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The effect of semi-natural habitats on aphids and their natural enemies across spatial and temporal scales

Audrey Alignier^{a,b,c,1}, Lucie Raymond^{a,b}, Marc Deconchat^{a,b}, Philippe Menozzi^d,
Claude Monteil^{a,b}, Jean-Pierre Sarthou^{a,c}, Aude Vialatte^{a,b}, Annie Ouin^{a,b,*}

^a University of Toulouse, INP-ENSAT, BP 32607, 31326 Castanet Tolosan, France

^b INRA, UMR 1201 DYNAFOR, BP 52627, 31326 Castanet Tolosan, France

^c INRA, UMR 1248 AGIR, BP 52627, 31326 Castanet Tolosan, France

^d CIRAD, UPR 102, 34398 Montpellier, France

A B S T R A C T

Semi-natural habitats in agricultural landscapes are generally assumed to enhance the biological control of insect pests based on native beneficial insects, by providing alternative prey and hosts, resources and refuges for overwintering. We hypothesized that natural enemies of winter wheat aphids should arrive sooner in fields near semi-natural habitats. We compared aphid, hoverfly (larvae and eggs) and parasitized aphid (mummies) abundances in 54 winter wheat fields located in southern France from 2003 to 2007. Six surveys were recorded each spring and were split into the early period (defined as the period before the peak of aphid growth) and the late period (after the peak). The wheat fields differed by their surrounding landscape composition measured as the proportion of semi-natural habitats (woods, hedges and grasslands), at three different spatial scales: 200 m, 500 m, and 1200 m. Despite great variability in abundance data between years, the abundance of hoverflies appeared more sensitive to landscape composition than aphid abundance was. Early abundance for both aphids and hoverflies was positively related to wood cover, but not late abundance in spring. The abundance of hoverflies was positively related to hedge and grassland cover at all spatial scales and both periods considered. Aphid parasitism was higher near hedges at the small spatial scale late in the spring. Our results confirmed that higher proportions of semi-natural habitats in agricultural landscapes enhance the biological control of pests, but this effect depends on the spatial scale, the time period in the spring and the natural enemies considered.

Keywords:
Biocontrol
Landscape
Seasonality
Aphid
Hoverfly
Parasitism

* Corresponding author at. University of Toulouse, INP-ENSAT, BP 32607, 31326 Castanet Tolosan, France. Fax: +33 5 34 32 39 01.

E-mail address: ouin@ensat.fr (A. Ouin).

¹ Present address: INRA, UR 0980 SAD-PAYSAGE, CS 84215, 35042 Rennes, France.

1. Introduction

The structural heterogeneity of agricultural landscapes influences biodiversity, and notably many groups of arthropods providing services to crop production e.g. pest control, pollination (Burel et al., 1998; Weibull et al., 2003; Schmidt et al., 2004; Tschardt et al., 2005a). Some of these organisms are mobile and their presence depends on resource availability that is segregated from the location or time where ecosystem services are provided (Kremen et al., 2007). Many authors argue that habitat management at a landscape-scale is needed to enhance ecosystem services such as pollination or pest biological control by effective habitat management (Tschardt et al., 2007). To disentangle the effects of landscape complexity on pests as well as on their natural enemies, it is necessary to identify the appropriate landscape elements, spatial scales and time periods to be considered (Kremen et al., 2007; Chaplin-Kramer et al., 2013).

The landscape elements involved in the life cycle of many beneficial arthropods are quite well documented. It is now known that most of the natural enemies of crop pests do not complete their life cycles in cultivated fields (Hani and Boller, 1998), but use semi-natural habitats (such as hedges, field margins, beetle banks, meadows and fallows) in the agricultural landscape (Landis et al., 2000; Gurr et al., 2004). Semi-natural habitats favour populations of natural enemies and improve their efficiency as control agents by providing alternative prey and hosts, nectar and pollen resources (Marino and Landis, 1996; Thies and Tschardt, 1999), and refuges against unfavourable weather conditions (i.e. “winter refuge”, Corbett and Rosenheim, 1996; Sarthou et al., 2005). Thus, semi-natural habitats can represent important sources of natural enemies colonizing crop fields, and proximity to such habitats may result in increased control of agricultural pests (i.e. “spill over hypothesis”, Rand et al. 2006). Spatial scales at which species respond to landscape heterogeneity revealed different responses according to species or groups (Purtauf et al., 2004; Schmidt et al., 2008).

