



White clover pollinators and seed set in relation to local management and landscape context

Veronica Hederström^{a,*,1}, Silvia Johansson^a, Maj Rundlöf^b, Glenn P. Svensson^b,
Olle Anderbrant^b, Ola Lundin^c, Mattias C. Larsson^{a,2}, Åsa Lankinen^{a,2}

^a Swedish University of Agricultural Sciences, Department of Plant Protection Biology, Alnarp SE-230 53, Sweden

^b Lund University, Department of Biology, Lund SE-223 62, Sweden

^c Swedish University of Agricultural Sciences, Department of Ecology, Uppsala SE-750 07, Sweden

ARTICLE INFO

Keywords:

Bee abundance
Bee species richness
Farming practice
Landscape land use
Seed set
Trifolium repens

ABSTRACT

Bees are declining, which is worrisome since they both have intrinsic conservation value and play a major role as pollinators in both natural and managed ecosystems. Land use change and lack of suitable habitats are often suggested as driving forces of bee decline. To propose mitigation measures to halt bee decline, it is important to understand how land use relates to bee abundance and diversity, and to explore consequences for their provision of pollination services. White clover, *Trifolium repens*, is an outcrossing mass-flowering crop, which could serve as an abundant, although ephemeral, food resource for bees. We investigated how the bee community in 39 fields of white clover grown for seed, related to local field management (organic, conventional without insecticides and conventional with insecticides) and landscape context (proportion semi-natural land), and how this pollinator community related to white clover seed set. The honey bee, *Apis mellifera*, was the most commonly observed bee species, and two generalist bumble bee species, *Bombus terrestris* and *B. lapidarius*, were the subsequently most common. We observed fewer non-*Apis* bees, and a lower bee species richness in organic white clover seed fields compared to conventional fields independent of insecticide treatment. Bee species richness in both conventional and organic fields were positively related to the proportion of semi-natural land in the landscape, likely because of a larger species pool in such landscapes. Initial seed set in immature inflorescences was positively related to bee abundance, whereas final seed set in mature inflorescences was unrelated to bee abundance, possibly as a consequence of seed-eating weevils consuming a large proportion of the seeds. We conclude that both bee visitation and seed set in white clover benefit from conventional management and that landscapes rich in semi-natural habitats will make future crop production more resilient. The observed positive relationship between bee abundance and initial seed set suggests that if we can mitigate pest impacts and increase bee abundance in clover seed fields, the final seed yield can be increased. Thus, bee decline should be considered and mitigated both to maintain biodiversity in general and for crop seed production specifically.

1. Introduction

The sexual reproduction of many plants is dependent on animal-mediated pollination (Ollerton et al., 2011), and plant-pollinator interactions are essential for seed production in both natural and human-managed ecosystems (Kearns et al., 1998). Insects, and among them bees, play a major role as animal pollinators (Klein et al., 2007; Abrol, 2012; Rader et al., 2016). Abundance and distribution of

pollinators in agricultural landscapes are to a high degree driven by land use (Ricketts et al., 2008; Carre et al., 2009; Goulson et al., 2010; Potts et al., 2010; Kennedy et al., 2013), including availability of flowering crops and wild plants as food resources as well as availability of undisturbed habitats for nesting and hibernation (Kennedy et al., 2013; Liczner and Colla, 2019). Pollinators need pollen and nectar from suitable flowers during their whole activity season (Carvell et al., 2017), i.e. crops flowering only part of the season cannot provide sufficient food

* Corresponding author.

E-mail address: veronica.hederstrom@cec.lu.se (V. Hederström).

¹ Present address: Lund University, Centre for Environmental and Climate Science, Lund SE-223 62, Sweden.

² Authors contributed equally.

resources for species with longer activity periods. In intensively cultivated landscapes with little semi-natural areas there is often a lack of complementary food resources, e.g. from wild flowers or a high diversity of flowering crops, and a lack of nesting sites and material (Kennedy et al., 2013; Vanbergen et al., 2013). Increased coverage of large and homogenous agricultural fields is linked to declines in bee species richness (Senapathi et al., 2015). Likewise, bee species richness decreases with reduced cover of semi-natural habitats, since such habitats contribute with both bee nesting habitats and food resources (Öckinger and Smith, 2007; Ricketts et al., 2008; Garibaldi et al., 2011).

Farmland managed organically without inorganic fertilizers or synthetic pesticides supports higher levels of biodiversity compared to conventionally managed farmland (Batáry et al., 2011; Tuck et al., 2014; Lichtenberg et al., 2017), including higher abundance and species richness of crop-visiting bees (Kennedy et al., 2013). Inorganic fertilizers and herbicides can reduce plant diversity and thereby reduce food resources for insects (Kleijn et al., 2009; Schmitz et al., 2014). An increased biodiversity supported by organic farms may not necessarily translate into more visits to flowers in a pollinator dependent crop, depending on species' flower preference, but an increased pollinator diversity has been shown to increase production in some crops (Malling and Gratton, 2015; Alomar et al., 2018). Local field management can interact with the landscape context in its influence on biodiversity (Batáry et al., 2011; Kennedy et al., 2013). For example, differences in bee abundance and species richness between organic and conventional farmland increase with the proportion of arable land, used as a proxy for landscape context, in the surrounding landscape (Holzschuh et al., 2007; Rundlöf et al., 2008). Thus, to understand the influence of organic farming on mobile organisms such as bees, it is important to also consider the landscape context.

Clover is a valuable crop in many parts of the temperate world, both for animal feed and as green manure (Baker and Williams, 1987). White clover, *Trifolium repens*, is completely dependent on insect pollination to set seed, and is pollinated by honey bees, bumble bees and solitary bees (Free, 1993). Mass-flowering white clover fields for seed production have a protracted flowering period, starting in early June and lasting until late July in southern Sweden (Lundin et al., 2017), and could serve as an abundant food resource for bees during this time (Harris and Ratnieks, 2022). Abandonment of clover leys as soil fertilizers with the introduction of inorganic fertilizers has been suggested to play an important role in the decline of bumble bees during the last century (Goulson et al., 2005; Carvell et al., 2006; Kleijn and Raemakers, 2008; Bommarco et al., 2012). With reports of a declining insect fauna in general (Conrad et al., 2006; Hallmann et al., 2017; Wagner et al., 2021) and a declining bee fauna in particular (FAO, 2008; Bartomeus et al., 2013; Senapathi et al., 2015; Zattara and Aizen, 2021) it is of great concern to explore how agricultural management and land use relate to bee community composition and the pollination services that bees provide.

Here we use data from 39 white clover fields over three years to explore effects of local field management and landscape context on the pollinator community, and links to seed set. In a previous study we found that wild bee densities were higher in insecticide-treated parts of conventional white clover seed fields compared to in organic fields, but that pollinator abundance was unrelated to the final seed set (Lundin et al., 2017). The seed-eating weevil pest *Protapion fulvipes* was instead identified as the main cause of low seed set. Because the role of pollinators for seed set may be masked when seed-eating weevils consume a large proportion of the seeds, as shown in Lundin et al. (2017), we here aimed to also quantify seed set at an earlier crop stage, i.e. before the major pest damage. To co-manage pests and pollinators (i.e. implement integrated pest and pollinator management, IPPM (Biddinger and Rajotte, 2015; Egan et al., 2020; Lundin et al., 2021)) it is important to understand the interrelation and factors that drive both groups of organisms and their relation to crop yield (Knapp et al., 2022). Compared to the previous study (Lundin et al., 2017), we here expand to include

additional years of data, relate bee variables to landscape context rather than just local management, and distinguish the relation between the bee pollinator community and initial vs final seed set, respectively. We ask the following specific questions:

- i. Is the bee pollinator community in white clover seed fields related to local field management, landscape context and their interaction?
- ii. Are the initial or final seed sets in white clover fields related to the bee pollinator community and the local field management?

2. Methods

2.1. Study system

Our system consisted of white clover grown for seed production and, in line with the specific study questions, the crop plant and the seed production may be impacted by both pests and beneficial organisms which may respond to local management and landscape context similarly or differently (Lundin et al., 2021, Knapp et al., 2022). We differentiated three types of local management: organic without any pesticides, conventional without insecticides or conventional with insecticides - indicating an increasing reliance on pesticides for pest control and possibility for non-target effects on beneficial insects. Landscape context is here quantified as the proportion of arable or semi-natural land and the bee community as bee abundance, species richness and diversity.

We conducted pollinator surveys during three consecutive years (2014–2016) in a total of 39 white clover seed fields in southern Sweden (12, 14, 13 fields in 2014, 2015, 2016, respectively, Fig. 1). The white

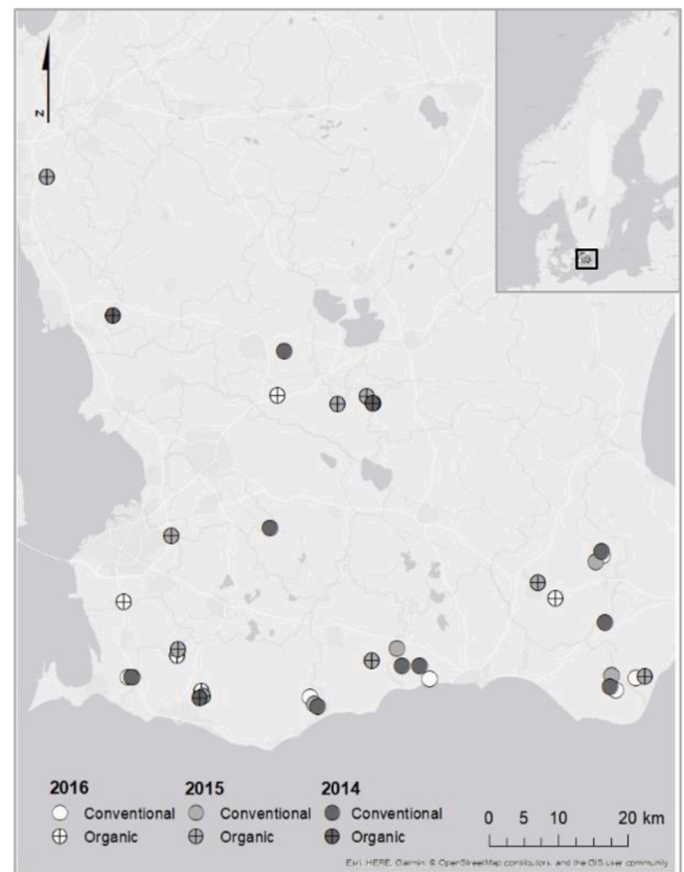


Fig. 1. Map of Scania (and its place in Scandinavia in upper right corner) with study fields in 2014 (dark grey), 2015 (light grey) and 2016 (white). Open circles represent conventional fields and circles with a cross organic fields.

