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Floral richness and seasonality influences bee and non-bee flower interactions in urban community gardens

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Abstract

Pollinating insects are essential for food production. Both bee and non-bee pollinators are undergoing dramatic declines due to land use intensification and its consequences on native ecosystems. While interactions between crops and bee pollinators are well studied, our understanding of the pollination service provided by non-bee flower visitors including flies, ants, beetles and others is still limited. Moreover, the effects of landscape urbanization and changes in floral and nesting resource availability on the network structure of pollinators with both cultivated and wild plants have been poorly studied. We assessed which common bee and non-bee flower visitor groups dominate the interactions with both wild (e.g. *Trifolium pratense*, *Taraxacum officinales*) and cultivated plants (e.g. *Fragaria ananassa*, *Cucurbita pepo*) in urban community gardens in Berlin and Munich and explored how these interactions between flower visitor groups and plants change over the growing season. We further investigated the effect of changes in urbanization surrounding community gardens, and the availability of floral and nesting resources within gardens on the complexity (i.e. nestedness, linkage density, connectance) of interaction networks. We observed 20 focal plant species and 13 common bee and non-bee flower visitor groups in 30 urban community gardens. We found that dominant plant visitors changed over the growing season, with non-bee flower visitors including ants and flies as dominant early season visitors, and bee pollinators as important visitors later in the season. Nestedness of the flower visitor network increased with increases in floral richness in community gardens, while neither floral abundance nor the impervious surface surrounding the community gardens, garden size or the availability of nesting resources in gardens strongly influenced the flower visitor networks. Our findings suggest that high floral richness in community gardens may ensure the complexity and, thus, the stability of flower visitor networks. Findings further suggest that the role of non-bee flower visitors should be considered for pollination service provision especially in the shoulder seasons. Finally, our results emphasize that urban gardeners play a key role in mediating flower visitor interactions through their gardening practices.

Keywords Plant-pollinator interactions · Ecological networks · Non-bee flower visitor · Temporal dynamics · Floral resources · Imperviousness

Introduction

The majority of vegetables, fruit and nut crops produced in agriculture for human consumption around the world are pollinated by arthropods (Klein et al. 2007). While both managed and wild pollinators are essential for food production in agricultural systems, insect pollinators are undergoing dramatic declines due to the intensification of land use, habitat loss, the lack of flowers, climate change, invasive species and disease (Panziera et al. 2022; Wood et al. 2020; Sánchez-Bayo and Wyckhuys 2019; Goulson et al. 2015; Smith et al. 2015; Winfree et al. 2009).

Diverse pollinator communities improve pollination services in agricultural and natural systems through resource use complementarity due to variations in morphology and behaviour among pollinator taxa (Dainese et al. 2019; Garibaldi et al. 2013; Albrecht et al. 2012; Winfree and Kremen 2009). For example, within bees (clade: Anthophila), species have different feeding specializations (e.g. generalist vs. specialist), socialities (e.g. solitary vs. social), as well as body sizes (e.g. bumble bees

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(large) vs. sweat bees (small)). In addition, the diversity of non-bee flower visitors (e.g. beetles, flies, butterflies, moths) can provide pollination services at different times of the day (i.e. moths pollinate at night), over larger temporal ranges, and in weather conditions unfavourable to some bee species (Rader et al. 2016, 2011; McCall and Primack 1992). Non-bee flower visitors may also differ in how they use floral resources by visiting different parts of the flower or visiting different flowers within a plant, which could complement pollination service provided by bees and therefore enhance the overall pollination service (Rader et al. 2016; Hoehn et al. 2008). How these diverse assemblages of bee and non-bee pollinators interact with both cultivated and wild plants in agricultural systems is therefore likely different, yet our understanding of the complexity of plant-pollinator interactions in agricultural systems is still limited. Furthermore, although non-bee pollinators may be as important as bee pollinators for the production of a variety of crops (Cusser et al. 2021; Howlett et al. 2021; Földesi et al. 2021; Rader et al. 2020, 2009; Jauker and Wolters 2008), our understanding of their interactions with plants is still limited compared to bees. Accordingly, understanding the role of both bee and non-bee pollinators and how they interact with cultivated and wild plants in agricultural systems may benefit sustainable food production.

Urban agricultural systems, or ‘urban agroecosystems’, are food-production oriented ecosystems within cities. The sustainable production of food and flowers in these agroecosystems is increasingly relevant to growing urban human populations (e.g., 15–20% of the global food production is already taking place in or close to urban areas) (Nicholls et al. 2020; Thornton 2008; Armar-Klemesu 2000). Urban agroecosystems may also have complex yet largely understudied plant-pollinator interactions, which underly food and flower production. In particular, urban community gardens often host species-rich communities of flowering plants that provide nectar and pollen resources throughout the season and thereby serve as important refuges for pollinators within cities (Cohen et al. 2021; Egerer et al. 2020; Olsson et al. 2021; Baldock et al. 2019; Levé et al. 2019; Hall et al. 2017; Lowenstein and Minor 2016; Hülsmann et al. 2015). Yet, it is unclear how a relatively high diversity of floral resources may influence how (e.g., visitation frequency) flower visitors interact with cultivated and wild plant species, to thereby influence pollination provision.

