



Aphids and their natural enemies are differently affected by habitat features at local and landscape scales

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HIGHLIGHTS

- ▶ Landscape simplification benefits predatory carabids and coccinellids.
- ▶ Margin distance affect aphid, parasitoid and coccinellid populations.
- ▶ The generalist predators' effect on aphids is comparable to the specialist one.
- ▶ Different predator guilds has non-additive effect in suppressing cereal aphids.
- ▶ Landscape and local features modulates biocontrol by acting differentially on the diverse predator guilds.

GRAPHICAL ABSTRACT



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ABSTRACT

Biological control, an essential ecosystem service to agriculture, can be affected by ecological processes operating at landscape scales. Here we assessed the effect of landscape complexity, measured as proportion of arable land (PAL), on the abundance of aphids, parasitoids, and specialist and generalist predators. In addition we set up cage experiments to test the ability of these groups of enemies to suppress aphid densities. Landscape context did not significantly explain differences in aphid or parasitoid densities between fields. However, aphid densities were significantly higher in field interior compared to the margin. Coccinellid (specialist predator) abundance showed a similar pattern, with higher density in the field interior, indicating an aggregative response to aphid prey. In addition, Coccinellid abundance increased with PAL, but only in field interiors and not at the field margins. The abundance of carabids (generalist predators) increased with PAL, suggesting that they benefit from landscape simplification. The cage experiment revealed that specialist as well as generalist predators were able to reduce the number of aphids on barley tillers and that a combination of both guilds did not provide a greater reduction of aphids.

Our results suggest higher densities of generalist predators with increasing PAL. Nonetheless, the greater abundance of coccinellids and carabid beetles in cereal fields embedded in simple landscapes does not necessarily imply better pest control since natural enemies may compete, thereby limiting their ability to control pests.

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1. Introduction

Current large-scale biodiversity losses in agricultural landscapes in the northern hemisphere may negatively affect the flow of ecosystem services such as biological control. In agricultural landscapes, biological control is exerted by a wide assemblage of natural enemies, in particular arthropods. Evidence from previous studies suggests that non-cropped habitats close to the crop fields may play a crucial role in maintaining natural enemy abundance and diversity in agroecosystems (Bianchi et al., 2006; Gardiner et al., 2009; Griffiths et al., 2008; Gurr et al., 2003; Tscharrntke et al., 2007; Werling and Gratton, 2010). However, processes at larger spatial scales may also affect their population dynamics (Tscharrntke et al., 2007). In particular, different taxa of biocontrol agents may respond differently to landscape complexity (Gardiner et al., 2010; Woodcock et al., 2010).

The effectiveness of biological control may also depend on the effect of landscape complexity differing between groups of natural enemies in combination with variation in their relative effect on their prey. For instance, a higher natural enemy abundance (Östman et al., 2001) or diversity (Snyder et al., 2006) may not automatically lead to improved biological control, because prey other than the pest species may be preferred. In this sense, our understanding of biological control is hampered by the lack of studies simultaneously examining the importance of agricultural landscape complexity on the abundance of specialist and generalist natural enemies and their ability to suppress pest prey (Bianchi et al., 2006).

Cereal aphids are specialist herbivores (Dixon, 1998) and major pest insects in cereal crops in northern Europe (Sigsgaard, 2002). The entomophagous arthropods that attack aphids can be divided broadly into specialists and generalists. Specialists include potentially important control agents of aphids such as parasitoids (Hymenoptera: Braconidae, Aphidiinae), and aphidophagous predators: coccinellids (Coleoptera, Coccinellidae), lacewings (Neuroptera, Chrysopidae), and hoverflies (Diptera, Syrphidae (Müller and Godfray, 1999)). Generalists include euryphagous predators such as ground beetles (Coleoptera, Carabidae) and spiders (Lang, 2003). The close dynamic link between specialist natural enemies and prey populations has resulted in a focus on specialists as potential biological control agents (Bianchi et al., 2006; Gurr et al., 2003). However, there are also examples where assemblages or specific generalist predators have been important complements to, or even more effective than, specialists at controlling pests (Murdoch et al., 1985; Symondson et al., 2002).

The research reported here aimed to examine the influence of landscape complexity, estimated as the proportion of annually cultivated land at the landscape scale, on communities of cereal aphids, parasitoids, and specialist and generalist predators in order to facilitate the design of appropriately scaled habitat conservation strategies. To accomplish this, we focused on two approaches. First, we investigated the influence of landscape complexity on the abundance and community composition of aphid natural enemies and on cereal aphid field populations. We hypothesised that relative abundance of aphids and their different predator guilds may change in relation to landscape complexity. In addition, we expected that some local factors such as position within-field, cover crop or weed cover would also have an effect on cereal aphids and their natural enemies. Second, to assess if shifts in natural enemy community composition might affect aphid biological control we performed cage experiments in two locations embedded in contrasting landscape contexts in a factorial experiment. We examined whether aphids suffer lower rates of mortality when attacked by flying predators and parasitoids alone, ground-dwelling predators alone, or a combination of the two. In addition, the

experiment was designed to test if these two groups have an additive effect on the control of aphid populations.

