



Assessing the contribution of lawns and semi-natural meadows to bee, wasp, and flower fly communities across different landscapes

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Abstract

Land conversion and intensive vegetation management are major drivers of shifts in insect communities, including economically valuable species. We evaluated the impact of lawns and meadows across agricultural, residential, and industrial landscapes in structuring bees, wasps, and flower flies communities. We carried out plant and insect inventories on 18 lawns and 18 meadows distributed evenly among agricultural, residential, and industrial landscapes within the Greater Quebec City region (Quebec, Canada). Insect sampling was conducted five times using bowl traps and entomological nets, from June to September 2020. Results indicate taxon-specific responses to landscape matrix and site maintenance. Agricultural landscapes negatively influenced bee abundance compared to urban areas, while the opposite trend was observed for flower flies. Wasp abundance and richness were negatively influenced by both agricultural and industrial matrices compared to residential landscapes. Regarding site maintenance, bees and wasps were 3 and 12 times more abundant and 2 and 6 times more species-rich, respectively, in meadows than in lawns as per the data aggregated across the sampling date. Flower fly abundance was higher in meadows than in lawns for agricultural and residential landscapes only, while richness was consistently higher (2 times greater) in meadows compared to lawns. Some species of the sweat bee genus *Lasioglossum* and the flower fly margined calligrapher (*Toxomerus marginatus*) were dominant in lawns, while meadows hosted a more balanced community among genera and supported pollinators with wide-ranging resource requirements. Our results suggest that conservation actions should consider both landscape and local management to conserve central-place foragers, such as bees and wasps, and for structuring flower fly species composition.

Keywords Urbanization · Rural · Land use · Biodiversity · Floral diversity · Turfgrass

Résumé

Les changements d'utilisation des sols, ainsi que la gestion intensive de la végétation ont des impacts majeurs sur les communautés d'insectes. Nous avons évalué l'impact des paysages agricoles et urbains et le rôle respectif des gazons et des prairies semi-naturelles pour soutenir les communautés d'abeilles, de guêpes et de syrphes. Des inventaires de plantes et d'insectes ont été réalisés sur 18 gazons et 18 prairies semi-naturelles réparties entre les paysages agricoles, résidentiels et industriels de l'Agglomération de Québec (Québec, Canada). L'échantillonnage des insectes a été effectué à cinq reprises à l'aide de pièges-bol et de filets fauchoirs, de juin à septembre 2020. Les zones agricoles étaient négativement associées à l'abondance

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et à la richesse des abeilles, alors que la tendance inverse s'observait pour les syrphes. Les zones agricoles et industrielles influençaient négativement l'abondance et la richesse des guêpes comparativement aux quartiers résidentiels. Les abeilles et les guêpes étaient respectivement 3 et 12 fois plus abondantes et 2 et 6 fois plus riches en espèces au sein des prairies que dans les gazons pour les données compilées sur la saison entière. L'abondance des syrphes était supérieure dans les prairies semi-naturelles comparativement aux gazons dans les paysages agricoles et résidentiels seulement, alors que la richesse était toujours supérieure dans les friches que dans les gazons (2 fois supérieures en moyenne). Certaines espèces d'abeilles (*Lasioglossum* spp.) et de syrphes (*Toxomerus marginatus*) étaient davantage associées aux gazons, mais les prairies abritaient des communautés ayant des besoins en ressources plus variés. Nos résultats suggèrent que les actions de conservation doivent tenir compte autant du paysage que de la gestion locale des espaces verts pour le maintien des insectes pollinisateurs.

Introduction

Bees (Hymenoptera: Anthophila), Vespidae wasps (Hymenoptera: Vespidae), and flower flies (Diptera: Syrphidae) play fundamental roles within ecosystems by pollinating angiosperms (Klein et al. 2007) and regulating arthropod populations (Nelson et al. 2012; Southon et al. 2019). Insect-mediated pollen dispersion is crucial for plant reproduction and crop yield: roughly 78% of flowering plants in temperate regions (Ollerton et al. 2011), and more than 70% of dominant crops globally (Klein et al. 2007), show improved reproductive success via animal pollination. For agricultural production, pollinators represent an annual value of US\$350 billion globally (IPBES 2016). Insect-mediated pollination efficiency depends on the frequency of plant visits and the ability of pollinators to transport and deposit compatible pollen on flower stigma. In that respect, the bees' foraging behavior and hairiness make them highly valuable pollinators (Rader et al. 2016). However, pollination by other insects, like wasps and flower flies, are far from negligible as they account for ~40% of crop flower visits (Rader et al. 2016). In addition, wasps and flower flies play a crucial service in regulating crop pests. For instance, wasps are biological controllers of lepidopteran larvae (Prezoto et al. 2019; Southon et al. 2019), while flower flies reduce aphid populations (Dunn et al. 2020; Nelson et al. 2012). In essence, bees are vital pollinators in both natural and managed ecosystems, while wasps and flower flies provide dual ecosystem services by pollinating plants and regulating arthropod pests.

Agricultural and urban expansion are the main drivers of habitat loss (Eigenbrod et al. 2011). Agricultural

and urban landscapes are planned to meet fundamental and non-essential human needs often ignoring that their composition and configuration influence food, nesting, and reproductive substrates for insects, as well as dispersal capacity of individuals at the landscape scale (Viana et al. 2012). Rural areas surrounded by natural habitats host a greater diversity of Hymenoptera than those predominantly composed of annual crops (Theodorou et al. 2020; Verboven et al. 2014). This may occur due to landscape simplification by monoculture, habitat loss and high mortality caused by pesticides (Le Féon et al. 2010; Theodorou et al. 2020; Verboven et al. 2014). Unlike Hymenoptera, flower fly diversity is generally less impacted by habitat conversion in agricultural owing to their higher dispersal ability as well as their capability to exploit aphid colonies for egg-laying (Dunn et al. 2020; Udy et al. 2020). Within the urban matrix, contrasting pollinator responses to urbanization have been reported (Wenzel et al. 2020). Some studies observed no change (Williams and Winfree 2013), or even an increased bee diversity with urbanization, explained by higher environmental heterogeneity benefiting several synanthropic species (Banaszak-Cibicka et al. 2018; Theodorou et al. 2020). Others have showed reduced bee diversity with urbanization, explained by increased isolation of feeding and nesting sites (Birdshire et al. 2020) and the reduction of floral and nesting resources (Harmon-Threatt 2020). This can be due to a lower proportion of semi-natural areas and reduced landscape connectivity in dense city centers compared to low density residential landscapes (Wenzel et al. 2020; Winfree et al. 2007). Man-made structures (residences, garages, fences, etc.) can favor specific groups of pollinators, such as social wasps, through the nesting opportunities they offer (Akre et al. 1981; Silagi et al. 2003). Nevertheless, urbanization can have a greater negative impact on flower flies, due to the deficit of food resources for the larvae compared to agricultural areas (Udy et al. 2020). The vital role of bees, wasps, and flower flies is thus jeopardized by both agriculture and urbanization and ensuring sustainable pollination services to crops requires a deep understanding of how they are affected by different landscape matrices.

Local habitat quality is a key component of pollinator community assembly (Potts et al. 2003). For instance, floral diversity (Wilson and Jamieson 2019) and the presence of native plant species increase reproductive success (Sexton et al. 2021) and richness of pollinators (Hülsmann et al. 2015). Floral composition, in turn, determines the availability of resources and breeding sites, affecting arthropod diversity (Francoeur et al. 2021; Normandin et al. 2017). Lawns cover up to 70% of green spaces in urban matrices, being endorsed by aesthetic

norms and social pressure (Burr et al. 2018, Ignatieva et al. 2015). Lawns commonly host few flowering weeds species such as dandelion (*Taraxacum officinale*) and white clover (*Trifolium repens*), providing foraging resources throughout the growing season and attracting several species of bees and flower flies (Larson et al. 2014; Lerman and Milam 2016). However, maintenance intensity (mowing frequency and use of pesticides) can negatively impact pollinators, due to shortages in floral resources (Larson et al. 2013; Lerman et al. 2018). How lawn maintenance practices and floral resource homogeneity structure assemblages of different insect taxa remain unclear. Meadows, which result from spontaneous colonization of abandoned lots, are less common than lawns in urban landscapes (Millard 2004). They are not frequently mowed, have a higher proportion of forbs, increased flower height and cover, and support richer invertebrate communities compared to lawn (Francoeur et al. 2021; Norton et al. 2014; Robinson and Lundholm 2012). The ecological value of these ecosystems is often ignored in landscape planning despite their importance in harboring biodiversity (Klaus 2013; Millard 2004; Milligan 2015). Increasing our knowledge of the ecological role of meadows relative to lawns for supporting pollinator diversity would improve decision-making about landscape development and management.

This study aimed to understand the relationships between different insect taxa and anthropogenic habitats on landscape and local scales. We determined bee, wasp and flower fly assemblage responses to landscape matrix (agricultural, residential and industrial) and site maintenance (lawn versus meadows). We expected that landscape matrix acts as an ecological filter modifying species composition, allowing us to identify disturbance-tolerant species related to each landscape. Also, we expected that lower floral cover and uniformity of lawns reduce feeding and nesting resource diversity, resulting in pollinator assemblages depleted of individuals and species when compared to meadows.

