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CROP AND LANDSCAPE FACTORS AFFECTING VARIATION IN COMPOSITION AND BEHAVIOUR OF THE POLLINATOR COMMUNITY IN FIELD BEAN CROPS

Capstick LA[1]*, Connelly J[1], McHugh NM[1], and Holland JM

[1]*Farmland Ecology Unit, Game and Wildlife Conservation Trust, Fordingbridge, Hampshire SP6 1EF, UK*

Abstract—The global decline in pollinators is likely to negatively affect the yield of insect pollinated crops such as field beans (*Vicia faba*). To understand the impact of such declines it is important to investigate how the abundance, composition and behaviour of the pollinator community relates to crop yield.

We observed pollinators (specifically *Bombus* spp. and *Apis mellifera*) foraging in field bean fields. Some bees actively pollinated flowers whereas others robbed the nectar without actively pollinating the flowers. As legitimate foraging visits are more likely to pollinate the crop, we explored infield and landscape scale factors affecting this variation in behaviour. Infield factors included sowing time (winter/spring) and plant density. Landscape factors were the area of flower-rich habitat, and of mass-flowering crops within 1 km of the bean field. We also explored how the abundance and behaviour of different functional groups (short-tongued bumblebees, long-tongued bumblebees or honeybees) responded to these factors. Finally, we assessed how the abundance and behaviour of these pollinators affected field bean yield.

Pollinators were more abundant in bean crops that were spring sown and where there was a smaller area of mass-flowering crops in the landscape. Functional groups varied in their predominant foraging behaviour and in how their behaviour was influenced by external factors. There was no relationship between pollinator abundance and bean yield however the proportion of pollinators legitimately foraging was negatively related to yield. Our findings align with previous research in suggesting that the benefits of insect pollinators for field beans are context specific. Additional work is required to develop pollinator conservation measures that will facilitate crop pollination.

Keywords—Pollination, pollinators, *Apoidea*, *Vicia faba*, floral resources, crop yield

INTRODUCTION

Pollinator populations are threatened by numerous factors including climate change, pesticide use, and land-use intensification (Powney et al. 2019; Dicks et al. 2021). These factors are causing widespread decline in pollinator populations which could negatively impact the yield of the 87 global food crops which are dependent to some extent on pollination (Klein et al. 2007). A loss of pollination services can reduce crop yield, quality and resilience and is likely to have significant economic consequences (Gallai et al. 2009), estimated at £400 million per year in the UK (Mancini 2022). The proportion of yield that is reliant on pollination (so-called pollination dependence) varies depending on biotic and abiotic factors (Bartomeus et al. 2015; Garratt et al. 2021), consequently the relationship between pollinator numbers and crop yields is not straightforward.

The effect of pollination on field bean (*Vicia faba*) yield depends on crop cultivar (Bishop et al., 2020), abiotic conditions (Bishop et al. 2016) and environmental context (Raderschall et al. 2021). The way in which the plant nectar and pollen is accessed by the pollinator will also impact pollination success. Field beans can be pollinated by three mechanisms: cross pollination, trigger pollination and self-pollination (Hanna & Lawes 1967). Cross pollination requires a pollinator to enter through the front of the flower and transfer pollen from another flower to the stigmatic

surface. Trigger pollination is mechanical self-pollination when the keel petal is depressed, and the stigma and style are released, and the stigmatic pupae are ruptured (Holden & Bond 1960; Kambal et al. 1976). Finally, field beans can self-pollinate without mechanical stimulation, this is known as auto-fertility (Hanna & Lawes 1967).

Trigger pollinated field bean plants can have higher yields than self-fertilised plants (Holden & Bond 1960; Bishop et al. 2020). The benefits of cross-pollination over mechanical self-pollination, are less clear (Free & Williams 1976), but there are some indications that outcrossing can have benefits under environmental stress (Bishop et al. 2017).

Pollinators can increase levels of cross and mechanical self-pollination in field beans (Kendall & Smith 1975); pollinators can cross-pollinate by legitimately foraging in the front of the corolla for pollen and nectar, and then transferring pollen between flowers, or they can trigger pollinate by causing physical disturbance to the flower structure. One way they cause this physical disturbance is by robbing from the flowers by biting the back of the corolla to access the nectar (Kendall & Smith 1975). Insect visitation to plants can therefore positively impact several measures of yield including pod set (Garratt et al. 2014) and bean size (Aouar-sadli et al. 2008; Benachour et al. 2007).

Numerous studies have shown that pollinator species tend to exhibit the visitation behaviour most suited to their morphology (Poulsen 1973; Balfour et al. 2013; Beyer et al. 2022). Fabaceae flowers (like field beans) have relatively long corollas which mean that long-tongued species (e.g., *B. hortorum*) are better able to access the nectar and pollen (Goulson et al. 2008). Long-tongued bumblebee species are therefore more likely to forage, and short tongued bumblebee species are more likely to rob from plants with long corollas (Beyer et al. 2022). Smaller pollinators (such as honeybees or solitary bees) may not be able exert the operative force required to either press the keel petal and enter the front of the flower to effectively forage (Bailes et al. 2018) or bite a hole in the back the corolla (Kendall & Smith 1975; McGregor 1976). These pollinators are therefore not optimally suited to either behaviour, therefore they may avoid foraging in field bean

crops, however honeybees do rob nectar from holes made by other species (Poulsen 1973; Marzinzig et al. 2018).

As pollinator species differ in their field bean visitation behaviour, the composition of the community could affect prevalence of robbing or legitimate foraging. The abundance of different species groups can be affected by habitat around the bean crop. Availability of semi-natural habitat in agricultural areas can provide foraging and nesting opportunities for pollinators and consequently increase the abundance of pollinators in crops (Woodcock et al. 2013; Raderschall et al. 2021). The type of habitat can influence the group of pollinators supported. For example, the number of long-tongued bumblebees in margins was found to be increased by the number of pollen and nectar agri-environment options (a legume rich flower mix) in the landscape (Pywell et al. 2006).

