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ORIGINAL PAPER

Functional plants supporting predatory ladybirds in a peach orchard agroecosystem

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Abstract

Predatory ladybirds are key natural enemies of a diversity of crop pests. Conserving ladybirds in agroecosystems to benefit from their biocontrol potential requires to understand the ecological interactions between them and functional plants. A diversity of functional plants is known to offer resources improving ladybirds' fitness and pest control effects. Yet, there is a lack of knowledge on the relationship between a diversity of functional plants found at the field scale and the dynamic of ladybird population. In this study conducted over three consecutive years, we investigated from early May to mid-August, the weekly abundance of predatory ladybirds on 15 functional plants and peach trees (*Prunus persica*) in a peach orchard agroecosystem in the Beijing Province of China. Seven plant species hosted 90% of the ladybird population throughout the study period. Through them, two abundance peaks of ladybirds were observed, with *Vitex negundo* and *Prunus persica* supporting the ladybirds in the first peak, *Artemisia sieversiana*, *Vigna unguiculata*, *Cosmos bipinnata*, *Zea mays* and *Helianthus annuus* playing a major role in the second peak. The plant species were either at their seedling, blooming or fructification stage when hosting the ladybirds, suggesting that these lasts used the diversity of resources (prey, nectar and pollen of flowers and extra-floral nectar) offered at the agroecosystem level. The present results enrich the screening of functional plants supporting predatory ladybirds in perennial agroecosystems and emphasize the need to pay attention to the long-standing plants in the surrounding habitats. It suggests that maintaining and managing a diversity of functional plants at the field scale is needed to offer a spatial and temporal continuity of resources to ladybirds.

Keywords Agroecosystem diversification · Coccinellidae · Secondary plants · Conservation biological control · Phenological periods · Population dynamic

Introduction

The modernization of agriculture has contributed to the simplification of agroecosystems, and orchards are no exception. It went along with high use of synthetic pesticides, causing a significant reduction of biodiversity in agricultural ecosystems, and leading to a gradual weakening of service functions including the regulation of pests, food safety issues and ecological environment damage (Geiger et al. 2010; Pretty et al. 2018; Zhou et al. 2023). In this context, restoring ecological regulations in agroecosystems is possible by increasing plant diversity (Nicholls and Altieri 2004). Against insect pests, conservation biological control consists in managing the environment to protect and enhance local natural enemies—among which predatory ladybirds (Obrycki et al. 2009)—to reduce the detrimental effects of herbivores on crops (Rayl et al. 2018).

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The use of functional plants, also called secondary plants (*sensu* Parolin et al. 2012), is key when designing pest suppressive agroecosystems (Hatt et al. 2018). Functional plants are sown or preserved with the objective of enhancing the delivery of one or more ecosystem services and are not necessarily harvested. Certain functional plant species can have direct effects on the pests, through repellence, or by attracting them away from the cash crop (Wang et al. 2022a). Functional plants can also benefit to pest predators. Predatory ladybirds (Coleoptera: Coccinellidae) can benefit from the provisioning of high-quality alternative food resources such as pollen and nectar (Wang et al. 2020; He et al. 2021) or alternative prey (Wang et al. 2022b), and use functional plants as shelter against disturbances (Tooker et al. 2020). Specific integrated strategies make use of functional plants for biological control in 'push-pull' and 'attract-reward' systems (Xu et al. 2018a; Simpson et al. 2011). Promising results showed that increasing plant diversity at the field scale allows reducing insecticide uses without decreasing yield, *in fine* favouring economic gains (Gurr et al. 2016; Li et al. 2021).

