

Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies

Zi-Hua Zhao · Cang Hui · Da-Han He ·
Feng Ge

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Abstract The spatial structure of agricultural landscapes can have a strong impact on the distribution and diversity of insects. Here we studied the effects of within-field position (edge or center) as well as adjacent habitats on the community structure of the natural enemies of cereal aphids. Twelve agricultural sites were included in the study, with two spring wheat fields selected for each site (one adjacent to an alfalfa field, the other adjacent to a corn field). We sampled two rows per field (1 and 20 m from the edge) using pitfall trapping for ground-dwelling predators, sweep netting for leaf-dwelling predators and hand collecting of aphid

mummies for parasitoids. Adjacent alfalfa areas, as opposed to corn fields, can significantly increase the abundance and diversity of leaf-dwelling predators and parasitoids near the field edges. Abundance and diversity were found significantly higher near the edges than in the centers of fields adjacent to alfalfa areas. In contrast, no significant differences were found between edges and centers of fields adjacent to corn fields. Of the fifteen most abundant species, *Aphidius avenae* (Haliday), *A. gifuensis* (Ashmead), *Hippodamia variegata* (Goeze) and *Chrysopa sinica* (Tjeder) were significantly more abundant near the edge than in the center. Being adjacent to alfalfa habitats could enhance parasitism and predator/prey ratios of leaf-dwelling predators at the edges, but has no effects on ground-dwelling predators. In conclusion, the effect of within-field position and adjacent habitats on natural enemies of agricultural pests was species specific. This should be considered for designing efficient plans of biological control.

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Z.-H. Zhao · F. Ge (✉)
State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, People's Republic of China
e-mail: gef@ioz.ac.cn

Z.-H. Zhao
e-mail: zhaozihua@ioz.ac.cn

C. Hui
Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University, Matieland 7602, South Africa
e-mail: chui@sun.ac.za

D.-H. He
Agricultural Schools, Ningxia University,
Yinchuan 750021, People's Republic of China
e-mail: hedahan@163.com

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Introduction

Farming activities have posed strong impacts on the diversity of insects in many natural habitats for centuries (Purtauf et al. 2005; Thies et al. 2011). Indeed, the intensification of agriculture, together with the rapid loss of perennial and natural habitats, is one

main driver of the extinction of many natural enemies of agricultural pests (Tscharrntke et al. 2012; Zhao et al. 2012). However, there is increasing consensus that these natural enemies can strongly and rapidly suppress agricultural pests (Janssen et al. 2007; Anjum-Zubair et al. 2010). Agricultural policies should, therefore, emphasize the role of these natural enemies for achieving efficient and sustainable biological control. This includes the use of entomopathogens (Entomophthoraceae), insect predators and parasitoids (Hassell and May 1986). We excluded pathogens from this study but only focused on the latter groups: ground-dwelling predators, leaf-dwelling predators and parasitoids (Brewer and Elliott 2004; Yu et al. 2012). They are important natural control agents of cereal aphids (Brewer and Elliott 2004; Messelink et al. 2013).

Kleijn and Sutherland (2003) reviewed the effectiveness of European agricultural policy in conserving insect predators and parasitoids and confirmed that good agricultural policies can significantly proliferate the abundance and diversity of insect predators and parasitoids. For instance, mixing native flowering plants with crops can enhance the abundance of insect predators by providing them more niches, resources and shelters (Wäckers et al. 2008; Zaller et al. 2008) and, thus, has been proposed for efficient biological control in agricultural landscapes (Schmidt and Döbeli 2009). Insect predators and parasitoids are capable of controlling pest populations below damage levels (Schmidt et al. 2005), and a diverse suite of these natural pest controllers can result in successful agricultural management (Leslie et al. 2009).

Agricultural practices and urbanization can affect the viability of these natural pest control agents, but at different levels. For instance, some ground-dwelling predators are found largely insensitive to man-caused disturbance (Thies et al. 2011), whereas others can be affected to a certain degree by the loss and fragmentation of perennial agricultural habitats (e.g. the loss of grassy margins and woodland areas; Brewer and Goodell 2012; Tscharrntke et al. 2012). In contrast, leaf-dwelling predators and parasitoids are often strongly affected by agricultural practices and inter-annual landscape changes (Thies et al. 2011; Opatovskiy et al. 2010). Overall, landscape changes have led to a dramatic loss of biocontrol service in agroecosystems throughout the world (Tscharrntke et al. 2012).

To mitigate the detrimental effect of agricultural practices and landscape changes on biocontrol services, perennial habitats (e.g. wildflower patches) have been established in the agricultural landscape of European countries during the last decade (Frank et al. 2012). Similar actions have been followed in China. For instance, alfalfa fields are one type of perennial habitat proposed in China's Agricultural Environment Program. Alfalfa (*Medicago sativa* Linn) areas are typically sown either inside crop fields or along their edges and are maintained for up to ten years (Zhao et al. 2013). These alfalfa fields are designed to restore the perennial habitats, insect diversity and serve to connect natural and perennial habitats, thus enhancing habitat connectivity in the agricultural landscape (Brewer and Goodell 2012). In recent years, the alfalfa fields keep expanding in the regional agricultural landscapes for soil and water conservation and preventing desertification. Sometimes, the alfalfa is also harvested to meet the demand of forage for livestock. However, regulating services (e.g. the regulation of climate, pests, and trophic chain) produced by alfalfa are the main function.

