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Responses of Cereal Aphids and Their Parasitic Wasps to Landscape Complexity

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ABSTRACT The intensification of agriculture has caused a decline in the complexity of agricultural landscapes because of the expansion of arable lands and the removal of natural habitats. These landscape changes, which have substantial effects on natural enemies (e.g., parasitoids) and on biological control services, have received considerable attention recently. In the current study, we analyzed the effects of landscape complexity on cereal aphids and their parasitic wasps in 24 sites during a period of 3 yr. In total, 11 primary parasitoid species and 6 hyperparasitoid species, comprising 5,220 individuals, were collected in our experiments. With the exception of two primary parasitic wasps (*Trioxys asiaticus* Telenga and *Toxares* sp.) and one hyperparasitic wasp (*Dendrocerus carpenteri* [Curtis]), most species were sensitive to landscape complexity after ≥1 yr. Species diversity, primary parasitism, and hyperparasitism increased with increasing landscape complexity. However, the relationship between the population density of active primary parasitoids (effective primary parasitoids) and landscape complexity was indicated by a quadratic function, not a linear function. The effective population density of primary parasitoids was maximal (2.04 individuals per 100 wheat stems) if the percentage of noncrop habitat was 38%. The hypothesis that landscape complexity may enhance the activity or higher diversity of primary parasitoids and hyperparasitoids was well-supported by our study. However, the hyperparasitoids had a more sensitive response to landscape complexity than the primary parasitoids. Further studies should aim to enhance the biological pest control of primary parasitoids and suppress hyperparasitoids by habitat manipulation. This technique could be used effectively for pest management in mosaic landscapes through habitat rearrangement and reorganization.

KEY WORDS biological control, hyperparasitism, mosaic landscape, noncrop habitat, primary parasitism

Modern intensive agriculture has dramatically changed the arrangement of arable lands and noncrop habitats and has caused frequent outbreaks of many pests (Wu et al. 2008, Gagic et al. 2011, Cobbold and MacMahon 2012). A linkage between landscape complexity and local biodiversity in arable lands has been confirmed in several groups of organisms (Finke and Snyder 2010, Holzschuh et al. 2010). Landscape simplification in modern agriculture may be unfavorable to many natural enemies that always require alternative hosts and food in noncrop habitats (Toledo and Burlingame 2006, Géneau et al. 2012). Structurally complex landscapes can support multiple ecosystem services besides biological pest control because of the high proportion of noncrop habitats in these landscapes, e.g., hedgerows, woodlands, streams, fallows, and grassland (Wratten et al. 2012). These noncrop habitats may enhance species diversity or the abundance of natural enemies in arable lands, and thereby suppress pest populations effectively (Clough et al. 2007). Insect parasitoids include a diverse set of taxa with the potential to reduce pest populations (Menalled et al. 1999, Bianchi et al. 2006, Tscharntke et al. 2012). Primary parasitoids are important as natural enemies in the control of cereal aphids in China (Zhao et al. 2012). Landscape complexity can affect species interactions, including parasitism by insect parasitoids (Brewer et al. 2008, Zhao et al. 2013a). In agricultural landscapes, parasitoids could benefit from extra crop field habitats because of the supply of food, shelter, favorable microclimates, alternative hosts, or a combination of these resources (Landis et al. 2000, Gagic et al. 2011). Therefore, the presence of diverse noncrop habitats in structurally complex landscapes may greatly enhance the activity and abundance of parasitoids (Schmidt and Tscharntke 2005, Steingrover et al. 2010).

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Recent empirical studies have demonstrated that the abundance of noncrop habitats within agricultural landscapes significantly affects the occurrence of parasitoids (With et al. 2002, Tscharntke et al. 2005). Increased landscape complexity has also been shown to increase primary parasitism and hyperparasitism (Schmidt et al. 2008, Gagic et al. 2011, Segoli and Rosenheim 2012). Most studies have focused on the relationship between primary parasitoids and landscape complexity (Roschewitz et al. 2005, Gagic et al. 2011, Macfadyen et al. 2011). However, primary parasitoids may simultaneously be disrupted by hyperparasitoids, which may affect the biological control of cereal aphids. In addition, the effects of landscape complexity on hyperparasitoids and on biological pest control are poorly understood (Thies et al. 2005, Gagic et al. 2011). The relationships among cereal aphids, primary parasitoids, hyperparasitoids, and landscape complexity remain largely unknown because of the joint effects of hyperparasitoids and landscape composition on the primary parasitoids of cereal aphids (Costamagna et al. 2004, Gagic et al. 2011).

In China, agricultural landscapes have been changed from an original complex pattern, including a large proportion of natural habitat, to a simple landscape, including a large proportion of arable lands (Zhao et al. 2012, 2013c). During the past decade, for example, 1.5 million ha of natural habitat has been converted to arable lands in Ningxia Province, China. The cereal aphids in wheat fields in North China are attacked by a range of primary parasitoid species (Hymenoptera: Aphidiidae), which are attacked by hyperparasitoids (Hymenoptera: Pteromalidae; Cynipoidea: Charipidae). These primary parasitoids are solitary endoparasites and can act as important biological control agents in wheat fields (Thies et al. 2005, Gagic et al. 2011). In this study, we examined the species composition and abundance of primary parasitoids and hyperparasitoids in landscapes of different complexity in spring wheat fields. We tested two hypotheses: 1) the species diversities of primary parasitoids and hyperparasitoids are higher in complex landscapes than in simple ones and 2) hyperparasitoids will offset the effect of complex landscapes on primary parasitoids, and therefore the level of biological pest control may remain unchanged or decline in complex landscapes.

