

Bidirectional movement of aphid parasitoids (Braconidae: Aphidiinae) between crops and non-crop plants in agroecosystems of central Argentina

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Abstract The movement of predators and parasitoids between natural and cultivated habitats is a common process in agroecosystems, which may be affected by different biotic and abiotic factors, mostly related to the availability of resources. Here, through a broad approach, we aimed to obtain an overview of factors affecting the bidirectional movement of aphid parasitoids (Braconidae: Aphidiinae) across cultivated habitats and their natural vegetated borders. Using bidirectional flight traps, we measured the number of parasitoids moving from borders to crops and vice versa, in fields of three common crop species (alfalfa, oat and wheat) in the Pampean region, Santa Fe, Argentina. The effects of the abundance of aphid prey, abundance and richness of flowers in both habitats, as well as temperature and wind speed on parasitoid movement, were assessed through generalized mixed models, considering sampling date and field as random factors. The relationship between parasitism percentages and parasitoid movement from the borders to the crops was explored separately for three pest aphid

species: *Aphis craccivora* Koch, *Rhopalosiphum padi* (L.) and *Schizaphis graminum* (Rondani). Overall, we found a prevalence of parasitoids moving in the border-crop direction, mainly in wheat and alfalfa crops. Aphid abundance in the arrival habitat affected parasitoid movement in both directions. A link between parasitoid movement and parasitism percentages was observed for the aphid species *S. graminum* in wheat, suggesting a beneficial role of natural vegetation in pest control.

Keywords Aphid pest species · Non-crop vegetation · Parasitoid movement · Parasitism rates · Natural enemy

Introduction

The movement of predators and parasitoids between natural and cultivated habitats is a common process in agroecosystems (Ekbom et al. 2000). The presence of natural vegetated habitats in the surroundings of crop fields has been repeatedly shown to be effective in providing nectar, pollen, sap, alternative hosts or prey, and moderate microclimates for natural enemies, thus increasing their populations, enhancing their fitness, and consequently improving their pest control services (Gurr et al. 2004; Landis et al. 2005; Chaplin-Kramer and Kremen 2012; McClure and Frank 2015). These habitats also facilitate the gradual recolonization of crop areas where natural enemy populations have been reduced by a disturbance (Ekbom et al. 2000; Holland et al. 2000; Lee et al. 2001).

Parasitoids, the most important natural enemies of herbivorous insects in some ecosystems (La Salle 1993), tend to display strong dependence on the resources offered by non-crop habitats since adults need to periodically locate food to avoid starvation, as suggested by longevity and

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survival studies (Azzouz et al. 2004; Irvin et al. 2006). Movement enables parasitoids to find resources such as alternative food and hosts, and to escape from adverse conditions, which is critical to ensure the persistence of populations in crop fields (Feng et al. 2015). The movement of parasitoids may be affected by different biotic and abiotic factors, mostly related to the availability of resources (Holt and Hochberg 2001; Ries et al. 2004). Meteorological conditions, particularly winds, play a role in the initiation or termination of parasitoid movement across habitats (Schellhorn et al. 2014), although these factors have a slight effect on biological control programs (Jerbi-Elayed et al. 2015). Host plant stimuli, such as color, architecture, height, etc., may also elicit a flight response in parasitoid females (Jang et al. 2000). Moreover, parasitoid females are able to locate their hosts and discriminate the occurrence of hosts in plants by flying upwind toward volatile substances emitted by the host or plant–host complex (Vinson 1981). Host density in a plant patch may also be assessed by parasitoid females using olfactory and visual cues from a distance (Bora and Deka 2014).

