Landscape complexity benefits bumble bee visitation in faba bean (*Vicia faba* minor L.) but crop productivity is not pollinator-dependent

Ola Lundin [*], Chloé A. Raderschall

Swedish University of Agricultural Sciences, Department of Ecology, SE-750 07 Uppsala, Sweden

ABSTRACT

Faba bean (*Vicia faba* minor L.) is partially dependent on insects for pollination, but the degree of pollinator-dependency and whether crop productivity is limited by insufficient insect pollination remain unknown. We monitored insect pollinators and their foraging behaviors (i. e., legitimate flower visitation, nectar robbing and extra-floral nectary visitation) in a total of 20 faba bean fields of a single cultivar (Tiffany) 2018–2019. Focal fields were situated along a gradient of landscape complexity. In each field, a pollination experiment was established, where plants were either bagged to exclude pollination by insects or remained open for pollinator visits. In addition, all flowers on half of the bagged and open-pollinated plants were pollinated by hand to measure the degree of pollen limitation. We found that bumble bee abundance was higher, and legitimate flower visitor abundance tended to be higher, in complex landscapes with more semi-natural habitat, indicating that the faba bean pollination potential is higher in complex landscapes. The pollination experiment showed that the number of beans per pod was lower in bagged plants compared with other treatments in one of the years, but the lower number of beans per pod was compensated for by a higher individual bean weight, such that there was no pollinator-dependency or effect of hand pollination on total bean mass per plant. We conclude that to be able to characterize the value of insect pollination services in faba bean we need an improved understanding of how pollinator-dependency varies across modern cultivars, and how environmental conditions can increase or, as in our case, cancel this pollinator-dependency.

1. Introduction

Animal pollination, mainly performed by bees, benefits over 75% of the world's most common crops and is a key ecosystem service supporting the nutritional needs and wellbeing of people globally (Klein et al., 2007; IPBES, 2016; Dainese et al., 2019). Managed honey bees and wild bumble bees (Apidae: Bombus) are particularly important crop pollinators in temperate agroecosystems (Garibaldi et al., 2013; Kleijn et al., 2015). While the abundance of managed honey bees in crops is largely driven by beekeeping practices, bumble bee abundances in crop fields are supported by nearby semi-natural habitat (SNH), which provides spatiotemporal continuity of nesting and foraging resources (Ricketts et al., 2008; Kennedy et al., 2013).

Wild bees are declining (Goulson et al., 2015; Zattara and Aizen, 2021) yet the production of pollinator-dependent crops is increasing concurrently (Aizen and Harder, 2009). Especially long-tongued species of bumble bees are declining in Europe (Dupont et al., 2011; Bommarco et al., 2012), probably largely as a result of loss of SNH rich in Fabaceae

plants, which long-tongued bumble bee species are specialized in gathering pollen from (Goulson et al., 2005). These trends suggest that pollen limitation, due to insufficient insect pollination, is increasingly limiting crop yields, especially for crops benefitting from visits by long-tongued bumble bees, but this is poorly documented. Pollen limitation in crops is usually not experimentally quantified, but instead inferred from positive correlations between bee abundances and crop yields (or proxies thereof) across sites (Garibaldi et al., 2013, 2016; Reilly et al., 2020, but see Gemmill-Herren and Biesmeijer, 2014). However, an important caveat of such a correlative approach is that alternative hidden drivers of crop production that correlate with bee abundance, such as pest control due to shared environmental drivers (Lundin et al., in press), cannot be excluded from being responsible for the relationships observed (Petersen and Nault, 2014).

Faba bean (*Vicia faba* minor L.) is an important nitrogen-fixing legume crop grown worldwide, which improves soil fertility and produces protein-rich seeds used for fodder and human consumption (Jensen et al., 2010; Karkanis et al., 2018). Faba bean is partially

---

dependent on insect pollinators for pollen transfer (Stoddard and Bond, 1987; Free, 1993). Honey bees and bumble bees are the most common pollinators of faba bean in Northern Europe (Poulsen, 1973; Bartomeus et al., 2014; Garratt et al., 2014). Bees display variation in functionally important foraging behaviors when visiting faba bean (Tasei, 1976; Marzinzig et al., 2018). They can either (1) legitimately visit flowers whereby the bee inserts its proboscis into the opening of the corolla to collect pollen and nectar (Fig. 1), (2) rob nectar whereby the bee extracts nectar through a pierced hole at the base of the corolla without getting in contact with the flower's sexual parts, or (3) collect nectar from extra-floral nectaries (EFN) located on stipules below the flowers. Legitimate visits are the most beneficial for crop pollination, since it is the only behavior, which facilitates pollen outcrossing (Kendall and Smith, 1975). Nonetheless, nectar robbing is more beneficial than no visits at all, likely because visitation by nectar robbing bees promotes self-pollination of the flower (Kendall and Smith, 1975). There is no evidence, however, that EFN visits contribute to pollination. Bee species differ in their dominant foraging behavior, with long-tongued bumble bees almost exclusively visiting flowers legitimately, whereas short-tongued bumble bees and honey bees predominantly rob nectar or visit EFN (Tasei, 1976; Marzinzig et al., 2018). Because bumble bees are more abundant in complex landscapes with less arable land and more SNH, the frequency of legitimate flower visits might be higher in faba bean fields in complex landscapes, but this has not been tested.

Estimates of the benefit of insect pollination for plant reproduction in faba bean vary greatly from zero or even negative (Bishop et al., 2020) to up to 185% yield increases (Nayak et al., 2015), with several more intermediate estimates between these extremes (Riedel and Wort, 1960; Free, 1966; Poulsen, 1975; Cunningham and Le Feuvre, 2013; Bartomeus et al., 2014). Because of this great variation in pollinator-dependency, the benefit of insect pollination in modern faba bean cultivars remains unclear (but see Bishop and Nakagawa, in press). Faba bean is, in addition, a suitable model crop to experimentally quantify pollen limitation, as each plant produces a reasonable number of flowers (ca 50–80, Free, 1993), which can be pollinated by hand in the field (Birkin and Goulson, 2015).

Our aims were to (1) compare the abundances of faba bean pollinators and their foraging behaviors between simple landscapes dominated by arable fields and complex landscapes with more SNH, (2) quantify the pollinator-dependence of the crop, and (3) determine whether plant reproduction is limited by insufficient pollination by insects. We expected (1) higher abundances of bumble bees and pollinators legitimately visiting flowers in complex landscapes with more SNH, (2) higher bean mass per plant in open-pollinated plants compared with plants where insect pollinators were excluded from visiting flowers, and finally (3) that hand pollination of open-pollinated plants would increase bean mass per plant in simple but not complex landscapes, due to insufficient ambient levels of insect pollination in simple landscapes.

Fig. 1. *Bombus terrestris* agg. worker legitimately visiting a faba bean (*Vicia faba*) flower.

2. Materials and methods

2.1. Study design

We conducted the study in 20 conventionally managed faba bean fields of the cultivar Tiffany (Scandinavian Seed) in the province of Västergötland in southwestern Sweden in 2018 (n = 10) and 2019 (n = 10, Fig. 2). We selected this cultivar because it is the most commonly grown in the area. Fields were selected along a gradient of landscape complexity, with proportion of SNH and arable land within 2 km from the each field center varying from 0.013 to 0.67 and from 0.30 to 0.91, respectively. All field sites were at least 2 km apart. Faba bean field sizes varied between 5 and 40 ha. Proportion of SNH was strongly negatively related to proportion of arable land across fields (r = 0.97, p < 0.001), while faba bean field size tended to be negatively correlated with proportion of SNH (r = − 0.40, p = 0.083) and positively correlated with proportion of arable land (r = 0.40, p = 0.077). The tendency for larger field sizes in simple landscapes with less SNH was not due to a bias in the selection of fields, because field sizes in simple landscapes are on average larger than in complex landscapes (Persson et al., 2010). Due to the potential relationship between landscape complexity and faba bean field size, we included field size as an additional covariate in all statistical analyses.

