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Shelterbelts in agricultural landscapes enhance ladybeetle abundance in spillover from cropland to adjacent habitats

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Abstract The natural enemies of herbivorous pests in cropping systems may relocate to adjacent habitats in response to declining habitat quality in heterogeneous landscapes. In this study, we measured the cross-edge spillover of ladybeetles from wheat fields to shelterbelts, and tested how landscape variables at various spatial scales influence ladybeetle populations. We conducted a large-scale sampling study of agricultural landscapes differing in structural complexity during 2012 and 2013. The effects of landscape variables (i.e., landscape diversity and the percentage of woody habitats) on the ladybeetle abundance were investigated. *Propylea japonica* (Thunberg) and *Harmonia axyridis* (Pallas) were the dominant ladybeetle species. The abundances of ladybeetles in spillover were positively correlated with the percentage of woody area, and negatively correlated with landscape diversity and edge density of crop habitats. It indicates that a low diversity landscape with a large area of shelterbelts supports larger ladybeetle abundance in spillover compared with a high diversity landscape with a limited area of shelterbelts. By contrast, greater numbers of within-field ladybeetles were associated with landscape diversity increase. Landscape features at the spatial scale of 2.5–3 km could best predict the abundance of ladybeetles in spillover, whereas the best prediction model for ladybeetle abundance within field was at the 1.5 km scale. These results suggest that the landscape variables influence ladybeetle abundance differently in spillover and within fields. The introduction of shelterbelts in the agricultural landscape could enhance the conservation of ladybeetle populations.

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Introduction

Agronomic intensification has transformed many agricultural landscapes into expansive monocultures with little natural habitat, which has resulted in a loss of biodiversity, including arthropods (Meehan et al. 2011). This landscape simplification is widely expected to increase insect pest pressure on crops, leading to increased use of insecticides (Meehan et al. 2011; Tscharntke et al. 2005). As an ecosystem service, biological control of crop pests can reduce the need for costly chemical pesticides. Biological control can be enhanced by increasing vegetation diversity through the provision of non-crop habitats such as forests, grass strips and remnant vegetation (Landis et al. 2000). At the landscape scale, natural enemies of herbivorous pests in cropping systems often benefit from the presence of natural or non-crop habitats in surrounding landscapes, as they provide food and shelter resources (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Thies et al. 2003). Woody vegetation around agricultural fields is a common element in the landscape of many areas. Farmers often view these borders as harboring weeds and insect pests and reducing insolation and drying of the soil by wind action. Shelterbelts introduce heterogeneity to the agricultural field that may modify the dynamics of pests and natural enemies. Increased biological control by natural enemies has been reported in landscape with increased woody habitats (Bianchi et al. 2005, 2008). The benefits from adjacent woody border on natural enemies have been demonstrated at spatial scales (Perovic et al. 2010; Thomson and Hoffmann 2013). However, a number of studies found no influence of woody vegetation on the abundance of natural enemies (Holland and Fahrig 2000; Smits et al. 2012).

Ladybeetles are conspicuous predators of aphids and are sometimes the most abundant predators of aphids in wheat fields and corn fields. Ladybeetles have a wide habitat range, and can easily move to and from crop and non-crop habitats (Osawa 2011). Using local-scale vegetation management to enhance ladybeetle abundance has been widely studied (e.g., Dong et al. 2012; Muller and Godfray 1997). Crop rotation of winter wheat and corn is common in North China. The spillover of natural enemies from cropland to adjacent habitats is an important process affecting pest populations in fragmented landscapes (Rand et al. 2006). Natural enemies move to escape disturbance and find resources scattered in space and time (Schellhorn et al. 2014). Previous studies showed that ladybeetles originating from wheat could enhance the control of cotton aphids (Men et al. 2004). The spatial resource template at the landscape scale could determine ladybeetle abundance (Bianchi et al. 2007). Networks of forest belts on farmland are very popular in the agricultural landscape in North China. This planting pattern offers a good system to study the landscape effects on the spillover of ladybeetles. Their abundance is important to controlling aphids in adjacent habitats and reentering crop fields in the late growing season. Conservation biological control in the agroecosystem requires a landscape management perspective, because most arthropod species experience their habitat at spatial scales beyond the plot level, and there is spillover of natural enemies across the crop and non-crop interface (Tscharntke et al. 2008). Landscape structure can influence the abundance of ladybeetles as shown by Elliott et al. (1999) where the effect of the surrounding landscape on abundance differed among ladybeetle species (also see Gardiner et al. 2009b; Rand and Tscharntke 2007).

Despite the potential importance of shelterbelt or tree rows, we know little about how the landscape variables affect abundance of ladybeetles that spill from agricultural fields to shelterbelts. Our research questions are: 1) whether the landscape variables affect the abundance of ladybeetle spillover from wheat fields to shelterbelt; and 2) if it has effects, whether these effects differ from landscape effects on the ladybeetles within field.

Materials and methods

Study site

Sampling was undertaken in the area surrounding Yucheng Experimental Station of the Chinese Academy of Sciences, Shandong Province, north China (116°36′ E, 36°57′ N). The area is in a temperate, seasonal, semi-humid monsoon climate where the mean annual temperature is 13.1 °C. Mean annual precipitation is 582 mm and concentrated in the summer months. Wheat (*Triticum aestivum* L.) was grown in rotation with maize (*Zea mays* L.). Networks of forest belts on farmland are built to reduce the effects of the wind. This type of intercropping of poplar (*Populus alba* L.) and the agricultural crop began several decades ago.

We selected 28 study sites, which covered a gradient from extremely simple landscapes to relatively complex landscapes. The study sites were all located within approximately 600 km^2. Each site was separated by 0.2–4 km from other sites. All study fields were maintained using similar management practices with the use of local traditional herbicides (tribenuron-methyl) and insecticides (mainly imidacloprid insecticide). Field geospatial data were collected using a handheld GPS receiver.

