



Abundance of aphid natural enemies on flowering service plants is associated with aphid prey and floral resources

Mengxiao Sun^{a,b,c}, Bing Liu^a, Felix J.J.A. Bianchi^c, Wopke van der Werf^{b,*}, Yanhui Lu^{a,*}

^a State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing 100193, China

^b Centre for Crop Systems Analysis, Wageningen University & Research, Wageningen, the Netherlands

^c Farming Systems Ecology, Wageningen University & Research, Wageningen, the Netherlands

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ABSTRACT

Natural enemies of agricultural pests are dependent on alternative prey and floral food resources that may be scarce in intensively managed agricultural landscapes. Introduction of flowering service plants may provide food resources, but context-specific information on plant species and associated plant traits attractive and supportive to natural enemies is often lacking. Here, we assessed aphid natural enemies on 39 native and non-native service plant species in a replicated field experiment in Korla, Xinjiang, China, in 2020 and 2021. The natural enemy communities and aphid abundance on these plants were assessed using visual counts and sweepnetting. Flowering period, corolla type, and presence of extrafloral nectar on the plants were assessed as possible predictors for attractiveness to natural enemies. *Gossypium hirsutum*, *Melilotus officinalis*, *Medicago sativa*, *Anethum graveolens*, and *Foeniculum vulgare* were associated with relatively high natural enemy abundances, but *G. hirsutum*, *M. officinalis* and *M. sativa* also hosted cotton or cowpea aphids. Ladybeetles, predatory bugs and parasitoids showed positive responses to aphid densities on plants. Ladybeetle adults showed consistent positive responses to extrafloral nectar, open corollas and flowering across two years, while for other natural enemies this was only found in one out of two years. Our findings indicate that besides the provision of floral resources, aphid prey on service plants is an important characteristic that influences the attractivity of service plants to natural enemies. Service plants that host aphids that do not infest crops can therefore be useful for habitat management programs aiming to conserve and augment natural enemies.

1. Introduction

Natural enemies are essential for the natural suppression of agricultural pests, but depend on prey, plant-based food resources and shelter which may be scarce in simplified agricultural landscapes (Rusch et al., 2016; Dainese et al., 2019). Considerable attention has been given since the 2000's to the importance of service plants that provide floral food and prey resources to support natural enemy communities (Pickett and Bugg, 1998; Landis et al., 2000, 2005; Hatt et al., 2018). While the use of service plants in natural enemy augmentation has had some notable successes (Fiedler et al., 2008; Gontijo, 2019; Albrecht et al., 2020), care is needed in the selection of flowering plant species to make sure that they are suitable for the local agroecological context, do not support agricultural pests and support locally relevant natural enemy species (Karamaouna et al., 2019). However, context-specific information on the suitability of plant species for natural enemies is often

lacking in Central Asia (Hatt et al., 2019b), indicating the need for experimental testing of service plants.

The identification of favourable plant traits can help inform the selection of locally adapted service plants. For instance, the accessibility of nectar and pollen moderates the attractiveness of plants for hoverflies and parasitoids (Winkler et al., 2009; van Rijn et al., 2013; van Rijn and Wäckers, 2016), and it enhances the longevity of lacewings and ladybeetles (Bertrand et al., 2019; Stowe et al., 2021), and their biological control potential (Heimpel and Jervis, 2005; Snyder, 2019). The combination of flower architecture and morphology of the mouthparts of natural enemies determines the accessibility of floral nectar (Patt et al., 1997; Wäckers, 2004). Flowers with short corollas offer nectar that is accessible to natural enemies with short mouthparts, such as parasitoids and hoverflies (Campbell et al., 2012; van Rijn and Wäckers, 2016). In addition, extrafloral nectar provides easily accessible sugar for parasitoids, hoverflies and ladybeetles, but it may also attract ants that can

* Corresponding authors.

E-mail addresses: wopke.vanderwerf@wur.nl (W. van der Werf), luyanhui@caas.cn (Y. Lu).

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defend aphids against attackers (Samuel and Rastogi, 2022). Furthermore, the flowering period of plant species determines the temporal availability of floral resources (Fiedler and Landis, 2007a, 2007b; Hatt et al., 2019a). Therefore, service plants have multiple traits that influence their suitability for augmentation of natural enemies.

Besides flower traits, the presence of prey can attract natural enemies to service plants. For instance, aphids and caterpillars on service plants can support parasitoids, ladybeetles, larvae of lacewings and hoverflies when herbivore populations in crops are low (Verheggen et al., 2008; Wäckers and van Rijn, 2012; Fei et al., 2023). Continuous provision of prey and floral resources can support natural enemies for prolonged periods in the growing season (Perović et al., 2018; Iuliano and Gratton, 2020), but prey availability is particularly important in the early season to retain natural enemies close to crop fields to enable effective top-down control of crop pest later in the season (Chailleux et al., 2014). Yet, care is needed that service plants do not support crop pests or diseases (Frank, 2010). No studies to our knowledge have made an integral assessment of how plant traits and their capacity to support prey influence the selection of plants by natural enemies.

The aim of this 2-year study in Korla, Xinjiang, China, was to assess the relationships between natural enemy abundance, plant traits associated with food resources for natural enemies, and aphid abundance on 39 flowering plant species. Specifically, we assessed (i) the natural enemy communities on these plants, and (ii) determined how the abundance of natural enemies was influenced by aphid abundance, floral nectar accessibility, presence of extrafloral nectar and presence of flowers. This information can be used to inform the selection of flowering service plant species to support natural enemies of aphids in Xinjiang and the wider region of central Asia.

2. Materials and methods

2.1. Study area

The Korla region, Xinjiang, China, is a prime irrigated agricultural production area located at the edge of the Tarim desert in the south and immediately adjacent to the Tianshan mountain range to the north. The climate of the Tarim basin is classified as cold arid desert (BWk) according to the Köppen-Geiger climate classification (Kottek et al., 2006). Korla has low rainfall (163 mm/year) and high evaporative demand (1256 mm/year) (Dong et al., 2020; Hu et al., 2021), but irrigation water is available by snowmelt from the Tianshan mountain range, which receives much more precipitation than the low-lying arid and semi-arid plains. Besides cotton (*Gossypium hirsutum*), which is the main crop in Korla, fruit production is a major economic activity that supports local livelihoods. The large difference between day and night temperature and the prevailing sunny weather offer excellent conditions for producing high quality fruit, such as Korla fragrant pear (*Pyrus sinkiangensis*), Aksu apple (*Malus domestica*), and Turpan grape (*Vitis vinifera*). Other crops are fodder crops such as silage corn (*Zea mays*) and alfalfa (*Medicago sativa*), cash crops such as chili (*Capsicum annuum*) and sugar beet (*Beta vulgaris*), and medicinal crops like liquorice (*Glycyrrhiza uralensis*) and goji (*Lycium chinense*). Pesticide use, including insecticides, is generally high to protect crops from weeds, diseases and insect pests, but this can also affect communities of beneficial insects and have other adverse environmental impacts (Pan et al., 2023). The agricultural practices in Korla are representative of agriculture in Xinjiang. Xinjiang is the most important fruit and cotton production area of China (NBSC, 2023).

