Do flower mixtures with high functional diversity enhance aphid predators in wildflower strips?

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Abstract. Among the semi-natural elements in agricultural landscapes, wildflower strips sown at field margins or within fields are potential habitats for the natural enemies of insect pests. As insects are sensitive to a variety of flower traits, we hypothesized that mixtures with high functional diversity attract and support a higher abundance and species richness of aphid flower visiting predators than mixtures with low functional diversity. During a field experiment, repeated over two years (2014 and 2015) in Gembloux (Belgium), aphid predators (i.e., lacewings, ladybeetles and hoverflies) were pan-trapped in five sown flower mixtures (including a control mixture, with three replicates of each mixture) of low to high functional diversity based on seven traits (i.e., flower colour, ultra-violet reflectance and pattern, start and duration of flowering, height and flower class, primarily based on corolla morphology). In both years, the species of flowering plants in the sown mixtures (i.e., sown and spontaneous flowers) were listed, and the realized functional diversity in each plot calculated. Over the two years, a high functional diversity was not associated with high abundance and richness of aphid predators. Moreover, ladybeetles, which made up the majority of the predators trapped, were more abundant in mixtures with very low or intermediate functional diversity at sowing, especially in 2014. We hypothesize that certain flowers, which were abundant in certain mixtures (and not in those exhibiting the highest functional diversity), attracted predators and were sufficiently abundant to support them. Our results present novel information that could be used for developing flower mixtures that provide effective ecosystem services, such as pest control.

INTRODUCTION

Wildflower strips (WFS) are one of several types of habitats used by insects in agricultural landscapes (Holland et al., 2016). There is extensive evidence that, when sown at field margins, WFS support a higher abundance and diversity of insects compared to adjacent crops (reviewed by Haaland et al., 2011). Indeed, WFS provide insects with floral food (such as nectar and pollen), as well as alternative prey and hosts for insect predators and parasitoids, respectively. WFS also provide insects with overwintering sites and shelters against adverse conditions, such as pesticide spraying (Landis et al., 2000). For these reasons, subsidizing the sowing of WFS is part of the agri-environmental policy in the European Union (EU) and some other countries in Europe. Indeed, within the EU, part of the direct payments is conditional on farmers implementing various ecological measures, including the maintenance of "ecological focus areas", such as field margins (i.e. "greening of direct payment" in Pillar 1, Hodge et al., 2015). Moreover, agri-environmental schemes (Pillar 2), which may be adopted by farmers on a voluntary basis, were developed to "reduc[e] environmental risks associated with modern farming on the one hand, and preserve nature and cultivated landscapes on the other hand" (European Commission, 2005). More recently, there have been calls to diversify agri-environmental schemes to include measures enhancing

ecosystem services, in addition to approaches that purely aim to support biodiversity (McKenzie et al., 2013; Ekroos et al., 2014). Among other ecosystem services (Zhang et al., 2007), the natural regulation of insect pests is of particular interest when considering the damaging effects of insecticides on human health and the environment (Devine & Furlong, 2007; Baldi et al., 2013) and the resistance of pests to insecticides (Foster et al., 2007).

Conservation biological control is defined as "the use of tactics and approaches that involve the manipulation of the environment (i.e., the habitat) of natural enemies so as to enhance their survival, and/or physiological and behavioural performance, and resulting in enhanced effectiveness" (Barbosa, 1998). When applied to WFS, such manipulations consist of sowing mixtures that support natural enemies. Yet, enhancing natural enemies through habitat management might not necessarily lead to pest control. In addition to the five hypotheses proposed by Tscharntke et al. (2016), the resources and shelter provided by WFS might retain natural enemies, limiting their ability to control pests in adjacent crops (Rand et al., 2006). Moreover, simply sowing flowers might not generate a higher abundance of key beneficial species in strips, and reduce the abundance of pests in adjacent crops (Uyttenbroeck et al., 2016). One explanation is that some natural enemies might not be attracted to the species of flowers that are sown, or, if they are, might not find the resources that they need (Wäckers, 2004). Therefore, several studies have explored the effects of specific flower species on insect behaviour in order to select the species that effectively attract and support the beneficial ones (Tooker et al., 2006; Fiedler & Landis, 2007a; Van Rijn & Wäckers, 2010; Carrié et al., 2012). However, the *functional traits* of flowers must be assessed in order to understand why some flower species are suitable for insects, and why some are not.

Traits are defined as "any morphological, physiological or phenological feature measurable at the individual level" (Violle et al., 2007). When traits are considered in the environment in which a plant grows, they may affect ecological processes, and are qualified as functional (Díaz & Cabido, 2001). Several studies have explored the effect of flower traits on the behaviour of natural enemies using laboratory experiments, monospecific plots in fields or plants in pots (Mondor & Warren, 2000; Schaller & Nentwig, 2000; Fiedler & Landis, 2007b; Miller et al., 2013; Van Rijn & Wäckers, 2016). The shape of the corolla is another flower trait, which determines how insects access the food provided by flowers. This trait has been extensively studied because many natural enemies need pollen and nectar at certain stages in their development (Lu et al., 2014; Van Rijn et al., 2016). Other morphological traits, such as colour and ultra-violet (UV) reflectance, are involved in host plant recognition and, thus, flower attractiveness (Chittka et al., 1994; Campbell et al., 2010), while plant height might affect their flight (Wratten et al., 2003). Finally, phenological traits, such as the month of the onset and duration of flowering, might be important, because the food provided by flowers must be available when the insects need it (Colley & Luna, 2000).

