

RESEARCH ARTICLE

Home sweet home: Evaluation of native versus exotic plants as resources for insects in urban green spaces

Doris Lerch¹  | Nico Blüthgen¹ | Karsten Mody^{1,2}

¹Ecological Networks, Technical University of Darmstadt, Darmstadt, Germany

²Department of Applied Ecology, Hochschule Geisenheim University, Geisenheim, Germany

Correspondence

Doris Lerch

Email: d.lerch65@t-online.de

Karsten Mody

Email: karsten.mody@hs-gm.de**Funding information**

Technische Universität Darmstadt

Handling Editor: Molly Mitchell**Abstract**

1. Insect decline and loss of biodiversity not only affect large-scale agricultural landscapes, but are increasingly recognized in urban environments. It is undisputed that a greater supply of flowers in urban green spaces can provide insects with more food and habitat. However, it is still controversial whether native wild plants or non-native ornamental plants and varieties are the right choice.
2. To answer this question we investigated the number of insects interacting with different types of plants: twelve ornamental and six related wild perennials. In this context, the number of flower visitors per plant species and plot was recorded at 10-minute observation intervals, as well as the feeding damage caused by insect herbivores on the leaves and stems of the study plants. We established 18 plant species in ten independent study plots in the city of Darmstadt, Germany. The plants were six native wild plant species, six ornamental plant species related to the wild plants from the same genus or family and six exotic ornamental plant species from other genera and families than the wild plants.
3. Native insects (wild bees, flies, beetles, wasps) that feed on pollen and nectar visited wild perennials significantly more often (67% of all visits) than related ornamental (24%) and unrelated exotic plants (9%). In contrast, honey bees (*Apis mellifera*) showed no preferences to any of the three target plant groups and interacted with other plant species than most of the native insects in our study according to analyses of interaction networks.
4. The assessment of leaf damage caused by insect herbivores on the individual plants confirmed a similar and significant difference in the insects' choices. Leaves from wild plants showed the highest herbivory (mean 2.3% of the leaf area), followed by related ornamental plants (0.8%), whereas unrelated exotic plants were hardly consumed (0.1%) by herbivores.
5. *Practical implication.* Our study shows that in urban green spaces, both flower-visiting and leaf-feeding insects are more likely to use native wild plants as a food source than closely related and exotic ornamental plants.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Author(s). *Ecological Solutions and Evidence* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

KEYWORDS

biodiversity, herbivores, honey bee, insects, leaf damage, native plants, non-bees, non-native plants, pollinator, urban green space

1 | INTRODUCTION

Insect decline and biodiversity loss have become terms we are confronted with on a regular basis. In 2017, the so-called “Krefeld Study” drew the attention of the general public to this topic. The core finding of the study was the decline of the biomass of all flying insects by 75% over 27 years (Hallmann et al., 2017). These alarming observations were supported by further work in the following years. For example, Seibold and colleagues demonstrated a similarly strong decline in individual and species numbers across all trophic levels between 2008 and 2017 in 150 grasslands (Seibold et al., 2019). If this trend is not halted, living conditions in the world will change drastically for us humans. Without the pollination services of insects, for example, 35% of global food production, including most fruits and vegetables, would be lost (Schowalter, 2020). In principle, only a high species richness at the various trophic levels can maintain ecosystem functions (Soliveres et al., 2016).

Already today, almost 60% of wild bees are considered endangered in Germany (Chemnitz et al., 2020). However, the honey bee (*Apis mellifera* L.) is still very popular with people, and the number of bee colonies in Germany has increased by 52% between 2007 and 2021 (Ahrends, 2022). The honey bee, which originates mainly from beekeeping, is no longer considered a wild insect, having been adapted to the needs of beekeeping through decades of breeding work (Tiesler et al., 2016). In addition to bees, the so-called non-bee pollinators also play an important role in the pollination performance of insects in agricultural landscapes. The non-bees include flies (Diptera), beetles (Coleoptera), moths and butterflies (Lepidoptera), wasps (non-bee and non-ant Hymenoptera) and ants (Hymenoptera, Formicidae). Non-bees provide 25–50% of the total number of flower visits (Rader et al., 2016). For example, cherry trees are 50% pollinated by flies (Larcenaire et al., 2021). Another advantage of non-bees is that they may be less sensitive than bees to changes in land use (Rader et al., 2016). If non-bees and bees pollinate the same crops, increased ‘response diversity’ may lead to stabilization of pollination performance (Elmqvist et al., 2003; Schmack & Egerer, 2023). Furthermore, visitation by diverse wild bees and non-bees promotes fruit and seed set of crops more than increased visitation by honey bees (Rader et al., 2016). In addition to pollination services, flower-visitors such as parasitic wasps, predatory flies/larvae and beetles are of great importance in biological crop protection (Khan et al., 2018). The value of natural pest control by insects has been estimated at 4.5 billion USD per year for the United States alone (Losey & Vaughan, 2006).

The causes of insect decline are manifold, but one of the main causes is the massive loss of suitable habitats due to agriculture

(Chemnitz et al., 2020), soil sealing (Umweltbundesamt, 2022), but also general urbanization (Wagner et al., 2021). Cities are rapidly expanding, and by 2060, two-thirds of the world's population is expected to live in cities (Menke, 2016). Living green spaces in cities today are an important tool for improving the urban climate, reducing pollution and creating recreational opportunities and social meeting places for people as well as habitats for animals and plants, including refuges from impacts by pesticides and intensive agriculture (Menke, 2016). With regard to animals and plants in urban areas, it is now known that private gardens, which can provide a high quality and quantity of flowers and nesting sites in a confined space, can make an important contribution to increasing biodiversity (Baldock et al., 2015; Hall et al., 2017; Wenzel et al., 2020). For example, 115 species of wild bees were observed in a 320-m² private garden in Tübingen, Germany (Zurbuchen & Mueller, 2012). Can public urban green spaces also help to protect the insect fauna? Until a few years ago, frequently mown park lawns and changing beds of flowering plants, also called flower borders, were the typical planting of urban green spaces. These areas, often re-planted annually or up to three times a year, were characterized by a rich display of flowers and colours. To achieve this, non-native ornamental plants and varieties were often used. In recent years, some municipalities have changed their maintenance practices so that they now only mow once or twice and create permanent planting beds to counteract the decline in insects (Mody et al., 2020).

It is undisputed that a wider range of flowers in public green spaces can provide insects with more food (Erickson et al., 2022; Wenzel et al., 2020). However, it is still controversial whether native wild plants (“**NATIVE**”; in our study: indigenous species according to FloraWeb; FloraWeb, 2024), or closely related, non-native ornamental and long-established plants from neighbouring flora areas (hereinafter “**RELATED**”), or the so-called exotics that come from other continents (“**EXOTIC**”) are the right choice for the targeted promotion of insects (Ayers & Rehan, 2021; Berthon et al., 2021). The value and attractiveness of plants vary widely to pollinating and herbivorous insects (Baisden et al., 2018; Garbuzov & Ratnieks, 2014). In addition, breeding-related changes, e.g. in flower or leaf characteristics, can have a negative impact on the number or species composition of plant-associated insects (Comba et al., 1999; Wenzel et al., 2020).

To answer the general questions (a) which plant groups (NATIVE, RELATED or EXOTIC plants) are more suitable as food source and habitat for native wild insects and (b) whether there are differences between insect groups, including honey bees, in terms of their plant preferences, we addressed the following research questions:

1. Which plant group is most attractive to flower-visiting insects and supports the highest number of species?

- Are there differences in the use of flowers by “wild” flower visitors and *Apis mellifera*?
- Are flower visitor-interactions more specialised among native than non-native plants, and more generalised for honey bees?
- Which plant group is most suited as a host for herbivorous insects?

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted in the independent city of Darmstadt (160.000 inhabitants, 122km² urban area) in southwest Germany (49°52'20"N, 8°39'10"E). The permit to remove and, if necessary, kill wild insects was issued by the Darmstadt Environmental Agency on 14 September 2020 under the reference UNB.60.012. In autumn 2020, a total of 10 planting beds were created in the urban area in spatially separated plots of nine square metres each for next year's survey. These planting beds are referred to below as study plots. The existing vegetation was removed, and a total of 328 native wild perennials (NATIVE) and 606 ornamental perennials were planted. The ornamental perennials were divided into the groups of native plant-related ornamental perennials (RELATED) and exotic perennials (EXOTIC).

The plots for the planting beds were chosen to be spatially independent (the distance between the individual plots was between 150 and 2.100metres) on the one hand, and to reflect the diversity of inner-city green-spaces on the other. The degree of greening around the planting beds varied greatly. It ranged from complete sealing by surrounding footpaths to narrow green strips between buildings, car parks or streets to larger or extensively greened areas such as parks and cemeteries.

The study plants (Table 1) were selected in a stepwise procedure. Ornamental perennials were chosen on the basis of a list of all ornamental plant species used in the urban area compiled by the Darmstadt Parks Department. For the group of RELATED ornamental perennials, six plant species from five different families were selected, for which there are native perennials that are related at genus or family level and are similar to the ornamentals in flower morphology (*Achillea clypeolata* 'Moonshine', *Campanula portenschlagiana* 'Birch', *Centaurea dealbata*, *Knautia macedonica* 'Mars Midget', *Salvia verticillata* 'Purple Rain', *Thermopsis chinensis*). Accordingly, six native wild plant species representing the NATIVE group were selected to match the RELATED ornamental plants (*Achillea millefolium*, *Campanula rotundifolia*, *Centaurea jacea*, *Knautia arvensis*, *Salvia pratensis*, *Lotus corniculatus*). The second group of ornamental plants, the EXOTIC ornamentals, were also chosen on the basis of a list of all ornamental plant species used in the urban area compiled by the Darmstadt Parks Department. EXOTIC ornamentals included species whose plant families are only sparsely represented in Europe (*Asclepias tuberosa*,

TABLE 1 Overview of plants used in the study.