Methods and Materials

Our experimental site was located on the Yinchuan Plateau in northwest China (38° 26′03″ N, 106° 27′02″ E, Fig. 1). Two different regions (towns) differing in landscape complexity (a noncrop-dominated region and a crop-dominated region) were selected in our experiments. The highly noncrop-dominated agricultural region was located in Junmachang town, Xingqing District, Yinchuan city. This region includes heterogeneous landscape with a high percentage of noncrop habitats. Approximately 81% of the 3,769 ha area in this region was covered by arable or grassland mosaic. The remaining area was characterized by patchily distributed fragments of natural and seminatural habitats, such as woodlands, wetlands, residential areas, roads, and barren land. Nearly 50% of the grassland sites in this region consist of meadows (nearly half of which are extensively managed by mowing at most three times a year), and approximately half of the grassland sites consisted of extensively and intensively managed pasture. In the noncrop-dominated region, 13 landscape sites, each with a 500 m radius, along a landscape complexity gradient were selected for our experiments. Each landscape site included from five to eight wheat fields. These landscape sites formed a continuous gradient, from simple landscapes with intensive land use (63% arable land) to complex landscapes with a high percentage of noncrop habitats (39.6% arable land). Furthermore, we used the percentage of noncrop habitats in each landscape to indicate the landscape complexity, which was an appropriate method for landscape analysis and has been used in many empirical experiments (Roschewitz et al. 2005, Schmidt et al. 2008, Zhao et al. 2013b). The minimum distance between landscapes sites was 1,000 m. Wheat (*Triticum aestivum* L.) was sown and managed according to the guidelines for integrated production. The crop-dominated agricultural region was located in Zhangzhen town, Xingqing District, Yinchuan city, in which most of the land cover consisted of arable land. Approximately 87% of the 2,138 ha area of this region was covered by arable land. The crops grown on these lands included maize (*Zea mays* L.), rice (*Oryza sativa* L.), soybean [*Glycine max* (L.)], potato (*Solanum tuberosum* L.), Chinese wolfberry (*Lycium chinense* Miller), and sorghum [*Sorghum bicolor* (L.)]. The remaining area was characterized by seminatural habitats such as grasslands, woodlands, and barren land. In the crop-dominated region, 11 landscape sites, each with a radius of 500 m, were selected, with three to six wheat fields in every landscape site and located along the same type of landscape complexity gradient as that used in the

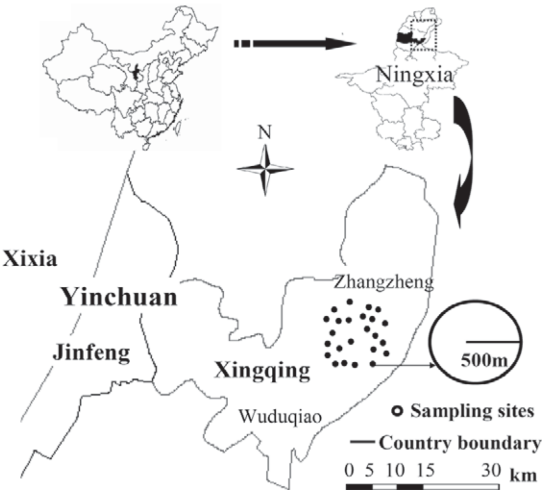

Fig. 1. Map of the study area in North China: 24 collection sites.

noncrop-dominated region. These landscape sites were situated along a gradient from simple landscapes with intensive land use (89.3% arable land) to complex landscapes with a high percentage of noncrop habitats (61% arable land). The distances between different landscape sites were all >1,000 m. In addition, these landscape sites were separated by an agricultural matrix and by other crops, such as maize and rice. This crop-dominated region contains a low percentage of noncrop habitats and is characterized by landscape simplification (intensive agriculture).

The total 24 landscape sites selected in our experiment formed a continuous gradient, from simple landscapes with a low percentage of noncrop habitats to complex landscapes with a high percentage of noncrop habitats. In every landscape site, three wheat fields were selected for insect investigation. The selected wheat fields in different landscape sites were located at least 1,000 m apart, and the fields within one landscape site were always closer than 600 m to each other. The 24 different landscapes sites in which our samples were collected were identified using a Global Positioning System and were investigated in 2009, 2010, and 2011. These 24 landscape sites were selected to encompass landscape complexity gradients from crop-dominated to noncrop-dominated landscapes.

