the word homogeneous

- Changed accordingly.

Lines 89-91 reword, Apples are a main pollinator-dependent global fruit crop (FAO, 2016), of which China is the most important global producer, accounting for 35% of the production . . .

- Thanks for this suggestion. We actually decided to split this sentence to further increase the fluency of the text: “Apples represent an insect pollinator-dependent global fruit crop (FAO, 2016). China is the most important apple producer, with the country’s orchards account for 35% of the global production (Chen et al., 2010).” Please see lines 82-85.

Line 152 just because pesticides were not used during bloom one can no assume that there is no effect on pollinators. Populations are certainly affect by pesticides applied at other times and these will influence the numbers and identities of bees present. Also there may be residual pesticide affects. In any case I think just need to acknowledge for example although residual pesticide effects might influence visitation . . . we focus on ground vegetation in the orchards as the main local . . . .

- Thanks for your comments and suggestions. This sentence has been changed to “In that context, although residual pesticides might influence bee diversity, we focus on the ground vegetation in the orchards as the main local management variable affecting bees in this study”. Please see lines 149-151.

Line 287 change high to abundant

- Thanks. Changed accordingly.

-Reviewer 3

Authors have done a nice job addressing my major concerns. A few follow-up comments below:

- Thanks for your suggestions and comments. We have now thoroughly revised the manuscript based on the reviewers’ suggestions. Please see the following, more detailed responses:

1. In title, consider changing "diversity" to "communities" because you are looking at both species richness and abundance; consider adding "in Beijing, China" given a major contribution of this paper is the study of pollinators in an understudied system.

- Many thanks for this suggestion. We decided to use “assemblages” instead of “diversity”, since we were uncertain if the assemblages we observe actually represent set communities, and have added the location according to your kind suggestion.

2. In this second read, the introduction seems a bit choppy from LL 40-77. And transition to this study's aims/goals is not strong. Would like to see a paragraph that starts with some overarching statement of goal like L 79-83, then go into details of management and hypotheses.

- We have now carefully revised the entire introduction, also in view of comments we received from the other reviewer (see above). We hope that this section now reads much better.

3. Statistics. Analyses section is greatly improved! L 183, one still needs to check for overdispersion in negative binomial models. When I look at Figure 4 built up areas v. bee responses, the data look random and no strong pattern there. Often for species richness, the data are normal or easily transformed to normal.

- Thanks for your suggestions. We have checked the normality of species richness of small bees and overdispersion in negative binomial models for Figure 4. The results showed that the variable of species richness of small bees was normally distributed, and we did not detect significant overdispersion in both the full glm.nb model (explanatory variables including distance from natural shrubland, percent of plantation forest, orchards and build-up area, and their interaction with flowering ground-cover) or the final glm.nb model resulting from the model average (explanatory variables included percent of plantation forest, orchards and build-up area, Table 1) using the testDispersion function (R package ‘DHARMa’, Hartig, 2019; the full model: dispersion = 1.2729, p-value = 0.4242; the final model: dispersion = 1.1566, p-value = 0.6869).

We also transformed the response variable accordingly and plotted the figure again, but the patterns remained unchanged.

The significance level of the response in wild bee species richness to percent of build-up area is relatively low (P=0.038, Table 1), which may explain the lack of a clear pattern in Figure 4. Based on these outcomes, we decided to leave the results as they are.

Hartig, F., 2019. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.4.

4. Discussion L238 "shrublands" should be singular, "disturbance" should be plural. L 239 Add" likely " before "provide floral resources", take out "hence"

- Thanks. Changed accordingly.

5. L242, change "a wide range" to " a large body"

- Changed accordingly.

6. L245 change "the differences in their" to "reduced", L247, add "small" before "body size" and take out "differences".

- Changed accordingly.

7. L 248 add reference - see Greenleaf and Kremen on body size and foraging distance relationship.

- Thanks. Changed accordingly.

8. L303 change "under: to "while"

- Changed accordingly.

9. Missing acknowledgements
- Thanks for your reminder. Acknowledgements were actually placed on the title page, but they could not be seen by the reviewers in this location.

Contrasting effects of natural shrubland and plantation forests on bee assemblages~~diversity~~ at~~in~~ neighboring apple orchards in Beijing, China

Abstract

Wild bees provide important pollination services for crops and wild plants. While land use intensification has resulted in steep declines of wild bee diversity across agricultural landscapes, the creation of semi-natural habitats has been proposed as a counter-measure. However, the relative value of semi-natural and natural habitats in promoting wild bees has rarely been studied, especially for China that harbors the world's largest plantation forest area, characterized by intensively managed, mono-dominant stands of wind-pollinated tree species. We sampled wild bees in apple orchards to assess how their assemblages were influenced by semi-natural habitats in the surrounding landscape and the local flowering ground-cover. Bee abundance declined with increasing isolation from natural shrubland. In contrast, wild bee diversity and abundance were negatively linked to plantation forests. For the abundance of large bees, this effect was partly ameliorated by local flowering ground-cover. Maintaining or restoring wild bee assemblages in agricultural landscapes therefore requires careful evaluations of restoration measures such as forest planting. Availability of local flower resources and nearby natural shrubland appeared particularly important to enhance wild bees and their potential services in apple orchards.

Keywords

dispersal ability, flowering ground-cover, habitat restoration, landscape composition, pollinator

1. Introduction

~~In agricultural landscapes, b~~Bees provide essential pollination services for both wild plants (~~Ashman et al., 2004;~~ Ollerton et al., 2011) and crops (Klein et al., 2007). With regard to this ecosystem service, wild bees are typically more effective pollinators than managed honey bees (Winfree et al., 2007; Garibaldi et al., 2013)~~.~~ ~~The growing demand for pollinator-dependent crops (Aizen and Harder, 2009) highlights the~~ , while both of these groups have experienced widespread ~~importance to identify key factors causing the dramatic recent~~ declines~~ in wild bee diversity~~ in recent decades (Potts et al., 2010).

Research into the decline of wild bee ~~bio~~diversity regularly identifies agricultural intensification and urbanization, associated with a loss and fragmentation of semi-natural habitats (Kremen et al., 2007; Krauss et al., 2010; Seto et al., 2012; Tscharntke et al., 2012), as ~~an~~ important factors.

In Europe, agri-environmental schemes targeting the protection and restoration of semi-natural habitats in agricultural landscapes have been widely used in response to biodiversity losses (Batáry et al., 2015), with the Farm Bill in the United States (Cain and Lovejoy, 2004) and afforestation projects in Beijing (Xue and Fan, 2018) claiming similar aims and using similar approaches.

However, t~~T~~he association of bees with restored habitats in comparison to remnant natural, successional habitats is currently poorly understood (Morandin and Kremen, 2013). Most studies combine various natural and restored habitats into one habitat class like 'semi-natural habitats' (Ricketts et al., 2008; Garibaldi et al., 2011), thereby disregarding differences ~~in~~between habitats in their vegetation, nesting and food resources they offer as well as the specific habitat management ~~, –~~ all factors known to affect wild bee assemblages (Potts et al., 2003; Potts et al., 2005; Forrest et al., 2015~~Kennedy et al., 2013~~).

In contrast to persistent uncertainties regarding the promotion of wild bees by restored habitats, n~~N~~atural habitats with diverse plant species and nesting resources that experience little human disturbance are widely~~have been~~ regarded as ~~the most~~highly ~~important~~beneficial ~~habitat~~ for ~~wild~~ bees (Kremen et al., 2007; Garibaldi et al., 2011). Responses of ~~Different wild bee~~pollinator species ~~nonetheless respond~~ to ~~distances from natural~~ such habitats in the surrounding landscape vary~~at different spatial scales –~~ due to differences in their dispersal ability (Winfree et al., 2007; Jauker et al., 2009)~~. Generally, this dispersal ability is positively~~ related to body size (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007)~~,. The bodysize-specific perception of the surrounding landscapes by wild bee species is, therefore, important in order to understand their distribution patterns in agricultural landscapes.~~

~~The importance of the proximity of natural or restored habitat on pollinator diversity may furthermore change with~~ the crop system (Joshi et al., 2016), the investigated pollinator group or taxon (Jauker et al., 2009; Carvalheiro et al., 2010) and the biogeographical context (Garibaldi et al., 2011). M~~M~~ost ~~pollinator~~ studies of agricultural pollinator assemblages originate from North America and Europe, where large agricultural fields commonly dominate the landscape, whereas field sizes are generally much smaller in rural China (Zou et al., 2017)~~.~~. Our understanding of the links between restored and semi-natural habitats and pollinator assemblages particularly in China's ~~The effect of differences in semi-natural habitat type and~~ management and the wider landscape structure on wild bee diversity within smallholder-dominated landscapes has remained very limited~~received limited attention so far~~ (Steward et al., 2014; Zou et al., 2017).~~Most pollinator studies originate from North America and Europe, where large agricultural fields commonly dominate the landscape, whereas field sizes are generally much smaller in rural China (Zou et al., 2017). The effect of differences in semi-natural habitat type and management and the wider landscape structure on wild bee diversity within smallholder-dominated landscapes has received limited attention so far (Steward et al., 2014; Zou et al., 2017).~~

In addition, g~~G~~rowing evidence demonstrates ~~the influence of~~ that local management practices (Kennedy et al., 2013; Shackelford et al., 2013)~~, such as pesticide applications (Tuell and Isaacs, 2010; Kovács-Hostyánszki et al., 2011;~~

~~Carvalheiro et al., 2012; Mallinger et al., 2015) and flower cover (Veddeler et al., 2006; Carvalheiro et al., 2010)~~ and their interactions with landscape structure also influence ~~on~~ pollinator diversity (Kennedy et al., 2013; Park et al., 2015; Westphal et al., 2015). For example, ~~A~~agricultural landscapes with higher proportions of organic crops support more diverse wild bees (Holzschuh et al., 2008~~).~~); w~~W~~ild bee diversity declines with increasing pesticide use in orchards, but this negative effect is partly buffered by increasing proportions of natural habitat in the surrounding landscape (Park et al., 2015~~).~~); and ~~Wildflowers~~ wildflower-rich~~in the~~ ground-cover promote~~s~~s the abundance of wild bees (Blaauw and Isaacs, 2014; Campbell et al., 2017) and honeybees (Földesi et al., 2016) and of the associated pollination services (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014). In our study ~~region~~area, ~~controlling ground-cover by~~ mowing, plowing or herbicide application to control ground-cover vegetation are conventional management measures in apple orchards to limit the growth of weeds that compete with apple trees for nutrients and water. Plantation forests in this agricultural landscape represent restored habitats characterized by homogenous stands of wind-pollinated tree species under intensive management (Cao, 2008; Xu, 2011) that have been planted to limit environment degradation like soil and water erosion. In comparison, natural shrubland is a natural habitat characterized by diverse assemblages of insect-pollinated plant species experiencing little human interference. Again, ~~., such as pesticide applications (Tuell and Isaacs, 2010; Kovács-Hostyánszki et al., 2011; Carvalheiro et al., 2012; Mallinger et al., 2015) and flower cover (Veddeler et al., 2006; Carvalheiro et al., 2010)However,~~ the~~e importance of~~ effects local management and its interaction with ~~landscape~~ natural and restored habitats in the wider landscape have on wild bee assemblages in orchards of our study region remain~~s~~ poorly understood~~ for China's agricultural landscapes, due to the distinct manag~~.~~ement practices and resulting landscape structure, as well as the little-developed pollinator research in China.~~ In this area, orchards are dominated by a

~~In this study, plantation forests represent habitats restored to limit environment degradation like soil and water erosion, and to improve biodiversity. They are characterized by homogenous of wind-pollinated tree species under intensive management (Cao, 2008; Xu, 2011). In comparison, natural shrubland is a natural habitat characterized by diverse assemblages of insect-pollinated plant species and little human interference. A~~pple~~s~~ trees, which therefore also represent the focus of our study. Apples represent an insect pollinator-dependent ~~main~~ global fruit crop (FAO, 2016). China is the most important apple producer, with the country's orchards~~, with China being the most important global apple producer,~~ account~~ing~~ for 35% of the global production (Chen et al., 2010).

