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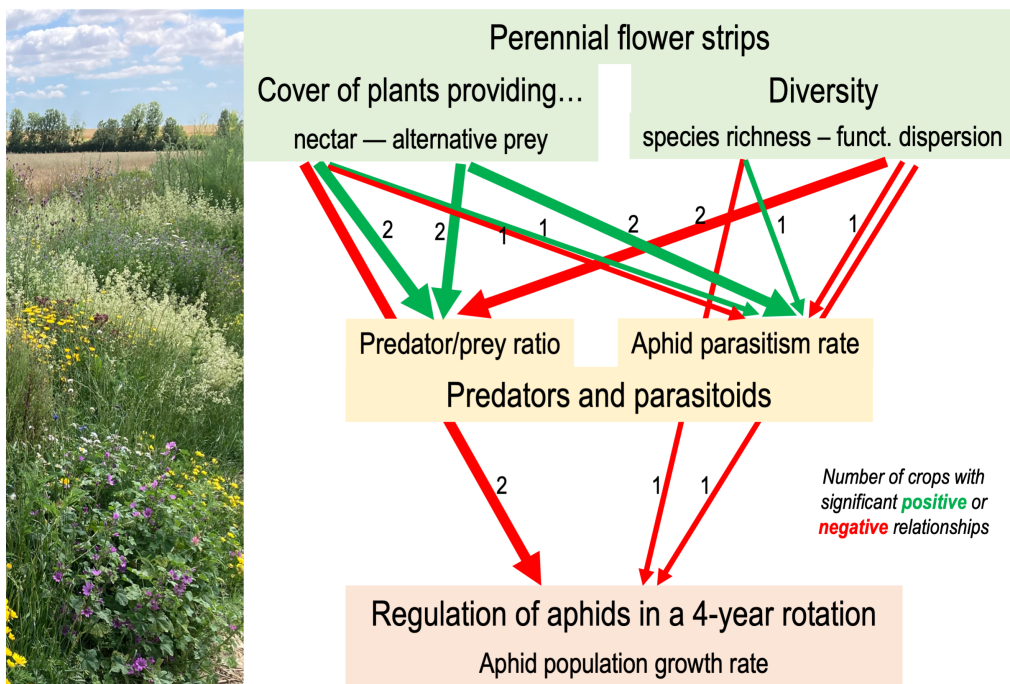
Aphid biological control in arable crops via flower strips: the predominant role of food resources over diversity effects

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Abstract

1. Plant taxonomic and functional diversity promotes interactions at higher trophic levels, but the contribution of functional diversity effects to multitrophic interactions and ecosystem functioning remains unclear. In agroecosystems, flower strips can be sown to promote biodiversity and associated services, but their plant composition is poorly considered from a functional diversity perspective so as to promote multitrophic interactions.

2. In a field experiment, aphid biological control was compared across contrasting flower strip mixtures, over a four-year arable crop rotation. The effects of plants providing food resources, i.e. nectar and legumes supporting alternative hosts and prey, and the effects of plant species richness and functional dispersion were investigated on the biological control of aphid populations.

3. In general, increases in the percentage of plant cover providing nectar and alternative prey (Fabaceae) to natural enemies increased predator-prey ratios and aphid parasitism, and decreased aphid population growth rates. These effects however depended on the crop species.

4. Species richness and the functional dispersion of traits involved in plant-arthropod interactions were of lesser importance and the directions of their effects were crop-specific.

5. *Synthesis and applications.* These findings provide useful insight for designing perennial plant mixtures for creating or restoring habitats supporting aphid regulation. It is not adequate to sow any mixture containing simply flowering plants. Plant mixtures should comprise a large proportion of plant species supporting alternative prey, like legumes, and species producing nectar being easily accessible to natural enemies (corollas with non-deep nectar). To be efficient over a crop rotation, with aphids being present at different seasons, these nectar resources should be provided throughout the year thanks to a diversity of plant flowering periods.

Keywords

Conservation biological control; nectar; parasitism; predator; trait-matching; wildflower strip.

Résumé

1. La diversité taxonomique et fonctionnelle des plantes favorise les interactions aux niveaux trophiques supérieurs, mais la contribution des effets de la diversité fonctionnelle aux interactions multitrophiques et au fonctionnement des écosystèmes reste incertaine. Dans les agroécosystèmes, des bandes fleuries peuvent être implantées pour favoriser la biodiversité et les services associés, mais leur composition végétale est peu réfléchiée sous un angle de diversité fonctionnelle de manière à favoriser les interactions multitrophiques.
2. Dans un essai en parcelle expérimentale, des bandes fleuries, semées avec mélanges de plantes contrastés, ont été comparées vis-à-vis de leurs effets sur la lutte biologique des pucerons, au cours d'une rotation de quatre ans en grandes cultures. Les effets des plantes fournissant des ressources alimentaires, c'est-à-dire du nectar, légumineuses hébergeant des proies et des hôtes alternatifs, l'effet de la richesse des plantes et l'effet de la diversité fonctionnelle ont été étudiés sur le contrôle biologique des populations de pucerons.
3. En général, l'augmentation du pourcentage de couverture végétale fournissant du nectar et des proies alternatives (Fabaceae) aux auxiliaires augmente le ratio prédateurs-proies et le taux de parasitisme des pucerons, et il diminue le taux de croissance des populations de pucerons. Ces effets dépendent toutefois de la culture en place.
4. La richesse des espèces et la dispersion fonctionnelle des traits impliqués dans les interactions plantes-arthropodes ont une importance moindre et le sens de leurs effets sont dépendants de la culture suivie.
5. Synthèse et applications. Ces résultats fournissent des indications utiles pour la conception de mélanges de plantes pérennes en vue de créer ou de restaurer des habitats favorisant la régulation des pucerons. Il ne suffit pas de semer un mélange contenant uniquement des plantes à fleurs. Les mélanges doivent comprendre une grande proportion d'espèces favorisant des proies alternatives, comme les légumineuses, et des espèces produisant du nectar facilement accessible aux auxiliaires (corolles avec nectar peu profond). Pour être efficace à l'échelle d'une rotation de cultures, les pucerons étant présents à différentes saisons, ces ressources alimentaires doivent être fournies tout au long de l'année via des plantes ayant des floraisons étalées toute l'année.

Introduction

Biodiversity and multitrophic interactions are at the very heart of the functioning of ecosystems. In the current context of declining biodiversity, there is an urgent need to improve our understanding of the relationships between plant and animal communities (Wood *et al.* 2015). Plant taxonomic and functional diversity promotes interactions at multiple trophic levels and contributes to a wide range of ecosystem services (Mouillot *et al.* 2011; Soliveres *et al.* 2016). The relationship between the functional composition of plant communities and productivity or soil fertility services has been investigated (Mouillot *et al.* 2011; Gross *et al.* 2017), but less is known about the contribution of plant functional diversity to multitrophic interactions across trophic levels (Dassou & Tixier 2016; Gross *et al.* 2017; Koricheva & Hayes 2018), and to the resulting services, such as pest control.

In crop-dominated landscapes, species-rich habitats, such as spontaneously developing linear field margins and sown wildflower strips, support populations of arthropods, including predators, parasitoids and pollinators, beneficial to diversity across trophic levels (Wratten *et al.* 2012; Holland *et al.* 2017). These habitats provide overwintering sites to many organisms (Griffiths *et al.* 2008), refuges protecting populations of predators and parasitoids against disturbances in the vicinity of cropped habitats, together with the food resources required for completion of their life cycles (Gardarin *et al.* 2018).

The plant functional composition of flower strips determines how they can impact natural enemies (van Rijn & Wäckers 2016; Mei *et al.* 2021) and biological control (Wäckers, van Rijn & Bruin 2005), especially depending on the food resources they provide. These resources consist of floral and extrafloral nectar, pollen, honeydew supplying energy and nutrients. Plants in flower strips can also harbour alternative prey when they are not present in the crop. For instance, wild legumes can serve as a reservoir for *Acyrtosiphon pisum* (Kordan *et al.* 2018). *A. pisum* is parasitised by cornerstone “generalist” parasitoids (Stary & Havelka 2008), such as *Aphidius spp.* and *Praon spp.* (Ichneumonidea, Braconidae) and this aphid can serve as a prey for various predators (Harwood & Obrycki 2005). These alternative prey help to establish and maintain predator and parasitoid populations when there is no aphid in the crop. This allows early colonisation of the crop by natural enemies as soon as pest aphids arrive in the crop. These alternative prey do not necessarily represent reservoirs of aphids pests towards the crop (Vialatte *et al.*, 2007).

These habitats have a generally positive effect on populations of natural enemies (Begg *et al.* 2017) and flower strips increase pest control, with an exponentially decreasing intensity with distance from them (Albrecht *et al.* 2020). However, these effects are highly variable, which limits the reliability and robustness of biological control strategies (Begg *et al.* 2017). This variability is not explained by the flower strip *per se*, but by its botanical composition. For instance, the cover and richness of wildflowers in field margins best explain ground-dwelling natural enemies (Mei *et al.* 2021). There are several hypotheses according to which species richness of plant communities has bottom-up effects on the abundance and diversity of higher trophic levels, such as predators. Indeed, increases in plant species richness may provide more niches for consumer species, promoting niche complementarity and lowering competition, thereby increasing consumer diversity, particularly if the species concerned have different ecological requirements (Potts *et al.* 2004; Ebeling *et al.* 2018; Goulnik *et al.* 2020).

An increase in plant species richness can result in a higher functional diversity, but very few studies have, however, experimentally manipulated the taxonomic and functional diversity of plant communities, and compared the simultaneous effects of such manipulations on biological control. The few results published to date suggest that high plant functional diversity alone does not necessarily result in abundant, diversified communities of aphid predators (Balzan, Bocci & Moonen 2014; Hatt *et al.* 2017b), and that the amount of flower resources, here available nectar provided by sown and unsown species among the observed vegetation, plays a predominant role. There is no consensus concerning the relative importance of plant community species composition and functional structure (Costanzo & Barberi 2014) for multitrophic interactions and biological control (Gagic *et al.* 2015; Garibaldi *et al.* 2015).

The objective here was, therefore, to distinguish between the respective influences of taxonomic richness, functional diversity and dominance effects of plants providing nectar and alternative prey on the dynamics of aphid populations, widespread insects affecting a large range of crops (Dedryver, Le Ralec & Fabre 2010). A field experiment was performed in which the plant community composition of flower strips was manipulated and assessed their contribution to the seasonal dynamics of aphids over a four-year crop rotation. The relative effects of the plants providing nectar and alternative prey, species richness and functional dispersion (as a measure of functional diversity) were investigated on predator/aphid ratios, aphid parasitism and on the temporal dynamics of aphid populations.

A hypothesis (H1) was that the cover of plants, in flower strips, providing accessible nectar to natural enemies would increase predator-prey ratios and aphid parasitism rates (Heimpel 2019), thereby limiting aphid population growth in the crop (Ammann *et al.* 2022). Wild legumes (Fabaceae) in flower strips would also improve predator-prey ratios and aphid parasitism rates (H2) as these plants support alternative hosts and alternative prey for aphid parasitoids and predators (Ramsden *et al.* 2015). In addition to the effect of nectar and alternative hosts and prey provisioning, a positive effect of functional dispersion on predator-prey ratio and on aphid parasitism (Ebeling *et al.* 2018), and a negative effect on the dynamics of aphid populations, were expected (H3). Since diversity effects were supposed to be explained by the functional dispersion of plant traits involved in interactions with insects, no additional effect of richness was expected (H4). Finally the effects of flower strips should be greater close to the strips rather than further out in the field (H5; Albrecht *et al.* 2020).

Materials and methods

Design of species mixtures with contrasting species and functional diversities

Eight mixtures of native and perennial plants were designed (Supplementary methods), differing in terms of species richness (low, medium or high), diversity of the traits involved in plant-arthropod interactions (low or high) and species identity (two sets of species). The chosen traits are involved in plant-arthropod interactions and were easily accessible in databases (Table S1): (1) flower resources, i.e. floral and extrafloral nectar or pollen, (2) accessibility of the resource, depending on flower shape, (3) temporal availability of the resource, i.e. the duration of the flowering period and (4) height of the plant at flowering.

Seed mixtures were constituted with commercial seeds (Table S2), with ecotypes of local origin (northern part of the Parisian Basin, France) where possible. Within each mixture, the species were

present in the same proportions in terms of seed numbers, based on the measured thousand-seed weight of each batch of seed. These different mixtures were used to create gradients of species richness and functional dispersion. In the main text, we focus on their analysis via continuous descriptive variables to characterise the resulting plant communities. All applicable international, national, and institutional guidelines relevant for the use of plants were followed.

Experimental design

The experiment was conducted between 2013 and 2017 in two adjacent 6.5 ha fields (fields A and B, Fig. 1) at Grignon, France (48.837°N, 1.956°E), on a deep loamy clay soil. Each field was divided into three blocks running north to south. In each field, each mixture was sown in October 2013 on a 6×44 m² strip, with three replicates (Fig. 1), with each mixture represented once per block. A control treatment, sown with the same crop species as the rest of the field, and managed similarly, was also included in the experimental design, resulting in nine experimental treatments per block. The strips were mown once a year in November, and residues were removed.

From the autumn of 2013 to the 2017 harvest, the crop rotation in field A was winter barley – maize – faba bean – oilseed rape, whereas that in field B was maize – spring pea + spring barley intercrop – oilseed rape – wheat. Crops were managed without insecticide treatment, but with a mean of 0.75 fungicide and 1.25 herbicide treatment frequency index each year (sum, for each product, of the applied dose divided by the dose recommended by the national regulation). For comparison, the mean annual TFI (all products) for all the crops grown in the experiment was 4.9 in the study area. No ethical approval was required for the conduct of this study.

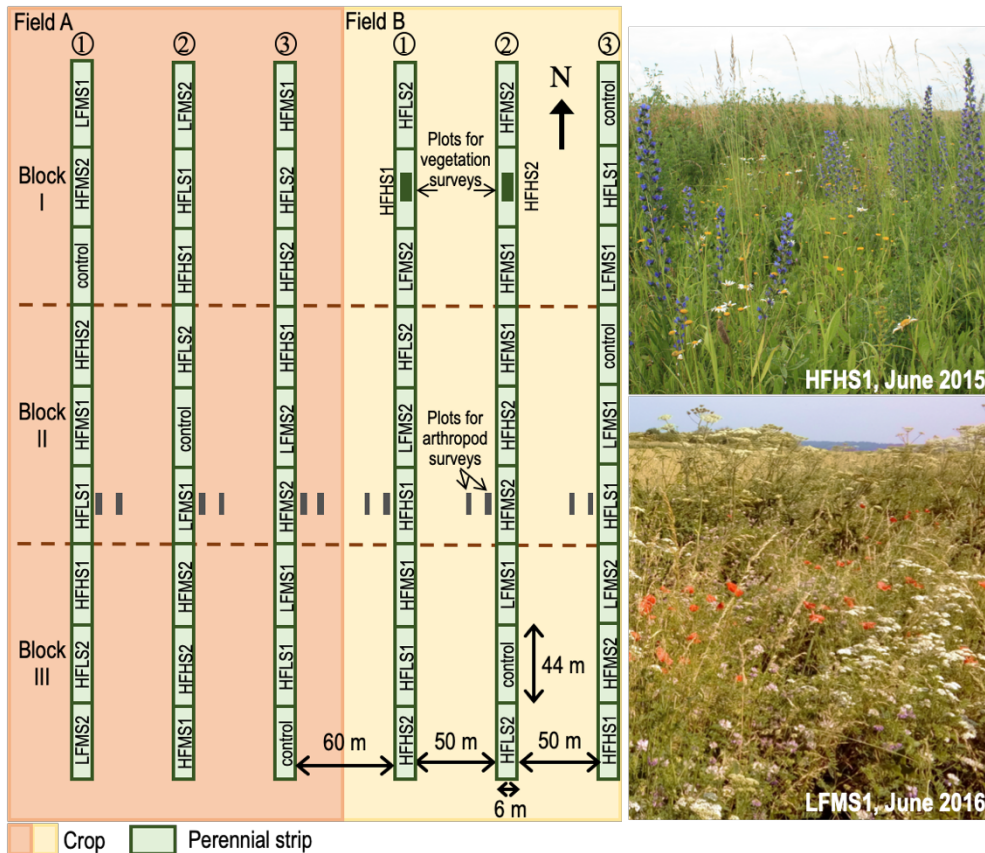


Figure 1. Design of the experiment (left), which was duplicated in two adjacent fields (A and B), grown with two different crops between 2013 and 2017, and illustration of different plant mixtures (right – Photo credit: A. Gardarin). In the perennial flower strips, the eight plant mixtures had a low or high functional diversity (LF or HF), a low, medium or high species richness (LS, MS or HS) and were composed of species from two different lists (1 or 2). They were compared with a control plot sown with the crop.

