

# RELATIONSHIP BETWEEN THE ABUNDANCE OF APHIDS AND THEIR NATURAL ENEMIES IN CEREAL FIELDS AND LANDSCAPE COMPOSITION

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## ABSTRACT

We investigated, over the course of two years, the association between the abundance of aphids and their natural carabid enemies and landscape, which may help in the development of effective strategies for reducing the incidence of aphid outbreaks in agricultural crops. This was undertaken in 12 wheat and 12 maize fields each year in an agricultural landscape in western France. Our study area was characterized by hedgerows surrounding arable fields and permanent grassland. Some areas have not changed much for several decades, while field enlargement and removal of hedges occurred in some areas following agricultural intensification. This paper aims to determine if the abundance of aphids in crops (either directly, or indirectly via their natural enemies) is associated with the landscape around fields and if so, is it dependent on the landscape scale considered. We observed that the abundance of aphids in fields was associated with landscape composition at a large scale (500 m and 800 m). There was a positive correlation between the abundance of aphids and the proportion of the area under woodland and grassland at these scales. There was a negative correlation between the abundance of carabids and the proportion of grassland and hedgerow around crop fields. The species richness of carabids was positively correlated with the proportion of hedgerows. We found that the abundance of aphids in wheat fields was negatively and in maize fields positively associated with the proportion under grass strips. At a large scale carabid abundance in both types of culture was positively correlated with the proportion under grass strips.

**Keywords:** agroecosystems, landscape structure, crop pests, aphids, biological control, semi-natural habitats

## Introduction

The increasing demand of the human population for food resulted in the necessity to increase agricultural yields and subsequently in the intensification of agriculture (Gardner 1996; Krebs et al. 1999), which among other things resulted in an increasing use of pesticides (Lewis et al. 1997; Oerke and Dehne 2004; Ameixa and Kindlmann 2011a). However, the use of pesticides has not completely prevented pest outbreaks and subsequent losses of yield (Wilson et al. 2001; Oerke 2006), because the pests have either become resistant to pesticides and/or there has been a breakdown in ecological processes like pollination, ecological functioning of the soil and biological control (Lewis et al. 1997; Plantegenest et al. 2007). In addition, there are many reports of pesticides adversely affecting man (Benton 2003; Lee 2004; Ameixa and Kindlmann 2011a). Therefore, effective alternatives to pesticides have to be found.

One alternative is to use ecosystem services, such as natural enemies, to suppress the abundance of agricultural pests (Kindlmann and Růžička 1992; Altieri 1999; Kindlmann and Dixon 1999; Plantegenest et al. 2001; Benton 2003; Wratten et al. 2003). In this respect landscape complexity, both in terms of composition and structure can be important (Burel and Baudry 1995; Kindlmann et al. 2005). Agricultural intensification leads to simplification of landscape structure by increasing the

size of the fields, homogenization of cultures and fragmentation of semi-natural habitats (hedges, grasslands, woodlands), which has resulted in a reduction in the biodiversity in agroecosystems, including that of natural enemies, (Stoate et al. 2001; Robinson and Sutherland 2002). This undermines the efficiency of natural biological control at a local and landscape scale (Östman 2001; Krauss 2011), because regulation of pests by their natural enemies is more likely in a heterogeneous landscape (Bianchi et al. 2006; Maisonhaute and Lucas 2012). This is also supported by a meta-analysis of the results published in 209 papers, which shows that 52% of herbivorous insects are significantly less abundant in polycultures than in monocultures (Andow 1991).

Aphids (Hemiptera: Aphididae) are among the most important pests globally (Dixon et al. 1996; Dixon and Kindlmann 1998; van Emden and Harrington 2007; Ameixa and Kindlmann 2011b; Šipoš et al. 2012). They are harmful to crops because they both consume phloem sap and thus deprive plants of nutrients (Fievet et al. 2007; Giordanengo et al. 2007), and are vectors of viruses, which can seriously damage plants (Nault et al. 1997).

Non-flying polyphagous generalist predators, like carabids, are important natural enemies of aphids. It is believed that predation by carabids can regulate aphid abundance and reduce the incidence of outbreaks (Symondson et al. 2002). However, their regulatory effect on aphids is still not fully understood, because it is rarely

studied in the field and the composition of the diet of carabids is not well known (Holland 2002; Symondson et al. 2002; Sunderland 2003; Ameixa and Kindlmann 2008).

Landscape composition, in terms of the relative proportion and size of patches of vegetation of different types and their spatial configuration, is important for both aphids and carabids. Because of their poor dispersal ability, many species of carabids are very sensitive to landscape fragmentation and changes in land use (Petit and Burel 1998; Holland 2002; Keller and Largiadèr 2003). The presence and abundance of aphids in crops is also associated with the structure of the landscape (Ricci et al. 2009). This is because both aphids and their natural enemies do not overwinter in fields but in semi-natural habitats such as woodland and grassland (Carter et al. 1982; Corbit et al. 1999; Pywell et al. 2011). These habitats provide a source of both aphids and their natural enemies, which colonize cereal fields in spring (Winder et al. 1999; Levie et al. 2005; Martinez et al. 2005; Bianchi et al. 2006; Grez et al. 2008). Therefore, the effect of semi-natural habitats on aphid abundance can be both positive and negative, depending on relative abundance of aphids and their natural enemies in the semi-natural habitats (Vanbergen et al. 2010; Vandewalle et al. 2010; Woodcock et al. 2010).

The aim of this study is to determine the association between the abundance of aphids and their natural enemies and landscape, which may help in the development of effective strategies for reducing the incidence of aphid outbreaks in agricultural landscapes. Here we test the hypothesis that the abundance of aphids in fields is influenced by landscape composition (either directly, or indirectly via their natural enemies) and this is dependent on the landscape scale considered.