clover fields were commercially grown for seed production, of varying size, cultivar and management practice (20 conventionally managed with pesticides, including plots excluding insecticides (see Section 2.2), and 19 organically managed without pesticides) (Table A1). Organic fields had a larger size range (5–52 ha, mean = 20 ha) than conventional fields (5–24 ha, mean = 11 ha) (Table A1). Because field size may influence pollinator abundance and diversity (Hass et al., 2018), we accounted for this by including this variable in the statistical analyses (see below). The distance between fields was at least 2.1 km within each year. We made sure no other clover field was within this distance. Other mass flowering crops usually grown in the area (oilseed rape and red clover) do not flower at the same time as white clover. We did not account for cultivar differences, however, an earlier study suggests that e.g. nectar production is similar among white clover cultivars (Norris, 1985). Honey bee, *Apis mellifera*, hives were placed by the farmers at 36 of the 39 fields, thus three fields were without added honey bees, and for four fields we got no information on the stocking density from the farmers (Table A1). Commercial bumble bee, *Bombus terrestris*, colonies were placed by the farmers at 11 of the 39 fields (Table A1). *B. terrestris* is native to Sweden, and it is the most common wild bumble bee species in the investigated area. Note that the data on bee abundance from 2014 are the same as in Lundin et al. (2017), but here we also use data from 2015 to 2016.

2.2. Pollinator surveys

Pollinator surveys were modified Pollard transect walks (Pollard, 1975) along two 50 × 1 m transects in parallel to and 8–12 m from the field border. In conventional fields, which in contrast to organic fields are treated with agrochemicals, one transect was situated within a 24 × 50 m control plot excluded from insecticide treatment, and the other transect in an adjacent plot treated as the rest of the field. Both transects in organic fields were managed as the rest of the field. This setup, also used in previous clover management-focused studies (Lundin et al., 2012, 2017; Rundlöf and Lundin, 2019; Knapp et al., 2022), enabled us to not only compare organic vs. conventional management, but also effects of the insecticide treatment within conventional fields.

Pollinator surveys were conducted on three occasions during bloom in each transect (2014, June 9 – July 17; 2015, June 20 – July 22; 2016, June 6 – July 12). To avoid bias due to diurnal bee activity patterns, the same field was visited at different times of day among survey occasions. On the majority of occasions, we collected pollinator data on days with temperatures of at least 17°C, no more than moderate wind (<8 m/s), and with at least 30 % sun and no rain. Exceptions were made in 8 out of 234 surveys, which were conducted during temperatures of 15–16°C. During a survey, all flower visiting bees along the transect were counted and collected for later identification in the laboratory, except bumble bee queens and honey bees, which were identified directly in the field and not collected. Honey bees and bumble bees were identified to species level, except for *B. terrestris*, *B. lucorum*, *B. cryptarum* and *B. magnus*, which were instead grouped into *B. terrestris* coll. because of difficulty to separate the species morphologically (Murray et al., 2008). Non-*Apis* and non-*Bombus* bee species were not identified to species but instead grouped as “solitary bees”.

Inflorescence density was measured during each pollinator survey by counting the number of inflorescences in bloom (>5 open florets) in three 0.25 m² squares along each transect. A mean value from the three squares was used as a covariate in the statistical analyses.

2.3. Initial and final seed set

To assess the initial seed set in relation to the concurrent pollinator community, we marked three inflorescences in full bloom (>70 % open florets) in one transect per field, directly after each pollinator survey in 2015 and 2016. In conventional fields this was done for the insecticide-treated transect, because it represents the local management practiced

by the farmer. We marked the inflorescences, and left them to mature in the field for two weeks (±2 days), thereafter we collected the inflorescences and stored them in a freezer to not lose seeds to seed-eating pests. We later counted the number of florets per inflorescence and then the number of seeds per pod, under a dissecting microscope, in 25 randomly picked healthy florets per inflorescence. Weevil damaged florets, as indicated by the calyx having a bite hole (Fig. A2), were omitted from the counts in order to exclude the effect of pests. Bite holes from nectar robbers are in contrast to bite holes from weevils situated higher up on the corolla and not through both the calyx and corolla, whereas bite marks from weevils are on the calyx. Even though seeds were unripe in these inflorescences, it was possible to separate developing seeds from undeveloped or aborted ovules due to the larger size of the former.

To determine the final seed set, we collected fully withered, mature inflorescences from each transect a few days before commercial harvest. From each of 20 randomly selected inflorescences per transect we counted the number of florets per inflorescence and counted the number of seeds per pod in five randomly selected florets per inflorescence. We also noted whether these florets were weevil damaged. This made it possible to investigate the final seed set in all pods and in undamaged pods, respectively.

2.4. Landscape context analysis

We calculated the proportions of semi-natural and arable land in a buffer zone with 1 km radius surrounding the survey transects using ArcGIS software 10.6 (ESRI, 2017) and a combination of land use data from the Swedish land cover map (Nationella Marktäckedata, NMD) and agricultural crop cover data from the Integrated Administration and Control System (IACS) from the Swedish Board of Agriculture. The 1 km radius was chosen because it captures the foraging ranges of most wild bees in Sweden (Kendall et al., 2022). Semi-natural land included uncultivated permanent grasslands that are grazed or cut, different types of fallows, including those aimed at supporting biodiversity, and field border areas, calculated as the perimeter length of agricultural parcels assuming a 1 m width (see caption in Table A1 for exact codes that were included from NMD and IACS). The grasslands in the region are generally grazed and are considered to be bee friendly (Öckinger and Smith, 2007, see also Persson et al., 2010 for a more general description of the grasslands and land use in the region). We did not include forests as semi-natural land as the forest cover was very low at our sites (mean = 2.4 %, median = 0.4 % in the 1 km buffer surrounding our sites). Arable land was defined as annually tilled land grown with annual crops. Proportion arable and semi-natural land were negatively correlated (Kendalls tau = -0.38, z = -4.89, p < 0.001, Fig. A1), and therefore always treated in separate statistical models.

2.5. Statistical analysis

Data analyses were performed using R version 4.1.2 (R Core Team, 2021). We performed generalized linear mixed models (GLMMs) and linear mixed models (LMMs) using package glmmTMB (Brooks et al., 2017) to test our hypotheses. Model validation was done following Zuur et al. (2009, 2010), and using package DHARMA (Hartig, 2022). In addition to checking multicollinearity in models using variance inflation factors (VIFs), a correlation matrix, testing collinearity between variables is shown in Fig. A1. We also tested for and found no spatial or temporal autocorrelation in our models (using package DHARMA, Hartig, 2022). Covariates that were non-significant (p > 0.05) and reduced the model fit, as determined by Akaike information criterion (AIC) and residual patterns, were excluded from the final models. Test of significance was obtained from type II Analysis of Deviance Table (type III was used in case of a significant interaction) with Wald chi-square tests (package: car, lmerTest, Fox and Weisberg, 2019; Kuznetsova et al., 2017). Post-hoc tests, multiple comparisons between groups, were

computed using estimated marginal means (function `emmeans`, and `emmeans` in package `emmeans`, Lenth, 2022). The estimated marginal means show the mean response for each factor, adjusted for any other variables in the model. To visualize our results we used package `ggplot2` (Wickham, 2016), `multcompView` (Graves et al., 2019), `ggeffects` (Lüdtke, 2018) and `sjPlot` (Lüdtke, 2022).

We checked if there were any pairwise correlations between honey bee, non-*Apis* bee and total bee abundance using Pearson correlation when the assumption of normality was met, and Kendall correlation when this assumption was not met. Using Kruskal-Wallis rank sum test, we also tested if the landscape variables, field size or added bee hives or colonies per ha differed depending on management.

2.5.1. Bee abundance

To investigate what affects bee abundance and to understand under what conditions the number of flower visitors to an insect-pollinated crop is maximized, we related bee abundance, i.e. the number of bees per transect and year (aggregating data over survey round), as i) number of non-*Apis* bees (bees other than *A. mellifera*), ii) number of honey bees, and iii) total number of bees (all bees) to local management and landscape context using GLMMs with negative binomial distribution and log link. The independent variables were proportion of semi-natural (or arable) land, local management (organic, conventional insecticide-treated or conventional untreated), year, field size, mean temperature and mean inflorescence density during the three survey rounds, added honey bees (yes or no) (in the models for honey bees and all bees), added bumble bees (yes or no) (in the models for non-*Apis* bees and all bees), and the interaction between local management and landscape context. We also included the interaction between management and year to evaluate if the results on bee abundance in Lundin et al. (2017) were consistent across years. The reason for including the variables added honey bees and added bumble bees was because *A. mellifera* hives, and to a lesser extent *B. terrestris* colonies, were placed in the field by the farmer. We chose the binary (yes or no) variable for the final models, but also ran the same models with continuous variables for added honey bees (hives/ha) and added bumble bees (colonies/ha) but this had to be done on a slightly smaller dataset when the added honey bees variable were included as we lack information on the stocking densities of honey bee hives from four fields (where we know that honey bees were deployed, Table A1). We present the results for these models where any of the added bees per ha variables remained after model selection, in Appendix B, but we also discuss the result in the main text. As proportions of semi-natural and arable land were correlated, they provide similar information on the landscape context; we therefore focus on semi-natural land in the main text and show the result for arable land in Appendix B. Continuous independent variables were standardized to a mean of zero and variance of one. To account for fields having two transects, and for fields being on the same farm between years, we added field identity nested in farm as random variables. Although we included inflorescence density in the models (to account for phenology differences among fields) we also confirmed that neither the inflorescence density ($\text{chisq}_{df} = 1.14_1$, $p = 0.29$) nor the number of florets per inflorescence ($\text{chisq}_{df} = 1.78_2$, $p = 0.41$) differed depending on local management.

