SCAPE Joint Special Issue

COMPLEMENTARY INSIGHTS FROM TRANSECT OBSERVATIONS AND PALYNOLOGICAL ANALYSES ON *ANDRENA* AND *LASIOGLOSSUM* FORAGING IN FIELD MARGINS

Manuela Giovanetti[1,]*, Laura Zavatta[1,2], Simone Flaminio[1,3], Francesca Corvucci[1], Francesca-Vittoria Grillenzoni[1], Rosa Ranalli[1,4], Marino Quaranta[1], Laura Bortolotti[1], Gherardo Bogo[1]

[1]CREA Research Centre for Agriculture and Environment, via di Corticella 133, 40128, Bologna, Italy.
[2] Department of Agriculture and Food Sciences, University of Bologna, Via Giuseppe Fanin 42, Bologna, 40127, Italy.
[3]Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Place du parc 20, 7000 Mons, Belgium.
[4]Department of Biotechnology and Biosciences, University of Milano-Bicocca, Piazza della Scienza2, 20126, Milano, Italy

Abstract—Field margins support wild bees by providing richer floral resources than most crops. While transect-based hand netting offers insight into bee–plant interactions, it underrepresents the full range of each bee's foraging activity. To uncover more of each bee's foraging behaviour, we complemented transect data with palynological analysis of pollen loads from captured bees. In 2021 and 2022, we collected 58 *Andrena* and 176 *Lasioglossum* females plus males during transect surveys. Sixty-six plant species were identified along the transects, at least to genus level. All bee specimens were identified to species level by a taxonomist, and their pollen loads (pollen carried on the body in various positions) analysed in the lab. The 19 *Andrena* species were mostly active in spring, showing a succession of species, whereas the 18 *Lasioglossum* species were more common in summer, with some overlap. Field observations showed *Crepis* species were the most frequently visited, with 52.7% of *Andrena* and 58.2% of *Lasioglossum* collected on them. *Cichorium intybus* was also a common resource for *Lasioglossum* (17.6%). Pollen analysis identified 63 taxa (40% overlapping with transect data) substantially expanding the list of visited plant species. Our findings highlight the crucial role of palynological analyses in revealing bee foraging preferences, even pointing to an underappreciated role of trees, and the importance of considering also male individuals. Yet, some observations on transects revealed unexpected food sources. For better understanding of lesser-known Apoidea species, we recommend incorporating planned pollen analyses into transect monitoring. Both bee and pollen identification require specialised expertise, but this integrated approach provides vital insights into plant-pollinator dynamics.

Keywords—Wild bees, pollen analyses, plant-pollinator networks, agroecosystems, transect

Journal of Pollination Ecology, 40(6), 2026, pp 77-97

DOI: 10.26786/1920-7603(2026)880

Received 9 June 2025, accepted 26 March 2026

*Corresponding author: manuela.giovanetti@gmail.com

INTRODUCTION

Accurate knowledge of floral resources actually collected by wild bees is crucial both for basic ecological understanding and for applied conservation. Ecologically, such data illuminate where, when, and how bees obtain their pollen and nectar, revealing niche breadth and overlap among species (Wood et al. 2016; Vaudo et al. 2020), foraging ranges (Zurbuchen et al. 2010; Beil et al. 2008), and resilience or vulnerability under environmental change (Rasmont et al. 2016). From a conservation standpoint, this knowledge underpins restoration efforts, habitat planning (Mandelik et al. 2012; Ghisbain et al. 2021), and interventions like wildflower planting (Hoffmann Black et al. 2009; Weber et al. 2023) or agri-environment schemes (Wood et al. 2016; McHugh et al. 2022; Giovanetti and Bortolotti, 2023). Yet, our current knowledge remains partial and biased, largely derived from floral visitation records rather than from the actual pollen and nectar resources collected by bees. Many wild bee species are underrepresented in datasets, and direct observations often fail to capture hidden dependencies on less conspicuous or temporally restricted plant species.

Palynological and molecular pollen analyses revealed that wild bees use a broader and sometimes markedly different set of plants than those detected by visual foraging records alone. Beil et al. (2008) demonstrated that pollen loads from 56 wild bee species in German sandy grasslands included tree pollen from *Acer pseudoplatanus* L. and *Tilia* spp., despite bees being observed mainly on herbaceous plants, showing that reliance on woody taxa is underestimated in field observations. In Michigan, analyses of pollen loads from 152 wild solitary bee species showed that in spring and early summer, trees and shrubs (e.g. *Acer, Prunus, Salix, Cornus, Vaccinium*) comprise a large fraction of pollen collected, shifting to herbs only later in the season; moreover, non-native plants become important when native herb resources decline. Therefore, studies that focus solely on herbaceous visitation risk overlooking crucial resources, such as pollen from trees and shrubs that sustain bee populations outside the main flowering season of herbs. Not only shrubs and trees may be overlooked. Kobayashi-Kidokoro & Higashi (2010) demonstrated that the seemingly generalist *Ceratina flavipes* Smith, 1869, exhibited strong floral constancy, selectively foraging on specific plant taxa while bypassing more abundant species. Similarly, Giovanetti et al. (2006) identified unexpected pollen sources, such as *Marrubium vulgare* L. and *Cistus albidus* L., in the Brassicaceae-oligolectic *Andrena agilissima* (Scopoli, 1770), suggesting flexibility and potential resilience in foraging under resource scarcity. Fisogni et al. (2018) found that pollen loads from wild bees foraging on *Dictamnus albus* L. contained a much higher diversity of plant taxa than expected from visitation data, expanding the perceived foraging niche of local bee communities. These findings highlight that observational data alone may underestimate the breadth or specialization of bee diets.

From a cost–benefit perspective, the relative time investment and efficiency of different methods to investigate plant sources must also be considered. It is now widely recognized that any monitoring programme on wild bees should aim for both community-level and species-level identification (Gonzalez et al. 2013; Portman & Tepedino 2021; Potts et al. 2021). This is particularly important in biodiversity hotspots, where ecological networks are more complex (Watts et al. 2016; Dorchin et al. 2018; Liang et al. 2021), implying that plant species should also be identified and quantified. In agroecosystems, the situation is often exacerbated by the limited floral resources available in human-modified landscapes, which can lead to oversimplified and potentially misleading conclusions about local plant–pollinator networks. Accurate identification of pollen grains requires specialist expertise and access to robust reference collections. Manual pollen analysis is labour-intensive and often constrains the number of samples processed or the number of grains analysed per sample. It also depends on the availability of comprehensive identification libraries. Some of these limitations may soon be mitigated by automated approaches, such as the method proposed by Olsson et al. (2021) which applies deep learning convolutional neural networks (CNNs) and was tested on pollen samples from bumblebees. It remains challenging to select one method over the other; yet, a combination of observational and palynological approaches undoubtedly provides the most reliable and comprehensive information to guide conservation efforts.

Andrena Fabricius, 1775 (Andrenidae) and *Lasioglossum* Curtis, 1833 (Halictidae) are two highly common genera of wild bees, found across a wide range of environments, from mountains and plains to urban areas. *Andrena* species are distributed almost worldwide, with the exception of Oceania and South America; *Lasioglossum*, by contrast, is also present in these two regions (Michener 2007). According to the current global checklist (Ascher & Pickering 2020), there are 1,619 recognised species of *Andrena* and 1,841 of *Lasioglossum*. Despite the high number of species in both genera, information on their foraging behaviour remains scattered and limited to a small subset of well-studied species. Published pollen-load or quantified flower-preference data exist for at least several dozen *Andrena* species (e.g., Chambers 1968; Wood & Roberts 2017), and regional or species-specific studies continue to expand this knowledge base (e.g., Wood 2023; Zenga et al. 2024; Tourbez et al. 2024). However, given the ~1,600 described *Andrena* species worldwide, most remain uncharacterized regarding detailed food sources. Similarly, for *Lasioglossum* species no comprehensive global synthesis has yet been compiled, even if several *Lasioglossum* species are among the best-studied wild bees in Europe with regard to their floral diets. For example, *Lasioglossum calceatum* (Scopoli, 1763) shows broad pollen use but strong seasonal and regional variation, often exploiting Asteraceae, Brassicaceae, and Rosaceae, as revealed by pollen-load analyses from farmland and semi-natural habitats in the United Kingdom (Wood et al. 2016). In contrast, *Lasioglossum villosulum* (Kirby, 1802) often exhibits a narrower diet, showing marked preferences for yellow Asteraceae and other open corollas (Wood et al. 2016; Heuel et al. 2024). These studies illustrate a limited diversity of foraging strategies within the genus *Lasioglossum* but highlight how diet breadth and floral specialization vary even among closely related species.

Since transects are a widely employed methodology for evaluating pollinator biodiversity in agroecosystems, we aimed to assess their contribution to understanding the pollen sources exploited by the most abundant bee genera. Our study integrates transect-based field observations with palynological analyses to investigate foraging behaviour at field margins. Monthly monitoring was conducted over two consecutive seasons along a 200 m × 2 m transect in the Emilia-Romagna region of Italy. Individuals of *Andrena* and *Lasioglossum* (the dominant genera in these agroecosystems) were collected and identified by an expert taxonomist, and the pollen loads they carried were analysed using classical palynological methods. Flowering plants along the transect were also identified to complement the visual observations. The results are discussed in relation to methodology, bee species phenology and the diversity of floral resources revealed through both transect observations and pollen analyses.

MATERIALS AND METHODS

STUDY SITE

The sampling was conducted in a Natura 2000 site (SCI-SPA IT4050001) located within the "Parco dei Gessi Bolognesi e Calanchi dell'Abbadessa" Natural Park in the Bologna province, Italy (92 m a.s.l., 44°25'39.08'' N, 11°23'58.62'' E). This site is part of a network of locations monitored during the BeeNet project (Giovanetti & Bortolotti 2021), all selected within agricultural landscapes. It can be classified as a semi-natural agroecosystem (CORINE Land Cover - CLC 2.4.2: heterogeneous agricultural areas) and is characterized by a cultivated wheat field adjacent to a wooded area.

