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Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity

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Abstract

Beneficial insects in agro-ecosystems provide humans with many invaluable ecosystem services including crop pollination and pest control. The creation of wildflower strips has emerged as a key tool to conserve beneficial insect groups in these systems. Yet, the efficacy of these schemes in delivering multiple ecosystem services is usually limited by our poor understanding of how plant species composition, functional traits and trait diversity affect insect visitation and resource use. Here we investigate the effects of plant floral traits and trait diversity on flower visitation by three functionally distinct beneficial insect groups, which provide crop pollination and pest control services: bumblebees, hoverflies and parasitoid wasps. We created plots that contained plants with either long or short-corolla flowers, as well as mixed plots, which contained plants presenting both floral traits concurrently. In functionally simple plots, insect groups exhibited distinct floral associations, with bumblebees being almost exclusively associated with long-corolla flower plots, whereas parasitoids and hoverflies strongly favoured plots with short-corolla flowers. When these flower types were planted in combination (mixed-trait plots), bumblebee and hoverfly visitation was maintained at the level of their respective preferred single-trait plot, but parasitoid visitation was reduced by 50%. Thus, the informed selection of functionally diverse flower patches can be an effective tool to attract a higher diversity of insect groups than functionally simple plots. However, this may increase interference competition between visitors and limit the value of floral resources for beneficials that are weak competitors.

Zusammenfassung

In Agrarökosystemen stellen nützliche Insekten viele unschätzbare Ökosystemfunktionen zur Verfügung, wie die Bestäubung von Nutzpflanzen und die Schädlingskontrolle. Die Schaffung von blühenden Ackerrandstreifen kam als eine wichtige Methode auf, um nützliche Insektengruppen in diesen Systemen zu bewahren. Dennoch ist die Wirksamkeit dieser Methode in Bezug auf die Bereitstellung der Ökosystemfunktionen normalerweise beschränkt, da es nur ein geringes Wissen darüber gibt, wie die Pflanzenartenzusammensetzung, die funktionalen Eigenschaften und die Diversität der Pflanzeneigenschaften die Besuche von Insekten und die Ressourcennutzung beeinflussen. Hier untersuchen wir die Auswirkungen der Eigenschaften von Blüten und der Diversität der Pflanzeneigenschaften auf den Blütenbesuch von drei Gruppen funktional unterschiedlicher, nützlicher Insekten, die eine Nutzpflanzenbestäubung oder eine Schädlingskontrolle zur Verfügung stellen: Hummeln, Schwebfliegen und parasitoide Wespen. Wir legten Versuchsflächen an, die entweder Pflanzen mit langen oder kurzen Blütenröhren besaßen und gemischte Probeflächen die gleichermaßen Pflanzen mit kurz- bzw. langröhrigen Blüten enthielten. In den funktional einfachen Probeflächen zeigten die Insektengruppen bestimmte Blütenassoziationen, wobei die Hummeln fast ausschließlich mit den Flächen mit langen Blütenröhren assoziiert waren, während die Parasitoide und Schwebfliegen stark die Probeflächen mit

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kurzröhrigen Blüten bevorzugten. Wenn diese Pflanzentypen in Kombinationen gepflanzt wurden (Probeflächen mit gemischten Eigenschaften), wurde der Besuch durch Hummeln und Schwebfliegen nicht beeinflusst, der Besuch durch Parasitoide war jedoch um 50% gegenüber der bevorzugten Probefläche mit einfacher Eigenschaft reduziert. Deshalb kann die bewusste Auswahl von funktional verschiedenen Pflanzen auf den Flächen im Gegensatz zu funktional einfachen Flächen ein effektives Werkzeug sein, um eine höhere Diversität von Insektengruppen anzuziehen. Dies könnte jedoch auch die Konkurrenz zwischen den Besuchern erhöhen und damit den Wert der Blütenressourcen für diejenigen Nützlinge vermindern, die schwache Konkurrenten sind.