The proportions of SNH and arable land were quantified within a radius of 2 km from each field center. SNH included pastures and forests, which both are important habitat types for bumble bees (Öckinger and Smith, 2007; Proesmans et al., 2019; Söber et al., 2020). The proportions of pastures and arable fields were calculated using data obtained from the Integrated Administration and Control System, administered by the Swedish Board of Agriculture. To estimate forest cover we used a digitized map layer (Terrängkartan, Lantmäteriet, Gävle) in ArcMap 10.4.1 (ESRI, Redlands, CA). Pesticide use was uncommon across our fields because most farmers had committed to not use pesticides in faba bean fields as part of agri-environmental schemes. In one field, a herbicide was applied early in the season, and in another field, an insecticide against broad bean weevil (*Bruchus rufimanus*) was applied during late crop bloom. The insecticide was, however, not applied in our sampling area (see below). Managed honey bees are common in the area, but none of our experimental fields were supplemented with honey bee hives.

2.2. Pollinator abundances and foraging behavior

Pollinators were surveyed by walking along one transect in each field for 10 min net observation time, stopping the clock for handling caught insects. Four to eight pollinator surveys were conducted per field during crop bloom. All insects that visited faba bean flowers or EFN were collected with a net for later identification in the laboratory using Løken (1973), Prys-Jones and Corbet (1986), Edwards and Jenner (2005) and Falk (2015). Bumble bee species were categorized as having short (< 7 mm) or long (> 7 mm) tongues based on measurements reported in Persson et al. (2015). Honey bees were, however, not collected but instead identified and counted directly in the field. Transects were 50 m long and 2 m wide and situated 50 m into the field and parallel to the field edge. Surveys were conducted between June 12 and July 4 in 2018 and June 13 and July 3 in 2019 between 9.00 and 19.00 hrs when temperatures were at least 15 °C, wind speeds less than 8 m s^{-1} (four or lower on the Beaufort scale) and skies at least partly sunny or brightly overcast. For each observation, we noted whether insects were legitimately visiting flowers, robbing nectar from flowers or collecting nectar from EFN. Apart from bees, we observed 13 wasp individuals and one hoverfly visiting EFN, and three moths and two butterflies legitimately visiting flowers, but these non-bee insects were not considered further in any analyses due to their low numbers. *Bombus terrestris*, *B. lucorum*, *B. cryptarum* and *B. magnus* were treated as one species complex, denoted as *B. terrestris* agg., due to difficulties separating collected specimens of these species morphologically (Murray et al., 2008). Crop
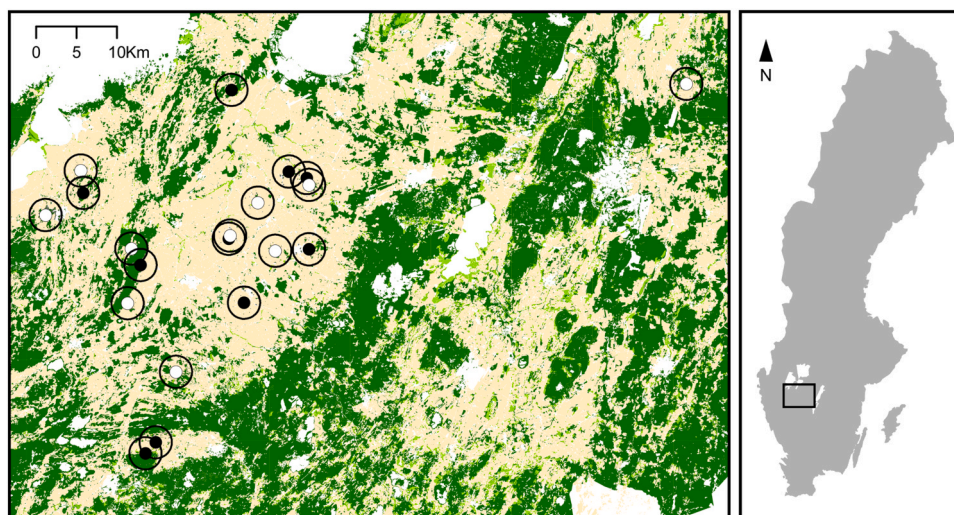
Fig. 2. Faba bean field locations in Västergötland (left panel), southwestern Sweden (right panel) in 2018 (white circles) and 2019 (black circles). Arable land is shown in beige, forest in dark green and pastures in light green. Circles around fields indicate the landscape buffers with 2 km radii from focal fields. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

bloom was determined alongside each pollinator survey by counting the number of open faba bean flowers in four 0.36 m^2 quadrats per transect.

2.3. Pollination treatments

In each transect, we selected five (2018) or six (2019) quadruplets of faba bean plants of similar height and growth stage (Weber and Bleiholder, 1990) shortly before the onset of crop bloom. Plants within quadruplets were ca. 1 m apart and quadruplets were separated by ca. 10 m along the transect. Two plants in each quadruplet were excluded from insect pollination by bagging them with a tulle net (2 by 2 mm mesh size), while the other two plants remained unbagged and open to insect pollination. Bags were adjusted regularly during crop bloom so that only open flowers remained bagged, and we removed the bags when all flowers on the plant had started to wilt. In addition, we hand-pollinated all open flowers on one bagged and one open plant in each quadruplet every second or every third day during crop bloom. Because faba bean flowers are open for 3 days or more (Osborne et al., 1997), we estimated that each flower on hand-pollinated plants received supplemental pollen at least once. Saturating all flowers of a plant with pollen is important when quantifying pollen limitation. This is because the degree of pollen limitation might be overestimated if only a subset of the flowers on a plant receive supplemental pollen, due to within-plant reallocation of resources to the hand-pollinated flowers (Knight et al., 2006). The bagged plus hand-pollinated treatment was included to verify the hand pollination and bagging treatments. If bagging successfully removed insect pollination without having any additional side effects, and hand pollination successfully removed pollen limitation, then we expected plant reproductive output to be equal in both hand pollination treatments.

The procedure for hand pollination followed details described in Birkin and Goulson (2015). Anthers visibly confirmed to contain pollen were removed from nearby non-experimental donor plants of the same cultivar in the field. Open flowers on hand-pollinated plants were opened by gently pulling down the lower petals (wings and keel) such that the anthers of the donor flower could be brushed across the stigma of the experimental flower. No more than three experimental flowers were hand-pollinated with anthers of the same donor flower (Birkin and Goulson, 2015) to avoid depletion of the donor pollen. Experimental plants were harvested at pod maturity and placed in individual paper bags. In the laboratory, we dried plants at 65 °C for 48 h, counted pods per plant and beans per pod and weighed dry bean mass per plant. We

calculated individual bean weight by dividing bean mass with the total number of beans per plant.

2.4. Crop yield

To estimate faba bean yield, we manually harvested faba bean pods from four 0.36 m^2 quadrats randomly placed in each transect shortly before farmers harvested fields. Pods were dried at 65 °C for 48 h, after which all beans were weighted. Crop yield was recalculated and expressed as kg dry beans per hectare.

