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RESEARCH PAPER

Partitioning pollination services to faba bean (*Vicia faba* L.) between managed honeybees and wild bees

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Abstract

Animal pollination of crops is an important ecosystem service provided especially by managed honeybees and wild bees, but the relative importance of these taxa for crop pollination remains debated. Faba bean (*Vicia faba* L.) is a grain legume crop grown worldwide for food and feed which is partially dependent on insects for pollination. I determined the relative contribution of honeybees and wild bees to faba bean pollination. Visitation rates and foraging behaviours of pollinators were measured in a total of 20 faba bean fields over two years (10 fields per year) in Sweden, and the bean mass per flower visit for different pollinator taxa was quantified in a field experiment which was repeated over two years in a single site. By combining information on visitation rates, foraging behaviours and gains in bean mass from single visits to flowers, I estimate that 47% of insect pollination services to faba bean is delivered by honeybees, 40% by short-tongued bumblebees, 6% by long-tongued bumblebees and 8% by solitary bees. I conclude that both managed honeybees and wild bees, especially short-tongued bumblebees, contribute substantially to faba bean pollination in Sweden, and I recommend faba bean farmers to manage for both these pollinator taxa.

Keywords: *Apis mellifera*; *Bombus*; Fava bean; Field bean; Single visit

Introduction

Animal pollination increases yields in approximately three quarters of the world's most common crops and is an important ecosystem service that supports the nutritional needs and wellbeing of people globally (Klein et al., 2007; IPBES 2016). Managed honeybees and wild bees, in particular, are both recognised crop pollinators (Garibaldi et al., 2013; Kleijn et al., 2015), but there is a longstanding debate on the relative importance of managed honeybees versus wild bees and other unmanaged pollinators for pollination of crops worldwide (Morse, 1991; Winfree et al., 2008; Aebi et al., 2012; Ollerton et al., 2012; Garibaldi et al., 2013; Rader et al., 2016). To manage for pollination in a particular crop (e.g., deciding whether to rent honey bee hives for crop pollination) the relative contributions of different pollinator taxa to crop pollination need to be understood.

Two main components need to be assessed when determining taxon-specific contributions to crop pollination: flower visitation rate and pollination benefit per visit (Rader et al., 2009). Flower visitation rate incorporates information on both the abundance of a given pollinator and how many flowers each individual visits per unit time (Herrera, 1987, 1989; Madjidian et al., 2008). The pollination benefit per visit can be defined in terms of contribution to pollination

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(e.g., stigmatic pollen deposition) or plant reproductive success (e.g., seed set) (Ne’eman et al., 2010). From an agronomic point of view, the ultimate impact of a pollinator visit on plant reproductive success (or harvestable crop mass) is arguably of most interest when determining the pollination benefit per visit. Compared to visitation rate data, much less information on per-visit pollination benefits for different pollinator taxa is available for crops (Kleijn et al., 2015).