Botanical name	Short name	Family
Wild plants = NATIVE		
<i>Achillea millefolium</i>	Ach_mil	Asteraceae
<i>Campanula rotundifolia</i>	Cam_rot	Campanulaceae
<i>Centaurea jacea</i>	Cen_jac	Asteraceae
<i>Knautia arvensis</i>	Kna_arv	Dipsacaceae
<i>Salvia pratensis</i>	Sal_pra	Lamiaceae
<i>Lotus corniculatus</i>	Lot_cor	Fabaceae
Ornamental plants = RELATED		
<i>Achillea clypeolata</i> 'Moonshine'	Ach_cly	Asteraceae
<i>Campanula portenschlagiana</i> 'Birch'	Cam_por	Campanulaceae
<i>Centaurea dealbata</i>	Cen_dea	Asteraceae
<i>Knautia macedonica</i> 'Mars Midget'	Kna_mac	Dipsacaceae
<i>Salvia verticillata</i> 'Purple Rain'	Sal_ver	Lamiaceae
<i>Thermopsis chinensis</i>	The_chi	Fabaceae
Exotic plants = EXOTIC		
<i>Asclepias tuberosa</i>	Asc_tub	Asclepiadaceae
<i>Kniphofia uvaria</i> 'Grandiflora'	Kni_uva	Asphodelaceae
<i>Agastache × cultorum</i> 'Blue Boa®'	Aga_cul	Lamiaceae
<i>Gaura lindheimeri</i> 'Whirling Butterfly'	Gau_lin	Onagraceae
<i>Helenium × cultorum</i> 'Rubinzweg'	Hel_cul	Asteraceae
<i>Cerastigma plumbaginoides</i>	Cer_plu	Plumbaginaceae

Cerastigma plumbaginoides, *Kniphofia uvaria* 'Grandiflora'). This group included the Asclepiadaceae, which occur predominantly in the tropics (Asclepiadaceae, 2001), the Plumbaginaceae, which are native to semi-deserts and steppes as well as coastal and dune landscapes worldwide (Plumbaginaceae, 2001), and the Asphodelaceae, whose main distribution area is southern Africa (Asphodelaceae, 2001). On the other hand, cultivated lines of North American plants widely used in private and public flowerbeds were selected, including the Fragrant Nettle *Agastache × cultorum* 'Blue Boa®' with one Asian (*Agastache rugosa*) and one unknown parent (Google Patents, 2022), *Gaura lindheimeri* 'Whirling Butterfly' and *Helenium × cultorum* 'Rubinzweg'.

The planting of the 18 study plant species took place on all plots according to a previously determined planting scheme. The position of each species per plot was determined by drawing lots, whereby the pairs of ornamental/wild plant were not allowed to stand exactly next to each other. Each plant species was allocated half a square metre as planting bed. Depending on the expected plant size, three to seven plant individuals per species were used, a specification based on the planting recommendations of the Gaißmayer perennial nursery (Gaißmayer, 2020) (Figure 1A).

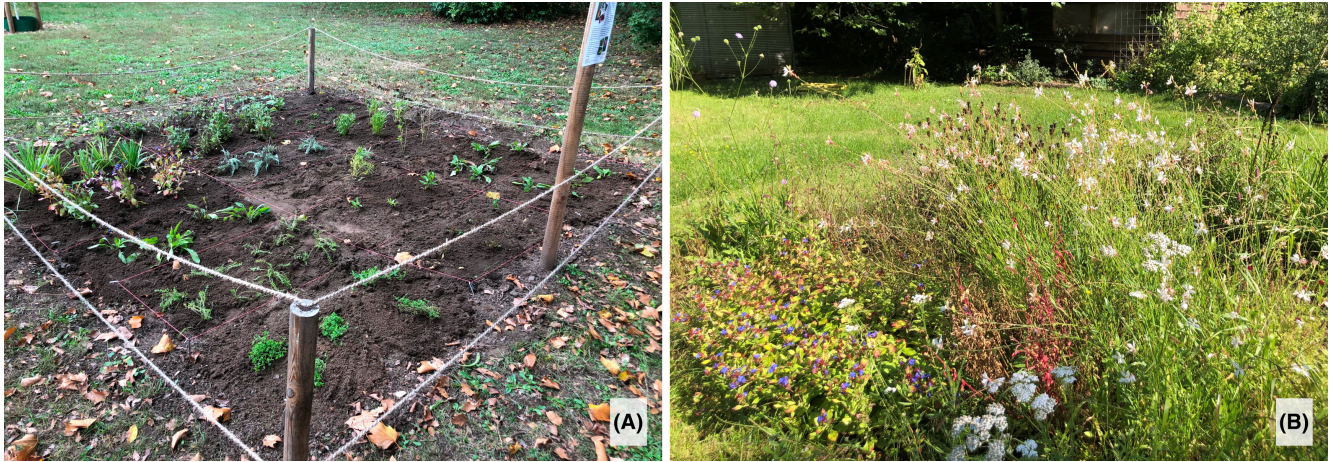


FIGURE 1 (A) Example of a freshly planted bed; (B) Example of a flowering bed at the time of data collection.

2.2 | Recording of flower visitors

Data were collected between 29 May and 19 September 2021 at the time of peak flowering of each plant species (Figure 1B). All flower visitors were surveyed once during a continuous 10-minute survey period per plant species and plot between 9:15am and 5:00pm (1550minutes in total). Insect individuals that could not be clearly identified in the field were collected and later identified in the laboratory. Identification was based on the specific literature for each insect order or family. For example, wild bees were identified using the identification tables of Scheuchl (Scheuchl, 1996). It was not always possible to identify the species precisely, so that the taxa designated as species also contained individuals that could only be identified at the family or genus level. These flower visitors were then designated as morphospecies, for example, *Andrena* 1 and *Andrena* 2 (Table 2). To address potential differences in their relationship to flower characteristics, we considered flower visitors in total as well as specific target groups including: (1) “Total Visitors” excluding *Apis mellifera* and Heteroptera; (2) “*Apis mellifera*”; (3) “Wild Bees” excluding *Bombus*; (4) “*Bombus*”; (5) “Non-Bees” such as Lepidoptera, Coleoptera, Diptera and (6) “Wasps”, which included members of the Crabronidae, Chrysididae, Ichneumonidae, Vespidae and Chalcidoidea.

True bugs (Heteroptera) were excluded from some analyses or considered in a separate way as they feed predominantly on plant juices or as predators. Honey bees (*Apis mellifera*) originated from domesticated beehives (Büchler et al., 2008) and were thus treated separately.

2.3 | Recording of interaction networks

Pollination is a central part of the life cycle of seed plants, and many plant species have a reciprocal relationship with animals (Futuyma & Slatkin, 1983). The plant–pollinator interaction network describes the links between the interacting communities of plant species and plant-visiting insect species (pollinators); (Olesen et al., 2007). In our

study, the plant–pollinator networks comprised 17 plant species (*T. chinensis* did not flower on any plot and was therefore not used) and 91 insect species. These interactions are typically heterogeneous, and many species have a low number of interaction partners and few species have a high number (Jordano et al., 2003). We used two indices to describe the exclusiveness (specialisation) of interactions: H_2' (at the network level) and d' (at the species level), as both are unbiased by variation in species abundance and the total number of observations (Blüthgen, 2010). Values of H_2' and d' are standardized between 0 and 1, with larger values indicating higher specialization. The experimental design of this study did not allow all interactions between flower visitors and each flower to be recorded. The insects were recorded once when they visited the observation area and settled on a flower.

2.4 | Recording of feeding damage

In addition to recording the flower visitors, the feeding damage was determined on those plants that were suitable for automatic damage measurement. The two *Achillea* species, whose leaves are pinnate, as well as the two *Campanula* species and *L. corniculatus*, whose very small leaves were not suitable for software-assisted evaluation, were excluded. For the other plant species, namely *C. dealbata*, *C. jacea*, *K. macedonica*, *K. arvensis*, *S. verticillata*, *S. pratensis*, *A. tuberosa*, *K. uvaria*, *A. x cultorum*, *G. lindheimeri* and *C. plumbaginoides*, five leaves per target plant species were taken blindly and randomly from different plant individuals in three-dimensional space.

The leaves were photographed directly on site in a picture frame with anti-reflective glass using a Canon EOS 40D camera. The percentage of leaf damage was then evaluated in the laboratory using “BioLeaf”, a mobile application for measuring leaf damage caused by insects (Machado et al., 2016). In the case of leaves whose leaf contours had been lost due to insect damage, auxiliary lines were drawn before the analysis in order to reconstruct the original leaf shape (Mody & Linsenmair, 2004).

TABLE 2 Overview of sampled insect taxa.

