Landscape structure alters the abundance and species composition of early-season aphid populations in wheat fields

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ABSTRACT

Agricultural landscape composition is reported to have effects on the occurrence of natural enemies in fields, but the responses of herbivorous pests to landscape features have rarely been studied. Our previous landscape-level study in northern China found that natural enemies had no significant effects on the population growth of wheat aphids at the colonization stage. Hence, we hypothesised that the initial aphid population in wheat fields may largely depend on immigration events from other habitats. In this study, we investigated the effects of landscape pattern on wheat aphid abundance and species composition at the colonization stage by surveying population densities of different aphid species along a landscape gradient. We found that noncrop habitats such as woodlots, fallow lands and vegetation around dwellings or wetlands in the landscape all had positive correlations with aphid abundance in wheat fields because they provided a source for aphid colonization. More specifically, the proportion of woodlots, fallow lands, dwellings, and other crops increased the abundance of *Rhopalosiphum padi* (L.), and the existence of water and dwellings in an agricultural landscape facilitated the occurrence of *Sitobion avenae* (Fabricius). Likewise, the abundance of *Schizaphis graminum* (Rondani) in wheat fields was found to be significantly promoted by the presence of water. The habitats around water and dwellings usually provide the overwintering sites for the aphids. Furthermore, wheat production acreage had a significant negative correlation with the abundance of *R. padi*, *S. avenae* and *S. graminum*. Landscape characteristics had a significant effect on the species composition of wheat aphids. Our study suggests that noncrop habitats in a landscape enhance aphid occurrence at the population colonization stage, and differences in overwintering host plants among aphid species may be responsible for the differing responses of the abundance of different aphids to landscape variables, which greatly altered aphid population composition across different landscapes. These results highlight the need for taking landscape effects on the pest itself into consideration when designing landscape-level pest management strategies.

1. Introduction

The composition of agricultural landscapes is known to have significant effects on the population dynamics and community structure of arthropods in crop fields (Tscharntke et al., 2005; Bianchi et al., 2006; Fraterrigo et al., 2009; Rusch et al., 2010; Chaplin-Kramer et al., 2011). Most arthropods, including both pests and natural enemies, are unable to complete their life cycles in cereal fields alone and require resources from surrounding habitats (Landis et al., 2000; Veres et al., 2013). In agricultural landscapes, natural or seminatural habitats (woodlots, fallow lands, and vegetation around dwellings) facilitate pest and natural enemy populations by providing alternative or supplemental food

resources, shelter, or overwintering refuges (Landis et al., 2000; Alignier et al., 2014). As noncrop habitats commonly serve as sources of arthropods colonizing crop fields (Schellhorn et al., 2014), the population of arthropods in fields is mediated by both direct (landscape effects on arthropods themselves) and indirect effects (landscape effects on the interaction between arthropods) of the landscape pattern (Chaplin-Kramer et al., 2011; Maisonhaute et al., 2017).

For insects in an agricultural landscape ecosystem, different habitats in the landscape mosaic serve different functions (Schellhorn et al., 2015; Janković et al., 2017). Habitats with high-quality host plants enhance the populations of herbivorous insects by providing preferred conditions that can facilitate insect population growth. Habitats with

low-quality host plants usually have the opposite effect, depressing the densities of herbivorous pests (Kennedy and Storer, 2000; Chaplin-Kramer, 2010; Tsafack et al., 2013, 2015). Habitats dominated by nonhost plants may still influence pests indirectly by promoting natural enemies (Gardiner et al., 2009a) or directly via physical pathways (such as windbreaks barring the immigration of aphids into crop fields) (Marrou et al., 1979), or by creating a particular microclimate (Dyer and Landis, 1997). Landscape-level studies provide a method to detect habitat functionality for insects at a particular time in the season, which is critical for the successful use of area-wide pest management through landscape manipulation (Schellhorn et al., 2014, 2015).

A large body of theoretical and empirical evidence suggests that natural enemy abundance in fields is enhanced by natural habitats in agricultural landscapes and that such habitats favorable to natural enemies improve control of some pests (Gardiner et al., 2009a; Chaplin-Kramer et al., 2013; Liu et al., 2016). However, natural habitats (such as grass margins) can constitute a source of pests, increasing pest density and subsequently affecting pest distribution and abundance in the neighboring crop fields (Ramsden et al., 2016). In many studies, larger populations of natural enemies in the field did not lower pest density because the pest immigration offset the biological control effects of those natural enemies (Roschewitz et al., 2005; Thies et al., 2005; Chisholm et al., 2014). Thies et al. (2005) found that while complex landscapes promote higher parasitism rates, this effect can be offset by greater aphid colonization rates, resulting in no difference in aphid densities along a landscape gradient.