Methods

Study area

The study was conducted in the Quebec City metropolitan community (QCM) and partly in Côte-de-Beaupré region (Quebec, Canada; Fig. 1). QCM corresponds to an area of 550 km² and a population of 548 996 inhabitants (Gouvernement du Québec 2020). In brief, 39% of the territory is covered by built areas, 36% by forests, 9% by wetlands, and 11% by crop fields (corn, soybeans, and hay being the main crops). The climate is continental humid with a mean annual temperature of 2 °C (17 °C in

July and -15 °C in January) and 1000 mm mean annual precipitation, of which 25% falls as snow (Environment and Climate Change Canada 2012).

Landscape classification and site selection

Following the zoning established by the administration of Quebec City (Ville de Québec 2020b), we divided the study area into three categories: agricultural, residential, and industrial. Twelve sites were selected within each of them (six lawns and six meadows), all positioned at least 250 m from its boundaries (apart from one agricultural site where a small residential area was situated 100 m from the sampling site). Also, within the 500-m buffer zone surrounding each site, the land cover category (agricultural, residential, or industrial) was consistent, with at least 70% of the area corresponding to the land cover category from the sampling site's location. The agricultural landscape (112 km²) was characterized by a few buildings and low-rise constructions (1%) and comprised predominantly cultivated land (46%) as well as extensive woodlands (44%), and a few lawns (4%), meadows (4%), water bodies (< 1%) and open wetlands (< 1%). The residential landscape (133 km²) had 32% of impervious cover including residential buildings and low-rise constructions (e.g., roads and parking lots). Pervious surfaces corresponded to isolated trees (17%), scattered forest remnants (13%), lawns (35%) and meadows (2%), cultivated land (< 1%), water bodies (< 1%) and open wetlands (< 1%). The industrial landscape (38 km²) was characterized to a large extent by impervious surfaces, covering 56% of the area. Woodlands covered approximately 18% of industrial zones, croplands 1%, water bodies < 1%, open wetlands 1%, while isolated trees made up 3%. Lawns and meadows accounted both for about 10% of this landscape. We obtained geospatial data on land cover types (impervious, agricultural, forest, isolated trees, lawns, and meadows) for each of the three landscape matrices, using maps from Quebec City (Ville de Québec 2020a), sentinel-2 aerial images (Copernicus Sentinel data 2020), MERN (2020), MFFP (2020a, b), MELCC (2018) and FADQ (2020).

We sampled six lawns and six meadows in each of the three landscape matrices (n = 36; Fig. 1). Lawns were defined as managed sites dominated by seeded grasses, sometimes mixed with *T. repens*, which are mowed weekly during the growing season and generally do not exceed 10 cm in height. We preselected 40 lawns on private land having a minimal lawn cover of 300 m² (10 × 30 m; the area in which we sampled plants and pollinators) well distributed in each landscape (Ville de Québec 2020c) based on aerial images (Google Earth Pro 2020). From this selection, 18 lawns were randomly chosen, six in each

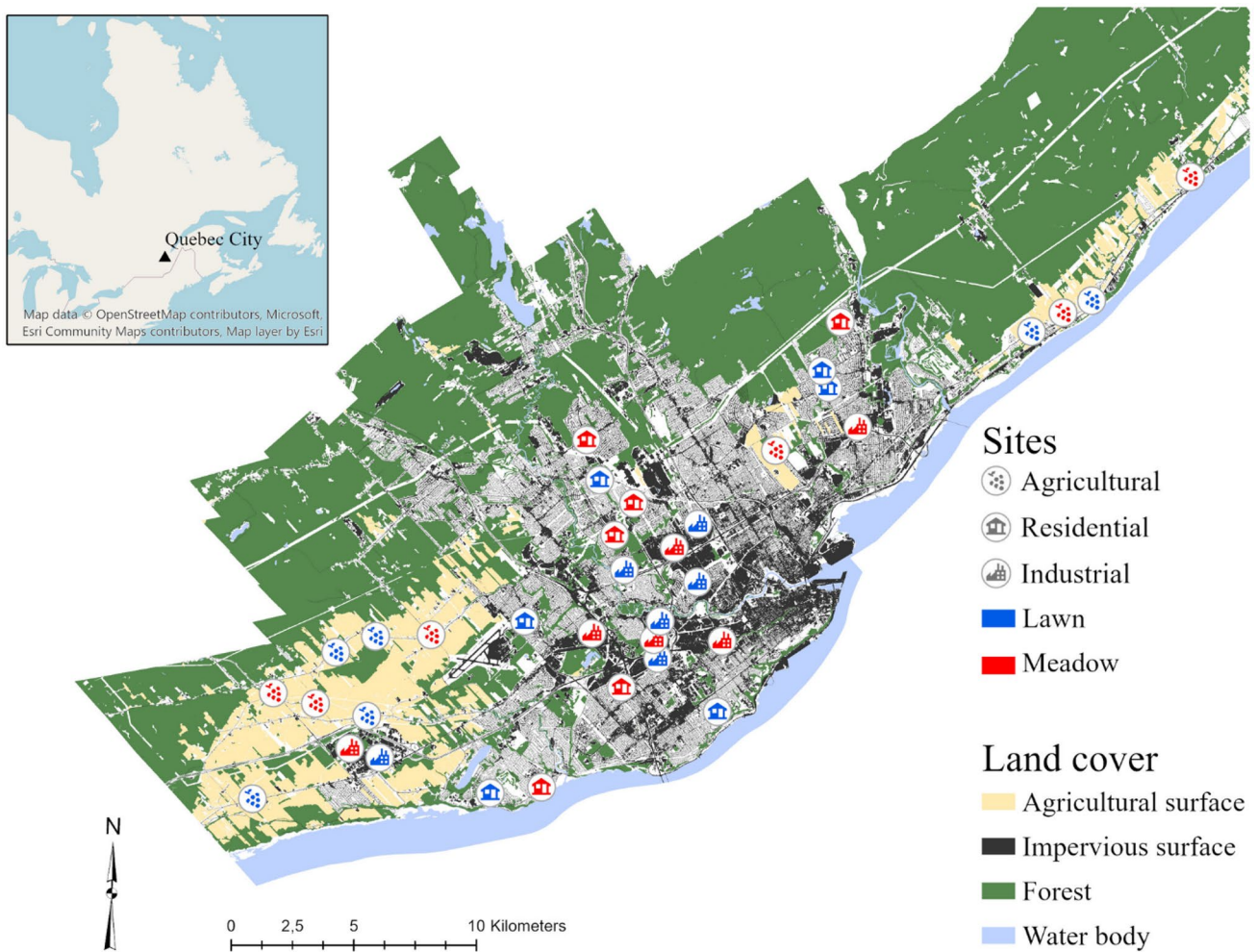


Fig. 1 Location of the 36 sites from the three landscape matrices (agricultural, residential, and industrial) and the two maintenance levels (lawn and meadow) sampled in 2020 in the Greater Quebec City

region. Location of the study area in the province of Quebec, Canada is shown in the upper left corner box (indicated by a triangle)

landscape. Meadows were defined as sites covered by spontaneous herbaceous vegetation, submitted to sporadic mowing (once or twice per year) and therefore presenting a more variable height compared to lawns. To identify meadow sites, we first selected vacant lots (as meadows often occur on vacant lots) with a minimal cover of 300 m² using a map of soil occupancy (Ville de Québec 2020c). Then, using LiDAR data (MFFP 2020b), we retained only vacant lots with low vegetation (shorter than one meter), thereby avoiding shrubby or forested vacant lots. From the remaining sites, we randomly selected six in each landscape ($n = 18$). Field truthing was used to validate that the selected sites were dominated by spontaneous vegetation. A minimal distance of 500 m between all sites was respected. We characterized the environment of each site by calculating the area of land cover (impervious, agricultural, forest, isolated trees, lawns, and meadows) within a 1-km radius (Table 1).

