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Flower strips, crop management and landscape composition effects on two aphid species and their natural enemies in faba bean

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Abstract

Wildflower strips and biodiversity-friendly management are promoted as ways of enhancing biodiversity and natural pest control in agroecosystems. Their efficacy for providing resources and shelters for natural enemies has been well studied, but little is known about how wildflower strip efficacy is mediated by local field management and landscape composition. In this study, we explored the effects of floral resources in perennial flower strips on faba bean aphids and their antagonists in contrasting cropping systems and landscapes. We surveyed 13 faba bean crops in northern France in 2019, and 19 in 2020. We sampled aphids (*Aphis fabae* and *Acyrtosiphon pisum*) and their antagonists (Syrphidae, Coccinellidae and mummy-forming parasitoids) on three dates during the spring, by visual observation. We assessed the floral resources provided by wildflower strips and spontaneous field margins and collected data on field management practices and land use in the surrounding landscape. We found that the percentage of flowering species in field edges providing accessible nectar to natural enemies had a positive effect on the abundance of Syrphidae and aphid mummies on faba bean plants. The positive effect of nectar resources on Syrphidae and aphid mummies decreased with increases in the proportion of semi-natural habitats in the landscape, but no interaction was observed with local management techniques. The growth rate of *Aphis fabae* and *Acyrtosiphon pisum* populations were unaffected by their antagonists. The growth rate of *A. fabae* populations was driven principally by local management practices (i.e. insecticide spraying and tillage). Conversely, the growth rate of *A. pisum* populations was driven principally by landscape composition (i.e. the proportion of semi-natural habitats and leguminous plants) and was negatively related to insecticide use. Nevertheless, insecticide spraying did not prevent increases in the growth rates of both aphid species, highlighting the need for alternative methods for controlling aphid populations.

Keywords: *Aphis fabae*, *Acyrtosiphon pisum*, conservation biological control, Coccinellidae, Syrphidae, nectar resources

1. INTRODUCTION

Chemical control to keep pest populations below damage thresholds in agriculture has its limitations. On the one hand, increasing numbers of pest species are becoming resistant to insecticides (e.g. *Myzus persicae*; Bass et al., 2014), and on the other hand, many molecules cause (i) direct deleterious effects (mortality and sublethal effects) on natural enemies (predators and parasitoids), favouring subsequent pest outbreaks (Cloyd, 2012; Desneux et al., 2007), and (ii) indirect deleterious effects on trophic networks and higher trophic levels feeding on pests, such as birds, by reducing trophic resources, and through the accumulation of pesticide residues (Benton et al., 2002; Chaiyarat et al., 2014; Hallmann et al., 2014). There is growing evidence to suggest that semi-natural habitats, by considering their proportion and heterogeneous spatial arrangement in agricultural landscapes, can enhance pest control (Chaplin-Kramer et al., 2011; Martin et al., 2019; Rusch et al., 2016), although they may also favour the colonisation of fields by pests, such as aphids in winter wheat (Alignier et al., 2014).

Conservation biological control (CBC) aims to improve pest regulation through the conservation of natural enemies in agroecosystems (Gontijo, 2019). CBC involves habitat manipulation and agricultural practices designed to favour the development and survival of natural enemies (Landis, 2017; Landis et al., 2000). Conflicting results have emerged from different studies on the response of natural enemies to landscape variables and the effect of natural enemies on pests. Further studies are required to determine how landscape effects can be modulated by local farm management (Karp et al., 2018). Cropping practices and field edge management are also important levers that can be used in the framework of agroecological crop protection (Deguine et al., 2017). In this context, one alternative to chemical control is enhancing the regulation of crop pests by their natural enemies through conservation biological control.

Wildflower strips are a promising way to enhance biological control by providing nectar and pollen resources or shelters to a wide range of predators and parasitoids (Bianchi et al., 2006; Holland et al., 2008; Pollier et al., 2019; Tschumi et al., 2016a, 2015). For instance, Hatt et al. (2017) reported the presence of significantly fewer aphids in wheat plots between wildflower strips than in control wheat plots. This result may reflect the larger amounts of adult hoverflies found in the presence of wildflower strips, whereas no significant difference in abundance was observed for adult lacewings, ladybirds and parasitoids (Hatt et al., 2017). In a recent meta-analysis, Albrecht et al. (2020) found that flower strips enhanced pest control services in adjacent fields by 16% on average, but with a high degree of variability. This supports the assertion made by Begg et al. that “the greatest limitation to the development of effective CBC lies [...] in its ability to deliver effective, reliable and robust biological control of pests” (Begg et al., 2017). There are several possible reasons for variability in the efficacy of flower strips to enhance pest control services.

First, it is the plant species composition of the flower strip, rather than its simple presence, that determines the level of provision of trophic resources and physical habitats for predators and parasitoids (Balzan, Bocci, and Moonen 2014; van Rijn and Wäckers 2016). Indeed, the effect of flower strips depends on their functional composition and structure, including the amount of available and accessible nectar they provide for predators (van Rijn and Wäckers, 2016). Tschumi et al. (2016) reported that flower strips with compositions targeting particular species to favour biological control could reduce the number of aphids in adjacent potato crops by 75%.

Second, the efficacy of flower strips for CBC interacts with the landscape context, resulting in contrasting results. Wildflower strips have been reported to have a stronger effect on the abundance of

Syrphidae and species richness further away from woodlands or in simplified landscapes (Haenke et al. 2009; Saunders and Luck 2018). By contrast, other studies have found that the addition of flower strips most strongly affects natural enemies within landscapes of intermediate (Grab et al. 2018) or high complexity in terms of the proportion of semi-natural habitat (Woltz, Isaacs, and Landis 2012).

Third, agricultural practices would be expected to modulate the CBC response to flower strips. The interaction between landscape and agricultural practices has been studied (Ricci et al., 2019), but interactions between flower strips and agricultural practices, in terms of their effects on the fauna and CBC, have yet to be investigated (but see Marshall and Moonen, 2002, mostly for plants). Some Coccinellidae and Syrphidae species overwinter in the soil (e.g. *Coccinella septempunctata*, (Hodek et al., 2012); *Episyrphus balteatus*, *Sphaerophoria scripta* (Raymond et al., 2014)) and might therefore be disadvantaged by tillage. For these species, a perennial strip would provide a less disturbed complementary habitat with resources non-substitutable from those in different habitats (Ganser et al., 2019 ; Jeanneret et al., 2021). Moreover, some predators and parasitoids need pollen and nectar resources to extend their longevity and fecundity (He et al., 2021). Weeds can provide alternative food sources that play a role in pest control, for instance for omnivorous carabid beetles that also feed on aphids and slugs (Petit et al., 2011) or could benefit to aphidophagous predators and parasitoids by providing alternative prey, nectar and pollen as a complementary resource (Amaral, 2014; Norris and Kogan, 2000). Nevertheless, such resources may be lacking in cropping systems with high rates of tillage or herbicide application (Marshall et al., 2003). In this context, flower strips may provide supplementary resources (i.e., providing substitutable, additional resources in similar, nearby patches). However, flower strips may also act as an ecological trap, depending on their management, with mowing or ploughing during the summer or winter (Ganser et al., 2019; Timberlake et al., 2021). Insecticide sprayed on the field may also limit the benefits of predator spill over from the flower strips into the field. Thus, compensatory effects, synergies or antagonisms may occur between local resources within the flower strip and field management over the season.

In summary, the many possible interactions between field management, flower strips and landscape context limit our ability to understand and develop efficient conservation biological control strategies.

The aim of our study was to evaluate how perennial wildflower strips, agricultural practices and their interactions with landscape context affect aphid control by predators and parasitoids in faba bean crops. Leguminous crops have several agronomic advantages (e.g. crop diversification, nitrogen input; Kumar and Goh, 2002; Kumar et al., 2018), but are susceptible to pests, including the aphids *Acyrtosiphon pisum* (Harris, 1776) and *Aphis fabae* (Scopoli, 1763). *A. fabae* can reduce the growth of the plant (Nuessly et al., 2004). Its sucking activity can result in yield losses and even the death of the whole plant (Völkl and Stechmann, 1998). *A. pisum* causes similar damage on pea and faba bean, through both direct feeding damage and the transmission of mosaic viruses (Nuessly et al., 2004), such as cucumovirus in snap bean (Nault et al., 2004), broad bean wilt virus (Ferriol et al., 2013) or pea enation mosaic virus (Lee et al., 2021). It can affect all stages of the crop (Stoddard et al., 2010). Cereal aphids have been the focus of many CBC studies (Hatt et al., 2017; Holland et al., 2008; Tschumi et al., 2016b), but few studies have investigated legume crops, in which the effect of natural enemies is generally weaker, perhaps due to a high concentration of nitrogen in tissues leading to a more rapid growth of aphid populations (Diehl et al., 2013).