Short name	Taxon	Short name	Taxon	Short name	Taxon
A_mel	<i>Apis mellifera</i>				
Wild Bees		Wild Bees		Coleoptera	
Col_sp	<i>Colettes</i> sp.	Las_4	<i>Lasioglossum</i> sp. (4)	Col_6	Coleoptera (6)
Ch_dis	<i>Chelostoma distinctum</i>	Las_5	<i>Lasioglossum</i> sp. (5)	Col_5	Coleoptera (5)
Ch_rap	<i>Chelostoma rapunculi</i>	No_sex	<i>Nomada sexfasciata</i>	An_ver	<i>Anthrenus verbasci</i>
Ce_cya	<i>Ceratina cyanea</i>	An_nan	<i>Anthidium nanum</i>	Col_4	Coleoptera (4)
Las_sp	<i>Lasioglossum</i> spec.	An_obl	<i>Anthidium oblongatum</i>	Col_3	Coleoptera (3)
And_1	<i>Andrena</i> sp. (1)	He_cre	<i>Heriades crenulatus</i>	Col_2	Coleoptera (2)
And_2	<i>Andrena</i> sp. (2)	He_tru	<i>Heriades truncorum</i>	Col_8	Coleoptera (8)
An_wil	<i>Andrena wilkella</i>	Meg_sp	<i>Megachile</i> sp.	Cur_1	Curculionidae (1) / <i>Miarus</i>
An_cur	<i>Andrena curvungula</i>			Ot_lig	<i>Otiorhynchus ligustici</i>
Da_hir	<i>Dasygaster hirtipes</i>			Va_vill	<i>Variimorda villosa</i>
Hy_sp	<i>Hylaeus</i> sp.			Psy_sp	<i>Psylliodes</i> sp.
Hal_goldi	Halictidae			Cr_vit	<i>Cryptocephalus vittatus</i>
Hy_nig	<i>Hylaeus nigritus</i>			Oe_vir	<i>Oedemera virescens</i>
Osm_1	<i>Osmia</i> sp. (1)			Oe_nob	<i>Oedemera nobilis</i>
Os_niv	<i>Osmia niveata</i>			Ma_bi	<i>Malachius bipustulatus</i>
Osm_3	<i>Osmia</i> sp. (3)			Tr_api	<i>Trichodes aparius</i>
Osm_4	<i>Osmia</i> sp. (4)			Cr_aur	<i>Cryptocephalus aureolus</i>
Os_bic	<i>Osmia bicornis</i>			Cur_2	Curculionidae (2)
Ha_sca	<i>Halictus scabiosae</i>			Oe_pod	<i>Oedemera podagrariae</i>
Ha_sex	<i>Halictus sexcinctus</i>			Ps_liv	<i>Pseudovadonia livida</i>
Ha_leu	<i>Halictus leucaheneus</i>			Ct_fla	<i>Cteniopis flavus</i>
Las_1	<i>Lasioglossum</i> spec. (1)			Ox_fun	<i>Oxythyrea funesta</i>
Las_2	<i>Lasioglossum</i> sp. (2)			Tr_hir	<i>Tropinota hirta</i>
Las_3	<i>Lasioglossum</i> sp. (3)			Cur_3	Curculionidae (3)
Bombus		Diptera		Heteroptera	
Bom_1	<i>Bombus</i> sp. (1)	Dip_1	Diptera (1) / <i>Empis</i>	De_lut	<i>Deraeocoris lutescens</i>
Bom_2	<i>Bombus</i> sp. (2)	Dip_2	Diptera (2)	Sy_rho	<i>Syromastus rhombeus</i>
B_pra	<i>B. pratorum</i>	Dip_3	Diptera (3)	Pt_sta	<i>Pterotmetus staphyliniformis</i>
B_terr	<i>B. terrestris</i>	Dip_4	Diptera (4)	Ph_mel	<i>Phylus melanocephalus</i>
B_pas	<i>B. pascuorum</i>	Lom_sp	<i>Lomatia</i> sp.	Le_anc	<i>Lepidargyrus ancorifer</i>
Lepidoptera		Cal_sp	<i>Calliphoridae</i>	Het_1	Heteroptera (1)
Ly_phl	<i>Lycaena phlaeas</i>	Dro_sp	<i>Drosophila</i> sp.	Het_3	Heteroptera (3) / Miridae
Ma_jur	<i>Maniola jurtina</i>	Car_sp	<i>Carpomya</i> sp.	Het_4	Heteroptera (4) / Miridae
Pi_rap	<i>Pieris rapae</i>	Coe_sp	<i>Coenosia</i> sp.	Het_5	Heteroptera (5)
Wasps		Me_equ	<i>Merodon equestris</i>	Het_6	Heteroptera (6) / Miridae
Le_cly	<i>Lestica clypeata</i>	Er_ten	<i>Eristalis tenax</i>		
Chry_1	Chrysididae	Sp_sci	<i>Sphaerophoria scripta</i>		
Ho_fas	<i>Holopyga fastuosa generosa</i>	My_flo	<i>Myathropa florea</i>		

(Continues)

TABLE 2 (Continued)

Short name	Taxon	Short name	Taxon	Short name	Taxon
Crab_1	Crabronidae	He_tri	<i>Helophilus trivittatus</i>		
Ce_ryb	<i>Cerceris rybyensis</i>	Si_ferr	<i>Sicus cf. ferrugineus</i>		
Ich_sp	<i>Ichneumonidae</i> sp.	Sy_pip	<i>Syricta pipiens</i>		
Anc_sp	<i>Ancistrocerus</i> sp.	Eu_lun	<i>Eupeodes luniger</i>		
Di_pic	<i>Dinetus pictus</i>				
Cha_1	Chalcidoidea				

2.5 | Statistical analysis

The statistical analyses were performed with PAST 4.03 (Hammer et al., 2001) and the network analyses with R version 4.1.1 (R Core Team, 2021) using the R-package “bipartite” (Dormann et al., 2016). We used Patefield’s null model (Patefield, 1981) to compare the observed networks with expected patterns from random associations. This null model maintains the structure of the network, namely the number of plant and pollinator species and the total interaction frequencies per species (i.e. the marginal totals of the matrix), and randomly allocates the individual interactions. We used the Patefield’s algorithm implemented as *r2dtable* in R and performed 10,000 randomizations per network.

Of the possible 180 plant species–plot combinations, 155 could be used for the statistical analysis, as *T. chinensis* did not flower on any plot and 15 other species plots remained without a flowering plant (Table 3). Mean numbers of individuals and species of flower visitors using the three target plant groups (NATIVE, RELATED, EXOTIC) in the different plots were compared using the non-parametric Friedman paired-samples test, followed by pairwise Wilcoxon post-hoc tests with sequential Bonferroni correction using PAST 4.03 (Hammer et al., 2001). The same analysis was performed for insect herbivore feeding damage (percentage feeding damage averaged from five leaves per plant species per plot).

3 | RESULTS

In the course of the survey, 674 flower visitors belonging to around 100 species were recorded in the 10 study plots. Bees including Wild Bees, honey bees and bumblebees were the most abundant flower visitors, followed by beetles, flies, Wasps, true bugs and butterflies (Table 3).

3.1 | Flower visitors

During the 155 observation periods on the ten plots, a total of 511 flower visits from native insects feeding on pollen and nectar were recorded (Wild Bees, *Bombus*, Lepidoptera, Coleoptera, Diptera, and Wasps; excluding *Apis mellifera* and Heteroptera) (Table 3). More flower visits were observed in the NATIVE perennials, with

an overall percentage of 67.1%, compared to 23.5% in the RELATED and 9.4% in the EXOTIC perennials (Figure 2). This highest number of visits to the NATIVE perennials was consistently observed in the different study plots, regardless of the surroundings of the study plot, which seemed to have a strong influence on the number of flower visitors (Figure S1). The highest number of 19 visits in total during an observation period was recorded for *K. arvensis*, followed by *C. rotundifolia* with 18 visits (Figure 2A). The average number of Total Visitors differed significantly between the three target plant groups. It was highest for NATIVE, followed by RELATED perennials. Lowest numbers were found for EXOTIC perennials (Figure 2A). Thus, there was a marked decline in insect numbers from the frequently visited NATIVE to the RELATED to the least visited EXOTIC perennials. This was also reflected in the absolute number of visits per target plant group. NATIVE perennials were visited 343 times, RELATED perennials 120 times and EXOTIC perennials 48 times.

With a total of 241 flower visits, Wild Bees accounted for 37% of the total number of recorded visits. The average number of flower visits by Wild Bees was significantly higher on NATIVE than on RELATED and the least visited EXOTIC perennials (Figure 2B). The number of flower visits by Wild Bees was not significantly different between the RELATED and the EXOTIC perennials. The difference between NATIVE perennials and the other plant groups was also reflected in the total number of visits, with 158 flower visits observed for the NATIVE compared to 62 visits for the RELATED and 21 visits for the EXOTIC perennials.

A total of 232 flower visits by Non-Bees was observed, accounting for 36% of the total number of visits. The highest number of visits during one observation period was recorded for *A. millefolium*, followed by *K. arvensis* and *L. corniculatus* (Figure 2C). Like for Wild Bees, the average number of visits by Non-Bees was significantly higher for NATIVE than for RELATED and EXOTIC perennials. No significant difference in number of visits was found between the RELATED and the EXOTIC perennials (Figure 2C). NATIVE perennials experienced 157, RELATED perennials 50 and EXOTIC perennials 25 flower visits in total.

For *Apis mellifera*, a total of 136 flower visits was observed, accounting for 21% of total visits. The average number of flower visits by *Apis mellifera* did not differ significantly between the three target plant groups (Figure 2D). *Apis mellifera* visited the EXOTIC perennials 52 times, the NATIVE perennials 46 times and the RELATED perennials 38 times. *Apis mellifera* visited the group of EXOTIC plants

TABLE 3 Results on flower visitor target groups.

	Total	Without <i>A. mell</i> and HETE	<i>A. mell</i>	Wild Bees	BOMB	LEPI	COLE	DIPT	Wasps	HETE
Flower visits										
Total	674	511	136	241	38	22	102	59	49	27
NATIVE	393	343	46	158	28	8	61	48	40	4
<i>A. millefolium</i>		80	3	6	0	0	11	26	37	
<i>C. rotundifolia</i>		62	0	38	0	0	24	0	0	
<i>C. jacea</i>		90	26	67	7	7	1	6	2	
<i>K. arvensis</i>		58	9	23	13	1	8	13	0	
<i>S. pratensis</i>		17	8	6	8	0	2	1	0	
<i>L. corniculatus</i>		36	0	18	0	0	15	2	1	
RELATED	179	120	38	62	8	6	33	6	5	21
<i>A. clypeolata</i>		18	0	5	0	0	6	3	4	
<i>C. portenschlagiana</i>		40	1	20	0	0	19	1	0	
<i>C. dealbata</i>		41	4	32	1	0	8	0	0	
<i>K. macedonica</i>		12	3	3	1	6	0	1	1	
<i>S. verticillata</i>		9	30	2	6	0	0	1	0	
EXOTIC	102	48	52	21	2	8	8	5	4	2
<i>A. tuberosa</i>		4	18	1	0	2	0	0	1	
<i>K. uvaria</i>		1	12	0	0	0	1	0	0	
<i>Agastache</i>		14	3	10	2	1	0	1	0	
<i>G. lindheimeri</i>		15	7	6	0	0	6	1	2	
<i>Helenium</i>		13	12	4	0	5	1	2	1	
<i>C. plumbaginoides</i>		1	0	0	0	0	0	1	0	
Species	101	90	1	32	5	3	24	17	9	10
Flower visits						Non-Bees				
<i>p</i> -value		0.00007	0.3	0.0006		0.0002				
Chi ² _(2,27)		19.05	2.45	13.95		16.8				
Species										
<i>p</i> -value		0.0001								
Chi ² _(2,27)		17.45								
Feeding damage (%)		Total								
<i>p</i> -value		0.0001								
Chi ² _(2,27)		18.2								

Note: Total: total of flower visitors; Flower visitors, species and feeding damage (%) that used the three target plant groups (RELATED, NATIVE, EXOTIC perennials) were compared for averaged numbers per plant group and plot using repeated-measures Friedman tests, *p* < 0.05.