2.5.2. Bee species richness and diversity

From the data of observed bees, we calculated for each transect and survey round i) species richness, i.e. the number of observed bee species (or species groups in the case of solitary bees and *B. terrestris* coll.), and ii) Shannon's diversity index ($H = -\sum p_i \ln(p_i)$), using function 'diversity' in the r-package `vegan` (Oksanen et al., 2018), where p_i is the frequency of occurrence of each species (Shannon, 1948; Morris et al., 2014). We used LMMs to test if bee species richness and bee species diversity were related to local management and landscape context. The independent and random variables were almost the same as specified for bee abundance above. The interaction between management and year

was however omitted here as we did not need to check for consistency with years included in Lundin et al. (2017). Because the data were on survey round level, we added survey round as an independent variable and round nested within field as random variables and we used the original temperature and inflorescence density values per transect and survey round instead of the mean. Bee species richness and diversity was highly correlated ($r = 0.76$, $t_{df} = 17.88_{232}$, $p < 0.001$), and results for the latter are therefore shown in Appendix B.

2.5.3. Initial and final seed set

To analyze how pollinator abundance and species richness (and diversity, in Appendix B) were related to initial and final seed set we specified LMMs with either initial seed set, final seed set from all pods, or final seed set calculated from only undamaged pods (average number of seeds per pod, in all cases) as dependent variable. The predictor was either bee abundance (separate models for abundance of non-*Apis* bees, honey bees and total number of bees), bee species richness or diversity. Local management and year were specified as independent variables. For the initial seed set the data were on survey round level, and we therefore added survey round as an independent variable and round nested within field as random variables. As the final seed set was on transect level we specified field as a random variable. The interaction between the insect variables and year was also investigated. The interaction term and local management were dropped if they were non-significant and reduced the model fit. The random variable farm, to account for fields being on the same farm between years, was omitted as it had very low variance ($< 1.14e-08$), and hence had no effect on the results for the fixed effects of the model, but reduced the model fit as determined by inspection of residual patterns.

We tested the relationship between initial and final seed set (the latter separately for all pods and undamaged pods) on the field level with LMMs. Year was included as an independent variable and we also tested if there was an interaction between year and seed set. Farm was included as random variable. Finally, we tested if the initial and final seed set differed depending on local management in a LMM with mean number of seeds per pod as dependent variable. Seed set measure (initial seed set, final seed set from undamaged pods or final seed set from all pods), local management, year and the interaction between seed measure and management were the independent variables. As data were on transect level, field was added as random variable to account for fields having two transects. Farm was omitted as its variance was 0 and caused a singular fit. Dropping it from the model had no effect on the result for the fixed effects of the model.

3. Results

We observed 15 bee species or species groups visiting clover flowers during 234 pollinator surveys conducted over three years in 39 white clover fields. Of the total number of observed bees, *A. mellifera*, *B. terrestris* coll. and *B. lapidarius* were most common, accounting for 68 %, 22 % and 8 %, respectively (Table 1).

The total number of bees was positively correlated to the number of honey bees ($r = 0.86$, $t = 14.80$, $df = 76$, $p < 0.001$) and also to the number of non-*Apis* bees ($\tau = 0.42$, $z = 5.38$, $p < 0.001$). There was no correlation between abundance of honey bees and non-*Apis* bees ($\tau = 0.069$, $z = 0.88$, $p = 0.39$). When testing if proportion semi-natural land, proportion arable land, field size, added bumble bees per ha, or added honey bees per ha differed among management types (organic, conventional untreated or conventional insecticide-treated i.e. the variables used in the latter analyses), we found no relations except that adding bumble bees was more common in conventional fields (Table 2, Fig. B1, Table A1). When instead checking if the above variables differed among conventional and organic fields (i.e. not the division of management types used for analyses later on but the field type), we found that field size was larger for organic fields, that organic fields to a higher degree were surrounded by semi-natural land, and that they had less added

Table 1

Total number of observed bee individuals per species (or species group) during 234 pollinator surveys conducted over three years in 39 white clover seed fields. The number of surveys conducted per year was 72, 84, and 78 in 2014, 2015 and 2016, respectively.

| Species or species group | Number of observed individuals | | |
|----------------------------|--------------------------------|------|------|
| | 2014 | 2015 | 2016 |
| <i>A. mellifera</i> | 2931 | 2456 | 1815 |
| <i>B. terrestris</i> coll. | 629 | 1451 | 271 |
| <i>B. lapidarius</i> | 328 | 423 | 118 |
| <i>B. sylvanum</i> | 5 | 26 | 15 |
| <i>B. subterraneus</i> | 22 | 6 | 3 |
| <i>B. soroeensis</i> | 14 | 6 | 2 |
| <i>B. hortorum</i> | 13 | 3 | 8 |
| <i>B. rudericus</i> | 5 | 2 | 8 |
| <i>B. pascuorum</i> | 3 | 10 | 1 |
| <i>B. pratorum</i> | 3 | 1 | 0 |
| <i>B. hypnorum</i> | 1 | 1 | 0 |
| <i>B. muscuorum</i> | 0 | 2 | 1 |
| <i>B. bohemicus</i> | 0 | 1 | 0 |
| <i>B. rupestris</i> | 0 | 0 | 1 |
| Solitary bee | 9 | 14 | 6 |

Table 2

Kruskal-Wallis rank sum test results with chi-square values, degrees of freedom (df) and p-values (p) for testing if proportion semi-natural land, proportion arable land, field size, added bumble bees per ha or added honey bees per ha differed among management types (Org = organic, Conv T = conventional insecticide-treated or Conv U = conventional untreated, i.e. the variables used in the analyses) as well as between conventional and organic fields (i.e. not the division of management types used in analyses, but the field type). Boxplot of raw data (with median, first and third quartiles) are shown in Fig. B1.

| x | y | chisq _{df} | p |
|-------------------------|---------------------------------------|---------------------|----------|
| | Management(Conv T, Conv U, Org) | | |
| Prop. semi-natural land | 5.20 ₂ | | 0.074 |
| Prop. arable land | 2.82 ₂ | | 0.24 |
| Field size | 4.94 ₂ | | 0.085 |
| Added bumble bees/ha | 14.04 ₂ | | < 0.0010 |
| Added honey bees/ha | 2.80 ₂ | | 0.25 |
| | Management (Conventional, Organic) | | |
| Prop. semi-natural land | 5.20 ₁ | | 0.023 |
| Prop. arable land | 2.82 ₁ | | 0.093 |
| Field size | 4.94 ₁ | | 0.026 |
| Added bumble bees/ha | 14.09 ₁ | | < 0.0010 |
| Added honey bees/ha | 2.80 ₁ | | 0.094 |

bumble bees per ha as compared to conventional fields (Table 2, Fig. B1).

3.1. Bee abundance in relation to local management and landscape context

Abundance of non-*Apis* bees was related to local management, year, field size and inflorescence density (Table 3, Fig. B2). Post-hoc tests showed that there were more non-*Apis* bees in conventional insecticide-treated and conventional untreated transects compared to organic transects (Fig. 2a), and most bees in 2015. Number of non-*Apis* bees decreased with field size and increased with inflorescence density (Fig. 2b, c, Fig. B2). The non-*Apis* bee abundance was not related to the proportion of semi-natural land (Table 3, Fig. B2).

Honey bee abundance was positively related to temperature and addition of honey bee hives, but was not related to proportion semi-natural land, management or year (Table 3, Fig. B2). The abundance of all bees was related to the interaction between management and year, with less bees in organic fields in 2016 compared to all other

combinations of year and management (Table 3, Fig. 2d). The abundance of all bees was also positively related to temperature and inflorescence density, but was not related to proportion semi-natural land, field size or addition of bumble bee colonies (Table 3, Fig. B2).

Models with proportion arable land as predictor showed similar results for all bee groups as proportion semi-natural land, with the exception that inflorescence density had no effect in the “all bees”-model, and that abundance of honey bees was positively related to the proportion of arable land (see Appendix B1.1, compare Table 3 and Table B1, see Fig. B2).

To investigate the effect of number of added bees (per ha) as a continuous variable instead of a categorical variable (yes or no), we used models on slightly smaller datasets (where the number added bees was known) for the abundance of honey bees and all bees, respectively. We found that the density of added honey bees was positively related to the abundance of honey bees, but there was no effect of density of any of the added bees on the abundance of all bees (Table B1, B2, Fig. B2). With non-*Apis* bees as response variable, the added bumble bees per ha variable had no effect and were removed during model selection. Differences between models using the categorical (full dataset) versus continuous variables (smaller dataset) were for the models with honey bees and arable land and the models with all bees and semi-natural land, that the positive effect of field size on abundance was marginally significant with the full dataset, but significant with the smaller dataset (Table B1, Table 3, Table B2). For the model with all bees and semi-natural land, the interaction between proportion semi-natural land and management was removed during model selection when using the full dataset, whereas the interaction remained and was significant when using the smaller dataset (Table 3, Table B2). Post hoc test show that the abundance of all bees in the conventional insecticide-treated plots increased with the proportion semi-natural land in the surrounding (Fig. B3a).

3.2. Species richness and diversity in relation to local management and landscape context

Bee species richness was lower in transects in organic fields vs. conventional fields no matter treatment, and positively related to semi-natural land in the surrounding landscape (Table 3, Fig. 3). Furthermore, species richness was positively related to inflorescence density, negatively related to increasing temperature, higher in 2015 compared to 2016 and 2014, higher during round three than round one, and higher when no bumble bee colonies were added (Table 3, Fig. B4). As can be seen in Appendix B (B1.3), bee species richness was negatively related to proportion arable land. However, when proportion arable land was the predictor in the model instead of semi-natural land, there was no effect of added bumble bees and there was only a difference between 2015 and 2016, with more in 2015, in all else the results were similar. When analyzing the effect of the density of added bees instead of categorical (yes/no) in the slightly reduced datasets, only added bumble bees per ha remained after model selection and only in the model with semi-natural land as predictor. Added bumble bees per ha had a negative relation to species richness (Table B2, Fig. B2). A difference between the model with the categorical vs continuous variable was that the negative relationship between temperature and species richness was significant in the former, but only marginally significant in the latter (Table 3, Table B2).