Several studies have focused on the influence of natural environments on the biodiversity of agroecosystems (see review in Bianchi et al. 2006; Chaplin-Kramer et al. 2011), but just a few have been designed to measure the directionality of insect movement between crop and non-crop habitats (Duelli et al. 1990; Macfadyen and Muller 2013; Macfadyen et al. 2015; González et al. 2016). In this study, we focused on the movement of aphid parasitoids between crop and non-crop plants in field borders. Aphids (Hemiptera: Aphididae) represent a major pest of agricultural crops worldwide (Ahmad and Wani 2014), and aphidophagous parasitoids (Braconidae: Aphidiinae) are the biological agents most widely used to control aphid populations in many regions of the world (Bortolotto et al. 2015). Recent research has shown that, in the same study region, aphid pests in crop fields with higher proportions of natural vegetated borders tend to suffer higher parasitism rates than fields with a lower proportion of such habitats (Zumoffen et al. 2012, 2015). Considering the scarce published evidence regarding the movement of parasitoids in agricultural settings of the Pampean region, the aim of this study was to obtain an overview of factors affecting the bidirectional movement of Aphidiinae parasitoids across cultivated habitats and their natural vegetated borders. We also explored whether increased parasitoid movement from natural vegetated borders to the cultivated plants provided enhanced control of *Aphis craccivora* Koch, *Rhopalosiphum padi* (L.), and *Schizaphis graminum* (Rondani), important pest species limiting the production of alfalfa (*Medicago sativa* L.), oat (*Avena sativa* L.), and wheat (*Triticum aestivum* L.), respectively, in the study region (Basigalup and Ustarroz 2007).

Materials and methods

Study area

The study was carried out at the Rafaela Experimental Station [Instituto Nacional de Tecnología Agropecuaria (INTA)] in the locality of Rafaela, Santa Fe, Argentina (31°11'S, 61°29'W). The study site has a typical Argiudoll soil, which is deep and moderately well drained. The zone is characterized by plains and extensive landscapes. The annual average rainfall is 1050 mm (west–east variation, 125 mm), distributed with an iso-hygro regime, with 70% of the rainfall in spring–summer, 23% during autumn and only 7% in winter. The annual mean temperature is 18.0 °C (north–south variation, 1.0 °C), with means of 26.0 and 12.7 °C in January and July, respectively (the hottest and coldest months of the year, respectively), and with an average thermal amplitude of 13.3 °C (Panigatti and Mosconi 1982). In the area, prevailing winds blow from the east (<http://siga2.inta.gov.ar/en/datoshistoricos/> consulted in November 2014).

The three crop species studied here, alfalfa, oat, and wheat, are intensely cropped in the region (Basigalup and Ustarroz 2007; Basigalup and Rossaningo 2007; Rimski-Korsakov et al. 2015). Alfalfa is a perennial legume, the vegetative regrowth and flowering stages of which start in September (Basigalup and Rossaningo 2007), whereas oats and wheat are annual cereals, usually sown in June and harvested in December (Rimski-Korsakov et al. 2015). Vulnerability to insect herbivory for all these crop species is enhanced after winter (end of September) when aphid populations increase, favored by higher temperatures, coinciding with regrowth in alfalfa and spike formation in oats and wheat (Bannerman and Roitberg 2014; Lacoste et al. 2015).

In this area, two fields of each crop species, separated by a minimum of 0.15 km and a maximum of 4.5 km, were selected. Fields were chosen for having an edge of spontaneous vegetation (i.e., a 4- to 6-m-wide strip, hereinafter called “border”) on the eastern side. These borders were composed of grasses, scattered bushes and vines (0.3–1.5 m high) and an herbaceous layer including annual and perennial plants mainly in the families Asteraceae, Apiaceae, Brassicaceae, Asclepiadaceae and Malvaceae; grasses were dominant [see details of plant species lists in Bertolaccini et al. (2008)]. In addition, all selected fields were of a similar size (1.8–2.5 ha) and surrounded by fields with the same crop at a similar phenological stage. No insecticides were sprayed on plants during the sampling period.