Faba bean (*Vicia faba* L.) is a grain legume crop grown worldwide for food and feed (Jensen et al., 2010) which is partially dependent on insects for pollination (Stoddard & Bond, 1987; Free, 1993). Estimates of the benefit of insect pollination in faba bean vary greatly (e.g., Bishop et al., 2020), but yield reductions without insect pollination have been estimated to 21−43% in a recent meta-analysis (Bishop & Nakagawa, 2021). The most common pollinators of faba bean in Northern and Central Europe are managed honeybees and wild bumblebees (Poulsen, 1973; Bartomeus et al., 2014; Garratt et al., 2014; Marzinzig et al., 2018; Raderschall et al., 2021a; Beyer et al. 2022). When collecting pollen and nectar from faba bean, bees either legitimately visit flowers and insert their proboscis into the opening of the corolla, rob nectar through a pierced hole at the base of the flower or collect nectar from extra-floral nectaries (EFN) on stipules below the flowers (Tasei, 1976; Fig. 1). Predominating foraging behaviours differ among bee species in relation to their body sizes, as visitors need a large enough body size to pull down the keel petals of the faba bean flowers and access its rewards (Bailes et al., 2018). Foraging behaviours also depend on visitor tongue lengths, as a long tongue length is required to access nectar at the base of the deep corolla tube. Honeybees and short-tongued bumblebees (e.g., *Bombus terrestris*) predominantly rob nectar or visit EFN, whereas long-tongued bumblebees (e.g., *B. hortorum* and *B. subterraneus*) almost exclusively visit flowers legitimately (Tasei, 1976; Marzinzig et al., 2018; Raderschall et al., 2021a; Fig. 1). Experiments, where the contribution of single flower visits to faba bean pod and seed set was examined, have either shown no differences in per-visit pollination benefits among legitimately visiting bee species (Kendall & Smith, 1975), or higher seed set following visits by the long-tongued bumblebee species *B. hortorum* (Marzinzig et al., 2018). Nectar robbing contributes less to pod set than legitimate visits, but is still more beneficial for pod set than no visits at all, likely because nectar robbing promotes self-pollination (Kendall & Smith, 1975). In a cage experiment, which manipulated the average amount of visits to faba bean flowers, visits by bumblebees led to more pods per node compared to visits by honeybees (Garratt et al., 2014). In line with these results, a meta-analysis found indications that pollination benefits in faba bean are lower for honeybees compared to bumblebees (Bishop & Nakagawa, 2021). So far, however, the two components flower visitation rate and pollination benefit per visit have not been combined, in order to determine taxon-specific pollinator contributions to faba bean pollination (for examples using other crops such as watermelon and buckwheat see e.g., Kremen et al., 2002; Liu et al., 2020).

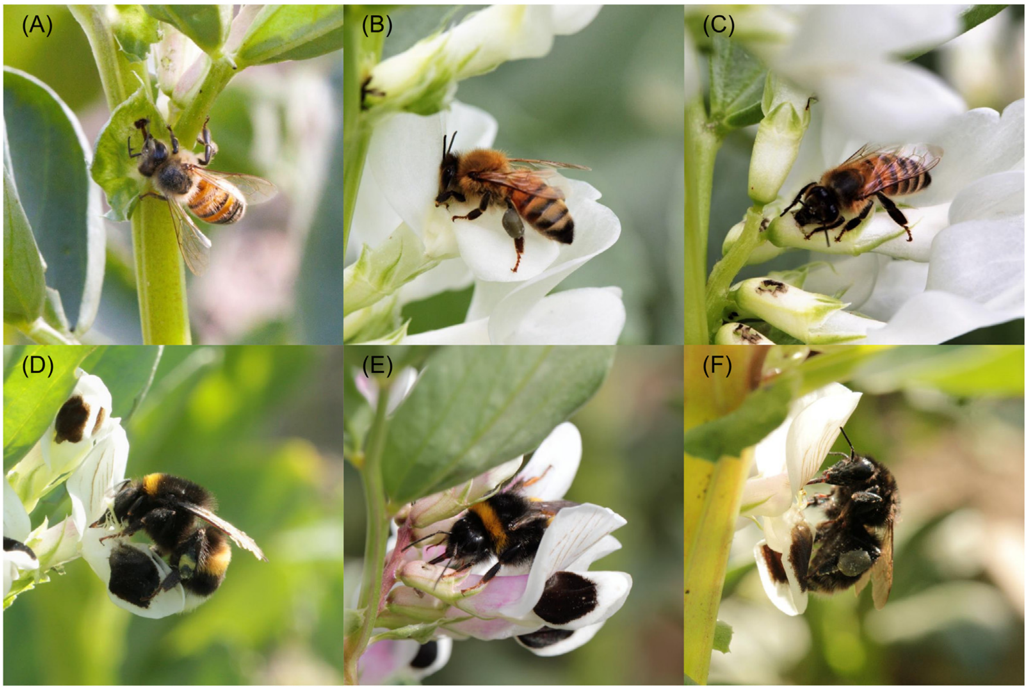

Fig. 1. Pollen and nectar collecting bees and their behaviours in faba bean. A honeybee (A) visiting an EFN, (B) visiting a flower legitimately or (C) robbing nectar, a short-tongued bumblebee (*B. terrestris* agg.) (D) visiting a flower legitimately or (E) robbing nectar and (F) a long-tongued bumblebee (*B. subterraneus*) visiting a flower legitimately. Photos by Chloë Raderschall.