In our study, we aim to address persisting knowledge gaps regarding the links between restored and natural habitats on wild bee assemblages in agricultural landscapes, using apple orchards as the 'target crop'. In this context, we specifically test the~~We~~ hypothes~~ize~~es that 1) natural shrubland supports a highly diverse assemblage of wild bees, acting as bee source habitat for neighboring apple orchards, so that wild bee~~s~~ abundance decreases with increasing distance from natural shrubland patches; 2) plantation forests in our study area exert~~s~~ a negative effect on wild bee assemblages and their diversity due to the flower scarcity and intensive management typical for these habitats; and 3) flowering ground-cover in orchards interacts with landscape structure~~composition~~, partly buffering negative effects associated with landscape-scale parameters.

2. Materials and methods

2.1. Study area

The study was conducted in Changping District (40°2′–40°23′ N, 115°50′–116°29′ E) in the northwestern suburbs of Beijing City, China in 2016. The local climate is continental, with an average annual temperature of ~12 °C and an average annual rainfall of ~550 mm. The area is located in the transitional zone between the Yan and Taihang Mountains and the North China Plain, with an altitudinal range from 30 m to 1400 m. The mountains are dominated by natural shrubland that experiences very limited human disturbance, and it is characterized by a low canopy cover from trees and a high diversity of flowering species, with *Vitex negundo*, *Cotinus coggygria*, *Gleditsia sinensis*, *Lespedeza bicolor* and *Wikstroemia chamaedaphne* forming important components of this vegetation. The plain area is dominated by urban areas, plantation forest and orchards. The plantation forest has been newly planted after 2012 under the ‘Plain Reforestation Project’, aimed to ~~merely~~ restore semi-natural habitat ~~for~~ to improv~~ing~~e the environmental conditions and enhanc~~ing~~e biodiversity in Beijing, rather than~~but not~~ for timber or fruit production. It is dominated by intensively managed monocultures of wind-pollinated tree species forming dense canopies. Plantation forest management comprises grass pruning, plowing and the application of pesticides. The main tree species planted are *Pinus tabulaeformis*, *Ginkgo biloba*, *Populus tomentosa*, *Platycladus orientalis* and the non-native legume *Robinia pseudoacacia*.

In 2016, we selected a total of 22 Fuji apple orchards, located along gradients of increasing distance from natural shrubland, for bee surveys during the apple blossom period (Fig. 1). The distance between investigated apple orchards was standardized at about 500 m, and the distance from apple sites to natural shrubland ranged from 0.02 km to 2.49 km.
Fig. 1. (2-column, black-and-white)

2.2. Bee sampling and classification

Bees (Hymenoptera: Apoidea) were sampled continuously during the Fuji apple blooming period (12^{th} to 25^{th} April) using pan traps. At each site, three parallel transect lines of 40 m length were established at distances of 10 m, with a distance from the orchard edges of at least 15 m. At each transect, three pan traps (yellow, white and blue following Westphal et al., 2008, with a 21 cm diameter and 10 cm depth) were placed on metal brackets at a height of about 1.3 m (Tuell and Isaacs, 2010; Mallinger et al., 2015), and three sets of traps were spaced at 20 m intervals along each transect line. Pan traps were filled with about 400 ml water solution with two drops of detergent added per five L of water, with traps being emptied and refilled every 3 days. All bee specimens were identified to species level based on the taxonomic literature (Wu, 1965, 2000 and 2006). The occurrence of *Apis mellifera* was strongly associated with temporary hives set by beekeepers in the study region during the apple blossom, and their abundance in the orchards was therefore only affected by the distance from these hives (Pearson's correlation, p-value= 0.0005, r= -0.68). Therefore, specimens of *A. mellifera* were disregarded in this study.

The body size of each wild bee species was measured using a Nikon SMZ800N stereomicroscope. For all species contained with >4 individuals in the samples, the body length was measured in four randomly selected specimens, while otherwise all individuals were measured. Bees were divided into small (≤11.5 mm) and large species (>11.5 mm), following the advice of Tscheulin et al. (2011) and accounting for the distinct gap between small and large bees observed in our samples (Fig. S1). For the analysis, wild bee data from nine traps at the same site were pooled for the entire sampling period.

2.3. Local management survey

All orchards were conventionally managed. In line with local practices, farmers did not apply any pesticides or fungicides during the apple flowering period to protect pollinators. In that context, although residual pesticides might influence bee diversity, we focus on the ground vegetation in the orchards ~~was recognized~~ as the main local management variable affecting bees in this study. Five 1 m × 1 m plots were established in the four corners and the center of the bee sampling area (20 m × 40 m) covered by three parallel transects during the apple bloom. In each plot, coverage of each flowering insect-pollinated plant species was recorded during the apple blossom period, and these values were added to calculate the total coverage of flowering ground-cover in each plot, subsequently averaged as the mean value for each study site.

2.4. Landscape parameters

Land use surrounding the focal orchards was quantified at radii between 250 m and 1000 m, based on extensive field inspections in May 2016 and on satellite imagery (at 0.91 m resolution from 29th March ~~2016~~2015). Wild bee assemblages were dominated by solitary bees, whose dispersal distance is usually <1000 m (Steffan-Dewenter et al., 2002; Zurbuchen et al., 2010). Habitats were classified into 'natural shrubland', 'plantation forest', 'orchard', 'built-up area', 'grassland', 'water' and 'other'. The first four habitat types were used in the following analysis to assess their specific effects on bees. Natural shrubland represents the main natural habitat in this region. 'Grassland' comprised both abandoned fields and natural grassland. Apples were the main orchard crops, but there were also a few peach, cherry and pear orchards encountered in the study region. ~~To assess the response of wild bees to increasing isolation from natural shrubland, w~~We selected three radii, 250, 500 and

1000 m, to assess the response of wild bees to the % area of each habitat type on increasingly larger spatial scales surrounding each sampling site (Table S1) using the connecting analysis tools to construct landscape models in ModelBuilder in ArcGIS 10.2 (ESRI, 2014). The distance from the center of each site to the nearest edge of a natural shrubland patch was calculated using the Near Tool of Analysis tools in ArcGIS 10.2.

2.5. Data analysis

The responses of wild bee abundance and species richness to the landscape variables, local flowering ground-cover and their interacting effects across spatial scales were analyzed using generalized linear models with a negative binomial distribution (R package 'MASS', Ripley et al., 2018), because of overdispersion in the ~~poisson~~ generalized linear model based on a Poisson distribution (Zuur et al., 2009). Mathematically independent major variables (Table S2), including distance from natural shrubland, percent of ~~and~~ plantation forest, orchards, build-up area, local flowering ground-cover and the interactions between the landscape variables and local flowering ground-cover, were included as explanatory variables in full models, with abundance and species richness of overall and different body size groups of wild bees included as response variables, respectively. Full models were constructed for each response variable in the surrounding landscapes at spatial scales of 250, 500 and 1000 m. The dredge function (R package 'MuMIn', Barton, 2018) was then used to select the optimal model and spatial scale for each response variable based on the corrected Akaike Information Criterion (AICc). The spatial scale of 500 m was selected as the optimal scale for each response variable in the following analysis, due to ~~where were~~ the smallest~~lowest~~ AICc values obtained at this scale (Table S4). Where several ~~Then, if more than one~~ models showed a ΔAICc<2, the model average function (R package 'MuMIn', Barton, 2018) was used to estimate the model parameters. Spatial autocorrelation was assessed by calculating Moran's I values based on geographic coordinates and the different wild bee diversity variables using the R package 'spdep' (version 0.7-9, Bivand, 2018), and no significant spatial autocorrelation was detected in any case (-0.12<Moran's I<-0.05, *p*-value>0.51 in all cases). We validated the models based on visual inspection of the plotted residuals versus the predicted values. All analyses were performed using R (version 3.5.1, R Core Team, 2018).

3. Results

3.1. Species composition of wild bees

Overall, the pan traps collected 4341 wild bee specimens representing 74 species in 12 genera (Table S3). Samples included 3050 small bees (55 species) and 1291 large bees (19 species). The most dominant species in the study area was the small bee *Andrena minutula* (Kirby, 1802), accounting for 32.23% of all sampled specimens. We also collected 2231 honeybees.

3.2. Effects of landscape structure, flowering ground-cover and their interaction on the diversity of wild bees

Distance from natural shrubland was negatively linked to the abundance of overall, small and large bees (Table 1, Fig. 2). Plantation forest area was negatively linked to all response variables except for large bee abundance. The area of orchards in the surrounding landscape similarly showed negative effects on abundance and species richness of overall and small bees. Abundance of overall and small bees and the species richness of small bees also responded negatively to the area of build-up area (Table 1, Fig. 3). In contrast, honeybee abundance was not significantly linked to any explanatory variable (null model with the lowest AICc).

Table 1.

Fig. 2. (1-column, black-and-white)

The percent of local flowering ground-cover interacted with distance of natural shrubland and percent of plantation forest, in partly countering the negative effects of isolation from shrubland and presence of plantation forests on large bee abundance (Table 1, Fig. 4).

Fig. 3. (2-column, black-and-white)

Fig. 4. (2-column, color)

4. Discussion

In this study, we found that plantation forests negatively impacted wild bee assemblages in neighboring apple orchards. For the abundance of large bees, this trend was partly counterbalanced by a high percentage of flowering ground-cover in the orchards. In contrast, natural shrubland benefited wild bee assemblages in the orchards.

In accordance with our first hypothesis, abundance of overall bees in orchards therefore declined with increasing isolation from natural shrubland. This may be linked to the fact that natural shrubland experiences limited human disturbances and likely provides floral resources, nesting material and nest sites, ~~hence~~ supporting a large abundance of wild bees in nearby orchards that spread into the surrounding landscape in search of food. This positive influence of natural habitats on wild bees in orchards is in line with a large body~~wide range~~ of previous studies (Ricketts et al., 2008; Garibaldi et al., 2011; Kennedy et al., 2013). The steeper decline in the abundance of small bee species in orchards with increasing isolation from shrubland when compared to large bees may be explained by ~~the difference in their~~reduced dispersal ability associated with their small body size~~ differences~~ (Greenleaf et al., 2007). Large bees can commonly utilize more distant pollen and nectar resources, while small bees usually prefer to search for floral resource in closely adjacent habitats. Furthermore, large bees commonly show larger resource requirements than small bees, possibly rendering them more sensitive to intensively managed agricultural landscapes (Martins et al., 2013). Considering the dominance of small bees and the sensitivity of large bees to agricultural landscape management, it appears critical to protect natural habitats and increase landscape connectivity by reconstructing natural habitat corridors in intensively managed agricultural landscapes to improve wild bee diversity and associated pollination services (Garratt et al., 2017).

