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ARTICLE

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Plant identity determines pollinator, natural enemy, herbivore, and decomposer abundances in flower plantings

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Abstract

Flower plantings in agricultural landscapes can contribute to sustainable crop production by enhancing pollination and biological control services. However, selecting plant species that promote multiple ecosystem services is challenging, since plants that favor pollinators may not equally foster natural enemies, and potential trade-offs, such as inadvertently promoting crop pests, must be considered. This complexity increases when accounting for belowground effects. We evaluated 27 candidate plant species for their ability to host functionally important above- and belowground organisms—pollinators, natural enemies, herbivores, and decomposers—and assessed how plant characteristics such as floral area, timing of peak bloom, life cycle, and plant cover affect these organism groups. We found that certain plant species have the potential to support several groups of beneficial organisms, suggesting they can enhance multiple ecosystem services. Annual plants had higher abundances of both above- and belowground beneficial organisms compared to perennials. Greater plant cover was positively associated with hoverfly abundance. Several functionally important organism groups were positively correlated across plant species, but these positive correlations were not explained by shared responses to plant characteristics. Our findings underscore the significance of plant species identity and characteristics in designing flower plantings for enhancing biodiversity and ecosystem services and highlight the importance of including belowground organisms like nematodes in future studies. Our results for specific plant species and plant characteristics can be used to design flower mixtures supporting several ecosystem service providers while considering potential trade-offs, thereby increasing the efficiency of flower plantings.

KEYWORDS

aboveground organisms, arthropod, belowground organisms, biological control, decomposition, ecosystem service, flower strip, leaf-dwelling, nematode, parasitic wasp, pollination, wild bee

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INTRODUCTION

Ensuring long-term sustainability of agricultural systems requires integrating functionally important biodiversity and its associated ecosystem services into crop production (Cardinale et al., 2012; Tilman et al., 2014). Adopting management practices that rely on beneficial organisms providing key ecosystem services—rather than relying solely on external inputs like pesticides and mineral fertilizers—is crucial for achieving this sustainability (Bommarco et al., 2013). This has been particularly recognized for aboveground ecosystem services such as pollination and biological control. Pollinators are essential for crop production, contributing to the yield of around 75% of globally important crops (IPBES, 2016; Klein et al., 2007) and providing an estimated economic worldwide benefit of US$235–577 billion annually (Potts et al., 2016). Additionally, crop losses due to pests and diseases are estimated to range between 20% and 30% globally (Savary et al., 2019), with the economic value of pest control provided by natural enemies in the United States alone estimated at over US$4.5 billion per year (Losey & Vaughan, 2006). In contrast, while belowground biodiversity plays a critical role in ecosystem services such as climate regulation, nutrient cycling, and food production (Bardgett & van der Putten, 2014; Rillig et al., 2023; Wagg et al., 2014), our understanding of its functioning is still relatively limited compared to aboveground services (Guerra et al., 2020).

Managing agricultural systems to promote aboveground ecosystem services, such as crop pollination and pest control, typically involves restoring, maintaining, or creating habitats that provide essential resources like food, nesting sites, overwintering sites, and protection from agricultural disturbances during critical periods when the surrounding environment fails to supply them (Landis et al., 2000; Wratten et al., 2012). The establishment of areas with flowers, such as flower strips, is among the most widely implemented strategies to achieve these objectives (Albrecht et al., 2020; Haaland et al., 2011; Wratten et al., 2012). While these habitats support many beneficial organisms (Boetzl et al., 2021; Lundin et al., 2023), studies often find limited effects on pollination or pest control in adjacent fields, with an average increase of only 16% in pest control services (Albrecht et al., 2020). This underscores significant potential for optimizing their design and implementation to further enhance their effectiveness. Furthermore, the benefits vary depending on factors such as the synchronization between flower resource availability and the phenology of target organisms, the surrounding landscape complexity, and the type of adjacent crops (Albrecht et al., 2020; Landis et al., 2000). Moreover, the influence of flower strips on belowground biodiversity and ecosystem services remains little understood. Recent studies indicate that perennial flower strips significantly increase earthworm abundance and biomass, enrich potworm populations, and enhance microbial diversity compared to annual flower strips or adjacent cropped fields (Bednar et al., 2023; Pelosi et al., 2024). However, the impact of flower strips on nematode communities is unknown, even though nematodes are the most numerous and functionally diverse soil animals, with substantial effects on soil ecosystem processes and plant community structure (van den Hoogen et al., 2019). Nematodes can either positively contribute to nutrient cycling, organic matter decomposition, and promoting plant health or negatively affect crops as plant parasites (van den Hoogen et al., 2019; Yeates et al., 1993). Though no specific research on nematodes has been done in flower strips, it is known that nematode abundance and composition are greatly affected by plant species identity (Viketoft et al., 2005).

A key challenge is optimizing flower strips to maximize the abundance and diversity of beneficial organisms. Flower strips are most effective and cost-efficient when they incorporate plants that consistently provide abundant resources to multiple beneficial arthropod groups (Morandin et al., 2016). However, selecting plant species for multiple functionally important organism groups is complex, as plants optimal for pollinators might not benefit natural enemies, and vice versa (e.g., see Isaacs et al., 2009, Lavandero et al., 2006, Lundin et al., 2019 for some examples). Moreover, it is crucial to consider potential trade-offs, such as inadvertently promoting crop pests while aiming to boost biological control (Lavandero et al., 2006; Winkler et al., 2010). This complexity might be further exacerbated when considering belowground effects, where interactions and benefits are less well understood. Research on identifying plants that host various functionally important organism groups (e.g., Fiedler & Landis, 2007; Lundin et al., 2019; Rowe et al., 2021) provides valuable insights but has predominantly focused on arthropod pollinators and natural enemies while giving less attention to insect herbivores and belowground organisms such as nematodes.

The crucial first step in designing and implementing multifunctional plantings is to identify the most appropriate plant species. However, this assessment requires region-specific evaluations due to organism community variation across sites. Identifying plant characteristics that can reliably predict abundances of beneficial and detrimental organism groups (i.e., ecosystem service and disservice providers) can enhance the efficacy of biodiversity management practices aimed at sustaining ecosystem services in agricultural systems (Rowe et al., 2021). To date, research on how plant characteristics influence multiple functional organism groups simultaneously has been limited, and there is a lack of studies addressing both above- and belowground communities at the same time. Floral area has been positively associated with the visitation of several pollinator groups as well as natural enemies (Fiedler & Landis, 2007; Lundin et al., 2019; Rowe et al., 2021; Tuell et al., 2008). The timing of peak bloom also influences insect visitation, though effects are variable: earlier bloom periods increased parasitic wasp numbers (Lundin et al., 2019) but later blooming resulted in higher numbers of predators (Fiedler & Landis, 2007). It is uncertain whether plant life cycle (annual vs. perennial) can serve as an indicator for functionally important organisms when selecting plants for flower strips. Perennial species might offer extended opportunities for beneficial organisms compared to annual species due to their regrowth and flowering over multiple years (Albrecht et al., 2020; Boetzl et al., 2021; Hatt et al., 2020).