## Materials and methods

### Study site

This study was conducted during 2009 and 2010 within an agricultural landscape situated in the “ZA Armorique” in the vicinity of Pleine-Fougères, which is located in the south of Mont Saint Michel’s Bay (Brittany, Western France, 48°36’N, 1°32’W). The locality is a long-term ecological research site (Burel et al. 1998; Baudry et al. 2000). It is representative of the “bocage” landscape, characteristic for Brittany, with a mixture of cultivated fields and grassland with a dense network of hedges (Baudry et al. 2000). This site also has a gradient of landscapes (Fig. 1) ranging from a fine-grain landscape with a complex network of hedgerows (160 m/ha) enclosing small fields and a heterogeneous landscape structure (Le Coeur et al. 1997) to a more open landscape with fewer meters of hedgerow per hectare (70 m/ha) enclosing large fields (Baudry et al. 2000). The main crops in this area are ce-

reals, maize, oilseed rape and vegetables. The main agricultural activity is mixed farming and milk production.

To estimate the variations in the landscape at the scale of this area, the experimental fields were chosen within an area of 24 km<sup>2</sup>, distributed along the landscape gradient in each year (Baudry et al. 2006), depending on the features of the surrounding landscape. The software CHLOETM 3.1 and ZAZIETM1.0 (Baudry et al. 2006) was used to verify that the fields were representative of the gradient in openness of the landscape within the study area.

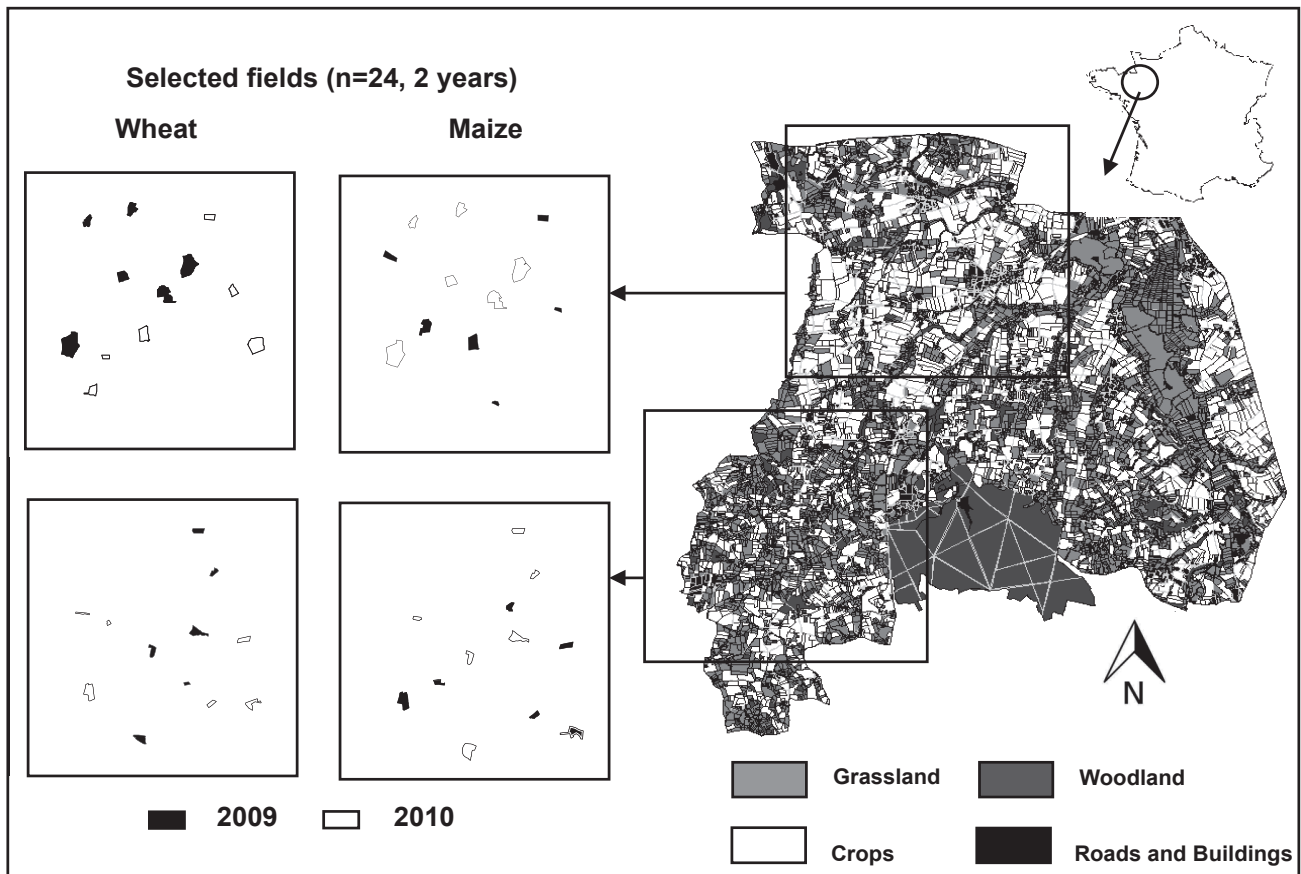
### Monitoring

In each year (2009 and 2010), 12 wheat and 12 maize fields were chosen at random within the experimental area (because of crop rotation they differed between years). In each of these fields, six sampling points were randomly selected using ArcGIS software (version 9.1, ESRI) and geo-referenced using a GPS (Juno™ ST, Software ArpentGIS 4.5). In each year, sampling was performed 5 times during the season for wheat and 6 times for maize fields, every 2 weeks: between May 1 and July 15 in wheat and June 20 and September 5 in maize fields. This period covers the time when aphids are most abundant on these crops.

