Small wild bee abundance declines with distance into strawberry crops regardless of field margin habitat

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Abstract

The preservation of pollinator habitat on croplands in the form of hedgerows, wildflower strips, and natural and semi-natural areas can help maintain and enhance wild bee populations in agricultural landscapes. However, there have been few comparisons of the effectiveness of different types of field-margin pollinator habitat in maintaining bee diversity and pollination of the focal crops. We compared wild bee abundance, species richness and community composition between strawberry crops bordered by hedgerows, and those bordered by larger expanses of natural land (forests). Strawberry is an ideal crop in which to investigate pollinator export from field margins as the rows are covered with straw, which reduces habitat for ground-nesting bees within the crop; thus, most wild pollinators need to enter the crop from the margins. We sampled bees in six strawberry fields with hedgerow margins and six strawberry fields with forested margins of at least 200 m in length, using a paired design. We examined strawberry pollen deposition at regular intervals into the fields, and the magnitude of pollinator export from the field margins towards the centre of the crops. We found that bees as a group were no more species-rich or abundant in crops bordered by forests than in crops bordered by hedgerows, although

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large-bodied bees were more abundant in the former than the latter. Regardless of field-margin type, we found that small wild bee abundance declined significantly from the edge to the centre of the crop, but honey bee (*Apis mellifera* L.) and large-bodied bee abundance did not. Strawberry pollen deposition also did not decline with distance into the crop. Although previous work indicates that small wild bees are more effective (yield-increasing) pollinators of strawberry on a per-visit basis, their limited foraging ranges suggest they may only pollinate areas near the crop margins, given typical field sizes in our area.

Keywords: Bees; strawberry; crop pollination; cross-habitat spillover; hedgerow; forest

Introduction

The movement of organisms from one type of habitat to another (cross-habitat spillover) influences the composition of ecological communities (Ricketts et al. 2008; Blitzer et al. 2012). As natural lands are increasingly converted to croplands (Lambin & Meyfroidt, 2011), especially pollinator-dependent crops (Aizen et al. 2019), cross-habitat spillover becomes vital to the preservation of pollination services provided by wild animals in agricultural landscapes (Tscharntke et al. 2012). Wild bees are highly effective pollinators, and can increase the quantity and quality of certain crops relative to managed honey bee pollination (Garibaldi et al. 2013). As wild bees are largely unmanaged, the availability of suitable floral resources and nesting habitat influences their ability to persist in agricultural landscapes. Thus, the preservation of non-crop habitat components such as hedgerows, wildflowers, and natural and semi-natural areas can enhance wild bee populations (Kremen et al. 2004; Williams et al. 2015) and pollination services in croplands (Morandin & Winston 2006;

Holzschuh et al. 2012; Carvalheiro et al. 2012). Despite the cited importance of cross-habitat spillover, comparisons of pollinator diversity between different non-crop habitat types, and the impact of those habitats on crop pollination, are limited (Kohler et al. 2008; Morandin & Kremen 2013). Such comparisons are necessary to determine which types of field margins can maximize spillover from non-crop areas to crop fields and preserve a diversity of wild bees and pollination services in agroecosystems.

Although honey bees can travel several kilometres in search of food (Visscher & Seeley 1982), the foraging ranges of small-bodied bees (e.g., *Hylaeus* spp.) can be less than 150 metres (Greenleaf et al. 2007; Zurbuchen et al. 2010). Consequently, a lack of nesting habitat (e.g., dead wood, bare ground) in close proximity to crops can reduce the suitability of agroecosystems for many wild bee species, even those that readily forage on flowers of crop plants. In addition to nesting habitat, the availability of a diversity of floral resources in croplands is necessary to support bees with suitable pollen and nectar outside the period of crop bloom. On the other hand, the presence of a diverse floral community on the field margin could have a negative effect on crop pollination, if it results in transfer of heterospecific pollen to crop flowers. Further, if floral resources and nesting habitat are plentiful only at or beyond crop edges, bees (especially small-bodied bees) may prefer to remain within these areas instead of foraging further into the centre of the focal crop (Lander et al. 2011). Thus, the limited foraging range of small-bodied bee species and the availability of floral resources at crop edges has the potential to limit wild bees and pollination to areas near the crop perimeter (e.g. Kohler et al. 2008).

Strawberry (*Fragaria* × *ananassa* D.) represents an ideal crop for studying wild bee diversity and cross-habitat spillover. Strawberry flowers are an attractive pollen and nectar source for wild bee species, and the yield and quality of the crop has been known to increase with insect pollination (Chagnon et al. 1993; MacInnis & Forrest 2019; Klatt et al. 2014). Further, in conventional strawberry cultivation, the area between crop rows is covered with straw, and plastic mulches are increasingly used within crop rows (OMAFRA 2016). This lack of bare ground within strawberry crops may reduce the habitat available for ground-dwelling bees within the crop interior, and force most wild pollinators to nest beyond the crop margins. In this study, we investigated the influence of field-margin type on bee community composition in strawberry fields bordered by forests or hedgerows, the most common field perimeters in the study area. Hedgerows are narrow, linear strips of trees or shrubs, which generally contain fewer native plants than do large natural habitats (Roy & de Blois 2006; Schmucki & de Blois 2009). Given that forested areas contain larger expanses of undisturbed areas than hedgerows and may have bee communities that differ from those of agricultural areas (Harrison et al. 2019), we expected that first: bee community composition would differ between strawberry fields with forested and hedgerow margins, and that species richness and bee abundance would be less in hedgerow margins compared to forested margins. Second, with the lack of within-field nesting habitat and the limited foraging ranges of many (especially small) wild bee species, we expected that regardless of margin type, pollinators and pollination would decline with distance from strawberry field edges, with this effect being stronger on small-bodied bees. Third, we expected field margins containing abundant and/or diverse flowering plant communities would promote more heterospecific pollen deposition within the crop. By testing all three predictions, we can assess the benefits of different types of field-margins for crop pollination and wild bee communities.