In orchard agroecosystems, functional plants can be managed between tree rows and/or in semi-natural habitats in the direct surrounding (Jaworski et al. 2019). Flowering forbs such as *Cnidium monnieri* (Apiaceae), *Tagetes patula* (Asteraceae) or *Ocimum basilicum* (Lamiaceae) sown between tree rows can support predatory ladybirds including *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) and *Propylea japonica* (Thunberg) (Coleoptera: Coccinellidae) (Zhang et al. 2022; Song et al. 2013). In the natural habitats potentially surrounding orchards, shrubs and trees hosting *H. axyridis* include *Sambucus sieboldiana* (Caprifoliaceae) or *Quercus glauca* (Fagaceae) in its native range (Osawa 2011). In a semi-natural environment (i.e. a botanical garden in Kyoto, Japan), Osawa (2000) showed that from April to July, *H. axyridis* beetles make use of a diversity of other plant species such as *Spiraea* spp. (Rosaceae), *Salix* spp. (Salicaceae), *Typha angustifolia* (Typhaceae) and peach trees *Prunus persica* (Rosaceae).

Population dynamic of predatory ladybirds is known to follow the population dynamic of their prey, especially aphids (Hemiptera: Aphididae) (Osawa 2000; Hodek and Honek 1996), explaining the key role of alternative prey on functional plants to support population of natural enemies of crop pests (Alhmedi et al. 2009). Yet, the fitness of aphids and therefore their availability as prey may depend on the growth stage of their host plants (Guldemond et al. 1998; Karley et al. 2004). In addition, ladybirds are known to visit flowers. Ultra-violet pattern of inflorescences (i.e. ultra-violet reflectance of the internal flower part differing to that of the external flower part) (Hatt et al. 2019a), short corolla depth implying accessible nectar (Hatt et al. 2019b) and the presence of extra-floral nectar (Mathews et al. 2016) are functional traits of plants attracting predatory ladybirds. It suggests that the phenological stages of functional plants can be critical to support populations of ladybirds, and that understanding ladybird-functional plant interactions considering plants' growth stage should help tailoring agroecosystem designs benefiting to pest natural enemies.

With the objective of supporting natural enemies of pests in peach orchard agroecosystems towards enhancing conservation biological control in the Beijing province of China, the aim of the present study was (i) to identify functional plant species and their development stage supporting predatory ladybirds at the field scale, and (ii) to evaluate whether different suitable functional plant species would complement each other to support ladybird populations through the whole cropping season. While predatory ladybirds can migrate short distances from plant species to others looking for food resources (Osawa 2000), ensuring the continuity of resources through time is supposed to be key to bolster ecosystem services such as pest control (Schellhorn et al. 2015).

Materials and methods

Study species and study site

Twenty functional plants were selected for this experiment (Table 1). These species were selected from native plants around the peach orchard agroecosystem in Beijing, or from varieties with potential application effects reported in other regions. The initial plants were derived from the surrounding natural ecosystems or seedlings cultivated by the Plant Protection Institute of Beijing Academy of Agriculture and Forestry Sciences. Functional plant plots were set around a peach orchard (Fig. 1) in Changping district experimental station in Beijing, China (116° 2′ E, 40° 10′ N), for three consecutive years in 2019, 2020 and 2021, with one plot for each plant species, each plot comprising 25 plant individuals. The plant layout in each plot was carried out according to 5 rows × 5 columns (the plant spacing of each species is indicated in Table 1). The field layout of all plants was similar for three consecutive years, some perennial plants (i.e. *Vitex negundo*, *Salvia miltiorrhiza*, *Artemisia sieversiana*) were planted 1 year before the experiment, the seeds or seedlings of other annuals plants were derived from Beijing Academy of Agriculture and Forestry Sciences, field planting or transplanting of these species was completed in March–April. No pesticide was used in the whole area during the whole duration of the experiment.

