Fruit orchards and woody semi-natural habitat provide complementary resources for pollinators in agricultural landscapes

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Abstract
Context To safeguard insect pollinators and their pollination services, we need to understand how landscape structure regulates the distribution of resources that sustain pollinator populations. However, evidence of how pollinator communities benefit from the variety of resources distributed across different habitat types is scarce.

Objectives To explore complementary resource provision, we conducted a field study to examine the resources available to pollinators in fruit orchards and woody semi-natural habitat.

Methods We studied 13 landscapes containing both habitat types in Flanders, Belgium. In every habitat element, we surveyed nesting resources, floral resources and wild pollinators (i.e. wild bees and hover flies) during three consecutive time periods in the season (once before- and twice after mass-flowering of the fruit orchards).

Results We concluded that the composition of nesting resources for wild bees was clearly different between both habitat types. Woody semi-natural habitat also provided more diverse- and a higher cover of floral resources compared to fruit orchards. In addition, the composition of these floral resources became more and more distinct between the two habitat types as the season progressed. Based on the plant – pollinator network we identified key plant species for inclusion in management schemes to support pollinators.

Conclusions Our study highlights that fruit orchards and woody semi-natural habitat provide a set of different, complementary resources during the flight season, for pollinating insects. Due to the higher diversity and abundance of resources in woody semi-natural habitat, conservation of woody semi-natural habitat is essential for the support of pollinators in agricultural landscapes.

Keywords Biodiversity · Bees · Hover flies · Floral resources · Nesting resources · Land use
Introduction

Loss and fragmentation of habitat has been a major driver of biodiversity loss and global environmental change (Foley et al. 2005; Tscharntke et al. 2005). Specifically, over the last decades, declines in populations of wild bees and other pollinating insects have been observed (Carvalheiro et al. 2013; Ollerton et al. 2014; Powney et al. 2019). These pollinator declines have been linked with reductions in the diversity and abundance of available floral resources in landscapes (Scheper et al. 2014; Balfour et al. 2018), the reduction of semi-natural habitat (Winfree et al. 2011), and the expansion of intensive agriculture (Goulson et al. 2015; Batáry et al. 2017). This raises concerns about the maintenance of pollination services, as wild pollinators are essential for human food production (Garibaldi et al. 2013; Dainese et al. 2019). To conserve pollinator diversity and pollination services, it is therefore essential to understand how landscape structure and resource supply affects pollinator populations in agricultural landscapes (Tscharntke et al. 2005, 2012).

During the course of their activity period, bees and other pollinating insects require sufficient floral resources and suitable nesting sites to complete their life cycle (Potts et al. 2005; Williams and Kremen 2007; Steffan-Dewenter and Schiele 2008). Within intensively managed agricultural landscapes, these resources are distributed over a mosaic of crops, pastures and semi-natural habitat. At a landscape scale, resources for pollinators are provided by semi-natural habitat (Kennedy et al. 2013; Eeraerts et al. 2019), linear landscape elements such as hedgerows and tree rows (Dainese et al. 2017; Van Den Berge et al. 2018), urban areas (Baldock et al. 2019), and to a certain extent by mass-flowering crops (Mallinger et al. 2016; Martins et al. 2018). Depending on the specific plant community composition in different land use types, the phenology and resulting distribution of floral resources are likely to vary considerably throughout the flight season in patches of different land use types. For instance, mass-flowering crops provide a pulse of floral resources during a short period when the crop is in full bloom, whereas semi-natural habitat provide a more fluctuating amount of floral resources throughout the year (Mallinger et al. 2016; Timberlake et al. 2019). In addition to floral resources, the presence of suitable nesting habitat is also necessary for reproduction and maintenance of viable populations. Nesting resources for wild bees are associated with different land use types and landscape characteristics, such as semi-natural habitat (Potts et al. 2005; Sardínias and Kremen 2014) and a variety of field edges (Kells and Goulson 2003; Purvis et al. 2020).

Mobile organisms such as pollinating insects are able to track the available resources in patches of different habitat types at different times throughout the flight season (i.e. complementary habitat use; Dunning et al. 1992). This implies that heterogeneous landscapes have higher landscape quality for pollinators, and might support more abundant and diverse pollinator populations, compared to homogeneous landscapes dominated by intensive agriculture (i.e. landscape heterogeneity hypothesis; Fahrig et al. 2011; Tscharntke et al. 2012). Indeed, recent studies conclude that the diversity and abundance of pollinating insects and other beneficial arthropods is higher in agricultural landscapes with a high diversity and heterogeneity of land use types (Martin et al. 2019; Sirami et al. 2019). However, empirical evidence regarding what particular resources these more heterogenous landscapes provide, in order to support pollinator communities, is largely lacking (but see Mandelik et al. 2012; Mallinger et al. 2016). A better understanding of the distribution and usage of different resources in different habitat types will enable us to improve landscape management in agricultural landscapes, in order to enhance biodiversity conservation and crop pollination. An assessment of how nesting- and floral resources interact in different habitat types, together with the identification of key resources in these habitat types in a single study, will build on previous research concerning complementary resource and habitat use.