Abbreviations: *A. mell*, *Apis mellifera*; BOMB, *Bombus*; COLE, Coleoptera; DIPT, Diptera; HETE, Heteroptera; LEPI, Lepidoptera.

The values in bold show the plant species most frequently visited by the individual target groups.

relatively more often (38% of all visits by *Apis mellifera*) than Non-Bees (11%) and Wild Bees (9%).

3.2 | Species numbers

A total of 101 different insect taxa were identified, which could not always be determined to species level (Table 3). The further evaluations were made only with the 90 species of insects that feed on pollen or nectar (excluding *Apis mellifera*). The highest number of

species, a total of ten different species, was found in one observation period on *C. jacea*, followed by *K. arvensis* with nine species (Figure 3). *A. millefolium* and *C. jacea* were the two plant species with the highest number (23) of different insect taxa.

The average number of species of Total Visitors differed significantly between the three target plant groups (Figure 3). The NATIVE plants were visited by more species than the RELATED perennials and EXOTICS and the RELATED perennials were visited by more species than the EXOTICS. The number of insect species visiting the target plants thus decreased, from NATIVE to RELATED to EXOTIC plant

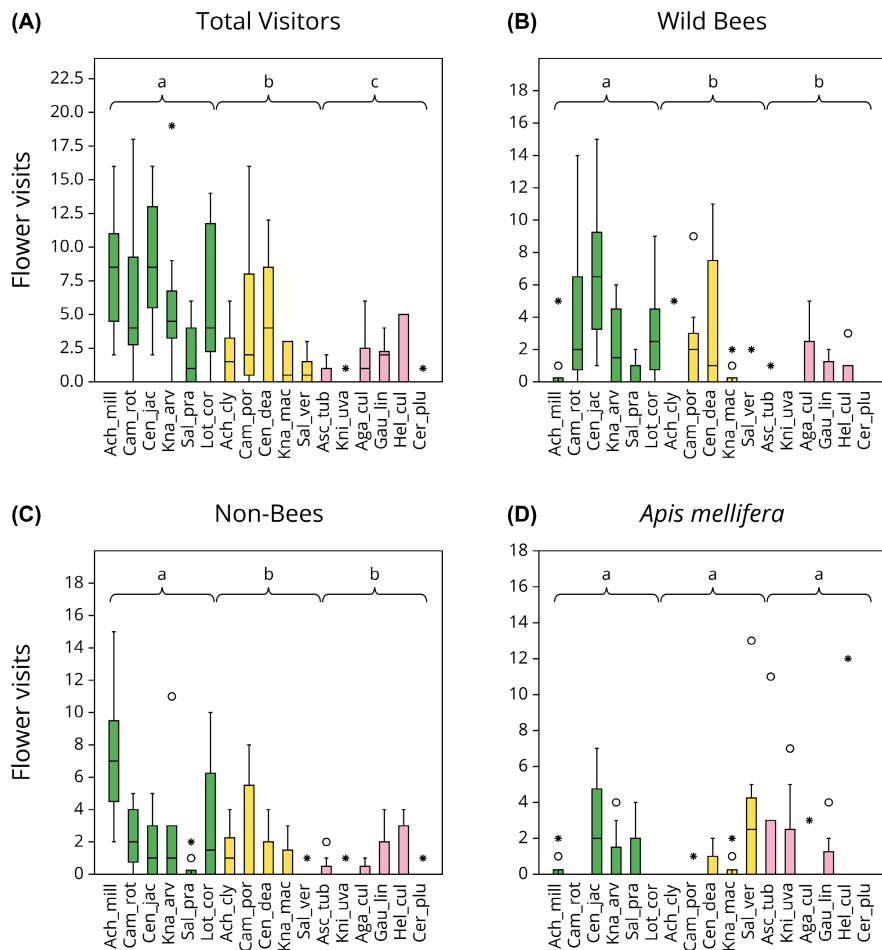


FIGURE 2 Comparison of the number of flower visits for seventeen different plant species belonging to the target plant groups NATIVE (green), RELATED (yellow) and EXOTIC (pink); outliers are displayed in the form of circles or stars. (A) Total Visitors excluding *Apis mellifera* and Heteroptera, (B) Wild Bees, (C) Non-Bees and (D) *Apis mellifera*. Different letters above grouped boxplots indicate significant differences between target plant groups (Friedman test followed by pairwise Wilcoxon post hoc tests, $p < 0.05$). Plant species as follows: Ach_cly = *Achillea clypeolata*, Cam_por = *Campanula portenschlagiana*, Cen_dea = *Centaurea dealbata*, Kna_mac = *Knautia macedonica*, Sal_ver = *Salvia verticillata*, Ach_mill = *Achillea millefolium*, Cam_rot = *Campanula rotundifolia*, Cen_jac = *Centaurea jacea*, Kna_arv = *Knautia arvensis*, Sal_pra = *Salvia pratensis*, Lot_cor = *Lotus corniculatus*, Asc_tub = *Asclepias tuberosa*, Kni_uva = *Kniphofia uvaria*, Aga_cul = *Agastache x cultorum*, Gau_lin = *Gaura lindheimeri*, Hel_cul = *Helenium x cultorum*, Cer_plu = *Ceratostigma plumbaginoides*.

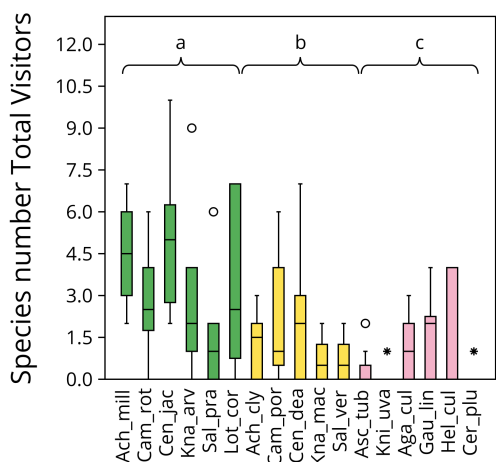


FIGURE 3 Comparison of the number of species of Total Visitors (excluding *Apis mellifera* and Heteroptera) for seventeen different plant species belonging to the target plant groups NATIVE (green), RELATED (yellow) and EXOTIC (pink); outliers are displayed in the form of circles or asterisks. Different letters above the grouped boxplots indicate significant differences between target plant groups (Friedman test followed by pairwise Wilcoxon post hoc tests, $p < 0.05$); for further details on plant species names see Figure 2.

species. The NATIVE perennials were visited by 73 different species, the RELATED perennials by 37 and the EXOTIC perennials by 26.

3.3 | Network analyses

For the entire plant-flower visitor network (Figure 1A), a medium-high degree of specialization was found ($H_2' = 0.52$). Flower visitor specialization was highest for the NATIVE and RELATED plant species (subnetwork native: $H_2' = 0.69$; related plants: $H_2' = 0.77$), whereas a much lower degree of specialization was found for the EXOTIC plants ($H_2' = 0.43$). All subnetworks were significantly more specialized than random associations ($p < 0.0001$). Among the insect species, the highest specialization was found for the wild bee *Chelostoma distinctum* ($d' = 0.61$) and a weevil of the genus *Miarus* ($d' = 0.57$). Both species interacted mainly with *C. rotundifolia*, which in turn showed the highest specialization among the plants ($d' = 0.78$). Similarly, *A. millefolium* ($d' = 0.74$) and *L. corniculatus* ($d' = 0.72$) were also only used by certain insect taxa.

Quantitative interaction networks of the seven investigated insect groups and the three target plant groups illustrated that the EXOTIC perennials were mainly visited by *Apis mellifera*, which

accounted for 52% of the total interactions of this plant group (Figure 4B). The total interactions of *Apis mellifera* were evenly distributed among the three plant groups (EXOTIC=38.2%, NATIVE=33.8%, RELATED=27.9%). In contrast, Wild Bees, *Bombus*, Diptera and Wasps showed a clear preference for the NATIVE perennials. Interactions with NATIVE perennials accounted for 81.6% of all interactions for Wasps, 81.4% for Diptera, 73.7% for *Bombus* and 65.6% for Wild Bees. Coleoptera used both NATIVE (59.8%) and RELATED (32.4%) perennials, whereas Lepidoptera used all plant groups to roughly the same extent (NATIVE=36.4%, RELATED=27.3% and EXOTIC=36.4%) (Figure 4B).

When analysing the interactions of insect groups with individual plant species, it became clear that several NATIVE perennials had a relatively specific set of visitor taxa, shown by a high degree of exclusiveness (d') (Figure 5A). *A. millefolium* (far right) had the highest d' value of 0.47 in this network. The group of Wasps with a d' value of 0.51 almost exclusively used *A. millefolium* as an interaction partner. The two plant species on the far left, *K. uvaria* and *S. verticillata*, with d' values of 0.33 and 0.35, showed an almost exclusive interaction with *Apis mellifera*. This network had a relatively low degree of specialization ($H_2' = 0.34$), but was significantly more specialized than random associations ($p < 0.0001$; Figure 5A).

When focusing on the bees alone, differences between Wild Bees and *Apis mellifera* became visible (Figure 5B). The degree of specialization (H_2') decreased from 0.57 in the pure Wild Bee network to only 0.47 in the network of Wild Bees and *Apis mellifera* due to the broad

interaction spectrum of *Apis mellifera* (Figure 5B). The two *Campanula* species and *L. corniculatus* were visited only by Wild Bees, of which *Chelostoma distinctum* and *Chelostoma rapunculi*, which only visited *Campanula* species, had particularly high d' values of 0.74 and 0.55, respectively. The exclusivity of these interactions is also reflected in the high d' values of the plants, with a d' value of 0.79 for *C. rotundifolia* and a d' value of 0.76 for *L. corniculatus*. *Centaurea jacea*, on the other hand, had many different interaction partners and a low d' value of 0.29. The EXOTIC perennials were mainly approached by the generalist *Apis mellifera* and had low d' values (*H. x cultorum* $d' = 0.11$, *K. uvaria* $d' = 0.23$, *A. tuberosa* $d' = 0.27$, *S. verticillata* $d' = 0.33$).