Data collection

The population dynamics of predatory ladybirds, with a focus on Coccinellinae, on functional plants and peach trees

Table 1 Species and spacing of functional plants

Number	Family	Latin name	Growth cycle	Type	Plant classification	Blooming period	Spacing (cm)
1	Asteraceae	*Cosmos bipinnata*	Annuals/perennial	Herb	Native	Jun.–Aug.	10
2		*Hemistepta lyrate*[a]	Annuals	Herb	Native	Mar.–Aug.	15
3		*Zinnia elegans*	Annuals	Herb	Naturalized	Jun.–Sep.	15
4		*Artemisia sieversiana*	Annuals/biennial	Herb	Native	Jul.–Aug.	30
5		*Helianthus annuus*	Annuals	Herb	Native	Jul.–Sep.	50
6	Lamiaceae	*Lagopsis supina*[a]	Perennial	Herb	Native	Mar.–Apr.	10
7		*Nepeta cataria*	Perennial	Herb	Native	Jul.–Sep.	15
8		*Salvia miltiorrhiza*	Perennial	Herb	Native	Apr.–Aug.	15
9		*Perilla frutescens*	Annuals	Herb	Native	Aug.–Nov.	30
10	Liliaceae	*Hosta plantaginea*[a]	Annuals	Herb	Native	Aug.–Sep.	15
11		*Anemarrhena asphodeloides*	Perennial	Herb	Native	May–Jun.	15
12		*Polygonatum odoratum*	Perennial	Herb	Native	May–Jun.	15
13	Fabaceae	*Medicago sativa*[a]	Perennial	Herb	Native	May–Jul.	15
14		*Vigna unguiculata*	Annuals	Herb	Naturalized	May–Aug.	30
15	Solanaceae	*Solanum lycopersicum*	Annuals	Herb	Naturalized	May–Jun.	30
16	Iridaceae	*Iris pallida*	Perennial	Herb	Naturalized	May–Jun.	30
17	Brassicaceae	*Orychophragmus violaceus*[a]	Annuals/biennial	Herb	Native	Apr.–May	15
18	Rosaceae	*Rosa chinensis*	Perennial	Woody	Native	May–Sep.	30
19	Gramineae	*Zea mays*	Annuals	Herb	Naturalized	Sep.–Oct.	50
20	Verbenaceae	*Vitex negundo*	Perennial	Woody	Native	MayvJul.	60

[a]These species, although sown in the field, were not monitored for ladybird beetle abundance

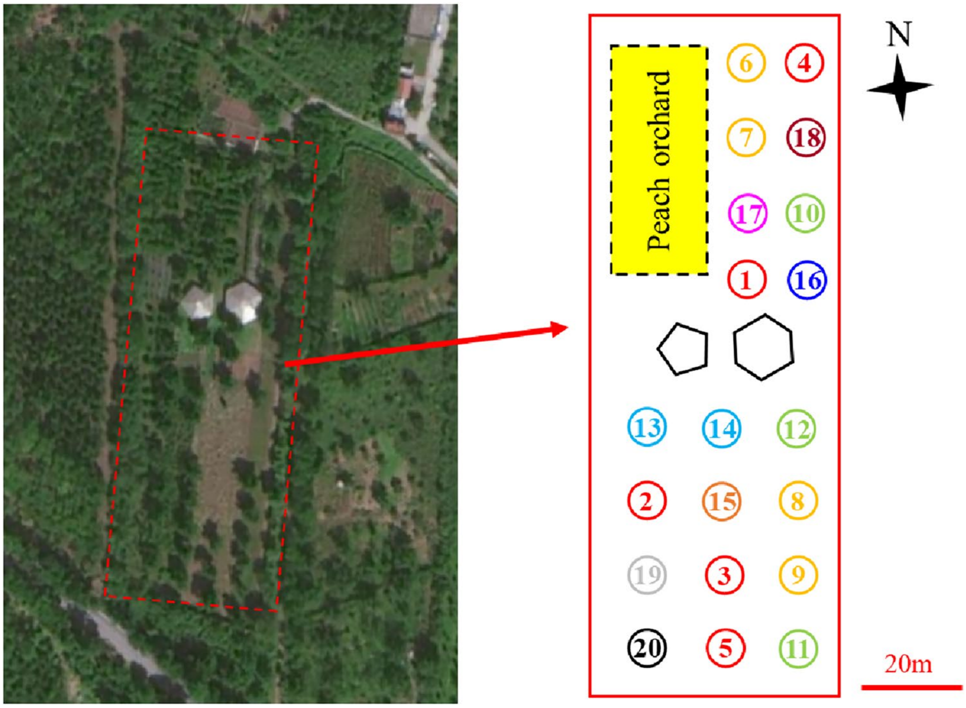

Fig. 1 Field layout of functional plants and the peach orchard. The numbers in the figure correspond to the plant species in Table 1. Different colour numbers represent different botanical families. The yellow area is the peach orchard, and the pentagon and hexagon are field greenhouses

