

Immature hoverflies overwinter in cultivated fields and may significantly control aphid populations in autumn



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ABSTRACT

This study was based on broad monitoring of spring emergence of hoverflies and of aphid populations in two French agro-ecosystems. Its aim was to determine whether hoverflies overwinter in agricultural fields and/or in field margins at immature stages and to what extent local and large-scale landscape features influence the abundance of immature overwintering individuals and the associated biological control. Our results show that the influence of the landscape on the abundance of immature overwintering hoverflies varies among trophic groups. Non-aphidophagous species plus some aphidophagous species, which occasionally feed on crop aphids, preferentially overwinter in field margins near wooded land. Conversely, aphidophagous species, which mainly feed on crop aphids, preferentially overwinter within the fields and are less influenced by semi-natural features. This work also shows a strong negative correlation between the abundance of hoverflies that overwinter at immature stages within the fields and the abundance of aphids in the spring, which suggests a biological control by the hoverflies in autumn. Because they may provide a significant service of biological control, the hoverflies that overwinter within agricultural fields should be taken in consideration in the management of croplands, through agricultural practices for example. The landscape configuration also should be considered in order to maximize the hoverflies community in agricultural landscapes, and to maximize the ecosystem services it provides.

This study provides valuable insights on overwintering of hoverflies at pre-imaginal stages in agricultural landscapes and on the role of this overwintering strategy in the biological control of aphid populations. It shows that a landscape mostly composed of cultivated land can provide significant service of biological control if semi-natural features are arranged in a convenient way for natural enemies.

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1. Introduction

In autumn-sown crops, pest predation in autumn may reduce the initial level of pest population in the following spring, as well as reduce the transmission of autumn occurring viruses such as Barley Yellow Dwarf Virus (Kendall et al., 1991). Winter survival of beneficial insects may determine their potential for biological control in the spring by conditioning the population levels at the end of

the winter. The ecology of pests and of beneficial insects in the cold months is nevertheless largely under-considered in the current literature (Eitzinger and Traugott, 2011). In the case of aphids which are major crop pests (Dedryver et al., 2010), the impact of biological control by natural enemies in autumn is poorly documented.

Insects which overwinter without migrating often require special habitats to survive unfavorable winter conditions (Bale, 1993). Semi-natural landscape features such as field margins, woodlands, or hedges are known to be favorable winter habitats for many beneficial insects as they provide alternative prey and hosts, floral resources, and protection against inhospitable climatic conditions (Landis et al., 2000; Gurr et al., 2004). However, cultivated fields may also provide suitable conditions for overwintering, and may be sources of some ecosystem-service providers throughout the year (Sotherton, 1984; Eitzinger and Traugott, 2011). For example, in some predatory beetles such as carabids and cantharids, active

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larvae which overwinter within crop fields are major contributors to adult spring populations (Fadl et al., 1996; Noordhuis et al., 2001). The quality of cultivated lands as overwintering sites and their functionality for conservation biological control may vary with the type of crop, crop phenology, and land use intensity (Herzog et al., 2006). Veres et al. (2013) point to the need for better consideration of the functionality of cultivated lands when assessing the influence of the landscape on pest regulation. The spatial arrangement of cultivated fields, with respect to each other, and with respect to semi-natural features, influences the abundance, distribution, and persistence of organisms in the landscape, and consequently the production of various ecosystem services in the agro-ecosystem (Fahrig et al., 2011). Under certain management conditions, the cultivated fields themselves may benefit ecosystem-services providers. In this way, they may enhance agricultural ecosystem services without necessarily requiring the addition of semi-natural features in the agricultural landscapes.

