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World Bee Day pollinators in urban environments 2022

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World Bee Day 2022: Pollinators in urban environments

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Pollinator cultivar choice: An assessment of season-long pollinator visitation among coreopsis, aster, and salvia cultivars

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Documented pollinator declines have encouraged the installation of pollinator plantings in residential, commercial and agricultural settings. Pollinator visitation among cultivars of coreopsis, salvia and asters was compared on 40 dates in a 2-year study resulting in 6,911 pollinator observations across all plant taxa with bees, butterflies and syrphids well-represented. Diversity of insect visitors was represented differently within the broad plant taxa salvia, coreopsis and asters. The most frequent visitors to coreopsis were the small bees with over 77% of visitors falling into this category. Salvia was most frequently visited by honey bees (36.4%) and carpenter bees (24%), although all the groups were represented. Syrphids were the group most commonly observed on asters (58.5%) with nearly 40% of the visitors being bee species. Nectar analysis was performed on salvia cultivars. However, differential attraction of pollinators to salvia cultivars could not be explained by volume of nectar produced per plant. Results from our cultivar comparisons provide data-based information to assist consumers in plant choice and present opportunities for future plant-specific pollinator census initiatives across a broader geographic range.

KEYWORDS

biodiversity conservation, ecosystem services, bees, perennials, cultivar choice, ornamentals, pollinators

Introduction

Attracting beneficial arthropods to garden and landscape areas can increase insect biodiversity, promote arthropod-mediated ecosystem services, and overall ecological health (Häussler et al., 2017). Documented pollinator declines have encouraged the installation of pollinator plantings in residential, commercial and agricultural settings. An analysis of wild bee population dynamics over time (Turley et al., 2022) found that about one third of bee species showed at least some evidence of decline in a 6-year span. Prendergast et al. (2022) conducted a comprehensive review of native bee assemblages in urban landscapes, reviewing 215 studies. Recommendations from their review included having plant managers (gardeners, homeowners, nurseries and landscape managers)

TABLE 1 Bee species collected in 2017 and 2018, from ornamental cultivar trials in the University of Georgia Research and Education Garden (Spalding Co., GA; 33°24′67″N, 84°26′40″W).

Species	Asters	Salvia	Coreopsis	Total	Months collected
Andrenidae					
Calliopsis andreniformis Smith, 1853	5	26	0	31	Aug–Sep
Halictidae					
Agapostemon virescens (Fabricius, 1775)	0	1	0	1	Aug
Augochlora pura (Say, 1837)	2	0	0	2	Oct
Halictus ligatus/poeyi Say, 1837	63	18	28	109	Jun–Oct
Lasioglossum spp.	18	38	15	71	May–Oct
Megachilidae					
Megachile exilis Cresson, 1872	0	2	0	2	May, Jun
Megachile mendica Cresson, 1878	0	3	0	3	Jun, Aug
Megachile petulans Cresson, 1878	0	1	0	1	Jun
Megachile rotundata (Fabricius, 1787)	1	0	0	1	Oct
Apidae					
Ceratina calcarata Robertson, 1900	0	0	1	1	Jul
Ceratina cockerelli H. S. Smith, 1907	0	3	6	9	Jun–Sep
Ceratina strenua Smith, 1879	0	1	6	7	Jul, Jun
Xylocopa micans Lepeletier, 1841	0	1	0	1	Jul
Xylocopa virginica (Linnaeus, 1771)	0	7	0	7	Jun–Aug
Bombus bimaculatus	0	8	0	8	May, Jun, Aug
Bombus griseocollis	0	2	0	2	Jun, Jul
Bombus impatiens Cresson, 1863	7	10	0	17	May–Oct
Bombus pensylvanicus DeGeer, 1773	0	23	0	23	May–Sep
Holcopasites calliopsidis (Linsley, 1943)	0	2	5	7	May–Jul
Apis mellifera Linnaeus, 1758	0	2	0	2	Jun
Melissodes tepaneca Cresson, 1878	0	1	0	1	Jul
Melissodes dentiventris Smith, 1854	2	5	0	7	May–Jul, Sep, Oct
Melissodes druriellus Kirby, 1802	10	2	0	12	Jun, Jul, Oct

focus on flowers that have been demonstrated to be visited by wild bees in the region, especially native species.

Regionally appropriate plant lists of trees, shrubs and flowers that attract and support pollinators are good resources to consult for landscape design or renovation (e.g., Harris et al., 2016; Braman et al., 2017; Braman and Quick, 2018; Mach and Potter, 2018; Smitley et al., 2019). Non-native, non-Apis bees were determined to be significantly more abundant visitors to non-native vs. native plants, especially *Osmia* taurus Smith and *Megachile sculpturalis* (Smith) (Potter and Mach, 2022). Those offers suggested that planting of favored non-native hosts could have the unintended consequence of facilitating the spread of non-native, non-*Apis* bees in urban areas. As improved propagation methods facilitate breeding and production (Lewis et al., 2020) and our understanding of the influence of cultivars vs. species increases (Poythress and Affolter, 2018), more native plant species and cultivars will become available in the ornamental plant trade that have been bred specifically to attract and support pollinators. Currently there are a great many ornamental plant cultivars available on the market, yet there is little empirical information available to guide consumer choice regarding attractiveness to pollinators (Garbuzov and Ratnieks, 2014; Rollings and Goulson, 2019). Here we present data on the attractiveness of 19 cultivars of salvia, coreopsis and asters.

Materials and methods

Plants and trial plots

This study was conducted at the University of Georgia Research and Education Garden on the UGA Griffin Campus

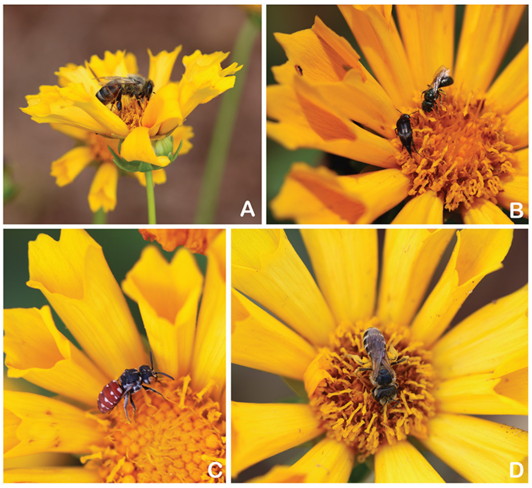

FIGURE 1
Flower visitors observed on coreopsis: **(A)** *Apis mellifera*, **(B)** *Ceratina* sp., **(C)** *Holcopasites* sp., and **(D)** *Halictus* sp.

FIGURE 3
Flower visitors observed on aster: **(A)** *Melissodes* sp., **(B)** *Svastra* sp., and **(C)** Syrphidae, **(D)** Syrphidae.

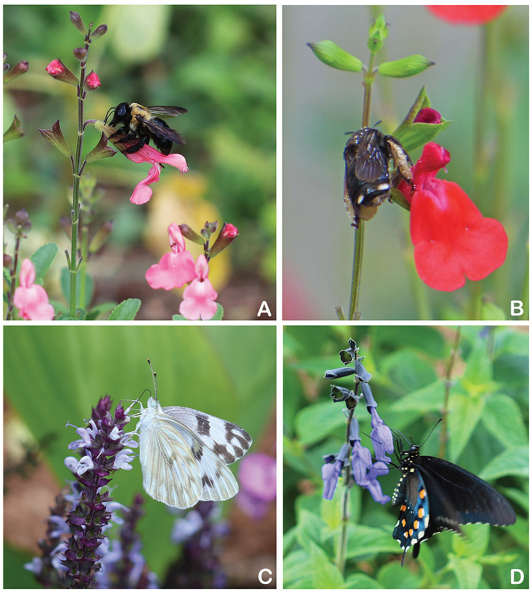

FIGURE 2
Flower visitors observed on salvia: **(A)** *Xylocopa* sp., **(B)** *Melissodes* sp., **(C)** Pieridae, and **(D)** Papilionidae.

(Spalding Co.; 33°24'67"N, 84°26'40"W). Cultivar trial plots were established during fall 2016. Salvia, coreopsis, and aster cultivars were each established in their own separate plots within the 24.3-hectare Research Garden. Plants were chosen to reflect new series and standards in the horticulture industry and commercial availability. Salvia cultivars included in this study were *Salvia greggii* "Radio Red", *Salvia guaranitica* "Black and Blue", *Salvia microphylla* x *greggii* "Heat Wave Blast", "Heat Wave Blaze", "Heat Wave Glitter", "Heat Wave Sparkle" and *Salvia nemorosa* "Steel Blue". Coreopsis cultivars were *Coreopsis lanceolata* hybrid "Desert Coral", a hybrid cross of *Coreopsis auriculata* "Zamfir" (female parent) and *Coreopsis lanceolata* "Early Sunrise" (male parent) "Jethro Tull", *Coreopsis verticillata* Sizzle and Spice? series "Hot Paprika", *Coreopsis* Solanna? "Golden Sphere" and *Coreopsis verticillata* "Sylvester". Aster cultivars were *Ampelaster carolinianus* "Climbing Aster", *Symphyotrichum grandiflorum* "Wild Blue", *Symphyotrichum ericoides* "Heath Aster", *Aster oblongifolius* "Jane Bath", *Aster oblongifolius* "Rachel Jackson", *Aster tataricus* "Jindai" and *Symphyotrichum novae-angliae* "English Countryside". Plants were provided by regional plant nurseries as trade-gallon size transplants and were planted on 0.9 m centers. There were three plants per replication and six to eight replications per cultivar (six asters, seven coreopsis and eight salvia replications × three plants per replication) planted in a randomized complete block design. Blocks were 4.6 m apart. Plots= blocks were mulched with pine bark and drip irrigated with water being applied at first sign of wilt.

Insect observations

Insect observations began at first flowering and were made weekly during the flowering period for 2 years. Observations were made between 1,000 and 1,400 h unless rain or high wind impeded observations. While some pollinators are active before and after this window, it is a standard period for assessment

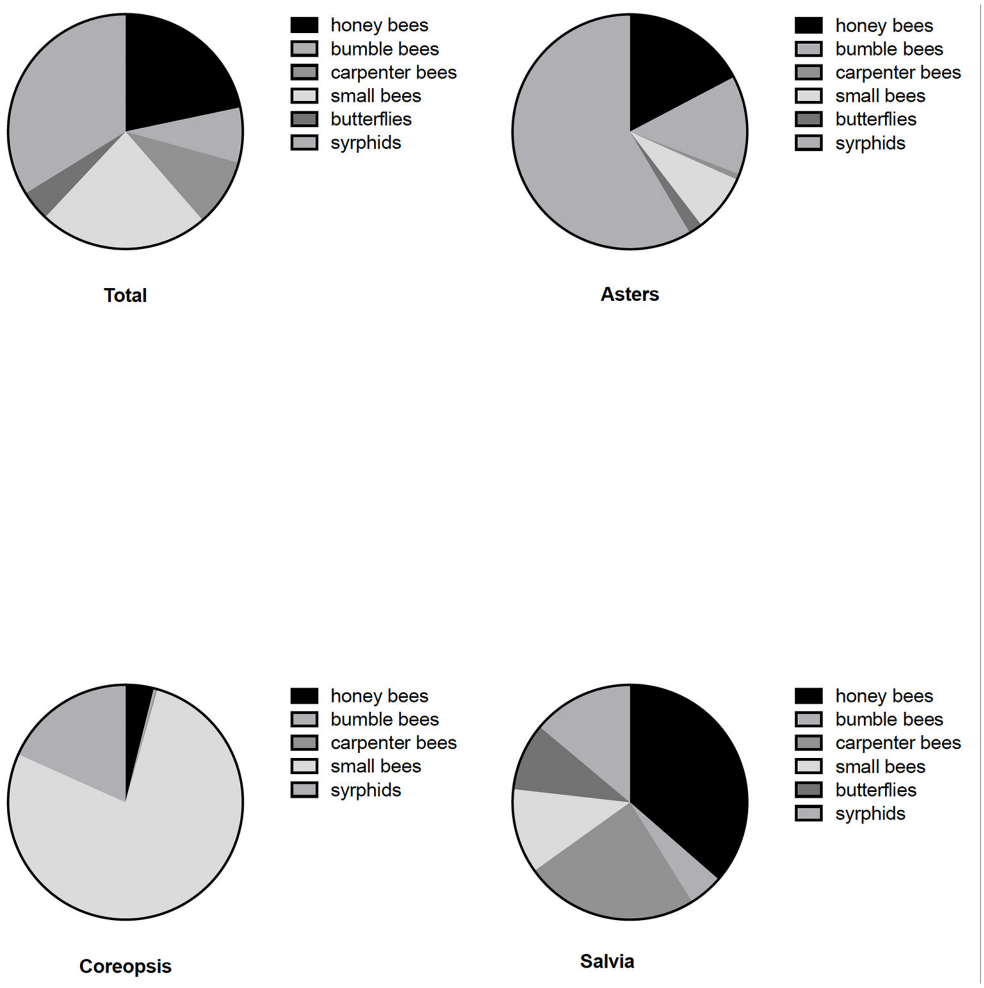

FIGURE 4
Relative abundance of insects in six main groups (legend moves clockwise in each figure) recorded over 2 years at the University of Georgia Research and Education Garden on asters, salvia and coreopsis. More detailed taxonomic breakdowns of bee species are given in Table 1.

when flower visitation is most frequent. All plants that had reached anthesis were observed on the same day. Number of insect visitors during a 1-min time span per replication was recorded in six categories: honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), carpenter bees (*Xylocopa* sp.), small (all other) bees (Hymenoptera), hoverflies (Diptera: Syrphidae) and butterflies (Lepidoptera). Visual observations were recorded on 14 dates for asters in September and October over 2 years, 25 dates for coreopsis from May-August, and 40 dates for salvia from April-October spanning 2 year's growing seasons. Additional hand netting approximately monthly allowed finer taxonomic resolution of some bees visiting the plants. Bees were mounted and identified to the lowest possible taxonomic resolution (Table 1) using a combination of print and online keys (Mitchell, 1960; Bouseman and LaBerge, 1978; http://www.discoverlife.org; Ascher, 2017).

Salvia nectar analysis

In mid-June 2017, five of the salvias were subjected to nectar sampling. *Salvia nemorosa* "Steel Blue" was excluded because by that time, it had passed peak anthesis. For comparison purpose, an additional cultivar, *Salvia microphylla* x *greggii* "Hot Lips" in nearby demonstration gardens was also included in the analysis. Nectar was allowed to accumulate for 24 h in flowers from which insects were excluded by means of fine netting (organza bags placed over five flower spikes per plant). A hand-held refractometer was used to measure sugar content as degrees Brix (°Bx, grams of sugar in 100 g solution). Following methodology by Hicks et al. (2016) microcapillary tubes (5 μL) were used to remove nectar, with individual flowers yielding 2–3 μL of fluid. The refractometer was rinsed with deionized water and dried after each sample. The number of open flowers was counted

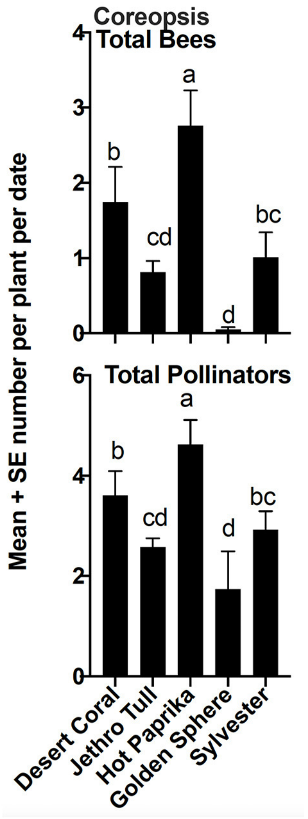

FIGURE 5
Mean ± se total bees and total flower visitors (pollinators) comparison among coreopsis cultivars in a 2-year study in central Georgia, USA. The superscript alphabets means with the same letters are not significantly different, $p > 0.05$.

and recorded for each plant and total sugar content per plant calculated as a product of sugar and number of flowers.

Data analysis

Visual observations of insect visitors to the cultivars were analyzed for each main plant taxon. The data were analyzed using a generalized linear mixed model (PROC GLIMMIX, SAS Institute Inc., 2013). Differences in least square means were determined by pairwise *t*-tests (alpha = 0.05) as the multiple comparisons *post-hoc* test to determine significant differences between levels of all factors. Data from coreopsis, salvia and asters were analyzed separately, and no direct comparison among these main taxa was attempted. Data analysis on salvia flower nectar and number of flowers was performed using ANOVA with mean separation through Tukey's Honestly Significant Difference Test.

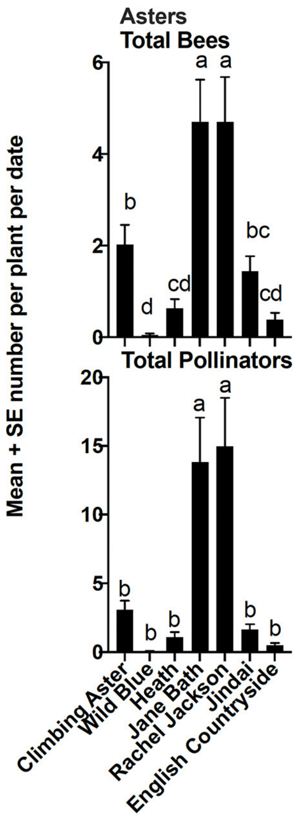

FIGURE 6
Mean ± se total bees and total flower visitors (pollinators) comparison among aster cultivars in a 2-year study in central Georgia, USA. The superscript alphabets means with the same letters are not significantly different, $p > 0.05$.

Results

Insect observations

Data collected during this two-year study comprised 6,911 pollinator observations across all plant taxa with bees, butterflies and syrphids well-represented (Figures 1–3). Relative abundance of insect taxa across all plant taxa and both years (Figure 4) revealed 62% bees, 4.2 % butterflies, and 33.8% hover flies. Among the bees, 21.7% were honey bees, 7.6% were bumble bees, 9.3% carpenter bees and 23.5% other or small bees. This diversity of insect visitors was represented differently within the broad plant taxa salvia, coreopsis and asters (Figure 4). The most frequent visitors to coreopsis were the small bees with over 77% of visitors falling into this category. Salvia was most frequently visited by honey bees (36.4%) and carpenter bees (24%), although all the groups were represented. Syrphids were the group most commonly observed on asters (58.5%) with nearly 40% of the visitors being bee species.

Of the 325 individual bees collected for greater taxonomic resolution, 23 bee species representing four families and 12 genera were collected between February and October from the aster, salvia, and coreopsis flower cultivars and plots (Table 1). Six species were collected from coreopsis cultivars, 20 species from salvia cultivars and eight species from asters. Additional species collected during preliminary sampling in the plot area prior to regular sampling included *Svastra obliqua* (Say) on asters, *Lasioglossum (Dialictus) imitatum* (Smith) on asters and coreopsis, *Lasioglossum (Dialictus) mitchelli* Gibbs on Coreopsis and *Colletes americanus* Cresson on asters.

Relative abundance of the six insect groups evaluated varied significantly among cultivars within plant taxa (Figures 5–7). "Hot Paprika" coreopsis was the most frequently visited cultivar by bees and by total flower visitors ($P < 0.0001$; Figure 5) although all cultivars were visited by the insects of interest. Total bees and total flower visitors were most often and equally observed on "Jane Bath" and "Rachel Jackson" asters among the cultivars evaluated ($P < 0.0001$; Figure 6). Total bees and total flower visitors were most frequently observed on the Heat Wave series cultivar "Blaze" salvia ($P < 0.0001$; Figure 7), with "Glitter" being visited least often by total flower visitors.

While the above-mentioned cultivars were the most or least-frequently visited across the trial period, expected seasonal variation did occur. All salvia cultivars, for example, were visited by pollinators during the course of the 2-year study, with frequency of visitation by cultivar not surprisingly also varying by date ($P < 0.0001$; Figure 8). Cultivar "Steel Blue", for example, was often most frequently visited earlier in the season, corresponding with bloom. "Blaze", the overall most frequently visited cultivar, was more often visited as the season progressed compared to early visitation observed on "Steel Blue".

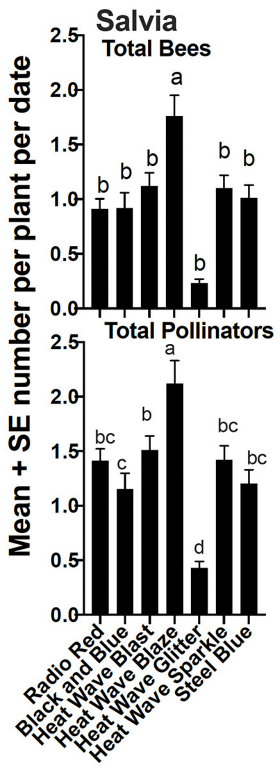

FIGURE 7
Mean ± se total bees and total flower visitors (pollinators) comparison among salvia cultivars in a 2-year study in central Georgia, USA. The superscript alphabets means with the same letters are not significantly different, $p > 0.05$.

Salvia nectar analysis

Nectar sugar content in salvias ranged from 22.9 to 30.4°Bx, and did not differ statistically among the six cultivars ($P > 0.05$; Figure 9). Number of open flowers ranged from 10 to 39, and was highest in *S.* "Radio Red", and lowest in *S.* "Hot Lips". When total amount of nectar (product of number of flowers and Bx) was calculated, *S.* "Hot Lips" had the lowest value, while *S.* "Radio Red" had the highest (data not shown). Yet, *S.* "Blaze," which had the highest number of flower visitors, did not differ significantly from either cultivar with respect to total amount of nectar. Therefore, the higher attraction of pollinators to *S.* "Blaze" could not be explained by volume of nectar produced per plant. Flower tube length has been shown to be important in impacting the type of pollinators; nectaries at the bottom of longer corolla typically can be accessed by insects with longer tongues (e.g., long-tongued bees and lepidopterans). The corolla width is also important as wider corollas allow access of smaller bees which crawl inside to reach the nectaries. In our study, flower number did vary significantly among salvia cultivars, with "Radio Red" having the highest number, and "Hot Lips" the lowest number. While "Blaze" had the highest number of visitors, it did not differ significantly from either of these cultivars in terms of total nectar volume it produced. The number of flowers were not significantly different between "Blaze" and "Radio Red". Based on our findings, flower number could not explain the different number of pollinators observed on the salvia cultivars.

Discussion

These data show that there is a wide variety of options among cultivars of salvia, coreopsis, and asters for garden design that will attract a diverse community of pollinators and meet the goal of making pollinator-friendly spaces. The plant taxa selected, while representing a small faction available to consumers (limited by our space and funding), are known to attract pollinators. Yet, there was considerable variation in the visitation rates by pollinators among the cultivars. This variation could be attributed to a variety of sources. Previous studies have

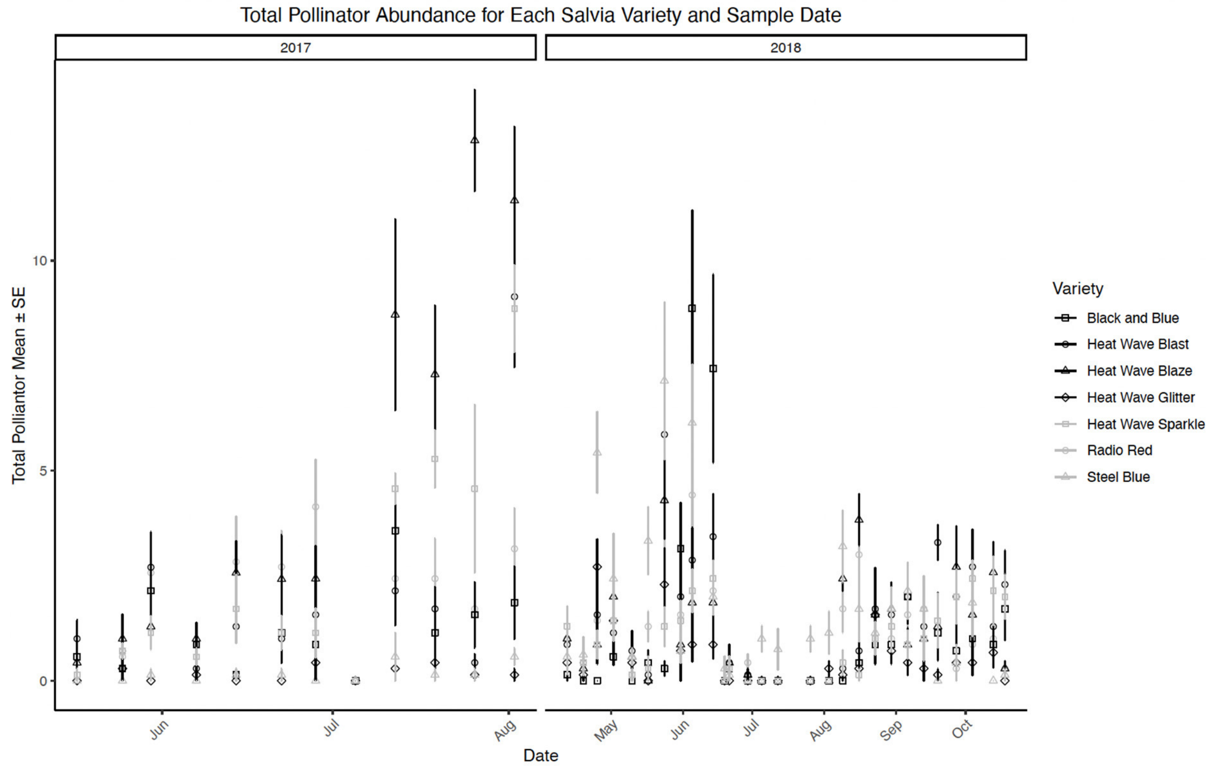

FIGURE 8
Mean ± se total flower visitors (pollinators) comparison among salvia cultivars by date in a 2-year study in central Georgia, USA.

demonstrated that floral abundance and nectar quality positively affect insect visitation (e.g., Fowler et al., 2016). However, these results do not support this relationship as the higher attraction of pollinators to *S.* "Blaze" could not be explained by the volume of nectar produced per plant. Other site-specific variables could account for this variation.

Other sources of variation we observed over the 2 years is believed to be (at least in part) due to natural seasonal or annual variation in insect populations. Insects, especially bees and hoverflies can be attracted in large numbers with a demonstrated season-long difference in distribution among the plant taxa studied here. While it is common to consider how variation in location, soil type, or other microclimatic conditions could affect localized response of pollinator plant choice, previous related studies (e.g., Garbuzov and Ratnieks, 2014) show that results can apply generally to a wider area and are not necessarily year- or location-specific. Most insect species or groups we recorded are commonly observed, so they would be present in almost any area, but not necessarily in the same proportions. This further supports the generalizability of our findings.

In other pollinator-related studies, data collection methods are commonly considered for how they affect external application of the results (Packer and Darla-West, 2021). Methods for recording visual observations of pollinator visitation used in this study lend themselves well and have been used in citizen science initiatives to promote awareness, increase pollinator spaces, and gather useful data via "the Great Georgia Pollinator Census," now in its fourth year (Griffin and Braman, 2018, 2021; Griffin et al., 2021, 2022). Observation and recording of broad taxonomic categories loses taxonomic resolution, but provides opportunity for citizen engagement by large numbers of samplers/observers who can be trained to recognize the broader taxonomic categories. One important goal of the census is to promote the creation of sustainable pollinator habitat. The maps shown on the Pollinator Census website https://ggapc.org/census-data-2/ show the 1,861 gardens across Georgia created as a result of the project by year. Clearly, there is increasing interest in planting for pollinators (Braman and Griffin, 2022). A recent study (Janvier et al., 2022) reported results from pan trap sampling 50 residential sites in and around Athens, Clarke Co., GA and documented 110 species of bees occurring in these urban and peri urban habitats. Twenty-two of the bee species collected directly from flowers reported in the present study were also represented in Janvier et al., thus further demonstrating the similarity and reliability of our collection methods.

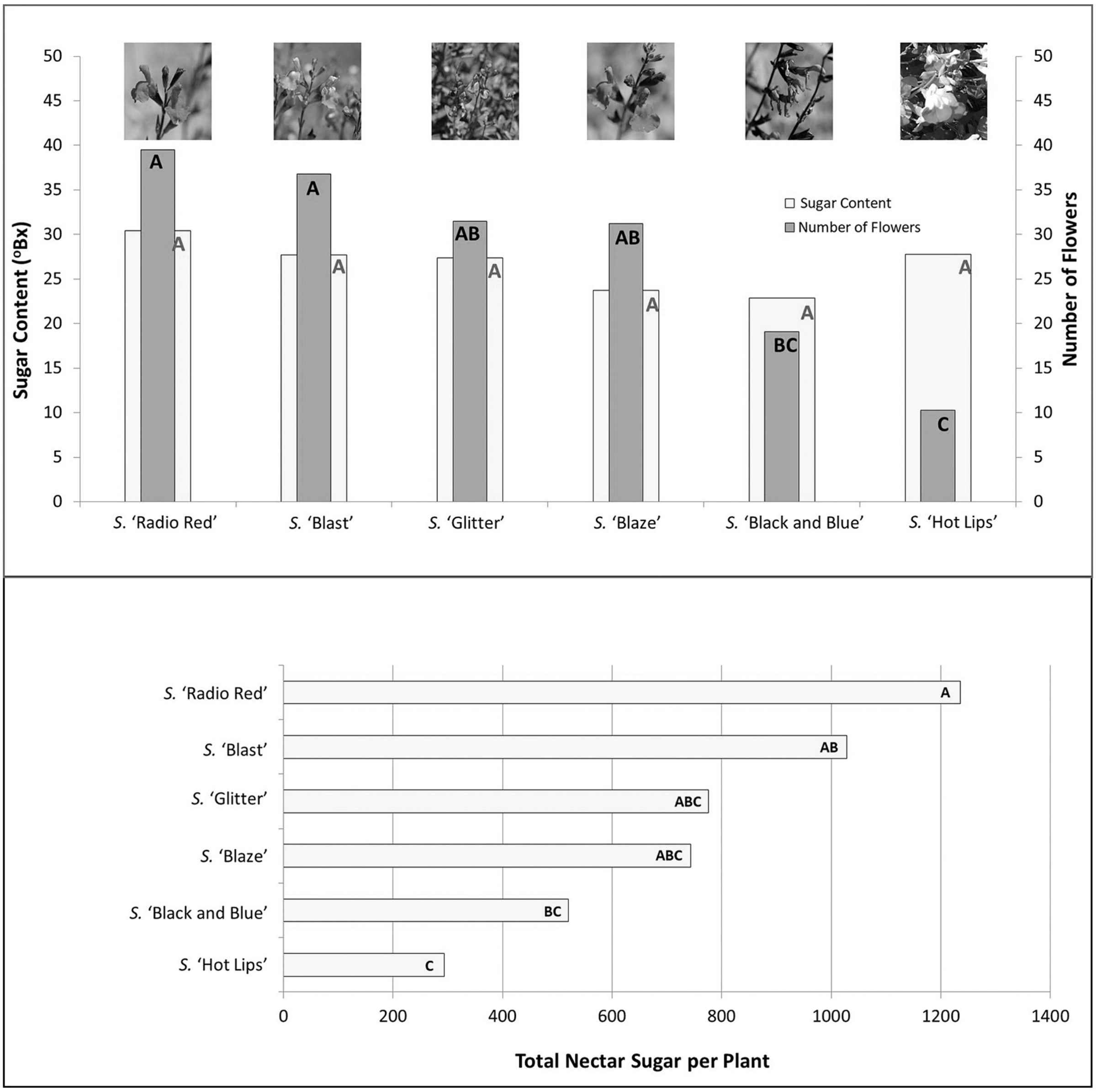

FIGURE 9
Salvia nectar sugar content, number of flowers and total nectar per plant for six salvia cultivars measured in mid-June 2017. Bars that share the same letters are not significantly different at $P < 0.05$ level.

Conclusion

Results from our cultivar comparisons in the present project provide additional data-based information to assist consumers in plant choice. While specific recommendations are limited, as these results are not the result of exhaustive comparisons, we can identify some target cultivars to consider for future study. Furthermore, our findings support more detailed assessment of floral characteristics that may determine pollinator preference to floral cultivars and species. As pollinator communities continue to suffer declines, and the need for providing floral resources increases across many urban areas, we advocate for future plant-specific pollinator census initiatives across a broader geographic range.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Release experiments as an indicator of flying activities of stingless bees in urban areas

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Contemporary urban ecology views cities as heterogeneous and dynamic ecosystems, composed of biotic, physical, social, and man-made systems. In this context, urban beekeeping stands out as a growing practice that demands further studies. Many species of stingless bees (tribe Meliponini) have adapted to urban areas, while others are more sensitive. The composition of the surroundings where the beehive is located is important for the health of the nests and quality of the bee products. This work used bee capture and release techniques to evaluate the use of this methodology for releasing and monitoring native bees in urban areas and to identify whether proportion of green and gray urban nature areas affect the flying activities of stingless bees in an urban landscape. We used nests of *Melipona quadrifasciata* (mandaçaia), a species of stingless bee native to the Atlantic Rainforest, from three meliponaries located in different parts of the city of São Paulo. The travel time of bees in the landscape were related to the green urban areas up to 900 m in diameter from the meliponaries. Although we did not find a relationship between green areas and bee return times and numbers, it was noticeable that there was variation between the study areas, indicating that the release and monitoring methodology can be used in urban areas following the recommended modifications.

KEYWORDS

urban ecology, urban biodiversity, urban green nature, urban gray nature, urban meliponaries, stingless beekeeping, *Melipona quadrifasciata*, mandaçaia

1. Introduction

Within the contemporary scope of the urban ecology, cities are studied as heterogeneous and dynamic ecosystems, composed of biotic, physical, social and built complexes (Cadenasso and Pickett, 2008). Wachsmuth and Angelo (2018) defined two representations of urban nature that can characterize urban sustainability policy: green urban nature and gray urban nature. Green urban nature encompasses all vegetation forms that can be found in urban areas (e.g., street trees, gardens, plazas, grass), while gray urban nature includes other sustainable urban spaces, such as dense urban cores and buildings (Wachsmuth and Angelo, 2018). About gray urban nature features, urban areas have a high percentage of impermeable surfaces and buildings, which influence the local microclimate not only by replacing natural forest areas and altering the natural flow of water systems, but also by intensely absorbing solar radiation, creating heat islands (Yuan and Bauer, 2007; Hamblin et al., 2018). A road, for example, can act as a barrier to flying insects, and the composition of these organisms can differ between the two sides of the road (Andersson et al., 2017).

Regarding green urban nature features, urban areas not only contain remnants of patches of vegetation (Pickett and Cadenasso, 2012), but also feature resources not native to the region, distributed in gardens and green areas (Kaluza et al., 2016; Silva and Kleinert, 2020), and resource heterogeneity distinctly influence both bee dynamics and diet (Banaszak-Cibicka et al., 2016; Dylewski et al., 2019). Urban gardens, for example, can act as providers of floral resources and refuge for bees and other pollinators when resources are scarce (Langellotto et al., 2018), and urban green areas can provide habitat for several species of nesting bees pre-existing cavities (Rocha-Filho et al., 2020).

In this context, meliponiculture, the breeding and management of stingless bees (Meliponini tribe), is an increasingly common modern practice in urban areas in the west hemisphere that demands further studies (Cortopassi-Laurino et al., 2006; Venturieri et al., 2013). Brazil has a great diversity of stingless bee species which increasingly attract the interest of society, whether to produce specialty honeys and marketable products, for conservation and educational purposes or as a leisure activity (Koser et al., 2020). Recent updates in federal (Brasil, 2020) and state (São Paulo, 2021) legislation have helped regulate the practice of rearing these native bees, which have advantages over honeybees (*Apis mellifera* Linnaeus, 1758) because they are native, have special honeys and are not harmful to humans.

Some species such as "yellow jataí" (*Tetragonisca angustula* Latreille, 1811) and "arapuá" (*Trigona spinipes* Fabricius, 1793) have adapted to urban areas and live in anthropic habitats (Sousa et al., 2002), being able to nest both in tree trunks and in artificial structures, such as hollow walls (Silveira et al., 2002). Other species, however, such as those of the genus *Melipona*, are more sensitive and have not adapted so well to these new environments (Pioker-Hara et al., 2014). *Melipona* bees can suffer adverse effects of deforestation and can be considered indicators of landscape change (Brown and Albretcht, 2001), mainly due to the necessity of finding large cavities for nesting, such as large trees, which are rare in urban areas (Pioker-Hara et al., 2014). Thus, their breeding requires experience of the stingless beekeeper and additional handling of nest, as well as greater availability and diversity of plant species in the area where they are located (Oliveira-Abreu et al., 2014; Andrade et al., 2019), in addition to beekeeping programs that aim to maintain regional biodiversity (Brown and Albretcht, 2001). However, the potential of *Melipona* bees for beekeeping is excellent, even in urban areas, not only for the creation and commercialization of unique bee products, but also to contribute to the conservation of this endangered species, combining the need to increase the number of these individuals with the conservation of forest remnants and their plant-pollinator interactions.

Although beekeepers provide their hives with energy and protein artificial supplements, it is essential for the maintenance of the nests that the bees forage and seek natural sources of nectar and pollen to meet all their nutritional needs that maintain the health of the colony. Thus, it is known that the composition and proportion of the landscape directly affect the richness of resources (pollen) collected by stingless bees (Machado et al., 2020). The arrangement and distribution of trees and shrubs and the presence of tall structures such as buildings (Forman, 2016), for example, are green and gray interferences that affect organisms in urban areas. In addition, stingless bees have diversified flight ranges, which define how far a bee can go to reach best quality floral resources. Maximum flight distances can reach more than 2,000 m for *Melipona* bees (Roubik and Aluja, 1983). However, in methodologies involving capture and release, bees typically do not return to the colonies when they are released at distances greater than 1,000 m, and only stingless bees of the genera *Melipona* and *Trigona* return from these distances (Araújo et al., 2004; Greenleaf et al., 2007). Still, the real distances that bees travel for foraging depend on the attractiveness of the resources to compensate for their distance from the nest and on the availability of alternative resources nearby, so that they usually do not exceed 500 m (Heard, 1999). Nevertheless, none of the mentioned studies were carried out in urban areas, so nothing is known about the flight ranges of these bees in this landscape context.

In this context, the bee flying activities on urban landscapes need further studies to better understand their foraging and pollination dynamics. In this work we used bee capture and release techniques to identify whether green infrastructure affect the activity of stingless bees and to evaluate the effectiveness of this method in an urban landscape. Therefore, we aimed to answer: can the methodology for releasing and monitoring native bees be used in urban areas? What is the role of green and gray infrastructure in the capacity and return time of bees to the hive?

2. Materials and methods

2.1. Study area and species

The study was carried out in the city of São Paulo, state of São Paulo, Brazil, and the target species chosen was *Melipona quadrifasciata* Lepeletier 1836 (typically called mandaçaia). São

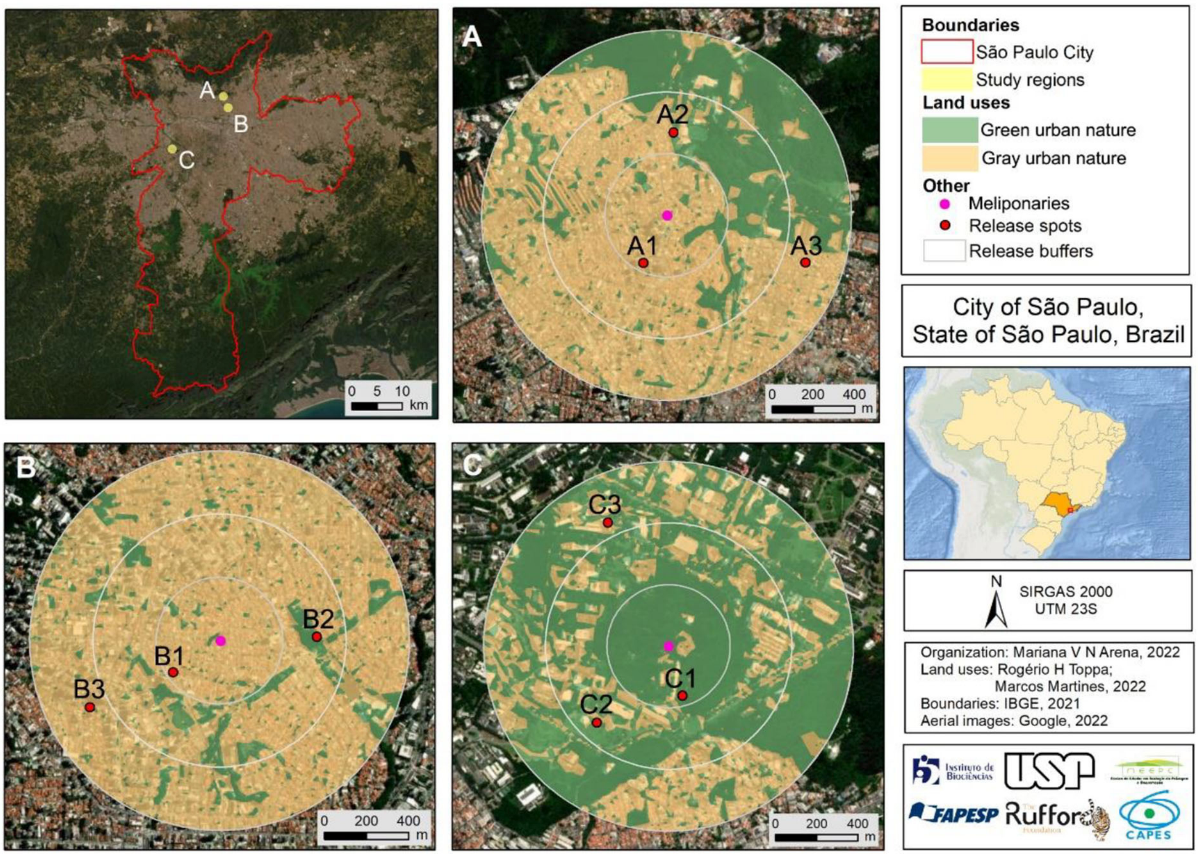

FIGURE 1
Location of study areas **(A–C)** (meliponaries) in the city of São Paulo, state of São Paulo, Brazil, showing coverage regions, urban green and gray nature areas, and bees' release spots and coverage regions.

Paulo is a large metropolis, being the most populous city in Brazil and the fifth most populated in the world, with more than 20 million inhabitants (World Population Review, 2022). Of the total area of the municipality, 735.99 km² (48.18%) are composed of vegetal cover, including areas of natural cover, regeneration, reforestation, etc., being 21% of natural Atlantic Forest vegetal cover (São Paulo, 2020). The municipality's rural area represents 31.78% of the territory, from which 79.37% are vegetation cover, while the urban area represents 68.22% of the territory, from which only 33.65% are of vegetation cover (São Paulo, 2020).

Mandaçaia is an important species native to the Atlantic Forest (Nogueira-Neto, 1997; Michener, 2007; Camargo et al., 2013) and is commonly breed in meliponaries in the state of São Paulo. This species is typical from forest environments (Silveira et al., 2002), so it is very sensitive to the loss of habitat, that is the reality of urban areas. Mandaçaia was chosen because it is native to the region, it has a valuable potential for the beekeeper, and it is one of the favorites among breeders, mainly in urban areas.

2.2. Data collection

Three landscapes were selected to compose a gradient of green-gray urban nature, where meliponaries used to collect bees for the experiment were located (Figure 1). To ensure that all hives of mandaçaia were in similar condition, nests were monitored during 6 months (autumn and winter) and fed with syrup (sugar solution: 50% water; 50% organic sugar). The experiments took place in early spring (September 2022). For each study area (meliponary) the bees were randomly divided into three groups of 15 individuals ($n = 45$), and bees were marked with a water-based colored pen (POSCA PC-5M), so that each group was assigned to a color. Bees were placed in plastic pots (100 ml) according to their groups, and immediately transported in thermic boxes with ice. Considering that bees typically do not return to the colonies when they are released at distances greater than 1,000 m (Araújo et al., 2004; Greenleaf et al., 2007), we established a maximum release distance of 900 m. For each study area, groups of bees were released at three distances from the nest: 300 m (subbuffer 1),

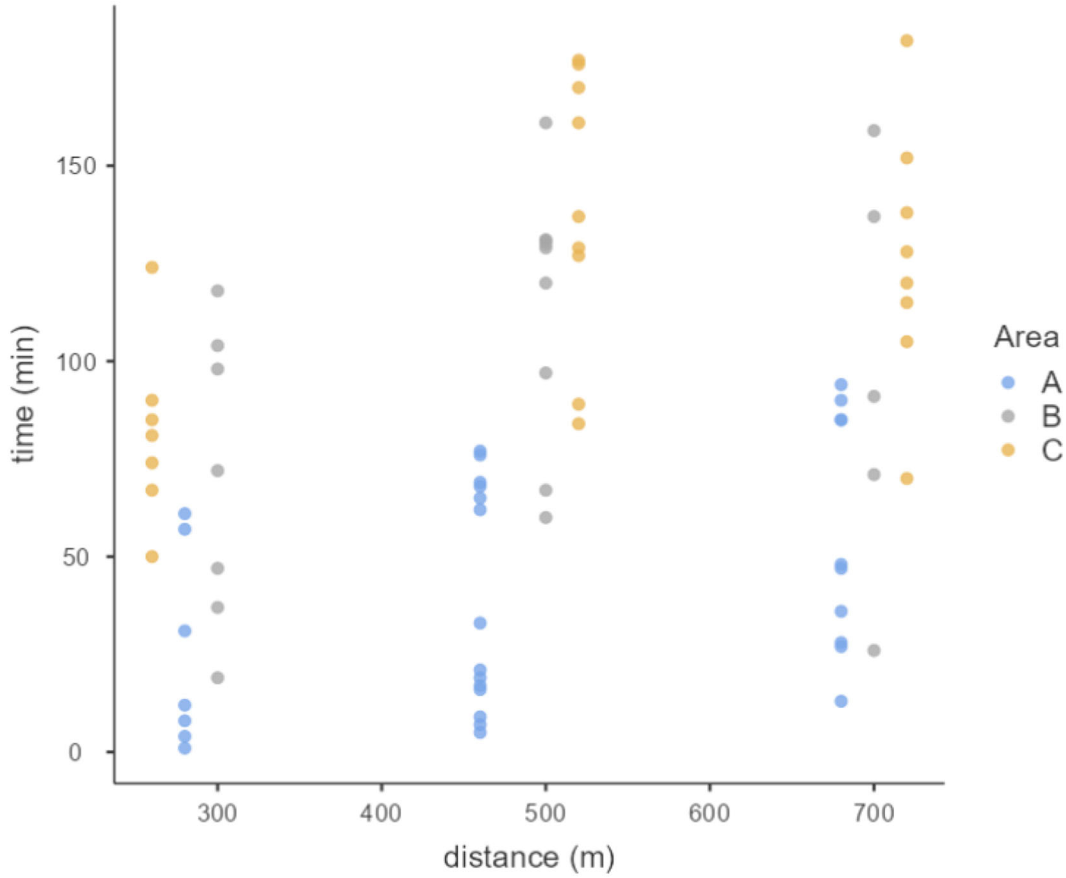

FIGURE 2
Dispersion graph showing the return time (minutes) of each bee according to the release point distance for each study area (A, B, C).

600 m (subbuffer 2), and 900 m (subbuffer 3), and the direction in which the releases were made was randomized (Figure 1).

The releases of bees from each nest were carried out on the same day of collection, on sunny days, between 8:00 am and 9:00 am. The releases started from the closest point (300 m) to the farthest (900 m), and the exact time of each release was noted. A video camera monitoring system was used to check how many individuals returned to the nests and how long they took to return. A webcam was installed at the entrance of the nest and connected to a notebook to record the bees arriving to the hive, for 3 h after the last bee was released. The images were analyzed to obtain the arrival times of the bees of each release group (visually identified by color) to the nest.

2.3. Spatial analysis

The land cover for each study area was classified as "green urban nature" and "gray urban nature" (Figure 1). The classification was performed with Sentinel satellite images, using as a filter the temporal space of 1 year (08/30/21 to 22), to obtain the median with the most characteristic classification of the spectral response of that image. Having the meliponaries as a central point, 900 m radius buffers were generated to demarcate the coverage regions around each study area. Filters were created based on the NDVI and EVI bands, in order to obtain specific responses regarding the presence of vegetation cover. The automatic classification of land uses was performed using the Earth Engine platform using the "random forest" classifier, and the training was performed 1,000 times to verify the best classification. Finally, to confirm the accuracy of the classification, confusion matrices were generated.

2.4. Data analysis

For each bee individual that returns to the nest, the difference between the time of release and the time of record was calculated to obtain the number of individuals that returned per nest and the return times (in minutes). Generalized

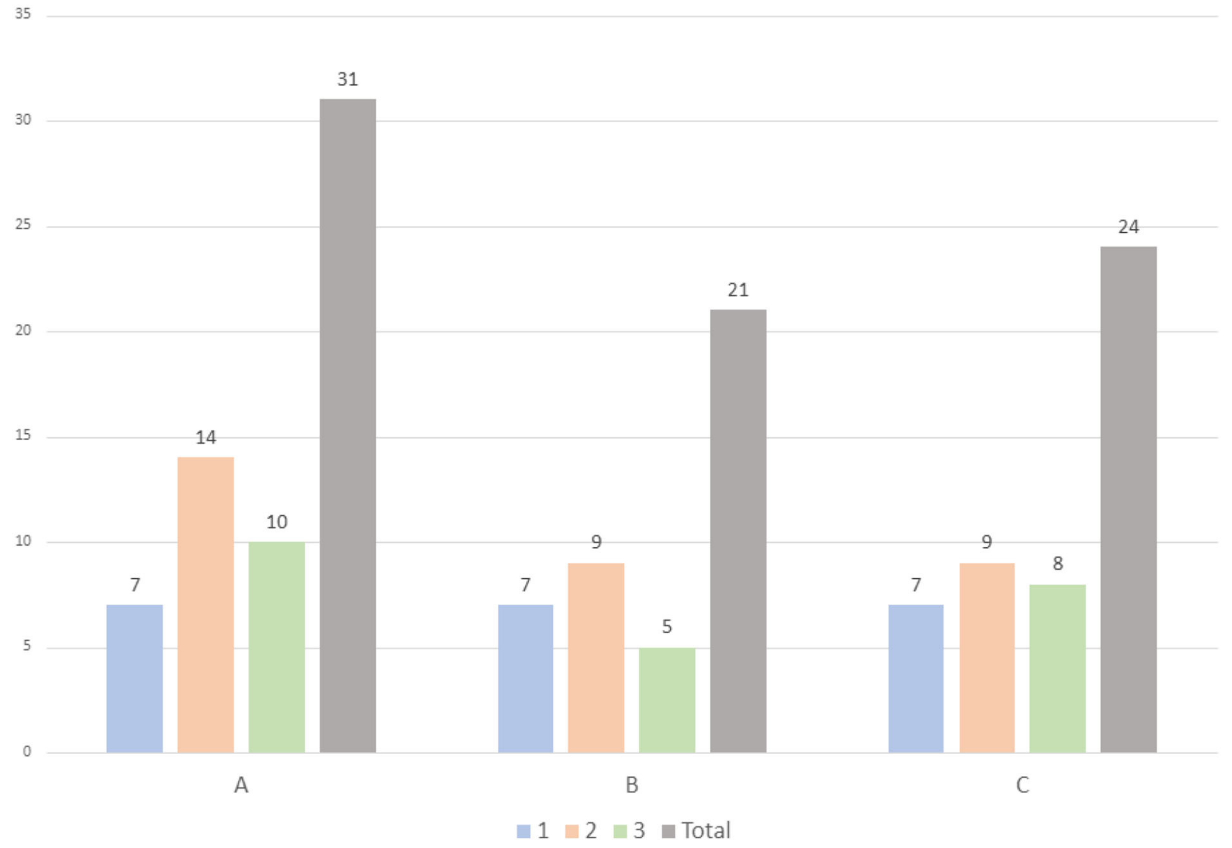

FIGURE 3
Total number of returning bees per study cover regions (A, B, C) and subbuffers (1, 2, 3, and total).

linear models (GLMs) with gamma and poisson distributions were created to verify the relationship between the response variables and the predictor variables, in order to identify which parameters influenced the return time intervals (minutes) of bees. Data were organized in Excel and statistical analysis were performed using the Jamovi 2.2.5 software.