were investigated every seven days from early May to mid-August (16 times per year in total) in 2019, 2020 and 2021. For 15 functional plant species (i.e. five plant species were finally not monitored during the whole period because the abundance of ladybirds on the five plants was extremely low on all dates and therefore were excluded from the analysis; Table 1), 10 individual plants were visually investigated in each plot between 9:00 am and 11:00 am to assess the abundance of ladybird larvae and adults (excluding eggs and pupae) (Li et al. 2021). The growth status of the plants (seedling stage, blooming or fructification) was noted for each monitoring date. To investigate the population dynamics of predatory ladybirds on peach trees, five points were selected at equal distances through the diagonal of the peach orchard, and two peach trees were selected at each point. On each of these two trees, 10 branches were randomly chosen and visually observed over 15 cm from the top of the new tip to record the abundance of predatory ladybirds (larvae and adults).

Statistical analyses

All statistical analyses were performed using R Core Team (2020). Difference between years (2019, 2020, 2021) in the abundance of ladybirds was evaluated by fitting a generalized linear mixed model (GLMM), including years as a fixed factor, and the plant species nested within years as a random factor. The random factor allowed integrating the repeated measurements done on the different plant species every year. A negative binomial distribution (function *glmmTMB*, package *glmmTMB*, Brooks et al. 2017) was used to solve the overdispersion of the data observed when using a Poisson distribution. The effect of years on ladybird abundance was tested using a Wald Chi-squared test. Difference in abundance of ladybirds was also compared between the first (5 May to 23 June) and the second (30 June to 18 August) half of the study period. The potential interactive effects of time phases and years were evaluated by fitting a GLMM with negative binomial distribution, with phases (5 May–23 June, 30 June–18 August), years (2019, 2020, 2021) and their interaction as fixed factors, the plant species nested within years as a random effect, the model tested using a Wald Chi-squared test.

The effect of plant species on the abundance of ladybirds was analysed by fitting a GLMM using a negative binomial distribution, including plant species as a fixed factor and the years as a random factor. Abundances over the sampling dates were pooled per plant species for each year separately. The effect of plant species was tested using a Wald Chi-squared test, and comparisons between species were performed using a post hoc test of Tukey (function *glht*, package *multcomp*, Hothorn et al. 2008). Similar analyses were performed by considering the first and second 8-week phases separately (i.e. 5 May–23 June and 30 June–18 August, respectively).

Considering separately the first and the second half of the study period was explained by the temporal dynamic of ladybird abundance, that was analysed over the whole study period by fitting a GLMM using a negative binomial distribution, with time (i.e. the successive sampling dates) as a fixed factor, years as a random factor, and tested using a Wald Chi-squared test.

Finally, whether ladybirds were significantly more observed on a plant species at a specific plant development stage (seedling, blooming or fructification) was analysed using an exact binomial test (function *binom.test*). The 'hypothesized probability of success' was fixed at 0.5. Summed ladybird abundances over the 3 years were considered for each development stage per plant species.

Results

Ladybird species observed were *H. axyridis*, *Coccinella septempunctata* (Linnaeus) and *Propylea japonica*. On average, 372 ± 25 (mean ± SE) ladybird individuals were observed every year, without significant differences between years ($df = 2$; $\chi^2 = 0.57$; $P = 0.752$). Over the whole study period, plant species identity had a significant effect on the abundance of ladybirds ($df = 15$; $\chi^2 = 222$; $P < 0.001$; Fig. 2a). Seven plant species statistically equally contributed (i.e. without significant differences between them) at supporting altogether 90 % of the ladybird population, namely *V. negundo* (20.43%), *Vigna unguiculata* (12.81%), *A. sieversiana* (12.63%), *Cosmos bipinnata* (9.77%), *Zea mays* (8.51%), *Helianthus annuus* (6.99%), as well as the peach trees *Prunus persica* (19.53%) (Fig. 2a; Table S1).