In addition to spatial scales, there is a growing interest in considering the temporal scale in order to identify the relationships between pest densities, natural enemies dynamics and pest control services (Chaplin-Kramer et al., 2013). Past empirical studies generally consider short-term data sets (i.e. a few weeks), making it difficult to understand the mechanisms behind the response patterns and the long-term dynamics of species. Although one of the laws to prevent pest infestations is “the earlier the natural enemies, the better the control” (Altieri and Nicholls, 2004), the time periods during which beneficial arthropods exploit particular landscape elements remain unclear (but see Bianchi and van der Werf, 2004; Sarthou et al., 2005). This is a crucial aspect of any recommendations for the enhancement of ecosystem services by landscape management, as for example in planning the mowing or reaping of grassland or the pruning of hedges.

Aphids (Hemiptera: Aphididae) are major invertebrate pests in agriculture and especially in cereal crops. In winter wheat fields, in south western France as well as in western Europe as a whole, the herbivore community is dominated for a short period by three species of generalist cereal aphids: *Sitobion avenae* (F.), *Metopolophium dirhodum* (W.) and *Rhopalosiphum padi* (L.), Hoverflies (Diptera: Syrphidae), mainly represented by *Episyrphus balteatus* (De Geer), *Sphaerophoria scripta* (L.) and *Melanostoma mellinum* (L.) are important natural enemies of cereal aphids in Western Europe. Parasitoid wasps (Hymenoptera: mainly Aphidiidae) occupy the same trophic level and specialize in one or more aphid host species. The most abundant aphid parasitoids on the three species of cereal aphids are *Aphidius ervi* (H.), *Aphidius rhopalosiphii* (De Stefani-Perez) and *Praon volucre* (H.) (Sigsgaard, 1997). All three parasitoids overwinter in mummies of aphids that served as host (Langer, 2001). All

these taxa (aphids, hoverflies, parasitoid wasps) are assumed to be enhanced by semi-natural habitats providing resources and overwintering sites (Thies et al., 2005) but not necessarily at the same time period (Bianchi et al., 2006).

Here, we investigated how semi-natural habitats in the agricultural landscape affect both aphid and their natural enemies abundance, at three different spatial scales (200 m, 500 m, 1200 m) representative of the range of dispersal of studied species. We surveyed the spring abundance of aphids, hoverflies and mummies (parasitized aphids) in 54 winter wheat fields in south-western France. Our study aimed at testing the following hypothesis for both scales:

- (1) Semi-natural habitats such as woods, hedges and grasslands support biological control by favouring hoverflies and parasitoids abundance much more than aphids and thus decreasing aphid abundance in winter wheat-field.
- (2) According to the “winter refuge” (Corbett and Rosenheim, 1996; Sarthou et al., 2005) and the “spill over” hypotheses (Rand et al., 2006), natural enemies abundance should be greater in the early spring near semi-natural habitats than in the late spring.

2. Methods

2.1. Study area

The study region lies between the Garonne and Gers rivers, in south-western France (approximately 43°N 1°E). This region is hilly (alt. 200–400 m), composed of south-north valleys, within a sub-Atlantic climate zone subject to both Mediterranean and mountain influences. The hillsides are sculpted in molasse, an argilo-calcareous detrital formation. Forest covers 15–30% of the area and is composed of multiple small, private forest fragments (Balent and Courtiade, 1992). The southern part of the study region (Wooded zone), near the Pyrenees, is slightly hillier and more wooded, with 27% of forest cover, than the northern part (Less Wooded zone) with 15% of forest cover. Landscapes include a mix of crops (winter cereals, oilseed rape and sunflower, with maize in irrigated lowland), pastures, and small coppice woods. Semi-natural habitats are woodlots, woodlot edges, hedges, field margins, grasslands (wet in the valleys and dry on the hill tops) and fields lying fallow.

2.2. Spring recording of hoverflies, aphids and mummies

Hoverfly, aphid and mummy abundances were studied in winter wheat fields with the same argilo-calcareous soil characteristics and arable management practices (i.e. ploughing, pesticides uses; farmers were questioned before and after the experiment). Each of the fields was larger than 1 ha (6 ha ± 4) and had a similar slope. Due to crop rotation, the fields differed from year to year. Twelve winter wheat fields were studied in spring 2003 and fourteen from spring 2004 to spring 2007.

Aphids, mummies (parasitized aphids) and hoverflies (eggs, larvae and pupae) were counted in a 20 m × 20 m square plot (400 m²), every 2 weeks (i.e. 6 records each year), from the end of March (to detect early colonization process) to the beginning of June (corresponding to the wheat stem elongation, heading, grain-filling). The 400 m² square plot was placed at a distance of 20 m from the field borders in the south western corner of the field. All farmers undertook to avoid biocide (herbicide, fungicide) spraying in the square plot itself. In each plot, ten neighbouring wheat-stalks were cut at 10 different subplots in the square. Each subplot was chosen after an active search for aphid colonies lasting 3 min (if no aphid colony was found, the observer cut ten stalks

randomly). This active search strategy was used to mimic female hoverfly search of aphid colonies and thus avoid too many zero data particularly in early colonisation time. Stalks were placed in plastic bags and stored in the fridge (+5 °C) for 2–3 days in the lab, after which aphids, preimaginal hoverflies and mummies were counted without species determination. Due to a severe drought in summer 2003, the field data of the year 2004 showed very low abundance in aphids, mummies and hoverflies, and were thus removed from the rest of the analysis. So, a total of 68 fields was surveyed over the study period and 54 were used in the subsequent analysis.