SAMPLING

Wild bee collections and plant surveys were carried out monthly from March to October in both 2021 and 2022, with the exception of May 2021, when mowing prevented sampling. Surveys were conducted along a fixed transect measuring 200 × 2 m.

For bee sampling, trained personnel walked the transect twice per survey day (once in the morning and once in the afternoon, one hour each). Bees observed within the transect were captured using a hand net, placed into individual vials, and stored in a refrigerated thermal bag. Individuals belonging to the genera *Andrena* and *Lasioglossum* were washed to recover pollen, then pinned and identified to species level by a taxonomist at the Laboratory of Entomology of CREA Research Centre for Agriculture and Environment (Bologna, Italy). Both males and females were caught, and male retained when pollen was abundant. Throughout the text, the term "load" will refer to the pollen that both, males and females, were carrying.

Simultaneously, botanical surveys recorded all entomophilous flowering plants within the transect. These were identified to the species level, or to the genus level when species identification was uncertain. Identification was carried out directly in the field, by using the PLANTNET© app. More details on the monitoring protocol are available (in Italian) at: https://www.reterurale.it/flex/cm/pages/ServeBLOB.php/L/IT/IDPagina/24820.

POLLEN ANALYSIS

In 2021, we selected specimens that visually carried a notable quantity of pollen. In 2022, all individuals showing visible pollen traces were considered, but only those carrying more than 25 pollen grains were retained for analysis. Each bee was washed by adding 1 ml of distilled water directly into the vial and agitating the contents for 2 minutes using a vortex mixer. After carefully checking the specimens, if any pollen was still visible on the bee body the process was repeated. The resulting pollen suspension was centrifuged at 14,000 rpm for 20 minutes (modified from Louveaux et al. 1978). After centrifugation, excess water was removed, leaving just enough to resuspend the pollen. A drop of the resuspended sediment was placed on a microscope slide using a Pasteur pipette and spread over an area of approximately 18 × 18 mm. Once dry, a coverslip with a drop of glycerine jelly was applied to mount the sample.

Palynological analysis followed the methodology described by Nicholson et al. (2024). Each slide was examined at 400× magnification using a Zeiss Axiolab re optical microscope. A maximum of 500 randomly selected pollen grains per specimen were counted and identified to the lowest possible taxonomic level. The majority of individuals (70.7% of *Andrena* and 77.8% of *Lasioglossum*) carried more than 500 pollen grains (> 500 grains: 41 *Andrena* specimens -5 of which were males- out of 58; *Lasioglossum*: 137 specimens -5 males- out of 176). Identification was guided by reference literature and by comparison with the CREA Reference Slide Collection, maintained at the CREA Research Centre for Agriculture and Environment. For each pollen type (hereafter referred to as a "pollen taxon"), the percentage relative to the total number of grains was calculated.

STATISTICAL ANALYSIS

We assessed the palynological diversity by evaluating both the number of pollen taxa (taxa richness) and the Shannon diversity index, using the relative abundance (%) of each identified pollen type. The Shannon index (H), reflecting the diversity in pollen composition, was calculated according to Bogo et al. (2025). To visually explore interaction patterns between plants and pollinators, we built two separate matrices for *Andrena* and *Lasioglossum* species and the corresponding pollen specimens found on each individual. We then generated bipartite networks using plotweb function from bipartite package (Dormann et al. 2008). Networks visualization was performed with R software version 4.4.1. All data are presented as mean ± SE.

RESULTS

WILD BEE COLLECTIONS

Over the two-year period, we collected 58 *Andrena* individuals (of which 18 were males) and 176 *Lasioglossum* individuals (23 males), identifying 19 *Andrena* species and 18 *Lasioglossum* species. Males accounted for 31% of all *Andrena* specimens, while *Lasioglossum* males represented only 13.1%.

Among the total sample (Fig. 1A), the majority of individuals belonged to the genus *Lasioglossum*, comprising three-quarters of all specimens collected. The most abundant species were *L. marginatum* (Brullé, 1832), *L. villosulum* (Kirby, 1802), and *L. nigripes* (Lepeletier, 1841), with 62, 41, and 16 individuals respectively. These were followed by *Andrena stabiana* Morice, 1899 ($N = 12$) and *A. livens* Pérez, 1895 ($N = 9$).

The phenology of the two genera was largely overlapping, although *Andrena* species tended to appear slightly earlier in the season, while *Lasioglossum* species were also collected in late summer (Fig. 1B). The full list of species and their phenological patterns is provided in Fig. 2, where individual abundance reflects frequency of collection. The figure highlights a distinct pattern among *Andrena* species: they were predominantly active in spring, with a clear succession observed across spring months. Many *Andrena* species had a restricted period of activity, often being captured in a single month. Only a few species, such as *A. distinguenda* Schenck, 1871, *A. minutula* (Kirby, 1802), and *A. stabiana*, were recorded in consecutive sampling rounds. Notably, *A. afzeliella* (Kiby, 1802) was recorded in two non-consecutive surveys, in accordance with the expected bivoltinism.

Lasioglossum species exhibited a different pattern. Most were collected over consecutive months, suggesting a longer activity period, with the majority active later in the season (June to

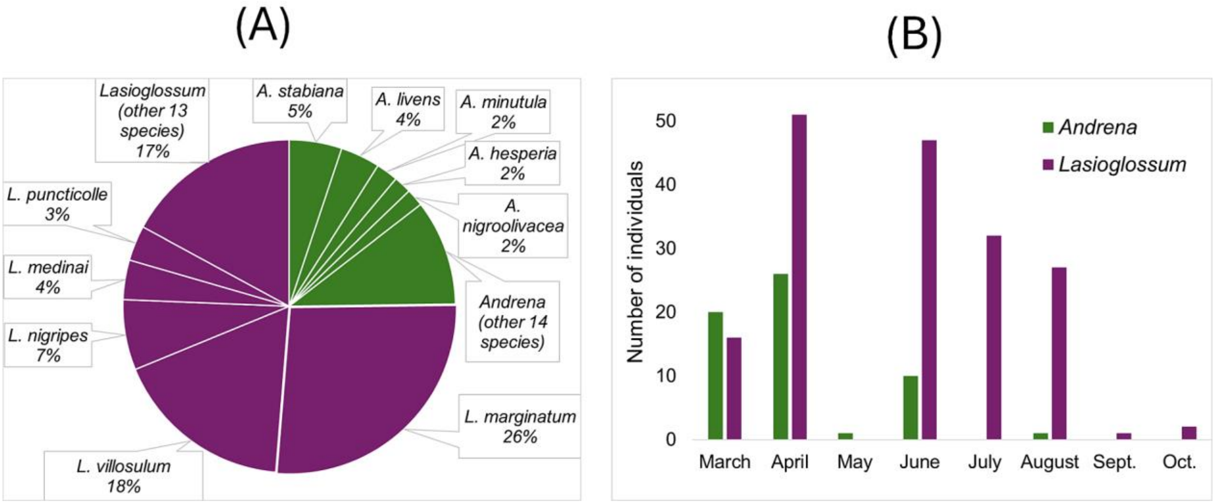

Figure 1. (A) Species composition of the individuals belonging to the genera *Andrena* (N = 58) and *Lasioglossum* (N = 176), collected monthly in the years 2021-2022. Percentages are according to total number of individuals; the first five more numerous species are represented individually, the others are grouped under the genus name. (B) Annual distribution of the individuals according to the genus they belong to. For each month (apart May), data refers to the two years combined.

species	March	April	May	June	July	August	September	October
Andrena pusilla	2							
Andrena truncatilabris	2							
Andrena viridescens	2							
Andrena distinguenda	1	1						
Andrena minutula	4	1						
Andrena stabiana	9	3						
Andrena aeneiventris		1						
Andrena ranunculi		1						
Andrena hesperia		4						
Andrena nigroolivacea		4						
Andrena livens		9						
Andrena senecionis			1					
Andrena afzeliella		2		1				
Andrena labialis				1				
Andrena ovatula				1				
Andrena humilis				2				
Andrena ventricosa				2				
Andrena flavipes				3				
Andrena pellucens						1		
Lasioglossum medinai	1			2	6			
Lasioglossum calceatum	1			2				
Lasioglossum villosulum	1			15	7	16	1	1
Lasioglossum marginatum	13	48						1
Lasioglossum morio		1			1			
Lasioglossum albipes		2						
Lasioglossum crassepunctatum				1				
Lasioglossum politum				1	1			
Lasioglossum malachurum				1	2	2		
Lasioglossum leucozonium				2	2	1		
Lasioglossum puncticolle				3	3	2		
Lasioglossum quadrisignatum				3				
Lasioglossum corvinum				6		1		
Lasioglossum nigripes				11	2	3		
Lasioglossum discus					2	1		
Lasioglossum glabriusculum					3			
Lasioglossum interruptum					3			
Lasioglossum griseolum						1		

Figure 2: Distribution of *Andrena* (above) and *Lasioglossum* (below) species records along following monitoring months, with the number of individuals.