The extensive literature available on how flower traits affect natural enemy behaviour highlights that different insect species respond differently to the same trait. Therefore, it is hypothesized that mixing flower species with different values for these traits, generating a high functional diversity (FD) at the mixture level, will attract and support a high diversity and abundance of insects. Previous studies showed that plant mixtures with high FD benefit both natural enemies and pollinators (Fontaine et al., 2006; Campbell et al., 2012; Balzan et al., 2014). However, the high FD in these studies was based on an increased diversity in types of corolla, which determines the availability of food resources. Because insects are sensitive to several other flower traits, the present study aimed to explore whether a high FD in flower mixtures based on a multiplicity of traits enhances their use by flower visiting aphid predators. Our results are expected to provide baseline information for developing effective WFS mixtures for use in agricultural landscapes.

MATERIAL AND METHODS

Study design

Field experiments were conducted during the 2014 and 2015 growing seasons in a 9 ha field of the experimental farm belonging to Gembloux Agro-Bio Tech (University of Liège), Namur Province, Belgium (50°34′03″N; 4°42′27″E). The field was characterized by a loamy soil that drains naturally (Service Public de Wallonie, 2014). Before starting this experiment, the field was managed conventionally (i.e. synthesised fertilisers and pesticides were applied), and winter wheat was grown the previous year. No particular soil treatments were implemented before the experiment. A forest (i.e. l'Escaille natural reserve) is present on the north-west side of the field, while a young agroforestry system (planted in 2013) is present on the north-east side. Five WFS (125 m × 8 m) were sown in 2013. Each strip was divided into five equally sized plots (25 m × 8 m), i.e., a total of 25 plots. These plots were sown with five different flower mixtures in a Latin square design. Three out of the five strips were assessed due to logistic constraints and work force limitation (Fig. 1). Four of the five mixtures contained seven flower species and three grass species (*Festuca rubra*, *Agrostis* spp. and *Poa pratensis*). The fifth mixture (control, C) only contained the three grass species (Table 1). All flowering plants are native perennial species that are commonly found in Belgian grasslands (benefits of such species, compared to exotic and/or annual species are reviewed by Fiedler & Landis, 2007a), are typically used in agri-environmental schemes in Wallonia, Belgium, and are available commercially (seeds were obtained from ECOSEM, Belgium). Flower species (0.5 kg.ha⁻¹ of each, see Table 1) and grass species (*Festuca rubra*: 11.5 kg.ha⁻¹; *Agrostis* spp.: 5 kg.ha⁻¹; *Poa pratensis*: 5 kg.ha⁻¹) were sown on 6th June 2013. Equal seed masses of the flower species were sown so that the species were similarly abundant. Species with lower seed mass are expected to suffer a greater mortality and, thus, might need more seeds compared to species with higher seed mass in order to obtain the same abundance (Turnbull et al., 1999). Each year, WFS were mown at the end of June and September. Adjacent to WFS, oilseed rape (*Brassica napus* L.) was grown from September 2013 to June 2014, while winter wheat (*Triticum aestivum* L.) was grown from October 2014 to July 2015.
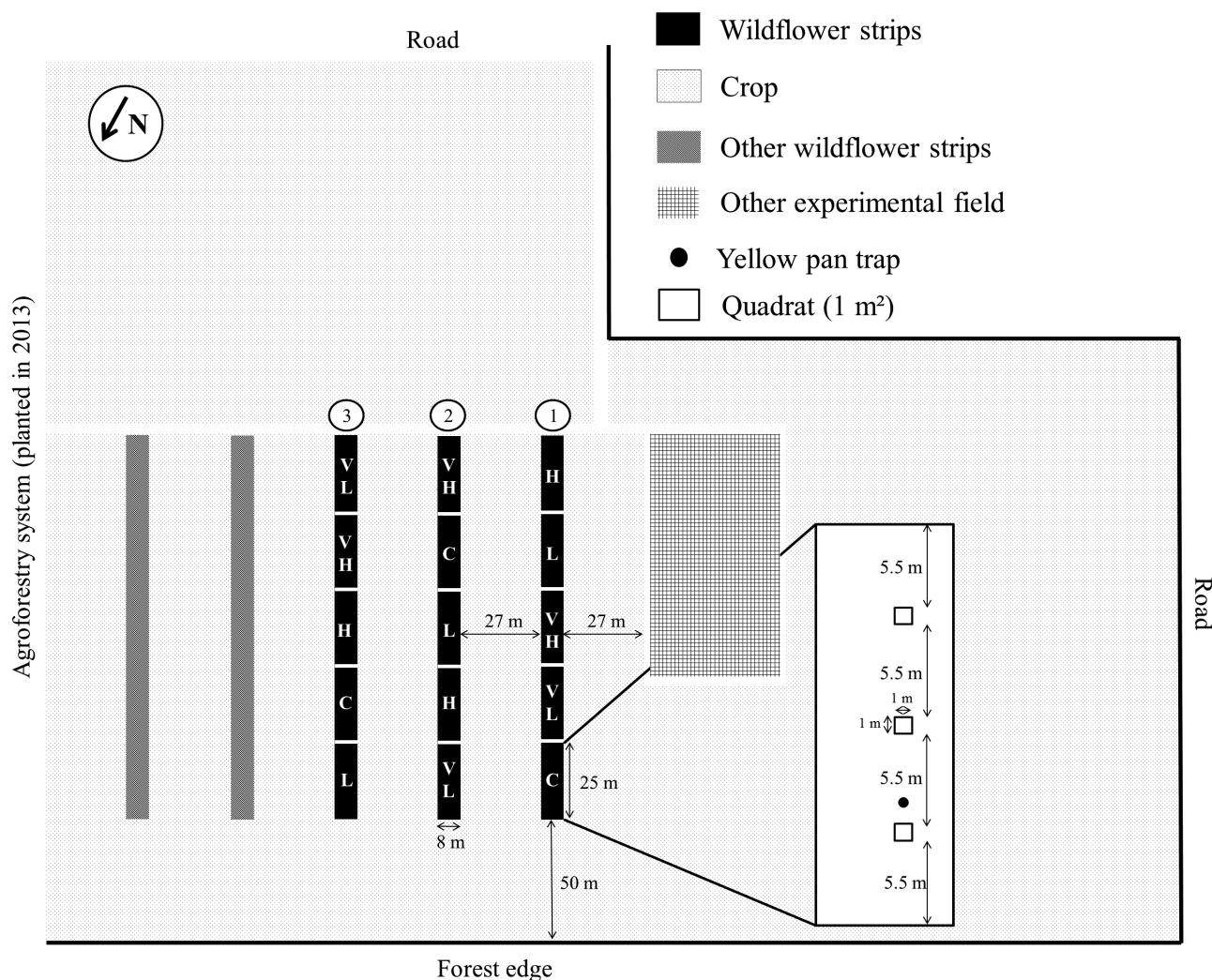
Fig. 1. Experimental field design. C – control, VL – very low, L – low, H – high, and VH – very high are the five flower mixtures sown described in terms of their functional diversity at sowing.

