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RESEARCH ARTICLE

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Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes

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Abstract

1. Continuous availability of food resources, such as pollen, is vital for many insects that provide pollination and pest control services to agriculture. However, there is a lack of knowledge about the shared or complementary use of floral resources by such species, which hampers more effective landscape management to simultaneously promote them in agroecosystems.
2. Here, we simultaneously quantified pollen use by a bumblebee (*Bombus terrestris*) and a mason bee (*Osmia bicornis*), two bee species recognized as important crop pollinators, as well as a lacewing (*Chrysoperla carnea*) and a ladybeetle species (*Harmonia axyridis*), both common predators of crop aphids, throughout the season in 23 agricultural landscapes in Germany and Switzerland.
3. Pollen diets were more diverse and similar among *C. carnea* and *H. axyridis* compared to the two bee species, but all four species shared key pollen types early in the season such as *Acer*, *Quercus*, *Salix* and *Prunus*. All species exhibited a pronounced shift in pollen sources from primarily woody plants (mainly trees) in spring to primarily herbaceous plants in summer. The majority of pollen (overall ≥64%) came from non-agricultural plants even in crop-dominated landscapes.
4. *Synthesis and applications*. Our results highlight the importance of trees as pollen sources for many insect species, particularly early in the season. Our findings support incentives that promote heterogeneous agricultural landscapes including both woody and herbaceous semi-natural habitats, ensuring phenological complementarity of floral resources for insect species that can provide pollination and pest control services to agriculture. The identified key plant species can help to design and optimize agri-environment schemes to promote these functionally important insects.

KEYWORDS
bumblebee, floral resources, foraging habitat, landscape resources, mason bee, pollen diet, resource specialization

1 | INTRODUCTION

Insects critically contribute to biodiversity in agroecosystems and provide ecosystem services sustaining crop production, such as crop pollination and pest control. Those services are of paramount economic and non-monetary value for human well-being (IPBES, 2016; Losey & Vaughan, 2006). Bees and other crop pollinators, as well as many natural enemies of crop pests such as syrphids, lacewings and ladybeetles, feed on nectar or pollen provided by flowering plants. Floral resources dominate the diet of bees, regardless of their development stage. The larvae of natural enemies, on the other hand, are predators primarily feeding on animal prey including major agricultural pests such as aphids, whilst adults regularly consume nectar and pollen as a sole food source (e.g. most lacewings) or to supplement their diet with key nutrients lacking in insect-only diets, in particular during periods of prey scarcity (e.g. ladybeetles; Lundgren, 2009). Hence, adequate floral resources may enhance these functionally important insects in agricultural landscapes (e.g. Carvell et al., 2017; Isaacs, Tuell, Fiedler, Gardiner, & Landis, 2009; Wäckers & Van Rijn, 2012; Williams, Regetz, & Kremen, 2012). The loss and degradation of semi-natural vegetation – and the concomitant loss of floral resources – is considered a principal cause of the decline of pollinators and pest enemies and the services they provide (Benton, Vickery, & Wilson, 2003; IPBES, 2016; Scheper et al., 2014). Therefore, promoting adequate floral resources at the right place and time is critical for successful habitat management (Isaacs et al., 2009; M'Gonigle, Ponisio, Cutler, & Kremen, 2015; Sutter, Jeanneret, Bartual, Bocci, & Albrecht, 2017) and can be highly effective to promote pest control (Tschumi, Albrecht, Entling, & Jacot, 2015; Wäckers & Van Rijn, 2012) and pollination services (Blaauw & Isaacs, 2014) provided by insects.

Most common crop pollinators and pests' natural enemies consuming floral resources are dietary generalists; that is, they collect floral resources from multiple plant taxa from both crop and non-crop habitats (e.g. Villenave, Thierry, Al Mamun, Lodé, & Rat-Morris, 2005; Walther-Hellwig & Frankl, 2000). However, even the diets of generalist flower visitors are usually dominated by certain floral resource types (e.g. Sutter et al., 2017; Wäckers & Van Rijn, 2012). Only a subset of resources offered by the flowering plant community in agroecosystems is accessible, available at the right time, of adequate chemical composition and attractive to different insect species. For instance, spatial resource use and accessibility depend on species' mobility and foraging ranges (e.g. Walther-Hellwig & Frankl, 2000). Furthermore, mass-flowering crops may offer abundant floral resources, but are ephemeral and only available during short periods. Spatio-temporal complementarity and thus continuous provisioning of floral resources by non-crop vegetation is, therefore, vital to ensure population persistence of pollinators and many important pest enemies, and the ecosystem services they provide (Schellhorn, Gagic, & Bommarco, 2015).

Yet, there is a lack of knowledge about the spatio-temporal dynamics of floral resource use (but see e.g. Grab, Blitzer, Danforth, Loeb, & Poveda, 2017) by co-ocurring pollinators and pest enemies, which hampers more effective landscape management to simultaneously promote them in agroecosystems. Regarding pollen – a main source of protein for many functionally important insects – it remains unclear what proportions of pollen consumed by different species come from crop and non-crop plants or from different vegetation types such as woody (e.g. woodlots or hedgerows) or herbaceous (e.g. grasslands, herbaceous field margins) habitats. Information regarding the extent of overlap or divergence in pollen use by multiple species over time is also missing. Thus, to increase the effectiveness of measures to concomitantly promote service providing insects, we need to simultaneously examine how different plant resources contribute to their requirements, and how similar or complementary their use of floral resources is (Rollin et al., 2013; Shackelford et al., 2013). Such knowledge is a prerequisite to better assess and predict the distribution of these functionally important insect taxa in agricultural landscapes, and to guide scientists and land managers in identifying and promoting habitats and specific floral resources that are vital to sustain them.

The main objective of this study was to compare the spatio-temporal use of pollen resources between two pollinator and two aphid enemy insect species commonly found in Central European agricultural landscapes and that rely on pollen for at least part of their life cycle. The bumblebee *Bombus terrestris* and the mason bee *Osmia bicornis* were used as pollinator model taxa. These two species rely on pollen for development and adult survival, and are among the most abundant wild bees in the studied agroecosystems (e.g. Kleijn et al., 2015; Westphal et al., 2008) that provide pollination services in a wide range of crops, such as pumpkin (Pfister, Eckerter, Schirmel, Cresswell, & Entling, 2017), field beans and oilseed rape (Garratt et al., 2014), or fruit trees and strawberries (Gruber, Eckel, Everaars, & Dormann, 2011; Klatt et al., 2014). Aphid enemies that rely on pollen include hoverflies, ladybeetles and lacewings. We selected the lacewing *Chrysoperla carnea* s.l. due to its high abundance in annual cropping systems (McEwen, New, & Whittington, 2007; Pfister, Schirmel, & Entling, 2017). The ladybeetle *Harmonia axyridis*, despite being invasive in Europe (Roy et al., 2012), was also included as a model taxon since it became one of the most dominant aphid predators in European agroecosystems in the past years (e.g. Pfister, Schirmel, et al., 2017; Stutz & Entling, 2011). For *C. carnea* and *H. axyridis* adults, pollen is either an obligatory (*Chrysoperla*) or complementary (*Harmonia*) part of their diet, which can be vital in particular during periods of prey scarcity (Berkevens et al., 2010; Lundgren, 2009).

We addressed the following questions:

1. What are the main pollen types used by the studied bee, lacewing and ladybeetle species?
2. To what extent does pollen use overlap among the four species? Do they share important pollen taxa that could be targeted by habitat management schemes?
3. What is the relative importance of different pollen sources (i.e. woody/herbaceous plants, crop/non-agricultural plants)? How does the use of pollen sources change over the season and does

the pollen use of the four insect species show similar temporal dynamics?