The family of Diptera Syrphidae, also called hoverflies, consists in more than 6000 species belonging to 200 genera distributed all over the world. Apart from extremely rare exceptions, all hoverflies are pollinators at the adult stage as they feed on flowers. Larval ecology is more diverse and varies with the genera and species. Some species, called aphidophagous, have predatory larvae, which are predators of a wide range of crop aphid species (Chambers and Adams, 1986; Tenhumberg and Poehling, 1995). Hoverflies have developed different strategies to survive winter conditions. They can migrate southwards to warmer climes (Aubert and Goeldlin, 1981; Gatter and Schmid, 1990), or they can remain in the summer sites and overwinter as adults (Schneider, 1948; Sarthou et al., 2005), or as diapausing larvae or pupae (Dusek and Laska, 1974; Sarthou et al., 2005). In some species including *Episyrphus balteatus*, several strategies may be used simultaneously in proportions which remain unclear and which probably vary over time and with the region (Hart et al., 1997; Hondelmann and Poehling, 2007; Raymond et al., 2013). In the case of aphidophagous species, the dynamics of each overwintering strategy determines the active period of the predatory larvae responsible for biological control. Locally overwintering adults are known to be more precocious in the spring than immigrants which arrive later from the south (Pollard, 1971; Tenhumberg and Poehling, 1995). Little is known about individuals that spend the winter at immature stages except that they overwinter in the soil (Sarthou et al., 2005; Bokina, 2012) and that they enter in diapause at the beginning of the winter and emerge in the spring (Dusek and Laska, 1974; Hart et al., 1997). Knowledge about the suitable habitats for these overwintering individuals, their distribution and their dynamics is lacking. The precise periods of emergence of adults from the overwintering larvae and pupae remain poorly known and the potential of cultivated fields to host pre-imaginal overwintering hoverflies has never been investigated.

The aim of this work was thus to determine (i) what hoverfly species overwinter at pre-imaginal stages in French agro-ecosystems, (ii) what is the influence of the landscape at large and local spatial scales on the abundance of hoverflies overwintering at pre-imaginal stages, (iii) what is the contribution of pre-imaginal overwintering hoverflies to biological control of aphids. The study was based on the monitoring of hoverflies emerging in spring associated with the abundance of aphids in crop fields, in two French agro-ecosystems with different landscapes and climates.

2. Material and method

Post overwintering emerging hoverflies were collected in spring at two French sites located more than 400 km apart. The study site “Vallées et Coteaux de Gascogne” (VCG) is a 220 km² hilly area

located in south-western France (43°17'N, 0°54'E). The study site “Plaine et Val de Sèvre” (PVS) is located in central western France (46°23'N, 0°41'W). It is a flat farmland area of 450 km² where mainly cereal crops are grown. The VCG study site is part of the Long Term Ecological Research network (LTER.EU.FR.003), and the PVS study site of the Zone Atelier network (ZAPVS).

2.1. Field sampling

Adults emerging from the pre-imaginal overwintering hoverflies were caught using emergence traps in 2011 and 2012 from the end of the winter to the beginning of the summer, covering most of the adult emergence period (Dusek and Laska, 1974). The operating principle of emergence traps is to seal hermetically a soil area and to collect all the insects that emerge within this area. Traps were placed in agricultural fields (within the fields and/or in the adjacent field margins) selected according to a gradient of density of the surrounding woodland (0–50% within a 500-m radius from the sampling location). In each sampling field, the positions of the traps in the field margin and inside the field were randomly chosen. Traps were set up during the second half of March and were collected every fortnight from the 15th of April until the first week in July.

In 2011, hoverfly emergences were only monitored in the VCG study site. Twenty large traps (surface area 1.8 m², a modified Malaise trap to the design of M.C.D. Speight; B&S Entomological Services, Co. Armagh, N. Ireland, UK) were set up in the margins of five oilseed rape fields and five winter wheat fields. In 2012, emergences were monitored in both study sites, both inside the fields and in the field margins, in 49 fields in the PVS site and in 35 fields in the VCG site. In each field, one trap was placed in the field itself, and one in the field margin. Crops in the fields were winter cereals ($N=52$), oilseed rape ($N=18$) or alfalfa ($N=14$). The traps used in 2012 were small (surface area: 0.36 m², Soil Emergence trap 96 × 26 mesh, Black, MegaView Science Co., Ltd., Taichung, Taiwan). Collection bottles in all the traps were filled two thirds full with 70° ethanol and were replaced every fortnight. The use of different size emergence traps was due to the availability of the material.

