Identification of flower functional traits affecting abundance of generalist predators in perennial multiple species wildflower strips

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Abstract

In agricultural fields, wildflower strips can be sown to enhance conservation biological control of insect pests. However, issues remain regarding the composition of flower mixtures to effectively attract and support large communities of natural enemies. Trait-based approaches are promising for this purpose. In the present study, conducted in an agricultural field of Belgium in 2014 and 2015, 15 flower mixtures were considered to explore the relation between the abundance of trapped generalist predators (i.e., lacewings [*Neuroptera*: *Chrysopidae*], ladybeetles [*Coleoptera*: *Coccinellidae*] and hoverflies [*Diptera*: *Syrphidae*]) and the community-weighted means of seven flower traits. Through a redundancy analysis, it was found that the presence/absence of flower ultra-violet pattern and the morphology of the corolla (that determines the accessibility of floral resources) were the traits that significantly affected the abundance of the generalist predators in the flower mixtures. The ladybeetles *Harmonia axyridis* and *Propylea quatuordecimpunctata* as well as the lacewings *Chrysoperla carnae* were more abundant in mixtures with a high cover of flowers showing an ultra-violet pattern, while the opposite was observed for the ladybeetle *Coccinella septempunctata*. As for hoverflies, *Episyrphus balteatus* and *Eupeodes corollae* were more abundant in mixtures with a high cover of flowers with open nectar. These results bring new knowledge regarding how a range of natural enemy species reacts to flower cues in diversified plant communities and should help in elaborating flower mixtures that enhance conservation biological control.

Keywords: Conservation biological control; *Coccinellidae*; *Syrphidae*; *Chrysopidae*; Community-Weighted Mean; Ultra-violet pattern; Corolla morphology

Introduction

Spatial diversification of agroecosystems is prerequisite for the delivery of ecosystem services in agricultural landscapes (Wratten et al. 2012; Hatt et al. 2018). The natural regulation of insect pests is one of these ecosystem services (Letourneau et al. 2011; Dassou and Tixier 2016; Rusch et al. 2016). It can be enhanced by manipulating habitats to increase the abundance, diversity and efficacy of pest natural enemies (i.e., conservation biological control, Barbosa 1998). At the field scale, crop habitats can be diversified by cultivating variety mixtures (Grettenberger and Tooker 2017) or multiple crops simultaneously (Lopes et

al. 2016). Moreover, semi-natural habitats can be implemented and managed adjacent to crops (Holland et al. 2016).

Wildflower strips (WFS) are one these semi-natural habitats. Over the last two decades, several studies explored whether sowing and/or managing WFS in agricultural landscapes allow enhancing the provision of ecosystem services (for a review: Uyttenbroeck et al. 2016). Recent studies have shown that sowing WFS adjacent to crops enhances biological control of insect pests due to an increased abundance of natural enemies (Tschumi et al. 2016; Hatt et al. 2017a; Toivonen et al. 2018). Indeed, generalist predators such as hoverflies (*Diptera*: *Syrphidae*), ladybeetles (*Coleoptera*: *Coccinellidae*) and lacewings (*Neuroptera*: *Chrysopidae*) commonly consume nectar and pollen from flowers at some—or at all—of their development stages in addition to prey food (Lundgren 2009a; Lu et al. 2014). Hence, flowering plants can attract and support them particularly when prey is scarce. Nevertheless, the studied WFS may not succeed in significantly increasing the diversity (i.e., richness and evenness) of these natural enemies in adjacent crops (Hatt et al. 2017a), thus questioning the ability of WFS to enhance biological control of several pest species in the long term. Indeed, the strength and stability of biological control may need a high functional diversity and redundancy of natural enemies, which is favoured by a high species richness and evenness within their community (Letourneau et al. 2009; Crowder et al. 2010; Jonsson et al. 2017).

Trait-based approaches have been increasingly used to understand how vegetation composition and management affect natural enemy abundance and diversity towards biological control (Gardarin et al. 2018; Perovic et al. 2018). The use of functional traits instead of taxonomic diversity allows an easier generalization of the observed patterns and mechanisms to other agroecological contexts. Indeed, whereas certain species are found in relatively specific ecological ranges, traits are attributes that can be shared across species and ecological ranges. As stated by McGill et al. (2006), 'statements about traits give generality and predictability, whereas nomenclatural ecology tends towards highly contingent rules and special cases'.

For flower-insect interactions, previous research has identified the flower traits and their values that determine natural enemy attractiveness (Sutherland et al. 1999; Koski and Ashman 2014; Song et al. 2017), their ability to collect floral resources (Nave et al. 2016; Van Rijn and Wäckers 2016) and the benefits they obtain from these resources (Vattala et al. 2006). Most of these studies used artificial devices or assessed the paired interaction between a certain flower species and a given insect species in relatively controlled environments. In field conditions, Fiedler and Landis (2007) identified that among six traits measured on 48 plants

sown in separate plots, an increased floral size and a late peak bloom increased the abundance of natural enemies approaching flowers. Additionally, Van Rijn and Wäckers (2016) showed that hoverflies more often visit flowers with accessible nectar in species-rich WFS. However, few studies to our knowledge have identified the various floral traits and their values that affect the abundance of an array of natural enemy species in multiple species WFS.