2. Material and methods

2.1. Study region and experimental design

The study was carried out in the province of Skåne in southern Sweden, which is characterized by a mixture of intensively farmed homogeneous plains and heterogeneous mixed farmland (Rundlöf and Smith, 2006). Within this region, 12 non-overlapping circular sectors, each with a 2-km radius, were chosen resulting in a gradient from structurally simple sectors, with >95% annually-tilled arable land and large fields (7.5 ha), to structurally rich ones, with 10% of annually-tilled arable land and small fields (1.6 ha). The landscape sectors were selected according the proportion of arable land within each landscape sector in order to avoid as far as possible, the north–south or east–west gradients, which may imply such problems as correlations between landscape complexity and abiotic factors like microclimate and soil fertility. In each landscape sector we selected two cereal fields with spring sown cereal (barley or wheat), altogether 24 fields were assessed. All selected fields were organically-managed for at least 3 years to guarantee that studied prey–natural enemy interactions were not affected by the impact of pesticides. As distance between fields within a landscape sector ranged from 260 to 2490 m, we determined individual estimates of landscape complexity for each field.

The landscape complexity around each field was characterized by the proportion of annually tilled arable land (hereafter PAL) within a 1000 m radius from the field centre. The PAL was chosen because it represents a relatively simple, but robust and useful parameter for characterizing landscape complexity (Persson et al., 2010). Landscape characteristics were determined using spatially explicit information on agricultural land-use analysed in ArcGIS 9.2.2.

In each field, we established two 100 m-transects parallel to the field edge, one 3 m from the first drill row (hereafter edge transect) and the other 30 m further into the field (hereafter interior transect) where aphid and natural enemies populations were assessed. Additionally, some agronomic measures were taken into account to assess the effects of local habitat characteristics. Cereal height was recorded from 20 randomly selected tillers in each field, whereas growth stage was evaluated with 10 shoots (Zadoks et al., 1974). Crop establishment and weed abundance were also studied in five randomly-distributed 1 m² squares per field. The cover of crop species and each weed species was recorded in each plot by means of a ground cover scale. We did not distinguish between narrow- and broad-leaved weeds.

2.2. Arthropods monitoring

Aphids were identified and counted on 100 randomly-selected cereal shoots by destructive whole-plant counts in the first 50 m of the two 100-m transects. The number of winged and wingless adults, nymphs and mummies (mummified aphids hosting parasitoids) for each aphid species on each cereal shoot were counted.

The natural enemy abundance was estimated from the count of aphid mummies and predators. Mummies were collected, reared in the laboratory and the hatched adult parasitoids were identified to species. The predator abundance was recorded using three sampling methods. First, larvae of lacewings and hoverflies were counted on the same shoots used to count the aphids. Second, flying predators, mainly coccinellids, were recorded visually by

walking along the second 50 m of the two 100 m-transects. The walking speed was 2 m min⁻¹ and all predators within 1 m on either side of transect were counted. Third, the ground-dwelling predators were caught using pitfall traps. Three pitfalls were positioned along the interior transect at 30-m intervals. The traps, with a diameter of 12 and 15 cm deep, were dug down to ground level. They were filled to three quarters with a NaCl-solution as a preservative solution and a drop of detergent to decrease the surface tension. Transparent plastic covers (25 × 25 cm) were placed above the traps to prevent flooding by rain.

Aphids and flying predator transects were inspected between 10:00 and 19:00 h and only during fair weather (no precipitation, light or no wind, minimum temperature of 17 °C). Ambient air temperature and percentage of relative humidity were measured prior to and just after transect sampling because these meteorological variables are known to affect the activity of some aphid predators (Elliott et al., 1998). Sampling was carried out at cereal flowering stage from June 7th to 14th, 2007, and at milk-ripe stage between July 14th and 20th, 2007. The traps were opened for two one-week sampling periods in June and July. As one sampling campaign lasted 5–6 days, the 24 fields were sampled in random order to prevent bias due to the phenological stage of cereal. Apart from larval stages of some predators, the entire arthropod community was determined to species. In addition, carabid beetles were sorted into trophic groups: predators, granivores and omnivores, according to the feeding type of adults (Purtauf et al., 2005).

