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REVIEW ARTICLE

Landscape potential for pollen provisioning for beneficial insects favours biological control in crop fields

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Abstract

Context The importance of landscape complexity for biological control is well-known, but its functional roles are poorly understood.

Objectives We evaluated the landscape capacity to provide floral resources for beneficial insects and its consequences for biological control in fields.

Methods The gut contents of adult hoverflies sampled in 41 cereal fields were analysed to determine which plant species are exploited. The relative value of each habitat in providing adequate pollen resources was evaluated by vegetation survey. Then 15 cereal fields were selected along a gradient of landscape complexity, where the abundance of aphids, hoverfly larvae and aphid parasitism was monitored. The habitat's proportions in landscape buffers surrounding these fields were used as landscape descriptors and to assess the potential level of pollen resources provision (LP index).

Results Aphid abundance significantly decreased with an increase of the LP index mainly sustained by grassy strips and weeds in fields. However, hoverfly larvae abundance also decreased with the increasing LP index. The enhancement of the aphid parasitism rate with the LP index suggests that aphid parasitoids may benefit from the same floral resources as hoverflies. Their crop habitat specialism may give them a competitive advantage in fields where both aphid and floral resources are abundant.

Conclusions Complex interaction networks involved in biological control may disrupt the expected direct effects of floral resource provisioning for a focal beneficial species. We highlighted fields and grassy strips as habitats provisioning floral resources for which the LP index could be very helpful to optimize agroecological management strategies.

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Introduction

It is widely assumed that biological control of agricultural pests and pollination, two important ecosystem services provided to agriculture, are improved in presence of non-crop habitats in agricultural landscapes (e.g. Chaplin-Kramer et al. 2011; Holzschuh et al. 2012). Non-crop habitats provide seasonal refuges, nesting sites and various food resources to insect predators, parasitoids and pollinators, resulting in a spill-over of beneficial insects from these habitats into crop fields (Landis et al. 2000; Kremen et al. 2004; Tscharntke et al. 2005; Klein et al. 2007). A positive effect of non-crop habitats on beneficial insects has been demonstrated either globally through assessment of the relative area covered by the non-crop (e.g. Steffan-Dewenter et al. 2002; Bianchi et al. 2006; Holzschuh et al. 2012) or by focusing on one particular type of non-crop habitat such as woodlots and hedgerows (e.g. Rusch et al. 2012), grasslands (e.g. Ockinger and Smith 2007; Meyer et al. 2009), or grassy/floral strips (e.g. Gillespie et al. 2011; Ernoult et al. 2013). The influence of plant composition of these habitats has been particularly well studied with the aim of increasing beneficial insect population abundances (Altieri and Whitcomb 1979; Cowgill et al. 1993; White et al. 1995; Hickman and Wratten 1996; Patt et al. 1997; Rebek et al. 2005). The distances between crop fields and non-cultivated habitats have also been shown to affect the diversity of beneficial insects and the biocontrol service provided in crop fields (e.g. Garibaldi et al. 2011).

However, even if the abundance and diversity of beneficial populations is generally enhanced by landscape complexity, the influence of non-crop habitats on realised ecosystem services in terms of biological control appears more variable (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Tscharntke et al. 2016). On the one hand, while native vegetation in non-cultivated habitats has been shown to support predator reproduction across seasons, its influence on biological control in crop fields is unclear (Bianchi et al. 2013). On the other hand, crop fields appear to be important overwintering sites for some major beneficial species and confer a significant effect on biological control (Raymond et al. 2014). It would appear that some beneficial populations are strongly associated with crop habitat throughout their ecological

cycles and consequently could be rather insensitive to the presence in the landscape of non-crop habitats. Our poor understanding of the ecological processes and functions involved means that the design of landscape management strategies for improving biological control service provision remains a central challenge. In this study we investigated the landscape functionality [i.e. landscape patterns in relation to their function (Forman and Godron 1986)] in terms of floral resource provisioning to beneficial insects and assessed how it affected the biological control of pests.

There is increasing evidence that the provision of floral resources in agricultural landscapes enhances the performance of parasitoids as part of conservation biological control (Tena et al. 2015; Jonsson et al. 2015). Adult parasitoids require both nectar and pollen as a source of energy (Tenhumberg et al. 2006) and a source of protein for reproduction (Rivero and Casas 1999). As floral resources, particularly nectar, are often scarce in agricultural ecosystems (Heimpel and Jervis 2005), the incorporation of targeted non-crop vegetation in agricultural landscapes can help support biological control (Landis et al. 2000).

Hoverflies (Diptera: Syrphidae) are another common and important group of beneficial insects in agroecosystems. They have been shown to provide significant pollination services to wild flowers and crops (Fontaine et al. 2006; Jauker and Wolters 2008). Moreover, some hoverfly species, aphidophagous at the larval stage, are among the most common natural enemies of aphids in crops (Tenhumberg and Poehling 1995; Schmidt et al. 2003; Brewer and Elliott 2004). Adult hoverflies feed on floral resources found in several types of habitats, with individuals moving from one habitat patch to another to find the resources they need to complete their entire life-cycle (Dunning et al. 1992). Hoverfly adults require floral resources for their high-energy flight, ovary maturation and egg production (Chambers 1988).

Studies on the use of flowers by aphidophagous hoverflies in intercropping flower strips or field margins have demonstrated a large spill-over of hoverflies from non-crop habitats to crop habitats (Cowgill et al. 1993; Gillespie et al. 2011). Explorative routine movements for daily resource-searching (pollen for feeding or aphids for egg laying) occur at small spatial scales, typically less than 200 m (Wratten et al. 2003). However, aphidophagous hoverflies exhibit long-distance dispersal behaviour as well (up

to 1000 m) for movements associated with life-cycle stages and seasonality (Arrignon et al. 2007; Meyer et al. 2009). Hence, it has been found that landscape properties affect aphidophagous hoverfly diversity, abundance and the ecosystem services they provide, at both small and large spatial scales (Jauker et al. 2009; Meyer et al. 2009; Power and Stout 2011; Ernoult et al. 2013; Alignier et al. 2014).