In the UK current conservation mechanisms for pollinators on farmland include agri-environment scheme supported measures such as planting nectar-rich wildflower areas (Holland et al. 2015; Nichols et al. 2019). The provision of this habitat may therefore increase the number of pollinators, particularly long-tongued pollinators in field bean crops.

In addition to the provision of semi-natural habitats, the presence of other mass flowering crops in the landscape can also provide foraging resources. The predominance of mass-flowering crops within the landscape can therefore also influence pollinator distribution. Higher coverage of mass-flowering crops at a landscape scale can increase bumblebee density both in the landscape and in crop (Beyer et al. 2020, 2021) but has also been shown to reduce bee species richness in the crop (Shaw et al. 2020). The influence of landscape context on the abundance and composition of the pollinator community in a specific field may depend on whether provision of additional resources increases pollinator numbers or dilutes the existing pollinators across the resources (Shaw et al. 2020).

Landscape context may also affect pollinator behaviour. Pollinators forage for both pollen and nectar but have been shown to preferentially forage for pollen from plants, such as field bean,

with protein-rich pollen (required for larval development (Vaudo et al. 2016)). Nectar is relatively less abundant in field beans compared to other plants, so in landscapes where other nectar sources are present, such as semi-natural habitats, bumblebees might be more likely to legitimately forage for pollen rather than nectar in field beans flowers (Raderschall et al. 2021).

Habitat factors within field bean fields have also been shown to affect pollinator abundance. Wild pollinators may be less prevalent earlier in the season when winter sown crops are in flower compared to later flowering spring sown crops (Stoddard 1986). Local field bean flower cover can positively affect pollinator abundance (Nayak et al., 2015). The effect of crop plant density and flower colour/type has also been explored (Stoddard 1986; Stoddard & Bond 1987). The temporal variation in these attributes, depending on abiotic conditions and plant phenology, could also influence pollinators.

Time of year can also affect the abundance of different pollinators and their behaviour. Some long-tongued bumblebees, which preferentially forage in field beans, have a relatively late emergence time (Goulson et al. 2005) and are more abundant in agricultural landscapes later in the flowering season (Beyer et al. 2021). However, the proportion of short-tongued bees robbing may increase over the crop flowering period (Poulsen 1973). Robbing is a learned behaviour so could be socially transmitted through the population (Leadbeater & Chittka 2008). In addition, as the number of holes in flowers increases, smaller bees, which cannot perforate the flowers themselves, are able to rob more frequently (Poulsen 1973).

Increasing the number of foraging pollinators in field beans crops could increase crop yield and promote outcrossing. It would be beneficial to understand the factors moderating the abundance and behaviour of pollinators in field bean crop. The aim of this study is therefore to explore the effect of infield factors (plant density and crop sowing time) and landscape factors (area of flower-rich habitat including agri-environment options and area of mass-flowering crops) on the pollinator community. We examined the effect of these factors on total pollinator abundance, visitation behaviour of all pollinators and

visitation behaviour of different functional groups (long-tongued bumblebees, short-tongued bumblebees and honeybees). Finally, we explored the relationship between pollinator abundance and predominate pollinator behaviour on field bean yield.

MATERIALS AND METHODS

STUDY DESIGN

13 field bean (*Vicia faba*) fields were selected across the North Sea Region of England as defined by the Interreg North Sea Region programme (Table 1) (North Sea Region Programme 2015). The sampled field bean fields were separated by > 2 km to reduce spatial autocorrelation and possible overlap in pollinator community. In the case of block cropping (several bean fields sited contiguously), a field was selected at random for sampling.

Twelve sample points, hereafter grid points, were positioned in regular 50 x 50 m grid pattern situated in the centre of each field. The 12 grid points were 3 x 4 in cardinal orientation. This sampling designed accounted for within field variation and reduced the influence of edge effects.

Each field was visited twice during the flowering period. Between 01-03/06/2021 and 11-13/06/2021 for winter sown beans which flowered earlier ($N = 5$) and between 13-26/06/2021 and 24/06-08/07/2022 for spring sown beans ($N = 8$). Fields were also visited once just before harvest to collect plant pods for yield calculations.

At each grid point the density of bean plants was measured. The number of plants within a 1 x 1 m quadrat (placed adjacent to the treated plants) were recorded. The type of beans (spring sown or winter sown) was recorded (Processors and Growers Research Organisation 2023).

To identify floral resources in the vicinity of the fields the area within 1 km of the centre point of each field was mapped. Habitat maps were based on the Ordnance Survey MasterMaps GIS vector layer (© Crown copyright and database rights [2021] Ordnance Survey 0100031673). Additional habitat such as agri-environment scheme options were mapped based on satellite imagery, information from landowners and ground truthing.

Table 1. Summary of bean and habitat variation between sites. Pollinator and yield data is taken from sampling round 1 as for some sites there was no yield data for sampling round 2. MFC - mass flowering crops.