We estimated if there were differences in the return times between subbuffers within buffers, assuming subbuffers categories as predictor variables. To find if there were differences due to the distances of the release points (subbuffers) within coverage regions (buffers), we generated GLMs for buffer A considering subbuffers A1 (300 m), A2 (600 m), and A3 (900 m); for buffer B considering subbuffers B1 (300 m), B2 (600 m), and B3 (900 m); and for buffer C considering subbuffers C1 (300 m), C2 (600 m), and C3 (900 m).

Additionally, we answered if there were differences in return time between the cover regions, assuming buffers as predictor variables. Finally, we wanted to know if there was a relationship between the vegetation amount and the return time. Therefore, data was organized considering the total vegetation area (Km^2) and number of patches (NP) as predictor variables.

3. Results

Exploratory analysis showed that in study area C bees took longer to return from the release points to the nest, followed by the bees from the areas B and A, respectively (Figure 2). Study area A presented the higher number of returning bees (31), followed by areas C (24) and B (21) (Figures 2–4).

Models regarding return time comparisons between subbuffers within coverage buffers (Table 1; Figure 5) showed no significant differences, except for subbuffers C1 and C3 ($p < 0.001$). Differences in return time between buffers showed significant differences between study areas A and B and between areas A and C (Table 2; Figure 6). We did not find statistically significant differences between the vegetation area and the return time or between the number of patches and the return time (Table 3). Detailed results of the generated models are available in the Supplementary material.

4. Discussion

Although we did not find a relationship between vegetation and bee return times and numbers, it was noticeable that there

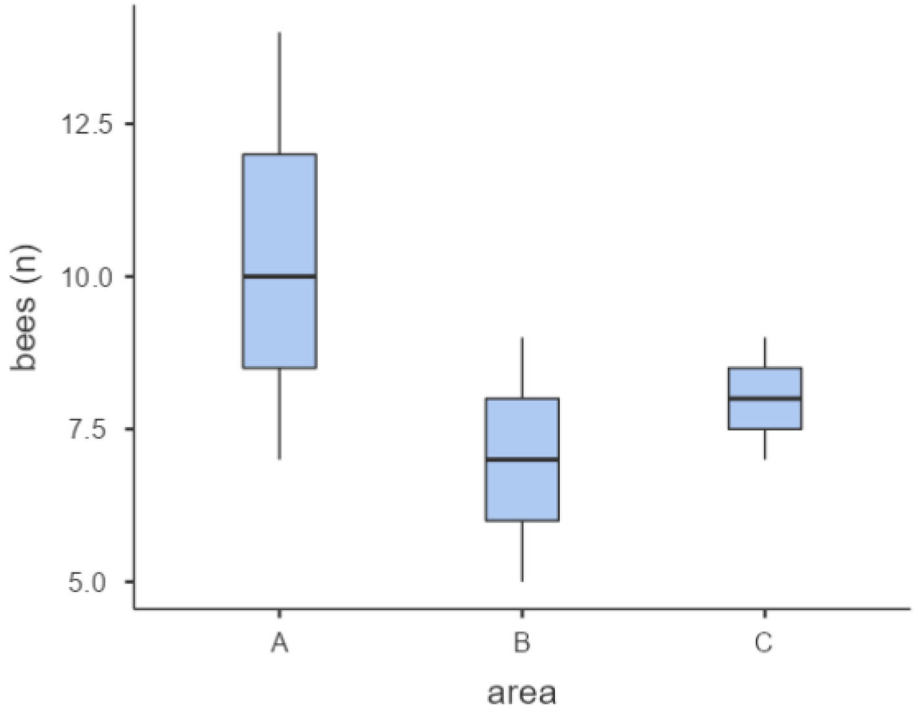

FIGURE 4
Plots accounting the number of bees that returned to the nest after release for each study area (A,B,C).

TABLE 1 *Post-hoc* comparison tests for the generalized linear models regarding differences between subbuffers.

Subbuffer	Subbuffer	Difference	SE	Z	$P_{bonferroni}$
A1	A2	−14.0	10.5	−1.33	0.551
A1	A3	−30.7	15.0	−2.05	0.121
A2	A3	−16.7	15.4	−1.09	0.827
B1	B2	−43.3	20.0	−2.163	0.092
B1	B3	−26.1	23.2	−1.122	0.786
B2	B3	17.2	22.1	0.777	1.000
C1	C2	−57.3	14.7	−3.887	<0.001
C1	C3	−44.7	14.4	−3.106	0.006
C2	C3	12.6	17.0	0.741	1.000

was variation between the study regions, showing that the release and monitoring methodology can be used in urban areas. We obtained satisfactory bee return rates of 46.6% (21 out of 45 bees in area B), 53.3% (24 out of 45 bees in area C), and 68.8% (31 out of 45 bees in area A). Marking techniques have been widely applied in studies with several conservation purposes and with a variety of permanent and impermanent methods (see Briggs et al., 2022). Our study proved that the method of marking and releasing bees can also be successful on different green-gray urban nature gradients. Additionally, we used a very wide spatial scale in this work in order to cover the green-gray gradient. To efficiently develop conservation strategies for local bees in urban landscapes, it is necessary to consider different spatial scales (Zanette et al., 2005). Thus, our findings report a new context for studies applied to the ecology of the movement of pollinating organisms in urban environments. Accordingly, it would be interesting to carry out a new study that uses greater spatial detail to investigate the influences of different elements of the urban landscape, such as street trees, paved roads or vacant lots.

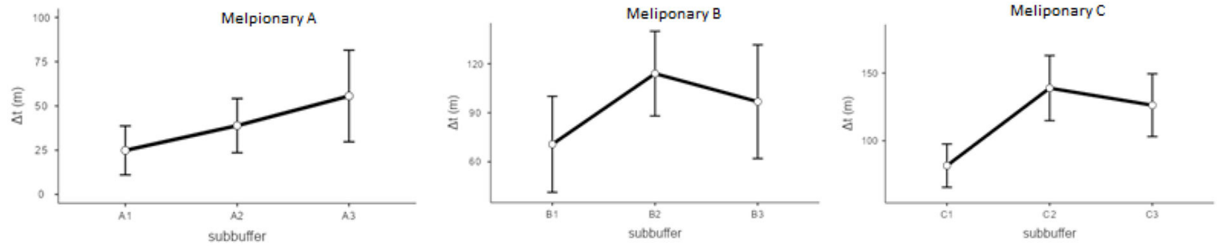

FIGURE 5
Plot results for the generalized linear models regarding differences between subbuffers.

TABLE 2 *Post-hoc* comparison tests for the generalized linear models regarding differences in return time between buffers.

Study area	Study area	Difference	SE	Z	$P_{\text{bonferroni}}$
A	B	−54.4	10.30	−5.28	<0.001
A	C	−76.9	9.91	−7.76	<0.001
B	C	−22.5	10.89	−2.06	0.117

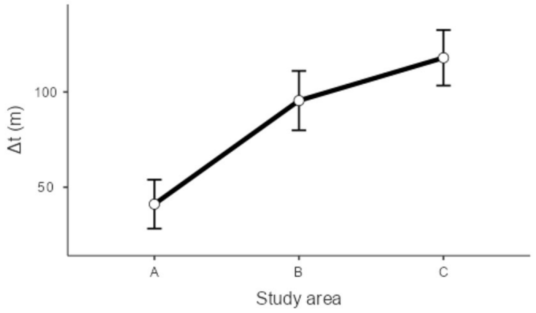

FIGURE 6
Plot results for the generalized linear models regarding differences in return time between buffers.

In order to be able to infer whether variations between study regions occurred due to the landscape around the nests and not to other factors (such as intercolonial variations), it would be suitable to repeat the experiment with a greater number of study areas. We suggest, for a next experiment, that more releases be carried out, at different distances, in order to cover a better representation of the landscape around the meliponaries. Bees are organisms that carry out recursive movement, defined as repeated visits to the same locations in a systematic way, between series of known points ("traplines"), in search of renewable resources, such as pollen and nectar (Berger-Tal and Bar-David, 2015). Thus, understanding how bees move and interact with anthropic landscapes, both in search of resources and in pollination, is extremely important both for the conservation of bees and the resources they need, and for good agricultural productivity (Heard, 1999; Machado et al., 2020; Silva and Kleinert, 2020).

Unfortunately, the technique used is limited to identify the routes of the bees returning to the hive. For this, there would be necessary to use more modern but expensive technologies for monitoring bee activity, such as harmonic radar. Although transmitter sizes have recently become small enough to allow tracking of insects under natural field conditions, they are still too big for most bee species and are still too expensive (Kissling et al., 2014; Nunes-Silva et al., 2019). It is also important to highlight that no marked bees were recorded returning with floral resources, demonstrating that during the return journey of the bees to the hive they did not carry out collection activities, focusing only on their return. Thus, there is no need to assess which resources are available in the vegetation to carry out this type of experiment, which allows the focus of the analyzes to be concentrated only on the type of urban element present in the landscape.

Bee flight capacities are an important factor that determines the area that a colony can exploit (Costa et al., 2021). *Tetragonisca angustula* and *T. spinipes*, for example, stingless bees commonly found in urban areas, can reach distances up to 1,000 m (Van Nieuwstadt and Iraheta, 1996; Araújo et al., 2004; Greenleaf et al., 2007). Typically, *M. quadrifasciata* can reach a flight distance of 2,100 m (Roubik and Aluja, 1983). However, recent studies using RFID tracking technology have revealed that *Melipona* bees can reach much greater flight ranges, with foraging flight distances from 1,000 to 2,000 m, and a maximum homing distance from 5 to 10 km (Nunes-Silva et al., 2019; Costa et al., 2021). Therefore, it is fundamental to study in detail the movement of bees and their relationship with the landscape elements in a radius of 1,000 m around the colony in order to assign the best conservation and management strategies of the meliponary and its surroundings. It is also important to highlight that, in both mentioned studies, the releases were carried out in forest areas, emphasizing the originality and importance of our survey and other studies that evaluate the movement of native bees in urban areas.

TABLE 3 Parameter estimates for the generalized linear models regarding differences between the vegetation area and the return time for buffers A, B, and C.

			95% Confidence interval			
Buffer A	**Estimate**	**SE**	**Lower**	**Upper**	**Z**	**P**
(Intercept)	41.097	5.76	31.67	55.11	7.135	<0.001
veg_CA_km2	37.098	19.15	3.11	86.96	1.938	0.063
other_CA_km2	0.450	1.36	−2.30	3.50	0.332	0.742
Buffer B	**Estimate**	**SE**	**Lower**	**Upper**	**Z**	**P**
(Intercept)	95.5	8.66	78.5	112.5	11.02	<0.001
veg_CA_km2	1,080.1	560.37	−18.2	2,178.4	1.93	0.070
other_CA_km2	−152.0	85.74	−320.1	16.0	−1.77	0.093
Buffer C	**Estimate**	**SE**	**Lower**	**Upper**	**Z**	**P**
(Intercept)	118	6.51	106	132	18.11	<0.001
other_CA_km2	−695	246.92	−1,218	−237	−2.81	0.010
veg_cakm2	430	141.17	168	729	3.04	0.006

Although some studies about the flight ranges of native bees have been successfully developed in natural areas, there is a lack of studies about the dynamics of these organisms in urban landscapes. Research that considers the new anthropic scenario to which native bees are submitted is of unquestionable importance for the development of public and conservation policies that concern biodiversity and urban ecology. Thus, our study presents a relevant suggestion for new research within this modern context. We conclude that, although some modifications are necessary, studies involving the marking, release and monitoring of bees can be of great value for the development of urban ecology studies, in order to better understand how these organisms interact in these landscapes and, thus, develop better conservation and maintenance strategies for native bees in urban areas.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the animal study because no authorization is required for ex-situ collection and transport of invertebrates. Written informed consent was obtained from the owners for the participation of their animals in this study.

Author contributions

MA, RT, and IA-d-S contributed to conception and design of the study. MA and RT organized the database. MA, RT, and MM performed the statistical analysis. MA wrote the first draft of the manuscript and sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2022.1103835/full#supplementary-material

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Citizen science initiatives increase pollinator activity in private gardens and green spaces

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Wild insect pollinators are essential to cultivated and natural ecosystems globally. Today, many pollinator species are declining. One reason is a general lack of flowering habitats at landscape scales. However, urban areas, including private gardens, may provide flowers, and constitute beneficial habitats for pollinators. Here, we evaluate the ecological outcomes of a citizen science campaign run by the Swedish Society for Nature Conservation (SSNC) (called "Operation: Save the bees"), encouraging citizens to incorporate interventions beneficial to wild pollinators (garden meadows, flower plantings, and bee hotels) in their gardens. Data on insect observations and flowering plants were collected through online questionnaires at the end of the growing season. In total, we received 3,758 responses for the three interventions. We found that participants were more likely to observe many pollinators (as opposed to few or none) in more species rich garden meadows, and in larger and older plantings. The surrounding environment also affected pollinator abundance: fewer pollinators were observed in plantings in dense urban areas. Direct counts of pollinators during 10-min surveys correlated strongly to the simplistic abundance assessment (none, few, or many insects seen over the summer season). Bee hotel occupancy was positively related to local flower availability and bee hotel age. Smaller nest holes (<10 mm) were more occupied than larger holes (11–15 mm) and hotels in rural gardens and natural/semi-natural sites were more occupied than those in urban gardens. This study demonstrates that flower-rich private gardens provide integral habitat for wild pollinators and that citizen science programs can provide a tool for implementing and evaluating conservation practices. However, longer lasting commitment resulting in older interventions are preferable and should be encouraged in future campaigns.

KEYWORDS

pollinator conservation, urban green space (UGS), bee hotel, garden meadow, flower plantings

1. Introduction

Wild insect pollinators are essential to both natural and managed ecosystems. Globally, around 90% of flowering plants (Ollerton et al., 2011) and 75% of crop species (Klein et al., 2007) are, to some degree, dependent on pollinators for seed or fruit set. Bees are the most well-documented insect pollinators but also, e.g., flies, beetles, moths, butterflies, wasps, and ants can act as pollinators (Rader et al., 2016). However, many wild pollinator species are declining (Biesmeijer et al., 2006; Zattara and Aizen, 2021), e.g., due to anthropogenic land use change, which has reduced the area of suitable habitat for foraging and nesting, mainly flower rich grasslands such as traditional meadows and pastures (Goulson et al., 2015; IPBES, 2016). One way to increase the availability of flower-rich habitats is to integrate them and promote their uptake into private gardens and green spaces. Gardens and backyards cover as much as 30% of urban areas (Goddard et al., 2010) and have the potential to act as a pollinator refuges, both in urban (Baldock, 2020) and rural (Samnegård et al., 2011) areas. Importantly however, this potential is moderated by pollinator ecological and life history traits. For example, hoverflies are more sensitive to urbanization than bees (Verboven et al., 2014; Persson et al., 2020), most likely because their larval stage is often connected to specific habitats largely lacking in urban areas, e.g., shaded wooded habitats with dead organic matter (Bartsch, 2009). For bees, above-ground (cavity) nesting, social, and generalist species tend to benefit from moderate urbanization (Fortel et al., 2014; Wenzel et al., 2019; Fauviau et al., 2022), and especially in comparison to land use dominated by agriculture (Wenzel et al., 2019). For bee body size, the results are so far inconclusive, and both large and small species have been shown to benefit from different aspects of urbanization (Wenzel et al., 2019; Gathof et al., 2022). Hence, the effects of increasing the cover of flower-rich habitats in urban gardens are expected to vary between taxa and trait groups.

It is well-established that more local flower resources will attract pollinators and potentially benefit populations, both in urban (e.g., Quistberg et al., 2016; Baldock et al., 2019) and rural agricultural (e.g., Jönsson et al., 2015) settings. So called "urban meadows," can be created either by reducing the intensity of mowing, or by sowing or planting seedlings of native herbaceous plants. They have been shown to benefit invertebrates in general (Garbuzov et al., 2015; Norton et al., 2019) and insect pollinators in particular (Blackmore and Goulson, 2014; Fischer et al., 2016), and to increase local insect pollinator diversity (Griffiths-Lee et al., 2022). Promoting meadow-like vegetation in private gardens and green spaces may thus benefit pollinators across urban residential areas. Traditional flowerbeds dominated by ornamental and non-native plants will mainly benefit generalist pollinator species (Hanley et al., 2014; Wenzel et al., 2019). As generalists are particularly common in urban areas, such resources can be expected to benefit a large proportion of urban pollinator communities (Wenzel et al., 2019). For example, small-scale additions of an exotic ornamental plant species in urban sites resulted in increased abundance and species density of small sized Halictid bees, with species density further increasing the following year (Simao et al., 2018). The rationale behind promoting bee hotels (often made from cut bamboo sticks or drilled holes in blocks of wood) is to benefit solitary cavity nesting bee populations through increased availability of nest sites. There is evidence from rural settings that man-made nests can led to increased populations (Steffan-Dewenter and Schiele, 2008), although the actual benefits of bee hotels are contested (MacIvor and Packer, 2015).

Given that urban areas are human-dominated landscapes, citizen science initiatives provide an outlet for engaging the public in pollinator conservation efforts, as well as to assess the effects of such efforts on pollinator communities. Residents invest both their time and money in gardens, allotments, and other private green spaces in order to provide, e.g., space for recreation (Barnes et al., 2020), and gardening of pollinator dependent crops (Lin and Egerer, 2017). There is thus great potential to introduce biodiversity friendly interventions and management of gardens (Goddard et al., 2013). To engage residents in local biodiversity conservation may also be important in the transition toward a more sustainable society, e.g., through the so called Pigeon paradox, hypothesizing that encounters with biodiversity where people live and work may lead to an increased understanding and engagement in biodiversity conservation (Dunn et al., 2006). Previous research has shown that people's perceived behavioral control (feeling able to help pollinators) is an important predictor of pro-pollinator actions (Knapp et al., 2021). Hence, it is important to evaluate to what degree people draw conclusions about the level of success of interventions based on the ecological outcomes, in this case pollinator activity and abundance.

Citizen science is a way for researchers to collect amounts of data that would not otherwise be possible by including society and individual voluntary citizens in the process (Bonney et al., 2009). Research is thus facilitated while the public is engaged and made aware of important issues. Internationally, there are several examples of successful citizen science projects focusing on pollinators [e.g., Bumble Bee Watch (North America), the Bumblebee Conservation trust's "Bee walk" (UK), and Spipoll (France)]. Such projects have the potential to generate data and knowledge relevant to pollinator conservation (e.g., Deguines et al., 2012; Bates et al., 2015; Griffiths-Lee et al., 2022).

The campaign "Operation: Rädda bina" ("Operation: Save the bees" in English), was run by The Swedish Society for Nature Conservation (SSNC) during 2018–2021. The aim was to benefit wild pollinators and especially bees by encouraging the public to increase the flower density in private gardens and green spaces, either through establishment of meadows or plantings, and to put up bee hotels (SSNC., 2022). Here, we aim to evaluate the citizen science project carried out in connection with the above-mentioned campaign. To this end, we use data from 2020 on three pollinator friendly interventions collected through online questionnaires administered by the SSNC. In addition, in order to verify the robustness of the simple pollinator assessment, we use data on direct pollinator counts from a follow-up survey done in 2021. We subsequently compare standardized counts with the simple assessment method.

We evaluate whether the campaign has given the desired result, that is, to what extent garden meadows, flower plantings, and bee hotels have attracted wild pollinators, and how the surrounding environment may have affected the outcome. The following ecological questions are examined:

(i) How is the abundance of pollinators in flower interventions (garden meadows and plantings) affected by the local quality of interventions in terms of size, age, and flower species richness?
(ii) How is the occupancy of bee hotels related to size of nesting cavities, bee hotel age, and surrounding flower availability?
(iii) How is the presence of pollinators in interventions moderated by the surrounding environment?
(iv) (How) does the abundance of pollinators observed affect how successful participants judge their flower intervention to be?

We expected that more pollinators would be observed in interventions that were larger, older and more flower-rich, and that bee hotels in moderately urbanized areas would be more occupied than in either highly urbanized or rural areas. We further expected that observing more insects would lead to a higher score for intervention success.

2. Materials and methods

2.1. Data collection

Data on the three interventions were collected in 2020 within the citizen-science SSNC campaign "Operation: Save the bees" using an online questionnaire prepared by the lead author (AP) in collaboration with officers at the SSNC. The campaign started in 2018 when volunteers in Sweden could register pollinator-friendly interventions that they had carried out in their gardens and other green spaces. The campaign encouraged three different interventions: (i) flowering "garden meadows," (ii) bee-friendly flower plantings, and (iii) bee hotels. Those who registered that they had undertaken an intervention received an email with a link to questionnaires with queries regarding their intervention(s) at the end of the growing season in September 2020 (Table 1 and Supplementary material). Separate surveys were provided for each type of intervention. Hence, if a participant registered more than one type of intervention they received, and potentially answered, two or three separate surveys. The surveys were sent to all who had registered interventions between 2018 and 2020. Note that respondents could register interventions that had been established before the start of the campaign in 2018.

In the questionnaires, the participants were asked about flower-visiting insects in general, i.e., potential pollinators. Hereafter, we refer to them as pollinators. Participants were not asked to distinguish between different insect taxa. We used the questions related to the abundance of pollinators observed, the size, age, and floweriness or flowering plant species richness of the intervention, and the type of surrounding habitat for further analyses, Table 1. The assessment of abundance of insects in flower interventions was answered as either: "no insects," "a few," "many," or "I do not know," Table 1. Note that participants were not given any instruction on the definitions of "a few" and "many" insect pollinators.

2.2. Data curation

Responses to the number of insects seen stating "I do not know" were removed from further analyses, as were interventions accidently stated to have been established before year 1900 or after September 2020, responses with an incorrect number of digits for year of establishment, and responses stating zero or >50 flowering plants species in flower interventions. One bee hotel, listed with a 1 million nest holes (a straw roof) was removed prior to analysis, resulting in a range of bee hotels with 1–2,500 nest holes. We also excluded responses where the number of occupied nest holes exceeded the total number of nest holes listed for the bee hotel, or where the number of nest holes per size category did not match the total number of nest holes listed. Collectively, this resulted in 370 responses being removed prior to analyses.

The number of insects seen in meadows and plantings was transformed into a binomial variable for further analyses, where 0 = No, or few, insects seen, and 1 = Many insects seen. We used year of establishment to infer age of intervention as a numerical factor 1–5, where interventions established before 2016 were merged into the oldest category (5) and years 2017–2020 were kept as four separate categories (4, 3, 2, 1). For the number of flowering plant species, responses of zero species were removed and the remaining responses were categorized in to five-step intervals: 1–5, 6–10, 11–15, 16–20, and >20 species. To assess potential effects of surrounding environment, the three non-garden categories (agricultural landscape, forestry landscape, and nature, Table 1) were merged into category *rural*. Gardens of urban single-family houses and allotment gardens were merged into category *urban garden*. Balconies and yards of multi-family houses were merged into category *dense urban*. Single-family rural gardens were kept as a single category, hereafter called *rural*

TABLE 1 The questions used to evaluate the success of interventions to benefit pollinators, with answer alternatives stated in parenthesis.

Garden meadow	Flower planting	Bee hotel
Did you see insects in your meadow during summer? (No; Yes a few; Yes many; I do not know)	Did you see insects in your planting during summer? (No; Yes a few; Yes many; I do not know)	How many nest holes did your bee hotel contain? Answer per size category (diameter), 2–5, 6–10, 11–15 mm
How large area does your meadow cover (square meters)?	How large area does your planting cover (square meters)?	How many nest holes were occupied in your bee hotel per size category (diameter), 2–5, 6–10, 11–15 mm?
Approximately how many flowering plant species does your meadow contain?	Approximately how many flowering plant species does your planting contain?	How much flowers did the close surrounding, within 50 m, contain? (Likert scale 1–5, where 1 = very few flowers of few species, 5 = many flowers of several different species)
When was your meadow established? (month/year)	When was your planting established? (month/year)	When was your bee hotel established? (month/year)
In which environment did you create the meadow? (In an urban area, e.g., back yard to a multifamily house; In the garden of a single-family house in a city or town; In the garden of a single-family house in a rural area; In an allotment; In the farmland landscape; In a forest production landscape; In nature)	In which environment did you create the planting? (In an urban area, e.g., back yard to a multifamily house; In the garden of a single-family house in a city or town; In the garden of a single-family house in a rural area; In an allotment; In the farmland landscape; In a forest production landscape; In nature)	In which environment did you put up a bee hotel? (In an urban area, e.g., back yard to a multifamily house; In the garden of a single family-house in a city or town; In the garden of a single family-house in a rural area; In an allotment; In the farmland landscape; In a forest production landscape; In nature)
How successful was your meadow? (Likert scale 1–5)	How successful was your planting? (Likert scale 1–5)	
In which municipality was your meadow placed?	In which municipality was your planting placed?	In which municipality was your bee hotel placed?
How engaged are you in issues regarding biodiversity? (Likert scale 1–5)	How engaged are you in issues regarding biodiversity? (Likert scale 1–5)	How engaged are you in issues regarding biodiversity? (Likert scale 1–5)
Year of birth	Year of birth	Year of birth
Gender (female, male, other/do not want to state)	Sex (female, male, other/do not want to state)	Sex (female, male, other/do not want to state)

Complete questionnaires are provided in the Supplementary material.

garden. Thus, in total four environment categories were used for further analyses.

For the evaluation of how successful the respondents perceived their intervention to be (1–5, Likert scale), answers were grouped into three categories: low success (1–2), medium success (3), and highly successful (4–5).

To evaluate the accuracy of the simple assessment of pollinator abundance (none, few, or many insects seen in flower interventions), we used data from 2021 collected through another online questionnaire. Similar to 2020, this questionnaire was sent to all participants in the campaign 2018–2021, asking them to assess the abundance of insects in their intervention(s). In 2021, however, participants were also asked to complete a 10-min survey of 50 m^2 of their garden, which included their flower intervention, and to count all flower visiting insects into five groups (bees and wasps, hoverflies, butterflies, beetles, and other insects). The survey was to be performed sometime between 11.00 and 16.00 on a calm, sunny, and warm day ($>16^\circ$C) in July.

2.3. Statistical analyses

We modeled to what extent flowering interventions (meadows and plantings) were visited by pollinators using generalized linear models (GLM), with binomial error distribution. We specified separate models for meadows and plantings. The proportion of participants who stated they observed "many insects" (as opposed to "none, or few, insects"), were modeled as a function of intervention area (categorical), intervention age (numeric: 1–5), species richness of flowers (categorical), and the type of surrounding environment (categorical). We assessed if flower intervention age and plant species richness was correlated using Spearman rank correlations, for meadows and plantings separately.

We modeled bee hotel occupancy using a GLM, specified with a beta binomial distribution. Occupancy was modeled as a function of environment (categorical), nest size category (categorical: 2–5, 6–10, and 11–15 mm wide), degree of flowering (numeric: 1–5), and bee hotel age (numeric: 1–5). We accounted for zero-inflation in the response. We assessed the interaction between environmental and nest size category but this was non-significant ($p = 0.8$) and removed from the presented model.

We evaluated if seeing many pollinators affected the feeling of having established a successful flower intervention (meadow or planting) using GLMs, with a binomial error distribution. We modeled the proportion of participants that stated they observed "many insects" (as opposed to "none, or few"), as a function of perceived intervention success.

We evaluated the accuracy of the simple pollinator assessments using a GLM with a negative binomial distribution, modeling meadows ($N = 165$) and plantings ($N = 218$) separately. We summed counts of the three major pollinator groups counted during surveys in 2021 (bees and wasps, butterflies, and hoverflies) to assess how pollinator abundance related to participants simple scores of insect abundance ("many insects," as opposed to "none, or few").

All analyses were carried out in R v 4.1.1 (R Core Team, 2021). Model assumptions were checked with package *DHARMa* (Hartig, 2020). Variance inflation factors (VIF) for models of meadows and plantings were checked with package *car* function vif (Fox and Weisberg, 2019), while VIF for bee hotels were checked with package *performance* (Lüdecke et al., 2021). Contrasts between groups (for example different sizes of plantings) were analyzed using Tukey's test for *post-hoc* analysis in the *Emmeans* package (Lenth, 2022). Test results were obtained from Analysis of Deviance Table using Wald Chi-square tests (package *car* function Anova, Fox and Weisberg, 2019) and the *ggplot2* package was used to visualize data and create graphs (Wickham, 2016).

Respondents' gender, year of birth, and engagement in issues related to biodiversity (self-rated, Likert scale 1–5) were compiled to describe whom the campaigned had reached and involved. All respondents from the meadow- and flower-planting surveys were included, even if their answers had previously been removed from analyses of ecological questions due to incomplete data. We were interested in how changes to vegetation quality affects peoples' perception of their garden, and therefore did not include data from bee hotel-respondents. Moreover, in contrast to added flower resources, the benefits of bee hotels are contested.

3. Results

In total, 3,758 survey responses were received for registered interventions: 898 for meadows, 1,281 for flower plantations, and 1,580 for bee hotels. After data curation (see above) 809 remained for meadows, 1,232 for plantations, and 1,210 for bee hotels. Approximately 19% of meadows, 23% of plantings, and 20% of bee hotels were situated in the 10 most populated cities/municipalities of Sweden (Stockholm, Göteborg, Malmö, Uppsala, Upplands Väsby and Sollentuna, Västerås, Örebro, Linköping, Helsingborg, and Jönköping), all situated in the southern third of the country. The vast majority of intervention were carried out in single-family residential gardens, in either urban or rural locations: 83% of meadows, 75% of plantings, and 82% of bee hotels.

3.1. Meadows

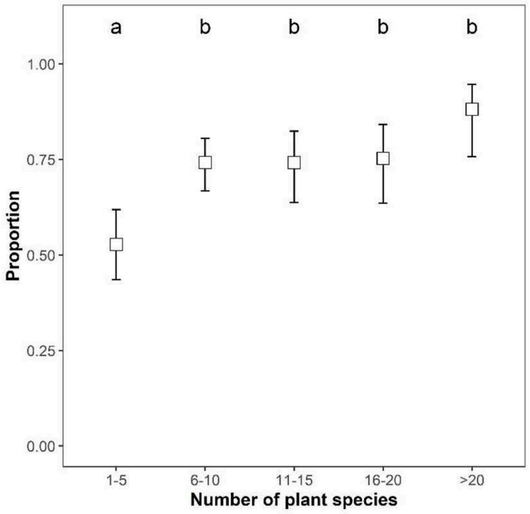

FIGURE 1
The proportion (estimated marginal means ± 95% confidence levels) of participants that reported having seen "many insects" in relation to flowering plant species richness in meadows. Pairwise comparisons of estimated marginal means are indicated by compact letter display, where plant species richness categories sharing a letter are not significantly different.

The number of participants who saw many pollinators was related to the number of flowering species in the meadow ($\chi^2 = 40.247$, $df = 4$, $p < 0.001$). *Post-hoc* tests revealed that fewer participants had reported many pollinators in meadows that contained 1–5, as compared to >5, flowering plant species (Figure 1). The meadow size and its surrounding environment had no significant effect on the likelihood of reporting many pollinators (size: $\chi^2 = 6.899$, $df = 4$, $p = 0.141$; environment: $\chi^2 = 2.057$, $df = 3$, $p = 0.561$), while meadow age showed a non-significant positive trend (age: $\chi^2 = 3.122$, $df = 1$, $p = 0.077$). Meadow age and plant species richness were positively correlated (rho = 0.24, $p < 0.001$), but not strong enough to preclude inclusion in the same models (checked with VIFs, as above).

3.2. Plantings

The proportion of participants that saw many pollinators was positively related to the age and size of the planting (age: $\chi^2 = 9.35$, $df = 1$, $p = 0.002$; size: $\chi^2 = 31.24$, $df = 2$, $p < 0.001$; Figures 2A, B). A lower proportion of participants saw many pollinators when plantings were situated in *dense urban*, compared to the other environments ($\chi^2 = 19.08$, $df = 3$, $p < 0.001$, Figure 2C). The number of flowering plant species had no significant effect on the abundance of pollinators seen ($\chi^2 = 2.17$, $df = 4$, $p = 0.71$). As for meadows, age and plant species richness were positively correlated (rho = 0.36, $p < 0.001$), but not strong enough to preclude inclusion in the same models (checked with VIFs, as above).

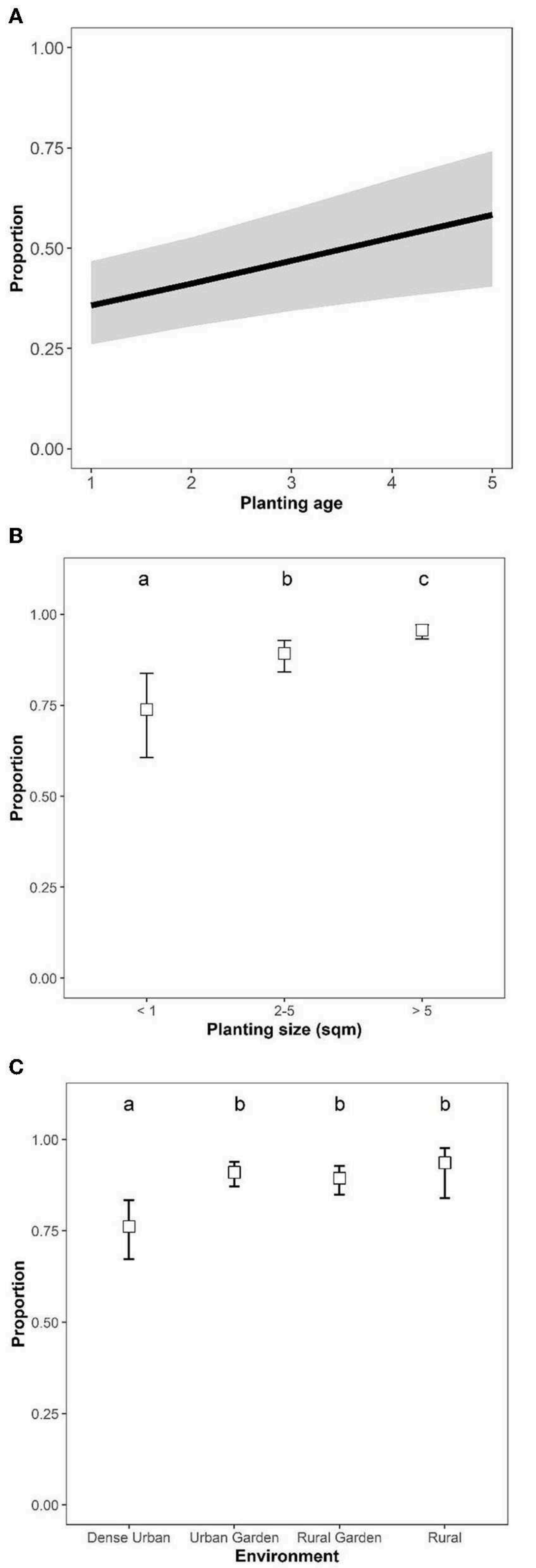

FIGURE 2
The proportion of participants (estimated marginal means ± 95% confidence levels) who reported having seen “many

(Continued)

FIGURE 2 (Continued)
insects” in their plantings in relation to **(A)** planting age, **(B)** planting size, and **(C)** the surrounding environment. Pairwise comparisons of estimated marginal means are indicated by compact letter display such that environments sharing a letter are not significantly different.

3.3. Success of flower interventions

A higher proportion of participants who reported having seen many pollinators also viewed their meadow as successfully established ($\chi^2 = 108.46$, $df = 2$, $p < 0.001$, Figure 3A). More participants reported they had observed many pollinators in meadows with the highest success rating, compared to meadows of either medium or low success, while participants with a medium success rate were in between the low and highly successful. Similarly, a higher proportion of participants who viewed their plantation as succesfull reported to have seen many insects, compared to those with a low or medium success rating ($\chi^2 = 87.85$, $df = 2$, $p < 0.001$, Figure 3B).

3.4. Bee hotels

Bee hotel occupancy rates were positively related to both local flower availability ($\chi^2 = 20.5$, $p < 0.001$, Figure 4A) and bee hotel age ($\chi^2 = 69.85$, $p < 0.001$, Figure 4B). Furthermore, occupancy rates differed between nest size categories ($\chi^2 = 101.99$, $p < 0.001$, Figure 4C). Occupancy was significantly higher in small and medium sized holes (2–5, 6–10 mm diameter), than in large holes (11–15 mm). Occupancy rates differed significantly between environment types ($\chi^2 = 74.69$, $p < 0.001$, Figure 4D). In particular, occupancy was significantly higher in both rural environments than either of the urban environments.

3.5. Accuracy of pollinator assessments

For both meadows and plantings, the pollinator abundance assess by 10-min surveys was highly positively related to if participants reported having seen “none or few” or “many” insects (meadows: $z = 3.668$, $p < 0.001$; plantings: $z = 5.167$, $p < 0.001$).

3.6. Demographics of respondents

The vast majority (80%) of survey respondents were women and most (47%) were aged 41–60 years, while the categories aged 20–40 and 61–80 years made up 27% and 25%, respectively. The majority (69%) considered themselves to have a strong

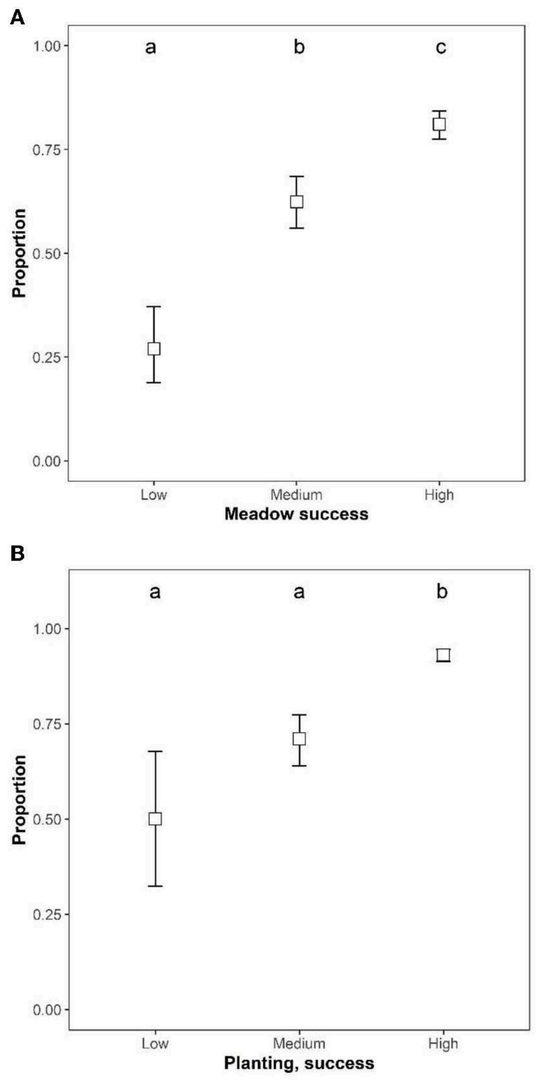

FIGURE 3
The proportion of participants (estimated marginal means ± 95% confidence levels), with meadows **(A)** or plantings **(B)** that reported having seen "many insects" in relation to their perception of intervention success. Pairwise comparisons of estimated marginal means are indicated by compact letter display. Success levels sharing a letter are not significantly different.

engagement (4–5 on a 1–5 Likert scale) in issues related to biodiversity conservation, while 26% classified themselves as equally committed as the societal average (3).

4. Discussion

Using data collected by citizens, we show that the ecological benefits of simple measures to enhance foraging resources for pollinators in private gardens and green spaces were moderated by flower species richness (for meadows), age and size (for plantings): older, more species rich, and larger flower interventions attracted more pollinators than newly established, species poor, or small ones. Similarly, the added nesting resources for bees (bee hotels) were more occupied when they were older and situated in more flower-rich gardens, compared to younger hotels in flower-poor gardens. In addition, smaller nest holes (2–10 mm wide), were more occupied than large ones (11–15 mm wide). There was a negative effect of urban environments, as both bee hotels and plantings situated in urban gardens and/or dense urban areas were less visited by pollinators. We also found that flowering interventions were perceived as more successful when they attracted many pollinators.

4.1. Flower richness increases pollinator activity in gardens

Positive effects of local flower species richness and abundance on the diversity and abundance of pollinator communities has previously been reported using traditional research methods, both in urban gardens (Quistberg et al., 2016; Del Toro and Ribbons, 2020), in rural experimental (Hegland and Boeke, 2006; Ebeling et al., 2008), and in agricultural settings (Potts et al., 2009; Jönsson et al., 2015). In addition, a citizen science project using standardized sampling methods showed that sown garden meadows enhanced local pollinator abundance and diversity over a 2-year period (Griffiths-Lee et al., 2022). Our results corroborate these findings, and in addition show that a very simple measurement, such as perceived pollinator abundance estimated by citizen scientists, may be used as a proxy for abundance to assess and compare the value of pollinator enhancement interventions.

The availability of local flower resources has been highlighted as a key factor for urban pollinator abundance and diversity (e.g., reviewed by Wenzel et al., 2019; but see Gathof et al., 2022) and may even buffer bee populations against the negative effects of landscape scale urbanization (Burdine and McCluney, 2019). Although we cannot evaluate the effects on pollinator populations in the wider landscape, even small-scale flower enhancements may result in population level effects if implemented on a large enough scale. For example, based on research in agricultural landscapes (e.g., Cong et al., 2014; Jönsson et al., 2015), one may expect that neighborhoods where uptake of interventions is high can support more pollinators at the landscape scale.

There was no effect of plant species richness in plantings on pollinator abundance. This may be because flowerbeds in general are highly dominated by ornamental and non-native plant species (Loram et al., 2007; Lowenstein and Minor, 2016), and therefore mainly cater for generalist pollinator species (Corbet et al., 2001; Wenzel et al., 2019). Adding more plant species to a flowerbed may then still only benefit the same

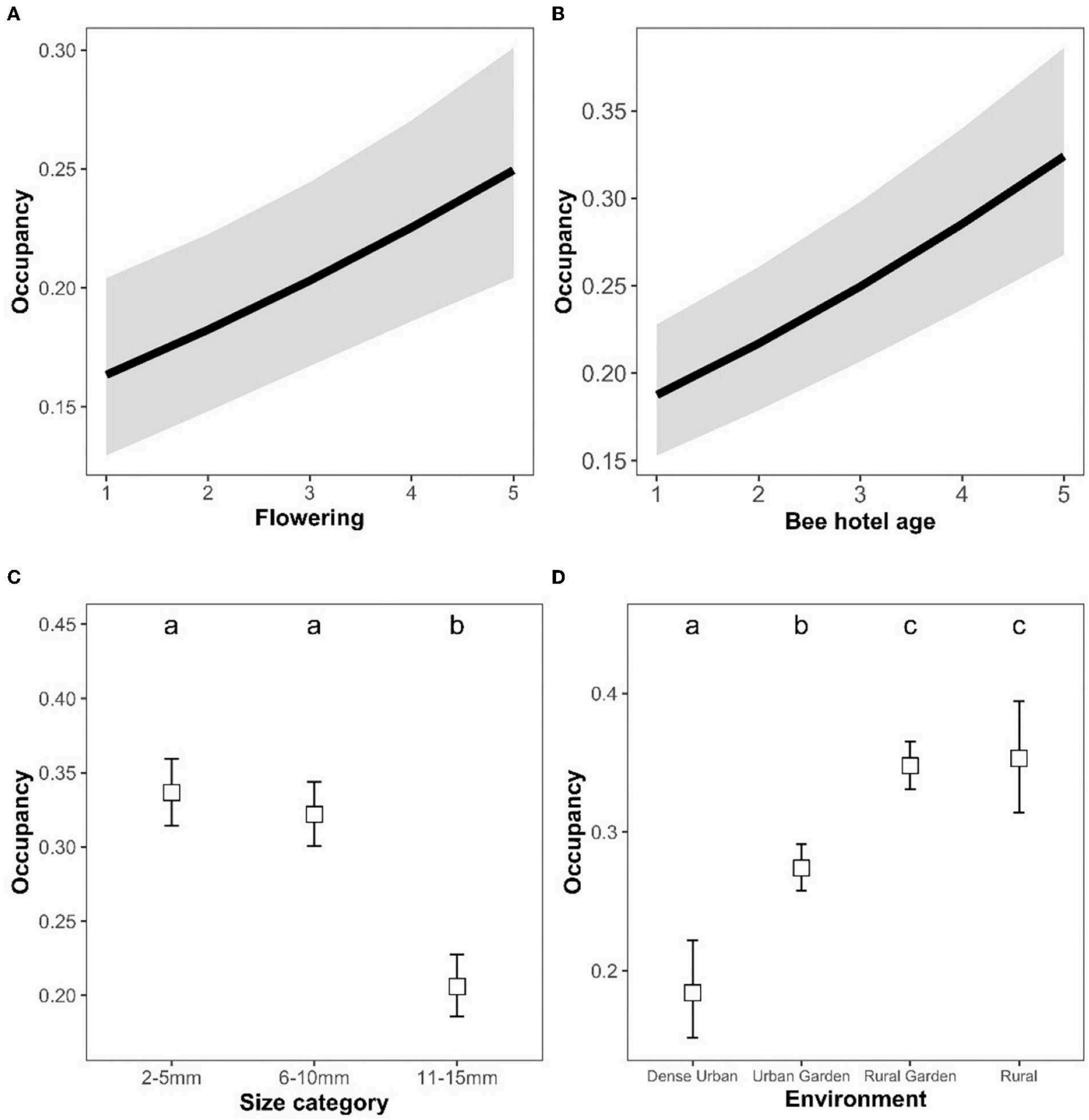

FIGURE 4
Bee hotel nest occupancy (estimated marginal means ± 95% confidence levels) in relation to **(A)** local flower availability, **(B)** bee hotel age, **(C)** nest hole size (diameter), and **(D)** surrounding environment. Pairwise comparisons of estimated marginal means **(C, D)** are indicated by compact letter display. Means (of size category and environment, respectively) sharing a letter is not significantly different.

part of the pollinator community and thus to a lesser degree attract more pollinators of other species (but see Simao et al., 2018; Staab et al., 2020). Simao et al. (2018) also show that, for small generalist bees, additions of urban flower resources had the strongest (positive) effect at low surrounding resource levels, whereas at higher levels the effect was unpredictable. Most (75%) of respondents reported plantings from single-family housing areas and we expect a generally high level of flowering of ornamental plants in such locations. In contrast, adding more plant species to a garden meadow dominated by native plants may increase the attractiveness of the garden to a wider array of pollinator species, including some specialists. Participants were only asked about the number of plant species present in their meadows or plantings, not about the abundance. It is therefore possible that we had seen a positive effect of flower abundance on pollinator activity in both meadows and plantings (as we did for occupancy of bee hotels), had we measured this variable. Indeed, the size of plantings, which is likely positively related to flower abundance, had a positive effect on pollinator abundance.

4.2. The value of interventions increase with time

Our results highlight the enhanced benefit of older flowering elements and bee hotels, and thus the need for gardeners to make more lasting commitments to changes in garden design and management. The significant positive effect of planting age (and the non-significant positive trend for meadows) could be because perennial plants, which are often preferred by bumblebees (Fussell and Corbet, 1992), often require several years to establish and flower from seed. Gardeners may make several attempts at sowing or planting new species into an intervention, thus intentionally increasing plant richness over time. In addition, spontaneous establishment of plant species, especially in garden meadows, may lead to increased plant diversity over time (Norton et al., 2019). Age and plant diversity were indeed positively correlated. Another explanation could be that beneficial micro-habitats build up over time in gardens and flower beds, including bare patches of soil for ground nesting bees, dead wood and stems with hollows for cavity nesters, and dead organic matter for some hoverfly taxa, allowing a delayed response of pollinator populations to an intervention. For bee hotels, the philopatric behavior of many solitary bee species may explain why occupancy builds up over time. The increased occupancy of older nests has previously been described for the common species *Osmia bicornis* (Steffan-Dewenter and Schiele, 2004; Fortel et al., 2016).

4.3. Nest size determine bee hotel occupancy

The largest nest cavities (11–15 mm) were far less inhabited than smaller ones (2–5 and 6–10 mm). Most likely, this is due to there being few bee or wasp species in Sweden that use nests larger than 10 mm; Recommendations for bee hotels in temperate regions rarely stretch past 12 mm (e.g., Naturhistoriska Riksmuseet, 2013; Bauer et al., 2015; Winter, 2018). Clear information about preferred size and design of bee hotels may thus increase the occupancy of hotels in future campaigns.

Bee species differ in their requirements for nesting conditions. Of Sweden's approximately 250 solitary bee species, around 70% are ground nesters, and only a small fraction of species are known to nest in bee hotels (Linowski et al., 2004; Naturhistoriska Riksmuseet, 2013). Despite this, bee hotels may be useful bio-indicators for insect pollinators in general (Tscharntke et al., 1998). A garden where a bee hotel is highly occupied can thus be expected to host many other pollinating insects, either nesting in and/or visiting the garden to forage.