2.2. Plant selection and experimental design

We selected 39 plant species to assess their potential as candidate service plants for beneficial insects based on the following criteria: 1) the plants have been used for habitat diversification in other parts of the world, thus may include native and exotic plants, or the plants are

known to be attractive for pollinators and natural enemies; and 2) the plants are expected to be adapted to the environmental conditions in Xinjiang. We first 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) (Fig. S1, Table S1).

The field trial was conducted in two subsequent years, 2020 and 2021, at the CAAS-IPP (Chinese Academy of Agricultural Sciences-Institute of Plant Protection) experimental station (85.81°E, 41.75°N) in Korla, Xinjiang, China. The trial consisted of a randomized complete block design with 3 blocks and 40 7×6 m² plots per block. Plant species were randomly assigned to plots each year and grown in each plot as a pure stand. Plots were separated by 1.5 m-wide paths, which contained a mulch layer and were hand weeded monthly (Fig. S2). Cotton was sown in two plots in each block as it is the main crop species in Xinjiang, and we were interested in natural enemies on pesticide free cotton plots, and also in the enemy community on cotton as a reference for the other plant species.

Plots were fertilized according to standard practice (150 kg/ha urea, 450 kg/ha diammonium phosphate and 150 kg/ha potassium sulphate), tilled and covered with plastic mulch before sowing to reduce evaporation and suppress weeds. Plastic mulch is a standard practice in Xinjiang due to the high evaporative demand. The plots were sown each year during late April. The trial was irrigated every two weeks, and no pesticides were used. Thirty-eight and 35 plant species established successfully in 2020 and 2021, respectively.

2.3. Arthropod sampling

We assessed the arthropod community on plants by visual counts and sweepnetting. Sampling was done weekly on days without precipitation from late May to early September for a total of 13 sampling rounds in 2020 and 15 rounds in 2021. In each plot, we manually inspected 25 individual plants (5 plants \times 5 points in an X pattern), and recorded the numbers and life stages of the focal insect species (see below).

After making the visual counts, we sampled the plots by taking 20 sweeps with a sweepnet, covering five subplots of 1 m² with four sweeps in each subplot. The sweepnet had a 30 cm diameter and the handle was 115 cm long. Insects collected by sweepnetting were put in ziploc plastic bags (180 \times 250 mm²), brought to the laboratory, and stored at -20°C until species identification. Four plant species did not have sufficient vegetation cover for sweepnetting: *Centaurea cyanus*, *Vicia villosa* and *Allium tuberosum* in 2020, and *Glycine max* in 2021. In these cases we used only visual counts.

Samples were sorted and specimens were identified to species whenever possible. Unknown species were pinned and sent to a specialist for identification. Based on the morphology of the aphids and the plant species on which they were found we distinguished the following species: *Myzus persicae* (e.g., on *Celosia cristata*), *Hyadaphis coriandri* (on Apiaceae, e.g., *Anethum graveolens*), *Uroleucon* sp. (on Asteraceae, e.g., *Carthamus tinctorius*), *Aphis gossypii* (e.g., on *Gossypium hirsutum*), *Brevicoryne brassicae* (on Brassicaceae, e.g., *Brassica campestris*) and *Aphis craccivora* (on Leguminosae, e.g., *Medicago sativa*). We also collected natural enemies of aphids, including aphid mummies (i.e. the larval plus pupal stages of parasitoids; only in visual counts), adult parasitoid wasps (only in sweepnetting), spiders (only in sweepnetting), lacewing larvae, hoverfly larvae, predatory bugs (*Orius similis* (Hemiptera: Anthoridae), *Deraeocoris punctulatus* (Hemiptera: Miridae), *Geocoris pallidipennis* (Hemiptera: Lygaeidae), ladybeetle larvae and adults (*Hippodamia variegata*, *Coccinella undecimpunctata*, *Coccinella septempunctata*, other ladybeetle species).

2.4. Assessment of plant traits

To assess whether the floral nectar was accessible to natural enemies, we assessed the corolla type for each plant species from June to August

in 2021. We took photos of a cross section through the longitudinal axis of ten flowers per species (Fig. 1) and classified the flower type as "open corolla", "short corolla" and "long corolla". Open corolla flowers provide freely accessible floral nectar and pollen (e.g., Apiaceae), while short corolla flowers present nectar in corollas that are wide or short and are therefore accessible to a wide range of species (e.g., *Fagopyrum esculentum*). The long corolla flowers hold nectar in narrow and deep corollas or spurs (e.g., *Cichorium intybus*) and can only be accessed by long-tongued insects such as bumblebees and butterflies, but not (or with difficulty) by natural enemies. The classification of flower type was cross-checked with Campbell et al. (2012) and van Rijn and Wäckers (2016). Information on the availability of extrafloral nectar was obtained from visual observation and cross-checking with other studies (Table 1, Fig. 1, Table S1). Three plant species (*Arctium lappa*, *Lotus corniculatus* and *Allium tuberosum*) did not germinate in 2021. Moreover, four plant species were not flowering during the plant traits assessment from June to August 2021 (*Glycine max*, *Glycyrrhiza uralensis*, *Melilotus officinalis* and *Allium cepa*). Therefore the corolla type of these seven species was assessed using wild specimens (Table 1). Plant flowering periods were assessed by recording whether flowers were present in each plot during each sampling round, and were categorized as early, peak or late flowering periods (Table 1) (Fiedler and Landis, 2007a).

2.5. Statistical analyses

We conducted Principal Component Analysis (PCA) to explore associations between plant species and insect taxa. Separate analyses were conducted for visual counts and sweepnetting data in both years. We calculated cumulative insect abundance per plot per year by pooling the insect catches for the sampling rounds in each year. We used $\log_{10}(N + 1)$ transformed data for the abundance of aphids, mummies, parasitoids, predatory bugs, ladybeetle larvae and adults. Data were centred (subtracting the mean for each variable) but not scaled and therefore the PCA results reflect covariances, and not correlations. We used the PCA() function in the 'FactoMineR' package (Lê et al., 2008), and the fviz_pca_biplot() in the package 'factoextra' to visualize PCA biplots (Kassambara and Mundt, 2017).

Relationships between natural enemy abundances as response variables and plant traits and aphid abundance together as predictors were analysed using generalized linear mixed models (GLMMs) with a negative binomial error distribution. Response variables included were abundances of mummies, parasitoids, predatory bugs, ladybeetle larvae or ladybeetle adults, while the explanatory variables were corolla type (open/short/long corolla), extrafloral nectar (present/absent), flowers (present/absent) and aphid abundance ($\log_{10}(N + 1)$ -transformed). We used sampling round and plant species as crossed and interacting random effects ((1| Sampling round) + (1| plant ID) + (1| Sampling round*plant ID)) in the models. Data from visual counts and sweepnet samples in 2020 and 2021 were analysed separately. We used the function glmer.nb() in the 'MASS' package (Ripley et al., 2013) to fit the generalized linear mixed models. We used simulateResiduals() in the 'DHARMa' package to validate model assumptions (Hartig, 2018) and lsmeans() in the 'lsmeans' package to conduct post-hoc tests of differences in insect abundance between the three corolla types (Lenth, 2016). The proportion of variance explained uniquely by each fixed explanatory variable (unique R^2), the proportion of variance explained by all fixed factors (marginal R^2) and the proportion of variance explained by all fixed and random factors (conditional R^2) were calculated using the glmm.hp() function in the 'glmm.hp' package (Nakagawa and Schielzeth, 2013; Stoffel et al., 2021; Lai et al., 2022).