Insect sampling

In each field ($n = 6$), two bi-directional flight-interception traps were placed at 70 cm from the ground and separated by 8–10 m from each other, parallel to the edge between

the crop and the border. Traps were set up in open sites to intercept actively flying insects. By doing so, we obtained quantitative data about the direction and intensity of parasitoid movement between the two adjacent habitats. Traps consisted of transparent polycarbonate sheets of 20 × 20 cm, with two faces smeared with aluminum grease (ZKL, used for wheel bearings, which is water-repellent and resistant to high temperatures). Bi-directional traps are useful tools to quantify movement across habitats and help to avoid biases due to the use of color as bait (Boiteau 2000). Traps remained active simultaneously in the three crop species in the period of maximum activity of insects, from September to December 2012 (Southwood and Henderson 2000). The start of spring, September is a critical period for all three crop species, due to regrowth in alfalfa and spike formation in oat and wheat. In December, the sampling ended with the harvest of oats and wheat, and alfalfa cutting. Adult Aphidiinae parasitoids captured weekly on each side of traps were counted and removed, obtaining a total of ten captures per trap. Given that our interest was centered on all aphidiinae species as potential aphid control agents, in addition to the impossibility of obtaining specific identifications of glued specimens, parasitoids captured in the traps were identified to subfamily level.

On the same sampling dates, seven transects (50 cm long × 30 wide each) were established within the crops (2 m from the crop edge) and their borders, and the following variables estimated:

1. Abundance of pest aphids in crops. This variable was estimated as the total number of aphid adults and nymphs counted in all crop plants along transects.
2. Abundance of alternative hosts, estimated as the total number of adults and nymphs of innocuous aphid species observed on non-crop plants border transects.
3. Parasitoid abundance in crops, estimated as the total number of mummies counted in crop transects.
4. Parasitism percentages observed for the pest aphid species associated with each crop (*A. craccivora* in alfalfa, *R. padi* in oat, and *S. graminum* in wheat). Parasitism percentages were calculated as (total number of mummified aphids/total number of aphids) × 100, in crop transects.
5. Flower/inflorescence abundances in the crops, estimated as the number of flowers and inflorescences observed by transects, in the crops.
6. Flower/inflorescence abundances in the borders, estimated as the number of flowers and inflorescences observed by transects, in borders.
7. Species richness of plants with flowers or inflorescences in border transects. Samples of unidentified species were collected and later identified by specialists.
8. Temperature.
9. Wind speed. Data of temperature and wind were obtained from a weather station located in INTA-Rafaela Argentina (<http://siga2.inta.gov.ar/en/datosdiarios/> consulted in November 2014), and averaged by week for inclusion in the analyses.

Data analysis

A generalized linear mixed models (GLMMs) approach, with a Poisson error distribution and a log link function, was used for data analysis. To explore differences in the magnitude of parasitoid movement (i.e., abundance of parasitoids captured in traps, the response variable), we performed a model including the crop species (three levels—oat, wheat, alfalfa), direction of capture (two levels—border to crop, crop to border) and their interaction as the fixed factors (model 1). To account for the dependence of data, two random factors were included: sampling date (a factor with ten levels), and traps nested within fields (trap < field).

The effects of the different variables on the parasitoid movement were assessed in a second pair of models (model 2), in which data were partitioned according to the direction of movement, from border to crop (model 2.1) and from crop to border (model 2.2), pooling data from the two traps for each field. A two-step approach was applied: firstly, a univariate analysis was conducted to select explanatory factors potentially associated with the movement of parasitoids in models 2.1 and 2.2 (crop species and variables 1, 2, 5, 6, 7, 8, and 9, described above) and those having a *P* value ≤ 0.15 were selected for multivariate analysis (Dohoo et al. 1996). Only the explanatory variable with the lowest *P* value was selected for the multinomial model when two of them may have explained similar results and were statistically associated (collinearity evaluation). Secondly, a GLMM approach, with a Poisson error distribution and a log link function, was used to evaluate the effect of the selected explanatory factors and their interactions on the parasitoid movement, including two random factors in the models: sampling date (a factor with ten levels), and field.

Moreover, correlated variables ($r > 0.6$) were deleted from the original models to avoid multicollinearity (Freckleton 2011). Most parsimonious models were selected via backward elimination of non-significant variables and interactions using Akaike (1987) information criterion values (Dohoo et al. 1996).

Under the premise that the percentage of parasitism in herbivores could be considered as a good estimator for the outcome of biocontrol (Hawkins and Gross 1992), we tested the explanatory power of the number of parasitoids moving from borders to crops on one date (*t*) for the parasitism rates in the following week (*t* + 1) through GLMMs (with a binomial error distribution and a logit link function), including sampling date and field as random factors. In these

analyses, parasitism of the three most important aphid species on each crop (*A. craccivora*, *R. padi*, and *S. graminum*) was separately used as response variables. All analyses were performed using the package lme4 (Bates et al. 2011) in R software version 3.1.1 (R Core Team 2014).