2.3. Landscape analysis

To investigate the spatial scales at which insects' abundance in wheat fields were correlated to semi-natural habitats, three circular buffer zones with a radius of 200 m, 500 m and 1200 m were computed around each 20 m × 20 m square plot. The smaller buffer size (200 m) corresponded to the grain size of our landscape (mean field size near 1 ha). The largest buffer size (1200 m) corresponded to the range of distances relevant to dispersal of studied species (Sarthou et al., 2005). A map of land-cover derived from automated classification of two satellite SPOT 5 images of 10 m resolution (June and November 2005) was used to measure the proportion of crops (*Crop*), woods (*Wood*), grasslands (*Grassland*) and hedges (*Hedge*) around the square plots in each buffer (Table 1). *Crop*, *Wood*, *Grassland* and *Hedge* in each buffer did not vary significantly according to year (ANOVAs for paired data, $p < 0.05$ for all tests). We checked for correlations between landscape variables with Spearman correlation tests (Appendix 1). As *Crop* and *Wood* displayed strong correlation ($>|0.7|$) irrespective of buffer size, we only kept the variable *Wood* and excluded *Crop* from further analyses (Dormann et al., 2013).

2.4. Data analysis

The data set was split into two periods: *Early* and *Late* spring. The *Early* period referred to records before the peak of aphid growth whereas the *Late* period referred to records after the peak. The peak of aphid growth corresponded to a sharp increase (more than four times) of aphid abundance between two records and was determined for each field an additive way only. By consequence, the peak was not always at the same date for each field (the fourth or the fifth record). Abundance of aphids, hoverflies and mummies were summed over these two periods.

In order to compare the effects of landscape variables in space and time on aphids, hoverflies and mummies, we performed

Table 1
Mean proportion (\pm SD) of landscape elements in the buffers (200, 500, 1200 m of radius) around the 54 winter wheat fields according to year.

| Year | Buffer (m) | Crop (%) | Grassland (%) | Wood (%) | Hedge (%) |
|------|------------|-------------|---------------|-------------|------------|
| 2003 | 200 | 78 \pm 21 | 12 \pm 18 | 7 \pm 12 | 3 \pm 2 |
| | 500 | 74 \pm 17 | 14 \pm 10 | 8 \pm 10 | 3 \pm 11 |
| | 1200 | 72 \pm 15 | 16 \pm 10 | 8 \pm 7 | 4 \pm 1 |
| 2005 | 200 | 73 \pm 19 | 16 \pm 11 | 7 \pm 11 | 4 \pm 2 |
| | 500 | 70 \pm 20 | 17 \pm 13 | 9 \pm 9 | 4 \pm 1 |
| | 1200 | 68 \pm 19 | 19 \pm 12 | 9 \pm 8 | 4 \pm 1 |
| 2006 | 200 | 72 \pm 18 | 15 \pm 13 | 8 \pm 10 | 4 \pm 3 |
| | 500 | 72 \pm 16 | 15 \pm 10 | 8 \pm 9 | 4 \pm 2 |
| | 1200 | 70 \pm 18 | 16 \pm 11 | 9 \pm 8 | 4 \pm 1 |
| 2007 | 200 | 66 \pm 22 | 19 \pm 14 | 11 \pm 12 | 3 \pm 2 |
| | 500 | 66 \pm 19 | 19 \pm 12 | 11 \pm 10 | 4 \pm 1 |
| | 1200 | 68 \pm 18 | 19 \pm 12 | 9 \pm 7 | 4 \pm 1 |