It is worth pointing out that different adjacent habitats can have completely different effects on insect diversity and biological control (Frank et al. 2012). Specifically, landscape simplification or homogenization could reduce the number of herbivore prey consumed by their natural enemies (Schmidt and Döbeli 2009; Géneau et al. 2012). This suggests that adjacent landscapes may be detrimental to biological control via changes in the diversity of pests and their natural enemies, thus altering food-web interactions (Diehl et al. 2013). In order to enhance the activity of these insect predators and parasitoids, their perennial habitats have often been designed in agricultural landscapes to enhance their biocontrol service (Diehl et al. 2012). Furthermore, within-field position (distance from the habitat interface: edge or center) also affects the performance of these biological control agents (Anjum-Zubair et al. 2010). However, quantitative studies on how adjacent habitats and within-field position affect biocontrol success are rare (Purtauf et al. 2005; Wäckers et al. 2008).

Many researchers have reported that perennial habitats could enhance the effectiveness of biological control (Schmidt et al. 2005; Poveda et al. 2012). For instance, adding areas with alfalfa adjacent to crop fields can increase the abundance and diversity of

these natural biocontrol agents (Géneau et al. 2012). Some researches have found that natural enemies of pests are found in relatively high species diversity and abundance in refuges such as perennial habitats adjacent the crop fields (Zaller et al. 2012; D'Alberto et al. 2012; Géneau et al. 2012). Although alfalfa areas are one of the most important and rapidly expanding perennial habitats in the agricultural landscape of China, the influence of these alfalfa areas and grassy edges on insect predators and parasitoids within the wheat fields is still largely unknown (Melnychuk et al. 2003; Thies et al. 2005). Here, we assess the effects of within-field positions (i.e. edges versus centers) and adjacent habitats (i.e. the perennial habitat of alfalfa areas versus the annual crop of corn fields) on the abundance and diversity of aphid predators and parasitoids. According to the above information, we expected higher species diversity and abundance of insect predators and parasitoids (i) at field edges than at field centers, and (ii) in wheat fields adjacent to alfalfa areas than in wheat fields adjacent to corn fields. Pathogens are not considered in this experiment due to their specific pathway and cycle of infection.

Materials and methods

Study sites

The study sites were located in the city of Yinchuan, Ningxia Hui Autonomous Region in Northwest China. This region has experienced dramatic loss and fragmentation of natural habitats in the past several decades due to agricultural intensification. The mosaic landscape consists of different habitat patches of crops, pasture and woodlands, with relatively long edges of crop fields due to adjacent different habitats (perennial habitat or ephemeral crop habitat). These adjacent habitats could affect the population dynamics of the natural enemies. Twelve sites were selected for this study, with the minimum distance between these sites larger than 1 km to avoid potential interactions of the insect populations from different sites. As a result, these sites were regarded as replicates in the following analysis. In each site, two wheat fields (*Triticum aestivum* Linn.) were chosen in 2009–2011: one adjacent to an alfalfa area, the other adjacent to a corn field. The corn (*Zea mays* L.) fields ranged from 0.9 to 2.3 ha, and the about-ten-year-old alfalfa (*M.*

sativa) areas varied from 0.2 to 1.7 ha. The alfalfa areas were at least 20 m in width and have not been treated with herbicides or insecticides. Alfalfa was cut three times per year for grass fodder (in the early of June, at the end of July and October). The corn fields were also at least 20 m in width and are sown each year in mid March. No pesticides but only fertilizers were applied in the corn fields. The annually-planted wheat fields (planted in early March; fields ≥ 20 years old) were ~ 60 m wide and were treated with mineral fertilizers. No pesticides were applied in the sampled wheat fields. The alfalfa, corn and wheat fields were all 80 m long and had a rectangular shape, with two edges used as walking paths and the other two directly adjacent to other fields. The wheat density was 400–450 plants m^{-2} with an extra 5 % initially sown to allow loss from agricultural practices (e.g. weeding).

Insect sampling

The two cereal aphid species *Sitobion avenae* (Fabricius) and *Schizaphis graminum* (Rondani) were the most important pests in wheat fields in China. These two species often show outbreaks in mixed populations and share a suite of natural enemies (Purtauf et al. 2005), including parasitoids, ground- and leaf-dwelling predators. Parasitoids in wheat fields live through their larval stage mainly in the mummies of cereal aphids. Aphidiidae parasitoids were sampled on warm and mostly sunny days at the same time that we sampled cereal aphids. The mummies were collected in two rows by hand. The distance between these two rows and habitat interface was 1 and 20 m respectively. Each row was sampled at five randomly-selected points, and the sampling at each point included visual inspection for about 15 min of 100 wheat tillers for parasitoids and about 5 min of 100 wheat tillers for cereal aphids. The short sampling period allowed us to sample all 24 spring wheat fields in a relatively simultaneous fashion. Alfalfa was first harvested in the early of June. Therefore, we sampled the aphids and parasitoids three times (10–15th, 15–20th, and 20–25th of May) before the harvest of alfalfa to avoid the crowding effects of these insects into the wheat fields (Blitzer et al. 2012; Zhao et al. 2013). All mummies were transferred individually to gelatin capsules (5 cm high and 10 cm in diameter) and reared in the laboratory for 30 days. The hatched

adult parasitoids were collected and identified to species (Zhao et al. 2012).