Bee diversity showed similar results to bee species richness (see Appendix B, B1.4), however, in the model with semi-natural land as predictor, there was no relation to added bumble bees, and in the model with arable land as predictor there was no effect of management and a negative relation to field size. For models including added bees as continuous variables, only added honey bees per ha remained (of the added bees variables) after model selection in the model with semi-natural land as predictor. Shannon diversity had a negative relationship with the density of added honey bee hives per ha (Table B2, Fig. B4). Differences between the model with the categorical vs

Table 3

Statistical results with chi-square (chisq), degrees of freedom (df) and p-values, for bee abundance (non-*Apis* bees, honey bees and all bees) and species richness in relation to proportion semi-natural land, local management (organic, conventional insecticide-treated, conventional untreated), year, field size, ambient temperature and inflorescence density in transects, presence of commercial bumble bee colonies (yes or no), presence of managed honey bee hives (yes or no), round (survey round one, two, three), interaction between proportion semi-natural land and management (mgmt.), and interaction between management and year. For abundance models, where data was on year level, round was not relevant (“-”) and the mean temperature and inflorescence density per year and field was used. Terms that were non-significant and reduced the model fit (as determined by AIC, BIC and residual patterns) were excluded from the final model and are not shown (blank cells). Statistically significant p-values (< 0.05) are shown in bold. Regression coefficients with confidence interval are shown in Fig. B2.

| | Abundance | | | | | | Species richness | |
|-------------------------|-----------------------|--------------------|---------------------|--------------------|---------------------|--------------------|---------------------|--------------------|
| | Non- <i>Apis</i> bees | | Honey bees | | All bees | | chisq _{df} | p |
| | chisq _{df} | p | chisq _{df} | p | chisq _{df} | p | | |
| Prop. semi-natural land | 0.49 ₁ | 0.48 | 0.58 ₁ | 0.45 | 2.47 ₁ | 0.12 | 6.33 ₁ | 0.012 |
| Management | 7.17 ₂ | 0.028 | 0.14 ₂ | 0.93 | 2.64 ₂ | 0.27 | 15.41 ₂ | < 0.0010 |
| Year | 66.92 ₂ | < 0.0010 | 5.51 ₂ | 0.064 | 0.53 ₂ | 0.77 | 19.70 ₂ | < 0.0010 |
| Field size | 5.64 ₁ | 0.018 | | | 3.26 ₁ | 0.071 | | |
| Temperature | | | 9.15 ₁ | 0.0025 | 17.92 ₁ | < 0.0010 | 4.18 ₁ | 0.041 |
| Inflorescence density | 10.67 ₁ | 0.0011 | | | 6.09 ₁ | 0.014 | 18.71 ₁ | < 0.0010 |
| Added bumble bees | | | - | | 1.45 ₁ | 0.23 | 5.32 ₁ | 0.021 |
| Added honey bees | - | - | 23.34 ₁ | < 0.0010 | | | | |
| Round | - | - | - | - | - | - | 6.61 ₂ | 0.037 |
| Prop. semi:Mgmt. | | | | | | | | |
| Management:Year | | | | | 18.14 ₄ | 0.0012 | | |

continuous variable were that the positive effect of proportion semi-natural land was significant in the former, but not in the latter, management was significant in the former but only marginally significant in the latter, whereas field size was not significant in the former but was in the latter (Table B2).

3.3. Seed set

Initial seed set was positively related to the abundance of honey bees and all bees (Fig. 4a, b), but not related to the abundance of non-*Apis* bees or bee species richness (Table 4). Initial seed set differed between years (Table 4), with more seeds in 2015 compared to 2016. Survey round was related to initial seed set only in the model with all bees (Table 4), with more seeds in round three compared to both round one and two. Final seed set was, however, not related to either bee abundance or species richness (Table 4). Initial seed set was positively related to final seed set, but only in 2016 (Seeds:Year chisq_{df} = 6.69₁, p = 0.0097, Fig. 4c). The relationship between initial seed set and final seed set only from undamaged pods was also positive (chisq_{df} = 14.41₁, p < 0.001, Fig. 4d), but there was no influence of year (chisq_{df} = 0.49₁, p = 0.49).

Final seed set was, in contrast to initial seed set, only related to local management, and not to bee abundance or any other variable (Table 4). Posthoc tests showed that final seed set was highest in insecticide-treated conventional transects, intermediate in untreated conventional transects and lowest in organic transects (Fig. 5a). Similar results were obtained for final seed set from undamaged pods only, but here year was also influential (Table 4). For final seed set in undamaged pods, post hoc tests showed that seed set was higher in both conventional treated and untreated transects compared to organic transects (Table B4).

Neither initial nor final seed set were related to bee diversity (see Appendix B1.5 and Table B3).

We also compared the different seed set measures (initial seed set, final seed set in all pods, and final seed set in only undamaged pods) between local management practices and found that there was an interaction between management and seed set measure (chisq_{df} = 12.43₂, p = 0.0020), and an influence of year (chisq_{df} = 15.76₁, p < 0.001). Post-hoc tests showed that final seed set in all pods in organic fields was lower than all other seed set measures, and that final seed set in undamaged pods was higher in conventional fields than all seed set measures in organic fields (Fig. 5b). There was no difference between initial seed set and final seed set in undamaged pods in organic fields, no difference in initial seed set between organic and conventional fields,

and no difference between any seed measures in conventional fields (Fig. 5b).

4. Discussion

We observed fewer non-*Apis* bees, i.e. bumble bees and solitary bees, and a lower bee species richness in organically managed fields compared to both in insecticide-treated and untreated plots within conventional fields in our three-year study in white clover seed fields. Bee species richness increased with the proportion of semi-natural land in the landscape, independent of local management. We found that initial seed set, i.e. in inflorescences collected early in the flowering season before major damage by seed-eating pest weevils, was positively related to honey bee and total bee abundance, but we found no such relationship for final seed set, i.e. when both pollinators and pests had affected the seed set.

4.1. Bee abundance, management and landscape context

Our results are in contrast to a global meta-analysis, which found that organic field management increased bee abundance in crop fields (Kennedy et al., 2013). In line with our previous two-year study in white clover fields (Lundin et al., 2017), we found a lower abundance of non-*Apis* bees in organic fields compared to conventional fields. In addition, we found that the total number of bees was lower in organic fields in 2016 than in any other management and year combination. We have previously suggested that the lower non-*Apis* bee abundance in organic white clover fields is related to bees being deterred by pest-damaged flowers, as the main pests were more common in organic fields compared to insecticide-treated conventional fields (Lundin et al., 2017). As in Lundin et al. (2017), surveys of the main seed-eating weevil pest (*P. fulvipes*), confirmed that there were more pests in organic fields compared to conventional insecticide-treated fields, but no difference in pest abundance between organic and untreated conventional plots (Hederström et al., 2022).

The higher abundance of pests in conventional untreated compared to insecticide-treated plots, while non-*Apis* bee abundance was equally high in both treatments, indicates that the lower bee abundance in organic fields cannot be fully explained by higher pest abundance. Possible factors explaining the lower non-*Apis* bee abundance in organic compared to conventional fields, which could be explored further, are differences between organic and conventional management in crop fertilization and crop growth regulation by cutting, which might affect

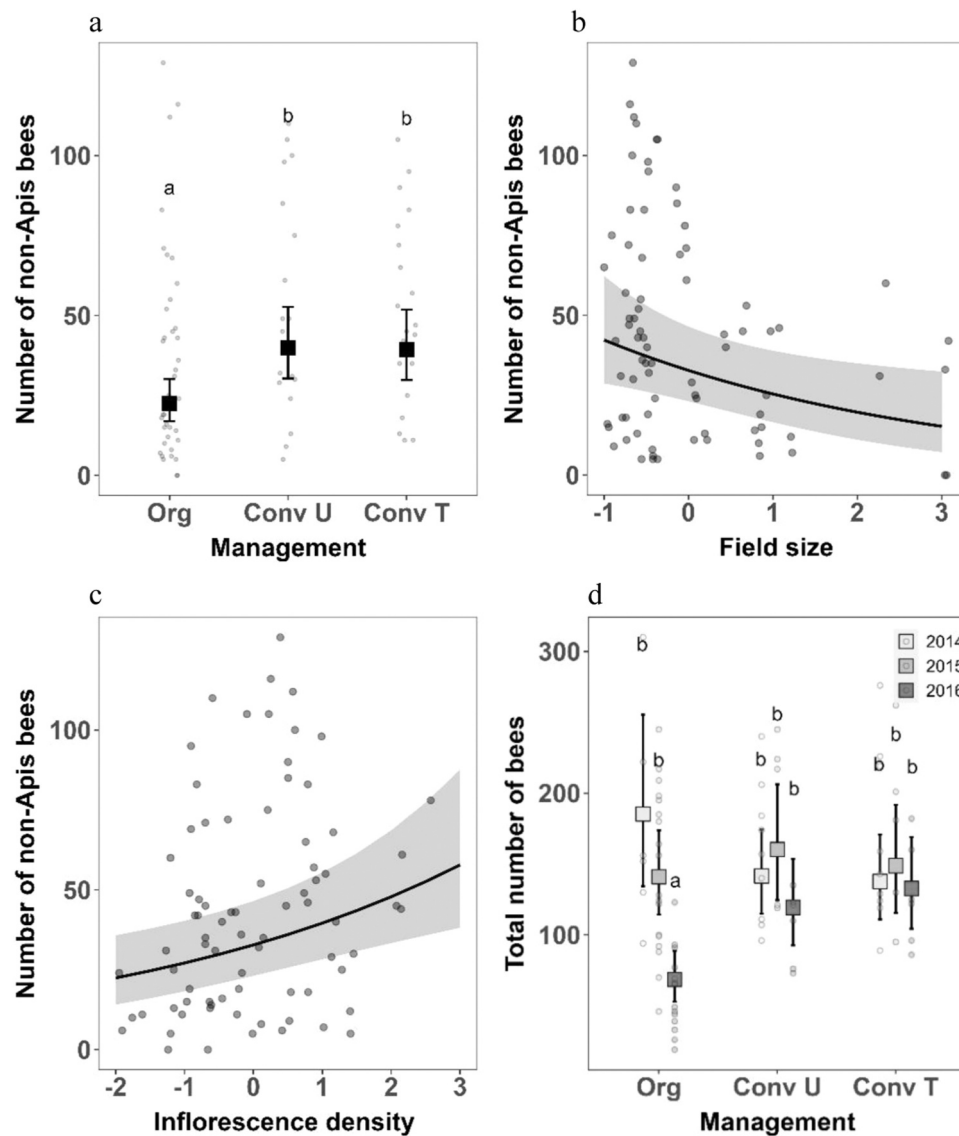


Fig. 2. Bee abundance in relation to local management, field size and inflorescence density. Model estimated means and confidence limits (95 %) for number of non-*Apis* bees in relation to (a) local management, (b) field size, (c) inflorescence density, and (d) total number of bees per transect in relation to local management and year (Org = organic, Conv U = conventional untreated, Conv T = conventional insecticide-treated). Pairwise comparisons of estimated means are indicated by letters in (a) and (d). Means sharing a letter are not significantly different ($p > 0.05$). Continuous independent variables were standardized to mean zero and variance one. Raw data shown as dots.