The overall aim of our study was to identify individual plant species and general plant characteristics across species that determine the abundances of functionally important organism groups above and below ground. Above ground, our focus was on arthropod pollinators, natural enemies, and herbivores and below ground, we concentrated on predatory, herbivorous, and decomposer nematodes. Specifically, we aim to (1) identify multifunctional plant species that host high abundances of ecosystem service providers while minimizing benefits to ecosystem disservice providers, (2) assess whether visitation by these organisms can be predicted by the plant characteristics floral area, timing of peak bloom, life cycle, or plant cover, and (3) determine whether abundances of the different functionally important organism groups are correlated. We predict that (1) abundances of functionally important organism groups will differ among plant species, with some plants having the potential to enhance multiple beneficial organism groups; (2) larger floral areas will lead to higher abundances of pollinators and leaf-dwelling natural enemies but will not have an effect on nematodes; (3) increased aboveground arthropod activity will be related to peak bloom periods, whereas nematodes will not be affected by the peak bloom period; (4) perennial plants will have higher abundances of several organism groups above and belowground; and (5) the abundances of functionally important organism groups that respond similarly to specific plant characteristics will be positively correlated across plant species.

MATERIALS AND METHODS

Study sites and experimental design

The study was conducted over two consecutive seasons 2020–2021 at two sites, Lönnstorp in Scania county, southernmost Sweden (55°40′08.1″ N 13°06′49.4″ E), and Lövsta in Uppsala county, south-central Sweden (59°50′34.1″ N 17°48′34.5″ E). Thirty plant species (Table 1) were selected to be evaluated based on previous studies on attractiveness for pollinators and natural enemies (Fiedler et al., 2008; Lundin et al., 2019; Russell, 2015), results from Swedish pilot trials (E. Ögren, Swedish Board of Agriculture, personal communication) and previous practical experiences and opinions of farmers and advisors in both agricultural and horticultural production. At both sites, the plant species were grown in monospecific 5 m by 2 m plots in a completely randomized block design with four replications per site. Plots within blocks were separated by 2 m, and blocks were separated from each other by 4 m. The space in between plots was sown with winter wheat as a means of standardizing the surrounding cover and limiting the presence of spontaneous flora.

Seeds were purchased from Olssons Frö AB (Helsingborg, Sweden). Annual species were sown in both years while perennial species were only sown in the first year of the study. In Scania, plants were sown on 11 and 19 May in 2020 and 2021, respectively. In Lövsta, plants were sown on 3 June in 2020. Due to an unusual rainy spring in 2021, annual plants could not be sown in Lövsta and only perennial species were surveyed. Sowing rates were adjusted for each species; see Table 1 for details.

Functionally important organism groups

Pollinators

We surveyed all plots with open flowers twice a week between 7:30 and 18:00 for 60 s each when temperatures were at least 15°C, wind was low (28 km/h or less), and the sky was at least partly sunny or brightly overcast. To account for diurnal patterns in pollinator activity, one of the two weekly observations in each flowering plot was in the morning and the second in the afternoon of the same day. During each observation, all flower visitors were counted and identified to the lowest taxonomic level possible. Unknown flower visitors were collected with a sweep net, frozen, and later identified in the laboratory. The observation time was paused during handling of the collected specimens. Flower visitors were classified into

TABLE 1 Characteristics of the herbaceous plant species evaluated, including family and scientific name, life cycle (annual, biennial, or perennial), origin (archaeophyte, native, neophyte), growth form, sowing rate, presumed (Mossberg & Stenberg, 2018) and observed blooming periods (earliest and latest bloom months observed in our study across years and sites), observed peak bloom (month and week number), plant cover at peak bloom, and floral area at peak bloom.

Plant species scientific name	Family	Life cycle	Origin	Sowing rate (kg/ha)	Theoretical blooming period	Observed blooming period	Observed peak bloom	Plant cover (% cover/1 m^2)	Floral area (cm^2/m^2)
Ammi majus	Ap	A	Neo	20	Aug–Sep	Jul–Sep	Aug 32.7 [31.6, 33.9]	78.5 [67.1, 90]	24,986 [8129, 76,800]
Anthemis tinctoria	As	P	Arc	10	Jun–Sep	Jun–Sep	Aug 31.4 [30.3, 32.6]	82.8 [71.4, 94.2]	6232 [2026, 19,163]
Anthriscus cerefolium	Ap	A	Arc	3.4	May-Jul	Aug–Sep			
Borago officinalis	Bo	A	Neo	10	Jun–Aug	Jul–Sep	Jul 29.5 [28.4, 30.7]	68.7 [57.3, 80.1]	1921 [628, 5870]
Carum carvi	Ap	B	N	8	May-Jul	Jun–Jul	Jun 25.4 [23.6, 27.2]	50.9 [31.2, 70.6]	4996 [1192, 20,930]
Centaurea cyanus	As	A	Arc	20	Jun–Sep	Jul–Sep	Jul 30.2 [29, 31.4]	87.4 [76, 98.9]	7116 [2302, 21,995]
Centaurea jacea	As	P	N	40	Jul–Sep	Jul–Sep	Aug 32.5 [31.4, 33.5]	68 [58.1, 77.8]	2968 [994, 8862]
Cichorium intybus	As	P	Arc	5	Jul–Sep	Jul–Sep	Aug 32 [30.6, 33.3]	78.5 [64.5, 92.5]	3832 [1141, 12,874]
Coriandrum sativum	Ap	A	Neo	18	Jun–Sep	Jul–Sep	Jul 30.2 [29, 31.3]	61.2 [49.8, 72.6]	3186 [1043, 9727]
Cosmos bipinnatus	As	A	Neo	20	Jul–Oct	Jul–Sep	Aug 31.8 [30.5, 33.2]	93.3 [79.3, 107.3]	3260 [972, 10,936]
Echium plantagineum	Bo	A	Neo	17	Jul–Oct	Jul–Sep	Jul 29.8 [28.5, 31.2]	87.8 [73.8, 101.8]	1346 [404, 4483]
Fagopyrum esculentum	Po	A	Neo	60	Jul–Aug	Jul–Sep	Jul 29.5 [28.3, 30.6]	84.3 [72.8, 95.7]	2389 [776, 7353]
Fagopyrum tataricum	Po	A	Neo	60	Jul–Sep	Jul–Sep	Aug 34.1 [32.9, 35.2]	93.9 [82.5, 105.4]	44 [14, 137]
Foeniculum vulgare	Ap	P	Neo	12	Jul–Aug	Aug–Sep			
Helianthus annuus	As	A	Neo	16.7	Aug–Sep	Jul–Sep	Aug 34.6 [33.4, 35.7]	64.5 [53.1, 76]	3239 [1033, 10,158]
Leucanthe-mum vulgare	As	P	N	10	Jun–Aug	Jun–Sep	Jul 29.4 [28.3, 30.6]	76 [64.6, 87.4]	14,496 [4637, 45,316]