Table 1. Flower mixtures sown in June 2013, constituting a gradient of functional diversity based on Rao's index. C – control, VL very low, L – low, H – high, VH – very high. All flowering species were perennial species that are commonly found in Belgian grasslands and used in agri-environmental schemes in Wallonia, Belgium.

Family	Species	Mixtures / Functional diversity (Rao's index)				
		C / 0	VL / 0.08	L / 0.11	H / 0.15	VH / 0.19
	Flowering species					
Apiaceae	*Anthriscus sylvestris*		x		x	x
Apiaceae	*Heracleum sphondylium*		x			
Asteraceae	*Achillea millefolium*		x	x	x	x
Asteraceae	*Crepis biennis*			x		
Asteraceae	*Hypochaeris radicata*			x		
Asteraceae	*Leontodon hispidus*			x	x	
Asteraceae	*Leucanthemum vulgare*		x		x	
Dipsacaceae	*Knautia arvensis*		x	x		
Fabaceae	*Lotus corniculatus*					x
Fabaceae	*Medicago lupulina*					x
Fabaceae	*Trifolium pratense*		x			
Geraniaceae	*Geranium pyrenaicum*				x	
Lamiaceae	*Origanum vulgare*				x	
Lamiaceae	*Prunella vulgaris*				x	x
Lythraceae	*Lythrum salicaria*			x		x
Malvaceae	*Malva moschata*					x
Rubiaceae	*Galium verum*		x	x		
	Grass species					
Poaceae	*Agrostis* spp.	x	x	x	x	x
Poaceae	*Festuca rubra*	x	x	x	x	x
Poaceae	*Poa pratensis*	x	x	x	x	x

Sown functional diversity

The four flower mixtures (the fifth one being the control) were chosen based on their FD values using Rao's quadratic index (Botta-Dukát, 2005). To create the mixtures, 20 flower species were chosen and described based on seven of their functional traits that were retrieved from Lambinon et al. (2008) and the TRY database (Kattge et al., 2011) (Table S1). The seven traits were chosen based on their potential effect on flower visitors. First, visual cues are known to be decisive for insects when selecting a plant (Campbell et al., 2010). Hence, the following traits were considered: (i) flower colour, (ii) UV reflectance of the peripheral part of the flower, and (iii) whether the UV reflectance of the internal flower part differed from that of the external part (also called "UV pattern"). Second, flowering phenology determines whether floral resources are available when target insects need them (Colley et al., 2000). Therefore, (iv) the month of the onset of flowering and (v) the duration of flowering were chosen. Third, (vi) vegetation height was included, because it might affect insect flight (Wratten et al., 2003). Fourth, (vii) flower class after Müller (1881) was used, because it provides a measure of the the availability of nectar for insects that visit flowers, which determines whether WFS are able to support natural enemies (Van Rijn et al., 2016). All of the possible combinations of mixtures of seven species were listed, and their FD value was calculated (R function "divc", package "ade4"; Dray & Dufour, 2007). Combinations with the lowest and the highest FD were selected, as well as those with a value closest to the 33rd and the 67th percentile of the range. As a result, four mixtures were generated with contrasting FD, termed very low (VL), low (L), high (H) and very high (VH) (Table 1).

Realized functional diversity

To evaluate the effect of the realized FD of the mixtures on flower visiting aphid predators, the effective composition of the flower mixtures was assessed each year. In three 1 m*1 m permanent quadrats in each plot (Fig. 1), flower species were recorded and their relative cover estimated on 18–19 June 2014 and 19–23 June 2015 (before mowing). The nomenclature of Lambinon et al. (2004) was followed. Based on the species of flowers listed (both sown and spontaneous), their traits and their relative cover in the quadrats, the realized FD of the mixture in each plot was calculated.