Assessment of densities of aphids, their predators and parasitism rates

In the adjacent fields, over the whole rotation, at 5 and 20 m from each wildflower strip, the densities of aphids and their antagonists were assessed, at one to three sampling dates in spring and summer, during the peak abundance of these species. The distance close to the strip (5 m) was chosen to prevent confounding effects with other nearby strips, as the effect of flower strips is known to be strongest in the first few metres of the field adjacent to them (Albrecht *et al.* 2020). Assessments were also made further away from the flower strip (20 m) to determine whether the strips promoted biological control at field level, while taking into account the spatial constraint of the distance between strips (50 m between opposing strips). Sampling methods were adapted to each crop and aphid species and are detailed in the Supplementary methods (Assessment of aphid populations, of their parasitism rate and of their predators). Briefly, at each distance, aphids, their predators (mainly Syrphidae, Coccinellidae and Chrysopidae) and mummies were counted by a meticulous visual examination of randomly chosen plants, or with a D-vac in the case of highly mobile organisms (Staphylinidae) on faba bean. At each distance, strip and date, we surveyed 10 plants in maize, 20 tillers in winter wheat, winter and spring barley, 20 plants in spring pea and in oilseed rape and 40 plants in faba bean.

Aphid and natural enemy abundances were close to zero on all plots for winter barley (2014, field A), maize (2015, field A) and oilseed rape (2017, field A). Only the five remaining crop×year trials in which aphid infestations and natural enemies occurred were therefore analysed. For each date, the abundances of predators were summed across taxonomic groups, and predator-prey ratios were calculated by dividing the summed abundance of predators by the number of aphids (total across aphid species, where applicable) on each cropped species. Aphid parasitism rate was estimated by dividing the total number of living mummies (no adult parasitoid exit hole) by the total number of aphids and living mummies. The growth rate r of aphid populations between the two successive counts (except for maize, for which there was only one count) was calculated as follows:

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

N_t is the number of aphids at date t , N_{t+1} is the number of aphids at date $t+1$ and Δt is the number of days between two observations (generally 14 days).

Botanical assessments and functional characterisation of plant communities

Botanical assessments were conducted in each year, in June. For each flower strip, the vegetation was assessed in $3 \times 15 \text{ m}^2$ permanent plots located within a representative position of the strip, 1.5 m from each edge to avoid the interface zone between the crop and the strip. The percentage of the ground covered by each sown or spontaneously growing plant species (weeds) was estimated by eye, by a single observer, over the whole experiment. In the control plots (sown with the crop species only), the nectar provided by weed species was taken into account. The production of extrafloral nectar (*Centaurea cyanus*, *C. scabiosa* and *Vicia sativa*) was also noted by observing the floral buds or all the stipules on 10 randomly chosen plants per treatment every two weeks between early March and late June. No secretion of extrafloral nectar was observed on the cropped *Vicia faba*.

The functional characterisation of plant communities was based on the plant traits assumed to be involved in plant-arthropod interactions (Gardarin *et al.* 2018). The corresponding hypotheses are summarised in Supplementary Table S3. These traits were related to the provision of food resources, the temporal availability of the resource, flower attractiveness, nectar accessibility and

the provision of physical habitats. The trait database used for creating the plant mixtures was expanded with measurements of additional traits that were not available in the literature, like flower morphological traits (so that trait values corresponded to the really observed plants during the experiment).

Traits were collected and measured for all 151 sown and spontaneously occurring species in the plant communities (Gardarin, Pigot & Valantin-Morison 2021). All traits relating to flower morphology, phenology and nectar provision were measured. The traits used to calculate functional dispersion, as a measure of functional diversity, were flower colour and UV reflectance pattern, leaf distribution, vegetative and flowering height which were retrieved from previous publications and online databases. Overall, for the traits measured and retrieved from databases, the trait matrix was complete for more than 95% of the species, accounting for 99.6% of total plant cover.

On the basis of the botanical surveys and the measured traits, four explanatory continuous variables were calculated to describe the provision of nectar resource, alternative hosts and prey, plant functional dispersion and plant species richness (Table 1).

Table 1. List, meaning and method of calculation of the continuous variables used to describe the plant communities of the flower strips.

Variable name	Proxy of...	Description	Calculation	Range of variation
Nectar resource	The most limiting food resource	Cover of plants (%) providing available and accessible nectar to predators and parasitoids.	The cover of flowering plants (%) providing accessible nectar to predatory Syrphidae, Coccinellidae, Chrysopidae and aphid parasitoids was determined based on a morphological model matching flower size and the size of the head and mouthparts of insects (Supplementary methods). These metrics included plants producing extrafloral nectar, with no constraint of accessibility. This approach was previously developed to assess nectar accessibility for parasitoids of coleopteran pests of oilseed rape and faba bean (Gardarin, Pigot & Valantin-Morison 2021). Ten to 36 of the 110 plant species observed, depending on the year and crop species, produced nectar that was available during the period of aphid counting and accessible to natural enemies according to the trait-matching approach (Table S5). Except for <i>Vicia sativa</i> producing extrafloral nectar, Fabaceae did not provide accessible nectar to natural enemies.	18.2 ± 20.3
Legume cover	Alternative prey and hosts, being another food resource	The Fabaceae cover in the strips (%) was used as a proxy of plants providing alternative hosts and alternative prey for aphid parasitoids and predators.	The percent cover of legume species was summed, as all species are potentially hosts of <i>Acyrtosiphon pisum</i> (Van Emden 2017).	11.1 ± 17.1
Functional dispersion	Plant functional diversity	Functional diversity is a conceptual variable that was characterised here through the species which best reflect niche diversity.	Functional dispersion is the abundance-weighted mean distance (Gower distance) of individual species from the centroid of all species in the trait space (Laliberté & Legendre 2010). It was calculated on the basis of all the previously described traits (Table S3). Due to the experimental design, functional dispersion was not independent of species richness. The functional dispersion was estimated independently of species richness, by standardising it according to species richness with null models (see Supplementary methods).	-0.78 ± 1.25
Species richness	Plant taxonomic diversity	Number of plant species recorded during the botanical assessments		17.3 ± 10.1

Statistical analyses

Effect of crop type, type of sown seed mixture and distance from the flower strip on aphid abundance, aphid growth rates, predator-prey ratio and parasitism rate

In a preliminary analysis, the effects of the type of mixture as a factor (varying according to sown species richness and diversity of functional traits), distance to the strip (factor) and their interaction were investigated on four kinds of response variables: aphid abundance, aphid population growth rate, predator-prey ratio and aphid parasitism (details in Supplementary information). Since the species diversity and functional diversity varied during the experiment (Figure S1), this approach is not developed in the main text. In general, the statistical models were better supported (lower AIC) for plant communities described in terms of the resources (nectar and alternative hosts and prey) they provided and diversity (approach described below), rather than mixture types as factors (Supplementary results).

Effects of nectar resources, legume cover, species and functional dispersion in flower strips on predator-prey ratios, aphid parasitism rates and population growth rates

Then, analyses investigated whether food resources (nectar and legumes supporting alternative hosts and prey) and diversity in flower strips affected predator-prey ratios, aphid parasitism rates and the temporal dynamics of aphid populations. Two explanatory variables were related to the dominance of plants providing resources to predators and parasitoids, i.e. (1) percentage of plant cover providing available and accessible nectar as an energy source, and (2) percentage of legume plant cover, hosting aphids as alternative hosts and prey. Two other variables were related to plant diversity, i.e. (3) observed plant species richness as a measure of taxonomic diversity and (4) observed plant functional dispersion as a measure of functional diversity, the latter being a broader concept (Table 1). The models also included the first-order interaction between these four variables and distance to the strip, an interaction between nectar resources and functional dispersion, distance to the strip (factor) and plot number nested within transect number as a random effect. The “nectar resource” variable was not included in the case of faba bean crop because the main predators (Staphylinidae and Araneae) do not feed on nectar and because no parasitism has been observed. The continuous explanatory variables were standardised to account for the large differences in scale between them.

Analyses were performed for all the crops studied, separately at each counting date. When there were several counting dates, parasitism was analysed only on the second date, because parasitism rates were low or undetectable at the first counting. Generalised linear mixed models were used (lme package, Bates *et al.* 2015), assuming a negative binomial error distribution for predator-prey ratios, a binomial error distribution for parasitism rate and a Gaussian error distribution for aphid population growth rates. A multimodel inference procedure was used (Burnham & Anderson 2002) to test models including all possible combinations of the fixed-effect predictors, ranked according to the Akaike information criterion fitted by maximum likelihood methods. Models with a $\Delta\text{AIC} < 4$ were selected and the results for the conditional averaged model are presented. Pseudo- R^2 was calculated with the *r.squaredGLMM* function. The distribution of model residuals (normality, homoscedasticity and outliers) was checked and confirmed with the DHARMA package (Hartig 2019). Statistical analyses were performed with R software version 3.1.3 (R Development Core Team, 2015).

Results

Flower strip establishment

The sown mixtures were generally well established. The plant communities contained a total of 85 species over all the surveyed plots (54 flower strips \times 15 m² plots per strip), including 41 of the 55 sown species. On average over the four years, the sown species accounted for 92.8% of total plant cover. About two thirds of the sown species persisted in the fourth year of the experiment. After sowing, plant communities were well and remained differentiated in terms of observed species richness and functional dispersion (Fig. S1).

Effect of crop type, type of sown seed mixture and distance from the flower strip on aphid abundance, aphid growth rates, predator-prey ratio and parasitism rate

At peak aphid levels, their abundance was low in maize (mean \pm SE = 7 ± 6 aphids/plant), spring barley (2 ± 1 aphids/tiller) and winter wheat (1 ± 0.5 aphid/tiller, Fig. S4). Infestation was moderate in faba bean (5 ± 2 aphids/plant) and spring pea (6 ± 4 aphids/plant). Large, dense colonies were observed in oilseed rape (909 ± 325 aphids/plant). In general, aphid populations were smaller at 5 m from the flower strips than those at 20 m and aphid population growth rates were lower at 5 m than at 20 m (Supplementary results).

At peak aphid levels, predator abundance was very low in wheat (mean \pm SE = 0.03 ± 0.03 predators/tiller), intermediate in oilseed rape (0.1 ± 0.2 predators/plant), faba bean (0.2 ± 0.2 predators/plant) and in the spring pea+barley intercrop (0.2 ± 0.2 predators/plant or tiller), and it was the highest in maize (1.9 ± 0.8 predators/plant). In oilseed rape, wheat and the pea-barley intercrop, predator populations were dominated by Syrphidae larvae (89, 90 and 90% of all predators, respectively, on both dates). In maize, the predators belonged to Chrysopidae (56%) and Coccinellidae (36%), whereas Staphylinidae (66% of all predators on both dates) and Araneae (17%) predominated in faba bean.

No parasitism was observed in faba bean, and parasitism rates were very low in oilseed rape (mean of $0.07\% \pm 0.09$), moderate in pea ($3.0 \pm 2.6\%$), barley ($3.6 \pm 8.3\%$) and wheat ($3.8 \pm 5.7\%$) and highest in maize ($7.9 \pm 10.3\%$; Fig. S6).

Effects of distance, nectar resources, legume cover, plant species richness and functional dispersion on predator-prey ratios and aphid parasitism rates

For both response variables, distance to the flower strip, the percentage of plant cover providing nectar resources and legume cover (supporting alternative hosts and prey) in the strips were the 3 variables, alone or in interaction, most frequently selected by multimodel inference and with the highest Akaike weight (Tables 2 and 3). Distance had a negative effect when significant, except for the predator-prey ratio in the intercrop (date 2) and for aphid parasitism in oilseed rape. Plant species richness was rarely selected in the best models, except for a positive effect on aphid parasitism in pea ($p\text{-value}=4.16 \cdot 10^{-4}$).

Table 2. Effects of the amount of nectar resources, legume cover, plant species richness and functional dispersion in flower strip plant communities and distance to the flower strip on predator-prey ratio. All possible combinations of the fixed-effect variables and their interactions were tested and results for the averaged best models ranked according to their AIC are presented. Only the slopes for variables with a significant or marginally significant effect or with an Akaike weight > 0.70 are reported. The full results are provided in Supplementary Table S10.

	Maize 2014	Spring barley + pea 2015		Faba bean 2016		Oilseed rape 2016		Wheat 2017	
	–	Date 1	Date 2	Date 1	Date 2	Date 1	Date 2	Date 1	Date 2
Distance 20 m (ref=5 m)	-0.301 ***	0.099	0.434 **	-0.505 ***			0.174		-1.163 **
Nectar resource		0.351 •		–			0.577 ***		0.277
Nectar resource × Distance 20 m				–			0.452 ****		
Nectar resource × Functional disp.	-0.372 •	0.410 *		–			-0.603 ****		
Legume cover	0.203 •						0.296 **		
Legume cover × Distance 20 m		0.517 *					-0.872 ****		
Species richness		-0.386 •							
Functional dispersion	-0.299 *								
Functional disp. × Distance 20 m							0.988 ****		

• $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 10^{-3}$, **** $p < 10^{-4}$; nectar resources were not tested in faba bean due to the absence of nectar feeding predators.

Table 3. Effects of the amount of nectar resources, legume cover, plant species richness and functional dispersion in flower strip plant communities and distance to the flower strip on parasitism rate. See the legend to Table 2 for more details on the method. The full results are provided in Supplementary Table S11.

	Maize 2014	Spring barley 2015	Spring pea 2015	Faba bean 2016	Oilseed rape 2016	Wheat 2017
Distance 20 m (ref=5 m)	-0.562 **	-0.737	-0.036 ****	not run,	0.791 ****	-1.340 ***
Nectar resource	0.502 *			no	0.531 •	
Nectar resource × Distance 20 m	-0.536 *			parasitism observed	-0.530 ***	
Nectar resource × Functional disp.		-0.872 •				
Legume cover	0.663 **	1.203 •	0.130 ****			
Legume cover × Distance 20 m	-0.892 **					
Species richness	0.161		0.167 ***			
Functional dispersion	-0.756 ***					
Functional disp. × Distance 20 m	0.863 **					

The cover of plant providing nectar increased predator-prey ratios significantly in oilseed rape (p-value= $1.78 \cdot 10^{-4}$) and marginally in the pea-barley intercrop (p-value=0.089; Table 2). The effect of nectar resources depended on the level of plant functional dispersion, with a positive interaction in the pea-barley intercrop (p-value=0.047) and with negative interactions in oilseed rape (p-value $<10^{-4}$) and in maize (p-value=0.062). As a result of these interactions, nectar resources increased predator-prey ratios at low (maize), at medium and high (pea-barley intercrop), or at all (oilseed rape) levels of functional dispersion, depending on the crop (Fig. 2). Increasing legume cover in the flower strips also significantly increased predator-prey ratios in the pea-barley intercrop (20 m), in maize (trend) and in oilseed rape (Table 2).