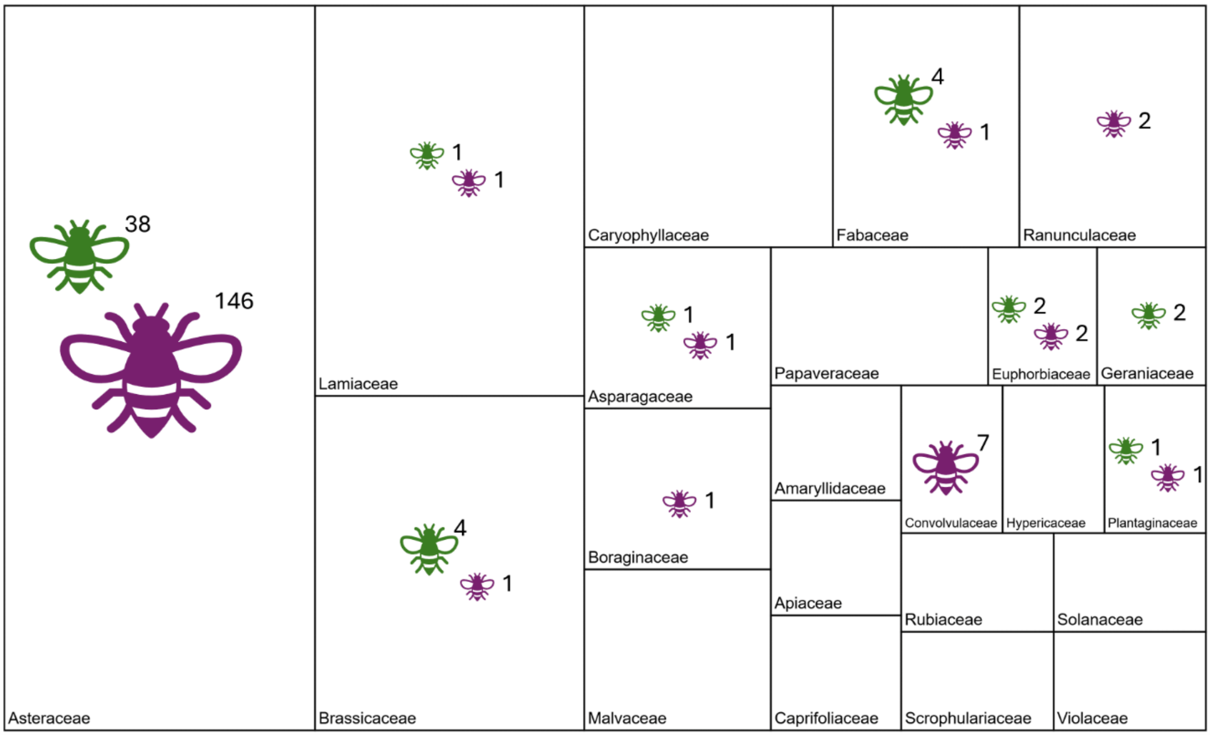

Figure 3. Taxonomic composition of plant records of the transect. The number of species in each family defines the size of the corresponding mosaic piece. Bee icons and corresponding numbers represent collected individuals of *Andrena* (green icon) and/or *Lasioglossum* (purple icon).

August). *L. marginatum* was mainly active in April and was particularly abundant. Apart from this species, most others were represented by few individuals, and in some cases, such as *L. medinai* (Vachal, 1895), *L. calceatum* (Scopoli, 1763), *L. morio* (Fabricius, 1793), and *L. corvinum* (Morawitz, 1876), records were not from consecutive months.

PLANT SURVEY AND PALYNOLOGICAL ANALYSES

Within the transect, we recorded a total of 66 plant species, belonging to 58 genera and 22 families. The most represented families were Asteraceae, Lamiaceae, and Brassicaceae (Fig. 3). With few exceptions, only one species per genus was recorded. In the families Geraniaceae and Euphorbiaceae, two species were identified within the common genera *Geranium* and *Euphorbia*, respectively. Similar cases were observed for the genera *Ranunculus* (Ranunculaceae) and *Silene* (Caryophyllaceae), represented by two and three species, respectively. An exception was the genus *Trifolium* (Fabaceae), for which four species were recorded. Bees were collected while visiting 16 plant species, representing only 24.2% of the total plant species recorded in the botanical survey, and roughly half of the flowering families (Fig. 3). *Crepis* sp. was by far the most visited plant. More than half of both *Andrena* (52.7%) and *Lasioglossum* (58.2%) individuals were collected on *Crepis* sp. A notable proportion of *Lasioglossum* individuals (17.6%) were also collected on another member of the Asteraceae family, *Cichorium intybus* L.

Palynological analyses identified a total of 63 pollen taxa. The most frequent and abundant pollen types were the Compositae H-form and Compositae T-form, both for each bee genus and overall (Table 1). Among the plant species recorded within the transect, the Compositae H-form corresponded to *Bellis perennis*, *Dittrichia viscosa* (L.) Greuter, *Erigeron annuus* (L.) Desf, *Eupatorium cannabinum* L. and *Senecio vulgaris* L., while Compositae T-form included *Crepis* sp., *Cichorium intybus* L., *Lactuca saligna* L., *Sonchus asper* All. and *Taraxacum* sect. *Taraxacum* F.H.Wigg.

By combining the plant list (N = 63) obtained from the transect survey with the taxa list (N = 73) derived from palynological analyses, we recorded a total of 73 unique pollen taxa. Of these, 86.3% were identified through palynological analysis, while the transect survey accounted for over 50%. The overlap between the two methods was

Table 1: List of species with information related to the floral resources. Calculations refer to the dataset obtained from the palynological analyses. Literature utilized to retrieve information on lecty include: (Wood 2023) (Zenga et al. 2024) (Standfuss & Standfuss 2010) (Praz et al. 2022) (Westrich, 1989). In red: taxa referring to tree species or groups comprising trees. F=female; M=male

Species	Number of individuals	From the literature	Collected on		From palynological analyses			
			Plant taxa	Taxa richness	Plant taxa	Taxa richness total	Taxa richness mean±SE	Shannon index mean±SE
Andrena aeneiventris	1F	Possibly broadly oligolectic	*Ornithogalum umbellatum*	1	Geraniaceae; Liliaceae	2	2.00 ± 0	0.68 ± 0
Andrena afzeliella	3M	Polylectic, preference for Fabaceae	*Geranium molle; Trifolium nigrescens*	2	*Clematis*; Geraniaceae; Ranunculaceae	3	1.33 ± 0.33	0.18 ± 0.18
Andrena distinguenda	1F 1M	Polylectic	*Bellis perennis; Capsella bursa-pastoris*	2	*Capsella bursa-pastoris*; Compositae T form; Ranunculaceae; *Quercus robur* gr.	4	2.00 ± 1.00	0.55 ± 0.55
Andrena flavipes	3F	Polylectic	*Crepis* sp.	1	Compositae H form; *Convolvulus*; *Medicago*	3	1.67 ± 0.33	0.08 ± 0.04
Andrena hesperia	4F	Broadly oligolectic	*Bellis perennis; Crepis* sp.	2	Compositae H form; Compositae T form	2	1.25 ± 0.25	0.02 ± 0.02
Andrena humilis	2F	Broadly oligolectic	*Crepis* sp.	1	Compositae H form; Papaver	2	1.50 ± 0.50	0.05 ± 0.05
Andrena labialis	1F	Broadly oligolectic	*Crepis* sp.	1	Compositae H form	1	1.00 ± 0	0 ± 0
Andrena livens	8F 1M	Broadly oligolectic	*Bellis perennis; Crepis* sp.; *Taraxacum* sect. Taraxacum	3	Brassicaceae <20 µm; Compositae H form; Compositae T form; Ranunculaceae; *Malus/Pyrus* f.; Oleaceae	6	1.89 ± 0.31	0.25 ± 0.11
Andrena minutula	5F	Polylectic	*Crepis* sp.; *Euphorbia helioscopia; Veronica persica*	3	Compositae H form; Compositae T form; *Euphorbia* f.; *Lamium* f.; *Veronica*; *Acer*; *Malus/Pyrus* f.; *Prunus* f.	8	2.60 ± 0.51	0.59 ± 0.24
Andrena nigroolivacea	4F	Broadly oligolectic	*Crepis* sp.	1	Compositae T form; *Acer*; *Quercus robur* gr.	3	1.50 ± 0.50	0.10 ± 0.10
Andrena ovatula	1M	Broadly oligolectic for Fabaceae	*Trifolium nigrescens*	1	*Trifolium repens* gr.	1	1.00 ± 0	0 ± 0
Andrena pellucens	1F	Oligolectic	*Cichorium intybus*	1	Compositae T form	1	1.00 ± 0	0 ± 0

Tab.1 continued

Species	Number of individuals	From the literature	Collected on		From palynological analyses			
			Plant taxa	Taxa richness	Plant taxa	Taxa richness total	Taxa richness mean±SE	Shannon index mean±SE
Andrena pusilla	2F	Polylectic	*Crepis* sp.; *Euphorbia helioscopia*	2	Brassicaceae <20 µm; Compositae T form; *Euphorbia* f.; *Lamium* f.	4	2.50 ± 0.50	0.48 ± 0.34
Andrena ranunculi	1M	Narrowly oligolectic	*Bellis perennis*	1	Compositae H form; Ranunculaceae	2	2.00 ± 0	0.16 ± 0
Andrena senecionis	1F	Broadly oligolectic	*Taraxacum* sect. Taraxacum	1	Compositae T form; *Ligustrum* f.	2	2.00 ± 0	0.21 ± 0
Andrena stabiana	3F 9M	Broadly oligolectic	*Capsella bursa-pastoris; Crepis* sp.; *Fumaria officinalis; Lamium purpureum*	4	Compositae H form; Compositae T form; Populus	3	1.17 ± 0.11	0.05 ± 0.04
Andrena truncatilabris	1F 1M	Polylectic	*Capsella bursa-pastoris*	2	Capsella bursa-pastoris; Compositae H form; Euphorbia f.; Lamium f.	4	2.00 ± 0	0.19 ± 0.09
Andrena ventricosa	2F	Polylectic with a strong preference (Fabaceae)	*Trifolium nigrescens; Trifolium repens*	1	*Trifolium pratense* gr.; *Trifolium repens* gr.	2	1.50 ± 0.50	0.16 ± 0.16
Andrena viridescens	2F	Polylectic	*Capsella bursa-pastoris*	2	Brassicaceae <20 µm; *Capsella bursa-pastoris*	2	1.00 ± 0	0 ± 0
Lasioglossum albipes	2F	Polylectic	*Bellis perennis; Ornithogalum umbellatum*	2	Compositae H form; Compositae T form; Geraniaceae; Ranunculaceae; Quercus robur gr.	5	3.00 ± 1.00	0.63 ± 0.55
Lasioglossum calceatum	2F 1M	Polylectic	*Crepis* sp.; *Trifolium nigrescens*	2	Apiaceae; Compositae H form; Compositae T form; *Lamium* f.; Plantago; Poaceae	6	3.00 ± 0.58	0.70 ± 0.24
Lasioglossum corvinum	4F 3M	Polylectic	*Centaurea jacea; Cichorium intybus; Convolvulus arvensis*	3	Compositae H form; Compositae J form; Compositae T form; Convolvulus; Labiatae M form; *Plantago*; Poaceae; *Castanea; Ligustrum* f.	9	2.43 ± 0.57	0.45 ± 0.17
Lasioglossum crassepunctatum	1F	Polylectic	*Convolvulus arvensis*	1	Compositae T form; Labiatae S form; *Plantago*	3	3.00 ± 0	0.98 ± 0
Lasioglossum discus	1F 2M	Polylectic	*Centaurea jacea; Cichorium intybus*	2	Compositae J form; Compositae T form	2	1.00 ± 0	0 ± 0

