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RESEARCH ARTICLE

Does temporal variability in floral resources at the landscape scale impact wild bee diversity and watermelon pollination?

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Abstract

Context The stability of flower resources in agricultural landscapes affects wild bee communities. Mass flowering crops provide monospecific resource pulses for pollinators in rural landscapes, while semi-natural habitats provide biodiverse plant communities and more continuous flower resources.

Objectives In this study, we hypothesized that organically-managed watermelon fields and those surrounded by landscapes with high cover of semi-natural habitats would: i) provide abundant and stable flower resources, ii) host abundant, diverse and stable wild bee communities, iii) offer a high and stable pollination service for watermelon production.

Methods We studied wild bee communities and estimated pollination in 59 organic and conventional watermelon fields of various sizes in north central California at three periods during the watermelon flowering season. Semi-natural habitats and flower resources and their temporal variability were mapped to investigate their effects on the abundance, diversity, and stability of wild bee communities and an estimation of watermelon pollination based on flower visitation.

Results Wild bee abundance and richness were significantly higher in small organic watermelon fields. A high proportion of semi-natural habitats and land cover diversity were both positively linked to wild bee functional diversity. In contrast, the proportion of land cover offering flower resources and its variability were negatively linked to wild bee abundance, presumably due to a dilution effect of mass flowering crops. The stability of watermelon flower pollination was higher in landscapes providing high flower abundance in early spring (March).

Conclusion Our study highlights the importance of early spring as a crucial time window for wild pollinators and stability of watermelon pollination.

Keywords Floral resources · Pollination services · Agroecosystem · Organic crops

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Introduction

Crop pollination services provided by wild pollinators depend critically on pollinator diversity. Indeed, with carbon sequestration, crop pollination shows the most consistently positive of any biodiversity-ecosystem service (ES) relationships (Ricketts et al. 2016). Insect mediated pollination depends on the number of visits (pollinator abundance) and the diversity of visitors (Garibaldi et al. 2013). The presence of semi-natural habitats (SNH) in farmland supports wild bee abundance and diversity by offering floral resources and nest sites (Kremen et al., 2002; Garibaldi et al. 2011; Connelly et al. 2015). Flowering crops themselves also provide "pulsed" flower resources during short periods for some wild bees, and increase bee densities (Westphal et al. 2003; Shaw et al. 2020). However, a recent review concluded that such mass-flowering crops also dilute rather than enhance visits to any single mass flowering crop (Holzschuh et al. 2016). Cropland mosaics provide floral resources from the crops themselves but also from weed flora, wild agricultural plants (Bretagnolle and Gaba 2015; Alignier et al. 2023) and field margins (Meek et al. 2002; Burgio et al. 2006; Olson and Wackers 2007; Woodcock et al. 2007).

Quantifying the importance of the succession of resources in time and space has been identified as a research frontier in agroecology to promote ecosystem services provided by wild insects in farmland (Mandelik et al. (2012) Schellhorn et al. 2015). argues that shifts in habitat and resource use between complementary habitats enable bees to persist in highly dynamic agricultural landscapes. Williams et al. (2012) showed that resources at landscape-scale promoted colony growth, with a stronger effect of early than later season resources, but with no effect on reproductive success of bumble bees (*Bombus vosnesenskii*). The importance of early (Malfi et al. 2019) and continuous resources (Hemberger et al. 2023) was also pointed out by experimental studies on bumble bee pollination (respectively *Bombus vosnesenskii* and *B. impatiens*). Some studies have already pointed out the negative effects of resource spatial discontinuity on bumble bee occurrence in the US (Hemberger et al. 2023) and pollination of broad bean used as phytometer (Eckerter et al. 2022). To our knowledge, few studies have investigated the effect of flower resource stability at landscape scale on wild bee communities and pollination service for a commercial crop.

The role of biodiversity in providing stable ecosystem service delivery, like pollination, has received much more theoretical with the "insurance hypothesis" (Tilman, 1996; Yachi and Loreau, 1999) than experimental tests. The quantitative results from a meta-analysis showed contrasting biodiversity effects on buffering of environmental variance depending on the nature of the perturbation (nutrient versus warming) and amplitude (Balvanera et al. 2006). The importance of SNH to support stable biodiversity and thus providing stable ES was demonstrated by a meta-analysis based on 29 studies on pollination (Garibaldi et al. 2011). They showed that stability of flower-visitor richness, visitation rate and fruit set of various crops decreased with the isolation from SNH.

In this study, we explore the link between floral resource stability in the landscape, considering wild plants and crops, on bee species/taxonomic diversity, bee functional diversity and pollination service to watermelon (*Citrullus lanatus*) in organic and conventional fields in the California Central Valley, USA. Watermelon relies entirely on insect pollination to produce fruits (Lonsdorf et al. 2009; Delgado-Carrillo et al. 2024) and can depend more on wild bees than honeybees in some contexts (Winfree et al. 2007). Moreover, watermelon production stability contributes to the economic sustainability of the farms. We use the watermelon-wild bee system to test if organically-managed watermelon fields and those surrounded by landscapes with high cover of semi-natural habitats would: i) provide abundant and stable flower resources, ii) host abundant, diverse and stable wild bee communities, iii) offer a high and stable pollination service for watermelon production.

Materials and methods

Study sites and field sampling

The study was conducted in the Central Valley of California, USA in a 64×49 km region including parts of Yolo and Solano Counties (Fig. 1). The area is characterised by intensive agriculture of tree fruit orchards (almond and walnut) and diverse annual row crops, with remnants of semi-natural habitats including chaparral, oak woodland, oak savannah and open