Investigating the responses of pest populations together with those of natural enemy populations to landscape factors gives a complete and more accurate measure of the ecosystem services provided by a landscape (Chaplin-Kramer, 2010; Chaplin-Kramer et al., 2013; Chisholm et al., 2014). Unfortunately, fewer studies have examined pest responses in a landscape context compared with studies on natural enemies, especially pertaining to the pest population at the initial colonization stage (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Moreover, these studies provided divergent conclusions (Veres et al., 2013). For example, Alignier et al. (2014) found that seminatural habitats in an agricultural landscape appeared to have no temporal pattern of effects on aphid abundance, as noncrop habitats affected aphids directly and indirectly, both negatively and positively. These results and the scarcity of studies on the subject suggest a need to pay more attention to the effects of different habitats on pests at the landscape scale to promote landscape-level pest control.

Aphids (Hemiptera: Aphididae) are important agricultural pests, causing economic damage to cereal crops. In wheat fields in northern China, the wheat aphid community is composed of four species: *Rhopalosiphum padi* (L.), *Sitobion avenae* (Fabricius), *Schizaphis graminum* (Rondani), and *Metopolophium dirhodum* (Walker). The first three species are the most important cereal pests, reducing yield and quality in the study region (Lu and Gao, 2016). In this study, we investigated the effects of landscape composition at four different spatial scales (0.5, 1.0, 1.5 and 2.0 km), on aphid population density at the early season, crop-colonization stage. Here, we chose early spring as the time to conduct our study because it is the main period for aphid colonization of wheat fields from aphid overwintering habitats. Our previous study showed that a relatively low density of natural enemies at the time of colonization was considered to have no significant effect on aphid populations (Yang et al., 2018), and hence variation in wheat aphid populations among different wheat fields may be due to features of the surrounding landscape. We surveyed aphid complex populations in wheat fields in 2015 and 2016 to test the following hypotheses: (1) The abundance of aphids will be higher in wheat fields within a landscape dominated by noncrop habitats due to immigration from surrounding natural habitats. (2) The abundance of aphids will be lower in wheat fields within a landscape dominated by wheat production due to a dilution effect. (3) Aphid species will respond to landscape features according to their biological property of overwintering. (4) Aphid species

assemblages will vary according to landscape features and the biological properties of individual species.

2. Materials and methods

2.1. Study area

The survey was conducted in 48 winter wheat fields (29 fields in 2015 and 19 in 2016) in Hebei Province, Beijing and Tianjin Cites, northern China (Fig. S1), 24 sites (17 sites in 2015 and 7 in 2016) of which had been examined in a previous study (Yang et al., 2018). The study region is one of the major winter wheat producing areas in China, with a temperate semihumid monsoon climate, and a landscape mosaic consisting mainly of crop lands, fallow lands, shelterbelts and dwellings (and associated plants) during the spring-summer season. The study sites were selected along a gradient of landscape composition ranging from simple landscapes with a high proportion of crop fields to complex landscapes dominated by noncrop habitats (Table S1). Within a given year, the minimum distance between any two sites was more than 4 km. The size of sampled wheat fields averaged 11.33 ha (range: 0.51–37.00 ha), and none of the fields were treated with insecticides before the survey.

2.2. Aphid sampling

Aphid densities were sampled twice each year, from April 16 to 29 in 2015 and from April 24 to May 5 in 2016, at approximately 10-day intervals during the wheat elongation stage. At each site, three plots (20×30 m^2 each with an interval of 10 m between two neighboring plots) were randomly selected, and aphid population abundances were surveyed by visual observation at five randomly selected points within each plot; 10 tillers were surveyed for each point. Each selected tiller was at least 10 m from any field edge. The abundance of aphids was calculated as individuals per 100 tillers, and data collected from these two surveys were pooled together.

