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Weeds, aphids, and specialist parasitoids and predators benefit differently from organic and conventional cropping of winter cereals

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Abstract The aphid–natural enemy interaction in winter wheat fields constitutes a complex system that has been frequently studied because of its implication for biological control. However, not all of the aphids living in cereal fields are crop pests, as there are also aphids living on weeds that may serve as alternative hosts or prey for aphid parasitoids or predators. In this context, a concomitant survey of the plant and insect communities was conducted to understand how different plant communities affect the abundance and richness of aphids and the interactions with their natural enemies. The plant community was split into functional groups (grasses, legumes and forbs), and the aphid community was divided into feeding groups according to their host preferences (specialists in grasses or

forbs). The grass aphids, which dominated the total aphid catches, responded positively to grass cover, which was particularly enhanced in the conventional fields. Conversely, the forb aphids, which mainly conditioned the total species richness of the aphids, were closely correlated with the local abundance of legumes. The system of cereal aphid–parasitoids was enhanced in the conventional fields, where the abundance of grasses was higher, whereas the legumes of the organic fields indirectly played a key role in enhancing the richness of the parasitoids and the abundance of predators. Our findings indicate that a bottom-up effect exists throughout the plant community, aphids, and aphidophagous insects and that plant community characteristics should be considered to better understand cereal aphid control.

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Introduction

Cereal aphids are major pests in several temperate areas around the world (Fuentes-Contreras and Niemeyer 2000), and yield losses are commonly avoided by the use of insecticides (Östman et al. 2001). In Catalonia (NE Spain), cereal aphids cause direct damage to winter cereals but rarely exceed the economic injury threshold (Pons et al. 1993). One of the main reasons for this limited damage appears to be the availability of natural enemies (Pons and Eizaguirre 2000). In fact, Lumbierres et al. (2007) outlined that the large reservoir of aphid parasitoids in the Catalan dry land cereal fields during winter appeared to offer a good potential for aphid control in cereals because the parasitoid activity in the winter and early spring is a significant factor in maintaining aphid populations below the injury threshold level during the spring (Legrand et al. 2004).

The entomophagous arthropods that attack aphids can be divided broadly into aphidophagous specialists and generalist predators (Müller and Godfray 1999). There are examples where assemblages or specific generalist predators have been important complements to the specialists in controlling pests (Murdoch et al. 1985; Symondson et al. 2002). Nonetheless, the close dynamic link between the specialist natural enemies and prey populations has resulted in a large body of research that is focused on the specialists as potential biological control agents (Bianchi et al. 2006; Gurr et al. 2003).

The interaction between cereal aphids and their specialist natural enemies constitutes a complex system that has been widely studied from many different points of view. For example, studies on the effect of the environmental conditions on the parasitism rate (Zamani et al. 2006) or the feasibility of the Integrated Pest Management of certain parasitoids that naturally occur under fluctuating conditions (Desneux et al. 2006) has been addressed. However, a wider perspective on the maintenance of natural aphid–natural enemy interactions is lacking, as not all aphids living in cereal fields are crop pests and those living on weeds or hedgerows may serve as alternative hosts or prey for the parasitoids and predators that are controlling cereal aphids populations (Norris and Kogan 2000).

In this sense, the study of organic and conventional cereal fields that differ in their weed communities appears to be a suitable model to explore the effect of the plant community on the aphid–natural enemy interactions further. This approach is particularly interesting, considering that the weed assemblage is of central importance to the food webs of arable systems (Hyvönen and Huusela-Veistola 2008).

The relationships amongst the plant community, aphids and their specialist natural enemies were tested in two key stages of cereal development, flowering and the milk-ripe stage. Furthermore, the comparison of fields under organic

and conventional insecticide-free management in a Mediterranean context allows the avoidance of the indirect effects of insecticide applications on the plant–arthropod interactions (Hole et al. 2005).

We hypothesised that the farming system would have a significant effect on the plant community characteristics and that we might detect individual patterns of the abundance and richness of aphids, parasitoids and predators in relation to the plant community characteristics because each group has specific foraging and reproduction requirements. The research reported here aimed to examine the following: (1) the effect of farming type (organic vs. conventional) on the plant community; (2) the effect of the cover of grasses, forbs and legumes on the abundance and species richness of aphids, parasitoids and predators and (3) the correlation amongst aphids and their natural enemy communities.

