



Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield

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ABSTRACT

Agricultural intensification has led to the conversion of natural habitats into agricultural fields, increased field sizes and simplified crop rotations. The resulting homogenisation of the landscape has led to a decline in bees, which provide an essential ecosystem service to agriculture. It has been suggested that an increase in landscape crop diversity supports higher biodiversity by providing more diverse and continuous resources without taking land out of agricultural production. We selected 14 faba bean (*Vicia faba* minor L.) fields in southern Sweden along uncorrelated gradients of landscape crop diversity and proportion of semi-natural habitat within 1.5 km radii surrounding focal fields. Pollinator surveys and pollinator exclusion experiments were conducted to assess whether landscape crop diversity affected pollinator densities, pollinator foraging behaviour (i.e. legitimate flower visitation, nectar robbing or extra-floral nectary visitation), pollination and yield formation. Landscape crop diversity enhanced bumble bee densities. Insect-pollinated faba bean plants produced, on average, 27 % higher bean weight per plant than bagged plants and the insect pollination benefit decreased with increasing semi-natural habitat cover. Bumble bee and honey bee densities, the proportion of nectar robbing bees as well as faba bean yield increased with increasing proportion of semi-natural habitat. Pollinator densities were not the driver of high yields associated with higher proportions of semi-natural habitat because the observed yield increase was unrelated to pollinator densities and driven by bagged plants that were excluded from pollinator visits. Insect pollination, however, clearly decreased the yield gap associated with low proportions of semi-natural habitat in the landscape. Our results highlight that agri-environmental policies should promote the retention of existing semi-natural habitats and encourage landscape crop diversity to provide pollinators with sufficient food and nesting resources.

1. Introduction

A main component of intensified crop production over the last century has been the conversion of natural habitats into agricultural fields, increased field sizes and simplified crop rotations (Robinson and Sutherland, 2002). The resulting homogenisation of the landscape has led to a stark decline in biodiversity (Biesmeijer et al., 2006; Kleijn et al., 2009). Particularly alarming are the reported wild bee declines (Biesmeijer et al., 2006; IPBES, 2016; Zattara and Aizen, 2020), whose pollination provision increases yield in many economically important crops (Aizen et al., 2009; Klein et al., 2007). Bees are central-place foragers and their foraging options are limited by their flight range around their nest (Gill et al., 2016). The loss of nearby nesting and foraging resources in homogenous agricultural landscapes is considered

a key driver of bee declines (Biesmeijer et al., 2006; Goulson et al., 2008). Retention of semi-natural habitats (SNH) such as forests and grasslands can support higher bee densities (Kennedy et al., 2013; Proesmans et al., 2019; Svensson et al., 2000; Williams and Kremen, 2007) and enhance crop pollination (Garibaldi et al., 2011; Ricketts et al., 2008). However, given global demand for agricultural products (Alexandros and Bruinsma, 2012; Godfray et al., 2010; Tilman et al., 2011), taking land out of crop production might become increasingly challenging to realise (Hodge et al., 2015).

Enhancing landscape crop diversity, which is defined as increasing the richness and evenness of crops grown in a landscape, has been proposed as a strategy to reverse the negative effects of homogenous agricultural landscapes without taking land out of crop production (Fahrig et al., 2011). By providing a more diverse matrix of food

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resources and habitats for nesting and dispersal, increased landscape crop diversity might support higher pollinator densities (Fahrig et al., 2011). Furthermore, different crops are associated with different weed communities (Hyvönen and Salonen, 2002), which can provide complementary food resources for pollinators (Bretagnolle and Gaba, 2015; Carvalho et al., 2011). Effects of landscape crop diversity on bees and pollination have only recently begun to be explored. Bee abundances (Hass et al., 2018) and species richness (Martin et al., 2020) have been shown to decline or be unaffected (Fahrig et al., 2015; Aguilera et al., 2020) by increased landscape crop diversity. Instead, landscapes with smaller field sizes supported higher bee abundances (Hass et al., 2018), bee diversity (Fahrig et al., 2015) and bee richness (Martin et al., 2020). In yet another case, bee richness increased with increasing crop diversity in landscapes with more than 11 % SNH cover while bee richness declined when SNH cover was low (<4 %) (Sirami et al., 2019). The only investigation of landscape crop diversity effects on pollination found no effect of landscape crop diversity on the seed-set of phytometer plants (Hass et al., 2018). It remains unknown whether increased landscape crop diversity benefits pollinator densities, pollination and yield of mass-flowering crops at field scale.

To maximise pollination and yield in insect pollination-dependent crops, not only the density or species richness of flower visitors is important. Their foraging behaviour also plays a role because not all flower visitors necessarily pollinate. Bees, for example, exhibit different behaviours when foraging for pollen or nectar (Sprenkel, 1793), these are: 1) legitimate pollination visits, whereby bees insert the proboscis into the flower tube to collect pollen and nectar, thereby transferring pollen to the stigma (Tasei, 1976); 2) nectar robbing, where bees extract nectar without getting in contact with the flowers' sexual parts, often by biting a hole in the flower tube (Inouye, 1980; Tasei, 1976); and 3) extra-floral nectary (EFN) visitation, where bees collect nectar from nectaries located outside flowers without providing pollination (Bond and Poulsen, 1983). Predominant behaviours depend to some degree on flower morphology and, thus, not all three behaviours can be observed in all crops. Faba bean (*Vicia faba minor* L.) is suitable for investigating factors affecting foraging behaviour because bees are using all three behaviours to forage on its pollen and nectar (Tasei, 1976). Despite being self-fertile, faba bean benefits from insect pollination (Free, 1966; Kendall and Smith, 1975; Nayak et al., 2015). Bee behavioural switches in faba bean are associated with crop stage, with pollinators preferring to visit flowers rather than EFN when faba bean flower abundance is high (Marzinzig et al., 2018). It is not known whether higher flower abundance at landscape-level, for example due to higher proportion of SNH or higher landscape crop diversity providing alternative nectar sources (Danner et al., 2016; Timberlake et al., 2019), could also increase pollen foraging and thereby legitimate pollination visits in faba bean. A higher abundance of alternative nectar resources in the landscape might promote foraging for pollen rather than nectar in faba bean fields since faba bean nectar abundance is low and difficult to access (Bailes et al., 2018) while its pollen is particularly rich in protein (Hanley et al., 2008; Pamminger et al., 2019).