The ground-dwelling predators of cereal aphids (e.g. Carabid beetles and spiders) have been extensively studied both theoretically and experimentally (Elliott et al. 2002). They often occurred on the ground surface as the result of movement among plants or dislodgment from plants (Brewer and Elliott 2004) and were collected using pitfall traps for estimating the relative population density (Hjältén et al. 2010; Lange et al. 2011). Of each of the 24 spring wheat fields, traps were set up in two rows: one near the edge (about 1 m to the edge), and the other in the centre (about 20 m to the edge) (Anjum-Zubair et al. 2010). Five traps were set up in each row, with increasing distances between traps (2.5, 5, 10 and 20 m) for assessing distance-dependent trapping efficiency. The traps were 0.2-l plastic cups (6.5 cm in diameter and 11 cm high), filled with 60 ml mixture of vinegar, sugar, propylene glycol and water at a ratio of 2:1:1:20. To break the surface tension of the water, an odorless detergent was added to the mixture. In total, 240 traps were set up three times for five days during the most active season of these ground-dwelling predators, starting from the 10 to 25th of May each year from 2010 to 2011. The whole experiment was also conducted before harvesting the alfalfa so that the spillover of these ground-dwelling predators could be avoided. We were, however, aware that trapping for such a short period could miss some over-wintering larval which only mature in late summer.

Leaf-dwelling predators of aphids (coccinellids, syrphids and lacewings) were sampled near the pitfall traps using sweep netting during the same period of the pitfall trapping. Fine mesh nets (200 meshes) were used to avoid escape of small predators. We sampled by sweeping ten times (sweeps) per point of the five-point sampling and thus 50 times (sweeps) per row in the wheat fields. The insect samples collected in the nets were transferred into specimen bottle. Then 80 % ethanol was added to kill and preserve all the insects for identification in the lab. Population density of leaf-dwelling predators was calculated in individuals per ten sweeps. All adult parasitoids, ground- and leaf-dwelling predators were identified to species.

Statistical analysis

Individuals in the five pitfall traps, ten sweeps, or on 100 wheat tillers per row were pooled for further

analyses. Predator/prey ratio ($=N_{\text{predator}}/N_{\text{aphid}}$) and proportion parasitism ($=N_{\text{parasitoid}}/(N_{\text{aphid}} + N_{\text{parasitoid}})$) were then calculated by combining the individuals from the same trophic level (two levels: aphids, predators and parasitoids). We ignored other differences between sites but only examined the effects of within-fields position and adjacent habitat on the diversity and density of these arthropods. As no effect of sampling time was found on species diversity and abundance, we also ignored the sampling time in the following analysis.

To analyze the effects of within field position (at the edge versus in the center) and adjacent habitats (alfalfa versus corn field) on species diversity and abundance of cereal aphid natural enemies, we applied a linear mixed-effect model (LMM) with the restricted maximum likelihood method (Lundy et al. 2012). To ensure correct degrees of freedom for each factor, we performed the LMM with the nested random effects of within field position and adjacent habitats on the diversity and abundance of cereal aphid natural enemies (SAS Institute Inc 2006). Specifically, within-field position (i.e. edge or center; $n = 48$ positions) was nested within adjacent habitat (i.e. the sampling wheat field being surrounded by either alfalfa or corn fields; $n = 24$ fields). Species diversity of aphid natural enemies was left untransformed but their densities were square root transformed to achieve normality of residuals. We used rarefaction curves to standardize the average species diversity and density per sampling unit (i.e. five pitfall traps, ten sweeps, and 100 wheat tillers) for the center and edge position of wheat fields adjacent to different habitats, respectively. Raw species counts were used as the response variable. Variance in parasitism and predator/prey ratios due to within field position and adjacent habitats were analyzed using an F test (SAS Institute Inc 2006).