In this study, we explored the effects of floral resources in perennial flower strips on faba bean aphids and their antagonists in contrasting cropping systems and landscapes. We first hypothesised that the number of aphid antagonists (Coccinellidae, Syrphidae and mummy-inducing parasitoids) would be

affected positively by flower resources and negatively by insecticides and soil tillage in faba bean fields. We also expected to see a negative effect of both aphid antagonists and disturbances (insecticides and tillage) on the growth rate of aphid populations. We hypothesised that wildflower strips would have a stronger effect in less disturbed fields (i.e. those with few insecticide applications or tillage operations). Finally, we expected the effect of flower resources to be weaker in landscapes with a higher proportion of semi-natural habitats than in homogeneous landscapes with few semi-natural habitats, due to a low contrast induced by the introduction of a wildflower strip in an environment already rich in plant resources (Scheper et al., 2015).

2. METHODS

2.1. Study sites

We studied 13 faba bean fields in 2019 and 18 in 2020. All these fields were located in northern France, a region dominated by the cultivation of arable crops (mostly cereals and oilseed rape) in open field landscapes.

We selected faba bean fields to cover a large gradient of resources provided by dicotyledonous species in their immediate surroundings. We chose 22 fields bordered by a spontaneous margin and we included nine fields (the maximum we found in the study area) in which farmers had sown wildflower strips in 2018 within their fields (each approximately 4 m x 500 m) to extent the gradient of floral resources. We studied this continuous gradient rather than the presence/absence of the flower strips. Each flower strip was sown with a mixture of 42 native, mostly perennial species, for a total sowing density at 13 kg/ha (See Table S2 for details per species). The plant species were selected so as to provide physical habitats and diverse trophic resources to arthropods throughout the year (Gardarin et al., 2018). The mixture of species sown was selected on the basis of the results of a previous analytical experiment comparing the effects of plant assemblages contrasting in terms of their specific and functional diversity (Gardarin et al., submitted).

These monitored strips (sown or naturally occurring) were located at the edges of fields subjected to various combinations of tillage and insecticide use practices (See section 2.4; Figure S1; Table S1). Sixteen fields were cropped with winter faba bean varieties, and 15 were cropped with spring faba bean varieties.

2.2. Invertebrate sampling: temporal dynamics of aphids and their antagonists

Aphids and aphid mummies were counted three times fortnightly between May and June, to estimate population dynamics and biological regulation. The sampling period encompassed the period after *A. fabae* colonisation, and the periods of exponential colony development and regression. Counts on spring faba bean varieties took place two weeks later than those on winter faba bean varieties, according to the phenological stage of the crop. Visual observations of invertebrates were performed 5 and 30 m from the wildflower strips or the field edge, on 30 plants randomly chosen along a 50 m row parallel to the field edge. We recorded the number of each species of aphid and the number of mummies on each plant. If the number of *A. fabae* visibly exceeded 200, the size of the colony was estimated by counting the number of aphids per centimetre and multiplying by the length of the colony and the number of colonised stem faces. We considered as mummies of *A. pisum* those having a golden aspect, of the same morphology as *A. pisum* and located on the lower strata of the vegetation (like their host). No mummy with the morphology of *A. fabae* and located at the apex of the plants (like *A. fabae* colonies) has been observed. The numbers of Syrphidae and Coccinellidae present on the plant were counted at the same

time, according to their stage of development (i.e. larva, pupa, and adult for Coccinellidae and larva and pupa for Syrphidae). We also noted the other predators, from the Araneae, Chrysopidae, Formicidae and Heteroptera, for example, seen on plants. At each date, for each predatory taxon (e.g. Coccinellidae, Syrphidae) we summed the abundances for the 30 plants per distance for each field.

For each species, the growth rate r of aphid populations between two successive counts (hereafter referred to as ‘T1-T2’ for growth of the population between the first two counts and ‘T2-T3’ for the growth of the population between the last two counts) was calculated as follows:

$$r = \frac{\ln(N_{t+1}+1) - \ln(N_t+1)}{\Delta t}$$

Where N_t = the number of aphids at date t , N_{t+1} = the number of aphids at date $t+1$ and Δt = the number of days between two observations.

2.3. Floristic survey to determine the nectar resources at the edge of the field

Botanical surveys were performed during the second aphid count, to assess the nectar resources provided to predators by sown wildflower strips and the spontaneous vegetation of the field margin (always herbaceous). The vegetation was assessed in 20 plots of 1 m² each, distributed along a 40 m transect (2 m between each plot), resulting in 20 m² of surface covered. In each plot, we attributed a cover class to each dicotyledonous species (as a putative nectar-producing resource) according to its percent cover (Class 1: 1% or less; Class 2: 2-10%; Class 3: 11-30%; Class 4: 31-75%; Class 5: 76-100%) and we noted the phenological stage of each species (vegetative, flowering, fruiting). We then calculated the cover of flowering plants (%) providing accessible nectar for predatory Syrphidae based on a morphological model coupling the size of the flower and the size of the head and mouthparts of Syrphidae, compiled for *Episyrphus balteatus*, *Eupeodes corollae*, *Sphaerophoria scripta* and *Syrphus ribesii* species (See details in Supplementary Materials Appendix B, Table S3 and Figure S2). This approach was not extended to the other predators as we lack knowledge on how they reach flower resources and we lack data on their feeding mouthparts. Coccinellidae and Chrysopidae adults, which can feed on aphids, should be though less dependent on nectar resources than Syrphidae. Similarly, we did not identify the parasitoids responsible of the mummies we observed, preventing us from extending our morphological trait-matching approach to parasitoids.

2.4. Description of cropping techniques and of the landscape

We noted the cropping techniques applied to each sampled field during interviews with farmers in 2019 and 2020. We collected detailed information about tillage operations, from soil preparation for sowing until harvest (e.g., ploughing, ploughing in of stubble, hoeing), and information about the insecticides sprayed on the crop (product name, date, dose and area treated). Based on this information, we calculated two continuous variables: the number of tillage operations carried out during the growing season and a treatment frequency index for insecticides (TFI: number of reference doses applied per hectare, Sattler, Kächele, and Verch 2007). Seven fields were cropped with no insecticide and no tillage, 19 fields were cropped with no insecticide but with one to six tillage operations, four fields were cropped with both insecticides (from 1 to 2.25 applications per hectare) and tillage management (from 1 to 5 operations) and one field was cropped without tillage but with insecticide treatment (Supplementary Materials Appendix A, Table S1). All insecticide treatments have been realized before the first count.

The land cover and land use about 500 m from the edge of each field was digitised from the “BD-Ortho 2014” (IGN: *Institut National de l'Information Géographique et Forestière*) in QGIS 2.18 and coupled to landscape surveys. We focused on a relatively small scale because we were interested in short-distance flights for foraging, the type of dispersal relevant for biocontrol in crop fields, rather than migratory flights, which take place over longer distances (Woltz et al., 2012). We calculated the proportion of semi-natural elements (including forest, bushes, hedges, grassland, fallow and other ecological areas, such as wildflower strips; Median=15.32% $\pm$ 16.89 SD; Min-Max=0.24 – 69.48%), and the proportion of leguminous crops (faba bean, pea and lentil) around each field.

We calculated the areal proportion of fields under organic farming in the surrounding environment (500 m) based on a national database updated in 2019 by the French authorities (<https://cartobio.org>). Indeed, previous studies highlighted that the presence of organic fields in the neighborhood of the surveyed fields decreased the number of aphids in both organic and conventional fields (Gosme et al., 2012). In addition, organic farming enhances biodiversity and biological control at a local scale (Muneret et al., 2018) and we could expect the same effect at a landscape scale. The areal proportion of fields under organic farming in the surrounding environment varied from 0% to 74.41% (Median=21.49% $\pm$ 22.17 SD).

2.5. Data analyses

2.5.1. Response of aphid antagonists to local and landscape variables

We assessed the effect of local and landscape variables on the abundance of predators *sensu lato*, i.e. Syrphidae (i.e. larvae and pupae), Coccinellidae (i.e. larvae, pupae and adults) and mummies of *A. pisum*. Araneae, Chrysopidae, Formicidae and Heteroptera could not be taken into account because their abundances were too low. We ran generalised linear mixed models based on maximum likelihood estimation and assuming a negative binomial distribution, “nbinom1” for Syrphidae and mummies, and “nbinom2” for Coccinellidae, with ‘Template Model Builder’ (glmmTMB package, Magnusson et al., 2020). This function provides two parameterisations of the negative binomial that differ in terms of the dependence of the variance (σ^2) on the mean (μ). For family = nbinom1, the variance increases linearly with the mean as $\sigma^2 = \mu(1 + \alpha)$, with $\alpha > 0$; for family = nbinom2, the variance increases quadratically with the mean as $\sigma^2 = \mu(1 + \mu/\theta)$, with $\theta > 0$ (Brooks et al., 2017). The parameter chosen for model adjustment (nbinom1 or nbinom2) was that giving the lowest AIC. The probability of producing a structural zero was modelled as equal for all observations with $ziformula = \sim 1$ (Brooks et al., 2017). As explanatory fixed-effect variables, we included the cover of plants providing accessible nectar in the field edge (spontaneous vegetation or wildflower strip), the number of tillage operations, the TFI for insecticides, the distance to the field edge (5 or 30 m), the total number of aphid individuals, the date of the visit (i.e. which count), the type of variety (winter or spring faba bean), the year (2019 or 2020), the areal proportion of semi-natural habitats, leguminous and organic fields in the landscape. We investigated interactions between local resources and local management or landscape context, by testing the first-order interactions between flower resources and (i) the number of tillage operations, the TFI for insecticides, the type of variety and (ii) proportion of semi-natural habitats. We considered the spatial and temporal dependence of observations between counting dates, by introducing field name as a random-effect variable. All variables were standardized to the same scale (i.e. by subtracting the mean and dividing by the standard deviation).

