



What makes a service plant attractive to pollinators? An exploration of the influence of plant traits among 38 flowering plant species

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ABSTRACT

Global declines of pollinator communities have triggered interest in flowering plants to support pollinators in agricultural areas. Flowering plants may differ in their attractiveness for pollinators, and it is not clear which plant traits (co-)determine the attractiveness of flowering plants for different pollinator groups. Here we assessed the communities of hoverflies and bees on 38 flowering plant species by visual counts and sweep net sampling in a replicated field experiment in Korla, Xinjiang, China. There were 13 sampling rounds in 2020 and 15 in 2021. Pollinators from sweep net samples were identified to species level and their body size recorded. Flower cover, corolla depth and width, plant height, and flowering duration were assessed. A total of 2751 hoverflies, 1350 honeybees and 621 wild bees were observed using the two sampling methods. *Diplotaxis tenuifolia*, *Foeniculum vulgare* and *Anethum graveolens* were the most frequently visited plants. The abundance of adult hoverflies and honeybees was negatively associated with corolla depth of flowering plants in 2020, while wild bee abundance was consistently negatively associated with corolla depth across both years. Plant flowering duration not only influenced the period of pollinator abundance, but longer flowering plants also hosted a higher abundance of hoverflies and wild bees in 2021. The abundance of pollinators was not associated with flower cover. The body length of hoverflies and wild bees was not associated with flowering plant traits. Our study demonstrates the potential of trait-based approaches to predict pollinator responses to inform the selection of flowering plants. However, it also reveals interannual variability in trait-pollinator relationships, highlighting the need for continued empirical testing to ensure effective plant selection for supporting local pollinator communities.

1. Introduction

Pollinators are crucial for the pollination of many crop species (Klein et al., 2007; Aizen et al., 2009), but pollinators may depend critically on pollen and nectar resources provided by flowering non-crop plants (Schmidt et al., 2022). Flower strips with entomophilous plants have been shown to support pollinators and enhance pollination in crops and orchards in Europe and the USA (Blaauw and Isaacs, 2014; Campbell et al., 2017). However, the attractiveness of flowering plant species for pollinators may vary geographically because of region-specific plant and pollinator communities (Page et al., 2021). Therefore, a region-specific approach for the selection and establishment of flowering plant species is needed to support local pollinator communities, potentially reducing pollination deficits and contributing to more resilient crop production.

Floral morphological traits influence plant attractiveness to

pollinators, while pollinator morphology determines which flowers can be effectively visited (Violle et al., 2007; Schleuning et al., 2015; Bergamo et al., 2020). For instance, plants with large flowers are attractive for many pollinator species, while flowers with deep and narrow corollas are usually accessible to only a few specialized pollinator species (Lázaro et al., 2020). However, the relationship between plant traits and pollinator abundance is still debated since these relationships are often moderated by local conditions, including the composition of wild pollinator communities (Lázaro et al., 2013; Harrison and Winfree, 2015). Hence, there is a need to explore which plant traits are relevant for the selection of flowering plant species to support pollinator communities in specific regions.

Plant-pollinator interactions are moderated by the combination of traits of flowering plants and those of pollinators (Junker et al., 2013; Naghiloo et al., 2021). For instance, pollinator body size is associated

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with dispersal capacity and can therefore indirectly govern their visitation of particular flowering plant species in the landscape (Stang et al., 2009; Benjamin et al., 2014). Hoverflies with a short proboscis mainly feed on flowers with shallow corollas (van Rijn and Wäckers, 2016), while larger bumblebees with a relatively long proboscis are equipped to feed from deeper flowers (Peat et al., 2005). Since proboscis length is linked with body length (Cariveau et al., 2016), the distribution of body sizes of flower visiting pollinator communities may indicate to what extent there is niche overlap between pollinators and competition between species for floral resources. In particular, Apidae with proboscis lengths similar to the honeybee exhibit high resource overlap (Cappellari et al., 2022). However, there is still a substantial information gap how different pollinator groups are associated with plant species with different traits. Linking the body size of pollinators with flower traits could provide further insights in possible relationships between particular groups of pollinators and flowering plants. Such understanding would enable a more targeted approach to support pollinator groups with tailored flowering plant species selection.

The aim of this 2-year study was to assess the community of hoverflies and bees on 38 candidate flowering service plant species and assess the relationship between the abundance and body size of pollinators and the traits of these flowering plants. Specifically, we assessed (i) the communities of the adult hoverflies and bees on these plant species, (ii) how plant traits (flower cover, corolla depth, plant height and flowering duration) influenced the abundance of hoverflies, honeybees and wild bees on the flowering plants, and (iii) how pollinator body size was related to these plant traits. This information can be used to inform the selection of flowering service plant species to support pollinators in Xinjiang, China, and the wider region of central Asia.

2. Materials and methods

2.1. Study area

The study was conducted in Korla, Xinjiang province, in northwest China, which is a major irrigated cropland area between the Tarim desert and the Tianshan mountains. The climate of the Tarim basin is classified as cold arid desert (BWk) according to the Köppen-Geiger climate classification while the mountains around it have a semi-arid climate (BSk) in the foothills and a tundra climate (ET) at higher elevations (Kottek et al., 2006). Korla has low rainfall (160 mm/year) and a high evaporative demand (1256 mm) (Dong et al., 2020; Hu et al., 2021), but irrigation water is available by snowmelt from the Tianshan mountains. Irrigated cotton (*Gossypium hirsutum*) is the main crop in Korla, but there is also widespread fruit production, such as Korla fragrant pear (*Pyrus sinkiangensis*), Aksu apple (*Malus domestica*), and Turpan grape (*Vitis vinifera*). Furthermore, there is cultivation of fodder crops such as silage corn (*Zea mays*) and alfalfa (*Medicago sativa*), cash crops such as chili pepper (*Capsicum annuum*) and sugar beet (*Beta vulgaris*), and medicinal crops such as liquorice (*Glycyrrhiza uralensis*) and goji (*Lycium chinense*). Pesticide use, including broad-spectrum insecticides, is generally high to protect crops from weeds, diseases and pests, but this can also impact beneficial insects, such as pollinators.

2.2. Plant selection and experimental design

We selected 38 plant species to assess their potential to enhance beneficial insects based on the following criteria: (i) the plants have been used for habitat diversification in other parts of the world; or (ii) the plants are known to be attractive for pollinators and natural enemies; and (iii) the plants are expected to be adapted to the environmental conditions in Xinjiang (Sun et al., 2025). We conducted a literature search for potential endemic and exotic entomophilous plant species, and checked the required environmental conditions using the *Flora of China* (Li, 2007).