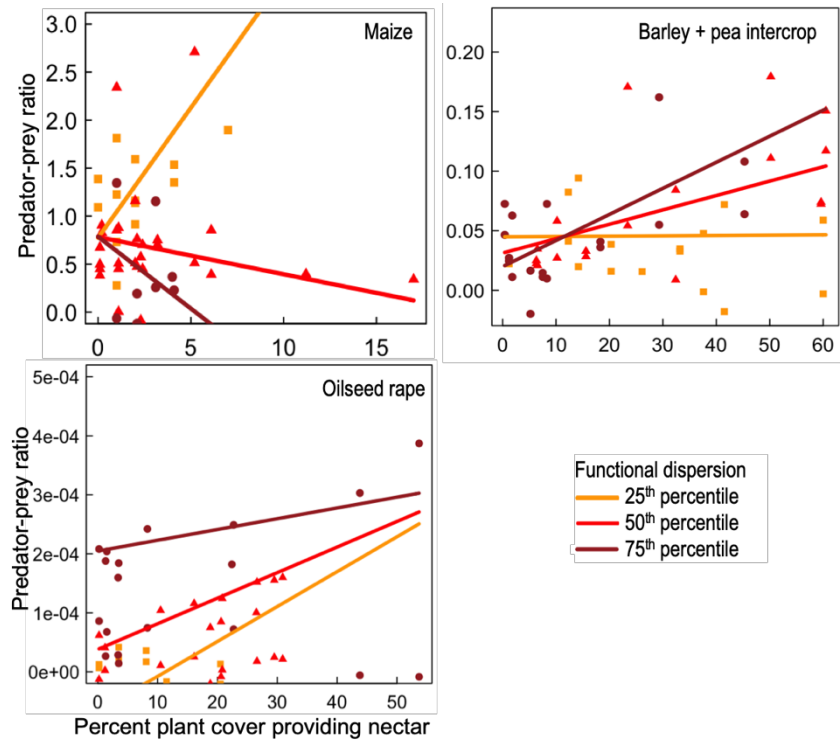


Figure 2. Effect of the percentage of plant cover providing accessible nectar to predators and functional dispersion on the predator-prey ratio in three crops where the interaction between these variables was significant or marginally significant. Partial regression plots were obtained with a generalised mixed model. The line represents the fixed-effect prediction with the best model and the partial residuals are shown by points. Regression lines are drawn for different levels of plant functional dispersion in flower strips: low (orange squares), medium (red triangles) and high (brown circles).

The effect of nectar resources on parasitism rates was more weak. For instance, there was only a positive in maize at 5 m (p -value=0.033), and a positive trend in oilseed rape at 5 m (p -value=0.078, Table 3). Aphid parasitism rates increased with the percentage of legume cover in the strips in maize (p -value=0.009), pea (p -value $<10^{-4}$) and barley (p -value=0.076, Fig. 3).

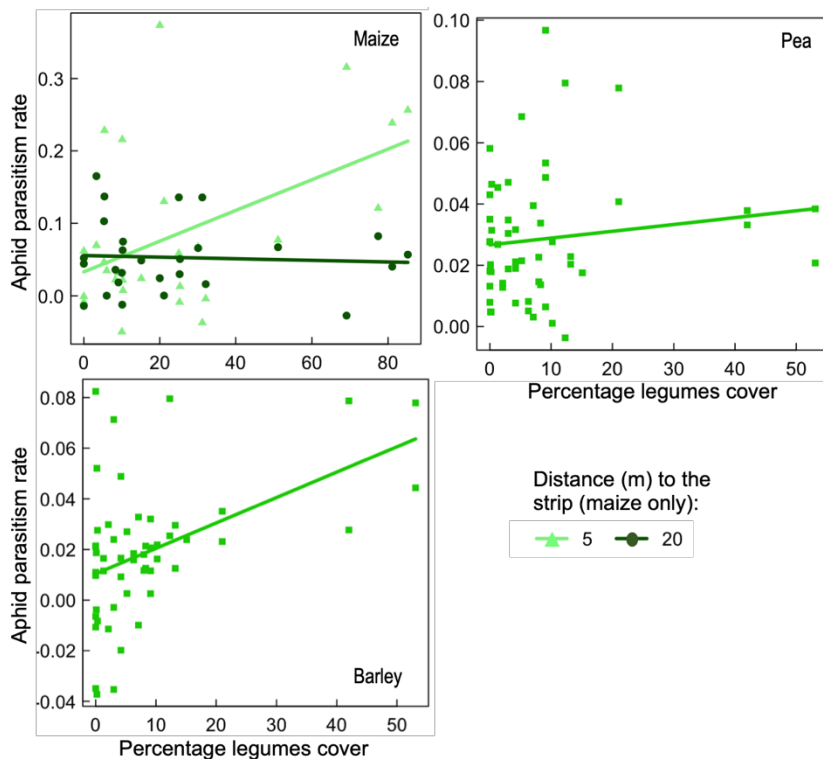


Figure 3. Effect of the percentage of legume cover in the flower strips on aphid parasitism rate in three crops in which this effect was significant or close to significance (Table 3). Partial regression plots were obtained with a generalised mixed model. The line represents the fixed-effect prediction with the best model and the partial residuals are shown as points. Regression lines are drawn for the two distances in maize (5 and 20 m from the strip, light green triangles and dark green circles, respectively) since an interaction between legume cover and distance has been found.

Effect of distance, nectar resources, legume cover, plant species richness and functional dispersion on the growth rates of aphid populations

Increases in the percentage of cover of plants providing accessible nectar resources had a negative effect on aphid population growth rates (Table 4, Table S12) in oilseed rape (p-value=0.028) and spring barley at 20 m (p-value=0.036). Finally, at 20 m from the strips, aphid population growth was negatively affected by increasing plant species richness in spring pea (p-value=0.031) and increasing plant functional dispersion in spring barley at 20 m (p-value =0.045), suggesting a better regulation of aphid populations.

Table 4. Effects of nectar resources, legume cover, plant species richness and functional dispersion of the flower strip plant communities and distance to the flower strip on aphid population growth rates between the two successive counts. See the legend to Table 2 for more details on the method. The full results are provided in Supplementary Table S12.

	Maize 2014	Spring pea 2015	Spring barley 2015	Faba bean 2016	Oilseed rape 2016	Wheat 2017
Distance 20 m (ref=5 m)	not run	0.006	-0.018***			No
Nectar resource	–			–	-0.076*	significant
Nectar resource × Distance 20 m	–	-0.344•	-0.010*	–		variable
Legume cover	–				0.023	nor with
Legume cover × Distance 20 m	–	-0.006•	-0.008•		-0.095•	Akaike
Species richness	–	-0.002				weight
Species richness × Distance 20 m	–	-0.008*				> 0.70
Functional dispersion	–		0.007			
Funct. dispersion × Distance 20 m	–		-0.010*			

Discussion

This study investigated the effects of food resources (nectar and legumes supporting alternative hosts and prey, H1 and H2), plant functional dispersion (H3) and plant species richness (H4) within plant communities, which were manipulated experimentally, on the ability of the flower strips to support biological control of aphids infesting six different crops, over a crop rotation. Such effects were not systematically observed in previous studies (Balzan, Bocci & Moonen 2016; Serée *et al.* 2022). Here, the percentage of plant cover providing resources to natural enemies (nectar and alternative hosts and prey) generally increased predator-prey ratios and aphid parasitism. The effects of plant species richness and plant functional dispersion were less clear. However, the significance and strength of these effects differed between crops. Most experimental studies of flower strips have assessed their effects on a limited number of pests and crops. By contrast, this study reveals general patterns for multiple pests at the scale of the crop rotation.

Food resources in wildflower strips promote aphid natural enemies and limit aphid population growth rates

Flower strips are known to have a positive, but highly variable effect on biological control (Albrecht *et al.* 2020). Here, this effect was mediated largely by the provision of food to natural enemies. These results tend to validate the initial hypotheses (H1 and H2) that the dominance of plant cover providing nectar, and hosting alternative prey to natural enemies (legumes), would

increase predator-prey ratios and aphid parasitism rates, thereby reducing aphid population growth rates.

A greater percentage cover of plants providing available and accessible nectar to predators (Syrphidae) increased predator-prey ratios in oilseed rape (and a trend in the pea-barley intercrop), and it reduced aphid population growth rates in oilseed rape and barley. Nectar is known to increase syrphids longevity, reproduction and dispersal (Wäckers, van Rijn & Bruin 2005; van Rijn & Wäckers 2016) as well as their abundance in field crops (Serée *et al.* 2022). In maize, there was no effect of nectar resources estimated for the main predators (Coccinellidae and Chrysopidae). At adult stage, ladybugs and lacewings are less restricted to nectar than syrphids and feed on pollen (Robinson *et al.* 2008), being more easily accessible than nectar. The range of variation in accessible nectar was also smaller for this crop than for the others, which may have limited our ability to measure its effect.

Nectar resources increased aphid parasitism rates in maize at 5 m, but these effects were cancelled at 20 m, perhaps due to a poor dispersal of parasitoids. In oilseed rape, results on parasitism rates should be interpreted with caution considering their very low values. The nectar provided by plants is not always exploited by parasitoids, which can feed on honeydew (Luquet *et al.* 2021) and this could explain the lack of effect in the other crops.

Alternative hosts for aphid parasitoids and alternative prey for predators can serve as complementary food increasing the abundance of natural enemies with a wide feeding niche and facilitating early-season pest control (Evans 2008). As a proxy for plants providing alternative prey, increases in the percentage of legume cover in flower strips would improve predator-prey ratios and aphid parasitism rates, as wild plants of this family regularly support aphid populations (Kordan *et al.* 2018). The corolla shape of the flowers of plants from this family results in the nectar not being accessible to predators and parasitoids (van Rijn & Wäckers 2016). Overall, increases in the percentage of Fabaceae cover increased predator-prey ratio (in the pea-barley intercrop, oilseed rape), and aphid parasitism rate (in maize, spring pea). Since aphids were not quantified in flower strips, it cannot be unequivocally attributed to the provision of alternative hosts and prey, but this finding is consistent with the hypothesis that legumes present in wildflower strips can act as reservoirs for aphids, sustaining populations of predators and parasitoids (Evans 2008; Ramsden *et al.* 2015).

The effect of nectar and legumes on predator-prey ratios and parasitism rates could explain the lower population growth rates of aphids in oilseed rape, spring barley. This study validates the positive contribution of flower strips to aphid biological control (Hatt *et al.* 2017a; Toivonen, Huusela-Veistola & Herzon 2018) in several arable crops at the scale of a rotation.

The secondary role of plant species richness and functional dispersion

The effects of plant species richness and functional dispersion were more contrasted and crop-specific. Functional dispersion had a positive effect only on predator-prey ratio in oilseed rape (20 m) and in the pea-barley intercrop when nectar resources were abundant (positive interaction). These findings are consistent with the hypothesis that functional dispersion would enhance the use

of nectar resources in flower strips (H3), with several possible explanations. High functional dispersion is more likely to provide the full range of resources and conditions required by predators to complete their cycle, and it can decrease negative interactions between predators (Finke & Denno 2006; Wilby, Anglin & Nesbit 2013).

Conversely, plant functional dispersion had a negative effect on predator-prey ratio and parasitism rates in maize. Analyses of predator-prey ratios revealed that plant functional dispersion also interacted negatively with nectar resources in oilseed rape and marginally in maize. This suggests that a high functional dispersion would “dilute” the relative importance of the plants producing nectar exploited by predators (and having a positive mass effect) among other plants providing unexploited resources. High dispersion probably also favoured the fourth trophic level, which includes hyperparasitoids, thereby disrupting aphid control by primary parasitoids, as shown for crop diversification (Jeavons *et al.* 2021). Indeed, Campbell *et al.* (2012) previously reported that rates of flower visitation by parasitoids were highest in stands of plants bearing only flowers with short corollas, and that these rates were much lower in plant stands bearing flowers with more diverse traits, due to higher levels of competition with bumblebees and hoverflies. Unfortunately, in the absence of data on flying parasitoids, this hypothesis could not be tested here.

Limits and perspectives

Despite a major effort to characterise plant communities from a functional perspective, part of the variability in predator abundance, parasitism and aphid dynamics remained unexplained. Beyond the provision of nectar, the sugar composition of nectar resources, which varies considerably between plant species, was not taken into account (Heimpel & Jervis 2005). The sugar composition of nectar affects pollinator preferences (Vattala *et al.* 2006) and nutritional quality (Lee *et al.* 2004). The role of epigeous predators, like carabids and spiders, being important aphid predators, was also largely ignored. These predators may also have responded to the gradients of flower resources and diversity in the flower strips (Brose 2003; Mei *et al.* 2021) and may also have contributed to aphid control (Ribeiro & Gontijo 2017). In wheat, no explanatory variable related to flower strips (except distance) explained predator/prey ratio, parasitoids and aphid dynamics. The very low aphid number on this crop, together with sporadic predators and mummies might have prevented us from detecting any flower strip effect. In addition, the range of plants providing nectar was narrow in comparison with other crops (from 0 to 26%), which could have limited the effect of nectar provision.

In general, flower strips increased predator/prey ratios, parasitism and decreased aphid abundance more at 5 m than at 20 m in the field. This could reflect a limitation of our experimental design. The treatments were close together and the distance to the different types of strip was more similar in the central parts of the field. We cannot exclude the possibility of confounding effects between adjacent flower strips. More generally, the pest control service also decreases exponentially with the distance to flower strips or hedges (Albrecht *et al.* 2020). To be efficient towards biological control, flower strips should therefore be implemented at regular intervals within fields, or next to small fields (Sirami *et al.* 2019). Weed management could also be adapted as some weeds can provide useful flower resources and contribute to increased pest parasitism (Serée *et al.* 2023).

Conclusion

This study investigated the simultaneous effects of plant species richness and functional composition on the ability of flower strips to support aphid natural enemies and to reduce aphid growth rates. The provision of nectar and alternative hosts and prey to natural enemies had a predominantly positive effect on these variables. Based on trait-matching between plants and insects (Ibanez 2012; Deraison *et al.* 2015), links were established between the functional composition of plant communities and the functions delivered by insect communities, in this case, the regulation of aphid populations. Matching traits have already been shown to be relevant to predict food web interactions, and they also have cascading effects on an ecosystem service here.

Functional dispersion and plant species richness also influenced natural enemies, but the direction of the effects observed was crop-specific, and there was an interaction with the dominance of plants providing nectar resources. It is, therefore, difficult to make general statements about the positive or negative role of plant diversity on interactions with higher trophic levels, as in other studies (Balzan, Bocci & Moonen 2014; Balzan, Bocci & Moonen 2016; Hatt *et al.* 2017b). Future studies should, therefore, try to clarify the circumstances and covariables modulating the effect of plant functional dispersion.

These results provide useful insight for the design of perennial plant mixtures for creating or restoring habitats supporting conservation biological control. These mixtures should not only include plants that flower, but they must produce nectar, being available when natural enemies need it, and being accessible to them according to their morphology and flower shape. Corollas with non-deep nectar often belong to Brassicaceae, Apiaceae and to some Asteraceae, but not only. Although they do not provide accessible floral nectar, wild legumes are also useful in attracting aphids and their related natural enemies, without promoting aphid colonisation of the adjacent crop (pea, faba bean). Our results on plant species richness and functional dispersion are ambiguous when analysing their effects on a crop-by-crop basis. However, crops have different growing cycles and are subject to aphid attacks at different periods of the year. For a flower strip to be adapted to a diversity of crops, this reinforces the need to design species mixtures with flowering periods that extend throughout the year. It does not suggest, however, that a diversity of other traits would be required.

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Data accessibility

The datasets generated during this study and analysed here are available from the Zenodo repository: <https://zenodo.org/record/6592207>.