Introduction

Managed and natural ecosystems can support a multitude of processes and services vital to food security and the overall well-being of human society (Daily et al. 2000; Hector & Bagchi 2007). Yet the mechanisms that bring about the provision of these services remain unclear (Yachi & Loreau 1999; Srivastava & Vellend 2005; Cardinale et al. 2006; Hector & Bagchi 2007). Many studies focus on species richness as a driver of ecosystem services and report a positive saturating relationship between species richness and ecosystem function (Cardinale et al. 2006; Haddad, Crutsinger, Gross, Haarstad, & Tilman 2011). Others argue that it is the underlying diversity of functional traits amongst species present, not the number of taxonomic units driving this relationship (Hooper et al. 2005; Flynn et al. 2009). A functional trait may be defined as any measurable aspect of an organism that mediates its interaction with the environment, other species or the ability to acquire resources, e.g., the structure of an organism's feeding apparatus (Flynn et al. 2009). Species may share traits, and be considered a functional group, creating functional redundancy amongst similar species (Schwartz et al. 2000). However, other species, or groups of species may differ, and these measurable differences in traits may determine ecosystem dynamics and processes.

The need to study the effects of changes in biological diversity is particularly pressing in managed ecosystems such as agricultural landscapes, where beneficial insect biodiversity provides crop growers with crop pollination and biological control services, which are key to food security and sustainability (Losey & Vaughan 2006). Several beneficial insect groups and the services they provide are currently under threat from the intensification of management practises within agro-ecosystems and the rapid reduction in semi-natural habitat surrounding productive areas (Thies & Tscharntke 1999; Kremen, Williams, & Thorp 2002; Ricketts 2004; Biesmeijer et al. 2006; Potts et al. 2010). It is pivotal that we understand the mechanisms that underlie Biodiversity-Ecosystem Function (BEF) relationships to provide accurate practical advice to policy makers setting agri-environment scheme prescriptions and practitioners managing the agricultural landscape (Carvalheiro et al. 2011).

Here we use experimental wildflower patches to investigate the effects of flower traits and trait diversity on the abundance of three functionally distinct beneficial insect groups (bumblebees, hoverflies and parasitoid wasps). Bumblebees are key pollinators, while parasitoids are representatives of biocontrol agents. Hoverflies, on the other hand, can act both as biocontrol agents and as pollinators (Jauker & Wolters 2008). All three insect groups feed upon plant-provided resources in the form of pollen and/or nectar (Colley & Luna 2000; Landis, Wratten, & Gurr 2000; Wäckers 2004; Carvell, Meek, Pywell, Goulson, & Nowakowski 2007). Therefore, their abundance, diversity and resultant ecosystem service provisioning may be enhanced by supplying suitable plant resources within agro-ecosystems (Irvin et al. 2006; Olson & Wäckers 2007; Carvalheiro et al. 2011; Haland, Naisbit, & Bersier 2011; Hogg, Bugg, & Daane 2011).

While all three groups depend on nectar and pollen, the range of floral resources each group exploits may vary as a function of plant traits and floral morphology, as well as insect innate preferences and foraging capabilities (Patt, Hamilton, & Lashomb 1997; Fontaine, Dajoz, Meriguet, & Loreau 2006; Campbell, Bischoff, Lord, & Robertson 2010; Wäckers & van Rijn 2012). For instance, long-tongued bees can exploit many flower types including the ones with nectar hidden in deep corollas and spurs (Pywell et al. 2005), whereas parasitoid wasps and hoverflies often lack specialised mouthparts and tend to feed on more open and accessible flowers (short-corollas) (Patt et al. 1997; Colley & Luna 2000; Wäckers 2004; Vattala, Wratten, Phillips, & Wäckers 2006). Different flower mixes have been developed and deployed to 'target' pollinators and biocontrol agents, respectively, with pollinator mixes often being dominated by Fabaceae, while the Apiaceae and other species with exposed nectaries dominate in biocontrol mixes, (Colley & Luna 2000; Pywell et al. 2005; Begum, Gurr, Wratten, Hedberg, & Nicol 2006; Carvell et al. 2007; Winfree 2010). While these commercially available flower mixes frequently target a particular insect group, it is often assumed that using them to diversify the agro-ecosystem benefits nectar and pollen feeder diversity in general. Alternatively, increasing the diversity of floral traits among flowering species may be a stronger driver of associated beneficial insect diversity than raising plant species diversity *per se* (Wäckers 2004; Fontaine et al. 2006;

Pontin, Wade, Kehrli, & Wratten 2006; Olson & Wäckers 2007).