The contrasting negative effects of both build-up area and orchards on bee diversity are~~is~~ possibly linked to natural habitat loss and fragmentation associated with these anthropogenic habitats (Bates et al., 2011; Geslin et al., 2016). Some studies have nonetheless highlighted the potential value of these habitats and areas for pollinators, in cases where diverse flowering plant communities occur in urban environments (Baldock at al., 2015; Threlfall et al., 2015) or for example at organically managed agricultural fields (Holzschuh et al., 2008; Kennedy et al., 2013). Improvement of resource availability for bees in these human-dominated habitats could therefore represent an important strategy for pollinator conservation (Baldock et al., 2015).

Similarly, the negative effects of plantation forests exerted on wild bees in orchards could be a direct result of flowering plant scarcity in these habitats due to their intensive management regime, including plowing, pruning and herbicide application, in combination with the dominance of anemochorous tree species. This intensive management results in plantation forests being characterized by a simple, homogeneous vegetation structure (Cao, 2008; Xu, 2011) lacking in both, food and nesting resources. These assumed causal links nonetheless require further more direct future testing, for example studying wild bee populations directly in plantation forests under different management regimes and in neighboring apple orchards.

Since widely undisturbed natural habitats are already chiefly located exclusively at the very edges of agricultural landscapes, their conservation can only play a part of any strategy to enhance pollinator assemblages and their pollination services. Given the potential positive effects of restored habitats (Morandin and Kremen, 2013; Ponisio et al., 2016), as well as their potential interaction with local management, restoring or creating semi-natural habitats may be feasible as a complementary means to promote key wild pollinator populations and associated pollination services in adjacent fields. Given the negative association between the semi-natural forest plantations and pollinator assemblages observed in our study region, this approach clearly requires a holistic perspective, considering reducing the degree of intensive management in both agricultural areas and any semi-natural habitats, and strat~~g~~eg~~t~~ically planning the composition and configuration of the agricultural landscape at larger spatial scales (Kennedy et al., 2013; Shackelford et al., 2013; Westphal et al., 2015).

Our results furthermore confirmed the importance of ~~high~~abundant flowering plant ground-cover for wild bees in orchards. Similar positive effects of flowering ground-cover or their interaction with landscape factors on pollinator abundance were already reported during crop bloom in apple orchards of south-west England (Campbell et al., 2017) and in other crops like mango in South Africa (Carvalheiro et al., 2012), sweet cherry in Germany (Holzschuh et al., 2012) or blueberry in the USA (Blaauw and Isaacs, 2014). Kammerer et al. (2016) reported that the relative abundance of bees benefited from floral resources on the ground throughout the entire apple growing season. They suggested that the ~~while~~ local enhancement of flowering ground-cover may mainly boost the abundance of species already present in the surrounding agricultural landscape matrix, and the large-scale conservation and restoration of natural and semi-natural habitats in agricultural landscapes may be more important to maintain and enhance the overall pollinator diversity in orchards (Kleijn et al. 2011; Carvalheiro et al., 2012; Campbell et al., 2017). Future research should further confirm the role of local flowering ground-cover and investigate which flowering plant species attract wild bees into the orchards (Martins et al., 2015), ~~under~~while simultaneously considering more local, adjacent and landscape factors, such as pesticides (Tuell and Isaacs, 2010), floral resources in adjacent habitats and surrounding landscapes (Grab et al., 2017).

Compared with Europe or the US, China’s agricultural landscapes and their management are unique, characterized by few organic fields and flower strips (Dai et al., 2015), but smaller field sizes (Zou, 2017) and often containing large areas of woodland like plantation forests or windbreaks (Cao, 2011; Zheng and Cao, 2015). Since 1978, China has launched large afforestation and reforestation programs to improve environmental conditions, such as Three North Shelterbelt Program (1978-2050) and the Grain For Green Project (2000-2020). Although these programs have increased the forest cover, they also show several drawbacks, partly related to the use of exotic fast-growing tree species, with few considerations or assessments of implications of these programs for biodiversity conservation. It is unsurprising that high tree mortality occurs at some of the afforested sites (Wang et al., 2012), and declines in native biodiversity have also been reported (Cao, 2011; Zheng and Cao, 2015), while studies reporting on positive implications of reforestation on biodiversity (Warren-Thomas et al., 2014; Zou et al., 2015) commonly stress the importance of the use of locally native species and the creating of structurally complex habitats and habitat mosaics. Multifunctional and sustainable restoration policies, reasonable management and monitoring of ecological impacts therefore need to be more strongly considered in ongoing and future reforestation programs across China. This suggests that, if plantation forest habitats in the study area were kept widely undisturbed and enriched with a wider variety of native tree species, allowing a rich community of perennial flowering plants to colonize the undergrowth, they may become much more valuable to bees by offering suitable microclimates, nesting sites and food resources (Joshi et al., 2016). To confirm this assumption and greatly enhance the conservation and ecosystem service value of existing plantation forests, we therefore suggest the planting of nectar and pollen rich tree or shrub species, and a reduced future forest management at least in plantation forests located in direct vicinity to orchards, a measure potentially conserving not only pollinators, but also other beneficial insects (Motzke et al., 2016).

5. Conclusion

Natural shrubland in our study area appears to provide crucial resources for a wide diversity of bee species across different body-size classes, and this habitat subsequently forms a key source habitat for wild bees in the wider landscape. In contrast, restored, currently intensively managed forest patches appear to trigger a decline in bee diversity in surrounding orchards, with this trend further influenced by local orchard management. These observations highlight the importance in distinguishing the pronounced potential differences in resource availability for bees between different types of natural and restored habitats. Habitat restoration in agricultural landscapes should diversify both vegetation structure and composition, and simultaneously reduce the management intensity to maintain rich wild bee resources and enhance associated pollination services in agricultural landscapes.

Acknowledgments

Supplementary data

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Fig. 1. The distribution of sampling sites in Changping District, Beijing

Fig. 2. Effects of distance from natural shrubland on wild bee abundance

Fig. 3. Effects of landscape composition on wild bee diversity

Fig. 4. Effects of the interaction between flowering ground-cover and distance from natural shrubland (a) and percent of plantation forest (b) on large bee abundance. Lines with 95% confidence intervals show predictions of negative binomial generalized linear models at 10% (low), 50% (medium) and 90% (high) quantiles of flowering ground-cover (FG)

Table 1. Model-averaged coefficients and relative variable importance for abundance and species of wild bees. Distance=distance from natural shrubland, PF=plantation forest, FG=flowering ground-cover, Oc=Orchard, Bu=Build-up area

	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	Relative variable importance
Overall bee abundance						
(Intercept)	6.9670	0.7342	0.7538	9.2430	<0.0001	
Bu	-0.0221	0.0067	0.0072	3.0630	0.0022	0.78
Distance	-0.3526	0.1009	0.1089	3.2390	0.0012	1.00
FG	0.0066	0.0058	0.0059	1.1250	0.2606	1.00
Oc	-0.0289	0.0081	0.0087	3.3430	0.0008	0.78
PF	-0.0599	0.0274	0.0286	2.0910	0.0365	1.00
FG:PF	0.0011	0.0005	0.0005	1.9270	0.0539	0.46
Small bee abundance						
(Intercept)	7.1614	0.5796	0.6129	11.6850	<0.0001	
Bu	-0.0282	0.0075	0.0080	3.5360	0.0004	1.00
Distance	-0.4202	0.1176	0.1243	3.3820	0.0007	1.00
FG	0.0060	0.0086	0.0089	0.6770	0.4986	1.00
Oc	-0.0344	0.0117	0.0123	2.7910	0.0053	1.00
PF	-0.0388	0.0168	0.0182	2.1330	0.0329	0.41
FG:Oc	0.0004	0.0002	0.0002	1.7910	0.0733	0.24
Large bee abundance						
(Intercept)	4.4710	0.2920	0.3068	14.5720	<0.0001	
Distance	-0.6644	0.3089	0.3157	2.1040	0.0354	1.00
FG	0.0062	0.0061	0.0063	0.9830	0.3257	1.00
PF	-0.09323	0.0465	0.0482	1.9330	0.0532	0.61
FG:PF	0.0014	0.0006	0.0006	2.2810	0.0226	0.40

Distance:FG	0.0086	0.0040	0.0043	2.0060	0.0449	0.24
Overall bee richness						
(Intercept)	4.0152	0.3233	0.3369	11.9180	<0.0001	
Bu	-0.00812	0.0041	0.0044	1.8510	0.0641	0.64
Oc	-0.0139	0.0049	0.0052	2.6940	0.0071	1.00
PF	-0.0297	0.0093	0.0098	3.0210	0.0025	1.00
FG	0.0023	0.0014	0.0015	1.5140	0.1300	0.22
Small bee richness						
(Intercept)	3.9136	0.3692	0.3844	10.1810	<0.0001	
Bu	-0.0098	0.0044	0.0047	2.0710	0.0384	0.70
Oc	-0.0166	0.0053	0.0056	2.9670	0.0030	1.00
PF	-0.0266	0.0104	0.0111	2.4070	0.0161	1.00
Large bee richness						
(Intercept)	1.8357	0.1612	0.1701	10.7890	<0.0001	
PF	-0.0385	0.0176	0.0188	2.0530	0.0401	1.00
FG	0.0032	0.0027	0.0029	1.1170	0.2638	0.31

Contrasting effects of natural shrubland and plantation forests on bee assemblages at ~~in~~ neighboring apple orchards in Beijing, China

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Contrasting effects of natural shrubland and plantation forests on bee assemblages at neighboring apple orchards in Beijing, China

Abstract

Wild bees provide important pollination services for crops and wild plants. While land use intensification has resulted in steep declines of wild bee diversity across agricultural landscapes, the creation of semi-natural habitats has been proposed as a counter-measure. However, the relative value of semi-natural and natural habitats in promoting wild bees has rarely been studied, especially for China that harbors the world's largest plantation forest area, characterized by intensively managed, mono-dominant stands of wind-pollinated tree species. We sampled wild bees in apple orchards to assess how their assemblages were influenced by semi-natural habitats in the surrounding landscape and the local flowering ground-cover. Bee abundance declined with increasing isolation from natural shrubland. In contrast, wild bee diversity and abundance were negatively linked to plantation forests. For the abundance of large bees, this effect was partly ameliorated by local flowering ground-cover. Maintaining or restoring wild bee assemblages in agricultural landscapes therefore requires careful evaluations of restoration measures such as forest planting. Availability of local flower resources and nearby natural shrubland appeared particularly important to enhance wild bees and their potential services in apple orchards.

Keywords

dispersal ability, flowering ground-cover, habitat restoration, landscape composition, pollinator

1. Introduction

Bees provide essential pollination services for both wild plants (Ollerton et al., 2011) and crops (Klein et al., 2007). With regard to this ecosystem service, wild bees are typically more effective pollinators than managed honey bees (Winfree et al., 2007; Garibaldi et al., 2013), while both of these groups have experienced widespread declines in recent decades (Potts et al., 2010). Research into the decline of wild bee diversity regularly identifies agricultural intensification and urbanization, associated with a loss and fragmentation of semi-natural habitats (Kremen et al., 2007; Krauss et al., 2010; Seto et al., 2012; Tscharntke et al., 2012), as important factors.

In Europe, agri-environmental schemes targeting the protection and restoration of semi-natural habitats in agricultural landscapes have been widely used in response to biodiversity losses (Batáry et al., 2015), with the Farm Bill in the United States (Cain and Lovejoy, 2004) and afforestation projects in Beijing (Xue and Fan, 2018) claiming similar aims and using similar approaches. However, the association of bees with restored habitats in comparison to remnant natural, successional habitats is currently poorly understood (Morandin and Kremen, 2013). Most studies combine various natural and restored habitats into one habitat class like 'semi-natural habitats' (Ricketts et al., 2008; Garibaldi et al., 2011), thereby disregarding differences between habitats in their vegetation, nesting and food resources they offer as well as the specific habitat management – all factors known to affect wild bee assemblages (Potts et al., 2003; Potts et al., 2005; Forrest et al., 2015).

