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Augmenting flower trait diversity in wildflower strips to optimise the conservation of arthropod functional groups for multiple agroecosystem services

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Abstract Sown wildflower strips are increasingly being established in Europe for enhancing arthropod conservation and the provision of ecosystem services, including biotic pollination and natural pest control. Here we use floral traits to identify different plant functional effect groups. Floral resources were provided in four experimental levels characterised by a cumulatively increasing flower trait diversity and vegetation stand complexity. The first level consisted of a bare control strip, whilst in each subsequent level three wildflower species with different functional traits were added (Level 0: control; Level 1: three Apiaceae species; Level 2: three Apiaceae and three Fabaceae species; Level 3: three Apiaceae, three Fabaceae species, and Centaurea jacea (Asteraceae), Fagopyrum esculentum (Polygonaceae), Sinapis alba (Brassicaceae)). Plots with sown wildflower strip mixtures were located adjacent to experimental plots of organically-managed tomato crop, which is attacked by multiple pests and partially relies on bees for fruit production, and hence dependent on the provision of pollination and pest control services. Results obtained here show that the inclusion of functionally diverse wildflower species was associated with an augmented availability of floral resources across time, and this increased the abundance of bees and

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anthocorids throughout the crop season. Several natural enemy groups, such as parasitoids, coccinelids and ground-dwelling predators, were not significantly enhanced by the inclusion of additional flower traits within the strips but the presence of flower resources was important to enhance their conservation in an arable cropping system.

Keywords Organic agriculture · *Solanum lycopersicum* L. · Natural enemies · Parasitoids · Pollinators · Predators

Introduction

Agricultural productivity and food security depend on agrobiodiversity and the numerous ecosystem services it can provide, such as biotic pollination and natural pest control (Cassman et al. 2005). The loss of natural pest control, an arthropod-mediated ecosystem service, and its replacement with human controls, such as pesticide applications and host plant resistance in intensive large monocultures, has important economic implications and it has been estimated that it would cost society between €40 billion and €74 billion to replace global biocontrol services (Naylor and Ehrlich 1997). Similarly, pollination services are important for maintaining crop productivity of 75 % of the leading global food crops and amounting to 35 % of the global production volumes (Klein et al. 2007). The total economic value of pollination worldwide has been estimated at €153 billion (Gallai et al. 2009), and the loss of pollination services from agricultural systems has been associated with lower productivity and yield growth for crops showing greater pollinator dependence, which has been compensated by the cultivation of more land (Garibaldi et al. 2011).



Many studies have investigated the use of habitat management strategies in arable systems that were aimed at increasing plant diversity and sowing wildflower strips to enhance the conservation of arthropods, including pollinators and natural enemies, and to maintain the services these groups provide in agroecosystems (Haaland et al. 2011). However, while it has often been suggested that the management of multiple ecosystem services is desirable and that synergistic effects may exist (Gurr et al. 2003; Kremen and Chaplin 2007; Fiedler et al. 2008; Bianchi et al. 2013), the compatibility of habitat management strategies for different agriculturally-functional arthropod groups and for ensuring the provision of pollination and pest control services has recently received more attention (Otieno et al. 2011; Campbell et al. 2012; Carrié et al. 2012; Wratten et al. 2012; Shackelford et al. 2013). Several natural enemy groups make use of non-pest plant-derived resources (Wäckers and van Rijn 2012), and in a recent review natural enemy enhancement, herbivore suppression and crop damage suppression were all higher in crops with increased plant diversity (Letourneau et al. 2011). Similarly, increased plant diversity has been shown to enhance the abundance of bees and pollinators (Nicholls and Altieri 2012).

Different wildflower strip mixtures have been used to attract and provide resources for different arthropod functional groups. Field margin seed mixtures have already been developed to provide resources for bees, butterflies and pest natural enemies. For example, flower mixtures dominated by Apiaceae and other species with exposed floral nectaries have dominated biocontrol studies whilst pollinator mixes are often dominated by Fabaceae species (Campbell et al. 2012). The use of different wildflower strip mixtures is a consequence of differential suitability of nectar and pollen resources to different functional groups depending on plant functional traits, including floral morphology, and food preferences and foraging risks for flower visitors (Wäckers 2005; Wäckers and van Rijn 2012). However, a concurrent research endeavour remains that of developing seed mixtures capable of conserving multiple functional groups of flower visitors for realising multiple ecosystem services in agroecosystems (Carrié et al. 2012). Increasing functional diversity within these strips, by providing more diverse floral traits, may play a particularly important role in maintaining multiple above-ground arthropod functional groups within arable habitats. Conversely, augmented vegetation cover, through the use of flowering strips may be more important for the conservation of ground-dwelling predators (Yardim and Edwards 2002; Hummel 2002).

The biodiversity-ecosystem function (BEF) relationship is one of the dominant issues of ecology, and is particularly important in the context of concurrent loss of biodiversity from ecosystems (Pullin 1997; Chapin III et al. 2000; Benton et al. 2002; Samways 2007; Tscharntke et al. 2007). Many BEF experiments have focused on the manipulation of plant species richness and measure the effect on an associated ecosystem function (Naeem et al. 1994, 1995; Tilman et al. 1996; Schwartz et al. 2000; Díaz and Cabido 2001). Whilst numerous studies have shown that species diversity can enhance ecosystem functions (Loreau and Hector 2001; Balvanera et al. 2006; Cardinale et al. 2006; Duffy et al. 2007; Isbell et al. 2011), results from BEF experiments have been attributed to two groups of mechanisms: complementary and sampling effects (Loreau et al. 2001). Traditionally, studies have used species diversity measures in quantifying BEF relationships (Naeem et al. 1994, 1995; Tilman et al. 1996; Schwartz et al. 2000; Díaz and Cabido 2001), but it has been argued that it is probably more important to understand the linkages between key species or functional groups and ecosystem functions (Bengtsson 1998; Moonen and Bàrberi 2008). This coarser categorisation of biodiversity into functional groups has revealed clearer patterns in many cases, indicating that there may be some level of functional redundancy among species in the provision of certain ecosystem functions (Hooper et al. 2005; Balvanera et al. 2006; Letourneau et al. 2009).