In 2020 and 2021, a field trial was conducted at the CAAS-IPP

experimental station in Korla, Xinjiang, China (85.81°E, 41.75°N). The trial was laid out as a randomized complete block design with three blocks. In each year plant species were randomly allocated to plots. There were therefore three plots per plant species, except for cotton which had six replicates (i.e., two plots per block) as cotton is the main crop species in Xinjiang. The size of each plot was $7 \times 6 \text{ m}^2$ and the spacing between plots was 1.5 m. The total area of the experimental field was $216 \times 54 \text{ m}^2$ and it was bordered by cotton fields on the south and east side, young fruit trees on the north side and an experimental field with various annual crops on the west side (Fig. S1).

The plots were fertilized, irrigated, tilled and covered with plastic mulch to reduce evaporation and suppress weeds. Plots were sown in late April. The trial was irrigated every two weeks and hand weeded monthly. No pesticides were used. Thirty-seven and 35 plant species established successfully in 2020 and 2021, respectively (Table 1, Table S1).

2.3. Insect sampling

We assessed the insect community on 38 plant species by visual counts and sweep net sampling (Table S1). Among the 37 established species in 2020, *Centaurea cyanus* and *Vicia villosa* were not sampled with sweep netting because of too little foliage cover, while in 2021 among the 35 established species, *Glycine max* was not sampled for this reason. Across the two years, all 38 species were sampled using sweep netting; 31 species in both years, four species only in 2020 and three species only in 2021. Assessments were done weekly on days without precipitation from late May to early September in each year. In total, 13 sampling rounds were conducted in 2020 and 15 rounds in 2021. In each plot, we observed the flying, foraging and resting insects on and near the five plants in five 1 m^2 subplots during 30 s, and recorded the number of adult hoverflies, honeybees, wild bees on the plants as broad categories. After completing the visual counts, we took 20 sweeps per plot (4 sweeps per subplot $\times$ 5 subplots) and sampled the insect community in the top 10 cm of the canopy. The sweep net had a 30 cm diameter and the handle was 115 cm long. Insects collected by sweep netting were put in ziplock plastic bags ($18 \times 25 \text{ cm}$), brought to the laboratory and stored at -20°C until processing. Sweep net samples were sorted into hoverflies, honeybees, and wild bees, and they were further identified to species level whenever possible. Unknown species were pinned and sent out to a specialist for identification.

2.4. Flowering plant traits

We assessed variables associated with plant phenology (flowering duration and peak bloom duration) throughout the season. Observations on plant morphology (plant height, height of the top flower, flower area, flower cover, corolla depth and width) were made once, at peak bloom in 2021. These traits are relevant for the detection of flowers by pollinators (e.g., flower cover) and the accessibility of nectar resources (e.g., corolla depth). Plant height and maximum flower height (i.e., distance from the highest flower to the ground) were measured with a measuring tape. A plant species was considered to be flowering if at least one flower was observed in any of the plots. We randomly selected ten flowers or floret clusters per plant species at peak bloom to assess corolla depth, width and flower area in laboratory. We took digital photos of longitudinal cross sections through the axis of each flower or floret, keeping a metric ruler as a reference to determine corolla depth and width (Fig. S2). Corolla depth and width were measured through ImageJ software (Fiedler and Landis, 2007). For most plant species, corolla depth was defined as the vertical distance from the base of the nectary to the upper edge of the petals. Width of a flower was the greatest diameter between the outer edges of the petals. For Asteraceae, corolla depth was the vertical distance from the base of the nectary to the edge of the tubiform floret, and corolla width was the tube width of the tubiform floret. For Apiaceae, the corolla depth was considered to be zero and the

Table 1
 Overview of 38 plant species and plant traits (plant height, height of top flower, flower area, flower cover, flower cover classification, corolla width, depth, flowering duration in 2020 and 2021, nativeness and life cycle). Means $\pm$ standard errors are presented. Flower cover was classified as Sparse (S; < 10 %), Medium (M; 10–20 %) or High (H; > 20 %).