Increasing urbanisation through urban densification and expansion may reduce pollinator richness, lower flower visitation rates, and reduce the diversity of interactions between plants and flower visiting insects due to landscape fragmentation and habitat loss (Udy et al. 2020; Harrison et al. 2019; Deguines et al. 2016; Bates et al. 2011) – with potential cascading effects on pollination services (Theodorou et al. 2021; Aguilar et al. 2006; Cheptou and Avendaño 2006; but see also Verboven et al. 2014b), as urbanization often drives the loss of nesting and floral resources (Theodorou et al. 2020a, b; Harrison and Winfree 2015; Williams et al. 2010). However, at the local habitat scale, the availability of floral resources, namely floral richness and abundance can have a positive effect on plant-pollinator interactions (Udy et al. 2020), pollinator diversity (Tasker et al. 2020; Woodard and Jha 2017; Wojcik and McBride 2012; Potts et al. 2003), flower visitation frequency (Gilpin et al. 2022; Ebeling et al. 2008; Hegland and Boeke 2006) and pollen deposition (Monasterolo et al. 2022; Cohen et al. 2021). In fact, flower-rich urban habitats often host a higher diversity of pollinators than do rural habitats (Baldock et al. 2015; Verboven et al. 2014a). Garden size also plays an important role in predicting pollinator diversity. For example, Quistberg et al. (2016) found that urban gardens along the California central coast that were larger in size hosted a higher abundance and diversity of bee pollinators than smaller gardens. Along with many other studies, they also found that the availability of bare soil is an important habitat feature that promotes pollinator richness and abundance by providing nesting habitat for ground nesting pollinator species (Felderhoff et al. 2023; Ballare et al. 2019; Quistberg et al. 2016). Thus, floral management – in particular increases in floral diversity – garden size and nesting resource availability – in particular increases in bare ground availability – can mediate the impacts of landscape urbanization on flower visitor interactions. (McDougall et al. 2022; Baldock 2020; Bloom et al. 2019; but see also Udy et al. 2020).

Studies on urban pollinator communities in urban agroecosystems have predominantly investigated the effect of urbanization (e.g., landscape imperviousness) on bee pollinators (Hernandez et al. 2009; Winfree et al. 2009). Yet we are still missing information on how both bee and non-bee pollinators interact with cultivated and wild plants in urban community gardens, and how this may vary based on both garden floral management, nesting resource availability and landscape urbanization. Flower visitor networks can help to understand the complex interactions between cultivated or wild plant species and their potential pollinators. As species are added to the network, increasing species richness, the number of possible interactions between them increases. This results in higher network complexity, measured by e.g., modularity and nestedness (Bascompte et al. 2003; Olesen et al. 2007). The complexity of flower visitor networks reflects the diversity and interdependence of species within the ecosystem and has important implications for ecosystem functioning and stability (see e.g., the diversity-stability debate; (MacArthur 1955; Bersier and Banasek-Richter 2009; Dunne et al. 2002)). Because larger habitats can support more species (*species-area relationship*, Schoener 1976), and, thus, support more interactions between species, the complexity and stability of networks is expected to increase with habitat area (Galiana et al. 2018). Testing how local agroecosystem management factors in the context of landscape urbanization influence diversity and interactions between plants and flower visitors can provide important information to our understanding of flower visitor networks, and how this may relate to stable pollination services in cities.

Here we investigate the effect of landscape imperviousness, garden size and changes in floral resource availability and nesting resource availability on the network structures of both bee and non-bee flower visitors with cultivated and wild plants in urban community gardens. We also determine the most frequent interactions between flower visitors and common garden plants, explore changes in flower visitor diversity over the growing season, and investigate how flower visitation by bee and non-bee visitors changes over the course of a growing season. Specifically, we ask: (1) What are the dominant pollinator groups that interact with common cultivated and wild plants? Here we consider 'dominance' of a pollinator group as the frequency of flower visits by individuals of that group compared to other pollinator groups. (2) How do diversity indices such as richness and diversity of flower visitor communities change over the growing season (3) How does the number of flower visits by bee and non-bee flower visitors change over the growing season?, and (4) How do flower visitor interactions change with changes in floral diversity, nesting resource availability, garden size and landscape urbanization? We hypothesized that: (a) the flower visits in urban community gardens are dominated by bee pollinators (honeybees, bumblebees, wild bees); (b) richness and diversity of flower visitor communities increase over the growing season; (c) the proportion of flower visits by bee pollinators to flower visits by non-bee flower visitors increases over the growing season; and (d) flower visitor networks will simplify (less interactions between plant species and flower visitors, represented by common network indices) with increasing landscape urbanization and decreasing floral diversity (richness and abundance) and nesting resource availability (Prendergast et al. 2022; Theodorou et al. 2020a, b).

Materials and methods

Urban community gardens

We conducted our research in 30 urban community gardens in Berlin (52.5200° N, 13.4050° E) and Munich (48.1351° N, 11.5820° E), Germany. From May to August 2021, 15 gardens were studied in Berlin (Northeast of Germany; area 891.7 km^2; population > 3.6 million) and 15 gardens in Munich (South of Germany; area 310.71 km^2; population > 1.4 million). The gardens ranged from 0.04 and 0.97 ha in size.

At the center of each community garden, we established a 400 m^2 (20 × 20-m or 40 × 10-m) sampling plot in which to concentrate our observations. We adjusted the size of the sampling plot where necessary (i.e., where gardens were more narrow than they were wide, we created a 40 × 10-m plot). We visited the gardens four times approximately every four weeks from May to August 2021 (henceforth 'sampling round'): 13.-23. May 2021, 14.-24. June 2021, 20.-30. July 2021, 17.-26. August 2021. Between three and seven gardens were visited each day and the order in which they were visited was selected so that each garden was visited twice in the morning (08:30–11:30) and twice in the afternoon (12:00–17:30).

Focal plant species

Observation of focal plants is a simple and standardised method for monitoring flower-visiting insects (Roy et al. 2016). To compare flower visitor networks across community gardens, we selected both focal cultivated and wild plant species in each garden that were (a) in flower and (b) the main flower resource (species with the highest flower abundance) in the garden at that time period on which to conduct flower visitor observations. We define "cultivated" species as those that were intentionally sown or planted native or nonnative species in the gardens, classified either by taxonomic criteria (taxa only known as cultivated species or varieties) or traces of cultivation (i.e., cultivation in rows or beds, promotion by weeding). "Wild" growing species were species with exclusively spontaneous occurrences, that were not directly planted by humans. In some instances, a plant species was observed in both categories. The number of observed focal plants varied with flower availability in the different community gardens and sampling rounds. Between two and six different focal plant species were observed per sampling round and garden. Gardens were heterogenous in their vegetation composition, with only one plant species (*Fragaria ananassa*) occurring in all 30 community gardens (see Table 1). Within each garden, patches with the highest amount of focal plant individuals in flower were chosen for observations (one patch per focal plant species per sampling round). Only those observations were included in the analysis where more than two patches of one focal plant species were observed in all community gardens in one sampling round.