Insect sampling

We sampled bees, wasps and flower flies every three weeks between June 9 and September 15, 2020, for a total of five surveys, varying the order of site sampling each time. We conducted sampling on sunny days with minimum 15 °C, light wind, and no precipitation. In each single sampling day, 36 sites were visited by two teams (18 sites per team). The only exception was the first sampling period, for which we completed the survey on two different days with similar meteorological conditions, one week apart. One team was responsible for visiting sites in the northeast of the study area, while the other covered the southwest. The areas covered by each team included sites of each landscape and maintenance type. To avoid bias related to the time of sampling, we visited sites of all three landscape categories and two maintenance types before and after noon. We captured insects using two methods: pan traps and hand-netting. On

Table 1 Site environmental characteristics for each landscape matrix (agricultural, residential, and industrial) and site maintenance (lawn and meadow)

	<i>Impervious</i> % (min–max)		<i>Cropland</i> % (min–max)		<i>Forest</i> % (min–max)		<i>Lawn</i> % (min–max)		<i>Meadow</i> % (min–max)	
Agricultural	8	(2-15)	52	(17-82)	16	(0-35)	10	(4-15)	6	(0-15)
Lawn	7	(2-13)	51	(32-78)	18	(7-35)	9	(4-14)	7	(0-13)
Meadow	9	(4-15)	53	(17-82)	12	(0-17)	12	(6-15)	6	(2-15)
Residential	36	(20-59)	0	(0-1)	15	(0-27)	29	(20-38)	5	(1-11)
Lawn	34	(24-41)	0	(0-1)	14	(5-20)	33	(26-38)	2	(1-6)
Meadow	37	(20-59)	1	(0-1)	15	(0-27)	26	(20-34)	7	(1-11)
Industrial	59	(39-74)	1	(0-6)	13	(1-24)	16	(10-25)	7	(2-11)
Lawn	57	(39-68)	1	(0-6)	10	(1-19)	18	(15-25)	7	(5-9)
Meadow	62	(46-74)	1	(0-4)	14	(2-24)	13	(10-23)	6	(2-11)

The average percentage of each surface cover type (impervious, cropland, forest, lawn, and meadow) within a 1-km buffer zone surrounding sampling sites. Minimum and maximum values in parentheses. Bold indicates mean value for each landscape

each site, we placed nine traps of three colors (yellow, white, and blue) in trios on a 20 m-transect, with 10 m between trios and 1 m between bowls of a single trio. We filled 12 oz. bowls three-quarters full of soapy water, which were laid directly on lawns and placed two feet above the ground on meadows. For each sampling date, we retrieved all traps 24 h after placement. We complemented pan trap samplings with hand-netting (Nielsen et al. 2011) on the same day. The latter consisted of walking along two 30 m-transects established five meters from each side of the pan-trap transect a single time in eight minutes, while sweeping the top of the vegetation with the net.

We stored collected specimens in 70% ethanol solution. Bees and wasps were then washed, rinsed, and pinned. Flower flies were put in a solution of half ethanol and half ethyl acetate for 6 h and another 6 h in pure ethyl acetate, before being pinned. We then identified each individual to the species level according to Ascher and Pickering (2018), Packer et al. (2007), Williams et al. (2014), Gibbs (2010), and with the assistance of an expert (Amélie Gervais) for bees, and the guides by Buck et al. (2008) for wasps, and those by Skevington et al. (2019) for flower flies. For bees and wasps, only wild bees (*Apis mellifera* was discarded) and species from the *Vespidae* family were considered, respectively. For flower flies, we pooled *Sphaerophoria asymmetrica*, *S. philanthus* and *S. abbreviata* as a single taxon, since it was impossible to differentiate females. Identification of male individuals showed that at least *S. philanthus* and *S. asymmetrica* were present in the landscape.

Floral resources

We estimated the floral resources on each site by calculating the total cover, the species relative cover and species richness of blooming plants (species cover and richness were

not recorded at the first sampling). Cover was estimated based on the surface occupied by reproductive stems and the flowers they bore. We performed these samplings the day after the insect survey, over a 10 × 30 m quadrat centered on the pan-trap transect. We estimated cover according to eight classes: < 1%, 1 – 5%, > 5 – 10%, > 10 – 25%, > 25 – 50%, > 50 – 75%, > 75 – 90%, > 90%. Grass and cyperaceous species were not considered since they are not significant sources of pollen and nectar for pollinators.

Data analyses

All analyses were conducted in R version 4.1.0 (R Core Team 2021). We combined captures from both pan-trapping and hand-netting in the analyses as these methods are complementary. For analyses of pollinator abundance and species richness, we discarded two sites from the first survey because three bowls fell on one site and two on another. We also discarded one site from the last survey due to inaccessibility caused by a new industrial development. Data were also grouped for the five sampling dates to better reflect the site compositional variation across the season. Data from the three sites with missing values were corrected as follows: for the two sites where bowls fell, we used the mean abundance of each insect species contained in the two-remaining bowls of the same color as an estimate of the number that would have been caught in the fallen bowls. For the inaccessible site, species abundances were estimated based on samples from the other five meadows of the same landscape matrix taken on the same sampling day.

Abundance and species richness

We assessed the influence of landscape matrices (agricultural, residential, industrial) and site maintenance (lawn vs.

meadow) on abundance and species richness (total number of species) of insects and cover as well as richness of blooming plants using a mixed-effect model. We have analyzed the results by pooling the data collected over the sampling date, but we also present a seasonal perspective when it provided valuable insights. For data compiled across seasons, abundance and richness of each insect group and the richness of blooming plants were analyzed with a generalized linear mixed model (GLMM). For cover of flowering plants, we log transformed the data to meet the assumption of homoscedasticity. Analysis of the residual plot supported this assumption, while we evaluated normality of the data using a normal quantile–quantile plot (Q-Q plot), which allowed the use of a linear mixed model (LMM). When sampling date was considered in the analysis, insect groups were still analyzed with a GLMM except that bee abundance and richness were log transformed and analyzed with a LMM. For the LMM and the GLMM, we considered landscape matrices, site maintenance, and the sampling date as fixed effects, while we used the study sites as a random effect. For significant results in the mixed-effect models, we used a Tukey multiple comparison test for pairwise comparisons. We used a Moran I test (DHARMA package in R) on each model to test for spatial autocorrelation. The Moran I test indicated a randomly distributed structure of models' residuals, except for the flower fly abundance and richness models (app. 6). We have taken this signal into account by including latitude in the models (app. 6).

Beta diversity

We compared beta diversity among landscape matrices as well as between site maintenance using tests for homogeneity of multivariate dispersions (PERMDISP; Anderson et al. 2006). Separate analyses for each group of insects (bee, wasp and flower fly) were performed. PERMDISP calculates the distance of each site to its group centroid (landscape matrices or site maintenance) in an ordination space (principal coordinate analysis; PCoA) and then tests whether the average distance is different between groups through permutation tests. To perform these analyses, we computed a site-by-species matrix of abundance for each group of pollinators. We then built site-by-site distance matrix using the Hellinger distance (Legendre and De Cáceres 2013). This distance matrix was used to compute the centroid of each group of sites (landscape matrices or site maintenance). The distance of each site to its associated group centroid was calculated, and the dispersion of these distances (within-group variance) was used to estimate beta diversity (the greater the within-group variance, the higher the beta diversity). These distances were subjected to an ANOVA with 9999 permutations to determine whether beta diversity differed between groups. When we found significant results for the three landscape matrices, we used a multiple comparison Tukey test for pairwise comparisons.

Shifts in species composition

To determine whether species composition differed with landscape matrices and site maintenance, we tested for location differences between centroids using permutational multivariate analysis of variance (PERMANOVA) while controlling for their interaction (Anderson 2001). The significance of PERMANOVA was assessed using pseudo-F ratios (9999 permutations). Because this test is sensitive to differences in multivariate dispersion (Anderson and Walsh 2013), PCoA was used to visually support the statistical tests. Whenever a factor significantly affected species composition, a redundancy analysis (RDA) was used to determine the species most associated with each type of habitat and visualize it in an ordination.

Species turnover and richness difference

To understand the mechanisms underlying variation in species composition between sites, we partitioned beta diversity into two components: species turnover and richness differences. We first transformed the site-by-species matrix of each pollinator group using the Sørensen dissimilarity index. We then decomposed the resulting dissimilarity matrix (i.e., beta diversity) into turnover and species difference for each site maintenance within each landscape matrix, following the Podani and Schmera framework (Podani and Schmera 2011).

Results

We collected 2,186 wild bee specimens belonging to 131 species (Table 2). Bees from five families were captured: *Halictidae* (n = 1, 297; 59% of all bees), *Apidae* (n = 335; 15%), *Megachilidae* (n = 261; 12%), *Colletidae* (n = 162; 7%) and *Andrenidae* (n = 131; 6%). The genus *Lasiosglossum* was the most abundant (n = 1, 117; 51%; 29 species), followed by *Bombus* (n = 270; 12%, 9 species), *Hylaeus* (n = 150; 7%, 7 species), *Megachile* (n = 122; 6%, 11 species), *Andrena* (n = 109; 5%, 18 species), *Halictus* (n = 105; 5%, 3 species), and *Chelostoma* (n = 74; 3%, 1 species). The most abundant species (at least 100 captures) were *Lasiosglossum ephialtum*, *Bombus impatiens*, *L. lineatulum*, *L. pilosum* and *L. imitatum*. At the beginning of the season, the genus *Andrena* was abundant with *A. wilkella* and *A. comoda*, while in July, *Megachile*, *Hylaeus*, and *Chelostoma* were more abundant. The genus *Bombus* was abundant from the end of July to mid-September, with *B. impatiens* and *Bombus rufocinctus* as its primary representatives.