3.4 | Feeding damage

Feeding damage by insect herbivores differed significantly between the three target plant groups. The NATIVE perennials were more frequently used as a food source by herbivores than the RELATED and EXOTIC perennials and the RELATED perennials were used as a food source more often than the EXOTIC perennials (Figure 6). This highest feeding damage to the NATIVE perennials was consistently observed in the different study plots, regardless of the surroundings of the study plot, which seemed to have a strong influence on the level of herbivory (Figure S2). On average, 2.3% of the leaf area of the NATIVE plants, 0.8% of the RELATED and 0.1% of the EXOTIC perennials were consumed by herbivores.

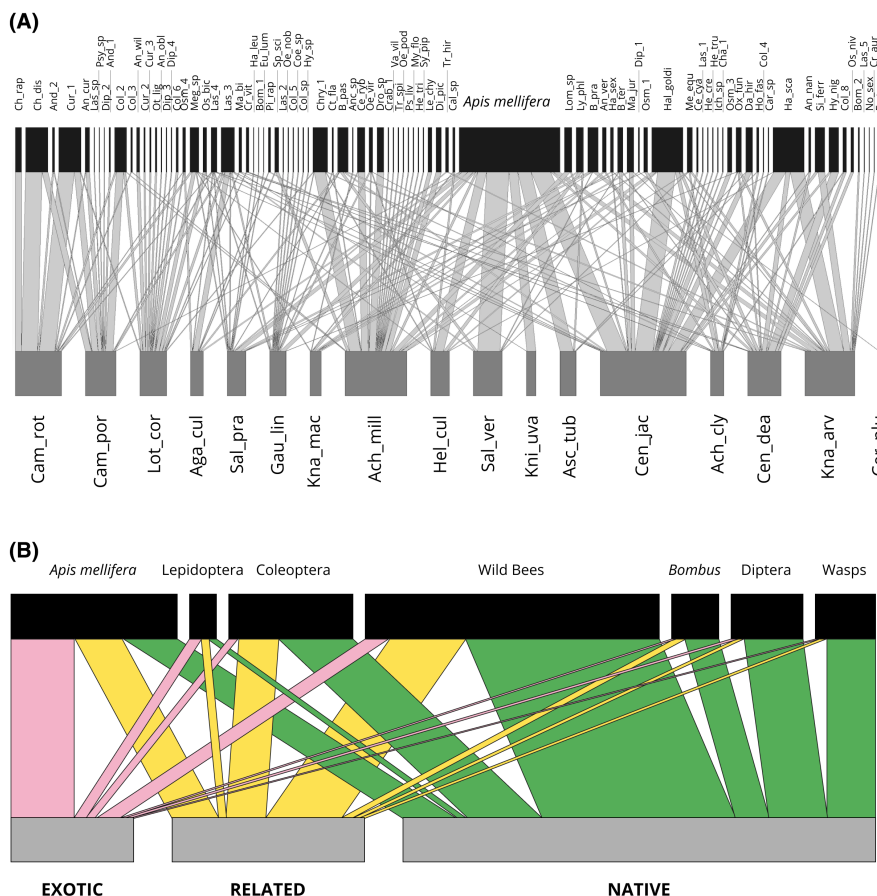


FIGURE 4 Quantitative network of (A) flower visitor-plant interactions (without Heteroptera). Each species is represented as a rectangle (plants=gray; insects=black). The widths of the black rectangles are proportional to the abundance of the insect species; those of the gray rectangles are proportional to the number of interactions of each plant species with insect individuals. Interactions are shown as connecting bars; their width reflects the number of interactions. Lines indicate interactions that were observed only once. Quantitative network of (B) insect group-plant group interactions. Plant groups: pink=EXOTIC, yellow=RELATED, green=NATIVE perennials. For further details on plant species names see Figure 2, and for further details on flower visitor names see Table 2.

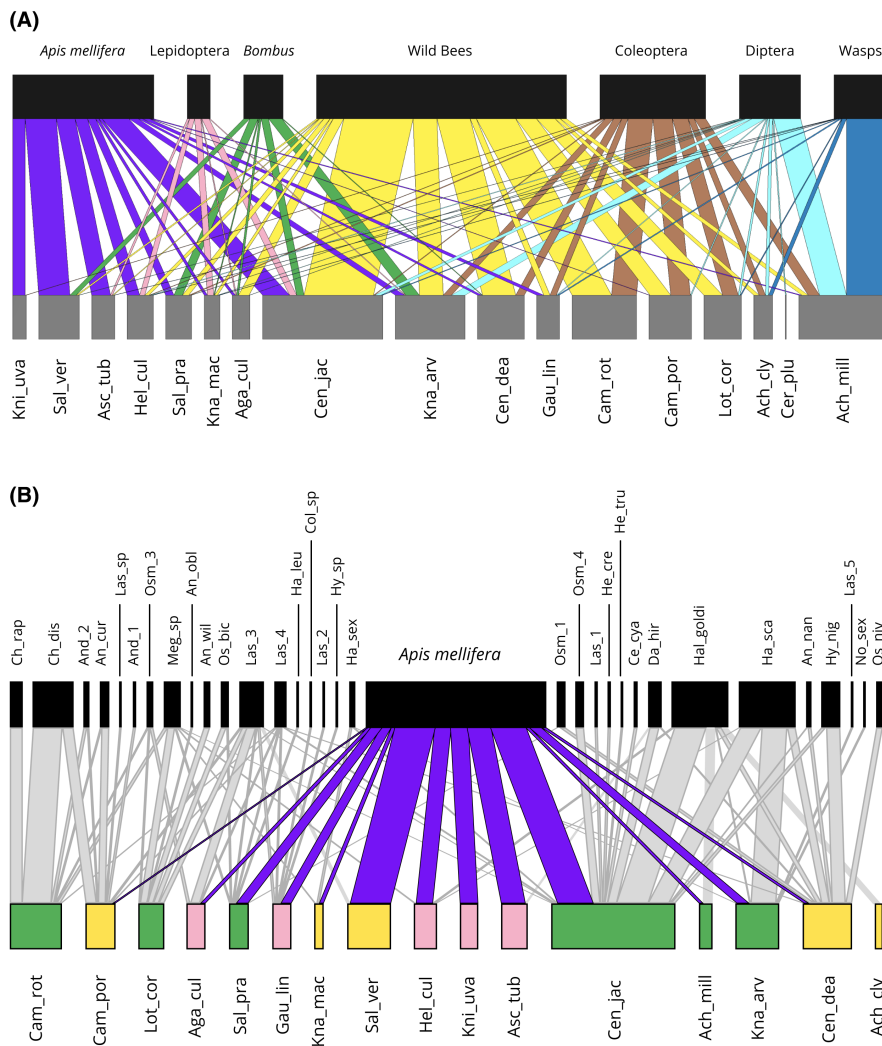


FIGURE 5 Quantitative network of (A) insect group-plant species interactions. Each group is shown as a rectangle (plant species = gray; insect groups = black). The widths of the black rectangles are proportional to the abundance of insect species; those of the gray rectangles are proportional to the number of interactions of each plant species with insect individuals. Interactions are shown as connecting bars; their width reflects the number of interactions. Lines indicate interactions that were observed only once. Flower visitor groups: purple = *Apis mellifera*, pink = Lepidoptera, green = *Bombus*, yellow = Wild Bees, brown = Coleoptera, turquoise = Diptera, blue = Wasps. Quantitative network of (B) Wild Bee-*Apis mellifera*-plant species interactions. Each species is shown as a rectangle. The widths of the black rectangles are proportional to the abundance of insect species, those of the green, yellow and pink rectangles to the number of interactions of each plant species with insect individuals. Plant species: gGreen = NATIVE, yellow = RELATED, pink = EXOTIC perennials. Interactions of *Apis mellifera* are shown in purple. For further details on plant species names see Figure 2, and for further details on flower visitor names see Table 2.

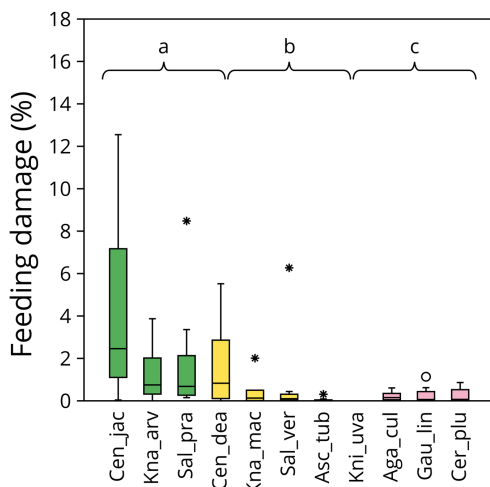


FIGURE 6 Comparison of percent feeding damage related to eleven different target plant species for which leaf area damage could be analysed. Different letters above the grouped boxplots indicate significant differences between groups (p -value < 0.05). Different colours indicate the different plant groups (green = NATIVE, yellow = RELATED, pink = EXOTIC). Outliers are displayed in the form of circles or asterisks. For further details on plant species names see Figure 2.

4 | DISCUSSION

4.1 | Flower visitors

Our study showed that the NATIVE perennials were used as a food source by flower visitors in urban green spaces to a greater extent than the RELATED and EXOTIC plants, and that there was a gradation in utilisation from the NATIVE to the EXOTIC plants. Greater utilisation of the NATIVE plants and intermediate utilisation of the RELATED plants was observed for most groups of flower visitors. As these flower visitors differ in the way they approach and use the flowers, this result suggests that not only one but several traits characterising the flowers of the NATIVE plants are involved in the preferential selection of the NATIVE plants by flower visitors.