To illustrate relationships between the abundance of aphids and natural enemies in graphs, we fitted ordinary linear regressions. Response variables included $\log_{10}(N + 1)$ -transformed abundances of mummies, parasitoids, predatory bugs, ladybeetle larvae and ladybeetle adults, and the explanatory variable was $\log_{10}(N + 1)$ -transformed aphid abundance. These linear regressions were performed using the

function lm() in the 'stats' package (Chambers and Hastie, 1992). We used the ggplot() in package 'ggplot2' to visualize regression biplots (Wickham, 2011). All data analysis was done in R 4.2.1 (R Development Core Team, 2022).

In the interpretation of results we take the occurrence of immature stages of natural enemies (ladybeetle larvae and mummies of parasitoids) as direct evidence that the plants were used as a reproduction site by natural enemies (Bianchi et al., 2013).

3. Results

3.1. Plant traits and aphid communities

Out of 39 plant species, three, nine and 27 plant species had open, short and long corollas, respectively (Table 1, Fig. 1). The time of flowering ranged from May to September, but there were only relatively few plant species that flowered in May. Arugula (*Diplotaxis tenuifolia*), sweet alyssum (*Lobularia maritima*) and buckwheat (*Fagopyrum esculentum*) had the longest flowering periods (Table 1). Nine plant species had extrafloral nectar.

Cotton (*Gossypium hirsutum*) had the highest aphid density (mostly cotton aphid, *A. gossypii*), while rape (*Brassica campestris*) and broad bean (*Vicia faba*) had high observed densities of *Brevicoryne brassicae* and *Aphis craccivora*, respectively (Fig. 2a and c, S3a, Table S1, S2). In May and June, *A. craccivora* was abundant on broad bean, but not on alfalfa (*Melilotus sativa*) (Table 1, Table S1). Sweepnetting data confirmed the high abundance of *A. gossypii* on cotton, and also indicated high abundances of *A. craccivora* on alfalfa and sweet clover (*Melilotus officinalis*) (Fig. 2b and d, Fig. S3b, Tables S1, S2).

3.2. Natural enemy communities

We counted 10,124 and 7,099 natural enemies on the plants in 2020 and 2021. Mummies (4747 + 3859; 50 %) and ladybeetles (5138 + 2789; 46 %) were the most numerous. Sweepnetting resulted in 7,094 and 4,657 natural enemies in 2020 in 2021, respectively, and ladybeetles (5819 + 1808; 65 %), parasitoids (513 + 1801; 20 %) and predatory bugs (618 + 752; 12 %) were the dominant groups (Fig. S4). Predatory bugs included 69 % *Deraeocoris punctulatus* (Hemiptera: Miridae), 21 % *Orius similis* (Hemiptera: Anthoridae) and 10 % *Geocoris pallidipennis* (Hemiptera: Lygaeidae) (Fig. S5a). Ladybeetle larvae and adults were mostly *Hippodamia variegata* (94 % of ladybeetle larvae and 98 % of ladybeetle adults; Fig. S5b and c).

The PCA of visual counts indicated that relatively high numbers of mummies were present on *G. hirsutum* and *M. sativa* (Fig. 2, S6a, Table S3) and many ladybeetle larvae on *G. hirsutum* (Fig. 2, Fig. S8a, Table S5). Sweepnetting indicated that adult parasitoid abundance was relatively high on *M. sativa* and *M. officinalis* (Fig. 2, Fig. S6b, Table S3), and that *M. sativa* and *G. hirsutum* hosted relatively high abundances of ladybeetle larvae (Fig. 2, Fig. S8b, Table S5). Both visual counts and sweepnetting showed that arugula (*D. tenuifolia*) hosted a relatively high abundance of predatory bugs (Fig. 2, Fig. S7, Table S4), and that ladybeetle adults were relatively abundant on fennel (*Foeniculum vulgare*) and cumin (*Anethum graveolens*), particularly late in the growing season (Fig. 2, Fig. S9, Fig. S10, Table S6).

The observed number of aphid mummies, predatory bugs and ladybeetle larvae were positively associated with aphid abundance in 2020 and 2021, but ladybeetle adults were not (Fig. 2a and c). The PCA of sweepnetting data indicated that in 2020 parasitoids and ladybeetle larvae were strongly associated with aphid abundance, while in 2021 this was only the case for ladybeetle larvae (Fig. 2b and d).

3.3. Relationships between natural enemies, aphids and plant traits

GLMM analysis for visual counts data confirmed that aphid mummies were positively associated with the abundance of aphids