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Supplementary information

Aphid conservation biological control in arable crops via flower strips: the predominant role of food resources over diversity effects

Gardarin A. (2023). Aphid biological control in arable crops via flower strips: the predominant role of food resources over diversity effects. *Journal of Applied Ecology*, 60: 2118–2131. <https://doi.org/10.1111/1365-2664.14495>

Appendix S1. Design of species mixtures with contrasting species and functional diversities

Species richness and functional diversity gradients were crossed orthogonally in an unbalanced design:

- Low functional diversity and medium species richness (14 species), LFMS;
- High functional diversity and low species richness (9 species), HFLS;
- High functional diversity and medium species richness (14 species), HFMS;
- High functional diversity and high species richness (29 species), HFHS.

The LFMS and HFMS mixtures aimed at testing the effect of plant functional diversity, independently of species richness, which was expected to increase predator-prey ratio, aphid parasitism and to reduce the dynamics of aphid populations. At high functional diversity (HF), the LS, MS and HS mixtures were used to assess if functional diversity effects remained similar whether richness was low, intermediate or high. The range of species richness was chosen to encompass the range of observed species richness in field margins in France (Alignier 2018; Fried, Villers & Porcher 2018). For each of these four categories, two mixtures with different species identities were designed, resulting in eight plant mixtures, to assess the genericity of species and functional diversity effects over communities with distinct taxonomic compositions.

Based on the BioFlor trait database (Kühn et al., 2004), plant species were classified into 12 functional groups (Table S1) according to their traits. As the interest was in mixtures enhancing conservation biological control, traits involved in plant-arthropod interactions, easily accessible in databases, were selected: (1) flower resources, i.e. floral and extrafloral nectar or pollen, (2) accessibility of the resource, depending on flower shape, (3) availability of the resource, i.e. the duration of the flowering period and (4) height at flowering. These traits were only used for creating the mixtures, but a larger range of traits has been used for the analyses presented in this study (see Materials and Methods).

The high functional diversity - medium species richness diversity (HFMS) mixtures were designed by choosing species from each of the 12 functional groups identified in Supporting information Table S1. The low functional diversity - medium species richness (LFMS) mixtures were obtained by reducing the number of functional groups to seven and increasing the number of species per group, so as to keep species richness constant. In the HFLS mixtures, only the species of the HFMS mixtures belonging to the most highly contrasting functional groups were retained, to obtain the highest diversity possible. Although the HFLS mixtures contain less functional groups (6) than the LFMS ones (7), the functional groups in the former are more contrasted than in the latter, with very early flowering species (functional group 9), short plant species (functional groups 8 and 9) and with species producing extrafloral nectar (functional group 10). In the HFHS mixtures, species richness was increased while keeping functional diversity as constant as possible by adding extra species with trait combinations closely resembling those already present in the HFMS mixtures.

The same three tussock grass species were added to each mixture, in similar quantities (Table S2).

The observed functional diversity in the sown mixtures was low and high, in the LF and HF mixtures respectively (Fig. S1), consistently with what was initially targeted (Gardarin & Valantin-Morison 2022).

Table S1. List of the plant functional groups included in the four types of mixtures (LF and HF mean a low or high functional diversity and LS, MS or HS mean a low, medium or high species richness respectively). Traits values were taken from the BiolFlor (Kühn *et al.*, 2004) and LEDA (Kleyer *et al.*, 2008) trait databases.

Functional group	Flower class after Müller	Flower type after Kugler (1970)	Month of flowering onset	Month of flowering end	Presence of nectar	Amount of pollen	Extra-floral nectar	Plant height	LFMS	HFLS	HFMS	HFHS
1	flowers with open nectar	disk flowers with nectar open	6-7	9	present	present	none	medium to tall	x	x	x	x
2	flowers with partly hidden nectar	disk flowers with nectar ± hidden nectaries at base of stamens	4	6	present	present	none	medium to tall	x	x	x	x
3	flower associations with totally hidden nectar	flower heads, Asteraceae, ray and disk flowers	6	9-10	present	present	none	medium to tall	x	x	x	x
4	flowers with open or partly hidden nectar	disk flowers with nectar open or nectar ± hidden in centre of flower	4-5	6-7	present	present	none	medium to tall	x		x	x
5	flowers with totally hidden nectar	stalk disc flowers, stamina and pistil within tube	5	7	present	present	none	medium to tall	x			x
6	flower associations with totally hidden nectar	flower heads, Asteraceae or non-Asteraceae	7	9-10	present	present	none	tall	x		x	x
7	hymenoptera flowers	flag blossom, Fabaceae type	6	7 to 9	present	present	none	medium to tall	x			x
8	hymenoptera flowers	flag blossom, Fabaceae type or true lip flowers	4-5	6 to 9	present	present	none	low		x	x	x
9	flowers with totally hidden nectar	several types	1 to 3	5	present	present	none	low		x	x	x
10	flower associations with totally hidden nectar or hymenoptera flowers	flower head or flag blossom	5 to 6	7	present	present	present	medium to tall		x	x	x
11	pollen flowers	pollen flowers	5 to 7	8 to 9	none	plenty	none	medium to tall			x	x
12	flowers with partly or totally hidden nectar	disk flowers with nectar ± hidden	5-6	8 to 9	present	present	none	medium to tall				x

Table S2. Composition of the eight mixtures differing in functional diversity and species richness.

Mixtures	LFMS1	LFMS2	HFLS1	HFLS2	HFMS1	HFMS2	HFHS1	HFHS2
Dicotyledonous species								
<i>Anthriscus sylvestris</i> (L.) Hoffm.	x						x	
<i>Arctium minus</i> (Hill) Bernh.	x						x	
<i>Foeniculum vulgare</i> Mill.	x						x	
<i>Hesperis matronalis</i> L.	x						x	
<i>Leucanthemum vulgare</i> Lam.	x						x	
<i>Medicago sativa</i> L.	x						x	
<i>Securigera varia</i> (L.) Lassen	x						x	
<i>Trifolium pratense</i> L.	x						x	
<i>Achillea millefolium</i> L.	x		x		x		x	
<i>Alliaria petiolata</i> Cavara&Grande	x		x		x		x	
<i>Heracleum sphondylium</i> L.	x		x		x		x	
<i>Cyanus segetum</i> L.			x		x		x	
<i>Trifolium repens</i> L.			x		x		x	
<i>Veronica hederifolia</i> L.			x		x		x	
<i>Centaurea scabiosa</i> L.					x		x	
<i>Euphorbia cyparissias</i> L.					x		x	
<i>Hypericum perforatum</i> L.					x		x	
<i>Tanacetum vulgare</i> L.					x		x	
<i>Verbascum densiflorum</i> Bertol.					x		x	
<i>Ajuga reptans</i> L.							x	
<i>Bellis perennis</i> L.							x	
<i>Capsella bursa-pastoris</i> (L.) Med.							x	
<i>Echium vulgare</i> L.							x	
<i>Galium odoratum</i> (L.) Scop.							x	
<i>Malva sylvestris</i> L.							x	
<i>Potentilla reptans</i> L.							x	
<i>Carum carvi</i> L.		x						x
<i>Cynoglossum officinale</i> L.		x						x
<i>Daucus carota</i> L.		x						x
<i>Hypochaeris radicata</i> L.		x						x
<i>Jacobaea vulgaris</i> L.		x						x
<i>Lotus corniculatus</i> L.		x						x
<i>Onobrychis viciifolia</i> Scop.		x						x
<i>Trigonella officinalis</i> (L.) Lam.		x						x
<i>Barbarea vulgaris</i> R. Br.		x		x		x		x
<i>Cota tinctoria</i> L.		x		x		x		x
<i>Pastinaca sativa</i> L.		x		x		x		x
<i>Medicago lupulina</i> L.				x		x		x
<i>Stellaria media</i> (L.) Vill.				x		x		x
<i>Vicia sativa</i> L.				x		x		x
<i>Cichorium intybus</i> L.						x		x
<i>Galium mollugo</i> L.						x		x
<i>Knautia arvensis</i> (L.) Coult.						x		x
<i>Plantago lanceolata</i> L.						x		x
<i>Verbascum lychnitis</i> L.						x		x
<i>Geum urbanum</i> L.								x
<i>Glechoma hederacea</i> L.								x
<i>Lamium album</i> L.								x
<i>Ranunculus repens</i> L.								x
<i>Reseda luteola</i> L.								x
<i>Taraxacum sect. Ruderalia</i>								x
Wiggers								x
<i>Veronica persica</i> Poir.								x
Poaceae								
<i>Arrhenatherum elatius</i> (L.) P.Beauv.	x	x	x	x	x	x	x	x
<i>Dactylis glomerata</i> L.	x	x	x	x	x	x	x	x
<i>Schedonorus arundinaceus</i> Schreb.	x	x	x	x	x	x	x	x

Table S3. Relationships between the plants traits used in this study and their functional significance toward plant-arthropod interactions.

Category	Trait (or plant strategy)	Type of trait	Functional significance
Provision of food resources	Amount of floral nectar	numerical	The carbohydrate and protein resources provided by plants increase the longevity, reproduction and dispersal of their consumers (Wäckers et al., 2005).
	Provision of extrafloral nectar	categorical	Extrafloral nectar is more easily accessible to arthropods with short mouthparts (Heimpel and Jervis, 2005). It generally has a higher sugar concentration than nectar (Lee et al., 2004).
Temporal availability of food resources	Week of onset of flowering	numerical	The phenological match between flowering period and arthropod floral resource requirements is crucial for completion of the life cycles of flower visiting arthropods (Welch and Harwood, 2014).
	Flowering duration	numerical	
Attractiveness of the food resource	Flower or inflorescence diameter	numerical	Visual signals, such as plant height, flower height, inflorescence size and colour, are involved in resource detection, and a high degree of visual attractiveness increases the abundance of natural enemies (Fiedler and Landis, 2007; Hatt et al., 2018).
	Basic flower colour	categorical	
	UV reflectance pattern	categorical	
Accessibility of the food resource	Nectar depth	numerical	A correlation between nectar holder depth and the proboscis length of the flower visitor has been observed in several insect groups, especially in pollinators. As a result, flower size is one of the most important variables determining the abundance and diversity of flower visitors (Heimpel and Jervis, 2005; van Rijn and Wäckers, 2016).
Provision of physical habitats	Leaf distribution	categorical	Plant structural traits shape arthropod habitats (Parolin et al., 2012). Plants with a complex morphology have higher invertebrate abundances and biomasses than plants with a simple morphology (Hansen et al., 2010).
	Flowering height	numerical	
	Raunkiær life form	categorical	

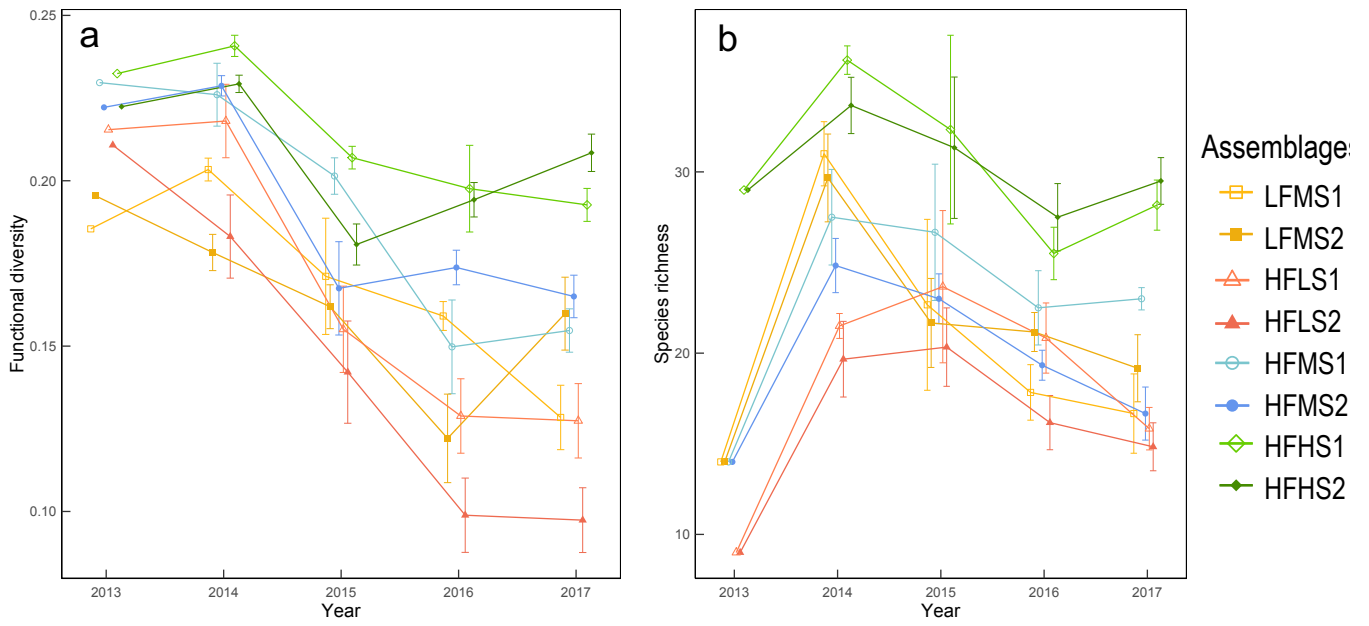


Figure S1. Dynamics of the functional dispersion (a) and species richness (b) of the eight sown plant mixtures (means \pm standard errors). The method for computing functional dispersion is described in the material and methods. The data for 2013 are based on the seed mixtures sown, and the data for the next four years were obtained from field observations. The eight plant mixtures have a low or high functional diversity (LF or HF), a low, medium or high species richness (LS, MS or HS) and are composed of species from two different lists (1 or 2).

Appendix S2. Assessment of aphid populations, of their parasitism rate and of their predators

Maize (field B 2014, field A 2015)

Aphids (dominant species: *Rhopalosiphum padi*), their predators and aphid mummies were counted by a meticulous visual examination on ten randomly chosen plants at each plot. A single counting was performed at anthesis (BBCH 55-63, mid-July). Sessile predators present on the plant were counted accordingly to their stage (i.e. egg, larva, pupa, and adult of Coccinellidae; egg, larva and pupa of Syrphidae; egg, larva and adult of Chrysopidae, Coniopterygidae and Hemerobidae).

Winter barley (field A in 2014) and winter wheat (field A in 2017)

Aphids (dominant species: *Sitobion avenae* and *Metopolophium dirrhodum*), their predators and aphid mummies were counted on 20 randomly chosen tillers at each plot. Counting occurred when ear emergence was complete (BBCH 59-60, early June) and three week later at dough stage (BBCH 83-85). Simultaneously, sessile predators present on the plant were counted accordingly to their stage (i.e. egg, larva, pupa, and adult of Coccinellidae; egg, larva and pupa of Syrphidae; egg, larva and adult of Chrysopidae and Hemerobidae).

Spring pea + spring barley intercrop (field B in 2015)

Counting occurred simultaneously for both cropped species at when ear emergence was complete (BBCH 59-60, early June) and three week later at dough stage (BBCH 83-85). On barley, aphids (dominant species: *Metopolophium dirrhodum* and *Sitobion avenae*) were counted by visually examining 20 randomly chosen tillers. On pea, aphids (*Acyrtosiphon pisum*) readily drop off plants when disturbed. The main stem of 20 randomly chosen plants was bent over a 600-cm² white plastic box and shaken to dislodge the aphids that were counted. Pea plant were then visually examined. Simultaneously, aphid mummies and sessile predators present were counted accordingly to their stage (i.e. egg, larva, pupa and adult of Coccinellidae; egg, larva and pupa of Syrphidae; egg, larva and adult of Chrysopidae and Hemerobidae).

Oilseed rape (field B in 2016, field A in 2017)

Aphid (*Brevicoryne brassicae*) abundance was estimated on the main raceme of 20 randomly chosen plants at two dates, i.e. at the beginning of flowering (in April, BBCH 60-61) and then at full flowering (in May, BBCH 65-66). In April, aphids were individually counted. In May, when colony size visually exceeded 1 cm length, the size of the colony was estimated by counting the number of aphids on one centimeter and multiplied by the length of the colony. Simultaneously, aphid mummies and sessile predators present were counted accordingly to their stage (i.e. egg, larva, pupa and adult of Coccinellidae; egg, larva and pupa of Syrphidae; egg, larva and adult of Chrysopidae).