Several types of metrics are used to understand plant-arthropod interactions in diversified ecosystems (Gardarin et al. 2018). Among them, the Community-Weighted Mean (CWM) is the 'mean of [trait] values present in the community weighted by the relative abundance of taxa bearing each value' (Lavorel et al. 2008). By considering the functional traits rather than the plant species *per se*, the CWM is a descriptor of the functional composition of a community and a predictor of ecosystem processes (Garnier and Navas 2012). Previously, Hatt et al. (2017b) related the abundance of specialist natural enemies (i.e., the parasitoids of *Meligethes* spp. [*Coleoptera*: *Nitidulidae*] and *Ceutorhynchus* spp. [*Coleoptera*: *Curculionidae*]) with the CWM of flower traits in perennial WFS. By following a similar approach, the present analysis aims at identifying those flower traits which affect the abundance of generalist predators (i.e., predatory lacewings, ladybeetles and hoverflies) in such semi-natural habitats.

Material and methods

Field setup

The study was conducted in a field of the AgricultureIsLife experimental farm of Gembloux Agro-Bio Tech (University of Liege) in Belgium (50°34′03″N; 4°42′27″E). The surrounding landscape comprised a matrix of crop fields and pastures, semi-natural habitats (woodlots, riverbanks, roadsides) and urban areas. In June 2013, five replicated WFS (125 m × 8 m) were sown in the centre of the field. Each WFS was separated by 27 m of crop (Fig. 1). Oilseed rape (*Brassicaceae*: *Brassica napus*) was cultivated from September 2013 to June 2014 and winter wheat (*Poaceae*: *Triticum aestivum*) from October 2014 to July 2015. Each WFS was divided into five plots (25 m × 8 m). Four of the plots were sown with a different flower mixture made of three *Poacae* species (*Festuca rubra*, *Agrostis* spp. and *Poa pratensis*) and seven perennial wildflower species that are commonly found in Belgian grasslands (seeds were purchased from Ecosem, Belgium). The fifth plot in each WFS was sown with only the three *Poacae* species. In total, 17 perennial flower species were sown in

the field (Table 1; for more details regarding the sowing protocol and the composition of each mixture at sowing, see Uyttenbroeck et al. 2015, 2017; Hatt et al. 2017c). The layout resulted in a Latin square design with 25 plots and in the present study, three out of the five WFS (in total 15 plots) were used (Fig. 1). Spontaneous plant species were allowed to grow into the plots (i.e., they were not removed) which increased the variability of the different plots in terms of plant composition.

Fig. 1 Experimental design. 1−15 are the flower plots considered. Mean cover of each flower species in every plot is given in Table S2
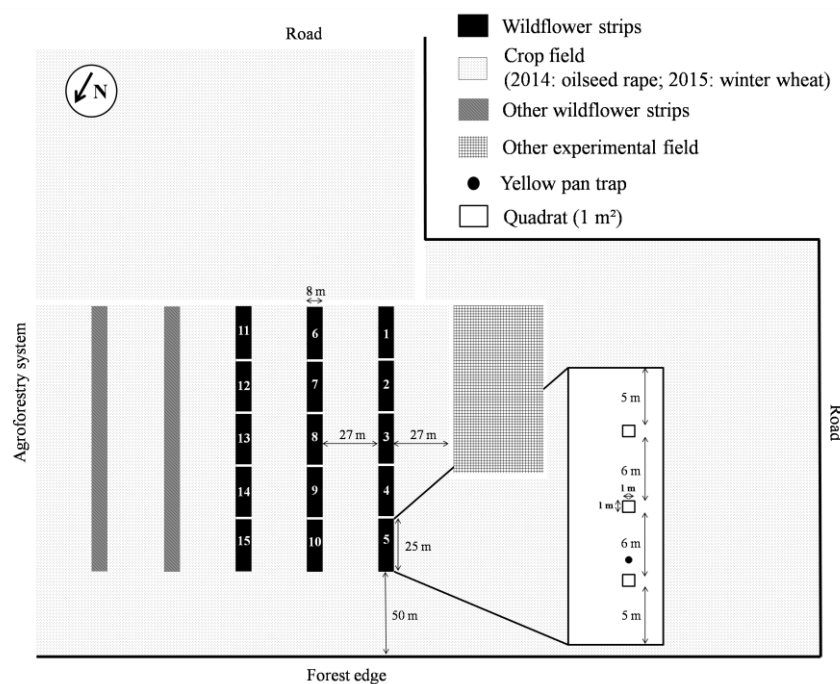

Flower species monitoring and plant traits

In each plot, three 1 m × 1 m quadrats were installed at a distance of 6 m to one another (Fig. 1). On 17th−18th June 2014 and 18th June 2015, the presence of each flower plant and their relative cover (%) were assessed in each quadrat following the nomenclature of Lambinon et al. (2004). Additionally, the blooming flower species were recorded by visual observations following a 20 m × 2 m transect in each plot in May 2014, June 2014 and June 2015. Although flower blooming was expected to change from May to June, it was hypothesised that plant diversity and relative cover were stable through this period.