Hoverflies were manually sorted, determined at the species level, and classified in three groups on the basis of larval diet. The species whose larvae are poly-aphidophagous and common predators of aphids in crops with known effective activity of biological control were classified “major aphidophagous species”. The species whose larvae are oligo-aphidophagous with unknown efficiency in biological control of crop aphids were classified “minor aphidophagous species”. The species whose larvae are not aphid predators were classified “non-aphidophagous species” (S1, supporting information). This classification was based on the databases Syrph the net (Speight et al., 2010) and SirfiGest (Rojo et al., 2003).

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In 2012, the abundance of aphids and hoverflies (eggs, larvae and pupae) was recorded in the fields in which the emergence traps had been placed. From the second week in April to the first week in July, they were counted every 15 days on 50 wheat stalks, 10 rape plants or 50 alfalfa plants randomly chosen in an area of 1 m² located near the emergence traps in the field. For each field, we determined (i) the “initial abundance of aphids in spring” (sum of the aphids counted in the recording area in the second week of April), (ii) the “total abundance of aphids in spring” (sum of all the aphids counted in the recording area in spring), (iii) the “total abundance of hoverflies in spring” (sum of all the eggs, larvae and pupae of hoverflies counted in the recording area in spring).

2.2. Landscape and local variables

Annual land use maps were drawn for the two study sites based on direct field observations, using ArcMap software, ArcGis for Desktop 10 version ArcInfo advanced (ESRI, 2012). Land use polygons were digitalized and attributed on the base of georeferenced numeric orthophotograph BDOrtho© (IGN, 2010). Three large-scale landscape descriptors were calculated in a circular buffer zone (radius 500 m) around each emergence trap using ArcToolBox scripts: (i) two landscape variables measuring the proportion of the buffer zone covered by different categories of semi-natural habitats (a) Woodlands, (b) Meadows, and (ii) the density of hedgerows (Hedges; *i.e.* total linear length of hedges within the buffer zone). For each trap, we also recorded local descriptors: the position of the trap (within the field or in the field margin), the type of crop in the field (winter cereal, oilseed rape, alfalfa), and the distance in m to the nearest semi-natural habitats (1) Distance to woodland, (2) Distance to hedge, and (3) Distance to meadow.

2.3. Statistical analysis

As different size traps were used, we calculated the number of emergences per m² (*i.e.* emergence density), in order to compare: (i) the emergence density of hoverflies in the field margins between years in the VCG study site, (ii) the emergence density of hoverflies between study sites in both fields and field margins in spring 2012, (iii) the emergence density of hoverflies between fields and field margins in the two study sites in spring 2012. The significance of all these comparisons was assessed by non-parametric Wilcoxon signed-rank tests.

Correlations between landscape variables were checked with Pearson correlation tests. As no pair of variables showed strong correlations (>|0.7|), all variables were retained for the analyses.

To investigate the effects of local and large-scale landscape variables on the abundance of spring emergence in the three hoverfly trophic groups, we first performed a generalized mixed effect model (GLMM) for each trophic group separately. In each model, the abundance of spring emergence of hoverflies was related to the local variables (Position of trap, Distance to woodland, Distance to hedge, and Distance to meadow) and the large-scale landscape variables (Wood, Grassland, and Hedge). Second, we performed a separate GLMM, considering only the emergence traps installed within the fields, to investigate the effect of the type of crop (Crop) and of the distance to the field margin on the abundance of spring emergence within field. This data subset involved only aphidophagous species (97% of major aphidophagous species and 3% of minor aphidophagous species).

All the GLMMs were additive models. We used a Poisson error distribution and a log link function for all the models. In order to conserve a Poisson distribution for the data, we considered the number of emergences per trap as the variable to explain and we added the trap area (in m²) as a fixed effect in the models. In all models, fixed effects were scale-centered to facilitate model convergence. The study site and the year were included as a single random effect ($N=3$, VCG-2011, VCG-2012, PVS-2012).