Materials and methods

Study sites and sampling protocol

This research was conducted at twelve sites in eastern Ontario, Canada, within the Ottawa municipality, primarily east and south of the National Capital Region (45°25′29″N 75°41′42″W). The landscape consisted of a mix of forest, urban, and agricultural areas. Approximately 35% of the area was designated for agriculture, with corn, soy beans, cereal grains, and hay being the most common field crops (Smith, 2015). However, all sites were located on farms that also grew a variety of fruit crops, specifically raspberry, strawberry, and apple. The forest patches on farms were part of the Great Lakes–St. Lawrence forest region which is dominated by a mix of hardwoods (*Acer* spp., *Betula* spp.) and coniferous trees (*Pinus* spp., *Tsuga canadensis*).

Six of the study fields had at least one margin bordered by a forest, and six fields had at least one margin bordered by a hedgerow. Most of the other field margins were bordered by another crop, typically soy or corn in the seedling stage. Each hedgerow site consisted of a strawberry field bordered by a narrow strip of trees (< 20 m wide) at the crop edge, whereas forested sites had a patch of contiguous trees at least 200 metres wide. All fields were 200 m to 300 m in length (i.e., distance from the field margin of interest); the width varied but all fields had 100 m to 150 m from the sampling transects to the nearest edge containing natural habitat. All sites were at least 1.5 km apart, exceeding the foraging range of most wild bees in our area, except *Bombus* spp., which were excluded from analyses for this reason (21 individuals). We used a matched-pairs design with each forest site paired with the closest hedgerow site (Appendix: Fig. 1A). We also determined the amount of natural habitat within a 1.2-km radius of each site (including any natural field-edge habitat). This distance corresponds to the maximal foraging range of most bee species in our region, and the amount of natural and semi-natural land at this scale has been positively correlated to wild crop pollinator services (Kremen et al. 2004). We used crop inventory maps (AAFC 2016) and image analysis software (ImageJ) to calculate the total area of natural land within the 1.2-km radius. 'Natural land' included forested regions (coniferous, broadleaf, mixed wood and undifferentiated), shrublands, wetlands, and grassland meadows and ranged from 10 % to 37% across sites (see Appendix: Fig. 1B for sites with a high and low percentage of natural land). The area of hedgerows and forest patches adjacent to each field site was calculated using ImageJ and Google Earth© satellite images.

All bee sampling was done on warm (> 18 °C), sunny days with little wind (< 2 m/s) over the strawberry bloom period (May 22 – June 6, 2018); paired fields were sampled on the same day. At each field site, 15 m sampling transects within the field and parallel to the field edge were marked at 0 m, 50 m, 100 m and 150 m from the field margin (Fig. 1A and B). To avoid sampling too close to the opposite field edge, only fields that were 300 m long were sampled out to a distance of 150 m from the field edge (7 fields); those that were only 200 m long (5 fields) were sampled to a distance of only 100 m from the field edge. Timed aerial netting was done at each transect, wherein two observers walked the length of the transects for 15 minutes each (30 minutes total per transect) collecting all wild bees that were seen actively foraging on strawberry flowers. Timing was stopped for each collection event and resumed when the observer was ready to continue searching for bees. Managed honey bee hives were present within a 2-km radius of all field sites. The location and number of colonies varied by site, so honey bee abundance within each field was quantified by counting all honey bees seen foraging on strawberry flowers along the transects during sampling periods.

Each site was sampled twice over the blooming period, once in the morning (9h00 to 12h00) and once in the afternoon (13h00 to 15h00). This resulted in a total of 240 minutes of collecting at fields that were 300 m long, and 180 minutes at fields that were 200 m long. All wild bees were identified to species using Ascher and Pickering (2018), two dichotomous keys (Gibbs, 2011; Gibbs et al., 2013), the assistance of an expert in bee taxonomy (see Acknowledgements), and the reference collection at the Biodiversity Centre of the Université de Montréal; voucher specimens are housed at this collection. We also measured the inter-tegular distance (ITD) of each bee species, averaged over 10 individuals (when available). ITD is the distance in millimetres between the two wings and is correlated with body size and foraging range (Greenleaf et al. 2007). Small bees were classified as those with an ITD of ≤ 2.0 mm and large bees were those with an ITD > 2.0 mm, following Greenleaf et al. (2007) and Benjamin et al. (2014). Greenleaf et al. (2007) suggested that bees with an ITD < 2mm have a foraging range of 200–500 m, and bees with an ITD > 2 mm were typically able to forage much further; Benjamin et al. (2014) found differences in bee responses to land uses at a similar size threshold.