4. How does the landscape context influence the use of different pollen sources?

2 | MATERIALS AND METHODS

2.1 | Study regions and pollen sampling design

The study was conducted in 2016 in southwestern Germany and northeastern Switzerland (see Appendix S1.A). In each region, 11 (Germany) to 12 (Switzerland) landscape sectors of 500 m radius were selected. The selected landscapes represent the typical range in the proportion of the two major land-use types characteristic for the study regions: agricultural land (e.g. arable crops, managed grassland, some horticulture; 38%–90%, mean = 68%, *SD* = 16%) and woody habitat (woodlots and hedgerows; 0%–51%, mean = 11%, *SD* = 12%; see Appendix S1.A; Figure S1). In each landscape sector three (Germany) to five (Switzerland) sampling points were selected: one central sampling point, as well as 2 to 4 further ones randomly spread across the landscape (see Appendix S1.B).

Samples of insects and pollen were collected approximately every 2 weeks from beginning of April–mid-July (see Table S2). At each sampling point, adults of *C. carnea* and *H. axyridis* were sampled using sticky traps. For each species, up to five individuals per sampling round and landscape sector were randomly selected for pollen analysis. Pollen collected by *B. terrestris* was obtained from the pollen sacs of up to 10 worker bees per sampling round and landscape sector upon return to colonies experimentally established at each landscapes' central sampling point ("Mini hive"; purchased from Biobest and containing 30–40 workers). Pollen collected by *O. bicornis* was obtained from up to five brood cell provisions per sampling round of experimentally established trap nests at each sampling point (Switzerland) or central sampling point (Germany; see Appendix S1.B; Figure S2).

2.2 | Pollen samples processing and analysis

Elytra and/or wings of sampled *C. carnea* and *H. axyridis* individuals were removed, and insects were thoroughly rinsed with ETOH to remove pollen from the exoskeleton to minimize the potential of including in the analysis pollen grains that were not consumed by the insects. Subsequently, insects were crushed and acetolysis was performed following Jones (2012).

All pollen samples belonging to the four insect species were treated chemically with acetolysis and KOH, and mounted in glycerine following standard palynological methods (Moore, Webb, & Collinson, 1991). Pollen grains were identified under a light microscope (400× magnification) based on palynological keys (Beug, 2004; Moore et al., 1991) and a photo atlas (Reille, 1992), as well as using the reference collection of the Institute of Plant Sciences of the University of Bern. Pollen grains were identified at species whenever possible, or at subgenus, genus, or family level (hereafter pollen types (=t.); see Table S1). About 1,070 samples were available for analysis (see Table S2). For each sample, we identified and counted up to 100 pollen grains whenever possible (i.e. between 30 and 100 grains).

2.3 | Data analysis

All statistical analyses were conducted using R 3.4.1 (R Core Team, 2017). To account for unequal numbers of pollen grains between samples or insect species, and as we were interested in pollen composition comparisons, data were always standardized to proportions (i.e. relative contributions with total 100), and analyses were performed using pollen types percentages. For analyses of temporal dynamics and to facilitate comparisons across the two study regions, four sampling periods were defined based on accumulated Growing Degree Days (GDD) (see Table S3).

To describe samples' pollen types diversity, we used pollen type richness (number of pollen types), as well as the Simpson diversity index, which represents the probability that two grains randomly selected from a sample will belong to different types ($1 - D$, with $D = \sum p^2$, p being the proportion of pollen grains belonging to one pollen type). Mean pollen type richness and mean Simpson diversity were compared for the four insect species with Kruskal–Wallis and Dunn tests.

To assess the degree of exclusiveness or overlap in pollen use among the four studied insect species, complementary specialization d' (Blüthgen, Menzel, & Blüthgen, 2006) was calculated for each species for each sampling period (R package "bipartite 2.08"; Dormann, Fründ, Blüthgen, & Gruber, 2009). The index d' measures how strongly the pollen types collected by a species deviate from that of other species (Kämper et al., 2016). The measure ranges from 0 (complete overlap in pollen types use, i.e. "opportunistic" species sharing all their pollen types with other species) to 1 (exclusive pollen types use, i.e. "specialized" species; Blüthgen, Fründ, Vázquez, & Menzel, 2008; Junker et al., 2013). Mean d' along the season was compared for the four species with Student t test. We also calculated H_2' which describes the average degree of complementary specialization for the four insect species (i.e. network specialization; Blüthgen et al., 2006). Network specialization equals the weighted sum of the specialization of its nodes (i.e. weighted sum of d' of all species). It also ranges from 0 (pollen types used by the four species completely overlap; "maximum niche overlap"; Schleuning et al., 2012) to 1 (each species uses a unique set of pollen types; "maximum exclusiveness" or "maximum niche divergence"; Blüthgen et al., 2008; Schleuning et al., 2012). The species-level index d' was used to compare the specialization levels of the four studied species within networks, while H_2' index was used for comparing the different networks across the season. The two study regions were analysed together, and for each sampling period all samples belonging to one insect species were pooled. Only pollen types that accounted for more than 1% of the total number of pollen grains were considered for the analyses.

To examine the importance of pollen from woody plants, pollen types were classified as "woody" or "herbaceous" (see Table S1). Pollen types that could not be identified at the species level potentially including both woody and herbaceous plants (5% ± 10% of the data) were excluded from these analyses. For each insect species and sampling period, samples within a landscape were pooled. We used generalized linear mixed models (GLMMs) with a binomial error distribution to test the impacts of the fixed factors sampling period, species (*B. terrestris*, *O. bicornis*, *C. carnea*, *H. axyridis*), study region (Germany/Switzerland) and their interactions and the random factor landscape sector, on the proportion of pollen from woody plants used by the insects. An observation level term was added as a second nested random effect to account for overdispersion (Lee & Nelder, 2000). Models were fitted with the R package "lme4 1.1-13" (Bates, Maechler, Bolker, & Walker, 2015). As there was no significant three-way interaction in the full model ($p = .64$), indicating consistent temporal patterns of pollen use across species in both regions, data of both regions were finally analysed together. Predictors' significance was tested with Wald chi-square tests. We also examined the importance of non-agricultural plants by classifying pollen types as "non-agricultural" (i.e. associated plant taxa can be unambiguously classified as non-agricultural plants, which includes plants from semi-natural habitats and crop weeds) and "potential crop" (i.e. associated plant taxa could potentially include crop or sown grassland plant species; see Table S1). We used similar GLMMs to those previously described, with the proportion of pollen from non-agricultural plants as the response variable, and sampling period, insect species and their interactions as fixed factors. In this case, as the significant three-way interaction of the full model indicated distinct patterns among the two study regions, they were analysed separately.

To examine the influence of the landscape context on pollen use, we calculated landscape metrics using ArcGIS 10.5 (ESRI) based on 2016 land-cover maps of the study regions. Maps were digitalized based on photo interpretation and were completed and validated with ground surveys. Land use was classified into five categories: woody semi-natural habitats (e.g. woodlands, hedgerows), woody crops (including vines and orchards), herbaceous crops (e.g. cereals), grasslands and "other land use" (including settlements). We calculated two metrics within each landscape sector of 500 m radius: the surface of woody semi-natural habitats, and the total surface of woody land-use types (including woody semi-natural habitats and woody crops). We used as a basis the GLMMs previously described, including pollen proportion from woody plants or from non-agricultural plants used by insects as the response variable, sampling period, insect species and their interactions as fixed factors, and landscape sector and observation-level term as random effects. We complexified those models by adding a landscape metric and interactions with sampling period and insect species as additional fixed factors. The total surface of woody habitat was used as a landscape metric for the first model including the pollen proportion from woody plants as the response variable, whereas the surface of woody semi-natural habitat was used for the second model including the pollen proportion from non-agricultural plants as the response variable. We confirmed that we had no remaining spatial autocorrelation in the models by checking residuals against spatial coordinates with correlogram plots using the ncf package in R (Bjornstad, 2019).