In order to evaluate the correlation between the abundance of hoverflies in autumn and in spring and the abundance of aphid in spring, we performed two GLMMs on the 2012 dataset. In the first GLMM, we linked the initial abundance of aphid in spring to the abundance of spring emergence of hoverflies within fields. In the second, we linked the total spring abundance of aphids to the abundance of spring emergence of hoverflies within fields and the total abundance of hoverflies in spring. The GLMMs were additive models with a Poisson error distribution and a log link function. The study site ($N=2$, VCG and PVS) and the type of crop ($N=3$, cereals, oilseed rape and alfalfa) were included as random effects.

Table 1

Densities of spring emergence of hoverflies observed during the two-year study period in the two sampling sites. Mean emergence density and standard deviation in number of emergence per m² (mean \pm SD), minimum emergence density in number of emergence per m² (min), and maximum emergence density in number of emergence per m² (max) for all the emergence traps are given for all hoverflies and for each trophic group (with N the number of samples that make up the mean and SD).

	Mean \pm SD	Min	Max	N
All hoverflies	1.56 \pm 3.82	0	25	62
Major aphidophagous	1.17 \pm 3.24	0	22.2	50
Minor aphidophagous	0.28 \pm 1.58	0	19.4	17
Non-aphidophagous	0.11 \pm 0.90	0	11.1	8

For all the GLMMs in the study, the significance of each fixed effect was tested by comparing model deviances fitted with and without each effect with a likelihood ratio test. GLMMs were systematically checked for data over-dispersion and randomness of the residuals.

3. Results

A total of 179 hoverflies (of which 158 were aphidophagous) were caught in the emergence traps in 2011 and 2012 and in the two study sites (Table 1). All the hoverflies observed emerged in 54 of the 187 traps (*i.e.* approximately 30%). Twenty-seven different species were identified, including six major aphidophagous species, 15 minor aphidophagous species and six non-aphidophagous species (S1, supporting information). In spring 2011, in the VCG study site, we observed hoverfly emerging from April 22nd to July 18th with the highest number emerging on June 3rd (Fig. 1). In spring 2012, in the two study sites, we observed hoverflies emerging from April 20th to July 2nd with the highest number emerging on July 2nd (Fig. 1).

Precocious adults of some species including *Melanostoma mellinum* and *Sphaerophoria scripta* have already been observed as early as the beginning of March (Speight et al., 2010). To avoid the risk of considering offspring of this first generation as spring emerging overwintering individuals, we discarded from further analyses all individuals found in the emergence traps before the beginning of May. Given that the developmental time from egg to adult is 5–6 weeks for a spring generation in polyvoltine aphidophagous hoverfly species (Barkemeyer, 1994; Dziock, 2002), if eggs or larvae from this precocious first generation were trapped while the traps were being set up (second half of March), they would have emerged before the beginning of May. In this way, 20 individuals (6 *M. mellinum*, 8 *S. scripta*, 1 *Melanostoma scalare*, 2 *Sphaerophoria ruepelli*, 1 *Epistrophe eligans*, 1 *Syrphus vitripennis*, 1 *Cheilosia ranunculii*) were discarded from further analyses.

We observed a non-significant difference in hoverfly emergence density between study sites in 2012 ($W=3852$, p -value=0.074) (Fig. 2a) and a significant difference between years in the VCG study site ($W=500.5$, p -value= 2×10^{-4}) (Fig. 2b). In spring 2012, in the two study sites, we observed a significantly higher density of hoverfly emergence within the fields than in the field margins ($W=3054.5$, p -value=0.047) (Fig. 2c). The major aphidophagous species accounted for 97% of the total spring emergence of hoverflies within the fields and for 43% in the field margins.

3.1. Influence of the landscape on hoverflies overwintering at immature stages

In the major aphidophagous species, the explanatory variable with the most effect on the abundance of spring emergence was the position of the trap: the abundance of spring emergence was significantly higher within the fields than in the field margins (Table 2).