In contrast to persistent uncertainties regarding the promotion of wild bees by restored habitats, natural habitats with diverse plant species and nesting resources that experience little human disturbance are widely regarded as highly beneficial for bees (Kremen et al., 2007; Garibaldi et al., 2011). Responses of pollinator species to such habitats in the surrounding landscape vary due to differences in their dispersal ability (Winfree et al., 2007; Jauker et al., 2009) related to body size (Gathmann and Tscharntke, 2002; Greenleaf et al., 2007), the crop system (Joshi et al., 2016), the investigated pollinator group or taxon (Jauker et al., 2009; Carvalheiro et al., 2010) and the biogeographical context (Garibaldi et al., 2011). Most studies of agricultural pollinator assemblages originate from North America and Europe, where large agricultural fields commonly dominate the landscape, whereas field sizes are generally much smaller in rural China (Zou et al., 2017). Our understanding of the links between restored and semi-natural habitats and pollinator assemblages particularly in China's smallholder-dominated landscapes has remained very limited (Steward et al., 2014; Zou et al., 2017).

In addition, growing evidence demonstrates that local management practices (Kennedy et al., 2013; Shackelford et al., 2013) and their interactions with landscape structure also influence pollinator diversity (Kennedy et al., 2013; Park et al., 2015; Westphal et al., 2015). For example, agricultural landscapes with higher proportions of organic crops support more diverse wild bees (Holzschuh et al., 2008); wild bee diversity declines with increasing pesticide use in orchards, but this negative effect is partly buffered by increasing proportions of natural habitat in the surrounding landscape (Park et al., 2015); and wildflower-rich ground-cover promotes the abundance of wild bees (Blaauw and Isaacs, 2014; Campbell et al., 2017) and honeybees (Földesi et al., 2016) and of the associated pollination services (Carvalheiro et al., 2012; Blaauw and Isaacs, 2014). In our study area, mowing, plowing or herbicide application to control ground-cover vegetation are conventional management measures in apple orchards to limit the growth of weeds that compete with apple trees for nutrients and water. Plantation forests in this agricultural landscape represent restored habitats characterized by homogenous stands of wind-pollinated tree species under intensive management (Cao, 2008; Xu, 2011) that have been planted to limit environment degradation like soil and water erosion. In comparison, natural shrubland is a natural habitat characterized by diverse assemblages of insect-pollinated plant species experiencing little human interference. Again, the effects local management and its interaction with natural and restored habitats in the wider landscape have on wild bee assemblages in orchards of our study region remain poorly understood. In this area, orchards are dominated by apple trees, which therefore also represent the focus of our study. Apples represent an insect pollinator-dependent global fruit crop (FAO, 2016). China is the most important apple producer, with the country's orchards account for 35% of the global production (Chen et al., 2010).

In our study, we aim to address persisting knowledge gaps regarding the links between restored and natural habitats on wild bee assemblages in agricultural landscapes, using apple orchards as the 'target crop'. In this context, we specifically test the hypotheses that 1) natural shrubland supports a highly diverse assemblage of wild bees, acting as bee source habitat for neighboring apple orchards, so that wild bee abundance decreases with increasing distance from natural shrubland patches; 2) plantation forests in our study area exert a negative effect on wild bee assemblages and their diversity due to the flower scarcity and intensive management typical for these habitats; and 3) flowering ground-cover in orchards interacts with landscape structure, partly buffering negative effects associated with landscape-scale parameters.

2. Materials and methods

2.1. Study area

The study was conducted in Changping District (40°2′–40°23′ N, 115°50′–116°29′ E) in the northwestern suburbs of Beijing City, China in 2016. The local climate is continental, with an average annual temperature of ~12 °C and an average annual rainfall of ~550 mm. The area is located in the transitional zone between the Yan and Taihang Mountains and the North China Plain, with an altitudinal range from 30 m to 1400 m. The mountains are dominated by natural shrubland that experiences very limited human disturbance, and it is characterized by a low canopy cover from trees and a high diversity of flowering species, with *Vitex negundo*, *Cotinus coggygria*, *Gleditsia sinensis*, *Lespedeza bicolor* and *Wikstroemia chamaedaphne* forming important components of this vegetation. The plain area is dominated by urban areas, plantation forest and orchards. The plantation forest has been newly planted after 2012 under the 'Plain Reforestation Project', aimed to restore semi-natural habitat to improve the environmental conditions and enhance biodiversity in Beijing, rather than for timber or fruit production. It is dominated by intensively managed monocultures of wind-pollinated tree species forming dense canopies. Plantation forest management comprises grass pruning, plowing and the application of pesticides. The main tree species planted are *Pinus tabulaeformis*, *Ginkgo biloba*, *Populus tomentosa*, *Platycladus orientalis* and the non-native legume *Robinia pseudoacacia*.

In 2016, we selected a total of 22 Fuji apple orchards, located along gradients of increasing distance from natural shrubland, for bee surveys during the apple blossom period (Fig. 1). The distance between investigated apple orchards was standardized at about 500 m, and the distance from apple sites to natural shrubland ranged from 0.02 km to 2.49 km.

Fig. 1. (2-column, black-and-white)

2.2. Bee sampling and classification

Bees (Hymenoptera: Apoidea) were sampled continuously during the Fuji apple blooming period (12th to 25th April) using pan traps. At each site, three parallel transect lines of 40 m length were established at distances of 10 m, with a distance from the orchard edges of at least 15 m. At each transect, three pan traps (yellow, white and blue following Westphal et al., 2008, with a 21 cm diameter and 10 cm depth) were placed on metal brackets at a height of about 1.3 m (Tuell and Isaacs, 2010; Mallinger et al., 2015), and three sets of traps were spaced at 20 m intervals along each transect line. Pan traps were filled with about 400 ml water solution with two drops of detergent added per five L of water, with traps being emptied and refilled every 3 days. All bee specimens were identified to species level based on the taxonomic literature (Wu, 1965, 2000 and 2006). The occurrence of *Apis mellifera* was strongly associated with temporary hives set by beekeepers in the study region during the apple blossom, and their abundance in the orchards was therefore only affected by the distance from these hives (Pearson's correlation, p-value= 0.0005, r= -0.68). Therefore, specimens of *A. mellifera* were disregarded in this study.

The body size of each wild bee species was measured using a Nikon SMZ800N stereomicroscope. For all species contained with >4 individuals in the samples, the body length was measured in four randomly selected specimens, while otherwise all individuals were measured. Bees were divided into small (≤11.5 mm) and large species (>11.5 mm), following the advice of Tscheulin et al. (2011) and accounting for the distinct gap between small and large bees observed in our samples (Fig. S1). For the analysis, wild bee data from nine traps at the same site were pooled for the entire sampling period.

2.3. Local management survey

All orchards were conventionally managed. In line with local practices, farmers did not apply any pesticides or fungicides during the apple flowering period to protect pollinators. In that context, although residual pesticides might influence bee diversity, we focus on the ground vegetation in the orchards as the main local management variable affecting bees in this study. Five 1 m × 1 m plots were established in the four corners and the center of the bee sampling area (20 m × 40 m) covered by three parallel transects during the apple bloom. In each plot, coverage of each flowering insect-pollinated plant species was recorded during the apple blossom period, and these values were added to calculate the total coverage of flowering ground-cover in each plot, subsequently averaged as the mean value for each study site.

2.4. Landscape parameters

Land use surrounding the focal orchards was quantified at radii between 250 m and 1000 m, based on extensive field inspections in May 2016 and on satellite imagery (at 0.91 m resolution from 29th March 2015). Wild bee assemblages were dominated by solitary bees, whose dispersal distance is usually <1000 m (Steffan-

Dewenter et al., 2002; Zurbuchen et al., 2010). Habitats were classified into 'natural shrubland', 'plantation forest', 'orchard', 'built-up area', 'grassland', 'water' and 'other'. The first four habitat types were used in the following analysis to assess their specific effects on bees. Natural shrubland represents the main natural habitat in this region. 'Grassland' comprised both abandoned fields and natural grassland. Apples were the main orchard crops, but there were also a few peach, cherry and pear orchards encountered in the study region. We selected three radii, 250, 500 and 1000 m, to assess the response of wild bees to the % area of each habitat type on increasingly larger spatial scales surrounding each sampling site (Table S1) using the connecting analysis tools to construct landscape models in ModelBuilder in ArcGIS 10.2 (ESRI, 2014). The distance from the center of each site to the nearest edge of a natural shrubland patch was calculated using the Near Tool of Analysis tools in ArcGIS 10.2.

2.5. Data analysis

The responses of wild bee abundance and species richness to the landscape variables, local flowering ground-cover and their interacting effects across spatial scales were analyzed using generalized linear models with a negative binomial distribution (R package 'MASS', Ripley et al., 2018), because of overdispersion in the generalized linear model based on a Poisson distribution (Zuur et al., 2009). Mathematically independent major variables (Table S2), including distance from natural shrubland, percent of plantation forest, orchards, build-up area, local flowering ground-cover and the interactions between the landscape variables and local flowering ground-cover, were included as explanatory variables in full models, with abundance and species richness of overall and different body size groups of wild bees included as response variables, respectively. Full models were constructed for each response variable in the surrounding landscapes at spatial scales of 250, 500 and 1000 m. The dredge function (R package 'MuMIn', Barton, 2018) was then used to select the optimal model and spatial scale for each response variable based on the corrected Akaike Information Criterion (AICc). The spatial scale of 500 m was selected as the optimal scale for each response variable in the following analysis, due to the smallest AICc values obtained at this scale (Table S4). Where several models showed a $\Delta AICc<2$, the model average function (R package 'MuMIn', Barton, 2018) was used to estimate the model parameters. Spatial autocorrelation was assessed by calculating Moran's I values based on geographic coordinates and the different wild bee diversity variables using the R package 'spdep' (version 0.7-9, Bivand, 2018), and no significant spatial autocorrelation was detected in any case ($-0.12<\text{Moran's I}<-0.05$, p-value>0.51 in all cases). We validated the models based on visual inspection of the plotted residuals versus the predicted values. All analyses were performed using R (version 3.5.1, R Core Team, 2018).

3. Results

3.1. Species composition of wild bees

Overall, the pan traps collected 4341 wild bee specimens representing 74 species in 12 genera (Table S3). Samples included 3050 small bees (55 species) and 1291 large bees (19 species). The most dominant species in the study area was the small bee *Andrena minutula* (Kirby, 1802), accounting for 32.23% of all sampled specimens. We also collected 2231 honeybees.

3.2. Effects of landscape structure, flowering ground-cover and their interaction on the diversity of wild bees

Distance from natural shrubland was negatively linked to the abundance of overall, small and large bees (Table 1, Fig. 2). Plantation forest area was negatively linked to all response variables except for large bee abundance. The area of orchards in the surrounding landscape similarly showed negative effects on abundance and species richness of overall and small bees. Abundance of overall and small bees and the species richness of small bees also responded negatively to the area of build-up area (Table 1, Fig. 3). In contrast, honeybee abundance was not significantly linked to any explanatory variable (null model with the lowest AICc).

Table 1.