Materials and methods

The study was conducted in Montblanquet (NE of Spain, 41°29'0.9"N, 1°7'16.4"E; 627 m.a.s.l.), an agricultural landscape dominated by woodlands, consisting of mainly pines (*Pinus nigra* subsp. *salzmannii* (Dunal) Franco) and evergreen and deciduous oaks (*Quercus ilex* L. and *Q. faginea* Lam.), scrublands and perennial grasslands. The field boundaries were mainly colonised by perennial grasslands dominated by *Brachypodium phoenicoides* (L.) Roem et Schultes and by a mixture of blackthorn-bramble hedgerows and thickets of *Rosmarinus officinalis* L. The climate is Mediterranean, with a mean annual precipitation of 450 mm and a mean annual temperature of 13°C.

Four organically and four conventionally managed winter wheat fields were selected in a homogeneous area of 2 × 2 km. The organic fields were randomly selected from the 12 available in the area, and the conventional fields were then selected at no more than 1 km apart, but detached from the organic fields. To characterise the boundary vegetation of the fields, we combined habitat field survey and photointerpretation methods in ArcMap version 9.1. The area of the habitats of the boundaries that covered at least 5 m of the field perimeter was measured on 1:5,000 orthophotomaps (ICC 2005). The habitats were categorised as perennial grasslands, blackthorn-bramble thickets, mixed holm-oak and deciduous oak woodlands, pine woodlands and deciduous woodlands. The average diversity of the habitats was computed for each field using the Shannon-Wiener index. The average habitat diversity did not differ significantly amongst the organic and conventional fields ($\chi^2_{1\text{ df}} = 0.70$, P value = 0.403). Therefore, our study of the organic and conventional cereal fields was focused on the intra-field plant community as the differing factor, as the organic and conventional fields shared the same vegetation along the boundary hedgerows.

Although we tried to select fields that were similar in size and shape, we considered the homogeneity of the boundary vegetation more important than the homogeneity of the field size and shape, as, in any case, the fields were relatively small. For this reason, the field size was significantly greater in the conventional (mean \pm SE; 4.08 ± 0.8 ha) than in the organic fields (2.19 ± 0.3 ha, $\chi^2_{1\text{df}} = 5.78$, P value = 0.016). In contrast, the perimeter-to-area ratio was significantly greater in the organic (mean \pm SE; 0.09 ± 0.01) than in the conventional fields (0.06 ± 0.01 ; $\chi^2_{1\text{df}} = 4.85$, P value = 0.028). The selected fields chosen were flat to avoid any bias in slope or aspect. The conventional fields were mainly cultivated with a cereal monoculture, whereas the organic fields relied on more-or-less complex rotations of cereals with legumes and green manure. In the latter, the weeds were controlled mechanically, and the fertilisation was composed of green manure and, occasionally, hen manure. In contrast, the conventional fields were regularly sprayed with herbicides and fertilised with a combination of pig slurry and mineral fertilisers. Pesticides other than herbicides were not applied under the conventional farming (for further details, see Appendix 1 in Supplementary Material), and the organic fields selected had been managed for more than one decade following organic guidelines and were certified by the Catalan Council for Organic Farming.

In each field, we established an 80 m transect diagonally across the centre of the field, starting at 55 m from the edge. Within each transect, five 1×1 m plots at 20 m intervals were surveyed. The arthropod sampling and plant surveys were conducted sequentially within each plot. The arthropods were sampled using a petrol-driven, Blow&Vac leaf-blower apparatus (McCulloch BVM250, Italy; sampling cylinder 60 cm in height and 12 cm in diameter) that was converted to a suction sampler according to Stewart and Wright (1995). The suction sampler was operated on full power, which produced an estimated constant airflow of $0.142 \text{ m}^3/\text{s}$ (manufacturer's data). The pipe was held vertically and carefully passed for 60 s over the wheat plants contained in the 1 m^2 quadrat. For each plot, the sampling bag was removed from the machine, enclosed in a labelled plastic bag and stored in a portable fridge to prevent the activity of the predators in the bag. All of the samples were collected by the same two individuals to reduce any variability of the sampling. This method has been shown to provide a sound representation of all of the trophic levels interacting with the vegetation (Letourneau and Goldstein 2001) and is used extensively to study arthropods on herbaceous crops (Caballero-López et al. 2010; Elliott et al. 2006; Stewart and Wright 1995).