We examined effects of landscape crop diversity and proportion of SNH in the landscape on pollinator densities, bee foraging behaviour, pollination and yield formation in 14 faba bean fields in southern Sweden. We hypothesise that both higher landscape crop diversity and higher proportion of SNH increase pollinator densities, proportion of legitimate pollinator visits, the insect pollination benefit, and ultimately faba bean yield.

2. Methods

2.1. Experimental design

We recorded densities of pollinators, pollinator foraging behaviour, insect pollination benefits for yield components in bagged and open-pollinated faba bean plants and calculated yield per hectare in 14

conventional faba bean fields in 2017. Fields were selected along uncorrelated ($r = 0.039$, $p = 0.90$) gradients of landscape crop diversity and proportion of SNH within a 1.5 km radius. We focused our analyses on 1.5 km landscape radii since bumble bees and honey bees are expected to be the main pollinators visiting faba beans (Free, 1993; Marzinzig et al., 2018). Bumble bees (Osborne et al., 2008) and honey bees (Steffan-Dewenter et al., 2002; Steffan-Dewenter and Kuhn, 2003) routinely forage within 1.5 km of their nest. To minimise spatial autocorrelation, field centres were located at least 2.9 km apart such that there was only minimal overlap among landscapes. All landscapes were located in Skåne, the southernmost province of Sweden, which spans across approximately 100 by 100 km of which approximately 40 % is arable land (Fig. 1) (Statistics Sweden, 2018). The dominant crops cultivated in this region are (in descending order) winter wheat, leys, spring barley and winter oilseed rape, but several other crops, including faba bean, are also grown (Statistics Sweden, 2018). The average size of our experimental fields was 15 ha (range 3–40 ha, Table S1). While each faba bean field was sown with a single cultivar, several cultivars differing in flower colour type (Duc, 1997) were grown among our experimental fields (white-flowered cultivars: 5 fields, coloured-flowered cultivars: 9 fields, Table S1). We set up two sampling areas in each field of 50 m by 24 m situated adjacent to each other along the field edge. Data was collected in each sampling area along a 30 m transect situated 12 m from the field edge. In one sampling area no insecticides were used, while the other sampling area and the rest of the field were assigned to receive conventional insecticide treatment. However, because insecticide use was not common among farmers only four fields were treated with insecticides before crop flowering and a fifth one after crop flowering. Consequently, we restricted the analysis of pollinator data, which was collected during crop flowering, to the 24 unsprayed sampling areas, and the analysis of faba bean data, which was collected at harvest, to the 23 unsprayed sampling areas across the 14 fields. The effect of insecticide was not analysed further.

2.2. Landscape gradients

The landscapes surrounding each faba bean field were characterised within a radius of 1.5 km from each field centre for landscape crop diversity (hereafter crop diversity) and proportion of semi-natural habitat (SNH), which included pastures and forests. Since our focus was to assess the role of crop diversity on pollinator abundances and pollination, we chose field sites in landscapes with high proportions of arable land (mean: 0.86, range: 0.75–0.93, Table S1). Pasture and crop data were obtained from the Integrated Administration and Control System (IACS), administered by the Swedish Board of Agriculture. Because crop identity information was missing in IACS for 6.2 % of the arable land, we complemented crop information by visually checking fields during the field season where possible, resulting in a final coverage of crop information for 96 % of the arable land across our landscape buffers. To estimate forest cover, we used a digitalised map layer (Terrängkartan, Lantmäteriet, 2018) in ArcMap software version 10.4.1 (ESRI, 2015).

To calculate crop diversity, we categorised all crops that are grown within the 1.5 km landscape buffers around the selected fields into 14 crop categories: beets, spring sown brassicas, winter sown brassicas, spring sown cereals, winter sown cereals, clovers, corn, fallow, leys, potato, pulses, trees, vegetables/fruits/berries and other (Fig. 1, Table S2). Percentage cover of each crop category in our landscape buffers and the number of landscape buffers including the respective crop category are given in Table S2. Agricultural land is divided and mapped into blocks in IACS. Block sizes contributing to each 1.5 km landscape buffer surrounding focal fields were extracted using ArcMap software (ESRI, 2015). Blocks are further divided into parcels of land cultivated with a certain crop. The parcels within each block are of known size but are unmaped. To estimate the proportion of each crop in each block within the landscape buffer, we therefore multiplied the parcel size of each crop grown in that block with the proportion of the block that was inside the