Fig. 2. (1-column, black-and-white)

The percent of local flowering ground-cover interacted with distance of natural shrubland and percent of plantation forest, in partly countering the negative effects of isolation from shrubland and presence of plantation forests on large bee abundance (Table 1, Fig. 4).

Fig. 3. (2-column, black-and-white)

Fig. 4. (2-column, color)

4. Discussion

In this study, we found that plantation forests negatively impacted wild bee assemblages in neighboring apple orchards. For the abundance of large bees, this trend was partly counterbalanced by a high percentage of flowering ground-cover in the orchards. In contrast, natural shrubland benefited wild bee assemblages in the orchards.

In accordance with our first hypothesis, abundance of overall bees in orchards therefore declined with increasing isolation from natural shrubland. This may be linked to the fact that natural shrubland experiences limited human disturbances and likely provides floral resources, nesting material and nest sites, supporting a large abundance of wild bees in nearby orchards that spread into the surrounding landscape in search of food. This positive influence of natural habitats on wild bees in orchards is in line with a large body of previous studies (Ricketts et al., 2008; Garibaldi et al., 2011; Kennedy et al., 2013). The steeper decline in the abundance of small bee species in orchards with increasing isolation from shrubland when compared to large bees may be explained by reduced dispersal ability associated with their small body size (Greenleaf et al., 2007). Large bees can commonly utilize more distant pollen and nectar resources, while small bees usually prefer to search for floral resource in closely adjacent habitats. Furthermore, large bees commonly show larger resource requirements than small bees, possibly rendering them more sensitive to intensively managed agricultural landscapes (Martins et al., 2013). Considering the dominance of small bees and the sensitivity of large bees to agricultural landscape management, it appears critical to protect natural habitats and increase landscape connectivity by reconstructing natural habitat corridors in intensively managed agricultural landscapes to improve wild bee diversity and associated pollination services (Garratt et al., 2017).

The contrasting negative effects of both build-up area and orchards on bee diversity are possibly linked to natural habitat loss and fragmentation associated with these anthropogenic habitats (Bates et al., 2011; Geslin et al., 2016). Some studies have nonetheless highlighted the potential value of these habitats and areas for pollinators, in cases where diverse flowering plant communities occur in urban environments (Baldock at al., 2015; Threlfall et al., 2015) or for example at organically managed agricultural fields (Holzschuh et al., 2008; Kennedy et al., 2013). Improvement of resource availability for bees in these human-dominated habitats could therefore represent an important strategy for pollinator conservation (Baldock et al., 2015).

Similarly, the negative effects of plantation forests exerted on wild bees in orchards could be a direct result of flowering plant scarcity in these habitats due to their intensive management regime, including plowing, pruning and herbicide application, in combination with the dominance of anemochorous tree species. This intensive management results in plantation forests being characterized by a simple, homogeneous vegetation structure (Cao, 2008; Xu, 2011) lacking in both, food and nesting resources. These assumed causal links nonetheless require further more direct future testing, for example studying wild bee populations directly in plantation forests under different management regimes and in neighboring apple orchards.

Since widely undisturbed natural habitats are already chiefly located exclusively at the very edges of agricultural landscapes, their conservation can only play a part of any strategy to enhance pollinator assemblages and their pollination services. Given the potential positive effects of restored habitats (Morandin and Kremen, 2013; Ponisio et al., 2016), as well as their potential interaction with local management, restoring or creating semi-natural habitats may be feasible as a complementary means to promote key wild pollinator populations and associated pollination services in adjacent fields. Given the negative association between the semi-natural forest plantations and pollinator assemblages observed in our study region, this approach clearly requires a holistic perspective, considering reducing the degree of intensive management in both agricultural areas and any semi-natural habitats, and strategically planning the composition and configuration of the agricultural landscape at larger spatial scales (Kennedy et al., 2013; Shackelford et al., 2013; Westphal et al., 2015).

Our results furthermore confirmed the importance of abundant flowering plant ground-cover for wild bees in orchards. Similar positive effects of flowering ground-cover or their interaction with landscape factors on pollinator abundance were already reported during crop bloom in apple orchards of south-west England (Campbell et al., 2017) and in other crops like mango in South Africa (Carvalheiro et al., 2012), sweet cherry in Germany (Holzschuh et al., 2012) or blueberry in the USA (Blaauw and Isaacs, 2014). Kammerer et al. (2016) reported that the relative abundance of bees benefited from floral resources on the ground throughout the entire apple growing season. They suggested that the local enhancement of flowering ground-cover may mainly boost the abundance of species already present in the surrounding agricultural landscape matrix, and the large-scale conservation and restoration of natural and semi-natural habitats in agricultural landscapes may be more important to maintain and enhance the overall pollinator diversity in orchards (Kleijn et al. 2011; Carvalheiro et al., 2012; Campbell et al., 2017). Future research should further confirm the role of local flowering ground-cover and investigate which flowering plant species attract wild bees into the orchards (Martins et al., 2015), while simultaneously considering more local, adjacent and landscape factors, such as pesticides (Tuell and Isaacs, 2010), floral resources in adjacent habitats and surrounding landscapes (Grab et al., 2017).

Compared with Europe or the US, China's agricultural landscapes and their management are unique, characterized by few organic fields and flower strips (Dai et al., 2015), but smaller field sizes (Zou, 2017) and often containing large areas of woodland like plantation forests or windbreaks (Cao, 2011; Zheng and Cao, 2015). Since 1978, China has launched large afforestation and reforestation programs to improve environmental conditions, such as Three North Shelterbelt Program (1978-2050) and the Grain For Green Project (2000-2020). Although these programs have increased the forest cover, they also show several drawbacks, partly related to the use of exotic fast-growing tree species, with few considerations or assessments of implications of these programs for biodiversity conservation. It is unsurprising that high tree mortality occurs at some of the afforested sites (Wang et al., 2012), and declines in native biodiversity have also been reported (Cao, 2011; Zheng and Cao, 2015), while studies reporting on positive implications of reforestation on biodiversity (Warren-Thomas et al., 2014; Zou et al., 2015) commonly stress the importance of the use of locally native species and the creating of structurally complex habitats and habitat mosaics. Multifunctional and sustainable restoration policies, reasonable management and monitoring of ecological impacts therefore need to be more strongly considered in ongoing and future reforestation programs across China. This suggests that, if plantation forest habitats in the study area were kept widely undisturbed and enriched with a wider variety of native tree species, allowing a rich community of perennial flowering plants to colonize the undergrowth, they may become much more valuable to bees by offering suitable microclimates, nesting sites and food resources (Joshi et al., 2016). To confirm this assumption and greatly enhance the conservation and ecosystem service value of existing plantation forests, we therefore suggest the planting of nectar and pollen rich tree or shrub species, and a reduced future forest management at least in plantation forests located in direct vicinity to orchards, a measure potentially conserving not only pollinators, but also other beneficial insects (Motzke et al., 2016).

5. Conclusion

Natural shrubland in our study area appears to provide crucial resources for a wide diversity of bee species across different body-size classes, and this habitat subsequently forms a key source habitat for wild bees in the wider landscape. In contrast, restored, currently intensively managed forest patches appear to trigger a decline in bee diversity in surrounding orchards, with this trend further influenced by local orchard management. These observations highlight the importance in distinguishing the pronounced potential differences in resource availability for bees between different types of natural and restored habitats. Habitat restoration in agricultural landscapes should diversify both vegetation structure and composition, and simultaneously reduce the management intensity to maintain rich wild bee resources and enhance associated pollination services in agricultural landscapes.

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Supplementary data

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Fig. 1. The distribution of sampling sites in Changping District, Beijing

Fig. 2. Effects of distance from natural shrubland on wild bee abundance

Fig. 3. Effects of landscape composition on wild bee diversity

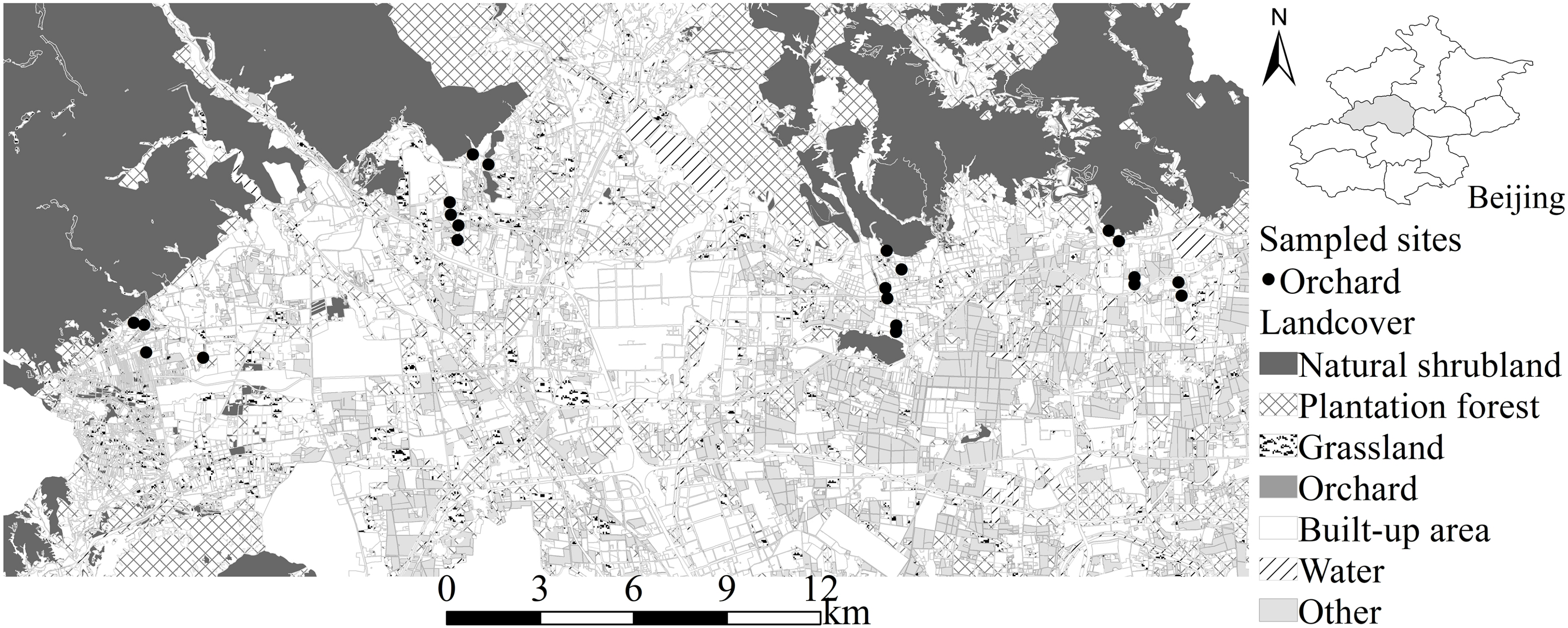
Fig. 4. Effects of the interaction between flowering ground-cover and distance from natural shrubland (a) and percent of plantation forest (b) on large bee abundance. Lines with 95% confidence intervals show predictions of negative binomial generalized linear models at 10% (low), 50% (medium) and 90% (high) quantiles of flowering ground-cover (FG)

Table 1. Model-averaged coefficients and relative variable importance for abundance and species of wild bees. Distance=distance from natural shrubland, PF=plantation forest, FG=flowering ground-cover, Oc=Orchard, Bu=Build-up area