3 | RESULTS

3.1 | Main types and diversity of pollen used

A total of 140 different pollen types were identified: 91 types were used by *B. terrestris*, 54 by *O. bicornis*, 99 by *C. carnea* and 82 by *H. axyridis* (see Table S1). Most individual samples contained at least two different pollen types (see Figure S3). Individual samples of pollen used by *C. carnea* and *H. axyridis* had a roughly three times higher pollen type richness than those of the two bee species (Dunn test, $p < .001$), and this pattern was consistent across the season (Figure 1). Simpson diversity of pollen types was also higher in samples from *C. carnea* and *H. axyridis* (0.54 ± 0.24 and 0.66 ± 0.18, respectively) than in those from *O. bicornis* (0.27 ± 0.22) and *B. terrestris* (0.17 ± 0.22; Dunn test: $p < .001$). Results were similar when pooling samples at the landscape level (see Figure S4).

Bombus terrestris collected mainly pollen from insect-pollinated plants (83% ± 25%) in contrast to *H. axyridis* which was mainly using pollen from wind-pollinated plants (67% ± 19%), whereas *O. bicornis* and *C. carnea* used pollen from both, insect- and wind-pollinated plants (see Table S4). More precisely, early in the season, *B. terrestris* collected *Salix*, *Prunus* t. (=type), *Acer* and Brassicaceae pollen (presumably oilseed rape; see Table S5), accounting for more than 80% of the pollen collected. Later in the season, mainly *Rubus*, *Papaver rhoeas* t., *Trifolium* (mainly *Trifolium repens* t.) and *Tilia* pollen were collected by this species (Figure 2). *O. bicornis* collected mainly *Acer* and *Quercus* pollen early in the season, accounting for more than 65% of the pollen collected, whereas *Acer* and *Ranunculus acris* t. (probably *Ranunculus* sp.) dominated in summer samples. *Prunus* t., *Betula*, *Salix*, *Carpinus*, *Acer*, *Fagus*, *Quercus* and Brassicaceae pollen covered more than 60% of the pollen diet of *C. carnea* early in the season, whereas Poaceae species dominated the pollen diet during the summer months. Finally, *H. axyridis* consumed mainly *Betula*, *Fagus*, *Carpinus*, *Quercus*, *Acer* and *Pinus* pollen early in the season, covering almost 60% of the pollen diet, whereas half of the pollen consumed in summer belonged to *Urtica* and Poaceae species (Figure 2).

3.2 | Overlap in pollen use among insect species

Complementary specialization at the species level was on average twice as high in the two bee species compared to *C. carnea* and *H. axyridis* (Figure 3; mean d' of 0.65 and 0.30 for the two bees and the two aphid enemy species, respectively; Student t test: $p < .001$). At the network level, the degree of complementary specialization (H_2'; i.e. mean complementary specialization of all four insect species) was low to intermediate, ranging from 0.33 to 0.53 across the sampling season (mean = 0.46; Figure 3). Overlap in pollen use

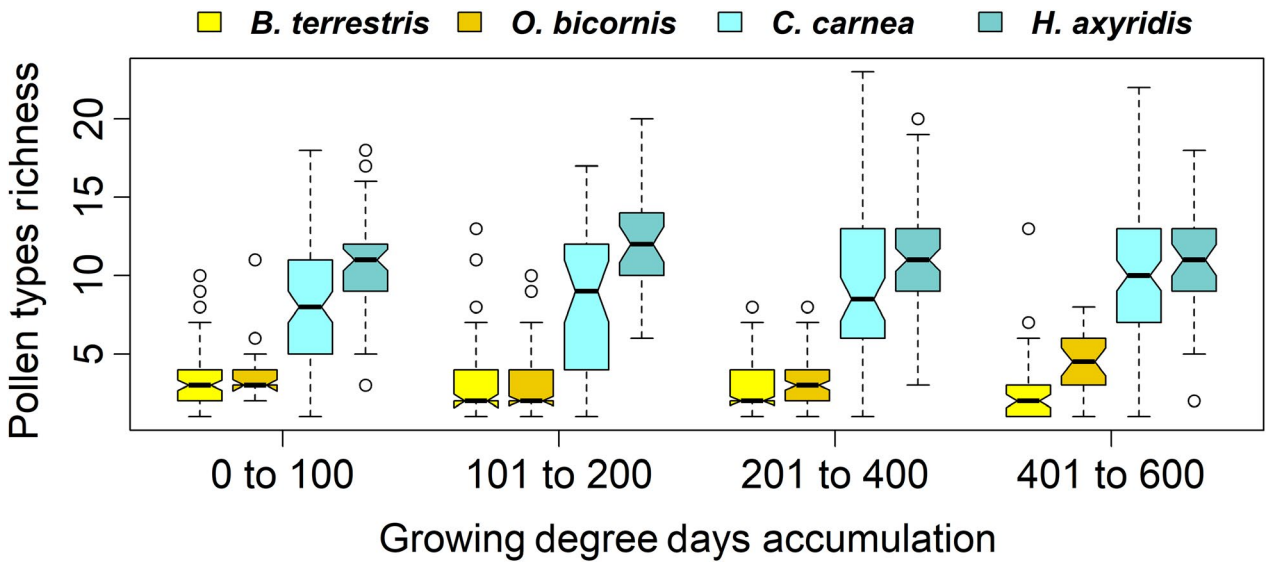


FIGURE 1 Changes in pollen type richness across the season for the pollen samples of *Bombus terrestris*, *Osmia bicornis*, *Chrysoperla carnea* s.l. and *Harmonia axyridis*. The notches indicate a 95% confidence interval of the median; if notches of two boxes do not overlap, this is a strong evidence that the medians differ. The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see Table S3)

between the four insect species was highest in May (GDD 100–200; H_2' = 0.33, i.e. less pronounced niche complementarity), primarily due to a relatively high proportion of shared pollen types from woody plants such as *Acer*, *Quercus*, *Fagus*, *Prunus* t. and *Salix*, as well as a fairly general use of Brassicaceae pollen (Figure 3). Further key pollen types shared by at least two species included *Betula* early in the season (April, GDD 0–100), and Poaceae, *Tilia*, *Papaver rhoeas* t. and *Ranunculus acris* t. later in the season (June to mid-July, GDD 201–600).

3.3 | Relative importance of different pollen sources, temporal shifts and landscape effects

For all insect species, the proportion of pollen from woody plants (collected from trees and shrubs) was high early in the year (April and May, GDD 0–200), but decreased significantly later in the season (June, GDD 201–400), indicating a shift from woody to herbaceous pollen sources (Table 1; Figures 2–4). The proportion of pollen from woody plants remained low until mid-July (GDD 401–600) for most species, but tended to increase again for *B. terrestris* because of the importance of *Tilia* pollen for this species in the late season. There was no significant relationship between the proportion of woody habitats in the landscapes and the proportion of pollen from woody plants collected by the insects (p > .05; see Table S6).