Until now, studies of pollen feeding by hoverflies have focussed on (1) analysing gut contents to determine visited plant species (Cowgill et al. 1993; Hickman et al. 1995), (2) testing consumption of various introduced flowering plants with the aim of making recommendations for the composition of the flower strips adjacent to crop fields (e.g. Hogg et al. 2011), and (3) using pollen as markers in studies of hoverfly dispersion from a controlled pollen source (e.g. Rader et al. 2011). Despite the significant amount of available information on pollen feeding by hoverflies, the floral sources actually exploited in agricultural landscapes are still unknown, with woodlands, hedgerows, grasslands, grassy strips or even weeds in crop fields being potential sources of pollen. By combining analyses of the gut content of adult hoverflies sampled in crop fields with a large vegetation survey of main non-crop and crop habitats, and an assessment of the proportion of these habitats covering the landscape surrounding crop fields in which aphid and larval hoverfly abundances have been monitored, we addressed two questions. What is the relative importance of non-crop and crop habitats as pollen sources for hoverflies? Does landscape functionality in terms of floral food provision to hoverflies influence aphid biological control in crop fields? We also consider the parasitoid community, through the aphid parasitism rate in monitored crop fields, in order to explore other effects of floral food supply.

Methods

Study area

The study took place in Brittany, a region of western France, in the Ille-et-Vilaine Department (Fig. 1). The study area is dominated by mixed dairy farming and is part of the Long Term Ecological Research (LTER) site "Zone Atelier Armorique" integrated in the Long-term Biodiversity, Ecosystem and Awareness Research Network (Alter-net). The area comprises a gradient of agricultural land-use intensity. The southern part is characterized by a dense hedgerow network and a large percentage of areas covered by grasslands and fodder crops. Farming systems are mainly oriented toward dairy production. The northern part of the study area is a more open landscape resulting from land re-allotment with agriculture mainly oriented toward mixed dairy-cattle and crop production and approximately 1/3 of the area covered by grasslands and fodder crops. As a result, there is a pronounced gradient from South to North with a decrease in the surface covered by grasslands and woody habitats and an increase in the surfaces devoted to annual crops associated with an increase in mean field size.

Dependent variables: monitoring of aphid, hoverfly and mummy abundance in focal cereal crop fields

In 2011, the respective abundance of aphids, aphid mummies and hoverflies (eggs, larvae and pupae) was recorded for 15 winter cereal fields in the "Zone Atelier Armorique" (Fig. 1). These fields were selected along a gradient of landscape complexity (Appendix 1 of supplemetary material). From the second week in April to the first week in July, the number of aphids, hoverflies and mummies were counted every 15 days on 50 wheat stalks randomly chosen in three 1 m^2 plots located at more than 20 m from the edge of the field. For each field, we calculated the total abundance of aphids, the total abundance of hoverflies (sum of all the eggs, larvae and pupae of hoverflies counted in the three samples over all dates of sampling) and the aphid parasitism rate (sum of all the mummies counted in the three samples over all dates of sampling/all live aphids and aphid mummies).

Land use maps of the "Zone Atelier Armorique" were drawn, based on direct field observations using ArcMap software, ArcGis for Desktop 10, version ArcInfo advanced. Land use polygons were digitalized and attributed, based on georeferenced numeric orthophotographs BDOrtho© (IGN, 2010). Landscape descriptors were calculated in five circular buffers of different sizes (with respective radii of 100, 250, 500, 750 and 1000 m) centered on the centroid of each monitored field using ArcToolBox scripts. The proportion of area covered by the six main non-crop and crop
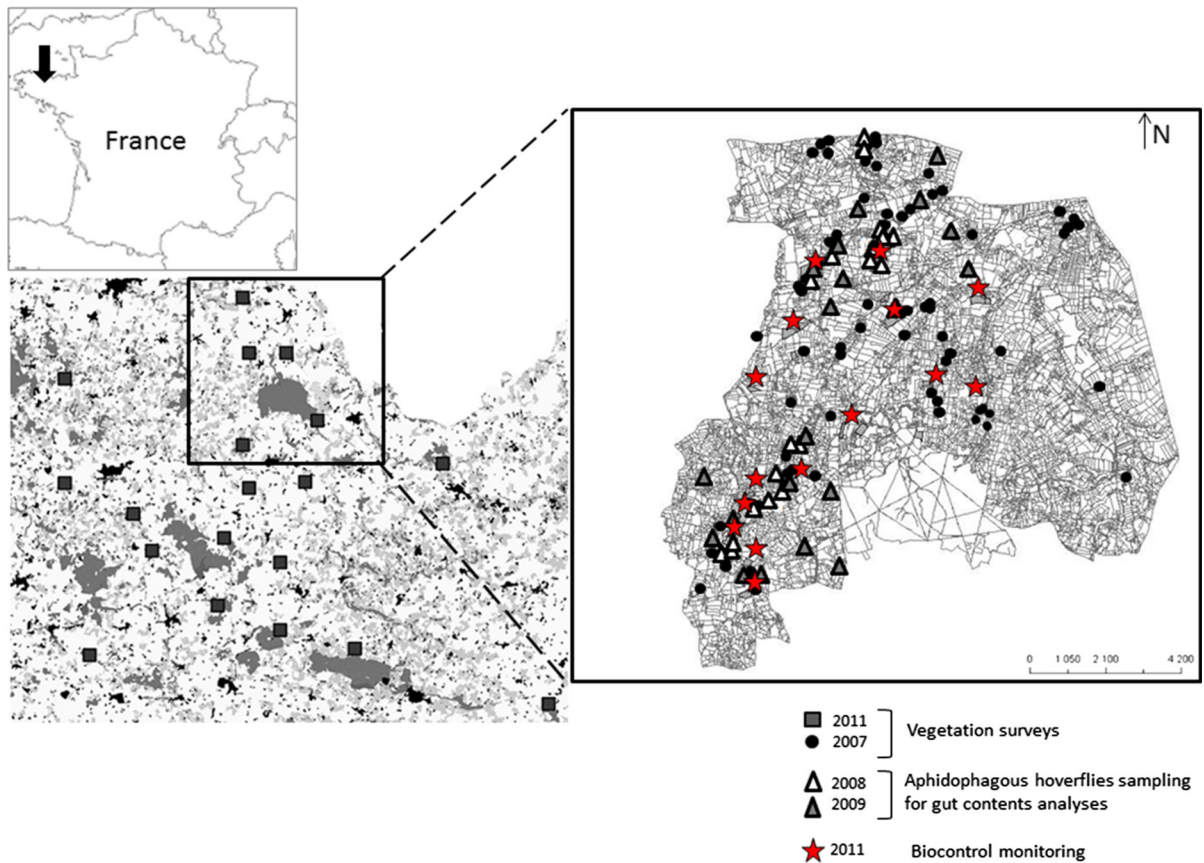
Fig. 1 Map of the study area localizing (1) vegetation surveys, (2) aphidophagous hoverfly sampling for gut content analyses, (3) crop fields monitored for aphid biological control.