2.5. Statistical analyses

Pollinator data was summed across the four to eight surveys in each field due to low numbers of observations in individual survey rounds, and analyzed using generalized linear models. Response variables were honey bee abundance, bumble bee abundance, bumble bee species richness, abundance of legitimate pollinators, nectars robbers and EFN visitors as well as the proportions of each of the three foraging behaviors. We chose to analyze both absolute abundances and proportions of foraging behaviors. This is because they are complimentary measures, where the abundances of behaviors are functionally important for pollination, whereas the proportions are measures of average community behaviors after controlling for any effects of overall abundances. Poisson distribution with a log link was used for species richness, negative binomial distributions and log links were used for abundances and binomial distributions with logit links were used for proportions. We chose negative binomial distributions for abundances as the data was overdispersed for Poisson distributions. For the binomial models, the ratio of Chi-square and its degrees of freedom indicated that the models were overdispersed, and thus we added an extra observation level random effect (random _residual_) to the models to account for this (Littell et al., 2006). Explanatory variables were proportion of SNH and year (2018 or 2019). Crop bloom (average number of faba bean flower per m^2 across the survey rounds in each field) and field size (ha) were added as covariates to the models but were only retained in final models if they had a significant effect (p < 0.05). The ln-transformed number of survey rounds was added as an offset to abundance and species richness models to account for the uneven sampling effort among fields (Schabenberger, 2005).

Pollination data was averaged per plant and analyzed using general and generalized linear mixed models. Response variables were pods per

plant, beans per plant, beans per pod, weight per bean and bean mass per plant. Negative binomial distribution and a log link was used for pods per plant and beans per plant and normal distributions with identity links were used for beans per pod, weight per bean and bean mass per plant. We chose negative binomial distribution for pods per plant and beans per plant as the data was overdispersed and the model did not converge, respectively with Poisson distribution. Explanatory variables were year (2018 or 2019), proportion of SNH, pollination treatment (bagged, open-pollinated, bagged plus hand-pollinated or open- plus hand-pollinated) and the interactions between proportion of SNH and pollination treatment, and between year and pollination treatment. Field size (ha) was added as a covariate to the models but was only retained in final models if it had a significant ($p < 0.05$) effect. Models were simplified by removing non-significant ($p > 0.05$) interactions. Wherever pollination treatment was involved in a significant interaction with year or landscape ($p < 0.05$), its simple main effects were examined separately for each year or landscape type using post hoc tests. Random factors were field and plant quadruplet identity nested within field. Significant effects of pollination treatment ($p < 0.05$) were followed by pairwise comparisons with Tukey adjustment.

Crop yield data was averaged across each field and analyzed using general linear models. The response variable was crop yield (kg dry beans per hectare), using normal distribution with an identity link. Explanatory variables were total bee abundance per transect, legitimate flower visitor abundance per transect and year. We also tested for quadratic relationships between total and legitimate flower visitor abundances and crop yield. Models were simplified by removing non-significant ($p > 0.05$) quadratic terms.

All statistical analyses were performed in SAS 9.4 (Proc Glimmix) for Windows (SAS, Cary, NC). Model assumptions were checked following Zuur et al. (2010). Variance inflation factors were below 2.3 in all cases. Degrees of freedom were estimated with the Kenward-Roger method (Littell et al., 2006).

3. Results

3.1. Pollinators

We observed 706 honey bees (76%), 227 bumble bees (24%) representing 10 species or species groups, of which 91% were short-tongued and 9% long-tongued species, and 2 solitary bees (< 1%) visiting faba bean flowers or EFN (Table S1).

Bumble bee abundance was positively related to, and total bee abundance (bumble bees, honey bees and solitary bees) tended to be positively related to proportion of SNH in the landscape (Fig. 3a, b, Table 1). Honey bee abundance and bumble bee species richness was not related to proportion of SNH, field size, crop bloom or year (Tables 1 and 2). Legitimate flower visitor and nectar robber abundance also tended to be positively related to proportion of SNH (Fig. 3c, d, Table 1), whereas EFN visitor abundance was not related to proportion of SNH, field size, crop bloom or year (Tables 1 and 2). The proportion of legitimate flower visitors, nectar robbers of EFN visitors was not related to proportion of SNH, field size, crop bloom or year (Tables 1 and 2).

3.2. Pollination treatments

The effects of pollination treatments differed between years and yield components. Pods per plant and beans per plant were only affected
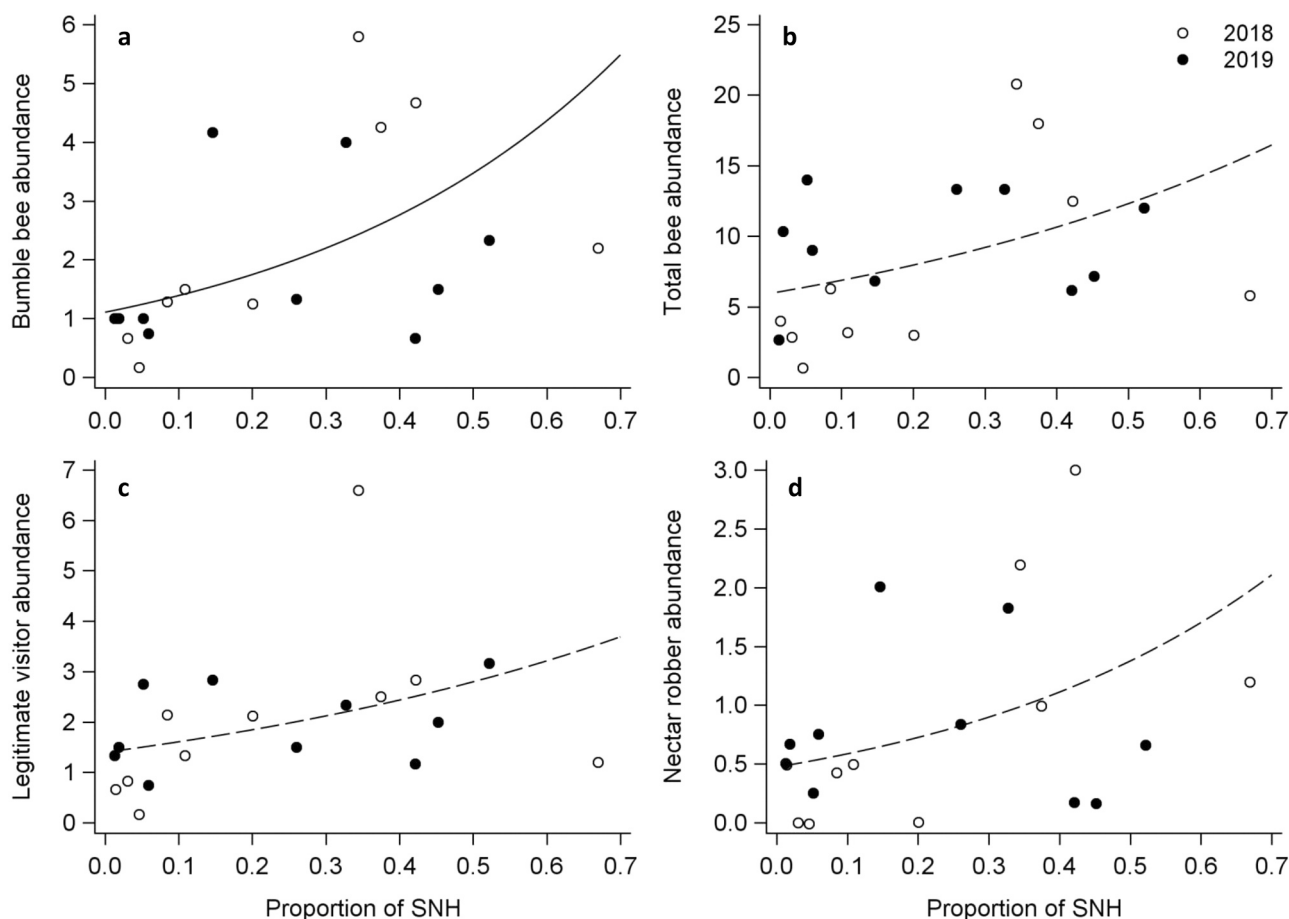

Fig. 3. (a) Bumble bee abundance increased (solid line) and (b) total bee abundance, (c) legitimate visitor abundance and (d) nectar robber abundance tended to increase (dashed lines) with proportion of SNH habitat in the landscape. All abundances are mean number of individuals per transect.

