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Is higher landscape heterogeneity associated with lower variation of abundances of pests and natural enemies?

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Abstract: While the influence of landscape heterogeneity on responses of both crop pest and natural enemy populations have been extensively studied, impacts on the variation of these responses are not. In this study, we aimed to determine how landscape heterogeneity affects the variation of densities of the soybean aphid and of the guild of natural enemies, and whether temporal variations are observed. We hypothesized that 1) landscape heterogeneity is associated with lower variation of densities of pests and natural enemies; and 2) the effect is stronger during the period of highest aphid population level. Respectively 29 and 31 soybean fields were weekly sampled in 2011 and 2012 in Quebec (Canada). For each field, a coefficient of variation was calculated regarding the density of the soybean aphid (*Aphis glycines*), of the entire guild of natural enemies, and of the different sub-guilds (predators, parasitoids, entomopathogens) during 1) the population peak of the soybean aphid (August 15-20), and 2) two weeks before (August 1-6). Landscape heterogeneity indices were calculated at a scale of 1.5 km radius around the fields: Crop richness, Crop diversity, Margin density, Landscape patchiness, and Proportion of woodlands. Overall, when considering aphids, predators, pathogens or the entire guild, results are in accordance with our 1st hypothesis: less variation in densities observed in heterogeneous landscapes. Finally, in accordance with our 2nd hypothesis, landscape heterogeneity has a stronger effect on the variation of natural enemy densities (but not on aphid density) during the population peak of the soybean aphid.

Key words: Spatial context, woodlands, field margins, coefficient of variation, spatial variability

Introduction

In agroecosystems, landscape heterogeneity influences both pest and natural enemy populations. Fahrig *et al.* (2011) discriminates between functional landscape heterogeneity (based on resource dependencies of species), structural landscape heterogeneity (based on physical characteristics), compositional heterogeneity (e.g., diversity of crop and/or non-crop habitats) and configurational heterogeneity (e.g., landscape patchiness, habitat fragmentation). However, most studies evaluated landscape complexity using the proportions of non-crop or semi-natural habitats in the landscape, where complex landscapes include high proportion of non-crop or semi-natural habitats. Many studies revealed negative effects of landscape heterogeneity on pest density and positive ones on natural enemy density and biocontrol

(Rusch *et al.*, 2016). Especially, landscape complexity showed positive effect on natural enemies in most studies, but less pronounced effects on pest control (Bianchi *et al.*, 2006).

Most of these population studies focused on abundance data instead of variation of abundance data (e.g., coefficient of variation). However, analysing the variance of data can provide relevant information. First, the coefficient of variation can reflect the variability of a population across habitats (spatial), with specialized species showing a higher coefficient of variation of density between habitat types than generalist species (Grez *et al.*, 2013). Second, the coefficient of variation can reflect the variability/stability of a population over time (temporal), with temporal variation of the coefficient of variation observed within a year (Gagic *et al.*, 2014) or throughout the years (Spitzer and Jaroš, 2009). Only few studies have evaluated the effect of the spatial context on the variability of populations. For instance, higher temporal variation of aphid abundance was found in low-intensity managed fields within complex landscapes than in high-intensity managed fields within simple landscapes (Gagic *et al.*, 2014). However, high variation of pest density can also be found between patches of habitat within a same landscape (Bianchi *et al.*, 2010).

In this study, we aimed to evaluate the effect of landscape heterogeneity on the spatial variability of insect populations. We formulated the hypothesis that 1) heterogeneous landscapes are associated with lower variation of densities of pests and natural enemies; and 2) the effect is stronger during the period of highest aphid population density.

Material and methods

Field samplings

In 2011 and 2012, respectively 29 and 31 soybean fields were sampled in the Montérégie area of Quebec (Canada). Samplings of soybean aphids (*Aphis glycines*) and natural enemies were performed according to the provincial phytosanitary surveillance network protocol, which includes the weekly observation of 30 soybean plants per field (6 stations, 5 plants each), from the beginning of July until the end of August (see Maisonhaute *et al.*, 2017 for more details). Once a week, the density of aphids and natural enemies (predators, parasitoids, entomopathogenic fungi) were recorded on each plant. The population peak of soybean aphid mainly occurred in mid-August in 2011 and in late August in 2012.

For each field, the within-field coefficient of variation (CV = standard deviation/mean) was calculated for 1) the soybean aphid density, 2) predator density, 3) parasitoid density, 4) entomopathogen density, and 5) the total density of natural enemies (predators, parasitoids, and entomopathogens). The CV was calculated for two periods: the aphid population peak (Peak populations, 2011: week of August 15th, 2012: week of August 20th), and two weeks before (Early populations, 2011: week of August 1st, 2012: week of August 6th). Aphid data were log-transformed in 2012 [$\log_{10}$(CV)].