Flower visitor observations

To determine how flower visitor interactions across all 30 community gardens change in relation to changes with local floral and nesting resource factors and landscape imperviousness, we conducted visual flower visitor observations during the four sampling rounds. Observations were conducted by one observer to minimise observer bias and

Table 1 Focal plant species with common and scientific names, the number of observations on each species, the number of urban community gardens in which the species was observed and the vegetation type (w = wild, c = cultivated, c/w = cultivated or wild)

Focal plant species scientific name	Focal plant species common name	Number of observations	Number of gardens	Vegetation type
Fragaria ananassa	Strawberry	124	30	c
Trifolium pratense	Clover	80	29	w
Calendula officinalis	Marigold	89	28	c
Origanum vulgare	Oregano	53	28	c
Taraxacum officinalis	Dandelion	65	27	w
Borago officinalis	Borage	83	26	c/w
Cucurbita pepo	Pumpkin	28	26	c
Erigeron sp.	Erigeron sp.	26	26	w
Helianthus annuus	Sunflower	25	25	c
Hypericum perforatum	St. Johnswort	22	21	w
Eruca versicaria	Rucola	15	15	c/w
Ranunculus repens	Buttercup	14	14	w
Achillea	Yarrow	13	8	w
Glechoma hederacea	Creeping Charlie	13	8	w
Capsicum frutescens	Chili	7	8	c
Symphytum officinale	Comphrey	7	5	c/w
Ajuga reptans	Bugle	5	3	w
Aegopodium podagraria	Ground Elder	5	2	w
Alchemilla vulgaris	Lady´s Mantle	4	4	w
Thymus vulgaris	Thyme	3	3	c

occurred between 09:00 and 17:00 on mostly sunny days with temperatures > 13 °C. During each five minute observation, within an observation area consisting of a semicircle with a radius of 70 cm (0.77 m^2) placed in the centre of each focal plant patch (Fig. 1), we recorded the interactions between one focal plant species and 13 flower visitor groups selected because they are common in our system: honeybees, bumblebees, wild bees, butterflies, moths, flies, hoverflies, beetles, bugs, thrips, ants, social wasps, and solitary wasps. We observed all insect visitors that were in contact with the reproductive organs of a flower, identified them to a flower visitor group and counted the number of visits (i.e., one flower visitor individual can land on one plant individual and interact with multiple inflorescences) for each individual until it left the observation area. Where the number of flower visits per individual as well as the number of individuals was too high to count simultaneously, we calculated visitation rates for the specific plant-flower visitor pair (e.g. *Apis mellifera* and *Origanum vulgare*) by recording the number of flowers that one individual visits in 30 s three times and then averaging the three observations. Because pollination surveys and experiments were running at the time of the observations, we did not collect pollinating insects. Visual identifications of pollinator groups were conducted by a researcher trained in insect identification.

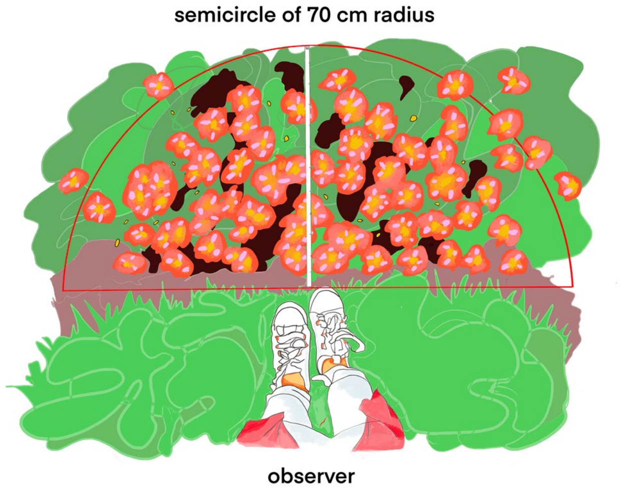

Fig. 1 Conceptual diagram of a flower visitor observation area consisting of a semicircle with a radius of 70 cm (0.77 m^2) placed in the centre of each focal plant patch, where all flower visitor interactions were recorded for five minutes. Illustration by Julia M. Schmack

Floral and nesting resources

We simultaneously measured floral resource availability (flower richness and abundance) as well as nesting resource availability (ground cover composition) within the community gardens for each sampling round at the same time as flower visitor observations. To do so, we randomly placed eight 1 × 1 m quadrats within the 20 × 20 m plots along four parallel 5 × 20 m transects (two random plots per transect) (following Seitz et al. 2022; Felderhoff et al. 2023; see for full description of vegetation sampling methods).

For floral resource availability, within these quadrats, we identified all flowering herbaceous plants (except grasses) to species level using Jäger (2016) and the Pl@ntNet app (https://plantnet.org/en/; Affouard et al. 2023) (see Seitz et al. 2022). In addition, we counted the total number of flowers within each quadrat. Flower species richness and total number of flowers was determined for each sampling round and then averaged per garden and across all four sampling rounds. When counting the number of flowers, we counted flowers inside inflorescences as individual flowers regardless of size.

For nesting resource availability, within each quadrat, we recorded the percentage of bare soil cover, mulch cover, rock cover, grass cover, herbaceous vegetation cover, and wood cover as our local garden scale land cover variables. We averaged ground cover data from these quadrats per garden and across all four sampling rounds. Here we consider bare soil cover as a proxy for nesting resources for ground nesting species following others (Felderhoff et al. 2023; Quistberg et al. 2016; Cohen et al. 2021).