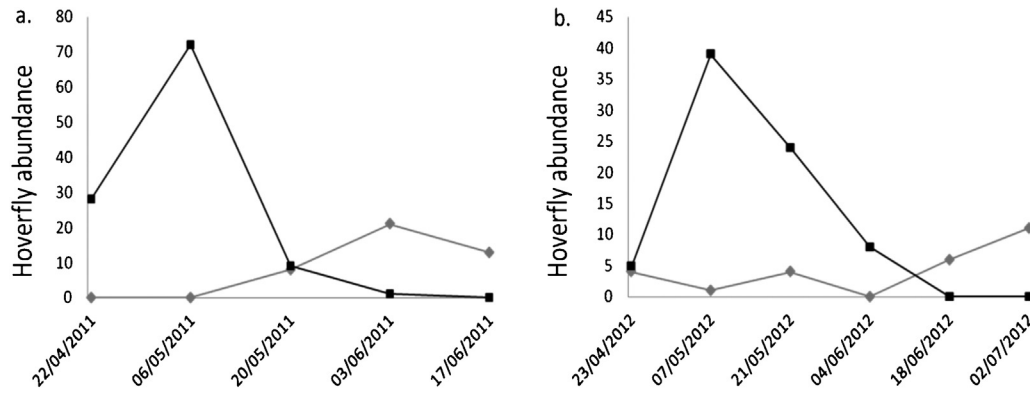


Fig. 1. Temporal dynamics of spring emergence of hoverflies and of hoverflies observed in the fields (eggs, larvae, pupae) in the VCG study site in spring in 2011 (a) and 2012 (b). Black line: total number of hoverflies (eggs, larvae, pupae) observed on 50 wheat stalks, 10 rape plants or 50 alfalfa plants randomly chosen in an area of 1 m², in 10 fields in 2011 (a) and in 35 fields in 2012 (b); gray line: spring emergence of hoverflies 20 large size emergence trap (1.8 m²) in 2011 (a) and in 70 small size emergence trap (0.36 m²) in 2012 (b).

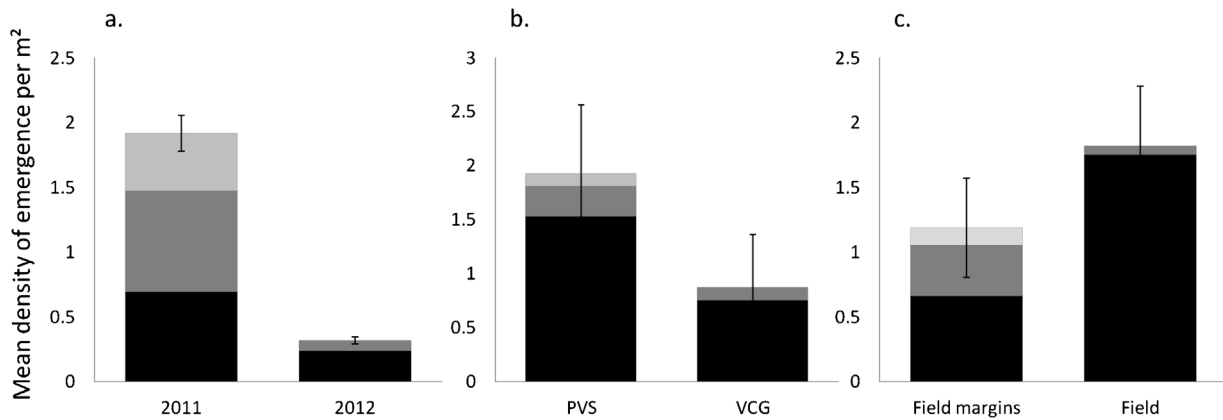


Fig. 2. Mean densities of spring emergence of hoverflies per m² according the year (study site VCG, field boundaries only) (a), to the study sites (year 2012, fields and field boundaries) (b), and the position of the trap (year 2012, both study sites) (c). Major aphidophagous species are in black, minor aphidophagous species are in dark gray, and non-aphidophagous species are in light gray. Standard errors are provided for all trophic groups combined.

Except for the proportion of meadows in a 500-m buffer zone, which had a negative effect, none of the landscape variables had a significant effect on the abundance of spring emergence.

Among the minor aphidophagous species, the abundance of spring emergence tended to be higher in the field margins than within the fields (Table 2). All the significant landscape effects were related to local variables: the abundance of spring emergence significantly increased with a decreasing distance to the nearest hedge and with an increasing distance to the nearest meadow.