Tab.1 continued

Species	Number of individuals	From the literature	Collected on		From palynological analyses			
			Plant taxa	Taxa richness	Plant taxa	Taxa richness total	Taxa richness mean±SE	Shannon index mean±SE
Lasioglossum glabriusculum	3F	Polylectic	*Cichorium intybus; Convolvulus arvensis; Crepis* sp.	3	Compositae H form; Compositae S form; Compositae T form; *Convolvulus; Papaver*; Ranunculaceae; *Cornus sanguinea; Rubus* f.	8	3.33 ± 1.20	0.59 ± 0.31
Lasioglossum griseolum	1F	Polylectic	*Centaurea jacea*	1	Compositae T form; Labiatae S form	2	2.00 ± 0	0.69 ± 0
Lasioglossum interruptum	3F	Polylectic	*Centaurea jacea; Cichorium intybus; Crepis* sp.	3	*Clematis*; Compositae T form	2	1.00 ± 0	0 ± 0
Lasioglossum leucozonium	4F 1M	Polylectic	*Cichorium intybus; Crepis* sp.	2	Compositae H form; Compositae T form; *Plantago*	3	1.20 ± 0.20	0.02 ± 0.02
Lasioglossum malachurum	3F 2M	Polylectic	*Centaurea jacea; Cichorium intybus; Convolvulus arvensis; Crepis* sp.	4	Compositae H form; Compositae J form; Compositae T form; *Rubus* f.	4	1.40 ± 0.25	0.15 ± 0.13
Lasioglossum marginatum	61F 1M	Polylectic	*Bellis perennis; Capsella bursa-pastoris; Crepis* sp.; *Euphorbia cyparissias; Euphorbia helioscopia; Ranunculus bulbosus; Sonchus asper; Taraxacum* sect. Taraxacum; *Veronica persica*	9	*Brassica* f.; Brassicaceae; *Capsella bursa-pastoris*; Caryophyllaceae; Compositae H form; Compositae T form; *Euphorbia* f.; Geraniaceae; *Lamium* f.; Liliaceae; *Papaver*; Poaceae; Ranunculaceae; *Trifolium repens* gr.; *Veronica; Acer*; Betulaceae; *Malus/Pyrus* f.; Oleaceae; *Populus; Quercus robur* gr.; *Salix*	22	2.21 ± 0.14	0.33 ± 0.05
Lasioglossum medinai	8F 1M	Polylectic	*Cichorium intybus; Crepis* sp.	2	Compositae H form; Compositae T form	2	1.00 ± 0	0 ± 0
Lasioglossum morio	2F	Polylectic	*Bellis perennis; Centaurea jacea*	2	Compositae J form; Compositae T form; *Convolvulus*; Geraniaceae; *Malus/Pyrus* f.	5	3.00 ± 0	0.51 ± 0.26
Lasioglossum nigripes	16F	Polylectic	*Cichorium intybus; Crepis* sp.	2	*Clematis*; Compositae H form; Compositae T form	3	1.06 ± 0.06	0.02 ± 0.02

Tab.1 continued

Species	Number of individuals	From the literature	Collected on		From palynological analyses			
			Plant taxa	Taxa richness	Plant taxa	Taxa richness total	Taxa richness mean±SE	Shannon index mean±SE
Lasioglossum politum	1F 1M	Polylectic	*Ballota nigra; Myosotis arvensis*	2	Brassicaceae; Compositae T form; *Fragaria/Potentilla*; *Helianthemum; Lotus; Plantago*; Ranunculaceae; *Coronilla/ Hippocrepis*; Oleaceae	9	5.00 ± 4.00	0.75 ± 0.75
Lasioglossum puncticolle	5F 3M	Polylectic	*Centaurea jacea; Cichorium intybus; Clematis vitalba; Crepis* sp.	5	*Clematis*; Compositae H form; Compositae J form; Compositae T form; Malvaceae; *Plantago*; Ranunculaceae; Oleaceae	8	2.00 ± 0.33	0.41 ± 0.13
Lasioglossum quadrisignatum	3F	Polylectic	*Cichorium intybus; Crepis* sp.	2	Compositae H form; Compositae T form	2	1.33 ± 0.33	0.11 ± 0.11
Lasioglossum villosulum	33 F 8M	Polylectic	*Ballota nigra; Centaurea jacea; Cichorium intybus; Crepis* sp.	5	*Brassica* f.; Brassicaceae; Brassicaceae <20 µm; Brassicaceae 25 µm; Compositae H form; Compositae T form; *Convolvulus*; Labiatae L form; *Lamium* f.; *Medicago; Papaver*; Ranunculaceae; *Cornus sanguinea*; *Malus/Pyrus* f.; *Populus*	15	1.37 ± 0.13	0.10 ± 0.04

approximately 40% (*N* = 29). A total of 39 taxa were detected exclusively through palynological analysis, over half of which were trees or shrubs (*N* = 14 and *N* = 4, respectively). Notably, members of the Poaceae family were identified solely via palynological data and were absent from the transect survey.

We listed all records in Table 1, where we also calculated taxa richness and the Shannon Index. The Shannon diversity index values showed considerable variation across samples, ranging from 0 to 0.98. The highest diversity was observed in one sample (mean ± SE: 0.98 ± 0), indicating a relatively even distribution of taxa. In contrast, several samples displayed very low diversity (e.g. 0 ± 0 and 0.02 ± 0.02), suggesting dominance by a single taxon or minimal species presence. Intermediate values reflect moderate diversity with higher variability among replicates. Notably, some samples with higher standard errors (e.g. 0.55 ± 0.55 and 0.75 ± 0.75) suggest inconsistency in diversity across replicates or subsamples. Finally, in Table 2 we summarised correspondence between food sources expected from the literature, observed from transect collections and recorded in pollen loads.

HIGHLIGHTS FROM THE NETWORK ANALYSES

We constructed plant-pollinator networks for each of the two bee genera, based on their observed floral visits. At first glance, *Lasioglossum* species display more generalist foraging patterns (Fig. 4), characterised by a complex web of interactions with many plant species, though individual links tend to show low interaction strength. Nonetheless, certain plant preferences emerged even within this context of polylectic behaviour. For example, *L. marginatum* exhibited stronger associations with both Compositae T- and H-forms, as well as members of the Oleaceae and Ranunculaceae families. Interestingly, it also showed notable interactions with anemophilous tree species such as *Quercus* and *Acer*.

Andrena species (Fig. 5) demonstrated a similar strong affinity for Compositae T- and H-forms. However, their foraging behaviour appeared more selective, with generally stronger links to each plant species visited. Tree species were also well represented in the *Andrena* network, including *Acer*, Betulaceae, *Quercus robur* gr., *Populus*, and, to a lesser extent, *Tilia*, *Quercus ilex*, and Pinaceae.

Various tree species appear in the list of palynological analyses (highlighted in red in Table 1 and in the last column of Table 2). Out of the ones already mentioned, we can list *Castanea*, *Malus*/*Pyrus* f., *Ligustrum*, *Salix*, and Oleaceae.

DISCUSSION

In this study, we began with the idea that monitoring efforts aimed at evaluating pollinator biodiversity in agroecosystems through transect methods could also provide valuable information for understanding the pollen sources exploited by bees. To verify this assumption, we integrated transect-based field observations with palynological analyses and data on flowering plants recorded along the transect. The results prompt a discussion concerning methodology, bee species phenology and foraging requirements, as well as the diversity of floral resources present at field margins.

Our data showed that the most commonly used method for identifying plants important to bees (the transect-based observational approach on which many conservation efforts currently rely) is a good proxy, but not entirely reliable as it yields incomplete results. A strong correspondence between the pollen types in bee loads and the plant species on which the bees were collected is a consistent finding in our study. Only 12 out 234 observational records mismatched the palynological records, and in 4 out of these 12 cases the pollen was actually present but as traces: for this reason, not included in the palynological list of taxa. Traces of given pollen could be informative also on nectar sources looked for by females and males. In a few cases, therefore, observational records added potential new plant species to a foraging list, as for *Andrena stabiana* that was recorded with 9 individuals with three plant species exclusive of the observational records. This clearly confirms the reliability of the observed plant–bee interactions recorded through the transect method. Yet, while each observation contributes valuable information to a broad picture, a single foraging event represents only a minimal snapshot of a bee's overall collection of pollen. Even with increased sampling effort, the picture resulting from observational data remains partial, as reported for *Lasioglossum marginatum* and *L. villosulum* in Table 1. This finding is not new

Table 2: List of species with comparison on resource expected, recorded during observations, and from the palynological analyses. Bee species are reported in alphabetical order (*Andrena* first, followed by *Lasioglossum*). Number of individuals are indicated separately for each sex (F=female; M=male). Hypotheses on lecty for each species are reported in the 4th column and if confirmed by our data present a green check mark (☑), if not they present a red cross (☒). The last three columns provide additional information about the number of records of plant species and consequently if all of them where or not confirmed from literature, plus we highlighted the presence of tree species. Asterisks (*) indicate cases in which pollen was not considered by palynological analyses since it was present as traces.