Site	Variety	Sowing time	Area of flower-rich habitat (km2)	Area of MFC (km2)	Total honey bees	Total short-tongued bumblebees	Total long-tongued bumblebees	Total pollinators	Average podset (number of pods per flower)
A	Lynx	Spring	0.018	0.283	3	89	2	94	0.278 ± 0.02
B	Tundra	Winter	0.016	0.237	18	26	0	44	0.217 ± 0.03
C	Tundra	Winter	0.038	0.138	12	24	5	41	0.334 ± 0.03
D	Wizard	Winter	0.007	0.427	56	35	1	92	0.232 ± 0.02
E	Tundra	Spring	0.000	0.375	7	74	5	86	0.255 ± 0.02
F	Cartouche	Spring	0.063	0.209	80	31	8	119	0.36 ± 0.03
G	Tundra	Spring	0.022	0.166	10	100	3	113	0.126 ± 0.03
H	Tundra	Winter	0.042	0.326	50	4	4	58	0.282 ± 0.03
I	Not recorded	Spring	0.067	0.108	2	280	19	301	0.241 ± 0.03
J	Tundra	Winter	0.000	0.277	80	30	3	113	0.382 ± 0.03
K	Lynx	Spring	0.033	0.091	60	36	4	100	0.166 ± 0.02
L	Lynx	Spring	0.025	0.191	79	18	3	100	0.302 ± 0.03
M	Lynx	Spring	0.000	0.171	82	111	12	205	0.418 ± 0.03

Habitats were classified according to likely provision of pollen and nectar. Key flower-rich habitat consisted of habitats specifically designed to provide floral resources such as wildflower areas or floral strips. This included management options available under the Countryside Stewardship agri-environmental scheme available in England (AB8: Flower-rich margins and plots and AB1: Nectar flower mix) (Rural Payments Agency, 2020) and flower strips put in by landowners independently. Total area of mass-flowering crops was also calculated. Mass flowering crops were defined as oil seed rape (*Brassica napus*) or field beans a priori, but only field beans were planted in the study landscapes. Hereafter mass flowering crops refers to field beans.

MEASURING POLLINATION

At each grid point, four sample plants were selected, with each plant approximately 2 m apart in a square. On each bean plant, a truss (stem that carries a cluster of flowers) was selected and marked. As the trusses do not flower synchronously only trusses with open flowers were selected; the selection alternated between higher and lower trusses of open flowers between plants. The number of flowers on each truss was counted.

On the second visit within the flowering period, the process was repeated on four additional plants in the 2 m by 2 m square around each grid point.

POLLINATOR ABUNDANCE AND BEHAVIOUR

At the same time as the pollination treatments, a survey of pollinator activity was carried out. A 5-minute timed transect was walked from the grid point 5 m to the west. Pollinators (*Bombus sp., Apis mellifera* and solitary bees) visiting bean flowers within 2 m of the transect line were identified to species where possible. Their behaviour was classified as foraging (legitimately entering the front of the flowers) or robbing (accessing the nectar in the flowers through holes in the base of the corolla).

Pollinator surveys were carried out under suitable conditions; between 10:00 – 17:00hr, temperature above 10°C, wind levels below 4 on the Beaufort scale and in the absence of rain or thick fog.

Bumblebees were categorised by tongue length according to values and classifications given in the literature (Goulson et al. 2008; Marzinzig et al.

2018); long-tongued bumblebees (tongue length > 8 mm) such as *B. hortorum* or short-tongued bumblebees (< 8 mm), such as *B. terrestris*. Honeybees were a separate category. Solitary bees were seen very few times so were excluded from analysis.

FIELD BEAN YIELD

Before harvest all the pods from marked trusses were collected. Pods were dried at 80°C until they reached a constant mass (> 24 hours). Yield was measured for each truss as pod set (proportion of flowers which produced pods). Pod set was used as a measure of yield (as opposed to bean weight for example) as previous studies have shown this yield measure can be affected by pollination level (Garratt et al., 2014; Nayak et al., 2015). The yield of each sample plant per grid point was calculated.

STATISTICAL ANALYSIS

Pollinator abundance and behaviour

To explore the effect of external factors on pollinator abundance and behaviour in field bean fields, we fitted two models to each response variable (Table 2). Model structure and model family varied depending on the response variable (Table 2). For the effect of in-field variation on pollinators we used crop density (number of plants per m^2 per grid point) and type (spring/winter) as explanatory variables. To examine the effect of landscape variation we used area of mass flowering crop within 1 km of the bean field and area of flower-rich habitat within 1 km of the bean field. Finally, to control for any effect of time in the flowering season, sampling round (first/second) was included as an explanatory variable in all models.

To examine effects on bee (*Bombus* and honeybee) abundance, the total number of bee individuals counted per grid point per site per sampling round was fitted as a response variable in a negative binomial generalised linear mixed model (GLMM). Site was fitted as a random effect to account for grid points being nested within site. For bee foraging behaviour, proportion of bees legitimately foraging (not robbing) per grid point per site per sampling round was used as a response variable in a binomial GLMM with site as random effect. To examine differences in behaviour between functional groups, we also fitted the models with proportion of short-tongued

bees foraging and proportion of honeybees foraging per grid point per site as the response variable in a binomial GLMM with site as a random effect (Table 2). As per Marzinzig et al. (2018), the long-tongued bees rarely engaged in robbing behaviour, and the sample size of long-tongued bees was small so the total number, of long-tongued bees per site per round, rather than proportion foraging per grid point was used as the response variable in a binomial GLM.

Functional group behaviour

We tested for an overall difference in behaviour between categories of pollinators. We fitted a negative binomial generalised linear model with bee behaviour (measured as total pollinators counted robbing or foraging per site per functional group) as a response variable. Interactions were fitted between behaviour and functional group and sampling round was included as a fixed effect.

Field bean yield

Finally, to assess the effect of pollinator abundance and pollinator behaviour on yield we fitted proportion of flowers which set pods (number of pods/number of flowers) as a binomial response in a generalised linear mixed-model. Pod set was measured per sampling plant, per grid point, per site so we fitted grid point nested in site as a random effect.

In the model assessing the effect of pollinator abundance we fitted total number of pollinators per grid point, sampling round and the first order interaction between the two as explanatory variables. We also included sowing time (winter/spring) as a fixed effect as this is known to influence crop yield. The model exploring pollinator behaviour had the same structure but proportion of pollinators legitimately foraging per grid point was used instead of total number of pollinators.