2.3. Landscape investigation and analysis

Landscape composition was measured outward from the center of each wheat field at four spatial scales (0.5, 1.0, 1.5 and 2.0 km), as landscape features at these scales usually have effects on wheat aphid population abundance (Thies et al., 2005; Alignier et al., 2014; Zhao et al., 2014; Chabert and Sarthou, 2017; Janković et al., 2017). The geographical coordinates of the center of each wheat field were collected using a handheld GIS unit (Model MG758, Beijing UniStrong Science & Technology Co., Ltd., China). We first obtained satellite imagery for the surrounding areas out to a radius of 2.0 km for each site from Google Earth maps using these coordinates. Then, we printed imagery maps and marked the land cover types on the maps by ground verification to eliminate inaccuracies caused by land use changes between the image date and study period (Liu et al., 2016). After that, we digitized the habitat types surrounding each study site and calculated the proportion of habitats in each radius buffer using ArcGIS 10.2 software (ESRI, 2013).

For each spatial scale, we measured the percentage of total area covered by each of six cover types: wheat, fallow, water, other crops (i.e., vegetables, greenhouse, fruit trees, pea, and maize), dwellings (i.e., roads and dwellings), and woodlots (i.e., poplar trees and reforested areas) (Table S1). The landscape surrounding sampled fields varied greatly among the 48 study sites and across all spatial scales, with wheat accounting for 1.62–87.96% and the percentage of woodlots ranging from 1.01 to 54.62% (Table S1). A Spearman correlation test was used to check for correlations among landscape variables (Table S2), and as wheat displayed strong correlations ($> |0.5|$) with the other variables at all spatial scales, we excluded the proportion of wheat in further analysis. The variance inflation factor (VIF) values for

the other five predictors were calculated at each scale and were found to be below 1.5 (Table S3), indicating that covariation between predictors was not a problem (Dormann et al., 2013).

2.4. Statistical analysis

To test the first hypothesis and investigate the effect of landscape composition on the population density of wheat aphids, linear mixed models (LMMs) were performed. We used an information-theory approach to determine the relationships between landscape variables at each scale and the abundance of each aphid species (*R. padi, S. avenae,* and *S. graminum*) due to their different overwintering biology. We did not analyze the occurrence of the fourth aphid species, *M. dirhodum,* because of its low abundance. The abundances of *R. padi, S. avenae,* and *S. graminum* were $\log_{10}(x+1)$ transformed before model fitting. In all models, the landscape variables (dwellings, fallow, other crops, woodlots, and water) were treated as fixed effects and scale centered to facilitate model convergence. Year was included as a random factor (Zuur et al., 2009). Explanatory variables in linear mixed models were considered in an additive way only, as interactions between explanatory variables were not taken into consideration in our hypotheses. To account for uncertainty in the model selection process and obtain robust parameter estimates, model averaging was performed (Burnham and Anderson, 2002). The 32 alternative candidate models were the linear combinations of explanatory variables (Table S4), which were compared and ranked using the bias-corrected Akaike's information criterion (AICc) corrected for a small sample size (Burnham and Anderson, 2002). To avoid redundant models and spurious results, we used the top 2AICc value to define the top model set for model averaging (i.e., models with a ΔAICc less than 2 were used in model averaging), and derived the coefficients for the best model from the top model set. When ΔAICc > 2, the most parsimonious model was treated as the best model (Markó et al., 2017). We also standardized the input variables using Gelman's approach to divide each numeric variable by two times its standard deviation, which was essential for interpreting parameter estimates (Gelman, 2008; Grueber et al., 2011). The model-averaging process gave the relative importance of explanatory variables based on the top model set to reveal the relationships between the response variable and explanatory factors (Burnham and Anderson, 2004). R^2 describes the amount of variance explained and provides an absolute value for the goodness-of-fit of a model; in this manuscript, we present the marginal and conditional R^2 values for the overall best model and all competing models (ΔAICc < 2). Marginal R^2 values indicate the amount of variation explained by fixed factors only, while conditional R^2 values represent the variance explained by both fixed and random factors (Nakagawa and Schielzeth, 2013).

Additionally, to test the second hypothesis and reveal relationships between wheat production and aphid population density more clearly, we used the proportion of wheat in the landscape as the only fixed factor to explain the variation in response variables, keeping year as a random factor.

Models were systematically assessed by examining model dispersion as well as the normality and homoscedasticity of residuals. We also conducted Moran's test with the residuals of all models to test for spatial autocorrelation, and we found no evidence of autocorrelation.