We conducted a field study to investigate habitat and resource use by pollinators, in order to test complementary provision of resources for pollinators through different habitat types in agricultural landscapes. We addressed the following research questions: (1) How does the composition of nesting resources for pollinators differ between woody seminatural habitat and fruit orchards? (2) How does abundance, diversity and composition of floral resources for pollinators differ between woody seminatural habitat and fruit orchards? (3) Can we identify key plant species for floral resource provision for both
dominant crop pollinators and non-crop pollinators? We expected that fruit orchards and woody semi-natural habitat contain different and complementary resources for pollinating insects, throughout their flight season. We also expected to identify key floral resources for dominant crop pollinators in both habitat types.

Material and methods

Study design and site selection

The study was conducted in Flanders, Belgium, where previous studies have highlighted the importance of wild pollinators to pollination service provision in a variety of crops (Eeraerts et al. 2017, 2019; Proesmans 2019; M. Pisman personal communications). In the study area, intensive agriculture (IA) is widespread and represents an important economic activity. We selected 13 study landscapes, each 1 km × 1 km in area, around a central intensive sweet cherry (Prunus avium) orchard. Cherry trees had been planted in a 4 m × 2 m planting scheme in each fruit orchard (FO). All farmers applied a conventional management scheme, so no organic FO were included. Based on thematic maps and aerial photographs, we mapped all semi-natural habitat and IA in each study landscape area around the central orchard, using GIS (De Saeger and Scheers 2016; QGIS Development Team 2018). Semi-natural habitat included all hedgerows, old droveways, tree rows, shrub vegetation, semi-natural grassland, field margins and forests. IA included all arable crops, intensively managed pastures and intensively managed fruit orchards. In these 13 study landscapes, the proportion of semi-natural habitat and IA was 11.3% ± 6.9% and 65.8% ± 15.5% (mean ± s.d.), respectively. This area for both semi-natural habitat and IA is representative for both apple and sweet cherry orchards in Flanders (Eeraerts et al. 2017, 2019; M. Pisman personal communications). The priority was to study how agricultural landscapes support pollinators before and after mass-flowering; thus, we opted to collect data before and after mass-flowering. In 2017 and 2018, we collected data in six and seven study landscapes, respectively. In each landscape, we sampled nesting resources, floral resources and pollinators.

Data collection

Bee nesting resource surveys

Bee nesting resources were surveyed once in each transect, in every study landscape, on the day of the first pollinator survey (March – April). Hence, five 1 m² quadrats were placed randomly along the 50 m transect. In each quadrat, eight different proxies for wild bee nesting resources were measured, based on the protocol of Potts et al. (2005):

1. Bare soil: the amount of exposed ground free of vegetation and plant litter (%).
2. Flat: the amount of ground with a slope < 30° (%)
3. Slope: the amount of ground with a slope between 30° and 60° (%)
4. Steep: the amount of ground with a slope > 60° (%)
5. Dead wood: the amount of dead woody substrate (%)
6. Stems: the number of exposed pithy- or hollow plant stems
7. Cavities: the number of large (> 2 cm diameter) cavities in trees, rocks and soil
8. Shells: the number of empty snail shells

Floral resource surveys

For the floral resource survey, we identified all tree (i.e. woody plants > 3 m height) and shrub (i.e. woody plants between 1.2 and 3 m height) species that were flowering, within 2 m of both sides of the entire 50 m transect; and the percent cover class of flowering resources was estimated (75 – 100%, 50 – 75%, 25 – 50%, 5 – 25%, 1 – 5%, < 1%; Hennekens 2009). For the herb layer vegetation (i.e. woody and herbaceous plants < 1.2 m), a representative plot of 2 m × 5 m was laid out along the 50 m transect. All plant species that were flowering in the herb layer within these 2 m × 5 m plots were identified, and their percent floral cover was estimated.