separated generalized linear mixed models (GLMMs) for the two periods (*Early* and *Late*) and for each buffer size. In a first step, abundances of aphids in the early and late spring were separately related to landscape variables (*Grassland*, *Wood*, *Hedge*) in each of the three buffer sizes using GLMMs with a Poisson error distribution and a log link function. In a second step, abundances of hoverflies, in the early and late spring, were related to landscape variables in each of the three buffers. As the abundance of hoverflies was expected to depend on aphid abundance, we added this as a fixed effect. Lastly, for the parasitism model, we used GLMMs with a binomial distribution for proportional data, i.e. the number of mummies among aphids. As previously, we tested the effect of landscape variables on parasitism, in the early and late spring. In all models, fixed effects were scale-centred to facilitate the model's convergence. The zone ($n = 2$, *Wooded* and *Less Wooded*) and the year ($n = 4$, 2003, 2005, 2006 and 2007) were included as random factors (i.e. random intercepts). Models were fitted by maximum likelihood (ML) and their suitability was assessed by checking normality and randomness of residuals. Explanatory variables in GLMMs were considered in an additive way only. The interactions between explanatory variables could not be explored by a global generalized linear mixed model, owing to the relatively large number of explanatory variables. To ensure robustness of our results, we performed 1000 bootstrap samples of each GLMM. The significance of each fixed effect for all GLMMs was tested by comparing model deviances fitted with and without each effect with an ANOVA test (Zuur et al., 2009). We checked whether collinearity was a potential problem by using variance inflation factors (VIF). VIF's which are not substantially greater than one and less than ten indicate that covariation between predictors is not a problem (Mayers, 1990). In our analyses, the range of VIF's was 1.01–4.59 (Appendix 2). GLMMs were also systematically checked for data overdispersion and spatial autocorrelation in model residuals. We did not find any significant data overdispersion or spatial structure in model residuals tested with Moran's correlograms. Statistical analyses were carried out using an lme4 package for mixed models and an ncf package for correlograms in R 2.15.1 (R Development Core Team, 2010).

3. Results

In total, we observed 36,683 aphids, 1159 hoverflies (764 eggs, 329 larvae and 66 pupae), and 688 mummies during the four years of the study. A large proportion of all the aphids (49%) and most of the hoverflies (63%) and mummies (53%) were counted in 2003 (Fig. 1).

3.1. Aphid abundance

Overall, abundance of aphids was negatively correlated with the proportion of grasslands and hedges, whatever the buffer size (200 m, 500 m and 1200 m) and period (*Early* and *Late*) (Table 2). We observed a higher abundance of aphids earlier in the spring in relation with a higher proportion of woods at 200 m (Fig. 2a) and later in the spring at 1200 m (Fig. 2b). But the abundance of aphids was negatively correlated with the proportion of woods in all other cases, except later in the spring at 500 m where no effect was detected (Fig. 2b; Table 2).

3.2. Hoverfly abundance

Overall, abundance of hoverflies was positively correlated with the abundance of aphids whatever the buffer size (200 m, 500 m and 1200 m) and period in the spring (*Early* and *Late*) (Table 3).