Plant species	Family	Plant height (cm)	Height of top flower (cm)	Flower area (cm ²)	Flower cover (%)	Flower cover classification (S/M/H)	Corolla width (mm)	Corolla depth (mm)	Flowering duration 2020 (weeks)	Flowering duration 2021 (weeks)	Nativeness	Life cycle
<i>Allium cepa</i>	Liliaceae	34 $\pm$ 1	—	—	—	—	—	—	—	0	Exotic	Perennial
<i>Anethum graveolens</i>	Apiaceae	107 $\pm$ 2	100 $\pm$ 2	0.28 $\pm$ 0.02	7.58 $\pm$ 0.46	S	1.8 $\pm$ 0.05	0 $\pm$ 0	10	12	Exotic	Annual
<i>Arachis hypogaea</i>	Leguminosae	17 $\pm$ 1	4 $\pm$ 0	1.23 $\pm$ 0.04	0.83 $\pm$ 0.03	S	4.77 $\pm$ 0.15	7.22 $\pm$ 0.23	6	8	Exotic	Annual
<i>Arctium lappa</i>	Asteraceae	—	—	—	—	—	—	—	0	—	Native	Biennial
<i>Borago officinalis</i>	Boraginaceae	93 $\pm$ 3	90 $\pm$ 3	2.83 $\pm$ 0.11	1.33 $\pm$ 0.05	S	5.16 $\pm$ 0.19	2.37 $\pm$ 0.12	12	13	Exotic	Annual
<i>Brassica campestris</i>	Brassicaceae	94 $\pm$ 1	94 $\pm$ 1	0.75 $\pm$ 0.03	13.79 $\pm$ 0.54	M	4.11 $\pm$ 0.12	4.27 $\pm$ 0.13	11	10	Native	Annual
<i>Capsicum annuum</i>	Solanaceae	44 $\pm$ 1	35 $\pm$ 2	2.14 $\pm$ 0.16	0.83 $\pm$ 0.06	S	5.87 $\pm$ 0.34	3.48 $\pm$ 0.21	7	7	Exotic	Annual
<i>Carthamus tinctorius</i>	Asteraceae	78 $\pm$ 2	73 $\pm$ 1	16.97 $\pm$ 0.68	9.67 $\pm$ 0.39	S	2.51 $\pm$ 0.18	8.38 $\pm$ 0.13	7	7	Native	Annual
<i>Celosia cristata</i>	Amaranthaceae	56 $\pm$ 1	56 $\pm$ 1	0.05 $\pm$ 0	0.75 $\pm$ 0.04	S	1.86 $\pm$ 0.08	5.43 $\pm$ 0.09	7	12	Exotic	Annual
<i>Centaurea cyanus</i>	Asteraceae	95 $\pm$ 2	87 $\pm$ 2	8.87 $\pm$ 0.34	17.84 $\pm$ 0.69	M	1.51 $\pm$ 0.05	2.44 $\pm$ 0.11	—	12	Exotic	Perennial
<i>Cichorium intybus</i>	Asteraceae	155 $\pm$ 4	139 $\pm$ 3	14.31 $\pm$ 0.42	9.87 $\pm$ 0.29	S	0.93 $\pm$ 0.04	1.76 $\pm$ 0.05	10	11	Native	Perennial
<i>Cirsium japonicum</i>	Asteraceae	122 $\pm$ 2	122 $\pm$ 2	8.65 $\pm$ 0.55	0.61 $\pm$ 0.04	S	1.98 $\pm$ 0.13	2.45 $\pm$ 0.15	9	10	Native	Perennial
<i>Cirsium setosum</i>	Asteraceae	160 $\pm$ 7	160 $\pm$ 7	11.23 $\pm$ 0.78	0.56 $\pm$ 0.04	S	2.18 $\pm$ 0.11	3.25 $\pm$ 0.22	9	10	Native	Perennial
<i>Coreopsis tinctoria</i>	Asteraceae	69 $\pm$ 3	58 $\pm$ 3	15.36 $\pm$ 0.41	—	—	0.75 $\pm$ 0.06	1.41 $\pm$ 0.08	12	—	Native	Perennial
<i>Coriandrum sativum</i>	Apiaceae	74 $\pm$ 2	71 $\pm$ 2	0.76 $\pm$ 0.04	3.65 $\pm$ 0.18	S	2.19 $\pm$ 0.04	0 $\pm$ 0	9	9	Exotic	Annual
<i>Diplotaxis tenuifolia</i>	Brassicaceae	46 $\pm$ 3	46 $\pm$ 3	0.97 $\pm$ 0.1	6.65 $\pm$ 0.71	S	5.47 $\pm$ 0.4	4.92 $\pm$ 0.26	9	15	Exotic	Annual
<i>Fagopyrum esculentum</i>	Polygonaceae	52 $\pm$ 1	52 $\pm$ 1	0.1 $\pm$ 0	12.83 $\pm$ 0.59	M	4.14 $\pm$ 0.15	1.23 $\pm$ 0.09	13	15	Native	Annual
<i>Foeniculum vulgare</i>	Apiaceae	107 $\pm$ 2	107 $\pm$ 2	1.79 $\pm$ 0.06	10.17 $\pm$ 0.37	M	3.09 $\pm$ 0.09	0 $\pm$ 0	9	11	Exotic	Annual
<i>Glycine max</i>	Leguminosae	—	—	—	—	—	—	—	5	—	Native	Annual
<i>Glycyrrhiza uralensis</i>	Leguminosae	101 $\pm$ 3	—	—	—	—	—	—	—	—	Native	Perennial
<i>Gomphrena globosa</i>	Amaranthaceae	56 $\pm$ 2	56 $\pm$ 2	5.22 $\pm$ 0.15	8.35 $\pm$ 0.24	S	1.39 $\pm$ 0.09	2.78 $\pm$ 0.16	12	13	Exotic	Annual
<i>Gossypium hirsutum</i>	Malvaceae	104 $\pm$ 2	66 $\pm$ 4	22.44 $\pm$ 1.4	2.02 $\pm$ 0.13	S	49.98 $\pm$ 2.54	49.97 $\pm$ 1.19	11	10	Exotic	Annual
<i>Helianthus annuus</i>	Asteraceae	127 $\pm$ 3	127 $\pm$ 3	83.09 $\pm$ 9.65	7.48 $\pm$ 0.87	S	1.76 $\pm$ 0.07	4.97 $\pm$ 0.23	6	9	Exotic	Annual
<i>Impatiens balsamina</i>	Balsaminaceae	68 $\pm$ 2	58 $\pm$ 3	10.65 $\pm$ 0.58	39.84 $\pm$ 2.18	H	20.06 $\pm$ 1.09	11.26 $\pm$ 0.51	11	10	Native	Annual
<i>Leonurus japonicus</i>	Labiatae	69 $\pm$ 2	67 $\pm$ 2	0.42 $\pm$ 0.01	7.02 $\pm$ 0.23	S	2.57 $\pm$ 0.09	6.8 $\pm$ 0.23	9	9	Native	Annual
<i>Lobularia maritima</i>	Brassicaceae	24 $\pm$ 1	24 $\pm$ 1	0.07 $\pm$ 0.01	8.29 $\pm$ 0.64	S	2.33 $\pm$ 0.15	0.88 $\pm$ 0.04	13	15	Exotic	Perennial
<i>Lotus corniculatus</i>	Leguminosae	—	—	—	—	—	—	—	13	—	Exotic	Perennial
<i>Medicago sativa</i>	Leguminosae	59 $\pm$ 2	56 $\pm$ 2	0.2 $\pm$ 0.02	0.45 $\pm$ 0.05	S	2.84 $\pm$ 0.26	4.49 $\pm$ 0.19	12	10	Exotic	Perennial

(continued on next page)

Table 1 (continued)