To test this, we created two functionally distinct flower mixes. The first was based on the pollen and nectar mix as developed for the UK Agri-Environment scheme, which is dominated by long-corolla flowers (Carvell et al. 2007). The second mix was based on a mix developed to support biocontrol in Dutch and UK vegetable production, and is characterised by short-corolla flowers (Wäckers & van Rijn 2012). We hypothesised that insects vary in their response to different flower types, with bumblebees able to forage upon both long/narrow and short/open corolla flowers, whilst parasitoids, and to a lesser extent hoverflies are restricted to open or short corolla flower resources. Second, we predicted that as plant functional trait diversity increased in a given flower patch, the abundance and diversity of insect groups would respond accordingly. To test this second hypothesis, the visitation of each insect group was compared between functionally simple (one flower category) and functionally diverse flower patches (mix of both flower categories). If, as predicted, flower mixes combining functional traits attract a higher diversity of beneficial insect categories, we can use this information to underpin the development of agri-environment scheme prescriptions that effectively 'stack' multiple ecosystem services (Fiedler, Landis, & Wratten 2008). Such multi-functional agri-environment prescriptions would be a powerful tool in supporting the sustainable production of safe and healthy food.

Materials and methods

Three flower treatments were sown in 2 m × 1 m plots along the centre of a grassy field, dividing a crop of potatoes and wheat at Stockbridge Technology Centre, North Yorkshire in April 2009. Each treatment was replicated four times in a randomised block design. Blocks were separated by a distance of 10 m from each other along the field, with a 4-m gap maintained between plots within these replicate blocks. Treatment 1 ('long-corolla mix') contained *Trifolium repens*, *Lotus corniculatus* and *Borago officinalis*, all of which have complex and deep flowers. Treatment 2 ('short-corolla mix') contained *Fagopyrum esculentum*, *Coriandrum sativum* and *Ammi majus*, all with easily accessible nectar and pollen (shallow, open nectaries) (see Appendix A, supplementary material). Treatment 3 ('mixed-trait mix') included all six plant species from treatments 1 and 2, at roughly 50% the abundance (in terms of floral resources) found in each of the 'targeted' mixes. *F. esculentum*, *C. sativum*, *A. majus*, and *L. corniculatus* were sown by hand in late April at densities recommended for UK environmental stewardship schemes (Defra 2006); whereas *B. officinalis* and *T. repens* individuals were transplanted into plots in early July. Other flowering species in and around the plot were manually removed throughout the study.

Floral resource abundance within plots was recorded three times over the study period (late June, early July and late July) using methods similar to those described in Carvell, Meek, Pywell, and Nowakowski (2004); whereby inflorescences of different species are considered equivalent units of each other. For example, a flower spike of *T. repens* and an umbel of *A. majus* were both considered as one floral unit. Abundance was standardised between plant species by setting maximum number of flowers found for each species to 1. This was achieved by dividing the number of flower units observed at one flower patch by the maximum number of flowers counted for that species across all replicates. Next we calculated the Shannon diversity index (H') for each plot to account for within-plot variation in floral resources.

Visitation

Visual observations of beneficial insects visiting plots were completed over nine (non-consecutive) days in July (peak flowering period), with each plot subject to 39, one-minute observation periods. All observations were performed between 10:00 and 15:00 h on warm, sunny days with minimal cloud cover, so to coincide with the period of peak insect activity, as well as to minimise the effects of variation in temperature on insect activity (Pontin et al. 2006). A 1-min pre-recording habituation period was used to reduce the observer effect (Wade, Zalucki, & Franzmann 2005; Pontin et al. 2006). The visitation frequencies of hoverflies (Diptera: Syrphidae), bumblebees (Hymenoptera: Apidae: *Bombus* spp.) and parasitoid wasps (super-family Hymenoptera: Parasitica) were recorded, along with the plant species visited. We recorded the visitation rates of six hoverfly species (*Platycheirus albimanus*, *Episyrphus balteatus*, *Eupeodes corollae*, *Syritta pipiens*, *Platycheirus clypeatus* and *Sphaerophoria scripta*). All remaining hoverflies were recorded as 'hoverfly'. Two bumblebee species could be identified by eye during observations (*Bombus pascuorum* and *Bombus lapidarius*), but *Bombus terrestris* and *Bombus lucorum* were classed as *B. terrestris/lucorum*, as workers are indistinguishable in the field (Prŷs-Jones & Corbet 1987). Solitary bees and honeybees were not considered during this study. All parasitoid wasps were recorded as 'parasitoid wasp'. Data for individual fly and bee taxa were too low and therefore pooled into groups (bumblebees and hoverflies) when analysed.