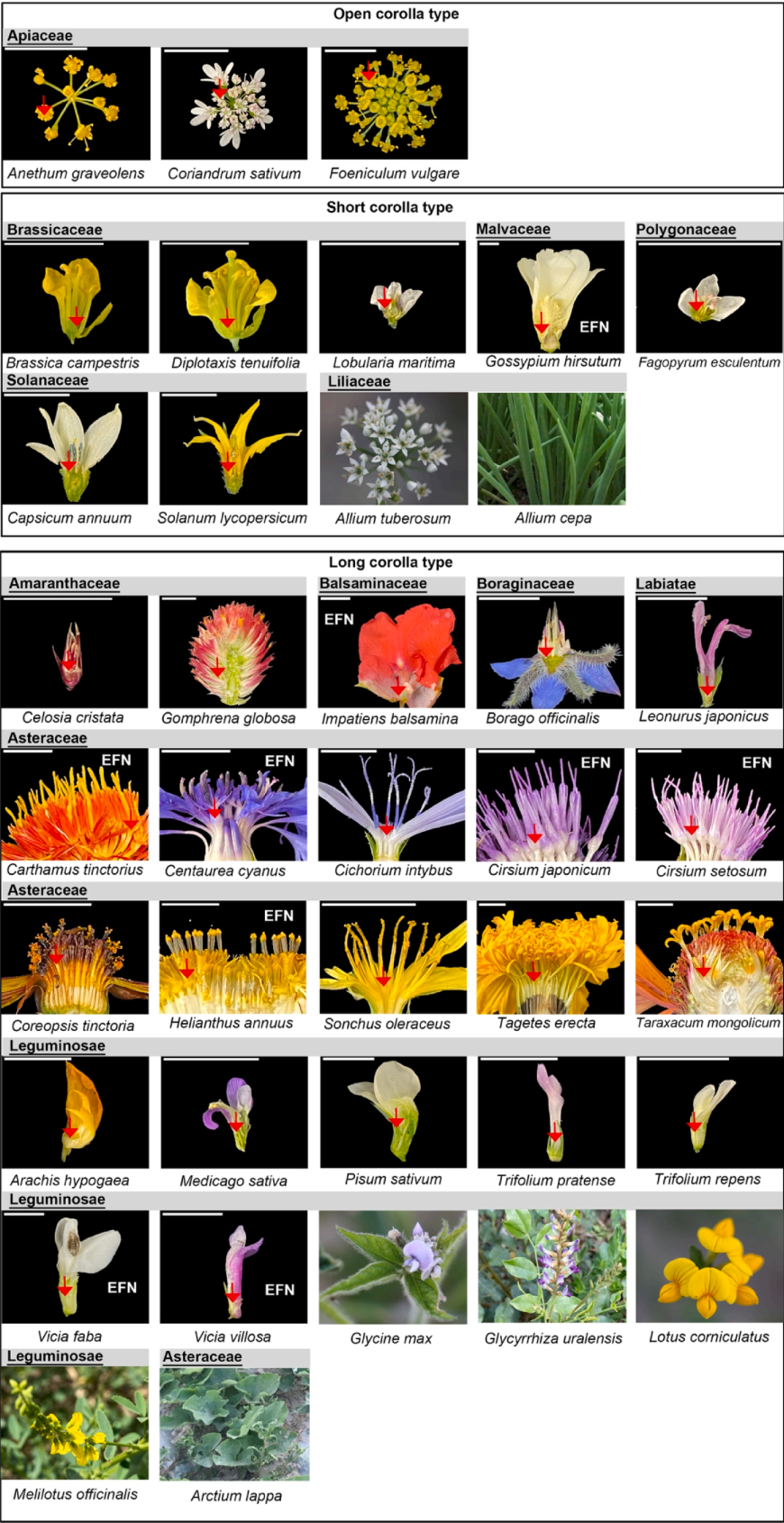


Fig. 1. Photos of 39 plant species included in the study, with longitudinal cross sections of 32 flowers to classify plants in corolla types (open corolla, short corolla and long corolla). A white bar in a panel indicate 1 cm. Red arrows indicate the location of the nectar.

Table 1

Overview of plant traits and aphid abundance for 39 flowering plant species. For every species, the table shows flowering (plus signs) and aphid abundance (numbers) per month of the year. The table further indicates for each plant species corolla type (long/short/open) and presence of extrafloral nectar (EFN) (yes/no). Flowering period is indicated as early or late flowering (+) and peak flowering (++). Aphid abundance is the average number per 25 plants per round in visual counts during two years.

No.	Species	Common name	Month					Corolla type	EFN
			May	Jun	Jul	Aug	Sep		
Amaranthaceae									
1	<i>Celosia cristata</i>	Cockscomb		+	++	++	++	long	no
			0	3	4	1	0		
2	<i>Gomphrena globosa</i>	Globe amaranth		+	++	++	++	long	no
			3	23	8	0	0		
Apiaceae									
3	<i>Anethum graveolens</i>	Cumin		+	++	+	+	open	no
			0	4	3	0	0		
4	<i>Coriandrum sativum</i>	Coriander		+	++	+		open	no
			6	20	18	0	0		
5	<i>Foeniculum vulgare</i>	Fennel		+	++	+	+	open	no
			1	2	5	0	0		
Asteraceae									
6	<i>Arctium lappa</i> †	Burdock						long*	no
				24	7	0	0		
7	<i>Carthamus tinctorius</i>	Safflower		+	++	+		long	yes
			4	50	30	3	0		
8	<i>Centaurea cyanus</i>	Cornflower		+	++	+	+	long	yes
			3	4	8	0	0		
9	<i>Cichorium intybus</i>	Chicory		+	+	+	++	long	no
			3	12	49	9	2		
10	<i>Cirsium japonicum</i>	Thistle			++	+	+	long	yes
			15	101	132	7	1		
11	<i>Cirsium setosum</i>	Small thistle			++	+	+	long	yes
			3	143	136	6	1		
12	<i>Coreopsis tinctoria</i> †	Snow daisy		+	++	++	+	long	no
				3	4	0	0		
13	<i>Helianthus annuus</i>	Sunflower		+	++	+		long	yes
			3	7	12	191	16		
14	<i>Sonchus oleraceus</i>	Sow thistle				+	+	long	no
			0	5	8	1	0		
15	<i>Tagetes erecta</i>	Marigold			+	++	+	long	no
			0	4	3	1	0		
16	<i>Zinnia elegans</i>	Zinnia		+	++	++	+	long	no
			1	86	44	5	1		
Balsaminaceae									
17	<i>Impatiens balsamina</i>	Jewelweed			+	++	+	long	yes
			0	6	5	1	0		
Boraginaceae									
18	<i>Borago officinalis</i>	Borage		+	++	+	+	long	no
			5	27	39	3	1		
Brassicaceae									
19	<i>Brassica campestris</i>	Rape	+	++	+	+		short	no
			24	272	259	0	0		
20	<i>Diplotaxis tenuifolia</i>	Arugula	+	++	++	++	++	short	no
			0	7	2	0	0		
21	<i>Lobularia maritima</i>	Sweet alyssum	+	++	++	++	++	short	no
			2	2	2	0	0		
Labiatae									
22	<i>Leonurus japonicus</i>	Leonurus		++	+	+		long	no
			0	1	2	0	0		
Leguminosae									
23	<i>Arachis hypogaea</i>	Peanut	+	++	+			long	no
			1	4	6	2	0		
24	<i>Glycine max</i>	Soybean	++	++				long*	no
			0	22	38	1	0		
25	<i>Glycyrrhiza uralensis</i>	Liquorice						long*	no
			0	35	12	3	0		
26	<i>Lotus corniculatus</i> †	Crowtoe		+	++	+	+	long*	no
				8	7	0	0		
27	<i>Medicago sativa</i>	Alfalfa			++	+	+	long	no
			1	24	19	2	0		
28	<i>Melilotus officinalis</i>	Sweet clover				+	+	long*	no
			2	18	11	4	4		
29	<i>Pisum sativum</i>	Pea		++	+			long	no
			44	7	10	1	0		
30	<i>Trifolium pratense</i>	Red clover			++	+	+	long	no
			13	31	18	4	1		
31	<i>Trifolium repens</i>	White clover			++	+	+	long	no
			0	8	9	2	0		

(continued on next page)

Table 1 (continued)

No.	Species	Common name	Month					Corolla type	EFN
			May	Jun	Jul	Aug	Sep		
32	<i>Vicia faba</i>	Broad bean	++ 415	++ 750	+ 27	+ 1	0	long	yes
33	<i>Vicia villosa</i>	Hairy vetch	1	+ 15	++ 4	+ 0	+ 0	long	yes
Liliaceae 34	<i>Allium cepa</i>	Onion	0	0	1	0	0	short*	no
35	<i>Allium tuberosum</i> †	Chinese chive		0	1	+	+	short*	no
Malvaceae 36	<i>Gossypium hirsutum</i>	Cotton	9	4057	++ 3510	+ 51	+ 2	short	yes
Polygonaceae 37	<i>Fagopyrum esculentum</i>	Buckwheat	++ 1	++ 9	++ 5	+ 3	+ 0	short	no
Solanaceae 38	<i>Capsicum annuum</i>	Chili	0	30	++ 43	+ 1	0	short	no
39	<i>Solanum lycopersicum</i>	Tomato	11	46	++ 32	+ 4	0	short	no

† aphid and natural enemy data only assessed in 2020;

* corolla type based on flowers obtained from wild plants.