At each of these points and instants, the numbers of aphids present on 25 tillers of wheat and 5 plants of maize were counted and their species and developmental stages and life form (larvae, unwinged and winged adults) were determined. Carabids were captured at the same sampling points, using pitfall traps (one trap per sampling point). Each trap was set when the aphids were counted and emptied 15 days later. The traps (polypropylene pots, H = 120 mm, Ø 8.5 cm) were buried in the ground and protected from rain by transparent plexiglas plates, positioned about two inches above each trap. Each trap contained a solution of 50% salt water and 50% propylene glycol (Bouget 2001). Captured carabids were stored in 70% alcohol and identified to the species level using the identification keys of Trautner and Geigenmüller (1987) and Forsythe (2000).

### Characterization of the landscape

In a 100 m wide buffer strip around each field and in circles with diameters 300, 500, and 800 m, centered in the centre of each the fields sampled, we measured six variables: percentage of land covered by (1) grassland, (2) woodland, (3) grass strips, (4) crops (wheat, maize, oilseed rape), (5) other elements (water, builtup areas, roads, railways, gardens) and the length in meters of (6) hedgerows. All these were identified and digitized with ArcGIS software (version 9.1, ESRI). In the subsequent text, the distance is indicated as a subscript to the landscape variable (e.g., grassland<sub>800</sub> means proportion of grassland in the circle with 800 m diameter). The distances used are a compromise between the scale to which the



**Fig. 1** Location and main land use in the study area. Distribution of the 24 wheat and maize fields sampled in the two years of the study.

landscape structure influences the maximum population of aphids and parasitoids: about 1 km (Rand and Tschantke 2007). The hedgerows were included, because they structure agricultural landscapes and thus are particularly important with respect to the movement of organisms in agroecosystems (Ricci et al. 2009).

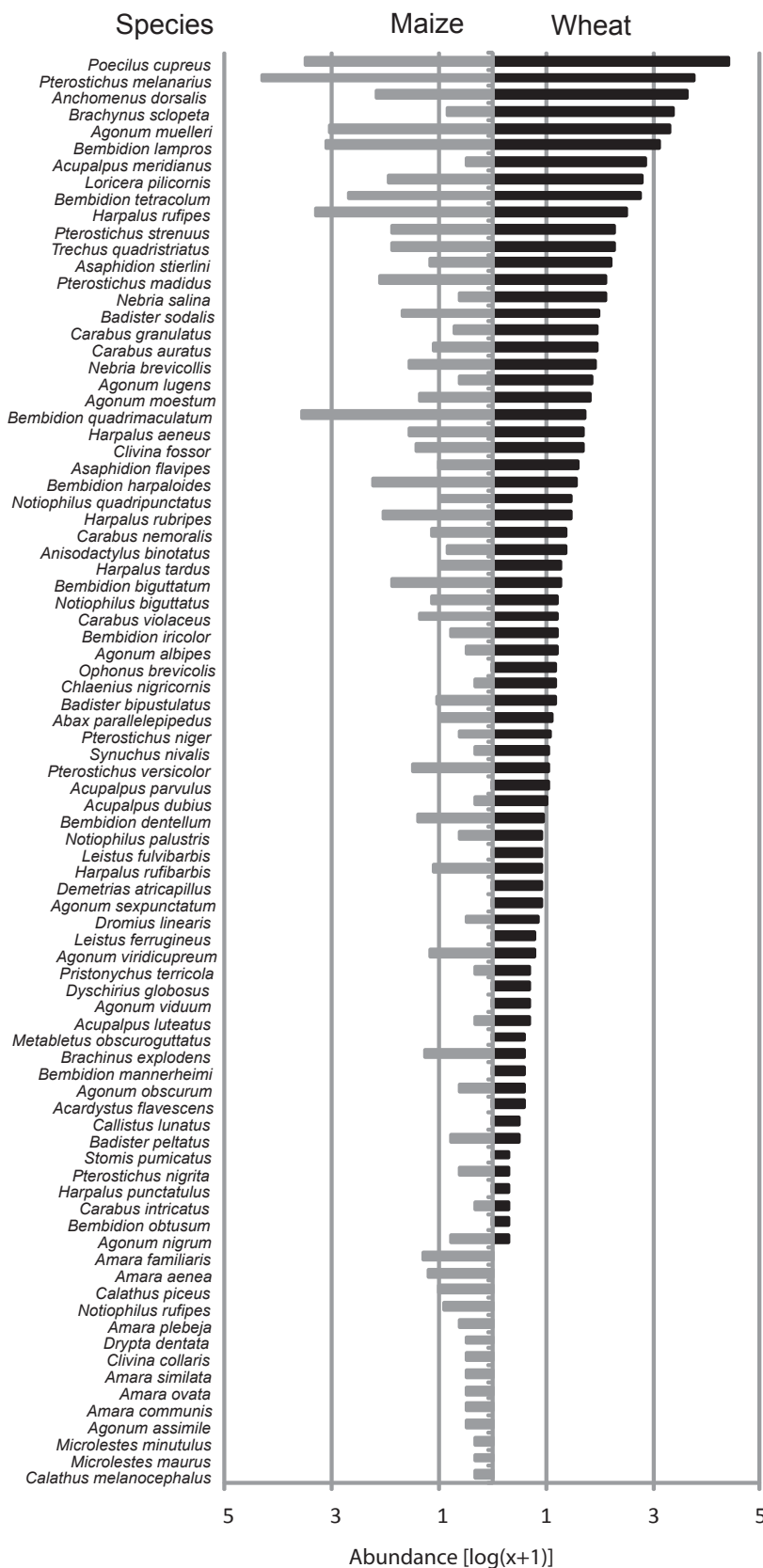
The abundance of aphids is determined by climatic factors (Hulle et al. 2010), and therefore we also included year as an explanatory variable. As we considered percentages, we had only 5 degrees of freedom among the 6 variables and one of them could be deleted. Because the percentage covered by grassland was strongly negatively correlated with that of the cultures, we deleted cultures from further analyses. This resulted in 21 variables: 5 types of landscape times 4 sizes of circles/buffer zones considered, plus year.