A sticky trap assay was included specifically as a second method for the monitoring of parasitoids. Sticky traps were 20-cm cylindrical tubes made of A4 acetate sheets treated with Agralan Insect Barrier glue (Agralan ltd., UK) and attached to 40-cm poles. Traps were transparent and free of volatiles. Four traps were set in each plot throughout July with the number of days each set of traps was left in the field varying between rounds (range = 4–10 days). As a result seasonal changes in parasitoid abundance could not be assessed. Following collection of the traps, the number of parasitoids

on each acetate sheet was counted and divided by the number of days the trap had been set for to estimate parasitoid catch per day.

Statistical methods

We used R (R 2.72, R Development Core Team 2009) for all analyses. Differences in bumblebee (pooled from three species), hoverfly (pooled from six species) and parasitoid wasp (considered as sub-order) abundance in each treatment were analysed using iterative GLM analysis for Poisson distributed errors in order to create the minimum adequate models (MAM) for each response variable. We used a mixed factor ANOVA to test for significance of model parameters (replicate, flower treatment, date, temperature, H' and total floral abundance) in explaining insect abundance. Data from Poisson GLMs was back-transformed before presentation. Plant-insect interaction networks were analysed using the bipartite package for R (ver. 0.93; Dormann, Fründ, Bluthgen, & Gruber 2009). We assessed upper trophic level dependence, i.e., what proportion of an insect's total plant interactions is made up by each plant species (Tylianakis, Laliberte, Nielsen, & Bascompte 2010). Only data for *B. pascuorum*, *E. balteatus*, *P. albimanus* and *Eu. corollae* were sufficient to be treated at species level. Sticky trap counts were analysed using independent t-test and iterative GLM using a multi-factorial ANOVA for Gaussian error distribution. All statistical models were considered at an overall significance level of $p < 0.05$.

Results

Insect-plant trait associations

During observations a total of 513 visits were observed (bumblebee: $n = 94$; hoverflies: $n = 187$; parasitoid wasps: $n = 232$). Bumblebee flower visitation frequency differed significantly between treatments ($p < 0.001$, df = 2, $n = 468$) being twenty five times higher in long-corolla plots than short-corolla plots (see Fig. 1). Bumblebee visitation also varied among observation dates ($p = 0.018$, df = 8, $n = 468$) and replicate blocks ($p = 0.0016$, df = 1, $n = 468$). Parasitoid wasp visits were most common in short-corolla plots (71.1% of observations) and were recorded twenty times less in long-corolla plots ($p < 0.001$, df = 2, $n = 468$). Observation date ($p < 0.001$, df = 1, $n = 468$) and floral diversity (H') ($p < 0.001$, df = 1, $n = 468$) significantly affected parasitoid visitation. Parasitoid abundance on sticky traps varied between collection dates ($F_{3,35} = 11.1137$, $p < 0.001$) and flower treatment ($F_{2,38} = 9.3542$, $p < 0.001$) (Fig. 2).

Hoverflies, pooled from the observations of six species, demonstrated the weakest response to plant trait treatments (Fig. 1). Still, hoverfly distribution patterns varied significantly among flower treatments ($p < 0.001$, df = 2, $n = 468$),
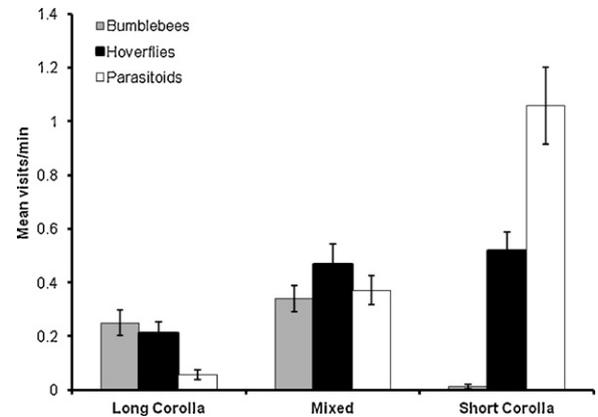

Fig. 1. Mean (±SE) visits/min of beneficial insect groups in each flower treatment. There are clear differences in the visitation frequencies of each insect group between long-corolla and short-corolla flower treatments, with parasitoids showing a clear preference for short-corolla flowers, and bumblebees for long-corolla flowers. Hoverflies were seen visiting flowers in both simple treatments, but were observed twice as often visiting flowers in short-corolla plots than long-corolla plots. All three insect groups were found also in mixed-trait plots but parasitoid visitation was greatly reduced relative to short-corolla plots.

with two times as many visits recorded at short-corolla plots compared to long-corolla plots suggesting some preference for short-corolla flowers. Observation date ($p < 0.001$, df = 1, $n = 468$) and the interaction between flower treatment and H' value ($p < 0.05$, df = 2, $n = 468$) were also significant in explaining hoverfly abundance.

