Flower strips as a bridge habitat facilitate the movement of predatory beetles from wheat to maize crops

Running title: Flower strips maximizing carryover of beetles from wheat to maize

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Abstract

BACKGROUND: Generalist predators play a key role in the biocontrol of insect pests in agricultural systems. However, predators are subject to frequent mortality events due to periodic disturbance regimes such as crop planting and harvest, which inevitably affect the population development of predators. Conservation of predators in this critical period is important for double-cropping systems such as winter wheat and summer maize, the most widely used cropping system in North China.

RESULTS: Planting *Cnidium monnieri* flower strips at field borders could not only serve as a bridge habitat to conserve the dominant predator *Propylaea japonica* in wheat fields during harvest but also help the predator immigrate to adjacent maize fields. The predator abundance was 7-fold higher on flower strips than that on natural vegetation strips during the wheat postharvest period and before the maize plant emergence for about a month, and its abundance in maize fields planted with flower strips was nearly 2-fold higher than that in maize fields planted with natural vegetation strips. Moreover, 77.56% of predators that entered maize fields were proven to originate from flower strips.

CONCLUSION: Our findings provided evidence that manipulating flower strips as a bridge habitat in wheat-maize rotation fields could conserve *P. japonica* during crop phenophase changes, and we quantified that the proportion of this predator in maize fields derived from flower strips. In practice, such a strategy may also be applied in other double-cropping and triple-cropping systems.

KEYWORDS: habitat management; flower strips; periodic disturbance regimes; generalist predator; molecular gut-content analysis; double-cropping and triple-cropping systems

1 INTRODUCTION

Generalist predators are major natural enemies and contribute to the top-down control of insect pests in agricultural systems.[1,2,3] However, these predators are subject to frequent mortality events because of crop periodic management practices such as planting and harvest.[4,5] In annual double-cropping and triple-cropping systems, predators are forced to emigrate from the crop habitats after crop harvest in the previous season, and predators' population must be reconstructed in the crop habitats in the following season after crop emergence.[4,5] It is obvious that there exists a resource shortage for enhancing predators' performance in these critical periods in these systems, especially in agricultural systems with disturbed non-crop habitats within the agricultural landscape.[6,7] Habitat management involves manipulating non-crop habitats such as flower strips at the within-crop, within-farm or landscape levels to provide available resources such as nectar, pollen, alternative prey for natural enemies, and shelter from unfavourable conditions.[8,9] Flower strips as bridge habitats within these agricultural systems have been manipulated as an ecological infrastructure to fill the resource shortage and provide available resources for predators during periods after crop harvest in the previous season and to help predators immigrate to crops after crop emergence in the following season. Manipulating flower strips as bridge habitats in these systems is essential for sustainable generalist predator conservation and maximizing biocontrol services.[5,6,7]

The patterns in abundance and species of predators in crops are relevant to specific non-crop habitats in the surrounding agricultural landscape.[10,11,12] When flower strips are manipulated as bridge habitats for predators in these systems, immigration to crops from flower strips has been suggested as a driver of these spatial patterns. It is vital to quantify the immigration time,[5] the transfer rate of predators from flower strips into crop habitats and the proportion of predators in crop habitats derived from flower strips,[5,8,9] but such a quantitative study is rare.[5] In turn, immigration is always confounded with local reproduction, and the elative contributions of immigration from flower strips and reproduction to population increase are not clear. Separating these processes would help researchers better understand the contribution of immigration from flower strips to population dynamics and the implications for pest suppression. In recent years, molecular gut-content analysis of food residuals in the guts of predators was widely used to reveal the explicit trophic relationships between predators and preys or alternative foods, and the food origins of predators.[13,14,15,16] Predatory beetles feed on plant floral resources (pollen or nectar) in flower strips manipulated as non-crop habitats within agricultural systems.[17] Recent studies have showed that internal transcribed spacer (ITS) is a suitable core barcode for seed plants[18] and could identify the plant species that insects have fed.[19,20] Previous studies have found that predators move between crops and non-crop habitats.[21,22] Thus, it is feasible to detect plant ITS in the guts of predators via molecular gut-content analysis and quantify the proportion of predators in crop habitats originally derived from flower strips. Moreover, the immigration time, the transfer rate of predators from flower strips into crops could be illustrated by detecting plant residuals in the guts of predators in crops at different sampling dates.

The winter wheat-summer maize rotation system is an annual double-cropping and the most widely used cropping system in North China.[23] The generalist predator *Propylaea japonica* Thunberg (Coleoptera: Coccinellidae) is among the dominant naturally occurring ladybeetles in North China [24] and effectively control cereal aphids, the most serious insect pests of wheat in spring,[25,26,27] and corn leaf aphids, an important insect pest of maize in summer.[22,28] Our previous study clarified that *P. japonica* has great dispersal ability between different crop and non-crop habitats.[22,29] In this rotation system, cereal aphids can be a source for *P. japonica* that reproduce in wheat fields, but this could end after a disturbance, resulting in ephemeral source habitats.[5,30] *P. japonica* in wheat fields are forced to emigrate into non-crop habitats during the wheat postharvest period. Additionally, *P. japonica* population must be reconstructed in maize fields after maize plant emergence.[28] The bridge habitats within wheat-maize rotation fields aim to conserve *P. japonica* in wheat fields postharvest and help it immigrate to maize fields. However, to date, few studies have reported that the manipulation of flower strips as a bridge habitat could conserve *P. japonica* in wheat-maize rotation fields.[6,7] More importantly, few studies have quantified that the immigration time, the transfer rate of *P. japonica* from flower strips into crop habitats and the proportion of *P. japonica* in crop habitats derived from flower strips.[6] In this study, we planted border flower strips as a bridge habitat in wheat-maize rotation fields to answer the following three questions: (i) can flower strips serve as a bridge habitat to conserve *P. japonica* in wheat-maize rotation fields; (ii) if so, what kinds of resources do flower strips provide for *P. japonica*; and (iii) if so, can the immigration time, the transfer rate of *P. japonica* from flower strips to maize fields and the proportion of *P. japonica* in maize fields derived from flower strips could be quantified?

2 MATERIALS AND METHODS

2.1 Study sites

Field experiments were conducted in Jiyang district, Jinan City (36° 58' 51"N, 116° 58' 23"E) in 2017 and in Decheng district, Dezhou City (37° 21' 48.01"N, 116° 20' 39.56"E) in 2018, respectively. The two research sites are about 50 km apart and in northwest of Shandong Province, China. Winter wheat and summer maize rotation system are widely used in this region covering about 200*200 km. The soil conditions, climatic conditions and so on are very similar in this region. In addition, the annual mean temperature and precipitation were 15.0 ℃ and 520.5 mm in Jinan in 2017 and 14.2 ℃ and 639.4 mm in Dezhou in 2018, respectively.

2.2 Experimental design

2.2.1 Experimental plot design

A randomized complete block design was adopted for the experimental plot arrangement. The experimental field was divided into three random blocks in Jinan (Fig. 1a) and six random blocks in Dezhou (Fig. 1b). Each block contained a treatment: a wheat/maize plot with flower strips and a control: a wheat/maize plot with natural vegetation strips (mainly composed of two herbaceous plants: *Amaranthus retroflexus* and *Abutilon theophrasti*). The length and width of each wheat or maize plot were 64 m and 13.5 m in Jinan, and 20 m and 14 m in Dezhou, respectively. The length and width of each flower strip plot were 13.5 m and 4 m in Jinan, and 20 m and 4 m in Dezhou, respectively. The line spacing among *C. monnieri* plants are about 0.3 meter in each flower strip plot. The flower strip plot or natural vegetation strip plot is adjacent to the first row of the wheat or maize and their spacing is about 0.3 metre. Wheat seeds were sowed in early

October and maize seeds were sowed in mid-June in next year. The wheat and maize cultivars are ‘Jimai 22’ and ‘Zhengdan 958’, respectively. The herbicide MCPA-dimethylammonium (CAS number: 2039-46-5, 75% purity, aqueous solutions) was purchased from Anhui Shalongda Biotechnology Co., Ltd (Hefei, Anhui Province, China). It was sprayed via Knapsack sprayer at wheat jointing stage and after maize seeds were sowed but before maize plant emergence. The herbicide was 15 gram per package and 750 milliliter were used for each hectare.