Vegetation surveys were conducted in 2007 (Ernoult et al. 2013) and 2011 (Duflot et al. 2015) in a total of five habitats representing the main habitats of the area

habitats (woodlands, meadows, grassy strips, hedgerows, winter cereal crops and other crops), and Shannon's diversity index were calculated for the five buffer sizes. The percentage of non-crop habitats around the monitored fields varied from 2% at the buffer size of 100 m for the lowest value to 74% at the buffer size of 250 m for the highest value (Appendix 1 of supplemetary material).

Reference data

Adult aphidophagous hoverflies (Dipterous, Syrphidae) were caught in cereal fields (winter cereal and maize) using yellow water traps. Three trap bowls (40 × 30 cm) were placed 20 m apart from each other in 19 winter cereal fields (at 50 m from the edge) for 12 weeks from April to July 2008 (Fig. 1). This period corresponds to the peak of flowering. From April to

July 2009, 11 winter cereal fields and 11 maize fields were monitored, following the same procedure. The traps were filled with water to which drops of liquid detergent were added and were emptied weekly. Adult hoverflies were identified to species level, when possible, according to van Veen (2004). They were stored individually in Eppendorf tubes at −20 °C, until their dissection. The guts were removed and opened on a slide to expose the pollen. After extraction of lipids using diethyl ether, the diverticulum was placed on a slide with glycerin jelly containing basic fuchsin to stain the pollen (Hyde and Adams 1958). Pollen was examined under an optic microscope at 400× magnification and determined to family or species level by comparison with the INRA—Le Magneraud's pollen collection (Aupinel et al. 2001).

The number of sampled adult hoverflies was low, ranging from 1 to 10 individuals (often 2 or 3) per

field, with only 1–2 pollen species in the individual guts. Consequently, the samples were merged in one group for a further analysis (see Jacobs index (D) calculation description). The group comprised all the hoverflies caught across the "Zone Atelier Armorique" (Fig. 1), distributed over an area covering 57 km^2 according to Al Hassan et al. (2013). In this area, large-scale landscape descriptors were calculated using ArcToolBox scripts for the proportions of the area covered by the main non-crop and crop habitats (woodlands, grasslands, grassy strips, hedgerows, winter cereal crops and other crops).

Previous studies have been conducted on vegetation in the studied area (for more details see Ernoult et al. 2013; Duflot et al. 2015). We used their data corresponding to surveys in five habitat types, representing the main habitats of the area: conventionally managed winter cereal crops (N = 40), hedgerows (N = 40), woodlands (N = 40), grasslands (N = 80) and grassy strips (N = 54, Fig. 1). We used the presence/absence data for each plant species (a total of 278 species) in the sample replicates to estimate its relative pollen availability for hoverflies in each of the five habitats. For example, a plant found in 10 hedgerows among the 40 surveyed hedgerows obtained a pollen availability index equal to 0.25 for this habitat. The presence/absence data were chosen as the pollen-vegetation relationship is non-linear because of the high variability in pollen productivity between species (Broström et al. 2008); this depends on many factors such as the number of flowers per inflorescence, pollen produced per flowers, but also climatic conditions etc. (e.g. Wroblewska and Stawiarz 2012). Hereafter, only the plant species effectively supplying pollen to aphidophagous hoverflies, i.e., found in the gut content analyses, were considered in the subsequent analyses.

Indices calculation

Gut content analyses provided the list of pollens consumed by aphidophagous hoverflies and an estimate of their consumption rate (CR). From the vegetation surveys in the main crop and non-crop habitats, we obtained an estimate of the availability of each pollen plant source in each habitat (PA). Finally, from the landscape habitat composition analyses, we calculated the proportion covered by each main crop and non-crop habitat (HP) (1) in the reference area of hoverfly sampling for gut content analyses at hand (2)

for each buffer size around the 15 cereal fields monitored for biological control.

All data were obtained between 2007 and 2011 in the same area. Yearly climatic conditions were equivalent during this period. As there were no major changes in agricultural practices during this period, flora diversity sampled in 2007 and 2011 in a large set of conventional crop fields and non-crop habitats appeared to be a relevant reference for hoverfly gut contents sampled in 2008.

Selectivity occurs when a feeder consumes available and co-occurring edible resources at different rates (Jacobs 1974). Jacobs's selection index allows comparing for a particular species its consumption frequency to its availability in the landscape. A positive Jacobs's selection index value indicates a preference (here called "over-selected" species) while a negative value indicates a lower consumption than expected from the resource abundance (here called "under-selected" species). We applied Jacobs's selection index D to the hoverfly selection preferences for pollen species i (Table 1), using:

$$D_i = CR_i - \sum_j \left(PA_{ij} \times HP_j\right) /$$
$$\left[CR_i + \sum_j \left(PA_{ij} \times HP_j\right) - 2CR_i \sum_j \left(PA_{ij} \times HP_j\right)\right],$$

where CR_i is the consumption rate for pollen of the species i (i = 1–40), PA_{ij} is the availability of pollen species i in habitat j (j = 1–5) and HP_j is the proportion of the referenced area covered by habitat j.

We explored the similarity between the set of plant species for which the pollen was consumed by the hoverflies and the set of plant species found in each habitat j by the Sørensen index (Sørensen 1948), calculated as:

$$S_j = 2A_j / \left(B_j + C_j\right),$$

where A_j is the number of species common to the two sets, B_j is the total number of species in the set of plant species for which the pollen is consumed by the hoverflies, and C_j is the total number of species found in the habitat j.