Sampling

Ladybeetles were sampled in wheat fields and their edges adjacent to shelterbelts. During the wheat harvest in 2012, samples were conducted in 19 fields. In 2013, samples were conducted in 18 fields from the wheat growing to harvest period. In each landscape site, we placed ten yellow sticky traps to sample ladybeetles in the edge of each field. Traps were located in marginal trees along one row, 5 m apart, adjacent to the crop field (within 1 m from field edge). The yellow sticky traps were 24 × 20 cm sheets attached to the poplar tree stem such that the bottom edge was approximately 1.7 m above the ground. We also sampled ladybeetles and aphids within fields. A single 50 × 50 m study plot in the field was established adjacent to the shelterbelt (within 1 m from shelterbelt edge). Sampling in the plot was conducted by suspending 15 yellow sticky traps from PVC pipes above the crop plants. These traps were located in three rows parallel to the shelterbelt and separated by 5-m long and 10-m across two rows. In 2012 sampling was conducted from 3 to 10 June. In 2013 there were three sampling periods: 23–30 April, 17–24 May and 4–11 June. Sticky cards were inspected a week after establishment. Sticky cards were returned to the lab, where we counted numbers of individual ladybeetle species. All ladybeetles were identified to species.

Landscape data

For each of the 28 sites, landscape structure was estimated in six circular sectors (0.5, 1, 1.5, 2, 2.5, and 3 km radiuses), representing a nested set of landscape sectors at six spatial scales. The landscape structure was analyzed from a commercially available digital map (Astrium10 m resolution; spot4-) using ArcGIS 10 (ESRI, Redlands, CA, USA). The area of arable land, woody vegetation, hedgerow, water area, road and settlement were measured. These represent six broad categories of land cover present within each landscape circle. The annual crop was mainly winter wheat. The woody vegetation included all shelterbelts, and was dominated by the poplar tree.

Landscape diversity, which reflects the diversity and composition of landscape context, was calculated using Shannon's diversity index (H). We measured landscape diversity at six spatial scales ranging from 0.5 to 3 km (at 0.5 km intervals) from the field center. We used edge density (ED) to measure the landscape fragmentation. The ED index refers to the amount of edge relative to the landscape area, reflecting the separation of the patches by edge. A high ED often means the high degree of fragmentation. All the variables were calculated using FRAGSTATS 4.1 (McGarigal et al. 2012).

Statistical analysis

To compare ladybeetle abundances in woody habitats with those in crop habitats, we introduced the variable, "fraction of ladybeetles in woody habitats" calculated as the number of ladybeetles in woody habitats divided by the combined number of ladybeetles within fields and in woody habitats. All analyses were performed using generalized linear models in the statistical program R version 2.15.3 (R Core Team 2013). Ladybeetle data were over-dispersed because of many zeroes in the dataset. According to Zuur et al. (2009), we fit generalized linear models assuming a negative binomial distribution using the "glm.nb()" function of the ''MASS'' package of R (Venables and Ripley 2002). Using this, we modeled the within field ladybeetles and marginal shelterbelt ladybeetles. For the fraction of ladybeetles in woody habitats, we fit generalized linear models assuming a binomial distribution using the "glm()" function. The independent variables were landscape variables at six spatial scales ranging from 0.5 to 3 km (at 0.5 km intervals) from the field center (Table 1). Each spatial scale was analyzed separately. AIC-based model selection statistics were used to select the model that best explained the abundances of ladybeetles. For each analysis, we present the log-likelihood estimate, the Akaike weights, and the minimum AICc value, which has the best support for the data and any other models with an AICc difference (ΔAIC) of less than 2. Models with a ΔAIC in this range are termed "competing models" and are considered to also have substantial support for the data (Burnham and Anderson 2002).

Results

Ladybeetle species and abundance

The number of ladybeetles collected and identified was 7,341 in 2012 and 6,161 in 2013. The composition of ladybeetles in 2012 was *Propylea japonica* (Thunberg) 89.3 %, *Harmonia axyridis* (Pallas) 10.4 % and *Coccinella septempunctata* L. 0.3 %. The species composition in 2013 was *P. japonica* 84.3 % and *H. axyridis* 15.7 %, and no *C. septempunctata* was found.

During the wheat harvest period in 2012, there were 19.5 ± 1.7 (mean ± SE) ladybeetles per sticky trap in the margin and 33.3 ± 2.5 within the field. No significant correlation was found between ladybeetles within-field and in spillover numbers. The fraction of ladybeetles in woody habitats averaged 0.38, with a range from 0.06 to 0.77. During the whole sampling period in 2013, there were 5.2 ± 1.4 ladybeetles per sticky trap in the margin and 6.7 ± 0.5 within fields. There was a weak negative correlation between ladybeetles in spillover and within fields ($r = -0.17$, $t = -2.45$, $df = 198$, $P = 0.02$). During the whole sampling period in 2013, the fraction of ladybeetles in woody habitats averaged 0.38, with a range from 0.09 to 0.90. The fraction of ladybeetles in woody habitats was quite low in April and May 2013, and reached high levels in June 2013 (Fig. 1).

Landscape effects

The landscape composition surrounding sampling fields varied markedly among the landscape sites (Table 1). For example, at the 1.5 km scale in 2012, the percentage of woody areas ranged from 6.29 to 21.36 %, whereas the percentage of crop ranged from 36.15 to 64.17 %.