Each flowering plant recorded in the quadrats was described through seven traits (Table S1) that are known to affect the behaviour of flower-visiting insects (e.g., Sutherland et al. 1999;

Wratten et al. 2003; Fiedler and Landis 2007; Adedipe and Park 2010; Koski and Ashman 2014; Van Rijn and Wäckers 2016). Traits related to visual cues were (i) flower colour (i.e., yellow, white, violet), (ii) the ultraviolet (UV) reflectance of the peripheral part of the flower (numerical value in % indicated as 'UV periphery') and (iii) the presence/absence of UV pattern (i.e., whether the UV reflectance of the internal flower part differed to that of the external flower part). Phenological traits were (iv) the month of the onset of blooming (i.e., numerical value from 1 to 12 with '1' being January) and (v) the number of blooming months (numerical value). Morphological traits were (vi) height (numerical value in cm) and (vii) the flower class that was delineated after Müller (1881) (indicated as 'Flower type') because it notably gives the accessibility of floral food source for flower-visiting insects (i.e., bee flowers, Hymenoptera flowers, flowers with open nectar, flowers with partly hidden nectar, flowers with totally hidden nectar, flower associations with totally hidden nectar). For each plant species, the values of the phenological traits and plant height were obtained from Lambinon et al. (2008), while those of the visual and resource accessibility traits were retrieved from the TRY database (Kattge et al. 2011).

Fig. 2 Mean number (± SE) per trap of lacewings (*Neuroptera*: *Chrysopidae*), ladybeetles (*Coleoptera*: *Coccinellidae*) and hoverflies (*Diptera*: *Syrphidae*) through time over the three sampling periods (May 2014, June 2014 and June 2015)
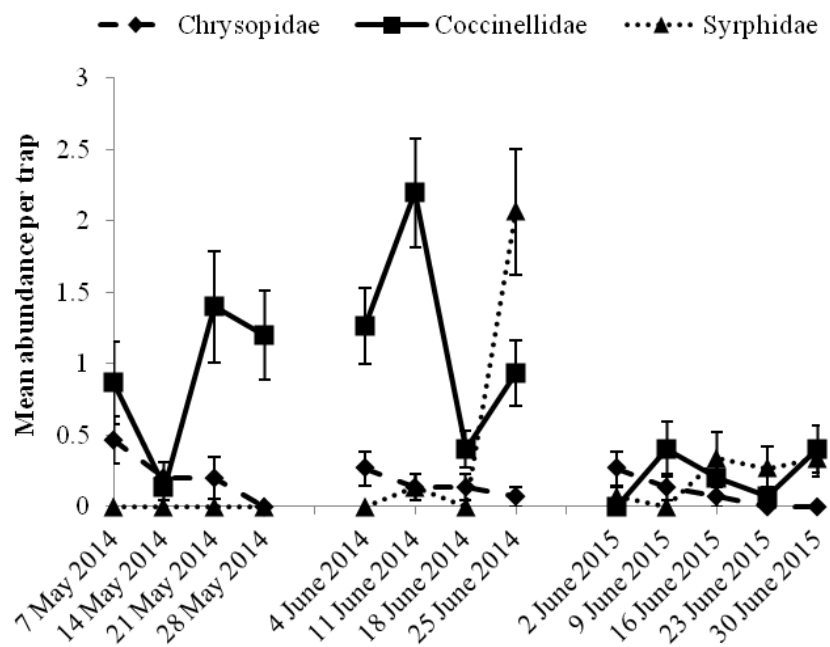
Table 1 List of flower species sown and that spontaneously grew, record of those that bloomed during the different sampling periods, and mean cover (% ± standard error) of each species through the different plots monitored on 17th–18th June 2014 and 18th June 2015.