Faba bean (field A in 2016)

Only *Acyrtosiphon pisum* aphids could be observed on the crop, together with highly mobile generalist predators, while no *Aphis fabae* and very few specialist predators could be observed. The former aphids readily drop off plants when disturbed. To facilitate their numbering, as well as for their generalist predators, aphids and predators were collected using a D-vac suction sampler (STIHL® SH 86C) on 40 randomly identified plants along a segment of about 20 m parallel to the margin, at each plot. A net bag was installed inside the vac pipe to collect the insects without damaging them. The collecting cone was placed over each plant, gently shaking the foliage for 5 s. After sampling, arthropods in D-vac bags were placed in a cool box à 0°C. Bags were then opened in the laboratory and arthropods were sorted to count *A. pisum* and their predators (i.e. by decreasing order of abundance, Staphylinidae, Araneae, Coccinellidae, Carabidae, and Chrysopidae).

Sampling occurred at three dates, vegetative growth 23rd March (vegetative growth, BBCH 36-38), 14th April (vegetative growth, BBCH 41-43) and 17th May (early flowering, BBCH 60-61). As almost no aphid was found in March, the first sampling date was discarded from the analyses. The last two count dates that were analyzed are therefore called date 1 and date 2. Due to time constraints in March, all modalities could not be monitored: only the LFMS1, LFMS2, HFLS1, HFLS2 and the control treatments were sampled.

Appendix S3. Estimation of nectar accessibility to predators and parasitoids

The amount of nectar provided by the plants was estimated by summing, in each treatment (flower strip or weeds in control treatments), the percent cover of, assessed in vegetation surveys, providing available and accessible nectar to aphid predators and parasitoids.

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 field observations, by selecting species at flower stage or producing extrafloral nectar between during aphid counts. Nectar **accessibility** depended on morphological matching between plants and predators or parasitoids. Extrafloral nectar, which is not enclosed in a perianth but produced on bracts or stipules, was considered to be always accessible. The **accessibility of floral nectar** was determined 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 *et al.*, 2021).

In spring barley intercropped with spring pea, in oilseed rape and in wheat, nectar accessibility to predators was determined for Syrphidae because they were dominant aphid predators in these crops. The adults require nectar as a source of energy and they have a limited access to floral nectar depending on morphological constraints. In maize and in faba bean, nectar accessibility to predators was determined for Coccinellidae and for Chrysopidae, which were the main predators depending on floral resources. Coccinellidae and Chrysopidae can feed on both prey and plant material in their juvenile as well as their adult stage (Wäckers *et al.*, 2005). Nectar accessibility to aphid parasitoids was also assessed without distinguishing the species being present in each crop.

Assessment of nectar accessibility to Syrphidae

To determine the access of aphidophagous Syrphidae to the nectar provided by plants, the size of their mouthparts and head, which limit corolla penetration, were retrieved from the literature (Table S4). Analyses focused on the four dominant aphidophagous species that were found in complementary unpublished observations. Passive interception traps (a kind a reduced malaise trap measuring 80 cm height, Sarthou, 2009) were placed from April to June each year, in each experimental treatment, within the flower strips and at 20 m from each strip, in the field crop. Among all trapped syrphids, 22.9% were *Eupeodes corollae*, 22.5% were *Episyrphus balteatus*, 18.5% were *Sphaerophoria scripta* and 16.0% were *Syrphus ribesii*. These four species represented 80 % of total Syrphidae abundance.

A decision tree (Figure S2) 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 (Gardarin *et al.*, 2021).

Using the decision tree, flower and insect traits were matched for all four Syrphidae species. In general, floral nectar accessibility was the same for all four species. Nectar was considered to be 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), nectar was considered to be not accessible in general to them.

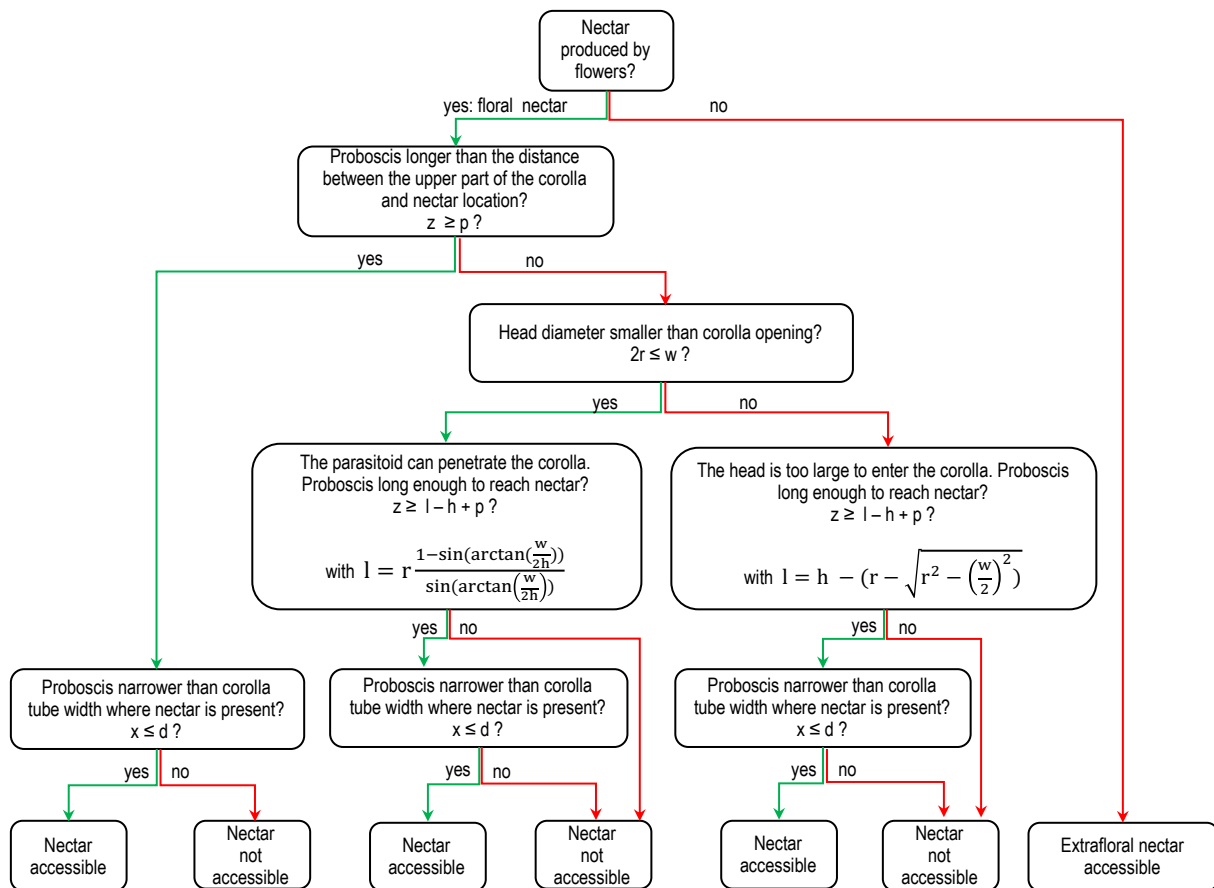


Figure S2. Decision tree from Gardarin *et al.* (2021) used to determine the accessibility of nectar to insects as a function of insect traits (radius of insect head r , proboscis length x and proboscis width z) and flower traits (width of flower opening w , corolla height h , nectar depth p , nectar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

Assessment of nectar accessibility to Coccinellidae and Chrysopidae

Coccinella septempunctata and *Harmonia axyridis* were the two dominant Coccinellidae observed at adult stage during aphid counts in maize. Chrysopidae were not identified. The individuals used had been collected in passive interception traps (see previous paragraph), and preserved in 70% ethanol, to measure their morphological traits. Morphological measurements were carried out on 13, 5 and 5 individuals of *C. septempunctata*, *H. axyridis* and Chrysopidae, respectively, under a binocular microscope (Table S4).

Assessment of nectar accessibility to aphid parasitoids

The measurement of parasitoid traits was not planned at the time of the experiment. To measure their morphological traits, 14 parasitoids kept in a collection were used. These parasitoids emerged from mummy rearing collected in oilseed rape in 2016 (5 individuals) and in wheat in 2017 (9 individuals) and were preserved in 70% ethanol. The parasitoids were not identified and the measurements on all individuals were averaged (Table S4).

Table S4. Morphological measurements of the head and mouthpart size of aphid predators and parasitoids.

	Head width (mm)	Absolute proboscis length* (mm)	Proboscis width **	Reference
<i>Episyrphus balteatus</i>	3.04	2.89	0.15	Gilbert, 1985a; Gilbert, 1985b
<i>Eupeodes corollae</i>	3.14	3.25	0.09	Gilbert, 1985a; Gilbert, 1985b
<i>Sphaerophoria scripta</i>	2.30	3.44	***	Gilbert, 1985a; Gilbert, 1985b
<i>Syrphus ribesii</i>	3.67	3.43	0.12	Gilbert, 1985a; Gilbert, 1985b
<i>Coccinella septempunctata</i>	1.69 ± 0.16	0.84 ± 0.11	0.14 ± 0.03	This study
<i>Harmonia axyridis</i>	1.42 ± 0.15	0.80 ± 0.19	0.11 ± 0.02	This study
<i>Chrysopidae</i>	1.24 ± 0.11	0.10 ± 0.02	0	This study
<i>Parasitoids</i>	0.511 ± 0.078	0.179 ± 0.061	0.029 ± 0.017	This study

* In Coccinellidae, the maxillary palps were measured.

** In Syrphidae, width of the labral sucking tube measured on Gilbert (1981).

*** No information was available for this species, the average value of the other three Syrphidae was used.

Table S5. Result of the morphological trait-matching decision tree to determine plant species providing available and accessible nectar (value = 3) to Coccinellidae and Chrysopidae (maize and faba bean) or to predatory Syrphidae (other crops). Among all the observed plant species each year (value different from zero), some species did not produce nectar (value = 1) or produced nectar that was not available or not accessible (value = 2).

Name	Status	Average cover over the whole experiment (%)	Maize, 2014	Pea-barley intercrop, 2015	Oilseed rape, faba bean, 2016	Wheat, 2017
		Total number of species	76	56	85	87
		Species with accessible nectar	13	19	36	10
<i>Achillea millefolium</i> L.	sown	2.000%	2	0	3	2
<i>Agrostis capillaris</i> L.	spontaneous	0.086%	0	0	1	1
<i>Agrostis gigantea</i> Roth	spontaneous	0.036%	1	1	1	1
<i>Ajuga reptans</i> L.	sown	0.001%	0	0	2	0
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande	sown	0.979%	0	2	0	0
<i>Allium vineale</i> L.	spontaneous	0.006%	1	1	0	0
<i>Anisantha sterilis</i> (L.) Nevski	spontaneous	0.138%	1	0	1	1
<i>Arrhenatherum elatius</i> (L.) P.Beauv.	sown	12.460%	1	1	0	0
<i>Artemisia vulgaris</i> L.	spontaneous	0.213%	0	0	1	1
<i>Avena strigosa</i> Schreb.	spontaneous	0.560%	1	1	0	0
<i>Barbarea vulgaris</i> R. Br.	sown	1.240%	2	3	3	2
<i>Bellis perennis</i> L.	sown	1.311%	2	3	3	2
<i>Bromus hordeaceus</i> L.	spontaneous	0.118%	1	0	0	1
<i>Capsella bursa-pastoris</i> (L.) Med.	sown	0.105%	0	2	0	0
<i>Centaurea scabiosa</i> L. s. l.	sown	0.726%	2	0	0	3
<i>Cerastium glomeratum</i> Thuill.	spontaneous	0.0003%	0	0	3	2
<i>Chenopodium album</i> L.	spontaneous	0.146%	0	0	1	1
<i>Cichorium intybus</i> L.	sown	0.819%	3	2	3	3
<i>Cirsium arvense</i> (L.) Scop.	spontaneous	0.666%	3	0	3	3
<i>Cirsium vulgare</i> (Savi) Ten.	spontaneous	0.148%	0	0	0	2
<i>Consolida hispanica</i> (Costa) Greuter &	spontaneous	0.0003%	2	0	0	0
<i>Convolvulus arvensis</i> L.	spontaneous	0.474%	2	0	2	3
<i>Coronilla varia</i> L.	sown	4.260%	0	2	2	2
<i>Cota tinctoria</i> (L.) J.Gay ex Guss.	sown	5.667%	2	0	3	2
<i>Crepis capillaris</i> (L.) Wallr.	spontaneous	0.004%	0	0	3	2
<i>Cyanus segetum</i> Hill	sown	5.441%	2	3	3	2
<i>Cynoglossum officinale</i> L.	sown	0.513%	0	2	0	2
<i>Dactylis glomerata</i> L.	sown	9.668%	1	1	1	1
<i>Daucus carota</i> L.	sown	0.377%	3	0	2	0
<i>Echium vulgare</i> L.	sown	0.132%	0	0	3	2
<i>Elytrigia repens</i> (L.) Desv. ex Nevski	spontaneous	0.447%	1	0	1	1
<i>Epilobium hirsutum</i> L.	spontaneous	0.011%	0	0	2	2
<i>Epilobium tetragonum</i> L. s. str.	spontaneous	0.436%	2	2	2	2
<i>Erigeron sumatrensis</i> Retz.	spontaneous	0.266%	2	0	0	0
<i>Ervilia hirsuta</i> (L.) Opiz	spontaneous	0.001%	0	0	2	2
<i>Euphorbia helioscopia</i> L.	spontaneous	0.037%	2	3	2	0
<i>Fallopia convolvulus</i> (L.) A. Löve	spontaneous	0.787%	3	0	2	0
<i>Foeniculum vulgare</i> Mill.	sown	0.050%	2	2	0	0
<i>Fumaria officinalis</i> L. s. l.	spontaneous	0.024%	2	0	0	0
<i>Galium aparine</i> L.	spontaneous	0.088%	2	3	3	2
<i>Galium mollugo</i> L. s. str.	sown	1.828%	2	0	2	2
<i>Geranium columbinum</i> L.	spontaneous	0.001%	0	2	0	0
<i>Geranium dissectum</i> L.	spontaneous	0.146%	2	3	3	2
<i>Geranium molle</i> L.	spontaneous	0.025%	2	3	3	2
<i>Geranium rotundifolium</i> L.	spontaneous	0.003%	0	3	0	0
<i>Geranium sp.</i>	spontaneous	0.020%	0	0	3	2
<i>Geum urbanum</i> L.	sown	0.126%	0	3	3	2
<i>Glechoma hederacea</i> L.	sown	0.678%	0	2	0	2
<i>Helminthotheca echioides</i> (L.) Holub	spontaneous	2.128%	3	3	3	3
<i>Heracleum sphondylium</i> L.	sown	1.906%	0	0	3	2