Specifying the plant phenological stages at which ladybirds were observed reveals contrasting situations. The seedling stage was preferred by ladybird beetles for *V. negundo* ($P < 0.001$) and *A. sieversiana* ($P < 0.001$), the blooming stage was preferred for *C. bipinnata* ($P < 0.001$) and *H. annuus* ($P < 0.001$), and finally the fructification stage was preferred for *V. unguiculata* ($P < 0.001$), *Z. mays* ($P < 0.001$) but also *P. persica* ($P < 0.001$) (Fig. 2a; Table S1).

The analysis of ladybird population dynamic, fitted as a fourth-degree polynomial regression ($df = 4$; $\chi^2 = 44.7$; $P < 0.001$), reveals an oscillation with two abundance peaks, first in mid-May, and second on early August (Fig. 3). Two phases of 8 weeks showing each an increase followed by a decrease of the abundance of ladybirds could be identified, i.e. from 5 May to 23 June, and from 30 June to 18 August. Abundance of ladybirds was not significantly different between the two phases ($df = 1$; $\chi^2 = 1.68$; $P = 0.195$), and no interaction between phases and years was identified ($df = 2$; $\chi^2 = 4.27$; $P = 0.118$).

During each phase, plant species identity had a significant effect on the abundance of ladybirds (phase 1: $df = 15$; $\chi^2 = 223$; $P < 0.001$; phase 2: $df = 15$; $\chi^2 = 176$; $P < 0.001$; Fig. 2b, c). The plant species hosting the most of ladybird individuals were different during the two phases (Fig. 2b, c). From 5 May to 23 June (phase 1), two species statistically equally contributed at supporting 80% of ladybird