The greater utilisation of native plants by flower-feeding insects does not seem surprising, as native insects and native wild plants have co-evolved over long periods of time and have developed complex feeding relationships (Schoonhoven et al., 2005). Our finding that the native plants are visited significantly more often and probably have a higher value for insects is thus consistent with the results of other studies (Jain et al., 2016; Pardee & Philpott, 2014; Webber et al., 2012). However, there are also studies that show no difference

between native and non-native plants (Philpott et al., 2023) or even a higher utilisation of non-native plants (Baker et al., 2020; Garbuzov & Ratnieks, 2014; Staab et al., 2020; Wenzel et al., 2020). A summarised meta-analysis found that native plants outperformed exotic plants in 43% of studies in terms of positive effects on biodiversity, while 33% of studies showed mixed effects, 17% showed neutral effects and exotic plants were superior in 8% of studies (Berthon et al., 2021). Understanding these contrasting results is certainly of great importance for optimising the use of plants to promote insects in urban areas. Based on our study and other studies, it is important which insects are considered in the study, as not all insects respond in a similar way to plant species and plant origin (Lowenstein et al., 2019).

For bees, which represent a dominant group of flower visitors in our study and are also the focus of many other studies on flower–insect interactions in urban areas, it seems helpful to consider the degree of flower specialisation when drawing conclusions about the suitability of native and non-native plants as food sources (Prendergast et al., 2022). While generalist (polylectic) bees, including the honey bee, most bumblebees and other polylectic wild bee species, appear to readily accept and utilise non-native plant species (Baker et al., 2020; Garbuzov & Ratnieks, 2014; Wenzel et al., 2020), more specialised (oligolectic) bee species tend to stick to native plants or their close relatives (Lowenstein et al., 2019). In our study, the different use of native and non-native plant species by specialised and generalist bees is nicely illustrated by the two strictly oligolectic scissor bees (*Chelostoma distinctum* and *Chelostoma rapunculi*), which used flowers (*Campanula*) that were not used by generalists such as the honey bee. The sole visitation of *Campanula* flowers by the specialist bees may be related to a strong adaptation to *Campanula* pollen as larval food (Praz et al., 2008), suggesting that specific nutritional requirements (here determined by pollen composition) are a driving force for flower use patterns (Ritchie et al., 2016; Wood et al., 2018). Answering the question of whether these specific requirements can be met less well by cultivation and selection requires more specific studies of the pollinators and herbivores concerned. However, it is known that the cultivation and selection of plant varieties can alter the quality of flowers for flower feeding herbivores and also for their natural enemies (Mody et al., 2015, 2017), as well as the chemical composition of nectar and pollen (Egan et al., 2018). This means that such cultivated plants, including the ornamental plants included in our RELATED and EXOTIC plants, may differ in terms of their usefulness as food for pollen-feeding insects.

If in the case of bees it is necessary to characterise and indicate the degree of specialisation of the bees studied in terms of plant use and suitability, what about other groups of flower-visiting insects? The strongest preference for NATIVE plants was found in the Non-Bee groups Wasps and Diptera. Both groups are very heterogeneous in size and feeding behaviour. Wasps can be social or solitary, and they can be predators or parasitoids requiring prey or hosts for larval development. Unlike bees, wasps visit flowers primarily to feed on nectar and sometimes to hunt prey, but not so often to collect flower products for rearing their offspring. Their relationship to individual plant species is therefore generally less

pronounced than that of bees (there are exceptions, e.g. wasp orchids), and the specialisation of interaction in wasp–flower networks may be less than in the overall pollination network (Mello et al., 2011). Nevertheless, there are certain flower characteristics that make flowers more attractive to wasps (Rosas-Guerrero et al., 2014). These traits include colour (pale colours and ultra-violet patterns), floral scent (e.g. sweet and spicy scents), nectar availability (flowers with easily accessible nectar are preferred, as wasps do not have specialised structures for nectar extraction from deep flowers) and flower shape (preference for open, flat flowers and for small and clustered flowers). Although this variety of floral traits provides the opportunity to distinguish between the NATIVE and EXOTIC plants, it is not possible on the basis of our study to determine which of these traits are responsible for the observed visitation patterns. However, *Achillea millefolium*, the most frequently visited plant species (much more than *A. clypeolata*), fulfilled the described attractive characteristics more than any other plant in the experiment. To better understand whether a direct, origin-related adaptation to *A. millefolium* or rather the combination of attractive traits is related to the strong preference for this plant species, specific tests with plants of different origins combining these traits in a comparable way would be required. Like wasps, dipterans typically lack the long proboscis of many bees and butterflies, making flowers with easily accessible nectar particularly attractive to dipterans. As with wasps, *A. millefolium* (also not *A. clypeolata*) was the most frequently used plant by dipterans, showing that the presence of very specific plant species can also be crucial for the occurrence of flower-visiting dipterans and wasps.

Flower-visiting beetles, the second largest group of flower visitors in our study, have been reported to not strongly respond to general availability of floral resources compared to other factors including area of built-up area in the surrounding of green spaces (Horak et al., 2022). Nevertheless, beetles may require specific floral traits that are distinctly different from those that determine bee use. In our study, beetles were not strongly restricted to a single plant species, but still showed a higher use of NATIVE and RELATED plants than of EXOTIC plants, suggesting that the floral traits that influence beetle use may also be related to plant origin, but to a lesser extent than for some other groups of flower visitors.

Of all the flower visitor groups studied, only Lepidoptera and especially the honey bee did not show higher visitation to NATIVE flowers. Lepidoptera were quite rare on the study plants, which is consistent with other studies showing that Lepidoptera are rather rare in urban areas compared to other flower visitor groups such as bees (Staab et al., 2020; Theodorou et al., 2020). Lepidoptera typically have a long, coiled proboscis that allows them to reach not only openly accessible nectar but also nectar hidden deep inside tubular flowers (Krenn, 2010). This adaptation is crucial for feeding on a wide range of flower shapes and sizes, which may explain the use of plants from all three study groups when nectar is available and colours are attractive. While we found a remarkably uniform use of the three plant groups for Lepidoptera, the honey bee was unique in its almost exclusive and strong use of many of the

EXOTIC plants. As a super-generalist that has also been bred for high productivity and efficiency (Büchler et al., 2008), the honey bee can use a wide variety of flowers to obtain nectar and pollen (Giannini et al., 2015). By using exotic plants not used by other flower visitors, it can avoid competition, although it can easily compete with native flower visitors for the floral resources of native plants (Urbanowicz et al., 2020). Although honey bees can use a wide variety of flowers, they prefer flowers that provide abundant and easily accessible nectar and produce large quantities of high-quality pollen. As many plants that are particularly useful to honey bees are not, or only marginally, useful to other groups of plant visitors, the current practice of tailoring seed mixtures or plantings to the needs of bees, or even specifically honey bees, may be detrimental to the important group of non-bee species, as it may be difficult to find suitable forage plants in these circumstances. An example of this is the seed mixtures sown by farmers in Germany (Hesse) as part of the Hessian programme of agri-environmental and landscape conservation measures, which mainly contain bee-friendly plants such as *Phacelia*, *Fagopyrum* or *Melilotus*, known as bee pastures (Brand, 2019; Decourtye et al., 2010). These plants are particularly rich in nectar and pollen and are therefore frequently visited by honey bees. For generalists, these often annual mixtures are a good food source. However, such seed mixtures or plantings, which are mainly adapted to honey bees, can hardly contribute to the conservation and promotion of biodiversity. This is because even many oligolectic wild bee species that specialise in low-nutrient pollen, such as bellflower scissor bees, would not find food for their offspring in such a flower mix or perennial planting. Typical bee flowers with larger amounts of nectar, such as the two *Salvia* species (Kadereit et al., 2021), are mainly of interest to large pollinators such as *Bombus* or other social bees such as honey bees. In particular, *Bombus* only collect nectar from the reservoir with large amounts of nectar (Kradolfer & Erhardt, 1995), because the larger the pollinator, the more nectar is consumed per visit (Pacini et al., 2003). The two *Salvia* species in our study were mainly visited by *Apis mellifera* and *Bombus* and only to a small extent by the Non-Bee group. On the other hand, the two *Campanula* species were not visited by *Bombus*. This result shows once again the importance of creating well-balanced flower mixtures or perennial plantings with a suitable species and family diversity to meet the needs of each insect group.

4.2 | Feeding damage

The results of the feeding damage analysis also support the hypothesis that NATIVE perennials are more suitable as a food resource for insects in urban green spaces than RELATED perennials or EXOTIC plants. The level of herbivory on NATIVE plants in our study is comparable to feeding damage in grasslands, which is reported to be between 0.5 and 15% damage, with most plants showing no more than 2% damage (Scherber et al., 2006; and references therein). In contrast, damage to RELATED plants, and

especially to EXOTIC plants, was lower than in grasslands, suggesting that these plants are of little use to insects. These results are consistent with other studies showing that herbivores in gardens can benefit from the presence of native plants (Salisbury et al., 2020). While the damage to NATIVE plants in our study shows that insect herbivores can occur in urban green spaces, the almost complete absence of damage to EXOTIC plants indicates that not all plants can be utilised by these herbivores. Whether the EXOTIC plants are not accepted as food or are unsuitable, i.e. the question of whether herbivore preference or performance determines the observed level of damage (Price et al., 2011), is not answered by our study.

In other study systems, it has been shown that varieties of native plants that have been improved by the horticultural industry for aesthetic value and disease resistance can differ from wild plants in terms of insect herbivory. It has also been observed that introduced species are less suitable for herbivores than comparable native species (Berthon et al., 2021; and references therein). For example, insect herbivory has been shown to be reduced in cultivars compared to wild-type woody plants due to anthocyanin enrichment, which changes leaf colour (Baisden et al., 2018). A study from the Netherlands compared the suitability of native mustard cabbage (*Brassica nigra*), native field mustard (*Sinapis arvensis*) and exotic oriental grouper (*Bunias orientalis*) as caterpillar food for two butterfly species specialized on different cruciferous plants (small cabbage white butterfly (*Pieris rapae*) and large cabbage white butterfly (*Pieris brassicae*)) (Harvey et al., 2010). The study showed that *B. orientalis* was highly toxic to the larvae of both pierids, with a mortality rate close to 100%. Analysis of glucosinolate concentrations in leaf tissues revealed considerable quantitative and qualitative differences in these secondary plant compounds among the three plant species (Harvey et al., 2010). Thus, non-native plant species may also represent a potential toxic trap for specialized herbivores. Changes in chemical and structural environmental conditions caused by non-native plants can alter the foraging behaviour and dispersal abilities of native insects (Bezemer et al., 2014; Heleno et al., 2009). One possible consequence is a decline in insects, as observed by Heleno and colleagues for insect biomass when native plants were replaced by non-native plants (Heleno et al., 2009).