<i>Hesperis matronalis</i> L.	sown	0.559%	2	2	2	2
<i>Hypericum perforatum</i> L.	sown	0.163%	1	1	1	1
<i>Hypochaeris radicata</i> L.	sown	0.069%	2	3	3	2
<i>Jacobaea vulgaris</i> Gaertn.	sown	0.061%	2	0	2	3
<i>Knautia arvensis</i> (L.) Coult.	sown	0.001%	3	2	2	2
<i>Lactuca serriola</i> L.	spontaneous	0.339%	3	0	3	2
<i>Lamium album</i> L.	sown	0.001%	0	0	0	2
<i>Lamium hybridum</i> Vill.	spontaneous	0.003%	0	0	2	0
<i>Lamium purpureum</i> L. s. l. p. p.	spontaneous	0.047%	0	0	2	0
<i>Lapsana communis</i> L.	spontaneous	0.003%	2	0	2	2
<i>Lepidium draba</i> L.	spontaneous	0.087%	0	2	3	2
<i>Leucanthemum vulgare</i> Lam. s. str.	sown	1.397%	2	3	3	2
<i>Lolium perenne</i> L.	spontaneous	0.039%	1	1	1	1
<i>Lotus corniculatus</i> L.	sown	0.847%	2	2	2	2
<i>Lysimachia arvensis</i> (L.) U.Manns & Anderb.	spontaneous	1.053%	1	0	1	1
<i>Malva sylvestris</i> L.	sown	0.253%	2	0	2	2
<i>Matricaria recutita</i> L.	spontaneous	0.082%	3	0	3	2
<i>Medicago lupulina</i> L.	sown	0.197%	2	0	2	2
<i>Medicago sativa</i> L.	sown	1.258%	2	2	2	2
<i>Melilotus officinalis</i> (L.) Lam.	sown	0.535%	2	2	2	2
<i>Mercurialis annua</i> L.	spontaneous	0.083%	1	0	1	1
<i>Myosotis arvensis</i> (L.) Hill	spontaneous	0.176%	2	3	3	2
<i>Onobrychis viciifolia</i> Scop.	sown	0.968%	2	2	2	2
<i>Papaver rhoeas</i> L.	spontaneous	0.966%	1	1	1	1
<i>Pastinaca sativa</i> L.	sown	1.945%	0	3	3	2
<i>Phacelia tanacetifolia</i> Benth.	spontaneous	0.088%	2	3	3	2
<i>Picris hieracioides</i> L. s. l.	spontaneous	1.327%	3	0	3	3
<i>Plantago lanceolata</i> L.	sown	2.692%	1	1	1	1
<i>Poa annua</i> L.	spontaneous	0.051%	1	1	0	0
<i>Poa pratensis</i> L.	spontaneous	0.074%	1	1	1	1
<i>Poa trivialis</i> L.	spontaneous	1.017%	1	1	1	1
<i>Polygonum aviculare</i> L. (s. l.)	spontaneous	0.106%	3	0	2	3
<i>Ranunculus repens</i> L.	spontaneous	0.120%	0	0	3	2
<i>Reseda luteola</i> L.	sown	0.002%	2	0	0	0
<i>Rubus fruticosus</i> L.	spontaneous	0.006%	0	0	0	3
<i>Rumex crispus</i> L.	spontaneous	0.017%	1	1	1	1
<i>Rumex obtusifolius</i> L.	spontaneous	0.027%	1	1	0	0
<i>Salvia verbenaca</i> L.	spontaneous	0.002%	0	0	2	2
<i>Schedonorus arundinaceus</i> (Schreb.)	sown	6.531%	1	1	1	1
<i>Senecio inaequidens</i> DC.	spontaneous	0.001%	2	0	0	0
<i>Senecio vulgaris</i> L.	spontaneous	0.329%	1	1	1	1
<i>Silene dioica</i> (L.) Clairv.	spontaneous	0.063%	2	2	2	2
<i>Silene latifolia</i> Poir.	spontaneous	0.024%	2	2	2	2
<i>Sinapis arvensis</i> L.	spontaneous	0.001%	0	0	3	2
<i>Sisymbrium officinale</i> (L.) Scop.	spontaneous	0.001%	0	0	3	2
<i>Solanum nigrum</i> L.	spontaneous	0.040%	1	0	1	1
<i>Sonchus asper</i> (L.) Hill	spontaneous	0.621%	3	3	3	2
<i>Stellaria media</i> (L.) Vill. s. str.	sown	1.448%	3	3	3	2
<i>Tanacetum vulgare</i> L.	sown	1.330%	3	0	0	0
<i>Taraxacum</i> sect. <i>Ruderalia</i> Wiggers	sown	0.459%	2	3	3	2
<i>Torilis arvensis</i> (Huds.) Link <i>subsp. arvensis</i>	spontaneous	0.148%	2	0	3	2
<i>Trifolium alexandrinum</i> L.	spontaneous	0.029%	2	0	0	0
<i>Trifolium pratense</i> L.	sown	1.099%	2	2	2	2
<i>Trifolium repens</i> L.	sown	1.802%	2	2	2	2
<i>Tripleurospermum perforatum</i> (Mérat) Lainz	spontaneous	0.006%	0	0	2	3
<i>Triticum aestivum</i> L.	spontaneous	0.904%	1	1	0	1
<i>Urtica dioica</i> L.	spontaneous	0.029%	0	0	1	1
<i>Veronica hederifolia</i> L. s. l.	sown	0.845%	0	2	2	2
<i>Veronica persica</i> Poir.	sown	0.286%	2	0	3	2
<i>Veronica polita</i> Fr.	spontaneous	0.060%	0	0	3	2
<i>Vicia sativa</i> L. s. str.	sown	3.678%	2	3	3	2

Appendix S4. Calculation of functional dispersion

Functional diversity was computed through the functional dispersion index (Laliberté and Legendre, 2010), on the basis of traits involved in plant-insect interactions (Table S3). These traits were very weakly correlated (Fig. S3), with few significant correlations and low correlation coefficients. Numerical traits with left skewed distributions (reproductive height, duration of flowering, flower size and nectar depth) were log-transformed before computing functional dispersion (Májeková *et al.*, 2016). Due to the experimental design, functional dispersion was not independent of species richness. To estimate functional dispersion independently of species richness, null functional dispersion values were generated using the name-shuffling approach (Swenson, 2014). Null models were realized by shuffling species names in the trait matrix. This approach maintains the observed patterns of trait co-variance and of community structure and calculated the expected distribution of functional dispersion values given the observed species richness in the mixture. This process was applied 1000 times to each observed plant mixture. Then, standardized effect sizes were calculated for each observed plant mixture, calculated as the observed functional dispersion minus the mean functional dispersion of the null distributions, and this value was divided by the standard deviation of the null distribution (Swenson, 2014). In the following, the term “functional dispersion” is used to refer to the standardized effect size of functional dispersion.

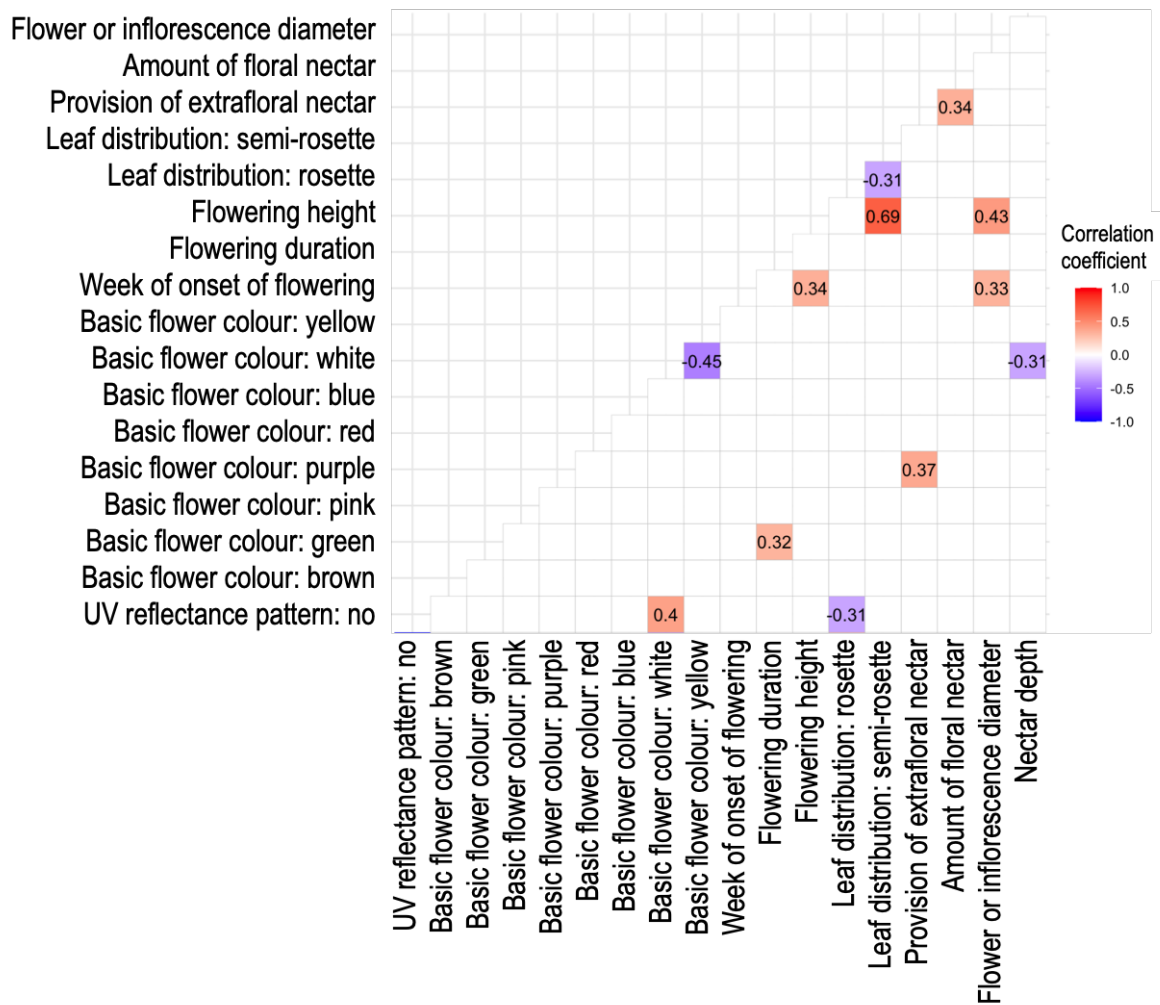


Figure S3. Correlation plot (drawn with the library `ggcorrplot` under R) between the traits involved in plant-arthropod interactions. Only Pearson correlation coefficients significant at $P < 0.05$ are shown. Factor levels were considered as separate variables for categorical traits. Correlations between the trait attributes within a single trait (e.g. between colours) are not interpreted as they are mutually exclusive.

Appendix S5. Effect of the sown species richness and the sown functional diversity on aphids, predator-prey ratios and parasitism rates

To investigate the effects of the sown species richness and the sown functional diversity (type of mixture as a factor), distance to the strip (factor) and their interaction, on aphid abundance, aphid population growth rate, predator-prey ratio and aphid parasitism, generalised linear mixed models were used with the *glmmTMB* package (Brooks *et al.* 2017). A negative binomial error distribution was used for aphid abundance and predator-prey ratios and a binomial error distribution for aphid parasitism rates. The models included plot number (numbered from 1 to 9 along the north-south transects) nested within transect number (from 1 to 6) as a random effect. Analyses were performed for all the crops studied, separately at each counting date. When there were several counting dates, parasitism was analysed only on the second date, because parasitism rates were low or undetectable at the first counting. The significance of the fixed effects was evaluated by type II analyses of deviance with Wald chi-squared tests, in the ANOVA function of the *car* package (Fox & Weisberg 2019). If a significant effect (p value < 0.05) was detected, Tukey-HSD post hoc tests were performed for pairwise multiple comparisons of the estimated marginal means of each treatment with the *multcomp* package (Hothorn, Bretz & Westfall 2008)

Appendix S6. Supplementary results

Effect of the sown species richness, sown functional diversity and distance on aphid population abundance and growth rate

Aphid populations were smaller at 5 m from the flower strips than those at 20 m, with significant effects in maize, faba bean and wheat and only trends in spring barley and spring pea. No effect of distance from the flower strip was observed in oilseed rape (Table S6). The sown mixtures had little effect on aphid populations (Table S6) and on their growth rates (Fig. S7, Table S9), and the observed effects were dependent on the crop considered. However, aphid numbers were generally higher in control treatments with no flower strip, for spring barley (p-value=0.005, date 2), spring pea (p-value=0.001, date 2) and faba bean (p-value= 0.052, date 2).

Effect of the sown species richness, sown functional diversity and distance from the flower strip on predator-prey ratios and parasitism rates

Predator-prey ratios (Fig. S5, Table S7) were higher 5 m from the strip than 20 m from the flower strip in maize (p-value= $1.17 \cdot 10^{-4}$), oilseed rape at date 2 (p-value=0.021), faba bean at date 1 (p-value= $1.11 \cdot 10^{-4}$) and wheat at date 2 (non-significant trend), but the reverse was observed for the pea-barley intercrop at date 2 (p-value=0.003). The type of sown mixture had almost no effect on predator-prey ratios, except in the LFMS2 mixture in maize, for which lower values were obtained at 5m for the control treatment (p-value $<10^{-4}$, Table S7).

Concerning aphid parasitism rate, some significant differences according to distance from the flower strip were identified, in maize and oilseed rape. The type of mixture had contrasting effects on parasitism rates in maize (p-value $<10^{-4}$), pea (p-value $<10^{-4}$), barley (p-value=0.0016) and oilseed rape at 20 m (p-value $<10^{-4}$, Table S8). The effects depended on the crop considered, but parasitism rates were often higher in LFMS2 and HFMS1 mixtures than in the HFMS2 mixtures and control treatments.

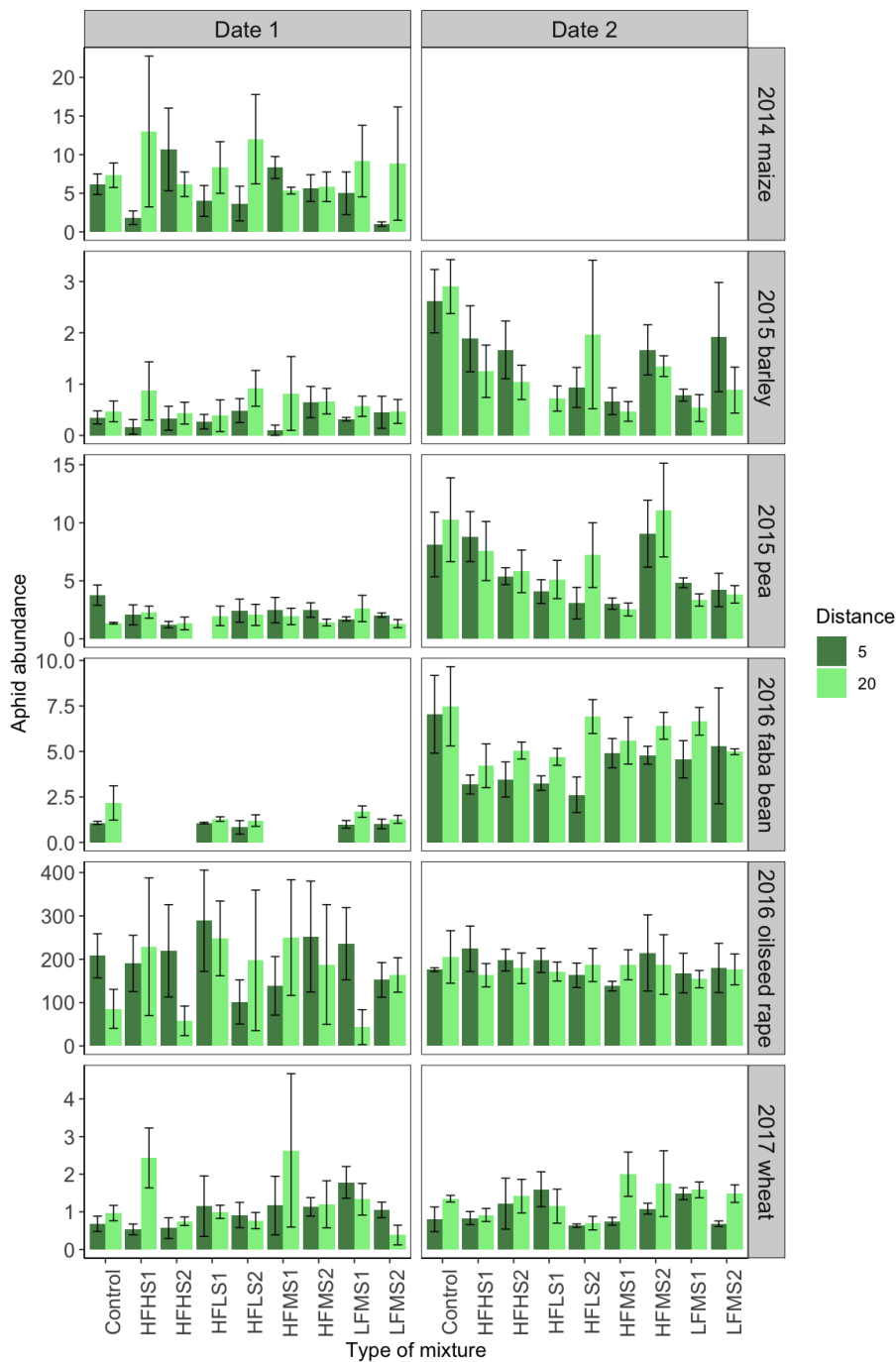


Figure S4. Effect of the type of plant mixture on the amount of aphids (number per plant , per raceme or per tiller) in the adjacent crop at the two counting dates where aphids occurred (except one date for maize). In oilseed rape at date 2, values were divided by 100 to enable their representation. The eight plant mixtures have a low or high functional diversity (LF or HF, respectively), a low, medium or high species richness (LS, MS or HS respectively), they are composed of species from two different lists (1 or 2), and they are compared with a control plot, on which the strip was sown with the same crop species as the field and managed in a similar manner. Not all treatments could be studied in faba bean at date 1.