There was no clear temporal trend in the proportion of pollen from non-agricultural plants used by studied insect species. Throughout the season, *O. bicornis* used higher percentages (82 ± 17%) of pollen from non-agricultural plants than *H. axyridis* (63 ± 15%), *B. terrestris* (57 ± 14%) or *C. carnea* (56 ± 9%; Table 2). At any time of the season and across all insect species, however, a significant part of the pollen diet was from non-agricultural plants (min ≥40%, mean ≥64%; Table 2). There was no significant relationship between the proportion of woody semi-natural habitats in the landscapes and the proportions of pollen from non-agricultural plants collected by the insects (p > .05; see Table S6).

4 | DISCUSSION

Our findings reveal: (a) a higher diversity and lower pollen diet specialization of the two potential aphid enemies *Chrysoperla carnea* and *Harmonia axyridis* compared to the two studied bee species; (b) some important pollen plant taxa (e.g. *Acer*) shared by all four species, in particular early in the season; (c) the importance of woody plants (primarily trees) as pollen sources early in the season and a pronounced shift from woody to herbaceous pollen sources during the season for all studied insect species; (d) a generally high proportion of pollen from weeds and non-agricultural sources used by all four species.

4.1 | Composition and diversity of pollen used

Our findings are in agreement with the general expectation that bees (*O. bicornis* and *B. terrestris*) – exclusively relying on pollen as protein source for offspring provisioning – more selectively use pollen taxa of high nutritional quality that can be collected at relative low energy costs (e.g. mass-flowering plants), while natural enemies (*C. carnea* and *H. axyridis*) are more opportunistic in their pollen use.

In spring as well as in summer, *Osmia bicornis* collected pollen mainly from a very limited number of plants: *Acer* and *Quercus* early in the year, and *Ranunculus acris* type (probably *Ranunculus*

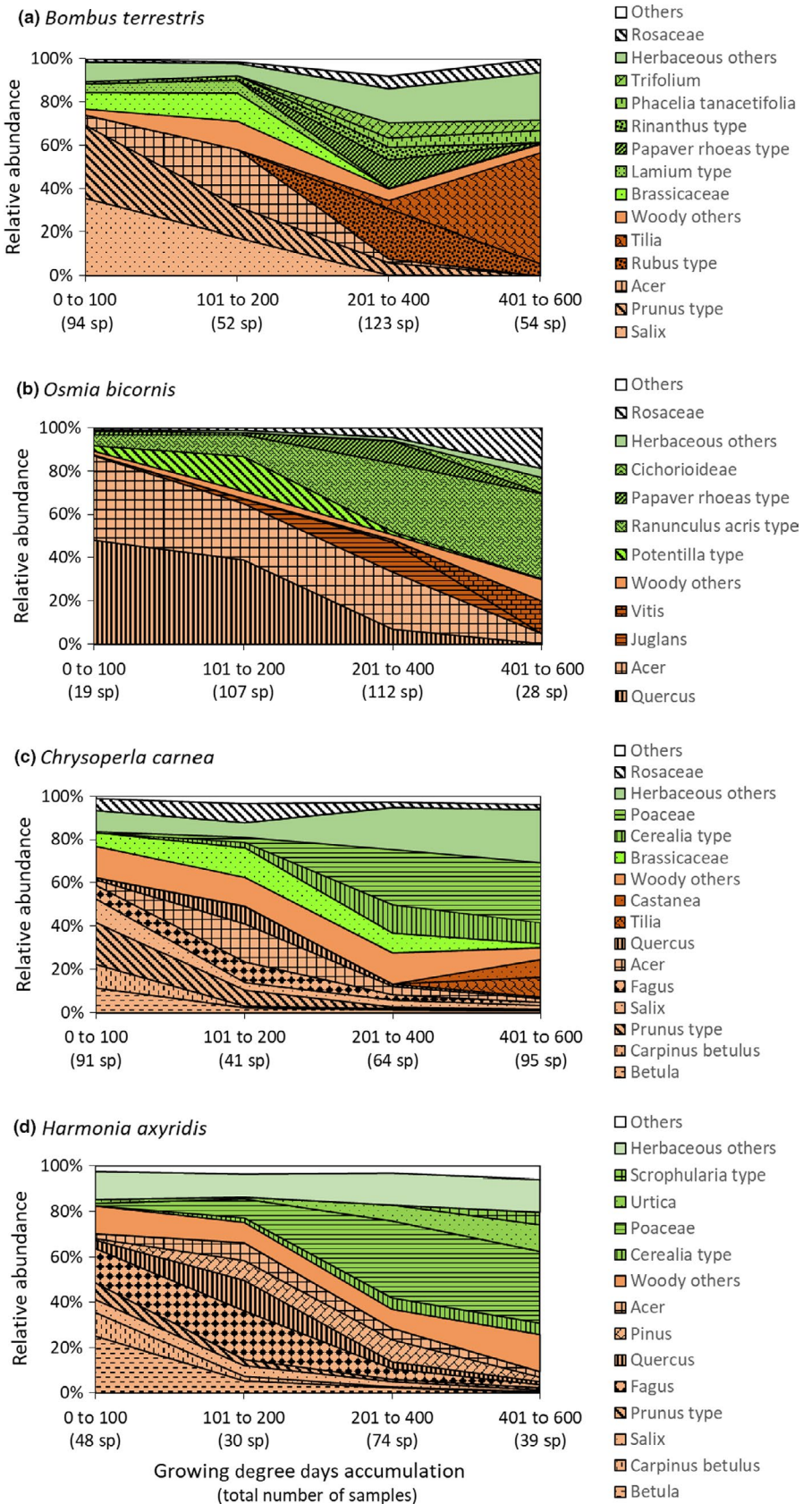
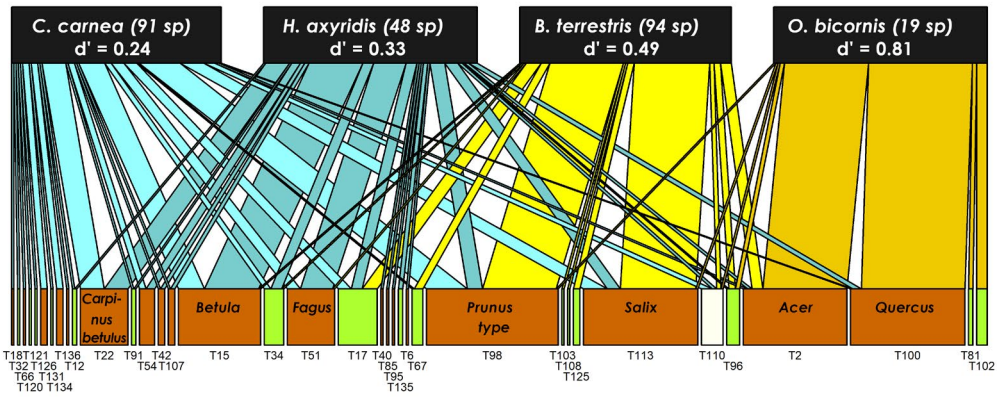