Results

A total of 476 specimens of hymenopteran parasitoids were captured on both sides of the traps. A majority (89%) belonged to the Braconidae, 4% to the Ichneumonidae and the rest to three other families (Pteromalidae, Encyrtidae and Ceraphronidae). The subfamily Aphidiinae was the most abundant among the braconids captured (86%), with their number varying across habitats and dates (Supplemental Fig. 1), equivalent in total to 2.38 parasitoids/cm² per date. Parasitoid movement was significantly higher from the natural vegetation to the crop than vice versa in wheat and alfalfa crops. A significantly lower number of moving aphids were detected in oat crops, without differences in movement direction (Fig. 1; Table 1).

Of the seven potential explanatory variables tested, three were selected after the univariate analysis for inclusion in the multivariable analysis for model 2.1 and two for model 2.2 (selected variables had a significance value of $P < 0.15$; Table 2). The number of parasitoids moving from the edges to the crops (model 2.1) was affected by two variables: crop species and the abundance of aphids in the cultivated plants, with a significant interaction between them. Movement was lower in oats than in the other crop species, whereas the

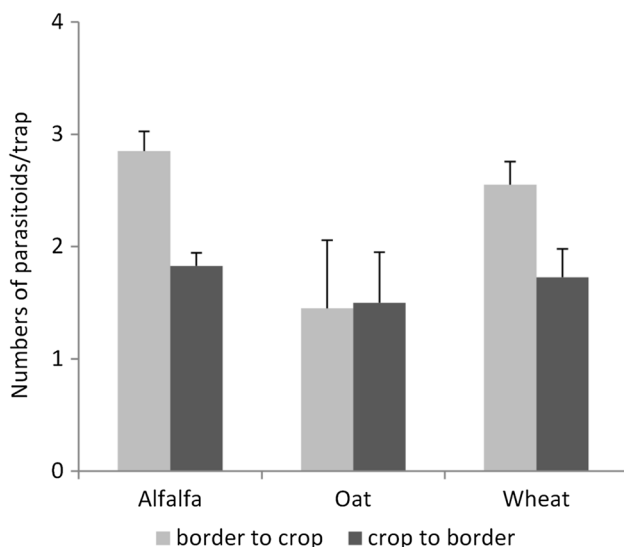


Fig. 1 Mean number of parasitoids moving across habitats in each crop species, according to the generalized linear mixed model (GLMM) (model 1). Error bars indicate SE

Table 1 Exploratory analysis (fixed effects) of the number of parasitoids moving across habitats in each crop species according to the generalized linear mixed model (GLMM) (model 1)

Variable	Estimate	SE	z value	P value
Model 1				
Crops				
Alfalfa (reference category)				
Oat	-0.676	0.161	-4.208	0.001*
Wheat	-0.111	0.136	-0.820	0.412
Movement	-0.446	0.149	-2.986	0.002*
Movement × Oat	0.479	0.236	2.029	0.042*
Movement × Wheat	0.055	0.215	0.255	0.799

* $P < 0.05$

available number of aphids in plants positively affected the number of parasitoids captured in wheat crops (Table 3; Fig. 2). The number of parasitoids moving from crops to edges (model 2.2) was not affected by crop species but was directly related to the abundance of non-pest aphid species feeding on the vegetation (Table 3; Fig. 3).