All yield analyses excluded the second round of winter bean crops as the lower flower trusses did not set any pods due to high temperatures and low rainfall.

The residuals of all models utilising abundance data were tested for overdispersion, and when the residuals were over dispersed the models were fitted with the negative binomial distribution instead of the Poisson distribution (Table 2). Model

Table 2. Response variables and structure of all models used in analysis. A, B and C are the models used examine effects of external factors on pollinator abundance and behaviour. With the exception of long-tongued bee abundance, which was analysed at the site level, the unit of analysis was the grid point. D is the model used to explore difference in behaviour between function group and was analysed at site level. MFC - mass flowering crops.

Variable	Response	Fixed effects	Random effect	Model family
A) Pollinator abundance	Total number of pollinators counted per grid point	Sampling round Sowing time (spring/winter) Crop density	Site	Negative binomial GLMM
	Total number of pollinators counted per grid point	Sampling round Area of MFC (km²) Area of flower-rich habitat (km²)	Site	Negative binomial GLMM
B) Pollinator behaviour	Proportion of pollinators foraging per grid point Proportion of short-tongued bees foraging per grid point Proportion of honeybees foraging per grid point	Sampling round Sowing time (spring/winter) Crop density	Site	Binomial GLMM
	Proportion of pollinators foraging per grid point Proportion of short-tongued bees foraging per grid point Proportion of honeybees foraging per grid point	Sampling round Area of MFC (km²) Area of flower-rich habitat (km²)	Site	Binomial GLMM
C) Long-tongued pollinator abundance	Total long-tongued bees counted per site	Sampling round Sowing time (spring/winter) Crop density		Negative binomial GLM
	Total long-tongued bees counted per site	Sampling round Area of MFC (km²) Area of flower-rich habitat (km²)		Negative binomial GLM
D) Pollinator functional group behaviour	Total of pollinators of each functional group (honeybee, short-tongued, long-tongued) and each behaviour (foraging or robbing)	Behaviour (foraging/robbing) Functional group (honeybee, short-tongued, long-tongued) Sampling round		Negative binomial GLM
E) Yield	Proportion of field bean flowers producing pods (podset)	Total pollinator abundance Sampling round Sowing time (spring/winter)	Grid point/Site	Binomial GLMM
	Proportion of field bean flowers producing pods (podset)	Proportion of pollinators foraging Sampling round Sowing time (spring/winter)	Grid point/Site	Binomial GLMM

assumptions were assessed using diagnostic plots (Thomas et al. 2015). Each model was tested for multicollinearity by calculating Variance Inflation Factors (VIFs) for each covariate. No VIFs exceeded 3 (Zuur et al. 2010). Non-significant interactions were excluded from final models and all fixed effects were retained (Crawley 2005).

All analyses were carried out in R ver. 4.2.2. (R Core Team, 2022). Generalised linear mixed models fitted with a binomial distribution were constructed using the lme4 package (Bates et al. 2015). Negative binomial generalised linear models were fitted using the MASS package (Venables & Ripley, 2002). Plots were produced using the ggplot2 package (Wickham, 2016).

RESULTS

Across the 13 field bean fields, we observed 1503 bumblebees (*Bombus* spp.) and 926 honeybees (*Apis mellifera*) visiting bean flowers.

A total of 12 bumblebee species were observed, 5 of which were cuckoo bumblebee species. The majority of visits (74.7%; 1122) were carried out by *Bombus terrestris* aggregate (*Bombus lucorum* and *Bombus terrestris* workers which cannot be accurately separated on the wing). Visits by the next most frequent visitors were much lower *B. lapidarius* (9.8%; 148), *B. hortorum* (4.7%; 70) and *B. pascuorum* (2.3%; 34).

We did observe solitary bees in the bean fields (*Andrena* spp., *Halictus* spp. and *Colletes* spp.) but these occurred in very low frequency (*N* = 16) and were excluded from analyses.

Most observed visits (87%) were bees robbing rather than foraging from bean flowers. Bee species exhibited behaviour expected from their species-specific morphology. Long tongued species (*B. hortorum* and *B. pascuorum* foraged legitimately more than they robbed (92% and 56% of visits respectively) whereas the short-tongued species (mainly *B. terrestris agg.*) robbed more than they foraged legitimately (91% of visits). Cuckoo bumblebees almost exclusively robbed from bean flowers (95% of visits). Although honeybees could not pierce holes in bean flowers, they robbed from holes made by other species the majority of the time (88% of visits).

TOTAL POLLINATOR ABUNDANCE AND BEHAVIOUR

In this study, the abundance of bees in bean fields was correlated with infield factors measured; bees were more abundant in the later flowering spring sown crops (Est =-0.648, SE = 0257, z = -2.522, *P* = 0.012), but numbers were not affected by crop plant density (Est = 0.003, SE = 0.006, z = 0.558, *P* = 0.577). Bees were less abundant when mass flowering crops (in this study only field beans) covered a wider area of the surrounding landscape (Est= -3.385, SE = 1.479, z = -2.288, *P* = 0.022) (Table 3, Fig. 1).

The behaviour of the pollinator community was moderated by some of the same external factors. Bees were more likely to forage rather than rob in winter as opposed to spring crops (Est=1.031, SE = 0.312, z = 3.307, *P* = 0.001), in the first sampling round (Est = -0.463, SE = 0.154, z = -3.017, *P* = 0.003) and when crop density was lower (Est = -0.022, SE = 0.011, z = -2.005, *P* = 0.045). However, neither the area of mass flowering crops (Est = 0.037, SE = 0.022, z = 1.671, *P* = 0.095) nor flower-rich habitat (Est = -0.018, SE = 0.101, z = -0.175, *P* = 0.861) influence bee behaviour (Table 4**Fehler! Verweisquelle konnte nicht gefunden werden.**).