My aim was to assess the relative contribution of different pollinator groups to faba bean pollination. I assessed the visitation rates and foraging behaviours of pollinators in 20 commercial faba bean fields over two years (10 fields per year) and quantified the bean mass produced from single visits of different groups of pollinators in a field experiment which was repeated over two years in a single site. I combine the information on visitation rates and gains in bean mass from single visits to flowers, in order to estimate the relative contributions of pollinator taxa to faba bean pollination.

Materials and methods

Visitation rates

Pollinator visitation rates were monitored in 20 conventionally managed spring faba bean (*Vicia faba* minor) fields of the cultivar Tiffany (Scandinavian Seed) in the province of Västergötland, Sweden in 2018 (n = 10) and 2019 (n = 10). Selected fields were located along a gradient of landscape complexity and at least 2 km apart (for further details see Lundin and Raderschall (2021)). Managed honeybees are common in the area, but honeybee hives were not supplemented to any of the fields. Pesticide use was uncommon across the fields surveyed because most of them were part of agri-environmental schemes, where the farmers had committed not to use any pesticides in the faba bean crop. A herbicide was applied early in the season in one field, and in one other field an insecticide was applied during crop bloom. The insecticide was, however, not applied in the part of the field where I sampled insects. In each field, a two by two meter quadrat was marked 50 m from the field edge, as it was determined in pilot observations that this was the maximum area one observer could monitor reliably. Visits to faba bean flowers or EFN inside the observation quadrat were monitored for 10 min during early to late crop bloom. Four to eight surveys per field (n = 4−8 and 4−6 in 2018 and 2019, respectively) were conducted between 9.00 and 19.00 hrs when temperatures were at least 15 °C, wind speeds less than 8 m s^{-1} (maximum four on the Beaufort scale) and skies at least partly sunny or brightly overcast between June 12 - July 4 in 2018 and June 13 - July 3 in 2019. The unequal sampling effort between fields was because unsuitable weather canceled surveys in some fields and because fields that flowered longer, or earlier or later compared to other fields included in the study could be surveyed more intensively. Each field was visited at different times of the day in different surveys. The inclusion of samples from morning to early evening meant that diurnal patterns in faba bean pollinator activity and foraging behaviours (Percival, 1955; Free, 1993) were accounted for. For each insect visiting flowers or EFN, species identity was determined visually and the number of visits to flowers or EFN within the quadrat was noted. *Bombus terrestris, B. lucorum, B. cryptarum* and *B. magnus* were grouped as *B. terrestris* agg. due to difficulties separating these species on the wing (Murray et al., 2008). At the end of each survey, crop plant density was determined by counting the number of plants in four 0.36 m^2 sub-plots within the observation quadrat, and crop flower density was assessed by counting the number of open flowers on five randomly chosen plants within each sub-plot (i.e., 20 plants per observation quadrat). Subsequently, I summed up for each field the number of visits by the following seven groups of visitors: (1) honeybees visiting EFN, (2) honeybees visiting flowers legitimately (3) honeybees robbing nectar, (4) short-tongued bumblebees visiting flowers legitimately, (5) short-tongued bumblebees robbing nectar, (6) long-tongued bumblebees visiting flowers legitimately or (7) solitary bees visiting flowers legitimately (see also Fig. 1). Short-tongued bumblebees included observations of *B. terrestris* agg. and *B. lapidarius*. Long-tongued bumblebees included observations of *B. hortorum* and *B. pascuorum.* A tongue length exceeding 8 mm (Goulson et al., 2005) was used to distinguish long-tongued from short-tongued bumblebees. Nectar robbing or visits to EFN by long-tongued bumblebees or solitary bees were not observed and are thus not included. Due to their low numbers, three visits by short-tongued bumblebees to EFN and three visits by wasps to EFN were also excluded. The number of open flowers in each observation quadrat and survey occasion was up-scaled by multiplying the average crop plant density with average number of flowers on the 20 plants in the four sub-plots. I then also summed up for each field, the total observation effort, calculated as the number of flower-minutes, i.e., if there were 100 open flowers in the observation quadrat during a 10 min observation period, the sampling effort was 1000 flower-minutes.