Pollinator surveys

Two pollinator surveys, 30 min each, were completed along the 50 m transect in every element, at midday (11:00 AM until 1:00 PM) and again in the afternoon (3:00 PM until 5:00 PM). During each survey, all flower-visiting pollinators were caught with a net along the transect. We focused on pollinator taxa that are relevant for crop pollination, specifically wild bees and hover flies. Collected specimens were identified, and the plant species on which they were...
foraging was recorded. To avoid counting a certain specimen multiple times, all specimens were kept in a conical tube and released after each 30-min survey. Pollinator specimens and visited plant specimens that could not be identified in the field were taken to the laboratory for identification. Because of the difficulty of distinguishing queens and workers of the species *Bombus terrestris*, *B. lucorum*, *B. magnus* and *B. cryptarum* we pooled these and noted them as *B. terrestris* agg. To ensure adequate pollinator activity, surveys were conducted only when weather conditions were suitable for pollinator sampling (i.e. low- or no wind, no rain, cloud cover < 50%, temperature > 13 °C).

During the pollinator surveys in the first sampling period, we collected nest-searching individuals of both solitary bees and bumble bees, both of which are used as a proxy for nesting habitat quality. Nest-searching bees display distinctive behaviors, including flying in low, zigzag patterns, and investigating holes in the ground between patches of vegetation. O’Connor et al. (2017) found that counts of nest-searching bumble bee queens are a good indicator of both quality of nesting habitat and actual nests later in the year.

Data analyses

**Nest-searching bees and nesting resource composition**

Data regarding nest-searching bees from the two 30-min surveys in the first sampling period were pooled, in order to obtain the total number of nest-searching bees per habitat element across each study landscape. A generalized linear mixed-effects model (GLMM) with a negative binomial error distribution was used to test the influence of habitat type (FO and WSNH), with landscape ID as a random factor, on the number of nest-searching bees (function *glmer.nb*, R package *lme4*; Bolker et al. 2019).

For analyzing the composition of bee nesting resources, data from the five plots were pooled to obtain the mean value for each of the eight nesting resources. To assess differences in nesting resource composition, a Bray – Curtis dissimilarity matrix was created using these mean values. We then used a permutation-based multivariate analysis of variance (PERMANOVA) to test the influence of habitat type on the composition of bee nesting resources (function *adonis*, R package *vegan*, Oksanen 2019). PERMANOVA accurately detects compositional differences among groups for balanced designs (Anderson and Walsh 2013). As this study has an unbalanced design of 13 FO- and 24 WSNH elements, it was necessary to check the multivariate homogeneity of group variance (i.e. dispersion) between habitat types. Before the PERMANOVA, the dispersion between the two habitat types was examined (function *betadisper*, R package *vegan*). To visualize nesting resource composition between habitat types, we used non-metric multidimensional scaling (NMDS) with two a priori chosen dimensions and a maximum of 999 permutations (function *metaMDS*, R package *vegan*). In addition, we determined which nesting resource parameters are indicators for a certain habitat type by calculating point-biserial correlation coefficients (rpb) for each parameter (function *multtpath*, R package *indicspecies*; De Caceres et al. 2010).

| Model parameter | Floral richness | df | X^2 | p     |
|-----------------|-----------------|----|-----|-------|
| Habitat type    | 1 15.6 < 0.001  |
| Time period     | 2 10.4 < 0.01   |
| Habitat type*Time period | 2 0.2 0.89  |

| Floral cover | df | F   | P     |
|--------------|----|-----|-------|
| Habitat type | 1 20.2 < 0.001 |
| Time period  | 2 19.7 < 0.001 |
| Habitat type*Time period | 2 5.8 < 0.01 |

| Floral composition | df | F   | P     |
|--------------------|----|-----|-------|
| Habitat type       | 1 21.3 < 0.001 |
| Time period        | 2 12.4 < 0.001 |
| Habitat type*Time period | 2 10.0 < 0.001 |
Floral resource abundance, richness and composition

Based on the pollinator surveys, lists of flowering plants that received at least one pollinator visit were generated. Such a list was made for each vegetation layer (tree, shrub and herbaceous layer), for each time period (Table A2). Based on these lists of visited flowering plant species, the data from the floral resource surveys were adjusted so that they only contained the visited flowering plant species for each vegetation layer. Regarding the floral cover of trees and shrubs, the average of the cover class was taken (e.g. the class 75–100% was assigned a mean coverage of 87.5%, and the class < 1% was assigned a mean coverage of 0.5%). The floral cover of herbaceous plant species retained their original, continuous, estimated cover from the field surveys. From this, both total cover and total species richness of visited flowering plants species, per element, per time period, were obtained by summing the data of visited flowering plants species, from each vegetation layer per site, per time period (see Mandelik et al. 2012; Mallinger et al. 2016). Prior to analysis, the total cover of visited flowering plant species (hereafter “floral cover”), and the total species richness of visited flowering plant species (hereafter “floral species richness”), were checked for outliers and normality. Square-root transformation was applied to assure normality of the floral cover data. A linear mixed-effects model (LME) was used to test the influence of habitat type, time period and the interaction between habitat type and time period, on floral cover, with study landscape ID included as random factor (function lme, R package nlme, Pinheiro and Bates 2019).