2.2.2 The establishment of flower strips

The species used in flower strips was selected through field investigation of native plants in Shandong Province for many years. Then we found a species of annual flowering herbaceous plant named *Cnidium monnieri* (L.) Cuss (Apiaceae: Cnidium), which harboured a great richness and abundance of predators including *P. japonica*.[31] *C. monnieri* seeds could be sowed in spring, summer and autumn[32]. However, *C. monnieri* seeds were sowed in autumn when wheat seeds were sowed at two sites, so the full-bloom stage of flower strips in next year were during periods after wheat harvest and before maize plant emergence. Then flower strips could act as a bridge habitat for *P. japonica*. *C. monnieri* seeds were sowed with a density of approximately 37.5 kg/ha. No pesticides were used in flower strip plots.

2.3 Sampling and collection

The arthropods in wheat, maize, flower strips and natural vegetation strips, and the flowering plant ratio of flower strips were all visually inspected. When sampling, four persons investigated from 8:00 am to 5:00 pm in a clear day to avoid the differences or variations. If it rained, the investigation had to postpone.

2.3.1 Arthropod sampling in wheat-maize rotation fields, flower strips and natural vegetation strips

2.3.1.1 Arthropod sampling on flower strips and natural vegetation strips

The arthropods sampling on flower strips was conducted at 3-day to 1-week intervals (for the sampling timeline, see Table S1 in the supporting online material). Each flower strip plot was equally divided into three subplots and five random locations were surveyed in each subplot. For each sampling event, predators' species and number were surveyed in a metal quadrat frame (0.25 m^2, 0.5 × 0.5 m) at each location. The abundances of other arthropods with weak or without flight ability were sampled on per 100 *C. monnieri* plants. Predators' investigation on natural vegetation strips was carried out during the same periods as that on flower strips (for the sampling timeline, see Table S1).

2.3.1.2 Arthropod sampling in wheat and maize fields

The visual inspection of arthropods was conducted at approximately 1-2-week intervals in wheat fields and 1-2-week intervals in maize fields (for the sampling timeline, see Table S1). The methods for sampling predators in wheat or maize was similar to that on flower strips. In each wheat or maize plot, five distance ranges of 0-2 m, 2-4 m, 4-8 m, 8-16 m and 16-32 m in Jinan and four distance ranges of 0-2 m, 2-4 m, 4-8 m, and 8-12 m in Dezhou outward from flower strips at the wheat or maize border were surveyed. Two dominant species of cereal aphids, *Sitobion avenae* F. and *Rhopalosiphum padi* L. occurred in two sites. They are the most serious wheat insect pests in North China.[25,26] Abundances of cereal aphids and other arthropods with weak or without flight ability in wheat plots were sampled per 100 tillers at each location.

Abundances of corn leaf aphids, *R. maidis* F. and other arthropods with weak or without flight ability in maize plots were also sampled per 100 plants at each location.

2.3.2 Sampling of the flowering plant ratio of flower strips

The sampling of the flowering plant ratio in flower strips was carried out in a 0.5 × 0.5 m quadrat frame at each location in each flower strip plot. The flowering plant ratio is the number of flowering plants that divided by the number of the sampled *C. monnieri* plants in a 0.5 × 0.5 m quadrat frame. Surveying and recording the flowering plant ratio were carried out concurrently with arthropod sampling on flower strips.

2.3.3 The adult predator and the plant collection

Samples of *P. japonica* adults from flower strips and maize fields were collected by hand (while wearing rubber gloves) in Dezhou. Once a sample was collected, a new rubber glove was replaced to collect a new sample to avoid surface contamination. Predators were evenly collected at four distance ranges in each maize plot. The sampling timeline and collected number of predators see Table S2. All samples collected were immediately placed in 95 % EtOH in 1.5-ml microcentrifuge tubes on ice before being transferred to a -20°C freezer. *C. monnieri* pollen and as many nontarget plants as possible were also collected to test for cross-reactivity against primer pairs that developed to target *C. monnieri* (for nontarget plant species see Table S3) Two familiar closely related species of *C. monnieri*, *Daucus carota* L. and *Apium graveolens*, were bought to test for cross-reactivity against the primer pairs developed to target *C. monnieri*.

2.4 Predator rearing and adult survival of the predator on *C. monnieri* flowers

The detailed descriptions of this part were showed in the supporting online material.

2.5 Molecular gut-content analysis of the residual *C. monnieri* in the guts of adult predators collected from flower strips and maize fields

A pair of specific primers targeting *C. monnieri* partial ITS (see Primer design and screening in the supporting online material) was used to detect *C. monnieri* in the guts of *P. japonica* collected from flower strips and maize fields. To analyse the predator movement process between flower strips and maize fields, the following formulas were used to calculate the proportion of predators fed on *C.monieri* (P_f) and the transfer rate of predators from flower strips to maize fields (P_t):

$P_f = N_f / N_t$

$P_t = P_m / P_{cm}$

N_f represents *C. monnieri*-positive detections of sampled predators, and N_t represents the total sampled predators. P_m and P_{cm} are the proportion of predators feeding on *C.monieri* that collected from maize fields and flower strips in a same sampling date, respectively.

DNA procedures included DNA extraction, primer design and screening, and detection of the residual *C. monnieri* in the guts of adult predators collected from flower strips and maize fields. These procedures are described in the supporting online material.

2.6 Data analysis

Generalized linear mixed-effects models (GLMMs) with a Poisson error distribution (log link function) were fitted using the Automatic Differentiation Model Builder (glmmADMB) package[33] to test flower strip effects on the abundances of cereal aphids, *P. japonica* adults in wheat fields, and *P. japonica* adults in maize fields. Full models of cereal aphid abundance in wheat fields and *P. japonica* adults in wheat or maize fields contained the fixed effects of flower strips (wheat fields with flower strips versus wheat fields with natural vegetation strips), distance from flower strips (five distance ranges:0-2 m, 2-4 m, 4-8 m, 8-16 m, 16-32 m in Jinan and four distance ranges: 0-2 m, 2-4 m, 4-8 m, 8-12 m in Dezhou), sampling dates and their interactions and were plotted in each random block as a random blocking factor. For sampling dates in the models above, seven dates in Jinan and three dates in Dezhou were used in the analysis of the abundance of cereal aphids and *P. japonica* in wheat fields. Three dates in Jinan and two dates in Dezhou were used in the analysis of *P. japonica* abundance in maize fields (for the detailed sampling dates, see Table S1). The statistical analyses described above were performed using R v. 3.1.2 software.[34] Model selection based on likelihood ratio tests was performed following the recommendations of Zuur *et al.*,[35] and minimum adequate models were used for statistical inference. The Chi-square values were calculated by model selection based on likelihood ratio tests.