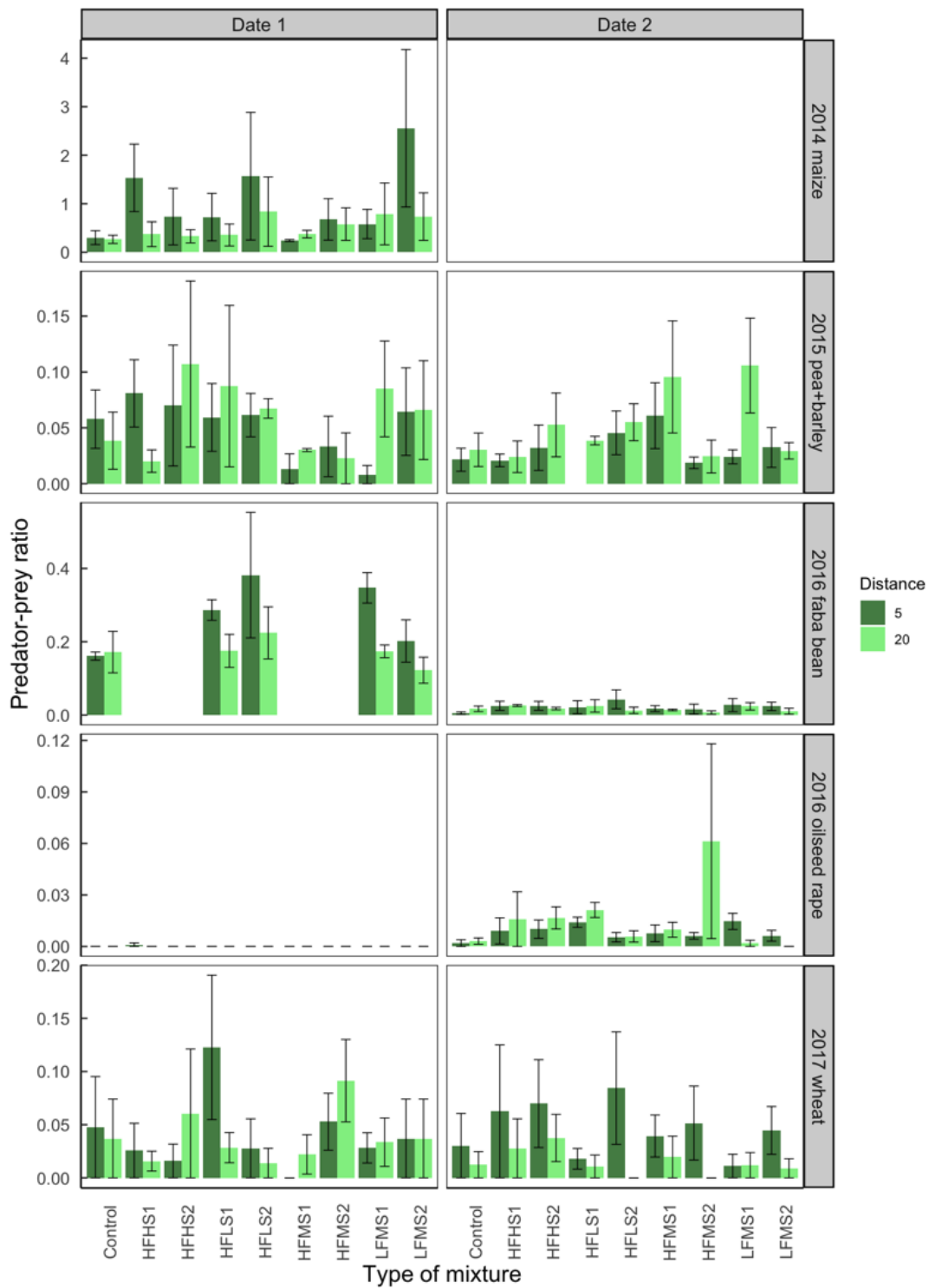


Figure S5. Effect of the type of plant mixture on the amount of the predator-prey ratio in the adjacent crop at the two counting dates where aphids occurred (except one date for maize). In oilseed rape at date 2, values were multiplied by 100 to enable their representation. In the pea-barley intercrop, data were pooled across the two cropped species since predators could prey on aphids of both species. The eight plant mixtures have a low or high functional diversity (LF or HF, respectively), a low, medium or high species richness (LS, MS or HS respectively), they are composed of species from two different lists (1 or 2), and they are compared with a control plot, on which the strip was sown with the same crop species as the field and managed in a similar manner. Not all treatments could be studied in faba bean at date 1.

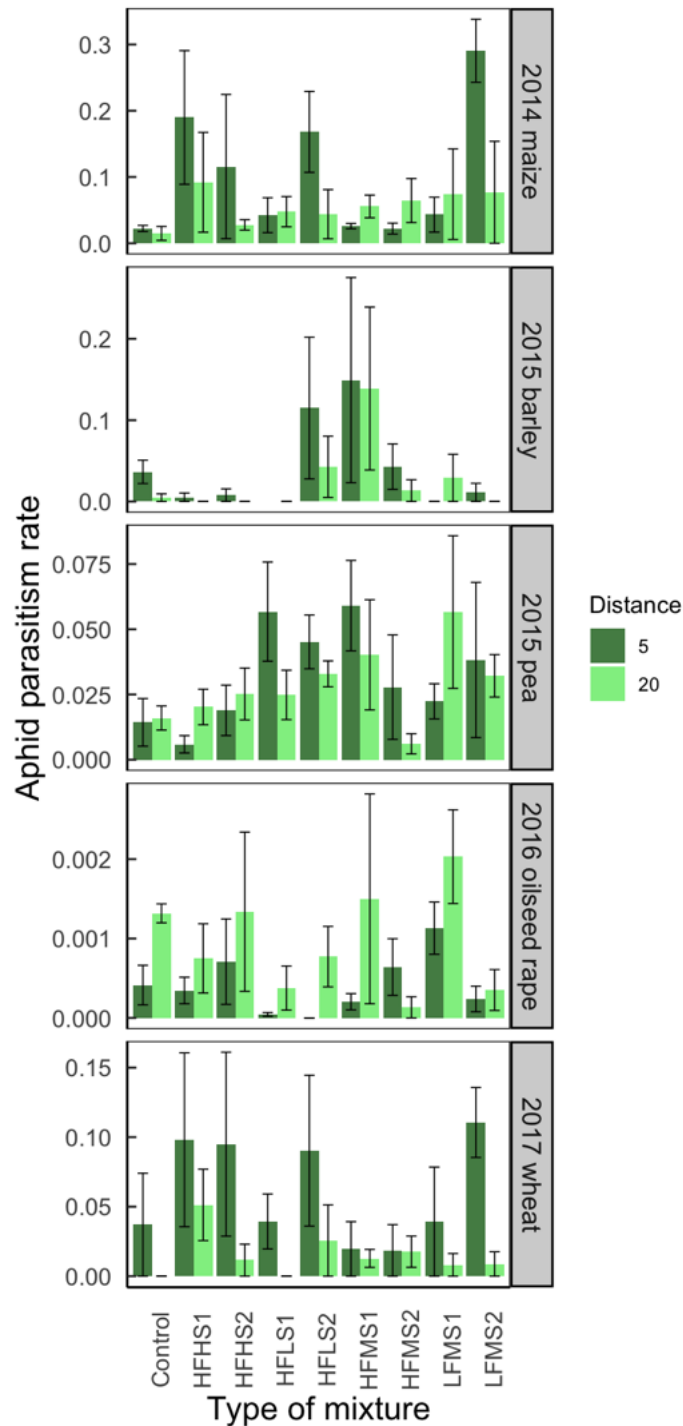


Figure S6. Effect of the type of plant mixture on the aphid parasitism rates in the adjacent crop. Parasitism was analysed at the last counting date only when there were several counts per crop. Parasitism was null in faba bean (not shown). The eight plant mixtures have a low or high functional diversity (LF or HF, respectively), a low, medium or high species richness (LS, MS or HS respectively), they are composed of species from two different lists (1 or 2), and they are compared with a control plot, on which the strip was sown with the same crop species as the field and managed in a similar manner.

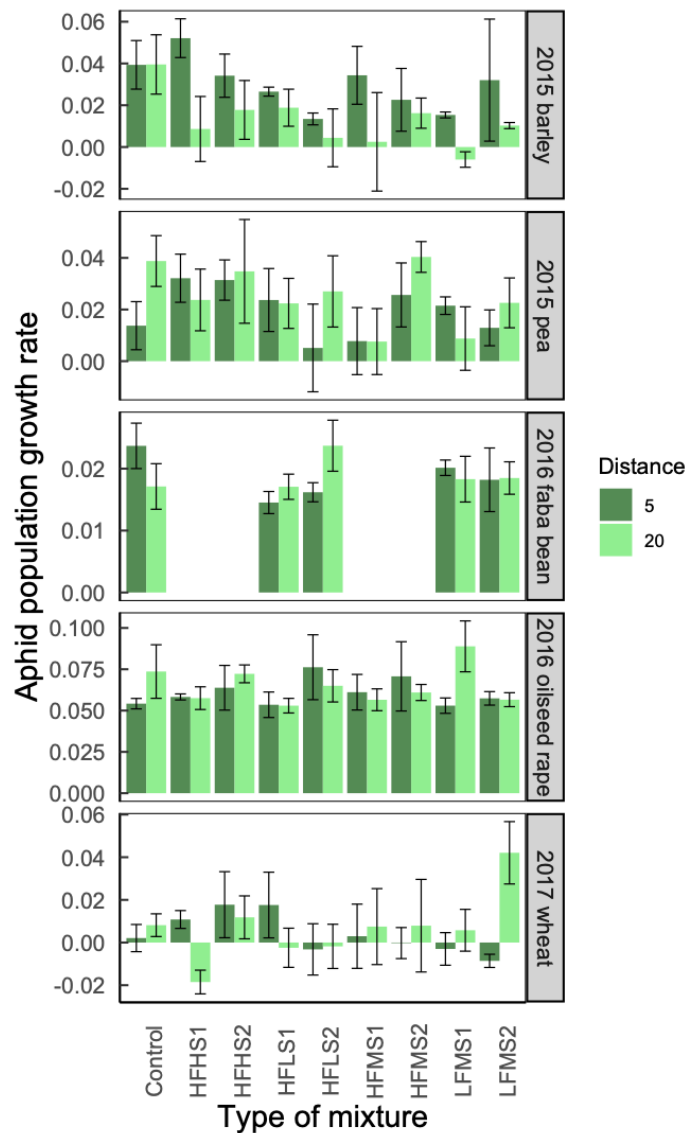


Figure S7. Effects of the type of mixture and distance to the flower strip on the growth rate of aphid populations on the crops for which two counts have been realized. The eight plant mixtures have a low or high functional diversity (LF or HF, respectively), a low, medium or high species richness (LS, MS or HS respectively), they are composed of species from two different lists (1 or 2), and they are compared with a control plot, on which the strip was sown with the same crop species as the field and managed in a similar manner.

Table S6. Effects of the type of mixture and distance to the flower strip on the number of aphids on six crop species where aphids occurred. Aphid number was recorded at one or two counting dates (see Supplementary methods). Generalised linear mixed effect models were used, assuming a negative binomial error distribution. Df are the degrees of freedom for explanatory variables. R²_m and R²_c are the marginal and conditional coefficients of determination of the models.

Crop		Variables	df	χ^2	P ($>\chi^2$)	Significant contrasts
Maize 2014		Mixture	8	5.727	0.678	
		Distance	1	5.742	0.017	5m < 20m
		Mixture × Dist.	8	15.054	0.058	<i>no significant contrast</i>
		R ² _m = 0.56; R ² _c = 0.99; AIC = 574.7				
Spring pea 2015	Date 1	Mixture	8	6.580	0.582	
		Distance	1	3.822	0.051	5m < 20m
		Mixture × Dist.	8	11.224	0.189	
		R ² _m = 0.55; R ² _c = 0.99; AIC = 502.4				
	Date 2	Mixture	8	25.195	0.001	HFMS1 < C, HFMS1
		Distance	1	0.896	0.344	
		Mixture × Dist.	8	11.229	0.189	
		R ² _m = 0.67; R ² _c = 0.99; AIC = 593.6				
Spring barley 2015	Date 1	Mixture	8	6.866	0.551	
		Distance	1	3.341	0.067	5m < 20m
		Mixture × Dist.	8	3.776	0.877	
		R ² _m = 0.85; R ² _c = 0.99; AIC = 383.3				
	Date 2	Mixture	8	21.876	0.005	HFMS1, LFMS1 < C
		Distance	1	1.489	0.222	
		Mixture × Dist.	8	7.589	0.475	
		R ² _m = 0.69; R ² _c = 0.99; AIC = 460.6				
Faba bean 2016	Date 1	Mixture	4	6.745	0.150	
		Distance	1	25.119	< 10 ⁻⁴	5m < 20m
		Mixture × Dist.	4	5.234	0.264	
		R ² _m = 0.44; R ² _c = 0.98; AIC = 270.1				
	Date 2	Mixture	8	15.367	0.052	HFHS1 < C
		Distance	1	11.949	0.001	5m < 20m
		Mixture × Dist.	8	8.008	0.433	
		R ² _m = 0.94; R ² _c = 0.99; AIC = 644.3				
Oilseed rape 2016	Date 1	Mixture	8	3.950	0.862	
		Distance	1	1.000	0.317	
		Mixture × Dist.	8	12.810	0.119	
		R ² _m = 0.55; R ² _c = 0.99; AIC = 684.6				
	Date 2	Mixture	8	2.355	0.968	
		Distance	1	0.334	0.563	
		Mixture × Dist.	8	14.749	0.064	
		R ² _m = 0.15; R ² _c = 0.99; AIC = 1095.1				
Wheat 2017	Date 1	Mixture	8	18.387	0.019	<i>no significant contrast</i>
		Distance	1	0.529	0.469	
		Mixture × Dist.	8	20.051	0.010	20m: LFMS2 < HFMS1, HFHS1
		R ² _m = 0.07; R ² _c = 0.11; AIC = 446.0				
	Date 2	Mixture	8	18.146	0.020	HFLS2, LFMS2 < LFMS1
		Distance	1	7.399	0.006	5m < 20m
		Mixture × Dist.	8	11.303	0.185	
		R ² _m = 0.86; R ² _c = 0.97; AIC = 431.9				

Table S7. Effects of the type of mixture (contrasting for their sown species richness and sown functional diversity) and distance to the flower strip on the predator-prey ratios in five crops where aphids occurred. Aphid and predators were recorded at one or two counting dates (see Supplementary methods). Generalised linear mixed effect models were used, assuming a negative binomial error distribution. Df are the degrees of freedom for explanatory variables. R^2_m and R^2_c are the marginal and conditional coefficients of determination of the models.