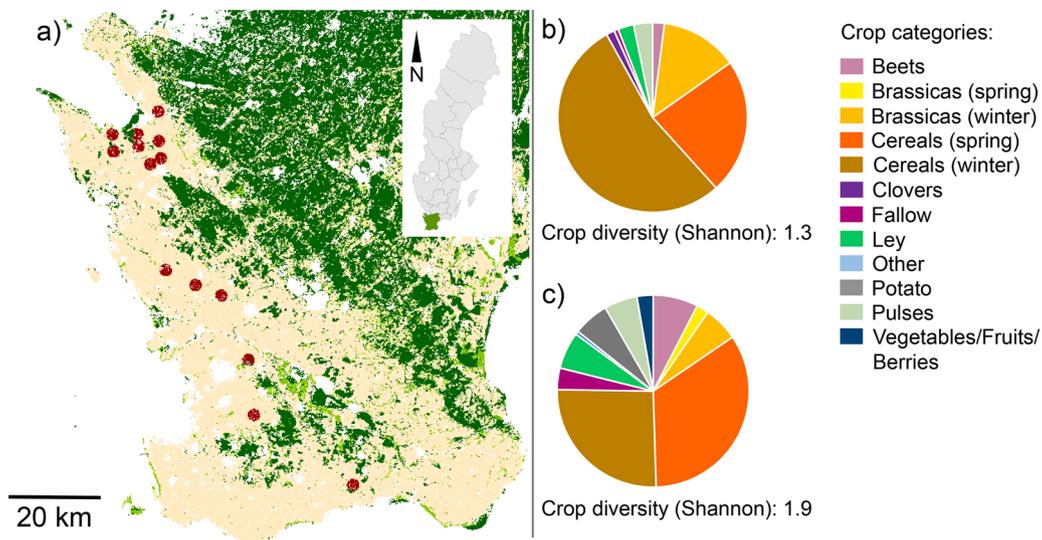


Fig. 1. Field locations in Skåne (a), Sweden (inset), with arable land in beige, forest in dark green and semi-natural grassland in light green. Red circles are the 14 landscapes of 1.5 km radii around our focal field sites. Proportional crop category contributions to the least crop diverse (b) and most crop diverse (c) landscapes are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

buffer.

Based on crop category and cover area, crop diversity was calculated using the Shannon index in the ‘vegan’ package in R (Oksanen et al., 2019). Crop diversity Shannon indices ranged from 1.3 to 1.9 (Fig. 1, Table S1). Proportion of SNH cover ranged from 0 to 0.15 across landscapes (Table S1). Correlations of crop diversity and proportion of SNH were low at the 1.5 km landscape scale ($r = 0.039$, $p = 0.90$), however, crop diversity correlated negatively with mean field size (MFS) ($r = -0.56$, $p = 0.036$, Table S3) in the landscape while the proportion of SNH correlated negatively with the proportion arable land in the landscape ($r = -0.73$, $p = 0.0033$, Table S3).

2.3. Pollinator densities and foraging behaviour

We sampled pollinators in both sampling areas using a standardised transect walk. Each transect was 30 m long and 1 m wide and located at 12 m from the field edge. We surveyed pollinators during faba bean bloom from mid-June until mid-July at weekly intervals two to four times depending on blooming duration (mean: 3.1). Sampling was restricted to days with conditions that were favourable for pollinator activity with air temperatures of at least 15°C, wind speeds of less than 8 m/s (Beaufort scale: “moderate breeze”), no rain within the last hour, and at least partly sunny or brightly overcast sky (Westphal et al., 2008). We sampled pollinator densities in each sampling area by slowly walking along the transect during 10 min net collection time and collected all pollinators that were visiting faba bean flowers or extra floral nectaries (EFN) with a net for later identification. Honey bees and bumble bee queens were counted but not collected and so bumble bee queens were not identified to species level. *Bombus terrestris*, *B. lucorum*, *B. cryptarum* and *B. magnus* were treated as one species complex, denoted as *B. terrestris aggr.*, because it is difficult to differentiate these species (Murray et al., 2008). In addition to honey bees and bumble bees, faba bean flowers and EFN were also visited by six ant individuals, three hoverflies, two wasps, one solitary bee and one soldier beetle, but due to low numbers these individuals were excluded from the analysis. For each observation, we also noted whether pollinators were 1) legitimately pollinating flowers by inserting their proboscis through the front of the flower opening, 2) robbing nectar by inserting their proboscis through a hole at the base of the flower tube to extract nectar or 3) visiting EFN located on stipules below leaves. Commercial honey bee hives are common in Skåne. We assessed honey bee hive presence within the 1.5 km landscape buffers through farmer questionnaires and

personal observations.

2.4. Pollination

To assess the contribution of insect pollination to faba bean yield, we selected five plant pairs in each transect (10 plant pairs per field except for one field, where the effect of insect pollination was not tested because early flowering made it impossible to bag plants). One of the plants in each pair was bagged with a tulle net (2 mm mesh size) once budding started but before anthesis, to exclude insect pollination. The second plant remained unbagged and open to insect pollination. The plants in each pair were chosen such that they had a similar growth stage and bud numbers. Bags were adjusted weekly for plant growth and flowers that started wilting were unbagged to minimise bagging effects on pod development. At pod maturity, all pods of bagged and unbagged plants were harvested. We counted pods per plant and beans per pod. We dried beans at 65°C for 48 h and weighed dry bean mass per plant. Individual bean weight was calculated by dividing bean mass with the total number of beans per plant.

2.5. Yield

Faba bean pods were manually harvested from four 0.36 m² quadrats randomly placed in each sampling area. Harvesting was done between 9–16 September 2017 when pods reached maturity, shortly before farmers harvested fields. To estimate crop plant density, we counted all faba bean plants per quadrat. We harvested all pods on five randomly chosen plants per quadrat. Beans were dried at 65°C for 48 h and then weighed. The average bean weight per plant in each quadrat was multiplied with crop plant density and then recalculated and expressed as kg dry beans per hectare.

2.6. Statistical analysis

All statistical analyses were done using linear mixed effects models or generalised linear mixed effects models (package ‘lme4’, Bates et al., 2015) in R version 3.6.1 for Windows (R Core Team, 2019) and the amount of variance that contributed to a sample by different factors was analysed with a type III ANOVA. To confirm that models were not overdispersed and to obtain residual diagnostics for models with Poisson and binomial error distributions we used the testDispersion and the simulateResiduals functions in R (package ‘DHARMA’, Hartig, 2019).