Propylaea japonica adult abundance on flower strips in comparison to that on natural vegetation strips was analysed using Kruskal-Wallis one-way ANOVA. A Mann-Whitney U test was used to compare the difference of the predator abundance between in Jinan and in Dezhou in wheat, maize or on flower strips, respectively. Three linear regression models (y = ax + b) with a normal error distribution were used to describe relationships between the adult predator abundance on flower strips and the flowering plant ratio of flower strips, the predator abundance on flower strips at early flowering stage and that in wheat fields during the same periods at wheat maturing stage, and the predator abundance in maize fields at its seedling and jointing stages to that on flower strips during the same periods, respectively. The abundances of five species of predators on flower strips during different growth stages were analysed for statistical significance using one-way ANOVA with the following least significant difference (LSD) post hoc test.

Data on the frequency of detection of *C. monnieri* DNA in *P. japonica* gut contents on flower strips at different sampling dates and that in maize fields with flower strips in July 4th and July 17th were analysed for statistical significance using one-way ANOVA with the following LSD test. Before analysis, these percentage data were arcsine square root transformed (asin(sqrt(p))) to obtain normally distributed residuals and avoid heteroscedasticity. Statistical analyses were performed using SPSS software (version 20.0; SPSS, Chicago, IL, USA)

3 RESULTS

3.1 The flower strip effects for the adult predator abundance in wheat fields, flower strips and maize fields

Fig. 1c showed photographs of wheat, maize and the flower strips at their different growth stages in Jinan. *P. japonica* (Coleoptera: Coccinellidae), *Harmonia axyridis* (Coleoptera: Coccinellidae), *Syrphus*.spp (Dipetra: Syrphidae) and *Chrysoperla*.spp (Neuroptera: Chrysopidae) are four predators that play an important role in wheat aphid biocontrol. The proportions of four predators above were 14.0 %, 80.8%, 5.0% and 0.2% in sequence. Four adult predators in wheat fields and *Coccinella septempunctata* (Coleoptera: Coccinellidae) were sampled on flower strips. *P. japonica* were the most dominant predator that accounted for 72% of all predators (Table 1).

And *P. japonica* was the only one of the five adult predators which have sampled in maize fields. Hence, the mutual dominant predator *P. japonica* in wheat, maize and flower strips was selected as the object of the study.

3.1.1 The adult predator abundance in wheat fields with flower strips

On average, 330 and 130 individuals of cereal aphids occurred on 100 wheat tillers for each sampling date in Jinan and Dezhou, respectively. *P. japonica* that reproduced in wheat fields in Jinan (Fig. 2a, black line) and Dezhou (Fig. 2b, black line) fed on cereal aphids. No significant flower strip effects and distance effects in wheat fields were found for cereal aphids in two sites (Jinan: Table S4, Fig. S1a; Dezhou: Table S4, Fig. S1b) or predators in Jinan (Table S5, Fig. S1c), respectively. No predators were found in *C. monnieri* monocultures during its seedling stage from late April to mid-May both in Jinan (Fig. 1c, Fig. 2a) and Dezhou (Fig. 2b). However, a few of adult predators inhabited in *C. monnieri* monocultures at early flowering stage from late May to early June in Jinan (Fig. 1c, Fig. 2a) and Dezhou (Fig. 2b).

3.1.2 The adult predator abundance on flower strips and natural vegetation strips

The predator abundance on flower strips increased during the periods at its full-bloom stage after wheat harvest compared with that at its early flowering stage before wheat harvest ($P < 0.05$, Table 1, Fig. 1c, Fig. 2). Moreover, the increase of the predator abundance on flower strips at its early flowering stage matched the decrease of the predator abundance in wheat fields at wheat maturing stage ($P > 0.05$, Table 2, Fig. 1c, Fig. 2). And the predator abundance on flower strips decreased at its fruit ripening and full ripening stage compared with that at its full-bloom stage ($P < 0.05$, Table 1, Fig. 1c, Fig. 2). Moreover, the decrease of the predator abundance on flower strips at its fruit ripening and full-ripening stages matched the increase of the predator abundance in maize fields at the maize seedling and jointing stages ($P < 0.05$, Table 3, Fig. 1c, Fig. 2). A total of 8371 and 436 *P. japonica* adults were recorded on flower strips in Jinan and Dezhou, respectively. The predator abundance on flower strips (10.48 ± 0.77 individuals/m^2, Mean ± SE, the same below) was approximately 7-fold higher than that on natural vegetation strips (1.41 ± 0.24 individuals/m^2) during the wheat postharvest period and before the maize jointing stage ($P < 0.001$, Fig. 3a). Moreover, the highest abundance of the predator on flower strips remained for about a month (mainly in June) at *C. monnieri* full-bloom stage in Jinan (Table 1, Fig. 1c, Fig. 2a) and Dezhou (Fig. 1c, Fig. 2b).

3.1.3 The adult predator abundance in maize fields with flower strips or natural vegetation strips

A total of 610 and 113 *P. japonica* were recorded in maize fields in Jinan and Dezhou, respectively. The predator abundance in maize fields with flower strips were 1.8-fold and 2.1-fold higher than that in maize fields with natural vegetation strips during the maize seedling and joint stages in Jinan ($P = 0.004$, $\chi^2 = 8.256$, Table 4, Fig. 4a) and Dezhou ($P < 0.001$, $\chi^2 = 12.052$, Table 4, Fig. 4b), respectively. The predator number was higher in maize fields with flower strips but only near flower strips (significant flower strips × distance interaction: Jinan, $P < 0.001$, $\chi^2 = 35.922$, Table 4, Fig. S2a; Dezhou, Table 4, $P < 0.001$, $\chi^2 = 2262.44$, Fig. S2b). Almost none corn leaf aphids and few thrips were sampled during the maize seedling and joint stages. During the same time, although none significant flower strip effects were found for cotton bollworms, *Helicoverpa armigera* (Hübner) in maize, about 65 and 22 larvae of cotton bollworms per 10000 maize plants were sampled in Jinan and Dezhou, respectively.

3.1.4 The difference of the predator abundance between in Jinan and in Dezhou in wheat, maize or on flower strips

The predator number in wheat fields in Jinan (0.35 ± 0.08 individuals/m^2) was higher than that in Dezhou (0.06 ± 0.03 individuals/m^2) during wheat whole sampling periods ($P = 0.01$). And the predator abundance on flower strips in Jinan (6.48 ± 0.40 individuals/m^2) was higher than that in Dezhou (0.78 ± 0.10 individuals/m^2) during the whole sampling periods of flower strips ($P < 0.001$). Then the predator abundance in maize fields in Jinan (1.09 ± 0.12 individuals/m^2) was higher than that in Dezhou (0.39 ± 0.07 individuals/m^2) during the maize whole sampling periods ($P < 0.001$).

3.2 Resources provided for the adult predator by flower strips

3.2.1 The floral resources for the adult predator

3.2.1.1 The relationship between the flowering plant ratio of flower strips and the predator number on flower strips

The average flowering plant ratios at early stage of flower strips were 26.95 ± 0.03 % in June 3rd in Jinan and 13.99 ± 0.01 % in May 28th in Dezhou. The average flowering plant ratios at full-bloom stage were 45.27 ± 0.03 %, 60.53 ± 0.03 %, 73.01 % ± 0.03 %, 78.77 ± 0.03 %, 86.21 ± 0.03 %, 100% and 100% in June 6th, 9th, 12th, 14th, 17th, 20th and 26th in Jinan, and 39.05 ± 0.02 %, 79.88 ± 0.14 % and 100% in June 5th, 8th and 15th in Dezhou, respectively. After June 26th in Jinan and June 15th in Dezhou, flower strips turned into the fruit-ripening stage. Moreover, the increase in the predator abundance on flower strips was correlated to a certain extent with an increase in the flowering plant ratio of flower strips both in Jinan ($y = 4.6917x - 1.1374$, $R^2 = 0.2090$, $P = 0.0074$, Fig. 3b) and Dezhou ($y = 2.0522x + 0.7306$, $R^2 =$

0.1333, $P = 0.0376$, Fig. 3c).