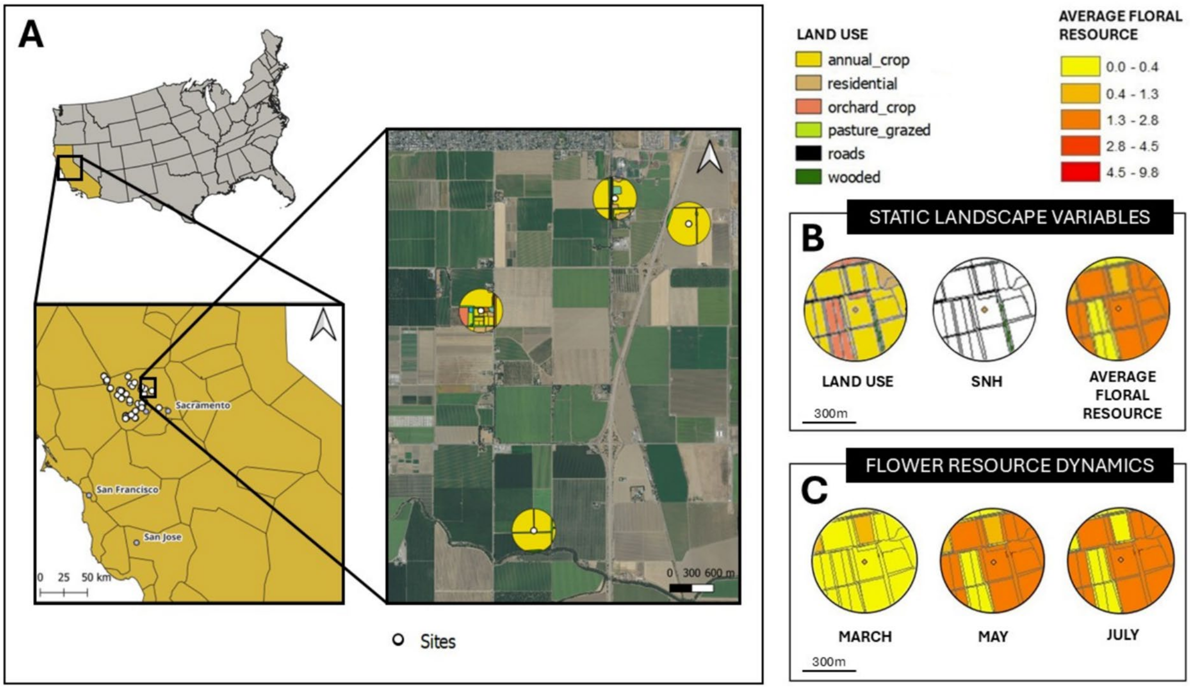

Fig. 1 **A**. Location of the 59 watermelon fields in California. **B**. example of static landscape variables (land use, Semi Natural Habitat, average flower resource) around a studied watermelon field. **C**. Dynamic of flower resource in a buffer of 330 m

riparian woodland (see Kremen et al. 2002 for a full description of the study region).

From 2010 to 2012, we studied 59 watermelon fields and their surroundings. Fields belonged to 33 farms under either organic ($n = 41$) or conventional ($n = 18$) management. In California, organic farms have no synthetic fertilizer, pesticide or herbicide use, organic farms do not use GMO seeds. In California, conventional farms are allowed to use synthetic fertilizer, pesticide and herbicide in their fields (see Lonsdorf et al. (2024) for a detailed list of the pesticide use). The fields varied in size from 183 to 42 544 m^2 (Table 1). It was not possible to fully disentangle management type from field size, because organic fields were typically smaller (16 035 ± 1 609 m^2; mean ± SE) than conventional ones (74 490 ± 9 766 m^2) ($F = 23.44$, $df = 1$, $p < 0.01$). Most of the farmers grows diploid varieties of watermelon (some also triploid varieties), it was not possible to study only one watermelon variety. For a given year, study fields were at least 1 km apart. However, according to crop rotation, some fields belonging to the same farm, were less than 1 km apart between years. Each field and its surrounding on-farm area was sampled on three separate dates (hereafter sample rounds) within a year during the watermelon flowering period, from June to August, separated by an average of 5 days within a farm site.

In each field and sample round, we first observed bee visitation on watermelon flowers, to estimate pollination service, and then we collected wild bees to assess taxonomic and functional diversity.

Observations of flower visitation and pollination service estimates

To assess visitation to watermelon flowers, we recorded bees visiting flowers during four replicated 17-min observation-periods along a 50 m transect in a row of watermelon during peak bloom. The four observation-periods were spaced between 8:00 and 13:00. To be considered as a visitor, a bee had to contact the central parts of the flower, i.e. the anthers or stigma, for at least 0.5 s. Few native bees are identifiable to species level in the field; we therefore identified native bees to four species groups: i) bumble bees, ii) large bees, other than bumble bees, iii) green bees and iv) small bees (for a full description of the groups, see

Table 1 Descriptive statistics of predictors used in the GLMM models (minimum, median, maximum values) at field (management type, field size) and landscape scales (floral resources abundance, diversity and temporal variability) for the two buffers (190 m, 330 m)

		190 m Buffer			330 m Buffer		
Variables	Description	Min	Med	Max	Min	Med	Max
Management	Farming system: organic (O) or conventional (C)	C: n = 18 / O: n = 41					
FieldSize	Field size (m^2)	183.5	10,530.9	242,544	183.5	10,530.9	242,544
Flo_Max	Maximum single-month value of flower abundance	175,359	555,379	1,878,509	329,606	1,700,990	5,504,989
Flo_Min	Minimum single-month value of flower abundance	0.0	7038.1	162,224.6	0.0	32,371	626,155
Flo_Mean	Mean value of flower abundance among months	71,416	224,319	505,400	173,252	703,380	1,486,559
Flo_CV	Coefficient of variation of flower abundance	0.496	1.011	1.990	0.391	1.047	1.936
Flo_%	The proportion of land cover providing flowers	0.187	0.673	1.000	0.183	0.591	0.996
Flo_Div	The diversity of land cover providing flowers	0.072	1.532	2.739	0.478	1.861	2.958
SNH_%	The proportion of semi-natural habitats	0.0	0.065	0.602	0.0	0.117	0.568
SNH_Div	The diversity of semi-natural habitats	0.0	0.901	2.082	0.0	1.169	2.011
LandCover_Div	The diversity of land cover	0.216	2.127	3.318	0.762	2.477	3.558

Winfree et al. (2007)). We also assessed the number of watermelon flowers observed in ten 1m^2 quadrats spaced along the transect, which allowed us to estimate the number of visits per flower per day.

To estimate pollination service, we first summed the total number of visits per flower per day per visitor class, based on our observations of watermelon flowers. We then multiplied this value by a pollen deposition coefficient for each class of visitor. The visitor classes and pollen deposit for each class is based on observational studies on watermelon fields in the study same area in California (Kremen et al. 2002). Coefficients were determined following Winfree et al. (2007) method by drawing the median value from 1000 random draws from the empirically determined distribution of pollen grains deposited on watermelon during single visits by that visitor class. The pollination service estimate variable was the mean per field (among the three sampling dates) of the estimated median pollen grains deposit per flower per observation date.

The variability of the pollination service estimates per field within a year, among the three sample rounds, was estimated by the coefficient of variation (CV = mean / SD*100).

For convenience, the term "pollination" was used hereafter in the text, instead of "pollination service estimates".