2.5.2. Response of aphid growth rate to antagonists, local and landscape variables

We analysed the growth rate of *A. fabae* and *A. pisum* separately, as a function of their predators and of local and landscape variables. We ran linear mixed models by maximum likelihood estimation and assuming a Gaussian distribution with the ‘lme’ function (nlme package, Pinheiro et al., 2017). We analysed each counting period (T1-T2 and T2-T3) separately. We introduced, as explanatory fixed-effect variables, the mean number of Syrphidae and Coccinellidae between two successive counts, the rate of parasitism for the *A. pisum* growth rate model, the cover of plants providing accessible nectar at the edge of the field, the TFI for insecticides, the number of tillage operations, the proportion of semi-natural habitat or leguminous crops and the proportion of organic fields. We also accounted for the distance to the field edge, the number of the other aphid species (e.g., *A. pisum* abundance was included as explanatory variable for *A. fabae* growth rate, and conversely, because each species could be considered as alternative prey for aphidophagous predators and decrease predation on the focal species), the type of variety (winter or spring faba bean) and the year (2019 or 2020). We assessed the effects of local resources and management on biological control by natural enemies, by testing the first-order interactions between aphid antagonist and (i) flower resources, (ii) the number of tillage operations, (iii) the insecticide TFI and (iv) type of variety. We accounted for the spatial and temporal dependence of observations between counting dates, by introducing field name as a random-effect variable.

All variables were standardized (i.e. by subtracting the mean and dividing by the standard deviation). Correlations between covariates in full models were assessed with variance inflation factors (all VIF < 5; James et al. 2013). All models were then simplified by a multi-model inference approach (Grueber et al., 2011; Harrison et al., 2018). Models were ranked according to Akaike’s information criterion (AICc; Burnham and Anderson 2002), which can be used to select the most parsimonious model from a set of candidate models. In the case of AICc differences of less than 2 with respect to the best models (Grueber et al., 2011), we used a model-averaging procedure to account for the uncertainty of model selection, and likelihood theory to produce parameter estimates with the ‘MuMIn’ package (Barton & Barton, 2015). Diagnostic residual plots of all full models confirmed a good fit for all. Spatial correlation in the residuals was checked with the ‘bubble’ function from the ‘sp’ package and with Correlogram (package ‘ncf’), and no spatial correlation was detected. All analyses were performed with a significance threshold of 5 % in R statistical software version 3.5.2 (2018-12-20).

3. RESULTS

In total, 88 dicotyledonous plant species flowered during the vegetation surveys, and the trait matching approach indicated that only 55 produced nectar accessible to Syrphidae (Table S4). Wildflower strips provided a significantly larger cover of flowering plants (mean=39.7 % ± 26.6 SD) and a larger cover of plants providing accessible nectar (31.5 % ± 25.4%) than spontaneous field margins (total resources: 17.0 ± 16.0 %; accessible nectar: 12.3 % ± 11.6 %; Fig. S3).

The abundance (mean number per field) of aphid antagonists was low at the beginning of the season. The abundance of Coccinellidae increased over time from 0.80 ± 1.32 individuals at T1 to 3.20 ± 5.05 at T2, and to 13.11 ± 22.11 at T3. The abundance of Syrphidae and mummies increased between T1 and T2, from 0.39 ± 1.11 individuals to 3.71 ± 3.86 individuals, and from 1.34 ± 3.38 mummies to 7.03 ±

14.87 mummies, decreasing slightly thereafter, between T2 and T3, to 3.03 ± 3.94 individuals for Syrphidae and 6.44 ± 9.73 mummies (Fig. S4).

The growth rates of *A. fabae* (0.10 ± 0.10 aphid·aphid⁻¹·day⁻¹) and *A. pisum* (0.06 ± 0.12) populations were positive during the first period (between T1 and T2). During the second period (T2-T3), *A. fabae* populations decreased strongly in size, with a negative growth rate (-0.19 ± 0.21), whereas *A. pisum* populations neither grew nor decreased in size (0.00 ± 0.10) (Fig. 1).

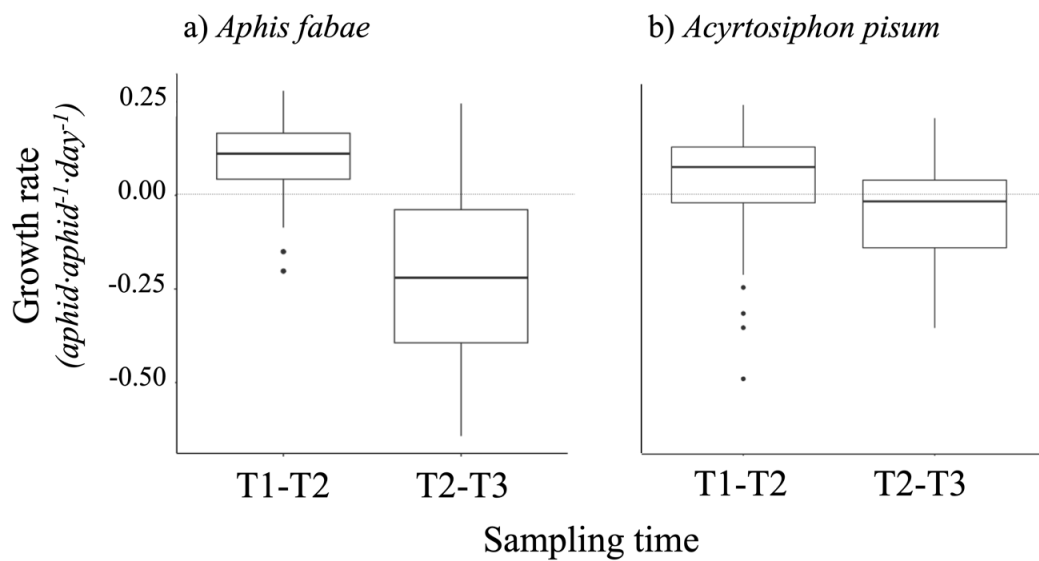


Figure 1: Growth rate of *Aphis fabae* (a) and *Acyrthosiphon pisum* (b) populations between two successive sampling time in faba bean crops.

3.1. Response of aphid antagonists to local and landscape variables

At field level, the abundances of Syrphidae, Coccinellidae and *A. pisum* mummies were positively related to the number of prey (Table 1). Agricultural practices had no significant effect on aphid antagonists other than a lower abundance of Syrphidae in spring faba bean than in winter faba bean crops and a higher abundance of Coccinellidae with a higher number of tillage (Table 1).

The abundances of Syrphidae and mummies were positively related to the cover of flowering species providing accessible nectar at the field edge (Table 1; Fig. 2), whereas no such relationship was observed for Coccinellidae. Interestingly, this local resource effect interacted with landscape composition. The positive effect of nectar resources on the abundance of Syrphidae and mummies weakened with increasing semi-natural habitat cover (in a 500 m landscape buffer zone; Table 1; Fig. 2). The abundance of Coccinellidae was not related to flower resources alone, but the effect of nectar resources weakened with increasing insecticides TFI (Table 1).

Table 1: Effect of local and landscape variables on the abundances of Syrphidae, Coccinellidae and parasitized aphids (mummies). Significant effects ($P < 0.05$) are indicated in bold typeface. All variables were standardised.