In the study region, the pest aphid species studied here (*Aphis craccivora*, *R. padi* and *S. graminum*) were parasitized by nine species of Aphidiinae: *Aphidius colemani* Viereck, *Aphidius ervi* Haliday, *Aphidius matricariae* Haliday, *Aphidius picipes* (Nees), *Aphidius rhopalosiphii* De Stefani-Perez, *Diaeretiella rapae* (McIntosh), *Lysiphlebus testaceipes* (Cresson), *Ephedrus plagiator* (Nees) and *Praon volucre* (Haliday) (Zumoffen 2014). Parasitism rates were variable across sites and sampling dates, although mean values were rather similar among species (Supplemental Fig. 2). On average, *A. craccivora* in alfalfa suffered higher parasitism ($\bar{X} = 33\%$; SE 10%, $n = 10$, range 20–60%) than *R. padi* in oat ($\bar{X} = 27\%$; SE 18%, $n = 10$, range 0–62%) and *S. graminum* in wheat ($\bar{X} = 21\%$; SE 13%, $n = 10$, range 0–62%). A significant relationship between the number of parasitoids moving from the border to the crop and parasitism rates recorded in the following week was detected only for the aphid *S. graminum* in wheat field crops ($R^2 = 0.38$, $P = 0.01$), but no relationship was found for the other two pest species (Table 4; Fig. 4).

Discussion

The role of natural habitats in enhancing the diversity and efficacy of natural enemies has been widely explored (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Veres et al. 2013), but evidence about the bidirectional movement of insects between natural habitats and agroecosystems and its consequences for pest control is relatively scarce (Macfadyen and Muller 2013; Macfadyen et al. 2015; González

Table 2 Explanatory variables (fixed effects) evaluated for the study of movement of parasitoids from the borders to the crop (model 2.1) and vice versa (model 2.2); GLMMs univariate

Models	Variable	Range	\bar{X}	Estimate	SE	<i>z</i> value	<i>P</i> value
Model 2.1	Crops						
	Alfalfa (reference category)						
	Oat	–	–	–0.676	0.16	–4.22	0.001*
	Wheat	–	–	–0.112	0.135	–0.822	0.411
	Abundance of pest aphids	0–583	101	0.002	0.001	3.973	0.001*
	Abundance of non-pest aphids	0–931	152	–0.001	0.001	–0.109	0.913
	Abundance of flowers in the crops	0–5	2	0.066	0.044	1.492	0.136
	Abundance of flowers in borders	0–3	1.7	0.161	0.083	1.95	0.051*
	Species richness of plants	0–5	2.2	–0.06	0.057	–1.052	0.293
	Temperature	15.4–24.3	20	–0.023	0.067	–0.346	0.729
Wind speed	8–18	13	–0.005	0.073	–0.068	0.946	
Model 2.2	Crops						
	Alfalfa (reference category)						
	Oat	–	–	–0.196	0.173	–1.136	0.256
	Wheat	–	–	–0.056	0.166	–0.735	0.735
	Abundance of pest aphids	0–583	101	0.001	0.001	1.031	0.302
	Abundance of non-pest aphids	0–931	152	0.001	0.001	2.669	0.008*
	Abundance of flowers in the crops	0–5	2	–0.061	0.054	–1.137	0.256
	Abundance of flowers in borders	0–3	1.7	0.165	0.085	1.957	0.050*
	Species richness of plants	0–5	2.2	0.024	0.068	0.352	0.725
	Temperature	15.4–24.3	20	–0.027	0.067	–0.395	0.693
Wind speed	8–18	13	–0.057	0.07	–0.822	0.411	

*Selected by *P* value >0.15**Table 3** Variables (fixed effects) affecting the number of parasitoids moving from the borders to the crop (model 2.1) and vice versa (model 2.2) according to the more parsimonious GLMMs

		Estimate	SE	<i>z</i> value	<i>P</i> value
Model 2.1	Crops				
	Alfalfa (reference category)				
	Oat	–0.263	0.427	–0.616	0.54
	Wheat	–0.189	0.367	–0.514	0.60
	Abundance of pest aphids	0.002	0.001	2.661	0.01*
	Oat × Abundance of pest aphids	–0.003	0.001	–1.89	0.06
	Wheat × Abundance of pest aphids	0.003	0.001	2.64	0.01*
Model 2.2	Abundance of flowers in borders	0.235	0.142	1.650	0.09
	Abundance of non-pest aphids	0.001	0.001	2.039	0.04*
	Abundance of flowers in borders	0.096	0.091	1.055	0.29