5 | CONCLUSION

In view of the global decline in insects (Hallmann et al., 2017; Janzen & Hallwachs, 2019; Seibold et al., 2019; Wagner et al., 2021), measures are being sought to promote insects. In this context, our study shows that planting urban green spaces with native plants as a food source for flower-visiting and leaf-feeding insects can be a way to promote various insect species in urban areas. Plantings or sowings that are only geared to the needs of honey bees are less suitable for the conservation and promotion of insect biodiversity in urban green spaces, as the flower preferences and needs of honey bees do not match those of most other insects. Based on our findings,

we recommend designing urban green spaces with a variety of predominantly native plants to meet the different food requirements of all insect species.

AUTHOR CONTRIBUTIONS

Doris Lerch and Karsten Mody: Conceptualization, methodology, formal analysis and software (equal). Karsten Mody and Nico Blüthgen: Validation and supervision (equal). Doris Lerch: Investigation, data curation, writing—original draft preparation, visualisation, project administration (lead). Karsten Mody and Nico Blüthgen: Writing—review and editing (equal). Nico Blüthgen: Funding acquisition (lead). All authors have read and agreed to the published version of the manuscript.

ACKNOWLEDGEMENTS

We would like to thank the Darmstadt Green Spaces Office, which not only made the municipal green spaces available to us for the study, but also provided active and also financial support in the selection of plant species. We thank the Darmstadt Environmental Office for providing exception permits for insect sampling. D.L. is grateful for the comprehensive training on Apidae identification provided by the BienABest project group of the University of Ulm. We further thank the employees of the AG Blüthgen and of the Botanical Garden of the Technical University Darmstadt for their support in establishing the plots. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1002/2688-8319.12380>.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.2ngf1vhz5> (Lerch et al., 2024).

ORCID

Doris Lerch  <https://orcid.org/0009-0005-1858-2701>

REFERENCES

Ahrends, S. (2022). *Anzahl der Bienenvölker in Deutschland in den Jahren 2007 bis 2021*. Retrieved from <https://de.statista.com/statistik/daten/studie/487925/umfrage/bienenvoelker-in-deutschland/>

Asclepiadaceae. (2001). Retrieved from <https://www.spektrum.de/lexikon/biologie-kompakt/asclepiadaceae/950>

Asphodelaceae. (2001). Retrieved from <https://www.spektrum.de/lexikon/biologie-kompakt/asphodelaceae/980>

Ayers, A. C., & Rehan, S. M. (2021). Supporting bees in cities: How bees are influenced by local and landscape features. *Insects*, 12(2), 128.

Baisden, E. C., Tallamy, D. W., Narango, D. L., & Boyle, E. (2018). Do cultivars of native plants support insect herbivores? *HortTechnology*, 28(5), 596–606.

Baker, A. M., Redmond, C. T., Malcolm, S. B., & Potter, D. A. (2020). Suitability of native milkweed (*Asclepias*) species versus cultivars for supporting monarch butterflies and bees in urban gardens. *PeerJ*, 8, e9823.

Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Stone, G. N., Vaughan, I. P., & Memmott, J. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, 282(1803), 20142849.

Berthon, K., Thomas, F., & Bekessy, S. (2021). The role of 'nativeness' in urban greening to support animal biodiversity. *Landscape and Urban Planning*, 205, 103959.

Bezemer, T. M., Harvey, J. A., & Cronin, J. T. (2014). Response of native insect communities to invasive plants. *Annual Review of Entomology*, 59, 119–141.

Blüthgen, N. (2010). Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology*, 11(3), 185–195. <https://doi.org/10.1016/j.baae.2010.01.001>

Brand, S. (2019). *Ackerbauliche Aspekte bei der Anlage von Blühmischungen beachten*. Retrieved from <https://lh.hessen.de/umwelt/biodiversitaet/ackerbauliche-aspekte-bei-der-anlage-von-bluehmischungen-beachten/>

Büchler, R., Drescher, W., & Tiesler, F. (2008). *Selektion der Honigbiene*. IWF Wissen und Medien GmbH. <https://tib.flowcenter.de/mfc/medialink/42/e2985b43d5c3087016341736f27fa8f3e6ba1c3cca0618e4371814a0b822ff8b059/c13136.pdf>

Chemnitz, C., Rehmer, C., & Wenz, K. (Eds.). (2020). *Insektenatlas: Daten und Fakten über Nütz- und Schädlinge in der Landwirtschaft* (1. Auflage, Januar 2020). Heinrich-Böll-Stiftung.

Comba, L., Corbet, S. A., Barron, A., Bird, A., Collinge, S., Miyazaki, N., & Powell, M. (1999). Garden flowers: Insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany*, 83(1), 73–86.

Decourtye, A., Mader, E., & Desneux, N. (2010). Landscape enhancement of floral resources for honey bees in agro-ecosystems. *Apidologie*, 41(3), 264–277.

Dormann, C., Fründ, J., & Gruber, B. (2016). Package 'bipartite'. Visualising bipartite networks and calculating some (Ecological) indices. Retrieved from <https://cran.r-project.org/web/packages/bipartite/bipartite.pdf>

Egan, P. A., Adler, L. S., Irwin, R. E., Farrell, I. W., Palmer-Young, E. C., & Stevenson, P. C. (2018). Crop domestication alters floral reward chemistry with potential consequences for pollinator health. *Frontiers in Plant Science*, 9, 1357. <https://doi.org/10.3389/fpls.2018.01357>

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, 1(9), 488–494. [https://doi.org/10.1890/1540-9295\(2003\)001\[0488:RDECAR\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2)

Erickson, E., Grozinger, C. M., & Patch, H. M. (2022). Measuring plant attractiveness to pollinators: Methods and considerations. *Journal of Economic Entomology*, 115(5), 1571–1582.

FloraWeb. (2024). *FloraWeb*. Retrieved from <https://www.floraweb.de/>

Futuyma, D. J., & Slatkin, M. (1983). *Coevolution*. Sinauer.

Gaißmayer. (2020). *Staudengärtnerei Gaißmayer: Pflanzen Sortiment*. Retrieved from <https://www.gaissmayer.de/web/shop/pflanzen-sortiment/stauden/203/>

Garbuzov, M., & Ratnieks, F. L. W. (2014). Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology*, 28(2), 364–374.

Giannini, T. C., Garibaldi, L. A., Acosta, A. L., Silva, J. S., Maia, K. P., Saraiva, A. M., Guimarães, P. R., Jr., & Kleinert, A. M. P. (2015). Native and non-native supergeneralist bee species have different effects on plant-bee networks. *PLoS One*, 10(9), e0137198.