Plant-trait diversity effects

No significant differences were found in hoverfly and bumblebee visitation frequency among their respective preferred single-trait plots and mixed-trait plots. Table 1 shows how flower preferences vary between hoverfly species and that
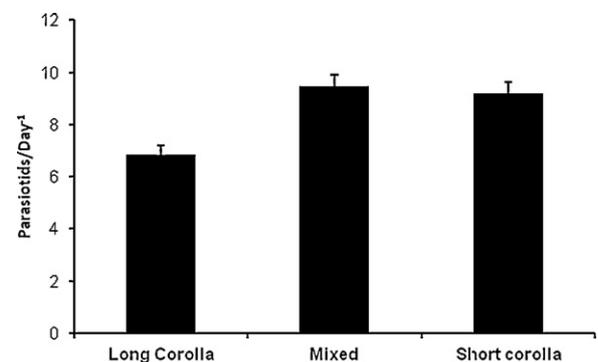

Fig. 2. Mean (±SE) number of parasitoids per day collected from sticky traps in three flower treatments to account for the variability in the number of days traps were set. The overall effect of treatment was significant ($p < 0.05$) but mean abundance counts from short-corolla plots and mixed-trait plots did not differ.

Table 1. The proportion of visits made by three hoverfly species to each plant species when in either single- or mixed-trait flower treatments. The middle line separates the three long-corolla species (top) from the three short-corolla species. The final row indicates total number of visits observed and how these were divided between long- or short-corolla flowers (#L/#S). In simple mixtures all 18 potential links between hoverflies and plants were found, whilst only 15 out of 18 links were observed in mixed-trait plots. In mixed-trait plots a preference for short-corolla plants was not observed as hoverflies utilised species from both simple mixes.

Treatment	P. albimanus		E. balteatus		Eu. corollae	
	Single	Mixed	Single	Mixed	Single	Mixed
B. officinalis	0.56	0.00	0.33	0.04	0.07	0.05
T. repens	0.22	0.36	0.33	0.15	0.60	0.35
L. corniculatus	0.22	0.18	0.33	0.00	0.33	0.10
F. esculentum	0.40	0.36	0.35	0.26	0.38	0.35
C. sativum	0.20	0.00	0.57	0.41	0.45	0.10
A. majus	0.40	0.09	0.09	0.15	0.17	0.05
#Visits (#L/#S)	14 (9/5)	11 (6/5)	26 (3/23)	27 (5/22)	44 (15/29)	20 (10/10)

these preferences are preserved in mixed-trait mixes. Some hoverflies such as *Eu. corollae* are generalist flower visitors; whilst others, such as *E. balteatus* almost exclusively feed from short-corolla flowers. Network analyses (Fig. 3) of bumblebee and hoverfly visitation show the strong affinity of bumblebees to long-corolla plants, even in mixed-trait plots (Fig. 3C) and that hoverfly preferences in functionally uniform plots (Fig. 3A and B) are also preserved in mixed-trait plots. However, in mixed-trait plots, despite the inclusion of favourable plant species, visitation by parasitoids was reduced by 2.5 fold relative to short-corolla plots (Fig. 1). Yet, no significant difference was found in the mean abundance of parasitoids collected from sticky traps at short-corolla plots versus mixed-trait plots, indicating that parasitoids are present in functionally diverse plots, but visiting flowers less frequently (Fig. 2).