Response variable	Explanatory variable	Estimate	Std. error	Z value	P-value
Syrphidae (larvae and pupae)	Intercept (Ref= 2019, 5 m, winter faba bean, Count T1)	-0.59	0.37	-1.62	0.106
	Year 2020	-0.21	0.19	-1.09	0.277
	Tillage	-0.09	0.11	-0.81	0.419
	Insecticide TFI	0.22	0.16	1.33	0.184
	Distance 30 m	0.21	0.15	1.44	0.151
	Variety (spring faba bean)	-0.63	0.28	-2.23	0.026*
	Number of aphids	0.13	0.06	2.09	0.038*
	Flower resources	0.90	0.25	3.64	<0.001***
	% Legumes	-0.12	0.10	-1.22	0.224
	% Organic fields	-0.21	0.13	-1.59	0.111
	% Semi-natural habitat	0.05	0.09	0.50	0.619
	Count T2	2.25	0.33	6.90	<10⁻⁴***
	Count T3	2.07	0.32	6.45	<10⁻⁴***
	Flower resources x tillage	-0.01	0.10	-0.08	0.933
	Flower resources x insecticide TFI	0.45	0.35	1.29	0.198
	Flower resources x crop (spring faba bean)	-0.66	0.33	-2.00	0.046*
	Flower resources x % semi-natural habitat	-0.37	0.14	-2.65	0.008**
Coccinellidae (adult, larvae and pupae)	Intercept (Ref= 2019, 5 m, winter faba bean, Count T1)	-0.07	0.40	0.16	0.870
	Year 2020	-0.45	0.33	-1.34	0.179
	Tillage	0.39	0.18	2.13	0.033*
	Insecticide TFI	-0.16	0.21	-0.77	0.443
	Distance 30 m	0.07	0.18	0.41	0.686
	Variety (spring faba bean)	-0.14	0.47	-0.29	0.770
	Number of aphids	0.31	0.13	2.40	0.016*
	Flower resources	-0.05	0.34	-0.15	0.885
	% Legumes	-0.08	0.15	-0.55	0.583
	% Organic fields	-0.24	0.21	-1.12	0.261
	% Semi-natural habitat	0.04	0.15	0.24	0.807
	Count T2	1.04	0.30	3.45	<0.001***
	Count T3	2.67	0.26	10.25	<10⁻⁴***
	Flower resources x tillage	0.17	0.19	0.87	0.384
	Flower resources x insecticide TFI	-0.69	0.34	-0.77	0.040*
	Flower resources x crop (spring faba bean)	0.53	0.45	1.17	0.243
	Flower resources x % semi-natural habitat	-0.15	0.20	-0.77	0.442
Parasitized aphids (mummies)	Intercept (Ref= 2019, 5 m, winter faba bean, Count T1)	0.11	0.38	0.29	0.772
	Year 2020	0.14	0.24	0.58	0.561
	Tillage	0.04	0.14	0.27	0.788
	Insecticide TFI	0.04	0.17	0.22	0.827
	Distance 30 m	0.22	0.17	1.29	0.196
	Variety (spring faba bean)	0.21	0.39	0.55	0.584
	Number of <i>Acyrtosiphon pisum</i>	0.35	0.05	6.44	<10⁻⁴***
	Flower resources	0.59	0.30	1.98	0.048*
	% Legumes	0.07	0.10	0.70	0.486
	% Organic fields	-0.29	0.19	-1.51	0.130
	% Semi-natural habitat	-0.07	0.13	-0.56	0.579
	Count T2	1.19	0.26	4.49	<10⁻⁴***
	Count T3	1.09	0.27	4.05	<10⁻⁴***
	Flower resources x tillage	0.14	0.12	1.19	0.233
	Flower resources x insecticide TFI	-0.12	0.33	-0.38	0.708
	Flower resources x crop (spring faba bean)	-0.51	0.40	-1.28	0.201
	Flower resources x % semi-natural habitat	-0.47	0.17	-2.75	0.006**

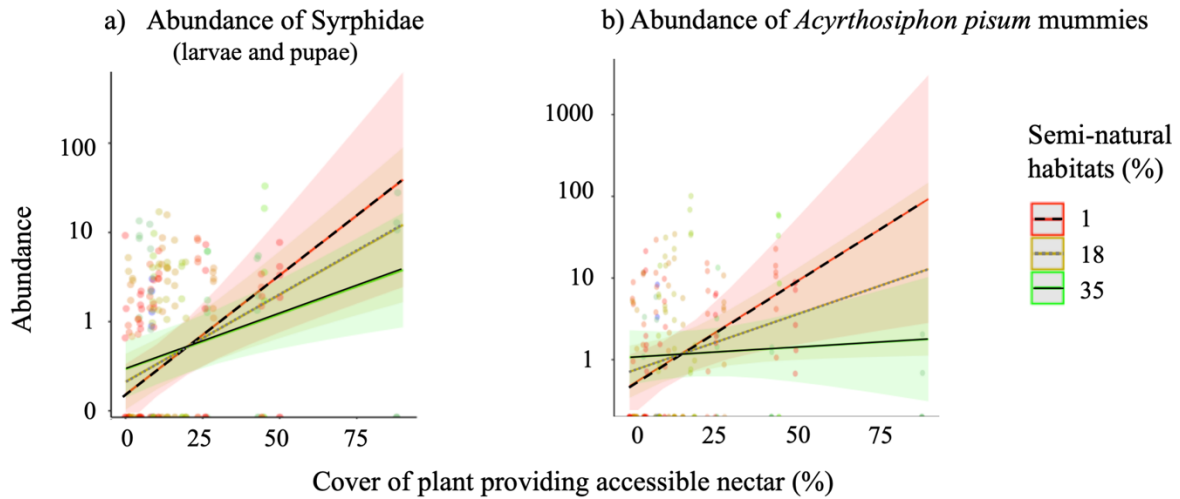


Figure 2: The abundance of (a) Syrphidae (larvae and pupae) and (b) *Acyrthosiphon pisum* mummies as a function of the percentage cover of plants providing accessible nectar (determined for Syrphidae) in interaction with the proportion of semi-natural habitats (500 m). The slope of the interaction is represented for the mean and the standard deviation value of semi-natural habitat ($18 \pm 17\%$).

3.2. Response of aphid population growth rate to antagonists, local and landscape variables

Population growth rate of aphids was not related to the percent cover of plants providing accessible resources at the field edge or the number of predators, for either of the aphid species considered.

During the first period, the growth rate of *A. fabae* populations displayed a weak negative relationship to insecticide TFI (Table 2), with no significant effect of other variables. During the same period, the growth rate of *A. pisum* populations was also negatively related to insecticide TFI, but increased with the proportion of semi-natural habitat in the surrounding landscape (Table 2).

During the second period, the growth rate of *A. fabae* and *A. pisum* populations increased with the number of aphids of the other species (Table 2). The growth rate of *A. fabae* populations displayed a weak positive relationship to insecticide TFI and was negatively related to the number of tillage operations (Table 2), with no effect of landscape variables. The growth rate of *A. pisum* populations was negatively related to the proportion of semi-natural habitats and increased with the proportion of legume crops in the landscape (Table 2).

Table 2: Effect of aphid antagonists, local and landscape variables on the growth rate of *aphid* populations. We only show the best models and explanatory variables, selected after multi-model inference for each species and each period. Estimates from the full average of best models are presented. Significant variables are shown in bold typeface ($P < 0.05$). All variables were standardized. ‘Imp’ is the sum of Akaike weights associated with each variable in all selected models.