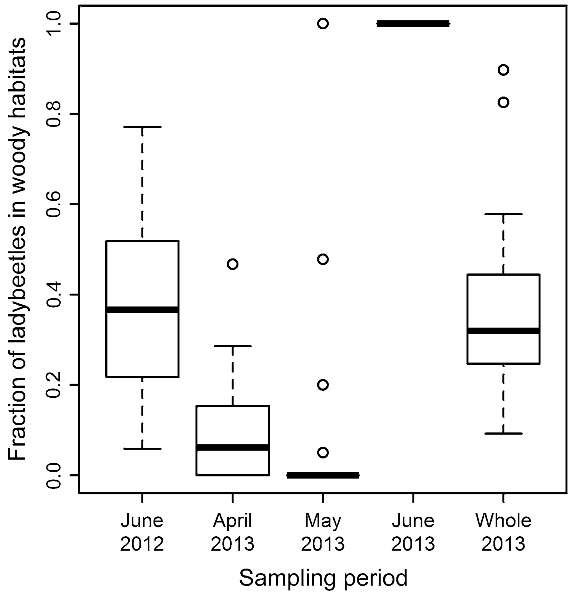

Fig. 1 The fraction of ladybeetles in woody habitats, calculated as the number of ladybeetles in woody habitats divided by the combined number of ladybeetles within fields and in woody habitats, in different sampling periods. The box corresponds to the interquartile range of the values, the thick line indicates the median, and whiskers indicate the minimum and maximum values. Dots represent outliers which are larger than 1.5 times of upper quartile

In 2012, ladybeetle abundance in marginal woody habitat was best predicted at a spatial scale of 3 km, having the lowest AICc value of any model at the six spatial scales examined. Competing models included the landscape diversity, percentage of crop and woody areas, and ED of crop habitats (Table 2). Ladybeetle abundance increased as the percentage of woody areas increased. The landscape diversity, negatively correlated with ladybeetle abundance, was also the best predictor at 0.5, 1, 1.5, 2 and 2.5 km. The abundance of ladybeetles within fields was best predicted at a spatial scale of 1.5 km by landscape diversity, ED of woody and crop area, and percentage of crop area (Table 3). This model had the lowest AICc of any model at the six spatial scales examined. The abundance of ladybeetles both in marginal woody habitats and within fields was negatively correlated with landscape diversity, ED of crop and percentage of crop areas. It indicated that ladybeetle abundance increased as the landscape diversity and crop area decreased. The fraction of ladybeetles in woody habitats was not significantly correlated with landscape variables at each of six spatial scales.

In 2013, ladybeetle abundances in margin woody habitats were best predicted by the landscape diversity, percentage of woody area and aphid number at a spatial scale of 2.5 km (Table 4). Competing models suggested that ladybeetle abundance in margin woody habitats was negatively correlated with the landscape diversity and aphid numbers, but positively correlated with the percentage of woody habitats. Abundance of ladybeetles within field was best predicted by landscape diversity at a spatial scale of 1.5 km, which had the lowest AICc value of any model at the six spatial scales examined (Table 5). There was a significant positive relationship between ladybeetle abundance within field and landscape diversity, indicating that ladybeetle abundance increased as landscape diversity increased. The fraction of ladybeetle in woody habitats could not be best predicted by any landscape variables at each of six spatial scales.

Discussion

Effects of landscape variable on ladybeetle abundances

The potentially high quality resources provided by cropping systems are ephemeral. The spillover of ladybeetles should result from the active emigration in response to wheat harvesting (Rand et al. 2006). This behavior can result in a transient spike in ladybeetle abundance in the field edges. This study was to determine whether landscape variables influence abundance of ladybeetles in spillover from cropland to shelterbelt. We found a significant relationship between ladybeetle abundance and landscape variables in both years. The competing models suggested that landscapes with a large area of woody habitats and low landscape diversity had more ladybeetles in spillover than those without these landscape features. However, for ladybeetle within fields, landscape effects on their abundance performed differently between two years. In 2012, greater numbers of ladybeetles were associated with increasing of landscape diversity, ED of crop and percentage of crop areas. On the contrary, abundance of ladybeetles in 2013 increased as the landscape diversity increased.

Table 1 Mean values of landscape variables for different spatial scales. Minimum and maximum are given in parentheses

Year	Scale (km)	P_{wd} (%)	P_{cp} (%)	ED_{wd} (m ha^{-1})	ED_{cp} (m ha^{-1})	H
2012	0.5	10.16 (3.05–27.97)	57.27 (28.80–78.85)	89.65 (53.37–175.01)	151.44 (97.75–219.45)	1.20 (0.74–1.70)
	1.0	11.95 (2.83–22.21)	50.28 (36.97–66.45)	113.72 (33.61–161.74)	141.08 (81.43–185.53)	1.39 (1.10–1.67)
	1.5	12.14 (6.29–21.36)	47.73 (36.15–64.17)	119.42 (75.09–158.09)	134.89 (103.40–171.79)	1.45 (1.16–1.59)
	2.0	11.90 (7.31–17.75)	48.01 (40.43–60.01)	118.71 (83.67–149.42)	136.72 (113.22–164.26)	1.46 (1.25–1.57)
	2.5	11.68 (6.79–15.79)	47.14 (42.49–56.64)	119.41 (80.28–148.19)	139.62 (115.27–167.93)	1.48 (1.33–1.58)
	3.0	11.37 (7.35–14.10)	47.43 (42.37–54.43)	118.24 (83.29–139.88)	142.73 (123.06–171.41)	1.47 (1.38–1.55)
2013	0.5	8.79 (3.05–27.97)	51.80 (25.53–68.60)	80.18 (53.38–151.37)	153.65 (97.75–219.45)	1.29 (0.97–1.70)
	1.0	9.31 (2.83–18.80)	46.43 (33.40–58.88)	101.30 (33.61–161.74)	146.03 (81.43–185.53)	1.43 (1.27–1.67)
	1.5	9.64 (4.60–20.57)	44.05 (36.15–53.48)	107.44 (75.09–151.87)	141.89 (103.40–177.59)	1.47 (1.27–1.61)
	2.0	10.01 (5.79–17.75)	44.47 (34.15–52.78)	109.33 (77.60–160.67)	143.90 (118.90–169.79)	1.48 (1.33–1.65)
	2.5	9.90 (6.23–15.79)	44.28 (35.37–52.16)	110.10 (80.28–149.20)	144.15 (121.21–167.93)	1.49 (1.38–1.64)
	3.0	9.84 (6.69–14.10)	44.87 (37.35–52.32)	109.93 (83.29–141.56)	146.08 (129.57–171.41)	1.48 (1.40–1.61)