For floral richness, a GLMM with a negative binomial error distribution was used. Here, the same fixed and random factors were applied as for the model of floral cover. To evaluate the influence of habitat type, in combination with the other parameters, on floral cover and floral richness, only the full model was tested and evaluated.

A Bray – Curtis dissimilarity matrix was created using floral cover per site, per time period. PERMANOVA was used to test the influence of habitat type, time period and the interaction between habitat type and time period on floral resource composition. Prior to the PERMANOVA, we examined the dispersion of floral resource composition between the two habitat types. NMDS was used to visualize floral resource composition between habitat types and time periods. Based on the floral cover data we determined which visited flowering plant species are indicator species for a certain habitat type and time period.

Key floral resources

Based on studies that address the influence of wild pollinator visitation on crop pollination in Flanders, Belgium (Eeraerts et al. 2017, 2019; Proesmans 2019; M. Pisman personal communications), we compiled a list of dominant crop pollinators for our study region (methodology according to Kleijn et al. (2015): dominant crop pollinators are pollinator species that comprise 5% or more of all crop visits in a single study; see Table A3). All other pollinator species were defined as non-crop pollinators as they do not forage on crops in relatively high numbers. Consequently, all encountered pollinator species in our study were classified as either dominant crop pollinator or non-crop pollinator.

To determine key plant species for floral resource provision (hereafter “key floral resources”), we pooled the plant-pollinator network data of each pollinator survey from each element of all landscapes, in order to obtain a pooled, weighted network dataset for each time period. We performed this pooling for both dominant crop pollinators and non-crop pollinators. Based on these pooled network datasets, a species level interaction diversity score was determined for each plant species in the network (function specieslevel, package bipartite; Dormann et al. 2020). This index gives the Shannon diversity index of the observed interactions for each plant species. Consequently, all plant species were ranked from high to low interaction diversity. Key floral resources were defined as the collective group of plant species with the highest interaction diversity, that accumulate up to 80% of the floral visits during the specific time period.

All analyses were performed in R version 3.5.1 (R Development Core Team 2018). For the LME and GLMM, the degree of collinearity of the explanatory factors was checked by variance inflation factor analysis (threshold value < 3). Model fit of the LMEs was evaluated by visually checking the normality of the model residuals (QQ-plot and plot of the residuals versus the fitted values) and with the Lilliefors test. For the GLMMs, the residual diagnostics and goodness-of-fit tests from the DHARMA R package were
used to evaluate the model fit (Hartig 2019). All LME and GLMM models were also performed with an extra fixed factor year in the model. As this factor was never significant and did not affect the overall results, we chose to report the models without a year as a fixed factor because we did not sample the same sites in the two sampling years.

Results

Field sampling results

Nesting resource surveys were conducted for all 37 distinct elements in the 13 study landscapes, i.e. 13 FO and 24 WSNH. In these 37 elements, vegetation surveys were conducted in 110 transects, and pollinator surveys were conducted in 220 transects. In one WSNH element, pollinator and vegetation surveys could not be conducted in June 2018, as a result of restoration work on the fence of the adjoining agricultural field.

In the different vegetation layers of all the elements, we identified 82 flowering plant species, of which 59 were visited at least once by a wild bee or hover fly (see Table A2 for a complete species list). The cover and richness of flowering plants was highly correlated to the cover and richness of visited flowering plants (Spearman rank correlation: $\rho = 0.91, p < 0.001$; and $\rho = 0.89, p < 0.001$; for floral cover and floral richness, respectively). A total of 1,169 foraging pollinators were recorded, accounting for a total of 57 pollinator species (619 and 550 pollinators, and 39 and 51 pollinator species, in 2017 and 2018 respectively). Of these, solitary bees comprised 172 flower visits by 26 species; bumble bees comprised 775 visits by 8 species; and hover flies comprised 222 visits by 23 species.