We also tested for spatial autocorrelation of model residuals using the testSpatialAutocorrelation function in R (package 'DHARMA', Hartig, 2019), which performs a Moran's I test. The residuals of the model for the number of beans per pod were spatially autocorrelated (Moran's I = 0.13, $p = 0.026$, Table S4). Hence we added a Gaussian spatial correlation structure (corGaus) to the model using the glmmPQL function (package 'MASS', Venables and Ripley, 2002) as suggested by Dormann et al. (2007). Marginal R-square values to represent the variance explained by the fixed effects for each model were calculated with the rsquaredGLMM function (package 'MuMin', Barton, 2019). For models with Poisson distribution we used the trigamma method for deriving the observation-level variances and for models using a binomial distribution the theoretical method (Nakagawa and Schielzeth, 2013; Nakagawa et al., 2017). As explanatory variables we used three landscape features unless specified otherwise: Crop diversity, proportion of SNH and mean field size (MFS) in the landscape. Since crop diversity and proportion of SNH were part of the experimental design, they were kept in the model irrespective of whether they significantly improved the model fit or not. We also kept MFS in the model as its correlation coefficient with crop diversity was below 0.7 (Dormann et al., 2013) and to account for its negative correlation with crop diversity (Table S3). Adding MFS to the models is important in order to separate effects of crop diversity from effects of landscape configuration due to smaller field sizes (Fahrig et al., 2015; Hass et al., 2018; Redlich et al., 2018). The variance inflation factor (vif) was tested for all models to verify that adding correlated variables did not cause strong collinearities (Dormann et al., 2013), and was below 1.8 in all cases (Zuur et al., 2010). Field identity was used as a random effect in the models unless specified otherwise, to account for data being collected from two unsprayed sampling areas in 9 out of 14 fields (see section 2.1)

Pollinator densities were evaluated in two separate models with 1) bumble bee and 2) honey bee densities as response variables using Poisson error distribution and a log link for honey bee densities and a negative binomial distribution and a log link for bumble bee densities. Bumble bee and honey bee densities were summed per transect and across the flowering season in each unsprayed sampling area ($N = 24$). The log-transformed number of sampling rounds was added to the model as an offset to account for variation in sampling effort among fields. We tested the effect of presence/absence information of honey bee hives on honey bee densities in the model with the three landscape variables but found no effect. Thus, we did not include hive information in the final model.

Foraging behaviour was analysed in three separate models with the proportions of 1) legitimate pollinators, 2) nectar robbers and 3) EFN visitors as response variables using binomial error distributions and a logit link. The proportion of individuals in the pollinator community that legitimately pollinated, robbed nectar or visited EFN were summed per sampling round and transect in each unsprayed sampling area ($N = 44$). We used the three landscape variables as explanatory variables. Sampling round nested within field identity was added as a random effect. The effect of faba bean cultivar type (white vs. coloured flowers) on foraging behaviour was tested in all three models together with the three landscape variables but had no significant effect on any of the response variables and was not included in the final models.

The effect of pollination treatment was investigated by comparing yield components of bagged and open pollinated plant pairs ($N = 193$ plants) and was replicated in all sampling areas ($N = 21$) across 13 fields. The effect of insect pollination treatment on yield components was evaluated in 12 separate models for 1) bean weight per plant, 2) number of pods per plant, 3) number of beans per pod and 4) individual bean weight as response variables. Normal distribution with a square root transformation and an identity link was used for bean weight per plant and weight per bean, and Poisson distribution and a log link were used for pods per plant and beans per pod. As explanatory variables in three separate models we used 1) landscape variables: crop diversity, proportion of SNH and MFS, 2) pollinator densities (mean number of

honey bees and bumble bees per sampling area) and 3) number of legitimate pollinators (mean number of legitimately pollinating honey bees and bumble bees per sampling area). Treatment, i.e., open-pollinated vs. bagged plants was added as explanatory variables to all three models. The interaction between treatment and all other explanatory variables was added and kept in the final model if that model had a lower Akaike information criterion (AIC) compared to the model without the interaction (Nakagawa and Schielzeth, 2013). Post-hoc tests for simple main effects of variables that interacted significantly with treatment were performed using the "emtrends" functions in R (package 'emmeans', Lenth, 2019). We used plant pair identity nested within field identity as random term. To analyse the number of beans per pod we used number of beans per plant as the response variable and added the log-transformed number of pods as an offset to the model. The effects of faba bean colour type (white vs. coloured flowers) and its interaction with treatment was tested in all models but had no significant effect on any of the response variables and was not included in the final models.

Yield was analysed with kg dry beans per hectare as response variable in three separate models assuming normal distribution with an identity link. Since yield was extrapolated from multiple quadrats per field ($N = 92$), we added field identity as a random term. As explanatory variables we used 1) landscape features: crop diversity, proportion of SNH and MFS, 2) pollinator densities (mean number of honey bees and bumble bees per sampling area) and 3) number of legitimate pollinators (mean number of legitimately pollinating honey bees and bumble bees per sampling area) in the respective models.

3. Results

3.1. Pollinator densities and foraging behaviour

We observed 493 honey bees and 144 bumble bees visiting faba bean flowers and EFN (Table S5). Bumble bee densities increased with increasing crop diversity (Fig. 2a) and proportion of SNH (Fig. 2b). Honey bee densities also increased with increasing proportion of SNH (Fig. 2c), but were not affected by crop diversity (Table 1).

In total, we determined foraging behaviour for 246 honey bees and 88 bumble bees. Of the honey bees, 70 individuals were legitimately pollinating flowers, 118 were robbing nectar and 58 visited EFN (Table S6). Of the bumble bees, 41 individuals were legitimately pollinating, 43 were robbing nectar and four visited EFN (Table S6). The proportion of nectar robbing increased with SNH (Fig. 2d) but we found no effect of landscape on the proportion of legitimate pollinator visits nor EFN visits (Table 2).