2.3. Cage experiment

The cage field experiment to test the effect of natural enemy guilds on aphid populations was carried out in two study sites selected from the 12 landscape sectors. One site was embedded in a relatively simple landscape (PAL = 92%), and the other in a relatively complex landscape (PAL = 65%). Based on the data obtained in the first sampling, we selected two sites to ensure they had similar aphid population densities. We chose three organically-managed spring barley fields as close as possible in each site.

In each selected field we established a 2 × 2 factorial design with an open control (O), ground-dwelling predator exclusion (G), flying predator and parasitoid exclusion (F), and total exclusion (T), which was the combination of G and F. We delimited 24 circular plots in each field with a diameter of 0.75 m, situated 2 m apart from each other. In late June the four treatments, each replicated six times in each field, were randomly assigned to each plot within each field. By locating plots in this way, they contained a low but random number of aphids at the beginning of the experiment. We placed plastic barriers to exclude ground-dwelling predators (e.g. spiders, carabids, staphylinids). The barriers were circular, 0.75 m in diameter, 30 cm high and were dug about 10 cm into the soil. Inside each barrier we placed a dry pitfall trap with a circular opening of 12 cm diameter that was permanently open throughout June and July. Ground-dwelling predators captured in these dry traps were counted and removed. All other animals caught were returned into the experimental plot. In addition, web-building spiders were removed by hand 4–5 times from the closed plots. Flying aphid predators and parasitoids were excluded by setting wire cages over the plots. The cages had a mesh size of 8 mm allowing airflow to avoid changes in microclimate conditions (Schmidt et al., 2003) and were covered with sticky glue to intercept or hinder flying predators and parasitoids from entering. The bottom edge of the cages was left without glue to permit ground-dwelling predators access (Schmidt). To impede ground-dwelling predators from climbing on shoots near the plastic barriers and preventing nearby shoots from sticking to the glued mesh, the surroundings of each sub-plot were mown at least 20 cm around the plot. This was done around all plots, so that any

microclimatic effect should not differ between treatments (for further information see [Supplementary material A](#)).

To estimate abundance of aphids and their natural enemies we performed destructive whole-plants counts. In each plot, 15 randomly selected cereal shoots were removed from the ground and the numbers of adult winged, adult wingless and nymphal aphids for each aphid species were counted on each plant. The number of mummified aphids and predators were also noted. Mummies were taken to the laboratory for rearing and identification. Predators were left on the plant (except in the total predator exclusion treatment). Ground-dwelling predators captured in the dry traps were released outside the barriers or taken to the laboratory if this was necessary for identification. The first aphid monitoring was carried out at late barley flowering, from 29th June to 2nd July, 2007. The plots of flying exclusion treatment were sampled just before the definitive installation of wire cages and that of the ground exclusion 2–3 days after the installation of the plastic barriers. The second sampling was at late milk-ripe stage, 21st to 22nd July, 2007, when the cages were removed. Plots were sampled on dry days after dew had evaporated from the plants.

2.4. Statistical analyses

The effect of landscape complexity on aphids and on their natural enemies was analysed using mixed-effects models, in which we included landscape sector and field (nested within landscape sector) as random factors to account for the non-independent errors in our hierarchically nested designs.

The effect of local factors on aphids and their natural enemies were initially tested by including margin distance, crop characteristics (cereal height, cereal growth stage, cereal cover and weed cover) and meteorological variables in all models. However, apart from margin distance, local factors did not contribute to explaining the variation in abundance of aphids and their natural enemies and were therefore not used as covariables in the final models.

Abundance of aphids and coccinellids and the proportion of infested shoots were analysed at the level of transects. As fixed factors we tested the effects of annually-tilled arable land (PAL) as a descriptor of landscape complexity, the distance to the field margin (edge and interior transect) and the sampling period. Interactions between PAL and field margin distance, and PAL and sampling period were also examined to check whether the responses to landscape complexity depended on the sampling period or the distance to the field margin. The model for parasitism rate did not include sampling period or the interaction with PAL because parasitism was only considered in the second sample due to very low parasitism in the first sample.

Species richness of coccinellids were analysed at the level of fields. Species richness and total densities of arthropods estimated from pitfall catches were also analysed at the level of fields, since pitfall traps were only installed at the interior transect. In these models we included, as fixed factors, the proportion of annually tilled arable land (PAL), sampling period and their interaction.

For the cage experiment, aphid density and parasitism rate were analyzed including landscape sector, ground-dwelling predator removal, flying predator plus parasitoid removal and their interaction as fixed factors. To account for the fact that data sampled in the same field are not independent, we included field (nested within landscape sector) as a random factor.

To meet the assumptions of the models, data were log-transformed when needed. After transformation, models had normally-distributed residuals (according to Shapiro–Wilk's test of normality), they were homoscedastic, and displayed good predictive power (observed *versus* fitted values).