et al. 2016). To our knowledge, our study is the first to examine the movement of Aphidiinae parasitoids between crops and their borders in agroecosystems of the central region of the Pampean region, Argentina. This quantification may be relevant to the implementation of aphid pest control in the region (Mazzi and Dorn 2012). Regarding aphids, since only winged adults have the ability to disperse, and considering that such morphotypes tend to appear in the colony at the ends of seasons (Blitzer et al. 2012), the alternating movement of individuals between crop and non-crop plants scarcely occurs. Moreover, flight in aphids is passive, and frequently aided by high-altitude air currents (Powell

et al., 2006). Bearing this in mind, crop borders seem to have greater relevance as a source of parasitoids rather than aphids to the crop field, but further research is necessary to examine this in more detail.

Overall, we found that a greater number of aphidiinae parasitoids moved from the border habitats to the crop fields than vice versa. This trend was observed in two of the three crop species studied (wheat and alfalfa), i.e., those in which parasitoid movement was higher. It is probable that traps detected the routine or “trivial” movement of insects, i.e., those movements associated with daily activities like foraging, mate location, seeking shelter or a resting place,

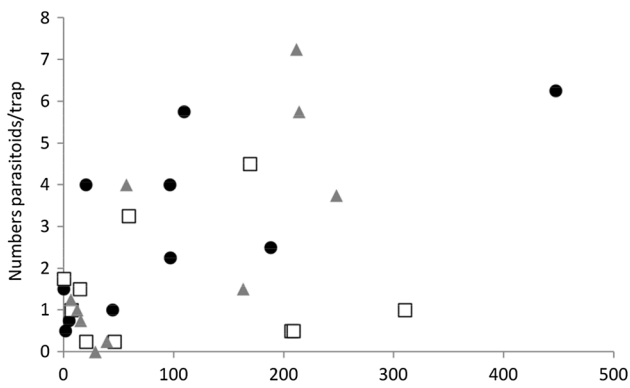


Fig. 2 Relationship between number of parasitoids moving from the borders to the crops and number of pest aphids in alfalfa (black circles), wheat (grey triangles) and oat (white squares) crops. Relationships were significant only in wheat crop, according to GLMM (see interaction between factors, model 2.1)

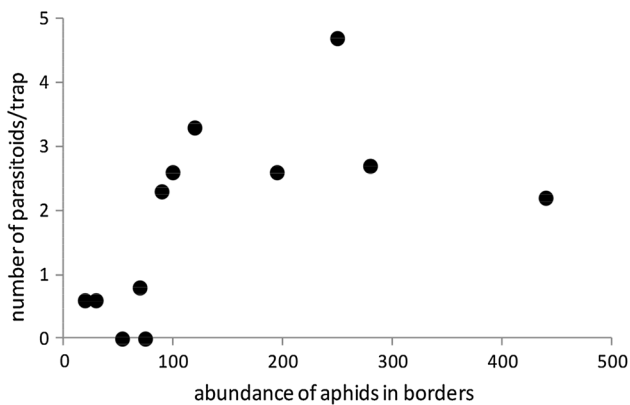


Fig. 3 Significant relationship between number of parasitoids moving from the crops to the borders and abundance of innocuous aphids in the natural vegetated borders. Adjusted means according to GLMM (model 2.2)

Table 4 Relationship between the number of parasitoids moving from the border to the crop in time t and parasitism rate in $t + 1$ according to the GLMMs

Response variable	Explanatory variable			
Parasitism rate (time $t + 1$)	Number of parasitoids moving from border to crop (time t)			
	Estimate	SE	z value	P value
<i>Aphis craccivora</i>	-0.015	0.023	-0.655	0.51
<i>Rhopalosiphum padi</i>	-0.037	0.035	-1.051	0.29
<i>Schizaphis graminum</i>	0.085	0.033	2.596	0.01

etc. (Van Dyck and Baguette 2005). Individuals found at the interface between habitats are the most likely to cross boundaries (Fahrig 2007), thus the detection of parasitoid movement, even through routine displacements, may have