For the verification of the fourth hypothesis, redundancy analysis (RDA) was used to analyze relationships between aphid species assemblages and landscape variables, with six landscape variables as environmental variables and the averaged aphid population density as the dependent variable. We eliminated variables that did not explain any significant variation in aphid species assemblages by a Monte Carlo permutation test (with 999 permutations). More specifically, at the 0.5 km scale, the variables Other crops and Fallow were eliminated and only Fallow was eliminated at the other three scales. Then, we conducted RDA on the significant variables to investigate the effects of landscape characteristics on species assemblages.

Statistical analyses were carried out using the "lme4" package for mixed models (Bates et al., 2015), "arm" package for model standardization (Gelman and Su, 2016), "MuMIn" package for model averaging (Bartoń, 2017), "piecewiseSEM" package for R^2 calculation (Lefcheck, 2015), and "vegan" package for redundancy analysis (Oksanen et al., 2018), all in R 3.4.2 (R Core Team, 2017).

3. Results

3.1. Aphid species composition

The average population abundance of aphids per 100 tillers was 289.1 ± 38.7 (mean ± SE) in 2015 and 130.4 ± 21.4 in 2016. The composition of aphids in 2015 was 63.0% *R. padi*, 33.9% *S. avenae*, 3.1% *S. graminum*, and no *M. dirhodum*. In 2016, the species composition was 5.9% *R. padi*, 82.0% *S. avenae*, 10.2% *S. graminum*, and 1.9% *M. dirhodum*. The percentages of the two most common species changed greatly between the two years; *R. padi* was the dominant species in 2015, while *S. avenae* was dominant in 2016.

3.2. Landscape effects on total aphid abundance

For total aphid abundance in 2015 and 2016, based on the null-hypothesis models with the lowest AICc values at the smaller landscape scales (0.5 and 1.0 km), the average model results indicated that the proportions of dwellings, fallow land, water areas, woodlots, and other crops are positively correlated with aphid abundance (Tables 1 & S5). At larger scales, i.e., 1.5 and 2.0 km, the variables fallow, woodlots and water are positively correlated with the abundance of aphids. The proportions of woodlots and water areas are the most important variables, as these showed the highest averaged coefficients and relative importance values (Table 1). Our results suggest that the 2.0 km scale is the best scale at which to observe the effect of landscape variables on aphid abundance, as competing models with this scale had the lowest AICc values (Table S5). We observed that fixed effects in the best model explained 28% of the variance in the distribution of aphid abundance in the landscape at the scale of 2.0 km (Table S5). Additionally, total aphid abundance was significantly negatively correlated with the area planted with wheat across the four scales (Table 2).

Table 1
Summary of the best model derived from the model-averaging procedure to assess landscape variable effects on aphid population abundance in 2015 and 2016. Only values for landscape variables included in the top model set determined by model averaging are shown. The effect sizes of the estimates have been standardized. Relative importance is the sum of Akaike's weight associated with each variable in models in the top model set. Significant differences were determined as $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$.

Scales (km)	Variable	Estimate	z value	Pr(> |z|)	Relative importance
0.5	Intercept	2.19	12.72	< 0.001***	
	Dwellings	0.18	1.98	0.048*	0.25
	Fallow	0.22	2.43	0.015*	0.35
	Water	0.23	2.45	0.015*	0.56
1.0	Intercept	2.19	13.58	< 0.001***	
	Dwellings	0.20	2.24	0.025*	0.29
	Fallow	0.21	2.52	0.012*	0.24
	Other crops	0.22	2.39	0.017*	0.18
	Woodlots	0.22	2.43	0.015*	0.44
	Water	0.25	2.65	0.008**	0.66
1.5	Intercept	2.19	13.57	< 0.001***	
	Fallow	0.20	2.59	0.010**	0.59
	Woodlots	0.28	3.37	0.001***	1.00
	Water	0.32	3.86	< 0.001***	1.00
2.0	Intercept	2.19	12.45	< 0.001***	
	Fallow	0.20	2.70	0.007***	0.64
	Woodlots	0.30	3.90	< 0.001***	1.00
	Water	0.33	4.23	< 0.001***	1.00

Table 2
Results of mixed-effects models to assess the effect of wheat proportion at each scale on the abundance of aphids. Wheat proportion at each scale was treated as the only fixed factor. Significance is presented as $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$.