Nest-searching bees and nesting resources

The number of nest-searching bees was significantly higher in WSNH compared to FO (habitat type: $X^2 = 14.9, p < 0.001$, Fig. 2a). Dispersion between habitat types was significantly higher for WSNH compared to FO ($F = 48.2, p < 0.001$). For unbalanced design, this implies that PERMANOVA gives a conservative result (Anderson and Walsh 2013). PERMANOVA indicated that habitat type had a significant effect on nesting resource composition

| Table 2 | Indicator values for visited flowering plant species, for the different time periods, across the two habitat types. Associated habitat type (FO = fruit orchard, and WSNH = woody semi-natural habitat). $r_{pb}$ = point-biserial correlation coefficients, and p-values are given. |
|---------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Time period | Plant species | Habitat type | $r_{pb}$ | p  |
| March–April | Bellis perennis | FO | 0.42 | < 0.01 |
|  | Taraxacum spp. | FO | 0.59 | 0.01 |
|  | Ficaria verna | WSNH | 0.39 | 0.01 |
|  | Prunus spinosa | WSNH | 0.36 | 0.02 |
|  | Glechoma hederacea | WSNH | 0.36 | 0.03 |
|  | Prunus avium | WSNH | 0.31 | 0.01 |
| May | Bellis perennis | FO | 0.92 | < 0.001 |
|  | Prunus avium | FO | 0.63 | < 0.001 |
|  | Taraxacum spp. | FO | 0.49 | < 0.001 |
|  | Crataegus spp. | WSNH | 0.38 | 0.01 |
|  | Lamium album | WSNH | 0.41 | 0.02 |
|  | Rubus spp. | WSNH | 0.50 | < 0.01 |
|  | Sambucus nigra | WSNH | 0.66 | < 0.01 |
| June | Bellis perennis | FO | 0.54 | < 0.001 |
|  | Trifolium repens | FO | 0.51 | < 0.001 |
|  | Taraxacum spp. | FO | 0.38 | < 0.001 |
|  | Rubus spp. | WSNH | 0.62 | < 0.001 |
|  | Sambucus nigra | WSNH | 0.35 | 0.02 |
The number of nest-searching bees in the two habitat types (a). NMDS plot based on the Bray–Curtis dissimilarity data, to compare the composition of bee nesting resources between the two habitats (b). The NMDS plot represents the data with reasonable low stress of 0.1. The identified indicator (F = 26.3, p < 0.001). The NMDS showed clear distinctions, regarding nesting resource composition, between the two habitat types (Fig. 2b). Concerning the different nesting resource parameters, flat ground was clearly associated with FO (r_pb = 0.74, p < 0.001). Sloped ground, steep ground and dead wood were all associated with WSNH (sloped ground: r_pb = 0.75, p < 0.001, steep ground: r_pb = 0.55, p < 0.01, dead wood: r_pb = 0.81, p < 0.001). An overview of the minimum, maximum and mean values of different nesting resource characteristics, per habitat type, is shown in Table A4.

Floral resources

Habitat type and time period both clearly affected richness- and cover of floral resources for pollinators (Table 1; Fig. 3a, b). A significant interaction effect between habitat type and time period was found for floral cover (Table 1). The dispersion of the flowering plant species composition was significantly greater for WSNH compared to that of FO (F = 18.8, p < 0.001). For unbalanced design this implies that PERMANOVA gives a conservative result. PERMANOVA indicated that habitat type, time period as well as the interaction between both factors had a significant effect on the flowering plant composition (Table 1). The NMDS also showed a clear distinction of the flowering plant composition between the two habitat types for each of the time periods (Fig. 3c–e). Different flowering woody and herbaceous plant species were associated with either of the two habitat types (Fig. 3c–e and Table 2).

Key floral resources

Of the 57 pollinator species identified in our study, 11 species were dominant crop pollinators of relevant pollination-dependent crops in Flanders, Belgium (Table A5). The key floral resources for dominant crop pollinators and non-crop pollinators, and their corresponding interaction diversity and total visits, are listed in Table 3. In total, 8 of the 13 plant species visited in March–April were identified as key floral resources for dominant crop pollinators; as well as 7 of the 27 plant species visited in May, and 3 of the 16 plant species visited in June. These key floral resources together supported all dominant crop pollinators during these periods. In total, 5 out of the 8 plant species visited in March–April were identified as key floral resources for non-crop pollinators; as well as 10 of the 27 plant species visited in May, and 12 out of 23 plant species visited in June. In March–April, these key floral resources supported each of the 13 non-crop pollinator species detected; as well as 23 of the 25 non-crop pollinator species detected in May, and 31 of the 35 non-crop pollinator species detected in June. Multiple key floral resources were associated with both habitat types as indicated in Table 3.
Discussion