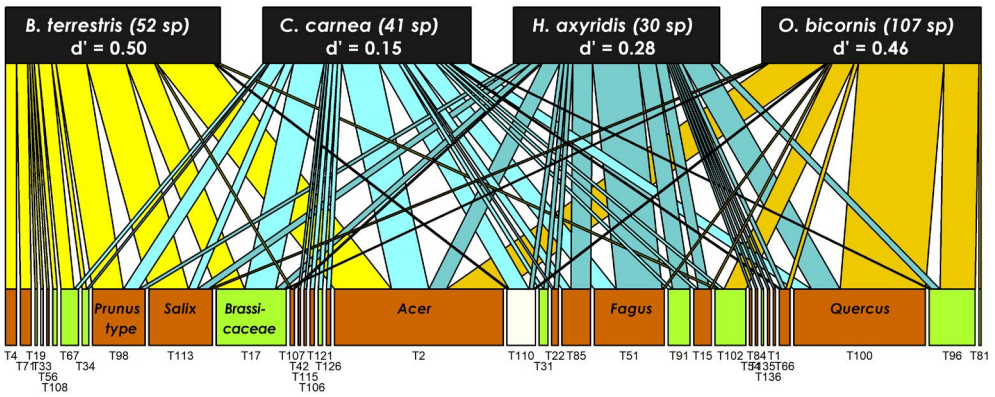
FIGURE 2 Relative abundance (%) of the main pollen types used across the season by (a) *Bombus terrestris*, (b) *Osmia bicornis*, (c) *Chrysoperla carnea* s.l., and (d) *Harmonia axyridis*. The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see Table S3). Number of samples is given in brackets next to sampling periods. Only pollen types accounting for more than 5% of the total number of pollen grains used by an insect species are detailed. Brown colours represent pollen from woody plants, green colours those from herbaceous plants and white those for which this information was not available or which comprise both woody and herbaceous plants (see Table S1)

sp.), *Acer*, *Juglans* and *Papaver* in summer. The similar pollen use of *O. bicornis* in different years and regions (Coudrain, Rittiner, Herzog, Tinner, & Entling, 2016; Radmacher & Strohm, 2010) indicates clear preferences among plants. These plants include mass-flowering trees such as *Quercus*, which is wind-pollinated but provides abundant and high-quality pollen for bees (Roulston,

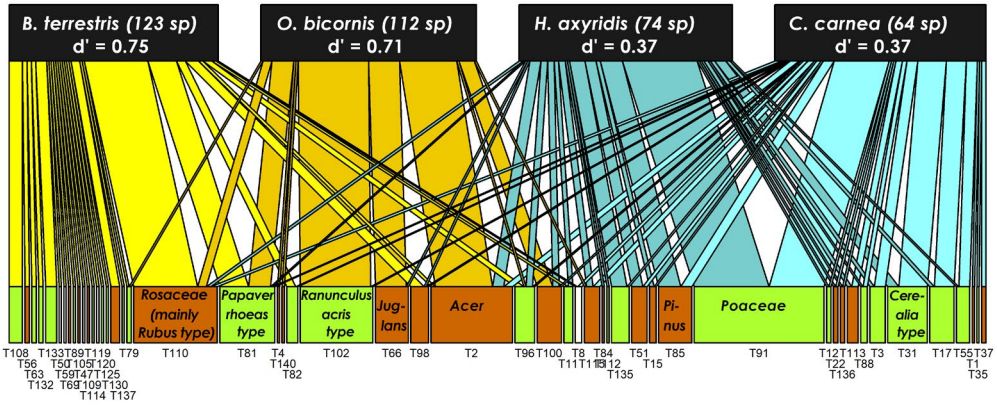
(a) GDD 0 to 100 ; H2' = 0.45



(b) GDD 101 to 200 ; H2' = 0.33



(c) GDD 201 to 400 ; H2' = 0.53



(d) GDD 401 to 600 ; H2' = 0.52

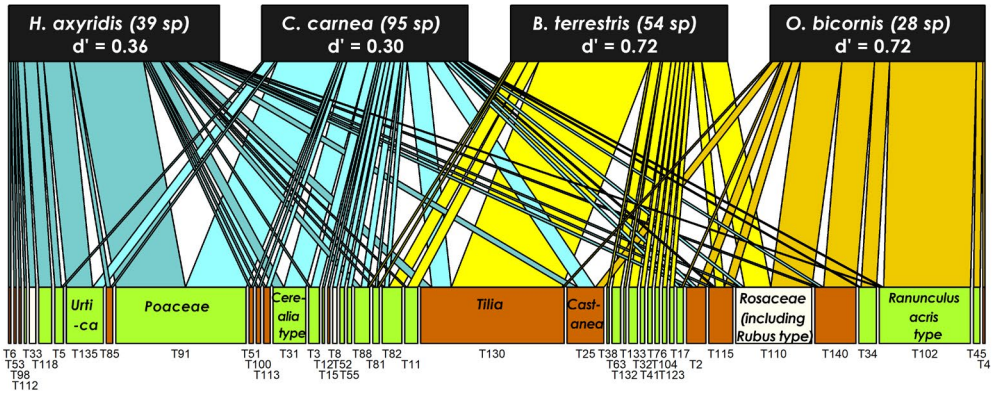


FIGURE 3 Pollen use network of the four insect species at each sampling period. Growing Degree Days (GDD) 0–100 correspond approximately to the month of April, 101–200 to May, 201–400 to June and 401–600 to end of June to mid-July (see Table S3). H_2' measures network specialization; it ranges from 0 for the most generalized (i.e. maximum niche overlap) to 1 for the most specialized network (i.e. high exclusiveness, or maximum niche divergence). Upper bars represent insect species and lower bars the average proportion of pollen types used across all insect species (see Table S1 for more information on pollen types). Brown colours represent pollen from woody plants, green colours those from herbaceous plants, and white those for which this information was not available or which comprise both woody and herbaceous plants. The width of the arrows between upper and lower bars represents the proportion of a pollen type used by an insect species. Number of samples is given in brackets next to species names, and values of species-level complementary specialization (d') are shown below. A high d' value indicates a high degree of specialization in pollen use of an insect species (high "exclusiveness"), whereas insect species sharing many pollen types with other taxa receive small d' values (i.e. "opportunistic" species)

TABLE 1 Analysis of deviance table (Type II Wald chi-square tests) of a generalized linear mixed model with binomial error structure testing for the effects of sampling period, insect species and their interaction on the proportion of pollen from woody plants used by insects

Predictor	χ^2	*df*	$p(>\chi^2)$
Insect species	3.85	3	.279
Sampling period	**143.91**	**3**	**<.001**
Insect species:Sampling period	15.59	9	.076

Note: Pollen use by *Bombus terrestris*, *Osmia bicornis*, *Chrysoperla carnea* and *Harmonia axyridis* was assessed during four sampling periods (roughly April, May, June and July; see Table S3). Significant values are highlighted in bold.

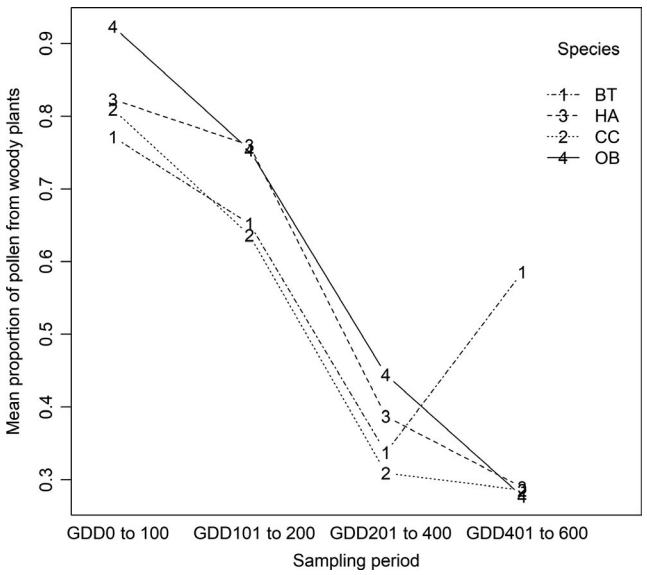


FIGURE 4 Mean proportion of pollen from woody plant taxa collected per landscape sector for each insect species and sampling period. The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see Table S3). Abbreviations: BT, *Bombus terrestris*; OB, *Osmia bicornis*; CC, *Chrysoperla carnea*; HA, *Harmonia axyridis*

Cane, & Buchmann, 2000), and some abundantly flowering, pollen-rich herbaceous plants including *Ranunculus*, which has been shown to be toxic to other bee species but not for *O. bicornis* (Sedivy, Müller, & Dorn, 2011).