P_{wd} percentage of woody habitats, P_{cp} percentage of crop, ED_{wd} edge density of woody habitats, ED_{cp} edge density of crop, *H* landscape diversity

Table 2 Model selection statistics for ladybeetle abundance in margin woody habitats during wheat harvest in 2012

Scale	Model	df	logLik	AICc	Delta	Weight
0.5	$9.646 - 0.0715\ P_{cp}^{**} - 2.245\ H^{*}$	4	−359.77	728.0	0.00	0.20
	$5.793 - 0.00461\ ED_{wd} - 0.0440\ P_{cp}^{**}$	4	−360.00	728.4	0.05	0.16
	$8.666 - 0.00280\ ED_{wd} - 0.0652\ P_{cp}^{**} - 1.522\ H$	5	−359.33	729.3	1.34	0.10
	$4.861 - 0.0347\ P_{cp}^{**}$	3	−361.84	729.9	1.96	0.08
1	$14.790 - 0.113\ P_{cp}^{**} - 4.489\ H^{**}$	4	−362.10	732.6	0.00	0.25
	$16.150 - 0.00383\ ED_{cp} - 0.117\ P_{cp}^{**} - 4.915\ H^{**}$	5	−361.44	733.5	0.90	0.16
	$13.800 - 0.109\ P_{cp}^{**} - 0.0203\ P_{wd} - 3.751\ H^{*}$	5	−361.65	734.0	1.33	0.13
	$13.600 - 0.00362\ ED_{wd} - 0.106\ P_{cp}^{**} - 3.579\ H^{*}$	5	−361.68	734.0	1.39	0.12
	$15.080 - 0.00445\ ED_{cp} - 0.00434\ ED_{wd} - 0.111\ P_{cp}^{**} - 3.953\ H^{*}$	6	−360.82	734.6	1.94	0.09
1.5	$15.580 - 0.00969\ ED_{cp}^{*} - 0.115\ P_{cp}^{**} - 0.0427\ P_{wd}^{*} - 3.716\ H$	6	−363.69	740.3	0.00	0.13
	$6.742 - 0.00834\ ED_{wd}^{*} - 0.0597\ P_{cp}^{**}$	4	−366.00	740.4	0.10	0.12
	$6.341 - 0.0602\ P_{cp}^{**} - 0.0468\ P_{wd}^{*}$	4	−366.07	740.6	0.25	0.11
	$7.346 - 0.00571\ ED_{cp} - 0.0602\ P_{cp}^{**} - 0.0528\ P_{wd}^{**}$	5	−365.03	740.7	0.41	0.10
	$15.500 - 0.00873\ ED_{cp} - 0.00666\ ED_{wd} - 0.112\ P_{cp}^{**} - 3.666\ H$	6	−364.10	741.1	0.81	0.08
	$7.434 - 0.00440\ ED_{cp} - 0.00856\ ED_{wd}^{*} - 0.0613\ P_{cp}^{**}$	5	−365.35	741.4	1.04	0.08
	$16.380 - 0.00941\ ED_{cp} - 0.114\ P_{cp}^{**} - 4.683\ H^{*}$	5	−365.47	741.6	1.28	0.07
	$9.137 - 0.00749\ ED_{wd} - 0.0754\ P_{cp}^{**} - 1.207\ H$	5	−365.79	742.3	1.93	0.05
	$6.684 - 0.00490\ ED_{wd} - 0.0612\ P_{cp}^{**} - 0.0232\ P_{wd}$	5	−365.82	742.3	1.98	0.05
2	$29.780 - 0.0207\ ED_{cp}^{**} - 0.202\ P_{cp}^{**} - 9.821\ H^{**}$	5	−364.06	738.8	0.00	0.50
	$31.180 - 0.0212\ ED_{cp}^{**} - 0.210\ P_{cp}^{**} + 0.0259\ P_{wd} - 10.690\ H^{**}$	6	−363.77	740.5	1.69	0.22
2.5	$59.430 - 0.0460\ ED_{cp}^{**} + 0.0141\ ED_{wd}^{*} - 0.375\ P_{cp}^{**} - 23.150\ H^{**}$	6	−357.39	727.7	0.00	0.44
	$46.830 - 0.0399\ ED_{cp}^{**} - 0.300\ P_{cp}^{**} - 16.440\ H^{**}$	5	−359.24	729.1	1.42	0.22
	$52.500 - 0.0427\ ED_{cp}^{**} - 0.331\ P_{cp}^{**} + 0.0665\ P_{wd} - 19.540\ H^{**}$	6	−358.18	729.3	1.59	0.20
3	$\mathbf{67.760 - 0.0636\ ED_{cp}^{**} - 0.425\ P_{cp}^{**} + 0.0954\ P_{wd} - 24.990\ H^{**}}$	**6**	**−355.57**	**724.1**	**0.00**	**0.34**
	$58.400 - 0.0578\ ED_{cp}^{**} - 0.370\ P_{cp}^{**} - 20.210\ H^{**}$	5	−356.92	724.5	0.43	0.29
	$60.170 - 0.0650\ ED_{cp}^{**} - 0.0216\ ED_{wd} - 0.381\ P_{cp}^{**} + 0.219\ P_{wd} - 20.310\ H^{**}$	7	−355.08	725.5	1.36	0.18
	$67.620 - 0.0606\ ED_{cp}^{**} + 0.0100\ ED_{wd} - 0.424\ P_{cp}^{**} - 25.290\ H^{**}$	6	−356.35	725.6	1.55	0.17