3.2.1.2 Adult survival of the predator on *C. monnieri* flowers

Adult predators survived an average of 7 days longer on *C. monnieri* flowers than on water alone (Fig. 3d). Specifically, adult females and males survived an average of 8 days and 6 days longer on *C. monnieri* flowers than on water alone, respectively (females, Fig. 3e; males, Fig. 3f).

3.2.2 Shelter for the predator

The compound umbel of *C. monnieri* provided favourable shelter for predator inhabitation during the wheat postharvest period (Fig. 3i). And the natural vegetation strips did not provide favourable geometric structure for the predator inhabitation.

3.3 The movement pattern of the predator between flower strips and maize fields

The average *C. monnieri*-positive rate of field-collected predators was 93.21 ± 0.02 % on flower strips during *C. monnieri* flowering stage (Fig. 1c, Fig. 4c). The immigration events of the predator from flower strips to maize crop first started at maize seedling stage (July 4th, Fig. 4d), and the transfer rate was 77.50 ± 0.07 % for the predator from flower strips to maize crop during this period (July 4th, Fig. 4e). Moreover, the proportion of the predators in maize fields derived from flower strips at maize seedling stage (July 4th, 77.56 ± 0.07 %) was higher than that at maize jointing stage (July 17th, 21.95 ± 0.06 %) ($P < 0.001$, Fig. 4d).

4 DISCUSSION

This study demonstrates that planting flower strips could create a bridge habitat for *P. japonica* in wheat-maize rotation fields after wheat harvest and then the predator could immigrate to maize fields at maize seedling and tillering stage. Importantly, this study quantified the immigration time, the transfer rate of predators from flower strips to maize and the proportion of predators in maize fields derived from flower strips, which showed the major contributions of flower strips to predators' conservation in rotation fields. Moreover, this study showed that floral and shelter resources are two important kinds of resources that flower strips provide for the predator. To the best of our knowledge, this is an important quantitative study systematically demonstrating that manipulating farmland vegetation can create a bridge habitat for sustainable natural enemy conservation in wheat-maize rotation fields.

4.1 The flower strip effects for the predator abundance in wheat fields, flower strips and maize fields

Generalist predators that provide biocontrol services in crops must often persist year round in agricultural landscapes and rely on the resources in the landscape.[36] Both crop and non-crop habitats can provide resources for predators, but crop habitats are inherently unstable because of periodic management practices such as crop planting and harvest.[5] Thus, predators' number that live in these disturbed crop habitats sharply declined.[37,38] It is vital to provide available resources for predators when crop habitats are unfavourable.[39,40] In wheat-maize rotation system, cereal aphids can be a source for *P. japonica* in wheat, but predators is forced to emigrate from wheat to disturbed non-crop habitats during the wheat postharvest period. This disturbance in wheat also results in a sharp decrease of the predator abundance. Fortunately, the successful establishment of a bridge habitat by planting flower strips has mitigated the harm to the predator caused by wheat harvest and maize planting and helped with the swift reconstruction of the predator population in maize fields. It should be noted that periods with high predator abundance on flower strips mismatched periods of aphid occurrence, which may lead to no significant flower strip effects for aphids in wheat-maize rotation system. Multiple flower strips should be arranged at different periods, which are able to not only conserve natural enemies during harvest but also be helpful for the biocontrol of important insect pests in this rotation system.

4.2 Resources provided for the predator by flower strips

Habitat management serves to establish a suitable ecological infrastructure within the agricultural landscape to provide available resources such as floral resources (nectar, pollen) for natural enemies, shelter and alternative prey/hosts from adverse conditions[8]. In this study, the increase of predators' abundance on flower strips was positively related to an increase in flowering plant ratio of flower strips. And laboratory survival experiment further showed that the floral resources of *C. monnieri* flowers prolonged the predator survival. These results indicated that flower strips provide available floral resources as alternative foods for the predator. Interestingly, *C. monnieri* are compound umbel, and the specific structure of inflorescence could provide favourable shelter for the predator from adverse conditions.[8, 9] It is worth mentioning that *C. monnieri* is a native species and therefore adapts to the environment and facilitates native enemy population increases to a greater extent than non-native species.[41]

4.3 The movement pattern of the predator between flower strips and maize fields

Generalist predators frequently move between crops and non-crop habitats in the surrounding landscape.[5] In this rotation system with flower strips, the increase of the predator abundance on flower strips at early flowering stage matched the decrease of the predator abundance in wheat fields at wheat maturing stage even if the linear regression model is not significant, it may conclude that a part of predators moved from wheat to flower strips. In addition, most of predators on flower strips at full-bloom stage may feed on preys in other non-crop habitats previously feeding on *C. monieri* after wheat harvest. Moreover, the decrease of the predator abundance on flower strips at its maturing stages matched the increase of the predator abundance in maize fields at its seedling and jointing stages. Thus, we may roughly speculate that most of predators in maize fields were derived from flower strips. Flower strips switched from its full-bloom stage to fruit ripening and full ripening stage and provided less favourable floral resources and shelter for the predator, this may be one reason why *P. japonica* left flower strips for maize at jointing stage. Previous research has shown that VOC profiles from maize leaf contain complex odor components including green leaf alcohols, aldehydes, derivate esters, terpenes, and sesquiterpenes. [42] Twelve-spotted lady beetle *Coleomegilla maculata* in the same Coccinellidae family as *P. japonica* showed electroantennographic responses to (*E*)-beta-farnesene, alpha-terpineol, 2-phenylethanol, and beta-caryophyllene that VOC profiles from maize leaves, respectively. [43] A good deal of terpenoid volatiles were released at maize seedling stage after they have been fed upon by caterpillars.[44] These volatiles may be produced in defense against herbivores but may also serve a secondary function in attracting natural enemies of these herbivores including predators. [44,45] These volatiles released by maize leaves per se or after maize leaves have been feeding upon by caterpillars such as cotton bollworms may attract *P. japonica* from flower strips to maize. Two reasons above may be the motivation for the beetles left flower strips for maize. We previously found the predator *P. japonica* fed on cotton aphids on cotton but inhabited on maize in maize and cotton intercropping system, which was clearly demonstrated by using stable carbon isotope analysis. [22] The maize with microclimate conditions of relative low temperature and high humidity are beneficial to maintain *P. japonica* in hot summer [46], which may be the reason for *P. japonica* inhabiting on maize.

To accurately assess the contributions of flower strips to *P. japonica* population establishment in maize fields, it is necessary to quantify the immigration time, the transfer rate of predators from flower strips to maize fields and the proportion of predators in maize fields derived from flower strips. Based on the detection results of the residual *C. monnieri* in the guts of predators, most of predators in maize fields were proven to originate from flower strips. Moreover, predators' population firstly reconstructed in maize fields mainly came from flower strips. *P. japonica* fed on floral resources of flower strips. *C. monnieri*-positive rate of predators in maize fields at maize seedling stage (July 4th, 77.56 ± 0.07 %) was significantly higher than that at maize jointing stage (July 17th, 21.95 ± 0.06 %). Thus, we may speculate that *P. japonica* on maize at its seedling stage mainly fed on *C. monnieri* floral resources. However, *P. japonica* may feed on few floral resources at maize jointing stage but at the fruit ripening stage of flower strips. And *P. japonica* needed to move to the nearby habitats to find preys but still inhabited on maize. It's worth noting that the DNA decay half-life of plant pollen is much longer than that of prey such as aphids,[47] which might make it easier to obtain a high *C. monnieri* positive rate of field-collected predators from flower strips and maize fields.