TABLE 1 (Continued)

Plant species scientific name	Family	Life cycle	Origin	Sowing rate (kg/ha)	Theoretical blooming period	Observed blooming period	Observed peak bloom	Plant cover (% cover/1 m^2)	Floral area (cm^2/m^2)
Lotus corniculatus	Fa	P	N	12	Jun–Aug	Jun–Sep	Jul 29.1 [28, 30.3]	67.6 [56.2, 79]	909 [299, 2767]
Medicago sativa	Fa	P	Arc	15	Jul–Sep	Jun–Sep	Aug 32.4 [31.3, 33.6]	77 [65.6, 88.4]	168 [55, 513]
Melilotus officinalis	Fa	B	Arc	20	Jul–Sep	Jun–Sep	Aug 30.9 [29.8, 32]	64.6 [54.5, 74.8]	1701 [570, 5079]
Phacelia tanacetifolia	Hy	A	Neo	10	Jun–Sep	Jun–Sep	Jul 28.5 [27.5, 29.6]	87.7 [77.8, 97.5]	4752 [1624, 13,905]
Plantago lanceolata	Pl	P	N	10	May–Aug	Jun–Sep	Jul 29.4 [28.3, 30.4]	77.8 [67.9, 87.6]	1320 [454, 3838]
Sinapis alba	Br	A	Neo	10	Jun–Sep	Jul–Sep	Aug 30.9 [29.5, 32.2]	64.5 [50.5, 78.5]	341 [101, 1148]
Trifolium alexandrinum	Fa	A	Neo	20	Jun–Aug	Jul–Sep	Aug 33.1 [31.9, 34.2]	45.4 [33.9, 56.8]	255 [83, 781]
Trifolium hybridum	Fa	P	Arc	10	Jun–Aug	Jun–Sep	Aug 31.2 [30.1, 32.4]	82 [70.6, 93.4]	1451 [467, 4504]
Trifolium incarnatum	Fa	A	Neo	20	Jun–Aug	Jul–Sep	Jul 30.6 [29.2, 31.9]	65.2 [51.2, 79.3]	1136 [339, 3807]
Trifolium pratense	Fa	P	N	10	May–Sep	Jun–Sep	Jul 30.1 [29.1, 31.2]	62.2 [52.3, 72.1]	668 [225, 1982]
Trifolium resupinatum	Fa	A	Neo	12	Jun–Aug	Jul–Sep	Aug 33.4 [32.2, 34.6]	57.7 [46.2, 69.1]	411 [134, 1260]
Tripleurospermum inodorum	As	A	Arc	3.3	Jun–Oct	Jul–Sep	Jul 30.4 [29, 31.9]	56.6 [41.7, 71.5]	862 [248, 2994]
Vicia sativa	Fa	A	Neo	60	Jun–Aug				
Vicia villosa	Fa	A/B	Neo	45	Jun–Aug	Jun–Sep	Aug 31.6 [30.4, 32.8]	70.4 [58.5, 82.3]	3632 [1145, 11,519]

Note: Values for observed peak bloom, plant cover, and floral area are averaged model predictions across years and sites (estimated marginal means ±95% CI). Blank cells indicate plant species that established too poorly to be included in the analysis.

Abbreviations: Family: Ap, Apiaceae; As, Asteraceae; Bo, Boraginaceae; Br, Brassicaceae; Fa, Fabaceae; Hy, Hydrophyllaceae; Pl, Plantaginaceae; Po, Polygonaceae. Life cycle: A, Annual; B, Biennal; P, Perennial. Origin: Arc, Archaeophyte (introduced and naturalized before 1800), N, Native (wild in Sweden); Neo, Neophyte (introduced after 1800).

hoverflies and wild bees (bumblebees and solitary bees) (Appendix S1: Table S1). Honey bees were not included in the study as they are a fully managed species in Sweden (Niklasson et al., 2024). Each flower visit was recorded as a new visit, regardless of whether it was by the same or a different individual. Plots were surveyed from July to September in 2020 (1 July to 11 September at Lönnstorp; 20 July to 4 September at Lövsta) and June to September in 2021 (1 June to 3 September at Lönnstorp; 7 June to 3 September at Lövsta).

Leaf-dwelling arthropods

Arthropods active in the vegetation layer were collected using vacuum sampling of the plots with open flowers. Samples were taken for 30 s with a modified leaf vacuum in a 1 m × 1 m quadrat located in the center of each plot and following the same weather criteria as for pollinators. In 2020, samples were taken fortnightly as long as the target plant species was in bloom. In 2021, each plot was sampled only when 50% or more of the target plant species in it was in bloom for a total of three times corresponding to three consecutive weeks. Additional samples were collected in 2021 in cases where blooming increased, ensuring that peak bloom was accurately captured. Vacuum samples were frozen and processed later in the laboratory. Due to the large number of samples, we limited the analyses to two samples per plot corresponding to the two consecutive samples with the highest number of floral units observed (defined as peak bloom). In these samples, we identified all arthropods caught to family level and classified them as herbivores, parasitic wasps, predators, or other (Appendix S1: Table S2) based on the broad trophic patterns of each family (Gibson et al., 2019).

Belowground organisms

Nematodes were sampled at the end of each survey season in both years: 21–27 September in 2020 and 13–19 September in 2021 at Lönnstorp; 28 September–4 October in 2020 and 27 September–3 October in 2021 at Lövsta. In each plot, three samples were taken using a soil corer (2 cm diameter) to a depth of 15 cm. The samples were taken at three distances (1.5, 2.5, and 3.5 m) along a central transect extending the length of each plot, unless the plot had sparse vegetation cover; in that case, the samples were taken in the vicinity of the target plant species. The three samples per plot were combined into a composite sample that was placed into a sealed plastic jar, transported to the laboratory in a cooling box, stored at 4°C and extracted with modified Baermann funnels (Viketoft et al., 2005) within 2 weeks after sampling. The nematodes were heat-killed, fixated in formalin, and counted under a stereomicroscope at low magnification (50×). Identification to family or genus level was done under a compound microscope (200×), and the specimens were classified as herbivores, predators (carnivores and omnivores), or decomposers (bacterial and fungal feeders) according to Yeates et al. (1993) (Appendix S1: Table S3).