The distance to the nearest woodland had no effect. We observed no significant effect of the large-scale landscape variables (Wood, Meadow and Hedges).

The abundance of spring emergence of non-aphidophagous species was significantly higher in the field margins than inside the fields (Table 2). The abundance of spring emergence tended to increase with an increasing distance to the nearest meadow and with an increasing proportion of woodland in a 500-m buffer zone. We observed no significant effect of the distances to the nearest

Table 2
Summary of generalized linear mixed models (GLMMs) for the abundance of spring emergence in the three trophic groups of hoverflies versus local and large-scale landscape variables. For each explanatory variable, the coefficient value \pm standard deviation (SD) and its level of significance are given (p -value of the likelihood ratio test between the models with and without the variable). AIC value of the model for each trophic group is given. ns: not significant.

Explanatory variable	Major aphidophagous species Model AIC = 312		Minor aphidophagous species Model AIC = 153		Non-aphidophagous species Model AIC = 59	
	Coefficient \pm SD	p	Coefficient \pm SD	p	Coefficient \pm SD	p
Intercept	-2.000 \pm 0.29		-3.631 \pm 0.51		-5.369 \pm 1.04	
Position of trap (field)	0.901 \pm 0.26	**	-1.239 \pm 0.78	ns	-17.178 \pm 3086	*
Distance to wood	0.187 \pm 0.13	ns	-0.580 \pm 0.37	ns	-0.565 \pm 0.79	ns
Distance to hedge	0.099 \pm 0.11	ns	-1.542 \pm 0.42	**	-0.378 \pm 0.51	ns
Distance to meadow	-0.049 \pm 0.15	ns	0.522 \pm 0.24	*	0.705 \pm 0.42	ns
Woodland	0.001 \pm 0.15	ns	-0.111 \pm 0.26	ns	0.702 \pm 0.37	ns
Hedge	0.176 \pm 0.13	ns	0.043 \pm 0.27	ns	0.608 \pm 0.49	ns
Meadow	-0.0329 \pm 0.13	*	0.108 \pm 0.20	ns	-0.455 \pm 0.42	ns
Trap area	1.418 \pm 0.23	**	1.884 \pm 0.32	**	2.537 \pm 0.70	**

* $p < 0.05$.

** $p < 0.01$.

Table 3

Summary of the GLMM for the abundance of spring emergence of hoverflies within the field versus crop type (Crop) and distance to the nearest field margin. The model AIC value is 165. For each explanatory variable, the coefficient value \pm standard deviation (SD) and its level of significance are given (p -value of the likelihood ratio test between the models with and without the variable). ns: not significant.

Explanatory variable	Coefficient \pm SD	p
Intercept	-0.409 ± 0.17	
Distance to the field boundary	-0.217 ± 0.15	ns
Crop type		*
Oilseed rape:	0.376 ± 0.30	
Cereals:	0	
Alfalfa:	-1.239 ± 0.40	

* $p < 0.05$.

woodland or to the nearest hedge, or of the proportion of meadows and hedges in the 500-m buffer zone.

The abundance of spring emergence of hoverflies within the fields was not significantly influenced by the distance to the field margins but was significantly higher in the oilseed rape fields than in the cereal fields and in the cereal fields than in the alfalfa fields (Table 3).

3.2. Correlations between abundance of aphids and hoverflies in autumn and spring

In the spring 2012, we observed 11,093 aphids and 104 hoverflies (eggs, larvae and pupae) in 52 cereal fields, 18 oilseed rape fields and 14 alfalfa fields. The initial abundance of aphids in spring within the fields decreased significantly with an increasing abundance of spring emergence of hoverflies within the fields, and the total abundance of aphids in spring decreased significantly with an increasing abundance of spring emergence of hoverflies within the fields as well as in the total abundance of hoverflies in spring (Table 4). According to the coefficients and the variations in AIC values associated with the two variables in the model, the effect of the abundance of the spring emergences of hoverflies within fields was greater than the effect of the total abundance of hoverflies in spring on the total abundance of aphids in spring.

