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Pollinator visitation to mass-flowering courgette and co-flowering wild flowers: Implications for pollination and bee conservation on farms

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Abstract

Managing the complex relationship between pollinators and their habitat requirements is of particular concern to growers of pollinator-dependent crop species, such as courgette (*Cucurbita pepo*). Naturally occurring wild flowers (i.e. agricultural weeds) offer a free, sustainable, and often underappreciated resource for pollinators, however, they may compete with crop flowers for visits. To understand the extent to which floral resources mediate pollinator visitation to courgette flowers and courgette fields, plant community and pollinator visitation data were collected at two spatial scales: field scale (in margins, and in the cropped area) and farm scale (500 m and 2000 m radii) for nine courgette fields across the UK. *Apis mellifera* (honeybees) and *Bombus* spp. (bumblebees) were the only pollinators observed to visit courgette flowers. Bumblebees were significantly more abundant on courgette flowers in areas with less semi-natural habitat. For both honeybees and bumblebees, their abundance in field margins did not significantly reduce their abundance on courgette flowers, suggesting that wild flowers were not competing with courgette flowers for pollinator visitation. Although solitary bees were not observed to visit courgette flowers, their abundance and species richness in courgette fields were significantly greater with more semi-natural habitat and a greater species richness of wild flowers. Therefore, allowing uncultivated areas around the crop to be colonised by species-rich wild flowers is an effective way of boosting the abundance of bumblebees, which are important visitors to courgette flowers, as well as the abundance and species richness of solitary bees, thereby benefitting pollinator conservation.

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Keywords: Cucurbit; Pollination; Landscape; Bee conservation

Introduction

Agricultural expansion and intensification has resulted in reduced ecological functioning of farmland ecosystems (Hooper, Chapin, & Ewel, 2005; Bommarco, Kleijn, & Potts, 2013). Sustainable management of these systems requires

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beneficial services such as pollination, pest control and nutrient cycling to be optimised whilst minimising any negative effects that they may have on other services. For example, effective biological weed control may reduce the availability of forage for pollinators and natural enemies, whilst areas planted for forage may compete with crop species for abiotic and biotic resources (Bretagnolle & Gaba, 2015). These factors are of particular concern to growers of pollinatordependent crop species who must manage the complex

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relationship between pollinators, their habitat requirements and other ecosystem services important for determining yield such as natural pest control (Bommarco et al., 2013).

Supplementing crop fields with managed bee species can bolster pollinator numbers (Garibaldi et al. 2014) to prevent yield declines. This has been common practice for growers of Cucurbitaceae (cucurbits or gourds) (Free, 1993; Nerson, 2007), which have an 'essential' requirement for insectmediated pollination (Klein et al. 2007, although see Knapp & Osborne 2017). However, introducing managed pollinator species does not address one of the primary drivers of pollinator decline: loss of available forage (Vanbergen, 2013). Instead, improving the quantity and quality of pollen and nectar resources available for pollinators, and allowing areas to remain undisturbed for mating, nesting, and hibernation will benefit pollinator populations beyond that of the focal crop (Carvell, Meek, Pywell, Goulson, & Nowakowski, 2007). At a field scale, floral resources can be increased by planting wild flower strips, allowing areas to be naturally colonised by wild flowers, or maintaining hedgerows. At a farm scale, proximity to, or quantity of natural and semi-natural habitat can increase pollinator abundance as species fly into crop areas from semi-natural habitat to forage (Garibaldi et al., 2011).