3.2. Pollination

There was an interaction between proportion of SNH and pollination treatment, where the benefit from insect pollination on bean weight per plant decreased with increasing proportion of SNH (Table 3, Fig. 3a). Post-hoc tests for simple main effects showed that bean weight per plant increased with increasing proportion of SNH in bagged (95 % CI -0.09–19.1 $p = 0.048$), but not in open-pollinated plants (95 % CI -6.15–12.9 $p = 0.45$). On average, open-pollinated faba bean plants produced 27 % higher bean weight per plant than bagged plants and increasing proportion of SNH was associated with higher bean weight per plant (Table 3, Fig. 3a). The bean weight per plant was neither affected by crop diversity, MFS, density of pollinators, density of legitimate pollinators, nor did any of these explanatory variables interact with the treatment (Table 3, Fig. 3b-d). The pollination benefit for bean weight per plant was driven by open-pollinated plants producing more pods per plants and more beans per pod than bagged plants, while individual bean weight did not differ between treatments (Table 3, Fig S1). Similarly to the overall effect on bean weight per plant, there was an interaction between the pollination treatment and the proportion of SNH on pods per plant (Table 3, Fig S1a), but tests for simple main

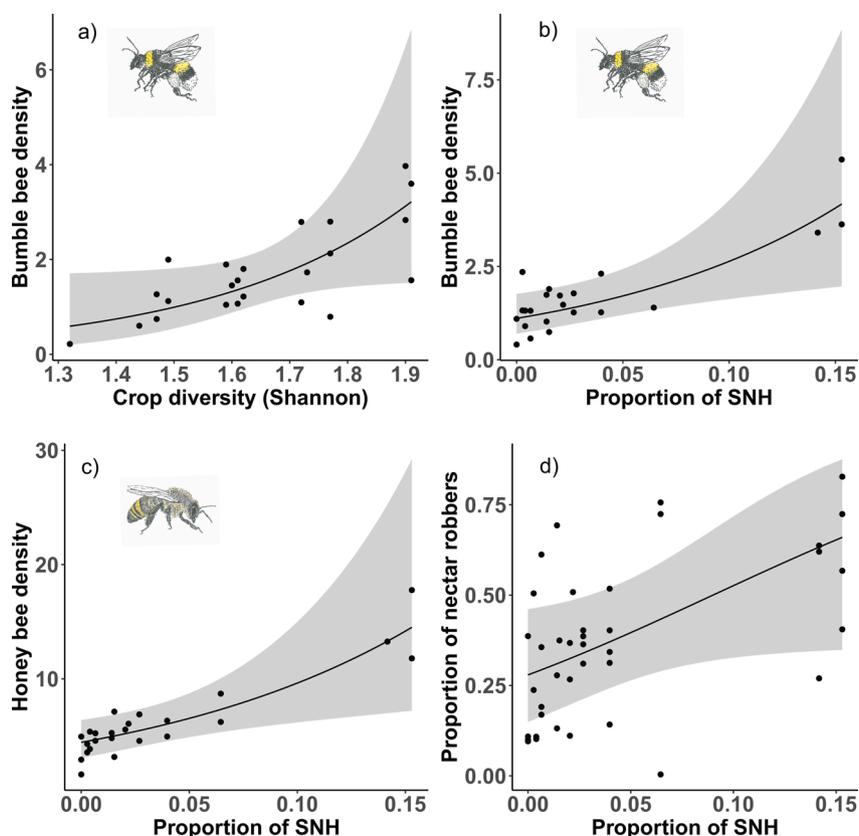


Fig. 2. Bumble bee densities per transect increased with crop diversity (a), and proportion of SNH (b). Honey bee densities per transect increased with proportion of SNH (c). The proportion of nectar robbing bees increased with increasing proportion of SNH (d). Shown are fitted lines with partial residuals (black dots) and shaded areas representing the 95 % confidence intervals.

Table 1

Results of generalised linear mixed effects models for bumble bee and honey bee densities per transect in relation to crop diversity, mean field size (MFS) and proportion of semi-natural habitat (SNH). Shown are Chi-square values (X^2), degree of freedom (df), estimates (e), standard errors ($s.e$) and p -values (p). P -values in bold are significant at the 0.05 level. Marginal R-square values (R^2) are given for each model to represent the variance explained by the fixed effects.

	Bumble bees				Honey bees			
	X^2 ($df = 1$)	e	$s.e$	p	X^2 ($df = 1$)	e	$s.e$	p
Intercept		-5.40				-0.28		
Crop diversity	4.52	2.87	1.35	0.033	0.62	0.79	1.00	0.43
MFS	2.00	0.12	0.08	0.16	1.06	0.07	0.07	0.30
SNH	8.23	8.65	3.02	0.0040	8.14	7.73	2.71	0.0043

Table 2

Results of generalised linear mixed effects models for the proportion of legitimate pollinators, nectar robbers and extra-floral nectary (EFN) visitors per transect in relation to crop diversity, mean field size (MFS) and proportion of semi-natural habitat (SNH). Shown are Chi-square values (X^2), degree of freedom (df), estimates (e), standard errors ($s.e$) and p -values (p). P -values in bold are significant at the 0.05 level. Marginal R-square values (R^2) are given for each model to represent the variance explained by the fixed effects.

	Proportion legitimate pollination $R^2 = 0.047$				Proportion nectar robbing $R^2 = 0.063$				Proportion EFN visits $R^2 = 0.11$			
	X^2 ($df = 1$)	e	$s.e$	p	X^2 ($df = 1$)	e	$s.e$	p	X^2 ($df = 1$)	e	$s.e$	p
Intercept		-2.86				-2.37				14.70		
Crop diversity	0.61	1.75	2.23	0.43	0.17	0.84	2.03	0.68	2.34	-10.51	13.28	0.13
MFS	0.25	-0.08	0.16	0.62	<0.01	<0.01	0.14	0.95	0.04	-0.20	0.52	0.84
SNH	0.34	-3.38	5.79	0.56	3.89	10.53	5.33	0.048	0.14	-3.66	17.66	0.71

effects indicated no significant relationships between number of pods per plant and the proportion of SNH in neither bagged (95 % CI -0.75–5.78, $p = 0.13$) nor open-pollinated plants (95 % CI -3.22–3.36, $p = 0.97$) (Fig S1a). There was also an interaction between pollination treatment and crop diversity on the number of pods per plant (Table 3, Fig S1b), but tests for simple main effects indicated no significant

relationships in neither bagged (95 % CI -1.25–1.07, $p = 0.88$) nor open-pollinated plants (95 % CI -1.81–0.48, $p = 0.26$) (Fig S1b).