(Table 2, Fig. 3a). Predatory bugs were positively associated with aphid abundance and presence of flowers in 2021, but not in 2020 (Table 2, Fig. 3c). Ladybeetle larvae and adults were significantly positively associated with aphid abundance, while ladybeetle adults were also positively associated with extrafloral nectar, open corollas and presence of flowers (Table 2, Fig. 3g and h).

Adult parasitoids in sweepnet samples were positively associated with aphid abundance and presence of flowers in 2021 and negatively associated with extrafloral nectar in 2020 (Table 3, Fig. 3b). Predatory bugs and ladybeetle larvae and adults in sweepnet samples showed mostly the same responses as found for visual counts, but we did not find in sweepnet data a positive association between ladybeetle adults and extrafloral nectar (Table 3, Fig. 3d, f and h). Aphid abundance and plant traits explained up to 12 % of the variation in natural enemy abundance (Tables 2 and 3).

Post-hoc tests for visual counts data confirmed that ladybeetle larvae in 2021 and ladybeetle adults in both years were significantly higher with open corollas than with long corollas. Post-hoc tests for visual counts data indicated the significant differences on abundance of aphid mummies in 2020 and ladybeetle adults between plants with open and short corollas (Table S7). No significant difference was found in post-hoc tests for sweepnetting data (Table S8).

4. Discussion

In this study we characterized aphid and natural enemy communities on 39 flowering plant species and assessed which resources (prey, plant traits) best explain the abundance of natural enemies on these plants. We found that *Gossypium hirsutum*, *Melilotus officinalis*, *Medicago sativa*, *Anethum graveolens*, and *Foeniculum vulgare* supported relatively high natural enemy abundances, but *G. hirsutum*, *M. officinalis* and *M. sativa* also hosted cotton or cowpea aphids. *Vicia faba* and *G. hirsutum* provided abundant aphids for natural enemies during the early and middle of the season, while *A. graveolens*, and *F. vulgare* provided pollen and nectar during the late season when aphids decreased on other plant species. All natural enemy groups showed positive responses to aphid densities on plants. Ladybeetle adults showed consistent positive responses to extrafloral nectar, open corollas and flowering across two years, while for other natural enemies this was only found in one out of two years. The relatively high density of ladybeetle larvae and aphid mummies on plants with many aphids indicates that these plants are used as reproduction sites, reflecting a reproductive response, while in the case of

adult natural enemies, the higher density on plants with more aphids could also indicate an aggregative response (Ives et al., 1993).

We observed large differences in insect communities on 39 plant species, which is in line with the findings of a common garden experiment with 43 plant species in the USA (Fiedler and Landis, 2007a), and we identified several plant species that have potential to support natural enemy communities in intensively managed agricultural landscapes in Xinjiang, China. Parasitoids, ladybeetles and predatory bugs showed positive aggregation responses to a limited number of plants, including *G. hirsutum*, *M. officinalis*, *M. sativa*, *A. graveolens*, *F. vulgare*, *C. setosum*, *C. japonicum*, *V. faba* and *C. tinctorius*, but not all of these plant species may be suitable for conservation biological control initiatives. For instance, cotton (*G. hirsutum*) hosted many cotton aphids (*A. gossypii*), which is a major pest in Xinjiang cotton. *M. officinalis* and *M. sativa* hosted cowpea aphids (*A. craccivora*), which can feed on alfalfa (*M. sativa*) that is sometimes grown as a fodder crop in the understorey of pear orchards. However, aphids cause little economic damage in alfalfa, and the benefit of supporting populations of parasitoids and ladybeetles may outweigh the damage caused by aphids (Schmidt et al., 2007). Natural enemies, including *H. variegata*, *Scymnus* sp., *Orius majusculus*, *Orius laevigatus* and *Orius minutus*, have been reported to move from alfalfa fields to nearby peach orchards when alfalfa is cut (Batuecas et al., 2021). However, since service plants are usually not disturbed as in the case of mown alfalfa, further research is needed to assess to which extent the enemies observed on the service plants move to target crops and contribute to pest suppression in these crops.

The plant species in our experiment provided variable levels of prey and floral resources at different times in the growing season. For instance, *V. faba* hosted aphids and floral resources during the early season, while *A. graveolens* and *F. vulgare* provided pollen and nectar later in the growing season. Ensuring temporal continuity of resources throughout the growing season can promote the recruitment of natural enemies, which can potentially contribute to pest suppression in nearby crops (Iuliano and Gratton, 2020). For the plant species considered in our study, combinations of, for example, *V. faba*, *A. graveolens* and *F. vulgare* could provide a combination of aphid and plant derived resources to attract and support natural enemies for the entire growing season of cotton, which is the main crop in the study area.

Parasitoid wasps and ladybeetle larvae showed strong positive responses to the aphid abundance on plants. The positive responses of ladybeetles can be explained by the fact that ladybeetles preferably oviposit egg batches at locations with high prey availability for their