Monitoring of insect species

Flower visiting predators were trapped from 7 May to 25 June 2014 and from 12 May to 30 June 2015 (i.e. for seven weeks in both years). In each plot, a yellow pan trap (Flora®, 27 cm diameter and 10 cm depth) was installed on a fiberglass stick and positioned at vegetation height. Its position was adjusted during the growing season to follow plant growth. Traps were filled with water containing a few drops of detergent (dish-washing liquid) to reduce the surface tension of the water. The traps were emptied and refilled every seven days, and the trapped insects were conserved in 70% ethanol. Aphidophagous ladybeetles (Coleoptera: Coccinellidae), as well as lacewings (Neuroptera: Chrysopidae) and hoverflies (Diptera: Syrphidae), the larvae of which prey on aphids, were identified to species using identification keys in San Martin (2004), van Veen (2010) and Roy et al. (2013), respectively. Because the adults of these predatory families are all highly mobile and able to traverse agricultural landscapes (Evans, 2003; Villenave et al., 2006; Almohamad et al., 2009), their dispersion through the different plots was comparable.

Statistical analyses

First, the linear relation between the sown and realized FD in each plot was tested for both years by using Pearson's correlation (P < 0.05).

Second, the effects of the sown mixtures on insect abundance (response variables: all predators pooled, and lacewings, ladybeetles, hoverflies individually) and total predator species richness (species of the three predator families pooled) were assessed by fitting generalised linear mixed effect models (R function "glmer", package "lme4"; Bates et al., 2014) with Poisson error distribution (log-link function). Mixtures (C, VL, L, H, VH), years (2014, 2015) and their interaction were included as fixed factors, and the plots included as random effects, as measures were repeated on seven consecutive occasions in the same plots each year. For every model, data over-dispersion was tested and found to occur for the summed predator, ladybeetle and hoverfly abundance. For these variables, generalised linear models with negative binomial error distribution were fitted (R function "glm.nb", package "MASS", Venables & Ripley, 2002), as suggested by Ver Hoef & Boveng (2007). The effects of fixed factors in every model were tested using likelihood-ratio tests (P < 0.05). When their interaction was significant, analyses were performed for each year separately.

Third, the effect of the realized FD on insect abundance (response variables: all predators pooled, and lacewings, ladybeetles, hoverflies individually) and total predator species richness (numbers of species of the three predator families pooled) were assessed for each year separately, as each year each plot potentially had a different value of FD, by fitting generalised linear mixed effect models. FD values were included as fixed factors and plots were included as random factors. Data over-dispersion was tested and found to occur for the summed predator, ladybeetle and hoverfly abundance in 2014. Thus, generalised linear models with negative binomial error distribution were fitted instead. The effects of realized FD in every model were tested using likelihood-ratio tests (P < 0.05). All analyses were done using R program (R Core Team, 2013).

RESULTS

Flower cover, species and functional diversity

Twenty-one and 20 flower species were recorded in the quadrats in 2014 and 2015, respectively (Table 2), out of which eight species in both years were not sown. Among these spontaneous species, *Cirsium arvense* and *Sinapis alba* had the highest cover in plots in 2014, whereas in 2015 it was *C. arvense* and *Rumex obtusifolius* (Table 2). The cover of all other spontaneous species never on average exceeded 3% of the quadrat surface in each plot. Conversely, three of the sown species, *Anthriscus sylvestris*, *Heracleum sphondylium* and *Lythrum salicaria*, were not recorded in either year, with *Origanum vulgare* also not recorded in 2015.

The values of the realized FD in 2014 and 2015 are given in Table 2. Except for the C plots, the values of the realized FD were lower than those of the sown mixtures. No significant correlations were found between the sown and realized FD in both 2014 (df = 13; r = 0.48; p-value = 0.071) and 2015 (df = 13; r = 0.22; p-value = 0.423).

Aphid predator abundance and diversity

Predators were significantly more abundant in 2014 than 2015 (i.e. 161 and 51 individuals trapped respectively, Ta-

Table 2. Realized functional diversity (FD, Rao's index) and mean cover (%) of each flower species in each plot (C – control, VL – very low, L – low, H – high, VH – very high; the numbers are the number of replicates of each mixture sown; see Fig. 1), based on the three 1 m² quadrats in each plot in 2014 and 2015. Flower cover was assessed at the end of June each year.