We captured 222 individuals from 21 species of wasps (Table 2). Social wasps of the genera *Vespula* (n = 142; 64%; 6 species), *Polistes* (n = 33; 15%; 2 species) and *Dolichovespula* (n = 21; 9%; 3 species) were more

Table 2 Total abundance and species richness of bees, wasps, and flower flies for each landscape matrix (agricultural, residential, and industrial) and site maintenance (lawn and meadow)

	<i>Bees</i>		<i>Wasps</i>		<i>Flower flies</i>	
	Abundance	Richness	Abundance	Richness	Abundance	Richness
Agricultural	478	69	37	11	332	19
<i>Lawn</i>	99	38	1	1	129	9
<i>Meadow</i>	379	62	36	10	203	16
Residential	921	103	131	16	176	12
<i>Lawn</i>	190	47	22	7	59	7
<i>Meadow</i>	731	89	109	16	117	10
Industrial	787	84	54	13	160	12
<i>Lawn</i>	272	38	5	3	91	3
<i>Meadow</i>	515	75	49	12	69	12

prevalent than solitaries from *Ancistrocerus* (n = 14; 6%; 4 species), *Eumenes* (n = 6; 3%; 1 species), *Euodynerus* (n = 4; 2%; 2 species), *Parancistrocerus* (n = 1; 1 species), and *Symmorphus* (n = 1; 1 species) genera. At the start of the season, the number of wasps captured was low, with only a total of 12 and 8 wasps in early June and July, respectively, followed by an increase, with a maximum of 104 captures in August.

We captured 668 flower flies of 24 species (Table 2). The most frequently seen species was *Toxomerus marginatus* (n = 375; 56%), followed by *Toxomerus geminatus* (n = 106; 16%) and species of the genus *Sphaerophoria* (n = 98; 15%; 3 species). In late August and mid-September, *Syrirta pipiens* (n = 40; 6%) and *Eristalis* spp. (n = 10; 1%; 4 species) were found more frequently in the landscape. Similarly to wasps, peak captures occurred at the end of August, with 313 individuals.

Impact of landscape matrix and site maintenance on pollinators

Abundance and Species Richness

The effect of landscape matrices and site maintenance on pollinator abundance and species richness varied among groups of pollinators. For bees, the landscape matrices

correlated with their abundance, but not their richness (Table 3). Bee abundance was lower in agricultural landscapes (30.1 95% CI [23.6,38.4]) compared to residential (57.7 [45.8,72.6]) and industrial ones (59.2 [47.1, 74.3]) (Table 3, Fig. 2). Wasp abundance and richness were higher in residential landscapes (abundance: 6.91 [4.45,10.73], richness: 3.49 [2.38, 5.13]) compared to industrial (abundance: 2.21[1.21,4.04], richness: 1.43 [0.8,2.56]) and agricultural ones (abundance: 0.65 [0.23, 1.81], richness 0.65 [0.23, 1.81]) (Table 3, Fig. 2). The abundance and richness of flower flies differed between landscapes in interaction with the green space maintenance (lawn or meadow) (Table 3). In lawns, their abundance was higher in agricultural (18.4 [13.61,24.9]) than residential environments (9.71 [6.84,13.8]), while richness was highest in agricultural environments (3.73 [3.01,4.61]), followed by residential (2.5 [1.99,3.13]) and industrial ones (1.49 [1.14,1.94]) (Fig. 2). In meadows, flower fly abundance was higher in agricultural landscape (30.47 [23.0, 40.4]) compared to industrial environments (11.25 [8.06, 15.7]), while richness was higher in agricultural (6.83 [5.51, 8.33]) compared to residential environments (3.74 [5.61,8.33]).

Abundance and species richness of both bees and wasps were lower in lawns (bee abundance: 26.7 [21.8, 32.6], bee richness: 13.8 [11.8, 16.0], wasp abundance: 0.67 [0.30, 1.49], wasp richness: 0.59 [0.27, 1.28]) compared to meadows (bee abundance: 82.2 [68.5, 98.7], bee richness: 30.6

Table 3 Effect of landscape matrix (agricultural, residential, and industrial), site maintenance (lawn and meadow), study sites (random effect) and their interaction on bee, wasp and flower fly abundance and richness using generalized linear mixed models

Source of variation	df	<i>Bees</i>				<i>Wasps</i>				<i>Flower flies</i>			
		Abundance		Richness		Abundance		Richness		Abundance		Richness	
		χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P	χ^2	P
<i>Landscape (l)</i>	2	16.65	<0.001	3.39	0.183	11.52	0.003	8.44	0.015	7.42	0.024	41.49	<0.001
<i>Maintenance (m)</i>	1	29.77	<0.001	20.76	<0.001	10.50	0.001	7.25	0.007	5.79	0.016	29.13	<0.001
<i>l x m</i>	2	5.51	0.064	0.02	0.988	2.88	0.237	2.80	0.246	7.28	0.026	18.39	<0.001

Bold indicates significant results (P < 0.05)

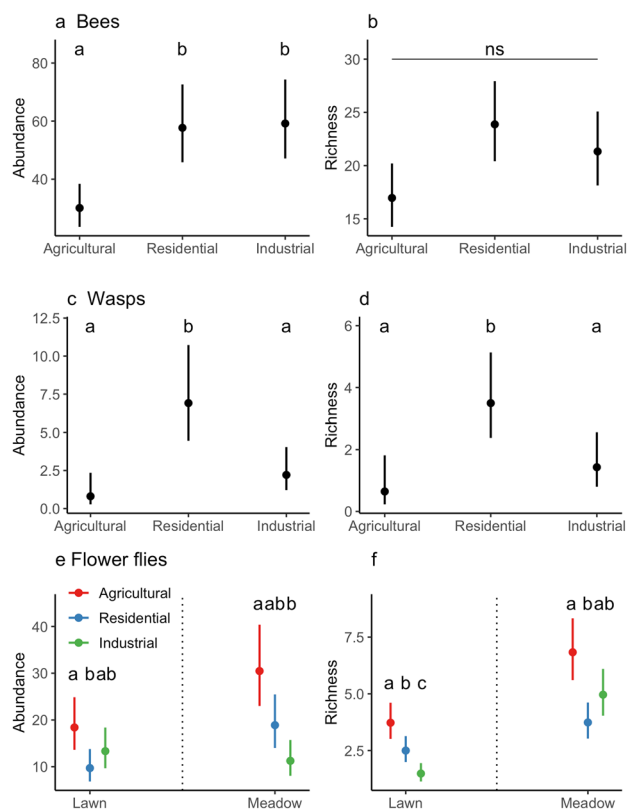


Fig. 2 Means and 95% confidence intervals of the abundance (a, c, e) and species richness (b, d, f) of bees, wasps and flower flies for each landscape (agricultural, residential and industrial) and the interaction with green space maintenance (e, f) estimated by a generalized linear model. Means with different letters differ significantly (Tukey <math>P < 0.05</math>)

[27.2, 34.4], wasp abundance: 7.96 [5.59, 11.33], wasp richness: 3.71 [2.72, 5.06]) (Table 3, Fig. 3). For flower flies, their abundance was 1.6 and 2 times higher in agricultural and residential meadows respectively, than in lawns, while it was similar between meadows and lawns in industrial landscapes. Flower fly richness was higher in meadows (5.02 [4.46, 5.65]) than in lawns (2.40 [2.09, 2.76]) (Fig. 3).

From a temporal perspective, the abundance, and species richness of bees between landscapes were only distinguishable from early July to late August (Fig. 4). The trend varied over time, but residential and industrial landscapes generally had a greater abundance and richness than agricultural settings during this time frame (Fig. 4). Flower fly abundance was relatively stable in lawns over time, while it increased in meadow at the end of August, widening the gap between the two green space maintenance at this moment (Fig. 4).

Beta diversity and shifts in species composition

Landscape matrices did not affect the beta diversity of any pollinator groups (Table 4, Fig. 5). Yet, beta diversity of bees was higher in lawns than in meadows (Table 4, Fig. 5),

indicating that bee species composition was more variable among lawns than among meadows.

Species composition of wasps and flower flies was similar across landscape matrices (Table 4, Fig. 4). In contrast, bee species composition varied across landscapes (Table 4, Fig. 5). A change in species composition was observed along the landscape gradient, from agricultural to industrial (Fig. 5), with communities associated to residential landscape intermediate to the two others. *L. ephialtum*, *L. pilosum*, *L. planatum*, *L. sagax*, *Hylaeus modestus*, *Melissodes desponsa* and *B. impatiens* were associated with industrial/residential landscapes (RDA; adjusted $R^2 = 0.07$, first two axes $P = 0.0008$ and 0.0329 ; Fig. 6), while *Ceratina mikmaqi*, *Andrena commoda*, *A. wilkella*, *Bombus ternarius*, *Chelostoma rapunculi* and *Lasioglossum zonulum* (Fig. 6) were rather found in agricultural/residential landscapes.

Bee and flower fly species composition differed between lawns and meadows, while wasp community composition did not (Table 4, Fig. 5). For bees, mainly *Lasioglossum* species, such as *L. ephialtum*, *L. planatum*, *L. pilosum* and *L. sagax*, were associated with lawns (adjusted $R^2 = 0.08$, axis $P = 0.0001$; Fig. 6). This genus represented 73% of the specimens sampled in lawns compared to 42% in meadows. More bee species were associated with meadows compared to lawns, such as *L. lineatulum*, *Halictus rubicundus*, *Hylaeus* spp., *Bombus* spp., *Megachile frigida*, *Augochlorella aurata*, *Ceratina mikmaqi* and *Chelostoma rapunculi* (Fig. 6). Among flower flies, only *T. marginatus* was related to lawns (RDA; adjusted $R^2 = 0.19$, axis $P = 0.0001$; Fig. 6). This species was indeed dominant in lawns and represented 79% of flower fly captures compared to 40% in meadows. In contrast, several flower fly species were associated with meadows (Fig. 6).