Since tomato (Solanum lycopersicum L.) is susceptible to attack by multiple pests (Lange and Bronson 1981; Flint 1998) and is partially dependent on flower-visiting insects for effective pollination and subsequent fruit production (Greenleaf and Kremen 2006), we chose this crop as a case-study crop to establish the impact of field margin strips with increasing levels of functional flower traits on both insect diversity and crop damage and production (Balzan 2013). Here we used flower traits to distinguish different plant functional effect groups, defined as ad hoc groups based on physiognomic attributes of the organisms within the ecosystem (Hooper et al. 2002). Floral resources were provided in four different levels, characterised by increasing flower trait diversity and vegetation stand complexity. Each level cumulatively augmented plant species and functional group richness in a replacement series. Floral resources were located adjacent to experimental plots of organically-managed tomato crop. We hypothesise that (H1) both sap-sucking bugs (alternate prey) and above-ground natural enemies (parasitoids and generalist predators) are associated with sown flower strips, which are composed of flowers with accessible nectaries, and that (H2) bee abundance is enhanced in flower strips with augmented availability of long-corolla Fabaceae species. We also predict that (H3) higher plant functional diversity in a given wildflower strip is associated with augmented abundance and diversity of above-ground arthropod functional groups. At the same time, it is



hypothesised that (H4) increased plant functional diversity is not associated with augmented abundance of ground-dwelling predators since these are not affected by the flower strip composition but by vegetation cover.

Materials and methods

Experimental design

Observations were carried out within a 2.5 ha experimental field of organic processing tomato at the Interdepartmental Centre for Agroenvironmental Research 'E. Avanzi' of the University of Pisa (lat. 43°40′N, long. 10°19′E) that were planted on the 20th May and harvested on 9th of September of 2011. Experimental plots consisted of subplot with the tomato crop (size 10 × 4 m) and an adjacent flowering strip plot (size 10 × 2 m). Soil steaming was carried in wildflower strip plots prior to sowing in order to reduce germination of weeds (Bàrberi et al. 2009). Wildflowers were then hand-sown on 2 separate dates (06/06/2011 and 21/06/2011) to increase the flowering period and were watered as needed using sprinklers placed within each strip. Each plot was separated by a distance of 8 m from other adjacent plots and inter-plot area was kept weed-free through mechanical weed control (harrowing and hoeing) in order to avoid effects of naturally occurring flowering plants other than the ones selected in the wildflower strips, on beneficial arthropod dynamics. Floral resources were provided in four different levels, consisting of different floral mixtures, with each level cumulatively increasing the species and functional group richness of flowering resources. Each level adds three different species in a replacement series (also termed substitutive design) (Appendix 1 of ESM). In substitutive designs alternate species replace some of the main plant species (Level 1 flowering resources, in this case) thereby reducing the sowing density of the latter in more diverse strips (Jolliffe 2000). A functional group is here defined as a group of species that are similar, and at least partially substitutable in their contribution to a specific ecosystem service (Naeem et al. 2002). The choice of functional effect groups here was based on the floral morphological traits of different plant species. The species used have often been included in wildflower strip mixtures, as they produce floral and extrafloral nectar, and are native or established within the Mediterranean region. Different levels of floral resources indicate different flowering strip species mixtures and represent the addition of new functional effect groups. Flowers of Apiaceae (Level 1) species are characterised by exposed and accessible floral nectar, making them highly attractive to several hymonepteran parasitoids and generalist predators with short mouthparts (Jervis et al. 1993; Wäckers and van Rijn 2012). The plant species introduced in Level 2 are Fabaceae species, which are characterised by flag-shaped flowers, making floral nectar relatively unavailable, and extra-floral nectar glands which can usually be successfully exploited due to their exposed nature. Plant species included in the third level represent different functional groups of flowering resources and have a diversified floral morphology (Table 1), and all three species have often been included in conservation biological control studies. Similar to other experiments manipulating plant functional effect groups (Hooper et al. 2002), the inclusion of increased plant species diversity in wildflower species mixtures is correlated with an increase in floral functional groups. These three levels of floral diversity were compared to a bare-soil control (Level 0). The Level

Table 1 Flower species used for this study, the respective experimental level and families, the position of nectaries and indication of floral nectar depth (0: < 0.2 mm, 1: 0.2–1.0 mm, 2: 1.0–2.0 mm, 3: 2.0–3.0 mm, 4: >3.0 mm) and corolla aperture (0: 0–1 mm, 1: 1–3 mm, 3: > 3.0 mm) for each flowering resource

Species	Family	Levels	Floral morphology	Floral resources	Floral Nectaries	Corolla depth	Corolla aperture
Anethum graveolens L.	Apiaceae	1,2,3	Dish-shaped	Nectar	Exposed	0	1
Coriandrum sativum L.	Apiaceae	1,2,3	Dish-shaped	Nectar	Exposed		
Foeniculum vulgare Mill.	Apiaceae	1,2,3	Dish-shaped	Nectar	Exposed		
Lotus corniculatus L.	Fabaceae	2,3	Flag-shaped	Nectar	Hidden	4	0
Phaseolus vulgaris L.	Fabaceae	2,3	Flag-shaped	Nectar; extra- floral nectar	Hidden		
Vicia faba L.	Fabaceae	2,3	Flag-shaped	nectar	Hidden		
Centaurea jacea L.	Asteraceae	3	Head-brush shaped	Nectar	Hidden	4	0
Fagopyrum esculentum Moench	Polygonaceae	3	Dish-shaped	Nectar	Exposed	0	3
Sinapis alba L.	Brassicaceae	3	Dish-shaped	Nectar	Partly hidden	4	3