	C1	C2	C3	VL1	VL2	VL3	L1	L2	L3	H1	H2	H3	VH1	VH2	VH3
2014															
Realized FD (Rao's index)	0.075	0.053	0.012	0.006	0.006	0.006	0.044	0.046	0.048	0.093	0.020	0.058	0.055	0.115	0.112
Flower cover (%)															
Achillea millefolium	0.67	0	0.67	9.67	11.67	4.67	5	14.33	12.67	1	15	9.67	8.33	3.67	1.33
Aethusa cynapium	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0
Capsella bursa-pastoris	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cichorium intybus	0	0	0	0.67	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	1	5.33	0.33	0	0	0.67	0.67	0	0.67	0	0	0	0	0	0.67
Conyza canadensis	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0	0
Crepis biennis	0	0	0	0	0	0	6	1.33	3.67	0	0	0	0.67	0	0
Galium verum	0.33	0	0	2	2	3.33	1.33	1	3.33	0	0.33	0	0	0	0
Geranium pyrenaicum	0	0	0	0	0	0	0.33	0	0	4.67	0.33	0.67	0	0	0
Hypochaeris radicata	0.67	0	0	0	0	0	11.33	13	20	0	0.33	0	0	0	0
Knautia arvensis	0	0	0	0	0	0.33	0.33	0	0.33	0	0	0	0	0	0
Leontodon hispidus	0	0	0	0	0	0	0	1	1.67	0	0	0	0	0	0
Leucanthemum vulgare	0.67	0	0	56.67	56.67	63.33	0	1	2	3.67	38.33	45	0	1	3
Lotus corniculatus	0	0	0	0	0	0	0	0	0	0	0	0	33.33	1.33	0.67
Malva moschata	0	0	0	0	0.33	0	0	0	0	0	0	1.33	2.33	1.33	4.33
Matricaria recutita	1	0.33	0.33	1	0	0	0	0	0	0.33	0	0	2.67	0	1.67
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	2.33	1	1.33
Origanum vulgare	0	0	0	0	0	0	0	0	0	0	0.67	0	0	0	0
Prunella vulgaris	0	0	0	0	0	0	0	0	0	0	1.67	8	1.33	2	1
Sinapis alba	1.33	1.33	0	0	0	0	0	0	0	0	0	0	0	5	0
Trifolium repense	0	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0
2015															
Realized FD (Rao's index)	0.096	0.000	0.036	0.008	0.011	0.005	0.057	0.051	0.059	0.059	0.018	0.026	0.075	0.041	0.069
Flower cover (%)															
Achillea millefolium	1	0	1.33	9.67	20	8.67	13.67	24	20.33	5.33	33.33	22.67	20	38.33	27.67
Silene latifolia	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0	0
Cirsium arvense	1.67	10.67	0.67	0	0	2	1.33	0	0.67	1	0.33	0.33	1	2	0.67
Crepis biennis	0	0	0	0	0	0	0.67	0.67	0	0	0	0	0	0	0
Galium verum	0.33	0	0.33	2.33	3.33	1.67	1.33	1	4	0	0	0	0.33	0	0
Geranium pyrenaicum	0	0	0	0	0	0	0.67	0	0	5.33	0.33	0	0	0	0
Hypochaeris radicata	0.33	0	0	0	0.33	0	3.33	22.33	8	0	0.33	0	0	0	0
Knautia arvensis	0	0	0	0	0	0.33	0.33	0	0	0	0	0	0	0	0
Leontodon hispidus	0	0	0	0	0	0	1	2.67	8.33	0	1.33	1	0	0	0
Leucanthemum vulgare	1.67	0	0	71.67	80	96	0	1.33	8	19.33	68.33	51.67	0	0.33	6.67
Lotus corniculatus	0	0	0	0	0	0	0	0	0	0	0	0	0.67	0	0
Malva moschata	0	0	0	0	0	0	0	0	0.67	0	0.33	0.33	1.67	1.33	4.33
Malva sylvestris	0	0	0	0	0	0	0	0	0.33	0	0	0	0	0	0
Medicago lupulina	0	0	0	0	0	0	0	0	0	0	0	0	0.33	0	0
Plantago major	0.33	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunella vulgaris	1.33	0	0	0.33	0.67	0	0	0	0	0	1.67	2.67	2	2	1.67
Rumex obtusifolius	0	0	0	3.33	0	0	0	1.33	0	0	0	0	10.33	0.67	0
Rumex crispus	2	0	0	0	0	0	0	0	0	0	0	0	0.67	0	0
Sonchus sp.	0	0	0	0.33	0	0	0.67	0	0	0	0	0	0	0	0
Trifolium sp.	0	0	0	0.33	0	0	0	0	0	0	0	0	0	0.67	0

bles 3–4). Ladybeetles were the most abundant predators in both years, especially in 2014, followed by hoverflies and lacewings (total abundance is presented in Table 3). Equal species richness was recorded for ladybeetles and hoverflies in 2014 (i.e., four species); however, hoverfly species richness was higher in 2015 (i.e. five and three species respectively, Table 3). During this two year experiment, only one species of lacewing was recorded.

Effect of sown mixtures and realized functional diversity on aphid predators

Only ladybeetle abundance was significantly associated with the mixtures sown (Table 4). As the interaction be-

tween mixture and year effects was also significant, annual analyses showed that mixtures had a nearly significant effect in 2014 (df = 4; χ^2 = 9.4; p-value = 0.052) and a significant effect in 2015 (df = 4; χ^2 = 12.4; p-value = 0.014). The mixtures had no significant effect on the sums of predators, lacewings and hoverflies and their species richness (Table 4). In 2014, ladybeetles were the most numerous in VL, L and H mixtures, whereas they were the least abundant in L and VH mixtures in 2015 (Fig. 2). Neither insect abundance (i.e., sum of predators, as well as every family separately) nor their species richness was significantly affected by the realized FD in either 2014 or 2015 (Table 5).

Table 3. Summed abundance of every aphid predator species trapped in each mixture (over a seven-week period from May to June in both years, three repetitions per mixture, one yellow pan-trap per repetition, which was emptied and refilled every week).