The habitat diversity in these 24 landscape sites also had a continuous gradient from high to low diversity. All selected wheat fields were managed under the same agricultural practices. The final plant density was 400–450 plants per square meter, with an extra 5% initially sown to allow losses produced by weeding. From March to June, none of the landscapes at any of our experimental sites were sprayed with insecticides. Wheat was fertilized once with N (nitrogen): P (phosphorus): K (kalium) = 12: 34: 12 during the establishment of the crop. In every landscape, the percentage of noncrop habitats in a circle of 500 m radius was used to indicate landscape complexity. This method is considered to furnish an appropriate scale for landscape analysis and has been used in many studies (Concepcion et al. 2008, Schmidt et al. 2008, Holzschuh et al. 2010, Jonsson et al. 2012). The same method has also been applied in many other empirical studies (Thies et al. 2005, Eilers and Klein 2009).

Field samples were collected to determine the species composition of cereal aphids and their parasitic wasp in different agricultural landscapes. Primary parasitoids and hyperparasitoids were collected during the peak of cereal aphid populations from 10 to 20 May in 2009–2011. Both visual observation and hand collection were performed on warm, mostly sunny days and not after rain. Every landscape around the wheat fields was examined based on a five-point sampling spread across as many wheat fields as possible (Zhao et al. 2012). As a result of crop rotation, the wheat fields within a landscape differed over the years 2009–2011. To avoid differences in species pools within the wheat fields, the size of the area sampled in the wheat fields was limited to a maximum of 100 by 100 m and a minimum of 30 by 30 m to reduce spatial autocorrelation (Winqvist et al. 2011). Every sample conducted for insect sample included 100 stems of wheat and consisted of 15 min of visual inspection of the wheat within each landscape (1 h total search time per sample). Specifically, 500 stems at every landscape site were screened, and the density (mummy and cereal aphids) was calculated in units of "individuals per 100 stems."

Both live and mummy aphids were collected simultaneously and taken to the laboratory for rearing (Lee et al. 2005, Zhao et al. 2012). Cereal aphids that died during rearing were dissected to determine whether they were parasitized. All field-collected mummies were stored in gelatin capsules until the emergence of adult parasitoids, after which they were identified. The gelatin capsules were kept in test tubes sealed with a damp cotton plug and placed in a climate chamber at 20°C with a photoperiod of 14:10 (L:D) h. The gelatin capsules with mummies were examined twice daily for the first month to detect the emergence of adults, and were examined once a day during the next month. Mummies from which a parasitoid did not emerge for two months were dissected to determine the cause of nonemergence and were classified as either aestivating or dead (Lee et al. 2005, Zhao et al. 2012). All adult parasitoids and hyperparasitoids were identified to the species level based on their morphological characteristics and taxonomic classification. Primary parasitism ($= N_{\text{primary parasitoid}}/(N_{\text{aphids}} + N_{\text{primary parasitoid}})$; i.e., the proportion of cereal aphids parasitized by the parasitic wasps) and hyperparasitism ($= N_{\text{hyperparasitoid}}/(N_{\text{primary parasitoid}} + N_{\text{hyperparasitoid}})$) were then calculated. The biocontrol efficacy was calculated as the ratio of the combined density of all parasitoids to the aphid density (Zhao et al. 2012).

Statistical Analyses. We evaluated the correlation between landscape complexity and the population density of cereal aphids, primary parasitoids, and hyperparasitoids. We conducted our analysis using Pearson correlation coefficients with a simultaneous autoregressive error term. The calculations were performed with PROC CORR (SAS Institute Inc. 2006, Cary, NC). Pearson correlation is a classical method to determine the relationship between variables. Owing to great variation in population densities among the study years, the data from different years were analyzed independently.

To determine the effects of landscape complexity and the year of sampling on population density of cereal aphids, primary parasitoids, and hyperparasitoids, a two-way analysis of variance was conducted to examine their relationships. In addition, interactions between landscape complexity and year of sampling were determined (GLM procedure, SAS Institute Inc. 2006). However, we did not find any significant effects of the year of sampling on population density of primary parasitism and hyperparasitism. For this reason, we did not conduct a time series analysis of population dynamics. Instead, we focused on the static relationship between landscape complexity and the biotic variables. Therefore, the 3 yr of data were combined to maximize the sample size. The use of this enlarged

Table 1. Pearson correlations between landscape complexity and pop densities of cereal aphids, primary parasitoid, or hyperparasitoid (* $P < 0.05$, **$P < 0.01$, ***$P < 0.001$; ns, nonsignificant)