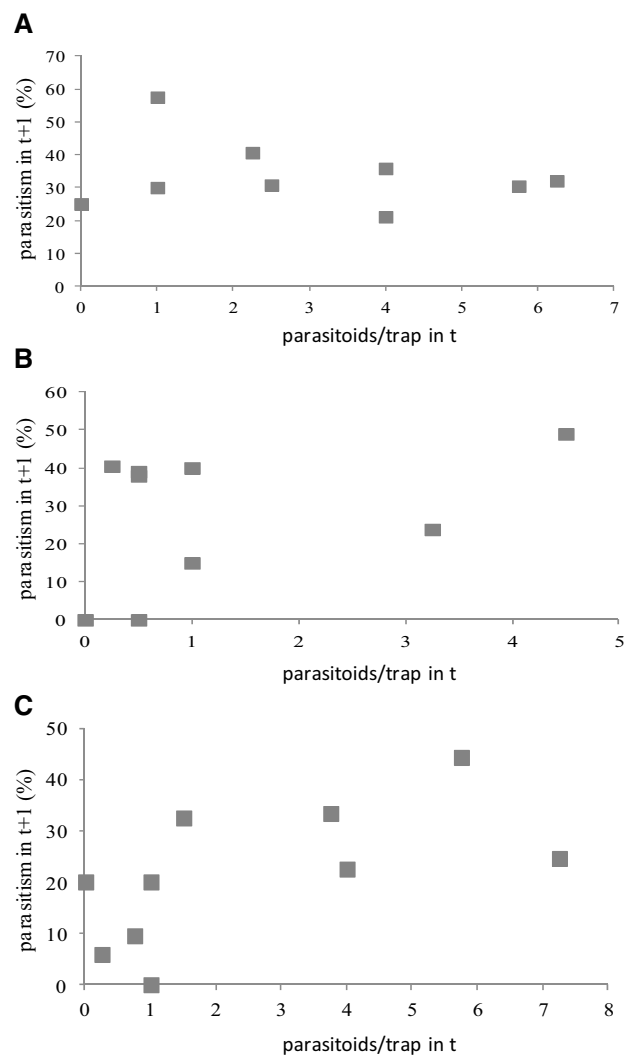


Fig. 4a-c Relationship between mean number of Aphidiinae parasitoids captured in traps facing the borders on date t and parasitism rates on date $t + 1$ of three aphid pest species. **a** *A. craccivora* in alfalfa, **b** *R. padi* in oat, and **c** *S. graminum* in wheat. Regression model: parasitism in *S. graminum* on $t + 1 = 12.88 + 3.33 \times$ parasitoids moving to the crop/trap on t

important implications in biological control (Blitzer et al. 2012). In this context, our data give general support to the idea that natural borders provide parasitoids to the crops, and thus may be considered as beneficial, at least when aphid pests are the target species for control.

Understanding the role of sinks or sources of parasitoids in agroecosystems is vital in studies of habitat manipulation to control pests (Lavandero et al. 2006). Bidirectional traps were set up at the field when studied crops were most vulnerable to aphids (regrowth in alfalfa and spike formation in oats and wheat). Thus, the gathered data on parasitoid movement could be used to predict the potential of these natural enemies in aphid regulation. The broad approach used in this study indicated that the only factors affecting

parasitoid movement were crop species and those related to aphid availability, whereas microclimatic conditions (wind velocity and temperature) showed no effect. The number of aphidiinae parasitoids moving in both directions was positively related to the abundance of aphids feeding in the “arrival habitat,” particularly in the wheat crop. This result agrees with our expectations, since parasitoids are guided mainly by chemical cues, and evidence indicates that parasitoids are capable of responding to differences in quality, without the need to make direct contact with host patches to assess their profitability (Fischbein et al. 2012).

The movement of parasitoids from borders to crop increased with an incremental rise in the abundance of flowers in the natural vegetation, but this effect was only evident in univariate regressions made as a previous step for model construction (see Table 2). The benefits obtained by parasitoids when feeding on carbohydrates have been widely documented (Williams and Roane 2007; Vollhardt et al. 2010a). It has also been demonstrated that the availability of such nutrients in agroecosystems is very limited (Vollhardt et al. 2010b). Consequently, parasitoids have to move periodically, mainly by flight, to obtain resources in the natural habitats surrounding crops.