inflorescence attractiveness for non-*Apis* bees, e.g. through alteration of nectar rewards, or surrounding flower resources on the farm. However, studies in red clover seed fields and of *B. terrestris* colonies indicate that inflorescence nectar production was not linked to insecticide treatment and that colonies grew equally large independent of local field management (Knapp et al., 2022). A more likely explanation for the lower numbers of bees detected in the organic white clover fields, could be the presence of preferred alternative foraging habitats around the field and in other fields on the farm, such as flower rich field borders, which are known to harbor floral and nesting resources for pollinators (Petersen et al., 2006; Williams and Kremen, 2007), or organically managed cereal fields which hold higher flower abundance than conventional equivalents (Holzschuh et al., 2007; Rundlöf et al., 2008; Carrié et al., 2018), both driven partly by lack of herbicide use in organic farming. Such flower resources could compete for flower visitors and create dilution in that clover field, similarly to a high proportion of mass-flowering crops in the landscape (Holzschuh et al., 2016). However, in this study the flower density in field borders or surrounding habitats was not

measured, and neither did we assess bee abundance or richness outside the white clover fields, but we encourage this in future studies. A similar dilution effect could be caused by the larger field size of organic compared to conventional white clover fields. This is supported by our analysis, where we found decreasing abundance of non-*Apis* bees with increasing field size. Similarly, Hass et al. (2018) found that increased field border density (as a result of smaller fields), had a strong positive effect on wild bee abundance. Although some bumble bee species and honey bees can forage over several kilometers, optimal foraging theory and observations suggest that most bees forage close to their nest (Heinrich, 1975; Walther-Hellwig and Frankl, 2000) and that realised foraging ranges are much smaller than potential foraging ranges in bees (Kendall et al., 2022). A larger field may have increased the distance from our transects to the bee nests, but it may also have diluted the bees over the larger flowering area (Holzschuh et al., 2016). Our observed abundances may hence reflect attraction, concentration and dilution effects (Persson and Smith, 2013) rather than population densities.

Moreover, the addition of honey bee colonies, both when analyzed as

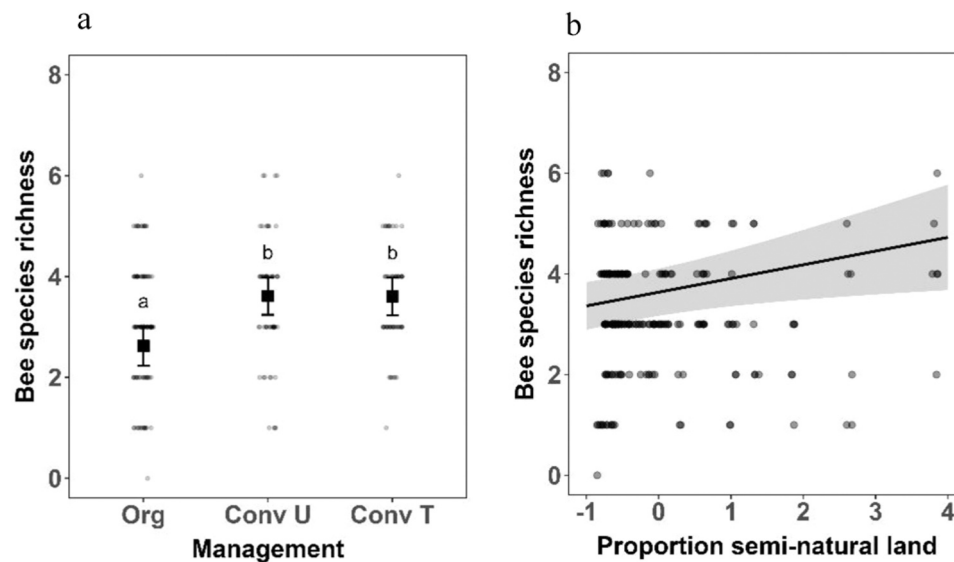


Fig. 3. Species richness in relation to local management and landscape context. Model estimates and confidence limits (95 %) for bee species richness in relation to (a) local management (Org = organic, Conv U = conventional untreated, Conv T = conventional insecticide-treated), and (b) landscape context quantified as proportion semi-natural land. Proportion land is standardized to mean zero and variance one. Pairwise comparisons of estimated means are indicated by letters in a, with means sharing a letter not significantly different ($p > 0.05$). Raw data shown as dots.

a categorical or continuous variable, increased the abundance of honey bees visiting clover flowers in the fields, but it did not have an effect on the total abundance of bees, neither did the addition of bumble bee colonies. The positive relationship between local honey bee hive presence or densities and honey bee abundance in the crop fields is expected, but far from universal (see [Eeraerts et al., 2023](#) and references therein), and could in our case be a result of white clover being a preferred foraging resource. Honeybee abundances was also positively related to the proportion agricultural land in the landscape, which could be because beekeepers place more hives for honey production or crop pollination in landscapes with more agriculture and flowering crops. Addition of commercial bumble bees was not important for the abundance of non-*Apis* bees either. These results were independent of if we compared the presence vs. absence of added bees or the density of the added bees, suggesting that the addition of bumble bee colonies as practiced by some of the farmers has a limited effect on bumble bee flower visitation in the crop. This study was not designed to explore the management of commercial honey bees and bumble bees and how it relates to crop pollination, but this is an interesting topic for future studies.

4.2. Bee species richness

In line with the results for bee abundance, bee species richness was also lower in organic compared to conventional fields. Similar to as suggested for non-*Apis* bee abundance, the negative effect of organic field management on bee species richness might be explained by more preferable bee foraging habitats outside the organic compared to conventional fields. Moreover, we found that species richness was positively related to the proportion of semi-natural land within 1 km. Our finding of bee species richness with proportion of semi-natural land is in line with previous studies ([Ricketts et al., 2008](#); [Garibaldi et al., 2011](#); [Rundlöf et al., 2008](#)). Semi-natural habitats provide flower resources and nesting habitats and can therefore harbor more species, which can then disperse into agricultural areas ([Öckinger and Smith, 2007](#)). If the negative effect on species richness from added bumble bees is due to competition between wild and managed bees, needs to be further explored. Honey bees have been shown to compete with wild bees ([Bommarco et al., 2021](#); [Herbertsson et al., 2016](#)), and there are many examples of when introduced *B. terrestris* compete with native bees

([Mallinger et al., 2017](#); [Iwasaki, Hogendoorn, 2022](#)). Furthermore, bumble bees have been shown to displace other insects through exploitative competition ([Wignall et al., 2020](#)), and it is therefore possible that also managed bumble bees within its native range compete with wild bees.

4.3. The influence of bee abundance and species richness on seed set

White clover is dependent on pollinating bees in order to set seed and therefore a sufficient number of pollinators or a species rich pollinator community may increase or stabilize seed yield in case some species are more efficient pollinators or more tolerant to unfavorable weather conditions. We have previously found that pest damage and not pollinator abundance is the most important yield-limiting factor in white clover seed production ([Lundin et al., 2017](#)). Here we were able to separate the effect of pollinators from that of seed-eating pests by further exploring the earlier stages of seed set leading up to final yield. We found a positive influence of honey bee and total bee abundances on initial seed set, but in accordance with our previous study, we found no such relationships with final seed set. A higher initial seed set does not necessarily result in a higher final seed set, even in the absence of seed-eating pests, due to e.g., seed abortion ([Bos et al., 2007](#)). However, final seed set, measured as mean number of seeds per pod in all pods, both from pods damaged and not damaged by seed-eating weevils, was lower than initial seed set in organic fields, but there was no difference between initial seed set and final seed set in undamaged pods only. This indicates that the lower final seed set (in all pods) is caused by seed consumption by weevils, and not due to seed abortion. The higher final seed set in undamaged pods observed for conventional fields compared to organic fields could be caused by indirect effects of weevil damage (e.g. pest damage weakening the plants, or redistribution of resources away from damaged inflorescences; [Haas and Lortie, 2020](#)).

Although our results suggest that an increased pollinator abundance, in addition to pest damage, contribute to seed set, a higher bee abundance will only translate into a higher final seed set if the pests are controlled. Indeed, pollination benefits are often enhanced under effective pest control ([Tamburini et al., 2019](#)), speaking for the benefits of co-managing pests and pollinators ([Lundin et al., 2021](#)). An alternative explanation as to why bee abundance is related to initial but not final seed set is that the initial seed set had a more direct link to the