FUNCTIONAL GROUP BEHAVIOUR

The difference in predominate visiting behaviour between functional groups was significant; long-tongued bees were less likely to rob than either short-tongued bees or honeybees (Est = -3.278, SE = 0.519, z = -6.312, *P* < 0.001) (Table 5 and Fig. 2).

Table 3. Results of negative binomial generalised linear mixed models analysing the effect of (A) infield factors and (B) landscape factors on total pollinators per grid point. Non-significant interaction terms are not presented. MFC – Mass flowering crop (*N* = 264, site = 13).

| A				
Fixed effects	Estimate	df	z-value	*P*-value
Intercept (Sowing time - Spring, Sampling round - 1)	2.323 ± 0.211		11.00	**< 0.001**
Sowing time (winter)	-0.648 ± 0.257	1	-2.522	**0.012**
Sampling round (2)	-0.115 ± 0.072	1	-1.599	0.110
Crop density (plants/m²)	0.003 ± 0.006	1	0.558	0.577
B				
Fixed effects	Estimate	df	z-value	P-value
Intercept (Sampling round - 1)	3.033 ± 0.468		6.481	**< 0.001**
Area of MFC (km²)	-3.385 ± 1.479	1	-2.288	**0.022**
Area of flower-rich habitat (km²)	-4.238 ± 6.702	1	-0.632	0.527
Sampling round (2)	-0.109 ± 0.072	1	-1.516	0.130
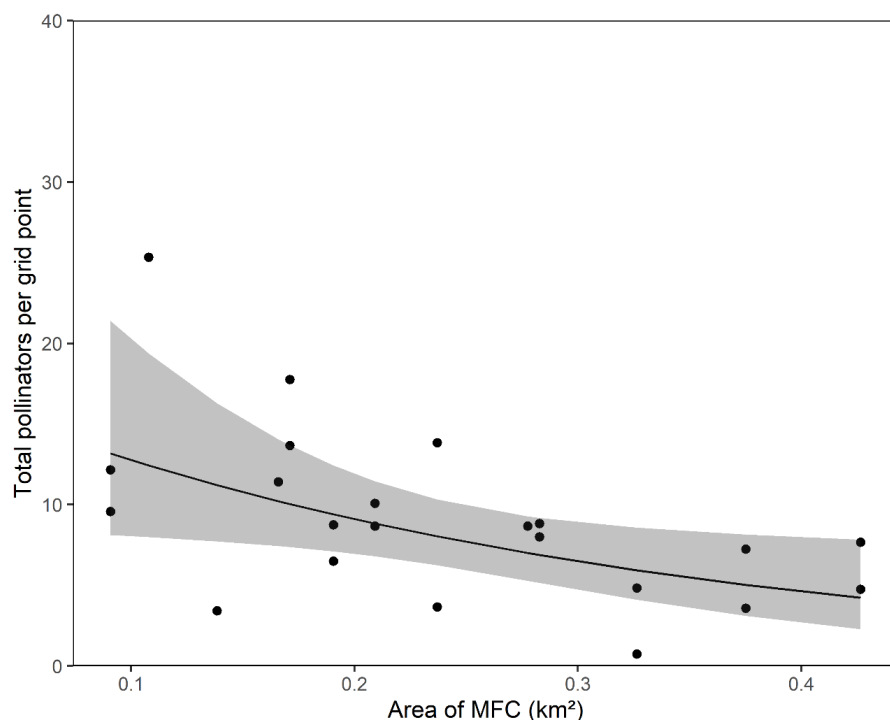
Figure 1. The relationship between average number of pollinators counted per grid point per site and the area of mass flowering crop (MFC) in the area within 1 km of the centre point of each field. The line represents the predicted values of the response (total pollinators per grid point) relative to the area of MFC. The predictions are adjusted relative to the effects of the other variables modelled. A 95% confidence interval is shown in grey around the predicted response.

Table 4. Results of binomial generalised linear models analysing the effect of (A) infield factors and (B) landscape factors on proportion of pollinators foraging per grid point site. MFC – Mass flowering crop (N = 252, site = 13).

A				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1, sowing time - spring)	-1.536 ± 0.329		-4.67	< 0.001
Sampling round (2)	-0.463 ± 0.154	1	-3.017	**0.003**
Sowing time (winter)	1.031 ± 0.312	1	3.307	**0.001**
Crop density (plants/m2)	-0.022 ± 0.011	1	-2.005	**0.045**
B				
Fixed effects	Estimate	df	z-value	P -value
Intercept (sampling round -1)	-2.425 ± 0.702		-3.454	0.001
Sampling round (2)	-0.462 ± 0.153	1	-3.014	**0.003**
Area of flower-rich habitat (km2)	-0.018 ± 0.101	1	-0.175	0.861
Area of MFC (km2)	0.037 ± 0.022	1	1.671	0.095

Table 5: Results of a negative binomial generalised linear model analysing the effect of functional group on pollinator behaviour per site. Response variable is number of bees of each functional group robbing or foraging per site. Non-significant interaction terms are not presented (N = 125).