Response variables	Period	Explanatory variables	Estimate	Std. error	Adjusted SEM	Z value	P-value	Imp
Growth rate of <i>Aphis fabae</i> populations	T1-T2	Intercept (Ref= 2019, 5 m)	0.10	0.02	0.02	5.88	<0.001	
		Year 2020	$-9.47 \cdot 10^{-8}$	$7.64 \cdot 10^{-5}$	$7.83 \cdot 10^{-5}$	$1.00 \cdot 10^{-3}$	0.999	<0.01
		Insecticide TFI	-0.04	0.02	0.02	2.37	0.018*	1.00
		Tillage	$-3.00 \cdot 10^{-5}$	$1.03 \cdot 10^{-3}$	$1.05 \cdot 10^{-3}$	0.03	0.977	<0.01
		Distance 30 m	$3.00 \cdot 10^{-8}$	$3.16 \cdot 10^{-5}$	$3.22 \cdot 10^{-5}$	$1.00 \cdot 10^{-3}$	0.999	<0.01
		Abundance of Coccinellidae	$8.91 \cdot 10^{-9}$	$1.42 \cdot 10^{-5}$	$1.46 \cdot 10^{-5}$	$1.00 \cdot 10^{-3}$	1.000	<0.01
		Flower resources	$3.13 \cdot 10^{-5}$	$1.05 \cdot 10^{-3}$	$1.06 \cdot 10^{-3}$	0.03	0.977	<0.01
		% Organic fields	$9.67 \cdot 10^{-4}$	$5.84 \cdot 10^{-3}$	$5.93 \cdot 10^{-3}$	0.16	0.870	0.04
		% Semi-natural habitat	$-6.09 \cdot 10^{-5}$	$1.46 \cdot 10^{-3}$	$1.48 \cdot 10^{-3}$	0.04	0.967	<0.01
	T2-T3	Intercept (Ref= 2019)	-0.20	0.03	0.03	7.28	< 10^{-4}	
		Year 2020	$8.06 \cdot 10^{-3}$	0.03	0.03	0.27	0.790	0.10
		Insecticide TFI	0.08	0.03	0.03	2.94	0.003**	1.00
		Tillage	-0.06	0.03	0.03	2.22	0.026*	1.00
		Abundance of <i>Acyrtosiphon pisum</i>	0.07	0.02	0.03	2.84	0.005**	1.00
		Abundance of Syrphidae	$3.93 \cdot 10^{-4}$	$4.41 \cdot 10^{-3}$	$4.53 \cdot 10^{-3}$	0.09	0.931	0.02
		Flower resources	$-5.04 \cdot 10^{-4}$	$5.27 \cdot 10^{-3}$	$5.42 \cdot 10^{-3}$	0.10	0.926	0.02
		% Organic fields	$6.05 \cdot 10^{-4}$	$6.14 \cdot 10^{-3}$	$6.33 \cdot 10^{-3}$	0.10	0.924	0.03
Growth rate of <i>Acyrtosiphon pisum</i> populations	T1-T2	Intercept (Ref= 2019)	0.105	0.027	0.082	3.70	$2.15 \cdot 10^{-3}$	
		Year 2020	-0.08	0.03	0.04	2.19	0.028*	1.00
		Insecticide TFI	-0.04	0.02	0.02	2.16	0.031*	1.00
		Abundance of Syrphidae	$1.19 \cdot 10^{-4}$	$1.51 \cdot 10^{-3}$	$1.54 \cdot 10^{-3}$	0.08	0.938	0.01
		% Semi-natural habitat	0.05	0.02	0.02	2.83	0.005**	1.00
		% Organic fields	$2.64 \cdot 10^{-4}$	$3.07 \cdot 10^{-3}$	$3.16 \cdot 10^{-3}$	0.08	0.934	0.02
	T2-T3	Intercept (Ref= 2019)	0.04	0.02	0.02	1.52	0.129	
		Year 2020	0.06	0.03	0.03	1.92	0.054	1.00
		Insecticide TFI	$1.59 \cdot 10^{-3}$	$6.68 \cdot 10^{-3}$	$6.75 \cdot 10^{-3}$	0.24	0.813	0.07
		Abundance of <i>Aphis fabae</i>	0.03	0.01	0.01	2.16	0.031 *	1.00
		Abundance of Coccinellidae	$-8.68 \cdot 10^{-4}$	$4.47 \cdot 10^{-4}$	$4.56 \cdot 10^{-4}$	0.02	0.985	0.98
		Abundance of Syrphidae	$4.72 \cdot 10^{-4}$	$3.69 \cdot 10^{-3}$	$3.72 \cdot 10^{-4}$	0.13	0.889	0.02
		Flower resources	$1.27 \cdot 10^{-9}$	$5.81 \cdot 10^{-6}$	$5.99 \cdot 10^{-6}$	0.00	0.999	<0.01
		% Semi-natural habitat	-0.03	0.01	0.01	2.23	0.026*	1.00
		% Legumes	0.03	0.01	0.01	2.59	0.010**	1.00
		Insecticide TFI x abundance of Syrphidae	$-1.41 \cdot 10^{-5}$	$5.77 \cdot 10^{-4}$	$5.82 \cdot 10^{-4}$	0.02	0.981	<0.01
		Flower resources x abundance of Syrphidae	$1.54 \cdot 10^{-9}$	$4.90 \cdot 10^{-6}$	$4.95 \cdot 10^{-6}$	0.00	0.999	<0.01

4. DISCUSSION

Our results show that increasing the percentage of flowering species with accessible nectar at the field scale by sowing wildflower strips in faba bean crops increases the abundances of Syrphidae and mummies. This positive effect of nectar resources decreased with the proportion of semi-natural habitats in the surrounding landscape, without interaction with local management practices. Nevertheless, this effect was not translated into greater regulation of the aphid population, because neither aphid predator levels nor aphid parasitism rates had any effect on aphid population growth rates at both sampling time.

4.1. Responses of aphid antagonists to local and landscape variables

Contrary to our initial hypothesis, insecticide use and tillage frequency had no significant effect on the abundance of Syrphidae or on the number of *A. pisum* mummies. The abundance of Coccinellidae was however positively affected by the tillage frequency and not affected by insecticide use. Ladybird first and second instars are known to be very sensitive to insecticides, but this susceptibility depends on species and type of insecticide (Afza et al., 2019). The insecticides used in these fields were mostly pyrethroids, rapid-action contact pesticides that are unlikely to prevent recolonization by insects after treatment. The positive effect of tillage frequency on the mean number of Coccinellidae per field could be due to an effect of organic farming. Indeed, in our study (Figure S1), and more generally (Puech et al. 2014), organic farming relies on a higher frequency of ploughing and other tillage methods than conventional ones. The lack of synthetic pesticides seems to predominate over the increased tillage intensity, explaining why organic cropping systems harbour a wide range of natural enemies, such as Coccinellidae (Makwela, 2019; Poupelin, 2012). The absence of a negative effect of tillage on Syrphidae and number of mummies suggests that these insects did not overwinter in the field and that their populations colonised the crop mostly from the surrounding landscape.

The abundances of Coccinellidae, Syrphidae and mummies increased with increasing aphid abundance, suggesting a prevailing bottom-up effect. Indeed, the principal natural enemies were aphidophagous and gravid Syrphidae, which usually oviposit close to their prey because first-instar larvae have a limited dispersal ability (Almohamad et al., 2009). Plants providing accessible nectar resources increased the abundance of Syrphidae and mummies, but were not related to the abundance of Coccinellidae, as shown in several other studies (Hatt et al., 2017; Ramsden et al., 2015). Adult insects require nectar, in addition to pollen, to enhance survival and reproduction (Lundgren, 2009; Rodríguez-Gasol et al., 2020). Hoverflies can make use of other resources (e.g. the extra-floral nectar of faba bean crops, aphid honeydew, flower pollen), but we have shown that nectar is generally a limiting resource that can be increased by planting wildflower strips. The lack of effect on the abundance of Coccinellidae may reflect a lower requirement for flower resources at the adult stage, because adults can also feed on prey, such as aphids (Weber and Lundgren, 2009). Floral resources may become important for ladybirds when prey is scarce (Lundgren, 2009), notably when individuals emerge and search habitats for mating and ovipositing. Flower resources alone are not nutritionally and metabolically sufficient for ovigenesis of most predatory ladybirds. However, combined with prey food (which is essential food for ladybird as they allow to reproduce them; Hodek, 1996), they accelerate oviposition (Hatt and Osawa, 2019). In this study, aphids were abundant (mean of 607 aphids per ladybird), potentially accounting for the lack of attractiveness of flowers to these insects. Our results showed that the number of mummies increased with the amount of available nectar resources, both at 5 m and 30 m. First of all, it is interesting to find a relationship to both distances in the field, since previous studies found decreasing levels of aphid parasitism with longer distance to flower strip (Tylianakis et al., 2004). In addition, like hoverflies, parasitoids can also feed on other sugar resources such as honeydew (Gillespie et al., 2016). Therefore,

the positive effect of the amount of nectar resources on the number of aphid mummies reinforces the importance of nectar provided by spontaneous or sown vegetation in the strips.

There was no interaction between the effect of flower resources and of local management on Syrphidae and mummies, suggesting that neither antagonism nor synergy occurred. For Coccinellidae however, a negative interaction was found between nectar resources and insecticide treatments. We do not think this result is robust because these variables had no significant effects alone (with additive effects only). Wildflower strips may, therefore, be valuable for predators and parasitoids in all cropping systems.

Interestingly, the positive effect of flower resources on the abundance of mummies and Syrphidae was smaller in landscapes containing higher proportions of semi-natural habitats than those with a low proportion. Highly complex landscapes may indeed benefit little from the addition of perennial habitats, because these areas already contain rich and abundant communities of beneficial insects such as natural enemies (Isaacs et al., 2009). Contrary to the intermediate landscape-complexity hypothesis (Tscharntke et al., 2012), the effect of nectar resources was the strongest in simple landscapes in our study, where flower created the largest ecological contrast with the surrounding landscape (Scheper et al., 2015). Moreover, we studied arthropods being mobile enough to recolonise quickly the studied fields, even in simple landscapes.

4.2. Effects of cropping techniques, aphid antagonists and landscape variables on the growth rate of aphid populations

As expected, the growth rate of *A. fabae* and *A. pisum* populations were influenced by cropping techniques, but *A. pisum* populations also responded to landscape composition. In addition, their responses to local and landscape variables change between sampling time.

Insecticides, which were all applied early, before the first count, had a negative effect on the growth rate of *A. fabae* and *A. pisum* populations during the first sampling time, although this growth rate remained positive (i.e. population size increased). However, the effect of insecticide treatment frequency index (TFI) on *A. fabae* populations was positive during the second period. Thus, insecticide treatments controlled aphid populations just after their application, but did not prevent the aphid population from growing again afterwards. The negative effect of tillage frequency on the growth rate of *A. fabae* populations could be linked to an organic cropping system effect. Indeed, biological control is often higher in organic than in conventional cropping systems (Muneret et al., 2018) despite soil disturbance caused by a higher tillage frequency in organic cropping systems (Puech et al., 2014). We moreover found that a low insecticide TFI was associated with a reduced aphid growth rate during the second sampling time (T2-T3).