Our assessment of resource provision and composition in both FO and WSNH during the flight season of pollinating insects, both before and after mass-flowering in FO, showed that WSNH offered greater floral cover and richness, compared to FO. This emphasizes the importance of WSNH conservation for supporting pollinator populations in agricultural landscapes. Both habitat types clearly differed in regard to both nesting- and floral resources for pollinators. For both habitat types, habitat-associated nesting- and floral resources differed. Thus, FO and WSNH together provided complementary floral resources for pollinators during their activity season. Based on the plant-pollinator network, a number of plant species were identified as key floral resources for both dominant crop pollinators and non-crop pollinators. This list of key floral resources can help farmers and other stakeholders to design targeted management schemes, in order to enhance crop pollination. Our findings highlight that conserving WSNH and enhancing the floral resources in and around FO may provide an abundance and diversity of resources that support pollinators in agricultural landscapes.

Complementary resource provision

An important finding from our study is that FO and WSNH each provide a unique set of nesting- and floral resources, thereby supporting a complementary distribution of resources (Fig. 2, 3; Tables 1, 2). The
significant effect of time-of-season, habitat type and their interaction on floral abundance and composition of floral resources, together with the identification of different indicator plant species, suggests that floral resources provided by each habitat type were complementary during the flight season of pollinators. The floral resources across WSNH were reasonably constant, whereas in FO, floral cover was more variable during the season, which likely explains the interaction effect observed. Furthermore, the floral composition and indicator species (which are often also key floral resources) suggest complementary resource provision. For example, *Taraxacum* spp. and *Trifolium repens* are indicator species in FO in June, and these plant species also represent key floral resources. Other indicator plant species are also linked to a specific habitat type and were identified as key floral resources during a specific period in the season.

### Table 3

Key plant species for floral resource provision, i.e. “key floral resources”, for both dominant crop pollinators and non-crop pollinators, for each time period. For each key floral resource, the interaction diversity (Int. Div.) and the total number of pollinator visits in this study are given. Plants that are identified as an indicator plant species for fruit orchards and woody semi-natural habitat are highlighted with an asterix (*) and a hash (#), respectively. EXFN = extra floral nectaries.

| March–April | May | June |
|-------------|-----|------|
| **Dominant crop pollinators** | **Key floral resource** | **Int. Div** | **Visits** | **Key floral resource** | **Int. Div** | **Visit** | **Key floral resource** | **Int. Div** | **Visits** |
| *Prunus spinosa*# | 2.07 | 28 | *Symphytum officinale* | 1.73 | 68 | *Rabas spp.*# | 1.59 | 160 |
| *Prunus avium*# | 1.66 | 16 | *Chelidonium majus* | 1.66 | 8 | *Taraxacum spp.*# | 1.28 | 14 |
| *Taraxacum spp.*# | 1.63 | 12 | *Taraxacum spp.*# | 1.64 | 31 | *Trifolium repens*# | 1.28 | 56 |
| *Salix alba* | 1.51 | 17 | *Ranunculus repens* | 1.58 | 14 | |
| *Ficaria verna*# | 1.05 | 5 | *Rabas spp.*# | 1.52 | 38 | |
| *Lamium album* | 1.04 | 4 | *Lamium album*# | 1.46 | 124 | |
| *Salix caprea* | 0.80 | 22 | *Crateagus spp.*# | 1.33 | 43 | |
| **Non-crop pollinators** | **Key floral resource** | **Int. Div** | **Visits** | **Key floral resource** | **Int. Div** | **Visit** | **Key floral resource** | **Int. Div** | **Visits** |
| *Taraxacum spp.*# | 1.75 | 7 | *Taraxacum spp.*# | 1.93 | 16 | *Rabas spp.*# | 2.34 | 79 |
| *Salix alba* | 1.39 | 4 | *Crateagus spp.*# | 1.72 | 11 | *Chaerophyllum temulm* | 2.06 | 27 |
| *Prunus spinosa*# | 1.10 | 3 | *Anthriscus sylvestris* | 1.54 | 7 | *Bellis perenis*# | 1.91 | 8 |
| *Prunus avium*# | 1.10 | 3 | *Ranunculus repens* | 1.52 | 9 | *Taraxacum spp.*# | 1.16 | 11 |
| *Glechoma hederacea*# | 1.04 | 4 | *Lamium album*# | 1.23 | 12 | *Hieracium spp.* | 1.10 | 3 |
| *Symphytum officinale* | | | 1.19 | 16 | *Castanea sativa* | 1.04 | 4 |
| *Chaerophyllum temulm* | | | 1.10 | 3 | *Trifolium repens*# | 0.87 | 6 |
| *Prunus avium* EXFN | 0.69 | 2 | *Digitalis purpurea* | 0.80 | 10 | |
| *Bellis perenis*# | 0.69 | 2 | *Silene dioica* | 0.80 | 7 | |
| *Rabas spp.*# | 0.69 | 2 | *Ranunculus repens* | 0.69 | 2 | |
| *Betonica officinalis* | | | | | | |
| *Centaurea jacea* | 0.65 | 18 | | | | |
(Tables 2, 3). To further demonstrate this, we have presented the complete plant–pollinator network for each of the three sampling periods in Fig A2. From this, we can conclude that a significant proportion of pollinators use key floral resources and indicator plant species from both FO and WSNH. Indeed, in March–April, 7 out of 24 pollinator species (accounting for 74% of all pollinator visits in March–April, Fig A2a) used different key floral resources in both FO and WSNH. Respectively, in May and June, 11 out of 36 pollinators (83%) and 11 out of 39 pollinators (77%) used key floral resources (Fig A2b, A2c). Thus, both habitat types exhibited shifts in key floral resources during the study period; and therefore, both habitat types contribute to the continuity and diversity of resources in agricultural landscapes, potentially enhancing pollinator populations. More accurate mapping of floral abundance instead of the use of floral cover as a proxy for floral abundance will allow this analysis to be further refined in the future (Timberlake et al. 2019).