4.4. Fewer pollinators seen in urban environments

We found that the surrounding environment moderated pollinator abundances in flower interventions, such that plantings in single-family urban or rural gardens and rural natural environments were more visited by pollinators, compared to yards and green spaces in dense urban areas. Similarly, bee hotels in both rural gardens and natural environments were more occupied compared to those in both types of urban sites. Our results thus corroborate previous research showing that urbanization is generally negative for insect abundance and diversity, including pollinators (Fortel et al., 2014; Geslin et al., 2016; Fenoglio et al., 2020; Piano et al., 2020). However, pollinator taxa and trait groups differ in sensitivity to urbanization. Butterflies (Fenoglio et al., 2020; Piano et al., 2020) and hoverflies (e.g., Verboven et al., 2014; Persson et al., 2020) are generally negatively affected by urbanization and, while a recent meta-analysis show that bee diversity is negatively affected by urbanization (Fenoglio et al., 2020), other studies have shown that cavity nesting and long tongued bee species may actually benefit from intermediate to high levels of urbanization (Fortel et al., 2014; Wenzel et al., 2019). Our results show that urban bee hotels were less occupied than those in rural sites, indicating that cavity nesting species were actually less abundant in urban areas of Sweden. This could partly be explained by the large geographical uptake of the campaign, whereby we likely included rural sites spanning from those embedded in production landscapes to those rich in semi-natural or natural habitats, where the latter may harbor high bee abundance and diversity. Alternatively, and a bit speculative, bee hotels in urban areas may be of lower quality than those in rural or natural sites; e.g., they may more often be store-bought rather than home-made or place-built, and/or placed in too exposed or too shaded sites. This may make them less attractive to nesting bees compared to those in rural/natural sites (von Königslöw et al., 2019).

Regarding bee body size, results are so far inconclusive. While some studies show that small bodied species may benefit from highly urbanized areas (Banaszak-Cibicka and Zmihorski, 2012; Gathof et al., 2022), other studies find the opposite (reviewed by Wenzel et al., 2019). In addition, body size and nesting substrate may be correlated, such that small bees more often are ground nesters (Banaszak-Cibicka and Zmihorski, 2012). Our results do not indicate that any size class of cavity nesting bees benefit from urban areas (non-significant interaction for environment and size class).

However, we have not assessed ground nesting species and may therefore have missed genera that are particularly well-adapted to urban environments.

4.5. High engagement in biodiversity among participants

Flowering interventions were seen as more successful when they attracted many pollinators, indicating that respondents evaluated their interventions based on the desired ecological outcome (to provide flowers and benefit pollinators). Previous research has shown that pro-pollinator actions may be conditional on the degree to which people perceive that their actions will indeed benefit pollinators (Knapp et al., 2021). Although not tested here, this may lead to a reinforcing loop, where perceived successful interventions remain, while less successful ones are terminated.

People who choose to design and manage their gardens to benefit biodiversity do so for a multitude of reasons, ranging from aesthetics and personal well-being to a sense of moral responsibility for nature (Freeman et al., 2012; Goddard et al., 2013; Knapp et al., 2021). People who are personally engaged and interested in biodiversity may also be more likely to perform acts beneficial to biodiversity (see e.g., Maiteny, 2002). This could explain why the majority of the respondents in this study stated that they are highly engaged in issues concerning biodiversity. Indeed, a growing number of studies highlight citizen science as a tool in the transition to a more sustainable society by strengthening, encouraging, and validating public participation in environmental and sustainability issues (Dickinson et al., 2012; Shulla et al., 2020).

5. Future directions and limitations to the study

While citizen science projects with appropriate organization and design have been shown to provide data with similar quality as that collected by professionals (Danielsen et al., 2014; Henckel et al., 2020), problems concerning data reliability and quality may occur (Bonney et al., 2014; MacPhail and Colla, 2020). For example, Mason and Arathi (2019) show that a citizen science program that included volunteer training gave reliable data concerning pollinator presence only at the level of morpho-species, while species specific mapping was less accurate. The campaign "Operation: Save the bees" did not include training of participants in doing insect observations. Respondents will thus have very different levels of understanding and knowledge about flower visiting insects and the research methods, and answers may therefore vary between rough estimates and exact answers. The lack of definition of "few" vs. "many" insects is another weakness. On the other hand, the questions asked here were kept simple precisely in order not to require prior knowledge on pollinator or plant species identification, and only 1% of respondents specifically stated that they found certain questions difficult to answer (data not shown). Our results align with expectations based on previous scientific studies, indicating that data is of acceptable quality in relation to the questions asked and statistical models used. However, our study may suffer from so called "expectation bias" regarding insect observations in flower interventions, such that respondents that have a more species rich flower interventions also expect to see more insects, and thereby report too high abundances. Our evaluation of the simple pollinator estimate, using a more structured flower visiting insect survey, indicate that the simple measure was valid. Even so, using a standardized survey protocol and adding surveys by trained staff as a control, would make possible proper evaluation of the simple method used. Training, e.g., through (online) instruction videos or workshops and interactions with campaign staff, and using photo and expert identification, could further improve both data quality and reporting frequency and allow the study of more complex research questions (e.g., Deguines et al., 2016; MacPhail and Colla, 2020). Training participants using multimedia, and using social media to promote citizen science projects and help participants with insect identifications, has been shown to be successful both in terms of project outreach and an increased interest and awareness of the benefits provided by insects (Griffin et al., 2021, 2022).

The majority of the respondents were middle-aged women highly engaged in biodiversity. There can be both age and gender differences regarding engagement, knowledge, roles, and responsibility in relation to biodiversity and (wildlife) gardening (Soga and Gaston, 2018; Jones and Niemiec, 2020; Hanson et al., 2021). Although we do not know to what extent respondents singlehandedly established and surveyed interventions, the results indicates that engagement and uptake of interventions could be further increased by engaging a more diverse group of participants, including more men and younger people in the campaign. Indeed, a recent study in Great Britain suggest that men are overrepresented in environmental citizen science programs (Pateman et al., 2021). Highlighting the science part of the campaign, e.g., through multi-media resources and outreach such as developed by Griffin et al. (2021), could therefore attract and involve more men.

6. Conclusions

Our results show that data collected by citizens can be a useful tool for evaluation of small-scale conservation interventions in private green spaces. Larger and more species rich flower interventions that last for multiple years, attracted more pollinators, and should thus be promoted in future campaigns. Supporting information and assistance on how to establish and manage garden meadows (e.g., through online fora) could increase the success rate and promote more species rich and long lasting interventions. In addition, differentiating the recommendations regarding plant choice based on soil type and surrounding environment (e.g., urban, rural, latitude/climate zone) may improve outcomes.

The results indicate that the flower interventions registered through "Operation: Save the bees" may have a positive effect on local insect pollinator abundance. The fact that private gardens can be efficient tools in supporting biodiversity in general (Goddard et al., 2010) and pollinators in particular (e.g., Samnegård et al., 2011; Martins et al., 2017; Baldock et al., 2019) merits further work on how to engage the public in biodiversity friendly gardening practices.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

SSNC and Lund University share the ownership and responsibility for the data collected through the campaign. The data used does not contain any personal information. People who participated in the campaign and completed the survey did so voluntarily.

Author contributions

AP conceived the idea, designed the study, and collected data together with officers at SSNC. IL, VH, and LK analyzed the data with input from AP and LN. IL wrote the first draft of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2022.1099100/full#supplementary-material

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Bee diversity on urban rooftop food gardens

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Green infrastructure on rooftops in urban areas can enhance important ecosystem services. In addition to mitigating water runoff and regulating building temperatures, green roofs can provide food and nesting resources for wildlife. Rooftop gardens can also be utilized to cultivate food crops, giving them the potential to attenuate instances of food insecurity which are commonplace in many urban areas. Given that many crops depend on bee pollination, it is imperative to characterize the rooftop bee community. Therefore, we sampled three urban food roofs near downtown St. Louis, MO during the 2017 and 2018 growing seasons. We found 38 bee species utilizing the rooftop farms. We then compared the rooftop bee communities to those of two nearby ground-level community gardens. The roofs had lower abundances of *Bombus* species than the ground-level sites while non-native cavity nesters in the genus *Megachile* were overrepresented. These results indicate that the rooftop bee communities represent a nested subset of the species found at ground level. This has important implications for the management of green roofs for growing crops, as this shift in bee community structure may play a role in determining which crops can be adequately supported with pollination services.

KEYWORDS

green roofs, food security, biodiversity, Hill numbers, pollination services

Introduction

Cities aiming to combat the negative impacts of impervious surfaces, including stormwater runoff, polluted water and air, and the urban heat island effect employ green infrastructure methodologies that marry engineering solutions with natural processes (Parker and Zingoni de Baro, 2019). One cost-effective solution, green roofs, can mitigate flooding events, help regulate building temperature, and lessen the impact of pollutants entering storm drains (Getter and Rowe, 2006). Green roofs also improve the aesthetics of urban landscapes, and can serve as public recreational spaces as seen from New York City's High Line, and Denmark's CopenHill. Additionally, green roofs have been found to provide habitat to a variety of birds (Wang et al., 2017; Belcher et al., 2018), arthropods (Madre et al., 2013; Wooster et al., 2022), and pollinators (Colla et al., 2009; Tonietto et al., 2011).

Although there have been many investigations into plants suitable for green roofs (e.g., Dvorak and Volder, 2010), a review of the literature examining bees on green roofs shows a relative paucity of research (Hofmann and Renner, 2018). Furthermore, most of the literature focuses on managed honeybees, with only a third of the papers ($n = 8$) focusing on wild bee species diversity. A positive conclusion by Hofmann and Renner (2018) was that green roofs may have the potential to host a large diversity of wild bee species. Primarily, the bee species found on green roofs tend to be pollen generalists, cavity nesters, and medium sized (MacIvor and Lundholm, 2011; Tonietto et al., 2011). Alternatively, in a more recent study conducted in Geneva, Switzerland, Passaseo et al. (2021) found the functional trait diversity among green roof bees was representative of the ground-level bee community. More research on a variety of green roof habitats could further elucidate the extent to which these spaces are being used by bees, and how their management can contribute to pollinator conservation.

The bee community on roofs is also influenced by the characteristics of the roofs themselves. In a study of wild bee diversity of green roofs in Vienna, Austria, bee diversity and abundance were positively correlated with percent of flower coverage (Kratschmer et al., 2018). Bee diversity also increased with the overall flower diversity, and as with other studies, cavity nesting bees were dominant. However, ground nesting bees increased in abundance and diversity as the amount of fine substrate soil on the roof increased (Kratschmer et al., 2018).

An emerging trend in green roof management is growing food crops (Cristiano et al., 2021). These so-called "food roofs" could be a tool to address food security *via* urban agriculture (Specht et al., 2014). Additionally, in many cities the soil is contaminated with harmful compounds such as lead, making certain crops grown in these soils unsafe to eat (Byers et al., 2020). Thus, importing clean soil to structures like roofs to grow crops can ensure that the food is safe to consume (Brown and Jameton, 2000).

The success of food roofs will depend in part on whether insect pollinators that visit the crops are both diverse and abundant enough to provide adequate pollination services. Previous research has suggested that green roof arthropod communities exhibit lower abundances and species richness when compared to nearby ground-level habitats (Wang et al., 2022). Thus, it is possible that decreased bee diversity may result in diminished pollination rates for animal-pollinated crops on green roofs (Ksiazek et al., 2012). Many crops, such as members of the families Cucurbitaceae (e.g., melon, squash, cucumber) and Solanaceae (e.g., tomato, pepper, eggplant), require insect pollination for fruit set (Stoner, 2020; Cooley and Vallejo-Marín, 2021). Most Solanaceae also require sonication for pollen release, which can only be performed by certain bee taxa including *Bombus* and some Halictidae (Cardinal et al., 2018). This will be critical in highly urbanized areas where the amount of impervious surface around roof gardens is extensive and therefore the distances between potential source habitats are greater. Furthermore, for potential pollinators to find these green roofs they must also be capable of ascending to high elevations. This represents a type of environmental filtering that selects for stronger flyers, which tend to be larger bodied bees like members of the genera *Bombus* and *Xylocopa* (Wojcik and McBride, 2012).

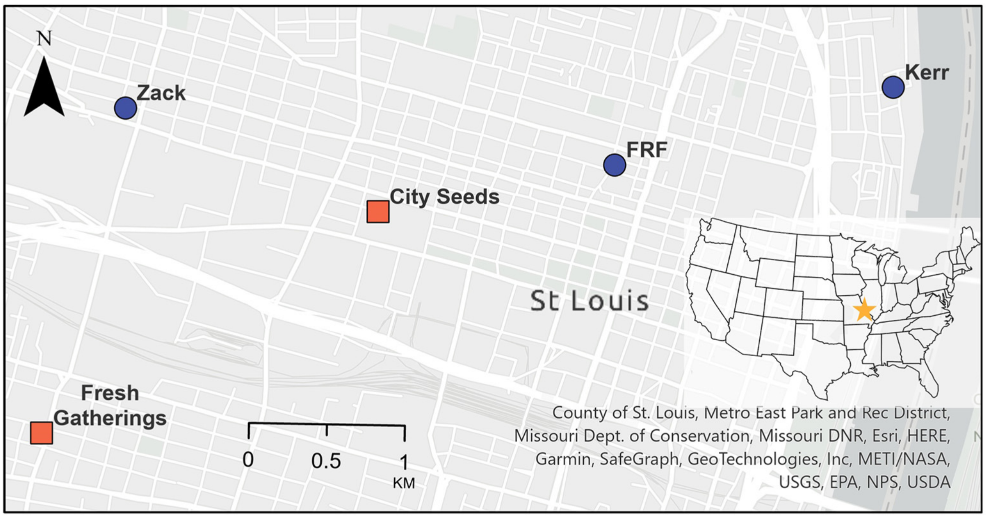
The goals of this study were 2 fold: (1) to document the bee community diversity of three urban food roofs in downtown St. Louis, MO; and (2) to compare the bee diversity of food roofs to nearby community gardens with similar crop diversity.

Materials and methods

Study sites

The three roof sites were in the downtown area of St. Louis, Missouri, USA (Figure 1). These rooftop farms were installed and maintained by the non-profit organization Urban Harvest STL. Food Roof Farm (FRF) was established in 2015 and featured a greenhouse, vegetated walls, and raised garden beds. The building is two stories (9 m), with a roof footprint of 790 m^2. The surrounding 500 m is 87% impervious surface at 1-meter resolution (East-West Gateway Council of Governments, 2017). During the time of study, FRF housed a large mix of native and non-native flowering plants including edible herbs, legumes, vegetables, and Missouri natives including *Echinacea* spp., *Asclepias* spp., and *Rudbeckia* spp.

The Kerr location was established in 2006 as a green roof using sedum Green Roof Blocks^{TM}, which are small self-contained units prefilled with growing substrate. Later, Urban Harvest STL partially converted the space into a food roof with the addition of modular Smart Pots$^{®}$, which are circular fabric pots. The building is one story (5 m) and the roof footprint is 165 m^2. It is adjacent to the Mississippi river (35% water within 500 m) and is surrounded by abandoned industrial buildings and overgrown lots. The surrounding 500 m is 50% impervious surface at 1-meter resolution. During the time of study, Kerr was growing vegetables such as squashes, tomatoes, and peppers, and herbs including basil and thyme, while still maintaining large amounts of sedum.



County of St. Louis, Metro East Park and Rec District, Missouri Dept. of Conservation, Missouri DNR, Esri, HERE, Garmin, SafeGraph, GeoTechnologies, Inc, METI/NASA, USGS, EPA, NPS, USDA

FIGURE 1
Map of collection locations in downtown/midtown St. Louis, Missouri. Food roofs sites are represented as blue circles, and ground-level community gardens are represented as orange squares.

TABLE 1 Species lists for roof locations.

			FRF		Kerr		Zack
Taxon	Status	Nest	2017	2018	2017	2018	2018
Andrenidae							
Calliopsis andreniformis	N	G	0	0	0	1	0
Apidae							
Bombus griseocollis	N	CL/G	2	3	0	1	2
Bombus impatiens	N	CL/G	1	0	0	0	2
Bombus pensylvanicus	N	CL/G	0	2	0	2	0
Ceratina calcarata	N	P	4	3	3	0	0
Ceratina strenua	N	P	0	0	6	8	0
Melissodes bimaculatus	N	G	14	47	0	0	2
Triepeolus lunatus	N	K	1	0	0	0	0
Xylocopa virginica	N	CV	5	4	2	0	1
Colletidae							
Colletes latitarsus	N	G	0	0	0	1	0
Hylaeus affinis/modestus	N	CV	0	0	0	1	0
Hylaeus illinoisensis/spA	N	CV	0	0	1	0	0
Hylaeus leptocephalus	I	CV	0	1	0	0	0
Hylaeus mesillae	N	CV	42	16	0	0	0
Halictidae							
Agapostemon virescens	N	G	0	9	6	73	6
Augochlorella aurata	N	G	0	0	0	2	0
Augochloropsis metallica	N	G	0	0	0	12	0
Halictus confusus	N	G/CL	2	2	8	7	0
Halictus ligatus	N	G/CL	1	14	13	12	0
Lasioglossum bruneri	N	G	0	0	0	1	0
Lasioglossum hitchensi	N	G	0	0	4	1	0
Lasioglossum imitatum	N	G	1	1	13	14	0
Lasioglossum sp1	N	G	4	1	0	0	0
Lasioglossum sp2	N	G	1	0	1	0	0
Lasioglossum tegulare	N	G	6	12	3	1	0
Lasioglossum zephyrus	N	G	0	0	2	4	0
Megachilidae							
Anthidium manicatum	I	CV	16	14	2	2	20
Anthidium oblongatum	I	CV	4	9	0	3	13
Coelioxys octodentatus	N	K	5	2	2	0	3
Heriades carinata	N	CV	1	0	0	0	0
Heriades leavitti/variolosa	N	CV	5	4	4	2	1
Megachile apicalis	I	CV	1	3	0	0	0
Megachile brevis	N	CV	5	2	0	0	0
Megachile concinna	I	CV	17	11	0	5	15
Megachile exilis	N	CV	10	7	0	0	0
Megachile mendica	N	CV/G	8	6	0	0	2
Megachile rotundata	I	CV	76	45	6	6	24
Megachile texana	N	G	41	37	1	3	16

Status denotes whether the species is native (N) or introduced (I) to the region. Nest denotes the nesting strategy of G (ground), CL (colony), CV (cavity), K (kleptoparasite), or P (pith).

The Zack location was established in 2018 using Recover Aerated Media Modules (RAMMs), which are portable fabric pots filled with growing media that are supported by plastic crates. The building is four stories (16 m) and the footprint is 315 m^2. The surrounding 500 m is 70% impervious surface at 1-meter resolution. The sampling of this food roof was done during its first active year, during which it was used to grow many herbs and vegetables, a few natives including *Asclepias* spp., and a variety of non-native ornamental flowers.

Sampling methodology

In 2017, we sampled FRF and Kerr 10 times between May and August. In 2018, each of the three roofs were sampled eight times each between June and August. Sampling occurred roughly weekly between the hours of 9:30 and 14:00 on days that ranged from sunny to partially cloudy. All pollinator sampling was performed *via* targeted aerial netting. FRF was sampled for 90 min during each visit whereas Kerr and Zack were sampled for 60 min. Sampling effort was comparable given the area covered by each garden. Honeybees, *Apis mellifera,* were not intentionally collected and were excluded from analyses. Bees were identified to species level by Nina Fogel and Michael Arduser utilizing regional taxonomic keys (Arduser, 2020; Ascher and Pickering, 2021). All specimens were pinned, labeled, processed, and housed in the insect collection of the biology department at Saint Louis University (catalog numbers jkr0001-jkr0889).

Rooftop species diversity analysis

To determine if there was a difference in species richness between the roofs, we utilized the “iNext” package (Hsieh et al., 2016) in the R computational environment (R Core Team, 2022). We used coverage-based rarefaction curves (Chao and Jost, 2012) to interpolate and extrapolate the data to obtain relevant metrics utilizing Hill numbers (Roswell et al., 2021). For Hill numbers (denoted as q), $q = 0$ is richness, $q = 1$ is the Shannon–Weiner diversity index, and $q = 2$ is equivalent to Simpson’s diversity index (Roswell et al., 2021).

We used coverage-based extrapolation in the rarefaction analysis with 95% confidence intervals to determine differences among sites. Since we lacked sampling data from Zack in 2017, we only compared specimens from 2018. An analysis of both years for the other two sites is provided in Supplementary material.

Comparison to ground-level sites

To determine if the roof community was a subset of the ground-level community, we compared the aggregated roof data to that of the two nearest community gardens. The community gardens, City Seeds (planted area ∼2,300 m^2) and Fresh Gatherings (planted area ∼550 m^2), are located an average distance of 1.7 and 3.2 km away from the food roofs, respectively (Figure 1). Both ground locations contained comparable crops to those found in the food roofs. They also have similar surrounding impervious surface cover at 500 m using 1-meter resolution; 82% for City Seeds, and 62% for Fresh Gatherings. The sites were sampled weekly during the summer months in 2015 and 2016 following the same protocol as the roofs. All ground and roof sites were located in the contiguous downtown/midtown area of St. Louis city. Furthermore, all sites were at least 1 km apart and therefore the data are spatially independent due to the small foraging distance of most bees (Greenleaf et al., 2007). Because the abundances of individual species vary year-over-year, and the sampling years differ from the roof and ground locations, we focused on the relative abundances at the genus level for our ground to roof comparisons. Singletons and doubletons were removed. A correlation test, using Kendall’s tau, was used to determine similarity between the pooled ground and pooled roof locations.

Additionally, we created a dendrogram of Euclidean distance and Ward’s clustering using the “hclust” and “dist” functions in the vegan package (Oksanen et al., 2019). The general expectation is that if roofs are not a challenge for bees to reach, then dissimilarities should be based on random sampling error, and cluster distances should be similar among all locations. Alternatively, if some bee taxa lack the ability to reach the roofs (or locate the resources on them), then dissimilarities will emerge, and food roofs should cluster together.

Results

There was variation in the bee abundance and community composition between the roofs. We collected a total of 889 individuals, from 17 genera and 38 species (Table 1). FRF had 273 collected individuals in 2017 and 255 in 2018; Kerr had 77 collected individuals in 2017 and 162 in 2018; and Zack had 107 collected individuals from 2018. Six introduced cavity nesting species accounted for 40% of the collected roof specimens. Of

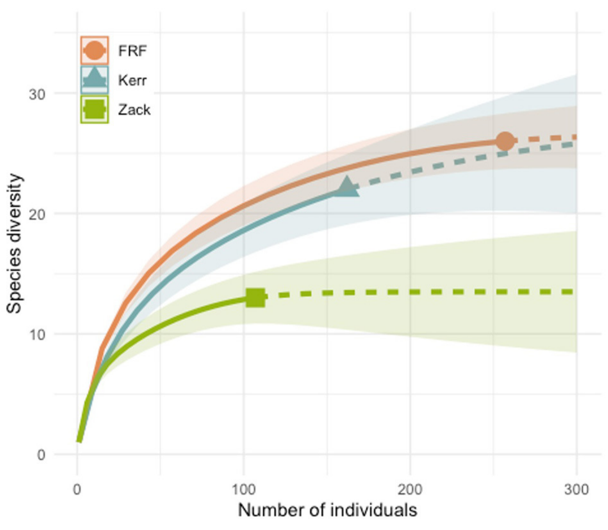


FIGURE 2
Species accumulation curves for the three roof sites for 2018. The solid lines denote rarefaction whereas the dotted lines are extrapolation. Confidence intervals are 95%.

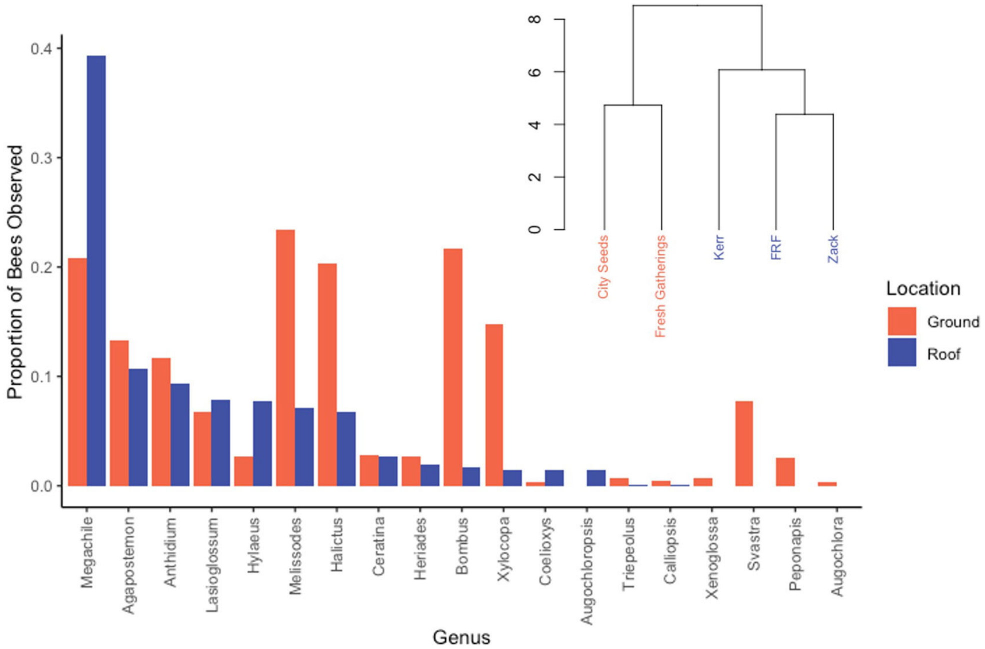


FIGURE 3
A comparison of community makeup at ground-level and roof-level by genus. The dendrogram indicates that the sites are grouped distinctly into two communities based on site type. The disparity in proportions of *Megachile* and several Apidae genera are the largest contributors to the difference in community composition.

the 60% of collected bees that are native, 22% ($n = 117$) nest above ground.

In 2018, the year that we have data for all three sites, there were differences in the species composition for the three roofs (Figure 2). We used diversity indices estimates based on coverage following Roswell et al. (2021). We found FRF had 26 observed species ($q = 0$), a $q = 1$ of 13.92 ± 0.91, and $q = 2$ of 9.6 ± 0.83. Kerr had 22 observed species ($q = 0$), a $q = 1$ of 8.55 ± 0.93 and $q = 2$ of 4.3 ± 0.61. Zack had the lowest diversity, with 13 observed species ($q = 0$), a $q = 1$ of 8.26 ± 0.71, and $q = 2$ of 6.78 ± 0.65. However, it is a possibility that the low diversity on Zack is because we sampled during the first season it was constructed, and thus there was low colonization, as compared to innate characteristics of the location.

The rooftop bee community differed significantly from the ground-level community (tau = 0.415, $z = 2.488$, $p = 0.012$). Roofs had a greater percentage of leaf-cutter bees (*Megachile* spp.), and decreased abundances of large bees including *Bombus* spp., *Melissodes* spp., and *Xylocopa virginica*, as well as fewer sweat bees in the genus *Halictus* (Figure 3). Additionally, the roof community was lacking the Cucurbitaceae specialists *Peponapis pruinosa* and *Xenoglossa strenua*, which were both present in the nearby ground sites. Only 12.6% of the ground specimens were introduced species. Cluster analysis further corroborated these results, with the two ground sites forming a cluster separate from the three roof sites (Figure 2). Furthermore, FRF and Zack were more similar to each other in community composition than they were to Kerr.

Discussion

The overall community structure of the food roofs does not represent a random assortment drawn from the city's species pool (Camilo et al., 2017). The high abundance and diversity of non-native species is not surprising given that previous research has found urbanization to be positively correlated with introduced species (Fitch et al., 2019; Gruver and CaraDonna, 2021). Additionally, green roofs have been found to have a higher percentage of non-native cavity nesting species than nearby ground-level habitats (Tonietto et al., 2011), which is consistent with our findings. It has been posited that cavity-nesting bees may be pre-adapted to flying at greater heights due to their nest searching behaviors (MacIvor, 2016), which may help explain why these species are more commonly observed in rooftop gardens.

Most non-native species tend to be generalists that can exploit a broad range of resources. Thus, the traits they exhibit allow them to take advantage of human-dominated landscapes (Russo et al., 2021). Introduced species can outperform natives' physiological thermal maxima allowing them to exploit resources when the natives cannot (da Silva et al., 2021). Thus, it is possible that the non-native species observed in the roof gardens can outperform the natives through an enhanced ability to ascend to rooftop elevations or tolerate the novel conditions located therein.

It is unclear from the literature whether green roofs filter for bees with larger or smaller body sizes. In this case, elevation does seem to represent a challenge. In our study, the food roof bee community differs greatly from the ground-level sites due in part to the absence of large bees. Large-bodied members of the family Apidae, especially members of the genera *Bombus*, *Svastra,* and *Xylocopa* were absent or had decreased abundances compared to nearby ground-level gardens. MacIvor et al. (2015) found that smaller bodied bees were significantly less common than medium to large-bodied bees on *Sedum* planted roofs and found the two most abundant species were *Megachile rotundata* and *Bombus griseocollis*. Alternatively, Ksiazek et al. (2012) found that bees with smaller body sizes dominated the specimens collected on Chicago green roofs. Determining which specific environmental filters and/or species traits are being acted upon will require further investigation.

The managers of the food roofs reported no observed pollination deficits. However, while it is easy to determine if pollination is grossly insufficient (due to low yield or misshapen fruits), it can be harder to assess if yields could further improve with additional pollination services (Webber et al., 2020). The roofs had a paucity of *Bombus* and *Xylocopa,* which are thought to be the main pollinators of many crops in the region because of their large size and ability to sonicate flowers (Cooley and Vallejo-Marín, 2021). However, other sonicating genera such as *Melissodes*, *Agapostemon* and the large, non-sonicating *Megachile texana* may be filling the gap (Cardinal et al., 2018). Many of the crops present were obligate outcrossers that require bees for pollination. Some crops, like those in the family Solanaceae, require specialized pollinators, while others require a great number of individual visits. Thus, the amounts and types of pollination deficits, as well as the need for specific types of pollinators must be addressed in future research.

As the number of green roof managers opting to grow bee-pollinated crops increases, understanding the potential limitations to attracting sufficient bee diversity becomes more relevant. It is important for organizations seeking to grow crops on roofs to understand that there may be pollination deficits, especially in dense urban areas. Thus, green roof managers should ensure that there are resources for pollinators all season, especially when crops are not in bloom.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JR and GC conceptualized the experiment. JR and JH performed fieldwork and processed specimens. NF curated the data. NF and GC did the analyses. All authors worked on the writing and editing of the draft. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2023.1100470/full#supplementary-material

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The conservation of urban flower visitors Down Under

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The majority of the human population now lives in urban environments and that proportion is forecast to increase dramatically by 2050. As urbanization increases, the urban environment will increasingly play a role in biodiversity conservation. Floral visitors, often erroneously referred to as pollinators, are integral to the maintenance of ecosystem services and function. Several floral visitors are capable of adapting to urban environments, but for comprehensive protection, management practices must be tailored to specific groups. Urban biodiversity conservation is usually discussed from the northern hemisphere perspective, which has a very different ecology than its southern counterpart. Here we compare and contrast conservation strategies for urban flower visitors in Australia and New Zealand to the northern hemisphere, with a focus on birds and bees. The differences in flower visitors and floral characteristics mean that unique management strategies, which consider the local evolutionary context and integrate native flora, are required to support urban flower visitors. An additional important difference is that neither honey bees nor bumble bees, which reach high local densities in many areas, are native to the region, and thus should be excluded from urban biodiversity schemes.

KEYWORDS
urbanization, beekeeping, pollinators, conservation, flower visitation

The urban environment as focal areas for biodiversity conservation

As the human population increases, more stress is being placed on remaining wild habitats. While it is always preferable to maintain native ecosystems, urban environments are increasingly prevalent, and can play an increasingly important role in biodiversity conservation. These areas cannot replace wild habitat, but they can help to protect a subset of biodiversity. Targeted, local strategies should be developed to reach the full capability of urban areas for biodiversity conservation. Here we explore such strategies for flower visiting species in Australia and New Zealand.

The percentage of people living in urbanized areas is forecast to grow from the current 55% to nearly 70% by 2050 (UNDESA, 2018). The concept of flower visitor conservation in urban areas is just one component of the broader goal of urban biodiversity conservation. Urban areas, while generally detrimental to biodiversity overall, are able to support significant concentrations of native flowering plants and hence populations of insect and bird flower visitors, especially when managed effectively (Normandin et al., 2017). In addition, urban environments have been shown to host more abundant and diverse communities of insects than farmland (Baldock, 2020). Cities can provide adequate habitat for many insect species due to their relatively small functional requirements (i.e., habitat range, life cycle, and nesting behaviors) as compared to other types of biodiversity (New, 2018). Importantly, planning opportunities to support bee biodiversity in urban environments can easily be promoted as these can provide mutual benefits for bees and humans, in particular because the former provide pollination for backyard fruit crops (Iwasaki and Hogendoorn, 2021).

However, bees that do well in urban areas are often exotics or generalists, such as honey bees, and as such may be the least threatened species (Cane et al., 2006; Baldock et al., 2015; Fitch et al., 2019). While these generalist and introduced bees deliver pollination services in urban gardens, exotic species can have further negative effects on native flower visitors, and particularly on species that have specific dietary requirements (Geldmann and González-Varo, 2018; Iwasaki and Hogendoorn, 2022). Pollinator declines are largely driven by losses of specific plant resources and associated habitats, and is especially pronounced for specialist species, which can result in subsequent losses of rare or dependent flowering plant species leading to mutual extinctions (Waser et al., 1996; Wood et al., 2019). In the face of pollinator declines, public attention is often directed toward well-known species, potentially to the detriment of native species (Senapathi et al., 2015), which can also be charismatic for the public (Figure 1). Thus, to properly conserve the biodiversity of flower visiting species in urban areas, attention must be paid to the identity and relative needs of each species, and in as far as possible, support should be provided for every aspect of their life history.

To maintain a diverse community of flower visiting bees and birds, year-round food availability is especially important as taxa have different seasonal patterns of emergence and resource requirements. Bees for example are completely reliant on pollen and nectar, and thus increasing floral resources (if nesting habitat is available) can increase local populations. Such an increase can be achieved not only by planting flowering plant species, but also by decreasing mowing frequency to allow weeds, crops, or ornamental species to flower (Wastian et al., 2016; Baldock, 2020). However, such measures will typically benefit generalist species the most (Baldock et al., 2015; Theodorou et al., 2017). For local native species, weeds and ornamentals may not provide the same food quality as the native plants that they have replaced and many species may not be used at all (Banaszak-Cibicka et al., 2016; Lowenstein et al., 2019). Therefore, it is key to evaluate the respective quality and quantity of useful floral resources available when managing urban green spaces. For example, specialist bees may be sustained by larger plantings of native plants in community gardens or collective efforts by neighboring gardeners.

The perspectives Down Under

Most insights into urban flower visitors are from the Northern Hemisphere, in particular Europe and North America (Baldock, 2020), and thus there is a gap in perspectives for the southern hemisphere, and particularly for Oceania. Due to their relative affluence, large population size, unique biodiversity, and high degree of urbanization (Cresswell and Murphy, 2017; UNDESA, 2018), Australia and New Zealand have the most relevance to urban pollinator conservation methods in Oceania. Therefore, and because of the large variation in geology, geography, and ecology within Oceania, we will restrict this review to these two countries.

North America and Europe, having had prehistoric geographic connectivity, share many plant and animal species with similar evolutionary lineages (80% of plant species from 15 families are shared; Rodriguez et al., 2006). Within Oceania, the Pacific Ocean has served as a significant barrier to colonization of bees in particular, but humans, prevailing winds, and currents have resulted in establishment of flora and fauna elements from Australasia on the relatively younger islands, which have largely been formed as a result of volcanic action (Groom and Schwarz, 2011; Dorey et al., 2021).

A prominent feature of the Australian environment is the prevalence of unpredictably but abundantly flowering nectar-rich shrubs and trees which feed a diverse range of vertebrates including honey eaters, parrots, bats, possums, as well as invertebrates (Armstrong, 1979; Ford et al., 1979; Woinarski et al., 2000; Gross, 2001; Cunningham et al., 2002; Abrol, 2012; Hermansen et al., 2014). Birds in the endemic family Meliphagidae (honeyeaters) are particularly significant flower visitors in Australia and New Zealand (Driskell and Christidis, 2004). In Australia, Gondwanan flora that is heavily utilized by bees and birds alike are representatives of the families Myrtaceae, Proteaceae, and Fabaceae (*Acacia*; Ford et al., 1979). Based on visitation records, Ford et al. (1979) suggest that about 100 plant species are bird pollinated, and many of these species belong to the group of Myrtaceae which have radiated throughout the continent in the last 35–60 million years (House, 1997). These species present large numbers of flowers that generally produce relatively weak nectar, which are thought to be adaptations to bird pollination (Ford et al., 1979). In addition, many species have either an unpredictable or an intermittent flowering phenology (House, 1997). New Zealand and most of the Pacific islands have no extant native *Eucalyptus*, but can have high abundances of other species in Myrtaceae (*Metrosideros* spp. in particular, which have been shown to be bird pollinated; Schmidt-Adam et al., 2009).

The areas also differ in their bee populations. Australia has a large and idiosyncratic bee fauna of over 1,700 bee species. Many Colletidae and Stenotritidae have a Gondwanan origin, while representatives of the families Halictidae, Megachilidae, and Apidae have colonized Australia from the north as the continent drifted closer to Eurasia (Houston, 2018). Most Australian bees are relative specialist and forage on Australian native plants in the family Myrtaceae (Michener, 1965). Many new species, possibly including endangered ones, are still being described (e.g., Leijs et al., 2018; Leijs and Hogendoorn, 2021). By contrast, New Zealand has a relatively poor bee fauna as a result of their recent origin and geographical isolation. The roughly 30 native bees in New Zealand are all closely related ground-nesting bees in the families Colletidae and Halictidae, and are likely derived from Australian progenitors relatively recently (i.e., ∼23 mya; Donovan, 2007; Scott et al., 2014). The recent arrival and low number of bee species may have caused New Zealand pollination syndromes to be relatively more generalized (Godley, 1979; Newstrom and Robertson, 2005).

Australia and New Zealand also differ from Europe in that honey bees (*Apis mellifera*) and bumblebees (*Bombus* spp.) are introduced species. The introduction of both these species has resulted in large numbers of feral colonies. Honey bees are present throughout temperate and Mediterranean climates in Australia, where they may compete with hollow nesting birds and mammals for nesting hollows and with flower visitors for floral resources (Paini, 2004; Cunningham et al., 2022). Bumblebees are present throughout New Zealand and on Tasmania, where they are significant pollinators of weeds and fruit trees. In studies on competition in New Zealand, introduced bees had clear preferences for European plants over native species, suggesting niche partitioning by respective geographic origin (Iwasaki et al., 2018). Regardless, honey bee centric conservation goals (Iwasaki and Hogendoorn, 2021) proposed mostly in Europe and often mistakenly applied to North American urban areas are not applicable to Australia

FIGURE 1
Charismatic bees of Australia and New Zealand. *Xylocopa aerata* (Australia, Remko Leijs), *Leioproctus fulvescens* (New Zealand, Jay Iwasaki), and *Amegilla* sp. (Australia, David Marquina Reyes).

and New Zealand. The dominant focus on bumble bee conservation found in the northern hemisphere also has no place Down Under.

Thus, distinctions must be made between conservation of urban flower visitors, urban pollinators, urban bee conservation, and urban beekeeping as they are not synonymous. While many concepts may be similar, flower visitors are not necessarily pollinators, and, Down Under, they are a diverse group of animals, which include many bird species. In addition, as honey bees are not native to Oceania and consume large amounts of pollen and nectar (Cane and Tepedino, 2017), urban beekeeping is inconsistent with biodiversity conservation, despite the fact that bee conservation and urban beekeeping is often perceived as identical by the public (Geldmann and González-Varo, 2018). Many conservation actions may benefit all flower visitors, but when defining urban flower visitor conservation, it is important to make clear distinctions and to clarify the objectives.

Conservation efforts for flower visitors primarily entails maintaining or increasing native floral resources for nectar foragers (bees, bats, and birds) and nesting habitat within Australian cities and suburbs. As a result of the high relative nectar requirements of vertebrates, conservation of flower visiting birds, bats, and mammals in Australia involves nectar producing trees and shrubs rather than lower plants. Unlike Australian flowering trees and shrubs (namely Myrtaceae and Proteaceae), introduced tree species do not necessarily provide floral resources for native birds or insects. In addition, many of the introduced plants in urban gardens that are attractive to honey bees are not or hardly visited by native bees, presumably because they have not co-evolved with them (Michener, 1965; Houston, 2018; Brown and Cunningham, 2019). Most bees specialize on native plants, and several species are oligolectic on a subset (Michener, 1965; Houston, 2018).

Many bird species are similarly adapted to specific groups of plants. For example cockatoos and lorikeets have a bulbous scaly tongue to harvest nectar from Myrtaceae, while the thin, long, brush-tipped tongues of the honey eaters allows nectar collection from Proteaceae (Ford et al., 1979). Nectar and pollen from Australian trees are also significant components of the diets of arboreal marsupials and large fruit bats, both of which have been shown to be effective pollinators (Armstrong, 1979; House, 1997).

The plants that native urban flower visitors rely on are sometimes not preferred for urban gardens. For example, the *Eucalyptus* species that many native bees, bird, and bat species strongly depend on may not be chosen in urban gardens because of their size and tendency to drop limbs. Other useful flowering plants that support specific species may not be preferred because they are hazardous, slow growing, or only flower for a limited period of time.

Many species of bees in urban environments are ground nesting species, and ground cover has been shown to have a negative correlation with bee abundance (Banaszak-Cibicka et al., 2016). This is of particular importance in parks and gardens, where open soil is often covered with either lawn or a thick layer of mulch to prevent evaporation. This may partly explain why, in urban areas, a larger proportion of bees are cavity nesters as compared to suburban or natural habitats, but the mechanisms behind such biases are as yet unknown (Hernandez et al., 2009). The degree of uncertainty in the factors driving urban bee ecology highlight the importance of future research in precisely how to maintain robust and diverse bee populations in urban environments.

While supplemental nesting habitat (nest boxes) cannot completely compensate for a lack of nesting hollows for vertebrate flower visitors, they can support bat, marsupial, and bird biodiversity in Australian cities (Le Roux et al., 2016; Macak, 2020). However, nest boxes can also provide habitat for invasive species, in particular European honey bees (Cunningham et al., 2022), and their placement can therefore be counterproductive to the conservation of native flower visitors (Macak, 2020). For bees, placement of bee hotels is very popular worldwide. While they help to encourage and maintain public awareness of the existence of solitary native bees, it is questionable whether their placement is an adequate conservation action (MacIvor and Packer, 2015). Bee hotels can host many introduced species (MacIvor and Packer, 2015). This is particularly likely to be an issue in New Zealand for example, where six of the 12 species that would use bee hotels are adventive (Donovan, 2007). In Australia, there are many native hollow nesting bee species that would potentially use bee hotels (Houston, 2018). However, even without promoting introduced species, the potential to benefit bee conservation is uncertain, as they may enhance the populations of predators and parasites (e.g., MacIvor and Packer, 2015; Geslin et al., 2020).

Flower visitors in New Zealand include birds, possums (introduced), and bats and these vertebrates known to be, or have been, important pollinators (Lord, 1991; Anderson, 2003). Invertebrate pollinators are thought to be mostly generalist, with flies and butterflies reflecting the greatest diversity of species (Anderson, 2003; Newstrom and Robertson, 2005). The New Zealand bee taxa is has relatively low diversity, but they have been shown to be efficient pollinators of several native plants (Bischoff et al., 2013). Referencing key plant species that are particularly important for native pollinators (Donovan, 2007) and maintaining urban forest reserves likewise are integral for maintaining urban biodiversity in New Zealand.

TABLE 1 List of key conservation actions for flower visitors in urban environments Down Under, including benefits and potential drawbacks.

Conservation action	Potential benefits	Potential drawbacks
Green space conservation, urban gardens, and floral enhancement	Increases resources available for flower visitors	Non-native plants may not provide resources for native species
		Plant choices may protect generalists more than specialist species
		Unwanted, expensive, or difficult horticulture
		Increased presence of fire prone vegetation
	Mitigation of urban heat island effects	
	Raises public awareness	
Preservation of nesting sites	Provides nesting habitat for flower visitors	Certain nesting habitat may not support specialist species
		Preservation of unwanted large, fire prone trees
Artificial nesting sites	Provides habitat for flower visitors	Artificial nesting sites may support unwanted species (e.g., honey bees in possum boxes)
		Artificial nesting sites may increase parasite populations
	Raises public awareness	
Controlling introduced pests	Reduces competition and/or predation	Lethal control of pests may be publicly unacceptable (e.g., cats, honey bees)

In addition, invasive species have contributed to significant declines in plant, marsupial, and bird communities in Australia and New Zealand, and there is significant public support for conservation efforts to reverse these trends, including in urban environments (Wittmer et al., 2018). As birds can be highly vulnerable to cat predation, urban pollinator conservation of avian flower visitors may require extensive removal of feral cats, limiting outdoor cat ownership, and trapping within urban areas (Kikillus et al., 2017). Regionally concerted efforts to establish strict feline control policies have been attempted within cities, but support from the general public for such strict rules has been limited (Grayson et al., 2002; Kikillus et al., 2017).

Controlling invasive species that have high public appeal also includes dissuading European honey beekeeping, which to the public is often the only bee they are familiar with. Urban beekeeping of honey bees is especially popular in Europe and in North America, where the public may be misled in thinking that honey bees are on the brink of extinction or otherwise imperiled (Egerer and Kowarik, 2020). In North America where honey bees are not native, urban beekeeping is more akin to maintaining livestock within cities and is not synonymous with maintaining or supporting local biodiversity (Colla and MacIvor, 2017). This is also the case in Oceania.

In Australia, native stingless bee can be kept in hives. Therefore, if hives are desired to be kept, native stingless bees, should be preferred for Australia. These species can thrive in urban areas (Kaluza et al., 2016) and have the potential to co-opt the focus on urban honey beekeeping. They also produce small quantities of unique honey, and can have greater foraging success in urban gardens than in forests or plantations (Kaluza et al., 2016). However, urban beekeeping of even a native species still may not align with the goals of urban pollinator conservation when it involves maintaining a single species at unnatural high densities. In those cases, the conservation benefits of artificially enhancing certain native bee species over others may be limited (Camps-Calvet et al., 2016).

The positive environmental effects of green spaces can also help to mitigate future threats from climate change, which will specifically increase harmful or catastrophic incidents from heat, fires, droughts, and flooding (Nicholson and Egan, 2020). The urban heat island effect is particularly exacerbated in urban environments, and in Australian capital cities the number of heatwave days are projected to triple within this century (Herold et al., 2018). Green spaces have the potential to mitigate some of the urban heat island effect, which may affect rarer specialist bees more negatively than generalists (Burdine and McCluney, 2019; Dew et al., 2019). Nevertheless, in the face of pollinator and biodiversity decline in general, conservation efforts in urban areas have great potential to protect biodiversity (Elmqvist et al., 2015). As urbanization increases, these efforts will become more important.

Conclusions

To summarize, habitat is the most important factor in supporting urban flower visitors. Habitat includes appropriate nutritional resources and nesting sites. In Australia and New Zealand in particular, unique flora and fauna means that northern hemisphere plant species may not provide the resources that native flower visitors require. Introduced mammalian predators also require control to protect predator-naïve species in urban areas (Table 1).

Generally, concepts in urban biodiversity management schemes follow universal principles and can be applied in Oceania, but also must address the local contexts regarding introduced species, relatively high urbanization rates, and fire dependent ecologies. Critically, an assessment of target goals following design implementation is crucial for determining successful design implementation and ensuring future sustainability (Garrard et al., 2018; Rega-Brodsky et al., 2022). Taken together, these approaches are integral for protecting biodiversity in the face of human population growth.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JI wrote the article. JI and KH contributed to conceptualization and extensively edited the manuscript. All authors contributed to the article and approved the submitted version.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Urban bee functional groups response to landscape context in the Southeastern US

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We investigated the influence of landscape cover on urban bee community functional groups. We observed a diversity of functional groups across primarily forested and primarily urban sites, however particular species were favored by forest/urban spaces. Results point to the importance of further investigating the nuance of land use impacts on pollinator communities, and in particular demonstrates the merit of investigating landscape heterogeneity. Conservation of forest remnants in urban environments can positively impact wild bees across multiple functional groups.

KEYWORDS

pollinators, bees, functional groups, forest, urban, land cover types, diversity

Introduction

As the landscapes of the world become increasingly urbanized, including within and near biodiversity hotspots, there is a growing need to incorporate cities, residential areas, and other anthropogenic habitats into conservation plans (Elmqvist et al., 2013). Although urbanization reduces the biodiversity of many taxa, there are ample opportunities to improve habitat quality for many organisms. This is particularly true for pollinators which, as a group, can be surprisingly resilient to development, provided that adequate floral and nesting resources are available (Wenzel et al., 2020). Conserving pollinators in anthropogenic habitats is important for a number of reasons. First, pollinators move readily between land use types so diverse urban pollinator communities have the potential to benefit neighboring habitats, including crops (Blitzer et al., 2012). Second, the pollination services provided by insects and other animals in urban habitats are critical to the reproductive success of many plants, including those planted in community or backyard gardens. Finally, improving conditions for pollinators in urban areas is likely to improve the quality of life for human inhabitants and will provide opportunities for children to develop a sense of connection with nature (McKinney, 2002; Ayers and Rehan, 2021; Fukano and Soga, 2021). Research shows that urban greening reduces human aggression and crime in inner cities, reduces ADHD (attention deficit hyperactivity disorder) symptoms in communities of all sizes, promotes self-discipline and academic achievement in children, promotes health across the lifespan by boosting the human immune system, can reconnect individuals with nature and encourage community involvement in conservation activities (Ayers and Rehan, 2021 and the references therein, Kuo, 2007, 2013; Kuo et al., 2018 and the references therein).

The extent to which urban areas can serve as a refuge for pollinators is an exciting area of expanding research (e.g., Hall et al., 2016; Langellotto et al., 2018; Braman and Griffin, 2022). Bee abundance response to local vs. landscape scale variables depended upon body size and nesting habit (Bennett and Lovell, 2019). In their study, pollination services to sentinel cucumber plants decreased with increasing hardscape, a standard metric for urbanization. They also reported that large-bodied bees, *Bombus* and *Apis* species, were positively associated with increasing amounts of impervious cover, while the abundance of small-bodied soil nesting *Halictus* species increased as the proportion of flower area, a local variable, increased. Urban/sub-urban settings can offer conservation opportunities especially for solitary and primitively eusocial bees in Britain (Sirohi et al., 2015). These researchers found the urban core to be more diverse and abundant in solitary and primitively eusocial bees compared to the meadows and nature reserves. They also found rare bee species, collectively demonstrating that urban settings can contribute significantly to the conservation of solitary and primitively eusocial bees in Britain.