Data were analysed using a generalised linear mixed model (Proc Glimmix) in SAS 9.4 for Windows (SAS, Cary, NC). Test statistics were obtained using type III sums of squares and degrees of freedom were estimated using the Kenward-Roger method. Total number of visits per quadrat was the response variable. Visitor group (1−7) and year (2018 or 2019) were fixed factors, field identity was a random factor and the ln-transformed number of flower-minutes observed in each field was added as an offset to account for the sampling effort (Reitan & Nielsen 2016). I used a negative binomial distribution with a log link, as the data was overdispersed for Poisson distribution. Overall statistically significant effects of visitor group ($p < 0.05$) were followed by pairwise comparisons with Tukey adjustment.

Pollination benefit per visit

To investigate the pollination benefit per visit, I established small (ca 0.1−0.2 ha) experimental fields of faba bean near the city of Uppsala in south central Sweden in 2017 and 2019. Faba bean cultivars used were Fanfare (2017) and Tiffany (2019). Cultivars differed between years due to differences in cultivar availability. Prior to the onset of crop flowering, six 2 by 2 by 2 m metal frame cages were erected in the fields, and covered with a net (Artes Politecnica SRL, Schio, Italy) with a mesh size of 1.6 by 0.6 mm. The net was dug approximately 10 cm into the soil to prevent any pollinating insects from entering the cages.

Once crop bloom had started, the nets were removed sequentially on one cage at a time between 10.00 and 20.00 hrs on days with favourable conditions for pollinator activity. Two observers monitored all faba bean plants in the 2 by 2 m area that had been caged for approaching flower-visiting insects. One person observed an approaching flower visitor and noted which flowers it visited, and whether the insect was visiting the flower legitimately or robbing nectar. The other observer made sure that no additional insects visited flowers in the previously caged observation area in the meantime. Each individual visitor was allowed a maximum of three visits to three different flowers on the same or different plants before it was chased away from the plot. I allowed more than one visit per individual to increase the sample size, while accounting for multiple visits per individual in analyses, and three visits represented an upper limit that the observer could register. Return visits to the same flower by any visitor were never observed. Flowers that had been visited once were marked and then bagged with a tulle net to avoid additional visits. The node number (first leaf pair at the bottom of the plant was assigned as node one etc.) of each flower visited was noted. In addition, the flower number within the raceme, assigning flower number one to the most proximal flower and up to flower number eight for the most distal flower on each node, was noted for each visited flower. Insects only visiting EFN were chased away if they approached the experimental plants. I did not include visits to EFN in the single visit experiment because I assumed (but did not verify) that these visits do not contribute to pollination. In addition to visited flowers, unvisited control flowers were also bagged, both on the same and different plants compared to those visited by bees, using similar node and flower numbers as for flowers visited. I used multiple cages because 2 by 2 m was a reasonable plot size for observing flower visitors, and a new cage could be opened once a substantial number of plants and flowers already had been visited in one cage. Opened cages remained open for the remaining duration of crop bloom and until harvest. Visited and unvisited control flowers were marked and pods produced from marked flowers were harvested at maturity. In the laboratory, I dried the pods at 65°C for 48 h and then weighed the beans.