Bombus terrestris foraged mainly on *Salix*, *Prunus* type, *Acer* and Brassicaceae (probably *Brassica* sp.) pollen in spring, and on *Rubus*, *Papaver*, *Trifolium* and *Tilia* pollen in summer (Kämper et al., 2016; Kleijn & Raemakers, 2008). Most of these plants are insect-pollinated and offer pollen of high protein content (Roulston et al., 2000), and except for *Papaver*, also relatively large amounts of nectar. In particular for the social *B. terrestris*, nectar availability may play a role in their preference for mainly insect-pollinated plants. Similar to *O. bicornis*, *B. terrestris* seems to primarily collect pollen of mass-flowering plants offering pollen of high nutritional quality (Kriesell, Hilpert, & Leonhardt, 2017). In fact, both quantity and quality of pollen collected by bumblebee workers are known to influence colony fitness (Génissel, Aupinel, Bressac, Tasei, & Chevrier, 2002; Kämper et al., 2016).

Although the total number of pollen types collected at the taxa level was similarly high between bumblebees, lacewings and ladybeetles (91, 99 and 82 types, respectively), individuals of *Chrysoperla carnea* and *Harmonia axyridis* were more generalistic in their pollen diet (i.e. using more diverse pollen spectra), suggesting that they are opportunistic pollen feeders when compared to the studied bee species (Berkvens et al., 2010; Villenave et al., 2005). This is also reflected by the higher proportions of pollen from wind-pollinated plants with relatively low nutritional quality such as *Betula*, *Carpinus betulus*, *Fagus* or Poaceae (Berkvens et al., 2010).

4.2 | Relative importance of pollen sources

Despite the observed differences in pollen use among the studied insect species, our results reveal several general patterns. First, all four species used high proportions of pollen from non-agricultural plants (overall ≥64%), despite the fact that most of the studied landscapes were dominated by agricultural land (ranging from 38% to 90%; mean = 68%). The percentage of pollen from non-agricultural plants could exceed 90% in the case of *O. bicornis* and was generally high early in the year, underpinning the crucial role of floral resources offered by weeds and non-crop vegetation to sustain functionally important insect populations outside crops' flowering periods (Requier et al., 2015). These percentages should be interpreted as conservative estimates since all pollen types that potentially include crop or sown grassland species were not considered. Evidence from North American agroecosystems support these findings for generalist pollinators (e.g. Russo & Danforth, 2017; Williams & Kremen, 2007).

Another important finding is that woody plant species play a crucial role in providing the studied insect species with

TABLE 2 Percentages of pollen used from non-agricultural plants

	GDD 0–100	GDD 101–200	GDD 201–400	GDD 401–600	Whole sampling season (mean ± *SD*)
Bombus terrestris	52%	68%	40%	69%	57% (±14%)
Osmia bicornis	95%	82%	92%	58%	82% (±17%)
Chrysoperla carnea	63%	63%	46%	51%	56% (±9%)
Harmonia axyridis	77%	74%	50%	51%	63% (±15%)
Mean	72%	72%	57%	57%	64% (±16%)

Note: Numbers represent percentages of pollen types that can be unambiguously classified as from non-agricultural plants (i.e. pollen types potentially including crops and sown grassland plants are not included; see Table S1). The four sampling periods (expressed in Growing Degree Days) correspond roughly to the months of April, May, June and July (see Table S3).

pollen resources early in the season (Kämper et al., 2016; Russo & Danforth, 2017; Villenave et al., 2005). The early season has been identified as a critical period during the life history of many important crop pollinators and pest enemies (e.g. Carvell et al., 2017; Kämper et al., 2016; Williams et al., 2012). This highlights the importance of maintaining woody habitats such as forest patches and hedgerows in agricultural landscapes. However, although we sampled 23 different agricultural landscapes spread over two countries and representing a high variability in landscape composition in terms of habitat and vegetation types, a rather low number of pollen types (2–8) represented more than 70% of the pollen collected by each insect species during the early season stage – in particular pollen types from flowering trees such as *Acer*, *Quercus*, *Salix*, *Fagus* or *Prunus*. These plants may also be important resources for other pollinator and natural enemy taxa such as honeybees (Requier et al., 2015) and hoverflies (Haslett, 1989). Moreover, the proportion of pollen collected from woody plants was not contingent on landscapes with high proportions of woody habitats (which ranged from 0% to 51%; mean: 11%).

Thus, maintaining even small amounts of woody habitats should receive high priority in landscape management. Key woody pollen types identified in our study (e.g. *Acer*, *Quercus*, *Salix*), which are of high nutritional value for insects (Roulston et al., 2000), are promising species for landscape management measures to simultaneously promote different pollinator and natural enemy species. Further research should focus on how the amount and spatio-temporal availability of the identified key resources may affect the distribution and dynamics of multiple insect assemblages. Maps that provide information on the spatial and temporal distribution of those specific resource plants (rather than broad land-use categories), at the right spatial scale (considering the foraging ranges of the target species), could significantly improve predictions of ecosystem service providing insects across agricultural landscapes. However, these predictions must also account for other factors such as intraguild predation (e.g. *H. axyridis* may prey upon *C. carnea* and conversely; Pell, Baverstock, Roy, Ware, & Majerus, 2008), which may lead to potential management conflicts. It should also be noted here that the invasive ladybeetle *H. axyridis*, despite being an effective aphid enemy, should not be specifically promoted by landscape management, because it threatens native biodiversity (and native ladybeetles in particular; Roy et al., 2012). However, our data show that due to its broad range of pollen use, and the strong dietary overlap with *C. carnea*, there appears to be little scope to selectively enhance either species by pollen resource provision. We hypothesize that the dominance of *H. axyridis* over native aphid predators can neither be countered nor exacerbated through pollen resource provisioning, but this topic requires further investigation.

4.3 | Seasonal shifts in pollen sources used

The four studied insect species exhibited similar temporal dynamics of pollen use during the season, characterized by a pronounced shift from woody to herbaceous pollen sources. This corroborates evidence of previous single-taxon studies focusing for example, on honeybees (Requier et al., 2015) or lacewings (*Chrysoperla* ssp.; Villenave et al., 2005). This pattern is likely at least partly driven by plant phenology: in most European agricultural landscapes, many dominant flowering trees and shrubs bloom relatively early and contribute more to floral resource availability early rather than later in the season (Williams et al., 2012; but see e.g. *Tilia* as an important exception). Yet, our results highlight the critical role of phenological complementarity among habitat types in providing food resources for multiple functionally important insect species throughout the year, and thus the importance of maintaining heterogeneous agricultural landscapes (Benton et al., 2003; Mallinger, Gibbs, & Gratton, 2016), including both species-rich woody and herbaceous habitats.

However, the high diversity of insects inhabiting agricultural landscapes that we could not investigate points to some limitations of our study. Further research is needed to confirm to what extent our findings could be generalized to natural bumblebee colonies and other important taxonomic groups of pollinators and crop pest enemies. Different functional groups such as parasitic wasps may show contrasting patterns of floral resource use (Patt, Hamilton, & Lashomb, 1997). Finally, monitoring over several years may help identify potential inter-annual variation in the observed pollen use patterns (e.g. due to varying phenologies of flowering plants and insects).