Plant species	Family	Plant height (cm)	Height of top flower (cm)	Flower area (cm ²)	Flower cover (%)	Flower cover classification (S/M/H)	Corolla width (mm)	Corolla depth (mm)	Flowering duration 2020 (weeks)	Flowering duration 2021 (weeks)	Nativeness	Life cycle
<i>Melilotus officinalis</i>	Leguminosae	—	—	—	—	—	—	—	0	0	Native	Biennial
<i>Pisum sativum</i>	Leguminosae	32 ± 1	30 ± 1	2.42 ± 0.07	1.84 ± 0.05	S	7.72 ± 0.43	11.23 ± 0.52	5	5	Exotic	Annual
<i>Solanum lycopersicum</i>	Solanaceae	54 ± 2	47 ± 2	1.59 ± 0.08	1.92 ± 0.09	S	7.09 ± 0.29	5.79 ± 0.28	7	9	Exotic	Annual
<i>Sonchus oleraceus</i>	Asteraceae	159 ± 4	153 ± 4	5.94 ± 0.27	—	—	0.63 ± 0.04	1.19 ± 0.08	8	—	Exotic	Annual
<i>Tagetes erecta</i>	Asteraceae	77 ± 2	75 ± 2	37.81 ± 2.5	20.42 ± 1.35	H	1.6 ± 0.1	3.69 ± 0.13	13	10	Exotic	Annual
<i>Trifolium pratense</i>	Leguminosae	64 ± 1	61 ± 2	5.26 ± 0.34	3.52 ± 0.22	S	1.92 ± 0.1	9.31 ± 0.41	10	10	Exotic	Perennial
<i>Trifolium repens</i>	Leguminosae	21 ± 1	21 ± 1	3.99 ± 0.3	1.28 ± 0.1	S	1.95 ± 0.07	6.29 ± 0.18	8	9	Exotic	Perennial
<i>Vicia faba</i>	Leguminosae	25 ± 1	22 ± 1	1.57 ± 0.07	0.91 ± 0.04	S	4.9 ± 0.11	13.44 ± 0.32	6	10	Exotic	Annual
<i>Vicia villosa</i>	Leguminosae	34 ± 2	21 ± 2	0.2 ± 0.03	0.86 ± 0.11	S	2.83 ± 0.06	11.64 ± 0.26	—	11	Exotic	Annual
<i>Zinnia elegans</i>	Asteraceae	135 ± 3	131 ± 3	63.39 ± 1.99	26.62 ± 0.84	H	6.1 ± 0.45	5.55 ± 0.51	13	13	Exotic	Annual

corolla width was taken equal to the width of a floret. To calculate flower area (i.e., the area of a single flower or floret) in the plane perpendicular to the flower axis, we marked the flower area in white in the ichnographic photos with Adobe Photoshop 2020, and then assessed the white area with ImageJ. The mean number of flowers (e.g., Asteraceae species), number of florets (e.g., *C. cristata*, *F. esculentum*, *L. maritima*), or number of inflorescences (e.g., Apiaceae plants, *A. graveolens*, *C. sativum*, *F. vulgare*) per subplot (1 m²) was calculated over 5 subplots per plot during peak bloom. The flower cover was then calculated by multiplying the mean number of flowers, florets or inflorescences per subplot with the average area per flower, floret or inflorescence as determined from the ichnographic photos (Fig. S3). We defined three categories of flower cover: Sparse (< 10 % of ground cover), Medium (10–20 %), and High (> 20 %). We recorded plant phenology during each insect assessment round as “no flowers”, “flowering” (at least one flower observed in any plot of the species) or “peak bloom” (> 80 % of the flowers were in full bloom).

2.5. Pollinator body size assessment

We measured the body length of each pollinator specimen from the point of antennal insertion to the end of the terminal abdominal tergite. Head width was measured using a digital calliper under a stereo microscope. For common pollinator species we measured at least 10 specimens per year, and if the number of specimens was less than ten all specimens were measured. Body size of pollinators was categorized as Small (< 7.5 mm), Medium (7.5–12 mm) or Large (> 12 mm) (Table S2). As a reference, honeybees (*Apis mellifera*) had a body length of 11.36 ± 0.14 mm (mean ± SEM).

2.6. Statistical analyses

Since sweep net samples on 38 plant species were identified to species level we used these data for all statistical analyses. We constructed plant-pollinator networks for hoverflies and bees using the ‘bipartite’ package in R (Dormann et al., 2008). As these networks focus on the visualization of all plant-pollinator associations, we summed all sampling rounds per year and constructed four separate networks: for hoverflies and bees, in 2020 and 2021. We used the ggplot() function in package ‘ggplot2’ to visualize the pollinator population dynamics (Wickham, 2011).

Relationships between the abundance of pollinator groups and plant traits were analysed using generalized linear models with a negative binomial error distribution. As this analysis focuses on the relationship between the traits of flowering plants, we summed the pollinator abundance data for each plot over all sampling rounds during which the plants were flowering. All analyses were done separately for the data of 2020 and 2021. Response variables included the abundances of hoverflies, honeybees, wild bees and all pollinators combined, and the explanatory variables were flower cover (%), corolla depth and width (mm), plant height (cm), height of the top flower (cm), duration of flowering (weeks), duration of peak bloom (weeks), and nativeness of the plant species (native or exotic). To account for differences in sampling effort for plant species with different flowering durations, we included log(number of sampling rounds when plants were flowering) as an offset variable, which means that in this analysis the estimated model coefficients predict the abundance observed per round. We checked the multicollinearity among explanatory variables via variance inflation factor (VIF) and found high correlations between corolla width and corolla depth, and between plant height and the height of the top flower (VIF scores > 10), and we also found considerable collinearity between duration of flowering and duration of peak bloom (VIF scores > 2.5). To avoid issues with collinearity, we used corolla depth, plant height and flowering duration as predictor variables in regressions, and discarded corolla width, height of the top flower and duration of peak bloom. The generalized linear models were constructed using the glm.nb() function

in the 'MASS' package (Ripley et al., 2013). We checked whether model assumptions were met using the `simulateResiduals()` function in the 'DHARMA' package (Hartig, 2018).

Relationships between the body size of pollinators and plant traits were analysed using linear regression. Body length and head capsule width of pollinators were strongly correlated ($R^2 = 82.4\%$), and therefore we only report the analysis for pollinator body length (Fig. S4, Table S2). We calculated abundance-weighted average body length of pollinators observed on each plant species to assess whether there is a relationship between plant traits and the average size of pollinators collected on them. We used the weighted body length of hoverflies and wild bees as response variables, and the explanatory variables were flower area (cm^2), corolla depth (mm), plant height (cm), and flowering duration (weeks). These regressions were conducted using the function `lm()` in the 'stats' package (Chambers and Hastie, 1992). All analyses were done separately for the data of 2020 and 2021.

For all analyses, we used a model selection and model averaging procedure to obtain robust parameter estimates with reduced bias and uncertainty using the `dredge()` and `model.avg()` functions in the 'MuMin' package (Barton, 2023). For the global models that included an offset, we fixed the offset in the `dredge()` function to ensure that all models in the selection set retained the offset term (Table S3). Bias-corrected Akaike's information criterion (AICc) was used to rank all candidate models derived from the full global model (Burnham and Anderson, 2004). Models within $\Delta\text{AICc} < 4$ were selected for the model averaging procedure to ensure sufficient model support while capturing the variability across plausible ecological hypotheses (Table S3 and S4) (Burnham and Anderson, 2002). The relative importance of each explanatory variable was assessed by summing the Akaike weights of all models in the top model set containing that variable (Grueber et al., 2011). We used the full averaged results (zero-averaging) in the `model.avg()` procedure such that a model without a given predictor contributed a value of 0 to the calculation of the weighted mean coefficient across models of that predictor (Grueber et al., 2011). All data analyses were conducted in R 4.2.1 (R Development Core Team, 2022).