4. Discussion

The present study clearly demonstrates that hoverflies use both cultivated and semi-natural habitats to overwinter at pre-imaginal stages in agro-ecosystems, and that they use different habitats according to their larval diet. The density of spring emergence of aphidophagous species was equivalent or even higher within the fields than in the field margins. This proves that although this phenomenon has not been previously observed, overwintering of aphidophagous hoverflies in cultivated fields is very common.

We observed a great variability in the abundance of emergence between traps and years. We also observed a difference between sites but this difference was not significant probably due to the low sample size in VCG in 2011 and to the great intra-site

variability. Climatic conditions may affect winter survival and/or the prevalence of the different overwintering strategies in the hoverfly populations at the end of the summer (Raymond et al., 2013). The fact that aphid population dynamics vary considerably between years and regions (Vialatte et al., 2007) may be also a determining factor in the abundance of pre-imaginal overwintering hoverflies. The difference in emergence abundance between traps is probably due to the patchy distribution of aphids (Winder et al., 1999), as 87% of observed emergences were emergences of aphidophagous hoverflies. The likely dependency on local conditions such as climatic conditions or aphid dynamics may influence the prevalence of the overwintering strategy at immature stages in the hoverfly population between regions, which in turn influences the biological control of aphids in agricultural fields.

4.1. Local and landscape determinants of the abundance of pre-imaginal overwintering hoverflies

Our results suggest that the abundance of hoverflies overwintering at pre-imaginal stages depends on the surrounding landscape composition and configuration. In our study, the relative influences of each landscape variable depended on the trophic group concerned and were consistent with the biology of the different groups.

Non-aphidophagous species appeared to preferentially exploit wooded landscapes, which is not surprising given that their trophic regimes are mainly based on decaying organic matter (*Caliprobola speciosa*, *Myathropa florum*, *Eristalinus sepulchralis*) or sap runs (*Volicella inflata*) (Speight et al., 2010). Minor aphidophagous species appeared to preferentially overwinter in field margins and in habitats close to hedges. This is also consistent with their trophic habits: although their larvae can be observed feeding on crop aphids, they feed mainly on root aphids (*Chrysotoxum* sp., *Xanthogramma* sp.), or on litter fauna (*M. scalare*) (Speight et al., 2010) which are more abundant in field margins than in the fields themselves.

Major aphidophagous species were shown to overwinter preferentially within the fields, with no strong influence of the landscape. The choice of their overwintering sites is probably mostly driven by the presence of aphid colonies in the crops in autumn. According to Syrph the Net (Speight et al., 2010), all the major aphidophagous species are on the wing until mid-November in western France, and can therefore lay their eggs on the first colonies of aphids to appear in winter wheat or oilseed rape fields in autumn. This supports the hypothesis of significant biological control in autumn at locations where emergence occurs in spring. We observed that the field's attractiveness to aphidophagous hoverflies depends on the type of crop. Oilseed rape was the most attractive crop (compared to cereals and alfalfa). This may be due to a higher density of aphids on plants in autumn or to more attractive microclimatic conditions within the plant cover. Indeed, oil seed rape vegetation is more developed in autumn than that of alfalfa or cereals because it is sowed earlier, and vegetation cover has already been shown

Table 4

Summary of GLMMs for the initial abundance of aphids in spring versus the abundance of spring emergence of hoverflies within the field, and for total abundance of aphids in spring versus the abundance of spring emergence of hoverflies within the field and the total abundance of hoverflies in spring. For each explanatory variable, the coefficient value \pm standard deviation (SD) and its level of significance are given (p -value of the likelihood ratio test between the models with and without the variable). AIC value of each model is given.

Response variable	Initial abundance of aphids in spring Model AIC = 4809		Total abundance of aphids in spring Model AIC = 23,159	
	Coeff value \pm SD	p	Coeff value \pm SD	p
Explanatory variable				
Intercept	2.040 ± 1.56		4.430 ± 1.15	
Abundance of spring emergence of hoverflies within field	-0.372 ± 0.04	**	-0.326 ± 0.01	**
Total abundance of hoverflies in spring	–	–	-0.028 ± 0.00	**

** $p < 0.01$.

to influence the overwintering density of other taxa (Frank and Reichhart, 2004). The crop attractiveness may also vary between years due to climatic conditions, comparative development of the plants and aphid colonization. Farming practices such as weed control, insecticide sprays and coated seeds may also have a significant influence on overwintering insects in the fields.