species	n individuals F=female M=male	Literature hypothesis	Confirmed / not confirmed	observed on	match with palynological record	tree species
Andrena aeneiventris	*1F*	Possibly broadly oligolectic	☑	1 species	☑	
Andrena afzeliella	*3M*	Polylectic, preference for Fabaceae	☑	2 species	☑☒	
Andrena distinguenda	*1F 1M*	Polylectic	☑	2 species	☑☒	present
Andrena flavipes	*3F*	Polylectic	☑	1 species	☒	
Andrena hesperia	*4F*	Broadly oligolectic	☑	2 species	☑☑	
Andrena humilis	*2F*	Broadly oligolectic	☑	1 species	☒	
Andrena labialis	*1F*	Broadly oligolectic	☒	1 species	☒	
Andrena livens	*8F 1M*	Broadly oligolectic	☒	3 species	☑☑☑	present
Andrena minutula	*5F*	Polylectic	☑	3 species	☑☑☑	present
Andrena nigroolivacea	*4F*	Broadly oligolectic	☑	1 species	☑	present
Andrena ovatula	*1M*	Broadly oligolectic for Fabaceae	☑	1 species	☑	
Andrena pellucens	*1F*	Oligolectic	☑	1 species	☑	
Andrena pusilla	*2F*	Polylectic	☑	2 species	☑☑	
Andrena ranunculi	*1M*	Narrowly oligolectic	☒	1 species	☑	
Andrena senecionis	*1F*	Broadly oligolectic	☑	1 species	☑	
Andrena stabiana	*3F 9M*	Broadly oligolectic	☒	4 species	☑☒☒☒	present
Andrena truncatilabris	*1F 1M*	Polylectic	☑	1 species	☑	
Andrena ventricosa	*2F*	Polylectic, strong preference for Fabaceae	☑	2 species	☑☑	
Andrena viridescens	*2F*	Polylectic	☑	1 species	☑	

Tab. 2 continued

species	n individuals F=female M=male	Literature hypothesis	Confirmed / not confirmed	observed on	match with palynological record	tree species
Lasioglossum albipes	*2F*	Polylectic	☑	2 species	☑☒	present
Lasioglossum calceatum	*2F 1M*	Polylectic	☑	2 species	☑☒	
Lasioglossum corvinum	*4F 3M*	Polylectic	☑	3 species	☑☑☑	present
Lasioglossum crassepunctatum	*1F*	Polylectic	☑	1 species	☒	
Lasioglossum discus	*1F 2M*	Polylectic	☑	2 species	☑☑	
Lasioglossum glabriusculum	*3F*	Polylectic	☑	3 species	☑☑☑	
Lasioglossum griseolum	*1F*	Polylectic	☑	1 species	☑	
Lasioglossum interruptum	*3F*	Polylectic	☑	3 species	☑☑ ☒*	
Lasioglossum leucozonium	*4F 1M*	Polylectic	☑	2 species	☑☑	
Lasioglossum malachurum	*3F 2M*	Polylectic	☑	4 species	☑☑☑☒	
Lasioglossum marginatum	*61F 1M*	Polylectic	☑	9 species	☑☑☑☑☑☑☑☑☑	present
Lasioglossum medinai	*8F 1M*	Polylectic	☑	2 species	☑☑	
Lasioglossum morio	*2F*	Polylectic	☑	2 species	☑☒	present
Lasioglossum nigripes	*16F*	Polylectic	☑	2 species	☑☑	
Lasioglossum politum	*1F 1M*	Polylectic	☑	2 species	☒ ☒*	
Lasioglossum puncticolle	*5F 3M*	Polylectic	☑	4 species	☑☑☑☑	present
Lasioglossum quadrisignatum	*3F*	Polylectic	☑	2 species	☑☑	
Lasioglossum villosulum	*33 F 8M*	Polylectic	☑	4 species	☑☑☑ ☒*	present

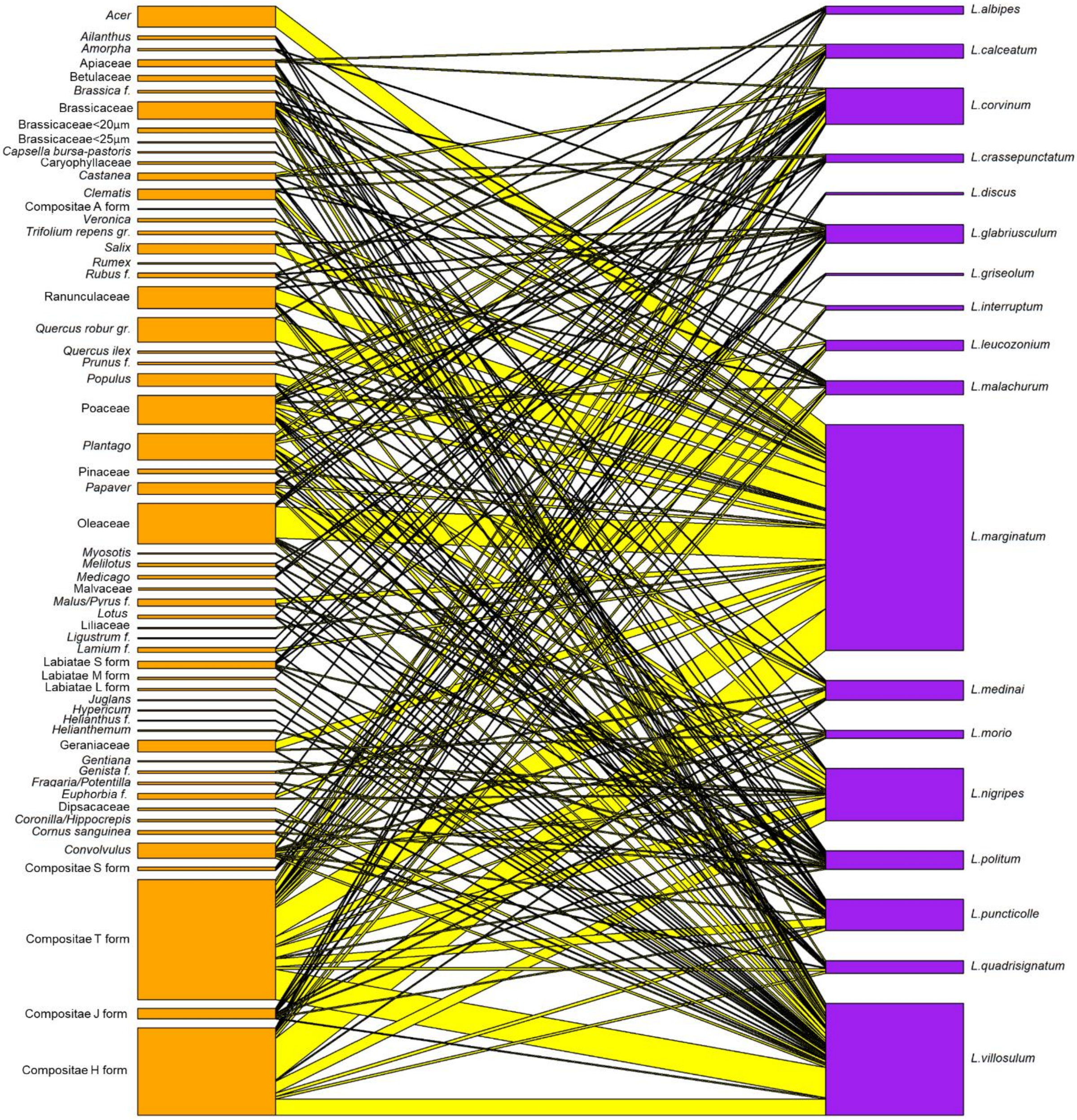

Figure 4. Plant-pollinator network depicting *Lasioglossum* species (on the right) food preferences as emerging from the palynological analyses.

in itself. Observational (visitation) records and palynological (pollen-based) data provide complementary, but not interchangeable, perspectives on bee foraging. Librán-Embid et al. (2024) recently found that only 37% of the total unique pairwise species interactions occurred in both pollen-transport and flower-visitation networks: a result strikingly similar to our overlap of approximately 40% of plant species. Palynological and molecular analyses of pollen loads, nest provisions, or body pollen reveal the actual plant taxa from which bees collect pollen and therefore uncover hidden interactions, seasonal diet shifts, differences in diet breadth and niche overlap, that visitation data alone often underestimate (Beil et al. 2008; Pornon et al. 2017; Wood et al. 2016). From a conservation perspective, this kind of information may result crucial to protect rare bee species as well as to sustain more common ones.