After the final sampling round at each site was complete, we collected 10 flowers in the male phase at random along each transect for pollen deposition analyses (*Fragaria* × *ananassa* D. is typically protogynous, so we assumed that pollen receipt was complete for male-phase flowers). On each of the flowers collected, the stigmas (10 minimum) at the apex of each receptacle were carefully removed with a scalpel and squashed on a microscope slide with a small cube of fuchsin gel (Dafni & Kevan 2005). We counted the number of strawberry and non-strawberry pollen grains at 400x magnification on the first 10 stigmas encountered under the microscope. The total pollen count was divided by 10 to determine the average number of strawberry and non-strawberry pollen grains per stigma at each distance (0 m, 50 m, 100 m, 150 m) from the field margin to the crop centre.

To determine whether floral diversity differed between field-margin types, floral density and richness were also measured at the field margin once at each site, during strawberry bloom. We placed 20 1-m2 quadrats along and within the hedgerow or forest at approximately 5-m intervals, parallel to the field edge, and counted all open flowers inside the quadrats. Ten quadrats were placed at the edge of the forest or hedgerow just beyond the tree line, and 10 quadrats were placed at 5 m inside the hedgerow or forest. For plants with many small, compact flowers such as *Cornus alternifolia*, each inflorescence was counted as one flowering unit (as in Fründ et al. 2010). All flowering plants were identified to species using Peterson and McKenny (1996). We also measured the abundance of all open strawberry flowers within the crops using 15 1-m2 quadrats placed along the length of the 15-m transects.

Statistical analyses

Field margin habitat and the crop bee community

Samples were pooled across transects and sampling periods and abundance and diversity metrics were calculated for the bee communities of each site. The bee communities at fields with forested and hedgerow margins were compared using non-metric multidimensional scaling, with Bray-Curtis distances (NMDS, package: vegan, Oksanen et al. 2019). A four-axis solution was used as it lowered the final stress below 0.10 and additional axes resulted in little improvement. To compare species richness for a given number of specimens, taxon sampling curves (rarefaction) were generated for all sites (package: vegan). We constructed generalized linear mixed-effect models (GLMMs, package: lme4, Bates et al. 2015) to compare total wild bee abundance, the abundance of small and large-bodies bees separately, and species richness between field-margin types. For each model, field-margin type was a fixed effect, and pair ID was a random effect. To account for overdispersion, a negative binomial distribution was used for the abundance models. A Gaussian distribution was used for species richness models with the rarified number of species as the response variable (abundance differed across sites despite consistency in sampling effort). Comparisons of bee diversity (Shannon index) between field-margin types were done in the same manner using LMMs. Field-margin flower data were pooled across quadrats at each site and we compared floral abundance and diversity between margin types with paired t-tests.

To further examine the responses of individual bee species to each field-margin type, we modeled changes in the relative abundance of the 20 most abundant bee species using multinomial models. The models were fitted using the package ‘mvabund’ (Yang et al. 2019), with the function ‘manyglm’. This function fits a separate generalized linear mixed model to each species in the abundance matrix. The abundance of each species was the response variable and field-margin type and distance were fixed effects; site ID nested within pair ID was included as a random effect in all models. We calculated the influence of predictor variables on individual species using likelihood-ratio tests.

Pollinator and pollen export

To examine the influence of distance into the crop and field-margin type on wild bee abundance, we constructed negative binomial GLMMs with distance into the field (continuous variable) and field-margin type as fixed effects, and site ID nested within pair ID as a random effect. In addition, we tested whether bee spatial distributions through the fields were affected by bee body size with a gamma GLMM. Here, average ITD in mm was the response variable, distance was a fixed predictor, and site ID nested within pair ID was a random effect. In addition, we tested the effect of distance on the number of bees in each size class separately (small or large, i.e. ITD $\leq$ or $>$ 2 mm) with negative binomial GLMMs. The abundances of small and large bees were response variables, distance from the field margin was a fixed predictor, and site ID nested within pair ID was included as a random effect. The influence of distance into the field on honey bee abundance was analysed with a separate negative binomial GLMM because the location of honey bee colonies varied by site and was not always at the natural habitat edge.

We also constructed LMMs to test for differences in strawberry flower abundance and quantities of strawberry pollen on stigmas in relation to field-margin type and distance into the field. Field-margin type and distance from the field edge were fixed effects, and site ID nested within pair ID was a random effect. For the pollen models, the average number of strawberry pollen grains per stigma was the response variable. To examine heterospecific pollen deposition with distance into the field, we used a zero-inflated negative binomial GLMM, package: pscl (Zeileis et al. 2008). The average number of heterospecific pollen grains per stigma was the response variable, distance from the field edge was a fixed numerical predictor and site ID nested within pair ID was included as a random effect.

Results

In total, we collected 784 individual wild bees comprising 70 species in 15 genera, and observed 1393 honey bee individuals foraging on strawberry flowers (see Appendix A: Table 1 for full species list). Only seven male bees were collected in total and were not included in analyses, as they do not collect pollen or depend on nesting habitat. Likewise, the five parasitic individuals found (*Nomada* spp., *Sphecodes* spp., see Appendix A: Table 1) were not included in analyses since their presence is more dependent on host species than habitat characteristics (Williams et al. 2010). Honey bees were not included in diversity or body size analyses.