However, the effectiveness of field-scale pollinatorsupporting practices are often variable and greatly depend on the complexity of the habitat surrounding a crop field, with more simplistic landscapes generally showing greater increases in pollinator species richness after interventions than in complex landscapes (Batáry, Báldi, Kleijn, & Tscharntke, 2011; Scheper et al., 2013). At a field scale, providing additional floral resources within fields (such as wild flowers) may attract or distract pollinators from the focal crop as they facilitate or compete for pollination services (Mitchell, Flanagan, Brown, Waser, & Karron, 2009; Nicholls & Altieri, 2013). At a farm scale, the area of massflowering crops may 'dilute' pollinator densities if large, or 'concentrate' pollinator densities if small (Holzschuh et al. 2016). This will be especially pronounced if additional food and nesting sites are not provided, meaning that pollinators move transiently between available forage rather than increasing their population size (Holzschuh et al. 2016). The complexity of field and farm-scale resources becomes further complicated when species-level responses are taken into consideration. Increasing the proximity of forage to suitable nesting sites may be more important for 'door step foragers' such as Bombus muscorum, B. pascuorum and B. lapidarius which are known to forage close to their nests (Osborne et al., 2008). Other species with longer flight distances (such as *B*. terrestris and Apis mellifera) are found in high abundance in large, intensively farmed fields, far away from available nest sites (Osborne et al., 2008). Since previous research has shown that B. terrestris and A. mellifera can fulfil the pollination requirements of courgette in the UK (Knapp & Osborne 2017) and that *Bombus impatiens* is an even more efficient pollinator of pumpkin than the specialist Peponapis *pruinosa* in the USA (Artz & Nault, 2011), increasing the proximity of forage to suitable nesting sites may be less important to cucurbit crops because they are primarily serviced by long-range, generalist pollinators. This highlights the need to match pollinator-supportive management practices with crops' individual requirements for pollination, since an increase in pollinator species richness may not necessarily be required for yield to be improved (Kleijn et al., 2015; Winfree, Fox, Williams, Reilly, & Cariveau, 2015).

The positive, mediating effect of forage availability on pollinator visitation and crop yield has been shown in many crops including pumpkin (Petersen & Nault 2014), strawberry (Connelly, Poveda, & Loeb, 2015), poppy (Hardman, Norris, Nevard, Hughes, & Potts, 2016), and coffee (Saturni, Jaffé, & Metzger, 2016). Likewise, several studies have looked at forage availability at different spatial scales, in terms of patch size (Heard et al., 2007), and field versus farm scale allocation of resources (Hardman et al., 2016). However, these analyses do not differentiate between pollinator visitors to the focal crop and all other pollinator species, thus increases in pollinator numbers may not necessarily benefit crop pollination.

This study focuses on pollinator visitation to massflowering courgette (*Cucurbita pepo*) and co-flowering wild flowers to further understand the extent to which available forage (at different spatial scales) may improve pollination and/or pollinator conservation in crop fields. To do this we ask: (1) Which pollinator species visit courgette flowers and which ones visit co-flowering wild flowers in crop fields? (2) How does forage availability and pollinator presence in field margins affect pollinator visitation to courgette flowers? And (3) How does forage availability affect the abundance and species richness of pollinators which do not visit courgette?

Materials and methods

Sites

In 2016, nine courgette (var. Tosca) fields were surveyed in three key courgette growing regions of England in Cornwall (five sites), Worcestershire (two sites) and Cambridgeshire (two sites), to represent a range of climatic variables. Tosca is a popular courgette variety in the United Kingdom, representing 37.9% of the market share (P.E. Simmons and Son, personal communication 1 April 2017). The total economic value of insect pollination to courgette is estimated to be worth £3398 per ha (Knapp & Osborne, 2017).

All courgettes were grown conventionally in outdoor conditions. Little or no herbicide is used on courgette fields due to the short picking intervals of the crop (P.E. Simmons and Son, personal communication 1st November 2017), which results in a high abundance and diversity of flowering weeds within the crop. The fields were managed by five horticultural growing companies: with similar farming practices checked using questionnaires. No foliar insecticides were applied at any

fields since courgette experiences little pest damage in the UK (P.E. Simmons and Son, personal communication 1st November 2017). Whilst all fields were subject to the same tillage regime (ploughed and harrowed), one site in Cornwall was consistently tilled at depths 4 cm less than other fields. Each field differed slightly in the number of herbicide (0–5 applications, median = 2.5), fungicide (0–4 applications, median = 2.5). All fields were planted with the same density of courgette and none were stocked with commercial pollinators, however, the density of managed pollinator colonies in the surrounding landscape was unknown.