I used bean mass (g) produced per visit as the main response variable in statistical analyses. This is because bean mass per visit incorporates effects of pollination on pod set, beans per pod and individual bean weight. I complemented this analysis, however, with analyses of the number of pods and beans per visit (Appendix A). Prior to statistical analyses, I averaged data over the one to three visits recorded for each flower visitor in order to reduce the number of zeros in the data. Flower treatments were grouped into either (1) unvisited control flowers (2) legitimately visiting honeybees, (3) legitimately visiting short-tongued bumblebees, (4) short-tongued bumblebees robbing nectar, (5) legitimately visiting long-tongued bumblebees or (6) legitimately visiting solitary bees. For solitary bees, only one Anthophora sp. individual was observed visiting two flowers. This observation was nevertheless included in analyses in order to obtain a point estimate of the pollination efficiency of solitary bees. I validated, however, that including or excluding solitary bees did not qualitatively affect any other model results. Honeybees robbing nectar were not observed in the single visit experiments, as all flowers were previously unvisited, and honeybee nectar robbing in faba bean requires previous piercing of the base of flowers by other insects (Free 1993). Short-tongued bumblebees included observations of *B. terrestris* agg. and *B. lapidarius*. Long-tongued bumblebees included observations of *B. hortorum* and *B. subterraneus*. Data was analysed using a general linear model (Proc GLM) in SAS 9.4 for Windows (SAS, Cary, NC) and test statistics were obtained using type III sums of squares. Bean mass (g) per visit was the response variable and year (2017, 2019), node number (4−14), flower number (1−8) and visitor group were explanatory variables. Explanatory continuous variables were uncorrelated and distribution of residuals was assessed visually in plots. A two-way interaction between year and visitor type was added to a preliminary model. This was done to test if the effect of flower visitors differed between years, especially as the cultivar was not the same in both years. The interaction term was, however, removed from the final model as it had no significant effect ($F = 0.01_{3,249}$, $p = 1.00$), indicating that the results are equally valid for both tested cultivars and years. In addition, I tested to add the number of visits recorded for each individual (1−3) as and additional explanatory variable, but it was not included in the final model as it had no significant effect ($F = 0.33_{1,251}$, $p = 0.56$). Overall statistically significant effects of visitor group ($p < 0.05$) were followed by pairwise comparisons with Tukey adjustment.

Combining visitation rates and pollination benefit per visit

The contribution to pollination of each visitor group was calculated as the product of the visitation rate and the increase in bean mass per visit relative to the control for a given visitor group (numerator), divided by the sum of the product of visitation rate and increase in bean mass per visit relative to the control for all visitor groups (denominator). Further details regarding these calculations are available in Appendix A.

Results

Visitation rates

Visitation rates differed among groups ($F_{df} = 8.31_{6,118}$, $p < 0.001$, Fig. 2) but not between the two years