Wild bees collection

Immediately after each of the four observation-periods in each day, bees visiting watermelon flowers were netted over 10 min along the same 50 m transect. Following netting on the watermelon field, we netted bees along a bee-walk transect in a 1 ha buffer around the field for 20 min in the morning and afternoon. The buffer area included field margins, additional non-watermelon crop fields and on farm semi-natural vegetation. During netting, we stopped the stopwatch while handling bees in the net and processing, to avoid differences in netting time between transects and minimize collector bias, given the differences in handling time among bee taxa. All field data were collected under good weather conditions: sunny and wind < 3 m/s. All netted bees were pinned and identified to species in the lab using keys and a comprehensive reference collection. Final identifications were confirmed by Robbin W Thorp (UC Davis). Bees netted in the watermelon field and around (the bee-walk transect) are considered hereafter as the whole community of bees, which was the community considered throughout this study.

Apis mellifera was present in all study fields. Hives are rented for watermelon pollination on all farms and for many crops flowering throughout the landscape. We hypothesized that honey bees were homogeneously present in the study area. This study aimed at focusing on wild bees only and *A. mellifera* was not recorded.

Bee taxonomic and functional diversity

Bee taxonomic diversity was assessed using species richness. Bee functional diversity was calculated from a database of functional traits maintained in the Williams lab (Forrest et al. 2015). We determined seven functional traits (inter tegular distance (ITD), median day of flight season, flight season duration, nest location, nesting behaviour, sociality and lecty) of all recorded bee species in our study. For 13 species which are not in the database, we measured traits directly from specimens at the Williams lab and Bohart Museum of Entomology UC Davis (ITD and flight season duration) and from published information (nesting, sociality and lecty) (complete database in SM 1). We used these traits to calculate functional dispersion (FDis) for the whole wild bee community at each site. FDis is the weighted mean distance in multidimensional trait space of individual species to the weighted centroid of all species, where weights correspond to the relative abundances of the species (Laliberté and Legendre 2010). FDis is, by construction, unaffected by species richness, can be computed from any distance or dissimilarity measures, can handle any number and type of traits (including more traits than species), is not strongly influenced by outliers, and can take into account species relative abundances. The variability of functional dispersion (CV_FDis) was defined as the coefficient of variation of FDis among the three sample rounds within a year. FDis was calculated using the "FD" package in R (Laliberté and Legendre 2010).

Landscape variables

Land cover data were composed hierarchically using diverse sources. We started with the crop commodity layers from the Sacramento Area Council of Governments Open Data Portal which provides crop identities for all agricultural parcels (https://data.sacog.org/datasets/7daf183f934c4131abd74447734b75e2_0/explore?location=38.616265%2C-121.943119%2C10.48). We then ground-truthed crop data, residential, non-crop commercial and municipal areas within a 330 m-radius around the transect centroid. Finally, we used aerial photographs (1 m resolution) to aid interpretation of areas we could not access via ground-truthing.

Roadside margins, which are often covered with weedy vegetation, were estimated from the regional transportation layer provided by Caltrans GIS Data portal (https://gisdata-caltrans.opendata.arcgis.com/search?tags=Highway) and buffered to 5 m on each side. Semi-natural habitats (SNH) corresponded to perennial habitats with low intensity management. It encompassed woody habitats (woods, riparian habitat, hedgerow, oak savanna) and open habitats (fallow, field margin, grassland and pasture). Eventually, 27 different types of land cover were kept in the analysis.

Land cover around each studied watermelon field was extracted using circular buffers (ArcGis 9.1). Landscape variables were assessed in circular buffers at two different radii corresponding to different bee communities: i) the bees netted on watermelon flowers only and ii) the whole community of bees netted in the watermelon field and in the 1 ha buffer. We estimated the distance moved by each species thanks to the equation proposed by Greenleaf et al. (2007) relating bee Inter Tegular Distance (ITD) with their typical homing distance (see SM 1 for the ITD). For each community we calculated an abundance weighted average distance (excluding the two Xylocopa species which exhibited a large ITD, represented only by 3 individuals in each community). The smaller radius (190 m) was obtained for the wild bees netted on watermelon flowers. This buffer includes the field margins and adjacent fields (mean field size ~ 1 ha, see Table 1). The larger radius (330 m) was obtained for the whole bee community. It captured potential larger-scale effects of resource availability in the landscape.

Flower resources

Land cover data were combined with estimates of floral density for different habitat types to calculate the quantity, diversity and temporal variability of flower resources at each study site. We obtained estimates of flower density from records conducted in the same study region in 2003–2004 in 20 different habitat types, five times during the growing season (Williams et al. 2012). We assumed that crops retain a similar flower density to what they were 6–10 years earlier, for example tomato fields and fruit orchards are grown at the same planting densities, or they remain the same orchards. Watermelon flower densities during the flowering period were based on surveys made following each bee observation period. When no data were available to estimate flower density a score of 0 was attributed (see SM 2 for the details of the flower density attributed to each land cover type). The "Unknown" land cover represented 13.4% of the total area covered by the 330 m buffers, of which 29% was built area and 39% annual crop.

Monthly average flower densities were calculated among all sites over the three study years. Total floral resource availability in each landscape for each month was then estimated by aggregating data for the different habitat types located within the 190 and 330 m radius buffers. We estimated the temporal variability of flower resources (Flo_CV) as the CV of flower resources among months. The minimum (Flo_Min) and maximum (Flo_max) values of flower resources in a month were also identified.

The diversity of land cover providing floral resources (FLO_Div) was estimated using the Shannon diversity index of land cover (based on their surface area) offering flowers during at least one month in the flowering period.

Statistical analysis

All the statistical analyses were performed using R 4.2.1 (R Core Team 2021).