Fields (average field size of 8.5 ± 1.9 ha (S.E.)) were all situated over 5 km apart (apart from two sites in Cornwall which were 3.5 km apart) so that pollinator communities are unlikely to be shared between fields (Vaissière, 2010), and each field was visited three times between 1st June and 31st July, during courgette blooming. Eight 50 m transects per field were established; four along each field margin and four within the crop (from the edge of the crop to the centre, 25 m apart).

Pollinator surveys

Transects were walked at a steady pace (\sim 5 min each) with observations made 1 m either side and in front of the recorder (over a length of 50 m). All bee species and the plant species they were on (if feeding or pollen collecting) were recorded to species level in the field, except workers from the *Bombus terrestris/Bombus lucorum* complex which cannot be reliably distinguished in the field (Murray, Fitzpatrick, Brown, & Paxton, 2008). In cases where species identification could not be made a voucher specimen was taken for identification in the laboratory. Sampling was conducted between 08:00 and 10:00 am (when flowers were open) on sunny to partly cloudy days.

Halfway along each transect, one pan trap (15 cm diameter plastic bowl sprayed with yellow UV paint) was placed 20 cm off the ground (average height of courgette flowers) for 24 h immediately after conducting a pollinator transect, to prevent any reduction in transect numbers by pan traps. Traps were filled with dilute scentless soapy water. All bees and hoverflies were identified to species level in the laboratory. Pollinator transects and pan traps were analysed separately (transects were used to calculate the number of pollinators on courgette flowers and pan traps were used to estimate the abundance and species richness of solitary bees (noncourgette pollinators)). Solitary bees were chosen for further analysis over hoverflies due to their effectiveness at pollinating other crop species such as oilseed rape (Garratt et al., 2014). Using this combination of survey techniques gave a better representation of overall species richness and an insight into plant-pollinator interactions (Westphal et al., 2008). In addition, network diagrams of pollinator/flower interactions in courgette fields, divided into field margins and the cropped area itself were constructed.

Floral surveys

Flowering plant surveys were conducted at the same time and location as the pollinator transects. To calculate the availability of non-crop floral resources (wild flowers), the numbers of open flowers or floral units (in the case of composites) of insect rewarding plant species (defined in Hardman et al. (2016)) were recorded.

Landscape variables

Since semi-natural habitat and mass-flowering crops can increase pollinator populations (Westphal, Steffan-Dewenter, & Tscharntke, 2003; Kremen, Williams, Bugg, Fay, & Thorp, 2004), the total area of semi-natural habitat (woodlands and heathland) and mass-flowering crops (courgette, oilseed rape, and field beans) were calculated in 500 m and 2000 m radii of each field (m²) using CEH Land Cover[®] plus: Crops (for information on annual crop types) and Land Cover 2007 (for information on habitat types (Centre for Ecology and Hydrology, 2011, 2016)) using ArcGIS 10.2.2.

Statistical analysis

All analyses were carried out using R (R Core Team, 2017). Linear mixed effect models (Bates, Mächler, Bolker, & Walker, 2015) were used to investigate how wild plant abundance and species richness at different spatial scales influenced (1) the abundance of bee species observed visiting courgette flowers (honeybees and bumblebees) and (2) the abundance and species richness of other bee species (solitary bees) which were not observed visiting courgette flowers.