4.4 Flower strips as a bridge habitat to protect natural enemies in other annual double-cropping and triple-cropping systems

Targeted measures that secure the continuity of resources for service-providing organisms, including generalist predators, bolster their biocontrol services in agricultural crop systems.[48] This study is not proven that *P. japonica* provided useful level of control in wheat or maize and against wheat or maize pests. However, the key point demonstrated by our study was how to manipulate flower strips as a bridge habitat to ensure that large numbers of predators persist from one cropping phase into a second crop species that follows the first one. The problem of natural habitat loss and fragmentation exists in most parts of the world,[49,50] and natural enemies of pests in other annual double-cropping and triple-cropping systems are also subject to high mortality events due to high levels of disturbance such as ploughing, planting, weeding, insecticide applications, crop senescence, and harvest.[5,8] These crop rotation fields mainly include rice-wheat rotation fields in northern India, Pakistan, Nepal, and southern China[51] and rice-maize rotation fields on the Indo-Gangetic Plain (IGP) of India, Bangladesh, Nepal and Pakistan.[24] Consequently, we developed the strategy of planting flower strips as a bridge habitat to realize sustainable natural enemy conservation in these annual double-cropping and triple-cropping systems. Flower strips as a bridge habitat have four fundamental characteristics (Fig. 5): (*i*) natural enemies immigrate to flower strips after crop harvest in the previous season; (*ii*) the plant species in flower strips provide sufficient resources for the targeted natural enemy; (*iii*) natural enemies in flower strips move to the crop after crop emergence in the following season; and (*iv*) the plant species should be native and not appealing to pests. We predict that the use of flower strips as bridge habitats will be helpful for natural enemy sustainable conservation to maximize biocontrol services and mitigate the negative impacts of periodic management practices in other annual double-cropping and triple-cropping systems.

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CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

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Tables

Growth stages			Mean (±1 SE) number of each adult predator per square meter				
Sampling date	flower strips	Wheat/ Maize	*P. japonica*	*H. axyridis*	*C.septempunctata*	*Chrysoperla.spp*	*Syrphus. spp*
May 20th	Seeding	Wheat grain-filling	0	0	0	0	0
May 28th, 31st; June 3rd, 6th,	Early flowering	Wheat maturing	0.21 ± 0.03 b	2.36 ± 0.90 a	0.04 ± 0.04 a	0 a	0.18 ± 0.18 a
June 8th		Wheat harvest					
June 9th,12th, 14th,17th, 20th, 26th; July 4th	Full-bloom	After wheat harvest	12.76 ± 3.07 a	2.61 ± 0.99 a	0.02 ± 0.02 a	0.05 ± 0.03 a	1.28 ± 0.42 a
June 20th		Maize emergence					
July 9th, 15th	Fruit-ripening	Maize jointing emergence	1. 28 ± 0.78 b	0.04 ± 0.04 a	0 a	0 a	0 a
The proportion of each adult predator number in total predators (%)			72.24	19.72	0.22	0.28	7.54

Table 1 Mean (±1 SE) number of each adult predator per square meter on flower strips at different *C. monnieri* growth stages in Jinan. Different lowercase letters during different growth stages for each predator indicate a significant difference at the $P < 0.05$ level according to one-way ANOVA with the LSD test.

Table 2. Linear regression models to describe relationships between the adult predator *P. japonica* abundance on flower strips at early flowering stage (y) and that in wheat fields during the same periods at wheat maturing stage (x). x and y represent *P. japonica* abundance per square meter in wheat fields and on flower strips, respectively.

Site	Regression model	R^2	F-Value	*df*	P
Jinan	$y = -0.359 x + 0.789$	0.039	0.523	1,13	0.482
Dezhou	$y = -0.051 x + 0.111$	0.03	0.68	1,22	0.419

Table 3. Linear regression models to describe relationships between the adult predator abundance in maize fields at seedling and jointing stages (y) and that on flower strips (x) during the same periods. x and y represent *P. japonica* abundance per square meter on flower strips and in maize fields, respectively.

Site	Regression model	R^2	F-Value	*df*	P
Jinan	$y = -0.049 x + 1.539$	0.444	7.984	1,10	0.018
Dezhou	$y = -0.207 x + 0.410$	0.161	4.216	1,22	0.052

Table 4. Summary of the main effects of treatment, distance from flower strips, sampling date, and their interactions on *P. japonica* adult abundance in maize fields in Jinan and Dezhou. Degrees of freedom (d.f.), chi-square values (χ^2) and P-values from likelihood-ratio tests of the model selection procedure (see Materials and Methods) are shown. P-values of explanatory variables that were included in the final model ($P < 0.05$) are in bold lettering.

	Jinan			Dezhou		
	d.f	χ^2	P	d.f	χ^2	P

Treatment	1	8.256	**0.004**	1	12.052	**< 0.001**
Distance	4	35.922	**< 0.001**	3	2262.440	**< 0.001**
Date	2	1.716	0.424	1	2258.400	**< 0.001**
Treatment x Distance	4	5.822	0.213	3	16.720	**< 0.001**
Treatment x Date	2	2.726	0.256	1	6.480	**0.011**
Date x Distance	8	29.304	**< 0.001**	3	10.420	**0.015**
Treatment x Distance x Date	8	65.466	**< 0.001**	3	520.390	**< 0.001**

Figure captions

Fig. 1. Spatial layout of the field experiment in two sites in northwest of Shandong Province, China and photographs of wheat, maize and flower strips at their different growth stages for each sampling date. (a) Spatial layout of the field experiment in Jinan. (b) Spatial layout of the field experiment in Dezhou. (c) Photographs of wheat, maize and flower strips at their different growth stages for each same sampling date during the whole sampling time periods in Jinan.

Fig. 2. Temporal changes in the abundance patterns of *P. japonica* adults in wheat-maize rotation fields with flower strips in Jinan (a) and Dezhou (b). Mean (±1 SE) number of the adult predators per square metre in wheat fields from the jointing stage to harvest (black line, a. Jinan, n = 495; b. Dezhou, n = 216), flower strips from the early flowering season to the last

stage of flowering (green line, a. Jinan, n = 1290; b. Dezhou, n = 432) and maize fields from the seedling stage to the jointing stage (red line, a. Jinan, n =180; b. Dezhou, n = 216).

Fig. 3. Relationships between flower strips and *P. japonica* on flower strips. (a) Mean (+1 SE) number of the adult predators per square meter on flower strips (grey column, n = 540) and on natural vegetation strips (white column, n = 270) after wheat harvest and before the maize emergence. (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). (b-c) Linear relationship between the abundance of the adult predators on flower strips (y) and the flowering plant ratio of flower strips (x) from early flowering stage to full-bloom stage in Jinan (b, $y = 4.6917x - 1.1374$, $R^2 = 0.2090$, $P = 0.0074$) and Dezhou (c. $y = 2.052x + 0.7306$, $R^2 = 0.1333$, $P = 0.0376$). Each point represents mean (±1 SE) number of adult predators in each subplot (vertical error bars) and mean (±1 SE) flowering plant ratio in flower strips in the same subplot (horizontal error bars) during each sampling event. (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). (d-f) Mean (+1 SE) number of days total adult predators (d), female adults (e) and male adults (f) survived on *C. monnieri* flowers (grey column, n = 15) and on distilled water only (white column, n = 15), respectively. (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). (g) Flower strip photographs. (h) Photographs of the predator, *P. japonica* on *C. monnieri* flowers. (i) Photographs of *P. japonica* inhibited in compound umbellate flowers of *C. monnieri*.