3. Results

3.1. Communities of hoverflies, honeybees and wild bees

Using visual counts, we observed 2854 pollinators on the 38 plant species in two years, comprising 1568 hoverflies (55 %), 1071 honeybees (37 %) and 215 wild bees (8 %). Sweep net sampling resulted in 1868 individuals on 38 plant species in two years, and the catch consisted of 1183 hoverflies (63 %), 279 honeybees (15 %) and 406 wild bees (22 %) (Fig. S5). *Sphaerophoria indiana* (595; 50 %) and *Eupeodes corollae* (295; 25 %) were the dominant hoverfly species and *Lasioglossum pseudannulipes* (245; 60 %) and *Pseudapis mandschurica* (64; 16 %) were the most abundant wild bee species in sweep net samples (Fig. 1). There was lower honeybee abundance in 2021 than in 2020, whereas wild bee abundance was higher in 2021 than in 2020 (Table S6, S7).

Visual counts and sweep net samples indicated that hoverflies were most abundant on arugula (*Diplotaxis tenuifolia*), fennel (*Foeniculum vulgare*) and dill (*Anethum graveolens*). Honeybees were abundant on fennel, arugula, borage (*Borago officinalis*) and dill, while wild bees were abundant on alfalfa (*Medicago sativa*) in 2020 and on arugula and sweet alyssum (*Lobularia maritima*) in 2021 (Fig. 1, Table S5, S6, S7). Hoverflies and wild bees showed similar plant species preferences as honeybees (Fig. S6). *D. tenuifolia*, *F. vulgare*, *A. graveolens*, *B. officinalis* and *L. maritima* had relatively long flowering durations of 12, 10, 11, 12 and 14 weeks (two-year average; Fig. 2, Table 1).

3.2. Flower trait-pollinator associations

The abundance of hoverflies, honeybees and total pollinators was

negatively associated with corolla depth of flowering plants in 2020, and wild bees were negatively associated with corolla depth in both years (Table 2). Furthermore, the average abundances per round of hoverflies, wild bees and total pollinators were positively associated with flowering duration in 2021.

3.3. Relationship between pollinator body size and flower traits

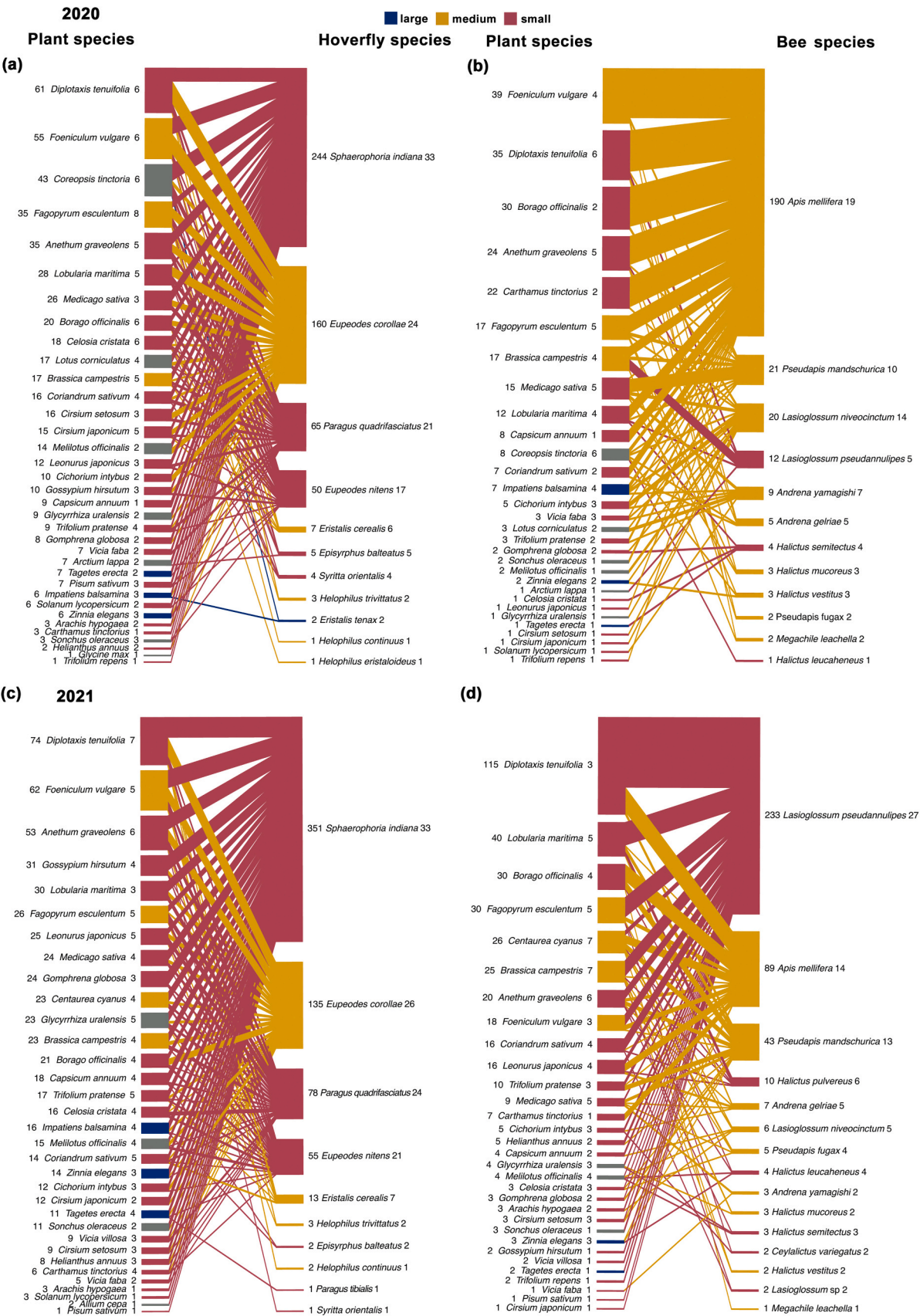
The body length of hoverflies ranged from 4.25 to 12.88 mm, and the head width ranged from 1.43 to 4.31 mm. The body length of honeybees was 11.36 ± 0.14 mm and the head width was 3.51 ± 0.07 mm. The body length of wild bees ranged from 3.72 to 9.18 mm, while the head width ranged from 0.95 to 3.05 mm (Table S2). The body length and head width of hoverflies and bees were strongly positively related ($R^2 = 82.4\%$; Fig. S4). The abundance-weighted body length of hoverflies and wild bees was not associated with any of the flower traits (Table 3).