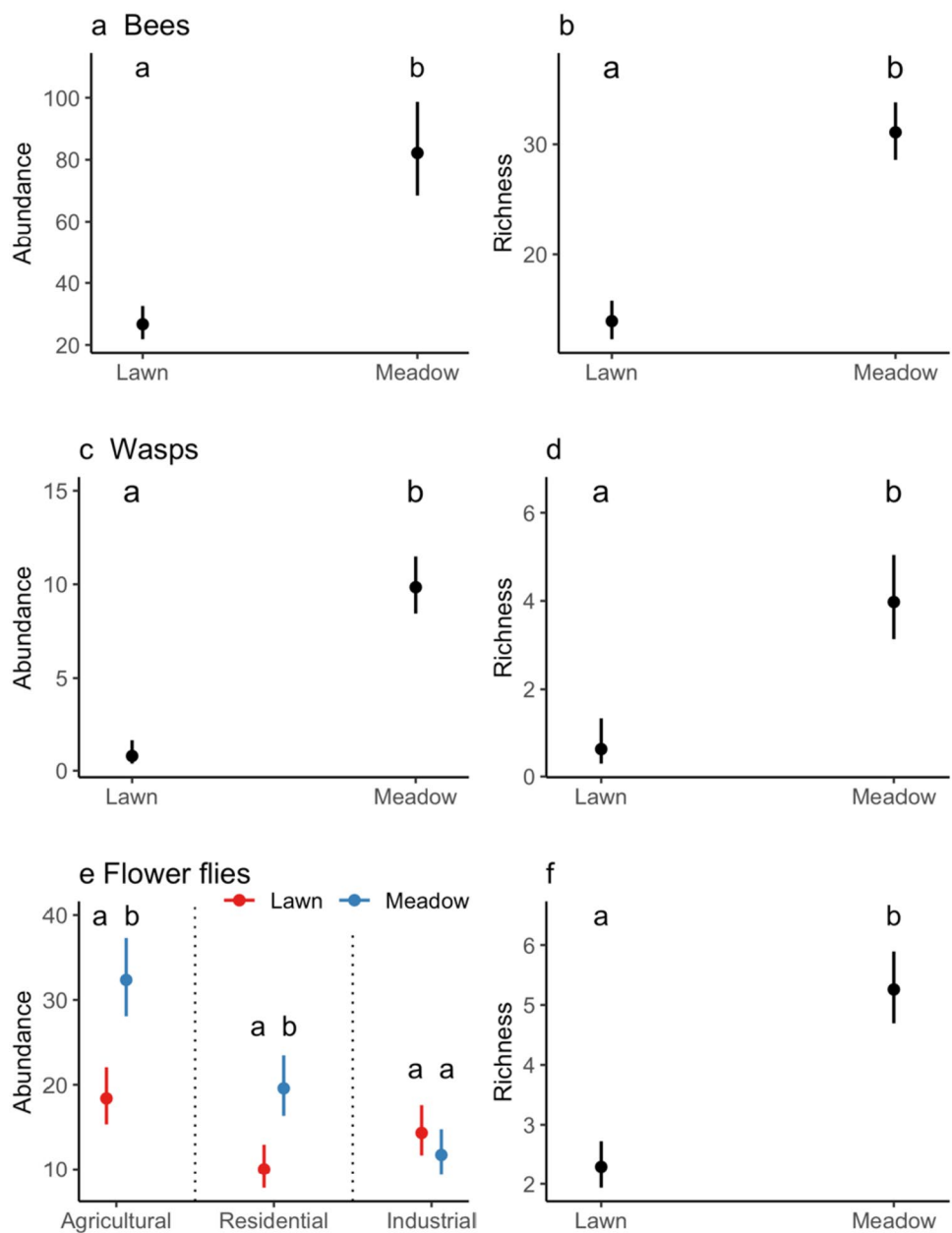
Species turnover and richness difference

Considering both lawns and meadows of each landscape matrix, variation in bee composition was mainly due to species turnover, and secondly richness difference, meaning that species captured in both lawns and meadows differed from site to site (Table 5). Variation in wasp species composition among lawns was mainly due to species turnover (Table 5), while in meadows species composition varied slightly more by richness difference (Table 5). Among the few captures of wasps on lawns, most were of meadow abundant species: *Vespa maculifrons*, *V. alascensis* and *Polistes dominula*. For flower flies, turnover was generally more important than species richness to explain composition variation, except for lawns in industrial landscapes (Table 5).

Availability of floral resources

The flower cover estimated for the season was greater in meadows (mean cover of ~5–10% per site) compared to lawns (<1%)

Fig. 3 Means and 95% confidence intervals of the abundance (a, c, e) and species richness (b, d, f) of bees, wasps and flower flies for each site maintenance (lawn and meadow) and the interaction with landscape (e) estimated by a generalized linear model. Means with different letters differ significantly (Tukey <0.05)

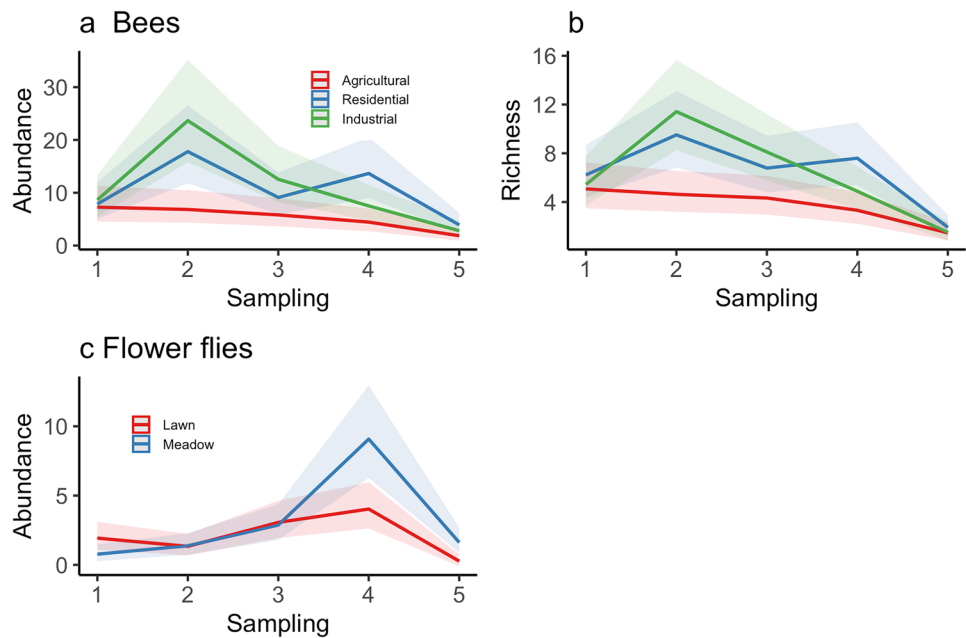


(Fig. 7). This difference strengthened over the season: the abundance of floral resources in lawns remained low throughout the summer, below 1% cover, while for meadows, it increased with time. In June, blooming plant cover in meadows (around 1–5%) was slightly higher to lawns (<1%) (Fig. 7) and then gradually increased up to 10–25% of the cover in August and remained stable until mid-September. We identified a total of 139 blooming plant species, 28 strictly associated with lawns, 65 with meadows, and 46 shared species. Over the season, lawns had an average of 11.42 [8.96, 14.57] blooming plant species per site, while meadows hosted on average 20.80 [17.39, 24.88] species

(Fig. 7). This difference was only significant over the season, but the gap faded when sampling was a factor considered. This was due to the return of the same species on the lawns from one sampling to the next, whereas different species emerged on the meadow over time.

Species composition of flowering plants was affected by the landscape matrix and site maintenance in interaction (PERMANOVA; interaction $P=0.0394$). Species composition of lawns differed from that of meadows and a lesser fraction of compositional variability was caused by the change in meadow species across landscape matrices (Fig. 6). The following

Fig. 4 Means and 95% confidence intervals of the abundance (a, c) and species richness (b) of bees and flower flies for landscape matrix (a, b) and site maintenance (c) according to the sampling date estimated by a linear mixed model (a, b) and a generalized linear model (c). Sampling date: 1 = beginning of June, 2 = beginning of July, 3 = end of July, 4 = end of August and 5 = mid-September



species were associated with lawns: *Prunella vulgaris*, *Trifolium repens*, *Oxalis stricta*, *Taraxacum officinale* and *Medicago lupulina* (RDA; adjusted $R^2=0.26$, axis 1 $P=0.0001$, axis 2 $P=0.0001$; Fig. 6). The plant species most common on meadows were *Solidago* spp., *Symphytotrichum lanceolatum*, *Vicia cracca*, *Ranunculus acris*, *Lathyrus pratensis*, *Tanacetum vulgare*, *Hypericum perforatum*, *Daucus carota*, *Cichorium intybus* and *Lythrum salicaria* (RDA; adjusted $R^2=0.26$, axis 1 $P=0.0001$, axis 2 $P=0.0001$; Fig. 6).