The significance of the explanatory variables was estimated using Markov Chain Monte Carlo (MCMC) sampling from the

posterior distribution of parameters. MCMC is a Bayesian approach that computes confidence intervals for estimated model parameters and allows evaluating the fitted models with respect to the stability of their parameters. This approach takes the uncertainty in both fixed- and random-effect parameters into account, capitalizes on the computational efficiency of maximum likelihood estimation and avoids the difficulties of estimating degrees of freedom in mixed-effects models (Bolker et al., 2009).

Analyses were performed using R 2.11 (R Development Core Team, 2010) with packages lme4 (Bates et al., 2008) and language R (Baayen, 2008) for mixed models.

3. Results

3.1. Arthropods monitoring

A total of 5076 cereal aphids were counted in the 24 organically-managed fields. Four aphid species were found, with *Rhopalosiphum padi* (63% of all aphid individuals) and *Sitobion avenae* (36%) dominating. Aphid abundance varied among sites, from 1 to 144 individuals per 50 cereal shoots at flowering and 5 to 203 at milk-ripe stage, but was not related to PAL (Table 1 and Fig. 1a). In contrast, the abundance of aphids was related to the distance to the field margin (Table 1), with higher values at interior (mean ± SE: 64.9 ± 13.1 individuals) than at edge transect (43.1 ± 6.4). The proportion of infested shoots followed the same pattern (Table 1) being greater at interior transects (mean ± SE: 35.2 ± 2.6%) than at the edge ones (26.0 ± 2.3).

A total of 208 parasitized aphid mummies, 180 (86.5%) *S. avenae* and 28 (13.5%) *R. padi*, were collected and reared in the laboratory. Out of these, 66 (31.7%) hatched in the laboratory and could be determined to species, whereas 93 (44.7%) already hatched in the fields, and 49 (23.6%) did not hatch. Those that did not hatch were dissected without finding any parasitoids, most likely because the parasitoids died from fungal attacks (Van Veen et al., 2008). Of the emerged parasitoids, 33.3% were primary parasitoids of the species *Aphidius uzbekistanicus* and *A. rhopalosiphii* (Hymenoptera, Braconidae, Aphidiinae), and the rest were hyperparasitoids such as *Asaphes suspensus*, *Dendrocerus carpenteri* and *Alloxysta victrix* (see Supplementary material B, for taxonomic details).

Aphid parasitism was about 1% at wheat flowering and 31.5% (± 6.4) by the end of the cropping season. There was a trend towards higher parasitism rates in landscapes with low PAL (Fig. 1b), but the large variability of parasitism rate ranging from 8 to 87% among landscape sectors, made it difficult to detect an effect of landscape complexity (Table 1). A higher proportion of the aphids close to the field margin were parasitized compared to the case further into the field (Table 1).

In total 440 predator individuals, representing four families, were recorded in the visual surveys. Coccinellids were the most abundant group, accounting for 88% of all individuals. Seven species of coccinellids were recorded, but the specialist aphidophagous