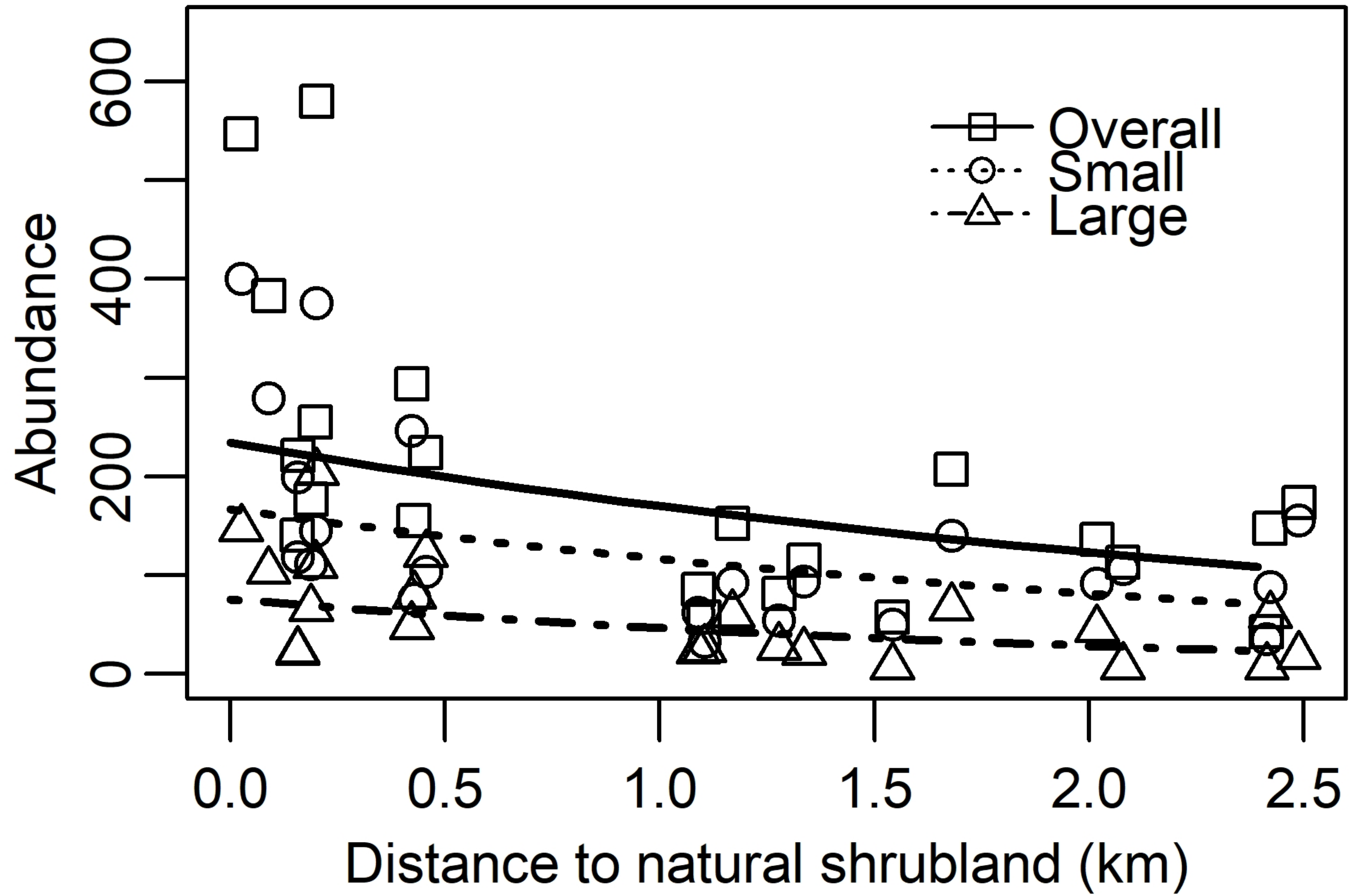
	Estimate	Std. Error	Adjusted SE	z value	Pr(>|z|)	Relative variable importance
Overall bee abundance						
(Intercept)	6.9670	0.7342	0.7538	9.2430	<0.0001	
Bu	-0.0221	0.0067	0.0072	3.0630	0.0022	0.78
Distance	-0.3526	0.1009	0.1089	3.2390	0.0012	1.00
FG	0.0066	0.0058	0.0059	1.1250	0.2606	1.00
Oc	-0.0289	0.0081	0.0087	3.3430	0.0008	0.78
PF	-0.0599	0.0274	0.0286	2.0910	0.0365	1.00
FG:PF	0.0011	0.0005	0.0005	1.9270	0.0539	0.46
Small bee abundance						
(Intercept)	7.1614	0.5796	0.6129	11.6850	<0.0001	
Bu	-0.0282	0.0075	0.0080	3.5360	0.0004	1.00
Distance	-0.4202	0.1176	0.1243	3.3820	0.0007	1.00
FG	0.0060	0.0086	0.0089	0.6770	0.4986	1.00
Oc	-0.0344	0.0117	0.0123	2.7910	0.0053	1.00
PF	-0.0388	0.0168	0.0182	2.1330	0.0329	0.41
FG:Oc	0.0004	0.0002	0.0002	1.7910	0.0733	0.24
Large bee abundance						
(Intercept)	4.4710	0.2920	0.3068	14.5720	<0.0001	
Distance	-0.6644	0.3089	0.3157	2.1040	0.0354	1.00
FG	0.0062	0.0061	0.0063	0.9830	0.3257	1.00
PF	-0.09323	0.0465	0.0482	1.9330	0.0532	0.61
FG:PF	0.0014	0.0006	0.0006	2.2810	0.0226	0.40
Distance:FG	0.0086	0.0040	0.0043	2.0060	0.0449	0.24
Overall bee richness						
(Intercept)	4.0152	0.3233	0.3369	11.9180	<0.0001	
Bu	-0.00812	0.0041	0.0044	1.8510	0.0641	0.64

Oc	-0.0139	0.0049	0.0052	2.6940	0.0071	1.00
PF	-0.0297	0.0093	0.0098	3.0210	0.0025	1.00
FG	0.0023	0.0014	0.0015	1.5140	0.1300	0.22
Small bee richness						
(Intercept)	3.9136	0.3692	0.3844	10.1810	<0.0001	
Bu	-0.0098	0.0044	0.0047	2.0710	0.0384	0.70
Oc	-0.0166	0.0053	0.0056	2.9670	0.0030	1.00
PF	-0.0266	0.0104	0.0111	2.4070	0.0161	1.00
Large bee richness						
(Intercept)	1.8357	0.1612	0.1701	10.7890	<0.0001	
PF	-0.0385	0.0176	0.0188	2.0530	0.0401	1.00
FG	0.0032	0.0027	0.0029	1.1170	0.2638	0.31