Species	Pearson correlation coefficient		
	2009	2010	2011
Cereal aphids			
S. avenae	-0.818^{***}	-0.796^{**}	-0.810^{***}
Sc. graminum	-0.684^{***}	-0.558^{**}	-0.431^{*}
Primary parasitoids			
A. avenae	-0.764^{***}	-0.628^{**}	-0.541^{**}
Aphidius gifuensis Ashmead	-0.356^{*}	−0.431ns	-0.274^{*}
Aphidius sichuanensis Chen & Shi	-0.453^{**}	−0.238ns	-0.394^{*}
T. asiaticus	−0.313ns	−0.419ns	−0.102ns
Trioxys sp.	-0.163^{*}	-0.097^{*}	−0.219ns
Lysiphlebus confusus (Tremblay & Eady)	−0.253ns	−0.083	−0.053ns
Praon volucre (Haliday)	-0.164^{**}	−0.103ns	-0.324^{*}
P. rhopalosiphum	-0.372^{**}	-0.298^{*}	-0.148^{*}
Toxares sp.	−0.094ns	−0.045ns	−0.019ns
Ap. albipodus	-0.234^{**}	-0.388^{**}	-0.327^{*}
Tetrastichus sp.	-0.174^{*}	−0.274ns	−0.208ns
Hyperparasitoids			
As. vulgaris	-0.253^{**}	-0.319^{*}	−0.318ns
As. suspensus	-0.453^{**}	−0.326ns	-0.287^{**}
P. aphidis	-0.786^{***}	-0.631^{**}	-0.549^{**}
Ah. aphidivorus	-0.364^{*}	−0.217ns	-0.198^{*}
D. carpenteri	−0.653ns	−0.124ns	−0.265ns
Alloxysta sp.	-0.476^{**}	-0.215^{*}	-0.369^{*}

sample could reduce the random error of the analyses to a considerable extent. The species diversity of primary parasitoids and hyperparasitoids were estimated with the Shannon diversity index in each landscape site. In addition, density, parasitism, and species diversity obtained from different landscape sites were treated as independent variables. Then, we examined the effects of landscape complexity on these independent variables using simple linear regression models at a given spatial scale (REG procedure, SAS Institute Inc. 2006). A nonlinear regression model (the quadratic function) was used to examine the relationship between landscape complexity and the effective population density of the primary parasitoid (SAS Institute Inc. 2006). In the entire analysis, only variables that attained a 0.05 level of significance were entered into the model.

Results

Three species of cereal aphids [*Sitobion avenae* (F.), *Schizaphis graminum* (Rondani), and *Rhopalosiphum padi* (L.)] were collected in our experiments. The first two species were the dominant species, which account for >95% of the total cereal aphids in every year (Table 1). The effects of landscape complexity on total population densities of cereal aphids were significantly negative ($R^2 = 0.2943$; $F_{1,71} = 21.98$; $P < 0.001$). However, landscape complexity had no significant effects on population density of single species (*S. avenae:* $R^2 = 0.3672$, $F_{1,71} = 1.47$, $P = 0.2294$; *Sc. graminum* $R^2 = 0.1983$, $F_{1,71} = 0.79$, $P = 0.3771$; Fig. 2). The effects of year of sampling and landscape complexity on density of total cereal aphids were significant. However, no interaction between year of sampling and landscape complexity was found (Table 2).

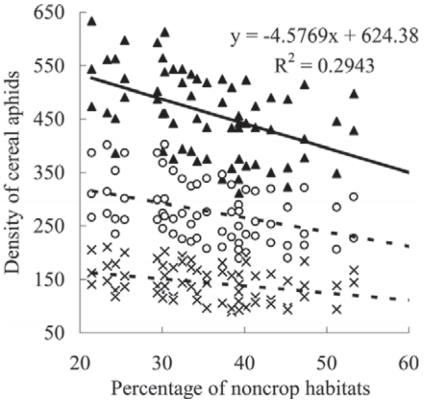

Fig. 2. Effects of landscape complexity on population density of cereal aphids [▲, total cereal aphids; O, *S. avenae* (F.); X, *Sc. graminum* (Rondani)]. Calculated using peak population densities.

In all, 5,220 individuals of primary parasitoid and hyperparasitoid species were collected in this experiment. Eleven species of primary parasitoids were identified. *Aphidius,* including three species, was the dominant genus and represented 90.54% of the total primary parasitoids. *Aphidius* was widely distributed in all landscape types. *Aphidius avenae* Haliday, the dominant species, represented 61.33% of all the primary parasitoids. Furthermore, the abundance of four parasitoid species from two family (Aphidiinae: *A. avenae*, *Trioxys* sp., and *Praon rhopalosiphum* Takada; Aphelinidae: *Aphelinus albipodus* [Hayat and Fatima]) was significantly affected by landscape complexity in all 3 yr (Table 1). In contrast, two parasitoid species (*Trioxys asiaticus* Telenga and *Toxares* sp.) were not affected by landscape complexity (Table 1).

Six species of hyperparasitoids were collected. Dominance among the hyperparasitoid species was not obvious. Three species (*Pachyneuron aphidis* [Bouche], *Asaphes suspensus* [Nees], and *Asaphes* sp.) had relatively large populations and attacked a wide range of primary parasitoids. The relationship be-

Table 2. Effects of year variable and landscape complexity on pop density of cereal aphids, primary parasitoid, and hyperparasitoid

Variables	*F* values	*P* values
Population density of cereal aphids		
Year	15.23	<0.001
Landscape complexity	23.14	<0.001
Year × landscape complexity	0.13	0.7195
Population density of primary parasitoid		
Year	0.16	0.6904
Landscape complexity	71.43	<0.001
Year × landscape complexity	0.02	0.8879
Population density of hyperparasitoid		
Year	0.21	0.6482
Landscape complexity	64.32	<0.001
Year × landscape complexity	0.08	0.7781