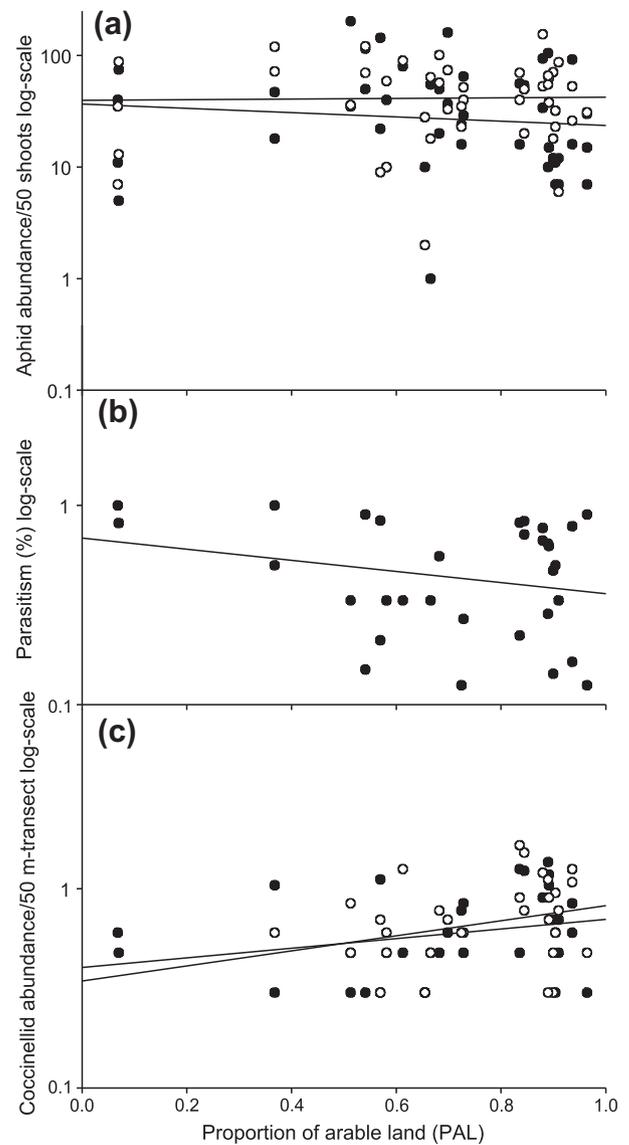


Fig. 1. Abundance of aphids (a), parasitism rate (b), abundance of coccinellids (c) in transects placed at 3 m (filled symbol) and 30 m (open symbol) from the field edge in relation to the proportion of annually tilled arable land at 1 km (diameter) surrounding the study field.

Coccinella septempunctata was the most abundant species (86.8%) and predator (76.1%). The low number of chrysopids (0.4 ± 0.2 individuals per 50 shoots) and hoverfly larvae (0.9 ± 0.3) prevented a detailed analysis (see species list on Supplementary material C).

Coccinellid densities showed a significant interaction between distance to field margin distance and PAL (Table 1). Coccinellid densities at the interior transects increased as PAL increased

Table 1

Effects of the proportion of annually tilled arable land (PAL), distance to the field margin (3 and 30 m), its interaction (PAL × Margin) and sampling period on count data of transect surveys. X ± SE is the estimates (coefficient) of the different variables. When the interaction was not significant it was excluded from the model. Significance for the different predictors included in the models was obtained using the Markov Chain Monte Carlo method. Bold font indicates significant relationships (p < 0.05).

	Aphid density		Infested shoots		Coccinellid abundance		Parasitism rate	
	X ± SE	p	X ± SE	p	X ± SE	p	X ± SE	p
Intercept	3.32 ± 0.58	0.000	0.20 ± 0.10	0.044	0.76 ± 0.44	0.081	0.63 ± 0.27	0.128
PAL	-0.18 ± 0.61	0.758	-0.04 ± 0.10	0.665	0.41 ± 0.54	0.452	-0.29 ± 0.37	0.804
Margin	0.47 ± 0.14	0.001	0.09 ± 0.02	0.000	0.92 ± 0.34	0.007	-0.49 ± 0.18	0.012
PAL × Margin					1.53 ± 0.45	0.006	0.56 ± 0.25	0.065
Sampling	0.00 ± 0.25	0.998	-0.03 ± 0.06	0.675	0.01 ± 0.27	0.956		

Table 2
Effects of the proportion of annually tilled arable land (PAL) and sampling period on catches in pitfall traps and on coccinellid and carabid richness. $X \pm SE$ is the estimates (coefficient) of the different variables. Significance for the different predictors included in the models was obtained using Markov Chain Monte Carlo methods. Bold font indicates significant relationships ($p < 0.05$).

	Carabid abundance		Spider abundance		Coccinellid richness		Carabid richness	
	$X \pm SE$	p	$X \pm SE$	p	$X \pm SE$	p	$X \pm SE$	p
Intercept	1.11 ± 0.60	0.065	3.87 ± 0.51	0.000	0.72 ± 0.48	0.120	5.56 ± 1.21	0.000
PAL	1.95 ± 0.68	0.004	0.58 ± 0.62	0.352	0.22 ± 0.48	0.639	1.29 ± 1.58	0.413
Sampling	0.37 ± 0.24	0.115	0.10 ± 0.16	0.615	0.84 ± 0.32	0.008	1.71 ± 0.62	0.050

(1.83 ± 0.57 , $t = 3.19$, $p = 0.001$, Fig. 1c), whereas such pattern was not seen at the edge transects (0.50 ± 0.55 , $t = 0.91$, $p = 0.36$, Fig. 1c). Coccinellid species richness was not related to PAL, while it was significantly related to the sampling period, with higher values at the second sample (Table 2).

In total, 20,555 arthropods were captured in the pitfall traps, with spiders being the dominant group (63.6% of the catch) followed by carabids (24.5%) and staphylinids (11.8%). A total of 5086 carabid beetles from 47 species were caught. The three most common were *Pterostichus melanarius*, *Harpalus rufipes* and *Bembidion lampros*, 77.6% of all carabids trapped (see Supplementary material D for a list of all species). Predators were the most abundant functional group (80%), followed by granivores (17.6%), and omnivores (2.4%). As our main interest was to disentangle the effect of predators on the aphid community only predatory carabids were included in the subsequent analyses.