- Google Patents. (2022, January 28). *Agastache plant named 'Blue Boa'*. Retrieved from <https://patents.google.com/patent/USPP24050P3/en>
- Hall, D. M., Camilo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J. S., Baldock, K. C., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M. E., Jackson, J. I., Langellotto, G., Lowenstein, D., Minor, E. S., Philpott, S. M., Potts, S. G., ... Frankie, G. (2017). The city as a refuge for insect pollinators. *Conservation Biology*, 31(1), 24–29.
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörrén, T., Goulson, D., & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, 12(10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). *PAST: Paleontological statistics software package for education and data analysis*. Retrieved from https://palaeo-electronica.org/2001_1/past/issue1_01.htm
- Harvey, J. A., Biere, A., Fortuna, T., Vet, L. E. M., Engelkes, T., Morriën, E., Gols, R., Verhoeven, K., Vogel, H., Macel, M., Heide-Fischer, H. M., Schramm, K., & van der Putten, W. H. (2010). Ecological fits, misfits and lotteries involving insect herbivores on the invasive plant, *Bunias orientalis*. *Biological Invasions*, 12(9), 3045–3059. <https://doi.org/10.1007/s10530-010-9696-9>
- Heleno, R. H., Ceia, R. S., Ramos, J. A., & Memmott, J. (2009). Effects of alien plants on insect abundance and biomass: A food-web approach. *Conservation Biology*, 23(2), 410–419.
- Horak, J., Šafářová, L., Trombik, J., & Menéndez, R. (2022). Patterns and determinants of plant, butterfly and beetle diversity reveal optimal city grassland management and green urban planning. *Urban Forestry & Urban Greening*, 73, 127609.
- Jain, A., Kunte, K., & Webb, E. L. (2016). Flower specialization of butterflies and impacts of non-native flower use in a transformed tropical landscape. *Biological Conservation*, 201, 184–191.
- Janzen, D. H., & Hallwachs, W. (2019). Perspective: Where might be many tropical insects? *Biological Conservation*, 233, 102–108.
- Jordano, P., Bascompte, J., & Olesen, J. M. (2003). Invariant properties in coevolutionary networks of plant-animal interactions. *Ecology Letters*, 6(1), 69–81. <https://doi.org/10.1046/j.1461-0248.2003.00403.x>
- Kadereit, J. W., Körner, C., Nick, P., & Sonnewald, U. (2021). *Strasburger–Lehrbuch der Pflanzenwissenschaften* (38. Auflage). Springer Spektrum. <https://doi.org/10.1007/978-3-662-61943-8>
- Khan, H. H., Naz, H., Sahu, P. S., & Ghongade, D. S. (2018). Biological control of pests. *Journal of Pharmacognosy and Phytochemistry*, 7(1), 2823–2825.
- Kradolfer, U., & Erhardt, A. (1995). Nectar secretion patterns in *Salvia pratensis* L. (Lamiaceae). *Flora*, 190(3), 229–235. [https://doi.org/10.1016/S0367-2530\(17\)30656-4](https://doi.org/10.1016/S0367-2530(17)30656-4)
- Krenn, H. W. (2010). Feeding mechanisms of adult lepidoptera: Structure, function, and evolution of the mouthparts. *Annual Review of Entomology*, 55(1), 307–327.
- Larcenaire, C., Wang, F., Holásková, I., Turcotte, R., Gutensohn, M., & Park, Y.-L. (2021). Characterization of the insect assemblage and associated floral volatiles of black cherry (*Prunus serotina*). *Plants (Basel, Switzerland)*, 10(10), 2195. <https://doi.org/10.3390/plant10102195>
- Lerch, D., Blüthgen, N., & Mody, K. (2024). Data from: Consistent temperature dependence of functional response parameters and their use in predicting population abundance. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.2ngf1vhz5>
- Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, 56(4), 311–323.
- Lowenstein, D. M., Matteson, K. C., & Minor, E. S. (2019). Evaluating the dependence of urban pollinators on ornamental, non-native, and 'weedy' floral resources. *Urban Ecosystems*, 22, 293–302.
- Machado, B. B., Orue, J. P. M., Arruda, M. S., Santos, C. V., Sarath, D. S., Goncalves, W. N., Silva, G. G., Pistori, H., Roel, A. R., & Rodrigues-Jr, J. F. (2016). BioLeaf: A professional mobile application to measure foliar damage caused by insect herbivory. *Computers and Electronics in Agriculture*, 129, 44–55.
- Mello, M. A. R., de Mendonça Santos, G. M., Mechi, M. R., & Hermes, M. G. (2011). High generalization in flower-visiting networks of social wasps. *Acta Oecologica*, 37(1), 37–42.
- Menke, P. (2016). Grüne Infrastruktur. *Standort*, 40(2), 117–122. <https://doi.org/10.1007/s00548-016-0424-2>
- Mody, K., Collatz, J., Bucharova, A., & Dorn, S. (2017). Crop cultivar affects performance of herbivore enemies and may trigger enhanced pest control by coaction of different parasitoid species. *Agriculture, Ecosystems & Environment*, 245, 74–82.
- Mody, K., Collatz, J., & Dorn, S. (2015). Plant genotype and the preference and performance of herbivores: Cultivar affects apple resistance to the florivorous weevil *Anthonomus pomorum*. *Agricultural and Forest Entomology*, 17(4), 337–346.
- Mody, K., Lerch, D., Müller, A.-K., Simons, N. K., Blüthgen, N., & Harnisch, M. (2020). Flower power in the city: Replacing roadside shrubs by wildflower meadows increases insect numbers and reduces maintenance costs. *PLoS One*, 15(6), e0234327.
- Mody, K., & Linsenmair, K. E. (2004). Plant-attracted ants affect arthropod community structure but not necessarily herbivory. *Ecological Entomology*, 29(2), 217–225.
- Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, 104(50), 19891–19896.
- Pacini, E., Nepi, M., & Vesprini, J. L. (2003). Nectar biodiversity: A short review. *Plant Systematics and Evolution*, 238(1–4), 7–21. <https://doi.org/10.1007/s00606-002-0277-y>
- Pardee, G. L., & Philpott, S. M. (2014). Native plants are the bee's knees: Local and landscape predictors of bee richness and abundance in backyard gardens. *Urban Ecosystems*, 17, 641–659.
- Patefield, W. M. (1981). Efficient method of generating random R × C tables with given row and column totals: Algorithm AS 159. *Applied Statistics*, 30(1), 91–97.
- Philpott, S. M., Lucatero, A., Andrade, S., Hernandez, C., & Bichier, P. (2023). Promoting beneficial arthropods in urban agroecosystems: Focus on flowers, maybe not native plants. *Insects*, 2023(14), 576.
- Plumbaginaceae. (2001). Retrieved from <https://www.spektrum.de/lexikon/biologie-kompakt/plumbaginaceae/9194>
- Praz, C. J., Müller, A., & Dorn, S. (2008). Specialized bees fail to develop on non-host pollen: Do plants chemically protect their pollen? *Ecology*, 89(3), 795–804. <https://doi.org/10.1890/07-0751.1>
- Prendergast, K. S., Dixon, K. W., & Bateman, P. W. (2022). A global review of determinants of native bee assemblages in urbanised landscapes. *Insect Conservation and Diversity*, 15(4), 385–405.
- Price, P. W., Denno, R. F., Eubanks, M. D., Finke, D. L., & Kaplan, I. (2011). *Insect ecology: Behavior, populations and communities*. Cambridge University Press.
- R Core Team. (2021). *A language and environment for statistical computing*.
- Rader, R., Bartomeus, I., Garibaldi, L. A., Garratt, M. P. D., Howlett, B. G., Winfree, R., Cunningham, S. A., Mayfield, M. M., Arthur, A. D., Andersson, G. K., Bommarco, R., Brittain, C., Carvalheiro, L. G., Chacoff, N. P., Entling, M. H., Foully, B., Freitas, B. M., Gemmill-Herren, B., Ghazoul, J., ... Woyciechowski, M. (2016). Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America*, 113(1), 146–151. <https://doi.org/10.1073/pnas.1517092112>
- Ritchie, A. D., Ruppel, R., & Jha, S. (2016). Generalist behavior describes pollen foraging for perceived oligolectic and polylectic bees. *Environmental Entomology*, 45(4), 909–919.
- Rosas-Guerrero, V., Aguilar, R., Martín-Rodríguez, S., Ashworth, L., Lopezariza-Mikel, M., Bastida, J. M., & Quesada, M. (2014). A

- quantitative review of pollination syndromes: Do floral traits predict effective pollinators? *Ecology Letters*, 17(3), 388–400.
- Salisbury, A., Al-Beidh, S., Armitage, J., Bird, S., Bostock, H., Platoni, A., Tatchell, M., Thompson, K., & Perry, J. (2020). Enhancing gardens as habitats for soil-surface-active invertebrates: Should we plant native or exotic species? *Biodiversity and Conservation*, 29, 129–151.
- Scherber, C., Mwangi, P. N., Temperton, V. M., Roscher, C., Schumacher, J., Schmid, B., & Weisser, W. W. (2006). Effects of plant diversity on invertebrate herbivory in experimental grassland. *Oecologia*, 147, 489–500.
- Scheuchl, E. (1996). *Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs. Band II: Schlüssel der Arten der Familien Megachilidae und Melittidae*. Eigenverlag Erwin Scheuchl.
- Schmack, J. M., & Egerer, M. (2023). Floral richness and seasonality influences bee and non-bee flower interactions in urban community gardens. *Urban Ecosystems*, 26, 1–14.
- Schoonhoven, L. M., van Loon, J. J. A., & Dicke, M. (2005). *Insect-plant biology*. Oxford University Press.
- Schwalter, T. D. (2020). *Insects and society*. CRC Press.
- Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarli, D., Ammer, C., Bauhus, J., Fischer, M., Habel, J. C., Linsenmair, K. E., Nauss, T., Penone, C., Prati, D., Schall, P., Schulze, E. D., Vogt, J., Wöllauer, S., & Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, 574(7780), 671–674. <https://doi.org/10.1038/s41586-019-1684-3>
- Soliveres, S., van der Plas, F., Manning, P., Prati, D., Gossner, M. M., Renner, S. C., Alt, F., Arndt, H., Baumgartner, V., Binkenstein, J., Birkhofer, K., Blaser, S., Blüthgen, N., Boch, S., Böhm, S., Börschig, C., Buscot, F., Diekötter, T., Heinze, J., ... Allan, E. (2016). Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. *Nature*, 536(7617), 456–459. <https://doi.org/10.1038/nature19092>
- Staab, M., Pereira-Peixoto, M. H., & Klein, A.-M. (2020). Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. *Oecologia*, 194(3), 465–480.
- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T. E., & Paxton, R. J. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*, 11(1), 576.
- Tiesler, F.-K., Bienefeld, K., & Büchler, R. (2016). *Selektion bei der Honigbiene* (Erstausgabe, 1. Auflage). Buschhausen Druck- und Verlagshaus. Retrieved from https://buschhausen-shop.de/leseproben/Leseprobe_Selektion_der_Honigbiene.pdf
- Umweltbundesamt. (2022, February 18). Siedlungs- und Verkehrsfläche. Retrieved from <https://www.umweltbundesamt.de/daten/flaechhe-boden-land-oekosysteme/flaechhe/siedlungs-verkehrsflaechhe#anhaltender-flaechenverbrauch-fur-siedlungs-und-verkehrszw-ecke->
- Urbanowicz, C., Muñiz, P. A., & McArt, S. H. (2020). Honey bees and wild pollinators differ in their preference for and use of introduced floral resources. *Ecology and Evolution*, 10(13), 6741–6751.
- Wagner, D., Grames, E., Forister, M., Berenbaum, M., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, 118(2), e2023989118.
- Webber, C. J., Peterson, A. J., Kelly, D., & Clemens, J. (2012). Native and exotic flower visitors in the Christchurch botanic gardens and their contrasting plant preferences. *New Zealand Natural Sciences*, 37–49. <https://ir.canterbury.ac.nz/bitstream/handle/10092/100623/webber.pdf?sequence=1>
- Wenzel, A., Grass, I., Belavadi, V. V., & Tschardt, T. (2020). How urbanization is driving pollinator diversity and pollination—A systematic review. *Biological Conservation*, 241, 108321.
- Wood, T. J., Kaplan, I., & Szendrei, Z. (2018). Wild bee pollen diets reveal patterns of seasonal foraging resources for honey bees. *Frontiers in Ecology and Evolution*, 6, 210.
- Zurbuchen, A., & Mueller, A. (2012). *Wildbienenenschutz - von der Wissenschaft zur Praxis. Bristol-Schriftenreihe: Bd. 33*. Haupt.

SUPPORTING INFORMATION

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

Figure S1. Comparison of the average number of flower visitors observed on the studied plant species per study plot, summarized for the target plant groups NATIVE (green), RELATED (yellow) and EXOTIC (pink).

Figure S2. Comparison of the mean feeding damage (%) observed for the studied plant species per study plot, summarized for the target plant groups NATIVE (green), CONVERTED (yellow) and EXOTIC (pink).

Table S1. Overview of plant species that have not flowered in the named plots.

How to cite this article: Lerch, D., Blüthgen, N., & Mody, K. (2024). Home sweet home: Evaluation of native versus exotic plants as resources for insects in urban green spaces. *Ecological Solutions and Evidence*, 5, e12380. <https://doi.org/10.1002/2688-8319.12380>