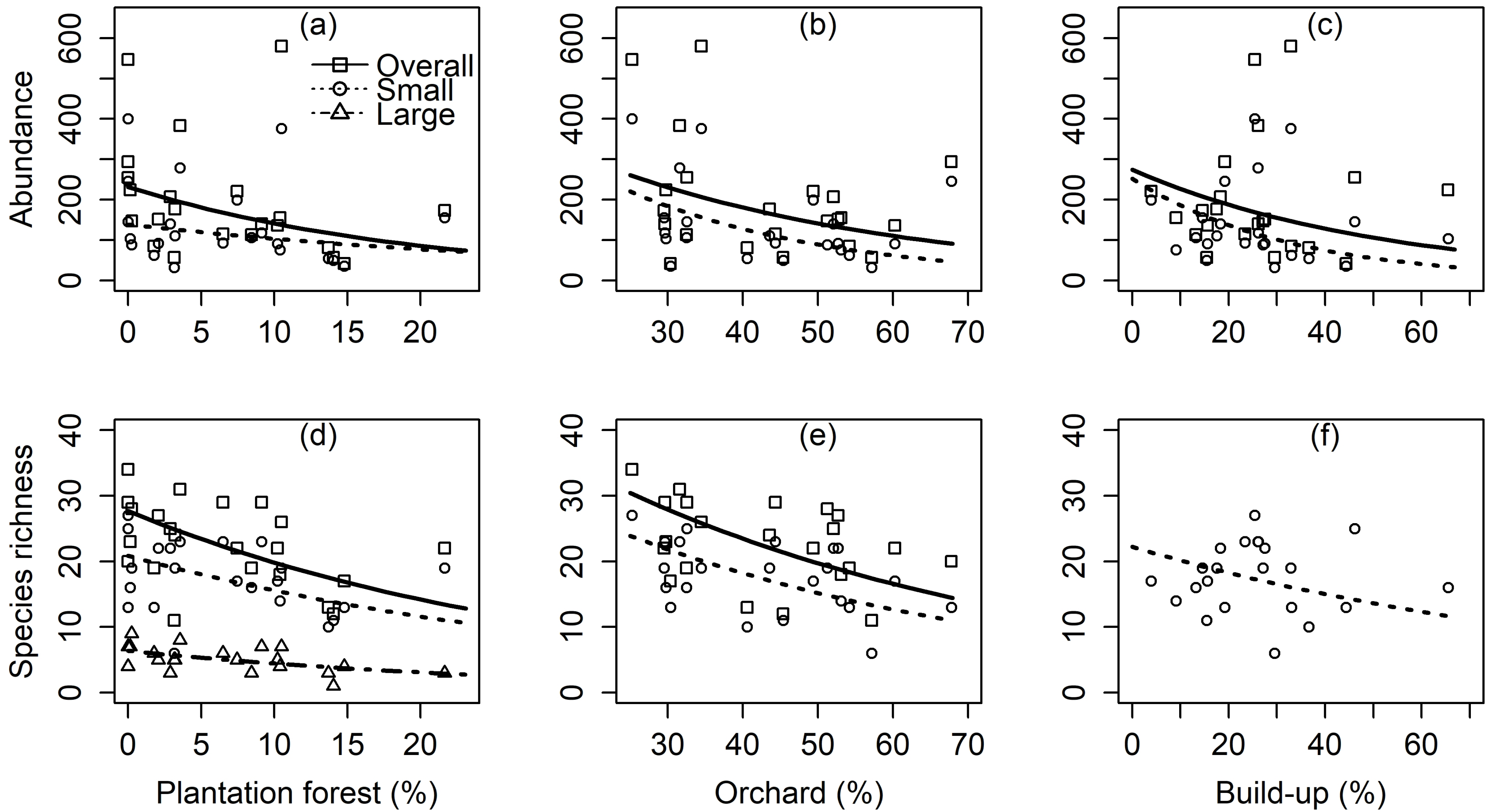
602



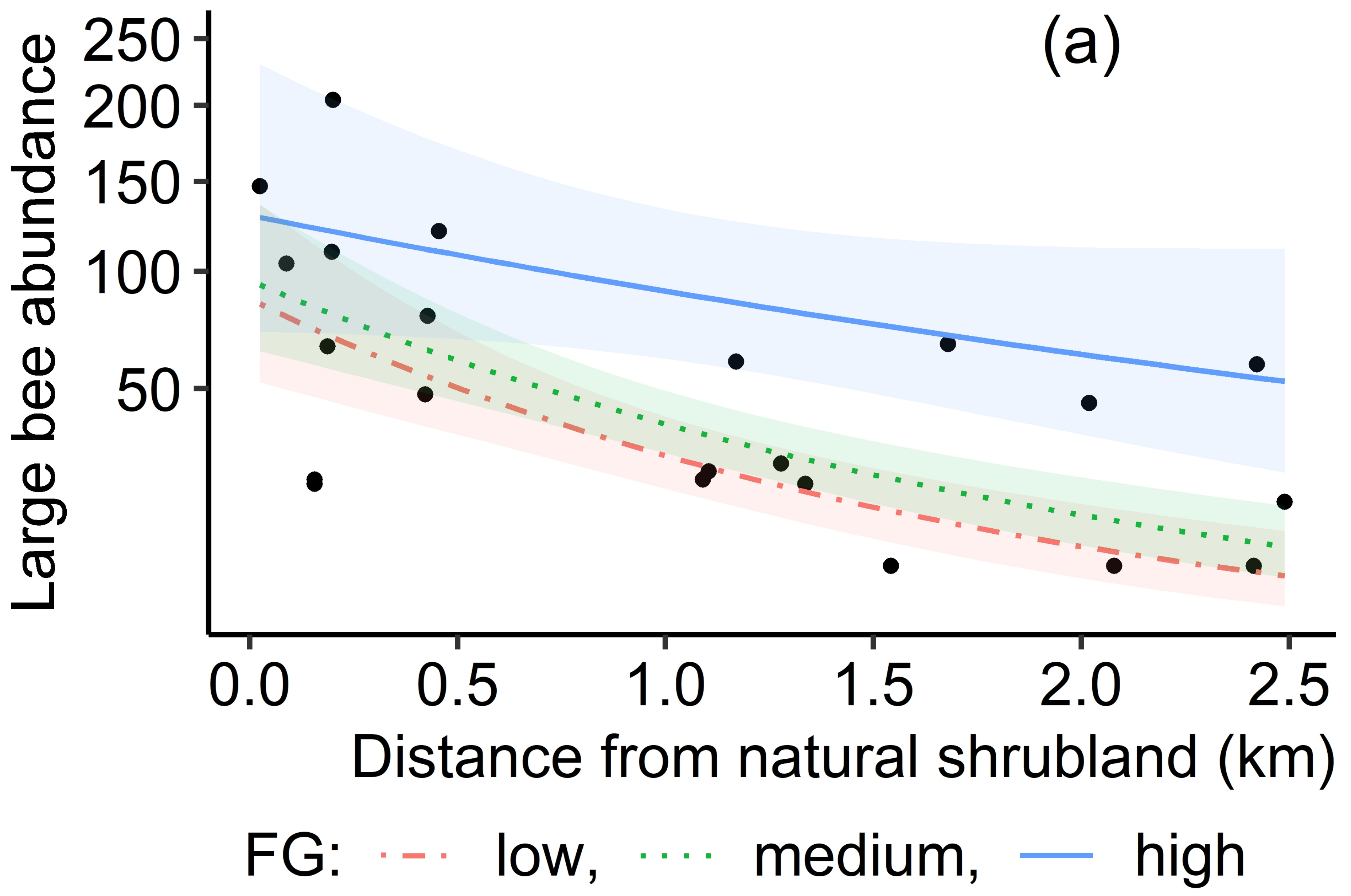
N
Beijing
Sampled sites
Orchard
Landcover
Natural shrubland
Plantation forest
Grassland
Orchard
Built-up area
Water
Other
0
3
6
9
12
km



Overall
Small
Large
Abundance
0
200
400
600
0.0
0.5
1.0
1.5
2.0
2.5
Distance to natural shrubland (km)



(a)
(b)
(c)
(d)
(e)
(f)
Overall
Small
Large
Abundance
Species richness
Plantation forest (%)
Orchard (%)
Build-up (%)
0
200
400
600
0
10
20
30
40
0
5
10
15
20
30
40
50
60
70
0
20
40
60


(a)
Large bee abundance
250
200
150
100
50
0.0
0.5
1.0
1.5
2.0
2.5
Distance from natural shrubland (km)
FG:
low,
medium,
high

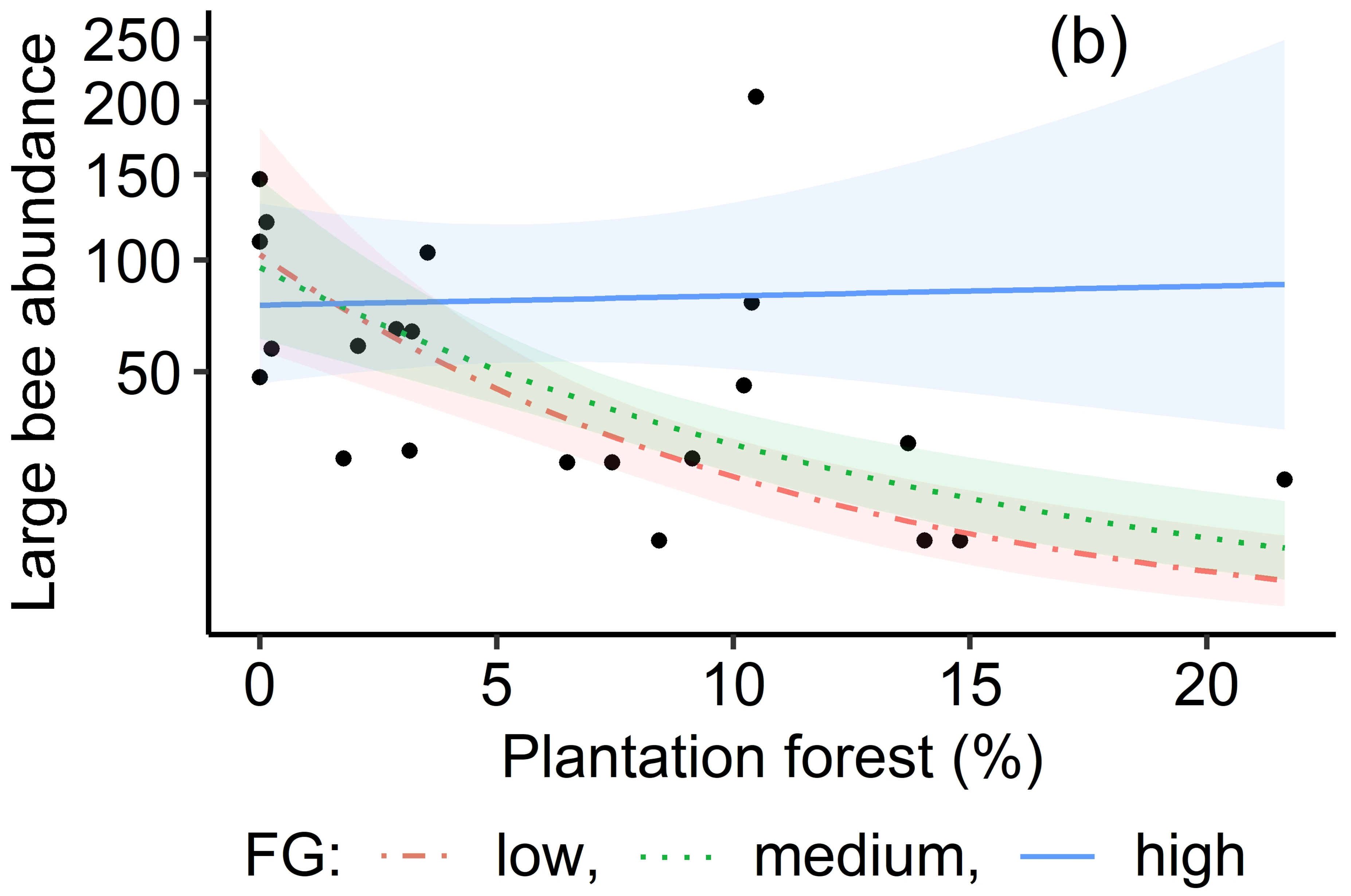

(b)
Large bee abundance
250
200
150
100
50
0
5
10
15
20
Plantation forest (%)
FG: low, medium, high

Table S1. Landscape composition at 500 m surrounding orchards in the Changping District of Beijing

Habitat type	Mean±SD (%)	Min (%)	Max (%)
Natural shrubland	9.07±13.43	0	40.08
Plantation forest	6.54±6.00	0	21.65
Grassland	2.76±2.90	0	9.40
Orchard	43.07±12.10	25.23	67.79
Built-up area	25.93±13.79	3.94	65.47
Water	2.42±2.93	0	9.50

Table S2. Correlation among explanatory variables based on spearman method due to variables not conforming to normality, except for correlation between orchard and build-up area based on the pearson method. Landscape variables were at the spatial scale of 500 m. Distance = distance from natural shrubland, NS = natural shrubland; PF = plantation forest, GL =grassland; FG = flowering groundcover, Oc = Orchard, Bu = Build-up area. Entries above the diagonal are correlation coefficients, and entries below the diagonal are p-values.

	Dis	NS	PF	GL	Oc	Bu	FG
Dis		-0.91	0.38	0.44	0.17	-0.09	0.19
NS	<0.01		-0.28	-0.36	-0.33	0.14	-0.12
PF	0.08	0.20		-0.05	-0.19	-0.31	-0.15
GL	0.04	0.10	0.83		0.18	-0.26	0.20
Oc	0.44	0.14	0.40	0.41		-0.39	0.19
Bu	0.70	0.52	0.16	0.24	0.07		0.08
FG	0.39	0.60	0.50	0.38	0.40	0.72	

Table S3. Species list of wild bees

Family	Species	Individuals	Length	Body class
Andrenidae	*Andrena* (*Andrena*) *aburana*	1	16.02	large
Andrenidae	*Andrena* (*Andrena*) *chinensis*	3	16.43	large
Andrenidae	*Andrena* (*Chlorandrena*) *taraxaci orienticola*	9	9.75	small
Andrenidae	*Andrena* (*Cnemidandrena*) *solidago*	31	11.84	large
Andrenidae	*Andrena* (*Euandrena*) *hebes*	119	7.83	small
Andrenidae	*Andrena* (*Euandrena*) *luridioma*	106	9.08	small
Andrenidae	*Andrena* (*Euandrena*) *subshawella*	256	8.05	small
Andrenidae	*Andrena* (*Hoplandrena*) *dentata*	36	9.39	small
Andrenidae	*Andrena* (*Larandrena*) *echizenia*	4	9.08	small
Andrenidae	*Andrena* (*Larandrena*) *geae*	130	8.58	small
Andrenidae	*Andrena* (*Melandrena*) *thoracica*	62	13.47	large
Andrenidae	*Andrena* (*Micrandrena*) *minutula*	1399	5.87	small
Andrenidae	*Andrena* (*Plastandrena*) *magnipunctata*	966	11.94	large
Andrenidae	*Andrena* (*Plastandrena*) *pilipes*	24	13.17	large
Andrenidae	*Andrena* (*Simandrena*) *wuae*	37	9.60	small