The abundance of carabids increased as PAL increased (Fig. 2a), while PAL did not contribute to explaining the variation in spider

abundance (Table 2 and Fig. 2b). The species richness of carabids was not related to PAL, but was higher in the second compared to the first sampling period (Table 2).

3.2. Cage experiment

Data from visual surveying and pitfall trapping in the experimental plots followed similar patterns (data not shown). The most numerous predators were polyphagous and ground-dwelling, with the pit-fall catches mainly including *P. melanarius* (Carabidae) and cursorial spiders (Lycosidae and Linyphiidae). Some specialist predators such as coccinellids, larvae of lacewings and nabids (Hemiptera) were present, but in lower numbers. Ambient (unmanipulated) densities of aphids and their natural enemies in the experimental fields are summarised in Supplementary material E.

A total of four species and 3827 individuals of aphids were recorded, with *Sitobion avenae* and *Rhopalosiphum padi* being the most abundant species. Before the experiment started, aphid densities were not significantly different among plots allocated to the different treatments or between the two landscape sectors (Table 3). However, by the end of the experiment, there were significant differences in abundance of aphids among treatments and landscape sector (Fig. 3). The inclusion of flying predators and parasitoids resulted in a 45.6% decrease in aphid density compared to when both groups were excluded, showing a significant control of aphid population by generalist predators such as ground-dwelling predators (Table 3). Similarly, the exclusion of ground-dwelling predators resulted in a 67.4% decrease in aphid densities compared to when no predators were allowed, which shows that natural levels of flying predators and parasitoids may inflict high levels of mortality on aphid population (Table 3). The total exclusion of the predator community resulted in a 54.7% increase in aphid densities compared to the open treatment. This figure is not much

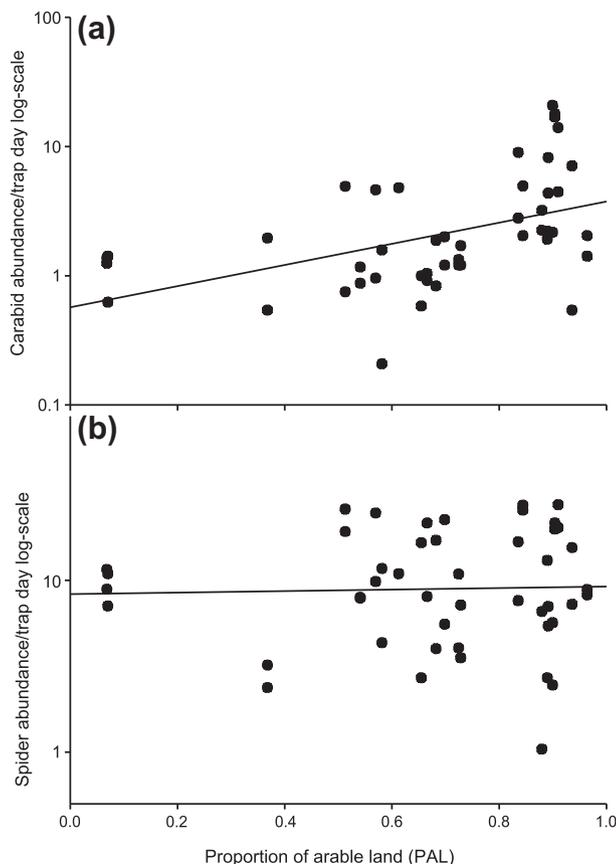


Fig. 2. Abundance of (a) carabids and (b) spiders per trap per day in relation to the proportion of annually tilled arable land at 1 km (diameter) surrounding the study field.

Table 3

Effects of treatment: flying predator and parasitoid exclusion (F), ground-dwelling predator exclusion (G), their interaction ($F \times G$), and study site (site) on aphid density and parasitism rates. Significance for the different predictors included in the models was obtained using Markov Chain Monte Carlo methods. Bold font indicates significant relationships ($p < 0.05$).

Aphid density					
First sample			Second sample		
	$X \pm SE$	p		$X \pm SE$	p
Intercept	2.27 ± 0.14	0.007	Intercept	2.39 ± 0.22	0.000
F	0.05 ± 0.15	0.733	F	-0.91 ± 0.20	0.000
G	0.13 ± 0.15	0.394	G	-0.49 ± 0.20	0.017
Site	0.13 ± 0.11	0.218	Site	-0.67 ± 0.27	0.049
$F \times G$	-0.12 ± 0.21	0.573	$F \times G$	0.71 ± 0.28	0.012
Parasitism rates					
Intercept	-4.06 ± 1.12	0.000	Intercept	-4.16 ± 1.04	0.000
F	0.09 ± 1.07	0.936	F	0.44 ± 0.87	0.609
G	0.10 ± 1.07	0.924	G	0.39 ± 0.88	0.654
Site	1.48 ± 1.00	0.140	Site	1.91 ± 0.90	0.035
$F \times G$	-0.51 ± 1.58	0.748	$F \times G$	-0.91 ± 1.25	0.465