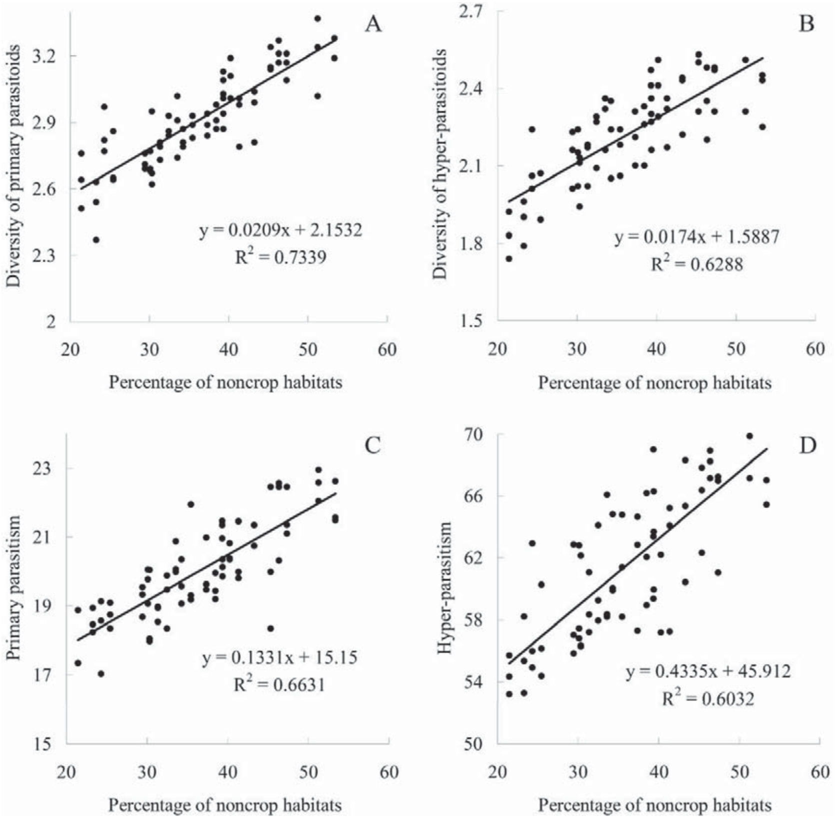

Fig. 3. Effects of landscape complexity on species diversity of parasitic wasps, primary parasitism, and hyperparasitism. A) The relationship of landscape complexity and diversity of primary parasitoids. B) The relationship of landscape complexity and diversity of hyper-parasitoids. C) The relationship of landscape complexity and primary parasitism. D) The relationship of landscape complexity and hyper-parasitism.

tween landscape complexity and abundance of the other three species (*Asaphes vulgaris* Walker, *Aphidencyrtus aphidivorus* [Mayr], and *Dendrocerus carpenteri* [Curtis]) varied greatly in different years. Almost all hyperparasitoid species were affected significantly by landscape complexity with the exception of one species, *D. carpenteri* (Table 1). The relationship between the species diversity of primary parasitoids, the species diversity of hyperparasitoids, and landscape complexity is shown in Fig. 3. Species diversity increased with increasing landscape complexity, and these two variables had a significant linear relationship (Fig. 3A and B; primary parasitoids, $R^2 = 0.795$, $F_{1,71} = 14.36$, $P < 0.001$; hyperparasitoids, $R^2 = 0.6288$, $F_{1,71} = 34.23$, $P < 0.001$).

Both primary parasitism and hyperparasitism increased with increasing landscape complexity (Fig. 3C and D). However, hyperparasitism was more sensitive to landscape complexity than primary parasitism, which had a higher slope than primary parasitism (hyperparasitism: 0.43 vs. primary parasitism: 0.13). The year of sampling had no significant effects (Table 2). In addition, no significant interaction effects between the year of sampling and landscape complexity were found for the primary parasitoids (Table 2). The level of hyperparasitism even reached 70% in complex landscapes (Fig. 3D). In addition, landscape complexity has significant effects on hyperparasitism. However, no significant interaction effects between the year of sampling and landscape complexity on density of hyperparasitoids were found (Table 2).

The total mummy population density and the population density of hyperparasitoids were significantly affected by landscape complexity and increased with increasing landscape complexity (Fig. 4A and B). The relationship between the effective population density of primary parasitoids (nonparasite) and landscape complexity was described well by a quadratic function (Fig. 4A; $R^2 = 0.4972$; $F_{1,71} = 26.37$; $P = 0.001$). As landscape complexity increased, the effective population density of primary parasitoids first increased and then decreased. The effective population density of primary parasitoids reached a maximum (2.04 individuals per 100 stems) when the percentage of noncrop habitat in the landscape was ≈38% (Fig. 4A).