Results

A total of 9,919 individuals of 97 species of cereal aphid natural enemies were observed in wheat fields adjacent to alfalfa areas, and 7,862 individuals of 72 species were found in wheat fields adjacent to corn fields. The total of 17,781 ($=9,919 + 7,862$) individuals include 49 ground-dwelling predators, 35 leaf-dwelling predators and 13 parasitoid species of cereal aphids, where 6,870 individuals of 76 species were

Table 1 Density (mean \pm SE) of cereal aphids and their main natural enemies in different types of wheat fields

Species	Adjacent to alfalfa areas		Adjacent to corn fields	
	Edge	Center	Edge	Center
Cereal aphids (individuals/100 tillers)				
Aphididae				
<i>Macrosiphum avenae</i> (Fabricius)	258 \pm 28	304 \pm 36	287 \pm 34	336 \pm 45
<i>Schizaphis graminum</i> (Rondani)	136 \pm 18	169 \pm 21	156 \pm 18	185 \pm 24
Leaf dwelling predators (individuals/ten sweeps)				
Coccinellidae				
<i>Propylea japonica</i> (Thunberg)	7.5 \pm 0.8	7.1 \pm 0.7	5.8 \pm 0.4	6.1 \pm 0.8
<i>Hippodamia variegata</i> (Goeze)	16.3 \pm 2.2	11.0 \pm 1.3	14.3 \pm 1.7	10.6 \pm 1.3
<i>Hippodamia tredecimpunctata</i> L.	4.3 \pm 0.7	3.5 \pm 0.4	4.1 \pm 0.5	3.7 \pm 0.6
<i>Harmonia axyridis</i> (Pallas)	3.5 \pm 0.5	2.7 \pm 0.3	2.9 \pm 0.5	2.1 \pm 0.2
<i>Coccinella septempunctata</i> L.	2.3 \pm 0.3	1.7 \pm 0.2	2.3 \pm 0.4	1.9 \pm 0.3
Syrphidae				
<i>Syrphus nitens</i> Zetterstedt	7.5 \pm 0.8	6.2 \pm 0.6	4.9 \pm 0.7	4.5 \pm 0.6
<i>Episyrphus balteatus</i> (De Geer)	1.7 \pm 0.3	1.5 \pm 0.5	1.9 \pm 0.3	1.5 \pm 0.1
Chrysopidae				
<i>Chrysopa sinica</i> Tjeder	9.5 \pm 1.1	5.5 \pm 0.7	7.8 \pm 0.9	4.6 \pm 0.5
<i>Sympetrum croceolum</i> Selys	2.2 \pm 0.3	1.7 \pm 0.4	1.7 \pm 0.5	1.9 \pm 0.1
Miridae				
<i>Deraeocoris punctulatus</i> Fallen	9.0 \pm 1.1	7.8 \pm 0.7	8.2 \pm 0.5	7.9 \pm 0.9
Anthocoridae				
<i>Orius minutus</i> (Poppius)	2.3 \pm 0.3	1.5 \pm 0.1	1.4 \pm 0.2	1.5 \pm 0.4
Ground dwelling predators (individuals/five traps)				
Carabidae				
<i>Calosoma chinese</i> (Kirby)	0.8 \pm 0.2	0.5 \pm 0.1	0.7 \pm 0.1	0.5 \pm 0.2
<i>Chlaenius pallipes</i> Gebler	1.7 \pm 0.3	1.5 \pm 0.3	1.1 \pm 0.3	1.0 \pm 0.2
<i>Scarites terricola</i> Bonelli	1.0 \pm 0.3	0.9 \pm 0.2	0.8 \pm 0.1	0.7 \pm 0.1
<i>Dolichus halensis</i> Schaller	2.6 \pm 0.5	1.2 \pm 0.3	2.3 \pm 0.5	1.5 \pm 0.4
<i>Harpalus crates</i> Bates	0.8 \pm 0.1	0.6 \pm 0.1	0.8 \pm 0.2	0.7 \pm 0.1
<i>Harpalus salinus</i> Dejean	1.4 \pm 0.2	0.8 \pm 0.2	1.1 \pm 0.3	0.8 \pm 0.1
Lycosidae				
<i>Pardosa astrigera</i> C. L. Koch	4.6 \pm 1.2	4.3 \pm 0.8	3.3 \pm 0.2	3.1 \pm 0.2
<i>Lycosa coelestris</i> L. Koch	3.3 \pm 0.8	3.7 \pm 0.4	3.4 \pm 0.5	3.7 \pm 0.4
Linyphiidae				
<i>Erigonidium graminicolum</i> Sundevall	5.1 \pm 0.7	4.9 \pm 0.7	3.0 \pm 0.3	3.7 \pm 0.3
<i>Erigone prominens</i> Boes. et Str.	3.4 \pm 0.4	3.5 \pm 0.5	2.6 \pm 0.5	2.4 \pm 0.2
Clubionidae				
<i>Misumenops tricuspoidatus</i> (Fabricius)	2.0 \pm 0.3	1.9 \pm 0.3	2.6 \pm 0.4	1.9 \pm 0.3
Parasitoids (Individuals/100 tillers)				
Aphidiidae				
<i>Aphidius avenae</i> Haliday	87.6 \pm 9.2	63.0 \pm 7.4	57.1 \pm 6.9	46.6 \pm 5.9
<i>Aphidius gifuensis</i> Ashmead	17.9 \pm 3.1	13.7 \pm 1.8	15.7 \pm 2.3	12.1 \pm 1.4
<i>Aphidius sichuanensis</i> Xiao	1.5 \pm 0.2	1.1 \pm 0.5	0.9 \pm 0.2	0.9 \pm 0.3
<i>Diaeretiella rapae</i> Mintosh	2.6 \pm 0.7	1.7 \pm 0.4	0.8 \pm 0.3	0.6 \pm 0.3