For each response variable, a set of candidate models were constructed using rescaled (between 0 and 1) predictor variables. For courgette visitors (honeybees or bumblebees), the full fixed effects model contained the abundance of the same species on field margins (either honeybees or bumblebees depending on the response variable), the overall abundance of either honeybees or bumblebees (opposite to the response variable as a measure of competition), abundance of wild flowers per crop transect, species richness of flowers per crop transect, total number of wild flowers per field (sum of wild flowers in the margins and cropped area), area of semi-natural habitat (m² in 500 m and 2000 m radii), area of mass-flowering crops (m² in 500 m and 2000 m radii), field size and the interaction between mass-flowering crops or semi-natural habitat and wild flowers per crop transect and wild flowers per field. Region and field size were entered as random effects, and a null model including random effects only included in the candidate model set. Abundance and species richness of floral resources were always tested in separate models due to collinearity, as were semi-natural

habitat and mass-flowering crops (at 500 m and 2000 m radii) (Appendix A: Fig. A1).

Non-courgette visitors (solitary bees) were analysed in similar models, but included data from both margins and cropped area (per transect) in the response variable. Transect location (margin or cropped area) was added as a fixed effect.

For each stage of the analysis, all possible combinations of the full model (all fixed effects) were compared to the null intercept-only model using Akaike's An Information Criterion for small sample sizes (AICc) (Barton, 2017), with the lowest AICc score defining the model that best describes the data (Symonds & Moussalli, 2011).

Models with a change in AICc of 2 or less when compared to the best fitting model were examined (model averaging was not carried out due to correlated predictor variables) and the most parsimonious of these (the one with the lowest AICc) further checked for multicollinearity using variance inflation factors (VIFs) (Fox & Weisberg, 2011). All covariates had VIFs <5. The full and best fitting models were visually checked to meet model assumptions (homogeneity of variance, normal distribution of residuals and the presence of influential values). The significance of fixed effects in the best fitting model were tested using summary *t* and *p*-values (Kuznetsova, Brockhoff, & Christensen, 2016).

Results

Pollinator community

Overall, a total of 958 pollinators of 53 different species were recorded during this study. All 53 species were recorded in pan traps and 9 species were recorded in pollinator transects (in the margin and cropped area of courgette fields). Pollinators caught in pan traps included 57% hoverflies, 31% solitary bees and 12% social bees (honeybees or bumblebees), while only social bees (84%) and hoverflies (16%) were observed during transect surveys. Nonetheless, three bee species and one hoverfly species accounted for 77% of all pollinator records: *Apis mellifera* (n = 379), *Bombus terrestris/lucorum* (n = 196), *Bombus lapidarius* (n = 55), and *Eupeodes corollae* (n = 110).

An average of 46% of pollinator species occurred in both the margin and within the crop, which included 6 bumblebee, 8 solitary bee, and 9 hoverfly species. Honeybees (and to a lesser extent bumblebees) were more abundant in the cropped area, whilst solitary bees were more abundant on field margins (Fig. 1A). Courgette was the most visited floral resource with 52% of all flower visits recorded (including margins) being to male or female courgette flowers. The next most frequently visited flower species were Sinapsis arvensis and Cirsium palustre which received just 8% and 6% of pollinator visits respectively. Out of all pollinator species visiting courgette flowers, A. mellifera and B. terrestris were the most abundant (Appendix A: Fig. A2). However, whilst B. terrestris visited both male and female flowers (male flowers = 45 visits, female flowers = 47 visits), A. mellifera showed a preference for female flowers (male flowers = 13visits, female flowers = 270 visits) (Appendix A: Fig. A2).

Floral resources

Across all regions floral species richness was greater in field margins than in the cropped area (mean margin = 29 ± 4 *SE*, crop = 12 ± 2 *SE*). Likewise, the number of flowers was generally greater in field margins than in the cropped area (mean margin = $23,273 \pm 5365$ *SE*, crop = $10,529 \pm 4838$ *SE*) (summed per transect) (Fig. 1B and C). The amount of seminatural habitat varied from 0–13% (median = 3%) in a 500 m buffer and 1–17% (median = 9%) in a 2000 m buffer. The percentage area of mass-flowering crops varied from 14–37% (median = 23%) in a 500 m radius and 2–13% (median = 3%) in a 2000 m radius. The majority of mass-flowering crop in the landscape (94%) was courgette and was therefore flowering simultaneously with courgette at the study sites.