3.3. Yield

Yield increased with increasing proportion of SNH in the landscape

Table 3
Results of linear mixed effects models for bean weight per plant and generalised linear mixed effects models for the number of pods per plant and the number of beans per pod in relation to pollination treatment (Treatment, open versus bagged), crop diversity, mean field size (MFS), proportion of semi-natural habitat (SNH), pollinator density and density of legitimate pollinators. Shown are Chi-square values (χ^2), t -values (t), degree of freedom (df), estimates (e), standard errors ($s.e$) and p -values (p). P -values in bold are significant at the 0.05 level. Interactions between landscape variables and pollination treatment that were not significant, and were not in the final model are indicated with a dash (-). Marginal R-square values (R^2) are given for each model to represent the variance explained by the fixed effects.

	Bean weight per plant				Number of pods per plant				Number of beans per pod				Weight per bean				
	χ^2	df	R^2	p	$s.e$	e	$s.e$	p	t	e	$s.e$	df	p	χ^2	df	R^2	p
Landscape model																	
Intercept	3.61		0.12			2.16		0.012		3.81		0.24				0.081	
Treatment, open	23.40	0.70		<0.001	0.15	1.19	0.47	0.012	7.73	0.36	0.05	94	<0.001	0.94	0.94		0.51
Crop diversity (CD)	0.06	-0.36	0.81	0.81	1.46	-0.09	0.59	0.88	-0.90	-0.49	0.55	9	0.39	0.37	0.37		-0.01
MFS	0.07	-0.03	0.11	0.79	0.11	<0.01	0.04	0.99	<0.01	<0.01	0.04	9	0.99	0.16	0.16		<0.01
SNH	5.03	9.60	4.28	0.025	2.52	2.52	1.67	0.13	1.31	2.00	1.52	9	0.22	1.68	1.68		0.60
SNH:Treatment, open	7.00	-6.21	2.35	0.0082	-2.45	-2.45	0.93	0.0084	-	-	-	-	-	-	-		-
CD:Treatment, open	-	-	-	-	-0.58	-0.58	0.29	0.044	-	-	-	-	-	-	-		-
MFS:Treatment, open	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		-
Organism model																	
Intercept	2.93		0.052			2.09		0.023		0.87		0.19				0.045	
Treatment, open	15.44	0.46		<0.001	0.12	0.15	0.05	<0.001	28.03	0.21	0.03		<0.001	0.96	0.96		0.61
Pollinators	0.66	0.03	0.04	0.42	0.04	<0.01	0.02	0.84	3.00	<0.01	<0.01	0.32	0.32	1.77	1.77		-0.01
Behaviour model																	
Intercept	3.09		0.042			2.11		0.023		0.95		0.16				0.020	
Treatment, open	15.44	0.46		<0.001	0.12	0.15	0.05	<0.001	54.61	0.21	0.03		<0.001	0.95	0.95		0.64
Legitimate pollinators	0.39	0.05	0.08	0.53	0.08	<0.01	0.03	0.94	0.18	<0.01	0.02	0.68	0.68	1.41	1.41		-0.01

(Fig. 4) but was not affected by any other landscape variables (Table 4). There were no relationships between yield and pollinator densities or legitimate pollinator densities (Table 4).

4. Discussion

We found that both increased crop diversity and proportion of SNH in the landscape enhanced bumble bee densities. The SNH gradient across our landscapes was limited because we selected landscapes with high proportions of arable land aiming to examine effects of crop diversity. Nonetheless, our results confirmed that SNH in the landscape increases densities of bumble bees in an insect pollinated crop (Garibaldi et al., 2011). Furthermore, the proportion of nectar robbing bees increased with the proportion of SNH in the landscape. Bean weight per plant was on average 27 % higher in open-pollinated compared with bagged faba bean plants. Faba bean yield benefits from insect pollination have been found before and vary substantially (17–185 %) (Bartomeus et al., 2014; Cunningham and Le Feuvre, 2013; Free, 1966; Nayak et al., 2015). The insect pollination benefit we observed was modified by the proportion of SNH in the landscape, with a higher pollination benefit in landscapes with low proportions of SNH. Increasing proportion of SNH in the landscape was associated with higher bean weight per plant but since this effect was stronger in bagged than in open-pollinated plants, we conclude that factors other than the higher pollinator densities increased yields.

4.1. Increasing crop diversity supports higher densities of bumble bees

Landscapes with both higher crop diversity and proportion of SNH supported higher densities of bumble bees visiting faba bean fields. Possible mechanisms are that a diversity of crops in the surrounding landscape creates more varied and continuous food resources (Fahrig et al., 2011; Schellhorn et al., 2015; Vasseur et al., 2013), while SNH provide pivotal foraging and nesting habitat (Öckinger and Smith, 2007). A potential caveat to our result is that crop diversity and MFS was negatively correlated across our landscape buffers ($r=-0.56$). Even though we accounted for this correlation in the statistical analyses we recommend that future studies explore the independent effects of crop diversity and MFS on pollinators across orthogonal landscape gradients. The positive effect of crop diversity on bumble bee densities contrast other observations showing that wild bee densities decrease (Hass et al., 2018) or are unaffected (Fahrig et al., 2015) by crop diversity and instead were responding positively to landscape configuration (i.e., smaller mean field sizes).