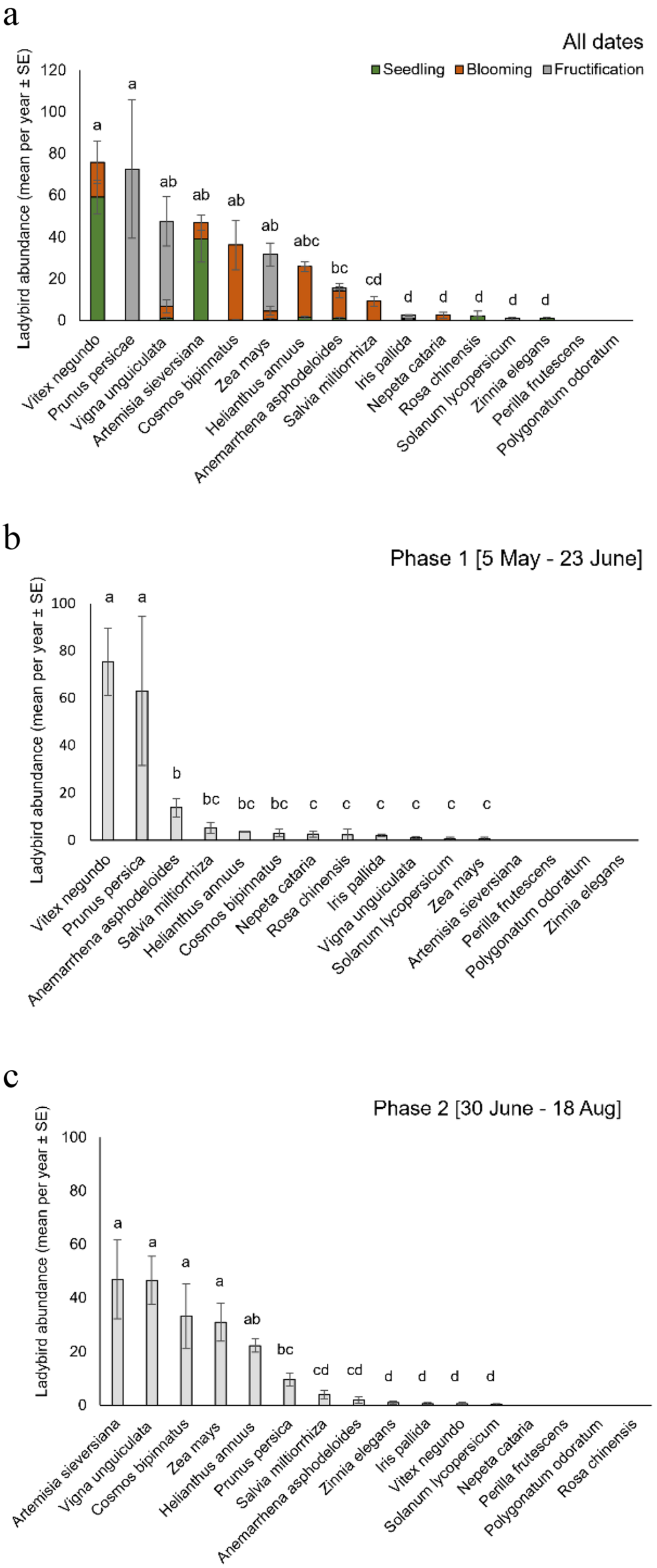

Fig. 2 Mean (± SE) abundance per year of ladybird beetles observed on companion plants and peach trees (*Prunus persica*) considering **a** all sampling dates (5 May to 18 August) with specifications on the plant's development stage, **b** only the first 8 weeks (i.e. phase 1, 5 May to 23 June), and **c** only the second 8 weeks (i.e. phase 2, 30 June–18 August)—see this figure for more details on ladybird beetles' population dynamics explaining the separate analysis of the two phases. Plant species sharing the same letters above the bars show no significant differences in the abundance of ladybird beetles.

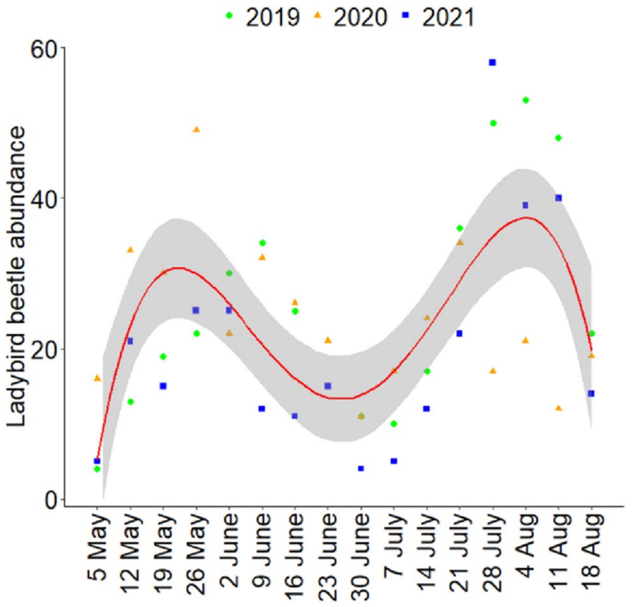

Fig. 3 Dynamic of ladybird beetles' abundance averaged over the 3 years of monitoring (2019–2021) considering all observed plants (i.e. each point being the summed abundance of ladybirds over the 15 monitored plant species and peach trees for a given sampling date and year). Grey shading indicates the 95% confidence interval in the polynomial regression

individuals: *V. negundo* and *P. persica* (mean ± SE: *V. negundo* 75 ± 14; *P. persica* 63 ± 31; Fig. 2b). From 30 June to 18 August (phase 2), five other plant species statistically equally contributed at supporting 90% of ladybird beetle individuals: *A. sieversiana*, *V. unguiculata*, *C. bipinnata*, *Z. mays* and *H. annuus* (mean ± SE: *A. sieversiana* 47 ± 15; *V. unguiculata* 47 ± 9; *C. bipinnata* 33 ± 12; *Z. mays* 31 ± 7; *H. annuus* 22 ± 2; Fig. 2c).