Discussion

The hypothesis that landscape complexity had substantial effects on the species diversity of primary

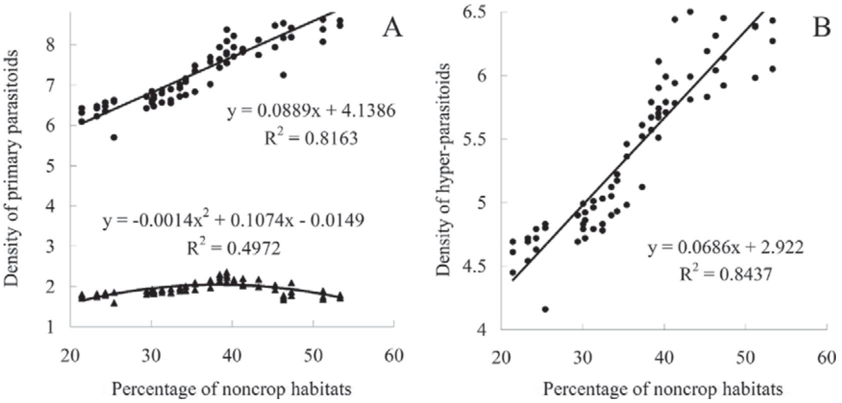

Fig. 4. Effects of landscape complexity on population density of primary parasitoid and hyperparasitoid (●, total mummy density; ▲, effective density of primary parasitoid [nonparasitized]). Calculated using peak population densities. A) The relationship of percentage of noncrop habitats and density of primary parasitoids. B) The relationship of percent of noncrop habitats and density of hyper-parasitoids.

parasitoids and hyperparasitoids was well supported in our study. The species diversity of the parasitic wasp increased with increasing landscape complexity. The results of this study can be explained in two ways. First, the primary parasitoids and hyperparasitoids appear to be closely linked spatially and temporally with noncrop habitats and may need to switch to alternative host species in autumn because the regions that are dominated by wheat typically cannot provide continued food resources and shelter (Kruess 2003, Thies et al. 2011). In addition, these species may also require alternative hosts to overwinter as prepupae within the host and hatch from mummies in the spring. Hence, within field populations of primary parasitoids and hyperparasitoids colonizing wheat fields in spring may be strongly affected by the habitat composition of the surrounding landscapes (Lindborg et al. 2008, Thies et al. 2011). These parasitoids may have evolved to adapt well to interannual landscape changes (Landis et al. 2000, Brewer and Elliott 2004). Second, many other alternative foods, including nectar-containing plants, could supply food resources and shelter to adult parasitoids in structurally complex landscapes (Kruess and Tscharntke 1994, Menalled et al. 1999). Many previous studies have found that nectar is often a more suitable food source than the honeydew produced by cereal aphids (Diekotter et al. 2007, Holzschuh et al. 2007). In this context, primary parasitoids and hyperparasitoids could have evolved adaptations to optimize the exploitation of nectar (Royama et al. 2005, Steingrover et al. 2010).

In this study, primary parasitism and hyperparasitism were also found to be significantly greater in the complex landscape than those in the simple landscape, as also reported by other studies (Tscharntke et al. 2005, Toledo and Burlingame 2006). The possible reason for the observed differences between complex and simple landscapes is that landscape complexity influences primary parasitism and hyperparasitism at a landscape scale (Thies and Tscharntke 1999, Kruess 2003). This result indicates that extra field habitats enhance the immigration and mobility of these species among different habitats (Chaplin-Kramer et al. 2011). Several previous studies have also demonstrated that landscape complexity enhances parasitoid populations because a higher percentage of noncrop habitats can provide food, shelter, favorable microclimates, alternative hosts, or combinations of these resources (Roland and Taylor 1997, Menalled et al. 1999, Brewer and Elliott 2004). However, several other studies have indicated that primary parasitism did not differ significantly among landscapes of different complexity (Costamagna et al. 2004). The possible reason for these findings was that landscape complexity created a contrast, and thus offset the effects of hyperparasitoids. More importantly, we hypothesize that "bank plants" existed in noncrop habitats, which can supply alternative food required by parasitoids and act as a rearing and release system in agricultural landscapes (Parolin et al. 2012a). Therefore, bank plants can release a large number of parasitoids into wheat fields to suppress cereal aphids (Parolin et al. 2012b). For these reasons, bank plants are important for pest management, and thorough screening is necessary to identify and preserve these plants (Landis et al. 2000). In the current study, the bank plants remained largely unknown. We refer to several studies that have focused research on the phenomenon of bank plants (Landis et al. 2000, Parolin et al. 2012b).

A mosaic landscape consisting of arable lands and noncrop habitats (grasslands and woodlands) could enhance biological pest control and suppress pest damage (Landis et al. 2000, Tscharntke et al. 2012). Because landscape complexity affects the activity of primary parasitoids, a landscape perspective is important for pest population management (Landis et al. 2000). The current study demonstrated that the population density of hyperparasitoids can also increase with increasing landscape complexity. More research is needed to clarify the ways in which landscape complexity can be optimized for biological pest control and for reducing the effects of hyperparasitoids (Jonsson et al. 2008, Gagic et al. 2011). Furthermore, the effects of landscape complexity on biological control services may be applied in habitat management (Costamagna et al. 2004, Lu et al. 2012).