Functional diversity or functional differences among species can be defined as the range, distribution and abundance of functional features of organisms in a given ecosystem, and these features can be morphological, phenological, physiological, or behavioral (Violle et al., 2007). Studies that take into account not only the diversity of species but also their functional diversity allow for a better understanding of the urbanization impact on bee communities (Banaszak-Cibicka and Dylewski, 2021). An understanding of urban wild bee functional ecology is critical to effective biodiversity conservation efforts and maintenance of ecosystem services (Bucholz and Egerer, 2020). However, in their review of 48 pollinator/landscape studies, only five studies considered functional diversity indices. They noted consistent trait characteristics for nesting, sociality, body size, diet and phenology. They proposed more research to develop a better understanding of how urbanization affects the functional ecology of urban wild bees to facilitate conservation efforts. In another example of how understanding the functional ecology of wild bees can inform conservation efforts, a study in a tropical forest system found that bee community abundance and diversity were lower in restoration plantings than in primary forest, but higher than anthropogenic wetlands and agricultural fields suggesting that restoration plantings could enhance pollinator community recovery (Montoya-Pfeiffer et al., 2020). Proximity to primary forest fragments in that study was deemed important to supply bee populations to restored sites. Effects on functional groups varied, with more effects on larger bee species with more restricted nesting and floral requirements. Overall, bee trait responses seemed to be primarily driven by an interaction between nesting location and body size. Larger bees nesting above ground were found to predominate in the more conserved habitats but were replaced by smaller bees that nest below ground in more degraded habitats. Younger trees in the restoration plantings and other degraded areas did not possess sufficient cavities and substrates for bees. Traits such as body size, social behavior, nesting site, and diet breadth have been indicated as principal predictors of species occurrence and abundance in disturbed and restored habitats (Montoya-Pfeiffer et al., 2020 and the references therein.) While local site variables influence pollinators and their services, understanding influences of landscape variables at multiple spatial scales can inform regional urban planning to protect pollinators (Grab et al., 2019). Previous studies have found pollinator diversity to be both negatively and positively influenced by forest, agriculture, etc., but few have looked at species-specific traits which may differ from general measures of diversity.

In this work, we assess these trait responses of bee communities in urban residential areas to the landscape level factors of amount of land cover ranked agricultural, forest, developed and streams. Previously, we sampled bees in residential settings in and around Clarke Co., GA. and showed landscape scale and land cover affected bee abundance and diversity (Janvier et al., 2022). In that study, development correlated positively with bee diversity at small ($<$2.5 square km) scales, while agriculture often correlated positively with bee diversity at larger ($>$2.5 km) scales. Forest cover correlated negatively with bee diversity at smaller scales, but positively at larger scales. Also in that study, generalized linear models were constructed to model the responses of individual species abundances to landscape covers for species that occurred in at least 10% of the sites and with a total count of more than 25 individuals revealing that bees respond to a complex assortment of landscape characteristics and this is driven by species-specific relationships with the land cover variables.

In the present study, to better understand the landscape effects on bee community functions, we examined how bee functional groups responded to landscape context. We took a closer look at communities based on what was learned from Janvier et al. (2022). For the present analysis, using bees collected in 2020, we identified the bees and their relative abundance in the following functional groups: Nesting guild, sociality, diet breadth, phenology (peak season of adult activity), and size class in order to test the hypothesis that urban bee functional groups respond to land cover type.

Materials and methods

Background on sample locations and bee identification

Sites sampled by Janvier et al. (2022) included 50 residential properties in northern Georgia, USA, a region that was largely deforested for cotton production beginning in the mid 1800's. Though reforestation accelerated in the early 20th century, this trend reversed in recent decades, as more forests were lost to development, particularly the creation of residential communities (Miller, 2012). Sites included several land cover types including development, agriculture and forest. All properties were at least 1,600 meters (m) apart to avoid spatial autocorrelation, and by design, represented a continuum from older properties within the city of Athens to peripheral suburban neighborhoods established on former agricultural land or forests.

Bee sampling

Bees were trapped using a set of three colored plastic pan traps (white, yellow, and blue) filled with soapy water (Dawn

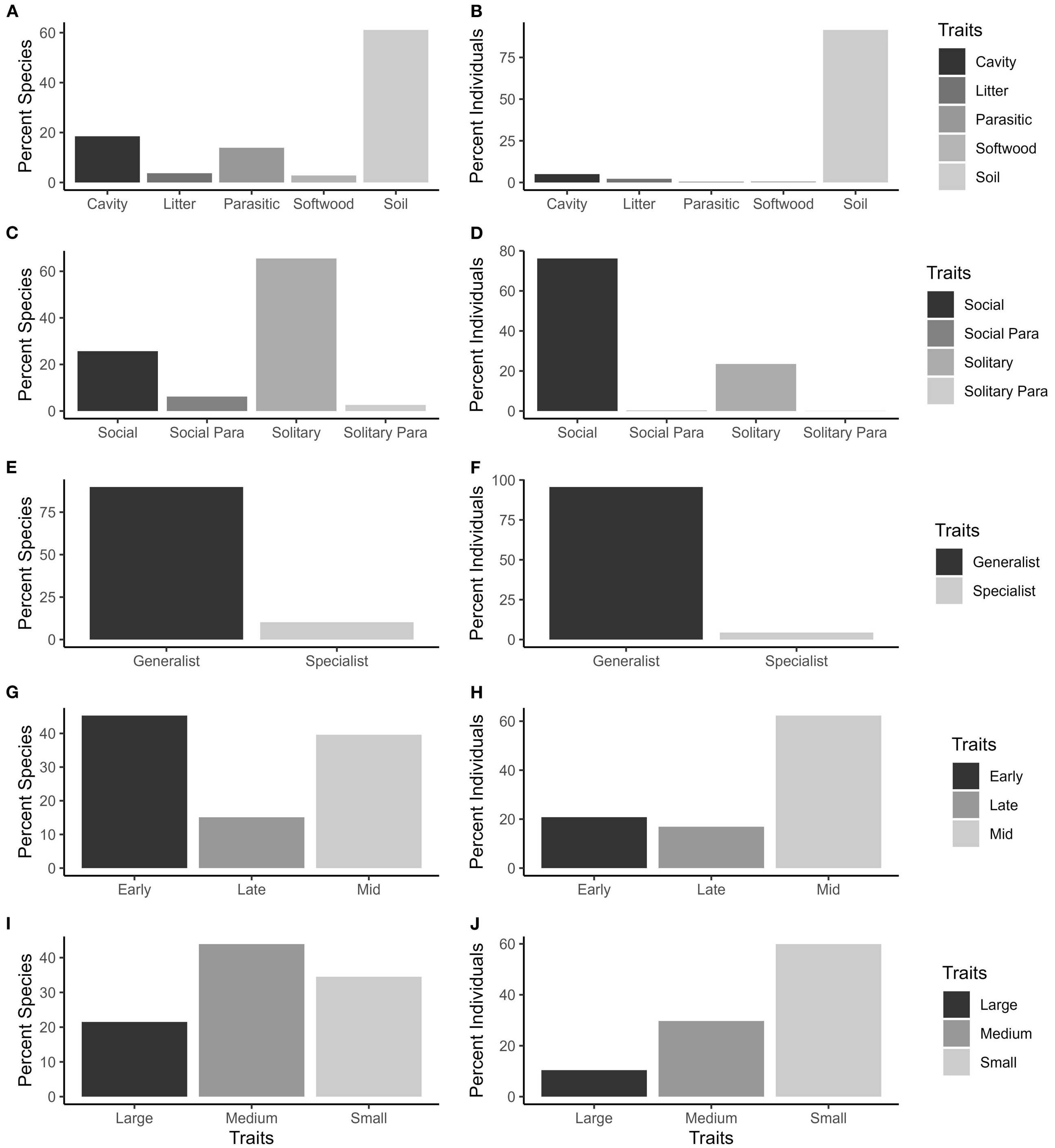

FIGURE 1
Percent bee species **(A, C, E, G, I)** and number of individuals **(B, D, F, H, J)** collected in pan traps from 50 residential properties in and around Clarke Co., Georgia, that represent varying functional traits. Nesting site **(A, B)**, sociality **(C, D)**, diet **(E, F)**, phenology-peak season **(G, H)** and size **(I, J)** trait variations are shown for urban bees collected on residential landscapes in the southeastern United States.

dishwashing soap). Although pan traps are known to capture smaller bees more effectively than larger bees (Cane et al., 2000; Roulston et al., 2007), they are a highly standardized and efficient method allowing simultaneous and consistent sampling of a large number of sites. The traps were placed in areas with direct sunlight, at least 10 m from the nearest mature tree, and were arranged in a straight line with 1 m separation. Wire stands were used to hold the traps in place about 30 cm above the ground. Sampling took place 2 days per week. The contents from the three bowls at each sampling site were combined into a single jar and returned to the laboratory. Insects were strained from the pooled water samples and stored in ethanol until bees could be sorted, pinned

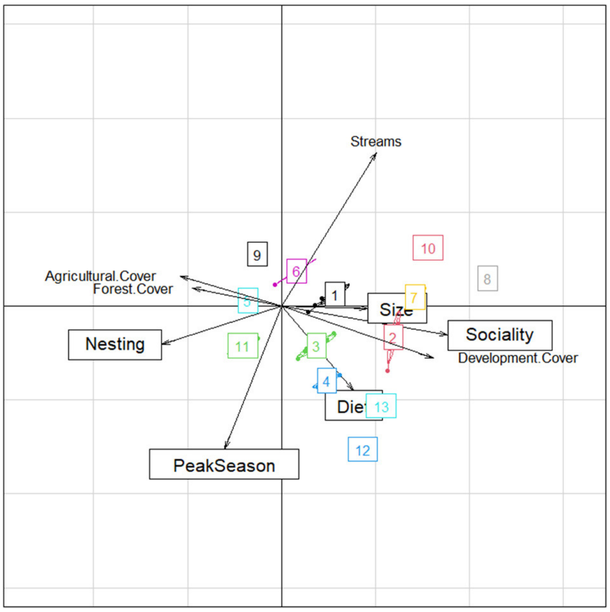

FIGURE 2
Site differences in the functional traits nesting site, sociality, diet, phenology-peak season and size. Visual results of Canonical Correspondence Analysis performed to evaluate differences among land cover types forest, development, and agriculture illustrating the most important variables separating bee functional traits. Numbers in boxes refer to hierarchical cluster analysis that identified functional response clusters of bee species responding similarly to cover use. See Supplementary Table 4 and Figure 1 for additional info on bees in each cluster.

and identified. They were identified by MDU using an established reference collection and a variety of printed and online resources (Mitchell, 1960, 1962; Gibbs, 2011; Gibbs et al., 2013; https://www.discoverlife.org). Voucher specimens are retained at the University of Georgia Natural History Museum.

Landscape analysis

Previously, we quantified landscape composition at 11 spatial extents (scales), ranging from ∼0.20 to 2.2 km in radius (i.e., 0.20–14.98 km^2). These scales were chosen as they encompass the extent of documented foraging ranges of bee species (Taki et al., 2007; Winfree et al., 2007; Watson et al., 2011). At each site the percent of the landscape occupied by each cover type for each spatial scale was calculated using the most recent USGS National Land Cover Database (NLCD) 2016 data. Land cover categories we considered included total forest cover, agriculture, and development. Further descriptions of landscape data are at: National Land Cover Database (https://www.usgs.gov/centers/eros/science/national-land-cover-database accessed 9/1/2021 date). Sites were classed into primary cover types between the most common cover types: agriculture, development, and forest.

We determined the "scale of effect" (Jackson and Fahrig, 2012) for each landscape variable and bee response variable combination. To do so we identified the spatial scales most highly correlated with each response variable (Holland and Yang, 2016). We used Pearson correlation coefficients for response variables with normal distributions and Spearman correlation coefficients for those with non-normal distributions. For each landscape cover type, the scale(s) with the highest and lowest correlation coefficients (to include negative correlations) were selected for initial analyses (Oksanen et al., 2020).

In the present study, we started by compiling a list of functional traits and developing a framework of functional group designations for all species for nesting, sociality, diet, phenology, and size. We used several sources in designating/verifying various functional groups including Mitchell (1960, 1962), Shinn (1967), Stockhammer (1967), Bouseman and LaBerge (1978), Brooks (1983), Cane (1991), Potts and Willmer (1997, 1998), Cane et al. (2007), Michener (2007), Fetridge et al. (2008), Matteson et al. (2008), Gibbs (2011), Rightmyer et al. (2011), Haider et al. (2013), Rozen and Go (2015), Lerman and Milam (2016), Wilson and Carril (2016), Ascher (2017), Langellotto et al. (2018), Danforth et al. (2019), and Fortuin and Gandhi (2021).

Nesting categories included cavity, litter, and soil dwelling bees. Cavity nesters nest in pithy stems or dead wood, and here, included soft wood nesters that require highly decayed wood. Litter dwellers are bees that tend to nest in leaf litter, wood piles, uppermost layer of soil organic matter, or perhaps existing animal burrows. Soil nesters excavate their nests underground. Sociality has two categories. Social where there is shared labor among colony members or solitary where females tend their own nests, although individual nests may be highly aggregated. Diet considered whether bees are generalists, utilizing a broad range of floral resources, or specialists that concentrate on a specific genus or perhaps family of plants for pollen. Phenology described whether a bee species occurs in early, mid, or late season, based on peak flight activity. Peak flight season—was divided into three categories: (1) early (February–April); (2) mid (May–July); or (3) late (August–November) seasons. For groups which are active across multiple seasons (i.e., Bombus spp. and other primitively eusocial groups), we selected the season for which their colony activity is at its peak. Size of bees, based on inter-tegular width from literature references, was divided into three categories according to the following criteria: (1) "small" $\leq$ 2 mm; (2) "medium" 2.1–3 mm; or (3) "large" $\geq$ 3 mm.

Statistical analysis

All analyses were done in R (R Core Team, 2022). We determined differences in relative abundance of bee functional trait groups and evaluated their response to primary land cover types, having previously demonstrated that land cover use types (agriculture, development, and forest) at particular spatial scales influence community composition (Janvier et al., 2022). Following Götzenberger et al. (2020), we utilized a "double Canonical Correspondence Analysis" (dCCA) to investigate the relationship of land cover use percentages at their most impactful scales to bee communities on differentiation in bee functional traits. Janvier et al. (2022) determined which of 15 landscape cover use scales most correlated with bee abundance and richness for these bee assemblages. The scale differed depending on the cover type. Forest cover and Developmental cover were

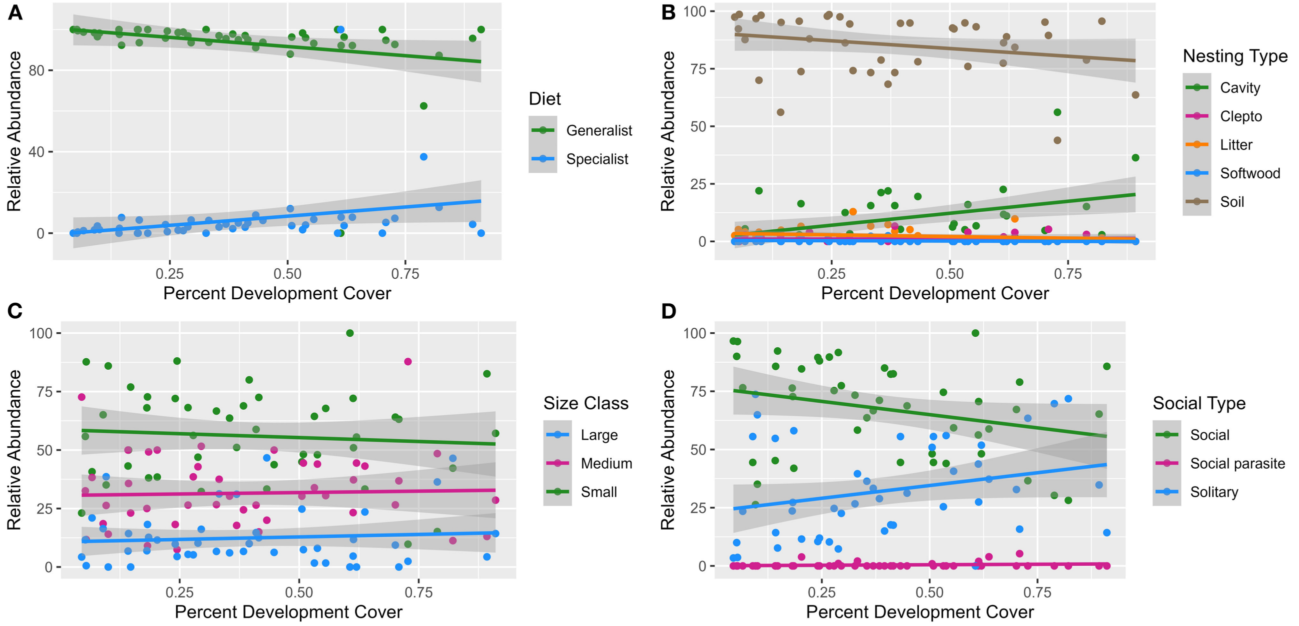

FIGURE 3
Linear models of the relationship between percent development land cover and bee abundance across the functional traits of diet **(A)**, nesting **(B)**, size **(C)** and sociality **(D)**. Each model trend line is graphed with a 95% standard error (the shaded portion around each line).

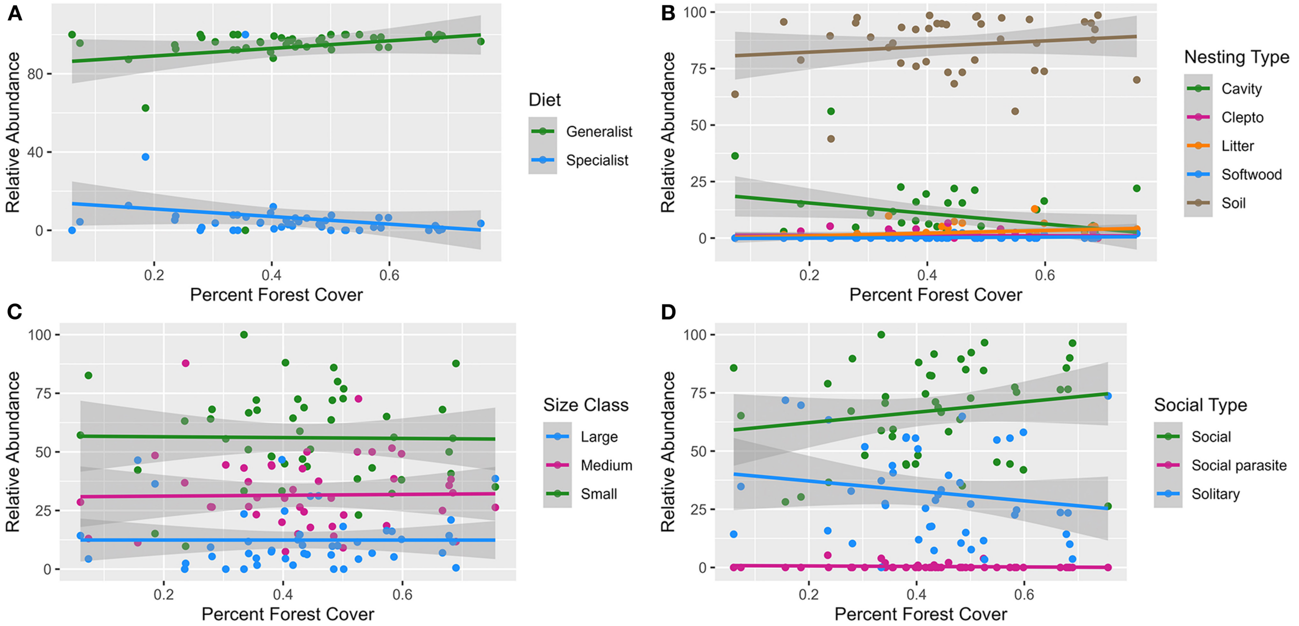

FIGURE 4
Linear models of the relationship between percent forest land cover and bee abundance across the functional traits of diet **(A)**, nesting **(B)**, size **(C)** and sociality **(D)**. Each model trend line is graphed with a 95% standard error (the shaded portion around each line.

analyzed at 14.9769 km^2 around the collection site, Agriculture cover was 2.5281 km^2, and Streams were 0.2025 km^2 as these particular scales were what was shown to be most correlated (i.e., had the appropriate, most impactful effect on pollinator abundance and richness) for their associated land cover types in prior analyses.

We followed the method for looking at both functional traits and environmental factors on communities across sample sites laid out in Götzenberger et al. (2020). The method is a double Canonical Correspondence Analysis, which first constrains the community matrix data by the environmental data in a Canonical Correspondence Analysis. It then also constrains the data, in the same CCA ordination, with the functional trait data using the dbrda function written by Kleyer et al. (2012). The relationship between bee species as an abundance matrix was first constrained with the land cover categories agriculture, development, forest, and streams in a Canonical Correspondence Analysis (CCA) using the dudi.coa function from the *ade4* package (Dray and Dufour, 2007). A permutational analysis of variance was run on the CCA to confirm significance of included land cover parameters. The resulting CCA of bee species was then doubly constrained by the species' functional traits (diet specialization, nesting habitat, peak seasonality, size, and sociality) using the code for the dbrda function provided in Kleyer et al. (2012). The resulting ordination plots bee species in ordination space, then vectorizes environmental data (landscape use and stream length) in addition to vectorizing shifting functional traits. Within that ordination, hierarchical cluster analysis identified functional response clusters of bee species responding similarly to cover use. The optimal number of meaningful clusters was determined using the hclust function (ward.D2 method) of the *stats* package (Murtagh and Legendre, 2014; R Core Team, 2022). Linear models were constructed with the geom_smooth function (method = "lm") of the *ggplot2* package. Model statistics were determined using the stat_poly_eq function of the *ggmisc* package. We used the *eulerr* package to generate Euler diagrams further illustrating the relationships among functional groups and land cover (Larsson, 2021).

Results

The 2,932 bees evaluated in the present study, representing 98 species from 27 genera in four families collected from residential landscapes, were dominated by soil nesting generalists (Figures 1A, B, E, F). Solitary bee species were more than twice as common as bee species displaying social behavior; however, the total number of individual bees (abundance) was greater for the social bees than the solitary bees (Figures 1C, D). Parasitic bees were collected, but in low numbers. Early, mid, and late season bees were all represented as were small, medium and large bees, with small bees being most numerous (Figures 1G–J).

Cover types significantly influenced bee community functional groups: Forest ($F = 1.78$, $P = 0.013$, df = 1, 42), development ($F = 2.69$, $P = 0.001$, df = 1, 42), agriculture ($F = 1.99$, $P = 0.001$, df = 1, 42), and stream ($F = 1.36$, $P = 0.04$, df = 1, 42) (Figure 2). Size, sociality, and diet breadth were more strongly influenced by degree of development, while nesting guilds and peak season of activity were more influenced by forest cover (Figure 2). Streams were a significant influence on community variation, particularly for bees in cluster 6, however streams appear to primarily influence bee traits not evaluated in our current data set (Figure 2). Clusters in Figure 2 and Supplementary Table 4, consist of species that are closely associated in the dCCA ordination space, which is vectorizing both land covers, and functional traits. A dendrogram (Supplementary Figure 1) further illustrates which bee species clustered together based on the relationships between bee nesting habitat, size, sociality, peak season of activity and diet and the land cover categories agriculture, development, forest and streams.

Linear models (Supplementary Table 5) showed the relative abundance of specialist, cavity dwelling, parasitic and solitary bees all tended to increase with increased development cover (Figures 3A, B, D), while the relative abundance of generalist, soil dwelling, and social bees decreased (Figures 3A, B, D). As the amount of forest cover increased, linear models showed generalist, soil dwelling, and social bee relative abundances tending to increase (Figures 4A, B, D), while specialist, cavity dwelling, parasitic and solitary bee relative abundances diminished (Figures 4A, B, D). Bee size appeared consistent with little influence contributed by the amount of forest or development land cover (Figures 3C, 4C).

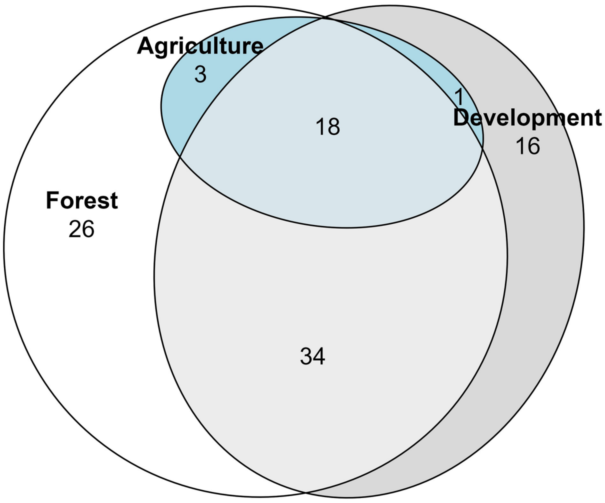

FIGURE 5
Euler diagram showing number of bee species unique to or in common with the land cover designations Forest, Development, or Agriculture. Bees were collected via pan traps from 50 residential properties in and around Clarke Co., Georgia.

During these 2020 surveys, primarily forested sites harbored 26 uniquely encountered species, while primarily development sites had 16 uniquely encountered species, with 56 species shared among our three landcover distinctions (Figure 5). Of the 85 encountered generalist feeders, 25 species were unique to primarily forested sites, and 12 were unique to primarily development (Figure 6A; Supplementary Table 1). All three land cover types shared 17 species, with no generalist feeder species unique to primarily agriculture sites (Figure 6A). For the nine specialist feeder species encountered, one species, *Lasioglossum lustrans* (Cockerell), was unique to forested sites and two species, *Andrena nigrae* Robertson and *Svastra obliqua* Say, were unique to development sites (Figure 6B).

Nesting strategies were diverse among cover types (Figure 7; Supplementary Table 2). Among the 16 cavity dwelling species, two, *Heriades carinatus* Cresson and *Megachile sculpturalis* Smith, were unique to forested sites as well as two species, *Hoplitis nemophillae* Neff and *Osmia subfasciatta* Cresson, to development sites (Figure 7A). Of the 61 soil dwelling species, 13 species were unique to forested sites, and ten were unique to development sites (Figure 7B). The litter dwellers, bumblebees (Supplementary Table 2), were present in all three cover types, with one species, *Bombus bimaculatus* Cresson, unique to forested sites (Figure 7C). Of the 64 solitary bee species, 17 species were unique to primarily forested sites, and 12 were unique to primarily

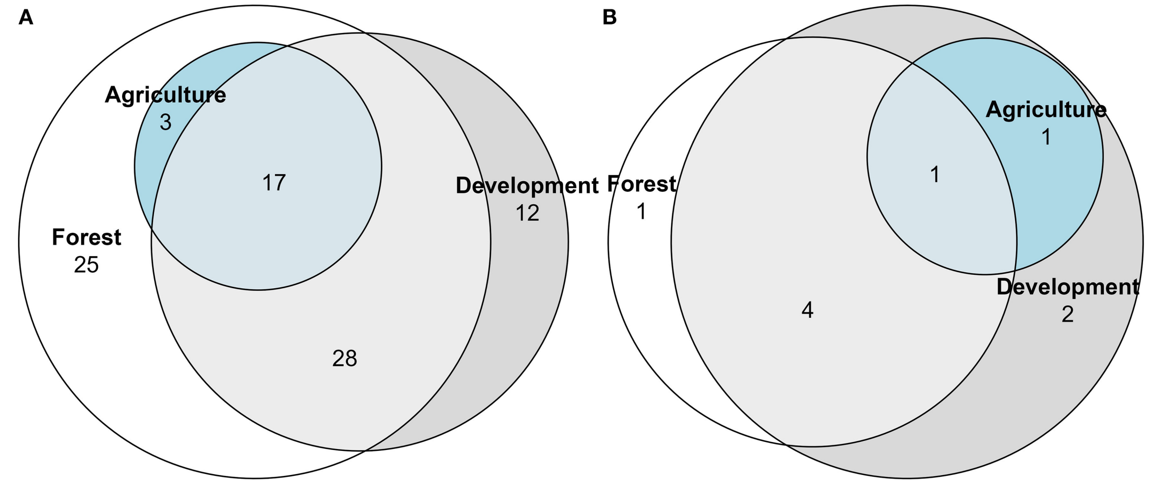

FIGURE 6
Euler diagram of diet functional groups showing number of generalist **(A)** or specialist **(B)** bee species unique to or in common with the land cover designations forest, development or agriculture. Bees were collected via pan traps from 50 residential properties in and around Clarke Co., Georgia.

development sites (Figure 8A; Supplementary Table 3). Of the 27 social bee species, seven were unique to primarily forested sites, with all others shared between multiple land cover types (Figure 8B).

Among all bees sampled, 26 species (26.5%) were unique to forest cover, but that number varied by functional group. Nesting guilds, for example, had differential responses among species to land cover with 2 (15%) cavity dwellers, 13 (26.5%) soil dwellers and 1 (33.3%) litter dweller unique to forest cover. Within the soil nesters there were sometimes similarities within genera. Three out of 4 *Eucera* species, for example, were encountered on landscapes characterized by primarily forest cover (Supplementary Table 2). Among the *Lasioglossum*, however, only 4 of 19 species were unique to forest cover, while two were unique to the development land cover sites. The exotic bees *Osmia taurus* Smith and *Megachile sculpturalis* Smith were found on sites characterized as primarily forest. Three specialist bees were unique to development, while only one specialist was unique to forested sites. Six parasitic bees were unique to forest cover sites.

Considering only those bee species that were represented on multiple sites and were represented by at least 15 individuals, 20 were generalists and two were specialists. Nine were solitary, while 13 exhibit some form of social behavior. Two were cavity dwellers, two litter dwellers and the rest are soil nesters. Among this group of bee species, those strongly favoring forested sites included *Augochlorella aurata* (Smith), *Bombus griseocollis* (De Geer), *B. impatiens* Cresson, *Ceratina strenua* Smith, *Halictus ligatus/poeyi* Say, *Lasioglossum bruneri* Crawford, *Lasioglossum callidum* Crawford, *L. hitchensi* Gibbs, *L. illinoense* (Robertson), *L. imitatum* (Smith), *L. tegulare*/(Robertson)/*puteulanum* Gibbs, *L. trigeminum* Gibbs, *L. zephyrum* (Smith), and *Osmia georgica* Cresson. This group included litter, cavity, and soil nesters. *Calliopsis andreniformis* Smith, in contrast, was more common in sites characterized by development (Supplementary Tables 1–3).

Discussion

Urban residential landscapes are characterized by numerous factors that could influence native bee abundance and diversity. These can be local (e.g., vegetation cover, floral resources, exotic plant cover, nesting resources, microclimate, green space size and habitat type.) or landscape level (e.g., landscape heterogeneity and fragmentation, surrounding land use?, impervious surfaces, urban heat island effects) (Ayers and Rehan, 2021). We examined the relationships of urban landscape -level land cover types with bee functional traits, with the aim of identifying those functional groups and the species that composed them that are vulnerable to increasing urbanization and could merit special consideration for conservation. In our study land cover types did significantly influence differentiation of urban bee community functional groups. Various studies have revealed trends in urban bees and functional traits and their response to urbanization, yet these trends are not always generalizable because of species-specific variation in response (Cariveau and Winfree, 2015; Bucholz and Egerer, 2020). While our study found a much greater abundance of generalists than specialists, consistent with numerous studies (Ayers and Rehan, 2021), the specialist bees from the 50 sites we surveyed tended to increase with increasing development cover. Although seven specialist bees were captured in our study (Supplementary Table 6), the vast majority of individuals were *Ptilothrix bombiformis* (Cresson) and *Peponapis pruinosa* (Say) the hibiscus bee and the squash bee, respectively, known to frequently visit plants typical of backyard gardens and ornamental plantings in residential landscapes in urban settings. An additional four species also specialize on plants characteristic of urban gardens and landscape settings, namely violets, false dandelions, mock orange and sunflowers.

Our study adds to a growing body of literature showcasing the complexity and multifaceted nature of considering community level responses of functional group traits. In the present study, specialist, cavity-dwelling and solitary bees tended to increase

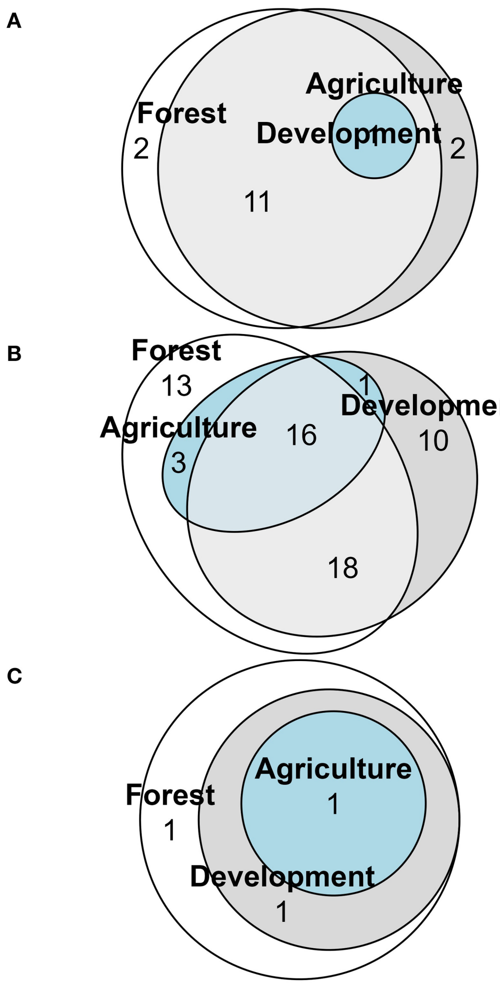

FIGURE 7
Euler diagram of nesting type functional groups showing number of cavity **(A)** soil **(B)** or litter **(C)** nesting bee species unique to or in common with the land cover designations forest, development or agriculture. Bees were collected via pan traps from 50 residential properties in and around Clarke Co., Georgia.

with increasing development cover, while soil-dwelling and social bees increased with increasing forest cover. In a study of bee functional groups in a Brazilian metropolis where stingless bees are an important component of the social functional group in tropical areas, however, social bees were more resilient to increasing urbanization (Graf et al., 2022). However, in that study as well as ours, above-ground bees were more resilient to increasing urbanization. Wilson and Jamieson (2019) determined that more urbanized sites supported a greater number of exotic, above-ground nesting, and solitary bees, but fewer eusocial bees. A study of bees in 55 cities across the globe explored how characteristics of cities influenced the taxonomic and functional trait profile of urban bees (Ferrari and Polidori, 2022). (Ferrari and Polidori, 2022) found that looking at the differences among cities across a wide geographical scale helped explain the previously observed variable response of some bee community traits across local urbanization gradients. They found, for example, that bigger cities host few parasitic and oligolectic species, along with more above-ground-nesting bees. Most sites in our present study were in and around Athens, Clarke County. With a 2020 population of 130,081, it is the 5th largest city in the state of Georgia and the 220th largest city in the United States. Spanning over 118 miles, Athens has a population density of 1,118 people per square mile (world population review https://worldpopulationreview.com/us-cities/athens-ga-population). As populations globally continue to rapidly develop urban cityscapes and suburban spaces like Athens, while also working toward creating more sustainable green spaces that support pollinator communities, understanding how landscape heterogeneity impacts pollinator communities is imperative to effective pollinator conservation.

Our study focused in particular on forested landcover as this area historically was primarily Oak and Pine woodlands. Thus, many native pollinators in this system likely originated in a well-forested landscape. Forest cover as part of these urban landscapes in the present study was associated with increased abundance of soil dwelling, generalist, and social bees. In our system at the urban/forest interface, softwood nesters also increased with increasing forest cover. Glenny et al. (2023) reported that the abundance of trees within the forest/grassland ecotone was positively associated with coarse woody debris (CWD), and in turn CWD had a positive association with bee richness and functional diversity early in the growing season and positive association with functional richness later in the growing season. Fortuin and Gandhi (2021) reported that nesting habitat indicators explained the majority of variation in bee communities in clearcut and managed hardwood and pine forests in the SE United States. In their study they concluded that mature hardwood forests promoted a wide diversity of functional groups and nesting guilds, and that nesting habitat by itself, without consideration for forage resources, is a strong predictor of wild bee community structure in southeastern forests, and therefore may also be a limiting factor for many groups. Research has demonstrated the importance of floral resources to mitigating the negative impacts of urbanization on pollinator communities, e.g., Birdshire et al. (2020). Our results imply that conservation of forest remnants in urban environments can also positively impact wild bees across multiple functional groups. We speculate that several aspects of urban forests could favor bees including increased availability of nesting habitat, diversity of pollen sources, including from plants that do not require bees for pollination, or even the availability of resin (e.g., *Megachile sculpturalis,* the giant resin bee). Future work could further address what are aspects of urban forests that most benefit wild bees and identify mechanisms to enhance engagement with municipal planners to best communicate these benefits.

Conclusion

In conclusion, it is clear from this work that landscape context strongly influences the functional composition of urban bee communities in our system. Forest cover has a particularly strong effect on bee assemblages, which is not surprising given that forests dominated our study region historically. Because forest-associated species, which may account for nearly a third of native bee diversity in the eastern US (Smith et al., 2021), are

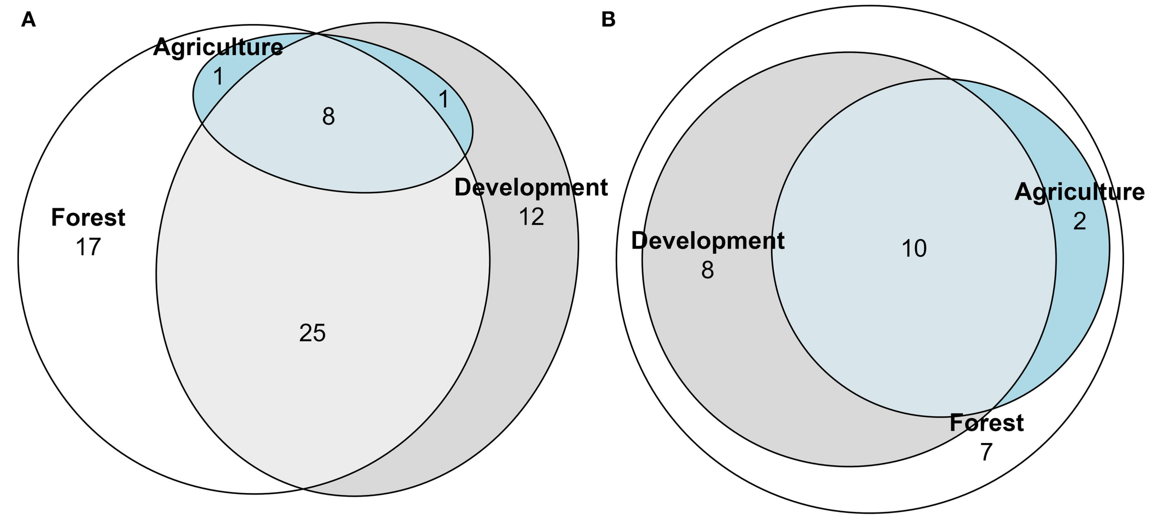

FIGURE 8
Euler diagram of social type functional groups showing number of solitary **(A)** or social **(B)** bee species unique to or in common with the land cover designations forest, development or agriculture. Bees were collected via pan traps from 50 residential properties in and around Clarke Co., Georgia.

largely lost from landscapes experiencing extensive deforestation (Ulyshen et al., 2023), forest cover is an important consideration for conservation planning in mixed-use landscapes. Many other taxa are less dependent on semi-natural habitats and can persist in urban areas as long as adequate floral and nesting resources are available. Future work can help us better understand how a suite of local efforts to improve conditions for pollinators (increasing floral resources, trees, nesting sites) can promote the diversity of these critical organisms. While much work has been done examining how increasing the abundance of these resources can affect pollinator communities, there remain gaps in our understanding that inhibit implementation of conservation measures. Future studies should continue to elucidate urban effects on bee functional traits with the recognition that trends may be regionally and species specific (Cariveau and Winfree, 2015; Ayers and Rehan, 2021). To better understand successful conservation of urban bee communities, future research should focus on identifying bees that demonstrate greater adaptive response to urban perturbations and why they are able to take advantage of available resources more effectively. In doing so, urban planning with a bee conservation mindset can make better informed decisions that promote the inclusion of bee friendly green spaces within the urban matrix (Hernandez et al., 2009). In particular the relationship between hardwood forest cover and pollinator diversity is poorly understood. For example, future research questions could include: can bees benefit from wind-pollinated oaks that are significant features of remnant forest in urban areas in our region? What is the total greenspace area needed to support wild bees and is this completely dependent on bee mobility or other factors as well?

Efforts to better communicate green space benefits for ecosystem and human health to those who can influence implementation including city planners, landscape designers and developers, home owners associations as well as the general public are needed to move the conservation needle more rapidly in the right direction. Our work addressed the need to investigate landscape effects on bee community ecology. Our results confirm the importance of inclusion of forest cover in urban planning whether they are remnant or restored. This forest cover impacts a wide array of bee functional diversity in these landscapes making it integral to effective conservation in planning urban greenspaces.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

SB and MU conceived the presented idea. CB developed the theory, performed the computations, and verified the analytical methods. EM encouraged the focus of investigating functional groups. ME-V, CT, and AJ contributed to data collection, processing, and analysis. All authors discussed the results and contributed to the writing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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Effects of urbanization on the structure of plant-flower visitor network at the local and landscape levels in the northern Argentinian Yungas forest

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Human population and cities are growing fast, with a concomitant modification of the land surface. Urbanization is driving biodiversity loss and biological homogenization, which impacts human wellbeing. In this study, we evaluated the influence of urbanization on flower visitor assemblage using an interaction network approach. We assessed the effect of different variables at the local and landscape scales on community parameters and network metrics along a gradient of urbanization located in a subtropical montane Yungas forest. We found that local variables affected the richness of flower visitors, which increased with greater flower coverage, high stability of floral resources, and the proportion of exotic plants. Moreover, local variables affected the diversity, nestedness (NODF), and specialization (H_2) of the interaction network. Landscape variables, such as altitude and proportion of impervious surface (a proxy of urbanization), affected both the richness of flower visitors and specialization. The effect of urbanization on the richness of flower visitors differed across the altitudinal gradient, with higher impact at higher altitudes. In conclusion, our results indicate that local and landscape variables affect community parameters and the structure of plant-flower visitor networks to different extents and strengths.

KEYWORDS

urbanization, flower visitor, assemblage, interaction network, network structure, Jujuy, local and landscape scale

Introduction

The field of complex ecological networks has grown in the last two decades [recently reviewed by Guimarães (2020)]. Network theory has become an important tool in community ecology as it provides an efficient representation and characterization of temporal and spatial patterns of community dynamics and the structure of ecological systems (Schwarz et al., 2020; Resasco et al., 2021). Ecological networks help to understand how communities respond to ongoing global environmental change (Schleuning et al., 2016; Tylianakis and Morris, 2017). Studies on network properties at local and landscape scales showed that habitat modification impacts system stability at the network level

(Marín et al., 2019) and outweighs the impact on species diversity (Tylianakis et al., 2007; Weiner et al., 2014). For example, habitat modification impacts both species themselves and their interactions, and it has been shown that loss of interactions precedes species loss (Valiente-Banuet et al., 2014). Thus, network analysis often provides a good assessment of the possible effects of changes in habitat on community stability (Kaiser-Bunbury et al., 2010; Sabatino et al., 2010), and the resilience of ecosystems to landscape modifications (Montoya, 2008).

One of the outstanding features of the Anthropocene is that most of the world's population lives in cities. By 2050, current projections indicate that two out of three world inhabitants will live in urban areas and that population growth during this period will happen entirely in cities (United Nations, 2019). Urbanization, a process that manifests through rapidly changing human population and land cover, is generally studied across urban–rural gradients, analyzing changes in plants and animals along a transect from the inner city to surrounding, less-altered ecosystems (McKinney, 2002). The impacts of urbanization on biodiversity occur mainly through the reduction in natural land cover, and also through fragmentation, the introduction of non-native species, and increased temperature (McDonald et al., 2013). Thus, urbanization is considered a major driving force of biodiversity loss and biological homogenization (Savard et al., 2000; Gupta, 2002; McKinney, 2002). In this context, there is recent and increased concern over the conservation of flower visitors in urban environments, considering that pollination is one of the major contributions of nature to human wellbeing (Díaz et al., 2006; Hall et al., 2017; Knight et al., 2018). We studied how the interactions between flower visitors and flowers are structured along an urbanization gradient.

Studies in the past decade revealed that bee community responses to urbanization are often mediated by local and landscape habitat conditions (Quistberg et al., 2016; Theodorou et al., 2020). At the local scale, floral resources are important for flower visitors, as the richness and cover of floral species (Ebeling et al., 2008; Grundel et al., 2010; McCune et al., 2019), constancy of floral resources over time (Stewart and Waitayachart, 2020), and the presence of abundant exotic plants in urban areas (Moroń et al., 2009; Martins et al., 2013; Fenesi et al., 2015) determine the richness of the flower visitor community. At the landscape scale, the most widely studied effects related to urban expansion are those caused by increased impervious surface (e.g., Geslin et al., 2016) and heat (e.g., McCune et al., 2019). In turn, the proportion of impervious surfaces is strongly associated with the composition of bee communities (Burdine and Mccluney, 2019). Urban areas are characterized by being significantly warmer than their surroundings, which can have a strong impact on ectotherms, such as insects (Briere et al., 1999), and thus on their survival rate and fecundity (Sales et al., 2018). Additionally, altitude has a negative effect on the total richness of flower visitors (Bates et al., 2011).

Nevertheless, the effects of urbanization on insects in general, and flower visitors in particular, remain ambiguous and are not completely understood (Threlfall et al., 2015). Existing studies report positive and negative effects, although the latter seems to prevail (McKinney, 2006, 2008). Some studies have found a decrease in the diversity and abundance of pollinating insects from a rural to urban gradient (Ahrne et al., 2009). However, the response to urbanization varies among species (Rodrigues et al., 1993; Osborne et al., 2008), and some bees are equally, or more abundant, in natural vegetation fragments within urban landscapes compared to extensive natural areas (McFrederick and LeBuhn, 2006; Osborne et al., 2008; Wenzel et al., 2020).

Assessing whether the impact of urbanization at the species level scales up to the community level is critical for the conservation of flower visitors and the ecosystem services they provide (Shwartz et al., 2013; Potter and LeBuhn, 2015). One way to assess the community stability in urban areas lies in the use of interaction networks between plants and their flower visitors (Baldock et al., 2015; Kaiser-Bunbury and Blüthgen, 2015), which allow a better understanding of the structure and dynamics of these systems (Vizentin-Bugoni et al., 2014; Knight et al., 2018). To achieve such an assessment, we propose to evaluate changes in the structure of interaction networks at the community level along an urbanization gradient, both at the local and the landscape scales. In particular, we looked at the effect of (1) local urban variables, such as the proportion of exotics plants, flower coverage, and temporal variation of floral coverage, and (2) variation in landscape variables, such as impervious surface (areas covered by buildings), altitude, and land surface temperature, on the structure of plant-flower visitor networks.

Methods

Study area and sites

This study was done in a natural–rural–urban gradient in the Yungas ecoregion of northwestern Argentina, which represents the southernmost extension of the neotropical Andean forest (Oyarzabal et al., 2018; Figure 1). It is one of the most diverse ecoregions in the country and has great importance in terms of the provision of ecosystem services (Malizia et al., 2012). In Argentina, the altitudinal gradient of the Yungas extends between 400 and 2,500 m a.s.l., along which it encompasses three main environmental forest tiers: piedmont (400–900 m a.s.l.), montane (900–1,600 m.a.s.l.), and montane cloud forest (1,600–2,500 m a.s.l.; Brown et al., 1985). Most of the larger urban developments are established in the montane forest valleys. The study area has a subtropical climate, where rainfall occurs mostly during the southern hemisphere summer (ranging between 600 and 2,000 mm annually) with a marked dry season (April–October), and a mean annual temperature that decreases up the altitudinal gradient from 21.5 to 11.5°C.

Jujuy province is the northernmost province of Argentina; it has a low degree of urbanization in general, but it has experienced a 30% population increase from 2001 to 2022 (from 611.888 to 797.955 inhabitants). The most populated area is the capital city, San Salvador de Jujuy (The National Institute of Statistics Censuses, 2022), which is located at 1,200 m a.s.l. The natural environment is represented by a montane forest. However, urban developments have extended to the montane cloud forest in recent years. Other main cities of Jujuy province grew spatially and demographically,

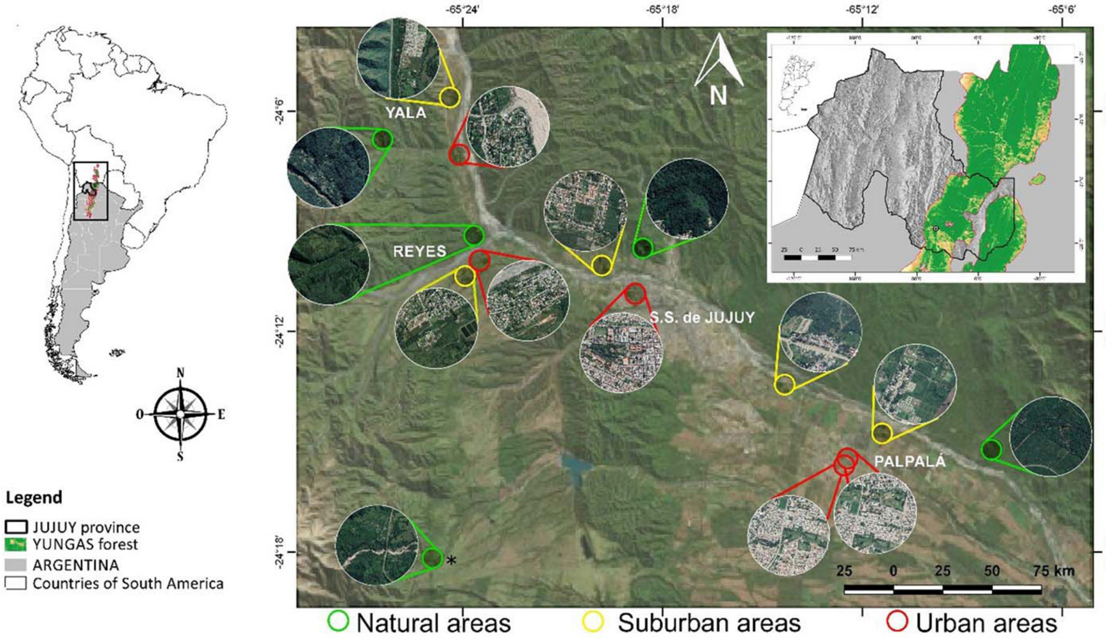

FIGURE 1
Distribution of the Yungas forest ecoregion in South America **(left)** and focused on Jujuy province **(right)**. Circles represent 15 sampling sites distributed within the Yungas ecoregion, showing a zoom-in of each. Small circles represent a 500-m ratio from the middle point of each site, where the landscape variables were recorded. Bigger circles represent a zoom-in of each site to visualize the degree of urbanization. Reference: urban sites (red circles); suburban sites (yellow circles), and natural sites nearby (green circles). (*) Natural site located in the Los Paños locality but belonging to one of the Palpalá gradients.

from a population of 82,000 inhabitants in the 1970's (National Population, Families and Housing Census, 1970)[1] to a current population of 335,406 inhabitants (Permanent Household Survey, fourth quarter of 2014). The main cause of this development lies in a double migratory process in search of work, both from rural areas of the province and from neighboring countries, mainly Bolivia (Boldrini and Malizia, 2017).