Crop		Variables	df	χ^2	P ($>\chi^2$)	Significant contrasts
Maize 2014 Predator-prey ratio		Mixture	8	12.134	0.145	
		Distance	1	14.830	$< 10^{-4}$	20m < 5m
		Mixture \times Dist.	8	57.068	$< 10^{-4}$	5m: C < LFMS2
		R ² _m = 0.07; R ² _c = 0.23; AIC = 464.5				
Spring barley + spring pea intercrop, 2015 Predator-prey ratio	Date 1	Mixture	8	5.855	0.664	
		Distance	1	0.232	0.630	
		Mixture \times Dist.	8	11.554	0.172	
		R ² _m = 0.12; R ² _c = 0.24; AIC = 227.5				
	Date 2	Mixture	8	14.002	0.082	<i>no significant contrast</i>
		Distance	1	8.623	0.003	5m < 20m
		Mixture \times Dist.	8	8.013	0.432	
		R ² _m = 0.06; R ² _c = 0.14; AIC = 286.6				
Faba bean 2016 Predator-prey ratio	Date 1	Mixture	4	8.729	0.068	LFMS2, C < LFMS1
		Distance	1	14.940	$1.1 \cdot 10^{-4}$	20m < 5m
		Mixture \times Dist.	4	1.9023	0.754	
	R ² _m = 0.04; R ² _c = 0.05; AIC = 175.3					
	Date 2	Mixture	8	6.783	0.560	
		Distance	1	1.679	0.195	
Mixture \times Dist.		8	10.426	0.236		
R ² _m = 0.05; R ² _c = 0.17; AIC = 266.6						
Oilseed rape 2016 Predator-prey ratio	Date 1	<i>Not enough predators</i>				
	Date 2	Mixture	8	9.971	0.267	
		Distance	1	5.294	0.021	20m < 5m
		Mixture \times Dist.	8	11.406	0.179	
		R ² _m = 0.82; R ² _c = 0.85; AIC = 209.1				
Wheat 2017 Predator-prey ratio	Date 1	Mixture	8	5.490	0.704	
		Distance	1	0.027	0.869	
		Mixture \times Dist.	8	1.050	0.998	
		R ² _m = 0.85; R ² _c = 0.85; AIC = 142.6				
	Date 2	Mixture	8	4.292	0.829	
		Distance	1	2.781	0.095	trend: 20m < 5m
		Mixture \times Dist.	8	1.739	0.988	
R ² _m = 0.96; R ² _c = 0.96; AIC = 130.4						

Table S8. Effects of the type of mixture and distance to the flower strip on aphid parasitism rate on six crops, measured at the last counting date. Generalised linear mixed effect models were used, assuming a binomial error distribution. Df are the degrees of freedom for explanatory variables. R²m and R²c are the marginal and conditional coefficients of determination of the models.

Crop	Variables	df	χ^2	P ($>\chi^2$)	Significant contrasts
Maize 2014	Mixture	8	33.807	$< 10^{-4}$	C < HFHS1, LFMS2
	Distance	1	7.136	0.007	20m < 5m
	Mixture \times Dist.	8	36.809	$< 10^{-4}$	5m: C, HFMS1, LFMS1 < HFLS2, LFMS2
	R ² m = 0.16; R ² c = 0.30; AIC = 253.4				
Spring pea 2015	Mixture	8	39.869	$< 10^{-4}$	HFMS2 < LFMS1, HFLS2, HFMS1
	Distance	1	0.522	0.469	C < HFLS2, HFMS1
	Mixture \times Dist.	8	12.013	0.151	HFHS1, HFHS2 < HFMS1
	R ² m = 0.07; R ² c = 0.08; AIC = 302.6				
Spring barley 2015	Mixture	8	24.844	0.001	C < HFMS1
	Distance	1	1.763	0.184	
	<i>(interaction not tested due to a lack of convergence)</i> R ² m = 0.22; R ² c = 0.27; AIC = 164.3				
Faba bean 2016	<i>No parasitism observed</i>				
Oilseed rape 2016	Mixture	8	10.906	0.207	
	Distance	1	40.768	$< 10^{-4}$	<i>no significant contrast</i>
	Mixture \times Dist.	8	74.171	$< 10^{-4}$	5 and 20m: HFLS2 < LFMS1
	R ² m = 0.84; R ² c = 0.87; AIC = 420.7				
Wheat 2017	Mixture	8	6.738	0.565	
	Distance	1	7.572	0.011	<i>no significant contrast</i>
	Mixture \times Dist.	8	2.839	0.944	
	R ² m = 0.92; R ² c = 0.93; AIC = 199.7				

Table S9. Effects of the type of mixture (contrasting for their sown species richness and sown functional diversity) and distance to the flower strip on the growth rate of aphid populations on the crops for which two counts have been realised. Generalised linear mixed effect models were used, assuming a binomial error distribution. Df are the degrees of freedom for explanatory variables. R²m and R²c are the marginal and conditional coefficients of determination of the models.

Crop	Variables	df	χ^2	P ($>\chi^2$)	Contrasts
Maize 2014	<i>no growth rate computed</i>				
Spring pea 2015	Mixture	8	6.070	0.639	
	Distance	1	2.254	0.133	
	Mixture \times Dist.	8	10.479	0.233	
	R ² m = 0.23; R ² c = 0.62; AIC = -118.4				
Spring barley 2015	Mixture	8	7.760	0.457	
	Distance	1	10.705	0.001	5 m > 20 m
	Mixture \times Dist.	8	5.576	0.694	
	R ² m = 0.29; R ² c = 0.48; AIC = -103.9				
Faba bean 2016	Mixture	4	2.888	0.578	
	Distance	1	0.042	0.839	
	Mixture \times Dist.	4	5.925	0.205	
	R ² m = 0.22; R ² c = 0.29; AIC = -114.8				
Oilseed rape 2016	Mixture	8	5.502	0.703	
	Distance	1	0.755	0.385	
	Mixture \times Dist.	8	9.589	0.295	
	R ² m = 0.22; R ² c = 0.33; AIC = -124.7				
Wheat 2017	Mixture	8	6.559	0.585	
	Distance	1	0.277	0.599	
	Mixture \times Dist.	8	16.903	0.031	20m: HFHS1 < LFMS2
	R ² m = 0.28; R ² c = 0.38; AIC = -119.3				

Table S10. Effects of food resources, species and functional diversity in flower strip plant communities (proportion of plant cover providing accessible nectar, cover of legumes, species richness and functional dispersion) and distance to the flower strip on the predator-prey ratio on the crops where aphids occurred. For each crop and each counting date, all possible combinations of the fixed effect variables and their interactions. The best models (ΔAIC from the best model < 4) were ranked according to their AIC and the results for the conditional averaged best model are presented. Generalised linear mixed effect models were used, assuming a negative binomial error distribution. All explanatory variables were scaled. For readability, the results for significant effects are reported here only or for variables with a relative importance (weight) greater than 0.70. R^2_m and R^2_c are the marginal and conditional coefficients of determination of the model.

		Explanatory fixed variables	Effect \pm SE	z-value	P ($> z$)	Weight
Maize 2014		Distance 20 m (ref=5m)	-0.301 \pm 0.082	3.586	0.0003	1
		Legume cover	0.203 \pm 0.114	1.734	0.083	0.74
		Functional dispersion	-0.299 \pm 0.118	2.480	0.013	1
		Nectar resource \times Functional disp.	-0.372 \pm 0.194	1.867	0.062	0.42
		$R^2_m = 0.04$; $R^2_c = 0.21$; AIC = 496.4				
Spring barley	Date 1	Distance 20 m (ref=5m)	0.099 \pm 0.203	0.476	0.634	0.95
+ spring pea		Nectar resource	0.351 \pm 0.201	1.701	0.089	0.86
intercrop, 2015		Nectar resource \times Functional disp.	0.410 \pm 0.201	1.981	0.047	0.41
		Species richness	-0.386 \pm 0.197	1.915	0.055	0.94
		Legume cover \times Distance 20m	0.517 \pm 0.204	2.460	0.013	0.95
		$R^2_m = 0.07$; $R^2_c = 0.15$; AIC = 209.3				
	Date 2	Distance 20 m (ref=5m)	0.434 \pm .141	3.004	0.003	1
		$R^2_m = 0.09$; $R^2_c = 0.16$; AIC = 273.6				
Faba bean 2016	Date 1	Distance 20 m (ref=5m)	-0.505 \pm 0.131	3.677	0.0002	1
		$R^2_m = 0.04$; $R^2_c = 0.06$; AIC = 167.8				
	Date 2	<i>No variable significant nor with weight > 0.7</i>				
Oilseed rape 2016	Date 1	<i>Not run, not enough predators</i>				
	Date 2	Distance 20 m (ref=5m)	0.174 \pm 0.130	1.304	0.192	1
		Nectar resource	0.577 \pm 0.152	3.748	0.0002	1
		Nectar resource \times Distance 20m	0.452 \pm 0.069	6.563	$< 10^{-4}$	0.59
		Nectar resource \times Functional disp.	-0.603 \pm 0.072	8.167	$< 10^{-4}$	1
		Functional disp. \times Distance 20m	0.988 \pm 0.115	8.395	$< 10^{-4}$	1
		Legume cover	0.296 \pm 0.094	3.070	0.002	1
		Legume cover \times Distance 20m	-0.872 \pm 0.175	4.930	$< 10^{-4}$	1
		$R^2_m = 0.22$; $R^2_c = 0.33$; AIC = 191.4				
Wheat 2017	Date 1	<i>No significant variable nor with $w > 0.7$</i>				
	Date 2	Distance 20 m (ref=5m)	-1.163 \pm 0.364	3.118	0.002	1
		Nectar resource	0.277 \pm 0.277	1.609	0.102	0.73
		$R^2_m = 0.18$; $R^2_c = 0.18$; AIC = 108.1				

Table S11. Effects of food resources species and functional diversity in flower strip plant communities (proportion of plant cover providing accessible nectar, cover of legumes, species richness and functional dispersion) and distance to the flower strip on the parasitism rate on the crop where aphids occurred. For each crop, all possible combinations of the fixed effect variables and their interactions. The best models (ΔAIC from the best model < 4) were ranked according to their AIC and the results for the conditional averaged best model are presented. Generalised linear mixed effect models were used, assuming a binomial error distribution. All explanatory variables were scaled. For readability, the results are reported here only for significant effects or for variables with a relative importance (weight) greater than 0.70. R^2_m and R^2_c are the marginal and conditional coefficients of determination of the model.

	Explanatory fixed variables	Effect \pm SE	z-value	P (>z)	Weight
Maize 2014	Distance 20 m (ref=5m)	-0.562 \pm 0.211	2.586	0.009	1
	Nectar resource	0.502 \pm 0.231	2.123	0.033	0.91
	Nectar resource \times Distance 20m	-0.536 \pm 0.254	2.049	0.040	0.75
	Functional dispersion	-0.756 \pm 0.230	3.212	0.001	1
	Funct. dispersion \times Distance 20m	0.863 \pm 0.306	2.749	0.006	1
	Legume cover	0.663 \pm 0.250	2.587	0.009	1
	Legume cover \times Distance 20m	-0.892 \pm 0.301	2.900	0.004	1
	Species richness	0.161 \pm 0.189	0.835	0.403	0.89
	$R^2_m = 0.11$; $R^2_c = 0.28$; AIC = 269.3				
Spring pea 2015	Distance 20 m (ref=5m)	-0.036 \pm 0.006	6.1326	$< 10^{-4}$	0.26
	Legume cover	0.130 \pm 0.011	11.196	$< 10^{-4}$	0.32
	Species richness	0.167 \pm 0.046	3.566	0.0004	0.44
		$R^2_m = 0.11$; $R^2_c = 0.16$; AIC = 239.3			
Spring barley 2015	Distance 20 m (ref=5m)	-0.737 \pm 0.498	1.443	0.149	1
	Legume cover	1.203 \pm 0.663	1.775	0.076	0.73
	Nectar resource \times Func. dispersion	-0.872 \pm 0.478	1.775	0.076	0.34
	$R^2_m = 0.22$; $R^2_c = 0.42$; AIC = 113.5				
Faba bean 2016	<i>No parasitism observed</i>				
Oilseed rape 2016	Distance 20 m (ref=5m)	0.791 \pm 0.089	8.646	$< 10^{-4}$	1
	Nectar resource	0.531 \pm 0.295	1.760	0.078	1
	Nectar resource \times Distance 20m	-0.530 \pm 0.122	4.270	0.0002	1
		$R^2_m = 0.10$; $R^2_c = 0.32$; AIC = 493.9			
Wheat 2017	Distance 20 m (ref=5m)	-1.340 \pm 0.265	3.262	0.001	1
		$R^2_m = 0.19$; $R^2_c = 0.27$; AIC = 129.1			

Table S12. Effects of food resources, species and functional diversity in flower strip plant communities (proportion of plant cover providing accessible nectar, cover of legumes, species richness and functional dispersion) and distance to the flower strip on the growth rate of aphid populations on six crop species where aphids occurred. For each crop, all possible combinations of the fixed effect variables and their interactions. The best models (ΔAIC from the best model < 4) were ranked according to their AIC and the results for the conditional averaged best model are presented. Generalised linear mixed effect models were used, assuming a Gaussian error distribution (after a log-transformation in the case of oilseed rape). All explanatory variables were scaled. For readability, the results for significant effects are reported here only or for variables with a relative importance (weight) greater than 0.70. R^2_m and R^2_c are the marginal and conditional coefficients of determination of the model.

	Explanatory fixed variables	Effect \pm SE	z-value	P (>z)	Weight
Maize 2014	<i>Only one count, no aphid population growth rate calculated</i>				
Spring pea 2015	Distance 20 m (ref=5m)	0.006 \pm 0.004	1.562	0.118	0.91
	Nectar resource \times Distance 20m	-0.344 \pm 0.004	1.682	0.092	0.28
	Species richness	-0.002 \pm 0.004	0.556	0.578	0.98
	Species richness \times Distance 20m	-0.008 \pm 0.004	2.156	0.031	0.78
	Legume cover \times Distance 20m	-0.006 \pm 0.004	1.670	0.095	0.35
	$R^2_m = 0.27$; $R^2_c = 0.62$; AIC = -263.1				
Spring barley 2015	Distance 20 m (ref=5m)	-0.018 \pm 0.005	3.523	4.261 $\cdot 10^{-4}$	1
	Nectar resource \times Distance 20m	-0.010 \pm 0.005	2.094	0.036	0.26
	Functional dispersion	0.007 \pm 0.005	1.562	0.118	0.74
	Funct. dispersion \times Distance 20m	-0.010 \pm 0.005	2.008	0.045	0.26
	Legume cover \times Distance 20m	-0.008 \pm 0.004	1.658	0.097	0.10
	$R^2_m = 0.28$; $R^2_c = 0.57$; AIC = -238.3				
Faba bean 2016	<i>No significant variable nor with Akaike weight > 0.70</i>				
Oilseed rape 2016 (log x+0.01)	Nectar resource	-0.076 \pm 0.034	2.193	0.028	1
	Legume cover	0.023 \pm 0.041	0.543	0.587	0.73
	Legume cover \times Distance 20m	-0.095 \pm 0.053	1.738	0.082	0.35
	$R^2_m = 0.25$; $R^2_c = 0.25$; AIC = 7.5				
Wheat 2017	<i>No significant variable nor with Akaike weight > 0.70</i>				

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