Family	Species	Sown Yes	Sown No	Blooming May 2014	June 2014	June 2015	Cover (%) Mean (±SE) 2014	Mean (±SE) 2015
	Flowering species							
Apiaceae	*Aethusa cynapium*		x	x	x		0.02 (± 0.09)	
Apiaceae	*Anthriscus sylvestris*	x						
Apiaceae	*Heracleum sphondylium*	x						
Asteraceae	*Achillea millefolium*	x		x	x	x	6.56 (± 5.36)	16.4 (± 11.96)
Asteraceae	*Cirsium arvense*		x			x		1.49 (± 2.63)
Asteraceae	*Crepis biennis*	x		x	x	x	0.78 (± 1.74)	0.09 (± 0.23)
Asteraceae	*Hypochaeris radicata*	x		x	x	x	3.02 (± 6.33)	2.31 (± 5.94)
Asteraceae	*Leontodon hispidus*	x		x	x	x	0.18 (± 0.49)	0.96 (± 2.18)
Asteraceae	*Leucanthemum vulgare*	x		x	x	x	18.09 (± 25.42)	27.00 (± 35.50)
Asteraceae	*Matricaria recutita*		x	x	x		0.49 (± 0.79)	
Brassicaceae	*Capsella bursa-pastoris*		x	x			0.02 (± 0.09)	
Brassicaceae	*Sinapis alba*		x	x	x		0.51 (± 1.33)	
Dipsacaceae	*Knautia arvensis*	x		x	x	x	0.07 (± 0.14)	0.04 (± 0.12)
Fabaceae	*Lotus corniculatus*	x		x	x	x	2.35 (± 8.57)	0.04 (± 0.17)
Fabaceae	*Medicago lupulina*	x		x		x	0.31 (± 0.69)	0.02 (±0.09)
Fabaceae	*Trifolium pratense*	x						
Fabaceae	*Trifolium repens*		x	x	x		0.02 (± 0.09)	
Geraniaceae	*Geranium pyrenaicum*	x		x	x	x	0.40 (± 1.20)	0.42 (± 1.37)
Lamiaceae	*Origanum vulgare*	x						
Lamiaceae	*Prunella vulgaris*	x						
Lythraceae	*Lythrum salicaria*	x						
Malvaceae	*Malva moschata*	x			x	x	0.64 (± 1.24)	0.58 (± 1.16)
Malvaceae	*Malva sylvestris*		x			x		0.02 (± 0.09)
Rubiaceae	*Galium verum*	x			x		0.91 (± 1.22)	

Predator species monitoring

Yellow pan traps (Flora®, 27 cm diameter and 10 cm depth) were used to monitor the abundance and diversity of adult lacewings, ladybeetles and hoverflies in the WFS. One pan trap was placed in the middle of each plot (Fig. 1), filled with water and few drops of detergent to reduce the surface tension of the water. The height of the pan traps was adjusted to the height of the vegetation throughout the experiment. Trapped insects were collected every seven days from 7th May to 28th May 2014, from 4th June to 25th June 2014 and from 2nd June to 30th June 2015 (i.e., four times in May 2014, four times in June 2014 and five times in June 2015). Traps were refilled each time with clean water and drops of detergent. Insects were kept in 70 % ethanol. The starting of insect trapping was delayed in 2015 compared to 2014 because flowers bloomed later in 2015 compared to 2014. Indeed, spring 2014 was especially warm: temperature was on average 2.7°C higher in March 2014 than that in March 2015, and 2.1°C higher in April 2014 than in April 2015 (Institut Royal Météorologique 2014, 2015). In the laboratory, predatory lacewings, predatory ladybeetles and hoverflies which larvae are predators were identified at the species level following the keys of San Martin (2004), Roy et al. (2013) and van Veen (2010), respectively. The identification of the hoverfly species was verified by a taxonomist in case of doubt (see Acknowledgements).

Statistical analyses

As the 15 plots were sown as three replications of five mixtures (see 'Field setup' above), their plant composition was theoretically related between each other. However, the 15 plots were considered independent here because in reality, the vegetation developed differently in each of them (Uyttenbroeck et al. 2015, 2017). Moreover, three sampling periods were considered (i.e., May 2014, June 2014 and June 2015) because the flower species blooming at these periods were different. Indeed, only those flower species blooming in the plots were considered in the analyses.

First, the mean cover of each flower plant (both sown and spontaneous ones) found in each plot was calculated from the three quadrats (i.e., for each plot, the summed cover of each plant species obtained from the three quadrats, divided by three) (Table S2). Then, by using the mean cover in each plot of the plants that bloomed during each period and the list of the plant traits (Table S1), the CWM of each flower trait was calculated for each plot and for the three sampling periods (R function 'dbFD', package 'FD', Laliberté et al. 2014). A single

CWM value per trait was obtained for numerical trait values and a single value for each class was obtained for class trait values (Table S3). The matrix of CWM was later considered as the matrix of explanatory variables. The matrix of the variables to be explained was the mean abundance per week of each insect species trapped in each plot during the three sampling periods (for each plot, the abundance of each insect species was divided by four for May 2014 as well as for June 2014, and by five for June 2015, to avoid any effect due to sampling effort) (Table S4).