Fig. 1. Boxplots of (A) honeybee, bumblebee, and solitary bee abundance, (B) species richness of wild flowers, and (C) abundance of wild flowers within courgette fields (light grey) and in the field margins (dark grey). (A) shows summed values from pan traps and transects, while (B) and (C) show summed values from transects, all from the three survey dates per season. Boxplots represent the median, interquartile range, and maximum and minimum recorded values.

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Fig. 2. Significant effects from best fitting models (lowest AICc) of (A) honeybee abundance on courgette flowers in relation to semi-natural habitat (SNH) in a 2000 m radius (m^2) surrounding courgette fields, and (B) bumblebee abundance on courgette flowers in relation to the species richness of wild flowers in the cropped area. Solid lines are predicted values from linear models and dashed lines are 95% confidence intervals calculated via bootstrapping of 200 simulations.

Effect of floral resources on courgette pollinators

Honeybee abundance on courgette flowers was negatively correlated to the quantity of semi-natural habitat in a 2000 m radius (m²) ($\beta = -0.10 \pm 0.13$, t = -7.44, p = 0.023) (Fig. 2A), as well as a decrease in species richness of wild flowers in the cropped area (summed per transect), although this was not statistically significant ($\beta = -0.22 \pm 0.1$, t = -1.83, p = 0.08) (Table 1).

Bumblebee abundance on courgette flowers was positively correlated with an increase in species richness of wild flowers in the cropped area (summed per transect) ($\beta = 0.73 \pm 0.2$, t = 33.44, p = 0.002) (Fig. 2B) (Table 1).

Effect of floral resources on solitary bees

The best fitting model for solitary bee abundance included transect location (margin or crop), an increase in field size, species richness of wild flowers in fields, semi-natural habitat in a 2000 m radius and the interaction between wild flower species richness and semi-natural habitat (Table 1). Solitary bee abundance was positively related to wild flower species richness (summed per transect) ($\beta = 0.93 \pm 0.33$, t = 2.78, p = 0.007) and there was a significant interaction between floral species richness (summed per transect) and seminatural habitat in a 2000 m radius (m²) ($\beta = -1.46 \pm 0.35$, t = -4.24, p < 0.001), with an increase in wildflower species richness positively correlated with solitary bee numbers in landscapes with low semi-natural habitat (Fig. 3A). For all other predictors in the best fitting model the relationship was not significant (margin transect location ($\beta = 0.76 \pm 0.5$, t = 1.50, p = 0.14; field size (Ha) $-\beta = 0.72 \pm 0.4, t = 1.63$, p = 0.11); semi-natural habitat in a 2000 m radius (m²) $\beta = -0.23 \pm 0.37, t = -0.61, p = 0.55.$

The best fitting model for solitary bee species richness included location (margin or crop), species richness of wild flowers in fields, semi-natural habitat in a 2000 m radius and the interaction between wild flower species richness and semi-natural habitat (Table 1). Solitary bee species richness was significantly greater in field margins than in the cropped area ($\beta = 0.74 \pm 0.32$, t = 2.35, p = 0.02) (Fig. 3A) and wildflower species richness had a positive relationship with solitary bee species richness in areas with low or medium levels of semi-natural habitat (overall interaction effect size $\beta = -0.57 \pm 0.2$, t = -2.35, p = 0.02, Fig. 3B). There was no significant relationship with wild flower species richness (summed per transect) ($\beta = -0.33 \pm 1.9$, t = 1.88, p = 0.07), or semi-natural habitat in a 2000 m radius (m²) ($\beta = -0.33 \pm 0.19$, t = -1.69, p = 0.12).