Table 1 continued

Species	Adjacent to alfalfa areas		Adjacent to corn fields	
	Edge	Center	Edge	Center
<i>Toxares</i> sp.	1.1 ± 0.4	0.6 ± 0.2	0.9 ± 0.5	0.5 ± 0.3
<i>Trioxys asiaticus</i> Telenga	1.7 ± 0.5	0.6 ± 0.3	0.3 ± 0.1	0.6 ± 0.2
<i>Praon volucre</i> (Haliday)	1.7 ± 0.4	0.6 ± 0.2	0.3 ± 0.1	0.0
<i>Praon rhopalosiphum</i> Takada	0.9 ± 0.4	0.5 ± 0.2	0.6 ± 0.2	0.4 ± 0.2
Eulophidae				
<i>Tetrastichus</i> sp.	1.1 ± 0.2	0.0	0.3 ± 0.1	0.0

Table 2 Effects of adjacent habitats on species diversity and abundance of three groups of aphid natural enemies

Variables	At the edge of wheat fields adjacent different habitats		In the enter of wheat fields adjacent different habitats	
	$F_{1,215}$	P	$F_{1,215}$	P
Density of cereal aphids	6.112	0.014	0.613	0.435
Density of leaf-dwelling predators	2.753	0.099	10.874	0.001
Diversity of leaf-dwelling predators	10.954	0.001	0.262	0.609
Density of ground-dwelling predator	9.983	0.002	0.113	0.737
Diversity of ground-dwelling predators	7.316	0.007	0.434	0.511
Density of parasitoids	8.239	0.005	0.141	0.708
Diversity of parasitoids	7.498	0.007	0.032	0.858

found in the center, and 10,911 individuals of 97 species were found on the edge. Here, we only listed 31 common species, representing 93.45 % of the total individuals (Table 1). The densities of most natural enemies adjacent to alfalfa were higher than those adjacent to the corn fields, and the densities of the two dominant cereal aphid species were significantly lower at the edges than in the centers (Tables 1, 2, 3). Of the 15 most abundant species (accounting for more than 80 % of all individuals), *A. avenae*, *A. gifuensis*, *H. variegata* and *C. sinica* were more abundant at edges than in the center, whilst *E. graminicolum*, *P. astrigera*, *E. prominens* and *S. nitens* were more abundant in the wheat fields adjacent to alfalfa than wheat fields adjacent to corn fields (Table 1). Other species were not affected by both within-field position and adjacent habitats.

Species diversity and density of ground-dwelling predators and parasitoids were significantly higher on the edges than in the centers of the wheat field adjacent to alfalfa (Fig. 1a, b, e, f; Table 3). Species diversity of leaf-dwelling predators was significantly higher in the centers than at the edges of wheat

fields adjacent to alfalfa (Fig. 1c; Table 3). However, their density was significantly higher at the edges than in the centers of fields adjacent to alfalfa (Fig. 1d; Table 3). The overall density of all natural enemies was significantly higher in the centers than at the edges of fields adjacent to alfalfa (Fig. 1b, d, f). In contrast, species diversity and density of these natural enemies were not different between the edges and the centers of wheat fields adjacent to corn fields (Fig. 2a–f; Table 2).

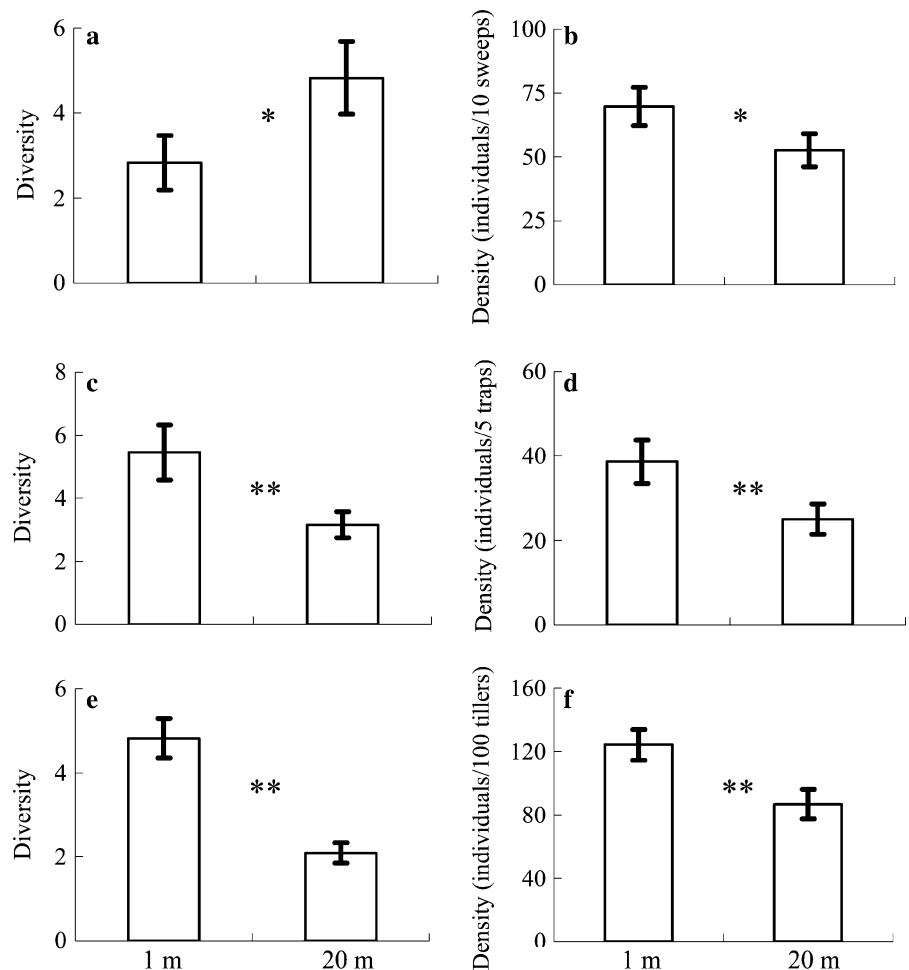
The densities of the main natural enemies which occurred in all 24 wheat fields during the two-year sampling duration were analyzed (Table 4). Two parasitoid species (*A. avenae* and *A. gifuensis*), three leaf-dwelling predators (*H. variegata*, *C. sinica* and *S. nitens*) and five ground-dwelling predators (*P. astrigera*, *E. prominens*, *Chlaenius pallipes*, *Scarites terricola* and *E. graminicolum*) were significantly affected by the position in the field (edge or centre) or adjacent habitat types (alfalfa or corn field). Only one species (*A. avenae*) was affected significantly by both within-field position and adjacent habitats (Table 4). The two most abundant parasitoid species *A. avenae*