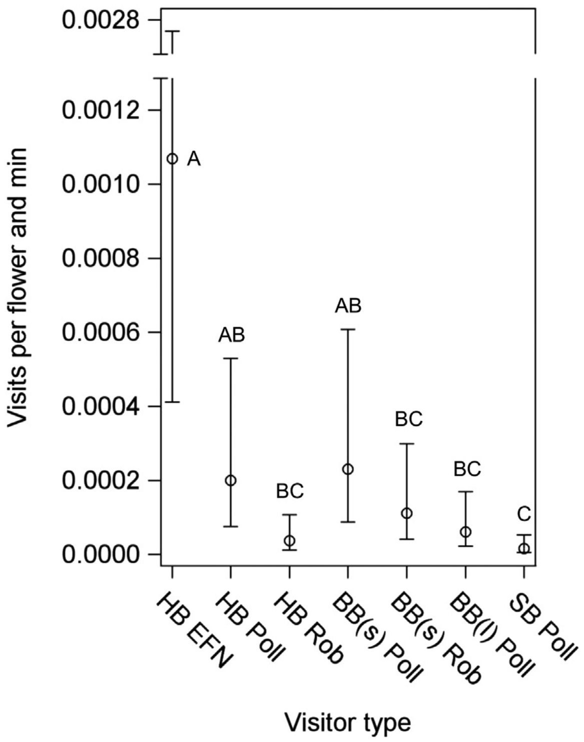

Fig. 2. Average visits per flower and minute for different visitor groups across 20 faba bean fields in 2018−2019. Shown are model-estimated means with 95% confidence intervals. Note that there is a break on the y-axis. HB EFN = honeybees visiting extra floral nectaries (n = 562), HB Poll = honeybees visiting flowers legitimately (n = 119), HB Rob = honeybees robbing nectar (n = 28), BB(s) Poll = short-tongued bumblebees visiting flower legitimately (n = 149), BB(s) Rob = short-tongued bumblebees robbing nectar (n = 94), BB(l) Poll = long-tongued bumblebees visiting flowers legitimately (n = 51) and SB Poll = solitary bees visiting flowers legitimately (n = 12, see also Fig. 1). Visitor groups not sharing the same letter are significantly ($p < 0.05$) different. Sample sizes (n) refer to the total number of visits recorded for each group.

($F_{df} = 0.66_{1,17}$, $p = 0.43$). Visits to EFN by honeybees were more common than other types of visits, except legitimate visits by honeybees and short-tongued bumblebees, which were intermediate and more common than legitimate visits by solitary bees (Fig. 2).

Pollination benefit per visit

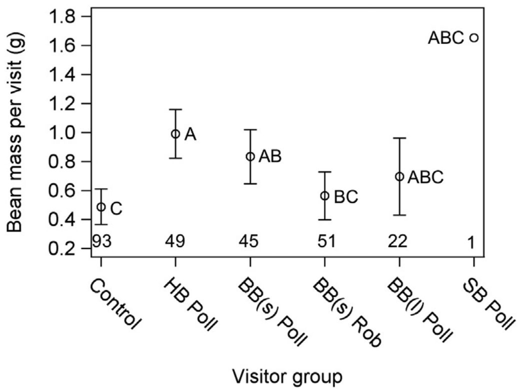

Fig. 3. Bean mass produced per flower visit for different types of visitors. Shown are model-estimated means with 95 percent confidence intervals. Control = unvisited flowers, HB Poll = legitimate flower visits by honeybees, BB(s) Poll= legitimate flower visits by short-tongued bumblebees *B. terrestris* agg. (n = 41) and *B. lapidarius* (n = 4), BB(s) Rob = nectar robbing by short-tongued *B. terrestris* agg. BB(l) Poll = legitimate flower visits by long-tongued bumblebees *B. hortorum* (n = 11) and *B. subterraneus* (n = 11), SB Poll = legitimate flower visits by a solitary bee (*Anthophora* sp., n = 1). Visitor groups not sharing the same letter are significantly ($p < 0.05$) different. Sample sizes (number of individuals) for each group are displayed below each error bar.

Bean mass per visit varied depending on visitor group (Fig. 3, Table 1) and was higher following legitimate visits from honeybees and short-tongued bumblebees compared with bean mass resulting from unvisited (control) flowers (Fig. 3). Bean mass following legitimate visits from honeybees was also higher compared with bean mass produced from flowers that had been robbed by short-tongued bumblebees (Fig. 3). Bean mass following visits from long-tongued bumblebees did not differ from those of any other group (Fig. 3). In addition, bean mass per visit was greater on lower nodes and in more proximal positions within a node, and was higher in 2017 compared with 2019 (Table 1). Similar results were obtained for pods and beans per visit (Appendix A).

Relative contribution to insect pollination

The relative contribution to insect pollination for each visitor group was estimated by combining information on

Table 1. Results from general linear model testing for differences in bean mass (g) per flower visit for different visitor groups (see Fig. 3). Shown are estimates with standard errors within parenthesis, F-values with degrees of freedom (df) and p-values for year (estimate is for 2019 compared with 2017), node number of flower on the faba bean plant (4−14) and flower number within node (1−8) for the flower visited. Significant effects, where $p < 0.05$, are indicated in bold. Bean mass (g) per flower was 1.05 (0.82−1.28, 95% confidence interval) in 2017 and 0.69 (0.47−0.90) in 2019.