Discussion

Enhancement of floral resources to increase pollinator populations is the primary basis for pollinator-supportive land management; however, less is known about how the scale of floral resources (field or farm) affects different crop pollinators. By understanding the dynamics more fully, pollinator-supportive land management can be targeted at *either* pollinator species which are known to visit the focal crop, with the aim of improving crop pollination, *or* at other pollinator species more generally, with the aim of improving species conservation; or both.

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Table 1. Top (maximum of three) best fitting models (with \triangle AICc < 2) describing the effect of field size and floral resources (at a local, and landscape scale) for (1) honeybees, and (2) bumblebees which were observed visiting courgette flowers, (3) solitary bee abundance, and (4) solitary bee species richness which were recorded over the whole courgette field. Only coefficient estimates for continuous fixed effects which occur in the best fitting models are presented in the table. Global models contained for 1 and 2: field size + (abundance of wild flowers in the cropped area + species richness of wild flowers in the cropped area) + total number of wild flowers in the field + margin honeybee abundance or Margin bumblebee abundance + overall honeybee abundance or overall bumblebee abundance + (semi-natural habitat (SNH) 500 m + semi-natural habitat 2000 m) + (mass-flowering crops (MFC) 500 m + mass-flowering crops 2000 m) + all measures of wild flowers * MFC/SNH. For 3 and 4 the global models were the same but included wild flowers over the whole field, transect location, and did not include honeybee or bumblebee abundance. Preceding brackets indicate where due to multicollinearity only one predictor variable for local floral resources and one variable for semi-natural habitat and mass-flowering crops were entered into the model. The R^2 (a measure of overall model fit) is divided into marginal R^2 (R^2_m) and conditional R^2 (R^2_C) following Nakagawa and Schielzeth (2013).

	Intercept	Field size	SR wild flowers (cropped)	Abundance of wild flowers	SR wild flowers	Margin bumblebee abundance	Margin honeybee abundance	SNH 2000 m	Location	SNH 2000 m* SR wild flowers	df	AICc	ΔAICc	Weight	R ² m	R ² c
	1.61		-0.22			-		-1.01	-		6	86.60	0.00	0.13	0.73	0.73
(1) Honeybee abundance	1.72					-	-0.06	-1.04	-		6	87.23	0.63	0.10	0.15	0.65
on courgette flowers	1.61					-		-1.06	-		5	87.27	0.68	0.09	0.70	0.71
									-							
(2) Bumblebee abundance on courgette flowers	1.53		3.06				-		_		5	127.50	0.00	0.15	0.09	0.80
	1.79		2.91			-0.06	-		-		5	128.84	1.35	0.08	0.09	0.80
(3) Solitary bee abundance in courgette field	-3.53	2.36	_		13.43	_	-		+Margin	-20.96	9	294.79	0.00	0.39	0.31	0.31
	-1.49		-		11.42	-	-		+Margin	-19.80	8	295.19	0.40	0.32	0.28	0.28
(4) Solitary bee SR in courgette field	-0.45		_		5.31	_	-		+Margin	-8.28	8	234.17	0.00	0.07	0.21	0.21
	0.50		-			-	-		+Margin		5	234.53	0.35	0.06	0.11	0.16
	0.36		-	0.97		-	-		+Margin		6	234.65	0.48	0.05	0.14	0.20

SR = species richness.

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Abundance and SR of wild flowers refer to a whole courgette field, unless otherwise stated.

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Fig. 3. Significant interaction effects from best fitting models (lowest AICc) of (A) solitary bee abundance, and (B) solitary bee species richness in courgette fields in relation to the species richness of wild flowers in courgette fields and semi-natural habitat (SNH) in a 2000 m radius (m^2) surrounding courgette fields. Solid lines are predicted values from linear models.