Table 3 Effects of within-field positions on species diversity and abundance of three groups of aphid natural enemies

Variables	Different position of wheat field adjacent alfalfa fields		Different position of wheat field adjacent corn fields	
	$F_{1,215}$	P	$F_{1,215}$	P
Density of cereal aphids	18.433	<0.001	1.523	0.219
Density of leaf-dwelling predators	6.344	0.013	0.112	0.738
Diversity of leaf-dwelling predators	5.681	0.018	2.886	0.091
Density of ground-dwelling predators	13.323	<0.001	0.978	0.324
Diversity of ground-dwelling predators	9.364	0.002	1.234	0.268
Density of parasitoids	13.763	<0.001	0.463	0.497
Diversity of parasitoids	13.822	<0.001	2.185	0.141

Fig. 1 Species diversity (left-hand side) and density (right-hand side) of ground-dwelling predators, leaf-dwelling predators, and parasitoids at the edge and in the centre of spring wheat fields adjacent to alfalfa areas (**a, b** leaf-dwelling predators, **c, d** ground-dwelling predators, **e, f** parasitoids). Graphs show the mean \pm SE;

* $P < 0.05$, ** $P < 0.01$



and *A. gifuensis* had 35 % higher densities at the field edges than in the centers. In addition, densities of *H. variegata* and *C. sinica* decreased by 31 % towards the field center (Table 4). Fifty percent more individuals of *A. avenae* were observed in fields adjacent to alfalfa

than in fields adjacent to corn fields. Parasitism, the predator/prey ratios of leaf-dwelling predators and ground-dwelling predators were significantly higher at the edge than in the center of wheat fields adjacent to alfalfa areas (Fig. 3). However, parasitism, the

Fig. 2 Species diversity (left-hand side) and density (right-hand side) of ground-dwelling predators, leaf-dwelling predators, and parasitoids present at the edge and in the centre of spring wheat fields adjacent to corn fields (**a, b** leaf-dwelling predators, **c, d** ground-dwelling predators, **e, f** parasitoids). Graphs show the mean \pm SE; * $P < 0.05$, ** $P < 0.01$