Another aspect that may be considered is pollen chemistry and nutritional quality. Not all pollen is equally valuable, so knowing which taxa

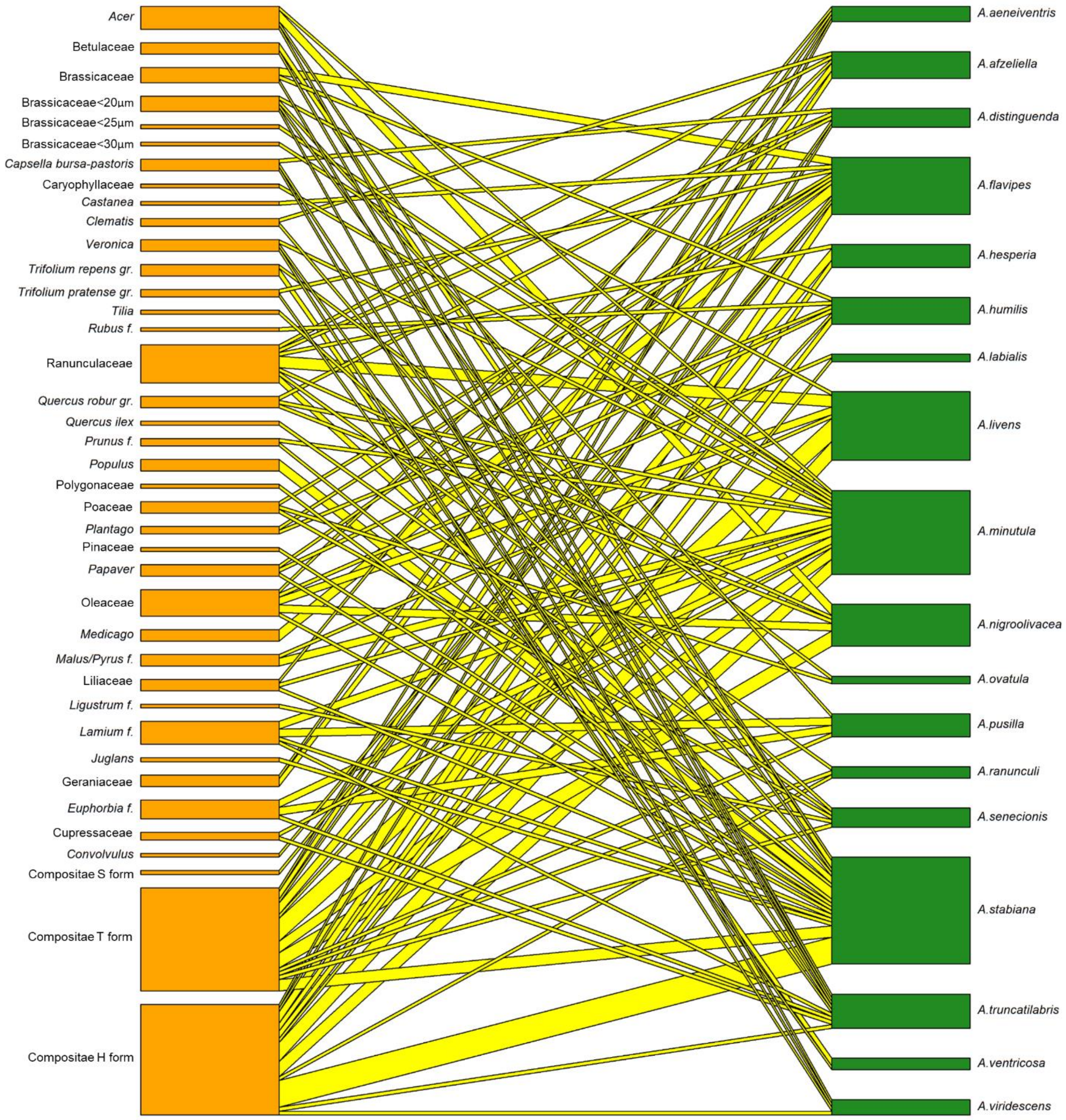

Figure 5. Plant-pollinator network depicting *Andrena* species (on the right) food preferences as emerging from the palynological analyses.

bees actually collect matters for interpreting ecological roles and for conservation planning (Vanderplanck et al. 2014). Our palynological analyses revealed greater complexity in local foraging behaviour, particularly highlighting the contribution of numerous tree species, many of which are associated to anemophilous (wind) pollination syndromes. The comparison of taxonomic richness between transect and palynological data shows a clear pattern. Among the 37 analysed bee species, for 26 species the richness in the transect data was lower than the total richness detected from palynological analysis, equal in 9 species, and higher in 2 species. This indicates that palynological analysis captures a greater number of plant–insect interactions than field observations alone, providing a more comprehensive view of the bees' overall diet. The Shannon index was not compared between the two methods because, within the transect dataset, it would yield only a single aggregated value per species, rendering it ecologically uninterpretable in this specific context. Trees (Table 1 and 2) were found in one third of the samples, with anemophilous species as *Quercus*, *Populus*, and *Acer* and herbs, such as *Plantago*. A broad review/meta-analysis shows that insect pollinators commonly collect pollen from wind-pollinated plants (over 200 records for 101 wind-pollinated genera), with grasses/sedges and genera like *Plantago* represented in the literature (Saunders 2018). *Plantago* (e.g., *P. lanceolata*, *P. major*) is generally considered anemophilous (wind-pollinated), but insect visitors including honey bees and wild bees do visit spikes and collect pollen under certain local conditions (Clifford 1962; Sabugosa-Madeira et al. 2008; Brodschneider et al. 2021). Borański et al. (2025) demonstrated a strong reliance of *Osmia bicornis* on *Quercus* pollen, both in their own palynological analyses and via cross-referenced results from five additional studies. Therefore, literature supports the concept that interactions with wind-pollinated taxa are widespread and ecologically relevant. In our case, the transect location likely favoured the acquisition of pollen from tree species, as several were present within a short distance. A wooded area was situated approximately 300 m from the transect site. Although we did not conduct direct observations of bee visits to trees, the presence of various taxa was confirmed. Adjacent to the transect, *Acer* and *Populus* species were recorded; *Acer* has been recently confirmed as a pollen source for pollinators (Chrzanowska et al. 2024). Fruit trees were present in private gardens about 100 m away; within the wooded area we detected *Quercus* spp., and *Salix* spp. were found along a nearby river. Finally, olive groves (*Olea europaea*) occurred on a hill approximately 250 m from the transect. Thus, palynological analysis was confirmed as the most effective means of detecting the presence and importance of tree pollen in wild bee diets.

Bee nutrition is frequently portrayed in simplified terms, with pollen viewed as the resource collected by females for larval provisioning and nectar regarded as the primary energy source for adults. However, this view is overly simplistic and old fashioned. Wild bee provisioning varies greatly in form and consistency, from the soupy mixtures used by Colletidae (Danforth et al. 2019) to the almost spherical pollen balls of *Andrena agilissima* (Giovanetti & Lasso 2005): therefore, nectar is often incorporated into larval provisions as well. Conversely, pollen is not exclusively for larvae; adults also consume it. Cane et al. (2017) detected pollen in multiple gut regions of female solitary Halictidae, underlining its dietary importance. In an earlier study, Cane (2016) demonstrated that pollen intake was crucial for egg maturation in a Megachilidae species. Similarly, Urban-Mead et al. (2022) found pollen in the guts of both male and female *Andrena* bees; less frequently in males, but sometimes in substantial quantities. A pollen-load study across many taxa showed male bees carry smaller but more diverse pollen loads than females, and that pollinator traits (including sex) strongly predict pollen composition (Cullen et al. 2021). Thus, examining pollen loads in both sexes can offer valuable insights into consumption patterns, preferences and pollination ecology.

The lecty of bee species is an issue that may strongly influence any conservation measure and is directly linked to its ecology. Most of the 19 *Andrena* species appeared in spring, following a clear sequence of emergence, whereas *Lasioglossum* species (18 in total) were more abundant during summer, with some overlap among species in activity periods. Many *Andrena* species are oligolectic. Literature sources identify eight species in our dataset as broadly oligolectic and one, *Andrena ranunculi,* as narrowly oligolectic. We collected a single male of this species on *Bellis perennis*, and most of the pollen grains it carried belonged to this plant. In the case of the *A. ranunculi* male, some pollen came from an evolutionarily distant species, provoking a renewed interest on the food requirement of this species. The fact that a male carried more than 500 pollen grains also underline the generally underestimated role of male bees in pollination. Polylectic species are generally considered more resilient to changes in floral composition. However, both diet breadth and the availability of key resources can influence even generalist foragers. Literature reports strong Fabaceae preferences in two *Andrena* species we monitored. Our findings support this for *A. ventricosa*, with females collected on *Trifolium* and showing a full pollen load of it. For the second species, only males were collected, which complicates interpretation, though such data contribute to our understanding of possible sexual differences in foraging, a topic still poorly documented (Roswell 2019). The case of *Lasioglossum* species differs slightly. While all the species we recorded are polylectic, social structure introduces additional considerations.

Foraging females of social species must provision not only themselves and offspring, but also queens, workers, and males staying in the nest. The needs of the colony influence floral choices, and proximity to the nest can increase sampling numbers. In our study, the social *Lasioglossum marginatum* (probably one of the more socially advanced) was the most frequently collected, with 63 females and only one male. Its record also corresponds to the highest number of plant taxa identified in palynological analyses for a single species, likely due to the combination of polylecty and large sample size. The second most abundant was *Lasioglossum villosulum*, a solitary species with 33 females and 8 males, with a number of plant taxa similar to that of *L. marginatum*. Probably the two species occupy different niches, since visited plants differ between the two: especially, we recorded more tree species visited by of *L. marginatum* and Euphorbiaceae too.