We calculated the value of each habitat j for the provision of pollen resources to hoverflies (H_j) by:

$$H_j = \sum_i (CR_i \times PA_{ij}),$$

Table 1 Definitions of parameters and indices used in the study

Type	Name	Definition	Data sources
Parameter	CR	Consumption rate for pollen of a plant species by adult hoverflies	Consumed pollen species (N = 40) in the hoverfly gut contents (N = 84)
Parameter	PA	Pollen availability in each habitat	Plant surveys (278 species in 254 habitats belonging to 5 categories)
Parameter	HP	Proportion of the referenced area covered by a habitat	GIS database (area of 57 km^2)
Parameter	HB	Proportion of the buffer size covered by a habitat around a monitored crop field	GIS database (radius from 100 m to 1000 m)
Index	D	Jacobs' selection index: hoverfly selection preferences for pollen species	
Index	S	Sørensen index: similarity between the set of plant species for which the pollen was consumed by the hoverflies and the set of plant species found in a habitat	
Index	H	Value of a habitat in the provision of pollen resources to hoverflies	
	HAII	Index considering all consumed plant species by adult hoverflies	
	H(+)	Index considering only over-selected plant species by adult hoverflies	According to D
	H(−)	Index considering only under-selected plant species by adult hoverflies	According to D
Index	LP	Index of landscape potential in pollen provisioning for aphidophagous hoverflies	
	LP All	Index considering all consumed plant species by adult hoverflies	
	LP(+)	Index considering only over-selected plant species by adult hoverflies	According to D
	LP(−)	Index considering only under-selected plant species by adult hoverflies	According to D

Data sources for calculating the parameters are specified. Indices are calculated based on parameters and according to formulas developed in the "Methods" section

where CR_i is the consumption rate for pollen of the species i (i = 1–40) and PA_{ij} is the availability of pollen species i in habitat j (j = 1–5).

Three different H_j indices were calculated for each habitat j, by considering alternatively (1) all plant species identified in the gut content analyses (H_{jAll}); (2) only the "over-selected" plant species ($H_{j+} = \sum i(PA_{ij} \times CR_i | D_i > 0)$), i.e. species exhibiting a positive Jacobs index (D_i); and (3) only the "under-selected" plant species ($H_{j-} = \sum i(PA_{ij} \times CR_i | D_i < 0)$), i.e. species exhibiting a negative Jacobs index.

We developed an index of landscape potential for pollen provisioning for aphidophagous hoverflies (LP index) taking into account landscape composition, by averaging habitat values as H_j, weighted according to their proportion in the landscape buffer:

$$LP\,index = \sum_j H_j \times HB_j,$$

where H_j is the value of habitat j in pollen provisioning for hoverflies and HB_j is the proportion of the area considered, covered by habitat j. HB_j values were calculated for the five buffer sizes with circular buffers centred on the centroids of each cereal field monitored for biological control.

We once again calculated three LP indices considering alternatively (1) all plant species identified in the gut content analyses (LP_{All}); (2) only the "over-selected" plant species (LP_+) and (3) only the "under-selected" plant species (LP_-), which is mainly related to the presence of weeds in the crops (cf. Results part). We also calculated the global contribution of each crop habitat j to the value of the LP index by means of the equation, LP index$_{/j}$ = $H_j \times HB_j$/LP index.

Statistical analyses

A log-transformation of the abundance data and an arcsine square root transformation of the parasitism

rate and hoverfly/aphid ratio were applied to normalize them.

First, predator–prey dynamics could imply that an initial increase of hoverflies may result in a later decrease due to lower aphid abundances. Consequently, few female hoverflies may lay their eggs when there are not many aphids. To deal with this time factor, we analysed (1) how later abundance of aphids was related to initial abundance of hoverflies and (2) how initial abundance of hoverflies was related to initial abundance of aphids. The first three sessions of insect sampling and the last three sessions were pooled to respectively form the initial and the later abundances. The relationship between parasitism rate and larval hoverfly abundance was analysed for the whole season to explore the possibility of a competitive relationship.

We performed random resampling by bootstrap method in the data of pollen consumption rate, using 1000 bootstrap samples to calculate the confidence intervals (2.5 and 97.5%) of D for each plant species. We then calculated H_+ for each habitat, including (1) all unconfident under-selected and over-selected species and the confident over-selected species (max), and (2) only the confident over-selected species (min, Fig. 3). The minimum and maximum H_- values were also calculated.

We performed standard Multiple Linear Models (LM) for each buffer size to investigate the effects of LP indices (LP_{All}, LP_+ and LP_-) on (1) larval hoverfly abundance (2) aphid abundance, (3) hoverfly/aphid ratio, and (4) aphid parasitism rate in the 15 cereal fields monitored. We compared this approach with the one based on landscape composition, using the proportional area covered by each of the six habitats (woodlands, meadows, grassy strips, hedgerows, winter cereal crops and other crops) for each buffer size as factors in the LM. Landscape variables were centred on their mean and scaled according to their standard deviation for each buffer size. In each model focusing on one buffer size, the insect abundances, their ratio or the parasitism rate were related to the LP index or the set of habitat proportions in simple or additive models respectively. The set of best-fitting models was selected based on Akaike's information criterion, corrected for small sample sizes (AICc, Burnham and Anderson 2002), and using the limit of two AICc units of the model with the lowest AICc. Estimates of model parameters are reported for these models. To complement these analyses, correlations between the three LP indices and the Shannon diversity index of landscape for each buffer size were calculated.

Statistical analyses were carried out using R 3.1.3 (R Development Core Team 2015) with the lme4, lmerTest, pgirmess and MuMIn libraries and the dredge function (Version 1.5.9).

Results

We caught 112 adult hoverflies using yellow water traps in crops belonging to 13 taxa. Most of them were successfully identified at species level. The entire sample comprised 31 individuals of *Eupeodes corollae*, 29 of *Melanostoma mellinum*, 21 of *Episyrphus balteatus*, 11 of *Spaerophoria scripta*, 6 of *Syrphus ribesii*, 4 of *Melanostoma* sp., 3 of *Platycherus* sp., 2 of *Syrphus* sp., 1 of *Eupeodes latifasciatus*, 1 of *Scaeva pyrastri*, 1 of *Pipezella* sp., 1 of *Platycheirus albimanus*, and 1 of *Platycherus granditarsus*. Twenty-five per cent of the insects had an empty gut. A maximum of 2 pollen types were found per individual, belonging to one of a total of 40 plant species (see list in Fig. 2). Pollen consumption rates varied from 0.01 to 0.16 (mean = 0.03, s.e. = 0.03). Pollens of six plant species were found only once in the gut of insects and belonged to plants that had not been recorded in the vegetation survey (*Aegopodium podagria*, *Bryonia dioica*, *Hemerocallis* sp., *Syringa* sp., *Trifolium campestre* and *Valeriana* sp.).

In monitored cereal crop fields, we counted 143–6866 aphids, 3–37 hoverflies at pre-imaginal stages and 10–157 mummies during the season, giving a mean count of 1695 aphids, 14 hoverflies and 64 mummies per field.