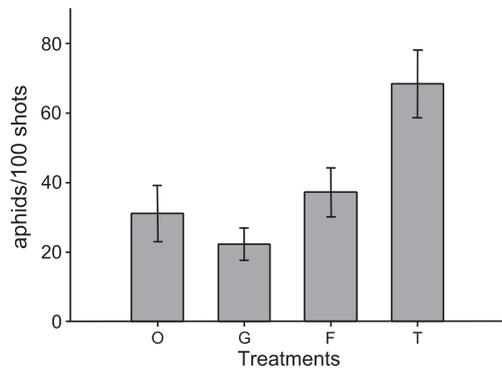


Fig. 3. Density of aphids (mean \pm SE) at the end of the experiment. O, open control; G, ground-dwelling predator exclusion; F, exclusion of flying predators and parasitoids; T, exclusion of all predators plus parasitoids (see text for details).

higher than the individual contributions of the two predator guilds, and the significant interaction between the removal treatments (Table 3) revealed that the effects of the two guilds on aphid populations were non-additive. The number of aphids at the end of experiment was also significantly different in the two places where the experiment was installed, with higher numbers in the simple site.

Aphids were attacked mainly by three species of primary parasitoids: *Aphidius rhopalosiphi*, *A. uzbekistanicus* and *A. ervi*. The proportion of aphids in the experimental plots that were parasitized was $20.51 \pm 6.6\%$ by the end of June, to increase to $37.54 \pm 18.06\%$ in the late season. Parasitism rates were not affected by either the exclusion of ground-dwelling predators' or the exclusion of flying predators and parasitoids. However, by the end of the experiment, there were significant differences in parasitism rate in the study site, indicating a greater parasitism in the complex site (Table 3).

4. Discussion

4.1. Aphids and coccinellids: local and landscape factors

Aphid abundance did not vary in relation to the PAL of the studied landscapes. This lack of relation between cereal aphids and landscape complexity was also found in another study (Vollhardt et al., 2008). Additionally, it has been reported that the influence of landscape features on biological control of cereal aphids is likely to vary over season (Östman et al., 2001; Thies et al., 2005) depending on abiotic factors and abundance of overwintering individuals (Östman et al., 2001). The strong relationship between aphid abundance and position within the field is consistent with a recent farm-scale assessment (Vialatte et al., 2007). This study revealed that despite the long-range dispersal potential of the grain aphid, its movement patterns and colonization dynamics in arable crops are much more determined by the landscape elements at a local scale.

One of the most influential factors explaining the variation in coccinellid abundance was the position within fields. Their densities were higher in the field interior as was cereal aphids. This suggests an aggregative response to prey in line with findings of Bianchi et al. (2007), that the distribution of *C. septempunctata* is highly dependent on availability of aphid prey in crops, in particular cereal ones, which served as their major reproduction habitat. Furthermore, the positive effect of a high PAL on coccinellid community was somewhat expected given that simplified landscapes with a high proportion of annually-tilled land have been shown to benefit aphidophagous insects such as *C. septempunctata* (Grez et al., 2008; Rand and Tschamtkke, 2007).

4.2. Parasitoids: local and landscape factors

The proportion of arable land did not seem to affect the abundance of aphid parasitoids, whereas the distance to the field margin had a negative effect on the proportion of aphids parasitized. A larger proportion of parasitized aphids close to the field margin indicate that aphid parasitoids respond to factors at a local scale revealing a higher biological control close to the margins. Tschamtkke et al. (2005) also found the strong dependence of parasitoids to resources at local rather than at the landscape scale, because of the poor dispersal abilities of the parasitoid compared to their host. This was also the case for Brewer et al. (2008) who reported the greater sensitivity of cereal aphid parasitoids to farm-scale vegetation than region-scale vegetation. Alternatively, the absence of a relationship between parasitoid abundance and isolation level, regardless of landscape complexity. This effect is probably stronger for the parasitoids than for their host, as the parasitoid colonization of habitat patches depends on both isolation from other patches and on the size of the host population (Viessler et al., 2009). It has also been suggested that parasitoid populations are more strongly influenced by inter-annually changing crop mosaics than their herbivorous hosts (Thies et al., 2008).