However, contrary to our expectations, we detected no direct top-down effect of the abundance of Coccinellidae or Syrphidae on the dynamics of *A. fabae* or *A. pisum* populations, despite the many reports of effective biological control by these aphidophagous predators (Thies et al., 2011; Tschumi et al., 2016b). We observed a bottom-up effect of aphids on their predators, but the numbers of these specialist predators over the growing season probably remained too small to prevent aphid population outbreaks (mean of 408 aphids per predator; Hasken and Poehling, 1995). Indeed, mostly studies have reported effective biological control of aphids by aphidophagous predators on wheat (Thies et al., 2011), on which the number of aphids is generally smaller than on legume crops because *A. fabae*, unlike *Rhopalosiphum padi* or *Sitobion avenae* on cereals, forms colonies of numerous aphids in a sleeve around the stems (Ighil et al., 2011). In addition, aphids feeding on legume crops achieve a higher

nutritional status than those on other crops, and this may enhance the growth and survival of aphid populations (Emden and Harrington, 2007). We detected no effect of the rate of parasitism on the growth rate of *A. pisum* populations. According to Thies et al. (2005), parasitoids would be able to control aphid populations only at low aphid densities, which was not the case here.

We also found that the growth rates of *A. pisum* and *A. fabae* populations late in the season increased with the number of aphids of the other species. This simultaneous increase in both populations may dilute the biological control effect due to the large increase in prey numbers, with any increase in one population favouring a decrease in predation on the other aphid population (Sánchez-Hernández et al., 2021).

Only *A. pisum* responded to landscape composition in our study. The growth rate of populations of this species increased with the proportion of semi-natural habitat, including fallow and grassland in the early part of the season, and with the proportion of legumes (i.e. mostly lentil, faba bean and pea) later in the season. Fallow and grassland may contain leguminous species (e.g. *Trifolium spp.*, *Medicago spp.*) that are host plants for *A. pisum*, like cultivated legume species (Kordan et al., 2018; Wale et al., 2000). Nevertheless, later in the season, the growth rate of *A. pisum* populations decreased with the proportion of semi-natural habitat, possibly due to an indirect positive effect of their natural enemies, leading to biological control. We found no relationship between landscape composition and aphid antagonist populations, but previous studies have reported beneficial effects of the proportion of semi-natural habitat on the biodiversity of predators (vertebrates or invertebrates) and pest control in the field (Chaplin- Kramer et al. 2011; Veres et al. 2013; Rusch et al. 2016; Holland et al. 2017; but see Karp et al. 2018).

Although our field sampling extended over a relatively large number of farms, a limit of our study is the number and frequency of count that probably was too low to capture the accurate temporal dynamics of aphids and how it is affected by the predators and by parasitoids. We also did not take into account the very beginning of the dynamics of potential aphids and the potential effects of generalist predators such as carabids and spiders (Thies et al., 2011), which also respond to flower strips and cropping systems (Ganser et al., 2019; Lys and Nentwig, 1992; Tamburini et al., 2016; Tuck et al., 2014). We thus recommend increasing the number of visits and starting earlier the sampling in next studies.

4.3. Application for management

Our results support the idea that, over and above the existing effects of landscape composition, the biological control of aphids can be managed through cropping practices in the field (e.g. by managing insecticide applications) and by planting flower strips (Begg et al., 2017). We found that it was not so much the simple presence of a flower strip, as the proportion of the plant cover within it providing accessible nectar that was strongly related to the presence of hoverfly larvae in the adjacent crop, as already reported for adult hoverflies (van Rijn and Wäckers, 2016). We also found that flower strips had a greater impact in simplified landscapes. These results provide a basis for the deployment of biological control in various landscape and agricultural contexts. However, the different responses of the two-aphid species studied to these levers limits the generic scope of our results and should encourage additional studies on a diversity of pests with contrasting patterns of behaviour.

AUTHOR CONTRIBUTIONS

LS, FC, MVM, and AG conceived the ideas and designed the methodology; LS, AG and AB collected the data; LS analysed the data; AG and LS wrote the manuscript. All authors contributed critically to the drafts and approved the final version for publication.

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Declaration of Competing Interest

We declare no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A: Overview of the cropping techniques implemented in the fields survey.

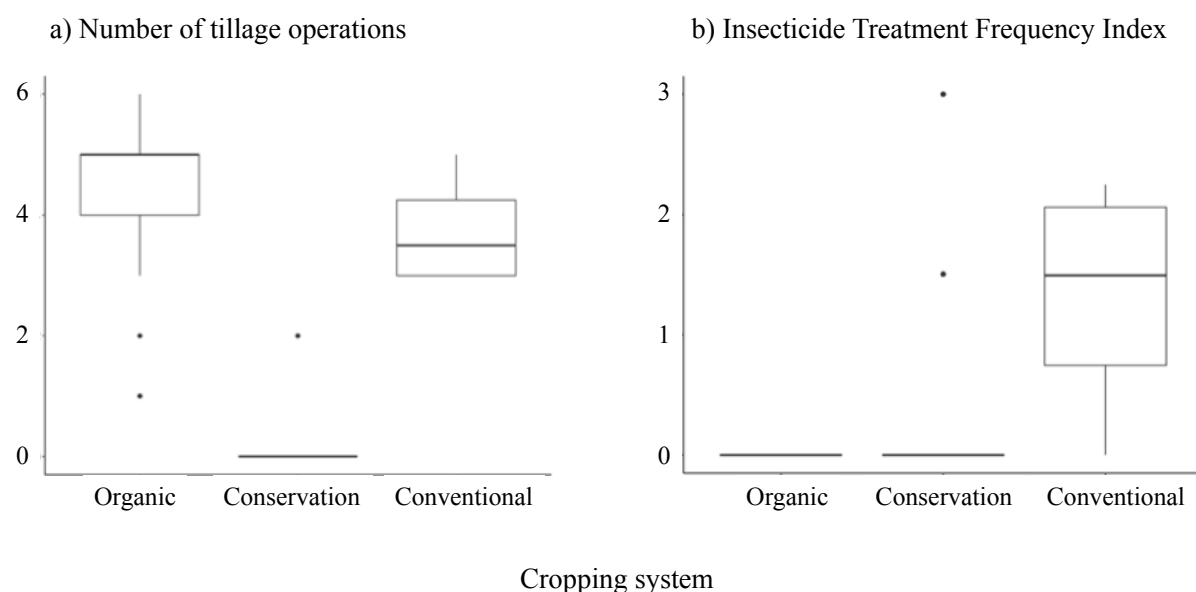


Figure S1: Mean number of tillage operations and Insecticide Treatment Frequency Index (TFI) depending on cropping system (organic, conservation or conventional). Organic farming was characterized by a high number of tillage operations but no insecticide sprayed compared to conventional and conservation cropping systems, while conservation systems do not perform ploughing and only a few employed superficial tillage.

Table S1: Number of fields surveyed depending on the combination of the number of tillage operations and insecticide Treatment Frequency Index (TFI) for spring or winter faba bean.

Variety	Number of fields		Number of tillage operations						
			0	1	2	3	4	5	6
Spring faba bean	Insecticide TFI	0	3		1	1	2	2	
		1-2		1				1	
		2-3	1			1	1		
Winter faba bean		0	3	1		2	6	4	2

Table S2: List of sown species and their density.

Sown species	Density (mg/m ²)
<i>Achillea millefolium</i>	1.79
<i>Alliaria petiolata</i>	9.27
<i>Anthemis tinctoria</i>	3.36
<i>Anthriscus sylvestris</i>	6.70
<i>Barbarea vulgaris</i>	49.77
<i>Bellis perennis</i>	4.19
<i>Carum carvi</i>	20.77
<i>Centaurea cyanus</i>	44.71
<i>Centaurea scabiosa</i>	52.59
<i>Cichorium intybus</i>	22.42
<i>Daucus carota</i>	21.82
<i>Echium vulgare</i>	28.30
<i>Festuca arundinacea</i>	163.17
<i>Galium mollugo</i>	4.22
<i>Geum urbanum</i>	33.28
<i>Glechoma hederacea</i>	10.97
<i>Hesperis matronalis</i>	28.53
<i>Hypericum perforatum</i>	6.35
<i>Knautia arvensis</i>	7.10
<i>Leucanthemum vulgare</i>	19.80
<i>Lotus corniculatus</i>	24.65
<i>Malva sylvestris</i>	27.02
<i>Medicago sativa</i>	27.29
<i>Melilotus officinalis</i>	32.80
<i>Onobrychis viciifolia</i>	183.34
<i>Origanum vulgare</i>	11.01
<i>Pastinaca sativa</i>	85.59
<i>Pimpinella saxifraga</i>	16.21
<i>Plantago lanceolata</i>	22.81
<i>Ranunculus acris</i>	15.06
<i>Reseda luteola</i>	1.31
<i>Securigera varia</i>	19.10
<i>Senecio jacobaea</i>	4.35
<i>Stellaria media</i>	1.90
<i>Tanacetum vulgare</i>	1.50
<i>Taraxacum officinale</i>	7.18
<i>Trifolium repens</i>	9.12
<i>Trisetum flavescens</i>	3.18
<i>Veronica hederifolia</i>	25.23
<i>Veronica persica</i>	1.88
<i>Vicia sativa</i>	131.40

Appendix B: Estimation of nectar accessibility to Syrphidae.