A particular high consumption rate (CR) by aphidophagous hoverflies was found for two pollen species (0.13 and 0.14 of the records respectively for both *Achillea millefolium* and *Lotus corniculatus*). These two plant species were not abundant in any habitat and were found mainly in grassy strips, but also in grasslands and winter cereal crops (Fig. 2). Both species had a positive Jacobs index (D) close to 1 (Fig. 3). In contrast, the most frequent plant species in habitats, *Rubus* sp., had a negative Jacobs index. Most of the plant species whose pollen was often consumed (ca. 6% of the records) or occasionally consumed (ca. 3% of the records) by hoverflies were present in all habitats. However, some of these species were found
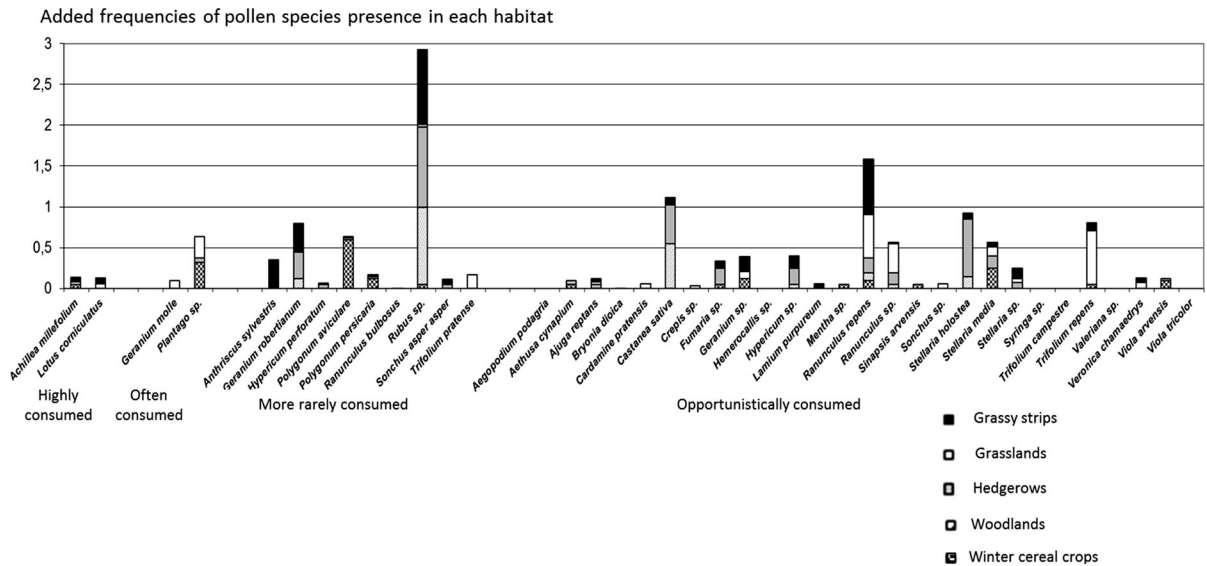
Added frequencies of pollen species presence in each habitat

Fig. 2 Availability of pollen species in each habitat, based on their presence rate found in the vegetation survey (PA). Pollen species are classified according to their consumption rate (CR) by aphidophagous hoverfly, into one of four categories: 'Highly consumed' when consumption rates are >10% of meals, 'Often consumed' when consumption rates are between 5 and 10% of meals, 'More rarely consumed' when consumption rates are between 2.5 and 5% of meals, and 'Opportunistically consumed' when pollen species were found only once in the set of meals

in only one habitat, such as *Anthriscus sylvestris* in grassy strips or *Geranium molle* and *Trifolium pratense* in grasslands (Fig. 2).

The Jacobs index (D) presented confident results for five over-selected pollen species and 8 under-selected pollen species (Fig. 3). The relative value of each habitat in pollen resources provision to hoverflies (H) appeared to differ from its expected value, based on the similarity between the set of plant species consumed by hoverflies and the set of plant species found in each habitat (Sorensen index S, Table 2). Grassy strips had the highest $H_{j\ All}$, followed by grasslands, hedgerows and crop fields. Woodlands had the lowest H_{jAll} (= 1.14). When considering only plant species having a positive Jacobs index, grassy strips still had the highest H_{j+} followed by hedgerows, grasslands, crop fields and woodlands. When considering only plant resources having a negative Jacobs index, crop fields had the highest H_{j-}, followed by grassland, grassy strips, hedgerows and woodlands.

The range of values of the three LP indices (*All*, (+) and (−), =landscape potential to offer pollen resources for aphidophagous hoverflies) according to buffer size is summarized in Appendix 2 of supplemetary material. The mean contribution of crop habitat to the value of the LP index was high, ranging for example for the LP_ from

56% (±13) for the buffer size of 1000 m to 86% (±11) for the buffer size of 100 m. No significant correlation was observed between any LP index value and the contribution of any habitat to this LP index value.

Correlations between all indices for the same buffer size are shown in Appendix 3 of supplemetary material. LP_ at 500 m was significantly correlated with LP_{All} at 500 m (r = 0.95, $P < 0.001$).

Correlations between the three LP indices and the Shannon diversity index were very variable and negative. The LP_ shared from 21% (at the buffer size of 100 m) to 62% (at the buffer size of 1000 m) common information with the Shannon diversity index (Appendix 4 of supplemetary material).

When considering the time factor and predator–prey dynamics, a non-significant relationship was recorded between late aphid abundance and early larval hoverfly abundance in cereal fields (t = −0.37, $P = 0.72$, $R^2 = 0.01$). No relationship was recorded between initial larval hoverfly abundance and initial aphid abundance (t = −1.77, $P = 0.10$, $R^2 = 0.13$). No relationship was recorded between larval hoverfly abundance and aphid parasitism rate in cereal fields for the whole season (t = −1.40, $P = 0.19$, $R^2 = 0.06$).