Plant characteristics

We collected information on several plant characteristics that were expected to affect the abundances of the functionally important organism groups above and belowground: floral area, timing of peak bloom, plant life cycle, and plant cover. Floral area and plant cover surveys were performed weekly within 2 days of sampling pollinators and leaf-dwelling arthropods (see above). Floral area and plant cover were recorded in a 1 m × 1 m quadrat at the center of each plot. In each quadrat, we estimated the percentage plant cover (using the Braun-Blanquet cover-abundance scale converted to percentage midpoints (Braun-Blanquet, 1932)) of the sown plant species and counted the number of floral units. A floral unit was equal to an individual flower in most species, but for Asteraceae and clovers (*Trifolium* spp.), we counted each inflorescence as a floral unit. To estimate the floral area in each plot, we measured the diameter (actinomorphic or composite flowers) or length and width (zygomorphic flowers) of five floral units of the target plant species. From these data, we calculated the average floral area per floral unit for each plant species and later multiplied it by the number of open floral units in each plot each week in order to calculate the weekly floral area per plot. The timing of peak bloom for each plant species was defined as the average week number between the two consecutive weeks with the highest number of open floral units. The life cycles of the plant species were classified as annual or perennial (perennial and biennial) following Mossberg and Stenberg (2018) (Table 1).

Data analysis

Plant establishment varied greatly among species, sites, and years (Table 1; Appendix S1: Table S4). Hence, only plots with at least 50% of vegetation cover of the target species at any one time point were included in the analyses of pollinators and nematodes, and only plots with at least 50% of vegetation cover during three consecutive time points during vacuum sampling were considered for the analyses of leaf-dwelling arthropods (Appendix S1: Table S5). After applying these criteria, three plant species were removed from the analysis due to insufficient establishment: *Anthriscus cerefolium* (L.) Hoffm., *Foeniculum vulgare* Mill., and *Vicia sativa* L. All data were summed on the observation plot level per site and year (Appendix S1: Table S5) and all analyses were conducted in R 4.4.2 for Windows (R Development Core Team, 2024).

In a first step, we assessed the effects of plant species identity on the abundance of eight different functionally important organism groups (hoverflies, wild bees, herbivorous arthropods, parasitic wasps, predatory arthropods, herbivorous nematodes, predatory nematodes, and decomposer nematodes) and richness of two groups (hoverflies and wild bees). For each functionally important organism group (count data), we fitted generalized mixed-effects models (package "glmmTMB," version 1.1.9-9000, Brooks et al., 2017) with "plant identity" (factor, 27 levels), "site" (factor, 2 levels), and "year" (factor, 2 levels) as fixed factors and the "block" nested within a combination of "site" and "year" as random intercept. All models used a negative binomial residual distribution. Sampling effort was not equal across plots in all sites and years. Visual pollinator observations were not available for all weeks with plants in bloom due to unfavorable weather conditions. In some cases, vacuum samples during peak bloom were missed due to unfavorable weather conditions. Despite sampling a constant soil volume, the final soil mass differed among plots (Appendix S1: Table S5). Each model hence contained one of three different offsets to control for uneven sampling effort: models for pollinator responses contained the number of weeks with pollinator observations divided by the number of weeks the respective plots were in bloom (i.e., where pollinators should have been observed), models for vacuum sample responses contained the number of samples taken, and models for nematodes contained the mass in grams of dry soil that had been extracted resulting in the proportion of samples gathered or the sample completeness. The offsets were log-transformed to fit the residual distributions used. From these models, we estimated marginal predictions for each of the eight functionally important organism groups in each of the 27 plant species. In models with offsets, these predicted values are given at the average sampling completeness or effort.

We found strong positive correlations between abundance and richness of hoverflies ($r = 0.60$, $p < 0.001$) and wild bees ($r = 0.71$, $p < 0.001$), across plant species, so we only included abundance but not richness of hoverflies and wild bees in subsequent analyses to maintain consistency among groups (Appendix S1: Table S6).

In a second step, we assessed whether the marginal predictions obtained for the different plants and functionally important organism groups were related to plant characteristics: floral area, the timing of peak bloom, life cycle, and plant cover. Apart from life cycle (annual vs. perennial), these characteristics were based on observations made in the field (as described above), and we obtained marginal predictions for each plant species as described above but using no offsets and a Gaussian residual distribution for peak bloom timing and plant cover and a negative binomial residual distribution for floral area. Before modeling, we correlated the values for plant cover and floral area for the whole season with those during peak bloom (the two consecutive weeks with the highest number of open flowers) using Pearson correlations. We found strong positive correlations in plant cover ($r = 0.83$, $p < 0.001$) and floral area ($r = 0.96$, $p < 0.001$) between the whole season and peak bloom (Appendix S1: Figure S1), so we used the values during peak bloom where data were consistently available and predictions are thus more reliable. Using the predictions for the eight functionally important organism groups in the 27 plant species obtained in the generalized mixed-effects models described above as responses, we fitted generalized linear models that included "life cycle" (factor, two levels), "peak bloom," "plant cover," and "floral area" (all continuous) as fixed effects. All continuous fixed effects were mean centered and scaled to multiples of their SD, and models used a negative binomial residual distribution, except the model for predatory nematodes, which used a lognormal residual distribution that improved the fit.

In a third step, we checked for correlations between the eight functionally important organism groups with Pearson correlations using the estimated marginal predictions for each plant species across sites and years obtained from the generalized mixed-effects models.

All model fits were evaluated for the suitability of the chosen residual distributions, collinearity, under- and overdispersion, and zero inflation using the packages "DHARMa" (version 0.4.7, Hartig, 2025) and "performance" (version 0.12.2, Lüdecke et al., 2021). We used type 3 Wald χ^2 tests with the command "Anova" (package "car," version 3.1-2) with corrected marginal contrasts (Al-Sarraj & Forkman, 2023) to test for statistical significance. All model predictions represent estimated marginal means with 95% CIs (command "ggemmeans," package "ggeffects," version 1.7.0, Lüdecke, 2018).

RESULTS

Functionally important organism groups

We observed 5246 hoverflies and 6452 wild bees. About 50% of the hoverflies belonged either to *Episyrphus balteatus* De Geer or to the genus *Sphaerophoria*. Among wild bees, the community was dominated by *Bombus lapidarius* L. and individuals belonging to the *Bombus lucorum* L. complex (almost 80% of the individuals) (Appendix S1: Table S1).

We identified a total of 55,796 leaf-dwelling arthropods (34,710 herbivores, 8937 predators and 12,149 parasitic wasps). The herbivore community was dominated by seed bugs (Lygaeidae), aphids (Aphididae) and thrips (non-Aeolothripidae Thysanoptera), representing about 66% of the herbivores collected. The most abundant predators were predatory thrips (Aeolothripidae), spiders (Araneae) and minute pirate bugs (Anthocoridae), accounting for about 80% of the predators collected (Appendix S1: Table S2).