We investigated the effects of the different field and landscape descriptors (at 190 and 330 m radii from the field) on wild bee species richness, abundance, functional dispersion, as well as their variability in time (i.e., the coefficient of variation among the three sample rounds within a year). Pollination (for the whole season, and the coefficient of variation) was only investigated at the 190 m scale as its estimation is based on the abundance of bees visiting watermelon flowers. This list of species was used to estimate the 190 m radius. All numeric explanatory variables at field and landscape scales (Table 1) were scaled. Our hypotheses were tested using generalized linear mixed models (GLMM) with a Gaussian error distribution (species richness, FDis, ln[Poll], CV_Ab, ln[CV_Richness], CV_FDis and ln[CV_Poll]) or a Poisson error distribution (abundance), and with farm and year as random factors. To avoid collinearity, variables with VIF > 4 were eliminated one by one from the models using a stepwise procedure and the function check_collinearity (package *performance* (Lüdecke et al. 2021)). Complete models (with all explanatory variables except those with a VIF > 4) were then analysed using a multimodel inference (MMI) procedure and model averaging, which deals with model selection uncertainty (Lukacs et al. 2009) and is useful when running complex mixed models(Zuur et al. 2009). Following the MMI procedure, we constructed models for each combination of the explanatory variables. All models, fitted by Maximum Likelihood (ML), were ranked based on the corrected Akaike information criterion (AIC). Then, we computed standardised average regression coefficients weighted by the Akaike weights across supported best models (Δ AIC < 2), using dredge function of the *MuMIn* package (Barton 2020). We report in the results the conditional model average. We calculated the relative importance of each variable (variable weight), which is the sum of the weights of all the models in which that factor was present in the set of best models. Variable weight reaches 1 for the more important variables, which appear in all top models, and is equal to zero if the variable is not present in any of the top models (Symonds and Moussalli 2010). All best models used for model averaging were checked individually for normality of residuals and homogeneity of variance using package DHARMa (Hartig and Hartig 2021). We thus estimated the variance explained by the models by calculating the R^2 statistic for all models within the subset of best models, and then calculating the mean of these values, weighted by Akaike weights. We report marginal R^2 (R^2m) which is the part of the variability explained by the fixed factors and is considered as a good indicator of the goodness of fit of the model (Nakagawa and Schielzeth 2013), and conditional R^2 (R^2c) which also takes into account the variance explained by the two random factors.

Results

A total of 3182 individuals belonging to 51 wild bee species were collected during the three years of the study (see SM 1 for complete species list). Two species comprised 74% of the individuals: *Lasioglossum (Dialictus) incompletem* (40%) and *Halictus tripartitus* (34%).

The effect of field and landscape variables on wild bee abundance, diversity and pollination service estimates

Wild bees were more abundant in organic farms than in conventional farms (Fig. 2, Table 2) and abundance also decreased with field size (Fig. 3A). At the landscape scale, variability of floral resources, the proportion of land cover providing flowers and land cover diversity negatively influenced wild bee abundance (Table 2, Fig. 3B, C, D). As was true for abundance, wild bee richness was higher at organic farms than conventional ones (Fig. 2, Table 2) but there were no significant effects of landscape variables.

Our results showed a higher functional dispersion of wild bee traits in landscapes exhibiting higher cover of SNH (Table 2, Fig. 3E). None of the variables we examined, explained variation in the estimated pollination of watermelon crops.

The effects of local and landscapes variable on the stability of wild bee abundance, diversity and pollination services estimates

The variability of wild bee abundance (i.e. the CV of abundance among sample rounds) was higher in landscapes with a higher temporal variability of flower abundance (Table 3, Fig. 4A). Wild bee abundance was also more variable over time at sites with higher proportions of land cover providing flower resources (Table 3, Fig. 4B).

The variability of bee species richness did not respond to any of the field or landscape variables (Table 3). The variability of wild bee functional dispersion among the three sample rounds was negatively influenced by the diversity of land covers (Table 3, Fig. 4C). Pollination variability was lower

Fig. 2 Comparison of wild bee abundance (**A**) and richness (**B**) in conventional and organic watermelon fields for the whole season. Boxes represent the 1st (bottom line), median and 3rd quartile (top line) of the distribution. Whiskers extend to 1.5 times the interquartile range. P-values are given for a t-test between conventional and organic management and indicate a significant difference between the means of the two variables

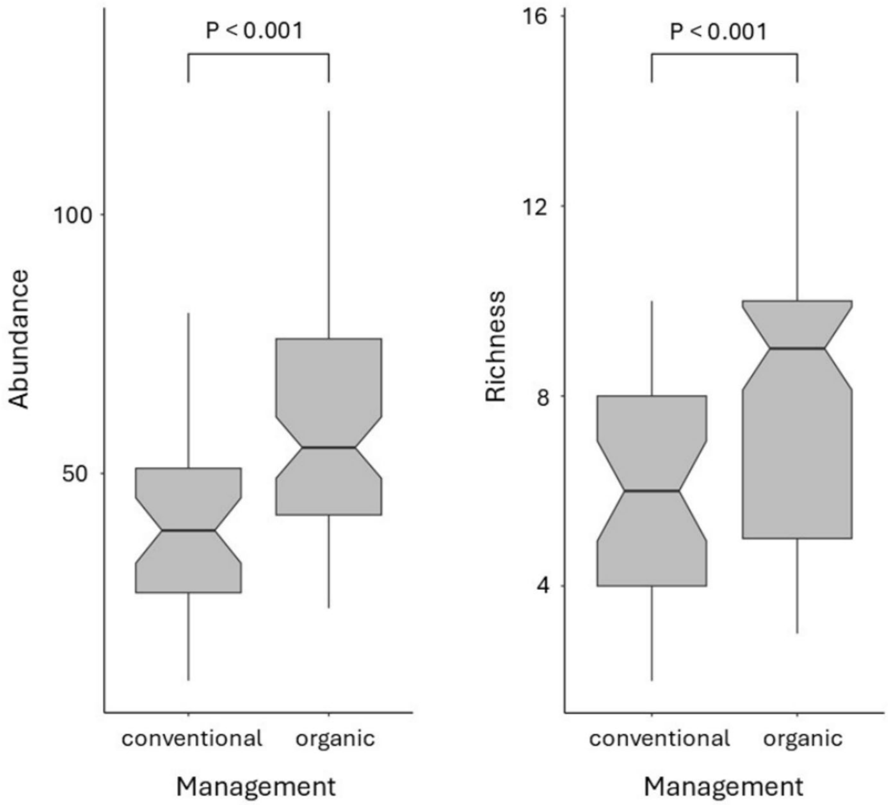

Table 2 Results of mixed models of wild bee abundance, richness, functional trait dispersion (FDis) and estimated pollination, as a function of field-scale and landscape-scale variables (in a 330 m buffer except for pollination) and resulting from multi-model inference and averaging. Weight, estimated coefficient, standard error (SE) and p-value are given. Conditional R^2 (R^2c—total R^2) and marginal R^2 (R^2m—only fixed effects) are weighted means of the R^2 of all models with $\Delta AIC < 2$. See Table 1 for full names of predictor variables. For readability, we report here the results for significant effects only or for variables with a relative importance (weight) greater than 0.60. Variables were listed according to their weight in the average model

Explanatory fixed variables	Estimate	SE	p-value	Weight
Abundance				
Flo_CV	− 0.14	0.04	0.002	1.00
Flo_%	− 0.12	0.04	0.001	1.00
Organic management	0.39	0.14	0.005	1.00
LandCover_Div	− 0.15	0.05	0.005	1.00
R^2m / R^2c	0.29 / 0.91			
Richness				
Organic management	2.31	0.84	0.007	1.00
R^2m / R^2c	0.19 / 0.38			
FDis				
SNH_%	0.03	0.01	0.001	1.00
R^2m / R^2c	0.26 / 0.36			
Pollination (190 *m radius buffer)*				
No significant effect				

in landscapes with high values of minimum floral resources (Fig. 4D) and was higher in landscapes (190 m radius buffer) with a greater diversity of SNH (Fig. 4E).