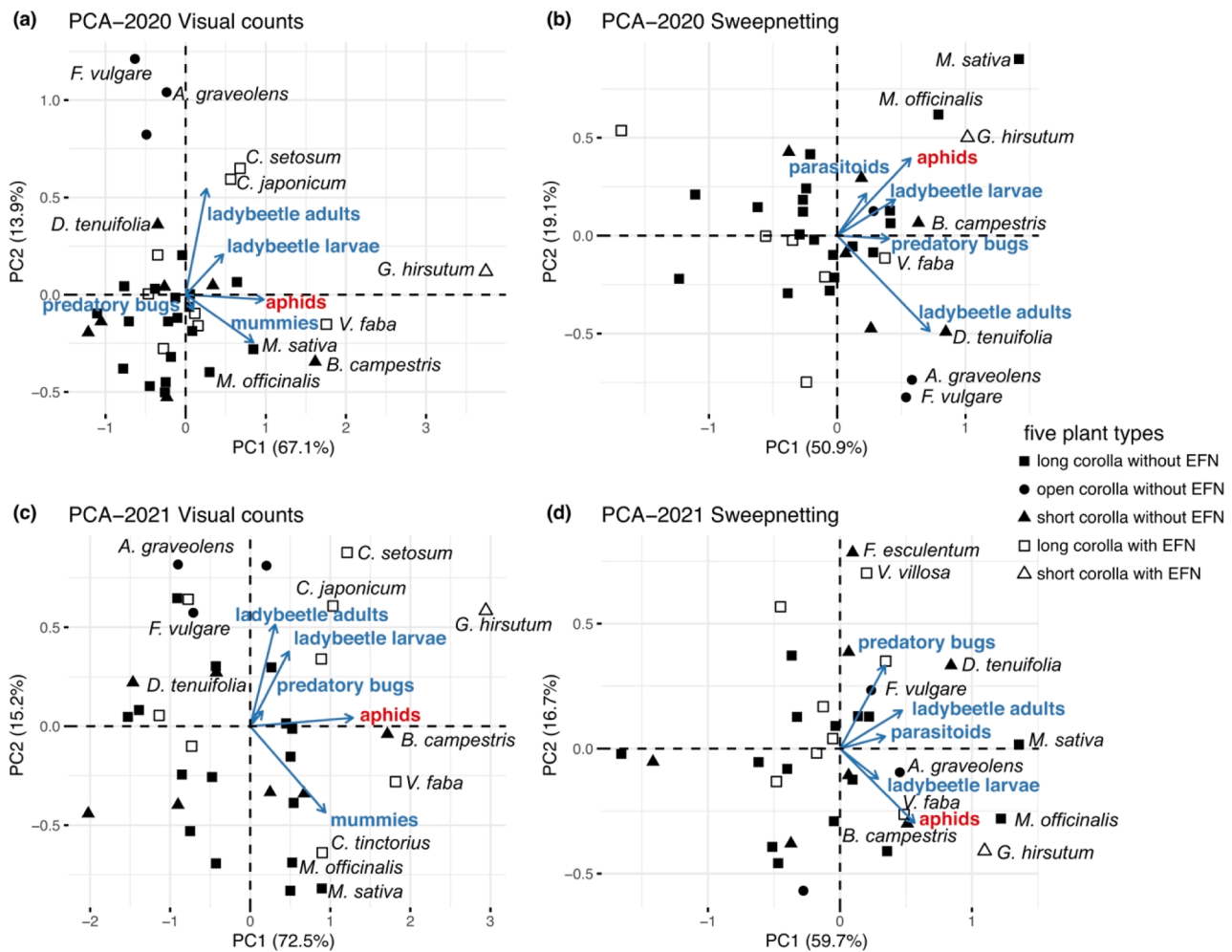


Fig. 2. Principal component analysis of cumulative aphids and natural enemies (aphid mummies, parasitoids, predatory bugs, ladybeetle larvae and adults) on 39 plant species. Panels show data for visual counts (left) and sweepnetting (right) and 2020 (top) and 2021 (bottom). Observations were made during 13 rounds in 2020 and 15 rounds in 2021. Visual counts are based on 25 plants, and sweepnetting data are based on 20 sweeps (5 m²). The length of arrows represents abundance of the $\log_{10}(N + 1)$ -transformed density of aphids, aphid mummies, parasitoid wasps, predatory bugs and ladybeetle larvae and adults. The angle between arrows represents positive (angle < 90°) or negative covariance (angle > 90°) among insects. Symbols indicate five plant types according to the corolla type and presence of extrafloral nectaries (EFN). Abbreviated names of plants with relatively high abundance of natural enemies and aphids are shown.: *Foeniculum vulgare* (*F. vulgare*), *Anethum graveolens* (*A. graveolens*), *Carthamus tinctorius* (*C. tinctorius*), *Cirsium japonicum* (*C. japonicum*), *Cirsium setosum* (*C. setosum*), *Brassica campestris* (*B. campestris*), *Diplotaxis tenuifolia* (*D. tenuifolia*), *Medicago sativa* (*M. sativa*), *Melilotus officinalis* (*M. officinalis*), *Vicia faba* (*V. faba*), *Vicia villosa* (*V. villosa*).

offspring (Kindlmann and Dixon, 1993; Evans, 2003). The relatively high explanatory power of aphids for natural enemy abundance suggests that availability of alternative prey on flowering plants plays an important role in attracting parasitoids and ladybeetle larvae. However, some plant species hosted aphids, but were not associated with many parasitoid wasps or ladybeetle larvae. This suggests that these plants hosted aphids that are not preferred by the natural enemies that are prevalent in the study area or that natural enemies prefer plants that provides both prey and floral resources (Suzuki and Ide, 2008). Indeed, plants that provided extrafloral nectar or open corolla flowers often had relatively high abundance of natural enemies, such as predatory bugs on *V. villosa* and ladybeetle adults on *F. vulgare* and *A. graveolens* (Fig. 3d, g and h). While flowering plants need to be carefully selected to provide resources for natural enemies but not for pests (Wäckers and van Rijn, 2012), we here show that ladybeetles, parasitoids (and aphid mummies) show relatively strong responses to aphid prey availability.

Plant species with open corollas, such as the Apiaceae species *A. graveolens* and *F. vulgare*, had the highest numbers of ladybeetle adults even though we did not find many aphids and ladybeetle larvae on these plant species. Most likely, these plants were attractive to ladybeetle

adults because of their accessible nectar and pollen (Wäckers, 2004; Campbell et al., 2017), which can enhance adult longevity and reproduction (Lundgren, 2009). However, we did not find a relationship between open corollas and parasitoid abundance (Tables 2 and 3). The absence of such a relationship may be explained by switching from nectar to honeydew feeding by parasitoids when aphid density is high and honeydew is readily available (Vollhardt et al., 2010). However, open corolla flowers were only present in the family Apiaceae, and therefore we cannot rule out the possibility that other traits of Apiaceae are also involved in the attractiveness to ladybeetle adults. Further study is needed to explore associations with other family plants with open corollas and ladybeetle adults.

We found a consistent pattern that plants with extrafloral nectar had a higher abundance of ladybeetle adults in our visual count data across two years than plants without extrafloral nectar (Table 2). This suggests that extrafloral nectar is an important trait for the selection of plant species that are attractive for ladybeetles. Indeed, extrafloral nectar is a valuable food resource for ladybeetles and parasitoids (Röse et al., 2006; Almeida et al., 2011; Choate and Lundgren, 2013; Mathews et al., 2016). Surprisingly, we found a negative association between extrafloral nectar

Table 2

Results of generalized linear mixed models with negative binomial error distribution for the relationship between the abundance of natural enemies and aphid abundance on plants ($\log_{10}(N + 1)$ -transformed), presence or absence of extrafloral nectar (EFN), accessibility of floral nectar (open/short/long corolla) and presence or absence of flowers on 39 plant species. Separate analyses are conducted for data obtained by **visual counts** in 2020 and 2021. Unique R^2 indicates the percentage of variance explained by individual factors. Marginal R^2 indicates the percentage of variance explained by fixed factors. Conditional R^2 indicates the percentage of variance explained by fixed and random factors. EFN absent, long corolla and flowers absent are references in all models. Significant relationships are indicated in bold.