Table 4 Difference in beta diversity (a) and composition (b) according to maintenance level (lawn vs. meadow) and landscape matrix (agricultural, residential, and industrial)

		a. Beta diversity		b. Composition	
		F-ratio	P	F-ratio	P
Bees	Landscape (L)	2.171	0.127	2.795	0.0001
	Site maintenance (S)	9.766	0.002	5.544	0.0001
	L x S			1.133	0.267
Wasps	Landscape (L)	0.358	0.697	0.622	0.843
	Site maintenance (S)	2.033	0.160	0.896	0.489
	L x S			1.409	0.149
Flower flies	Landscape (L)	0.459	0.636	1.864	0.060
	Site maintenance (S)	1.890	0.178	10.245	0.0001
	L x S			1.843	0.063

Bold indicates significant results ($P < 0.05$)

Beta diversity was evaluated using permutation tests for homogeneity of multivariate dispersion (dispersion around centroid) and composition with permutational multivariate analysis of variance (centroid location)

Discussion

Our study aimed to disentangle the effects of landscape matrices (agricultural, residential, and industrial) and site maintenance (lawn and meadow) on pollinator communities in managed ecosystems. We found that both landscape matrix and site maintenance structure bee, wasp, and flower fly communities. Bee abundance were negatively associated with agricultural areas compared to residential and industrial environments and this effect is particularly marked in mid-season, from early July to mid-August. Although the effect of landscape on richness was absent for the overall season, mid-season was also marked by lower bee richness in agricultural landscape compared to urban ones. Wasps were more abundant and species-rich in residential landscapes compared to agricultural and industrial settings. The link between flower flies and landscapes was not straightforward, but the tendency was for the agricultural environment to host a greater abundance and species richness than urban environments. Our results also showed that landscape matrices tended to harbor different bee species. As expected, we found that meadows supported a higher abundance and species richness of bees and wasps than lawns. Flower fly abundance was also higher in meadows than in lawns, apart from those located in industrial environments. Flower fly richness was always higher in meadow than in lawn. The latter also selectively favored a limited number of adapted bee (*L. epihaltum*) and flower fly (*T. marginatus*) species.

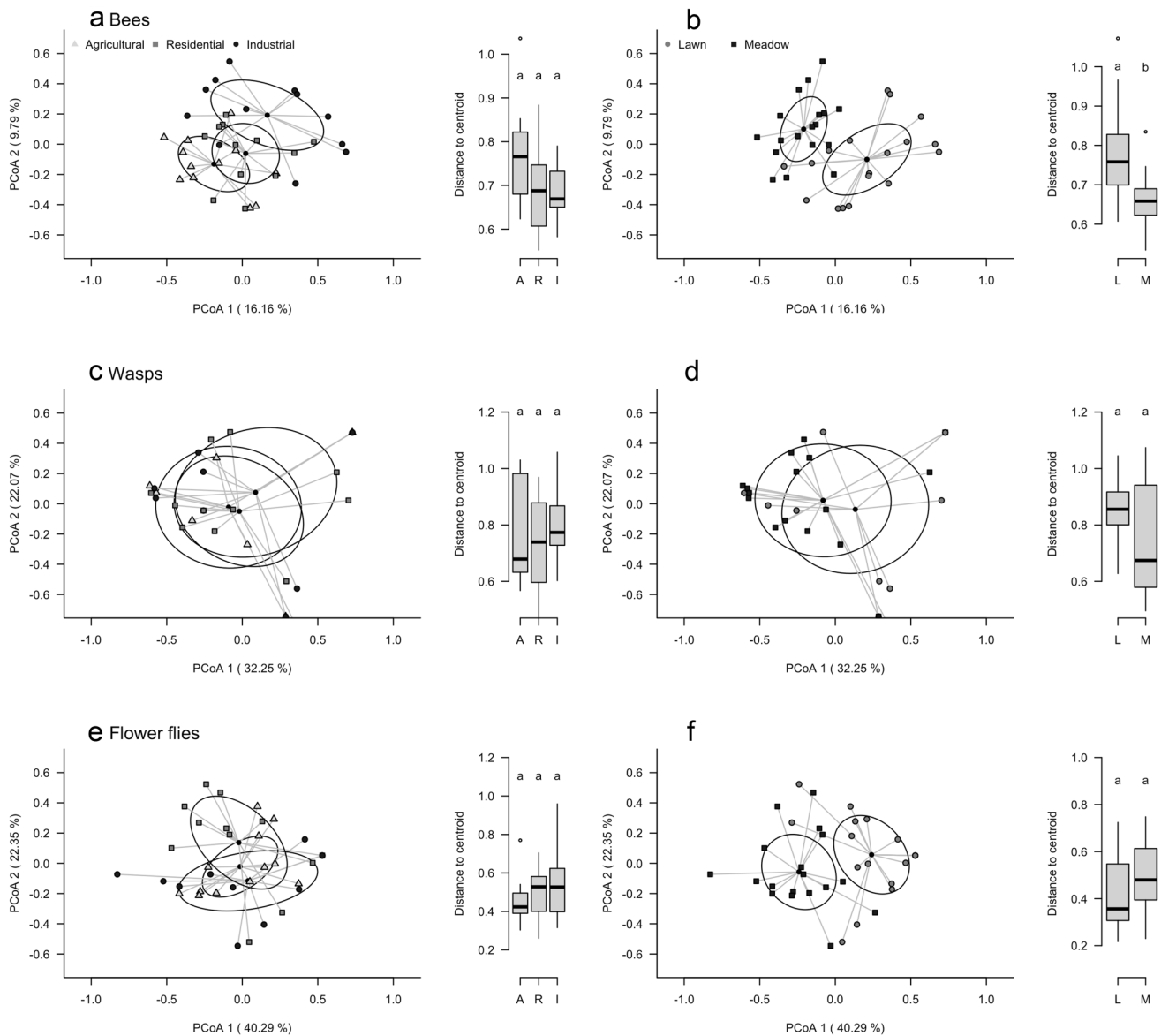


Fig. 5 Variation in species composition and beta diversity with landscape matrix (agricultural (A), residential (R) and Industrial (I); **a**, **c**, **e**) and site maintenance (lawn (L) and meadow (M); **b**, **d**, **f**) for bees, wasps, and flower flies. Beta diversity is estimated based on the distance of sites to their group centroid; this value is presented in the boxplots and by the dispersion of sites on the PCoA. A shift

in location of centroids shows a variation in community composition. To facilitate analysis, ellipses showing the standard deviation of the position of the centroids were plotted. Prior to analysis, the community matrix was transformed to obtain the Hellinger distance between sites. Means with different letters differ significantly (Tukey < 0.05)

Landscape matrix

Our results showed a reduction in bee abundance and richness (in mid-season only) in agricultural matrices compared to urban areas (residential and industrial), even if the mean proportion of semi-natural environment (forest and meadows) in the surroundings of our sites was similar between landscape matrices. Wasps also showed a decrease in abundance and richness in agricultural landscapes, but only when compared to residential areas. The 52%

of cultivated land around sites in agricultural landscapes (Table 1) may have a direct impact on forage and nesting availability by restricting ground nesting, offering little or no substrates for aerial nests and limiting floral resource quantity as well as its temporal availability. Indeed, intensive agricultural practices can involve insecticide and herbicide use, intensive tillage (Harmon-Threatt 2020), and lead to simplification of the landscape through the establishment of large monocultures, as well as loss of semi-natural areas, causing pollinator decline (Kremen et al. 2002).