Fig. 4. The movement pattern of *P. japonica* between flower strips and maize fields. (a-b) Mean (+1 SE) number of adult predators per square metre for each sampling date in maize fields with flower strips (grey column, a. Jinan, n = 135; b. Dezhou, n = 144) and maize fields with natural vegetation strips (white column, a. Jinan, n = 135; b. Dezhou, n = 96) at maize seedling

and jointing stages. (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$). (c-d). Mean (+1 SE) frequency of detection of *C. monnieri* DNA in gut contents of the predator collected on flower strips in different dates during *C. monnieri* flowering stage (c) and that in maize fields with flower strips on July 4th and July 17th (d) in Dezhou. Different lowercase letters indicate a significant difference at the $P < 0.05$ level. (e) The transfer rate of the predator from flower strips to maize fields on July 4th. (f) The diagram of the movement route of adult predators between flower strips and maize fields.

Fig. 5. Model of flower strips as the bridge habitat for sustainable natural enemy conservation in agricultural rotation fields. First, natural enemies prey on pests before last crop harvest, and the plants in flower strips were at seedling stage. Second, natural enemies on last crop immigrate into flower strips after last crop harvest and flower strips were at flowering stage. Finally, most of natural enemies on flower strips immigrate to next crop after its emergence.

Fig. 1

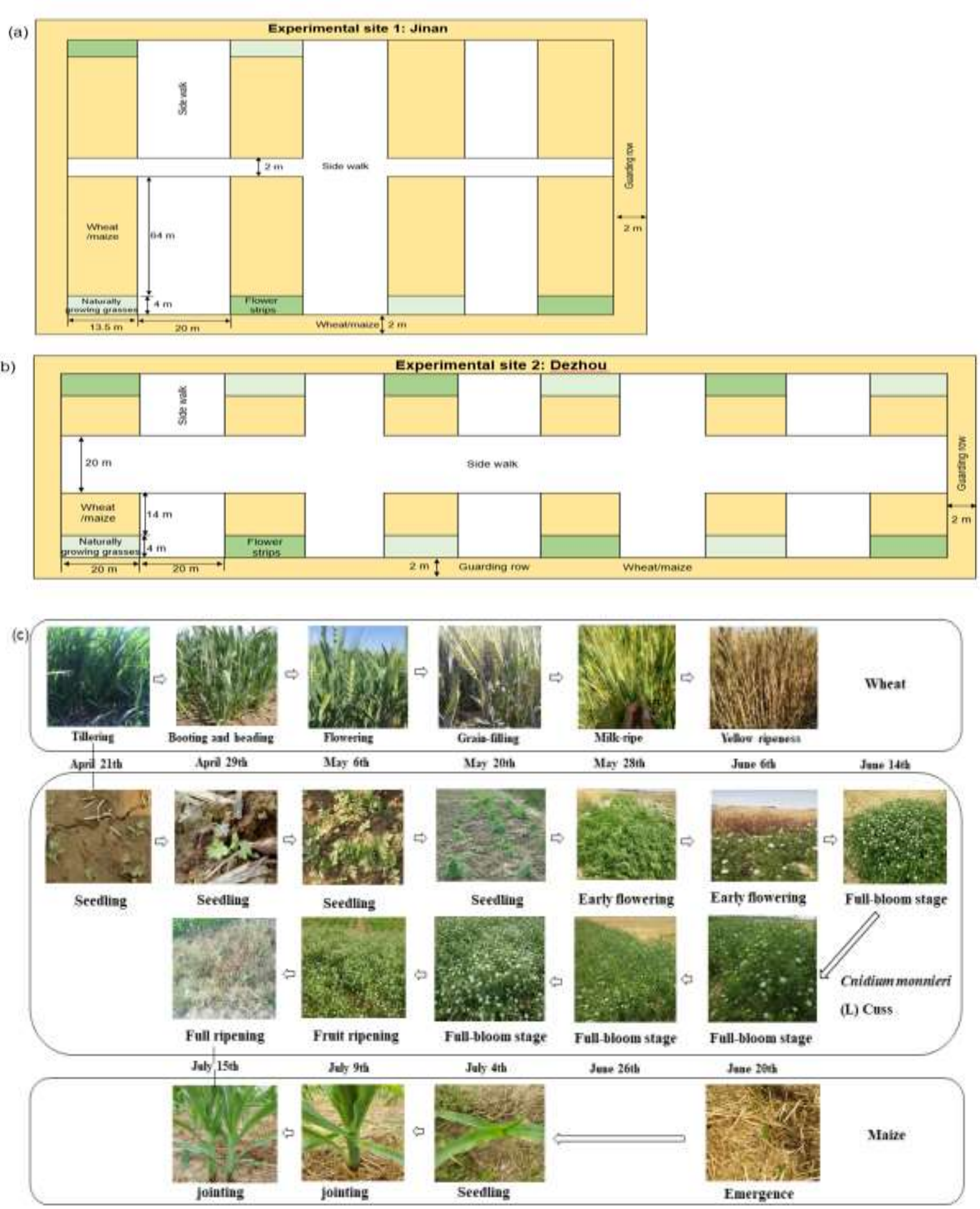

(a)
Experimental site 1: Jinan
Side walk
2 m
Side walk
Guarding row
2 m
Wheat /maize
64 m
4 m
Naturally growing grasses
Flower strips
13.5 m
20 m
Wheat/maize
2 m
(b)
Experimental site 2: Dezhou
Side walk
20 m
Side walk
Guarding row
2 m
Wheat /maize
14 m
4 m
Naturally growing grasses
Flower strips
20 m
20 m
2 m
Guarding row
Wheat/maize
(c)
Tillering
Booting and heading
Flowering
Grain-filling
Milk-ripe
Yellow ripeness
Wheat
April 21th
April 29th
May 6th
May 20th
May 28th
June 6th
June 14th
Seedling
Seedling
Seedling
Seedling
Early flowering
Early flowering
Full-bloom stage
Full ripening
Fruit ripening
Full-bloom stage
Full-bloom stage
Full-bloom stage
Cnidium monnieri
(L) Cuss
July 15th
July 9th
July 4th
June 26th
June 20th
jointing
jointing
Seedling
Emergence
Maize