Aphid species	Scales (km)	Estimate	Pr(> |z|)	Marginal R^2	Conditional R^2
Total population	0.5	−0.16	< 0.001***	0.20	0.41
	1.0	−0.17	< 0.001***	0.25	0.40
	1.5	−0.17	< 0.001***	0.24	0.40
	2.0	−0.17	< 0.001***	0.23	0.43
Rhopalosiphum padi	0.5	−0.28	< 0.001***	0.09	0.83
	1.0	−0.30	< 0.001***	0.11	0.83
	1.5	−0.29	< 0.001***	0.10	0.83
	2.0	−0.29	< 0.001***	0.09	0.84
Sitobion avenae	0.5	−0.09	0.030*	0.09	0.09
	1.0	−0.08	0.054	0.07	0.07
	1.5	−0.09	0.032*	0.09	0.09
	2.0	−0.10	0.016*	0.11	0.11
Schizaphis graminum	0.5	−0.17	0.004**	0.12	0.35
	1.0	−0.14	0.026*	0.08	0.31
	1.5	−0.14	0.025*	0.08	0.31
	2.0	−0.16	0.008**	0.11	0.33

3.3. Landscape effects on the population abundance of R. padi

Multimodel inference showed that the percentage of woodlots in an agricultural landscape had the strongest positive effect on *R. padi* population abundance as characterized by the highest averaged coefficients and the highest relative importance values whatever the spatial scale considered (Table 3). The area of dwellings and other crops within a 0.5 and 1.0 km radius also had significant positive effects on aphid abundance, while the area of fallow land at the 1.5, and 2.0 km scales showed a positive correlation with aphid abundance (Table 3). The percentage of variance explained by fixed factors in the top models at each spatial scale was between 3% and 6%, while the variance explained by both fixed and random factors (conditional R^2) ranged from 81% to 83% (Table S6). The 2.0 km scale is the best scale at which to assess the effect of landscape features on *R. padi* abundance (Table S6). The proportion of total area planted with wheat at each spatial scale was found to be significantly negatively correlated with *R. padi* abundance (Table 2).

3.4. Landscape effects on the population abundance of S. avenae

The results of model averaging showed that water areas had the strongest positive effect on *S. avenae* abundance, with the highest averaged coefficient and relative importance values at the four spatial scales. Dwellings also had a significant positive effect on aphid abundance at all scales. Fallow land showed a positive effect only at the 0.5 and 1.0 km spatial scales (Table 4). Across the four spatial scales, the percentage of variance explained by fixed factors in the top-ranked models varied between 0.13 and 0.39 (Table S7). Our results indicate that the 2.0 km scale is the best scale at which to evaluate the effect of landscape variables on the abundance of *S. avenae* (Table S7). The abundance of *S. avenae* was significantly negatively correlated with area planted with wheat at each spatial scale (Table 2).

3.5. Landscape effects on the population abundance of S. graminum

Water areas was the most important variable for *S. graminum* abundance over both years in the best models, with a significant positive correlation with *S. graminum* population abundance at the 1.0, 1.5 and 2.0 km spatial scales. The area of dwellings had a significant, positive correlation with the abundance of this aphid only at 0.5 km

Table 3
Summary of the best model to assess landscape variable effects on *Rhopalosiphum padi* population density. Only values for landscape variables included in the top model set determined by model averaging are shown. The effect sizes of the estimates have been standardized. Relative importance is the sum of Akaike's weight associated with each variable in models in the top model set. Significant differences are presented as $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$.

Scales (km)	Variable	Estimate	z value	Pr(> |z|)	Relative importance
0.5	Intercept	1.41	2.23	0.026*	
	Dwellings	0.25	1.96	0.050*	0.13
	Other crops	0.28	2.09	0.036*	0.53
	Woodlots	0.32	2.39	0.017*	0.69
1.0	Intercept	1.42	2.43	0.015*	
	Dwellings	0.24	1.99	0.046*	0.20
	Other crops	0.26	2.11	0.035**	0.52
	Woodlots	0.42	3.16	0.002**	1.00
1.5	Intercept	1.42	2.35	0.019*	
	Fallow	0.22	1.85	0.064	0.33
	Woodlots	0.47	3.75	< 0.001***	1.00
2.0	Intercept	1.42	2.26	0.024*	
	Fallow	0.23	1.99	0.047*	0.31
	Water	0.21	1.70	0.089	0.19
	Woodlots	0.49	4.07	< 0.001***	1.00

Table 4
Summary of the best model to assess landscape variable effects on *Sitobion avenae* population density. Only values for landscape variables included in the top model set determined by model averaging are shown. The effect sizes of the estimates have been standardized. Relative importance is the sum of Akaike's weight associated with each variable in models in the top model set. Significant differences are presented as $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$.