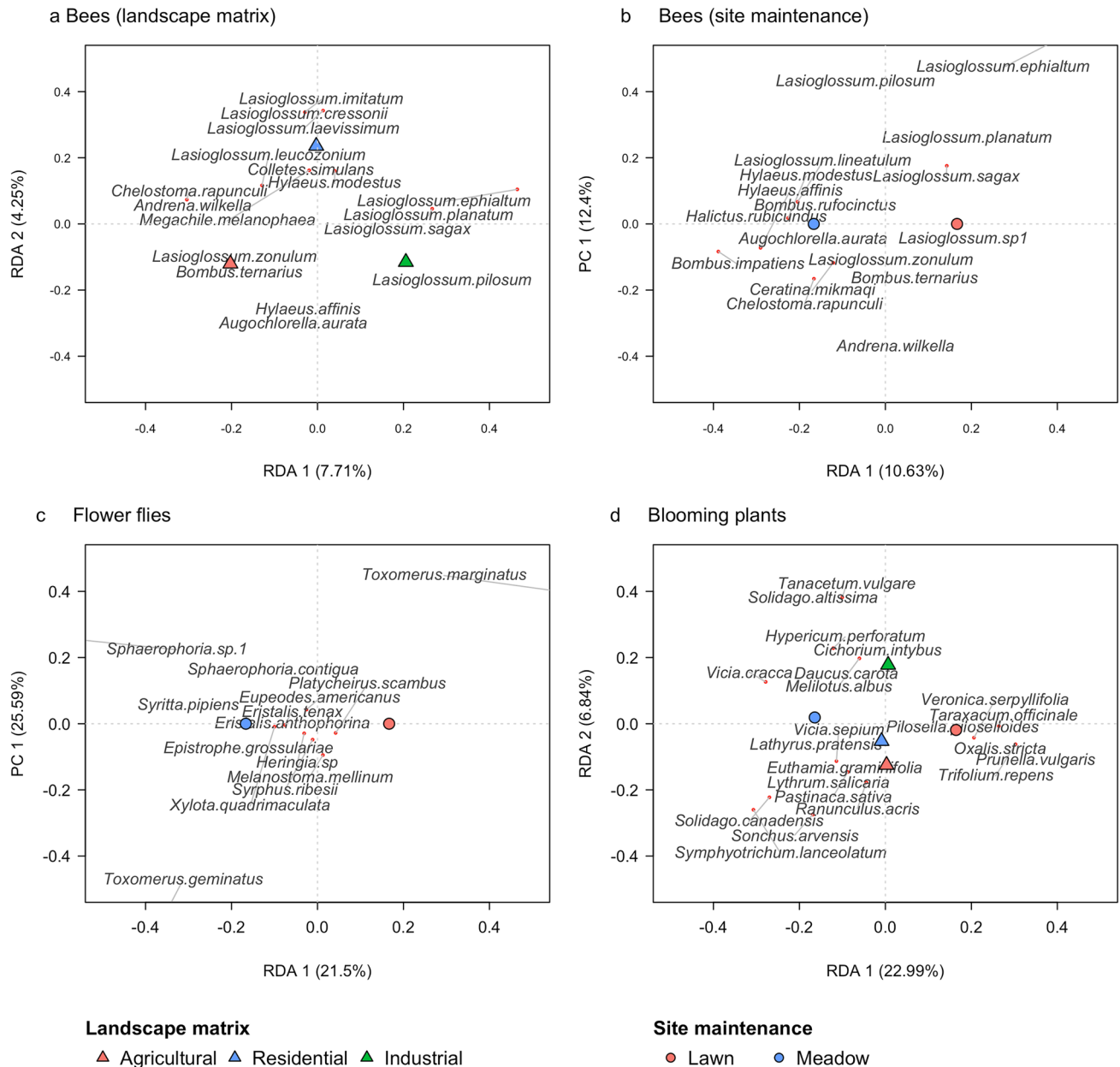


Fig. 6 Redundancy analysis (RDA) ordination relating landscape matrix (a), site maintenance (b, c) or the interaction of both factors (d) (circles and triangles show the landscape matrix and site maintenance centroid) and species (red dots were used to avoid overlapping species names) for bees (a, b), flower flies (c) and blooming plants (d). Only species most fitted to the model are shown

Residential and industrial landscapes equally supported bee abundance and richness. Industrial landscapes were characterized by large impervious surfaces covering more than half of their area. Still, 40% of them were covered by forest fragments, urban trees, lawns, and meadows which offer resources that can maintain bee diversity. Contrary to our results, Burdine and McCluney (2019) observed a decline in bee diversity with impervious cover with a cumulative effect for resource-poor sites. For the case of industrial landscapes in our study area, bee communities

did not seem hindered by an average of 60% impervious cover (compared to ~35% impervious cover in residential matrices). Residential and industrial matrices also hosted specialist pollinators in similar proportions (4% of captures in each landscape) and shared substantially the same species, including *Lasioglossum planatum*, *Perdita octomaculata* and *Melissodes desponsa* (Normandin et al. 2017). Our results are consistent with those suggesting that urban environments, offering open and early successional habitats (Winfree et al. 2011) and ornamental flowers (Erickson et al.

Table 5 Partition of beta diversity (BD) into turnover and species richness difference (reported as a percentage of total beta diversity) for all sites and among site maintenance (lawn and meadow) of each landscape matrix (agricultural, residential, and industrial) for bees, wasps, and flower flies

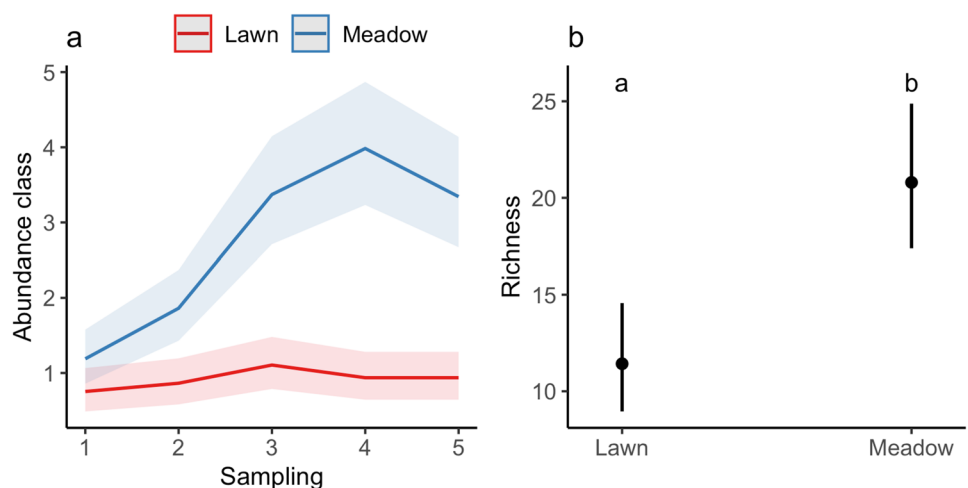
			<i>BDtotal</i>	<i>Turnover (%)</i>	<i>Richness difference (%)</i>
Bees	<i>All sites</i>		0.3292	56	44
		<i>Agricultural</i>			
		<i>Lawn</i>	0.3951	67	33
		<i>Meadow</i>	0.2623	66	34
	<i>Residential</i>	<i>Lawn</i>	0.3318	68	32
		<i>Meadow</i>	0.2536	70	30
	<i>Industrial</i>	<i>Lawn</i>	0.2587	63	37
		<i>Meadow</i>	0.2615	68	32
Wasps	<i>All sites</i>		0.3694	48	52
		<i>Agricultural</i>			
		<i>Lawn</i>	-	-	-
		<i>Meadow</i>	0.394	49	51
	<i>Residential</i>	<i>Lawn</i>	0.3744	72	28
		<i>Meadow</i>	0.3146	39	61
	<i>Industrial</i>	<i>Lawn</i>	0.4167	1	0
		<i>Meadow</i>	0.376	40	60
Flower flies	<i>All sites</i>		0.2341	37	63
		<i>Agricultural</i>			
		<i>Lawn</i>	0.2106	66	34
		<i>Meadow</i>	0.2075	65	35
	<i>Residential</i>	<i>Lawn</i>	0.2467	58	42
		<i>Meadow</i>	0.1947	71	29
	<i>Industrial</i>	<i>Lawn</i>	0.1333	25	75
		<i>Meadow</i>	0.188	58	42

2020), have the potential to support a high diversity of bees (Theodorou et al. 2020) compared to landscapes dominated by cultivated land.

Residential environments positively affected wasp abundance and richness compared to industrial and agricultural areas, despite efforts of citizens to destroy nests near their residences. This suggests that residential areas offer more food resources, nesting substrates or less natural enemies for wasps compared to the two other landscape matrices. Many human-made residential constructions provide numerous opportunities for nesting, such as the eaves of houses, attics, sheds, fences, and garages (Akre et al. 1981). A few species

effectively use these structures as well as natural substrates, facilitating their survival within urban environments (Silagi et al. 2003). This is the case of the exotic species *Polistes dominula*, which was much more abundant than its native counterpart *Polistes fuscatus* in urban areas, partly due to the ability of the former for seeking out human-made structures for nesting (Silagi et al. 2003). Sorvari (2018) also suggested that several species of wasps, such as *Vespula germanica*, are attracted to urban centers for their warmer climate than rural area, but our study shows that, despite higher potential of industrial areas as heat islands (CERFO 2013), the lack of nesting resources seems to be a more limiting factor for

Fig. 7 Means and 95% confidence intervals of the flower abundance class (a) for each site maintenance (lawn and meadow) and sampling date and the species richness (b) of blooming plant pooled over the season for each site maintenance (lawn and meadow). Means with different letters differ significantly (Tukey < 0.05). Sampling date: 1 = beginning of June, 2 = beginning of July, 3 = end of July, 4 = end of August and 5 = mid-September



wasp establishment, making this matrix less hospitable than residential areas.