| Fixed effects		Estimate	df	z-value	P-value
Intercept (behaviour - foraging, sampling round -2, Functional group - honeybees)		1.714 ± 0.240		7.129	**< 0.001**
Behaviour (robbing)		1.892 ± 0.312	1	6.071	**< 0.001**
Functional group	Long-tongued	-0.293 ± 0.329	2	-0.890	0.374
	Short-tongued	0.082 ± 0.323		0.253	0.801
Sampling round (1/2)		-0.217 ± 0.195	1	-1.113	0.266
Behaviour * Functional group	Robbing:Long-tongued	-3.278 ± 0.496	2	-6.610	**< 0.001**
	Robbing:Short-tongued	0.503 ± 0.439		1.114	0.253
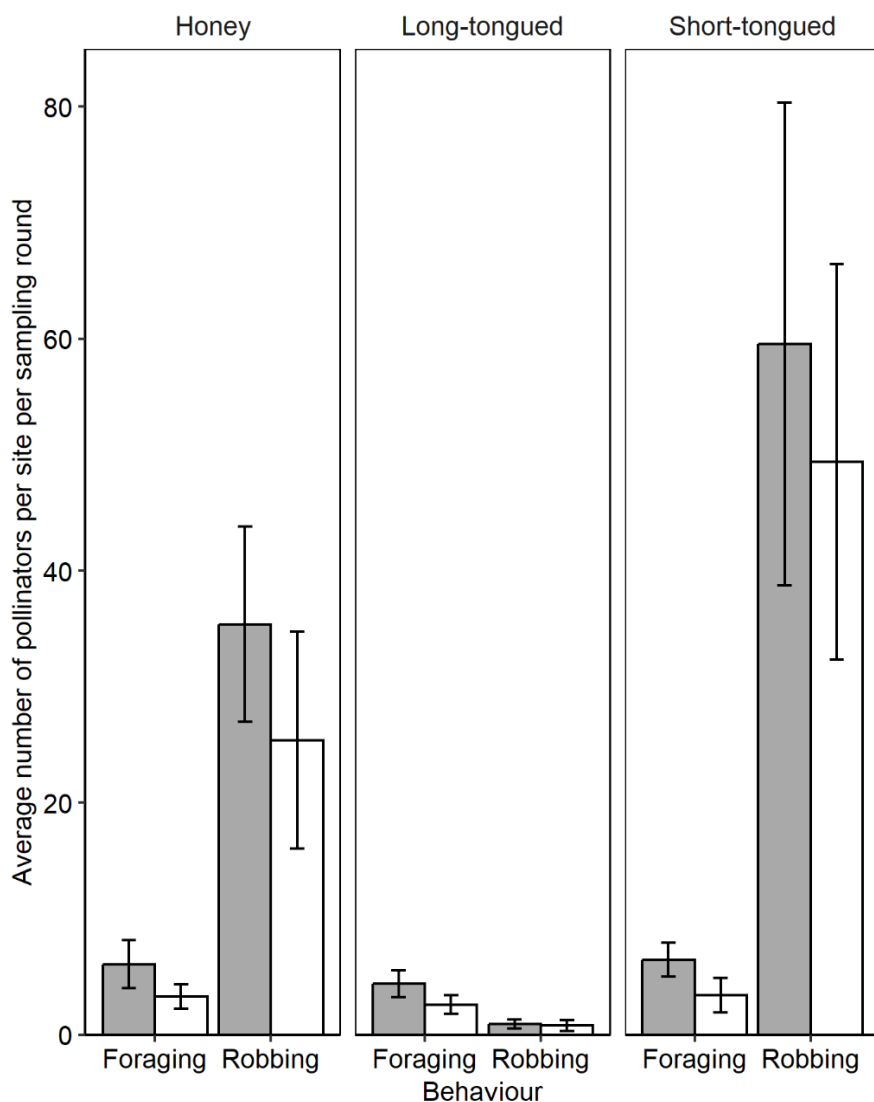
Figure 2. The difference between functional groups (short-tongued bumblebees, long-tongued bumblebees and honeybees) in foraging behaviour in field bean crops. Dark grey bars - sampling round 1, white bars - sampling round 2. Error bars are SE.

Separately analysing the behaviour of functional groups (honeybees and short-tongued bumblebees) showed that although short-tongued bumblebees were less likely to forage legitimately in winter beans (Est = 1.886, SE = 0.64, z = 2.947, P = 0.003) and in the first sampling round (Est = -0.911, SE = 0.261, z = -3.496, P < 0.001), honeybee behaviour was not affected by external factors (Table 6).

The long-tongued bees were observed in much smaller numbers and very rarely robbed < 20% of visits (as per. Burns & Stanley, (2023); Marzinzig et al., (2018)). Their behaviour could not be analysed separately. Their abundance was not affected by any of the external factors we assessed (Table 4).

FIELD BEAN YIELD

Flowers on trusses that were open in the second round of sampling (later in the flowering period)

formed fewer pods than those open in the first round of sampling (Est = -0.343, SE = 0.079, z = -4.357, P = <0.001). Pollinator abundance did not influence pod set (Est = -0.005, SE = 0.008, z = -0.65, P = 0.515) but on sites where the proportion of pollinators legitimately foraging was lower the proportion of flowers setting pods was higher (Est = -0.489, SE = 0.17, z = -2.872, P = 0.004) (Table 7).

DISCUSSION

We identified external factors which influenced the abundance and behaviour of *Bombus spp.* and honeybees within field beans crops. Pollinator abundance was greater in spring sown crops and when the area of mass flowering crops in the landscape was smaller. These pollinators predominantly robbed rather than foraged legitimately when they visited field bean flowers and were more likely to rob in spring sown crops.

Table 6. Results of binomial generalised linear models analysing the effect of (i) infield factors and (ii) landscape factors on proportion of pollinators of different pollinator functional groups foraging per grid point per site*. Impacts are shown for short-tongued bumblebees (no. of observations = 252, site = 13), honeybees (no. of observations = 252, site = 13). Due to low sample size for - long-tongued bumblebees a general linear model with total long-tongued bees as the response per site were used (no. of observations = 20). MFC – Mass flowering crop.