The nematode community was dominated by decomposers (1042 nematodes per 100-g dry soil), followed by herbivorous nematodes (117 nematodes per 100-g dry soil) and predatory nematodes (40 nematodes per 100-g dry soil). Among the decomposers, Rhabditidae and Cephalobidae were the most abundant families, accounting for about 62% of the decomposers identified. Among plant feeders, spiral nematodes (*Helicotylenchus* spp.) and root-lesion nematodes (*Pratylenchus* spp.) dominated the community adding up to 72% of the herbivorous nematodes identified. Almost 50% of the predatory nematodes belonged to the genus *Clarkus* (Appendix S1: Table S3).

Plant identity effects on functionally important organism groups

All eight functionally important organism groups differed in abundance across the plant species (Figure 1, Table 2; Appendix S1: Tables S7 and S8). Most functionally important organism groups differed across sites or years (Appendix S1: Tables S8 and S9). There were twice as many wild bees and herbivorous nematodes, and more than six times as many predatory nematodes, in Lövsta than in Lönnstorp (Appendix S1: Tables S8 and S9). Additionally, the abundance of wild bees, herbivorous arthropods, parasitic wasps, predatory arthropods, herbivorous nematodes, and decomposer nematodes was consistently higher in 2021, with most groups showing two- to threefold increases compared to 2020 (Appendix S1: Tables S8 and S9).

Plant characteristics predicting organism abundances across plant species

Herbivorous nematodes tended to be more abundant in species with smaller floral area. Hoverflies tended to be more abundant on plant species with an earlier peak bloom, while parasitic wasps tended to be more abundant on plants with a later peak bloom. The abundances of decomposer nematodes were higher, and wild bees and predatory arthropods tended to be higher in annual compared to perennial plant species (Figure 2; Appendix S1: Table S10). Finally, hoverflies were more abundant in plant species with higher plant cover (Appendix S1: Figure S2 and Table S10).

Correlations across functionally important organism groups

The abundances of parasitic wasps and predatory arthropods were positively correlated. The density of decomposer nematodes was positively correlated with the abundances of hoverflies and wild bees and with the density of herbivorous nematodes (Figure 3).

DISCUSSION

Our study of 27 candidate plant species for inclusion in flower plantings in agricultural landscapes demonstrated that plant species identity and plant characteristics influence the abundance of both above- and belowground organisms. Certain plant species hosted high populations of beneficial organisms across multiple functional groups, suggesting their potential to enhance several ecosystem services simultaneously. Life cycle (annual vs. perennial) tended to affect the abundances of several beneficial organism groups both above and belowground, with annuals having higher abundances compared to perennials. Surprisingly, floral area was not related to the abundance of any functionally important organism group. Notably, we observed that plant species and their characteristics affected nematodes, underscoring the need to integrate belowground organisms in future studies. Correlations among functionally important organism groups were not related to shared responses to plant characteristics.

Plant identity effects on functionally important organism groups

Abundances and densities of all functionally important organism groups varied across plant species, with several plant species, such as *Echium plantagineum* L. and *Centaurea cyanus* L., showing potential to support multiple beneficial organism groups, in agreement with our first prediction (Figure 1, Table 2; Appendix S1: Table S7). For instance, *E. plantagineum* simultaneously had high numbers of hoverflies, wild bees, predatory arthropods, and decomposer nematodes. While the attractiveness of this species to pollinators and predators has been previously reported (Atakan & Tunç, 2010;