Table 1

Statistical test results with F-values, numerator and denominator degrees of freedom (df) and p-values for the effects of year (2018 or 2019), crop bloom (average number of open faba bean flowers per m^2), field size (ha) and proportion of semi-natural habitat (SNH) on the number of honey bees, bumble bees, bumble bee species, total bees, legitimate flower visitors, nectar robbers and EFN visitors per transect, as well as the proportions of each foraging behavior. Significant effects, where $p < 0.05$, are indicated in bold.

	Year		Crop bloom		Field size		Prop. SNH	
	F_{df}	p	F_{df}	p	F_{df}	p	F_{df}	p
Honey bee abundance	$2.19_{1;17}$	0.157	$0.20_{1;16}$	0.662	$0.40_{1;16}$	0.537	$2.75_{1;17}$	0.116
Bumble bee abundance	$0.12_{1;17}$	0.735	$0.40_{1;16}$	0.538	$0.01_{1;16}$	0.935	**$6.95_{1;17}$**	**0.017**
Bumble bee richness	$1.86_{1;17}$	0.190	$0.31_{1;16}$	0.585	$0.67_{1;16}$	0.424	$0.67_{1;17}$	0.424
Total bee abundance	$1.49_{1;17}$	0.239	$0.21_{1;16}$	0.650	$0.34_{1;16}$	0.569	$4.29_{1;17}$	0.054
Legitimate v. abundance	$0.00_{1;17}$	0.981	$2.87_{1;16}$	0.110	$0.00_{1;16}$	0.953	$3.67_{1;17}$	0.072
Nectar robber abundance	$0.13_{1;17}$	0.720	$0.01_{1;16}$	0.918	$0.02_{1;16}$	0.902	$3.18_{1;17}$	0.092
EFN visitor abundance	$2.05_{1;17}$	0.171	$0.01_{1;16}$	0.933	$0.56_{1;16}$	0.467	$2.94_{1;17}$	0.105
Prop. legitimate visitors	$1.88_{1;17}$	0.188	$1.92_{1;16}$	0.185	$0.21_{1;16}$	0.651	$0.20_{1;17}$	0.658
Prop. nectar robbers	$0.55_{1;17}$	0.468	$0.22_{1;16}$	0.646	$0.11_{1;16}$	0.746	$0.25_{1;17}$	0.622
Prop. EFN visitors	$2.12_{1;17}$	0.164	$0.62_{1;16}$	0.442	$0.30_{1;16}$	0.594	$0.01_{1;17}$	0.930

Table 2

Number of honey bees, bumble bees, bumble bee species, total bees, legitimate flower visitors, nectar robbers or EFN visitors per transect, as well as the proportions of each of the three foraging behaviors in relation to year (2018 or 2019), crop bloom (average number of open faba bean flowers per m^2), field size (ha) and proportion of semi-natural habitat (SNH). Numbers indicate least square mean values and the 95% confidence limits within parenthesis back-transformed using the ilink option for categorical variables and the model-estimated slopes for continuous variables with standard errors within parenthesis. Significant effects, where $p < 0.05$, are indicated in bold.

	Year 2018	2019	Crop bloom Slope	Field size Slope	Prop. SNH Slope
Honey bee abundance	4.9 (3.1–7.9)	7.9 (4.9–13)	-0.0019 (0.0043)	-0.012 (0.019)	1.5 (0.90)
Bumble bee abundance	2.0 (1.3–3.0)	1.8 (1.3–2.8)	-0.0023 (0.0037)	0.0017 (0.020)	**2.2 (0.85)**
Bumble bee richness	0.54 (0.37–0.79)	0.37 (0.23–0.59)	0.0016 (0.0029)	-0.015 (0.018)	0.57 (0.69)
Total bee abundance	6.9 (4.5–10)	9.7 (6.4–15)	-0.0017 (0.0037)	-0.010 (0.018)	1.7 (0.81)
Legitimate v. abundance	1.9 (1.3–2.8)	1.9 (1.3–2.8)	-0.0050 (0.0030)	-0.00096 (0.016)	1.4 (0.72)
Nectar robber abundance	0.71 (0.36–1.4)	0.83 (0.43–1.6)	-0.00061 (0.0059)	0.0041 (0.033)	2.3 (1.3)
EFN visitor abundance	4.2 (2.6–7.1)	6.9 (4.2–11)	-0.00041 (0.0048)	-0.016 (0.021)	1.7 (0.97)
Prop. legitimate visitors	0.29 (0.20–0.39)	0.21 (0.15–0.29)	-0.0060 (0.0044)	0.0097 (0.021)	-0.39 (0.86)
Prop. nectar robbers	0.11 (0.062–0.19)	0.085 (0.047–0.15)	0.0027 (0.0058)	0.0096 (0.029)	0.59 (1.2)
Prop. EFN visitors	0.60 (0.48–0.71)	0.71 (0.60–0.79)	0.0037 (0.0047)	-0.012 (0.023)	0.080 (0.90)

by year, with more pods per plant and beans per plant in 2019 compared with 2018 (Tables 3 and 4). Beans per pod was affected by an interaction between pollination treatment and year, such that in 2019 beans per pod was lower in bagged plants compared with open-pollinated, bagged plus hand-pollinated and open- plus hand-pollinated plants, whereas in 2018 there were no differences among pollination treatments (Fig. 4a, Table 3). Weight per bean was also affected by an interaction between pollination treatment and year, such that in 2019 weight per bean was higher in bagged plants compared with open-pollinated, bagged plus hand-pollinated and open- plus hand-pollinated plants, whereas in 2018 there were no differences among pollination treatments (Fig. 4b, Table 3). Bean mass per plant was only affected by year, with higher bean mass per plant in 2019 compared with 2018 (Tables 3 and 4). Field

size tended to increase beans per plant, beans per pod and bean mass per plant (Tables 3 and 4). Boxplots with raw data from the pollination experiment are presented in Fig. S1.

3.3. Crop yield

Crop yield was higher in 2019 compared with 2018 ($F = 44.15_{1;16}$, $p < 0.001$), but was not related to total bee abundance ($F = 0.49_{1;16}$, $p = 0.494$), legitimate flower visitor abundance ($F = 1.18_{1;16}$, $p = 0.293$), or quadratic terms of either total bee abundance ($F = 0.16_{1;15}$, $p = 0.698$) or legitimate flower visitor abundance ($F = 0.20_{1;15}$, $p = 0.659$, Fig. S2, Table 5).