	2020							2021						
	Estimate	Std. Error	z value	P value	Unique R^2	Marginal R^2	Conditional R^2	Estimate	Std. Error	z value	P value	Unique R^2	Marginal R^2	Conditional R^2
Aphid mummies														
Intercept	−4.55	0.63	−7.24	< 0.001		20.94 %	80.34 %	−3.96	0.63	−6.24	< 0.001		15.67 %	86.43 %
Log ₁₀ (aphids+1)	0.53	0.08	7.00	< 0.001	9.97 %			0.52	0.05	9.53	< 0.001	11.09 %		
EFN	0.80	0.57	1.41	0.16	2.20 %			0.13	0.61	0.22	0.83	0.37 %		
Open corolla	−2.15	1.22	−1.77	0.08	8.24 %			−0.90	0.98	−0.91	0.36	1.50 %		
Short corolla	0.91	0.59	1.54	0.12				0.07	0.64	0.11	0.91			
Flowers	−0.10	0.33	−0.31	0.76	−0.10 %			0.50	0.29	1.69	0.09	0.74 %		
Predatory bugs														
Intercept	−3.19	0.45	−7.07	< 0.001		1.23 %	18.99 %	−3.85	0.34	−11.24	< 0.001		7.64 %	22.49 %
Log ₁₀ (aphids+1)	0.02	0.10	0.23	0.82	0.03 %			0.17	0.05	3.07	< 0.001	0.93 %		
EFN	0.08	0.42	0.20	0.84	0.01 %			0.02	0.29	0.06	0.95	−0.02 %		
Open corolla	−1.36	0.81	−1.68	0.09	1.09 %			−0.25	0.48	−0.53	0.6	0.53 %		
Short corolla	−0.04	0.44	−0.10	0.92				0.40	0.29	1.39	0.16			
Flowers	0.17	0.29	0.59	0.56	0.07 %			1.34	0.25	5.27	< 0.001	4.78 %		
Ladybeetle larvae														
Intercept	−5.30	0.98	−5.38	< 0.001		5.21 %	90.65 %	−4.47	0.38	−11.78	< 0.001		11.35 %	47.88 %
Log ₁₀ (aphids+1)	0.26	0.07	3.87	< 0.001	2.45 %			0.44	0.06	7.10	< 0.001	8.01 %		
EFN	1.02	0.37	2.74	0.01	2.25 %			0.32	0.35	0.89	0.37	0.47 %		
Open corolla	0.89	0.58	1.52	0.13	0.76 %			1.29	0.52	2.50	0.01	1.61 %		
Short corolla	−0.33	0.41	−0.8	0.43				0.00	0.37	0.01	0.99			
Flowers	0.52	0.29	1.77	0.08	0.70 %			0.28	0.30	0.92	0.36	0.38 %		
Ladybeetle adults														
Intercept	−1.76	0.41	−4.27	< 0.001		12.76 %	75.11 %	−2.31	0.31	−7.46	< 0.001		15.09 %	63.81 %
Log ₁₀ (aphids+1)	0.14	0.04	3.21	< 0.001	1.60 %			0.16	0.04	4.00	< 0.001	2.02 %		
EFN	0.90	0.25	3.62	< 0.001	4.16 %			0.79	0.30	2.65	0.01	3.73 %		
Open corolla	1.98	0.38	5.18	< 0.001	6.74 %			1.47	0.45	3.24	< 0.001	3.87 %		
Short corolla	0.36	0.26	1.38	0.17				−0.22	0.32	−0.69	0.49			
Flowers	0.62	0.16	3.94	< 0.001	2.18 %			0.88	0.20	4.49	< 0.001	4.14 %		

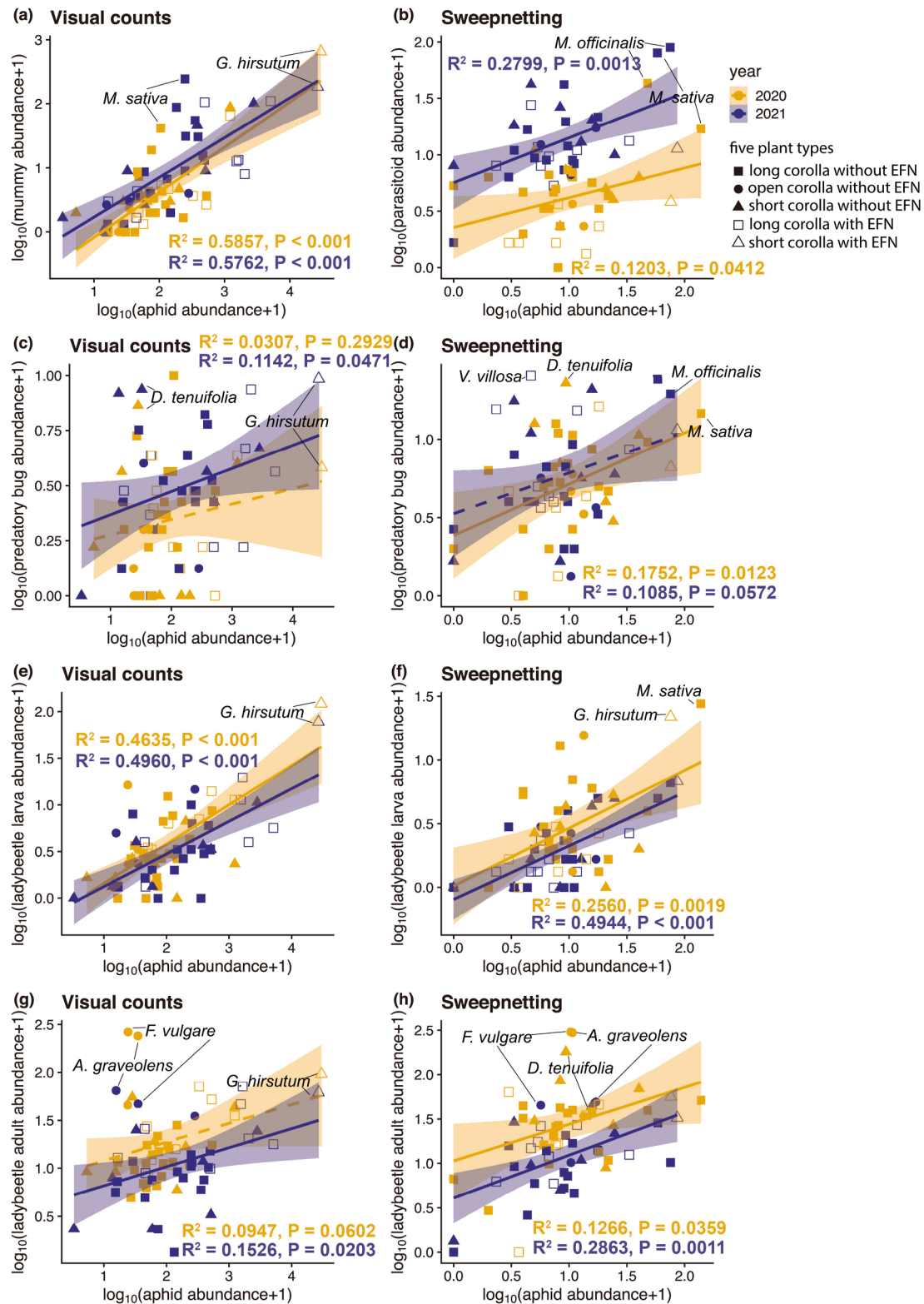


Fig. 3. Relationships between the abundance of mummies and aphids (a), abundance of parasitoids and aphids (b), predatory bugs and aphids (c, d), ladybeetle larvae and aphids (e, f), ladybeetle adults and aphids (g, h) on 39 plant species in 2020 and 2021. All abundances are $\log_{10}(N + 1)$ transformed. Panels show data for visual counts (left) and for sweepnetting (right). The two years are indicated with different colours (orange for 2020 and purple for 2021) and symbols indicate five plant types according to the corolla type and presence of extrafloral nectaries (EFN). Every symbol represents the results obtained for one plant species, based on sampling in three plots during the growing season. Observations were made on 25 plants per plot, and an area of 5 m² per plot was sampled with sweep nets (20 sweeps). Thirteen rounds were conducted in 2020 and 15 rounds in 2021. Solid and dash lines indicate significant ($P < 0.05$) and non-significant linear relationships, respectively. Abbreviated plant species names: *Foeniculum vulgare* (F. vulgare), *Anethum graveolens* (A. graveolens), *Diplotaxis tenuifolia* (D. tenuifolia), *Medicago sativa* (M. sativa), *Melilotus officinalis* (M. officinalis), *Vicia villosa* (V. villosa).