Landscape imperviousness

To classify community gardens according to the degree of landscape urbanization, we used the amount of landscape imperviousness (i.e. sealed surface) surrounding the gardens as a proxy (von der Lippe et al. 2020). We collected publicly available data on landscape imperviousness for Berlin and Munich. We used the Geographical Information Systems software ArcGIS 10.5.1 (Environmental Systems Research Institute (ESRI) 2011) and the Copernicus High Resolution Layer: Imperviousness Density (IMD) 2018 (European Union, Copernicus Land Monitoring Service, European Environment Agency (EEA)) to measure the impervious surface in a 1000 m buffer around each garden. We selected this scale to measure how larger-scale landscape urbanization (as opposed to local land use (100 m)) influences flower visitor interactions. Imperviousness ranged from 17 to 83%.

Data analysis

We: (1) determined the dominant pollinator groups for the common focal plants in urban community gardens; (2) compared pollinator group diversity indices (richness and Shannon index) for each sampling round (May, June, July, August); (3) compared the number of flower visits by bee and non-bee flower visitors for each sampling round; and (4) assessed the relationship between plant-flower visitor network indices, landscape imperviousness, floral richness and abundance, garden size, and the availability of nesting sites.

1. What are the dominant flower visitor groups that interact with common cultivated and wild plants?

To assess the dominant flower visitor groups for focal plants in our study sites, we first determined five plant species that were most common in the surveyed community gardens across all four sampling rounds and second, summed up the number of visits they received from the 13 different flower visitor groups. To determine the number of visits realized by each flower visitor group, we averaged their number of visits per sampling round.

2. How do diversity indices of flower visitor communities change over the growing season?

To assess changes in the flower visitor community over the growing season (i.e., between monthly sampling rounds), we calculated the Shannon index and species richness for flower visitor groups for each round using the *vegan* package for R (Oksanen et al. 2007; R Development Core Team 2021) and compared them between each sampling round, using a non-parametric Kruskal–Wallis test and the non-parametric Dunn´s test (p-values adjusted with the Bonferroni method) to determine significant differences between sampling round means.

3. How does the number of flower visits by bee and non-bee flower visitors change over the growing season?

To test the contribution of bee and non-bee flower visitors to overall flower visitation, we summed flower visitor groups into bee pollinators (bumblebees, honeybees, wild bees) and non-bee flower visitors (butterflies, flies, hoverflies, moths, ants, bugs, beetles, thrips, social wasps, solitary wasps) and compared their average flower visits using the unpaired two-samples Wilcoxon rank sum test for non-parametric data. To assess the contribution of bee and non-bee flower visitors to overall flower visitation across the monthly sampling rounds, we compared the average flower visits of bee and non-bee flower visitors, respectively, using a non-parametric Kruskal–Wallis test and the non-parametric Dunn´s test (p-values adjusted with the Bonferroni method). We also tested for differences in the number of flower visits between bee and non-bee flower visitors across the monthly sampling rounds using non-parametric Wilcoxon Signed Rank tests.

4. How do flower visitor networks change with changes in floral diversity, nesting resource availability and landscape imperviousness?

To explore how flower visitor networks change with changes in landscape imperviousness and with changes in floral richness and abundance, we created bipartite networks of flower visitor interactions using the "bipartite" package in R (v. 2.13, Dormann et al. 2008). Bipartite networks are used to visualize interactions within webs consisting of two levels, in our case plants and flower visitors, and calculate indices commonly used to describe ecological networks (see below) (Bascompte and Scheffer 2022; Daniels et al. 2020; Ballantyne et al. 2017). We created bipartite networks using the data of visual counts of visits between arthropods grouped into flower visitor groups and the flowering structure of a focal plant. The resulting networks allow for testing hypotheses about flower visitor diversity and network complexity across differences in amounts of landscape imperviousness, garden size, nesting resource availability and floral richness and abundance.

We used the *networklevel* function in "bipartite" (Campbell et al. 2011; Mariani et al. 2019) to calculate multiple indices that describe network structure and interactions within a network. For our study, three network-level indexes were chosen to represent a variety of commonly used indexes in community ecology: i) connectance, ii) linkage density, and iii) nestedness (*NODF*). Connectance (C) measures the fraction of interactions that occur in the network, out of all possible interactions. Linkage density (*LD*) is calculated as the average number of links per species in a network, but weighted by the average number of interactions across the species (Dormann et al. 2009; Bersier et al. 2002). Nestedness describes the extent to which specialists interact with a subset of species that also interact with generalists; this metric is based on overlap and decreasing fill. Nestedness can have important implications for network stability; a highly nested network is thought to be more robust to species extinctions, as species that interact with fewer partners are more likely to be lost due to environmental disturbance or stress (Almeida-Neto et al. 2007).

To examine which environmental factors drive changes in flower visitor networks, we used generalized linear models (GLMs) with the glm function in R (R Development Core Team 2021). We used connectance, linkage density, and nestedness (NODF) as dependent variables. For our predictor variables, we first identified variables that were significantly correlated with one another (using the *cor* function in "stats" (R Core Team)) and selected the one with the highest correlation coefficients with other variables to include in the analysis. Floral richness was not correlated with the level of urbanization within a 1000 m buffer around the community gardens (Spearman's rho = -0.068, $P > 0.05$). We selected a total of five explanatory variables: percent landscape imperviousness surface (1000 m buffer), garden size, floral richness (number of flowering plant species), floral abundance (number of flowers), percent bare soil cover. For all dependent variables, we tested for normal distribution using the Shapiro Wilk test and since they followed normal distribution, we used a Gaussian distribution as this provided the best fit. We used model selection and model averaging (Burnham and Anderson 2002). We fitted separate global models for the three response variables linkage density, nestedness and connectance. We derived a full set of models with all possible combinations of fixed effects from each global model. Next, we applied an information theoretic approach to determine a set of best models, including all models within a range of $\Delta\text{AICc} \leq 2$ (Akaike's information criterion for small sample sizes) relative to the best model. To gain weighted averages of parameter estimates from the respective set of best models, model averaging was used (Burnham and Anderson 2002). The *stats* (R Core Team) package was used to fit GLMs (Bates et al. 2012), and the "MuMIn" package was applied for model averaging (Barton 2016).