Landscape and statistical analyses

Landscape heterogeneity was evaluated by analysing the effect of five variables at scale 1.5 km radius around fields: Crop richness (number of different crops), Crop diversity (Simpson index), Landscape patchiness (number of patches of crop and non-crop habitat), Field margin density (mean perimeter-to-area ratio of all fields), and Proportion of woodlands (%).

Statistical analyses were performed using the software R. For both aphid and natural enemy models, a forward selection procedure was used (‘‘forward.sel” function of R package ‘‘packfor”, 999 permutations, threshold alpha = 0.05) to select variables showing significant effect on the coefficient of variation. Regressions were then carried out with the selected variables, with calculated of adjusted R^2 (R^2_a) and p-value.

Results and discussion

Variation of aphid density

In Peak populations, the variation of aphid density was negatively influenced by the field margin density in 2011, while no effect of landscape heterogeneity was found in 2012 (Table 1). In Early populations, the variation of aphid density was not influenced by landscape heterogeneity in 2011, while it was negatively influenced by the field margin density in 2012 (Table 1). These results are in accordance with our 1st hypothesis that a higher landscape heterogeneity is associated with lower variation of densities of pests. Similarly, previous studies showed that more field margins in the landscape increased pest biological control (Östman *et al.*, 2001; Holland *et al.*, 2016). According to contrasting results, it is impossible to conclude for our 2nd hypothesis that the effect of landscape heterogeneity was stronger during the period of highest aphid density.

Table 1. Effect of landscape heterogeneity on the within-field variation of soybean aphid and natural enemy (NE) densities during the soybean aphid population peak (Peak) and two weeks before (Early). CV: coefficient of variation. NS: non-significant. NA: not applicable.

Year	Period	Group	CV (mean ± SE)	Variables (effect)	R^2_a	p
2011	Early	Soybean aphid	0.924 ± 0.113	NS	-	-
		All NE indexes	-	NS	-	-
	Peak	Soybean aphid	0.566 ± 0.036	Field margin (-)	0.134	0.029
		Predators	1.535 ± 0.110	NS	-	-
		Parasitoids	2.302 ± 0.432	Patchiness (+) and Diversity (-)	0.224	0.014
		Entomopathogens	1.610 ± 0.249	Field margin (-)	0.173	0.014
		Total NE	1.428 ± 0.095	NS	-	-
2012	Early	Soybean aphid	0.748 ± 0.058	Field margin (-)	0.178	0.010
		All NE indexes	-	NS	-	-
	Peak	Soybean aphid	0.597 ± 0.030	NS	-	-
		Predators	1.887 ± 0.203	Woodland (-)	0.149	0.018
		Parasitoids	2.117 ± 0.447	NS	-	-
		Entomopathogens	-	NA	-	-
		Total NE	1.845 ± 0.205	Woodland (-)	0.102	0.045

Variation of natural enemy (NE) densities

During aphid Peak populations in 2011, the variation of entomopathogen density was negatively influenced by the margin density, while no significant effect was found for predator density and for the total NE density (Table 1). Higher crop diversity provided lower variation of parasitoid densities, while higher landscape patchiness was associated with higher variability in parasitoid densities. In 2012, the variations of predator density and of total NE density were negatively influenced by the proportion of woodlands, while no effect was found on the variation of parasitoid density. In Early populations in both years, no variable significantly influenced the variation of total NE, predator, parasitoid and entomopathogen densities (Table 1). Data on predators, entomopathogens, and total NE support our 1st hypothesis that a higher landscape heterogeneity is associated with lower variation of NE densities, while it is not possible to conclude for parasitoids. In addition, the second hypothesis (stronger effect during the period of highest aphid density) is supported for all groups of NE. According to previous results, landscape heterogeneity, especially woody elements, have beneficial effects on NE (Holland *et al.*, 2016) and provided higher functional diversity of NE, which was associated with higher natural control (Maisonhaute *et al.*, 2017).

Overall, our results show that a heterogeneous landscape provides lower within-field population variability for both pest (aphid) and natural enemies, although the associated landscape variables are different. Finally, aphid natural control is clearly linked to landscape heterogeneity, not only according to the impact on aphid densities, but also according to the variability of their densities in the field. Further studies should be conducted to specifically evaluate the complex links between landscape, entomological variation and biocontrol.

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