Discussion

In this study, the abundance of predatory ladybirds was monitored on 15 plant species over 3 years from May to August in a peach orchard agroecosystem. We found that seven plant species, including peach trees, accounted for almost all the ladybird population mostly made of *H. axyridis*, *C. septempunctata* and *P. japonica*. During the study period, two abundance peaks of the ladybirds were observed, and during each peak period they used two distinct groups of plants. The plant species that hosted the ladybirds during the first phase (i.e. *V. negundo* and *P. persica*) had a significantly reduced hosting capacity during the second phase, when other plant species (i.e. *A. sieversiana*, *V. unguiculata, C. bipinnata*, *Z. mays* and *H. annuus*) were used. It suggests that sustaining predatory ladybirds in a peach orchard agroecosystem from spring to summer, i.e. throughout the production period of peach trees, requires preserving and managing a diversity of key functional plant species at the field scale.

Three of the highly attractive plant species in the present study belong to the Asteraceae (*A. sieversiana, C. bipinnata, H. annuus*). Previous studies also showed that Asteraceae is among the botanical family comprising plant species attractive to ladybirds (Losey et al. 2022). Yet, compared to Apiaceae which consistently benefit to ladybirds, variable effects of Asteraceae species are observed (Hatt et al. 2019b), which is confirmed in the present experiment. Here, *C. bipinnata* and *H. annuus* were attractive to ladybirds while blooming. While both have deep corolla making nectar hardly available to ladybirds (Wäckers and van Rijn 2012), *H. annuus* offers extra-floral nectar (Weber et al. 2015), which likely explain the observed attraction to ladybirds. The production of extra-floral nectar, which can occur at various development stages of plants (Marazzi et al. 2013), can also explain the attractivity of *V. unguiculata*, a Fabaceae which hosted the coccinellids while fruiting in the present study. Although nectar generally contributes to increase the survivability of ladybirds (He et al. 2021), aphids are their essential food (Hodek 1996). Xu et al. (2023) previously showed that the presence of ladybirds on *V. negundo* and peach trees is driven by the abundance of aphids on these plants. As for *Z. mays*, previous studies also highlighted the positive correlation between aphid and ladybird dynamics, especially in August in adjacent regions of Beijing (Pan et al. 2020).

The diversity of resources offered by the various functional plants at the field scale is central in the dynamic of the ladybird population (Osawa 2000). In the present study, it was oscillatory with two abundance peaks in the end of May and early August, respectively, and a reduced population in the end of June. In the first phase, hosts plants provided ladybirds with prey food (i.e. aphids) (as shown in a previous analysis, Xu et al. 2023) essential for the ladybird reproduction (Hodek 1996), allowing the population to increase which is critical for early pest control (Evans 2008). During the second phase, it is likely that food sources were more diverse, with non-prey food potentially allowing the ladybirds to survive in the absence of prey (Wolf et al. 2018). Previous studies attributed the oscillatory dynamic of ladybird population to the dynamic of aphids (Osawa 2000). The present results suggest that non-prey food, such as extra-floral nectar, can also significantly contribute to this oscillatory dynamic.