All analyses were performed in the R Statistical Environment (version 4.0.2; R Core Team 2021).

Results

In total, we conducted 692 visitor observations over 58 h of 22 focal plant species across all sampling rounds during which we observed a total of 3,503 flower visitor individuals and 76,638 flower visits.

The number of flower visits differed significantly between bee and non-bee flower visitor groups of focus ($P = 0.0034$), with bee-pollinators performing 22 times the number of flower visits compared to non-bee flower visitors. On average, across community gardens and sampling rounds, honeybee individuals visited 52.9 flowers (SD ± 583.3 flowers), wild bee individuals visited 4.7 flowers (SD ± 30.8 flowers), bumblebee individuals visited 48.6 flowers (SD ± 252.4 flowers), and hoverflie individuals visited 2.2 flowers (SD ± 5.3 flowers).

Dominant flower visitor groups for common garden plants

Interactions between the five most observed focal plant species and their flower visitor groups are presented in Table 2. Some focal plants were visited by either bee or non-bee flower visitors. For example, lavender (*Lavendula angustifolia)* was visited by bee pollinators, but not by non-bee flower visitors, while common yarrow (*Alchemilla vulgaris)* and daisies (*Bellis perennis)* were visited exclusively by non-bee pollinators.

Table 2 Number of visits between flower visitor groups and the five most frequently observed focal plants in the surveyed urban community gardens: strawberry (*Fragaria ananassa*), clover (*Trifolium pratense*), marigold (*Calendula officinalis*), dandelion (*Taraxacum officinale*), and oregano (*Origanum vulgare*)

Pollinator group	*Fragaria ananassa*	*Trifolium pratense*	*Calendula officinalis*	*Taraxacum officinalis*	*Origanum vulgare*
Bumblebees	0	466	27	0	14,929
Honeybees	57	801	351	42	36,899
Wild bees	89	78	267	15	656
Flies	66	29	95	45	599
Hoverflies	12	52	41	2	63
Butterflies	0	0	1	1	137
Moths	0	96	0	0	0
Beetles	24	24	92	47	8
Bugs	3	1	2	1	3
Ants	186	56	2	47	13
Thrips	4	4	60	0	0
Solitary wasps	2	4	6	4	20
Social wasps	2	0	1	0	3

Changes in diversity indices of flower visitors over the growing season

Average flower visitor diversity (Shannon index) varied significantly across sampling rounds (Kruskal–Wallis test, *Chi*=12.442, $p=0.006$) (Fig. 2). Flower visitor diversity was significantly lower in May than in August (Dunn´s test, $z=-3.203$, $p=0.004$). Richness of flower visitors varied significantly across sampling rounds (Kruskal–Wallis test, *Chi*=21.424, $p<0.001$). Flower visitor richness was significantly lower in the earlier than in the later sampling rounds; it was lower in May than in July (Dunn´s test, $z=-4.362$, $p<0.001$), in July than in August (Dunn´s test, $z=-3.086$, $p=0.005$), and in June than in July (Dunn´s test, $z=-2.812$, $p=0.01$).

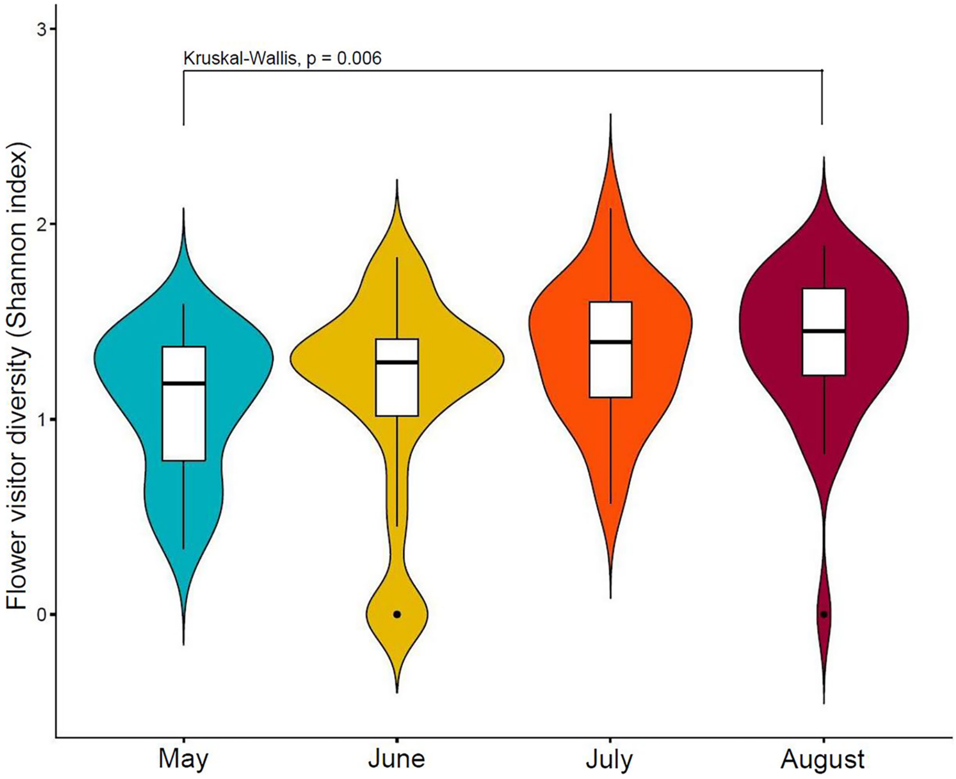

Fig. 2 Violin plots of flower visitor diversity (Shannon index) for each sampling round (May, June, July, August) where flower visitors were observed in 30 urban community gardens in Berlin and Munich, Germany. Violin plot outlines illustrate kernel probability density. Integrated boxplots indicate the median and quartiles with whiskers reaching up to 1.5 times the interquartile range