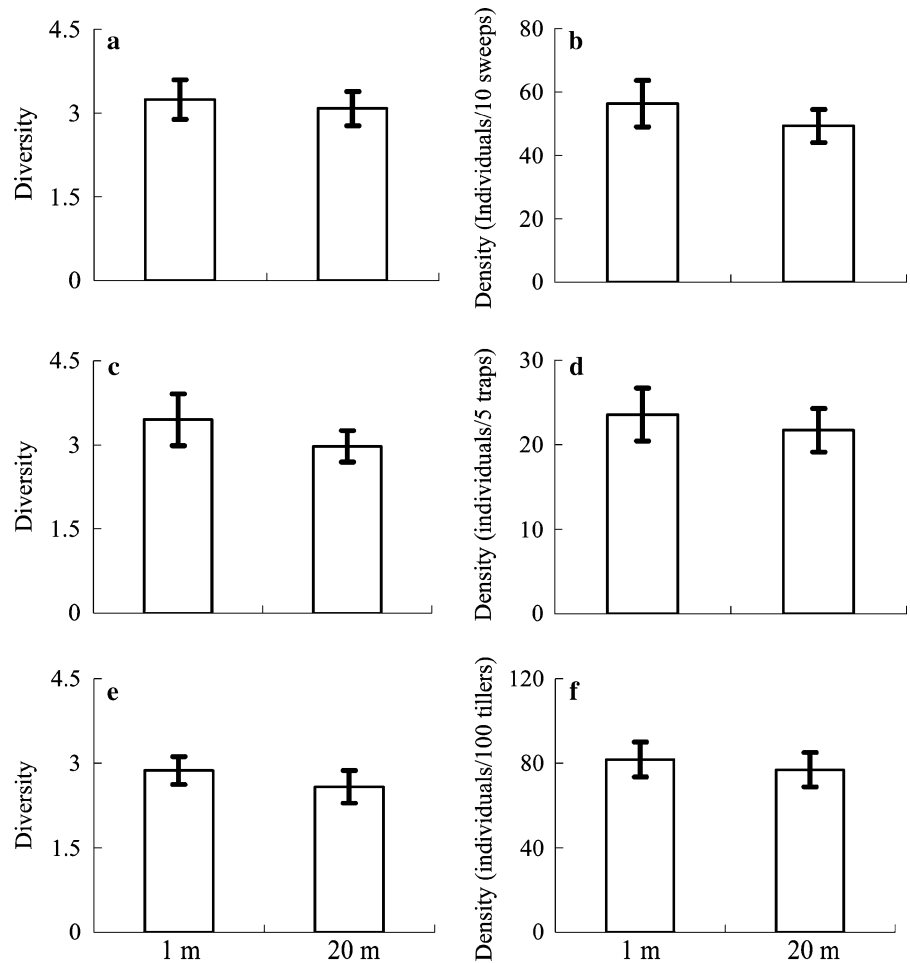


Table 4 Effects of within-field position and adjacent habitats on density of the main natural enemies, from a linear mixed-effect model with nested random effects

Dependent variable	Within-field position		Adjacent habitats	
	$F_{1,431}$	P	$F_{1,431}$	P
Parasitoids				
<i>A. avenae</i>	5.633	0.018	15.343	<0.001
<i>A. gifuensis</i>	5.142	0.024	2.292	0.131
Leaf-dwelling predators				
<i>H. variegata</i>	7.653	0.006	2.274	0.132
<i>C. sinica</i>	8.986	0.003	2.037	0.154
<i>S. nitens</i>	0.474	0.492	13.216	<0.001
Ground-dwelling predators				
<i>P. astrigera</i>	1.423	0.234	5.838	0.016
<i>E. prominens</i>	1.834	0.176	6.147	0.014
<i>C. pallipes</i>	0.572	0.45	7.136	0.008
<i>S. terricola</i>	1.743	0.187	6.117	0.014
<i>E. graminicolum</i>	0.254	0.615	9.014	0.003

predator/prey ratios of leaf-dwelling predators and ground-dwelling predators showed no significant differences in the center and at the edge of wheat fields adjacent to corn fields (Fig. 3).

Discussion

There is a growing body of evidence that both the within-field position and adjacent habitats affect pest regulation by natural enemies (Bianchi et al. 2010). In our experiments, the species diversity of ground-dwelling predators was higher at the edges than in the centers of the wheat fields adjacent to alfalfa areas, consistent with previous studies, which showed a higher species diversity of aphid natural enemies at the edge than in the center of a wheat field bordered by a perennial habitat (Bianchi et al. 2010). However, no trends of species diversity were detected for wheat

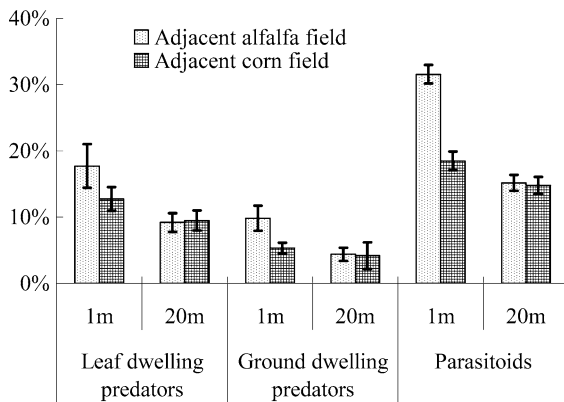


Fig. 3 Parasitism and the predator/prey ratios (%) of ground-dwelling predators and leaf-dwelling predators present at the edge and in the centre of spring wheat field adjacent different habitat types. Error bars represent SE

fields adjacent to corn fields. Because the species assemblages of ground-dwelling predators inhabiting perennial habitats are different from those of arable fields, some ground-dwelling predators from perennial habitats could have invaded the edges of wheat fields (Rand et al. 2006; Mody et al. 2011). Therefore, whether the observation of an increasing diversity of ground-dwelling predators towards field edges (Thies et al. 2011) is specific to fields adjacent to alfalfa areas or due to the edge effect still warrants further investigation.