Community networks of pollinators in courgette fields show that whilst field margins support a greater number of pollinator species, many of these species also occur within the cropped area, suggesting movement between the two areas. Of these species, A. mellifera and B. terrestris were the most abundant and occur in their greatest numbers within the cropped area. These two species also show a preference for courgette flowers, with B. terrestris showing a more equal preference than A. mellifera for male and female courgette flowers which may affect their relative effectiveness as pollinators (Ne'eman, Jürgens, Newstrom-Lloyd, Potts, & Dafni, 2010; Artz, Hsu, & Nault, 2011). These networks also show that several widespread, resilient species (rather than speciesrich communities) are the main pollinator visitors to courgette (see also Knapp & Osborne (2017)). Although these species respond positively to increased provision of floral resources their populations can be increased by beekeepers/farmers introducing managed colonies to an area. Honeybee density on crop flowers may also be intensified by their en masse recruitment to areas of good forage (von Frisch, 1967) and beekeepers may have placed more honeybee colonies into areas with more mass-flowering crop.

Bumblebee abundance on courgette flowers was correlated with an increase in species richness of wild flowers in the cropped area. As bumblebees have been observed to stay constant to an area of good forage (Osborne et al., 1999) it is likely that they are foraging between wild and crop flowers (due to their phenology) at a specific locality. Importantly, the abundance of honeybees or bumblebees on the field margin did not influence their abundance on courgette flowers, suggesting that wild flowers are not competing with crop flowers for pollinator visitation, supporting findings from almond orchards (Lundin et al., 2017). Nonetheless, honeybee foragers were more abundant on courgette flowers in areas with less seminatural habitat; and where there was lower species richness of wild flowers in the cropped area, suggesting that courgette may compete with co-flowering wild flowers for honeybee visits, although this was not statistically significant. Whilst in the short-term wild flowers within the crop may compete with courgette for pollination services, these wild flowers may improve pollinator populations and thus crop pollination in the long term (Mitchell et al., 2009). Unfortunately, no information is available on the abundance of honeybee hives or the location of apiaries within 10 km of the study sites. Therefore it is impossible to determine if honeybee forager abundance is moderated by the amount of semi-natural habitat in the landscape or beekeeping practices. The overall abundance of honeybee foragers at a site did not influence bumblebee abundance at courgette flowers and vice versa, nor interact with other landscape features, suggesting that these species are not in competition with each other for common resources and that the surrounding landscape is not moderating any potential competition between species (Herbertsson, Lindstrom, Rundlof, Bommarco, & Smith, 2016).

Floral species richness was more important for predicting solitary bee abundance and species richness (non-courgette visitors) in sites with less semi-natural habitat. This suggests that a higher species richness of wild flowers in courgette fields is needed if they are located in areas with less semi-natural habitat. Likewise, the abundance and species richness of solitary bees were higher in the margin (where there is a higher abundance and species richness of wild flowers) than the cropped area. These findings are likely due to solitary bees generally having broader dietary and

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nesting requirements, and much smaller foraging ranges (150-600 m) than honeybees and B. terrestris (the predominant bumblebee species) (Gathmann & Tscharntke, 2002; Greenleaf, Williams, Winfree, & Kremen, 2007). Wild flowers have been shown to be more effective at increasing pollinator abundance and species richness in simple landscapes (with less semi-natural habitat) compared to complex landscapes (Scheper et al., 2013). Since Scheper et al. (2013) and this study only analysed foraging individuals it is impossible to determine if differences in pollinator abundance and species richness between study sites were due to the transient movement of species between areas of forage, or due to an actual population increase. Floral resources on the field margin also increased the abundance of Eupeodes corollae, a hoverfly species whose larval stage is a natural predator of soft-bodied arthropods such as aphids (Gomez-Polo et al. 2014). Therefore, provisioning floral resources at the field scale may increase pollinator abundance, species richness, and natural enemies of pests (Blaauw & Isaacs, 2014; Wood, Holland, Hughes, & Goulson, 2015).

Data access statement

The research data supporting this publication are openly available from the University of Exeter's institutional repository at: https://doi.org/10.24378/exe.664.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.09.003.

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