Fig. 2

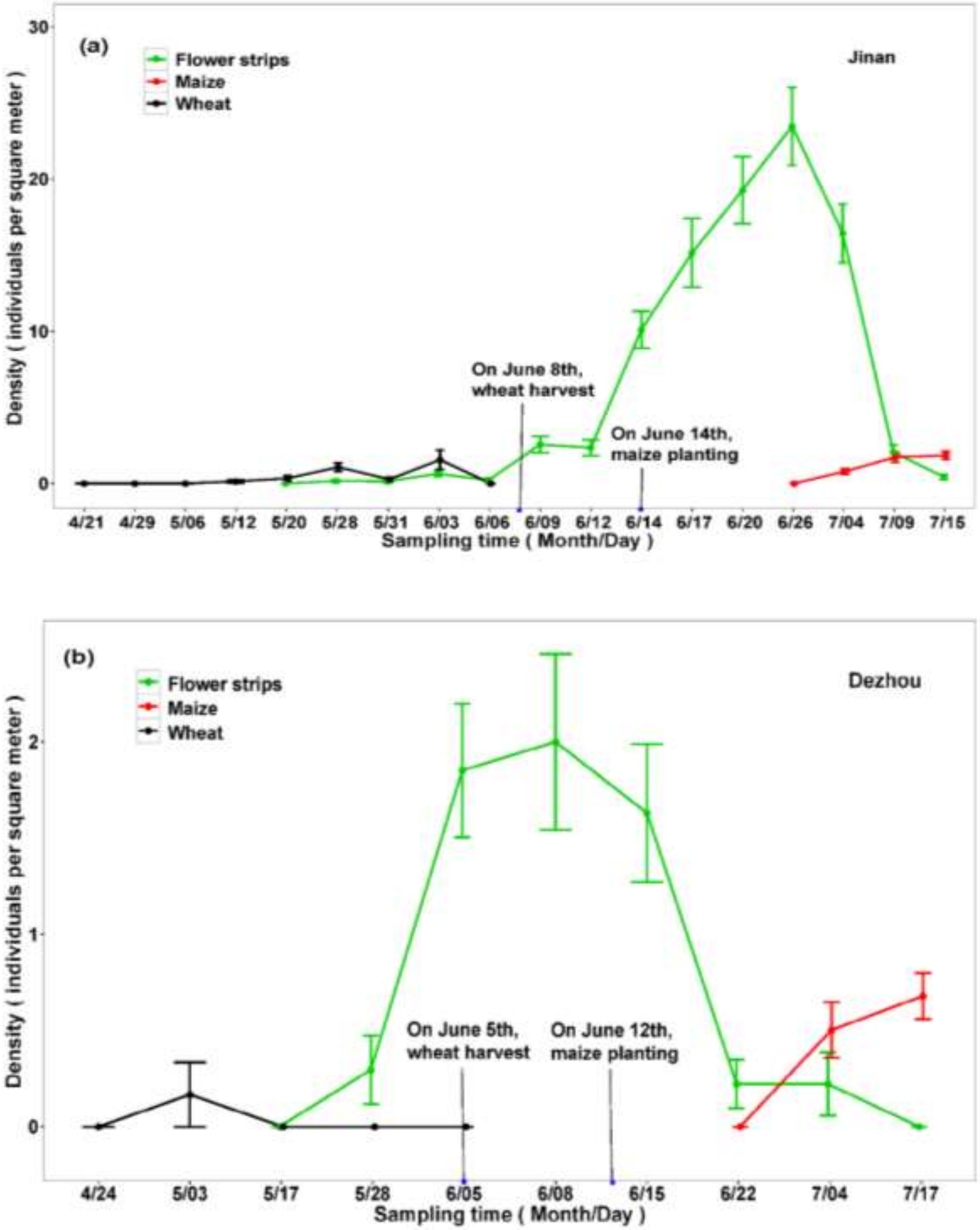
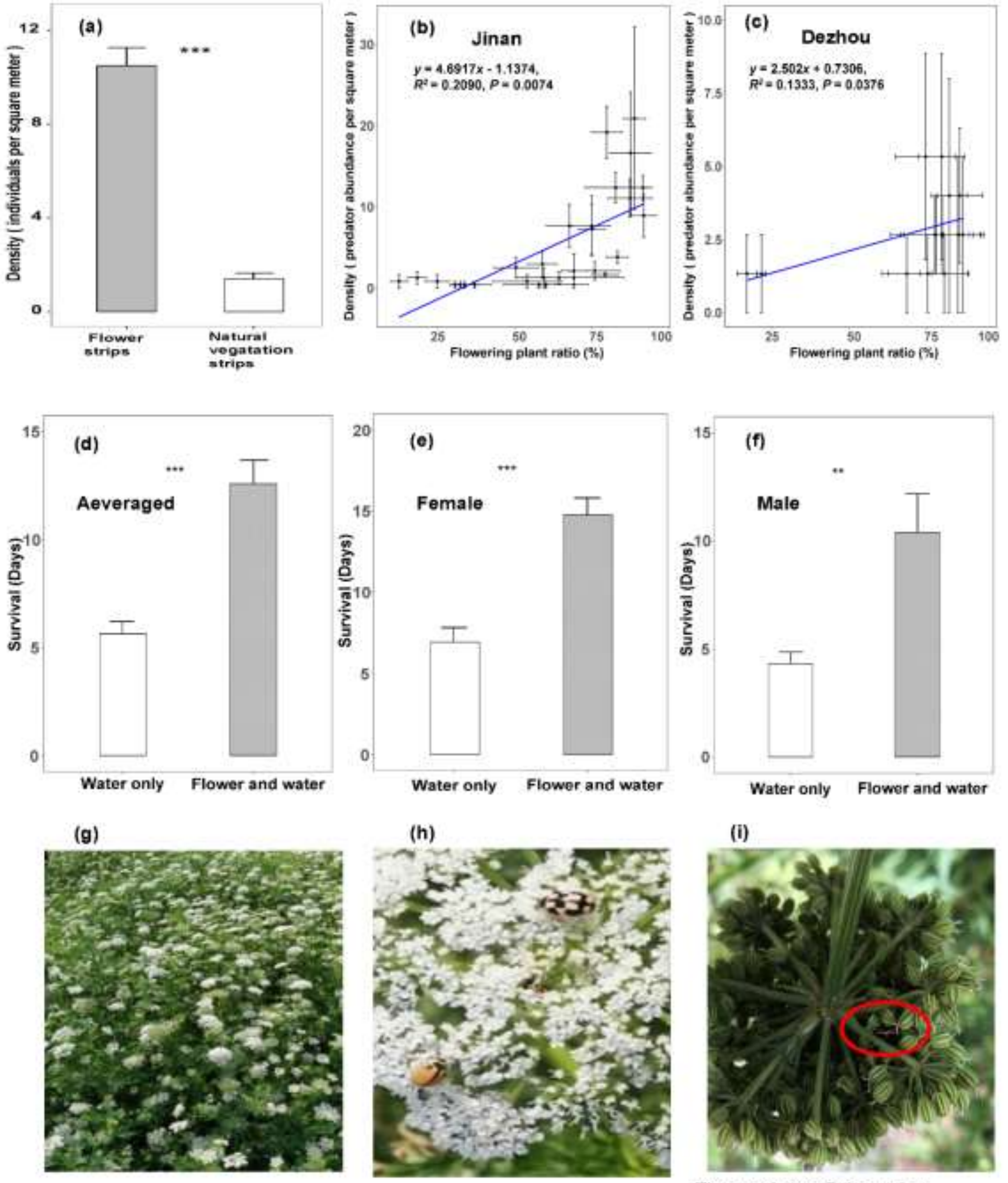

(a)
Flower strips
Maize
Wheat
Jinan
Density (individuals per square meter)
0
10
20
30
On June 8th, wheat harvest
On June 14th, maize planting
4/21
4/29
5/06
5/12
5/20
5/28
5/31
6/03
6/06
6/09
6/12
6/14
6/17
6/20
6/26
7/04
7/09
7/15
Sampling time (Month/Day)
(b)
Flower strips
Maize
Wheat
Dezhou
Density (individuals per square meter)
0
1
2
On June 5th, wheat harvest
On June 12th, maize planting
4/24
5/03
5/17
5/28
6/05
6/08
6/15
6/22
7/04
7/17
Sampling time (Month/Day)

Fig. 3



C. monnieri flower strips

The predator, *P. japonica* on *C. monnieri* flowers

The predator, *P. japonica* inhabited in compound umbellate flowers of *C. monnieri*