We provide three possible explanations for why positive effects of crop diversity on pollinators are not consistently observed. Firstly, the identity of crops that become more or less abundant with increasing crop diversity might be more important than crop diversity *per se*. In our study landscapes, the proportion of winter cereals, which provide relatively few resources for pollinators, decreased with increasing crop diversity (Table S2). If the crops that become more abundant with increasing crop diversity are, however, intensively managed and provide few resources for pollinators then higher crop diversity might negatively impact pollinators (Hass et al., 2018, 2019) and provide resource disruption rather than continuity as we hypothesised. For this reason, functional crop diversity, i.e., distinguishing crop types based on their importance for pollinators in providing resources (see Fahrig et al., 2011), could be a better predictor of pollinator responses than simple crop diversity based on crop identity. To test this hypothesis, it would be necessary to collect information on crop traits and associated weeds relevant for pollinators. Secondly, the effect of crop diversity on pollinators might vary as a result of variation in the availability of co-flowering resources from SNH and other crops in the landscape, which influence observed pollinator densities at a certain sampling location and time of sampling (Kleijn et al., 2018). For example, early flowering crops and weeds could have facilitated a build-up of pollinator

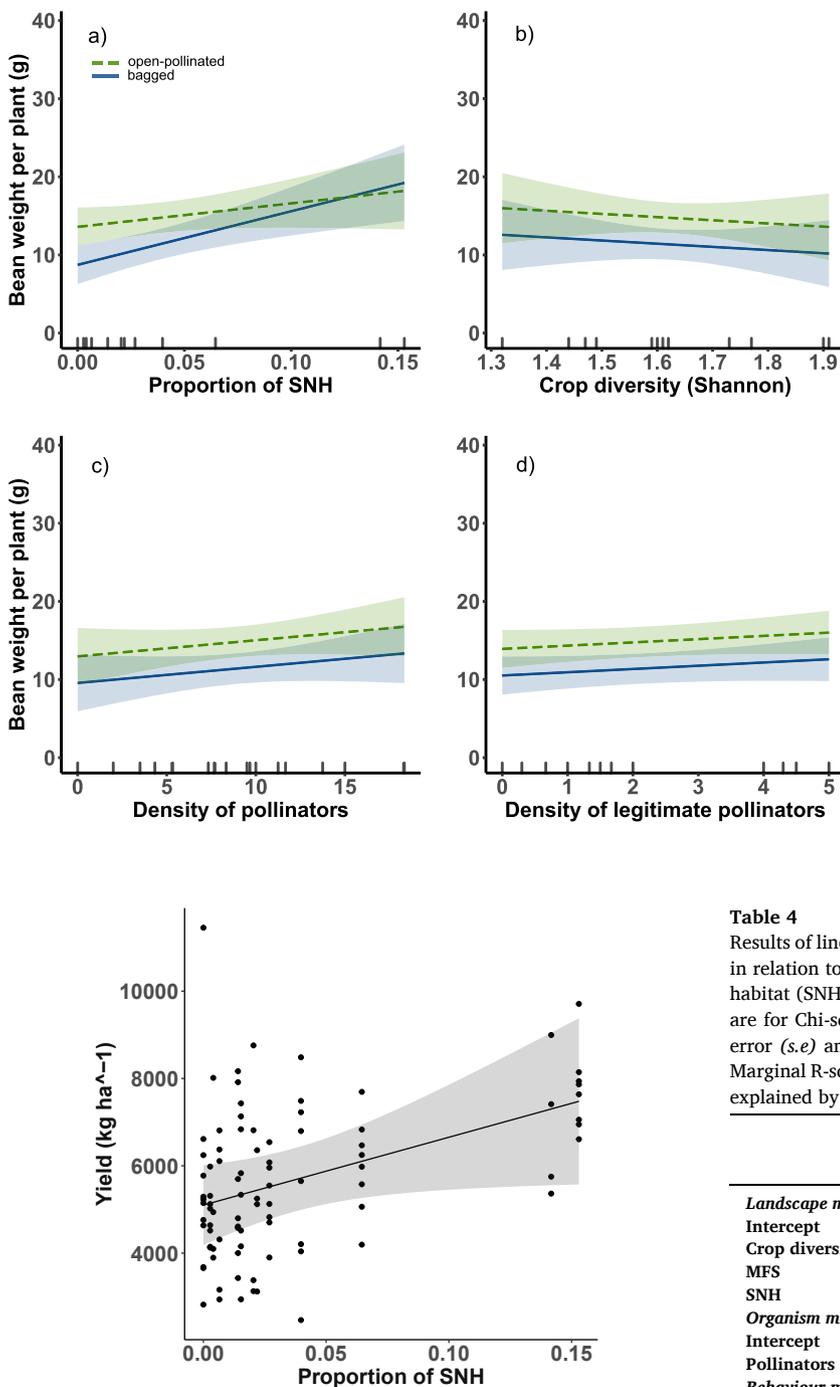


Fig. 3. Bean weight per plant (g) was higher in open-pollinated plants (green dashed line) than bagged plants (blue continuous line) and increased with proportion of SNH, but the effect of SNH was stronger for bagged than open-pollinated plants (a). Bean weight per plant was not affected by increasing crop diversity (b), pollinator densities per transect (c) nor the number of legitimate pollinators per transect (d). Shown are fitted lines and shaded areas representing the 95 % confidence intervals. Data spread is shown using rug marks along the x-axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 4. Yield (kg ha^{-1} , dry weight) increased with proportion of SNH. Shown are fitted lines with partial residuals (black dots) and shaded areas representing the 95 % confidence intervals.