Bold type indicates the best overall model. Competing models with a $\Delta AIC < 2$ are included

P_{wd} percentage of woody habitats, P_{cp} percentage of crop, ED_{wd} edge density of woody habitats, ED_{cp} edge density of crop, H landscape diversity, *df* are the degrees freedom; logLik are the log-likelihood values, *delta* are the AICc differences (ΔAIC), *weight* are the Akaike weights

Significance of variables is indicated as follows: * $P < 0.05$; ** $P < 0.01$

These results appeared to be inconsistent, which may be partly explained by the difference in sampling periods in these years. The samplings in 2012 were conducted only in the harvest period. During this period, the ladybeetles within fields were mainly expected to migrate from fields to adjacent shelterbelts. Consequently, the relationship between ladybeetles and landscape variables was similar in spillover and within fields. By contrast, the samplings in 2013 began with the wheat-growing period and ended after harvest. Ladybeetles stayed mostly in fields during the wheat-growing period, and moved from fields to nearby habitats after harvest. Therefore, ladybeetles in different periods may have different responses to landscape variables such as landscape diversity.

Our results suggest that landscape diversity could significantly affect the abundance of ladybeetles. During the wheat-growing season, ladybeetle abundance increased as the landscape diversity increased. However, in wheat harvesting time, abundance of ladybeetle spillover from fields to marginal woody habitats was negatively correlated with landscape diversity. That contradiction was possibly due to the

Table 3 Model selection statistics for ladybeetle abundance within field during wheat harvest in 2012

Scale	Model	df	logLik	AICc	Delta	Weight
0.5	$13.020 - 0.00857\ ED_{cp}^{**} - 0.0581\ P_{cp}^{**} - 4.122\ H^{**}$	5	−406.70	824.1	0.00	0.37
	$13.350 - 0.00947\ ED_{cp}^{**} - 0.0621\ P_{cp}^{**} - 0.0180\ P_{wd} - 3.946\ H^{**}$	6	−405.78	824.5	0.45	0.29
	$12.460 - 0.00887\ ED_{cp}^{**} - 0.00248\ ED_{wd} - 0.0542\ P_{cp}^{**} - 3.619\ H^{**}$	6	−406.22	825.4	1.33	0.19
1	$18.590 - 0.0121\ ED_{cp}^{**} + 0.00575\ ED_{wd} - 0.0890\ P_{cp}{}^{**} - 6.921\ H^{**}$	6	−403.61	820.2	0.00	0.44
	$15.850 - 0.0128\ ED_{cp}^{**} - 0.0708\ P_{cp}^{**} - 5.068\ H^{**}$	5	−405.20	821.1	0.88	0.28
1.5	$\mathbf{24.970 - 0.0164\ ED_{cp}^{**} + 0.00760\ ED_{wd}^{*} - 0.114\ P_{cp}^{**} - 10.200\ H^{**}}$	**6**	**−401.47**	**815.9**	**0.00**	**0.51**
2	$25.320 - 0.0178\ ED_{cp}^{**} + 0.0141\ ED_{wd}^{**} - 0.120\ P_{cp}^{**} - 0.0415\ P_{wd} - 10.300\ H^{**}$	7	−400.73	816.8	0.85	0.34
	$21.220 - 0.0113\ ED_{cp}^{*} + 0.00907\ ED_{wd} - 0.0951\ P_{cp}^{**} - 8.711\ H^{**}$	6	−407.95	828.9	0.00	0.23
2.5	$22.610 - 0.0135\ ED_{cp}^{*} + 0.0191\ ED_{wd}^{*} - 0.105\ P_{cp}^{**} - 0.0618\ P_{wd} - 9.456H^{**}$	7	−407.07	829.4	0.57	0.17
	$16.280 - 0.0109\ ED_{cp}^{*} - 0.0639\ P_{cp}^{*} - 5.647\ H^{**}$	5	−409.59	829.9	1.00	0.14
	$39.660 - 0.0303\ ED_{cp}^{**} + 0.0348\ ED_{wd}^{**} - 0.191\ P_{cp}^{**} - 0.153\ P_{wd}^{*} - 17.170\ H^{**}$	7	−404.43	824.1	0.00	0.63
3	$26.770 - 0.0373\ ED_{cp}^{**} - 0.124\ P_{cp}^{*} - 8.235\ H^{*}$	5	−408.03	826.7	0.00	0.27
	$39.710 - 0.0397\ ED_{cp}^{**} + 0.0140\ ED_{wd} - 0.195\ P_{cp}^{**} - 15.600\ H^{**}$	6	−407.00	826.9	0.21	0.24
	$31.400 - 0.0386\ ED_{cp}^{**} - 0.150\ P_{cp}^{**} + 0.0440\ P_{wd} - 10.760\ H^{**}$	6	−407.72	828.4	1.66	0.12
	$43.540 - 0.0393\ ED_{cp}^{**} + 0.0298\ ED_{wd} - 0.216\ P_{cp}^{**} - 0.103\ P_{wd} - 18.070\ H^{**}$	7	−406.56	828.4	1.67	0.12

Bold type indicates the best overall model. Competing models with a $\Delta AIC < 2$ are included