### Statistical analysis

Because the number of explanatory variables was large, we had to adopt a procedure for variable selection. This was conducted in two phases. First, we used a procedure for selecting variables used by Ricci et al. (2009). For each landscape variable and each distance, the Akaike index (Akaike Information Criterion, Akaike 1974) was calculated. The distance with the lowest AIC was selected for subsequent analyses. Then, the procedure *glmulti* (Calcagno and De Mazancourt 2010) was applied to select the combination of variables producing the best model

based on the AIC values. The default method in *glmulti* (method = "h") fits all candidate models. All 50 possible models containing all considered explanatory factors were fitted to the data and ranked according to their AIC values from the model with the lowest AIC value (Appendices 1, 2, 3, and 4). Top regression models, with the highest level of empirical support, were those within AIC units of the top-supported model (Burnham and Anderson 2002) and with informative parameters (Arnold 2010). Finally, the GLM including all variables selected by this procedure were adjusted to the data set. All data were pooled and analyses used Poisson error term and a Log link. The significance of the estimated parameters was tested using the chi-square test. These models were calculated using R Software (R Development Core Team, 2008).

Autocorrelation is problematic for classical statistical tests like regression, which rely on independently distributed errors (Legendre 1993), as it may lead to erroneous conclusions regarding the significance of covariates in studies of species-environment relationships (Christman 2008; Thornton et al. 2011). To account for this, the coordinates of each field were obtained using ArcGIS software® and used for subsequent tests of spatial autocorrelation between fields (Thébaud et al. 2006). In order to test for spatial autocorrelation of the residuals of the best model (GLM) for total aphid and carabid abundances in the field, we computed Moran's I indices for nearest-neighbour pairs of the fields sampled according



**Fig. 2** Rank abundance distribution of carabid species in wheat and maize fields. Only species recorded in wheat fields are ranked.

to the Delaunay network. The objective was to test the interdependence of the residuals of the model within our area. Under the hypothesis of spatial independence, the values of the residuals should be distributed at random among the locations of the coordinates of the fields

sampled (Thébaud et al. 2006). Spatial autocorrelation was tested using Passage 2.0 software (Rosenberg 2009). The significance of the coefficients of autocorrelation was tested against the null hypothesis of absence of a spatial arrangement ( $\alpha = 0.05$ ).

## Results

We recorded a total of 40,167 aphids in the wheat fields and 31,125 in the maize fields. In Western Europe, *Sitobion avenae*, *Metopolophium dirhodum* and *Rhopalosiphum padi* (Homoptera: Aphididae) are the three most abundant cereal aphid pests (Carter et al. 1982; Hill 1987). However, in this study, all three species were found only in maize fields: *S. avenae* (11,450 individuals), *M. dirhodum* (5250) and *R. padi* (14,425), but only *S. avenae* (31,897) and *M. dirhodum* (8270) were found in wheat fields. A total of 85 species of carabid were captured: 44,558 individuals of 71 species in wheat fields and 32,148 of 70 species in maize fields. The two crops shared 56 species. Rank-abundance values for all the species found in wheat and maize fields are plotted in Fig. 2.

### The association between abundance of aphids in wheat fields and landscape

The model that best described total aphid and *S. avenae* abundances, included year, woodland<sub>800</sub>, grassland<sub>300</sub>, grass strips<sub>800</sub>, and hedgerow<sub>800</sub> for total abundance of aphids and year, woodland<sub>800</sub>, grassland<sub>300</sub>, grass strips<sub>800</sub>, and hedgerow<sub>100</sub> for *S. avenae*. The model that best described the abundance of *M. dirhodum* included year, grassland<sub>100</sub>, grass strips<sub>300</sub>, and hedgerow<sub>500</sub> (see AIC values of the generalized linear model, Appendix 1).

The best models for total abundance and that of each aphid species in wheat fields are presented in Table 1. Estimated parameter values indicate that there are positive associations between total aphid abundance and woodland<sub>800</sub> and grassland<sub>300</sub> ( $\chi^2 = 5038.7$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 3380.6$ ;  $df = 1$ ,  $P < 0.0001$ , respectively) and that of *S. avenae* ( $\chi^2 = 5974.9$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 1943.7$ ;  $df = 1$ ,  $P < 0.0001$ , respectively). The abundance of *M. dirhodum* was positively correlated only with grassland<sub>100</sub> ( $\chi^2 = 66.103$ ;  $df = 1$ ,  $P < 0.0001$ ). The total aphid abundance was significantly negatively correlated with grass strips<sub>800</sub> and hedgerow<sub>800</sub> ( $\chi^2 = 3684.2$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 206.18$ ;  $df = 1$ ,  $P < 0.0001$ , respectively) as was that of *S. avenae* with grass strips<sub>800</sub> and hedgerow<sub>100</sub> ( $\chi^2 = 3432.8$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 1292.3$ ;  $df = 1$ ,  $P < 0.0001$ , respectively) and *M. dirhodum* with grass strips<sub>300</sub> and hedgerow<sub>500</sub> ( $\chi^2 = 61.067$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 54.613$ ;  $df = 1$ ,  $P < 0.0001$ , respectively). The year did not contribute significantly to explaining total aphid and species' abundances of aphids in wheat fields ( $\chi^2 = 419.52$ ;  $df = 1$ ,  $P = 0.0799$ ,  $\chi^2 = 122.26$ ;  $df = 1$ ,  $P = 0.0887$ ,  $\chi^2 = 41.1$ ;  $df = 1$ ,  $P = 0.1147$ , respectively).