Short-tongued bumblebees				
i)				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1, sowing time - spring)	-1.935 ± 0.581		-3.333	0.001
Sampling round (2)	-0.911 ± 0.261	1	-3.496	**< 0.001**
Sowing time (winter)	1.886 ± 0.640	1	2.947	**0.003**
Crop density (plants/m²)	-0.028 ± 0.017	1	-1.643	0.100
ii)				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1)	-3.027 ± 1.407		-2.151	0.032
Sampling round (2)	-0.858 ± 0.253	1	-3.388	**0.001**
Area of flower-rich habitat (km²)	-0.073 ± 0.206	1	-0.353	0.724
Area of MFC (km²)	0.058 ± 0.045	1	1.311	0.190
Honeybees				
i)				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1, sowing time - spring)	-2.539 ± 0.681		-3.728	<0.001
Sampling round (2)	-0.298 ± 0.278	1	-1.074	0.283
Sowing time (winter)	1.133 ± 0.660	1	1.716	0.086
Crop density (plants/m²)	0.008 ± 0.020	1	0.413	0.680
ii)				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1)	-3.004 ± 1.033		-2.907	0.004
Sampling round (2)	-0.388 ± 0.276	1	-1.407	0.159
Area of flower-rich habitat (km²)	-0.128 ± 0.165	1	-0.777	0.437
Area of MFC (km²)	0.059 ± 0.032	1	1.838	0.066
Long-tongued bumblebees				
i)				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1, sowing time - spring)	2.501 ± 0.836		2.991	0.003
Sampling round (2)	-0.245 ± 0.357	1	-0.685	0.493
Sowing time (winter)	-0.669 ± 0.46	1	-1.453	0.146
Crop density (plants/m²)	-0.029 ± 0.032	1	-0.908	0.364
ii)				
Fixed effects	Estimate	df	z-value	P-value
Intercept (sampling round -1)	1.771 ± 0.58		3.051	0.002
Sampling round (2)	-0.142 ± 0.328	1	-0.433	0.665
Area of flower-rich habitat (km²)	10.148 ± 8.197	1	1.238	0.216
Area of MFC (km²)	-1.954 ± 1.829	1	-1.068	0.285

Table 7. Results of a binomial generalised linear mixed model analysing the effect of total pollinators and proportion of pollinators robbing on pod set (proportion of field bean flowers that produced pods) (N = 911, grid = 156, site = 13).

Total pollinators			
Fixed effects	Estimate	z-value	*P*-value
Intercept (sampling round -1, sowing time - spring)	-0.906 ± 0.169	-5.372	<0.001
Total pollinators (per grid point)	-0.005 ± 0.008	-0.65	0.515
Sampling round (2)	-0.343 ± 0.079	-4.357	**<0.001**
Sowing time (winter)	-0.237 ± 0.236	-1.003	0.316
Proportion of pollinators robbing			
Fixed effects	Estimate	z-value	*P*-value
Intercept (sampling round -1, sowing time - spring)	-0.905 ± 0.149	-6.095	<0.001
Proportion of pollinators foraging (per grid point)	-0.489 ± 0.17	-2.872	**0.004**
Sampling round (2)	-0.351 ± 0.078	-4.482	**<0.001**
Sowing time (winter)	-0.107 ± 0.24	-0.444	0.657

Comparing factors affecting behaviour of different functional groups suggests that honeybee foraging behaviour was not influenced by the same factors that affected short-tongued bumblebee behaviour. We did not find a relationship between pollinator abundance and yield. We did find a negative relationship between proportion of pollinators foraging legitimately and yield.

POLLINATOR ABUNDANCE AND BEHAVIOUR

Bee abundance was higher in spring sown crops compared to winter sown ones. A lack of bee activity in winter sown crops has been attributed to their relatively early flowering period. The weather conditions earlier in the spring when winter-sown beans are in flower may not be favourable for foraging bees (Stoddard, 1986), particularly honeybees (Clarke & Robert 2018). The floral resources available in the wider landscape are lower earlier in the flight season which could limit populations (Williams et al. 2012). It is also possible that the relatively delayed colony development of later emerging bumblebee species will lead to lower overall numbers of workers early in the season (Goulson et al. 2005)

Some previous work has shown that field bean crops situated in more complex landscapes (with more nesting and foraging habitat) have more bees (Lundin & Raderschall 2021; Beyer et al. 2022), but other studies suggested that the presence of pollinator friendly habitat in the landscape does not always lead to increased crop visitation (Bartomeus et al. 2014; Image et al. 2022). We did not observe an effect of foraging habitat (flower-rich areas) in the surrounding landscape on bee abundance or behaviour. The lack of effect could be because the area of such habitat was an order of magnitude (Table 1) smaller than the area of mass flowering crop in our landscapes (Nayak et al. 2015). It is also possible that independent of the presence of mass flowering crops, the area of flower-rich habitats in our landscapes was not sufficient to effect pollinator population numbers. The area of wildflower habitat in our landscapes was lower than the 2% per 100 ha. suggested by Dicks et al. (2015) to be sufficient to support the pollen requirements of six common pollinator species.

Infield bee abundance was lower in landscapes with larger field bean areas which suggests that there could be some dilution effect (Holzschuh et al. 2011). Where pollinator numbers are limited by factors other than foraging resources (e.g. nest sites) increasing flowering crop area will not produce a proportional increase in bee density (Holzschuh et al. 2016; Shaw et al. 2020)

Some of the external factors which correlated with higher bee abundance in this study also correlated with bee behaviour; the proportion of bees legitimately foraging was lower in spring crops compared to winter crops. The proportion of foraging legitimately as opposed to robbing was also lower later in the season (the second sampling round). Robbing behaviour can be learned through pollinators observing holes in flowers made by others (Barker et al. 2018). The positive feedback effect of this social transmission will increase the number of individuals able to rob through time (Leadbeater & Chittka 2008) and, as spring beans

flower after winter beans, early emerging bumblebee species may have already learned robbing behaviour by the time spring beans are in flower. In addition, the increasing number of holes will allow species which can't bite holes themselves (such as honeybees) to rob rather than forage legitimately (Poulsen 1973). Honeybees may also be driven towards secondary robbing (through existing holes) as it is more energetically beneficial than legitimately foraging (Dedej & Delaplane 2005).