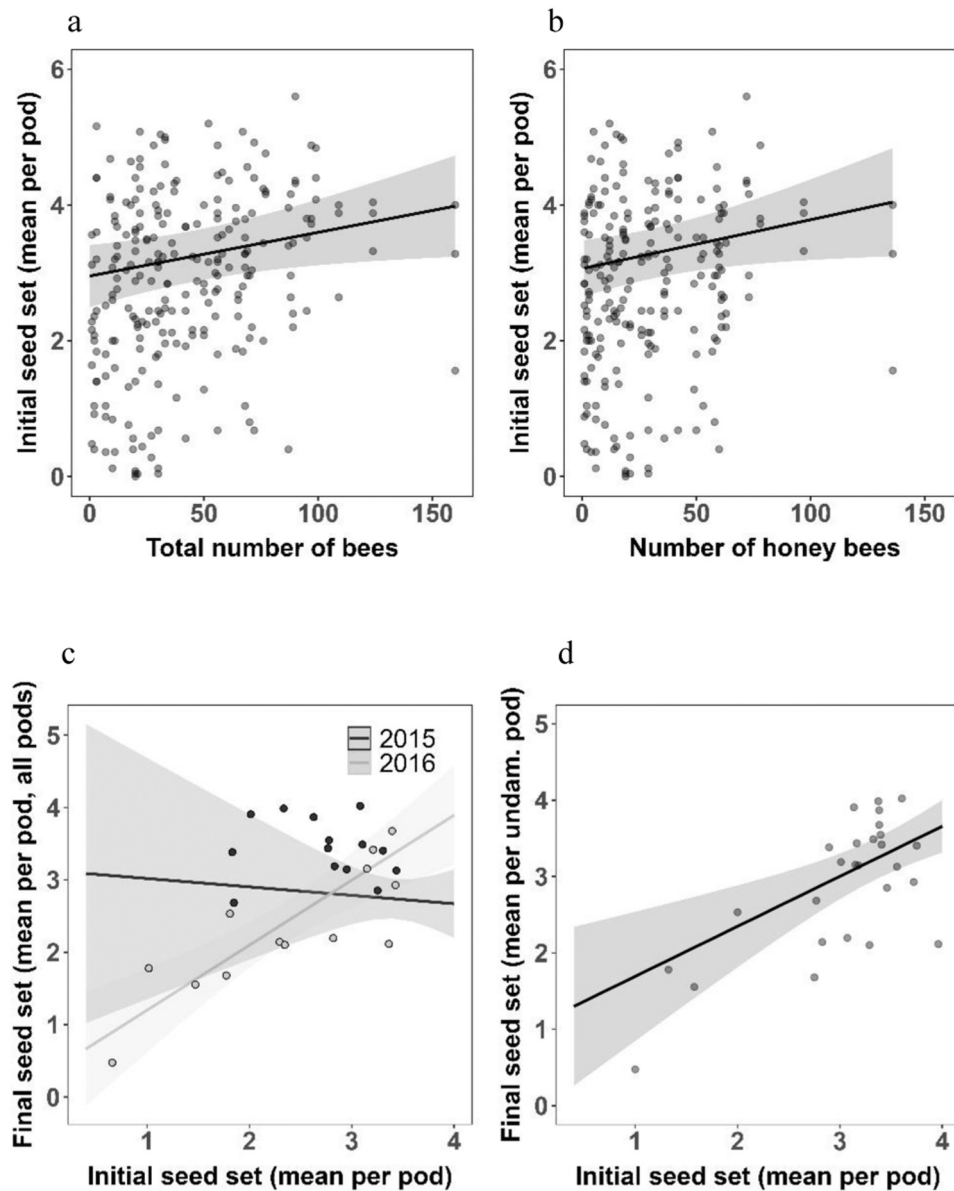


Fig. 4. Seed set. Model predicted means and confidence limits (95 %) for initial seed set in relation to (a) abundance of all bees and (b) honey bee abundance, and (c) final seed set in all pods depending on initial seed set, (d) final seed set in undamaged pods depending on initial seed set. Raw data shown as dots.

pollinator community that was observed during pollinator surveys, as it relates to flowers that were fully open at the time of surveys. Final seed set, however, as measured here is a result of the pollinator activity during the entire flowering season, and this pollinator activity might not be fully captured by only three pollinator surveys at each field. To further explore this it would be interesting to measure the final seed set in addition to the initial seed set in inflorescences marked during pollinator surveys.

Bee species richness or diversity did not affect initial seed set. This result potentially reflects that the most common species in our study – short-tongued honey bees and *B. terrestris* and *B. lapidarius* – are effective pollinators in white clover (Free, 1993), and that the addition of a few individuals of the rare long-tongued species did not improve seed set. Bumble bees can be slightly more efficient pollinators due to visiting more white clover florets per time unit, but less effective due to lower abundances compared to honey bees (Howlett et al., 2019). The most abundant species often contribute the most to crop pollination, as shown by Kleijn et al. (2015). It is possible that diversity of pollinators could have some influence on seed yield, such as in the case of summers with

low temperature, as honey bees are more sensitive to cold weather than bumble bees (Lundberg, 1980; Corbet et al., 1993). Our analyses showed that temperature positively influenced both honey bee and total bee abundance. Several studies on other crops highlights the importance of a diverse pollinator fauna for increased seed set (Mallinger and Gratton, 2015; Alomar et al., 2018; Katumo et al., 2022).

4.4. Conclusions

In conclusion, we found that bee abundance and species richness in mass-flowering white clover fields was influenced by local management, and species richness also by landscape context. While this crop is a food resource for bees, our study does not support that organic management favors bee abundance and species richness in white clover seed fields. On the contrary, we found that bee abundance and species richness is lower in organic fields, possibly caused by presence of preferred alternative foraging habitats around organically managed fields, or less rewarding inflorescences within organic fields due to differences in management practices. It should be pointed out that we investigated

Table 4

Initial seed set, final seed set in all pods and final seed set in undamaged pods (mean number of seeds per pod) in relation to non-*Apis* bee abundance, honey bee abundance and total bee abundance, year, survey round and management (organic, conventional untreated, conventional insecticide-treated), showing model results obtained from type II Analysis of Deviance Table, with Wald chi-square tests. Terms that were non-significant and reduced the model fit (as determined by AIC and residual patterns) were excluded from the final model and are not shown. Round was not relevant for final seed set. Statistically significant p-values (< 0.05) are shown in bold.

| Bee abundance and species richness | Initial seed set | | Final seed set, all pods | | Final seed set, undamaged pods | |
|---------------------------------------|---------------------|---------------|--------------------------|---------------|--------------------------------|-------------------|
| | chisq _{df} | p | chisq _{df} | p | chisq _{df} | p |
| Number of non-<i>Apis</i> bees | | | | | | |
| Abundance | 3.15 ₁ | 0.076 | 0.00 ₁ | 0.99 | | |
| Year | 9.45 ₁ | 0.0021 | 2.63 ₂ | 0.27 | 11.75 ₂ | 0.028 |
| Round | 4.67 ₂ | 0.10 | - | - | - | - |
| Management | | | 36.51 ₂ | < | 14.54 ₂ | <0.0010 |
| | | | | 0.0010 | | |
| Number of honey bees | | | | | | |
| Abundance | 4.48 ₁ | 0.034 | 0.47 ₁ | 0.49 | 0.57 ₁ | 0.46 |
| Year | 23.92 ₁ | < | 5.14 ₂ | 0.077 | 9.78 ₂ | 0.0074 |
| Round | 4.964 ₂ | 0.084 | - | - | - | - |
| Management | | | 39.43 ₂ | < | 14.04 ₂ | < |
| | | | | 0.0010 | | 0.0010 |
| Total number of bees | | | | | | |
| Abundance | 4.99 ₁ | 0.026 | 0.39 ₁ | 0.53 | | |
| Year | 15.56 ₁ | < | 3.27 ₂ | 0.20 | 11.75 ₂ | 0.0028 |
| Round | 9.14 ₂ | 0.010 | - | - | - | - |
| Management | | | 36.89 ₂ | < | 14.54 ₂ | < |
| | | | | 0.0010 | | 0.0010 |
| Species richness | | | | | | |
| Species richness | 1.51 ₁ | 0.22 | 0.20 ₁ | 0.66 | 0.00 ₁ | 0.95 |
| Year | 16.62 ₁ | < | 5.85 ₂ | 0.054 | 11.05 ₂ | 0.0040 |
| Round | 5.74 ₂ | 0.057 | - | - | - | - |
| Management | | | 40.66 ₂ | < | 14.49 ₂ | < |
| | | | | 0.0010 | | 0.0010 |

effects on a relatively restricted pollinator community dominated by honey bees (managed) and bumble bees in a single mass-flowering crop, and as such our results do not support that pollinator diversity overall is lower on organic farms. Despite the lack of a connection between bee abundance and the proportion of semi-natural land, we found that bee species richness was positively related to the proportion of semi-natural land in the landscape, independent of management. Although seed-eating pests rather than pollinators currently determine seed yield in white clover seed production (Lundin et al., 2017), we detected a positive relationship between bee abundance and initial seed set i.e. in flowers collected prior to most seed consumption by pests. This suggests that seed yield can be increased if actions can be implemented that increase bee abundance and control pests in the clover seed fields. The threat of a declining bee fauna should be taken into consideration both for the sake of the crop seed production and for a stable biodiversity in general. By increasing the amount of semi-natural land in the area surrounding clover fields we could support a diverse wild bee community and ensure resilient future crop production.

CRedit authorship contribution statement

Mattias C. Larsson: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Ola Lundin:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Åsa Lankinen:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Veronica Hederström:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maj Rundlöf:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Silvia Johansson:** Writing – review & editing, Investigation, Data curation. **Olle Anderbrant:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Glenn P. Svensson:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

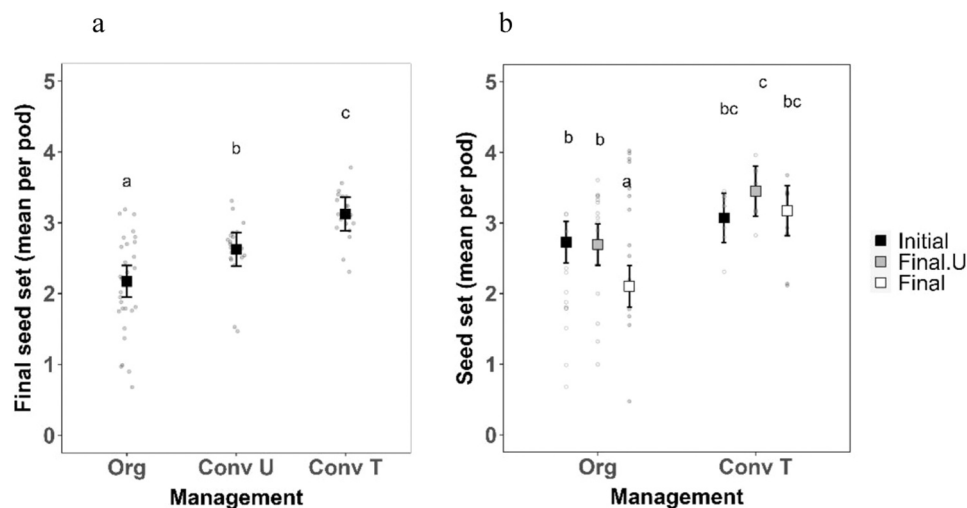


Fig. 5. Seed set in relation to management. Model predicted means and confidence limits (95 %) for (a) final seed set in all pods, related to management (Org = organic, Conv U = conventional untreated, Conv T = conventional insecticide-treated), and (b) mean number of seeds depending on seed measure (initial = initial seed set, Final.U = final seed set calculated from only undamaged pods, Final = final seed set calculated from both damaged and undamaged pods) and management. Pairwise comparisons of estimated means are indicated by letters, with means sharing a letter not significantly different ($p > 0.05$). Raw data shown as small dots.

Data availability

Data will be made available on request.

Acknowledgements

We thank all white clover seed farmers and landowners for allowing us to work on their land. We also thank Delphine Larivière, Maria Blasi Romero and Maya Johansson for field work and laboratory assistance, and Adam Flöhr for discussions on statistical analyses. Funding: This study was financed by grants from the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS) (grant 2014-00292), Swedish Farmers' Foundation for Agricultural Research (SLF) (grant H1333073), Partnerskap Alnarp, and by Sveriges Frö- och Oljeväxtodlare (SFO) (grant PA841). MR was supported by the Swedish Research Council VR (grant 330-2014-6439) and FORMAS (grants 2018-01020 and 2018-02283).