Scales (km)	Variable	Estimate	z value	Pr(> |z|)	Relative importance
0.5	Intercept	1.92	47.69	< 0.001***	
	Dwellings	0.18	2.27	0.023*	0.35
	Fallow	0.19	2.35	0.019*	0.40
	Water	0.24	2.74	0.006**	0.83
1.0	Intercept	1.92	47.13	< 0.001	
	Dwellings	0.17	2.20	0.028*	0.16
	Fallow	0.19	2.34	0.020*	0.42
	Water	0.24	2.77	0.006**	0.77
1.5	Intercept	1.92	51.54	< 0.001***	
	Dwellings	0.20	2.71	0.007**	0.74
	Other crops	0.20	2.65	0.008**	0.46
	Water	0.30	3.61	< 0.001***	1.00
2.0	Intercept	1.92	50.60	< 0.001***	
	Dwellings	0.16	2.11	0.035*	0.34
	Water	0.28	3.67	< 0.001***	1.00

Table 5
Summary of the best model to assess landscape variable effects on *Schizaphis graminum* population density. Only values for landscape variables included in the top model set determined by model averaging are shown. The effect sizes of the estimates have been standardized. Relative importance is the sum of Akaike's weight associated with each variable in models in the top model set. Significant differences are presented as $^*p < 0.05$; $^{**}p < 0.01$; and $^{***}p < 0.001$.

Scales (km)	Variable	Estimate	z value	Pr(> |z|)	Relative importance
0.5	Intercept	0.91	5.97	< 0.001***	
	Dwelling	0.32	2.69	0.007**	1.00
	Water	0.24	2.08	0.038*	0.43
1.0	Intercept	0.90	8.33	< 0.001***	
	Fallow	0.28	2.30	0.021*	0.44
	Water	0.34	2.63	0.009**	0.78
1.5	Intercept	0.90	8.20	< 0.001***	
	Fallow	0.22	1.90	0.058	0.33
	Other crops	0.27	2.18	0.029*	0.48
	Water	0.42	3.28	0.001***	1.00
2.0	Intercept	0.90	9.67	< 0.001***	
	Fallow	0.21	1.83	0.067	0.31
	Water	0.37	3.14	0.002**	1.00

(Table 5). The percentage of variance explained by fixed factors in the best models varied between 0.12 and 0.23, while that of both fixed and random factors ranged from 0.22 to 0.33 (Table S8). We found that the abundance of *S. graminum* was better predicted by landscape variables at larger scales (1.5 and 2.0 km), the models of which had lower AICc scores than did those for smaller ones (0.5 and 1.0 km). The abundance of this aphid species was also significantly negatively related to the area planted with wheat at four spatial scales (Table 2).

3.6. Landscape effects on aphid species assemblages

The RDA model explained a low but significant amount of variance in aphid species composition, i.e., 28.7, 38.4, 37.7 and 33.7% at 0.5, 1.0, 1.5, and 2.0 km, respectively (0.5 km: F = 4.33, P = 0.001; 1.0 km: F = 5.23, P = 0.001; 1.5 km: F = 5.07, P = 0.001; 2.0 km: F =

4.26, P = 0.001). Among the four spatial scales, a distinct distribution of species was found based on the landscape variables, with *R. padi* clearly associated with woodlots, other crops and dwellings, and *S. avenae* and *S. graminum* associated with water areas (Fig.1).