Table 3

Statistical test results with F-values, numerator and denominator degrees of freedom (df) and p-values for the effects of year (2018 or 2019), proportion of semi-natural habitat (SNH), field size (ha), pollination treatment (bagged, open-pollinated, bagged plus hand-pollinated or open- plus hand-pollinated) and interactions between pollination treatment and proportion of SNH or year respectively on the number of pods per plant, beans per plant, beans per pod, weight per bean (g) and bean mass per plant (g). Where pollination treatment was involved in a significant interaction with year, results from post hoc tests of its simple main effects are reported separately for each year using the slice option. Significant effects, where $p < 0.05$, are indicated in bold.

	Pods per plant		Beans per plant		Beans per pod		Weight per bean (g)		Bean mass per plant (g)	
	F_{df}	p	F_{df}	p	F_{df}	p	F_{df}	p	F_{df}	p
Year	**$40.47_{1;16}$**	**< 0.001**	**$36.92_{1;17}$**	**< 0.001**	**$7.18_{1;17}$**	**0.016**	**$5.53_{1;17}$**	**0.031**	**$80.59_{1;17}$**	**< 0.001**
Proportion SNH	$0.67_{1;17}$	0.424	$0.28_{1;17}$	0.602	$0.36_{1;17}$	0.557	$2.36_{1;17}$	0.143	$0.19_{1;17}$	0.670
Field size	$2.81_{1;16}$	0.113	$3.55_{1;16}$	0.078	$4.42_{1;17}$	0.051	$0.83_{1;17}$	0.376	$3.63_{1;16}$	0.075
Pollination treatment (P)	$0.50_{3;339}$	0.680	$0.99_{1;318}$	0.400	**$6.88_{3;323}$**	**< 0.001**	**$18.10_{3;322}$**	**< 0.001**	$1.16_{3;406}$	0.323
P: SNH	$0.85_{3;369}$	0.468	$0.11_{2;325}$	0.955	$1.21_{3;320}$	0.307	$0.27_{3;320}$	0.850	$0.62_{3;403}$	0.601
P: Year	$0.45_{3;427}$	0.717	$0.93_{3;347}$	0.425	**$2.91_{3;323}$**	**0.035**	**$6.84_{3;322}$**	**< 0.001**	$0.43_{3;403}$	0.730
P: 2018	–	–	–	–	$0.56_{3;323}$	0.641	$1.64_{3;323}$	0.181	–	–
P: 2019	–	–	–	–	**$10.20_{3;322}$**	**< 0.001**	**$25.75_{3;322}$**	**< 0.001**	–	–

Table 4

Number of pods per plant, beans per plant, beans per pod, weight per bean (g) and bean mass per plant (g) in relation to year (2018 or 2019), proportion of SNH, field size and pollination treatment (bagged, open-pollinated, bagged plus hand-pollinated or open- plus hand-pollinated). Numbers indicate least square mean values and the 95% confidence limits within parenthesis back-transformed using the ilink option for categorical variables and model-estimated slopes with standard errors within parenthesis for continuous variables. Significant effects, where p < 0.05, are indicated in bold. Pollination treatments indicated with different letters are significantly different from each other. Note that there are in addition significant interactions between pollination treatment and year on beans per pod and weight per bean, which are reported in Fig. 4.

| Variable	Level	Pods per plant	Beans per plant	Beans per pod	Weight per bean (g)	Bean mass per plant (g)
Year	2018	**4.2 (3.3–5.3)**	**12 (9.2–16)**	**2.9 (2.7–3.1)**	**0.37 (0.33–0.41)**	**5.0 (3.3–6.7)**
	2019	**11 (8.8–14)**	**35 (27–46)**	**3.2 (3.1–3.4)**	**0.43 (0.39–0.46)**	**15 (13–17)**
Proportion SNH	Slope	-0.32 (0.39)	-0.24 (0.46)	0.18 (0.30)	-0.097 (0.063)	-1.3 (2.9)
Field size	Slope	0.016 (0.0097)	0.021 (0.011)	0.015 (0.0071)	0.0015 (0.0016)	0.13 (0.070)
Pollination treatment	Bagged (B)	6.9 (5.8–8.2)	19 (16–24)	**2.9 (2.7–3.0) a**	**0.46 (0.43–0.49) a**	11 (9.3–12)
	Open (O)	6.7 (5.6–8.0)	21 (17–25)	**3.1 (3.0–3.3) b**	**0.38 (0.35–0.41) b**	10 (8.2–11)
	B + Hand	7.0 (5.9–8.3)	22 (18–27)	**3.1 (3.0–3.3) b**	**0.38 (0.35–0.41) b**	10 (8.8–12)
	O + Hand	6.5 (5.5–7.8)	21 (17–25)	**3.2 (3.0–3.3) b**	**0.38 (0.35–0.41) b**	10 (8.0–11)
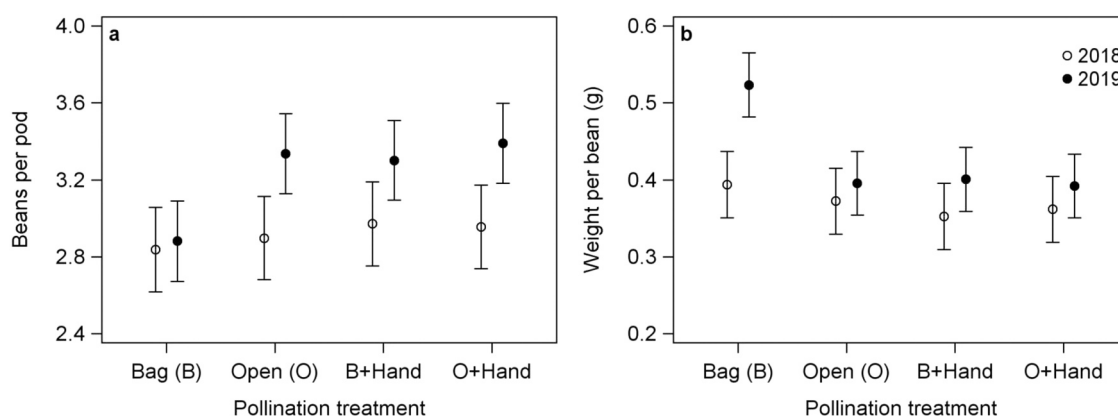
Fig. 4. (a) Beans per pod was higher in open-pollinated, bagged plus hand-pollinated and open- plus hand-pollinated compared with bagged plants in 2019, but not 2018. (b) Weight per bean was lower in open-pollinated, bagged plus hand-pollinated and open- plus hand-pollinated compared with bagged plants in 2019, but not 2018.

Table 5

Crop yield (kg dry beans per hectare) in relation to year, total bee abundance, legitimate flower visitor abundance, total bee abundance (squared) and legitimate flower visitor abundance (squared) per transect. Numbers indicate least square mean values and the 95% confidence limits within parenthesis back-transformed using the ilink option for categorical variables and the model-estimated slopes for continuous variables with standard errors within parenthesis. Significant effects, where p < 0.05, are indicated in bold.