Appendix A & B. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2024.108933](https://doi.org/10.1016/j.agee.2024.108933).

References

- Abrol, D.P., 2012. Biodiversity Conservation and Agricultural Production. *Pollination Biology*. Springer, Dordrecht. <https://doi.org/10.1007/978-94-007-1942-2>.
- Alomar, D., González-Estévez, M.A., Traveset, A., Lázaro, A., 2018. The intertwined effects of natural vegetation, local flower community, and pollinator diversity on the production of almond trees. *Agric. Ecosyst. Environ.* 264, 34–43. <https://doi.org/10.1016/j.agee.2018.05.004>.
- Baker, M.J., Williams, W.M., 1987. *White clover*. CAB International, Wallingford.
- Bartomeus, I., Ascher, J.S., Gibbs, J., Danforth, B.N., Wagner, D.L., Hedtke, S.M., Winfree, R., 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proc. Natl. Acad. Sci. USA* 110, 4656. <https://doi.org/10.1073/pnas.1218503110>.
- Batáry, P., Baldi, A., Kleijn, D., Tscharnkte, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proc. R. Soc. B* 278, 1894–1902. <https://doi.org/10.1098/rspb.2010.1923>.
- Biddinger, D.J., Rajotte, E.G., 2015. Integrated pest and pollinator management — adding a new dimension to an accepted paradigm. *Curr. Opin. Insect Sci.* 10, 204–209. <https://doi.org/10.1016/j.cois.2015.05.012>.
- Bommarco, R., Lindström, S.A.M., Raderschall, C.A., Gagic, V., Lundin, O., 2021. Flower strips enhance abundance of bumble bee queens and males in landscapes with few honey bee hives. *Biol. Conserv.* 263, 109363. <https://doi.org/10.1016/j.biocon.2021.109363>.
- Bommarco, R., Lundin, O., Smith, H.G., Rundlöf, M., 2012. Drastic historic shifts in bumble-bee community composition in Sweden. *Proc. R. Soc. B* 279, 309–315. <https://doi.org/10.1098/rspb.2011.0647>.
- Bos, M.M., Veddeler, D., Bogdanski, A.K., Klein, A.M., Tscharnkte, T., Steffan-Dewenter, I., Tylianakis, J.M., 2007. Caveats to quantifying ecosystem services: fruit abortion blurs benefits from crop pollination. *Ecol. Appl.* 17, 1841–1849. <https://doi.org/10.1890/06-1763.1>.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. *glmmTMB* balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9, 378–400.
- Carre, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyorgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M., Vaissiere, B.E., 2009. Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agric. Ecosyst. Environ.* 133, 40–47. <https://doi.org/10.1016/j.agee.2009.05.001>.
- Carrié, R., Ekroos, J., Smith, H.G., 2018. Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *Biol. Conserv.* 227, 48–55. <https://doi.org/10.1016/j.biocon.2018.08.022>.
- Carvell, C., Bourke, A.F.G., Dreier, S., Freeman, S.N., Hulmes, S., Jordan, W.C., Redhead, J.W., Sumner, S., Wang, J., Heard, M.S., 2017. Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature* 543, 547–560. <https://doi.org/10.1038/nature21709>.
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006. Declines in forage availability for bumblebees at a national scale. *Biol. Conserv.* 132, 481–489. <https://doi.org/10.1016/j.biocon.2006.05.008>.
- Conrad, K.F., Warren, M.S., Fox, R., Parsons, M.S., Woiwod, I.P., 2006. Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. *Biol. Conserv.* 132, 279–291. <https://doi.org/10.1016/j.biocon.2006.04.020>.
- Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., Smith, K., 1993. Temperature and the pollinating activity of social bees. *Ecol. Entomol.* 18, 17–30. <https://doi.org/10.1111/j.1365-2311.1993.tb01075.x>.
- Eeraerts, M., Rogers, E., Gillespie, B., Best, L., Smith, O.M., DeVetter, L.W., 2023. Landscape-level honey bee hive density, instead of field-level hive density, enhances honey bee visitation in blueberry. *Land. Ecol.* 38, 583–595. <https://doi.org/10.1007/s10980-022-01562-1>.
- Egan, P.A., Dicks, L.V., Hokkanen, H.M.T., Stenberg, J.A., 2020. Delivering integrated pest and pollinator management (IPPM). *Trends Plant Sci.* 25, 577–589. <https://doi.org/10.1016/j.tplants.2020.01.006>.
- ESRI, 2017. ArcGIS Desktop: Release 10.6. Environmental Systems Research Institute, Redlands, CA.
- FAO, 2008. *Rapid Assessment Of Pollinators' Status. A Contribution To The International Initiative For The Conservation And Sustainable Use Of Pollinators*. Food and Agriculture Organization of the United Nations, Rome.
- Fox, J., Weisberg, S., 2019. *An R Companion to Applied Regression*, third ed. Sage, Thousand Oaks, CA.
- Free, J.B., 1993. *Insect pollination of crops*. Academic Press, London.
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhofer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyorgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. *Biol. Conserv.* 122, 1–8. <https://doi.org/10.1016/j.biocon.2004.06.017>.
- Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L., Darvill, B., 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. *J. Appl. Ecol.* 47, 1207–1215. <https://doi.org/10.1111/j.1365-2664.2010.01872.x>.
- Graves, S., Piepho, H., Dorai-Raj, S., 2019. *multcompView: Visualizations of Paired Comparisons*. R package version 0.1-8, <<https://CRAN.R-project.org/package=multcompView>>.
- Haas, S.M., Lortie, C.J., 2020. A systematic review of the direct and indirect effects of herbivory on plant reproduction mediated by pollination. *PeerJ* 8, e9049. <https://doi.org/10.7717/peerj.9049>.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Horren, T., Goulson, D., de Kroon, H., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12, e0185809. <https://doi.org/10.1371/journal.pone.0185809>.
- Harris, C., Ratnieks, F.L.W., 2022. Clover in agriculture: combined benefits for bees, environment, and farmer. *J. Insect Conserv.* 26, 339–357. <https://doi.org/10.1007/s10841-021-00358-z>.
- Hartig, F., 2022. *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R package version 0.4.6, <<https://CRAN.R-project.org/package=DHARMA>>.
- Hass, A.L., Kormann, U.G., Tscharnkte, T., Clough, Y., Baillo, A.B., Sirami, C., Fahrig, L., Martin, J.L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Burel, F., Georges, R., Giralt, D., Marcos-Garcia, M.A., Ricarte, A., Siriwardena, G., Batáry, P., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. *Proc. R. Soc. B* 285, 20172242. <https://doi.org/10.1098/rspb.2017.2242>.
- Hederström, V., Nyabuga, F.N., Anderbrant, O., Svensson, G.P., Rundlöf, M., Lankinen, Å., Larsson, M.C., 2022. Dispersal and spatiotemporal distribution of *Protaplia fulvipes* in white clover fields: implications for pest management. *J. Pest Sci.* 95, 917–930. <https://doi.org/10.1007/s10340-021-01408-w>.
- Heinrich, B., 1975. Energetics of Pollination. *Annu. Rev. Ecol. Syst.* 6, 139–170. <https://doi.org/10.1146/annurev.es.06.110175.001035>.
- Herbertsson, L., Lindström, S.A.M., Rundlöf, M., Bommarco, R., Smith, H.G., 2016. Competition between managed honeybees and wild bumblebees depends on landscape context. *Basic Appl. Ecol.* 17, 609–616. <https://doi.org/10.1016/j.baae.2016.05.001>.
- Holzschuh, A., Dainese, M., Gonzalez-Varo, J.P., Mudri-Stojnic, S., Riedinger, V., Rundlöf, M., Scheper, J., Wickens, J.B., Wickens, V.J., Bommarco, R., Kleijn, D., Potts, S.G., Roberts, S.P.M., Smith, H.G., Vila, M., Vujic, A., Steffan-Dewenter, I., 2016. Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. *Ecol. Lett.* 19, 1228–1236. <https://doi.org/10.1111/ele.12657>.
- Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., Tscharnkte, T., 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *J. Appl. Ecol.* 44, 41–49. <https://doi.org/10.1111/j.1365-2664.2006.01259.x>.
- Howlett, B.G., Lankin-Vega, G.O., Jesson, L.K., 2019. *Bombus terrestris*: a more efficient but less effective pollinator than *Apis mellifera* across surveyed white clover seed fields. *N. Z. J. Crop Hortic. Sci.* 47, 32–47.
- Iwasaki, J.M., Hogendoorn, K., 2022. Mounting evidence that managed and introduced bees have negative impacts on wild bees: an updated review. *Curr. Res. Insect Sci.* 2, 100043. <https://doi.org/10.1016/j.cris.2022.100043>.
- Katumo, D.M., Liang, H., Ochola, A.C., Lv, M., Wang, Q.-F., Yang, C.-F., 2022. Pollinator diversity benefits natural and agricultural ecosystems, environmental health, and human welfare. *Plant Divers* 44, 429–435. <https://doi.org/10.1016/j.pld.2022.01.005>.
- Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. Endangered mutualisms: The conservation of plant-pollinator interactions. *Annu. Rev. Ecol. Syst.* 29, 83–112. <https://doi.org/10.1146/annurev.ecolsys.29.1.83>.

- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalho, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhofer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A. M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599. <https://doi.org/10.1111/ele.12082>.
- Kendall, L.K., Mola, J.M., Portman, Z.M., Cariveau, D.P., Smith, H.G., Bartomeus, I., 2022. The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology* 103, e3809. <https://doi.org/10.1002/ecy.3809>.
- Klein, A.-M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kleijn, D., Kohler, F., Baldi, A., Batáry, P., Concepcion, E.D., Clough, Y., Diaz, M., Gabriel, D., Holzschuh, A., Knop, E., Kovacs, A., Marshall, E.J.P., Tscharntke, T., Verhulst, J., 2009. On the relationship between farmland biodiversity and land-use intensity in Europe. *Proc. R. Soc. B* 276, 903–909. <https://doi.org/10.1098/rspb.2008.1509>.
- Kleijn, D., Raemakers, I., 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* 89, 1811–1823. <https://doi.org/10.1890/07-1275.1>.
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalho, L.G., Henry, M., Isaacs, R., Klein, A.M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Adamson, N. L., Ascher, J.S., Baldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauber, F., Jha, S., Knop, E., Krewenka, K.M., Le Feon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardinias, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissiere, B.E., Veldtman, R., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* 6, 7414. <https://doi.org/10.1038/ncomms8414>.
- Knapp, J.L., Bates, A., Jonsson, O., Klatt, B., Krausl, T., Sahlin, U., Svensson, G.P., Rundlöf, M., 2022. Pollinators, pests and yield—Multiple trade-offs from insecticide use in a mass-flowering crop. *J. Appl. Ecol.* 59, 2419–2429. <https://doi.org/10.1111/1365-2664.14244>.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest Package: Tests in Linear Mixed Effects Models. *J. Stat. Softw.* 82, 1–26. <https://doi.org/10.18637/jss.v082.i13>.
- Lenth, R.V., 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.2, <<https://CRAN.R-project.org/package=emmeans>>.
- Lichtenberg, E.M., Kennedy, C.M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Perez, N.A., Carvalho, L.G., Snyder, W.E., Williams, N.M., Winfree, R., Klatt, B.K., Astrom, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekoetter, T., Eigenbrode, S.D., Ekroos, J., Elle, E., Freitas, B.M., Fukuda, Y., Gaines-Day, H.R., Grab, H., Gratton, C., Holzschuh, A., Isaacs, R., Isaia, M., Jha, S., Jonason, D., Jones, V.P., Klein, A.-M., Krauss, J., Letourneau, D.K., Macfadyen, S., Mallinger, R.E., Martin, E.A., Martinez, E., Memmott, J., Morandin, L., Neame, L., Otieno, M., Park, M.G., Pfiffner, L., Pocock, M.J.O., Ponce, C., Potts, S.G., Poveda, K., Ramos, M., Rosenheim, J.A., Rundlöf, M., Sardinias, H., Saunders, M.E., Schon, N.L., Sciligo, A.R., Sidhu, C.S., Steffan-Dewenter, I., Tscharntke, T., Vesely, M., Weisser, W.W., Wilson, J.K., Crowder, D.W., 2017. A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Glob. Chang. Biol.* 23, 4946–4957. <https://doi.org/10.1111/gcb.13714>.
- Liczner, A.R., Colla, S.R., 2019. A systematic review of the nesting and overwintering habitat of bumble bees globally. *J. Insect Conserv.* 23, 787–801. <https://doi.org/10.1007/s10841-019-00173-7>.
- Lüdtke, D., 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. *J. Open Source Softw.* 3, 772. <https://doi.org/10.21105/joss.00772>.
- Lüdtke, D., 2022. sjPlot: Data Visualization for Statistics in Social Science. R package version 2.8.12, <<https://CRAN.R-project.org/package=sjPlot>>.
- Lundberg, H., 1980. Effects of weather on foraging-flights of bumblebees (Hymenoptera, Apidae) in a subalpine/alpine area. *Holarct. Ecol.* 3, 104–110. <https://doi.org/10.1111/j.1600-0587.1980.tb00715.x>.
- Lundin, O., Rundlöf, M., Jonsson, M., Bommarco, R., Williams, N.M., 2021. Integrated pest and pollinator management—expanding the concept. *Front. Ecol. Environ.* 19, 283–291. <https://doi.org/10.1002/fee.2325>.
- Lundin, O., Rundlöf, M., Smith, H.G., Bommarco, R., 2012. Towards integrated pest management in red clover seed production. *J. Econ. Entomol.* 105, 1620–1628. <https://doi.org/10.1603/EC12179>.
- Lundin, O., Svensson, G.P., Larsson, M.C., Birgersson, G., Hederström, V., Lankinen, A., Anderbrant, O., Rundlöf, M., 2017. The role of pollinators, pests and different yield components for organic and conventional white clover seed yields. *Field Crops Res* 210, 1–8. <https://doi.org/10.1016/j.fcr.2017.05.014>.
- Mallinger, R.E., Gaines-Day, H.R., Gratton, C., 2017. Do managed bees have negative effects on wild bees? A systematic review of the literature. *PLOS ONE* 12, e0189268. <https://doi.org/10.1371/journal.pone.0189268>.
- Mallinger, R.E., Gratton, C., 2015. Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *J. Appl. Ecol.* 52, 323–330. <https://doi.org/10.1111/1365-2664.12377>.
- Morris, E.K., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T.S., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S.A., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S., Rillig, M.C., 2014. Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecol. Evol.* 4, 3514–3524. <https://doi.org/10.1002/ece3.1155>.
- Murray, T.E., Fitzpatrick, U., Brown, M.J.F., Paxton, R.J., 2008. Cryptic species diversity in a widespread bumble bee complex revealed using mitochondrial DNA RFLPs. *Conserv. Genet.* 9, 653–666. <https://doi.org/10.1007/s10592-007-9394-z>.
- Norris, 1985. Flowering of contrasting white clover varieties in relation to temperature in controlled environments. *Ann. Bot.* 56, 317–322. <https://www.jstor.org/stable/42757547>.
- Öckinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J. Appl. Ecol.* 44, 50–59. <https://doi.org/10.1111/j.1365-2664.2006.01250.x>.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szocs, E., Wagner, H., 2018. vegan: Community ecology package. R. Package Version 2.5-2, <<https://CRAN.R-project.org/package=vegan>>.
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>.
- Persson, A.S., Olsson, O., Rundlöf, M., Smith, H.G., 2010. Land use intensity and landscape complexity—Analysis of landscape characteristics in an agricultural region in Southern Sweden. *Agric. Ecosyst. Environ.* 136, 169–176. <https://doi.org/10.1016/j.agee.2009.12.018>.
- Persson, A.S., Smith, H.G., 2013. Seasonal persistence of bumblebee populations is affected by landscape context. *Agric. Ecosyst. Environ.* 165, 201–209. <https://doi.org/10.1016/j.agee.2012.12.008>.
- Petersen, S., Axelsen, J.A., Tybirk, K., Aude, E., Vestergaard, P., 2006. Effects of organic farming on field boundary vegetation in Denmark. *Agric. Ecosyst. Environ.* 113, 302–306. <https://doi.org/10.1016/j.agee.2005.09.016>.
- Pollard, E., 1975. A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve in 1973. *Entomol. Gaz.* 26, 79–88.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- R. Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Rader, R.A., Bartomeus, I.B., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R. G., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R.A., Brittain, C.N., Carvalho, L.G., Chacoff, N.P., Entling, M.H., Foully, B.A., Freitas, B.M., Gemmill-Herren, B.U., Ghazoul, J.V., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipolito, J., Jaggard, S., Jauber, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindstroem, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattmore, D.E., Pereira, N.D., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schuepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyorgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *Proc. Natl. Acad. Sci. USA* 113, 146–151. <https://doi.org/10.1073/pnas.1517092111>.
- Ricketts, T.H., Regatt, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol. Lett.* 11, 499–515. <https://doi.org/10.1111/j.1461-0248.2008.01157.x>.
- Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumblebees. *Biol. Conserv.* 141, 417–426. <https://doi.org/10.1016/j.biocon.2007.10.011>.
- Rundlöf, M., Lundin, O., 2019. Can costs of pesticide exposure for bumblebees be balanced by benefits from a mass-flowering crop? *Environ. Sci. Technol.* 53, 14144–14151. <https://doi.org/10.1021/acs.est.9b02789>.
- Schmitz, J., Hahn, M., Brühl, C.A., 2014. Agrochemicals in field margins - An experimental field study to assess the impacts of pesticides and fertilizers on a natural plant community. *Agric. Ecosyst. Environ.* 193, 60–69. <https://doi.org/10.1016/j.agee.2014.04.025>.
- Senapathi, D., Carvalho, L.G., Biesmeijer, J.C., Dodson, C.A., Evans, R.L., Mc Kerchar, M., Morton, R.D., Moss, E.D., Roberts, S.P.M., Kunin, W.E., Potts, S.G., 2015. The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proc. R. Soc. B* 282, 20150294. <https://doi.org/10.1098/rspb.2015.0294>.
- Shannon, C.A., 1948. Mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–423. <https://doi.org/10.1002/j.1538-7305.1948.tb01338.x>.
- Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W.H., Marini, L., 2019. Pollination contribution to crop yield is often context-dependent: a review of experimental evidence. *Agric. Ecosyst. Environ.* 280, 16–23. <https://doi.org/10.1016/j.agee.2019.04.022>.
- Tuck, S.L., Winqvist, C., Mota, F., Ahnstrom, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *J. Appl. Ecol.* 51, 746–755. <https://doi.org/10.1111/1365-2664.12219>.
- Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: death by a thousand cuts. *Proc. Natl. Acad. Sci. USA* 118, e2023989118. <https://doi.org/10.1073/pnas.2023989118>.
- Walther-Hellwig, K., Frankl, R., 2000. Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). *J. Insect Behav.* 13, 239–246. <https://doi.org/10.1023/A:1007740315207>.

- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wignall, V.R., Broolly, M., Uthoff, C., Norton, K.E., Chipperfield, H.M., Balfour, N.J., Ratnieks, F.L.W., 2020. Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community. *Behav. Ecol. Sociobiol.* 74, 152. <https://doi.org/10.1007/s00265-020-02924-y>.
- Williams, N.M., Kremen, C., 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol. Appl.* 17, 910–921. <https://doi.org/10.1890/06-0269>.
- Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., Bryden, J., Budge, G.E., Bull, J.C., Carvell, C., Challinor, A.J., Connolly, C.N., Evans, D.J., Feil, E.J., Garratt, M.P., Greco, M.K., Heard, M.S., Jansen, V.A.A., Keeling, M.J., Kunis, W.E., Marris, G.C., Memmott, J., Murray, J.T., Nicolson, S.W., Osborne, J.L., Paxton, R.J., Pirk, C.W.W., Polce, C., Potts, S.G., Priest, N.K., Raine, N. E., Roberts, S., Ryabov, E.V., Shafir, S., Shirley, M.D.F., Simpson, S.J., Stevenson, P. C., Stone, G.N., Termansen, M., Wright, G.A., 2013. Threats to an ecosystem service: pressures on pollinators. *Front. Ecol. Environ.* 11, 251–259. <https://doi.org/10.1890/120126>.
- Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records suggest a global decline in bee species richness. *One Earth* 4, 114–123. <https://doi.org/10.1016/j.oneear.2020.12.005>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. <https://doi.org/10.1111/j.2041-210X.2009.00001.x>.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models And Extensions In Ecology with R*. Springer, New York.