Composition of nesting resources also differed between FO and WSNH, and in addition we also identified different indicator nesting parameters for both FO (i.e. flat soil) and WSNH (i.e. sloped ground, steep ground, dead wood; Fig. 2, Table 2). This further supports the rationale that these two habitat types complement each other via the resources they provide. The greater number of nest-searching bees in WSNH, in combination with multiple nesting parameters associated with WSNH, suggests that WSNH is of higher quality in terms of nesting habitat a finding consistent with that of O’Connor et al. (2017). Due to the diverse nesting habits of different bees and other pollinators, it is important to maintain a variety of nesting sites. Sloped soil, cavities, hollow plant stems, diverse field boundaries, etc. have all been associated with nesting activities of wild bees (Steffan-Dewenter and Schiele 2008; Sardinas and Kremen 2014; Buckles and Harmon-Threatt 2019). However, as bare soil was regularly detected in both WSNH and FO but not related to any specific habitat type, this might offer opportunities for nesting of solitary bees in both FO and WSNH as nesting activity of solitary bees has been related to the amount of bare soil (Steffan-Dewenter and Tscharntke 2000; Buckles and Harmon-Threatt 2019).

Concerning indicator plant species, an interesting result is that sweet cherry was an indicator species of WSNH before mass-flowering of the commercial sweet cherry cultivars in the orchards. Indeed, commercial sweet cherry cultivars in FO are present among their wild relatives that occur sparsely within the WSNH in the study area. The latter blooms a few weeks earlier (i.e. end of March) compared to commercial cultivars (i.e. early to mid-April), providing floral resources earlier in the active flight season of pollinating insects. In addition, a considerable number of pollinators were detected foraging on the extrafloral nectaries of sweet cherry during mid-May. Extrafloral nectar and honey dew are commonly collected by various pollinators, although this topic is not well studied (Requier and Leonhardt 2020). The flowering phenology of commercial- and naturally cultivars, in combination with their provisioning of extrafloral nectaries, extends the period whereby this plant species provides pollen and nectar for pollinators.

In general, most pollinator taxa collect diverse resources (Wood et al. 2015; Bertrand et al. 2019). These resources can be provided by different habitat types in agricultural landscapes, as pollinators are able to track available resources throughout the season, across different habitat types (Dunning et al. 1992). In accordance with Mandelik et al. (2012) and Mallinger et al. (2016), we conclude that during the flight season, pollinators make use of complementary floral resources between multiple habitat types (Fig. 3; Tables 1, 3). Indeed, during each sampling period, different key floral resources were detected in both FO and WSNH. Our work elaborates on previous research by including nesting resource surveys, as well as sampling of pollinators on shrubs and trees adjacent to herbaceous plants. Another advantage is that, based on the plant–pollinator network, we have determined which plant species are potentially most important for pollinating insects in our focal habitats and study region. Confirmation of this complementary resource provision serves as a solid rationale for the findings of previous studies which show that the heterogeneity of landscapes regulates biodiversity, such as the diversity of pollinating insects (Martin et al. 2019; Sirami et al. 2019). As many of the pollinator species detected in our study are relevant for crop pollination, it is possible that complementary habitat types in agricultural landscapes also contribute indirectly to crop yield, by enhancing crop pollinator populations (Martin et al. 2019). It is important to note that the proportion of FO in the landscape should not exceed a
certain threshold, as this can result in a level of landscape homogeneity that may be detrimental for bumble bee reproduction (Proesmans et al. 2019), as well as the provision of pollination services in fruit crops (Eeraerts et al. 2017).