Field edges contained 18 species of plants that were in flower during sampling. Hedgerow margins contained five flowering shrubs and two tree species. Forested margins contained four tree species and two shrubs. Both field-margin types included the same six flowering herbaceous species (see Appendix A: Table 2 for full flowering plant species list). The average number of flowering plant species in the field margin did not differ significantly between forested and hedgerow margins, nor did floral abundance (Table 1). Strawberry flower abundance did not change with field-margin type (Table 1) or with distance into the field ($\chi 2 = 1.03$, $p = 0.316$). On average, there was more natural land at forested fields than hedgerow fields within a 1.2-km radius (Table 1). The area of natural land directly adjacent to the fields was correlated with the amount of natural land within a 1.2-km radius of the fields (rp = 0.51).

Field margin habitat and the crop bee community

Overall wild bee abundance did not differ between field-margin types among the sites examined (Table 1). Similarly, species richness and Shannon diversity did not differ between fields bordered by forests and fields bordered by hedgerows (Table 1).

The ordination plot indicated that the bee communities did not differ between field-margin types, as there was complete overlap between ellipses (Fig. 2A). The hedgerow rarefaction curves were of similar shape to those of the forested sites, with the exception of two forested sites that contained fewer, more abundant species (Fig. 2B). Of the 20 most abundant bee species, only three differed significantly in abundance between field-margin types: There were more *Agapostemon sericeus, Andrena carlini*, and *Augochlorella aurata* individuals at forested sites (see Appendix A: Table 3). There were also more large bees (ITD > 2 mm) at forested sites than hedgerow sites, but small bee (ITD ≤ 2 mm) abundance was not affected by field-margin type (Table 1).

Pollinator and pollen export

Honey bee abundance did not decline significantly with distance into the crop (Table 2, Fig. 3A). The abundance of wild bees decreased with distance consistently across field-margin types (Table 2; Fig. 3B). This decline was driven by a decrease in the number of small bees, as ITD increased significantly with distance towards the crop centre ($\chi2 = 4.24$, $p = 0.039$, Fig. 3C). When categorized by body size, small bee abundance (ITD < 2 mm) declined with distance, but large bee abundance did not (Table 2). This general decline of small bees with distance was also observed in the analyses of the most abundant species, with 6 of 8 small-bodied species declining with distance (see Appendix A: Table 3). At 150 m into the field, the number of small bees was 44% less than at the field edge. The abundance of large wild bees was not influenced by distance into the crop (Table 2).

The amount of heterospecific pollen deposited within strawberry flowers was negligible, and was not significantly affected by field-margin type ($\chi2 = 0.73$, $p = 0.392$) or distance into the field (Table 2). This suggests that bees foraging in the field margins did not transport a significant amount of non-strawberry pollen into the crop. Strawberry pollen deposition was not affected by distance from the field edge (Table 2, Fig. 3D).

Discussion

Wild bees are effective crop pollinators that rely heavily on the habitat and floral resources in croplands and surrounding natural and semi-natural areas for survival (Garibaldi et al. 2011). Contrary to our expectations, the large area of natural land provided by forested field margins did not increase the richness and abundance of the bee communities throughout strawberry crops. Fields bordered by forests did not have more abundant or species-rich wild bee communities than fields bordered by narrow strips of natural land (hedgerows). Similar results have been found in cranberry (*Vaccinium macrocarpon* Ait.) agroecosystems northeast of our study area (Gervais et al. 2017).

Our unexpected results may be due to the similarity of floral resources available among field margin types, or the quality of floral and nesting resources within the field margins. Forests may not provide the ideal resources for most wild bees (Winfree et al. 2007; Mandelik et al. 2012), and the hedgerows at our study sites were not planted specifically to support wild pollinators with habitat or floral resources (G.M. pers. communication with growers). Bee abundance and species richness have been positively correlated with the abundance and richness of flowering plant species (Potts et al. 2003; Sutter et al. 2017). Although we did not measure floral resources deep within the forest, the diversity of floral resources near the field margin did not differ between forested and hedgerow sites. As June-bearing strawberries bloom early in the season, bee species richness might have increased at our study sites as more flowering plants and bees emerged, and differences between field-margin types might have appeared. However, this study was focused on wild pollinator services to strawberry crops, so plant or bee species that emerged after our sampling period (which encompassed the entire strawberry bloom) would not have influenced strawberry pollination. Most bee species found at our sites were also regionally common species. Wild bee communities in agroecosystems often consist of common species that are well-adapted to live near crops, and can persist despite declines in surrounding natural areas or flowering plant diversity (Kleijn et al. 2015). The wild bees in this system may have been more reliant on crop flowers than on floral resources in the surrounding landscape.

The similarity of the bee communities at forested and hedgerow sites could also have been due to larger-scale landscape composition being relatively similar between the two site types. When crops are grown within a mix of natural and uncultivated land, bee diversity and pollination services within crop fields are higher than in simplified landscapes (Ricketts et al. 2008; Carvalheiro et al. 2011, Shackelford et al. 2013), revealing the importance of the broader landscape context for local bee communities. Local habitat features like hedgerows may not influence pollinator populations above the background influence of heterogeneity in complex landscapes, as they do in more simplified landscapes (Tscharntke et al., 2012). As per Tschartke et al. (2012), the majority of our study sites (8 of 12) would be considered complex, as they contained at least 20% natural, or non-crop, land within a 1.2-km radius (see Appendix: Fig. 1B). The relative complexity of the landscape at this scale may explain why we did not find a difference in bee communities between crop margin types at the field scale.