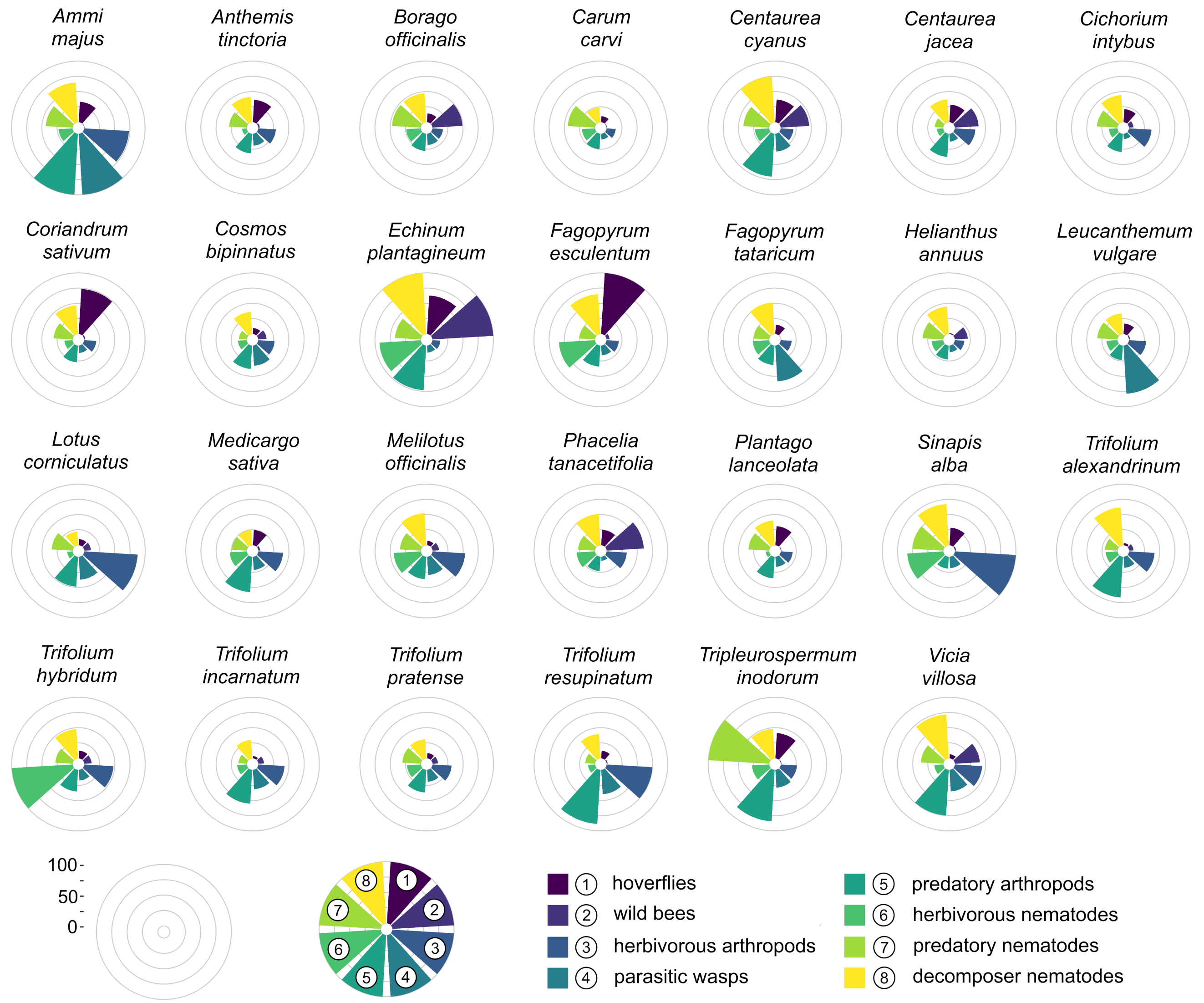

FIGURE 1 Estimated marginal means for the eight functionally important organism groups assessed on 27 sown plant species. Marginal means on the response scale are scaled relative to the highest marginal mean obtained for any plant species. Unscaled estimated marginal means are available in Appendix S1: Table S7. For statistics, see Appendix S1: Table S8.

Pinheiro et al., 2013; Reverté et al., 2023), our study is the first to reveal its potential to simultaneously promote multiple groups of ecosystem service providers above and belowground. Similarly, *C. cyanus* had high abundances of hoverflies, wild bees, and decomposer nematodes. This species is known for its high pollen production, which attracts pollinators such as honey bees, wild bees, bumblebees, hoverflies, and butterflies (Carreck & Williams, 2002; Jeavons et al., 2020).

Beneficial effects on ecosystem service providers, however, need to be balanced with possible trade-offs of simultaneously fostering ecosystem disservice providers. Some plant species can harbor herbivores either above or belowground, such as *E. plantagineum* which had large numbers of herbivorous nematodes. The herbivores could potentially harm nearby or subsequent crops, but might also serve as prey for beneficial predators when other food sources are limited (Lundin et al., 2019). Therefore, a thorough assessment of the overall composition and impact of each functionally important organism group associated with these plants is essential. In this respect, categorizing functionally important organisms into "beneficial" (e.g., pollinators) or "harmful" (e.g., herbivores) is not always straightforward, as their ecological roles might shift depending on the specific crop and context (Saunders et al., 2016). Selecting plant species to enhance ecosystem services should thus account for the crops being targeted, the desired ecosystem services, and local environmental conditions.

TABLE 2 Percentile-based rankings of the 27 plant species (derived from model-estimated marginal means with 95% CIs) for the eight functionally important organism groups evaluated in the field experiments.

Plant species	Hoverflies	Wild bees	Herbivorous arthropods	Parasitic wasps	Predatory arthropods	Herbivorous nematodes	Predatory nematodes	Decomposer nematodes
Ammi majus	+	−−	++	++	++	0	++	+
Anthemis tinctoria	+	−	0	0	−	−−	−	−
Borago officinalis	0	++	−−	0	−	+	++	0
Carum carvi	−	−−	−−	−−	−−	0	++	−−
Centaurea cyanus	++	++	−	0	+	0	+	++
Centaurea jacea	+	+	0	−	0	−−	−−	−
Cichorium intybus	0	0	0	−−	−	−	0	0
Coriandrum sativum	++	−	−	−−	−−	−−	0	0
Cosmos bipinnatus	−	+	−	+	0	−	−−	−
Echium plantagineum	++	++	−−	−−	++	++	+	++
Fagopyrum esculentum	++	0	−	−	−	++	−	++
Fagopyrum tataricum	0	−−	−−	++	−	+	−	+
Helianthus annuus	−−	+	−−	−−	−−	0	0	0
Leucanthemum vulgare	0	−	0	++	−−	−	0	−−
Lotus corniculatus	−	+	++	++	+	−−	+	−−
Medicago sativa	0	−	+	0	+	+	−−	−−
Melilotus officinalis	−−	0	++	+	0	++	+	+
Phacelia tanacetifolia	0	++	0	−−	−−	+	−	+
Plantago lanceolata	+	−−	−−	−	0	−−	0	−
Sinapis alba	+	−	++	0	−−	++	++	++
Trifolium alexandri-num	−−	0	+	−	+	0	−−	+
Trifolium hybridum	−	+	+	−	0	++	−	0
Trifolium incarnatum	−−	0	+	+	+	−	−−	−−
Trifolium pratense	−−	0	0	0	0	0	0	−−
Trifolium resupinatum	−	−−	++	++	++	−−	−−	−
Tripleuro-spermum inodorum	++	−−	−	+	++	+	++	0
Vicia villosa	−−	++	+	+	++	−	+	++

Note: Symbols denote percentile bins: "++," top 20%; "+," >20%–40%; "0," >40%–60%; "−," >60%–80%; "−−," bottom 20%.

Plant characteristics predicting organism abundances across plant species

The abundances of several functionally important organism groups were related to plant characteristics (Figure 2). Contrary to our expectations, our results did not support the second prediction that larger floral areas would lead to higher abundances of pollinators and leaf-dwelling predatory arthropods. Increased floral area has repeatedly been found to be positively correlated with higher visitation rates by aboveground natural enemies and wild bees (Boetzl et al., 2023; Lundin et al., 2019; Rowe et al., 2021; Tuell et al., 2008). In our study, the lack of effects of floral area on natural enemies and pollinators may be attributed to factors beyond floral area. For instance, these arthropod groups might rely on additional resources such as insect prey and the presence of extrafloral nectaries (Landis et al., 2000; Wäckers & van Rijn, 2012) or be attracted to other floral characteristics that we did not assess, such as floral shape (Campbell et al., 2012; Lundin et al., 2019; Wäckers & van Rijn, 2012), or the quality and quantity of nectar and pollen (Laubertie et al., 2012; Rowe et al., 2021). Furthermore, narrowing the focus to specific taxa, rather than grouping all natural enemies or wild bees, might reveal stronger associations between floral area and arthropod attractiveness (Blümel et al., 2024).