The interactions between the CWM of traits and the abundance of generalist predators were analyzed by (i) conducting a forward selection of the significant variables and (ii) performing a redundancy analysis (RDA). Predator abundances were $\log_{10}(x+1)$-transformed prior to the analysis. RDA combines multivariate multiple linear regression and principal component analysis (Borcard et al. 2011). The 'matrix of explanatory variables' was the matrix of the CWM values of each plot, and the 'matrix of centred response' was the matrix of predator abundance in each plot (respectively the matrices X and Y of Borcard et al. 2011). Through the forward selection process (R function 'ordistep', package 'vegan', Oksanen et al. 2015), the plant traits that significantly ($P < 0.05$) affected the abundance of predators were identified and those with the lowest Akaike Information Criterion (AIC) at each step were selected for inclusion in the RDA analysis. The interactions between the abundance of predators and the selected traits were analyzed through a Constrained Analysis of Principal Coordinates using Bray–Curtis distances (R function 'capscale', package 'vegan', Oksanen et al. 2015). The obtained ordination, as well as each of its axis, were tested with a permutation test ($n = 1000$, $P = 0.05$). All statistical analyses were performed with R software (R Core Team 2017).

Results

Flowers

Fourteen flower species were blooming in May 2014 and June 2014, and twelve in June 2015 (Table 1). Among the sown ones, five flower species were not found blooming during the sampling periods and three flower species were found blooming at only some of the sampling periods (Table 1). Seven flower species that were not sown were found blooming in the quadrats: *Aethusa cynapium* (*Apiaceae*), *Matricaria recutita* (*Asteraceae*), *Capsella bursa-pastoris* (*Brassicaceae*), *Sinapis alba* (*Brassicaceae*), *Trifolium repens* (*Fabaceae*) that

bloomed in 2014 only, and *Cirsium arvense* (*Asteraceae*) and *Malva sylvestris* (*Malvaceae*) that bloomed in 2015 only. Among all the flower species, *Leucanthemum vulgare* (*Asteraceae*) and *Achillea millefolium* (*Asteraceae*) were those with the highest cover in both years in the WFS (Table 1).

Predators

Ladybeetles were the most abundant predators trapped in May 2014, June 2014 and June 2015, followed by hoverflies and lacewings (Table 2). Ladybeetles were particularly abundant in May and June 2014, hoverflies in the end of June 2014, and the abundance of the predators remained relatively low in June 2015 (Fig. 2). *Propylea quatuordecimpunctata* (*Coleoptera*: *Coccinellidae*), *Harmonia axyridis* (*Coleoptera*: *Coccinellidae*) and *Coccinella septempunctata* (*Coleoptera*: *Coccinellidae*) were the three main species of ladybeetles trapped, however their abundance varied through time (Table 2): *H. axyridis* was not trapped in 2015, while *C. septempunctata* was trapped only in June in both years. Only *P. quatuordecimpunctata* was trapped throughout the experiment. *Episyrphus balteatus* (*Diptera*: *Syrphidae*) was the most abundant hoverfly trapped, followed by *Eupeodes corollae* (*Diptera*: *Syrphidae*) and *Sphaerophoria scripta* (*Diptera*: *Syrphidae*) (Table 2). Hoverflies were only trapped in June in both years (Fig. 2) and *S. scripta*, which was the most abundant hoverfly species in June 2015, was not trapped in 2014 (Table 2). Finally, *Chrysoperla carnae* (*Neuroptera*: *Chrysopidae*) was the only species of lacewing trapped (Table 2). It was found in a relatively low but stable abundance across the sampling periods (Fig. 2).

Effects of flower traits on predator abundance

The presence or absence of a UV pattern and the type of corolla 'open nectar' were the flower trait values that significantly affected the abundance of trapped predators in the WFS (Table 3). The ordination built with these variables significantly explained the spread of the predators in the different plots (F_{2-39} = 2.20; P = 0.001). 10.13 % of the total variance of the matrix of insect abundance was explained by these variables (axis 1 explained 6.37 % of the variance, F_{1-39} = 2.77; P = 0.001; axis 2 explained 3.76 % of the variance, F_{1-39} = 1.69; P = 0.03).

The abundance of ladybeetles was especially driven by the flower UV pattern (axis 1): *H. axyridis* and *P. quatuordecimpunctata* were correlated with a high cover of flowers showing a UV pattern while *C. septempunctata* was correlated with a high cover of flowers without a

UV pattern (Fig. 3). The abundance of *C. carnae* was also affected by the flower UV pattern (axis 1) and was correlated with a high cover of flowers with a UV pattern (Fig. 3). The abundance of hoverflies was mostly affected by the type of corolla (axis 2): *E. balteatus* particularly, and *E. corollae* to a lesser extent, were correlated with a high cover of flowers with open nectar (Fig. 3).

Table 2 Diversity and summed abundance of predators trapped during sampling periods.