The analysis revealed no spatial autocorrelation for the model residuals (GLM) of total aphid abundance at the level of the 12 fields sampled each year; aphids in 2009:  $I = -0.18$ ,  $p = 0.55$ ; aphids in 2010:  $I = -0.014$ ,

$p = 0.61$ . This means that the residuals exhibit no spatial structure and the fields sampled can be considered as independent spatial replicates.

### The association between total abundance and species richness of carabids in wheat fields and landscape

The best model describing total abundance of carabids included year, grassland<sub>800</sub>, other<sub>300</sub>, grass strips<sub>800</sub>, and hedgerow<sub>800</sub>. The best model describing species richness of carabids included other<sub>300</sub> and hedgerow<sub>800</sub> (see AIC values of the generalized linear model, Appendix 2).

The best models for total abundance and species richness of carabids in wheat fields are presented in Table 2. The total abundance of carabids was negatively associated with grassland<sub>800</sub>, and hedgerow<sub>800</sub> ( $\chi^2 = 94.165$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 9.8548$ ;  $df = 1$ ,  $P = 0.001694$ , respectively). There was a significant positive correlation between the total abundance of carabids and grass strips<sub>800</sub> and other<sub>300</sub> ( $\chi^2 = 853.46$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 470.51$ ;  $df = 1$ ,  $P < 0.0001$ ). The species richness of carabids was positively associated with the proportion covered by hedgerow<sub>800</sub> ( $\chi^2 = 6.3529$ ;  $df = 1$ ,  $P = 0.001742$ ). In the wheat fields, no association between species richness of carabid and the proportion of other was detected ( $\chi^2 = 4.3555$ ;  $df = 1$ ,  $P = 0.05689$ ).

The analysis revealed no spatial autocorrelations in the residuals of the model (GLM) for carabid abundance at the level of the 12 fields sampled each year; carabids in 2009:  $I = 0.154$ ,  $p = 0.09$ ; carabids in 2010:  $I = -0.005$ ,  $p = 0.56$ . This means that the residuals exhibit no spatial structure and the fields sampled can be considered as independent spatial replicates.

### The association between abundance of aphids in maize fields and landscape

The best model describing total abundance of aphids included woodland<sub>300</sub>, other<sub>500</sub>, grass strips<sub>300</sub>, hedgerow<sub>800</sub>, and grassland<sub>800</sub>. The best model describing the abundance of *S. avenae* included hedgerow<sub>800</sub>, grassland<sub>800</sub>, woodland<sub>500</sub>, and grass strips<sub>800</sub>. The best model describing the abundance of *M. dirhodum* included grassland<sub>800</sub>, grass strips<sub>500</sub>, and hedgerow<sub>100</sub>. For the abundance of *R. padi*, the best model included woodland<sub>300</sub>, grass strips<sub>300</sub>, and grassland<sub>500</sub> – see AIC values of the generalized linear model, Appendix 3.

The best models for total abundance and that of each aphid species in maize fields are presented in Table 3. We found that the total abundance of aphids was positively associated with woodland<sub>300</sub>, other<sub>500</sub>, grass strips<sub>300</sub>, and grassland<sub>800</sub> ( $\chi^2 = 1082.7$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 1397.4$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 1559.1$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 1125.9.1$ ;  $df = 1$ ,  $P < 0.0001$ , respectively), and *S. avenae* abundance positively with grassland<sub>800</sub>, woodland<sub>500</sub>, and grass strips<sub>800</sub> ( $\chi^2 = 220.72$ ;  $df = 1$ ,  $P = 0.00410$ ,  $\chi^2 = 14.45$ ;  $df = 1$ ,

**Table 1** Generalized Linear Model, including parameter estimates, which describes the total abundance of aphids and that of individual species in wheat fields; df: degrees of freedom,  $\beta$ : estimate of regression coefficient, SE: standard error,  $\chi^2$  = test value, P = significance of  $\beta$ . All sp.: Total aphid abundance; S.a.: *Sitobion avenae* abundance; M.d.: *Metopolophium dirhodum* abundance.

Parameters	Distance	df			$\beta$			SE			$\chi^2$			P			
		All sp.	S.a.	M.d.	All sp.	S.a.	M.d.	All sp.	S.a.	M.d.	All sp.	S.a.	M.d.	All sp.	S.a.	M.d.	
Year 2010					-2.468e-01		-1.720e+00	1.592e-01	1.208e-02	1.441e-02	3.097e-02	419.52	122.26	41.1	0.0799	0.0887	0.1147
Woodland	800 m	1	1	1	6.510e-02			7.862e-02	9.267e-04	1.046e-03		5038.7	5974.9		< 0.0001	< 0.0001	
Grassland	300 m	1	1	1	1.839e-02			1.551e-02	3.278e-04	3.519e-04		3380.6	1943.7		< 0.0001	< 0.0001	
Grassy strip	800 m	1	1	1	-1.722e+00			-1.869e+00	3.119e-02	3.565e-02		3684.2	3432.8		< 0.0001	< 0.0001	
Hedgerow	800 m	1	1	1	-1.507e-05				1.052e-06			206.18			< 0.0001		
Hedgerow	100 m	1	1	1				-3.092e-04		8.915e-06			1292.3		< 0.0001		
Grassland	100 m	1	1	1				5.168e-03			6.317e-04			66.103		< 0.0001	
Grassy strip	300 m	1	1	1				-1.144e-01			1.524e-02			61.067		< 0.0001	
Hedgerow	500 m	1	1	1				-3.151e-05			4.219e-06			54.613		< 0.0001	

**Table 3** Generalized Linear Model, including parameter estimates, which describes the total abundance of aphids and that of individual species in maize fields; df: degrees of freedom,  $\beta$ : estimate of regression coefficient, SE: standard error,  $\chi^2$  = test value, P = significance of  $\beta$ . All sp.: Total aphid abundance; S.a.: *Sitobion avenae* abundance; M.d.: *Metopolophium dirhodum* abundance; R.p.: *Rhopalosiphum padi* abundance.