4. Discussion

Pollinator communities and the flowering plant species they use remain largely undocumented in Xinjiang (Shi et al., 2024). This represents an important knowledge gap given the region's reliance on pollination-dependent fruit crops. Notably, Korla fragrant pear (KFP) orchards in Xinjiang experience high pollination deficits, and depend heavily on managed honeybees (*Apis mellifera*) to meet their pollination requirement (Li et al., 2022). In this study we characterized hoverfly and bee communities on 38 flowering plant species using visual counts and sweep netting and assessed the relationship between plant traits and pollinator abundance observed on the plants. We found that *Sphaerophoria indiana* and *Eupeodes corollae* were the dominant hoverfly species and *Lasioglossum pseudannulipes* and *Pseudapis mandschurica* were the most numerous wild bee species in sweep net samples. Several plant species, such as *Diplotaxis tenuifolia*, *Foeniculum vulgare*, *Anethum graveolens*, *Lobularia maritima* and *Borago officinalis*, were frequently visited by a wide range of pollinator species. Plants with shallow corollas attracted relatively many wild bees in two years, and honeybees and hoverflies in one year. Plants with longer flowering durations attracted relatively many hoverflies and wild bees in one year. Overall, plants with shallow corollas and long flowering durations, such as *D. tenuifolia*, *F. vulgare*, *A. graveolens*, are suitable to enhance pollinators in Xinjiang, but there is also considerable interannual variability in these plant trait-pollinator relationships.

S. indiana and *E. corollae* were the dominant hoverfly species on more than 30 plant species (Fig. 1a, c). The larvae of these hoverfly species are zoophagous, feeding mostly on aphids, and therefore these species do not only contribute to crop pollination, but also to pest suppression in crops (Pekas et al., 2020). *L. pseudannulipes* was the dominant wild bee species in 2021 and was most often observed on *D. tenuifolia* (Fig. 1d). Likewise, Li et al. (2025) found this species to be abundant in Korla fragrant pear orchards. *Lasioglossum* spp. are small ground-nesting wild bees that visit a wide range of native and exotic plant species (Shebl, 2012; Kleijn et al., 2015; Elliott et al., 2021). Although *L. pseudannulipes* carry relatively few pollen grains and move relatively slowly between rape flowers (Rader et al., 2009; Howlett et al., 2011), they can occur in relatively high numbers in areas with suitable habitat and can therefore still be locally relevant pollinators (Rader et al., 2012; Garantonakis et al., 2016; Pisanty et al., 2016). While hoverflies and wild bees, such as *S. indiana*, *E. corollae* and *L. pseudannulipes*, aggregated at flowering flower plots in our experiment, further studies are needed to evaluate the contribution of these species to pest suppression and pollination in crops.

Plants with shallow corolla flowers and long flowering durations, such as *D. tenuifolia*, *L. maritima*, *F. vulgare* and *A. graveolens*, attracted relatively many hoverflies, honeybees and wild bees when they were flowering. *D. tenuifolia* was also found to be attractive to bees and hoverflies in Spain (Barbir et al., 2015). The negative relationships



(caption on next page)

Fig. 1. Plant-hoverfly network and plant-bee network based on sweep net sampling data in 2020 (a, b) and 2021 (c, d). At the left of each panel, plant species are ranked by the total abundance of hoverflies or bees. Plant-specific flower cover at peak bloom is indicated in blue (> 20 %), yellow (10–20 %) and red (< 10 %). For plant species indicated in grey no flower cover was assessed because of poor establishment or no flowering during the assessment period in 2021. The numbers before the plant name indicate the number of specimens of hoverflies or bees captured on them and the numbers following the plant name indicates the richness of pollinator species that was found on the plant. At the right of each panel, hoverfly and bee species are ranked by their abundance, and relative body size is indicated in blue (> 12 mm), yellow (7.5–12 mm) or red (< 7.5 mm). The number before the pollinator name indicates the number of specimens captured and the number following the pollinator name indicates the number of plant species from which the species was collected. Lines connecting plant and pollinator species represent catches from sweep net samples and are weighted by the strength of association as represented by the number of pollinator individuals found on the plant species.

between corolla depth and pollinator abundance confirm that shallow flowers provide accessible nectar to diverse communities of hoverflies and short-tongued bees (van Rijn and Wäckers, 2016; Heuel et al., 2024). Plant species with relatively long flower durations attracted relatively many hoverflies and wild bees per sampling round. Due to their long flowering duration, these plants provide predictable nectar and pollen resources over an extended time, which possibly encourages pollinators to return frequently (Waser and Real, 1979; Goulson, 1999). Pollinators may learn to associate these plants with reliable food sources, enhancing visitation rates (Chittka and Raine, 2006). Although we found that plant species with long flowering durations attracted many pollinators, this was only the case in 2021, and not in 2020. In addition, there were exceptions as *Zinnia elegans* had a relatively long flowering duration while hosting relatively few pollinators. This indicates that flowering duration should not be the only criterion for plant species selection, and that other traits, such as corolla depth, quality and quantity of pollen and nectar, are also important (Somme et al., 2015). Besides the selection of plant species with shallow corollas and long flowering durations, the onset of flowering time can be manipulated by the time of sowing for annual plant species (Riedinger et al., 2014). The selection of plant species, such as *D. tenuifolia*, *L. maritima*, *F. vulgare* and *A. graveolens*, targeting specific pollinator groups, combined with optimized sowing dates, may enhance resource availability for pollinators and improve pollination services in pollination dependent crops.

Taller flowering plants were marginally more attractive for hoverflies (Table 2), which aligns with observations that flower visitation of hoverflies increased with plant height in the Czech Republic (Klecka et al., 2018). This suggests that taller plants stand out more and are easier to find for hoverflies (Hernández-Villa et al., 2020). Surprisingly, we did not find a positive relationship between flower cover and pollinator abundance. Studies that reported positive relationships between flower cover and bee visitation explained this by a higher availability of pollen and nectar at high flower cover levels (Makino and Sakai, 2007; Makino et al., 2007; Rowe et al., 2020). In our study, we assessed flower cover only once, during peak bloom, and we did not measure pollen and nectar quantity or quality of flowers, which limits our ability to explain this finding. Nevertheless, the contrasting findings of our study in Xinjiang and studies in other parts of the world indicate that recommendations for the selection of suitable plant species to support pollinator communities cannot always be generalized across geographic areas, and local testing remains necessary.