Bee species composition varied mainly between agricultural and industrial environments, while residential environment hosted species found in both landscapes. Some species adapt better to urban centers, while others prefer agricultural or rural environments (McCune et al. 2020; Verboven et al. 2014). Agricultural environments are usually stressful for most bees, but *Bombus ternarius*, *Lasioglossum zonulum*, *L. novascotiae*, *Andrena wilkella* and *Chelostoma rapunculi* seemed to thrive better there than in industrial environments. In contrast, some small species of *Lasioglossum* (*Dialictus*) were more related to residential and industrial landscapes and were virtually excluded from agricultural areas. Small species are generally less abundant in dense urban settings where feeding and nesting sites are far apart, as they disperse less efficiently (Birdshire et al. 2020; Greenleaf et al. 2007) but this was not the case in our study, possibly because our sampled industrial (~59% impervious) and residential landscapes (~36% impervious) were not densely built. This suggests that the habitat connectivity in the industrial and residential landscapes in our study region was similar and sufficient to allow the movement of species with low dispersal ability. The low abundance of some small species of *Dialictus* bees in agricultural landscape could be due to a long distance between suitable feeding or breeding sites, or to a reduced fitness of individuals caused by agricultural operations (chemical agents, soil tilling, etc.). Moreover, environment heterogeneity is a key factor in diversifying the forage and nesting resources supply, therefore attracting different taxonomic and functional groups (McCune et al. 2020). Residential neighborhoods potentially offer greater heterogeneity in terms of resources for foraging or nesting, attracting communities of bees associated with both agricultural and urbanized landscapes.

Despite the different characteristics of agricultural, residential, and industrial landscapes, the relationship between abundance and richness of flower fly with the landscape category was not straightforward and was influenced by the type of green space maintenance. In general, abundance and richness were higher in agricultural than in residential and industrial landscapes. This may be due to a higher prey diversity for larvae in agricultural compared to urban landscapes (e.g. a greater abundance of aphids) (Udy et al. 2020). However, lawns in industrial landscapes and meadows in residential areas had comparable flower fly abundance than agricultural landscapes, while meadows in industrial had comparable flower fly richness than agricultural meadows. Thus, urban environment could provide prey diversity for larvae which facilitates the establishment of communities similar to agricultural environments. This could be due to the high proportion of semi-natural

fragments. Also, flower flies are not central-place foragers, meaning they do not return to a nest with resources, instead moving more freely between forage sites (Rader et al. 2016) and they have a good dispersal ability (Udy et al. 2020). Consequently, flower flies easily navigate the landscape and reach food sources (Rader et al. 2016), which could explain the variability of results when comparing agricultural and urban landscapes.

Site maintenance

Our results indicated that the studied lawns were somewhat attractive to some bee species and flower flies. Common flowering weeds in lawns are attractive to pollinators (Larson et al. 2014). For example, open, shallow dandelion flowers can attract small-mouthed pollinators, while clovers, which have deeper corollas, commonly attract long-tongued pollinators (Larson et al. 2014). Lawn flowering weeds, which bloom several times from spring to autumn, benefit pollinators by providing foraging resources and improving the connectivity across green spaces when they remain unmowed (Lerman and Milam 2016). However, the generally complex plant communities and greater abundance of floral resources in meadows, as compared to lawns, attracted more bee, wasp and flower fly individuals and species. Plant population density increases the attractiveness: a single blooming plant is less attractive to pollinators and will be less visited than a dense patch (Fowler et al. 2016); meadows are thus more likely to be noticed and visited by pollinators than lawns. Moreover, meadows also reduce the energy cost of flower foraging activity by decreasing the trip duration required to gather sufficient resources because of greater abundance of flowers (Gathmann and Tscharrntke 2002).

Meadows offer more insect prey for consumption by wasp and flower fly larvae (Francoeur et al. 2021) making it more likely that organisms will choose meadow for feeding rather than lawns. Indeed, adult wasps supply the nest with predated insects and syrphid larvae depend on variable food sources to ensure their development (phytophagous, zoophagous or saprophagous) (Bańkowska 1980; Cervo et al. 2000; O'Neill 2001). The greater arthropod diversity of meadows (Francoeur et al. 2021; Norton et al. 2014) constitutes a more complex food web that can provide more rewarding sites than lawns on which to forage for prey. We observed a low wasp abundance in lawns with a species composition that mainly varied due to species turnover, meaning that turning to lawn resources is probably an opportunistic and uncommon behavior among wasps.

Due to the different resources provided by lawns versus meadows, bee, and flower fly species composition was dissimilar in those environments. *Lasioglossum* bees (mainly *Dialictus* subgenus) dominated the lawn inventory, indicating that they predominantly attract small-bodied, ground

nesting, and polylectic species (Packer et al. 2007), as observed by Lerman and Milam (2016). Fewer individuals of *Bombus* spp., which depend on resources throughout the season, and *Andrena* spp. (mainly *A. wilkella*), active in spring, were observed on both lawns and meadows. As meadows are not at the peak of their floral productivity in the spring, lawns are potentially an appealing foraging alternative for early active pollinators such as those genera. Also, as most bees captured in lawns have a short dispersal range from their nest (Greenleaf et al. 2007), bare soil within lawns (observed at 15 out of 18 lawn sites) could provide a substrate for building ground nests (Harmon-Threatt 2020; Lerman and Milam 2016). Among flower flies, *T. marginatus* dominated communities in lawns and was present at all sites. This species is adapted to a variety of habitats and has been observed as dominant in cranberry fields (Gervais et al. 2018). Our results confirm that many *Lasioglossum* (*Dialictus*) species and *T. marginatus* can take advantage of environments with low floral resources.

Bee and flower fly communities hosted by meadows were more diverse than those within lawns. *Lasioglossum* species were also abundant, but less dominant in meadows than in lawns. Both lawns and meadows attract several soil nesters, but meadow plant communities tend to favor a different pool of species. *Bombus* spp. were seven times more abundant in meadows than in lawns, with *B. impatiens*, *B. rufocinctus* and *B. bimaculatus* particularly associated to it. Bumblebees have higher energy needs and require more resources to feed their colony than solitary bees (Packer et al. 2007); they prioritize resource-rich habitats, but occasionally use scarce resources from lawns. Species of *Hylaeus*, *Chelostoma* and *Ceratina* genera were mostly found in meadows. These genera are often observed nesting inside hollow stems (Packer et al. 2007). *Rubus* spp. and *Rhus thyphina*, which were frequently present in the meadows sampled (observed on 12 out of 18 sites) compared to lawns (2 out of 18), can provide nesting sites inside their stems, promoting the presence of these bee genera in their surroundings (Lerman and Milam 2016; Packer et al. 2007). Among flower flies, community structure showed a weaker dominance of *T. marginatus* within meadows. Hence, other species such as *T. geminatus*, *Sphaerophoria* spp., and *Syrirta pipiens* were also abundant. Our results confirm that meadows provide floral and nesting substrates that attract and support diverse pollinator communities within fragmented urban and agricultural landscapes.

Contrary to our expectations, lawns supported more variable bee communities between sites than meadows (higher beta diversity). A core of common species, such as *Lasioglossum* species, was frequently observed using lawn resources, occasionally and circumstantially joined by other species, causing a higher variability between sites compared

to meadows. Spontaneous vegetation in lawns can thus offer valuable alternative resources to those sporadic visitors.

Implications for conservation

The agricultural sites had low impervious cover (less than 10% on average of the 1-km buffer around the sampling site) and a marked increase in agricultural land (around 50% of the area on average) compared to urban sites, but those landscapes have similar forest and meadow cover. This suggests that agricultural land cover is the cause, as mentioned by other authors, for a lower abundance and richness of pollinating insects, including bees and wasps, possibly caused by high mortality rates, due to the destruction of ground nests, the lack of surface for aerial nests and contamination by chemical agents (Harmon-Threatt 2020; Kremen et al. 2002). Agricultural methods that harm pollinator communities should be limited (e.g. by employing organic methods). In addition, meadows still encourage a greater diversity of insects in agricultural environments and should be favored over lawns or to replace some cultivated areas. Such measures could increase the diversity of wild pollinators and reduce both our dependence on honeybees for crop pollination as well as the use of pesticides to regulate insect pests by fostering the spillover of beneficial insects from adjacent rich environments (Kremen et al. 2002; Prezoto et al. 2019).

Lawns are particularly appreciated for their aesthetics and recreational possibilities (Ignatieva et al. 2015). Yet, they host poorer pollinator communities compared to meadows. If part of them is converted to meadows, pollinator biodiversity would be fostered with minimal impact on urban and suburban dwellers. In cases when converting is not possible, incentives should be put in place to increase wild-flower presence on residential lawns (by reducing mowing frequency) to preserve the ecological value of lawns since our results indicated they can provide alternative resources, including some spring-flowering species. Residential environments have a strong potential to attract a diverse community of pollinators compared to other managed ecosystems. The impressive lawn cover in residential matrices offers a great opportunity to increase the abundance of pollinating insects if lawns are converted to meadows, enhancing the resilience of insect communities, and encouraging the spillover of beneficial insects from urbanized to adjacent agricultural areas. Ideally, meadows conceived for biodiversity conservation should be mowed infrequently and section by section to maintain refuge sites and avoid creating ecological traps (Buri et al. 2014). Finally, as the composition of pollinator communities varies widely due to species turnover, we recommend sites in different landscapes to be targeted for conservation, to preserve a greater number of taxonomic and functional groups.

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Author contributions S.C., P.M., J.C.-M., S.P., and M.P. participated in the conception of the experimental design. All authors developed the methodology. S.C. did the data collection and analysis and wrote the original draft of the paper. All authors have reviewed drafts of the paper.

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Data availability The data that support the findings of this study are available in Appendix 4 of the supplementary material.

Declarations

Competing interests The authors declare no competing interests.

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