Increasing evidence indicates that only a subset of plant species provides nutritionally balanced pollen capable of sustaining larval development and long-term population viability (Filipiak 2019). This finding, combined with our results, suggests that floral abundance and high visitation rates must be viewed through a broader lens when selecting plants for bee conservation. Conservation strategies based exclusively on adult foraging activity may overlook critical dietary constraints operating at the larval stage. Field margins are widely recognized as resource-rich elements within agroecosystems, and their floral richness and structural characteristics are often positively associated with bee abundance and and morphospecies richness (Morrison et al. 2017). Shrubby field margins in southern Spain increased bee richness and abundance compared to herbaceous margins (Pérez-Marcos et al. 2023). The high frequency of Asteraceae, Brassicaceae, and Lamiaceae in our transects is linked to the ability of certain species to withstand farming practices (e.g. *Crepis* spp., *Bellis perennis* L., *Cichorium intybus* L., *Centaurea jacea* L., *Taraxacum* sect. *Taraxacum* F.H.Wigg, *Salvia pratensis* L., *Lamium purpureum* L., *Clinopodium nepeta* (L.) Kuntze, 1891, *Ballota nigra* L., *Capsella bursa-pastoris* (L.) Medik., 1792, *Eruca sativa* Mill.). However, their pollen was not always the most frequently recorded in the palynological analyses of *Andrena* and *Lasioglossum* specimens. While Asteraceae (Compositae H–J–T forms) were indeed abundant, Brassicaceae appeared to a lesser extent, and Lamiaceae even less so. This suggests selective foraging preferences by these bee genera in field margins, eventually related to morphological limitations, while other bees, e.g. bumblebees, probably sufficiently pollinated them. Tur et al. (2014) demonstrated heterogeneity in pollen use and foraging behaviour when network analyses were downscaled to the individual level, with such variability also present among conspecifics. Expanding existing datasets is therefore essential. Several limitations of the pollen load method were previously noted by Beil et al. (2008). First, the number of bees sampled may be limited, as not all individuals encountered in the field carry pollen loads. In addition, some bee species occur at low frequencies, meaning any data collected may only be indicative. Second, as Beil et al. (2008) also noted, pollen grain identification does not always reach species level: this is particularly true for the ecologically important and taxonomically challenging Asteraceae. Males and females differ in their floral interactions: males primarily seek nectar for their own energy needs, while females also collect resources for brood provisioning. Palynological analysis proved effective in highlighting these differences, revealing stronger plant associations in females while also showing similar levels of floral diversity between the sexes (Tourbez et al. 2023). Therefore, we share some of the conclusion of the colleague Filipiak (2019): the conservation of field margins and "bee-friendly" plants value depends not only on the quantity of floral resources provided, but also on their nutritional quality and functional relevance for different bee species and different developmental stages. Integrating information on pollen composition and larval nutritional requirements is therefore essential for designing field margins and floral enhancements that effectively support sustainable wild bee populations. Our findings further emphasise the role of wind-pollinated (anemophilous) and tree species, often excluded from pollination studies. We detected such pollen in both sexes, e.g., females carried pollen from *Acer* (3 bee species), Betulaceae (1), *Malus/Pyrus* (5), Oleaceae (3), *Populus* (2), *Prunus* (1), *Quercus* (3), and *Salix* (1); males from *Castanea* (1 bee species), Oleaceae (1), *Populus* (1), and *Quercus* (1). Historically, trees and hedgerows at field margins were a widespread and characteristic feature of many European agricultural landscapes, but decades of agricultural intensification, land consolidation and mechanization have driven large-scale removal and simplification of these woody boundary elements. Reviews and syntheses show that intensification reduced non-crop features (including hedgerows and isolated trees), with consequent declines in landscape heterogeneity and biodiversity (Forman & Baudry 1984; Stoate et al. 2001; Priyadarshana et al. 2024). Regional case studies confirm this trend at local scales: for example, photointerpretation and land-cover analyses in Tuscany documented substantial hedgerow and isolated-tree loss between the 1950s and 2016 (Vannucci et al. 2022).

In conclusion, we strongly recommend including both male and female bees in monitoring studies, including analyses of their respective pollination networks and complementing observational data with pollen analyses. We advocate for the integration of palynological analyses particularly for rare or poorly studied species, and underline that such data may also unveil innate preferences at the species, sex, or individual level in case of common species: information that could deeply help in the conservation of this important group of pollinators, as fostering restoration measures including trees.

ACKNOWLEDGEMENTS

We are indebted with the Parco Regionale Gessi Bolognesi e Calanchi dell'Abbadessa, which allowed the research in its area. The study was funded by the project BeeNet (Italian National Fund under FEASR 2014-2020) from the Italian Ministry of Agriculture, Food Sovereignty and Forestry (MASAF). We deeply appreciated the efforts of two anonymous reviewers, who contributed significantly to the improvement of the first version of this manuscript.

AUTHOR CONTRIBUTION

Concept and design MG, MQ, LB & GB, data collection LZ, SF, RR, data analysis FC, FVG, LZ, MG & GB, writing MG & GB, edits and approval for publication MG, LB & GB.

DISCLOSURE STATEMENT

There are no conflicts of interest to declare.

GENERATIVE AI DISCLOSURE STATEMENT

Gemini (Google): Used to suggest concise phrasing for the summary and to provide language polishing and grammatical corrections. This ensured a professional tone and clarity for a non-native English-speaking audience. The primary author reviewed and integrated suggestions based on their relevance to the intended meaning. ChatGPT (Free Version): Used as a brainstorming tool to expand the bibliography by inputting key findings to identify similar or contrasting studies. The AI served strictly as an initial search aid.

The authors maintained rigorous control over all AI-generated content. While Gemini's linguistic suggestions were frequently utilized, the vast majority of ChatGPT's bibliographical suggestions were rejected following manual verification. Every citation was cross-referenced against academic databases (such as Google Scholar) to confirm existence and relevance; all inaccurate or "hallucinated" citations were removed. Overall, more than 60% of all AI-generated suggestions were modified or discarded to ensure the integrity and accuracy of the final manuscript.

DATA AVAILABILITY STATEMENT

The data used to write this article are available as appendix.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Dataset employed.

REFERENCES

Ascher JS, Pickering J (2020) Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: *Anthophila*). http://www.discoverlife.org/mp/20q?guide=Apoidea_species. Accessed 16 July 2024

Beil M, Horn H, Schwabe A (2008) Analysis of pollen loads in a wild bee community (Hymenoptera: Apidae) – a method for elucidating habitat use and foraging distances. Apidologie 39: 456–467. https://doi.org/10.1051/apido:2008021

Bogo G, Albertazzi S, Capano V, Caringi V, Corvucci F, Dettori A, Giovanetti M, Grillenzoni FV, Guerra I, Vitti C, Medrzycki P, Bortolotti L (2025) Beebread pollen composition is affected by seasonality and landscape structure. Environmental Monitoring and Assessment 197: 1–14. https://doi.org/10.1007/s10661-025-13752-w

Borański M, Jachuła J, Pustkowiak S, Celary W, Splitt A (2025) Solitary bees (*Osmia bicornis*) avoid creating single-component pollen provisions from mass-flowering crops in favor of trees' pollen. Arthropod–

Plant Interactions 19: 1–16. https://doi.org/10.1007/s11829-025-10137-1

Brodschneider R, Kalcher-Sommersguter E, Kuchling S, Dietemann V, Gray A, Božič J, van der Steen JJM (2021) CSI Pollen: Diversity of honey bee collected pollen studied by citizen scientists. Insects 12: 987. https://doi.org/10.3390/insects12110987

Cane JH (2016) Adult pollen diet essential for egg maturation by a solitary *Osmia* bee. Journal of Insect Physiology 95: 105–109. https://doi.org/10.1016/j.jinsphys.2016.09.011

Cane JH, Dobson HE, Boyer B (2017) Timing and size of daily pollen meals eaten by adult females of a solitary bee (*Nomia melanderi*) (Apiformes: Halictidae). Apidologie 48: 17–30. https://doi.org/10.1007/s13592-016-0444-8

Chambers VH (1968) Pollens collected by species of *Andrena* (Hymenoptera: Apidae). Proceedings of the Royal Entomological Society of London. Series A, General Entomology 43: 155–160. https://doi.org/10.1111/j.1365-3032.1968.tb01018.x

Chrzanowska E, Denisow B, Strzałkowska-Abramek M, Dmitruk M, Winiarczyk K, Bożek M (2024) Nectar and pollen in *Acer* trees can contribute to improvement of food resources for pollinators. Scientific Reports 14: 27705. https://doi.org/10.1038/s41598-024-78355-w

Clifford HT (1962) Insect pollination of *Plantago lanceolata* L. Nature 193: 196. https://doi.org/10.1038/193196a0

Danforth BN, Minckley RL, Neff JL (2019) The solitary bees: biology, evolution, conservation. Princeton University Press, Princeton. https://doi.org/10.2307/j.ctvd1c929

Dorchin A, Dafni A, Izhaki I, Sapir Y, Vereecken NJ (2018) Patterns and drivers of wild bee community assembly in a Mediterranean IUCN important plant area. Biodiversity and Conservation 27: 695–717. https://doi.org/10.1007/s10531-017-1459-9

Dormann CF, Gruber B, Fruend J (2008) Introducing the bipartite package: Analysing Ecological Networks. R news 8: 8-11.

Filipiak M (2019) Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. Journal of Applied Ecology 56: 1410-1418. https://doi.org/10.1111/1365-2664.13383

Fisogni A, Quaranta M, Grillenzoni FV, Corvucci F, De Manincor N, Bogo G, Bortolotti L, Galloni M (2018) Pollen load diversity and foraging niche overlap in a pollinator community of the rare *Dictamnus albus* L. Arthropod–Plant Interactions 12: 191–200. https://doi.org/10.1007/s11829-017-9581-x

Forman RTT, Baudry J (1984) Hedgerows and hedgerow networks in landscape ecology. Environmental Management 8: 495–510. https://doi.org/10.1007/BF01871575

Ghisbain G, Radchenko VG, Cejas D, Molina FP, Michez D (2021) Assessment and conservation status of an endemic bee in a diversity hotspot (Hymenoptera, Melittidae, *Dasypoda*). Journal of Hymenoptera Research 81: 127-142. https://doi.org/10.3897/jhr.81.60811

Giovanetti M, Bortolotti L (2021) Report on a project: BeeNet at the start. Bulletin of Insectology 74(2).