4. Discussion

In this two-year study, we investigated the effects of landscape composition on wheat aphid population abundance and assessed the responses of the three most common aphid species, *R. padi*, *S. avenae*, and *S. graminum*, to landscape variables at different spatial scales during the field-colonization period of aphids. While great variation in aphid population abundance and species composition was found between the two years, the presence of noncrop habitats (woodlots, fallow land, water areas, and vegetation associated with human dwellings) increased aphid abundance in wheat fields at the field-colonization stage of aphids. In this study system, there was a relatively low abundance of natural enemies in wheat fields. Yang et al. (2018) showed that the abundance of natural enemies did not impact aphid abundance at the field-colonization stage, and the variation in aphid abundance in wheat fields was, therefore, largely determined by aphid colonization events. Aphid population abundance was positively correlated with noncrop habitats in the agricultural landscape and this relationship could be ascribed to aphid overwintering ecology, as cereal aphids usually lay eggs for the overwintering generation on a variety of grasses or perennial woody plants (Wratten, 1975; Hand, 1989; Leather, 1993; Pettersson et al., 1994; Qiao et al., 2009), which can be found in or around various noncrop habitats. These habitats provide shelter and host plants on which aphids can overwinter. These overwintered aphids can then serve as the main source of migrants that move back to wheat fields in early spring (Dean, 1974; Dixon, 1977). This finding is in accordance with a previous study that showed that a high availability of overwintering plant hosts for aphids in complex landscapes supported much larger aphid populations and reduced the efficacy of aphid biological control (Roschewitz et al., 2005).

Noncrop habitats (such as woodlots and dwellings) enhanced the abundance of *R. padi*, which may be due to the overwintering preferences of this species, which usually lays eggs on woody plants for
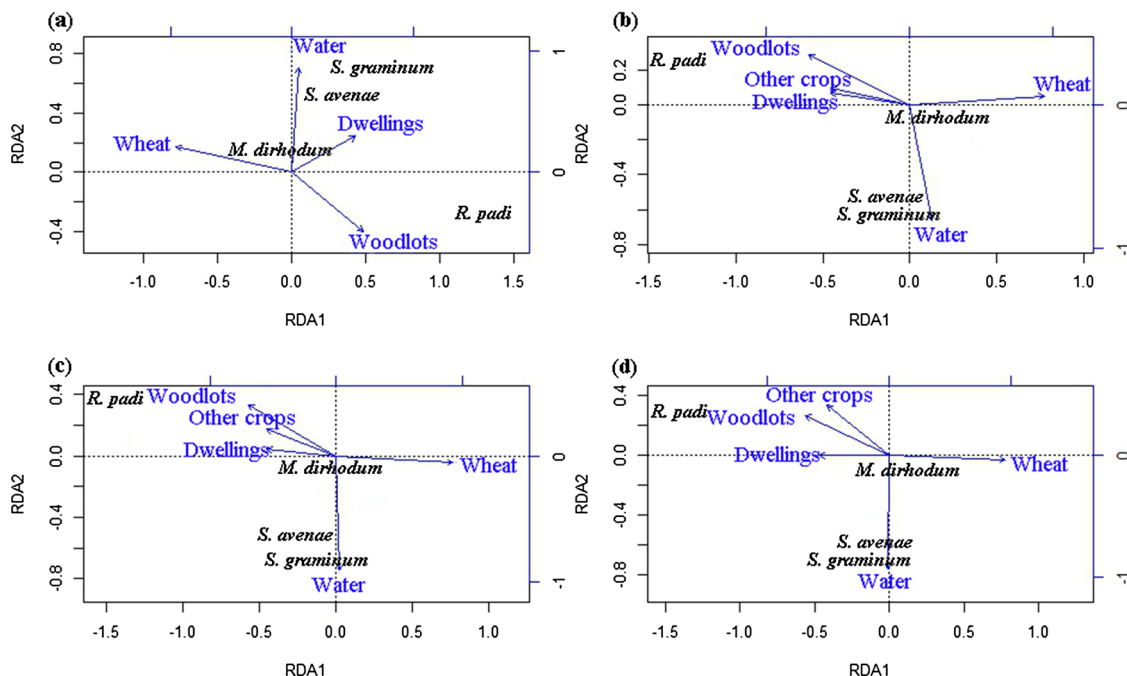

Fig. 1. Ordination diagrams from RDA of aphid species assemblages, constrained by significant landscape variables at (a) 0.5, (b) 1.0, (c) 1.5 and (d) 2.0 km spatial scales.

overwintering. In agricultural landscape ecosystems, the life cycles of aphids can be classified as autoecious, heteroecious, or anholocyclic, and *R. padi* is typically heteroecious in that it migrates between primary and secondary hosts (Dean, 1974; Leather, 1993; Vialatte et al., 2007). In northern China, *Prunus padus* (L.), *Prunus persica* (L.), *Prunus salicina* (Lindl.), *Amygdalus triloba* (Lindl.) Ricker and some other woody plants are the primary hosts of *R. padi* (Chen et al., 2004; Qiao et al., 2009), and these plants are easily found in woodlots, orchards and around dwellings (Flora of Hebei Editorial Committee, 1991), providing a source of migrant aphids for the following spring. Wheat acts as a secondary host for *R. padi*, and a large area of wheat will tend to have a negative effect on aphid abundance by diluting the population of spring migrants over a larger area (Grez et al., 2004; Zhao et al., 2013). Furthermore, fallow land facilitated the abundance of this aphid, possibly because *R. padi* can successfully overwinter in an anholocyclic form on some wild grasses in or around such fallow land when winter temperatures are sufficiently mild (Hand, 1989).