While the overall abundance of wild bees was unaffected by field-margin type, the abundance of large bees was higher in fields surrounded by forests rather than hedgerows. Studies in other systems have found that populations of large-bodied bees are affected by the composition of the landscape at larger spatial scales than small-bodied bees (Benjamin et al. 2014, Warzecha et al. 2016), which makes sense in light of the greater foraging ranges of larger-bodied bees (Gathmann & Tscharntke 2002; Greenleaf et al. 2007). Thus, small bees foraging within the strawberry crops may have only been those nesting in areas close to the field margins, whereas large bees would have the ability to nest in and travel further from the forest interiors. However, forest-margin fields also had more overall natural habitat in our study, so the effects of field-margin type on large-bodied bees cannot be separated from effects of broader landscape composition.

Although we predicted that strawberry fields with forested margins would host more species-rich and abundant bee communities due to their larger area of adjacent natural habitat, the distance from the field edge had more of an effect than field-margin habitat on the crop bee community. This suggests that landscape configuration, especially field size, may be more important than natural land area for preserving wild bee richness, abundance, and pollination services within crops (see also Fahrig et al. 2015; Smith et al. 2020). If small wild bees increase cross-pollination and strawberry yield compared to managed honey bees (as in MacInnis & Forrest 2019), the decrease in abundance of small bees toward the centre of crop fields has the potential to reduce the quality of pollination services to large (> 200 m long) strawberry fields. The larger bee species (e.g. *Halictus rubicundus, Agapostemon* spp., *Andrena* (*Melandrena*) spp., see Appendix A: Table 1) benefited from forested margins, were unaffected by distance from the field margin and may be able to provide wild pollination services further into strawberry fields. However, the number of honey bees observed visiting flowers in field interiors was more than double that of large wild bees. Since strawberry pollen deposition did not decline with distance into the field, this suggests that honey bees were likely providing more pollination than wild bees, and are necessary to ensure pollination of large strawberry fields in our region.

Conclusions

Spillover of insects or other animals from natural or semi-natural habitats into agroecosystems can be beneficial for a suite of ecosystem services, including pest control and pollination. Presently, the provision of pollinator habitat is not a requirement on Canadian farms, and the choice to preserve or remove potential pollinator habitat belongs to the growers. For strawberry, wild bee pollination can increase berry size and quality; thus, increases in yield may justify the costs of taking a portion of land out of production for pollinator habitat. In this study, the limited foraging range of small-bodied bees and a lack of within-crop nesting habitat most likely limited wild bee abundance within the crop. Although several studies have found that wild pollinator populations increase with the amount of natural land in agricultural landscapes, further work is needed to determine how natural habitat needs to be distributed in agricultural lands to sustain wild pollinator diversity and pollination services in crops. It is also important to note that simple measures of species richness and abundance cannot detect differences in the species composition of bee communities or the effects of landscape characteristics on individual species or functional groups (e.g. large and small bees). Measuring species-specific responses to habitat type, amount, and configuration is vital to preserve and enhance bee diversity and ecosystem services in human-dominated landscapes, and to reduce dependency on managed honey bees.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Figure 1 A,B

Fig. 1. Sampling design and field-margin types. (A) Strawberry field with hedgerow margin and (B) strawberry field with forested margin. Sampling transects and distances from the field margin are marked in white.

Figure 2 A,B

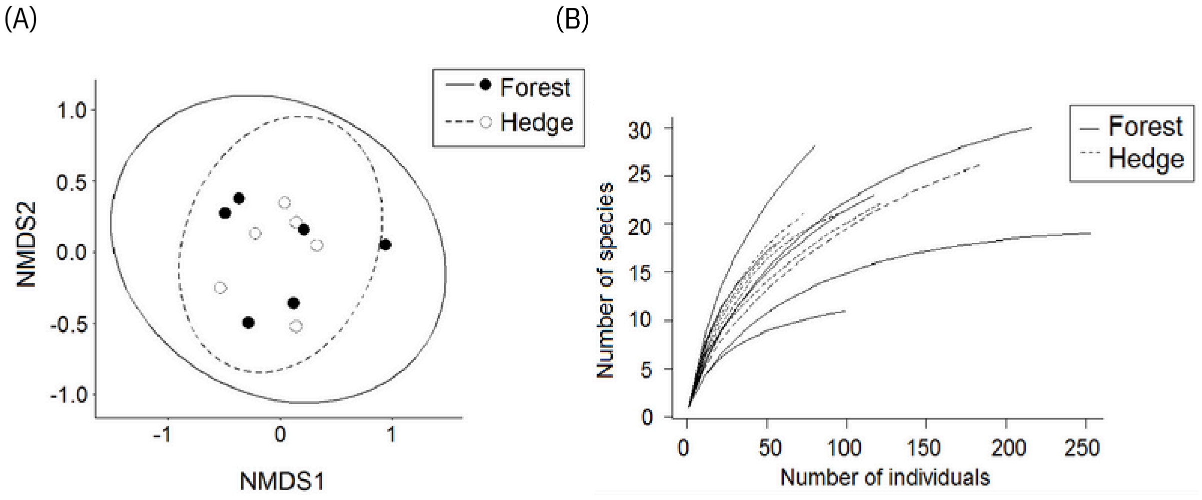


Fig. 2. Bee community composition at strawberry fields with forested and hedgerow field margins. (A) Non-metric multidimensional scaling of the 12 sites based on species abundance (Bray-Curtis dissimilarities). Hedgerow sites are represented by open circles and the dotted ellipse. Forested sites are filled circles surrounded by a solid ellipse. (B) Rarefaction curves for the 12 sites; forested sites are solid lines, hedgerow sites are dotted lines.