Resource requirements can also affect the bee's decision to rob field beans (primarily for nectar) or forage (for both pollen and nectar) (Poulsen 1973). Pollen primarily provides protein and lipids whereas nectar provides carbohydrates (Vaudo et al. 2015). There may be seasonal changes in resource requirements; *Bombus spp.* and honeybees can moderate foraging in relation to colony state (Requier et al. 2020, Fewell & Winston 1996). Both *Bombus spp.* and honeybees may favour legitimate foraging for pollen (for protein) early in the season to support worker population growth and robbing nectar (for carbohydrates) later in the season to build up overwinter energy resources (Vaudo et al. 2015).

The relative availability of other nectar and pollen resources in the landscape could influence infield pollinator behaviour. However, previous studies have shown varying effects of landscape on bee behaviour in field bean fields. Raderschall et al., (2021) found a higher proportion of bees robbing in field bean crops in landscapes with more semi-natural habitat whereas Beyer et al. (2022) found more bees robbing when there was a higher proportion of field bean crops in the landscape. We saw proportionally less robbing behaviour in landscapes with more field beans, but this was not significant. There is clear variability in infield pollinator response to landscape context. A more detailed analysis of the resources available within the foraging range of the pollinator species observed might provide more insight into these results.

FUNCTIONAL GROUP BEHAVIOUR

Interspecific differences between bee species in their predominant foraging behaviour in field beans is well-established and has been linked to their morphology (Bailes et al. 2018; Marzinzig et al. 2018). Short-tongued bees were far more likely

to rob than forage legitimately from field bean flowers and, like the community as a whole, the proportion of bees foraging legitimately was lower in spring sown beans and later in the flowering period. As honeybees rely on the holes created by short-tongued bees to rob, we might expect that the proportion of honeybees robbing would increase with the proportion of short-tongued bees robbing. In our study honeybee behaviour did follow the same trend as short-tongued bee behaviour although not significantly.

FIELD BEAN YIELD

Numerous studies have failed to identify a positive relationship between pollinator numbers and field bean yield (Raderschall et al., 2021) and field bean yield is not always dependent on pollination (Bishop et al., 2020).

However, the lack of relationship we observed between pollinator abundance and bean yield may also be because the pollinators present were not effective in increasing yield. The number of legitimately foraging pollinators was relatively low in all fields (15% of total visits observed). Foraging legitimately is expected to increase yield more than robbing (Marzinzig et al. 2018). In addition, the foraging visits we observed may not have represented efficient pollination. Long-tongued bees (particularly *B. hortorum* which was the most frequently observed long-tongued bumblebee in our study) have been shown to be more efficient field bean pollinators (Burns & Stanley 2023). The number of long-tongued bees seen was much lower than other functional groups. This meant that even though they legitimately foraged for a relatively large proportion of their visits, the overall number of foraging visits made by long-tongued bees was lower than foraging visits by the more abundant short-tongued bumblebees or honeybees. Nevertheless, this would not explain the negative relationship between proportion of pollinators foraging legitimately and yield we observed. The trend seen in this study, field bean yield increasing with a decreasing proportion of pollinators legitimately foraging and an increased proportion robbing, has not been observed previously to our knowledge. Given we expect robbing to lead to less efficient pollination than legitimate foraging, this result is unexpected. It may be that the bean cultivars included in this study were less reliant on

cross-pollination and more receptive to self-pollination, consequently foraging may not have had the expected effect on yield (Bishop et al. 2020).

The factors affecting the abundance of pollinators and proportion of those pollinators legitimately foraging in field beans is likely to be context specific. This study aligns with previous research, which has shown high variability in pollinator activity and behaviour in field beans and in any relationship between pollinators and field bean yield. Further research into understanding this variability is necessary to inform crop pollination management.

Management interventions which aim to increase pollinator numbers in agricultural areas are encouraged and, in some cases, funded through agri-environment schemes, but evidence that these measures increase pollinator populations and diversity is mixed (Carvell et al. 2013; Wood et al. 2015) and may be dependent on landscape context (Scheper et al. 2013). These measures may not always have the benefits expected for crop pollination (Carvell et al. 2007).

The results of this study and previous research suggest that long-tongued bees are most likely to legitimately forage in field bean flowers, which can facilitate pollination and outcrossing. Focusing conservation on farmland on increasing numbers of long-tongued bumblebees, such as *B. hortorum*, might be beneficial for field bean pollination. However, long-tongued bees are relatively rare in farmland due to their narrow diet breadth and their decline has been attributed to the loss of habitat which is naturally rich in Fabaceae species such as in unimproved grassland (Goulson et al. 2005). Existing agri-environment options may not provide sufficient floral resources for all pollinator species (Carvell et al. 2007; Nichols et al. 2022) and focusing management on providing foraging resources for long-tongued bees may be beneficial.

The conservation of other bee species observed in this study could also be beneficial for field bean crops as they also engaged in some legitimate foraging behaviour and their robbing behaviour did not detrimentally impact yield in our study. Employing measures that support pollinator populations on farmland generally, such as providing foraging resources through the flight season (Timberlake et al. 2019), reducing possible competition or disease transmission from honeybees (Wermuth & Dupont 2010) and providing nest sites would also be advantageous (Wood et al. 2015).

AUTHOR CONTRIBUTION

Concept and design JH, LC & NM, data collection LC & JC, data analysis LC, writing LC, edits and approval for publication LC, JC, NM & JH.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

DATA AVAILABILITY STATEMENT

The data is available from the corresponding author on request.

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