| | 2014 | | | | | | 2015 | | | | | | 2014–2015 |
	C	VL	L	H	VH	Total	C	VL	L	H	VH	Total	Total
Lacewings	4	5	3	2	1	15	1	2	3	2	1	9	24
Chrysoperla carnae (Stephens, 1836)	4	5	3	2	1	15	1	2	3	2	1	9	24
Ladybeetles	15	31	23	30	14	113	5	6	–	9	3	23	136
Coccinella 7 punctata (Linnaeus, 1758)	–	8	3	4	–	15	1	4	–	3	1	9	24
Harmonia 4 punctata (Pontoppidan, 1763)	–	–	–	–	–	–	–	–	–	1	–	1	1
Harmonia axyridis (Pallas, 1773)	7	11	9	12	8	47	–	–	–	–	–	–	47
Propylea 14 punctata (Linnaeus, 1758)	9	12	10	14	5	50	4	2	–	5	2	13	63
Tytthaspis 16 punctata (Linnaeus, 1761)	–	–	1	–	1	2	–	–	–	–	–	–	2
Hoverflies	6	6	9	6	6	33	6	1	2	6	4	19	52
Episyrphus balteatus (De Geer, 1776)	5	5	8	4	4	26	1	1	–	–	3	5	31
Eupeodes corollae (Fabricius, 1794)	–	1	1	–	1	3	1	–	2	1	–	4	7
Melanostoma mellinum (Linnaeus, 1758)	–	–	–	2	–	2	–	–	–	2	–	2	4
Platycheirus manicatus (Meigen, 1822)	–	–	–	–	–	–	–	–	–	1	–	1	1
Sphaerophoria scripta (Linnaeus, 1758)	–	–	–	–	–	–	4	–	–	2	1	7	7
Syrphus ribesii (Linnaeus, 1758)	–	–	–	–	1	1	–	–	–	–	–	–	1
Total	25	42	35	38	21	161	12	9	5	17	8	51	212

"–" indicates that no individuals of these species were trapped.

DISCUSSION

Our study indicates that a high abundance and richness of flower visiting aphid predators is not necessarily associated with a high FD of flower mixtures. Only ladybeetles, which made up the majority of the predators trapped in both years, were affected by the sown mixtures. Ladybeetles were mostly trapped in plots where the FD of the mixture was very low or intermediate at sowing, especially in 2014.

A surprisingly low number of predators was trapped. In the case of hoverflies, we trapped on average 30 times more per week per trap in the crops growing adjacent to the WFS in 2015 (Hatt et al., 2017) while Tschumi et al. (2016) trapped on average 20 times more per week per trap in WFS adjacent to potato crops in June and July in Switzerland. A reason for this might be that hoverfly abundance often peaks in July in such regions, as was the case in 2015 in adjacent crops (Hatt et al., 2017). In the present experiment, insects were trapped in the WFS only up to the end of June. As for ladybeetles, a slightly higher number than recorded in these previous studies was trapped in 2014, but three times less was recorded in 2015. Indeed, insect abundance differed in the two years of the study. The higher abundance of predators, especially ladybeetles, in 2014 might be due to the early summer in that year, favouring greater insect occurrence in early spring compared to 2015. In addition, other studies conducted in the same region report a very low density of ladybeetles in 2015, indicating that their abundance was low that year in the region of Gembloux (Fassotte, 2016; Hatt et al., 2017). Similar annual variability in ladybeetle abundance is reported in Belgium (Vandereycken et al., 2013).

The results recorded for the effect of FD contradicted our hypothesis. We expected the abundance and richness of natural enemies to be positively associated with FD,

Table 4. Effect of mixtures sown (C, VL, L, H, VH) and years (2014, 2015), and their interaction, on the abundance and species richness of predators. Signs of estimates were retrieved from the selected models when significant, "–" means that the values for 2015 were lower than those for 2014. Degree of freedom (df), χ²- and p-values were obtained from the likelihood ratio tests performed on the selected model. * P < 0.05; *** P < 0.001.

	Estimate	df	χ²	p-value
Abundance				
Predators				
Mixture		4	7.75	0.101
Year	–	1	45.6	< 0.001 ***
FD:Year		4	6.18	0.186
Lacewings				
Mixture		4	3.41	0.476
Year		1	1.52	0.212
FD:Year		4	1.74	0.784
Ladybeetles				
Mixture		4	12.2	0.016 *
Year	–	1	55.3	< 0.001 ***
FD:Year		4	9.82	0.044 *
Hoverflies				
Mixture		4	1.12	0.891
Year		1	1.99	0.158
FD:Year		4	2.74	0.602
Species richness				
Predators				
Mixture		4	7.12	0.130
Year	–	1	33.7	< 0.001 ***
FD:Year		4	5.67	0.225

Table 5. Effect of realized functional diversity (Rao's index) on predator abundance and species richness of predators in 2014 and 2015. Signs of estimates were retrieved from the selected models. Degree of freedom (df), χ²- and p-values were obtained from the likelihood ratio tests performed on the selected models.

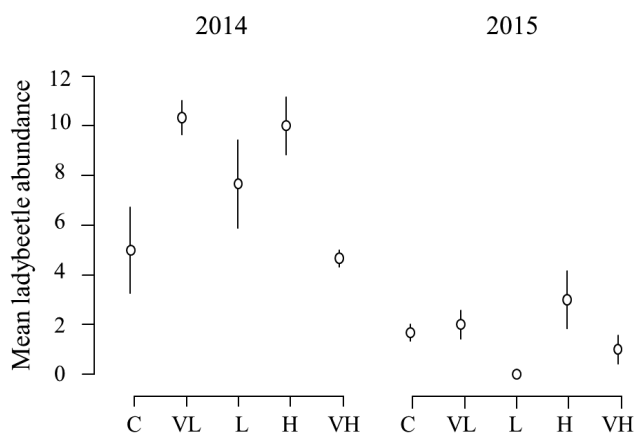| | 2014 | | | | 2015 | | | |
	Estimate	df	χ²	p-value	Estimate	df	χ²	p-value
Abundance								
Predators	–	1	2.78	0.096	–	1	0.04	0.846
Lacewings	–	1	2.18	0.140	–	1	0.12	0.73
Ladybeetles	–	1	2.93	0.089	–	1	1.70	0.192
Hoverflies	–	1	<0.01	1	+	1	2.09	0.148
Diversity								
Species richness	–	1	2.75	0.097	–	1	0.63	0.428