Giovanetti M, Bortolotti L (2023) Pollinators and policy: the intersecting path of various actors across an evolving CAP. Renewable Agriculture and Food Systems 38: e27. https://doi.org/10.1017/S1742170523000200

Giovanetti M, Lasso E (2005) Body size, loading capacity and rate of reproduction in the communal bee *Andrena agilissima* (Hymenoptera; Andrenidae). Apidologie 36: 439-447. https://doi.org/10.1051/apido:2005028

Giovanetti M, Luppino S, Zola R (2006) Preliminary note on the relative frequencies of two bees on wild Brassicaceae: oligolectic *Andrena agilissima* vs polylectic *Apis mellifera*. Bulletin of Insectology 59: 153

Gonzalez VH, Griswold T, Engel MS (2013) Obtaining a better taxonomic understanding of native bees: where do we start? Systematic Entomology 38(4). https://doi.org/10.1111/syen.12029

Heuel KC, Haßlberger TA, Ayasse M, Burger H (2024) Floral trait preferences of three common wild bee species. Insects 15: 427. https://doi.org/10.3390/insects15060427

Hoffmann Black F, Sheperd M, Vaughan M, LaBar C, Hodges N (2009) Farming for bees: Guidelines for providing native bee habitat on farms. The Xerces Society for Invertebrate Conservation. Publication No. 15-007_0. https://www.xerces.org/

Kobayashi-Kidokoro M, Higashi S (2010) Flower constancy in the generalist pollinator *Ceratina flavipes* (Hymenoptera: Apidae): an evaluation by pollen analysis. Psyche: A Journal of Entomology 2010: 891906. https://doi.org/10.1155/2010/891906

Liang H, Zhao YH, Rafferty NE, Ren ZX, Zhong L, Li HD, Li DZ, Wang H (2021) Evolutionary and ecological factors structure a plant-bumblebee network in a biodiversity hotspot, the Himalaya-Hengduan Mountains. Functional Ecology 35: 2523-2535. https://doi.org/10.1111/1365-2435.13886

Librán-Embid F, Grass I, Emer C, Alarcón-Segura V, Behling H, Biagioni S, Ganuza C, Herrera-Krings C, Setyaningsih CA, Tscharntke T (2024) Flower–bee versus pollen–bee metanetworks in fragmented landscapes. Proceedings of the Royal Society B: Biological Sciences 291: 20232604. https://doi.org/10.1098/rspb.2023.2604

Louveaux J, Maurizio A, Vorwohl G (1978) Methods of melissopalynology. Bee World 59: 139-157. https://doi.org/10.1080/0005772X.1978.11097714

Mandelik Y, Winfree R, Neeson T, Kremen C (2012) Complementary habitat use by wild bees in agro-natural landscapes. Ecological Applications 22: 1535-1546. https://doi.org/10.1890/1051-0761-22.5.1535

McHugh NM, Bown B, McVeigh A, Powell R, Swan E, Szczur J, Holland J (2022) The value of two agri-environment scheme habitats for pollinators: Annually cultivated margins for arable plants and floristically enhanced grass margins. Agriculture, Ecosystems & Environment 326: 107773. https://doi.org/10.1016/j.agee.2021.107773

Michener CD (2007) The Bees of the World, 2nd Edition. Johns Hopkins University Press, Baltimore.

Morrison J, Izquierdo J, Plaza EH, González-Andújar JL (2017) The role of field margins in supporting wild bees in Mediterranean cereal agroecosystems: Which biotic and abiotic factors are important? Agriculture, Ecosystems & Environment 247: 216-224. https://doi.org/10.1016/j.agee.2017.06.047

Nicholson CC, Knapp J, Kiljanek T, Albrecht M, Chauzat MP, Costa C, Pilar De la Rúa, Klein AM, Mänd M, Potts SG, Schweiger O, Bottero I, Cini E, de Miranda JR, Di Prisco G, Dominik C, Hodge S, Kaunath V, Knauer A, Laurent M, Martínez-López V, Medrzycki P, Pereira-Peixoto MH, Raimets R, Schwarz JM, Senapathi D, Tamburini G, Brown MJF, Stout JC, Rundlöf M (2024) Pesticide use negatively affects bumble bees across European landscapes. Nature 628: 355-358. https://doi.org/10.1038/s41586-023-06773-3

Olsson O, Karlsson M, Persson AS, Smith HG, Varadarajan V, Yourstone J, Stjernman M (2021) Efficient, automated and robust pollen analysis using deep learning. Methods in Ecology and Evolution 12: 850–862. https://doi.org/10.1111/2041-210X.13575

Pérez-Marcos M, Ortiz-Sánchez FJ, López-Gallego E, Ibáñez H, Carrasco A, Sanchez JA (2023) Effects of Managed and Unmanaged Floral Margins on Pollination Services and Production in Melon Crops. Insects 14: 296. https://doi.org/10.3390/insects14030296

Portman ZM, Tepedino VJ (2021) Successful bee monitoring programs require sustained support of taxonomists and taxonomic research. Biological Conservation 256: 109080. https://doi.org/10.1016/j.biocon.2021.109080

Potts SG, Dauber J, Hochkirch A, Oteman B, Roy D, Ahnré K, Biesmeijer K, Breeze T, Carvell C, Ferreira C, Fitzpatrick Ú, Isaac N, Kuussaari M, Ljubomirov T, Maes J, Ngo H, Pardo A, Polce C, Quaranta M, Settele J, Sorg M, Stefănescu C, Vujic A (2021) Refined proposal for an EU Pollinator Monitoring Scheme (EUR 30416 EN). Publications Office of the European Union. https://doi.org/10.2760/881843

Praz C, Genoud D, Vaucher K, Bénon D, Monks J, Wood TJ (2022) Unexpected levels of cryptic diversity in European bees of the genus *Andrena* subgenus *Taeniandrena* (Hymenoptera, Andrenidae): implications for conservation. Journal of Hymenoptera Research 91: 375-428. https://doi.org/10.3897/jhr.91.82761

Priyadarshana TS, Martin EA, Sirami C, Woodcock BA, Goodale E, Martínez-Núñez C, Lee MB, Pagani-Núñez E, Raderschall CA, Brotons L, Rege A, Ouin A, Tscharntke T, Slade EM (2024) Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. Ecology Letters 27: e14412. https://doi.org/10.1111/ele.14412

Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts SPM, Biesmeijer JC, Castro L, Cederberg B, Dvorák L, Fitzpatrick Ú, Gonseth Y, Haubruge E, Mahé G, Manino A, Michez D, Neumayer J, Ødegaard F, Paukkunen J, Pawlikowski T, Potts SG, Reemer M, Settele J, Straka J, Schweiger O (2015) Climatic Risk and Distribution Atlas of European Bumblebees. Biorisk 10 (Special Issue), 246 pp. https://doi.org/10.3897/biorisk.10.4749

Roswell M, Dushoff J, Winfree R (2019) Male and female bees show large differences in floral preference. PLOS ONE 14: e0214909. https://doi.org/10.1371/journal.pone.0214909

Sabugosa-Madeira B, Ribeiro H, Cunha M, Abreu I (2008) The importance of plantain (*Plantago* spp.) as a supplementary pollen source in the diet of honey bees. Journal of Apicultural Research 47: 77-81. https://doi.org/10.1080/00218839.2008.11101427

Saunders ME (2018) Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. Insect Conservation and Diversity 11: 13–31. https://doi.org/10.1111/icad.12243

Standfuss K, Standfuss L (2010) *Andrena pellucens* Pérez, 1895 und *Nomada argentata* Herrich-Schäffer, 1839 in Griechenland. Bembix 30: 35-40.

Stoate C, Boatman ND, Borralho RJ, Carvalho CR, de Snoo GR, Eden P (2001) Ecological impacts of arable intensification in Europe. Journal of Environmental Management 63: 337–365. https://doi.org/10.1006/jema.2001.0473

Tourbez C, Gómez-Martínez C, González-Estévez MA, Lázaro A (2024) Pollen analysis reveals the effects of uncovered interactions, pollen-carrying structures, and pollinator sex on the structure of wild bee–plant networks. Insect Science 31: 971–988. https://doi.org/10.1111/1744-7917.13267

Tur C, Vigalondo B, Trøjelsgaard K, Olesen JM, Traveset A (2014) Downscaling pollen-transport networks to the level of individuals. Journal of Animal Ecology 83: 306–317. https://doi.org/10.1111/1365-2656.12130

Urban-Mead KR, Walter E, McArt SH, Danforth BN (2022) Nearly half of spring-flying male *Andrena* bees consume pollen, but less than female conspecifics. Apidologie 53: 49. https://doi.org/10.1007/s13592-022-00951-4

Vanderplanck M, Moerman R, Rasmont P, Lognay G, Wathelet B, Michez D (2014) How does pollen chemistry impact development and feeding behaviour of polylectic bees? PLOS ONE 9: e86209. https://doi.org/10.1371/journal.pone.0086209

Vannucci A, Andreoli M, Rovai M (2022) Land use change and disappearance of hedgerows in a Tuscan rural landscape: a discussion on policy tools to revert this trend. Sustainability 14: 13341. https://doi.org/10.3390/su142013341

Watts S, Dormann CF, Martín González AM, Ollerton J (2016) The influence of floral traits on specialization and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes. Annals of Botany 118: 415-429. https://doi.org/10.1093/aob/mcw114

Vaudo AD, Biddinger DJ, Sickel W, Keller A, López-Uribe MM (2020) Introduced bees (*Osmia cornifrons*) collect pollen from both coevolved and novel host-plant species within their family-level phylogenetic preferences. Royal Society Open Science 7: 200225. https://doi.org/10.1098/rsos.200225

Weber M, Diekötter T, Dietzsch AC, Erler S, Greil H, Jütte T, Krahner A, Pistorius J (2023) Urban wild bees benefit from flower-rich anthropogenic land use depending on bee trait and scale. Landscape Ecology 38: 2981-2999. https://doi.org/10.1007/s10980-023-01755-2

Wood TJ (2023) The genus *Andrena* Fabricius, 1775 in the Iberian Peninsula (Hymenoptera, Andrenidae). Journal of Hymenoptera Research 96: 241-484. https://doi.org/10.3897/jhr.96.101873

Wood TJ, Roberts SPM (2017) An assessment of historical and contemporary diet breadth in polylectic *Andrena* bee species. Biological Conservation 215: 72–80. https://doi.org/10.1016/j.biocon.2017.09.009

Wood TJ, Holland JM, Goulson D (2016) Diet characterisation of solitary bees on farmland: dietary specialisation predicts rarity. Biodiversity and Conservation 25: 2655-2671. https://doi.org/10.1007/s10531-016-1191-x

Zenga E, Cilia G, D'Agostino M, Zavatta L, Ranalli R, Bortolotti L, Flaminio S (2024) New ecological insights on wild pollinator *Andrena hesperia*. Journal of Pollination Ecology 37: 303–325. https://doi.org/10.26786/1920-7603(2024)796

Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S (2010) Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143: 669–676. https://doi.org/10.1016/j.biocon.2009.12.003