Source: Baggen et al. (1999); Lavandero et al. (2006); Vattala et al. (2006); Winkler et al. (2009); Wäckers and van Rijn (2012)



1 wildflower strip consisted of three Apiaceae species, Anethum graveolens L., Coriandrum sativum L., Foeniculum vulgare Mill., while in Level 2 three additional Fabaceae species, Lotus corniculatus L., Phaseolus vulgaris L., Vicia faba L., were added to the seed mixture. Finally, Level 3 was composed of a more diverse floral mixture and in addition to the 6 species from the previous level included Centaurea jacea L., Fagopyrum esculentum Moench. and Sinapis alba L..

Establishment of experimental flower strips

Establishment and flowering of the sown plant species was recorded during weekly visits throughout the crop cycle. Cover of sown plant species and naturally emerging weeds was recorded at the end of the crop growing season in a standardised belt transect at the centre of the strip. Species cover was recorded along five equally spaced quadrats $(0.5 \times 0.5 \text{ m})$ along this central belt transect. The quadrat was subdivided into 25 smaller sectors and the abundance of each species within each quadrat was recorded as the number of sectors within which the species is represented, either in whole or in part, and this figure was expressed as a proportion of the total number of sectors in the quadrat (Kent and Coker 1995). Subsequently the mean of the five quadrats was calculated. This procedure provides a rapid,

replicable and objective methodology for assessing patterns of species abundance and richness.

Flower visiting and ground-dwelling arthropods

Surveys of arthropod visitors to flower strips were initiated after flowering of the sown wildflower species in each level and were carried out every 14 days, through standardised aspiration two times along the whole length of the plot for a total of five plots per level and excluding the bare control plots. Pitfall traps were also used to determine the influence of different floral strips on ground-dwelling organisms. These traps were placed in the centre of each wildflower (Levels 1, 2 and 3) and control (Level 0) strip and filled with 70 % alcohol for the preservation of captured arthropods. Rain covers were positioned approximately 10 cm above each trap to prevent flooding by rain or irrigation. The traps were set up soon after the flowering of sown strips, and were sampled on a weekly basis up to the harvest date. Collected arthropods were stored in 70 % ethanol for taxonomic determination. Subsequently, all arthropods were identified to the Order, with pre-determined sets of species taken further taxonomically and assigned to functional groups. The functional groups used were: pest; natural enemy; pollinator; conservation (for groups of either direct conservation interest-i.e. butterflies and bees) and alternate prey (for groups of particular benefit as prey and/or

Table 2 Functional groups into which sets of arthropods were classified according to the taxonomic level shown

Order	Sub-order/ group	Super-family/family/ group	Genus/species	Ground- dwelling/ above-ground	Functional group
Araneae	_	Araneidae		Above-ground	Natural enemy
		Linyphidae			
		Oxyopidae			
		Salticidae			
		Tetragnathidae			
		Thomisidae			
	_	Araneidae		Ground-dwelling	Natural enemy
	Corinnidae Dysderidae				
		Dysderidae			
		Gnaphosidae			
		Linyphiidae			
	Gnaphosidae				
		Salticidae			
		Scytodidae			
		Tetragnatidae			
		Theridiidae			
		Thomisidae			
Coleoptera	_	Carabidae		Ground-dwelling	Natural enemy
	_	Coccinelidae	Hippodamia variegata Goeze	Above-ground	Natural enemy
	_	Staphilinidae		Ground-dwelling	Natural enemy



Table 2 continued

Order	Sub-order/ group	Super-family/family/ group	Genus/species	Ground- dwelling/ above-ground	Functional group
Diptera	Brachycera	Syrphidae		Above-ground	Natural enemy; pollinators
Hemiptera	Heteroptera	Nabidae	Nabis sp. Latreille	Above-ground	Natural enemy
		Anthocoridae	Orius sp. Wolff	Above-ground	Natural enemy
	_	Miridae		Above-ground	Pest; alternate
		Pentatomoidea			prey
		Lygaeidae			
	Homoptera			Above-ground	Pest; alternate prey
	_	Aphididae		Above-ground	Pest; Alternate prey
Hymenoptera		Formicidae		Ground-dwelling	Natural enemy
				Above-ground	
	Parasitica	Ichneumonoidea, Chalcidoidea,		Above-ground	Natural enemy
		Platygastroidea, Proctotrupioidea,			
		Cynipoidea,			
		Diaprioidea,			
		Chrysidoidea			
	Honey bees	Apidae	Apis mellifera L	Above-ground	Conservation; pollinators
	Bumblebees	Apidae	Bombus spp. Latreille	Above-ground	Conservation; pollinators
	Wild bees	Colletidae,		Above-ground	Conservation;
		Andrenidae,			pollinators
		Halictidae,			
		Melittidae,			
		Megachillidae,			
		Antophoridae,			
		Apidae (other)			
Lepidoptera	-	-		Above-ground	Conservation; pest
Thysanoptera	Terebrantia	-		Above-ground	pest
	Tubulifera	_		Above-ground	Alternate prey