4.3. Carabids and spiders: landscape factors

The abundance of predatory carabids increased with the proportion of arable land in the surrounding landscape. This suggests that a reduced complexity at landscape scale can actually enhance the communities of these predators. Our results add to a growing body of work that indicates the positive effects of surrounding agricultural habitats on highly mobile predators (Elliott et al., 1998; Bianchi et al., 2007; Rand and Tschamtkke, 2007), potentially able to benefit from the high availability of resources within cropping systems. In addition, this finding is also in accordance with the hypothesis of Schmidt et al. (2008), postulating that species that are well adapted to the focal habitat, in this case arable fields, will respond negatively to the diversity of habitats in the surrounding landscape. This would indicate that *P. melanarius*, the main representative of the predatory carabid group in the studied agricultural landscapes, is one of the species better adapted to agriculturally-dominated landscapes and benefit from arable fields as has been suggested by Woodcock et al. (2010).

Conversely, the activity density of spiders did not exhibit any relation to landscape complexity. This contradicts previous European studies (Öberg et al., 2007; Öberg et al., 2008), which suggested that a diverse landscape with easy access to perennial crops and forest would augment both the number of lycosid and linyphiid spiders. This was also the case for Gardiner et al. (2010) in USA who also found that activity density of spiders increased in soybean fields in landscapes with an abundance of forest and grasslands. However, our result reinforce those of Schmidt et al. (2005) who suggested that variables acting on small scales, such as more favourable habitat conditions were more important than landscape context in terms of activity density of spiders. According to Clough et al. (2005) within field location of the traps was one the best predictors of activity density of spiders, with greater abundances in field edges. Other authors, in turn, suggested that species specific behavior may condition the outcomes in analyses of arthropod response to landscape complexity. As example, Schmidt et al. (2008) found that 19 species out of the 40 tested responded positively to the percentage of non-crop habitats in the surrounding landscape, and five responded negatively. Depending on the species, the spatial scales with the highest explanatory power ranged from 95 m to 3 km radius around the study fields, potentially reflecting dispersal distances.

4.4. Cage experiment

The experimental manipulations showed that flying natural enemies as well as ground-dwelling predators were able to reduce the overall number of aphids on barley tillers. The fact that aphid density in F and G was not different to that in the open treatment indicates that both groups can exert the same pressure on aphids by themselves when the other group was excluded (see Fig. 3). Few other exclusion studies have attempted to measure the impact of different natural enemy guilds under natural densities in field conditions (Holland et al., 2008; Schmidt et al., 2003). These studies found that flying predators and parasitoids were more effective than ground-dwelling predators alone. Conversely, our cage experiment revealed that the effect of ambient levels of ground-dwelling predators on suppressing aphids was as important as the effect of flying predators plus parasitoids. However, as the abundance of parasitism did not differ between treatments and coccinellids constituted the major group of flying predators, the control of aphid populations by flying predators can be entirely attributed to coccinellids.

Multiple enemy species may act synergistically on their shared prey (Colfer and Rosenheim, 2001; Losey and Denno, 1998). By contrast, if one predator species kills another predator (“intraguild predation”) or interferes with its foraging behavior, the enemy interaction is antagonistic and fewer prey than expected will be killed by their combined action (Losey and Denno, 1998). Our work shows that, over the short term, the effects of flying-predators plus parasitoids and ground-dwelling predators were non-additive (Fig. 3). Our results, therefore, add to a long list of non-additive effects between natural enemies that have now been shown to occur among a number of different taxa (Ferguson and Stiling, 1996; Müller and Brodeurb, 2002). For instance, aphids are caught by spiders when they drop from the vegetation, a behavior that allows escape from *Aphidius* wasps (Longley and Jepson, 1996) or in response to foliar-foraging predators (Gross, 1993). *P. melanarius* disrupt the biological control of parasitoid wasps by preying on the aphid mummies (Snyder and Ives, 2001). *P. melanarius*, is also known to frequently prey on spiders in the field (Lang, 2003). Nonetheless, our design did not enable us to identify intraguild effects of the main ground-dwelling predators such as spiders and carabids.

4.5. Implications

The negative relationship between densities of coccinellids and predatory carabids in cereals fields to the complexity of surrounding agricultural landscapes may suggest more efficient biological control in fields embedded in a simplified context. However, the lack of response of aphids in relation to landscape complexity, such that the apparent reduced number of predators in complex sites maintain the aphid populations at the same level as in the simple landscapes, suggests that this may not be so. This potentially contradictory result shows that we are just starting to appreciate the complexity of the assemblage of aphid natural enemies. In addition, through the findings of the cage experiment we now understand that competition between natural enemies may counteract the higher density of natural enemies and limit their efficiency in controlling pests.

The clear response of aphids, parasitoids and coccinellids to local factors such as the position within-field hint at the importance of small scale factors within extensive agricultural landscapes. In the same line, the lack of a relationship between landscape complexity and parasitoid abundance call for more studies in order to better understand the relative role of isolation and fragmentation of non-cropped habitats, regardless of landscape complexity.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2012.03.012>.

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