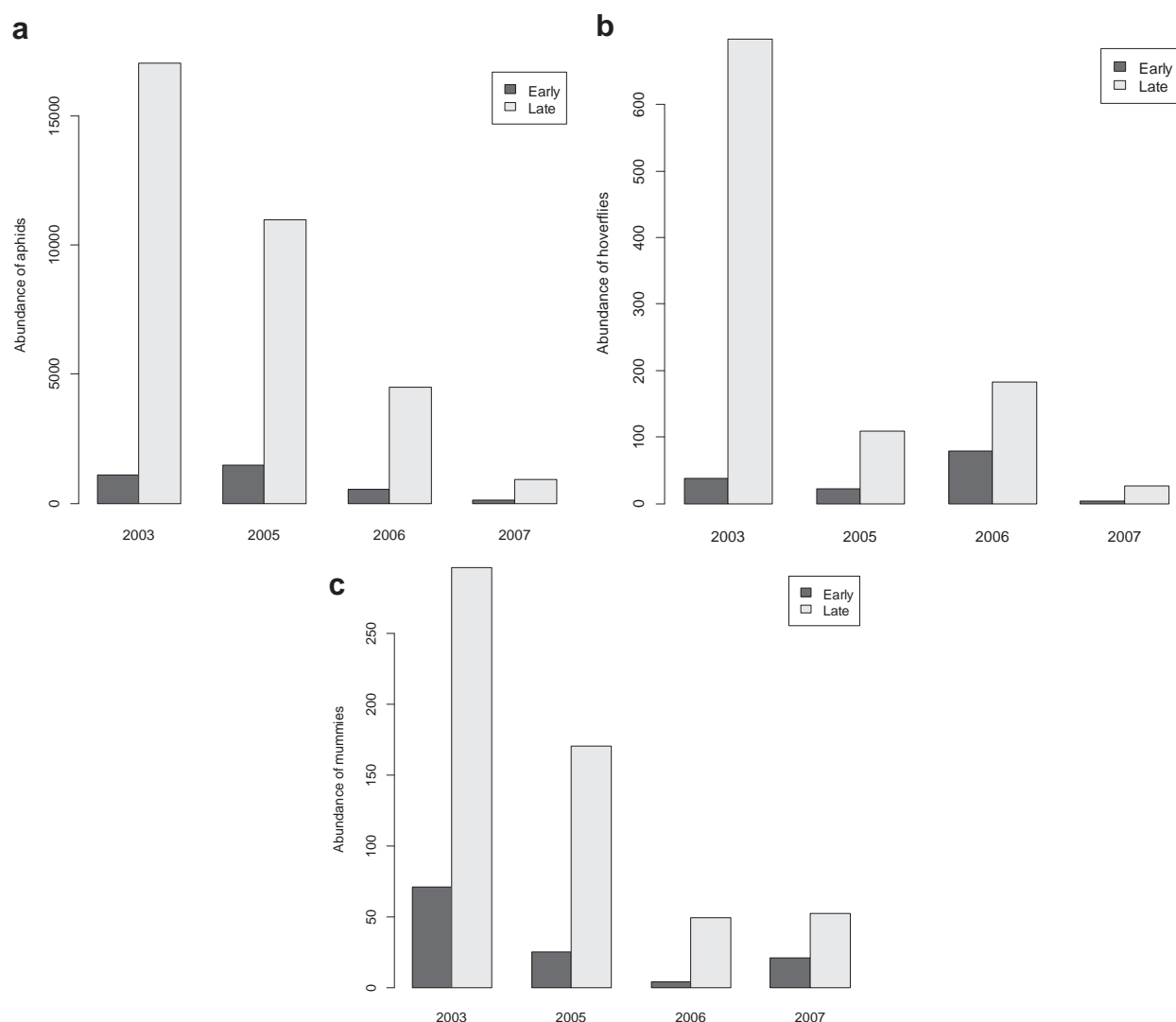


Fig. 1. Total abundance of (a) aphids, (b) hoverflies and (c) mummies (parasitized aphids) according to the year and the time period in spring (*Early* or *Late*).

Table 2
Summary of GLMMs for aphid abundance at the three buffer sizes and the two time periods.

| Spatial scale | Explanatory variable | 200 m | | | 500 m | | | 1200 m | | |
|---------------|----------------------|----------------------------|----------|---------------|----------------------------|----------|---------------|----------------------------|----------|---------------|
| | | Coefficient value \pm SD | <i>P</i> | AIC (R^2) | Coefficient value \pm SD | <i>P</i> | AIC (R^2) | Coefficient value \pm SD | <i>P</i> | AIC (R^2) |
| Early spring | Intercept | +3.7 \pm 0.5 | ** | 2367 (0.05) | +3.7 \pm 0.6 | ** | 2379 (0.10) | +3.7 \pm 0.6 | ** | 2415 (0.13) |
| | Grassland | -0.08 \pm 0.02 | ** | | -0.37 \pm 0.05 | ** | | -0.46 \pm 0.07 | ** | |
| | Wood | +0.24 \pm 0.02 | ** | | -0.07 \pm 0.04 | * | | -0.08 \pm 0.07 | * | |
| | Hedge | -0.04 \pm 0.02 | (Inf) | | -0.16 \pm 0.03 | ** | | -0.15 \pm 0.03 | ** | |
| Late spring | Intercept | +5.9 \pm 0.6 | ** | 16,673 (0.03) | +5.9 \pm 0.6 | ** | 17,666 (0.01) | +5.9 \pm 0.6 | ** | 17,499 (0.03) |
| | Grassland | -0.09 \pm 0.01 | ** | | -0.09 \pm 0.08 | ** | | -0.15 \pm 0.02 | ** | |
| | Wood | -0.01 \pm 0.01 | * | | -0.01 \pm 0.01 | ns | | +0.20 \pm 0.01 | ** | |
| | Hedge | -0.26 \pm 0.01 | ** | | -0.21 \pm 0.01 | ** | | -0.18 \pm 0.01 | ** | |

For each explanatory variable, the coefficient value \pm standard deviation (SD) after 1000 bootstrap samples and its level of significance (*p*-value of the ANOVA between models with and without the variable) are indicated. AIC values of the model for each spatial scale and time period are given. R^2 corresponding to marginal R^2 (i.e. the variance explained by fixed factors only) are provided in brackets. ns: not significant; (Inf) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

Woods were significantly and positively related to early hoverfly abundance at 200 m and 500 m. Later in the spring, the abundance of hoverflies was positively correlated with *Hedge* at 500 m and 1200 m, with *Grassland* at 500 m and negatively correlated with *Grassland* at 200 m (Table 3).