P_{wd} percentage of woody habitats, P_{cp} percentage of crop, ED_{wd} edge density of woody habitats, ED_{cp} edge density of crop, H landscape diversity, *df* are the degrees freedom, *logLik* are the log-likelihood values, *delta* are the AICc differences (ΔAIC), *weight* are the Akaike weights

Significance of variables is indicated as follows: * $P < 0.05$; ** $P < 0.01$

ecological functions of landscape diversity. Wheat fields serve as the major reproduction habitat of ladybeetles. Moreover, increased diversity of crop and non-crop habitats will provide more ladybeetles to wheat fields. Similarly, Gardiner et al. (2009a) found that landscape diversity benefited ladybeetle abundance based on the increase of non-crop habitats (forests and grasslands). During wheat harvest, spillover of ladybeetles to marginal woody habitats would not benefit from an increase in diversity, because ladybeetles may move to other habitats in a diversified landscape. Therefore, a measure of diversity per se may not be sufficient to characterize functional diversity. In the North China Plain, land cover pattern is characterized by dense villages and cropland. Fields are often small, and fields with different land uses may be mixed at fine spatial scales. Although some sites were quite close together (<0.5 km) leading to overlapping circles at larger spatial scales, most of the sampling sites varied markedly in landscape composition. Our results could still reflect the actual situation of landscape effects.

Previous studies have shown that the presence of woody borders near cropland is particularly important in determining the local abundance of some ladybeetle species (Elliott et al. 2002). The majority of studies about landscape effects on natural enemies have been performed within fields, and few have focused on the spillover of natural enemies. Our results show the negative correlation between ladybeetle abundance in spillover and the ED of crop habitats, which suggests that a landscape with fragmented cropland patch tends to have lower numbers of ladybeetles in spillover. That may be explained by limited resources provided by fragmented crop habitats. The number of aphids caught by field margin traps which reflected the dynamics of cereal aphids in wheat fields was negatively correlated with ladybeetles in spillover. It should be considered that ladybeetle abundance in spillover increased as cereal aphid population declined, because the poplar trees did not harbor any aphids during that time.

For ladybeetles within field, it is unexpected that their abundance was not predicted by aphid abundance. The wheat-cropping system is prone to aphid outbreaks, which in turn provides potentially high quality resources to ladybeetle populations. However, the land use intensity, such as level of input (especially insecticides) could cause pressure on pests and natural enemies. Zhou et al. (2014) showed that insecticide

Table 4 Model selection statistics for ladybeetle abundance in margin woody habitats during wheat growing and harvest period in 2013