Discussion

Our study confirmed that wild bee abundance and species richness were strongly affected by management type, both being higher in organic fields. However, organic fields were also smaller than conventional ones in our study system ($F = 23.44$, $df = 1$, $p < 0.01$), so it is quite difficult to disentangle the size effect and the management type in our study. In the same study area, it was shown that the combination of organic field and proximity of SNH, could provide full pollination service to watermelon production (Kremen et al. 2002). The benefits of organic farming systems for wild bee pollinators have been reported by other studies in other context, for example Carrié et al. (2018a) have shown that among-year stability of bumblebee species richness was higher in organic than in conventional cereal fields. Regarding field size, small scale conventional agriculture with high field border density consistently increases wild bee abundance and seed set of Radish (*Raphanus sativus*) across European agricultural landscapes (Hass et al. 2018). Field size, together with crop heterogeneity were shown to positively influence multitrophic diversity, including wild bees, in European and Canadian landscapes (Sirami et al. 2019). In our study area, organic farming leads to higher input of compost adding considerable soil organic matter, higher flowering weed diversity at some times of the season and greater local scale crop diversity both spatially and temporally. Wild bee abundance and diversity could have benefit from all these factors and our study was not designed to disentangle these positive effects on biodiversity.

In our study, three components of the landscape influenced bee diversity and pollination: floral resources, semi-natural habitats and land cover diversity. We showed that the proportion of habitats offering floral resources in the landscape had a negative effect on wild bee abundance, but also on the stability of their abundance. These unexpected results are in opposition with an important literature demonstrating the positive effect of flower resources on wild bee abundance and diversity (Potts et al. 2003; Crone and Williams 2016; Orford et al. 2016). In our study, habitats offering flower resources included flower resources coming from semi-natural habitats and from crops. In our Californian system, high cover of flowers was mainly due to mass flowering crops (MFC) which provide abundant floral resources only during a short period of time (watermelon, sunflower, orchards). While flowering, sunflower and orchards could pull bees away from the studied watermelon field. Additionally, they may not provide adequate resources to sustain bee populations. The current literature on the effects of MFC on pollinators and pollination shows scale dependent, positive as well as negative effects. Westphal et al. (2003) advocate that mass flowering plants enhance pollinator densities at a landscape scale. Similarly, early flowering oilseed rape has a beneficial effect on colony growth but no effect on sexual offspring of bumblebees (Kennedy et al. 2013). However, other studies have shown a

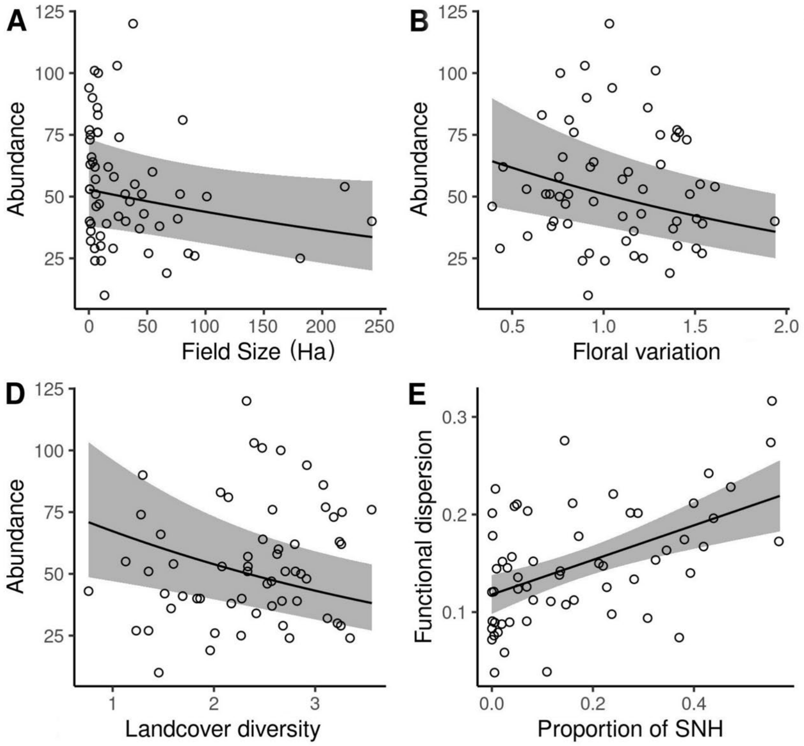

Fig. 3 Responses of wild bee abundance (**A–D**) and functional dispersion (**E**) to the significant variables ($p < 0.05$). Shaded area indicates 95% confidence interval

transient pollinator dilution and reduced pollination of wild plants because of increased competition between crop plants and grasslands (Klein et al. 2012; Brittain et al. 2013; Van Reeth et al. 2018). A recent simulation study has shown a negative effect on crop pollination of flower patches if they are located close to the insect pollinated crop field (less than 1 km) but a positive effect for more remote insect pollinated crop fields (between 1 and 2 km) (Desaegher et al. 2021). Moreover, the study of Beyer et al. (2021)) shows a positive effect of past MFC and a transient dilution effect of the current MFC on wild bee densities.

In our study, flower resource variability around the studied watermelon fields also showed consistent negative effects on bee abundance and its stability. The variability of flower abundance reflects a lack of resource continuity for pollinators. Planting even small areas of late-blooming flowers of red clover to increase resource continuity removed the flower resource bottleneck and markedly enhanced the abundance and reproductive success of bumble bees in the landscape, during and after blooming (Rundlöf et al. 2014). A similar positive effect of continuous flowering of purple tansy (*Phacelia tanacetifolia*) on total mass gain of *Bombus impatiens* colonies has been demonstrated in an experimental study comparing continuous versus pulsed resources (Hemberger et al. 2022). However, they found no effect on colony growth rate or total gyne production.