We selected five different urbanization gradients in the province of Jujuy, each consisting of three urbanization categories (hereafter called sites), classified according to the percentage of impervious surface in a 500-m radius from the center of the site with a GIS analysis technique used by Owen et al. (2006). Categories of sites were as follows: (1) Urban: 58.6% of the area, on average, occupied by buildings and houses (ranging from 33.1 to 86%), sampling was done in parks; (2) Suburban: areas nearby cities and residential sites, where buildings occupied 30.2% of the area, on average (ranging from 22 to 36.3%), most of the buildings are houses with backyards and sampling was done in vacant lots; (3) Natural: areas with Yungas forest, with <1.1% covered by buildings (ranging from 0 to 4.4%), and these sites were mostly natural reserves often used for tourism. The sites within each urbanization gradient were separated by at least 1.2 km from each other (Figure 1, Supplementary Table 1). Urbanization gradients were located in different cities, which was the "region" category, and were added as a random effect in the models.

Data collection

At each site, we delimited a one-hectare plot, where we observed plants to record flower visitors and measured local plant variables (see *Local and landscape variables*). Sampling plant-flower visitor interactions consisted of observation of a focal plant for 5 min and recording all plant visitors that made direct contact with the flower's reproductive parts. We aimed at completing three observation periods for each plant species, but in some cases, we did not find enough individuals. Data were collected between 9 am and 12:30 pm and between 1:30 pm and 5 pm by the same observer throughout the study. At each site, we recorded interactions with all flowering plants present in the plot, including herbaceous plants, shrubs, or trees. For the latter, we only included branches up to 1.80 m high.

When possible, we captured all insect flower visitors before they flew away, using entomological aspirators. Afterward, we labeled all captured individuals and took them to the laboratory for further identification by experts. Apoidea specimens were identified to the lowest taxonomic category possible with the help of experts, while most specimens from Coleoptera, Diptera, Vespidae, and Formicidae were identified as morphospecies. We also identified plants with the help of experts when needed (see Acknowledgments section). To ensure that our sampling included a representative percentage of the flower visitor community, we calculated the sampling completeness of the different levels of urbanization with the Chao1 estimator (Chao, 1987), following Chacoff et al. (2012). We estimated that we recorded 66% of flower visitors in natural

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[1] Available online at: https://www.censo.gob.ar/.

areas, 75% in suburban areas, and 68% in urban areas, which mean that our sampling is quite representative of the total flower visitor community in those sites (Amado De Santis and Chacoff, 2020; Supplementary Table 3).

Fieldwork was done during the peak flowering time for three consecutive seasons (2015–2018), between September and February (spring and summer) over five urbanization gradients, and each site was visited between four and six times (Supplementary material). Two of the gradients were sampled during two seasons, and three were sampled in only one season (Supplementary Table 2). This sampling totaled 21 networks.

Community and network metrics

We built a quantitative plant-flower visitor network for each site. For those sites that were assessed during two flowering seasons, we built a separate network for each year (we evaluated the influence of the different seasons and we did not find any effect). For each network, we extracted community and network metrics to analyze. The community metrics include the following: (1) *richness* (r) is the total number of flower visitor species; (2) *Shannon diversity index* (d) accounts for both abundance and evenness of the species present; network metrics include the following: (3) *specialization index* (H_2) measures the level of specialization in the entire network, which ranges from zero (extreme generalization) to one (extreme specialization), and is derived from the Shannon index. H_2 is not dependent on sample size, and therefore it is robust to changes in sampling intensity and to the number of interacting species in the network (Blüthgen et al., 2006); (4) *connectance* (c) describes the ratio between the total number of realized (observed) links in a network and the theoretical maximum number of possible links if all visitors and plants were connected (Jordano, 1987); finally, (5) *nestedness* (NODF) is a network metric that indicates how low-degree species (also called *specialists*) interact with the subsets of the species with which high-degree species (*generalists*) interact. Values range from 0 (not nested at all) to 100 (perfect nesting; Almeida-Neto et al., 2008).

Local and landscape variables

We measured environmental variables at the local and landscape scales, which were calculated for each site. *Local variables* include the following: (1) Flower cover: for each day of sampling, we calculated the percentage of flower cover in 10 random plots of 4 × 4 m, distributed within a 1-hectare plot, each time we visited the site (ranging from 4 to 6 times, Supplementary Table 2) and then we averaged those values to get one value per site. (2) Temporal variation of flower cover: we determined the temporal coefficient of variation (CV) of flower cover at each site throughout the season with the following formula: $CV_{fc} = (\sigma/\chi)^{*}100$ (χ: absolute mean value of flower cover throughout the flowering season and σ: standard deviation of flower cover), as a measure of the temporal stability of the flower resources offered at each site. (3) Proportion of exotic plant species was calculated per site in relation to the total number of native and exotic plant species.

Landscape variables

These variables were measured using a GIS analysis. (1) Percentage of impervious surface (area with buildings, paved roads, sidewalks, etc.) and natural vegetation cover: it is calculated for each site in a 500-m radius by considering four categories, namely dense and shrub vegetations, natural vegetation (with trees and shrubs), and impervious surface (area with buildings). (2) Ground surface temperature: the maximum ground surface temperature was extracted from MODIS images (Wan et al., 2015), from a series of values obtained from 2015 to 2018. Then, because the available data are reported on a per-year basis, and each season encompasses 2 years (September–March), we averaged the two values to obtain one mean value per season per site. (3) Distance to a natural area: natural vegetation could provide extra resources to flower visitors and thus influence their abundance and richness in urban areas. This variable was calculated as the distance in meters from the middle point of each site to the center of the nearest sector with at least 70% of forest cover in a 500-m radius. (4) Distance to a water body is calculated as the distance from the center of each site to the edge of a lotic water body (e.g., a river), and (5) Altitude is obtained with a GPS.

To avoid multiple tests, before the GLMM, we correlated the local and landscape variables by using Pearson's correlation test (Quinn and Keough, 2002). Variables that were highly correlated ($r > 0.70$) were discarded from subsequent analysis. At the local scale, we kept the three original variables because their coefficient of correlation was <0.70. At the landscape scale, we discarded distance to vegetation and a water body as they were highly positively correlated with urbanization. Therefore, we included only the percentage of impervious surface (urbanization), altitude, and surface temperature. We also discarded natural vegetation cover because it was highly negatively correlated with urbanization (Supplementary Table 8).

Statistical analyses

To test the effect of local and landscape-scale variables over the response variables—community and network metrics listed above—we standardized each explanatory variable by subtracting the mean and dividing by 2*SD (Gelman and Hill, 2007). We report the range and mean of the original values in Supplementary Table 4. We used generalized linear mixed models (GLMMs; Crawley, 2007; Logan, 2009; Zuur et al., 2009) to test local and landscape effects separately including three-way interactions. One of the models included community and network metrics as response variables and local-scale variables as explanatory variables. The other model included the same response variables and the landscape-scale variables as explanatory variables (Supplementary Table 5). For frequency data (richness), we used a negative binomial distribution to model the stochastic part of the model, because the data showed over-dispersion. For continuous response variables (*Shannon diversity index, specialization index, connectance,* and *NODF*), we used a Gaussian distribution.

We considered each network as an independent observation and thus had 21 networks for the analysis. To ensure that the two gradients (six sites) that were measured during two

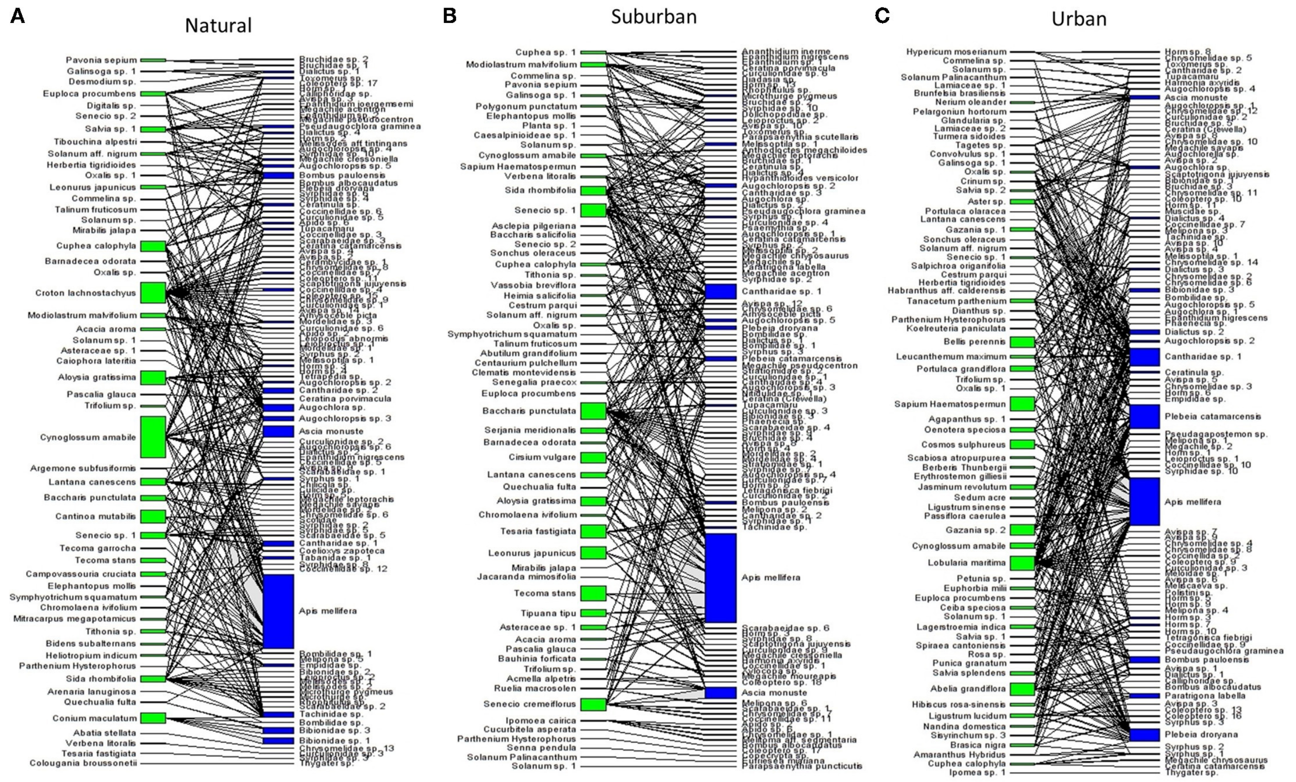

FIGURE 2
Total interactions of the sites in each urban category. References: **(A)** natural sites, **(B)** suburban sites, and **(C)** urban sites. Green boxes represent plant species/morphospecies and blue boxes represent flower visitor species/morphospecies, named right next to each box. Lines represent interactions and box width is proportional to the number of times that each species was recorded interacting.

flowering seasons (Supplementary Table 2) could be considered independent samples, we set season as a random nested factor (1|Region/Season). Because the overall results were not affected by this, we considered that it was justified to analyze all networks as independent observations. This avoided an unbalanced design and the need for more complex models. Only the region was kept as a random effect due to the structure of the sampling design.

For local and landscape effects, we selected the best model (those models that better adjust to our data) by using information-theoretic procedures (Burnham and Anderson, 2004). We considered models with all possible combinations of predictor variables. We calculated Akaike's information criterion corrected for a small sample size (AICc) for each model (Burnham and Anderson, 2004). We compared models based on ΔAICc, which is the difference between the lowest AICc value (e.g., best of suitable models), and AICc for all other models; when the difference between the best models was >2, we selected the model with the lowest AICc, but when the difference was <2, we used a weighted model selection criterion. The criterion to select the best or the weighted models was based on the AICc weight of a model (w_i), which represents the relative likelihood that the specific model is better than all the other models (Burnham and Anderson, 2004). We performed a multiple model selection for each model (Supplementary Tables 6, 7) and, if the model had w_i > 0.70, it was considered the best model. If no model reached that value, we calculated the 95% confidence interval limits (CL) for parameter estimates. The CL of the variables that excluded zero was considered significant. Because models of richness at the local and landscape scales exhibited overdispersion (c ËĘ = 1.38; c ËĘ = 2.03, respectively), we adjusted standard errors and used QAICc for model selection (Burnham and Anderson, 2004). Statistical analyses were done using lme4 (Bates et al., 2015) and MuMIn packages (Barton, 2019) for R software, version 3.5.3 (R Core Team, 2019).

Results

Overall characteristics of pollination networks

We recorded a total of 197 morphospecies of flower-visiting insects, of which 37 were identified at the species level and the rest at the genus, family, and superfamily levels. Hereafter, for the sake of simplification, we will talk about species for both species and morphospecies. We also recorded 121 species of plants; thus, the total number of species in the network was 318 (Supplementary Tables 9, 10). We documented a total of 3,310 visits; of which, 971 visits were recorded in natural areas, 1,120

TABLE 1 Estimates of community and network parameters, SE, and 95% confidence interval limits (CL) for explanatory variables at the local scale.

Model	Response variable	Explanatory variables	Parameter estimate ± SE	Confidence interval limits (CL)	
				2.5%	97.5%
Local	Flower visitors richness	(Intercept)	3,3252 ± 0.0544	3,2115	3,4390
		CV floral cover	−0.1641 ± 0.0937	−0.3609	0.0326
		Floral cover	−0.0678 ± 0.1276	−0.3300	0.1942
		Exotics	−0.0889 ± 0.1698	−0.4337	0.2559
		CV floral cover × Floral cover	**0.5527 ± 0.2251**	**−1,0301**	**−0.0753**
		CV floral cover × Exotics	**−0.6169 ± 0.2719**	**−1,1938**	**−0.0399**
		Floral cover × Exotics	0.0869 ± 0.4025	−0.7517	0.9257
		Floral cover × CV Floral cover × Exotics	**−1,8775 ± 0.8482**	**−3,7256**	**−0.0293**
	Shannon diversity index	(Intercept)	3.0526 ± 0.1006	2,8404	3,2648
		CV floral cover	**−0.4371 ± 0.1876**	**−0.8323**	**−0.0417**
		fl_cov	−0.3413 ± 0.2053	−0.7733	0.0908
		Exotics	0.1211 ± 0.2556	−0.4087	0.6510
	Specialization index H_2	(Intercept)	0.6018 ± 0.0354	0.5271	0.6764
		Exotics	**−0.1042 ± 0.0373**	**−0.1830**	**−0.0255**
		CV floral cover	0.0633 ± 0.0395	−0.0197	0.1464
		fl_cov	0.0602 ± 0.0409	−0.0257	0.1462
		CV floral cover × Exotics	0.1578 ± 0.0936	−0.0418	0.3575
		fl_cov × Exotics	0.1546 ± 0.1317	−0.1260	0.4353
		fl_cov × CV floral cover	**−0.2528 ± 0.0993**	**−0.4644**	**−0.0413**
	NODF	(Intercept)	9,4831 ± 0.7734	7,8275	1,1138
		fl_cov	−1,0586 ± 2,0037	−5,3092	3,1920
		CV floral cover	**5,3568 ± 1,4822**	**2,1756**	**8,5379**
		Exotics	**4,4301 ± 1,7772**	**0.6066**	**8,2536**

Explanatory variables with CL excluding zero are in bold. We only show the response variables that were affected by some explanatory variables. References: exotics: proportion of exotic plants; floral cover: flower coverage; CV floral cover: temporal variation coefficient of flower coverage.

in suburban areas, and 1,219 in urban areas (Figure 2). We found a total of 107 species of flower visitors in natural and suburban areas and 96 in urban areas. We captured 75 bee species (38% of the total recorded), 64 beetle species (32% of the total recorded), 31 fly species (15% of the total recorded), 14 wasp species (7% of the total recorded), and 12 ants species (6% of the total recorded). Within the bee group, 31 species belonged to Apidae, 19 to Megachilidae, 16 to Halictidae, 3 to Colletidae, and 3 to Andrenidae.

Local-scale effects over community and network metrics

The richness of flower visitors was explained by the relation among the proportion of exotic plants, flower coverage, and temporal variation of flower coverage (Table 1). The richness of flower visitors decreased with increasing variability in flower coverage. However, when the variability in flower coverage was low, the richness of flower visitors increased with increasing flower cover and proportion of exotics (Figure 3A). Moreover, high variability in floral resources negatively affected the diversity of interactions (Figure 3B, Table 2).

Specialization of the network (H_2) decreased when the proportion of exotics increased (Figure 3C). Furthermore, this index was also influenced by the interaction between flower coverage and its variability. When the variability in flower cover was low, the specialization index increased with increasing flower cover (thus high stability promoted specialization in the community), but when variability was high, the specialization index did not change with flower cover (Figure 3D). While the connectance of the network was not affected by any local-scale variable (Supplementary Table 6), nestedness (NODF) increased with an increasing proportion of exotic plants and variability in flower cover (Figures 3E, F, respectively).

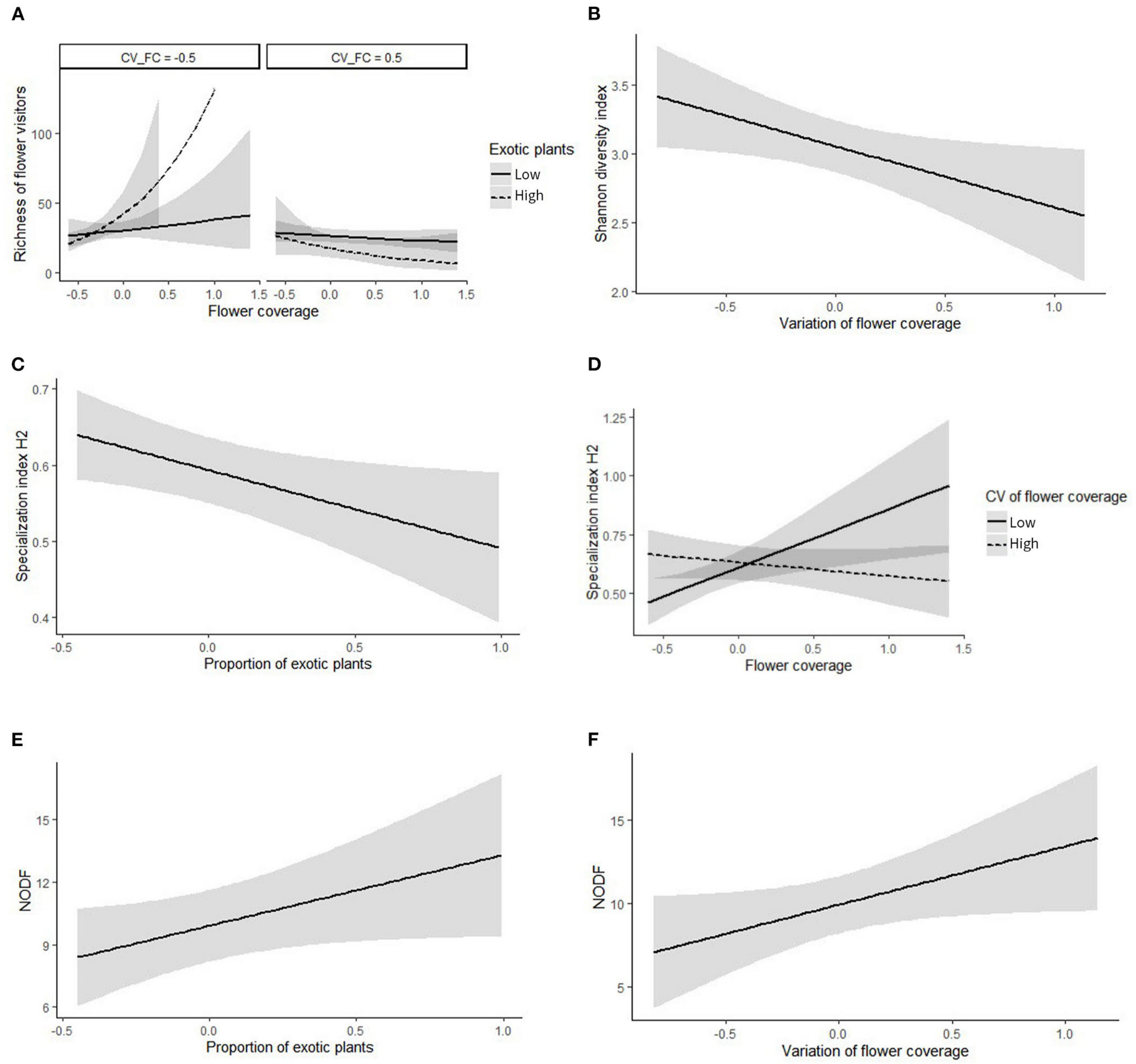

FIGURE 3
Response of community parameters and network metrics to different local scale variables. **(A)** Response of richness of flower visitors to flower coverage, for different proportions of exotic plants at two different values of the coefficient of temporal variation of flower coverage (CV_FC). The values of the explanatory variables are standardized, their equivalence is as follows: flower coverage −0.5 = 3%, 0.5 = 18%, 1 = 27%; coefficient of variation of flower coverage, CV_FC: −0.5 = 23% (low variation in floral resources), CV_FC: 0.5 = 75% (high variation in floral resources); the proportion of exotics plants: low = 4%; high = 46%. **(B)** Response of the Shannon diversity index to temporal variation of flower coverage; **(C)** response of the specialization index to the proportion of exotic plants; and the responses of NODF to **(D)** proportion of exotic plant species, and **(E)** temporal variation of flower coverage. References: the values of the explanatory variables are standardized. The equivalence of each value is as follows: proportion of exotic plants: −0.4 = 3%; 0 = 20%; 0.8 = 58%; temporal variation of flower coverage: CV_FC −0.5 = 23% (low resources variation), 0 = 50% (medium resources variation), CV_FC 0.5 = 75% (high resources variation). **(F)** Response of the specialization index H_2 to flower coverage, at two different levels and the coefficient of temporal variation of flower coverage. The value of the explanatory variables are standardized, we show the equivalence of each value: flower coverage −0.5 = 3%, 0.5 = 18%, 1 = 27%; temporal variation of flower coverage: low = 23% (low variation in floral resources), high = 75% (high variation in floral resources).

Landscape effect over community parameters and network metrics

We found that the effect of the percentage of impervious surface on flower visitor richness differs with altitude. At low altitudes, the richness of flower visitors increased when the proportion of impervious surfaces increased. But at high altitudes, richness decreases with increasing impervious surface (Figure 4A, Table 2).

The specialization of the network (H_2) was negatively affected by impervious surface, suggesting that urbanization induces a more

TABLE 2 Estimates of community and network parameters, SE, and 95% confidence interval limits (CL) for explanatory variables at the landscape scale.

Model	Response variable	Explanatory variables	Parameter estimate ± SE	Confidence interval limits (CL)	
				2.5%	97.5%
Landscape	Flower visitors richness	(Intercept)	3,326 ± 0.0527	3,2151	3,4371
		imp_sur	0.0740 ± 0.1032	−0.1414	0.2895
		sur_tem	0.0717 ± 0.0977	−0.1343	0.2778
		Alt	0.0249 ± 0.1236	−0.2328	0.2826
		Alt × imp_sur	**−0.6784 ± 0.2965**	**−1,3097**	**−0.0471**
		imp_sur × sur_tem	0.5656 ± 0.3261	−0.1236	1,2548
		Alt × sur_tem	0.3774 ± 0.3542	−0.3540	1,1088
	Specialization index H_2	(Intercept)	0.6029 ± 0.0354	0.5283	0.6775
		imp_sur	**−0.1013 ± 0.0341**	**−0.1732**	**−0.0294**
		sur_tem	0.0519 ± 0.0462	−0.0457	0.1495
		Alt	0.0237 ± 0.0684	−0.11761	0.1650

Explanatory variables with CL excluding zero are in bold. We only show the response variables that were affected by some explanatory variables. References: alt: altitude; sur_tem: surface temperature; imp_sur: impervious surface.

generalized assemblage (Figure 4B, Table 2). The Shannon diversity index was not affected by any landscape explanatory variable.

Discussion

In this study, we evaluated the influence of urbanization over the assemblage of flower visitors using an interaction network approach, in an area of Argentinian Yungas. We measured different variables at local and landscape scales and evaluated the effect of those variables over community and network metrics. We found that both local and landscape-scale variables differently affected community parameters and network metrics. At the local scale, specifically, temporal variability of resources had complex effects over most of the parameters evaluated, while landscape-scale variables affected both network specialization and flower visitor richness.

At the local scale, we found that the stability of flower resources affected the richness of flower visitors and the level of generalization of the network. Increasing the stability of floral resources increased the richness of flower visitors and diversity of interactions and decreased the level of nestedness. It has been shown that the constancy of floral resources over time can lead to a high richness of flower visitors (Stewart and Waitayachart, 2020). Conversely, the diversity of flower visitors was negatively affected by decreasing stability of floral resources as was documented previously by Winfree et al. (2011) who found that flower visitors respond to changes in floral resources. As was observed in other studies, the availability of floral resources can mitigate the effect of urbanization on flower visitors (Burdine and Mccluney, 2019; Baldock, 2020; Wenzel et al., 2020). Moreover, urban sites could be a better place than suburban and rural areas by offering large amounts of floral resources (Lynch et al., 2021) and nesting sites (Frankie et al., 2005; Matteson et al., 2008; Hülsmann et al., 2015), as well as a more stable availability of those resources over time, as plants are replaced periodically in parks within urban areas. Our findings highlight the importance of constant and reliable availability of floral resources within urban areas to maintain a high richness and diversity of flower visitors.

Increasing the proportion of exotic flowers within the community, usually used as ornamental in urban areas (Smith et al., 2005), also affected flower visitors and their interactions. Many studies report a negative effect of exotic plants over flower visitors (Moroń et al., 2009; Martins et al., 2013; Fenesi et al., 2015), while others show no effect of plant status (native or exotic) on network structure (Vilà et al., 2009). We found that exotic flowers, when constant, increased flower visitor richness, probably because they provide important resources. Additionally, we found that an increasing proportion of exotic plants leads to a more generalist and nested network. The increase in generalist interactions can result from having more generalist flower visitor species or generalist plants (exotic plants may have floral morphologies that are more accessible to any flower visitor). Yet in our sites, both generalist and specialist flower visitors (specifically bees) are found equally distributed in the gradient studied (Amado De Santis and Chacoff, 2020). Alternatively, increased generalization may be related to a reduction in the number of native plants, a common trend found in urbanization gradients (Bertin, 2002; Chocholoušková and Pyšek, 2003; Tait et al., 2005). As a result, specialized interactions between native plants and flower visitors might have been lost (Traveset and Richardson, 2006; Aizen et al., 2008). Moreover, exotic plants contribute to an increase in flower visitor niche overlap (Marrero et al., 2017), thus, an increasing number of exotic plants may be playing a key role in interspecific competition among flower visitors, which could lead to a more generalist behavior by flower visitors.

Nestedness, the most common structure of mutualistic networks (Bascompte et al., 2003), has been linked to resilience, in theoretical models, as increasing nestedness increased resilience (Thébault and Fontaine, 2010). We noticed that the prevalence

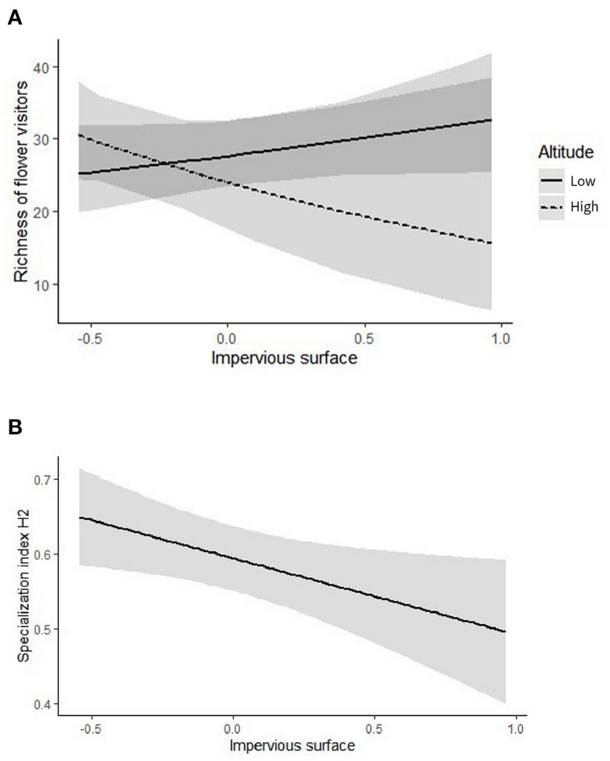

FIGURE 4
Response of community parameters and network metrics to different landscape scale variables. **(A)** Response of the richness of flower visitors to the interaction between the percentage of impervious surface and altitude. The value of the explanatory variables are standardized, we show the equivalence of each value: impervious surface −0.4 = 4%, 0.1 = 35%, 0.6 = 65%; low altitude = 1,120 m, high altitude = 1,550 m. **(B)** Response of the specialization index H_2 to the urbanization gradient. Each triangle represents a value of the specialization index H_2 for each of the 21 communities analyzed. The value of the explanatory variables are standardized, we show the equivalence of each value: impervious surface −0.4 = 4%, 0.1 = 35%, 0.6 = 65%.

of exotic plant species along with low floral resource stability throughout the flowering season increased the level of nestedness of the plant-flower visitor networks. This agrees with previous studies where they show a positive relationship between nestedness and the presence of exotics (Stouffer et al., 2014). Exotic plants are generally involved in generalist interactions, and it has been recently found that they can even contribute more than natives to nestedness in networks of urban areas (Zaninotto et al., 2023). Exotic plants can play an important role in increasing the level of nestedness, thus probably increasing the resilience of these communities in urban areas, as they provide resources in moments when native flowers are not flowering. In this case, the nested pattern may be related to the tendency of having bigger networks toward urban areas (Bascompte et al., 2003; Vázquez and Aizen, 2004) and an increased generalism in the interactions. This interpretation agrees with Pigozzo and Viana (2010), who suggested that nestedness could be related to the ability of different species to exploit the different range of resources (generalist vs. specialist). To our knowledge, low stability in floral resources followed by an increase in nestedness in the community is a new and interesting result, probably related to the different timing of flowering of native vs. exotics or to the increased phenological period of flowering. Further studies could confirm its generality and contribute to understanding the mechanisms behind it.

At the landscape scale, the percentage of impervious surface affected network structure, while temperature and distance to bigger natural areas had no detectable effects. We found that the effect of the percentage of impervious surface on flower visitor richness differs with altitude. At the lowest sites, the richness of flower visitors increased with an increasing proportion of impervious surfaces, but the effect was the opposite at high altitudes. Species richness of flower visitors has been shown to decrease with altitude (Arroyo et al., 1985; Hodkinson, 2005; Ramos-Jiliberto et al., 2010), as in our study, despite the narrow altitude range of our sites (1,031–1,681 m.a.s.l.). The differential effect of urbanization on the richness of flower visitors depending on altitude might be the result of a more specialized, restricted, or limited set of species toward higher altitudes, but further study to understand the mechanism behind this pattern would be needed.

The proportion of impervious surfaces negatively affected the specialization of the network. This result agrees with Aizen et al. (2012), who concluded that specialized plant-flower visitor interactions are particularly prone to be lost with increasing habitat fragmentation and other anthropogenic disturbances. Moreover, this could be related to a greater percentage of exotic plants in urban areas, which contribute to an increase in niche overlap among flower visitors, as exotic species often have less restricted morphologies, and therefore tend to be more generalistic, on average, than native species (Marrero et al., 2017). This scenario might favor mostly generalist flower visitors and could affect the reproduction of native plants present in these sites (Totland et al., 2006). In this sense, many species of flower visitors interact with generalist exotic plants in highly invaded networks, and there is a trend of increased dependency with time on those exotic species (Aizen et al., 2008). This situation could lead to a more generalist flower visitor assemblage.

Overall, our results suggest that, at the community level, flower visitors are affected by urbanization, although this is dependent on the spatial scale. Local-scale factors have strong effects on the parameters measured, and local and landscape effects both affect the richness and the specialization levels of the network in different ways. Therefore, our findings highlight the importance of factors at the local scale—i.e., the stability of floral resources in their effect on community and network metrics. Our results suggest that urban residents along with garden managers can promote the presence of pollinators by managing floral resources, specifically increasing their stability through the spring and summer. Our results are encouraging because local conditions can be relatively easily managed, while landscape or context variables, such as habitat cover, are more complex and economically costly to handle. With the information offered here, we encourage decision-makers to be very cautious in the implementation of development plans in urban environments located in forests at high altitudes. In conclusion, the network approach provides valuable information to achieve more sustainable development of urban expansion with respect to the flower visitor assemblages when managing territorial development plans and maintenance of public green spaces such as urban squares and parks.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

Data collection and analysis were performed by AA and NC. The first draft of the manuscript was written by AA. NC and SL commented on previous versions of the manuscript and read, discussed, and approved the final manuscript. All authors contributed to the study's conception and design. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2023.1086076/full#supplementary-material

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Local influence of floral resource attributes on urban bumble bee foraging activity

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Introduction: Urbanization diminishes the extent of uncompacted, exposed soil and the coverage of wild plant species, yet still supports diverse pollinator communities when their habitat is maintained within the built environment. Floral abundance and richness are known to influence bee foraging behavior, and these factors vary across the landscape, especially across heterogeneous urban extents. This study assesses how floral resources are distributed across the city of Madison, WI and how these factors influence the distribution of foraging bumble bees.

Methods: We conducted a systematic walking transect survey of bumble bees across Madison, WI. The resulting point location data associated with more than 5,000 non-lethally surveyed bumble bees were analyzed with regard to floral resource explanatory variables as well as underlying land use zoning on more than 700 transects. We used Moran's *I* correlograms to investigate spatial autocorrelation in floral resource variables and bumble bee counts, then we fitted a generalized linear model predicting transect bee counts based on floral cover, density, species richness and wild plant species richness on the distribution of foraging bees. We employed a geographically-weighted regression model to explore non-stationarity in the effects of floral resource explanatory variables across the study extent.

Results: We found significant positive influence of flower cover, species richness, and weakly significant positive influence of wildflower species richness on foraging bee counts within the model as well as a significant positive influence of the land use zoning categorical variable. The effects of floral resource predictors on foraging bumble bees varies based on landscape context across the city.

Discussion: The results of this study show that landscapes with high cover as well as floral diversity maximize bumble bee foraging, and the positive effect of wildflower species richness stands out where floral cover and overall richness are also present. Given that urban landscapes are not homogeneous and that floral resources are not consistently distributed across the cityscape, valuable pollinator habitat should be protected, and supplemented where gaps persist.

KEYWORDS

urban bees, floral resources, foraging ecology, geographically weighted regression (GWR), non-stationarity, bumble bees (Bombus), sustainable cities, pollinators

Introduction

Pollination is an essential ecosystem service that enables the production of fruits and seeds and maintains the diversity of most plant populations in almost all global ecosystems (Klein et al., 2007; Ollerton et al., 2011; Garibaldi et al., 2013). However, global declines of many pollinators have triggered international interest in conservation science to address risk factors and isolate the most influential variables that promote bee community resilience (Goulson et al., 2008; Tuell et al., 2008; Garbuzov and Ratnieks, 2014). Floral abundance and floral species richness are known factors that influence bumble bee colony growth and foraging activity (Jha and Kremen, 2013; Crone and Williams, 2016). These resources have been assumed to decrease in urban ecosystems compared to forb-rich, semi-natural land cover (e.g., prairie), yet recent work has revealed that urban ecosystems likely provide intermediate amounts of floral resources that surpass other types of natural land cover (e.g., forb-poor grassland) (Goddard et al., 2010; Threlfall et al., 2015; Lynch et al., 2021). Comprehensive investigation of the distribution of floral resources and foraging bumble bees across an urban extent may illuminate which aspects of floral resource distribution shape bumble bee foraging patterns most across an urban ecosystem.

Foraging for food is an energy intensive process that must be continuously accomplished to sustain bumble bee colonies through the growing season (Dornhaus and Chittka, 2005). Bumble bees do not store much surplus food within the colonies, so constant, efficient foraging on nutritionally appropriate pollen sources is a necessity (Vaudo et al., 2018). Bumble bees are central place foragers, known to fly long distances to visit resource rich floral assemblages (Redhead et al., 2016) and landscape scale floral resources have been shown to influence bumble bee foraging distances in studies based in multiple landscapes (Jha and Kremen, 2013; Pope and Jha, 2018). Bumble bee activities and resource use are difficult to assess at broad landscape scales and are known to differ depending on the composition of the landscape (Hemberger and Gratton, 2018; Pfeiffer et al., 2019; Rollings and Goulson, 2019). Spiesman et al. (2016) found no influence of landscape scale floral resources on bumble bee colony growth, when local dominance of resource-rich flowers was high.

Landscape-scale studies have been conducted to confirm the importance of floral cover and native plant species richness to sustain bee communities, and further consideration of the distribution of these factors may help to illuminate the degree of their influence in heterogeneous urban ecosystems (Williams et al., 2012; Requier et al., 2020; O'Connell et al., 2021). Many studies focus on components of urban landscapes in isolation, such as city parks or residential gardens, rather than the comprehensive urban landscape (Bhattacharya et al., 2003; McFrederick and LeBuhn, 2006; Osborne et al., 2008). Developing an understanding of the distribution of important foraging resources and their use by foraging bees across complex spatial extents is important to improve the capacity of landscapes to sustain robust pollinator populations (Pywell et al., 2006; Brosi et al., 2008; Goulson et al., 2010). Comparing the influence of various explanatory factors on the distribution of bumble bee foragers can help to tune conservation guidelines to the context of a particular ecotype (Galpern et al., 2012).

This study investigates the spatial distribution of floral resources and foraging bumble bees around the city of Madison, and tests the predictive capacity of four aspects of floral resource distribution to estimate the distribution of foraging bumble bees. We hypothesize that (1) floral resources and bumble bee abundance are not uniformly distributed across the urban extent, and (2) floral cover, density, species richness, and wildflower species richness increase bumble bee foraging activity. Additionally, (3) we expect that the importance of the various aspects of floral cover fluctuate across the city based on relevance to local limiting factors. Specifically, we expect that floral community composition will be most important where there is sufficient floral cover or density. We explore patterns of non-stationarity in the effect size of floral resource explanatory variables across the study extent using geographically weighted regression. The results of this study identify what aspects of floral resource distribution confer the strongest influence on observed frequency of bumble bee foragers, informing conservation practitioners based on local context.

Materials and methods

Study area

We conducted a systematic transect survey across a 125 km^2 extent covering the city of Madison, WI, USA to map the distribution of floral resources and foraging bumble bees in July and August of 2013 and 2014. The survey extent included the city of Madison, located on an isthmus bounded by a northern and southern lake, as well as the exurban agricultural land immediately adjacent to the eastern and western edges of the city. Several high density urbanized patches of mixed commercial/residential zones were located within both eastern and western residential zones, as well as the center of the grid (downtown Madison). Agricultural land was primarily located on the eastern and western edges of the city, across an approximately 6 × 3 km of surveyed terrain on each edge. The majority of the surveyed terrain was comprised by residential land use, characterized by a moderate range of impervious surface (∼20–30% based on 1 m resolution classification), and grass lawn, with scattered patches of woodland and semi-natural grassland or restored prairie scattered throughout the extent.

Transects

An ∼400 m transect was surveyed across each publicly accessible 400 × 400 m cell of the 125 km^2 grid, by walking a maximally straight line from one side of the grid cell to another between 9 am and 5 pm, in July and August of 2013 and 2014, the time of year when bumblebees are most prolific. Due to extremely-restricted accessibility of the urban landscape based on the layout of residential property, most transects were located along one side of a street, and half the transect area was comprised by impervious surface. Frequently, large parking lots also boosted the amount of impervious surface covered by the transect path. After the maximally straight, approximately 400 m, publicly-accessible path from one side of the cell to another side of the cell was selected, an observer walked the path across the cell as a 10 m wide transect, at which time the observer recorded a list of flowering plants in anthesis, and recorded GPS points marking the occurrences of bumble bees. The mean and median transect lengths was 389 m and 409 m, respectively, while the minimum and maximum transects were 210 m and 664 m. When bumble bees were observed within 5 m of the observer, GPS coordinates were collected and their species was recorded along with the plant morphospecies they were visiting in most cases (Williams et al., 2014). Most native plants were identified to species, however many ornamental plants and rare plants were identified by morphospecies alone (i.e., >90 percent of floral ids were at species level).

Explanatory variables

The floral resource explanatory variables estimated for each transect included percent cover, density, flowering plant species richness, and prairie and lawn species richness. During the transect walk, the observer estimated the total percentage area of the transect that could support vegetation (non-impervious), as well as the average density of flowers within that area of non-impervious cover. After completion of the data collection, all flower morphospecies were classified as lawn, prairie, or garden species based on the ecotype where they were most often observed. The lawn species included "weedy" morphospecies that commonly persisted in areas with mowed lawn, including white clover (*Trifolium repens*), red clover (*Trifolium pretense*), birds-foot trefoil (*Lotus corniculatus*), crown vetch (*Secuigera varia*), dandelion (*Taraxacum officinale*), heal-all (*Prunella vulgaris*), sweet clover (*Melilotus* spp.), plantains (*Plantago* sp.), and chickweed (*Cerastium* spp.). Prairie species included primarily native, perennial species commonly found in restored prairie ecotypes (as well as gardens), but whether spontaneous or cultivated, require reduced mowing to produce flowers such as Joe-pye weed (*Eutrochium purpureum*), Boneset (*Eupatorium perfoliatum*), Cone flower (*Echinacea purpurea*), milkweeds (*Asclepias* spp.), rosinweed (*Silphium integrifolium*), cup plant (*Silphium perfoliatum*), vervain (*Verbena* spp.), Queen Anne's lace (*Daucus carota*) and others. Most other species were classified as garden species found primarily in managed gardens and dominated by cultivars.

Mapped transects were compared with city parcel spatial data layers, and each transect was assigned a categorical land use zoning type, loosely based on city zoning of the parcels where the transect was surveyed. Commercial use was prioritized, so that mixed residential and commercial zones were coded as commercial. Residential zones were the most common land use category. Transects that passed through city parks were coded as city parks. Agricultural zoning qualifications in the city parcel data were much less accurately linked to observed land use, so agricultural land use zoning was determined based on observation during the transect survey.

Statistical analysis

To test our expectation that floral resource descriptors and bumble bee counts were not uniformly distributed (hypothesis 1), and spatial autocorrelated at local scales – meaning nearest neighbor transects or nearest few transects, or nearest 50 transects were more similar than expected based on the distribution of values across the whole dataset – we investigated the scale of spatial autocorrelation in each of these variables using correlograms. Correlograms estimate Moran's I correlation metrics between classes of points separated by increasing spatial lags to illustrate the scales at which either positive or negative spatial autocorrelation is observed and where it dissipates. Signals at the most distant lags should be ignored because they are based on very few comparisons, because they are calculated only based on the most distant points.

The number of bumble bees foraging on each transect was modeled using a generalized linear regression model to estimate the effect of floral resource explanatory variables and land use zoning on bumble bee frequency to test hypotheses 2. The variance in count data was greater than the mean, indicating a pattern of over-dispersion that breaks the assumptions associated with the Poisson distribution. Both negative binomial and quasi-poisson model fitting were applied, resulting in similar patterns of variable strength and significance. The robust quasi-poisson fitting was used for the Poisson model to accommodate overdispersion commonly observed in count datasets. This fitting adjusts the standard error with an appropriate scalar, although the coefficient estimates remain the same as the standard Poisson model. Interactions between land use type and each floral resource variable were included to test hypothesis 3. Before fitting the model, the variance inflation factor of the explanatory variables was calculated to ensure that multicollinearity would not overestimate the variance explained by the model. All VIF scores fell below 2, well below commonly used cut-off values of 5 or 10.

The Moran's I test of residuals based on spatially weighted 10 nearest neighbor points was used to check for spatial structure in the residuals of the model, and the alternative hypothesis that existing spatial structure in the dataset was not captured in the model. However, the test statistic ranging between -1 and 1, was calculated to be 0.062 ($p < 0.001$), very close to zero indicating only a very small proportion of the variance in bee frequency was explained by spatial structure with a ten nearest point ($k = 10$) neighborhood covering an approximately 1.5 km radius neighborhood. Similarly small spatial structure was observed using a 25 or 100 point neighborhood, with Moran's I test statistics estimated as 0.016 $p = 0.037$ or 0.013 $p = 0.001$. Robust standard error was calculated separately for each coefficient estimate in the glm model using the "sandwich" package in R (R Core Team, 2013; Zeileis et al., 2018). To account for the spatially autocorrelated variance, the robust standard error for heteroscedasticity was used (ie. vcovHC) with White's estimator for large sample sizes (i.e., "HC0"). This method is tailored to take into account leverage points.

In the final component of the study, we employed a local quasi-Poisson model fitted by the geographically-weighted quasi-Poisson regression method to investigate non-stationarity in floral resource coefficient estimates across the study extent (Kalogirou, 2018). This exploratory statistical method is a type of local regression whereby generalized linear regression models are fit across the study extent based on a moving window, and regression coefficients are calculated for each data point. This analysis was accomplished using the "lctools" R package. Local regression coefficients were calculated based on an adaptive geographic window including the

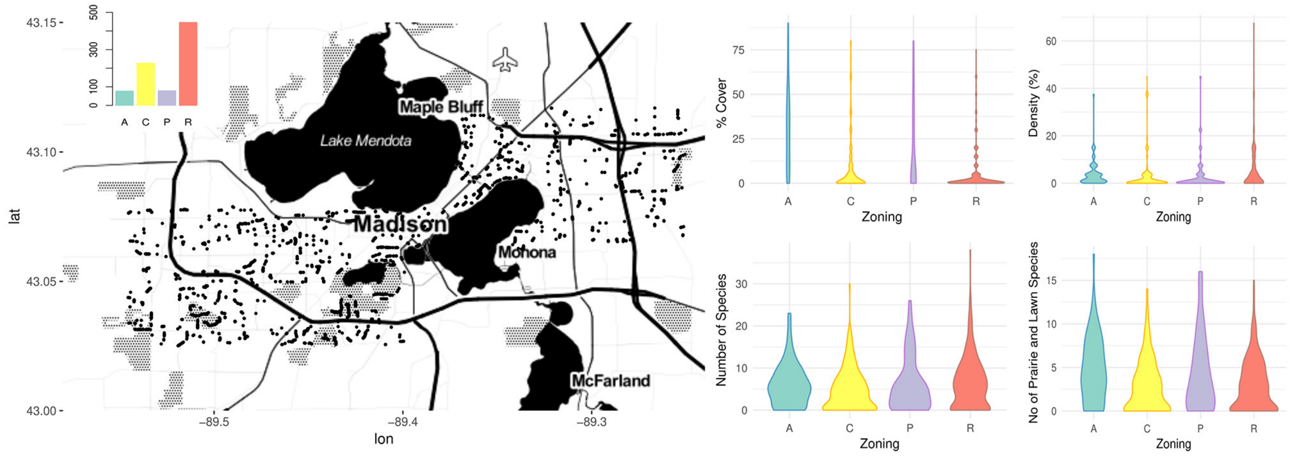

FIGURE 1
Map of the study extent and point locations of bumble bees observed along the transects. The upper left bar chart shows the number of transects sampled of each land use category (A – Agricultural, C – Commercial, P – Park, R – Residential), while the fiddle plots on the right show the distribution of flower resource explanatory variables by land use categorical variable zoning levels. Basemap data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org.

50 closest points and each included data point is weighted by geographic distance.

Results

Overall, 784 transect were surveyed, including 408 residential transects, 222 commercial transects, 77 agricultural transects, and 77 transects through city parks. Across the transects 5,574 foraging bumble bees were documented, primarily comprised by *Bombus impatiens*, *B. bimaculatus*, *B. vagans*, *B. griseocollis*, *B. rufocinctus*, *B. fervidus*, *B. auricomus*, also, *B. perplexus*, *B. sandersoni*, *B. ternarius*, *B. terricola*, and *B. affinis*. Floral cover, density, species richness, as well as the number of prairie and lawn species were documented, and while the range of each of these variables was similar across each of the land use zoning types, the distribution of values for several of these explanatory variables differed between land cover zoning categories (i.e., agricultural, commercial, residential, and park) (Figure 1). Transects in agricultural zoned areas and city parks were characterized by a more uniform distribution of flower cover compared to commercial and residential transects which were more frequently characterized by lower flower cover and higher impervious surface than agricultural and park transects. Commercial and residential transects included more low and high values of species richness, while agricultural and city park transects included more high values of lawn and prairie species compared to commercial and residential transects.

Floral resources were more spatially autocorrelated than bees

Positive spatial autocorrelation was observed in bee count data up to about 5 km, and in floral resource variables up to about 2 or 3 km (Figure 2). Maximum Moran's I estimates of bee count data at very short distances reached 0.1 (Figure 2A), while floral resource variables reached a higher maximum of just over 0.15 (Figures 2B–D), which indicate that only a small proportion of the variation could be attributed to local spatial autocorrelation.