5 | CONCLUSIONS

Our findings have several important implications for the promotion of multiple key insect species that can provide crop pollination and pest control services in agroecosystems. Among the most important findings is that pollen use overlapped only little among the four studied species, with the exception of *Chrysoperla carnea* and *Harmonia axyridis*. Nevertheless, the diet generally shifted from woody to herbaceous pollen collected from mostly weeds and non-agricultural vegetation sources. This strongly supports incentives to maintain or restore heterogeneous agricultural landscapes (Benton et al., 2003; Martin et al., 2019). Heterogeneous landscapes should be characterized by a high diversity of plants and vegetation types, including both woody and herbaceous vegetation providing complementary floral resources throughout the year (phenological completeness), a factor proposed to be critical for effective provision of pollination and pest control services in agroecosystems (Schellhorn et al., 2015). Such incentives may include floral enhancement measures, such as the establishment of flower-rich hedgerows or sown flower strips promoted through agri-environmental schemes, which mitigate the isolation of semi-natural areas, and have a high potential to enhance floral-resource consuming insects and the ecosystem services they provide (e.g. Blaauw & Isaacs, 2014; M'Gonigle et al., 2015; Sutter et al., 2017; Tschumi et al., 2015). Our results, however, highlight an important role of trees for the nutrition of all four studied insect species in the early (*Acer*, *Quercus*, *Salix*, *Fagus* or *Prunus*) or late (*Tilia*) season, questioning whether schemes based on herbaceous plants alone can always provide enough adequate pollen resources to meet the pollen dietary requirements of multiple functionally important insect species (see also Wood, Holland, & Goulson, 2017). The identified early flowering trees are promising targets for habitat management measures to simultaneously promote both crop pollinators and pest enemies and the multiple ecosystem services they can provide in European agroecosystems.

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AUTHORS' CONTRIBUTIONS

C.B., M.A., L.A., M.H.E., L.M. and F.H. conceived and designed the experiment. C.B., L.A. and L.M. performed the field surveys. C.B., P.E., E.G. and W.T. contributed to pollen sample preparation and identification. C.B. and M.A. performed the analysis. C.B. wrote the first draft of the manuscript, and all authors contributed substantially to writing. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.6836p06 (Bertrand et al., 2019).

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REFERENCES

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology & Evolution*, *18*(4), 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Berkvens, N., Landuyt, C., Deforce, K., Berkvens, D., Tirry, L., & De Clercq, P. (2010). Alternative foods for the multicoloured Asian lady beetle *Harmonia axyridis* (Coleoptera: Coccinellidae). *European Journal of Entomology*, *107*(2), 189–195. https://doi.org/10.14411/eje.2010.025

Bertrand, C., Eckerter, P. W., Ammann, L., Entling, M. H., Gobet, E., Herzog, F., … Albrecht, M. (2019). Data from: Seasonal shifts and complementary use of pollen sources by two bees, a lacewing and a ladybeetle species in European agricultural landscapes. Dryad Digital Repository, https://doi.org/10.5061/dryad.6836p06

Beug, H.-J. (2004). *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Munich, Germany: Verlag Dr. Friedrich Pfeil.

Bjornstad, O. N. (2019). ncf: Spatial covariance functions. R package version 1.2-8. Retrieved from https://CRAN.R-project.org/package=ncf

Blaauw, B. R., & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, *51*(4), 890–898. https://doi.org/10.1111/1365-2664.12257

Blüthgen, N., Fründ, J., Vázquez, D. P., & Menzel, F. (2008). What do interaction network metrics tell us about specialization and biological traits. *Ecology*, *89*(12), 3387–3399. https://doi.org/10.1890/07-2121.1

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*(1), 9. https://doi.org/10.1186/1472-6785-6-9

Carvell, C., Bourke, A. F. G., Dreier, S., Freeman, S. N., Hulmes, S., Jordan, W. C., … Heard, M. S. (2017). Bumblebee family lineage survival is enhanced in high-quality landscapes. *Nature*, *543*(7646), 547–549. https://doi.org/10.1038/nature21709

Coudrain, V., Rittiner, S., Herzog, F., Tinner, W., & Entling, M. H. (2016). Landscape distribution of food and nesting sites affect larval diet and nest size, but not abundance of *Osmia bicornis*. *Insect Science*, *23*(5), 746–753. https://doi.org/10.1111/1744-7917.12238

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*(1), 7–24. https://doi.org/10.2174/1874213000902010007

Garratt, M., Coston, D. J., Truslove, C. L., Lappage, M. G., Polce, C., Dean, R., … Potts, S. G. (2014). The identity of crop pollinators helps target conservation for improved ecosystem services. *Biological Conservation*, *169*, 128–135. https://doi.org/10.1016/j.biocon.2013.11.001

Génissel, A., Aupinel, P., Bressac, C., Tasei, J. N., & Chevrier, C. (2002). Influence of pollen origin on performance of *Bombus terrestris* microcolonies. *Entomologia Experimentalis Et Applicata*, *104*(2–3), 329–336. https://doi.org/10.1046/j.1570-7458.2002.01019.x

Grab, H., Blitzer, E. J., Danforth, B., Loeb, G., & Poveda, K. (2017). Temporally dependent pollinator competition and facilitation with mass flowering crops affects yield in co-blooming crops. *Scientific Reports*, *7*, 45296. https://doi.org/10.1038/srep45296

Gruber, B., Eckel, K., Everaars, J., & Dormann, C. F. (2011). On managing the red mason bee (*Osmia bicornis*) in apple orchards. *Apidologie*, *42*(5), 564–576. https://doi.org/10.1007/s13592-011-0059-z

Haslett, J. R. (1989). Interpreting patterns of resource utilization: Randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia*, *78*(4), 433–442. https://doi.org/10.1007/BF00378732

IPBES. (2016). The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany, 552 pp.

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., & Landis, D. (2009). Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment*, *7*(4), 196–203. https://doi.org/10.1890/080035

Jones, G. D. (2012). Pollen extraction from insects. *Palynology*, *36*(1), 86–109. https://doi.org/10.1080/01916122.2011.629523

Junker, R. R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Martin Schaefer, H., & Stang, M. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional Ecology*, *27*(2), 329–341. https://doi.org/10.1111/1365-2435.12005

Kämper, W., Werner, P. K., Hilpert, A., Westphal, C., Blüthgen, N., Eltz, T., & Leonhardt, S. D. (2016). How landscape, pollen intake and pollen quality affect colony growth in *Bombus terrestris*. *Landscape Ecology*, *31*(10), 2245–2258. https://doi.org/10.1007/s10980-016-0395-5

Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E., & Tscharntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1775), 20132440. https://doi.org/10.1098/rspb.2013.2440

Kleijn, D., & Raemakers, I. (2008). A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology*, *89*(7), 1811–1823. https://doi.org/10.1890/07-1275.1

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L. G., Henry, M., Isaacs, R., … Potts, S. G. (2015). Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications*, *6*, 7414. https://doi.org/10.1038/ncomms8414

Kriesell, L., Hilpert, A., & Leonhardt, S. D. (2017). Different but the same: Bumblebee species collect pollen of different plant sources but similar amino acid profiles. *Apidologie*, *48*(1), 102–116. https://doi.org/10.1007/s13592-016-0454-6

Lee, Y., & Nelder, J. A. (2000). Two ways of modelling overdispersion in non-normal data. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, *49*(4), 591–598. https://doi.org/10.1111/1467-9876.00214

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, *56*(4), 311–323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2

Lundgren, J. G. (2009). Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control*, *51*(2), 294–305. https://doi.org/10.1016/j.biocontrol.2009.05.016

Mallinger, R. E., Gibbs, J., & Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, *31*(7), 1523–1535. https://doi.org/10.1007/s10980-015-0332-z.