Table 3

Results of generalized linear mixed models with negative binomial error distribution for the relationship between the abundance of natural enemies and aphid abundance on plants ($\log_{10}(N + 1)$ -transformed), presence or absence of extrafloral nectar (EFN), accessibility of floral nectar (open/short/long corolla) and presence or absence of flowers on 39 plant species. Separate analyses are conducted for data obtained by **sweepnetting** in 2020 and 2021. Unique R^2 indicates the percentage of variance explained by individual factors. Marginal R^2 indicates the percentage of variance explained by fixed factors. Conditional R^2 indicates the percentage of variance explained by fixed and random factors. EFN absent, long corolla and flowers absent are references in all models. Significant relationships are indicated in bold.

	2020							2021						
	Estimate	Std. Error	z value	P	Unique R^2	Marginal R^2	Conditional R^2	Estimate	Std. Error	z value	P	Unique R^2	Marginal R^2	Conditional R^2
Parasitoids														
Intercept	-1.40	0.25	-5.5	< 0.001		4.49 %	13.40 %	-1.33	0.39	-3.45	< 0.001		6.18 %	64.39 %
$\log_{10}(\text{aphids}+1)$	0.19	0.12	1.53	0.13	0.19 %			0.40	0.07	5.44	< 0.001	1.73 %		
EFN	-1.30	0.39	-3.30	< 0.001	3.88 %			-0.39	0.31	-1.25	0.21	0.52 %		
Open corolla	-0.39	0.53	-0.74	0.46	0.23 %			-0.41	0.49	-0.83	0.40	0.42 %		
Short corolla	0.18	0.36	0.51	0.61				0.09	0.32	0.29	0.77			
Flowers	0.13	0.21	0.63	0.53	0.00 %			0.77	0.15	5.04	< 0.001	3.99 %		
Predatory bugs														
Intercept	-1.70	0.30	-5.66	< 0.001		3.35 %	27.96 %	-3.32	0.42	-7.98	< 0.001		10.55 %	51.31 %
$\log_{10}(\text{aphids}+1)$	0.37	0.11	3.39	< 0.001	1.29 %			0.30	0.12	2.51	0.01	0.57 %		
EFN	-0.53	0.37	-1.44	0.15	0.69 %			0.58	0.32	1.84	0.07	1.42 %		
Open corolla	-0.13	0.52	-0.25	0.80	1.07 %			-0.74	0.54	-1.38	0.17	1.28 %		
Short corolla	0.56	0.35	1.58	0.11				0.30	0.33	0.91	0.36			
Flowers	0.07	0.20	0.37	0.71	0.02 %			1.40	0.24	5.77	< 0.001	7.11 %		
Ladybeetle larvae														
Intercept	-4.72	0.84	-5.64	< 0.001		1.32 %	75.90 %	-5.23	0.71	-7.39	< 0.001		0.50 %	34.31 %
$\log_{10}(\text{aphids}+1)$	0.37	0.11	3.44	< 0.001	0.66 %			0.20	0.15	1.35	0.18	0.16 %		
EFN	-0.31	0.53	-0.58	0.56	0.12 %			-0.05	0.53	-0.10	0.92	0.00 %		
Open corolla	0.09	0.76	0.12	0.91	0.38 %			0.60	0.78	0.77	0.44	0.16 %		
Short corolla	0.45	0.52	0.88	0.38				0.12	0.54	0.22	0.83			
Flowers	0.01	0.41	0.03	0.98	0.00 %			0.32	0.45	0.71	0.48	0.16 %		
Ladybeetle adults														
Intercept	-1.10	0.49	-2.26	0.02		5.77 %	78.25 %	-2.18	0.47	-4.68	< 0.001		6.18 %	74.52 %
$\log_{10}(\text{aphids}+1)$	0.31	0.09	3.54	< 0.001	0.76 %			0.28	0.07	3.79	< 0.001	1.09 %		
EFN	0.07	0.41	0.17	0.86	0.05 %			0.42	0.32	1.28	0.20	0.85 %		
Open corolla	1.19	0.58	2.05	0.04	3.38 %			0.96	0.50	1.94	0.05	1.94 %		
Short corolla	0.63	0.40	1.56	0.12				0.29	0.34	0.85	0.39			
Flowers	0.53	0.18	2.97	< 0.001	1.17 %			0.78	0.19	4.12	< 0.001	2.98 %		

and parasitoid abundance in 2020 (Table 3). While the use of extrafloral nectar by parasitoids is well established (Jones et al., 2017), some plants without extrafloral nectar but high aphid abundance, such as *M. officinalis* and *M. sativa*, had a relatively high parasitoid abundance (Figs. S3b and S6b). This suggests that sugar resources were not limiting in our experiment and that parasitoids primarily used floral nectar or aphid honeydew and fed less on the less abundant and/or conspicuous extrafloral nectar (Géneau et al., 2013). Since different natural enemy groups showed different responses to plants with open nectaries, extrafloral nectar, high aphid densities and the associated honeydew, selecting a mix of service plants that provide these sugar resources could potentially support a wider diversity of natural enemy species (Zytynska et al., 2021).

While the use of service plants in flowering field margins is increasingly promoted and applied in many parts of the world, it is still hardly used in Xinjiang despite successes in other parts of China (Gurr et al., 2016). We identified plant species that grow well under Xinjiang conditions and were used by local natural enemy communities, which were dominated by ladybeetles, parasitoids and predatory bugs. Besides the well documented importance of floral and extrafloral resources, we found that the provision of aphid prey was a key plant characteristic attractive to natural enemies. This finding can help to inform farmers about what service plant species may be suitable for habitat diversification practices to conserve natural enemies on their farms, and are compatible with their production systems. Further work is needed to assess whether the service plants can contribute to the longer-term built up of natural enemy populations, biological control in target crops and reduce the dependency on insecticides.

CRediT authorship contribution statement

Mengxiao Sun: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Bing Liu:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Felix J. Bianchi:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Wopke van der Werf:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Yanhui Lu:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, 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.2025.109502.

Data availability

Data will be made available on request.

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