The most bee-attractive flower species were prairie and lawn species

Fourteen flower species each supported more than 1% of the bumble bees observed in the survey data (accounting for over 55 observations). These "*most visited species*" accounted for ∼70% of all bumble bee observations documented in our survey. These top visited species included, goldenrod (*Solidago spp.*) (12.4% of observations), white clover (*Trifolium repens*) (12.2%), thistle (*Cirsium spp.*) (11.2%), bee balm (*Monarda spp.*) (10.4%), garden mints (*Mentha spp.*) (5.6%), spirea (*Spirea spp.*) (5.5%), purple coneflower (*Echinacea purpurea*) (4.0%), and silphiums (*Silphium spp.*) (4%). Russian sage (*Perovskia atriplicifolia*), Birds-foot trefoil (*Lotus corniculatus*), knapweed (*Centaurea spp.*), crown vetch (*Secuigera varia*), joe pye weed (*Eutrochium purpureum*), and red clover (*Trifolium pretense)*, each supported between 1 and 3% of the bee visits. Most of these species were classified as either lawn or prairie species rather than garden species. While these species were commonly distributed across the city, there were other common species (Table 1) that were rarely visited, including hosta (*Hosta spp.*), bell flower (*Campanula latifolia*), and lillies (*Lilium spp.*). The most visited flowers classified as garden types included, mint, Russian sage, and spirea.

Floral cover and diversity positively influenced the number of foraging bumble bees

The quasi-Poisson generalized linear regression model fit for the transect count data evidenced significant influence of flower

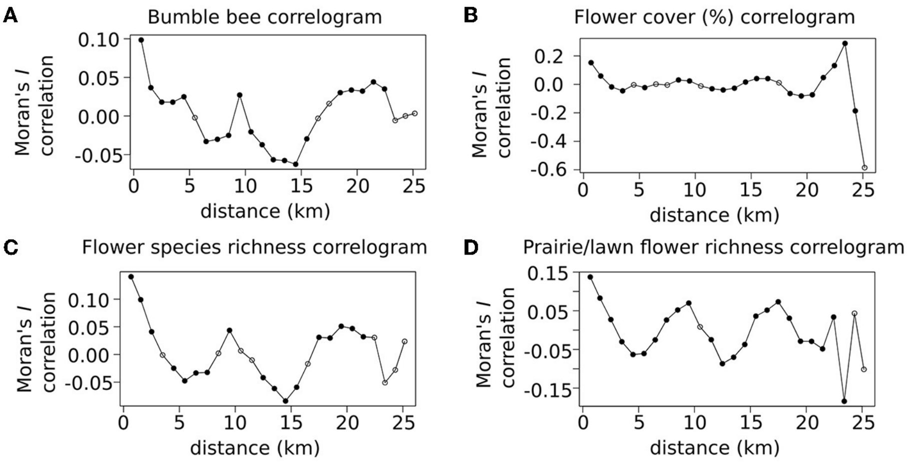

FIGURE 2
Correlograms depict the spatial structure of variance across scales within the study extent for **(A)** bee counts, as well as each floral resource variable, **(B)** floral cover, **(C)** floral species richness, and **(D)** Prairie/lawn flower species richness. Correlograms plot the Moran's *I* correlation statistic. Dark points in the correlogram indicate a statistically significant Moran's *I* value indicating positive or negative spatial autocorrelation between transects separated by the spatial lag value on the x-axis compared to the rest of the transects in the dataset.

TABLE 1 Most common species of each flower ecotype group ordered by observation frequency.

Lawn	Prairie	Garden
Trifolium repens	*Daucus carota*	*Hosta* spp.
Lotus corniculatus	*Cirsium* spp.	*Lilium* spp.
Taraxacum officinale	*Rudbeckia hirta*	*Lilium lancifolium*
Melilotus officeinalis	*Cichorium intybus*	*Campanula latifolia*
Phlox spp.	*Echinacea purpurea*	*Calendula officinalis*
Oxalis stricta	*Monarda fistulosa*	*Leucanthemum vulgare*
Securigera varia	*Liatris pycnostachya*	*Perovskia atriplicifolia*
Cerastium spp.	*Solidago canidensis*	*Spirea* spp.
Trifolium pretense	*Erigeron* spp.	*Rosa* spp.
Plantago lanceolate	*Achillea millefolium*	*Impatiens* spp.

TABLE 2 Global model summary information for the quasi-Poisson fit regression model used to test the influence of floral resource explanatory variables and land use zoning on foraging bumble bee transect count data.

Global quasi-poisson model summary			
Factors	Estimate	Robust error	*p*-value
Intercept	0.33	0.225	0.194
Cover	0.016	0.003	0.000 ***
Species richness	0.042	0.011	0.000 ***
Wild species richness	0.037	0.023	0.073 .
Commercial	0.755	0.222	0.004 **
Park	1.463	0.251	0.000 ***
Residential	0.628	0.223	0.015 *
Null deviance: 12821.6 on 783 degrees of freedom			
Residual deviance: 9085.1 on 777 degrees of freedom			
qAIC: 646.74			
Pseudo R^2: 0.29			

An additional GLM fitted using a negative binomial distribution is presented in Supplementary Table 1.
*$p < 0.05$ indicates that the variable is statistically significant at the 95% confidence level.
***$p < 0.001$ indicates high statistical significance.

cover as well as species richness, and a weakly significant influence of prairie and lawn flower species richness on the bee count data across the transects (Table 2). Additionally, the categorical factor of land use zoning, showed significant differences in the number of foraging bees where city parks supported 4 times more bumble bee foragers than agricultural transects on average, and residential and commercial transects supported about twice as many bees as agricultural transects (Figure 3C). The effect size of floral resource explanatory variables contrasted in terms of their unit increase influence on bee count in Figure 3. An additional global GLM fitted using a negative binomial distribution is presented in Supplementary Table 1, and shows similar patterns of predictive power for the explanatory variables. The negative binomial distribution model weighs small values more, while the quasi-poisson weighs the large values more.

Interactions between land use type and each floral resource variable were tested, yet interactions were only weakly significant in the full model, and when non-significant resource variable and zone class interaction subsets were eliminated, the weak significance dissipated, and more variance was explained by the primary floral resource factors.

Local models illustrated variance in effect sizes

A geographically-weighted generalized linear regression analysis was used to explore fluctuation of floral resource

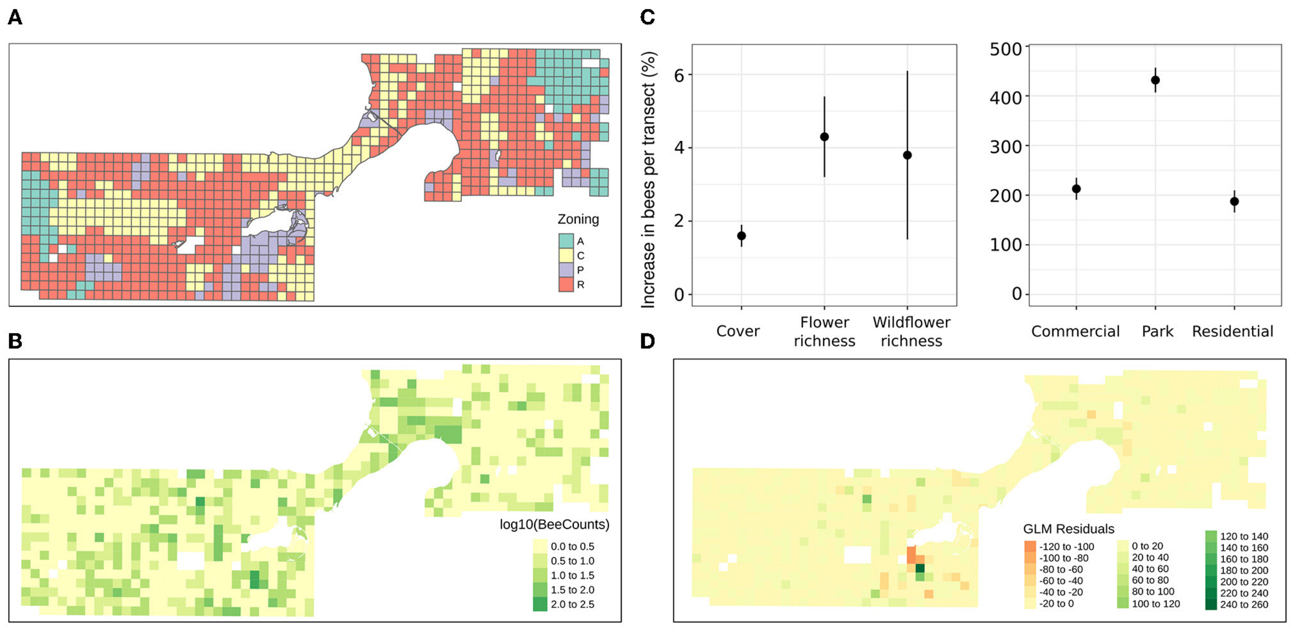

FIGURE 3
Transcript grid polygon layer symbolized by **(A)** land use zoning type **(B)** log base 10 of the number of foraging bumble bees counted on each transect (2 = 100 bees) **(C)** estimated effects of unstandardized explanatory variables (expected increase in bees per variable unit, i.e., percent or additional species), and **(D)** the residuals of the global GLM, based on the fitted model and observed bumble bee count data.

explanatory variable effect sizes across the study extent (Figures 4, 5). Local regressions were fit for each transect point, based on the data associated with the fifty closest transects, weighted by geographical distance so that data from the closest transects were more impactful in the regression model. The coefficients from each local regression model are plotted on each transect point to indicate the strength (Figure 4) and significance (Figure 5) of the explanatory variables in the local regression. Floral cover was the most consistently strong positive influence on bumble bee foraging counts across the study extent, consistent with the global quasipoisson generalized linear model. Density was the only non-significant floral resource explanatory variable. The slight positive influence of density was also widespread and highest in the agricultural and commercial areas.

While overall floral morphospecies richness and the richness of prairie and lawn flower morphospecies was positively correlated, this overall and non-managed subset of flower richness was distributed differently across land use zones. Commercial and residential areas sustained higher floral richness than parks and agricultural areas, however, parks and agricultural transects sustained rather higher richness of the lawn and prairie species subset. Across the study extent, the positive influence of overall species richness was more widespread and disappeared only in places where the positive influence of prairie and lawn species richness was particularly strong. These areas where prairie and lawn species richness stood out as the stronger effect in the glm regression model included areas with large, species-rich restored prairies (West – UW Madison Arboretum; East – Heritage Prairie, Elvehjem Park) surrounded by residential areas.

Discussion

The results of the study illustrate the spatial distribution of foraging bumble bees with regard to Madison's floral resources and the scales of spatial autocorrelation present in the bumble bee counts and floral resource variables. Furthermore, the global GLM of bumble bee abundance based on floral resources evidences the positive influence of floral cover and species richness, while the local regression results portray some variability in the influence of these floral resource variables across the urban extent.

Flower species and foraging bumble bees

Past studies have offered insight into bumble bee preferences for nutritious flower species by foraging bumble bees based on protein-lipid composition (Vaudo et al., 2016, 2018). Gardeners, pollinator enthusiasts, and ecologists have identified bumble bee-attractive flowers and encouraged the use of native plants in pollinator gardens for many years (Tuell et al., 2008; Williams et al., 2015). However, the benefit of lists or simplistic dichotomies has also been questioned, as pollinators tend to be generalists, and other nutritional or contextual factors may influence their foraging behavior (Garbuzov and Ratnieks, 2014; Rollings and Goulson, 2019). An investigation of urban plant-pollinator visitation networks between 24 pollinator morpho-types and 106 plant taxa revealed that elimination of all but four highly attractive plant taxa could maintain all observed pollinators (Lowenstein et al., 2018). Many flower species are likely useful to pollinators, and other factors like consistent

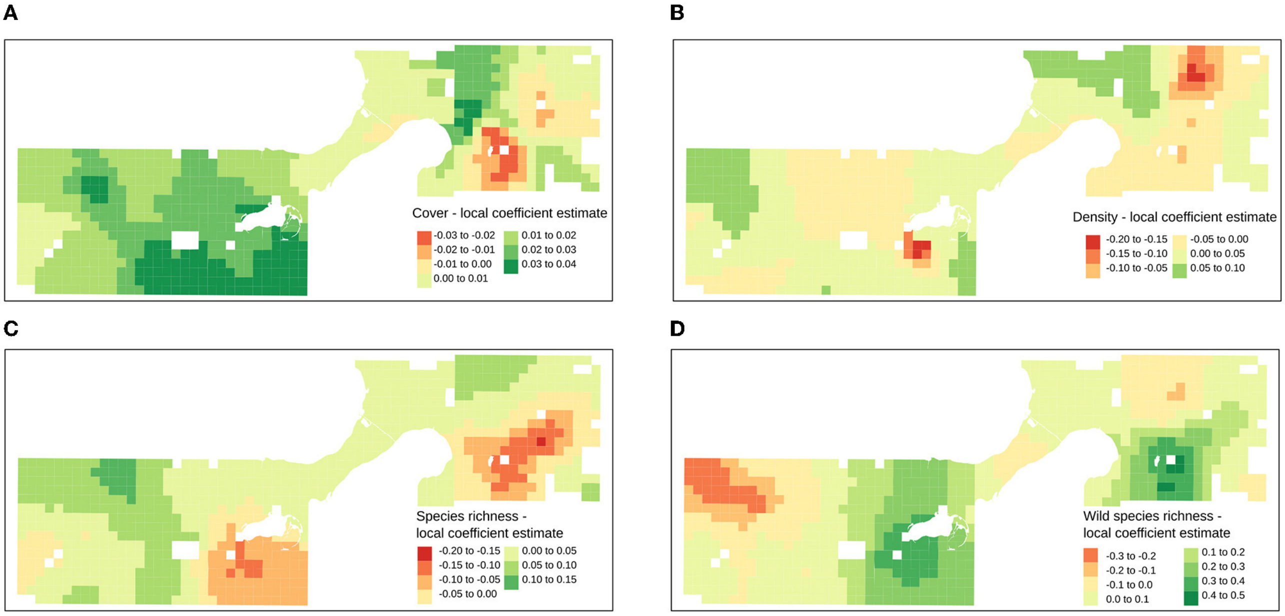

FIGURE 4
Raw explanatory variables and coefficient estimate results of geographically weighted regression mapped across study extent for **(A)** % flower cover **(B)** % flower density **(C)** flower species richness **(D)** wildflower species richness. Coefficient estimates can be interpreted as, −0.3 = 26%, −0.2 = 18%, −0.1 = 10% less bumble bees, 0.1 =11%, 0.2 = 22%, 0.3 = 35%, 0.4 = 49 % more bumble bees based on a marginal unit increase in the variable.

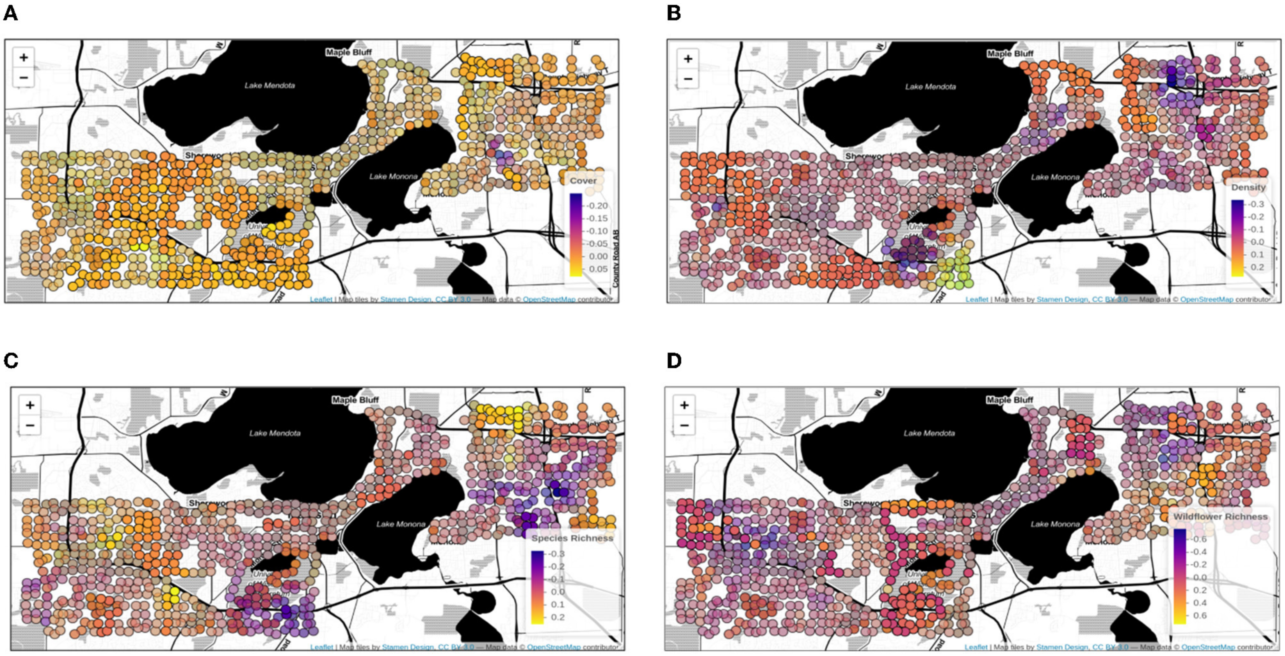

FIGURE 5
The geographically weighted regression coefficient estimates (same as Figure 4) mapped across study extent for **(A)** % flower cover **(B)** % flower density **(C)** flower species richness **(D)** wildflower species richness. Transparent dots indicate lack of statistical significance of variable effects within the local regression models, while opaque dots represent statistically significant coefficient estimates in the local regression models. Basemap data copyrighted OpenStreetMap contributors and available from https://www.openstreetmap.org.

availability of resources through the season might be more important factors to consider (Garbuzov and Ratnieks, 2014). Yet, dramatic differences in visitation across flower species (i.e., 14 species accounted for 70% of visits) underscore the variation in preference of foraging bumble bees (Lowenstein et al., 2018; Mach and Potter, 2018; Rollings and Goulson, 2019). To optimize pollinator habitat within urban gardens, selection of bee-attractive species that provide ample pollen and nectar resources is an important consideration.

Flower distribution and foraging bumble bees

Local significant positive spatial autocorrelation was observed for both floral resource variables and bumble bee observations, however autocorrelation levels were higher for floral resource variables and tapered off at shorter spatial lags (2 or 3 km) compared to bumble bee counts (5 km, Figure 2). The low positive Moran's I statistic values for the floral resource variables ($I \sim 0.15–0.2$), indicate that floral resources within a couple km are more similar to each other than the rest of the dataset, however not dramatically so. At a spatial lag of 4 or 5 km, almost all the floral resource variables exhibit negative spatial autocorrelation, indicating that variable values are more different from each other than the rest of the dataset. This appears to be driven by the dispersion of urban centers through the urban fabric, spacing heavily urbanized spaces between residential neighborhoods with lower coverage of impervious surface.

In recent years, an uptick in urban ecology studies has shed more light on the distribution of floral resources across cities (Ossola et al., 2019; Locke et al., 2021). A study of neighborhoods in Chicago revealed differences in the richness and composition of both spontaneous and cultivated plants between neighborhoods, with some differences explained by socioeconomic factors (Minor et al., 2023). Neighborhoods with lower racial or ethnic diversity had lower numbers of plants, while neighborhoods with intermediate numbers of Hispanic and white residents had the highest species richness, and a higher frequency of weedy species was reported in lower income neighborhoods (Lowenstein and Minor, 2016). Authors conclude that these patterns suggest evidence of disparities in plant-related ecosystem services.

Positive local autocorrelation of bumble bee counts ($I \sim 0.1$) was slightly less pronounced than autocorrelation of floral resource variables, and also extended for about twice as far. While this positive spatial autocorrelation is likely driven by differences in nesting or foraging resources between neighborhoods, the longer range of local autocorrelation is likely due to the mobility of the central place foraging bumble bees (Darvill et al., 2010). Differences in pollinator communities between urban spaces have been recorded in another recent urban pollinator study, wherein parks sustained higher richness and abundance of flower visiting insects than residential neighborhood blocks (Matteson et al., 2013), likely due to differences in habitat provisioned by these different land uses.

Global models and variance in the influence of floral resource variables on the number of foraging bumble bees

In the global GLM, we estimated average effect sizes of floral cover, density, overall floral richness, and wildflower richness for prediction of foraging bumble bees. This approach was used to test our hypotheses that our explanatory variables provided predictive capacity across our study extent. Consistent with other studies, we observed that these explanatory floral variables help predict bumble bee distribution (e.g., Matteson et al., 2013; Spiesman et al., 2016). However, we also expected that the influence of particular variables might differ based on local context. For instance, where floral resources are abundant and specious, the highest quality floral resource patches likely attract the most bumble bees. Investigating the residuals of the model could help to identify locations that surpass our expectations of foraging quality, and locations which fail to meet our predictions. In our map of global model residuals (Figure 3), we can see some high and low predictions of bumble bee foraging, especially several very attractive transects at the UW Madison Arboretum. We can hypothesize about what might cause this additional variation in bumble bee foraging, and set up new studies to test these hypotheses, but we also can explore potential variabilities in the strength of our predictor variables using geographically-weighted regression. This comprehensive investigation of fluctuation in the effect sizes of floral resource explanatory variables across the study extent contextualizes some differing results observed in studies that focus only on a particular ecotype within cities or exurban ecotypes.

In the global model, we tested for evidence of interactions between land use zoning class and floral resource variables, but finally none were statistically significant ($\alpha = 0.05$). Several interactions were weakly significant, including, the interaction between city parks and native flower species richness, boosting the number of foraging bumble bees when they occurred together.

Floral cover and density

Loss of habitat including nesting and foraging resources are likely the most important factors contributing to loss of pollinators around the world (Goulson et al., 2008; Williams and Osborne, 2009; Winfree et al., 2009; Potts et al., 2010). Yet, it is unclear in what contexts various aspects of floral abundance and distribution may be most critical for local bumble bees (Crone and Williams, 2016; Spiesman et al., 2016). The geographically weighted regression results in this study highlight the pervasive positive influence of flower cover, and the slight positive influence of flower density – which is most apparent in agricultural zones and commercial zones. Floral resources are a primary limiting factor for pollinator populations, but local circumstances of distribution and phenology should be also be considered in depth. Studies located in resource pulse landscapes have observed beneficial results of late blooming mass-flowering crops, but not early blooming mass-flowering crops, suggesting increased floral resources as colonies are reaching maximum size has a much different effect than a bump in floral food resources while the colony is still growing. Bumble bees store very little extra food resources in the nest, so continuous access to floral resources during the season is crucial (Dornhaus and Chittka, 2005). Recent studies have documented variation in foraging distance in response to floral abundance in the surrounding landscape evidencing flexibility that is essential for bumble bees to respond to variability in the spatial and temporal distribution of resources (Jha and Kremen, 2013; Vasseur et al., 2013).

Several recent studies have isolated the efficiency of foragers in resource collection as the primary driver of colony growth (Williams et al., 2012; Spiesman et al., 2016; Requier et al., 2020). One study found no influence of landscape scale floral resources when local resources were high, and in this case found high flower species dominance as the primary driver of colony growth (Spiesman et al., 2016). The association between transect scale floral cover and foraging bumble bees seems quite clear, and persistently positive across the study extent. It's possible that the spatial scale at which density was estimated, and the heterogeneity within a transect, obscured the usefulness of this metric in our study.

Floral species richness, floral type, and foraging bumble bees

Floral richness positively influenced the count of foraging bumble bees more than the richness of prairie and lawn species alone. While many common lawn and prairie species were highly attractive to foraging bumble bees and supported the majority of foraging visits, there were highly bumble bee-attractive garden plants as well, including mints, Russian sage, and spirea. As micronutrients may vary greatly between plant species, the need for diverse floral resources may vary based on the nutritional content of the available assemblage.

In two parts of the city, a strong, positive influence of native plant species diversity overcame the influence of overall species richness in the geographically weighted regression results. This phenomenon appeared to result in compensatory negative coefficients in the overall floral species richness variable, where the prairie and lawn species subset surpassed it as a strong influential explanatory variable. These areas represented localities where species rich prairies were nested in residential communities. While it seems that, generally, floral richness is an important predictor of foraging resource quality, in some circumstances, wildflower richness provides more explanatory capacity and comprises relatively better quality of floral resources. This result underscores the value of relatively large extents of restored prairie inside the urban matrix for bumble bees.

As cities grow, it is vital to maintain urban lands that provide bumble bee foraging resources, such that bumble bees can continue to maintain pollination services. This study demonstrated the importance of floral resource distribution on the prevalence of foraging bumble bees and potential disparities in plant and pollinator related ecosystem services across the city. The results of this study show that landscapes with high cover as well as floral diversity would maximize bumble bee foraging. In neighborhoods with ample floral resources or an abundance of ornamental cultivars, wildflower species presence is particularly important. Given that urban landscapes are not homogeneous and that floral resources are not consistently distributed across the cityscape, valuable pollinator habitat must be protected, and supplemented where gaps persist. Comprehensive consideration of cityscapes can help to prioritize conservation efforts to protect high value bumble bee foraging resources and ameliorate biodiversity "*deserts*." Future work could contribute to the understanding of floral phenology and bumble bee foraging behavior throughout the season.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

VP planned and executed the study. JS and JZ reviewed the data analysis. VP drafted the manuscript and all authors reviewed it. All authors contributed to the article and approved the submitted version.

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Conflict of interest

JS was employed by the Silvernail Studio for Geodesign, LLC.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2023.1103721/full#supplementary-material

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Assessing five decades of garden bee studies

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Urban garden spaces are potentially important habitats for bee conservation. Gardens can host diverse flora, which provide floral resources across foraging seasons for bee species. Recent reviews have focused on the impacts of cityscapes on urban bee assemblages in different green spaces. Urban gardens are distinct from other urban green spaces, and bee communities in urban spaces have been an increasing topic of study over the past few decades. We reviewed 28 urban garden bee studies spanning five decades and 14 countries to compile an original metadataset of bee species' functional traits to understand the conservation value of gardens, identify gaps in bee sampling efforts, and summarize the calls to action included by their authors. Studies of urban garden bees have documented between 674 (conservative count, excluding morphospecies) and 830 (liberal count, including morphospecies) bee species. Urban garden bee communities were taxonomically and functionally diverse, although bee species that were non-eusocial, ground-nesting, generalist foragers, and native were most common in garden habitats. The proportion of parasitic bee species and specialist foragers found in urban gardens was comparable to proportions for global bee taxa. This suggests that gardens contain the hosts and forage needed to support bees with specialized life history requirements, and thus represent high quality habitat for a subset of bee communities. Garden bee research was strongly biased toward the northern hemisphere, which signifies a large gap in our understanding of garden bee communities in other regions. The variety of, and non-standard sampling methods in garden bee research makes it difficult to directly compare results between studies. In addition, both intentional low taxonomic resolution and a lack of collaboration with taxonomists constrains our understanding of bee diversity. Our analyses highlight both successes of past urban garden bee studies, and areas of opportunity for future research as we move into a sixth decade of garden bee research.

KEYWORDS

Anthophila, pollinator, urban, ornamental landscapes, garden

1. Introduction

Native bees are critically important organisms that support biodiversity and crop production via their pollination services (Klein et al., 2007; Winfree et al., 2008; Ollerton et al., 2011). Animals pollinate 87% of flowering plant species, with the majority of animal-mediated pollination conferred by bees (Ollerton et al., 2011; Christmann, 2019) making them the primary pollinators of most agricultural crops and wild plants (Potts et al., 2010). Substantial losses of bees have been widely reported (Biesmeijer et al., 2006; Potts et al., 2010; Goulson et al., 2015; Zattara and Aizen, 2021), although evidence is sparse for most species, outside of bumble bees (Bartomeous et al., 2013; Soroye et al., 2020) and mason bees (LeCroy et al., 2020). While large-scale seasonal losses of managed western honeybee colonies have been reported recently, the number of global colonies has increased by 45% (Potts et al., 2016).

Despite disagreement about the extent to which bee species (beyond bumble bees and mason bees) are in decline (Goulson and Nicholls, 2016) and about the causes of potential declines, media coverage about bee population losses has increased public attention and enthusiasm for bee conservation (Wilson et al., 2017). In particular, public attention on bees has highlighted opportunities to promote bee conservation in public and private urban spaces (Sirohi et al., 2015; Threlfall et al., 2015; Turo and Gardiner, 2019; Hall and Martins, 2020; Hane and Korfmacher, 2022). Cities can provide an array of habitat options for bees, including urban gardens and parks. Recent reviews have examined the influence of urban landscapes on bee communities across a broad range of habitats, including gardens, but also including cemeteries, vacant lots, wastelands, parks, and remnant native vegetation (Ayers and Rehan, 2021; Prendergast et al., 2022). Although these reviews have advanced our understanding of urban bee communities, we suggest that gardens are distinctly different from other urban habitats, and thus deserve separate consideration.

Urban gardens are characterized by a diverse and heterogeneous plant assemblage that is actively tended by gardeners (Threlfall et al., 2016). The extremely high diversity of plants in garden sites, relative to other urban greenspaces, reflects the large pool of plants available to gardeners via the nursery trade (Thompson et al., 2003). In addition, management and maintenance decisions made by gardeners ultimately contributes to high within-garden heterogeneity, compared to most other urban greenspaces (Thompson et al., 2003). For example, gardeners' decisions might result in areas dedicated to fruit trees, annual vegetables, lawn, shade trees and plants adapted to growing in shade, ornamental cultivars, and/or native plants, all within a single garden. Urban parks, golf courses, or cemeteries in contrast, are typically planted with species from a limited plant palette, and subject to management practices that tend to homogenize plant communities across urban green spaces (Threlfall et al., 2016). Other urban habitat types, including wastelands and vacant lots are often minimally cultivated or managed (Gardiner et al., 2013; Twerd and Banaszak-Cibicka, 2019), and offer limited opportunities for public engagement. Thus, garden plant assemblages vary considerably over small scales, whereas urban parks, golf courses, and cemeteries are typically more homogenous.

Gardens also offer opportunities to engage the general public in bee conservation efforts via science-based planting and management practices (Anderson et al., 2022), unlike vacant lots and other minimally managed urban greenspaces. The management of urban gardens, though, can also vary widely, both within and between individual gardens, including those gardens with vigorous maintenance and frequent mowing (Ayers and Rehan, 2021) and those that use more natural landscaping approaches (McCarthy, 2018). Smaller urban gardens, including home, allotment, or community gardens, can harbor nearly as much diversity as larger urban parks and adjacent natural areas (Fetridge et al., 2008; Normandin et al., 2017; Baldock et al., 2019). There is value, then, in zooming in to bee communities within urban gardens, to better understand their bee communities, and to share with gardeners which practices might enhance or impede bee conservation efforts.

The conservation value of gardens has repeatedly been referenced in the literature (Tommasi et al., 2004; Matteson et al., 2008; Pawelek et al., 2009; Lerman and Milam, 2016; Plascencia and Philpott, 2017; Lanner et al., 2020). In fact, an interest in urban gardens as a space for insect conservation dates back to 1941, when entomologist Frank Lutz documented 1,402 insect species in his suburban 15,000 m^2 garden in Ramsey, NJ, a suburb of New York City, USA (Lutz, 1941). Gardens can provide nest sites (Cane, 2001; Tonietto et al., 2011) and diverse floral resources which can provide pollen and nectar across the entire foraging season for many bee species (Tommasi et al., 2004; Burdine and McCluney, 2019; Lanner et al., 2020). Gardens may also be sites of heavy pesticide use (Meftaul et al., 2020), which can have lethal or sublethal effects on native bees (Hladik et al., 2016). Highly bred ornamental plants, with reduced floral rewards of nectar and/or pollen, often dominate garden plant assemblages, which may limit the usefulness of urban gardens for bees (Comba et al., 1999; Corbet et al., 2001; Wenzel et al., 2020). However, gardeners' enthusiasm for bee conservation also has potential to drive plant purchases toward native species (Anderson et al., 2021), which tend to attract more diverse bee assemblages (Williams et al., 2011; Morandin and Kremen, 2013; Pardee and Philpott, 2014; Salisbury et al., 2015; Anderson et al., 2022). Although we have a general sense of the types of management practices that enhance or exclude bee taxa in gardens, we also have an opportunity to look at the types of bees that are relatively abundant or sparse in garden systems. Doing so may reveal more specific garden design and management practices that can enhance bee conservation efforts. A recently published review (Rahimi et al., 2022) focused on functional traits of bees in urban gardens, though only dominant garden bee species (the most abundant bee species from each study) were examined. Additionally, most bees were categorized to the family or genera level, with the exception of European honeybees (a non-native and managed species across most areas of the globe), which precludes consideration of species-specific patterns.

We thus compiled a metadataset (a dataset of datasets) of urban garden bee study characteristics and the functional traits of species identified, using studies which took place over the past 50 years. We used these data to address three objectives. First, we characterized the state of urban garden bee research, including geographic extent and methodologies used to study bees in home, community/allotment, or rooftop gardens. Second, we characterized the abundance and richness of bee species that have been found in urban gardens, as well as bees' functional traits, to better understand the types of bee taxa that are more or less common in garden bee communities. Finally, we evaluated the bee conservation recommendations that have emerged from these papers, which we refer to as a "call to action".

2. Methods

To assemble the garden bee research literature, we conducted standardized searches of the databases WebofScience, AGRICOLA (EBSCOHost), and CAB Direct on January 19, 2022, using the

Boolean search term: (pollinator* OR bee OR Apoidea) AND garden AND (urban OR community) AND (visitation OR richness OR diversity OR "functional diversity") NOT (beekeeping OR apiculture). We used the Boolean operator of NOT (beekeeping OR apiculture) to exclude the multitude of studies on honeybee biology, which was not the focus of this review.

The initial search yielded 227 peer-reviewed publications after the removal of duplicates. To be included in the metadataset, studies had to have been conducted in urban garden spaces: home gardens (i.e., a home garden cultivated for the personal use of the tenants or homeowners); community/allotment gardens (i.e., shared, semi-public space, typically containing several different plots cultivated by different individuals); or rooftop gardens (garden on the rooftop of a multi-tenant building). Non-garden urban bee studies, including those conducted in parks, vacant lots, remnant habitats, or other non-garden green spaces, were not included in this review. Additional criteria for inclusion were that studies had to have identified at least 50% of bee taxa to species level and had to present bee data separate from (rather than pooled with) other taxa. Species level determinations were necessary in order to ensure that we were accurately categorizing bees' functional traits (e.g., nesting habit, sociality, native status, foraging breadth). Though we considered including two papers that were just under this 50% threshold (Lowenstein et al., 2015, 2019), these papers were ultimately excluded due to low taxonomic resolution in combination with only utilizing sight identification, thus making it difficult to evaluate identifications. Coarse groupings of bees as "small" and "large" bees (e.g., Fukase and Simons, 2016) precluded functional trait assignments to garden bees from some studies. It is possible that a lack of available taxonomists (Drew, 2011) might have limited taxonomic resolution in these and other urban garden bee studies. Papers that reported bee communities in both urban and non-urban sites, or both garden and non-garden sites, were included if it was possible to identify and specifically extract bee data associated with only the urban garden sites. Papers from all geographical regions and publication dates were included, provided the above criteria were met (Figure 1).

We initially screened abstracts for relevancy (i.e., urban garden studies that identified bees to species), and then screened the full text of papers that passed initial screening prior to coding them. After application of the inclusion and exclusion criteria, we retained 19 papers, including studies of bees on urban farms (Sivakoff et al., 2018), botanical gardens (Pardee and Philpott, 2014), and a university garden (Wojcik et al., 2008). These studies were retained in our metadataset because study sites were similar in size and flowering plant diversity to typical home or community gardens. Another six papers were included after searching the bibliographies of these 18 papers for additional references. Four papers were added during the review process, including two that were published after our initial literature search (Ollerton et al., 2022; Prendergast et al., 2022). The Ollerton et al. (2022) paper was a collaborative effort across the globe by different scientists, and some sites were gardens; we were able to include 40 garden sites from this paper. Two papers (Halder et al., 2013; Del Toro and Ribbons, 2020) were later removed from the metadataset due to concerns related to species identifications. Del Toro and Ribbons (2020) was retracted by the publisher in November 2022. Halder et al. (2013) was removed from our dataset due to multiple species misspellings and identifying species far outside of their known range (e.g., *Xylocopa nigrita* only occurs in Africa, and *Xylocopa calens* only occurs in Madagascar; Pauly, 2016). We also included one book in this review (Owen, 2010). Although not peer-reviewed, the extensive and decades-long sampling of a single garden space was meticulously documented and reported, such that the book met all inclusion criteria. The early documentation of insects from Lutz (1941) was excluded because only order-level identifications were listed. Our garden bee metadataset was thus drawn from 27 journal articles published from, 1990 to 2022, and one book published in 2010 (Table 1).

To better understand the current state of garden bee research, as well as any gaps, we extracted the following data from each paper: study location (city/cities, country) and biome; type of garden (community, home, garden-scale urban farm, garden-scale botanical garden, rooftop) and number of plots/gardens sampled; cumulative area (m^2) of urban garden(s) studied and sampled and timeframe of the study (total number of active sampling months to account for those that spanned multiple years); type of sampling methods employed (pan traps, aerial netting, malaise trap, visual search, trap nest, vane trap, hand collection); number of bee species found (species richness), and bee species' functional traits, if identified (sociality, diet breadth, and nesting location). Biome was determined using the World Wildlife Fund Terrestrial Ecoregions of the World (Olson et al., 2001). When data were not available in the paper or supplementary material, we contacted authors for additional information. Information on site size was not available for Hostetler and McIntyre (2001), Colla et al. (2009), Sivakoff et al. (2018), and Persson et al. (2020). These studies were not included in estimates of cumulative urban garden area sampled. Active sampling months was not available for Frankie et al. (2009).

For all studies, we noted the prevalent research themes (including, but not limited to, baseline pollinator assessment, comparative landscape study, and effects of urbanization), to identify areas that have been investigated across urban garden bee studies (Table 2). We also recorded whether a study included a call to action. The Cambridge Dictionary defines a call to action as "something as a speech, piece of writing, or act that asks for or encourages people to take action about a problem" (Call to action, 2022). To identify a call to action from general recommendations, we searched for command words, including but not limited to "should," "must," "we ask," "we recommend,", followed by a set of actions (i.e., "gardeners should reduce the frequency of lawn mowing and plant more flowers where possible"). Calls to action were coded as being one or more of these categories: "more flowers" called for more flowering plant species in urban gardens; "native flowers" specifically called for more native flowering plant species in urban green spaces; "more greenspace" called for more urban green space area; "exotic bees" specifically mentioned exotic bees as driving out native pollinators and called for fostering habitats to support native bees; "further research" called for more research on bees in urban gardens; "remnant vegetation" called for prioritizing remnant/native habitats in urban spaces, and "reduced disturbance" called for reduced mowing, soil disturbance, and/or pesticide and herbicide use.

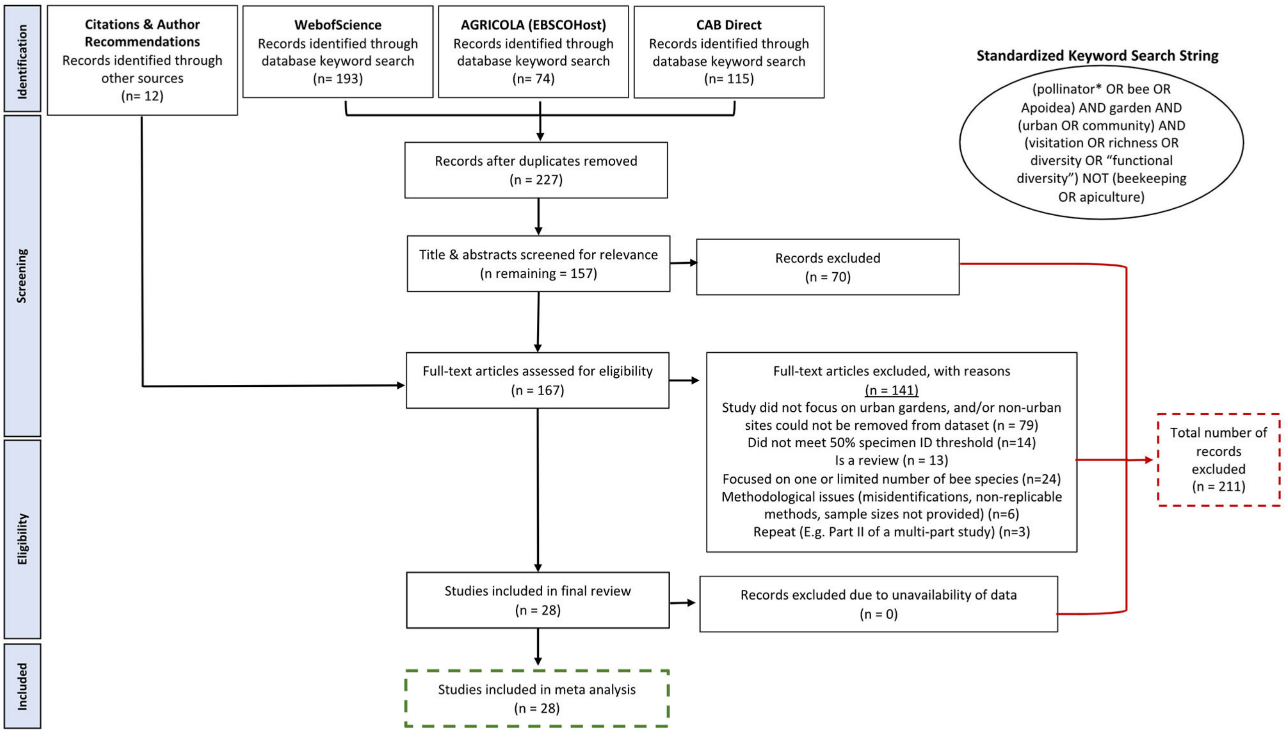

FIGURE 1
PRISMA flow diagram depicting the databases searched with a standardized keyword search string, and the process to finalize the 28 publications included in this review.

To better understand the abundance, diversity, and types of bees that have been found in urban garden studies, we compiled, validated, and updated a master list of garden bee taxa reported across all papers (referred to in this paper as the garden bee metadataset). Validating and updating the master list involved correcting numerous misspellings, as well as updating genera and epithets to account for nomenclature changes and/or to correct synonyms. Examples include updating correct use of *Lasioglossum heterognathum* from *Lasioglossum* (*Dialictus*) *heterognathus* (Fetridge et al., 2008) and updating to the correct use of *Pseudoanthidium nanum* from *Anthidium nanum* (Lanner et al., 2020). Other examples include updating *Afranthidium repetitum* to *Pseudoanthidium [Immanthidium] repetitum* and updating *Lasioglossum (Dialictus) mitchelli* Gibbs to *L. (Dialictus) hitchensi*). In another case, *Lasioglossum* (*Dialictus*) *tegulariforme* (cited in Pawelek et al., 2009) was combined with *L. helianthi* due to likely misidentification after conferring with a taxonomic expert on the *Lasioglossum* genus (J. Gibbs, personal communication). One species, *Lasioglossum (Sphecodogastra) leucopymatum*, was removed from the dataset because its identification in Gotlieb et al. (2011) is unlikely in Israel; the native region of this species is not known to extend beyond Afghanistan and surrounding countries (Ebmer, 1995, as cited in Astafurova and Proshchalykin, 2020). These types of taxonomic updates and quality control checks help to ensure that future efforts to describe urban garden bee communities are as accurate and up to date as possible.

Bee taxon abundance and functional traits for each paper (if reported) were initially coded by N.B., J.H., M.M., and G.L. Entries were reviewed for accuracy by N.B. and J.H., and ultimately confirmed or corrected by J.A. To identify which bee species are relatively common in garden habitats (i.e., dominant garden bee species), we noted the number of studies where each bee species had been collected. In addition to noting frequency of species across studies, we also recorded relative abundance across studies, when available. We also recorded the geographic region and garden type where each study occurred. Species' functional traits were extracted from a publication (when listed) or were determined by cross-referencing bee taxa with species-specific ecological data embedded in Discover Life (Cane, 2003; Giles and Ascher, 2006; Lerman and Milam, 2016; Ascher and Pickering, 2020). We recorded the nesting substrate (e.g., soil, cavity, hive, wood excavator, aerial nest), sociality (e.g., eusocial, non-eusocial, subsocial, semi-social, parasitic), floral specificity (e.g., polylectic, oligolectic, or no pollen for parasitic species), and native status (e.g., native or exotic to the region where study was conducted) (Table 3). In instances where species' functional trait information was not available, we inferred traits from closely related congeneric species. Native status for bees found in North American studies was determined using Cane (2003) and Giles and Ascher (2006). Native status for bees found in studies outside of North America was sourced directly from studies or through Discover Life (Ascher and Pickering, 2020), and verified by J. A.

We estimated the cumulative number of bee species collected from urban gardens, across all studies, in two ways. First, we generated a liberal estimate of the upper end of the range of species represented, by including specimens identified to

TABLE 1 List of garden bee studies included in this review, and study characteristics.

References	City or region (state), country	Ecoregion	Garden type(s)	Active sampling months	Total area sampled (m^2)	Sampling methods used	Bee species richness	Call to action code
Archer (1990)	Leicester, England	TBMF	H	84	688	AN MT	37	None
Baldock et al. (2019)	Bristol, Reading, Leeds, Edinburgh (UK)	TBMF	H, C	11	8,800	AN	48	More Greenspace, More Flowers, Native Flowers
Birdshire et al. (2020)	Denver, USA	TGSS	H, C	4	2,632	AN PT	37	More Flowers Native Flowers More Greenspace Reduced Disturbance
Choate et al. (2018)	Meadville, USA	TBMF	H	8	316	PT VT	55	None
Cohen et al. (2022)	Monterey and Santa Cruz (California), USA	MFWS	C	4	7,200	PT AN	59	None
Colla et al. (2009)	Toronto, Canada	TBMF	R	12	NC	PT	45	None
Egerer et al. (2019)	Monterey, Santa Cruz, and Santa Clara (California), USA	MFWS	C	4	7,600	AN	48	More Flowers Native Flowers More Greenspace
Fetridge et al. (2008)	Westchester County (New York), USA	TBMF	H	6	62,879	PT HC	110	None
Frankie et al. (2009)	Ukiah, USA	MFWS	H	NA	120	VS	68	None
Gotlieb et al. (2011)	Jordan Rift Valley, Israel	MFWS	H	6	10,000	AN	64	Further Research
Langellotto et al. (2018)	Portland (Oregon), USA	TCF	H	3	117,119	PT HC	48	Further Research
Lanner et al. (2020)	Vienna, Austria	TCF	C	5	14,090	AN	113	Native Flowers More Flowers, Reduce Disturbance
Lerman and Milam (2016)	Springfield (Massachusetts), USA	TBMF	H	10	12,648	PN AN	114	None
Makinson et al. (2017)	Sydney, Australia	TBMF	C	5	59	AN TN	12	Further Research More Flowers
Matteson et al. (2008)	New York City, USA	TBMF	C	13	17,262	PT AN	58	Exotic Bees Further Research Reduced Disturbance
Hostetler and McIntyre (2001)	Phoenix, USA	TGSS	H	2	NC	PT	21	None

(Continued)

TABLE 1 (Continued)

References	City or region (state), country	Ecoregion	Garden type(s)	Active sampling months	Total area sampled (m^2)	Sampling methods used	Bee species richness	Call to action code
Ollerton et al. (2022)	Multiple locations	TBMF, MFWS, TGSS, TSGSS, TSMBF, TCF	H, C, R	7	6,422	VS		None
Owen (2010)	Leicester, England	TBMF	H	182	741	MT	59	None
Pardee and Philpott (2014)	Toledo, USA	TBMF	H, B	4	128	PT AN VS	66	Native Flowers More Flowers
Pawelek et al. (2009)	San Luis Obispo, USA	MFWS	C	15	4,000	AN VS	40	None
Persson et al. (2020)	Malmö, Sweden	TBMF	H	1	NC	PT	40	More Flowers
Prendergast et al. (2022)	Perth, Australia	MFWS	H	10	70,000	PT AN	93	Remnant Vegetation Native Flowers
Sivakoff et al. (2018)	Cleveland, USA	TBMF	U	12	NC	PT	70	More Greenspace
Staab et al. (2020)	Frieburg, Germany	TBMF	H	7	16,627	PT	119	More Flowers Native Flowers More Greenspace
Threlfall et al. (2015)	Melbourne, Australia	TBMF	H	6	31,200	AN PT	9	Further Research Remnant Vegetation More Flowers Native Flowers
Tonietto et al. (2011)	Chicago, USA	TBMF	R	5	1,200	PT AN VS	19	None
Wilson and Jamieson (2019)	Southeast Michigan, USA	TBMF	C, U	3	104,679	PT AN	118	More Flowers More Greenspace
Wojcik et al. (2008)	Berkeley, USA	MFWS	C	7	180	PT AN	32	None

Ecoregion was determined with the World Wildlife Fund Terrestrial Ecoregions of the World (Olson et al., 2001) and coded as: TGSS, Temperate grassland, savannas, and shrubland; TCF, Temperate coniferous forest; MFWS, Mediterranean forests, woodlands, and scrub; TBMF, Temperate broadleaf and mixed forest; TSGSS, Tropical and subtropical grasslands, savannas, and scrubs; TSMBF, Tropical and subtropical moist broadleaf forest. Garden type was coded as: R, rooftop garden; H, home garden; C, community garden; U, garden-scale urban farm; B, garden-scale botanical garden. Active sampling months was calculated as the total number of months spent sampling an urban garden. When the total area sampled could not be calculated, it was coded as NC. Sampling methods used was coded as: PT, pan traps; VS, visual search; AN, Aerial Net; TN, Trap Nest, HC, Hand Collected (with aspirator or jar); MT, Malaise Trap; VT, Vane Trap. Bee Species Richness represents the total number of bee taxa identified. Call to Action was coded as; None, no call to action included in the paper; More Flowers (called for more flowering plant species in urban gardens), Native Flowers (called for more native flowering plant species in gardens), More Greenspace (called for more urban green space area), Reduced Disturbance (called for reduced mowing, soil disturbance, and/or pesticide and herbicide use), Exotic Bees (mentioned exotic bees as driving out native pollinators and called for fostering habitats to support native bees), Further Research (called for more research on bees in urban gardens), Remnant Vegetation (called for prioritizing remnant/native habitats in urban spaces).

TABLE 2 Major research themes, definitions, and key-word examples emanating from the 28 studies included in this review.