	May 2014		June 2014		June 2015		Total	
	Abundance	%	Abundance	%	Abundance	%	Abundance	%
Chrysopidae	**13**		**9**		**7**		**29**	
Chrysoperla carnea	13	100,0	9	100,0	7	100,0	29	100,0
Coccinellidae	**54**		**73**		**16**		**143**	
Propylea quatuordecimpunctata	27	50,0	28	38,4	6	37,5	61	42,6
Harmonia axyridis	27	50,0	28	38,4	0	0	55	38,5
Coccinella septempunctata	0	0	15	20,5	9	56,2	24	16,8
Tytthaspis sedecimpunctata	0	0	2	2,7	0	0	2	1,4
Harmonia quatripunctata	0	0	0	0	1	6,3	1	0,7
Syrphidae	**0**		**32**		**15**		**47**	
Episyrphus balteatus	0	0	26	81,2	4	26,7	30	63,8
Eupeodes corollae	0	0	3	9,4	4	26,7	7	14,9
Sphaerophoria scripta	0	0	0	0	6	40,0	6	12,8
Melanostoma mellinum	0	0	2	6,3	1	6,6	3	6,4
Syrphus ribesii	0	0	1	3,1	0	0	1	2,1

Table 3 Permutation test ($n = 1000$) of forward selection of explanatory variables affecting the community of predators through the sampling period (May 2014, June 2014, June 2015). * $P < 0.05$; ** $P < 0.01$. Values used in analysis (i.e., the community-weighted means, CWM) of traits and predator abundances in each plot, are given in Tables S3 and S4, respectively.

Explanatory variables		Step 1			Step 2			Step 3		
Trait	Value	AIC	F	P(>F)	AIC	F	P(>F)	AIC	F	P(>F)
UV Pattern	Yes	14.607	2.71	0.005 **						
UV Pattern	No	14.607	2.71	0.005 **						
Flower type	Open nectar	15.724	1.59	0.040 *	14.868	1.65	0.035 *			
Colour	Violet	16.049	1.27	0.130	15.435	1.10	0.225	15.858	0.93	0.575
Colour	Yellow	16.067	1.25	0.135	15.474	1.07	0.340	15.990	0.80	0.830
Blooming duration	Numerical	16.151	1.17	0.215	15.308	1.22	0.145	15.567	1.20	0.190
Blooming start	Numerical	16.242	1.08	0.305	15.434	1.10	0.330	15.657	1.11	0.205
Flower type	Associations with totally hidden nectar	16.307	1.02	0.400	15.435	1.10	0.265	16.063	0.74	0.960
Flower type	Bee flower	16.383	0.94	0.430	15.562	0.98	0.395	15.801	0.98	0.425
UV Periphery	Numerical	16.327	0.99	0.445	15.518	1.02	0.350	15.643	1.13	0.280
Flower type	Hymenoptera flower	16.384	0.94	0.505	15.477	1.06	0.340	15.665	1.10	0.300
Flower type	Partly hidden nectar	16.416	0.91	0.595	15.588	0.96	0.530	15.534	1.23	0.135
Maximum height	Numerical	16.431	0.90	0.595	15.606	0.94	0.510	15.842	0.94	0.585
Colour	White	16.480	0.85	0.715	15.704	0.85	0.705	16.038	0.76	0.885
Flower type	Totally hidden nectar	16.794	0.55	1.000	16.005	0.56	1.000	16.225	0.59	1.000

Fig. 3 Factorial map of redundancy analysis (RDA) carried out on the community of trapped predator species. Grey triangles represent flower plots. Variance explained by each axis is given, as well as the effect of selected factors (i.e., those with the lowest AIC—see Table 3) on them (Permutation test: $n = 1000$; *$P < 0.05$; ***$P < 0.001$)
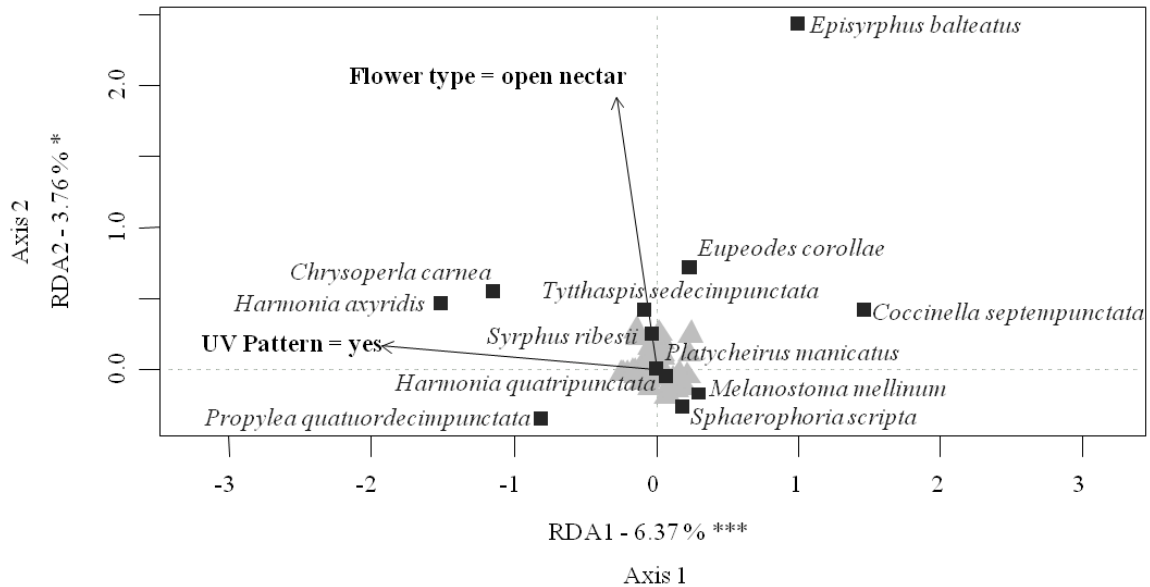
Discussion