A model comparison based on AICc identified the LP_ (for a buffer size of 500 m) as the variable

Fig. 3 Selectivity of pollen sources by aphidophagous hoverflies (Jacobs index D). An index value >1 indicates a higher relative abundance of the pollen species in hoverfly gut compared to the vegetation survey (consumption preference), whereas a value <1 indicates a negative selection for the pollen species. Species with * present a confident positive or negative D, following the calculation of the confidence intervals (2.5 and 97.5%) with bootstrap resampling in pollen species data
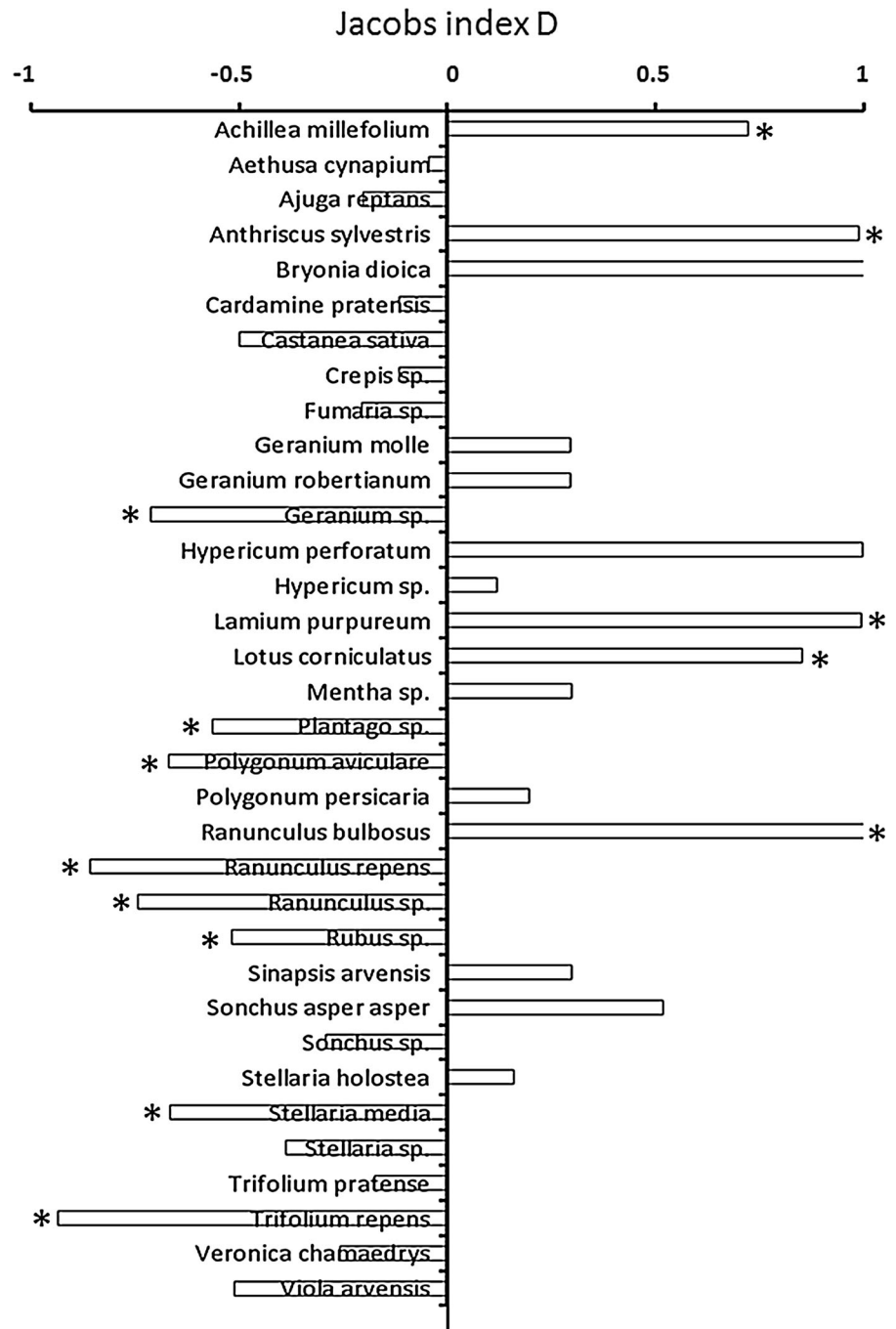
best fitting larval hoverfly and aphid abundances and aphid parasitism rate in cereal crop fields, with the lowest AICc and the highest adjusted R^2 (Table 3). Both aphid and larval hoverfly abundances were significantly lower with higher LP_ (t = −3.18, R^2 = 0.44, P = 0.01 and t = −3.21, r^2 = 0.45, P = 0.01 respectively, Fig. 4), while the aphid parasitism rate was significantly enhanced with the LP_ (t = 2.42, R^2 = 0.26, P = 0.03). A positive effect of LP$_{All}$ was recorded for the aphid parasitism rate at buffer sizes of 500 m, but with a marginal trend toward significance. No effect of any LP index was recorded on the hoverfly/aphid ratio in cereal fields.

Table 2 Relative importance of each habitat in offering pollen resources to aphidophagous hoverflies

Habitat j	Number of plant species in habitat j	Number of common species with consumed pollen species set	s_j	H_{jAll}	H_{j+} (min; max)	H_{j-} (min; max)
Grassy strips	118	14	0.18	4.63	3.25 (2.55; 4.10)	1.39 (0.53; 2.08)
Grasslands	125	18	0.22	3.24	1.31 (0.81; 2.14)	1.93 (1.10; 2.43)
Hedgerows	162	18	0.18	3.14	2.13 (1.38; 2.44)	1.01 (0.70; 1.76)
Crop fields	93	13	0.20	3.10	0.95 (0.52; 1.53)	2.14 (1.57; 2.58)
Woodlands	102	5	0.07	1.14	0.46 (0.00; 0.65)	0.68 (0.49; 1.14)

S_j is the Sorensen index of similarity between the two sets of plants (consumed by hoverflies and found in the habitat); H_j is the relative importance of each habitat to offer pollen resources to hoverflies, which combines the pollen consumption frequency by hoverflies with the species frequency in each habitat. *All*: for all the pollen source species; (+): for only pollen species with a positive Jacobs index (D); (−): for only pollen species with a negative Jacobs index; (min, max): minimum and maximum values of H_+ and H_- for each habitat, including respectively (1) only the confident over-selected pollen species, and (2) all unconfident under-selected and over-selected pollen species and the confident over-selected (for H_+) or under-selected (for H_-) pollen species (see Fig. 3)

Table 3 Results of model selection for the analyses of aphid biological control in cereal crop fields according to landscape potential for offering pollen resources for aphidophagous hoverflies (LP index)