Changes in the number of flower visits by bee and non-bee flower visitors over the growing season

Across all focal plant species and all observations, there was a significant difference in flower visitation (Wilcoxon test, $W = 260{,}499$, $p = 0.002$) between bee pollinators (bumblebees, honeybees, wild bees) (mean flower visits = 106 ± 654.75) and non-bee flower visitors (butterflies, flies, hoverflies, moths, ants, bugs, beetles, thrips, social wasps, solitary wasps) (mean flower visits = 4.77 ± 23.67), with bee pollinators visiting significantly more flowers over the entire sampling than non-bee flower visitors. Flower visitation by both bee pollinators and non-bee flower visitors changed significantly across the growing season (Kruskal–Wallis test, $Chi = 120.91$, $p < 0.001$; $Chi = 11.184$, $p = 0.011$, respectively) (Fig. 2). Bee pollinators visited significantly less flowers in May than in June, July and August (Dunn´s test, $z = -3.802$, $p < 0.001$, $z = -9.893$, $p < 0.001$, $z = -8.318$, $p < 0.001$; respectively), and in June than in July and August (Dunn´s test, $z = -6.204$, $p < 0.001$; $z = -4.523$, $p < 0.001$, respectively). Non-bee flower visitors visited significantly more flowers in May than in June (Dunn´s test, $z = 3.297$, $p < 0.001$).

In May, non-bee flower visitors visited significantly more flowers than bee flower visitors (Wilcoxon test, $W = 8618$, $p < 0.001$) (Fig. 3), with bees providing 1.02 ± 2.55 mean flower visits and non-bees providing 2.56 ± 2.97 mean flower visits (number of visits averaged per season). There was no significant difference in the number of flowers visited by bee and non-bee visitors in June ($p > 0.05$). In July and August, bee pollinators visited significantly more flowers than non-bee flower visitors (Wilcoxon test, $W = 18{,}552$, $p < 0.001$, $W = 20{,}981$, $p < 0.001$, respectively).

The effect of changes in floral resources, nesting resources, garden size and landscape imperviousness on flower visitor networks

Flower visitor networks increased in nestedness (nestedness) with increasing floral richness in community gardens (Table 3 and Fig. 4). The best model explaining nestedness included floral richness abundance and garden size, however, only floral richness was siginificantly correlated. The availability of nesting resources (percent bare soil cover) and floral abundance and garden size was not significantly associated with changes in flower visitor networks (linkage density and connectance). Floral abundance was included in the best model explaining changes in likage density and floral abundance and richness, garden size and landscape urbanization were included in the best model explaining changes in connectance (Table 3).

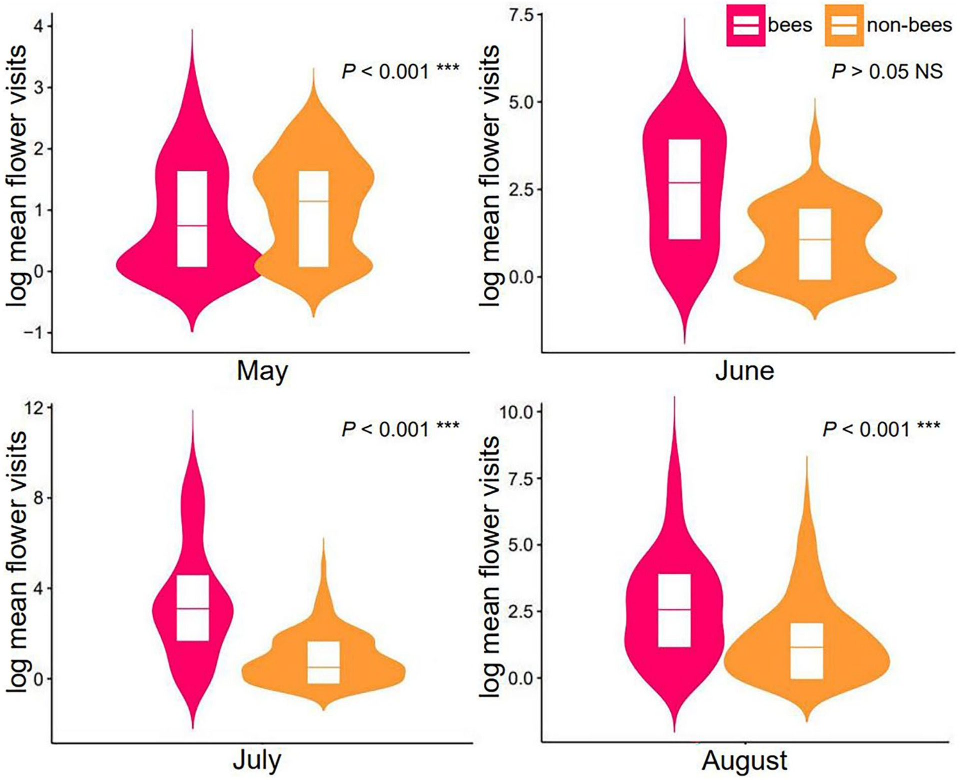

Fig. 3 Violin plots of mean number of flower visits for bee pollinator groups (honeybee, bumblebee, wild bee) and non-bee flower visitor groups (butterflies, moths, flies, hoverflies, beetles, bugs, thrips, ants, social wasps, solitary wasps) per sampling round (May, June, July, August). Axes of response variables (number of flower visits) are logtransformed.. Violin plot outlines illustrate kernel probability density. Integrated boxplots indicate the median and quartiles with whiskers reaching up to 1.5 times the interquartile range

Table 3 Results of Generalized Linear Models examining the relationships between environmental factors floral richness and abundance, garden size and landscape urbanization (imperviousness in a 1000 m buffer around the community gardens) of urban community gardens and flower visitor network metrics across all studied gardens. Presented are the fully averaged results of the best models after model selection. The availability of nesting resources was not significantly associated with changes in flower visitor interactions and not included in any of the selected models