We found a positive effect of the minimum monthly value of flower abundance in the landscape on the stability of watermelon pollination. In our study, this minimum value always corresponded to the first flower records in March. Winfree et al. (2015) identified three bee species abundant on watermelon flowers and depositing a high number of pollen grains per individual: *Halictus tripartitus*, *Lasioglossum incompletem* and *Xenoglossa pruinosa*. The first two exhibited a median day of flight season slightly before the average of the 51 recorded species (respectively 6 and 4 days before the average) and the latter 9 days after the average. *Halictus tripartitus* and *L. incompletem* are not the earliest-emerging species of the data set, and they are respectively partially

Table 3 Results of mixed models of variation of wild bee abundance (CV_Ab), richness (CV_Richness), functional trait dispersion (CV_FDis) and estimated pollination (CV_Poll), as a function of field-scale and landscape-scale variables (in a 330 m buffer except for pollination) and resulting from multi-model inference and averaging. Weight, estimated coefficient, standard error (SE) and p-value are given. Conditional R^2 (R^2c—total R^2) and marginal R^2 (R^2m—only fixed effects) are weighted means of the R^2 of all models with $\Delta AIC < 2$. For readability, we present the results for significant effects only or for variables with a relative importance (weight) greater than 0.60 Variables were listed according to their weight in the average model

Explanatory fixed variables	Estimate	SE	p-value	Weight
CV_Ab				
Flo_%	0.08	0.03	0.010	1.00
Flo_CV	0.06	0.03	0.045	0.89
R^2m / R^2c	0.20 / 0.20			
CV_Richness				
No significant effect				
CV_FDis				
LC_Div	− 0.12	0.05	0.017	1.00
R^2m / R^2c	0.16 / 0.20			
CV_Poll *(190 m radius buffer)*				
Flo_Min	− 0.30	0.11	0.008	1.00
SNH_Div	0.23	0.11	0.037	0.81
R^2m / R^2c	0.12 / 0.28			

social and eusocial species. Abundant early season resources are important for colonies of social bees even if their median day of flight is not early in the season, as demonstrated by Malfi et al. (2019) for *B. vosnesenskii*. The two species, *H. tripartitus* and *L. incompletem,* strongly influenced the pollination estimates (by their high pollen deposition) and thus the trend seen in the relationships with landscape variables. Their relatively early flight, sociality and high abundance in the data set may explain why pollination stability was greater for high values of minimum monthly flower abundance. Our results suggest that: i) early flower abundance (corresponding to March) could be a bottleneck in our study system, ii) a high cover of flower abundance, early in the season, when the flower resources are scarce, and close to watermelon fields (within a radius of 190 m) benefits pollination stability.

Variables related to SNH were not often selected in the models, perhaps because some of their positive effect on wild bees, i.e. providing floral resources, was partly captured by the floral resource variables. We showed a positive effect of SNH proportion on wild bee functional diversity but a negative effect of SNH diversity on pollination stability. The positive effect of SNH on bee diversity is supported by many other studies (Garibaldi et al. 2011). Eeraerts et al. (2019) found a positive effect of the proportion of SNH at a small scale (100 m) on wild pollinator abundance in sweet cherry orchards. Semi-natural habitats provide abundant and diverse floral and nesting resources, and in this way support many bee species with different functional traits (Potts et al. 2005; Ockinger and Smith 2007; Rivers-Moore et al. 2020). In our study, the positive effect of the proportion of SNH habitat on functional dispersion might thus reflect a higher availability and diversity of nesting sites (in addition to flower resources) for below ground, above ground and stem nesting wild bees, in grasslands (Carrié et al. 2018b) and in forest edges (Bailey et al. 2014). The availability in nesting sites has been poorly investigated up to now because nests are not easily detected in the field. Remote sensing could be a useful tool to determine carrying capacity in some herbaceous SNH such as grassland, using slope and proportion of bare ground (Carrié et al. 2018b), but additional studies are needed to investigate nest site availability in other types of SNH.

Our result on the negative effect of SNH diversity on the stability of pollination service estimate is not convergent with recent studies showing a positive effect of SNH habitat diversity on the continuity of floral resources (Rivers-Moore et al. 2020) and wild bee richness (Maurer et al. 2022). The two most abundant and strongest contributors to pollination in our study (*H. tripartitus and L. incompletem)* are broad generalist feeders, and ground nesting bees. Forrest et al. (2015) compared bee functional diversity in organic, conventional fields and natural habitats and showed that farms of both types hosted bee communities distinct from those of natural sites. The bee communities hosted by farmland showed similar functional traits (such as below ground nesting sites), filtered by framing practices. Therefore, diversity of SNH, by adding woody semi-natural habitats, may not have been in favour to the social, ground nesting wild bee species, and strongly involved in pollination. Finally, we showed that land cover diversity was negatively related to wild bee abundance, and positively to functional dispersion stability. A possible negative

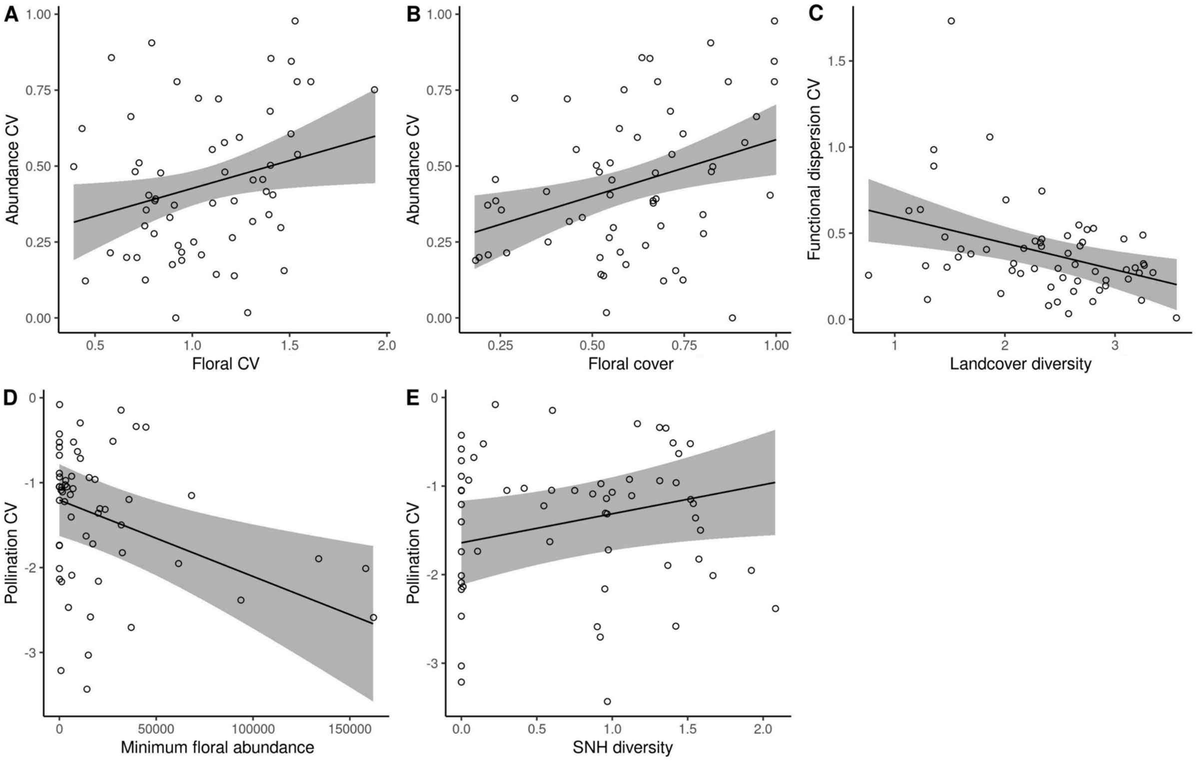

Fig. 4 Responses of the variability of wild bee abundance (**A, B**), functional dispersion (**C**) and pollination (**D, E**) to the significant landscape variables ($p < 0.05$) in a radius of 330 m. Shaded area indicates 95% confidence interval