3.3. Parasitism

Early in the spring, there were no significant relationships between parasitism and the proportion of semi-natural habitats, whatever the buffer size (Table 4). Later in the spring, *Hedge* was

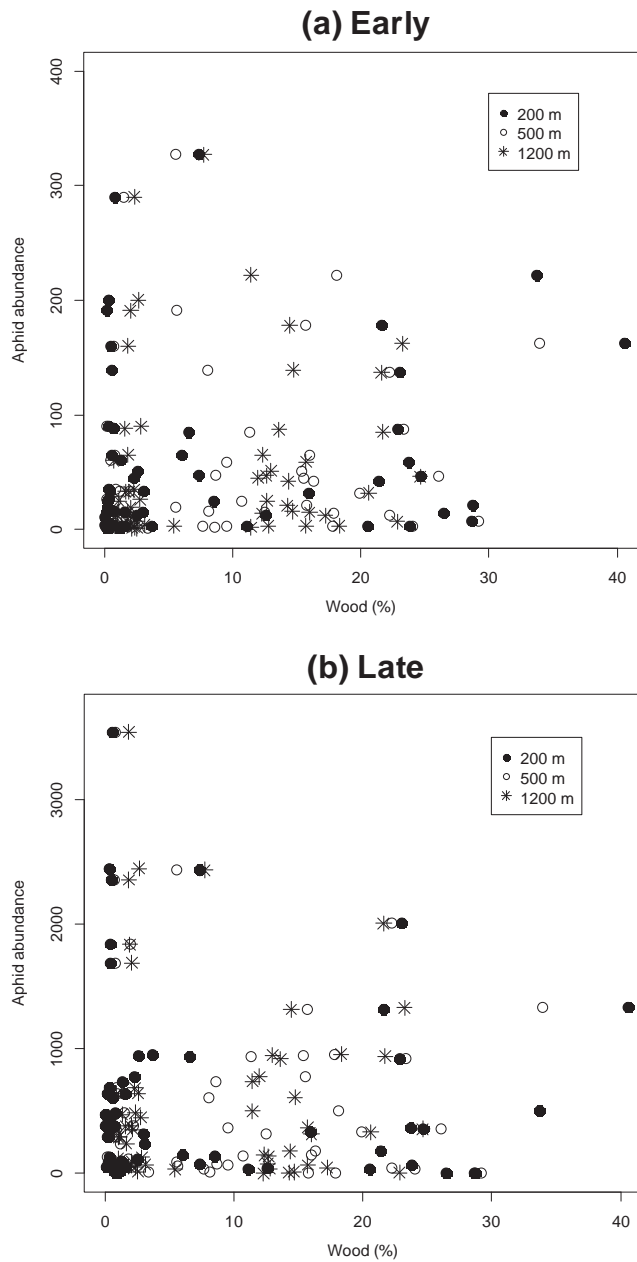


Fig. 2. (a) Early and (b) late spring aphid abundance according to the proportion of woods in the 200 m, 500 m, 1200 m buffers.

positively related to parasitism at 200 and 500 m, whereas *Wood* was negatively related to parasitism at 200 m (Table 4).

4. Discussion

Our study showed high variability of aphid and hoverfly abundance between years. Such an inter-annual variability of aphid populations and their specialist natural enemies has already been observed (e.g. Bianchi and van der Werf 2004). The variability of aphid population dynamics could be due to weather conditions, particularly in winter (Thies et al., 2005). The presence or absence of generalist species controlling aphids early in the season was also pointed out to explain variability of aphid population dynamics in various studies (Plantegenest et al., 2001; Lang, 2003).

Despite this great variability, which was amplified by the exceptional drought of 2003, the positive responses of natural enemies (hoverflies and parasitoids) to wooded semi-natural elements of the landscapes (woods, hedges) were robust and often significant at the studied scales (except a negative and significant effect of woods on parasitism at small spatial scale suggesting intra-guild competition). Thus, we validated our first prediction about the importance of semi-natural habitats, mainly for the wooded ones, in sorting natural enemies of aphids. We also showed that the role displayed by landscape elements depended not only on the spatial scale considered but also on the time period as demonstrated by Vinatier et al. (2013).

4.1. No temporal pattern in the response of aphid abundance to semi-natural habitats

Whatever the period in the spring and the spatial scale, aphid abundance responded in the same way to landscape elements, except for woods. We showed that aphid abundance decreased with grasslands and hedges. Hedges could form barriers to dispersal for aphids. Marrou et al. (1979) showed that windbreaks slowed down the migration of aphid vectors of the Cucumber Mosaic Virus (CMV). In addition, Bianchi et al. (2006) showed that hedges and grasslands favoured the presence of natural enemies and thus reduced aphid abundance.