Scale	Model	df	logLik	AICc	Delta	Weight
0.5	$7.381 - 0.0485\ \mathrm{Aphid}^{**} - 0.016\ \mathrm{ED}_{cp}^{**} + 0.0259\ \mathrm{ED}_{wd}^{**} - 0.0613\ \mathrm{P}_{wd} - 3.766\ \mathrm{H}^{**}$	7	−412.81	840.2	0.00	0.22
	$0.811 - 0.0494\ \mathrm{Aphid}^{**} - 0.0162\ \mathrm{ED}_{cp}^{**} + 0.0172\ \mathrm{ED}_{wd}^{**} + 0.0457\ \mathrm{P}_{cp}^{**} - 0.05\ \mathrm{P}_{wd}$	7	−413.00	840.6	0.38	0.18
	$0.235 - 0.0487\ \mathrm{Aphid}^{**} - 0.0149\ \mathrm{ED}_{cp}^{**} + 0.0111\ \mathrm{ED}_{wd}^{**} + 0.0541\ \mathrm{P}_{cp}^{**}$	6	−414.24	840.9	0.71	0.15
	$-8.096 - 0.0497\ \mathrm{Aphid}^{**} - 0.0156\ \mathrm{ED}_{cp}^{**} + 0.112\ \mathrm{P}_{cp}^{**} + 4.948\ \mathrm{H}^{*}$	6	−414.66	841.8	1.57	0.10
	$7.999 - 0.0477\ \mathrm{Aphid}^{**} - 0.0143\ \mathrm{ED}_{cp}^{**} + 0.0199\ \mathrm{ED}_{wd}^{**} - 4.471\ \mathrm{H}^{**}$	6	−414.71	841.9	1.67	0.10
1.0	$12.770 - 0.0426\ \mathrm{Aphid}^{**} - 0.0192\ \mathrm{ED}_{cp}^{*} + 0.0203\ \mathrm{ED}_{wd}^{**} - 7.307\ \mathrm{H}^{**}$	6	−414.25	840.9	0	0.34
	$17.81 - 0.0421\ \mathrm{Aphid}^{**} - 0.02\ \mathrm{ED}_{cp}^{*} + 0.0224\ \mathrm{ED}_{wd}^{**} - 0.0362\ \mathrm{P}_{cp} - 9.882\ \mathrm{H}^{**}$	7	−413.99	842.6	1.62	0.15
1.5	$-1.774 - 0.0491\ \mathrm{Aphid}^{**} - 0.0182\ \mathrm{ED}_{cp}^{*} + 0.0201\ \mathrm{ED}_{wd}^{**} + 0.0865\ \mathrm{P}_{cp}^{**}$	6	−412.97	838.4	0	0.19
	$-3.682 - 0.0471\ \mathrm{Aphid}^{**} + 0.0799\ \mathrm{P}_{cp}^{**} + 0.187\ \mathrm{P}_{wd}^{**}$	5	−414.27	838.8	0.47	0.15
	$12.220 - 0.0461\ \mathrm{Aphid}^{**} - 0.0271\ \mathrm{ED}_{cp}^{**} + 0.0290\ \mathrm{ED}_{wd}^{**} - 6.702\ \mathrm{H}^{**}$	6	−413.32	839.1	0.70	0.13
	$-1.485 - 0.0512\ \mathrm{Aphid}^{**} - 0.0120\ \mathrm{ED}_{cp} + 0.0743\ \mathrm{P}_{cp}^{**} + 0.163\ \mathrm{P}_{wd}^{**}$	6	−413.49	839.4	1.03	0.11
	$3.479 - 0.0476\ \mathrm{Aphid}^{**} - 0.0214\ \mathrm{ED}_{cp}^{*} + 0.0237\ \mathrm{ED}_{wd}^{**} + 0.0562\ \mathrm{P}_{cp} - 2.620\ \mathrm{H}$	7	−412.79	840.2	1.79	0.08
2	$-4.972 - 0.0536\ \mathrm{Aphid}^{**} + 0.0879\ \mathrm{P}_{cp}^{**} + 0.270\ \mathrm{P}_{wd}^{**}$	5	−411.88	834.1	0	0.16
	$8.953 - 0.0531\ \mathrm{Aphid}^{**} + 0.362\ \mathrm{P}_{wd}^{**} - 7.369\ \mathrm{H}^{**}$	5	−412.03	834.4	0.30	0.14
	$10.500 - 0.0508\ \mathrm{Aphid}^{**} + 0.0198\ \mathrm{ED}_{wd} + 0.234\ \mathrm{P}_{wd}^{**} - 9.032\ \mathrm{H}^{**}$	6	−411.45	835.3	1.27	0.08
	$-7.087 - 0.0481\ \mathrm{Aphid}^{**} + 0.0321\ \mathrm{ED}_{wd}^{**} + 0.117\ \mathrm{P}_{cp}^{**}$	5	−412.6	835.5	1.47	0.08
	$1.444 - 0.0535\ \mathrm{Aphid}^{**} + 0.0506\ \mathrm{P}_{cp} + 0.314\ \mathrm{P}_{wd}^{**} - 3.506\ \mathrm{H}$	6	−411.62	835.7	1.61	0.07
	$-5.809 - 0.0521\ \mathrm{Aphid}^{**} + 0.0114\ \mathrm{ED}_{wd} + 0.0976\ \mathrm{P}_{cp}^{**} + 0.184\ \mathrm{P}_{wd}^{*}$	6	−411.63	835.7	1.64	0.07
2.5	$\mathbf{12.340 - 0.0551\ Aphid^{**} + 0.381\ P_{wd}^{**} - 9.707\ H^{**}}$	**5**	**−410.89**	**832.1**	**0**	**0.26**
	$-6.044 - 0.0538\ \mathrm{Aphid}^{**} + 0.112\ \mathrm{P}_{cp}^{**} + 0.274\ \mathrm{P}_{wd}^{**}$	5	−411.58	833.5	1.37	0.13
	$13.720 - 0.0553\ \mathrm{Aphid}^{**} - 0.00674\ \mathrm{ED}_{cp} + 0.375\ \mathrm{P}_{wd}^{**} - 9.939\ \mathrm{H}^{**}$	6	−410.80	834.0	1.95	0.10
3	$15.060 - 0.0506\ \mathrm{Aphid}^{**} + 0.0644\ \mathrm{ED}_{wd}^{**} - 13.840\ \mathrm{H}^{**}$	5	−412.80	835.9	0	0.18
	$-9.051 - 0.0502\ \mathrm{Aphid}^{**} + 0.0398\ \mathrm{ED}_{wd}^{**} + 0.141\ \mathrm{P}_{cp}^{**}$	5	−413.24	836.8	0.89	0.12
	$14.510 - 0.0517\ \mathrm{Aphid}^{**} + 0.0457\ \mathrm{ED}_{wd}^{*} + 0.143\ \mathrm{P}_{wd} - 13.020\ \mathrm{H}^{**}$	6	−412.46	837.3	1.45	0.09
	$-6.623 - 0.0529\ \mathrm{Aphid}^{**} + 0.121\ \mathrm{P}_{cp}^{**} + 0.291\ \mathrm{P}_{wd}^{**}$	5	−413.58	837.5	1.57	0.08

Bold type indicates the best overall model. Competing models with a ΔAIC < 2 are included

P_{wd} percentage of woody habitats, P_{cp} percentage of crop, ED_{wd} edge density of woody habitats, ED_{cp} edge density of crop, *H* landscape diversity, *df* are the degrees freedom, *logLik* are the log-likelihood values, *delta* are the AICc differences (ΔAIC), *weight* are the Akaike weights

Significance of variables is indicated as follows: * $P < 0.05$; ** $P < 0.01$

use in corn fields negatively affected ladybeetle populations in the North China Plain. Although we did not record the insecticide use in each sampling site, we observed that farmers in Yucheng usually spray insecticide twice or more in wheat. Accordingly, the agricultural practices possibly disturbed the effects of aphids on ladybeetle populations.

Scale of landscape effects

Previous studies have found that the spatial scales matter for determining species richness and abundance for many species (Miyashita et al. 2012; Tscharntke et al. 2005). In the present study, we examined the effects of landscape variables on ladybeetle abundance at six spatial scales, with landscape radii varying from 0.5 to 3 km. Landscape features at the spatial scale of 2.5–3 km could best predict the abundance of ladybeetles in spillover, whereas the best prediction model for ladybeetle abundance within field was at a 1.5 km scale. For ladybeetles within fields, landscapes of a similar spatial scale have proved important in predicting ladybeetle abundances. Gardiner et al. (2009a) found that landscape diversity

Table 5 Model selection statistics for ladybeetle abundance within field during wheat growing in 2013