Dependant variable	Model							
	Landscape descriptors (buffer)	Estimates	t value	P	AICc	Δi	Adjusted R²	P
Hoverfly abundance	LP. index (500 m)	−1.22	−3.18	0.007**	2.08	0.00	0.44	0.007**
	LP. index (250 m)	−1.34	−2.95	0.01*	3.05	0.97	0.34	0.01*
Aphid abundance	LP. index (500 m)	−1.96	−3.21	0.005**	16.12	0.00	0.45	0.006**
	LP. index (750 m)	−1.93	−2.94	0.01*	17.21	1.09	0.35	0.01*
Hoverfly/aphid ratio	Model null				−47.6	0.00		
	LP. index (750 m)	0.02	1.31	0.22 NS	−46.3	1.34	0.05	0.22 NS
	LP. index (1000 m)	0.02	1.28	0.22 NS	−46.2	1.40	0.04	0.22 NS
	LP_{All} index (750 m)	0.01	1.18	0.26 NS	−45.9	1.70	0.03	0.26 NS
	LP. index (500 m)	0.01	1.14	0.28 NS	−45.8	1.76	0.02	0.28 NS
Aphid parasitism rate	LP. index (500 m)	0.25	2.42	0.03*	−34.7	0.00	0.26	0.03*
	LP_{All} index (500 m)	0.19	2.18	0.05*	−33.8	0.9	0.21	0.05*
	LP. index (750 m)	0.23	2.07	0.06 NS	−33.4	1.31	0.19	0.06 NS

Biological control was explored using aphid abundance, larval hoverfly abundance, hoverfly/aphid ratio and aphid parasitism rate in 15 fields. Explanatory variables are four landscape descriptors: three LP indices (LP_{All}, LP_+ and LP_-) for five buffers with radii ranging from 100 to 1000 m. Only the univariate and multivariate models within two AICc units (Δi) of the model with the lowest AICc are shown, including their estimates with the related t value and its level of significance

NS not significant

* $P < 0.05$; ** $P < 0.01$

Using habitat proportions as landscape descriptors, a model comparison systematically identified the % of grassy strip in the landscape as a significantly positive or negative variable fitting the insect abundances, the hoverflies/aphids ratio or the parasitism rate in cereal crop fields (Table 4). A significant effect of the % of winter cereal crop was also recorded on larval hoverfly abundance for a buffer size of 500 m (t = −4.64, $P = 0.0006$), while significant effects of the % of grassland and woodland were observed on the aphid abundance for a buffer size of 500 m (t = 4.15, $P = 0.002$ and t = 3.77, $P = 0.03$ respectively). A
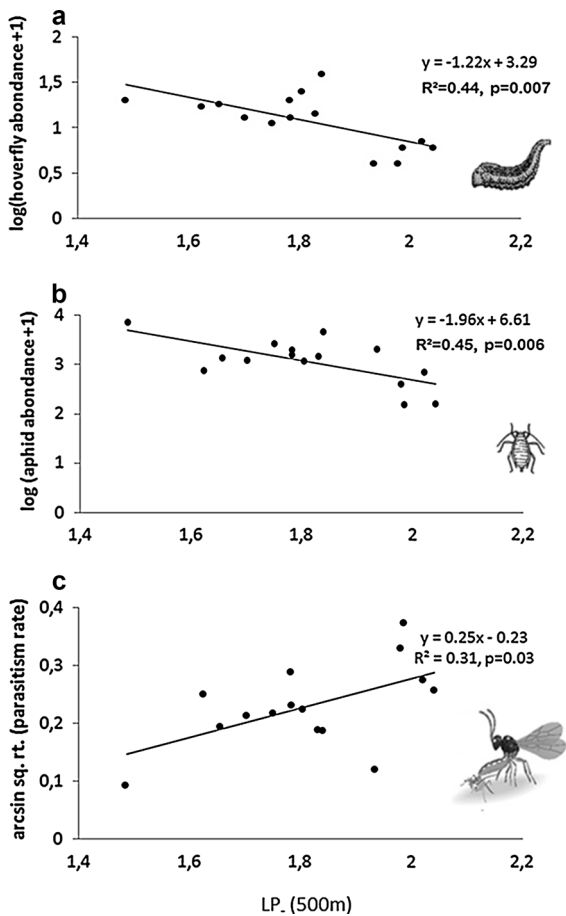
Fig. 4 Regression between aphidophagous hoverfly abundance (**a**), aphid abundance, (**b**) or aphid parasitism rate, (**c**) in crop fields and the LP index (i.e. landscape potential for offering pollen resources for aphidophagous hoverflies) for buffer size of 500 m around the crop fields. The LP index considered takes into account pollen species with a negative Jacobs index (D). Coefficient of determination (R^2) of the linear regressions and its level of significance are presented

significant effect of the % of woodland was recorded on parasitism rate for a buffer size of 1000 m (t = −3.52, $P = 0.004$). The adjusted R^2 of the models were high, from 0.43 ($P = 0.005$) for the model explaining the aphid parasitism rate to 0.79 ($P = 0.0001$) for the one explaining aphid abundance.

Discussion

By combining data on pollen found in the gut of aphidophagous hoverflies, with the availability of the corresponding plants in different habitat types and

then by correlating indices of suitability of different habitats in landscapes with natural enemies and prey abundances, we explored the value of different landscapes for biological control of cereal aphids. As our approach is novel, some limits have to be discussed. First, the relative pollen availability for hoverflies was estimated based on the presence-absence of plant species in habitats. Estimating pollen productivity remains a great scientific challenge, notably in archeological palynology, because of the non-linear relationship between pollen and vegetation abundances, which is related to the high variability in pollen productivity between plant species (Broström et al. 2008). Then, presence-absence data appears at present to enable the least-biased estimates of the relative pollen availability in habitat. The developing data bases of the life-history traits of plants, such as the LEDA-Traitbase concerning the Northwest European flora (Kleyer et al. 2008) or the TRY Database (Kattge et al. 2011), offer promising perspectives for precisely estimating pollen productivity when this trait is available. Second, we have based the floral preferences of hoverflies on consumed pollen, but nectar may also be an important floral resource for selecting flowers as clearly demonstrated recently by Van Rijn and Wäckers (2016). The two sets of plant species used do not match, but it is interesting to note that the most consumed two pollen species in our study, *Achillea millefolium* and *Lotus corniculatus*, reveal respectively accessible nectar and non-accessible nectar according to Van Rijn and Wäckers (2016). The combination of plant species presenting a high rate of pollen consumption by beneficial insects and easily accessible nectar offers promising perspectives for preserving or introducing a plant community in and around crop fields favouring these insects.