Variable	Level	Estimate
Year	2018	**2100 (1400–2800)**
	2019	**5100 (4400–5700)**
Total bee abundance	Slope	44 (62)
Legitimate visitor abundance	Slope	-270 (250)
Total bee abundance^2	Slope	-3.8 (9.5)
Legitimate visitor abundance^2	Slope	-34 (75)

4. Discussion

We found that complex landscapes with more SNH benefitted bumble bee abundances, and tended to benefit total bee abundance, in faba bean fields, which is in line with findings by Nayak et al. (2015) and Raderschall et al. (2021a). Increased bumble bee abundances in complex landscapes were likely supported by higher amounts of semi-natural grasslands and forest patches, and more abundant field border vegetation as a result of smaller field sizes, which provided nesting and foraging resources (Öckinger and Smith, 2007; Rundlöf et al., 2008; Kennedy et al., 2013; Hass et al., 2018; Martin et al., 2019; Söber et al., 2020). In addition, landscape complexity tended to favor a higher abundance, but not proportion, of bees legitimately visiting flowers and

robbing nectar. The possibly higher abundance of legitimate flower visitors in complex landscapes with more SNH was likely driven by *B. terrestris* agg. abundances, which was the most common bumble bee species group observed legitimately visiting flowers. In contrast, long-tongued bumble bees such as *B. hortorum* and *B. subterraneus* were not as important for pollination as initially hypothesized. Although these two species were exclusively observed legitimately visiting flowers, the total number of legitimate visits from *Apis mellifera* and *B. terrestris* agg. were higher due to their overall much higher abundances (see also Kleijn et al., 2015). *B. terrestris* agg. was also likely influential for the possibly positive relationship between proportion of SNH in the landscape and the abundance of nectar robbers, as it was the most common species group observed robbing nectar. Although legitimate flower visits are most beneficial for pod set in faba bean, likely due to promoting cross-pollination, robbed flowers still set more pods than unvisited flowers, probably because nectar robbing increases self-pollination of the flower (Kendall and Smith, 1975). Taken together, our results indicate that the supply of pollination services to faba bean is higher in complex landscapes with more SNH.

The pollination experiment revealed, however, that bean mass per plant did not differ between bagged, open-pollinated, bagged plus hand-pollinated or open- plus hand-pollinated plants. While open-pollinated, bagged plus hand-pollinated and open- plus hand-pollinated plants had a higher number of beans per pod compared with autonomously self-pollinated (bagged) plants in 2019, the individual bean weight was higher in bagged plants compared with other treatments in 2019, thus compensating for the lower number of beans per pod. This suggests that insect and hand pollination increase fertilization, but that faba bean plants are able to compensate for reduced pollination by a greater

investment into individual bean weight. A higher individual bean weight following lack of insect pollination in faba bean has been found previously (Free, 1966; Poulsen, 1975; Hebblethwaite et al., 1984). The environmental context-dependency and physiological limits to this compensation mechanism are poorly known. Compensation should, however, be more likely when insect pollination benefits on seed set are limited and the supply of other resources (light, nutrients, water) is high late in the season, during the pod-filling stage of the crop. We found no effect of pollination treatment on any of the yield parameters in 2018. Due to unusually dry and warm weather during spring and summer (Toreti et al., 2019), average yields in 2018 were on average less than half of those in 2019 in our fields, and this might have canceled any pollination benefit in our experiments in 2018. This would be in contrast with experimental findings that heat-stress increase pollinator dependency in faba bean (Bishop et al., 2016, 2017). In the experiments performed by Bishop et al. (2016, 2017), non-stressed pollen donor plants from which pollinators could transfer pollen to stressed plants were available in both heat-stressed and control treatments. In commercial faba bean fields, the availability of such non-stressed plants might be limited during a major drought such as that in 2018, in which case insect pollination would not be able to overcome yield limitation caused by lack of fertile pollen.

In general, the insect pollination benefit in faba bean is extraordinary complex and variable, with large variation both within and among cultivars (Bishop et al., 2020). Some of this variation and context-dependency is driven by cultivar differences (Bishop and Nakagawa, in press), and variation in abiotic factors such as soil conditions that modify the pollination benefit (St-Martin and Bommarco, 2016). In experiments with the same cultivar (Tiffany) as here, where cages in a faba bean field were either supplemented with bumble bees or autonomously self-pollinated, we found clear benefits of insect pollination on both bean mass per plant and beans per pod, but no effect on individual bean weight (Raderschall et al., 2021b). The insect pollination benefit was conserved across experimentally established levels of water stress and aphid herbivory (Raderschall et al., 2021b). This raises the question whether pollinator dependency can vary also between different seed batches of the same cultivar, or if unmeasured environmental conditions such as *Bruchus rufimanus* pest pressure, differed between the two studies and modified the outcome.

To our knowledge, this is the first study where pollen limitation of faba bean has been experimentally explored by hand-pollinating entire faba bean plants in crop fields. Since we did not find any evidence for pollinator-dependency of crop productivity, we are limited in what conclusions we can make regarding faba bean yield limitation due to insufficient pollination. The similar positive response of open-pollinated, bagged plus hand-pollinated and open- plus hand-pollinated plants on beans per pod in 2019, suggests, however, that ambient pollinator abundances were sufficient for pollen delivery and fertilization even in simple landscapes with lower abundances of flower-visiting bees. Bean mass per plant could have been limited by other factors across all landscapes in both years, such as lack of water, nutrients or pest control, such that insect pollination only would have a positive effect if these other yield-limiting factors were overcome. This would be in contrast with earlier findings that crop yields are often co-limited by lack of pollination and other ecosystem services (Garibaldi et al., 2018). Proportion of SNH in the landscape had no impact on any yield components, either as a main effect or in interaction with the pollination treatments. This suggests that the proportion of SNH mainly was associated with pollination service delivery, but not other yield-affecting factors such as soil fertility or pest control. Hand pollination of bagged plants increased beans per pod to the levels of open-pollinated plants in 2019, indicating that we can exclude errors in the hand pollination method we used as a factor affecting our results. Our results are in contrast with earlier experiments, where partial hand pollination of open-pollinated faba bean plants in commercial crop fields generally increased seed set of hand pollinated flowers (Free and Williams, 1976).

In summary, growing faba bean in complex landscapes, characterized by high proportions of SNH, seems to increase the supply of pollination services to the crop because bumble bee abundances increase, and the abundance of legitimate flower visitors tend to increase. Yet, faba bean fields sown with the cultivar Tiffany, when grown under the conditions of the current study, had no demand for insect pollination, as lower numbers of beans per pod was compensated for by higher individual bean weight. This is in spite of recent evidence that plants of the same cultivar benefit from insect pollination (Raderschall et al., 2021b). We conclude that to be able to characterize the value of pollination services in faba bean we need a better understanding of how pollinator-dependency varies across and within modern cultivars, and how environmental conditions modify this pollinator-dependency (Tamburini et al., 2019).

CRediT authorship contribution statement

Ola Lundin: Conceptualization (lead), Data curation (lead), Formal analysis (lead), Funding acquisition (lead), Investigation (lead), Methodology (lead), Project administration (lead), Resources (lead), Validation (lead), Visualization (equal), Writing - original draft (lead), Writing - review & editing (equal). **Chloé A. Raderschall**: Formal analysis (supporting), Methodology (supporting), Visualization (equal), Writing - review & editing (equal).

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.

Acknowledgements

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107417.

References

Aizen, M.A., Harder, L.D., 2009. The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr. Biol. 19, 915–918.

Bartomeus, I., Potts, S.G., Steffan-Dewenter, I., Vaissiere, B.E., Woyciechowski, M., Krewenka, K.M., Tscheulin, T., Roberts, S.P.M., Szentgyörgyi, H., Westphal, C., Bommarco, R., 2014. Contribution of insect pollinators to crop yield and quality varies with agricultural intensification. PeerJ 2, e328.

Birkin, L., Goulson, D., 2015. Using citizen science to monitor pollination services. Ecol. Entomol. 40, 3–11.

Bishop, J., Jones, H.E., Lukac, M., Potts, S.G., 2016. Insect pollination reduces yield loss following heat stress in faba bean (*Vicia faba* L.). Agric. Ecosyst. Environ. 220, 89–96.