Overall, the results of the study support the hypothesis that landscape complexity enhances the population density of primary parasitoids and hyperparasitoids. In addition, species at a higher trophic level (hyperparasitoids) were more sensitive to landscape complexity than those at a lower trophic level (primary parasitoids). The factors causing these differences are complex and cannot be generalized in a short-term context (French et al. 2001, Hui et al. 2012, Segoli and Rosenheim 2012). Further interpretation of these differences will require studies of interspecific relationships caused by species specific, realized host range, overwintering requirements, and microclimate requirements of primary parasitoids and hyperparasitoids (Kavallieratos et al. 2004, Lu et al. 2012). The effects of landscape complexity on tritrophic interactions should be considered in sustainable management of cereal aphids.

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References Cited

Bianchi, F.J.J.A., C.J.H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. R. Soc. B 273: 1715–1727.

Brewer, M. J., and N. C. Elliott. 2004. Biological control of cereal aphids in North America and mediating effects of host plant and habitat manipulations. Annu. Rev. Entomol. 49: 219–242.

Brewer, M. J., T. Noma, N. C. Elliott, A. N. Kravchenko, and A. L. Hild. 2008. A landscape view of cereal aphid parasitoid dynamics reveals sensitivity to farm- and region-scale vegetation structure. Eur. J. Entomol. 105: 503–511.

Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. Ecol. Lett. 14: 922–932.

Clough, Y., A. Kruess, and T. Tscharntke. 2007. Local and landscape factors in differently managed arable fields affect the insect herbivore community of a non-crop plant species. J. Appl. Ecol. 44: 22–28.

Cobbold, S. M., and J. A. MacMahon. 2012. Guild mobility affects spider diversity: links between foraging behavior and sensitivity to adjacent vegetation structure. Basic Appl. Ecol. 13: 597–605.

Concepcion, E. D., M. Diaz, and R. A. Baquero. 2008. Effects of landscape complexity on the ecological effectiveness of agri-environment schemes. Landsc. Ecol. 23: 135–148.

Costamagna, A. C., F. D. Menalled, and D. A. Landis. 2004. Host density influences parasitism of the armyworm *Pseudaletia unipuncta* in agricultural landscapes. Basic Appl. Ecol. 5: 347–355.

Diekotter, T., K. J. Haynes, D. Mazeffa, and T. O. Crist. 2007. Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects. Oikos 116: 1588–1598.

Eilers, E. J., and A. M. Klein. 2009. Landscape context and management effects on an important insect pest and its natural enemies in almond. Biol. Control 51: 388–394.

Finke, D. L., and W. E. Snyder. 2010. Conserving the benefits of predator biodiversity. Biol. Conserv. 143: 2260–2269.

French, B. W., N. C. Elliott, S. D. Kindler, and D. C. Arnold. 2001. Seasonal occurrence of aphids and natural enemies in wheat and associated crops. Southwest. Entomol. 26: 49–61.

Gagic, V., T. Tscharntke, C. F. Dormann, B. Gruber, A. Wilstermann, and C. Thies. 2011. Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. Proc. R. Soc. B 278: 2946–2953.

Géneau, C. E., F. L. Wäckers, H. Luka, C. Daniela, and O. Balmer. 2012. Selective flowers to enhance biological control of cabbage pests by parasitoids. Basic Appl. Ecol. 13: 85–93.

Holzschuh, A., I. Steffan-Dewenter, D. Kleijn, and T. Tscharntke. 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. J. Appl. Ecol. 44: 41–49.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? J. Anim. Ecol. 79: 491–500.

Hui, C., C. Boonzaaier, and L. Boyero. 2012. Estimating changes in species abundance from occupancy and aggregation. Basic Appl. Ecol. 13: 169–177.

Jonsson, M., S. D. Wratten, D. A. Landis, and G. M. Gurr. 2008. Recent advances in conservation biological control of arthropods by arthropods. Biol. Control 45: 172–175.

Jonsson, M., H. L. Buckley, B. S. Case, S. D. Wratten, R. J. Hale, and R. K. Didham. 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. J. Appl. Ecol. 49: 706–714.

Kavallieratos, N. G., Z. Tomanovic, P. Stary, C. G. Athanassiou, G. P. Sarlis, O. Petrovic, M. Niketic, and M. A. Veroniki. 2004. A survey of aphid parasitoids (Hymenoptera : Braconidae : Aphidiinae) of southeastern Europe and their aphid-plant associations. Appl. Entomol. Zool. 39: 527–563.

Kruess, A. 2003. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. Ecography 26: 283–290.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological-control. Science 264: 1581–1584.

Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45: 175–201.

Lee, J. H., N. C. Elliott, S. D. Kindler, B. W. French, C. B. Walker, and R. D. Eikenbary. 2005. Natural enemy impact on the Russian wheat aphid in southeastern Colorado. Environ. Entomol. 34: 115–123.

Lindborg, R., J. Bengtsson, A. Berg, S.A.O. Cousins, O. Eriksson, T. Gustafsson, K. P. Hasund, L. Lenoir, A. Pihlgren, E. Sjodin, et al. 2008. A landscape perspective on conservation of semi-natural grasslands. Agric. Ecosyst. Environ. 125: 213–222.