Sitobion avenae (Fabricius) and *S. graminum* population abundance responded similarly to landscape variables, with both being facilitated by water areas, land around human dwellings, and fallow habitats in the agricultural landscape. The life cycles of *S. avenae* and *S. graminum* are autoecious, and the species can exist on their host plants all year round, usually laying eggs on hosts to overwinter while anholocyclic overwintering occurs simultaneously (Dean, 1974; Leather, 1993; Vialatte et al., 2007). In agricultural ecosystems, these two aphids occur on cultivated plants and wild grasses, hibernating on perennial grasses (such as *Poa annua* L., *Phragmites australis* (Cav.) Trin. ex Steud. and *Alopecurus aequalis* Sobol.) and wheat (Hand, 1989; Leather, 1993; Vialatte et al., 2007; Qiao et al., 2009); the former are common plant species around waterbodies and can be seen around dwellings and in fallow land in northern China (Flora of Hebei Editorial Committee, 1991). For these two aphid species, the dilution effect provided by wheat fields was not as noticeable as that for *R. padi*, possibly because wheat may be an overwintering host for them, as suggested by Vialatte et al. (2007).

The species composition of insects (such as aphids) is generally driven by species-specific responses to biotic and abiotic factors, which from the perspective of landscapes are usually driven by the differences in habitat use or dispersal ability of the individual herbivore species (Bianchi et al., 2006; Gardiner et al., 2009b; Yasuda et al., 2011; Jonsson et al., 2012; Alison et al., 2017). Weibull and Östman (2003) found, for example, that both landscape features and habitat type at the farm level affected the species composition of butterflies and carabids but that the effect of landscape features was greater for butterflies due to their greater mobility. Variation in overwintering behaviors, host plants and dispersal ability among herbivorous pests can induce different responses to a landscape (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Veres et al., 2013). In our study, the three common aphid species in wheat fields responded to landscape variables differently, suggesting that species composition along landscape gradients may be affected by characteristics of the surrounding landscape. More woodlots in a landscape may induce a higher proportion of *R. padi* than a landscape dominated by wheat production, as the former habitats provide more sources of *R. padi* to immigrate into wheat fields.

The aphid species we focused on differed in their reproductive capacities, tolerance to extreme temperatures, resistance to insecticides, ecological niches, and even their efficiencies as vectors of different plant viruses (Dixon, 1977; Yang et al., 1986; Liu et al., 2001; Qureshi and Michaud, 2005; Seabloom et al., 2009; Alford et al., 2014). Differences in species composition of aphids in many crops would change pest management decisions (Dixon, 1977). Aphid composition during the immigration period may determine the relative abundance of a particular species at a later stage. Therefore, landscape effects on the species composition of wheat aphids at the colonization stage should be taken into consideration when developing an integrated pest management program. In the future farmers can adjust the pest management strategy according to the effects of landscape context on pest density and composition.

5. Conclusions

While many studies have suggested that natural or seminatural habitats in a landscape can contribute to the abundance of natural enemies potentially contributing to biological control of aphids (Gardiner et al., 2009a; Plećaš et al., 2014; Zhao et al., 2014), our results found much higher aphid abundance at the colonization stage in fields surrounded by more noncrop habitats. Future studies should examine the effects of landscape on pests and natural enemies together to evaluate the biological service provided by varying agricultural landscapes. Moreover, the different responses of individual species to landscape features can alter the population composition of a pest guild, and such responses need to be taken into account during pest management. Improving areas of habitat that benefit natural enemies but have negative or neutral effects on pests ensures resource continuity for natural enemies while interrupting resource continuity for pests, thereby eliminating the positive effects that can be provided by a landscape to pests (Fahrig et al., 2011; Chisholm et al., 2014; Schellhorn et al., 2015).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2018.07.028.

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