In the WFS, the abundance of predatory ladybeetles and lacewings was significantly affected by visual cues (i.e., the presence or absence of flower UV pattern) while the abundance of hoverflies which larvae are predators was affected by the flower morphology (i.e., the shape of the flower corolla).

Effects of UV

Despite variations among taxa, it is known that most insects are sensitive to UV due to UV-absorbing visual pigments (in addition to blue- and green-absorbing pigments) that constitute the photoreceptors of their compound eyes (Briscoe and Chittka 2001). Experiments in controlled environments evaluating the effect of various wavelengths on insect phototactic behaviour showed that *C. carnea* (Kral and Stelzl 1998), *C. septempunctata* (Agee et al. 1990; Lin 1993; Zhou et al. 2013) and *P. quatuordecimpunctata* (Chen et al. 2009) are sensitive to UV. Other experiments using blacklight traps (which have the specificity to emit UV wavelength) in open fields reported the sensitivity to UV of *H. axyridis* (Nalepa 2013) and

confirmed the sensitivity of *P. quatuordecimpunctata* (Ma and Ma 2012). Whereas some flower species generally reflect or absorb UV, others show a UV pattern that is often characterized by UV-reflecting peripheral flower parts and UV-absorbing centre parts, a type of pattern termed 'bull's-eye' (Silberglied 1979).

The bull's eye UV pattern participates in the attraction of pollinators such as bees (*Hymenoptera*) and flies (*Diptera*) (Koski and Ashman 2014) and can guide them to the centre of the flower (Jones and Buchmann 1974; Lunau 1992) where floral pollen and nectar are produced (in the present experiment, none of the flower species growing in the plots produced extrafloral nectar, Weber et al. 2015). To our knowledge, the present study is the first to report the relation between flower UV pattern and a high abundance of some ladybeetle and lacewing species. Although they are more often considered predators than pollinators, *H. axyridis* (Berkvens et al. 2008), *P. quatuordecimpunctata* (Pervez and Omkar 2011) and *C. carnae* (Villenave et al. 2005, 2006) commonly consume flower pollen and nectar (Lundgren 2009b). Hence, flower UV pattern may have attracted and guided these species to such floral food sources. However, the UV pattern is considered an important cue in the attraction of insects at close range only because of the low spatial resolution of insect eyes (Kevan et al. 1996). Hence, we can hypothesize that UV pattern here participated in maintaining the populations of *H. axyridis*, *P. quatuordecimpunctata* and *C. carnae* that had already flown into the WFS, rather than attracting them from a long distance. More controlled experiments assessing the effect of UV pattern on the attractiveness of these predators, as previously conducted with bees and flies (Jones and Buchmann 1974; Lunau 1992; Koski and Ashman 2014), could confirm the present observations.

Similar to other ladybeetle species, *C. septempunctata* is also a pollen and nectar feeder (Triltsch 1999; Ricci et al. 2005). However, it was found abundant in plots with a high cover of flower species without a UV pattern. This result suggests that the attracting and guiding effects of UV pattern vary among ladybeetle species and that *C. septempunctata* may use other cues to locate floral nectar and pollen. This difference in the sensitivity to UV pattern among species of ladybeetles might participate in segregating their habitats, leading in avoiding inter-specific competition and intra-guild predation. Roy et al. (2012), assessing the role of *H. axyridis* arrival in the decline of native ladybeetle species in the UK and Belgium, indeed explained that the non-decline of *C. septempunctata* was partly due to the segregation of its habitat with *H. axyridis*. In contrast, intra-guild predation of *H. axyridis* on *P. quatuordecimpunctata* (both sharing the same habitat according to the present study) has been

reported in Belgium (Hautier et al. 2011) and the decline of *P. quatuordecimpunctata* after the arrival of *H. axyridis* was shown by Roy et al. (2012).