Figure 3 A,B,C,D

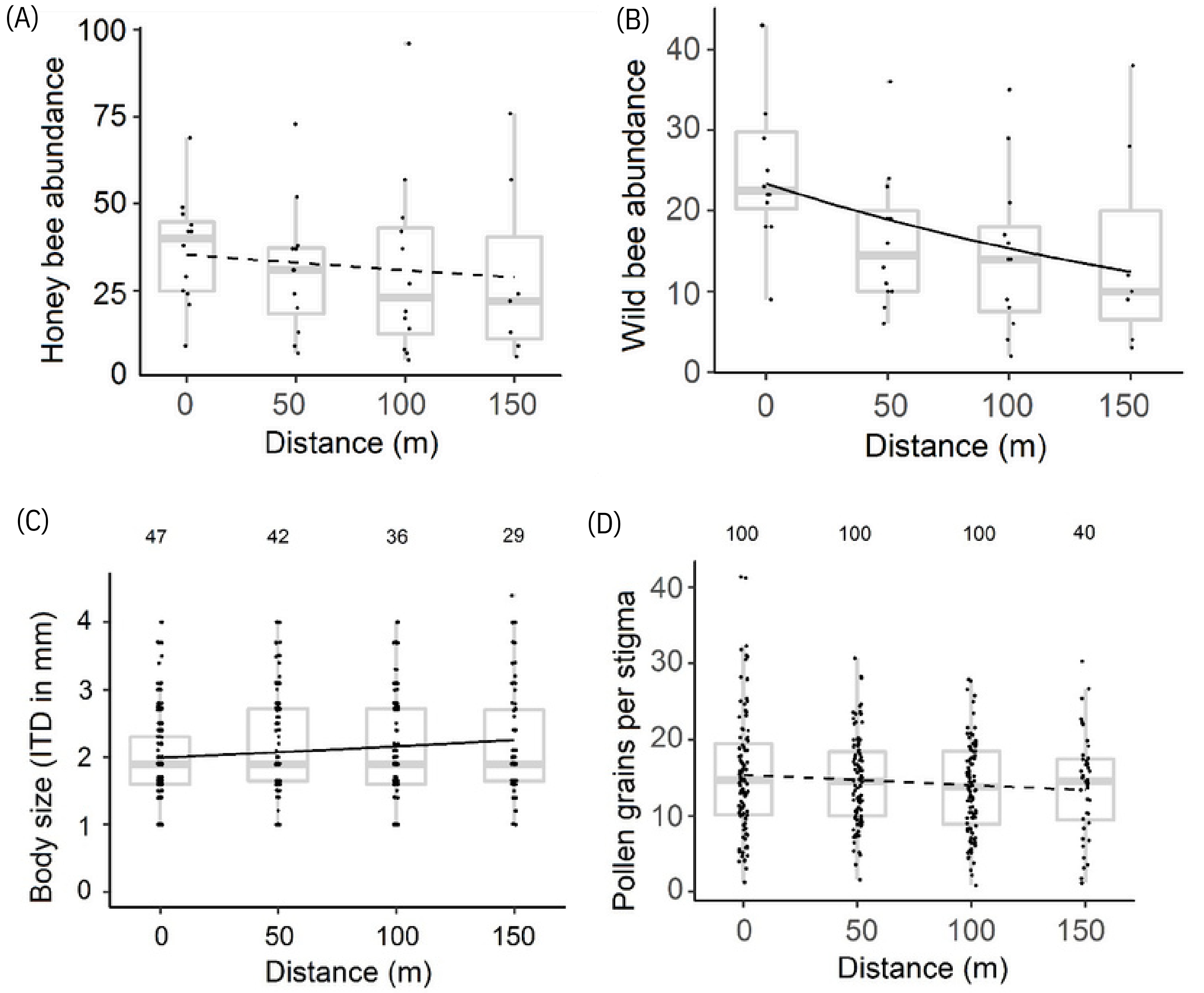