2014   2015

Fig. 2. Mean (summed abundance recorded during seven weeks of trapping each year divided by the three repetitions ± SEM) lady-beetle abundance in each mixture sown, based on their functional diversity at sowing: C – control, VL – very low, L – low, H – high, VH – very high.

because these predators have different nutritional requirements and might react differently to different flower traits at different times. However, our findings are consistent with Balzan et al. (2014, 2016), who report that FD had no effect on the abundance of flower visiting natural enemies. Furthermore, these authors report that mixtures with intermediary FD support a higher natural enemy richness. Balzan et al. (2014, 2016) increased FD by increasing the diversity of flower corolla types, which determines the ability of natural enemies to benefit from flower nectar (Vattala et al., 2006; Van Rijn & Wäckers, 2016). Insect abundance and diversity recorded in this study, however is not associated with FD based on seven traits. Balzan et al. (2014, 2016) suggest that the presence of certain species of plants, particularly those attractive to natural enemies (i.e., *Apiaceae* spp. in their case), might mask the effect of FD on flower visitors. This might also have affected our results, especially as some flowering species covered a large surface area in some plots, whereas others that were sown were not even recorded (Table 2).

There are several explanations for the unequal establishment of different species of plants, despite similar seed weights being sown. For instance, competition for space and resources might result in the establishment of the most competitive species. Alternatively, the conventional farming practices used in the field before the experiment (especially the application of nitrogen fertilisers) might have favoured the most productive species, which limited the establishment of diversified mixtures (Pywell et al., 2002). In our experiment, the Asteraceae *Leucanthemum vulgare* was the most abundant species in VL and H mixtures (Table 2). The high abundance of this species, compared to others, may account for the lower than expected values of realized FD in H and the low values in VL plots. However, most of the predators trapped, especially ladybeetles, were trapped in the H and VL plots. *Leucanthemum vulgare* is typically visited by hoverflies, ladybeetles and lacewings (Ricci et al., 2005; Carrié et al., 2012; Wäckers & Van Rijn, 2012), because it is a rich source of nectar and pollen (Brodie et

al., 2015). This resource might be of particular benefit to ladybeetles, for which pollen is one its most nutritious non-prey food sources, enabling them to complete their development and survive when prey are scarce (Berkvens et al., 2008; Lundgren, 2009).

Adult hoverflies exclusively feed on flowers, with pollen providing a source of proteins that directly influence their fecundity, while nectar is a source of sugars, providing energy and increasing their longevity and foraging capacity (Laubertie et al., 2012; Van Rijn et al., 2013). Thus, any flower that was abundant in the mixtures and produced nectar (i.e. flowers with shallow florets, because hoverflies have a short proboscis; Van Rijn & Wäckers, 2016) and pollen are likely to be attractive. For instance, the Asteraceae, *Achillea millefolium*, is typically visited by hoverflies (Salveter, 1998; Tooker et al., 2006; Carrié et al., 2012) and enhances their longevity (Van Rijn & Wäckers, 2016). In our study, *A. millefolium* was present in every flower mixture, and was quite abundant in most plots (Table 2). The presence of this species might have resulted in hoverflies being equally distributed across the different treatments. Moreover, ladybeetles and hoverflies are sensitive to colour, especially yellow (Sutherland et al., 1999; Mondor et al., 2000). Hoverflies are also sensitive to flowers with a contrasting UV-pattern (Koski & Ashman, 2014). Some species with these traits might have been attractive. For instance, *Hypochaeris radicata* was quite abundant in L mixtures, especially in 2014, and might have attracted hoverflies, resulting in their being slightly (but not significantly) more numerous in plots with these than other mixtures.

Lacewings were less abundant than other predators in both years. They might also have benefited from a large variety of flowers in the strips, as they are considered to be opportunistic (Villenave et al., 2006). In addition, some spontaneous weeds, such as *C. arvense* and *R. obtusifolius* (the most abundant spontaneous plants listed in several plots), might have attracted predators, as they often host aphids that are prey for ladybeetle adults and the larvae of all three predators studied (Salveter, 1998). This phenomenon might also explain why some individuals were trapped in the control plots, even when few floral resources were available but with the values of the functional traits differed enough to result in higher than expected values of realized FD.

The presence of prey in adjacent crops might also have attracted natural enemies out of the flower strips, potentially explaining their generally low abundance in the mixtures. Indeed, hoverfly adults for instance search for aphid colonies in which to lay their eggs after having fed on flowers (Almohamad et al., 2009). While further analyses are needed to confirm such a hypothesis, a higher abundance of natural enemies in adjacent crops than in WFS, would enhance biological pest control. Despite the higher FD of VH mixtures at sowing, and to some extent in 2014 and 2015 (Table 2), the low attraction of the WFS to natural enemies might also be explained by the limited establishment of some of the species sown. The cover of

sown flower species in the quadrats was low (except for *A. millefolium*, which was also abundant in other mixtures) and, some sown species, like *Lythrum salicaria,* were not even recorded in the quadrats (Table 2). Moreover, some of the plant species that established successfully could a priori not provide food for hoverflies, ladybeetles or lacewings, because of their flower morphology. This is the case for plants of both Fabaceae and Malvaceae, which have a corolla that is too deep for e.g. hoverflies to access their nectar (Wäckers & Van Rijn, 2012).