hosts to natural enemies). The abundance of Hymenoptera (Ichneumonoidea, Chalcidoidea, Platygastroidea, Proctotrupioidea, Cynipoidea, Diaprioidea, Chrysidoidea) parasitoids and pollinators (Hymenoptera: Apoidea: Apiformes) visitors was calculated (Table 2). Similarly, the availability of nontarget prey was calculated by measuring the abundance of Hemiptera (sap-sucking) bugs. Several species that make part of this functional group (sucking bugs) are also secondary pests of tomato (Flint 1998), and including the polyphagous species *Lygus* spp. and *Nezara viridula* L. (Awan et al. 1990; Balzan and Moonen 2014; Flint 1998). Another, polyphagous Miridae pest in agroecosystems is *Adelphocoris lineolatus* Goeze, which together with the aforementioned bugs is reported to be

an important and widespread pest species in Italy and in many other European countries (Pansa et al. 2012). To investigate the influence of habitat management strategies diversity of sapsucking bugs, members of these species collected from flowering strips were identified to the species taxonomic level and their abundance for each plot at different sampling dates recorded. The abundance of ground-dwelling predators was calculated by measuring the abundance of Carabidae and Staphylinidae (Coleoptera), Formicidae (Hymenoptera), Opiliones and Araneae. Several species of these taxa have been listed as natural enemies for the invasive *Tuta absoluta* Meyrick (Desneux et al. 2010) and the polyphagous *Helicoverpa armigera* Hübner (van den Berg 1993; van den Berg and Cock



1993; Watmough and Kfir 1995; Cherry et al. 2003; Mansfield et al. 2003; Lange et al. 2008).

Data analyses

The relationship between abundance of different arthropod groups was first graphically investigated using a non-metric multidimensional scaling (NMDS) analysis. This analysis aims at representing the main relationships among objects in a reduced and specified number of dimensions (axes) and can produce an ordination diagram from any distance matrix (Clarke 1993; Legendre and Legendre 1998). A dissimilarity matrix was built, based on the Bray-Curtis index and used as input for the NMDS (Oksanen et al. 2013). Generalised linear mixed-effect models (GLMMs) were used to investigate the influence of functional floral diversity on the abundance of different arthropod groups. Given that the influence of time on different arthropod groups is likely to change with group identity, and to vary between different levels of floral strips according to the flowering period of the different plant species, 3 models were performed for each of the recorded arthropod groups. The first two models included both treatment level and sampling date set as fixed variables and plot as a random effect to account for spatial autocorrelation: one GLMM (model 1) included treatment level (L) and time (T) as fixed variables and their interaction (L:T), while the second model (model 2) deployed level and time as fixed variables but their interaction was not considered (L + T). The last model (model 3) considered time and plot as a random effect and used only the treatment parameter (L) as a fixed effect. The three different models were performed in order to take account of the influence of temporal variability on different arthropod groups in separate experimental treatments, in which abundance may be influenced differently by time in different experimental treatments (model 1), similarly across experimental treatments (model 2) or there is no overall effect of time (model 3). The most parsimonious model was selected as that with the lowest Akaike information criterion with a second-order correction (AICc) (Burnham and Anderson 2002). The significance of the interactions between variables was tested using a Poisson error distribution (Bates et al. 2013). This approach aims at selecting the least complex model without losing important information on interactions between the experimental factors, time and spatial autocorrelation.

Results

Establishment of experimental flower strips

The sown wildflower strips established well and provided a gradient of species and flowering resources (Appendix 2 of



Table 3 Phenology data for flowering plant species in sown strips

Flowering species	Level	Sampling Occasion (Date)								
riowering species	Level	12/07	20/07	02/08	12/08	19/08	26/08			
C. sativum	1,2,3									
F. vulgare	1,2,3									
P. vulgaris	2,3									
V. faba	2,3									
F. esculentum	3									
S.alba	3									

Dark grey squares indicate 'peak/full bloom' while soft grey indicates flowers that were 'in bloom'

ESM). One species from each experimental level, that is *A. graveolens*, *L. corniculatus* and *C. jacea*, did not produce flowers even though these were recorded during vegetation surveys. A number of weed species were recorded from the wildflower strips, however the main flowering resources were provided by sown species and the most dominant weeds for all strips were Cyperaceae and Poaceae species (Appendix 2 of ESM). The flowering period varied for different species, with Level 3 species (*F. esculentum* and *S. arvensis*) being the first to flower while sown Level 1 species (*C. sativum* and *F. vulgare*) flowered later during the growing season (Table 3).

Influence of increased plant functional diversity on arthropod diversity for ecosystem services

A total of 12,459 arthropods were collected from the flower strips, of which 7,938 were recorded from periodical aspiration. The most abundant groups from the arthropods collected by aspiration were sap-sucking bugs of the order Hemiptera and Diptera, which made up 35.1 and 28.6 % respectively of the total sample. Members of the Order Thysanoptera made up 13.2 % of the total sample size, while the hymenopteran groups Parasitica, Apiformes and Formicidae accounted for 18, 1.8 and 0.71 % of the total sample size respectively. Hoverflies (Syrphidae: Diptera) only made a small proportion (0.57 %) of all dipterans recorded within this study. Similarly, honeybees (Apis mellifera L.) only made a small fraction (0.06 %) of the bees collected by aspiration, whilst wild bees (excluding bumblebees which were not recorded during this study) accounted for the rest. Lepidoptera adults accounted for 0.46 % of the total sample size, and coccinelids made a relatively small fraction (0.94 %) of the arthropods collected from the flower strips and were dominated by Hippodamia variegata Goeze (92.0 %). Thomisidae were the most important Araneae predators collected from aspiration and accounted for 70.2 % of this cohort.