Parameters	Distance	df			$\beta$			SE			$\chi^2$			P			
		All sp.	S.a.	M.d.	R.p.	All sp.	S.a.	M.d.	R.p.	All sp.	S.a.	M.d.	R.p.	All sp.	S.a.	M.d.	
Woodland	300 m	1			1	8.16e-02			0.10	2.48e-03		1082.7		892.42		< 0.0001	< 0.0001
Other	500 m	1				8.51e-02				2.30e-03		1397.4				< 0.0001	
Grassy strip	300 m	1			1	3.56e-01			0.82	8.83e-03		1559.1		5305.60		< 0.0001	< 0.0001
Hedgerow	800 m	1				-5.81e-05				1.43e-06		1759.7	761.24		< 0.0001	< 0.0001	< 0.0001
Grassland	800 m	1	1	1	2.462e-02	1.691e-02	1.682e-02		7.388e-04	1.143e-03	1.044e-03	1125.9	220.72	254.44	0.0410	0.0410	< 0.0001
Woodland	500 m	1				1.32e-02				3.47e-03			14.45			0.0001	
Grassy strip	800 m	1				4.18e-01				4.57e-02			86.69			< 0.0001	
Grassy strip	500 m		1	1			3.46e-01				5.72e-02					< 0.0001	< 0.0001
Hedgerow	100 m		1	1			-1.30e-04				2.21e-05					< 0.0001	< 0.0001
Grassland	500 m			1					0.03					1108.00			< 0.0001

**Table 2** Generalized Linear Model, including parameter estimates, which describes the total abundance and species richness of carabids in wheat fields; df: degrees of freedom,  $\beta$ : estimate of regression coefficient; SE: standard error,  $\chi^2$  = test value,  $P$  = significance of  $\beta$ .

Parameters	Distance	Carabid abundance					Species richness of carabids				
		df	$\beta$	SE	$\chi^2$	P	df	$\beta$	SE	$\chi^2$	P
Year 2010		1	7.009e-02	1.019e-02	47.363	0.0599					
Grassland	800 m	1	-6.148e-03	6.315e-04	94.165	< 0.0001					
Other	300 m	1	3.123e-02	1.463e-03	470.51	< 0.0001	1	-2.697e-02	1.297e-02	4.3555	0.05689
Grassy strip	800 m	1	6.010e-01	2.019e-02	853.46	< 0.0001	1				
Hedgerow	800 m	1	-4.223e-06	1.347e-06	9.8548	0.001694	1	2.252e-05	6.561e-06	6.3529	0.001742

**Table 4** Generalized Linear Model, including parameter estimates, which describes the total abundance and species richness of carabids in maize fields; df: degrees of freedom,  $\beta$ : estimate of regression coefficient; SE: standard error,  $\chi^2$  = test value,  $P$  = significance of  $\beta$ .

Parameters	Distance	Carabid abundance					Species richness of carabids				
		df	$\beta$	SE	$\chi^2$	P	df	$\beta$	SE	$\chi^2$	P
Woodland	100 m	1	-8.945e-03	2.228e-03	16.18	< 0.0001					
Grassland	100 m	1	-4.128e-03	4.277e-04	93.81	< 0.0001					
Other	500 m						1	-4.145e-02	1.695e-02	2.2793	0.05626
Grassy strip	300 m	1	2.402e-01	1.087e-02	522.18	< 0.0001					
Hedgerow	800 m		-6.802e-05	1.564e-06	2043.40	< 0.0001	1	1.800e-05	8.154e-06	4.8647	0.02741

$P = 0.0001$ ,  $\chi^2 = 86.69$ ;  $df = 1$ ,  $P < 0.0001$ , respectively). The association with grassland<sub>800</sub> and grass strips<sub>500</sub> was positive for *M. dirhodum* ( $\chi^2 = 254.44$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 35.87$ ;  $df = 1$ ,  $P < 0.0001$ , respectively). The abundance of *R. padi* was significantly positively correlated with woodland<sub>300</sub>, grassy strip<sub>300</sub>, and grassland<sub>500</sub> ( $\chi^2 = 892.42$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 5305.60$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 1108.00$ ;  $df = 1$ ,  $P < 0.0001$ , respectively). The total abundance of aphids, *S. avenae* and *M. dirhodum* were significantly negatively correlated with hedgerow<sub>800</sub> and hedgerow<sub>100</sub> ( $\chi^2 = 1759.7$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 761.24$ ;  $df = 3$ ,  $P < 0.0001$ ,  $\chi^2 = 34.84$ ;  $df = 1$ ,  $P < 0.0001$ , respectively).

The analysis revealed no spatial autocorrelation for the model residuals (GLM) of total aphid abundance at the level of the 12 fields sampled each year; aphids in 2009:  $I = -0.12$ ,  $p = 0.13$ ; aphids in 2010:  $I = -0.21$ ,  $p = 0.43$ . This means that the residuals exhibit no spatial structure and the fields sampled can be considered as independent spatial replicates.

### The association between total abundance and species richness of carabids in maize fields and landscape

The best model describing the total abundance of carabids included woodland<sub>100</sub>, grassland<sub>100</sub>, grass strips<sub>300</sub>, and hedgerow<sub>800</sub>. The best model describing species richness of carabids included other<sub>500</sub> and hedgerow<sub>800</sub> – see AIC values of the generalized linear model, Appendix 4.