The non-significant correlations between the sown and realized FD indicate that it is difficult to obtain a certain realized FD by sowing flower mixtures. This may be due to various factors such as the presence of spontaneous species, the better development of the most productive and competitive, and the non-development of some sown species. Considering the optimal growing conditions (e.g. exposure to sun, humidity, soil disturbance) for the different species on the one hand, and better balancing of the number of seeds between the different species by also considering their productivity and competitiveness (and not only considering their weight as in this study) on the other hand, may result in more diversified mixtures. Moreover, rather than relying on mixture FD, sowing flower species that are known to support natural enemies might enhance their presence in WFS, and even favour pest control in adjacent crops. This is the "pick and mix" approach developed by Wäckers & Van Rijn (2012) and successfully tested in the field by Tschumi et al. (2014, 2015, 2016). Nevertheless, WFS have to provide multiple ecosystem services, including pollination, and participate in the conservation of insect species that are endangered in agricultural landscapes (Ekroos et al., 2014; Batáry et al., 2015). Within this context, a higher diversity of arthropods could potentially occur in flower mixtures with a high FD. Indeed, Balzan et al. (2014) report that the abundance of wild bees (Hymenoptera) increases with FD. Depending on the objectives assigned to WFS (i.e. enhancing pest control, pollination, conservation, or all of these combined), different strategies could be used when formulating flower mixtures.

Within an agricultural context, sowing WFS is proposed to enhance biodiversity conservation and ecosystem services, with doubts being raised about whether they will be a source of pests infesting adjacent crops (Frank, 1998; Hatt et al., 2015; Tscharntke et al., 2016). Moreover, it is worth establishing the threshold at which increasing the mixture of FD also improves its attraction for predators and shelters pests. For instance, aphids use visual and olfactory cues to locate host plants (Döring, 2014). Thus, increasing plant functional diversity might increase the chance of including more colours, UV patterns and odours that are attractive to aphids. It is also possible, a higher diversity of trait values might confuse aphids. For instance, when a high diversity of colours is present, the attractive ones might be masked. In parallel, if a large variety of odours is present, it might not be possible to distinguish attractive cues. This effect of diversified plant systems was first theorised by Root (1973) in the *Resource concentration hypothesis*. This suggests

that diversified cropping systems (e.g. intercropping), or, in the present case, diversified flower strips, might be less attractive to pests than monospecific systems (Letourneau et al., 2011; Lopes et al., 2016).

The present study investigated an array of traits; however, the selection was not exhaustive. Other traits could have been chosen; for instance, traits related to the abundance and quality of nectar and pollen (rather than just availability, as used here in the context of "flower type" based on the classification of Müller, 1881) or the profile of semiochemical volatiles emitted by flowers. Indeed, flower visiting insects, particularly aphid predators, respond to nectar and pollen abundance and quality, as well as odour (Laubertie et al., 2006; Adedipe & Park, 2010; Laubertie et al., 2012). Thus, it is necessary to screen a variety of flower species for these traits and establish their ability to attract and support aphid predators, in order to advance our knowledge in this field of research. As the value of the FD being tested depends on the chosen traits, further field-based research assessing different mixtures based on several other traits should be implemented, with the objective of enhancing the ability of WFS to deliver multiple ecosystem services in agriculture.

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Table S1. Traits of each flower species considered to constitute the mixtures. Traits were retrieved from Lambinon et al. (2008) and the TRY database (Kattge et al., 2011).

Flower species	Colour	UV periphery (%)	UV pattern	Blooming start	Blooming duration (months)	Max. height (cm)	Flower type (Müller, 1881)
Achillea millefolium	White	3.5	No	June	6	45	Associations with totally hidden nectar
Anthriscus sylvestris	White	3.5	No	May	2	120	Open nectaries
Crepis biennis	Yellow	33.5	Yes	June	3	120	Associations with totally hidden nectar
Galium verum	Yellow	3.5	No	May	5	80	Open nectaries
Geranium pyrenaicum	Violet	76	Yes	May	5	60	Totally hidden nectar
Heracleum sphondylium	White	3.5	No	June	3	150	Open nectaries
Hypericum perforatum	Yellow	53	Yes	July	3	60	Pollen flowers
Hypochaeris radicata	Yellow	33.5	Yes	June	4	60	Associations with totally hidden nectar
Knautia arvensis	Violet	3.5	No	June	4	60	Associations with totally hidden nectar
Leontodon hispidus	Yellow	53	Yes	June	5	40	Associations with totally hidden nectar
Leucanthemum vulgare	White	3.5	No	May	4	60	Associations with totally hidden nectar
Lotus corniculatus	Yellow	3.5	No	May	5	30	Bee flowers
Lythrum salicaria	Violet	76	Yes	June	4	150	Totally hidden nectar
Malva moschata	Violet	53	Yes	July	3	80	Totally hidden nectar
Medicago lupulina	Yellow	3.5	No	April	7	50	Hymenoptera flowers
Origanum vulgare	Violet	11.5	No	July	3	80	Totally hidden nectar
Prunella vulgaris	Violet	76	Yes	July	3	50	Hymenoptera flowers
Ranunculus acris	Yellow	21.5	Yes	May	5	90	Partly hidden nectar
Silene latifolia	White	21.5	Yes	May	6	90	Moth flowers
Trifolium pratense	Violet	3.5	No	May	6	50	Bee flowers