A total of 4,521 individuals were collected from pitfall traps during 7 sampling dates. Members of Carabidae and Formicidae were the most abundant groups and made up a

Table 4 Influence of flowering resources on arthropod and functional group abundance in pitfall traps, measured through GLMM models when using a Poisson error distribution

Arthropod/functional group	Model	df	L1	L2	L3	Control	Time (T)	L1:T	L2:T	L3:T	Control: T	AICc
Araneae	Model 3	7	1.002	1.377	0.300	-0.795						393.4
			< 0.0001	0.285	0.036	< 0.0001						
Carabidae	Model 1	9	0.560	0.869	0.185	-0.822		0.058	0.058	0.056	0.0032	741.9
			0.016	0.355	0.298	0.012		< 0.0001	0.906	0.717	0.0013	
Staphilinidae	Model 3	7	0.587	1.114	0.536	-3.043						344.6
			0.030	0.197	0.902	< 0.0001						
Formicidae	Model 3	7	1.383	1.279	1.090	0.681						804.3
			< 0.0001	0.821	0.529	0.134						
Ground-dwelling predators	Model 3	7	3.103	3.283	2.678	1.144						956.3
			< 0.0001	0.474	0.095	< 0.0001						
Aphididae	Model 3	7	-0.177	_	1.109	-18.65						337.4
			0.692	0.841	0.184	0.992						
				0.536								
Hemiptera	Model 3	7	0.767	0.264	- 0.110	-0.394						416.1
			0.009	0.258	0.118 0.051	0.0009						
Orthoptera	Model 2	6	-0.200	_	_	-1.393	0.018					305.9
<u></u>			0.586	0.554	0.240	0.031	0.0004					
				0.495	0.937							
Ground-dwelling	Model 3	7	1.434	1.008	1.046	0.257						484.6
herbivores			< 0.0001	0.209	0.250	0.0009						

AICc values were used to indicate the most parsimonious models. The p values for experimental levels 2, 3 and control indicate differences from baseline treatment 1. Estimates shown for each experimental treatment indicate the intercept while those for time (or time:treatment level interaction) indicate the slope, and the second value in each cell represents the p value when using a Poisson error distribution

total of 24.9 and 17.3 % of the total number of collected ground-dwelling organisms, while Staphylinidae predators accounted for 6.3 %. Araneae individuals made a total of 8.41 % of the cohort collected from pitfall traps, and Lycosidae (61.1 %) and Linyphiidae (24.7 %) spiders were the dominating groups. Independent of the species composition, flowering strips around tomato plots significantly increased the abundance of ground-dwelling predators collected from pitfall traps, with the exception of Formicidae abundance that did not differ between plots (Table 4). Augmented plant functional group richness (in Level 2 and 3 strips) did not increase the abundance of ground-dwelling predator groups, and the strips with the highest level of plant functional group richness (Level 3) appeared to have lower abundance of ground-dwelling natural enemies (Fig. 1). All of the groups, with the exception of Carabidae, were not significantly influenced by time suggesting that the phenological stage of the sown mixtures does not play an important role in regulating their abundance. The presence of the sown flower strips was associated with increased abundance of ground-dwelling herbivores collected in pitfall traps but increased vegetation diversity within these experimental strips did not have

a significant effect on the abundance of these herbivores (Table 4).

Vegetation diversification in sown strips influenced different flower-visiting arthropod groups in an idiosyncratic manner (Table 5). The ordination plot (Fig. 2) for abundance of above-ground visitors to flower strips indicates that several predator groups, including Coccinelidae (Coleoptera), Thomisidae (Araneae), and several parasitoid wasps (Chalcidoidea, Ichneumonidae, Braconidae, Platygastroidea: Hymenoptera), appear to be enhanced by the presence of Apiaceae species that dominate the Level 1 strips, and subsequent addition of flower functional groups do not augment their abundance. Furthermore, GLMM analyses show that the abundance of the aforementioned groups was not significantly different between experimental levels (Table 3). While the addition of flower trait diversity in subsequent experimental levels (Levels 2 and 3) attracts other arthropod groups, relatively few natural enemies appear to benefit from this increase. The abundance of the ladybird *H. variegata* did not vary significantly between experimental treatments and increased with time for all experimental levels (Fig. 3a). Similarly, parasitoids (Hymenoptera) increased with time in all flower strip mixtures but their abundance was not significantly



Fig. 1 Total temporal attractiveness of different wildflower mixtures to ground-dwelling a Carabidae and b Staphylinidae beetles and c spiders. *Error bars* represent standard error from the mean. Abundance of carabids increased with time for all experimental levels but not for staphylinids and Araneae

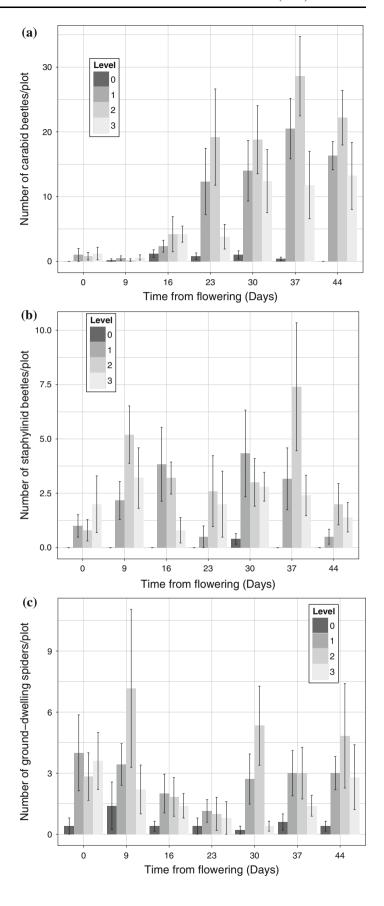




Table 5 Influence of flowering resources on arthropod and functional group abundance of flower visitors, measured through GLMM models