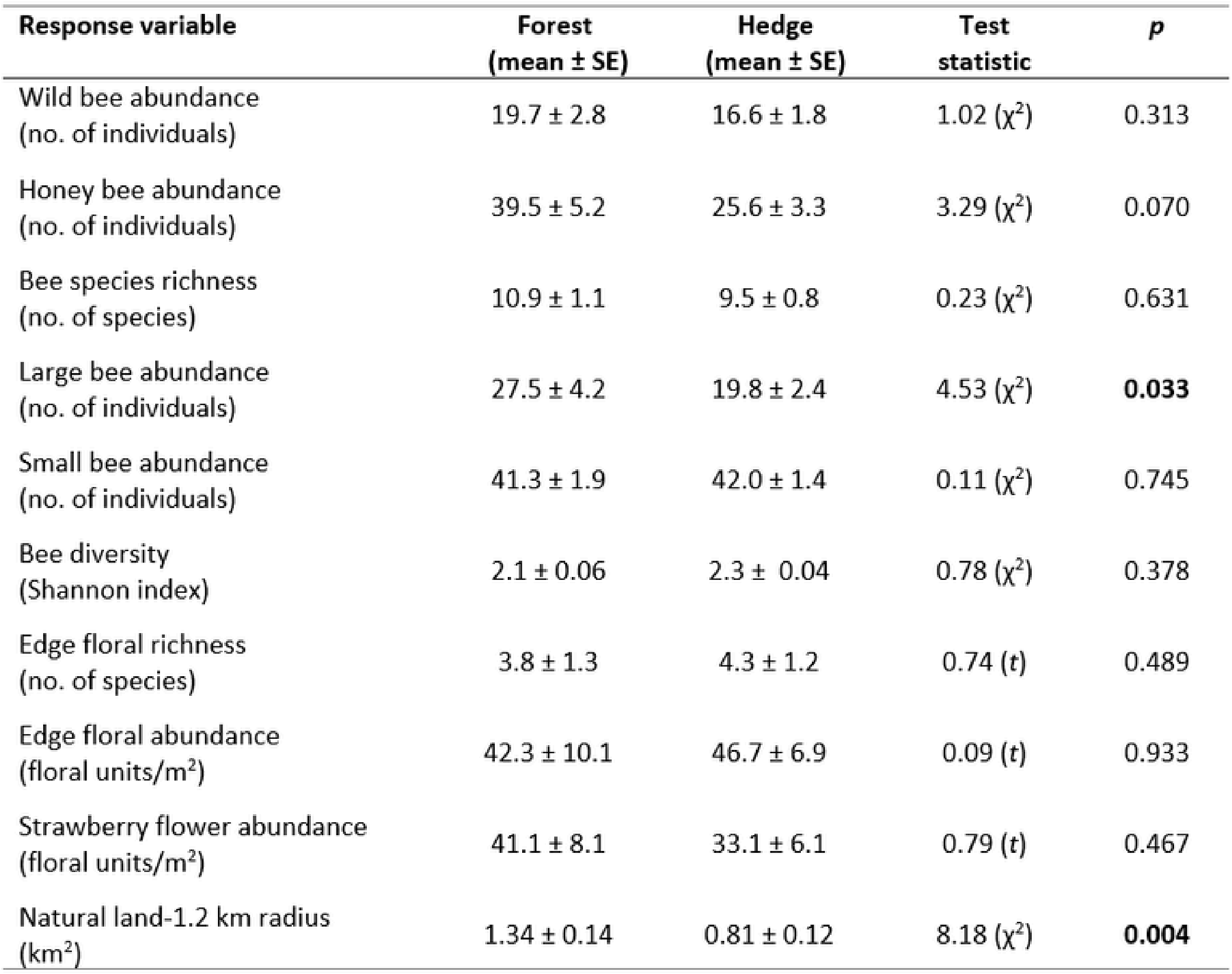