We estimated the amount of nectar provided by the plants by summing, in each field margin (spontaneous vegetation or flower strip), the percent cover of, assessed in vegetation surveys, providing available and accessible nectar to Syrphidae. We focused on Syrphidae because (1) they were dominant aphid predators in our study, (2) the adults require nectar as a source of energy and (3) they have a limited access to floral nectar depending on morphological constraints.

Plant species producing floral or extrafloral nectar were selected from vegetation surveys. Nectar was considered to be **available** when it was produced during the period of predator observations, by selecting species at flower stage or producing extrafloral nectar between the first and the third aphid count. Nectar **accessibility** depended on morphological matching between plants and predators. Extrafloral nectar, which is not enclosed in a perianth but produced on bracts or stipules, was considered to be always accessible. We determined the **accessibility of floral nectar**, with a mechanistic trait-based approach, by adapting the geometric model proposed by van Rijn et Wäckers (2016).

Flower traits related to nectar availability (presence of floral and extrafloral nectar) and accessibility (flower opening diameter, corolla height, nectar depth and nectar tube diameter) were measured in a previous study (Gardarin, Pigot, et Valantin-Morison 2021).

To determine the access of aphidophagous Syrphidae to the nectar provided by plants, we retrieved from the literature the size of their mouthparts and head, which limit corolla penetration. We focused on the four dominant aphidophagous species (Table S3) that were found in malaise traps in a complementary unpublished experiment. Altogether, these four species represented 91 % of all Syrphidae trapped individuals.

Table S3: Morphological measurements of the head and mouthpart size of the Syrphidae, retrieved from the literature (Gilbert, 1985a; Gilbert, 1985b).

	Head width (mm)	Absolute proboscis length (mm)
<i>Episyrphus balteatus</i>	3.04	2.89
<i>Eupeodes corollae</i>	3.14	3.25
<i>Sphaerophoria scripta</i>	2.30	3.44
<i>Syrphus ribesii</i>	3.67	3.43

A decision tree (Gardarin *et al.*, 2021) was built to take into account the three constraints limiting nectar accessibility: (1) ability of the insect to penetrate the flower, which is dependent on head size and flower opening, (2) ability to reach the nectar, which depends on proboscis length, nectar depth and corolla height, and (3) proboscis width and nectar tube diameter in the presence of nectar (Figure S2). Here, we hypothesized that there was no constraint related to the proboscis width (width of the labral sucking tube) with regards to nectar tube diameter, and that sucking was always possible, even in narrow tubes (Gilbert, 1981).

Using the decision tree, we matched flower and insect traits for all four Syrphidae species. In general, floral nectar accessibility was the same for all four species. We considered that nectar was accessible in general to Syrphidae when it was the case for the four selected species. If results on nectar accessibility were not congruent across Syrphidae species (situation met in only a few instances), we considered that nectar was not accessible in general to these predators.

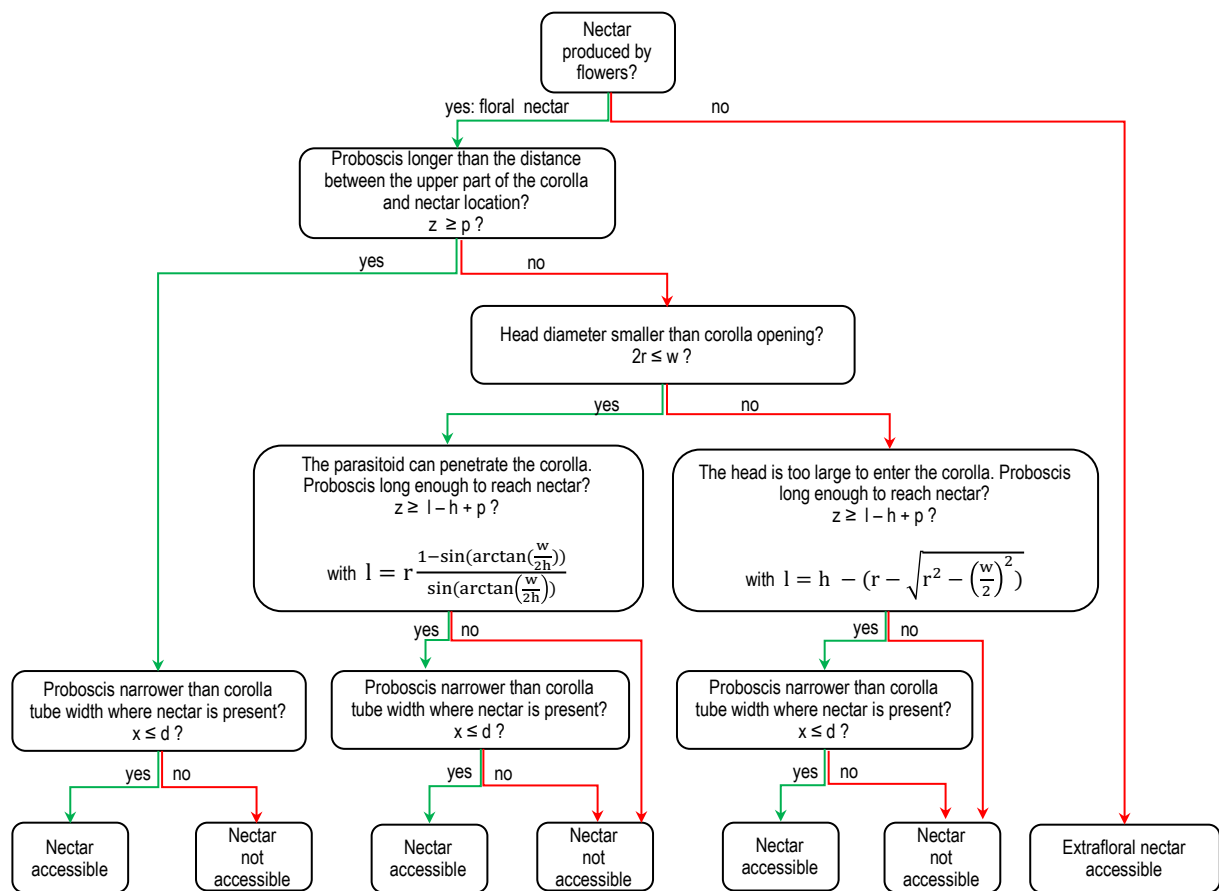


Figure S2. Decision tree from Gardarin *et al.* (2021) used to determine the accessibility of nectar to insects as a function of insect traits (radius of insect head r , proboscis length x and proboscis width z) and flower traits (width of flower opening w , corolla height h , nectar depth p , nectar tube diameter d).

Table S4: List of flowering species sampled with nectar accessible or not to Syrphidae according to the previous morphological model. The mean cover (with standard deviation SD) of each plant species per field and its cumulated sum among all fields sampled is given (No standard deviation is given when the specie was found only once across fields).