Arthropod/functional group	Model	df	L1	L2	L3	Time	L1:time	L2:time	L3:time	AICc
Araneae	Model 2	5	-0.268	0.197	-0.378	-0.006				168.5
			0.485	0.261	0.789	0.508				
Anthocoridae	Model 1	7	-2.109	-0.414	1.152		0.059	0.03	-0.026	246.2
(Orius sp.)			0.006	0.071	< 0.0001		0.002	0.218	< 0.0001	
Nabidae	Model 3	6	0.029	0.133	-0.794					141.5
(Nabis sp.)			0.907	0.768	0.024					
Coccinelidae (Hippodamia variegata)	Model 2	5	-2.779	-2.173	-2.884	0.073				145.3
			< 0.0001	0.171	0.817	< 0.0001				
Formicidae	Model 2	5	-0.461	-0.176	0.232	-0.040				123.1
			0.442	0.712	0.309	0.0002				
Parasitica	Model 2	5	2.093	2.157	1.695	0.009				409.6
			< 0.0001	0.774	0.057	0.0007				
Apiformes	Model 1	7	-1.614	-2.546	1.212		0.055	0.075	-0.055	204.2
			0.008	0.400	< 0.0001		< 0.0001	0.482	< 0.0001	
Terebrantia (Order: Thysanoptera)	Model 3	6	0.595	0.723	0.642					361.4
			0.062	0.783	0.908					
Phlaeothripidae (Order: Thysanoptera)	Model 3	6	2.6101	1.662	1.150					709.3
			< 0.0001	0.060	0.001					

AICc values were used to indicate the most parsimonious models. The p values for experimental levels 2 and 3 indicate differences from baseline treatment L1, while p value for L1 indicates a significant effect of L1 on measured parameter. Estimates shown for each experimental treatments indicate the intercept while those for time (or time:treatment level interaction) indicate the slope, and the second value in each cell represents the p value when using a Poisson error distribution

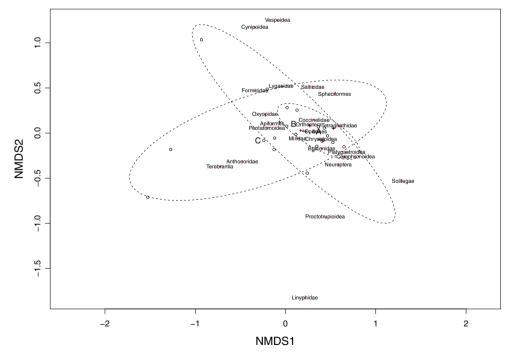


Fig. 2 Nonmetric multidimensional scaling ordination plot showing arthropod groups association to floral strip functional diversity (only the most dominant groups are included to reduce clutter in the ordination plot, Oksanen et al. 2013). *Ellipses* represent 95 %

confidence intervals of point scores from the covariance matrix for each level, while *letters* represent the centroid position for each level (level 1 = A; level 2 = B; level 3 = C)



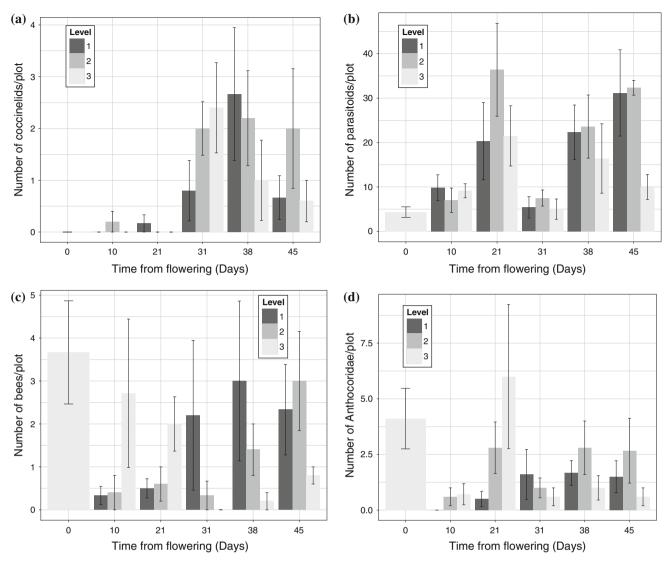


Fig. 3 The abundance of **a** ladybird beetles and **b** parasitoids increased with time for all flowering mixtures. Abundance of **c** wild bees and **d** flowerbugs was enhanced in Level 3 strips soon after initiation of flowering, whilst Level 1 and 2 strips appear to be more

important later in the season. *Error bars* represent standard error from the mean. Data for presented groups was collected from standardised aspirations across the flowering strips

different between the different experimental levels (Fig. 3b). Contrastingly, the predominantly zoophagous *Nabis* sp. bugs were recorded in lower abundance in Level 3 strips. Vegetation diversification within the experimental plots had no significant effect on Araneae and Formicidae abundance, while the abundance of the latter group decreased with time in all strips.

The abundance of wild bees varied with time and flower strip mixtures and relatively high wild bee abundance was recorded initially in Level 3 strips, which flowered earlier, but subsequently declined within this experimental level (Fig. 3c). Contrastingly, the abundance of bees in Level 1 and 2 strips increased exponentially with time as these flowered later. Similarly, earlier flowering of Level 3 strips was also associated with augmented abundance of

Anthocoridae flowerbugs (Fig. 3d), which are considered as being important predators of insect pests in agroecosystems. In addition to the prey they also feed on plant material such as plant juices, pollen and nectar, which can increase their longevity when the prey is rare (Wäckers and van Rijn 2012). The abundance of flowerbugs declined soon after blooming of Level 3 strips. We also observed an increase in the abundance of flowerbugs in Level 1 and 2 strips with time, that is when flowers became more concentrated in these strips (Table 3), and indicating that the availability of flower resources is particularly important for the conservation of these arthropod groups in agroecosystems.