Discussion

All three insect groups, but particularly bumblebees and parasitoid wasps, differed clearly with regard to their floral association, demonstrating that floral traits largely determine insect visitation patterns (Fig. 1). Bumblebees demonstrated a strong affinity to plots containing long-corolla flowers, whilst parasitoid visitation was highest at plots containing short-corolla flowers. Parasitoid wasps may be morphologically excluded from foraging on structurally complex flowers as they lack the mouthparts required to extract nectar from such flowers (Patt et al. 1997). Hoverflies utilised both long and short flowers and exhibited some preference for the latter. This result may be a reflection of pooling data from six ecologically distinct species, each with their own specific floral preferences. Gilbert (1981) suggests that the feeding niche of a hoverfly is strongly determined by the length of its mouthparts, with many aphidophagous species limited to feeding from flowers with short-corollas of less than 3 mm in depth. When the floral associations (proportion of visits) of the three most abundant hoverfly species are considered (Table 1), in conjunction with interaction web analyses (Fig. 3), it is clear that flower preferences vary between hoverfly species. For example *Eu. corollae* was found foraging frequently on all plant species irrespective of treatment (simple or mixed-trait); whereas *E. balteatus* only formed strong associations with short-corolla flowers, particularly coriander (in both simple and mixed-trait plots). These interaction web analyses clearly demonstrate that the foraging preferences of hoverflies and bumblebees in single-trait plots can be preserved in mixed-trait plots.

The three surprising outcomes of the study were: (1) the almost absolute partitioning of bumblebees and parasitoids between long and short-corolla plots; (2) the affinity of bumblebees to long-corolla flowers, even though they should have been able to exploit short-corolla flowers as well; (3) the notable reduction in flower visitation by parasitoids in mixed-trait plots despite the presence of preferred short, open corolla flower species. Unlike the absence of parasitoid wasps from long-corolla flowers, lack of access cannot explain why bumblebees rarely visited short-corolla flowers both in single trait mixes and mixed-trait mixes. Plant traits other than flower structure may also drive insect visitation frequency; including visual cues (Begum, Gurr, Wratten, & Nicol 2004), plant volatiles (Dotterl & Vereecken 2010; Randlkofer, Obermaier, Hilker, & Meiners 2010) and/or resource quality and quantity (Wäckers 2005; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies 2005). Short-corolla flowers may present a lower quantity of available nectar, as these flowers can be exploited by a larger pool of nectar-feeding insects. Nectar quality can also be affected by floral traits, as nectar in open flowers tends to become more viscous through evaporation (Winkler, Wäckers, Kaufman, Larraz, & van Lenteren 2009) and tends to have higher glucose and fructose levels, whereas long-corolla flowers often have sucrose-dominated nectar (Percival 1961). Overall, these results support our first hypothesis; that beneficial insect groups are highly specific in their response to different flower types.
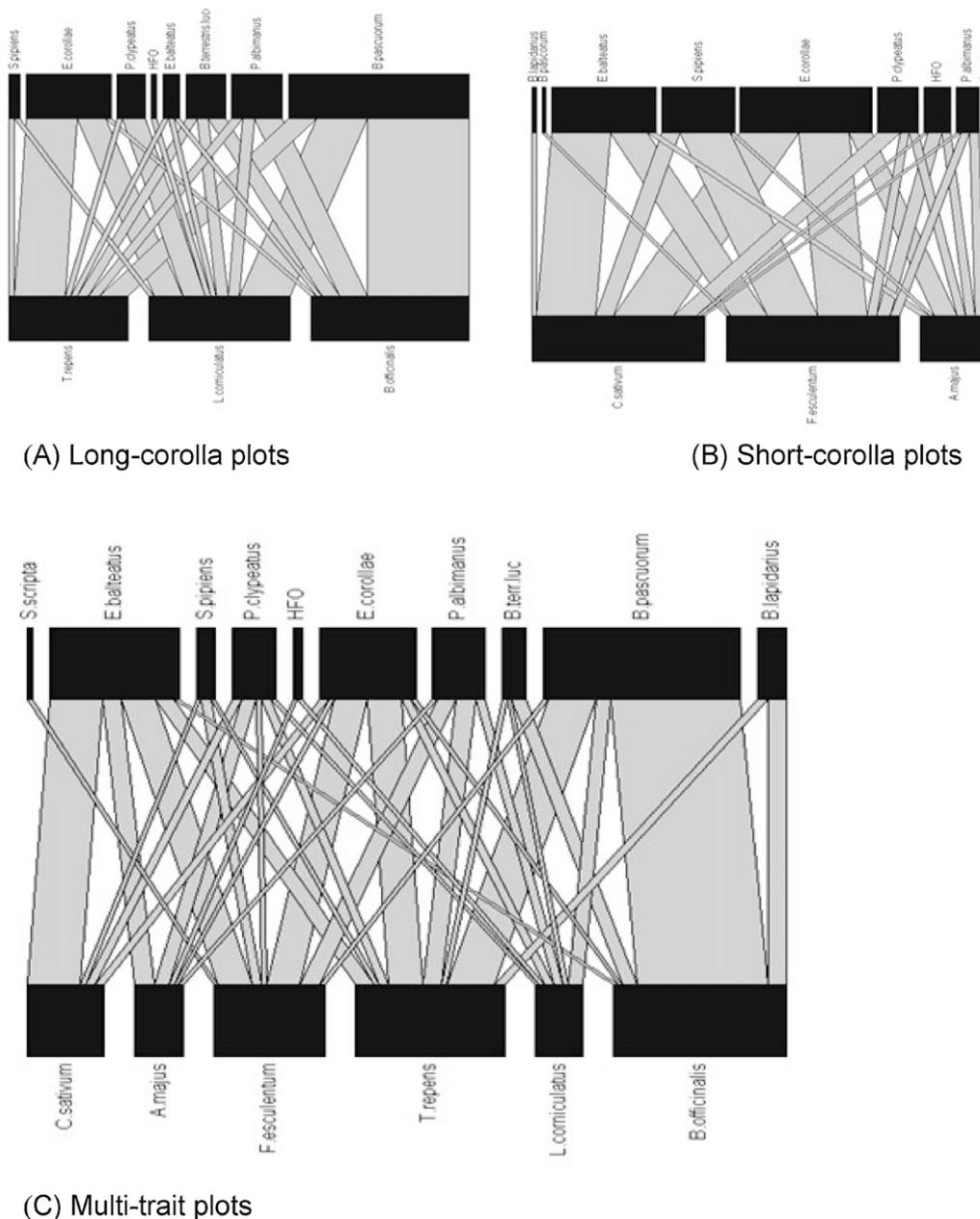
Fig. 3. Interaction webs demonstrating changes in hoverfly and bumblebee visitation to six plant species in single-trait plots ((A) long-corolla plots, (B) short-corolla plots) and (C) mixed-trait plots. HFO denotes unidentified hoverflies.