The spill-over of natural enemy insects from surrounding habitats or native plants to crops is key for conservation biological control (Jaworski et al. 2023; Zaviezo and Muñoz 2023). According to our observation in the present study, ladybirds may have transferred from *V. negundo* to peach trees before moving again to other plant species (Fig. S1). The movement of insect from one habitat type to another in agricultural landscapes determines their abundance and distribution in space and time (Mazzi and Dorn 2012). The existence or density of (alternative) prey, in addition to nectar and pollen, is a significant driver of natural enemy distribution (Gurr et al. 2017; Wang et al. 2022b; Zhang et al. 2022). Yet, previous studies conducted in other agroecosystem contexts did not consistently show such a movement of ladybirds between a variety of plant species available at the field scale. In field crops, *C. monnieri* sown as a flower strip is used as a bridge habitat to facilitate the movement of *P. japonica* from wheat to maize (Yang et al. 2021). However, in an apple orchard, the abundance of *H. axyridis* peaked synchronically on all the four functional plants tested [i.e. *Brassica napus* (Brassicaceae), *Vicia villosa* (Fabaceae), *Schizonepeta tenuifolia* (Lamiaceae) and *C. monnieri*] suggesting a redundancy in the use of resources (Zhang et al. 2022). In the present study, woody species in addition to forbs were considered. The high attractivity of *V. negundo* in the earlier phase highlights the key role that woody plants can play to support ladybirds at crop vicinity. While predatory ladybirds are known to use both trees and forbs (Osawa 2000; Burgio et al. 2004), the present results suggest a complementary between both, with trees playing a significant role in the early phase of population development, forbs being more attractive in the second phase.

Beyond food sources and shelter, attractivity of functional plants to predators is partly driven by chemical cues, i.e. plant volatiles (Turlings and Erb 2018). Large range of plant volatiles attracting predators are induced by herbivores, and therefore released by plants as indirect defences. By using Y-tube olfactometer, Xu et al. (2023) demonstrated that aphid-infested *V. negundo* attracts adults of *H. axyridis*, and identified sclareol, eucalyptol, nonanal and a-terpineol as key plant volatiles involved in *H. axyridis* attraction. Methyl-salicylate (MeSA) is another herbivore-induced plant volatile (HIPV) known to be highly attractive to natural enemies of pests including ladybirds (Rodriguez-Saona et al. 2011). Complementing the use of functional plants, and more generally plant diversity in agroecosystems, with the release of HIPVs such as MeSA was successful in enhancing predatory ladybirds and promoting biological control (Jaworski et al. 2019; Xu et al. 2018b).

More generally, stacking practices to attract and support natural enemies was proposed as a key principle to design pest suppressive agroecosystem (Hokkanen 2017; Hatt and Döring 2023). It is supposed to enhance the resilience of regulating processes by increasing the redundancy in ecological functions. It is not trivial as several plant species tested in the present experiment did not support ladybirds as expected. It is the case of *Nepeta cataria*, which was as efficient as other functional plant species to support predatory ladybirds in previous studies (Wan et al. 2015). It is also the case of *Perilla frutescens*, which floral resources can enhance the longevity of ladybirds, and even bolster their fecundity if associate with prey food (Hatt and Osawa 2019). However, *P. frutescens* is a relatively late blooming species, i.e. flowering in September, which was beyond the study period in the present research. Finally, the limited attractivity of *Medicago sativa* was surprising. Regulation by other natural enemies (e.g. parasitoids), or aphid-ant symbiosis (Stadler and Dixon 2005) can explain that plant species usually hosting alternative preys may not support targeted predators such as ladybirds.

In the present study, six functional plant species supporting ladybirds in a peach orchard agroecosystem were identified. It was demonstrated that together, they can sustain the predators throughout the peach production period from spring to summer. It offers practical information for future research, in which these six functional plants could be implemented in peach orchards to quantify their effect on pest reduction on peach trees. While the forb species could be sown between tree rows as flower strips, *V. negundo* could be planted as hedgerows at orchard margins. The effect of these functional plants on other pest natural enemies, such as predatory hoverflies (Diptera: Syrphidae) and lacewings (Neuroptera: Chrysopidae) as well as parasitoids (Hymenoptera), could be evaluated.

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Author contributions CW, QX, SW and XG contributed to the study conception and design. CW, SW and QX completed the field investigation. CW, SH, DX and QX analysed experiments data. CW, SH and QX wrote and revised the paper. All authors have read, commented on and approved the final manuscript.

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Data availability Authors can provide relevant data.

Declarations

Competing interests The authors have no conflict of interests in this contribution.

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