Sown flower strip mixtures can also provide resources and conditions required by pest species, including several polyphagous sap-sucking true bugs (Hemiptera) that are



Table 6 Influence of functional plant diversity on abundance of sap-sucking bugs, and that of 3 important polyphagous pests belonging to this group

Arthropod abundance	Model	L1	L2	L3	Time	AICc	df
Sucking bugs (Hemiptera) abundance	Model 3	3.299 <0.0001	3.315 0.901	2.767 <0.0001	-	426.1	6
Adelphocoris lineolatus abundance	Model 2	-1.889 <0.0001	-1.01 0.151	-0.773 0.050	_	95.2	5
Nezara viridula abundance	Model 2	-3.218 <0.0001	-3.396 0.850	-1.799 0.034	0.030 0.077	69.1	5
Lygus spp. abundance	Model 3	-0.512 0.176	0.430 0.064	0.515 0.030	-	169.4	6

The p values for experimental levels 2 and 3 indicate differences from baseline treatment level 1. Values indicate the intercept for different treatments (L1, L2, L3), while variable Time indicates slope for change in dependent variable across growing season, and the second value in each cell indicates the p value

considered as being pests of tomato, and this may enhance their fitness and abundance. The GLMM results indicate that the abundance of sap-sucking bugs, which cause damage to the tomato crop and fruit, was significantly associated with flowering strips (Table 6). However, increasing plant diversity reduces the abundance of this group and a lower abundance was recorded in Level 3 strips. The abundance of the three polyphagous pests A. lineolatus, Lygus spp. and N. viridula was also investigated. The species Lygus gemellatus Herrich-Schäffer, L. pratensis L. and L. rugulipennis Poppius were recorded from the surveyed flower plots, and subsequent analyses included these as the functional group Lygus spp.. GLMM results for these pests show that increasing vegetation diversity is associated with increased abundance of these species.

Discussion

Potential pest control service

Results presented here indicate that the sown flower strip mixtures are important for the conservation of parasitoids and generalist predators, supporting hypothesis H1. Similarly, other studies have suggested that increased availability of flowering plants is likely to provide synergistic effects for several functional groups (Balzan and Moonen 2014; Fiedler and Landis 2007a, b; Noordijk et al. 2010; Carrié et al. 2012; Wratten et al. 2012; Pisani Gareau et al. 2013). No major significant differences in functional group abundance were recorded between Levels 1 and 2 flower strip mixtures but enhanced vegetation functional diversity in Level 3 strips was associated with increased abundance of Anthocoridae bugs and wild bees. Thus, results obtained here only partially support hypothesis H3, and concur with observations made in other studies that for the management of sustainable ecosystems it is probably more important to focus on functional identity and linkages between key species and functional groups rather than focusing on species diversity (Bengtsson 1998; Moonen and Bàrberi 2008). In this study, this may have been caused by the efficiency of temperate Apiaceae in attracting large numbers of flower visitors (Memmott 1999; Olesen et al. 2007) and therefore play a key role in the conservation of insect diversity and the provision of ecosystem services in arable systems. The Apiaceae included have dish-bowl flower morphology, which (together with bell-funnel and head-brush flowers) have a higher generalisation level than flag, gullet and head-brush flowers (Olesen et al. 2007). Since most hymenopteran parasitoids and many predators have short mouthparts these can fulfil their energy needs by feeding on accessible sugar resources, such as exposed floral nectaries found in several Apiaceae species (Jervis et al. 1993; Wäckers 2005; Wäckers and van Rijn 2012), and enhancement of these through the provision of nectar may be important for pest suppression (Chaney 1998; Baggen and Gurr 1998; Baggen et al. 1999; Winkler et al. 2006; Masetti et al. 2010; Skirvin et al. 2011; Woltz et al. 2012; Balzan and Wäckers 2013). However, members of the Parasitica may have represented hyperparasitoid species (at the fourth trophic level), in addition to primary parasitoids, with the former having the potential to have a negative impact on pest control (Carrié et al. 2012; Lavandero et al. 2006).

The sown flowering strips augmented the abundance of ground-dwelling arthropod predators but this was not significantly enhanced by increased vegetation diversity in Levels 2 and 3 strips. These results support the hypothesis (H4) that the abundance of ground-dwelling arthropods is not affected by the flower strip composition and concur with previously made observations that the abundance of ground-dwelling predator groups is mainly influenced by vegetation cover (Yardim and Edwards 2002; Hummel 2002) and that ground-dwelling predators also benefit from the presence of uncropped margins sown with wildflower



and grassy mixtures (van Rijn et al. 2008; Noordijk et al. 2010; Hof and Bright 2010; de Lange et al. 2012).

Potential disservices of wildflower strips

More diverse flower strips (Levels 2 and 3) were generally less attractive to the sap-sucking bug functional group and a lower abundance was recorded but these strips had a higher abundance of these pests of tomato (A. lineolatus, Lygus spp. and N. viridula). In a previous study, conducted in organically-managed tomato fields, we have demonstrated that sown wildflower strips hold potential as a trap crop for these pests and a lower fruit damage was recorded in the crop adjacent to these strips (Balzan and Moonen 2014). Similarly, several plant species have been shown to hold some potential as trap crops for the suppression of N. viridula (Rea et al. 2002; Tillman 2006; Mizzel et al. 2008; Smith et al. 2009) and Lygus spp. (Accinelli et al. 2005; Swezey et al. 2007; Bensen and Temple 2008). Augmented abundance of these polyphagous pests in more diverse strips could be due to a bottom-up effect caused by the presence of multiple host plants that become available in more diverse plots. Nonetheless, in another study investigating the effects of these flower strips on pest damage, we have not found an increased crop damage from these pests (Balzan 2013).