The abundance of pollinator species and the relationships between plant traits and pollinator visitation showed interannual variation. For instance, in 2020 honeybee abundance was relatively high while wild bee abundance was relatively low, and this pattern was reversed in 2021. The variation in honeybee abundance may be caused by yearly differences in the number of managed beehives in the vicinity of the experiment, although direct evidence to support this explanation is lacking. In the case of wild bees, such as *L. pseudanulipes*, which was approximately 20 times more abundant in 2021 than in 2020 (Table S2), this increase may suggest that ground-nesting females foraged within the flowering plots during the first year and subsequently established nests nearby. Given that most small-bodied bee species are considered to have limited dispersal capabilities of a few hundred meters (Zurbuchen et al., 2010; Antoine and Forrest, 2021; Nelson et al., 2023), such local nesting behaviour could account for the marked rise in the abundance of *L. pseudanulipes* in the second year. Similarly, the inconsistent

relationships between plant traits and pollinators between 2020 and 2021 indicate that trait-based predictions of suitable plant species are not universally stable, and are likely influenced by environmental factors and annual fluctuations in pollinator populations. Overall, our findings demonstrate the potential of trait-based approaches to guide plant selection for pollinators, but also emphasize the need to consider temporal variability in trait-based frameworks.

We did not find differences in pollinator abundance on native and exotic plant species (Table 2), which is in line with findings of other studies (Nienhuis et al., 2009; Williams et al., 2011). Native plants share a longer evolutionary history of interactions with native pollinators than exotic plant species, which is expected to result in a higher diversity of pollinator species associated with native plants (Chrobok et al., 2013). In some cases long-term pollinator-plant associations have led to specialized, strongly mutually dependent relationships (Fenster et al., 2004). However, in our study the far majority of pollinator species visited multiple plant species and there were relatively few specialists, if any (Fig. 1). For our experiment we selected plant species of which we expected that they would be suitable for growing under Xinjiang conditions and attract local pollinators. The exotic plant species *A. graveolens*, *B. officinalis*, *D. tenuifolia*, *L. maritima* were attractive for pollinators and these plant species have already been introduced as ornamentals, spice plants or salad vegetables in China for years (Li, 2007). Therefore, we expect that the use of these exotic plant species as pollinator service plants in Xinjiang poses a limited risk.

In contrast to our expectation, the body size of pollinators was not related to plant traits of visited plants. Positive relationships between proboscis length and corolla depth of visited plants have earlier been reported for bees and hoverflies (Branquart and Hemptinne, 2000; Inoue and Yokoyama, 2006). Possibly, pollinators with a short proboscis were still able to feed on pollen and nectar on flowers with a deep corolla when the nectar level was high (Vlašánková et al., 2017). The fact that we did not confirm the relationship between body size and corolla depth suggests that this relationship is not as robust as previously thought, and may be specific for different pollinator families (Cariveau et al., 2016). Therefore, caution is needed for generalizing pollinator-plant trait relationships across geographic areas.

In conclusion, our study provides region-specific information on the relationships between flower traits and flower visitation of common groups of pollinators, which can be used to inform plant selection for pollinator conservation. While our study offers basic information on flowering plant visitation by pollinators, further work on the management (e.g., sowing dates) and the identification of compatible plants for specific crops is needed. For instance, early-flowering Korla fragrant pear is an important crop in Xinjiang (Li et al., 2024), which would require the selection of early flowering pollinator service plants that support pollinator communities that are active at the end of March before pear flowering and do not compete with the crop for pollinators. Although honeybee keeping is a common practice in China, farmers may not be familiar with the use of flowering service plants or don't know which plant species are suitable to conserve beneficial insects. Providing successful examples of pollinator conservation management that is compatible with farmer's practices will therefore be essential to raise farmers' interest.