Our original approach enables significant insight into the mechanisms underlying previously well-studied relationships between landscape composition, habitat quality and indicators of pest control (e.g. Parry et al. 2015; Schellhorn et al. 2015). Non-cultivated habitats clearly play unequal roles in floral food supply to hoverflies, despite hosting the same common plant species. Grassy strips appeared to provide the highest quantity of pollen resources to hoverflies. This habitat hosted both over-selected plant species and under-selected plant species. We also showed that crop fields significantly provided pollen resources consumed by adult hoverflies. In contrast,

Table 4 Results of model selection for the analyses of aphid biological control in cereal crop fields according to landscape composition

Dependant variable	Model							
	Landscape descriptors (buffer)	Estimates	t value	P	AICc	Δi	Adjusted R^2	P
Hoverfly abundance	% grassy strip (500 m)	−0.18	−3.44	0.005**				
	+ % winter cereal crop (500 m)	−0.25	−4.64	0.0006***	0.5	0.00	0.62	0.001**
Aphid abundance	% grassy strip (500 m)	−0.26	−4.52	0.0009***				
	+ % grassland (500 m)	0.24	4.15	0.002**				
	+ % woodland (500 m)	0.21	3.77	0.003**	8.6	0.00	0.79	0.0001***
Hoverfly/aphid ratio	% grassy strip (100 m)	0.03	4.02	0.002**				
	+ % woodland (100 m)	0.01	1.99	0.07 NS	−53.7	0.00	0.51	0.005**
	% grassy strip (100 m)	0.03	3.23	0.007**	−53.3	0.46	0.40	0.007**
	% grassy strip (100 m)	0.03	3.26	0.007**				
	+ % winter cereal crop (100 m)	−0.02	−1.82	0.09 NS	−53.1	0.63	0.49	0.007**
	% grassy strip (250 m)	0.03	2.98	0.01*	−52.2	0.50	0.36	0.01*
Aphid parasitism rate	% grassy strip (250 m)	6.08	3.42	0.005**	−38.7	0.00	0.43	0.005**
	% woodland (1000 m)	−0.05	−3.52	0.004**				
	+ % grassland (1000 m)	−0.03	−2.07	0.06 NS	−37.1	1.60	0.47	0.009**

Biological control was explored using aphid abundance, larval hoverfly abundance, hoverfly/aphid ratio and aphid parasitism rate in 15 fields. Explanatory variables are the proportion of area covered by six habitats (woodlands, meadows, grassy strips, hedgerows, winter cereal crops and other crops) for each buffer size ranging from 100 to 1000 m. Landscape variables were centred on their mean and scaled according to their standard deviation for each buffer size. Only multivariate models within 2 AICc units (Δi) of the model with the lowest AICc are shown, including their estimates with the related t value and its level of significance

NS not significant

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

woodlands made the lowest contribution to pollen provisioning. However their role as overwintering habitats for adult hoverflies could nevertheless mean that they are important landscape elements for maintaining biological control (Arrignon et al. 2007).

To evaluate landscape functionality in providing floral resources to hoverflies, we calculated an original index taking into account the landscape composition (the LP index) by combining hoverfly's pollen preferences, the plant frequency in each habitat and the proportion of each habitat in the landscape. A comparison of the LP index with the classical Shannon diversity index attested its originality as a landscape descriptor. Their negative relationship may be due to the important contribution of crop fields in floral food supply. Indeed, a high crop proportion in landscape is generally associated with a low Shannon diversity index (e.g. Fahrig et al. 2011). The LP index brings new insights on the results of analyses using habitat proportions, which mix the different ecological roles

that these habitats may play in pest biological control, such as resource supply, overwintering sites, reproduction sites, refuges or corridors for a set of natural enemies (Bianchi et al. 2006). Even if many natural enemies could be important in suppressing aphids, by considering the landscape through the prism of floral food supply for one taxonomic group (the aphidophagous Syrphidae), we obtained significant results that explicitly link aphid control with the level of the floral resources used by hoverflies and that are available in and around the crop field. The results obtained with these two approaches are strongly concordant and complement one another; they highlight the important role of floral resource supply for natural enemies and its consequences on biological control. They notably point out the role of grassy strips in floral provision for natural enemies.

The landscape potential for pollen provisioning based on over-selected plant species (LP_+) was not correlated to aphid and hoverfly abundance in fields.

These plants are more abundant in non-crop habitats and may attract hoverflies away from a field (Landis et al. 2000). In contrast, the LP_ index, whose value is influenced by the presence of weed plants in crop fields, was significantly and negatively correlated to aphid abundances in fields, with the highest correlation for a buffer size of 500 m. However, an unexpected negative correlation was observed between this LP index and the abundance of predatory hoverfly at larval stages, while the aphid parasitism rate was positively correlated with this LP index. First, results on aphid and hoverfly abundance could in part be due to fewer hoverfly eggs being laid where there are fewer aphids present, but no relationship has been found between initial aphid and hoverfly abundances. Even if the ratio of hoverflies to aphids is positively related to the LP_ index, suggesting that there are more hoverflies among aphid colonies, the results were not significant. Second, another question to be considered is how much the LP index is specific to hoverflies. A comparison with the list of pollen consumed by another group of natural enemies of pests in the same pseudo-climatic region, *Chrysoperla* species (Neuroptera: Chrysopidae, Villenave-Chasset et al. 2006), showed that only two species were shared. But aphid parasitoids, which also consume floral resources, appeared to benefit from the same floral resources as hoverflies in the landscape. These floral resources concerned only the under-selected plant species, i.e., mainly weeds in crop fields. Our results are strongly consistent with those of Tylianakis et al. (2004) who demonstrated that floral resources significantly increase the aphid parasitism rate in cereal fields when these floral resources are very close (< 14 m). Moreover, as pest aphid parasitoids are highly specialised to crop habitat (Derocles et al. 2014), and according to the resource concentration hypothesis (Root 1973), they may be favoured by a high proportion of crop field area in the landscape in which both aphid and floral resources are abundant. The presence of mummies among aphid colonies limits hoverfly egg-laying (Almohamad et al. 2008). Consequently, even if hoverflies are more abundant in the landscape owing to the pollen resources offered by the different habitats, competition with parasitoids limits them in the crop fields.

Altogether, the present results suggest that crop fields form habitats that have been largely underestimated in their capacity to sustain pest control services, as recently hypothesised by Tscharntke et al. (2016). Our study illustrates how crop fields, even when conventionally managed as in our case, could play a prominent ecological role in agricultural landscapes, being more than just sink habitats of beneficial populations from surrounding non-crop habitats. Practically, our results call for combining (1) the management of grassy strips through the choice of species composition at initial sowing or the tuning of the mowing dates in order to enhance strips' function of providing floral resources to hoverflies, and (2) the development of weed-control practices balancing in an optimal way the negative effect of weeds caused by competition with crops and their positive effects as beneficial insect supports. The original LP index proposed in this study may contribute to the design and assessment of such agricultural management strategies at a landscape scale in order to significantly improve biological control for a sustainable crop production.

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