Scale	Model	df	logLik	AICc	Delta	Weight
0.5	$0.024 - 0.027\ P^{*}_{wd} + 1.625\ H^{**}$	4	−411.32	830.9	0.00	0.12
	$-0.0397 - 0.00650\ \text{Aphid} - 0.0298\ P^{*}_{wd} + 1.741\ H^{**}$	5	−411.06	832.6	1.64	0.05
	$0.810 + 0.841\ H^{*}$	3	−413.29	832.8	1.83	0.05
	$0.00126 + 0.00171\ ED_{wd} - 0.0332\ P_{wd} + 1.578\ H^{**}$	5	−411.17	832.8	1.86	0.05
	$0.371 - 0.00158\ ED_{cp} - 0.0287\ P^{*}_{wd} + 1.555\ H^{**}$	5	−411.16	832.8	1.87	0.05
1	$-0.450 + 1.641\ H^{*}$	3	−412.78	831.7	0.00	0.11
	$2.791 - 0.0194\ P_{cp}$	3	−413.30	832.8	1.03	0.06
	$-0.619 - 0.0210\ P_{wd} + 1.893\ H^{*}$	4	−412.24	832.8	1.05	0.06
	$0.0509 - 0.00173\ ED_{cp} + 1.467\ H$	4	−412.71	833.7	1.98	0.04
	$-0.461 - 0.00108\ ED_{wd} + 1.725\ H^{*}$	4	−412.72	833.7	1.99	0.04
1.5	$\mathbf{-1.712 + 2.439\ H^{*}}$	**3**	**−411.96**	**830.1**	**0.00**	**0.13**
	$-2.357 - 0.0275\ P_{wd} + 3.052\ H^{**}$	4	−411.22	830.7	0.63	0.09
	$-2.093 - 0.00335\ ED_{wd} + 2.938\ H^{**}$	4	−411.55	831.4	1.31	0.07
2	$3.189 - 0.00292\ P_{cp}$	3	−413.39	833.0	0.00	0.09
	$-0.975 + 1.934\ H$	3	−413.45	833.1	0.11	0.09
	$-1.860 - 0.00476\ ED_{wd} + 2.879\ H$	4	−412.88	834.1	1.10	0.05
	1.902	2	−415.01	834.1	1.14	0.05
	$-1.844 - 0.0313\ P_{wd} + 2.728\ H$	4	−412.91	834.1	1.15	0.05
	$1.139 - 0.00175\ P_{cp} + 1.031\ H$	4	−413.21	834.7	1.75	0.04
2.5	$3.267 - 0.0312\ P_{cp}$	3	−413.50	833.2	0.00	0.09
	$-1.276 + 2.126\ H$	3	−413.57	833.3	0.15	0.09
	1.902	2	−415.01	834.1	0.93	0.06
	$-2.033 - 0.00508\ ED_{wd} + 3.006\ H$	4	−413.07	834.4	1.26	0.05
	$1.191 - 0.0190\ P_{cp} + 1.033\ H$	4	−413.39	835.1	1.90	0.04
	$-1.642 - 0.0170\ P_{wd} + 2.483\ H$	4	−413.44	835.2	1.99	0.03
3	1.902	2	−415.01	834.1	0.00	0.11
	$2.913 - 0.0227\ P_{cp}$	3	−414.29	834.8	0.65	0.08
	$-0.118 + 1.362\ H$	3	−414.56	835.3	1.20	0.06
	$2.093 - 0.00173\ ED_{wd}$	3	−414.95	836.1	1.97	0.04

Bold type indicates the best overall model. Competing models with a $\Delta AIC < 2$ are included

P_{wd} percentage of woody habitats, P_{cp} percentage of crop, ED_{wd} edge density of woody habitats, ED_{cp} edge density of crop, *H* landscape diversity, *df* are the degrees freedom, *logLik* are the log-likelihood values, *delta* are the AICc differences (ΔAIC), *weight* are the Akaike weights

Significance of variables is indicated as follows: * $P < 0.05$; ** $P < 0.01$

and composition at a spatial scale of 1.5 km surrounding the focal field explained the greatest proportion of ladybeetle abundance. It is possible that a landscape of this size encompasses their ecological neighborhood, containing the diversity of habitats utilized by ladybeetles (Gardiner et al. 2009a). The number of ladybeetles in spillover was correlated with landscape variables at a larger spatial scale, suggesting that the spatial scale does not simply reflect dispersal ability, but that some sink habitats and source habitats would also affect the spatial scale. We illustrate here that the scale at which ladybeetles respond to landscape variables results from the interaction of the dispersal-distance function of the ladybeetle population with the frequency distributions of distances among suitable habitat patches in the landscape (Rusch et al. 2013). When wheat is harvested, woody habitats tend to be most suitable habitats for ladybeetle. Their response scales were therefore different between ladybeetle spillover and within field numbers. Further studies need to consider the possible functions of the different habitat types (Veres et al. 2013).

Modeling studies suggest that spillover or cross-edge movement by predators from source habitats, where they receive resource subsidies, can suppress prey species occurring within adjacent recipient fields (Bianchi and van der Werf 2003, 2004). Our study focuses on the sink function of margin woody habitats during wheat harvest. The variable "fraction of ladybeetles in woody habitats" indicates that ladybeetles stayed mostly in fields during the wheat-growing period. When their food resources decrease, ladybeetles disperse from field to margin shelterbelts as temporary habitats. Conservation of ladybeetle populations could be enhanced by maintaining shelterbelts in the agricultural landscape to serve as refuges. The large area of woody habitats and unfragmented crop patches will benefit ladybeetle populations at the landscape scale.

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Zhaoke Dong This research is part of a post-doctorate work of Zhaoke Dong devoted to the analysis of the effects of shelterbelts on ladybeetle populations at the landscape scales.

Fang Ouyang is studying conservation biological control, especially on habitat management.

Fei Lu is involved in developing field experiments for testing the effect of landscape variables.

Feng Ge is a principle investigator. His studies mainly focus on insect physiological ecology, behavior ecology, population ecology and integrated pest management.