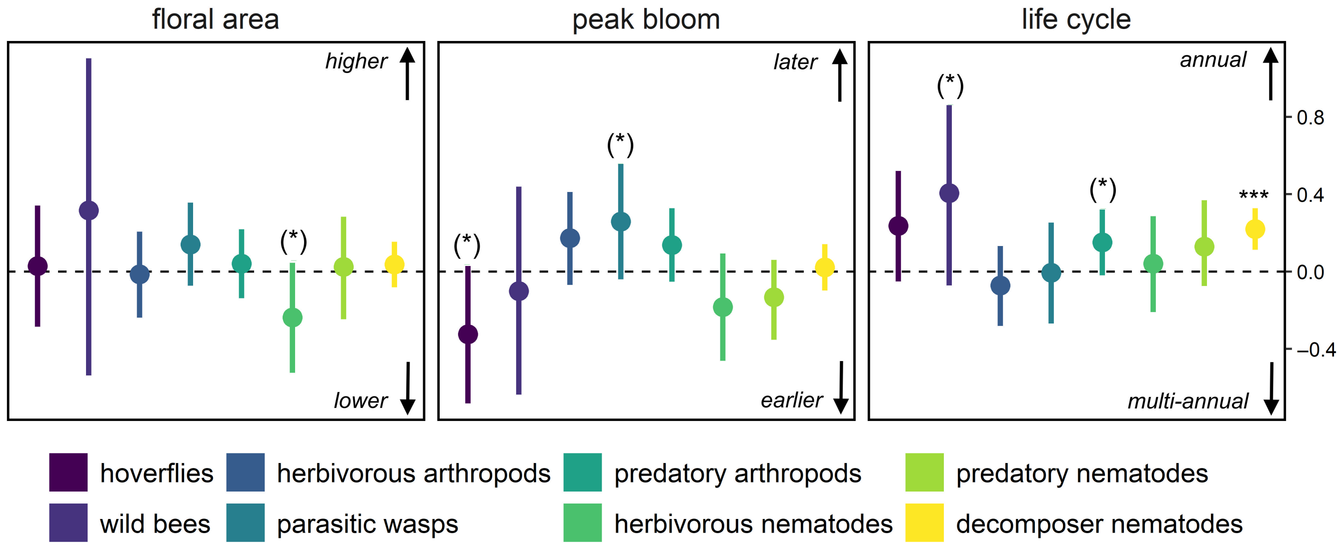

FIGURE 2 Estimated marginal means with 95% CI for the eight functionally important organism groups in relation to plant life cycle (annual vs. perennial) and the marginal predictions for floral area and peak bloom calculated from the monofloral plots in both locations and years. For statistics, see Appendix S1: Table S10.

Below ground, the abundance of herbivorous nematodes tended to be negatively related to floral area, something not anticipated in our second prediction. Plants can adjust their resource allocation to optimize growth and development (Bloom et al., 1985), and allocating resources to reproduction can reduce growth in vegetative tissues (Harris & Pannell, 2008; Tuomi et al., 1983). Consequently, one potential explanation for the negative trend observed in our study is that plants with a larger floral area have allocated fewer resources to root development, reducing resources for herbivorous nematodes. Alternatively, nematodes feeding on roots might have impaired the plant's ability to produce flowers (Masters et al., 2001; Wurst et al., 2008). The observed relationship could, however, also simply be coincidental.

Hoverflies tended to be more abundant in early-blooming plants, whereas parasitic wasps tended to be more abundant in late-blooming plants, providing some support for the third prediction. The timing of peak bloom can influence the number of pollinators and natural enemies visiting the plant species (Fiedler & Landis, 2007; Lundin et al., 2019; Rowe et al., 2021), with higher visitation often corresponding to periods of increased insect abundance (Lundin et al., 2019; Rowe et al., 2021). For example, hoverflies might show increased visits to early-blooming plants due to the arrival of migratory species like *E. balteatus* from southern Europe (Wotton et al., 2019). Apart from being aligned with the phenology of beneficial organisms, the provision of flower resources, however, also needs to ensure resource availability during critical times in which surrounding habitats fail to provide enough resources (Landis et al., 2000; Wratten et al., 2012). Hence, the preference for specific blooming periods could also indicate a scarcity of alternative resources at those times. Thus, late-blooming plants might benefit parasitic wasps by offering essential resources not readily available in the surrounding environment, highlighting the importance of continuous resource provisioning.

Our results did not support the fourth prediction that perennial plants would have higher abundances of both above- and belowground organisms due to their extended period of resource availability. Contrary to this expectation, decomposer nematodes were more abundant in annual plants than in perennials, with similar trends for wild bees and predatory arthropods. In our study, the pollinator community was predominantly composed of generalist bumblebees like *B. lucorum* and *B. lapidarius* (Redhead et al., 2016). Notably, these pollinators were particularly abundant in several annual plants including *Borago officinalis* L., *C. cyanus*, *E. plantagineum*, and *Phacelia tanacetifolia* Benth. These annual species are recognized for providing high nectar rewards and are known to attract both pollinators and natural enemies (Carreck and Williams 2002; Geneau et al., 2012; Laubertie et al., 2012). Consequently, the observed elevated abundances of pollinators and leaf-dwelling predators in these annual plants may be coincidental, potentially influenced by other unmeasured characteristics or traits, such as the quality, quantity, or accessibility of the floral resources they provide. Moreover, some perennial plants need a longer time to properly establish and reach full flower production than annuals, which could have also influenced the results. Therefore, taking the implications of both plant life cycles into account is