The best models for total abundance and species richness of carabid in maize fields are presented in Table 4; the total abundance of carabids is significantly negatively associated with woodland<sub>100</sub>, grassland<sub>100</sub>, and hedgerow<sub>800</sub> ( $\chi^2 = 16.18$ ;  $df = 1$ ,  $P < 0.0001$ ,  $\chi^2 = 93.81$ ;  $df = 3$ ,  $P < 0.0001$ ,  $\chi^2 = 2043.40$ ;  $df = 1$ ,  $P < 0.0001$ , respectively). We found a significant positive correlation between the total abundance of carabids and grass strips<sub>300</sub> ( $\chi^2 = 522.18$ ;  $df = 1$ ,  $P < 0.0001$ ). The species richness of carabid was significantly positively correlated with hedgerow<sub>800</sub> ( $\chi^2 = 4.8647$ ;  $df = 1$ ,  $P = 0.02741$ ).

The analysis revealed no spatial autocorrelations in the residuals of the model (GLM) for carabid abundance at the level of the 12 fields sampled each year; carabids in 2009:  $I = 0.11$ ,  $p = 0.15$ ; carabids in 2010:  $I = 0.23$ ,  $p = 0.05$ . This means that the residuals exhibit no spatial structure and the fields sampled can be considered as independent spatial replicates.

## Discussion

### Association between abundance of aphids and landscape

Composition of the landscape is associated with abundance of insect pest species in different ways (den Belder et al. 2002). For example, Bianchi et al. (2006) recently demonstrated that pest pressure recorded in more complex landscapes is lower in 45% and higher in 15%

of the publications they reviewed. In our study, the abundance of aphids in the field was associated with landscape composition at a large scale (500 m and 800 m). There was a positive correlation between the abundance of the aphids and the proportion of woodland and grassland at these scales. Aphid abundance in wheat and maize field was negatively and positively, respectively, correlated with the proportion of grass strips. We also found that the abundance of aphids at these scales in both types of crop is negatively associated with the proportion of hedgerows.

The semi-natural habitats at a large scale are key factors in determining pest pressure (Rusch et al. 2010). In general, semi-natural habitats are more stable and so provide refuges for aphids from human disturbances (e.g., pesticides) and hibernation sites from which they can colonize crops in spring (Dixon 1973, 1985; Carter et al. 1982). Thus semi-natural habitats are sources and cereals sinks in aphid source-sink dynamics, as suggested by Dunning et al. (1992) and Dias (1996).

#### **Association between abundance and species richness of carabids and landscape**

There was a negative correlation between the abundance of carabids in wheat fields and the proportion of grassland and hedgerow at a large scale. There is a similar negative correlation for maize fields but with the proportion of grassland and woodland at a small scale. Carabid abundance was positively correlated with the proportion of grassy strips at a large scale in both types of crop. Carabid species richness was significantly positively correlated with the proportion of hedgerows at a large scale in both types of crop.

The semi-natural habitats promote the diversity of carabids, but their impacts on different species are debated (Holland 2002). Carabids are particularly sensitive to landscape structure, especially at a large scale (Holland 2002; Aviron et al. 2005). In our study, the relative proportions of semi-natural habitats such as woodland, grassland and hedgerows were negatively correlated with the abundance of carabids at two different scales. This may be because the dominant species in our study were *Poecilus cupreus* and *Pterostichus melanarius* (Fig. 2), which made up 71% of all the carabids captured. These species mainly occur in fields (Thiele 1977; Kromp 1999; Ameixa and Kindlmann 2008).

The proportion of hedgerows was positively correlated with species richness of carabids. This may be because hedgerows can be a habitat or a corridor for forest species (Petit and Burel 1998), which may venture into adjacent fields. Thus the carabid community in landscapes rich in hedgerows might have been enriched by species, which would not be present here if there were no hedgerows. Also the proportion of other elements was positively correlated with the abundance of aphids and carabids. This may be due to factors such as the presence of diversified

resources and spread over time (e.g., flower of gardens) or a micro-climate (high temperatures in winter or spring).

#### **The association between the abundance of aphids and carabids and the proportion of the landscape under grass strips**

We found that the proportion of grassy strips was negatively correlated with the abundance of aphids in wheat fields, and positively in maize fields at different scales. Carabid abundance was positively correlated with the proportion of grass strips at large scales in both types of crop. Similarly, Collins et al. (2002) showed that there is a greater abundance of carabids in fields surrounded by grass strips, but their abundance decreased rapidly with distance from the strip. Pywell et al. (2011) show that grass strips promote abundances of predators. Carabids were more active and more abundant in fields bordered by grassy margins (Varchola and Dunn 2001; Hof and Bright 2010). Thus, even if it is not possible to draw any strong conclusions based on the results of our study, published data support the idea that grass strips may compensate for the loss of semi-natural habitats and the negative effect this has on beneficial insects, like carabids. This is particularly interesting since despite their cost, grass strips were not designed to be ecologically multifunctional: their initial – and only official – goal in France was to protect water against agricultural inputs (Delattre et al. 2011). However, some studies like Marshall et al. (2006) indicate that there are not more carabids in fields surrounded by 6m wide uncultivated strips.

Grass strips have been a part of agricultural landscapes for many years, but their ecological role is still not fully understood (Marshall and Moonen 2002). Undoubtedly, they play an important role in increasing the amount of semi-permanent and semi-natural habitat in the landscape, thereby favouring beneficial species. They may thus partly compensate for the loss of semi-natural habitats and ameliorate the negative effects of the intensification of agriculture (Woodcock et al. 2010).