Arthropod sampling was carried out between 10:00 and 19:00 h in sunny weather conditions (temperature $>20^\circ\text{C}$)

and performed twice at different stages of the wheat's development (Zadoks et al. 1974): at the beginning of the anthesis stage between May 25th and 27th and the mid-milk-ripe stage between June 24th and 26th in 2004. As one sampling campaign lasted two days, the eight fields were sampled in random order to prevent a systematic bias due to the time of day.

Target groups

The arthropod samples were frozen for sorting and identification at a later date. The aphid species (Hemiptera: Aphididae) were classified according to their host preferences (Blackman and Eastop 2000, 2006) into two feeding categories: grass aphids and forb aphids. Grass aphids feed on the wheat crop and grass weeds, whereas forb aphids do not have an impact on the wheat plants and comprise a wide range of aphid species, which mainly thrive on the many weeds available in arable fields and on plant species in hedgerows.

The entire community of parasitoids and predators were counted and sorted to the family level, but only the aphidophagous parasitoids and the specialist aphidophagous predators were investigated further. The Aphidiinae sub-family (Hymenoptera: Braconidae) was the main group of aphidophagous parasitoids, insects that deposit their eggs inside the still-living aphid; the parasitised aphid continues to live and grow (Starý 1988), but its reproduction is diminished or suppressed. Information related to the potential hosts of parasitoid species was obtained from specific literature (Kavallieratos et al. 2006; Michelena-Saval and González-Funes 1987; Michelena-Saval and Oltra-Moscardó 1987; Noyes 2007; Starý 1974, 1976, 1981; Tomanovic et al. 2003). The species of specialist aphidophagous predators belonged mostly to the families of coccinellids (Coccinellidae: Coleoptera) and lacewings (Chrysopidae: Neuroptera). Coccinellids are active predators in the larval and adult stages, whereas lacewings are only predators during their larval stage.

The vegetation was surveyed twice, concomitant with the suction-sampling. The cover of the crop species and each weed species was recorded for each plot by means of a ground cover scale. The weed species were identified according to Bolòs et al. (2005), and the plant species were classified into three functional groups (grasses, forbs and legumes). The legumes were considered apart from the other forbs due to the generally higher nitrogen content of their tissues, which would make them a higher quality resource for herbivores, and the grasses have tough tissues with low nitrogen contents and structural characteristics that deter many plant-feeders.

Data analysis

Models of the total plant cover and for the different functional plant groups (grasses, forbs and legumes) were analysed in terms of the farming system (conventional/organic) and sampling period (first/second) as the fixed factors.

The aphids (grass and forb aphids) and parasitoids were analysed considering the sampling period (first/second) and a common set of covariables (cover of forbs, legumes and grasses) as the fixed factors. The predator model did not include the sampling period, as all of the specimens were captured during the second sampling. In addition, due to their different ecological requirements, the models of the parasitoids and predators also included several additional variables, which were of different types depending on the focus of the analysis. When we modelled the species richness of the parasitoids or predators, we included the richness of the grass aphids and forb aphids, which could act as potential hosts. When the focus was on the abundance of the parasitoids or predators, we included the abundance of the different aphid groups.

All of the models displayed are full models; they were analysed by means of linear mixed models with normal error distribution, and the field was included as a random effect term to account for the fact that the samples in the same fields were not independent (Pinheiro and Bates 2000). No model simplification was used to avoid the inherent bias of stepwise regression. Prior to the analysis, the collinearity of the sets of independent variables included in the models was evaluated with the variance inflation factor, $1/(1 - R^2)$, to check the robustness of the model (Kutner et al. 2004). Assumptions of linearity, normality and homogeneity of the variances were evaluated through the examination of the residuals, and the data were log-transformed when needed. All of the analyses were performed using R 2.11 (R Development Core Team 2010); library lme4 (Bates et al. 2008) was used for the model fitting, and library languageR (Baayen 2008) was used to determine the significance of the predictors using Markov Chain Monte Carlo methods.

Results

Plants

In total, 40 weed species from 17 families were recorded in the 8 winter wheat fields; 26 of these were forbs, 8 were legumes and 6 were grasses. In the organic fields, 35 species were recorded (24 forbs, 8 legumes and 3 grasses), whereas in the conventional fields, 15 were found (10 forbs and 5 grasses). Most of these species appeared in only one

or two fields, indicating a high variability in the local occurrence (Appendix 2 in Supplementary Material).