numbers that subsequently increased pollinator visits in faba bean fields, which flower late in the season when competition with other flowering crops for pollinators is low (Grab et al., 2017; Holzschuh et al., 2016; Riedinger et al., 2014). In contrast, Hass et al. (2018) sampled pollinators in field edges, non-flowering crops and in oilseed rape fields mainly after crop flowering. These habitats might be less attractive for pollinators and also compete for pollinator visits with late flowering crops such as red clover or faba bean. Thirdly, it is possible that different wild pollinator groups (i.e., bumble bees, solitary bees, and syrphid flies) respond differently to crop diversity. Previous assessments of crop diversity on wild pollinators have included solitary bees and syrphid flies

Table 4

Results of linear mixed effects models for area-based yield (kg ha^{-1} , dry weight) in relation to crop diversity, mean field size (MFS), proportion of semi-natural habitat (SNH), pollinator density, and density of legitimate pollinators. Shown are for Chi-square values (X^2), degree of freedom (df), estimate (e), standard error ($s.e$) and p -values (p). P -values in bold are significant at the 0.05 level. Marginal R-square values (R^2) are given for each model to represent the variance explained by the fixed effects.

	Yield			
	X^2 ($df = 1$)	e	$s.e$	p
Landscape model	$R^2 = 0.12$			
Intercept		5191.02		
Crop diversity	<0.01	-92.47	2689.93	0.97
MFS	<0.01	8.83	184.19	0.96
SNH	4.17	15533.12	7607.56	0.041
Organism model	$R^2 = 0.059$			
Intercept		5000.49		
Pollinators	1.20	76.91	70.34	0.27
Behaviour model	$R^2 = 0.0092$			
Intercept		5820.36		
Legitimate pollinators	0.26	-80.58	159.14	0.61

in their analyses (Fahrig et al., 2015; Hass et al., 2018). Solitary bees and syrphid flies rarely collect faba bean resources, and except for one single solitary bee we only found bumble bees and honey bees to visit faba beans and can only base our conclusions on these two groups. It is thus possible that bumble bees respond positively to crop diversity while solitary bees and syrphid flies do not.

4.2. Crop diversity does not influence pollinator foraging behaviour but SNH increases nectar robbing

We found no evidence that crop diversity affected the foraging behaviour of pollinators but the proportion of nectar robbing increased with SNH. Considering the importance of crop flower density of faba

bean for driving changes in foraging behaviour (Marzinzig et al., 2018), it might not be crop diversity *per se* affecting pollinator foraging behaviour, but rather the abundance and quality of alternative pollen and nectar resources provided by mass-flowering crops in the landscape. Individuals might shift from foraging for nectar, which they extract from flowers and EFN, to foraging for pollen in faba bean, which requires legitimate pollination, when alternative nectar providing crops are abundant in the landscape. This hypothesis is supported by the fact that pollen from the family Fabaceae, which includes faba bean, is particularly rich in protein (Hanley et al., 2008; Pamminer et al., 2019), and bees increase pollen foraging in plants that have pollen with high protein-lipid ratios (Vaudo et al., 2016). Nectar, on the other hand, is less abundant in faba bean and difficult to access for short-tongued bees (Bailes et al., 2018; Bommarco et al., 2012; Norgaard Holm, 1966) making faba bean potentially less attractive when other nectar resources are available. To test this hypothesis, it would be interesting to assess the landscape level floral resource abundance including flowering crops, wild plants and also tree species and conduct experiments that observe foraging behaviour in focal fields surrounded by landscapes with varying proportions of flowering resources. The fact that nectar robbing increases with the proportion of SNH in the landscape, however, contradicts this hypothesis, considering that SNH would also provide alternative nectar sources. It is possible that the proportion of SNH in the landscape affects the bumble community composition in faba bean fields and favours generalist bumble bee species such as *Bombus terrestris* *aggr.*, which predominately robbed nectar in our faba bean fields (Table S6). To test this hypothesis we would need to analyse the effect of SNH on individual bumble bee species, but unfortunately our bumble bee numbers were too low to conduct such analyses.

4.3. SNH effects on insect pollination benefits and yield

Faba bean yield was higher in landscapes with higher proportions of SNH, which was uncorrelated with other landscape features. This yield increase was driven by factors other than increased pollinator densities that we could neither control for nor measure such as variation in soil properties or pest pressure associated with the SNH gradient (Bartomeus et al., 2015). Positive relationships between landscape features, pollinator visitation, and yield are commonly found in many crops, but these positive relationships do not rule out the possibility that landscape features may be associated with crop yield, independent of pollinator visits to flowers (Petersen and Nault, 2014). The use of bagged and open-pollinated plants in our experimental design allowed us to strengthen the conclusion that observed yield increases with increasing proportion of SNH in the landscape cannot be attributed to higher pollinator densities.

We further found that the benefit of insect pollination decreased with increasing SNH. The decrease in insect pollination benefit could be due to plants being able to compensate better for poor pollination when they are growing in otherwise favourable conditions in landscapes with higher proportions of SNH due to e.g., improved soil conditions for faba beans or reduced pest pressure (Tamburini et al., 2019). In line with this general mechanism, insect pollination benefit in oilseed rape is greater in plants that were nitrogen deficient (Marini et al., 2015) and under high pest attack (Bartomeus et al., 2015). Similarly, the insect pollination benefit in faba bean yield increased from 15.5 % in plants growing under control temperatures to 52.5 % in heat-stressed plants (Bishop et al., 2016).

5. Conclusions

We found that increasing crop diversity in agricultural landscapes benefits bumble bees in particular, and that crop diversity complemented SNH in the landscape rather than replacing it. Landscapes with high proportions of SNH supported higher densities of both wild and managed bees. From an agricultural perspective, increasing SNH in

the landscape also increases yield in faba beans. Thus, the retention of SNH benefits both pollinator conservation and crop production. We recommend that future agri-environmental schemes and agricultural policies strongly support an increase in crop diversity in agricultural landscapes, by incentivising the lengthening of crop rotations for example, while the conservation of existing SNH should be maintained.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:10.1016/j.agee.2020.107189.

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