Although, in the present study, we could not demonstrate effects of abiotic factors, we can make some suggestions. Regarding wind, many species of parasitoids locate hosts and host habitats via anemotactic responses to airborne odors emanating from host insects or their host plants (Tumlinson et al. 1993), but responses to wind in field conditions are very complex (Messing et al. 1997). Here, the predominant recorded movement of parasitoids was from borders to crops, in the direction opposite to the prevailing winds (averaging 13 km/h in the study period). Moreover, we found no relationship between parasitoid captures and wind speed, which suggests that parasitoids were able to actively orient their flight upwind following plant and host cues, which were probably stronger in the crops. It is important to note that, even though very small, most parasitoid species can actively fly, and change flight direction and height in response to host availability (Takasu et al. 2004; Petit et al. 2008). Regarding temperature, this variable has been shown to be the main elicitor of activity of poikilothermic animals, with demonstrated effects on survival, development, fertility, oviposition time and dispersion of parasitoids (Flinn and Hagstrum 2002; Rouse et al. 2009). In terms of flight activity, several studies have shown that increases in temperature tend to increase parasitoid movement (Idris and Grafius 1998; Rouse et al. 2009). Normal flight in parasitoids occurs at 16–32 °C, with an optimum temperature range between 22 and 30 °C (Yu et al. 2009). In our study, parasitoid movement was affected neither by temperature nor by winds, probably due to the low thermal amplitude in the period studied (average weekly minimum 15 °C and

maximum 24 °C) and the low velocity of winds, which never surpassed the threshold mentioned for parasitoid flight (Juillet 1964; Jerbi-Elayed et al. 2015).

Our data indicated that, along the study period, all three pest aphid species were parasitized. Parasitism rates of *A. craccivora* in alfalfa fields were never below 20% and frequently surpassed 30%, levels which indicate possible success of parasitoids in controlling their hosts (Hawkins et al. 1993). Lower and more variable parasitism rates were observed for *R. padi* and *S. graminum*. The explored relationship between parasitism percentages and the movement of these parasitoids from border to crops 1 week earlier was only significant for data obtained in wheat fields (pest aphid *S. graminum*). Previous studies in the same system indicate that nine of the plant species spontaneously growing in the borders of the wheat fields harbor aphids parasitized by *L. testaceipes* and *A. colemani* (Zumoffen 2014), which are two species of generalist aphidiinae very common at both regional and local scales, and were also found parasitizing *S. graminum* in this study. An incremental increase of the interception area used to trap flying parasitoids in relation to total crop field area could probably enhance the probability of detecting a relationship between parasitism and parasitoids moving across habitats in the other two studied species, and this aspect deserves further research.

In recent studies in the same region, it has been demonstrated that several native plant species spontaneously growing in borders of alfalfa agroecosystems act as sources of *L. testaceipes*, the most important biocontrol agent of *A. craccivora* (see Zumoffen et al. 2015). Moreover, smaller aphid pest populations and higher parasitism rates in alfalfa fields with higher proportions of natural borders have been observed (Zumoffen et al. 2012). However, our present results did not establish a relationship between enhanced parasitism and the number of parasitoids moving from the borders in alfalfa fields. It should also be taken into consideration that borders in the studied fields were fairly thin (4–6 m wide strip), thus traps could potentially have captured parasitoids flying from one adjacent field to another (over the border). Thus, further detailed studies including alfalfa fields adjacent to another alfalfa field (i.e., without border vegetation) should be made to give a better understanding of the beneficial effects of margins previously reported for the region (Zumoffen et al. 2012).

In conclusion, we found a bidirectional interchange of Aphidiinae parasitoids across crops and their borders with a prevalence of parasitoids moving in the border-crop direction. Aphid abundance in the arrival habitat was one of the factors influencing parasitoid movement. Another factor influencing parasitoid movement was the quantity of floral resources, which was directly related to the number of parasitoids provided by the border to the crop. A link between parasitoid movement and parasitism percentages was

observed for the aphid species *S. graminum* in wheat, suggesting a beneficial role of natural vegetation in pest control.

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