The mean total plant cover was significantly higher in the conventional than in the organic fields, which was closely related to the also greater percentage of grass cover (GC) in the conventional fields (Fig. 1). The wheat cover represents 97.2% of the GC in the conventional fields and 91.4% in the organic fields. However, the mean relative cover of forbs (mainly Brassicaceae and Polygonaceae) was significantly higher in the organic than in the conventional fields. Furthermore, the legumes thrived exclusively in the organic fields, either as weeds or volunteer crops (e.g. *Vicia ervilia*). The mean wheat height differed only slightly between the conventional (mean \pm SE; 87.9 cm \pm 1.36) and organic fields (81.3 cm \pm 3.5), and the differences were not significant ($\chi^2_{1\text{ df}} = 0.345$, P value = 0.56).

Aphids

A total of 1,728 aphids, including 18 species, were collected. The grass aphids belonged to nine species and represented 92.2% of the total catch; *Sitobion avenae* (Fabricius) and *Metopolophium dirhodum* (Walker) were the most commonly captured species. The remainder was composed of forb aphids, represented by nine species. The complete list of species is provided in Appendix 3 in Supplementary Material.

The catches of grass and forb aphids mainly depended on the wheat developmental stage, revealing a higher number and more diverse captures in the milk-ripe stage (Table 1). However, the abundance of grass aphids was also positively affected by a greater cover of grasses. Conversely, a higher GC decreased the number of forb

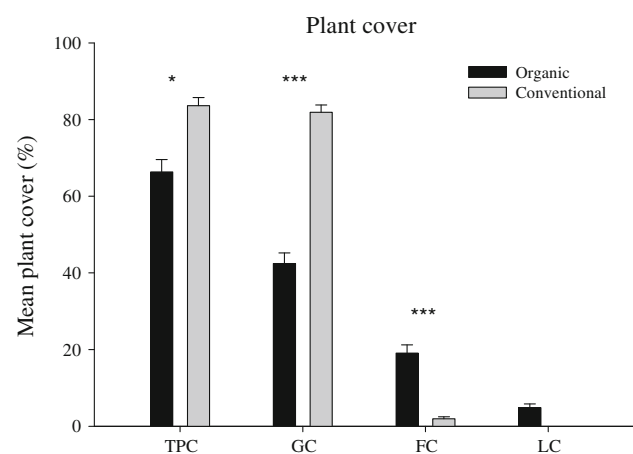


Fig. 1 The effects of farming system on the total plant cover (TPC), grass cover (mainly explained by the wheat cover, GC), forb cover (FC) and legume cover (LC). Data are the means with standard errors. Level of significance from the linear mixed models is shown. * $P < 0.05$; *** $P < 0.001$

aphids, whereas a greater cover of legumes benefited the abundance and richness of the forb aphids (Table 1).

Natural enemies

Overall, 494 parasitoids, belonging to 17 families, were collected and identified. Of these, 153 of the individuals were aphidophagous parasitoids and all belonged to the Aphidiinae subfamily (Hymenoptera: Braconidae). From these specimens, seven species were found, and the *Aphidius* genus was the most common (Appendix 3 in Supplementary Material). In accordance with our literature review, all of the identified species of the primary parasitoids prey on the main species of grass aphid that was captured (Kavallieratos et al. 2006; Michelena-Saval and González-Funes 1987; Michelena-Saval and Oltra-Moscardó 1987; Noyes 2007; Starý 1974, 1976, 1981; Tomanovic et al. 2003), but some of the species of aphids categorised as forb specialists can also serve as hosts (Appendix 4 in Supplementary Material).

The parasitoid abundance was considerably enhanced by the presence of the grass aphids (Table 2), revealing a

significant relationship between the parasitoid community and the presence of their potential host. The richness of the parasitoids was significantly and negatively related to the GC and positively associated with the species richness of the forb aphids (Table 2), suggesting that the richness of the parasitoids was mostly explained by the structure of the plant cover and the local host richness.

In total, 1,107 predatory individuals, belonging to 4 orders and 19 families, were collected. Of these, a total of 218 aphidophagous predators were considered, representing five species and three families (Appendix 3 in Supplementary Material). Chrysopid larvae constituted the most abundant group, accounting for 72% of all of the individuals, followed by the specialist aphidophagous, *Coccinella septempunctata*, in both the adult and juvenile stages.