Fig. 4

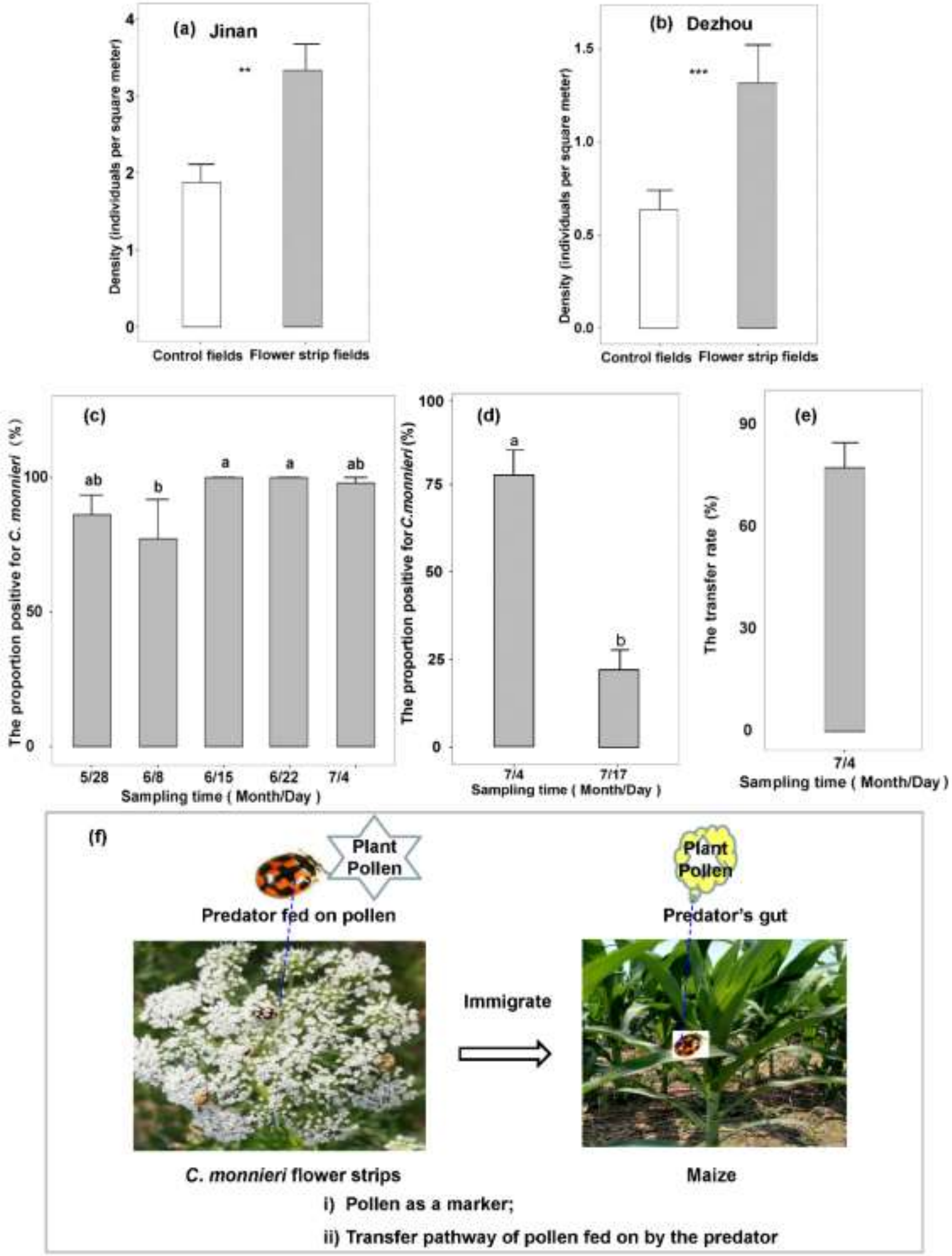
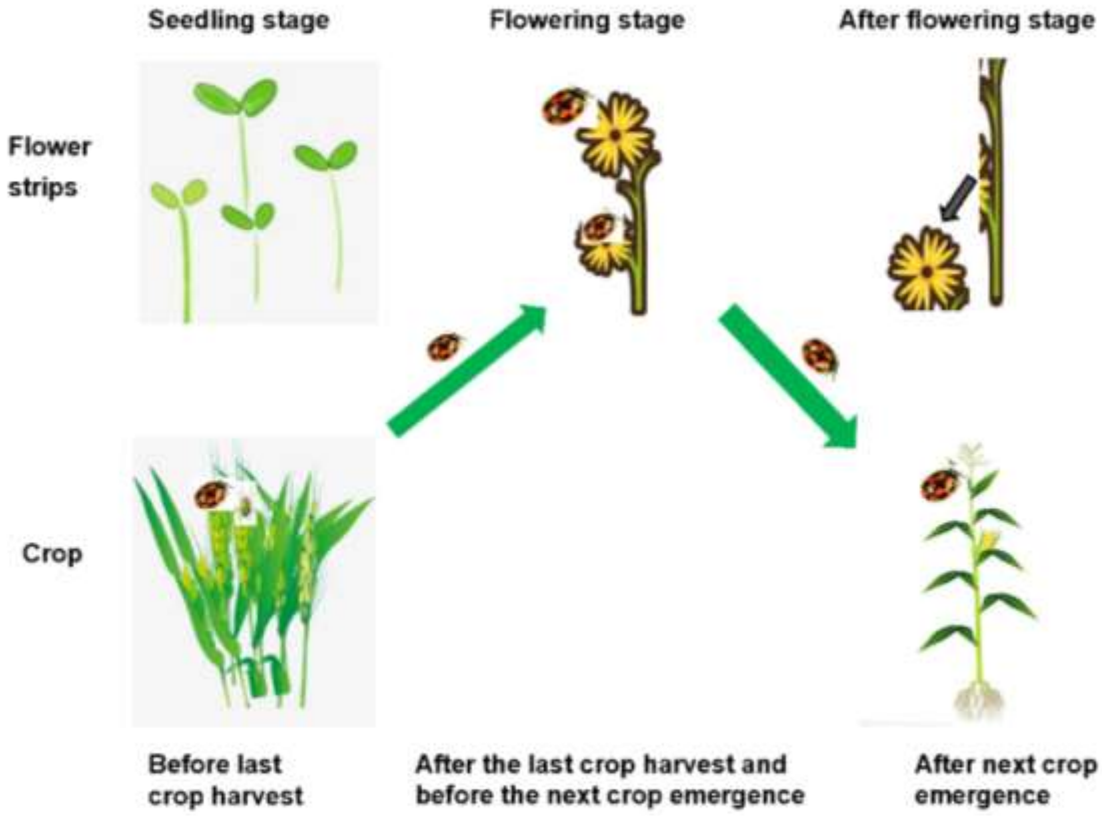

(a) Jinan
Density (individuals per square meter)
0
1
2
3
4
**
Control fields
Flower strip fields
(b) Dezhou
Density (individuals per square meter)
0.0
0.5
1.0
1.5
***
Control fields
Flower strip fields
(c)
The proportion positive for C. monnieri (%)
0
50
100
ab
b
a
a
ab
5/28
6/8
6/15
6/22
7/4
Sampling time (Month/Day)
(d)
The proportion positive for C.monnieri (%)
0
25
50
75
100
a
b
7/4
7/17
Sampling time (Month/Day)
(e)
The transfer rate (%)
0
30
60
90
7/4
Sampling time (Month/Day)
(f)
Plant Pollen
Predator fed on pollen
Plant Pollen
Predator's gut
Immigrate
C. monnieri flower strips
Maize
i) Pollen as a marker;
ii) Transfer pathway of pollen fed on by the predator

Fig.5


Seedling stage
Flowering stage
After flowering stage
Flower strips
Crop
Before last crop harvest
After the last crop harvest and before the next crop emergence
After next crop emergence