Bishop, J., Jones, H.E., O'Sullivan, D.M., Potts, S.G., 2017. Elevated temperature drives a shift from selfing to outcrossing in the insect-pollinated legume, faba bean (*Vicia faba*). J. Exp. Bot. 68, 2055–2063.

Bishop, J., Garratt, M.P.D., Breeze, T.D., 2020. Yield benefits of additional pollination to faba bean vary with cultivar, scale, yield parameter and experimental method. Sci. Rep. 10, 2102.

Bishop, J., Nakagawa, S. Quantifying crop pollinator dependence and its heterogeneity using multi-level meta-analysis. J. Appl. Ecol. in press.

Bommarco, R., Lundin, O., Smith, H.G., Rundlöf, M., 2012. Drastic historic shifts in bumble-bee community composition in Sweden. Proc. R. Soc. B 279, 309–315.

Cunningham, S.A., Le Feuvre, D., 2013. Significant yield benefits from honeybee pollination of faba bean (*Vicia faba*) assessed at field scale. Field Crop. Res. 149, 269–275.

Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L.G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L.A., Ghazoul, J.,

Grab, H., Jonsson, M., Karp, D.S., Kennedy, C.M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D.K., Marini, L., Poveda, K., Rader, R., Smith, H.G., Tscharntke, T., Andersson, G.K.S., Badenhausser, I., Baensch, S., Bezerra, L.A., Bianchi, F.J.J.A., Boreux, V., Bretagnolle, V., Caballero-Lopez, B., Cavigliasso, P., Ćetković, A., Chacoff, N.P., Classen, A., Cusser, S., Silva, F.D.S., Groot, G.A., Dudenhöffer, J.H., Ekroos, J., Fijen, T., Franck, P., Freitas, B.M., Garratt, M.P.D., Gratton, C., Hipólito, J., Holzschuh, A., Hunt, L., Iverson, A.L., Jha, S., Keasar, T., Kim, T.N., Kishinevsky, M., Klatt, B.K., Klein, A., Krewenka, K.M., Krishnan, S., Larsen, A.E., Lavigne, C., Liere, H., Maas, B., Mallinger, R.E., Pachon, E.M., Martínez-Salinas, A., Meehan, T.D., Mitchell, M.G.E., Molina, G.A.R., Nesper, M., Nilsson, L., O'Rourke, M.E., Peters, M.K., Plećaš, M., Potts, S.G., Ramos, D.L., Rosenheim, J.A., Rundlöf, M., Rusch, A., Nilsson, A., Scheper, J., Schleuning, M., Schmack, J.M., Sciligo, A.R., Seymour, C., Stanley, D.A., Stewart, R., Stout, J.C., Rundlöf, L., Takada, M.B., Taki, H., Tamburini, G., Tschumi, M., Viana, B.F., Westphal, C., Willcox, B.K., Wratten, S.D., Yoshioka, A., Zaragoza-Trello, C., Zhang, W., Zou, Y., Steffan-Dewenter, I., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5 eaax0121.

Dupont, Y.L., Damgaard, C., Simonsen, V., 2011. Quantitative historical change in bumblebee (*Bombus* spp.) assemblages of red clover fields. PLoS One 6, e25172.

Edwards, E., Jenner, M., 2005. Field guide to the bumblebees of Great Britain and Ireland. Ocelli Limited, Eastbourne.

Falk, S.J., 2015. Field Guide to the Bees of Great Britain and Ireland. Blomsbury, London.

Free, J.B., 1966. The pollination requirements of broad beans and field beans (*Vicia faba*). J. Agric. Sci. 66, 395–397.

Free, J.B., 1993. Insect Pollination of Crops, second ed. Academic Press, London.

Free, J.B., Williams, I.H., 1976. Pollination as a factor limiting the yield of field beans (*Vicia faba* L.). J. Agric. Sci. 87, 395–399.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J. H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipolito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013. Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339, 1608–1611.

Garibaldi, L.A., Carvalheiro, L.G., Vaissiere, B.E., Gemmill-Herren, B., Hipolito, J., Freitas, B.M., Ngo, H.T., Azzu, N., Saez, A., Åström, J., An, J., Blochtein, B., Buchori, D., Chamorro Garcia, F.J., da Silva, F.O., Devkota, K., Fátima Ribeiro, M., Freitas, L., Gaglianone, M.C., Goss, M., Irshad, M., Kasina, M., Pacheco Filho, A.J.S., Piedade Kiill, L.H., Kwapong, P., Nates Parra, G., Pires, C., Pires, V., Rawal, R.S., Rizali, A., Saraiva, A.M., 1975. Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. Science 351, 388–391.

Garibaldi, L.A., Andersson, G.K.S., Requier, F., Fijen, T.P.M., Hipólito, J., Kleijn, D., Pérez-Méndez, N., Rollin, O., 2018. Complementarity and synergisms among ecosystem services supporting crop yield. Glob. Food Sec. 17, 38–47.

Garratt, M.P.D., Coston, D.J., Truslove, C.L., Lappage, M.G., Polce, C., Dean, R., Biesmeijer, J.C., Potts, S.G., 2014. The identity of crop pollinators helps target conservation for improved ecosystem services. Biol. Conserv. 169, 128–135.

Gemmill-Herren, B., Biesmeijer, K., 2014. Introduction to special issue of the Journal of Pollination Ecology on crop pollination deficits. J. Pollinat. Ecol. 12, 0.

Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S., Knight, M.E., 2005. Causes of rarity in bumblebees. Biol. Conserv. 122, 1–8.

Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347, 1255957.

Hass, A.L., Kormann, U.G., Tscharntke, T., Clough, Y., Bosem Baillod, A., Sirami, C., Fahrig, L., Martin, J.L., Baudry, J., Bertrand, C., Bosch, J., Brotons, L., Burel, F., Georges, R., Giralt, D., Marcos-García, M.Á., Ricarte, A., Siriwardena, G., Batáry, P., 2018. Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in Western Europe. Proc. R. Soc. B 285, 20172242.

Hebblethwaite, P.D., Scott, R.K., Kogbe, J.O.S., 1984. The effect of irrigation and bees on the yield and yield components of *Vicia faba* L. In: Hebblethwaite, P.D., Dawkins, T. C.K., Heath, M.C., Lockwood, G. (Eds.), *Vicia faba*: Agronomy, Physiology and Breeding. Springer, Dordrecht, pp. 71–93.

IPBES, 2016. In: Potts, S.G., Imperatriz-Fonseca, V.L., Ngo, H.T. (Eds.), The Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination and Food Production. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn.

Jensen, E.S., Peoples, M.B., Hauggaard-Nielsen, H., 2010. Faba bean in cropping systems. Field Crop. Res. 115, 203–216.

Karkanis, A., Ntatsi, G., Lepse, L., Fernández, J.A., Vågen, I.M., Rewald, B., Alsina, I., Kronberga, A., Balliu, A., Olle, M., Bodner, G., Dubova, L., Rosa, E., Savvas, D., 2018. Faba bean cultivation – revealing novel managing practices for more sustainable and competitive European cropping systems. Front. Plant Sci. 9, 1115.

Kendall, D.A., Smith, B.D., 1975. The pollinating efficiency of honeybee and bumblebee visits to field bean flowers (*Vicia faba* L.). J. Appl. Ecol. 12, 709–717.

Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., Carvalheiro, L.G., Chacoff, N. P., Cunningham, S.A., Danforth, B.N., Dudenhöffer, J.H., Elle, E., Gaines, H.R., Garibaldi, L.A., Gratton, C., Holzschuh, A., Isaacs, R., Javorek, S.K., Jha, S., Klein, A.

M., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L., Neame, L.A., Otieno, M., Park, M., Potts, S.G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B.F., Westphal, C., Wilson, J.K., Greenleaf, S.S., Kremen, C., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecol. Lett. 16, 584–599.

Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A. –M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. Nat. Commun. 6, 7414.

Klein, A.M., Vaissiere, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tscharntke, T., 2007. Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B 274, 303–313.

Knight, T.M., Steets, J.A., Ashman, T.L., 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. Am. J. Bot. 93, 271–277.

Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. SAS System for Mixed Models, second ed. SAS Institute, Cary.

Løken, A., 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). Nor. J. Entomol. 20, 1–218.

Lundin, O., Rundlöf, M., Jonsson, M., Bommarco, R., Williams, N.M. Integrated pest and pollinator management - widening the concept. Front. Ecol. Environ. in press.

Martin, E.A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M.P.D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S.G., Smith, H.G., Al Hassan, D., Albrecht, M., Andersson, G.K.S., Asís, J.D., Aviron, S., Balzan, M.V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E.D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C.F., Duflot, R., Entling, M.H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L.A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., Steffan-Dewenter, I., 2019. The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. Ecol. Lett. 22, 1083–1094.

Marzinzig, B., Brünjes, L., Biagioni, S., Behling, H., Link, W., Westphal, C., 2018. Bee pollinators of faba bean (*Vicia faba* L.) differ in their foraging behaviour and pollination efficiency. Agric. Ecosyst. Environ. 264, 24–33.

Murray, T.E., Fitzpatrick, Ú., Brown, M.J.F., Paxton, R.J., 2008. Cryptic species diversity in a widespread bumble bee complex revealed using mitochondrial DNA RFLPs. Conserv. Genet. 9, 653–666.

Nayak, G.K., Roberts, S.P.M., Garratt, M., Breeze, T.D., Tscheulin, T., Harrison-Cripps, J., Vogiatzakis, I.N., Stirpe, M.T., Potts, S.G., 2015. Interactive effect of floral abundance and semi-natural habitats on pollinators in field beans (*Vicia faba*). Agric. Ecosyst. Environ. 199, 58–66.

Öckinger, E., Smith, H.G., 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. J. Appl. Ecol. 44, 50–59.

Osborne, J.L., Awmack, C.S., Clark, S.J., Williams, I.H., Mills, V.C., 1997. Nectar and flower production in *Vicia faba* L. (field bean) at ambient and elevated carbon dioxide. Apidologie 28, 43–55.

Persson, A.S., Olsson, O., Rundlöf, M., Smith, H.G., 2010. Land use intensity and landscape complexity - analysis of landscape characteristics in an agricultural region in Southern Sweden. Agric. Ecosyst. Environ. 136, 169–176.

Persson, A.S., Rundlöf, M., Clough, Y., Smith, H.G., 2015. Bumble bees show trait-dependent vulnerability to landscape simplification. Biodivers. Conserv. 24, 3469–3489.

Petersen, J.D., Nault, B.A., 2014. Landscape diversity moderates the effects of bee visitation frequency to flowers on crop production. J. Appl. Ecol. 51, 1347–1356.

Poulsen, M.H., 1973. The frequency and foraging behaviour of honeybees and bumble bees on field beans in Denmark. J. Apic. Res. 12, 75–80.

Poulsen, M.H., 1975. Pollination, seed setting, cross-fertilization and inbreeding in *Vicia faba*. J. Plant Breed. 74, 97–118.

Proesmans, W., Bonte, D., Smagghe, G., Meeus, I., Decocq, G., Spicher, F., Kolg, A., Lemke, I., Diekmann, M., Bruun, H.H., Wulf, M., Van Den Berge, S., Verheyen, K., 2019. Small forest patches as pollinator habitat: oases in an agricultural desert? Landsc. Ecol. 34, 487–501.

Prys-Jones, O.E., Corbet, S.A., 1986. Bumblebees. Cambridge University Press, Cambridge.

Raderschall, C.A., Bommarco, R., Lindström, S.A., Lundin, O., 2021a. Landscape crop diversity and semi-natural habitat affect crop pollinators, pollination benefit and yield. Agric. Ecosyst. Environ. 306, 107189.

Raderschall, C.A., Vico, G., Lundin, O., Taylor, A.R., Bommarco, R., 2021b. Water stress and insect herbivory interactively reduce crop yield while the insect pollination benefit is conserved. Glob. Chang. Biol. 27, 71–83.

Reilly, J., Artz, D.R., Biddinger, D., Bobiwash, K., Boyle, N.K., Brittain, C., Brokaw, J., Campbell, J.W., Daniels, J., Elle, E., Ellis, J.D., Fleischer, S.J., Gibbs, J., Gillespie, R. L., Gundersen, K.B., Gut, L., Hoffman, G., Joshi, N., Lundin, O., Mason, K., McGrady, C.M., Peterson, S.S., Pitts-Singer, T.L., Rao, S., Rothwell, N., Rowe, L., Ward, K.L., Williams, N.M., Wilson, J.K., Isaacs, R., Winfree, R., 2020. Crop

production in the USA is frequently limited by a lack of pollinators. Proc. R. Soc. B 287, 20200922.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng, A., Potts, S.G., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? Ecol. Lett. 11, 499–515.

Riedel, I.B.M., Wort, D.A., 1960. The pollination requirement of the field bean (*Vicia faba*). Ann. Appl. Biol. 48, 121–124.

Rundlöf, M., Nilsson, H., Smith, H.G., 2008. Interacting effects of farming practice and landscape context on bumble bees. Biol. Conserv. 141, 417–426.

Schabenberger, O., 2005. Introducing the GLIMMIX procedure for generalized linear mixed models. SAS Users Group International 30, 196.

Sõber, V., Leps, M., Kaasik, A., Mänd, M., Teder, T., 2020. Forest proximity supports bumblebee species richness and abundance in hemi-boreal agricultural landscape. Agric. Ecosyst. Environ. 298, 106961.

St-Martin, A., Bommarco, R., 2016. Soil compaction and insect pollination modify impacts of crop rotation on nitrogen fixation and yield. Basic Appl. Ecol. 17, 617–626.

Stoddard, F.L., Bond, D.A., 1987. The pollination requirements of the faba bean. Bee World 68, 144–152.

Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W.H., Marini, L., 2019. Pollination contribution to crop yield is often context-dependent: a review of experimental evidence. Agric. Ecosyst. Environ. 280, 16–23.

Tasei, J.N., 1976. Les insectes pollinisateurs de la féverole d'hiver (*Vicia faba* equina L.) et la pollinisation des plantes mâle-stérile en production de semence hybride. Apidologie 7, 1–38.

Toreti, A., Belward, A., Perez-Dominguez, I., Naumann, G., Luterbacher, J., Cronie, O., Seguini, L., Manfron, G., Lopez-Lozano, R., Baruth, B., van den Berg, M., Dentener, F., Ceglar, A., Chatzopoulos, T., Zampieri, M., 2019. The exceptional 2018 European water seesaw calls for action on adaptation. Earths Future 7, 652–663.

Weber, E., Bleiholder, H., 1990. Explanations of the BBCH decimal codes for the growth stages of maize, rape, faba beans, sunflowers and peas-with illustrations. Gesunde Pflanz. 42, 308–321.

Zattara, E.E., Aizen, M.A., 2021. Worldwide occurrence records reflect a global decline in bee species richness. One Earth 4, 114–123.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.