Fixed Parameter	# Models	Estimate	SE	P
Linkage density				
Floral abundance	1	-2.584e-04	2.845e-04	0.373
Connectance				
Floral abundance	1	3.121e-05	3.533e-05	0.387
Floral richness	2	1.413e-02	1.662e-02	0.405
Garden Size	3	-3.467e-06	5.694e-06	0.549
Urbanization	4	3.149e-03	6.249e-04	0.620
Nestedness				
Floral abundance	1	0.001009	0.003292	0.759
Floral richness	2	9.012957	2.595239	0.001 ***
Garden Size	3	-0.000281	0.000698	0.695

Discussion

The interactions between plants and their flower visitors underly a key ecosystem function in urban agroecosystems, namely pollination. Our study on flower visitor interactions in 30 urban community gardens in two of Germany's most populated cities shows that both bee and non-bee flower visitors are important visitors of common wild (e.g. *T. pratense, T. officinale*) and cultivated (e.g. *F. ananassa, C. pepo*) garden plant species. Yet, who are the most frequent flower visitors changes over the growing season, with bee flower visitors dominating most of the season and non-bee flower visitors providing the majority of visits in the early season (May).. Neither landscape imperviousness nor garden size, floral abundance and nesting resource availability strongly influenced flower visitor networks, but floral richness increased network nestedness. Thus, city residents through their gardening practice, play a key role in mediating plant-pollinator interaction stability, and thereby, likely pollination provision.

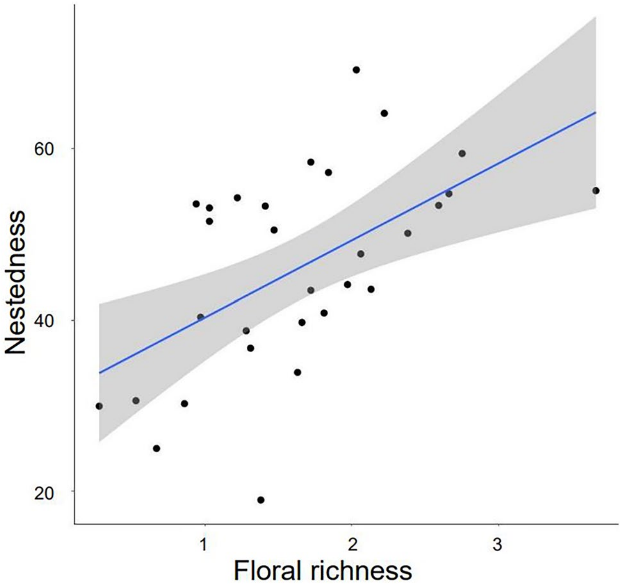

Fig. 4 Nestedness (NODF) of the networks in 30 urban community gardens (network indices calculated for each garden) was best explained by average floral richness. Closed circles denote mean values for each garden. Shaded area around fitted trend line indicates 95% confidence interval. Significance taken at alpha = 0.05

Most frequent flower visitors of common garden plants

Not just bee, but non-bee flower visitors are common visitors of plants that are prevalent in urban community gardens. We found that wild bees, bumblebees and honeybees were the dominant flower visitors in the urban community gardens. However, non-bee flower visitors (butterflies, moths, flies, hoverflies, beetles, bugs, thrips, ants, social wasps, solitary wasps) are important flower visitors particularly early in the growing season when early blooming and economically important crops (i.e., strawberry) need insect pollination, but also when many wild plants including spring ephemerals are in bloom. Thus, for these plants, non-bee flower visitors may fill a temporal niche in pollination function for early flowering wild and cultivated plants, and potentially play an important role as 'back-up' pollinators in cooler conditions in the early season.

Our results support the importance of non-bee flower visitors belonging to the orders Diptera, Coleoptera and Hymenoptera for crop production. In a recent meta-analysis of 1,022 studies, Rader et al. (2020) show that 77% of 105 crops analyzed were visited by both bee and non-bee pollinators, and that the second most dominant flower-visiting order was Diptera (72% of crops), followed by Lepidoptera (54%) and Coleoptera (51%). In particular, hoverflies (order; Diptera; family Syrphidae) were the most dominant non-bee flower visitors, visiting over half of all crop species (Rader et al. 2020). In addition, our results are in line with a study from 33 farms in the UK, which found that non-syrphid Diptera comprise a majority of all flower-visiting Diptera (on average 82% abundance and 73% species richness), providing an estimated 84% of total pollen transport (Orford et al. 2015). We see similar dominance patterns in our system: ants and beetles and flies dominated overall flower visits early in May. The life histories of these common non-bee flower visitors may suggest resource use complementarity among non-bee visitors in the community gardens. For example, flies are often attracted to white flowers, ants to those flowers that offer high nectar rewards or extrafloral nectaries, while beetles to bowl-shaped flowers (Campbell et al. 2010; Fenster et al. 2004; Faegri and Van der Pijl 1979). In addition, these species all have large differences in their thermoregulation, a key factor in the foraging energetics of flower-visiting insects (Hegland et al. 2009). While ants are able to utilize flowers in spring and early summer when temperatures are still cool, many wild bees can only utilize flowers when average temperatures increase later in the summer. This may explain why we see shifts in pollinator floral visitation over the growing season.

Flower visitor communities, and their interactions with plants, change over the growing season

The shifts in flower visitation dominance over the growing season suggests that bee and non-bee flower visitors may provide complimentary pollination services over time in these community gardens. On average, bee pollinators deposit more pollen than non-bee pollinators (Rader et al. 2016; Orford et al. 2015) due to high efficiency, visitation rates and population numbers. However, even if non-bee flower visitors are less efficient at pollen deposition, these pollinators were the most frequent flower visitors in the early season here. This suggests that these flower visitors may be important pollinators for early spring flowering crops and ephemerals in community gardens. Although we include ants in our analysis as they are present in the system, we acknowledge that ants may be less efficient or even disruptive pollinators (Samra et al. 2014; Beattie et al. 1984; but see also Natsume et al. 2022).