To test our second hypothesis, that an informed increase in floral trait diversity within flower patches helps attract a greater number of insect groups, we compared functionally simple plots (single trait) with functionally diverse plots (mixed-trait). In contrast to single-trait plots, which almost entirely excluded at least one insect group, we found that all three insect groups were recorded in abundance in mixed-trait plots (Fig. 1). Nevertheless, parasitoid visitation was reduced by 50% in mixed-trait plots relative to preferred short-corolla plots (Fig. 1). This reduction could reflect an equivalent reduction in suitable floral resources, having been diluted by a factor two in the mixed-trait mix (short, open corolla flowers making up 50% in the mixed-trait plots). This is a common problem of biodiversity-ecosystem function studies, where more diverse treatments concurrently diminish the abundance of each individual species involved (Cardinale, Harvey, Gross, & Ives 2003). Alternatively, the reduced visitation could be a negative response to the addition of the other plants, as parasitoids can be repelled by the volatiles of some plant species (Wäckers 2004). Yet sticky trap assays revealed no difference in the number of parasitoids caught at the preferred short-corolla plots to those from mixed-trait plots, suggesting that parasitoid wasps were present in both treatments, but visited flowers more frequently in single-trait plots. Furthermore, similar declines in visitation rate in mixed-trait plots were not witnessed in other insect groups

such as bumblebees, despite a similarly strong affinity to only one of the two available corolla-trait groups (long-corolla flowers). This implies a possible competitive effect of other flower visitors on parasitoid wasps. Dominance hierarchies at flower patches and strong direct and indirect competition between even distantly related insect groups for food resources have been well documented (Reader, MacLeod, Elliott, Robinson, & Manica 2005; Pontin et al. 2006; Hogg et al. 2011).

Our results strongly indicate that biodiversity-ecosystem service relationships are driven by the diversity of functional traits amongst species present rather than the number of taxonomic units. Although we accept that it would be better to use a fully factorial design (random three species treatments from the pool of six plant species) to study this relationship it is clear from our findings that wildflower mixes that lack plant trait diversity may not benefit a broad suite of beneficial insects. Our study underlines that joint optimisation of multiple ecosystem services and insect conservation objectives requires insight in floral associations and resource requirements of target organisms. Furthermore, the observed response of parasitoid wasps indicates that separate plots targeting each group rather than a fully mixed design might be more effective to reduce negative competitive effects between insect groups.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.baae.2012.04.003.

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