Variable	Estimate	F_{df}	P
Intercept	**2.58 (0.65)**		
Year	**−0.37 (0.09)**	$\mathbf{18.56_{1,252}}$	**<0.001**
Node number	**−0.08 (0.02)**	$\mathbf{13.06_{1,252}}$	**<0.001**
Flower number	**−0.13 (0.03)**	$\mathbf{21.07_{1,252}}$	**<0.001**
Visitor group	**see** Fig. 3	$\mathbf{5.81_{5,252}}$	**<0.001**

Table 2. Estimated contribution of different groups of visitors (for explanations of abbreviations see legend of Fig. 2) to faba bean pollination. Visitation rate = average number of visits per flower and minute. Bean mass per visit (g) = estimated additional bean mass produced per visit (calculated by subtracting bean mass for unvisited control flowers from estimates in Fig. 2). Numbers within parentheses are 95% confidence intervals. Visits to EFN are assumed to not contribute to bean mass production. Percent contribution = estimated percent contribution to pollination, calculated as the product of visitation rate and bean mass per visit, divided by the sum of the product of visitation rate and bean mass per visit for all visitor groups.

Visitor group	Visitation rate	Bean mass per visit (g)	Percent contribution
HB EFN	0.001069 (0.000413−0.002770)	(0)	0.0%
HB Poll	0.000201 (0.000076−0.000530)	0.504 (0.198−0.809)	45.2%
HB Rob	0.000037 (0.000013−0.000107)	*0.076 (−0.226−0.378)**	1.3%
BB(s) Poll	0.000231 (0.000088−0.000608)	0.346 (0.018−0.673)	35.7%
BB(s) Rob	0.000112 (0.000042−0.000299)	0.076 (−0.226−0.378)	3.8%
BB(l) Poll	0.000062 (0.000022−0.000170)	0.208 (−0.219−0.634)	5.8%
SB Poll	0.000016 (0.000005−0.000053)	1.166	8.3%

*Due to lack of data, nectar robbing by honeybees is assumed to contribute to bean mass production to the same extent as nectar robbing by bumblebees. Given the larger bodyweight of bumblebees and that honeybees only perform secondary robbing, the estimate likely represents and upper limit of how much nectar robbing honeybees contribute to pollination.

visitation rates with the additional gain in bean mass per visit (Table 2). Forty-seven percent of faba bean pollination was delivered by honeybees, 40% by short-tongued bumblebees, 6% by long-tongued bumblebees and 8% by solitary bees (Table 2).

Discussion

Honeybees were numerically the most common group visiting faba bean flowers or EFN, followed by short-tongued bumblebees and long-tongued bumblebees. These results are generally in line with findings from Denmark (Poulsen, 1973), Germany (Marzinzig et al., 2018; Beyeret al., 2022) and southern Sweden (Raderschall et al. 2021a, 2022). In the UK, bumblebees (primarily *B. terrestris* agg.) were more common legitimate flower visitors than honeybees (Garratt et al., 2014). However, that study was performed in winter-sown faba bean, which flowers earlier than spring-sown faba bean. Since bumblebees are more active at lower temperatures early in the season compared to honeybees, this might explain why bumblebees were relatively more numerous than honeybees in winter compared to spring faba bean. Taxon-specific behaviours were also in line with expectations, with only a minority of visits by honeybees being legitimate, whereas long-tongued bumblebees exclusively performed legitimate visits (Tasei, 1976; Marzinzig et al., 2018). Approximately two thirds of visits by short-tongued bumblebees were, however, legitimate, which is higher compared to results found earlier (Poulsen, 1973; Tasei, 1976; Marzinzig et al., 2018; Raderschall et al., 2021a). It could be that short-tongued bumblebees in the studied landscapes had access to nectar from other plants, but lacked alternative pollen sources, and therefore to a higher extent collected pollen from faba bean, which only can be done by legitimate visits. The high proportion of legitimate visits by bumblebees could in turn also have limited nectar robbing by honeybees, as nectar robbing by honeybees requires previous piercing of the flowers by other insects (Free, 1993). The pollination service of honeybees might thus vary depending on the context.