The abundance of predators was significantly and negatively related to the number of forb aphids, and greater abundances occurred in those plots with a higher cover of legumes. The predator species richness did not seem to be related to the plant community or the abundance of potential prey (Table 3).

Table 1 Effects of GC, FC, LC and sampling period (second vs. first) on the abundance and richness of grass and forb aphids

	Grass aphids abundance		Grass aphids richness		Forb aphids abundance		Forb aphids richness	
	X ± SE	P	X ± SE	P	X ± SE	P	X ± SE	P
Intercept	2.47 ± 0.46	0.002	1.29 ± 0.57	0.047	0.76 ± 0.37	0.084	0.25 ± 0.39	0.597
GC	0.03 ± 0.01	0.009	−0.01 ± 0.01	0.420	−0.02 ± 0.01	0.029	−0.01 ± 0.01	0.242
FC	−0.00 ± 0.01	0.613	0.01 ± 0.01	0.690	−0.01 ± 0.01	0.322	−0.00 ± 0.01	0.906
LC	0.00 ± 0.02	0.733	0.02 ± 0.02	0.382	0.04 ± 0.02	0.022	0.06 ± 0.02	0.007
Sampling	1.88 ± 0.26	0.000	0.86 ± 0.23	0.000	1.42 ± 0.21	0.000	1.48 ± 0.22	0.000

Significant relationships at α = 0.05 are indicated in bold

Level of significance for the different predictors included in the models was obtained by means of Markov Chain Monte Carlo methods

Table 2 Effects of GC, FC, LC and sampling period (second vs. first) on the abundance and richness of primary parasitoids

	Primary parasitoids abundance		Primary parasitoids richness		
	X ± SE	P	X ± SE	P	
Intercept	0.44 ± 0.39	0.317	Intercept	0.97 ± 0.44	0.060
GC	−0.01 ± 0.01	0.383	GC	−0.02 ± 0.01	0.034
FC	0.01 ± 0.01	0.397	FC	−0.00 ± 0.00	0.835
LC	−0.00 ± 0.00	0.838	LC	−0.02 ± 0.02	0.395
Sampling	0.02 ± 0.20	0.875	Sampling	0.20 ± 0.35	0.604
GAA	0.01 ± 0.00	0.044	GAR	−0.00 ± 0.15	0.913
FAA	0.01 ± 0.02	0.449	FAR	0.41 ± 0.17	0.022

Significant relationships at α = 0.05 are indicated in bold

Grass aphids, in terms of the abundance (GAA) or richness (GAR), and forb aphids, in terms of abundance (FAA) or richness (FAR), were also included in the models. Level of significance for the different predictors included in the models was obtained by means of Markov Chain Monte Carlo methods

Table 3 Effects of GC, FC, LC and sampling period (second vs. first) on the abundance and richness of aphidophagous predators

	Predator abundance			Predator richness	
	X ± SE	P		X ± SE	P
Intercept	6.05 ± 2.57	0.062	Intercept	2.11 ± 1.22	0.021
GC	0.01 ± 0.03	0.713	GC	0.03 ± 0.02	0.109
FC	−0.02 ± 0.05	0.689	FC	−0.00 ± 0.02	0.198
LC	0.18 ± 0.08	0.046	LC	0.06 ± 0.03	0.130
GAA	−0.01 ± 0.02	0.788	GAR	−0.66 ± 0.31	0.704
FAA	−0.17 ± 0.07	0.048	FAR	−0.14 ± 0.19	0.304

Significant relationships at $\alpha = 0.05$ are indicated in bold

Grass aphids, in terms of the abundance (*GAA*) or richness (*GAR*), and forb aphids, in terms of abundance (*FAA*) or richness (*FAR*), were also included in the models. Level of significance for the different predictors included in the models was obtained by means of Markov Chain Monte Carlo methods

Discussion

In agreement with previous studies (Hyvönen et al. 2003; Romero et al. 2008), our data support the notion that the farming system has an effect on the plant assemblage in cereal fields. In the dryland cereal agroecosystem studied, a higher cover of grasses was found in the conventional fields due to the greater wheat cover. Conversely, the organic farming promoted weed diversity, as a richer plant community was found in the organic cereal fields. As stated by Romero et al. (2008) in a Mediterranean context, the exclusive presence of legumes in organic cereal fields might imply major consequences on the insect community; this is discussed below.