Fig. 3. (A) Honey bee abundance in relation to distance from the field edge. Points represent the number of honey bees found foraging at each distance from the field margin at each of the 12 sites. (B) Wild bee abundance in relation to distance from the field edge. Points represent the number of wild bee individuals found foraging on strawberry flowers at each of the 12 sites. (C) Body size of wild bees with distance from the field edge. Points are the ITD values for each bee species at each distance from the field edge over the 12 sites. Sample size is listed above. Size was measured as the distance between the tegula of representatives of each bee species. (D) The number of strawberry pollen grains per stigma at the field edge inward to 150 m for six fields, and to 100 m for four of the fields. Sample size is listed above. All grey boxes show the interquartile range, the median is indicated by a horizontal line, and whiskers indicate the data range. Solid lines are the regressions from the generalized linear mixed models. Dotted lines are non-significant regression lines. All points are jittered horizontally for clarity.

Table 1

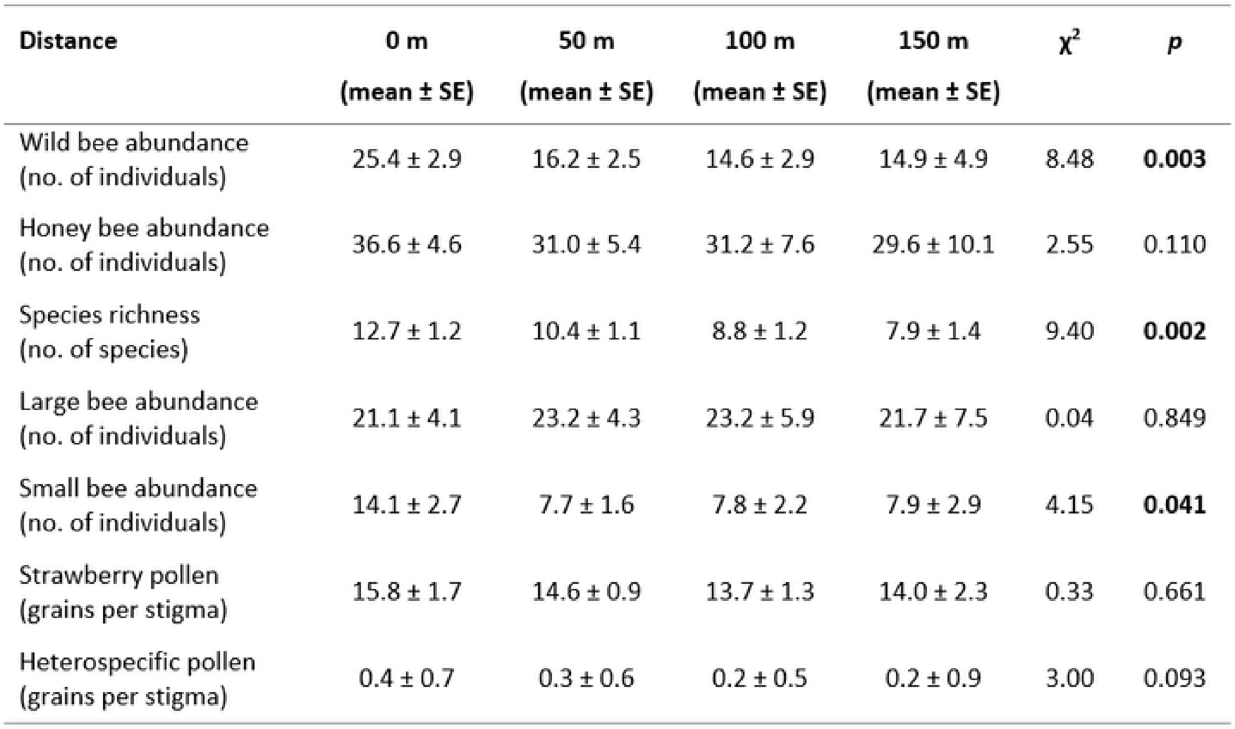
Table 1. Average bee and floral diversity in strawberry fields bordered by forests and hedgerows and the results of the comparisons of each diversity metric. Bee abundance was based on a total of 240 minutes of collecting at large (300 m) fields and 180 minutes at small (200 m) fields. The rarefied number of species was based on 40 individuals, the lowest number of individuals found at any site. N = 6 each for forested and hedgerow sites. $\chi 2$ indicates the Wald chi-squared test statistic, and t indicates a t-test was used for comparisons. p is the significance.



Response variable	**Forest (mean ± SE)**	**Hedge (mean ± SE)**	**Test statistic**	***p***
Wild bee abundance (no. of individuals)	19.7 ± 2.8	16.6 ± 1.8	1.02 (χ^2)	0.313
Honey bee abundance (no. of individuals)	39.5 ± 5.2	25.6 ± 3.3	3.29 (χ^2)	0.070
Bee species richness (no. of species)	10.9 ± 1.1	9.5 ± 0.8	0.23 (χ^2)	0.631
Large bee abundance (no. of individuals)	27.5 ± 4.2	19.8 ± 2.4	4.53 (χ^2)	**0.033**
Small bee abundance (no. of individuals)	41.3 ± 1.9	42.0 ± 1.4	0.11 (χ^2)	0.745
Bee diversity (Shannon index)	2.1 ± 0.06	2.3 ± 0.04	0.78 (χ^2)	0.378
Edge floral richness (no. of species)	3.8 ± 1.3	4.3 ± 1.2	0.74 (*t*)	0.489
Edge floral abundance (floral units/m^2)	42.3 ± 10.1	46.7 ± 6.9	0.09 (*t*)	0.933
Strawberry flower abundance (floral units/m^2)	41.1 ± 8.1	33.1 ± 6.1	0.79 (*t*)	0.467
Natural land-1.2 km radius (km^2)	1.34 ± 0.14	0.81 ± 0.12	8.18 (χ^2)	**0.004**

Table 2

Table 2. Summary of bee diversity and pollen deposition as functions of distance from field margins in strawberry fields bordered by hedgerows and forests (N=12). Large bees had an inter-tegular distance of greater than 2 mm, small bees had an inter-tegular distance of less than or equal to 2 mm. χ2 is the value of the Wald chi-squared test statistic. p is the significance value. Significant relationships are indicated in bold.



Distance	**0 m (mean ± SE)**	**50 m (mean ± SE)**	**100 m (mean ± SE)**	**150 m (mean ± SE)**	**χ^2**	***p***
Wild bee abundance (no. of individuals)	25.4 ± 2.9	16.2 ± 2.5	14.6 ± 2.9	14.9 ± 4.9	8.48	**0.003**
Honey bee abundance (no. of individuals)	36.6 ± 4.6	31.0 ± 5.4	31.2 ± 7.6	29.6 ± 10.1	2.55	0.110
Species richness (no. of species)	12.7 ± 1.2	10.4 ± 1.1	8.8 ± 1.2	7.9 ± 1.4	9.40	**0.002**
Large bee abundance (no. of individuals)	21.1 ± 4.1	23.2 ± 4.3	23.2 ± 5.9	21.7 ± 7.5	0.04	0.849
Small bee abundance (no. of individuals)	14.1 ± 2.7	7.7 ± 1.6	7.8 ± 2.2	7.9 ± 2.9	4.15	**0.041**
Strawberry pollen (grains per stigma)	15.8 ± 1.7	14.6 ± 0.9	13.7 ± 1.3	14.0 ± 2.3	0.33	0.661
Heterospecific pollen (grains per stigma)	0.4 ± 0.7	0.3 ± 0.6	0.2 ± 0.5	0.2 ± 0.9	3.00	0.093