I found that legitimate visits from either honeybees or short-tongued bumblebees resulted in higher bean mass produced compared to unvisited flowers, and that legitimate visits from honeybees resulted in higher bean mass produced per visited flower compared to flowers robbed by *B. terrestris* agg. Similar results were obtained for pods and beans per visit. This result adds to a wealth of evidence that although unvisited flowers also produce some beans, plant reproduction is enhanced by insect pollination in faba bean (Riedel & Wort, 1960; Free, 1966; Poulsen, 1975; Cunningham & Le Feuvre, 2013; Bartomeus et al., 2014; Nayak et al., 2015; Raderschall et al., 2021a, 2021b; Bishop & Nakagawa, 2021). The benefit of pollination was determined on the flower scale and might not hold true on the plant scale due to within-plant reallocation of resources to visited flowers (Knight et al., 2006). The bean mass per flower following visits from long-tongued bumblebees was numerically in between control flowers and those visited by either honeybees or short-tongued bumblebees, but was statistically indistinguishable from any other group. In previous studies, either no differences in per-visit efficiencies among legitimately visiting bee species (Kendall & Smith, 1975), or higher seed set following visits by the long-tongued bumblebee species *B. hortorum* (Marzinzig et al., 2018) were found. The fact that visits by long-tongued bumblebees were not associated with the highest bean mass as opposed to in Marzinzig et al. (2018) could be due to several factors. Firstly, sample sizes for long-tongued bumblebees were lower compared to other groups (except solitary bees). This increases the uncertainty in the estimate of the average bean mass produced per visit, which therefore should be interpreted carefully. Additionally, I grouped the two long-tongued species

B. hortorum and *B. subterraneus*, while *B. hortorum* was the only long-tongued bumblebee species observed by Marzinzig et al. 2018. Interspecific variation in pollinating efficiency between *B. hortorum* and *B. subterraneus* could therefore have played a role, but additional data collection would be needed to explore this further.

Incorporating taxon- and behaviour-specific visitation rates and gains in bean mass from each visitor group, I estimate that 47% of pollination services to faba bean is delivered by honeybees, 40% by short-tongued bumblebees, 6% by long-tongued bumblebees and 8% by solitary bees. Important factors that re-scale the pollination contribution when not only taking into account visitation rates but also foraging behaviour and pollination benefit per visit, is (1) that a majority of honeybees in faba bean do not visit the flowers, but instead collect nectar from EFN and (2) that long-tongued bumblebees and solitary bees were exclusively observed visiting faba bean flowers legitimately. A caveat is that the estimate for solitary bees in particular is uncertain and likely overestimated, as the flowers visited by the only solitary bee observed in the single visit experiment produced high bean masses. The estimate for solitary bees might thus not be representative for the solitary bee species observed, let alone for other species of solitary bees, but nevertheless indicates that solitary bees contribute to faba bean pollination to an extent which is yet to be more closely determined. On a per-capita basis, long-tongued bumblebees and solitary bees were the most efficient pollinators because they exclusively visited flowers legitimately. Honeybees and short-tongued bumblebees were, however, much more frequent resource collectors of nectar and pollen from flowers and EFN in faba bean. Even though honeybees mostly visited EFN, the proportional minority of legitimate flower visits were still sufficient for making them the most common legitimate flower visitor. As a result, the honeybee was estimated as the species contributing most to faba bean pollination, followed by short-tongued bumblebees. My results are in line with the more general finding that visitation rates override effects of per-visitation pollination benefits when determining taxon-specific contributions to pollination (Kleijn et al., 2015).

I conclude that both managed honeybees and wild bees, especially short-tongued bumblebees, contribute substantially to faba bean pollination in Sweden. For this reason, I recommend faba bean farmers to manage for pollination by both these groups of pollinators. Promotion of especially long-tongued bumblebees and solitary bees is, however, also a strategy with potential for enhancing faba bean pollination, as these taxa were exclusively observed performing legitimate flower visits. Managing for a diversity of pollinators also has the added benefit of stabilising pollinator abundance and species richness, and pollination service delivery (Senapathi et al., 2021; Lemanski et al., 2022). An important next step is to test the generality of these findings for faba bean pollination in a wider set of locations and under different growing conditions.

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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Supplementary materials

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