correlation between wild bee abundance and functional dispersion is understandable: functional dispersion is by construction independent from species richness and could be negatively linked to species abundance, particularly when abundance is driven by only two species, exhibiting similar ecological traits. However, their opposite link with land cover diversity is hardly explainable. Landscapes with high land cover diversity may contain unfavourable land cover types such as built areas (towns, roads), not in favour of the two bee species driving the abundance but favouring species with life history traits different from those of these two dominant species.

In our study, some variables showed opposing effects depending on the variable explained or when temporal variability was taken into account. For example, it could seem contradictory that SNH cover had a positive effect on functional dispersion while SNH diversity had a negative effect on pollination stability. Similarly, land cover diversity had a negative effect on wild bee abundance but a positive effect on the stability of functional dispersion. (Galpern et al. 2021) investigated wild bee responses to cropland landscape complexity and found evidence for a temporally-variable and taxon-specific abundance response by wild bees across a broad gradient of conditions. They conclude that non-crop land covers in agricultural landscapes may not have unified benefits for the whole bee community. In our case, variables favouring the abundance of the most dominant species and thus driving the responses of abundance-related variables may not favour taxonomic and functional diversity of wild bees.

One other limitation of our study is the choice to not consider honey bees, which are also important pollinators of watermelon (Reilly et al. 2020). However, wild native bees are generally more effective pollinators than honey bees on a per visit basis (Page et al. 2021). Wild insect visitation almost universally increases crop pollination, whereas honey bee abundance only sometimes increases yield (Garibaldi et al. 2013). It is also hard to say whether the same landscape factors that support wild bees in our system could be applied to honey bees. Access to native prairie habitat has been shown to benefit honey bees in other systems (Dolezal et al. 2019), although the migratory nature of commercial beekeeping in the U.S. makes it harder to determine when and where these resources are most useful in supporting managed honey bee populations. Ultimately, understanding how SNH and flower plantings can simultaneously support wild and managed bees remains an important and fruitful field for future study.

Conclusion

Our study confirmed that organic management had a strong, consistent and positive effect on richness and abundance of wild bees. We showed that the proportion of the land cover offering flower resources and its variability were negatively linked to wild bee abundance and its stability, presumably due to an ambiguous effect of MFC. We also revealed the positive effect of a high proportion of SNH in the landscape on functional dispersion. Our approach based on the temporal variability of flower resources allowed us to shed light on early spring as a crucial time window for pollination stability. As such, our results suggest that providing flower resources at the very beginning of the growing season and maintaining or restoring a high proportion of SNH in the close vicinity of small and organic crops would increase bee abundance, functional diversity and the stability of watermelon pollination by wild bees.

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Author contributions N.M. W. led the study conception and data collection. Data analyses were performed by A. O., A. C., J. R. M., C. A. B. and M. L. P. The first draft of the manuscript was written by A. O. N. M. W. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

References

Alignier A, Lenestour N, Jeavons E et al (2023) Floral resource maps: a tool to explain flower-visiting insect abundance at multiple spatial scales. Landsc Ecol 38(6):1511–1525

Bailey S, Requier F, Nusillard B, Roberts SPM, Potts SG, Bouget C (2014) Distance from forest edge affects bee pollinators in oilseed rape fields. Ecol Evol 4:370–380

Balvanera P, Pfisterer AB, He JS, Nakashizuka T, Raffaelli D, Shmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9:1146–1156

Barton K (2020) MuMIn: multi-model inference. R Packag Vers 1(43):17

Beyer N, Gabriel D, Westphal C (2021) Contrasting effects of past and present mass-flowering crop cultivation on bee pollinators shaping yield components in oilseed rape. Agric Ecosyst Environ 319:107537

Bretagnolle V, Gaba S (2015) Weeds for bees? A review. Agron Sustain Dev 35:891–909

Brittain C, Williams N, Kremen C, Klein AM (2013) Synergistic effects of non-Apis bees and honey bees for pollination services. Proc Biol Sci 280(1754):20122767

Burgio G, Ferrari R, Boriani L, Pozzati M, Van Lenteren J (2006) The role of ecological infrastructures on Coccinelidae (Coleoptera) and other predators in weedy field margins within northern Italy agroecosystems. Bull Insectol 59:59–67

Carrié R, Ekroos J, Smith HG (2018a) Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. Biol Conserv 227:48–55

Carrié R, Lopes M, Ouin A, Andrieu E (2018b) Bee diversity in crop fields is influenced by remotely-sensed nesting resources in surrounding permanent grasslands. Ecol Indic 90:606–614

Connelly H et al (2015) Landscape simplification decreases wild bee pollination services to strawberry. Agri Ecosyst Envi 51-56

Crone EE, Williams NM (2016) Bumble bee colony dynamics: quantifying the importance of land use and floral resources for colony growth and queen production. Ecol Lett 19(4):460–468

Delgado-Carrillo O, Marten-Rodriguez S, Ramirez-Mejia D et al (2024) Pollination services to crops of watermelon (*Citrullus lanatus*) and green tomato (*Physalis ixocarpa*) in the coastal region of Jalisco, Mexico. PLoS ONE 19(7):e0301402

Desaegher J, Sheeren D, Ouin A (2021) Optimising spatial distribution of mass-flowering patches at the landscape scale to increase crop pollination. J Appl Ecol 58(9):1876–1887

Dolezal AG, St Clair AL, Zhang G, Toth AL, O'Neal ME (2019) Native habitat mitigates feast-famine conditions faced by honey bees in an agricultural landscape. Proc Natl Acad Sci U S A 116(50):25147–25155

Eckerter PW, Albrecht M, Bertrand C et al (2022) Effects of temporal floral resource availability and non-crop habitats on broad bean pollination. Landsc Ecol 37(6):1573–1586

Eeraerts M, Smagghe G, Meeus I (2019) Pollinator diversity, floral resources and semi-natural habitat, instead of honey bees and intensive agriculture, enhance pollination service to sweet cherry. Agric Ecosyst Environ 284:106586

Forrest JRK, Thorp RW, Kremen C, Williams NM (2015) Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. J Appl Ecol 52:706–715

Galpern P, Best LR, Devries JH, Johnson SA (2021) Wild bee responses to cropland landscape complexity are temporally-variable and taxon-specific: evidence from a highly replicated pseudo-experiment. Agric Ecosyst Environ 322:107652

Garibaldi LA, Steffan-Dewenter I, Kremen C et al (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol Lett 14(10):1062–1072

Garibaldi LA, Steffan-Dewenter I, Winfree R et al (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339(6127):1608–1611

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153(3):589–596

Hartig F, Hartig MF (2021) Package 'dharma'. R-project. org/Package 'dharma'.