Species	Accessible	Mean cover $\pm$ SD (%)	Cumulated sum (%)
<i>Achillea millefolium</i>	yes	0.14 $\pm$ 0.05	0.55
<i>Agrimonia eupatoria</i>	yes	0.65	0.65
<i>Althaea hirsuta</i>	no	0.35	0.35
<i>Ammi majus</i>	yes	0.05	0.05
<i>Anagallis arvensis</i>	no	2.99 $\pm$ 3.40	17.95
<i>Anthemis tinctoria</i>	yes	5.26 $\pm$ 6.01	31.58
<i>Anthriscus sylvestris</i>	yes	0.05	0.05
<i>Aphanes arvensis</i>	yes	1	1
<i>Barbarea sp.</i>	yes	2.35	2.35
<i>Barbarea vulgaris</i>	yes	0.63 $\pm$ 0.60	3.15
<i>Bellis perennis</i>	yes	2.30 $\pm$ 1.98	25.30
<i>Capsella bursa-pastoris</i>	yes	0.20 $\pm$ 0.22	0.60
<i>Carduus nutans</i>	no	0.05	0.05
<i>Centaurea cyanus</i>	yes	3.77 $\pm$ 6.28	33.90
<i>Centaurea scabiosa</i>	yes	0.94 $\pm$ 0.77	3.75
<i>Cerastium glomeratum</i>	yes	0.1	0.10
<i>Cicuta virosa</i>	yes	0.10	0.10
<i>Cirsium arvense</i>	yes	0.3	0.30
<i>Cirsium vulgare</i>	yes	0.08 $\pm$ 0.04	0.15
<i>Convolvulus arvensis</i>	yes	1.23 $\pm$ 1.33	9.85
<i>Cornus sanguinea</i>	yes	0.05	0.05
<i>Crepis setosa</i>	yes	0.53 $\pm$ 0.64	1.60
<i>Crepis sp.</i>	yes	0.10	0.10
<i>Echium vulgare</i>	yes	0.55 $\pm$ 0.42	1.10
<i>Erigeron acris</i>	no	0.30	0.30
<i>Euphorbia helioscopia</i>	yes	0.40	0.40
<i>Fallopia convolvulus</i>	yes	9.25	9.25
<i>Filago vulgaris</i>	no	2.25	2.25
<i>Fumaria officinalis</i>	no	0.05	0.05
<i>Galium aparine</i>	yes	0.83 $\pm$ 1.16	6.60
<i>Galium mollugo</i>	yes	4.68 $\pm$ 6.11	18.70
<i>Geranium dissectum</i>	yes	3.56 $\pm$ 4.70	67.73
<i>Geranium molle</i>	yes	1.55 $\pm$ 2.35	10.85
<i>Geranium pusillum</i>	yes	8.04 $\pm$ 11.30	16.08
<i>Geum urbanum</i>	yes	0.20	0.20
<i>Hesperis matronalis</i>	no	0.15 $\pm$ 0.14	0.60
<i>Hypericum perforatum</i>	no	0.38 $\pm$ 0.04	0.75
<i>Hypochaeris radicata</i>	yes	0.05 $\pm$ 0.00	0.10
<i>Knautia arvensis</i>	no	0.55 $\pm$ 0.52	1.65
<i>Lactuca serriola</i>	yes	0.10	0.10
<i>Lamium album</i>	yes	0.50	0.50
<i>Lapsana communis</i>	no	3.95	3.95
<i>Lepidium draba</i>	yes	6.93	6.93

<i>Leucanthemum vulgare</i>	yes	9.62 ± 8.02	48.08
<i>Lotus corniculatus</i>	no	1.00	1.00
<i>Lythrum hyssopifolia</i>	no	0.30	0.30
<i>Malva sylvestris</i>	no	0.72 ± 0.81	2.15
<i>Matricaria perforata</i>	yes	0.77 ± 1.04	3.85
<i>Matricaria recutita</i>	yes	14.48 ± 25.08	159.30
<i>Medicago lupulina</i>	no	0.86 ± 1.32	4.30
<i>Medicago sativa</i>	no	14.95 ± 28.53	59.80
<i>Melilotus officinalis</i>	no	0.68 ± 0.55	2.05
<i>Myosotis arvensis</i>	no	0.38 ± 0.04	0.75
<i>Onobrychis viciifolia</i>	no	1.30 ± 1.02	10.40
<i>Papaver rhoeas</i>	no	1.49 ± 1.91	10.40
<i>Pastinaca sativa</i>	yes	1.75 ± 2.85	7.00
<i>Picris echioides</i>	yes	3.61 ± 5.04	7.23
<i>Plantago lanceolata</i>	no	3.83 ± 4.06	11.48
<i>Polygonum persicaria</i>	no	0.95 ± 1.13	1.90
<i>Potentilla reptans</i>	yes	1.51 ± 1.44	7.53
<i>Ranunculus acris</i>	yes	1.45	1.45
<i>Ranunculus arvensis</i>	yes	0.40	0.40
<i>Ranunculus bulbosus</i>	yes	1.10 ± 0.71	2.20
<i>Reseda lutea</i>	no	0.12 ± 0.03	0.35
<i>Reseda luteola</i>	no	0.05	0.05
<i>Rumex crispus</i>	no	0.05 ± 0.07	0.10
<i>Senecio jacobaea</i>	yes	0.10	0.10
<i>Senecio vulgaris</i>	no	0.63 ± 0.69	1.90
<i>Sherardia arvensis</i>	yes	0.35	0.35
<i>Silene inflata</i>	no	0.05	0.05
<i>Silene latifolia</i>	no	0.29 ± 0.24	1.75
<i>Sinapis arvensis</i>	yes	0.98 ± 1.60	4.90
<i>Sisymbrium officinale</i>	yes	0.43 ± 0.53	1.70
<i>Sonchus asper</i>	yes	0.41 ± 0.58	5.30
<i>Stellaria media</i>	yes	0.15	0.15
<i>Taraxacum officinale</i>	yes	0.92 ± 1.13	9.20
<i>Tordylium maximum</i>	yes	3.65	3.65
<i>Torilis arvensis</i>	yes	5.83 ± 7.81	11.65
<i>Trifolium campestre</i>	no	7.43 ± 10.43	14.85
<i>Trifolium pratense</i>	no	0.06 ± 0.03	0.25
<i>Trifolium repens</i>	yes	1.18 ± 1.06	5.90
<i>Veronica arvensis</i>	yes	0.32 ± 0.36	1.90
<i>Veronica persica</i>	yes	0.86 ± 1.17	7.70
<i>Vicia hirsuta</i>	no	1.42 ± 2.24	4.25
<i>Vicia sativa</i>	no	2.70 ± 3.22	40.55
<i>Viola arvensis</i>	no	0.65 ± 0.49	1.30
<i>Vicia faba</i>	no	0.10	0.10

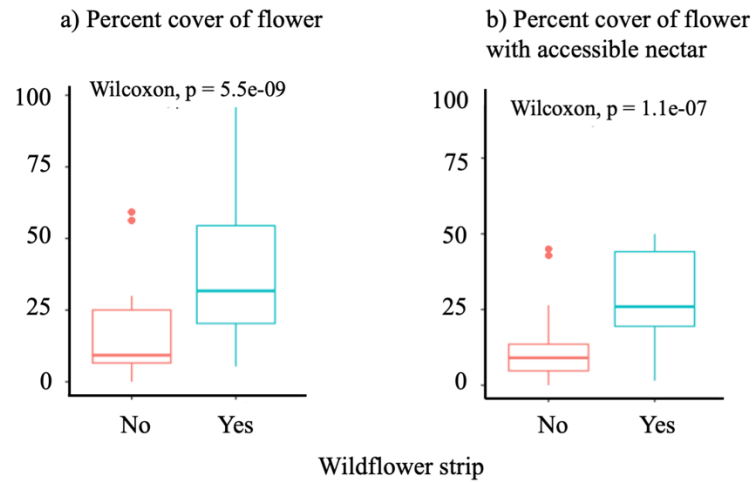


Figure S3: Percent cover of all dicotyledonous flowering species with or without the presence of a wildflower strip for a) all species recorded and b) for species providing accessible nectar to Syrphidae.

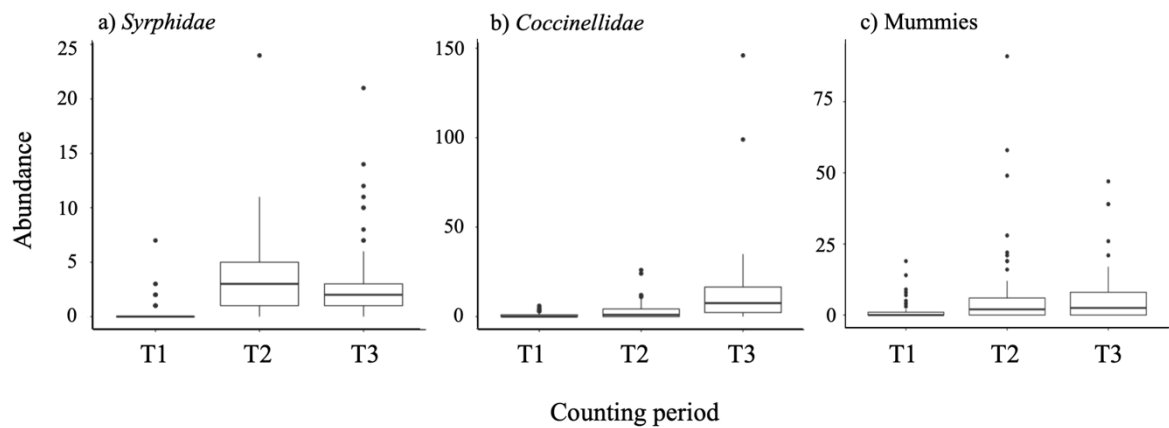


Figure S4: Temporal dynamics of the abundance of a) *Syrphidae* (larvae and pupae), b) *Coccinellidae* (adult, larvae and pupae) and c) Mummies of *Acyrthosiphon pisum* per counting date (T1, T2 and T3) in faba bean.

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