Lu, Y., K. Wu, Y. Jiang, Y. Guo, and N. Desneux. 2012. Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. Nature 487: 362–367.

Macfadyen, S., P. G. Craze, A. Polaszek, K. van Achterberg, and J. Memmott. 2011. Parasitoid diversity reduces the variability in pest control services across time on farms. Proc. R. Soc. B. 278: 3387–3394.

Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999. Does agricultural landscape structure affect parasitism and parasitoid diversity? Ecol. Appl. 9: 634–641.

Parolin, P., C. Bresch, N. Desneux, R. Brun, A. Bout, R. Boll, and C. Poncet. 2012a. Secondary plants used in biological control: a review. Int. J. Pest Manage. 58: 91–100.

Parolin, P., C. Bresch, C. Poncet, and N. Desneux. 2012b. Functional characteristics of secondary plants for increased pest management. Int. J. Pest Manage. 58: 369–377.

Roland, J., and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386: 710–713.

Roschewitz, I., M. Hucker, T. Tscharntke, and C. Thies. 2005. The influence of landscape context and farming practices on parasitism of cereal aphids. Agric. Ecosyst. Environ. 108: 218–227.

Royama, T., W. E. MacKinnon, E. G. Kettela, N. E. Carter, and L. K. Hartling. 2005. Analysis of spruce budworm outbreak cycles in New Brunswick, Canada, since 1952. Ecology 86: 1212–1224.

SAS Institute. 2006. SAS User's Guide, version 9.1.2. SAS Institute, Cary, NC.

Schmidt, M. H., and T. Tscharntke. 2005. Landscape context of sheetweb spider (Araneae : Linyphiidae) abundance in cereal fields. J. Biogeogr. 32: 467–473.

Schmidt, M. H., C. Thies, W. Nentwig, and T. Tscharntke. 2008. Contrasting responses of arable spiders to the landscape matrix at different spatial scales. J. Biogeogr. 35: 157–166.

Segoli, M., and J. A. Rosenheim. 2012. Should increasing the field size of monocultural crops be expected to exacerbate pest damage? Agric. Ecosyst. Environ. 150: 38–44.

Steingrover, E. G., W. Geertsema, and W.K.R.E. van Wingerden. 2010. Designing agricultural landscapes for natural pest control: a transdisciplinary approach in the Hoeksche Waard (The Netherlands). Landsc. Ecol. 25: 825–838.

Thies, C., and T. Tscharntke. 1999. Landscape structure and biological control in agroecosystems. Science 285: 893–895.

Thies, C., I. Roschewitz, and T. Tscharntke. 2005. The landscape context of cereal aphid-parasitoid interactions. Proc. R. Soc. B 272: 203–210.

Thies, C., S. Haenke, C. Scherber, J. Bengtsson, R. Bommarco, L. W. Clement, P. Ceryngier, C. Dennis, M. Emmerson, V. Gagic, et al. 2011. The relationship between agricultural intensification and biological control: experimental tests across Europe. Ecol. Appl. 21: 2187–2196.

Toledo, A., and B. Burlingame. 2006. Biodiversity and nutrition: a common path toward global food security and sustainable development. J. Food Compos. Anal. 19: 477–483.

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecol. Lett. 8: 857–874.

Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batary, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, et al. 2012. Landscape moderation of biodiversity patterns and processes-eight hypotheses. Biol. Rev. 87: 661–685.

Winqvist, C., J. Bengtsson, T. Aavik, F. Berendse, L. W. Clement, S. Eggers, C. Fischer, A. Flohre, F. Geiger, J. Liira, et al. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. J. Appl. Ecol. 48: 570–579.

With, K. A., D. M. Pavuk, J. L. Worchuck, R. K. Oates, and J. L. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. Ecol. Appl. 12: 52–65.

Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and N. Desneux. 2012. Pollinator habitat enhancement: benefits to other ecosystem services. Agric. Ecosyst. Environ. 159: 112–122.

Wu, K., Y. Lu, H. Feng, Y. Jiang, and J. Zhao. 2008. Suppression of cotton bollworm in multiple crops in China in areas with Bt toxin-containing cotton. Science 321: 1676–1678.

Zhao, Z. H., D. H. He, and C. Hui. 2012. From the inverse density-area relationship to the minimum patch size of a host-parasitoid system. Ecol. Res. 27: 303–309.

Zhao, Z. H., C. Hui, D. H. He, and F. Ge. 2013a. Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. Biocontrol 58: 765–776.

Zhao, Z. H., C. Hui, F. Ouyang, J. H. Liu, X. Q. Guan, D. H. He, and F. Ge. 2013b. Effects of inter-annual landscape change on interactions between cereal aphids and their natural enemies. Basic Appl. Ecol 14: 472–479.

Zhao, Z. H., P. J. Shi, X. Y. Men, F. Ouyang, and F. Ge. 2013c. Effects of crop species richness on pest-natural enemy systems based on an experimental model system using a microlandscape. Sci. China Life Sci. 56: 818–822.

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