Our study makes the assumption that all individuals belonging to the order Lepidoptera are of conservation value. However, this need not be the case as there are several Lepidoptera pests of tomato that are the cause of substantial yield loss within the study area (Balzan and Moonen 2012), and the indiscriminate use of nectar plants to provide nutrients to biological control agents may actually enhance pest fitness (Baggen et al. 1999; Lavandero et al. 2006). Moreover, previous research has indicated that T. absoluta, a recently introduced invasive alien pest of tomato, is able to utilise nectar resources from a relatively wide range of flowers (Balzan and Wäckers 2013). Nevertheless, in another study investigating the impact of the flower strips used here on crop damage from key tomato pests we did not record an increase in Lepidoptera-caused crop damage, and thus cannot confirm that flower strips provided agroecosystem disservices through increased yield loss (Balzan 2013).

Potential pollination service

Sown flower strip mixtures augmented the abundance of wild bee visitors, and these were more abundant than visits by honey bees. Similarly, several previous studies have investigated the conservation of pollinator diversity in field margins, suggesting that the inclusion of wildflower strips benefits pollinator diversity (Haaland et al. 2011). Moreover, results presented here complement previous research that has

indicated that wild bees and honey bees utilise different flowering resources within agricultural landscapes, where wild bees were tightly associated with semi-natural habitats while honey bees were mainly recorded from mass-flowering crops (Rollin et al. 2013). Wild bees are key components of insect communities in arable crops as they provide important contributions to the crop pollination, but also to the pollination of wild plants (Klein et al. 2007; Petanidou and Potts 2006). Previous research has indicated that the presence of natural habitats can enhance the abundance of pollinators, which increase the production field-grown tomato (Balzan 2013; Greenleaf and Kremen 2006). Our results also support observations that wild bees in agricultural landscapes have a wide trophic niche and have access to different flower functional groups (Rosa García and Miñarro 2014; Miñarro and Prida 2013). In a study investigating the effects of sown wildflower strips on pollination services and species diversity, it was observed that the benefits of these strips were largely independent of the experimentally varied strip properties, including species composition (Korpela et al. 2013). Rather, ensuring the presence of flowering plant species appears to be more important for increasing the abundance of wild bees and honey bees (Rosa García and Miñarro 2014). This contrasts with observations made by Carrié et al. (2012) suggesting that flowering period alone is a poor indicator of plant suitability to insects and that certain plant species can be more 'generalist' in their attractiveness than others.

Diversity in wildflower strips and the associated increase in the bloom period duration were observed to be particularly important for the conservation of wild bees in arable crops. Thus these results do not support our initial hypothesis H2 that increased abundance of Fabaceae species is associated with augmented abundance of wild bees within the study area, and contrast with previous observations that areas sown with pollen and nectar rich mixtures (Fabaceae) attract the highest number of honey bees and wild bees (Haaland et al. 2011). In this field experiment, the abundance of wild bees within the three sown flower strip mixtures changed with time and they were mainly associated with strips where flower resources were more concentrated. Indeed, the addition of long-corolla Fabaceae species in Level 2 did not increase the abundance of wild bees with respect to flowering Apiaceae species (Level 1). This may have been caused by the presence of short-tongued wild bees (e.g. Colletidae, Andrenidae and Halictidae), which are able to access the shallow flowers of Apiaceae species. Thus, from a conservation management perspective, if the aim is to improve the conservation of wild bees to enhance crop productivity, it may be more effective to introduce several flower strips with a few species flowering at a time to increase the temporal availability of pollen and nectar resources across the growing season of field-grown arable crops.



Conservation value of wildflower strips in arable systems

Our results show that the conservation of farmland insect biodiversity is possible through the maintenance of plant diversity in agroecosystems and habitat management techniques involving the use of sown flowering strips mixtures. The inclusion of flower resources in arable systems can be important for the conservation of several important arthropod functional groups, and an augmented abundance of wild bees, parasitoids, coccinelids and ground-dwelling predators (Lycosidae and Linyphiidae (Araneae), Carabidae and Staphylinidae (Coleoptera)) has been recorded during this study. Increased plant functional group richness was also associated with an augmented availability of floral resources across time, which appears to augment the abundance of wild bees and anthocorids. The augmented abundance of several functionally important groups, namely parastioids, predators and pollinators, highlights the importance of these field margins for providing ecosystem services to agriculture and from a conservation perspective. Wildflower strips can be established as Ecological Focus Areas (EFAs) under the ("Pillar 1") European Union Common Agricultural Policy (CAP) for 2014-2020, which should be applied to at least 5 % of arable land of farms where arable land covers more than fifteen hectares. EFAs should be established for safeguarding and improving biodiversity on farms. Contrastingly, tomato grown for processing within the study area is characterised by large-scale cultivations and farmers often remove various weeds and herbaceous species in uncultivated areas, including field margins, through the use of chemical and mechanical techniques (Balzan and Moonen 2012). Results obtained here, and in a previous study (Balzan and Moonen 2014), indicate that the use of wildflower strips in tomato crop can enhance the conservation of multiple arthropod groups in these agroecosystems. Ensuring a longer flowering period of sown wildflower strips, through the use of different species within the same strip or throughout the agricultural matrix, is particularly important since our results indicate that several arthropod groups are able to utilise multiple floral resources. Indeed, several studies have similarly suggested that different flowering species can enhance the insect conservation in arable systems and that intensively managed field margins are typically associated with the reduced arthropod diversity (Anderson et al. 2013; Carrié et al. 2012; Haaland et al. 2011; Meek et al. 2002; Thomas and Marshall 1999). In conclusion, the establishment of the flowering strips of varying species and functional composition, and increased availability of flower resources, augmented the abundance of several flower-visiting and ground-dwelling arthropods, and wildflower strips are important for ensuring the conservation of insect functional and species diversity and the provision of multiple ecosystem services in agricultural landscapes.

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