We observed a negative influence of the proportion of meadowland in a 500-m buffer zone on the abundance of spring emergence of major aphidophagous species, and a positive influence of the distance to the nearest meadow on the abundance of the emergence of minor- and non-aphidophagous species. The negative influence of meadows may be due to a dilution effect considering that meadows are attractive overwintering sites for hoverflies. It may also be due to a smaller area of croplands in the landscapes in which meadows are abundant, what leads to lower aphid populations and therefore to lower hoverfly populations. An alternative hypothesis is that meadows are sources of parasitoid natural enemies of hoverflies, mainly *Diplazontinae* (Hymenoptera: Ichneumonidae) (Weems, 1954). Parasitism of hoverflies in autumn may be greater in landscapes with a higher proportion of meadows, which allow the wasps to reproduce and multiply more easily throughout the vegetative season thanks to more available flowers (notably legumes).

Finally, our findings suggest that the abundance of aphidophagous hoverflies emerging in the spring is more related to the distances to the nearest semi-natural features than to the amount of land occupied by these features in the surrounding landscape. This highlights the importance of the landscape configuration and the proximity of different types of habitat patches to each other (Fahrig et al., 2011). This supports the hypothesis that the amount of semi-natural features in the landscape is not the only important feature to take into consideration for biological control, and suggests that a landscape mostly composed of cultivated land can provide significant biological control service if semi-natural features are arranged in a convenient way for natural enemies.

4.2. Hoverflies overwintering at immature stages and biological control

Our observations support the hypothesis that most hoverfly spring emergence occurs quite late in the spring. Because they overwinter at pupal stage or at the last larval instar, the individuals that spend the winter at immature stages do not perform predation on aphid populations after overwintering. Biological control service in the spring may be provided by the predatory larvae of the next generation. Whatever the study site and the year, the peak of hoverfly emergence was observed after the end of May. Comparing this dynamics of emergence to the dynamics of aphids and of predatory larvae (with few eggs and pupae) in the fields, we first conclude that the contribution of the pre-imaginal overwintering hoverflies to biological control in spring is limited. Biological control by predators in spring is known to be more efficient when it occurs early after pest colonization of fields (Altieri and Nicholls, 2004). In the particular case of aphidophagous hoverflies, Tenhumberg and Poehling (1995) showed that syrphid larvae have a greater impact on aphid populations when the larvae are present in cereal fields early in the spring.

However, our findings suggest that pre-imaginal overwintering hoverflies had a major influence on aphid populations in spring thanks to their significant contribution to biological control in autumn. We showed that the abundance of spring emergence of hoverflies was negatively correlated with the precocious abundance of aphids in spring, suggesting biological control of young aphid colonies on winter crops in autumn. Autumn biological control may not only reduce the initial populations of aphids in the fields in spring, but may influence aphid population dynamics

throughout the spring season. Our results support the hypothesis that the influence of hoverfly larvae in autumn on the total aphid population in spring is even more important than the influence of predatory hoverfly larvae in the beginning of the spring. Biological control is probably divided between autumn and spring: in autumn, biological control may reduce the populations of the first colonies of aphids, and in spring, predation may control the remaining colonies and the colonies arising from the spring colonization of agricultural fields by immigrating aphids. The biological control of aphids in autumn could also play an important role in controlling viruses that occur in autumn such as Turnip Yellowings Luteovirus in oilseed rape (Büchs, 2007) or Barley Yellow Dwarf Virus in cereals (Kendall et al., 1991), which cause serious damage and economic losses.

5. Conclusion

This work is the first to demonstrate that cultivated lands are favorable habitats for the overwintering of aphidophagous hoverflies, and to highlight a possible biological control of aphids by hoverflies in autumn. Biological control in autumn may limit the propagation of autumn occurring plant viruses and significantly decrease pest populations.

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