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., … Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: New pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, https://doi.org/10.1111/ele.13265

McEwen, P. K., New, T. R., & Whittington, A. E. (Eds.). (2007). *Lacewings in the crop environment*. Cambridge: Cambridge University Press.

M'Gonigle, L. K., Ponisio, L. C., Cutler, K., & Kremen, C. (2015). Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecological Applications*, *25*(6), 1557–1565. https://doi.org/10.1890/14-1863.1

Moore, P. D., Webb, J. A., & Collinson, M. (1991). *Pollen analysis* (2nd ed.). Oxfrod, UK: Blackwell Scientific Publications.

Patt, J. M., Hamilton, G. C., & Lashomb, J. H. (1997). Foraging success of parasitoid wasps on flowers: Interplay of insect morphology, floral architecture and searching behavior. *Entomologia Experimentalis Et Applicata*, *83*(1), 21–30. https://doi.org/10.1046/j.1570-7458.1997.00153.x

Pell, J. K., Baverstock, J., Roy, H. E., Ware, R. L., & Majerus, M. E. (2008). Intraguild predation involving Harmonia axyridis: A review of current knowledge and future perspectives. *BioControl*, *53*(1), 147–168. https://doi.org/10.1007/s10526-007-9125-x

Pfister, S. C., Eckerter, P. W., Schirmel, J., Cresswell, J. E., & Entling, M. H. (2017). Sensitivity of commercial pumpkin yield to potential decline among different groups of pollinating bees. *Royal Society Open Science*, *4*(5), 170102. https://doi.org/10.1098/rsos.170102

Pfister, S. C., Schirmel, J., & Entling, M. H. (2017). Aphids and their enemies in pumpkin respond differently to management, local and landscape features. *Biological Control*, *115*, 37–45. https://doi.org/10.1016/j.biocontrol.2017.09.005

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Radmacher, S., & Strohm, E. (2010). Factors affecting offspring body size in the solitary bee *Osmia bicornis* (Hymenoptera, Megachilidae). *Apidologie*, *41*(2), 169–177. https://doi.org/10.1051/apido/2009064

Reille, M. (1992). Pollen et spores d'europe et d'afrique du nord. Marseille, France: Laboratoire de Botanique historique et Palynologie.

Requier, F., Odoux, J. F., Tamic, T., Moreau, N., Henry, M., Decourtye, A., & Bretagnolle, V. (2015). Honey bee diet in intensive farmland habitats reveals an unexpectedly high flower richness and a major role of weeds. *Ecological Applications*, *25*(4), 881–890. https://doi.org/10.1890/14-1011.1

Rollin, O., Bretagnolle, V., Decourtye, A., Aptel, J., Michel, N., Vaissière, B. E., & Henry, M. (2013). Differences of floral resource use between honey bees and wild bees in an intensive farming system. *Agriculture, Ecosystems & Environment*, *179*, 78–86. https://doi.org/10.1016/j.agee.2013.07.007

Roulston, T. H., Cane, J. H., & Buchmann, S. L. (2000). What governs protein content of pollen: Pollinator preferences, pollen–pistil interactions, or phylogeny? *Ecological Monographs*, *70*(4), 617–643.

Roy, H. E., Adriaens, T., Isaac, N. J. B., Kenis, M., Onkelinx, T., Martin, G. S., … Maes, D. (2012). Invasive alien predator causes rapid declines of native European ladybirds. *Diversity and Distributions*, *18*(7), 717–725. https://doi.org/10.1111/j.1472-4642.2012.00883.x

Russo, L., & Danforth, B. (2017). Pollen preferences among the bee species visiting apple (*Malus pumila*) in New York. *Apidologie*, *48*(6), 806–820. https://doi.org/10.1007/s13592-017-0525-3

Schellhorn, N. A., Gagic, V., & Bommarco, R. (2015). Time will tell: Resource continuity bolsters ecosystem services. *Trends in Ecology & Evolution*, *30*(9), 524–530. https://doi.org/10.1016/j.tree.2015.06.007

Scheper, J., Reemer, M., van Kats, R., Ozinga, W. A., van der Linden, G. T. J., Schaminée, J. H. J., … Kleijn, D. (2014). Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(49), 17552–17557. https://doi.org/10.1073/pnas.1412973111

Schleuning, M., Fründ, J., Klein, A.-M., Abrahamczyk, S., Alarcón, R., Albrecht, M., … Blüthgen, N. (2012). Specialization of mutualistic interaction networks decreases toward tropical latitudes. *Current Biology*, *22*(20), 1925–1931. https://doi.org/10.1016/j.cub.2012.08.015

Sedivy, C., Müller, A., & Dorn, S. (2011). Closely related pollen generalist bees differ in their ability to develop on the same pollen diet: Evidence for physiological adaptations to digest pollen. *Functional Ecology*, *25*(3), 718–725. https://doi.org/10.1111/j.1365-2435.2010.01828.x

Shackelford, G., Steward, P. R., Benton, T. G., Kunin, W. E., Potts, S. G., Biesmeijer, J. C., & Sait, S. M. (2013). Comparison of pollinators and natural enemies: A meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews*, *88*(4), 1002–1021. https://doi.org/10.1111/brv.12040

Stutz, S., & Entling, M. H. (2011). Effects of the landscape context on aphid-ant-predator interactions on cherry trees. *Biological Control*, *57*(1), 37–43. https://doi.org/10.1016/j.biocontrol.2011.01.001

Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology*, *54*(6), 1856–1864. https://doi.org/10.1111/1365-2664.12907

Tschumi, M., Albrecht, M., Entling, M. H., & Jacot, K. (2015). High effectiveness of tailored flower strips in reducing pests and crop plant damage. *Proceedings of the Royal Society B*, *282*(1814), 20151369. https://doi.org/10.1098/rspb.2015.1369

Villenave, J., Thierry, D., Al Mamun, A., Lodé, T., & Rat-Morris, E. (2005). The pollens consumed by common green lacewings *Chrysoperla* spp. (Neuroptera: Chrysopidae) in cabbage crop environment in western France. *European Journal of Entomology*, *102*(3), 547–552.

Wäckers, F. L., & Van Rijn, P. C. (2012). Pick and mix: Selecting flowering plants to meet the requirements of target biological control insects. In G. M. Gurr, S. D. Wratten, W. E. Snyder, & D. M. Y. Read (Eds.), *Biodiversity and insect pests: Key issues for sustainable management* (pp. 139–165). Oxford: John Wiley & Sons Ltd.

Walther-Hellwig, K., & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, *124*, 299–306. https://doi.org/10.1046/j.1439-0418.2000.00484.x

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., … Steffan-Dewenter, I. (2008). Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*, *78*(4), 653–671. https://doi.org/10.1890/07-1292.1

Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, *17*(3), 910–921. https://doi.org/10.1890/06-0269

Williams, N. M., Regetz, J., & Kremen, C. (2012). Landscape-scale resources promote colony growth but not reproductive performance of bumble bees. *Ecology*, *93*(5), 1049–1058. https://doi.org/10.1890/11-1006.1

Wood, T. J., Holland, J. M., & Goulson, D. (2017). Providing foraging resources for solitary bees on farmland: Current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, *54*(1), 323–333. https://doi.org/10.1111/1365-2664.12718

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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