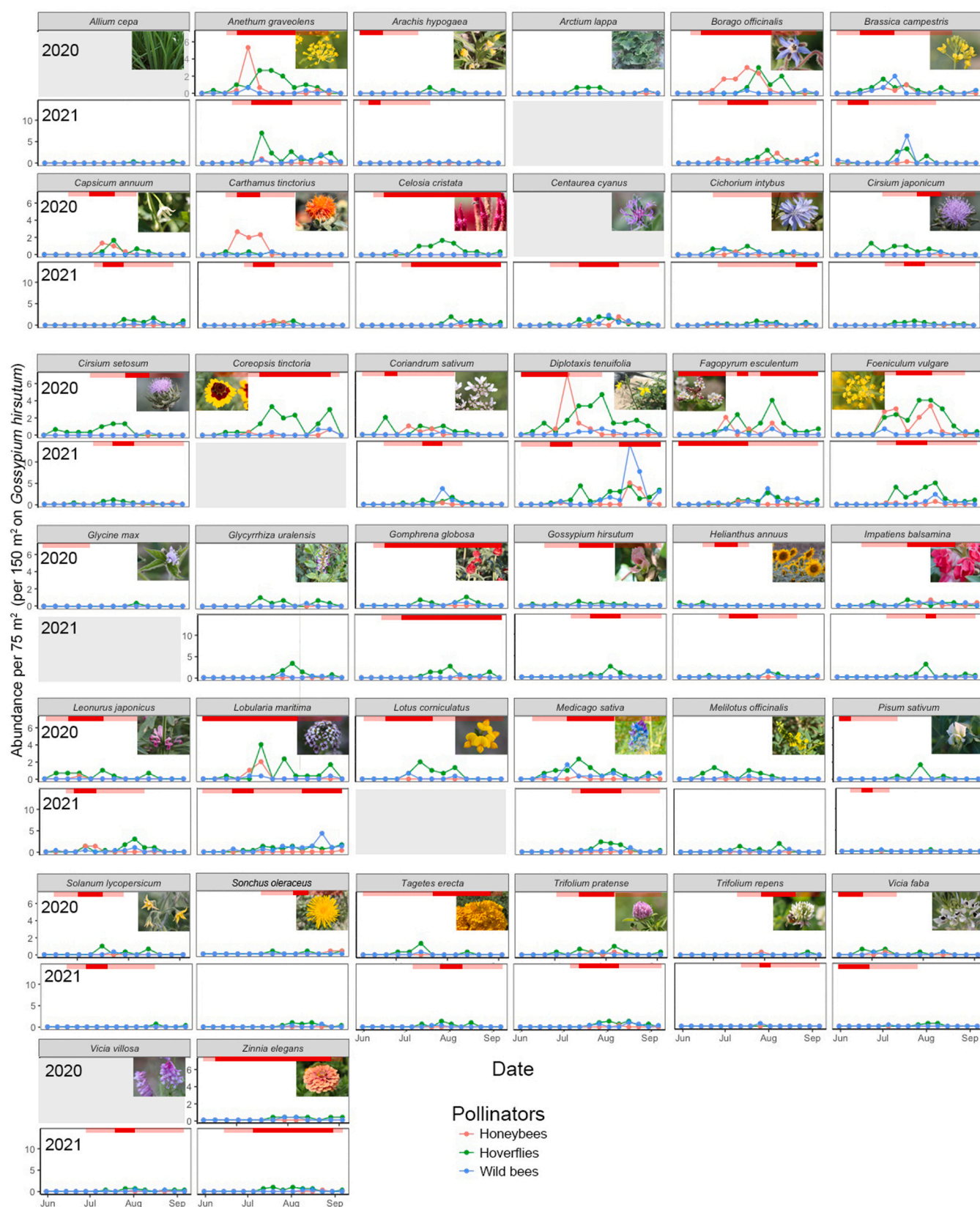


Fig. 2. Pollinator abundance assessed by sweep net sampling on 38 flowering plants during 13 sampling rounds in 2020 and 15 sampling rounds in 2021. For each round, abundance data from three replicate plots were summed (and from six plots for cotton). Red, green and blue lines represent honeybees, hoverflies and wild bees, respectively. The light and dark red bars at the top of the panels indicate flowering and peak bloom periods, respectively. Grey backgrounds indicate that the plant species was not included in the pollinator assessment because of poor establishment or too sparse foliage for sweep netting.

Table 2

Model averaging results of generalized multiple linear models with negative binomial error distribution for the relationship between the abundance of pollinators, hoverflies, honeybees and wild bees, and flower cover, corolla depth, plant height, flowering duration and nativeness of 38 plant species during flowering in 2020 and 2021. Pollinator abundance was assessed by sweep net sampling during flowering and expressed as number per plot per round. The number of sampling rounds when plants were flowering was used as an offset variable. Significant relationships are indicated in bold.

	Variables	2020				2021			
		Estimate	Std. Error	z value	p value	Estimate	Std. Error	z value	p value
Pollinators	Intercept	-0.23	0.43	0.53	0.594	-2.86	0.55	5.16	< 0.001
	Flower cover	-0.07	0.54	0.13	0.899	0.08	0.51	0.16	0.870
	Corolla depth	-0.49	0.12	4.16	< 0.001	-0.05	0.08	0.68	0.496
	Plant height	0.00	0.00	0.19	0.850	0.00	0.00	0.81	0.418
	Flowering duration	0.02	0.04	0.53	0.594	0.23	0.04	5.28	< 0.001
Hoverflies	Origin: Native	-0.03	0.13	0.23	0.818	0.05	0.13	0.35	0.729
	Intercept	-1.22	0.62	1.95	0.052	-3.17	0.54	5.79	< 0.001
	Flower cover	-0.70	1.23	0.57	0.570	0.07	0.44	0.16	0.870
	Corolla depth	-0.42	0.11	3.67	< 0.001	-0.01	0.04	0.20	0.843
	Plant height	0.00	0.00	0.29	0.768	0.01	0.00	1.92	0.055
Honeybees	Flowering duration	0.07	0.06	1.17	0.242	0.19	0.04	4.51	< 0.001
	Origin: Native	-0.11	0.21	0.54	0.590	-0.01	0.08	0.07	0.949
	Intercept	0.69	1.53	0.45	0.653	-5.52	2.16	2.54	0.011
	Flower cover	0.68	1.90	0.36	0.721	-0.18	1.20	0.15	0.881
	Corolla depth	-1.87	0.78	2.37	0.018	-0.57	0.65	0.87	0.386
Wild bees	Plant height	0.00	0.00	0.42	0.677	0.00	0.00	0.09	0.931
	Flowering duration	-0.14	0.13	1.02	0.310	0.26	0.16	1.61	0.108
	Origin: Native	0.12	0.32	0.36	0.716	1.06	0.78	1.35	0.176
	Intercept	-3.57	1.02	3.48	0.001	-4.20	0.77	5.42	< 0.001
	Flower cover	0.19	0.94	0.20	0.843	-0.48	1.14	0.42	0.678
	Corolla depth	-0.68	0.34	1.99	0.047	-0.52	0.20	2.50	0.013
	Plant height	0.00	0.00	0.02	0.984	0.00	0.00	0.17	0.869
	Flowering duration	0.13	0.09	1.38	0.167	0.28	0.06	4.38	< 0.001
	Origin: Native	0.13	0.26	0.52	0.603	0.00	0.13	0.02	0.984

Table 3

Model averaging results of linear regression models for the relationship between the abundance weighted average body length of hoverflies and wild bees and individual flower area, corolla depth, plant height, and flowering duration of 38 plant species in 2020 and 2021. There were no significant relationships.

	Variables	2020				2021			
		Estimate	Std. Error	z value	p value	Estimate	Std. Error	z value	p value
Hoverflies	Intercept	6.81	0.83	8.00	< 0.001	6.75	0.35	18.89	< 0.001
	Flower area	-0.01	0.01	0.69	0.493	0.00	0.00	0.35	0.729
	Corolla depth	-0.21	0.35	0.60	0.550	-0.01	0.04	0.16	0.871
	Plant height	0.00	0.00	0.45	0.653	0.00	0.00	1.20	0.231
	Flowering duration	0.05	0.07	0.67	0.502	0.01	0.02	0.36	0.720
Wild bees	Intercept	7.80	0.55	13.8	< 0.001	5.87	0.76	7.47	< 0.001
	Flower area	0.00	0.01	0.33	0.740	0.00	0.00	0.14	0.890
	Corolla depth	0.18	0.32	0.56	0.576	-0.01	0.09	0.14	0.889
	Plant height	0.00	0.00	0.17	0.867	0.00	0.00	0.01	0.995
	Flowering duration	-0.02	0.05	0.41	0.683	0.02	0.06	0.31	0.756

CRedit authorship contribution statement

Yanhui Lu: Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Mengxiao Sun:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Bing Liu:** Writing – review & editing, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Wopke van der Werf:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Bianchi Felix J. J. A.:** Writing – review & editing, Validation, Supervision, Methodology, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2025.110134](https://doi.org/10.1016/j.agee.2025.110134).

Data Availability

Data will be made available on request.

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