Research theme	Definition	Key phrase example	References
Baseline pollinator community assessment	Studies seeking to describe and or census the current bee community in a given area.	"…with the goal of attracting local native California bee species to assess emerging patterns of diversity" (Wojcik et al., 2008)	Archer, 1990; Fetridge et al., 2008; Wojcik et al., 2008; Pawelek et al., 2009; Owen, 2010; Choate et al., 2018; Ollerton et al., 2022
Comparative landscape assessment	Studies that compared sites along an urban-rural gradient, or examined two or more different kinds of landscapes (rooftop vs. park, urban farm vs. vacant lot)	"…we surveyed bee communities at 15 farms and gardens across an urban-rural gradient" (Wilson and Jamieson, 2019)	Hostetler and McIntyre, 2001; Colla et al., 2009; Gotlieb et al., 2011; Tonietto et al., 2011; Threlfall et al., 2015; Makinson et al., 2017; Choate et al., 2018; Sivakoff et al., 2018; Baldock et al., 2019; Egerer et al., 2019; Wilson and Jamieson, 2019; Birdshire et al., 2020; Lanner et al., 2020; Persson et al., 2020; Cohen et al., 2022; Prendergast et al., 2022
Conservation value of gardens	Studies that referred to the potential of gardens to serve as refuges for bees or to support abundance and diversity of bee communities	"…these results suggest that urban development can be designed to promote the conservation of bees" (Hostetler and McIntyre, 2001)	Hostetler and McIntyre, 2001; Fetridge et al., 2008; Matteson et al., 2008; Wojcik et al., 2008; Colla et al., 2009; Frankie et al., 2009; Gotlieb et al., 2011; Threlfall et al., 2015; Lerman and Milam, 2016; Langellotto et al., 2018; Sivakoff et al., 2018; Baldock et al., 2019; Lanner et al., 2020; Ollerton et al., 2022
Effects of urbanization	Studies that examined the impacts of urban features such as impervious surfaces on bee communities, or were on an urban-rural gradient	"…we found that the proportion of impervious surface and number of greenspace patches in the surrounding landscape strongly influenced bee assemblages" (Sivakoff et al., 2018)	Hostetler and McIntyre, 2001; Matteson et al., 2008; Tonietto et al., 2011; Makinson et al., 2017; Choate et al., 2018; Sivakoff et al., 2018; Egerer et al., 2019; Wilson and Jamieson, 2019; Birdshire et al., 2020; Lanner et al., 2020; Persson et al., 2020; Cohen et al., 2022; Prendergast et al., 2022
Effect of plant diversity/abundance/species	Studies that included analyses of how plant diversity, abundance, or particular species impacted bee communities	"…only elements within the gardens had an effect on [bee] species richness, with flower frequency as the major positive driver" (Lanner et al., 2020)	Hostetler and McIntyre, 2001; Wojcik et al., 2008; Frankie et al., 2009; Gotlieb et al., 2011; Tonietto et al., 2011; Pardee and Philpott, 2014; Threlfall et al., 2015; Lerman and Milam, 2016; Baldock et al., 2019; Egerer et al., 2019; Wilson and Jamieson, 2019; Birdshire et al., 2020; Lanner et al., 2020; Staab et al., 2020; Cohen et al., 2022; Prendergast et al., 2022
Plant-pollinator networks	Studies that examined plant-pollinator networks	"Plant pollinator networks constructed from floral visitation observations revealed…" (Sivakoff et al., 2018)	Gotlieb et al., 2011; Sivakoff et al., 2018; Staab et al., 2020

TABLE 3 Definitions used to code bees' ecological traits were coded for nesting substrate (soil, cavity, hive, wood excavator, or aerial nest), sociality (eusocial, non-eusocial, parasitic), and floral specificity (polylectic, oligolectic, no pollen).

Nesting substrate	Sociality	Floral specificity
Soil: species which primarily nest in the soil, e.g., *Andrena (Melandrena) commoda.*	Eusocial: species that exhibit cooperative brood care, overlapping generations within a colony of adults, and division of labor, e.g., *Apis (Apis) mellifera.*	Polylectic: species which collects pollen from the flowers of a variety of plant families.
Cavity: species which nest in pre-existing cavities, such as dead wood or pithy stems, e.g., *Megachile (Eutricharaea) rotundata.*	Non-eusocial: encompasses truly solitary bees, where a single female builds and provisions each nest. Also includes communal species, where females sometimes share nest entrances. Sub-social and semi-social species were also included in this group.	Oligolectic: species which exhibit narrow pollen collection preferences, typically for one plant family.
Hive: species which nest in hives, which are built structures that include the construction of pollen pots, e.g., *Bombus (Pyrobombus) vosnesenskii.*	Parasitic: species that enter nests of pollen-collecting bees and kill host egg/larvae. These bees do not collect pollen.	No pollen: species which is parasitic, and thus does not collect pollen.
Wood excavator: species that excavates a tunnel in wood to create nest sites, e.g., *Xylocopa (Xylocopoides) virginica virginica.*		
Aerial nest: species that constructs a free-standing nest out of resin, e.g., *Anthidiellum (Loyolanthidium) notatum.*		

the species level, the morphospecies level, and two species identified to the subspecies level. For example, *Hylaeus (Hylaeus) mesillae, Hylaeus (Hylaeus) mesillae cressoni* would count as two separate species, using this method. Likewise*, Osmia (Osmia) lignaria lignaria* and *Osmia (Osmia) lignaria propinqua w*ould account for two species in the liberal estimate. The conservative estimate was calculated by excluding specimens identified only to the morphospecies level (unless no species-level identifications for that genus were listed), and the compilation of the two species identified to the subspecies level. Species identified to the genus level were included in the analysis of bee functional traits and in the liberal estimate of species richness, but not in the conservative estimate of bee species richness.

Specimens identified as *nr.* (exact identification cannot be vertified; e.g., *Megachile nr. relativa)* or *aff.* (having affinities to a particular species, but may not be that species; e.g., *Hylaeus aff. affinis*) were not double counted. For example, *Megachile nr. relativa* and *Megachile relativa* were counted as one species. Those specimens that were identified as either/or species were not double counted, when that species was already represented in the dataset (e.g., *Agapostemon angelicus/texanus, Agapostemon angelicus*, and *Agapostemon texanus* were collectively counted as two species).

To better understand the types of bees that are common in urban gardens, we noted the five most abundant species in each paper. Bee abundance was not available for Frankie et al. (2009), Langellotto et al. (2018), Lanner et al. (2020), and Staab et al. (2020). Bee abundance was only sporadically reported in Ollerton et al. (2022), so it was not included in abundance counts. Pawelek et al. (2009) and Owen (2010) did not record the abundance of *Apis mellifera*, but honeybees were included in the top five most abundant species for these two papers, due to authors' noting that the species was highly abundant. Honeybees were excluded from analysis and abundance counts in Egerer et al. (2019) and Persson et al. (2020). The six most abundant species were included for Pardee and Philpott (2014), because two species had the same recorded abundance. Bees identified only to the genus level were not included in the bee abundance dataset. We performed the same functional trait analysis on the most abundant bees across papers as we did on the garden bee metadataset.

Summary statistics for the species functional traits were generated in R Studio (22.07.02) using the "dpylr" (Wickham et al., 2022) and "magrittr" (Bache et al., 2022) packages, and the "count" function to generate frequency counts, which were then used to manually calculate proportions within each of the functional trait categories.

3. Results

Across the 27 articles and one book we used to compile our garden bee metadataset, 466 individual garden spaces were sampled, including 644 home gardens, 161 community gardens, 12 urban farms, and 9 rooftop gardens.

3.1. Garden study characteristics

Most of the studies took place in the United States ($n = 16$). Other studies took place in Australia ($n = 3$), the United Kingdom ($n = 3$), and Canada, Germany, Austria, Sweden, and Israel ($n = 1$, each). All but four studies were conducted in the northern hemisphere (Threlfall et al., 2015; Makinson et al., 2017; Prendergast et al., 2022; sites in Ollerton et al., 2022; Figure 2). The most studied biome was temperate broadleaf and mixed forest ($n = 16$), followed by Mediterranean forests, woodlands, and scrubs ($n = 7$), temperate coniferous forest ($n = 2$), and temperate grassland, savannas, and shrubland ($n = 2$). Out of the 40 garden sites that met inclusion criteria in Ollerton et al. (2022) (see included sites in Supplementary Table 1), most were in Europe (United Kingdom, Ireland, Germany, Spain, Italy; $n = 29$ sites), though the United States ($n = 4$ sites), Australia ($n = 3$ sites), Brazil ($n = 2$ sites), Algeria ($n = 1$ site), and Mexico ($n = 1$ site) were also represented. The biomes represented in the included sites from Ollerton et al. (2022) were mostly temperate broadleaf and mixed forest ($n = 32$), though Mediterranean forest, woodlands and scrubs ($n = 3$), tropical and subtropical moist broadleaf forest ($n = 2$), temperate grasslands, savannas, and shrublands ($n = 1$), tropical and subtropical grasslands, savannas, and shrublands ($n = 1$), and temperate coniferous forest ($n = 1$) were also represented.

Netting was the most common method used to sample garden bees ($n = 19$), followed by pan traps ($n = 17$). Only six studies sampled bees by visual search. Six studies included other sampling methods, including hand collection with aspirators or collection jars. Most studies used either two sampling methods ($n = 13$), or one sampling method ($n = 13$), and three studies used three sampling methods.

Across the 27 studies that reported sampling period, the mean number of active sampling months was 16.1 months ± 35.8 (SD), whereas the median number of active sampling months was 6 months. The Owen (2010) study skewed the mean, since it took place over 30 years. Excluding the Owen study, the mean number of active sampling months was 9.8 months ± 15.3 (SD). Across the 24 studies that reported site size, the cumulative area of all study sites covered 2.9 km^2. Mean cumulative area sampled was 20,991 $\text{m}^2 \pm 32{,}527\ \text{m}^2$ (median size 7,400 m^2). Studies with multiple garden study sites, such as Langellotto et al. (2018) and Wilson and Jamieson (2019) skewed the mean, with cumulative areas sampled of over 100,000 m^2 each.

3.2. Bee functional traits

The total number of bee species found across all urban garden studies was between 674 (excluding morphospecies) and 830 bee species (Supplementary Table 2). The mean number of species found per study was 63 ± 35.7 (median 57 species). Across all garden bee species, 18.6% were eusocial ($n = 154$), 64.9% were non-eusocial ($n = 539$), 13.3% were parasitic ($n = 110$), and 3.2% had unknown social behaviors ($n = 27$). Most nested in the soil (53.6%; $n = 445$), followed by cavity nesters (32.9%, $n = 273$), and species that nest in hives (5.8%, $n = 48$). The remaining

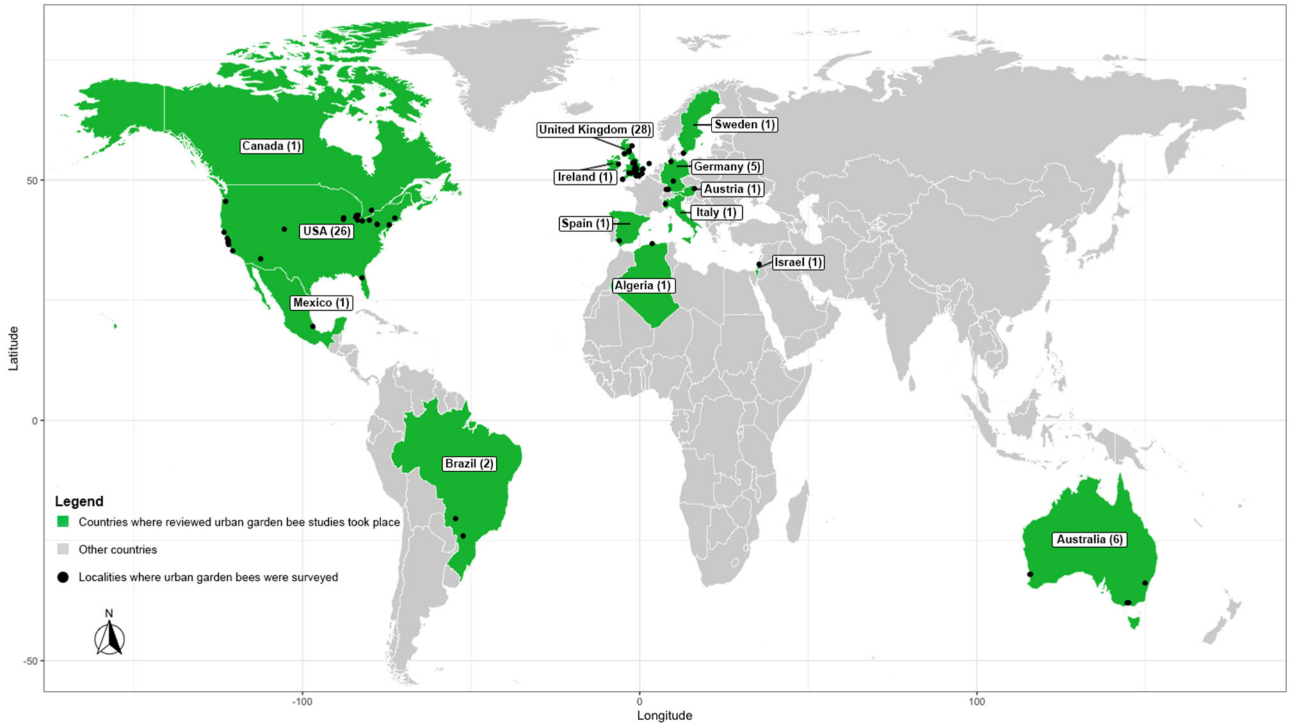

FIGURE 2
Map depicting where reviewed urban garden bee studies were conducted.

species' nesting habits were unknown (6.1%, n = 51) or had other nesting habits (wood excavation or aerial nests; 1.6%, n = 13). Generalist foragers comprised 64.4% of bee species found in gardens (n = 535); specialist foragers comprised 13.3% of species found (n = 110). Other species were parasitic, and do not forage for pollen (13.3%, n = 110), or their diet breadth was unknown (9.0%, n = 75) (Figure 3). The most abundant bee family represented was Halictidae (31.3%, n = 260 species), followed by Megachilidae (22.5%, n = 187 species) and Apidae (21.6%, n = 179 species) (Figure 4). The families Colletidae (12.7%, n = 105 species), Andrenidae (11.1%, n = 92 species), and Melittidae (0.80%, n = 7 species) were also represented. Across all bees, with 16 species duplicated due to differing native/exotic status depending on region, only 2.9% of bee species were exotic to the region studied (n = 24 species). Most garden bee species (92.5%) were native (n = 768 species). The native status of the remaining 4.6% was unknown (n = 38 species). We identified the dominant garden bee species across studies by recording the number of papers in which a particular species was recorded. Across all studies, the five most frequently reported bee species were *Apis (Apis) mellifera* (n = 20 studies), *Halictus (Odontalictus) ligatus* (n = 17 studies), *Anthidium (Anthidium) manicatum* (n = 17 studies), *Megachile (Eutricharaea) rotundata* (n = 16 studies), and *Halictus (Protohalictus) rubicundus* (n = 15 studies). Although eusocial, non-native species were a minority in the full dataset, the most dominant garden bees were eusocial (60%, n = 3) and non-native to the region where they were studied (60%, n = 3). All five species were polylectic, but represented three different nesting strategies: soil (40%, n = 2), cavity (40%, n = 2), and hive (20%, n = 1).

When looking at the 5 (or 6, for Pardee and Philpott, 2014) most abundant bee species within each study where abundance was reported (n = 23 papers), there were 73 species after the removal of duplicates (Supplementary Table 3). Across entries, 31.5% were eusocial (n = 23 species), 65.8% were non-eusocial (n = 48 species), and 2.7% had unknown social behaviors (n = 2 species). Most nested in the soil (53.4%, n = 39 species), followed by cavity nesters (31.5%, n = 23 species), and species that live in hives (12.3%, n = 9 species). The remaining species were wood excavating (1.4%, n = 1 species) or had unknown nesting habits (1.4%, n = 1 species). Most species were generalists (94.5%, n = 69 species), with only 4.1% of the most abundant species being specialist foragers (n = 3 species), and one species' diet was unknown (1.4%, n = 1 species). Most abundant garden bees were native (91.8%, n = 67 species), with 8.2% of abundant bee species being exotic to the region in which they were studied (n = 6 species). The most abundant bee family represented was Halictidae (46.6%, n = 34 species), followed by Apidae (30.1%, n = 22 species. The families Colletidae (12.3%, n = 9 species), Megachilidae (9.6%, n = 7 species), and Andrenidae (1.4%, n = 1 species) were also represented.

3.3. Prevalent research themes and calls to action

The most prevalent research themes from garden bee studies included investigations of the effects of plant

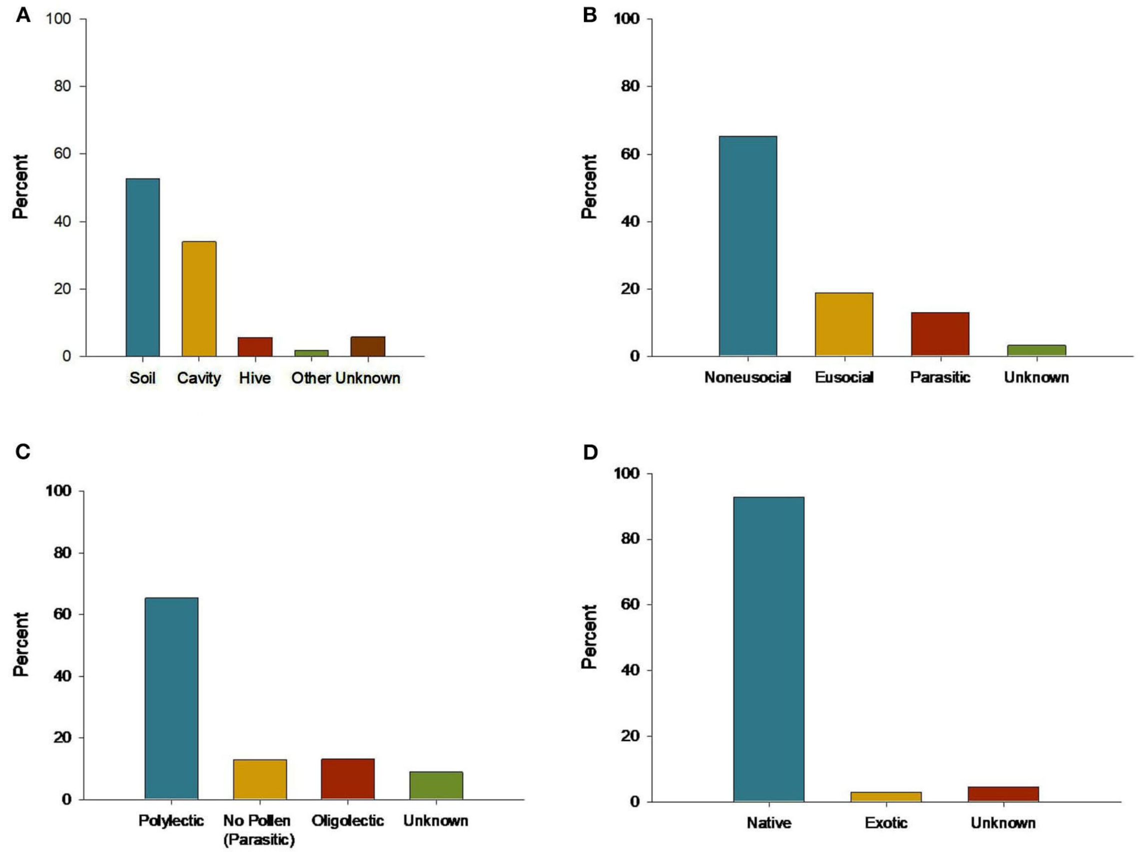

FIGURE 3
Distribution of functional traits across urban garden bee taxa: **(A)** nest type, **(B)** sociality, **(C)** floral specificity, and **(D)** native status.

diversity/abundance/species on bees ($n = 16$) and comparative landscape assessments ($n = 16$), followed by studies of the conservation value of gardens ($n = 14$), and the effects of urbanization on bees ($n = 13$). Other research themes included baseline pollinator community assessments ($n = 8$) and plant-pollinator networks ($n = 3$). While 13 of the 14 studies that included the conservation value of gardens as a major theme concluded that they are valuable conservation sites, Gotlieb et al. (2011) asserted that gardens do not promote species richness compared to more natural areas.

We identified 15 papers that included calls to action in the reviewed literature, with several papers containing more than one (Figure 5). The most common calls to action were for gardeners to plant more flowering plant species in gardens ($n = 10$), for gardeners to include more native flowering plant species in gardens ($n = 8$), advocating for more urban green space ($n = 6$), and for scientists to conduct further research ($n = 5$). Other calls for actions included suggesting gardeners reduce habitat disturbance ($n = 3$), leave remnant vegetation where possible ($n = 2$), and a call for habitat to specifically support native bees, rather than exotic bees ($n = 1$).

4. Discussion

Between 674 (conservative estimate) and 830 (liberal estimate) bee species have been collected from urban garden habitats included in our review, representing six of the seven extant bee families. These bees have been identified from a relatively small number of studies, biased to the northern hemisphere. Bees from the family Stenotritidae were not represented. This is not surprising since this family is comprised of 21 species isolated to Australia (Danforth et al., 2019), although we did include four studies with sites located in Australia in our review (Threlfall et al., 2015; Makinson et al., 2017; Ollerton et al., 2022; Prendergast et al., 2022). While there are estimated to be over 20,000 bee species worldwide (Danforth et al., 2019; Orr et al., 2021), urban areas can present harsh conditions for many bees (Cardoso and Gonçalves, 2018), including heat stress (Hamblin et al., 2017), homogenization of forage plants (Groffman et al., 2014), increased landscape disturbance (Threlfall et al., 2015; Lerman and Milam, 2016), competition from exotic species (LeCroy et al., 2020), and a decrease in forage and nesting site availability (Bates et al., 2011; Choate et al., 2018; Birdshire et al., 2020; Lanner et al., 2020). This can result in significant declines in pollinator abundance and species richness, when compared with more rural sites (Bates et al., 2011; Birdshire et al.,

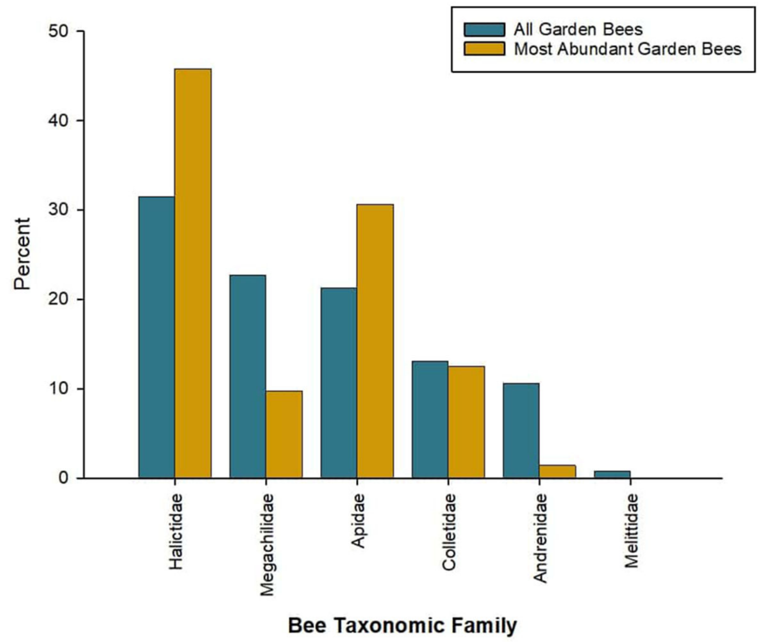

FIGURE 4
Percent of bee taxonomic family distribution for most abundant taxa collected from urban gardens, for all taxa collected from urban gardens, and globally. Abundant taxa were determined by selecting the five most abundant bee species from each study that reported abundance.

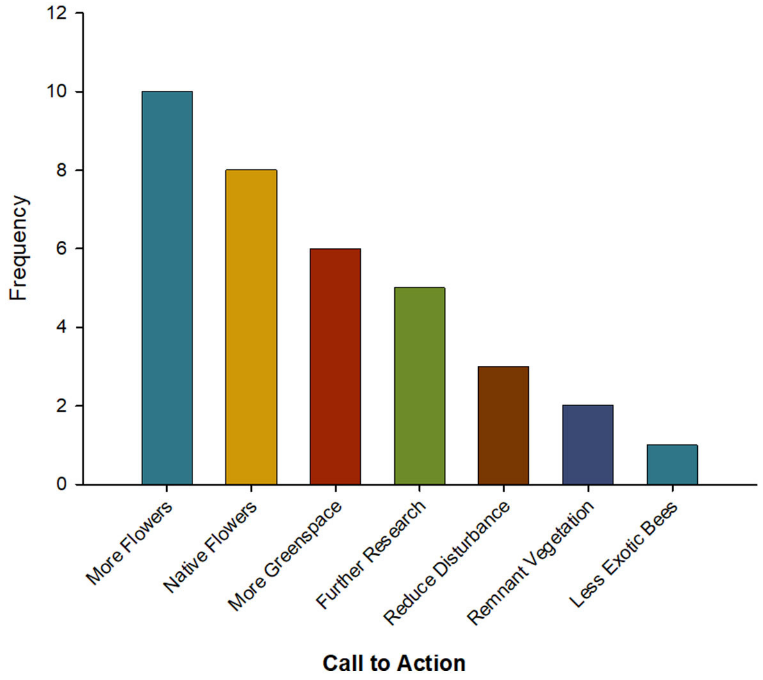

FIGURE 5
Proportion of various calls to action included in garden bee studies. Calls to action included "More Flowers" or "Native Flowers" (in urban gardens); "More Greenspace" (in urban landscapes), "Exotic Bees" (noted the negative impact of exotic bees on native pollinators and called for fostering habitats to support native bees); "Further Research" (on bees in urban gardens,) "Remnant Vegetation" (called for prioritizing remnant/native habitats in urban spaces); and "reduced disturbance" (including mowing, soil disturbance, and/or pesticide and herbicide use).

2020; Millard et al., 2021), although this is not always the case (Kearns and Oliveras, 2009; Baldock et al., 2015; Sirohi et al., 2015).

Across all studies in the metadataset for which the total area sampled was available, ∼2.9 km^2 of cumulative garden area was sampled. Small garden spaces can, in fact, host bee communities that are representative of bee communities found in larger, more intact habitat (Fetridge et al., 2008; Kearns and Oliveras, 2009). This suggests the potential conservation value of urban gardens to bees, particularly if gardeners emphasize the availability of forage plants (Tommasi et al., 2004; Matteson and Langellotto, 2010; Burdine and McCluney, 2019; Lanner et al., 2020) and nesting resources (Cane, 2001; Tonietto et al., 2011).

4.1. Bee functional traits

Across all garden bee species documented in this review, 64.4% were polylectic (generalist foragers). This aligns with general estimates of bee foraging habits in the United States, where between 65 and 75% of bee species are estimated to be polylectic (Fowler, 2020a,b; Fowler and Droege, 2020). That oligolectic, specialist foragers made up 13.3% of the bees identified from garden study sites, suggests that gardens can support the specialized life history requirements of some bee species, which could be an area to build upon for continued urban bee conservation efforts. Fowler (2016) emphasizes that strategies to conserve pollinator populations should specifically target specialist species.

It is important to note that because the metadataset is biased to the northern hemisphere, the data compiled for the most abundant garden bee species is skewed toward North America and Europe. All the dominant garden bees documented in this review were generalist foragers. Three specialist bees were present, however, when considering the 5–6 most common garden bee species within each urban garden study. These abundant specialists included *Colletes daviesanus, Megachile (Pseudomegachile) aff. flavipes, and Melissodes (Eumelissodes) robustior*. *C. daviesanus* and *M. robustior* both specialize on plants in the Asteraceae (Müller and Kuhlmann, 2008; Fowler, 2020b). Many of the specialist bees found in urban gardens, such as bees from the family Andrenidae and bees from the genus *Melissodes*, also specialize on plants in the Asteraceae (Cameron et al., 1996; Michez et al., 2008). In a study of bee associations with native plants, Douglas' aster (*Symphyotrichum subspicatum*) was observed to support 19 different bee species, and estimated to support up to 74 bee species (Anderson et al., 2022). Though many bees specialize on Asteraceae, host plant specialization is not limited to this one botanical family (Larkin et al., 2008), suggesting that a broad representation of plant families in a garden may be best suited to supporting oligolectic species.

While some studies have found a high richness and abundance of exotic bee species in urban gardens (Matteson et al., 2008; Gruver and CaraDonna, 2021), we found a relatively low number of exotic species ($n = 24$, or 3%) across our metadataset. To date, the proportion of exotic species remains low in urban garden systems, though some exotic bee species are numerically abundant and dominant components in urban gardens. It is important to note, though, that the percent of exotic bee species increased as we examined the most abundant bees in urban garden studies (8.3%) and the dominant bees across all studies (60%), compared to just 3% of garden bee species in our metadataset, suggesting that exotic species are disproportionately benefitting from urbanization (Fitch et al., 2019). The most common exotic species (though specimen abundance was not reported for every paper) were *Apis (Apis)* mellifera ($n = 3{,}206$ specimens), *Hylaeus (Spatulariella) hyalinatus* ($n = 207$ specimens), and *Hylaeus (Hylaeus) leptocephalus* ($n = 195$ specimens).

Urban gardens also support a relatively high number of parasitic bee species ($n = 110$, 13.3% of urban garden bee species found in our review), which is reflective of estimated proportions of bee social parasites in North America (15%; Bohart, 1970). No parasitic bee species were represented when we examined the most abundant species in urban gardens. Parasitic bees (kleptoparasites) can act as indicator species for bee communities, because they respond to disturbances in a manner that is reflective of the entire bee community (Sheffield et al., 2013). As with specialist foragers, the relatively high proportion of parasitic bees collected from garden studies suggests that gardens can support the specialized life history requirements of at least some bee species.

Though floral resources are often emphasized as being predictive of pollinator abundance in urban spaces (Matteson and Langellotto, 2010; Plascencia and Philpott, 2017; Hyjazie and Sargent, 2022), less attention has been given to the importance of nest sites. Nest resources are particularly important for smaller-bodied bees, as body size can be predictive of foraging range (reviewed in Greenleaf et al., 2007). The existence of nest sites or nesting resources in gardens, then, may influence what bee species are able to persist in urban spaces. We found the percentage of cavity nesting bees in this metadataset relatively low (32.9% of species) in contrast with those of previous studies and reviews that have examined urban bee communities across a broad range of habitats, and have found cavity nesters to be dominant in urban environments (reviewed in Buchholz and Egerer, 2020; Ayers and Rehan, 2021; Fauviau et al., 2022). In contrast, soil nesting bees, the most common nesting strategy of all solitary bees (Danforth et al., 2019; Antoine and Forrest, 2021), were relatively abundant in urban gardens (53.6% of species), though ground nesting bees are estimated to represent between 65 and 70% of all bees (Danforth et al., 2019; Sgolastra et al., 2019). Opportunities to enhance nesting resources in gardens to support the abundance of wild bee species with varying nesting strategies including provisioning patches of bare soil (Cunningham-Minnick et al., 2019), and woody additions, such as small logs (Pawelek et al., 2015).

We found that bees from the family Halictidae were somewhat overrepresented (31.3% of bee species) in our metadataset compared to expected global representation of ∼22% (Danforth et al., 2019). Others have found that urban bee assemblages are dominated by Halictidae (in particular Halictinae; Fortel et al., 2014; Geslin et al., 2016; Villalta et al., 2021). This may be in part explained by the bias of pan-traps toward smaller bees (Cane, 2001; Portman et al., 2020), given that 17 studies sampled with pan-traps. Another explanation could be the tendency for eusocial bees to dominate urban settings (Zanette et al., 2005) due to social traits enhancing the spread and competitiveness of certain species (Chapman and Bourke, 2001). Of all the halictids found in urban gardens, 41.1% were eusocial, 35.9% were non-eusocial, 13.0% were parasitic, with the social structure of 10.0% of the halictids unknown. Bees from the family Andrenidae are underrepresented in the dataset (11.1% of bee species) compared to global expected proportions of 15% (Danforth et al., 2019), particularly when we examine the most abundant and dominant bees in urban settings. Because most andrenids (in particular, the majority of *Andrena* species) are spring-flying bees, their underrepresentation could be related to sampling periods focusing more on summer months, or due to lack of spring-flowering forage in gardens (Matteson et al., 2008). Global totals for Andrenidae are also enhanced by a uniquely large radiation of perditine (genera *Perdita* and *Macrotera*) and protandrenine (*Protandrena* sensu lato) in deserts and of *Andrena* in Mediterranean areas (Wood, 2021; Bossert et al., 2022). All but four of the garden bee studies included in this review were from different regions and/or biomes less favorable to this family (Table 1). Bees within the Apidae were among the most abundant bees found in urban gardens. For example, the European honeybee (*Apis mellifera*), was documented as one of the most abundant species in seven papers and held exotic status in all of them. When honeybees are present, they may have negative impacts on native bee communities, including depletion of nectar and pollen resources (Carneiro and Martins, 2012), which particularly puts pressure on oligolectic species (Cane and Tepedino, 2017).

4.2. Considerations for bee-friendly gardens

Urban gardens are often dominated by ornamentally modified and exotic plant species (Threlfall et al., 2016), and the impact of exotic plant species on native insect species is varied (Sunny et al., 2015). While generalist bees are more likely to forage on invasive or non-native plant species than specialists (Lopezaraiza-Mikel et al., 2007; Tepedino et al., 2008), there is abundant evidence to support generalist bees' preference for native plant species (Williams et al., 2011; Morandin and Kremen, 2013; Pardee and Philpott, 2014; Salisbury et al., 2015; Anderson et al., 2022), suggesting that even generalist bees may be facultative specialists (Synge, 1947; Percival, 1974; Wills et al., 1990). Preserving and planting native flowering plant species as a means to sustain wild bee communities was specifically recommended by five of the studies in our dataset (Table 1; Figure 5). In a recent study of bee associations with native and non-native garden plants, Anderson et al. (2022) documented significant associations between several native bees known to be polylectic (including *Halictus ligatus, Halictus tripartitus, Bombus caliginosus*) and specific native plants (*Symphyotrichum subspicatum, Eschscholzia californica,* and *Phacelia heterophylla*, respectively) even when bee-attractive, non-native garden plants were nearby. This suggests that generalist bees may prioritize foraging from certain native plants, perhaps to meet nutritional needs (Roulston et al., 2000; Wood et al., 2018) and/or to take advantage of efficient foraging opportunities (Williams et al., 2011). Despite the potential benefits of native plant species to garden bees, there is a general lack of concordance between the native plants that bees found most attractive, and the ones gardeners found most attractive (Anderson et al., 2022), with some of the top plants for bees described by gardeners as being "weedy" or "unattractive" (Anderson et al., 2021). Fortunately, gardeners' perception of native plants can significantly improve when short messages are shared regarding a plant's value to native bees (Anderson et al., 2021), highlighting the value of informal outreach and education efforts.

Beyond gardeners' perceptions, changing a garden's vegetative composition to include more native plants and other bee-friendly practices does not come without barriers. Many home gardens, particularly in the United States, are regulated entities, and municipal ordinances can limit the height of grasses, the presence of "weedy" looking species, and woody debris (Larson et al., 2020). Gardens come with their own sets of social norms that prioritize a tidy aesthetic that may require synthetic chemical inputs, and/or reduce bee nest site availability (Nassauer et al., 2009; Locke et al., 2018). Studies have also reviewed the potential benefits of adding "cues to care" (e.g., fences and tidy paths, bright flowers) in urban gardens, which imply the presence of a garden caretaker, thus creating a more ecologically-minded space that may appease societal, and sometimes municipal, expectations (Nassauer, 1995; Li and Nassauer, 2020).

Beyond any nutritional advantages that native plants may confer to native bees, increasing their planting in urban garden spaces might reduce exploitative and/or interference competition with exotic bees (Stout and Morales, 2009). For example, even though plants were cultivated at a common field site, non-native honeybees were much more abundant on non-native plants (e.g., "Grosso" lavender, *Lavandula* x *intermedia* "Grosso"; oregano, *Origanum vulgare*; and catnip, *Nepeta cataria*) than on native plants highly attractive to native bees (e.g., globe gilia, *Gilia capitata*; Douglas' aster, *Symphyotrichum subspicatum*; yarrow, *Achillea millefolium*; California poppy, *Eschscholzia californica*; and Oregon sunshine, *Eriophyllum lanatum*) (Anderson et al., 2022). This suggests that intermixing non-native with native plants in garden spaces might facilitate niche-partitioning and co-existence between non-native and efficient foragers, such as honeybees, and the native bee community (Comba et al., 1999; Salisbury et al., 2015; Pei et al., 2023).

4.3. Geographic bias

The studies included in this review were biased to the northern hemisphere. Most study sites were located at mid-latitudes, which host the highest levels of bee biodiversity (Orr et al., 2021), and most studies were also located in either temperate or xeric regions, which are also hotspots of bee diversity (Cheng and Ashton, 2021; Orr et al., 2021). Studies are underway in regions not represented in this analysis, but they may not yet be published (Hui, 2021), did not meet inclusion criteria (Wen et al., 2013), or may have been filtered out of our search, since search terms were exclusively in English. No studies from the southern hemisphere were excluded solely for identifying fewer than 50% of specimens to the species level. Instead, studies were screened out because they did not occur in urban gardens (Sing et al., 2016; Stewart et al., 2018). Nonetheless, the lack of studies from the southern hemisphere, particularly Africa (De Palma et al., 2016), and less studied regions of the northern hemisphere, such as Asia (De Palma et al., 2016), represents a huge gap in our understanding of garden bee communities. Some taxonomic biases, such as the relative scarcity of Colletidae, may also reflect geographic biases, since this family is most species-rich in Australia and in temperate South America.

As our review and other studies have shown, urban bee data (including garden bee data), is centered around the northern hemisphere, especially the United States and Europe (De Palma et al., 2016; Brant et al., 2022). Although this is a recognized deficiency, it is important to note that this has been an identified area of concern in bee ecology for at least 20 years (Liow et al., 2001; Hernandez et al., 2009; Buchholz and Egerer, 2020; Shackleton et al., 2021; Prendergast et al., 2022). The rate of urbanization is increasing globally (United Nations, 2018), particularly in developing regions [United Nations Population Fund (UNFPA), 2007]. We know that urbanization leads to large-scale habitat loss and fragmentation (Morse et al., 2003; Miller et al., 2014; Baldock et al., 2019), and percent impervious surface cover is associated with declines in species richness (Choate et al., 2018; Burdine and McCluney, 2019; Birdshire et al., 2020), but bee species richness and abundance in urban areas is highly trait- and scale-dependent (Archer, 1990; Wenzel et al., 2020). City gardens have the potential to be a refuge for wild bees (Tommasi et al., 2004; Matteson et al., 2008; Lowenstein et al., 2014; Baldock et al., 2019; Hall and Martins, 2020), to provide important social benefits (Dunnett and Qasim, 2000), and to fulfill socio-cultural needs (Sturiale et al., 2020), creating a synergistic effect between social and ecological benefits (Dennis and James, 2017). Understanding urban garden bee communities in the southern hemisphere and other understudied regions, such as Asia, should be prioritized, to create more context- and region-specific recommendations for gardeners.

4.4. Recommendations for gardeners and researchers

Urban garden bee research spans decades, and recommendations to create standardized sampling methods and conservation opportunities date back nearly as far (Cane et al., 2000; Cane, 2001; Frankie et al., 2009; Williams et al., 2011; Buchholz and Egerer, 2020; Wenzel et al., 2020). While standardized sampling methods have been developed for monitoring bee populations (LeBuhn et al., 2003; Droege et al., 2016), these recommendations are not amenable to urban garden habitats. Specifically, established protocols require long transects and/or large sampling spaces (e.g., 1 hectare), which are unrealistic, given the heterogeneity and relatively small size of most urban garden habitats. Studies included in this review had a broad range in active sampling months (1–182 mo), total area sampled (59–117, 119 m^2), and the number of sampling methods employed (1–3 methods). There was a lack of standardized sampling across studies, with a total of seven different methods used. Because pan-trapping is known to be biased toward smaller bees and tends to miss specialist bees (Cane, 2001), supplementing pan-traps with aerial netting can provide better insight into an area's true species richness (Williams et al., 2011). Previous reviews of urban garden bee ecology also recommend that studies have temporal depth, or span over many seasons, to account for the variances in bee community structure over multiple years (Cane, 2001; Williams et al., 2011). Although the studies we examined display a wide range in sampling methods, garden bee sampling is complicated by needing access to dispersed, and often private or gated, parcels of land. Even if sampling access is granted for one season, it may be difficult to maintain access for multiple years, thus complicating the fulfillment a multi-year study. An example where access was not an issue, and thus there were 182 active sampling months, was Owen (2010). The study took place in her own backyard, leading to a 30-year dataset.

Based on the results of this review, we make the following recommendations that may benefit future urban garden bee studies:

1. Create standardized sampling methods for gardens. Although standardized sampling methods exist for bee communities (e.g., LeBuhn et al., 2003; Droege et al., 2016), they are not amenable to garden habitats. Consistency in sampling across studies would allow for comparison across studies, as well as comparisons across time.
2. Researchers should work with, and advocate for, collaboration with taxonomists. Collaboration is necessary to avoid identification mistakes (e.g., Halder et al., 2013; Del Toro and Ribbons, 2020), which can delay or misguide our understanding of bee communities. In addition, training taxonomists should be a priority to account for identification demands (Drew, 2011).
3. Prioritize and fund research of urban bee communities in the southern hemisphere and understudied regions of the northern hemisphere. This is of particular importance because the rate of urbanization is high in developing countries, amplifying pressures on bee populations.

The studies included in this review represent data collected over the past five decades. As we move into a sixth decade of extensive garden bee studies amidst massive global change events (e.g., urbanization, climate change), it becomes more important than ever to create and tend urban spaces that yield multiple benefits. Gardens provide important social benefits (Dunnett and Qasim, 2000) and fulfillment of socio-cultural needs (Sturiale et al., 2020), while also providing habitat for a diversity of wildlife (e.g., Owen, 2010; Marzluff, 2015; Hall and Martins, 2020) and urban plants (Doody et al., 2014). Thus, gardens are somewhat uniquely positioned for creating a synergistic effect between social and ecological benefits (Dennis and James, 2017). We hope that the metadataset we compiled, as well as our associated summary of key findings and current research gaps, might be useful to current and future urban ecologists who study urban garden spaces.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

NB: Conceptualization, Data curation, Formal analysis, Methodology, Writing—original draft, Writing—review & editing. JA: Data curation, Validation, Writing—review & editing. JH: Data curation, Writing—review & editing. MM: Data curation, Writing—review & editing. GL: Conceptualization, Data curation, Funding acquisition, Methodology, Supervision, Writing—review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2023.1102360/full#supplementary-material

SUPPLEMENTARY TABLE 1
Site information from Ollerton et al. (2022).

SUPPLEMENTARY TABLE 2
List of bee taxa found across studies in our metadataset, including bee functional trait data.

SUPPLEMENTARY TABLE 3
List of the most abundant bee taxa found across studies that reported abundance in our metadataset, including bee functional trait data.

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Holistic wild bee management in urban spaces

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Projects promoting bees in urban areas are initiated in cities around the world but evidence-based conservation concepts at a city-wide scale are scarce. We developed a holistic approach for assessment of bee and flowering plant diversity in a medium-sized city. In addition to standard mapping approaches in bee hotspots, we initiated citizen science projects for participative urban bee research to be able to collect comprehensive bee data across the entire city. We identified 22 hotspots of bee diversity, analyzed connectivity between those hotspots and evaluated the impact of flower patches planted in collaboration with the municipal gardens department as stepping stones for oligolectic bee species throughout the city. Participation by urban citizens in bee identification trainings was high (c. 630 persons) but their subsequent contribution through observation reports was relatively low (1,165 records by 140 observers). However, we identified a total of 139 bee taxa, seven of them only discovered by citizen scientists. Total species richness was higher in extensively managed orchards than in semi-natural and wasteland areas. Half of the stepping stone flower patches were occupied by the target oligolectic bee species in the year of planting. After 3 years, all but two species could be confirmed. We suggest a 5-step concept for bee management in cities: (1) identification of bee hotspots combined with standardized surveys, especially of rare species; (2) training of citizen scientists at two different levels for comprehensive surveys in all parts of the city: (a) half-day introductions to wild bee diversity, ecology and conservation in order to create more awareness and (b) 2-weeks workshops for in-depth training of a small number of dedicated citizen scientists; (3) extensive management of existing habitats and special conservation programs for very rare species; (4) creation of high-value habitats which take into account the varied resource needs of bees within flight ranges of only a few hundred meters; (5) creation of stepping stone habitats as floral and nesting resources, integrating educative and participative aspects.

KEYWORDS

biodiversity, bee conservation, citizen science, meadow orchard, river dike corridor, urban ecology, wasteland

1 Introduction

Global insect, pollinator and wild bee declines have received increased research attention in the last years (Hallmann et al., 2017; Powney et al., 2019; Zattara and Aizen, 2021). Habitat loss and changes in habitat quality were identified as main drivers for this decline (Potts et al., 2010; Sánchez-Bayo and Wyckhuys, 2019; Wagner et al., 2021). In light of global urban expansion (Seto et al., 2012; van Vliet, 2019), understanding the effects of urbanization on wild bee communities is highly relevant. The growing body of research on the topic indicates a loss of bee diversity with increased urbanization (Cardoso and Gonçalves, 2018). An increase of impervious surfaces (Geslin et al., 2016), fragmentation (Burdine and McCluney, 2019), and parasitism (Theodorou et al., 2016) have been identified as factors negatively impacting wild bees in urban environments. At the same time, cities have been shown to harbor diverse wild bee communities (Baldock, 2020; Theodorou et al., 2020) and many studies have identified hotspots and conservation potential in a range of urban habitat types and structures: community and residential gardens (Baldock et al., 2019; Felderhoff et al., 2022), urban parks (Banaszak-Cibicka et al., 2018; Daniels et al., 2020), urban grasslands (Buchholz et al., 2020), botanical gardens (Hofmann et al., 2018), gravel pits (Hofmann and Fleischmann, 2020), wastelands (Fischer et al., 2016; Twerd and Banaszak-Cibicka, 2019; Vereecken et al., 2021), green roofs (Kratschmer et al., 2018), flower strips (Blackmore and Goulson, 2014; Hofmann and Renner, 2020; Weweler et al., 2022), urban trees (Hausmann et al., 2016; Somme et al., 2016), roadsides, railway and power line corridors, and riparian corridors (Twerd et al., 2021; Villalta et al., 2021; Zhang et al., 2022).

The explanation for these seemingly contradictory findings might be that urbanization favors some functional groups of bees while others cannot survive in cities, leading to changes in patterns of functional diversity. There seems to be a general tendency for urbanization to favor cavity nesting, generalist and smaller sized species (e.g., Buchholz and Egerer, 2020; Ayers and Rehan, 2021; Fauviau et al., 2022). This would mean that although cities can be important strongholds for a large number of bee species, they might not be suitable habitats for the more specialized and larger bee species.

One of the biggest problems in our current biodiversity crisis is the lack of awareness and the increasing emotional distance of a large proportion of the urban population to nature and wild organisms. In order to slow down the loss of species, it is crucial to raise general awareness and knowledge about insects and other neglected groups (Wilson et al., 2017; Drossart and Gérard, 2020; Hall and Martins, 2020; Harvey et al., 2020; Wagner et al., 2021). In our current situation, citizen science projects, originally implemented mainly for conspicuous and easy to identify taxa like birds and mammals, could play an important role also in the conservation of smaller and less popular organisms. A number of community and citizen science projects for wild bees have been developed in recent years to carry out species inventories (Wilson et al., 2020; Flaminio et al., 2021; Vereecken et al., 2021), study bee-plant interactions (Bloom and Crowder, 2020) and nesting ecology (Lye et al., 2012; Graham et al., 2014; Noël et al., 2021). Overall, evaluation of data quality, educational impact and motivation of participants revealed that not only data of reasonable quality but also a strong educational impact can be achieved (Toomey and Domroese, 2013; van der Wal et al., 2015; Falk et al., 2019; Mason and Arathi, 2019; Christ et al., 2022). Many of these projects are carried out in cities, where outreach potential is particularly high.

Even though the current state of research suggests urban habitats could be important for bee conservation, evidence-based concepts at a city-wide scale are still rare (but see www.bienenstadt-braunschweig.de). We developed a holistic approach for the assessment of bee diversity and distribution and habitat management in Freising, a medium-sized German city. We (1) explored possibilities of a photography-based survey approach combining systematic specialist surveys with citizen scientist surveys; (2) analyzed wild bee taxon richness and community composition in sites representative of different habitat types and management intensities, and (3) analyzed connectivity between urban bee hotspots. We hypothesized that (a) the river dike, a semi-natural dry grassland corridor traversing the city, is an important connection to more distant nature reserves and source area for bees colonizing the city. This should be reflected in a higher species number and more oligolectic species compared to the rest of the city; (b) the city center with very few green patches and a high proportion of impervious surfaces constitutes a colonization barrier between the southern part of the city (including the river dike) and habitats in the rest of Freising. This should result in significantly reduced species numbers in the northern part of the city; (c) stepping stone flower patches allow oligolectic bees to cross unsuitable areas of the city and colonize the more isolated patches of suitable habitat.

2 Materials and methods

The study was carried out in the city of Freising in southern Bavaria, Germany, which has a total area of c. 89 km^2 and a population of about 50 000 inhabitants (www.kreis-freising.de). The climate is temperate with annual rainfall of 806.21 mm and temperatures ranging from −14.13°C to +33.46°C (long-term average based on the values of the years 2012 to 2021, www.wetter-by.de). For additional information about the city and its location, see Supplementary Data 1, Supplementary Figures 1, 2. A total of 521 wild bee species have been recorded in Bavaria, and c. 300 species in the administrative district of Freising (Bayerisches Landesamt für Umwelt, 2001, 2021). The main semi-natural habitat types in the city are lawn-dominated public parks, rivers and smaller streams with lines of trees. Less common but more relevant for bees are meadow orchards, wastelands and the semi-natural river dikes.

We first identified the potentially most important habitat types for wild bees in the city: flower-rich meadow orchards and wastelands as well as a river dike mostly covered by dry grassland which traverses the city and forms a semi-natural corridor connecting Freising and several dry grassland nature reserves in the region. We performed systematic surveys of wild bee and flowering plant diversity in these habitats using standard mapping approaches. To be able to collect comprehensive bee data across the entire city, we initiated a citizen science project for participative urban bee research. Based on the results of the systematic surveys and the citizen science data, we analyzed the bee communities of each of the main habitat types as well as the effect of different management intensities or succession stages on bee diversity. We analyzed connectivity between wild bee hotspots and evaluated the impact of flower patches planted as stepping stones for oligolectic bee species in collaboration with the municipal gardens department.