Apidae	*Anthophora* (*Anthophora*) *melanognatha*	4	12.89	large
Apidae	*Bombus* (*Bombus*) *ignitus*	3	19.30	large
Apidae	*Bombus* (*Melanobombus*) *pyrosoma*	1	17.95	large
Apidae	*Ceratina* (*Ceratina*) *iwatai*	1	4.99	small
Apidae	*Ceratina* (*Ceratinidia*) *flavipes*	12	6.70	small
Apidae	*Eucera* (*Eucera*) *longicornis*	2	12.51	large
Apidae	*Eucera* (*Synhalonia*) *floralia*	9	11.89	large
Halictidae	*Halictus* (*Monilapis*) *tsingtauensis*	21	10.40	small
Halictidae	*Halictus* (*Seladonia*) *aerarius*	1	5.68	small
Halictidae	*Halictus* (*Seladonia*) *confusus*	1	6.05	small
Halictidae	*Halictus* (*Seladonia*) *verarius*	2	6.09	small
Halictidae	*Halictus* (*Vestitohalictus*) *ferreotus*	1	6.15	small
Halictidae	*Halictus* (*Vestitohalictus*) *pseudovestitus*	24	6.83	small
Halictidae	*Halictus calceatus*	1	11.26	small
Halictidae	*Halictus* (*Protohalictus*) *rubicundus*	3	11.74	large
Halictidae	*Halictus* (*Halictus*) *quadricinctus*	1	14.54	large
Colletidae	*Hylaeus* (*Hylaeus*) *paulus*	24	3.85	small
Colletidae	*Hylaeus* (*Hylaeus*) *perforatus*	4	6.64	small
Colletidae	*Hylaeus* (*Paraprosopis*) *nigricallosus morawite*	7	5.41	small
Halictidae	*Lasioglossum* (*Ctenonomia*) *halictoides*	18	4.71	small
Halictidae	*Lasioglossum* (*Ctenonomia*) *kumejimense*	1	8.36	small
Halictidae	*Lasioglossum* (*Ctenonomia*) *sinicum*	58	5.52	small
Halictidae	*Lasioglossum* (*Ctenonomia*) sp1	5	7.72	small
Halictidae	*Lasioglossum* (*Ctenonomia*) sp2	2	6.29	small
Halictidae	*Lasioglossum* (*Dialictus*) *epiphrom*	2	6.07	small
Halictidae	*Lasioglossum* (*Dialictus*) *gorge*	1	5.50	small
Halictidae	*Lasioglossum* (*Dialictus*) *orpheum*	1	5.09	small
Halictidae	*Lasioglossum* (*Dialictus*) *pallilomun*	76	5.96	small
Halictidae	*Lasioglossum* (*Dialictus*) *politum*	1	8.01	small
Halictidae	*Lasioglossum* (*Dialictus*) sp1	1	7.95	small
Halictidae	*Lasioglossum* (*Evylaeus*) *metisi*	7	4.47	small
Halictidae	*Lasioglossum* (*Evylaeus*) *pallilomun*	13	5.97	small
Halictidae	*Lasioglossum* (*Evylaeus*) *politum*	97	8.20	small
Halictidae	*Lasioglossum* (*Evylaeus*) *sakagamii*	1	6.54	small
Halictidae	Lasioglossum (*Evylaeus*) sp1	1	3.96	small
Halictidae	Lasioglossum (*Evylaeus*) sp2	1	8.20	small
Halictidae	Lasioglossum (*Evylaeus*) sp3	2	7.05	small
Halictidae	*Lasioglossum* (*Evylaeus*) *vulsum*	370	5.51	small
Halictidae	*Lasioglossum* (*Lasioglossum*) *halictoides*	56	5.05	small
Halictidae	*Lasioglossum* (*Lasioglossum*) *kansuense*	6	8.86	small
Halictidae	*Lasioglossum* (*Lasioglossum*) *mutilum*	47	8.09	small
Halictidae	*Lasioglossum* (*Lasioglossum*) *nipponicola*	39	10.24	small
Halictidae	*Lasioglossum* (*Lasioglossum*) *proximatum*	9	8.63	small

Halictidae	*Lasioglossum* (*Lasioglossum*) *scitulum*	1	9.01	small
Halictidae	*Lasioglossum* (*Lasioglossum*) sp1	1	8.52	small
Halictidae	*Lasioglossum* (*Lasioglossum*) sp2	4	8.21	small
Halictidae	*Lasioglossum* (*Lasioglossum*) sp3	2	8.81	small
Halictidae	*Lasioglossum* (*Lasioglossum*) sp4	2	9.04	small
Halictidae	*Lasioglossum* (*Lasioglossum*) *subopacum*	2	8.35	small
Megachilidae	*Megachile* (*Xanthosarus*) sp1	1	12.90	large
Megachilidae	*Megachile* (*Megachile*) *nipponiaca*	2	10.22	small
Megachilidae	*Melecta sibirica*	1	13.14	large
Megachilidae	*Osmia* (*Helicosmia*) *mengolica*	12	8.60	small
Megachilidae	*Osmia* (*Helicosmia*) *satoi*	7	7.30	small
Megachilidae	*Osmia* (*Osmia*) *taurus*	7	9.92	small
Megachilidae	*Osmia* (*Osmia*) *cornifroms*	4	12.15	large
Megachilidae	*Osmia* (*Osmia*) *excavata*	29	11.51	large
Apidae	*Tetralonia* (*Tetralonia*) *chinensis*	139	12.56	large
Apidae	*Xylocopa* (*Alloxylocopa*) *appendiculata*	7	21.33	large
Total	74	4341		

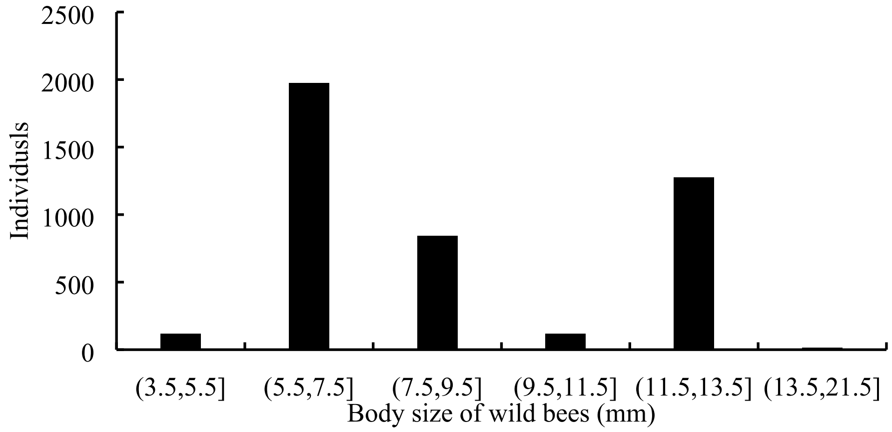


Fig. S1. Histogram of body size of wild bees. Small bees≤11.5 mm, large bees>11.5 mm

Table S4. Model estimates of generalized linear models with a negative binomial distribution for each response variable at the corresponding scale. Explanatory variables incorporated in each model are listed for each response variable individually. Distance=distance from natural shrubland, PF=plantation forest, FG=flowering ground-cover, Oc= Orchard, Bu=Build-up area. Significance level, ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$

Response variable	Scale (m)	AICc	Explanatory variable	Estimate	Sd. Error	z value	*p*-value
Overall bee abundance	250	261.1135	(Intercept)	5.8627	0.2079	28.1940	<0.0001***
			Distance	-0.7741	0.1488	-5.2020	<0.0001***
			Bu	-0.02043	0.0081	-2.5320	0.0113*
			FG	0.0039	0.0035	1.1050	0.2692

			Distance:FG	0.0060	0.0028	2.1100	0.0349*
	500	258.0239	(Intercept)	7.3457	0.4616	15.9150	<0.0001***
			Distance	-0.3662	0.0965	-3.7960	0.0001***
			PW	-0.0430	0.0157	-2.7430	0.0061**
			Oc	-0.0309	0.0075	-4.0910	<0.0001***
			Bu	-0.0235	0.0064	-3.6520	0.0003***
			FG	0.0107	0.0021	5.0360	<0.0001***
	1000	258.9059	(Intercept)	6.8894	0.4140	16.6410	<0.0001***
			Distance	-0.4607	0.0974	-4.7320	<0.0001***
			Bu	-0.0264	0.0081	-3.2640	0.0011**
			Oc	-0.0275	0.0091	-3.0320	0.0024**
			FG	0.0096	0.0024	4.0610	<0.0001***
Small bee abundance	250	249.5817	(Intercept)	5.4708	0.1983	27.5940	<0.0001***
			Distance	-0.3666	0.1141	-3.2140	0.0013**
			PW	-0.0554	0.0231	-2.3960	0.0166*
			Bu	-0.0233	0.0087	-2.6700	0.0076**
			FG	0.0063	0.0027	2.3560	0.0185*
	500	245.3888	(Intercept)	7.3522	0.4950	14.8540	<0.0001***
			Distance	-0.3441	0.1034	-3.3280	0.0009***
			PW	-0.0388	0.0168	-2.3070	0.0211*
			Oc	-0.0347	0.0081	-4.2910	<0.0001***
			Bu	-0.0321	0.0069	-4.6400	<0.0001***
			FG	0.0102	0.0023	4.4910	<0.0001***
	1000	247.8199	(Intercept)	6.8227	0.4593	14.8550	<0.0001***
			Bu	-0.0321	0.0090	-3.5720	0.0004***
			Distance	-0.3807	0.1076	-3.5390	0.0004***
			FG	0.0089	0.0026	3.3970	0.0007***
			Oc	-0.0329	0.0101	-3.2720	0.0011**
Large bee abundance	250	212.7698	(Intercept)	4.4626	0.2491	17.9140	<0.0001***
			Distance	-1.0900	0.2164	-5.0380	<0.0001***
			FG	0.0048	0.0049	0.9830	0.3257
			Distance:FG	0.0086	0.0040	2.1500	0.0316*
	500	211.7198	(Intercept)	4.6442	0.2481	18.7180	<0.0001***
			Distance	-0.4294	0.1467	-2.9270	0.0034**
			FG	0.0021	0.0047	0.4560	0.6484
			PW	-0.1175	0.0361	-3.2580	0.0011**
			FG:PW	0.0014	0.0006	2.4550	0.0141*
	1000	212.7698	(Intercept)	4.4626	0.2491	17.9140	<0.0001***
			Distance	-1.0900	0.2164	-5.0380	<0.0001***
			FG	0.0048	0.0049	0.9830	0.3257
			Distance:FG	0.0086	0.0040	2.1500	0.0316*
Overall bee richness	250	145.3155	(Intercept)	3.2191	0.0654	49.2200	<0.0001***
			PW	-0.0301	0.0131	-2.2980	0.0216*
	500	141.4229	(Intercept)	4.1374	0.2716	15.2350	<0.0001***

			Bu	-0.0073	0.0039	-1.8950	0.0581
			Oc	-0.0147	0.0043	-3.4250	0.0006***
			PW	-0.0318	0.0088	-3.6130	0.0003***
	1000	146.7740	(Intercept)	4.1523	0.3005	13.8190	<0.0001***
			PW	-0.0275	0.0121	-2.2810	0.0225*
			Oc	-0.0147	0.0060	-2.4730	0.0134*
			Bu	-0.0141	0.0046	-3.0540	0.0023**
Small bee richness	250	139.9405	(Intercept)	2.9593	0.0748	39.5910	<0.0001***
			PW	-0.0288	0.0149	-1.9360	0.0529
	500	135.6789	(Intercept)	4.0737	0.3057	13.3250	<0.0001***
			PW	-0.0293	0.0098	-2.9760	0.0029**
			Oc	-0.0181	0.0049	-3.7120	0.0002***
			Bu	-0.0098	0.0044	-2.2200	0.0264*
	1000	138.6997	(Intercept)	3.7303	0.2948	12.6530	<0.0001***
			Oc	-0.0136	0.0064	-2.1350	0.0328*
			Bu	-0.0155	0.0055	-2.8040	0.0051**
Large bee richness	250	97.1951					
	500	94.4784	(Intercept)	1.8785	0.1321	14.2240	<0.0001***
			PW	-0.0396	0.0176	-2.2510	0.0244*
	1000	94.9779	(Intercept)	1.9446	0.1590	12.2280	<0.0001***
			PW	-0.0497	0.0230	-2.1620	0.0306*