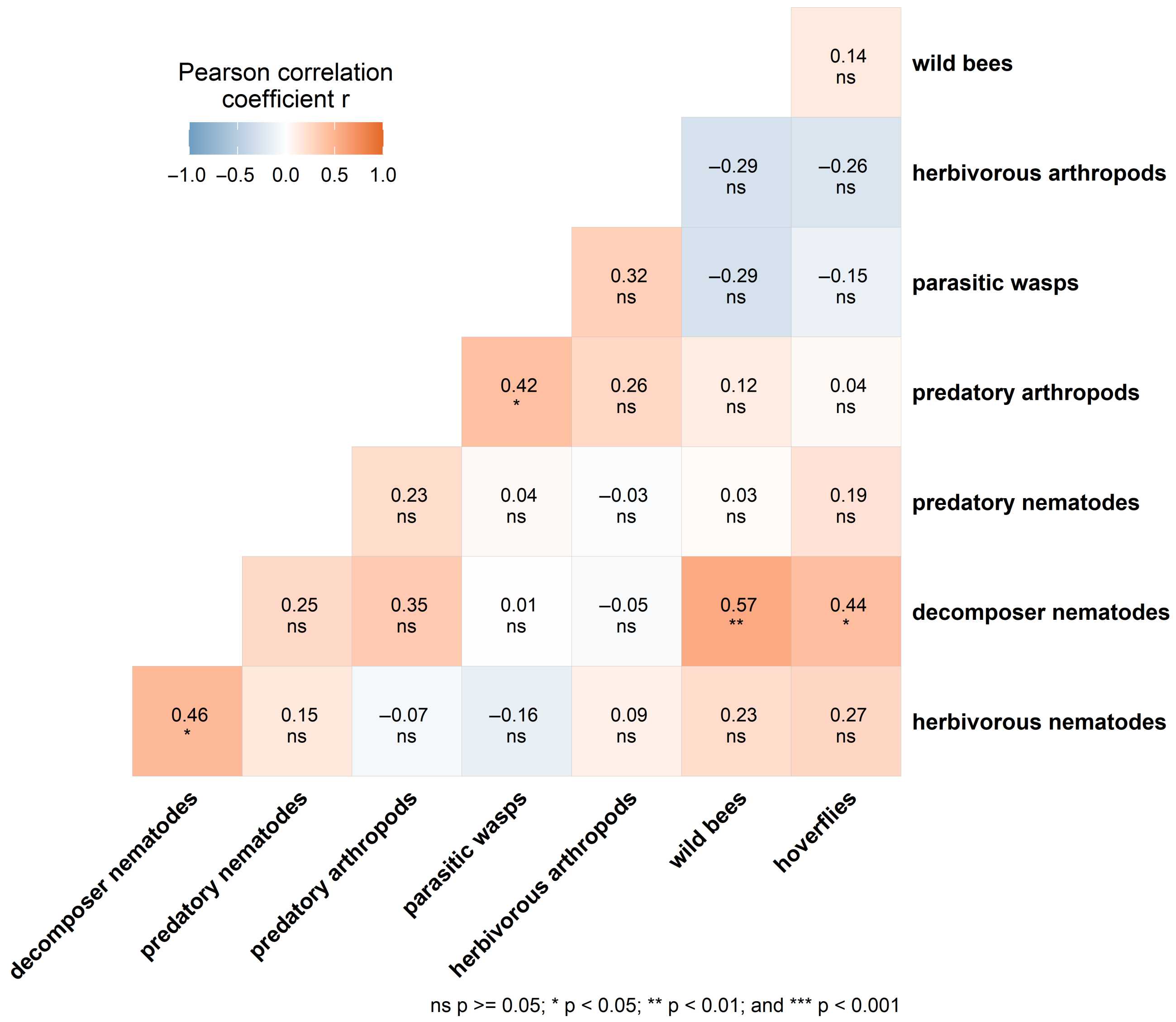

FIGURE 3 Correlation matrix plot showing Pearson's correlation coefficient between the eight functionally important organism groups.

important when selecting species for flower plantings. Annual plant species might offer more cost-effective seed options and are easier to deploy in agricultural systems constrained by yearly crop rotations (Carreck & Williams, 2002; Hatt et al., 2020). Perennial species, on the other hand, can provide multiple years of regrowth and flowering without additional management and thereby offering greater nesting and overwintering opportunities for natural enemies and pollinators (Boetzl et al., 2021; Hatt et al., 2020). The duration and spatial scale of our study were, however, insufficient to capture such effects.

The higher abundance of decomposer nematodes in annual plants can be attributed to differences in soil management based on the plants' life cycles. Annual plots were tilled before sowing in each year, while perennial plots were left undisturbed after the first year, allowing these plant species to persist. Decomposer nematodes, characterized by short life cycles and high reproductive rates, are less affected by disturbances like tillage compared to other nematode trophic groups (Bongers & Ferris, 1999). Additionally, tillage increases the accessibility of plant litter to bacteria, promoting their growth and increasing food availability for decomposer nematodes. Consequently, a greater abundance of these nematodes is found in conventionally tilled soils compared to non-tilled ones (van Capelle et al., 2012). A final consideration is that, in contrast to the highly mobile aboveground organisms such as pollinators, belowground organisms exhibit slower dispersal capacity. Consequently, nematode communities are likely still adapting to the new environmental conditions, that is, recently established plants. Hence, a longer study duration may capture stronger associations (Mahaming et al., 2009).

We largely controlled for plant cover by excluding plots with poor establishment, thereby reducing the likelihood of observing a strong effect of plant cover on the abundances of our functionally important organism groups. Nonetheless, our observations indicated that adult hoverflies visited more flowers from plant species with higher plant cover. Hoverflies primarily rely on visual cues for locating flowers (Rodríguez-Gasol et al., 2020); hence, higher plant cover might signal a higher probability of finding these resources.

Correlations across functionally important organism groups

Contrary to our fifth prediction, while we found positive correlations between the abundance of several organism groups, these groups responded differently to the plant characteristics evaluated (Figure 3). Above ground, the abundances of parasitic wasps and predatory arthropods were positively correlated across plant species. It is likely that both natural enemy groups were drawn by overlapping responses to unmeasured cues from plants like floral rewards or greater prey availability (Lundin et al., 2019; Rowe et al., 2021). Furthermore, decomposer nematodes were positively correlated with herbivorous nematodes, wild bees, and hoverflies. Decomposer nematodes contribute to soil nutrient cycling by breaking down organic material, thereby making more nutrients available to plants. As observed by Wurst et al. (2008) for earthworms, this nutrient boost can enhance plant growth and contribute to increased root biomass. This could have indirectly provided more food resources for herbivorous nematodes, which feed on plant roots. Additionally, increased nutrient availability allows plants to allocate more resources to blooming, which might indirectly benefit pollinators (Nötzold et al., 1998; Poveda et al., 2003). However, since we did not directly measure these nutrient-driven interactions, future studies are needed to confirm these relationships. Another possibility is that these organism groups co-occurred due to shared environmental preferences rather than direct interactions. Deepening our understanding of these relationships could help identify specific plant characteristics that foster beneficial interactions across functionally important organism groups.

CONCLUSION

In this study, we present results that can be used for the optimization of flower plantings. By demonstrating that some plant species can support several beneficial organism groups above and belowground and highlighting possible trade-offs with potential crop pests, this study indicates that with careful plant selection, flower strips can be designed to promote multiple ecosystem services above and belowground. The identification of specific plant characteristics that attract various functional organism groups helps refine the development of flower mixtures to maximize ecological benefits. Ultimately, our results can be used to strengthen the effectiveness of habitat management programs, ensuring that both above- and belowground biodiversity are fully considered in strategies aimed at enhancing beneficial organisms and ecosystem services in agricultural landscapes.

AUTHOR CONTRIBUTIONS

Neus Rodríguez-Gasol: Data curation; investigation; methodology; project administration; validation; visualization; writing—original draft; writing—review and editing. **Fabian A. Boetzl:** Formal analysis; validation; visualization; writing—review and editing. **Elodie Chapurlat:** Investigation; methodology; project administration; validation; writing—review and editing. **Johan A. Stenberg:** Conceptualization; funding acquisition; methodology, supervision, writing—review and editing. **Mattias Jonsson:** Conceptualization; funding acquisition; methodology; supervision, writing—review and editing. **Ola Lundin:** Conceptualization; funding acquisition; methodology; supervision; writing—review and editing. **Maria Viketoft:** Conceptualization, funding acquisition; investigation; methodology; project administration; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Rodríguez-Gasol et al., 2025) are available from the Swedish National Data Service (Svensk nationell datatjänst): https://doi.org/10.5878/8q5t-3546.

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SUPPORTING INFORMATION

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

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