2.1 Study site

2.1.1 Surveyed habitats

Systematic surveys of wild bees and flowering plants were performed in 22 sites representative of different management types or succession stages of the three habitat types "river dikes," "meadow orchards" and "wastelands." The total surface area of the surveyed river dikes is 16.25 ha (Figure 1, sites D01–D03; Figures 2A–C) with a total length of 5.6 km on both sides of a 4.3 km long section of the Isar river. We divided the dike area in three different patches with regards to the mowing time, the western section is mown in September, the south-eastern section is mown in August/September, and the north-eastern section is mown in July. For the meadow orchard habitat, we surveyed a total area of 8.14 ha divided between five orchards of 0.8–4.25 ha (Figure 1, sites M01–M05; Figures 2D–F), each with 50–216 fruit trees of up of ten different species ranging in age between 10 to >50 years. The meadow orchards have been subject to different management types and intensity ranging from fallow to grazing, mowing and multiple mulching per season. The total wasteland area surveyed was 9.37 ha, divided between 14 plots ranging from 0.09–2.08 ha (Figure 1, sites W01–W14; Figures 2G–I). We classified the wastelands into different succession stages according to the proportion of bare ground, herb layer, shrub layer and tree layer on each site (see Supplementary Table 1). Bare ground was most prominent on early succession stage wastelands but also occurred locally on the extensively managed meadow orchards (fallow, grazed, and mixed), and on the river dikes. In each of the studied sites, we mapped all insect-pollinated flowering plant species in the herb-, shrub, and tree layer. The surveys took place over the entire season and stopped when the sites had been mown.

2.1.2 Stepping-stone flower patches

In 2019, we planted in collaboration with the municipal gardeners ten flower patches as stepping-stones between flower-rich parts of the city (Figure 1, orange dots; Figures 2J–L). In each patch, we planted a minimum of 30 individuals of a plant species chosen to provide pollen and nectar for specific oligolectic bee species: several bellflower species (*Campanula persicifolia, C. rotundifolia, C. rapunculoides, C. trachelium, C. latifolia* var. *macrantha,* and *C. poscharskyana*) for the rampion scissor bee, *Chelostoma rapunculi*; *Hesperis matronalis* to attract the threatened mason bee species *Osmia brevicornis; Lysimachia punctata* for the loosestrife oil bees, *Macropis europaea* and *M. fulvipes; Reseda lutea* for the large yellow-face bee, *Hylaeus signatus*; *Lathyrus latifolius* for the leaf cutter bee *Megachile ericetorum*; *Stachys byzantina* to attract the wool carder bee, *Anthidium manicatum*; *Echium vulgare* for the mason bee species *Osmia* (*Hoplitis*) *adunca*; *Lythrum salicaria* for the blunthorn bee, *Melitta nigricans*; *Knautia arvensis* for the sand bee *Andrena hattorfiana*; and *Cichorium intybus* for the pantaloon bee, *Dasypoda hirtipes.* The accompanying information boards provide photos and a few interesting details on each plant species and the respective target bee species.

2.2 Bee survey

2.2.1 Standardized surveys

Bee records were collected between 2017 and 2021 with most observations between April and August 2018. Systematic bee surveys were performed between 9 AM and 6 PM and only in dry, sunny weather with temperatures over 12°C. Additional observation time of 1 h in September was dedicated to the late flowering plant species *Hedera helix* to obtain occurrence data of the ivy bee, *Colletes hederae*, which is specialized on the flowers of ivy, which open in very late summer. Pollen and nectar offering plants in the herb and shrub layer were systematically observed for periods of 10–15 min to assess the visiting bees. We additionally identified potential nesting sites to assess the presence of nesting bees. In the meadow orchards, we dedicated an additional 101 h and 40 min of systematic observations on the following fruit tree species: plum (*Prunus domestica*), cherry plum (*Prunus cerasifera*), sweet cherry (*Prunus avium*), sour cherry (*Prunus cerasus*), pear (*Pyrus communis*, and apple (*Malus domestica*) (see Weissmann et al., 2021). Occurrence data for the ten selected oligolectic bee species was collected on existing and newly established flower patches throughout the city in 2019 and 2021.

Wild bees were photographed directly in the field or caught and cooled down on a cold pack to take high-resolution pictures for later identification (a specific permit to catch bees had been granted by the local conservation authorities at the Regierung von Oberbayern). In order to identify bees to species level from photographs, we developed a field identification guide (Weissmann and Schaefer, 2022). In this guide, species that are not distinguishable in the field (e.g., *Colletes daviesanus, Colletes similis,* and *Colletes fodiens*) are treated as species groups, a concept we also adopted for our surveys. For each recorded bee taxon and habitat type, at least one photograph has been uploaded on the iNaturalist platform, where we set up a specific project for wild bee observations in Freising (https://www.inaturalist.org/projects/wildbienen-in-freising-urban-pollinators-bees-in-freising). On this platform, the photographs are accessible by everybody and identifications can be checked and confirmed or updated.

2.2.2 Citizen scientist surveys

For the citizen science project, we set up a project webpage and directly contacted conservation NGOs, community garden groups, allotment gardens, beekeeper associations, schools and kindergartens. We offered public talks and guided walks advertised on the project website and through local media, as well as through personal visits in people's gardens to give an introduction to the most common bee genera and species, their morphology, behavior, nesting sites, and host plants, and identification methods. In 2018 and 2019, we offered eleven guided walks, seven talks and information events, as well as visits to six classes (sixth and eighth grade) in three schools and two elementary school children's groups (Supplementary Table 2). Eleven articles were published in local media about the project. Citizen scientists contributed observations through forms on the project website and via the iNaturalist project page. We did not perform specific surveys of citizen scientists' motivation or background.

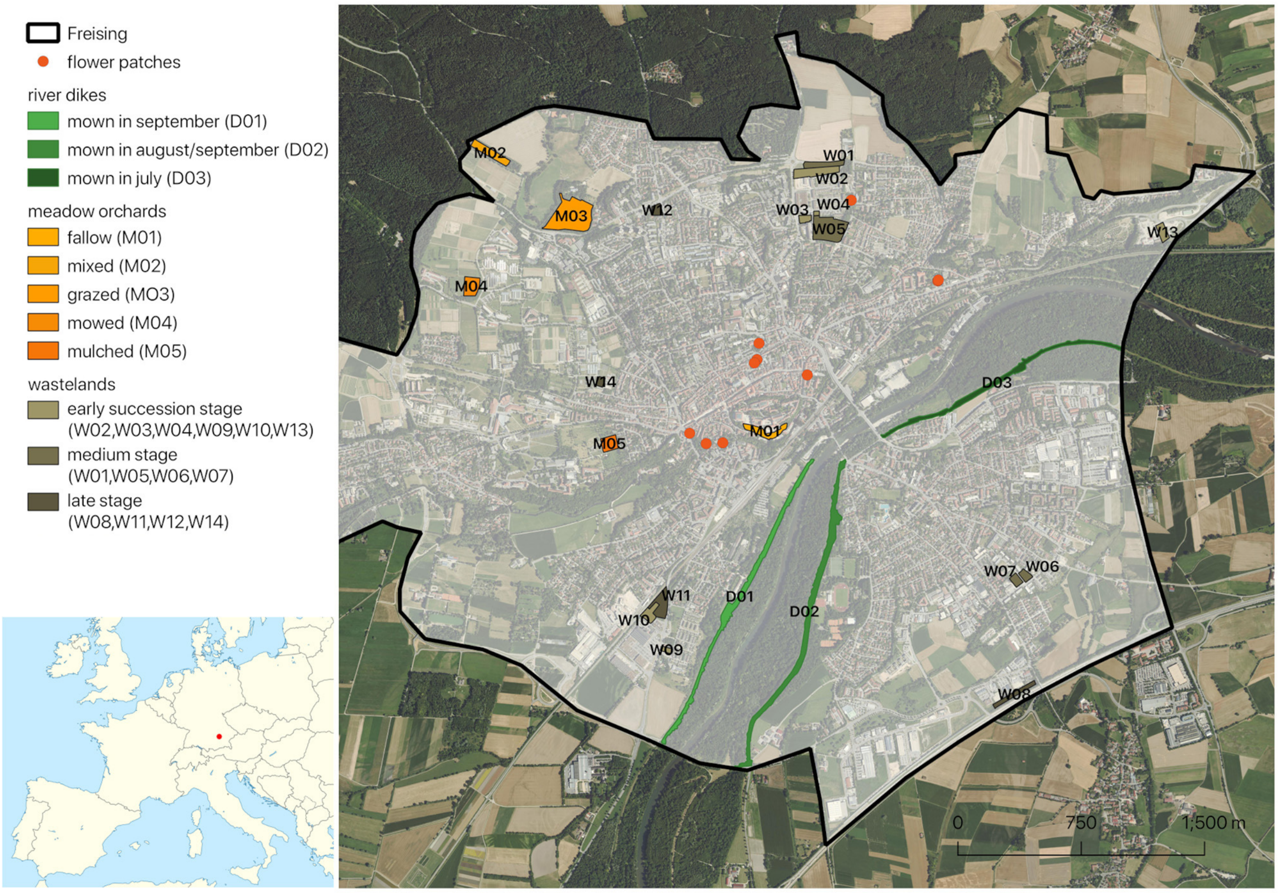

FIGURE 1
Location of Freising in Europe (inset) and distribution of bee rich habitats and stepping-stone flower patches in the city of Freising [basemaps: Bayerische Vermessungsverwaltung, 2023 (main map) & Wikimedia (inset)].

2.3 Trait analyses

To characterize and compare the bee communities of the different parts of the city, we analyzed the following traits: threat level (Germany and Bavaria), life form, nesting type, nesting resources, lecty, female body size, preferred host plants (oligolectic bees), host species (parasitic bees). The trait information was compiled from Westrich (2018) for life form, nesting type, nesting resources, lecty, pollen sources of oligolectic species, hosts of parasitic species. Information on threat level was compiled from Bayerisches Landesamt für Umwelt (2021) for Bavaria and Westrich et al. (2011) for Germany. For species that are not distinguishable in the field, we chose a conservative approach and used the trait values of the most common, widespread and least threatened species in the species group based on Weissmann and Schaefer (2022) (e.g., *Colletes daviesanus* as representative of the species group *C. daviesanus, C. similis, C. fodiens*). In a few cases, frequency, distribution and threat level did not differ. Here, we chose the species based on the alphabetic order (e.g., *Lasioglossum albipes* for *L. albipes/L. calceatum*). To determine female body size, we calculated the average of the size range given in Dathe et al. (2016), Weissmann and Schaefer (2022) for *Hylaeus*, and Martin (2023) for *Bombus* (workers), and *Psithyrus* (queens). For parasitic species, we assigned the nesting type of the main host(s) according to Westrich (2018) (see Supplementary Data 2).

2.4 Statistical analyses

All statistical analyses were performed in R version 4.2.3 (R Core Team, 2023) and the packages vegan v.2.6-4 (Oksanen et al., 2022), VennDiagram v.1.7.3 (Chen, 2022), tidyverse v. 2.0.0 (Wickham et al., 2019), reshape 2 v.1.4.4 (Wickham, 2007) and patchwork v.1.1.2 (Pedersen, 2022) (see Supplementary Data 6 for the code for the analyses and the datasets).

2.4.1 Bee taxa richness

For each site, the cumulative wild bee taxa richness and the flowering plant species richness were summarized from all observation periods (22 sites, 586 h of total observation time). To study the effects of the site characteristics "species diversity of flowering plants," "habitat type," and "distance from the river dikes" on wild bee diversity, we performed a poisson regression model (function glm). To account for different mapping intensity on each

FIGURE 2
Bee habitats in Freising: **(A)** river dike mown in September; **(B)** river dike mown in August/September; **(C)** river dike mown in July; **(D)** meadow orchard fallow; **(E)** meadow orchard grazed; **(F)** meadow orchard mulched; **(G)** wasteland early succession stage; **(H)** wasteland medium succession stage; **(I)** wasteland late succession stage; **(J)** flower patch with *Hesperis matronalis*; **(K)** flower patch with *Reseda lutea*; **(L)** flower patch with *Echium vulgare* [**(A–C)** © RR, **(D–F)** © IW, **(G–I)** © SR, **(J–L)** © JW].

site, we included total observation time in hours as offset (Zuur et al., 2009).

2.4.2 Bee community composition

We compiled the wild bee taxa list for each succession stage from the fourteen sites of the habitat type "wasteland" to obtain cumulative wild bee taxa lists for each habitat and management type (three management types for the habitat type "river dike," five management types for the habitat type "meadow orchard," three succession stages for the habitat type "wasteland;" 586 h of total observation time). We applied Non-metric Multi-dimensional Scaling (NMDS) to assess similarities in wild bee community composition between habitat type. To test whether there is a relationship between habitat type and wild bee community composition, we performed an Analysis of similarities (ANOSIM) and calculated the Sörensen index IA to evaluate the similarity between bee communities of the different habitat types with $IA = (2g/(a+b)) * 100$ (g = total number of bee taxa occurring in habitat type A and B; a = total number of bee taxa occurring in habitat type A; b = total number of bee taxa occurring in habitat type B).

2.4.3 Bee taxa traits

To test whether the number of bee species per trait (sociality, nesting, lecty) is similarly distributed across all habitat types, we performed Pearson's Chi-squared test (function chisq.test). Because some of the counts were less than five in the sociality and lecty tables, we confirmed that Fisher's Exact Test for Count Data (function fisher.test) gave similar results. To test significant differences in the sizes of bee species occurring in the different habitat types, we performed a Kruskal-Wallis rank sum test (function Kruskal.test) for each habitat type because the assumptions for an ANOVA were not met.

3 Results

3.1 Involvement of citizen scientists

Participation by citizen scientists in public talks, guided walks, and bee identification trainings was high (c. 630 persons, see Supplementary Table 2) but their subsequent contribution through observation reports was much lower (c. 1,165 records). A total of 140 observers (excluding the authors) contributed observations to our iNaturalist project but only six of them contributed more than thirty observations.

3.2 Bee fauna of Freising

3.2.1 Bee taxa diversity

We identified 139 wild bee taxa in the city of Freising in 586 h of systematic observation plus an unknown amount of time for the non-standardized citizen scientist observations all over the city. The most diverse habitats were the meadow orchards with 98 taxa, followed by wastelands with 80 taxa, and then the river dikes with 77 taxa (see Figure 3, Supplementary Table 3, and Supplementary Data 2 for an extended taxon list). The two species *Andrena clarkella* and *Osmia brevicornis* have been reported but the photographs are not sufficient for unequivocal identification. Seven bee species have been observed and well-documented by citizen scientists only but not during the standardized surveys in the city (*Andrena ventralis*, *Coelioxys afra, Epeoloides coecutiens, Melitta leporina, Nomada flavopicta*, *Pseudoanthidium nanum* and *Rophites quinquespinosus*) plus two remarkable species in the administrative district of Freising outside the city (*Melitta tricincta* and *Osmia spinulosa*) (see Supplementary Data 3).

The overall bee community of Freising comprises at least 27 genera. The largest genera in the city are *Andrena* (24 taxa), *Bombus/Psithyrus* (18 taxa), *Nomada* (15 taxa), and *Hylaeus* (12 taxa). In the mid-range genera, *Osmia/Hoplitis* (8 taxa) is followed by *Lasioglossum* (7 taxa), *Megachile* (7 taxa), and *Halictus* (6 taxa). The remaining genera are only represented by five or fewer taxa. When compared to the other habitat types, the meadow orchards have the highest number of taxa of the genera *Andrena*, *Nomada*, *Lasioglossum*, *Osmia*, *Anthophora*, and *Chelostoma*. The genera *Stelis*, *Panurgus*, *Anthidiellum,* and *Xylocopa* were found in meadow orchards and other parts of the city (e.g., some private gardens) but not on the river dikes and in the wasteland patches. The river dikes have the highest richness of the genera *Bombus* and *Sphecodes*. The genus *Megachile* has the highest richness in wastelands and the parasitic genus *Epeolus* was found exclusively in wastelands (Supplementary Figure 3).

3.2.2 Bee trait diversity

With 59% of the taxa (82 taxa), the majority of Freising's bees is solitary. Much less common are social species (mostly *Bombus*) with 13.7% (19 taxa), and 2.2% (3 taxa) of the species have a communal life form (Figure 4A). No significant differences were detected across site types by Fisher's Exact Test for Count Data (P-value = 0.95).

Regarding the nesting sites, 69.8% nest in the ground (97 taxa), while 40.3% have their nests above-ground (56 taxa) [for parasitic species, we assigned the nesting type of the main host(s)]. Some species are flexible in their nesting behavior and were counted as above- and below-ground taxon. The majority of the ground-nesting bees lives in self-excavated tunnel systems in the soil, usage of pre-existing cavities is relatively rare (Figure 4B). No significant differences were detected across site types by Pearsons's Chi-squared test (P-value = 0.93).

More than half of Freising's bee taxa are generalists (51.1%, 71 taxa), 23% (32 taxa) are oligolectic bees that rely on the pollen of a single or few plant species. Parasitic taxa represent 25.2% of the bee fauna of the city (35 taxa) (Figure 4C). No significant differences were detected across site types by Fisher's Exact Test for Count Data (P-value = 0.97).

The average size of female bees for all taxa recorded in Freising is 10.9 mm. When comparing the different habitats, there is no significant difference in body size (Supplementary Figure 4) (Kruskal-Wallis rank sum test: P-value = 0.57). On the river dike, however, bees are slightly larger (on average 11.52 mm compared to 10.98 mm and 10.91 mm on meadow orchards and wastelands). This difference disappears when the genus *Bombus* is excluded.

3.2.3 Threat level

Of the bee taxa recorded in Freising, 15 species are listed as "near threatened" in the Bavarian Red List (Bayerisches Landesamt für Umwelt, 2021), 12 are classified as "threatened," one species, *Bombus subterraneus* from the river dikes, is classified as "highly threatened" and one species, *Rophites quinquespinosus*, is classified as "threatened with extinction." We found the highest number of threatened bee species in the meadow orchards (8 near threatened, 5 threatened) and the lowest number of threatened species in the wastelands (4 near threatened, 4 threatened) (Table 1). In total, Freising harbors 11.3% of the red list species of Bavaria [categories V (near threatened), R (extremely rare), G (threat of unknown extent), 3 (threatened), 2 (highly threatened), 1 (threatened with extinction)] (Bayerisches Landesamt für Umwelt, 2021).

3.3 Bee hotspots

3.3.1 Bee communities in different habitat types

The bee communities of the different habitat types were similar across all sites. No significant inter-group and intra-group differences were detected by the ANOSIM (R-value = 0.191, P-value = 0.1184). Both the ANOSIM (Supplementary Figure 5) and the results of the Sörensen Index (Supplementary Table 4) indicate that the highest similarity was found between wastelands and meadow orchards, the lowest between wastelands and

FIGURE 3
Some of the bee species observed in Freising: **(A)** *Andrena agilissima* on *Sinapis arvensis*; **(B)** *Andrena hattorfiana* on *Knautia arvensis*; **(C)** *Melitta haemorrhoidalis* on *Campanula* spec.; **(D)** *Melitta nigricans* on *Lythrum salicaria*; **(E)** *Chelostoma campanularum/distinctum*; **(F)** *Megachile ericetorum* on *Lathyrus latifolius*; **(G)** *Dasypoda hirtipes* on *Cichorium intybus*; **(H)** *Colletes hederae* on *Hedera helix*; **(I)** *Megachile nigriventris* on *Baptisia australis*; **(J)** *Megachile pilidens*; **(K)** *Eucera nigrescens* on *Lathyrus pratensis*; **(L)** *Anthophora furcata* on *Nepeta grandiflora*; **(M)** *Halictus subauratus* on *Ranunculus* spec.; **(N)** *Anthidium punctatum* on *Lotus corniculatus*; **(O)** *Osmia caerulescens* on *Onobrychis viciifolia*; **(P)** *Anthidium oblongatum* on *Lotus corniculatus*; **(Q)** *Hylaeus nigritus* on *Leucanthemum vulgare*; **(R)** *Stelis punctulatissima* on *Calamintha nepeta*; **(S)** *Bombus subterraneus*; **(T)** *Bombus humilis* on *Calamintha nepeta*; **(U)** *Nomada sexfasciata*; **(V)** *Coelioxys* cf. *inermis*; **(W)** *Anthidium manicatum* on *Stachys byzantina*; **(X)** *Megachile* cf. *pilidens*; **(Y)** *Osmia leucomelana* nesting in *Rubus* sect. *Rubus* [**(B, N, V)** © IW, **(J)** © SR, **(S)** © RR, **(A, C–I, K–M, O–R, T, U, W–Y)** © JW].

river dikes. According to the NMDS (Supplementary Figure 6), wasteland late succession stage, meadow orchard mowed and meadow orchard mixed were the sites most distinct in their composition from all other sites while all river dikes, the meadow orchards fallow, mixed and grazed, as well as the wasteland sites of early and mid-succession stages, respectively, were similar in wild bee community composition.

Twenty taxa were recorded only in the meadow orchards (Figure 5): six of those taxa are on the red list for Bavaria [*Andrena hattorfiana* (3), *Osmia* cf. *niveata* (3), *Panurgus calcaratus* (V), *Anthophora furcata* (V), *Andrena lathyri* (V), *Stelis minima* (data deficient)]; six are oligolectic (*Andrena hattorfiana, A. proxima, Colletes hederae, Osmia* cf. *niveata, Panurgus calcaratus,* and *Andrena lathyri*) and *Osmia cornuta* is a typical pollinator of fruit trees flowering early in the season; three have specific nesting requirements [*Anthidiellum strigatum* (builds nests attached to rocks and walls; resin), *Anthophora furcata, Xylocopa violacea* (rotten wood)]; seven are parasitic (*Nomada fucata, Nomada lathburiana, Nomada signata, Stelis* cf. *ornatula, S. minima, S. punctulatissima,* and *S.* cf. *breviuscula*) and three are unspecific (*Halictus* cf. *eurygnathus, Lasioglossum zonulum,* and *Hylaeus difformis*).

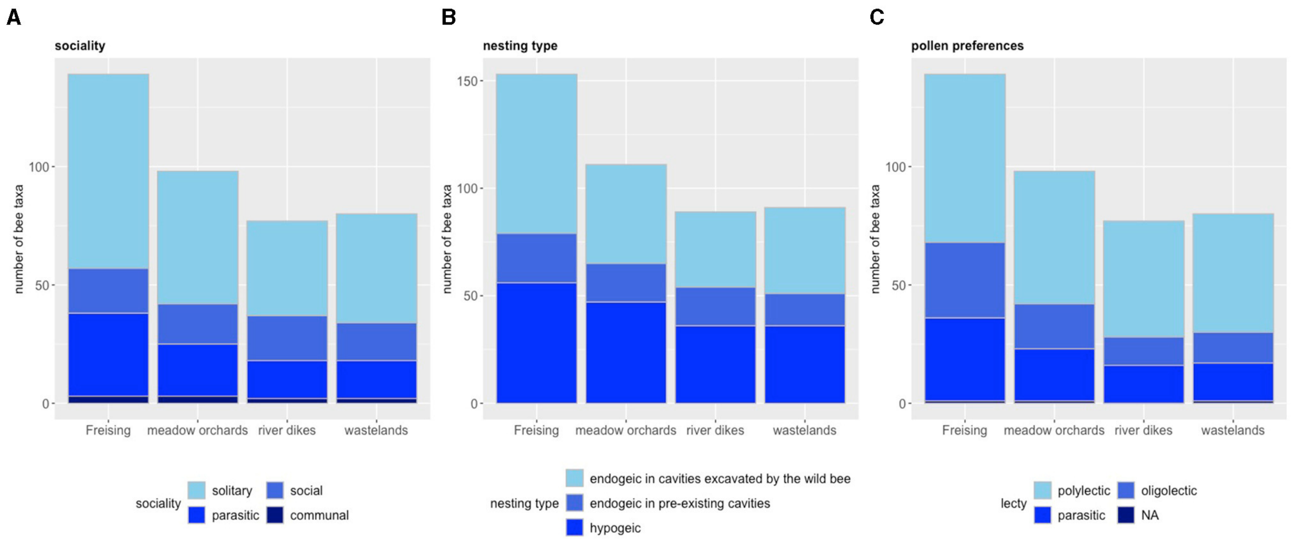

FIGURE 4
Sociality **(A)**, nesting type **(B),** and pollen preferences **(C)** of bee taxa according to habitat type. Total bee taxon richness = 139 taxa, total observation time = 586 h of systematic observation plus additional non-standardized observations all over the city.

Eleven taxa were unique to the wastelands (Figure 5): two of those taxa are on the red list for Bavaria [*Anthophora aestivalis* (3), *Halictus sexcinctus* (V)], two are oligolectic (*Andrena* cf. *praecox, Megachile lapponica*), one has specific nesting requirements (*Osmia aurulenta* nests in empty snail shells); five are parasitic (*Epeolus variegatus, Nomada fulvicornis*, *Nomada striata*, *Nomada* cf. *sheppardana*, and *Nomada fabriciana*) and one is unspecific (*Andrena nigroaenea*).

Nine taxa were unique to the river dikes (Figure 5): five of those taxa are on the red list for Bavaria [*Bombus subterraneus* (2), *Bombus ruderarius* (3), *Coelioxys aurolimbatus* (3), *Coelioxys rufescens* (3), *Hylaeus variegatus* (V)]; two are oligolectic (*Hylaeus signatus, Andrena vaga*); three are parasitic (*Coelioxys aurolimbatus, Coelioxys rufescens,* and *Sphecodes monilicornis*) and one is unspecific (*Colletes cunicularius*).

Sixteen taxa were recorded outside the hotspot habitats: eight of those are on the red list for Bavaria [*Rophites quinquespinosus* (1), *Pseudoanthidium nanum* (2), *Anthophora quadrimaculata* (3), *Dasypoda hirtipes* (3), *Melecta albifrons* (V), *Melitta leporina* (V), *Melitta nigricans* (V), *Nomada sexfasciata* (V)]; seven are oligolectic (*Andrena ventralis, Pseudoanthidium nanum, Dasypoda hirtipes, Melitta leporina, Melitta nigricans, Melitta haemorrhoidalis*, and *Rophites quinquespinosus*); five have specific nesting requirements (*Pseudoanthidium nanum* requires pre-existing cavities and plant hair, *Anthophora quadrimaculata* requires vertical walls, *Dasypoda hirtipes* requires sandy soil, *Megachile nigriventris* requires dead wood and leaf cuttings, *Megachile* cf. *pilidens* requires leaf cuttings); five are parasitic (*Coelioxys afra, Epeoloides coecutiens, Melecta albifrons, Nomada sexfasciata,* and *Nomada flavopicta*); one is unspecific (*Andrena tibialis*), two were found on the flower patches and not on the study sites (*Melitta nigricans* and *Melitta haemorrhoidalis*); seven were solely recorded by citizen scientists (*Andrena ventralis, Melitta leporina, Pseudoanthidium nanum, Coelioxys afra, Epeoloides coecutiens, Nomada flavopicta,* and *Rophites quinquespinosus*). Two additional species were found outside of the city in the surroundings of Freising: *Melitta tricincta* [threatened, oligolectic on *Odontites* (Orobanchaceae)], *Osmia spinulosa* (near threatened, oligolectic on Asteraceae, nests in empty snail shells) (see Supplementary Data 3).

3.3.2 Influence of management-intensity and succession stage on bee taxon richness

Within a particular habitat type, bee taxon richness differed depending on succession stage or management type. The highest number of bee taxa occurred in fallow and grazed meadow orchards (67 and 68 bee taxa respectively), the river dike area with the latest mowing date (62 bee taxa), and in the wastelands of early succession stage (57 bee taxa) (Supplementary Data 2, Supplementary Table 5). This pattern is mirrored in flowering plant diversity, which was highest in fallow and grazed meadow orchards (85 and 82 species respectively), in the wastelands in early and mid-succession stage (137 and 122 species respectively—these are the cumulative species numbers of all wasteland sites with the respective succession stage) and on the river dike sections mown in September and August (117 and 114 species respectively) (Supplementary Data 4, Supplementary Table 5). In our poisson model, the number of flowering plant species on a site had a positive impact on wild bee taxa richness on site for our dataset (estimate: 1.358e-03), but the result cannot be generalized (*P*-value = 0.48636). According to the model, assuming a set observation time and a set number of plant species on site, one would expect on average 1.5 times more bee taxa on a wasteland site compared to a meadow orchard site (estimate: 3.946e-01, *P*-value = 9.98e-05 ***) and on average 0.6 times as many bee taxa on a river dike site compared to a meadow orchard site (estimate: −4.420e-01, *P*-value = 0.00293 **) (Supplementary Table 6).

TABLE 1 Threatened and near threatened species found in Freising, according to the Bavarian Red List (Bayerisches Landesamt für Umwelt, 2021).

	River dikes	Meadow orchards	Wastelands	Freising
Near threatened (V)				
Andrena viridescens		1	1	1
Andrena lathyri		1		1
Anthidiellum strigatum		1		1
Anthophora furcata		1		1
Bombus sylvarum	1	1	1	1
Bombus soroeensis	1	1		1
Eucera longicornis				1
Eucera nigrescens		1		1
Eucera longicornis/E. nigrescens	1		1	-
Halictus sexcinctus			1	1
Hylaeus variegatus	1			1
Melecta albifrons				1
Melitta nigricans				1
Melitta leporina				1
Nomada sexfasciata				1
Panurgus calcaratus		1		1
Osmia spinulosa				1*
Threatened (3)				
Andrena hattorfiana		1		1
Andrena agilissima	1	1	1	1
Anthophora quadrimaculata				1
Anthophora aestivalis			1	1
Bombus humilis	1	1	1	1
Bombus ruderarius	1			1
Coelioxys aurolimbatus	1			1
Coelioxys inermis		1	1	1
Coelioxys rufescens	1			1
Dasypoda hirtipes				1
Osmia cf. niveata		1		1
Pseudoanthidium nanum				1
Osmia brevicornis		?		?
Melitta tricincta				1*
Highly threatened (2)				
Bombus subterraneus	1			1
Threatened with extinction (1)				
Rophites quinquespinosus				1
Data deficient (D)				
Stelis minima		1		1

*Taxa observed outside of the city but within the administrative district of Freising.

? existence in Freising is currently doubtful (identification based on the provided photograph not unequivocal).

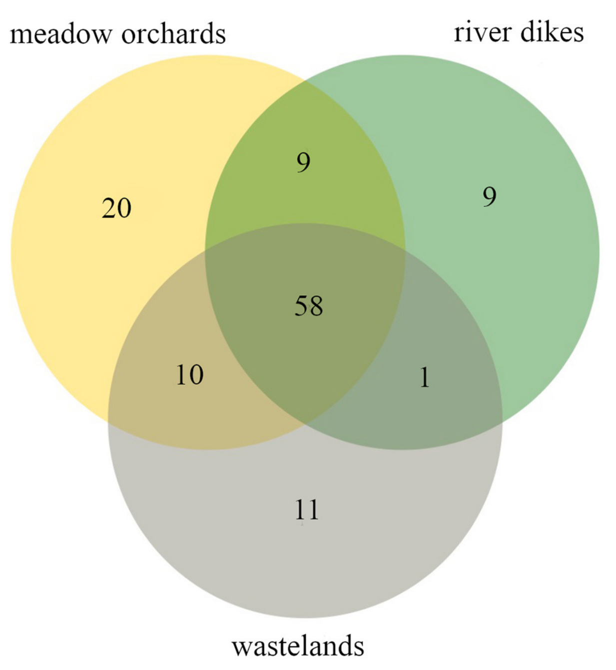

FIGURE 5
Bee taxa shared between the three habitat types (wild bee taxa found on meadow orchards in yellow, wild bee taxa found on the river dikes in green, wild bee taxa found on wastelands in gray). Total wild bee taxon richness = 118 taxa, total observation time = 586 h of systematic observation.

3.3.3 Distribution of bee hotspots across the city

Two of the hotspots (meadow orchard M01, wasteland W09) are within 400 m distance of the river dikes; two are within 600 m (wastelands W10 and W11); seven within 1,000–2,000 m (meadow orchard M05 and wastelands W05 to W08, W13, and W14), five within 2,000–3,000 m (wastelands W01 to W04, W12, and W13) and three within 3,000–4,000 m (meadow orchards M02 to M04). The flower patches are within or close to the areas of continuous urban fabric according to the CORINE classification and within 800–2,100 m distance from the river dikes (Supplementary Figure 7). The number of bee taxa does not decrease with increasing distance from the dikes. Distance from the river dikes did not have a significant effect on the number of bee taxa in our poisson regression model (estimate: −7.540e-06; P-value = 0.84736) (Supplementary Table 6). The two most taxon rich patches are one of the closest and one of the most distant meadow orchards.

3.3.4 Colonization of stepping-stone patches

In six of ten flower patches we observed the target oligolectic bee species already in the first flowering season. Eight of ten were colonized in the third year after planting (Supplementary Table 7). We did not find *Dasypoda hirtipes* on the patch of *Cichorium intybus* planted to attract it but we found this bee species in two other locations at 2.6 km and 2.8 km distance of the flower patch. Similarly, *Osmia brevicornis* could not be observed in the planted patch of *Hesperis matronalis* but in another site nearby (unfortunately, the photograph is not detailed enough, so its existence in Freising remains somewhat doubtful). Other species were also found to profit from the patches, e.g., *Melitta haemorrhoidalis*, a bellflower specialist, and many generalist species.

4 Discussion

4.1 Survey method: challenges and opportunities of participative approaches

Our species identification approach based on photographs instead of collected bees leads to an underestimation of total species numbers, especially in species-rich difficult genera like *Hylaeus*, *Lasioglossum,* and *Sphecodes*. For those genera, pan trap or direct collecting allow more precise identification and therefore longer species lists. However, these lethal methods require collecting permits and citizen scientists are unlikely to be granted such permits even if they could be convinced to go through the trouble of applying. For citizen science projects, identification by photographs seems therefore the only realistic option. Since this approach is easier in some genera than in others (Weissmann and Schaefer, 2022), comparing diversity per genus or comparing diversity values between different studies gets more complicated. The real diversity and number of rare species in Freising can be expected to be higher than in our list but it seems unlikely that overall patterns would change dramatically when all our taxon groups were fully resolved into single species. Our approach delivers in-depth data for the bee communities systematically surveyed in urban bee hotspots, while the citizen scientist data helps to cover all the less accessible sites (e.g., private gardens and allotments).

Interest in bee talks and identification trainings was high, which resulted in a large number of people getting some basic understanding of bee diversity, bee ecology and the problems that bees are facing in our cities. Some participants of these basic introductions became really interested in the topic, continued to attend our program, and contributed large numbers of observations to our webpage and the iNaturalist portal. This, in combination with self-studies allowed them to reach advanced levels of identification knowledge in a few years' time. In the end, these people have not only contributed a large percentage of the total records but even discovered some rare species we had not found in our systematic surveys. While this is a fantastic result, we encountered two main challenges to reach larger numbers of dedicated participants. First, wild bees are often difficult to identify to species level even for specialists. Since they are often small and fast, taking high-quality photographs is a challenge and needs patience and persistence. Without such high-quality pictures, even experienced specialists or the best artificial intelligence algorithm will not be able to reliably identify the species. Second, reporting of bee observations and species identifications should be as easy as possible, ideally with one or two clicks on the smart phone. To tackle the first challenge, we developed a field guide focusing only on the pool of bee species occurring in the region (here: Bavaria) to make the identification based on photographs more accessible (Weissmann and Schaefer, 2022). In this field guide, we acknowledge that some species cannot reliably be distinguished with photographs alone and propose a system to group those species into consistent taxon groups. This enables comparisons of diversity between projects following the same system. The approach could be easily expanded to other regions of Europe. Regarding the second challenge, we realized that iNaturalist (www.inaturalist.org) is the perfect platform for quick and easy reporting of wild bee observations and species identification by observers of different levels of experience. A strength of this approach lies in its potential to provide continuous data in space, including private gardens, and time: wild bee observations are continuously added to our iNaturalist project while the funding period for in-depth surveys is limited in time. Moreover, iNaturalist includes an artificial intelligence species identification algorithm, which gets better the more correctly identified photographs of a particular species are uploaded for a particular geographic region. So, over time, the need for specialists to provide and review identifications should go down. It is, however, clear that regular trainings by bee specialists would be very helpful, for example as part of targeted communal survey events (e.g., Bioblitz; Roger and Klistorner, 2016) to provide additional in-depth snapshots. Ideally, these projects should be combined with university courses and specialist surveys (Paradise and Bartkovich, 2021; Vereecken et al., 2021). This would allow to maximize data availability, minimize bee capture, and focus the very limited specialist capacities on the most relevant (endangered) species and habitats. The fact that some of the most endangered species in our study were not discovered during our (or other) specialist surveys but through chance observations of citizen scientists shows that a large community of trained citizens can be more efficient than few specialists.

4.2 Is the city a hotspot or a refugium for wild bees?

Overall, with 139 wild bee taxa recorded in 2017–2022 (29% of the 472 bee species currently known in Bavaria), the total wild bee taxon richness in Freising (c. 90 km^2) is comparable to results from other central European cities: 331 species have been recorded in Munich (c. 310 km^2) since 1841 (Schuberth and Bräu, 2022) and 232 species have been re-observed or newly observed in 1997–2017 (Hofmann and Renner, 2020); 104 species have been recorded in Poznan (Poland, c. 260 km^2, 2006–2008) (Banaszak-Cibicka and Zmihorski, 2012), 87 species in Paris (France, c. 100 km^2, 2011–2016) (Ropars et al., 2018); 291 in the Lyon Metropolis (France, c. 530 km^2, 2012–2014) (Fortel et al., 2015); 210 in the Brussels-Capital Region (Belgium, c. 160 km^2, 1999–2020) (Vereecken et al., 2021), 170 in Zurich (Switzerland, c. 9 km^2) (Casanelles-Abella et al., 2021). In the nearby area protected under the Habitat's directive (Fauna Flora Area) "Isarauen von Unterföhring bis Landshut" and the protected area "Isarauen zwischen Hangenham und Moosburg," both natural riverine forest and gravel bank habitats, a total of 118 wild bee species was recorded during specialist surveys in 2015 (Mandery, 2016; Bayerisches Landesamt für Umwelt, 2021).

Freising harbors 11.3% of the red list species of Bavaria (categories 1, 2, 3, G, R, V) (Bayerisches Landesamt für Umwelt, 2021). The share of oligolectic taxa in Freising (23%) is comparable to that of Bavaria (23.3%). This is in contrast to other studies that tend to show that generalist species are more prevalent in urban areas (Buchholz and Egerer, 2020) but it is possible that generalist diversity is underrepresented due to our identification approach. The share of parasitic taxa in Freising (25.2%) is comparable to that in Bavaria (25.6%), which is remarkable because in these genera, species-level identification based on photographs is often impossible. The share of hypogeic species (excluding parasitic species) was higher in Freising (31.1%) than in Bavaria (23.5%), a pattern that has been related to urbanization (Wilson and Jamieson, 2019), although Gathof et al. (2022) have shown that urban dry grassland can be a favorable habitat for ground-nesting species. Overall, although common species are predominant, we found that Freising harbors a relatively species-rich wild bee community including some rare and specialized taxa regarding pollen/nectar requirements, but also regarding nesting requirements: resin (*Anthidium strigatum* and *Megachile ericetorum*), dead/rotting wood (*Anthophora furcata*, *Megachile nigriventris*, and *Xylocopa violacea*), empty snail shells (*Osmia aurulenta*, *O. bicolor*, and *O. spinulosa*).

The following taxa were recorded by us in addition to the 230 species recorded for the administrative district of Freising since 1856 (Bayerisches Landesamt für Umwelt, 2023): *Andrena agilissima*, *Anthophora quadrimaculata*, *Coelioxys afra*, *Coelioxys aurolimbatus*, *Coelioxys inermis*, *Coelioxys rufescens*, *Colletes hederae*, *Epeoloides coecutiens*, *Hylaeus dilatatus*, *Hylaeus variegatus*, *Megachile lapponica*, *Megachile rotundata*, *Melitta tricincta*, *Nomada flavopicta*, *Nomada sexfasciata*, *Nomada* cf. *sheppardana*, *Osmia* cf. *brevicornis*, *Osmia cornuta*, *Rophites quinquespinosus*, *Sphecodes albilabris*, *Stelis minima*, *Stelis* cf. *ornatula*, and *Xylocopa violacea*. The taxa *Dasypoda hirtipes*, *Coelioxys afra, Rophites quinquespinosus*, *Megachile lapponica,* and *Nomada* cf. *sheppardana* were recorded during our study but not yet in Munich, where 331 wild bee species have been recorded since 1841 (Schuberth and Bräu, 2022). For the taxa that could not unequivocally be identified, verification through capture and barcoding would be useful. Considering that more than twice as many bee taxa have been recorded in Munich in 150 years of surveys compared to our findings in Freising, it is evident that bee surveys should ideally be performed over long time scales. Although some of the species recorded for the administrative district of Freising and for Munich are difficult to detect with our method, they also include numerous taxa that we would have identified to species level from photographs. This shows that there is potential for additional species including rare ones to be found in Freising in the coming years.

4.3 Urban hotspots and their specific contribution to a diverse wild bee community

Overall, the river dike hosts a large part of the wild bee communities of the city, which is comparable to studies on river dikes along the Rhine (Westrich, 1985) and Loire (Villalta et al., 2021). The dikes had ten Red-List-species, and were particularly attractive for bumblebees, including the species with the highest threat level in the city (*Bombus subterraneus*). This might be related to the high availability of abandoned rodent holes in the dike (see also McFrederick and LeBuhn, 2006). The high share of *Sphecodes* bees on the dikes, a parasitic genus specialized mainly on *Andrena* and halictid bee hosts, indicates availability of nesting sites for its ground nesting host bee species. Two species only found on the dikes, the *Reseda* specialist *Hylaeus signatus* and the willow specialist *Andrena vaga* probably did not find enough host plants in the other habitat types.

We found the highest number of bee taxa in the meadow orchards and also the highest total number of near threatened and threatened species, and the highest share of oligolectic species. Two specialists of rotten wood (*Anthophora furcata* and *Xylocopa violacea*) and the resin specialist *Anthidiellum strigatum* were only found here. Although, we know of only one other study from urban orchard meadows (Rada et al., 2023), meadow orchards in general (usually located in the surroundings of small villages far from cities) have been found to be important wild bee habitats in other parts of Germany and Europe (Steffan-Dewenter, 2003; Steffan-Dewenter and Leschke, 2003; Schwenninger and Wolf-Schwenninger, 2012; Horak et al., 2013; Saure, 2016).

Although the wastelands had the lowest species number among our main study sites and the lowest number of threatened species, they were still hotspots within the city with 80 taxa and particularly important for *Megachile* and *Epeolus*. The willow specialist *Andrena praecox*, *Megachile lapponica* which needs *Epilobium*, and *Osmia aurulenta* which needs empty snail shells were only found on wastelands. Studies focusing on wasteland bee communities in other European cities revealed even higher numbers: 112 species in Freiburg (Germany) (Klatt, 1989), 127 species in Brussels (Belgium) (Vereecken et al., 2021), and 201 species of bees in Bydgoszcz (Poland), which is 42% of all bee species reported from Poland (Twerd and Banaszak-Cibicka, 2019). This demonstrates the huge importance of these ephemeral and often overlooked habitats, which often have large proportions of bare ground and favorable microclimatic conditions resulting in good nesting and foraging conditions for bees until succession or development projects put an end to the bee community in this site and new wastelands nearby are needed.

As river valleys can be important corridors for wild bees (see e.g., Braun-Reichert et al., 2021), we hypothesized that the river dike in Freising would be the main bee hotspot of the city. Contrary to our expectations, meadow orchards and not the river dikes had the highest species richness. This might be partly explained by the fact that the studied river dike sections were relatively uniform overall while there was more structural diversity within the different meadow orchard (and wasteland) sites we studied. Furthermore, since we were unable to locate nesting sites of most species, we do not know if the observed foraging habitats are also suitable for nesting. In fact, many studies highlight the importance of the availability of non-floral resources (Potts et al., 2005; Appenfeller et al., 2020; Requier and Leonhardt, 2020). Providing bare soil for ground nesting bee species is a relatively easy measure in in urban environments that can have a large impact (Noël et al., 2021).

4.4 Management of hotspots

We recorded the highest bee diversity on two patches of extensively managed meadow orchards, on the river dike area with the latest date of mowing (September), and on wastelands in early succession stages. Those were also the sites with the highest flowering plant species diversity. Our findings support extensive management of green spaces with grazing animals or late summer/autumn mowing (1–2 times per year), always leaving some stripes or patches unmown. Besides protecting natural areas and fostering flower- und structure-rich parks and gardens, the importance of wasteland in early succession stages should not be overlooked. These habitats tend to be short-lived in cities but will reappear whenever new demolition or construction sites appear.

4.5 Promoting connectivity—and at which scale?

Overall, the bee community composition in the hotspots was relatively similar. Bee species richness on a site is not related to the distance from the river dikes, and the city center does not seem to be a barrier. This might partly be explained by the relatively small size of Freising and of its highly urbanized areas. The particular topography of the city might also play a role, as bees might be more easily displaced by wind from elevated hill sites. Body size of female bees was overall very similar in the different habitats. A slightly larger size found on the river dikes is an effect of the higher number of bumblebee species on the dikes. The lack in size patterns is in contrast to other studies (e.g., Greenleaf et al., 2007) suggesting higher dispersal potential for larger-sized bees.

Our stepping-stone flower patches were very successful, similar to the results of Hofmann and Renner (2020), who found that flower strips in Munich already supported a quarter of Munich's bee species in the first year with oligolectic species not being underrepresented compared to the city's overall species pool. This suggests that some oligolectic bee species are relatively well established in cities, where they find their specific host plants in gardens (e.g., *Campanula* spp. as ornamental plants) or on wasteland and roadsides (e.g., *Echium vulgare* or *Reseda lutea*). In a way, this might be misleading since they do not rely on additional stepping-stones. Maybe more attention should be given to those species with more specific needs who will take some time to colonize the new patches (e.g., *Osmia brevicornis* or *Dasypoda hirtipes*).

Overall, our results indicate that, for cities to harbor diverse bee communities including rare species, it might be more important to provide small-scale connectivity between foraging and nesting resources than to provide continuous connectivity between floral resources throughout the entire city. While foraging ranges are estimated to reach only a few hundred meters especially in the smaller bee species (Hofmann et al., 2020), flight ranges for colonization of new habitats are probably larger and bees might occasionally be able to cross local physical barriers. For species nesting in above-ground structures, dispersal by human transport of rocks, wood, or building materials might be common in cities. And even ground-nesting species could be transported with soil or sand for construction and landscaping. Providing continuous corridors e.g., in areas mainly covered with impervious surfaces or along road axes might come with the price of creating partial habitats (Westrich, 1996) and in the worst case could form sinks/traps e.g., by attracting bees to sites with heavy traffic (Martin et al., 2018; Dániel-Ferreira et al., 2022a,b). Nevertheless, flower patches in densely populated areas have an important potential to raise awareness for the very specific habitat needs of wild bees when accompanied e.g., by information boards. They might be more important in larger cities with larger areas of impervious surface if the goal is high bee diversity throughout the city. However, if the goal is to provide hotspots and refugial areas for rare and threatened species, we argue the better approach is to create structurally diverse habitats taking into account the resources within a few hundred meters radius (Hofmann et al., 2020) of the three-fold needs of wild bees by providing: (1) pollen and nectar sources: ideally flowering plants species of different plant families flowering throughout the season and with a special focus on the host plants of oligolectic bees; (2) nesting sites: shifting the focus from the very popular provision of nesting aids for cavity nesting bees [which are usually colonized only by very common species (Geslin et al., 2022)] toward the needs of ground-nesting species. Also, dead wood specialists (Eckerter et al., 2021) and bees nesting in pithy plant stems suffer from the lack of “wild” places in parks and private gardens and need special help [e.g., unmown grass patches during winter (Unterweger et al., 2018) and leaving dry *Verbascum* or *Rubus* stems for at least two winters]; (3) nesting materials: e.g., moist clay for mason bees, and hairy plant species for wool carder bees.

4.6 Implications for bee conservation

We suggest the following concept for bee-friendly management of urban spaces: (1) identification of bee hotspots and systematic surveys for rare species (also considering habitat corridors at a larger scale); (2) training of citizen scientists at two levels for comprehensive surveys across the city: half-day introductions to bee diversity, bee ecology and bee conservation to create general awareness, and 2-weeks workshops for in-depth training in bee identification of a small number of dedicated citizen scientists; (3) extensive management of existing habitats and targeted conservation of rare species; (4) creation of high-value habitats to account for all resource needs of bees within flight ranges of only a few hundred meters; (5) creation of stepping stone habitats (with particular attention to rare oligolectic species) as floral and nesting resources, integrating educative and participative aspects. When integrated into the general green space management of a city and with the support of local NGOs, schools, and universities, this approach can be very cheap. Even though it is a time-consuming task to map and identify bees, using the suggested citizen science approach will not only make this more efficient than a traditional scientific study, it will also produce as a side-effect a lot of new bee-enthusiasts and even some future bee specialists, which are desperately needed for long-term conservation work of this fascinating group of insects.

Data availability statement

The datasets presented in this study can be found in online repositories. The observation data for this study can be found in our project on the iNaturalist platform at https://www.inaturalist.org/projects/wildbienen-in-freising-urban-pollinators-bees-in-freising and in the Supplementary Data 5 of this publication.

Author contributions

JW and HS designed the study and wrote the first draft of the manuscript. JW, SR, RR, IW, JP, and KS collected data. JW organized the database and performed the statistical analysis. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/frsc.2023.1155714/full#supplementary-material

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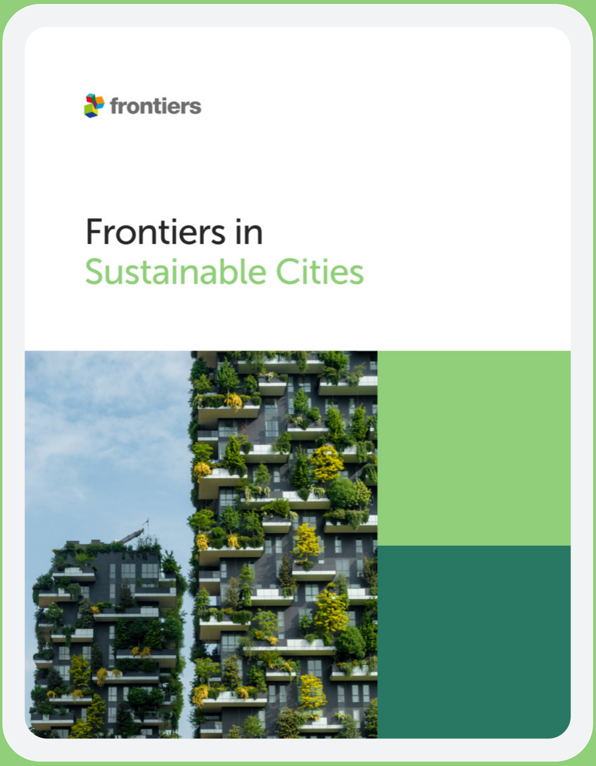
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