Our work shows that we should consider the role of non-bee flower visitors for early season pollination service provision. These early season flower visitors may be increasingly important for the stability and maintenance of pollination in urban ecosystems, especially given bee pollinator declines and temporal variability that threatens bees. Future research should investigate the importance of non-bee flower visitors in the “shoulder” (early, late) seasons and explore potential synergies across multiple ecosystem services, such as natural pest control (Lundin et al. 2021). For example, some insect taxa are both efficient flower pollinators and pest predators in their adult stages (wasps and tachinid flies, Brock et al. 2021; Klein et al. 2002) or larval stages (hoverflies, Hodgkiss et al. 2018; Orford et al. 2015; Jauker and Wolters 2008). This may be especially important in the early season when some crops are flowering, but also young crops are most vulnerable to pests. Understanding how these complementary services can be utilized in an agricultural context may reduce pesticide applications and therefore lower the pressure on the beneficial insect communities (Egan et al. 2020). Our work emphasizes that urban gardeners play a key role in influencing interactions between their garden plants as well as wild plants and flower visitors, and thereby likely in pollination service provision.

In our study, we observed both wild and cultivated flowering plants in the community gardens, and some differences between plant type may explain the structure of networks. While the main pollinators of *O. vulgare* and *C. officinalis* were honeybees and wild bees, *T. pratense* and *T. officinale*) were mainly visited by non-bee flower visitors (ants and hoverflies, ants and beetles, respectively). The main flower visitors of *F. ananassa* were ants and wild bees. We note that focal plant species varied across community gardens due to garden heterogeneity, meaning that some flower visitors may be specialized on certain plant species that only occurred in some gardens (i.e. *Thymus vulgare*) and we could not control for this. Future research could expand to longer observations on e.g., experimental plants (Rivkin et al. 2020) to account for this variation. We further note that flowering woody species in the community gardens may have had an effect on network structure because they can offer prolific nectar and pollen resources, and can reduce focal plant visitation (‘dilution effect’, Yamamura 1999). Yet our work provides a realistic picture of common garden plants in situ, and their common flower visitors and interaction networks.

Floral diversity, but not landscape imperviousness nor nesting resource availability or garden size, modulates flower visitor interactions

In support of our hypothesis, network complexity (nestedness) increased with floral richness in community gardens. The influence of floral resources has been shown to support pollinators and influence their interactions over the season (Staab et al. 2020; Tasker et al. 2020). Yet, surprisingly, contrary to our hypothesis, neither landscape imperviousness nor nesting resource availability or garden size strongly influenced flower visitor interactions. We would expect that urban landscape imperviousness would alter flower visitor networks by reducing the number of flower visitor species (Bates et al. 2011) and changing the number of interactions between plant and flower visitor species (Geslin et al. 2013).

The lack of an effect of landscape could be explained by the local-scale effect of floral resource availability shown here and elsewhere (Wenzel et al. 2020), where floral resources mediate potential landscape-scale resource loss on network complexity. Flower visitor network complexity (nestedness) may increase or maintain network stability in urban habitats if floral resources are available and diverse, also if floral resources are low in the surrounding rural landscape (Theodorou et al. 2017). Yet studies show largely mixed results on these ‘mitigation effects’. Udy et al.

(2020) show that although plant richness increased along an urbanization gradient (from city to village to farmland habitat), plant-pollinator network complexity decreased with increasing landscape imperviousness, concluding that cities hold rather poor pollinator communities and unstable networks. A study from Germany also found that although floral richness was higher in urban than in rural areas, bees visited a lower proportion of the available plants in cities than in rural habitats (Theodorou et al. 2017).

Of course, the differences in how network complexity responds to floral resources or landscape imperviousness largely depends on how the individual pollinators respond to these factors. For example, some pollinator groups, particularly bees, thrive in urban ecosystems and even exceed rural agricultural ecosystems in species richness and reproductive success (Casiker et al. 2021; Theodorou et al. 2020a, b; Theodorou et al. 2017; Baldock et al. 2015; Turrini and Knop 2015), while other pollinator groups such as hoverflies, are negatively affected by increases in landscape imperviousness (Persson et al. 2020; Bates et al. 2011; but see also Olsson et al. 2021). Geslin et al. (2013) conclude that hoverflies and solitary bees are more impacted by landscape imperviousness than bumblebees because they mostly visit open flowers while bumblebees visit flowers belonging to a different functional group.

The structure of flower visitor networks, and how it changes across land-use gradients, is relevant because network complexity can in turn influence pollination service provision (Tscharntke 2021), where increased pollinator richness and visitation can increase fruit and seed weight of crop plants (Lowenstein et al. 2015). Rivkin et al. (2020) have shown that negative effects of landscape imperviousness on flower visitor networks result in reduced plant reproductivity. What remains to be determined is how network complexity relates to pollination services of wild and cultivated plants in urban community gardens.

Conclusion

In sum, in our system, the main flower visitor communities change over the growing season, with bee and non-bee flower visitors differing in visitation dominance. Furthermore, the availability of flower resources, especially floral richness determines flower visitor network complexity, suggesting that local habitat scale factors and thus gardeners can influence flower visitor interactions in their gardens. Interestingly, and perhaps counterintuitively, this is regardless of the extent of urbanization surrounding the gardens and garden size. Here, gardeners can enhance floral diversity through both crop and non-crop plants that flower at different times of the season to their urban community gardens. Such efforts may provide benefits to gardeners through pollination provision, and may also help to mitigate the loss of insect habitats due to urban land use change and promote insect diversity and conservation at the local habitat scale.

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Author contributions JMS and ME designed the study; JMS collected the data, analysed the data, prepared the figures and led the writing; all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Summarised data will be uploaded on Dryad Digital Repository upon instruction.

Declarations

Ethics approval Not applicable.

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