Ground-dwelling predators often need alternative prey and habitats and thus move frequently between habitat patches. This pattern is observed during the growing season of wheat from March to July, or when breeding carabids move from grassy boundaries towards wheat field centers in early spring (Elliott et al. 2002; Purtauf et al. 2005). These previous observations are consistent with our results of a higher density of carabids in field edges. This suggests that ground-dwelling predators are often generalists that tend to utilize multiple food resources in different habitat. The movement of ground-dwelling predators from one distinct habitat to another may cause the significant differences at the edge and in the center of wheat field adjacent to alfalfa fields, which could produce cross-habitat spillover processes (Birkhofer et al. 2010). Several studies have demonstrated an increased number of natural enemies in fields adjacent to perennial habitats due to the spillover effect on natural enemies that disperse from high-density alfalfa habitats into arable fields (Elliott et al. 2002). Our

results indicate that these natural enemies increase towards alfalfa margins emphasizing the importance of using adequate controls to distinguish the possible benefits of boundary habitats from unspecific edge effects (Tscharntke et al. 2012).

Leaf-dwelling predators and parasitoids in cereal fields are largely oligophagous (Brewer and Elliott 2004) because cereal aphids alone can satisfy their need for resources (i.e. food or host). However, these natural enemies need emigrate out of cereal fields to search for alternative resources (nectar and pollen) in the absence of pests in crop fields (Bianchi et al. 2010; Chaplin-Kramer et al. 2011). This could explain why significant differences of both the abundance and diversity of leaf-dwelling predators and parasitoids were found between samples from edges and centers of wheat fields adjacent to alfalfa fields. In contrast, corn fields could not supply these food resources, and consequently the abundance and diversity of these natural enemies were not enhanced in wheat fields adjacent to corn fields.

Perennial vegetation can serve as reservoir for natural enemies (Kleijn and Sutherland 2003; Frank et al. 2012). Field margins, hedgerows, and other perennial habitats adjacent to arable lands can host a large variety of parasitoids and predators (Géneau et al. 2012). These natural enemies that spillover from perennial habitats to crop fields can be beneficial due to the consumption of agricultural pests (Rand et al. 2006; Tscharntke et al. 2012). This spillover edge effect was the overall movement of predatory insects from the perennial habitat to the arable habitat (Blitzer et al. 2012). Predator/prey ratios of leaf-dwelling predators and parasitism are higher when adjacent to alfalfa areas, supporting the idea that using habitat management in agro-farming landscape can enhance sustainable pest control. Perennial habitats can provide alternative hosts and prey for predators and parasitoids (Langer and Hance 2004; Purtauf et al. 2005), and are also important refuge for egg parasitoids and predator larvae to hibernate in winter (Clough et al. 2007; Klingenberg et al. 2010).

The density of leaf-dwelling predators declined towards the center of the wheat field, whereas the diversity increased. This was because the dominant species (such as *H. variegata*) had higher densities at the edges than in the centers (Rand et al. 2006). In addition, mobility of natural enemies are sensitive to the differences in habitat quality (e.g. for hibernation;

Blitzer et al. 2012) and may be an important aspect to cause uneven distributions in mosaic landscapes (Dahms et al. 2010). Hence, that the presence of alfalfa areas can offer suitable overwintering conditions may explain why high abundance and diversity of natural enemies were found in wheat fields adjacent to alfalfa areas. Similarly, other perennial habitats adjacent to crop fields could also enhance biological control service (Blüthgen et al. 2012; Cobbold and MacMahon 2012). The proliferation effect of being near an alfalfa area is mainly on natural enemies because alfalfa areas can supply a large amount of alternative resources (e.g. nectars and hosts) and shelters for natural enemies (Opatovsky et al. 2010; Diehl et al. 2012). However, intraguild interactions of natural enemies need to be further examined on whether biological control services could be enhanced at the edge of wheat field adjacent to perennial habitat (Janssen et al. 2007; Messelink et al. 2013).

In conclusion, the natural enemies of cereal aphids in wheat fields responded strongly to the within-field position and adjacent habitat type, with the within-field position being a more dominant factor (MacFadyen et al. 2009). Modern agricultural landscapes have been shaped by using land for crop production (Perdikis et al. 2011). Since the within-field position and adjacent habitat around the crop field can have a strong influence on the abundance and distribution of these aphid natural enemies (Purtauf et al. 2005), agricultural landscape should be better designed to enhance the efficiency of biological control by increasing perennial habitats in farmlands (Zhao et al. 2012).

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Author Biographies

Zi-Hua Zhao is a postdoctoral fellow at the Institute of Zoology, Chinese Academy of Sciences. This research is part of his Ph. D. project (Ningxia University, China) on the effects of habitat structures on agricultural pests. His current research

focuses on pest management via habitat manipulation and biological control.

Cang Hui is a senior researcher at DST-NRF Centre of Excellence for Invasion Biology (CIB), Stellenbosch University, South Africa. His research interests lie in proposing models and theories for explaining emerging patterns in community ecology, macroecology and evolution.

Da-Han He is a professor at Ningxia University, China, with research in the field of agroecology, integrated pest management and landscape ecology.

Feng Ge is a professor at the Institute of Zoology, Chinese Academy of Sciences. His research interests include biological control, habitat management, and climate change biology.