#### **Conclusions**

Because species differ in the scales at which they use resources and perceive their environment (Wiens 1989), studying the scale-dependent effect of local and landscape factors on pest abundance is a pre-requisite for conceiving ecologically-based pest management strategies at large scales. Our study demonstrated that the abundance of aphids and their natural carabid enemies was associated with the composition of the landscape at a large scale. We found a strong positive association between the abundance of the aphids and the proportion of woodland and grassland in the landscape. This result is supportive of Rusch et al. (2001) finding that semi-natural habitats at large scales have



an important role in determining pest pressure. Thus, movement of aphids from semi-natural habitats into cereal crops can be considered as source-sink dynamics, as suggested by Dunning et al. (1992) and Dias (1996). Carabid abundance was negatively associated with the proportion of these semi-natural habitats. In our study, the carabid community was dominated by typical field species, which are known to be impeded by semi-natural habitat, such as dense hedgerows, which act as barriers and prevent dispersal. Carabids were more abundant in crop fields surrounded by grass strips while aphids showed a similar trend only in maize fields.

Further research is needed to clarify the relationships between the abundance of aphids and carabids and the composition of the landscape if we are to improve our ability to predict their dynamics in agricultural landscapes. This will help in the development of agroecosystems that are sustainable, conserve species diversity and maximize the service provided by natural enemies in controlling pest populations.

## Acknowledgements

This study was funded by a grant from the ANR “Landscaphid” (French National Research Agency, ANR-09-STRA-05) for the LTER “Armorique” study area and two grants to PK: VOL/11/E036 of the GA CR, and CZ.1.05/1.1.00/02.0073 of the MSMT. Diab Al Hassan was funded by a PhD fellowship from the Syrian Minister of Higher Education. We thank Noémie Guillaud, Jessica Thevenot, Yann Rantier and Olivier Jambon who contributed to field work, data collection and/or data analysis.

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**Appendix 1** Comparison of AIC (Akaike Information Criterion) values of the four best generalized linear models of total and aphid species abundances in wheat fields. Best models are in bold.

Total aphid abundance					
Parameters	Distance	<b>Model1</b>	Model2	Model3	Null model
Year 2010		×	×		
Woodland	800 m	×	×	×	
Grassland	300 m	×	×	×	
Grassy strip	800 m	×	×	×	
Hedgerow	800 m	×	×	×	
Other	500 m		×	×	
(AIC)		<b>5164.7</b>	5568.9	5782.3	31420
<i>Sitobion avenae</i> abundance					
Year 2010		×			
Woodland	800 m	×	×	×	
Grassland	300 m	×	×	×	
Grassy strip	800 m	×	×	×	
Hedgerow	100 m	×	×	×	
Other	800 m		×	×	
(AIC)		<b>4102.9</b>	4423.2	5493.2	35927
<i>Metopolophium dirhodum</i> abundance					
Year 2010		×	×		
Woodland	500 m		×	×	
Grassland	100 m	×	×	×	
Grassy strip	300 m	×	×	×	
Hedgerow	500 m	×	×		
(AIC)		<b>1360.0</b>	1365.3	1413.3	6095

**Appendix 2** Comparison of AIC (Akaike Information Criterion) values of the four best generalized linear models of total and species richness of carabids in wheat fields. Best models are in bold.

Carabid abundance					
Parameters	Distance	<b>Model1</b>	Model2	Model3	Null model
Year 2010		×	×	×	
Grassland	800 m	×	×	×	
Other	300 m	×	×	×	
Grassy strip	800 m	×	×	×	
Hedgerow	800 m	×	×		
Woodland	100 m		×		
(AIC)		<b>12305</b>	12317	12325	14877
Species richness of carabids					
Grassland	500 m		×		
Grassy strip	300 m		×	×	
Hedgerow	800 m	×	×	×	
Other	300 m	×			
(AIC)		<b>147.64</b>	150.55	158.5	155

**Appendix 3** Comparison of AIC (Akaike Information Criterion) values of the four best generalized linear models of total and aphid species abundances in maize fields. Best models are in bold.

Total aphid abundance					
Parameters	Distance	<b>Model1</b>	Model2	Model3	Null model
Year 2010			×	×	
Woodland	300 m	×	×		
Other	500 m	×	×	×	
Grassy strip	300 m	×	×	×	
Hedgerow	800 m	×	×	×	
Grassland	800 m	×	×	×	
(AIC)		<b>4759.5</b>	4765.2	5718.3	14475
<i>Sitobion avenae</i> abundance					
Year 2010			×	×	
Hedgerow	800 m	×	×	×	
Grassland	800 m	×	×	×	
Woodland	500 m	×	×		
Grassy strip	800 m	×		×	
Other	800 m		×	×	
(AIC)		<b>1613.7</b>	1620.7	1631.8	7931
<i>Metopolophium dirhodum</i> abundance					
Year 2010			×		
Woodland	300 m		×	×	
Grassland	800 m	×	×		
Grassy strip	500 m	×	×	×	
Hedgerow	100 m	×	×	×	
Other	800 m			×	
(AIC)		<b>783.22</b>	798.46	805.76	1455.333
<i>Rhopalosiphum padi</i> abundance					
Year 2010			×	×	
Woodland	300 m	×	×	×	
Grassy strip	300 m	×	×	×	
Grassland	500 m	×	×		
Hedgerow	800 m			×	
Other	800 m		×	×	
(AIC)		<b>8107.1</b>	8171.9	8268.8	19013.92

**Appendix 4** Comparison of AIC (Akaike Information Criterion) values of the four best generalized linear models of total and species richness of carabids in maize fields. Best models are in bold.

Carabid abundance					
Parameters	Distance	<b>Model1</b>	Model2	Model3	Null model
Year 2010				×	
Woodland	100 m	×	×	×	
Grassland	100 m	×	×	×	
Other	500 m		×	×	
Grassy strip	300 m	×			
Hedgerow	800 m	×	×	×	
(AIC)		<b>6234.9</b>	6305.1	6386.5	12852
Species richness of carabids					
Woodland	300 m		×	×	
Hedgerow	800 m	×	×	×	
Other	500 m	×		×	
(AIC)		<b>139.29</b>	143.3	143.3	143