Management implications

Our work emphasizes the importance of WSNH conservation, as WSNH provided diverse and abundant nesting opportunities for pollinators (Fig. 2, Table A4). The fact that both cover and richness of floral resources was higher in WSNH further highlights the idea that conservation and establishment of well-developed WSNH is vital for providing essential resources to support pollinator populations in agricultural landscapes. Given that previous research has shown that semi-natural habitat represents and harbors crucial resources for pollinating insects (Öckinger and Smith 2007; Winfree et al. 2011), conservation of this habitat type remains an essential management measure. However, due to a perceived lack of available space and financial incentives, it is often difficult or unfeasible for farmers and policymakers to create semi-natural habitat in and around farms to support pollinator diversity in agricultural landscapes. Mitigation measures, such as agri-environmental schemes to promote floral resources that support pollinator functional diversity, have been implemented by governments, as floral resources are regarded as one of the most limiting factors for pollinator populations (Roulston and Goodell 2011; Science for Environmental Policy 2017). However, these measures have delivered mixed results due to the influence of landscape structure (Scheper et al. 2013), and because the floral composition of these measures is not tailored to certain target species (Wood et al. 2015). Here we have identified key plant species that can provide floral resources for multiple dominant crop pollinators, as well as non-crop pollinator species, during the active flight season (Table 3). Most key floral resources that support dominant crop pollinators are also beneficial for non-crop pollinators. However, to conserve these non-crop pollinators, it is also necessary to conserve diverse WSNH that contain a more diverse set of resources (Pywell et al. 2011; Sutter et al. 2017).

In Flanders and elsewhere in Europe, WSNH such as hedgerows and tree rows have been declining in agricultural landscapes over the last 50 years (Senapathi et al. 2015; Van Den Berge et al. 2019). Therefore, promoting woody plant species such as *Prunus spinosa*, *Salix caprea*, *Crateagus* spp., etc., and planting them where there is space in and around farms, may represent a cost-efficient and targeted action for farmers to support pollinating insects. To date, trees and shrubs are only included to a lesser extent in these mitigation measures, compared to herbaceous plants in flower strips and cover crops; whereas it has been shown that trees and shrubs can function as sources of abundant pollen and/or nectar for pollinating insects (Bertrand et al. 2019; Timberlake et al. 2019). Trees and shrubs can be planted in a very limited area, and require less maintenance over the years, compared to flower strips. Next to woody plants, we also identified some herbaceous plant species as important plants for pollinators in both FO and WSNH. With regards of the management of FO, ruderal herbaceous plants such as *Bellis perennis*, *Taraxacum* spp. and *Trifolium repens* are interesting. Other studies also showed that such herbaceous plants can be an important food source for crop pollinators (Wood et al. 2015; Bertrand et al. 2019). Provided the appropriate management is put into place, FO could provide additional floral resources in agricultural landscapes, and be complementary to the floral resources in WSNH elements, without requiring extra available space. Here, possible effects of pesticide use on pollinators and other beneficial insects should be a topic of future research, in order to integrate an adapted mowing regime in the management scheme of FO (Park et al. 2015).

Conclusion

Our FO and WSNH study sites provide complementary nesting and floral resources during the flight season for pollinating insects in the study region. Our findings highlight the importance of an integrated approach to conserve pollinators and enhance crop pollination, including the protection of WSNH and managing FO to maximize floral resources before and after mass-flowering. Other habitat types that were not included in this study, such as species rich grasslands, heathlands or urban areas, can be expected to provide other unique resources that further complement the habitat types we studied, in accordance with the landscape heterogeneity hypothesis (Fahrig et al. 2011;
Tscharntke et al. 2012). Including other habitat types in future studies will further improve our understanding of how to conserve and promote farmland biodiversity and associated ecosystem services.

Acknowledgement The authors declare no conflict of interest. ME was funded by the Research Foundation Flanders PhD grant 1S71416N. We gratefully acknowledge Delphine Parmentier, Anne-Sophie Sacré, Veerle Stro and Lieve Van Lysebetten for their assistance in the field. We also thank the farmers for providing access to their orchards, and Jonathan Willow for his useful comments and linguistic review of the manuscript.

Data availability Data is available from the Dryad Digital Repository https://doi.org/10.5061/dryad.44j0zpcbh

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