Hass AL, Kormann UG, Tscharntke T et al (2018) Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc Biol Sci. https://doi.org/10.1098/rspb.2017.2242

Hemberger J, Witynski G, Gratton C (2022) Floral resource continuity boosts bumble bee colony performance relative to variable floral resources. Ecol Entomol 47(4):703–712

Hemberger J, Bernauer OM, Gaines-Day HR, Gratton C (2023) Landscape-scale floral resource discontinuity decreases bumble bee occurrence and alters community composition. Ecol Appl :a 33(7):e2907

Holzschuh A, Dainese M, Gonzalez-Varo JP et al (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol Lett 19(10):1228–1236

Kennedy CM, Lonsdorf E, Neel MC et al (2013) A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol Lett 16(5):584–599

Klein A-M, Brittain C, Hendrix SD, Thorp R, Williams N, Kremen C (2012) Wild pollination services to California almond rely on semi-natural habitat. J Appl Ecol. https://doi.org/10.1111/j.1365-2664.2012.02144.x

Kremen C, Williams NM, Thorp RW (2002) Crop pollination from native bees at risk from agricultural intensification. Proc Natl Acad Sci U S A 99(26):16812–16816

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from mutliple traits. Ecology 91:299–305

Lonsdorf E, Kremen C, Ricketts T, Winfree R, Williams N, Greenleaf S (2009) Modelling pollination services across agricultural landscapes. Ann Appl Biol 103(9):1589–1600

Lonsdorf EV, Rundlöf M, Nicholson CC, Williams NM (2024) A spatially explicit model of landscape pesticide exposure to bees: development, exploration, and evaluation. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2023.168146

Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D (2021) Performance: an R package for assessment, comparison and testing of statistical models. J Open Source Softw 6(60):3139

Lukacs PM, Burnham KP, Anderson DR (2009) Model selection bias and Freedman's paradox. Ann Inst Stat Math 62(1):117–125

Malfi RL, Crone E, Williams N (2019) Demographic benefits of early season resources for bumble bee (*B. vosnesenskii*) colonies. Oecologia 191(2):377–388

Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. Ecol Appl 22(5):1535–1546

Maurer C, Sutter L, Martínez-Núñez C, Pellissier L, Albrecht M (2022) Different types of semi-natural habitat are required to sustain diverse wild bee communities across agricultural landscapes. J Appl Ecol 59(10):2604–2615

Meek B, Loxton D, Sparks T, Pywell R, Pickett H, Nowakowski M (2002) The effect of arable field margin composition on invertebrate biodiversity. Biol Conserv 106:259–271

Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142

Ockinger E, Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. J Appl Ecol 44:50–59

Olson DM, Wackers FL (2007) Management of field margins to maximize multiple ecological services. J Appl Ecol 44:13–21

Orford KA, Murray PJ, Vaughan IP, Memmott J (2016) Modest enhancements to conventional grassland diversity improve the provision of pollination services. J Appl Ecol 53(3):906–915

Page ML, Nicholson CC, Brennan RM et al (2021) A meta-analysis of single visit pollination effectiveness comparing honeybees and other floral visitors. Am J Bot 108(11):2196–2207

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P (2003) Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84:2628–2642

Potts SG, Vulliamy B, Roberts SPM et al (2005) Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology 30:78–85

Reilly JR, Artz DR, Biddinger D et al (2020) Crop production in the USA is frequently limited by a lack of pollinators. Proc Biol Sci 287(1931):20200922

Ricketts TH, Watson KB, Koh I et al (2016) Disaggregating the evidence linking biodiversity and ecosystem services. Nat Commun 7:13106

Rivers-Moore J, Andrieu E, Vialatte A, Ouin A (2020) Wooded semi-natural habitats complement permanent grasslands in supporting wild bee diversity in agricultural landscapes. InSects. https://doi.org/10.3390/insects11110812

Rundlöf M, Persson AS, Smith HG, Bommarco R (2014) Late-season mass-flowering red clover increases bumble bee queen and male densities. Biol Conserv 172:138–145

Schellhorn NA, Gagic V, Bommarco R (2015) Time will tell: resource continuity bolsters ecosystem services. Trends Ecol Evol 30(9):524–530

Shaw RF, Phillips BB, Doyle T et al (2020) Mass-flowering crops have a greater impact than semi-natural habitat on crop pollinators and pollen deposition. Landscape Ecol 35(2):513–527

Sirami C, Gross N, Baillod AB et al (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc Natl Acad Sci https://doi.org/10.1073/pnas.1906419116

Symonds MRE, Moussalli A (2010) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65(1):13–21

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Tilman D (1996) Biodiversity: population versus ecosystem stability. Ecology 77:350-63

Van Reeth C, Caro G, Bockstaller C, Michel N (2018) Current and previous spatial distributions of oilseed rape fields influence the abundance and the body size of a solitary wild bee, *Andrena cineraria*, in permanent grasslands. PLoS ONE 13(5):e0197684

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6:961–965

Williams NM, Regetz J, Kremen C (2012) Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. Ecology 93(5):1049

Winfree R, Williams NM, Dushoff J, Kremen C (2007) Native bees provide insurance against ongoing honey bee losses. Ecol Lett 10:1105–1113

Winfree R, Fox JW, Williams NM, Reilly JR, Cariveau DP (2015) Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. Ecol Lett 18(7):626–635

Woodcock BA, Potts SG, Pilgrim E et al (2007) The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms. J Appl Ecol 44:60–69

Yachi S, Loreau M (1999) Biodiversity and ecosystem functionning in a fluctuating environment: the insurance hypothesis. Proc Natl Acad Sci USA 96:1463-1468

Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed Effects Models and Extensions in Ecology with R Springer