Effects of resource accessibility

Hoverflies were affected by the morphology of the corolla and the most abundant ones *E. balteatus*, and *E. corollae* to a lesser extent, were found abundant in plots with a high cover of flowers with open nectar. This result is in accordance with the BIOLFLOR database (Kolz et al. 2002) indicating that flowers with open nectar are commonly pollinated by hoverflies. Hoverfly species mostly feed on flower nectar and pollen at the adult stage, while it is their larvae that feed on a diversity of prey (at least, for the hoverfly species considered in the present study) (van Veen 2010). It is especially the case for *E. balteatus* (Van Rijn et al. 2013) to which nectar accessibility determines flower choice and abundance in flowering fields (Van Rijn and Wäckers 2016). Moreover, flowers with open nectar benefit *E. balteatus* longevity and reproduction (Laubertie et al. 2012; Wäckers and Van Rijn 2012). However the corolla morphology may not be a trait that intervenes in the long-distance attractiveness of hoverflies. Instead, it more likely determines flower choices by flies hovering above a diversity of flowers (Van Rijn and Wäckers 2016). Hence, we can hypothesize that the high cover of flowers with available nectar has participated in maintaining the populations of *E. balteatus*, and also *E. corollae*, which have flown into the WFS.

Long-distance vs. close-range effects

Colour is an important cue for the long-distance attraction of insects to flowers. Yellow attracts *E. balteatus* (Sutherland et al. 1999), *H. axyridis* (Mondor and Warren 2000; Adedipe and Park 2010) and *C. septempuctata* (Maredia et al. 1992), but contradictory results were found for *C. carnae* (Maredia et al. 1992; Koczor et al. 2017). However, here colour did not determine the abundance of generalist predators in the WFS and instead traits that participate in the orientation to flower food source (UV pattern) and their accessibility (corolla morphology) were important. This result suggests that in multiple species WFS, where flowers with various colours are mixed, generalist predators can fly to the mixtures in a first step, search for suitable flowers within these mixtures in a second step, and spend more time in the mixtures if they find the food source they searched for. Hence, the efficiency of sowing flowering plants to support natural enemies relies not only on long-distance attractiveness but

also on their ability to orient and offer to the visitors the floral food source they are searching for.

Perspectives

In a previous analysis, Hatt et al. (2017b) showed that UV pattern, corolla morphology, as well as colour, also determine the number of parasitoids of oilseed rape beetle pests in the WFS. Present and previous results were obtained by using pan traps. Pan traps present the advantage of continually collecting insects; however, they do not allow assessing a real contact between insects and flowers. Hence, monitoring flower visitations and collecting visitors with a net would be a complementary method to evaluate predator-flower trait interactions (Amy et al. 2018). Still, these results suggest that UV pattern, corolla morphology, as well as colour are the flower traits to take into account when choosing flower plants to compose multiple species WFS towards conservation biological control. Mixtures with a high proportion of yellow flowers, providing accessible nectar, some with a UV pattern and some without, should be suitable to attract and conserve a diversity of generalist predators as well as parasitoids of oilseed rape beetle pests. These findings support the hypothesis that the complementarity between diverse plant functions enhances the large community of natural enemies required to regulate a community of pests (Gardarin et al. 2018). Nevertheless, previous research did not find that an increased functional diversity (i.e., measuring the diversity of functional trait values and range within a community, Díaz and Cabido 2001) at the mixture level increased natural enemy abundance and diversity (Balzan et al. 2014, 2016; Hatt et al. 2017c). Therefore, rather than augmenting the diversity of functional trait values *per se*, tailored flower mixtures could comprise different flower species bearing a diversity of key trait values known to attract and support a variety of natural enemy species. Still, some questions remain: what would be the proportion of each key trait value in the mixture (i.e., the CWM)? What would be the ratio of trait complementarity / trait redundancy? Factorial studies comparing mixtures with a gradient of CWM for some key trait values, or a gradual ratio of trait complementarity / trait redundancy, could provide answers to these novel issues. In addition, although attracting and conserving natural enemies is the first step towards biological control, it will also be necessary to evaluate the efficiency of such tailored flower mixtures on pest suppression in adjacent crops. Finally, considering traits involved in the delivery of additional ecosystem services (e.g., pollination, soil conservation, nutrient

cycling—noticing that there are synergies, but also trade-offs, between them) would furthermore be required to develop multifunctional WFS for sustainable agriculture.

Acknowledgements

Compliance with ethical standards

Conflicts of interest: The authors declare that they have no conflicts of interest.

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Supplementary materials

Table S1 Theoretical trait values for each flower species. The values on blooming start, blooming duration and plant height were obtained from Lambinon et al. (2008), while those on colour, UV periphery, UV pattern, and the flower type were retrieved from the TRY database (Kattge et al., 2011).

Table S2 Mean cover (%), calculated from the three quadrats in each plot, of each blooming flower species found. Sum of percentage may be less than 100 as grass cover and bare soil was also considered when assessing flower cover.

Table S3 Community-Weighted Mean (CWM) calculated for each plot based on the average cover of each flower species found in the quadrats and blooming (see Table S2) and the traits of each species (see Table S1).

Table S4 Weekly mean abundance per trap of each predator species collected in each plot for each sampling period.