The positive effect of woods on early aphid abundance in the spring, at the smallest spatial scale, could reflect a positive effect of forest edges, from which a primary colonisation process of crop fields associated occurs through local dispersal. The predation pressure of generalist ground-dwelling predators in the vicinity of overwintering habitats, such as forest edges and woods, drive the movement of aphid populations towards crop fields. This is in accordance with previous study which showed that carabids had little direct impact on aphids, apparently because aphids

Table 3
Summary of GLMMs for hoverfly abundance at the three buffer sizes and the two time periods.

| Spatial scale | Explanatory variable | 200 m | | | 500 m | | | 1200 m | | |
|---------------|----------------------|----------------------------|----|---------------|----------------------------|----|---------------|----------------------------|----|---------------|
| | | Coefficient value \pm SD | P | AIC (R^2) | Coefficient value \pm SD | P | AIC (R^2) | Coefficient value \pm SD | P | AIC (R^2) |
| Early spring | Intercept | +2.7 \pm 0.7 | ** | 177 (0.31) | +3.1 \pm 0.7 | ** | 182 (0.33) | +2.8 \pm 0.5 | ** | 188 (0.26) |
| | Grassland | -0.1 \pm 0.1 | ns | | +0.2 \pm 0.1 | ns | | +0.1 \pm 0.2 | ns | |
| | Wood | +0.4 \pm 0.1 | ** | | +0.4 \pm 0.1 | * | | +0.2 \pm 0.2 | ns | |
| | Hedge | +0.1 \pm 0.1 | ns | | +0.3 \pm 0.2 | ns | | +0.2 \pm 0.2 | ns | |
| | Aphid abundance | +5.6 \pm 0.8 | ** | | +5.8 \pm 0.7 | ** | | +5.6 \pm 0.7 | ** | |
| Late spring | Intercept | +2.2 \pm 0.6 | ** | 373 (0.07) | +2.2 \pm 0.6 | ** | 375 (0.06) | +2.2 \pm 0.6 | ** | 363 (0.07) |
| | Grassland | -0.17 \pm 0.06 | ** | | +0.16 \pm 0.05 | ** | | +0.1 \pm 0.1 | ns | |
| | Wood | -0.01 \pm 0.06 | ns | | +0.06 \pm 0.05 | ns | | -0.1 \pm 0.1 | ns | |
| | Hedge | +0.06 \pm 0.05 | ns | | +0.17 \pm 0.04 | ** | | +0.34 \pm 0.07 | ** | |
| | Aphid abundance | +0.15 \pm 6.69e-05 | ** | | +0.19 \pm 0.04 | ** | | +0.21 \pm 0.04 | ** | |

For each explanatory variable, the coefficient value \pm standard deviation (SD) after 1000 bootstrap samples and its level of significance (p -value of the ANOVA between models with and without the variable) are indicated. AIC values of the model for each spatial scale and time period are given. R^2 corresponding to marginal R^2 (i.e. the variance explained by fixed factors only) are provided in brackets. ns: not significant; (Inf) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

Table 4

Summary of GLMMs for aphid parasitism at the three buffer sizes and the two time periods.

| Spatial scale | Explanatory variable | 200 m | | | 500 m | | | 1200 m | | |
|---------------|----------------------|----------------------------|----------|---------------|----------------------------|----------|---------------|----------------------------|----------|---------------|
| | | Coefficient value \pm SD | <i>P</i> | AIC (R^2) | Coefficient value \pm SD | <i>P</i> | AIC (R^2) | Coefficient value \pm SD | <i>P</i> | AIC (R^2) |
| Early spring | Intercept | -3.4 ± 0.7 | ** | 116 (0.02) | -3.4 ± 0.7 | ** | 116 (0.02) | -3.4 ± 0.7 | ** | 117 (0.02) |
| | Grassland | -0.1 ± 0.2 | ns | | -0.2 ± 0.2 | ns | | -0.02 ± 0.31 | ns | |
| | Wood | -0.1 ± 0.2 | ns | | -0.2 ± 0.2 | ns | | -0.23 ± 0.32 | ns | |
| | Hedge | $+0.2 \pm 0.1$ | ns | | -0.8 ± 0.1 | ns | | $+0.1 \pm 0.2$ | ns | |
| Late spring | Intercept | -3.9 ± 0.3 | ** | 218 (0.04) | -3.9 ± 0.2 | ** | 228 (0.10) | -3.9 ± 0.3 | ** | 245 (0.01) |
| | Grassland | -0.03 ± 0.06 | ns | | -0.01 ± 0.06 | ns | | -0.1 ± 0.1 | ns | |
| | Wood | -0.16 ± 0.07 | * | | $+0.01 \pm 0.06$ | ns | | $+0.07 \pm 0.09$ | ns | |
| | Hedge | $+0.26 \pm 0.06$ | ** | | $+0.26 \pm 0.05$ | ** | | $+0.10 \pm 0.06$ | ns | |