Grass aphids, with *Sitobion avenae* and *Metopolophium dirhodum* as the main representatives, were more abundant where the GC was greater, which usually occurred in the conventional fields and, in turn, receive higher N supplies. This is not surprising given that *Sitobion avenae* and *Metopolophium dirhodum* are known to benefit from higher nitrogen supplies in winter wheat fields (Duffield et al. 1997; Hasken and Poehling 1995). However, our study did not enable us to distinguish which of these factors is the most relevant for explaining the grass aphids' pattern.

The abundance of parasitoids appears to be closely associated with the abundance of grass aphids, which may account for an aggregation response to the prey (Evans 2008; Pareja et al. 2008). The significant relationship between the abundances of grass aphids and of parasitoids could be addressed as a cascade-up mechanism that is mediated by density-dependent factors, since many of the parasitoid species identified in our study attack grass aphids, such as those of the *Sitobion* and *Metopolophium* genera (see Appendix 4 in Supplementary Material). The response between the grass aphids and parasitoids is in agreement with studies that have reported a density-dependent

relationship between aphids and specialist aphidophagous parasitoids (Colfer and Rosenheim 2001; Helms et al. 2004; Murphy and Volkl 1996). Nevertheless, in no case was the density-dependent parasitism by parasitoids sufficient to prevent an exponential population growth of the aphids within the growing season (Helms et al. 2004). The population densities of the parasitoids might also appear to be strongly correlated in space and time with the aphid densities because the parasitoids can exploit a sugar resource, such as the honeydew offered by their sap-producing hosts (Wäckers et al. 2008). However, information on how the aphid honeydew may impact the tri-trophic relationships and what the implications may be on biological control is still rather limited (Hogervorst et al. 2007).

Whereas the aphid number was enhanced with a greater GC, the parasitoid community responded negatively to a higher GC. This result was in accordance with the findings of Desneux et al. (2009) and Obermaier et al. (2008), who demonstrated that complex plant assemblages reduce the parasitoid mobility and impact its foraging behaviour. In addition, Obermaier et al. (2008) highlighted that aphids and their parasitoids were influenced in opposite ways by the habitat structure therefore, suggesting the existence of a parasitoid-free space for the herbivores where a complex vegetation occurs. Conversely, the response of the predator abundance to a higher cover of legumes may also be understood as the predator community benefiting from a more complex plant community structure. These outcomes were previously addressed by other authors (Moreby et al. 1994; Norris and Kogan 2000), who assessed the importance of the plant community structure on the predatory groups in influencing the movement, duration of stay and risk of predation mortality; however, information on this subject is rather limited. The positive correlation shown between the predators and legume cover (LC) may also be explained by a direct enhancement of alternative food

supplies, such as floral resources (Hodek and Honek 1996; Norris and Kogan 2000).

Predators had a significantly negative correlation with forb aphid abundance (Table 3), indicating they would not be effective at regulating aphid forb populations. Although most of the predators observed were known as active predators of cereal aphids, predator abundance did not appear to be related to grass aphids. However, it was perhaps not surprising given that in previous studies it was pointed out that there was no significant periodicity in the dynamics of the aphid or predators, suggesting that there was no clear predator–prey cycle (Leslie et al. 2009). It is also likely that other factors were involved such as the ability of aphids to move of their colonies and to develop rapidly (Winder et al. 1999) or the difficulty to estimate the impact of predators because of the ephemeral interactions with the aphid prey (Fievet et al. 2007). There were also indications that weather directly affected peak density of *M. dirhodum* and its impact on the spatial distribution of *Coccinella septempunctata* populations (Leslie et al. 2009).

The presence of legumes seems to be playing a key role in enriching the forb aphid community, which, in turn, increases the diversity of natural enemies such as parasitoids. The correlation between the richness of the parasitoids and forb aphids is in accordance with the results of Norris and Kogan (2000), and it reveals that aphids living on weeds or hedge-rows close to arable fields may also serve as alternative hosts or prey for the natural enemies when the grass aphids disappear from the field. In addition, these findings concurred with the patterns that have emerged from the comparison of correlation coefficients amongst the richness of herbivores and parasitoids described in previous studies (Caballero-López et al. 2010; Haddad et al. 2001; Koricheva et al. 2000).

The clear response of the aphids, aphidophagous parasitoids and predators to local factors, such as the grass and legume cover, indicates that, or such as the GC and LC, indicates that to better understand the interactions amongst the organisms of different trophic levels, small-scale factors, such as the intra-field plant community, must be taken into account in future studies.

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