For each explanatory variable, the coefficient value \pm standard deviation (SD) and its level of significance (*p*-value of the ANOVA between models with and without the variable) are indicated. AIC values of the model for each spatial scale and time period are given. R^2 corresponding to marginal R^2 (i.e. the variance explained by fixed factors only) are provided in brackets. ns: not significant; (Inf) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

actively avoided carabids (Snyder and Ives, 2001). Woods also had a negative effect on early abundance of aphids at a large scale and on late abundance at a small scale, though less than its positive effects. Woods provide habitats and resources for additional beneficial arthropods, such as ladybirds and carabids. In turn, the auxiliary insects spill over from woods to neighbouring field crops and feed on aphids (Tscharrntke et al., 2005b; Roume et al., 2011).

4.2. Woods favoured early spring abundance of hoverflies

First of all, we found evidence of a positive relationship between abundance of aphids and hoverflies irrespective of the spatial scale and the time period. The link between aphid and hoverfly population dynamics has already been demonstrated (Tenhumberg and Poehling, 1995), as well as for other aphid enemies such as coccinellids (Elliott et al., 2002). Aphidophagous hoverfly species (except *M. mellinum*) are known to search actively for aphid colonies before laying their eggs (Chandler, 1968).

We showed that early hoverfly abundance in wheat fields was positively related to woods whereas the effect of hedges and grasslands was not significant. Wheat fields near woodlots benefit from early spring eggs laid by post-overwintering females (Sarhou et al., 2005), unlike wheat fields remote from woodlots. Our result was in accordance with those of Pollard (1971) who observed in polyvoltine hoverfly species that the first generation was more localised near wooded habitats. He explained this result by the need for shelter, which is greater during the early part of the spring when the weather is cooler.

In later records, woods no longer affected hoverfly abundance whatever the spatial scale. One explanation is that hoverflies use woods for overwintering refuge (Sarhou et al., 2005) and then spread across the landscape using hedges for connectivity between uncultivated habitats (Tscharrntke et al., 2005b) and are mainly looking for nectar and aphid resources. This hypothesis is supported by the positive role of hedges (at 500 m and 1200 m) and grasslands (only at 500 m) observed in late spring. Indeed, both hedges and grasslands are nectar providers for hoverflies and favour egg laying by females (Cowgill et al., 1993; Hickman, Lövei and Wratten, 1995; Hickman and Wratten, 1996; Pontin et al., 2012). The negative effect showed by grasslands at small spatial scale in late period is not in accordance with these hypotheses. That may reflect a limitation in our land cover map classification because it does not discriminate the temporary non-flowering grasslands from the permanent flowering meadows.

4.3. Hedges favoured aphid parasitism in late spring

A significant effect of landscape variables on aphid parasitism was observed only in late spring and at the smaller scales. The

few number of significant relationships, whatever the spatial scale, is explained by the fact that parasitoids are poor dispersers (Weisser and Völkl, 1997). As for hoverflies, the positive hedges influence on parasitism could be due to the additional floral resources they provide. By the reverse, the negative influence of woods is explained by indirect competition between predators for aphids as feeding resources (Snyder and Ives, 2003). We hypothesized that hoverflies in the favourable environment of woods early in spring fed on aphids which were no longer available for parasitoids late in the season. Moreover, the presence of hoverfly larvae and eggs among aphid colonies is also known to affect egg laying by parasitoids (risk of predation by aphid parasites) (Müller and Brodeur, 2002).

4.4. Implications for conservation biological control

According to Barbosa (1998), the conservation biological control enhance the performance and local abundance of the existing community of natural enemies in terms of fecundity, longevity, search ability and prey conversion efficiency. Semi-natural elements in the landscape provide mainly resource subsidies enhancing fecundity and longevity. In our study, woods, grasslands and hedges were in majority positively related to the abundance of natural enemies (hoverflies and parasitoids) whatever the spatial scale. Therefore, implementing landscape with an increased proportion of semi-natural habitats providing food and shelter appears to be one of the promising strategies to increase natural enemies and favour biological control in winter crop fields.

We highlighted the role of woods for sustaining the potential aphid biocontrol in agricultural landscape, in early spring at small spatial scale scales. However, we also showed a positive relationship between woods and aphid abundance in the surroundings of wheat fields in the early spring. To our knowledge, this is one of the first studies which demonstrates intra-seasonal antagonism of semi-natural habitats upon a pest and its natural enemies. This temporal variability in the response patterns of aphids and their natural enemies to semi-natural habitats leading us to consider the landscape as "ambivalent" in accordance with Rusch et al. (2012). Thus, in our landscape context, meadows and hedges are the semi-natural elements to be favoured as they do not present any ambivalent effect for pest biological control.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocontrol.2014.06.006>.

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